UNIVERSITY OF SOUTHAMPTON

TESTING HYPOTHESES RELATED TO CHANGES IN ABUNDANCE AND DISTRIBUTION OF WARM-TEMPERATE INVERTEBRATES ON ROCKY SHORES ALONG THE SOUTH COAST OF ENGLAND

By Roger J. H. Herbert

Thesis submitted for the degree of Doctor of Philosophy
School of Ocean & Earth Science

Faculty of Science

March 2001

I declare that the work contained in this thesis was completed by myself
while a part-time postgraduate student registered at the
University of Southampton.

Roger J.H.Herbert

March 2001

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

SCHOOL OF OCEAN AND EARTH SCIENCES

Doctor of Philosophy

TESTING HYPOTHESES RELATED TO CHANGES IN ABUNDANCE AND DISTRIBUTION OF WARM-TEMPERATE INVERTEBRATES ON ROCKY SHORES ALONG THE SOUTH COAST OF ENGLAND

by Roger J.H. Herbert

Surveys of southern invertebrates found on rocky shores along the south coast of England have been carried out since the 1930s. Following exceptionally warm summers in the 1990s, new comparative surveys have been undertaken to determine whether changes have occurred since the last major studies in the late 1970s and early 1980s. Particular attention has been given to the barnacles *Chthamalus montagui*, *C. stellatus* and *Balanus perforatus*, while other species, including the trochid molluscs *Gibbula umbilicalis* and *Osilinus lineatus* and limpets *Patella depressa* and *P. ulyssiponensis* have been dealt with in less detail. A hypothesis testing approach was then commenced to investigate the various physical and biological constraints on life cycles that might be contributory to the discontinuous distribution of these species along the central south coast of England.

Chthamalus montagui and *C. stellatus* are now found at Bembridge on the Isle of Wight; 8km and 26km beyond eastern limits observed in the late 1970s. The abundance of *Chthamalus* appears to have risen on the south coast of the Isle of Wight subsequent to the last surveys in the 1970s, when densities were observed to have dropped since the 1950s. *Balanus perforatus* was recorded as far as Eastbourne in Sussex, an eastward extension of 75km. The topshell *Gibbula umbilicalis* is still not found east of Bembridge on the Isle of Wight but is now 'common' at Freshwater Bay and 'frequent' at Bembridge, where populations have increased by ten-fold over the past decade.

A second theme to the work aimed to identify principal factors setting geographic limits of *Chthamalus* spp, *B.perforatus*, *G.umbilicalis* and *Osilinus lineatus* in the Channel. Investigations were conducted on the reproductive development and fecundity of *C. montagui* and *B. perforatus* and the growth and mortality of *C. montagui*. Yet no obvious biological constraints on benthic life stages were observed at the extreme geographic limits.

Experiments were carried out to determine the effect of rock-type on the recruitment and mortality of *C. montagui*. Recruitment was found to be greater on the roughest samples, including chalk, and least on the smooth Kimmeridge dolomite. Mortality over the first year was more variable, but generally greater on the chalk.

Between 1994-1999, annual recruitment of *Chthamalus*, *G.umbilicalis* and *O. lineatus* was measured up to the geographic limits. Recruitment was significantly greater in the warmer years of the study, yet the results showed a marked gradient in the magnitude of recruitment between Portland Bill and the Isle of Wight. In 1999, a broad-scale study measured recruitment of *S.balanoides* *C.montagui* and *Elminius modestus* within four coastal cells between Torbay and Beachy Head. Data analysis, which included hierarchical analysis of variance, showed that recruitment in the region between Selsey Bill and Portland Bill was low for all species.

A hierarchy of factors setting geographic limits is proposed for each species. It is considered that problems associated with eastward larval transport and dispersal are most important. The small intertidal area combined with smooth and soft rocks along the Purbeck coast must also reduce population growth rate of *C.montagui*.

CONTENTS

Testing hypotheses related to changes in abundance and distribution of warm-temperate invertebrates on rocky shores along the south coast of England

Chapter 1. Introduction

Chapter 2. The physical environment of the south coast of England: A review of existing knowledge and observations over the study period 1994-1999.

Chapter 3. Recent changes and current geographic limits of southern species on rocky shores along the south coast of England.

Chapter 4. Reproduction of *C.montagui* & *B. perforatus* along the south coast of England

Chapter 5. Recruitment, growth & mortality of *Chthamalus* & other barnacle species along the south coast of England.

Chapter 6. Observations on the recruitment & growth rate of *Gibbula umbilicalis, Osilinus lineatus and Balanus perforatus*

Chapter 7. The effect of rock type on the recruitment & mortality of *Chthamalus montagui*

APPENDICES

Acknowledgements

First and foremost, thanks must go to my wife Gill and boys Sam and Mike for their patience, love and support while I have been doing this study. I am also extremely grateful to the staff and fellow directors of the Medina Valley Centre, past and present, who have supported me during this period and have made this project possible. I am particularly indebted to Keith Marston for his field assistance at Lyme Regis. Considerable thanks to my supervisor Dr.Martin Sheader and also Professor Stephen Hawkins for his enormous help and encouragement. I am very grateful to Professor Alan Southward and Dr. Eve Southward for their kind hospitality, encouragement and discussions over the years, and for access to field notebooks and database.

English Nature provided financial assistance for the establishment of monitoring sites. A Richard Newitt Award from the University of Southampton was also helpful. Major J.C. Mansell of Smedmore Estates and Peter Tinsley of the Dorset Wildlife Trust allowed access to Kimmeridge Bay and Tony Tutton of the National Trust gave permission to establish monitoring sites and carry out fieldwork at Hanover Point and St.Catherine's Point on the Isle of Wight. Thanks to *SP Systems*, and David Cripps in particular, for provision of *WetWork* resin. I am extremely grateful to Mark Collins for photographic help, computer expertise and numerous cups of tea. Martin Cade, warden of the Portland Bird Observatory, was always very hospitable and even showed some interest in barnacles! Alan & Ruth Swinney made me feel very welcome in Torbay. Mike Kendall of PML and John Hawthorne of the Dorset Wildlife Trust provided useful information on the distribution and ecology of trochidae along the south coast. Meteorological data was kindly provided by Mr. F.G Thomas (Dover), Durlstone Country Park, MAFF (Weymouth and Shoreham) and Mr. E. Freed (Torbay). Chris Hill and Ben Barton were extremely helpful while I was using the GIS in the *Geodata Unit*. Many useful discussions were had with those within the *Rocky Shore Research Group* in the Biodiversity and Ecology Division: special thanks to Drs. Tas Crowe, Richard Thompson, Mark Johnson and Adam Kent. Mr. Bob Jones and Dr. Ian West in the Geology Dept. and Andrew Speyer in the Engineering Dept. were always extremely helpful and I am grateful to Paula Moschella for valuable collaboration on the effect of rock type on barnacle settlement and microbial films.

Chapter 1

Introduction

1.1 Initial observations

Following the exceptionally hot summers of 1989 and 1990, I was interested to determine whether southern (warm-temperate) species of intertidal animals on rocky shores had significantly extended their range eastwards along the English Channel. A broad-scale survey by Crisp & Southward (1958) showed that several southern species of barnacles and molluscs, common in the south-west of England, had their geographic limits along the coast of Dorset and in the vicinity of the Isle of Wight. Subsequent monitoring continued at several sites by Crisp & Southward until the late 1970s (Crisp *et al.*, 1981; Southward *et al.*,1995; Southward pers. comm) albeit more intermittently at the more eastern localities. Recently, an analysis of a 40 year time-series of barnacle population density at a site near Plymouth in south-west England has demonstrated a correlation between rising sea temperature and an increase in the southern genus *Chthamalus* (Southward, 1991). Studies of other species have also reported a greater prevalence of southern forms in the western Channel in warmer years (Southward & Boalch, 1989, 1994; Southward *et al.*, 1988, 1995). My own observations and records of southern species on the Isle of Wight since 1982 have included a rapid colonisation of the nudibranch *Aeolidiella alderi* (Collins *et al.*,1990), an increase in reported sightings of the mantis shrimp *Rissoides desmaresti* and Gilthead bream *Sparus auratus* (Herbert,1991,1994,1997) and first record of Marbled electric ray *Torpedo marmorata* (Herbert,1997). In March 1999 the rare saccoglossan *Heamiopsis variopicta* was found at Bembridge - only the second record off the coast of England (Herbert, 2000). With the prospect of further hot summers and mild winters as a result of global warming (Houghton, 1994) it was decided to investigate further:

a) the current distribution and density of southern barnacle and gastropod species on rocky shores on the English side of the Channel and to establish geographic limits.

b) possible constraints on benthic stages of life-history as they approach their geographical limits.

c) the likely rate they might extend eastwards to the North Sea should current predictions of environmental change be sustained.

Nomenclature for British species is according to Howson & Picton (1997) unless otherwise stated. *Chthamalus stellatus* (Poli) was separated into *Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli) (Southward,1976). Records of *C.stellatus* prior to1976 are shown in parentheses.

1.2 General Marine Biogeography

Due largely to the establishment of marine laboratories and commissioning of research vessels in the mid-late nineteenth century the North-East Atlantic, and in particular the coastal waters of the British Isles, have had a relatively long history of marine biological and oceanographic research (Forbes & Goodwin-Austen,1859; Briggs,1974; Southward & Roberts,1984; Hiscock, 1998). Survey work yielded many new species and with the growing interest in ecology in the early twentieth century (Elton, 1927), there was an increasing amount of research into the probable causes of observed geographical distribution and in particular the influence of air and sea temperature (Appleöff, 1912; Orton,1920; Hutchins,1947; Eckman,1953; Southward,1958).

Angel (1997) has reviewed several factors on different time and spatial scales that must be considered and appreciated to understand the present geographical location of marine species. Firstly, the origins of species must be linked to long-term changes in the morphology and size of the ocean basins that have been formed by plate tectonics. Since the fragmentation of the ancient continent of Pangea the circulatory patterns of gyres and currents have been considerably modified and coastlines have both coincided and drifted apart. Rising and falling sea levels associated with either tectonic or climatic changes have opened up or closed inter-oceanic connections, such as the opening of the Drake Passage and the closure of the Indonesian Seaway. During the Miocene period the Mediterranean was subject to episodes of desiccation and re-flooding when Tethyan relict species were largely replaced by those of Atlantic origin and which have since undergone genetic changes (Southward *et al.*,1995; Pannacciulli *et al.*,1997). In geological terms the Atlantic is still relatively young compared to the Pacific and influxes of African species may still be continuing. It is possible that the Atlantic communities have not yet stabilised and are therefore much more subject to climatic change (Southward *et al.*, 1995). Many of the northern elements of the eastern Atlantic intertidal fauna have close relatives or conspecifics in the north-west Atlantic and north Pacific (e.g. *Semibalanus balanoides*, *Mytilus, Nucella,* littorinids and fucoids). According to Vermeij (1991) many of these represent outliers of a former pan-boreal fauna that occupied the arctic during a climatic optimum. The barnacle species *Chthamalus montagui* is thought to be of Pacific origin, having spread via the north-west passage or along the Siberian coast during the Pliocene, whereas *Chthamalus stellatus* appears to have close relatives in the tropical eastern Pacific and the Caribbean (Dando & Southward, 1980; Crisp *et al.*, 1981). Some of the warm-water species of topshells (*Gibbula* spp.) and patellid limpets found in the North Atlantic are not found along the American coast and may have affinities with the fauna of the south Atlantic or derived from the circumtropical/Tethyan fauna (Vermeij, 1991, 2000).

In addition to tectonic changes there are global climatic oscillations induced by the eccentricity and precessionary characteristics of the Earth's orbit known as Milankovitch cycles (see Hays *et al.*, 1976). These have resulted in ice ages that have caused considerable changes in global sea levels. They have been large enough to close sea-ways during glacial periods and reopen them during interglacials, including the English Channel (Meijer & Preece, 1995).

Although the geological history of a region imposes restraints on the pool of species present, or likely to naturally colonise part of the coast or ocean basin, the current broad-scale biogeography is determined by regional and climatic factors that impose latitudinal gradients on the distributions of species. In his synthesis concerned with the influence of temperature on north-south geographical zonation of species, Hutchins (1947) concludes that species zonal limits are to be interpreted in terms of summer and winter temperatures and emphasises two general types of relationship. Firstly, that distribution may be checked by the inability of individuals to survive temperature extremes; either winter chilling at the poles or summer heat stress at the equator, and secondly that temperature extremes may result in a failure to successfully reproduce and repopulate the area. *Both survival and re-population are necessary for sustained permanent establishment.* Four types of latitudinal zonation are proposed which are illustrated diagrammatically in Fig.1.1. Type 1 species includes those whose geographical distribution is limited by the survival of individuals toward the polar and equatorial extremes of temperature. Type 2 species are those whose adult stages may survive at or toward the polar and equatorial extremes of temperature but are either totally or partially incapable of successful reproduction and the completion of life cycles necessary for re-population. The distribution of these species is likely to be limited by summer temperatures at the poles and winter temperatures at the equator. Types 3 & 4 are combinations with one boundary being determined by survival tolerances and the other by requirements of some phase within the re-population process. Type 3 species are those whose northerly distribution is determined by an inability to breed successfully outside a narrow summer temperature range which might result in inadequate larval supply necessary for re-population, and a southern boundary beyond which adults are unable to tolerate high summer temperatures. Type 4 species are similar but whose distribution is limited by winter conditions.

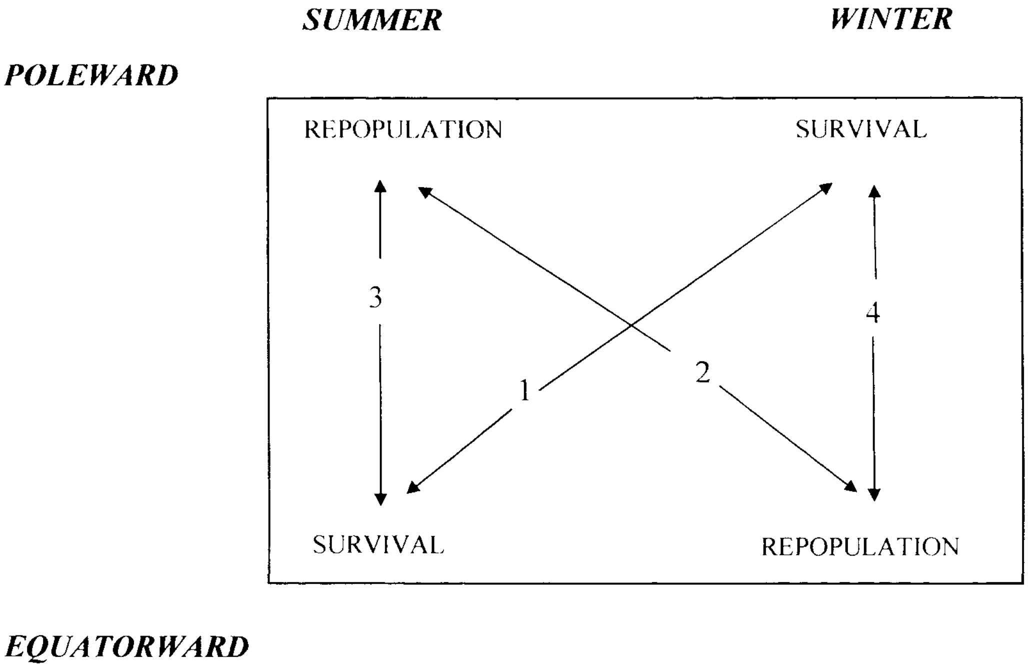


Fig.1.1 From Hutchins (1947). Diagram illustrating the four basic types of zonation evident in geographical distribution. See text for further details.

The illustration serves to aid the general interpretation of broad-scale species distribution patterns, although relationships between species tolerances and zonal types only becomes clear when there are well marked breaks in distribution and temperature.

The climatic factors that are responsible for these latitudinal gradients in temperature are themselves caused by variations in solar radiation which strongly influence ocean - atmosphere interactions, surface wind field and water circulation patterns. Some of these interactions have been found to have a periodicity of between 30-40 years (Stoker, 1994). Of particular interest to this work is the North Atlantic Oscillation (NAO) which appears to have a significant influence on sea surface temperature and precipitation over the northern hemisphere with a periodicity of about a decade or so (Hurrell, 1995). The distributions of organisms may extend or retreat from the boundaries of their mean zonal limits in response to these oscillations. One of the most famous studies undertaken was that carried out in the western English Channel by Sir Frederick Russell and co-workers, whose observations and analysis of changes in plankton and nutrient levels between the 1930s and early 1970s is now known as the Russell Cycle (Russell, 1936; Russell *et al.*,1971; Cushing & Dickson, 1976). Although largely interpreted at the time as changes in response to the movement of different water masses it is now more generally considered a response to changes in climate over that period (Southward, 1963, 1980; Southward *et al.*, 1995).

Within these shifting climatic gradients there are finer scale abiotic conditions that determine location and biodiversity of marine organisms. For example there might be differences in substratum type, nutrient levels, tidal elevation or wave exposure. These particular factors are especially pertinent to the ecology of rocky shores that owing to their two-dimensional nature and relative ease of study must be the most thoroughly investigated and intensively sampled marine habitats in Britain, if not throughout the world. Much of the earlier published information was descriptive and related to the observed patterns of intertidal zonation and the horizontal gradient of wave exposure (Ballantine, 1961a; Stephenson & Stephenson, 1972). A detailed overview of the patterns of zonation, effects of wave exposure, and importantly, geographical distribution was contained in the classic text *The Ecology of Rocky Shores* (Lewis, 1964). In more recent decades much attention has been given to the observed spatial and temporal variability in the abundance and diversity of species on rocky shores (for review see Raffaelli & Hawkins, 1996). On semi-exposed rocky shores, studies of the interactions between limpets, dog-whelks, seaweeds and barnacles have revealed the dynamic and often cyclical nature of such communities (Connell,1961b; Dayton,1971; Menge,1976; Hartnoll & Hawkins,1985). Many of the processes identified are relatively predictable or deterministic, for example the growth of seaweeds (*Fucus* spp) in response to locally reduced limpet grazing pressure. Yet less predictable 'stochastic'events such as recruitment variation, due perhaps to the uncertainties of larval supply, can reinforce or considerably modify the interactions between species. For example, onshore winds have been shown to promote the settlement of the barnacle *Semibalanus balanoides* (Hawkins & Hartnoll, 1982a; Bertness *et al.*,1996). Should a dense barnacle population develop on the shore as a result of high recruitment, then in such situations, limpet recruitment can be reduced and inefficient grazing over dense barnacles enables fucoids to 'escape' in old barnacle shells (Hartnoll & Hawkins, 1985).

The realisation that recruitment variation, due to the arrival of different quantities of propagules, can have a major effect on the structure of communities has led to the development of 'supply-side' ecology (Gaines & Roughgarden, 1985; Underwood & Fairweather, 1989).

The organisation of communities might also be considered in terms of their trophic structure (Paine,1980; Menge,1976,1992,2000a). The level of primary production could determine how many trophic levels can exist in a community. 'Top-down' control operates by reducing the dominance of a limited number of species by selective predation or grazing, whereas 'bottom-up' processes operate through the primary producers, perhaps in response to nutrient levels. The extent to which 'top down' predators or grazers influence the structure of communities has resulted in considerable discussion, not least concerning the identification of 'key-stone species' – those that have a major controlling influence on the density of their prey (Paine,1980; for review see Raffaelli & Hawkins,1996). Paine (1994) now refers to those species that have a major influence on community structure and organisation as 'critical species'. Yet on rocky shores at least, carefully controlled exclusion experiments have demonstrated a hierarchy of competitive and predatory relationships that maintain the coexistence of species and biodiversity (Connell,1961b; Dayton,1971; Menge,1976; Menge & Sutherland, 1976).

1.3 European Latitudinal Gradient

An outline of the biogeography of the European-Atlantic seaboard, so far as it influences the coast of Britain, has been usefully summarised by Hiscock (1998). The identification of distinct regions where the biota was similar or different to other parts of the coast was recognised by natural historians in the mid 19th Century (Forbes & Goodwin-Austen,1859). Forbes identified four main provinces extending from the Arctic Circle south to the Mediterannean: Arctic, Boreal, Celtic and Lusitanean. The Celtic was incorporated into the Boreal province by Eckman (1953). The Lusitanean province extends northwards from the Mediterranean to the entrance of the English Channel. Yet because many species found within this area are also recorded along the south-west and western coasts of the British Isles an intermediate 'Boreal-Lusitanean' zone is proposed, stretching north to the Irish Sea and east to the Isle of Wight (Hiscock, 1998). A similar Lusitanean-Boreal area is also suggested from the north-west coast of France south to the Gironde estuary.

Apart from records of species distribution, empirical evidence supporting the suggestion that the communities within these provinces were largely determined by temperature variation had been gathered since the early part of the 20th century (Orton, 1920). A study of the biology of the southern warm-water barnacle *Chthamalus 'stellatus'* (Poli) by Moore & Kitching (1939) revealed that the species was confined to the western coast of the British Isles and was considered to be associated with Atlantic water. After World War II there was a renewed interest in the distribution of intertidal species and particularly barnacles. Much of the discussion was centered on Moore & Kitching's hypothesis, yet further records of *Chthamalus* from the Isle of Man in the Irish Sea suggested an equally plausible link with air temperature, as the known distribution appeared to coincide with the 7 °C winter isotherm (Southward, 1950). Crisp (1950) supplied further records of *Chthamalus* from the Irish Sea and provided experimental evidence suggesting that its distribution was limited due to the vulnerability of larval stages rather than adult mortality at low temperatures. Nevertheless, research into the changes in abundance of *Chthamalus* and *Semibalanus* (as *Balanus balanoides*), around the British Isles between the 1930s and early 1950s, seemed to show evidence of a link with the prevailing climatic conditions; *Chthamalus* was observed to increase in density during the warmer years (Fischer-Piette, 1936; Southward & Crisp, 1952,1954,1956).

Lewis (1986) has reviewed trends in reproduction and recruitment for several warm-temperate intertidal species found on rocky shores along the European Atlantic north-south gradient. These included limpets *Patella ulyssiponensis* (as *P.aspera*) and *P. depressa*, topshells *Osilinus lineatus* (as *Monodonta lineata*) and *Gibbula umbilicalis*, and the barnacle *Chthamalus montagui*. Lewis concluded that northern populations were characterised by short reproductive periods in the summer, frequent recruitment failures and a low density of large sized individuals with long life-spans. In southern Europe, breeding periods of the molluscan species were shown to lengthen, with a likelihood of fewer recruitment failures and a higher density of smaller short-lived individuals. The barnacle *Chthamalus montagui* also showed similar latitudinal trends. It was considered that for the barnacles, the vulnerable planktonic larval phase was primarily responsible for recruitment failure rather than inadequate gonad development. Crisp *et al.*, (1981) suggested that the cool summers around the north of Scotland would prohibit breeding of *C. montagui*. Yet Lewis (1986,1991) reports that nauplii had been released in Scotland every year since 1970 and Kendall (1988) concluded that re-population failure in the north is due not to a failure of the gonads to develop normally, but the reduced breeding season produces insufficient larvae to overcome planktonic mortality and physical or hydrographic barriers. Connel (1961a) found that adult populations of *Chthamalus* in SW Scotland were restricted to the upper shore due to competition for space from the faster growing Boreal species *Semibalanus balanoides*, which will further reduce the supply of *Chthamalus* larvae.

Lewis (1986) observed that the gonads of the molluscan species investigated also underwent normal development at their northern geographic limits, but that temperature sensitivity of the young spat was primarily responsible for re-population failure. In the southern part of their range, the trochids *Gibbula* and *Osilinus* settle later in the year, probably so as to avoid heat stress. In the north, where summer temperatures are lower, settlement occurs earlier between July and September enabling a longer growing period necessary to withstand a cold winter. Kendall & Lewis (1986) and Kendall *et al.*, (1987) found that winter mortality of *Gibbula* spat was highly variable but correlated well with temperature, with an almost total failure during the coldest years. *Osilinus* was shown to be less variable (Kendall, 1987) and yet observations suggesting a climatic mechanism setting the northern limit were not conclusive.

1.4 Non-Latitudinal Factors

In attempting to identify the role of latitudinal or climatic factors in setting geographical limits of species, Lewis (1986) discusses the importance and extent to which local or non-latitudinal factors are influential, such as unsuitability of substratum or habitat, and the effects of offshore currents on larval supply and dispersal. For example, with *Gibbula umbilicalis*, the lack of suitable sheltered habitats on the steep and exposed north coast of Scotland might so reduce the adult population density as to further decrease larval supply, already low due a shorter breeding period. Reference is also made to the failure of *Osilinus lineatus* to bridge the 15-25km gap between Northern Ireland and south-west Scotland, due perhaps to high larval dispersal because of strong currents running parallel to the coast. Similar hydrographic barriers could also account for the species northern limits set on the British mainland near Anglesey in North Wales, which also coincide with that of the limpet *Patella depressa* (Crisp & Knight-Jones,1954). The absence of *P.depressa* and the barnacle *Balanus perforatus* on the Irish coast is probably due to the failure of larvae of both species to cross the St. Georges Channel: perhaps because of late colonisation of northern Europe the barnacle *Balanus perforatus* on the Irish coast is probably due to the failure of larvae of both species to cross the St. Georges Channel; perhaps because of late colonisation of northern Europe that occurred after the severance of Ireland from mainland Britain (Crisp & Southward,1953; Lewis,1976). Comparatively narrow sea barriers are influential in determining the distribution and evolution of intertidal animals and plants (Crisp & Southward,1953). It may be argued, however, that similar hydrographic and physical barriers occur within the species range but do not set limits, for example between the north Devon coast and south Wales.

Crisp (1958) considers the effect of barriers on the dissemination of larvae and the colonisation of favourable sites beyond (Fig.1.2). Due to random marginal dispersal, at increasing distances from the parent stock, larval density within the water column falls asymptotically to zero. Not taking account of post-settlement and post-recruitment mortality, the successful establishment of a new breeding colony will only occur if the density of larvae reaching the shore equals or exceeds the minimum density necessary for successful reproduction (critical breeding density) of the species. The maximum distance from the adult population over which colonisation is likely to occur (critical colonising distance) will be determined by the distance at which the curve of potential settlement intersects the critical breeding density. The distance will be further from the parent population if the fecundity of the species increased, but substantially more should there be water movement in the direction of potential new habitat. For alien species such as the Australasian barnacle *Elminius modestus* which can settle on the undersides of ships hulls, sea barriers can potentially be overcome by remote dispersal (Crisp & Southward,1953; Crisp,1958).

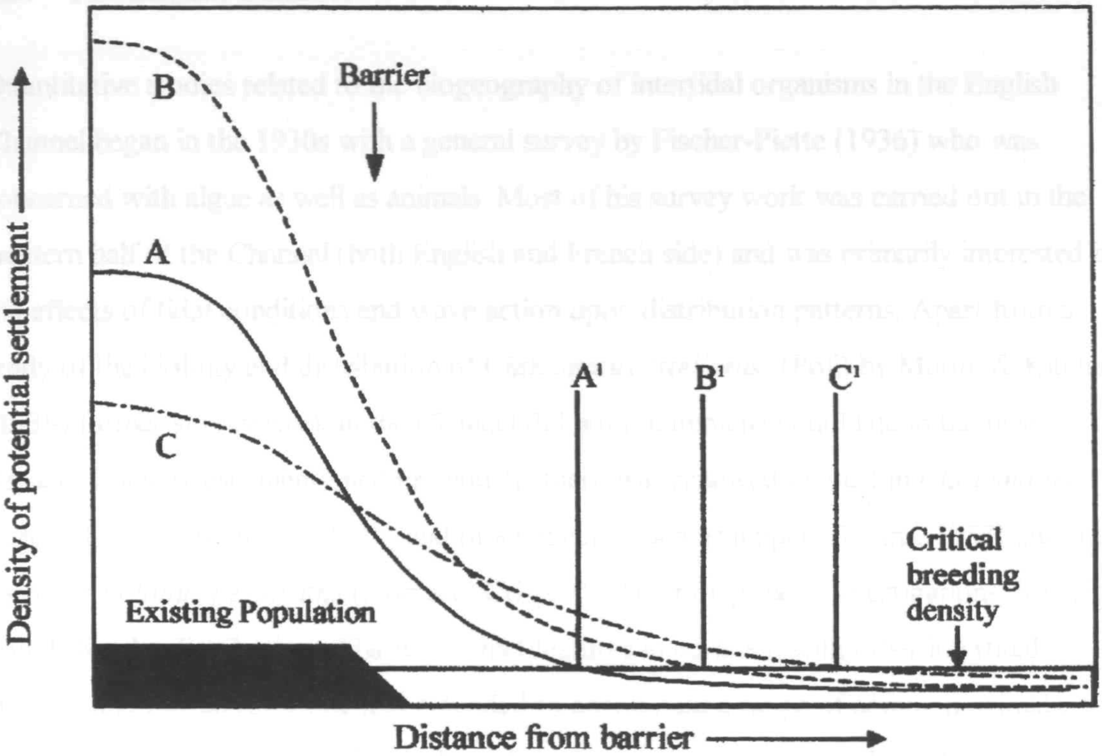


Fig.1.2. Diagram (from Crisp,1958). showing effect of a barrier on the dissemination of larvae liberated from a parent population and potential colonisation. Curve A shows random dispersal offshore from parent population. Curve B shows effect of increased fecundity of parent population and Curve C shows pattern of dispersal modified by water movement. Points A^1 , B^1 and C^1 are the locations of new colonies established beyond barrier (critical colonising distance) where settlement density equals the minimum density necessary for breeding success (critical breeding density).

Crisp (1989) develops a strong argument for the influence of tidal fronts on the distribution of intertidal flora and fauna, and in particular thermal fronts at the boundaries between cool mixed and warm stratified water. Obviously only those species with pelagic larvae will be affected, which include many gastropod and barnacle species, and these will only be influenced by near-shore fronts. Using correspondence analysis and drawing upon survey data from the Irish coast, Crisp found a high association between the presence of stratified water and the abundance of southern Lusitanian species including *Osilinus lineatus*, *Gibbula umbilicalis, Sabellaria alveolata* and *Chthamalus montagui.* There were however some anomalies including the northern species *Acmaea testuinalis* and *Balanus balanus*. Negatively associated were northern forms *Gibbula cineraria* and *Semibalanus balanoides*, but also the Lusitanian limpet *Patella ulyssiponensis* (= *P.aspera*).

1.5 The English Channel

Quantitative studies related to the biogeography of intertidal organisms in the English Channel began in the 1930s with a general survey by Fischer-Piette (1936) who was concerned with algae as well as animals. Most of his survey work was carried out in the western half of the Channel (both English and French side) and was primarily interested in the effects of tidal conditions and wave action upon distribution patterns. Apart from a study of the biology and distribution of *Chthamalus 'stellatus'* (Poli) by Moore & Kitching (1939) further survey work in the Channel did not recommence until late in the next decade, when as was mentioned previously, there was renewed interest in *Chthamalus* (Crisp, 1950; Southward, 1950) and other species such as limpets (Evans, 1953) and the barnacle *Balanus perforatus* (Norris & Crisp, 1953). During these investigations, it was noted that the distribution of barnacles had features in common with other intertidal species, and the survey work was extended to encompass a range of common animals. By including these other species it was hoped to gain a greater understanding of the many possible factors controlling the distribution of intertidal organisms.

The survey results from along the coast of the English Channel (Crisp & Southward, 1958) have become a bench-mark for future survey work and monitoring. They clearly identified that the main trend in the Channel is from east to west, with northern (Boreal) cold-water species being found throughout the Channel, albeit more abundant in the east. However many southern warm-water species, which were found to be common in the western Channel, did not penetrate the eastern basin, which, in their absence was relatively impoverished. They considered that these trends were due to temperature differences, with the eastern limits determined not from a lethal winter minimum temperature, but from '*a generally lower efficiency*' of these animals compared to northern species, as the temperature falls. However during the exceptionally severe winter of 1962-63, there was considerable mortality of several southern species along the English Channel coast notably the trochid gastropods *Osilinus lineatus* and *Gibbula umbilicalis*, limpet *Patella depressa* and barnacle *Balanus perforatus* (Crisp (ed.),1964). *Chthamalus* was not as badly affected on the English coast as it was on the French side (Barnes & Barnes, 1966).

In addition to a generally reduced efficiency at low temperatures, Crisp & Southward (1958) considered that there must be several other factors responsible for the major discontinuity in species distribution on the south coast of England. The change in aspect of the coast on the southern tip of the Isle of Wight exposes the shore to cold north and east winds which could increase juvenile and adult mortality. Prominent headlands such as Portland Bill and St. Catherine's Point could potentially cause significant offshore dispersal of larvae. The limited extent and suitability of rocky substratum in the eastern Channel was also considered to be an important factor restricting the eastward penetration of southern fauna.

Lewis (1964), noting that the southern species of limpet *Patella ulyssiponensis* (= *aspera*), small periwinkle *Melarhaphe neritoides* (= *Littorina neritoides*), and anemone *Anemonia viridis* (= *sulcata*) all extend northwards to Norway, yet fail to penetrate significantly into the eastern Channel and North Sea, came to the '*inescapable conclusion*' that abiotic factors other than temperature had an overriding effect on species distribution.

The geographical distribution of marine algae in the eastern and western basins of the Channel, observed by Crisp & Southward (1958), was later confirmed from more detailed surveys by Tittley & Price (1978). These authors concluded that not only is temperature an important limiting factor setting algal limits in the English Channel, but so also is the quantity of suspended silt, which causes insufficient light penetration through the water column.

Extensive work carried out offshore by Holme (1961,1966) concluded that while there were localised species assemblages associated with sediment variation, the main faunistic boundary is between the summer-stratified western half of the Channel and the eastern half, where vertical mixing of the water column occurs throughout the year. Cabioch *et al.*,(1977) also identified eastern boundaries of subtidal epibenthic species in the Channel. The abundance and species diversity of coccoliths in the Channel is considered to be under thermocline control with fewer species found in the more tidally mixed waters of the eastern Channel (Houghton, 1988).

Longhurst (1998) suggests that his Northeast Atlantic Shelves Province (NECS) may be further subdivided into seven areas of which the English Channel, from Dover west to Ushant, is the region of primary interest in this work. However he goes on to recommend that the region is more realistically divided up at known tidal front boundaries between mixed and thermally stratified water that occur in the spring and summer, largely determined by Pingree & Griffiths (1978). The development of stratification on the shelf causes these fronts to migrate seasonally. Inevitably, where thermoclines breakdown at the boundaries of these fronts, such as off headlands, there is a likelihood of water turbulence or strong currents. It remains unclear therefore whether those species associated with stratified conditions, determined by Crisp (1989), are dependent upon a thermal, chemical or ecological quality of stratified water, or just the presence of a relatively stable water column that minimises larval dispersal and facilitates high recruitment. Undoubtedly, southern species at their latitudinal limits, which are dependent on high water temperatures for successful reproduction and larval development, would benefit from warmer seas. Yet the evidence put forward does not exclude the possibility that development might proceed just as favourably in warm mixed-water. Indeed, at many sites along the north French coast between Brest and St. Malo, *Osilinus lineatus*, *G.umbilicalis* and *C. montagui* are either common or abundant (Crisp & Southward, 1958). Yet according to frontal boundaries illustrated in Pingree & Griffiths (1978) and reproduced in Crisp (1989) there is no inshore stratification here and the shores are shown to be bathed with mixed water.

1.6 Aims of this work

To further our understanding of faunistic limits in the English Channel, Holme (1966) suggests that further progress could be made by studies on species feeding, growth, reproduction and spat settlement in different years. Recognising the challenges of ecological monitoring on rocky shores, Lewis (1976) suggests that studies on the reproduction and recruitment of selected key species should be a priority.

It is the purpose of this current work to investigate which of the many possible factors are particularly important in controlling the distribution of southern rocky shore species along the English side of the Channel. The study area is the short 150 mile (241km) section of coastline between Torbay in South Devon and Eastbourne in East Sussex, where the greatest changes in populations appear to occur. Interactions between possible physical and biological factors influencing geographical limits of Lusitanian species on rocky shores are summarised in Fig.1.3.

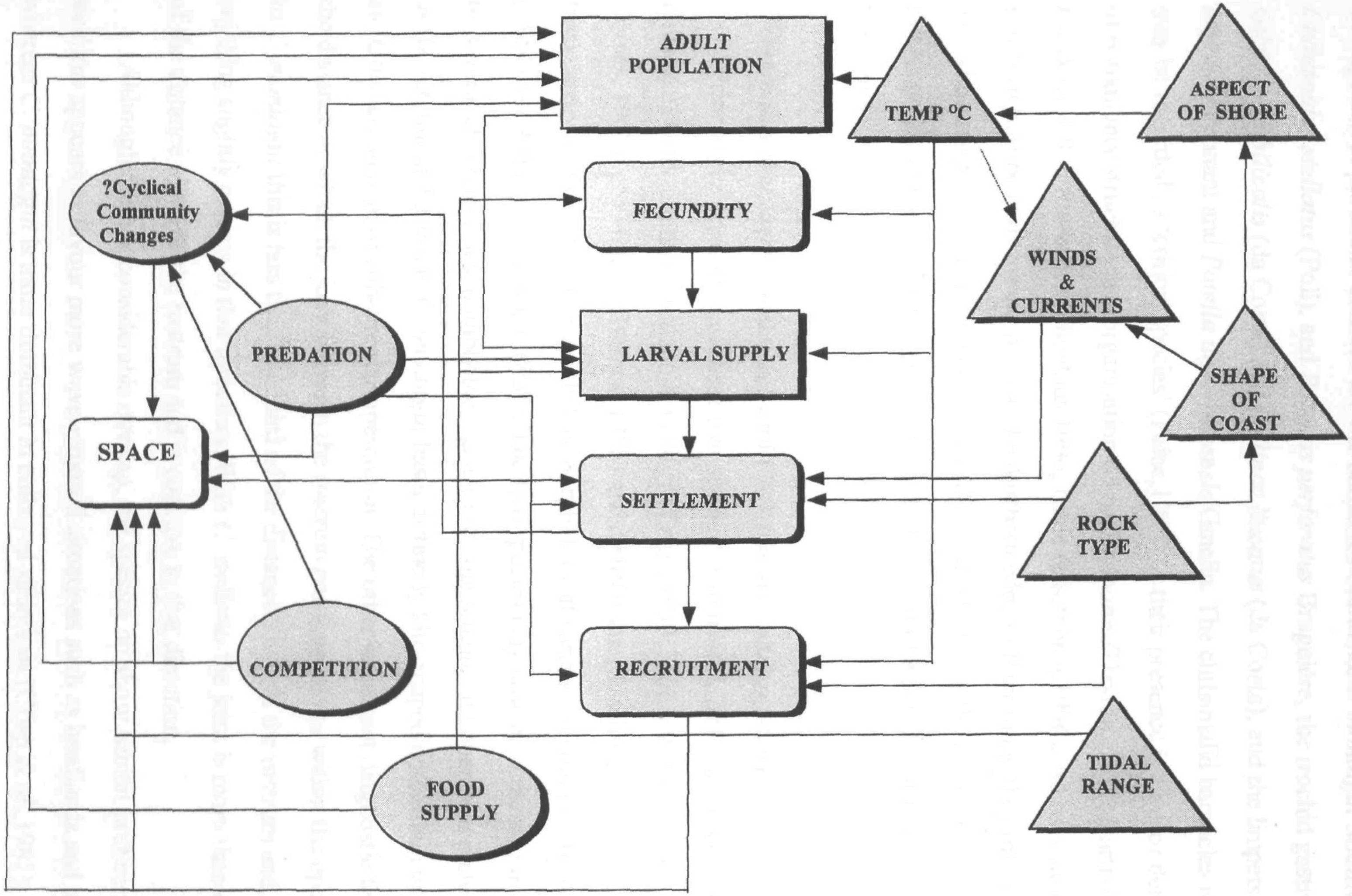


Fig.1.3 Flow chart showing factors potentially affecting population size of southern invertebrate species on rocky shores along the south coast of England.

1.6.1 Species of particular interest in this study

The species of particular concern are the barnacles *Chthamalus montagui* Southward, *Chthamalus stellatus* (Poli), and *Balanus perforatus* Bruguière, the trochid gastropods *Gibbula umbilicalis* (da Costa) and *Osilinus lineatus* (da Costa), and the limpets *Patella depressa* Pennant and *Patella ulyssiponensis* Gmelin. The chthamalid barnacles and limpets may be regarded as 'critical species' (Paine,1994) as their presence is a major determinant of community structure and organisation on rocky shores (Dayton, 1971; Hartnoll & Hawkins. 1985; Raffaelli & Hawkins,1996; Little & Kitching,1996). All have an essentially southern European distribution, so at the northern edge of their range they may be regarded as 'indicator species' of climate change (Southward, 1991; Southward *et al.*, 1995). The European distribution of these species and a selection of others relevant to the investigation is shown in Fig. 1.4.

***Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli)**

Prior to the separation of these two species (Southward, 1976) a considerable amount of work on the reproductive biology (Crisp, 1950; Barnes & Crisp, 1956; Barnes & Barnes, 1958), growth rate (Barnes, 1956) and distribution (Southward & Crisp, 1956) had been carried out on animals, regarded as morphological varieties recognised by Darwin (1854) as *Chthamalus stellatus* (Poli). The two species may now be separated in the field by several characteristics; notably the shape of the operculum and opercular plates known as the tergum and scutum. *C. montagui* has a distinctly kite-shaped operculum whereas *C. stellatus* has an oval or sub-circular operculum. The other important diagnostic feature is the distance at which the joint between the rostrum and tergum lies within the operculum. In *C. montagui* this is less than one third of the distance towards the rostrum and is if anything slightly convex in that direction. With *C. stellatus* the joint is more than one third of the distance towards the rostrum and is concave in that direction.

Although there is considerable overlap, the species do show habitat preferences; *C. stellatus* appears to favour more wave-exposed situations such as headlands and islands, whereas *C. montagui* is more dominant in embayed situations (Crisp *et al.*,1981). Generally speaking, in mixed populations *C. montagui* is found higher up the shore than *C. stellatus*. The two species occur together along the whole of the Atlantic coasts of Britain, Ireland, France, Spain and North Africa and the Mediterranean Sea (Crisp *et al.*, 1981; Pannacciulli *et al.*, 1997). Being essentially southern species, in the UK they breed between May and October, with the main settlement period between July and September (Burrows,1988; Burrows *et al.*,1992; Pannacciulli,1995). In the Mediterranean, larval development of *C. montagui* begins in February and continues in to October (Relini, 1983; Pannacciulli & Falautano, 1999). *C.stellatus* matures later and releases larvae from May to September (Pannacciulli & Falautano, 1999). *Chthamalus* settlement can occur throughout the year in the Mediterranean but is principally in July, August and September (Pannacciulli & Relini, 1999). In northern Spain, *Chthamalus* settles by the end of May (Myares,1986). Larval culture experiments found evidence to suggest that *C. stellatus* has a longer development period than *C. montagui*, which may enable the species to exploit islands and headlands not reached by other barnacle species (Burrows,1988; Burrows *et al.*,1999a).

The major predator of adult barnacles are muricid gastropods such as the dog-whelk *Nucella lapillus* (Crothers,1985). Burrows (1988) observed that dog-whelks feed preferentially on *C. stellatus* because of its larger size and that *C. montagui* was prised off the rock whereas *C. stellatus* was drilled. Individuals of *Chthamalus* have been known to survive 20 years at the northern extremities of their range in northern Scotland (Lewis,1986). Enzyme electrophoresis confirmed the specific rank of the two species (Dando & Southward,1980). Both species are known to exhibit genetic variation throughout their geographic range and occur in distinctly different Atlantic and Mediterranean forms (Dando *et al.*, 1979; Dando & Southward, 1981; Pannacciulli, 1995), although little if any genetic variation exists along the open seaboard of the NE Atlantic.

***Balanus perforatus* Bruguiere.**

This is one of the largest intertidal barnacles on British coasts, with basal diameter up to 35mm, and usually occupies the lower half of the littoral zone and the shallow sublittoral (Norris & Crisp,1953). Compared to the genus *Chthamalus* there has been relatively little work done on its biology and particularly the species general ecology. It is a somewhat enigmatic species, appearing in variable density on a wide range of hard substrata including wave-beaten coasts and estuaries, where it has been found to tolerate reduced salinities (Norris & Crisp,1953). Fischer-Piette (1936) noted the species preference for embayed situations near the limits of distribution on the French coast and Channel Islands where they also appear larger. Geographically the species occurs between West Africa and South Wales, but is not found in Ireland (Crisp & Southward, 1953). In south-west England it is known to breed during the summer months (Patel & Crisp, 1960ab). In the Mediterranean, mature gonads may be found throughout the year, although major brood releases occur in August (Lepore *et al.*,1979). Anderson (1981) has described the cirral feeding activity, which is different from other species of *Balanus*; in addition to captorial feeding it is also an efficient filter feeder, utilising a powerful exhalent jet of water produced from the mantle cavity.

Gibbula umbilicalis **(da Costa)** and ***Osilinus lineatus*** **(da Costa),**

The recruitment and population ecology of the topshells have not been studied in as much detail as some of the barnacles. These gastropods are conspicuous grazing animals although their relative importance in the community appears poorly understood. *G. umbilicalis* reaches its northern limits on the north coast of Scotland and occasional specimens have been found in the Orkney Islands (Rendall, 1956 cited by Kendall & Lewis, 1986). It is absent from the North Sea, although extends along the north coast of France as far as Calais and on the English side of the Channel as far as the Isle of Wight (Crisp & Southward, 1958). The southern limit is less certain but is suspected as being near Cap Blanc on the west African coast (Fischer-Piette,1955). The distribution of *Osilinus lineatus (= Monodonta lineata)* extends between the coast of Morocco in the south (Fischer-Piette,1955) to the north coast of Ireland (Crisp & Southward,1954). On the British mainland the northern limits occur abruptly at the Lleyn Peninsula. Both species have single sexes and gametogenesis lasts approximately one year. Short spawnings occur during the summer months, although the exact time appears to vary between years (Garwood & Kendall, 1985; Kendall *et al.*,1987). Fertilization is external and eggs develop into a lecithotrophic trochophore larva and rapidly into a veliger larva. Larval life is short, being between 4-6 days (Fretter & Graham, 1994). In Britain, recruits of both species may be found on the shore from mid-August. The lifespan of *Gibbula* is between 8-12 years at the northern limits of its range in Scotland and 2 years in Portugal. *Osilinus* also shows a reduction in longevity as the southern limits are approached with 10-15 years recorded in the UK but only 4-5 years in Spain (Lewis, 1986).

***Patella ulyssiponensis* Gmelin** and ***Patella depressa* Pennant**

The distribution of *Patella ulyssiponensis* (formally *P.aspera* Roding) extends between N.Africa and S.Norway (Fischer-Piette, 1935,1941,1948; Crisp & Southward, 1958; Lewis,1976; Bowman & Lewis, 1986), although on the north coast of the Channel it does not extend eastwards beyond the Isle of Wight (Crisp & Southward, 1958). The species is characteristic of exposed rocky shores and may be found on the mid to lower tidal levels in permanently wet *Lithothamnia* and coralline covered areas including pools. The main spawning period is between July and November, and if anything is earlier in north-east England than in the south-west (Ballantine,1961b; Bowman & Lewis,1986). Multiple spawnings are probable and in north-east England, newly emerged spat have been found on the shore as early as July, though more usually October (Bowman, 1981; Bowman & Lewis, 1986). The growth rate in south-west England is considered to be relatively slow, with juveniles rarely exceeding 6mm after one year (Bowman,1981). On the Isle of Wight, adult individuals may reach 80mm across (pers. obs).

Patella depressa occurs between North Africa and North Wales (Fischer-Piette, 1935, 1941, 1948; Crisp & Knight-Jones,1954; Crisp & Southward, 1958; Lewis, 1976). It is locally abundant in the western Channel, favouring rocky shores of moderate exposure where it may be found on the middle and lower shore. At Freshwater Bay on the Isle of Wight, Hatch (1977) found spawning individuals in June, July and September and ripe gonads were present throughout the autumn and over the winter. Multiple spawnings in this species are not confirmed (Orton & Southward, 1961; Bowman, 1981). Growth rate in the UK has been found to be slow and it is not certain when the main recruitment period is. Bowman (1981) suggests that 5mm animals on the shore in May could only be 3 years old.

1.6.2 Hypotheses:

1) On the south coast of England, the eastern geographic limits of *Chthamalus* spp., *Balanus perforatus*, *Gibbula umbilicalis*, *Osilinus lineatus*. *Patella depressa* and *P. ulyssiponensis* all occur in either Dorset or the Isle of Wight and have been subject to minor fluctuations in response to changes in air and sea temperatures over the past 50 years. Warm summers in 1989 and during the 1990s will therefore have increased the density of populations at the eastern limits of distribution. **See Chapter 3**.

2a) Breeding of *Chthamalus montagui* at the extreme eastern limits in the English Channel is likely as the species is known to produce broods in somewhat cooler conditions in the north of Scotland. Yet the onset of brooding will be later than in the western Channel i.e. late May or June and finish earlier in the autumn. **See Chapter 4**.

2b) Breeding of *Balanus perforatus* at the extreme limits of distribution is unknown although Norris & Crisp (1953) suspected a high degree of sterility. It is considered that in warm summers they will breed normally. **See Chapter 4**.

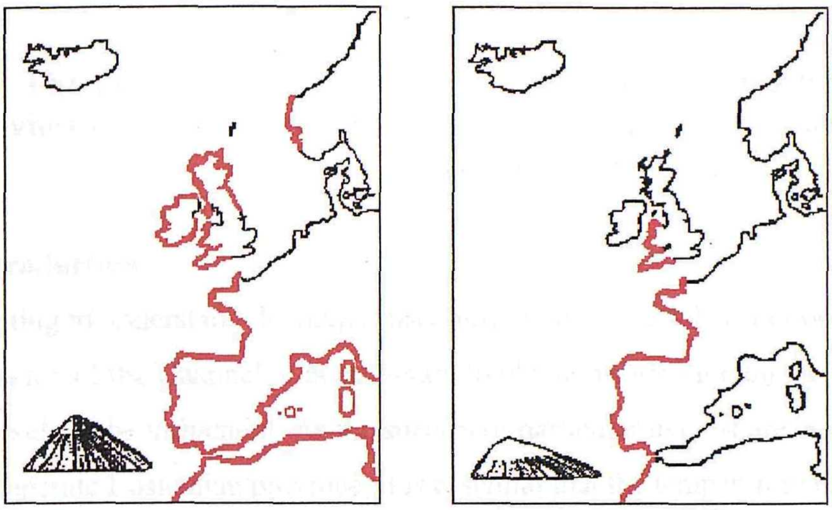
3a) The magnitude of annual recruitment of *Chthamalus* spp, *B. perforatus, Gibbula umbilicalis* and *Osilinus lineatus* is determined ultimately by breeding success influenced by sea and air temperatures. The higher the sea and air temperatures between May and September, the greater will be the annual recruitment. **See Chapters 5 and 6**.

3b) The magnitude of *Chthamalus* recruitment to the east of major headlands and peninsulas will be low, owing to strong offshore currents and gyres that cause considerable reductions in the number of larvae reaching the shore. **See Chapter 5**.

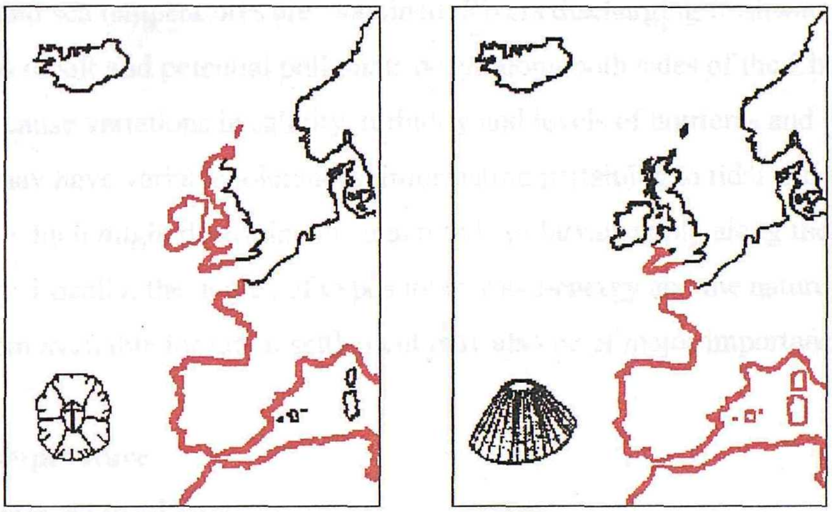
3c) Post-recruitment mortality of *Chthamalus montagui*, *Gibbula umbilicalis* and *Osilinus lineatus* will be greater in the eastern Channel because of cooler winters. **See Chapters 5 and 6**.

4a) The growth rate of *Chthamalus montagui, Gibbula umbilicalis* and *Osilinus lineatus* will diminish as the eastern limits of distribution are approached because of cooler winters **See Chapters 5 and 6**.

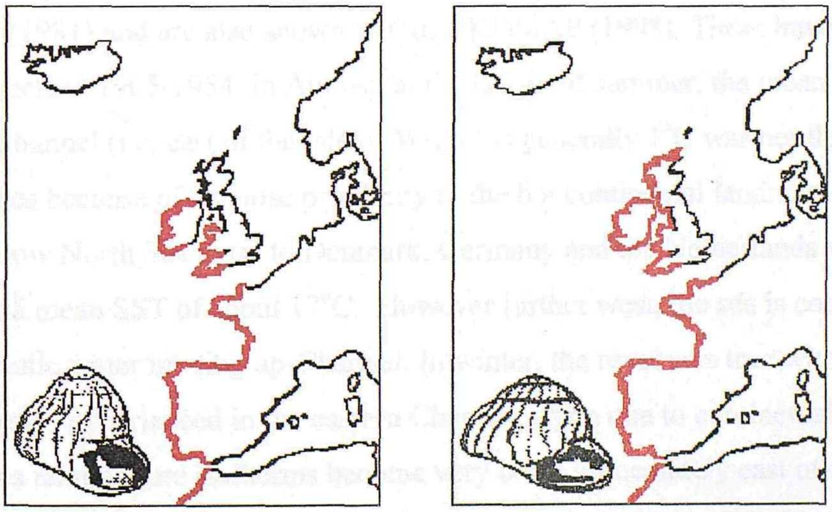
5) The success of both *Chthamalus* recruitment and the magnitude of post-recruitment mortality will be influenced by rock type with reduced recruitment success and higher mortality on softer rocks. **See Chapter 7**.



Patella ulyssiponensis *Patella depressa*



Chthamalus spp. *Balanus perforatus*



Osilinus lineatus *Gibbula umbilicalis*

Fig 1.4 The European distribution of selected species of invertebrates found on rocky shores. From Southward *et al.*, (1995).

Chapter 2

The physical environment of the south coast of England: A review of existing knowledge and observations obtained over the study period 1994-1999

2.1 Introduction

In attempting to understand the major discontinuity in species distribution within the central region of the Channel, it is necessary to obtain information on the abiotic factors that are likely to be influential. As the species of particular interest are essentially from the warm-temperate Lusitanian province, it is essential that the temperature regime of the Channel must be considered in detail. Moreover, for intertidal species, it is important that both air and sea temperatures are examined. Rivers discharging freshwater and various quantities of silt and potential pollutants occur along both sides of the Channel and are likely to cause variations in salinity, turbidity and levels of nutrients and toxins, to which species may have variable tolerances. Information pertaining to tidal and wind-driven currents, which might determine the magnitude of larval supply along the coast, is also necessary. Locally, the degree of exposure to wave-energy and the nature of the substratum available for larval settlement may also be of major importance.

2.2 Temperature

2.2.1 East-west gradients

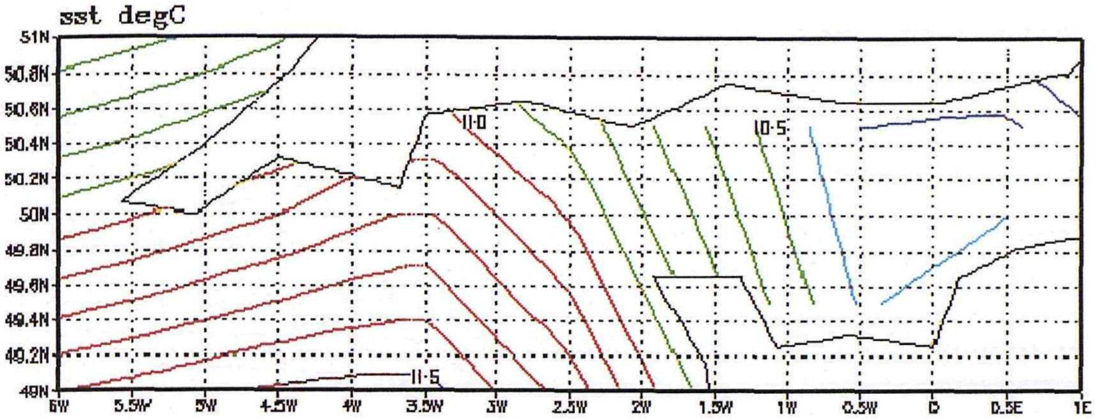
Mean sea temperature isotherms for the English Channel are presented in Lee & Ramster (1981) and are also shown within UKDMAP (1998). These have been compiled over the period 1905-1954. In August, at the height of summer, the mean SST of the eastern Channel (i.e. east of the Isle of Wight) is generally 1°C warmer than the western approaches because of its close proximity to the hot continental landmass of Euro-Asia. The shallow North Sea close to Denmark, Germany and the Netherlands warms quickly, reaching a mean SST of about 17°C. However further west, the sea is cooled by relatively cold Atlantic water moving up-Channel. In winter, the reverse is true with coldest temperatures experienced in the eastern Channel, again due to continental influences. The winter sea temperature isotherms become very close immediately east of the Isle of Wight, where the mean temperature for February, the coldest month, is 7°C. The western approaches in Devon and Cornwall are kept relatively mild in the winter due to the continuation of the Gulf Stream known as North Atlantic Current, and mean SST is between 9-10°C.

A broad-scale assessment of the pattern of sea surface temperature in the English Channel over the main six-year study period between 1994 -1999 was determined by plotting isotherms from Reynolds SST data provided by the NOAA-CIRES Climate Diagnostics Centre and obtained from their web-site (Climate Diagnostics Centre, 2000). The optimum interpolation (OI) SST analysis is produced weekly on a one-degree grid, with data available from 1981 to present. The analysis uses *in situ* and satellite SST's (Reynolds & Smith, 1994). Fig. 2.1 shows the mean winter SST isotherms to illustrate the typically warmer western approaches and cooler eastern basin of the Channel. A maximum and minimum temperature of 11.7 and 9.6 °C were recorded over the 1994-95 winter period within the area shown. There is a noticeably abrupt change in the direction of the isotherms off Prawle Point, east of which the temperatures appear to drop quickly at the rate of approximately 0.1°C per 0.25° longitude. Temperature decreases from 11.1 °C in the west of Lyme Bay to 10.5 °C off the Isle of Wight. A similar pattern of isotherms was evident during the winters 1997-98 and 1998-99.

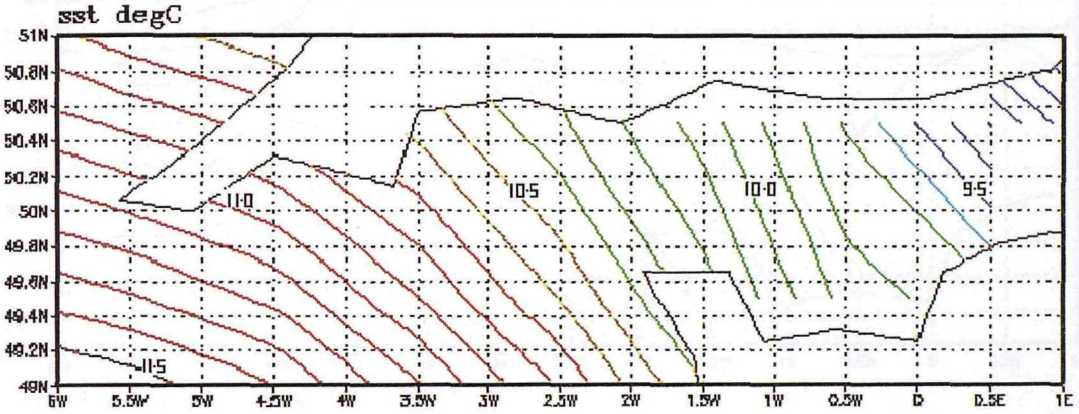
The western approaches of the Channel were cooler during the 1995-96 and 1996-97 winters. The temperatures immediately opposite on the French side of the Channel generally remain warmer, although this was less evident in the 1997-98 and 1998-99 winters where isotherms are almost vertically aligned, at least in the eastern Channel. Mean March-May temperatures (spring temperatures) were typically of the same order with a maximum of 12.08 °C in 1998 and minimum of 7.8 °C in the spring of 1996. Fig.2.3 shows the mean summer (July-September) isotherms for 1994 -1996. Overall, the summer of 1999 was the warmest and those of 1994 and 1996 the coolest. The isotherms during the warm summer of 1995 are much more widely spaced than those for 1999, which may indicate less surface mixing.

Compared to the western approaches, the eastern Channel experiences a greater range of temperature due largely to much cooler winters. The situation further inshore, however, is often complicated by land masses, the movement of water around headlands from potentially warmer embayments, and the effect of less saline estuarine discharges.

December 1994-February 1995



December 1995-February 1996



December 1996-February 1997

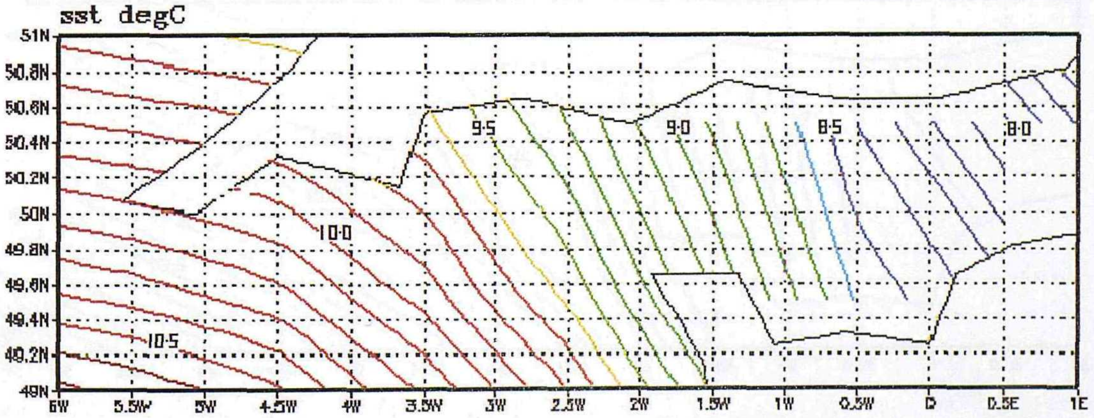
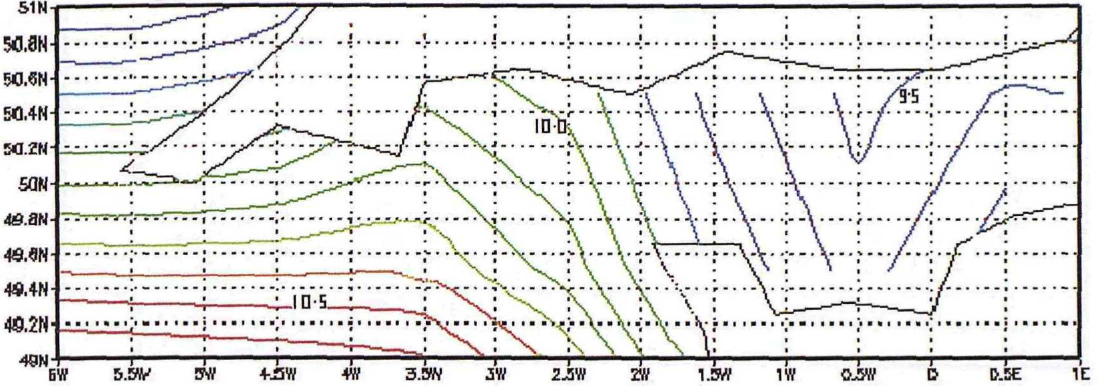
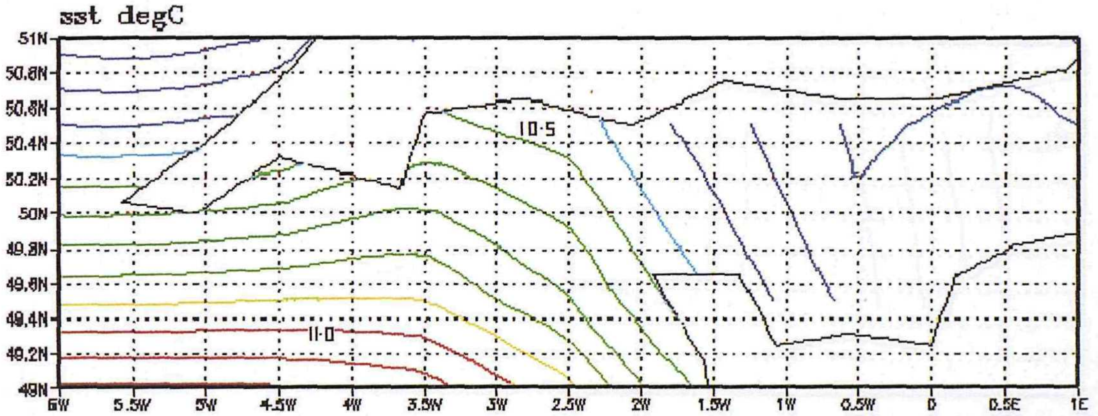


Fig.2.1 Mean winter Reynolds SST isotherms for the English Channel. Data obtained from the NOAA-CIRES Climate Diagnostics Centre (Climate Diagnostics Centre, 2000). Isotherms are at 0.1° C intervals. See text for further details.

March-May 1994



March-May 1995



March-May 1996

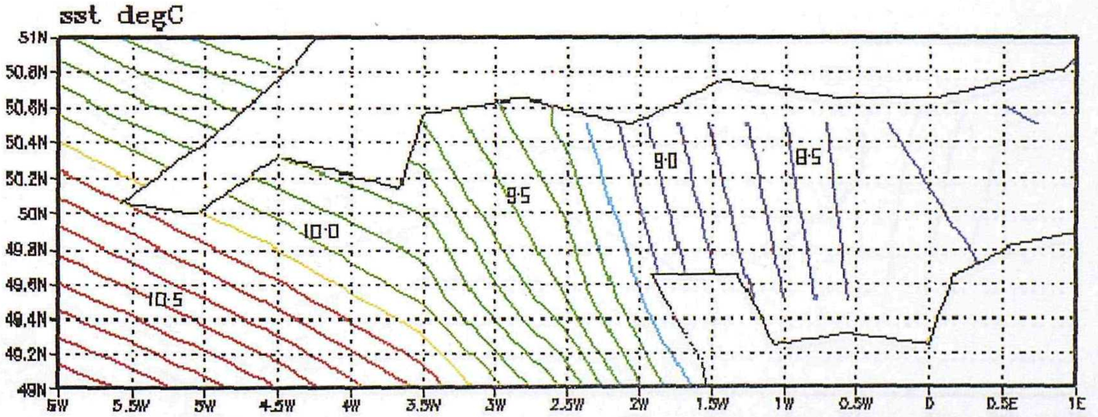
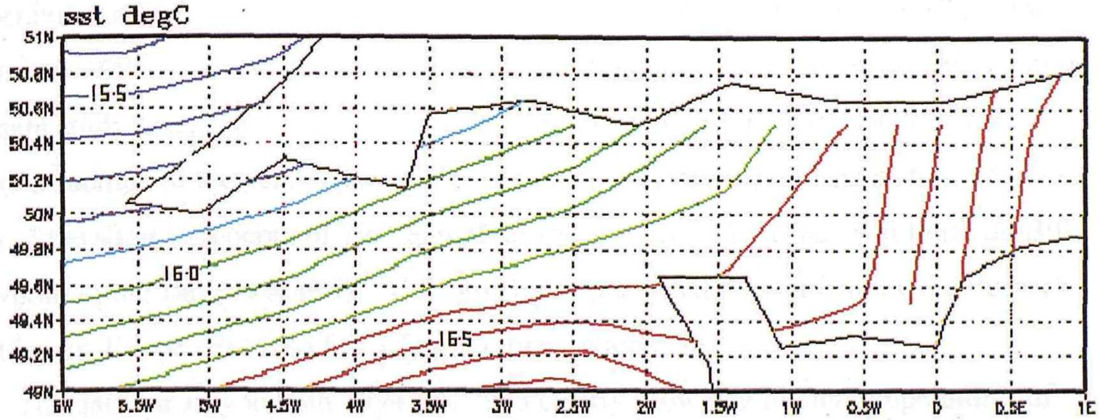
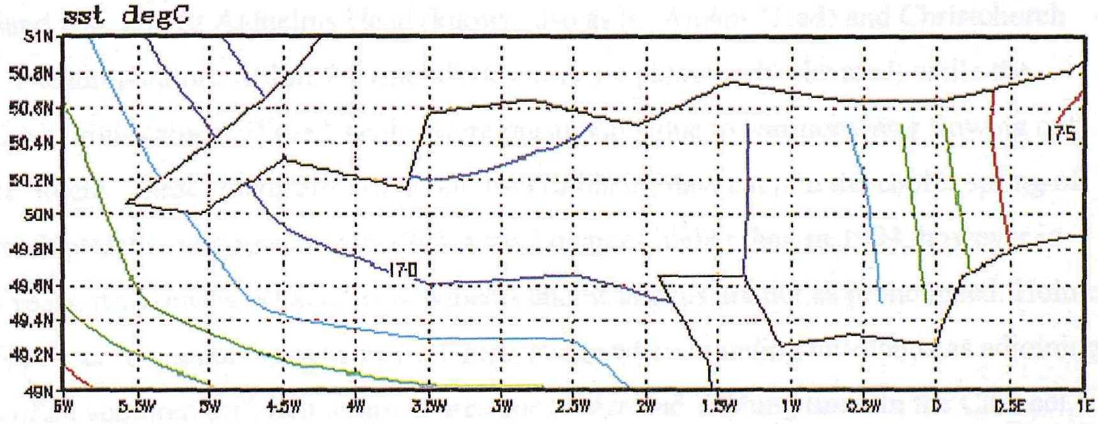


Fig.2.2 Mean spring Reynolds SST isotherms for the English Channel. Data obtained from the NOAA-CIRES Climate Diagnostics Centre (Climate Diagnostics Centre, 2000). Isotherms are at 0.1° C intervals. See text for further details.

July-September 1994



July-September 1995



July-September 1996

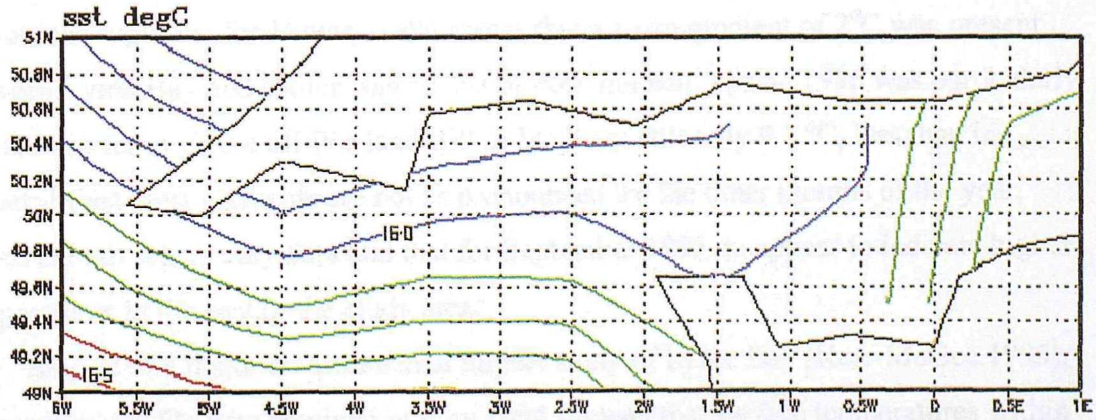


Fig.2.3 Mean summer Reynolds SST isotherms for the English Channel. Data obtained from the NOAA-CIRES Climate Diagnostics Centre (Climate Diagnostics Centre, 2000). Isotherms are at 0.1° C intervals. See text for further details.

2.2.2 Inshore transect data

Data obtained from the Environment Agency, who routinely measured sea temperature and other determinands along a transect between Torbay and St. Catherine's Point from 1994-1996, provides a more detailed inspection of the inshore situation within the main study area. Fig 2.4 shows a graphical presentation of the data obtained for different months of the year. Measurements were taken using a profiling instrument within 5 km of the shore at a depth of 1m. Sampling stations between Torbay and Portland Bill are within Lyme Bay; stations St. Aldhelms Head and Anvil Point are along the Purbeck coast in east Dorset. See also Fig 3.7 (p74) for location map.

The data for July in both 1994 and 1995 clearly show that higher temperatures of between 18-21°C were observed within embayments such as Lyme Bay and Christchurch Bay (at Hengistbury Head). In 1994 a 2°C difference was recorded between Seaton and Portland Bill, and St Aldhelms Head (known also as St. Albans Head) and Christchurch Bay. The temperature within Weymouth Bay was not particularly elevated, while the relatively high values off the Needles were presumably due to warmer water flowing out of the Solent. These trends are just about discernible in May, even in the cooler spring of 1996. September temperatures in 1995 were 2 degrees higher than in 1994, however in both years, differences between embayments and headlands are not as pronounced. Holme (1966) observed major changes in sea temperatures when rounding headlands as adjoining bays often acquired different temperatures due to size and flushing time. In the Channel, one of sharpest changes in sea temperature occurs off St. Aldhelms Head in Dorset (Holme,1966 citing Lumby,1953). Unfortunately no complete data are available for mid-winter, although that for January 1996 shows that a sharp gradient of 2°C was present between Lyme Bay and cooler waters east of Portland Bill. Spring 1996 was particularly late and the temperature off Portland Bill in May was still only 9.7 °C, less than in January! East-west gradients are not as pronounced for the other months of the year, however both sets of July data and that for September 1995 do appear to indicate higher temperatures in the east of the study area.

As part of a major environmental impact study of Lyme Bay (Kerr-McGee,1995), temperature profile data obtained in May 1994 showed that surface temperatures within the Bay varied between 10.6 and 12.4°C. Significant insolation effects on surface layers are evident from the profile data, particularly in the shallower areas of weaker tidal flows.

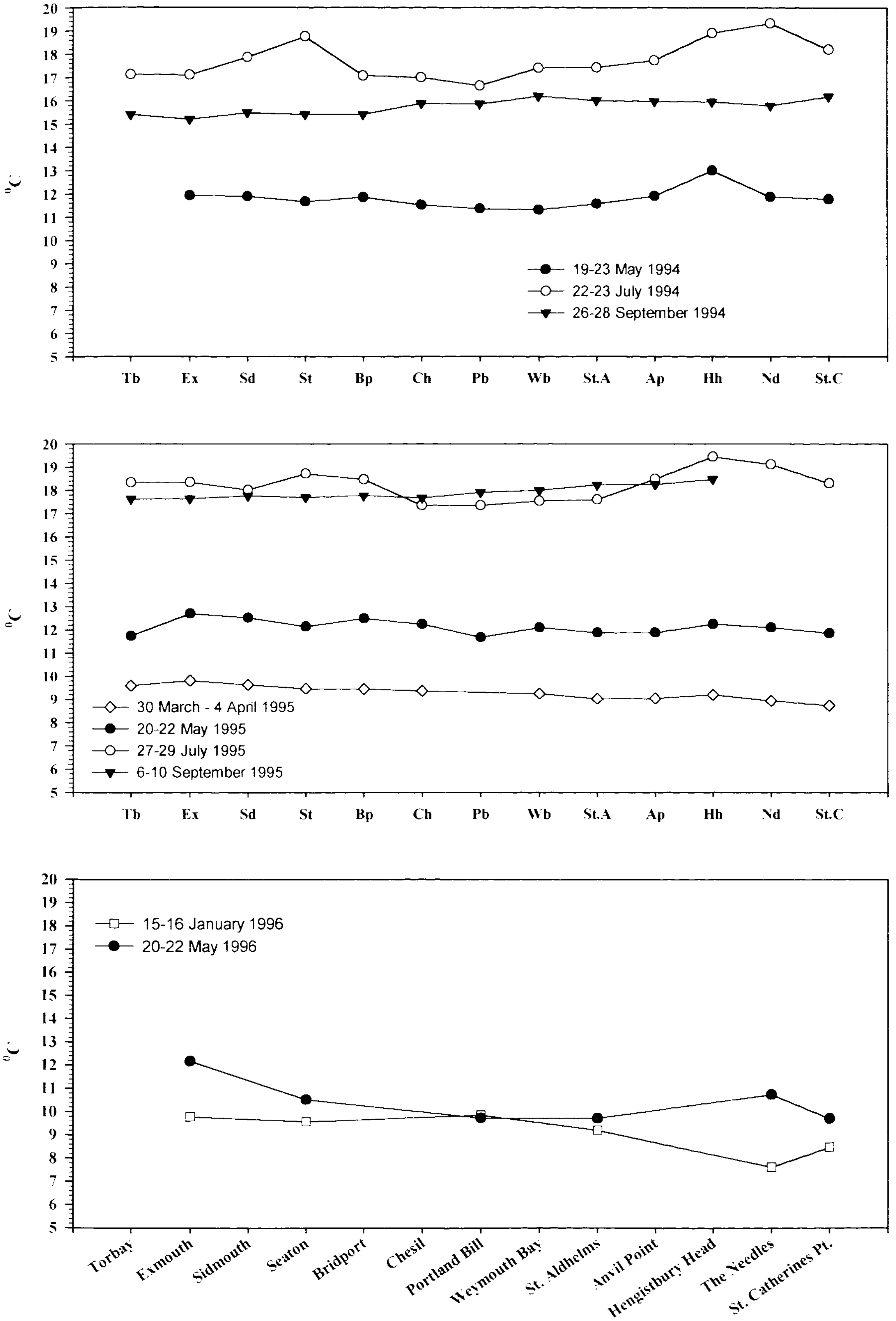


Fig 2.4 Sea temperature measured at 1m depth at stations along the south coast of England as part of the Environment Agency Baseline Survey 1994-1996. Stations are listed from west to east.

In the deeper faster flowing areas around Portland, well-mixed conditions are maintained. Warmest summer conditions were found in Weymouth Bay and Portland Harbour. The authors conclude that as a result of insolation, temperature stratification can occur in the area between March and August.

Pingree *et al.*, (1983) found evidence of a marginal frontal region in Lyme Bay between tidally stirred waters and thermally stratified conditions. Elevated chlorophyll-α values were shown up on Coastal Zone Colour Scanner (CZCS) images taken in the summer months. It is suggested that the high primary productivity measured along the crescent-shaped frontal zone is caused by cooler (16.0°C), mixed waters flowing around Portland Bill meeting warm (>17°C) stable conditions in the shallower parts of the Bay. Charts in UKDMAP (1998) indicate the probability of summer stratification occurring within the water column and show contours of the Simpson stratification parameter 'S', which is roughly quantified as $\log_{10} H/U^3$ where 'H' is the depth of water and 'U' the maximum tidal stream velocity. In general, areas with S>2 tend to become summer stratified. On the charts for the English Channel these regions only occur west of Start Point and therefore indicate that stratification within most of the Channel is unlikely. Yet, higher resolution maps are required to examine the situation closer inshore, which is the main area of concern of this work. Pingree & Griffiths (1978) show that stratified conditions (S >2) are likely to occur in the north-west of Lyme Bay and shores in south Devon and Cornwall. Conditions transitional between stratified and mixed (S = 1.5) are also projected for close inshore along the Dorset coast and off parts of the east Sussex and Kent coast. As a consequence of recent studies into the design of long sea outfall discharge pipes, Sherwin & Jonas (1994) found evidence of thermal stratification in Lyme Bay, Poole and Christchurch Bay and even in the eastern Solent on the north coast of the Isle of Wight. This was, however, in May 1990 when sea temperatures were exceptionally warm (15-16°C). The duration of such conditions at these more eastern localities, where thermally mixed waters were thought to be the norm, is not reported. The authors do point out that the persistence of stratification in certain areas and the conditions under which it breaks down requires more research.

2.2.3 Monthly monitoring of sea and air temperature at coastal stations 1994-1999

Mean air and sea temperatures from four main coastal stations are shown in Tables 2.1-2.6. Difficulties were encountered in obtaining complete sea temperature time-series along the south coast as several stations had just closed, or were closing e.g. Swanage. The administration of the meteorological recording in Torbay changed in 1998 with the arrival of an automatic station. Yet, although no sea temperature data were obtained at Torquay Marina during the summer of 1998, recording has since been resumed. The mean summer sea temperature value of 16.88°C in 1998 shown in Table 2.2 has therefore been estimated from air temperature data, for which there is a close correlation. It compares well with the value of 16.91°C obtained from the Met Office weather buoy positioned in the east of Lyme Bay (Met Office data, Bracknell)

Sea temperatures at Torquay are obtained daily at a depth of 1m from the marina. Air temperatures were obtained from Torre Abbey and measured daily at 0900 GMT. Sea temperatures at Weymouth and Shoreham are measured about ten times per month by staff of the MAFF laboratories (see Jones & Jeffs (1991) for earlier data). Unfortunately, no sea temperatures for Shoreham were obtained after July 1999. Sea temperatures from Dover in the eastern Channel are taken five to seven times a month while air temperatures are measured daily at 0900 GMT. Air temperatures from Shanklin on the Isle of Wight are measured daily at 0900 GMT.

Table 2.1 Sea temperatures (°C) from coastal stations obtained over study period 1994-1999. Shown are lowest and highest monthly means, and the annual mean. 'nd' denotes no data due to incomplete series.

Station	**Value**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**
Torquay	***Lowest***	*7.3*	*8.9*	*6.7*	*6.0*	nd	nd
	Highest	17.2	18.9	17.0	18.4	nd	18.2
	Mean	**12.3**	**13.0**	**12.4**	nd	nd	nd
Weymouth	***Lowest***	*7.2*	*8.3*	*5.2*	*4.5*	*7.9*	*7.2*
	Highest	17.5	18.3	17.0	17.1	17.3	17.7
	Mean	**11.8**	**12.3**	**10.7**	**11.6**	**12.0**	**12.0**
Shoreham	***Lowest***	*5.6*	*7.6*	*5.3*	*5.1*	*6.3*	6.*1*
	Highest	21.3	20.5	20.2	19.5	17.8	nd
	Mean	**13.2**	**13.7**	**12.6**	**12.6**	**11.7**	nd
Dover	***Lowest***	*6.5*	*7.3*	*5.1*	*3.8*	*6.5*	*6.9*
	Highest	18.6	19.4	17.7	18.7	17.8	19.4
	Mean	**12.0**	**12.3**	**11.2**	**12.2**	**12.1**	**12.8**

Table 2.2 Mean Summer (July-September) sea temperatures (°C) from coastal stations obtained over study period 1994-1999. Rank order given in brackets. 'nd' denotes no data due to incomplete series.

Station	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**
Torquay	16.23 (6)	17.63 (2)	16.53 (5)	17.27 (3)	16.88 (4)	17.72 (1)
Weymouth	16.45 (3)	17.19 (1)	15.83 (6)	16.23 (5)	16.43 (4)	17.13 (2)
Shoreham	19.67	19.32	18.80	18.50	16.96	nd
Dover	17.23 (4)	17.87 (2)	16.63 (6)	17.70 (3)	17.07 (5)	18.90 (1)

Table 2.3 Mean Winter (Dec-Feb) sea temperatures (°C) from coastal stations obtained over study period 1994-1999. Rank order given in brackets. 'nd' denotes no data due to incomplete series.

Station	**94/95**	**95/96**	**96/97**	**97/98**	**98/99**
Torquay	10.2	8.50	7.47	nd	nd
Weymouth	9.26 (1)	6.97 (4)	6.23 (5)	9.00 (2)	8.16 (3)
Shoreham	8.78 (1)	7.12 (3)	6.60 (5)	6.97 (4)	7.37 (2)
Dover	7.23 (3.5)	7.23 (3.5)	6.37 (5)	8.47 (1)	7.77 (2)

Table 2.4 Air temperatures (°C) from coastal stations obtained over study period 1994-1999. Shown are lowest and highest monthly means, and the annual mean. 'nd' denotes no data due to incomplete series.

Station	**Value**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**
Torquay	***Lowest***	*6.3*	*3.2*	*1.8*	*2.5*	*4.7*	*4.7*
	Highest	22.1	24.5	21.7	22.4	22.1	nd
	Mean	**11.7**	**12.1**	**10.9**	**12.0**	nd	nd
Shanklin (IOW)	***Lowest***	*5.0*	*6.1*	*3.6*	*2.9*	6.6	6.0
	Highest	16.9	19.3	16.3	18.7	16.8	17.8
	Mean	**11.1**	**11.4**	**9.8**	**11.1**	**11.1**	**11.4**
Dover	***Lowest***	*4.0*	*5.5*	*2.8*	*2.3*	*6.5*	*4.9*
	Highest	19.3	19.0	15.9	19.9	10.7	17.4
	Mean	**11.1**	**11.0**	**9.4**	**11.0**	**11.0**	**11.3**

Table 2.5 Mean Summer (July-Sept) air temperature (^{o}C) from coastal stations obtained over study period 1994-1999. Rank order given in brackets. 'nd' denotes no data due to incomplete series.

Station	1994	1995	1996	1997	1998	1999
Torquay	16.40	17.95	16.43	17.23	16.97	nd
Shanklin (IOW)	16.20 (4)	17.30 (1)	15.53 (6)	16.87 (3)	15.93 (5)	17.17 (2)
Dover	16.88 (4)	17.20 (3)	15.23 (6)	17.37 (2)	16.02 (5)	17.52 (1)

Table 2.6 Mean Winter (Dec-Feb) air temperature (^{o}C) from coastal stations obtained over study period 1994-1999. Rank order given in brackets. 'nd' denotes no data due to incomplete series.

Station	94/95	95/96	96/97	97/98	98/99
Torquay	8.28 (5)	6.98 (4)	6.08 (2)	5.95 (1)	6.15 (3)
Shanklin (IOW)	7.40 (5)	4.63 (1)	4.80 (2)	6.93 (4)	6.75 (3)
Dover	6.78 (5)	4.87 (4)	3.58 (1)	3.95 (2)	4.17 (3)

Coolest temperatures are measured in February while highest temperatures are normally reached in August, although over the past 100 years the warmest ever Channel temperatures have been in September (Raynor *et al.*, 2000). Table 2.1 shows the annual mean sea temperatures over the main study period and indicates that 1996 was overall the coolest year while 1995 and 1999 were the warmest. The mean of 13.7 ^{o}C for Shoreham in 1995 exceeded the previous record of 13.2 ^{o}C in 1989. The mean summer temperatures (July-September) were slightly higher at the eastern stations of Shoreham and Dover, which is consistent with the broad-scale temperature gradient in the Channel discussed previously. Warmest summers were 1995 and 1999, the latter being slightly warmer overall, although the highest mean monthly sea temperature recorded over the study period was 20.54 ^{o}C at Shoreham in August 1995. The sea temperature in September 1999 was exceptionally warm and was the highest ever recorded for the month at Dover.

The coolest winter (December-February) sea temperatures at coastal stations were those of 1995-96 and 1996-97, the latter having the lowest mean. The 1997-98 winter sea temperatures at Shoreham were marginally less than those of 1995-96. Slightly cooler conditions occurred at the eastern sites of Shoreham and Dover compared to those at Weymouth and Torquay although differences were no greater than 1.5 °C . The coldest month was January 1997 when mean temperatures were 3.8 °C at Dover, 5.1 °C at Shoreham, 4.5 °C at Weymouth and 6 °C at Torquay. The slightly cooler conditions measured at Weymouth could have been due to the influence of freshwater discharge from the River Wey.

The rank-order annual mean air temperatures closely follow those of sea temperature with warmest years being 1995 and 1999 and coolest in 1996. The measurements of air temperature are however more susceptible to local microclimatic differences. At Dover, sub-zero winter mean-minimum temperatures were recorded in February 1996 (-0.02 °C) and January 1997 (-0.6 °C). At Torquay, no sub-zero mean minima were recorded, although short periods of air frost may have occurred. The winter 1994-95 was the mildest during the study period. The highest mean monthly air temperature recorded was 24.6 °C at Dover in August 1997. Other short-term data obtained during the study period confirmed the general patterns described above. At Kimmeridge, sea temperatures were recorded intermittently in 1995 and 1996 from a sensor attached to a buoy in the Bay at a depth of 2m. A maximum value of 22°C was recorded on 30th July 1995. A sensor inserted into the rock at mid-shore level measured a fall in mean temperature from 11.8-7.7 °C between 19th November and 31st December 1995. A minimum of -2.7°C was recorded on 24th of December 1995. In 1996, sub-zero temperatures were recorded intermittently between January and March and maximum rock temperatures reached 41°C in mid-July.

At Durlston Head near Swanage, a temperature sensor was positioned 400m offshore at a depth of 11m. Data were collected intermittently between July 1994 and May 1997. Summer temperatures were maximum in 1995 when they reached 19.1°C (L.Browning pers.comm)

2.2.4 Long-term temperature time-series

Fig 2.5 shows an annual mean SST time-series for the central English Channel (box 50-51° N, 1-2° W) from 1871-1999. Data have been extracted from the HadISST1 data set (Raynor *et al.*, 2000). A linear regression line through the series indicates a rise in temperature of about 0.7 °C between 1871 and 1999.

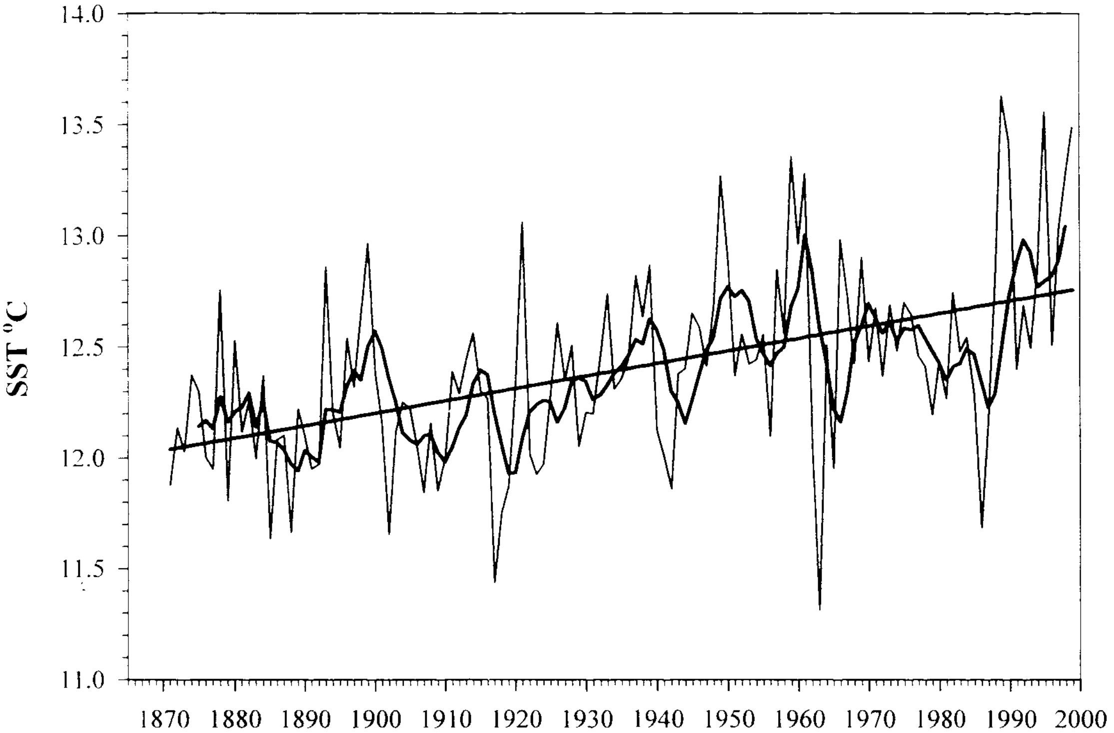


Fig.2.5 Sea surface temperature (SST) of central English Channel (50-51° N, 1-2° W) from 1871-1999, shown as annual mean (thin line) and smoothed 5 year mean (thick line). Linear regression fitted using least squares method ($r^2 = 0.24$, $F = 40.1$, $p < 0.0001$). Data extracted from the HadISST1 data set (Raynor *et al.*, 2000).

Cool periods of several years exist all the way through the series, as do warm phases. The early 1900's were particularly cool and more recently the period 1975 to 1986, which culminated in the third coolest year over the whole series (11.69 °C). The coldest winter was 1962-63 when many harbours and estuaries froze for several weeks. The SST of 6.34 °C for February 1963 is the lowest monthly mean of the whole time-series and the exceptionally cold winter contributed to the lowest annual mean of 11.31°C. The other notably cold years were 1917 (11.44 °C) and 1942 (11.86 °C). Seven particularly warm years have occurred since the middle of the twentieth century and four of those have been over the past decade; 1989 (13.63 °C); 1990 (13.42 °C); 1995 (13.56 °C) and 1999 (13.49 °C). The year of 1989 has been the warmest of the time-series although the warmest month was September 1949 (18.02 °C), closely followed by September 1939 (17.98 °C) and September 1999 (17.97 °C). The particularly warm September in 1999 contributed to the warmest ever mean summer (July-September) SST over the time-series of 17.46 °C.

Over the period 1861-1997, annual global surface temperatures have risen by 0.57°C. (Jones *et al.,* 1999; Climate Research Unit, 2000). The 1990s were the warmest decade in the series with 1998 the warmest on record. Analyses of over 400 proxy climate series (from trees, corals, ice cores and historical records) show that the 1990s was the warmest decade of the millennium and the 20th century the warmest century. The warmest year of the millennium was 1998 and the coldest was probably 1601 (Jones *et al,* 1999; Climate Research Unit, 2000). While cyclical warm and cool periods are acknowledged, much debate has arisen concerning anthropogenic influences on global temperatures as a result of the increase in greenhouse gases from burning fossil fuels (see Houghton (1994) for review). In its most recent report, the inter-governmental panel on climate change (IPCC) stated *"the balance of evidence suggests a discernible human influence on the climate system"* (Houghton *et al.,* (eds.).1995). Attempts to predict the magnitude of future climate change have required the construction of models coupling ocean and atmosphere heat circulation (General Circulation Models). Of particular interest is the examination of periodicity within time-series. Of special relevance to the SST of the English Channel is the decadal variation in climate thought to be associated with the North Atlantic Oscillation (NAO) (Hurrel, 1995; Hurrel & VanLoon, 1997). In simple terms, this temperature see-saw occurs due to atmospheric pressure differences between the arctic and the Azores. When pressure is low near Iceland there is a tendency for it to be high near the Azores and south-west Europe. The sea level pressure difference between these two locations has been converted to an index (Hurrel, 1995). The high index for the mild winters/springs of 1989,1990 and 1995 was caused by a deep 'Icelandic Low' and an extensive 'Azores High', which strengthened westerlies over the North Atlantic Ocean. Strong westerlies bring more warm moist air over the European continent and give rise to milder maritime winters. The low index for the winter/springs of 1917, 1936,1963 and 1969 was associated with a southward displacement of the 'Icelandic Low', a breakdown of the 'Azores High' and weaker westerlies over the North Atlantic Ocean, with corresponding colder than normal European winters. The winter temperature has a major effect on the annual mean temperature for that year. Fig.2.6 shows an overlay between the mean Channel SST and the Winter NAO index. Although not perfect the two variables correlate well ($r = 0.5$, $p = 0.001$, $n = 50$). Aphasic correlation's are not statistically significant: NAO v SST year +1 , $r = 0.05$, $p = 0.71$, $n = 49$; NAO v SST year +2, $r = 0.04$, $p = 0.78$. $n = 48$. In the past twenty years most of the NAO indices have been positive.

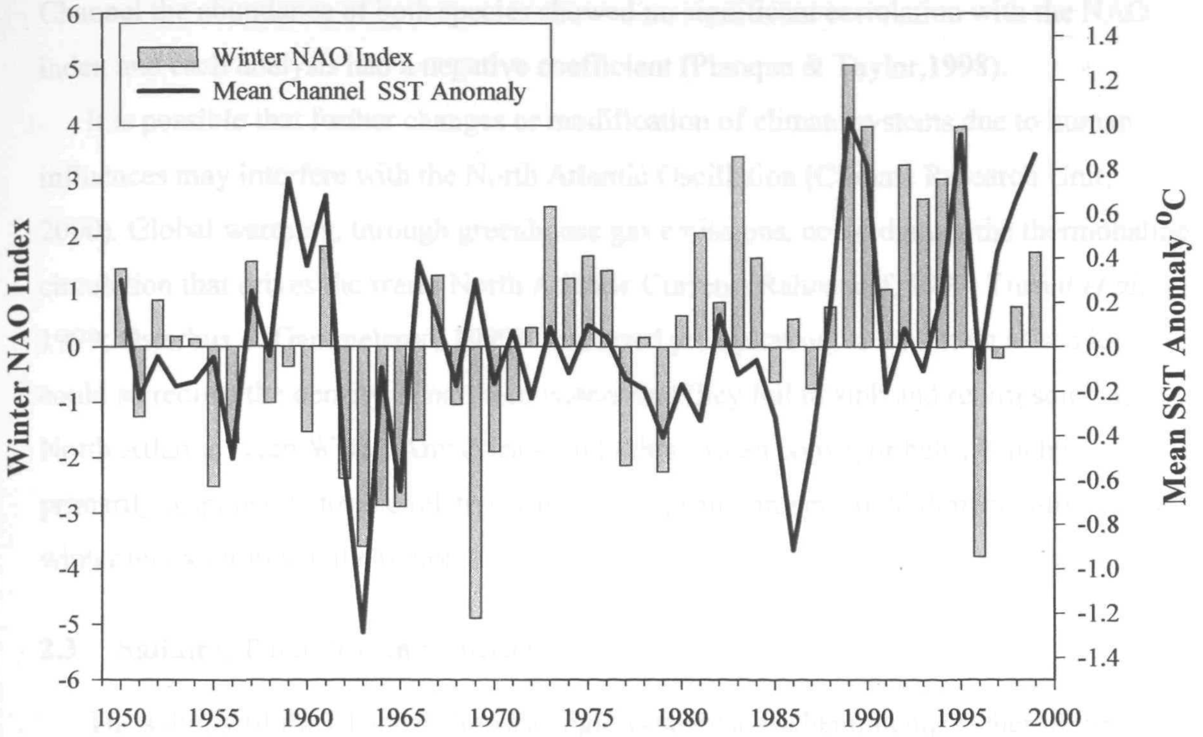


Fig.2.6 Mean Channel SST anomaly and Winter NAO index 1950-1999. Channel SST data from the HadlSSST1 time-series (Raynor *et al*, 2000). Winter NAO index is as calculated by Hurrel (1995) and obtained from D.Stephenson's website (Stephenson, 2000).

The intense warm current known as the Gulf Stream, which leaves the eastern seaboard of the United States and progresses eastwards across the North Atlantic, plays a major role in the transfer of heat from ocean to atmosphere. Taylor & Stephens (1998) have shown that over the past thirty years, the latitude of the north wall of the Gulf Stream is clearly correlated with the NAO; high values of the NAO index favour more northerly paths of the Gulf Stream about two years later. Moreover, the Gulf stream is also displaced northwards by El Nino-Southern Oscillation (ENSO) events so storm tracks over the Northwest Atlantic are linked to ocean-atmosphere events in the Tropical Pacific (Taylor *et al.*,1998). Taylor (1995) and Planque & Taylor (1998) have investigated relationships between these various climatic indices and plankton abundance around the British Isles. For example the position of the north wall of the Gulf Stream correlates well with the total copepod abundance in the northern North Sea (Taylor, 1995). In the thermally stratified regions of the northern North Sea, significant positive associations occur with the NAO index and abundance of *Calanus helgolandicus* and negative associations with *C. finmarchicus.* Yet in the western approaches and central English Channel the abundance of both species showed no significant correlation with the NAO index and each analysis had a negative coefficient (Planque & Taylor,1998).

It is possible that further changes or modification of climate systems due to human influences may interfere with the North Atlantic Oscillation (Climate Research Unit, 2000). Global warming, through greenhouse gas emissions, could disrupt the thermohaline circulation that drives the warm North Atlantic Current (Rahmstorf, 1997; Turrell *et al.*, 1999; Østerhus & Gammelsrød, 1999). Increased precipitation, and melting of sea ice could so reduce the density of northern waters that they fail to sink and return south as North Atlantic Deep Water. Any disruption to this 'ocean conveyor belt', which is primarily responsible for the relatively mild European winters, could dramatically reduce winter temperatures in the region.

2.3 Salinity, Turbidity and Nutrients

The salinity of the Channel shows a slight east-west gradient, being higher in the west than in the east (Lee & Ramster, 1981). The data, which are also presented in UKDMAP (1998) shows a winter sea surface salinity isohaline of 35ppt extending across Lyme Bay. Slightly reduced salinities of 34.75ppt occur within the Solent region and along the Sussex coast. Reduced salinity may of course be more important to pelagic larval stages than to adults living within the intertidal zone that are exposed to the direct effects of rainfall at low tide. As the southern species of interest spawn during the summer months, any exposure of the larvae to reduced salinities offshore must be minimal. The water turbidity of the Channel correlates well with the pattern of salinity, as much sediment is discharged into the sea via rivers, which are larger in size and more frequent in the east. However, the mobility and lithology of the seabed substratum, to some extent, also determine the turbidity of the water. The shores of the western Channel, that is along the Devon and Cornish coast, are generally of harder substratum than those further east and the more steeply shelving coastline and deeper water reduces wave disturbance of the sea bed, resulting in lower turbidity. In contrast, water further east contains much particulate material, and apart from reduced light penetration which could influence algal growth, the continual abrasion of the shores might create conditions that are inimical to many intertidal species by causing interference with filter-feeding and respiratory mechanisms.

Yet most Lusitanian species of interest are currently common along parts of the Dorset coast that are backed by rapidly eroding cliffs that contribute large quantities of mud silt and sand across the intertidal zone. Mud-flows are frequently observed at Lyme Regis and Charmouth where all the species of concern in this work are common. Offshore, the sea remains comparatively clear until the Channel narrows to the east of the Isle of Wight, where the water becomes continuously turbid (Crisp & Southward, 1958). As far as water quality is concerned, most pollutants are discharged from estuaries, although there has been particular nutrient enrichment in the vicinity of holiday resorts such as Bournmouth in Dorset. With European legislation necessitating the construction of longer sea-outfalls, discharging waste water and treated sewage into deeper water at a greater distance from the coast, the impact of nutrient enrichment upon intertidal species may become less. Fig.2.7 shows chlorophyll-α measurements obtained between 1994 -1996 along a transect from Torbay and Southampton Water, undertaken by the Environment Agency. Water samples were taken at a depth of 1m. Compared to the east Devon and Dorset coast, considerably higher spring and summer measurements were obtained in Christchurch Bay and around the Isle of Wight, close to the nutrient enriched waters of the Solent. In May 1995, smaller peaks also occurred in Torbay, Exmouth and near St. Albans Head on the Purbeck coast. In these cases, elevated readings may be related to sewerage discharges in the near vicinity. There is little evidence of elevated values in Lyme Bay that could indicate the edge of a front, although this might only be detected by continuous monitoring along the transect.

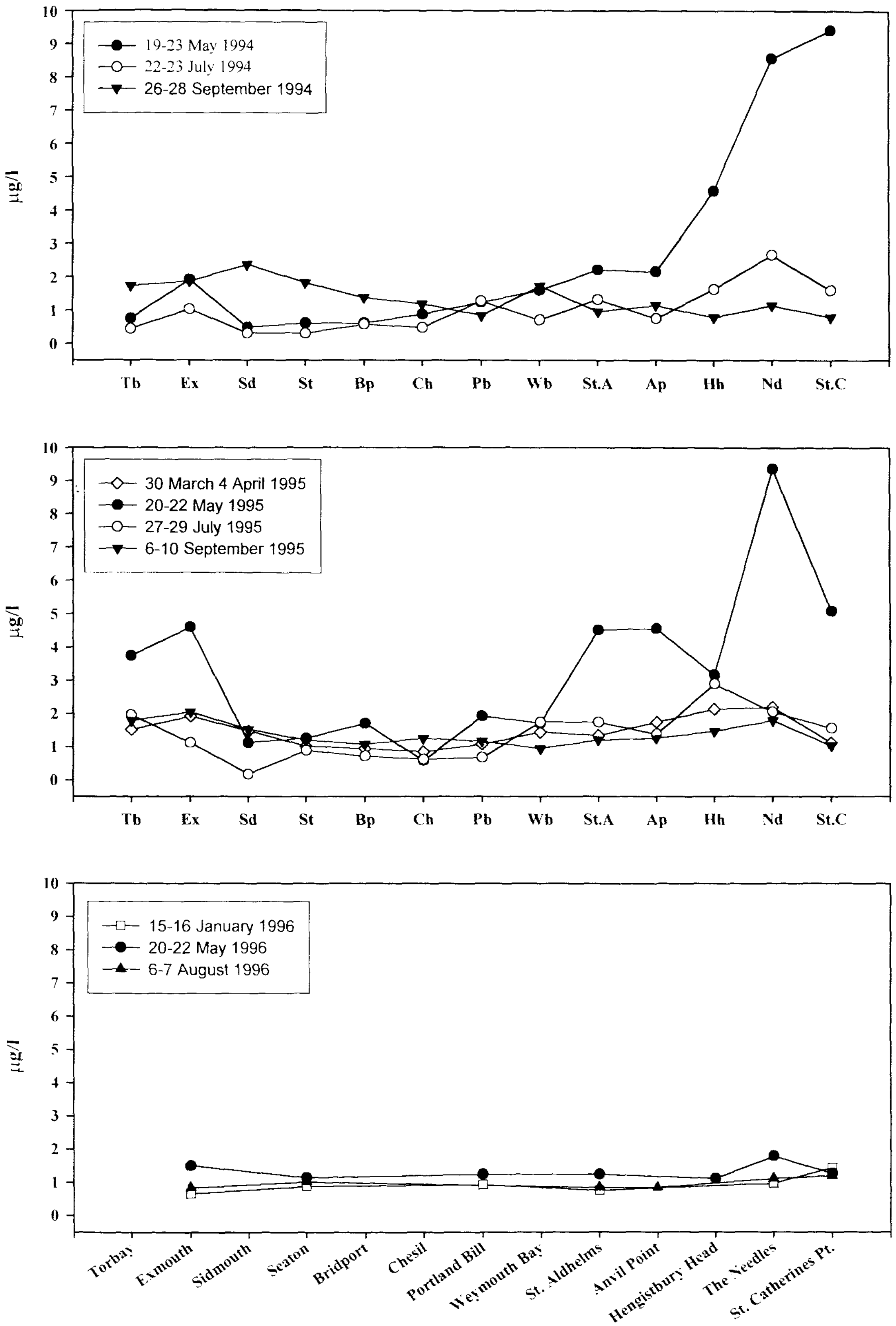


Fig.2.7 Chlorophyll-α measurements taken at 1m depth along the south coast of England as part of the Environment Agency Baseline Survey 1994-1996.

2.4 Hydrography

The English Channel may be divided into two tidal basins, roughly along a line between Swanage in England and Cherbourg in France. Along the English coast the smallest tidal range of 2m occurs at Swanage. The range increases both to the east and west of this amphidromic point, reaching 4m at Portsmouth and Torbay respectively. Distortion of the tidal curves is a common feature of the region due to a combination of factors which include sea floor topography, shallow water, coastline configurations and in particular the division of tidal flow around the Isle of Wight. This results in unusual tidal phenomena, such as the double low waters observed at Kimmeridge, Weymouth Bay and Portland which extend the period of low tide, and the double high water that increases the stand at high tide in the Solent and around the Isle of Wight (Pingree & Maddock, 1977; Barne *et al.*, (eds.). 1996a). Tidal ranges increase offshore, reaching a maxima of 8-9m around the Channel Islands and the Gulf of St. Malo on the north coast of France.

Because the tides are out of phase in the east and west Channel, there is a 6 hour difference between the time of high water (and low water) spring tides. West of Swanage, low water spring tide occurs at around midday and midnight, whereas to the east of St.Albans Head, they occur in the early morning and evening. Potentially, this could have a major influence on the ecology of the shores, particularly lower levels, as those to the west will be exposed to summer heat at midday. To the east, submergence during the hottest part of the day may reduce the risk of desiccation, but exposure to early morning frosts could be more damaging to Lusitanian fauna.

While weak (<0.5 $m.s^{-1}$) inshore tidal currents occur in Lyme Bay and off parts of the Sussex coast, fast streams occur in many areas, reaching between 1.75-3.0 $m.s^{-1}$ off Portland Bill during spring tides (Barne *et al.*, (eds.).1996a; Bruce & Watson, 1998). Fast currents and turbulence also occur off other major headlands such as St. Albans Head in Dorset and at the Needles and St. Catherines Point on the Isle of Wight. Either side of these headlands, tidal eddies may occur such as at Portland Bill (Pingree & Maddock, 1977). Tidal-stream charts for inshore waters along the Dorset coast, prepared by local sailors and fisherman, are presented in Bruce (1989). More recently, this local knowledge has been combined with more quantitative tidal information generated by oil companies and HR Wallingford Ltd. who have used Ocean Surface Current Radar (OSCR) together with the French modelling programme Telemac-2D to describe the situation in greater detail (Bruce & Watson, 1998).

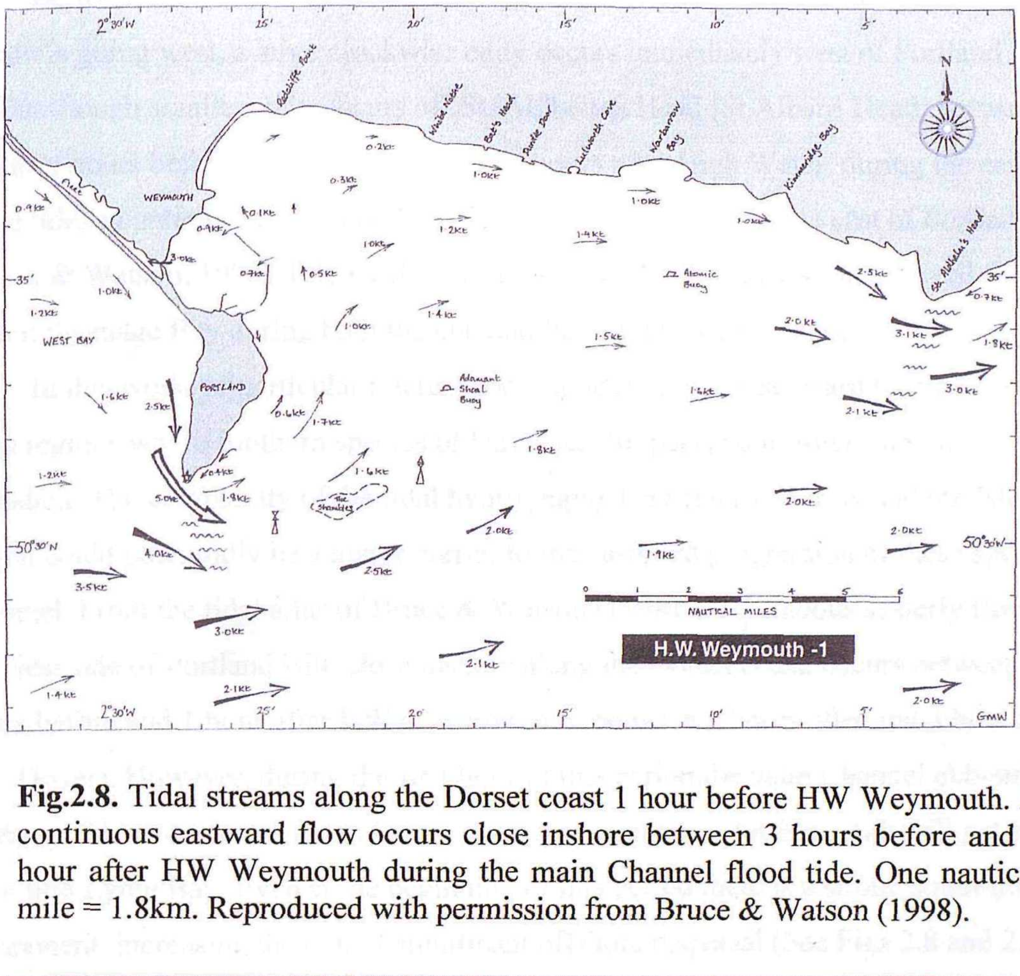


Fig.2.8. Tidal streams along the Dorset coast 1 hour before HW Weymouth. A continuous eastward flow occurs close inshore between 3 hours before and 1 hour after HW Weymouth during the main Channel flood tide. One nautical mile = 1.8km. Reproduced with permission from Bruce & Watson (1998).

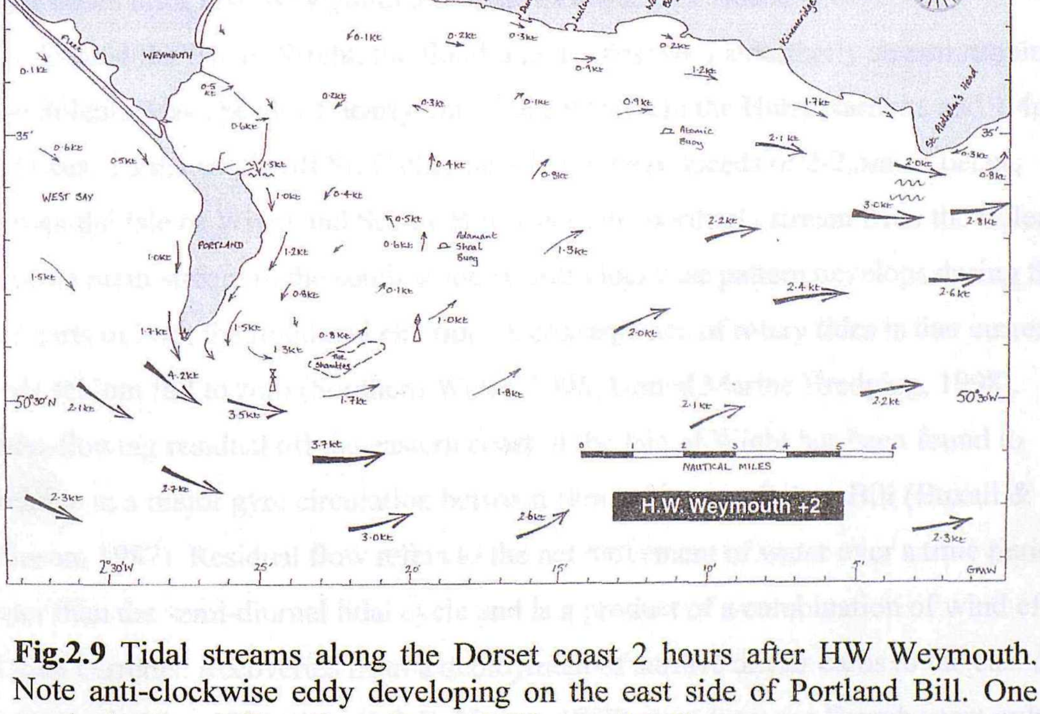


Fig.2.9 Tidal streams along the Dorset coast 2 hours after HW Weymouth. Note anti-clockwise eddy developing on the east side of Portland Bill. One nautical mile = 1.8km. From Bruce & Watson (1998).

Between six and two hours before High Water at Weymouth, when the main ebb stream is going west, a large clockwise eddy occurs immediately west of Portland Bill. A similar though smaller eddy occurs off St. Aldhelms Head (St.Albans Head) between six and four hours before High Water. For three hours after High Water, during the east-going flood tide, an anticlockwise eddy develops in Weymouth Bay to the east of Portland (Bruce & Watson, 1998). Eddies also occur between Durlston Head and Peveril Point and within Swanage Bay during both the ebb and flood tide (Bruce,1989).

In this work, of particular interest and importance is the eastward transport of larvae from regions where southern species of barnacles, limpets and topshells are most abundant. The complexity of the tidal hydrography between Lyme Bay and the Isle of Wight could potentially be a major barrier to the eastward progression of these species up-Channel. From the tidal atlas of Bruce & Watson (1998), a continuous easterly flow from the west side of Portland Bill, close inshore along the Dorset coast, occurs between 3 hours before and 1 hour after HW at Weymouth (between 5 hours after and 3 hours before HW Dover). However, during the first hour of this period the main Channel ebb-stream further offshore is westward, so larvae just a few kilometres further south will get swept back into Lyme Bay. Even at the beginning of this period there is a strong south-going component, increasing the risk of significant offshore dispersal (See Figs 2.8 and 2.9). From 1 hour after HW the continuous eastward inshore flow from Lyme Bay is interrupted by the development on an anti-clockwise eddy. Strong southward inshore currents occur from 2 hours after HW Weymouth along the east side of Portland.

Around the Isle of Wight, the flood tide divides, with a northerly stream running in to the Solent. Peak speeds of nearly $2m.s^{-1}$ occur through the Hurst Narrows and $1.4m.s^{-1}$ off Cowes. To the south, off St. Catherine's Point, peak speeds of $2\text{-}2.5m.s^{-1}$ occur. Between the Isle of Wight and Selsey Bill, where the northerly stream from the Solent meets the main stream to the south, a rotary anti-clockwise pattern develops during the latter parts of both the flood and ebb tide. A consequence of rotary tides is that current speeds seldom fall to zero (Southern Water, 1996; United Marine Dredging, 1998). A west-flowing residual off the eastern coast of the Isle of Wight has been found to culminate in a major gyre circulation between Bembridge and Selsey Bill (Boxall & Robinson, 1987). Residual flow refers to the net movement of water over a time period greater than the semi-diurnal tidal cycle and is a product of a combination of wind effects and tidal currents. Recoveries from a deployment of surface drifter cards to the east of Bembridge in May 1984 (Boxall & Robinson, 1987) were from the French coast only, 57 days later. Those deployed to the south of the Isle of Wight were recovered on the French coast 27 days later but none arrived on the south coast of England. A repeat experiment in June 1986 provided further evidence that the residual tide in this region is west-flowing or south-going. Drifter cards deployed west of Selsey Bill were only recovered from the Isle of Wight and Selsey, while those deployed east of Selsey were recovered 30 days later on the French coast. In May and June 1995, studies using Ocean Surface Current Radar (OSCR) confirmed the existence of the gyre at the eastern approaches to the Solent and found it to be strongly seasonal, forming only during period April to May and persisting during the summer months (S. Boxall pers comm; Guyard, 2000).

Guyard (2000) attempted to measure the dispersal of particles from different positions in the eastern approaches to the Solent and to the west of the Isle of Wight using a computer model of the Channel developed by IFREMER (Institut Francais de Recherche pour l'Exploitation de la Mer), Brest, and based upon the tidal circulation simulated by models of Salomon & Breton (1991,1993). Wind data were measured at La Hague on the Contentin Peninsula and a series of diffusion and mortality functions were added to the equations. Model simulations run for 2-4 weeks in June, July and August showed that in light winds, particles released between the Isle of Wight and Selsey Bill were generally retained within that region. Only during moderate to strong south and west winds of 9-12 $m.s^{-1}$ (Beaufort Force 5 or 6) was there any appreciable transport to the east of Selsey Bill.

A detailed study of the local and regional oceanography of the south-eastern coast of the Isle of Wight has recently been carried out in response to the application for a long-sea sewage outfall in Sandown Bay (Southern Water,1996). Using drogues from the outfall point, maximum excursions on spring tides were 15km eastwards on the flood and 24km westward on the ebb. During neaps, drogues travelled 11km eastwards on the flood and 19km westward on the ebb. Both drogue tracks never returned any closer than 1km offshore. Due to the irregular nature of the seabed, causing rapid and turbulent flow, no evidence of thermal stratification was found during the study.

East of the Isle of Wight, peak current speeds rise to $1 m.s^{-1}$ off Selsey Bill, but then reduce inshore to $0.25\ m.s^{-1}$ between Shoreham and Brighton (Hydraulics Research, 1993). Apart from a strong south-going component off Selsey Bill, tidal residual flow patterns off Brighton and the Sussex coast and in the eastern Solent are generally west-flowing but relatively weak (United Marine Dredging, 1999).

Of additional relevance to this work is the hydrogrphy of the coast of northern France as it may be possible for larvae to colonise English shores from the large populations that exist on the north coast of Brittany and Gulf of St. Malo. FLUXMANCHE radio-tracer measurements, following the fate of ^{125}Sb discharged from Cap de La Hague nuclear reprocessing plant near Cherbourg, indicate that transport of soluble radionuclides between La Hague and the Dover Straits takes between 3-7 months (Guegueniat *et al.*, 1995). This is strongly dependent on meteorological conditions and whether the slower coastal route, hugging the Normandy shoreline, or the much faster central route was taken. What is also apparent from the work is that measurements significantly above background levels are not detected west of Beachy Head in Sussex. If planktonic larvae behave similarly, any eastward transport around the Contentin peninsula would arrive on the English shoreline between Beachy Head and Dover, or carry on through to the North Sea. It is however quite likely that plankton behaves very differently and is influenced more by surface wind conditions (Hawkins & Hartnoll,1982a ; Bertness *et al.*, 1996).

Studies of sea bed sediment transport, which might be correlated with tidal or wind driven currents, have been summarised by Motyka & Brampton (1993) who divided up the coast of England and Wales into a number of 'cells' whose sediment transport characteristics were largely independent of other cells. Major boundaries were classified either as 'Littoral drift divides' where for example beach material on both sides of a headland moves away from it, or 'sediment sinks' where sediment transport paths meet and beach material tends to build up. Around the coast of England and Wales, eleven such cells have been identified. The main region of interest in this work falls within three of these, namely Region 4 between the Thames and Selsey Bill; Region 5 between Selsey Bill and Portland Bill; and Region 6 between Portland Bill and Lands End. Within each main cell are several sub-cells, largely differentiated by headlands (drift divides) or estuaries (sediment sinks).

Along the south-coast of England, the prevailing wind throughout the year is from the south-west, with the strongest winds occurring in winter (Barne *et.al.*, eds.1996a). The wind-rose at Portland Bill shows that south-easterly winds are the least frequent, although during anticyclonic conditions associated with high pressure, easterly winds have been a feature of recent warm summers. Hawkins & Hartnoll (1982a) demonstrated that onshore winds are influential in determining the magnitude of recruitment of the barnacle *Semibalanus balanoides* on the Isle of Man. Several studies of the onset of Sea Breezes in the region have been reviewed during the Environmental Impact Assessment associated with the construction of the long-sea outfall pipe in Sandown Bay (Southern Water, 1996). In the Solent area there is a significant correlation between the onset of the Sea Breeze and the time of local High Water. Studies made at Thorney Island in Chichester Harbour suggest that a typical year will produce some 75 events at the coast. Some of these could reach $10m.s^{-1}$, especially when combined with onshore gradient winds.

Information on the rate at which water within neighbouring bays is exchanged might help our understanding of larval retention and dispersal. In the Solent, it takes 6 ¼ days for all the water, effluents and freshwater discharges to be totally replaced (Dyer & King, 1975). This is a relatively short period compared with most estuarine systems and the region is therefore able to cope with the dispersal of nutrients and pollutants comparatively swiftly (Tubbs, 1999).

2.5 Coastal Geology and Geomorphology

The geology and geomorphology of the coast may have a direct and indirect effect on species distribution. The shape of the coastline is largely determined by the lithology of the rocks, and the presence of rocky headlands can have a major influence on hydrography, discussed in the previous section. As the aspect changes around the headland so does the wave energy climate. Change in aspect might expose animals to unfavourable air temperatures, risk of desiccation or frost damage and dislodgement by high wave energy. The lithology of rocky substrata may also influence settlement behaviour of barnacle cyprids, and if too soft, prevent adequate adhesion of spat. Geology and lithology also influences the topography of the shore where the angle of dip of the intertidal reefs or presence of boulders is often determined by the orientation of the bedding planes and marine erosion. Softer rocks also create more turbid conditions during rough weather. During storms, the water at the foot of chalk cliffs appears milky-white, and that along coasts of iron-rich Ferruginous Sands (Cretaceous:Lower Greensand) is very often a rust colour (pers.obs).

The present coastline of southern England is comparatively recent, and has been revealed since the last ice age 20,000-14,000 BP. In the west of Lyme Bay, the oldest Devonian limestones, shales, slates and schists occur, which have complex folded and faulted structures. Jurassic limestones, shales and clays predominate on the Dorset coast between Lyme Regis and Swanage. Cretaceous strata, including chalk, are a feature of the southern shores of the Isle of Wight and Sussex coastline (Durrance & Laming (eds.),1982; Insole *et al.*,1998; West, 2000).

Of principal interest in this work is the extent of hard substrata within the study area between Prawle Point at the extreme western end of Lyme Bay and Beachy Head on the East Sussex coast. In Lyme Bay, rocky coastline is almost continuous between Torbay and Lyme Regis, with sandstones, breccia and limestones predominating. At Beer, just to the west of Lyme Regis, there are chalk cliffs above an Upper Greensand platform. The chalk here is unusually hard and sandy and only fallen boulders are present below MHW. The discontinuity in rocky shore habitat in the east of Lyme Bay, caused by the 30km shingle ridge known as Chesil Beach, is thought to be a major contributory factor in reducing the population size of Lusitanian species to the east of Portland (Crisp & Southward, 1958). On the western side of Portland, rocky habitat consists mainly of limestone boulders, much of which is landslip. The Jurassic limestones around Portland Bill have been famously worked for building stone for hundreds of years and as a consequence, many of the ledges on the south-eastern side of the 'Bill' have been created or extended by quarrying. Most of the Purbeck coast consists of limestone cliffs, with some old quarry workings near Swanage. Chalk shore platforms are formed near Lulworth Cove and at Old Harry Rocks. The Jurrassic Corralian limestones, sandstone and gritstone form the intertidal ledges and boulders at Osmington Mills and within Ringstead Bay (West, 2000). At Kimmeridge there are bituminous shales and hard dolomite platforms known as 'cementstone'. On the mainland coast between Swanage in Dorset and Brighton in Sussex there are no significant rocky shores. Yet on the Isle of Wight there are chalk platforms in the west, between the Needles and Freshwater, and also at Culver Cliff in the extreme east of the island. On the south-west coast of the island there are soft clay or marl platforms with scattered exposures of hard iron-rich sandstone, notably at Hanover Point. From St. Catherine's Point eastwards to Shanklin, much of the natural shoreline consists of large boulders of Upper Greensand. This is largely old landslip debris with some chalk, clay and harder chert mixed in. Just to the north of Culver Cliff are extensive flat ledges of Bembridge Limestone. These also outcrop as much smaller exposures on the Solent coast of the island, for example in Gurnard Bay and Hamstead Ledge. East of the Isle of Wight, there is then a gap of approximately 75km until natural rocky shores appear again, below the chalk cliffs of the Sussex coast. Because of the larger tidal range here, the ledges are relatively extensive. The quantity of flint within the chalk varies along this part of the coast. It is very evident on the shore near Brighton, but less so further east. In some parts of the platform considerable weathering of the chalk has occurred below the flint bands resulting in a hard flint capping to the shore.

2.5.1 Method to determine area of intertidal rock within study area

The area of intertidal rocky ledge was determined using *MapInfo* v5 Geographical Information System (GIS) at the Geodata Unit at Southampton University. The coastline between Prawle Point at the west of Lyme Bay and Beachy Head in Sussex was traced from the 1:25000 O.S maps (Leisure and Explorer Series). The perimeter of all rock between MHW and MLW defined on the O.S maps as either 'Outcrops' or Boulders' was also traced and the area of each polygon determined. Broad geological categories were assigned to the rock polygons using the 1:50000 series geology maps, however because the type of intertidal rock is not always shown, definition was supplemented with local knowledge. The vertical component of the overall intertidal zone area was calculated by measuring the length of each rocky section of coast and multiplying this by the spring tidal range for that location, as shown on UKDMAP (1998). Coastal cell divisions (based on Motyka & Brampton, 1993) were also applied to aid the division of the coastline and for the purposes of testing hypotheses related to larval supply and habitat availability. The cell 'Lyme' extends from Prawle Point to Portland Bill, cell 'Purbeck' between Portland Bill and Handfast Point, cell 'Wight' between Handfast Point and Selsey Bill and cell 'Sussex' between Selsey Bill and Beachy Head.

The approximate total area (TA) of intertidal rock along a section of coast was therefore considered to be: $TA = A_{RI} + L_{RC}\ T$

Where A_{RI} =Area of intertidal outrops & boulders (km^2)

L_{RC} = Length of Rocky Coast (km)

T = Tidal range (km)

2.5.2 Results

Maps showing the location of rocky coastline and extent of rocky reefs within the study area are presented in Fig.2.10. The length of rocky shoreline in each cell is shown in Table 2.7. The total area of intertidal rock for each coastal cell is shown in Fig.2.13. Lyme Bay has almost twice the length of rocky coast as neighbouring 'Purbeck' and this is further reduced to the east within 'Wight' and 'Sussex'. Yet the area of intertidal rocky shore is by far the greatest on the Sussex coast due to the wide chalk reefs and greater tidal range. The area of rocky shore within 'Wight' is larger than 'Purbeck', because of the broad and extensive limestone reefs around Bembridge and the boulder shores of the 'Undercliff' between St. Catherine's Point and Shanklin.

Table 2.7 Length of rocky and non-rocky coastline within study area. The total 603.4 km does not include perimeter of estuaries, harbours or the inner shoreline of the Fleet in Dorset. See Fig 2.10 for map and cell boundaries. Note the figures for cell 'Wight' includes the Hampshire coast.

Coastal Cell	Rocky (km)	Non-rocky (km)	Total (km)
Lyme	100.8	83.6	184.4
Purbeck	51.9	74.5	126.4
Wight	34.4	166.0	200.4
Sussex	23.7	68.5	92.2

Table 2.8 Area of rocky outcrops and boulders as shown on O.S maps and determined using GIS. Note values do not include vertical component.

Coastal Cell	Rocky Outcrops (km^2)	Rock Boulders (km^2)
Lyme	1.50	0.65
Purbeck	0.33	0.14
Wight	0.95	0.37
Sussex	2.13	0.44

The relative area of intertidal rocky outcrops and boulder shores as measured using the GIS alone is shown in Table.2.8. The vertical component of the tidal range has not been added to this estimate and therefore the figures are based on the area shown on the O.S. maps. On this basis, about 30% of the rocky intertidal area within 'Lyme', 'Purbeck' and 'Wight' cells are boulder shores. That within the Sussex cell is about 17%. Estimates of surface area for boulder shores are extremely difficult from map work alone and figures quoted are likely to be severely underestimated. This might be particularly important for the extensive boulder shores along the 'Undercliff' of the Isle of Wight.

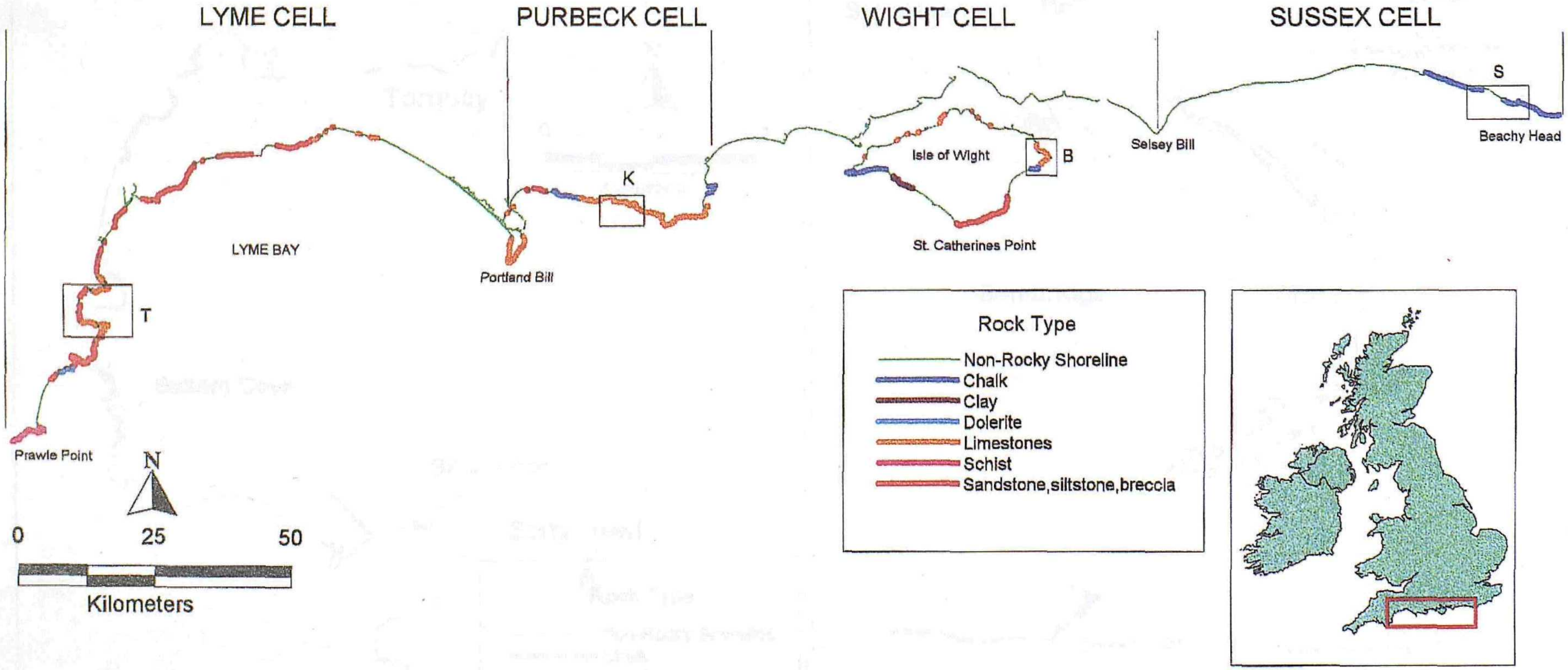


Fig. 2.10 Map of the central south coast of England showing the location of main rock types on shores within the four coastal cells in the study area. See Figs 2.11 and 2.12 for detailed maps of boxed regions; Torbay (T); Kimmeridge (K); Bembridge (B) and Seaford (S).

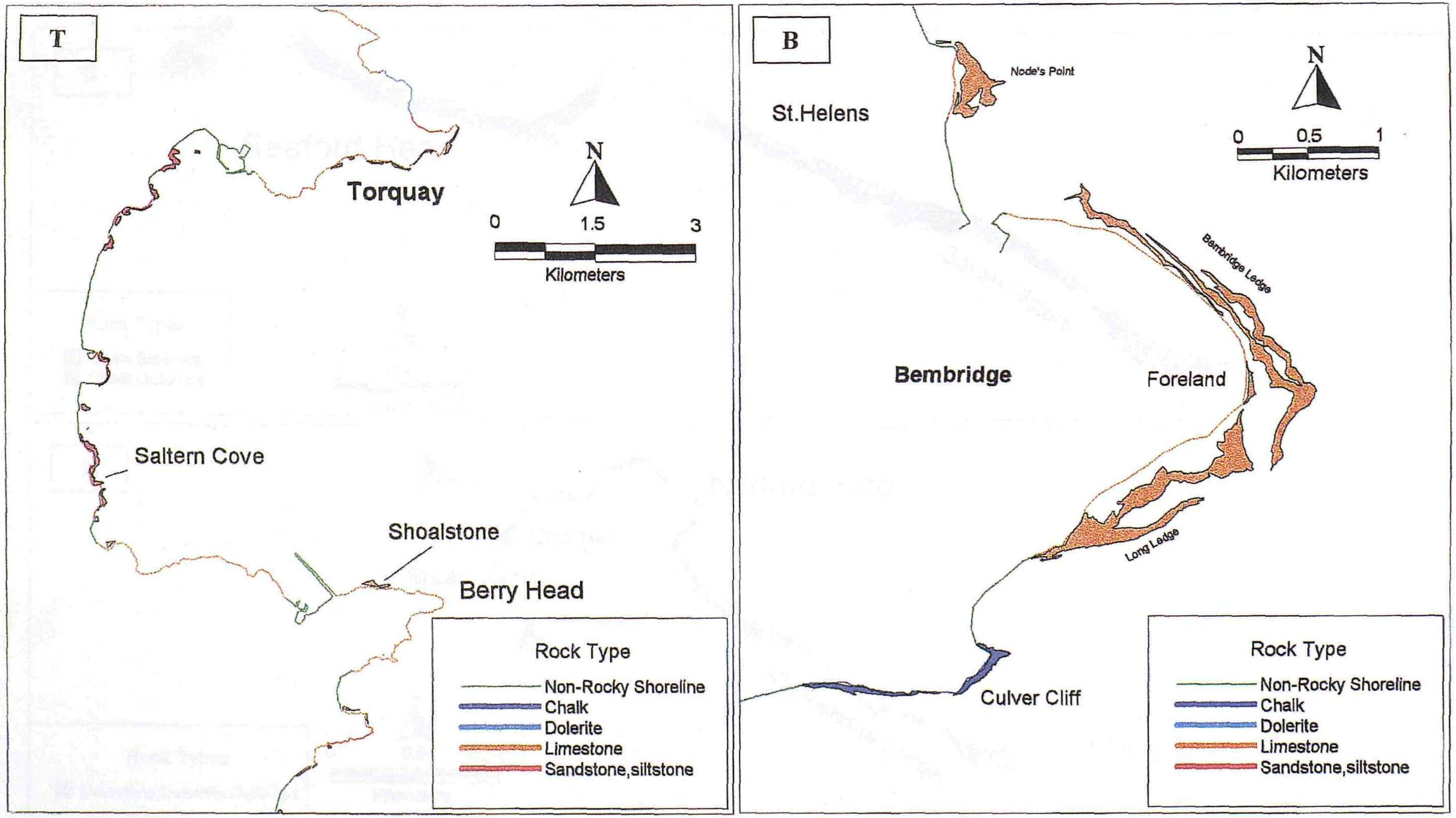


Fig. 2.11. Maps showing location, geology and type of rocky shores within Torbay (T) and at Bembridge (B). See Fig 2.10 for location along the south coast of England.

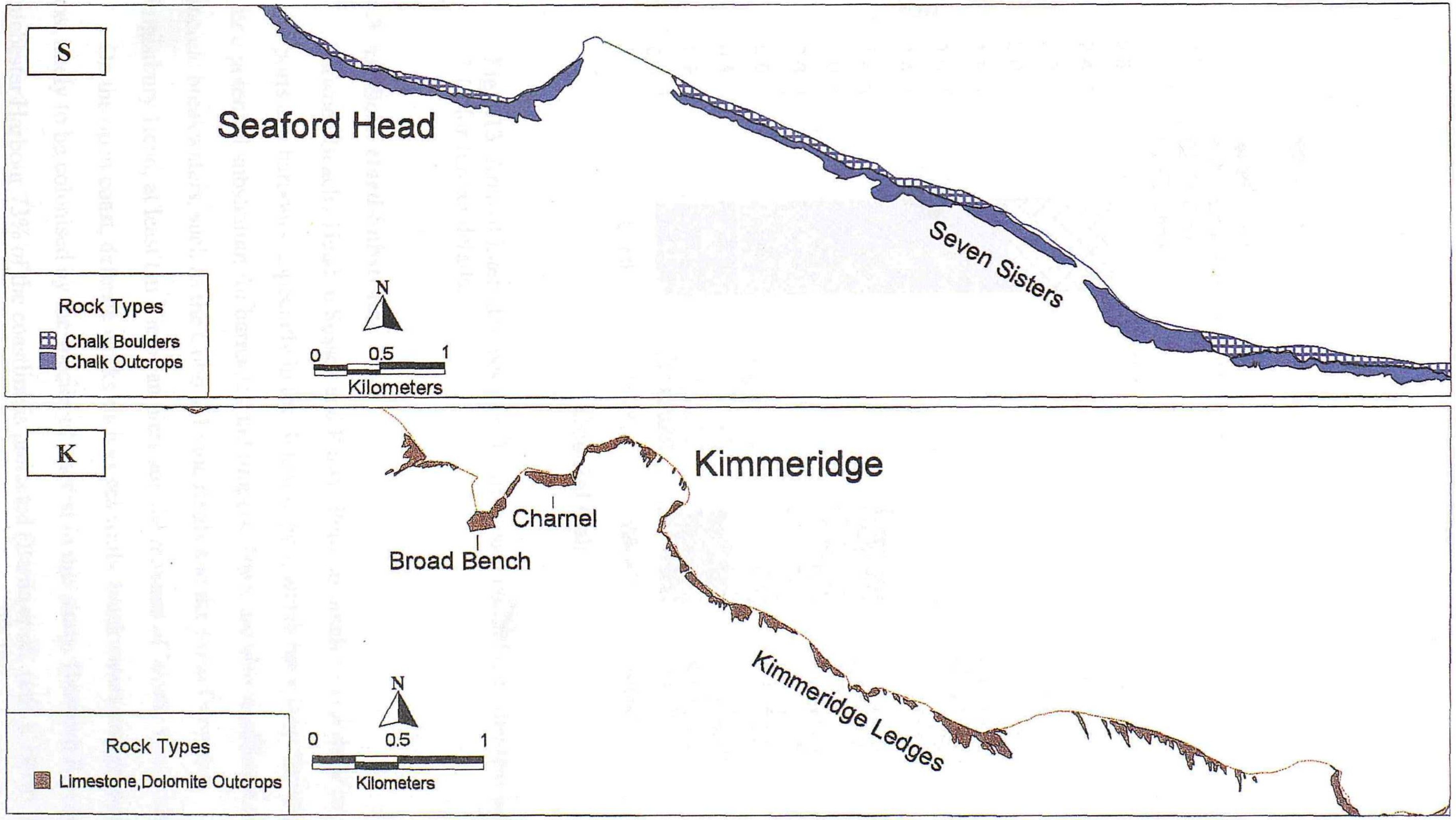


Fig. 2.12 Maps showing location, geology and type of rocky shores at Seaford (S) and at Kimmeridge (K). See Fig 2.10 for location along south coast of England.

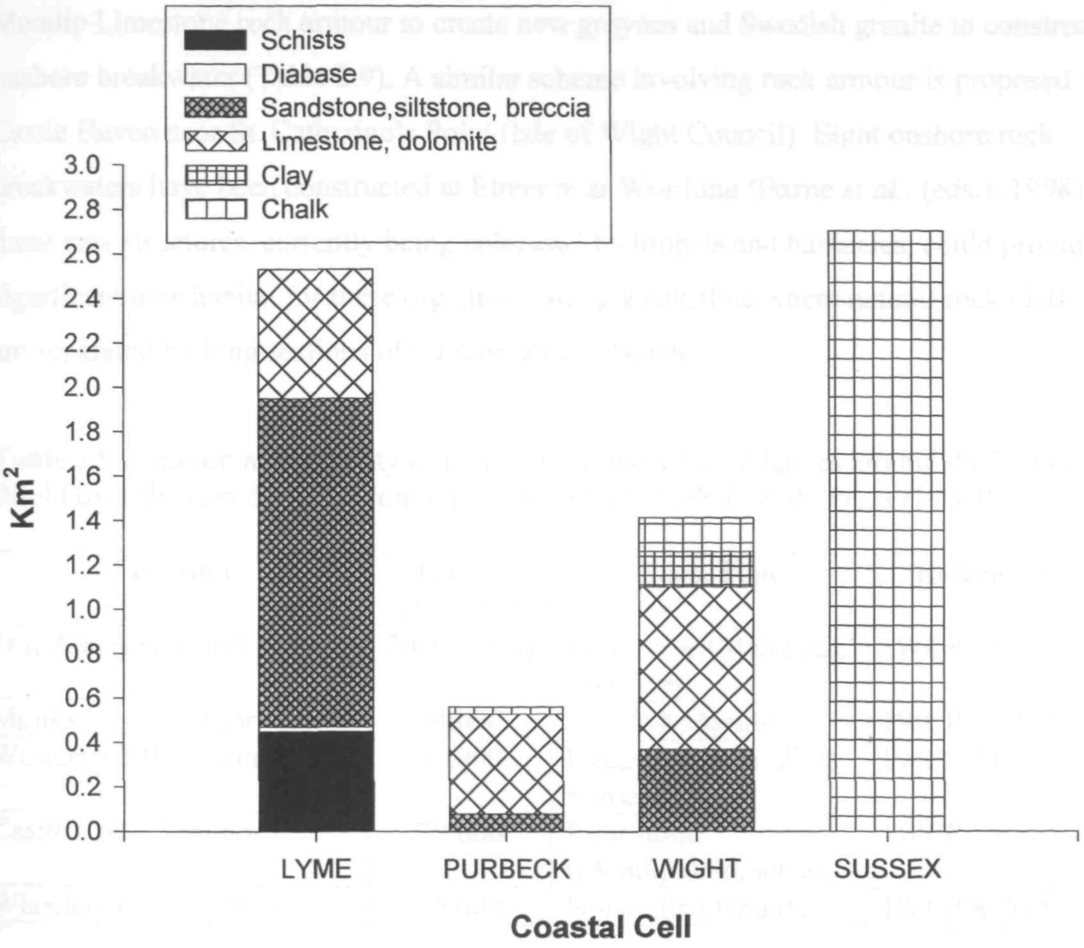


Fig.2.13 Area of intertidal rock (km^2) within each coastal cell. See text and Fig. 2.10 for further details.

2.5.3 Artificial Hard-Substrata

Between Beachy Head in Sussex and Prawle Point in South Devon there are several major ports and harbours, especially in the Solent region, which have large frontages that offer a potential substratum for barnacles and limpets. There are also significant stone or concrete breakwaters, such as the Cobb at Lyme Regis and the Long Groyne at Hengistbury Head, at least ten Victorian piers and the remains of World War II structures.

On the open coast, defence works such as sea walls, breakwaters and groynes are most likely to be colonised by the species of interest in this study. Between Rye and Chichester Harbour 73% of the coastline is protected (Barne *et al.,* (eds.), 1998), from Hayling Island to Lyme Regis 41.9% (Barne *et al.*, (eds.), 1996a) and between Lyme

Regis and Torbay 35.4% (Barne *et al.*, (eds.), 1996b). Over the past twenty years there have been new innovative defences along the south-east coast using piles of large blocks of natural rock. On the Isle of Wight, a scheme at Monks Bay near Ventnor utilised Mendip Limestone rock armour to create new groynes and Swedish granite to construct an onshore breakwater (Table 2.9). A similar scheme involving rock armour is proposed for Castle Haven near St. Catherine's Point (Isle of Wight Council). Eight onshore rock breakwaters have been constructed at Elmer near Worthing (Barne *et al.*, (eds.). 1998). All these new structures, currently being colonised by limpets and barnacles, could provide a significant new habitat for these organisms along a coastline where natural rock platforms are separated by long sections of sand or shingle beach.

Table 2.9 Location and quantity of rock armour placed as defences around the Isle of Wight over the past decade. From reports in *Isle of Wight County Press* (IWCP).

Location	Tonnes (Length)	Rock Type	Reference
Fort Albert, Totland	7000 (90m)	Limestone (Mendips), Somerset	IWCP 24/9/93
Monks Bay, Ventnor	24,000	Swedish Granite	IWCP 26/1/96
Western Cliffs, Ventnor	30,000	Limestone (Mendips) Somerset)	IWCP 31/2/97
Castle Cove, Ventnor	28,000	Limestone (Mendips),Somerset	IWCP 19/7/00
Wheelers Bay, Ventnor	15,000	Norwegian Granite	IWCP 8/2000

Chapter 3

Recent changes and current geographic limits of southern species on rocky shores along the south coast of England

3.1 Introduction

Following publication of their initial survey of rocky shore organisms along the Channel (Crisp & Southward, 1958), Southward and Crisp regularly re-surveyed many of the sites, together with more detailed annual monitoring within specific shores e.g. Cellar Beach in Devon and other sites in south-west England (Crisp *et al.*, 1981; Southward, 1991; Southward *et al.*, 1995). The more eastern localities, including the Isle of Wight, were re-surveyed least often, and yet it is here that the limits of distribution of several southern species occurred up until the last survey by Southward in October 1975 and by Crisp in 1979 (Crisp *et al.*, 1981; Southward, pers.comm). Time-series have also been maintained for limpet species at several sites on the south coast including Freshwater Bay on the Isle of Wight (Southward *et al.*,1995; Hawkins, pers. comm). During the late 1980s and early 1990s, there have been exceptionally warm summers and mild winters, notably 1989 and 1990, so before embarking on detailed monitoring and experimental investigations it was considered important to re-survey the south coast between Torbay in east Devon and Beachy Head in Sussex. The shores of the Isle of Wight, reported as the most eastern limits of several species (Crisp & Southward, 1958; Crisp *et al.*, 1981), are of particular interest so it was also decided to undertake a detailed survey of the barnacle species *Chthamalus montagui*, *C. stellatus* and *Balanus perforatus*. A description of survey sites is given in Appendix I.

The specific aims of this chapter are:

i) to establish the current biogeography of selected Lusitanian intertidal species on rocky shores along the central south coast of England.

ii) to measure the population size-frequency and determine which stage in the life cycle fails when geographical limits are reached. Where survival sets the limits, populations will be biased towards juveniles, however populations with missing size classes, or skewed towards the older (larger) animals may be limited by the processes of reproduction or recruitment failure (Hutchins, 1947; Kendal, 1987).

iii) to review evidence for recent changes in population size.

3.2 Methods

3.2.1 Minimum quadrat and sample size experiments for barnacles *Chthamalus* spp. *Semibalanus balanoides* & *Elminius modestus*.

Prior to an estimation of mean barnacle density, minimum quadrat area and sample size experiments were considered necessary as population densities at any particular location can vary over several orders of magnitude. At various sites and tidal levels, cumulative species density was recorded with increasing sampling area, initially using a quadrat marked with 25 square centimetres on a plastic petri-dish. When plotted graphically, the minimum quadrat size was chosen when major fluctuations in density ceased. The minimum number of quadrats of chosen area necessary to obtain a representative estimate of species density was similarly obtained by plotting cumulative species density against number of randomly placed quadrats. Fluctuations less than 5% of estimated density ceased after placing more than between 10 and 15 quadrats. See Figs 3.1-3.6 for examples of plots. Quadrat areas chosen for *Chthamalus montagui* at different sites and tidal levels are shown in Table 3.1.

Table 3.1 Size of quadrat used to determine density of *Chthamalus montagui* for survey work on shores along the central south coast of England in 1994.

	Tidal Level		
Site	**MHW**	**MTL**	**LWN**
Shoalstone Beach & Saltern Cove, Torbay, Devon.	6cm^2	6cm^2	6cm^2
Broad Ledge, Lyme Regis, Dorset.	25cm^2	6cm^2	6cm^2
Portland Bill, Dorset.	12cm^2	12cm^2	12cm^2
Osmington Mills, Dorset.	100cm^2	12cm^2	12cm^2
Kimmeridge, Dorset.	100cm^2	25cm^2	25 cm^2
Warden Ledge, Colwell, IOW.	400cm^2	400cm^2	400cm^2
Hanover Point, Brook, IOW.	400cm^2	400cm^2	400cm^2
St. Catherines Point, IOW.	400cm^2	400cm^2	400cm^2
Bembridge, IOW.	400cm^2	400cm^2	400cm^2

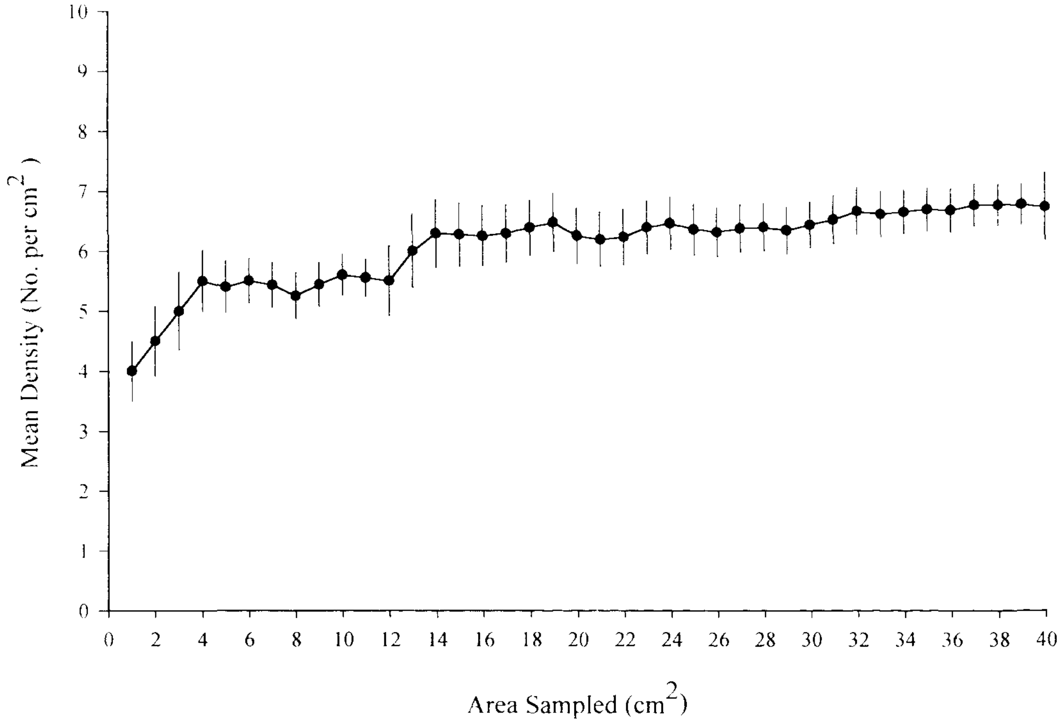


Fig.3.1 Study to determine minimum quadrat area necessary to obtain reasonable estimate of population density of *Chthamalus montagui* on the middle shore of Shoalstone beach at Brixham, Devon. It was concluded that a quadrat area of 6cm^2 (3x2cm) was sufficient. Bars show ± SE.

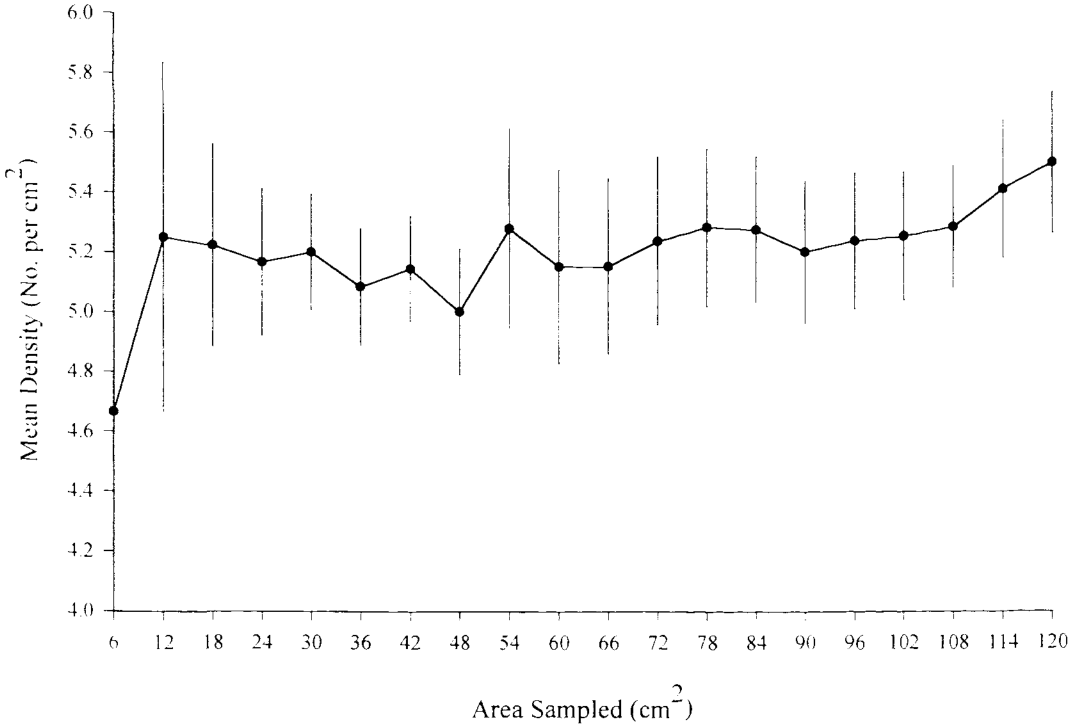


Fig.3.2 Graph showing results of study to determine minimum number of 6cm^2 quadrats required to obtain reasonable estimate of population density of *C. montagui* on the middle shore of Shoalstone beach at Brixham, Devon. Major fluctuations disappear after placing 12 quadrats. Bars show ± SE.

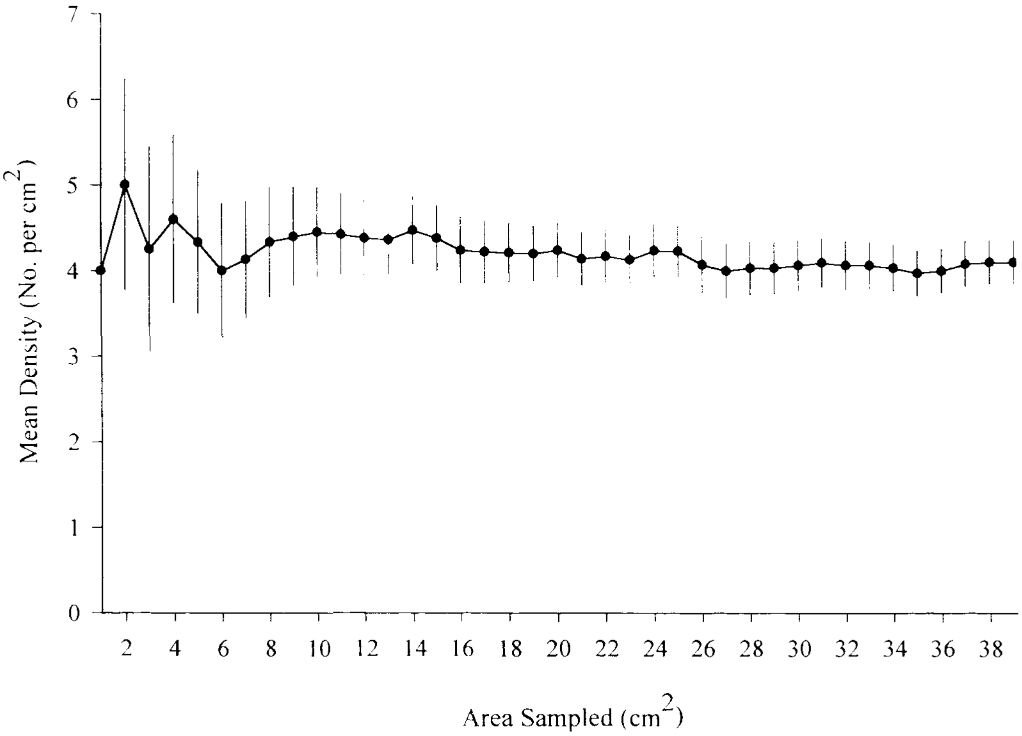


Fig.3.3 Study to determine minimum quadrat area necessary to obtain reasonable estimate of population density of *Chthamalus montagui* on the middle shore at Portland Bill, Dorset. It was concluded that a quadrat area of 12cm^2 (4x3cm) was sufficient. Bars show ± SE.

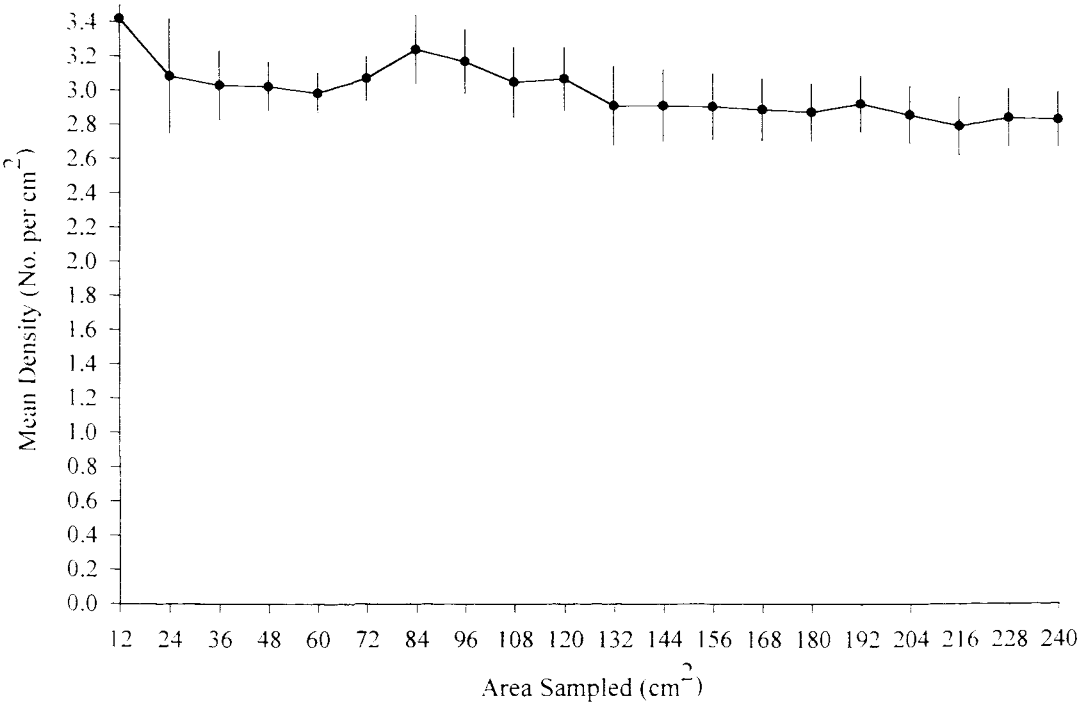


Fig.3.4 Graph showing results of study to determine minimum number of 12cm^2 quadrats required to obtain reasonable estimate of population density of *C. montagui* on the middle shore at Portland Bill, Dorset. Major fluctuations disappear after placing 12 quadrats. Bars show ± SE.

For *Semibalanus balanoides* and *Elminius modestus*, similar quadrats were used depending on observed density.

3.2.2 The broad-scale distribution of selected biogeographical indicator species along the south coast of England.

A broad-scale assessment of species distribution was made along the south coast of England in the autumn of 1994. Sites along the Hampshire and Sussex coast were surveyed during spring tides in early September and those along the Isle of Wight, Dorset and Devon coast in mid-October. Sites were selected from those used in earlier surveys by Crisp & Southward (1958), although precise localities where survey work was carried out do differ. For example at Portland Bill, earlier surveys were undertaken nearer to Pulpit Rock, further to the west of the site chosen for this work. However the extremely exposed location of this site was considered unworkable for other planned investigations where permanent photographic sites were required.

The density of barnacle species *Semibalanus balanoides*, *Elminius modestus* and *Chthamalus* spp. was recorded at three tidal levels using quadrats of various sizes between 6cm^2 and 400cm^2 depending on abundance (see Table 3.1 above). Surveys were carried out on flat or gently sloping surfaces except where these were not a characteristic feature of the shore. In such cases, species densities on all accessible surfaces and aspects were recorded. If a species was not observed within any of the quadrats a 30min timed search was carried out. The abundance of limpets (*Patella* spp.) was determined by placing between ten and fifteen 0.25m^2 quadrats randomly on the upper, middle and lower shore.

The abundance of other species, including topshells, dog-whelks and sea anemones was immediately converted to the semi-quantitative scale presented in Crisp & Southward (1958), a part of which is shown in Table 3.2. Particular care was made to observe any evidence of settlement or recent recruitment, which for many of these species should have been visible after the summer brooding period. Other conspicuous species were also noted, as were general observations on the extent of algal zones. The topography of the shore, magnitude of tidal scour and evidence of recent sediment movement was also recorded.

Table 3.2. Abundance scale used by Crisp & Southward (1958). Only selected species shown.

Anemones

A Many in almost every pool and damp place.
C Groups in pools and damp places.
F Isolated specimens in few places.
R A small number, usually under 10, found after 30 min searching.

Barnacles

For *Chthamalus* spp., *Semibalanus balanoides* and *Elminius modestus:*

A More than 1 per cm^2; rocks well covered.
C 0.1 to 1.0 per cm^2; up to one third of rock space covered.
F 0.01 to 0.1 per cm^2; individuals never more than 10 cm apart.
O 0.0001 to 0.01 per cm^2; few within 10 cm of each other.
R Less than 1 per m^2; only a few found in 30 min searching.

For *Balanus perforatus*:

A Over 0.1 per cm^2; close groups on most vertical faces, often up to MTL.
C 0.01 to 0.1 per cm^2; adjacent groups, not always above LWN.
F Less than 0.01 per cm^2; adjacent in crevices.
O Less than 0.01 per cm^2; rarely adjacent even in crevices.
R Only a few found in 30 min searching.

Limpets (Patella)

A Over 50 per m^2 or more than 50% of limpets at certain levels.
C 10 to 50 per m^2, 10 to 50% at certain levels.
F 1 to 10 per m^2, 1 to 10% at certain levels.
O Less than 1 per m^2 on average, less than 1% of *Patella* spp.
R Only a few found in 30 min searching.

Topshells (Gibbula & Osilinus)

A Exceeding 10 per m^2 generally.
C 1-10 per m^2, sometimes very locally over 10 per m^2.
F Less than 1 per m^2, locally sometimes more.
O Always less than 1 per m^2.
R Only one or two found in 30 min searching.

A, abundant; C, common; F, frequent; O, occasional; R, rare; N, not found.

3.2.3 The distribution of *Chthamalus montagui*, *C. stellatus* and *Balanus perforatus* around the coast of the Isle of Wight, 1992-1999.

So that the current work could be compared with earlier surveys, the methodology is based on that employed by Crisp & Southward (1958) and Southward (pers.comm). For the purpose of mapping the species distribution and assessing population density, the coast was divided into 'squares' (in reality trapezia) of 1 minute latitude x 1 minute longitude as had previously been undertaken by Light & Killeen (1990) for their molluscan survey. All squares containing hard substrata, either natural or man-made, were surveyed between August 1992 and January 1994. For *Chthamalus* spp., twelve quadrats of size 400cm^2, subdivided into 25cm^2, were placed randomly at Mean High Water, Mid Tide Level and Mean Low Water Neaps on flat or gently sloping surfaces. If these were not a characteristic feature of the shore then other surfaces, including verticals, were investigated. If no *Chthamalus* could be found within the quadrats then a 30 minute timed-search was undertaken and the numbers of individuals observed were recorded.

For *Balanus perforatus*, the shore between Mean Tide Level and Low Water Springs was surveyed, with particular attention directed towards crevices and overhangs where the species is often found along the south-west coast of England. Where densities were considered measurable, a 400cm^2 quadrat was placed randomly to assess abundance, however a timed-search was more often employed.

A total of 33 sites were surveyed for *Chthamalus* spp. and 30 for *Balanus perforatus*; there being fewer suitable sites for the latter species. The density of the other barnacle species *Semibalanus balanoides* and *Elminius modestus* was determined using various sized quadrats depending on abundance. Key community indicator species including macroalgae, dog-whelk *Nucella lapillus*, limpets *Patella* spp., topshells *Gibbula* spp. & *Osilinus lineatus* and anemones *Actinia equina* and *Anemonia viridis* were also recorded using the Crisp & Southward semi-quantitative abundance scale (Table 3.2).

3.2.4 Size-frequency of *Chthamalus* spp. and *Balanus perforatus* along the south coast of England.

For locations in Devon and Dorset, the size-frequency of *Chthamalus* populations was determined from measurements on photographs taken randomly at three tidal levels. An Olympus OM1n SLR camera with a 50mm lens and small Vivitar extension tube was fixed to a laboratory tripod giving a field of view of 8 x 5 cm. A single Prima 100M flash gun was mounted on either side of the camera and the photographs taken using Ilford

Delta 100 ASA black & white film. A 5p coin (18mm diameter) was placed in view as a scale reference and six photographs were taken at each level on the shore. Developed negatives were then projected on a screen; the size of the enlarged image being 34cm by 50.5cm. A sheet of perspex, marked with 50 point dots whose co-ordinates were generated from random numbers, was then placed over the screen and individual barnacles nearest each mark were selected for measurement. Measurements of the basal diameter along the rostro-carinal (RC) axis and tergal-scutal (TS) diameter (opercular diameter) were made using vernier callipers. Between 200 and 300 measurements were obtained for each tidal level. Densities of *Chthamalus* on the Isle of Wight were so low that photographic methods described above were impractical to obtain samples of sufficient size. Instead, field measurements were made using callipers. Quadrats, size 400cm^2, were placed at random at MHW, MTL and LWN. The rostro-carinal diameter and tergal-scutal diameter of all barnacles within the quadrat were measured.

For *Balanus perforatus* field measurements of the rostro-carinal diameter were measured for accessible barnacles at the edge of ledges or beneath overhangs.

3.2.5 Size-frequency of *Gibbula umbilicalis* and *Osilinus lineatus* on the south coast of England.

Because the major objective of this investigation was to assess the magnitude of recent recruitment, searches were concentrated in the main nursery areas. For *G.umbilicalis* these are beneath cobbles and flat stones in shallow pools between MTL and MLW, and for *Osilinus*, under stones lying over damp gravel or bed rock between MHWN and MLWN. Because of the varied nature of shore topography, it was not possible to use a random sampling technique for obtaining an estimate of the species density. Although tending to overestimate the abundance of spat, comparisons of abundance were made using replicate timed searches of 5-minute duration on different parts of the shore. All animals seen were placed in separate polythene bags. Searches continued until about 200 snails had been collected, although at sites near to the species eastern limit, where animals were more scarce, searches were terminated after 30 minutes and the number of snails were counted. The maximum basal diameter of the shell of each animal was then measured to the nearest 0.1mm using vernier callipers. Attempts were made to age the *Osilinus* by counting growth rings using the procedure in Williamson & Kendall (1981). Animals were then returned to the shore.

3.2.6 Size - frequency of *Patella depressa* and *P. ulyssiponensis* at Freshwater Bay, Isle of Wight

This investigation was not carried out until May 1996 as field experience was found necessary to separate both the adults and juveniles of each species from each other and the more common *P. vulgata*. Freshwater Bay is 30km west of the eastern limits of both species at Bembridge however they become too uncommon to permit adequate size-frequency estimates here. Even further west, it was not always possible to find the settlement sites despite higher adult densities. Studies were centred on the main settlement and recruitment sites, which for both species tend to be permanently wet areas on the lower shore and *Lithothamnia* in pools. Juveniles and adults were identified from morphological characteristics described by Bowman (1981). Quadrats of area $0.25m^2$ were placed at random on the shore and, without disturbance, the shell length of each individual was measured to the nearest 0.1mm with vernier callipers.

3.2.7 Assessment of long-term changes in the abundance of *Chthamalus* and *Semibalanus balanoides* along the south coast of England and calculation of Warm Index.

Between 1955 and 1987 several sites within the study area were visited by A.J. Southward to monitor changes in population size, with the aim of determining relationships with climate change. Since 1994 the density of these species has been measured annually from most of these shores although the precise locations do differ. The earlier surveys involved the placement of approximately ten quadrats of various sizes depending upon density, although of no greater area than $100cm^2$. In 1994, thirty quadrats of various sizes (see Table 3.1) were placed at each of three tidal levels and in subsequent years the mean of two or three patches, each of 15 quadrats placed at three tidal levels, was used to calculate the mean species density. This was done to obtain a measure of population variance so that differences in species abundance between years could be tested using hierarchical analysis of variance (Underwood.1997). See also Chapter 5.

Indices developed by Southward (1991) have been calculated to describe the species composition of the barnacle community at different sites and may be correlated with temperature and shore type. Of particular interest here is the Warm Index:

Warm index $WI = CT / (CT + SB)$

CT = total *Chthamalus* (*C. montagui* + *C. stellatus*), SB = *Semibalanus balanoides*

The index has been calculated from the sums of the mean density of each species obtained from grouped tidal levels (HW, MTL and LW). The ratios are based on the knowledge that *Chthamalus* is a warm-water Lusitanian species and *Semibalanus* a Boreal cold-water species. Therefore the greater the proportion of warm-water *Chthamalus* in the barnacle community the higher the index.

3.3 Results

3.3.1 The current status of selected indicator species on the central south coast of England.

A map showing the location of survey sites along the south coast is shown in Fig.3.7 (p74). A more detailed map of the Isle of Wight is presented in Fig.3.13 (p80). The broad-scale distribution of ten selected indicator species between Torbay in Devon and Beachy Head in Sussex are shown in Figs 3.8 - 3.12. The semi-quantitative scale and symbols utilized in Crisp & Southward (1958) and Crisp *et al.*, (1981) are employed for comparative purposes. More details of species abundance are presented in Appendix II.

Barnacles

Between Devon and the Isle of Wight, the density of all species of barnacles decreases eastwards and there is a noticeable increase in free available space within the upper and middle levels of the intertidal zone. On the south coast of the Isle of Wight, between St. Catherine's Point and Ventnor, barnacle density is extremely low and there is only a narrow band of *S. balanoides* at LWN and scattered *Chthamalus* spp. above. On the north coast of the island, barnacle densities are generally higher (2-4 per cm^2), especially near the estuaries and within harbours. Between the Isle of Wight and Beachy Head, total barnacle density increases eastwards, and on the sandstone reefs of Cow Gap, near Eastbourne, densities are equivalent to or exceed those in Devon.

Chthamalus spp.

C. montagui and *C. stellatus* show similar patterns of distribution with the eastern limits along the Channel occurring on the Isle of Wight (Fig.3.8). *C. montagui* is the most abundant; between MTL and LWN mean densities of between 4-6 per cm^2 were recorded at sites in Lyme Bay and where a maximum of 10.25 per cm^2 was recorded at LWN at Lyme Regis. To the east of Portland Bill the density of adults at these tidal levels decreases along the Purbeck coast from 2-3 per cm^2 at Osmington to 0.5-1 per cm^2 at Kimmeridge. Although still 'common ' on the Long Groyne at Hengistbury Head, the species density diminishes rapidly on the Isle of Wight. While a few individuals have been found on the north-east coast of the island, the largest populations are to be found on the southern shores, particularly at Hanover Point and between St. Catherine's Point and Ventnor (Fig.3.14, p81). The species was found on a variety of rock types including the chalk on Culver Cliff near Bembridge. A single individual was found near the lifeboat station at Bembridge in 1995, which is 8km further east of previous records from Bonchurch by Crisp *et al.*, (1981).

The vertical distribution of barnacle species on the Isle of Wight is comparable with the pattern observed in the western Channel where *Chthamalus montagui* is most abundant between the mid and upper shore. The main difference between the eastern and western shores is the high density and broad extent of the *Semibalanus / Elminius* zone between the Isle of Wight and Beachy Head, which extends above mean tide level.

Chthamalus stellatus was less abundant than *C. montagui* within the study area, with mean shore densities never rising above 1 per cm^2. As had been noted by Crisp *et al.*, (1981), in the western Channel *C. stellatus* is more commonly found on the lower regions of the limpet-barnacle zone, but was occasionally observed to extend above the *C. montagui* zone near its eastern limits. Maximum densities of 0.75 per cm^2 were measured on the middle shore at Portland Bill although the species still only accounted for less than 5% of the total *Chthamalus* recorded here. Mean densities diminished east of Portland, however maxima continued to be relatively high along the Purbeck coast with 0.6 per cm^2 recorded at Kimmeridge and mean densities accounting for over 12% of total *Chthamalus* on the lower shore here in 1994. On the Isle of Wight the species was generally 'occasional' along the south-coast and as with *C. montagui*, the eastern limits were found to be close to Bembridge (Fig.3.15, p82). This is 26 km east of previously recorded limits at Hanover Point (Crisp *et al.*, 1981).

Semibalanus balanoides & Elminius modestus.

S.balanoides was ubiquitous within the study area although mean shore densities were higher east of the Isle of Wight (Fig.3.9). Densities of up to 11 per cm^2 were measured on the sandstone rocks at Cow Gap near Eastbourne in Sussex and mean densities at LWN were over 5 per cm^2. On the chalk at Hope Gap near Seaford, mean shore densities of nearly 3.5 per cm^2 were recorded and up to 12 per cm^2 on the flints. Even at HWN the species can be common with up to 2 per cm^2 recorded at Shoreham. At shores in Lyme Bay the species was hardly ever seen at this tidal level, where *Chthamalus* occupies nearly 100% shore cover at many localities. However at LWN, maximum densities of 1-1.5 per cm^2 were recorded at Shoalstone and Saltern Cove and at Lyme Regis maxima of 2.5 per cm^2 were measured at MTL.

The Australasian immigrant *Elminius modestus* was most common near to the more estuarine localities where the species was first recorded (Stubbings, 1950). Highest densities were measured at Southsea (not shown in Fig 3.9) where maxima of 4 per cm^{2} were recorded at HWN and where the mean shore density exceeds 1 per cm^{2}. At Selsey Bill and at Worthing the species is also 'common' or 'abundant'. At Shoalstone in Torbay, a maximum of 2.3 per cm^{2} was recorded at LWN. The species is known to foul the undersides of boats so the population here may be dependent on animals 'imported' on the fishing boats at nearby Brixham Harbour.

Balanus perforatus

This species was found to be 'abundant' beneath overhangs and in rock crevices within Lyme Bay and around Portland (Fig.3.10). At both locations in Torbay it was also found to be common on the open shore immediately below the *Semibalanus* zone at LWN. On shores along the Purbeck coast the species was mainly found in crevices. Yet in May 1997 an inspection of 100-year-old wooden piles, removed during the restoration of Swanage Pier, revealed that the species was 'abundant' (max 0.34 per cm^{2}) below LWN and at densities much greater than on the shore. The species zone was 1.8m wide and extended into the sublittoral, where it was mixed with *Balanus crenatus*. On the Isle of Wight, occasional adjacent groups were found among rock boulders at the northern end of Alum Bay. In 1993 the species could be found on most shores along the south coast of the Isle of Wight and was most densely recorded at the eastern end of Reeth Bay near St. Catherine's Point (Fig 3.17, p84). At Bembridge, only a few individuals were found around the lifeboat station. The previous most easterly records of the species in the Channel are from Chichester Harbour where adults were seen on submerged fouling test panels during the 1960s (Stubbings & Houghton, 1964). It was therefore particularly interesting to discover four individuals amongst dense *S. balanoides* between MTL and LWN on the western sides of piles on Worthing Pier in September 1994. Five years later, in September 1999, the population had significantly increased and the species could at least be regarded as 'frequent'. On some piles, adult density exceeded 10 per dm^{2} (0.1 per cm^{2}) and there was evidence of new recruitment, with spat densities of up to 16 per $25cm^{2}$ quadrat. On the same day, a single specimen was also found near Cow Gap at Eastbourne. The known range of this species has therefore been extended eastward by about 75km. Yet the abundance at Bembridge has not noticeably changed over the survey period.

Grazers

Grazer densities were also highly variable between shores with lowest densities of *Patella* spp. at Lyme Regis and Kimmeridge (30-35 per m^2 at LWN) and highest at Portland Bill and Freshwater Bay (160-200 m^2 at LWN).

Patella depressa and *P. ulyssiponensis.*

Neither of these species was found on shores east of the Isle of Wight. Moderate to high densities may however be found close to the species distributional limits (Fig.3.11). *P. depressa* was found to be most abundant at Saltern Cove in Torbay, where mean densities between MTL and LWN were 47 per m^2. Yet at nearby Shoalstone, average densities were only 14 per m^2. In terms of the proportion of adult *Patella* spp. on the shore at Saltern Cove the species represents between 31-53% at MTL and LWN respectively. At Shoalstone this is between 21-25%. At Freshwater Bay, on the Isle of Wight, there is an extremely high limpet population on the chalk cliffs and platform, yet although *P. depressa* densities of 32 per m^2 were found at MTL and LWN they represented only 16% of the total limpet population. Single specimens were recorded near the lifeboat station at Bembridge in November 1995 and June 1997.

P. ulyssiponensis was found to be most abundant around the exposed headland of Portland Bill in Dorset and at Freshwater Bay on the Isle of Wight. At Freshwater Bay the maximum density recorded was 120 per m^2 and mean of 69 per m^2. At MLW the species accounts for an average of 36 % of total *Patella*. At Portland Bill the maximum was 220 per m^2 with mean of 43 per m^2. Here the proportion in terms of the total *Patella* at MLW is on average 28%. At Bembridge, at the species extreme limits, densities are only 1.2 per m^2 at MLW with most individuals close to the edges of the outer reefs.

Osilinus lineatus and *Gibbula umbilicalis.*

Only a semi-quantitative assessment of abundance was made for these species which are sometimes hidden beneath small cobbles or weed (Fig.3.12). *Osilinus* was 'abundant' at Shoalstone, Saltern Cove and Lyme Regis and was 'common' below Golden Cap near Seaton. Maximum densities were between MTL and HWN. In May 1996 the species was also found at Clay Ope on the western side of Portland Bill, where it could be regarded as 'occasional' amongst the large boulders here. East of Portland, single 'O' class specimens were found at Osmington Mills on 14th November 1997 and in October 1999. Two adult specimens were found there on 4th October 1998. A very large, worn and old-looking specimen was found at Kimmeridge on 17th August 1997.

Gibbula umbilicalis was most abundant in Lyme Bay and while high densities also exist on shores along the Purbeck coast they are not as abundant as further west (Fig.3.12). The species can be reliably found at Freshwater Bay on the Isle of Wight, close to the species eastern limits, and may generally be regarded as 'frequent-common' with densities up to 3 per m^2 recorded in 1994. It was particularly noticeable how clustered the adults were, with groups often grazing on the same chalk boulder. Although not shown in Fig.3.12, single specimens have been found on the north coast of the Isle of Wight at Thorness Bay, Gurnard Ledge and on East Cowes breakwater. In 1994 the species was 'rare' on the ledges at Bembridge however in 1999 it was 'frequent' and turning up regularly in student collections on the shore.

Other species

Anemonia viridis.

Both colour morphs of this anemone are abundant within shallow rock pools in Torbay and Lyme Regis. They are also 'frequent' along the Purbeck coast. On the Isle of Wight, it is extremely abundant at Freshwater Bay and in 1994 was common at Bembridge (Fig.3.10, p77)). However since 1996 there has been a dramatic decline of this species at Bembridge and it is currently scarce here. On the Sussex coast a single specimen was found at the base of Worthing Pier in 1994 and I have sublittoral records from near Beachy Head.

Nucella lapillus.

To the west of the Isle of Wight, dog-whelks, which are a major predator of barnacles, were common or abundant at all sites with the exception of Portland Bill, where extreme wave exposure is probably a limiting factor. Here, they were only occasionally seen in the shelter of crevices on vertical surfaces. The Solent and Isle of Wight shores have been badly polluted by tributyltin (TBT) antifouling paints (Langstone *et al*. 1994) with the result that populations of *Nucella* have become extinct at many sites in the Solent and reduced at others on the island's southern coast (Herbert, 1989; Bray & Herbert 1998; Herbert *et al.*, 2000). In 1994 no dog-whelks were found at Colwell or Freshwater Bay, although there appeared to be some recovery of the population at Bembridge. East of the island, dog-whelks were frequent on the rock groynes at Selsey Bill and were extremely abundant on the piles of Worthing Pier. Although absent from the outer wall of Newhaven Harbour, there were large populations on the chalk platforms at Newhaven, Birling Gap, Seaford, Beachy Head and Cow Gap, where they were observed feeding on dense populations of *S. balanoides*.

No detailed survey of the marine algae was undertaken at the sites, however the southern species *Cystoseira tamariscifolia* was observed at Kimmeridge and the brown alga *Padina pavonica* was seen at Lyme Regis and Kimmeridge in Dorset and at Hanover Point and Bembridge on the Isle of Wight. Both these species have known eastern limits in this area (Lewis, 1964; Titley & Price, 1978).

3.3.2 Size-frequency of *Chthamalus* spp.

The objective here was to determine whether there is any evidence of recent recruitment and interactions between other species that could influence size, growth and mortality. The main limitation of basal diameter and opercular measurements is that they are influenced by population density. The growth of adjacent individuals causes the animal to grow vertically, forming a columnar structure or hummock. However, Burrows (1988) found that the opercular diameter and biomass of the prosoma and thorax, which are attached to the opercular plates, were very highly correlated. Therefore the opercular diameter can justifiably be used as the parameter to describe growth. On photographic negatives, the outline of the operculum appears distinct and dimensions may be measured accurately. Size-frequency histograms of *C. montagui* populations at three tidal levels are shown for all the major survey sites in Figs 3.18-3.23. The largest individuals were close to the species eastern limit at Hanover Point on the Isle of Wight, where on the upper shore the mean RC diameter and TS diameter were 6.13 and 3.12mm respectively. Here, there is the greatest difference in size-frequency between tide heights, with small size classes found only on the lower shore. The Portland Bill population also consists of large individuals that may benefit from higher growth rates at this location. The smallest individuals were found at Lyme Regis and Kimmeridge in embayed situations. A chi-squared test was used to determine whether there was any association between size and shore level. The results, shown in Table 3.3, indicate that on most shores the population size-frequency varies significantly with tidal level, with the largest animals being on the upper shore and smallest size classes predominantly on the lower shore. Yet no differences were found at Portland Bill where the animals are considerably larger than at all other sites.

At Osmington Mills there was a significantly higher number of small individuals on the upper shore where there had been a relatively dense recruitment.

Table. 3.3 Results of Chi^2 tests to determine whether population size classes of *C. montagui* are associated with tidal level. Measurements of opercular diameter from upper, middle and lower shore were put into 2mm size categories. * denotes significant association;** denotes highly significant association; *** denotes very highly significant association. See also Figs.3.18-3.23 for histograms.

Location	df	χ^2	P	Source of major contribution to χ^2
Shoalstone	2	65.8	<0.0001***	Higher no. of smaller individuals on lower shore.
Lyme Regis	2	94.7	<0.0001***	Higher no. of smaller individuals on lower shore and larger animals on middle shore.
Portland Bill	2	3.01	0.22 ns	No significant association between size and tidal level.
Osmington	2	28.2	<0.0001***	Higher no. of smaller animals and lower no. of larger individuals on upper shore.
Kimmeridge	2	8.42	0.015*	Higher no. of smaller individuals on lower shore.
Hanover Point	2	52.9	<0.0001***	Higher no. of smaller individuals on lower shore.

C.stellatus was not found to be sufficiently common to justify a size-frequency analysis, however data from selected sites are shown in Fig.3.24 (p91). There was a notable absence of small size classes at any site, however some indication of more recent recruitment is shown at Portland Bill and at Osmington Mills. At Portland the largest populations are to be found within the study area.

3.3.3 Size-frequency of *Balanus perforatus* populations.

Size-frequency histograms for the populations on Broad Ledge at Lyme Regis, Warden Ledge near Totland and Reeth Bay near St. Catherine's Point on the Isle of Wight, are presented in Fig.3.25 (p92). Owing to the species preference for crevices and overhangs, only accessible individuals were measured. The populations on the Isle of Wight were measured in the early spring of 1994 whereas the size-frequency of the Lyme Regis population was not ascertained until the autumn. Consequently, young recruits appear on the Lyme-Regis histogram but not from the other sites. However, visual assessments at the Isle of Wight sites during the autumn did not reveal the presence of any new recruitment. The observations of Norris & Crisp (1953) on the relationship between the degree of shelter and animal size were confirmed. Warden Ledge, in the western Solent, had the largest specimens of up to 18mm basal diameter, whereas the most exposed site at Reeth Bay near St. Catherine's Point had a population of smaller individuals, most of which appeared old and were encrusted with *Lithothamnion* sp.

3.3.4 Size-frequency of *Osilinus lineatus* and *Gibbula umbilicalis*

Size-frequency histograms of the maximum basal diameter of *G.umbilicalis*, obtained from six sites between Torbay and the Isle of Wight in the autumn of 1994, are presented in Fig.3.26 (p93). Most populations had a tri-modal distribution, with 'O' class individuals being more abundant at the east Dorset sites of Osmington and Kimmeridge. Here the size of the 'O' class varied between 1- 6.5mm and there is some evidence of a bi-modal distribution within the 'O' class, suggestive of prolonged settlement and or gametogenesis. Large individuals dominated populations east of Kimmeridge. A single 'O' class individual was found at Freshwater Bay on the Isle of Wight, close to the species' limit. *Osilinus* was only found in measurable populations in Torbay and Lyme Bay, but in 1996 a small population was discovered on Portland Bill, where J. Hawthorne reported animals surviving the cold winter of 1962-63 (Hawthorne, 1964,1965,1966). Size-frequencies of these populations are shown in Fig.3.27 (p94). Attempts were made at ageing *Osilinus* by counting the growth rings (Williamson & Kendall, 1981; Kendall, 1987). However for the majority of specimens from Torbay and Lyme Regis, the rings were insufficiently distinct to obtain reliable estimates of age beyond two to three years. Williamson & Kendall (1981) found similar difficulties with some specimens. Both populations of *Osilinus* show a tri-modal distribution, with the 'O' class already slightly larger at Shoalstone. The size of the 'year 1' (1993) cohort at Shoalstone is significantly larger than that of Lyme Regis. The specimens from Portland Bill collected in 1996 were considerably larger than those from Lyme Regis and Shoalstone, and yet from their shell condition appeared to be young individuals. For both species, adult size is expressed as the maximum diameter of the shell at the 90th percentile of a cumulative frequency plot so as to minimise any distortion and bias caused by sampling within the tail of a size-frequency distribution (Kendal & Lewis, 1986). For *G. umbilicalis*, a scatter diagram showing the significant negative correlation between maximum basal diameter and abundance of snails is presented in Fig.3.28 (Spearman rank correlation coefficient $r = -0.93$, $p < 0.001$). Similarly, Fig.3.29 shows the significant correlation between shell size and distance east from Devon towards the species limit at Bembridge (Spearman rank correlation coefficient $r = 0.95$, $p < 0.001$).

3.3.5 Size-frequency of *Patella depressa* and *P. ulyssiponensis* at Freshwater Bay, IOW.

Size-frequency histograms for both species, obtained in May 1996, are presented in Fig.3.30. Gaps in the size-frequency histograms for both species are probably due to the low numbers of individuals measured, owing to their relative rarity, rather than missing age classes. A tri-modal shape is just about recognisable for *P. ulyssiponensis*

3.3.6 Long-term time-series of *Chthamalus* and *Semibalanus* for selected shores on the south coast of England.

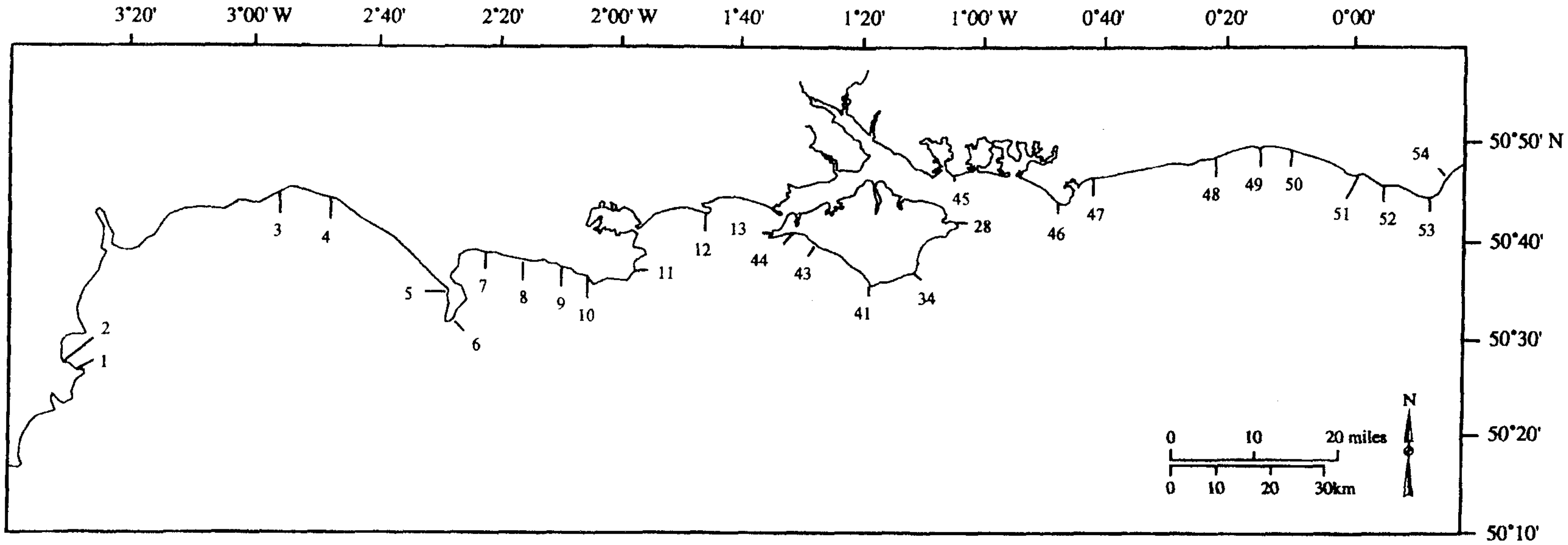
Figs. 3.31-3.34 show the mean shore densities of adult *Chthamalus* and *Semibalanus balanoides* at sites along the south coast of England; the earlier data was provided by A.J. Southward. Most of the counts obtained by Southward were during the spring, while those since 1994 have been carried out in the autumn. It is possible that spring counts may be slightly less than autumn counts due to winter mortality. For the data from Shoalstone, Lyme Regis and Osmington Mills, there is an inverse relationship between the abundance of the two species; when *Chthamalus* densities are high, *Semibalanus* densities are generally low. The Spearman rank correlation coefficient of the abundance of *Chthamalus* v *Semibalanus* is highly significant for each of these three time-series (see figs for p values). The time-series for both Shoalstone and Lyme Regis show similarities in that *Chthamalus* abundance was generally high during the late 1950s and early 1960s before *Semibalanus* became more prevalent during the 1970s. The data obtained since 1994 shows that *Chthamalus* is again the dominant species on these shores. This applies to the data for Osmington Mills also, however this time-series is not as complete. The data for Peveril Point do not show any significant correlation between the abundance of the two species. The densities here are relatively low compared to the other shores, and being close to the species eastern limits, the shore may receive too infrequent recruitment to reveal clear patterns. The measurements were taken from the outer north-facing ledge, which during this work was surveyed in 1994 and 1998 only.

Fig.3.35 shows the Warm Indices calculated for Shoalstone, Lyme Regis and Portland Bill. Portland Bill is included because the time-series is more complete than that for Osmington Mills. The lowest indices were obtained during the 1970s, with maxima occurring in the early 1960s and late 1990s. Prior to this work, no data have been obtained for Shoalstone since 1980 and data collection for Portland and Lyme Regis ceased in 1987.

Table 3.4 Results of Spearman Rank correlation tests on matched Sea Surface Temperatures, Mean barnacle Warm Index for the combined locations on the south coast and the North Atlantic Oscillation Index. See Chapter 2 for SST and NAO data sources.

Correlation	**n**	**r**	**p**
Summer Mean Channel SST v Winter NAO (1954-99)	46	0.48	>0.001
Mean S.Coast Warm Index v Mean *Annual* Channel SST (1955-1999)	38	0.31	0.057ns
Mean S.Coast Warm Index v Mean *Annual* Channel SST *one year earlier* (1955-1999)	38	0.35	0.036
Mean S.Coast Warm Index v Mean *Annual* Channel SST *two years earlier* (1955-1999)	37	0.166	0.32ns
Mean S.Coast Warm Index v Mean *Summer* Channel SST (1955-1999)	38	0.38	0.02
Mean S.Coast Warm Index v Mean *Summer* Channel SST *one year earlier* (1955-1999)	37	0.45	0.006
Mean S.Coast Warm Index v Mean *Summer* Channel SST *two years earlier* (1955-1999)	36	0.18	0.28ns
Mean S. Coast Warm Index v Winter NAO (1955-1999)	38	0.27	0.1ns
Mean S. Coast Warm Index v Winter NAO *one year earlier* (1955-1999)	37	0.4	0.016
Mean S. Coast Warm Index v Winter NAO *two years earlier* (1955-1999)	37	0.32	0.053ns

Correlations between the combined barnacle Warm Index and sea surface temperature are shown in Table 3.4. The best correlation is between the Warm Index and the Summer SST *the previous year*, supporting earlier findings (Southward & Crisp 1954,1956; Southward, 1967,1991; Southward *et al.*, 1995) that high summer temperatures favour *Chthamalus* recruitment, which is revealed in adult counts the following year. High recruitment and greater survival of *Semibalanus* during cooler years could potentially reduce the Warm Index calculated in the autumn following spring recruitment, as this species reaches adult size within four to six months. The correlation between the Warm Index and annual mean SST was not significant (p=0.057). Yet the correlation between the Warm Index and Summer SST measured in the same year was significant (p=0.02). This may perhaps be a reflection of success or otherwise of *Semibalanus* survival during hotter or cooler summers. The good correlation between the Warm Index and NAO index is unsurprising considering the strong relationship between the North Atlantic Oscillation and Sea Temperature (see also Chapter 2).



▲ ABUNDANT

▲ COMMON

▲ FREQUENT

▲ OCCASIONAL

▲ RARE

△ ABSENT

Fig. 3.7 See Table 3.1 for Abundance Scale.

Key to Location Map

DEVON
1. Shoalstone
2. Saltern Cove

DORSET
3. Lyme Regis
4. West Bay
5. Portland Bill (Clay Ope)
6. Portland Bill (Collar ledge)
7. Osmington Mills
8. Lulworth Cove
9. Kimmeridge
10. Chapmans Pool
11. Peveril Point
12. Hengistbury Head

IOW
13. Alum Bay
28. Bembridge
34. Bonchurch
41. St. Catherine's Pt
43. Hanover Point
44. Freshwater Bay

HAMPSHIRE
45. Southsea

WEST SUSSEX
46. Selsey Bill
47. Bognor Regis
48. Worthing
49. Shoreham

EAST SUSSEX
50. Brighton
51. Newhaven
52. Hope Gap
53. Beachy Head
54. Cow Gap

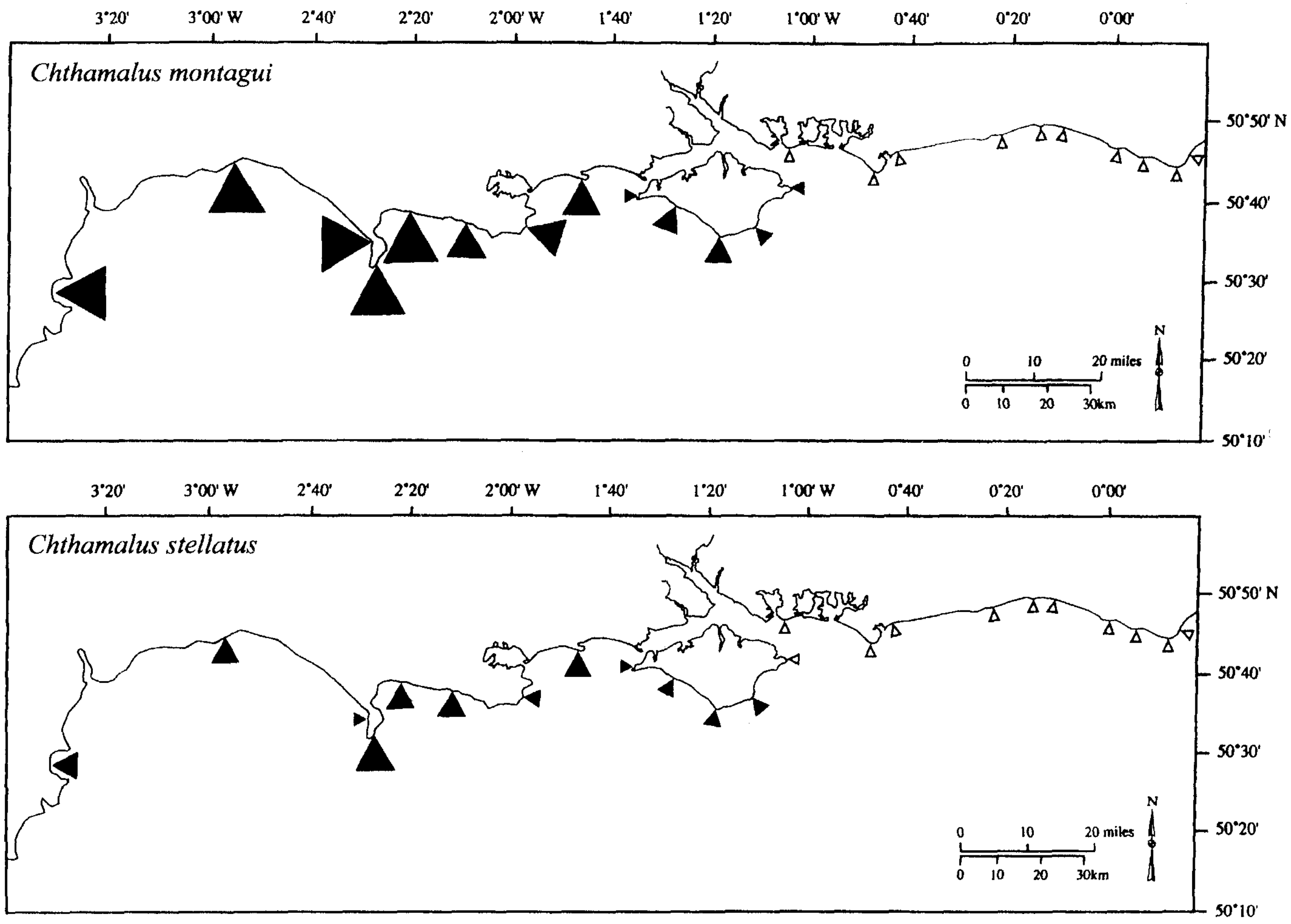


Fig.3.8 Distribution of *Chthamalus montagui* and *C. stellatus* along the south coast of England. Symbols show maximum mean shore abundance during main survey between 1992-94. New record of *C. montagui* at Bembridge in 1995 also shown. See Figs. 3.14 and 3.15 for detailed distribution around the Isle of Wight and Fig.3.7 for map and key.

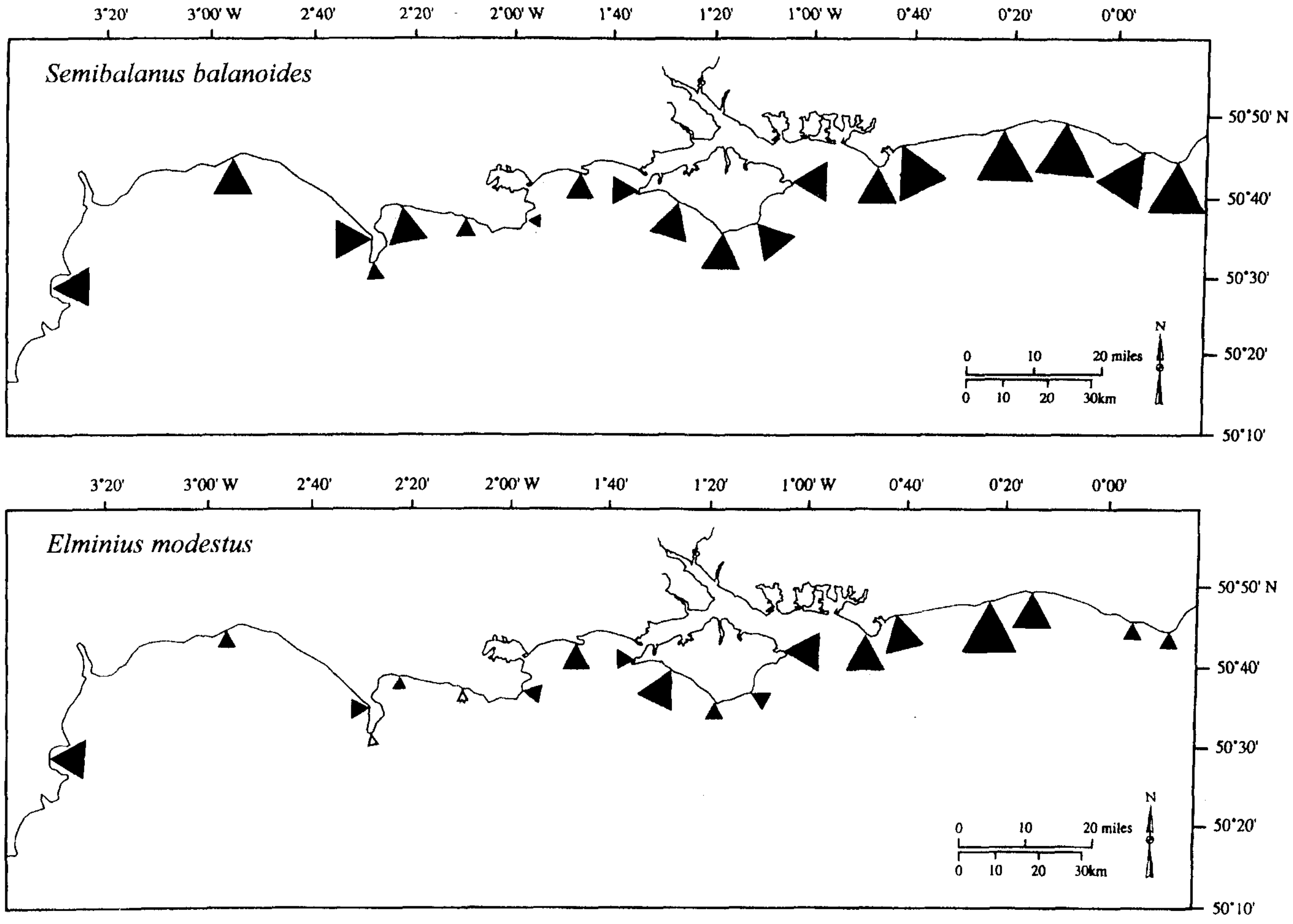


Fig.3.9 Distribution of *Semibalanus balanoides* and *Elminius modestus* along the south coast of England. Symbols show maximum mean shore abundance between 1992-94. (see Fig.3.7).

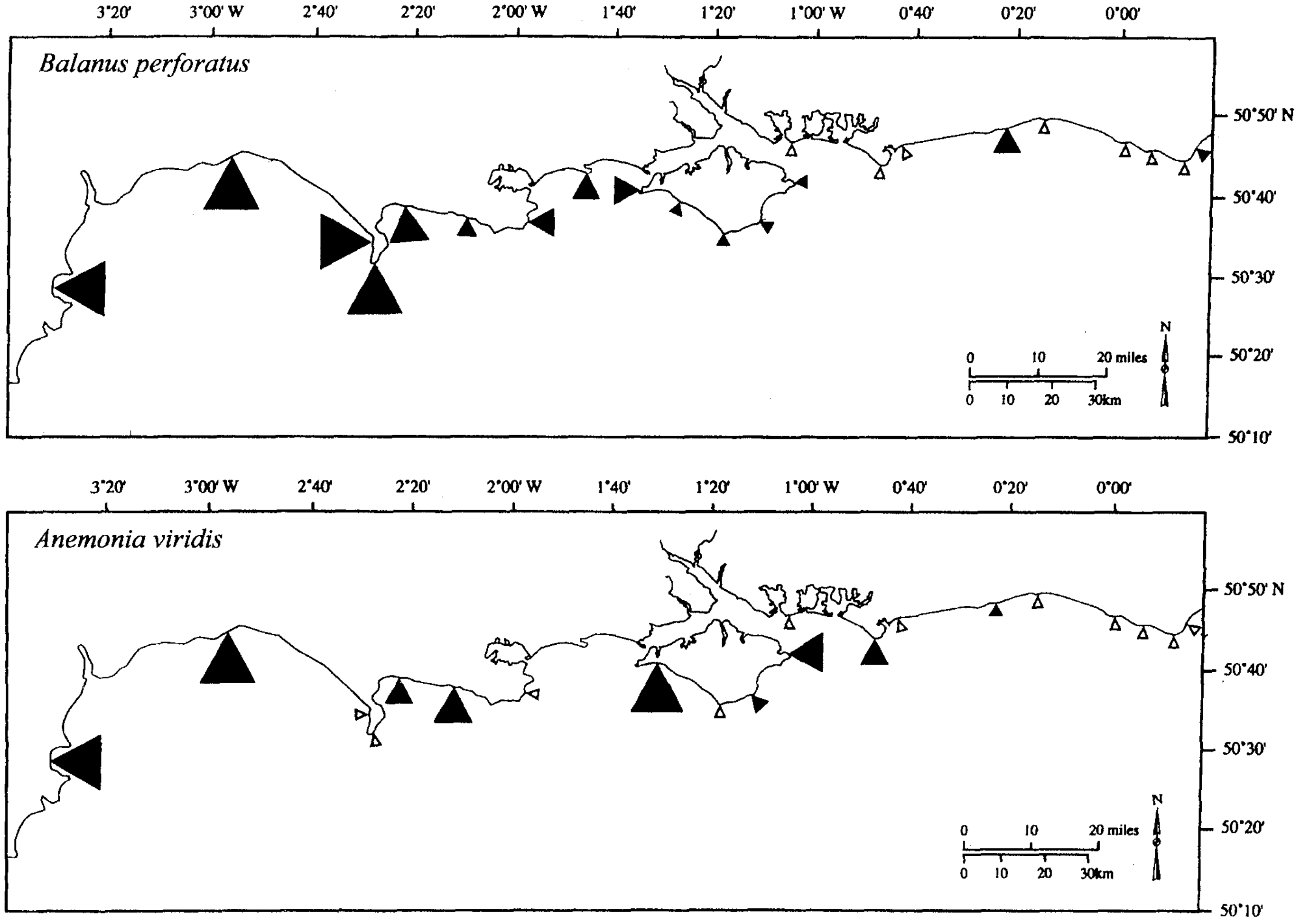


Fig.3.10 Distribution of *Balanus perforatus* and *Anemonia viridis* along the south coast of England. Symbols show maximum mean shore abundance during main survey between 1992-94 New records of *B. perforatus* at Worthing and Eastbourne in 1999 also shown. See also Fig.3.17 for detailed distribution of *B. perforatus* around the Isle of Wight and Fig 3.7 for key.

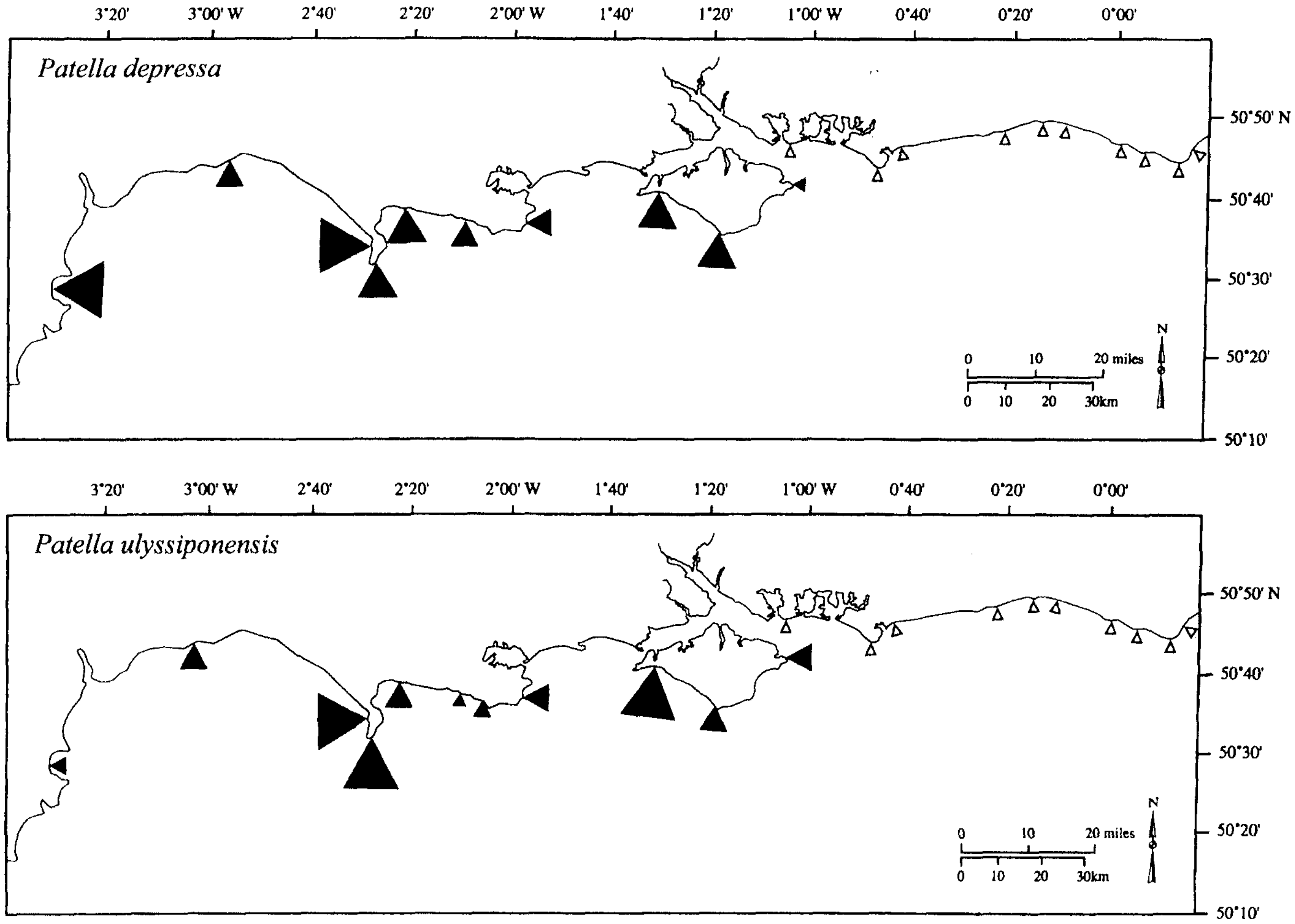


Fig.3.11 Distribution of *Patella depressa* and *P. ulyssiponensis* along the south coast of England. Symbols show maximum mean shore abundance in 1994 (see also Fig.3.7)

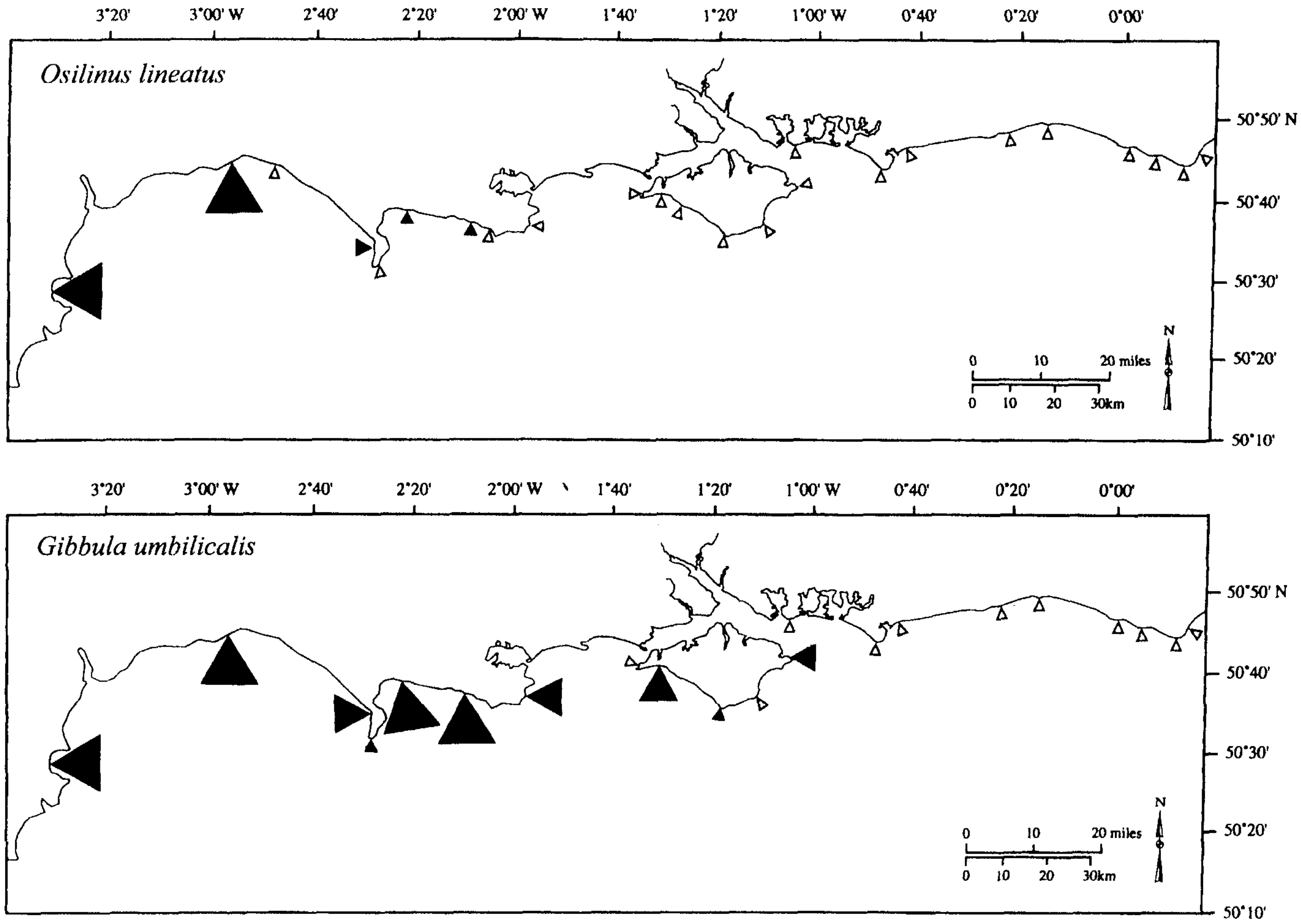


Fig.3.12 Distribution of *Osilinus lineatus* and *Gibbula umbilicalis* along the south coast of England. Symbols show maximum mean shore abundance during main survey in 1994 plus additional records of *Osilinus* along Dorset coast 1994-1999. (see also Fig.3.7).

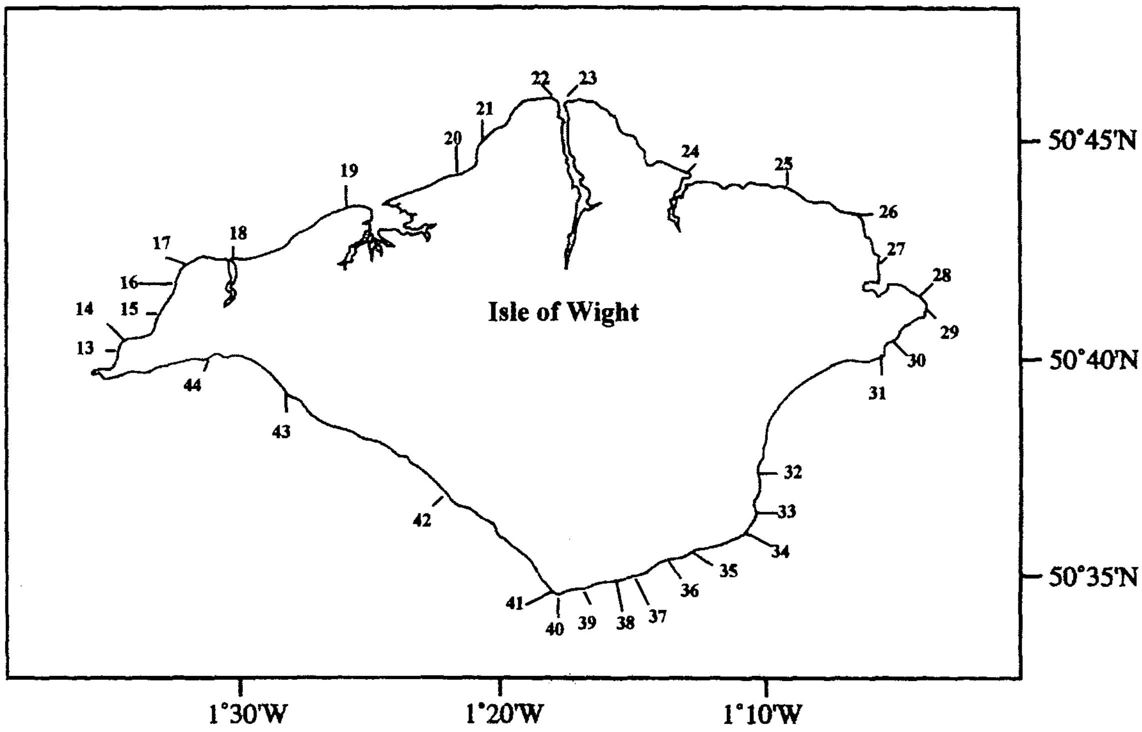


Fig.3.13. Map showing location of main survey sites on the Isle of Wight.

Mainland sites 1-12 and 45-54 together with symbols used in Figs. 3.14-3.16 is shown in Fig.3.7.

Locations

13. Alum Bay
14. Hatherwood Pt.
15. Colwell
16. Fort Albert
17. Fort Victoria
18. Yarmouth
19. Hamstead Ledge
20. Thorness Bay
21. Gurnard Ledge
22. Cowes
23. East Cowes
24. Woodside
25. Pelhamfield
26. Seaview
27. Nodes Pt.
28. Bembridge (Ethel Pt)
29. Forelands
30. Black Rock
31. Culver Cliff
32. Horse Ledge
33. Luccombe
34. Bonchurch
35. Ventnor
36. Steephill Cove
37. Woody Pt.
38. Binnel Pt.
39. Reeth Bay
40. St. Catherine's Pt.
41. Watershoot Bay
42. Atherfield Ledge
43. Hanover Pt.
44. Freshwater Bay

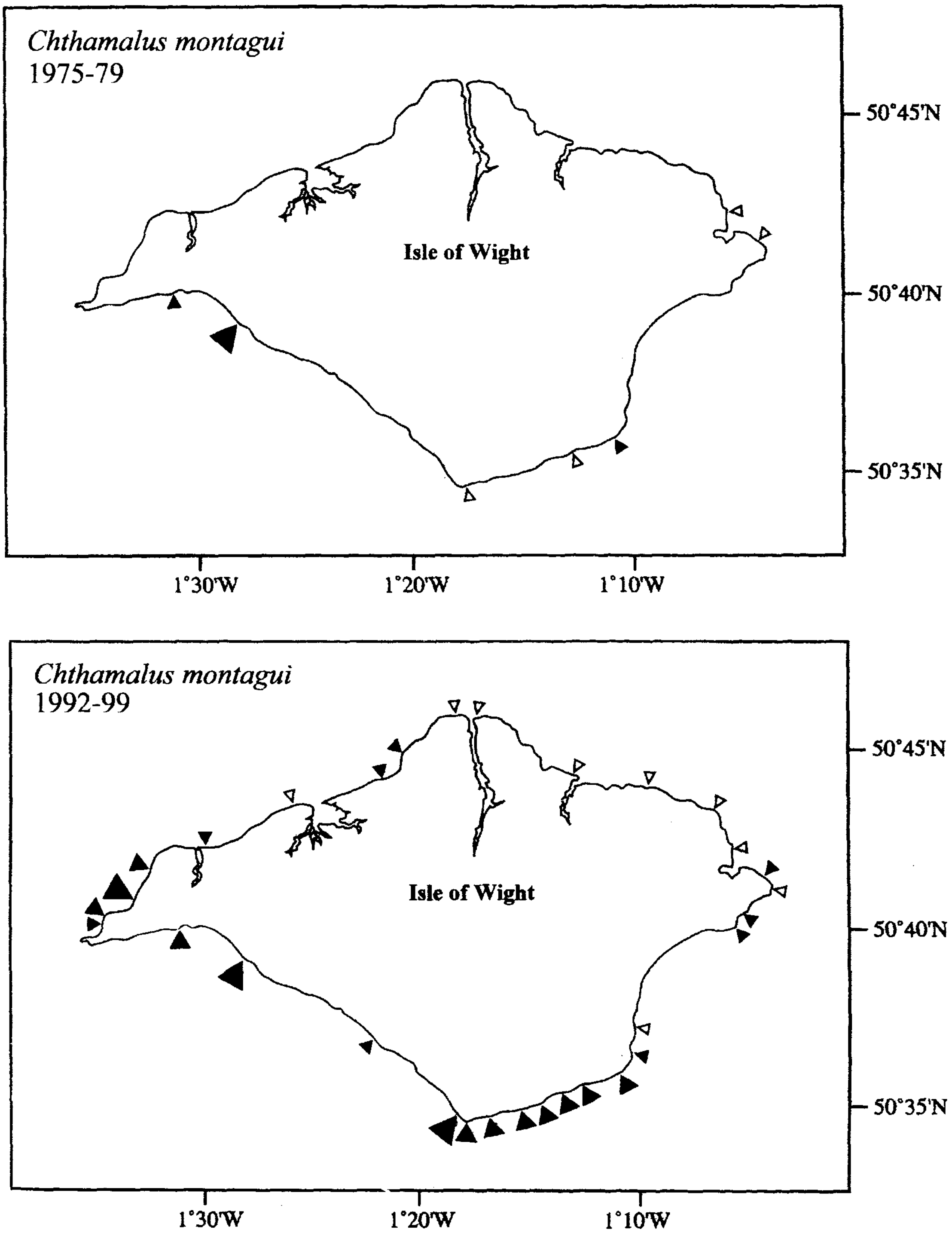


Fig. 3.14 Distribution and abundance of *Chthamalus montagui* around the Isle of Wight. Symbols show maximum mean abundance at HWN during period shown (see also Figs 3.7 & 3.13). Data for 1975-79 from Crisp *et al.*, 1981.

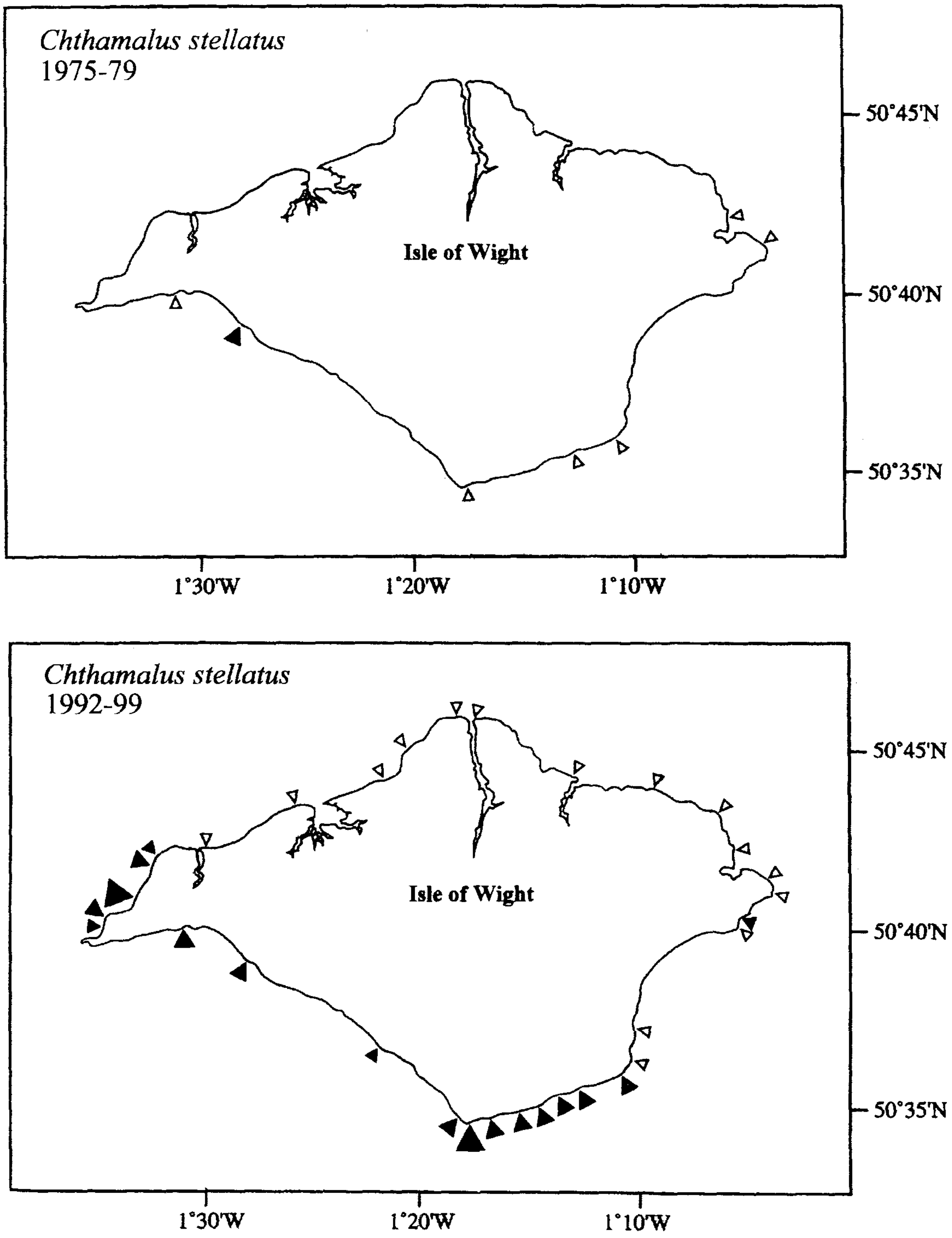
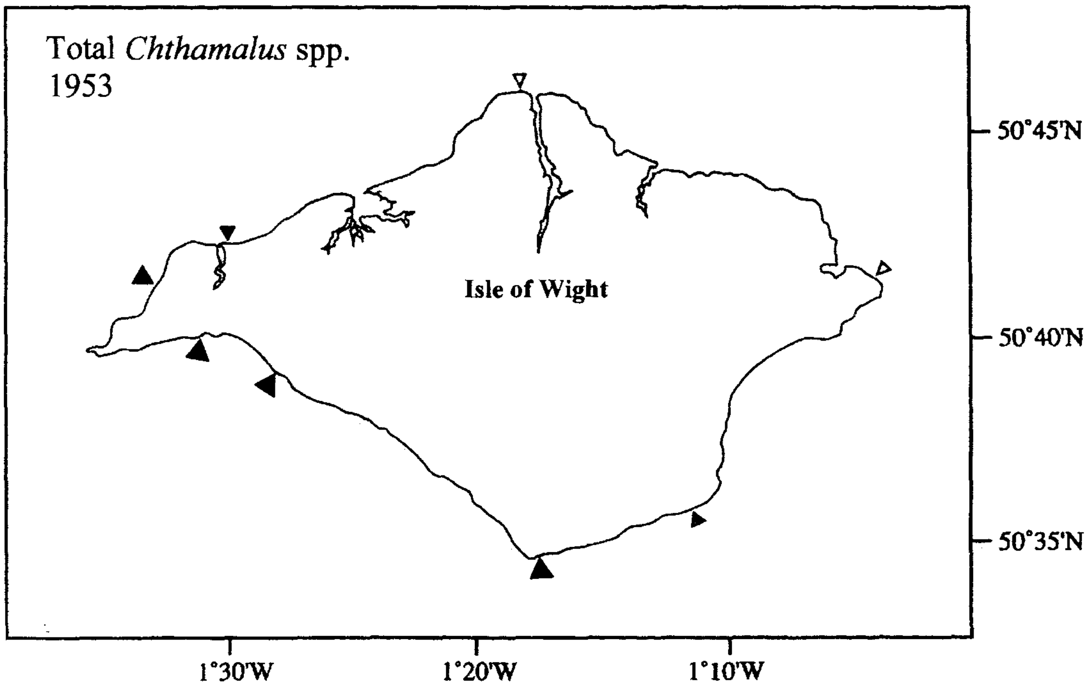


Fig. 3.15 Distribution and abundance of *Chthamalus stellatus* around the Isle of Wight. Symbols show maximum mean abundance at HWN during period shown (see Figs.3.7-3.13). Data for 1975-79 from Crisp *et al.*, 1981.



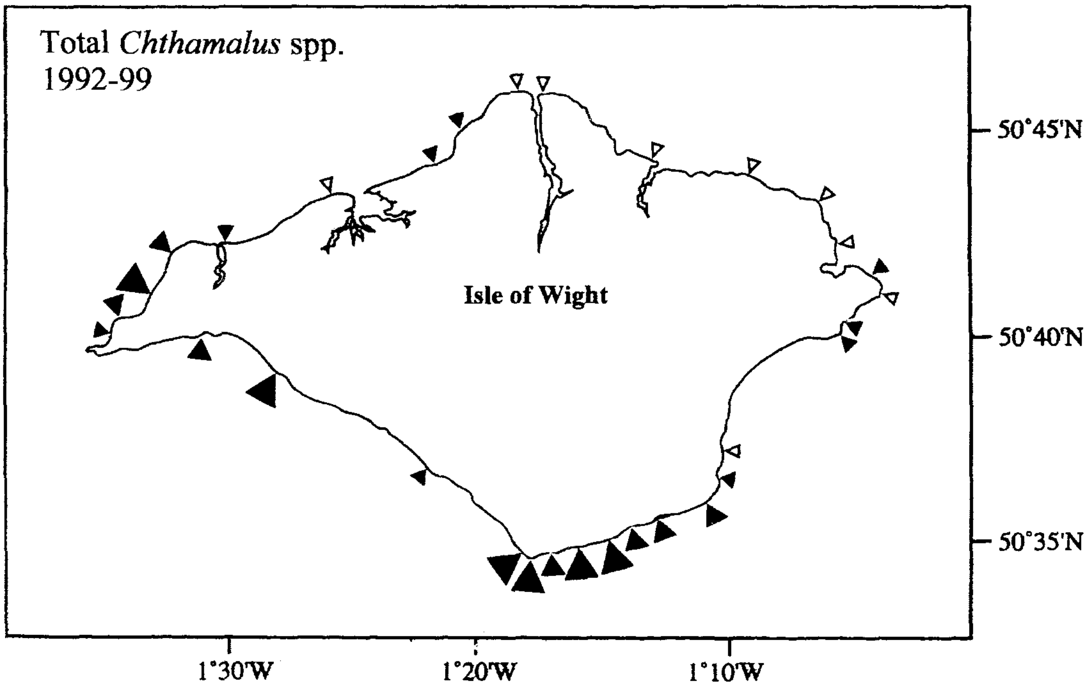


Fig.3.16 Distribution and abundance of both *Chthamalus* spp around the Isle of Wight. Symbols show maximum mean abundance at HWN during period shown (see Figs.3.7-3.13). Data for 1953 from Crisp & Southward (1958).

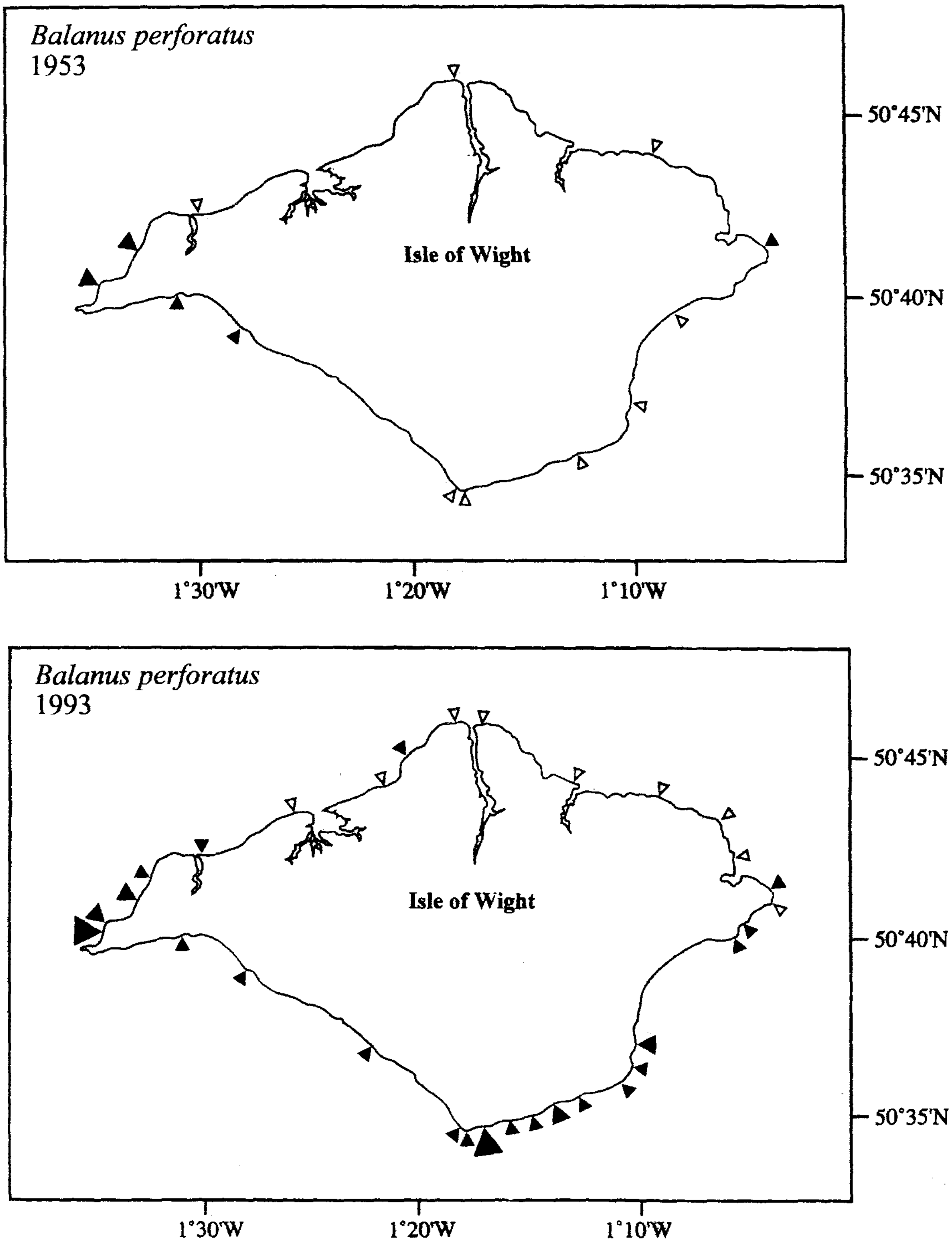


Fig.3.17 Distribution and abundance of *Balanus perforatus* around the Isle of Wight. Symbols show mean abundance (see Fig.3.7 & 3.13). Data for 1953 from Crisp & Southward (1958).

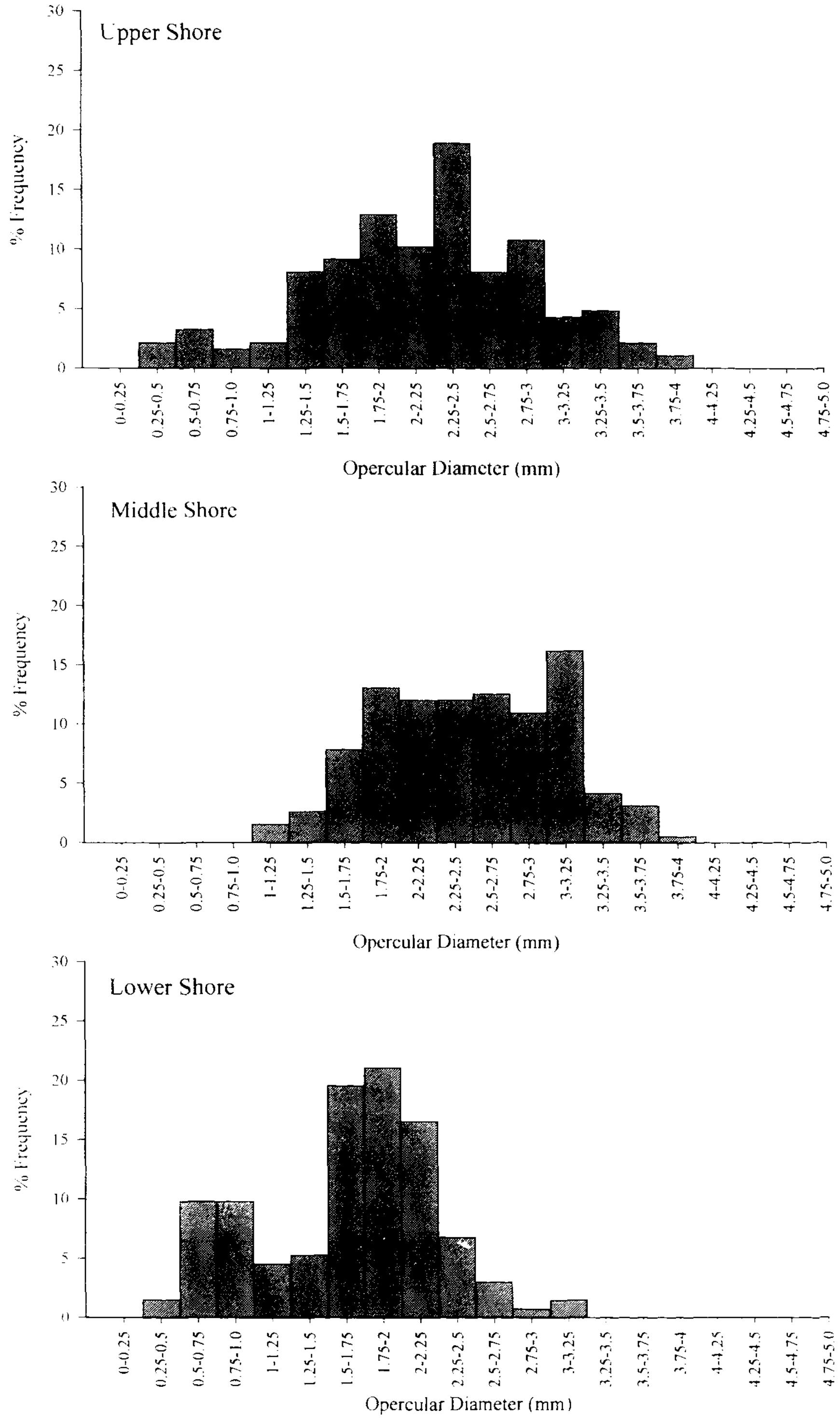


Fig.3.18 Population size-frequency histogram of *Chthamalus montagui* at Shoalstone beach, Brixham in south Devon in October 1994. Upper shore n = 185; Middle shore n = 191; Lower shore n = 133.

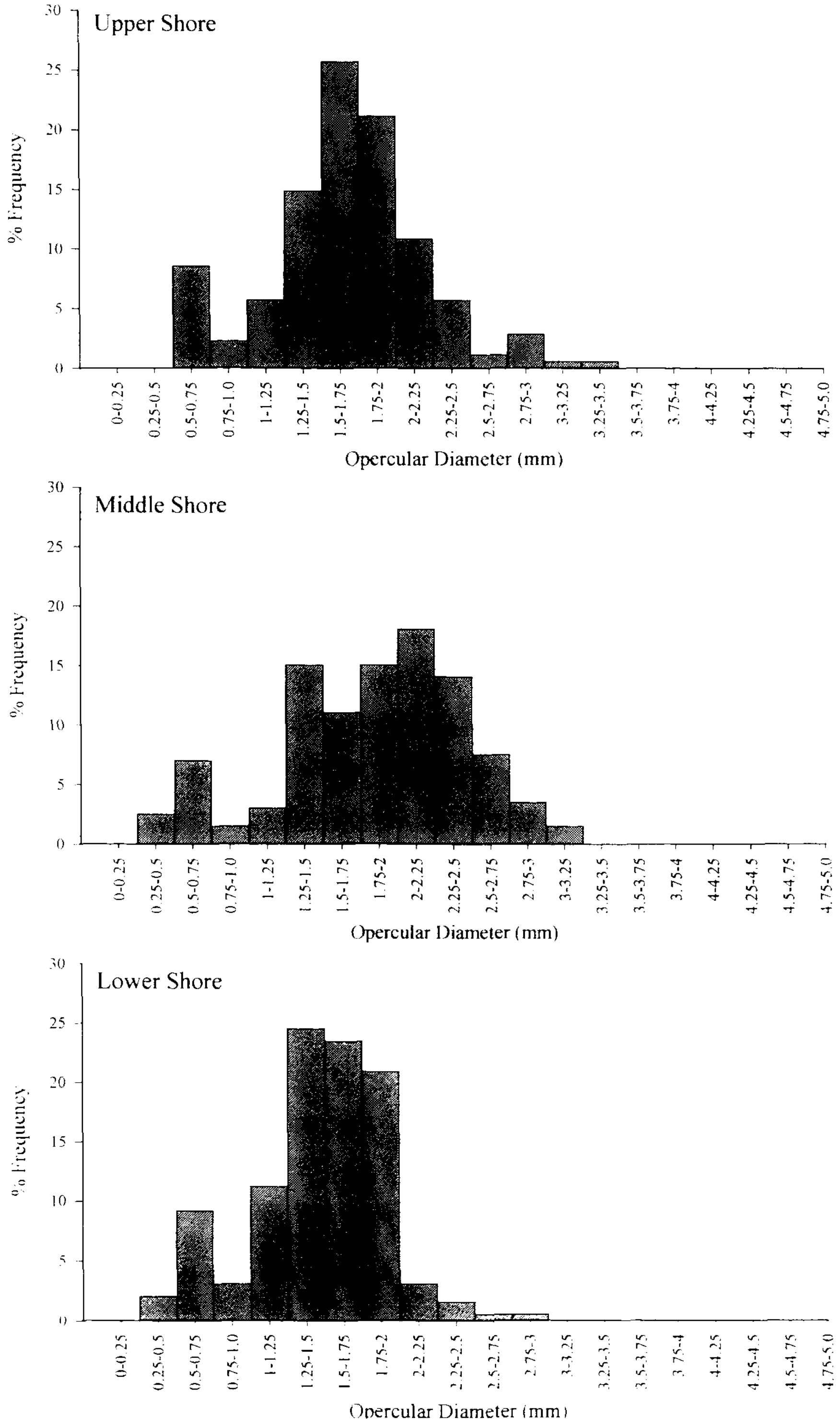


Fig. 3.19 Population size-frequency histogram of *Chthamalus montagui* at Lyme Regis, Dorset in October 1994. Upper shore n = 175; Middle shore n = 199; Lower shore n = 176.

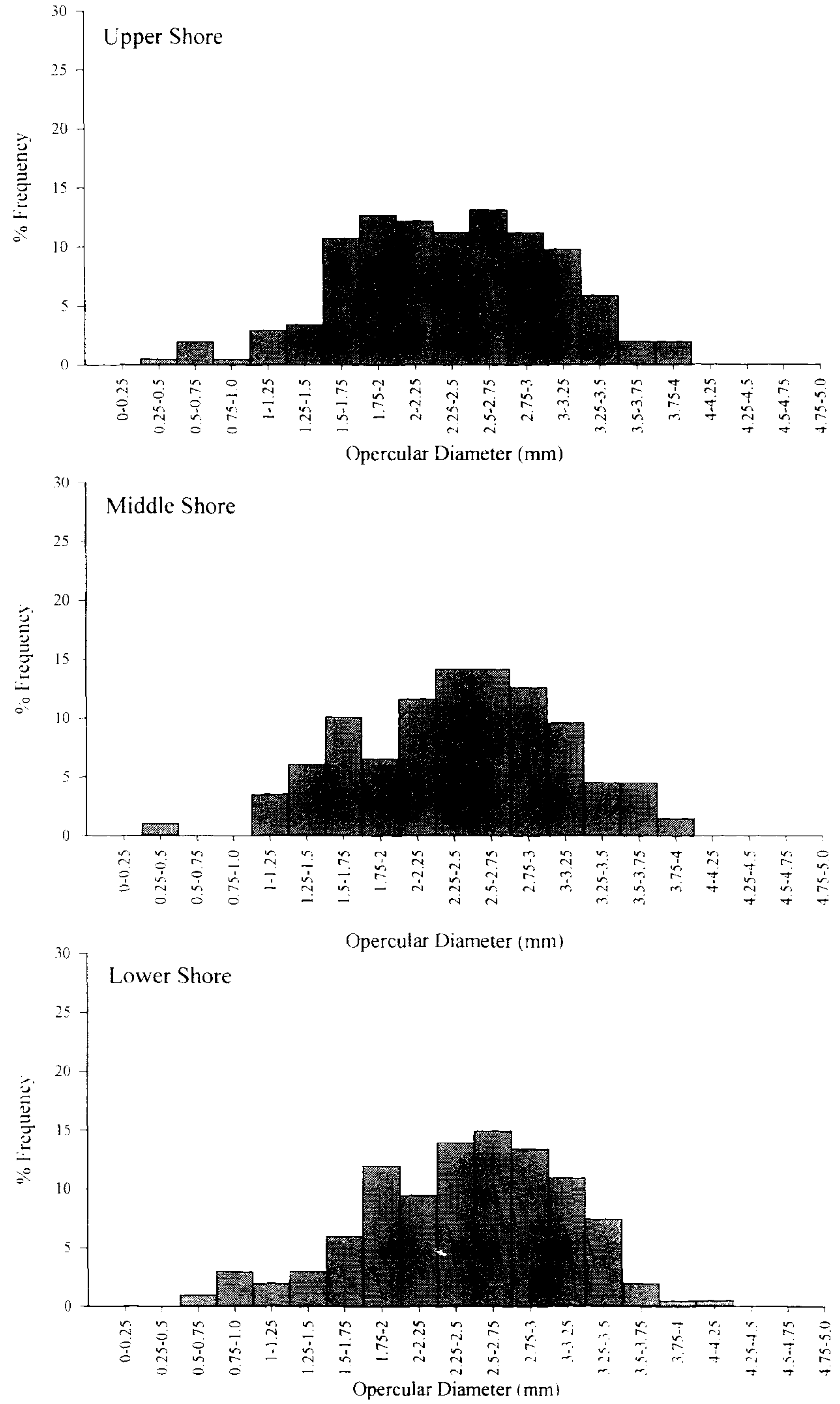


Fig.3.20 Population size-frequency of *Chthamalus montagui* at Portland Bill, Dorset in October 1994. Upper shore n = 205; Middle shore n = 198; Lower shore n = 201.

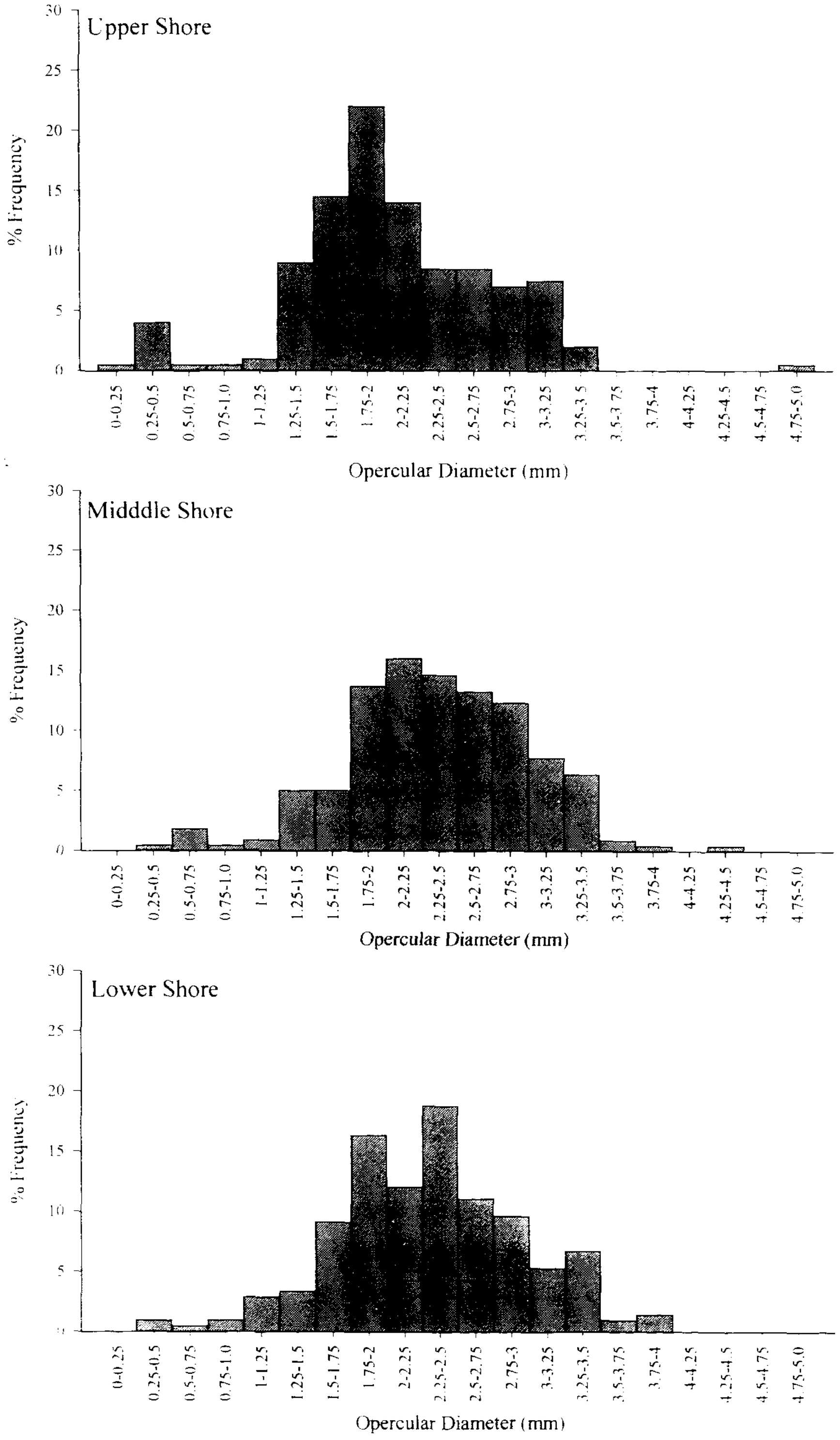


Fig. 3.21 Population size-frequency histogram of *Chthamalus montagui* at Osmington Mills, Dorset in October 1994. Upper shore n = 200; Middle shore n = 218; Lower shore n = 208.

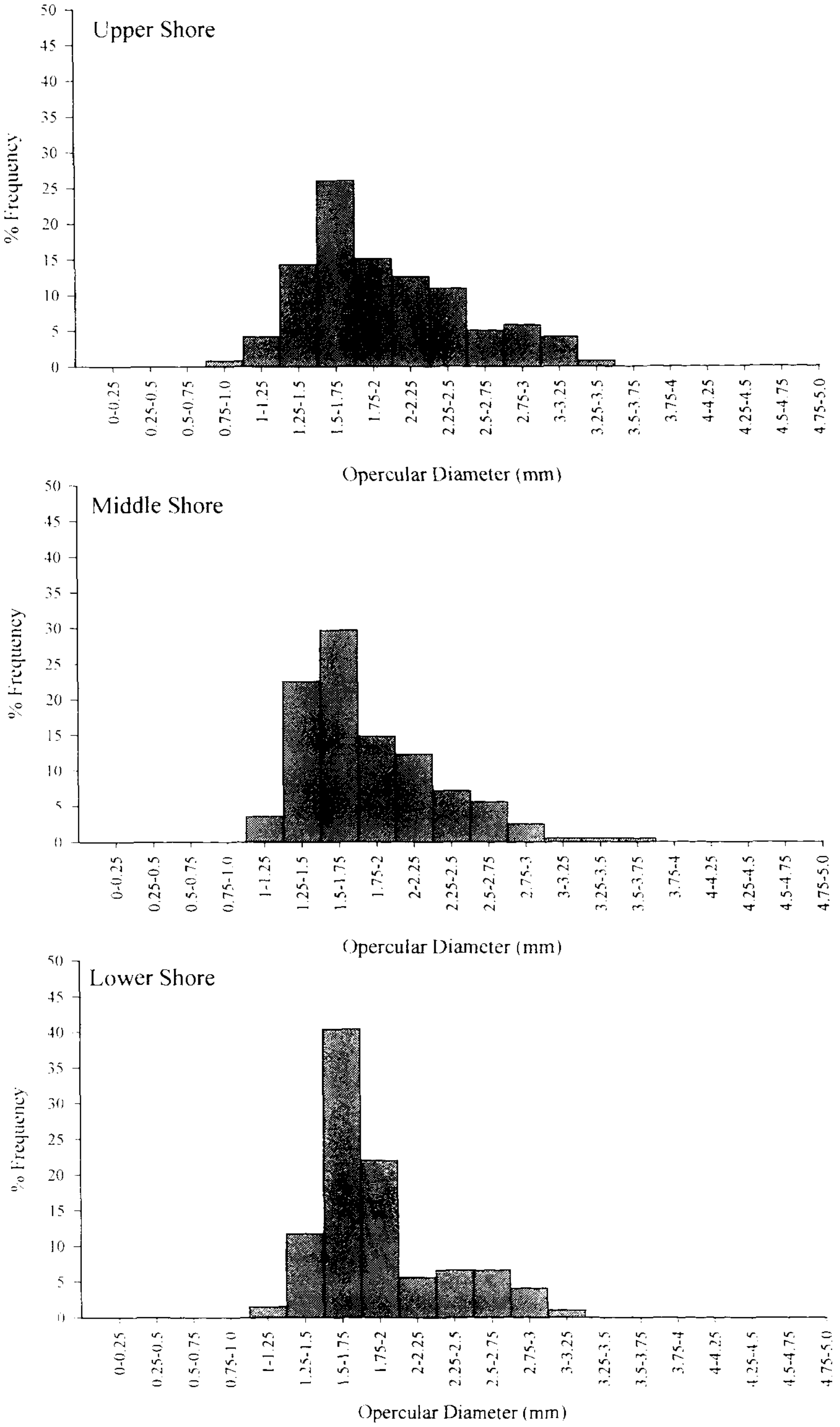


Fig. 3.22 Population size-frequency of *Chthamalus montagui* at Kimmeridge, Dorset in October 1994. Upper shore n = 119; Middle shore n = 195; Lower shore n = 195.

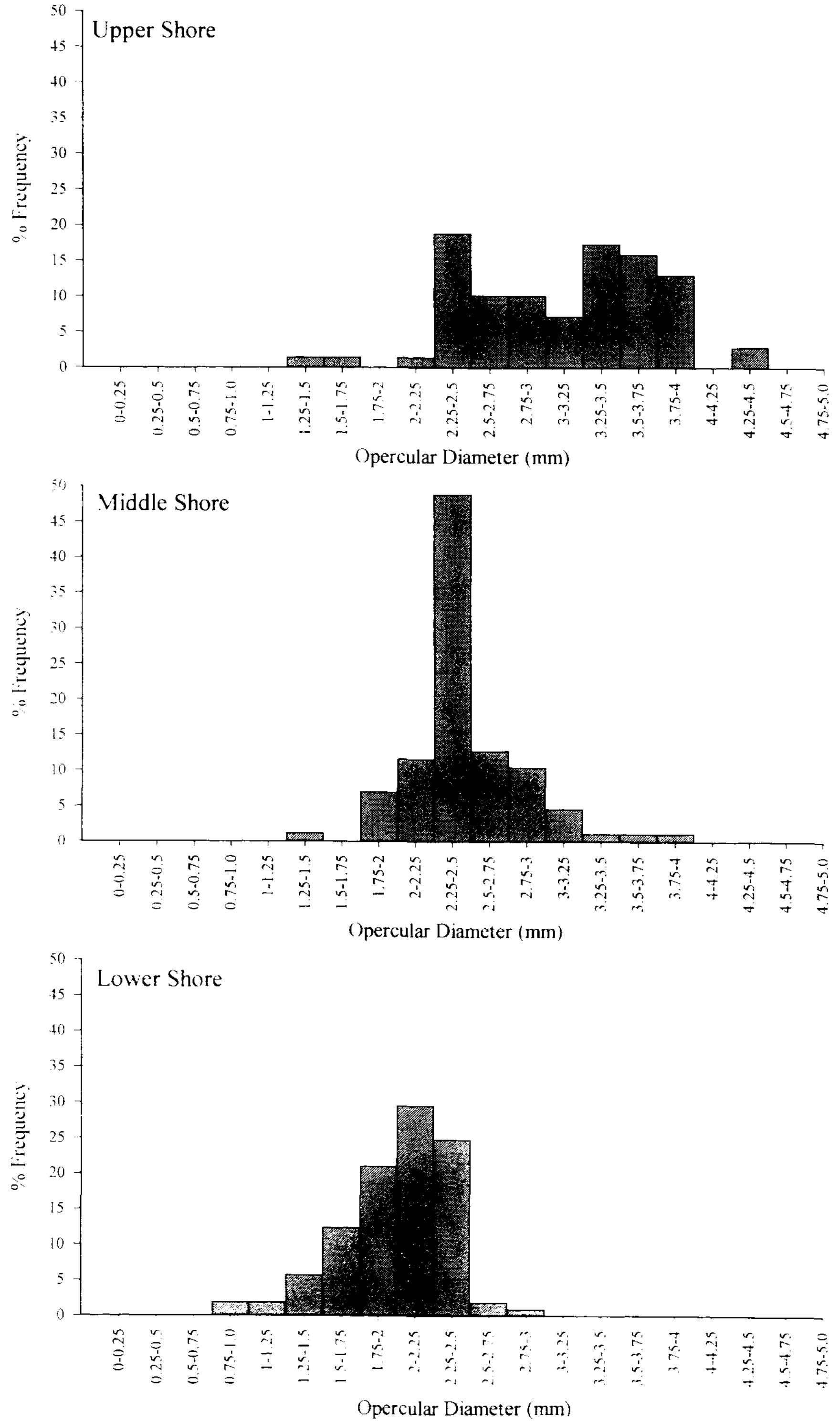


Fig.3.23 Population size-frequency histogram of *Chthamalus montagui* at Hanover Point, Isle of Wight, in October 1994. Upper shore n = 58; Middle shore n = 86; Lower shore n = 105.

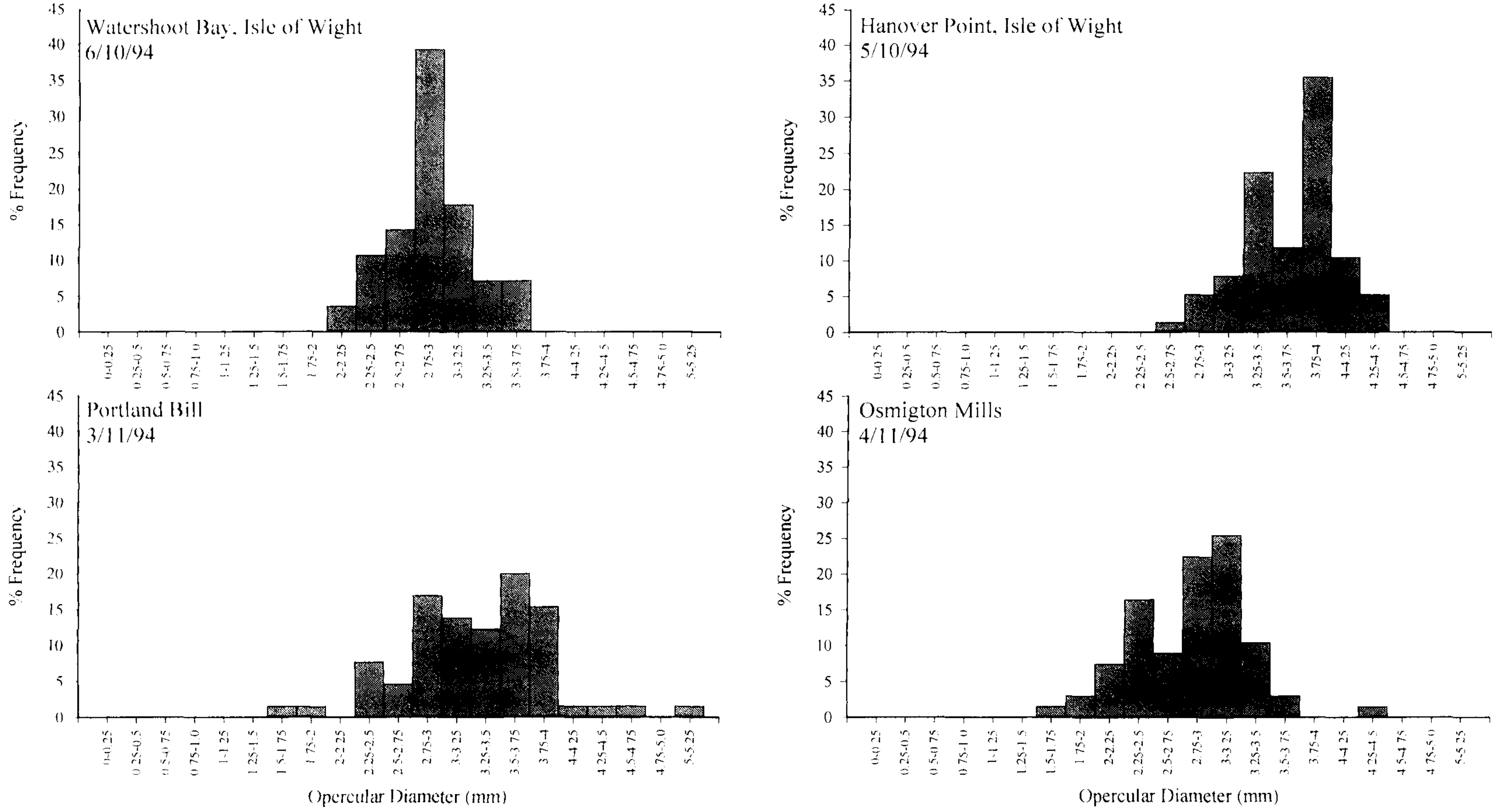


Fig.3.24 Size-Frequency of *Chthamalus stellatus* in autumn of 1994. Portland Bill n = 65; Osmington Mills n = 67; Watershoot Bay n = 28; Hanover Point n = 76.

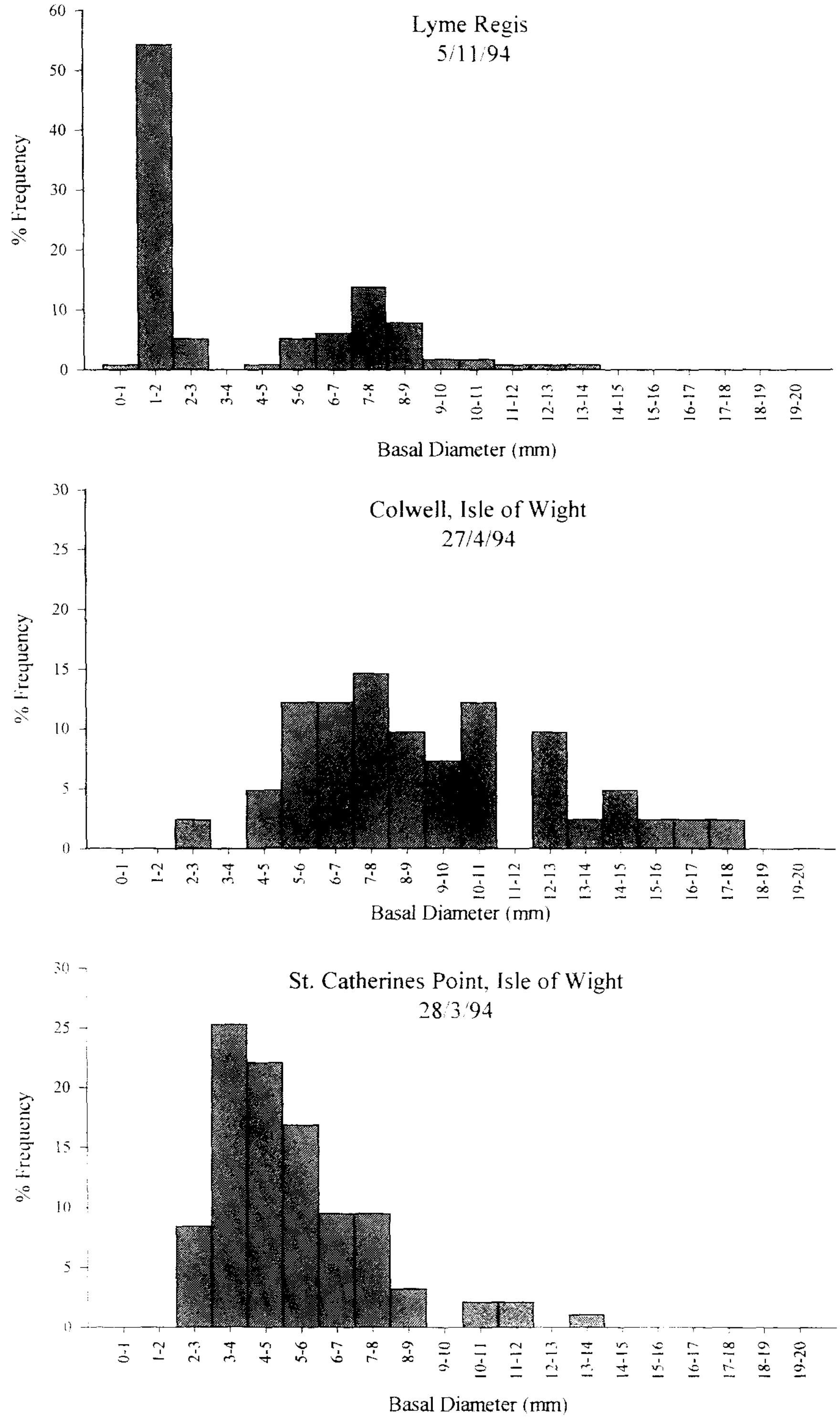


Fig. 3.25 Population size-frequency histograms of *Balanus perforatus* at shores approaching eastern Channel limits. Lyme Regis, n = 116; Colwell, n = 41; St. Catherines Point, n = 95.

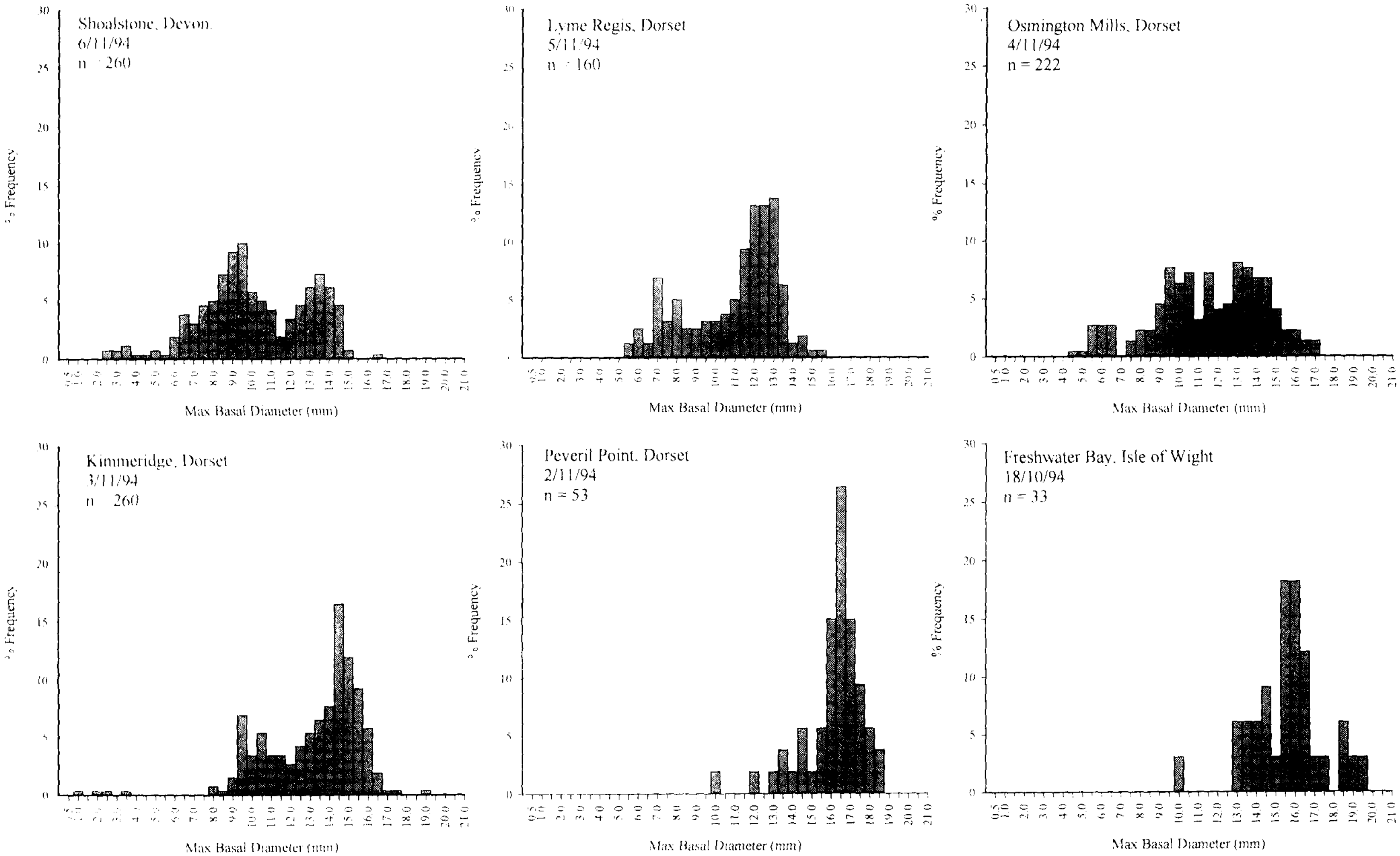


Fig.3.26 Population size-frequency histograms of *Gibbula umbilicalis* at shores approaching eastern Channel limits in autumn 1994.

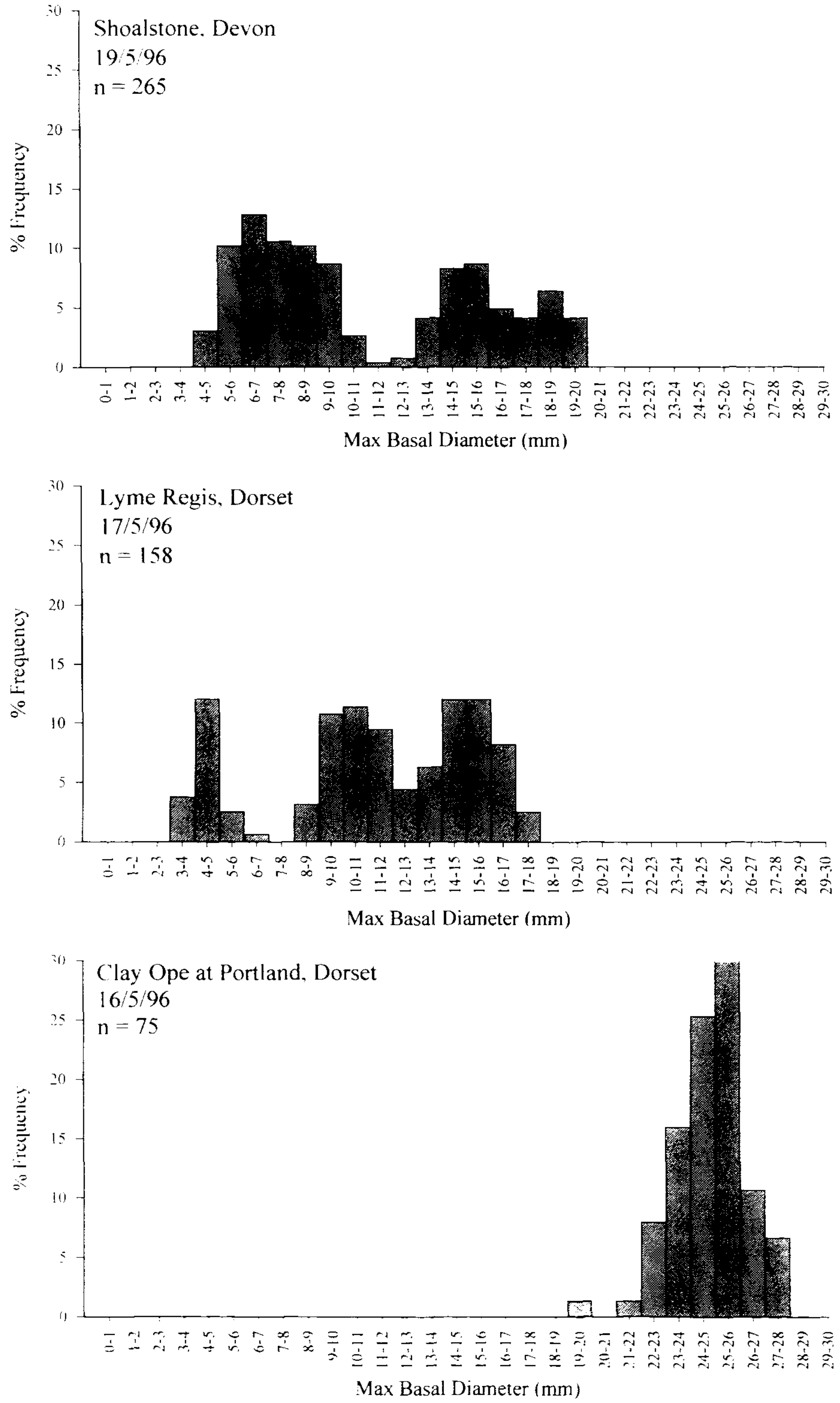


Fig.3.27 Population size-frequency histograms of *Osilinus lineatus* at shores approaching eastern Channel limits in May 1996.

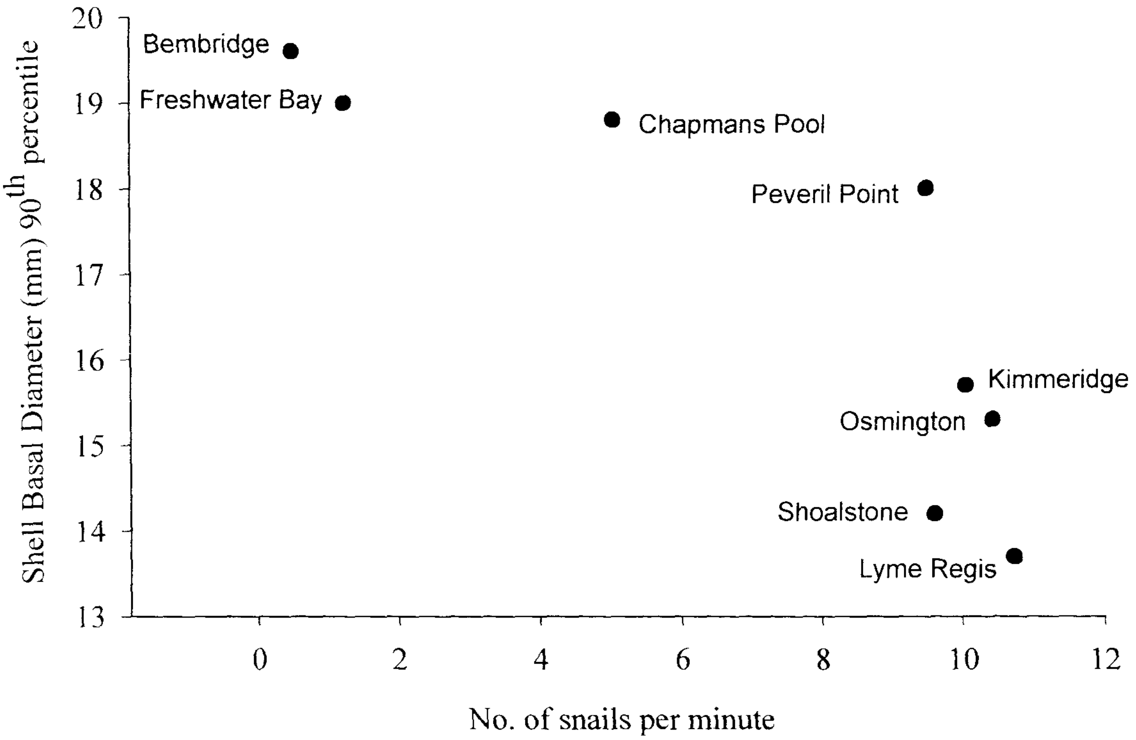


Fig.3.28 Relationship between abundance of *Gibbula umbilicalis* and the shell basal diameter at the 90th percentile of a cumulative frequency plot. Spearman rank correlation coefficient r = - 0.93, n = 8, p <0.01.

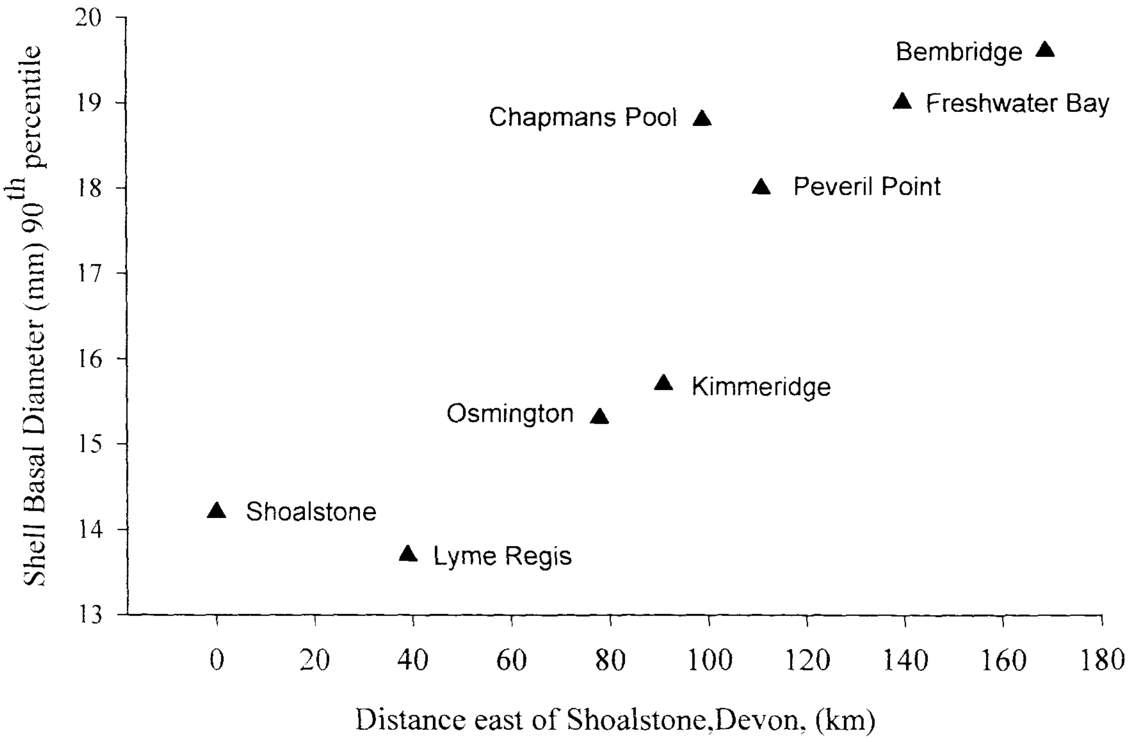


Fig. 3.29 Scatter diagram of shell basal diameter of *G. umbilicalis* populations against distance east of Shoalstone in Devon. Spearman Rank correlation coefficient r = 0.95, n = 8 , p < 0.01.

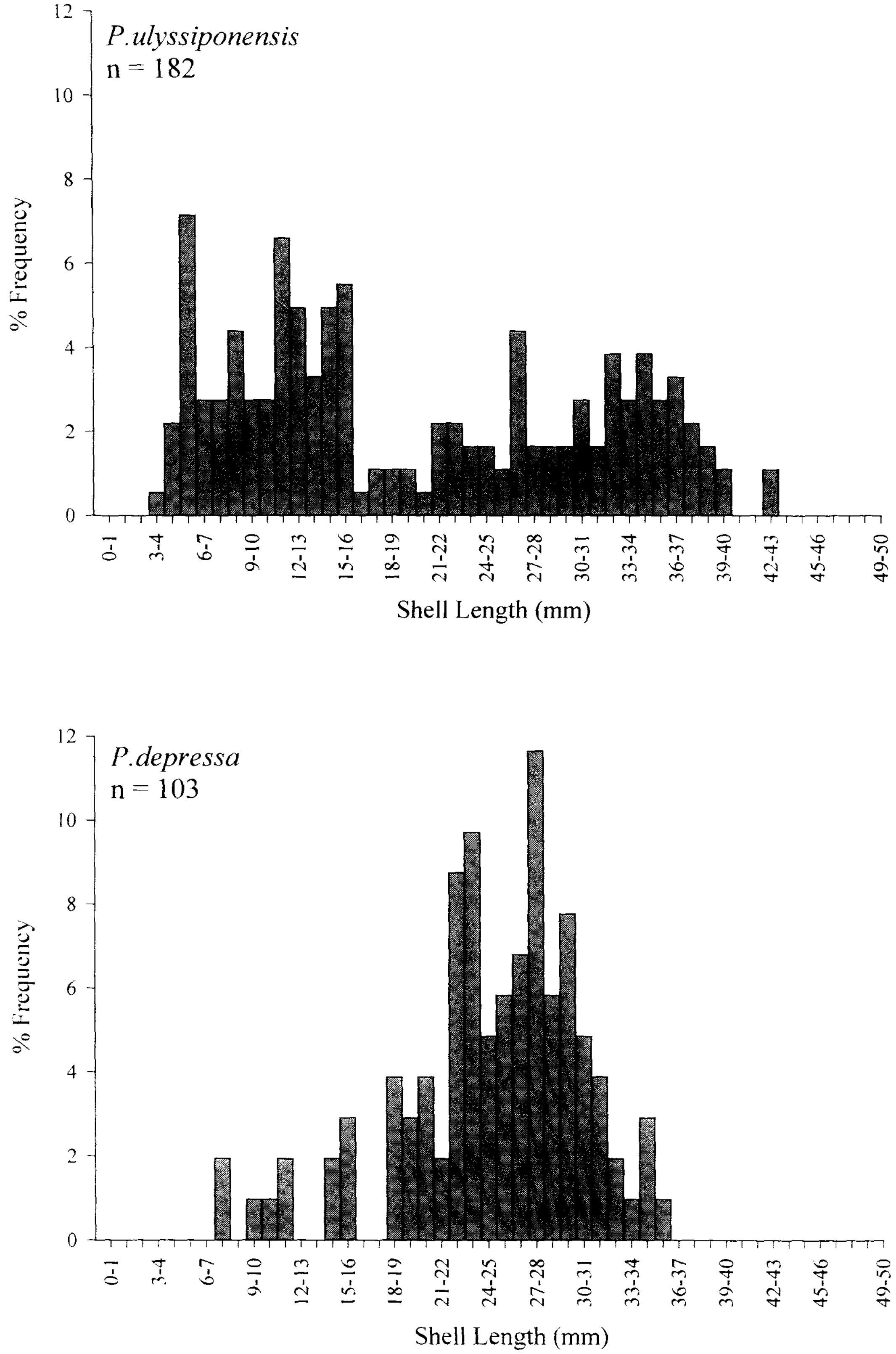


Fig. 3.30 Population size-frequency histograms of *Patella ulyssiponensis* and *P. depressa* at Freshwater Bay, Isle of Wight on 14/ 5/1996.

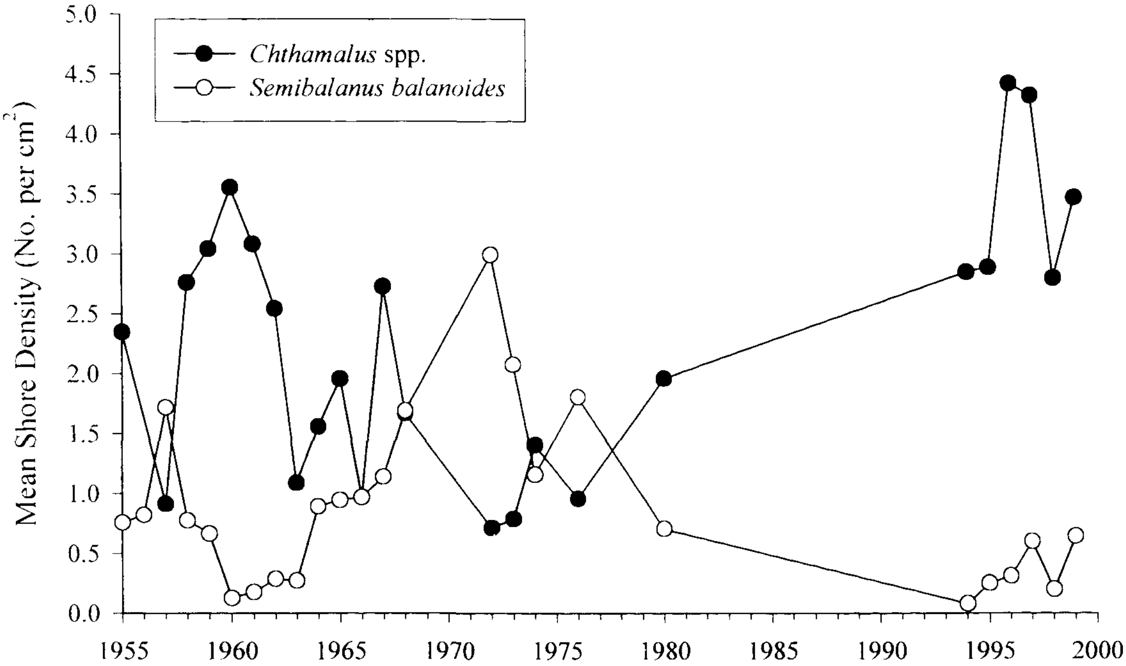


Fig.3.31 Time-series showing mean shore density of *Chthamalus* spp. and *Semibalanus balanoides* at Shoalstone beach, Brixham, Devon. Data from 1955-80 supplied by A.J. Southward. Spearman rank correlation coefficient of density of two species = -0.76, $p<0.001$, n=29.

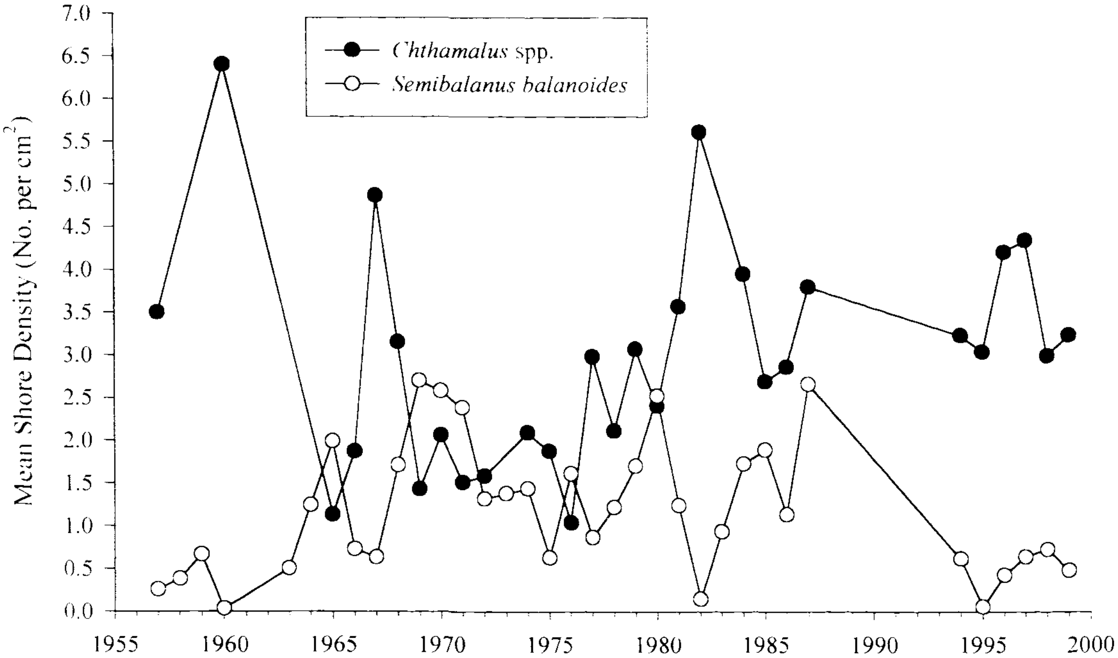


Fig.3.32 Time-series showing mean shore density of *Chthamalus* spp. and *Semibalanus balanoides* at Lyme Regis, Dorset. Data from 1957-87 supplied by A.J. Southward. Spearman rank correlation coefficient of density of two species = -0.53, $p<0.003$, n=29.

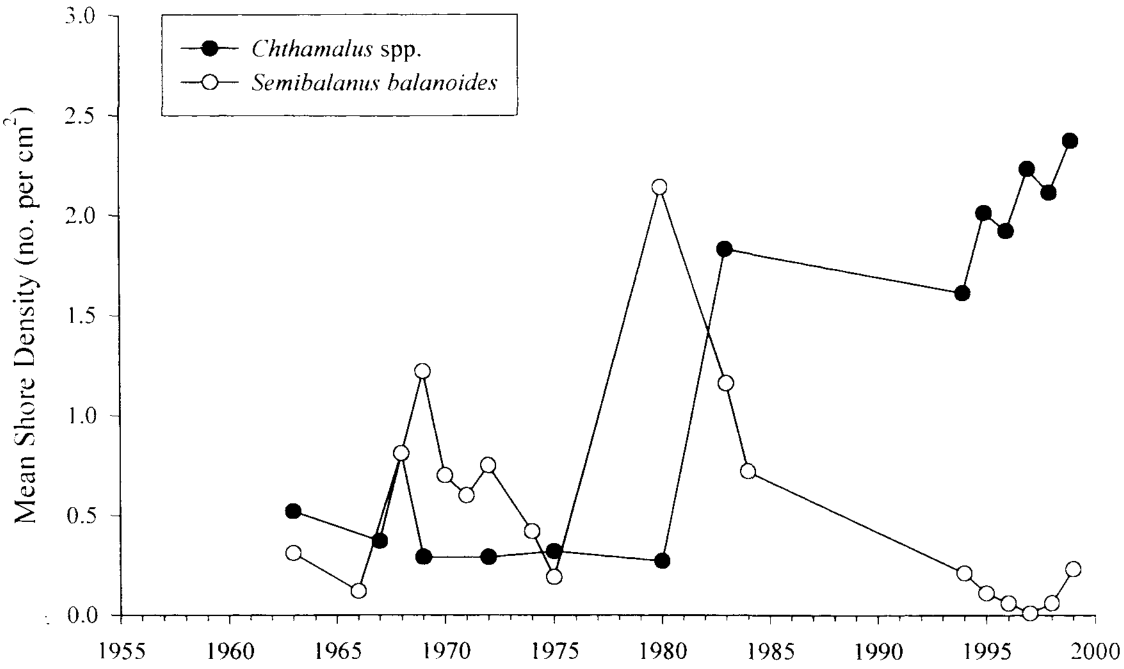


Fig.3.33 Time-series showing mean shore density of *Chthamalus* spp. and *Semibalanus balanoides* at Osmington Mills, Dorset. Data from 1955-84 supplied by A.J. Southward. Spearman rank correlation coefficient of density of two species = -0.7, p = 0.006, n = 13.

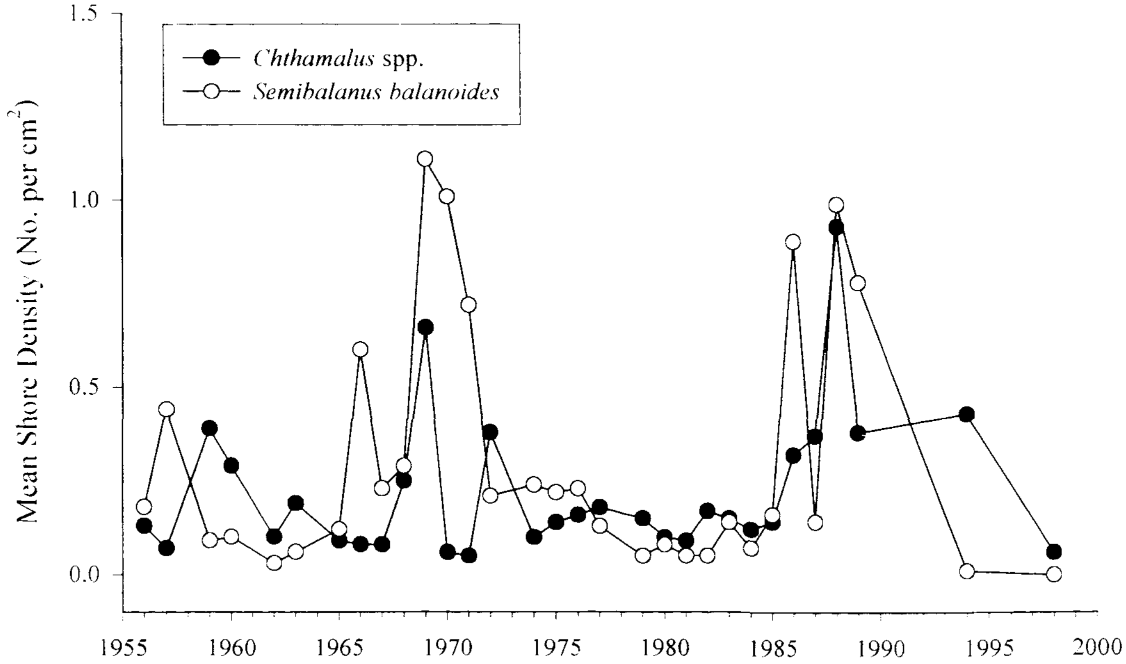


Fig.3.34 Time-series showing mean shore density of *Chthamalus* spp. and *Semibalanus balanoides* at Peveril Point. Dorset. Data from 1955-89 supplied by A.J. Southward. Spearman rank correlation coefficient of density of two species =0.06, p = 0.74. n = 31.

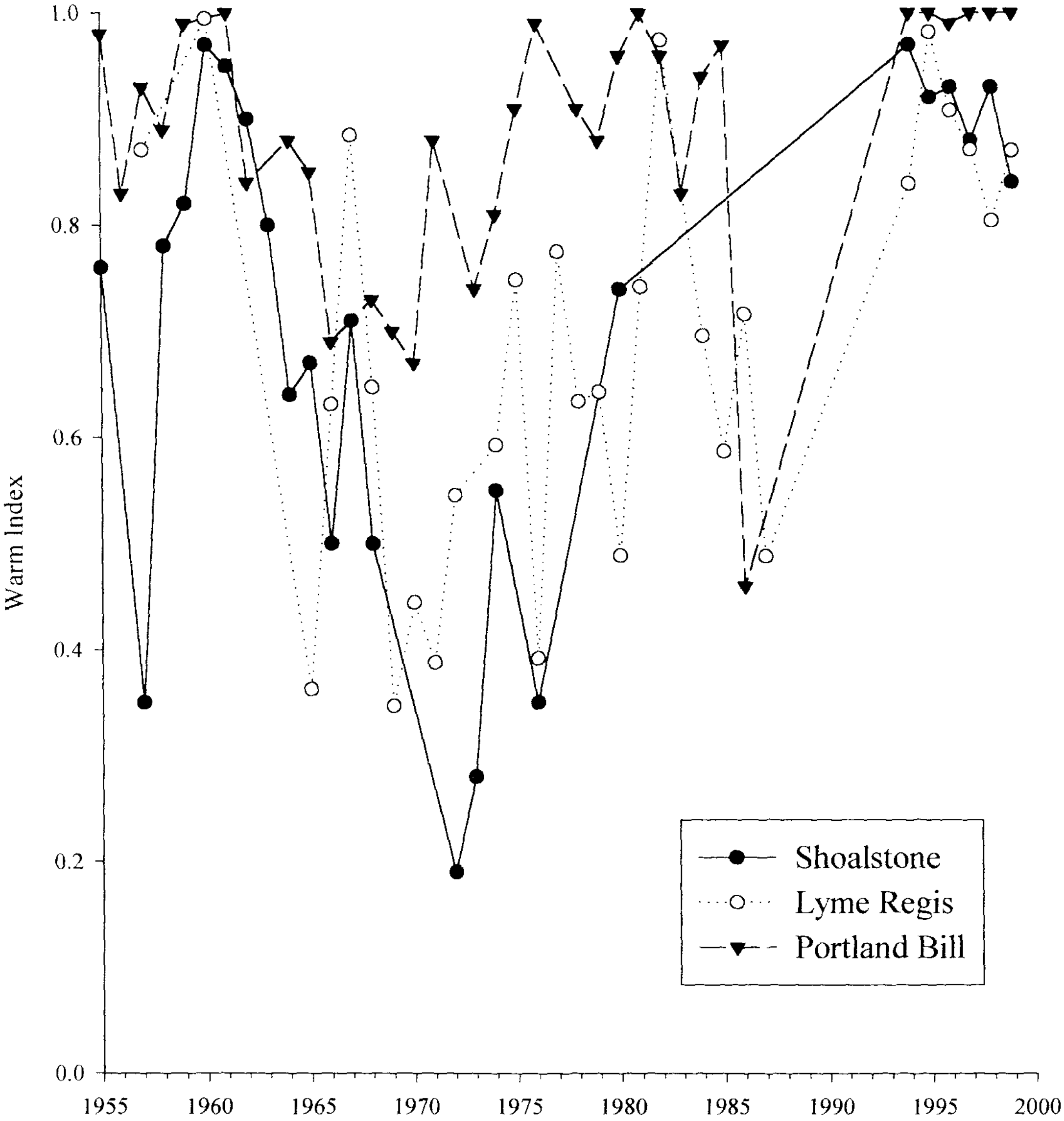


Fig.3.35 Warm indices calculated for Shoalstone (Brixham, Devon), Lyme Regis and Portland Bill (Dorset). Data from 1955 – 1987 supplied by A.J. Southward. See section 3.27 for calculation of index.

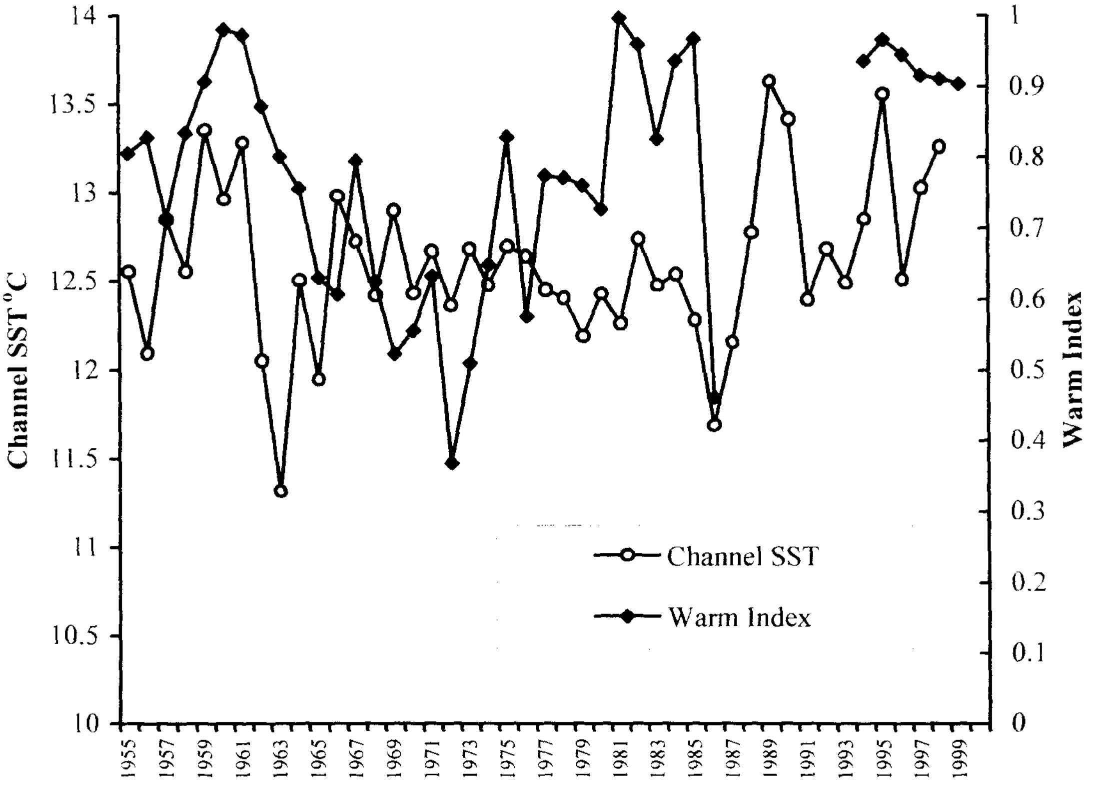


Fig.3.36 Mean Warm Index (Brixham, Lyme Regis and Portland) and Mean Channel SST between 1955 and 1999. The two variables show a significant correlation when Warm Index is compared with sea temperature one year earlier (Spearman rank r =0.347, p = 0.036, n = 38). See text for further details.

3.5 Discussion

With the exception of *Balanus perforatus* and *Anemonia viridis*, the eastern limits of all the selected Lusitanian species occur in either east Dorset or the Isle of Wight, where there has been a recovery of populations to densities equal or above those recorded prior to the severe 1962-63 winter. *Balanus perforatus* was found at Eastbourne, 75 km east of earlier known limits within Chichester Harbour where fully grown individuals were recorded on submerged fouling test-panels in the 1960s (Stubbings & Houghton, 1964). However its abundance at Bembridge, on the eastern tip of the Isle of Wight, does not appear to be at levels recorded by R.Wells of Portsmouth Grammar School between 1959-63 (Portsmouth Grammar School records and reference collection). Intertidally, the anemone *Anemonia viridis* was found as far east as Worthing, although I have sublittoral records obtained from divers as far east as Beachy Head. This species has also recovered since the ice winter when it was killed on Isle of Wight shores (Crisp (ed.),1964; O.Frazer pers.comm).

The trochids *Osilinus lineatas* and *Gibbula umbilicalis*, also killed at their eastern limits during the cold winter of 1962-63, have now recolonised their former sites in Dorset and the Isle of Wight; the recent discovery of several specimens of *Osilinus lineatus* east of Portland suggest that densities of this species are back to levels found prior to the ice winter (Hawthorne,1965). On the Isle of Wight, *Gibbula umbilicalis* may now reliably be found between MTL and LWN at Freshwater Bay, its main stronghold on the island prior to the 1962-63 winter when the population was killed. Even in 1987 the species was quite scarce here as only a total of 11 specimens were found in a 20 minute search by six workers (Herbert,1989). The limpets *Patella ulyssiponensis* and *P. depressa* may still be found as far east as Bembridge, where they were previously recorded by Crisp & Southward (1958). Large *P.ulyssiponensis* may be easily found on the outer ledges.

Despite a decade of high air and sea temperatures (Chapter 2), with particularly mild winters and exceptionally hot summers recorded in 1989, 1990 and 1995, there has not so far been any major eastward extension of *Chthamalus* and *G. umbilicalis* beyond the limits observed by Crisp & Southward (1958). Nevertheless, the barnacles *Chthamalus montagui* and *C. stellatus* do appear to have increased in density on the south coast of the Isle of Wight and have now both been found at Bembridge, 8 km and 25km beyond the previously observed limits at Bonchurch and Brook (Crisp & Southward 1958; Crisp *et al.*,1981). Moreover, they have been seen below MTL. Thus at the extreme limits there appears to have been a slight extension of *Chthamalus*. George *et al.*,(1989) recorded a few *C.montagui* on the chalk shore below Culver Cliff on the Isle of Wight in July 1988, and it is possible that earlier surveys overlooked this species at the eastern end of the Isle of Wight. Near the edge of a species range, fluctuations in the abundance may be more easily measured than nearer the centre of distribution, and interest in the intertidal barnacles *Chthamalus* and *Semibalanus* has been the observed correlation with temperature. The SST data for the English Channel in Fig 2.5 shows that there was a general increase in sea temperature between 1920 and 1960 followed by a period of cooling. This was most marked during the 1970s to about 1981, since when there has been another rise in temperature. From the quantitative evidence contained in earlier work (Fischer-Piette, 1936; Southward & Crisp, 1956) and observations since, the following changes in boundaries within the Channel were inferred (Crisp *et al.,* 1981):

a) Between the 1930s and 1951, *Chthamalus* advanced eastwards from St. Albans Head near Swanage in Dorset to the Isle of Wight, where the most easterly record was at Bonchurch near Ventnor.

b) Between 1930s and 1949-51, *Semibalanus balanoides* retreated eastwards from the south coast of Cornwall.

c) Between 1962 and 1979 there was a considerable fall in numbers of *Chthamalus* on the English side of the Channel, which was most marked east of Portland and on the Isle of Wight.

Earlier, Southward & Crisp (1956) refuted the view held by Moore & Kitching (1939) that the abundance and distribution of *Chthamalus* was related to a beneficial effect of Atlantic water, as the density of *Chthamalus* in Cornwall had risen between 1930 and 1950 when there had been no corresponding increase in the proportion of water of Atlantic origin.

From the results of this current work, *Chthamalus* appears to have again increased in density, supporting the view that temperature is crucially important in determining species distribution and abundance. Moreover, when the long-term time series are examined there are strong inverse relationships between the abundance of *Chthamalus* and that of *S. balanoides* for three different locations along the coast.

An analysis of a forty year time-series (1951-1991) from the River Yealm near Plymouth in Devon also identified a relationship between the abundance of *Chthamalus montagui, Semibalanus balanoides* and inshore sea temperature (Southward, 1991).

Counts were made at twelve tidal levels along a transect laid across the shore and maximum fluctuations were observed on the lower third of the intertidal zone. The proportion of *Chthamalus* adults at MTL and LWN was correlated with annual mean inshore temperature two years earlier, while the proportion of *S. balanoides* was negatively so correlated. The author suggests that good settlement at these levels, perhaps resulting in an earlier onset of gametogenesis, is a major factor resulting in increases in the adult *Chthamalus* population, but that other factors must also be important e.g. predation by dog-whelks. The author also points out that the survival of *Semibalanus* juveniles was noticeably higher during the cooler periods 1963-64, 1973-74, and 1974-80. Similar data published for Wembury shore near Plymouth also shows comparable relationships between the abundance of *Chthamalus* and *Semibalanus* (Southward *et al.*, 1995) with peaks in *Semibalanus* coinciding with the cooler period between the late 1960s and late 1970s.

In this work the Warm Index, calculated using data from three shores, was significantly correlated with Channel sea surface temperature one year earlier (Fig.3.36; Table 3.4) indicating that warmer years would appear to sufficiently favour recruitment of *Chthamalus* to be revealed in counts the following year. The precise mechanisms are uncertain but it could be due to:

a) an earlier onset of gametogenesis which would yield a higher production of planktonic larvae.

b) a greater survival of planktonic naupliar and/or cyprid stages due to temperature alone or because of a better match between naupliar abundance and food abundance within the water column.

c) the greater onshoreness of winds (sea breezes) and more stable water column often associated with warm summer periods.

The decline in *Semibalanus* abundance during warmer phases has been assumed to be due to the greater desiccation of young spat, as shown by studies by Kendall *et al.*, (1985). As yet, attempts to show any failure of gonad or larval development in warmer waters has failed. However a succession of warmer summers might also have the effect of so increasing the *Chthamalus* population that space availability at MTL and HWN for *Semibalanus* recruits diminishes. The annual larval production from the increasingly smaller adult population, now only surviving at lower tidal levels, would therefore also decline. The pre-emption of longer-lived *Chthamalus* may influence larval output of *Semibalanus* for several years, resulting in periods of low adult density.

The contribution made by the strongly positive North Atlantic Oscillation phase to the recent high SST in the Channel is undoubtedly a strong one. The correlation between SST and the North Atlantic Oscillation (NOA) was very significant (Table 3.4). The relationship between the barnacle Warm Index and the winter NAO one year earlier was also statistically significant. However as Larkin (1970) warns, "Virtually any set of stock-recruit data is sufficiently variable to inspire hypotheses about the effects of trends in environments, especially with the wealth of meteorological and oceanographic data that can be mined for real and fortuitous correlation's."

The biological effects of previous climatic changes have been well reviewed by Cushing & Dickson (1976) who discusses the many and various periodicity's that have been observed with particular reference to fish stocks. The Russell Cycle (Russell, 1973) shows an apparent correlation between the macro-plankton present in the western approaches to the Channel and winter phosphorous levels between 1930-1970; during the 1930s both decline and were at low levels until the early 1960s, when a rise comparable with the earlier observations was detected.

Southward *et al.*, (1975) detected a secular trend in warming that peaked about 1945, when catches of hake and of summer pilchard eggs were correlated positively with the short term trends, whereas catches of cod and of autumn pilchard eggs were correlated negatively. A change therefore occurred in the abundance of warmer water species to more Boreal forms and a shift in pilchard spawning from summer to autumn during the cooler period. Since 1970 there has been a period of relative instability in spawning intensity (Southward *et al.,* 1995). Southward's interpretation of the period between 1930 and early 1970s was therefore a more general one that states that with an increase in temperature in the waters of the western Channel, considerable changes in species distribution occurred. The earlier methodology used in the measurement of phosphorus levels upon which Russell based his cyclical hypothesis, has recently been questioned (Joint *et al.*, 1997) and cross calibration using new techniques indicate that the nutrient data suggest a more random pattern.

According to Southward *et al.*. (1995) southern species abundance's greater than those observed in the 1950s are necessary to show "conclusively" a marine biological response to global warming. Current monitoring shows that these levels have not yet generally been exceeded, although mean shore adult population densities of *Chthamalus* at Brixham in 1996, following good recruitment in 1995, were the highest recorded in the time-series. Densities have since dropped. The time-series for Osmington Mills is more intermittent, however recent measurements since 1994 have shown a steady increase in mean shore abundance, particularly at upper and middle levels (see Chapter 5 Fig. 5.37). Unfortunately, no measurements of species density were obtained immediately following the exceptionally hot summers of 1989 and 1990. Hawkins (pers.comm) noted recent settlement of *C.montagui* during visits to Brook in 1986 and St.Catherine's Point in 1993. However over the past five years monitoring, large inter-annual fluctuations in abundance have been measured at most sites. If populations of *Chthamalus* are going to significantly increase east of Portland then the frequency of 'good' recruitment years must become greater to offset population mortality.

Southward *et al.*, (1995) also report on the changes in population size of the limpet *Patella depressa* and topshell *Osilinus lineatus*. Although not as complete as the barnacle time-series, data collected by S.J. Hawkins on *Patella depressa* from Dorset and Devon since 1980 and Southward between 1950s and 1980s, correlate well with temperature. The species formed a higher proportion of the mid-shore limpet population in the warmer 1950s than in the cooler 1960s & 70s, when *P. vulgata* was very much more dominant. In the early 1980s *P.depressa* was still relatively uncommon. Yet at Duckpool and at Bude in North Devon there had been a marked increase in density during the late 1980s and early 1990s. At Portland Bill, populations have still not reached levels observed in the 1950s, although further to the east, at Peveril Point near Swanage, there has been a greater recovery. *Osilinus* also appears to have been more abundant during the warmer periods, possibly as a result of increases in recruitment.

Estimates of the proportion of *P. depressa* in the total midshore limpet population made in 1995 were comparable with, but less than, those presented for Swanage, Portland Bill and Lyme Regis in Southward *et al.*, (1995, Fig. 17.). This could be due to inexperience in identification or within-site variability. The estimates for the Isle of Wight sites were between 10 and 20%, which is consistent with the upward trend apparent from the published graphs.

Evidence from Bronze Age, Iron Age and Roman middens suggests that these southern molluscan species were prevalent on the Isle of Wight during these periods. Preece (1993) records the presence of *Osilinus lineatus* (as *Monodonta*) in Bronze Age deposits from the south of the Isle of Wight. Recently, several specimens of *Osilinus*, *Gibbula umbilicalis*, *Patella depressa* and *P. ulyssiponenis* have been brought to me from a Roman midden deposit near St. Catherine's Point by Mr. K.Trott. Clearly there may have been large populations of these species on the island during that period.

The size-frequency data for *Chthamalus* populations indicate that in Devon and Dorset there appears to be evidence of recent recruitment and growth to adult stages at all tidal levels. However at Hanover Point on the Isle of Wight, there is very little evidence of recent recruitment on the upper and middle shores, although a tri-modal distribution is just about discernible at the higher level. On the lower shore, small individuals dominate the population, which either infers recent recruitment, a failure to grow to adulthood or both. Possible causes might either be predation, competition for space by other barnacle species, limpet bulldozing or a combination of factors. Several workers point out that *Chthamalus* settlement is higher on the lower levels and thus a larger proportion of smaller individuals are more likely here (Kendall & Bedford, 1987; Burrows,1988). But the presence of adults on the middle and higher levels of the shore indicates a tolerance to high summer temperatures and frost damage in winter. From their size and weathered appearance of the shell plates, many of these individuals look very old, so are likely to have been present for several years. Similar characteristics are apparent within the eastern populations of *Gibbula umbilicalis*. The dominance of large individuals is very evident within the relatively small populations at Freshwater Bay and at Bembridge. Studies of *G. umbilicalis* at the extreme northern limits in Scotland (Kendall & Lewis, 1986) also found that populations were characterised by larger individuals and suggest that density-dependent competition is important in influencing the size/age structure of gastropod populations here.

It would appear from the observations of current distribution and size-frequency measurements that the eastern limits of distribution are due to re-population failure rather than survival of the adult stages. The only exception being populations of *Chthamalus* on the lower shore, which are lacking in adults. It is possible that a failure to develop gonads, and thus to successfully reproduce, is an important factor in the eastern Channel that is exposed to lower winter temperatures. The reproductive biology of these species seems worthy of further study and is explored in the next chapter.

Chapter 4

Reproduction of *Chthamalus montagui* and *Balanus perforatus* along the south-coast of England

4.1 Introduction

Although recognised as being of crucial importance by Appleöff (1912), the significance of sea temperature in determining the breeding period of marine animals and its relationship with species distribution was first discussed by Orton (1920). Through a review of the literature and by experimental work on the seasonal growth and development of sexual maturity in marine animals, he concluded that breeding, defined as fertilization resulting in subsequent development, is dependent on some kind of temperature stimulus, such as the attainment of a minimum temperature. He also proposed that should sufficient information on the physiological tolerances of species also be available, then it would be possible to map their geographical distribution.

One of the key areas to be examined is the reproductive capability of species as the geographic limits are approached. It could just be that temperature, food supply or some aspect of water chemistry reduces the efficiency, delays or even interferes with the necessary processes of gonad development, copulation, fertilization and development of embryos. For *Chthamalus* there is every good reason to believe that successful development will occur. The translocation experiments by Crisp (1950) demonstrated that *Chthamalus* '*stellatus*' could survive the winter and produce normal nauplii outside its existing geographic range on the coldest parts of the Northumberland coast at Whitley Bay and in north Norfolk. Earlier work on the south-west coast of England by Bassindale (1936) and Moore & Kitching (1939) concluded that *Chthamalus* '*stellatus*' was a southern species that bred during the summer in northern Europe. There are other well documented accounts of the reproductive biology of *Chthamalus* '*stellatus*' close to the northern limit of its range in Scotland (Barnes,1956; Barnes & Barnes,1965,1968; Lewis, 1986). At Aberystwyth, on the west coast of Wales, Kendall & Bedford (1987) found that individuals of *Chthamalus montagui* were brooding embryos between mid-May and the end of August. More recent work on *C. montagui* and *C. stellatus* at Plymouth in Devon (Burrows, 1988; Burrows *et al.*, 1992) and south-west Ireland (O'Riordan, 1992; O'Riordan *et al.*,1991,1992) found that both these species have almost identical summer brooding periods, ranging between late April and early October in both areas, and exceptionally earlier in Ireland. Moreover, both authors found evidence of multiple brooding in both species with the number of broods dependent on age, level of the shore and degree of wave exposure. Lewis (1986), commenting on multiple brooding in *Chthamalus*, suspects that at the species' northern limit in Scotland only a single brood is possible, succeeding only in warm summers.

Also of importance is the evidence of self-fertilization that has been observed in the genus *Chthamalus* (Barnes & Crisp, 1956; Barnes & Barnes, 1958). Crisp *et al.*, (1981) suggest that the capability to self-fertilize could be especially important in the maintenance of barnacle populations where densities are very low, such as at the limits of distribution. The viability of apparently self-fertilized egg masses was found to be reduced, although they can be capable of full development and hatch to give swimming nauplii (Barnes & Crisp, 1956).

Barnacle larvae pass through six naupliar stages before metamorphosis to the non-feeding cypris stage (Darwin,1854; Southward (ed.), 1987; Anderson,1994). There is evidence that the pelagic stage of *C.stellatus* is longer than that of *C. montagui* (Burrows,1988; Burrows *et al.*, 1999b). In cultures, 50% of *C.montagui* nauplii reached Stage V in 8-10 days, with the longest development period at the coolest temperature. Estimates for *C stellatus* indicated a longer naupliar development period that up to Stage V was 45-70% greater than *C. montagui* (Burrows *et al.*, 1999b). Burrows (1988) estimated that between 17.6 °C and 22.6 °C it would take 14-18 days for 50% of *C. montagui* larvae to reach cypris stage and 22-31 days for 50% of *C.stellatus* larvae.

Compared to *Chthamalus*, there has been relatively little research on the reproductive biology and larval settlement of *B.perforatus* and successful reproductive development at the eastern geographic limits is more uncertain. Norris & Crisp (1953) refer to animals found growing on exposed locations close to their distributional limits as small and sterile, including localities on the Hampshire and Isle of Wight coast. However at Torbay in south Devon, the authors did observe fertilized egg masses in the mantle cavity between mid-June and August. Egg development was rapid and nauplii were liberated into the plankton in late June, with settlement commencing in late July and continuing through August and into September. Further observations at Barnstaple Bay on the north Devon coast indicated a slightly later onset of breeding. The authors go on to infer that larvae of *Balanus perforatus* should not be present in plankton hauls taken north of Aberystwyth on the Welsh coast, in the North Sea or in the Channel east of the Isle of Wight. Barnes & Crisp (1956) found evidence for self-fertilization, which could be important as isolated individuals are common on the open shore and within clumps of dead barnacles. Through serial sampling of a population from the Gower peninsula in Swansea in South Wales, Patel & Crisp (1960a) suggested that *Balanus perforatus* probably had more than one brood annually. As the authors point out however, the methodology is less than conclusive as it is assumed the broods develop synchronously throughout the population, which has mixed age classes.

In the Mediterranean, Lepore *et al.*, (1979) found that animals which had a minimum basal diameter of 1cm contained mature gonads throughout the year, although multiple broods were unconfirmed. The major brood release was in August and maximum settlement in September. Barnes & Klepal (1971), sampling at Arcachon in southern Brittany, suggest that the species does have multiple broods and that the spermatozoa mature while the eggs of one brood are developing and the ova of the next are being produced.

It appears fundamental then, that for both species, the ability to produce nauplii at the Channel limits needs to be ascertained. Moreover, the period over which brooding can occur also requires investigation. Crisp (1950) suggested that in the UK, fertilization of *Chthamalus 'stellatus'* occurs right up to the limit of distribution wherever individuals are sufficiently close together, and that brooding commenced later with increasing latitude and with easterly longitude. If proven, this might limit the number of broods produced annually and therefore the fecundity of *Chthamalus* as the eastern limits are approached.

The specific aims of this chapter are:-

i) to determine whether species at their eastern geographic limits develop gonads and produce viable larvae.

ii) to ascertain whether brood size decreases as the eastern limits are approached.

iii) to establish whether there is any delay in the onset of brooding as the eastern limits are approached.

iv) to determine whether brooding occurs earlier in warmer years.

4.2 Methods

4.2.1 Reproduction of translocated *Chthamalus montagui* at Bembridge, Isle of Wight.

To establish whether the species is able to breed at the extreme eastern edge of its range in the English Channel, where it is exposed to colder winters, small numbers of barnacles were translocated to the species limit at Bembridge on the Isle of Wight. In November 1994, small rock chips bearing adult *Chthamalus montagui* were removed from mid-tide level at Shoalstone beach near Brixham in Devon, where the species is extremely abundant, and within 15 hours were glued to the shore at mid-tide level at Bembridge, using *WetWork* resin (SP Systems, Newport, Isle of Wight) which cures underwater. The barnacles were kept moist during transit by laying seaweed over the rocks and leaving them immersed in seawater overnight.

In January 1995, and thereafter at monthly intervals, a few of the translocated rock chips were removed from the shore at Bembridge and taken to the laboratory. Within four hours of collection, animals were separated from the rock chips with a scalpel, and gonad development was scored according to the scale described by Crisp (1954) and modified by O'Riordan (1992), (Table 4.1). Only contiguous groups of barnacles were included, with the assumption made that copulation and cross-fertilization could have occurred between adjacent individuals. The barnacles were examined under a stereo binocular microscope at x30 magnification. It was sometimes necessary to remove ovarian tissue for closer examination under higher magnification using a monocular microscope. Samples taken between May and September contained brooding individuals and the stage of development of each brood was determined using the score system in Table 4.2, devised by Achituv & Barnes (1976) and utilised subsequently by Burrows (1988) and O'Riordan (1992). Embryos were also compared with illustrations shown in Groom (1894). The minimum sample size necessary to obtain a reasonable mean gonad index and estimate of percentage brooding embryos was determined graphically by plotting a running mean index against number of barnacles examined (Fig 4.3). Results showed that fluctuations were sufficiently reduced after the examination of 40 barnacles. The basal diameter (R-C axis) and opercular diameter (T-S axis) was also measured under a microscope using an ocular micrometer to ensure that subsequent samples of barnacles were comparable in size. The presence of parasites or cysts in the mantle cavity was noted. The mean indices of 40 barnacles were then calculated to determine the stage of development of the sample.

To determine whether the *WetWork* resin had any effect on the reproductive behaviour of the barnacles, rock chips were also stuck down on the shore in Devon and examined the following May, when their reproductive development was compared with that of the undisturbed population on adjacent rock.

Table 4.1 Gonad condition scoring criteria based on Crisp (1954) and modified by O'Riordan (1992).

Male Development:

<u>Testes</u>

0. Absent.
1. Poorly developed, visible only on dissection or teasing out.
2. Moderately developed, occupying a small part of the body and just visible through the cuticle, transparent to slightly white/opaque in colour.
3. Well developed, occupying much of the body cavity and clearly visible from the outside, transparent to slightly white/opaque in colour.

<u>Vesiculae seminales</u>

0. Absent or present as thin strands of tissue.
1. Thin linear sacs with little sperm.
2. Moderately developed; sacs cylindrical of diameter about equal to that of the gut, clearly visible through the cuticle, opaque white in colour.
3. Well developed, sacs large and bloated exceeding diameter of gut, seminal fluid readily expelled, opaque white in colour.

Female Development:

<u>Ovary</u>

0. Absent, no ovary or eggs visible.
1. Poorly developed, rudimentary ovary, grey to off-white in colour, only a thin layer in the basal membrane, eggs minute, few cells, normally grey-orange in colour.
2. Moderately developed, filling about a third of the mantle cavity, eggs multicellular, having a smooth fatty appearance, but not of full size nor completely filling the tubules, orange in colour.
3. Well developed ovary filling the greater part of the mantle cavity, eggs with a clearly defined shape, often rounded or slightly oval, orange in colour and filling the ovarian tubules.

Table 4.2 Stages of barnacle embryonic development after Achituv & Barnes (1976).

1. Early development from newly laid to few cells.
2. Multicellular.
3. Limb Buds appear.
4. Nauplius eye present.

4h. Nauplii hatch on disturbance of mantle cavity.

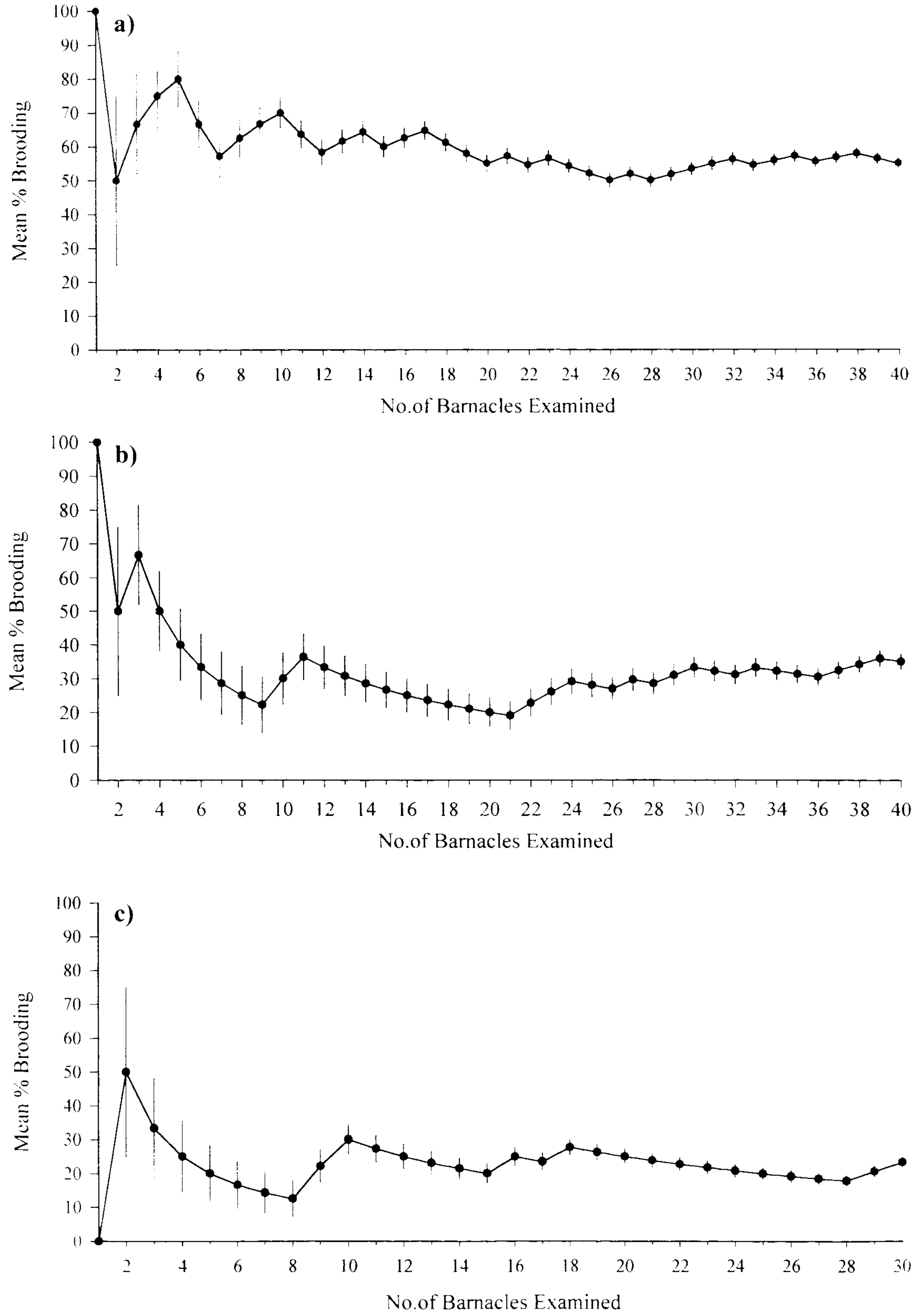


Fig.4.1 Determination of minimum number of barnacles requiring examination to obtain reasonable estimate of percentage brooding. a) *Chthamalus montagui* 14/5/95 at MTL from Kimmeridge; b) *C. montagui* 20/5/95 at MTL translocated to Bembridge; c) *Balanus perforatus* 15/9/95 at LWN translocated to Bembridge. Error Bars show ± SE. For *C. montagui* major fluctuations of running mean diminish after examination of 30 individuals and for *B. perforatus* about 20.

4.2.2 Variation in the stage of reproductive development of *Chthamalus montagui* at sites along the south coast of England between Devon and the Isle of Wight.

In mid-May of 1995, 1996, 1997 and 1998, rock chips colonised by adult *Chthamalus montagui* were obtained from mid tide level at seven sites along the south coast of England between Torbay in Devon and Kimmeridge in east Dorset. Barnacles translocated from Torbay to Bembridge on the Isle of Wight the previous autumn (4.2.1 above) were also removed. In 1995, 40 barnacles in each sample were scored for gonad development, the % brooding embryos and the stage of embryonic development (Table 4.1 & 4.2 above). Between 1996 and 1998, two samples of 40 barnacles were obtained at MTL but from different areas of the shore to assess the variability of reproductive development within each site. Ideally, all samples should have been taken on the same tide, however this proved logistically impossible. The order in which sites were visited was often dictated by prevailing weather conditions, especially around Portland Bill, but so as to overcome any temporal bias in the sampling programme, attempts were made to avoid collecting from east to west. The time difference between examination of the most western samples from Torbay and the most eastern sample at Bembridge was 15 hours. All samples were examined and reproductive development scored within 4 hours of collection.

4.2.3 Brood size of *Chthamalus montagui* from different sites along the south coast of England.

In mid June 1996, ovigerous lamellae were removed from barnacles taken from mid tide level at Shoalstone, Portland Bill and Bembridge. The embryo masses were placed in a few drops of seawater contained within a Sedgewick raft cell, to which was then added a drop of concentrated hypochlorite to break the retaining membrane and release the embryos. The hypochlorite was rendered inactive by the addition of a few drops of Sodium thiosulpate solution. The number of embryos within the brood was then counted under a stereo binocular microscope. With large numbers of embryos, a sub-sample was taken by counting the number of embryos along twenty rows of the raft cell, and with subsequent multiplication an estimate was obtained of the total number of embryos in the brood. The tergal-scutal diameter of the operculum of each barnacle was measured and the somatic tissue, excluding adductar muscle, was retained and temporarily preserved in 70% IMS. The somatic tissue samples were then dried in an oven for 72 hours at 80 ^{o}C before weighing. Dry weights were then correlated with opercular diameter and the number of embryos the barnacles contained. The brood size for a 'standard barnacle' of 0.5mg dry weight was then determined graphically using Type 1 linear regression model.

4.2.4 Assessment of brooding in isolated and contiguous *C.montagui* at Colwell Bay, Isle of Wight.

To establish whether there was any local evidence for self-fertilization in *C. montagui* a brief assessment was made at Colwell Bay, at the western end of the Isle of Wight, during the middle of the breeding season. On 11th June 1998, 40 contiguous and 40 isolated individuals of adult *C. montagui* were carefully removed from the surface of concrete boulders near HWN tide level. Here, populations were considered sufficiently large enough for removal of specimens. Isolated individuals were at least 5cm from nearest conspecific; maximum penis lengths for *C. montagui* were found to be about 12mm (O'Riordan, 1992). Contiguous individuals were those whose plates were in contact or fused with each other. Animals were placed in glass vials and frozen for later examination. The condition of the gonads and developmental stages of embryos was scored using the criteria shown in Tables 4.1 and 4.2.

4.2.5 Reproduction of translocated *Balanus perforatus* at Bembridge, Isle of Wight.

In November 1994, small boulders and cobbles densely colonised by *Balanus perforatus* were removed from LWN on Broad Ledge at Lyme Regis, and placed in buckets of seawater. Two days later, the boulders were wedged into rock crevices at LWN at Bembridge, Isle of Wight. While in transit, the seawater in the buckets was changed daily. In January 1995, and at monthly intervals thereafter, one or two boulders were taken back to the laboratory and barnacles removed from the rock with a robust scalpel or pen knife, and the basal diameter (R-C axis) measured with verniar callipers. For the larger individuals, the calcareous base of the shell was carefully chipped away with a scalpel to reveal gonads and any ovigerous lamellae. With the smaller animals, the whole body including gonads, ovigerous lamellae and valves could be successfully removed by pushing a blunt seeker into the aperture and out through the thin calcareous base. Barnacles were scored for gonad stage, and if brooding, embryonic development according to criteria in Tables 4.1 & 4.2 above. Illustrations shown in Groom (1894) were also useful. By plotting mean gonad index against number of barnacles examined, the minimum sample size necessary to obtain a reasonable estimate of mean gonad index was obtained. From Fig 4.1, fluctuations are sufficiently reduced after the examination of between 18 and 25 animals. A minimum number of 20 animals were examined thereafter. In October 1995, a further quantity of boulders with *Balanus perforatus* were translocated from Lyme Regis to Bembridge to assess for a second year the peak percentage brooding and to determine brood size.

4.2.6 Brood size of *Balanus perforatus* at Bembridge and Lyme Regis.

In mid-August 1996, ovigerous lamellae were removed from barnacles taken from Lyme Regis and those translocated from Lyme Regis to Bembridge the previous October. The embryo masses were placed in a few drops of seawater contained within a Sedgewick raft cell to which was then added a drop of concentrated hypochlorite to break the retaining membrane and release the embryos. The hypochlorite was rendered inactive by the addition of a few drops of Sodium thiosulpate solution. The number of embryos within the brood was then counted under a stereo binocular microscope. With large numbers of embryos, sub-samples were taken by counting the number of embryos along twenty rows of the raft cell, and with subsequent multiplication an estimate was obtained of the total number of embryos in the brood. The basal diameter of each barnacle was measured and the somatic tissue, excluding adductar muscle, was retained and temporarily preserved in 70% IMS. The somatic tissue samples were then dried in an oven for 72 hours at 80 °C before weighing. Dry weights were then correlated with basal diameter and number of embryos the barnacles contained. The brood size for a 'standard barnacle' of 3mg dry weight was then determined graphically using Type 1 linear regression model.

4.3 Results

4.3.1 Reproduction of translocated *Chthamalus montagui* at Bembridge, Isle of Wight, in 1995.

Shortly after gluing the barnacle encrusted rocks on to the beach in October 1994, it became evident that a considerable loss of animals would occur due to erosion of the broken barnacle matrix, and by November 1995, only 15 individuals remained on the translocated rocks. Consequently no barnacles were scored for gonad development in December 1995. Graphs showing the seasonal change in female and male gonad development and production of embryos during 1995 are presented in Fig 4.2. The mean gonad index was calculated and compared with work from other localities (S. Ireland, O'Riordan, 1992; Plymouth, Burrows, 1988), although with numerical score systems of this nature, the median or modal score may be more appropriate. The ovaries developed simultaneously with the male gonads, and fully developed eggs (Stage 3) were present in the ovarian tubules between May and July (Fig.4.3) and also in October (3% of sample). Fully developed testes (Stage 3) were first observed in March, when they were present in 5% of the sample, and by May this was characteristic of all barnacles scored. By September, 20% were at Stage 3, but none were seen to be fully mature thereafter. The development of the vesiculae seminales appeared to be slightly behind that of testes but by June, those of all individuals appeared to be mature and readily expelled seminal fluid. The proportion of the sample with Stage 3 vesiculae seminales dropped slowly from June onwards, yet were still observed in 3% of sample in October.

Embryos deposited in to the mantle cavity, as a pair of 'ovigerous lamellae', were first observed in May, when they were present in 33% of the sample, and were seen in subsequent months until September. Yet as part of another study, the examination of 1994 cohort specimens (translocated on a piece of slate and also fixed to the shore in autumn 1994) revealed one brooding individual with Stage 4 embryos on 12th October 1995. Of all brooding individuals examined, only one brood, seen on 15th September, had a single ovigerous lamella. Stage 4 embryos were first seen in May when they were observed in 3% of the sample, and those at the hatching stage, releasing nauplii upon disturbance of membrane, were observed during July and August (10% and 5% of sample respectively).

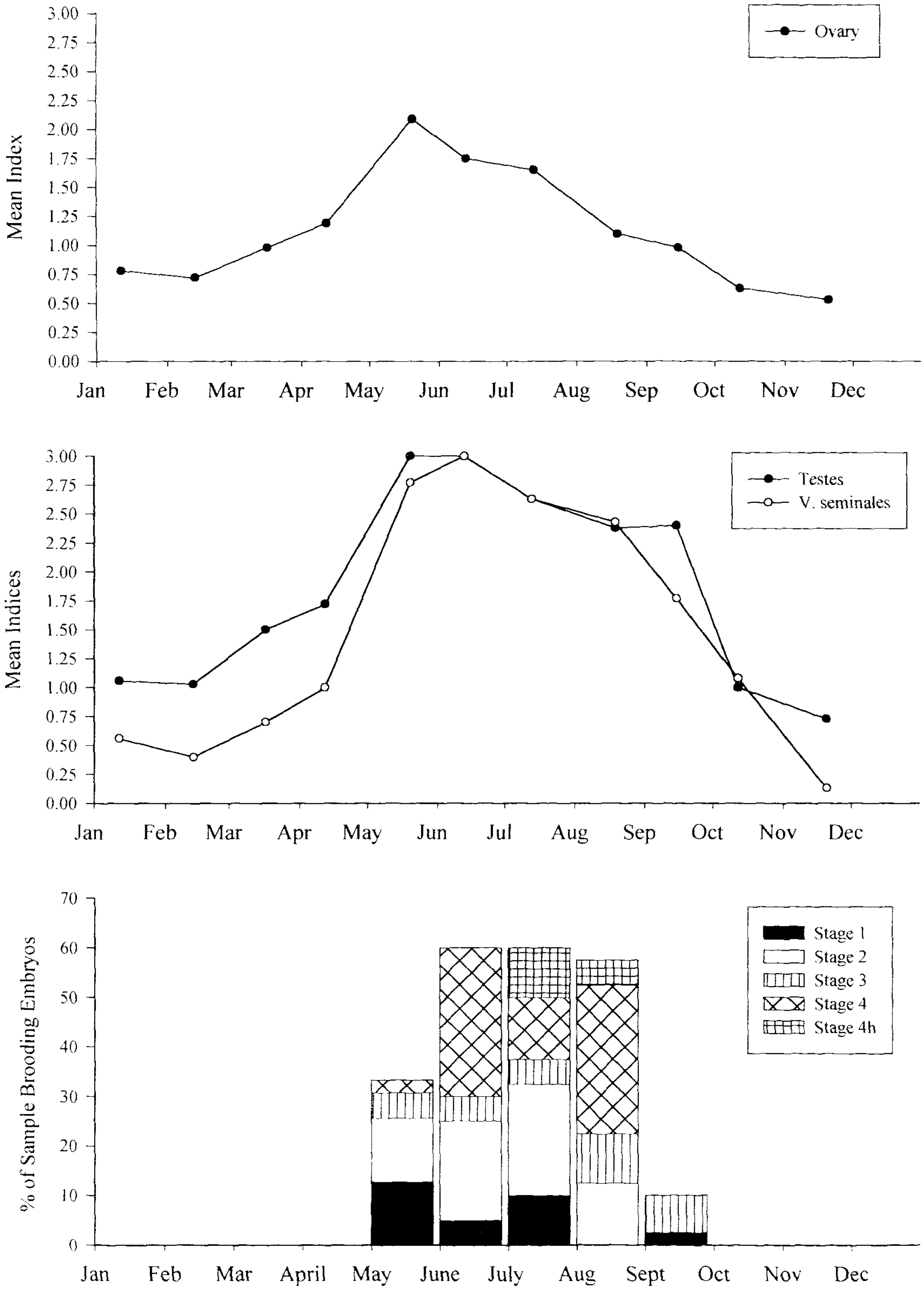


Fig.4.2 Seasonal development of gonads and embryos in *Chthamalus montagui* during 1995. Animals translocated to Bembridge, Isle of Wight in October 1994.

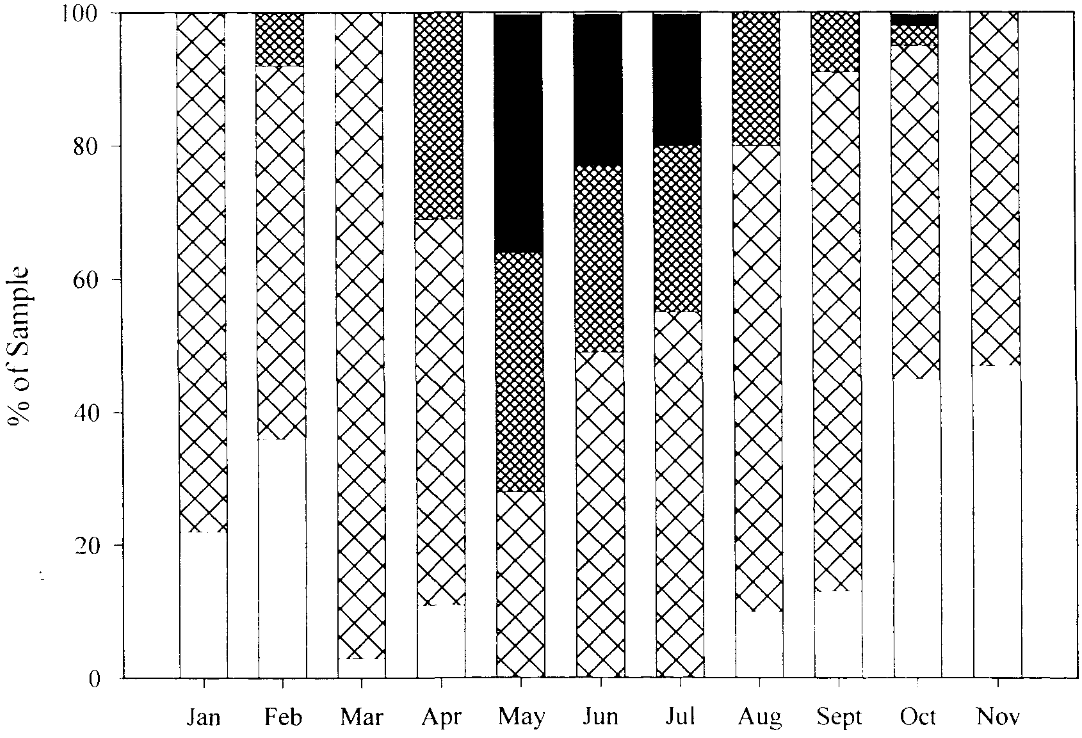
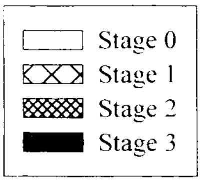


Fig.4.3 Stages of ovarian development within translocated *C.montagui* at Bembridge, Isle of Wight, in 1995.



Stage 3 embryos, which have limb buds, were relatively uncommon. This either indicates a failure to differentiate adequately from those at Stage 2, or that this stage is of short duration. None of the barnacles examined had cysts, but the occasional nematode worm and copepod were seen in the mantle cavity.

4.3.2. Variation in the stage of reproductive development of *Chthamalus montagui* at sites along the south coast of England between Devon and the Isle of Wight.

Having established in 4.3.1 that embryonic development is possible right up to the current eastern geographic limits at Bembridge, the stage of reproductive development at several sites between Torbay and the Isle of Wight was compared in mid-May between 1995 and 1998. At each site the percentage of the sample brooding embryos was calculated: since 1996 this was the mean of two samples, n = 40 (Fig.4.4).

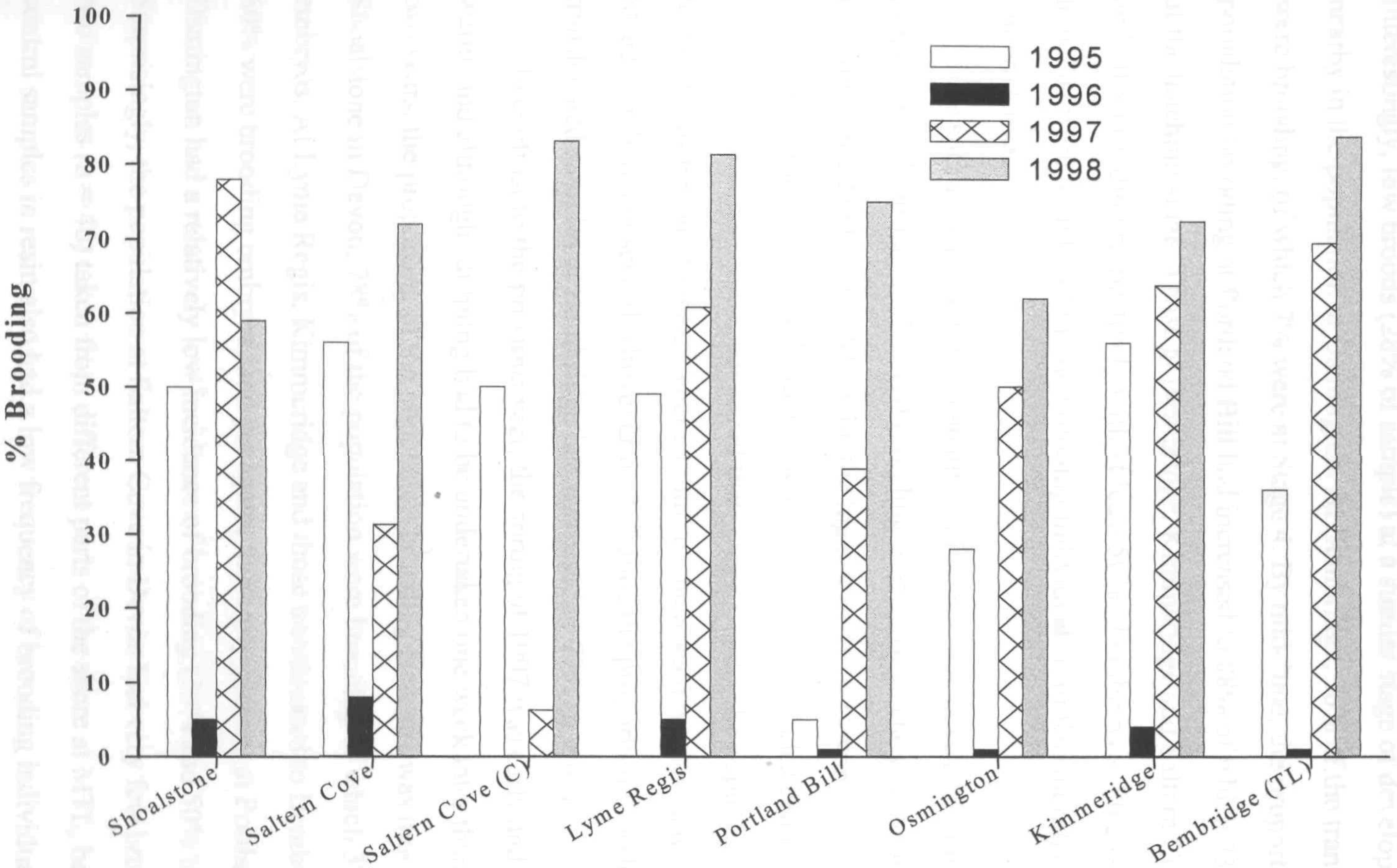


Fig.4.4 Proportion of *C. montagui* population at MTL brooding embryos in mid-late May at shores along the south coast of England between 1995-1998. Those at Bembridge were translocated (TL) from Saltern Cove. At Saltern Cove, samples were taken from both natural populations and from controls (C). These controls were lost in 1996. Estimates for 1995 were from single samples of n = 40. From 1996-1998 estimates are means of two samples, each n = 40. Sampling dates were 15-20 May 1995; 15-21 May 1996; 23-29 May 1997; 25-30 May 1998.

In 1995, the proportion of the population brooding embryos in mid-May varied between 5-56%, with populations in Devon, Lyme Regis and Kimmeridge being highest and having the largest proportions of Stage 4 embryos. The lowest value (5%) was from the end of Portland Bill, where embryonic development was not beyond Stage 2. Interestingly, few broods (28% of sample) at a similar stage of development were also seen nearby in the population at Osmington. At Bembridge, 36% of the translocated barnacles were brooding, of which 7% were at Stage 4. By mid-June, the proportion of the population brooding at Portland Bill had increased to 88% of which 23% of embryos were at the hatching stage. Those at Bembridge, Kimmeridge and Saltern Cove had 60 %, 63% and 70% brooding respectively with at least 50% of embryos at Stage 4. Single ovigerous lamellae were found within one brooding individual from Kimmeridge and one from Saltern Cove.

The spring of 1996 was unusually cold which may have accounted for the very low proportions of barnacles observed brooding in mid-May. The percentage of the population brooding varied between 1-8%, with the highest again in Devon and lowest at Portland Bill, Osmington and at Bembridge, where only 1% of barnacles examined were observed with broods and none more advanced than Stage 1. Only the population at Kimmeridge had embryos beyond Stage 2, where a third of those seen were at Stage 3. At no sites were Stage 4 embryos observed. However by 25th June the proportion brooding within the translocated samples at Bembridge had increased to 77% ($n = 65$).

In contrast to the previous year, the spring of 1997 was early and exceptionally warm, and although sampling had to be undertaken one week later than in the previous two years, the proportion of the population brooding embryos was much higher. At Shoalstone in Devon, 78% of the population were brooding of which 39% had Stage 4 embryos. At Lyme Regis, Kimmeridge and those translocated to Bembridge in excess of 60% were brooding embryos, and yet again, those populations at Portland Bill and Osmington had a relatively low incidence of brooding (39% and 50% respectively). Surprisingly, the population at Saltern Cove in Devon had very few brooding; the mean of two samples ($n = 40$) taken from different parts of the shore at MTL, being only 31%. The control samples in resin also had a low frequency of brooding individuals ranging from 0% to 12.5% (mean = 6.25%). Considering that a much a higher figure was obtained for Shoalstone beach, just 5km away, disease, parasitism or lack of food, rather than temperature is suspected to have suppressed reproductive development at Saltern Cove. Of those brooding at Saltern Cove, Stage 4 embryos were seen in similar proportions to those at other sites, but while male gonad development appeared to be progressing normally for the time of year, ovarian and egg development was very poor, with 90% of ovaries still at Stage 1 and none developed beyond Stage 2. Although looked for, there was no evidence of a higher frequency of parasitic copepoda, isopoda or nematoda.

The spring of 1998 was the warmest of the four years during which measurements of brooding frequency were determined. On all shores, with the exception of Shoalstone, the highest ever proportion with embryos was recorded. Interestingly, it was the animals translocated to Bembridge that had the highest percentage brooding (84%). These were from the 1995 cohort that had been part of growth rate studies (see Chapter 5) so most were producing embryos for the first or second season.

Of the controls at Saltern Cove, which were the same age as the Bembridge specimens, 83% had embryos. This was slightly higher than those taken from the natural population on the shore where 72% were brooding. However, although a minimum size animal (more than 4mm R-C diameter) was selected, this sample will have contained a higher proportion of older animals. Beyond two years, it is not known how the age of animal effects brooding.

To determine whether the act of fixing rock chips or plates to the shore in any way affects barnacle reproductive development, a comparison was made of the barnacles glued/fixed to the shore at Saltern Cove (controls) with those in the natural population. This was only possible with the samples from 1997 and 1998 as those to be examined in May 1996 were lost.

For samples taken in 1997 and 1998, a two-way ANOVA was carried out, using arcsine transformed data, to determine differences in the mean percentage brooding within natural populations at Saltern Cove, those fixed to the shore at Saltern Cove and those translocated and fixed to the shore at Bembridge, n = 2 samples of 40 barnacles. The results, shown in Table 4.3, indicate that while there were significant differences between 'Years' (the % brooding in 1998 was greater than in 1997), there was no significant difference in brooding frequency between those fixed to the shore at Saltern Cove in Devon and those translocated and fixed to the shore at Bembridge on the Isle of Wight ($p > 0.05$). Differences between those fixed to the shore and in natural populations could not be resolved using SNK test, however in two of the three years when comparisons could be made, the proportion of those brooding that were fixed to the shore was less than that in natural populations. If indeed the process of glueing or fixing samples onto the shore does impair reproductive development, then one might be justified in elevating the stage of reproductive development of the translocated samples at Bembridge.

Table 4.4 shows the results of a two-way ANOVA to compare the proportion of different shore populations brooding embryos in mid-May between 1996 and 1998. The data for 1995 could not be used as only one sample was taken. The results indicate that there is a highly significant difference between 'Shores' and 'Years' but that these differences are dependent upon what shore or year is considered (Year x Shore interaction highly significant, $p = 0.0007$). Because of the small number and unequal variances of the samples a Friedman non-parametric test (Sokal & Rohlf, 1995) was carried out to determine whether there were any differences between years with respect to the proportion of the populations brooding embryos. For each of the four years studied, the shores were placed in rank order of percentage brooding embryos. The result (Table 4.5) showed a highly significant difference between years ($p < 0.001$); the coolest spring (1996) and the warmest spring (1998) having the fewest and highest proportion brooding embryos respectively, when sampled in mid-late May. It was also apparent from the data that populations from Portland Bill and Osmington Mills often had a low proportion brooding embryos. A Friedman test was applied to the data to determine whether there was any difference between shores with respect to the proportion of the populations brooding embryos.(Table 4.6). However although this proved not to be significant ($p = 0.337$) the median rank of the Portland Bill and Osmington Mills populations were the lowest of the seven shores included in the analysis.

In addition to using the proportion of the population brooding embryos as an indicator of reproductive performance, the stage of embryonic development was also assessed in mid-May of each year and plotted on cumulative frequency graphs (Figs. 4.5 & 4.6). For each year, Kolmorgorov-Smirnov two-sample tests (Sokal & Rohlf, 1995) were applied to the pair of sites showing greatest differences in cumulative percentage frequency of stage of embryonic development (Table 4.7). Highly significant differences were obtained but there was no evidence of retarded development at the most eastern sites studied. In fact those commonly showing least embryonic development were populations at Portland Bill and Osmington Mills. The most eastern sites, Kimmeridge and Bembridge, generally showed either moderate or relatively advanced development.

Table.4.3 Two-way ANOVA of % brooding *C. montagui* determined at MTL in 1997 and 1998 from natural populations at Saltern Cove, those stuck to shore in resin or plates (1998) at Saltern Cove and rocks translocated and stuck to shore in resin or on plates at Bembridge. Two samples of 40 barnacles examined from each shore. Data arcsine transformed.

Source of Variation	**df**	**MS**	***F***	**P**
Year	1	0.69	11.4	0.012*
Shore	3	0.12	1.91	0.22
Residual	7	0.06		
Total	11	0.15		

SNK Tests on Years: '>' denotes significant difference. P<0.05.

Year	1998 > 1997
Mean % Brooding	79.3 > 32.5

It was also resolved that there was no significant difference between samples in resin at Saltern Cove and those translocated and fixed in resin at Bembridge (p >0.05)

Table. 4.4 Two-way ANOVA of % brooding *C. montagui* determined at MTL on seven shores along the central south coast of England in 1996, 1997 and 1998. Two samples of 40 barnacles examined from each shore. Data for 1995 not included as only a single sample taken. Data arcsine transformed.

Source of Variation	**df**	**MS**	***F***	**P**
Year	2	3.02	402.5	<0.0001
Shore	6	0.03	3.94	0.0085
Year x Shore	12	0.04	4.99	0.0007
Residual	21	0.007		
Total	41	0.17		

SNK Tests on Years; '>' denotes significant difference. P<0.05.

Year	1998 > 1997 > 1996
Mean % Brooding	72.9 > 57.1 > 37.5

The following differences between Shores were also resolved (p<0.05): Lyme Regis > Osmington Mills, Portland Bill and Saltern Cove.

Table. 4.5 Rank order 'Years' of % brooding *C. montagui* examined in mid-late May at seven sites along the south coast of England between 1995 and 1998. In 1995 only a single sample (n =40 barnacles) was examined and in subsequent years two samples. Rank 1 is highest % brooding. Onset of brooding was therefore latest in 1996 and earliest in 1998. SST is mean for April-May and is taken from HadISST1 time series (Rayner *et al.*, 2000).

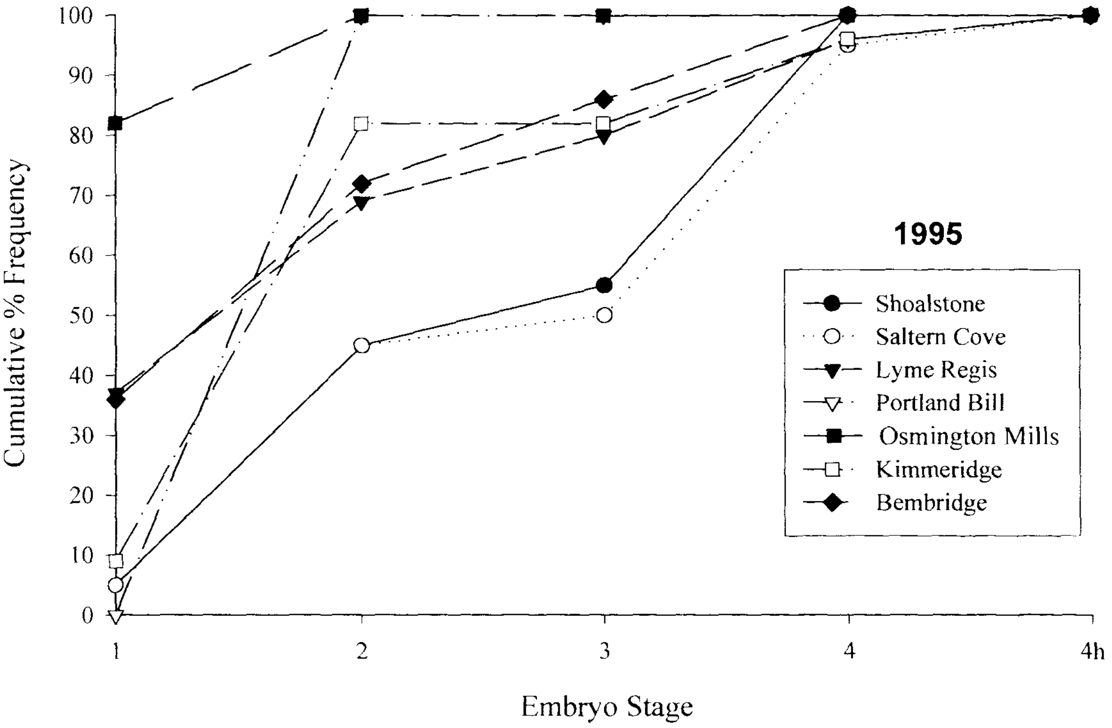
	1995	1996	1997	1998
Shoalstone	3	4	1	2
Saltern Cove	2	4	3	1
Lyme Regis	3	4	2	1
Portland Bill	3	4	2	1
Osmington Mills	3	4	2	1
Kimmeridge	3	4	2	1
Bembridge	3	4	2	1
Median	**3**	**4**	**2**	**1**
Rank SST	**2.5**	**4**	**2.5**	**1**

Results of Friedman test (Sokal & Rohlf, 1995) Null Hypothesis: ' Years have same median % brooding embryos'
χ^2 = 18.8, n = 7, df = 4, p <0.001***. Reject H_0 and accept H_1 that years differ.

Table. 4.6 Rank order 'Shores' of % brooding *C. montagui* examined in mid-late May at seven sites along the south coast of England between 1995 and 1998. In 1995 only a single sample (n =40 barnacles) was examined and in subsequent years two samples. Rank 1 is highest % brooding. Control sample at Saltern Cove omitted.

	1995	1996	1997	1998	Median Rank
Shoalstone	3	2.5	1	7	2.75
Saltern Cove	1.5	1	7	5	3.25
Lyme Regis	4	2.5	3	2	2.75
Portland Bill	7	6	6	3	6
Osmington Mills	6	6	5	6	6
Kimmeridge	1.5	4	4	4	4
Bembridge	5	6	2	1	3.5

Results of Friedman test (Sokal & Rohlf, 1995) Null Hypothesis:
'Shores have same median % brooding embryos'
χ^2 = 6.83, n = 4, df = 6, p = 0.337. Accept H_0.



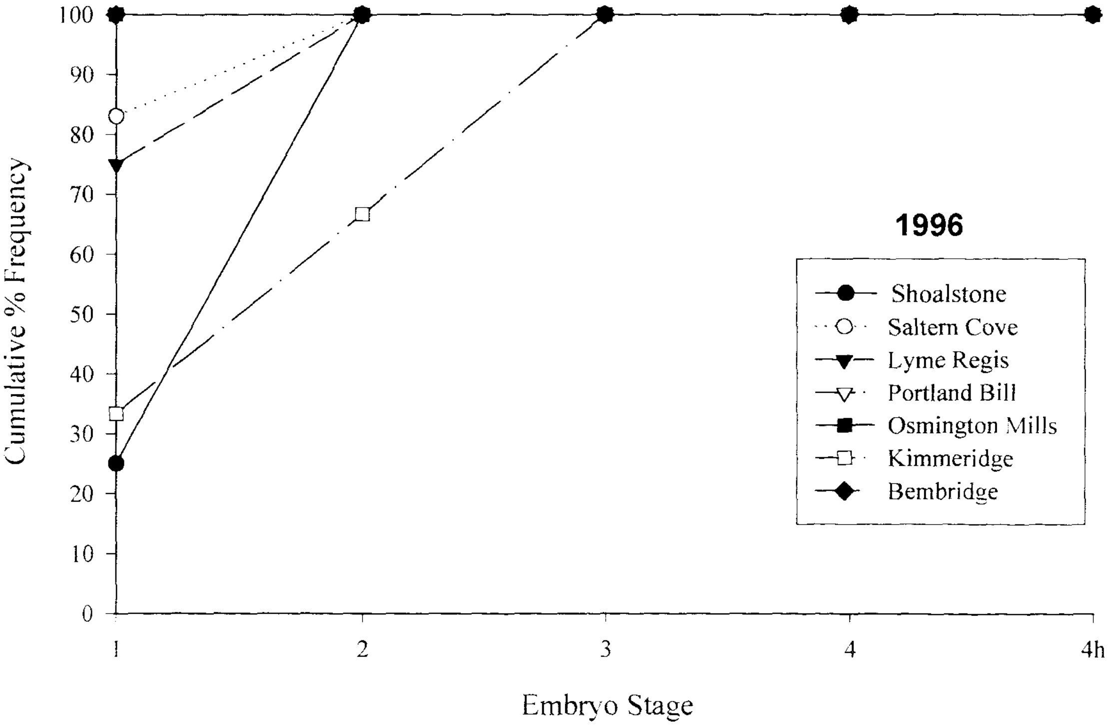
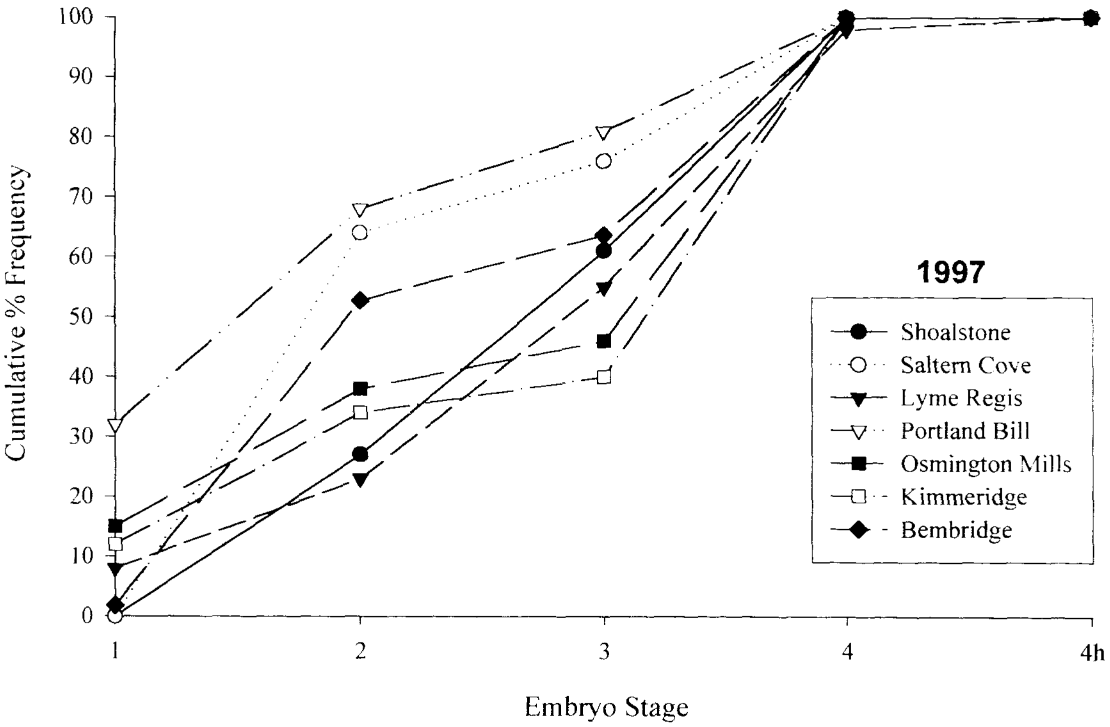


Fig.4.5 Stage of *C. montagui* embryo development at MTL at shores along the south coast of England sampled in mid-late May of 1995 and 1996.



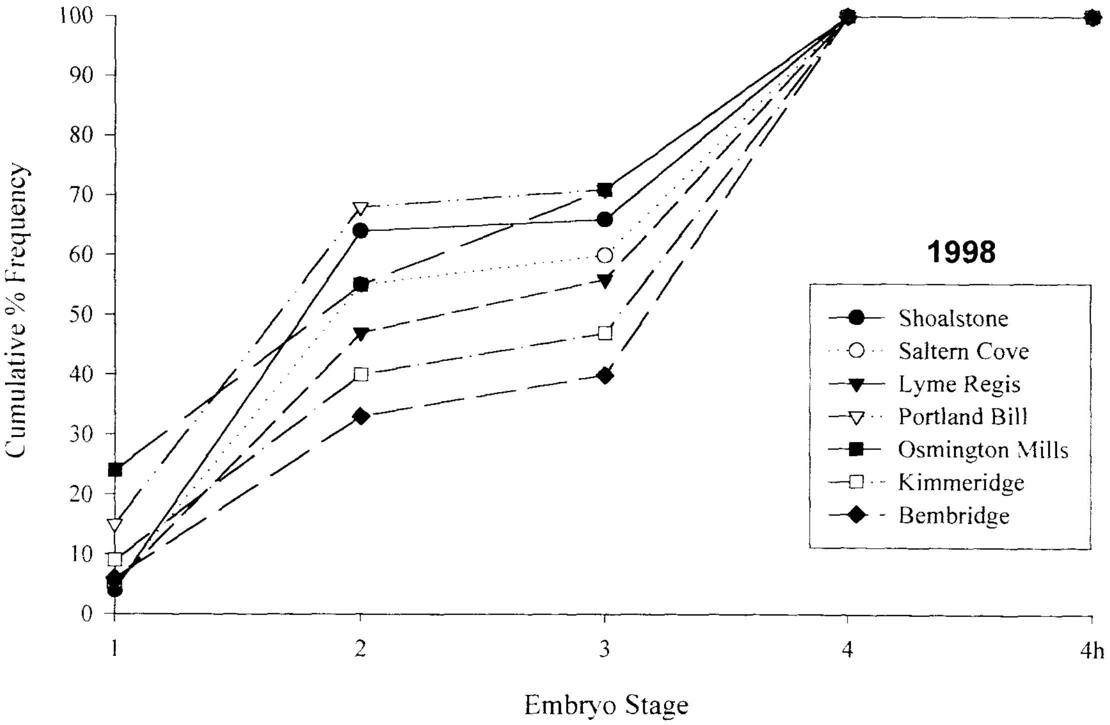


Fig.4.6 Stage of *C. montagui* embryo development at MTL at shores along the south coast of England sampled in mid-late May 1997 & 1998.

Table.4.7 Kolmogorov-Smirnov two-sample tests (Sokal & Rohlf, 1995) on stage of embryonic development of *C. montagui* from shores showing greatest differences as shown in Figs.4.5 & 4.6. Samples taken from MTL in mid-late May. In 1996 insufficient numbers in the populations were brooding embryos.

Year	**Site 1 (n_1)**	**Site 2 (n_2)**	**Maximum Difference (D) in cumulative proportions**	***P* two-tailed**
1995	Osmington Mills (11)	Saltern Cove (20)	0.77	<0.001***
1997	Portland Bill (30)	Kimmeridge (50)	0.4	0.005**
1998	Portland Bill (67)	Bembridge (59)	0.35	0.001***

Table 4.8 Kolmogorov-Smirnov two-sample tests (Sokal & Rholf, 1995) on stages of embryonic development of *C.montagui* sampled from natural populations and those fixed to the shore at Saltern Cove, Devon at MTL in mid-late May. The fixed samples were lost in 1996.

Year	**Natural Population (n_1)**	**Fixed (n_2)**	**Maximum Difference (D) in cumulative proportions**	***P* two-tailed**
1995	20	18	0.22	0.74ns
1997	25	5	0.24	0.97ns
1998	42	52	0.14	0.72ns

Table 4.9 Kolmogorov-Smirnov two-sample tests (Sokal & Rholf, 1995) on stages of embryonic development of *C.montagui* sampled from those fixed to the shore at Saltern Cove, Devon, and on rocks translocated and fixed to the shore at Bembridge, Isle of Wight at MTL in mid-late May. The fixed samples were lost from Saltern Cove in 1996.

Year	**Saltern Cove (n_1)**	**Bembridge (n_2)**	**Maximum Difference (D) in cumulative proportions**	***P* two-tailed**
1995	18	13	0.21	0.59ns
1997	5	55	0.13	1.00ns
1998	52	67	0.12	0.62ns

The effect of fixing rocks to the shore, using either resin or plates, upon the stage of embryonic development was again investigated using Kolmogorov-Smirnov two-sample tests. The results showed that there was no significant difference between frequency of embryonic stages in natural populations and those fixed to the shore at Saltern Cove (Table 4.8), or between those fixed at Saltern Cove and translocated and fixed to the shore at Bembridge, Isle of Wight (Table 4.9). All broods examined had the normal two ovigerous lamellae except one from Lyme Regis. The data from 1995 were analysed further to assess whether there was any evidence for a succession of broods and ovarian regeneration after embryos had been deposited in the mantle cavity. Table 4.10 shows the frequency of association between ovarian and embryonic stages at three sites: Torbay (Shoalstone & Saltern Cove combined), Kimmeridge and Bembridge. The data are also shown graphically in Fig. 4.7.

Table 4.10 Contingency tables showing the frequency of ovarian developmental stages with developing embryos of *C. montagui*. Samples obtained from MTL in May and June 1995.

Bembridge (Translocated)

	Ovary Developmental Stage			
Embryo	**1**	**2**	**3**	**Total**
1	9	0	0	**9**
2	8	5	0	**13**
3	1	3	0	**4**
4 /4h	5	4	0	**9**
Total	**23**	**12**	**0**	**35**

Kimmeridge

	Ovary Developmental Stage			
Embryo	**1**	**2**	**3**	**Total**
1	2	0	0	2
2	11	4	5	20
3	2	1	0	3
4/ 4h	15	3	2	20
Total	**30**	**8**	**7**	**45**

Torbay

	Ovary Developmental Stage			
Embryo	**1**	**2**	**3**	**Total**
1	9	4	0	13
2	19	4	1	24
3	6	2	0	8
4/4h	15	14	10	39
Total	**49**	**24**	**11**	**84**

Results from a Spearman Rank correlation between ovary and embryo developmental stages are presented in Table 4.11. Significant correlation's for Torbay and Bembridge provide some evidence of regeneration of ovaries and development of eggs as deposited embryos mature.

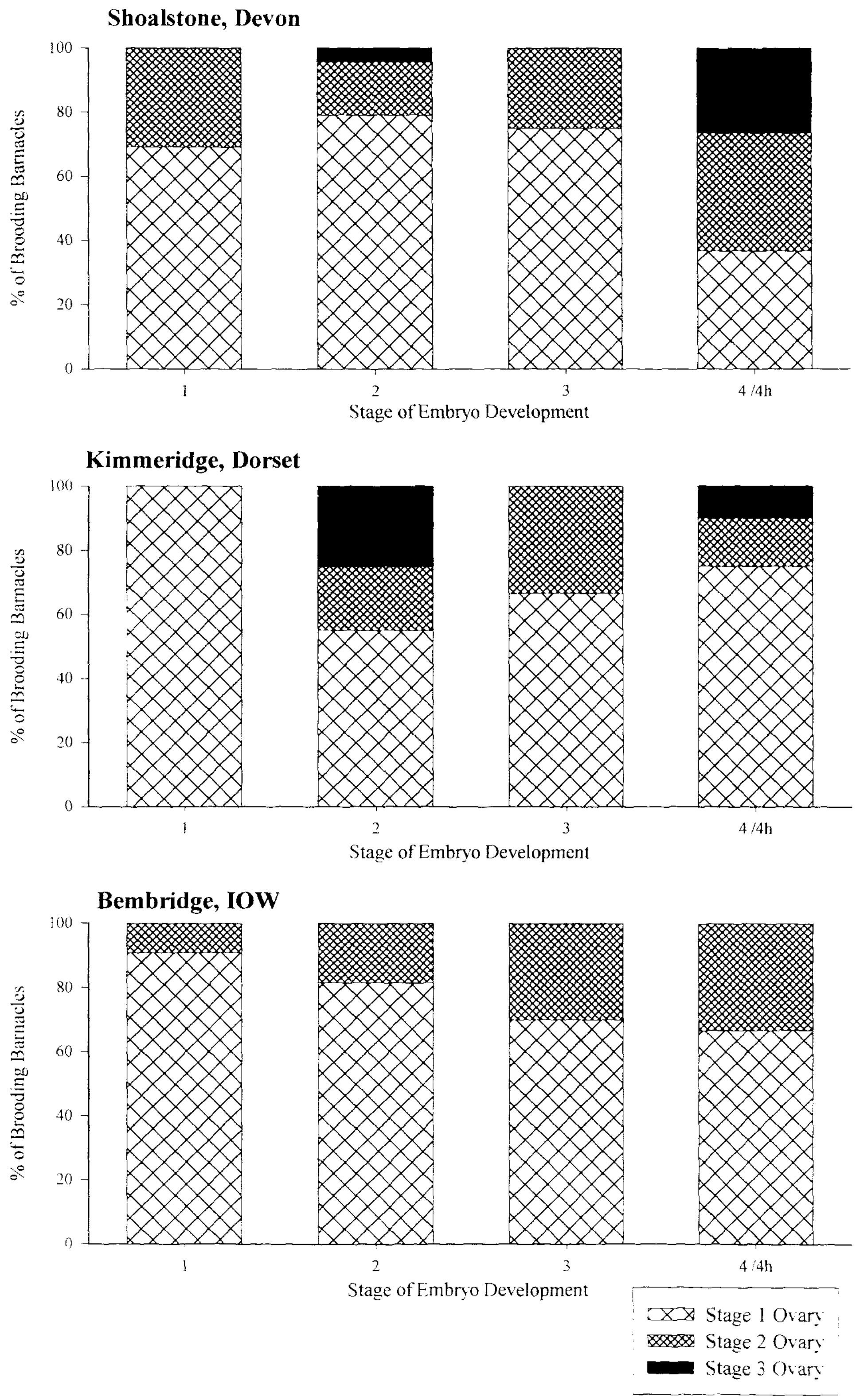


Fig.4.7 Ovarian regeneration within brooding individuals of *C. montagui* examined 14-20th May 1995 at three shores. Those at Bembridge had been translocated from Saltern Cove, Devon in October 1994.

Table. 4.11 Spearman Rank correlation between ovarian and embryonic development of *C. montagui.* from three shores.

Site	**n**	**r_s**	**p**	**Conclusion**
Torbay	82	0.4	< 0.01 **	Highly significant correlation indicating regeneration of ovaries and development of eggs as deposited embryos mature.
Kimmeridge	45	-0.138	0.36 ns	No significant correlation indicating that evidence for a succession of broods is unconfirmed.
Bembridge (TL)	35	0.38	0.023 *	Significant correlation indicating regeneration of ovaries and development of eggs as deposited embryos mature.

4.3.3 Brood size of *Chthamalus montagui* from different sites along the south coast of England

Figs 4.8 - 4.10 show relationships between body weight, opercular diameter and brood size. The opercular diameter of the sample varied between 2.1- 4.5mm and the dry mass between 0.057- 0.4mg. Animals from MTL at Shoalstone were found to have between 65-1715 embryos per brood. The sample from Portland Bill were larger animals whose opercular diameter varied between 2.5 - 5mm, but were of relatively low dry weight. Brood size was found to be between 219-1781 embryos. The translocated sample from Bembridge had an opercular diameter of between 2-4.4mm and dry weight in the range 0.016-0.506mg. The brood size was found to vary between 148-1482 embryos. The results of Type 1 linear regression of brood size against dry weight for *C.montagui* from the three sites is shown in Table 4.14. The regression equations for samples from Shoalstone and Portland Bill are statistically significant ($p < 0.05$), although that from Bembridge was not significant ($p = 0.065$). For barnacles of 0.5mg, the brood size at Shoalstone was determined to be 1288; Portland Bill 1472 ; and Bembridge 927. An analysis of covariance (ANCOVA) found there to be no significant difference in brood size between sites using opercular diameter as covariate (Table 4.15). A similar analysis using body weight as covariate was not possible owing to the non-significance of the linear regression of brood size against dry weight for the Bembridge samples.

4.3.4 Brooding in isolated and contiguous *C. montagui.*

No differences were observed between the development of male and female gonads in isolated and contiguous specimens. However the proportion of *C. montagui* brooding embryos in contiguous animals (70%) was over twice that of isolated individuals (32.5%). A Chi-squared test, with Yates correction for continuity, showed that there was a highly significant association between the presence or otherwise of contiguous individuals and the proportion brooding embryos ($\chi^2 = 9.04$, df = 1, $p = 0.0026$). Yet a Kolmogorov-Smirnov test showed there to be no significant difference in the observed frequency of embryonic stages in the two samples (Fig 4.11; Table 4.16).

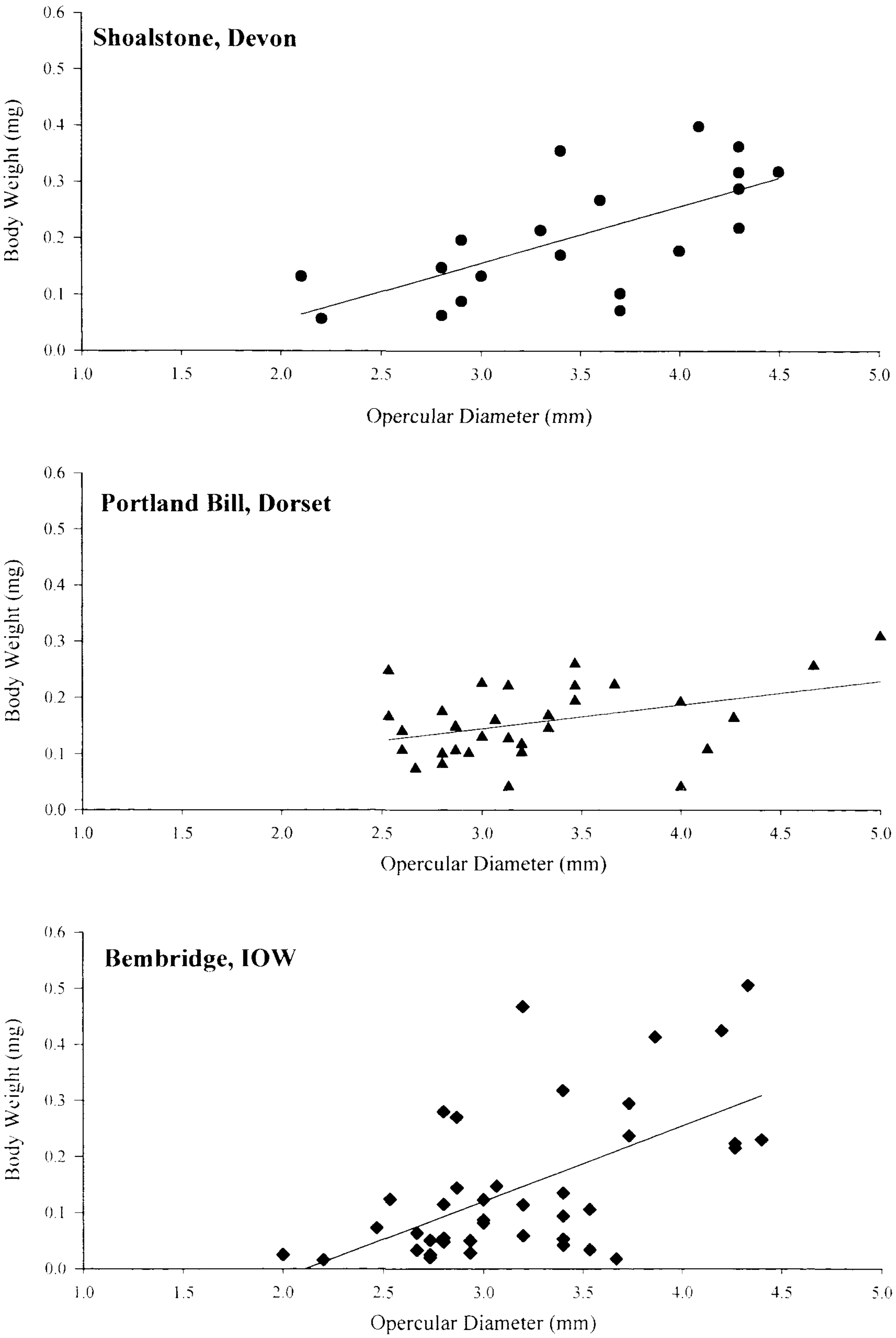


Fig.4.8 Scatter diagrams showing relationship between opercular diameter and body weight of *C. montagui* at MTL from three shores. Animals collected in June 996. Type 1 Linear Regression line shown. See Tables 4.12 for *F*-values.

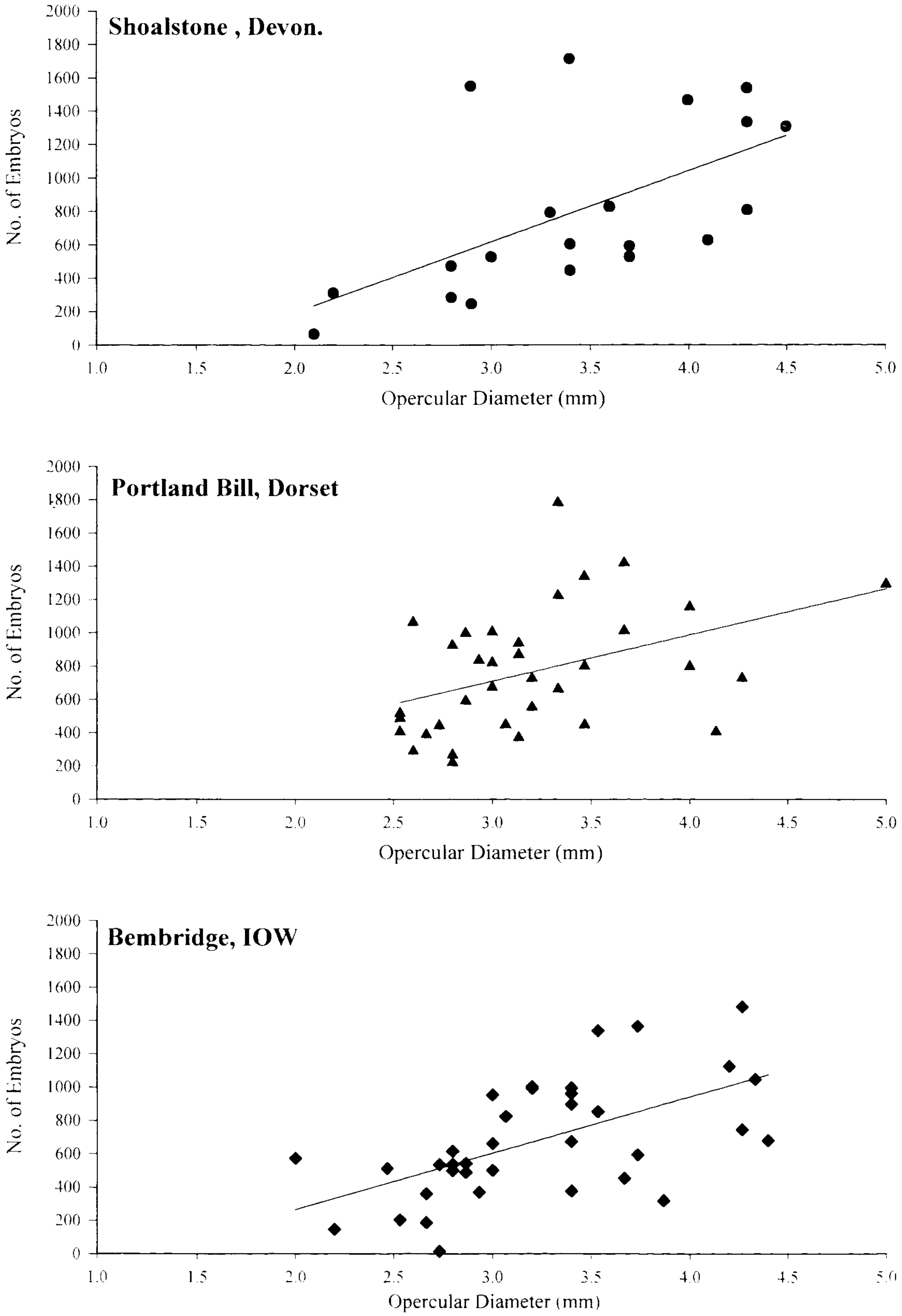


Fig 4.9 Scatter diagrams showing relationship between brood size and opercular diameter of *C. montagui* at MTL from three shores. Animals collected in June 1996. Type 1 Linear Regression line shown. See Table 4.13 for F-values.

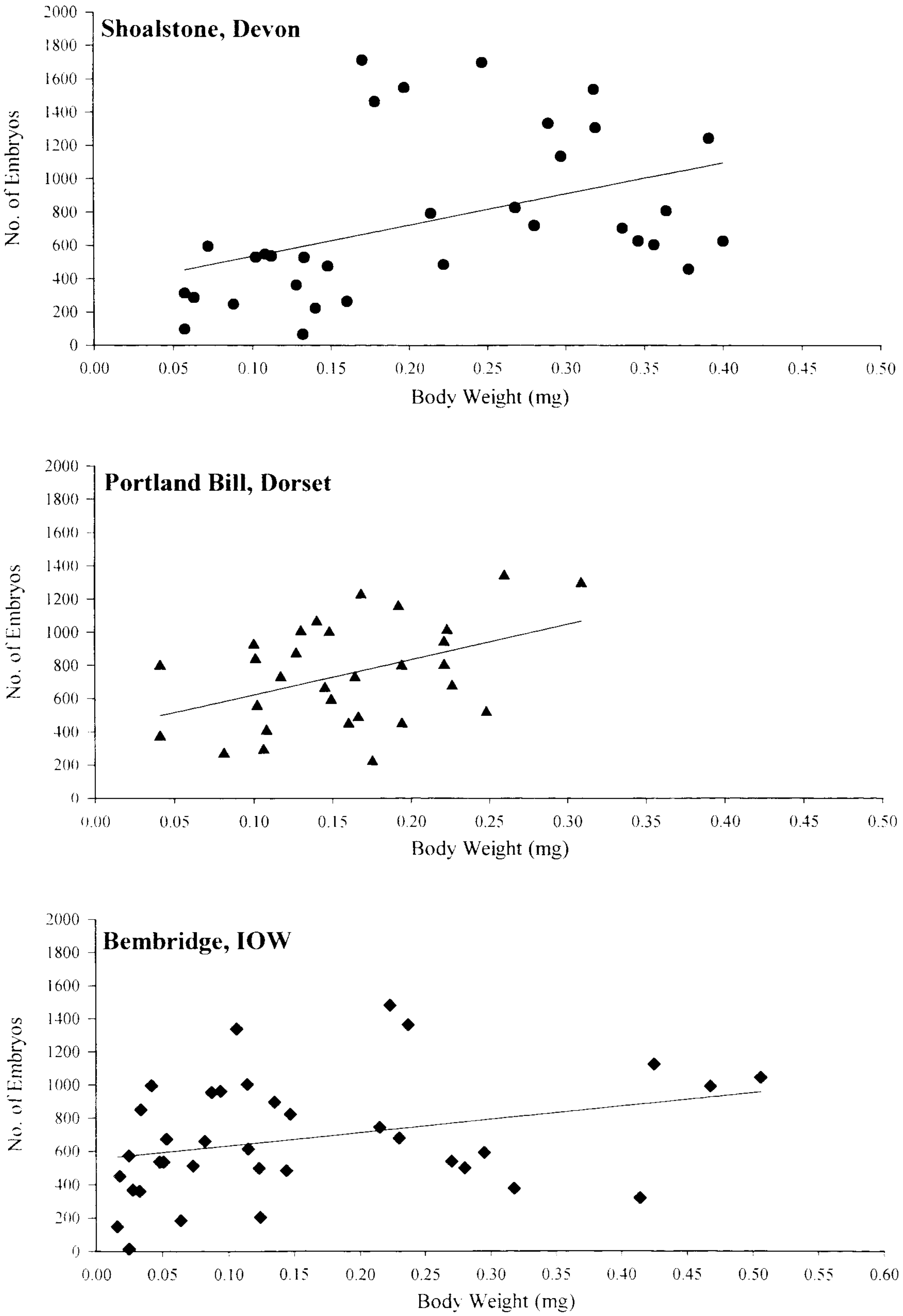


Fig.4.10 Scatter diagrams showing relationship between brood size and body weight of *C. montagui* at MTL from three shores. Animals collected in June 1996. Type 1 Linear regression line shown. See Table 4.14 for *F*-values.

Table 4.12 Type 1 Linear Regression and significance levels for relationships between Opercular Diameter and Body Weight of *C. montagui* collected at three shores at MTL in June 1996. See also Fig.4.8.

Shore	**n**	$\mathbf{r^2}$	*F*	**p**
Shoalstone, Devon	20	0.44	15.1	0.0011**
Portland Bill, Dorset	31	0.16	5.71	0.023*
Bembridge, IOW (Translocated)	39	0.35	19.6	< 0.001***

Table 4.13 Type 1 Linear Regression and significance levels for relationships between Brood Size and Opercular Diameter of *C. montagui* collected at three shores at MTL in June 1996. See also Fig.4.9.

Shore	**n**	$\mathbf{r^2}$	*F*	**p**
Shoalstone, Devon	20	0.35	9.6	0.006**
Portland Bill, Dorset	35	0.18	7.11	0.012*
Bembridge, IOW (Translocated)	36	0.34	17.5	0.002**

Table 4.14 Type 1 Linear Regression and significance levels for relationships between Brood Size and Body Weight of *C. montagui* collected at three shores at MTL in June 1996. See also Fig.4.10.

Shore	**n**	$\mathbf{r^2}$	*F*	**p**
Shoalstone, Devon	33	0.19	7.19	0.0012**
Portland Bill, Dorset	30	0.19	6.36	0.018*
Bembridge, IOW (Translocated)	37	0.1	3.64	0.065

Table 4.15 ANCOVA of *C. montagui* brood size from Shoalstone, Portland Bill and sample translocated to Bembridge. 'No. of eggs' being the dependent variable, 'Shores' the main effect and 'Opercular Diameter' the covariant. The p values confirm that the effect of opercular diameter as a covariate is highly significant, however there is no significant difference in brood size between shores.

Source of Variation	**df**	**MS**	***F***	**p**
Opercular Diameter	1	3838185.3	33.8	<0.0001***
Shore	2	80311.8	0.71	0.50
Residual	87	113732.2		
Total	90			

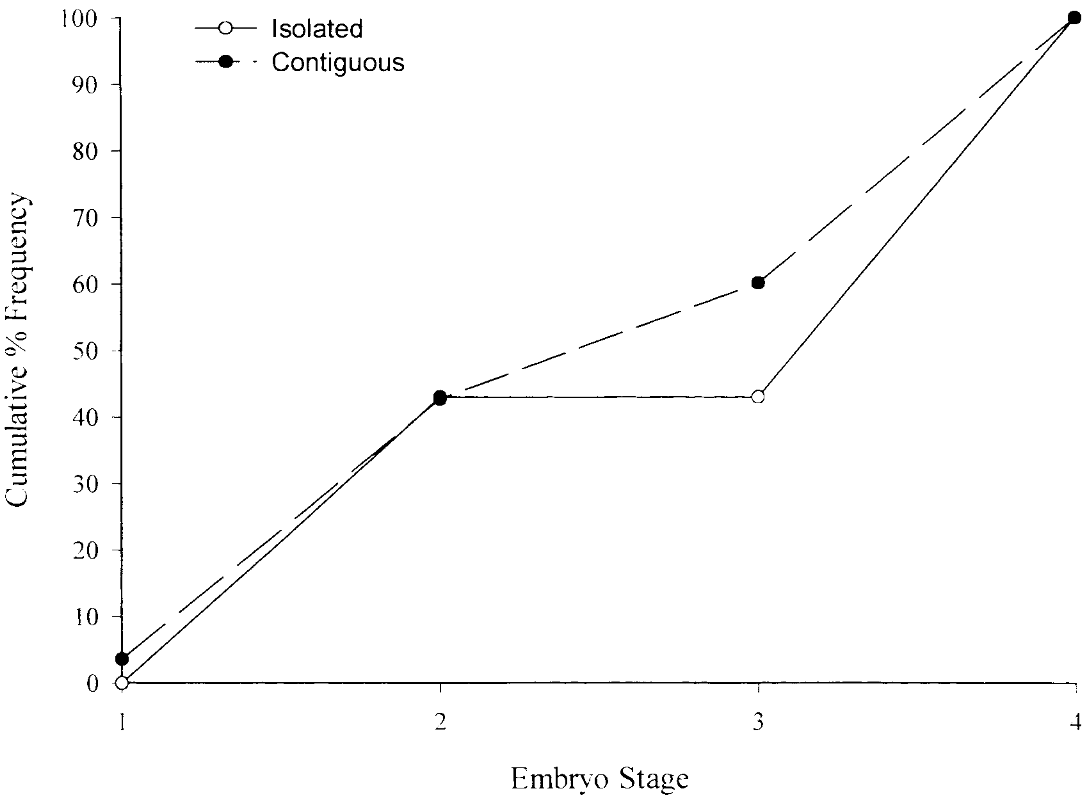


Fig.4.11 Stage of embryo development in contiguous and isolated individuals of *C.montagui* from Colwell, Isle of Wight 11/6/1998. Isolated animals were more than 5cm apart. Both samples from HWN, n = 40.

Table 4.16 Kolmogorov-Smirnov two-sample test (Sokal & Rohlf, 1995) on stage of Isolated and Contiguous *C.montagui* brooding embryos at Colwell Bay, Isle of Wight, 11/6/98. See also Fig 4.11.

Isolated (n_1)	**Contiguous (n_2)**	**Maximum Difference (D) in cumulative proportions**	**P (Two-tailed)**
13	28	0.027	1.00ns

4.3.5 Reproduction of translocated *Balanus perforatus* at Bembridge, Isle of Wight during 1995.

The number of barnacles examined in January, February, October and November were lower than the desired minimum of 18-20 required to obtain a reasonable assessment of the proportion brooding embryos (Fig.4.1). However when it came to examine the rocks and break open the barnacle shells, many were empty or were full of silt. When the rocks were collected from Lyme Regis it was not possible to determine the number of live barnacles present as the opercular plates are often sunken well below the small aperture. Whether the barnacles were already dead or had died subsequent to translocation is therefore uncertain. As the species is known to breed during the summer and the purpose of this investigation was to determine whether brooding was possible at the geographic limits, it was considered prudent to conserve those rocks with the highest density of individuals for examination between July and September. The seasonal development of male and female gonads and production of embryos is shown in Fig.4.12. The process of development was much slower than in *C. montagui* and fully ripe ovaries were not seen until July, when they were present in 5% of the sample. Surprisingly, however, a single individual was seen with Stage 2 embryos on May 20th - earlier than previously recorded in UK waters. Stage 3 ovaries were observed until October but reached a maximum of 40% of the sample in September. The male gonads appeared to develop earlier than the ovaries with Stage 3 testes present between May and September, reaching a maximum of 50% of sample in August. Stage 3 vesiculae seminales were present between May and October, reaching a maximum of 60% in August. The testes were more opaque in colour than the cream or white of *Chthamalus* and the ripe ovaries were yellow compared to the orange colour of *C. montagui*. There was an increase in density of the yellow pigment as the eggs and ovarian tissue developed. As previously mentioned, brooding was first observed in May, but no further broods were seen until July when they were present in almost 10% of the sample. Embryos at the hatching stage (Stage 4h) were seen in samples taken in August and September, where they comprised of 50% and 40% respectively of those individuals observed brooding. The maximum percentage of sample brooding embryos was only 23% and occurred in September. A single ovigerous lamella was found within one barnacle examined in July, all the remainder of those seen brooding had the normal two lamellae. An isolated individual examined in September had Stage 4h embryos, which appears to confirm the species ability to undergo self-fertilization.

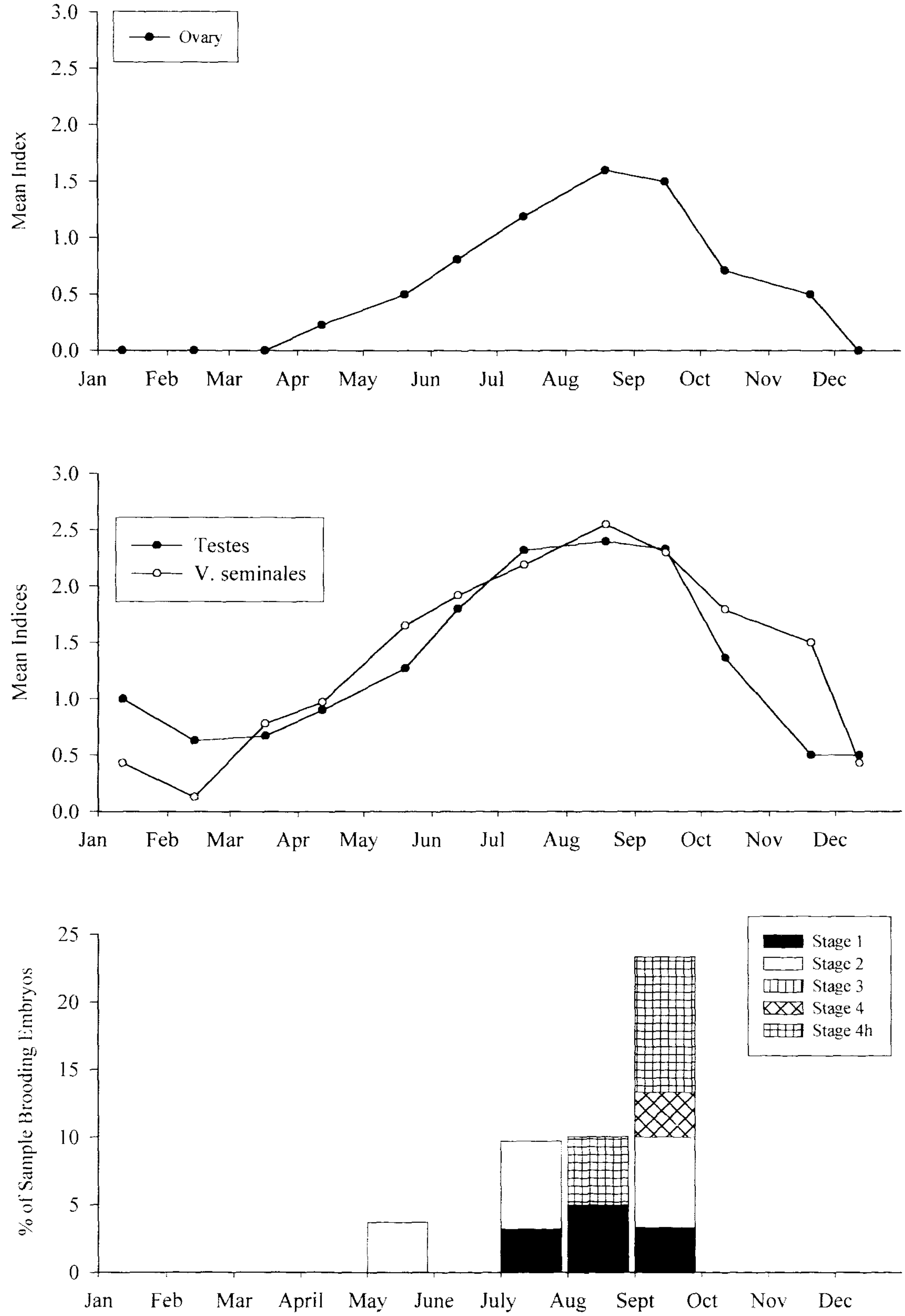


Fig.4.12 Seasonal development of gonads and embryos in translocated *Balanus perforatus* at Bembridge. Isle of Wight, during 1995.

4.3.6 Stage of reproductive development in *Balanus perforatus* from Bembridge and Lyme Regis in August 1996.

Five rocks bearing barnacles, that were translocated from Lyme Regis to Bembridge in October 1995, were removed from the shore on 22nd August 1996. Each of four rocks were treated as separate samples and the percentage brooding embryos varied between 12-47% (mean 27.3%, n = 120). Of the 31 with broods, plus an additional 16 removed from the fifth rock, 45% were at Stage 4 and 30% at the hatching stage. Three broods had a single lamella. At Lyme Regis, the percentage of the population brooding embryos was much higher, varying between 62-74% (mean 66%, n = 64). Of those with embryos, 32% were at Stage 4 and 39% at the hatching stage. The cumulative frequency of embryo stages from brooding barnacles at Bembridge and Lyme Regis is shown in Fig.4.13.

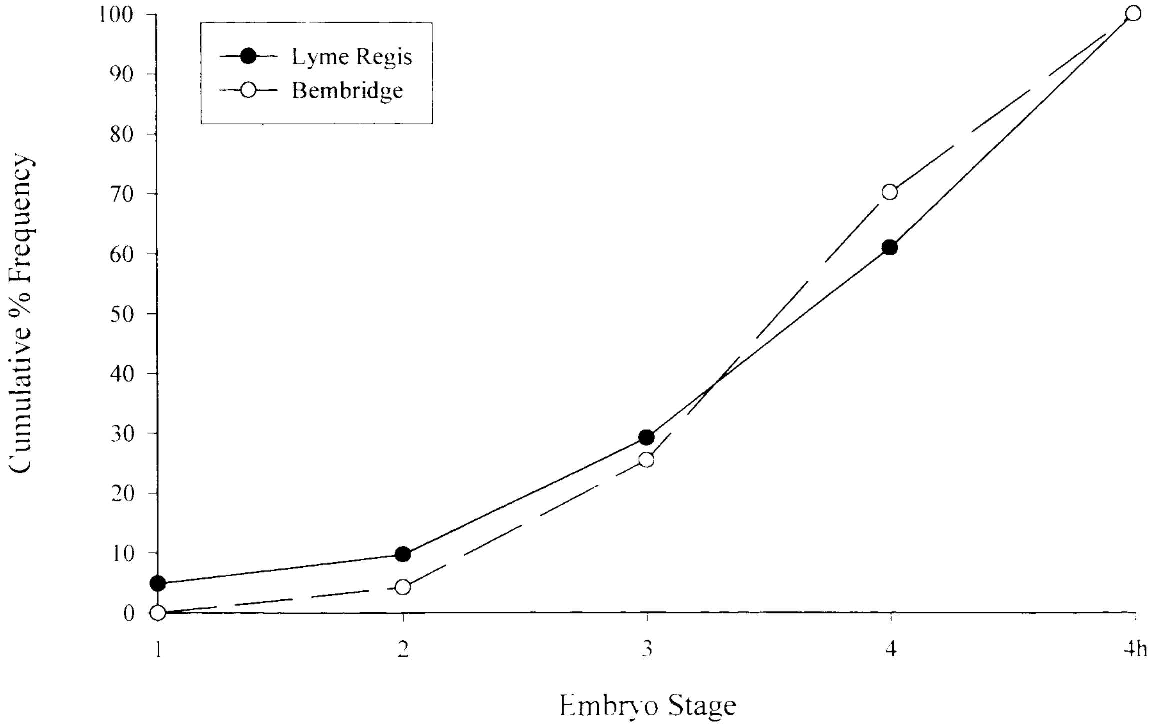


Fig.4.13 Stage of embryo development in *Balanus perforatus* from natural populations at LWN in Lyme Regis, west Dorset, and those translocated to Bembridge, Isle of Wight, sampled between 20-27th August 1996.

Table 4.17 Kolmogorov-Smirnov two-sample test (Sokal & Rohlf. 1995) on stage of embryonic development of *Balanus perforatus* from Lyme Regis and those translocated to Bembridge. Samples taken from LWN in August 1996.

Site 1 **(n_1)**	**Site 2** **(n_2)**	**Maximum Difference (D) in cumulative proportions**	**P** **Two-tailed**
Lyme Regis (44)	Bembridge (47)	0.071	1.00ns

A Kolmogorov-Smirnov two-sample test applied to compare the observed frequency of embryonic stages showed no significant difference (Table. 4.17). At Bembridge, brooding barnacles were found with Stage 1 ovaries only, but at Lyme Regis 17% of those with embryos had ovaries at Stage 2. A Spearman Rank test, applied to determine whether there was a correlation between embryonic and ovarian development (Table 4.18), showed no significant relationship at either of the two sites. Thus there is little evidence for regeneration of ovaries and a succession of broods in *B. perforatus* within the populations studied.

Table. 4.18 Results of Spearman Rank correlation between embryonic and ovarian development of *Balanus perforatus*.

Site	**n**	**r_s**	**p-value**	**Conclusions**
Lyme Regis	43	0.112	0.47	No significant correlation between embryonic and ovarian development.
Bembridge	30	0.054	0.77	No significant correlation between embryonic and ovarian development.

4.3.7 Brood size of *Balanus perforatus* at Bembridge and Lyme Regis.

Relationships between body weight, basal diameter and brood size are shown in Figs 4.14 - 4.16. Animals from Lyme Regis had broods of between 104 and 7550 embryos and body weight between 0.1 and 3.14mg. Broods were observed in animals with a basal diameter as low as 5.7mm. The translocated sample at Bembridge had a similar size range with body weight between 0.2-2.9mg. Brood size varied between 80-4242 embryos and ovigerous lamellae were seen in the smallest animal in the sample of basal diameter 6.8mm. Type 1 linear regression equations of brood size against animal size for both sites were very highly significant ($p < 0.0001$) and are presented in Tables 4.21 and 4.22. Barnes & Barnes (1968) gave a brood size of 7250 for a standard barnacle of body weight

3mg from the French coast. From the regression equations for Lyme Regis and Bembridge, brood sizes for a 'standard barnacle' are 6731 and 3272 embryos respectively. An analysis of covariance (ANCOVA) found there to be a significant difference in brood size between sites using body weight as a covariant (Table 4.23).

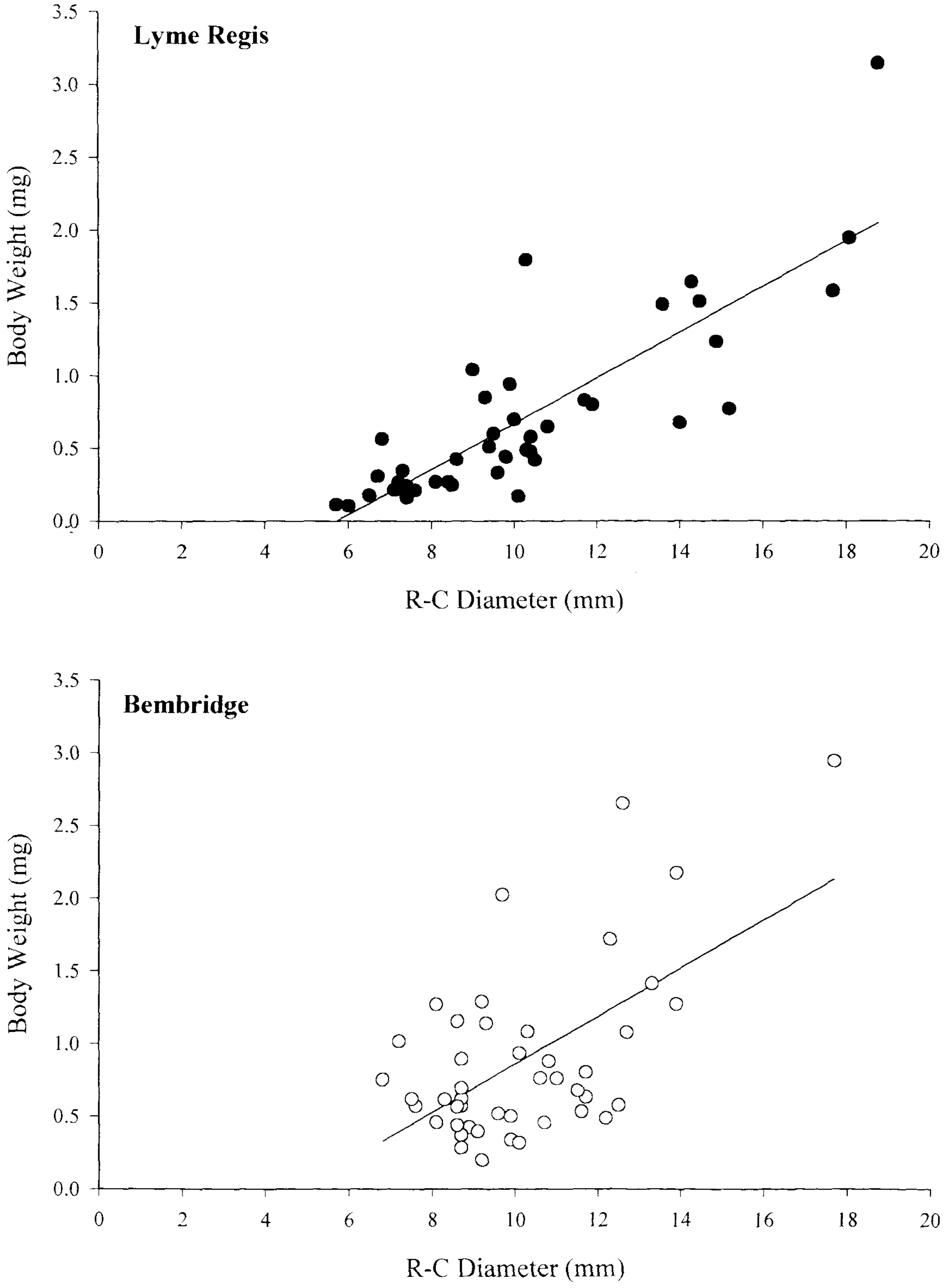
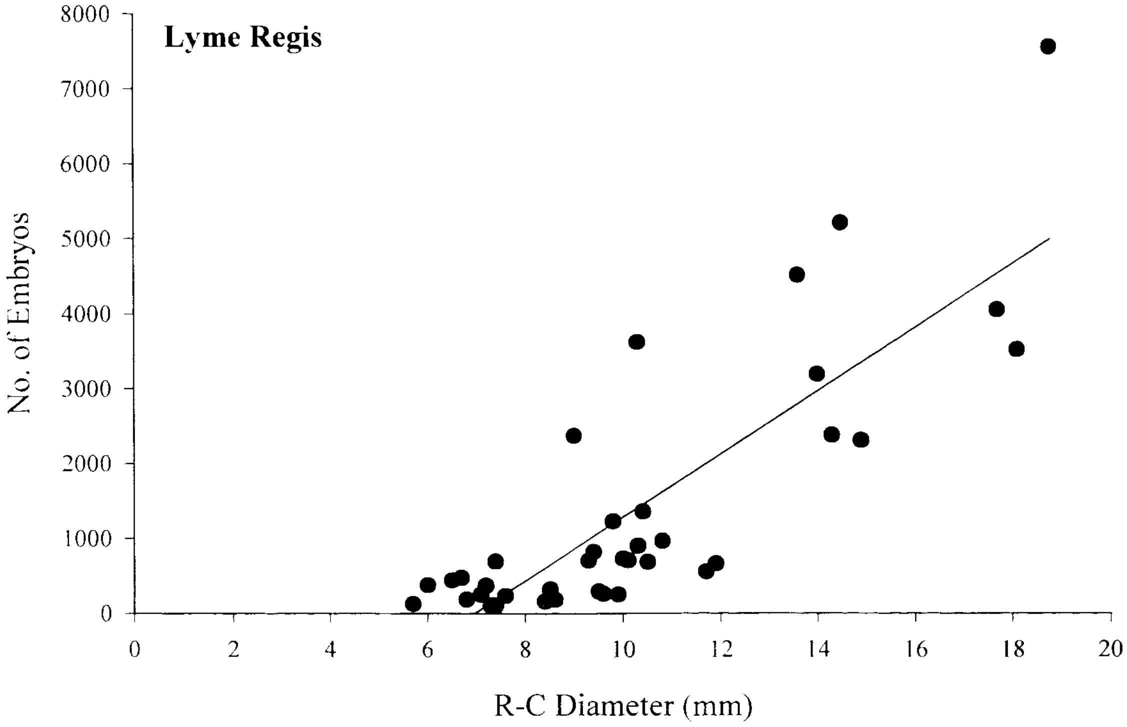


Fig.4.14 Scatter diagrams showing relationship between body weight and basal diameter (R-C axis) of *Balanus perforatus* at Lyme Regis and those translocated to Bembridge, Isle of Wight. Animals collected from LWN in August 1995. Type 1 Linear Regression line shown. See Table 4.20 for *F*-values.



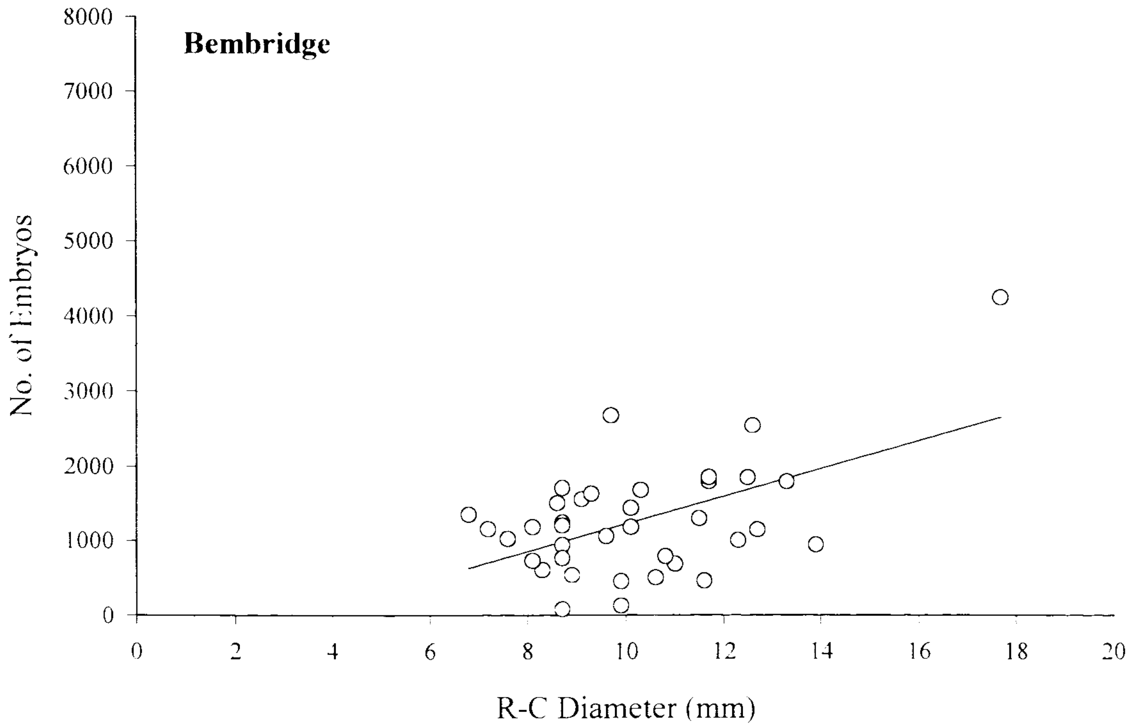


Fig.4.15 Scatter diagrams showing relationship between brood size and basal diameter (R-C axis) of *Balanus perforatus* at Lyme Regis and those translocated to Bembridge, Isle of Wight. Animals collected from LWN in August 1995. Type 1 Linear Regression line shown. See Table 4.21 for *F*-values.

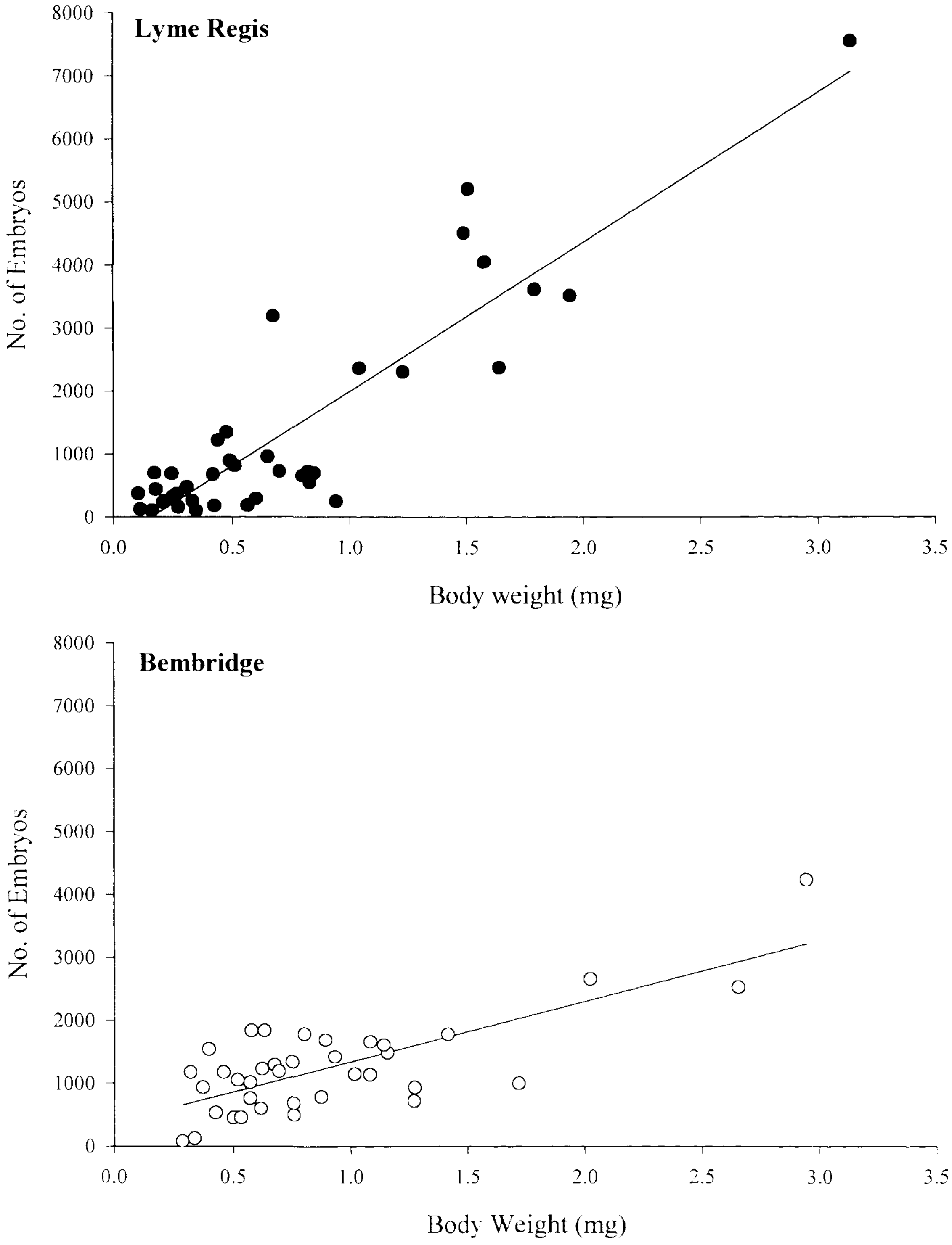


Fig.4.16 Scatter diagrams showing relationship between brood size and body weight of *Balanus perforatus* at Lyme Regis and those translocated to Bembridge. Isle of Wight. Animals collected from LWN in August 1995. Type 1 Linear Regression line shown. See Table 4.22 for *F*-values.

Table 4.20 Type 1 Linear Regression and significance levels for relationships between Basal Diameter and Body Weight of *B. perforatus* collected at LWN in August 1996. See also Fig.4.13.

Shore	**n**	r^2	*F*	**p**
Lyme Regis, Dorset	41	0.69	85.4	<0.0001***
Bembridge, IOW (Translocated)	45	0.35	22.7	<0.0001***

Table 4.21 Type 1 Linear Regression and significance levels for relationships between Brood Size and Basal Diameter of *B. perforatus* collected at LWN in August 1996. See also Fig.4.14.

Shore	**n**	r^2	*F*	**p**
Lyme Regis, Dorset	44	0.68	75.7	<0.0001***
Bembridge, IOW (Translocated)	38	0.27	13.1	0.0009***

Table 4.22 Type 1 Linear Regression and significance levels for relationships between Brood Size and Body Weight of *B. perforatus* collected at LWN in August 1996. See also Fig.4.15.

Shore	**n**	r^2	*F*	**p**
Lyme Regis, Dorset	39	0.8	146.5	<0.0001***
Bembridge, IOW (Translocated)	37	0.57	46	<0.0001***

Table 4.23 ANCOVA of *B. perforatus* brood size from Lyme Regis and sample translocated to Bembridge. 'No. of eggs' being the dependent variable, 'Shores' the main effect and 'Body weight' the covariant. The p values confirm that the effect of body weight as a covariate is highly significant, and there is also a significant difference in brood size between shores.

Source of Variation	**df**	**MS**	*F*	**p**
Body Weight	1	86235733	138.2	<0.0001***
Shore	1	3206896.8	5.14	0.026*
Residual	73	624127.4		
Total	75			

4.4 Discussion

The main objective was to confirm whether breeding was possible at the eastern edge of the species' known range, and to determine if there was any evidence of retardation or impairment within the reproductive process that could severely limit the species ability to repopulate this part of the coast. For *Chthamalus montagui*, the development of male and female gonads, fertilized eggs and embryos was found to occur right up to the Channel limits at Bembridge on the Isle of Wight. Moreover, there appeared to be no delay in the onset of brooding at the most eastern shores or early cessation compared to SW England, where the species is abundant. Burrows (1988) found that brooding at Plymouth commenced in mid-April when sea temperatures rose above 10 °C. In the Ligurian Sea (Mediterranean), at the centre of the species geographic range, late embryonic stages are observed in February (Relini, 1983) when the mean SST is about 12-13 °C (Climate Diagnostics Centre, 2000). In SW Scotland, at the extreme northern limits, it does not start until early June (Barnes, 1972). Samples from muddy rocks, collected at the Alvor Estuary in the Algarve, southern Portugal on April 8th 1996 had between 20-52% brooding of which 78% had Stage 4 embryos (pers. obs). In SW Ireland, O'Riordan (1992) concluded that brooding commenced slightly earlier than in SW England and that a small percentage of the population had embryos during the winter months. Here, the warm influence of the North Atlantic Current may be responsible for the observed non-degeneration of the gonads. Patel & Crisp (1960b) found that *Chthamalus* specimens brought into the laboratory in mid winter produced embryos after being kept for 2-3 weeks at 15-16 °C. All the available evidence points to temperature as the main factor determining the onset of brooding and is undoubtedly the cause of the latitudinal gradient in reproductive development. Yet although there are differences in the proportion of the population brooding at different sites, when assessed in mid-May, there is no clear W-E gradient along the Channel coast. Higher temperatures in 1995 and 1998 resulted in an earlier development of embryos at nearly all sites, whereas the late spring in 1996 severely delayed brooding. The populations at Portland Bill and Osmington Mills had slightly retarded development. This could be due to the cooler Channel waters off Portland Bill (see Chapter 2). At Osmington in Weymouth Bay, the warmer coastal waters would normally be expected to accelerate development. Although unsupported from the temperature data obtained, it is just possible that at this time of year the Bay receives cooler Channel water brought in as a result of the anticlockwise gyre to the east of the headland. This may also affect the production cycle and therefore food supply to the developing embryos. Patel & Crisp (1960b) found that unfed individuals of several species including *Chthamalus 'stellatus'*, did not breed at any of the temperatures investigated. Hines (1978) showed empirical evidence that the availability of food has an effect on the proportion of *C. fragilis* population brooding on the Californian coast. Local factors must also be responsible for the poor proportion brooding at Saltern Cove in 1997. Parasitism or disease is suspected although no evidence could be found of the isopod *Hemioniscus balani*, which destroys the ovary and reduces somatic growth in *S. balanoides* (Crisp, 1960).

Another important indicator of reproductive efficiency is the extent to which the species is able to produce multiple broods. The production of several broods is advantageous in case of failure within the hazardous planktonic larval phase of the life history and could be especially important at the species geographic limits, not least because of the complex hydrography of the region. Crisp (1950) was the first to suggest that unlike *Semibalanus balanoides*, *C. 'stellatus'* gives rise to a succession of broods in British waters.

At all sites, even those at the extreme eastern limits, different stages of embryonic development were observed at any one time, suggesting that there is evidence of asynchronous multiple broods within a defined breeding season between May and October (Burrows, 1988; O'Riordan, 1992).

Burrows (1988) estimated that full embryonic development took about 23 days *in vivo* at 15 °C. And yet at Bembridge, the translocated barnacles sampled during 1995 had embryos within the mantle cavity between May and September. Moreover, there was evidence of ovarian regeneration and development of eggs as embryos within the mantle cavity matured. Burrows *et al.*, (1992) calculated that at Plymouth in SW England, *C. montagui* has annually on average 1.5-2.1 broods on the high shore, 2.2-3.2 broods on the middle shore and 2.6-3.5 broods on the lower shore. This was calculated by applying the formula:

$$N_B = L_B / L_E$$

Where N_B is the No. of broods released; L_B is the effective length of time that an individual spends carrying embryos and L_E is the time for complete development of embryos from oviposition to release (i.e. 23 days).

For the barnacles translocated to Bembridge at MTL the first broods were observed when sampled on May 20th 1995 and last on September 15th 1995. It will be assumed therefore that the brooding period is from May to September inclusive = 153 days. The effective length of time that an individual spends carrying embryos L_B is given as (Burrows *et al.*, 1992, equation 2):

$$L_B = \Sigma P_B \times \Delta t$$

Where P_B is the average proportion of the population with embryos over the brooding season and Δt is the time interval between successive samples.

Using the data for Bembridge this is:

L_B = 59.66 Days

Using L_E = 23 days, the number of broods produced by the translocated animals at Bembridge at MTL in 1995 is estimated as:

L_E = 59.66/23 = 2.6

This is comparable with the estimates of between 2.2 and 3.2 calculated for shores in the Plymouth area at MTL (Burrow *et al.*, 1992). The estimates assume that each brood has an equal development period. Patel & Crisp (1960a) note that in cirripedes, the release of nauplii is frequently delayed after embryos have become fully developed: the hatching being dependent on the secretion of hatching substance (Crisp, 1956), which is highly correlated with feeding. It is also possible that the retention times of the different broods vary due to food availability. Crisp & Davies (1955) observed that in *Elminius modestus* grown on glass slides, the retention of mature embryos was greater in the autumn than in spring and suggested that this may have been due to the higher quantities of suspended food available to the earlier broods.

O' Riordan (1992) also found that both *Chthamalus* spp. showed a succession of broods in SW Ireland. In Lough Hyne, *C. montagui* was capable of producing up to 2 broods in their first summer, although this was dependent on size attained; no brooding was observed in animals of less than 4.5mm R-C diameter. A single specimen of the 1994 cohort translocated to Bembridge was found to be brooding embryos on 12th October 1995, when it had an R-C diameter of 4.5mm and T-S of 2.2mm. The attainment of this size will be dependent on growth rate and time of settlement the previous summer. The reproductive output by the population is therefore affected by age or size structure and varies across the shore according to the duration of immersion, which will determine feeding period, and emersion which will affect the temperature within the mantle cavity. Southward & Crisp (1956) noted that the interval between broods was shorter at higher temperatures so in warmer summers the larval output is likely to be greater. The proportion brooding at different tidal levels was not investigated within this study but interesting variations may exist due to the prolonged stand of high water during spring tides around the Isle of Wight, and extended periods of low water springs around Portland Bill. O'Riordan (1992) found differences in embryo production at different tidal levels with reduced numbers on the upper shore. However, higher numbers of embryos were found at a site with faster flowing water, presumably because of greater food availability. Barnes & Barnes (1968) found that the number of eggs per brood in European *C. 'stellatus'* was smaller in the most sheltered areas where suspended sediment load was high and salinity reduced. However Burrows (1988) found that there was a greater production of larvae at the most sheltered of his study sites and attributed this to the greater food production in the bay compared to the exposed headland. For *C. 'stellatus'* Barnes & Barnes (1968) gave estimates of between 500-1500 eggs per brood for an animal of 0.5mg body weight. Burrows found considerable variability but a comparable figure of between 1400-1900 was obtained. In SW Ireland O'Riordan *et al.*, (1991) found between 1500-3000 embryos in a standard 0.5mg barnacle, with the higher values in the faster flowing channel at the mouth of Lough Hyne. In this work figures of 1300,1500 and 900 were obtained for Shoalstone, Portland Bill and those translocated to Bembridge, respectively. Again high variability was found within sites and comparative analysis showed no significant differences.

The fecundity of barnacles, defined as the number of larvae released per year by an individual, is given by (Burrows *et al.*, 1992):

$$R_N = N_B \times N_E$$

Where N_B is the number of broods released and N_E is the number of larvae per brood. Assuming the average number of embryos produced per brood is similar, using N_B calculated earlier, the fecundity for each of the translocated barnacles at Bembridge :

= 2.6 x 927 = 2410 larvae per year.

Further investigations are required to determine within-site variability and to determine embryo numbers in the small natural populations on the Isle of Wight.

The brief examination of isolated and contiguous *C. montagui* at Colwell showed that the frequency of brooding in isolated *C. montagui* was less than half that in contiguous animals. This supports the observations of Barnes & Crisp (1956) and Barnes & Barnes (1958) and provides evidence for self-fertilization in this species. That the frequency of brooding was substantially less in isolated individuals is important, as isolation is typically the norm within these small populations; on average only 10% of all *C. montagui* mapped on Isle of Wight shores were truly contiguous (see Chapter 5). This could therefore considerably influence the larval output from small populations at the species extreme geographic limits. While embryonic development appears possible in isolated individuals, self-fertilization, as opposed to the passive drift of sperm liberated from nearby animals, still requires confirmation. Only molecular investigations into the DNA of adults and embryos will be able to confirm parentage. There then still remains considerable uncertainty as to whether survival rates of larvae produced as a result of self-fertilization are similar to those of larvae released following cross-fertilization.

Balanus perforatus translocated to Bembridge on the Isle of Wight, near to the extreme eastern Channel limits, was also found to undergo full reproductive development of gonads and embryos, however the peak period of development was about 3 months later than *Chthamalus*. During the winter, no recognisable ovarian tissue could be identified. Patel & Crisp (1960b) noted that the species had a fatty ovary during the winter period when their laboratory experiments were carried out. The maximum proportion observed brooding was much smaller than for *Chthamalus*, although the effects of the translocation process could not be controlled in this species due to its cryptic habitat. Yet only 28% of animals examined in mid-August at Arcachon (southern Brittany) had egg masses (Barnes *et al.*,1971).

Compared to *Chthamalus*, very little work has been undertaken on the reproductive biology of this species. However in laboratory experiments, Patel & Crisp (1960b) found that the species did not commence brooding until the water temperature was 15°C, when over the 35 day period of the investigation 5% of the sample were observed with embryos; this rose to 60% at a temperature of 19°C. In 1995, the spring was early and the sea temperature measured from the shore was 18.5 °C in May. Yet June was cool and the inshore temperature dropped back to 15.5 °C . July and August were particularly warm with measured temperatures between 21 °C and 23 °C. The samples taken from the shore at

Lyme Regis in August 1996 had much higher proportions brooding than those translocated to Bembridge, although temperatures measured at Bembridge were a degree higher.

Reduced food availability and higher sediment load may have been responsible, however the species is not unknown in estuaries (Norris & Crisp, 1953). The particularly high temperatures in May 1995 could well have accelerated the developmental process resulting in a single brooding animal being observed on the 20th of the month. It is significant that no broods were observed in June, which was unusually cool. Norris and Crisp (1953) state that in Torbay, egg masses of *B.perforatus* rarely occur before mid-June. Broods seen in May are therefore the earliest reported in UK waters, although Burrows (1988) observed Stage IV nauplii off Plymouth in early June 1984. In the Mediterranean, nauplii are abundant in the plankton as early as April (Lockhead, 1936), however they become less common later in the season, suggesting that higher temperatures may limit production or there is insufficient food. Because of the July-August breeding period and observations of a slightly later onset of breeding further north in Barnstaple Bay, Norris & Crisp (1953) concluded that nauplii would not be present in plankton hauls taken on the south coast east of the Isle of Wight, on the North Sea coast and further north of Aberystwyth on the west coast of Wales. Subsequent observations of settlement at Worthing Pier, together with confirmed brooding at Bembridge even in the cooler summer of 1996, refute this claim.

Patel & Crisp (1960b) found that *in vitro,* the species has a rapid rate of embryonic development that at 14.5°C was observed to be 6 days and at 20°C as short as 4 days.

Theoretically therefore, despite late summer brooding, there is plenty of time available for several broods. Using the methods of Burrows *et al.*, (1992) described above, the estimated number of broods for the animals translocated to Bembridge and sampled monthly in 1995 are:

$N_B = L_B/L_E = 7.63/6 = 1.3$ Broods per year at 14.5°C

$= 7.63/4 = 1.9$ Broods per year at 20°C

The sea temperature at Bembridge during the mid-summer was between 21-23 °C, so theoretically it is possible that some barnacles could have released more than one brood. Yet there was no evidence of ovary redevelopment as the embryos in the mantle cavity matured. Only single broods were observed by Patel and Crisp (1960b) when animals were exposed to temperatures between 15-28 °C. In Plymouth Sound, Burrows

(1988) considered that the sudden increases in abundance of Stage II nauplii observed in late July, August and September may be due to two synchronised releases per year.

The brood size of *B. perforatus* has never before been fully investigated. Barnes & Barnes (1968) provide a figure of 7250 eggs for an animal of 3 mg body weight from Arcachon, in south Brittany. The figure of 6731 obtained in this work from Lyme Regis is comparable, yet significantly greater than the estimate of 3721 embryos from Bembridge. Again, the within-site variance needs to be fully investigated here before any conclusions are drawn from the data, however the smaller brood size at Bembridge may be due to the relatively high suspended sediment load present in the eastern Solent.

Chapter 5

Recruitment, growth and mortality of *Chthamalus* and other barnacle species along the central south coast of England

5.1 Introduction

As discussed in Chapter 1, the decreasing dominance of southern intertidal species eastwards along the Channel has been thought due to unfavourable climatic and neritic conditions which could potentially affect breeding, growth rate and mortality of various species (Crisp & Southward, 1958). Yet in Chapter 4 it was shown that the minor differences in reproductive behaviour observed in translocated *Chthamalus montagui* and *Balanus perforatus,* compared to natural populations further west, were too small to explain the major changes in species distribution that occur in the vicinity of the Isle of Wight. It was therefore decided to investigate annual recruitment, growth rate and winter mortality of *Chthamalus* spp. as the geographic limits are approached and, where possible, obtain information on the recruitment of other potentially competitive species e.g. *Semibalanus balanoides* and *Elminius modestus*.

According to Connell (1985), whose definitions are used in this work, barnacle settlement refers to cyprid exploration of, or cementation to, the substratum, metamorphosed barnacles are known as recruits, while older barnacles are either juveniles or adults dependent on age. Recruitment combines settlement with any early mortality that has occurred on the substrate up to the time of the first census. Because of their sessile nature and relative ease of obtaining quantitative data, there has been a considerable amount of research into barnacle settlement and recruitment (Connell 1961a, 1985; Kendall *et al.*, 1982; Hawkins & Hartnoll, 1982a; Hawkins, 1983; Gaines & Roughgarden, 1985; Bertness *et al.*,1992). Importantly, Connell (1985) found that the level of recruitment had a major influence on the structure of intertidal barnacle communities. Moreover, alluding to his earlier work in the Clyde (Connell, 1961a), he concluded that existing models of community structure mainly apply to sites with high rates of settlement or recruitment.

Holm (1990) showed that recruitment correlated well with larval settlement rate and subsequent work on *Semibalanus balanoides* by Minchenton & Scheibling (1991) demonstrated a strong positive relationship between cyprid availability and settler density and recruitment. Nearly 80% of the variability in recruitment density could be explained by settler density recorded over the settlement period. Adult density and total settler density were also highly correlated except where post-recruitment mortality, attributed to predation, was high. Sutherland (1987) noted that the decline of a population of the Pacific barnacle *Tetraclita panamensis* could be attributed to low larval supply to the area. Hawkins & Hartnoll (1982a) found that higher settlement rates of *S.balanoides* around the Isle of Man were associated with on-shore winds, which increased the quantity of cyprids arriving on to the shore. Shanks (1986), however, found no correlation between settlement intensity and wind speed and direction, yet showed a positive correlation between settlement and maximum daily tidal range. Peaks of settlement occurred from between one and four days before a spring tide. Bertness *et al.,* (1992) concluded that larval supply to a shore increases with wave exposure but decreases with tidal height. At a smaller spatial scale, gregariousness of cyprids has been observed in many species with larvae settling preferentially adjacent to or in close proximity to other barnacles and particularly conspecifics (Knight-Jones & Stevenson,1950; Crisp & Meadows,1963; Gabbott & Larman,1987). This would seem to be particularly advantageous to those species that are incapable of self-fertilization and require adjacent conspecifics to undergo successful reproduction. Cracks and pits in the substratum are known to be attractive to cyprids (Crisp,1961; 1976) and there is much evidence of other chemical and biological settlement cues (Gabbott & Larman,1987; Thompson *et al.*,1998). There are known seasonal differences in settlement between different species. In the UK, cyprids of *S. balanoides* arrive on the shore between March and end of June (Crisp,1959; Jenkins *et al.*, 2000) whereas *Chthamalus* settles later between July and early October (Burrows,1988; O'Riordan,1992). The Australasian immigrant *E. modestus* settles between May and November, with a peak in late summer (Crisp & Davies,1955: Crisp, 1958).

Much discussion has centred on the methodology used to measure settlement and recruitment and of the relative importance of post-settlement mortality and post-recruitment mortality in affecting size of adult populations. (Denley & Underwood,1979; Hawkins & Hartnoll 1982a; Caffey 1982, 1985; Connell, 1985; Wethey, 1985, Minchinton & Scheibling,1991, 1993ab; Bertness *et al.*, 1992; Menge, 2000b). Both physical and biological factors may cause mortality amongst settling cyprids and newly calcified recruits. Desiccation and intolerance to changes in salinity of shore water cause considerable physiological stress among intertidal organisms (Lewis, 1964) and temperature in particular has been found to mediate competition between barnacle species (Wethey, 1983). Barnacle cyprids and young recruits are recognised as being particularly vulnerable to desiccation owing to their greater surface area to volume ratio. Low temperatures and freezing conditions can inhibit cirral activity and cause starvation (Southward, 1955,1964). Intensive wave action can cause high mortality amongst intertidal organisms including barnacles. Barnacles living within a dense matrix of fused shell plates can be vulnerable should the matrix be damaged, exposing the edges to wave erosion. Hummocking, resulting from high recruitment and forcing rapid upward growth of the shell can result in clumps suddenly breaking away from the remainder of the population (Barnes & Powell, 1950; Bertness *et al.*, 1998)). Along the Ligurian coast in Italy, an exceptional storm killed 92% of total *Chthamalus* spp. at an exposed site (Relini & Galizia, 1991). The bulldozing affect of limpets and other grazers can also damage and dislodge larvae and new recruits (Dayton,1971; Hawkins,1983). The sweeping movement of large fucoid seaweeds may prevent settlement and recruitment (Hawkins,1983; Jenkins *et al.*, 1999). The parasitic isopod *Hemioniscus balani,* found in all intertidal barnacle species, can sufficiently weaken individuals as to increase risk of mortality (Naylor, 1972). Known predators of young intertidal barnacles in UK waters include polychaetes and nudibranchs (Hurley, 1975), nemertean worms (Paine, 1981), shannies (Burrows *et al.*, 1999a) and dog-whelks *Nucella lapillus* (Connell, 1961b; Crothers, 1985). The extent to which dog-whelk predation is currently affecting barnacle communities will vary according to how much local populations have been damaged by tributyltin (TBT) pollution (Bryan *et al*,1986; Gibbs *et al.*,1987). Populations in the vicinity of major ports and marinas have been particularly affected, including those on Isle of Wight shores (Herbert, 1989; Bray & Herbert, 1998; Herbert *et al.*, 2000). Human disturbance upon barnacle communities due to trampling has been found not to have long-term effects, but oil pollution and use of dispersants do influence the structure and stability of intertidal communities (Southward & Southward, 1978; Hawkins & Southward, 1992).

In an analysis of published data on two barnacle species (*Semibalanus balanoides* (L.) & *Tesseropora rosea* (Krauss.)), Connell (1985) found that mortality in the first few weeks after settlement was independent of settler density, and therefore recruitment density, determined at the end of the settlement season, was a positive function of the magnitude of settlement. Juvenile and adult mortality was not significantly influenced by initial density when recruitment was light, but heavy recruitment (above 25 per cm^2) can result in over-crowding and higher adult mortality. Therefore juvenile and adult mortality was found to be density-independent when recruitment is light and density-dependent when recruitment is heavy. For the North American species *Chthamalus dalli*, recruitment was shown to be a stronger determinant of adult density than post-recruitment processes, while for *Balanus glandula*, post-recruitment processes were more important (Menge, 2000b). Apart from intraspecific relationships, higher recruitment of one species may exclude another if there is overlapping settlement, as is the case at Millport with *Chthamalus* and *Semibalanus balanoides* (Connell,1961a).

Other published studies on the recruitment and mortality of *Chthamalus* spp. are limited but Kendall & Bedford (1987) working at Aberystwyth in mid-Wales concluded that the observed poor recruitment of *C. montagui* was as a result of low numbers of cyprids reaching the shore, rather than post-settlement mortality. Burrows (1988) found that recruitment of *Chthamalus* around Plymouth in south Devon was greatest at levels below the maximum density of adults, suggesting that post-recruitment mortality was higher further down the shore. He also showed that, over a three-year study, there were consistent differences in the magnitude of recruitment between the species, with higher levels of *C. montagui* at sheltered locations and *C. stellatus* at more exposed sites. Most of the recruitment of *C. stellatus* occurred below MLWN whereas that of *C. montagui* was higher on the shore. Burrows (1988) suggests that *C. montagui* may require greater exposure to the air to harden its shell plates satisfactorily, which could reduce survival on the lower shore. The author also found that recruitment of *C. stellatus* was much more variable than *C. montagui*, thought due to its longer larval life and greater dispersal.

The zonation of the two *Chthamalus* spp. was attributed to differential post-settlement mortality, with that of *C. stellatus* being greater at high shore levels and *C. montagui* on the lower shore (Burrows,1988; O'Riordan, 1992). Pannacciulli (1995) showed that survival of early cohorts of *Chthamalus* was greater than those that settled later.

Space availability and the magnitude of any competitive interactions is partially dependent on species' growth rate and it is possible that this may vary throughout geographical range. Barnacle growth can be influenced by a variety of factors including supply and competition for food, parasitic infection, tidal level, degree of exposure and temperature (Crisp & Bourget, 1985). For *S.balanoides*, the authors considered that tidal level, current flows and degree of exposure far outweighed latitudinal influences. Individuals exposed to high flow rates feed more frequently and grow to a larger size than those in lower flow rates (Bertness *et al.*, 1991). Algal cover in close vicinity has also been shown to inhibit growth by limiting access to food or interference with cirral beat (Barnes, 1955). Early work on the growth of *Chthamalus 'stellatus'* was carried out by Moore & Kitching (1939) at Plymouth and Barnes (1956) at Millport on the Isle of Cumbrae in Scotland. Both showed that there are seasonal differences in growth rate with a cessation of growth during winter and higher rates during the spring. Burrows (1988) found no differences in the growth rate of *C. montagui* at different tidal levels but did observe that *C.montagui* grew faster than *C. stellatus* at a sheltered site in Plymouth Sound, and that *C. stellatus*, grew faster than *C. montagui* on the lower shore at a more wave-exposed site. When transferred to continuous immersion, *Chthamalus* from the upper shore were found to increase their growth rate by increasing cirral activity (Crisp & Southward, 1961). Growth of *S. balanoides*, investigated by Moore (1934), showed that it was more rapid at lower tidal levels and was reduced during the winter. The growth rate of the immigrant species *Elminius modestus* can be extremely rapid, reaching a shell length of 5-7mm in only two months (Crisp & Patel, 1961).

Of particular interest in this work on the population dynamics of *Chthamalus* was to determine the impact of good or poor recruitment on overall population density and to identify any correlation with air or sea temperature. Kendall & Bedford (1987) found no relationship between summer air temperatures and recruitment of *C. montagui* during a seven-year study at Aberystwyth in mid-Wales. However over a forty-year time series for a single shore in south Devon, Southward (1991) has demonstrated a significant correlation between the proportion of *Chthamalus* within the barnacle community and the annual mean inshore temperature two years earlier. Moreover, at lower tidal levels there was also a significant correlation (at 5% level) between the intensity of settlement and adult population density two years later, and at mean tide level a correlation one and two years after settlement.

The specific objectives of this chapter are :

i) to assess the magnitude of *Chthamalus* recruitment and where possible that of other potentially competing species at different locations along the south coast of England approaching the species geographical limits.

ii) to determine whether there are any differences in post-recruitment mortality and adult mortality of *C. montagui* at the different sites approaching the geographical limits.

iii) to measure the growth rate of *C. montagui* and to determine whether it is reduced towards the species eastern geographical limits.

iv) to determine whether interspecific competition between barnacle species is a major factor affecting the size of the *Chthamalus* populations as the distributional limits are approached.

v) to monitor changes in size of barnacle populations at the survey sites and to assess, albeit over a relatively short period of six years, any relationship with recruitment and sea temperature.

Plate 5.1. Adult *Chthamalus montagui* (Cm) dominant at MTL, Osmington Mills, Dorset, 3rd March 1994. Single *C.stellatus* (Cs) can be seen at top centre and bottom left of photograph. A few adult *Semibalanus balanoides* (Sb) are also present towards the bottom right of picture.

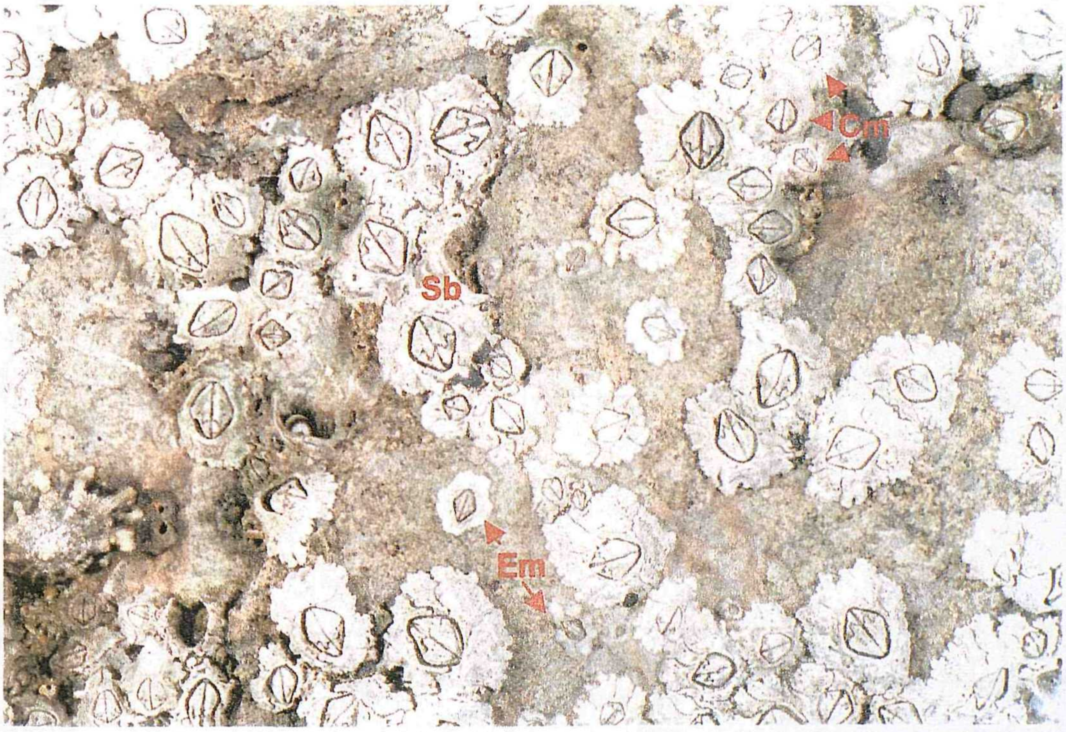


Plate 5.2. Adult *Semibalanus balanoides* (Sb) dominant at LWN, Osmington Mills, Dorset, 3rd March 1994. A few *Elminius modestus* (Em) and *Chthamalus montagui* (Cm) can also be seen. Note relatively large area of open space.

5.2 Methods

5.2.1 Minimum clearance size experiments

An investigation to determine the minimum size of clearance necessary to overcome the problem of underestimating *Chthamalus* spp. recruitment at thinly populated sites, due to lack of settlement cues from neighbouring adults barnacles, was carried out at MTL on Shoalstone beach at Brixham. Because settling cyprids have been observed to congregate around adult barnacles, resulting in higher densities of recruitment immediately adjacent to the neighbouring adult population, clearances were created with a 1cm border within which recruitment was ignored. Ten clearances of area 9, 49, 121 and 484 cm^2 (referred to hereafter as 'areas' 'countable areas' or 'clearances' of $1cm^2$, $25cm^2$, $100cm^2$ and $400cm^2$ respectively) were made using a paint scraper and wire brush in late May, and the density of recruits counted in each area at the end of October (Fig.5.1). Results from a one-way ANOVA showed that a minimum area of $100cm^2$ was necessary; there being significantly higher estimates ($p < 0.05$) obtained from the two smaller clearance sizes, but differences between the 100 and 400 cm^2 areas were not significant.

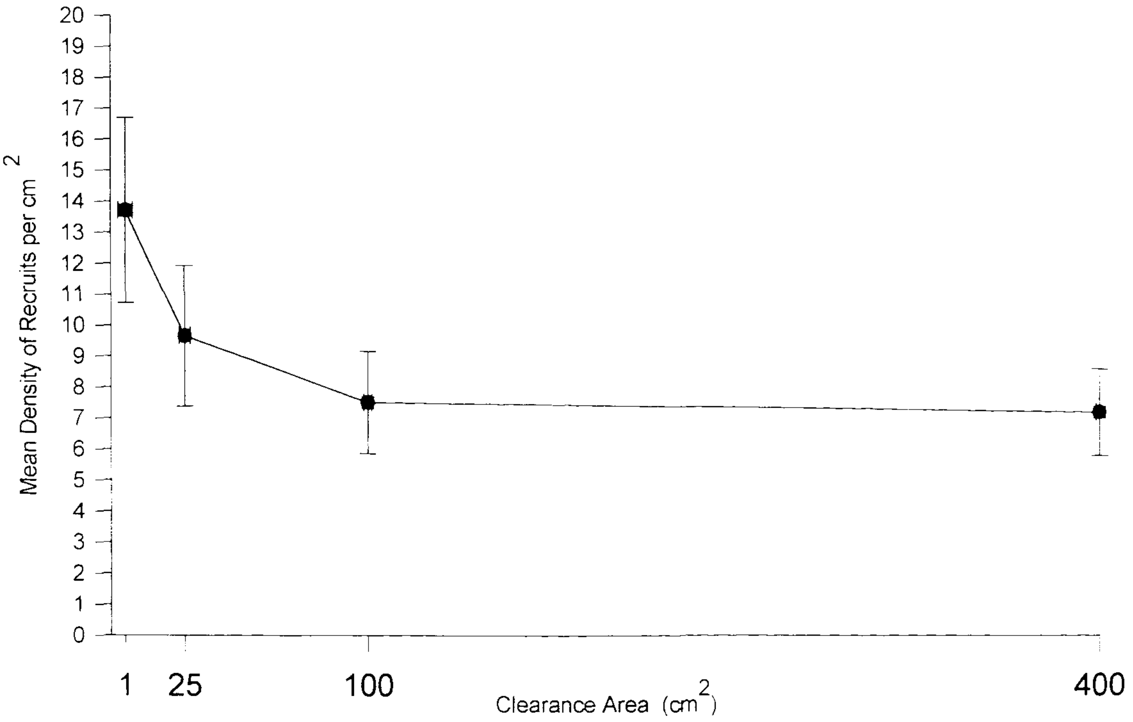


Fig 5.1 Effect of increasing clearance size on the estimated recruiment density of *Chthamalus* at MTL at Shoalstone in Devon, October 1995. Quadrat n =10 for each area. Error bars show ± SE.

5.2.2 Recruitment of *Chthamalus* along the Devon & Dorset coast.

Although clearances of area 100cm^2 would have been adequate where recruitment is high, clearances of area 400cm^2 were created to increase the range of microhabitat and surface topography thought to be important at low recruitment sites, especially in the eastern localities. By creating large clearances at all sites, the problem of underestimating recruitment on shores with low adult populations is reduced.

In June 1994, prior to settlement, six 400cm^2 clearances were created on the upper, middle and lower section of the limpet-barnacle zone at five sites between Torbay in Devon and Swanage in east Dorset. Six additional clearance sites were also made at Mean High Water either side of the Long Groyne at Hengistbury Head near Christchurch in Dorset. Because the density of settlement has been found to vary considerably within a site, due to local surface topography, microhabitat and hydrography, it was decided that comparative annual estimates of recruitment should be made at exactly the same points on the shore. The creation of a larger number of clearances was considered to be irresponsible where population densities were low at the eastern sites, as was also the creation of new clearances on an annual basis. The clearances were therefore re-scraped annually. This technique, used by Hawkins & Hartnoll (1982a) and Kendall *et al.*,(1982) for investigating recruitment and settlement patterns of *Semibalanus balanoides*, and Kendall & Bedford (1987) for recruitment estimates of *Chthamalus montagui*, can underestimate the magnitude of potential recruitment in populations where there is considerable competition for space. Habitat and site details of the recruitment sites are summarised in Table 5.1 and location shown in Fig 3.7 (p74). Sites also described in Appendix II.

Table 5.1 Shores where permanent *Chthamalus* recruitment monitoring stations established on the mainland coast of southern England.

Site	Rock Type	Max Rock Angle °	Coastal Aspect	Other Details
Shoalstone, Torbay DEVON	Limestone	15	N	
Saltern Cove, Torbay DEVON	Sandstone	15	E	Established in 1995
Broad Ledge,Lyme Regis DORSET	Limestone	<5	S	Middle & Lower
	Concrete	<5	S	Upper shore only
Collar Ledge, Portland Bill, DORSET	Limestone	<5	SE	
Osmington Mills, nr Weymouth, DORSET	Sandstone	10	S	
Kimmeridge, DORSET	Dolomite	<5	S	Established in 1995
Peveril Point, Swanage, DORSET	Limestone	25	S	
Long Groyne, Hengistbury Head, DORSET	Concrete	Vertical E and W facing	S	Discontinued after 1994

A 20 x 20cm quadrat was placed in the centre of the clearance and two corners were permanently marked on the rock by either a drilled hole or a stainless steel screw fixed in the hole. Holes were drilled using a *Ryobi* petrol drill with a 6.5mm SDS bit. In mid-October, at the end of the *Chthamalus* settlement season, a grid quadrat was positioned exactly over the screws marking the cleared area and the number of young recruits were counted with the aid of a x4 hand-lens. Where densities were very high, sub-samples were taken and an estimate of recruits in the whole quadrat calculated. Recruitment at Hengistbury Head was only estimated in 1994. In 1995, two additional recruitment monitoring sites were created at Saltern Cove in Torbay and at Kimmeridge in Dorset. There were two reasons for this: firstly, the other site in Torbay at Shoalstone beach is much visited and there were concerns related to trampling damage, and secondly it was felt important to obtain a better estimate of the variability in recruitment along each section of coast. The Kimmeridge site is also popular with visitors but the monitoring site is distant from the most intensively used areas. Each site was also checked in August during the middle of the settlement season to determine if there was any delay in settlement at the eastern localities and whether a higher density of recruitment was evident that may not have survived until the October count date.

5.2.3 Recruitment of *Chthamalus* spp. on the Isle of Wight.

In view of the low densities of *Chthamalus* recorded on the Isle of Wight the creation of large clearances was considered unjustifiable. Instead, because of the generally high availability of bare rock space on these shores, new recruits were counted within three patches of randomly placed 400cm^2 quadrats (n = 3 x 15) at three tidal levels in late October of each year.

5.2.4 Recruitment of *Semibalanus balanoides*, *Chthamalus* spp. and *Elminius modestus* on vertical surfaces along the south coast of England in 1999.

To establish the pattern of recruitment of other intertidal species of barnacles that might compete for space with *Chthamalus*, it was decided to undertake a broad-scale study to include neighbouring coastal cells to the east of the Isle of Wight. Whereas the annual assessment of *Chthamalus* recruitment has been determined on flat or slightly sloping rock platforms, it was considered that this habitat was insufficiently represented within the central and eastern parts of the study area to make an adequate comparison between coastal cells. It was therefore decided to make clearances on vertical surfaces: mixing where possible those on man-made structures, such as pier-piles, with natural rock platforms. The coast from Torbay to Beachy Head was divided into four cells, broadly based on those cells or sub-cells identified as having independent sediment transport characteristics and differentiated largely by major headlands or hydrographic barriers (Motyka & Brampton,1993; Chapter 2 of this work). These were named: '*Lyme*' (Prawle Point-Portland Bill); '*Purbeck*' (Portland Bill to Handfast Point; '*Wight*' (Handfast Point to Selsey Bill; and '*Sussex*' (Selsey Bill to Beachy Head). Within each cell three shores were chosen. To determine within-shore variability, three random patches of 100cm^2 clearances (n=10) were made at each of three tidal heights approximating to MHW, MTL and MLWN. Settlement of *S. balanoides* begins in March and early April along the Channel coast so clearances were made well in advance in January and February. New clearances in different areas of each shore were made in May, prior to the settlement period of *Chthamalus* and *Elminius modestus*. When counting, each quadrat was scanned with a x4 lens. Quadrat size varied between 1-400cm^2 according to the density of recruits observed. When the smaller quadrats were employed, sub-sampling was used to calculate the mean density within each 100cm^2 clearance. The density of limpets and dog-whelks was also measured by placing ten 0.25m^2 random quadrats. For logistical reasons it was not possible to determine density of recruits on the different shores during the same tide, and therefore it is conceivable that some post-recruitment mortality and additional settlement may have occurred during the intervening period between shore visits. The shores and dates of counts are shown in Table 5.2 See Chapter 2 for site descriptions.

Table 5.2 Shores surveyed and count dates of barnacle recruits within clearances made on vertical surfaces during 1999.

Cell	**Shores**	**Dates of Counts *S.balanoides***	**Dates of Counts *Chthamalus & Elminius***
Lyme	Saltern Cove	18 May	12 October
	Lyme Regis	17 May	13 October
	Chesil	16 May	16 October
Purbeck	Osmington Mills	16 May	28 October
	Kimmeridge	15 May	25 October
	Swanage	13 May	24 October
Wight	Colwell	21 May	7 November
	East Cowes	24 May	4 November
	Watershoot Bay	22 May	6 November
Sussex	Selsey Bill	29 May	25 September
	Worthing Pier	27 May	24 September
	Newhaven	28 May	23 September

5.2.5 The growth of *Chthamalus montagui* along the south coast of England.

The growth-rate of *C.montagui* along the mainland coast was measured periodically from photographs taken at four locations: Saltern Cove in Devon, and Lyme Regis, Portland Bill and Kimmeridge in Dorset. At all locations, six photographic monitoring stations were established at each tidal level. Three holes were drilled in to the rock with a *Ryobi* petrol drill to locate the camera tripod. A third hole was drilled in the middle of the field- of -view and a stainless steel screw fixed into the rock, both to act as a scale bar and to aid re-location of the site. Where adult population densities were high, and available space for settlement minimal, the rock was cleared of barnacles within the camera field-of-view, which was approximately 8 x 5cm. The photographic apparatus consisted of an Olympus OM1n SLR camera with 50mm lens and No.1 Vivitar extension tube fitted to a laboratory tripod. A steel bar was welded across the back of the tripod to support two small Prima 100M flash units. Photographs were taken using Ilford Delta 100 ASA black & white film each May, August and October until August 1997, when the animals were about two years old. The developed negatives were projected on to a screen, enlarging the image to 34 x 50.5cm, and the 1995 recruits were marked on an A2 sheet of tracing paper. At Saltern Cove and Lyme Regis the density of new recruits was so high, that for growth-rate studies, between 15-20 barnacles were randomly selected from each photograph, enabling 100 size measurements to be obtained for each tidal level. The basal diameter across the rostro-carinal axis and opercular diameter (tergal-scutal diameter) was measured on the screen using vernier callipers. Individual recruits of *C.montagui* from the 1994 & 1995 cohorts, identified within permanent quadrats at Watershoot Bay, Hanover Point and Colwell on the Isle of Wight, were also photographed and measured periodically over two years.

5.2.6 Growth and mortality of translocated *Chthamalus montagui* recruits at Bembridge, Isle of Wight.

During May 1995, twelve 10 x 10cm settlement plates made of 4mm perspex were screwed down to the shore at MTL at Saltern Cove in Devon. To encourage settlement, shallow grooves were cut in to each plate. During the summer, a very high density of spat settled on the plates and at the end of October it had been hoped that six whole plates could have been taken to Bembridge. However most of the plates were damaged, and in the end only two whole plates and two half sized pieces were taken. Three full sized plates were left at Saltern Cove. These were unscrewed and supported by a square piece of 10mm marine plywood, for extra strength. They were re-secured to a different patch of rock, to create a measure of disturbance that might be comparable to that encountered by those translocated to Bembridge. The plates removed for translocation to Bembridge were kept damp with seaweed during transit, and occasionally immersed in seawater. Fifteen hours later, the plates were fixed to the shore at MTL at Bembridge, using stainless steel screws and supported with marine plywood. The recruits were photographed monthly until October 1996, then bimonthly from January 1997. Mortality and growth rate were measured as described above (5.2.5). Growth on the control plates and natural populations at Saltern Cove was similarly measured, with photographs being taken in May August and October of each year.

Individual recruits of *C.montagui* from the 1994 & 1995 cohorts identified within permanent quadrats at Watershoot Bay, Hanover Point and Colwell on the Isle of Wight (see 5.2.5 above) were also photographed and measured periodically over two years.

5.2.7 Mortality of *Chthamalus montagui* along the mainland coast of southern England.

The mortality of the 1994 and 1995 cohorts and adults of *C. montagui* was measured photographically at six sites at each of two or three tidal levels on five shores (Shoalstone, Saltern Cove, Lyme Regis, Portland Bill and Kimmeridge). Up to 25 individual barnacles from each photograph (n = 6 at each tidal level) were mapped onto A2 tracing paper and their presence or absence recorded at successive sampling occasions. Of particular interest was the mortality of the new recruits during their first winter, determined between October post-settlement and the following May.

5.2.8 Mortality of *Chthamalus montagui* on the Isle of Wight.

On the Isle of Wight the mortality of new recruits and adult *Chthamalus* spp. were measured within permanent quadrats. Each quadrat was 400cm^2 and its location marked at two corners by the insertion of stainless steel screws into holes drilled in the rock with a *Ryobi* petrol drill. The number of quadrats established at each location together with site description is shown in Table 5.3. During the initial survey, all adult and juvenile *C.montagui* and *C.stellatus* from each quadrat were marked on to a separate 3mm perspex square map using a waterproof pen, and their subsequent presence or absence was recorded at three-monthly intervals. During the settlement season and the following spring, new recruits were also mapped and progress followed during subsequent months.

Should the barnacles *Semibalanus balanoides* or *Elminius modestus* come into contact with *Chthamalus*. then this was also marked on the map, and all species continued presence checked during each visit. Dead barnacles with valves removed, yet opercular plates intact, were differentiated from those that had been dislodged. The potential competitive interference from these other faster growing species could then be monitored and its impact assessed. As from February 1997 the seasonal variation in the amount of available space within the quadrats was also determined during each visit.

Table 5.3 Locations on the Isle of Wight where permanent monitoring sites were established to measure mortality of *Chthamalus* spp.

Location	Tidal Level	No of Quadrats	Slope Angle & Aspect	Substrate	Date Quadrats Established
Colwell Bay	MTL	10	75^0 NW	Concrete Sea Defence	9 October 1994
Hanover Point	HWN	10	25^0 N	Sandstone Reef	1 December 1994
Hanover Point	MTL	10	25^0 N	Sandstone Reef	22 February 1994
Hanover Point	LWN	10	20^0 N	Sandstone Reef	19 April 1996
Watershoot Bay	HWN	3	90^0 E	Sandstone Boulders	1 July 1994
Watershoot Bay	MTL	10	Flat	Sandstone Boulders	1 July 1994
Watershoot Bay	LWN	3	90^0 S	Sandstone Boulders	1 July 1994

5.2.9 Monitoring barnacle populations along the east Devon, Dorset and Isle of Wight coast 1994-1999.

In mid-October 1994, counts of intertidal barnacle species were made within thirty random quadrats, placed at three tidal levels. However due to the high variability in species density across the shore, particularly at the species eastern limits, a hierarchical design (Underwood, 1997) was initiated from October 1995 onwards. This, it was hoped, would improve the estimation of within-shore variance and help to determine whether differences in mean abundance between years were genuine, or more likely to be due to random variability.

Counts of adult barnacles were made within three random patches at MHW, MTL and LWN on nine shores: Shoalstone and Saltern Cove in Devon, Lyme Regis, Portland Bill, Osmington Mills, Kimmeridge and Peveril Point in Dorset and Hanover Point and Watershoot Bay, Isle of Wight. Patches were usually 10-15m apart and between ten and fifteen quadrats were placed in each patch, depending on tidal and weather conditions. Quadrat sizes were as shown in Chapter 3 (Table 3.1), with the exception that a smaller quadrat of $6cm^2$ was used at all tidal levels at Portland Bill, Osmington Mills and on the upper shore at Lyme Regis. Counts were usually made in mid-October and all barnacle species that appeared of adult age (a minimum basal diameter of about 4mm) were included. On all shores, quadrats were placed on flat or gently sloping surfaces except on the boulder shore at Watershoot Bay where representative sampling required the inclusion of a variety of slope angle and aspect. Quadrats falling within rock pools were ignored.

The % cover of each barnacle species, fucoids, limpets and free space was determined from 6 photographs taken within permanently marked areas at each of three tidal levels. The camera field of view was 8 x 5 cm (see 5.2.5 for details of photographic equipment).The developed B&W negatives were projected onto a screen that enlarged the image to 34 x 50.5cm. A sheet of perspex marked with 100 evenly spaced dots was placed over the screen to measure % cover. Photographs were taken in October and May between 1994 and 1999. In some years, photographs were also taken in August.

5.3 Results

5.3.1 **Recruitment of *Chthamalus***

5.3.1.1 Annual estimates of *Chthamalus* recruitment along the south-coast of England, 1994-99.

Figs. 5.2 - 5.4 show the annual recruitment of *Chthamalus* spp. within the cleared quadrats measured between mid-October and mid-November of each year (note Log_{10} scale). A consistent pattern was obtained with shores in Lyme Bay having much greater recruitment than those in Weymouth Bay and along the Purbeck coast. In Lyme Bay, all three shores studied had annual recruitment densities of at least 1 per cm^2, except for Shoalstone in 1997 (0.8 per cm^2). The highest mean recruitment recorded in Lyme Bay was 20 per cm^2 on the lower shore at Lyme Regis in 1999, when a maximum of 27 per cm^2 was recorded from one quadrat. There was an order of magnitude reduction in recruitment immediately east of Portland Bill at Osmington Mills in Weymouth Bay, with densities exceeding 1 per cm^2 in 1999 only. Densities were further reduced along the Purbeck coast to Peveril Point where the mean was never greater than 0.02 per cm^2 (8 per $400cm^2$ quadrat). At some shores there were also consistent differences in recruitment with tidal level. Shoalstone, Saltern Cove and Osmington Mills generally had higher recruitment on the middle shore, whereas at Lyme Regis, Portland Bill and Kimmeridge, densities were usually greater at lower tidal levels. The annual data between 1995-1999 were subject to three-way analysis of variance using GMAV5 (Underwood *et al.*, 1998) with the main hypothesis being that recruitment was significantly different in the western cell (Lyme Bay) compared to that in Weymouth Bay and along the Purbeck coast (eastern cell). To ensure a balanced design for the analysis the shore at Portland Bill was omitted. This was also considered reasonable because of its central location and extreme exposure to wave energy. The results of the ANOVA are shown in Table 5.4. Factor 'Cell' is orthogonal and fixed; factor 'Shore' is nested in 'Cell' and is random; factor shore 'Height' is orthogonal and fixed. There were six replicates. The results indicate that there was a significant ($p<0.05$) or highly significant ($p< 0.001$) difference in recruitment between coastal cells each year except 1997, and in 1998 the difference was dependent on tidal height examined. Apart from 1998 there were highly significant differences between shores and that each year the recruitment at a particular tidal height was dependent on shore.

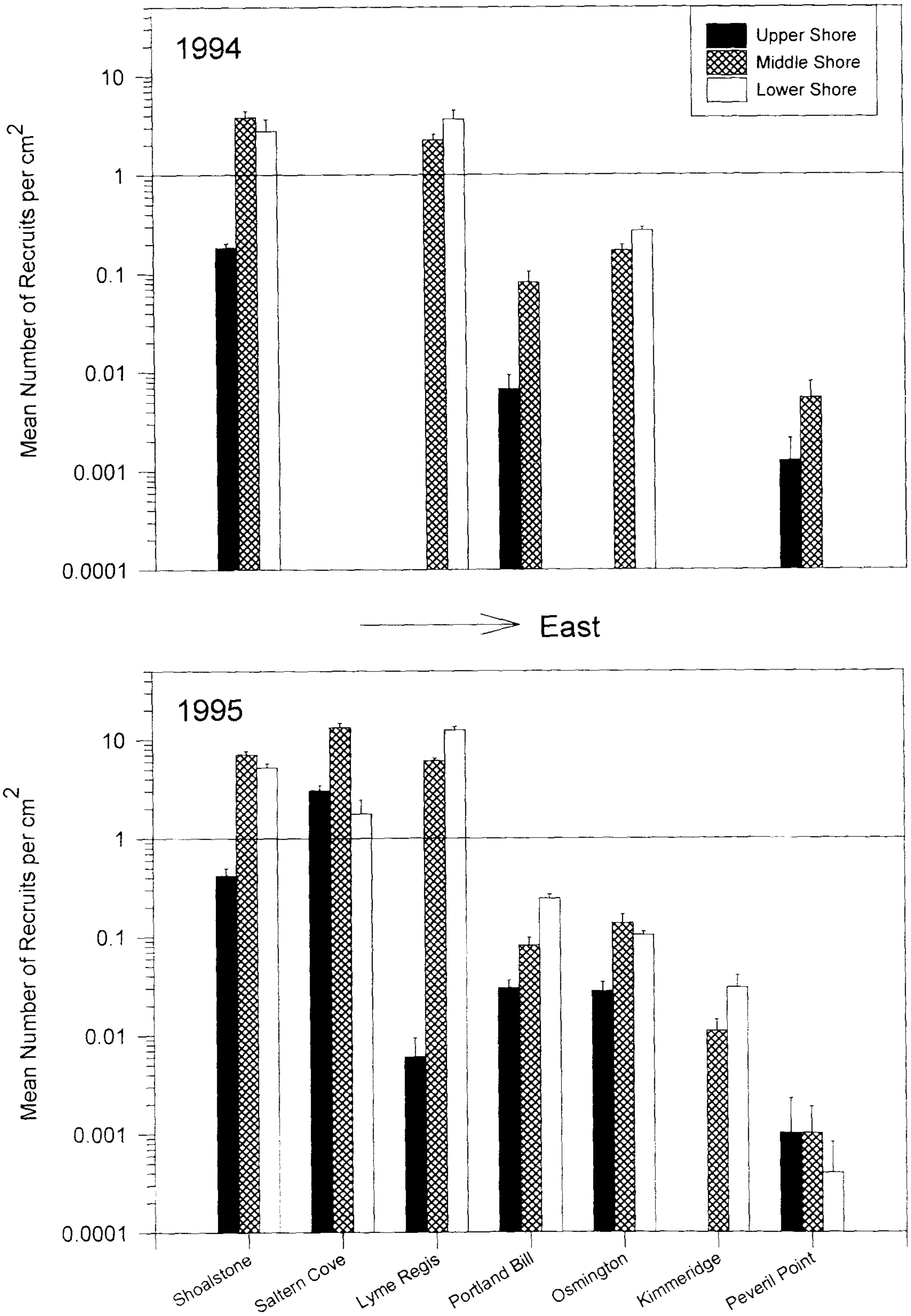


Fig. 5.2. Mean *Chthamalus* recruitment at three tidal levels along the south coast of England in 1994 and 1995. Counts made in mid-autumn within cleared $400cm^2$ quadrats (n = 6 at each level). Note Log scale. Error bars show +SE. Sites at Saltern Cove, Kimmeridge and lower shore of Portland Bill was not established until 1995.

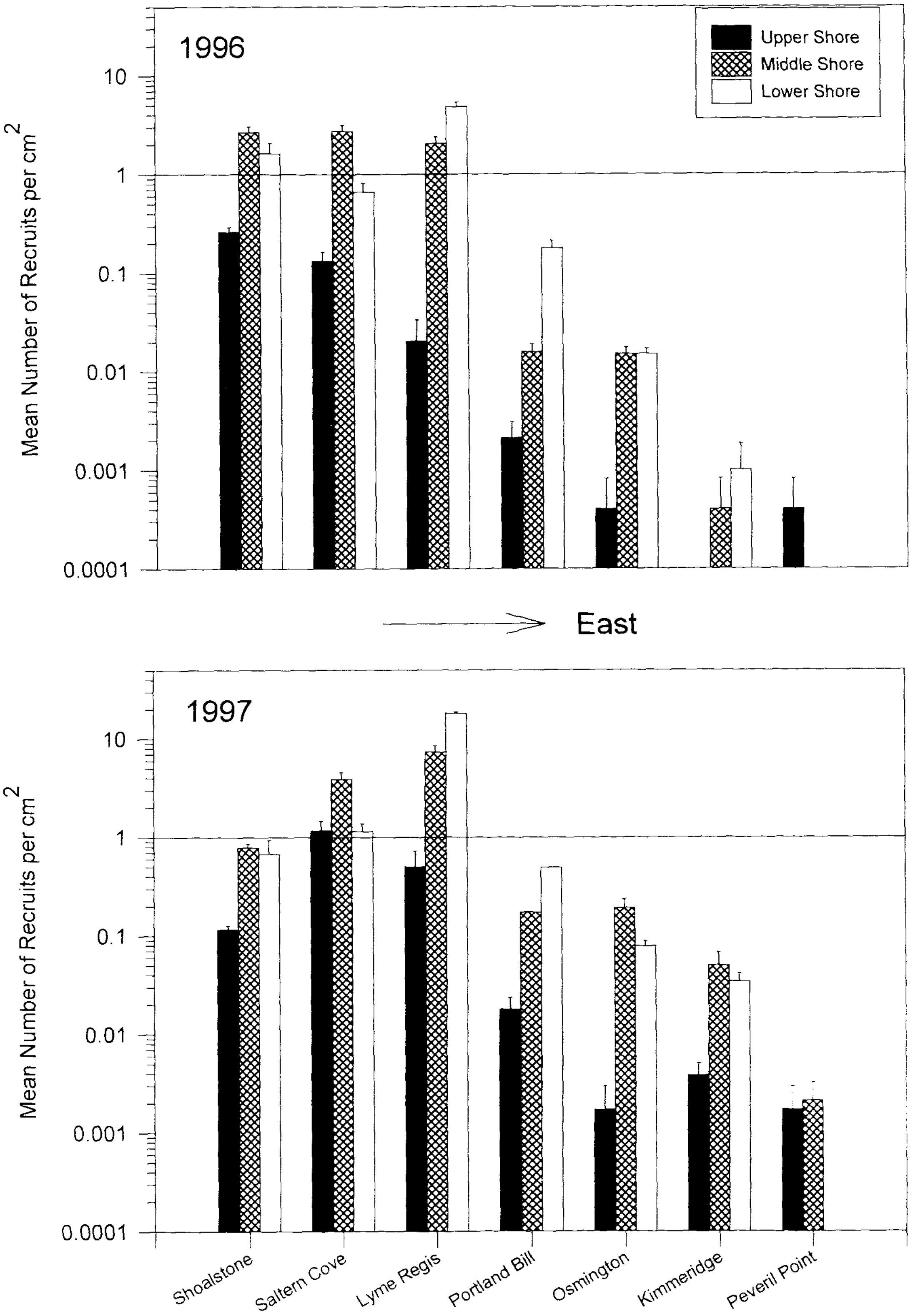


Fig 5.3 Mean *Chthamalus* recruitment at three tidal levels along the south coast of England in 1996 and 1997. Counts made in mid-autumn within cleared 400cm^2 quadrats (n = 6 at each level). Note Log scale. Error bars show +SE.

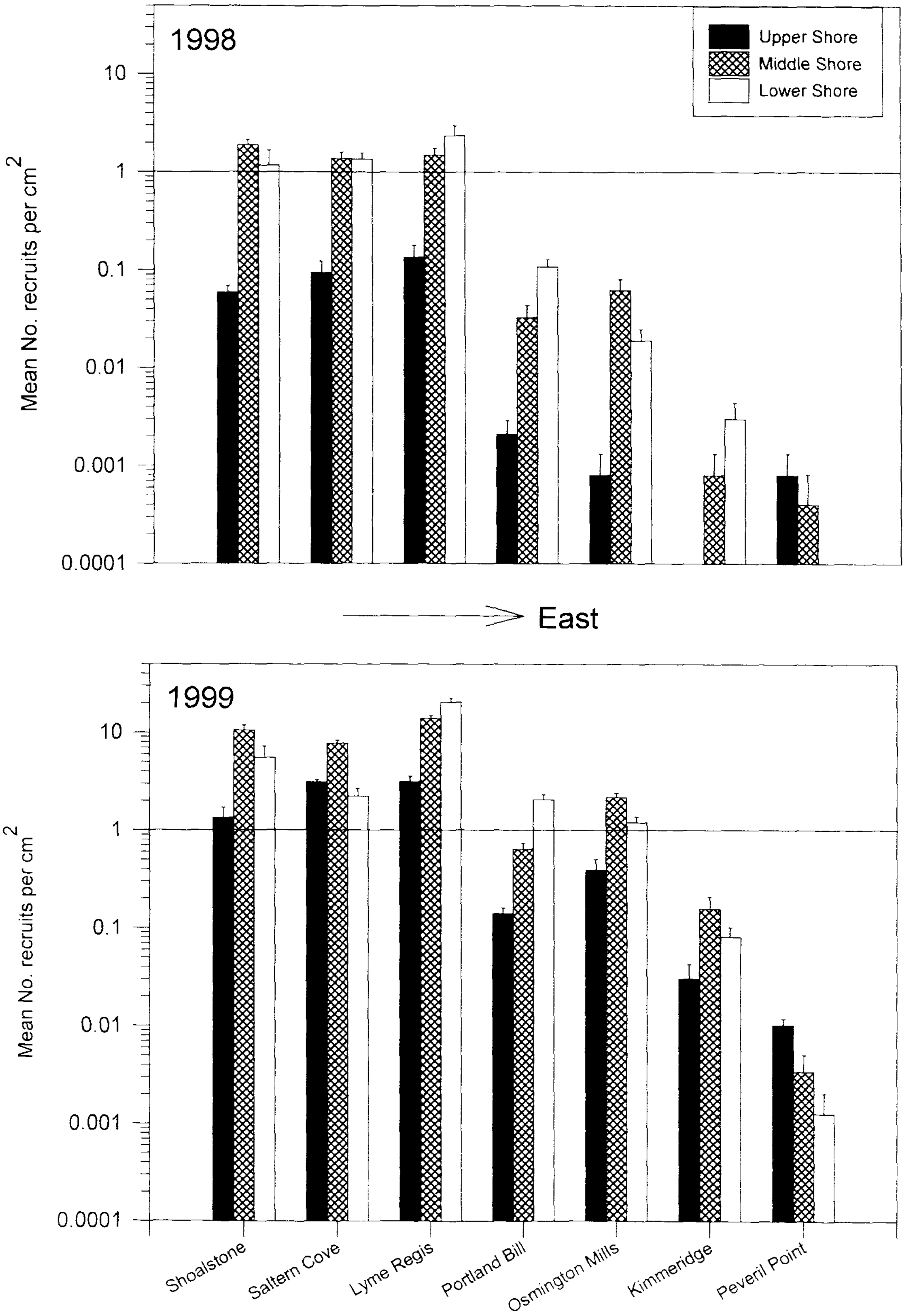


Fig 5.4. Mean *Chthamalus* recruitment at three tidal levels along the south coast of England in 1998 and 1999. Counts made within cleared 400cm^2 quadrats (n = 6 at each level) in mid-autumn. Note Log scale. Error bars show +SE.

Table 5.4a Three-way ANOVA of annual mean *Chthamalus* recruitment density (No. per cm^2) within cleared patches at shores West and East of Portland Bill (known as West and East coastal cells). See Figs 5.2-5.4 and text for further details. Data are untransformed; Cochrans test $p<0.01$ for each year. *P* values: * denotes $p< 0.05$,** denotes $p < 0.01$,*** denotes $p<0.001$

YEAR		1995			1996	
Source of variation	**df**	**MS**	***F***	**df**	**MS**	***F***
Cell = C	1	805.38	73.85***	1	74.38	25.06***
Shore = S (C)	4	10.91	5.48***	4	2.97	9.34***
Height =H	2	141.02	2.11	2	15.82	2.69
C X H	2	138.00	2.07	2	15.68	2.67
H X S (C)	8	66.81	33.6***	8	5.88	18.5***
Residual	90	1.99		90	0.32	

YEAR		1997			1998	
Source of variation	**df**	**MS**	***F***	**df**	**MS**	***F***
Cell = C	1	369.05	2.22	1	32.06	86.22***
Shore = S (C)	4	166.00	169.35***	4	0.37	1.32
Height =H	2	83.04	1.04	2	6.92	12.86
C X H	2	80.85	1.02	2	6.68	12.41**
H X S (C)	8	79.61	81.22***	8	0.54	1.91**
Residual	90	0.98		90	0.28	

YEAR		1999	
Source of variation	**df**	**MS**	***F***
Cell = C	1	1530.6	11.12*
Shore = S (C)	4	137.6	13.35***
Height =H	2	134.89	1.33
C X H	2	97.20	0.96
H X S (C)	8	101.1	9.81***
Residual	90	10.31	

SNK tests. '=' denotes no significant differences. * denotes $p< 0.05$,** denotes $p < 0.01$.

YEAR	**1995**	**1996**	**1997**	**1998**	**1999**
Cells	W>E	W>E	W = E	W>E	W>E
Means	5.5>0.035**	1.66>0.004**	3.74=0.04	1.01>0.01**	7.98>0.45*

Conclusions

Recruitment was significantly greater in the western cell than in the eastern cell in all years except 1997. In 1998, the difference between cells was dependent on the shore tidal height examined. There are significant differences between shores each year except in 1998. Each year the recruitment at a particular tidal height is dependent on shore.

Table 5.4b SNK multiple comparison tests *post* ANOVA in Table 5.4a on (i) recruitment density between shores and (ii) tidal height between shores
‘ ’ denotes no significant difference; ‘< >’ denotes significant difference $p < 0.05$.

(i) Shores within Cells: West Cell (Lr - Lyme Regis; Sc – Saltern Cove; Sh – Shoalstone).
East Cell (O - Osmington; K – Kimmeridge; P – Peveril Pt)

YEAR	**1995**	**1996**	**1997**	**1998**	**1999**
West Cell:	Lr = Sc >Sh	Lr > Sc = Sh	Lr > Sc > Sh	Lr = Sc = Sh	Lr > Sc = Sh
Mean No per cm^2	6.2 =6.06 > 4.23	2.3 > 1.18 = 1.52	8.62 > 2.06 > 0.53	1.33 = 0.94 = 1.03	12.42 > 5.75 = 5.76
East Cell:	O = K = P	O = K = P	O = K = P	O = K = P	O = K = P
Mean No per cm^2:	0.09 = 0.014 =0.001	0.01 = 0.0006 = 0.00	0.09 = 0.03 = 0.001	0.03 = 0.001 = 0.0004	1.25=0.09 = 0.003

(ii) Tidal heights between shores; Shore (Cell X Height):

UPPER SHORE

YEAR	**1995**	**1996**	**1997**	**1998**	**1999**
West Upper:	Sc > Sh = Lr	Sh = Sc = Lr	Sc = Lr = Sh	Lr = Sc = Sh	Sh < Sc > Lr
Mean No per cm^2:	3.05 > 0.42 = 0.006	0.26 = 0.13 = 0.02	1.17 = 0.5 = 0.12	0.1 = 0.09 = 0.05	1.34 < 7.3 > 3.13
East Upper:	O = K = P	O = K = P	O = K = P	O = K = P	O = K = P
Mean No per cm^2:	0.028 = 0.0004 = 0.001	0.0004 = 0.0 = 0.0	0.002 = 0.004 = 0.002	0.0008 = 0.0008 = 0.0	0.38 = 0.03 = 0.005

MIDDLE SHORE

YEAR	**1995**	**1996**	**1997**	**1998**	**1999**
West Middle:	Sc > Sh = Lr	Sh = Sc = Lr	Lr > Sc > Sh	Sh = Lr = Sc	Sc < Lr = Sh
Mean No per cm^2:	13.37 > 7.05 = 6.11	2.67 = 2.74 = 2.04	7.35 > 3.88 > 0.79	1.88 = 1.5 = 1.4	7.7 < 13.9 = 10.45
East Middle:	O = K =P	O = K = P	O = K = P	O = K = P	O = K = P
Mean No per cm^2:	0.14 = 0.01 = 0.001	0.02 = 0.0004 = 0.0	0.19 = 0.05 = 0.002	0.062 = 0.0008 = 0.0004	2.16 = 0.16 = 0.003

LOWER SHORE

YEAR	**1995**	**1996**	**1997**	**1998**	**1999**
West Lower:	Lr > Sh > Sc	Lr > Sh > Sc	Lr > Sc = Sh	Lr > Sc = Sh	Lr > Sh = Sc
Mean No per cm^2:	12.48 > 5.22 > 1.77	4.82 > 1.63 > 0.66	18 > 1.15 = 0.68	2.35 > 1.4 = 1.2	20.3 > 5.5 = Sc
East Lower:	O = K =P	O > K > P	O = K = P	O = K = P	O = K = P
Mean No per cm^2:	0.1 = 0.03 = 0.0004	0.015 = 0.001 = 0.0	0.08 = 0.03 = 0.0004	0.02 = 0.003 = 0.0	1.2 = 0.08 = 0.001

Table 5.4c SNK multiple comparison tests post ANOVA in Table 5.4a on (iii) differences between tidal height within shores ‘=’ denotes no significant difference; ‘< >’ denotes significant difference $p < 0.05$.

Upper shore (U);Middle shore (M); Lower shore (L).

(iii) Height (Cell X Shore)

YEAR	1995	1996	1997	1998	1999
Shoalstone (W)	M > L > U	M > L > U	U = M = L	M > L > U	M > L > U
Mean No per cm^2	7.05 > 5.21 > 0.42	2.67> 1.63 > 0.26	0.12 = 0.79 = 0.68	1.88 > 1.16 > 0.06	10.5 > 5.5 > 1.34
Saltern Cove (W)	M > L = U	M > L = U	M > U = L	M = L > U	M = U > L
Mean No per cm^2	13.4 > 1.8 = 3.04	2.74> 0.66 = 0.13	3.9 > 1.17 = 1.16	1.36 = 1.35 > 0.09	7.7 = 7.3 > 2.2
Lyme Regis (W)	L > M > U	L > M > U	L > M > U	L > M > U	L > M > U
Mean No per cm^2	12.5 > 6.1 > 0.006	4.82 > 2.04 > 0.02	18 > 7.4 > 0.5	2.35 > 1.5 > 0.14	20.3 > 13.9 > 3.1
Osmington (E)	U = M = L	U = M = L	U = M = L	U = M = L	U = M = L
Mean No per cm^2	0.03 = 0.13 = 0.1	0.0004 = 0.015 = 0.015	0.002 = 0.19 = 0.08	0.0008 = 0.62 = 0.02	0.4 = 2.2 = 1.2
Kimmeridge (E)	U = M = L	U = M = L	U = M = L	U = M = L	U = M = L
Mean No per cm^2	0.0004 = 0.01 = 0.03	0.0 = 0.0004 = 0.0013	0.004 = 0.05 = 0.03	0.0 = 0.008 = 0.003	0.28 = 0.16 = 0.08
Peveril Point (E)	U = M = L	U = M = L	U = M = L	U = M = L	U = M = L
Mean No per cm^2	0.001 = 0.001 = 0.0004	0.0 = 0.0 = 0.0	0.002 = 0.002 = 0.0004	0.008 = 0.0004 = 0.00	0.005 = 0.003 = 0.001

An SNK multiple comparison test revealed that, in the western cell, Lyme Regis frequently had significantly higher recruitment than either Saltern Cove or Shoalstone ($p < 0.01$), but this was largely because of the much greater densities found on the lower shore ($p < 0.01$). In 1997 the recruitment at Saltern Cove was greater than that at Shoalstone due to considerably higher densities at middle shore levels ($p < 0.01$). There is no natural rock platform above MTL/HWN at Lyme Regis so clearances were made on the flat upper surface of a concrete groyne. In some years however this was covered in shingle or had been badly scoured by sand. Differences between shores in the eastern cell were not resolved by SNK analysis because of the much larger variances, and considerably higher values in the west. A separate analysis was carried out on the eastern cell, which showed that the recruitment at Osmington Mills was greater than both Kimmeridge and Peveril Point but there was again a significant Height x Shore interaction ($p < 0.05$). Observations during August did not indicate any higher level of recruitment on the eastern shores that could have suffered mortality over the later summer months, perhaps due to high rock temperatures. Indeed during most years, no cyprids or metamorphosing recruits were seen at localities east of Portland Bill.

Because of the problem of inadequate spatial and temporal independence within the experimental design, i.e. use of same clearance sites each year to assess recruitment, it is difficult to analyse and present the data to show differences between years without violating statistical principles. Of particular interest, considering that *Chthamalus* is a southern species, was to find any evidence for an association between the magnitude of recruitment and sea temperature. However interannual differences in recruitment might theoretically be dependent on the density of recruits the previous year, as it is known that settling cyprids are attracted to arthropodin (Gabbott & Larman, 1987) which might have persisted on the rock surface since clearance was made. If recruitment was heavy at Year_1 then the recruitment in Year_2 might also be heavy because of the attractive residues left by the previous year's recruits. Similarly, if recruitment was light at Year_1 then recruitment might be similarly light in Year_2, unless of course independent factors were of greater importance. Temporal dependence was investigated using the data from Saltern Cove, with the hypothesis that the variance in recruitment with increasing separation between years might increase. This was examined by comparing the between-year variance in recruitment at three tidal levels at Saltern Cove. Fig. 5.5 shows a scatter graph of recruitment variance against increasing separation between years for six clearances on the lower shore. As there is no indication of a positive slope it can be concluded that measurements from the same quadrat in adjacent years are temporally independent. However spatial aspects of independence are not party to this analysis, and unless different quadrats are compared each year, the variability associated with the main factors of time, tidal height and shore would, arguably, be unreasonably reduced. During the five years of study between 1995-99, four years were sufficiently different to be classified as either warm or cool (see Chapter 2): 1995 and 1999 were distinctly warmer than 1996 and 1998. An analysis of variance with 'Year' nested within 'Temperature' was designed to compare the mean *Chthamalus* recruitment in warm and cool years.

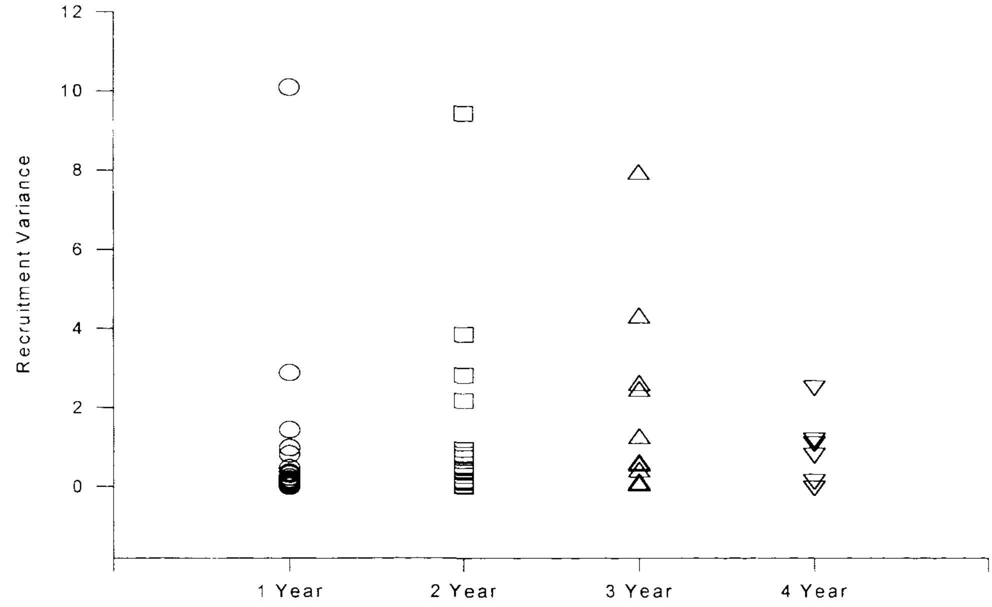


Fig. 5.5 Recruitment variance of *Chthamalus* spp. against increasing separation between years for six clearances on the lower shore at Saltern Cove, Devon. Column '1 Year' shows variance in mean recruitment between 1995 & 1996, 96 & 97, 97 & 98, 98 & 99; column '2 Year' shows variance in mean recruitment between 95 & 97, 96 & 98, 97 & 99; Column '3 Year' shows variance in mean recruitment between 95 & 98 and 96 & 99; Column '4 Year' shows variance in mean recruitment between 1995 & 1999.

Two different pairs of quadrats out of the six replicates from each site were used for three out of the four years, with a fourth pair being re-used after three years. The result of the ANOVA proved statistically insignificant($p>0.05$) but the design was abandoned due to the inadequate number of replicates. The annual deviation from 1995-99 mean recruitment is shown for each shore in Figs. 5.6 and 5.7. It will be observed that all shores along this section of coast had highest recruitment in 1999 except for Saltern Cove, where recruitment was marginally greater in 1995. The higher frequency of anticyclonic easterly winds during the summer of 1995 may have been responsible for the higher recruitment densities observed at both Torbay sites in that year. Similarly, all shores, except for Shoalstone, had their lowest recruitment in the cooler years of 1996 and 1998. The annual deviations in recruitment for each shore were correlated against each other to measure the degree of similarity; the coefficient values are shown in Table 5.6. All comparisons had 'r' values either equal or greater than 0.5, and of the twenty-eight correlation's made, half were statistically significant. Of the fourteen that were not significant, twelve were between one of the two Torbay sites and other shores. The correlation between the two Torbay sites, Shoalstone and Saltern Cove, was statistically significant. Using a Friedman test (Sokal & Rholf, 1997) the median recruitment of each year between 1995-1999 was compared across all eight sites from Saltern Cove in Devon to Hanover Point on the Isle of Wight. The result (Table 5.7) was highly significant ($\chi^2 = 22.8$, n = 8, df 4, $p < 0.001$) indicating that there is a high degree of consistency in the magnitude of *Chthamalus* recruitment at shores along the whole of this section of coast. This pattern would seem to imply that broad-scale factors, such as temperature and (or) wind direction, are responsible for recruitment variability rather than local factors such as wave exposure and shore aspect. It was decided to analyse the relationship with sea temperature in more detail. The mean July-September sea temperature was calculated for each year using data from Torquay and Weymouth (see Chapter 2). Burrows (1988) found that cyprid survival of *Chthamalus* spp. was greater at higher sea temperatures and concluded that the main larval settlement period along the south-west coast of Britain was between July and September. An examination of temperature data over the period of early gametogenesis and naupliar development, i.e. April-June, did not correlate well with the observed level of recruitment on the shore ($p > 0.05$). Fig. 5.8 shows a scattergraph of mean *Chthamalus* recruitment for the three shores in Lyme Bay against summer sea temperature. Linear regression was statistically significant: $r^2 = 0.47$, $F = 11.3$, $p = 0.005$, n = 15.

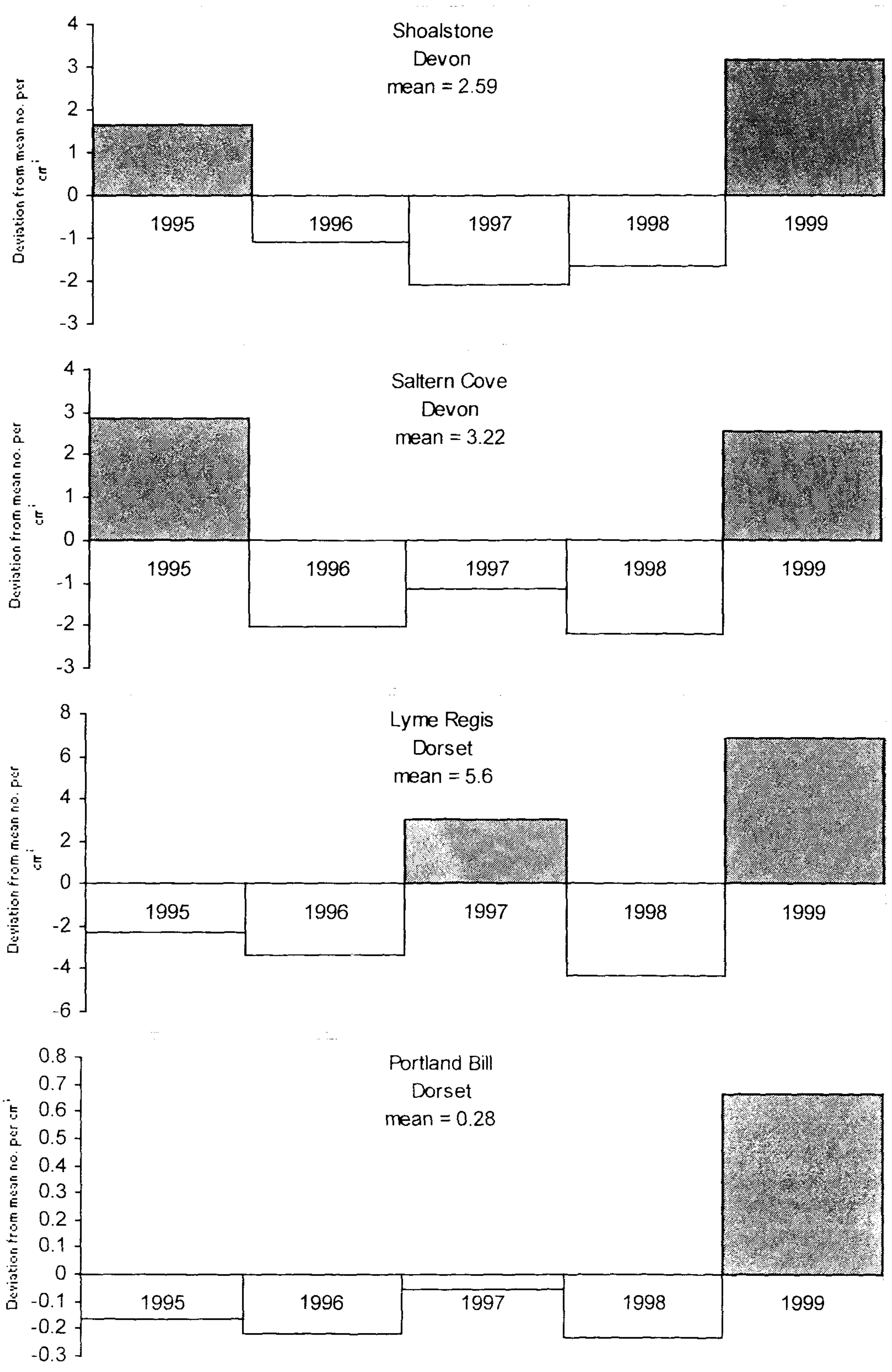


Fig. 5.6. Deviation from mean shore recruitment (1995-1999) of *Chthamalus* (No's per cm^2) at western sites. Measured within cleared areas (n = 6) at MHW, MTL and LWN.

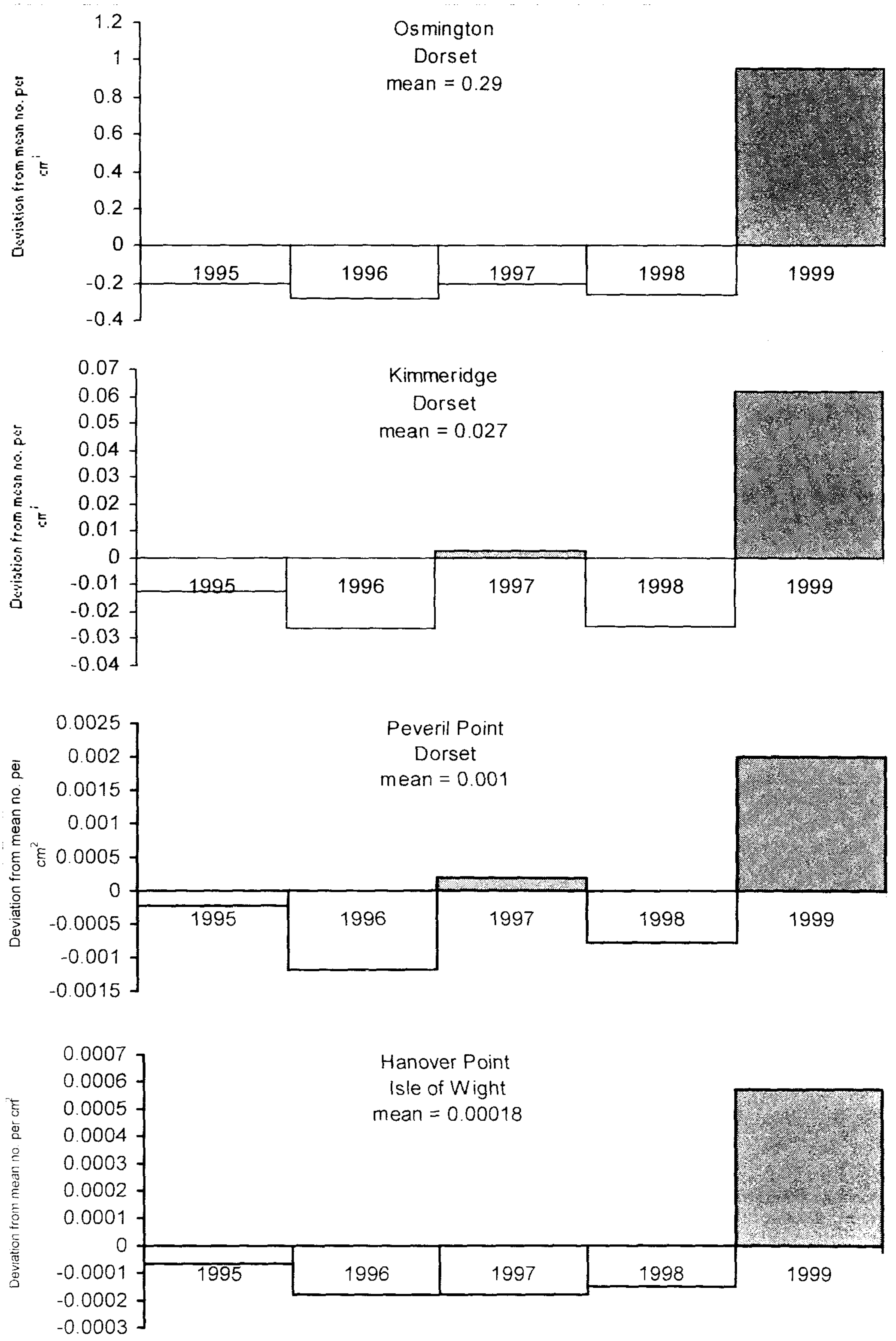


Fig. 5.7. Deviation from mean shore recruitment (1995-1999) of *Chthamalus* (No's per cm^2) at eastern sites. Measured within cleared areas (n = 6) at MHW, MTL and LWN.

Table 5.6 Correlation matrix showing 'r values' of annual departures from five-year mean shore recruitment of *Chthamalus* between 1995 and 1999 at sites along the south coast of England (see Figs 5.6 & 5.7). $p<0.05$*, $p<0.01$**, $p<0.001$***.

	Saltern Cove	**Lyme Regis**	**Portland Bill**	**Osmington**	**Kimmeridge**	**Peveril Point**	**Hanover Point**
Shoalstone	0.92*	0.5	0.73	0.78	0.72	0.52	0.84
Saltern Cove		0.5	0.59	0.6	0.62	0.68	0.67
Lyme Regis			0.9*	0.83	0.95*	0.94*	0.78
Portland Bill				0.97**	0.99**	0.96**	0.97**
Osmington					0.96**	0.93*	0.99***
Kimmeridge						0.99**	0.94*
Peveril Point							0.91*

Table 5.7 Rank order recruitment of *Chthamalus* at sites along 100km section of the south coast of England between 1995-1999. Rank 1 is highest recruitment. Rank 1 SST is highest mean July-September sea temperature. Results of Friedman test applied with H_0 'Years have same median recruitment' $\chi^2 = 22.8$, $n = 8$, df 4, $p < 0.001$***. Reject H_0 and accept H_1 that years differ.

	1995	**1996**	**1997**	**1998**	**1999**
Shoalstone	2	3	5	4	1
Saltern Cove	1	4	3	5	2
Lyme Regis	3	4	2	5	1
Portland Bill	3	4	2	5	1
Osmington	3	5	2	4	1
Kimmeridge	3	5	2	4	1
Peveril Point	3	5	2	4	1
Hanover Point (IOW)	2	4.5	4.5	3	1
Median Rank	**3**	**4.25**	**2**	**4**	**1**
Rank SST (Torquay)	**2**	**5**	**3**	**4**	**1**

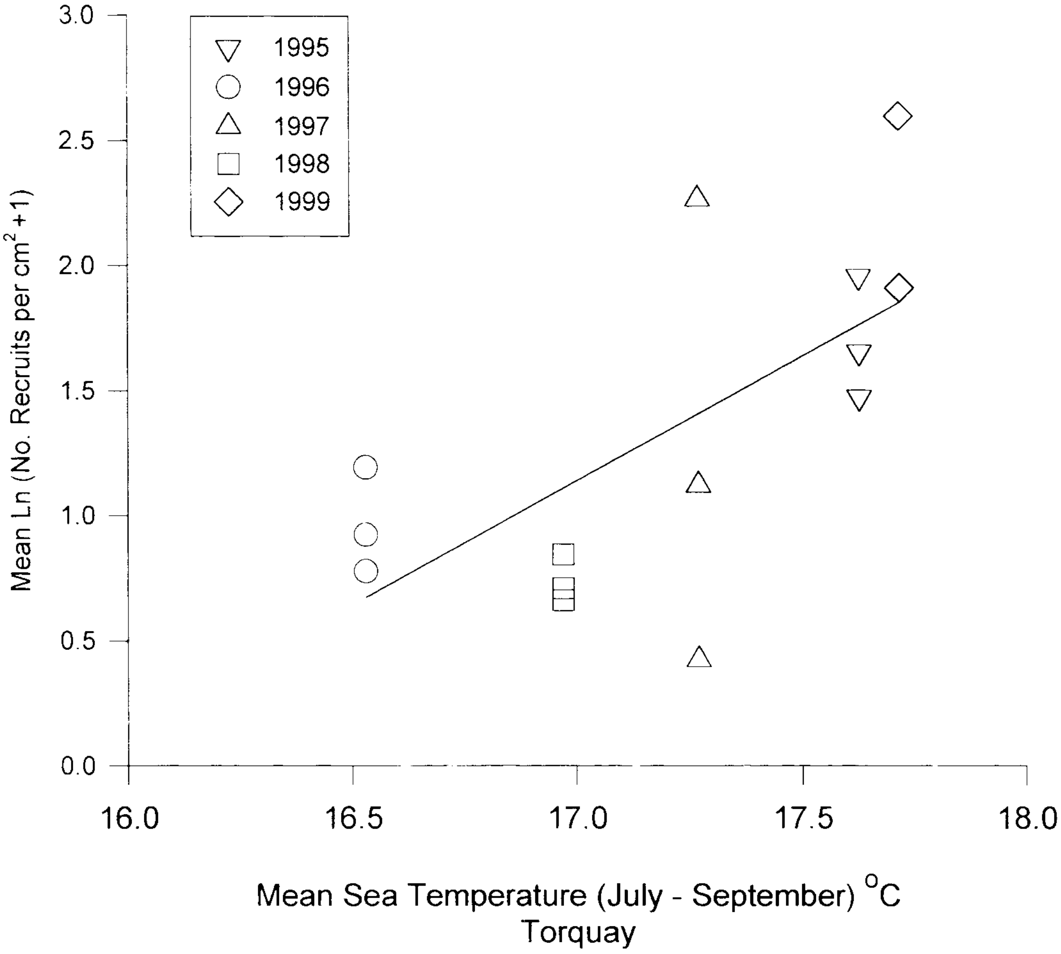


Fig 5.8. Mean shore recruitment of *Chthamalus* spp. at three shores within Lyme Bay against mean summer (July-September) sea temperature measured at Torquay. Linear regression $r^2 = 0.47$, $F = 11.3$, $p = 0.005$**, $n = 15$.

Individual shores along the Purbeck coast were examined separately and Fig.5.9 shows a scattergraph of mean recruitment against summer sea temperature for Osmington and Kimmeridge. The Kimmeridge and Osmington data are for the lower shore only and both show significant relationships with the mean July-September sea temperature measured at Torquay (Kimmeridge, $r^2 = 0.395$, $F = 18.2$ $p<0.001$; Osmington, $r^2 = 0.39$, $F = 17.9$, $p<0.001$).

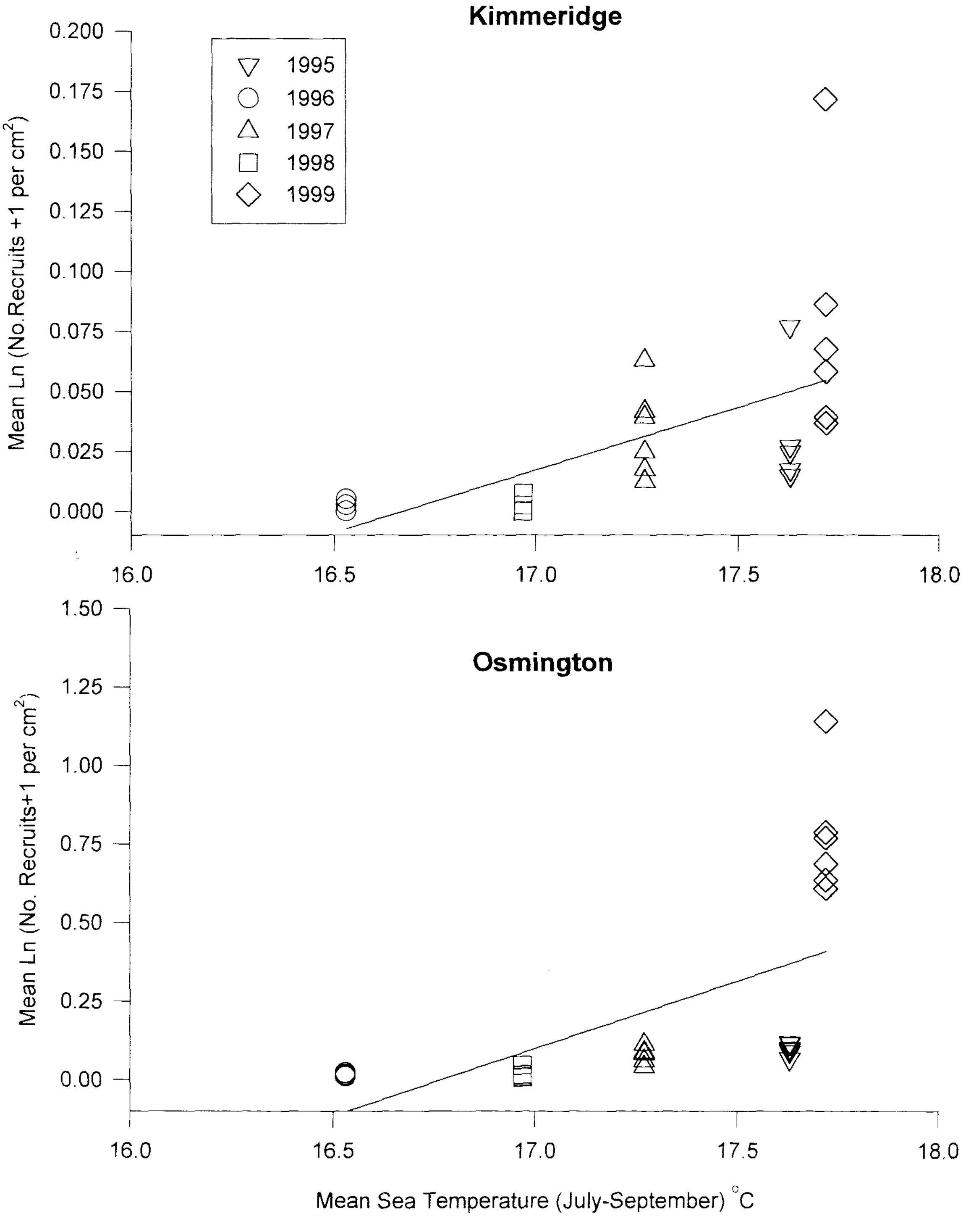


Fig 5.9 *Chthamalus* recruitment within lower shore patches (n = 6) against mean July-September sea temperature measured at Torquay. Kimmeridge:Linear regression $r^2 = 0.395$, $F = 18.2$, $p = <0.001$***. Osmington: Linear Regression. $r^2 = 0.39$, $F = 17.9$, $p = <0.001$***.

5.3.1.2 Recruitment of intertidal barnacle species on vertical surfaces at shores along the south coast of England during 1999.

Figs. 5.10 - 5.12 show the recruitment of *Semibalanus balanoides*, *Chthamalus* spp. and *Elminius modestus* within cleared quadrats made on vertical surfaces at shores within four coastal cells between Torbay and Beachy Head in 1999. From observations made on the Isle of Wight, *S. balanoides* settlement commenced in early April and was nearly over by the middle of May. Counts along the whole of the study area between Torbay and Beachy Head were made over a sixteen-day period between 13 – 29 May. The graphs strongly indicate that recruitment of *S. balanoides* was far greater along the Sussex coast than in any other cells further west. Densities were greatest on the piles of Worthing Pier, where mean and maximum densities of 22 and 30 per cm^2 respectively were measured on the upper shore. Considering the high space occupation and columnor growth of the recruits, which even in mid May was approaching 10mm, this is likely to be a gross underestimate of settlement density as considerable post-settlement mortality must have occurred due to intraspecific competition. Densities were so great that 'hummocking' was frequent in places. The upper shore densities are probably greater than that of middle and lower levels because of later settlement and reduced growth rate. There is a marked contrast between the high recruitment densities along the Sussex coast and that observed around the Isle of Wight and in east Dorset. Even in the relatively sheltered waters of the Solent the recruitment density at East Cowes was, in comparison, relatively low with a mean of 1.6 per cm^2 at one patch on the lower shore. At Kimmeridge, where *S. balanoides* recruitment on flat surfaces was almost zero, there were higher densities observed on vertical ledges, with a mean of 0.2 per cm^2 at one patch on the lower shore. In the east of Lyme Bay, relatively high recruitment densities were observed at Saltern Cove and Lyme Regis of 8 and 11 per cm^2 respectively. However at each of these sites there was considerable variability both between tidal levels and within tidal level. Table 5.8 shows the results of a four-way ANOVA to determine whether there was a significant difference in the magnitude of recruitment between coastal cells. It was not possible to stabilise variances through transformation. Differences between shores were dependent on tidal height examined (Height x Shore interaction $p < 0.01$).

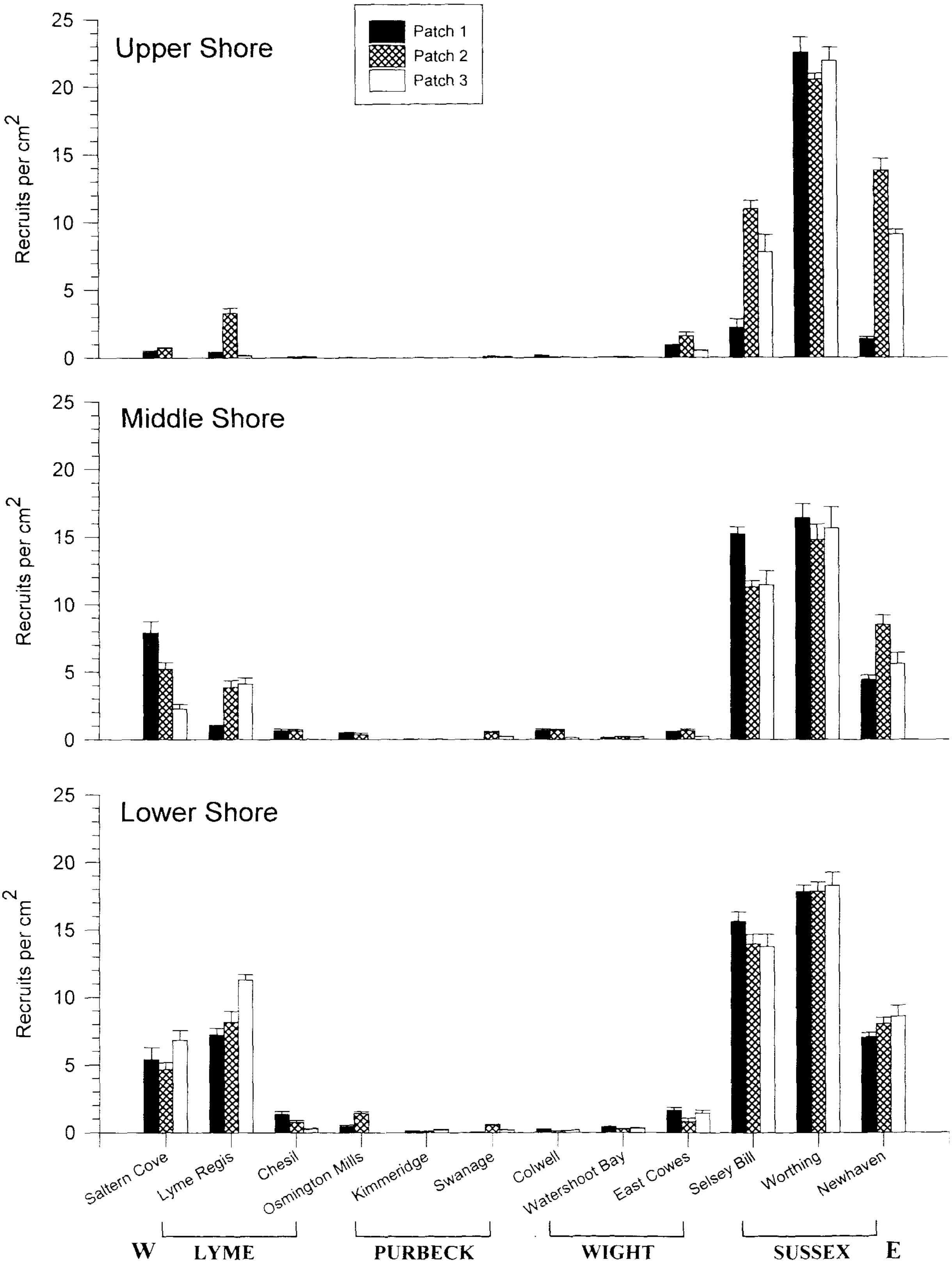


Fig 5.10 Mean recruitment of *Semibalanus balanoides* on vertical surfaces at shores along the central south coast of England in 1999. Counts made in mid-May; three patches of cleared 100cm^2 quadrats (n =10) at each tidal level. Error bars show + SE. Coastal cells shown in brackets below shore names.

The main conclusions from the analysis, followed by SNK multi-comparison procedure, are that there is a significant difference in recruitment between coastal cells (*F* = 10.98, $p < 0.01$) with the Sussex cell having greater recruitment than the other three cells further west ($p < 0.01$). The differences between shores were dependent on tidal height examined (Height x Shore interaction $p < 0.01$).

Table 5.9 Four-way ANOVA of *Semibalanus balanoides* recruitment within four cells along the south coast of England in May 1999. Three shores are located within each cell, and counts were made in 100cm^2 clearances ($n = 10$) in three separate patches at each of three tide heights: MHW, MTL and LWN. See Fig 10 and text for further details. Data are untransformed; Cochran's test $p < 0.01$. *P* values: * denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$.

(i) Analysis

Source of Variation	**df**	**MS**	***F***
Cell = C	3	8892.16	10.98**
Shores = S (C)	8	809.53	30.85***
Height = H	2	232.69	1.97
Patch = P (C X S X H)	72	26.24	12.79***
C X H	6	106.57	0.9
H X S (C)	16	118.32	4.51***
Residual	972	2.05	

SNK tests. '=' denotes no significant differences. * denotes $p<0.05$, **denotes $p<0.01$

(ii) Coastal Cells

Cell	**Lyme Bay (L)**	**Purbeck (P)**	**Isle of Wight (W)**	**Sussex (S)**
Mean No/cm^2	2.87	0.18	0.43	12.38

S > L**; S > P**; S > W**; L= P; W = P; L = W.

(iii) Shores (Cell)

Shores: Saltern Cove (Sc); Lyme Regis (Lr); Chesil (Ch); Osmington Mills (Om); Kimmeridge (Km); Swanage (Sw); Colwell (Cw); Watershoot Bay (Wb); East Cowes (Ec); Selsey Bill (Ss); Worthing Pier (Wo); Newhaven (Nh).

Cell	**Lyme Bay (L)**	**Purbeck (P)**	**Isle of Wight (W)**	**Sussex (S)**
Shores	Lr > Ch < Sc	Om = Km = Sw	Cw = Wb = Ec	Wo > Ss > Nh
Mean No/cm^2	4.5 > 0.4 < 3.7	0.3 = 0.05 = 0.2	0.2 = 0.2 = 0.9	18.4 >11.3 > 7.4

In May 1999, new clearances were made at each shore to prepare for measurement of *Chthamalus* and *Elminius* recruitment during the summer. Observations at Lyme Regis indicated that *Chthamalus* settlement commenced in late July, but that light *Elminius* recruitment had already occurred. There was a particularly heavy settlement of *Chthamalus* at Lyme Regis and at other shores in Lyme Bay during September, and so counts did not commence until later that month when spat could be more readily seen. Counts were made between 23th September and 7th November. The Sussex coast was visited first, in case the expected higher *Elminius* recruitment quickly smothered any *Chthamalus* recruits. To in some way compensate for this earlier examination at the limits of the species range, the Isle of Wight shores in the neighbouring cell were visited last to determine whether any late settlement had occurred. Fig 5.11 clearly illustrates the high densities of *Chthamalus* observed in Lyme Bay and Purbeck and the near absence in the adjacent Isle of Wight cell. The highest mean patch density was 28 per cm^2 on the lower shore at Lyme Regis, but at Chesil it was the upper shore that had greatest recruitment (17 per cm^2). The most eastern site where recruitment was observed was at Watershoot Bay near St. Catherines Point on the Isle of Wight. Again there was considerable variability between patches at each tidal level. The results of a four-way ANOVA and SNK *post hoc* test, shown in Table 5.10, demonstrates that there is a significant difference between cells, with the Lyme Bay cell having a significantly higher recruitment than the other cells further east ($F = 13.12$, $p < 0.01$). A strong Height x Shore interaction indicates that differences between shores depends on the tidal height examined. The recruitment of *Elminius* along the south coast is presented in Fig.5.12. Highest counts were along the Sussex coast with 16 and 23 per cm^2 being the mean and maximum recorded for a single patch at Selsey Bill. Higher counts were expected for the Solent as the species is known to tolerate low salinities. The graph clearly shows differences between the Sussex cell and the other three cells to the west, yet because of the high variances, ANOVA, presented in Table 5.11, failed to resolve any differences between cells and differences between shores were dependent on tidal height examined.

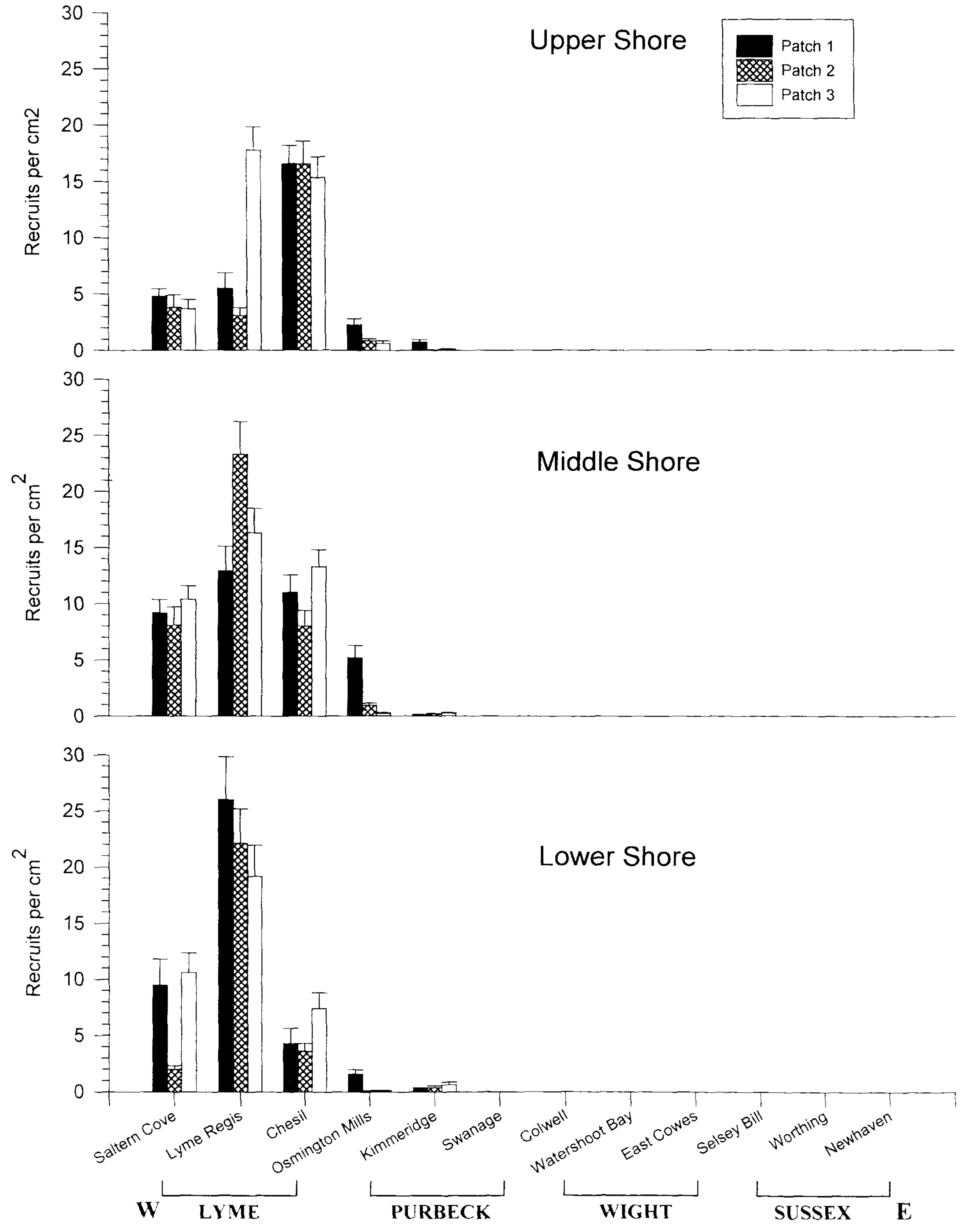


Fig 5.11. Mean recruitment of *Chthamalus* spp. on vertical surfaces at shores along the south coast of England during 1999. Counts made between September and November; three patches of cleared 100cm^2 quadrats (n =10) at each tidal level. Error bars show +SE. Coastal cells in brackets beneath shore names.

Table 5.10 Four-way ANOVA of *Chthamalus* spp. recruitment within four coastal cells along the south coast of England in autumn 1999. Three shores are located within each cell. and counts were made in $100cm^2$ clearances (n = 10) in three separate patches at each of three tide heights: MHW. MTL and LWN. See Fig 5.11 and text for further details. Data are untransformed; Cochran's test $p < 0.01$. *P* values: * denotes $p< 0.05$, ** denotes $p < 0.01$, *** denotes $p<0.001$.

(i) Analysis

Source of Variation	**df**	**MS**	***F***
Cell = C	3	9099.99	13.12**
Shores = S (C)	8	693.82	14.91***
Height = H	2	63.86	0.19
Patch = P (C X S X H)	72	46.53	6.11***
C X H	6	57.95	0.18
H X S (C)	16	327.77	7.04***
Residual	972	7.62	

SNK tests. '=' denotes no significant differences. * denotes $p<0.05$, **denotes $p<0.01$

(ii) Coastal Cells

Cell	**Lyme Bay (L)**	**Purbeck (P)**	**Isle of Wight(W)**	**Sussex (S)**
Mean No.per cm^2	11.78	0.54	0.0003	0.0

L > P**; L >W**; L > S**; P = W; P = S; S = W

(iii) Shores (Cell)

Shores: Saltern Cove (Sc); Lyme Regis (Lr); Chesil (Ch); Osmington Mills (Om); Kimmeridge (Km); Swanage (Sw); Colwell (Cw); Watershoot Bay (Wb); East Cowes (Ec); Selsey Bill (Ss);Worthing Pier (Wo); Newhaven (Nh).

Cell	**Lyme Bay (L)**	**Purbeck (P)**	**Isle of Wight (W)**	**Sussex (S)**
Shores	Lr > Ch > Sc	Os = Km = Sw	Cw = Wb = Ec	Ss = Wo = Nh
Mean No. per cm^2	17.8> 10.7 > 6.9	1.3 = 0.3 = 0.003	$6 \times 10^{-4} = 3 \times 10^{-4} = 0$	0= 0 = 0

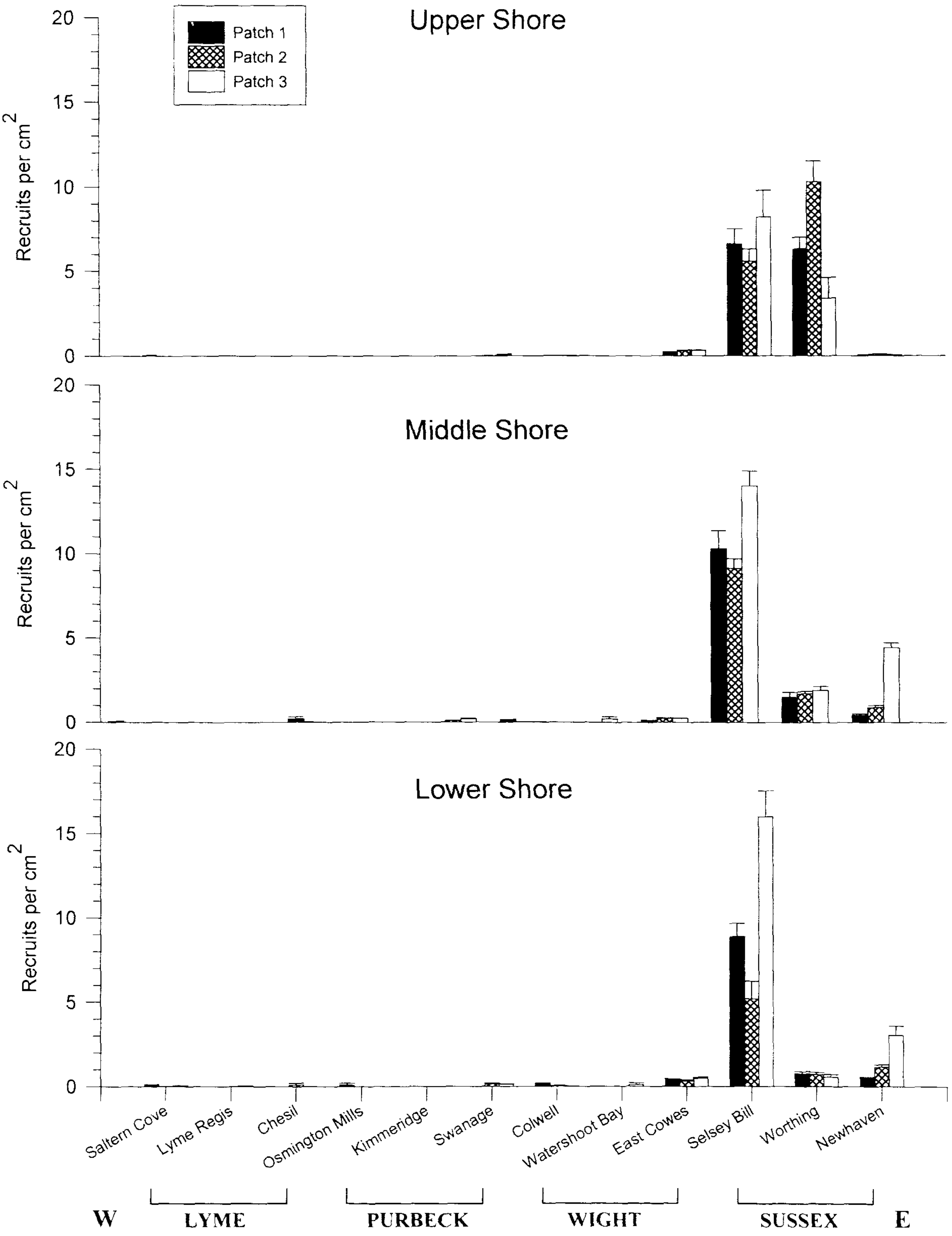


Fig. 5.12. Mean recruitment of *Elminius modestus* on vertical surfaces at shores along the south coast of England during 1999. Counts made between September and November; three patches of cleared 100cm^2 quadrats (n=10) at each tidal level. Error bars show +SE. Coastal cells shown below shore names.

Table 5.11 Four way ANOVA of *Elminius modestus* recruitment within four coastal cells along the south coast of England in autumn 1999. Three shores are located within each cell, and counts were made in 100cm^2 clearances ($n = 10$) in three separate patches at each of three tide heights: MHW, MTL and LWN. See Fig 12 and text for further details. Data are untransformed; Cochran's test $p < 0.01$. *P* values: * denotes $p< 0.05$, ** denotes $p < 0.01$, *** denotes $p<0.001$.

(i) Analysis

Source of Variation	**df**	**MS**	***F***
Cell = C	3	1324.55	3.22
Shores = S (C)	8	411.35	25.81***
Height = H	2	3.22	0.05
Patch = P (C X S X H)	72	15.94	11.76***
C X H	6	4.34	0.07
H X S (C)	16	59.39	3.73***
Residual	972	1.35	

SNK tests. '=' denotes no significant differences. * denotes $p<0.05$, **denotes $p<0.01$

(ii) Coastal Cells

Cell	**Lyme Bay (L)**	**Purbeck (P)**	**Isle of Wight (W)**	**Sussex (S)**
Mean No. per cm^2	0.068	0.036	0.12	4.5

S>W*; L = P; L = W; L = S; P = W; P = S.

(iii) Shores (Cell)

Shores: Saltern Cove (Sc); Lyme Regis (Lr); Chesil (Ch); Osmington Mills (Om); Kimmeridge (Km); Swanage (Sw); Colwell (Cw); Watershoot Bay (Wb); East Cowes (Ec); Selsey Bill (Ss); Worthing Pier (Wo); Newhaven (Nh).

Cell	**Lyme Bay (L)**	**Purbeck (P)**	**Isle of Wight (W)**	**Sussex (S)**
Shores	Sc = Lr = Ch	Os = Km = Sw	Cw = Wb = Ec	Ss > Wo > Nh
Mean No. per cm^2	0.2 = 0.006 = 0.01	0.04 = 0.001 = 0.07	0.05 = 0.03 = 0.2	9.3> 3.0 > 1.2

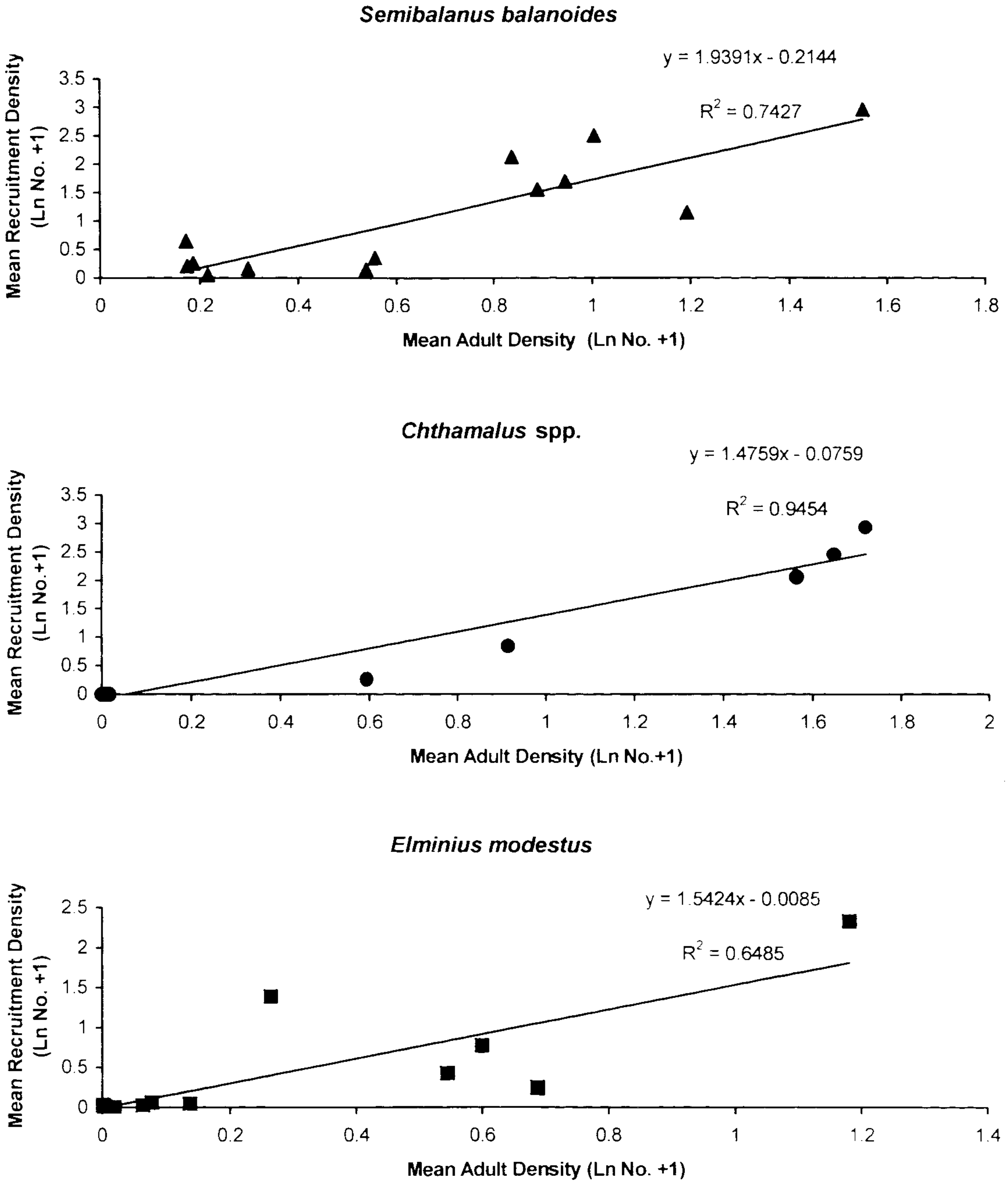


Fig. 5.13 Mean shore density of recruits (1999 cohort) plotted against the mean shore background density of adults for each species at different shores along the south coast of England. Counts on vertical surfaces. For all species there is a strong correlation coefficient: (*S. balanoides*, $r = 0.86$, $p<0.001$; *Chthamalus* spp., $r = 0.97$, $p<0.001$; *E. modestus* $r = 0.8$, $p<0.001$).

There are good correlations between recruitment density and background adult density (Fig 5.13). This could indicate that although the magnitude of recruitment might vary from year to year the pattern across the south coast in recent years is likely to have been similar to that observed during 1999.

5.3.1.3 Model of Recruitment

Table 5.11 column (o) shows the recruitment of *Chthamalus* in 1995 within different coastal cells as a proportion of the estimated annual larval output. Because barnacle populations are essentially open systems, larvae arriving on to the shore are unlikely to originate totally from the parental population. An attempt is therefore made to consider the magnitude of recruitment at the coastal process cell level (column a). The overall area of intertidal rock (column b) within each cell was determined in Chapter 2. Because of the decline in adult population density along the Purbeck coast, the cell has been divided into three sections (see Table 5.11 legend for details). The barnacle zone on each shore was estimated on average to be 75% of the total rock area (c). This figure was then divided in to upper, middle and lower zones (d-g). Adult densities were determined in October of 1995. The annual mean number of broods per year (h) is an average figure taken from (Burrows,1988) who estimated that barnacles on the upper shore had between 1-2 broods, middle shore 2-3 broods and lower shore 2.5-4 broods annually. The number of larvae released per brood has been determined for the mean opercular diameter size-class within that cell, based on the regression lines shown in Chapter 4 (Fig.4.9;Table 4.13). The recruitment within each cell or sub-cell was measured in October. The results for 1995 show that the percentage of larval production that recruit on to the shore is proportionally reduced towards the eastern geographic limits of the species. Of particular note is the reduction from 0.16% to 0.0028% between Lyme Bay and Purbeck. A further order of magnitude reduction occurs along the east Purbeck coast, which could partly be due to a lower number of embryos produced by the Kimmeridge population because of their relatively small adult size.

			Mean Adult Density per cm^2							Recruitment on shore No. per cm^2				
a	b	c	d	e	f	g	h	i	j	k	l	m	n	o
Cell	Rock area km^2	Zone Area cm^2	Upper zone	Mid zone	Low zone	Total No. in cell	No. of Broods per year	No. of eggs Per brood	Total No. of larvae per cell	Upper zone	Middle zone	Lower zone	Recruits per Cell	% Recruitment
Lyme	2.53	6.33×10^{9}	2.17	5.4	2.7	6.48×10^{10}	2.6	400	6.7×10^{13}	1.16	8.84	6.49	1.04×10^{11}	1.6×10^{-1}
Purbeck a	0.18	4.61×10^{8}	0.82	3.0	3.4	3.29×10^{9}	2.6	600	5.1×10^{12}	0.03	0.11	0.17	1.44×10^{8}	2.8×10^{-3}
Purbeck b	0.34	8.41×10^{8}	0.07	0.4	0.7	9.35×10^{8}	2.6	600	1.5×10^{12}	0.0004	0.01	0.03	3.51×10^{7}	2.4×10^{-3}
Purbeck c	0.03	7.76×10^{7}	0.13	0.0	0.0	1.37×10^{7}	2.6	200	7.1×10^{9}	0.0013	0.0013	0.0004	2.26×10^{5}	3.2×10^{-4}
Wight	1.10	2.75×10^{9}	0.02	0.0	0.0	1.08×10^{8}	2.6	400	4.2×10^{11}	0	0.0003	0.0001	9.17×10^{5}	8.2×10^{-4}
Sussex	2.70	6.75×10^{9}	0	0	0.0	0	0	0	0	0	0	0	0	0

Table 5.11. Estimate of larval production and % recruitment of *Chthamalus* within coastal cells approaching eastern geographic limits. Data for adult and recruitment density is from 1995. Coastal Cell Boundaries: *'Lyme'* -Prawle Point to Portland Bill; *'Purbeck (a)'* -Portland Bill to Lulworth Cove; *'Purbeck b'* -Lulworth to St.Albans Head; *'Purbeck (c)'* -St.Albans Head to Studland; *'Wight'* -Studland to Selsey Bill; *'Sussex'* -Selsey Bill to Beachy Head. Rock area data obtained using GIS (Chapter 2). Area of each zone is 25% of total rock area. No.of annual broods is mean shore figure (Burrows,1988; Chapter 4 of this work). Value 'No. of eggs per brood' has been determined for mean size class (opercular diameter) within that cell (Chapter 3 & Chapter 4). Percentage recruitment is proportion of total larvae produced per cell that recruit onto shores within that cell (measured in mid-October). See text for further detail.

5.3.2 **Growth rate of *Chthamalus montagui***

5.3.2.1 Growth of 1994 and 1995 cohorts on shores along the south coast of England

Although both the rostro-carinal diameter and opercular diameter were measured for all barnacles, the correlation between opercular diameter and biomass (Chapter 4) was sufficiently strong to use this parameter as an indicator of animal size. The size of the 1994 cohort measured in May 1995 is presented in Fig.5.14.

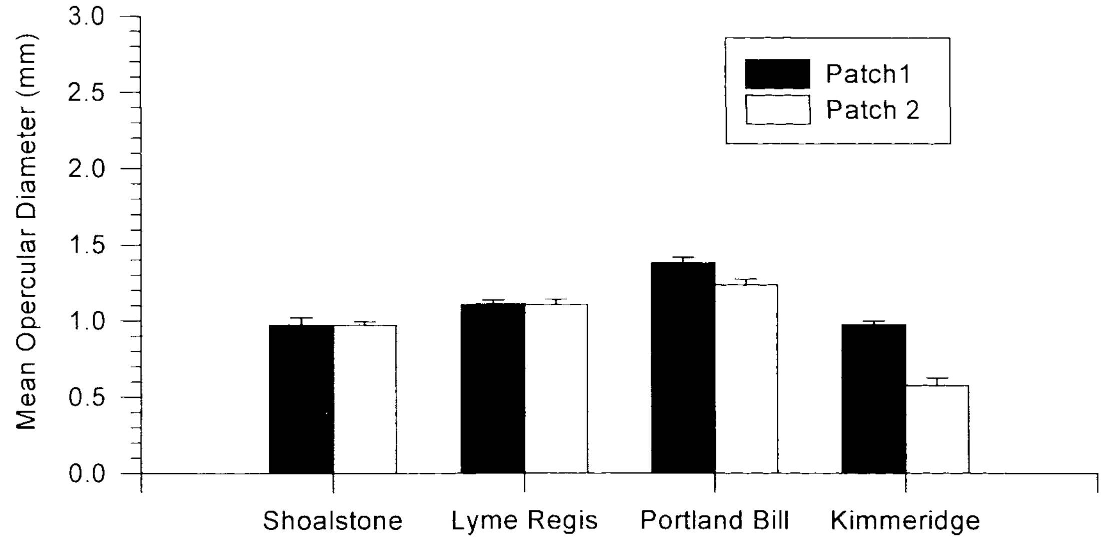


Fig 5.14 1994 cohort of *C.montagui* measured in two patches on four shores along the south coast of England at MTL in May 1995. Error bars show +SE. Shoalstone, n = 6 & 6; Lyme Regis, n = 12 & 12; Portland, n = 8 & 12; Kimmeridge, n = 5 & 2).

Because of observed differences, and particularly the smaller size reached by the most eastern population at Kimmeridge, a more detailed examination of growth rate was undertaken with the 1995 cohort. In Figs.5.15-5.16 seasonal growth curves for the 1995 cohort of *C.montagui* are presented for Saltern Cove, Portland Bill and Kimmeridge at three tidal heights. The same animals were followed for nearly two years. It was not possible to visit these sites over the mid-winter period so the detailed pattern of growth over the coldest months has not been established. It was observed that there was already a significant difference in the initial size of recruits measured in October 1995, both between shores and tidal heights. Table 5.12 shows the results of a two-way ANOVA that indicates that the differences are highly statistically significant, with the smallest animals being at high tidal levels at Kimmeridge. However a comparison of the growth

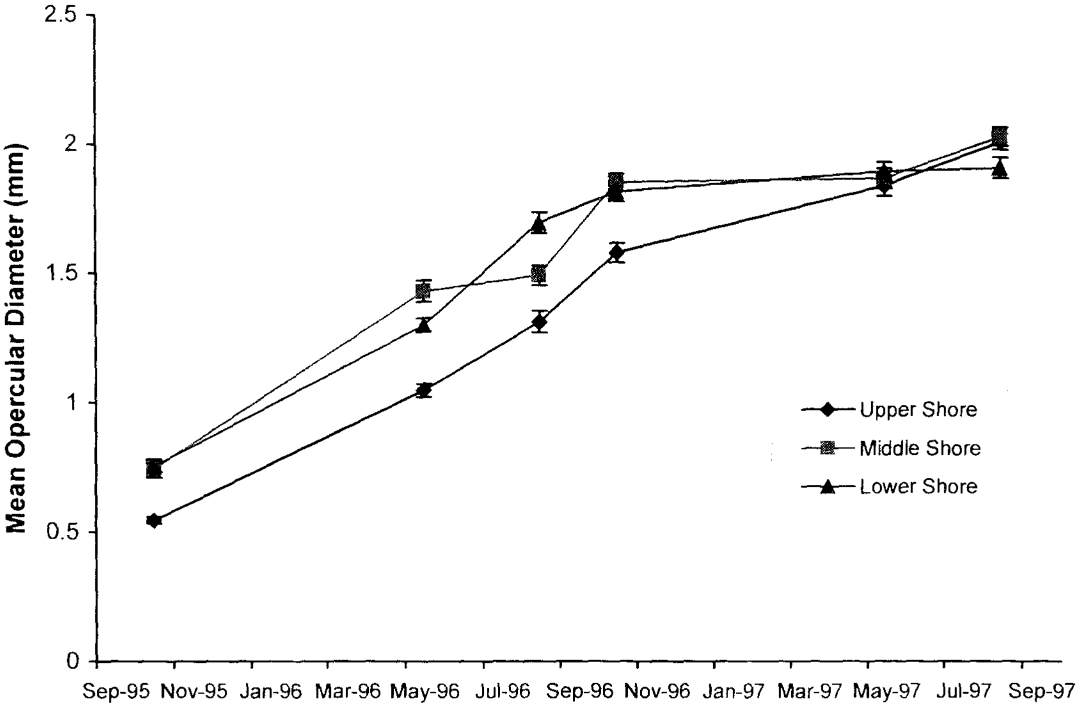


Fig 5.15 Growth of 1995 cohort *C.montagui* at Saltern Cove, Devon . Error bars show ± SE. Upper, n = 21-25; Middle, n = 25; Lower, n = 25.

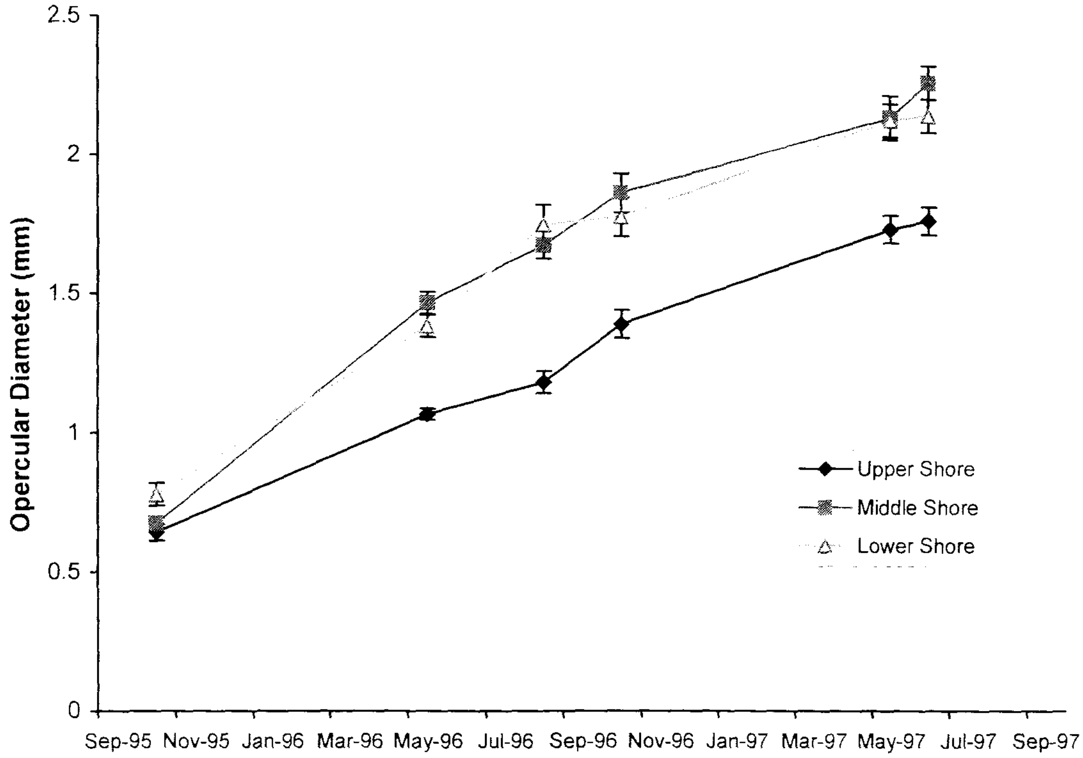


Fig 5. 16. Growth of 1995 cohort *C. montagui* at Portland Bill, Dorset. Error bars show ±SE. Upper, n = 15-11; Middle, n = 18-9; Lower, n = 21-9.

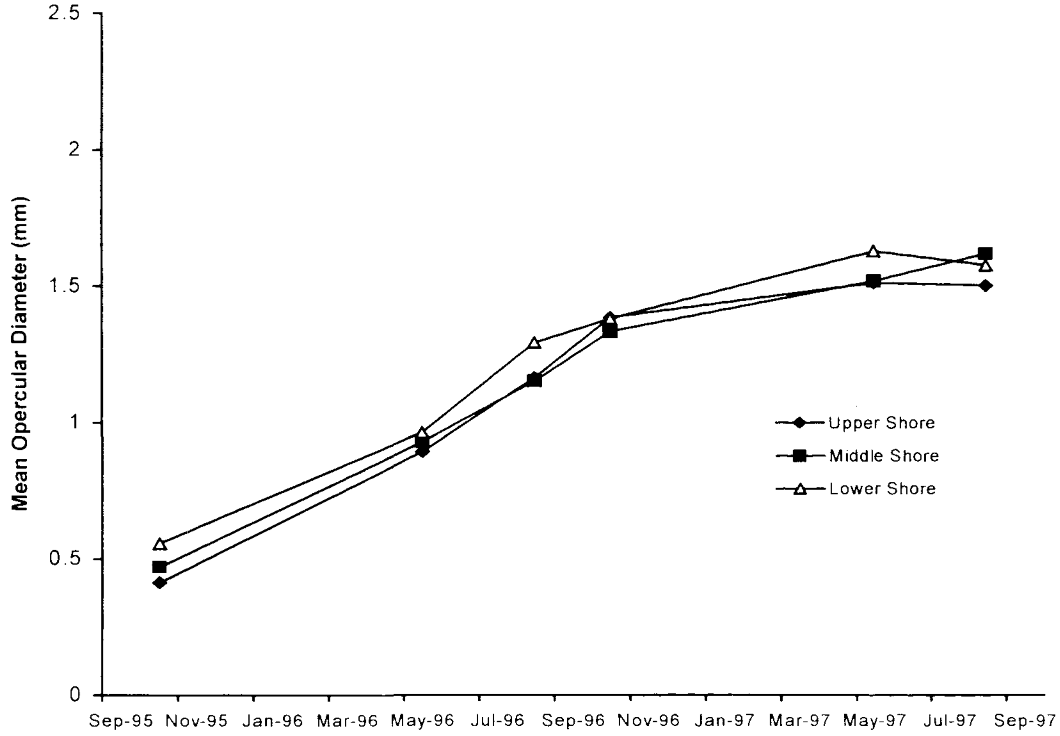


Fig 5.17. Growth of 1995 cohort *C. montagui* at Kimmeridge, Dorset. Error bars omitted for clarity. Upper, n = 12-4; Middle, n = 23-15; Lower, n = 25-16.

rates over the first winter did not reveal any statistically significant differences between shores (Table 13), although those at higher and mid tidal levels at Saltern Cove and Kimmeridge grew significantly faster than animals on the lower shore (Tables 5.14 - 5.16). Differences in growth rate between shores measured between October 1995 and the middle of the second summer in August 1997 were not significant ($p = 0.086$), although there was a highly significant difference in growth rate at different tidal heights and a significant Height x Shore interaction (Table 5.17). Animals on the upper shore at Saltern Cove had higher growth rate than those on the upper shore at Portland Bill, although at middle shore heights, those at Kimmeridge grew faster. The faster growth rates at higher tidal levels may be an attempt to compensate for the initially small size resulting from later settlement.

Table 5.12 Two-way ANOVA of opercular size of 1995 cohort of *Chthamalus montagui* measured in October 1995 at three tidal heights on three shores; Saltern Cove (n = 10), Portland Bill (n =10) and Kimmeridge (n = 10). Data were Log_e transformed.

Source of variation	df	MS	*F*	*P*
Shore	2	1.213	38.62	<0.001***
Height	2	0.645	20.54	<0.001***
Shore x Height	4	0.0156	0.5	0.739
Residual	80	0.0314		
Total	88	0.0713		

SNK Tests on Shores; '=' denotes no significant difference, '>' denotes significant difference, p <0.05. Saltern Cove (SC); Portland Bill (PB); Kimmeridge (KM).

Shores	PB > SC > KM
Mean size (mm)	0.706 > 0.622 > 0.476

SNK Test on Height: Upper (U); Middle (M); Lower (L)

Height	L > M > U
Mean size (mm)	0.69 > 0.595 > 0.519

Table 5.13 Two-way ANOVA of winter opercular growth rate of the 1995 cohort of *Chthamalus montagui* measured at Saltern Cove (n = 10), Portland Bill (n = 9), and Kimmeridge (n = 10) on upper, middle and lower shore. Growth rate expressed as Ln(opercular diameter May 1996) – Ln (opercular diameter October 1995). K-S Normality test p = 0.555; Levene equal variance test p = 0.0851. *P* values: * denotes p< 0.05,** denotes p < 0.01,*** denotes p<0.001.

Source of variation	df	MS	*F*	*P*
Shore	2	0.024	0.512	0.60
Level	2	0.377	8.14	<0.001***
Shore x Level	4	0.072	1.56	0.19
Residual	80	0.046		
Total	88	0.055		

There is no significant difference between shores.

Shores	SC = PB = KM
Mean Rate	0.672 = 0.626 = 0.678

SNK Test on shore levels. Upper Shore (U); Middle Shore (M); Lower Shore (L). '=' denotes no significant differences. > denotes p< 0.05.

Shore Levels	U = M > L
Mean Rate	0.669 = 0.766 > 0.541

Table 5.14 One-way ANOVA of winter opercular growth rate (October 1995-May 1996) of the 1995 cohort of *Chthamalus montagui* measured at three tidal levels (n = 10) at Saltern Cove.

Source of Variation	**df**	**MS**	***F***	***P***
Levels	2	0.16	4.12	0.0275*
Residual	27	0.039		
Total	29			

SNK Test on shore levels. Upper Shore (U); Middle Shore (M); Lower Shore (L).
'=' denotes no significant differences. > denotes $p< 0.05$.

Shore Level	M > L = U
Mean Rate	0.798 > 0.544 = 0.674

Table 5.15 One-way ANOVA of winter opercular growth rate (October 1995-May 1996) of the 1995 cohort of *Chthamalus montagui* measured at three tidal levels at Portland Bill. Upper and Middle n = 10, Lower, n = 9.

Source of Variation	**df**	**MS**	***F***	***P***
Levels	2	0.114	2.27	0.123
Residual	26	0.05		
Total	28			

Shore Level	U = M = L
Mean Rate	0.546 = 0.748 = 0.584

Table 5.16 One-way ANOVA of winter opercular growth rate (October 1995-May 1996) of the 1995 cohort of *Chthamalus montagui* measured at three tidal levels (n = 10) at Kimmeridge.

Source of Variation	**df**	**MS**	***F***	***P***
Levels	2	0.255	5.16	0.013*
Residual	27	0.049		
Total	29			

SNK Test on shore levels. Upper Shore (U); Middle Shore (M); Lower Shore (L).
'=' denotes no significant differences. > denotes $p< 0.05$.

Shore Level	U = M > L
Mean Rate	0.786 = 0.753 > 0.494

Table 5.17 Two-way ANOVA of growth rate of 1995 cohort of *Chthamalus montagui* over two years at three tidal levels on three shores: Saltern Cove (n = 10), Portland Bill (n =10) and Kimmeridge (n = 7). Growth rate expressed as Ln (opercular diameter August 1997) – Ln (opercular diameter October 1995). Equal variance test p = 0.36. Levene equal variance test p = 0.16; K-S test for normality 0.82.

Source of variation	**df**	**MS**	***F***	***P***
Shore	2	0.083	2.54	0.086
Height	2	0.284	8.76	<0.001***
Shore x Height	4	0.166	5.1	<0.001***
Residual	72	0.033		
Total	80	0.048		

SNK Tests on Shores: '=' denotes no significant difference, '>' denotes significant difference.

p <0.05. Saltern Cove (SC); Portland Bill (PB); Kimmeridge (KM).

Shores	PB = SC = KM
Mean Rate	1.08 = 1.18 = 1.08

SNK Test on Height: Upper (U); Middle (M); Lower (L)

Height	L < M = U
Mean Rate	1.02 < 1.21 = 1.1

Despite similarities in growth rate between shores, the proportional differences in opercular diameter observed shortly after recruitment in October 1995 were maintained over the following months. Fig.5.18 shows the mean opercular diameter of the 1995 cohort of *C. montagui* growing in different patches of the shore at MTL at different locations along the south coast of England in mid-May 1996, October 1996 and August 1997. Between October 1996 and August 1997, two of the patches at Portland Bill could not be found. The mean opercular diameter of animals growing on four shores were compared in May 1996 and in August 1997 using two-way ANOVA (Tables 5.18 and 5.19). Ten animals from two different patches were compared on each date to ensure temporal and spatial independence. By May 1996, after the first winter, the animals at Portland Bill were significantly larger than those at Lyme Regis and Kimmeridge but not significantly different from those on the shore at Saltern Cove. By August 1997

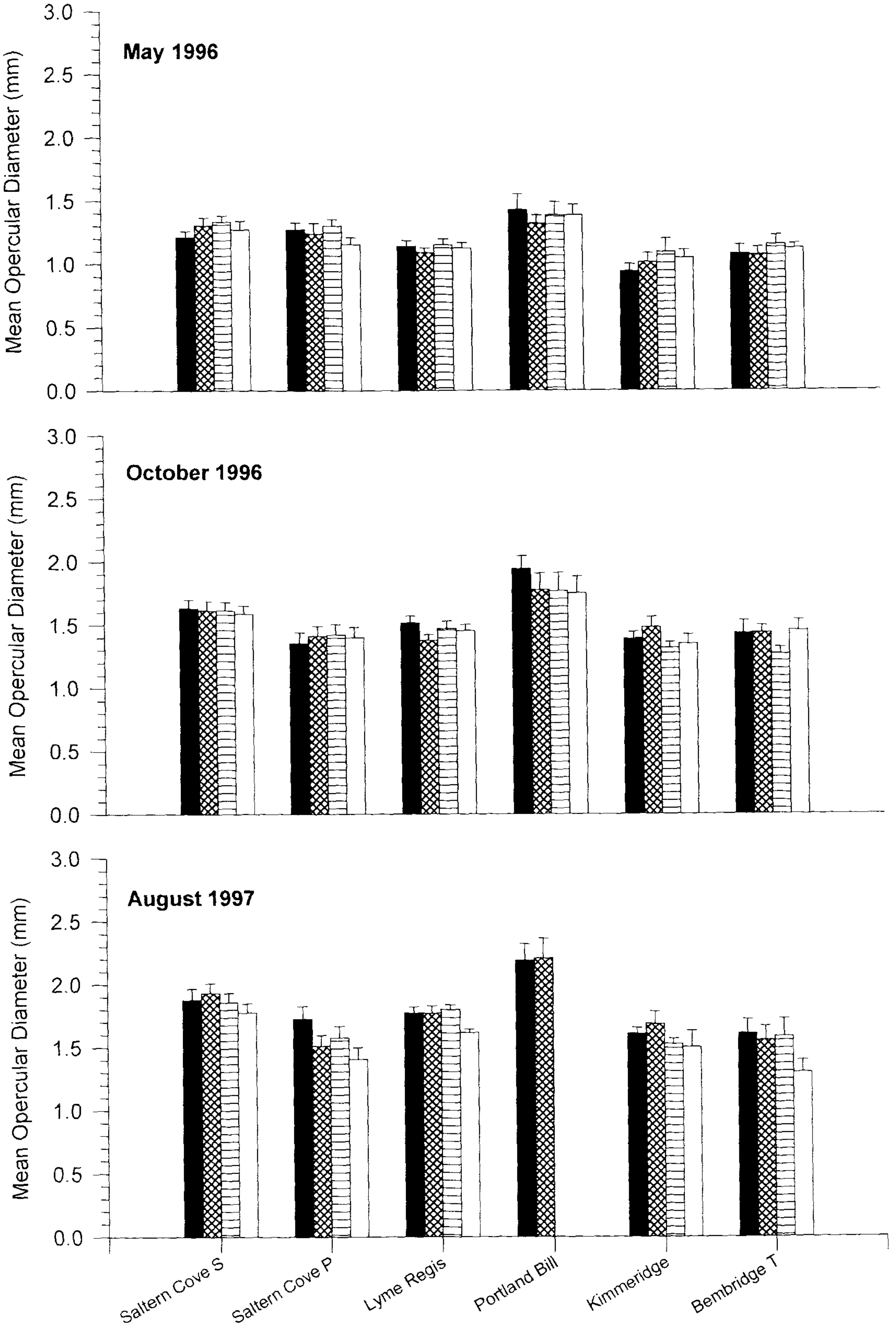


Fig 5.18. Mean opercular diameter of 1995 cohort *Chthamalus montagui* in different patches on shores along the south coast of England at MTL measured in May 1996, October 1996 and August 1997. Saltern Cove on shore (S); Saltern Cove on plates (P); translocated to Bembridge Isle of Wight (T). All patches n = 8 - 25. Error bars show 95% confidence levels.

continued rapid growth at Portland Bill over the summer had resulted in a mean opercular diameter of 2.16mm which was significantly larger than that of any of the other shores (Table 5.19). Animals at Kimmeridge were significantly smaller than those of any shore both in May 1996 and August 1997.

Table 5.18 Two-way ANOVA of opercular diameter of the 1995 cohort of *Chthamalus montagui* measured in two patches (n = 10 per patch)) at MTL on four shores along the south coast of England in mid-May 1996. K-S Normality test p = 0.047; Levene equal variance test p = 0.014. Data were untransformed.

Source of Variation	**DF**	**MS**	***F***	***P***
Shore	3	0.63	27.73	<0.001***
Patch	1	0.01	0.27	0.607
Shore x Patch	3	0.03	0.27	0.27
Residual	72	0.02	1.33	
Total	79	0.05		

SNK Test: '=' denotes no significant difference, '>' denotes significantly different, p < 0.05.
Portland Bill (PB); Saltern Cove (SC); Lyme Regis (LR); Kimmereidge (KM).

Shores	PB = SC > LR > KM
Means (mm)	1.37 = 1.28 > 1.12 > 0.97

Table 5.19 Two-way ANOVA of opercular diameter of the 1995 cohort of *Chthamalus montagui* measured in two patches (n = 10 per patch) at MTL on four shores along the south coast of England in August 1997. K-S Normality test p = 0.12; Levene equal variance test p = 0.002. Data were untransformed.

Source of Variation	**DF**	**MS**	***F***	***P***
Shore	3	1.37	39.11	<0.001***
Patch	1	0.11	3.25	0.077
Shore x Patch	3	0.04	1.07	0.37
Residual	71	0.03		
Total	78	0.09		

SNK Test: '=' denotes no significant difference, '>' denotes significantly different, p < 0.05.
Portland Bill (PB); Saltern Cove (SC); Lyme Regis (LR); Kimmeridge (KM).

Shores	PB >SC = LR > KM
Means (mm)	2.16 >1.81 = 1.7 > 1.55

5.3.2.2 Growth of 1995 cohort *C. montagui* translocated to Bembridge, Isle of Wight

Fig.5.19 shows the seasonal growth of the 1995 cohort of *C. montagui* at Saltern Cove in Devon, both on the shore and on perspex plates, with that of animals translocated on plates to Bembridge on the Isle of Wight. The same animals were followed through over the two year period of study, n = 25. Fig 5.20 shows the growth rate of the translocated animals together with that of animals found in natural populations on the south-west coast of the Isle of Wight (n =5). All animals on the shore and on plates were of the same size in October 1995, however between October 1995 and May 1996 those at Bembridge had grown at a significantly reduced rate compared to those left on plates at Saltern Cove (Table 5.20). The mean size of the animals within natural shore populations on the SW coast of the Isle of Wight, measured in May, was comparable with that of the translocated sample (Fig. 5.20). During the summer there was a major increase in growth rate of those animals on shore compared to those on plates at Saltern Cove.

For comparative purposes, the opercular diameters of animals growing at MTL in separate patches on plates from Saltern Cove and Bembridge are shown with those from the other shores in Fig.5.18. A separate two-way ANOVA was carried out to determine whether the mean opercular diameter of the animals growing at Saltern Cove was different to those translocated to Bembridge. Two different patches of ten animals were compared in both May 1996 and August 1997; the results are presented in Tables 5.21 and 5.22. SNK *post hoc* procedure indicates that the opercular size of animals translocated to Bembridge, measured in May 1996, was significantly less than that of animals both on plates and on the shore at Saltern Cove, whereas the controls on plates at Saltern Cove were not significantly different from those on the shore. However, by the end of the experiment in August 1997, those on the shore at Saltern Cove were significantly larger than those on the plates, suggesting that feeding or growth was impaired by being on a plate. Those on plates at Saltern Cove and at Bembridge were now not of significantly different sizes.

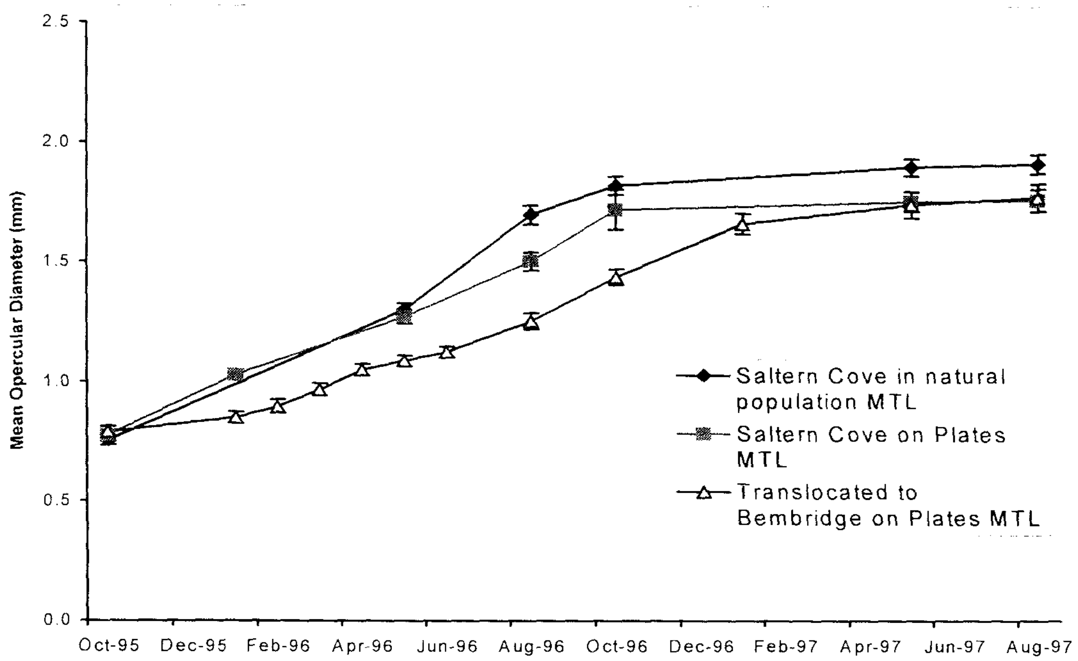


Fig 5.19 Growth of 1995 cohort of *C.montagui* on shore (n = 24) and on plates (n = 23) at Saltern Cove and those translocated to Bembridge, Isle of Wight (n = 25). Error bars show ± SE.

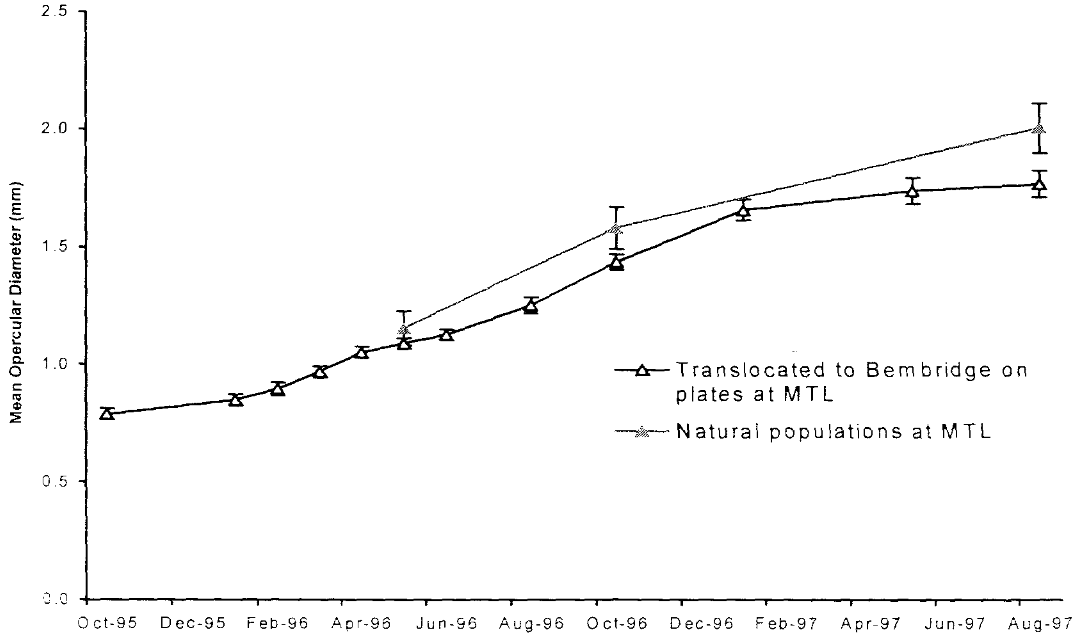


Fig 5.20. Growth of 1995 cohort *C.montagui* on plates translocated to Bembridge (as in Fig.5.19), and those in natural populations on shores in south-west of Isle of Wight (n = 4-6). Error bars show ± SE.

Table 5.20 One-way ANOVA of growth rate of 1995 cohort *Chthamalus montagui* over first winter at Saltern Cove and those grown on plates translocated to Bembridge, Isle of Wight (n = 25). Growth rate expressed as Ln (opercular diameter May 1996) – Ln (opercular diameter October 1995). Equal variance test p = 0.36.

Source of Variation	df	MS	*F*	*P*
Sites	2	0.34	14.5	<0.001
Residual	71	0.02		
Total	73			

SNK Test: '=' denotes no significant difference, '>' denotes significant difference, p <0.05.

Saltern Cove 'Shore' (SCs); Saltern Cove 'Plates', Bembridge Translocated Plates (BT).

Sites	SCs = SCp > BT
Mean Rate	0.552 = 0.503 > 0.327

Table 5.21 Two-way ANOVA of opercular diameter of the 1995 cohort of *Chthamalus montagui* measured in two patches (n = 10 per patch) at MTL on shore at Saltern Cove, on plates at Saltern Cove and on plates translocated to Bembridge, Isle of Wight, in mid May 1996. K-S Normality test p = 0.49; Levene Equal variance test p = 0.49.

Source of Variation	DF	MS	*F*	*P*
Shore	2	0.35	16.01	<0.001***
Patch	1	0.004	0.17	0.68
Shore x Patch	2	0.009	0.4	0.67
Residual	54	0.02		
Total	59	0.03		

SNK Test: '=' denotes no significant difference, '>' denotes significantly different, p < 0.05.

Saltern Cove 'Shore' (SCs); Saltern Cove 'Plates' (SCp); Bembridge Translocated Plates (BT)

Shores	SCp = SCs > BT
Means (mm)	1.3 = 1.28 > 1.06

Table 5.22 Two-way ANOVA of opercular diameter of the 1995 cohort of *Chthamalus montagui* measured in two patches (n = 10 per patch) at MTL on shore at Saltern Cove, on plates at Saltern Cove and on plates translocated to Bembridge, Isle of Wight, in August 1997. K-S Normality test p = 0.47; Levene Equal variance test p = 0.01. Data were untransformed.

Source of Variation	DF	MS	*F*	*P*
Shore	2	0.55	9.3	<0.001***
Patch	1	1.13	18.93	<0.001***
Shore x Patch	2	0.15	2.5	0.09
Residual	54	0.06		
Total	59	0.09		

SNK Test: '=' denotes no significant difference, '>' denotes significantly different, p < 0.05. Saltern Cove 'Shore' (SCs); Saltern Cove 'Plates' (SCp); Bembridge Translocated Plates (BT)

Shores	SCs > SCp = BT
Means (mm)	1.81> 1.56 =1.50

5.3.3 **Mortality of *Chthamalus montagui***

5.3.3.1 Mortality of 1994 and 1995 cohort at shores along south coast of England

Of particular interest was the winter survival of the young recruits at the eastern edge of the species distribution. Fig.5.21 shows the results of a pilot study over the 1994-95 winter, which was relatively mild.

Fig 5.21. Mean first winter mortality rate of the 1994 cohort *C. montagui* at upper, middle and lower shore levels at Shoalstone, Devon and Isle of Wight. Shoalstone upper n = 5, middle and lower n = 6; Isle of Wight, upper n = 11, middle n = 7, lower, n = 3. Error bars show +SE.

The results indicate that the winter mortality rate at the most western site was greater than on the Isle of Wight. At Shoalstone in Torbay, the mortality within quadrats between October 1994 and May 1995 was highly variable and ranged from between 8-50% on the upper shore to 0-70% on the lower shore. Overall, the mortality here was 31%. In contrast, the mean mortality of the 51 recruits monitored within twenty-one quadrats at Colwell, Watershoot Bay and Hanover Point on the Isle of Wight was only 4 %, and no mortality at middle shore levels was observed at all.

The winter 1995-1996 was the second coldest recorded over the study period. Fig 5.22 shows the mean winter mortality rates of the 1995 cohort for six shores at three tidal levels between Shoalstone and the Isle of Wight.

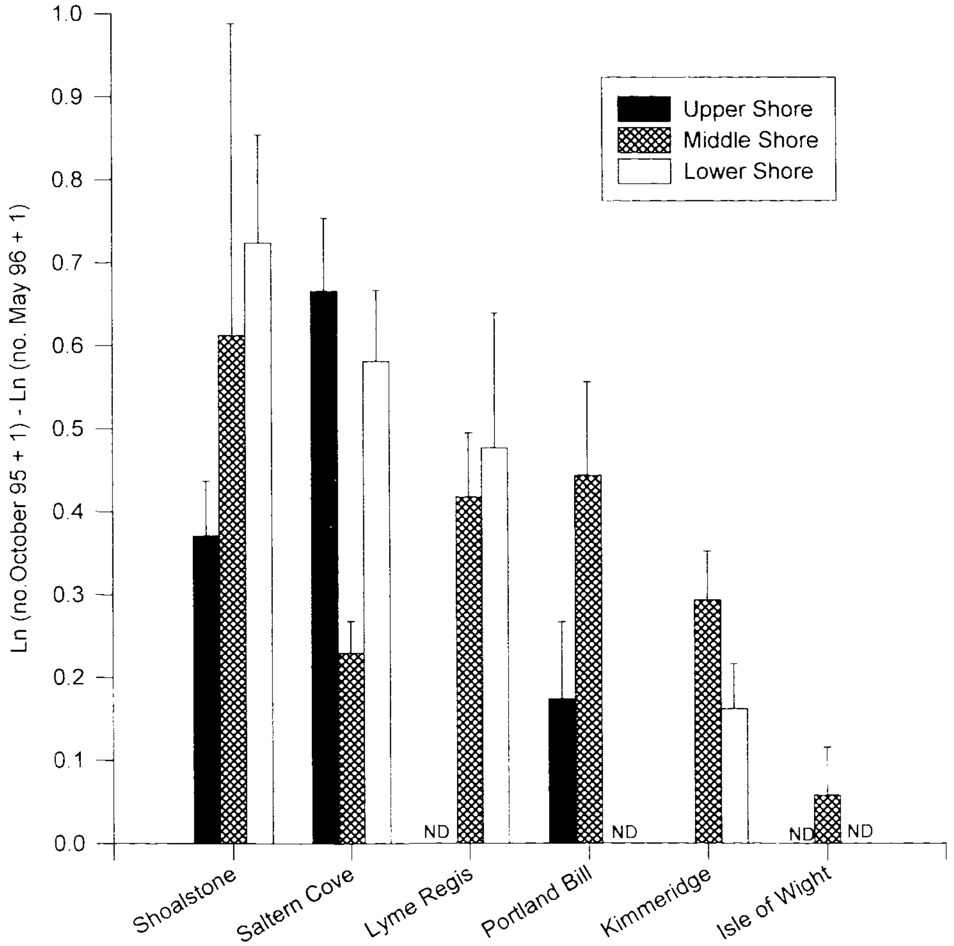


Fig 5.22. Mean first winter mortality rate of the 1995 cohort *C. montagui* at different shores heights on shores along the south coast of England. On mainland shores, counts are within photographs with field-of-view 40cm^2 (n = 8-12). On Isle of Wight, counts are within 400cm^2 quadrats (n =5). Error bars show + SE. ND denotes no data obtained.

Highest winter mortality rates were observed at the western end of the study area where populations are largest and where recruitment was greatest. There was also great variability in the mortality rate at different tidal heights, although it is generally highest on the middle and lower shore levels. At Saltern Cove the mean mortality on the upper shore was the highest recorded for that location (49%). However at Kimmeridge, at the eastern end of the study area there was no winter mortality observed on the upper shore, where highest rates might be expected should frost damage be of significance. On the highly exposed shore at Portland Bill, where abrasive damage might occur during winter gales, recorded mortality was 22% on the upper shore and 42% on the middle shore. No data were obtained here for lower shore levels. On the Isle of Wight, recruitment was less than the preceding year (1994) and by October, fourteen recruits were observed in the marked quadrats on the three shores; only one of which had died by the following May. Although overall mean mortality rates varied between sites, a one-way ANOVA of the winter mortality rates of the mid shore populations at each location showed no significant difference between shores (Table 5.23).

Table 5.23 One-way ANOVA of mean winter mortality of the 1995 cohort of *C.montagui* at middle tidal levels at shores along the central south coast of England. Mortality expressed as Ln(no.October 1995 +1) - Ln (no.May 1996 +1). The differences in the mean values are not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference.

Shore	**n**	**Mean Rate**
Shoalstone	8	0.61
Saltern Cove	10	0.23
Lyme Regis	12	0.42
Portland Bill	8	0.44
Kimmeridge	11	0.29
Isle of Wight	5	0.06

Source of Variance	**df**	**MS**	***F***	***P***
Shores	5	0.25	1.19	0.33
Residual	47	0.21		
Total	52			

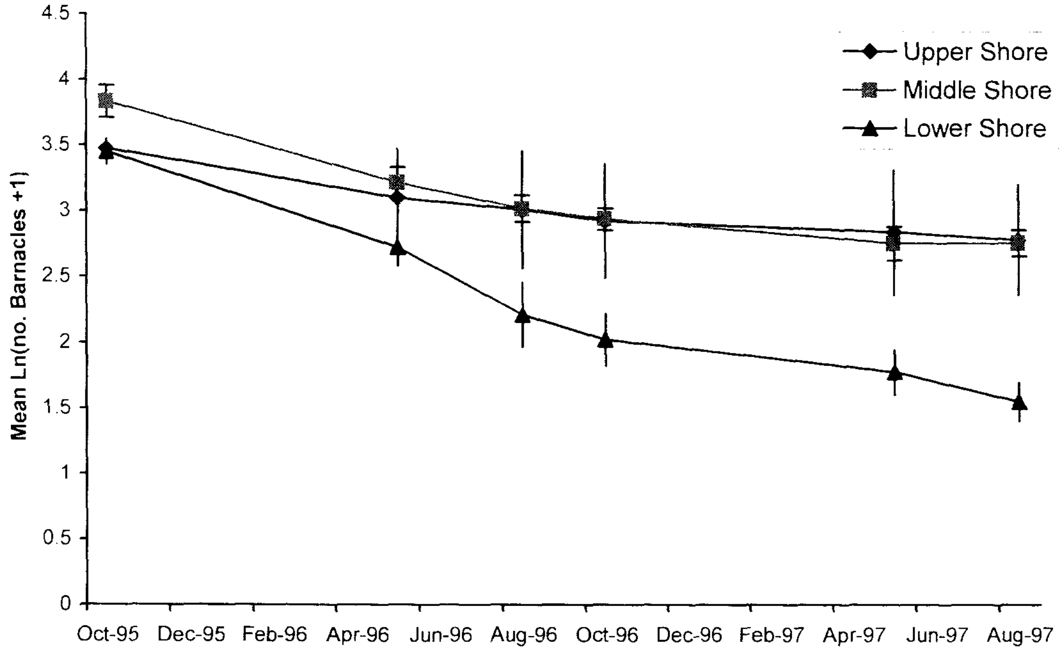


Fig 5.23. Mean number of the 1995 cohort *C. montagui* at Shoalstone,Devon. Counts within photographs. Upper n = 10, Middle n = 8, Lower n = 9. Error bars show ± SE.

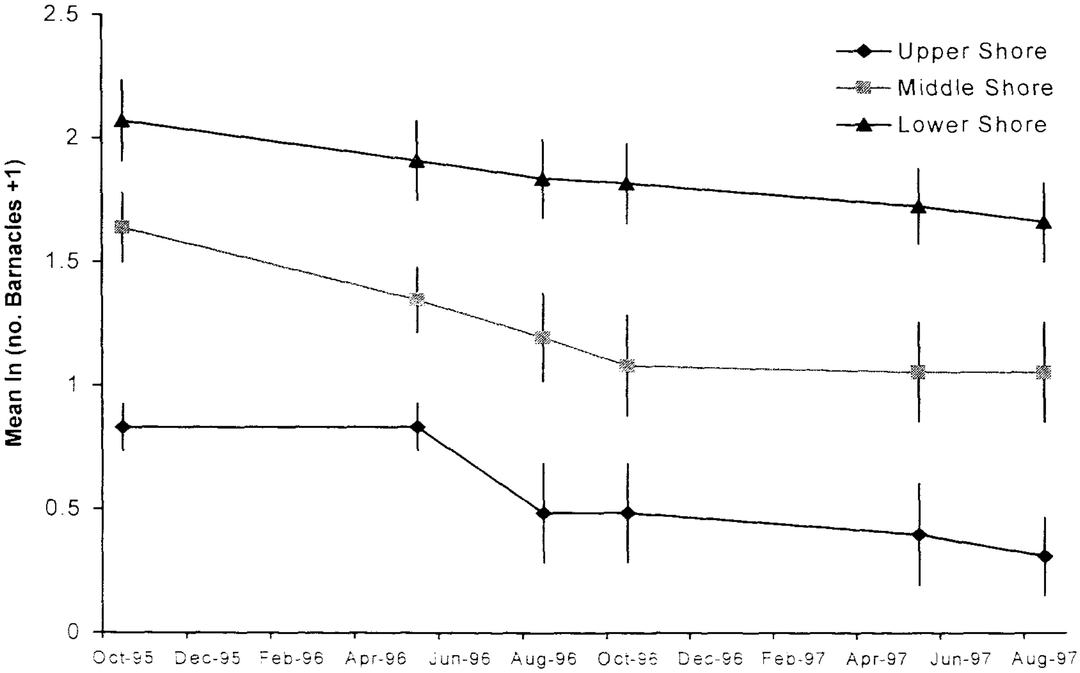


Fig 5.24. Mean number of the 1995 cohort *C. montagui* at Kimmeridge, Dorset. Counts within photographs. Upper n = 8, Middle n = 11, Lower, n = 12. Error bars show ± SE.

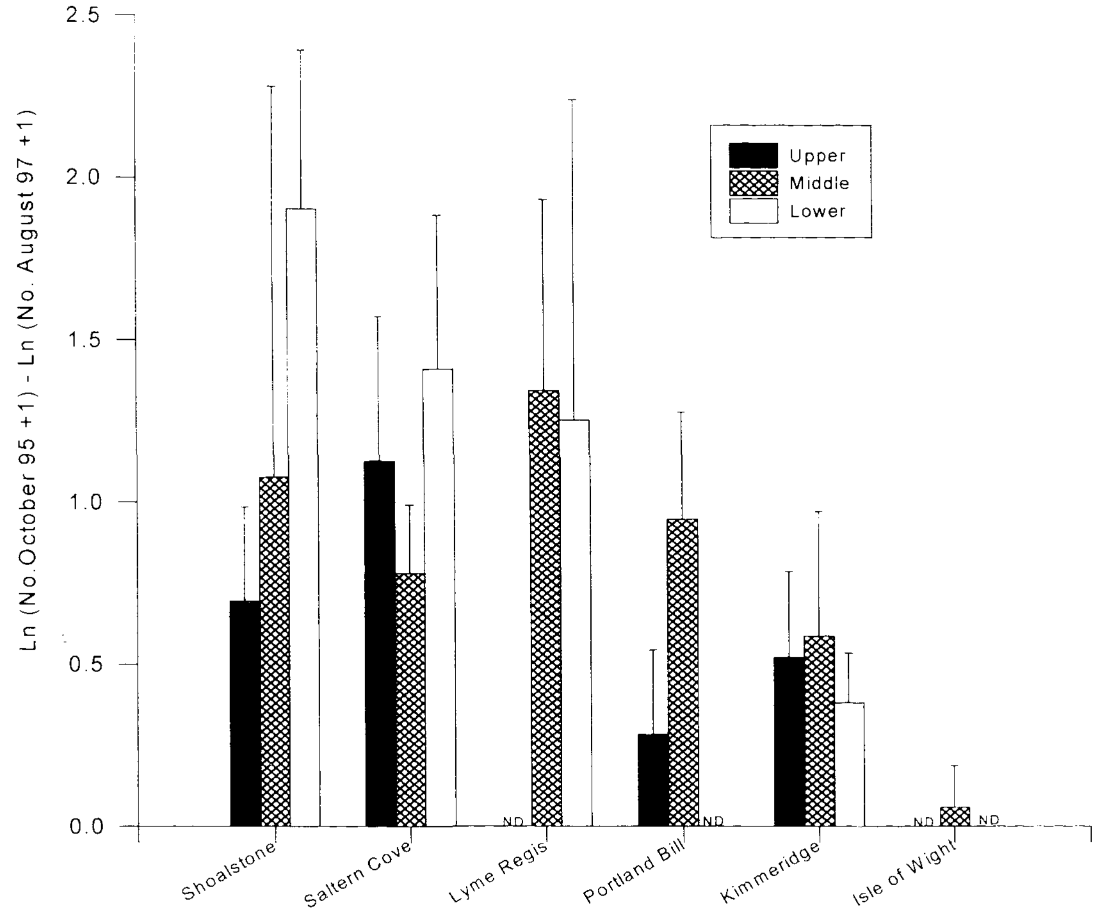


Fig 5.25. Mean mortality rates of 1995 cohort *C. montagui* between October 1995 and August 1997 at different tidal heights on shores along the south coast of England. Counts on mainland shores within photographs (n = 8-12). Isle of Wight counts within $400cm^2$ quadrats (n = 5). Error bars show +SE. ND denotes no data obtained.

Table 5.24 One-way ANOVA of mean mortality of the 1995 cohort *C.montagui* after nearly two years at middle tidal heights on shores along the south coast of England. Mortality expressed as Ln (no.October 1995+1) – Ln(no.August 1997 +1).

Shore	n	Mean Rate	Shore	n	Mean Rate
Shoalstone	8	1.08	Portland Bill	7	0.95
Saltern Cove	9	0.78	Kimmeridge	11	0.59
Lyme Regis	12	1.34	Isle of Wight	5	0.06

Source of Variance	df	MS	*F*	*P*
Shores	5	1.466	4.09	0.0037**
Residual	46	0.359		
Total	51			

SNK Test. The following comparisons were resolved at $p < 0.05$.
'=' denotes no significant difference. '>' denotes significant difference.
Lyme Regis (LR); Isle of Wight (IOW); Kimmeridge (KM); Portland Bill (PB); Saltern Cove (SC); Shoalstone (SH). LR > IOW; LR >KM; LR = SC ; PB = IOW; SC >IOW; SH = KM

Figs 5.23 and 5.24 show the size of the Shoalstone and Kimmeridge populations monitored within photographs between October 1995 and August 1997. It will be observed that the greatest mortality occurs not in the winter but during the summer months, where there is potential damage from desiccation. A graphical comparison of the mortality rates of the 1995 cohort at each shore level between October 1995 and August 1997 is shown in Fig.5.25. Highest rates were again recorded in the western locations but there was considerable variability between shores and that recorded at different tidal heights. A one-way ANOVA (Table 5.24) did however show a significant difference in the mean mortality at mid shore heights after two years, with subsequent SNK test resolving differences between the lower rates of eastern shores at Kimmeridge and on the Isle of Wight with those of Lyme Regis and Saltern Cove. The higher mortality rates recorded in the western localities, where the recruitment and adult populations are so much greater, suggests dependence not on winter temperatures but on population density. Where data from more than one tidal level were obtained, the mean-shore winter mortality rate was calculated and plotted against the mean shore recruitment density for 1995 (Fig.5.26). A one-way ANOVA comparing the mean shore mortality of the three high recruitment localities with that of the three low recruitment sites showed a significant difference (df=5, F = 16.4, p = 0.015).

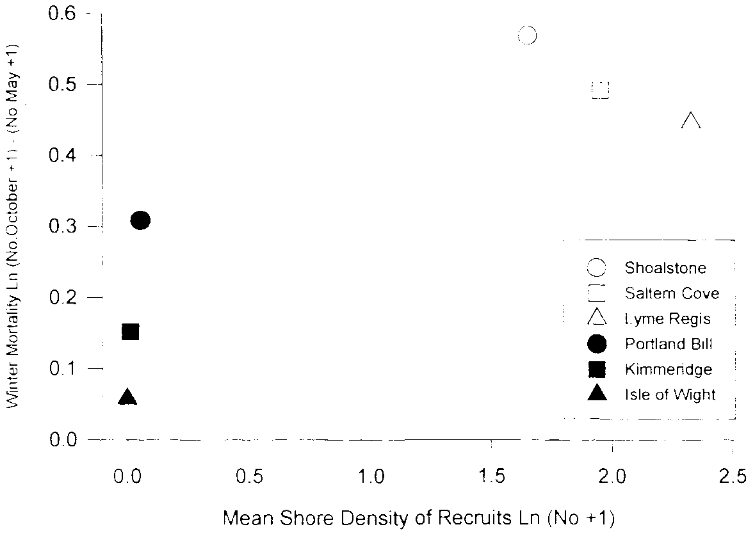


Fig 5.26. Mean shore winter mortality rate of 1995 cohort *C. montagui* plotted against mean shore density of recruits

5.3.3.2 Mortality of the 1995 cohort *C.montagui* translocated to Bembridge, Isle of Wight

The mortality of the new *Chthamalus* recruits monitored on Isle of Wight shores was recorded at locations in the south and west of the island. One consideration given by Crisp & Southward (1958) was that winter mortality could significantly increase with change of shore aspect from southerly to easterly, as one rounded St. Catherines Point. Because no recruitment had been recorded east of St. Catherine's Point, spat collected on plates from Saltern Cove in October 1995 were translocated to Bembridge at the eastern tip of the island. In Fig.5.27 the mean mortality rates of the translocated individuals are plotted with those measured both on plates and on the shore at Saltern Cove in Devon and those within quadrats in natural populations in the south and west of the Isle of Wight.

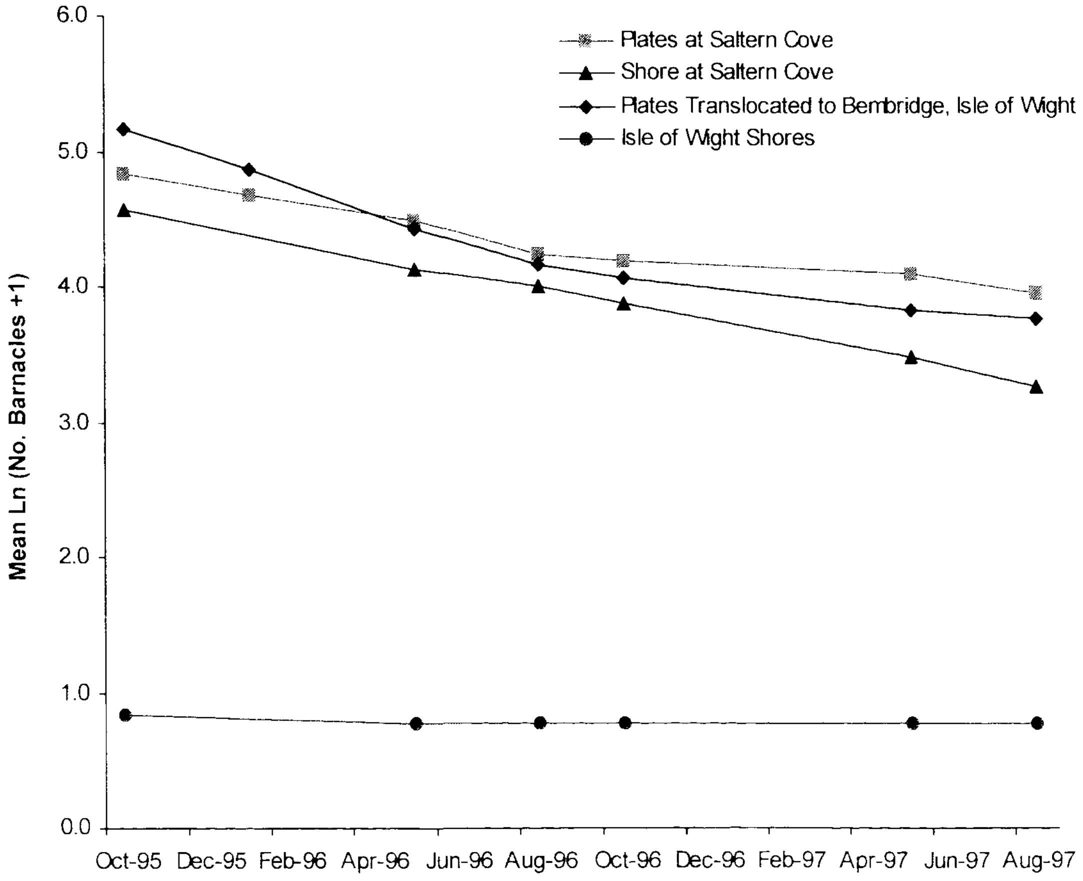


Fig 5.27. Mean mortality of 1995 cohort *C.montagui* on plates (n = 6 patches 40cm^2) and on shore at Saltern Cove (n = 6 patches 40cm^2), those translocated to Bembridge, IOW (n = 6 patches 40cm^2) and natural shore populations on the Isle of Wight (n = 5 quadrats 400cm^2). Error bars omitted for clarity.

Two analyses were carried out to determine differences in first winter (October 1995-May 1996) mortality and that over the period October 1995 to August 1997. Cold easterly winds were frequent over the winter 1995-96 and this may account for the higher mortality on the plates at Bembridge compared to those at Saltern Cove, although this shore also has an easterly aspect. Initial mortality due to disturbance during translocation may have been partially responsible, however an examination of the slopes on the graph in Fig.5.27 suggests that the high mortality rate recorded between October 1995 and January 1996 was maintained between January and May.

A one-way ANOVA was carried out to determine differences in the mean mortality rates over the period October 1995-May 1996 (Table 5.25). Results show that mortality at Bembridge was significantly greater than both treatments at Saltern Cove, but there was no statistical difference between the controls on plates and those in natural populations in Saltern Cove.

Table 5.25 One-way ANOVA of mean winter mortality of the 1995 cohort of *C.montagui* translocated on plates from Saltern Cove in Devon to Bembridge, Isle of Wight, compared to natural shore population and controls on plates at Saltern Cove (n = 6 patches). Mortality expressed as Ln(no.October 1995 +1) – Ln (no.May 1996 +1).

Source of Variance	**df**	**MS**	***F***	***P***
Sites	2	0.259	8.06	0.0042**
Residual	15	0.032		
Total	17			

SNK Test. '=' denotes no significant difference, '>' denotes significant difference at p <0.05.

Bembridge Transplants (BT); Saltern Cove on plates (SCp); Saltern Cove on shore(SCs).

Sites	BT > SCp = SCs
Mean Rate	0.747 > 0.349 = 0.445

Between May 1996 and October 1996 there was no significant difference in the mortality rates of the three areas ($p = 0.65$). Those on plates, both at Bembridge and at Saltern Cove, then continued to expire at the same rate until the end of the experiment in August 1997. Those on the shore at Saltern Cove, however, showed significantly higher mortality from October 1996 onwards ($p < 0.05$). It is possible that those growing on the plates, being slightly raised above other biota, were protected from interspecific interactions on the shore including dog-whelk predation (Crothers,1985) and limpet bulldozing effects (Hawkins,1983). No dog-whelks were seen on any of the plates over the two years although a juvenile limpet (<10mm) was observed on one occasion. It is also possible that the grooves made in the plates to encourage settlement also facilitated anchorage during growth, thereby improving survival. Over the two years of the experiment there was no statistically significant difference in the mortality rates between the three areas (Table 5.26).

Table 5.26 One-way ANOVA of mean mortality of the 1995 cohort of *C.montagui* over two years translocated on plates from Saltern Cove in Devon to Bembridge, Isle of Wight compared to natural shore population and controls on plates at Saltern Cove (n = 6). Mortality expressed as Ln(no.October 1995 +1) – Ln (no. August 1997 +1).

Source of Variance	df	MS	*F*	*P*
Shores	2	0.449	2.77	0.095
Residual	15	0.162		
Total	17			

Conclusion. The differences in the mean values are not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference.

Sites	BT = SCp = SCs
Mean Rate	1.401 = 0.891 = 1.319

5.3.3.3 Mortality of adult *Chthamalus* spp. on shores along the south coast of England

The mean mortality rates of adult *C. montagui* at eight shores between October 1995 and August 1997 is shown in Fig.5.28. Those on the lower shore generally had higher mortality than those on the upper shore levels, suggesting that damage resulting from low winter temperatures has a relatively insignificant effect. The highest rate was on the lower shore at Lyme Regis where the largest density of dog-whelks (mean 10.25 per m^2) were observed over this study period. High mortality was also recorded on the lower shore at

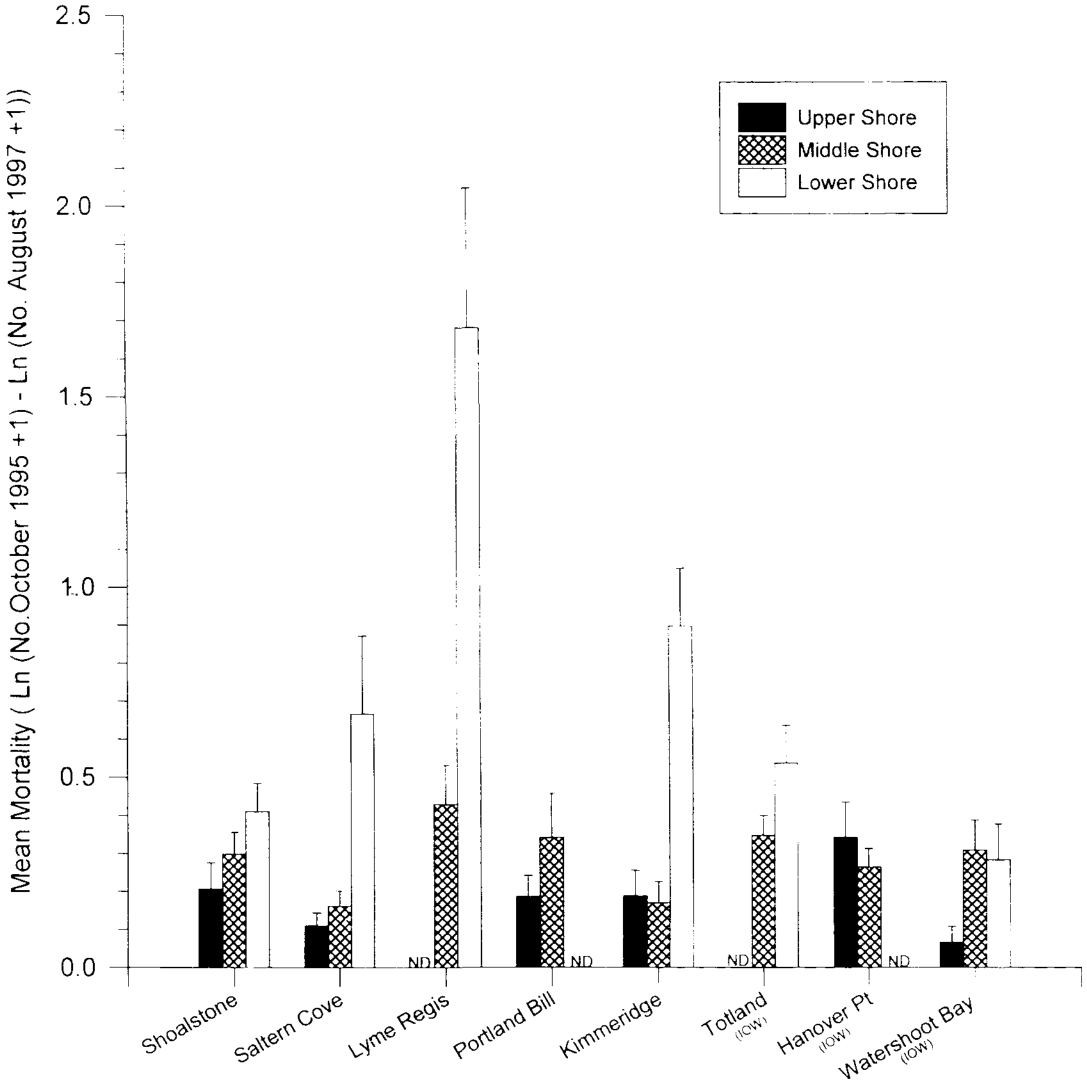


Fig 5.28. Mean mortality rate of adult *C. montagui* between October 1995 and August 1997 at different tidal heights on shores along the central south coast of England. Counts on mainland shores within photographs (n = 7-12), field of view 40cm^2. Isle of Wight counts within 400cm^2 quadrats (n = 3-10). Error bars show + SE. ND denotes no data obtained.

Kimmeridge. This site has a very low limpet density (25-35 per m^2) and mean dog-whelk density of only 0.5 per m^2. On the gently sloping cementstone platforms, where the study site was located, there was also a virtual absence of *Semibalanus balanoides* and *Elminius modestus*, so mortality due to possible competitive exclusion from these faster growing species can be eliminated. The density of chthamalid barnacles is also low (0.8 per cm^2) yet it is possible that the high proportion of isolated individuals without the protection of a firm barnacle matrix causes higher mortality. From Fig.5.28, there does not appear to be any east-west gradient in adult mortality, nor any suggestion of the strong density-dependent relationships evident in the data for new recruits, discussed above.

The mortality of adult *C.montagui* between 1994 and 1997 within quadrats at three Isle of Wight shores is shown in Figs.5.29-5.31. The data have been plotted on an arithmetic scale to enable easier inspection of seasonal mortality. At high and mid tidal levels, annual

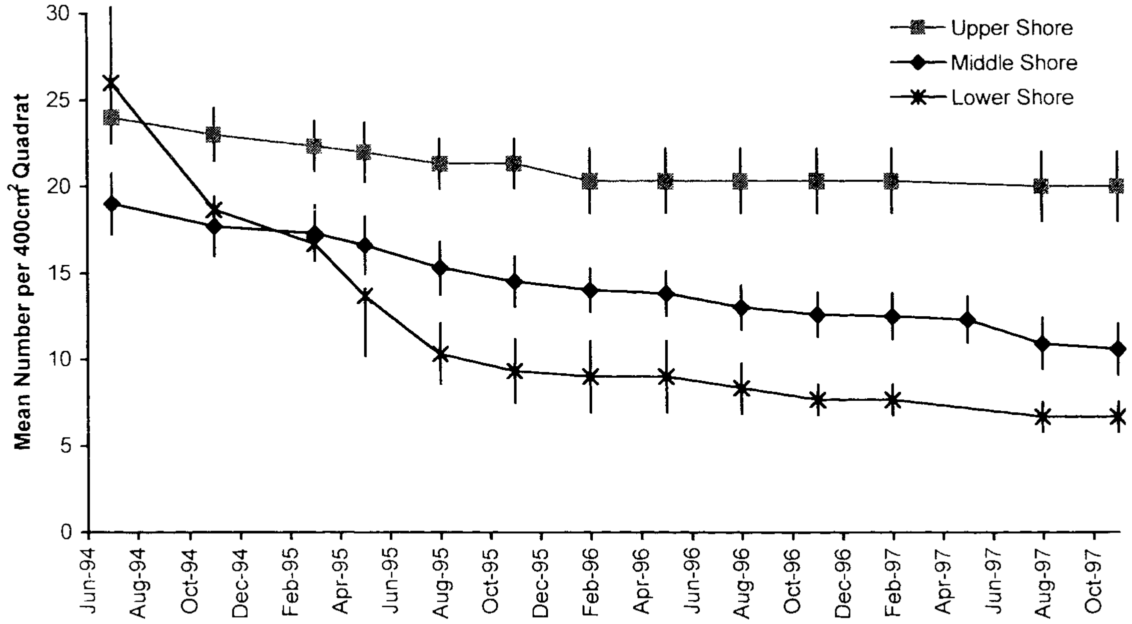


Fig 5.29. Size of adult *C. montagui* population monitored at Watershoot Bay near St. Catherines Point, Isle of Wight between July 1994 and November 1997. Quadrats on the middle shore were on flat surfaces (n =10). Those on the upper and lower shore were on vertical surfaces (n =3). Error bars show ± SE.

mortality is slight, both being on average 14%. On the lower shore however, there was significant mortality at Watershoot Bay between July 1994 and August 1995. During this period, dog-whelks, normally at very low density here, were particularly frequent within the study site. At Colwell too, at the western end of the island, mortality on the lower shore was greatest. There does not appear to be any significantly higher mortality during the winter: if anything, slopes appear to be greater during the summer months as may be observed in Fig.5.31 on the middle shore of Hanover Point.

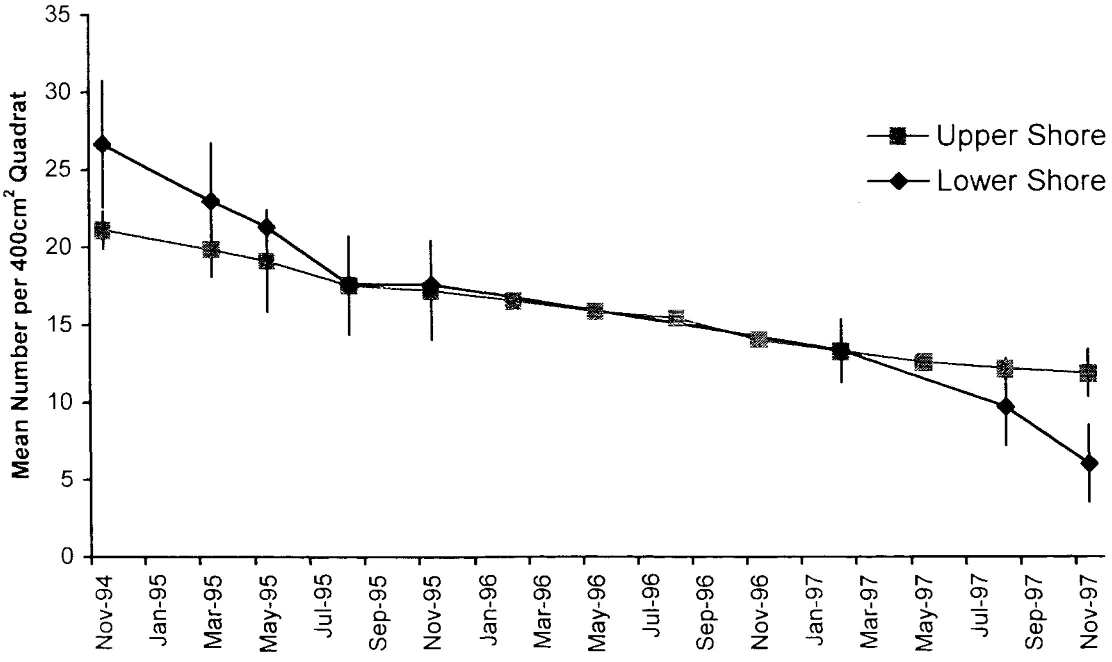


Fig 5.30. Size of adult *C. montagui* population monitored at Colwell, Isle of Wight. Quadrats on north-west facing steeply sloping surfaces (Upper shore n =7); Lower shore n = 3) Error bars show ± SE.

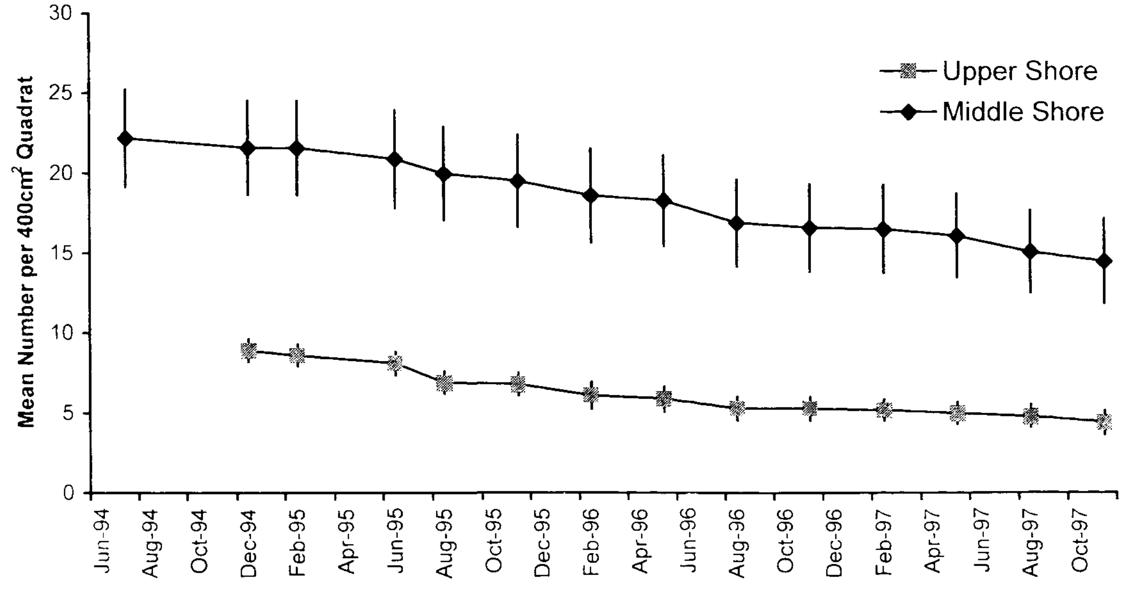


Fig 5.31. Size of adult *C. montagui* population monitored at Hanover Point, Isle of Wight. Quadrats on north facing surfaces (Upper shore, n =10); Middle shore, n = 10) Error bars show ± SE.

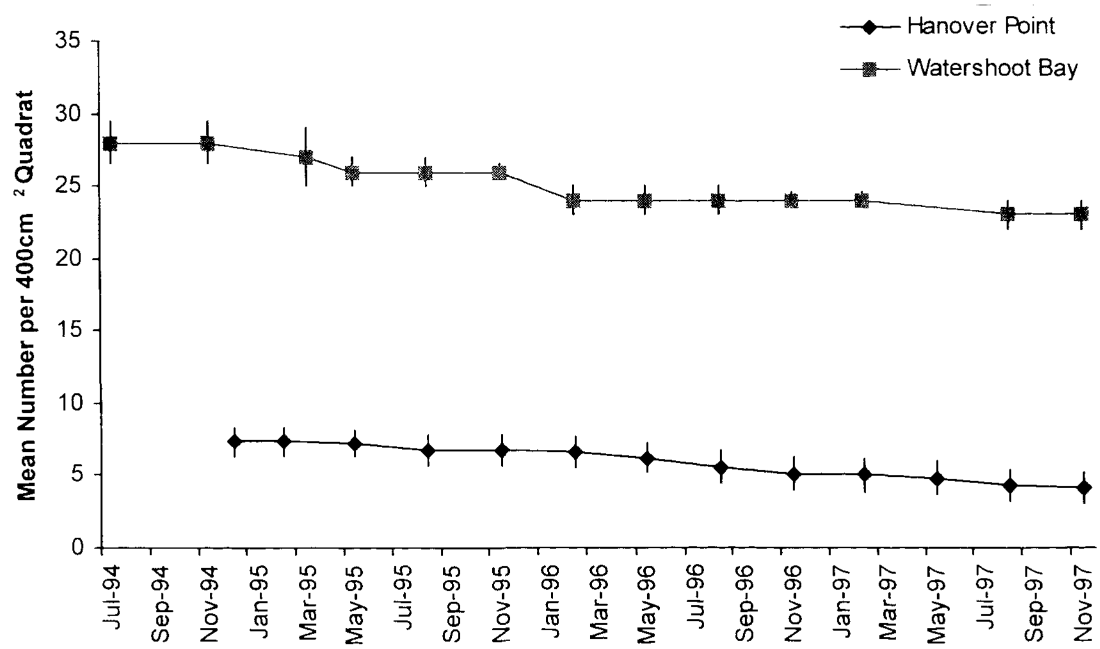


Fig 5.32 Size of adult *Chthamalus stellatus* population monitored at high tidal levels on two Isle of Wight shores. Hanover Point (n =10) and Watershoot Bay (n = 2). Error bars show ± SE.

Fig.5.32 shows the mortality of *Chthamalus stellatus* on the higher shore levels at Hanover Point and Watershoot Bay, where the species was most frequent. Again, mortality was very slight over this period and comparable with *C. montagui.*

5.3.3.4 Influence of interspecific competition on mortality of *Chthamalus* within Isle of Wight populations.

The contribution to overall mortality of adult *C. montagui* from competition by faster growing *Semibalanus balanoides* and *Elminius modestus* was investigated at Hanover Point and Colwell on the Isle of Wight. As shown in Figs 5.30 and 5.31, the overall adult mortality was relatively low, but having mapped the location of individual barnacles and noted contact with other species during the course of the year it was possible to record their fate in more detail. Mortality was said to have occurred only if an individual had been dislodged or overgrown and not if the valves were missing, as this could be due to predation by dog-whelks. However, no barnacles were observed in this condition at these particular sites, probably because dog-whelk density was very low. The monitoring year began and finished in November with additional observations made in

February, May and August. Over the years studied, only the 1994 cohort at Colwell were mapped in sufficient numbers to make any worthwhile analysis of the fate of young recruits. Because of the small numbers of *E.modestus* that came into contact with *Chthamalus* they were combined with *S.balanoides*. The total number of barnacles monitored and the overall % mortality is shown in Table 5.27.

Table 5.27. Total number of *C. montagui* monitored at Isle of Wight shores to compare mortality of isolated individuals with those in contact with other species and conspecifics. Barnacles were mapped within marked 400cm^2 quadrats; Hanover Point MTL n =10, Colwell (LWN) n =3.

Location	**Year**	**In contact with *S.b/E.m***	**Isolated**	**In contact with *Cm/Cs* only**	**Total**	**Overall % Mortality**
Hanover Pt	1994-1995	162	44	11	217	10.6
Hanover Pt	1995-1996	155	27	6	188	14.9
Hanover Pt	1996-1997	136	20	4	160	13.1
Colwell	1994-1995	51	26	4	81	40.7
Colwell (1994 cohort)	1994-1995	12	3	0	15	13.3

The percentage mortality of the number of *C.montagui* in contact with other barnacles and those isolated is shown in Figs 5.33 and 5.34. At Hanover Point the annual mortality during the three years of study was only between 10-15%, yet interestingly, the percentage mortality of *C. montagui* that came into contact with either *S.balanoides* or *E. modestus* was not only small but substantially less than the mortality of those that were isolated or in small contiguous groups. The exception being during the 1995-1996 season when the mortality of isolated individuals was also low. At Colwell the mortality during the 1994-1995 season was just over 40%, but again, the percentage mortality of those in contact with *S.balanoides or E.modestus* was relatively small compared to isolated individuals.

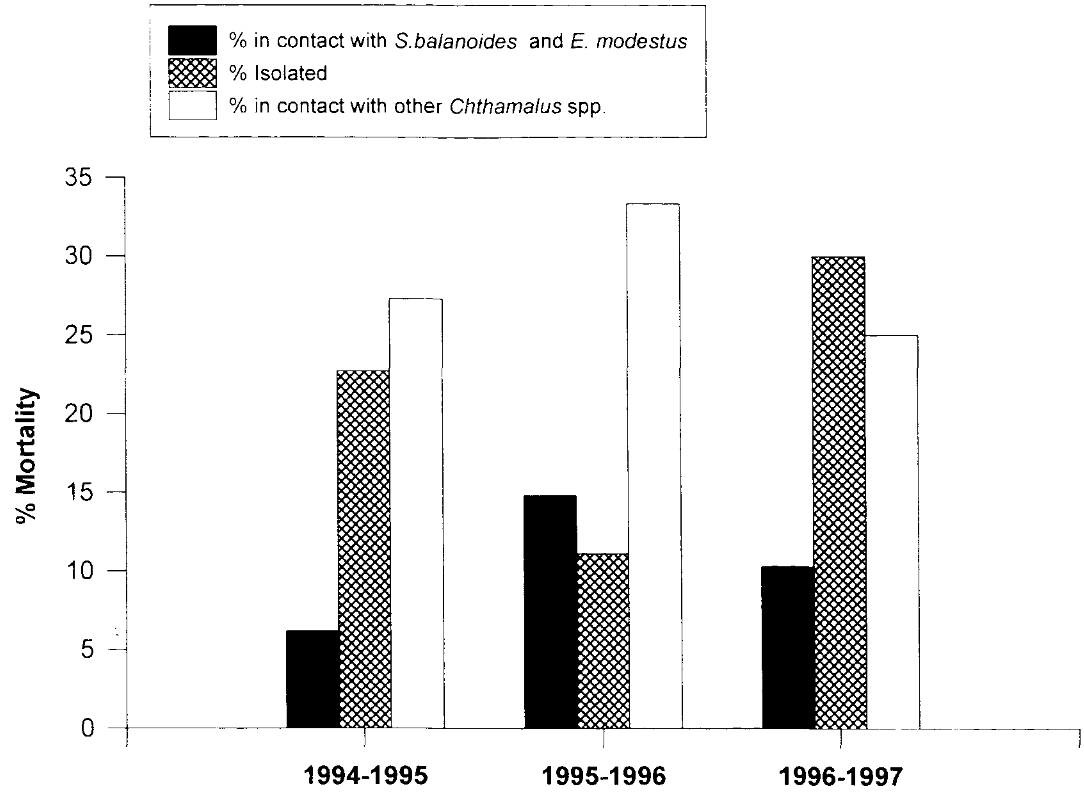


Fig 5.33 Annual % mortality of isolated *C.montagui* and those that came into contact with *S.balanoides* plus *E. modestus* or other chthamalids during that year (November –November) at MTL, Hanover Point Isle of Wight. See text and Table 5.27 for further details.

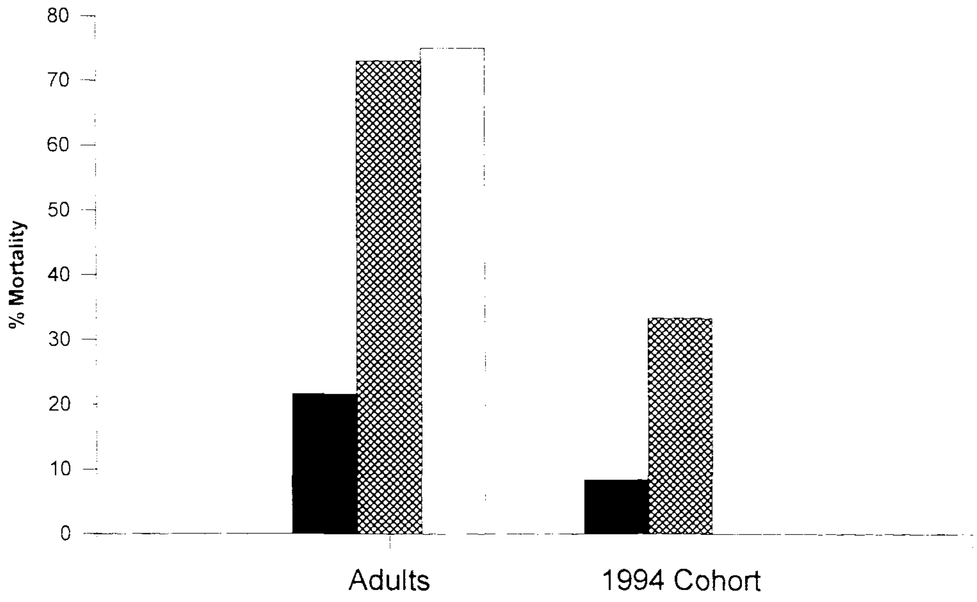


Fig 5.34 Annual % mortality of isolated *C.montagui* and those that came into contact with *S.balanoides* plus *E. modestus* or other chthamalids at LWN, Colwell (IOW) between Nov 1994 and Nov 1995. See Fig 5.33 for legend and text and Table 5.27 for further details.

Table 5.28. Results of chi-squared analysis of proportions of adult *C.montagui* that survived each year when in contact with *S.balanoides/E.modestus*, isolated or in contact with other chthamalids. For all tests, more than 20% of expected frequencies were below 5 in value.

Location	**Year**	**df**	χ^2	***P***
Hanover Pt	1994-1995	2	35.2	<0.0001
Hanover Pt	1995-1996	2	1.91	0.38
Hanover Pt	1996-1997	2	6.45	0.039
Colwell	1994-1995	2	21	<0.0001

Although a small sample size, of the twelve 1994 recruits that came into contact with non- chthamalids during the following spring and summer, only one had died by October 1995. Table 5.28 shows the results of a chi-squared analysis on the proportional survival of adult *C. montagui* in contact with other species, isolated or in contact with other chthamalids. Although the results are to be interpreted cautiously, due to low expected frequencies within some cells, three of the four tests revealed either a significant or highly significant association between survival and barnacle contact. Numbers of the 1994 cohort at Colwell were too low to use in any statistical analysis. It is possible that the isolated individuals, not having the protection afforded by a dense matrix of barnacles, are more vulnerable to dislodgement by waves or perhaps limpets. Even contact with a single individual of *S.balanoides* may significantly increase the anchorage of chthamalids and provide higher resistance to dislodgement. The higher percentage mortality of small groups of chthamalids might appear to contradict this hypothesis, however these were often old individuals, no more than four in number, and as their plates were closely welded together they could arguably be regarded as a single unit. If one individual became damaged the whole group might therefore be at risk. The dislodgement of whole contiguous groups was occasionally recorded on all shores studied.

5.3.4 **Changes in adult populations of *C.montagui* 1994-1999**

Figs 5.35-5.39 show changes in the mean adult density of *C. montagui* at MHW, MTL and LWN at nine shores along the central south coast of England between 1994 and 1999. Values for 1994 are the means of thirty quadrats, whereas those from 1995 onwards are means of two separate patches (n = 10). Also shown is the mean *Chthamalus* recruitment measured in October of that year within cleared quadrats (see 5.2.2 & 5.3.1.2). Density values for adult *C. stellatus* have been omitted from the graphs as the species frequently accounted for less than 5% of total *Chthamalus*, and no more than 10% at Portland Bill, where the species is most abundant. Fig 5.35 shows the population changes recorded at Shoalstone beach and Saltern Cove within Torbay. Consistent overall changes can be observed both between tidal levels and the two shores, with peak densities in 1996 following the high recruitment in the warm year of 1995. Recruitment in the cooler year of 1996 was, however, low; at most sampling stations, populations fell over the following two years. A further rise in adult populations was observed at both shores in 1999, which followed better recruitment at Saltern Cove in 1998. However, recruitment at Shoalstone, while improved, was still relatively poor that year. Fig 5.36 shows the population changes on Broad Ledge at Lyme Regis and at Portland Bill. On the upper shore groynes at Lyme Regis, populations fell until 1998 largely because of the mortality incurred as a result of abrasion and frequent smothering by sand and shingle. On the middle shore at Lyme, recruitment and population density has varied widely, yet good recruitment in 1995 resulted in higher population densities in 1996 and 1997, and the poor recruitment in 1996 may have been responsible for the fall in adult density observed in 1998. Adult densities of both the upper and middle shores were observed to have increased between 1998 and 1999, presumably due to the good recruitment in 1997. On the lower shore at Lyme Regis the pattern of recruitment was very similar to that of middle and upper levels of the shore and by 1996, populations were observed to have risen as a result of the good recruitment in 1995. Population levels then fell for the rest of the monitoring period. Mortality may have been due to dog-whelk predation; densities of 3.75 per m^2 in 1996 were significantly higher than in other years. There was also a corresponding increase in the recruitment of *Fucus serratus* within the main sampling areas which raised mean cover from 0-10% over the period of study. This may not only have reduced space occupation for adults, but frond movement may have caused damage and reduced feeding efficiency (Hawkins,1983; Jenkins *et al.*,1999). Both these changes in shore community can be a consequence of high barnacle recruitment, such as that observed in 1995 and 1997 (Hartnoll & Hawkins,1985). There was also a significant increase in the density of *Semibalanus balanoides* at the lower shore levels from 0.01 in 1995 to 0.9 per cm^2 in 1996, following good recruitment (non-quantitative observation). The species continued to increase in density to 2 per cm^2 following another good recruitment year in 1998, which was again cooler. While no detailed observations of interspecific interactions between *Chthamalus* and *Semibalanus* were made at Lyme Regis, qualitative observations of *Semibalanus* recruitment over the monitoring period indicated that it may have been great enough to cause some exclusion of *Chthamalus*. Yet from six (8 x 5 cm) photographs taken of the barnacle community over these years, space occupation by *S. balanoides* never exceeded 14%. Moreover, during the period October 1995 to October 1996, four out of the six photographs showed a fall in *Semibalanus* cover, while between October 1997 and October 1998 three of the six photographs showed a fall in *Semibalanus* cover. Obviously, such a small number of samples cannot accurately estimate cover changes occurring over the whole shore, however it appears unlikely that any interactions between the two species have significantly altered space occupation in favour of *Semibalanus*. At Portland Bill (Fig 5.36) and all other shores eastwards, the annual *Chthamalus* recruitment is considerably lower than that for shores within Lyme Bay. There is also less concordance in population density changes between tidal levels, although there is some evidence of an overall population increase following better recruitment in 1997; this is also evident on the upper and middle shores at Osmington Mills (Fig 5.36). At Kimmeridge (Fig 5.37), adult population densities are considerably less than those at Osmington, however changes between shore levels over the monitoring period have been remarkably consistent, with high peaks in 1997. Because initial growth rate of *Chthamalus* has been found to be low here (5.2.3.1, Fig 5.17) and adult-sized individuals are the smallest within the study area, it is possible that individuals are not noticed in counts until two years later, particularly if they have settled in small pits or crevices. The rise in density observed in 1997 may therefore have been due to the 1995 recruitment which was the third highest over the five year period. Figs 5.38 and 5.39 show the population changes at Peveril Point in east Dorset and at Hanover Point and Watershoot Bay on the Isle of Wight. Annual recruitment at these sites has been extremely sparse over the monitoring period and, as a consequence, populations at these sites have generally declined since 1995. Large variances are indicative of a very patchy distribution on the boulder shore at Watershoot Bay. Of the 27 monitoring stations (nine shores and three tidal levels), 20 show a decrease in density of *C. montagui* between October 1996 and October 1998 following particularly low recruitment in 1996. This decline is mirrored in the changes in % cover of the species measured at fixed photographic points: of the sixty six photographs examined, taken at all three Lyme Bay sites, Portland Bill and Kimmeridge, 69.7% showed a reduction in the chthamalid percentage cover over the same period. The positive or negative changes (C) in species percentage cover over this period were tested against the null hypothesis that $C+ = C- = 0.5$ using the binomial distribution (Table 5.29). The result was highly significant indicating that there was general decline in species % cover along the south coast over this period.

Table 5.29. No.of photographs showing +ve or –ve changes in % cover of *C.montagui* at different tidal heights on shores along the south coast of England between October 1996 and October 1998. Total number of photo sites at each tidal level = 6. Using 2-tailed Binomial test p = 0.002; highly significant.

Location	Tidal Height	+ve Change	-ve Change
Shoalstone	U	2	3
Shoalstone	M	0	4
Shoalstone	L	0	5
Saltern Cove	U	6	0
Saltern Cove	M	0	5
Saltern Cove	L	1	5
Lyme Regis	M	1	4
Lyme Regis	L	3	3
Portland.Bill	U	3	3
Portland Bill	M	1	4
Kimmeridge	U	2	3
Kimmeridge	M	1	3
Kimmeridge	L	0	5
	Total	**20**	**46**

The annual count data between 1995 and 1999 were tested for overall differences in density of *C. montagui* between years using a four-way ANOVA with GMAV5 (Underwood *et al*.,1998). Although mean densities for three random patches (n =15) were obtainable for most sites over the monitoring period, due to poor weather and other logistical difficulties, there were occasions when this was not possible. To ensure a balanced design for the ANOVA just two patches (n =10) were used. Factors 'Year' and 'Shore' were random, factor tidal 'Height' was fixed and orthogonal and factor 'Patch' was nested in 'Year', 'Shore' and 'Height'. The results, shown in Table 5.30, indicate that overall differences in the density of *C. montagui* across the nine shores investigated between 1995 and 1999 was not significant ($p = 0.0582$), however there was a strong Year x Shore interaction which was investigated further using SNK multiple comparison procedure. Significant differences between years were resolved ($p < 0.05$) for Shoalstone, Saltern Cove, Lyme Regis and Peveril Point and largely indicate that densities were significantly higher in 1996 prior to the general decline.

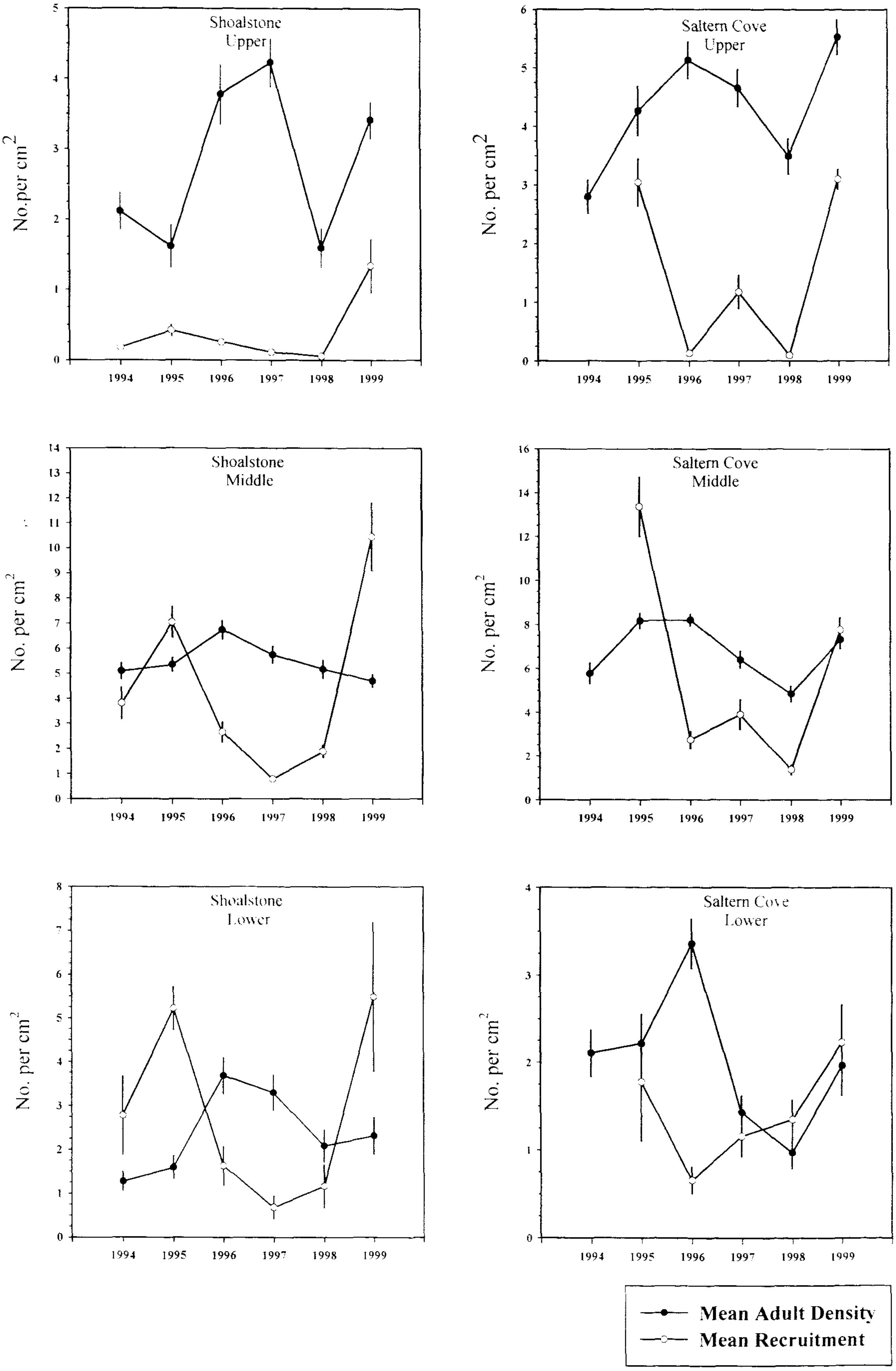


Fig.5.35. Mean *Chthamalus* recruitment and adult density of *Chthamalus montagui* at three tidal levels at Shoalstone and Saltern Cove in Torbay, Devon, 1994-1999. Error bars show ± SE.

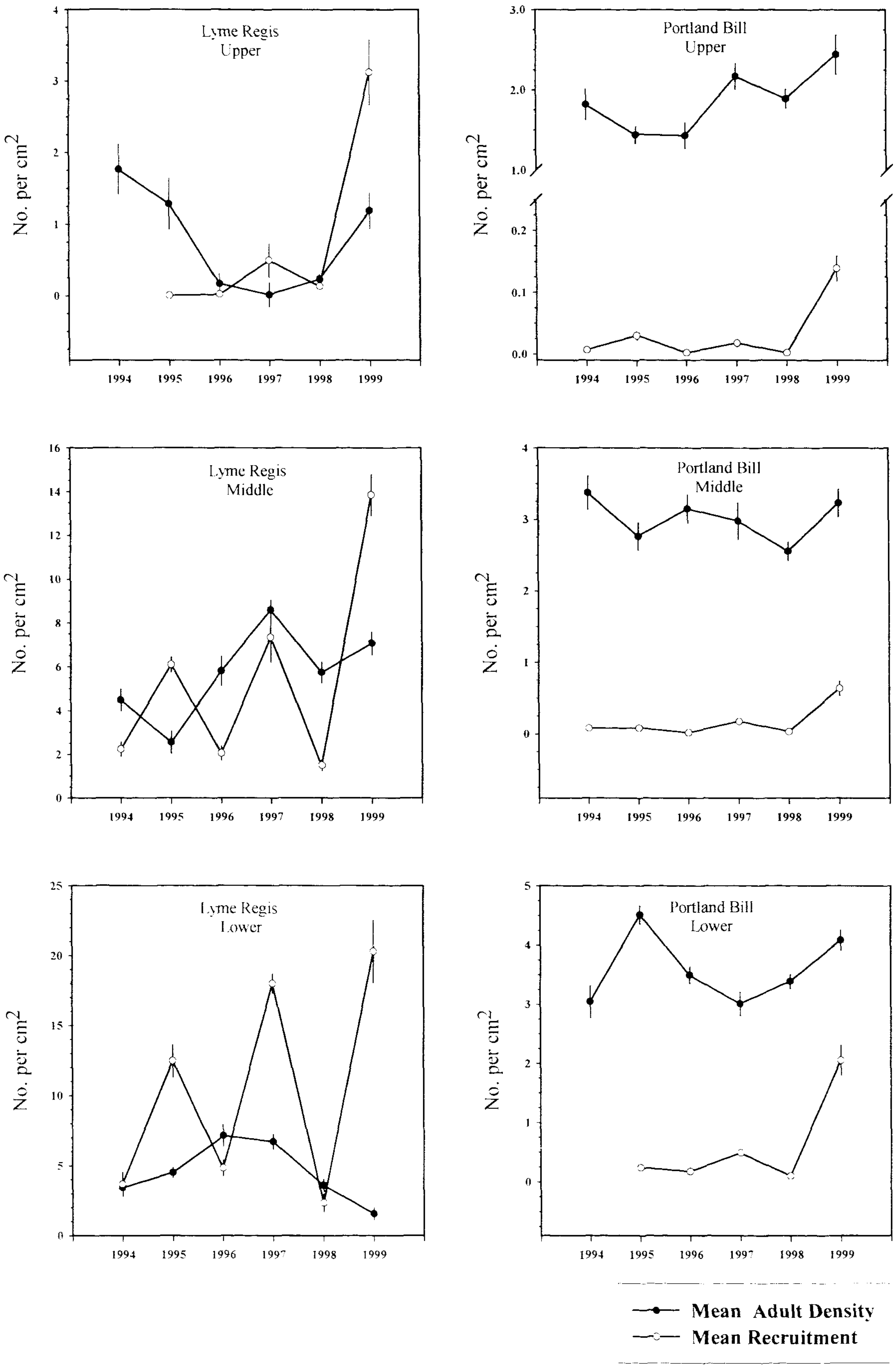


Fig.5.36. Mean *Chthamalus* recruitment and adult density of *Chthamalus montagui* at three tidal levels at Lyme Regis and Portland Bill, Dorset, 1994-1999. Error bars show ± SE.

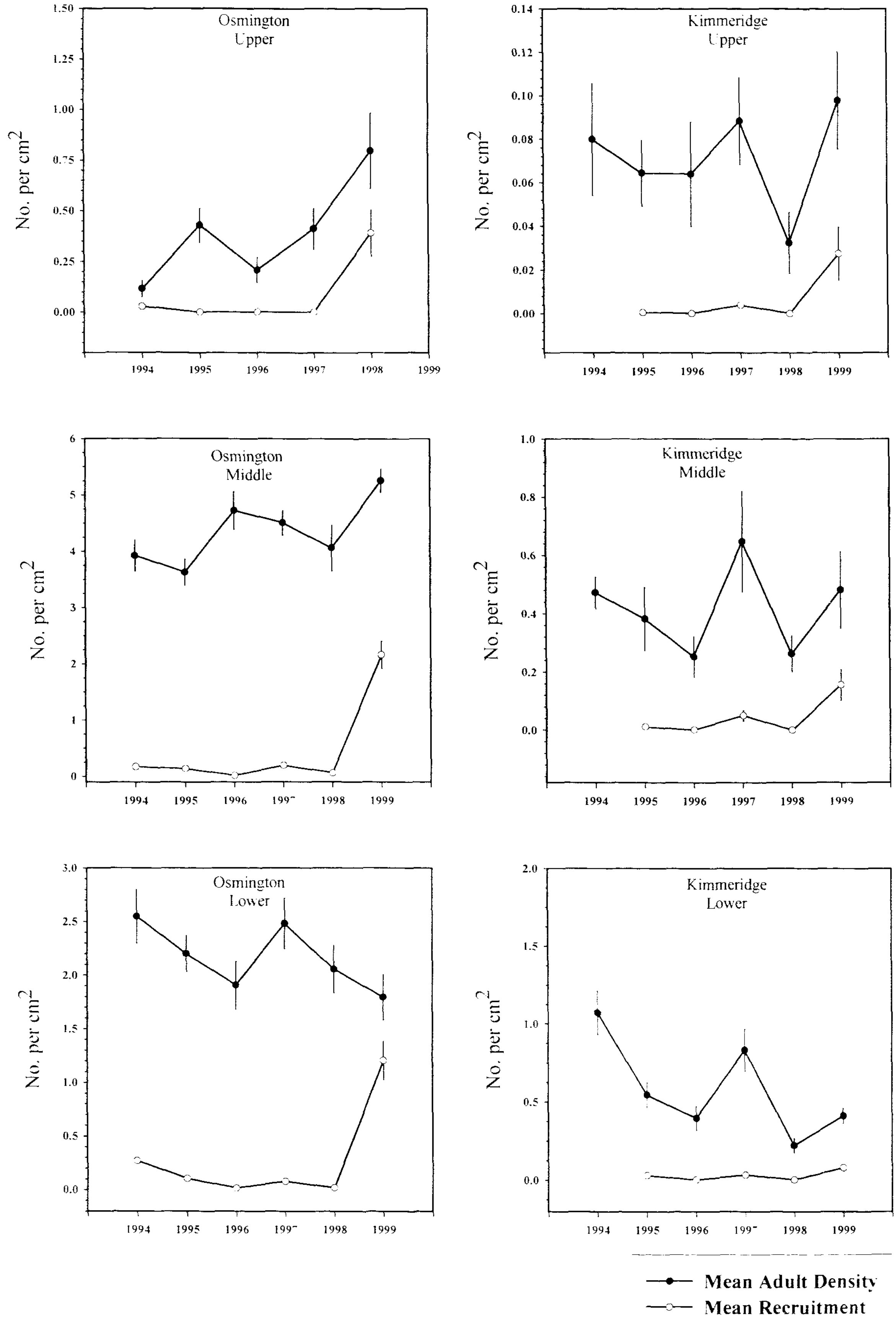


Fig.5.37. Mean *Chthamalus* recruitment and adult density of *Chthamalus montagui* at three tidal levels at Osmington Mills and Kimmeridge,Dorset, 1994-1999. Error bars show ± SE.

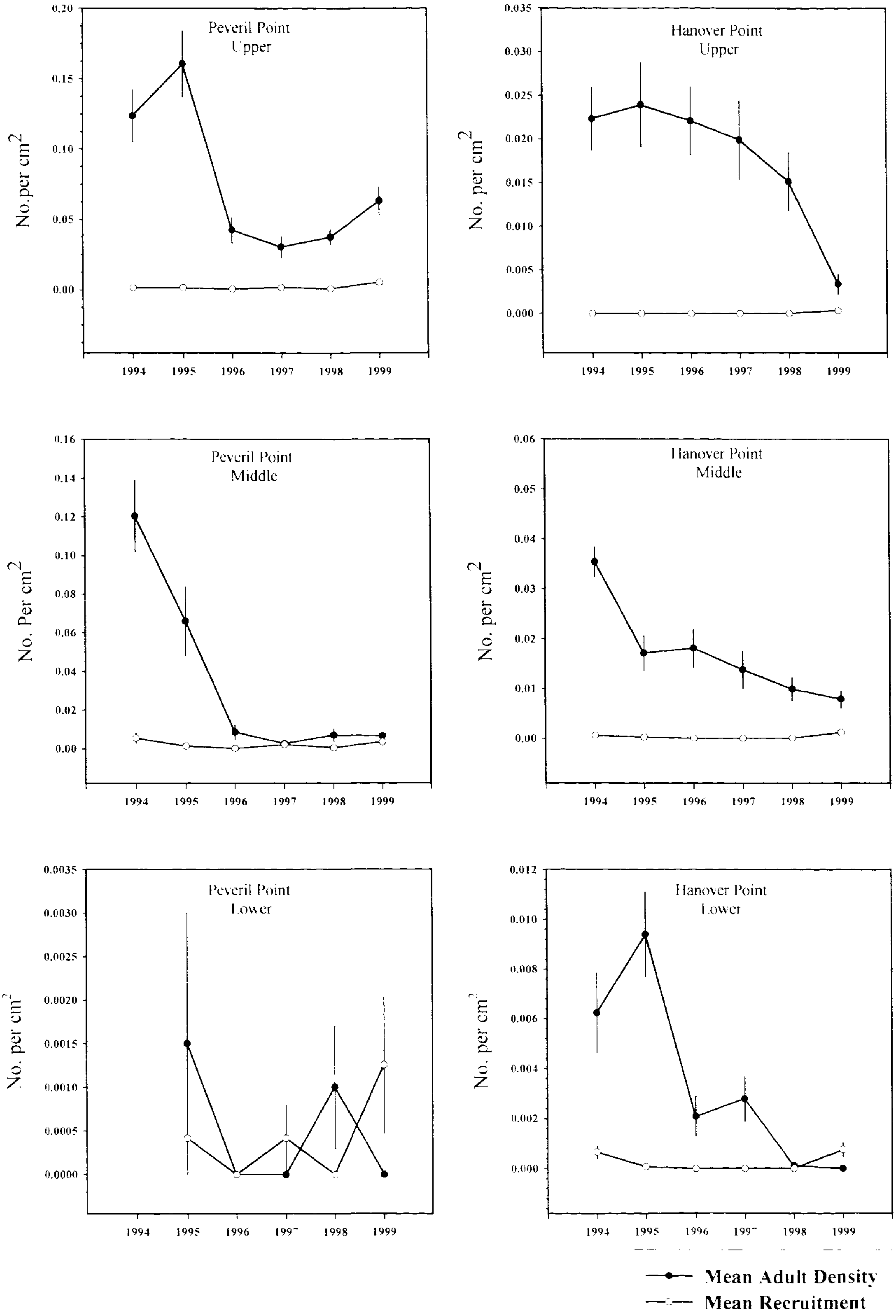


Fig.5.38. Mean *Chthamalus* recruitment and adult density of *Chthamalus montagui* at three tidal levels at Peveril Point, Dorset, and Hanover Point, Isle of Wight, 1994-1999. Error bars show ± SE.

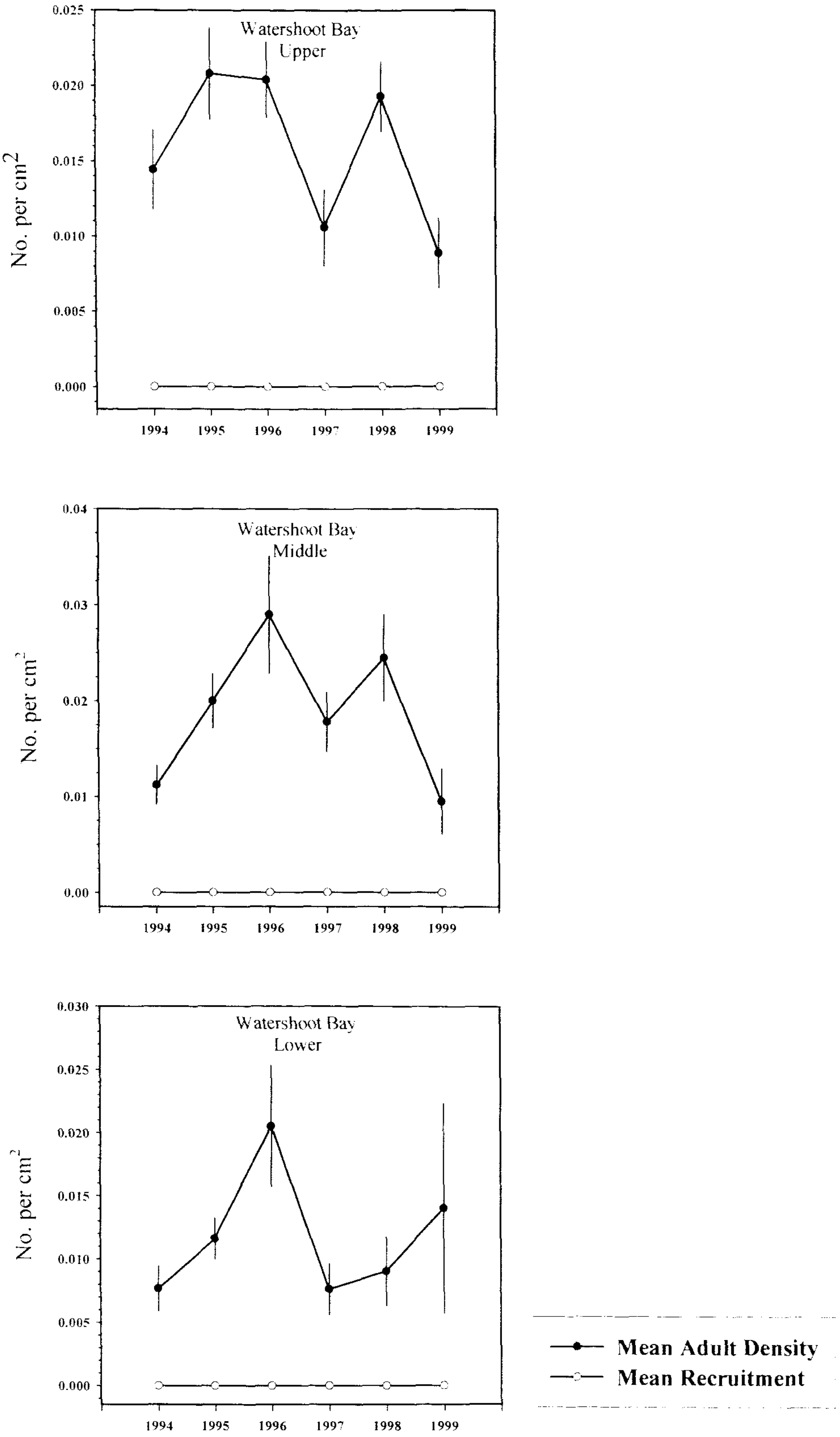


Fig.5.39. Mean *Chthamalus* recruitment and adult density of *Chthamalus montagui* at three tidal levels at Watershoot Bay, Isle of Wight, 1994-1999. Error bars show ± SE.

Table 5.30. Four-way ANOVA of annual mean adult density of *Chthamalus montagui* (No.per cm^{2}) at nine shores along the south coast of England between 1995 and 1999. See Figs5.35-5.39 and text for further details. Data are untransformed: Cochrans test p<0.01.

Source of variation	**df**	**MS**	***F***	***P***	**F versus**
Year = Y	4	38.87	2.55	0.0582	Y X S
Shore = S	8	1035.83	67.93	<0.001	Y X S
Height =H	2	719.68	-	-	NO TEST
Patch (Y x S x H)	135	2.53	2.46	<0.001	RES
Y x S	32	15.25	6.03	<0.001	P (Y x S x H)
Y x H	8	10.7	0.94	0.49	Y x S x H
S x H	16	181.95	16	<0.001	Y x S x H
Y x S x H	64	11.37	4.49	<0.001	P (Y x S x H)
Residual	430	1.03			
Total	699				

While overall differences between years were not quite significant (p = 0.0582) the strong Y x S interaction was investigated further using SNK multiple comparison procedure. Differences in *Chthamalus montagui* density between years were resolved for the following shores: '=' denotes no significant differences. '>' denotes p< 0.05.

Shoalstone

Year	**1995**	**1996**	**1997**	**1998**	**1999**
Mean Shore Density	2.86	4.73	4.42	2.95	3.48

1996 =1997 >1999 = 1998 = 1995

Saltern Cove

Year	**1995**	**1996**	**1997**	**1998**	**1999**
Mean Shore Density	4.87	5.57	4.16	3.1	4.93

1996 > 1999 = 1995 >1997 > 1998

Lyme Regis

Year	**1995**	**1996**	**1997**	**1998**	**1999**
Mean Shore Density	2.78	4.37	5.11	3.19	3.27

1997 > 1996 > 1999 = 1998 = 1995

Peveril Point

Year	**1995**	**1996**	**1997**	**1998**	**1999**
Mean Shore Density	0.08	0.02	0.01	0.02	0.02

1995 > 1996 = 1997 = 1998 = 1999

5.4 Discussion

Recruitment

Between 1994-1999, studies of *Chthamalus* recruitment between east Devon and the Isle of Wight have shown that although there have been consistently high densities (typically 1-10 per cm^2) recorded at sites in Lyme Bay, there is an 'order of magnitude' reduction immediately east of Portland Bill. Moreover there is a recruitment gradient east along the Purbeck coast, with the consequence that almost negligible recruitment is measured at Swanage and on the Isle of Wight. The rank-order of recruitment was consistent amongst the shores between 1995-99.

So how reliable is this observed pattern? What are the main assumptions being made? Firstly, no attempt has been made to separate the contribution made to total recruitment by the different species *C. montagui* and *C. stellatus*. While an aid to field identification of newly metamorphosed recruits is provided by Burrows (1988) this was not used. In the same study, even when using biochemical techniques to separate recruits, *C. stellatus* typically only accounted for less than 5% of total *Chthamalus* recruits examined in 1983 and 1984 at shores near Plymouth. On the most exposed shore, at Queener Point, this proportion rose to between 10-15%. Because both *C. montagui* and *C. stellatus* are regarded as warm-temperate species it was not considered of great importance to distinguish the recruits for the purposes of this study. It is acknowledged however that due to the longer planktonic life of *C. stellatus* (Burrows.1988) recruitment of this species may be greater at headlands such as Portland Bill and towards the east of the *Chthamalus* range e.g. St Catherine's Point on the Isle of Wight.

Secondly, a fully quantitative estimate of recruitment at the different sites was only made at the end of the settlement period, typically between mid and late October. Minchinton & Scheibling (1993b), working in Nova Scotia, found that variations in sampling procedure and frequency seriously affected recruitment estimates of *Semibalanus balanoides*. Estimates of recruitment and post-settlement mortality were found to decrease exponentially as the sampling frequency decreased. The estimate of recruitment made by sampling every 2.1 days during the 44 -day period of the study was 77% smaller than the estimate made by sampling every 1.3 days.

During this study of *Chthamalus,* no detailed measurement of daily settlement and post-settlement mortality was undertaken. The recruitment estimates made at the end of the summer are therefore likely to be a gross underestimate of the total settlement that occurred during the season, particularly at those shores when high densities were recorded. In most years, a mid-season check was made in August at a selection of sites along the coast and yet cyprids or metamorphosing recruits were extremely scarce east of Portland Bill. Whereas in Lyme Bay, recruitment was often very advanced by mid-August and it is quite possible that in some years, notably 1999, certain parts of the shore did approach saturation point. In 1995, quadrats were particularly densely colonised on the middle shore at Saltern Cove and it was evident that recruitment was also high further up the shore, beyond the main adult zone. This could have indicated that space lower down the shore had become saturated and that cyprids were having to settle at below-optimum sites where available space was still present. More frequent clearance during the settlement period may therefore have resulted in higher density estimates obtained, although a precise estimate of total settlement can only be determined by following the fate of individual cyprids and newly calcified individuals.

While the magnitude of overall settlement may have been underestimated because of low sampling frequency, the pattern of recruitment, and particularly the relative differences either side of Portland Bill, would only be affected if there were significant differences in post-settlement mortality rate. Experiments were not possible east of Portland because of the scarcity of cyprids; they had either died on contact, perhaps due to desiccation or predation, or their abundance was so low that they were overlooked. However even in Lyme Bay, while metamorphosing barnacles ('pink spat') were very obvious by mid -August, cyprids were not so easy to find. Power *et al.*, (1999) suggest that the relative scarcity of *C. montagui* cyprids found on the shores of south-west Ireland may be due to early calcification of the shell plates, perhaps as an adaptation to resist desiccation on the shore.

Of the three shores studied in Lyme Bay, two were in relatively close proximity within Torbay. Indeed Torbay itself should arguably have been excluded from the study because of the small size of the embayment in relation to the remainder of the study area. Shoalstone beach was originally chosen because of the possibility of comparative studies with that of earlier work at this location (Southward & Crisp,1954, 1956). However because of concerns related to visitor pressure, the nearby nature reserve of Saltern Cove was also included. Yet over the study period, both these sites had remarkably similar recruitment. Other data collected from Chesil in 1999, as part of the broad-scale studies undertaken (Fig 5.11), do however support the assertion that Lyme Bay may generally be regarded as a high recruitment area for this species. That high densities should be observed at this site is particularly interesting considering the 40km distance east from Lyme Regis and the intervening Chesil beach; a highly mobile shingle structure offering unsuitable substratum. The inadequate rocky habitat between Lyme Regis and Portland has been regarded as a major factor responsible for setting the limits of southern species along the Channel (Crisp & Southward 1958). In Lyme Bay, high recruitment densities, albeit non-quantitative, were also observed at Dawlish in 1994 and at Seatown in 1996. Studies carried out using 78cm^2 quadrats by Dr.A.Kent in 1998 (pers. comm) gave densities of between 3-10 per cm^2 at Sidmouth and 0.3-1 per cm^2 at Portland Bill.

At the design stage of the investigation, careful consideration was given to the use of permanent quadrats, as opposed to making new clearances on the shore on an annual basis. While clearing new patches would have been acceptable at those shores with high recruitment and rapid recovery, it was considered inappropriate and unnecessarily destructive to carry out this type of sampling at low recruitment sites such as those east of Portland Bill. At Osmington Mills near Weymouth, a new series of clearances was made at mid tide level in 1995 and those created the previous year were never re-cleared. Although adult cover was approximately 100% prior to clearance, after five years the original quadrats still have less than 20% cover of *Chthamalus*, due to low recruitment. However at Shoalstone, all the patches made to determine optimum clearance size in 1995 (Fig.5.1) had been totally re-colonised (90-100% cover) after two years.

One possibility was to have used a 100cm^2 quadrat instead of 400 cm^2. However at the low recruitment sites it was thought that a larger clearance area would be necessary to capture sufficient recruits to make a quantitative assessment suitable for comparative purposes. In retrospect, this smaller size would have probably been satisfactory. The use of permanent quadrats throughout this part of the study has to some extent confounded statistical analysis because of the non-independent nature of the design, with the consequent loss of spatial and temporal replication required for an examination of the time-series. Yet no evidence could be found that the patches became either more or less attractive to new recruits during the monitoring period (Fig.5.5). In October 1998, six new clearances were made at Saltern Cove within five metres of those that had been cleared annually over the previous four years. The recruitment density in both sets of quadrats was measured in October 1999. Although the mean densities within the new quadrats were higher than those in the original clearances a Mann-Whiney 'U' test applied to the data showed no significant difference in density estimates obtained (p = 0.065).

The broad-scale study of *Chthamalus* recruitment on vertical surfaces, carried out during 1999, support other observations that there is a steep recruitment gradient along the Purbeck coast. Though interestingly, the same is apparent for *Semibalanus balanoides*, which also had particularly low recruitment along the Purbeck coast and around the Isle of Wight. Additional data for *S. balanoides* (Dr.A.Kent pers.comm) from Sidmouth in Lyme Bay during 1998, showed that maximum densities varied between 2 and 10 per cm^2 but that those at Cowes on the Isle of Wight were between 0.3 and 2 per cm^2. There is therefore strong evidence for consistency in the pattern of barnacle recruitment along the south coast; a pattern that correlates well with adult density. The Australasian immigrant *Elminius modestus* had surprisingly low recruitment around the Isle of Wight and especially in the Solent where the species is common on pilings and as fouling on the undersides of boats moored within estuaries. It is possible that the high flushing rate of the Solent causes considerable larval dispersal, thereby reducing recruitment on the open coast. The species is also known not to tolerate high wave exposure (Crisp, 1958) so its absence from Portland Bill was unsurprising.

Within-shore recruitment patterns were also remarkably consistent, with highest recruitment densities generally found at the mid-shore level (HWN-MTL). This is also the zone of largest adult populations. The notable exception being at Portland Bill, where highest recruitment was found at the lower end of the shore. It is possible that overall recruitment estimates here may have been elevated due to the settlement preferences of *C.stellatus* on the lower zones of exposed shores. However, while not every recruit counted in October was examined closely, no *C. stellatus* was identified the following May, or showed up in subsequent photographs. It is interesting that Burrows (1988) working in Plymouth found that *Chthamalus* recruitment was greatest at HWN on relatively sheltered shores and at LWN on the most exposed location. It may be that predation by dog-whelks or other species on these highly exposed coasts is reduced, enabling greater survival at lower tidal levels. The lower recruitment found at LWN on the other shores may be due to poor settlement or higher post-settlement mortality. Highest settlement densities for *C. montagui* have been found on the lower shore (Kendall & Bedford, 1987; Burrows, 1988) however post-settlement mortality was also shown to be greatest at this level (Burrows, 1988; Pannacciulli, 1995). This has been mainly attributed to predation by dog-whelks or other species.

Previous studies on the settlement of *S. balanoides* have shown that there is strong concordance between the magnitude of settlement and the supply of cyprids to the shore (Minchinton & Scheibling, 1991). In Nova Scotia, 79% of variation in *S.balanoides* recruitment density at the end of the settlement period was explained by settlement density. Moreover, between 73-86% of variation in adult density was explained by total settlement density, except where post-recruitment mortality was high due to predation. Bertness *et al.*,(1992) concluded that site differences in the magnitude and timing of settlement are primarily an expression of larval dynamics and that local features of variation in settlement, due to microhabitats, tidal height, and presence of conspecifics were of secondary importance relative to variations in larval supply. This is important to consider, as the observed low *Chthamalus* settlement and recruitment on the eastern shores could well be due to inadequate cues because of low adult population densities. A negative feedback situation might then ensue whereby population densities could remain low for long periods. At Osmington Mills near Weymouth, large areas of the intertidal zone have a 100% cover of *Chthamalus*, yet recruitment density is typically ten times less than in Lyme Bay.

There is therefore empirical evidence for the suggestion that recruitment density may be used as a surrogate for a measure of larval supply. Gaines *et al.*,(1985) showed that even spatial variation in settlement of *Balanus glandula* on natural substrata located tens of metres apart reflected the spatial distribution of cyprids in the water column, and that larval density explained 86% of variation in weekly settlement. At Port Erin, in the Isle of Man, Chelazzi *et al.*, (1997) found that there was also a strong correlation between cyprid abundance, both within the water column and in traps, and settlement of *S.balanoides* on the shore. It is therefore likely that the major differences in *Chthamalus* recruitment measured in Lyme Bay and along the Purbeck coast reflect differences in larval abundance between the two coastal cells and supply of cyprds to the shore.

From the model (Fig.5.11) there are proportionally fewer recruits per adult reaching the shore at lower adult densities. There could therefore be an Allee-effect (Allee,1931), where because adult densities are so low in the east Dorset coast and on the Isle of Wight, the minimum distance between individuals necessary for cross-fertilization, and therefore larval production, is seldom reached. In *Chthamalus*, the maximum penis size is about 12mm (O'Riordan,1992), so adults more than 2cm apart would not be able to breed successfully. However, in *Chthamalus*, this difficulty may be partly overcome by self-fertilization (Barnes & Crisp, 1956; Barnes & Barnes, 1958; Chapter 4 of this work).

The considerable reduction in recruitment is probably also due to the physical and hydrographic barrier created by Portland. Similarly, for the other species, barriers to the westward larval transport of both *Semibalanus balanoides* and *Elminius modestus* appear to occur at Selsey Bill and the turbulent waters around Isle of Wight. One can envisage 'High Larval Dispersal Zones ' off Selsey, St.Catherine's Point and Portland Bill that, for barnacles at least, significantly reduces shore settlement and consequent recruitment. Portland Bill was considered to be an important barrier to the westward dispersal and colonisation of *E. modestus* (Crisp,1958). Of course this can only be confirmed by studies of larval abundance and associated settlement rates on the different shores within the area over many more years. It might be, for example, that there is differential larval survival due to predation or food supply and (or) quality of some hitherto unknown physical or chemical constituent of the water.

In the case of *Chthamalus*, larval survival should theoretically be greater in the eastern Channel because of higher summer temperatures. Burrows (1988) found that *Chthamalus* nauplii reared in the laboratory survived better at higher temperatures, which may account for the recruitment failure of broods released in the late spring and early summer when sea temperatures may not yet be warm enough to aid survival

Although this work only covers a five year period it has been evident that higher recruitment of *Chthamalus* has occurred during the warmer summers, with maxima recorded during the warmest summer of 1999 and the lowest in the cooler years of 1996 and 1998. Moreover there has been remarkable concordance in the level of recruitment at different locations along the whole coast. This suggests that inspite of the locally variable tidal regime, rock type and shoreline configuration, the magnitude of recruitment appears to be ultimately determined by some climatic or meteorological factor. Lewis (1991) suggested a correlation between *Chthamalus* recruitment and summer temperatures in Scotland, but the relatively poor regional synchrony also pointed to strong wind influences on this highly irregular coastline, as with *Semibalanus* in this area. At Aberystwyth, on the Welsh coast, Kendall & Bedford (1987) did not find any association between recruitment and summer air temperature. High summer temperatures are often associated with relatively calm and settled anticyclonic conditions, when onshore sea breezes are common during the afternoon. During these periods, winds from an easterly direction can be relatively frequent along the south coast of England. Hawkins & Hartnoll (1982a) found that settlement of *S. balanoides* around the Isle of Man was strongly correlated with onshore winds. Relatively calm seas with light onshore winds are likely to provide good conditions for larval settlement of any intertidal species, and so it is difficult to separate wind effects from sea temperature. The greater frequency of easterly winds during the summer of 1995 may have been responsible for the particularly high recruitment of *Chthamalus* observed within Torbay, which has an eastern aspect.

Growth

The results of the initial pilot study on the growth of the 1994 cohort (Fig.5.14) showed that by May 1995, opercular size differences were apparent between shores. Individuals at Kimmeridge, the most eastern site investigated, appeared to have grown least over this period and so a more detailed study of the 1995 cohort was commenced. It was not possible to obtain size measurements between October and May from any of the mainland study sites and so any cessation of growth during the winter months could not be established. It is however apparent from the growth curves for Portland Bill and Saltern Cove (Figs 5.15-5.17) that the opercular diameter of the recruits approximately doubled between October 1995 and May 1996. Yet although there was no significant difference in first 'winter' growth rate between shores, it was evident that the Kimmeridge animals were still much smaller than those both at Saltern Cove and at Portland Bill. Moreover the size differences of the new recruits, which had existed shortly after settlement in October, had been maintained during the following seven months. This would suggest that the initial growth within the first few weeks after settlement largely determines size attained by the following May. It is possible that this initial size difference may be a consequence of later settlement. It was certainly apparent that no settlement had occurred at this site by mid-August, whereas it had been advanced to the west of Portland Bill. Kimmeridge is relatively distant from estuarine sources of nutrient input and this may be partly responsible for poor initial growth. The size of the new recruits may also be a consequence of cyprid size at the time of settlement. It is possible that should the cyprids arriving on to the shore at Kimmeridge be of local parental origin, then they may be smaller due to reduced growth during the naupliar, feeding stage, of development. Smaller cyprids may also be expected should they have been at sea for particularly long periods, perhaps as a result of offshore dispersal due to the strong currents off Portland Bill, or because of the inability to find suitable substrata for settlement. What is clear is that even after two years growth, *C. montagui* at Kimmeridge was significantly smaller compared to those on the other shores. An examination of the size-frequency histograms for *C. montagui* at Kimmeridge in Chapter 3 (Fig.3.23) shows that the population consists of unusually small animals. A comparison with other data from the Plymouth area (Burrows,1988; Pannacciulli,1995) concords with this work that the opercular diameter of two year old animals is generally about 1.7-2.0mm; those at Kimmeridge however were approximately 1.5mm. The animals at Portland Bill were consistently and significantly larger than those on the other shores, even shortly after settlement. This is unsurprising considering the high degree of wave action on this shore, which for filter feeding species must enhance feeding efficiency. The large size of animals within this population, determined from the size-frequency histograms in Chapter 3, can now be attributed to rapid early and sustained growth rate.

Although there were no differences in winter growth rate between shores, highly significant differences do occur between tidal levels, with lowest rates measured on the lower shore. These differences were particularly apparent at Kimmeridge and Saltern Cove. At all shores the initial size of recruits diminished with increasing tidal height and it may be that higher growth rates at elevated levels in some way compensate for the smaller size. Crisp & Southward (1961) found greater cirral activity rates of *C. 'stellatus'* at higher tidal levels. This ability to compensate for 'below optimum size' might possibly have been expected to extend to the whole Kimmeridge population by increased growth rates at all tidal levels. Although not statistically significant it is worth noting that the mean shore winter growth rate for Kimmeridge was larger than that measured for the other two shores.

To determine if growth rate was inhibited beyond the current adult range, animals of the 1995 cohort were collected on perspex plates and translocated to Bembridge, the most eastern extremity of the Isle of Wight. Here the animals were measured more frequently and it was apparent that little growth occurred between October 1995 and mid-January 1996. At Shanklin on the Isle of Wight, the mean air temperature over these months was the second coolest over the five-year study period (8.5°C). At Torquay, the mean air temperature over the same months was nearly a degree warmer at 9.33 °C .Those growing on control plates at Saltern Cove in Devon grew faster over this same period and by May 1996 the animals at Bembridge were significantly smaller than those both on plates and in natural populations at Saltern Cove. It is therefore possible that the lower air temperatures experienced at Bembridge over the winter period suppressed cirral activity, or indirectly reduced food availability. A nested experimental design (Underwood, 1997) encompassing other shore localities in both regions would be necessary to demonstrate any effect of low winter temperatures on growth rate. Although in May 1996, the four recruits measured in natural populations on the south-west coast of the Isle of Wight were of comparable size to those translocated to Bembridge. From May 1996, the animals within natural populations on the shore at Saltern Cove grew significantly faster than those on plates. From the growth observed it is possible that the grooves sawn into the perspex plates, within which most animals settled, severely restricted summer growth, either physically or by causing reduced feeding efficiency. The animals on the shore however had greater space available for shell growth. Interestingly, from the summer of 1996 till the end of the experiment in August 1997 there was no significant difference in growth rate between those on plates at Bembridge and at Saltern Cove. One would expect therefore that if animals had settled on the shore at Bembridge they would have grown at a faster rate than those on the perspex plates and would therefore have been of similar size to those growing in Devon at the western end of the study area. It is probable that they would also be larger than those in the Kimmeridge population. The few individuals followed in natural populations on the Isle of Wight were larger than the translocated specimens when measured in October 1996 and August 1997. It is concluded that while there is some evidence for reduced winter growth rate of *C. montagui* at the extreme eastern edge of its current range, the differences are sufficiently small not to affect the species ability to attain an adequate size for reproduction and resistance to predation.

Mortality

Of particular interest in this part of the investigation was the first-winter survival of the new recruits, as it has been suggested that the colder winters experienced in the east of the species range causes higher mortality and limits species distribution (Crisp & Southward, 1958). For this reason, it was considered unnecessary to examine in detail the mortality during the first few weeks after settlement (post-settlement mortality). This work was primarily concerned therefore with post-recruitment mortality of *Chthamalus* over the first winter i.e. between mid-October and the following May, with the initial hypothesis that mortality would increase at the eastern end of the study area. Yet a comparative study of the 1994 cohort at Shoalstone in Devon, and at sites on the Isle of Wight showed that, if anything, mortality was greater in the west and therefore independent of cooler air or sea temperature. A more extensive study the following winter also revealed this trend, however there were no statistically significant differences between shores. It is very evident that there is considerable within-shore variability in mortality and that differences between shore levels were not consistent, although survival was generally less on the middle and lower shore. This concords with recent work near Plymouth by Burrows (1988) and Pannacciulli (1995), who both found that mortality of *C. montagui* was greater at lower tidal levels.

The measurement of mortality may have been confounded by differences in number of individuals followed, which were much smaller at the eastern shores because of lower recruitment. Nevertheless, the results suggest that post-recruitment mortality may be density-dependent, with higher rates measured where recruitment is greatest in the west. Indeed the mean-shore winter mortality of the three low-recruitment sites examined was significantly less than that of the three high-recruitment shores (Fig. 5.26). The mechanisms responsible for higher mortality are not clear. Overall dog-whelk abundance was greater in the western localities which may have increased mortality rates due to predatory activity at lower levels on these shores. However the mortality above the dog-whelk zone was also greater in these locations. Bulldozing by limpets could also be important and undoubtedly occurs; photographs showed that areas cleared of new recruits were often observed in the close vicinity of older limpets. Total limpet densities on the eastern shores were comparable with localities in Lyme Bay; the exception being Kimmeridge where lowest densities were recorded. Significant overcowding with subsequent intraspecific competition, due to overgowth and undercutting, is also unconvincing as space was always available, albeit less at the most western localities. Even on the upper shore, mortality was still greater in the west, where frost damage might be least. The importance of other predators such as fish, which are able to extend their influence over the whole shore, may be underestimated. It is likely that predator density will be greater where the prey is in good supply. However there may also be other factors or agents associated with high population density that are influential in raising mortality. Although rarely referred to in the literature, mortality may occur due to the spread of bacterial, viral and fungal disease or parasites. The risk of fatal outbreaks is likely to be greater when densities are high and new recruits are probably most vulnerable. The isopod *Hemioniscus balani* is known to have a debilitating effect on barnacles and although its presence was not observed within adult *Chthamalus*, the new recruits were not examined. Connell (1985) re-analysed several sets of data collected from various workers in an attempt to find evidence for density-dependent mortality in marine intertidal communities. As far as barnacles were concerned he concluded that post-settlement mortality was independent of settler density. Using data on *C. 'stellatus'* collected by Hatton (1938) at three sites in northern France he also examined post-recruitment mortality (from end of settlement to age 1 year) on the upper and middle shore. Using log-transformed densities he found that although the regression slope indicated positive density-dependence, the data was statistically insignificant. A close examination of the graph (his Fig.3B) shows a particularly anomalous point where 60-70% mortality was recorded at recruitment densities of about 0.1 per cm^2, which was the probable cause of statistical insignificance. However, using untransformed data the relationship was significant ($p < 0.05$) and the highest mortality (90-100%) was recorded where densities were greatest (between 8-20 per cm^2). Post-recruitment density-dependent mortality was demonstrated for *Semibalanus balanoides* at Millport in Scotland and in Maine, U.S.A. These particular shores were both characterised by recruitment densities in excess of 25 per cm^2 whereas other shores investigated where recruitment was lighter showed density-independent mortality. In this work, *Chthamalus* recruitment densities reached a maximum of 20-27 per cm^2 on the lower shore at Lyme Regis in 1999.

The suggestion that cooler winter temperatures may be unimportant in setting species limits is somewhat undermined by the translocation experiment undertaken at Bembridge. The mortality of translocated *Chthamalus* during the relatively cold winter months was nearly twice that on the control plates in Devon. However this may be due to one or a combination of several other factors that differ between the sites, such as food availability or the degree of exposure. It may also have been due to a greater degree of disturbance during the process of translocation. The settlement plates appear not to effect early mortality as there was no significant difference in mortality on plates and in natural populations in Saltern Cove. However at lower temperatures, such as those experienced at Bembridge, the local microclimate within grooves on the plates may not necessarily be as favourable. After one year, the higher mortality experienced within natural populations suggests that greater protection is afforded by the plates. Therefore one might expect greater mortality within natural populations, had they existed, on the shore at Bembridge. Arguably, the important result was that over half the 1079 recruits followed on the plates at Bembridge survived until the following May as did six of the seven monitored in natural populations elsewhere on the island. While survival of winter temperatures may be important it appears not to be critically so.

Observations on the survival of adult *Chthamalus 'stellatus'* during the 1962-63 winter were mixed. Crisp (1964) reported relatively little effect in England whereas Barnes & Barnes (1966) found considerable mortality on shores in southern Brittany.

Between October 1995 and August 1997 the mortality of adult *Chthamalus* on the Isle of Wight was comparable with that in the west of the study area and there does not appear to be any evidence of the density-dependent mortality that was evident in young recruits. On Isle of Wight shores, slightly higher mortality appears to occur during the summer months, which may either be due to heat stress, greater predatory activity or trampling pressure from visitors.

The higher mortality of isolated individual chthamalids observed within Isle of Wight populations may be a significant consequence of low recruitment. The observations are at variance with those of Barnes & Powell (1950) who suggested that animals living within a dense matrix are more vulnerable, should it be damaged and exposed to wave erosion. Although 'hummocking' at high densities by *S. balanoides* causes eventual weakness of the barnacle matrix, Bertness *et al.*, (1998) argue that crowding may benefit northern acorn barnacles by buffering them from heat and desiccation stress.
However the overall annual mortality of the adult populations on these shores was usually under 15% and as discussed above was no greater than populations in Devon.
It is important to appreciate that the presence of adults alone indicates that the environment has been generally suitable for survival, and from the condition of the shell plates appears to have been so for several years.

All the evidence obtained suggests that, should recruitment occur, the probability of winter survival and subsequent growth to adult size is, at the very least, no less than in the west of the species range.

Population changes

The time lag between annual recruitment, determined by sea temperatures, and observed changes in adult population density was suggested by Southward (1991) to vary between one and two years depending on tidal level. Relationships over a five-year time-series are more difficult to identify, however in Lyme Bay, the peaks in recruitment do appear to coincide with peaks in adult density one year later at most tidal heights considered. The exceptions being on the upper shore at Shoalstone, where the peak in recruitment in 1995 was not observed until 1997, and on the upper shore at Lyme Regis, where the sampling areas were located on a concrete groyne that was frequently smothered by sand and shingle. At Lyme Regis the heavy recruitment in 1997 had not reversed the population decline when last measured in October 1999. It is possible that at lower tidal levels, where there is intensive dog-whelk predation, even consistently high recruitment may not always impact upon adult population density. At Portland Bill, the rising adult densities measured in 1999 may be a consequence of the better recruitment in 1997, observed at all tidal levels. This is just about discernible at Osmington, except on the lower shore where the population remains in decline. At Kimmeridge, a two-year time lag appears to be evident. This may be because the smaller sized individuals here are not noticed in counts. The major fall in adult density measured in 1998 could be partly due to recruitment failure two years earlier in 1996. This, together with consistently poor recruitment at Peveril Point and Hanover Point is undoubtedly responsible for the decline in *Chthamalus* observed at the extreme limits of the species range.

Chapter 6

Observations on the recruitment and growth rate of other species: the trochid gastropods *Gibbula umbilicalis* and *Osilinus lineatus* and barnacle *Balanus perforatus*

6.1 Introduction

Studies on the reproductive biology, recruitment and growth rate of British populations of the trochid gastropods *Gibbula umbilicalis* and *Osilinus lineatus* were largely carried out by the NERC Rocky Shore Surveillance Group between 1977-1986 (Williamson & Kendall, 1981; Garwood & Kendall, 1985; Kendall & Lewis, 1986; Kendall, 1987; Kendall *et al.*, 1987). Their work was primarily concerned with the identification of latitudinal factors affecting distribution and recruitment and although sites in the western approaches to the Channel were included in their monitoring programmes they were not investigating factors setting eastern geographic limits. For *Osilinus lineatus*, the population at Portland Bill was not specifically studied, and the most eastern population of *Gibbula umbilicalis* included in their work was Osmington Mills. Kendall (1987), however, suspected that the eastern limits of *Osilinus* were set by hydrographic barriers at Portland Bill, where there are strong offshore currents.

Earlier work on the reproductive biology of both *G. umbilicalis* and *Osilinus* (Williams 1964, 1965; Underwood, 1972) indicated that the species had prolonged spawning periods of between 3-4 months, during which there was a gradual release of gametes. However at Aberaeron in mid-Wales, both sexes of each species reached maturity when two years old, gonad development commenced in April or May and major releases were detected in July for *Osilinus* and in August for *G. umbilicalis* (Garwood & Kendall, 1985). Very little is known about the duration of larval stages for these species, although Fretter & Graham (1994) quote a figure of 4 -6 days.

Studies on the recruitment of *G. umbilicalis* by Kendall & Lewis (1986) showed that in NW Scotland, close to the species northern limit, recruitment was generally poor and populations were of low density and dominated by large old individuals. Yet within enclosed embayments close to the northern limits, such as Loch Eriboll, there existed large populations with small body size. Further south, in Wales and in SW England, recruitment was usually more regular and populations more dense with smaller individuals. Yet, in populations examined at the most eastern sites in the Channel (Osmington Mills and Lyme Regis) between 1976-1984, recruitment was considered to have succeeded only in 1979 at Lyme. Kendall *et al.*, (1987), working on both *G. umbilicalis* and *Osilinus* at Aberaeron in Mid-Wales, observed regular recruitment, even though the site was close to the northern limits of both species. The size of animals found close to the northern limits is considered to be density-dependent. Lewis (1986) noted the decline in maximum basal diameter of *G.umbilicalis* from the extreme northern limits in Scotland to Portugal. He also observed that dense populations in Britain and Ireland are of small size "apparently as a result of intraspecific competition". *Osilinus lineatus* transplanted to the North Yorkshire coast survived the cold 1978-79 winter and grew faster than animals in the population from which they were taken and spawned normally (Williamson & Kendall, *unpub* cited in Kendall & Lewis, 1986; Kendall, 1987). Studies on the recruitment of *Osilinus* on English and Welsh shores between 1974 and 1986 (Kendall, 1987) showed that failure years were unusual, as were particularly successful years. A relationship between size and density was also observed, again suggesting density dependence.

No previous attempts to measure the recruitment success of *Balanus perforatus* in British waters appear to have been published. The species cryptic habit does not easily permit direct quantitative assessment on the rock surface. Norris & Crisp (1953) found that at Torbay in south Devon, egg development was rapid and occurred between mid-June and August. Nauplii were liberated into the plankton in late June, with settlement commencing in late July and continuing through August and into September. Further observations by these authors at Barnstaple Bay on the north Devon coast indicated a slightly later onset of breeding.

In the Mediterranean, Lepore *et al.*, (1979) found that maximum settlement was in September. Between early May and the end of October, Geraci & Romairone (1986) analysed the proportion of different naupliar stages of a variety of *Balanus* spp. off the Italian coast. Stage II larvae of *B.perforatus* were found at the beginning of the sampling programme and stage VI peaked in mid-late June, although they were still present in samples at the end of October. Large reductions in the proportions of the larval stages present in hauls were attributed to high mortality. Total *Balanus* settlement showed two distinct periods; in mid-June and in September, however cyprids and young spat were unfortunately not speciated.

In this work (Chapter 4) *B. perforatus* translocated to Bembridge were shown to have broods between May and September. Because of the species southern distribution and likelihood of earlier reproductive development in warmer seas, it was considered worth attempting to develop a technique by which recruitment could be monitored and growth measured. The growth rate of *B.perforatus* has also received little attention. Single observations of 14μm linear growth per day (5.04mm per year) for intertidal animals at Brixham and 122μm per day for submerged animals on rafts, are reported in Crisp & Bourget (1985).

The specific aims of this chapter are:

i) To investigate the presence of any 'near-limit' characteristics of trochid populations at extreme eastern limits of distribution i.e. frequent recruitment failure and large adult size in sparse populations.

ii) To examine in detail the growth rate of trochids as eastern limits are approached.

iii) To ascertain whether there is a relationship between trochid recruitment and summer sea temperature.

iv) To determine if there is any concordance between the recruitment success of these southern trochid species and with that of *Chthamalus* spp.

v) To develop techniques to measure the growth and recruitment of *Balanus perforatus*.

6.2 Methods

6.2.1 Annual recruitment of *Gibbula umbilicalis* and *Osilinus lineatas*

From population size-frequency histograms of the 1994 and 1995 cohorts (Figs 6.3-6.7 and Figs 6.10-6.11) it was possible to identify, by eye, the modal class for each age cohort and therefore the size range of the shell maximum basal diameter over the first year of growth. The maximum size of new recruits of both species at each location, measured in the autumn (mid-October to early November) and the following spring (May) after the first winter, is shown in Table 6.1. A visual assessment of shell condition was also made to confirm age class. Four five-minute timed searches for new recruits were carried out at each location within suitable recruitment areas: shallow pools at MTL-MLWN with loose stones for *G. umbilicalis* and beneath damp stones and boulders at HWN-MTL for *Osilinus*. Because of the cryptic nature of young spat, this technique was preferred over density estimates within quadrats and was employed for comparative purposes with data obtained by Kendall & Lewis (1986). For both autumn and spring estimates the mean number of new recruits per five-minute count was calculated separately.

Prior to using perspex plates to obtain a settlement of *Chthamalus* for translocation experiments, trials using pieces of roofing slate glued and screwed to marine plywood boards (270x110x12mm) were carried out at LWN at Shoalstone in Devon and at Portland Bill in Dorset. Unfortunately, the slate became badly cracked and this technique was abandoned. However upon removal of the boards at Shoalstone, several young recruits of *G.umbilicalis* were observed both attached to the underside of the board and on the rock immediately beneath.

Table 6.1. Maximum size (mm) of 'O' class measured at different locations along the central south coast of England in October/November of year of recruitment and in May following first winter. Parameter used is maximum basal diameter of shell. Sizes determined from frequency histograms for the 1994 and 1995 cohorts.

	Gibbula umbilicalis		***Osilinus lineatus***	
Location	**Autumn**	**Spring**	**Autumn**	**Spring**
Brixham (Shoalstone) Devon	≤ 6.0	≤ 7.5	≤ 10	≤ 12
Lyme Regis (Broad Ledge) Dorset	≤ 6.0	≤ 7.5	≤ 7	≤ 8
Osmington Mills, Dorset	≤ 6.5	≤ 9.5	N/A	N/A
Kimmeridge, Dorset	≤ 6.5	≤ 9.5	N/A	N/A
Freshwater Bay, Isle of Wight	≤ 6.5	≤ 9.5	N/A	N/A

It was decided to use the boards to create artificial 'removable crevices' as an alternative technique to timed searches for measuring recruitment. The boards were re-fixed to the shore and removed each subsequent visit in the spring and autumn, when the underside of the board and rock beneath was cleared of all colonists. All six boards survived on the shore for six years.

6.2.2 Measurement of growth rate of *Gibbula umbilicalis* and *Osilinus lineatus*

For each species, the size of the 1994 cohort was monitored for two years and that of the 1995 cohort for one year. The size-frequency of the *G.umbilicalis* population was measured at LWN at five stations between Shoalstone in Devon and Freshwater Bay on the Isle of Wight. Each year, the maximum basal diameter was measured with callipers in May, August and October/November. Data were plotted as size-frequency histograms and the position of modal class sizes determined by eye. The mean diameter of each cohort was then calculated for the months sampled. Attempts were made at aging *Osilinus* by observing winter growth checks (Williamson & Kendall, 1981). However some difficulty was encountered, particularly at Lyme Regis where growth rings were relatively indistinct. This could indicate continued growth during the milder winters over the study period. Kendall (1987) refers to similar difficulties in aging French samples where a microscopic examination was required.

6.2.3 Measurement of recruitment and growth of *Balanus perforatus*

When the marine plywood boards (see 6.2.2 above) were removed from the shore at Portland Bill, young recruits of *Balanus perforatus* were observed that had settled on the rock beneath. In many localities the species is most common in relatively inaccessible places, such as crevices and beneath boulders, making recruitment estimates particularly difficult. It was therefore decided to assess the suitability of this technique for monitoring recruitment and growth of the species at this location. In June 1994, six pieces of marine plywood 270 x 110 x 12mm were screwed down to the rock just below LWN using 5 stainless steel 6.5mm screws. Holes for the screws were made using a *Ryobi* petrol drill. The wooden boards were first removed in May 1995 and the number of recruits from the previous summer and autumn were counted under each board and the basal diameter across the R-C axis measured with vernier callipers. Other colonists (e.g. mussels) were removed and the boards were re-fixed to the shore. The 1994 cohort was re-examined and measured in October 1995, May 1996 and August 1996. By this time, further studies of barnacle growth were considered impractical as individuals of the 1994 cohort were now limited by the space available beneath each board. The rocks beneath the boards were then scraped clean of all barnacles and other growth prior to the 1996 settlement season. The number of recruits were then counted in October and the following May, when the rocks were cleaned again. To determine if growth proceeded at the same rate closer to the known eastern limits. some cobbles. bearing new spat of *Balanus perforatus*, were translocated from Lyme Regis in October 1995 to Bembridge on the Isle of Wight and wedged into crevices at LWN. These and native spat from Lyme Regis were then photographed after one year in mid-August 1996 and measurements of the basal diameter made from enlarged negatives.

6.3 Results

6.3.1 Recruitment of *Gibbula umbilicalis* along the south coast of England

The annual recruitment between 1994 and 1999 is shown in Fig.6.1. Some of the data from earlier timed searches were not separated and therefore error bars are shown only for the more recent years. Recruitment at the extreme eastern site at Freshwater Bay on the Isle of Wight was approximately ten times less than at other sites examined along the Devon and Dorset coast. With the exception of the 1995 cohort at Freshwater Bay and 1996 cohort at Shoalstone, spat counts were greater in the May following the first winter than in the autumn immediately after the settlement period. This is considered to be due to greater ease of finding larger animals rather than a major extension of the settlement period in to the autumn and suggests that winter mortality has been relatively minimal. The highest mean count of 42 spat (1997 cohort) was close to the eastern site of Kimmeridge in May 1998. No specimens of the 1996 cohort could be found at Freshwater Bay in either the autumn or in the following spring. With the exception of Lyme Regis, recruitment in this, the coldest year, was generally the lowest over the study period. The warmer years of 1995 and 1999 generally had high recruitment. Casual observations at the species extreme limits at Bembridge on the Isle of Wight, indicated that recruitment occurred in 1994, 1995 and 1997. In Table 6.2 results of a Friedman test showed that despite variability across the five sites sampled there was a significant difference in the magnitude of recruitment between years ($p = 0.03$). This indicates that there was a measure of concordance in good and poor years at sites along this section of coast (Table 6.3).

Fig 6.2 shows a scatter diagram of recruitment estimates at Shoalstone using two different techniques. Although in May 1996 the highest mean count on the shore coincided with the highest count beneath the wooden boards, there was no significant correlation between the two recruitment estimates ($r = 0.37$, $p = 0.089$, $n = 11$)). This may in part be due to the small number of counts. The high count beneath boards in October 1995 (mean 7.7) was not reflected in the shore counts, yet shore counts the following spring were very high. This confirms the difficulties in recruitment estimation from shore counts due to the cryptic nature of young spat. The apparent advantages of counts beneath boards were, however, inconsistent as much higher figures were obtained from shore counts, particularly in later years.

This could be due to a deterioration of the undersides of the board, some of which were showing signs of rot, and changes in the faunal community beneath the boards that had developed over the six-year period. This appeared to encourage the entrapment of silt and possible deterioration of the crevice habitat, making it increasingly unsuitable for young spat. It is also possible that toxins released from the plywood may have been a deterrent.

6.3.2 Growth of *G. umbilicalis*

The early growth of the 1994 and 1995 cohorts for five populations from the south coast of England may be followed in the size-frequency histograms (Figs 6.3-6.7). The size-frequency histogram for October 1996 is not shown. The size range for each cohort, measured in May, August and October, was determined from a visual examination of these histograms and identification of modal size-classes. The mean size in the months sampled was then calculated and is plotted in Fig.6.8. Growth rate measurements of both species have been determined by following age class modes on size-frequency histograms. Grant *et al.*, (1987) discuss the merits of various graphical methods for estimating demographic parameters compared to more rigorous mathematical techniques. They conclude that graphical techniques should be avoided except where the modes on the size-frequency histogram are clear and sample sizes are large. In this work, growth rate estimates over the first year for both species are considered to be reasonably reliable as the modal classes are well separated. Size-classes of *Osilinus* are better defined than those of *G.umbilicalis*, as are populations at lower density. At Brixham and Lyme Regis, newly settled spat measured in October or early November were usually under 6mm and 0.5mm larger at sites further east. Yet at all sites, spat found in the autumn were commonly under 3mm. At Kimmeridge, two distinct modal classes are evident in the 1995 cohort, measured in October shortly after settlement, suggesting two main settlement periods.

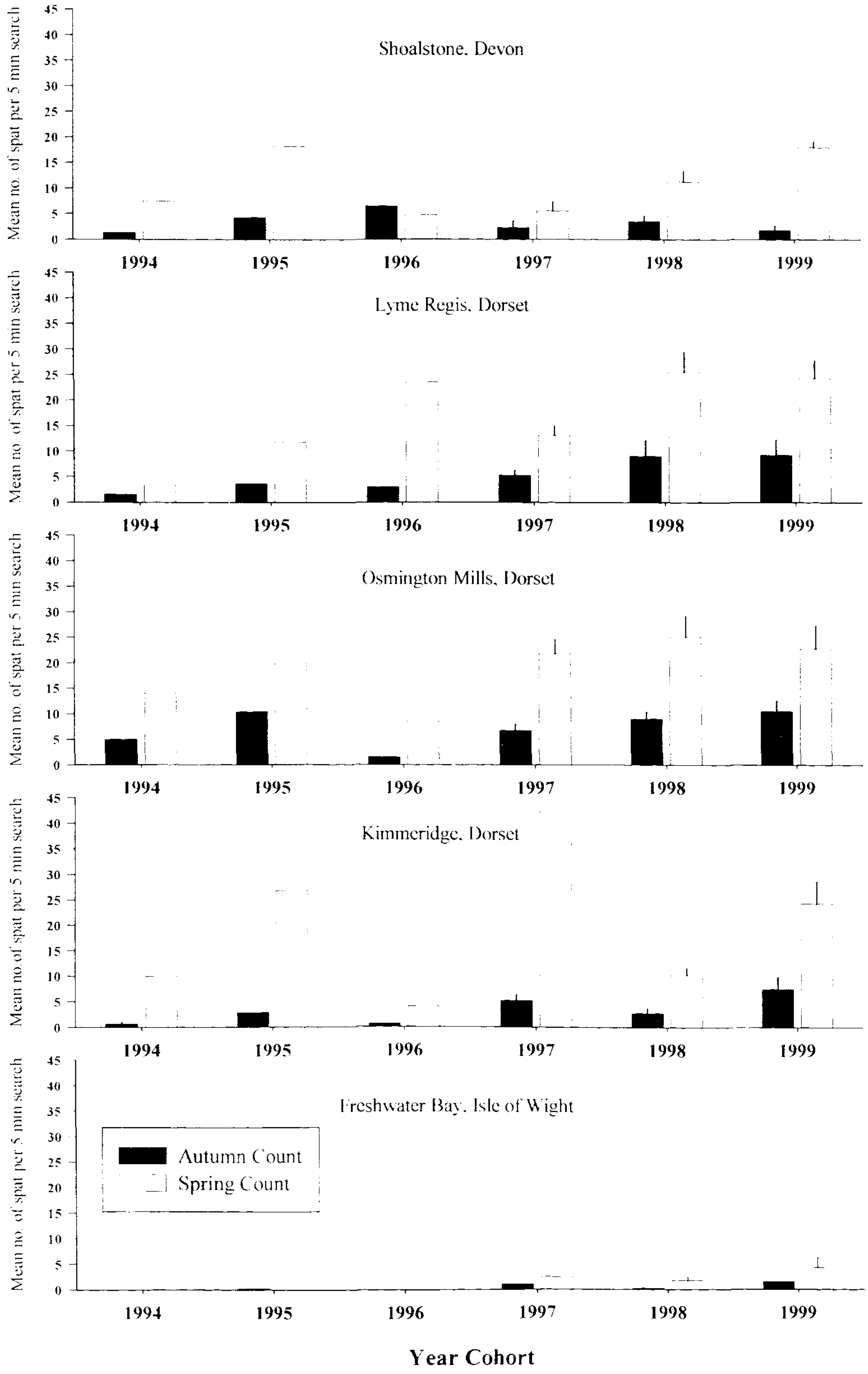
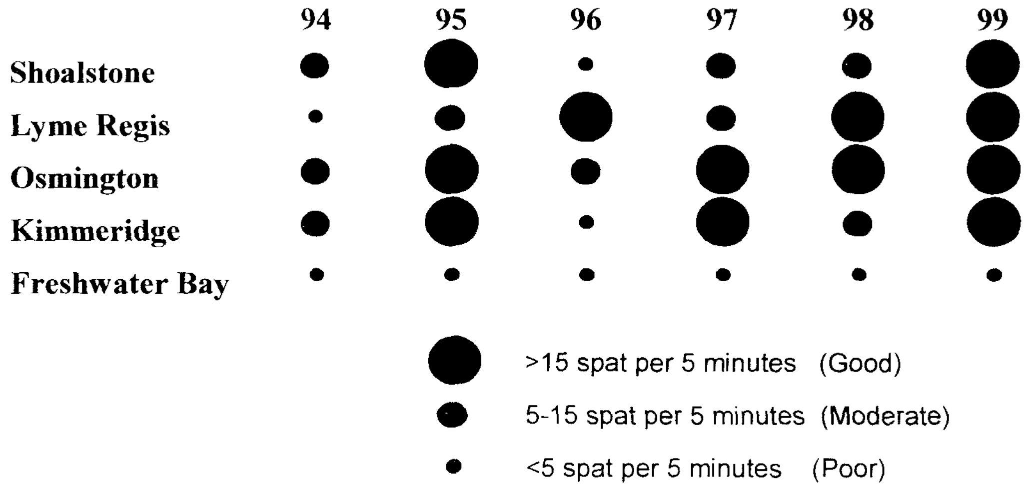


Fig.6.1 Annual recruitment of *Gibbula umbilicalis* at sites approaching limits of distribution along the south coast of England. Autumn counts were made between mid-October and early November. Spring counts were obtained in May, after the first winter. Bars show mean of four counts. Error bars on later counts show +SE.

Table.6.2 Rank order recruitment (spring counts) of *G. umbilicalis* at sites along the central south coast of England between 1994 and 1999. Rank 1 is highest recruitment. Results of Friedman test applied with H_0 'Years have same recruitment' $\chi^2 = 12.36$, df 5, $p = 0.03$*. H_0 rejected: accept H_1 that years differ.

	1994	1995	1996	1997	1998	1999
Shoalstone	4	1	6	5	3	2
Lyme Regis	6	5	3	4	1	2
Osmington	5	4	6	3	1	2
Kimmeridge	4	2	6	1	5	3
Freshwater Bay	5.5	4	5.5	2	3	1

Table.6.3 Summary of annual recruitment success of *G.umbilicalis* at sites approaching eastern Channel limits between 1994 and 1999. Counts made in May following first winter.



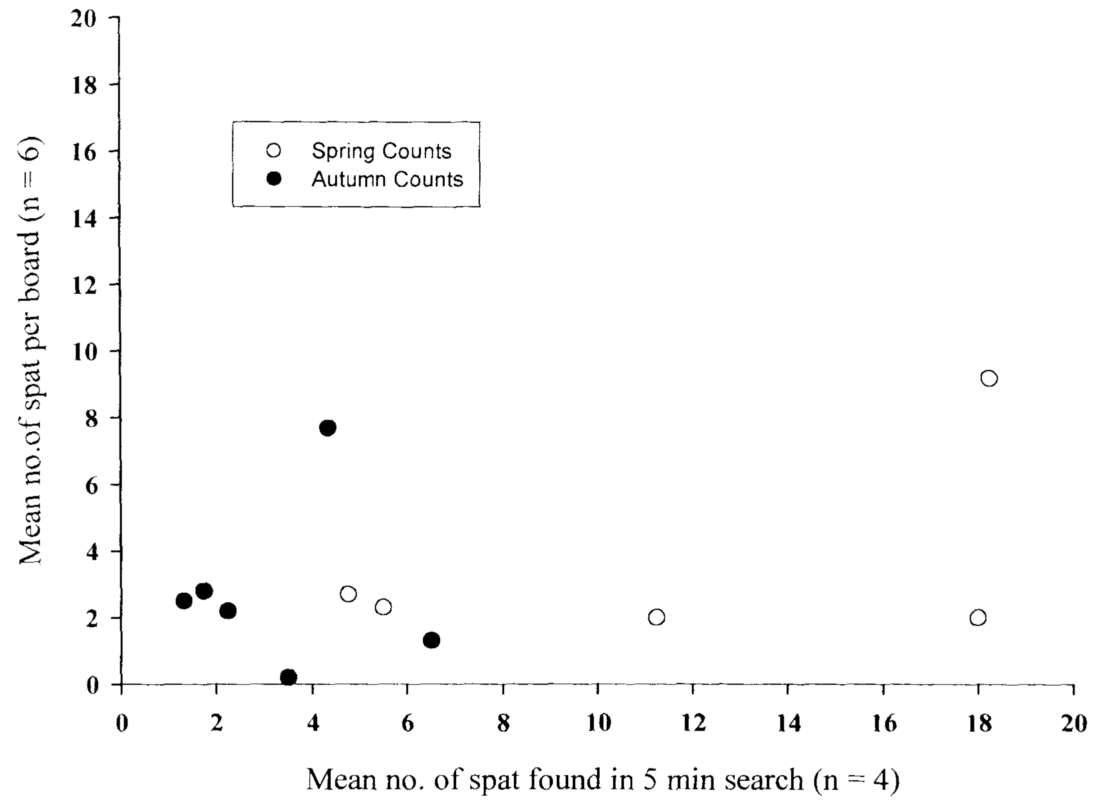


Fig.6.2 Correlation between results of two different techniques for estimating recruitment of *G. umbilicalis* at Shoalstone, Devon: timed searches and counts from beneath fixed boards. Counts made between May 1995 - May 2000. Correlation coefficient 'r' = 0.37; p = 0.089, n =11.

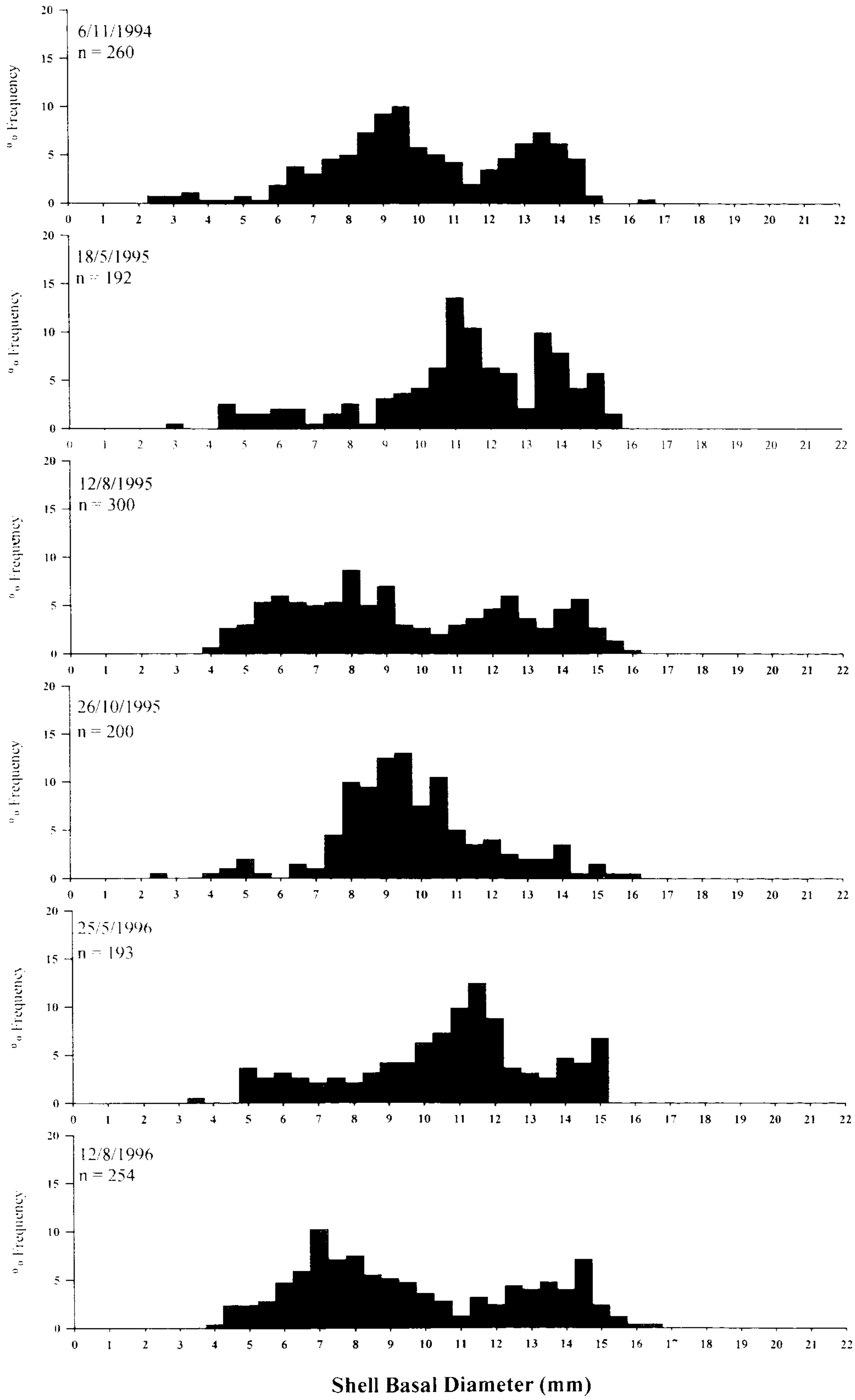


Fig.6.3 Size-frequency histograms of *G.umbilicalis* population at Shoalstone, Devon.

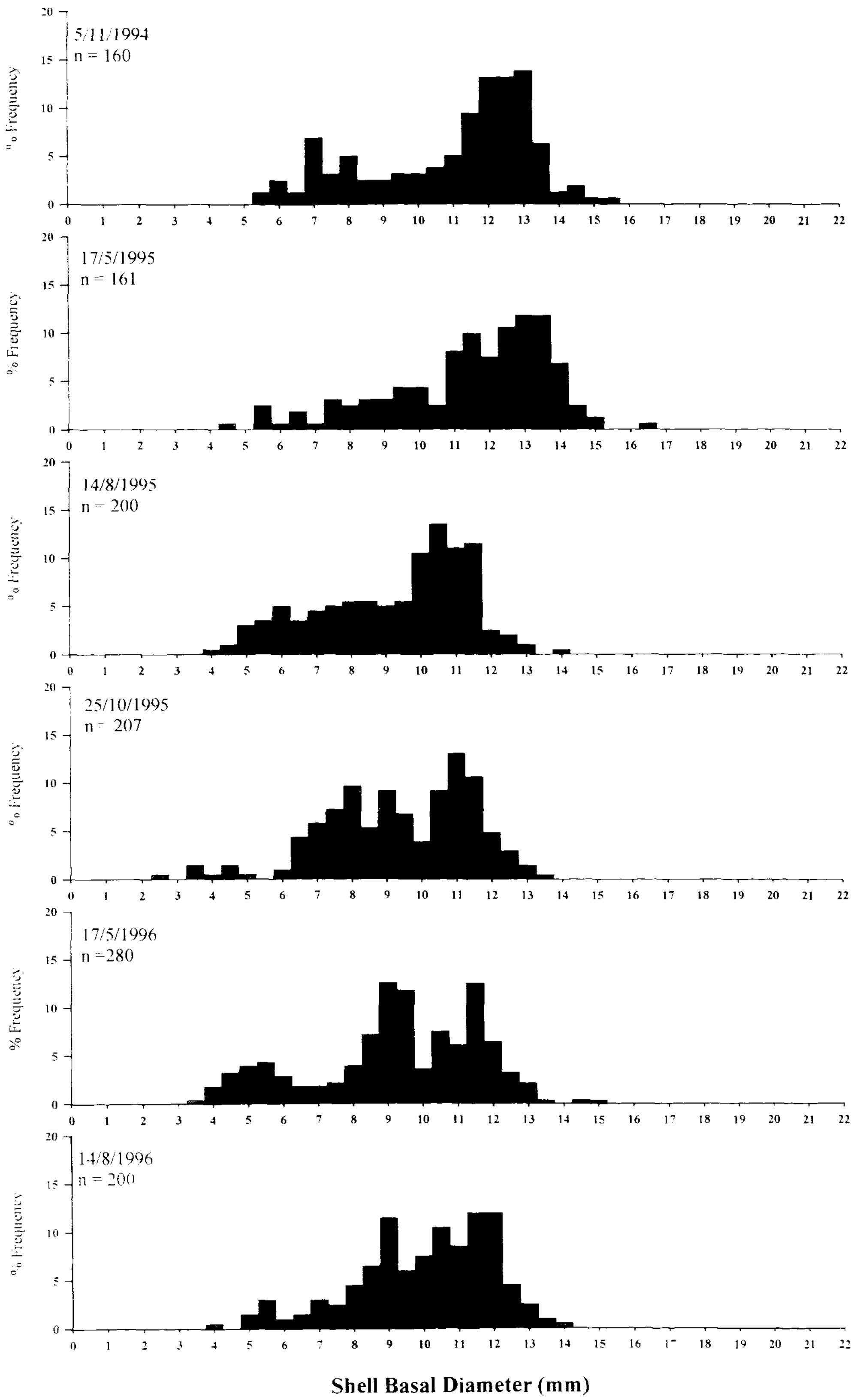


Fig.6.4 Size-frequency histograms of *G. umbilicalis* population at Lyme Regis, Dorset.

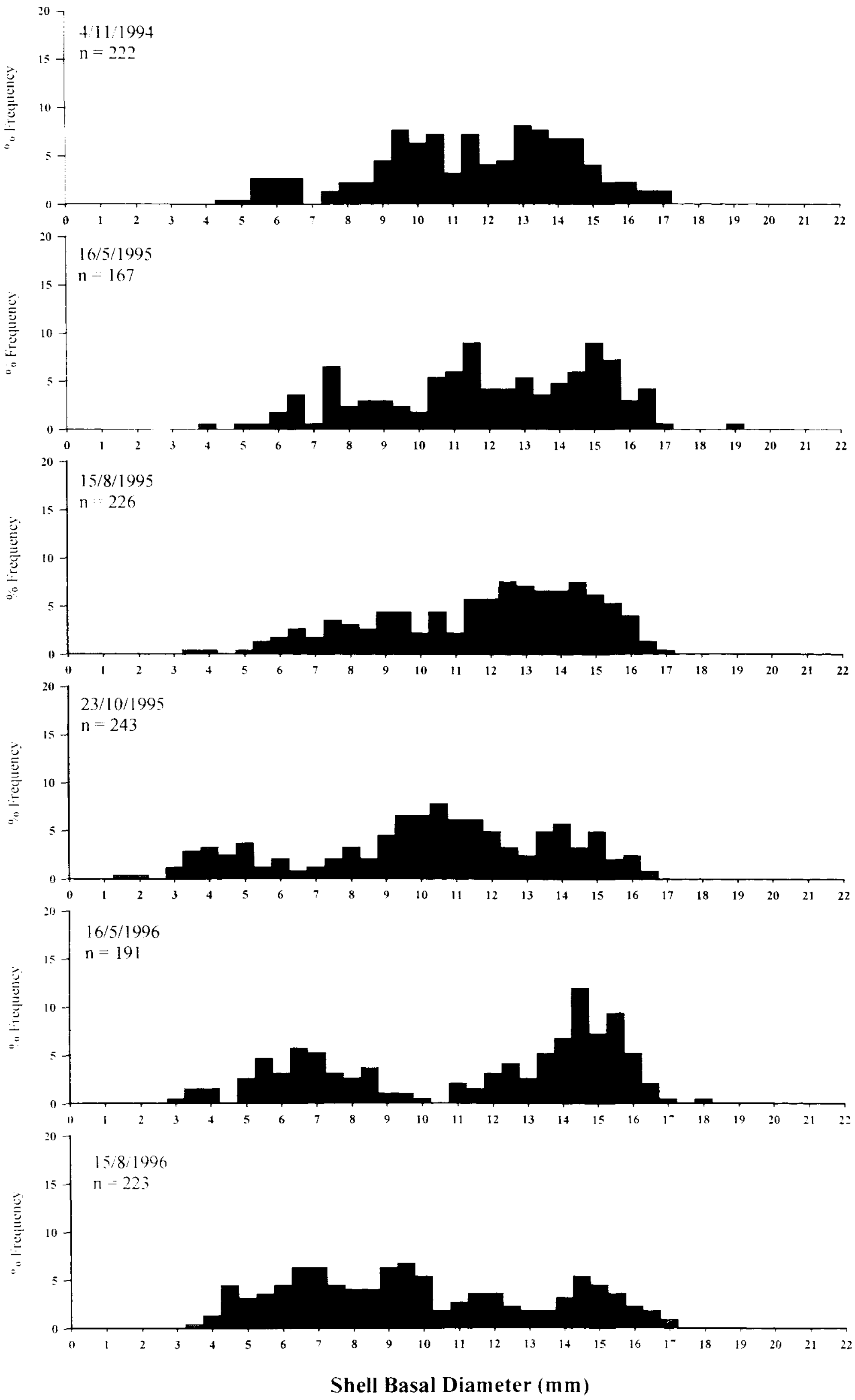


Fig.6.5 Size-frequency histograms of *G.umbilicalis* population at Osmington Mills, Dorset.

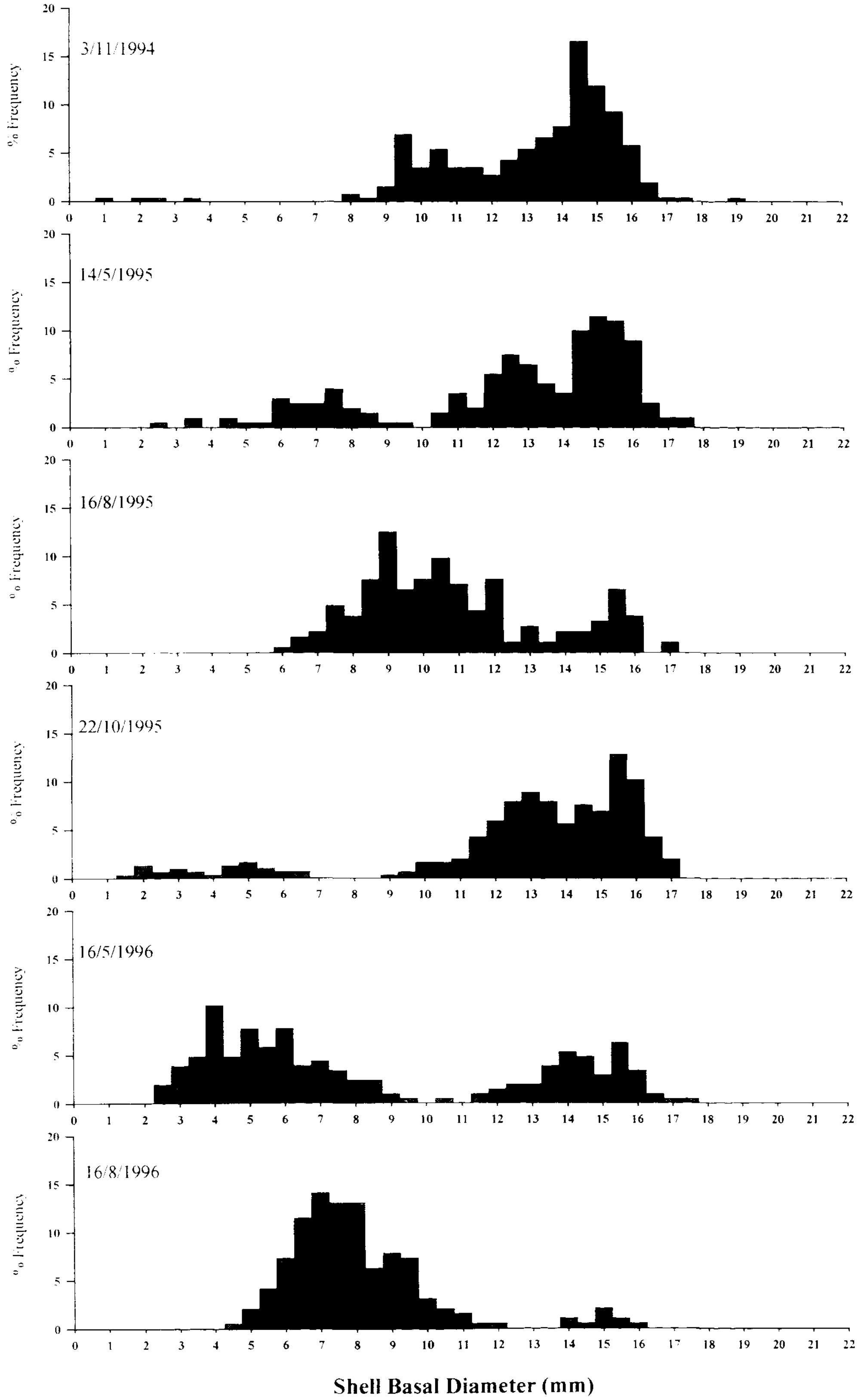


Fig.6.6 Size-frequency histograms of *G.umbilicalis* population at Kimmeridge, Dorset.

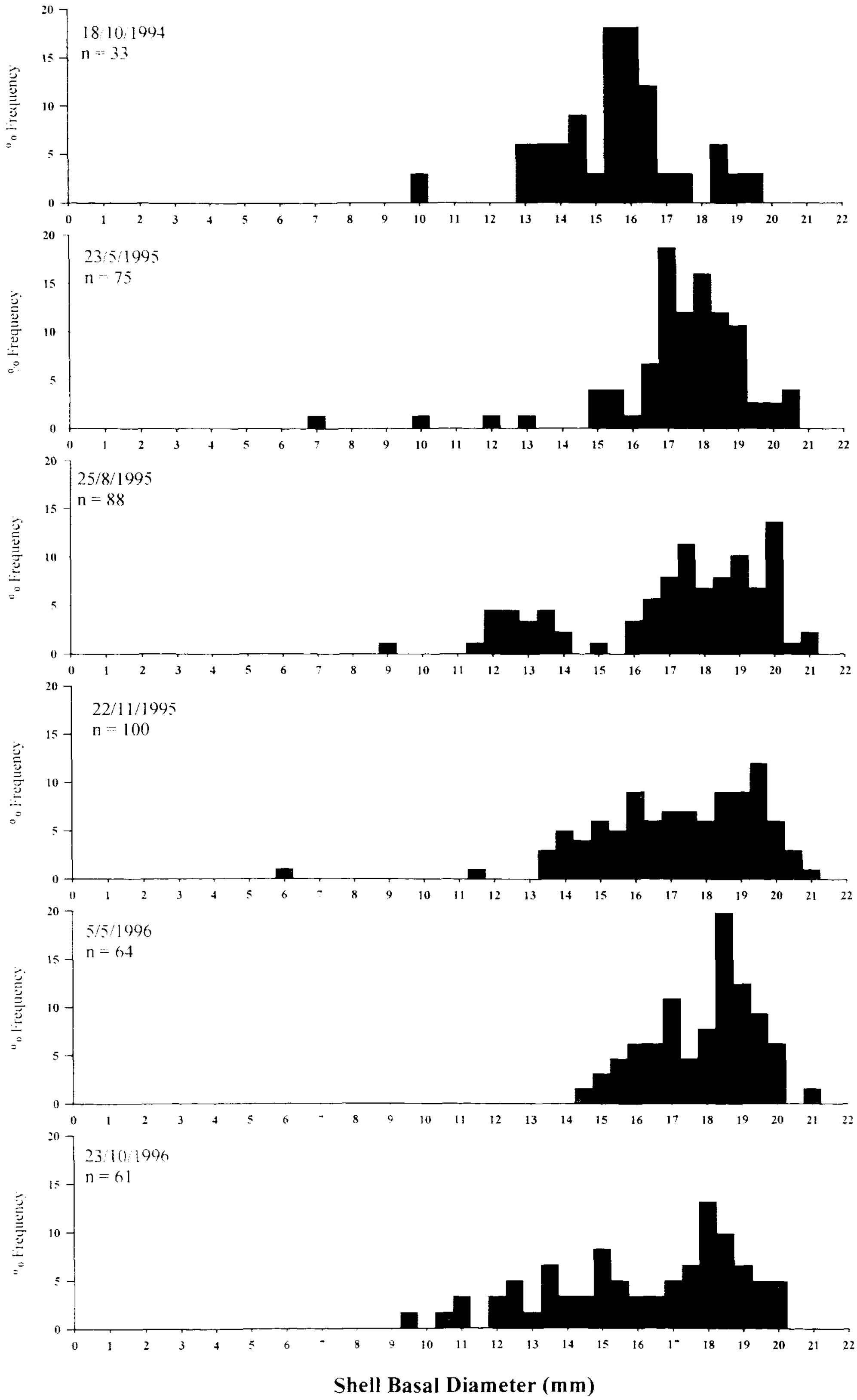


Fig.6.7 Size-frequency histograms of *G.umbilicalis* population at Freshwater Bay, Isle of Wight.

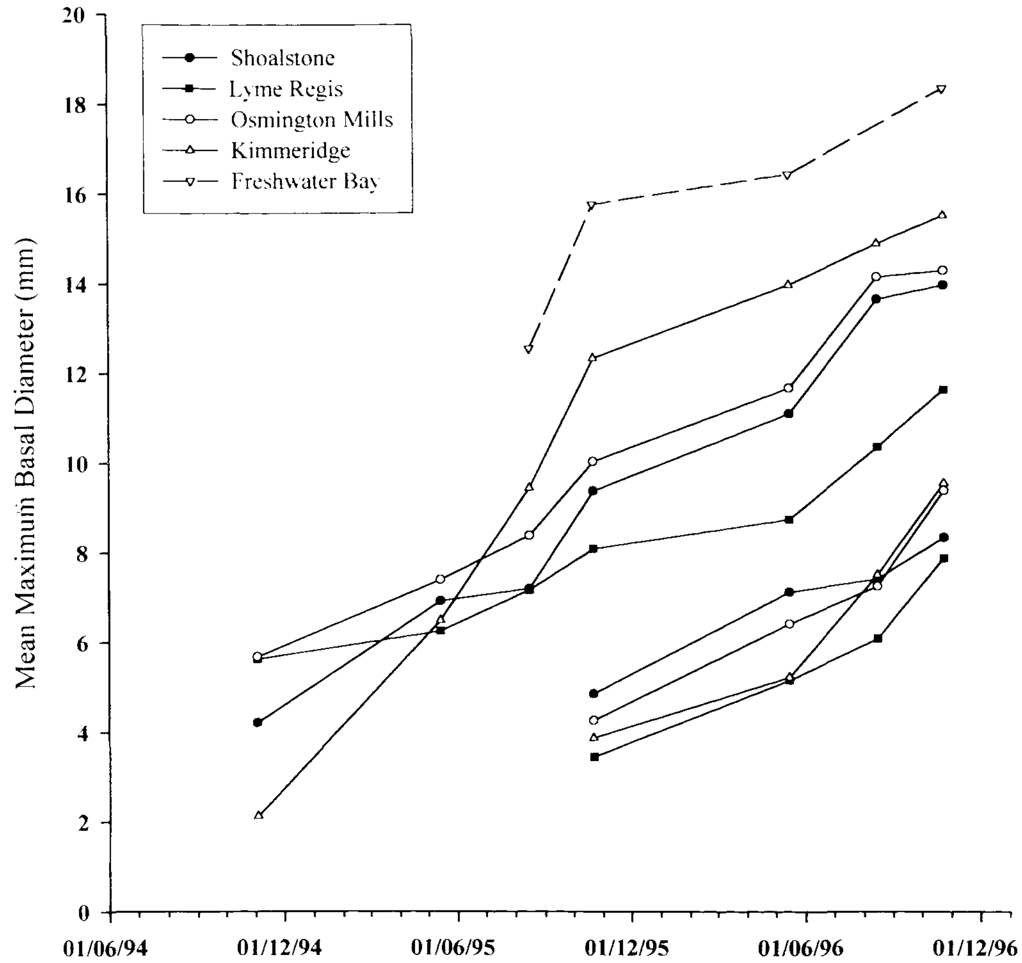


Fig.6.8 Growth of 1994 and 1995 cohorts of *G. umbilicalis* at shores approaching eastern geographic limits on the central south coast of England. Error bars omitted as means determined visually from cohorts in size-frequency histograms. Less confidence applied to data from Freshwater Bay due to few well-defined modes - hence dashed line. See text for further details.

By May, after the first winter, spat size ranges differed considerably, both within shores and between sites. At Kimmeridge, sizes of both the 1994 and 1995 cohorts measured this month varied between 2.5 and 9.5mm. In both 1994 and 1995, growth appeared to be most rapid at the more eastern sites of Osmington and Kimmeridge. Early growth at Freshwater Bay could not be determined because of difficulty in finding new recruits. The growth line for this most eastern site shown in Fig 6.8 is therefore more speculative. However the well-defined mode of 12-13mm present in August 1995 could well be that of the 1994 cohort. If so, the growth on this shore was the most rapid of all sites. Of the two locations sampled west of Portland, growth at the more densely populated shore at Lyme Regis was less than that at Shoalstone beach near Brixham. The overall pattern of growth along the south coast appears to be density-dependent with animals at the more eastern sites growing more quickly and attaining a larger size. So after one year, animals at Freshwater Bay, at the extreme east of the species range, may have attained a basal diameter of 16mm, whereas those in Lyme Bay could be only half the size. In each population, growth was more rapid during the first summer when the greatest divergence in size occurs between sites. The early growth rate of the 1995 cohort was slightly less than that of the previous year, due perhaps to the cooler winter and spring of 1996.

6.3.3 Recruitment of *O.lineatus* along the south coast of England.

The annual recruitment of *Osilinus* at Shoalstone beach near Brixham and at Lyme Regis over the period 1994-1996 is shown in Fig 6.9. Earlier counts were pooled, so error bars are not shown. At Shoalstone, all spring counts after the first winter were higher than in the autumn immediately after settlement, however at Lyme Regis, spring counts of the 1995 and 1997 cohorts were slightly less. Highest counts were of the 1997 cohort at Lyme Regis made in the spring of 1998. Counts for the 1997 year cohort were also large at Shoalstone, although spring counts were greater for the 1995 and 1999 cohorts.

No concordance could be found in the magnitude of recruitment at the two sites (Table 6.4: Friedman test, p = 0.34). A clearer pattern may have been more evident with more study sites. The population at Portland was considered too small and the habitat unsuitable for easy estimation of summer settlement. However in October 1997 and October 1999, recruits <4mm were found further east at Osmington Mills while sampling in pools for *G. umbilicalis* spat.

Table.6.4 Rank order recruitment (spring counts) of *O. lineatus* at sites along the south coast of England between 1994 and 1999. Rank 1 is highest recruitment. Results of Friedman test applied with H_0 'Years have same recruitment' $\chi^2 = 5.71$, df 5, p = 0.34: accept H_0.

	1994	1995	1996	1997	1998	1999
Shoalstone	5	1	6	4	3	2
Lyme Regis	6	5	3	4	1	2

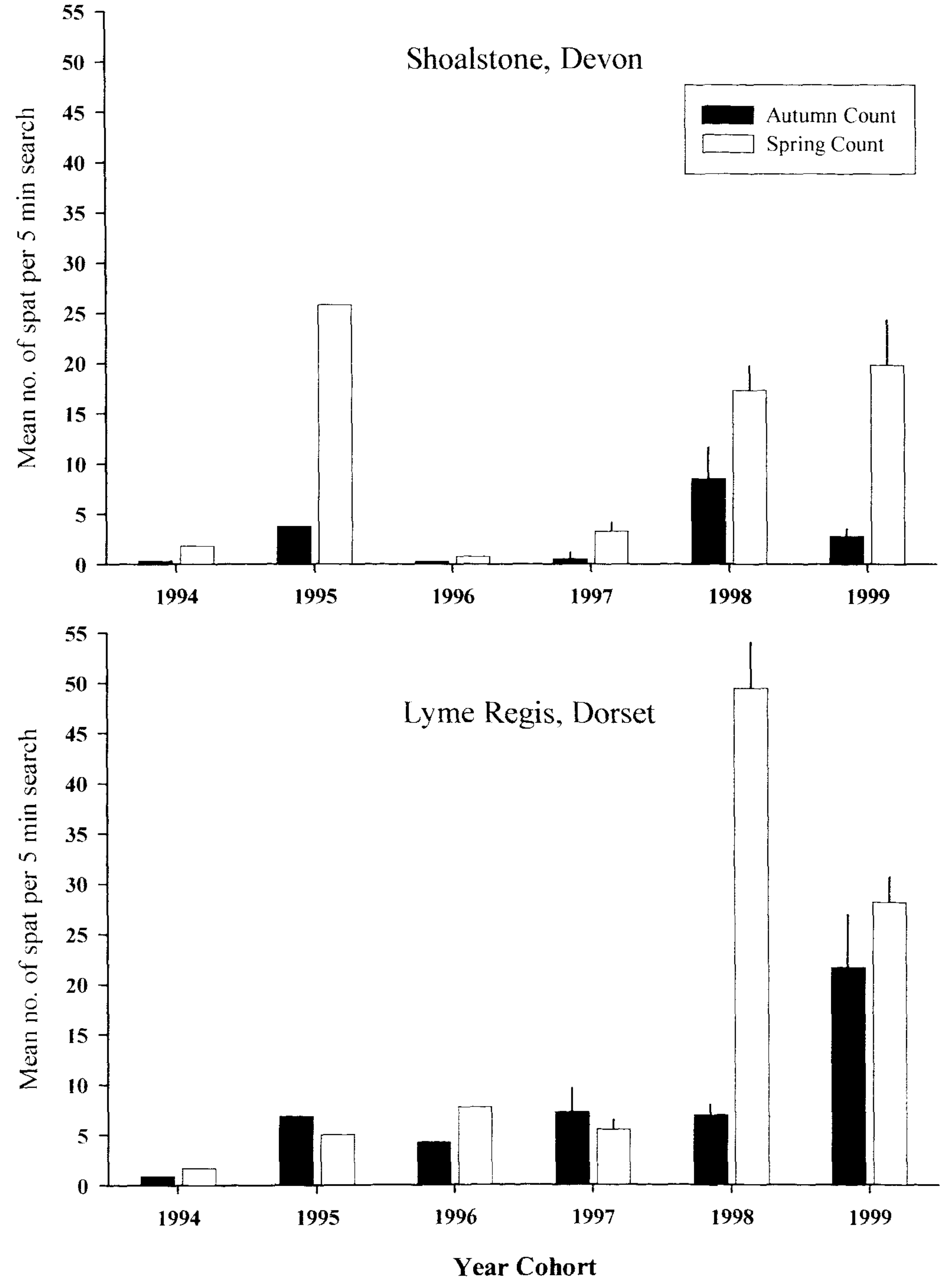


Fig.6.9 Annual recruitment of *Osilinus lineatus* at Shoalstone near Brixham in Devon and at Lyme Regis in Dorset. Autumn counts were made between mid October and early November. Spring counts were obtained in May, after the first winter. Bars show mean of four counts. Error bars on later counts show +SE.

Table.6.5 Mean rank order recruitment of *G.umbilicalis*, *O.lineatus* and *Chthamalus* spp. at sites along the south coast of England between 1995 and 1999. Rank 1 is highest recruitment. Spring counts used for the trochids and autumn counts for *Chthamalus* (see Table 5.7). Results of Friedman test applied with H_0 'Years have same recruitment' $\chi^2 = 9.42$, df 4, $p = 0.051$: accept H_0.

	1995	**1996**	**1997**	**1998**	**1999**
G.umbilicalis	4	5	4	2	1
O.lineatus	3	5	4	1.5	1.5
***Chthamalus* spp.**	3	5	2	4	1

It is clear that 1996 was a poor year for all species studied, and 1999 the best. Yet a Friedman test applied to data for *G.umbilicalis*, *Osilinus* and *Chthamalus* (Chapter 5) with the hypothesis that all species show the same rank order of annual recruitment was not quite significant (Table 7.5, p = 0.051).

6.3.4 Growth of *O. lineatus*

Histograms showing the size-frequency of the Lyme Regis and Shoalstone populations are shown in Figs 6.10 and 6.11. In most months of the year a clear tri-modal pattern is evident and the size range of each year cohort can be clearly followed. The early growth of the 1994 and 1995 cohorts is plotted in Fig. 6.12. Both year cohorts at each site showed more rapid growth between May and October. As with *G.umbilicalis*, density dependence is again suspected as growth was rapid at the less densely populated site at Shoalstone. Even when first sampled, in the October or November shortly after settlement, there was a 1mm difference in the mean size of recruits. By the end of the first year, the gap had widened to over 2mm. As with *G. umbilicalis*, the early growth of the 1995 cohort was slightly less than that of the previous year, due possibly to the cooler spring of 1996. The small population at Portland was not sampled immediately after the main settlement period. However at the end of May 1995, distinct modes at 19 and 24mm could be identified. These are much higher than the other two sites sampled and it is likely that the lower mode, where animals ranged in size between 15.6 and 21mm represents the 1993 cohort. If this is so then growth rate at this sparsely populated site is much more rapid than the others sampled, where equivalent modes for Shoalstone and Lyme Regis appear at 17mm and 11mm respectively.

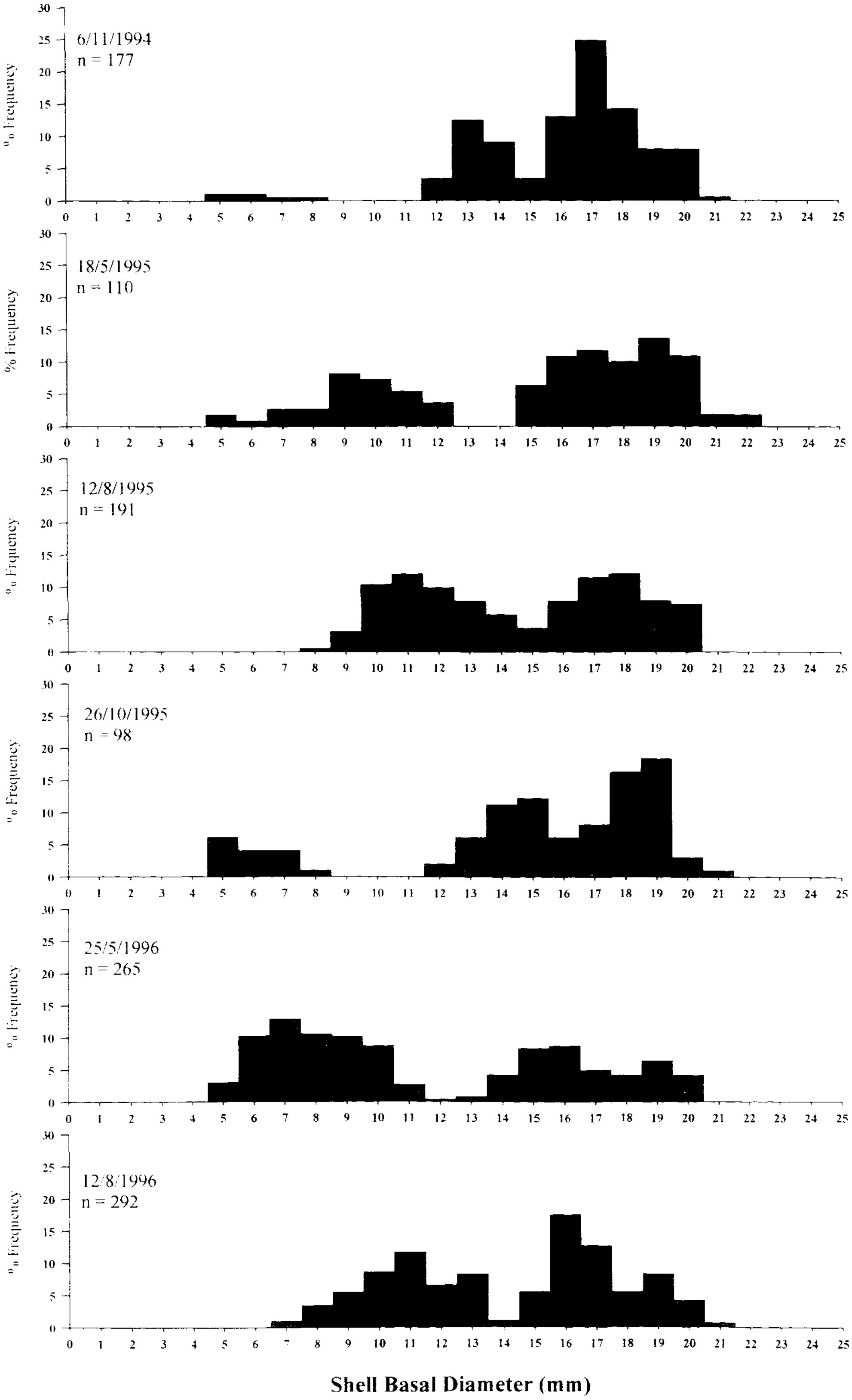


Fig.6.10 Size-frequency histograms of *Osilinus lineatus* population at Shoalstone, Devon.

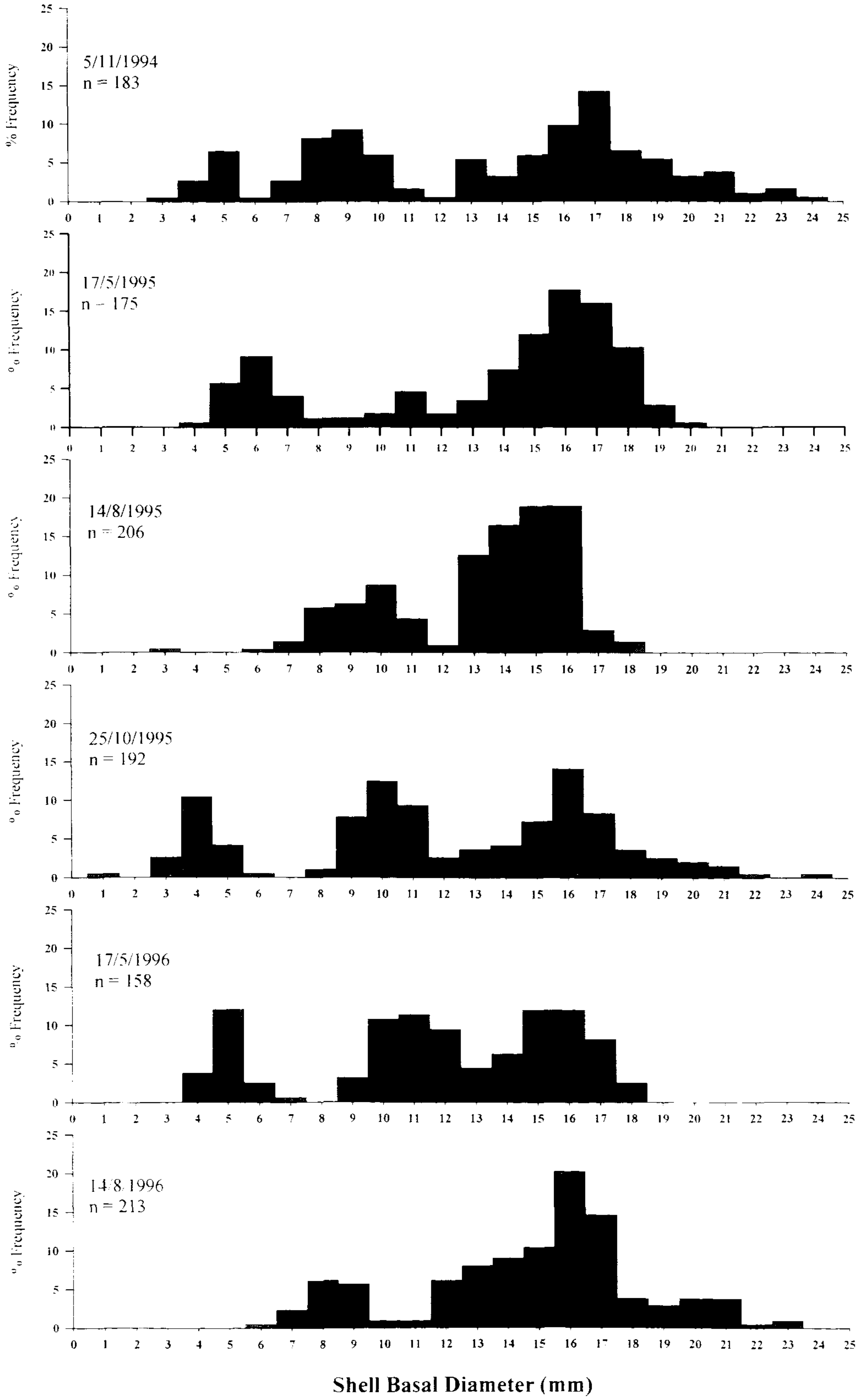


Fig.6.11 Size-frequency histograms of *Osilinus lineatus* population at Lyme Regis.

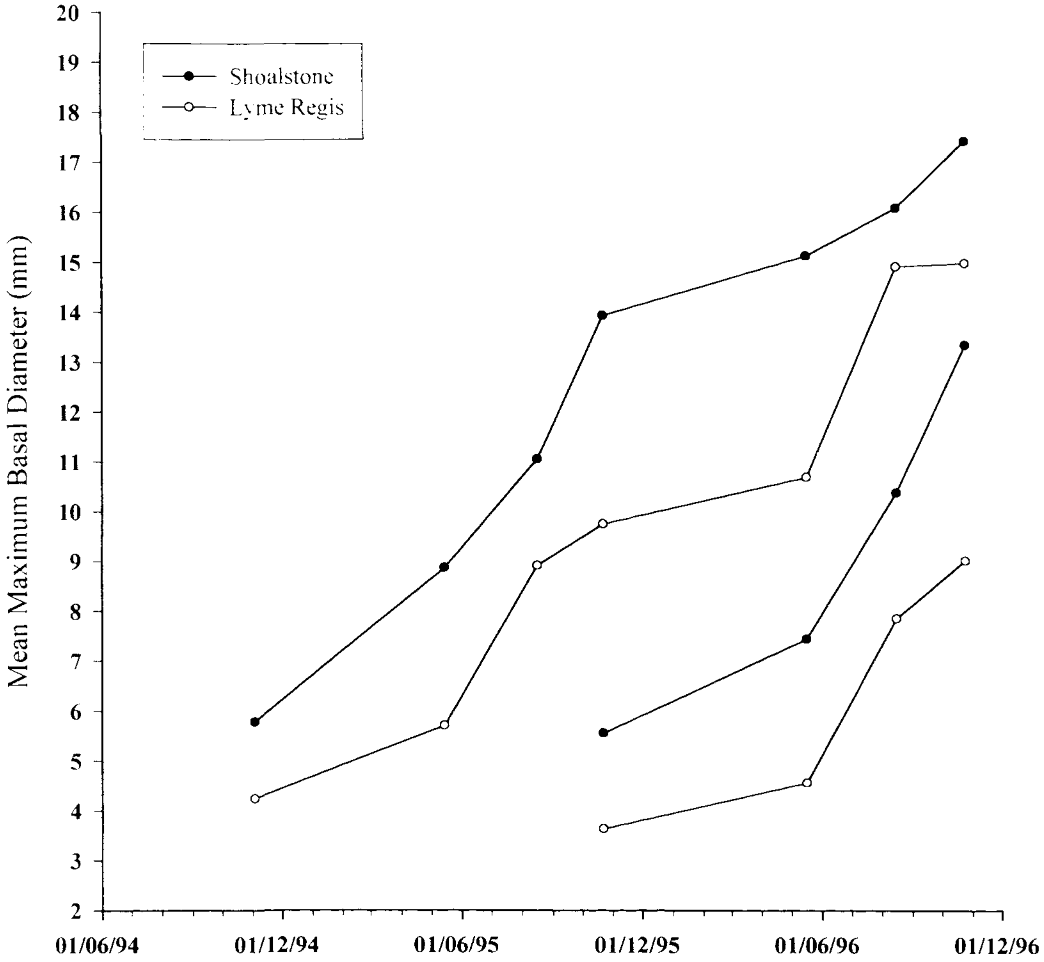


Fig.6.12 Growth of 1994 and 1995 cohorts of *Osilinus lineatus* at Shoalstone and Lyme Regis. See text for more details.

6.3.5 Recruitment and early growth of *Balanus perforatus*

Of the six boards that were screwed down on the lower shore at Portland Bill in 1994 two were lost between May and August 1996. However some of the barnacles were still present, suggesting that although preferred settlement is in cryptic habitats such as crevices, survival and early growth is possible on the open shore. Damaged and missing boards were replaced and the sites continued to be monitored till May 1999 when all boards had been lost, presumably during winter storms. The boards provided shelter for a good variety of other fauna including small shanny fish (*Blennius pholis*), amphipods, juvenile crabs, gastropods *Nucella lapillus* and *Gibbula umbilicalis* and the anemone *Bunodactis verrucosa*.

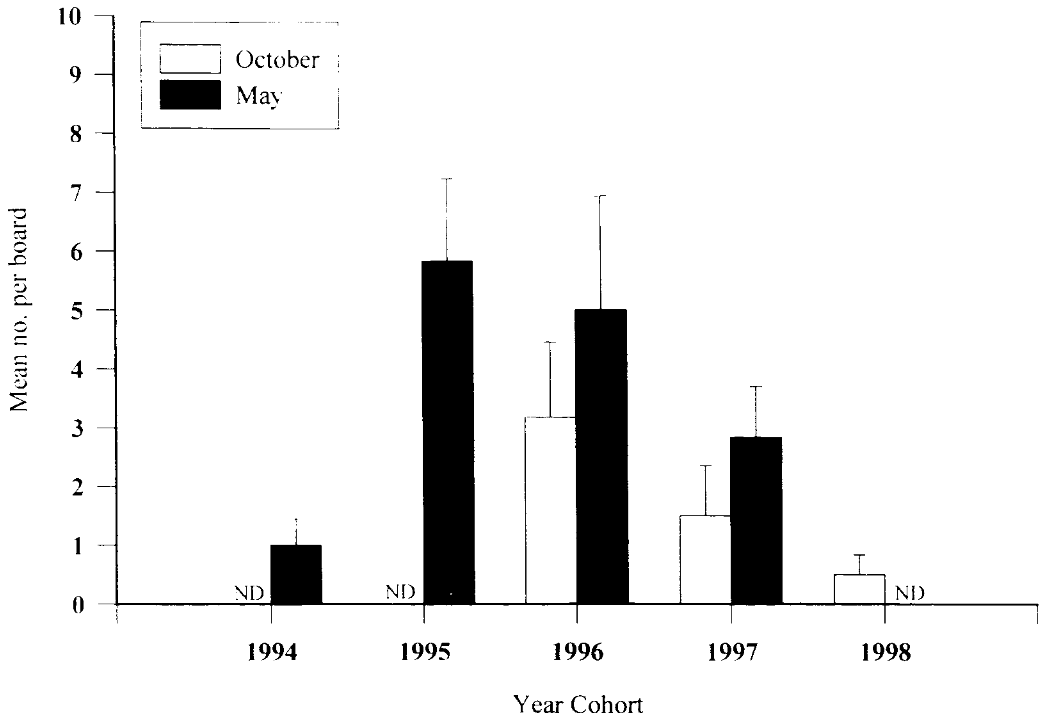


Fig.6.13 Recruitment of *Balanus perforatus* beneath wooden boards fixed to the shore at MLW at Portland Bill. No data (ND) was collected in the autumn of 1994 and 1995 and in May 1996 the boards had been lost. Error bars show +SE.

During the five years the boards were down, the rock beneath also became colonised by additional sessile species, particularly *Spirorbidae*. The mean number of recruits beneath the boards counted in October and May is shown in Fig 6.13. The young recruits are usually very visible in October, being between 1-2mm in diameter, however the May count is probably the more reliable as some settlement may continue into the late autumn. Although the data are incomplete, the 1995 cohort was largest of years 1994-1997. Yet because of the changes that occurred beneath the boards and the deterioration of the boards themselves it is not possible to attribute differences in number of recruits to variations larval supply. The recruits were not mapped on the shore so it was not possible to measure mortality.

Fig 6.14 shows the mean basal diameter of the 1994 and 1995 cohorts, growing at different locations and in varied situations, measured in mid-August after one year's growth. By the end of their first year, animals of the 1994 cohort growing beneath boards at Portland Bill had a basal shell diameter of between 5-7.2mm (mean 6.2mm). By August 1996 the mean basal diameter had increased to

10.2mm (range 8.2-11mm). Further growth may have been limited by the space beneath the board. The mean basal diameter of the 1995 cohort translocated from Lyme Regis to Bembridge is shown for comparative purposes alongside measurements for the natural population at Lyme Regis. By the end of their first year those at Lyme Regis were on average 1mm larger than the translocated animals at Bembridge.

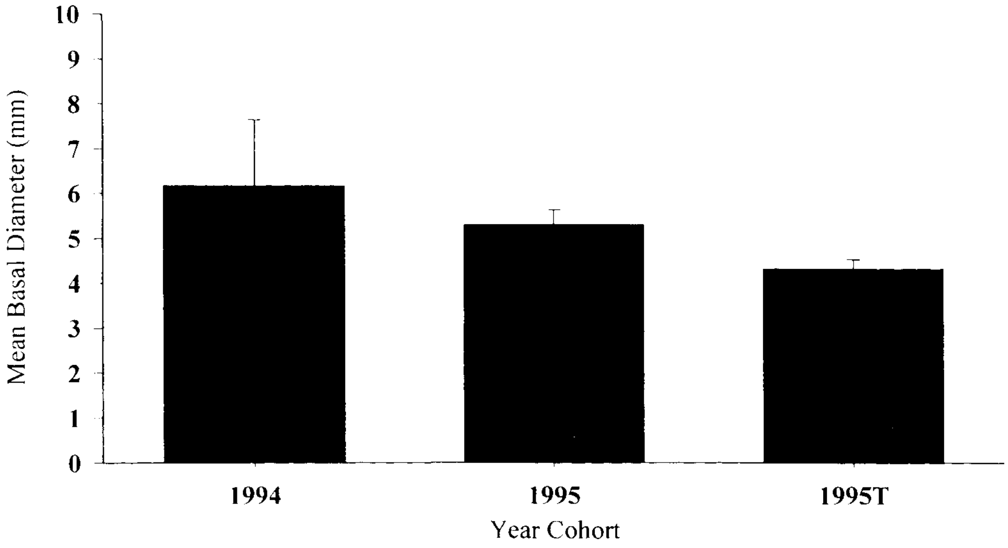


Fig.6.14 Mean shell basal diameter at end of first year of 1994 cohort of *Balanus perforatus* measured at Portland Bill (n = 4), 1995 cohort at Lyme Regis (n = 38) and animals translocated from Lyme Regis to Bembridge, Isle of Wight (1995T, n = 28). See text for further details. Error bars show +SE. See text for further details.

6.4 Discussion

As suspected by previous workers (Kendall & Lewis, 1986; Lewis, 1986), the Channel limits of both trochid species investigated appear to be currently set by recruitment failure. In the case of *Gibbula umbilicalis* this failure occurs very abruptly over a 60km stretch of coastline between Kimmeridge in Dorset and Freshwater Bay on the Isle of Wight. Along this section a ten-fold reduction in recruitment density was measured. Of course the numbers of recruits collected may be a reflection of terrain complexity, and not recruitment density. As pointed out by Kendall *et al.*, (1987) the intensity of recruitment of both trochid species is strongly influenced by the physical characteristics of the shore, which include the degree of wave exposure and the availability of suitable nursery areas for spat. This difficulty was partially reduced by choosing sites that were similar with respect to habitat and wave exposure. Shores where recruitment was monitored were embayed situations with cobbles and shallow pools and were therefore similarly suitable nursery sites. Recruitment within the *Osilinus* population on Portland was not monitored, mainly because of the unsuitable nature of the shore, which consisted of large boulders and wave-swept gullies.

Over the six-year study period, not only was frequent recruitment of *Gibbula umbilicalis* measured close to the eastern limits at Kimmeridge, but the highest spat densities were also recorded here. In their broad-scale surveys between 1976-1984, Kendall & Lewis (1986) only considered two sites on the south coast; Lyme Regis and Osmington Mills. Combined with data from Widemouth in North Devon they concluded that the frequency of poor recruitment increases west to east along the Channel. Recruitment at Osmington failed each year and good settlement at Lyme Regis only occurred in 1979. In this work, annual recruitment at Osmington was found to be at least as high if not higher than that measured at Lyme Regis and Torbay. However although both the earlier and current work employed a timed search technique for spat measurement, strictly comparative assessments are difficult because of inevitable between-worker variability. It is also possible that different areas of the shore were visited. Certainly, recruitment estimation beneath fixed boards, carried out at Shoalstone, has potential in overcoming these difficulties although their location would need to be changed each year to avoid problems associated with successional community development beneath the board.

An alternative way of collecting spat could be the use of plastic mesh pan-scrubbers to mimic algal turf (Myers & Southgate, 1980) although these again would need replacing on a regular basis. Higher recruitment during the warmer years of 1995 and 1999 and low recruitment in the cooler year of 1996 is unsurprising considering the southern distribution of the species. It might also explain the apparently higher recruitment at the more eastern sites surveyed compared to the earlier surveys between 1976-1984. During this period the Channel SST was approximately 0.5°C cooler than in the mid to late 1990's (Chapter 2). Crothers (1998) working along the coast of Somerset also found a higher than normal settlement of *Osilinus* (as *Trochococlea*) during the long warm summer of 1995. It remains uncertain whether higher sea temperature, onshore winds or warm post-settlement conditions facilitate higher recruitment.

Along the Dorset coast the adult population of *Osilinus lineatus* is now back in densities prior to the severe winter of 1962-63 (see Hawthorne,1965). Again, recruitment drops suddenly over 40km between the large population at Lyme Regis and the small but significant population on Portland. Although spring spat measurements were not made at Portland, the shell size-frequency and condition, determined in August 1996, indicated that recruitment had occurred at least in the year previously. Other measurements made in May 1995 by J. Hawthorne (pers. comm) showed that recruitment had also occurred in 1994. The new recruits found at Osmington Mills in October 1997 and 1999 are presumed to have originated from larvae produced from the main populations to the west of Portland at Lyme Regis or below Golden Cap near Seatown. Assuming larvae are in the surface water, rapid transport could have occurred around Portland Bill, although this might be dependent on the coincidence of favourable tidal and wind driven surface currents. Although they are known to be short-lived, surviving up to 5-6 days (Fretter & Graham,1994), there is a measure of uncertainty regarding the position of trochid larvae in the water column, and to what extent they could be benthic. Attempts to collect larvae with plankton net, during a period of major larval release at Aberaeron, failed completely (Kendall pers. comm). Yet the high recruitment densities of *G. umbilicalis* in enclosed Scottish Lochs (Kendall & Lewis,1986) do seem to indicate that water movements are likely to be important. High larval retention in Torbay, which has an easterly aspect, may have facilitated recruitment of both species at Shoalstone during easterly winds in the summer of 1995. This could also help to explain the relatively unexceptional recruitment at Lyme Regis the same year, should there have been significant westward transport of larvae in Lyme Bay. Earlier work on recruitment variation of *Osilinus* in southern Britain between 1978-1986 (Kendall, 1987) found that both particularly successful and particularly weak cohorts were unusual. These assessments were made from size-frequency histograms when the animals were 18 months old, i.e. after they had survived two winters. On this basis, only the 1980 and 1981 cohorts at Lyme Regis were considered to be particularly weak. For the 1981 cohort this is also evident from the lack of recruits present in the histogram of spring 1982. Failure of the 1980 cohort appears to have occurred after the second winter, as a reasonable number of recruits are shown in the graph for spring 1981. Between 1978 and 1983, winter mortality of *Osilinus lineatus* spat was found to be significant at Aberaeron in mid-Wales (Kendall *et al.*, 1987), where spring counts were usually less than counts made shortly after settlement the previous autumn. In the current work, spring counts at Shoalstone in Torbay were always higher than those made the previous autumn, however spring counts of the 1995 and 1997 cohorts at Lyme Regis were slightly less. Overall, these observations may indicate that winter mortality over this mild study period has been relatively insignificant. Yet Crothers (1998) observed that the colder winters of 1995/96 and 1996/97 caused significant juvenile and adult mortality of the *Osilinus* population along the Somerset coast and concluded that winter cold is the main restraint to the eastern advance of *Osilinus lineatus* in the Bristol Channel.

Recruitment at Shoalstone was particularly good during the warmer summers of 1995 and 1999 and least during the cooler year of 1996. In northern Spain, spawning of *Osilinus lineatus* begins in June and in some individuals continues till November (Bode *et al.*, 1986). In southern Brittany, two reproductive periods occur annually; in the spring (April to June) and in the autumn between September and October (Daguzan, 1991). Further north at Aberaeron in west-Wales, spawning has been reported only in July and August (Garwood & Kendall, 1985; Kendall *et al.*, 1987). Warmer summers are therefore likely to extend the spawning period or enable multiple spawnings. However both trochid species appear to settle slightly later with decreasing lattitude. In northern Spain, settlement of *Gibbula* and *Osilinus* occurs in September and November (Bode *et al.*, 1986) whereas in Britain new recruits may be found on the shore in August (Lewis, 1986; Kendall, 1986;

pers. obs). It is suggested (Lewis, 1986) that at the extreme southern limits high summer temperatures could result in severe mortality of spat. Successful settlements therefore occur later in the autumn.

The advantage of higher temperatures is not thought to enable earlier settlement and rapid growth prior to the onset of winter, but to prolong the spawning season and raise the probability of a better match between gamete release, larval food availability and onshore breezes (assuming larvae are within the surface water). The frequency of recruitment failure thus diminishes further south and 'better matches' yield high recruitment densities. This enables the maintenance of high population densities; in Portugal, densities of *G.umbilicalis* may be 2-4 times greater than in Britain (Lewis, 1986).

The first year growth rate of the 1994 and 1995 cohorts of both species appears to be density dependent with the largest sizes being attained at the eastern edge of the species distribution where densities are least. This helps to explain the significant correlation between population density and adult size of *G.umbilicalis* shown in Chapter 3 (Figs.3.29 & 3.30). Size-ranges of *G. umbilicalis* recruits from all populations, measured in the autumn after settlement and following spring, are comparable with those shown for the 1984 cohort at Aberaeron (Kendall *et al.*, 1987). Williams (1964) also measured growth rate of a population in west-Wales, yet the mean size of both the 1960 and 1961 cohort (his Fig.4), measured in the first spring, appears to be almost half that obtained in this work. Nevertheless, growth was apparently rapid during late summer and the mean size at the end of their first year is similar to that obtained in this work. Higher winter growth rates found in this work could be a consequence of milder winter conditions. Kendall *et al.*, (1987) observed differences in early growth rate between two successive year cohorts, one of which had two distinct modes attributed to early and late spawning periods. Many of the smaller animals, which resulted from the later spawning, were apparently lost during the winter. The 1995 cohort from Kimmeridge examined in this work also shows evidence of two distinct settlement periods. Yet both early and late settlers appear to have survived the cooler 1995-1996 winter and emerge strongly within the size-frequency histogram for May 1996 and during their first summer. This extended spawning period during a warm summer followed by successful winter survival is an important and significant observation when considering the effect of climate change on populations near the extreme edge of the species distribution.

The growth rate of *Osilinus* varied markedly between the two sites, with the recruits at Shoalstone growing significantly faster than those at Lyme Regis. The mean size of recruits measured after one year in west-Wales (Williams,1965) was intermediate between the sizes found at the two sites surveyed in this work, but after two years was similar to that of the 1994 cohort measured at Lyme Regis. Kendall (1987) found that 18 month-old animals from the 1984 cohort sampled at Lyme Regis had a shell diameter of 15mm, which is almost identical to the mean size attained by the 1994 cohort measured in this work. Those within the more dense population at Churston (Torbay) only reached 12.9mm. This is nearly 4mm less than the size attained by the 1994 cohort at nearby Shoalstone, however the population density here is relatively low (pers.obs).

Measurements and examination of growth checks in the small *Osilinus* population at Portland on May 31st 1995 indicate that the 1994 cohort had attained a size of between 15.6 and 19mm (J. Hawthorne, pers.comm). This far exceeds the sizes achieved by the larger populations at Lyme Regis and Shoalstone over the same period and provides further evidence to suggest that growth rate and size attained is density dependent. Underwood (1976) found strong evidence for intraspecific competition amongst the Australian intertidal grazing gastropod *Nerita atramentosa* when juveniles and adult animals were kept in cages on the shore at different densities. While the growth rate of juveniles decreased with increasing density, mortality was not significantly different. However mortality of adults increased linearly as density increased. Food rather than space competition was inferred as the animals roamed about randomly and showed no homing behaviour (as in *Osilinus* and *Gibbula*, pers.obs). The possibility of population density regulation by food competition was postulated as heavy recruitment of *Nerita* would cause reduced growth of juveniles and increased adult mortality till populations dropped. Juveniles would then increase their growth rate and become adult. Such population density regulation is also suggested for *Osilinus* and *Gibbula* within dense populations near to the species southern limits (Bode *et al.* 1986).

Of course the question arises as to whether the faster growth observed in individuals at low population density enables adequate energy resources to be made available for gonad development and spawning. Daguzan (1991) found that *O.lineatus* in southern Brittany had become sexually mature after one year, reaching a mean basal diameter of 14.6mm. In Britain, both sexes of each species first reach maturity as they approach two years old (Williams, 1964,1965; Underwood, 1972; Garwood & Kendall, 1985), although most of the data come from dense populations in west Wales and Plymouth. Desai (1966) has observed spawning *O.lineatus* aggregated in shallow pools and it may be that ripe males induce females to spawn. The highly clumped population of *G.umbilicalis* at Freshwater Bay on the Isle of Wight (pers obs) suggests that individuals may be chemically attracted to one another. Further investigations into gonad development and spawning could be undertaken within these small populations. Yet Kendall (1987) reports that adult *O.lineatus* were successfully transplanted to the North Yorkshire coast, survived the 1978-1979 winter, grew faster than the animals within the population from which they were taken "*and spawned normally*" the following summer.

Inferences regarding the frequency of recruitment of *Balanus perforatus* at Portland Bill are difficult considering the successional changes that occurred beneath the boards and their deterioration over the study period. However of particular interest was survival and continued growth after the shelter of the boards had been lost. Although the species is commonly found within crevices and beneath overhangs it is also on the open shore, as observed at Saltern Cove in Devon, suggesting that cryptic habitats are not necessarily required for successful settlement. In UK waters, no other field experiments have been published on the settlement of this species. Laboratory experiments on the relative tenacity of cyprids to low and high shear biofilms have been carried out by Neal & Yule (1994). The authors found that both *Balanus perforatus* and *Elminius modestus* cyprids attached more strongly to thin dense biofilms associated with high shear conditions compared to low shear filmed surfaces. *B. perforatus* cyprids also had higher tenacity on unfilmed surfaces compared to thick low-shear biofilms. They concluded that both barnacle species may detect differences in bacterial communities grown under different shear regimes. The shear conditions on the edge of crevice habitats are likely to be less than on the open shore, but reduced light intensity in these habitats may favour the development of particularly thin algal biofilms on these surfaces. Deeper within crevices, silt deposition would presumably deter barnacle settlement, although the species may be found in sheltered estuaries. *B. perforatus* was discovered on vertical pier piles at Swanage in Dorset and at Worthing in Sussex, which are likely to be high-shear habitats where filter feeding may be favourable. Translocation of recruits from Lyme Regis to Bembridge confirmed that growth was possible at the then known limits of the species range, albeit at a reduced rate compared to recruits at Lyme. The smallest individual in which brooding embryos have been observed was 5.7mm (Chapter 4) which may just about be attained by animals after one years growth. The estimates of size after one year's growth are almost identical to with those quoted for intertidal animals at Brixham in Crisp & Bourget (1985). Further work on the growth rate of the species in different habitats would be valuable.

Chapter 7

The effect of rock type on the recruitment and mortality of *Chthamalus montagui*

7.1 Introduction

Of all the possible factors that might be influential in determining the geographic limits of barnacle species, the availability of suitable substratum, upon which to settle and survive to reproductive maturity, must rank as being of fundamental importance. However, the specific attributes of the substratum that are favoured by settling cyprids are many and varied; these include rugosity, thermal capacity, colour, surface energy and charge and elemental composition (Crisp, 1974; Lewis, 1977; Holmes *et al.*, 1997). Of additional importance may be the thickness and species composition of microbial films that develop on these surfaces which are also known to influence settlement of marine larvae (Holmstroem *et al.*,1992; Wieczorek *et al.*,1996; Thompson *et al.*, 1998).

The influence of rock type upon barnacle settlement has received relatively scant field investigation in comparison to studies on other natural and artificial substrata (see Holmes *et al.*, 1997, for bibliography). Moreover, the studies that have been undertaken have resulted in somewhat conflicting results. Hatton (1938) found no difference in settlement density of *S. balanoides* on three types of granite and diabase. Caffey (1982) investigated settlement and early survival of the Australian intertidal barnacle *Tesseropora rosea* in a four-factor experiment that assessed variation on three spatial scales and on different rock types; shale, sandstone, mudstone and gabbro. While there was usually significant differences in settlement and early survival at the different spatial scales studied, there were no consistent patterns of settlement due to the influence of rock type alone, nor in interaction with factors representing spatial variation at two scales. Holmes *et al.*, (1997) investigated the effect of fifteen different rock types on the settlement of *Semibalanus balanoides* cyprids. Polished samples were suspended from a pier at Millport in Scotland. Significant differences in settlement preferences were obtained that were independent of any potential effect of surface rugosity or colour cues.

Caffey (1988) argues that, because in nature, larvae are never exposed to single factor dichotomous choices, experiments on settlement must enable larvae to respond to an integrated series of substratum characteristics, which therefore must involve naturally weathered substrata. McGuinness (1989) also makes a strong case for the use of natural substrata because of the many interactions between variables that occurred when experiments were conducted in the field.

Moore & Kitching (1939), working along the Dorset coast, made a detailed study of the influence of rock surface texture on the distibution of *Chthamalus 'stellatus'* at Tilly Whim caves near Swanage (now inaccessible due to rock falls). Here, there is a vertical succession of different bands of limestone and chert, which had been differentially weathered exposing varied surface texture. They found that adult populations of *Chthamalus 'stellatus'* preferred hard, rough limestone to a soft smooth one. Larval preferences for a more rugose substrata were inferred from their work although other possibilities might be less-visible surface features, different films, differential activities of grazers or predators, or fortuitous small scale (<10m^2) patchiness of settling cyprids (De Wolf, 1973). In discussing factors influencing larval settlement Crisp (1974) made an appropriate distinction between surface 'texture' i.e. small-scale relief, and 'contour' which are relatively large features compared to the size of larvae e.g. cracks, holes and raised areas. Walters & Wethey (1996) found that *Balanus* sp. larvae settled almost exclusively in the location that provided individuals with the best refuge: the crevices formed where the bases of roughness elements intersect with flat surfaces.

In experiments to investigate the influence of surface contour on settlement of *S.balanoides* and *Chthamalus fragilis* on the Atlantic coast of N.America, Wethey (1986) found that both species settled in identical locations on replicate casts from the same mould. The results largely supported the observations of Crisp (1961, 1976) who noted that *S.balanoides* larvae preferred pits to grooves, and small pits were preferred to large pits. He also noted that the bottoms of pits were preferred to the edges, which have lower shear.

The importance of settlement cues at different spatial scales is described using empirical data by Le Tourneux & Bourget (1988) who concluded that at the smallest scale (<300µm, equal to the average maximum width of *S.balanoides* larvae) the micro-heterogeneity of surface immediately beneath the larva was most important. Fractal measurements showed that larvae were apparently able to discriminate micro-heterogeneity levels below a step length of 35µm, which is approximately the size of diameter of antennular discs (40µm) used to explore the substratum and attach.

On chalk, Moore & Kitching (1939) reported that *C. 'stellatus'* in Dorset could only be found in positions sheltered from violent wave action such as at Swyre Head or Arish Mell Gap, or on flints. The authors found that both *C. 'stellatus'* and *Semibalanus* (as

Balanus) *balanoides* were similarly distributed along the Dorset coast. The only exception was at Old Harry Rocks near Swanage where *Chthamalus* was absent, yet *Semibalanus* 'plentiful'. The undesirability of chalk for *Chthamalus* was attributed to the fact that it affords insecure holding (either for larvae or for adults) because of its smooth surface, or that being porous it allows the barnacles to be desiccated from below in dry weather.

No experiments have been carried out on the settlement preferences of *Chthamalus montagui* or *C.stellatus*, although Raimondi (1988) found that recruitment of *Chthamalus anispoma* on basaltic rocks was significantly lower than on granite, due to higher post-settlement mortality. He also found that settlement was not greatest on the roughest surface of his four treatments.

The specific aims of this chapter are:

i) To measure settlement and recruitment of *C.montagui* on samples of different rock types, including chalk, found at the species current geographic limits.

ii) To investigate whether there are differences in the mortality of new recruits on the different rock types.

7.2 Methods

7.2.1 Description of rock types used in the experiment

Because the heterogeneity of mineralogy of different rock types has been suggested to influence barnacle recruitment (Holmes *et al.*1997) it was considered important to describe more accurately the physical and chemical nature of the rocks included in the experiment. This was felt especially important considering the complex stratigraphy of sedimentary rocks within the region. The rocks chosen were Bembridge Limestone (Oligocene) from Bembridge, Isle of Wight; Chalk (Cretaceous) from Freshwater Bay, Isle of Wight; Kimmeridge Cementstone (Jurrassic) from Kimmeridge, and Blue Lias Limestone (Jurrassic) from Lyme Regis. All are calcareous rocks that form significant intertidal shore platforms along the central south coast of England towards the extreme geographic limits of *C. montagui.* Thin sections of each of the rocks were prepared, examined under the microscope and photographed. Analysis of the relative mineral composition of the rocks was carried out by X-ray diffraction. The porosity of the rocks was measured indirectly by determining rock density. A 1cm^3 cube of each rock was cut accurately and weighed on an electronic balance. The thermal capacity of the different rocks was also simply compared by exposing rock samples of 1 cm^3 to a heat lamp and measuring rise in surface temperature.

7.2.2 Preparation of rock samples and measurement of surface parameters

Small boulders of each rock type were collected from above EHWS. The rocks were selected for having a visually similar weathered surface profile to that of the shore platform and were assumed not to have been recently colonised by barnacles or algae from the lower shore. Lyme Regis was chosen for the experiment because over the previous five years, the shore was found to be a consistently high settlement and recruitment site and therefore a large supply of cyprids was likely to be available (see Chapter 5). After one-year of indoor storage, the boulders were taken to the Department of Geology and cut with a diamond tipped saw into approximately equal sized pieces, 6cm x 4cm x 1.5cm, with one face being left naturally weathered.

As cyprids of *Semibalanus balanoides* are known to favour surfaces with microbial films (Thompson *et al.*, 1998) considerable thought was given to the best way of sterilising or cleaning the rock samples so as to remove any remaining algal cells and chemical cues e.g. the integumental protein arthropodin. Various techniques such as scrubbing, heating with a blow-lamp and autoclaving have been carried out in previous studies (e.g. Homes *et al.*, 1997; Thompson *et al.*, 1998). The sedimentary rocks used in the study are by their very nature soft and fragile, especially chalk, and vigorous brushing may well effect the natural rugosity and surface profile of the samples. Heating the rocks, even in an autoclave, may also cause damage and any remaining proteins or chemicals will not necessarily be removed. Heating may cause an amalgamation of chemicals that might further complicate the problem. It was finally decided to scrub the weathered surface of each rock with a nylon toothbrush for one minute to remove any loose microbial film and algal cells.

In collaboration with P. Moschella (University of Southampton), six chips of each rock type were then checked for the presence of microbial film with scanning electron microscopy (SEM) at fixed magnification (x250). Three random fields were photographed from each rock chip and negatives observed on a light box or under a light microscope, however no presence of any micro-organisms was detected

The hardness of each of the rock types was determined using a Vickers instrument in the Engineering Materials Department. The diameter of a diamond-shaped impression made into the rock is measured using a magnifying eyepiece. Because of difficulty in defining the impression made in chalk, a small area was coloured with a black marker pen prior to measurement. Ten measurements were made for each of the rock types and the mean hardness calculated.

The rugosity of each rock sample was measured along a trace of length 20-30mm using a Taylor-Hobson Form Talysurf 120L. Surface irregularity (Ra) is the universally recognised and the most used international parameter of roughness. It is the arithmetic mean of the absolute departure of the roughness profile from the mean line.

7.2.3 Measurement of recruitment of *C.montagui* on prepared samples

On 14th May 1999, ten replicates of each of the four rock types were embedded in resin (*WetWork*, SP Systems Newport, IOW) and stuck to the flat shore platform at MTL in each of two patches, 15m apart, on Broad Ledge at Lyme Regis. Within each patch, rocks were located randomly and approximately 25cm apart, with the naturally weathered surface uppermost. To avoid the possibility of differential settlement being as a result of varying chemical cues from the surrounding adult barnacle population, rocks were positioned in areas of similar adult density. The resin around the edges of the rock samples was smoothed to facilitate movement of grazing gastropods on to the rock samples to prevent them from becoming colonised by thick green algae.

To determine the effect of rock sample preparations on larval settlement and subsequent recruitment and mortality, counts were also made within ten cleared areas of the natural Blue Lias limestone platform and compared with the prepared Blue Lias limestone samples that were fixed to the shore. Each clearance was 8x6cm and counts made within the central 6x4cm and inner 8cm^2. A stainless steel screw (head diameter 9.8mm) was fixed into the centre of each clearance as a reference marker to aid identification of individual recruits in photographs.

The rocks were examined on four occasions during the settlement season between the end of July and mid-October. The number of cyprids and calcified recruits were counted in the central 8cm^2 (4x2cm) and on the whole of the upper surface of each rock.

Because differences in grazing pressure and predation could both influence settlement and mortality, the density of gastropods in the vicinity of each patch was determined by placing ten random quadrats in each area. For limpets and dog-whelks a quadrat of area 0.25 m^2 was used and for the topshells and periwinkles, 400cm^2.

7.2.4 Measurement of mortality on prepared rock samples

To determine the mortality of recruits, rocks were photographed on 13th October 1999, 8th January and 15th May 2000. Counts were made from enlarged black & white negatives (see Chapter 5 for details of photographic equipment). Between 15-25 individual recruits present in October 1999 were marked on to tracing paper, placed over the screen and their survival monitored on subsequent field visits. Because of difficulties, previously encountered, in locating recruits on photographs of Kimmeridge Cementstone, due to poor contrast against a dark background, mortality was determined from field counts within the central 8cm^2 of each sample.

7.2.5 Measurement of mortality in natural populations at Beer and Kimmeridge

While the settlement and mortality of *C.montagui* on all rock types is of interest, of particular importance is the reaction to chalk. Intertidal chalk is present at the extreme geographic range of the species at Freshwater Bay and Culver cliff on the Isle of Wight. Yet because of the recruitment gradient along the Dorset coast (determined in Chapter 5) its rarity on chalk may be as a result of too few cyprids arriving on the shore at these localities rather than adverse settlement preference. Chalk is however present at Beer

Head, 12 km east of Lyme Regis, where it forms high cliffs above reefs of upper-greensand. A few large chalk boulders, which had fallen from the cliffs above, were found between MTL and HWN. Adult *C. montagui* was abundant on the upper-greensand platform and was patchily distributed on the chalk boulders. In October 1999, ten photographic stations were established at MTL on a large flat chalk boulder that had fallen on to the shore at Beer. Holes (6mm) were made with a cordless drill in areas where there had been a reasonable settlement. Care was taken to avoid damage to the new recruits and monitoring site while drilling. Stainless steel screws were inserted into plastic 'Rawlplugs'. Photographs of new recruits were taken in October 1999, with the screw in the centre of the camera field of view. Twelve photographs were also taken of new recruits within the permanent stations at MTL on the cementstone platform at Kimmeridge (see Chapter 5 for details of photographic equipment). Photographs of both the sites were taken again in May 2000. Only eight of the original ten sites at Beer were re-located, and of the twelve permanent stations at Kimmeridge, new recruits could only be seen in seven photographs. The mortality of new recruits at both sites was determined from projected negatives using the same procedure as in 6.2.3 above; 15-25 recruits were mapped in each photograph from Beer and 2-20 from Kimmeridge. Because no settlement of *C. montagui* has ever been observed on the shore at Bembridge, photographic stations to monitor mortality were not established.

7.3 Results

7.3.1 Description of the physical and chemical nature of the rock types

From the prepared thin sections the following preliminary analysis of the four rock types was made using a polarising microscope:

Bembridge Limestone: Largely micrite and moderately porous, with pores well spaced out. Clay, kerrogen and pyrite content low.

Chalk: Coccolith micrite, highly porous although pores very small. Permeability low.

Blue Lias Limestone: Microsparite limestone with irregular patches of iron pyrite and low porosity.

Kimmeridge Cementstone: A ferroan dolomite (Calcium magnesium carbonate) with high iron and organic content. Dolomite rhombi about 30 μm. Has low porosity as pores are filled with iodine-rich kerrogen.

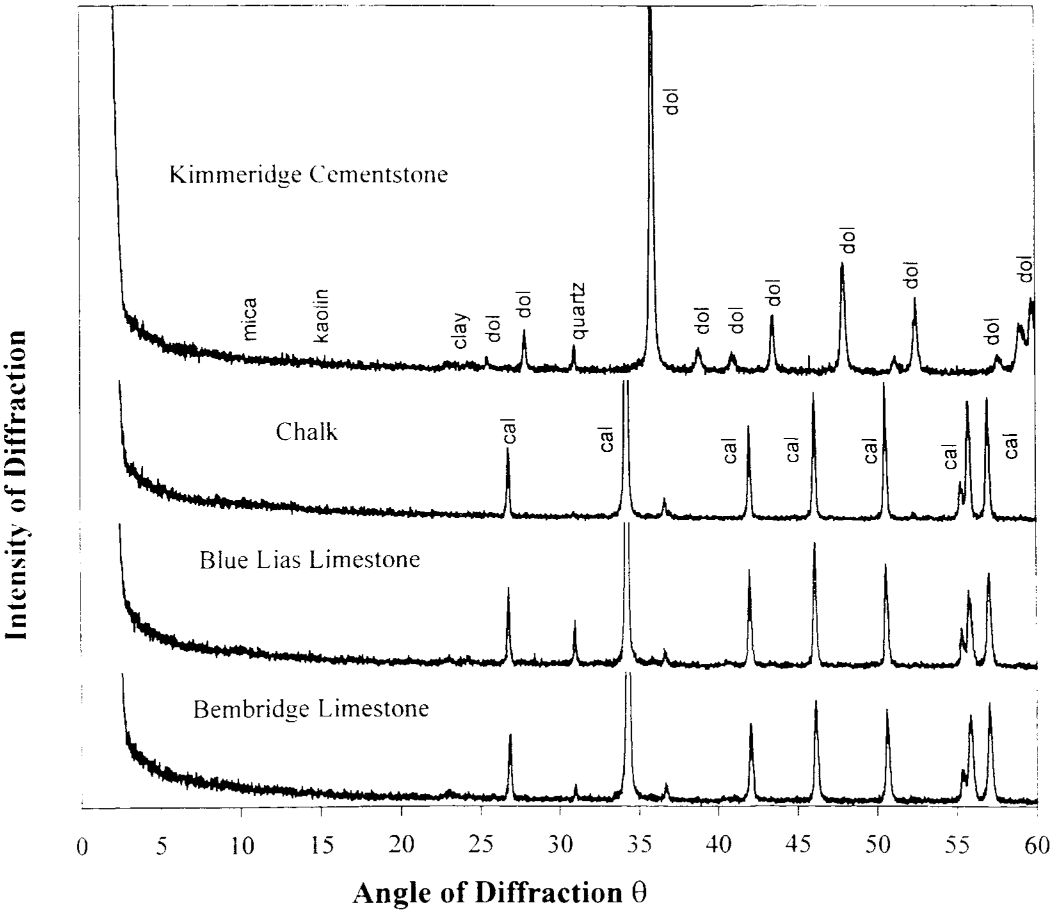


Fig.7.1 Results of X-Ray Diffraction analysis of four rock types used in the experiments 'dol' denotes dolomite; 'cal' denotes calcite.

Fig.7.1 shows the results of X-ray diffraction to determine the relative mineralogy of the different rock types. The Kimmeridge Cementstone is a dolomite (a double carbonate of calcium and magnesium, $MgCO_3.CaCO_3$) whereas the other three rocks are dominated by the presence of calcite. The quantity of quartz (Silica or silica dioxide) further differentiates these limestones. From the height of the peaks shown in Fig 7.1 chalk has negligible amounts whereas Blue Lias has just over twice the amount present in Bembridge Limestone. Kimmeridge Cemenstone also contains small amounts of quartz and various clay minerals. Blue Lias appears to contain small quantities of mica (aluminium silicate), yet quantitative differences between the four rock types are difficult to establish.

Table 7.1 Density of one cubic centimetre of each rock type and temperature attained after exposure under heat lamp for 5 minutes. Room temperature was 16.7°C.

Rock Type	**Density (g/cm^3)**	**Temp°C**
Chalk	2.35	25.1
Bembridge Limestone	2.28	32.4
Kimmeridge Cementstone	2.80	37.5
Blue Lias Limestone	2.54	31.6

Table 7.1 shows the density of the four rock types and the temperature attained by a sample 1cm^3 after exposure to a heat lamp for 5 minutes. The room temperature during the experiment was 16.7°C. The greater density and dark colour of the Kimmeridge Cementstone contribute to its lower thermal capacity.

7.3.2 Hardness and roughness measurements

The mean hardness of the Bembridge Limestone, Chalk, Kimmeridge Cementstone and Blue Lias limestone is shown in Fig 7.2. Chalk is the softest and Kimmeridge Cementstone the hardest of the four rock types. This is consistent with the relative amounts of dolomite, calcite and quartz contained in the rocks, described above. On the Mohs scale of hardness (Allman & Lawrence, 1972) calcite is 3.0 and quartz, the hardest, 7.0. A one-way ANOVA showed highly significant differences between hardness of the four rock types ($p<0.001$) and a subsequent SNK test showed that no two rock types had the same mean ($p<0.05$). The rocks of each type were divided in to two samples ($n = 10$) that would later form the two patches of rocks fixed to the shore. Fig.7.3 shows the mean roughness (Ra) of the four rock types in each of the two samples.

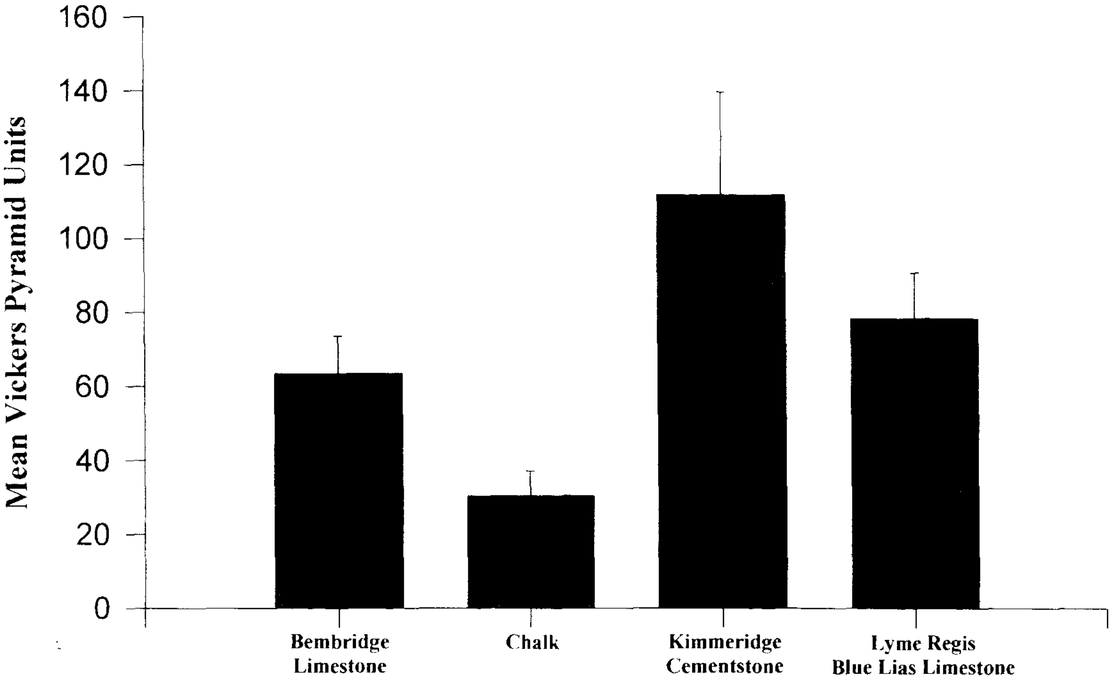


Fig.7.2 Mean hardness of four rock types used in experiment to investigate recruitment of *C. montagui*, n = 10. Error bars show +SE.

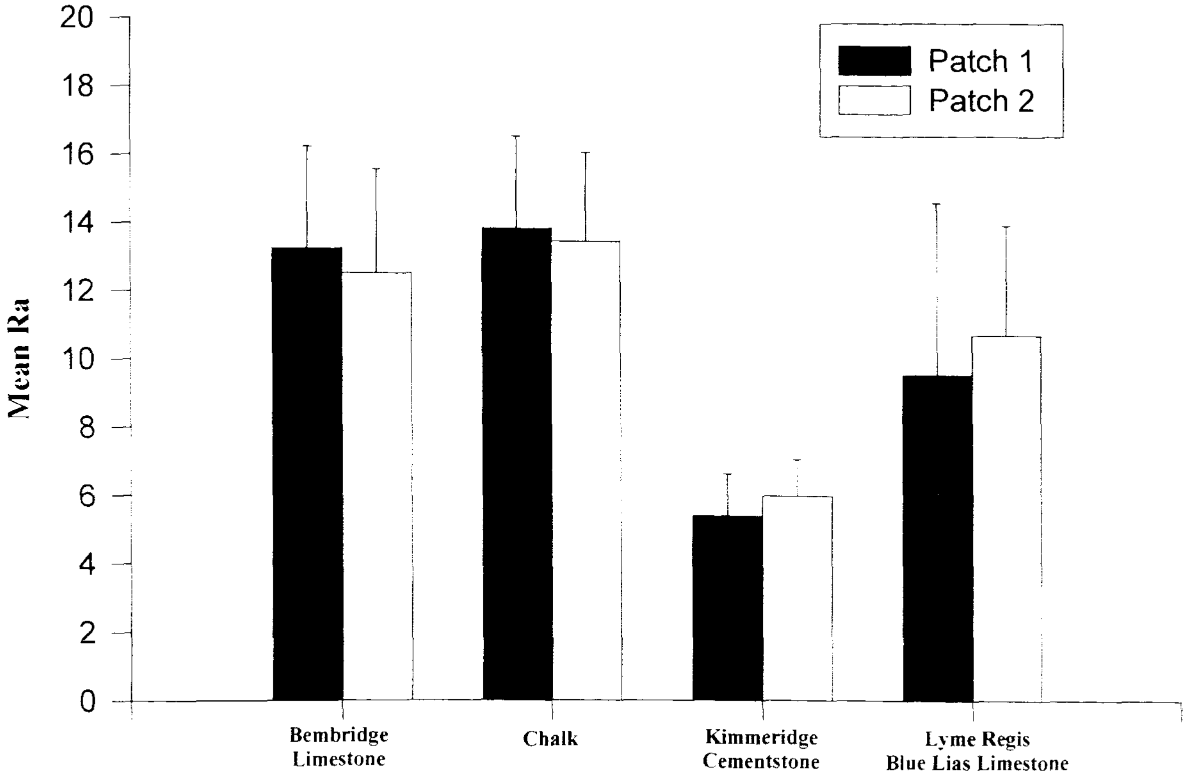


Fig.7.3 Mean roughness (Ra) of four different rock types placed in two patches on the shore at Lyme Regis. Error Bars show +SE, n = 10.

A two-way ANOVA showed significant differences in roughness between rock types (p=0.003), but not between patches (p = 0.8). A subsequent SNK test showed that the mean roughness of every combination of rock types was significantly different from each other ($p<0.05$) except for between Bembridge Limestone and chalk.

7.3.3 Recruitment of *C. montagui* on samples of different rock types.

Between July and October 1999, only two of the rock samples were lost, one from each patch. Some flaking had occurred on the surface of a few Bembridge Limestone and chalk samples between fixing in May and first examination in July, however no further obvious damage was observed on subsequent occasions.

Settlement was just beginning, both on the shore and on rock samples, when the rocks were first examined on July 28th. Fig. 7.4 shows the rate of recruitment on the different rock types and shore platform in each patch. By August 16th, spat densities within control clearances on the shore platform were already greater than on the rock samples, including that of Blue Lias. Cyprids were observed only on September 10th, when they were seen on the Kimmeridge Cementstone and Blue Lias samples. Considerable recruitment had by this time also occurred on the resin, within which the rock samples were embedded, indicating that this appears not to have any deleterious effect on the settling larvae.

From mid-August, the rate of recruitment on the shore platform and on all rock samples, except for Kimmeridge Cementstone, was very similar. It was noted that pits and cracks on the rock surface were the first areas to be colonised, irrespective of rock type. Some small spots of the alga *Hildenbrandia rubra* were observed on the chalk and Bembridge Limestone samples, looking uncannily like young spat. Recruitment on the Kimmeridge Cementstone samples remained low throughout the summer, though reached a maximum density of 8.75 per cm^2 on a single sample. The mean density of recruitment for all samples by mid-October is shown in Fig. 7.5. Highest mean densities were on the shore platform where the maximum counted in a single area was 25 per cm^2. This was slightly less than the maximum of 29 per cm^2 counted on a single sample of Bembridge Limestone. Recruitment on the chalk samples of both patches was surprisingly high with a maximum of 23 per cm^2 and minimum of 5 per cm^2. Overall, considerable variability in the magnitude of recruitment was evident within each rock type. Differences were tested using a two-way ANOVA with GMAV5 (Underwood *et al.*, 1998). Factor 'Rock Type' was orthogonal and fixed and the factor 'Patch' orthogonal and random (Table 7.2). The results showed a significant difference between rock types ($p = 0.0107$), but not patches: neither was there any interaction between factors.

Table 7.2 Two-way ANOVA of *C.montagui* recruitment on four different rock types fixed to the shore and in naturally cleared areas on the shore platform in two patches at Lyme Regis ($n = 9$). Counts made in October at end of settlement season. Data were Ln(x) transformed. Cochran's test $C = 0.23$ (ns). *P* values: * denotes $p< 0.05$,** denotes $p < 0.01$,*** denotes $p<0.001$. See Fig.6.4 and text for further details

Source of Variation	df	MS	*F*	*P*
Rock Type	4	13.07	15.32	0.0107*
Patch	1	0.54	0.57	0.45
Rock x Patch	4	0.85	0.9	0.47
Residual	80	0.95		
TOTAL	89			

SNK Test on rock types: Bembridge Limestone (BM); Chalk (CK); Kimmeridge Cementstone (KC); Blue Lias Limestone (BL); Shore (SH). '=' denotes no significant difference, '<' denotes $p < 0.05$.

Rock Types	KC < BL = SH = BM = CK
Mean Recruitment (no. per cm^2)	2.58 < 10.62 = 16.12 = 11.09 = 12.03

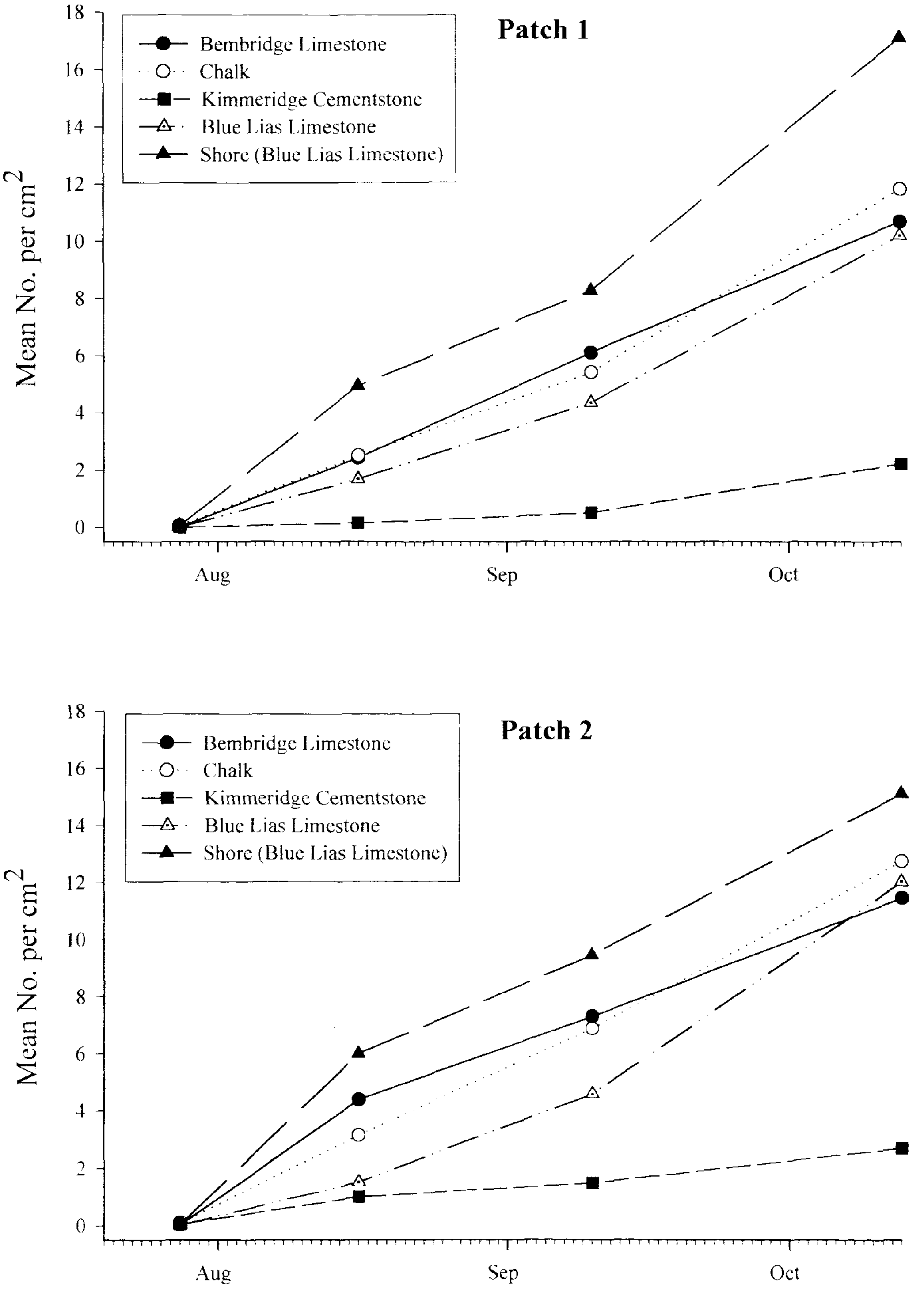


Fig.7.4. Mean recruitment of *Chthamalus montagui* on different rock types and control clearances in each patch during the main settlement season at Broad Ledge, Lyme Regis in 1999. Patches 15m apart at MTL. Error bars omitted for clarity. See text for further details.

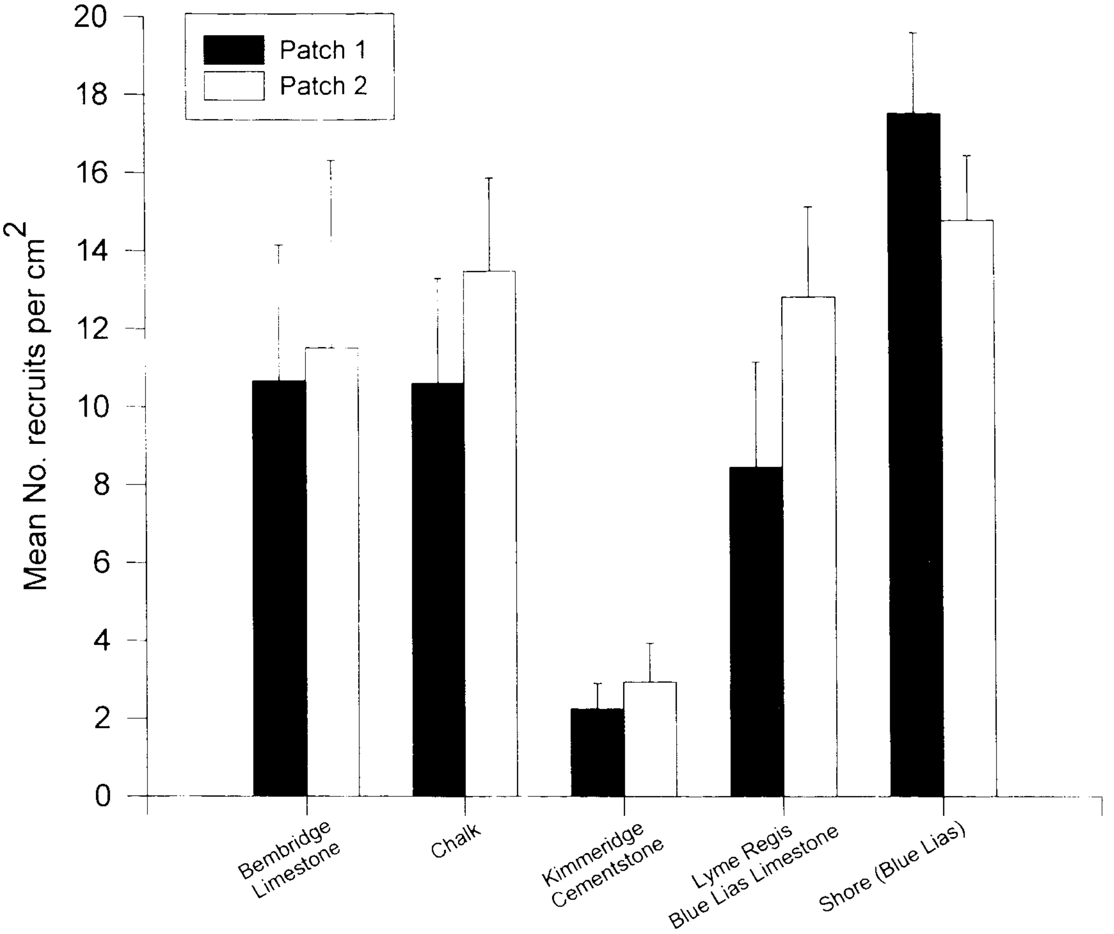


Fig.7.5 Mean recruitment of *Chthamalus montagui* on prepared samples of four different rock types and within clearances on the shore platform at Lyme Regis, Dorset. Rocks and clearances arranged in two patches 15m apart at MTL, n = 9 of each treatment per patch. Counts made on 13th October 1999 at end of settlement season. Error bars show + SE.

Subsequent SNK analysis showed that Kimmeridge Cementstone had significantly less recruitment than other rock types and controls ($p<0.05$), but no other differences were apparent. Recruitment in clearances on the Blue Lias shore platform was higher than on the Blue Lias samples, although not statistically significant. Although the mean density of recruits on each of the prepared samples was greater in patch 2, that of the control clearances was higher in patch 1. Differences between patches were not statistically significant, however, they may reflect a clumped distribution of cyprids within the water column as observed by De Wolf (1973).

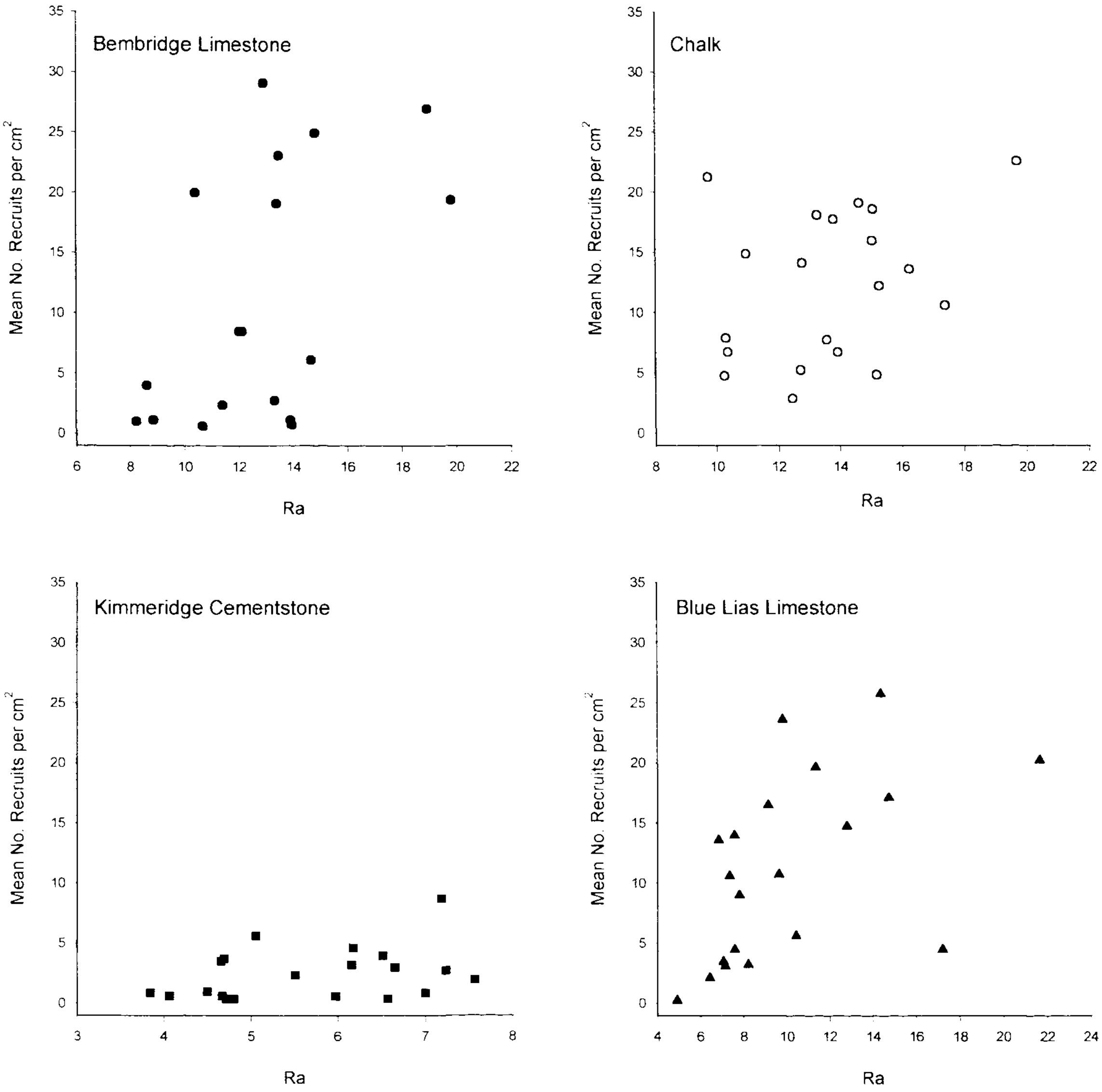


Fig.7.6 Scatter diagrams of *C.montagui* recruitment against roughness (Ra) of prepared samples of four rock types fixed to the shore at Lyme Regis. Both patches of rocks are combined. Recruitment measured at end of season on 13th October 1999. Note different scales on x and y axis. Correlation coefficients: Bembridge Limestone, $r = 0.53$, $n = 18$, $p = 0.0245$*; Chalk, $r = 0.33$, $n = 20$, $p = 0.158$ns; Kimmeridge Cementstone, $r = 0.35$, $n = 20$, $p = 0.132$ns; Blue Lias Limestone, $r = 0.52$, $n = 20$, $p = 0.02$*.

Fig.7.6 shows scatter diagrams of recruitment against roughness for each rock type. Positive trends are apparent for each type and correlation's for Bembridge Limestone and chalk are statistically significant. All samples from each rock type are combined in Fig 7.6. An analysis of covariance (ANCOVA) was carried out on the data with roughness as covariant. The main effect, 'Rock Type', was not significant indicating that differences in recruitment on the rock samples are largely due to variation in roughness (Table 7.3).

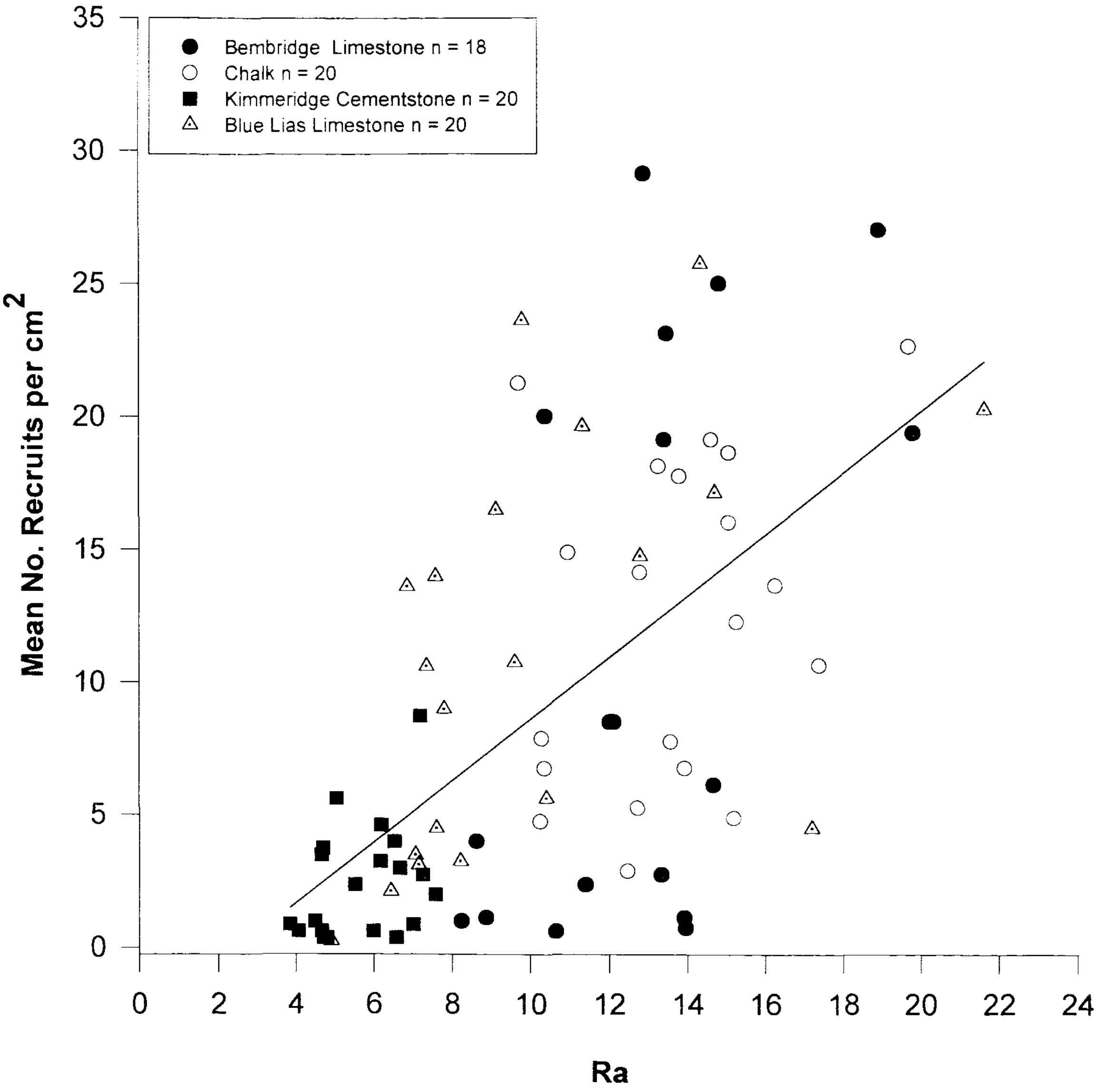


Fig.7.7 Scatter diagram of *Chthamalus montagui* recruitment on all rock samples with measured roughness (Ra). Counts made at end of settlement season in October 1999. Type 1 Linear Regression line shown, $n = 78$, $r^2 = 0.37$, $p < 0.001$.

Table 7.3 ANCOVA of recruitment of *C. montagui* on four different rock types with measured roughness (Ra) as covariate.

Source of Variation	**df**	**MS**	***F***	***P***
Covariate (roughness)	1	813.68	19.8	<0.001
Rock Type	3	53.48	1.3	0.28
Residual	73	41.1		
Total	77	65.57		

7.3.4 Mortality of *C. montagui* on different rock types

Figs 7.8 and 7.9 show the mean mortality of *C. montagui* on the different rock samples and within clearances between 27th October 1999 - 8th January 2000 and 27th October 1999 -15th May 2000 respectively. By May 2000, 70% of the rock samples still remained fixed to the shore. Several detached samples were found in rock pools within five metres of the patches but were not included in the analysis. Between October 1999 and January 2000, the extent of mortality was found to be very variable, with considerable differences on the chalk samples in each patch and between patches. Least mortality had occurred on the shore platform and on the Blue Lias samples. A two-way ANOVA using GMAV5 (Underwood *et al.*,1998) showed no significant differences in the mean mortality rates on rock types or between patches (Table 7.5). By the end of the experiment in May 2000, highest survival had occurred on both the Blue Lias samples and shore platform, and least on the Bembridge Limestone and Chalk samples. Apart from the Kimmeridge Cementstone samples, higher mortality had occurred in patch 2. A two-way ANOVA (Table 7.6) showed significant differences in mean mortality rates between rock types ($p = 0.033$) although these could not be resolved using a subsequent SNK test. The similarity in mortality between the Blue Lias samples compared to the shore would seem to indicate that the experimental procedure has no major effect on mortality rate. Slightly higher mortality on the shore could be due to predatory activity by dog-whelks and bulldozing by grazers such as topshells, periwinkles and limpets. Table 7.4 shows the densities of common gastropods in the vicinity of each patch determined in September 1999. Mann-Whitney 'U' tests showed no significant differences between patches ($p > 0.05$) in the density of any species.

Table 7.4 Densities of gastropod molluscs (per m^2) in immediate vicinity of two patches of rock samples, determined in September 1999. Adult *Patella* spp. *P*(a); Juvenile *Patella* spp. *P*(j); *Gibbula umbilicalis* ***Gu***; *Osilinus lineata* ***Ol***; *Littorina littorea* ***Ll***; *Nucella lapillus* ***Nl***. Figures show mean and SD of ten random quadrats.

	Patch 1						**Patch 2**					
	Gu	***Ol***	***Ll***	***P*(a)**	***P*(j)**	***Nl***	***Gu***	***Ol***	***Ll***	***P*(a)**	***P*(j)**	***Nl***
Mean	40	10	143	8	1	4	43	3	190	7	1	2
SD	57	17	112	3	1	1	33	8	151	2	1	0.4
n	10	10	10	10	10	10	10	10	10	10	10	10

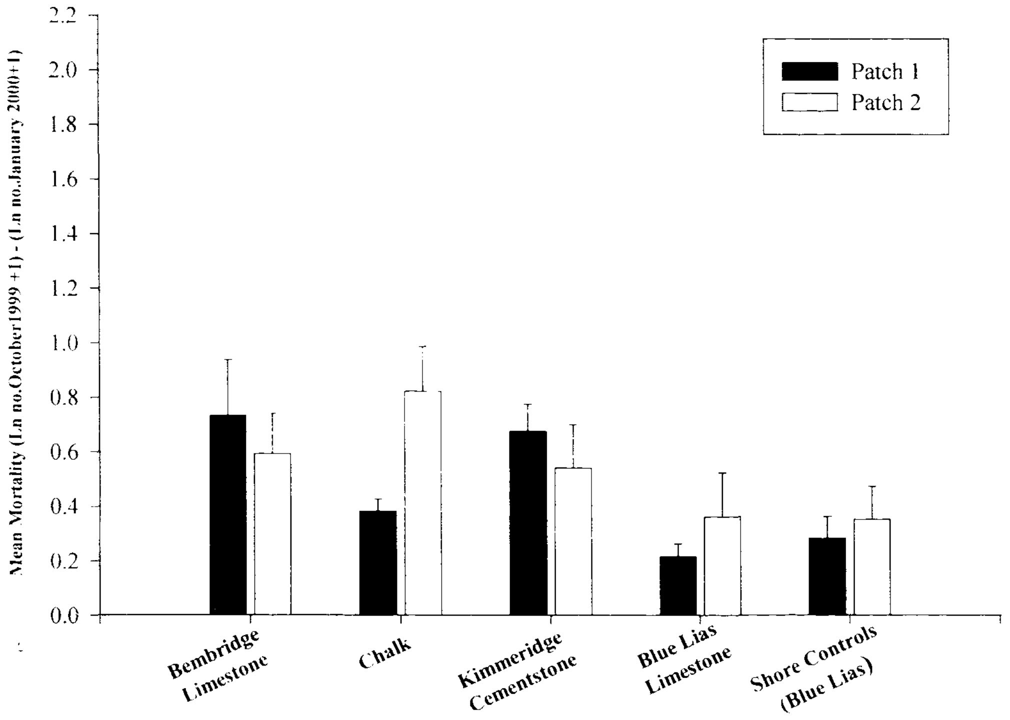


Fig 7.8. Mean mortality of *C. montagui* on four different rock types and controls in two patches (n = 7) at MTL between 27th October 1999 and 8th January 2000. Error bars show +SE.

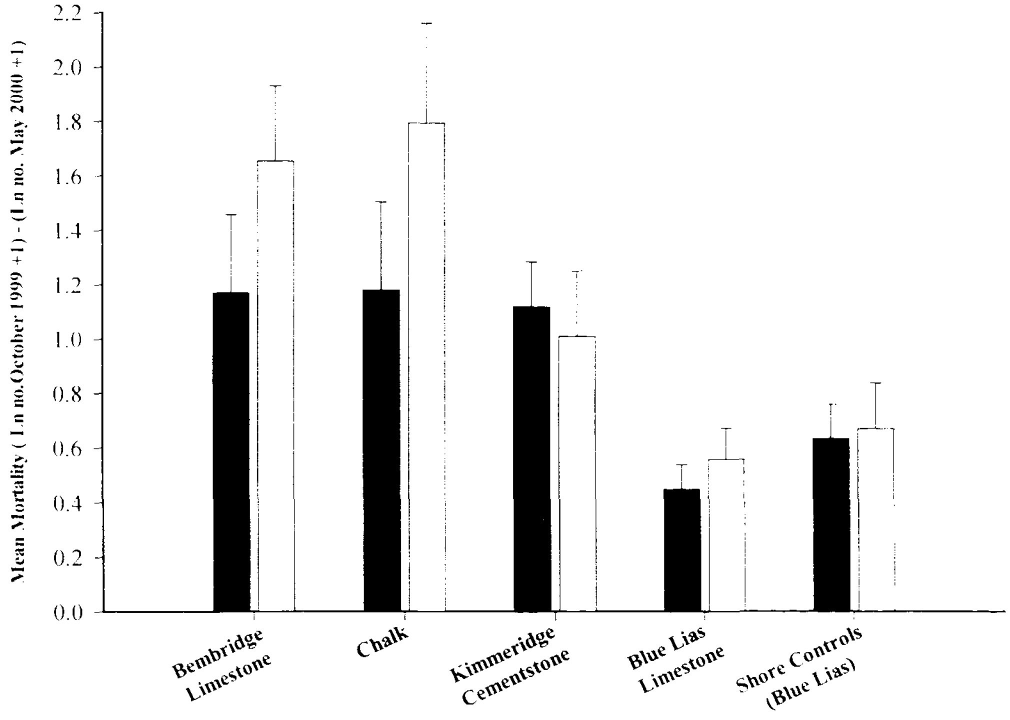


Fig 7.9. Mean mortality of *C. montagui* on four different rock types and controls in two patches (n = 6) at MTL between 27th October 1999 and 15th May 2000. Error bars show +SE.

Table 7.5 Two-way ANOVA of *C.montagui* mortality on four different rock types fixed to the shore and in naturally cleared areas on the shore platform in two patches at Lyme Regis (n = 7). Mortality expressed as (Ln no. in October 1999 +1) – (Ln no. in January 2000 +1). Data untransformed. *P* values: * denotes p< 0.05,** denotes p < 0.01,*** denotes p<0.001. See Fig.7.8 and text for further details.

Source of Variation	df	MS	*F*	*P*
Rock Type	4	0.45	2.25	0.23
Patch	1	0.10	0.82	0.37
Rock x Patch	4	0.19	1.60	0.19
Residual	60	0.12		
TOTAL	69			

Table 7.6 Two-way ANOVA of *C.montagui* mortality on four different rock types fixed to the shore and in naturally cleared areas on the shore platform in two patches at Lyme Regis (n = 6). Mortality expressed as (Ln no. in October 1999 +1) – (Ln no. in May 2000 +1). Data untransformed. *P* values: * denotes p< 0.05,** denotes p < 0.01,*** denotes p<0.001. See Fig.7.9 and text for further details.

Source of Variation	df	MS	*F*	*P*
Rock Type	4	2.33	8.20	0.033*
Patch	1	0.78	2.35	0.13
Rock x Patch	4	0.28	0.86	0.5
Residual	50	0.33		
TOTAL	59			

Differences between rock types could not be resolved using SNK analysis.

A correlation between recruitment density and mortality on the different rock treatments proved not statistically significant (p=0.08, n = 48) suggesting non density-dependence. However a correlation between mortality and roughness (Ra) did prove significant (0.34. n = 48, p = 0.017).

7.3.5 Recruitment and mortality of *C. montagui* in natural populations on the shore

Although the mean recruitment on the Kimmeridge Cementstone samples was the lowest of all rock types in the experiment (2.5 per cm^2), it was an order of magnitude greater than that observed on the shore at Kimmeridge (mean 0.16 per cm^2). The minimum density of recruits observed on the fixed samples (0.37 per cm^2) was the same as the maximum density recorded on Kimmeridge shore, the highest in five years of monitoring (see Chapter 5). The lower density estimates on the shore at Kimmeridge may in part be due to the larger clearance area (400 cm^2) within which counts were made. Yet similar estimates (0.2 per cm^2) were obtained from the examination of 8 x 5 cm photographs of uncleared areas. On the chalk boulders at Beer, recruitment density measured within cleared 8 x 5 cm quadrats was between 0.6 and 5.6 per cm^2 (mean 3.2 per cm^2). This was considerably less than that on the fixed samples of chalk at Lyme Regis (12.3 per cm^2).

In Fig 7.10, the mean mortality (October 1999-May 2000) at MTL of *C.montagui* recruits on fallen chalk boulders at Beer and on the shore at Kimmeridge is shown alongside the mean mortality of those that settled in the two patches cleared on the shore at Lyme Regis.

Mortality on the chalk at Beer was considerably higher, being on average 89%, compared to the other shores: Kimmeridge 30%; Lyme Regis 57%. A one-way ANOVA (Table 7.7) showed that mortality on the chalk boulders at Beer was greater than that on the other two shores.

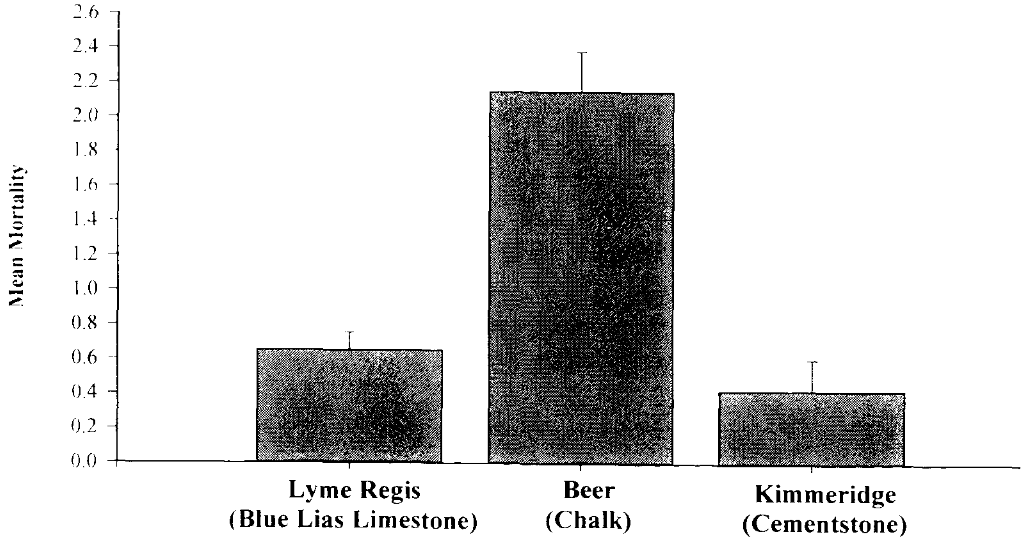


Fig.7.10. Mean mortality of *C. montagui* at MTL on three shores between October 1999 and May 2000. Error bars show +SE. Lyme Regis n = 12 (mean of two patches in Fig 6.6); Beer, n = 8; Kimmeridge, n = 7. Mortality expressed as (Ln no. October 1999 +1) – (Ln no. May 2000 + 1). See text for further details.

Table 7.7 One-way ANOVA of mean mortality of *C. montagui* on three rock types at different locations between October 1999 and May 2000. Mortality expressed as (Ln no. October 1999 +1) – (Ln no. May 2000 + 1).

Source of Variation	**df**	**MS**	***F***	***P***
Rock Type	2	7.16	30	<0.0001
Residual	24	0.24		
TOTAL	26			

SNK Test on rock types: Chalk at Beer (CB); Kimmeridge Cementstone at Kimmeridge (KC); Blue Lias Limestone at Lyme Regis (BL)

Rock Types/Locations	CB > BL = KC
Mean Mortality	2.15 > 0.65= 0.42

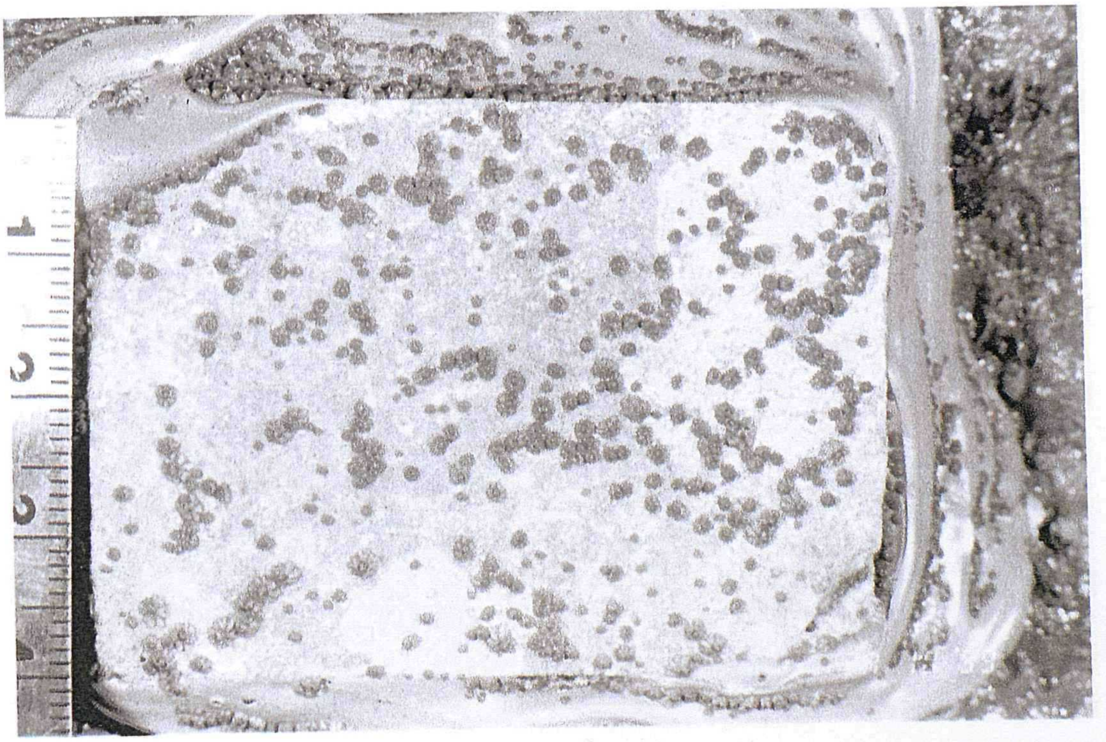


Plate 7.1. *Chthamalus montagui* recruitment on Chalk sample fixed to shore at Lyme Regis on 14th May 1999 and photographed on 27th October 1999. Note also recruitment on resin. Ruler divisions are (mm) See text for more details.

Plate 7.2 Chalk sample as 7.1 above, photographed on 16th May 2000. Ruler divisions are (mm).

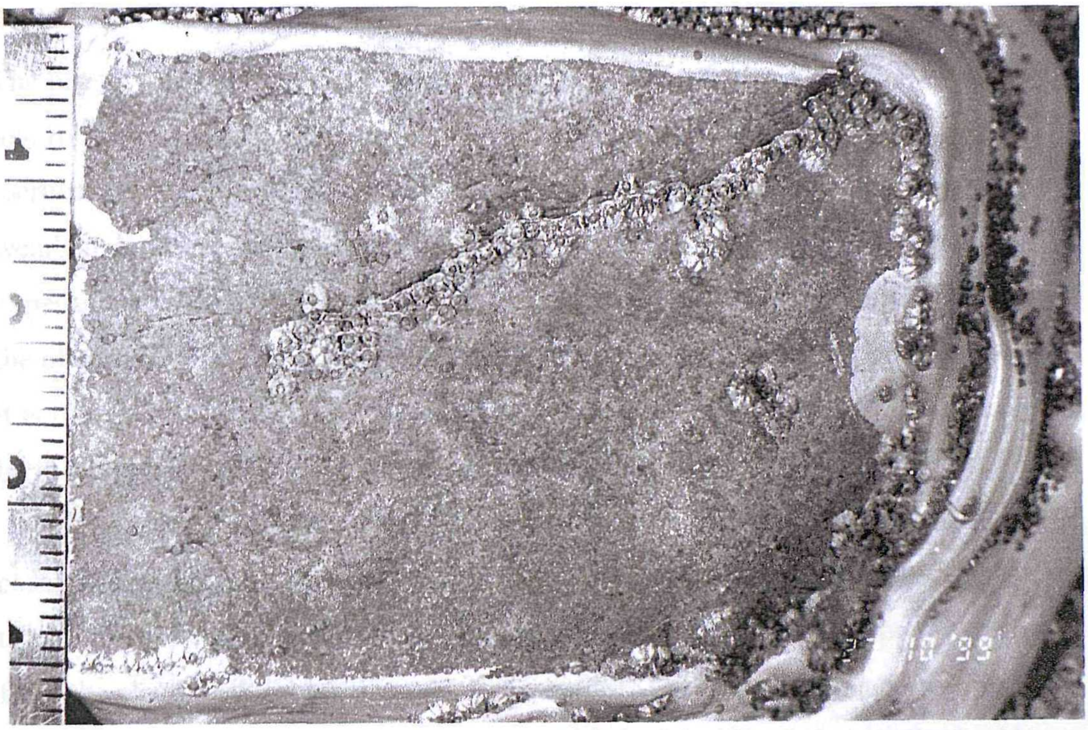


Plate 7.3. *Chthamalus montagui* recruitment on sample of Kimmeridge Cementstone (dolomite) fixed to the shore at Lyme Regis on 14th May 1999 and photographed 27th October 1999. Note recruitment in small crack running from top right of view. Ruler divisions are (mm). See text for more details.

Plate 7.4. Sample of Kimmeridge Cementstone (dolomite) as Plate 7.3 above photographed 16th May 2000. Ruler divisions are (mm). See text for more details.

7.4 Discussion

The primary objective was to determine whether there was any evidence to suggest that rock type could be responsible for the abrupt reduction in adult density and recruitment of *C.montagui* along the Dorset and Isle of Wight coast. Naturally weathered surfaces of important rocks found in the region were therefore used in the experiments. While efforts were made to ensure that samples were comparable with the observed microtopography evident on the shores from which the rocks originated it is possible that differences on a broader scale do exist and that the samples may not be fully representative of larger sections of the coast.

The higher recruitment in the control clearances on the shore at Lyme Regis compared to the Blue Lias samples, although not statistically significant, could be due to attractive chemical and/or biological cues form microbial films or protein residues from the cleared adult barnacles. Thompson *et al.*, (1998) found that *Semibalanus balanoides* cyprids selected filmed surfaces that had previously been colonised by barnacles in preference to unfilmed ones. Yet in field experiments, the proximity of conspecifics and traces of previous barnacle colonisation were found to be more important than cues from microbiota. However the relative importance of each of these might vary according to rock type and other shore variables. In this work, the rock samples were placed on the shore approximately eight weeks prior to the onset of settlement and simultaneous experiments conducted by P.Moschella (University of Southampton) using the same rock types showed that films did colonise these surfaces. After one month of exposure, the abundance of diatoms on the Blue Lias was significantly greater than on the Chalk and Kimmeridge Cementsone, whilst no differences were found between the Chalk and Cementstone. The Bembridge Limestone has not yet been examined (P.Moschella pers.comm).

In this work, surface roughness was found to be a significant factor determining the magnitude of *C. montagui* on the selected rock types, which could therefore account for the low levels of recruitment recorded on the Kimmeridge Cementstone, the smoothest of the rock samples chosen. Surface roughness has long been known to be an important parameter influencing *S.balanoides* settlement (Crisp & Barnes, 1954; Barnes, 1956b). Yet the major differences in settlement on fifteen rock types observed by Holmes *et al.*, (1997) could not all be attributed to variation in roughness; settlement on the smoother igneous and metamorphic rocks such as slate, quartz and marble was greater than the coarser grained rocks of sedimentary origin. They concluded that the finer grained rocks may have a greater heterogeneity of surface mineralogy which aids the antennular adhesive ability of the cyprid larvae. Another related factor discussed by the authors are differences in the sequestration and partitioning of organic and inorganic molecules in the electric double layer on the rock surface. The coarser grained rocks would absorb more compounds than the crystalline metamorphic and igneous rocks, resulting in reduced heterogeneity of surface chemistry. If this was an overriding factor amongst rock types used in this study, then chalk, the most homogenous in terms of surface chemistry, being almost entirely calcium carbonate, would be the least favoured by exploratory cyprids. This however proved not to be the case. With the Kimmeridge Cementstone samples, it is not unreasonable to suppose that oil residues from the underlying shales may have come into contact with the samples. Fortuitously, laboratory experiments on the effect of oil extract from Blackstone oil shale at Kimmeridge have been undertaken on the settlement of *S. balanoides* (Holland *et al,* 1984) and, interestingly, when painted on to slate panels, moderately thick films actually enhanced cyprid settlement.

Working on Mexican shores, differences in settlement and recruitment of *Chthamalus anispoma* on granite and basalt were found by Raimondi (1988). Although settlement and recruitment was much higher on the rougher treatments in his study, the highest overall settlement and recruitment was not on the rocks with the most surface texture, suggesting that the size of holes and pits were larger than those favoured by settling larvae. In this work, despite the strong correlation between surface roughness and recruitment, roughness only accounted for 37% of the variance in recruitment density. Indeed, the highest recruitment was observed on samples of Bembridge Limestone and Blue Lias limestone that had only half the Ra values of other samples. This may be attributed to the short trace length over which the Ra values were determined, or that the textural parameter 'Ra' does not fully describe the preferred scale of microtopography required by settling cyprids. In experiments conducted with *S.balanoides* larvae, Hills *et al.,* (1999) compared settlement on surfaces with different complexity which were mathematically described using both multiscale fractal dimensions (Minkowski fractal dimension, MFD) and an index referred to as 'potential settling sites' (PSS). This Euclidean description of the surface was based upon knowledge of the settlement behaviour, size and morphology of cyprid larvae. The PSS value is the number of symbolic cyprids that can be packed per horizontal 10mm of a scaled printout of the surface profile (Hills & Thomason, 1996). In field experiments, settlement density of *S.balanoides* was found to be positively correlated with both MFD and PSS. However further experiments that involved surface modification which reduced MFD, but not PSS, showed no change in settlement intensity. The authors concluded that the cyprids settle in response to characteristics of surface texture described by PSS. It is quite probable, therefore, that a re-analysis of the surfaces used in this work, to describe PSS, may yield an even better relationship with recruitment of *Chthamalus montagui.* The importance of organism-sized topographical components could be related to a number of different requirements such as a refuge in strong hydrodynamic conditions. Pits and micro-concavities may also facilitate anchorage and cementation to surfaces.

Raimondi (1988) attributed the differences in tidal elevation of Mexican *Chthamalus anisopoma* on basaltic and granite shores to differential post-recruitment mortality. Basalt is smooth, dark and has a lower thermal capacity than granite, and so rock temperatures on basaltic shores were much greater. At high tidal levels, survivorship of *C.anispoma* was significantly less than on granite. In this work, because a time interval of between 19 and 33 days elapsed between examination of the rocks, it is possible that higher cyprid settlement on the smooth darker Kimmeridge Cementstone samples did occur but was quickly killed due to desiccation on the rock surfaces. However on none of the four counts made during the settlement season were spat densities higher than the other rocks in the experiment.

Of the relatively few reported studies on the effect of different rock types on survival of barnacle settlers, most have only considered the initial process of attachment and cementation. Caffey (1982) followed individuals from between 30-60 days post-settlement, after which he regarded the individuals as 'recruits' because they were soon able to breed and were potential prey items. In this work, the recruits were followed for seven months after the end of the settlement season. By May 2000, a significant difference in mortality was found between rock types, although because of heterogeneity of variances it was not possible to determine which treatments differed. Graphical comparisons show considerable variability in mortality between patches, particularly with respect to the chalk and Bembridge Limestone, although this was not statistically significant. No differences were found in the density of gastropod grazers or predators between patch locations, although grazing or predatory activity on the rock samples could not be monitored; differentially attractive microbial film development at one patch could have encouraged higher grazer activity and subsequent bulldozing of newly metamorphosed settlers.

The significant positive correlation between mortality and rock roughness was surprising since survival of newly settled barnacles has been shown to be enhanced by complex surface topography, which could provide a refuge from competitors, predators (Walters & Wethey, 1996) and desiccation stress (Raimondi, 1988). A possible explanation could be that the 'rougher' of the different rock types used in this experiment were also the softest i.e. the chalk and Bembridge Limestone. Insufficient adhesion, undermining and erosion of the surfaces of these softer rocks could have contributed to the higher recorded mortality. Of the two harder rocks, the considerably smoother surface of the Kimmeridge Cementstone, compared to the Blue Lias, may have been responsible for the proportionally higher mortality observed. The darker surface of the Kimmeridge Cementstone, and lower thermal capacity might also cause greater desiccation stress, as Raimondi (1988) found on basalt. Barnacles on smoother rocks may also be vulnerable to higher shear due to the low frequency of cracks, crevices and raised areas that aid anchorage This could be somewhat reduced where the presence of adult barnacles and limpets in the vicinity can provide some shelter. The mortality on the shore at Kimmeridge was significantly less than on the samples of Kimmeridge Cementstone fixed at Lyme Regis. This may be due to lower interspecific interactions, because densities of grazers and dog-whelks are lower at Kimmeridge than on Broad Ledge. It is also possible that greater mortality occurred on the slightly raised fixed samples due to higher shear, compared to that on the shore platform itself. This might be more important on rocks that have smooth surfaces with few textural features than on comparatively rougher rocks like Blue Lias. Recruits monitored on the shore at Kimmeridge were in the close vicinity of adult barnacles and limpets that may have afforded a degree of protection from hydrodynamic shear forces.

In his work on the Australian barnacle *Tesseropora rosea,* Caffey (1982) concluded that there was no consistent effect of rock type on settlement and early survival. In a re-examination and discussion of Caffey's results McGuinness (1989) points out that the effects of rock type varied with time and place, perhaps due to different shore conditions and climate prevailing along the 600km section of coast. In fact unusually hot and dry conditions were recorded on two shores, which caused considerable mortality of new recruits. Thus the effects of different rock type might have been dependent on or over-ridden by climatic conditions prevailing during the period immediately post-settlement.

In the present work, significant differences in recruitment did exist between Kimmeridge Cementstone and other rock types. However it is possible that had simultaneous experiments also been carried out on wave-exposed shores e.g. Portland Bill, then such differences may not have been apparent, or that other interactions between variables may have resulted in a different rank-order of recruitment and/or survival. The main section of Dorset coast along which differences in recruitment of *C. montagui* have been observed is, compared to Caffey's study, relatively short (100km) and consists of alternating bays and headlands. During the summer settlement period, sea-state and air temperatures were very similar. However, winter conditions are very different and it is unlikely that wave-exposed conditions around headlands would in any way have reduced mortality on the softer or smoother rock types.

It is therefore concluded that as far as *Chthamalus montagui* is concerned, recruitment and early survival is influenced by rock type and that the significantly lower recruitment on the Kimmeridge Cementstone samples is largely due to the smooth nature of the rock surface. This will partially explain the low adult density of *C. montagui* observed on the shore at Kimmeridge and preference for the few cracks and crevices that exist. Low annual recruitment due to an unfavouable substratum will further accentuate problems of species colonisation caused by poor larval supply on the east side of Portland Bill. What is still uncertain is whether the cyprids might be present in good numbers within the water column at Kimmeridge but avoid settlement upon exploration of the rock surface because of inadequate settlement sites. Anecdotal evidence from the warden of Kimmeridge Marine Nature Reserve, who has undertaken plankton trawls within the bay, suggests that this is not the case (P.Tinsley pers.comm). Although the density of new recruits on Kimmeridge Cementstone samples fixed to the shore at Lyme Regis was much lower than those of other rock types, it was an order of magnitude greater than on the shore at Kimmeridge. This therefore suggests that although Kimmeridge Cementstone presents a relatively unfavourable substratum to *C. montagui*, a greater larval supply should result in increased barnacle cover, providing mortality is not unusually high. If larval supply to Kimmeridge became consistently greater, then although the rate of recruitment might initially be slow, an increase in adult density would further raise the number of

Potential Settlement sites (PSS) which would accelerate recruitment. The mortality rate may reduce because of the greater number of refuges amongst the growing adult population. Lively & Raimondi (1987) found that isolated individuals were more susceptible to desiccation or thermal stress than those in clusters.

The experiment also raises the question concerning the colonisation of *C. montagui* on chalk shores in the eastern Channel. The empirical evidence suggests that recruitment on chalk is possible and spat densities on the chalk boulders at Beer were between 0.6 and 5.6 per cm^2 (mean 3.2 per cm^2). However it would appear that high post-recruitment mortality would be an important factor limiting the establishment of populations. Despite relatively high recruitment, densities of adult *C. montagui* on the chalk boulders at Beer were on average only 0.1 per cm^2. Apart from the marine erosion of shore platforms, recent work on the bioerosion of chalk shores by limpets along the Sussex coast (Andrews & Williams, 2000) could further limit the species colonisation on this substratum.

Chapter 8

General Discussion

The aim of demographic studies is to predict the future structure of populations. This could be required to aid the management of species of conservation importance, whose extinction may be threatened, or to ensure the sustainable stocks of economically important species (Minchinton & Scheibling,1991). In this work, the major aim is to predict the future population size, structure and distribution of warm-temperate invertebrates on rocky shores in response to climate change (Houghton, 1994; Houghton *et al*, 1995). Earlier surveys and time-series have made it possible to establish the approximate rate of change for a variety of species since the 1930s (Fischer-Piette,1936; Crisp & Southward, 1958; Crisp *et al.*,1981; Southward *et al.*, 1995).

Changes in species abundance

New comparative surveys have been carried out to determine whether changes have occurred since the last major studies in the late 1970s and early 1980s. Particular attention has been given to the barnacles *Chthamalus montagui*, *C. stellatus* and *Balanus perforatus* while other species including the trochid molluscs *Gibbula umbilicalis* and *Osilinus lineatus* and the limpets *Patella depressa* and *P.ulyssiponensis* have been studied in less detail. A hypothesis testing approach was then commenced to investigate the various physical and biological constraints on life cycles suggested by Crisp & Southward (1958) that might be contributory to the discontinuous distribution of these species along the central region of the Channel.

The main findings from the survey work discussed in Chapter 3 were that both *Chthamalus montagui* and *C. stellatus* now occur as far east as Bembridge on the Isle of Wight; 8km and 26km beyond their previously known limits respectively. The abundance of *Chthamalus* appears to have risen on the south coast of the Isle of Wight subsequent to the last surveys in the 1970s, when densities were observed to have dropped since the 1950s. The larger barnacle species *Balanus perforatus* also occurs beyond previously known limits and is now recorded as far as Eastbourne in Sussex, an eastward extension of 75km. The topshell *Gibbula umbilicalis* is still not present east of Bembridge on the Isle of Wight but is now common at Freshwater Bay and frequent at Bembridge, where populations have increased by an order of magnitude over the past decade. The larger, toothed topshell, *Osilinus lineatus,* may be found in similar abundance and localities prior to the severe winter of 1962-63, having recovered from catastrophic mortality (Crisp (ed.) 1964; Hawthorne, 1964). The most eastern record of *Osilinus* during the survey period was at Kimmeridge on the east Dorset coast and 'O'class recruits were seen at Osmington. The population on the west side of Portland may be increasing. Crothers (1994) reports that *Osilinus lineatus* has extended its range eastwards along the Somerset coast by at least 20km over the past 50 years and may still be advancing. Crothers also cites evidence for the eastward extension of *Gibbula umbilicalis* up the Severn Estuary over the same period. The warm-temperate limpet species *Patella depressa* and *P. ulyssiponensis* have not extended beyond previously known localities on the Isle of Wight, yet relatively large populations at Freshwater Bay and St.Catherine's Point remain stable and there is evidence of recent recruitment.

In October 2000 a broad-scale survey was carried out around the Contentin Peninsula on the north coast of France, where the distribution of these species has been similarly followed over the past sixty years (Fischer-Piette,1936; Crisp & Southward,1958; Crisp *et al.*,1981). Similar range extensions were observed (Appendix III). Both *Chthamalus* species may now easily be found at sites near Cherbourg and as far east as Barfleur, 45km beyond previously known limits near Cap de la Hague, excluding the single specimen of *C.montagui* found by A.J.Southward at Cap Blanc Nez near Calais in 1964 (Crisp *et al.,* 1981). These mirror recent changes in nearby Guernsey where the density of *Chthamalus* spp. *Osilinus, Gibbula umbilicalis* and *G.pennanti* appear to have similarly increased (Jory, 1996). On the east coast of the peninsula, *Balanus perforatus* is now abundant at St.Vaast and at Port en Bessin near Omaha Beach. However the sublittoral records from off the port of Dunkirk in 1982 (Davoult *et al.*, 1993) suggest that the species may have been present in the eastern Channel for twenty years. *Osilinus lineatus*, which was previously only known as far east as St.Vaast, where it was rare (Crisp & Southward, 1958), is now abundant at this location and may now be found 35km east at Port en Bessin.

Over the past twenty years and at the end of the warmest decade of the millennium (Jones *et al.*. 1999; Climate Research Unit, 2000) the overall picture in this central region of the Channel is that there have been small to moderate range extensions and population increases of at least one order of magnitude. These changes appear to have been greater on the warmer, south side of the Channel. Of the species studied, *Balanus perforatus* has progressed the furthest on both the English and French side. Conversely, the *Patella* species have shown relatively little change and have not extended their range on either side of the Channel. Yet both *Patella depressa* and *P. ulyssiponensis* are more common at Bembridge now than in the 1980s (S.J.Hawkins pers.comm). On the French side near Cherbourg, densities of *P.depressa* appear to be less now than in the 1950s. Jory (1996) made similar observations of *Patella* spp. on Guernsey.

According to Southward *et al.*, (1995) an abundance of southern species greater than those observed in the 1950s is necessary to show "conclusively" a marine biological response to global warming. Survey work over the past six years shows that levels of *Chthamalus* have not yet generally been exceeded, although mean adult population densities of *Chthamalus* at Brixham in 1996 were the highest recorded in the time series following good recruitment in 1995. Densities have since dropped at Brixham and at the eastern limits of distribution on the Isle of Wight, where the mortality rate has exceeded that of recruitment. The barnacle *Balanus perforatus* appears to have extended its range to the greatest extent and thus it is tempting to conclude that this species is responding the most to climatic change. Yet, from the records and preserved specimens of R.Wells (Portsmouth Grammar School collection), the population at Bembridge on the Isle of Wight appears not to have reached densities that existed in the late 1950s. *Balanus perforatus* died on Isle of Wight shores during the extremely severe winter of 1962-63. (Crisp (ed.),1964; Southward, pers.comm). Deep sub-tidal populations would have survived the cold, and therefore recovery of this species may have been faster than others that are only distributed intertidally. The re-appearance of populations of southern species following the ice winter of 1962-63 (Crisp (ed.),1964), is itself an important indicator of potential future colonisation rates. *Gibbula umbilicalis* populations on the Isle of Wight now appear to be larger than those recorded in the 1950s, with increases of at least an order of magnitude over the past decade.

Of course with these general surveys there is likely to have been considerable variability in the approach made by the various workers involved. At some localities certain species may have been overlooked or their abundance measured or recorded differently. Crisp (1958) warns that records of scarce species will depend as much on the diligence of the observer as on the density of the species. In consultation with A.J.Southward and S.J.Hawkins at Plymouth, attempts have been made to carry out the survey work at locations that match as closely as possible those used in the earlier work. Exceptions include Portland Bill, where other criteria including the siting of photographic stations were important. Many of the general survey methods employed in this and in previous work usually involved placing between five and ten random quadrats at three or four tidal levels. A major development of this technique, which has been used in this work and other barnacle population surveys during the past six years (Benedetti-Cecchi *et al.*, 2000; Jenkins *et al.*, 2000) is a hierarchical sampling approach (Underwood, 1997). Using these techniques a measure of population variance may be established at a range of spatial scales and differences between years can be more confidently be attributed to either genuine inter-annual variations or random population variability. The use of permanent photographic stations was also useful in measuring small-scale changes in species space occupation, recruitment and mortality and their continued use is recommended as pictures can provide important voucher material for future workers.

Occasional surveys, while useful, do not clearly indicate the changes in population demography during the intervening years. A more complete understanding of population dynamics necessitates the kind of annual monitoring undertaken at Cellar Beach on the River Yealm (Southward, 1991). Other sites monitored by A.J.Southward until the mid-1980s were re-visited during this work between 1994 and 1999. Although some of the time-series are incomplete, when the recent surveys were combined with the earlier data a significant inverse correlation was found between densities of *Chthamalus* and *Semibalanus* for Shoalstone Beach near Brixham, Lyme Regis and Osmington Mills in Dorset. When a combined 'Warm Index' was calculated from these barnacle data (Southward, 1991; Chapter 3 of this work) a significant correlation was found between the Warm Index and both Mean Annual and Mean Summer SST one year earlier. The time lag would seem to indicate that it takes from one to two years for *Chthamalus* to reach a size that may be recorded in the count data. Importantly, the data analyses for these more eastern localities support the findings of work carried out in south-west England (Southward *et al.*,1995) that suggests broad-scale climatic influences on species abundance that extend to this central part of the Channel. Between 1995 and 1999 a significant correlation was found between the recruitment of *Chthamalus* and sea temperature for shores in Lyme Bay and two sites in Dorset. The high recruitment of *Chthamalus* observed at the western end of the study area during the warm summer of 1999 was also measured on the Isle of Wight at the extreme limits. The rank-order of recruitment across all the sites showed considerable consistency over the six-year survey period despite the presence of large headlands and unusual tidal phenomena. This would support the idea that sea temperature and / or onshore sea breezes, often associated with warm and settled weather, are of greater importance in determining the magnitude of recruitment than local hydrography.

The measurement of recruitment, used in this work as an estimation of the magnitude of larval supply, has to be interpreted cautiously because it takes no account of post-settlement mortality. Difficulties were encountered at the more eastern localities in finding cyprids or newly calcified recruits to measure post-settlement mortality. Only translocation experiments of a kind developed by O'Riordan (1994) might help resolve this difficulty.

Fluctuations in sea temperature over the past 50 years would appear to have been important in maintaining the coexistence of *Chthamalus* spp. and *Semibalanus balanoides* in this region of the Channel. Dial and Roughgarden (1998) attempt to explain the coexistence of space-limited benthic species with pelagic larvae in terms of the intermediate disturbance hypothesis. Their model considers the potential competitive relationship between a fast growing dominant species (*Balanus*) and a stress-tolerating subordinate (*Chthamalus*). Conventionally, only the benthic stages of a species' life history are considered. For example, Connell (1961a) found evidence for undercutting and overgrowth of the smaller *Chthamalus* (*montagui*) by the faster growing *Semibalanus* (as *Balanus*) and speculated that at high population densities of *Chthamalus* there might be insufficient space for settlement of *Semibalanus*. Intermediate disturbance theory states that at low levels of habitat disturbance, competitively dominant species will exclude subordinates and high levels of disturbance lead to local extinctions. Yet at intermediate levels of disturbance, coexistence is possible that will generally result in higher species diversity. However while disturbance of the rock surface might result in adult mortality and the freeing of potential space for competitors, larval mortality is unaffected. Therefore when applied to species with long-lived propagules, such as barnacles, the theory needs to couple adult and propagule dynamics (Gaines & Roughgarden, 1985; Roughgarden *et al.*, 1988; Dial & Roughgarden, 1998). If sea temperature influences larval output of *Chthamalus* then inter-annual variations in settlement and space occupation might be expected during periods of fluctuating temperatures. This environmental stochasticity (Stephan & Wissel, 1999) could be regarded as 'temporal disturbance'. During the cooler years, *Semibalanus* would occupy higher tidal levels when desiccation effects are reduced and space is available because of low settlement of *Chthamalus*. During warm periods, dense *Chthamalus* occupation would reduce the potential settlement space for *Semibalanus*, which might also suffer higher mortality due to desiccation. If either cool or warm years were frequent then 'disturbance' due to temperature fluctuations would be lessened, resulting in the domination of one or other species. In situations where physical disturbance is constant, species coexistence is therefore determined by the magnitude of settlement and available space. Long-term intermediate levels of recruitment within a particular region will also enable the survival of both species. Over the past decade, *Chthamalus* has been found to be prevalent on shores west of the Isle of Wight where *Semibalanus* is confined to a relatively narrow zone on the lower shore. On the flat reefs at Kimmeridge, *Semibalanus* is now extremely rare if not extinct in some areas, although this may be due to a combination of reduced larval supply and desiccation effects rather than pre-emption by *Chthamalus* as space is readily available. At Osmington Mills near Weymouth an average adult *Chthamalus* density of 2 per cm^2 appears to be maintained by an annual recruitment of between 0.05- 0.1 per cm^2 (5-10 per 100cm^2 quadrat). This would seem to be the minimum recruitment density required to maintain high space occupation (50-100%) between MHWN and LWN, aided by particularly successful years which occurred in 1995, 1997 and 1999. Taken to extremes, if annual temperature fluctuations were too large and frequent then populations of both species might suffer from their inability to maintain large persistent adult populations due to frequent recruitment failure and adult mortality. The 'inconstant' nature of the ecosystem of the western English Channel (Southward, 1980) has probably been responsible for the retention of many Boreal and Lusitanian species that have managed to colonise the area during alternating cool and warm periods.

That higher summer temperatures appear to increase the settlement of *Chthamalus* raises an important question. Why, in the eastern basin of the English Channel, where the highest summer temperatures are attained, is *Chthamalus* so rare or absent? The second theme in this work has attempted to investigate which of the many possible physical and biological constraints on the life cycle of *Chthamalus* and other southern species are particularly important factors setting geographical limits in this region.

Factors setting limits

Several hypotheses were suggested and tested concerned with reproductive development, growth and survival from juvenile to adult stages, interspecific competition with neighbouring species and the effect of rock type on settlement and mortality.

Initial studies on gonad development and subsequent embryonic growth involved the collection and translocation of adult *Chthamalus montagui* from shores in Devon to their current limit at Bembridge on the Isle of Wight. Bembridge, at the extreme eastern end of the Isle of Wight, can be very exposed to cold east winds in the winter that may potentially impair reproductive development of warm-water forms. Yet animals sampled monthly from rock chips fixed to the shore at Bembridge showed that breeding commenced no later and terminated no earlier than further west in the Channel. In some years brooding was more advanced here than at other shores further west. Crisp (1950) undertook similar translocation experiments and found that *Chthamalus* was able to produce embryos in the mantle cavity on some of the coldest shores in England. What is still as yet unknown is the fate of larvae released; the rate of subsequent naupliar development and metamorphosis to cyprid stages, predation rate and duration of the cyprid stage in coastal waters. This could be dependent on sea temperature, food availability, predation intensity or some hitherto unknown factor. Burrows *et al.*, (1992) found some evidence that the rate of development of nauplii was greater at higher temperatures. In this work, the recruitment failure during the cooler summer of 1996 and success in the warmer years support the hypothesis.

While the onset of breeding appears earlier in the warmer years, and larval survival may be greater at higher temperatures, the experiments carried out in this work do not indicate that the breeding and larval development period is currently an important factor setting geographic limits of *Chthamalus* in the English Channel.

The growth rate of *Chthamalus montagui* was investigated to determine whether any inhibition was identifiable as the limits of distribution were approached. Growth could be affected by food availability and/or temperature, which might impair the efficiency of feeding apparatus. Lower growth rate or the attainment of a smaller adult size might diminish competitive ability and resistance to predation, space occupation and the accommodation of embryos in the mantle cavity. The translocation experiments at Bembridge, at the extreme eastern limits of the species, showed that while growth rate of new recruits was reduced over the cold winter period (1995-1996) the size attained by the following summer on control plates in Devon was not significantly different from the translocated individuals. The minimum R-C diameter of 4.5mm necessary for reproduction and retention of embryos in the mantle cavity (O'Riordan, 1992) appears as attainable within the first year of growth at the extreme eastern geographic limits, as it does at sites in the western Channel (Burrows, 1988; Pannacciulli, 1995). The only exception, which might potentially be significant, was the particularly small size attained by the population at Kimmeridge, in east Dorset. While not specifically investigated at Kimmeridge, the generally linear relationship between body size and embryo number

(Burrows, 1988; Burrows *et al.*, 1992; O'Riordan, 1992; this work Chapter 4) may mean that there is a smaller larval release per capita from these animals, assuming number of annual broods is similar to that of other shores. Early brooding was observed here, yet although multiple broods were suspected they were unconfirmed. A low larval production rate at this particular point on the coast may be partially responsible for the critically low recruitment measured further east at Swanage and on the Isle of Wight.

The small size of the Kimmeridge animals was apparent soon after settlement. Although not suggested by the limited data available (Chapter 2), it is possible that growth immediately post-settlement is suppressed by nutrient-poor waters. An alternative and testable hypothesis is that the cyprids arriving on the shore are smaller, either due to poor naupliar development or an exhaustion of food reserves. Gaines & Bertness (1992) found that the lengths of *Semibalanus balanoides* cyprids from open coast habitats were smaller than those that had developed within nutrient-rich embayed habitats. These were used as markers of origin in an attempt to correlate settlement with water transport. Similar investigations between Devon and the Isle of Wight might be fruitful, provided sufficient cyprids can be found.

The results of experiments on the effect of rock type on the recruitment of *Chthamalus montagui* (Chapter 7) showed that the magnitude of recruitment on Kimmeridge Cementstone (dolomite) was significantly less than that on the other rock types investigated. Moreover, these differences were found to be due to the smooth nature of the rock surface, which provides few potential settlement sites for cyprids. That such differences were found when there was high recruitment and likely competition for space shows that this rock surface is particularly unfavourable to *Chthamalus* settlement. Such an unattractive surface can only accentuate problems associated with poor larval supply to the shore at Kimmeridge and contribute to the slow growth of adult populations here. Yet an increase in recruitment rate and the development of a larger adult population will create a more attractive surface because of the greater number of potential settlement sites formed. Each new barnacle that survives till the following settlement season provides surfaces and mini-crevices attractive to cyprids. It is conceivable that adult density on these shores could increase, with consequential increases in larval output when the animals become sexually mature. There is no doubt however that this part of the Purbeck coast, which initially appears to provide an expanse of suitable barnacle habitat, is in fact inimical to *Chthamalus* settlement and creates yet another barrier to the rapid growth of dense adult populations.

The experiments carried out on the Isle of Wight to investigate the severity of interspecific competition for space between *Semibalanus* and both juvenile and adult *Chthamalus* provide no evidence of the undercutting and overgrowth described by Connell (1961a). It would appear that in this region, where *Semibalanus* recruitment is moderate to low and that of *Chthamalus* very low, adequate space is available for both species. Although both adult and juvenile mortality of *Chthamalus* were generally greater on the lower shore within the *Semibalanus* zone, there was no evidence that this was a result of exclusion by the faster growing species. Indeed on the flat reefs at Kimmeridge, where *Semibalanus* is virtually absent, mortality of *Chthamalus* was at least as great as that measured on shores with *Semibalanus,* indicating that predation or relative ease of dislodgement may be of greater importance at these lower tidal levels.

A major part of the fieldwork and monitoring programme was devoted to the measurement of recruitment and mortality of *Chthamalus, Gibbula umbilicalis* and *Osilinus lineatus* along the Channel coast from where adult populations are large, right up to the current eastern limits of distribution. For *Chthamalus*, the work revealed that while recruitment in Lyme Bay was consistently high, there was a sharp reduction of one order of magnitude immediately east of Portland Bill. Recruitment eastwards along the Purbeck coast to Swanage diminished further by approximately two orders of magnitude. Several factors could be responsible for this recruitment gradient and require consideration. From the model presented in Chapter 5 (Table 5.11) there are proportionally fewer recruits per adult reaching the shore at lower adult densities. There could therefore be an Allee-effect (Allee, 1931), as discussed in Chapter 5. Other explanations for the sharp recruitment gradient of *Chthamalus* along the Purbeck coast that have not been investigated are severe offshore larval dispersal, larval predation while in the water column and post-settlement mortality of cyprids. There might also be greater attraction of cyprids to those shores with a higher density of con-specifics. Yet evidence from other studies (Minchinton & Scheibling, 1991; Bertness *et al.*, 1992) suggests that the measurement of recruitment is a useful surrogate for larval supply estimates, so the recruitment pattern, if not the order of magnitude, might still be valid. Clearly, studies of the plankton communities inshore along the coast would be extremely valuable, together with estimates of offshore dispersal. A proposal for this work was submitted during the study period but was not accepted.

The Channel limits of both trochid species *Gibbula umbilicalis* and *Osilinus lineatus* also appear to be set by recruitment failure, however true comparisons between shores are more difficult than for *Chthamalus* because differences between timed searches may be a reflection of the ease of survey and habitat heterogeneity. New techniques, such as the removable boards evaluated in this work, are required. Compared to *Chthamalus* a steeper recruitment gradient was observed for *Gibbula*, as high recruitment densities were obtained along the Purbeck coast within 75km of the geographic limits. The topshells shed male and female gametes into the water, where there is external fertilization. At low population densities, the probability of fertilization will be reduced due to low gamete concentrations in the water column, therefore an Allee-effect may be operative for these species also. The shorter larval life of the trochidae (Fretter & Graham, 1994) will reduce the ease and probability of transport across large sea barriers. Poor larval dispersal is thought to be responsible for the relative rarity of *Osilinus lineatus, Gibbula umbilicalis* and *Littorina littorea* on Lundy Island in the Bristol Channel, compared to the mainland coast of N. Devon (Hawkins & Hiscock,1983) and scarcity of *Patella depressa, Littorina littorea* and *Semibalanus balanoides* on the Scilly Isles compared to the Cornish coast (Crisp & Southward,1958). The Needles Channel must present a similar if not a greater obstacle to trochid larval dispersal from Dorset. Yet over the past decade, densities of *G.umbilicalis* have increased on the Isle of Wight. Compared to earlier work in the 1980s (Kendall & Lewis 1986; Kendall, 1987), higher levels of recruitment of *G. umbilicalis* were also obtained for sites in east Dorset. The precise mechanisms responsible for the observed increases in recruitment remain unclear, yet it is considered by Lewis (1986) that prolonged spawnings may result in better matches between larval production and food supply (Cushing & Dickson, 1976). The population characteristics of animals near their northern limits observed by Kendall (1987) and Kendall *et al.*,(1987) are applicable in places further south wherever recruitment is low. The large adult size attained within these populations is probably a result of rapid growth in consequence of low intraspecific competition for food. Studies of gametogenesis and larval production within these populations would be informative.

The suggestion by Crisp (1989) that tidal fronts and thermal stratification might be influential in setting geographic limits of southern intertidal species is not supported by observations during this study. While thermally mixed water might appear to set limits of *Osilinus lineatus* on the east coast of Ireland. the abundance of the species around the Contentin Peninsula in France contradicts this general view. Along this coast. where there is constantly moving water. turbulent flows and no thermal stratification. there are dense populations of *Osilinus lineatus*. *Gibbula umbilicalis* and *G.pennanti*. which certainly extend as far as St.Vaast on the east coast of the peninsula. These species, which are known to have short larval stages, may however benefit from the almost continuous granite shoreline around the peninsula, with large boulders and plenty of suitable settlement sites. While thermal stratification may enhance larval development and facilitate recruitment, the fronts do not appear impenetrable.

From the evidence obtained during this study, the importance of post-recruitment mortality in setting the geographic limits of *Chthamalus* spp. appears minimal. Even after the relatively cold winter of 1995-96, a large number of recruits survived on the translocated plates and there was no significant mortality in natural populations on the Isle of Wight. Adult mortality at the extreme limits was also low. This is in part consistent with the work of Menge (2000b) who concluded that for *Chthamalus dalli* on the Oregon coast of the USA, post-recruitment processes were generally unimportant in determining adult abundance compared to the magnitude of recruitment. In the present work, although there was evidence of density-dependent mortality at the western sites in the study area, recruitment density was still a generally good predictor of adult density. Minimal mortality over the relatively mild winters was also observed in the trochid populations. Yet Crothers (1998) concludes that winter mortality of new recruits is significant and primarily responsible for setting eastern limits in the Bristol Channel. This agrees with observations reported after the severe winter of 1962-63 that resulted in considerable mortality of *Osilinus* in Britain (Crisp (ed.),1964; Hawthorne,1965).

Although fluctuations in sea temperature appear to have underlain significant changes in species abundance in the west of the study area, the *Chthamalus* and *Gibbula umbilicalis* population front has been relatively stable over the past 40 years and has not extended eastwards beyond the Isle of Wight. Apart from a potential Allee-effect described above, there do not currently appear to be any major biological constraints (reproduction, fitness, growth rate and survival) that could potentially limit the eastward extension of the species on the north side of the Channel between the Isle of Wight and the North Sea. It is quite possible that before an Allee-effect becomes fully operative, physical factors reducing onshore larval supply are critically important. Principal among these must be the reduction in suitable habitat along the Purbeck coast and the region's complex hydrography. The situation around Portland is complex, with gyres forming on both sides of the headland. A gyre off St. Albans Head, the turbulent waters near the Needles off the Shingles Bank, the division of the tidal flow around the Isle of Wight and further strong offshore currents around the south-east of the Island provide additional obstacles for larvae to overcome. The easterly tidal flow of water inshore along the Purbeck coast might be expected to carry large numbers of barnacle larvae to the more eastern shores around Kimmeridge and Swanage, thus enabling potential settlement here. Yet the relatively low recruitment on these shores compared to potential larval output (Table 5.11) indicates that offshore dispersal, or long-term larval retention within gyres, is greater than eastward transport.

These hydrographic barriers, caused largely by complex coastal configurations and prominent headlands such as Portland Bill and Selsey Bill, would also be expected to hinder the westward transport of larvae from the eastern Channel. This was partially investigated by examining the recruitment of *Elminius modestus* and *Semibalanus balanoides* between Beachy Head in Sussex and Berry Head near Brixham in South Devon, again using recruitment as a surrogate for larval supply. Known boundaries of sediment transport cells (Motyka & Brampton, 1993) were used to test the hypothesis that biological propagules might be similarly contained within such cells. The results showed very high recruitment of *Semibalanus* to the east of Selsey Bill and moderately high recruitment to the west of Portland Bill, but very little along the Isle of Wight and Purbeck coast. *Elminius* was mainly confined to the east cell 'Sussex' and *Chthamalus* to the western cell 'Lyme'. This study needs to be repeated to confirm the pattern. However the results support the notion of high and low recruitment cells along the coast where larvae are largely retained or dispersed. Between Selsey Bill and Portland Bill offshore transport appears to be the more dominant process, whereas retention prevails within Lyme Bay and along the Sussex coast. Notable exceptions are off Poole Bay, and in summer between Bembridge and Selsey Bill where long-term larval retention within circular gyres may cause significant barriers to east-west transport (Guyard, 2000).

Techniques in molecular biology, which can provide an indicator of gene flow between localities (Cooksey (ed.)., 1998), could usefully clarify the extent to which these coastal 'cells', separated by physical and hydrographic barriers, are leaky or 'closed systems'. For species with a short larval life, such as *Gibbula umbilicalis and O. lineatus*, there is a probability that prolonged isolation from other populations will result in genetic differentiation and species divergence. Barnacle populations are generally regarded as more open systems where recruitment depends on colonisation from external sources and is independent of 'births' from the parent shore (Roughgarden *et al*, 1985; Todd, 1998; Kent, 2000). It would be useful to determine whether *Chthamalus* larvae arriving on Isle of Wight shores have parental origins on the Isle of Wight, Purbeck coast, Lyme Bay, or even the French coast. This would enable us to test various models of population dynamics. For example it may be appropriate to describe the population of *Chthamalus* at its eastern geographic limits conforming to an 'open metapopulation' (Boorman & Levitt, 1973; Hanski, 1999). This is an adaptation of classic island biogeography theory (MacArthur & Wilson, 1967) where the persistence of populations on islands was shown to be dependent on the rate of colonisation from a mainland source (those nearer to the source population had higher colonisation rates) and the extinction rate, which was greater on the smaller islands. In the current context the various fragmented populations of *Chthamalus* in Weymouth Bay, Kimmeridge and the Isle of Wight, isolated by headlands and hydrographic barriers, are reliant on colonisation from a mainland source habitat - possibly Lyme Bay. Because of large populations and consistently high recruitment in Lyme Bay, extinction here would be infrequent. Extinction on some of the more remote and isolated shores (such as the Isle of Wight) is quite probable, because the recruitment rate is currently low compared to the mortality rate and the intertidal area is small. Allee-effects may cause a metapopulation to go extinct even though suitable habitat is present (Amarasekare, 1998). The Isle of Wight populations could potentially be 'rescued' (Brown & Kodric Brown,1977) as a result of an increasing migration rate (larval supply) from neighbouring shores, should fecundity increase as a result of rising temperatures. However, shores on the Isle of Wight, being on the extreme edge of the species' range, would be more vulnerable due to zero larval supply from the east. It is considered that the reduction of adult *Chthamalus* on Isle of Wight shores since 1992 is largely caused by low and infrequent recruitment below the level necessary to reverse the decline. The higher densities at Hanover Point and Watershoot Bay, present at the start of this investigation, were probably due to a large '*pulse*' of cyprids arriving on the shore in the late 1980s, perhaps during the particularly warm summers of 1989 and 1990. The maintenance and growth of high populations at the species eastern limit will therefore require more consistent and greater recruitment than is occurring currently.

Larval Supply - implications for the community and conservation

Barnacles could be described as 'critical species' on rocky shores (Paine,1994) as their presence is a major determinant of community structure and organisation. A low and infrequent supply of barnacle larvae can influence the structure and composition of communities on rocky shores (Dayton, 1971; Hartnoll & Hawkins, 1985). On moderately exposed rocky shores, the observed patchiness of fucoid algae, limpets and barnacles has been shown to be cyclical; the intrinsic biological processes very often being driven by the intensity of recruitment of one or more species (Hartnoll & Hawkins, 1985; Hawkins *et al.*,1992). A dense settlement of barnacles, followed by post-recruitment survival, can modify grazing interactions because limpets graze very inefficiently over a dense barnacle matrix (Hawkins & Hartnoll,1982b,1983b). Young algal germlings are safe from grazers within a dense barnacle matrix. This can encourage fucoids to 'escape', with the consequence that clumps of *Fucus* plants grow and develop on the shore. These can provide shelter for limpets, dog-whelks and other species. Empty barnacle shells, often common within a dense matrix, may provide an important refuge for smaller grazers such as *Littorina neglecta* (Hawkins *et al.*,1992). A low barnacle larval supply rate, resulting in low adult densities on shores between Portland Bill and Selsey Bill, will therefore favour grazers on rocky shores within the region. This has visibly created much space on these shores above MTL, where fucoids are relatively uncommon and limpets dominant. Good examples being the boulder strewn coast between St.Catherine's Point and Ventnor on the Isle of Wight, Kimmeridge and Peveril Point in Dorset. The extraordinary high density of limpets on chalk shores (e.g. Freshwater Bay) may also be attributable in part to the absence or low density of barnacles at these sites.

If frequent poor larval retention and low recruitment rates were to be confirmed for a variety of rocky shore and subtidal reef species within the Isle of Wight cell then these habitats and species would be particularly vulnerable to anthropogenic disturbance and environmental perturbations. Most of this type of habitat falls within the boundary of the South-Wight Maritime candidate Special Area for Conservation (cSAC) (English Nature, 2000) because of its internationally high conservation value. Should there be widespread damage in the region, re-colonisation rates might be slow due to the relative isolation of these species from high adult populations on the mainland coast. Studies of sublittoral Lusitanian species at their northern limits have highlighted vulnerability due to slow growth rates and infrequent recruitment (Fowler & Laffoley, 1993; Hiscock,1994).

The rate of progression towards the North Sea

So what is the likelihood that these southern invertebrate species might colonise the Sussex coast and the southern North Sea? *Balanus perforatus*, now found east of Beachy Head and able to live subtidally, may already be beyond the Dover Straits. Crisp (1958) estimated that allowing for gregariousness, the critical breeding density of *Elminius modestus* was about 2 per m^2 ('occasional' on the abundance scale of Crisp & Southward, 1958). The critical colonising distance along the north coast of Wales, assuming marginal dispersal, was calculated to be about 48km (see Chapter 1 Fig.1.2 for explanation of terms). Although the viability of larvae has yet to be confirmed, the critical breeding density could be less, since it has been determined that self-fertilization is possible in *Elminius* (Barnes & Barnes,1958). The spread of *Elminius* between 1946-1955 varied between 19.5km and 52km per year depending on location. Interestingly, the lowest rates were recorded eastward from Plymouth, presumably due to the strong westerly residual flow. For *Chthamalus montagui,* bridging the 41km gap between St.Catherine's Point on the Isle of Wight (where the species is 'frequent') and Selsey Bill might seem a reasonable possibility. The duration of the planktonic phase is considered to be at least 18 and possibly 60 days (Burrows, 1988; Burrows *et al.*, 1999b). Assuming no horizontal water movement, to cover the distance would require an eastward rate of transport of between 0.03 and 0.008m.s^{-1}. Yet considering the west-flowing residual currents (Boxall & Robinson, 1987) and formation of a retentive gyre during the summer months between Bembridge and Selsey (Guyard, 2000) the probability of eastward dispersal and colonisation along the Sussex coast is likely to be extremely low. It is also unlikely that the Sussex coast will be colonised by *C.montagui* before there is a major rise in the population at Bembridge on the Isle of Wight, where the species is currently very rare. The successful transport of larvae, eastwards from the Isle of Wight and beyond Selsey Bill, might therefore be very infrequent. Of the two species of *Chthamalus, C. stellatus* is probably the more likely to reach Beachy Head, as there is growing evidence to suggest that it has a longer pelagic phase and is more tolerant of wave exposed coasts (Burrows,1988; Burrows *et al.*,1999b).

Fortuitously, a greater understanding of the colonisation and dispersal of living organisms in this region has been obtained by charting the progress of species introduced as a consequence of intensive shipping movements and world trade.

Crisp (1958) in his report of the spread of the Australasian barnacle *Elminius modestus*, which is thought to have been introduced to the Solent area in the early 1940s, found that Portland Bill was a significant barrier to the westward spread of the species in the English Channel and its colonisation of the eastern part of Lyme Bay. The eastern half of the Channel had already been well colonised by 1946, suggesting that eastward transport presented few problems. However, this species is able to settle on the hulls of boats and can therefore colonise new sites by remote dispersal. Several other factors will have facilitated colonisation: its rapid growth and attainment of sexual maturity during its first season, multiple brooding and self-fertilization capability (Barnes & Crisp,1956) and ability to survive in estuaries and to tolerate low salinities. The close proximity of Selsey Bill to the probable initial adult population centre in Chichester Harbour (Bishop, 1947; Stubbings, 1950) might also have enabled sufficiently high concentrations of larvae to have penetrated eastwards along the Sussex coast. Once around Selsey Bill, the high retention capability of this cell could have enhanced recruitment and population growth.

The arrival of the immigrant Pacific brown alga *Sargassum muticum* presented another opportunity to study the pattern of a species dispersal and colonisation in local waters. The alga was first observed at Bembridge on the Isle of Wight in 1973 (Farnham *et al.*, 1973), although it may have entered the Solent in the late 1960s, as a result of importations of spat of the Japanese oyster *Crassostrea gigas* into French oyster beds (Critchley *et al.*, 1983). The species bears fertile germlings on the frond, yet while a few of these propagules have been recorded 1.5km from the parent plants, most settle just within a few metres (Deysher & Norton, 1982). Long-range dispersal may occur through floating drift fronds that can become fertile en route (Deysher & Norton, 1982). The species will settle on hard substrata in shallow water and rock pools but not on open rock surfaces. The spread of the species throughout the Channel has been reported by Critchley *et al.*, (1983). Although drifting masses were sighted off the Sussex coast within the first two years of the species first record, initial colonists were confined to the east Solent ports and the Isle of Wight. It was not until late in 1976 that plants were found outside the Solent; at Chapmans Pool in Dorset and in the River Yealm, South Devon. Yet by 1981, plants had still not been recorded within Lyme Bay suggesting that Portland Bill was an important barrier to dispersal. The first colonisation east of Selsey Bill was not recorded until 1977 when attached plants were found at Brighton. This delay, so close to the growing population in the eastern Solent, could provide additional evidence for a significant hydrographic barrier between the Isle of Wight and Selsey Bill. The spread along the north coast of France east of the Contentin Peninsula appears to have been more rapid than along the south east coast of England.

Of course for successful colonisation of any species, suitable habitat has to be present. With the exception of *Balanus perforatus*, all the species of prime interest in this study require intertidal rock. Beyond Selsey Bill, which has some hard defences but no extensive rocky shores, the nearest habitat is the chalk platform between Brighton and Beachy Head. Although experiments (Chapter 7) showed that dense recruitment of *Chthamalus montagui* on chalk is possible, subsequent mortality is high. Further construction of sea defences in the eastern Channel, using granite or hard limestone, may provide suitable substrata, yet this may not be of sufficient area to maintain viable populations. As far as the topshells *Gibbula umbilicalis* and *Osilinus lineatus* and limpets *Patella depressa* and *P. ulyssiponensis* are concerned, there appears to be plenty of suitable habitat and recruitment sites along the Sussex coast. All of these species were prevalent on and amongst the fallen chalk boulders at Beer in Devon and, apart from *O.lineatus*, are common on the chalk at Freshwater Bay. The barnacle *Balanus perforatus* was also common on the undersides of chalk boulders at Beer. This species has a calcareous basis and may be more resistant to dislodgement and less vulnerable to desiccation on drying chalk compared to *Chthamalus*, which has a membranous base.

Further work

Although attempts have been made to model the diffusion and dispersal of larvae from an open coast (Barnes & Barnes, 1977; Richards *et al.*, 1995; Eckman, 1996), the complexity of local oceanography necessitates detailed tidal simulation models, combined with wind-forcing scenarios, to fully understand and predict the movements of larvae within the water column. Such studies have recently been attempted on the polychaete *Pectinaria koreni* along the French coast of the eastern Channel (Ellien *et al.*, 2000). Refinements to the tidal circulation models, developed for this region of the Channel (e.g. DHI MIKE21 hydrodynamic program at ABP Research Ltd., Southampton) will become invaluable tools to predict the future colonisation and dispersal of different species. Field studies, to include the enumeration of pelagic larvae, settlement and recruitment on the shore of a variety of species, will aid the calibration of these models and further our understanding of the effects of recruitment variation on the structure of communities. This should also identify regions of particularly low larval supply for a variety of 'critical' and rare species. An important anomaly in the hypothesis that the east Dorset and Isle of Wight coast is a low recruitment cell for intertidal reef species is the limpet *Patella vulgata*, which is ubiquitous along the whole coast. Widespread investigations into the recruitment of this species are particularly desirable.

Studies on the population genetics of species thought to have short pelagic phases (e.g.*Osilinus* and *Gibbula umbilicalis*) may also provide useful information on the frequency of larval transport between different sections of the coast and the extent of isolation between neighbouring bays such as Lyme Bay and Weymouth Bay.

Once larval supply and transport is better understood, the concept of dividing the coast in to cells based on sediment transport characteristics (which currently dominates

Coastal Zone Management within the region) could be usefully extended to include biological processes.

Continued maintenance of the Crisp & Southward time-series will be required to monitor the influence of climate change on rocky shores, both in Britain and in Europe. The methodology should include a hierarchical sampling design, the use of fixed marked quadrats and photographic points. A greater understanding of the general ecology of lesser known species, notably *Balanus perforatus* and *Patella depressa*, would be particularly valuable. Inclusion of other warm-water species in to the monitoring programme, such as the sublittoral barnacle species *Solidobalanus fallax*, recently recorded in British waters (Southward, 1995), would be worthwhile.

Research in to palaeoclimatic conditions, through the examination of mollusc shells in midden deposits, would be interesting. Preliminary studies of limpets and trochids in collections from Isle of Wight have been made.

Conclusions

In summary, there appears to be a hierarchy of factors setting geographic limits for the different species. Although increasing sea temperatures will undoubtedly result in an increase in population size of *Chthamalus* and the other species studied, the rate of eastward progression along the south coast is likely to be very slow. The current constraints upon populations increasing abundance or extending their geographical range eastwards in the Channel to the North Sea are summarised in Table 8.1.

Table 8.1. Importance of probable factors currently limiting the colonisation of selected species on rocky shores near and beyond present eastern geographic limits. Bold typeface denotes High confidence, regular typeface denotes Medium confidence and italics indicate Low confidence.

Factor	***Chthamalus***	***B.perforatus***	***G.umbilicalis***	***O.lineatus***
Breeding Period	LOW	MED	MED	MED
Fecundity	MED	MED	MED	MED
Juv.Winter Mortality	**LOW**	LOW	LOW	MED
Adult Winter Mortality	**LOW**	LOW	LOW	MED
Growth Rate	**LOW**	**LOW**	**LOW**	**LOW**
Competition	**MED**	LOW	**LOW**	**LOW**
Shore Type	**HIGH**	*MED*	MED	MED
Habitat Area	*HIGH*	LOW	MED	MED
Larval Dispersal	*HIGH*	*HIGH*	*HIGH*	*HIGH*

Larval dispersal or the 'uncertainties within the water column' are considered to be the most important factor overall setting geographic limits and causing low recruitment in this region. This might be a result of either offshore dispersal around headlands or long-term retention within re-circulation cells or gyres, with consequent prolonged exposure to predation and mortality prior to settlement. It is considered that Portland Bill must create both a significant physical and hydrographic barrier to eastward larval transport. The long pelagic phase of the barnacles makes them vulnerable to dispersal offshore whereas the shorter larval stages of the molluscs may limit opportunities for dispersal. An extension of the mollusc breeding period due to higher temperatures may facilitate greater recruitment by raising the probability of a better match between larvae and food availability. The importance of winter mortality and exposure to cold weather has been largely deduced from other work (Crisp (ed.), 1964; Kendall,1987; Kendall *et al.*,1987; Crothers,1998) as severely cold weather was not encountered during the study period. The Factor 'Shore Type' includes rock type and presence of suitable recruitment areas; for *Chthamalus* spp., chalk shores on the Sussex coast will not provide a very suitable habitat. Interspecific competition is considered to be relatively unimportant for the trochid species and *B.perforatus*. From experiments conducted on the Isle of Wight and observations in Dorset, interspecific competition between *Chthamalus* and *Semibalanus balanoides* does not appear to limit the size of *Chthamalus* populations. Yet, colonisation of the Sussex coast might prove difficult considering the high recruitment and space occupancy of *S.balanoides* and *Elminius modestus* measured in several areas within this cell.

Should global warming not only result in higher summer temperatures but improve conditions generally conducive to recruitment, then existing populations of these warm-temperate species can be predicted to increase on the south coast of England. The extreme eastern geographic limit, between Portland Bill and Beachy Head, is therefore an important region to monitor the marine environment.

The response of the climate system to global warming may be non-linear and vary considerably over the earth's surface. Increases in the frequency and intensity of Atlantic storms (Knutson *et al.*, 1998; Grevemeyer *et al.*, 2000) might have a negative effect on larval supply and settlement, and the abrasive damage to the shore community could affect species dominance and space occupation. Storms can also break up the retentive properties of seasonal gyres, such as that off Selsey (Guyard, 2000), and therefore increase the possibility of eastward larval transport.

There is a very real possibility of surprises (Houghton *et al.*, 1995). Consequently, changes in marine ecosystems may be similarly unpredictable because of the complexity of species interactions and life cycles. The continuation of physical and biological time-series is thus essential for the construction of accurate models, to both describe and predict environmental change in different regions.

References

Achituv.Y. & Barnes. H. (1976)
Studies in the biochemistry of cirripede eggs V. Changes in the general biochemical composition during development of *Chthamalus stellatus* (Poli). *J.Exp.Mar.Biol.Ecol.*, **22** : 263-267.

Allee.W.C. (1931)
Animal aggregations: a study in general sociology. Univerity of Chicago Press.

Allman. M. & Lawrence, D.F. (1972)
Geological Laboratory Techniques. Blandford Press, Dorset. 335pp.

Amarasekare. P. (1998)
Allee effects in Metapopulation dynamics. *The American Naturalist,* **152** (2):299-302.

Anderson. D.T. (1981)
Cirral activity and feeding in the barnacle *Balanus perforatus* Brugiere (Balanidae), with comments on the evolution of feeding mechanisms in thoracican-cirripedes. *Phil.Trans.Royal.Soc.Lond. B-biological sciences.*, **291** (1053):411-449.

Anderson, D.T (1994)
Barnacles. Structure,function,development and evolution. Chapman & Hall. 357pp.

Andrews. C. & Williams, R.B.G. (2000)
Limpet erosion of chalk shore platforms in southeast England. *Earth surface processes and landforms*, **25** (12):1371-1381

Angel, M.V. (1997)
Pelagic diversity. In: Ormond, R.F.G., Gage, J.D. & Angel, M.V (eds.). *Marine Biodiversity: patterns and processes.* Cambridge University Press. 449pp.

Appleöff. A.(1912)
Invertebrate bottom fauna of the Norwegian Sea and North Atlantic. The depths of the ocean. Murray & Hjort. London.

Ballantine.W.J (1961a)
A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies*,**1**:1-9.

Ballantine. W.J. (1961b)
The population dynamics of Patella vulgata and other limpets. *Ph.D Thesis. Queen Mary College. University of London.*

Barne. J.H.. Robson. C.F.. Kaznowska. S.S.. Doody. J.P. & Davidson. N.C.. (eds.) (1996a)
Coasts and seas of the United Kingdom. Region 9: Southern England: Hayling Island to Lyme Regis. Joint Nature Conservation Committee. (Coastal Directories Series) Peterborough.

Barne. J.H.. Robson. C.F.. Kaznowska. S.S.. Doody. J.P. & Davidson. N.C.. (eds.) (1996b)
Coasts and seas of the United Kingdom. Region 10: South-West England: Seaton to Roseland Peninsula. Joint Nature Conservation Committee. (Coastal Directories Series) Peterborough.

Barne. J.H.. Robson. C.F.. Kaznowska. S.S.. Doody. J.P.. Davidson. N.C. & Buck. A.L. (eds.) (1998).
Coasts and seas of the United Kingdom. Region 8: Sussex: Rye Bay to Chichester Harbour. Joint Nature Conservation Committee. (Coastal Directories Series) Peterborough.

Barnes. H. (1955)
The growth rate of *Balanus balanoides* (L.) *Oikos.* **6** (2):109-113.

Barnes, H. (1956a)
The growth rate of *Chthamalus stellatus* (Poli). *J.Mar.Biol.Ass.UK.*, **35** : 355-361.

Barnes, H. (1956b)
Surface roughness and the settlement of *Balanus balanoides* (L.) *Archivum Societatis Zoologicae Botanicae Fennicae Vananmo*, **10**:164-168.

Barnes, H. (1972)
The seasonal changes in body weight and biochemical composition of the warm-temperate cirripede *Chthamalus stellatus* (Poli). *J.Exp.Mar.Biol.Ecol.*, **8** :89-100.

Barnes, H. & Barnes, M. (1958).
Further observations on self-fertilisation in *Chthamalus* sp. *Ecology*, **39** (3) : 550.

Barnes, H. & Barnes, M. (1965)
Egg size, nauplius size and their variation with local geographical and specific factors in some common cirripedes. *J.Animal Ecology*, **34** : 391-402.

Barnes, H. & Barnes, M. (1966)
The recovery of *Chthamalus stellatus* from the effects of the severe winter of 1962-63 on the shores of Pornic, France. *Cahiers de Biologie Marine*, **7** :247-249.

Barnes, H. & Barnes, M. (1968)
Egg numbers, metaboloic efficiency of egg production and fecundity; local and regional variations in a number of common cirripedes. *J.Exp.Mar.Biol.Ecol.*, **2** : 135-153.

Barnes, H. & Barnes, M. (1977)
The importance of being a littoral nauplius, In: *Biology of benthic organisms: Proc. 11th Eur.Mar.Biol.Symp.*(eds.) B.F.Keegan, P.O'Ceidigh & P.J.S. Boadan. Oxford.Pergamon Press.

Barnes, H. & Crisp, D.J. (1956)
Evidence of self-fertilization in certain species of barnacles. *J. Mar.Biol.Ass.UK.*, **35** : 631-639.

Barnes, H. & Klepal,W. (1971)
Observations on the form and changes in the accessory droplet and motility of the spermatozoa of some cirripedes. *J.Exp.Mar.Biol. Ecol.*, **7**:173-196

Barnes, H. & Powell, H.T. (1950)
The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides* after a heavy initial settlement. *J.Animal. Ecol.*, **19**:175-179

Bassindale, R. (1936)
The developmental stages of three English barnacles, *Balanus balanoides*, (Linn.), *Chthamalus stellatus* (Poli.) and *Verruca stroemia* (O.F.Muller.). *Proc. zool. Soc. Lond.*, **106** : 57-73.

Benedetti-Cecchi, L., Acunto, S. Bulleri, F., & Cinelli, F. (2000)
Population ecology of the barnacle *Chthamalus stellatus* in the northwest Mediterranean. *Mar.Ecol.Prog.Ser.*, **198**:157-170.

Bertness, M.D., Gaines, S.D.,Bermudez, D. & Sanford, E. (1991)
Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Mar.Eco.Prog.Ser.*, **75**:91-100.

Bertness, M.D., Gaines, S.D., Stephens, E.G. & Yund, P.O. (1992)
Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus.) *J. Exp. Mar.Biol. Ecol.*, **156** : 199-215.

Bertness, M.D., Gaines, S.D. & Wahle, R.A. (1996)
Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar. Ecol. Prog. Ser.*, **137**:103-110

Bertness, M.D., Gaines, S.D. & Yeh, S.M. (1998)
Making mountains out of barnacles: The dynamics of acorn barnacle hummocking. *Ecology*, **79**: (4) 382-1394.

Bishop, M.W.H. (1947)
Establishment of an immigrant barnacle in British waters. *Nature*, **189**:1145.

Bode, A., Lombas, I. & Anadon, N. (1986)
The reproduction and population dynamics of *Monodonta lineata* and *Gibbula umbilicalis* (Mollusca,Gastropoda) on the central coast of Asturias (Spain). *Hydrobiologia*, **142**:31-39.

Boorman, S.A. & Levitt, P.R. (1973)
Group selection on the boundary of a stable population. *Theoretical population biology*, **4**:85-128.

Bowman, R.S. (1981)
The morphology of *Patella* spp. juveniles in Britain, and some phylogenetic inferences. *J. Mar.Biol. Ass.UK.*, **61** : 647-666.

Bowman, R.S. & Lewis, J.R. (1986)
Geographical variation in the breeding cycles and recruitment of *Patella* spp. *Hydrobiologia*, **142**:41-56.

Boxall, S.R. & Robinson, L.S. (1987)
Shallow sea dynamics from CZCS Imagery. *Advances in Space Research*, 7:37-46.

Briggs, J.C. (1974)
Marine Zoogeography. McGraw & Hill. New York.

Bray, S. & Herbert, R.J.H. (1998)
A reassessment of populations of the dog-whelk (*Nucella lapillus*) on the Isle of Wight following legislation restricting the use of TBT antifouling paints. *Proc. Isle. Wight. nat. Hist. archaeol Soc.*, **14** :23-40.

Brown, J.H. & Kodric-Brown, A. (1977)
Turnover rates in insular biogeography:effect of immigration and extinction. *Ecology*, **58**:445-447.

Bruce, P. (1989)
Inshore along the Dorset Coast. First Edition. Boldre Marine, Lymington, Hampshire.

Bruce, P. & Watson, G. (1998)
Tidal Streams between Portland Bill and St. Albans Head. Boldre Marine, Lymington, Hampshire.

Bryan, G. W., Gibbs, P.E., Hummerstone, L.G. & Burt, G.R. (1986)
The decline of the gastropod *Nucella lapillus* around South-West England: Evidence for the effect of Tributlytin from antifouling paints. *J Mar.Biol. Ass.UK.*, **66**: 611-640.

Burrows, M.T. (1988)
The comparative biology of *Chthamalus stellatus* (Poli.) and *Chthamalus montagui* Southward. *Ph.D thesis. University of Manchester.* 319pp.

Burrows, M.T., Hawkins, S.J. & Southward, A.J. (1992)
A comparison of reproduction in co-occuring chthamalid barnacles *Chthamalus stellatus* (Poli.) and *Chthamalus montagui* Southward. *J.Exp. Mar.Biol.Ecol.*, **160** (2) : 229-249.

Burrows, M.T., Kawai, K. & Hughes, R.N. (1999a)
Foraging by mobile predators on a rocky shore: underwater TV observations of movements of blennies *Lipophrys pholis* and crabs *Carcinus maenas*. *Mar.Ecol. Prog. Ser.*, **187**:237-250.

Burrows, M.T., Hawkins, S.J. & Southward, A.J. (1999b)
Larval development of the intertidal barnacles *Chthamalus stellatus* and *Chthamalus montagui*. *J.Mar.Biol.Ass.UK.*, **79**:93-101

Cabioch, L., Gentil, F.,Glaçon, R. & Retière, C. (1977)
Le macrobenthos des fonds meubles de la Manche:distribution génerale at écologie. In: *Biology of benthic organisms*. Keegan, B., O'Ceidigh, P. & Boaden, J. (eds.), Pergamon Press, 115-128.

Caffey, H.M. (1982)
No effect of naturally-occurring rock types on settlement or survival in the intertidal barnnacle *Tesseropora rosea* (Krauss.) *J.Exp.Mar. Biol.Ecol*, **63** : 119-132.

Caffey, H.M. (1985)
Spatial and temporal variation in settlement and recruitment of intertidal barnacles *Ecol. Monogr*, **55** : 313-332.

Chelazzi, G., Hughes, R.N., Myers, A., Hawkins, S.J., Aberg, P. (1997)
Interactions of physical and biological factors in the surf and swash zone of European rocky shores. EUROROCK first year report, 1/2/1996-31/1/1997.

Climate Diagnostics Centre (2000) website, www.cdc.noaa.gov

Climate Research Unit (2000) website, www.cru.uea.ac.uk

Collins, K.C., Herbert, R.J.H. & Mallinson, J.J. (1990).
The Marine Flora & Fauna of Bembridge and St. Helens, Isle of Wight. *Proc. Isle. Wight. nat. Hist. archaeol. Soc.*, **9** : 41-85.

Connell, J.H. (1961a)
The influence of interspecific competion and other factors on the barnacle *Chthamalus stellatus*. *Ecology*, **42** (4) : 710-723.

Connell, J.H. (1961b)
Effect of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.*, **31**: 61-104.

Connell, J.H. (1985)
The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J.Exp. Mar.Biol.Ecol.*, **93** : 11-45.

Cooksey, K.E. (ed.) (1998)
Molecular approaches to the study of the ocean. Chapman & Hall. 549pp.

Crisp, D.J. (1950)
Breeding and distribution of *Chthamalus stellatus*. *Nature*. **166** :311-312.

Crisp, D.J. (1954)
The breeding of *Balanus porcatus* (Da Costa) in the Irish Sea. J.*Mar.Bio. Ass.UK.*, **33**:473-496.

Crisp, D.J. (1956)
A substance promoting hatching and liberation of young in Cirripedes. *Nature*. **178**:263.

Crisp, D.J. (1958)
The spread of *Elminius modestus* Darwin in North-West Europe. *J. Mar. Biol.Ass.UK.*, **37**:483-520.

Crisp, D.J. (1959)
Factors influencing the time of breeding of *Balanus balanoides*. *Oikos*, **10** : 275-289.

Crisp, D.J. (1960)
Factors influencing growth-rate in *Balanus balanoides*. *J. Animal. Ecol.*, **29**: 95-116.

Crisp, D.J. (1961)
Territorial behaviour in barnacle settlement. *J.Exp Biol.*, **38**: 429-446.

Crisp, D.J. (ed.) (1964)
The effects of the severe winter of 1962-63 on marine life in Britain. *J.Animal Ecology*, **33** :165-210.

Crisp, D.J (1974)
Factors influencing the settlement of marine invertebrate larvae. In: Grant,P.T., Mackie, A.M (eds.). *Chemoreception in marine organisms*. Academic Press, London pp 177-267.

Crisp, D.J. (1976)
Settlement responses in marine organisms. In: Newell, R.C (ed.) *Adaptations to environment: essays on the physiology of marine animals*. Butterworths, London.

Crisp, D.J. (1989)
The influence of tidal fronts on the distribution of intertidal fauna and flora. *Scient. Mar.*, **53**(2-3):283-292.

Crisp, D.J. & Barnes, H.B (1954)
The orientation and distribution of barnacles at settlement with particular reference to surface contour. *J.Anim.Ecol.*, **23**:142-162.

Crisp, D.J. & Bourget, E. (1985)
Growth in barnacles. *Advances in Marine Biology*, **22**:199-244.

Crisp, D.J. & Davies, P.A. (1955)
Observations in vivo on the breeding of *Elminius modestus* grown on glass slides. *J. Mar. Biol. As.UK.*, **34**: 357-380

Crisp, D.J. & Knight-Jones, E.W. (1954)
Discontinuities in the distribution of shore animals in North Wales. *Bardsey Observatory rep.*, 29-34.

Crisp, D.J. & Meadows, P.S. (1963)
The chemical basis of gregariousness in cirripedes. *Proc.R..Soc.Lond.B*, **156**: 500-520.

Crisp, D.J. & Patel, B. (1961)
The interaction between breeding and growth rate in the barnacle *Elminius modestus* Darwin. *Limnology & Oceanography*, **6** (2): 105-115.

Crisp, D.J. & Southward, A.J. (1953)
Isolation of intertidal animals by sea barriers. *Nature*, **172** : 208-209.

Crisp, D.J. & Southward, A.J. (1958)
The distribution of intertidal organisms along the coasts of the English Channel. *J. Mar.Biol. Ass. UK.*, **37**:157-208.

Crisp, D.J. & Southward, A.J. (1961)
Different types of cirral activity of barnacles. *Phil. Trans. R. Soc.B*, **243**: 271-308.

Crisp, D.J., Southward, A.J. & Southward, E.C. (1981)
On the distribution of the intertidal barnacles *Chthamalus stellatus*, *Chthamalus montagui* and *Euraphia depressa*. *J. Mar.Biol.Ass. UK.*, **61**: 359-380.

Critchley, A.T., Farnham,W.F. & Morrell, S.L. (1983)
A chronology of new European sites of attachment for the invasive brown alga, *Sargassum muticum*, 1973-1981. *J.Mar.Biol.Ass.UK.*, **63**:799-811.

Crothers, J.H. (1985)
Dog-whelks: an introduction to the biology of *Nucella lapillus* (L.).*Field Studies*, **6**:2 91-360.

Crothers, J.H. (1994)
Student investigations on the population structure of the commmon topshell *Monodonta lineata* on the Gore, Somerset. *Field Studies*, **8**: 337- 355.

Crothers, J.H. (1998)
A hot summer, cold winters, and the geographical limit of *Trochocochlea lineata* in Somerset. *Hydrobiologia*, **378**:133-141.

Cushing, D.H. & Dickson, R.R. (1976)
The biological response in the sea to climatic changes. In: *Advances in marine biology* (ed.F.S Russell and M.Yonge), **14**: 1-122 London: Academic Press

Daguzan, J. (1991)
Research on the growth and ecology of *Monodonta lineata* (Da Costa) (Gastropoda, Prosobranchia, Trochidae) living on the Atlantic coast of Brittany. *Cahiers de Biologie Marine*, **32** (1): 3-22.

Darwin, C. R. (1854)
A Monograph on the Sub-Class Cirripedia..The Balanidae, The Verrucidae, etc. Ray Society, London.

Dando, P.R. & Southward, A.J. (1980)
A new species of *Chthamalus* (CRUSTACEA:CIRRIPEDIA) characterized by enzyme electrophoresis and shell morphology: with a revision of other species of *Chthamalus* from the western shores of the Atlantic Ocean. *J. Mar. Biol. Ass. UK.*, **60**: 787-831.

Dando, P.R. & Southward, A. J. (1981)
Existence of 'Atlantic' and Mediterranean' forms of *Chthamalus montagui* (Crustacea: Cirripedia) in the Western Mediterranean. *Mar. Biol. Lett.*, **2** :239-248.

Dando, P.R., Southward, A. J. & Crisp, D.J. (1979)
Enzyme variation in *Chthamalus stellatus* and *Chthamalus montagui* (Crustacea:Cirripedia) : evidence for the presence of *C. montagui* in the Adriatic. *J. Mar.Biol.Ass.UK.*, **59**: 307-320.

Davoult, D., Dewarumez, J-M., & Glaçon, R. (1993)
New additions to macrobenthic species from the French coasts of the eastern English Channel and North Sea (4): Miscellaneous groups. *Cahiers de Biologie Marine*, **34** (1):55-64.

Dayton, P.K. (1971)
Competition, disturbance and community organisation: The provision and subsequent utilisation of space in a rocky intertidal community. *Ecol. Monogr.*, **41** (4): 351-389

Denley, E.J. & Underwood, A.J. (1979)
Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *J.Exp Mar.Biol.Ecol.*, **36** :269-293.

Desai, B.N. (1966)
The biology of *Monodonta lineata* (da Costa). *Proc.malac.Soc.Lond.*, **37**:1-17.

De Wolf, P. (1973)
Ecological observations on the mechanism of dispersal of barnacle larvae during planktonic life and settling. *Neth. J. Sea.Res.*, **6** :1-129.

Deysher, L. & Norton,T.A. (1982)
Dispersal and colonisation in *Sargassum muticum* (Yendo) Fensholt. *J.Exp.Mar.Biol.Ecol.,* **56**:179-195.

Dial, R. & Roughgarden, J. (1998)
Theory of marine communities: The intermediate disturbance hypothesis. *Ecology,* **79** (4):1412-1424.

Durrance, E.M. & Laming, D.J.C. (Eds) (1982)
The Geology of Devon. University of Exeter Press.

Dyer, J.J. & King, H.L. (1975)
The residual water flow through the Solent, southern England. *Geophys. J.R.Astra.Soc.,* **42**:97-106.

Eckman, S. (1953)
Zoogeography of the sea. Sidgewick and Jackson. London. 417pp.

Eckman, J.E. (1996)
Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *J.Exp.Mar.Biol.Ecol.,* **200**: 207-237.

Ellien, C., Barney, A.S., Dauvin, J.C., Gentil, F. & Salomon, J.C. (2000)
The influence of variability in larval dispersal on the dynamics of a marine metapopulation in the eastern Channel. *Oceanol.Aacta.,* **23** (4): 423-442.

Elton ,C. S, (1927)
Animal Ecology. London: Sidgewick & Jackson.

English Nature, (2000)
South Wight Maritime European Marine Site. English Natures's draft advice given under Regulation 33(2) of the Conservation (Natural Habitats &c.) Regulations 1994. Consultation draft. November 2000.

Evans, R.G. (1953)
Studies on the biology of British limpets - the genus *Patella* on the south-coast of England. *Proc. zool. Soc. Lond.,* **132** : 357-376.

Farnham,W.F., Fletcher, R.K. & Irvine, L.M. (1973)
Attached *Sargassum* found in Britain. *Nature,* **243**:231-232.

Fischer-Piette, E. (1935)
Systématique et biogéographie. Les Patelles d'Europe et Afrique du Nord. *Journal de conchyliologie,* **78**:5-66

Fischer-Piette, E. (1936)
Etudes sur la biogéographie intercotidale des deux rivers de la Manche. *J. Linn. Soc. (Zool.),* **40** :181-272

Fischer-Piette, E. (1941)
Observations biométriques sur les Patelles de la Manche. *Journal de conchyliologie,* **84**:300-306.

Fischer-Piette, E. (1948)
Sur les éléments de prospérité des Patelles et leur specificité. *Journal de conchyliologie,* **88**: 45-96.

Fischer-Piette, E. (1955)
Repartition, le long des cotes septentrionales de l'Espagne,des principal especes peuplant les rochers intercotidaux. *Ann.Inst.Ocean.,* **31**:37-124.

Forbes, E. & Goodwin-Austen, R. (1859)
The natural history of the European seas. London,Van Voorst.

Fowler, S. & Laffoley, D. (1993)
Stability in Mediterranean-Atlantic sessile epifaunal communities at the northern limits of their range. *J. Exp. Mar. Biol. Ecol.*, **172** : 109-127.

Fretter, V.& Graham, A. (1994)
British Prosobranch Molluscs (2nd Edition), Ray Society, London

Gabbott, P.A. & Larman, V.N. (1987)
The chemical basis of gregariousness in cirripedes: A review (1953-1984). In: Southward, A.J. (ed). (1987) *Barnacle biology. Crustacean Issues.* A.A. Balkema, Rotterdam.

Gaines, S.D., Brown, S. & Roughgarden, J. (1985)
Spatial variation in larval concentrations as a cause of spatial variation in settlemnt for the barnacle *Balanus glandula. Oecologia*, **67**:267-272.

Gaines, S.D. & Roughgarden, J. (1985)
Larval settlement rate: a leading determinant of structure in ecological communities of the marine intertidal zone. *Proc. Natl. Acad. Sci. U.S.A.*, **82** : 3707-3711.

Gaines, S.D. & Bertness, M.D. (1992)
Dispersal of juveniles and variable recruitment in sessile marine species.
Nature, **360**: 579-580.

Garwood, P.R. & Kendall, M.A. (1985)
The reproductive cycle of *Monodonta lineata* and *Gibbula umbilicalis* on the coast of Mid-Wales.
J.Mar.Biol.Ass.UK., **65**: 993-1008.

George, J.D.,Tittley, I., & Price, J.H. (1989)
Macrobenthos of chalk shores in the Isle of Wight, Dorset and Devon. Report to the Nature Conservancy Council, CSD Report No.931.BM (NH) London, 111pp.

Geraci, S. & Romairone,V. (1986)
Larval stages and *Balanus* (Cirripedia) settlement in a port environment with a key to naupliar stages of Tyrrhenian species. *P.S.Z.N.I Marine Ecology*, 7 (2):151-164.

Gibbs, P.E., Bryan, G.W., Pascoe, P.L. & Burt, G.R. (1987)
Reproductive failure in populations of the dog-whelk *Nucella lapillus* caused by tributyltin from antifouling paints. *J. Mar.Biol. Ass. UK.*, **66**: 767-777.

Grant, A., Morgan, P.J. & Olive, P.J.W (1987)
Use made in marine ecology of methods for estimating demographic parameters from size-frequency data. *Mar Biol.*, **95**:201-208.

Grevemeyer, I, Herber, R, & Essen, H.H. (2000)
Microseismological evidence for a changing wave climate in the northeast Atlantic Ocean. *Nature*, **408** (6810): 349-352.

Groom,T.T. (1894)
On the early development of the Cirripedia. *Phil. Trans. Roy. Soc.* (B), **185** : 119-212.

Grubb, V.M. (1936)
Marine algal ecology and the exposure factor at Peveril Point, Dorset. *J.Ecol.* **24** : 392-423.

Gueguениat, P., Bailly du Bois, P., Salomon, J.C., Mason, M. & Cabioch, L. (1995)
FLUXMANCH radiotracers measurements: A contribution to the dynamics of the English Channel and North Sea. *J.Marine Systems*, **6**:483-494.

Guyard. P.H. (2000)
Effects of oceanographic factors in the mesozooplanktonic communities of the east Solent and outer approaches. *Ph.D Thesis. School of Ocean & Earth Sciences, University of Southampton.*

Hall, C.A. (1964)
Shallow-water marine climates and molluscan provinces. *Ecology*, **45** (2): 226-234.

Hanski, I. (1999)
Metapopulation ecology. Oxford University Press.313pp.

Hartnoll, R.G. & Hawkins, S.J. (1985)
Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia*, **24** :53-63.

Hatch, D.J. (1977)
The inter-relationships of three *Patella* spp. on the south coast of Britain. *Ph.D Thesis. University of Southampton.*

Hatton, H. (1938)
Essais de bionomis explicative sur quelques especes intercotidales d'algues et d'animaux. *Ann. Inst. Oceanogr. Monaco.*, **17**: 241-348.

Hawkins, S.J. (1983)
Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *J. Exp. Mar. Biol. Ecol.*, **62**, 271-283.

Hawkins, S.J. & Hartnoll,R. (1982a)
Settlement Patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977-1981)
J. Exp. Mar. Biol. Ecol. **62** : 271-283.

Hawkins, S.J. & Hartnoll, R. (1982b)
The influence of barnacle cover on the numbers, growth and behaviour of *Patella vulgata* on a vertical pier. *J.Mar.Biol.Ass.UK.*, **62**: 865-867.

Hawkins, S.J. & Hartnoll, R.G. (1983a)
Changes in a rocky shore community: an evaluation of monitoring. *Marine Environmental Research*, 9:131-181.

Hawkins, S.J. & Hartnoll, R.G. (1983b)
Grazing of intertidal algae by marine invertebrates. *Oceanogr.Mar.Biol.Ann.Rev.*, **21**:265-271.

Hawkins, S.J. & Hiscock, K. (1983)
Anomalies in the abundance of common eulittoral gastropods with planktonic larvae on Lundy Island, Bristol Channel. *J. Molluscan. Studies.*, **50** : 86-88.

Hawkins, S.J. & Southward, A.J. (1992)
The Torrey Canyon oil spill: recovery of rocky shore communities. In : *Restoring the Nations Environment*. Thayer, G.W. (ed.) Maryland Sea Grant, Maryland. pp583-631.

Hawkins S.J., Hartnoll, R.G., Kain, J.M. & Norton, T.A. (1992)
Plant-animal interactions on hard substrata in the north-east Atlantic. In: John, D.M., Hawkins, S.J. & Price, J.H. (eds.*) Plant-Animal Interactions in the Marine Benthos*. Systematics Association Special Volume No.46. Clarendon Press.Oxford.

Hawthorne, J.B. (1964)
Death of Marine Organisms in Dorset during February 1963. *Proc.Dorset. Nat. Hist. Arch. Soc*, **85** : 87-90.

Hawthorne. J.B. (1965)
The eastern limit of distribution of *Monodonta lineata* (da Costa) in the English Channel. *J. Conch.* **25** : 348-352.

Hawthorne. J. B (1966)
The limitation of the distribution of Monodonta lineata (da Costa) on the English Channel shore of Dorset. *M.Sc. Thesis. University of London.*

Hays. J.D., Imbrie, J. & Shakleton, N.J. (1976)
Variations in the earth's orbit: pacemaker of the ice ages. *Science,* **194**:1121-1132

Herbert, R.J.H. (1989)
A survey of the Dog-whelk *Nucella lapillus* (L.) around the coast of the Isle of Wight. *Proc. Isle. Wight. nat. Hist. archaeol. Soc..* **8** (3): 15-21.

Herbert. R.J.H. (1991).
Isle of Wight Marine Biological Report for 1989 and 1990. *Proc. Isle. Wight. nat. Hist. archaeol. Soc.,* **10** : 31-34.

Herbert, R.J.H. (1994).
Isle of Wight Marine Biological Report 1992. *Proc. Isle. Wight. nat. Hist. archaeol. Soc.,* **12** : 77-80.

Herbert, R.J.H. (1997)
Isle of Wight Marine Biological Reports 1993-1995. *Proc. Isle. Wight. nat. Hist. archaeol. Soc.,* **13** : 83-89.

Herbert. R.J.H. (2000)
Isle of Wight Marine Biological Report 1999. *Proc. Isle. Wight. nat. Hist. archaeol Soc.,* **16** : 91-92.

Herbert. R.J.H., Bray, S. & Hawkins, S.J.H. (2000)
Use of the Dog-whelk *Nucella lapillus* as a Bio-Indicator of Tributyltin (TBT) Contamination in the Solent and around the Isle of Wight: 307-310. In: Collins, M. & Ansell, K. (eds.) *Solent Science - a review.* Proceedings in Marine Science (1).Elsevier.

Hills. J.M. & Thomason, J.C. (1996)
A multi-scale analysis of settlement density and pattern dynamics of the barnacle, *Semibalanus balanoides. Mar.Ecol.Prog. Ser.,* **138**:103-115.

Hills. J.M., Thomason. J.C. & Muhl, J. (1999)
Settlement of barnacle larvae is governed by Euclidean and not fractal surface characteristics. *Functional Ecology,* **13** (6): 868-875.

Hines. A.H. (1978)
Reproduction in three species of intertidal barnacles from central California. *Biological Bulletin.* Marine Biological Laboratory, Woods Hole, Massachusetts. **154**: 262-281.

Hiscock. K. (1994)
Marine communities at Lundy - origins. longevity and change. *Biol.Journal.Linnean. Soc..* **51**:183-188.

Hiscock. K. (1998)
Introduction and Atlantic-European perpective: 3-70. In: Hiscock. K. (ed.) *Marine nature Conservation Review. Benthic marine ecosystems of Great Britain and the north-east Atlantic.* Peterborough. JNCC. (Coast and seas of the UK. MNCR series).

Holland. D.L., Crisp. D.J., Huxley. R. & Sisson. J. (1984)
Influence of oil shale on intertidal organisms: Effect of oil shale extract on settlement of the barnacle *Balanus balanoides* (L.). *J. Exp. Mar. Biol. Ecol.* **75** : 245-255.

Holligan, P.M. (1981)
Biological implications of fronts on the northwest European continental shelf. *Phil. Trans. R. Soc. Lond.* A., **302**: 547-562.

Holm. E.R. (1990)
Effects of density-dependent mortality on the relationship between recruitment and larval settlement. *Mar.Ecol. Prog. Ser.*, **60**: 141-146.

Holme, N.A. (1961)
The bottom fauna of the English Channel. *J. Mar. Bio. Ass.UK.*, **41**: 397-461.

Holme, N.A. (1966)
The bottom fauna of the English Channnel. Part 2. *J. Mar. Biol. Ass. UK.*, **46** : 401-493.

Holmes, S.P., Sturgess, C.J., & Davies, M. (1997)
The effect of rock-type on the settlement of *Balanus balanoides* (L.) cyprids. *Biofouling*, **11** (2):137-147.

Holmstroem,C., Rittschoff, D & Kelleberg, S. (1992)
Inhibition of settlement by larvae of *Balanus amphitrite* and *Ciona intestinalis* by a surface-colonizing baterium. *Appl Environ Microbiol.*, **58**: 2111-2115.

Houghton, J. (1994)
Global Warming: the complete briefing. Lion Publishing. Oxford.

Houghton, J.T., Meira, L.G., Filho, B.A., Callander, N.H., Kattenberg, A. & Maskell, K.(eds.) (1995) *Climate Change 1995-The Science of Climate Change: Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press.

Houghton, S.D. (1988)
Thermocline control on Coccolith diversity and abundance in recent sediments from the Celtic Sea and English Channel. *Marine Geology*, **83**:313-319.

Howson, C.M. & Picton, B.E.(eds.) (1997).
The species directory of the marine fauna and flora of the British Isles and surrounding seas. Ulster Museum and The Marine Conservation Society. Belfast and Ross-on-Wye.

Hurley, A.C. (1975)
The establishment of populations of *Balanus pacificus* (Cirripedia) and their elimination by predatory Turbellaria. *J.Animal Ecol.*, **44**:521-532.

Hurrell, J.W. (1995)
Decadal trends in the North Atlantic Oscillation and relationships to regional temperature and precipitation. *Science*, **269**: 676-679.

Hurrell, J.W. & VanLoon, H. (1997)
Decadal variations in climate associated with the north Atlantic oscillation. *Climate Change*, **36** (3-4): 301-326.

Hutchins, L.W. (1947)
The bases for temperature zonation in geographical distribution. *Ecol. Monogr.*, **17** (3) : 325-335.

Hydraulics Research Wallingford (1993)
South Coast Seabed Mobility Study. Report EX 2795.

Insole, A., Daley, B. & Gale, A. (1998)
The Isle of Wight. Geologists Association Guide No.60:132pp. The Geologists Association.

Jenkins, S.R., Norton, T.A & Hawkins, S.J (1999)
Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea:Cirripedia) and three species of fucoid canopy algae. *J.Exp.Mar.Biol.Ecol.*, **236**:49-67.

Jenkins, S.R., Aberg, P., Cervin, G., Coleman, R.A., Delany, J., DellaSantina, P., Hawkins, S.J., LaCroix, E., Myers, A. A.,Lindgarth, M., Power, A.M., Roberts, M.F. & Hartnoll, R.G. (2000)
Spatial and temporal variation in settlement and recruitment of the barnacle *Semibalanus balanoides* (L.) (Crustacea:Cirripedia) over a European scale. *J.Exp.Mar.Biol.Ecol.* **243**:209-225.

Joint, I., Jordan, M.B. & Carr, M.R (1997)
Is phosphate part of the Russell Cycle? *J. Mar.Biol.Ass.UK.*, 77: 625-633.

Jones, P.D., New, M. Parker, D.E., Martin, S. & Rigor, I.G. (1999)
Surface air temperature and its changes over the past 150 years. *Reviews of Geophysics,* **37**:173-199.

Jones, S.R. & Jeffs, T.M. (1991)
Near-surface sea temperatures in coastal waters of the North Sea, English Channel and Irish sea. *Data Rep., MAFF Direct. Fish. Res.*, Lowestoft, (24) : 70pp.

Jory, A.M. (1996)
Changes in the abundance of some of the intertidal indicator species in Guernsey over the past 45 years. *B.Sc. (Hons.) project (unpub).Dept.Biology. University of Southampton.*

Kerr-McGee (1995)
Lyme Bay Environmental Study. Volume 1:The Physical Environment: Hydrography. Ambios Environmental Consultants Ltd.

Kendall, M.A. (1987)
The age and size structure of some northern populations of the Trochid Gastropod *Monodonta lineata. J.Moll. Stud.*, **53** : 213-222.

Kendall, M.A. (1988)
Reproduction and recruitment of the barnacle *Chthamalus montagui* and the trochid gastropods *Monodonta lineata* and *Gibbula umbilicalis* close to the northern limit of their distributions. *Porcupine Newsletter,* **4** (2):36.

Kendall, M.A., Bowman, R.S. & Williamson, P. & Lewis, J.R. (1982)
Settlement patterns, density and stability in the barnacle *Balanus balanoides. Netherlands Journal of Sea Research,* **16**, :119-126.

Kendall, M.A., Bowman, R.S., Williamson, P. & Lewis, J.R. (1985)
Annual variation in the recruitment of *Semibalanus balanoides* on the North Yorkshire coast 1969-1981. *J. Mar. Biol. Ass. UK.*, **65** : 1009-1030.

Kendall, M.A. & Lewis, J.R. (1986)
Temporal and spatial patterns in the recruitment of *Gibbula umbilicalis. Hydrobiologia,* **142 :** 15-22.

Kendall, M.A. & Bedford, M.L. (1987)
Reproduction and recruitment of the barnacle *Chthamalus montagui* at Aberystwith (mid-Wales). *Marine Ecology Progress Ser.* **38** : 305-308.

Kendall, M.A., Williamson, P. & Garwood, P.R. (1987)
Annual variation in recruitment and population structure of *Monodonta lineata* and *Gibbula umbilicalis* populations at Aberaeron, mid-Wales. *Estuarine, Coastal & Shelf Science,* **24**: 499-511.

Kent, A. (2000)
Influence of recruitment on population persistence in open and closed systems. *Ph.D Thesis. University of Southampton.*

Killeen, I. (1964)
Marine molluscs from the Isle of Wight in the Leslie Prebble collections. *Proc.Isle.Wight.nat. Hist.archaeol.Soc.*, **12**: 71-75

Klepal, W. Barnes, H. & Barnes, M. (1979)
Studies on the reproduction of cirripedes.VII. The formation and fine structure of the fertilization membrane and egg case. *J.Exp.Mar.Biol. Ecol.*. **36**:53-78.

Knight-Jones, E.W. & Stevenson, J.P. (1950)
Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *J.Mar.Biol. Ass.UK.*, **29**:281-297.

Knutson,T.R.,Tuleya, R.E. & Kurihara, Y. (1998)
Simulated increase of Hurricane intensities in a CO_2-warmed climate. *Science*. **279**:1018-1019.

Larkin, P.A. (1970)
Some observations on models of stock and recruitment relationships for fishes. *ICES Symposium on Stock and Recruitment.* Document No. 17, 14pp.

Langston,W.J., Bryan, G.W., Burt, G.R. & Pope, N.D. (1994)
Effect of Sediment Metals on Estuarine Benthic Organisms. National Rivers Authority R&D Note 203.

Le Tourneux, F. & Bourget, E. (1988)
Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides. Mar.Biol.*, **97**:57-66.

Lee, A.J, & Ramster, J.W. (1981)
Atlas of the seas around the British Isles. Ministry of Agriculture, Fisheries and Food. Lowestoft.

Lepore, E., Sciscioli, M. & Gherardi, M. (1979)
Observations on the oogenesis and spermatogenesis in some cirripedes. *Mem. Biol. Mar.Ocean.*, **5** (5): 115-122.

Lepore. E., Sciscioli. M. & Gherardi. M. (1993)
Some ultrastructural aspects of oocytes during vitellogenesis in two species of *Balanus* (Crustacea,Cirripedia). *Oebalia,* **19**:79-87.

Lewis. C.A. (1977)
A review of substratum selection in free-living and symbiotic cirripedes. In: Chia. F.S., Rice. M. (ed.) *Settlement and metamorphosis of marine invertebrate larvae.* Elsevier, Amsterdam, p207-217.

Lewis. J.R. (1964)
The Ecology of Rocky Shores. Hodder & Stoughton. 323pp.

Lewis. J.R. (1976)
Long-term ecological surveillance: practical realities in the rocky littoral. *Oceanogr.Mar.Biol. Ann. Rev.*, **14** : 371-390.

Lewis. J.R. (1986)
Lattitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes. *Hydrobiologia.* **142** : 1-13.

Lewis J.R. (1991)
. Rationale methods and problems involved in the assessment and causes of recruitment fluctuations of some rocky shore species. In: Keegan B.F (ed*). Space and Time Series data analysis in coastal benthic ecology*. CEC Brussels 582pp

Light, J.M. & Killeen, I.J. (1990)
A survey to record the marine mollusca of the Isle of Wight. *Proc.Isle.Wight. nat. Hist. archaeol. Soc.*, **9** : 86-90.

Little, A.E., Dicks, B. & Crothers, J.H. (1986)
Studies of barnacles, limpets and topshells in Milford Haven. *Field Studies,* **6** (3) : 459-492.

Little, C. & Kitching, J.A. (1996)
The Biology of Rocky Shores. Oxford University Press. 240pp.

Lively, C.M. & Raimondi, P.T. (1987)
Desiccation, predation, and mussel-barnacle interactions in the northern Gulf of California. *Oecologia (Berlin)*, **74**:304-309.

Lockhead, J.H. (1936)
On the feeding mechanism of the nauplius of *Balanus perforatus* Bruguiere. *Proc. Linn.Soc.Lond. (Zool.)*, **39**:429-442.

Longhurst, A. (1998)
Ecological Geography of the Sea. Academic Press. 398pp.

Lumby, J.R. (1953)
Salinity and temperature of the English Channel. Atlas of charts. *Fishery Invest., Lond.*, Ser.2, **14** (3).

Lyme Bay and South Devon Coastline Group (1998)
Lyme Bay and South Devon Shoreline Management Plan. Volume 2. Posford & Duvivier.

MacArthur, R.H. & Wilson, E.O. (1967)
The Theory of Island Biogeography. Princeton University Press, Princeton, N.J.

McGuinness, K.A. (1989)
Effects of some natural and artificial substrata on sessile marine organisms at Galeta Reef, Panama. *Mar.Ecol.Prog.Ser.*, **52**: 201-208.

Meijer, T. & Preece, R.C. (1995)
Malacological evidence relating to the insularity of the British Isles during the Quaternary. In: Preece (ed.) *Island Britain: a Quaternary perspective*. Geological Society Special Publication No.96, p 89-110.

Menge, B.A. (1976)
Organisation of the New England rocky intertidal communities: roles of predation, competition, environmental heterogeneity. *Ecol. Monogr,* **46**:355-393.

Menge, B.A. (1992)
Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology,* **73** (3):755-765.

Menge, B.A. (2000a)
Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J.Exp.Mar.Biol.Ecol.,* **250**: 257-289.

Menge, B.A. (2000b)
Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. *Ecol Monogr.,* **70** (2):265-288.

Menge, B.A. & Sutherland, J.P. (1976)
Species diversity gradients: synthesis of the roles of predation, competition and spatial heterogeneity. *Am.Nat.*, **110**:351-369.

Minchinton,T.E. & Scheibling, R.E. (1991)
The influence of larval supply and settlement on the population structure of barnacles. *Ecology*, **72** (5) :1867-1879.

Minchinton,T.E. & Scheibling, R.E. (1993a)
Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Mar. Ecol. Prog. Ser.*, **95**: 233-244.

Minchinton,T.E. & Scheibling, R.E. (1993b)
Variations in sampling procedure and frequency affect estimates of recruitment of barnacles. *Mar. Ecol. Prog. Ser.*, **99**: 83-88.

Moore, H.B. (1934)
The biology of *Balanus balanoides*.I. Growth rate and its relation to size, season and tidal level. *J.Mar.Biol.Ass.UK.*, **19**:851-868.

Moore, H.B. & Kitching, J.A. (1939)
The biology of *Chthamalus stellatus* (Poli). *J.Mar.Biol. Ass. UK.*, **23**: 521-541.

Motyka, J.M. & Brampton, A.H. (1993)
Coastal Management - mapping of littoral cells. Oxford, HR Wallingford. (HR Wallingford Report SR 328).

Myares, M.P. (1986)
Estudio del horizonte de *Chthamalus-Patella* en el littoral Asturiano. *Ph.D Thesis, University of Oviedo.*

Myers, A.A & Southgate, T. (1980)
Artificial substrates as a mean of monitoring rocky shore cryptofauna. *J.Mar.Biol.Ass.UK.*, **60**:963-975.

Naylor, E. (1972). *British marine Isopods*. Academic Press. London.

Neal. A.L. & Yule, A.B. (1994)
The tenacity of *Elminius modestus* and *Balanus perforatus* cyprids to bacterial films grown under different shear regimes. *J. Mar.Biol. Ass. UK.*, **74** : 251-257.

Norris, E. & Crisp, D.J. (1953)
The distribution and planktonic stages of the cirripede *Balanus perforatus* Bruguière. *Proc. Zool. Soc. Lond.*, **123** : 393-409.

O'Riordan, R.M., Myers, A.A. & Cross, T.F. (1991)
Chthamalus stellatus (Poli) and *C. montagui* Southward (CIRRIPEDIA):- variation in embryo numbers with species, habitat and shore level. In: Myers, A.A., Little, C., Costello, M.J. & Partridge, J.C. (eds.). *The Ecology of Lough Hyne*. Proceedings of Conference 4-5 September 1990. Royal Irish Academy.

O'Riordan, R. (1992)
Reproduction and recruitment of two intertidal Chthamalid barnacles. *Ph.D Thesis.University College Cork.*

O'Riordan, R.M., Myers, A.A. & Cross, T.F. (1992)
Brooding in the intertidal barnacles *Chthamalus stellatus* (Poli)and *Chthamalus montagui* Southward in south-western Ireland. *J.Exp. Mar.Biol. Ecol.*, **164** : 135-145.

Orton, J.H. (1920)
Sea temperature, breeding and distribution in marine animals. *J.Mar. Biol.Ass.UK.*, **12** : 339-336.

Orton, J.H. & Southward, A.J. (1961)
Studies on the biology of limpets.IV. The breeding of *Patella depressa* Pennant on the north Cornish coast. *J.Mar.Biol.Ass.UK.*, **35**:149-176.

Osterhus, S. & Gammelsrød, T. (1999)
The abyss of the Nordic Seas is warming. *J.Climate*, 12:3297-3304.

Paine, R.T. (1980)
Foodwebs: linkage,interaction strength and community infrastructure. *J.Animal.Ecol.*, **49**:667-685.

Paine, R.T. (1981)
Barnacle ecology:the forgotten roles of disturbance and predation. *Paleobiology*, 7:553-560.

Paine, R.T. (1994)
Marine Rocky Shores and Community Ecology: An experimentalist's perspective. Ecology Institute, Germany.

Pannacciulli, F.G. (1995)
Population ecology and genetics of European species of intertidal barnacles. *Ph.D thesis. University of Liverpool.* 143pp.

Pannacciulli, F.G., Bishop J.D.D. & Hawkins, S.J. (1997)
Genetic structure of populations of *Chthamalus* (Crustacea:Cirripedia) in the north-east Atlantic and Mediterranean. *Mar Biol.*, **128** (1):73-82.

Pannacciulli, F.G. & Falautano, M. (1999)
Time of larval release in barnacles of the general *Chthamalus* and *Euraphia* in the Gulf of Genoa (Ligurian Sea) and in the Gulf of Trieste (North Adriatic Sea). *Biol.Mar.Medit.*, **6** (1):407-410.

Pannacciulli, F.G. & Relini, G. (1999)
Time of settlement in barnacles of the genus *Chthamalus* in the Gulf of Genoa (Ligurian Sea) and in the Gulf of Trieste (North Adriatic Sea). *Biol.Mar.Medit.*, **6** (1):411-414.

Patel, B. & Crisp, D.J. (1960a)
Rates of development of the embryos of several species of barnacles. *Physiol. Zool.*, **33** : 104-119.

Patel, B. & Crisp, D.J. (1960b)
The influence of temperature on the breeding and the moulting activities of some warm-water species of operculate barnacles. *J. Mar. Biol. Ass. UK.*, **39**: 667-680.

Pingree, R.D. & Maddock, L. (1977)
Tidal eddies and coastal discharge. *J. Mar. Biol. Ass.UK.*, **57**: 869-875.

Pingree, R.D & Griffiths, D.K. (1978)
Tidal fronts on the shelf seas around the British Isles. *Journ. Geophys. Res.*,
83: 4615-4622.

Pingree, R.D., Mardell, G.T. & Maddock, L. (1983)
A marginal front in Lyme Bay. *J.Mar. Biol. Ass.UK.*, **63** : 9-15.

Planque, B. & Taylor, A.H. (1998)
Long-term changes in zooplankton and the climate of the North Atlantic. *ICES Journal of Marine Science*, **55**:644-654.

Power, A., Delaney, J., Myers, A.A., O'Riordan, R.M. & McGrath, D. (1999)
Prolonged settlement and prediction of recruitment in two sympatric intertidal *Chthamalus* species from south-west Ireland. *J.Mar.Biol. Ass. UK.*, **79**: 941-943.

Preece, R.C. (1993)
Monodonta lineata (da Costa) from Archaeological sites in Dorset and the Isle of Wight. *J. Conch. Lond.*, **34** : 339-341.

Raffaelli, D. & Hawkins, S.J. (1996)
Intertidal ecology. London, Chapman & Hall.

Rahmstorf, S. (1997)
Risk of sea-change in the Atlantic. *Nature*, **388**:825-826.

Raimondi, P.T. (1988)
Rock type affects settlement, recruitment and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *J.Exp.Mar.Biol. Ecol.* **123**: 253-267.

Rayner, N.A., Parker,D.E., Horton, E.B., Folland, C.K., Alexander, L.V. and Frich, P. (2000)
The HadISST1 Global Sea-Ice and Sea Surface Temperature Data Set, 1871-1999.
Hadley Centre Technical Note 17. Unpublished manuscript available from the Hadley Centre for Climate Prediction and Research, The Met. Office, London Road, Bracknell, RG12 2SY, UK.

Relini, G. (1983)
Remarks on the ecology of chthamalids in the Ligurian Sea. Rapport et Proces-Verbaux des Reunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee **28** (3):273-275.

Relini, G. & Galiizia, C. (1991).
Effetti di una mareggiata sui popolamenti di Ctamali Atti del 53 Convegno UZI, 1-5 Ottobre 1990, Palermo: 106-107.

Rendall, R. (1956)
Mollusca orcadensia. *Proc. r. Soc. Edinb.* **66B**:131-201

Reynolds, R.W. & Smith, T.M. (1994)
Improved sea surface temperature analysis using optimum interpolation. *J.Climate*, **7**:929-948.

Richards, S.A., Possingham, H.P. & Noye, B.J. (1995)
Larval dispersion along a straight coast with tidal currents: complex distribution patterns from a simple model. *Mar.Ecol. Prog.Ser.*, **122**:59-71

Roughgarden, J., Iwasa,Y. & Baxter, C. (1985)
Demographic theory for an open marine population with space-limited recruitment. *Ecology*, **66**, (1):54-67.

Roughgarden, J., Gaines,. S.D. & Possingham,H. (1988)
Recruitment dynamics in complex life cycles. *Science*, **241**:1460-1466.

Russell, F.S. (1936)
The seasonal abundance of the pelagic young of teleostean fishes in the Plymouth area. Part III. The year 1935, with a note on the conditions as shown by the occurrence of plankton indicators. *J. Mar. Biol.Ass.UK.*, **20** :595-604.

Russell, F.S. (1973)
A summary of observations of the occurrence of planktonic stages of fish off Plymouth, 1924-1972. *J. Mar.Biol.Ass.UK.*, **53**: 347-355.

Russell. F.S., Southward. A.J.. Boalch. G.T. & Butler. E.I., (1971)
Changes in biological conditions in the English Channel off Plymouth during the last half century. *Nature*. **234**: 468-470.

Salomon. J.C. & Breton. M. (1991)
Courants residuals de maree dans la Mance. *Oceanol. Acta.*, **11**:47-53.

Salomon. J.C. & Breton. M. (1993)
An atlas of long-term current in the Channel. *Oceanol.Acta.*, **16**:439-448.

Sanford. E., Bermudez. D., Bertness, M.D. & Gaines. S.D. (1994)
Flow, food supply and acorn barnacle population dynamics. *Mar.Ecol.Prog.Ser.*, **104**:49-62.

Shanks, A.L. (1986)
Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesised mechanism for the cross shelf transport of cyprids. *Biol.Bull. (Woods Hole)*, **170**:429-440.

Sherwin,T.J. & Jonas, P.J.C. (1994)
The impact of ambient stratification on marine outfall studies in British waters. *Mar.Poll.Bull.*, **28** (9):527-533

Sokal. R.R. & Rohlf, F.J. (1995)
Biometry. The principles and practice of statistics in biological research. W.H. Freeman & Co. New York.

Southern Water Services Ltd. (1996)
Information to support NRA Consent Application for Sandown LSO. *Report No. 4. Oceanographic Overview.* Southern water services Ltd. Otterbourne. Hampshire.

Southward, A.J. (1950)
Occurrence of *Chthamalus stellatus* in the Isle of Man. *Nature*. **165** :408-409.

Southward, A.J. (1951)
Distribution of *Chthamalus stellatus* in the Irish sea. *Nature*. **167** :410-411.

Southward. A. J. (1955)
On the behaviour of barnacles.I. The relation of cirral and other activities to temperature. *J.Mar.Biol.Ass.UK.*, **34**: 403-422.

Southward. A.J. (1957)
On the behaviour of barnacles. III Further observations on the influence of temperature and age on cirral activity. *J. Mar. Biol. Ass. UK.*, **36**: 323-334.

Southward. A.J. (1958)
Note on the temperature tolerances of some intertidal animals in relation to environmental temperature and geographical distribution. *J. Mar. Biol. Ass. UK.*, **37**: 49-66.

Southward. A.J. (1960)
On changes of sea temperature in the English Channel. *J. Mar. Biol. Ass. UK.*, **39**: 449-458.

Southward. A.J. (1963)
The distribution of some plankton animals in the English Channel and Western Approaches.III. Theories about long-tem biological changes. including fish. *J.Mar.Biol.Ass.UK.*, **43**:1-29.

Southward. A.J. (1964)
The relationship between temperature and rhythmic cirral activity in some Cirripedia considered in connection with their geographic distribution. *Helgolander wiss Meersunters*. **10**:391-403.

Southward, A.J. (1967)
Recent changes in abundance of intertidal barnacles in south-west England: A possible effect of climatic deterioration. *J. Mar. Biol. Ass. UK.,* **47** : 81-95.

Southward, A.J. (1976)
On the taxonomic status and distribution of *Chthamalus stellatus* (Cirripedia) in the North-East Atlantic region: with a key to common intertidal barnacles of Britain. *J. Mar. Biol. Ass.UK.,* **56** : 1007-1028.

Southward, A.J. (1979)
Cyclic fluctuations in population density during 11 years recolonisation of rocky shores in west Cornwall following the Torrey Canyon oil spill in 1967. In: *Cyclic Phenomena in Marine Plants and Animals*. Naylor, E. and Hartnoll, R.G. (eds). Pergamon Press, Oxford.pp85-92.

Southward, A.J. (1980)
The western English Channel – an inconstant ecosystem? *Nature,* **285**:361-366.

Southward, A.J. (ed.). (1987)
Barnacle biology. Crustacean Issues. A.A. Balkema, Rotterdam.

Southward, A.J. (1991)
Forty years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. *J. Mar Biol. Ass UK.,* **71** : 445-513.

Southward, A.J. (1995)
Occurrence in the English Channel of a warm-water cirripede *Solidobalanus fallax*. *J. Mar. Biol. Ass. UK.,* **75** : 199-210.

Southward, A.J. & Boalch, G.T. (1989)
Aspects of long-term changes in the ecosystem of the western English Channel in relation to fish populations: 415-447. In: Wyatt, T. & Larrantea, M.G. (eds.) *Long-term Changes in Marine Fish Populations*. Vigo:Inst. Investigaciones Marinas.

Southward, A.J. & Boalch, G.T. (1994)
The effect of changing climate on marine life:past events and future predictions. In: *Man and the Maritime Environment*. Exeter Maritime Studies Volume 9. (ed. S.Fisher). University of Exeter Press, Exeter, UK.

Southward, A.J. & Crisp, D.J. (1952)
Changes in the distribution of the intertidal barnacles in relation to the environment. *Nature,* **170**: 416.

Southward, A.J. & Crisp, D.J. (1954)
Recent changes in the distribution of the intertidal barnacles *Chthamalus stellatus* (Poli) and *Balanus balanoides* L. in the British Isles. *J. Animal Ecol.,* **23** : 163-177.

Southward, A.J. & Crisp, D.J. (1956)
Fluctuations in the distribution and abundance of intertidal barnacles. *J. Mar. Biol. Ass. UK.,* **35** : 211-229.

Southward, A.J. & Roberts, E.K. (1984)
The Marine Biological Association 1884-1984. One hundred years of marine research . *Rep. Trans.Devon.Ass.Advmt.Sci.,* **116**:155-199.

Southward, A.J. & Southward, E.C. (1978).
Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the *Torry Canyon* spill. *J.Fish. Res. Board. Canada.,* **35**: 682-706

Southward, A.J., Boalch,G.T. & Maddock, L. (1988)
Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th Century. *J.Mar.Bio.Ass.UK.*, **68**:423-445.

Southward, A.J, Butler, E.I & Pennycuick,L. (1975)
Recent cyclic changes in climate and in the abundance of marine life. *Nature*, **253**: 5444: 714-717

Southward, A.J., Hawkins, S.J. & Burrows, M.T. (1995)
Seventy years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature.
J. therm. Biol., **20** No. 1. :127-155.

Stephan, T. & Wissell, C. (1999)
The extinction risk of a population exploiting a resource. *Ecological Modelling*, **115**:217-225.

Stephenson, T.A. & Stephenson, A. (1972)
Life between the tide marks on rocky shores. W.H. Freeman & Co.

Stephenson, D.B. (2000). www.rdg.ac.uk/cag/NAO

Stoker, T.F. (1994)
The variable ocean. *Nature*, **367**: 221-222.

Stubbings, H.G. (1950)
Earlier Records of *Elminius modestus* (Darwin) in British waters. *Nature*, **166** : 277-278.

Stubbings, H.G. & Houghton, D.R (1964). The Ecology of Chichester Harbour, S.England, with special reference to some fouling species. *Int Revuee ges. Hydrobiol.*, **49** (2) : 233-279.

Sutherland, J.P. (1987)
Recruitment limitation in a tropical intertidal barnacle: *Tetraclita panamensis* (Pilsbry) on the Pacific coast of Costa Rica. *J.Exp.Mar.Biol. Ecol.*, **113**:267-282

Taylor, A.H. (1995)
North-south shifts of the Gulf Stream and the climate connection with the abundance of zooplankton in the UK and its surrounding seas. *ICES J.mar.sci.*, **52**:711-721.

Taylor, A.H. & Stephens, J.A (1998)
The North Atlantic Oscillation and the latitude of the Gulf Stream. *Tellus*, **50A**:134-142.

Taylor, A.H., Jordon, M.B. & Stephens, J.A. (1998)
Gulf Stream shifts following ENSO events. *Nature*, **393** p638.

Thomason, J.C., Hills, J.M., Clare, A.S., Neville, A. & Richardson,M. (1998)
Hydrodynamic consequences of barnacle colonisation. *Hydrobiologia*, **375/376**: 191-201

Thompson, R.C., Norton,T.A. & Hawkins, S.J. (1998)
The influence of epilithic microbial films on the settlement of *Semibalanus balanoides* cyprids - a comparison between laboratory and field experiments. *Hydrobiologia*, **375/376**:203-216.

Tittley, I. & Price, J.H. (1978)
The benthic marine algae of the eastern English Channel: a preliminary floristic account.
Botanic Marina, **21**:499-512.

Todd, C.D. (1998)
Larval supply and recruitment of benthic invertebrates: Do larvae always disperse as much as we believe? *Hydrobiologia*, **376**:1-21.

Tubbs, C. (1999)
The Ecology, Conservation and History of the Solent. Packard Publishing Ltd. Chichester.West Sussex. 184pp.

Turrel, W.R., Slesser,G., Adams, R.D., Payne, R. & Gillibrand, P.A. (1999)
Decadal variability in the composition of Faroe Shetland Channel bottom water. *Deep-Sea Research* I, **46**:1-25

UKDMAP (1998)
UK Digital Marine Atlas (3rd Edition). British Oceanographic Data Centre, Bidston Observaory, Merseyside. UK.

Underwood, A.J. (1972)
Observations on the reproductive cycles of *Monodonta lineata, Gibbula umbilicalis* and *G. cineraria. Mar.Biol.*, **17**:333-340.

Underwood, A.J. (1976)
Food competition between age-classes in the intertidal Neritacean Neria atramentosa (Reeve) (Gastropoda:Prosobranchia). *J.Exp.Mar.Biol Ecol.*, **23**:145-154.

Underwood, A.J. (1992)
Competition and marine-plant interactions. *In Plant-Animal Interactions in the Marine Benthos* (ed. D.M. John, S.J. Hawkins and J.M. Price). Systematics Association special volume No. 46. Pp 443-475. Clarendon Press. Oxford.

Underwood, A.J. & Fairweather, P.G. (1989)
Supply-side ecology and benthic marine assemblages. *Trends in. Ecol.Evol.,* **4** :16-20

Underwood, A.J. (1997)
Experiments in ecology. Their logical design and interpretation using analysis if variance. Cambridge University Press. 504pp.

Underwood, A. J., Chapman, M.G. & Sage, M. (1998).
GMA V5 for Windows. Institute of Marine Ecology, University of Sydney.

United Marine Dredging Ltd. (1998)
Environmental Assessment for aggregate extraction from Inner Owers, English Channel. United Marine Dredging Ltd. UMA House, Chichester. W. Sussex

United Marine Dredging Ltd. (1999)
Area 433 Environmental Assessment for aggregate extraction from North Nab, English Channel. United Marine Dredging Ltd. UMA House, Chichester. W. Sussex.

Vermeij, G.J. (1991)
Trans-equatorial connections between biotas in the temperate eastern Atlantic. *Mar. Biol.*, **112:** 343-348.

Vermeij, G.J. (2000)
Community Assembly in the Sea: geologic history of the living shore biota. In: Bertness, M.D., Gaines, S.D.& Hay, M.E. (eds.) *Marine Community Ecology.* Sinauer Associates, Inc. Mass.U.S.A

Walters, L.J. & Wethey, D.S. (1996)
Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. *Mar. Ecol. Prog. Ser.*, **137**: 161-171.

West, I.M. (2000)
Wests Geology Directory.www.soton.ac.uk/~imw/index.htm. School of Ocean & Earth Sciences. Southampton University. UK.

Wethey, D.S. (1983)
Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chthamalus* in New England. *Biol. Bull. (Woods Hole)*, **165**:330-341.

Wethey, D.S. (1985)
Local and regional variation in settlement and survival in the littoral barnacle *Semibalanus balanoides* (L.): patterns and consequences. In: *The Ecology of Rocky Coasts*, eds. P.G.Moore & R.Seed: 194-202. London:Hodder & Stoughton.

Wethey, D.S. (1986)
Ranking of settlement cues by barnacle larvae: influence of surface contour. *Bull. Mar. Sci*, **39**:393-400.

Wieczorek, S.K., Murray, A.W.W. & Todd, C.D. (1996)
Seasonal variation in the effects of hard substratum biofilming on settlement of marine larvae. *Biofouling*, **19**:309-330.

Williams, E.E. (1964)
The growth and distribution of *Gibbula umbilicalis* (da Costa) on a rocky shore in Wales. *J.Animal. Ecol.*, **33**:433-442.

Williams, E.E. (1965)
The growth and distribution of *Monodonta lineata* (da Costa) on a rocky shore in Wales. *Field Studies*, **2**:189-198.

Williamson, P. & Kendall, M. (1981)
Population age structure and growth of the trochid *Monodonta lineata* determined from shell rings. *J. Mar.Biol.Ass.UK.*, **61**, 1011-1026.

APPENDIX I

Description of major survey sites

These sites were visited to assess the broad-scale distribution of species in the autumn of 1994 and subsequent monitoring.

Shoalstone Beach, Torbay, Devon. (National Grid Reference: SX 568936)

A north-facing moderately sheltered rocky shore on the southern coast of Torbay near Brixham Harbour. The survey site was 50m east of the outdoor swimming pool where there are steep and gently sloping Devonian limestone and sandstone reefs. Areas of small boulders and cobbles also occur between the reefs and rocky outcrops. The limpet-barnacle zone extends to about MLWN below which *Fucus serratus* dominates the lower shore. which is fringed with *Laminaria digitata*. At low-water shallow pools occur at all tidal levels. The site was regularly monitored by the late D.J Crisp (Southward & Crisp, 1954, 1956) and is included for comparative purposes, although it is now much visited by school parties. The close proximity of the fishing port and recent expansion of the marina may have contributed to changes in water quality in this part of Torbay.

Saltern Cove, near Goodrington Torbay, Devon. (National Grid Reference: SX 584897)

Concerns related to pollution and visitor pressure at Shoalstone beach made it necessary to find an alternative site nearby. This is an east-facing moderately exposed shore in the centre of the bay and is managed as a Local Marine Nature Reserve by Torbay Borough Council. The shore consists of a siltstone reef (Lower Devonian: Old Red Sandstone) backed by cliffs, and is gently sloping. The limpet-barnacle zone extends to about MLWN. Nearby are reefs of the sand-building tubeworm *Sabellaria alveolata*.

Broad Ledge, Lyme Regis, Dorset. (National Grid Reference: SY 345921)

A thin layer of limestone (Jurrassic: Blue Lias) forms a relatively hard wave-cut platform below Church Cliffs. just to the east of the town and sandy beaches. Beneath the limestone is much softer shale. which is also exposed on the shore and at the edges of the reefs. Apart from concrete groynes there is little hard substrate above mean tide level. Limpets and barnacles are most abundant on the edges of the reefs. although there are large and extensive patches elsewhere and on the surface of cobbles. At low tide. large

Peveril Point, Swanage, Dorset.(National Grid Reference:SY 041786)

At this location on the south coast of Swanage Bay, two parallel fingers of limestone (Jurrassic:Upper Purbeck) extend eastwards into the Bay; the northern ledge has a southern aspect, and the southern ledge has a northern aspect. Both ledges are steeply sloping, although more crevices divide the northern ledge, which is most accessible. There is a narrow limpet and barnacle zone below which is a mixed community of *Corallina officinalis* and *Laurencia* spp. Strong currents sweep across the ledges on the ebb and flood tide, although the tidal range of 2m is the lowest in Britain. A concrete sewer pipe runs parallel and to the north of the ledges.

Long Groyne, Hengistbury Head, Hampshire. (National Grid Reference: SZ 178903)

A shingle and sandy beach occurs either side of this long concrete structure that extends south into Christchurch Bay. The western aspect is the most exposed to wave energy. Variations in the age and roughness of the concrete rendering greatly influence the density of barnacles. Surveys were carried out on the vertical sides of the groyne.

Warden Ledge, Colwell, Isle of Wight. (National Grid Reference: SZ 324877)

This narrow limestone ledge (Oligocene: Osborne & Headon Beds), with a northwesterly aspect, extends out into fast currents at the western end of the Solent. Much of the ledge consists of weed covered boulders, although there are some rocky outcrops. The smaller barnacles (*Chthamalus*, *Semibalanus* & *Elminius*) and limpets were most abundant on the concrete boulders which had been placed at the foot of the esplanade, and it is here that population monitoring was carried out.

Freshwater Bay (West), Isle of Wight. (National Grid Reference: SZ 345855)

This is an exposed site on the south-west coast of the island. The western shore of this small embayment is sheltered by chalk cliffs, below which is a gently shelving chalk and flint platform with boulders and rock pools. Above mean tide level is a shingle and sandy beach. Running across the shore is a short redundant concrete sewer pipe.

Hanover Point, Brook, Isle of Wight. (National Grid Reference: SZ 379837)

A small area of hard sandstone reefs (Cretaceous:Wealden Beds) amongst a clay wave-cut platform and petrified forest. The sandstone reefs dip 10 degrees to the north and the seaward face is nearly vertical. Immediately around the reefs are variously sized boulders draped in algae or covered in sediment.

Watershoot Bay, St.Catherine's Point, Isle of Wight. (National Grid Reference: SZ 493754)

An exposed shore consisting of large predominantly sandstone boulders (Cretaceous:Upper Greensand), the lithology of which varies between hard chert and soft sandstone. The shore is backed by rapidly eroding cliffs derived from landslip debris.

Lane End, Bembridge, Isle of Wight. (National Grid Reference: SZ 659877)

Moderately exposed flat reefs (Oligocene:Bembridge Limestone) 300m south of the lifeboat station on the eastern tip of the island. Much of the ledges retain shallow water at low tide or are covered in algae, especially *Fucus serratus*. At the seaward edges of the reefs there is often a small strip of open rock with limpets and barnacles. This is more extensive on the outer ledges at Ethel Point.

Southsea Castle, Hampshire. (National Grid Reference:SZ 644979)

Below the castle is a small area of concrete blocks and stone boulders amongst a shingle and sandy beach. The shore is close to Portsmouth Harbour and marinas.

Selsey Bill, Sussex. (National Grid Reference: SZ 852922)

The survey was carried out below the Coast Guard station where there were concrete slabs and blocks. Most of the shore consisted of sand and shingle, although a clay reef was exposed at low-water spring tides

Bognor Regis, Sussex. (National Grid Reference: SZ 920984)

Concrete structure lying on sandy beach. The sides were covered in barnacles and limpets.

Shoreham, Sussex. (National Grid Reference: TQ 344045).

Inside the harbour entrance on the western shore are concrete boulders with sandy mud nearby. The boulders were draped with *Fucus* spp. and *Pelvetia canaliculata* was locally abundant. Between the boulders were extensive mussel beds. Barnacles and limpets were most abundant on vertical piles and the west-facing wall of the harbour.

Worthing Pier, Sussex.(National Grid Reference:TQ 150021)

All accessible structures were investigated during low spring tides. Much of the structure is colonized by limpets mussels and barnacles. Surrounding the pier is a sandy and shingle beach.

Newhaven, Sussex. (National Grid Reference:TV 437998)

Chalk wave-cut platform 1km west of the harbour breakwater. Moderately sized boulders occur at the foot of the cliff, and there are shallow coralline pools on the lower shore.

Hope Gap, Seaford, Sussex.(National Grid Reference: TV 512973)

An extensive chalk wave-cut platform with large boulders at the foot of the cliffs. Some shingle is present at the top of the beach. The chalk is rich in flint nodules that resist weathering and erosion. The Cuckmere river discharges into the sea nearby.

Birling Gap, Sussex. (National Grid Reference:TV 551961)

The shore below Birling Gap is sandy and disturbed, possibly from launching of boats. To the east, the limpet barnacle zone becomes increasingly well developed on a hard flint-capped platform where there are also rich coralline pools. To the west of Birling Gap the platform is well furrowed along the line of strike, and here a thick layer of flint is sandwiched between the chalk.

Beachy Head, Sussex. (National Grid Reference:TV 583951)

Chalk boulders dominate the shore at this exposed location although those lower down the shore provide significant shelter to the upper part of the intertidal zone. The granite blocks at the base of the lighthouse were also examined. Rich coralline pools are also present.

Cow Gap, Eastbourne, Sussex. (National Grid Reference:TV 596955)

Moderately exposed reefs and boulders consisting of hard sandstone (Cretaceous:Upper Greensand) covered by limpets and barnacles. There is little fucoid growth above low water neap tide level. Deep crevices exist between the boulders and within the reefs, which are of variable slope and aspect.

APPENDIX III

Results summary of survey along Contentin peninsula, France, 25-28 October 2000. Abundance scale follows Crisp & Southward (1958) shown in Table 3.2 ('P' indicates species present, but not counted); Barnacle densities are No. per cm^2.
Order of survey locations shown is from west to east side of peninsula.

	Tide Ht.	Cap de Carteret	Vauville	Baie Ecalgrain	Cap de la Hague	Pt.Racine. Anse St.Martin	Omonville-la-Rogue	Roch. du Castel-Venden	Nacqueville	Bretteville	Cap Levy	Pointe de Barfleur	Barfleur	St.Vaast	Grandcamp	Grandecamp / Pt.du Hoc	Port-en Bessin-Huppain
Chthamalus montagui (no. per cm^2)	HWS	0.12	0.06	0.01	0.002	0.002	0.001	0.002	0.03	R	0.002	N	R	N	N	N	N
	HWN	0.08	0.02	N	0.002	0.01	N	N			N	N	N	N	N	N	N
	MTL	0.006	0.002	N	N	0.002	N	N			N	N	N	N	N	N	N
	LWN	N	N	N	N	N	N	N			N	N	N	N	N	N	N
Chthamalus stellatus (no. per cm^2)	HWS	0.03	0.08	0.16	0.021	0.01	0.01	0.004	R	R	0.012	R	R	N	N	N	N
	HWN	0.08	0.02	0.07	0.008	0.04	0.03	0.02			0.05	N	N	N	N	N	N
	MTL	0.002	0.002	0.008	N	0.12	0.004	0.01			0.006	N	N	N	N	N	N
	LWN	N	N	0.002	N	N	N	N			N	N	N	N	N	N	N
Semibalanus balanoides (no. per cm^2)	HWS	0.01	0.56	0.6	0.92	0.03	0.08	0.08	0.5		0.26	0.07	0.67	0.03	F		
	HWN	1.2	A	A	A	0.14	A	A			0.31	1.2	2.52	1.2	C	A	
	MTL	3.5	A	A	A	A	A	A			0.27	4.7	2.15	0.43	A	C	A
	LWN	1.8	A	A	A	A	A	A			A	0.25		0.63	A		
Elminius modestus (no. per cm^2)	HWS	0.01	0.12	0.02	0.01	0.01	0.02	0.01	0.24		0.04	0.02	0.13	0.37			
	HWN	0.08	C	0.04	0.01	0.005	P	0.01			0.06	N	0.17	0.2			
	MTL	P	C	0.04	0.01	N	P	0.01			0.05	N	0.07	N			P
	LWN	0.04	F	0.02		N	R	P			P	N	0.05	0.03			
Balanus perforatus	LWN	F	F	C	F	F	O	N	N		A	F	C	A	N	R	A
Gibbula umbilicalis	LWN	A	A	A	A	A	A	A		C	A	A	A	A	A	A	A
G. pennanti	MLW	C	O	N	A	A	A				A	A		N	N	N	N
Osilinus lineatus	HWN	O	F	A	A	A	A	A	A	C	A	A	A	A	C	F	R
Patella vulgata	MTL	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
P.depressa	MTL	O	C	C	C	C	C	A	P	P	F	F	N	N	N	N	N
P. ulyssiponensis	MLW	N	F	F	C	F	F	C	P		F	F	N	N		N	N
Anemonia viridis	MLW	C		P							F			O			C