UNIVERSITY OF SOUTHAMPTON

POPULATION STUDIES OF A COMMERCIALLY FISHED BIVALVE, *MERCENARIA MERCENARIA* (L.), IN SOUTHAMPTON WATER

BY

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A thesis submitted to the University of Southampton for the degree of Doctor of Philosophy

DEPARTMENT OF OCEANOGRAPHY

JUNE 1988

ACKNOWLEDGEMENTS

I am greatly thankful to my supervisor, Dr. M.Sheader for his generous help and guidance throughout the course of this study.

I am grateful to Professor A.P.M. Lockwood for his personal interest and encouragement. My thanks are also due to Dr. D. Purdie. I also sincerely thank all the technical staff of the Oceanography Department, especially D. Hutchinson for his assistance in the boatwork.

I am particularly indebted to Dr. and Mrs. M. Nossier for their continuous advice and guidance during the study period.

The help with the computer programming by Khirulazhar and the help by H. Widatalah are appreciated.

I extend my gratitude to my parents and especially to my wife for their endless patience and moral support throughout the study period.

Finally my special thanks is due to the Directorate of Scholarship at the Ministry of Education in Bahrain for awarding me an extended scholarship.

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The hard shell clam Mercenaria mercenaria (L.) is a long-lived animal tolerating wide environmental variations. The animal is an important constituent of the macrobenthic fauna in Southampton Water. A study was made of various aspects of the population in relation to absence of cooling water discharge caused by closure of Marchwood power station, increased fishing activities and the frequent failure of settlement in recent years. The littoral population at 12 sites was sampled in two successive winters. The highest density of clams was at Netley and the lowest at Royal Pier, with actively growing and reproducing populations extending to Solent Breezes and Lee-on-Solent in the eastern Solent. The total stock estimated for littoral sites above Hamble Spit has shown a reduction of about 50% since 1970. The population at present is dominated by large and old individuals originating from settlements in 1971, 1972, 1973 and 1976. These year classes and a recent settlement in 1984 seem to coincide with low river flow during August, September and October of each year. The annual production of littoral Mercenaria populations at both Marchwood and Lee-on-Solent approximated to $3gm^{-2}yr.^{-1}$. Although Mercenaria dominates the biomass of the benthic fauna, energetically its role in the ecosystem has been diminished in recent years as a result of change in the population structure towards larger / older individuals.

Growth in Mercenaria was analyzed according to the Logistic, the Gompertz and the Monomolecular models. The Gompertz provides an accurate model of ontogenic growth in Mercenaria. Highest predictive growth rate in shell length was found in littoral population at Solent Breezes, Hamble Spit, Weston and Netley. Maximum growth rates in shell length were achieved during the 2nd and 3rd years, whereas maximum growth rates in flesh weight was recorded during the 4th and 5th years, indicating that during the early stages and before gonad maturation a greater proportion of energy is directed to formation of shell rather than in flesh.

Monthly gamete counts at Marchwood and Lee-on-Solent permitted assessment of the reproductive cycle, and the consequences of gamete production on variation of growth at both sites were discussed. It appears that at Marchwood a greater proportion of available energy is devoted to gamete production and less to somatic growth than at Lee-on-Solent. The gamete counting also revealed that the peak of spawning occurred at the end of summer and during autumn, this result was supporting data obtained by weekly monitoring of larvae. Results suggest that Mercenaria is capable of spawning at 16°C, which is a lower temperature than that reported in earlier works, indicating a physiological adaptation to local conditions. Growth, survival and environmental factors affecting abundance of planktonic larvae over an 8 days period were studied. It appears that larvae remain in the plankton for about 15 days, at summer temperature. The 12 hours survey of vertical distribution provides evidence that larvae are retained within Southampton Water through behavioural regulation during different stages of the tide. The distribution, seasonal growth and survival of spat throughout the estuary, were investigated. First settlement of the spat in 1984 took place in the latter part of August. The population is seen as stock in decline largely resulting from overfishing and failure of spat settlement in recent years.

CHAPTER ONE : GENERAL INTRODUCTION

The hard-shell clam, Mercenaria mercenaria (L.), family Veneridae, is a warm / temperate filter-feeding infaunal bivalve. The animal is widely distributed in the USA, where it typically occurs in the littoral and sublittoral zones of coastal embayments and estuaries from the Gulf of St. Lawrence to the Gulf of Mexico (Ansell, 1968).

Mercenaria is of great commercial importance, and various aspects of its biology in North American waters have been extensively studied, as exemplified by the voluminous literature. Kennish et al. (1984) reviewed all ecological works on Mercenaria in Barnegat Bay. Ansell (1968) determined growth characteristics for Mercenaria throughout its geographic range, based on all the previous works. The reproductive biology (Davis and Chanley, 1956; Loosanoff, 1937a, 1937b; Loosanoff and Davis, 1950; Porter, 1964, Dalton, 1977; Bricelj and Malouf, 1980; Eversole et al. 1980) and the occurrence of Mercenaria larvae and their settlement have also been investigated (Carriker, 1952, 1956, 1962; Davis and Calabrese, 1964; Landers, 1954; Loosanoff and Davis, 1950).

A growing knowledge on the effects of various environmental conditions, diseases and genetic history are rapidly accumulating from research in laboratories and commercial hatchery cultures in which various techniques have been developed for assessment of growth and mortality during larval development (Gallager and Mann, 1981; Gallager et al., 1986). The wide distribution of Mercenaria reflects its tolerance to a wide range of environmental conditions. Adult Mercenaria have been shown to tolerate low oxygen levels (less than 1

mgO_2l^{-1}) for 3 weeks (Savage, 1976) and can live for 8 weeks out of water with complete recovery on immersion (Green and Becker, 1977). Mercenaria has extremely high tolerance to NO_2^-, NO_3^-, NH_4^+ and orthophosphate (Epifanio and Srna 1975), and can regulate its uptake of certain metals. It tolerates high concentrations of copper at levels which prove to be toxic to Mya arenaria (Pringle et al., 1968). In addition food requirements of Mercenaria larvae are less restricted than in some other bivalves. Larvae seem to settle on bottoms ranging from sand to a mixture of sand and mud, containing sufficient loose materials to permit them to burrow as spat (Carriker, 1961; Keck et al., 1974). Pratt and Campbell (1956) observed that growth was relatively slow in sediment that contain quantities of silt-clay in comparison to sandy sediment, coarse gravel or shells. Thorson (1966) concluded that Mercenaria larvae may delay metamorphosis in nature until a favourable habitat is found, although they metamorphose readily in clean containers in the laboratory (Carriker, 1961).

In different geographic regions Mercenaria spawns at a wide range of temperature (20 - 30°C) depending on local temperature and availability of food. Although Mercenaria reproduces over a long period, the peak of spawning is restricted to the warmest summer months.

In Mercenaria there is little storage of food reserve and gonad development appears to take place when sufficient food is available (Bricelj et al., 1980).

In Southampton Water, the occurrence of the clam was first reported by Heppell (1961), and Mitchell (1974) suggested, citing evidence, that Mercenaria was first introduced to the estuary around

1925. Since 1925 the animal has become firmly established in Southampton Water. Ansell (1964a) attributed such colonisation to the decline of the indigenous but pollution intolerant Mya arenaria, therefore vacating a niche which became occupied by Mercenaria. Ansell (1961) also added that the warming effect caused by the cooling water at Marchwood power station enabled the clam to spawn more frequently, and Mitchell (1974) demonstrated that recruitment in the estuary relied on Mercenaria spawning in the upper reaches. Clam density in Southampton Water during 1974 compared well with the most productive beds in the USA, but serious deterioration in clam productivity has occurred over the years as a result of the combined effects of poor recruitment and overfishing. Condition and growth rates were reported to be lower than that of the clams at the typical USA sites (Ansell, 1964a; Coughlan 1972). Oyenken (1980) concluded that no successful settlement took place during 1978 - 1979, and production of the macro-infaunal community was dominated by large and old Mercenaria. This would indicate that production rates, growth rates and condition index values at present might be expected to be even lower than reported earlier, as a result of the change in the population structure towards old and large individuals.

Mercenaria is quoted as requiring a temperature of above 20°C for spawning in American waters, but in Britain it appears to be able to spawn at a slightly lower temperature, 18 - 19°C, (Mitchell, 1974).

In Southampton Water, although the spawning of Mercenaria lasts for several months and during some parts if not all the time, environmental factors that stimulate spawning of the animal and support survival and settlement of larvae must exist, failure of spatfall seems to be the case. It appears therefore that the planktonic larvae or spat do not seem to survive the different sources of mortalities such as predation, dispersion, flushing and starvation, that occur during the initial stages despite extremely high numbers of larvae produced in the water column each summer. If this supposition is false one might expect to find heavy and regular settlements in certain areas where larval dispersal is low and predators are scarce.

The main objectives of the present work were to assess changes in the characteristics of the Mercenaria population including changes in age and size structure, growth, biomass and production based on annual surveys of the littoral Mercenaria population throughout Southampton Water. Performance of the animal was investigated by estimating production and biomass at 2 sites characterised by different environmental conditions, Marchwood and Lee-on-Solent, which are situated at the northern and southern extremes of the sampling area, respectively.

Growth and growth rates were determined by the use of 3 mathematical models which have the advantage of reducing a large set of data and producing graphical representations of growth rates of the population over the years. Application of the growth models on the annual changes in shell length and the corresponding changes in tissue ash free dry weight, gave some indication of the pattern of utilisation of energy at different ages. Morphometric characteristics of different littoral population were investigated by observing readily measurable characters such as tissue dry and ash free dry weights, shell length,weight, height, width, breadth, curvature and thickness.

The clam larvae were investigated during several ecological surveys in which seasonal, spatial, daily abundance and vertical distribution of the larvae were determined. Behaviour of *Mercenaria* larvae in relation to a spring tide was monitored over a 12-hour tidal cycle.

The settlement of *Mercenaria* larvae was investigated throughout Southampton Water over one year and the subsequent growth rates and mortality of spat under natural conditions were calculated.

This information is essential for management of the clam fishery which has remained unmanaged up to the present time and during this study. The Ministry of Agriculture, Fisheries and Food (MAFF) has become interested in the clam stock only in recent years and has begun to survey the stock at two year intervals. As yet the stock is not managed, with no minimum size or quota system. With lack of management, the clam stock will be seriously depleted and become unprofitable in the near future.

CHAPTER TWO : POPULATION DYNAMICS

2.1 INTRODUCTION

The quahog or hard-shell clam, Mercenaria mercenaria L. is widely distributed in North America from the Gulf of St. Lawrence to the Gulf of Mexico, forming an important constituent of the fauna of many estuaries and coastal embayments (Ansell, 1968). The clam has great commercial importance and aspects of its biology have been intensively studied especially in the U.S.A. (Chesnut, 1952; Carriker, 1956 and 1959; Davis, 1958; Pratt, 1953; Loosanoff and Davis, 1950; Saila and Pratt, 1973; Rhoad and Pannella, 1970; Dalton, 1977, Bricelj and Malouf, 1980; and Eversole et al., 1980).

In Britain several studies have been initiated following the successful colonisation and reproduction of Mercenaria in Southampton Water. Heppell (1961) was the first to record the occurrence of Mercenaria in Southampton Water. Ansell (1963a) gave a brief summary on distribution of the animal around the British Isles, and followed its growth in selected places.

Coughlan and Holmes (1972) re-examined the Mercenaria population in Southampton Water and found no evidence of any change as far as distribution and age were concerned since Ansell's study. Mitchell (1974) investigated the structure and dynamics of the population in relation to spawning, recruitment, growth, mortality, larval distribution and followed seasonal biochemical changes in adults and settled spat. Oyenekan (1980) studied production of benthic macro-infauna in Southampton Water and found that Mercenaria emerged as the most productive and biomass dominant species.

In the present work different characteristics of the Mercenaria population in Southampton Water are investigated in order to assess changes and consequences of the closure of Marchwood power station and the increased fishery pressure on recruitment and future stocks.

2.2 MATERIAL AND METHODS

2.2.1 Survey of littoral population

Mercenaria populations in Southampton Water were extensively investigated on several occasions. Littoral populations of Mercenaria at 12 sites were sampled in winters (December, January and February) of 1983 and 1984 (Fig. 2.1). In addition monthly collections of Mercenaria were made at Marchwood and Lee-on-Solent from March 1985 to March 1986. The littoral populations were sampled randomly by hand raking the bottom sediment from the midlittoral area at the upper edge of the clam distribution to the water edge at low tide. At each site the numbers of clams within 5 to 10 of $0.2m^2$ quadrats was noted. For the annual surveys, a total of 70 or more individuals were collected within 2 to 3 hours spent at each site. In addition sediment was sieved through a 2mm sieve in order to collect small sized individuals. Air and sediment temperatures were measured at each site using a glass thermometer. Most of the sampling was carried out during spring low tides.

2.2.2 Surveys of Sublittoral Populations

Semi-quantitative samples of sublittoral populations were collected from different sites in Southampton Water, adjacent to the littoral sites, using an oyster dredge, 80cm wide and double mesh bag, with the inner bay having a 10mm mesh. The dredge was towed at a speed of approximately 1.5 knots for 10 minutes along a line parallel to the shore. Two tows were made at each site and an additional con firmatory one was made whenever the number of animals was low. The surveys were carried out at different times, in March, October 1984 and July, October 1985.

Quantitative samples of sublittoral Mercenaria were collected during February 1985 at a range of sites in the estuary using a Baird grab ($0.5m^2$). The survey was repeated in August 1985 using a Van Veen grab ($0.1m^2$). At each site 4 to 5 samples were collected and were sieved on board using a 1mm sieve.

2.2.3 Laboratory Treatment of Animals

In the laboratory all Mercenaria were kept in clean seawater for 24 hours then stored in a deep freeze at -20°C. Animals were removed a few days later from the freezer and left to thaw and gape for an hour after which the flesh was removed and the wet, dry and ash free dry weight were recorded as described in Chapter 3.

Empty shells were numbered and soaked in 10% (v/v) sodium hypochlorite solution which oxidises and removes the black reduced layer that stains the outer surface of the shell thus making observation of growth rings easier. Age of the animal was determined by counting the number of growth rings. Ansell (1964a) and Mitchell (1974) validated the use of annual growth rings in estimating the age and past growth history for Mercenaria, concluding that each ring represents a winter growth check. In older Mercenaria (more than 12

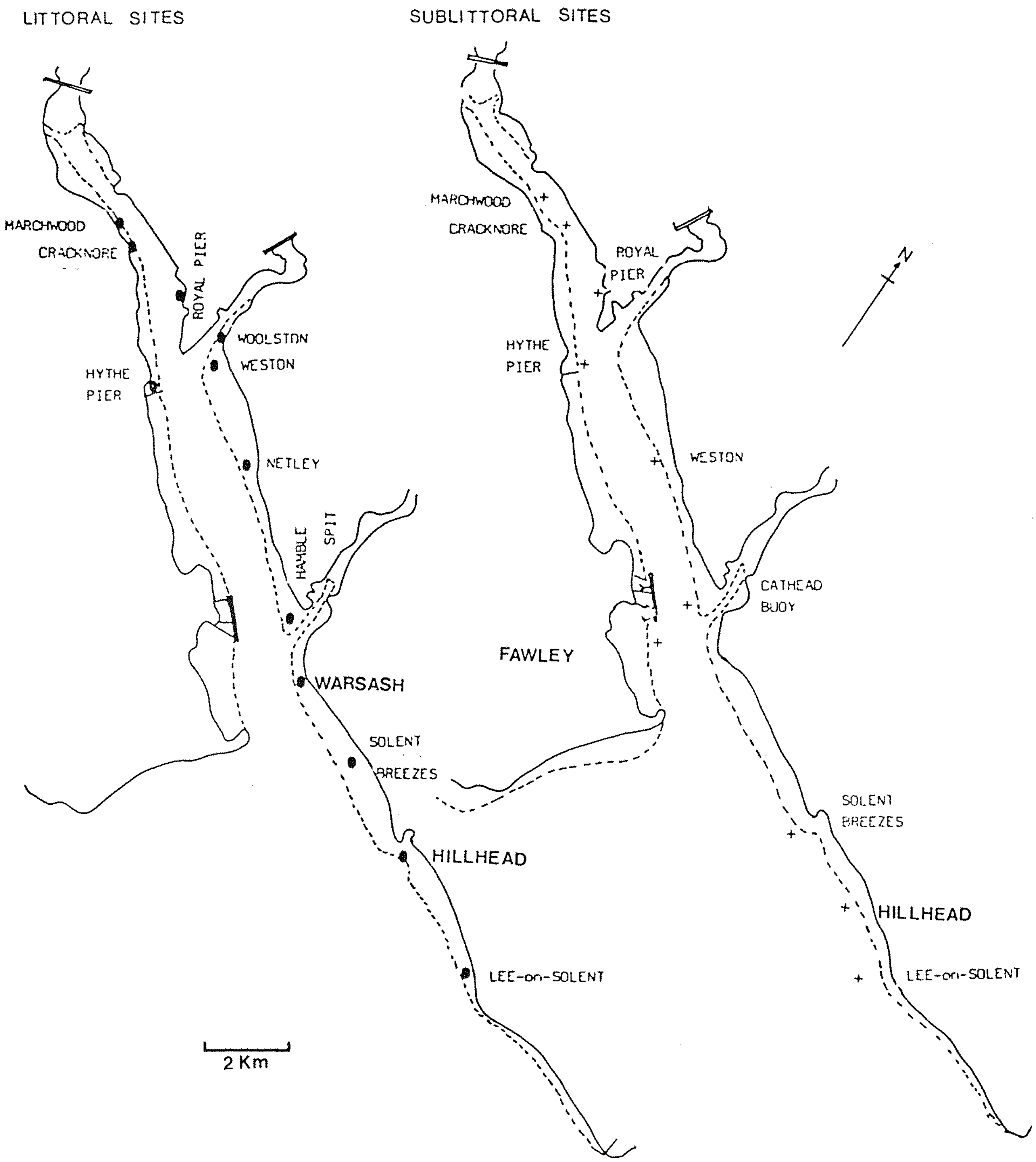


Fig. 2.1 Sampling sites of littoral and sublittoral Mercenaria populations in Southampton Water during 1983 - 1985

years) growth rings are formed closer together, and counting of growth rings, therefore becomes difficult. However, aging of older individuals was confirmed by a method similar to Mitchell (1974) where the edge of one valve was struck with a heavy knife. This gave a clean cleavage of the shell edge allowing growth rings to be seen more readily. Total length and length at each growth ring was measured along the anterior-posterior axis parallel to the hinge line. The measurements were made to the nearest 0.05mm using callipers.

2.2.4 Estimation of Mercenaria Stock

Estimation of the stock was restricted to the area between Marchwood and Hamble Spit because only small stocks are present at the lower end of the estuary. In addition, the stock size of *Mercenaria* calculated by MAFF, with which results of the present study were compared, was confined to the upper and central parts of the estuary. Stocks of the littoral and sublittoral areas were calculated separately. The littoral area was taken as the area which lies between the mean low water marks and the mean high water mark which are shown on Ordnance Survey maps (numbers SU40NE, SU41SW and SU41NE). Width and length of the littoral zone were measured at different points and a mean value was calculated. The area of the littoral zone was determined by multiplying mean width by the mean length for each section. A similar approach was followed in estimating the area of different parts of the sublittoral sites. The sublittoral zones was considered as the area that lies between the mean low water line and the dredged channel. The sublittoral zones was divided into different sections. Width and lengths for each section were used to calculate the area of each section. The mean number and mean weight of *Mercenaria* at each sampling site were extrapolated to the area of each littoral or sublittoral section, giving stock size and tonnage in each section. Summation of all the estimates gives stock size and tonnage for all the littoral and sublittoral areas. Such a procedure, was also followed to calculate the approximate stock of the animal, using data provided in the previous works of Mitchell (1974) and Hibbert (1976) on the littoral population, and Oyenekan (1980) on the sublittoral one.

The method used is obviously open to criticism, but aims to give a rough estimate of the total stock available within the area.

2.3 RESULTS AND DISCUSSION

2.3.1 **Density and Distribution**

The mean number of *Mercenaria* recovered at littoral and sublittoral sites in 1983 and 1984 and at the few sublittoral sites in 1985 are shown in Table 2.1. *Mercenaria* was widely distributed in Southampton Water, and showed a comparatively higher concentration in the littoral than the sublittoral sites, which can be mainly attributed to the greater fishing intensity in the sublittoral. The littoral population on the other hand was not reduced significantly between 1983 and 1984, indicating therefore less fishery pressure. The largest number of *Mercenaria* was recorded at Netley Hard during 1983 and the lowest number occurred at Royal Pier in 1984. In general a growing colony of *Mercenaria* seems to have been established in the lower part, of Southampton Water in recent years, mainly at Solent Breezes and Lee-on-Solent. Mitchell (1974) reported that the density of *Mercenaria* decreased at the seaward end of the estuary.

Table 2.1 : Density of individuals (mean no/m^2 $\pm$ S.D.) of littoral and sublittoral *Mercenaria* populations in Southampton Water in 1983 - 1985

Sites	Littoral		Sublittoral
	1983	1984	1985
Marchwood Outfall	N.S.	19.6±10.8	4±1.6
Marchwood	15.5±6.7	8.8±6.2	Q.S.
Royal Pier	N.S.	7.2±4.2	N.S.
Hythe Pier	N.S.	15.5±7.2	3±1
Woolston	N.S	15.5	Q.S.
Weston	11.3±3.9	N.S.	Q.S.
Netley Hard	24.2±10.9	12.2	6±4
Netley Great Dome	N.S.	N.S.	22±11.3
Hamble Spit	19.6±4.3	20.6±9.8	Q.S.
Warsash	N.S.	N.S.	Q.S.
Solent Breezes	18±10.8	11.8±5.7	Q.S.
Hill Head	N.S.	10.3	Q.S.
Lee-on-Solent	N.S.	16.3±6.7	Q.S.

N.S. = Not sampled.

Q.S. = Qualitative samples only.

2.3.2 Age and Size Structure

In this study, age and size of *Mercenaria* were determined. The year class was taken to represent the year in which the animal was spawned. The age composition of the littoral population in 1983 and 1984 are shown in Table 2.2 and Fig. 2.2. The results demonstrated that the year classes 1971, 1972 and 1973 were abundant throughout Southampton Water, with 1976 year emerging as the dominant year class at Solent Breezes, Hillhead and Lee-on-Solent. There were records of successful settlement years from other surveys prior to this study. Mitchell (1974) found the dominant year classes were 1959, 1961, 1965 and 1968. Hibbert (1976) on the other hand reported that year classes 1965, 1968 and 1970 dominated the population at Hamble Spit. He added that a successful spatfall in the local population only occurred irregularly (in 1959, 1961, 1968 and 1970) and all were good years. Oyenekan (1980) concluded from *Mercenaria* results, that no settlement was achieved in 1978 and 1979 (respectively). Irving (1983) reported that most of the *Mercenaria* she found were in the 8 to 9 age classes (i.e. spawned in 1975 and 1974).

In the present study, dominance of the year classes 1971, 1972, 1973 and 1976 cannot be explained by records of mean maximum temperature for August, September and October (Table 2.3) because temperature did not vary significantly between the summers of the different years. On the other hand data of river flow for the river Test (Table 2.3) showed that the mean flow in August, September and October of 1973 and particularly 1976 were the lowest on record. This might explain, therefore the dominance of 1973 and 1976 year classes at Marchwood, Royal Pier, Solent Breezes, Hillhead, Lee-on-Solent

Table 2.2a : Percentage age distribution of the littoral *Mercenaria* populations in 1983

NO. OF GROWTH RINGS	YEARS SPAWN ED	SITES						
		MARCHWOOD	ROYAL PIER	WOOLSTON	WESTON	NETLEY	HAMBLE SPIT	SOLENT BREEZES
0	1982	-	-	-				
1	1981	1.3	-	-				
2	1980	-	-	-				
3	1979	-	-	-				
4	1978	-	-	-	1.3			
5	1977	3.9	-	7.7	6.4	7.3	2	13.3
6	1976	1.3	-	5.8	5.1	4.9	2	30
7	1975	5.3	5.3	3.8	3.8	-	3	3.3
8	1974	11.8	5.3	7.7	5.1	2.4	15.2	3.3
9	1973	32.9	26.3	11.5	16.7	19.5	34.3	6.7
10	1972	18.4	42.1	32.7	34.6	26.8	32.3	10
11	1971	17.1	15.8	23.1	23.1	22	5.1	10
12	1970	6.6	5.2	3.8	2.6	7.3	5.1	10
13	1969	1.3	-	3.8	0	7.3	1	10
14	1968	-	-	-	1.3	2.4	-	-
15	1967	-	-	-	-	-	-	-
16	1966	-	-	-	-	-	-	3.3
17	1965	-	-	-	-	-	-	

Table 2.2b : Percentage age distribution of the littoral *Mercenaria* populations in 1984

NO. OF GROWTH RINGS	YEARS SPAWNED	SITES						
		MARCH-WOOD	ROYAL PIER	HYTHE PIER	WESTON SHORE	HILL-HEAD	SOLENT BREEZES	LEE-ON-SOLENT
0	1983	-						
1	1982	-						
2	1981	-	3.3					
3	1980	-	-					
4	1979	-	-					1.5
5	1978	-	13.3				7.1	3
6	1977	-	10	9.4		11.8	30	18.2
7	1976	1.5	-	15.6	2.6	47.1	31.4	18.2
8	1975	4.3	3.3	3.1	-	11.8	4.3	3
9	1974	18.8	6.7	3.1	2.6	-	-	3
10	1973	15.9	23.3	9.4	-	-	1.4	28.8
11	1972	34.8	16.7	18.8	7.7	5.9	-	16.7
12	1971	15.9	16.7	12.5	20.5	17.6	8.6	6.1
13	1970	5.8	6.7	6.3	41	5.9	8.6	1.5
14	1969	1.5	-	6.3	23.1	-	2.9	-
15	1968	-	-	-	2.6	-	2.9	-
16	1967	-	-	-	-	-	1.4	-
17	1966	-	-	15.6	-	-	-	-
18	1965	-	-	-	-	-	1.4	-

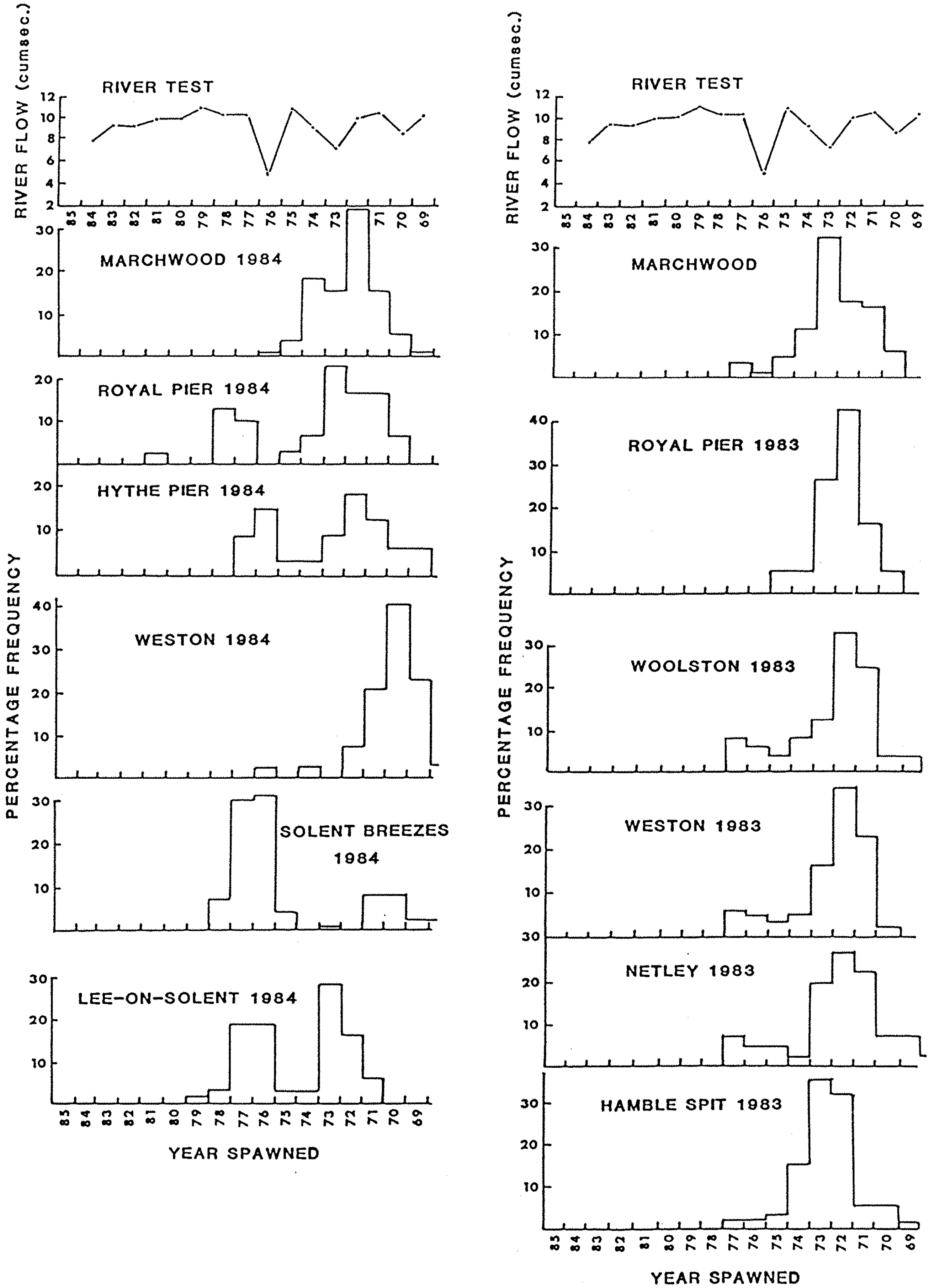


Fig. 2.2 Mean River Test flow (cumsec.) at Broadland in August, September, and October during 1970 - 1984 and percentage of age composition of Mercenaria in Southampton Water

Table 2.3: Mean of maximum temperature (°C) at Hythe Pier, and mean River Test flow (cumsec) at Broadland, in August, September and October from 1970 to 1983

Parameters	Years													
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
T°C	19.6	16	18.9	15.9	17.9	19	18	18.6	18.4	17.6	18.8		16.17	
River flow (cumsec)	10.70	10.13	7.26	9.16	10.97	4.80	10.40	10.27	11.09	9.91	9.87	9.25	9.55	7.9

(Fig. 2.2). The recent settlement in summer of 1984, mainly in the Hythe-Dibden Bay area also coincided with reduced river flow during the summer months.

The size structure of the littoral population throughout Southampton Waters in 1983 and 1984 is illustrated in Fig. 2.3. Spat settlements that occurred in summer 1984 is not included in the results, because no survey of the littoral population was carried out in the winter of 1985. A characteristic feature of the Mercenaria population during both surveys (1983 and 1984) was the high frequency of medium-sized individuals (60 - 80mm) forming 60% to 55% of the population, and on the other hand, individuals smaller than 50mm formed 2% of the population. Furthermore, there were differences in frequency of the size groups especially in brood (35 - 50mm) and juvenile individuals (10 - 35mm) between the two annual surveys. This might indicate that brood (35 - 50mm) individuals in 1983 have grown to the small-size category (50 - 65mm). It might also indicate that reduction in the remaining categories occurred as a result of fishing mortality.

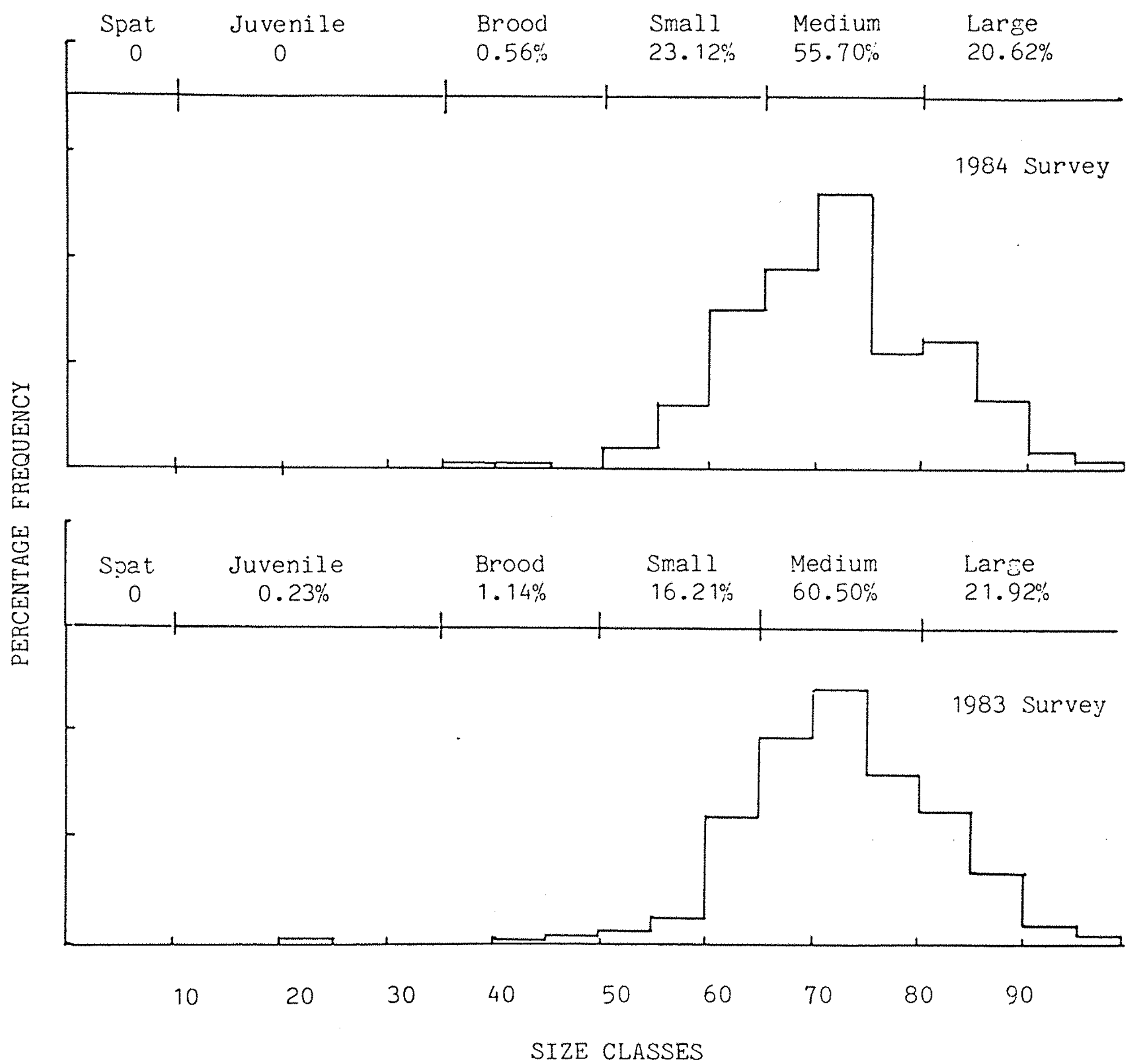


Fig. 2.3 Percentage of size class distribution of littoral population throughout Southampton Water during 1983 and 1984.

2.3.3 Mercenaria Stock

Estimation of the *Mercenaria* stock expressed in numbers and tonnage in different littoral and sublittoral areas above Hamble Spit from 1970 to 1985 are given in Table 2.4. The littoral areas seem to support comparatively higher numbers of *Mercenaria* than the sub-littoral areas. Although, some littoral sites (Weston, Netley, Hamble) have shown an increased stock since 1971, which can be attributed to successful settlement in 1971, 1972 and 1973 at those sites. However, in general the total littoral stock in all Southampton Water from 1970 to 1983 experienced a 75% and 47% reduction in the total numbers and tonnage, respectively. Reduction of the littoral stock has been slower than the sublittoral stock which has been reduced dramatically to 12% of the stock in 1979 according to a MAFF report in 1985. It is important to point out that MAFF estimate did not include *Mercenaria* from the littoral areas, where a higher density and biomass was found during this study.

Although the discrepancy in the estimate of the clam stock between the present study and MAFF, might be attributed to the different methods used, it might also indicate that the littoral stock has not been reduced as dramatically as the sublittoral stock which is under increased fishing pressure. The fishing boats that dredge for clams have been increased from 10 boats in 1979 to 40 or more in 1983. More recently a number of hydraulic suction dredgers, which have a higher fishing efficiency, have been seen dredging for clams in Southampton Water. In addition the intensive dredging has been shown to have deleterious effects on the benthic community. Sheader (1986) reported a decline in dominant species such as *Mercenaria* in areas of intensive dredging.

In addition to the increased fishery operations, several works (Mackenzie, 1979; Bricelj, 1980; Walker, 1985) have concluded that a characteristic feature of the clam fishery is the irregular and infrequent supply of recruits to the adult population.

Table 2.4 : Estimates of *Mercenaria* stocks at sampling sites and throughout Southampton Water during 1970 - 1985

Years	Sites		Total area (hectares)	Density ($No.m^{-2}$)	Mean biomass (flesh + shell) (kgm^{-2})	Total stock ($\times 10^6$)	Total tonnage (metric tons)
1970	Marchwood	(littoral)	6.98	54.6	2.95	3.8	205.90
1970	Weston	(littoral)	84.30	1.4	0.20	1.2	168.6
1970	Netley Hard	(littoral)	35.95	3.7	1	1.3	359.5
1970	Hamble Spit	(littoral)	91	14	1.60	12.7	1456
1976	Hamble Spit	(littoral)	91	16.9	0.71	15.4	646.1
1983	Marchwood	(littoral)	6.98	15.5	1.2	1.1	83.76
1983	Weston	(littoral)	84.30	11.3	2.1	9.5	1835.4
1983	Netley	(littoral)	35.95	24.2	3.16	8.7	1136
1983	Hamble Spit	(littoral)	91	19.6	1.72	17.8	1565
1970	All Southampton littoral areas		289.4	22.5	3.20	65.1	9260.8
1983	All Southampton littoral areas		289.4	16.92	1.49	48.9	4312.1
1980	All Southampton sublittoral areas		271	16.17	1.84	43.8	499.2
1985	All Southampton sublittoral areas		271	7.2	0.76	19.5	204.8

N.B. Density and biomass data in earlier years are taken from Mitchell (1974), Hibbert (1976) and Oyenekan (1980)

CHAPTER THREE : GROWTH

3.1 INTRODUCTION

Growth is an important feature of the study of a population. It provides an accurate picture of species performance in relation to environmental factors (Odum, 1971). There are several methods of studying growth in marine invertebrates, as outlined by Crisp (1984). One approach measures population growth based on the study of the periodical progression of size classes over time. The second approach is related to study of individual growth by means of measuring growth rings, where each ring represents an annual growth increment. The two concepts of growth rates are different and the values will not yield the same results. Crisp (1971) mentioned that individual growth rate and population growth rate are only equal if mortality is independent of size. Furthermore, Odum (1971) pointed out that a population has characteristics that differ from properties of an individual. Density, growth rates, mortality, age distribution, sex ratio and growth forms, are all characters of a population, whereas an individual has a life cycle, development, feeding and age but does not have a birth rate and death rate.

Recently new methods for studying growth rate over short time periods (for example during a tidal cycle, daily and seasonal growth) have been developed for animals with shells. Richardson (1979) estimated tidal growth of cockles using a peel acetate technique. Similarly Kennish and Loveland (1980) applied such a technique to study growth in dead assemblages of clams. Another method of studying growth rate over short time periods involves the use of Laser techniques (Stromgren, 1975).

Growth of bivalve lends itself very well to mathematical modelling because growth represents a continuous change of any shell characters with time. Causton (1983) mentioned that growth is one of the biological topics, where mathematical analysis has been repeatedly employed, either in the analysis of growth of cells, whole organism or populations. For such analysis, calculus which is a branch of mathematics that deals with rates is commonly used. The mathematical description of any function (e.g. growth) has the advantage of reducing a large set of data into few parameters which are interrelated and expressed by an equation. Other advantages of modelling according to Preece (1978) are:

1 - The reduction of a large amount of growth data collected on each individual, facilitating a comparison of the growth of individuals.

2 - Growth parameters of the model provide information on the relationships within the growth processes, in addition to the examination of the relationship between physical aspects of the growth and other observations.

There have been many attempts to represent the growth curve using mathematical functions. Nichols et al. (1985) described growth of Echinus esculentus according to a logistic growth model. Similarly Crossner (1977) reported that growth of the European starling Sturnus vulgaris follow a logistic function. Kennish and Loveland (1980) concluded that the Gompertz model can best represent growth of

Mercenaria mercenaria. The Gompertz growth model has also been used to describe human growth (Marubini, 1972) and the growth of tumour cells (Laird, 1964).

In the present study, 3 of the most widely used growth models namely the Logistic, Gompertz and Monomolecular models were applied to the growth data of Mercenaria, using the modification of the mathematical procedures of Kennish and Loveland (1980). A computer programme was developed to calculate various parameters of the growth models. The major objective of the work was to investigate which of these 3 models best represents growth of Mercenaria in Southampton Water, and subsequent calculation of growth rates. This requires fitting each equation to the growth data and selecting the best fitting model. Predictive growth curves can be constructed once parameters are estimated.

3.2 GROWTH MODELS

The application of growth models, involves linear transformation of the growth functions followed by linear regression of the transformed data from which values of different growth parameters are obtained. Determination of all the parameters permits the calculation of predictive growth curves.

3.2.1 The Logistic Model

The Logistic model was first proposed by Verhulst in 1883 and rediscovered by Raymond Pearl and J. Read (1920). It is basic and a simple form model used for the description of exponential growth of animal population in an unlimited environment. The basic form of the

Logistic model is given by:

$$dN/dt = rN$$

where dN/dt refers to the change in numbers (dN) per time interval (dt), with r as the specific growth rate.

Odum (1971) enlisted different forms of the Logistic equations as :

$$dN/dt = rN\,[(K - N)/K] \quad \text{or} \quad dN/dt = rN - r/K\,N^2$$

$$\text{or} \quad dN/dt = rN\,(1 - N/K)$$

Similarly there are different forms of integration of the Logistic model which are expressed as follows:

$$N_t = N_0\,e^{rt} \quad \text{or} \quad N_t = \frac{K}{1 + e^{a-rt}}$$

where N_t = number of individuals within a population at time t

N_0 = number of individuals at time zero

K = carrying capacity or maximum population size

a = constant of integration defining the position of the curve relative to the origin

r = intrinsic rate of increase or specific growth rate

Variations of the Logistic equation have been employed in the analysis of growth of cells (Laird, 1964) and growth of whole organisms (Marubini, 1972).

Here, a modified form of the Logistic model which has been suggested by Kennish and Loveland (1980) will be followed, with subsequent derivation of growth rate. Kennish and Loveland (1980) applied the following Logistic form for description of growth in <u>Mercenaria</u>:

$$L_t = L_{max} \left[1 + e^{-kt} \left(\frac{L_{max} - L_{(o)}}{L_{(o)}} \right) \right]^{-1} \qquad \text{-------------- (1)}$$

where L_{max} = maximum asymptotic length

$L_{(o)}$ = initial length

$L_{(t)}$ = length at time t

k = intrinsic growth factor

Growth rate which is a measure of change of length with time is given by differentiation of equation (1):

$$dL/dt = kL_t - bL_t^2 \qquad \text{------------------ (2)}$$

If we let $k/b = L_{max}$, then dividing equation (2) by L_t, we get:

$$\frac{dL}{dt.L_t} = k - bL_t \qquad \text{--------------------- (3)}$$

Equation (3) represents the linear form of the Logistic model (Kennish, and Loveland, 1980). The actual calculation of equation (3) is simple. The data on length of each growth ring L_t are converted into two additional arrays L_{avg} and dL_t / $dt.L_{avg}$, according to the following steps:

$$L_{avg} = \frac{L_t + L_{t+1}}{2} \quad \text{------------------------} \quad (4)$$

and

$$\frac{dL}{dt.L_{avg}} = \frac{L_{t+1} - L_t}{L_{avg}} \quad \text{------------------------} \quad (5)$$

Linear regression of L_{avg} (x-axis) and dL / dt.L_{avg} (y-axis) will result in a straight line of slope = -b and y-intercept of k. These results are used to calculate a predicted value of L_{max}, where L_{max} = k/b = intercept/slope

Knowing values of L_{max}, k and $L_{(o)}$, equation (1) can be used to calculate predicted length at each age.

3.2.2 <u>The Gompertz Model</u>

In 1825 Gompertz suggested that metazoan growth can be described by a growth equation which is now known as the Gompertz growth function. Medawar (1940) theoretically deduced that the growth of an embryo chicken is a sigmoid curve and can be described by the Gompertz equation, given as follows:

$$Y = ae^{-be^{-kt}}$$

where a = intercept with y-axis , b = slope

k = intrinsic growth factor , t = time or age

Various forms of the Gompertz equation have been used to fit experimental growth data for many embryos, organs and tumours (Laird, 1964, 1965, 1969). In a comprehensive study, the Gompertz curve has been used to fit the mean size data of a variety of solid and ascites tumours (Simpson _et al._, 1970).

However in the present study, the following Gompertz growth equation will be used:

$$L_t = L_{max} e^{-Pe^{-kt}} \qquad \text{(Ricklefs, 1967)} \text{ ------------- } (6)$$

where L_t = length of the clam at specific age (t)

L_{max} = maximum or asymptotic length

k = intrinsic growth factor

P = growth constant defining proportion of L_{max} which specifies the initial length $L_{(0)}$

e = base of natural logarithm

The differential form that measures growth rate is given by:

$$dL_t / dt = k.\ln L_{max} - k.\ln L_t \qquad \text{--------------------------- } (7)$$

Linear regression of $\ln L_{avg}$ against $dL / dt.L_{avg}$ will result in a linear data set with slope k and y intercept yielding L_{max}.

3.2.3 The Monomolecular Model

In 1938 Von Bertalanffy described the following model

$$S_t = S_\infty (1 - e^{-kt})$$

where S_t = size at time t

k = intrinsic growth factor

S_∞ = asymptotic size

e = base of natural logarithm

The majority of studies on invertebrate growth employ the Von Bertalanffy model and subsequently the Ford-Walford equation in the analysis of growth curves (e.g. echinoid growth (Ebert, 1973) and *Mercenaria* growth (Ansell, 1964; Mitchell, 1974; Hibbert, 1976)).

However, a different variation of the Von Bertalanfy has been used in this study, namely the Monomolecular model which was suggested by Price (1970) and used by Kennish and Loveland (1980). The Monomolecular model is a more general form of Von Bertalanfy equation, albeit equivalent when c = 1 is given by:

$$L_t = L_{max} (1 - ce^{-kt}) \quad \text{(Price, 1970)} \quad \text{------------} \quad (8)$$

where L_t = length at time t

L_{max} = maximum or asymptotic length

k = intrinsic growth factor

c = growth constant which sets the initial condition of L_0

Determination of L_{max} and value of k require linear regression of L_{avg} against dL_t/dt. However, it is necessary to calculate the value of c which determines the initial length L_0 (see Appendix 1).

3.3 PRODUCTION OF MERCENARIA AT MARCHWOOD AND LEE-on-SOLENT

3.3.1 Introduction

Early investigations in the field of benthic ecology were mainly concerned with collection of information on species and communities present in various types of deposit. Information on the dynamics (growth rate, recruitment, mortality and production) of the commoner species are believed to provide a better basis for comparing the performance of a species from one locality to another (Warwick, 1983). Furthermore, studies of the rate of production of organic matter by the various members of the benthic community and their trophic dependence on each other is of vital importance for the purpose of predicting predation rate and fishing yield (Crisp, 1971). Production studies on Mercenaria mercenaria in Southampton Water are few. Hibbert (1976) studied distribution, biomass and production of the littoral populations of bivalve at Hamble Spit, with the main emphasis on Mercenaria. He estimated that the mean annual bivalve production amounts to $14 gm^{-2} yr^{-1}$ (formalin fixed ash free dry weight) and Mercenaria production at the site ranged from 3.99 to $14 gm^{-2} yr^{-1}$. Oyenekan (1980) investigated the community structure of the benthic macro-infauna of Southampton Water. He found, Mercenaria to be the most productive and biomass dominant species throughout much of the Eastern side of Southampton Water. Both Hibbert (1976) and Oyenekan (1980) estimated secondary production by following periodical changes in the weight and number of individuals. In the present study, the secondary production of the littoral Mercenaria population at Marchwood and Lee-on-Solent was investigated over a one year period. Although the estimate represents production over a short period (one year) and may vary over a longer period, nevertheless, a clear picture of the condition of the animal in relation to the environmental factors at both sites, can be formed. Furthermore, the study aims to relate production to results obtained on growth and reproductive biology.

3.3.2 Materials and Methods

Mercenaria was collected as described in Chapter 2 from the littoral areas of Marchwood and Lee-on-Solent, which are situated in the upper and lower part of Southampton Water respectively (Fig. 3.1). Both sites are characterised by different environmental conditions (e.g. water currents, food, substrate). The animals were collected at approximately bimonthly intervals between March 1985 and March 1986. Temperatures of the air, water and sediment were recorded on each occasion. In the laboratory animals were cleaned and shells were scraped free of attached debris, and clams were stored in a freezer at -20°C for a few days. The animals were then taken from the freezer and defrosted at room temperature. Soft tissue was removed from the shell. The cleaned shells were numbered and soaked overnight in a dilute solution of sodium hypochloride, which removes the black stain from the outer surface of the shells and facilitates aging of the animals. Production was estimated following one of the methods outlined by Crisp (1971). The method uses changes in weight and numbers of each age group between each sampling occasion to estimate annual production. However, in the present study, a slightly modified procedure similar to that used by Warwick (1983) on *Ensis siliqua* was used to estimate production. The method allows estimates of production of species which are long-lived, with few individuals per year classes. *Mercenaria* occurs in low numbers in Southampton Water, and lives for a long period (maximum 19 years in this study) with relatively low mortality after the initial high larval and juvenile mortality.

On every occasion, *Mercenaria* collected from both sites,

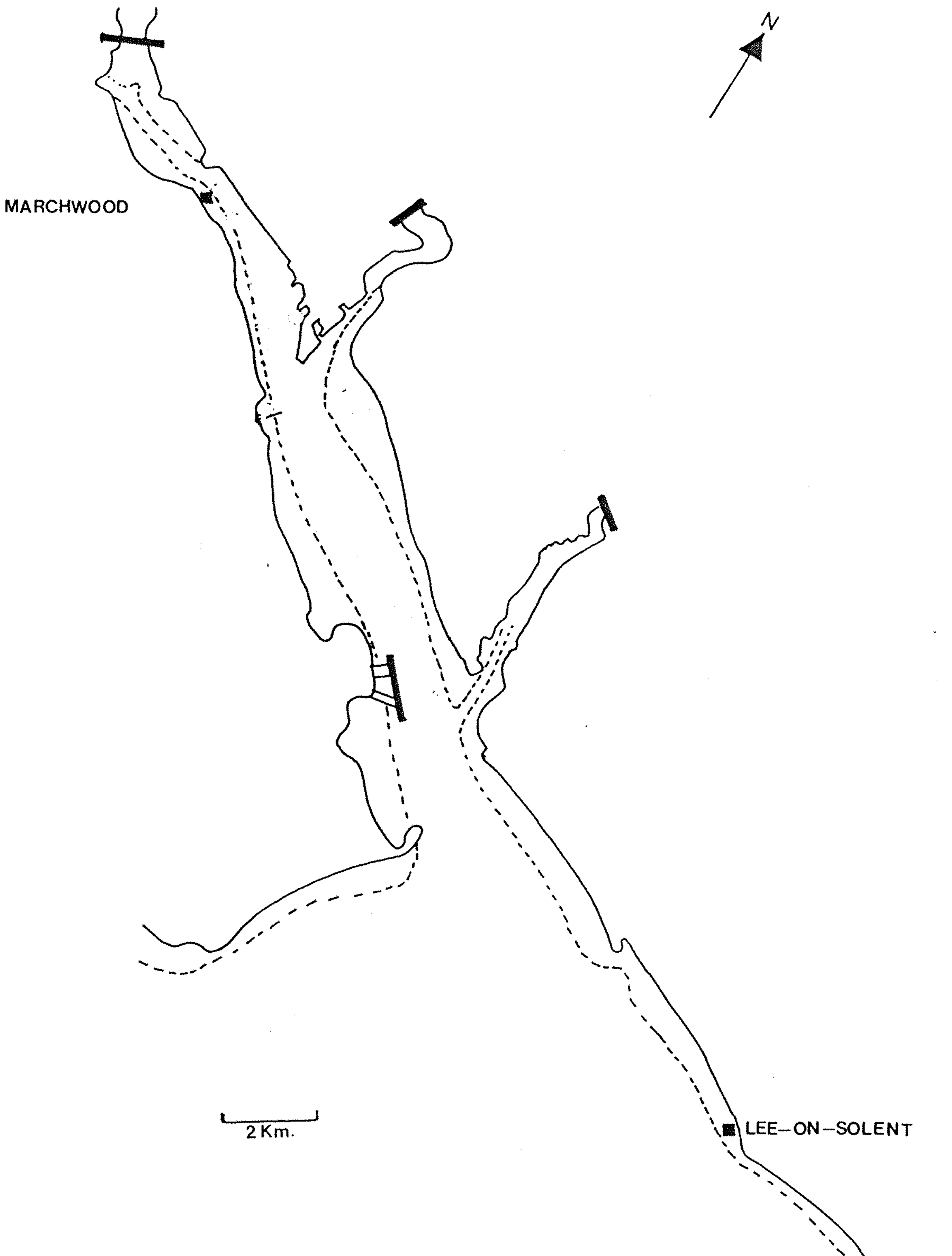


Fig. 3.1 Sampling of littoral Mercenaria population in Southampton Water during March 1985 - March 1986

were divided according to the ring counts, into different year classes, and the numbers occurring in each year class was recorded and expressed as m^{-2}. The mean annual number of individuals per square metre in each year class was then calculated. The mean length of individuals in each year class, was employed to calculate the corresponding mean weight of each year class using the length-weight relationship for each site. The annual production for each year class is given by the product of annual mean number of individuals ($\bar{N}$) at each year class and weight increment (Δw) gained by each age group during the sampling period ($\bar{N}\Delta w$) that is, over one year. Total annual production for all age groups was calculated by summation of production estimates obtained for all the year classes. Biomass of the individuals collected during each sampling intervals, was calculated by substituting the length of each individual in each year class in the length-weight relationship for each site. The total weight of individuals was converted to weight per square metre and taken to represent the biomass. The annual mean biomass of each year class was calculated from data of biomass of each age class obtained during sampling intervals. The total mean annual biomass was then calculated by summation of biomass of all age groups. Division of the total annual production by the total mean annual biomass gives the $P/\bar{B}$ ratio.

3.4 CONDITION INDEX

Various indices have been devised to assess the condition of bivalves of commercial importance. Mitchell (1974) gave a detailed account of characteristics of each index, and suggested that the percentage of the ratio of tissue dry weight to the dry shell weight accurately describes the condition of Mercenaria mercenaria in Southampton Water. Furthermore, such an index avoids the error that arises when dealing with wet biological materials. In the present work calculation of the condition index [(tissue dry weight / shell weight) x 100] was made on Mercenaria collected from littoral and sublittoral areas of Southampton Water.

3.5 LENGTH - WEIGHT RELATIONSHIP

3.5.1 Materials and Methods

To study length-weight relationship, clams covering a wide range of sizes were collected from each site in Southampton Water during winters of 1983 and 1984. The animals were kept in a circulating sea water aquarium for 24 hours, in order to void material from the guts. All materials and organisms attached to the outer surface of the shells were removed. Deformed shells were excluded from measurements. Animals from each site, were carefully labelled and stored in a deep freeze at -20°C, for approximately one month. The animals were than removed and left to thaw, shells gaped after 3 to 6 hours depending on the size of the animal. Each animal was numbered by water proof pen, and soft tissue was carefully removed, using a pair of scissors to cut the adductor muscle, and by means of a sharp scalpel all the attached soft tissue was removed. A standard procedure was followed to drain all external water from the soft tissue. The procedure involved repeated wrapping of the soft tissue in several layers of blotting paper until the soft tissue appeared dry. A pre-weighed cup of aluminium foil was used to record the wet weight of each individual. The soft tissues were then dried in an oven at 70°C, for 24 to 48 hours depending on weight of the tissue, until complete drying and total dehydration was achieved. The dried tissue and aluminium foil, were left to cool down to room temperature in a desiccater containing selica gel, before being reweighed on a 'Mettler' P1200 balance, and the tissue dry weight was obtained. The specimens were then carefully marked and ashed in a muffle furnace at 550°C for 6 hours, after which, they were stored in a desiccater, in order to settle to room temperature, and were subsequently reweighed using a 'Mettler' P1200 balance. The tissue ash free dry weight was calculated by substraction of ash weight from dry tissue weight.

3.6 MORPHOMETRY

3.6.1 Introduction

The recent advent of computers that are able to analyse multivariate data on morphometric characters, provides a better opportunity to study variation of growth and morphometric characters between different sites. In animals body characters may grow differently depending on environmental condition and age (Green, 1972). In studying growth, zoologists found that when linear measurement made on two different body parts (x and y) of a growing animal, were plotted in the form of log y against log x, a linear band of points appeared on the graph and can be mathematically approximated to a power function $\log y = \log a + b \log x$. Such a phenomenon is called allometry. It is either said that the two parts have an allometric relationship between them, or the two parts are growing allometrically. In the present study, morphometric characters are used to assess and distinguish between *Mercenaria* populations living in intertidal and subtidal areas of Southampton Water.

3.6.2 Materials and methods

Samples of Mercenaria collected during 1984 and 1985 from littoral areas of Marchwood, Royal Pier, Solent Breezes, Lee-on-Solent and sublittoral areas, were utilised for the measurement of morphometric characters. These sites were chosen, because they are exposed to different environmental conditions. A standard method of measurement of different aspects of the shell shape was adopted (Fig. 3.2a). Plastic vernier calipers was used to measure shell length (SL) , shell height (SH) and shell breadth (SB). All the linear measurements were recorded to the nearest 0.05mm. The shell length was taken to be the maximum shell dimension along the anterior posterior axis, whereas the shell height was represented by the maximum dimension perpendicular to the length axis. The shell breadth is the maximum dimension perpendicular to the directive plane. Shell curvature (SC) which is the peripheral distance from the umbone to the shell margin a along predetermined median axis, was measured by means of a thin paper strip and a metric ruler. Thickness of the centre of the posterior adductor muscle, was considered to represent shell thickness (ST). The thickness was measured to the nearest 0.01 using a modified micrometer with two pointed cones.

3.7 RESULTS AND DISCUSSION

3.7.1 Growth models

In the present study growth of Mercenaria is measured as increase in shell length. The growth curve (Fig. 3.2 b&c) revealed

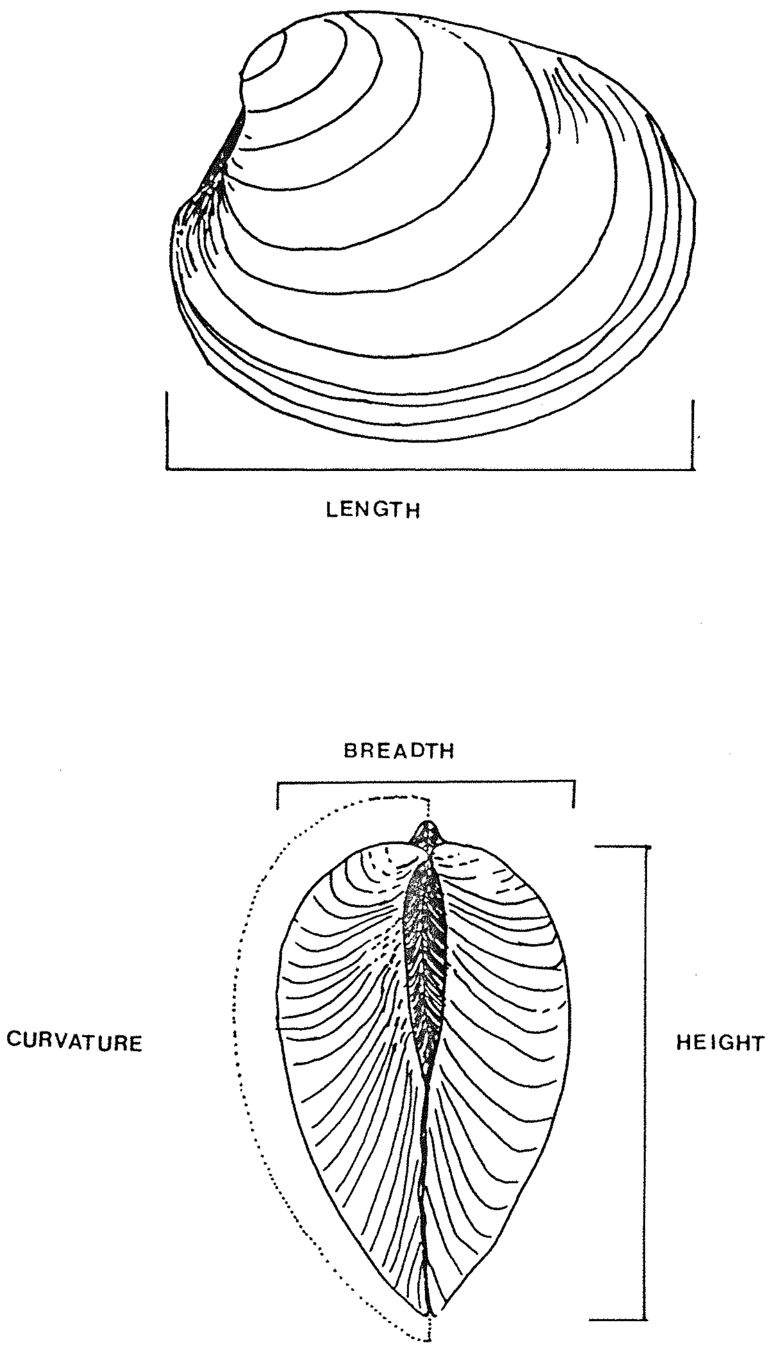


Fig. 3.2a Linear measurements of different shell morphometry of the clam

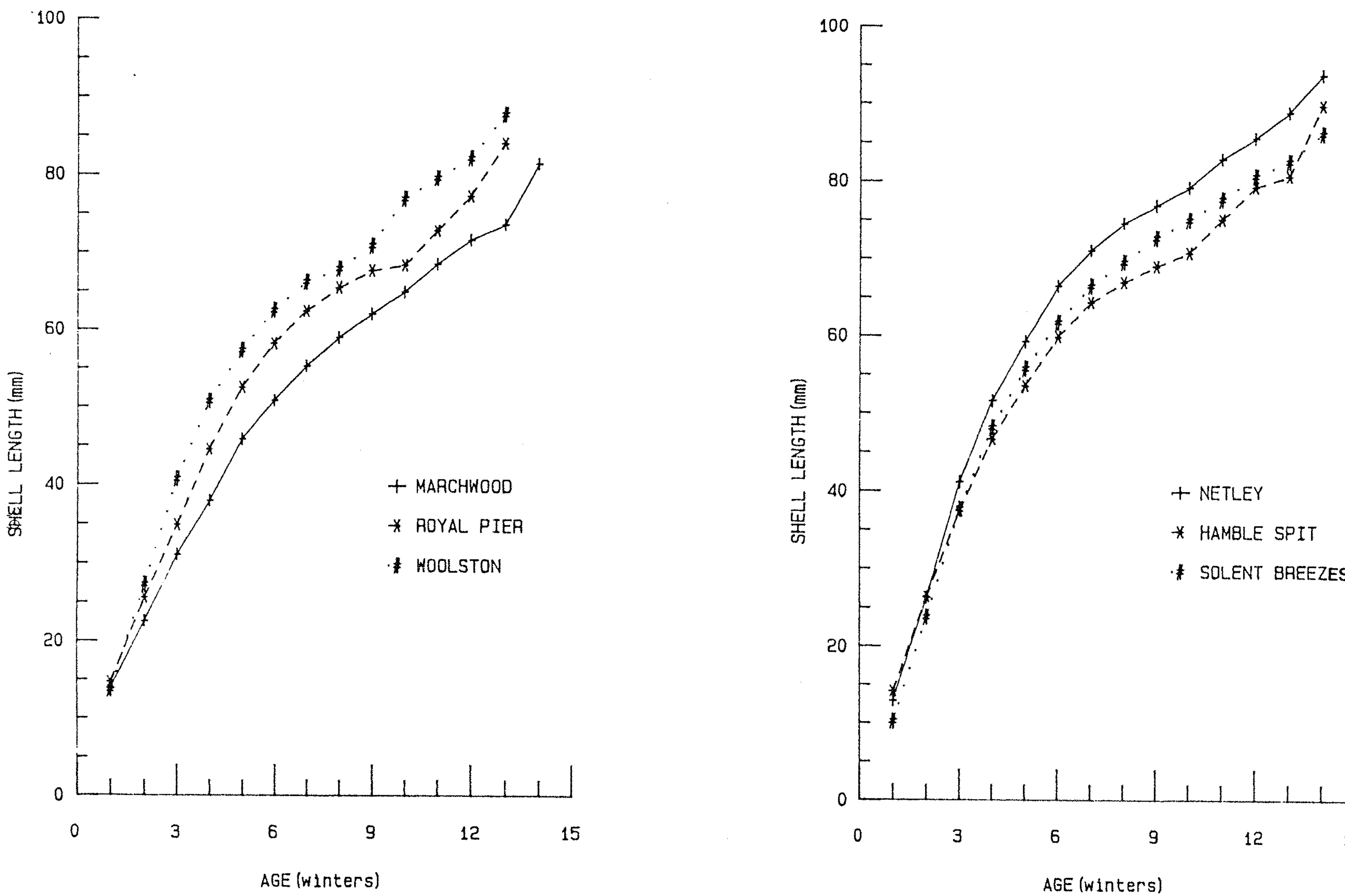
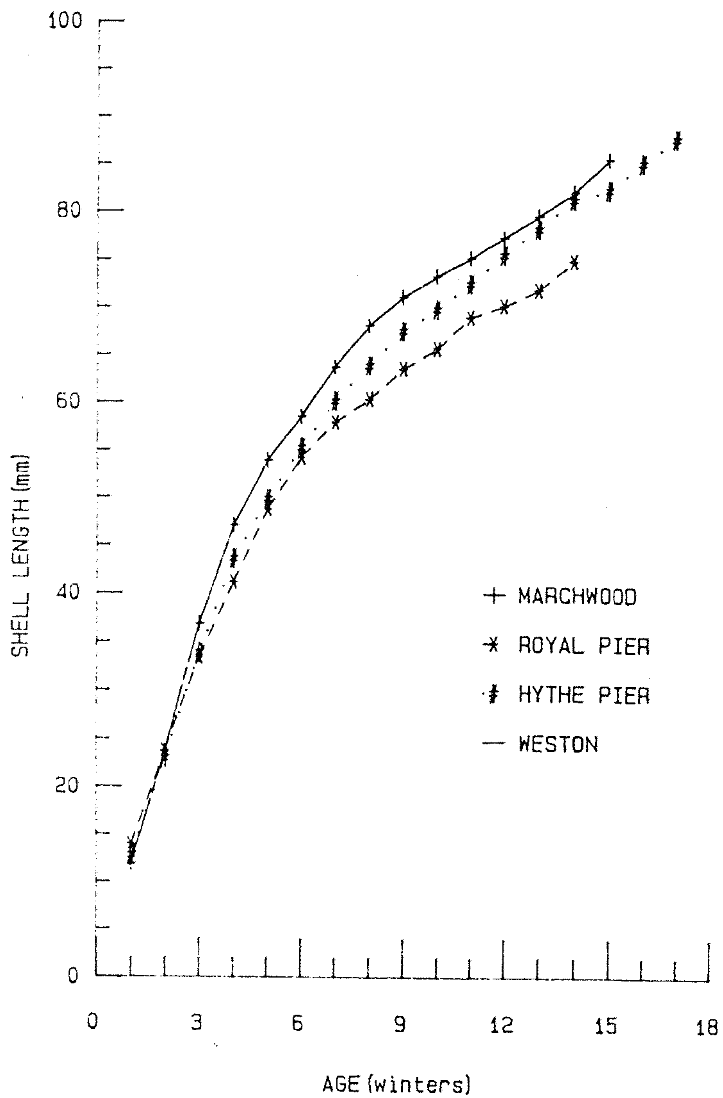


Fig. 3.2b Growth curves of <u>Mercenaria</u> population sampled at the beginning of 1983



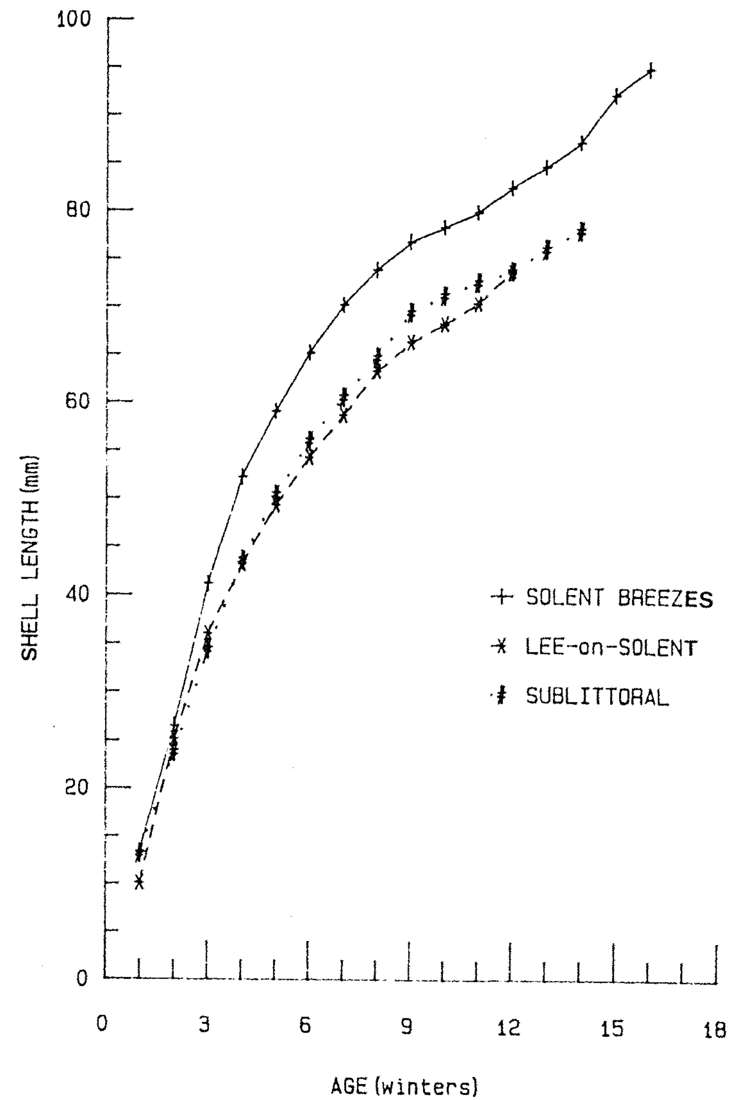


Fig. 3.2c Growth curves of <u>Mercenaria</u> population sampled at the beginning of 1984

that Mercenaria exhibits different rates of growth at different sites in Southampton Water. Highest growth occurred at Solent Breezes and Netley, wheareas lowest growth was recorded at Marchwood. Further analysis of growth involved the application of the three growth models, namely the Logistic, the Gompertz and the Monomolecular models for the purpose of mathematical description of growth and subsequent calculation and plotting of predictive growth rates. Because the growth of Mercenaria differs from one site to another, the 3 models were applied separately on growth data obtained at each site from Lee-on-Solent to Marchwood using a specially written computer programmes. The results are shown in Table 3.1. Initially the linear regression yielded the predictive values in order to determine initial sizes. The growth equations were iterated based on predicted parameters and initial conditions. The parameters b, c and p in the Logistic, Gompertz equation have no biological significance, therefore they cannot be compared between different models, for the purpose of selecting the best growth model. Similarly, the parameter k which has biological significance cannot be compared across parameters of the different models, because each model defines k differently. However, in the present study value of L_{max}, correlation coefficient, coefficient of determination and standard error of estimate as mentioned in Table 3.1 are the criteria employed for selecting best fit between models. Predictive growth curves for Marchwood and Lee-on-Solent are shown in Fig. 3.3 a, b and curves of growth rates for different sites are mentioned in Fig. 3.4

Statistically all the equations accurately describe the growth data of Mercenaria, as evident from the high correlation coefficient values in Table 3.1. However, the degree of fit is best

Table 3.1 : Constants (L_{max}), correlation coefficient (r), coefficient of determination (d) and estimated parameters (b, c, k, P) of the Logistic, the Gompertz and the Monomolecular growth models, applied on *Mercenaria* growth, at different sites in Southampton Water

3.1 a - MARCHWOOD

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	64.10	-0.833	0.010	-	0.641	-	0.695	0.113
Gompertz	69.65	-0.879	-	-	0.386	-2.895	0.773	0.097
Monomole-cular	85.91	-0.697	-	0.969	0.148	-	0.486	2.675

3.1 b - LEE-on-SOLENT

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	67.5	-0.869	0.010	-	0.675	-	0.756	0.090
Gompertz	68.27	-0.911	-	-	0.425	2.595	0.830	0.075
Monomole-culer	80.65	-0.710	-	1.004	0.187	-	0.517	2.766

3.1 c - ROYAL PIER

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	68.56	-0.652	0.009	-	0.617	-	0.425	0.177
Gompertz	75.47	0.655	-	-	0.349	2.236	0.430	0.176
Monomole-culer	90.12	-0.372	-	1.018	0.153	-	0.138	6.48

3.1 d - HYTHE PIER

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	74.13	-0.833	0.008	-	0.593	-	0.694	0.104
Gompertz	85.79	-0.783	-	-	0.290	2.511	0.613	0.117
Monomole-culer	92.82	-0.685	-	0.995	0.147	-	0.469	3.06

3.1 e - WESTON

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	72.4	0.786	0.010	-	0.724	-	0.618	0.145
Gompertz	78.85	-0.822	-	-	0.438	2.903	0.675	0.133
Monomole-culer	88.77	-0.547	-	1.049	0.198	-	0.299	5.82

3.1 f - NETLEY

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	69.2	-0.873	0.010	-	0.692	-	0.761	0.101
Gompertz	75.51	-0.910	-	-	0.404	2.627	0.829	0.086
Monomole-culer	91.59	-0.711	-	1.002	0.161	-	0.505	2.98

3.1 g - HAMBLE SPIT

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	69.00	-0.882	0.012	-	0.828	-	0.777	0.106
Gompertz	71.00	-0.944	-	-	0.548	3.122	0.890	0.075
Monomole-culer	79.02	-0.865	-	1.021	0.250	-	0.748	2.431

3.1 h - SOLENT BREEZES

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	82.40	-0.592	0.010	-	0.824	-	0.350	0.290
Gompertz	82.51	-0.948	-	-	0.482	2.961	0.899	0.072
Monomole-culer	95.30	-0.841	-	1.033	0.215	-	0.707	2.84

3.1 i - MEON-on-SEA

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	77.00	-0.705	0.010	-	0.770	-	0.497	0.208
Gompertz	81.96	-0.705	-	-	0.421	2.414	0.498	0.208
Monomole-culer	94.67	-0.456	-	-	0.191	-	0.208	7.48

3.1 j - SUBLITTORAL

Equation	L_{max}	r	b	c	k	P	d	std. error of estimate
Logistic	70.78	-0.833	0.009	-	0.637	-	0.694	0.110
Gompertz	77.02	-0.871	-	-	0.372	2.523	0.758	0.098
Monomole-culer	97.39	-0.456	-	0.995	0.191	-	0.454	2.944

for the Gompertz growth function in almost all the sites with a correlation coefficient value of 0.655 to 0.911 and with the highest coefficient of determination (40 - 80%). In addition, it has the lowest standard error of estimate. The Monomolecular model gives the poorest fit to the data ($r = 0.3$ to 0.7) lowest coefficient of determination (13 - 50%) and highest standard error of estimate.

The Logistic equation gave an intermediate fit ($r = 0.6$ to 0.8) and predicted highest asymptotic size (L_{max}) and growth rate, respectively. The monomolecular model not only gave poorest fit to the data, it also suffers from an inability to predict growth rates, because the predictive growth curve increases at a steadily decreasing rate but has no point of inflexion (Mason, 1983).

According to all the criteria employed, the Gompertz model can best describe the growth in length of _Mercenaria_ in Southampton Water. Similarly Kennish and Loveland (1980) concluded that the Gompertz model could best describe growth in height of _Mercenaria_ in Barnegat Bay (USA). More recently Mason (1983) found that the Gompertz model yields a reasonable fit for growth of the scallop (_Pecten maximus_) with Von Bertalanffy giving a better fit for older individuals.

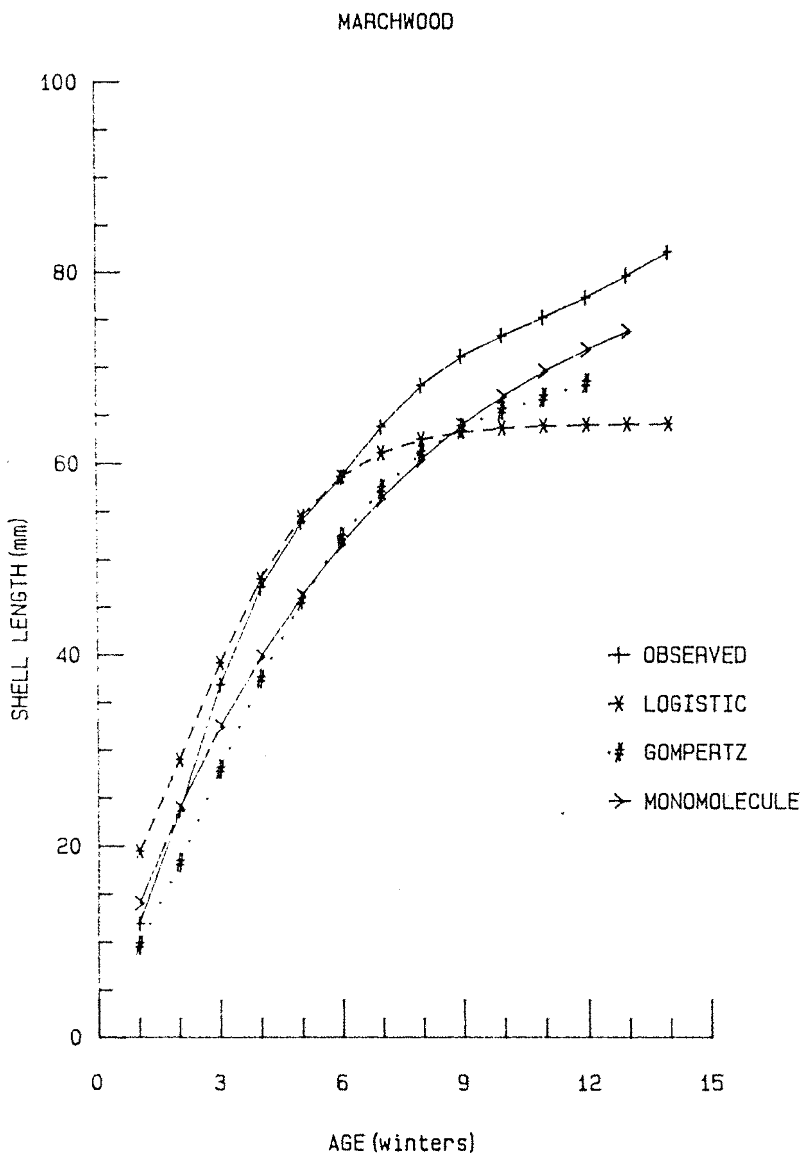


Fig. 3.3a Observed and predictive growth curves for *Mercenaria* sampled at Marchwood in 1984

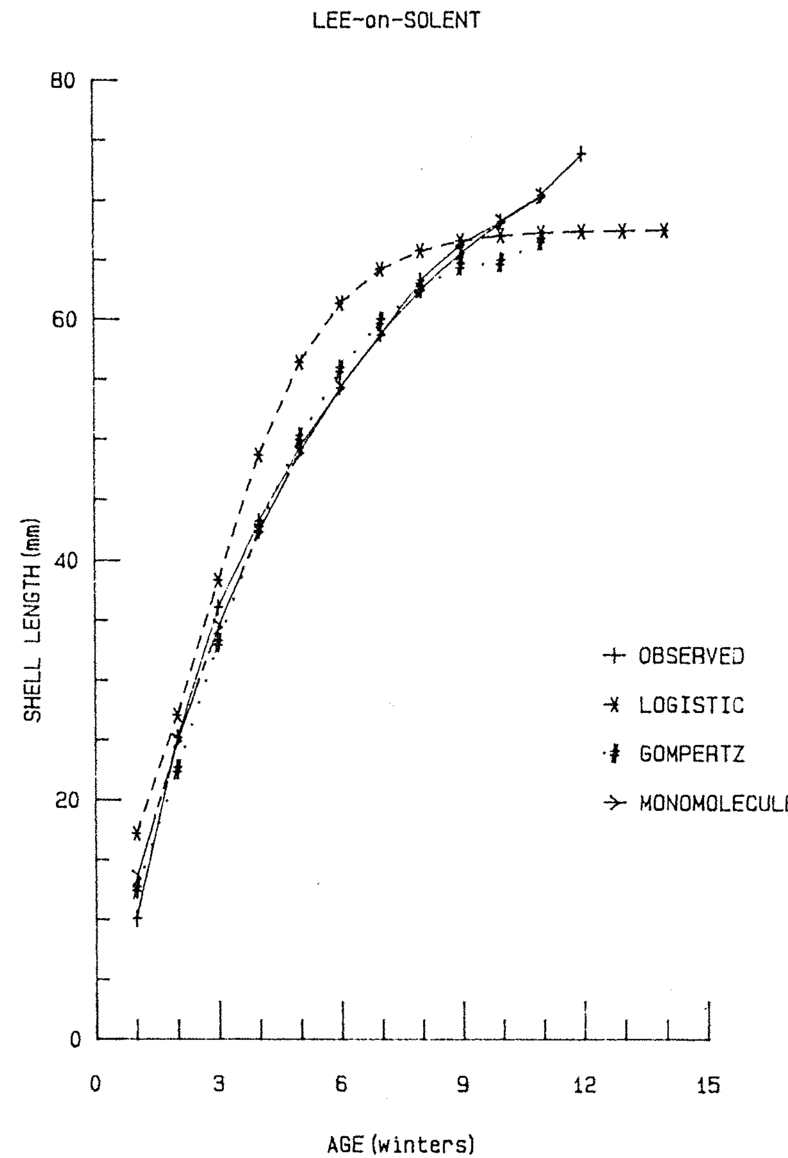


Fig. 3.3b Observed and predictive growth curves for *Mercenaria* sampled at Lee-on-Solent in 1984

3.7.2 Predictive Growth Rates for All Sites

Plotting of predictive growth curves and growth rates obtained by the Gompertz model makes comparison of growth rates across Southampton Water possible, as shown in Fig. 3.4. In almost all the sites maximum rate growth in terms of length was achieved during the second year of life, with the exception of Marchwood and Hythe Pier, where maximum growth rate was recorded during the third year, and was followed by a gradual reduction in the annual growth with increasing age. Furthermore, the results suggest that individuals with high growth rates during younger ages (1 - 4 years) tend to show lower growth rates at older ages (more than 4 years) as clear from the negative correlation coefficient between growth rates at the second and ninth years of individuals at all the sites (Table 3.2). Such results indicate that rapidly growing individuals tend to show a shorter growing period because they reach maximum length at earlier ages, than gradually growing individuals. Davidson (1981) carried out a detailed study on Mercenaria in Southampton Water, and reported that the maximum length increment occurred in the second, third and fourth years, and growth subsequently decline with increasing age. Furthermore, Eversole et al. (1986) monitored growth of Mercenaria in Clark Sound (USA), and reported that most of the growth occurred in the first 2 years. The result also illustrate that growth of littoral populations of Mercenaria showed wide variation between sites. Maximum predicted increase of shell length was found at Solent Breezes and minimum at Hythe Pier. In general a pattern of higher growth rates was shown at sites in the middle part (Solent Breezes, Hamble Spit, Meon-on-Sea) rather than by sites in the lower (Lee-on-Solent) and upper sections (Marchwood, Royal Pier, Hythe Pier) of Southampton Water.

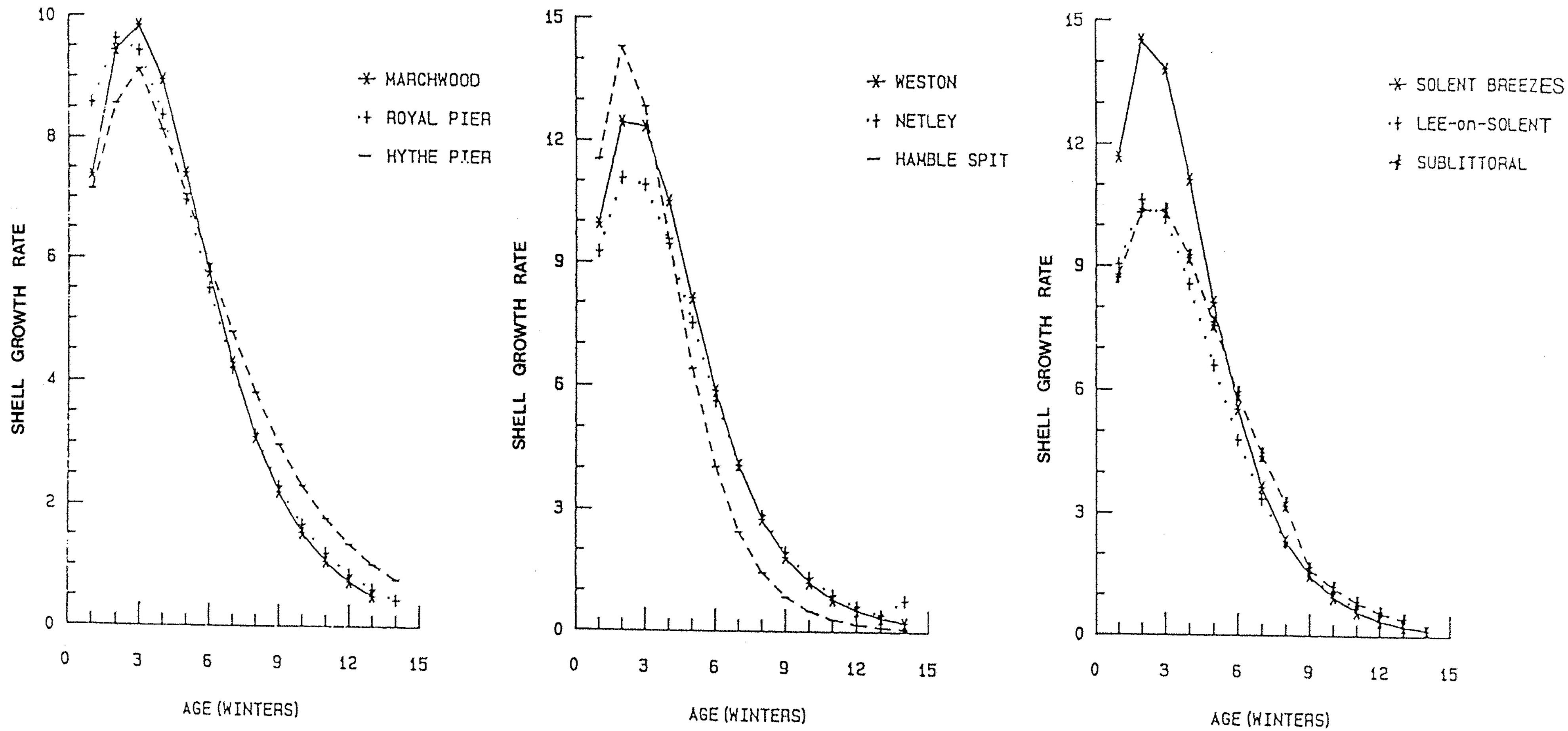


Fig. 3.4 Predictive growth rates in shell length (mm/yr.) using Gompertz growth model at different sites in Southampton Water during 1984 - 1985

Similarly, Mitchell (1974) found different growth rates in Mercenaria at different sites. He reported that highest and lowest growth rates occurred at Lee-on-Solent and Marchwood, respectively. Nossier (1981) also reported variation of growth rates of Cerastoderma edule between different sites in Southampton Water, with the population at Weston and Netley showing the highest growth rates compared to the lowest growth rates found among the population at Marchwood and South Hythe Pier.

Table 3.2 : Linear regression of growth rate (mm/yr) during second and ninth years using values predicted by the Gompertz model

Growth rate	Number of animals									
	1	2	3	4	5	6	7	8	9	10
Second year growth rate (mm/yr.)	9.439	9.633	8.573	12.264	11.076	14.302	14.518	12.683	10.618	10.357
Ninth year growth rate (mm/yr.)	2.205	2.312	2.993	1.840	1.971	0.857	1.480	1.783	1.549	1.649

Correlation coefficient(r) = - 808

Intercept (a) = 16.775

Slope (b) = - 2.902

3.7.3 Predicted Growth Rates in Length and Tissue Weight

Data of length and ash free dry weight of clams collected from Marchwood and Lee-on-Solent have been used to establish length-weight relationship, from which weight at each age was calculated. In this way it was possible to apply all of the three models to calculate weight data, and predicted growth curves and rate of growth in terms of weight increment were obtained. Plots of growth in length and weight for Marchwood and Lee-on-Solent are shown in Fig. 3.5a and 3.6a. The curve of growth in length has a higher gradient compared to growth in weight during the first years. The rate of growth in terms of length (Fig. 3.5b and 3.6b) shows that the animals at Lee-on-Solent have higher and faster growth, reaching a maximum value one year earlier than *Mercenaria* does at Marchwood. Similarly, the maximum rate of weight increase occurs one year earlier at Lee-on-Solent than at Marchwood. The results show that maximum rate of increase in length and weight occurred at different ages. At Marchwood, maximum rate of length increase was achieved during the second year, whereas maximum rate of weight increase occurred during the fourth year. At Lee-on-Solent, maximum rate of length and weight increment occurred during the third and fifth years of age, respectively. It is possible that *Mercenaria* spend a greater proportion of available energy in shell growth during its early life, and in tissue growth during later years.

3.7.4 Production at Marchwood and Lee-on-Solent

The annual mean number (m^{-2}) of individuals per age group and the weight of each age groups of *Mercenaria* sampled at Marchwood and Lee-on-Solent during the period March 1985 to March 1986 are given

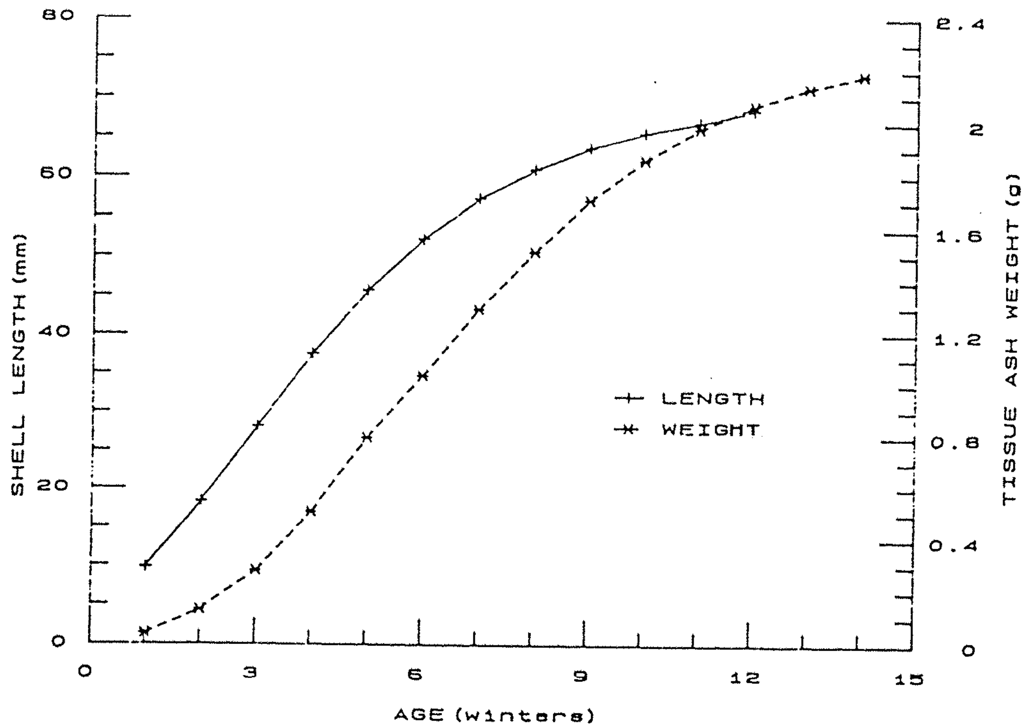


Fig. 3.5a Predictive growth curves in shell length and tissue ash free dry weight for Mercenaria at Marchwood (1984) using Gompertz model

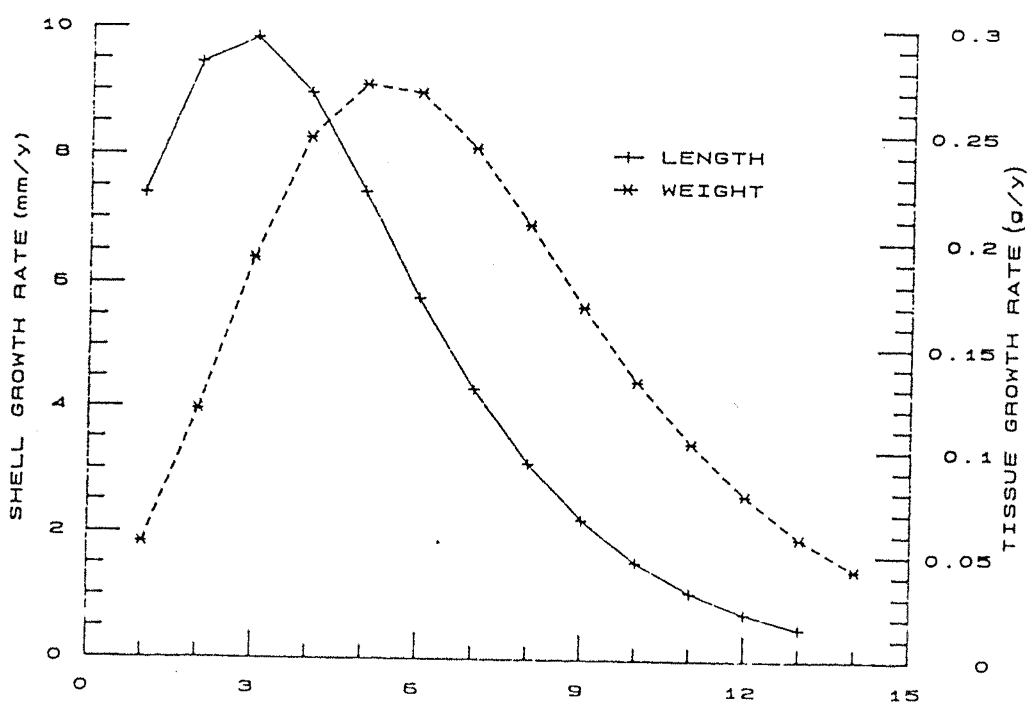


Fig. 3.5b Predictive growth rates in shell length and tissue ash free dry weight for Mercenaria at Marchwood (1984) using Gompertz model

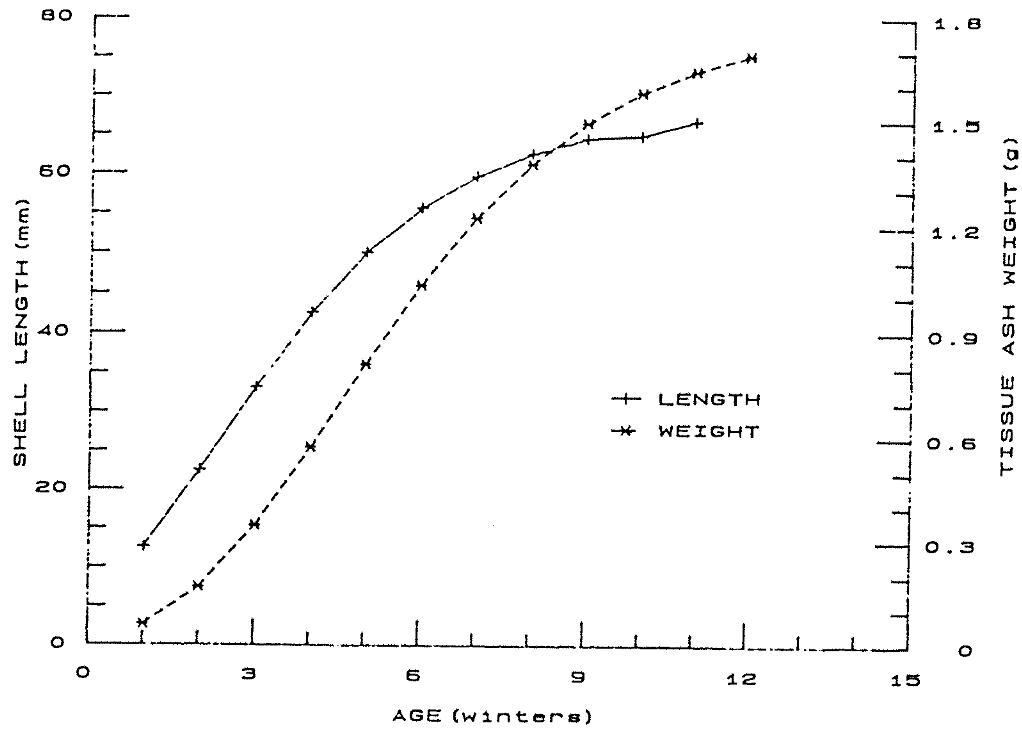


Fig. 3.6a Predictive growth curves in shell length and tissue ash free dry weight for Mercenaria at Lee-on-Solent (1984) using Gompertz model

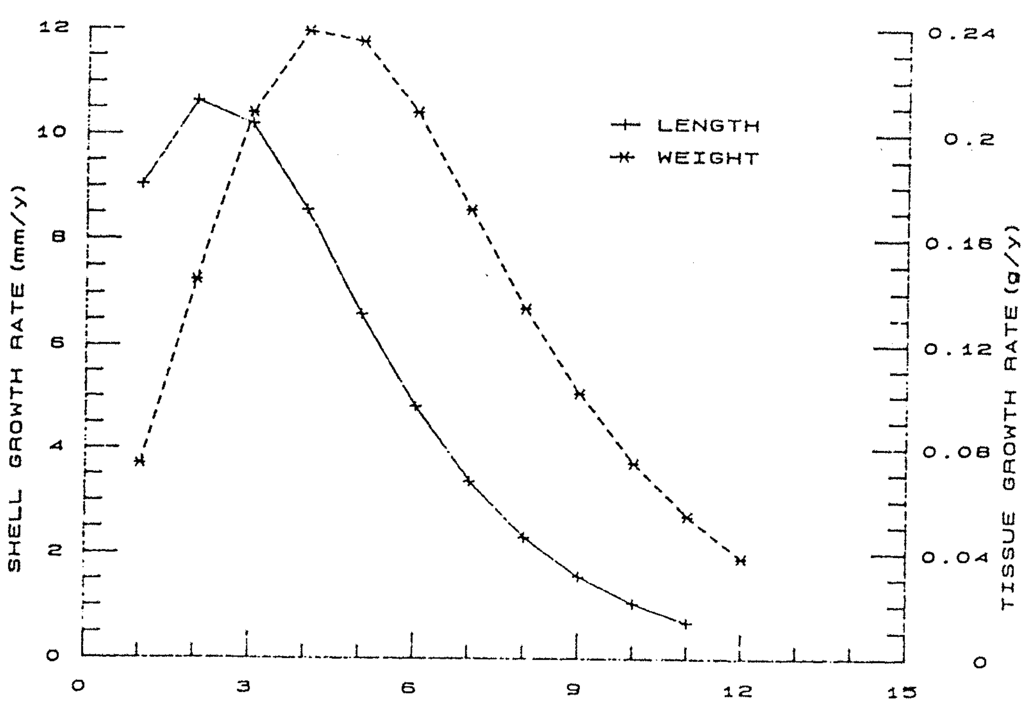


Fig. 3.6b Predictive growth rates in shell length and tissue ash free dry weight for Mercenaria at Lee-on-Solent (1984) using Gompertz model

in Tables 3.3 and 3.4. Estimates of the annual production at both sites are given in Tables 3.5 and 3.6 and illustrated in Fig. 3.7. Production estimates for both sites were similar amounting to 3.0166 and 2.7099 $gm^{-2}yr^{-1}$ for Marchwood and Lee-on-Solent, respectively. However, the distribution of production between year classes and the peak year classes in terms of production differed at each site. At Lee-on-Solent the peak of production was by the 8 and 9 year classes and again by the 12 and 13 year classes (Fig. 3.8). Similarly, the peak of the production, at Marchwood occurred as two peaks but between different year classes, in the 10 to 11 and again between the 13 and 15 year classes. Therefore, it appears that peak production at Lee-on-Solent occurred in animals approximately one year younger than at Marchwood. Furthermore, at Lee-on-Solent the production of animals less than 10 years of age gave a greater contribution to the total production than at Marchwood, where most of the production occurred among the older individuals (greater than 10 years).

The production, cumulated by age, for both sites is illustrated in Fig. 3.8. The advantage of such a plot is that it either shows a continuous increase or levelling off, of production and it clearly illustrates age groups where production is at a maximum or minimum. The plot further demonstrates that production fluctuates between the age groups and varies between both sites. The cumulative production increased more uniformly at Marchwood than at Lee-on-Solent. At Marchwood, production was low among the juvenile individuals (< 10 years) and showed a steep rise between the 12 and 15 year classes, levelling off at ages greater than 16 years. Whereas at Lee-on-Solent production follows a different pattern, with higher rates of production in the individuals less than 9 years and

Table 3.3 : Mean number ($no.m^{-2}$) and weight (g) of each age group of littoral Mercenaria population at Marchwood

Months	Age Groups													
	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+	19+
12.03.85	0	0	0.590	1.190	1.780	1.780	1.190	1.780	1.190	3.570	0.590	1.190	0	0.590
7.05.85	0	0	0	0.290	0.570	0.290	0	2.290	0.570	1.140	1.430	0	0	0.290
10.06.85	0	0	0	0	0	0.950	0.950	2.220	4.760	2.540	0.320	0	0.630	0.630
1.08.85	0	0	0	0.540	0	0	0	1.610	0.540	0	2.680	0.540	0	0
4.09.85	0	0	0	0	0	0	0.220	0.670	0.440	0.220	0.220	0.220	0	0
19.10.85	0.590	0	0	0.590	0.590	0	0	1.780	1.780	0.590	1.780	0.590	0	0
17.11.85	0	0	0	0.920	0	1.830	0	0.920	3.670	1.830	0	1.830	2.750	0
26.01.86	0	0	0	0	0	0	0.620	2.480	2.480	6.820	2.480	1.240	0	0
2.03.86	0.520	0	0	0	0	0	2.060	2.580	4.120	4.640	2.060	0.520	0	0
31.03.86	0	0	0	0	3.440	1.720	0	1.720	3.440	5.160	3.440	0	0	0
Mean no. of each age group	0.111	0	0.059	0.353	0.638	0.657	0.504	1.805	2.299	2.651	1.500	0.613	0.338	0.151
Ash free dry weight of each age group	0.885	1.0667	1.2843	1.4735	1.6503	1.8168	2.1465	2.2976	2.6796	3.0457	3.2460	3.4427	3.5619	3.7707

Table 3.4 : Mean number (no.m^{-2}) and weight (g) of each age group of littoral Mercenaria population at Lee-on-Solent

Months	Age Groups												
	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+
7.03.85	0.273	3.550	4.640	1.910	0.273	0.273	0	0.820	2.180	0.820	0	0	0
7.05.85	0	0.644	2.580	0.644	0	0	0.644	4.510	4.510	3.220	0	0	0
9.06.85	0	0.585	4.095	0.585	0	0.585	0.585	6.435	0	0	0	0	0
3.08.85	0	0.550	2.210	8.270	1.100	0	0	2.210	2.760	5.510	0	1.100	0
1.09 85	0	0	1.080	1.080	0	0	0.540	0.540	4.860	2.700	0	0.540	0
16.10.85	0	0	6.760	4.830	0.970	0.970	0	0	0	5.800	0	0	0
13.11.85	0	0.490	0	1.970	0.990	0	0	0.490	2.960	2.470	0.490	0.490	0
27.01.86	0	0	0	1.950	3.900	0	0	5.890	5.890	0	0	0	0
28.02.86	0	0.500	4.530	5.540	0.500	1.510	0.500	1.010	3.020	3.020	1.510	0.500	0.500
30.03.86	0	0.220	1.530	1.090	0.440	0	0.440	0.440	2.190	1.090	0.440	0.220	0
Mean no. of each age group	0.027	0.654	2.743	2.787	0.817	0.334	0.370	2.235	2.837	2.463	0.244	0.285	0.050
Ash free dry weight of each group	0.840	1.040	1.180	1.270	1.440	1.550	1.690	1.920	2.230	2.380	2.540	2.880	3.130

Table 3.5 : Annual production for *Mercenaria* at Marchwood

Age groups	Mean Number (No.m^{-2})	Initial Weight (g)	Final Weight (g)	Weight Increment Δw (g)	Production P (gm^{-2}yr^{-1})	Biomass $\bar{B}$ (gm^{-2})	P/$\bar{B}$ (yr.$^{-1}$)
6+	0.111	0.8552	1.0667	0.2115	0.0235	0.1393	0.169
7+	0	1.0667	1.2843	0.2176	0	0	0
8+	0.059	1.2843	1.4735	0.1892	0.0112	0.11179	0.100
9+	0.353	1.4735	1.6503	0.1768	0.0624	0.67894	0.092
10+	0.638	1.6503	1.8168	0.1665	0.1062	0.99291	0.107
11+	0.657	1.8168	2.1465	0.3297	0.2166	1.43186	0.151
12+	0.504	2.1465	2.2976	0.1511	0.0762	1.23445	0.062
13+	1.805	2.2976	2.6796	0.3820	0.6895	4.39816	0.157
14+	2.299	2.6796	3.0457	0.3661	0.8417	6.0123	0.140
15+	2.651	3.0457	3.2460	0.2003	0.5310	8.27137	0.064
16+	1.500	3.2460	3.4427	0.1967	0.2951	3.98677	0.074
17+	0.613	3.4427	3.5619	0.1192	0.0731	1.76497	0.041
18+	0.338	3.5619	3.7707	0.2088	0.0706	1.10335	0.064
19	0.151	3.7707	3.900	0.1293	0.0195	0.60811	0.032
					$\sum P$ = 3.0166	$\sum \bar{B}$ = 30.73435	P/$\bar{B}$ = 0.0982

Table 3.6 : Annual production for *Mercenaria* at Lee-on-Solent

Age groups	Mean Number (No.m^{-2})	Initial Weight (g)	Final Weight (g)	Weight increment Δw (g)	Production P ($gm^{-2}yr^{-1}$)	Biomass $\bar{B}$ (gm^{-2})	P/$\bar{B}$ ($yr.^{-1}$)
6+	0.0273	0.84	1.04	0.20	0.0055	0.0229	0.2402
7+	0.654	1.04	1.18	0.14	0.0916	0.9819	0.0925
8+	2.743	1.18	1.27	0.09	0.2469	4.6797	0.0528
9+	2.787	1.27	1.44	0.17	0.4738	4.7854	0.0990
10+	0.817	1.44	1.55	0.11	0.0899	0.9651	0.0932
11+	0.334	1.85	1.69	0.14	0.0468	0.5893	0.0794
12+	0.370	1.69	1.92	0.23	0.0851	0.7217	0.1179
13+	2.235	1.92	2.23	0.31	0.6929	3.8421	0.1803
14+	2.837	2.23	2.38	0.15	0.4256	5.7476	0.0740
15+	2.463	2.38	2.54	0.16	0.3940	6.5714	0.0600
16+	0.244	2.54	2.88	0.34	0.0830	0.7510	0.1105
17+	0.285	2.88	3.13	0.25	0.0713	0.8597	0.0829
18+	0.05	3.13	3.20	0.07	0.0035	0.1733	0.0202
					$\sum P$ = 2.7099	$\sum \bar{B}$ = 30.6991	P/$\bar{B}$ = 0.0833

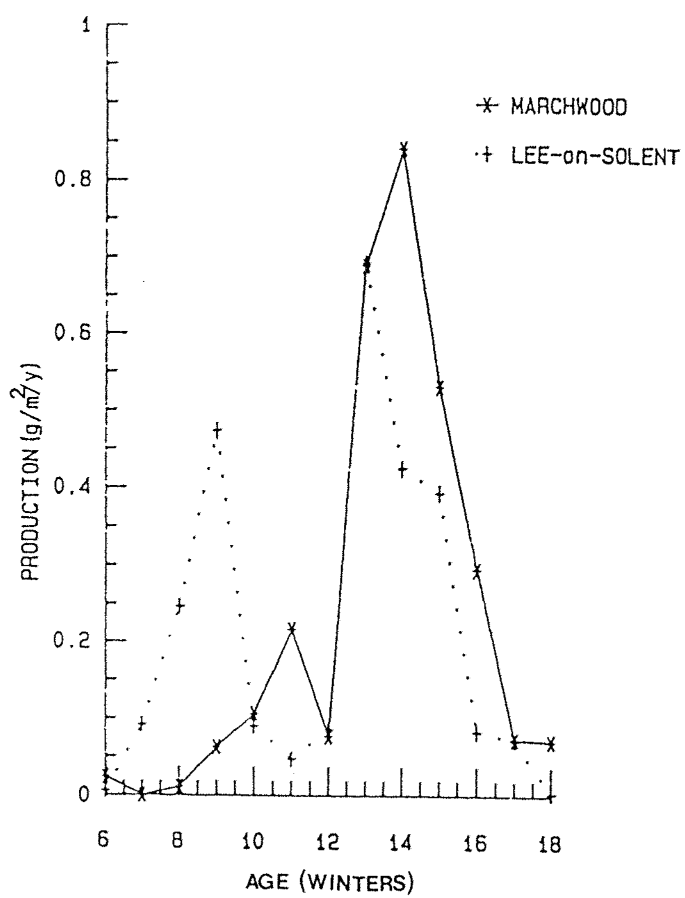


Fig. 3.7 Annual production ($gm^{-2}yr^{-1}$) of Mercenaria year classes at Marchwood and Lee-on-Solent during March 1985 - March 1986

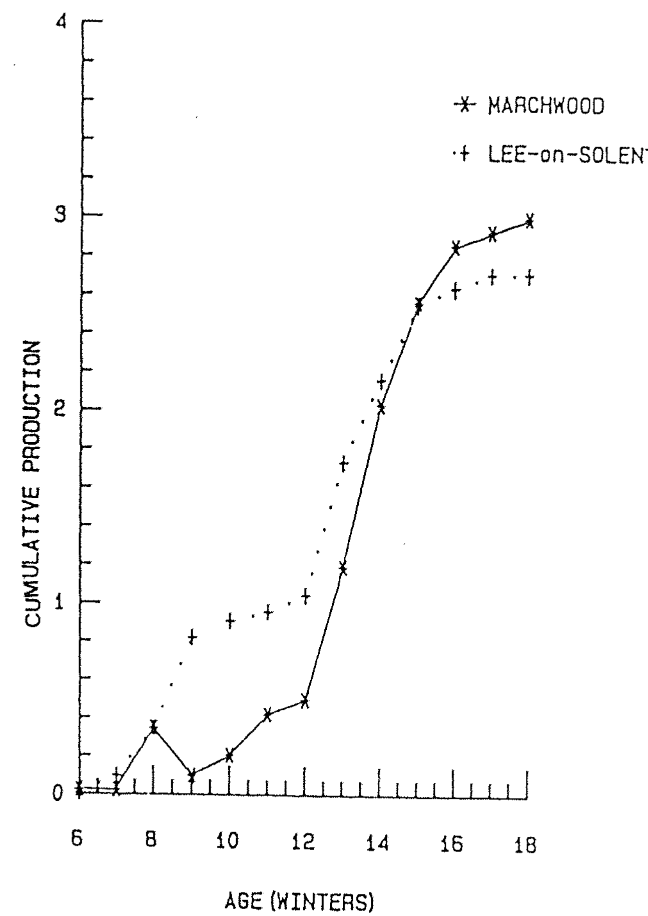


Fig. 3.8 Cumulative annual production of Mercenaria by age at Marchwood and Lee-on-Solent during March 1985 - March 1986

insignificant increase between 9 and 12 year classes, followed by a steep rise between 12 and 15 years, after which production levelled off. The annual mean biomass for each age group and the total annual mean biomass for the two sites are given in Table 3.7 and 3.8. The results showed that the total annual mean biomass values were similar at both sites and amounted to $30.7gm^{-2}$. However, the annual mean biomass of the individual age groups were different at each site and found to be marginally higher at Marchwood than at Lee-on-Solent, among the adult year classes.

In estimating production, the ratio of production to biomass ($P/\bar{B}$) is of more general significance than the production value itself (Greze, 1978). Furthermore, Hibbert (1976) mentioned that the $P/\bar{B}$ ratio gives a measure of rate of biomass turnover and this elucidates the ecological importance of the species in the aquatic community. The $P/\bar{B}$ ratio for all age groups are given in Table 3.9 and Fig. 3.9. The overall $P/\bar{B}$ values were found to be similar for both sites amounting to 0.098 and 0.088 for Marchwood and Lee-on-Solent, respectively. However, calculation of the $P/\bar{B}$ ratio for each age group at both sites showed marked variation (Fig. 3.9). At both sites peak of the $P/\bar{B}$ ratio occurred in individuals less than 7 years old. At greater age, the $P/\bar{B}$ become more or less constant at both sites varying between 0.02 and 0.25. In general a pattern of gradual decline of the $P/\bar{B}$ with age could be detected and was statistically confirmed by the least squares method. The analysis showed that log-linear regression gave the best fit model and the highest correlation coefficient, especially for Marchwood ($r = 0.717$) as shown in Table 3.10. According to Chambers and Milne (1975), the life cycle of animals can also influence estimates of production, as long-lived animals tend to have

Table 3.7 : Annual mean biomass (gm^{-2}) for <u>Mercenaria</u> at Marchwood

Months	Age Groups													
	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+	19+
12.03.85	0	0	1.1179	2.0157	3.6985	3.2347	2.6996	4.2634	3.3120	11.7972	1.9147	4.6023	0	2.872
7.05.85	0	0	0	0.8954	0.8518	1.0376	0.7346	0	2.0123	2.9126	4.2646	0	0	1.195
10.06.85	0	0	0	0	0	2.3559	2.5144	5.3712	10.6410	5.7168	0.6310	0	2.0895	2.086
1.08.85	0	0	0	1.4114	0	0	0	4.3631	1.3363	0	7.2987	1.5832	0	0
4.09.85	0	0	0	0	0	0	0.4422	1.9556	1.2422	0.6689	0.6667	0.8022	0	0
19.10.85	0.8325	0	0	1.0703	1.0822	0	0	4.0434	5.0126	1.4390	4.0612	1.7838	0	0
17.11.85	0	0	0	1.4402	0	3.3666	0	2.5594	9.7788	4.1005	0	4.6878	8.9440	0
26.01.86	0	0	0	0	0	0	1.7349	6.7228	7.4044	32.6847	8.6374	2.8378	0	0
2.03.86	0.5607	0	0	0	0	0	4.9535	6.0542	9.9069	11.8872	6.2702	1.3528	0	0
31.03.86	0	0	0	0	4.1108	4.6268	0	2.6660	9.4772	11.5068	6.1232	0	0	0
Mean Biomass of each age group	0.13932	0	0.1118	0.6789	0.9929	1.4319	1.234	4.3982	6.0124	8.2714	3.9868	1.7645	1.1034	0.6081

Table 3.8 : Annual mean biomass (gm^{-2}) for <u>Mercenaria</u> at Lee-on-Solent

Months	Age Groups												
	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+
7.03.85	0.2293	5.0888	7.6815	3.2376	0.4804	0.4149	0	1.8899	5.0419	2.2413	0	0	0
5.05.85	0	1.0501	4.6114	0.8954	0	0	1.2221	8.1695	10.3128	8.4310	0	0	0
9.06.85	0	1.0156	6.3379	1.0659	0	0.9705	1.0776	13.3526	0	0	0	0	0
3.08.85	0	0.7201	3.9745	15.7291	1.8764	0	0	4.9017	6.5462	14.1725	0	3.4572	0
1.09.85	0	0	1.9958	1.9175	0	0	1.1043	1.1556	11.8228	6.9903	0	1.5044	0
16.10.85	0	0	11.6905	9.2098	1.7272	1.4828	0	0	0	15.6415	0	0	0
13.11.85	0	0.8115	0	2.4973	1.8450	0	1.9884	0.9836	7.3661	7.5169	1.9184	1.4934	0
27.01.86	0	0	0	1.1756	2.0158	0	0	3.6796	3.7022	0	0	0	0
28.02.86	0	0.8544	7.9380	10.1110	0.9345	3.0245	0.9415	2.3488	6.8520	7.7980	4.4151	1.3896	1.7330
30.03.86	0	0.3586	2.5676	2.0146	0.7718	0	0.8833	1.9399	5.8317	2.9222	1.1763	0.7526	0
Mean Biomass at each age group	0.02293	0.9899	4.6797	4.7854	0.9651	0.7217	0.7217	3.8421	5.7476	6.5714	0.7510	0.8597	0.1733

lower $P/\bar{B}$ values.

The annual mean biomass and production obtained in the present investigation have been compared with biomass and production found in previous studies (Table 3.11). Although production and biomass of the present study seemed to be slightly lower than in previous studies, it fell within the range obtained by Hibbert (1976) for the littoral population of *Mercenaria* at Hamble Spit. However, figures of production for the sublittoral population of *Mercenaria* found by Oyenekan (1980) appeared to be exceptionally high and unlikely although in sublittoral area, conditions are less stressful and feeding is continuous. The discrepancy in the estimate of production between the present study and Oyenekan's work, may result from actual change in population density, together with errors which might have occurred in aging of clams in Oyenekan's study.

Table 3.9a : $P/\bar{B}$ ratio at each group for *Mercenaria* at Marchwood

	Age Groups												
	6+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+	19+
Mean production ($gm^{-2}y^{-1}$)	0.0949	0.0128	0.0668	0.1128	0.1094	0.1662	0.2727	0.8782	0.9705	0.3005	0.1206	0.0403	0.0350
Mean Biomass (gm^{-2})	0.1392	0.1117	0.6789	0.9929	1.4319	1.2345	4.3982	6.0124	8.2714	3.9868	1.7650	1.1034	0.6081
$P/\bar{B}$	0.6812	0.1145	0.0984	0.1136	0.0764	0.1346	0.0620	0.1461	0.1173	0.0754	0.0683	0.0365	0.0519

Table 3.9b : $P/\bar{B}$ ratio at each group for *Mercenaria* at Lee-on-Solent

	Age Groups												
	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+
Mean production ($gm^{-2}y^{-1}$)	0.0227	0.1177	4.6797	4.7854	0.9651	0.5893	0.7217	3.8421	5.7476	6.5714	0.7510	0.8597	0.1733
Mean Biomass (gm^{-2})	0.0229	0.9899	0.3840	0.3066	0.1307	0.0401	0.0444	0.4470	1.0497	0.3695	0.0390	0.0969	0.0125
$P/\bar{B}$	0.9900	0.1189	0.0821	0.0641	0.1354	0.0680	0.0615	0.1163	0.1826	0.0562	0.0519	0.1127	0.0721

Table 3.10 : Regression of the P/$\bar{B}$ with age group at Marchwood and Lee-on-Solent

Marchwood		Lee-on-Solent	
Age Groups	P/$\bar{B}$	Age Groups	P/$\bar{B}$
6+	0.17	6	0.24
8+	0.10	7	0.09
9+	0.09	8	0.05
10+	0.11	9	0.10
11+	0.15	10	0.09
12+	0.06	11	0.08
13+	0.16	12	0.12
14+	0.14	13	0.18
15+	0.06	14	0.07
16+	0.07	15	0.06
17+	0.04	16	0.11
18+	0.06	17	0.08
19+	0.03	18	0.02
Correlation Coefficient (r)	0.717		0.486
Intercept (a)	- 0.544		- 0.674
Slope (b)	- 0.040		- 0.032
Significance level	$P \leq 0.05$		$P \leq 0.05$

Table 3.11 : Mean biomass (gm^{-2}) and annual production of *Mercenaria mercenaria* in different studies in Southampton Water

Site / station	Biomass (gm^{-2})	Production ($gm^{-2}y^{-1}$)	P/$\bar{B}$	Source
Station 5 (sublittoral, Netley)	80.207	87.6955	1.09	Oyenekan (1980)
Hamble Spit I (littoral)	7.73	3.99	0.52	Hibbert (1976)
Hamble Spit II (littoral)	50.04	14.00	0.28	Hibbert (1976)
Hamble Spit IV (littoral)	36.54	6.19	0.17	Hibbert (1976)
Marchwood (littoral)	30.73	3.02	0.098	Present study
Lee-on-Solent (littoral)	30.70	2.71	0.088	Present study

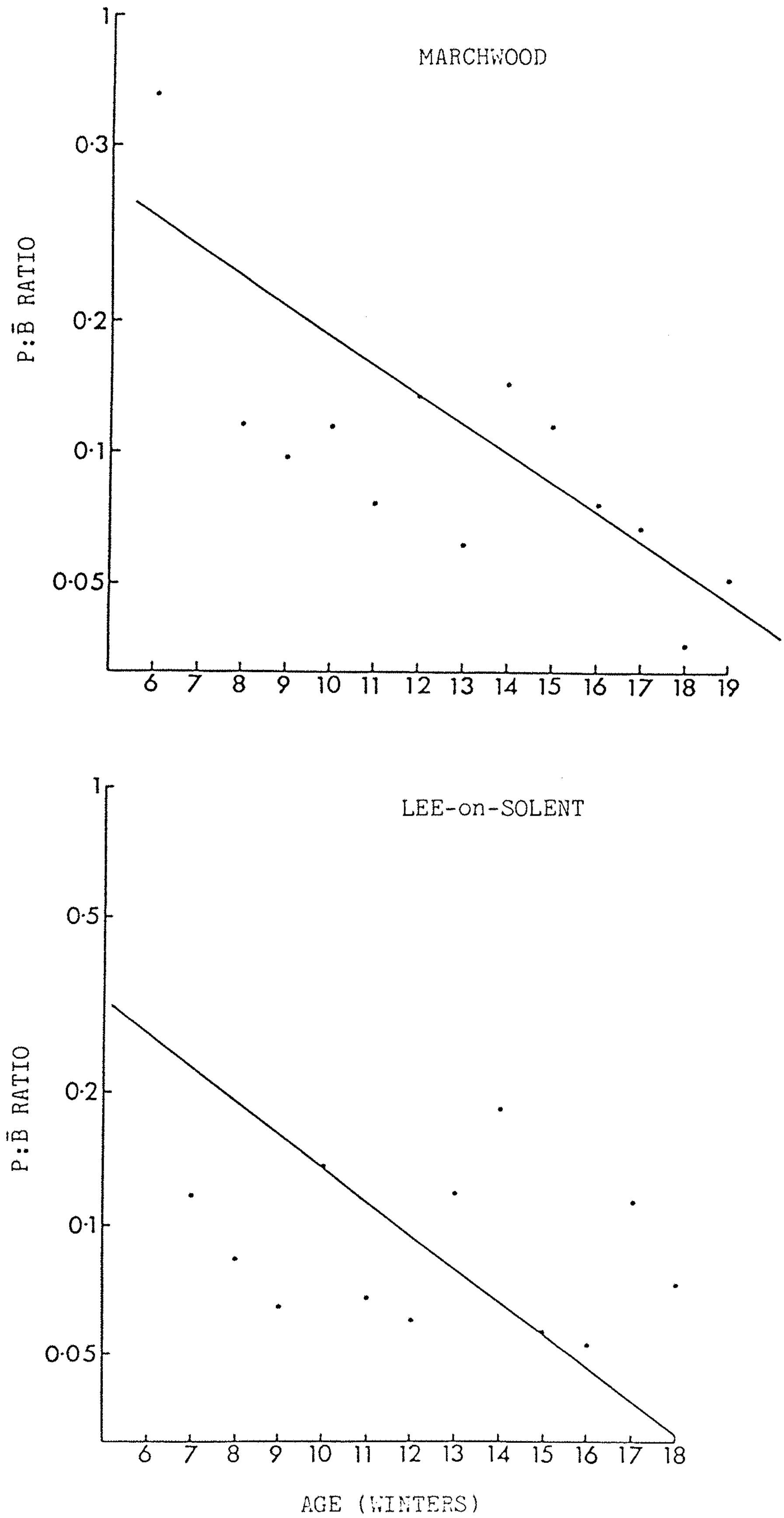


Fig. 3.9 Log-linear regression of P/B̄ ratio and age of Mercenaria population at Marchwood and Lee-on-Solent during March 1985 - March 1986

3.7.5 Condition Index

The percentage frequency distribution of the condition index for *Mercenaria* sampled at different sites during 1983, 1984 and 1985 are represented in Fig. 3.10. The condition index varied between sites. At Marchwood and Lee-on-Solent the modal class was between 2 and 3, whereas individuals at Royal Pier, Hamble Spit and Solent Breezes had their modal class between 3 and 4, with the sublittoral populations of *Mercenaria* having their modal class between 4 and 5. Individuals at Hamble Spit showed a broad spread of values ranging from 2 to 7 compared to the narrow distribution of values at Solent Breezes. Although the samples consist mainly of large and old individuals (aged 5 - 14 years) nevertheless comparison of condition index calculated for different size groups at different sites (Table 3.12 and Fig. 3.11) have been made using analysis of covariance. The condition index varied significantly between different size groups and between sites, respectively at $p < 0.05$ as shown in Table 3.13. The Sch effe multiple comparison test showed that condition indices at Hamble Spit, Lee-on-Solent and sublittoral sites were significantly different at $p \leq 0.05$ (Table 3.14). In general, the overall mean condition index revealed a distinct pattern of higher value at the middle littoral and sublittoral sites of the estuary. Relatively lower values for condition index was found at both the northern and southern parts of Southampton Water as shown in Table 3.12.

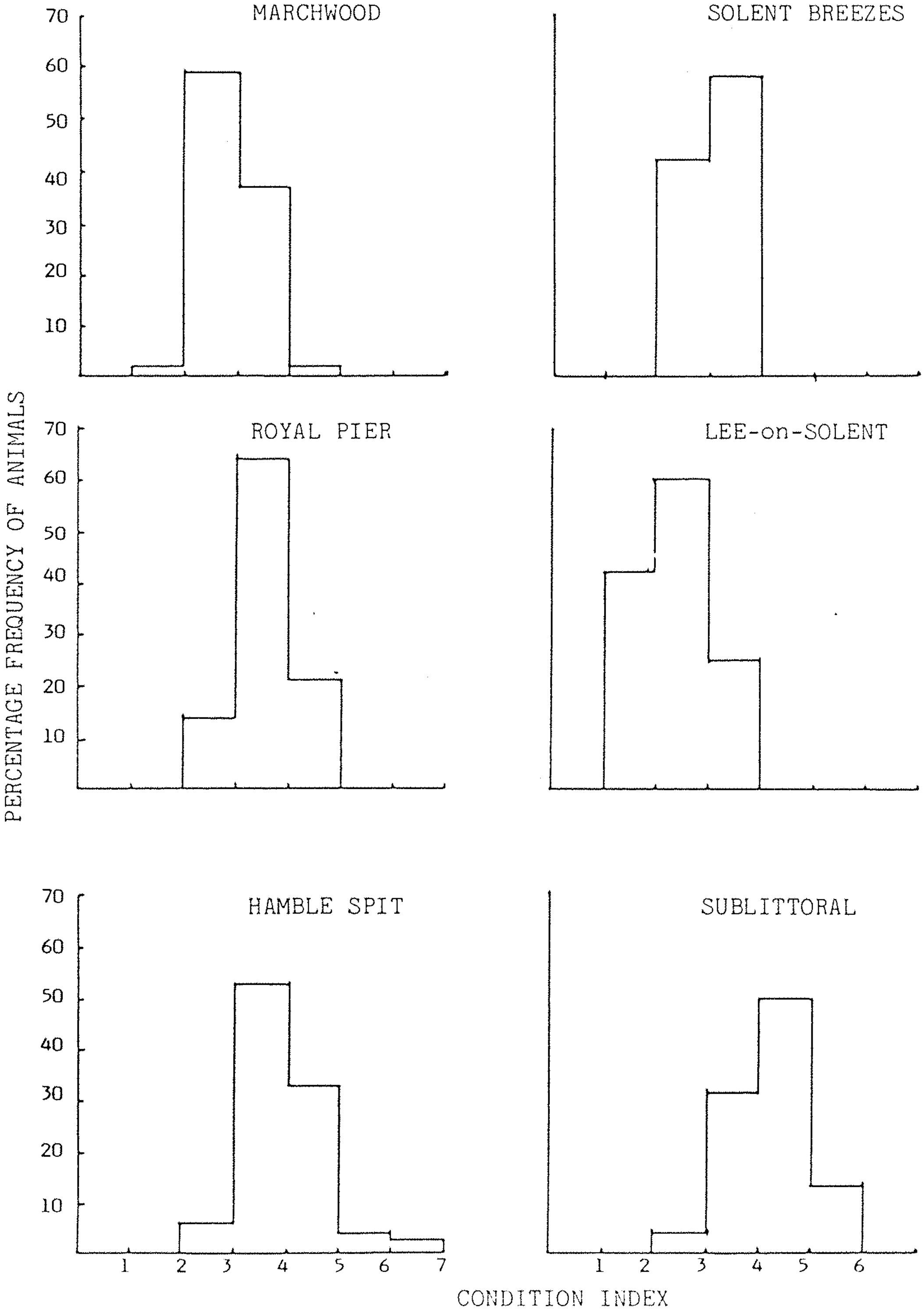


Fig. 3.10 Percentage frequency distribution of condition index throughout Southampton Water

Table 3.12 : Mean condition indices (C.I.) and standard deviation at each size group of littoral and sublittoral *Mercenaria* populations sampled in 1983 - 1985

size groups (mm)	Marchwood	Royal Pier	Hamble Spit	Solent Breezes	Lee-on-Solent	Sublittoral sites
46 - 48	3.55					
48 - 50	2.71±0.69					
50 - 52	2.79±0.35					
52 - 54	-					
54 - 56	2.73±0.24					
56 - 58	-					
58 - 60	-		2.76±0.00			
60 - 62	2.56±0.46		0			
62 - 64	2.76±0.46		4.33±1.15	3.03±0.00		
64 - 66	2.85±0.28		3.95±0.73	-	2.81±1.16	5.34±0.00
66 - 68	2.86±0.63	3.65±0.78	4.06±0.29	3.47±0.00	2.48±0.58	4.77±0.11
68 - 70	3.05±0.79	3.10±0.0	4.07±0.94	-	2.80±0.37	3.80±0.37
70 - 72	3.06±0.29	3.15±0.92	3.88±0.66	2.82±0.00	2.32±0.47	4.33±0.90
72 - 74	2.88±0.11	3.17±0.45	3.96±0.52	2.82±0.48	2.34±0.32	4.76±0.06
74 - 76	3.34±0.66	3.3÷0.26	3.64±0.51	2.87±0.36	2.26±0.98	-
76 - 78	3.06±0.54	4.10±0.0	4.07±0.67	3.26±0.0	3.05±0.00	4.32±0.55
78 - 80	3.16±0.59	3.10±0.0	3.44±0.70	-		4.72±0.00
80 - 82			3.05±0.00	2.91±0.19		4.58±0.00
82 - 84				0	-	-
84 - 86				3.53±0.0		4.79±1.66
86 - 88				3.23±0.0		
88 - 90				2.78±0.0		
90 - 92				2.93±0.0		
92 - 94				-		
94 - 96				-		
96 - 98				3.70		
98 -100						
Overall mean C.I.	2.94	3.37	3.74	3.11	2.55	4.60
Overall S.D.	±0.24	±0.38	±0.48	±0.32	±0.31	±0.42
Number of clams	14	7	11	12	11	9

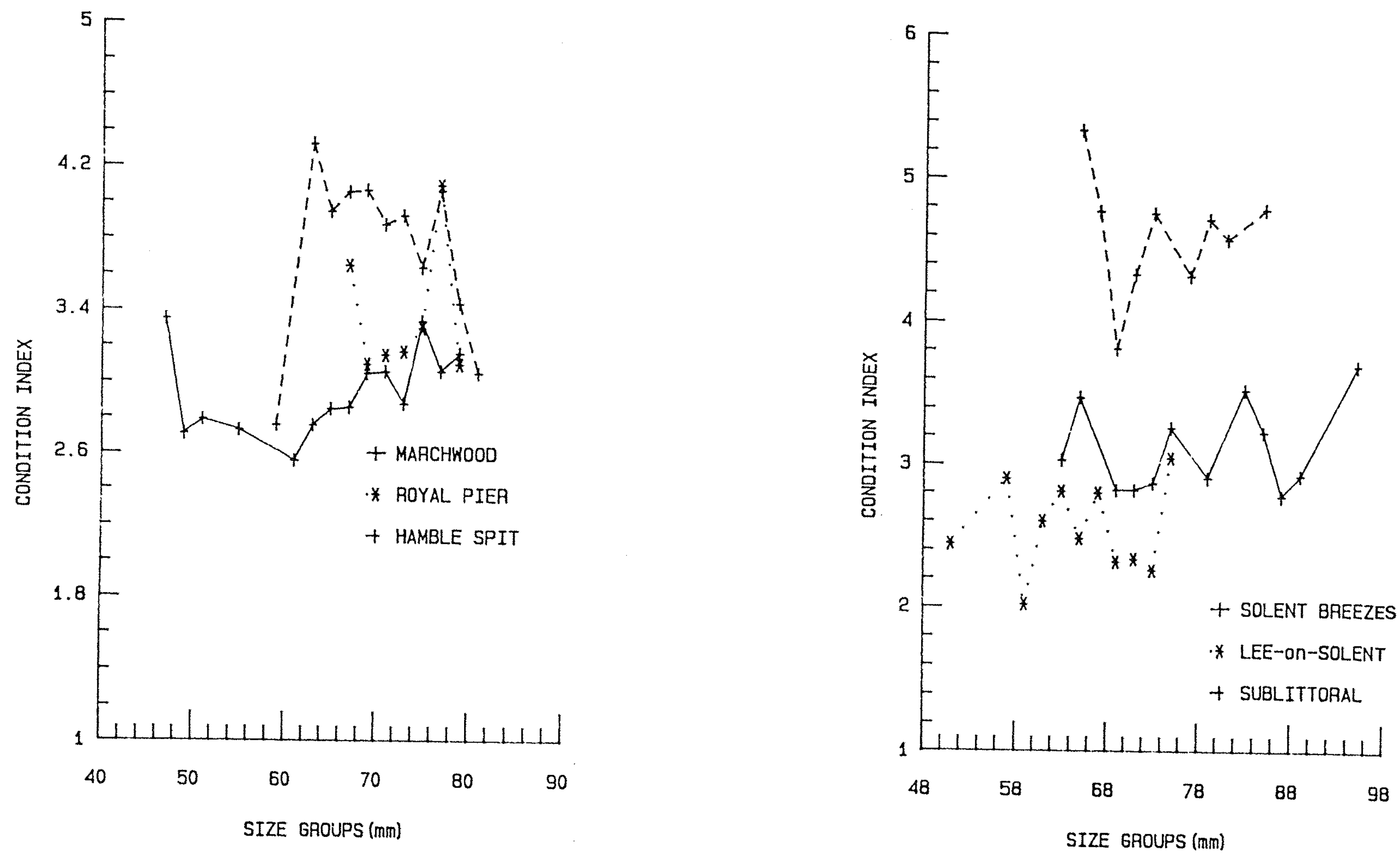


Fig. 3.11 Mean condition index at each size group of littoral and sublittoral populations of Mercenaria during 1983 - 1985.

Table 3.13 : Analysis of variance for condition index at different sites

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio
Covariates	6.824	1	6.824	19.536*
groups	6.824	1	6.824	19.536*
Main effects	70.837	5	14.167	40.557*
sites	70.837	5	14.167	40.557*
Residual	69.165	198	0.349	
Total (Corr.)	146.826	204		

* indicates statistically significant at P < 0.01

Table 3.14 : Multiple comparison test (Scheffe) for condition index at different sites

Site name	Site code	95 Percent Count	Scheffe Average	Homogeneous sites 4	1	3	6	5
Lee-on-Solent	4	24	2.533	*				
Marchwood	1	56	2.874		*			
Solent Breezes	3	18	3.051		*	*		
Royal Pier	2	14	3.314			*		
Hamble Spit	6	71	3.885				*	
All sublittoral sites	5	19	4.497					*

Sites with identical condition index are only shown and marked with astericks.

3.7.6 Length-Weight Relationship

Investigation of the relationship between the shell length and ash free tissue dry weight, was made on Mercenaria collected in the winters of 1983 and 1984 from different sites in Southampton Water. The relationship was found to be logarithmic and calculation therefore was made on logarithmically transformed data using the least square regression analysis. The appropriate regression constants a and b, correlation coefficient and the statistical significance of the relationships are shown in Table 3.15. Plot of the logarithmic relationship obtained throughout Southampton Water are shown in Fig. 3.12. The results illustrate that the association between shell length and tissue ash free dry weight is positively correlated ($r = 0.66 - 0.966$) and significant at $p < 0.05$ for all the sites, except at Royal Pier and Hamble Spit, where the correlation was low ($r = 0.41 - 0.61$) suggesting great individual variability in sizes and weights. The sublittoral population showed the best fit length-weight relationship ($r = 0.966$)

Table 3.15 : Regression constants (a) and (b), correlation coefficient (r) and significance level of the logarithmic length-weight relationship of *Mercenaria* at different sites

Number of clams	Site	Slope (b)	Intercept (a)	Correlation coefficient (r)	Coefficient of determination (d)	Standard error of estimate	Level of significance
16	Marchwood	2.826	-4.879	0.749	0.652	0.402	$P \leq 0.05$
10	Royal Pier	3.222	-5.608	0.617	0.405	0.592	$P \leq 0.05$
56	Woolston	3.512	-6.121	0.756	0.526	0.526	$P \leq 0.05$
34	Weston	3.387	-5.663	0.732	0.509	0.509	$P \leq 0.05$
36	Netley	3.371	-5.749	0.819	0.694	0.694	$P \leq 0.05$
39	Hamble Spit	1.598	-2.544	0.414	0.173	0.173	$P \leq 0.05$
18	Solent Breezes	2.815	-4.849	0.867	0.509	0.509	$P \leq 0.05$
25	Lee-on-Solent	2.672	-4.709	0.662	0.442	0.442	$P \leq 0.05$
26	Sublittoral	3.653	-6.344	0.966	0.828	0.828	$P \leq 0.05$

The relationship between the ash-free dry weight (W) and the clam length (L) is expressed by the following equation:

$$\text{Log}_{10}W = b\ \text{Log}_{10}L + a$$

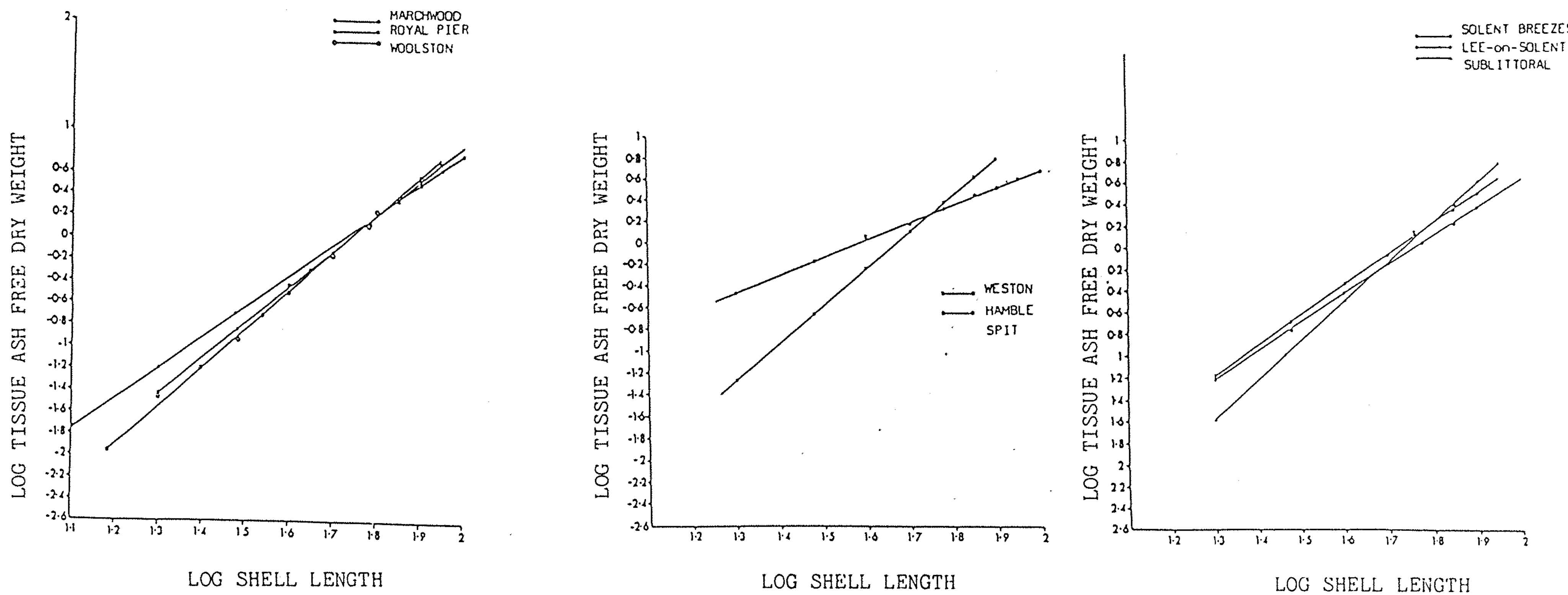


Fig. 3.12 Logarithmic regression of shell length and tissue ash free dry weight for Mercenaria populations throughout Southampton Water

3.77 Morphometry

The correlation matrix between various body parameters of the Mercenaria population sampled at Marchwood, Royal Pier, Solent Breezes, Lee-on-Solent and sublittoral sites in 1984 and 1985 are given in Tables 3.16 a, b, c, d, e. Although, there were many individual variations in characters of individuals of the same age, the correlation matrix showed that all body parameters were positively correlated with each other. Shell curvature gave the highest and most consistent correlation with other characters. On the contrary, shell thickness showed the lowest correlation. Mean values of body parameters by age at different sites are given in Table 3.17a,b,c,d,e,f . Plot of mean values of the characters at each age as a function of shell curvature for the 4 sites are illustrated in Fig. 3.13. All the parameters increased with shell curvature but to a different extent. Shell length, height and breadth showed a steady increase with shell curvature, whereas tissue dry weight, ash free dry weight and shell weight increased exponentially with shell curvature. All the measured parameters revealed that Mercenaria at Solent Breezes had the heaviest, thickest and widest shell, and greatest soft tissue weight, whereas clams at Marchwood had narrowest and thinnest shell (Table 3.17). Parameters of the shell volume (length, height and breadth) apparently increase at a lower rate than weight and thickness of the shell in all the sites. The length, height and breadth showed approximately linear relationship with the curvature, while the dry soft tissue weight, ash free dry weight, and shell weight gave an exponential relationship. From large number of measurements, on body parameters, the growth coefficient, b, of the allometric equation $Y = ax^b$, were computed for Mercenaria at different sites. The results are given in Table 3.18. The interrelationship between different body parameters (x and Y) are said to be showing negative allometry, when values of $b < 1$, indicating that x is increasing relatively faster than Y. Positive allometry occurs when $b > 1$, indicating that Y grows faster than x, whereas a value of $b = 1$ is indicative of isometric allometry i.e. the two variables grow equally. If variables are of different dimensions (e.g. length and weight), value of the growth coefficient $b = 1$ represents isometric growth (Gould, 1966).

The relationship between shell curvature and parameters of the shell volume (shell length, height and breadth) showed negative allometry in all the sites. This indicate that shell curvature grows relatively faster than length, height and breadth of the shell. The relationship of shell length with shell height and shell breadth resulted in negative allometry for all the sites. The length : shell weight relationship showed negative allometry in all the sites except at Solent Breezes, where the relationship displays positive allometry. The height shell : shell weight relationship was positively allometric with the exception of population at Royal Pier and the sublittoral populations, where the relationship was negatively allometric.

Table 3.16 a : Correlation matrix between different body parameters of littoral population of Mercenaria at Marchwood sampled in 1984

	Age	SL	SW	SH	SB	SC
Age	-					
SL	0.562*	-				
SW	0.669*	0.937*	-			
SH	0.589*	0.956*	0.933*	-		
SB	0.687*	0.871*	0.919*	0.866*	-	
SC	0.654*	0.948*	0.947*	0.975*	0.913*	-

* indicates statistically significant at P ≤ 0.01. Sample size was 48 individuals.

SL = shell length, SW = shell weight, SH = shell height,

SB = shell breadth, SC = shell curvature

Table 3.16 b : Correlation matrix of different characters of littoral population of Mercenaria at Solent Breezes sampled in 1984

	TWW	TDW	AFDW	SL	SW	SH	SB	SC	ST
TWW	-								
TDW	0.951*	-							
AFDW	0.965*	0.905*	-						
SL	0.838*	0.769*	0.777*	-					
SW	0.661*	0.630*	0.632*	0.722*	-				
SH	0.842*	0.764*	0.760*	0.973*	0.725*	-			
SB	0.097	-0.017	0.003	0.297*	0.209	0.306*			
SC	0.091	0.034	0.029	0.360*	0.237	0.384*	-		
ST	0.601*	0.514*	0.474*	0.799*	0.639*	0.775*	0.452*	-	

* indicates statistically significant at P ≤ 0.05. Sample size was 22 individuals.

TWW = tissue wet weight, TDW = tissue dry weight, AFDW = ash free dry weight, SL = shell length, SW = shell weight, SH = shell height, SB = shell breadth, SC = shell curvature, ST = shell thickness

Table 3.16 c : Correlation matrix of different characters of littoral population of Mercenaria at Lee-on-Solent sampled in 1984

	TWW	TDW	AFDW	SL	SW	SH	SB	SC	ST
TWW	-								
TDW	0.072	-							
AFDW	0.072	0.938*	-						
SL	0.172	0.518*	0.388*	-					
SW	0.239	0.657*	0.718*	0.554*	-				
SH	0.303*	0.645*	0.712*	0.479*	0.917*	-			
SB	0.002	0.522*	0.480*	0.206	0.416*	0.339*	-		
SC	0.362*	0.611*	0.652*	0.413*	0.872*	0.875*	0.266	-	
ST	0.181	0.130	0.197	0.251	0.329*	0.418*	0.140	0.338*	-

* indicates statistically significant at $P \leq 0.05$. Sample size was 22 individuals.

TWW = tissue wet weight, TDW = tissue dry weight, AFDW = ash free dry weight, SL = shell length, SW = shell weight, SH = shell height, SB = shell breadth, SC = shell curvature, ST = shell thickness

Table 3.16 d : Correlation matrix of different characters of sublittoral Mercenaria population throughout Southampton Water, sampled in 1985

	TWW	TDW	AFDW	SL	SW	SH	SB	SC	ST
TWW	-								
TDW	0.915*	-							
AFDW	0.929*	0.994*	-						
SL	0.577*	0.435*	0.443*	-					
SW	0.215	0.192	0.217	0.413*	-				
SH	0.467*	0.318*	0.342*	0.860*	0.437*	-			
SB	0.147	0.099	0.137	0.268	0.683*	0.183	-		
SC	0.512*	0.354*	0.361*	0.947*	0.561*	0.905*	0.297	-	
ST	0.425*	0.326*	0.321*	0.857*	0.459*	0.858*	0.128	0.876*	-

legends are same as above

Table 3.17 : Mean values of body parameters in relation to age at each site

a - Tissue dry weight (g)

Age	Solent Breezes	Lee-on-Solent	Sublittoral
4	-	-	0.63
5	-	0.77	0.76
6	2.28	0.93	2.1
7	3.52	1.19	-
8	2.59	1.68	2.64
9	3.25	-	2.89
10	-	1.85	3.93
11	-	2.00	3.59
12	-	2.10	-
13	3.11	2.11	-
14	5.59	-	4.21
15	-	-	5.48

b - Shell weight (g)

Age	Marchwood	Royal Pier	Solent Breezes	Lee-on-Solent	Sublittoral
5	-	-	-	36.57	-
6	-	39.82	76.21	37.94	49.4
7	-	56.7	82.73	49.21	48.32
8	-	-	106	53.67	75.12
9	54.52	68.7	-	52.87	77.05
10	58.23	56.85	-	71.29	86.17
11	59.85	76.43	-	71.34	-
12	73.52	82.2	-	78.28	-
13	73.33	84.79	-	86.4	-
14	82.69	89.3	146.7	-	94.95
15	-	-	152.6	-	-

c - Shell length (mm)

Age	Marchwood	Royal Pier	Solent Breezes	Sublittoral
4	-	-	-	46.25
5	-	-	-	50.80
6	-	55.18	79.1	63.00
7	-	64.67	73.78	-
8	-	-	75.48	66.49
9	64	-	79	71.68
10	66.72	63.9	-	75.67
11	64.99	72.4	-	78.45
12	70.57	72.48	-	-
13	69.55	72.72	88.8	-
14	70.7	74.90	86.9	73.9
15	-	-	91.3	83.1

d - Shell height (mm)

Age	Marchwood	Royal Pier	Solent Breezes	Sublittoral
4	-	-	-	40.05
5	-	-	-	44.85
6	-	44.87	58.95	53.55
7	-	55.6	61.2	-
8	-	-	61.13	56.05
9	53.2	-	66.9	57.73
10	56.32	55.45	-	63.25
11	54.8	59.85	-	69.05
12	58.66	61.72	-	-
13	60.03	61.74	-	-
14	58.25	64	72.70	-
15	-	-	74.4	72.07

e - shell curvature

Age	Marchwood	Royal Pier	Solent Breezes	Lee-on-Solent	Sublittoral
4	-	-	-	-	50
5	-	-	-	58.00	60
6	-	57	76.2	60.25	68
7	-	70	78.2	65.50	-
8	-	-	79.0	65.18	71
9	66	-	86	69.50	74.89
10	70.7	72	-	73.43	79
11	68.67	76.67	-	73.33	86
12	74.31	79.2	-	75.75	-
13	75.5	78.8	-	79.75	-
14	76	82	94.6	-	78.3
15	-	-	96	-	91.69

f- shell thickness

Age	Royal Pier	Solent Breezes	Lee-on-Solent	Sublittoral
4	-	-	-	2.71
5	-	-	3.28	2.87
6	3.55	4.43	3.78	3.48
7	3.87	4.36	3.58	-
8	-	4.26	3.65	3.81
9	-	5	3.66	4.13
10	4.08	-	4.16	4.89
11	4.50	-	4.29	5.51
12	4.62	-	4.19	-
13	4.66	-	4.35	-
14	4.53	5.28	-	4.60
15	-	6.93	-	4.77

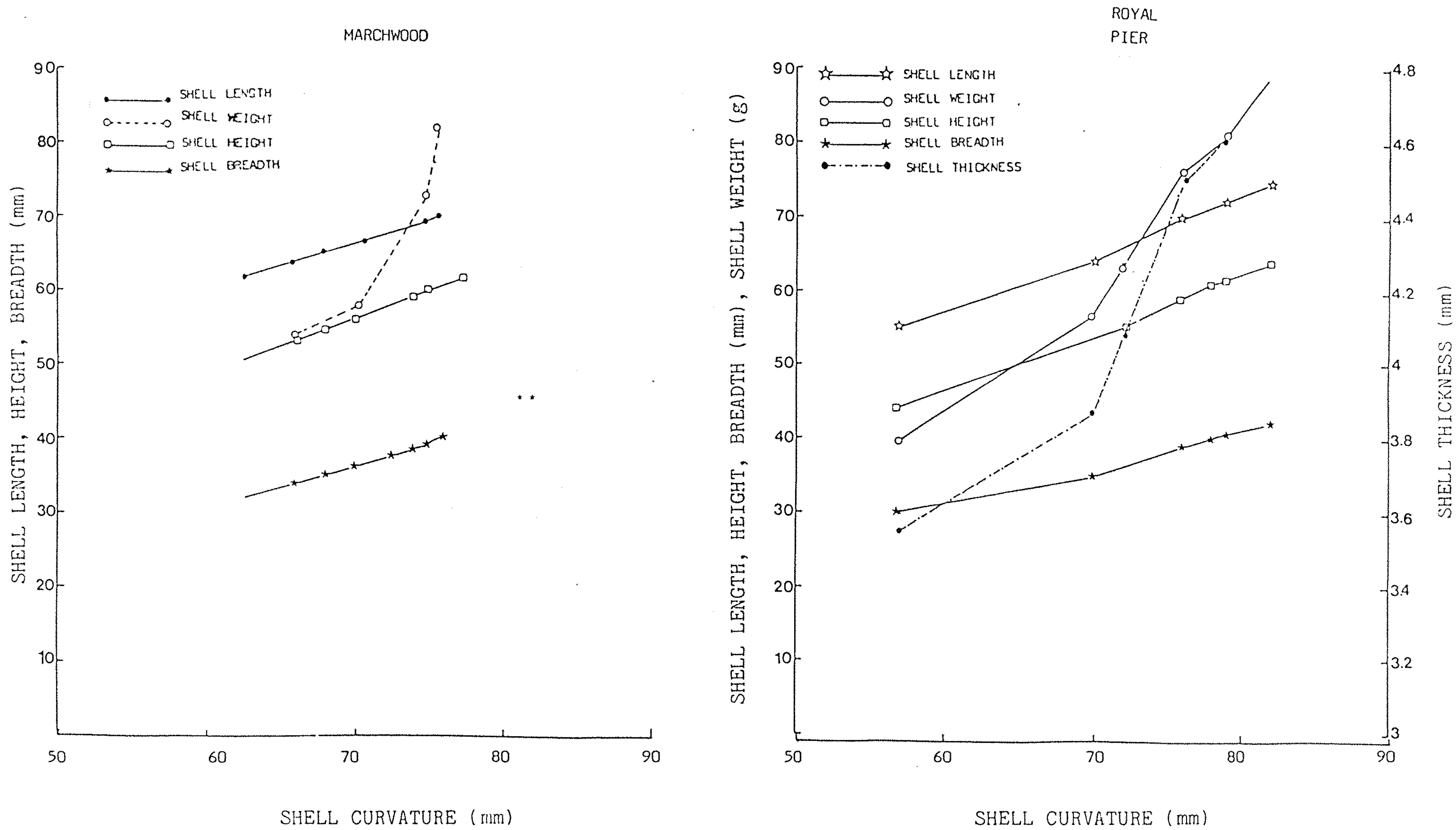


Fig. 3.13a Body parameters as a function of shell curvature in littoral *Mercenaria* populations at Marchwood and Royal Pier

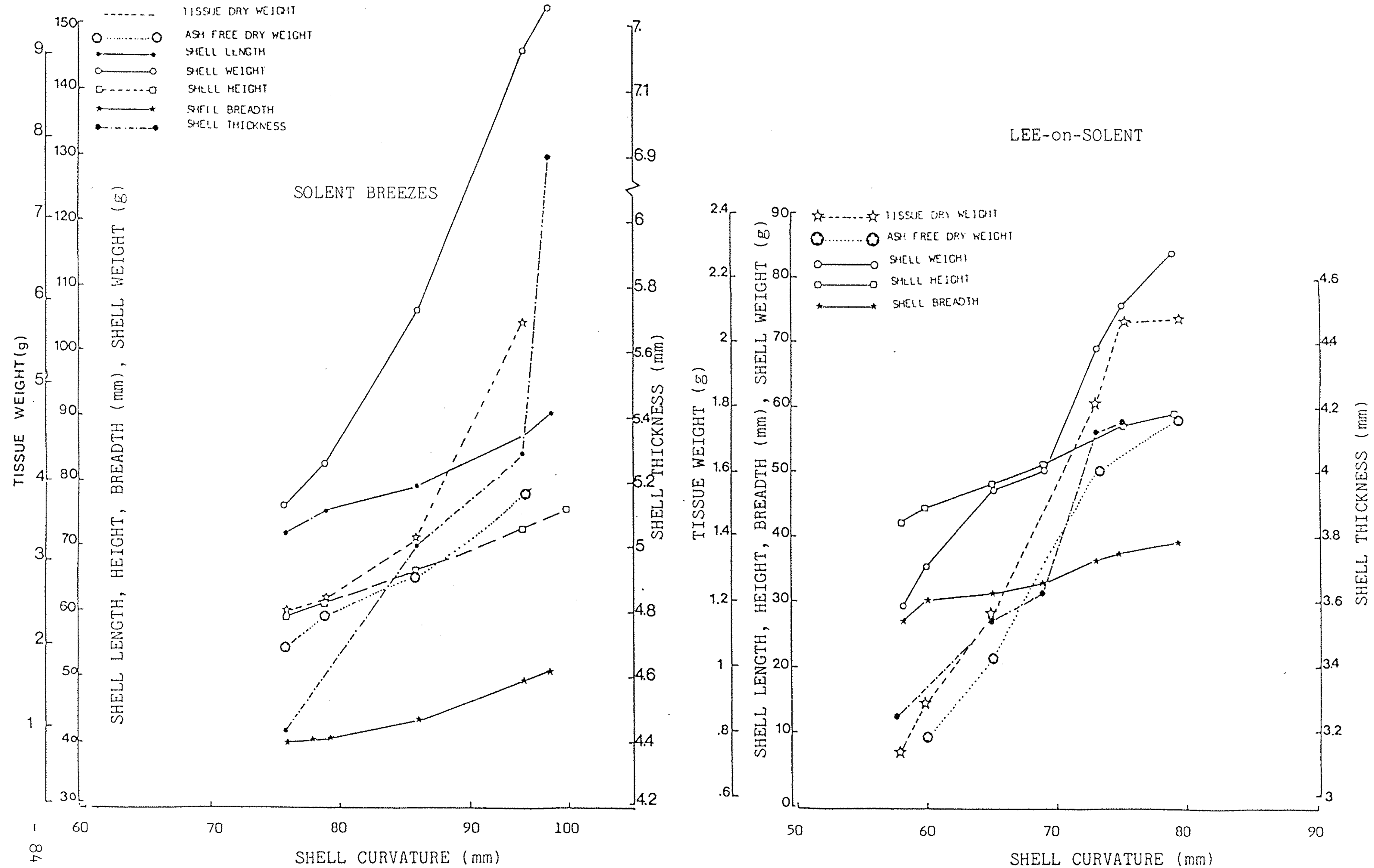


Fig. 3.13b Body parameters as a function of shell curvature in littoral Mercenaria populations at Solent Breezes and Lee-on-Solent

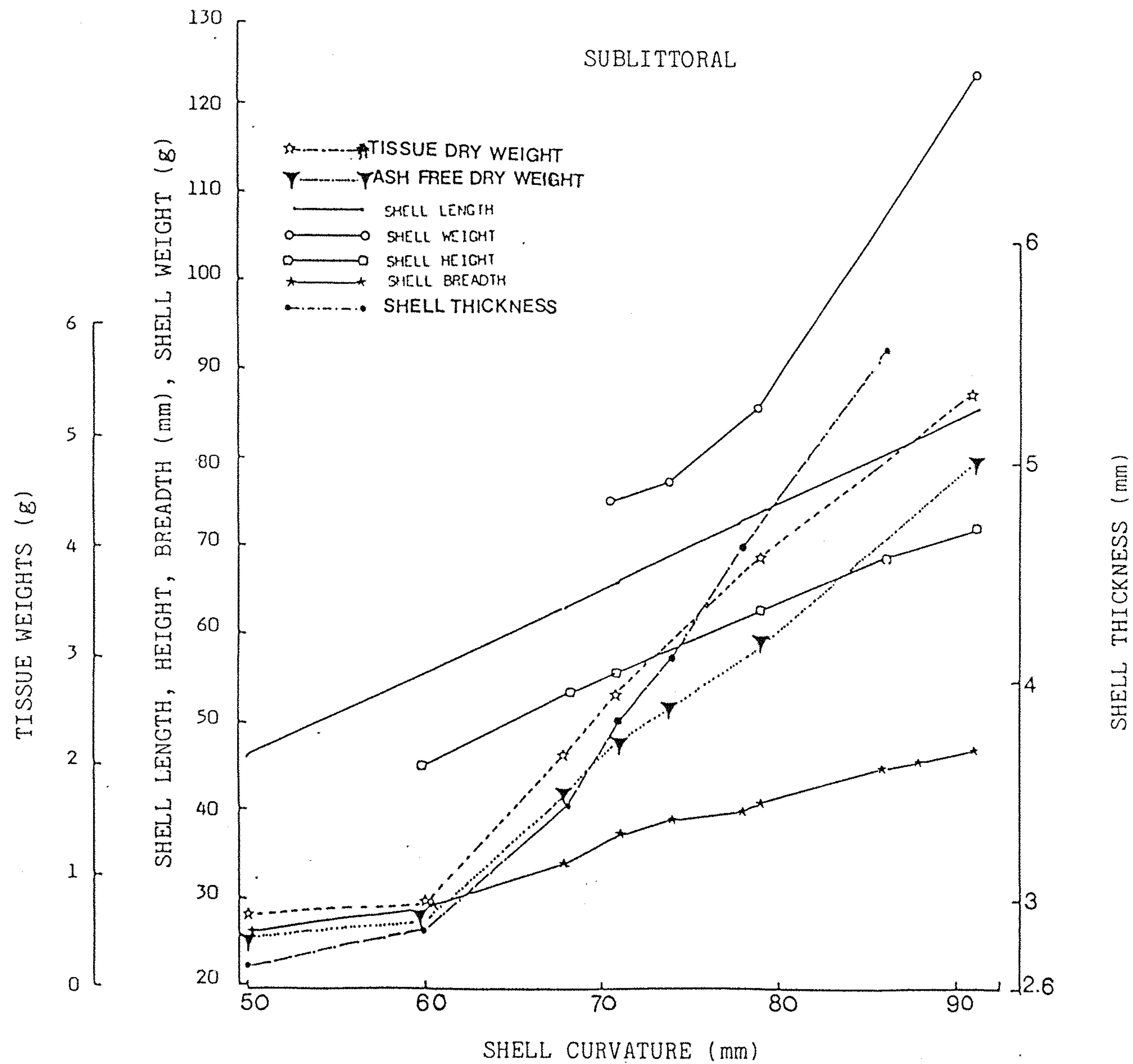


Fig. 3.13c Body parameters as a function of shell curvature in sublittoral *Mercenaria* population throughout Southampton Water

Table 3.18 : The growth coefficient b ±S.E. of the allometric equation $Y=aX^b$ for all possible pairs of variables of <u>Mercenaria</u> population from different sites

Variables	Marchwood		Royal Pier		Solent Breezes		Lee-on-Solent		Sublittorals	
	b	±S.E.	b	±S.E.	b	±S.E.	b	±S.E.	b	±S.E.
SC - SL	0.927	--- 0.046	0.869	--- 0.046	0.140	--- 0.082	0.466	--- 0.224	0.784	--- 0.063
SC - SH	0.740	--- 0.025	0.761	--- 0.027	0.133	--- 0.072	0.734	--- 0.089	0.762	--- 0.092
SC - SB	0.439	0.029	0.482	--- 0.02	0.131	--- 0.046	0.197	--- 0.156	0.222	--- 0.173
SC - ST	-	-	0.056	--- 0.006	0.014	--- 0.007	0.044	--- 0.027	0.067	--- 0.008
SL - SH	0.742	--- 0.034	0.844	--- 0.033	0.866	--- 0.046	0.356	--- 0.142	0.869	--- 0.122
SL - SB	0.429	--- 0.036	0.519	--- 0.036	0.188	--- 0.129	0.135	--- 0.140	0.238	--- 0.201
SL - ST	-	-	0.063	--- 0.007	0.068	--- 0.011	0.029	--- 0.024	0.077	--- 0.011
SL - SW	2.631	--- 0.144	2.225	--- 0.198	3.650	+++ 0.783	1.501	--- 0.492	1.426	--- 0.741
SH - SW	3.375	+++ 0.191	2.646	--- 0.201	4.302	+++ 0.915	3.338	--- 0.317	1.031	--- 0.765
SH - SB	0.549	--- 0.047	0.620	--- 0.030	0.220	--- 0.153	0.299	--- 0.181	0.050	--- 0.206
SH - ST	-	-	0.075	--- 0.007	0.074	--- 0.019	0.065	--- 0.031	0.070	--- 0.012
SB - ST	-	-	0.116	--- 0.012	0.0617	--- 0.026	0.025	--- 0.038	0.018	--- 0.020
SC - SW	2.599	--- 0.131	2.01	--- 0.174	0.488	--- 0.438	2.666	+++ 0.326	1.623	--- 0.596
SW - ST	-	-	0.026	--- 0.003	0.105	--- 0.003	0.014	--- 0.009	0.012	--- 0.004
SW - SB	0.161	--- 0.010	0.206	--- 0.018	-	-	0.010	--- 0.048	0.194	--- 0.037

--- negative allometry +++ positive allometry

SC = shell curvature; SL = shell length; SH = shell height; SB = shell breadth; ST = shell thickness; SW = shell weight.

3.8 CONCLUSION

Different aspects of population parameters (growth rate, production, biomass, condition index and morphometry) are summarised in Table 3.19.

In the analysis of growth of Mercenaria, three mathematical models namely, the Logistic, the Gompertz and the Monomolecular, were fitted on growth data collected from different sites in Southampton Water. The Gompertz model gave consistently highest correlation coefficient and coefficient determination, and the lowest standard error. Therefore, the Gompertz was considered the best model to describe growth of Mercenaria in Southampton Water. The subsequent calculation of growth rate in terms of shell length as predicted by the Gompertz model, revealed wide variation in growth rate between different sites. Maximum growth rate in terms of shell length occurred during the second year at all sites, with the exception of the population at Marchwood and Hythe pier, where maximum growth was in the third year. It appears that growth rate of Mercenaria depends on locality within the estuary. Highest growth rate (in shell length) were found in the littoral population of Mercenaria at Solent Breezes, Hamble Spit, Weston and Netley (Table 3.19). Those sites, represent different types of sediment (sand, mixed muddy sand). Mitchell (1974) concluded that comparison of growth rate at different sites, do not show a simple relationship between growth rates and sediment types, and suggested other factors such as availability of food, temperature and salinity might also influence growth rates. Recently, evidence for the effect of bottom current on growth of Mercenaria have been given by Wildish (1985) who found that production and growth of

Mytilus edulis is a function of current speed. He added that at lower current speed growth is limited by the seston depletion effect, while at an intermediate current speed no effect on mussel production could be detected.

In the present study populations showing greater shell growth during the first four years had reduced growth rate in older animals (Fig. 3.4). It follows, that individuals showing rapid initial growth have a shorter rapid growth phase, reaching maximum size over a shorter period, than do gradually growing individuals. The high growth rate recorded in young individuals may be favoured in areas where the mortality of young individuals relative to old individuals is high. Mortality of older individuals as a result of predation or hand picking seems to be relatively low in comparison to fishing mortality.

Differential growth rate in shell length and tissue ash free dry weight were investigated in populations at Marchwood and Lee-on-Solent. Although in comparing growth in shell length with growth in tissue weight, we are not comparing like with like, a significant relationship exist between shell length and weight. Growth in terms of shell length should therefore show similar trends to change in shell weight.

Results showed that maximum rate of increment in shell length and in tissue ash free dry weight was achieved at different ages. At Marchwood maximum rate of increment in shell length and ash free dry weight occurred during the third and fifth year of age, respectively, whereas at Lee-on-Solent, maximum growth rate in shell length and ash free dry weight was achieved during the second and

Table 3.19 : Population parameters of <u>Mercenaria</u> populations at different sites in Southampton Water

sites	Growth rate in length (mm yr.$^{-1}$)	Production $gm^{-2}yr.^{-1}$	Biomass gm^{-2}	Mean $no.m^{-2}$	Mean condition index	Length-weight relationship b	Length-weight relationship r	Tissue dry weight g	Shell weight g	Shell height mm	Shell breadth mm	Shell curvature mm	Shell thickness mm
Marchwood	9.848	3.020	30.70	15.5	2.94	2.826	0.749		82.69	58.25	40.85	76	
Royal Pier	9.633	1.635*	16.35*	10.0	3.37	3.223	0.617		89.30	64.00	42.40	82	3.53
Hythe Pier	9.139	3.828*	38.28*	14.0									
Woolston		3.795*	37.95*	11.3		3.512	0.756						
Weston	12.464	5.760*	57.60*			3.387	0.732						
Netley	11.076	12.284*	122.84*	24.2		3.371	0.819						
Hamble Spit	14.302	4.979*	49.79*	19.6	3.74	1.598	0.414						
Solent Breezes	14.518	3.624*	36.24*	11.8	3.11	2.815	0.867	5.59	146.7	72.70	49.20	94.6	4.42
Lee-on-Solent	10.618	2.710	27.10	16.0	2.55	2.672	0.662						2.78
All sub-littoral sites	10.362	2.674*	26.74*	10.7	4.60	3.653	0.966	4.21	94.95	61.70	40.43	78.3	3.43

Note: Values of production and biomass marked with asterisks are predictive, calculated according to the method outlined in the text, using a P:8 ratio of 0.1 each time. Morphometric value are compared at age 14 years old. Maximum growth rate at age 2.

fourth year respectively. Such differential growth of shell and soft parts were also reported by Mitchell (1974) when he monitored seasonal changes in condition and biochemical composition between small immature and large mature Mercenaria. He attributed the fall in condition index in the immature individuals (less than 3 years old) to greater growth of shell relative to growth of flesh. Also, Hibbert (1976) concluded from energy measurement on a Mercenaria population at Hamble Spit, that more than half (59%) of the energy obtained from food consumption is lost in faeces and pseudofaeces, whereas metabolic requirement accounts for much (64%) of the assimilated energy. He found that 19% of the assimilated energy is directed to flesh growth in younger individuals and 16% to reproductive output. It therefore seems that Mercenaria during the first three years of its life, spends a greater proportion of available energy in shell growth than it does at an older age. Peak tissue growth occurs two years later than peak shell growth. A clear advantage of early investment in shell growth is to avoid mortality by a range of predators such as Carcinus and wading birds and gulls which are the main predators on young Mercenaria in Southampton Water (Hibbert, 1976). Moreover, early rapid shell development is particularly advantageous to withstand damage by wave action and sediment abrasion especially on sandy shores.

More information on the littoral population of Mercenaria is given by the study of production and biomass at Marchwood and Lee-on-Solent. Although, the present estimate of production is applicable only to those sites studied, and to the year of the study, it serves to demonstrate performance of the animal at both sites.

The results showed that annual production, annual mean biomass and subsequently the annual $P/\bar{B}$ ratio, were similar at both sites and approximated to 3 ($gm^{-2}yr^{-1}$), 30 (gm^{-2}) and 0.1, respectively. The estimate of production was largely influenced by the number of individuals in each year class, which is directly dependent on survival in the post settlement period. This probably explains the high production recorded for some year classes at both sites. In addition, production was also influenced by the age structure, because younger year classes tend to show higher relative growth and production per unit biomass than older individuals.

One advantage of calculating a common $P:\bar{B}$ ratio for Marchwood and Lee-on-Solent was that it was possible to use the calculated $P/\bar{B}$ ratio of 0.1 yr^{-1} at sites throughout the estuary to estimate production using biomass data.

To calculate mean biomass at each site, the ash free dry weights of all Mercenaria was added together and divided by the total number of the animals, giving the mean weight per individual. The product of mean weight per individual and mean number of individuals per square metre gives a figure for the mean biomass which when multiplied by the common $P : \bar{B}$ ratio, yields a predictive estimates of production. Such a procedures was used to calculate production at each site giving values shown in Table 3.19. The results demonstrate, spatial variation in production between sites with highest production at Netley and lowest at Royal Pier. Several factors are well documented as influencing the $P : \bar{B}$ ratio. Low temperature, slow growth rate, and high predation rates, all lower the $P:\bar{B}$ ratio (Gray, 1981). However, in the present study, estimates of production are determined largely by the numerical density of Mercenaria at each site. Differences in abundance probably explain the low correlation between production and growth rates.

The study of seasonal changes in condition index and biochemical composition provide important information on the reproductive cycle, and indicate the optimal time of the year for harvesting molluscs for commercial purposes (Mitchell, 1974). Mitchell suggested that a better yield in terms of flesh weight would be obtained by harvesting Mercenaria in the summer when condition index is at its maximum as a result of continuous feeding on abundant phytoplankton and detritus. Ansell and Lander (1967) measured seasonal changes in condition index of different size groups, and found that the magnitude of changes was greatest in smaller individuals.

In the present study, condition index was measured in winter months, during which, flesh weight should be at its lowest value, due to reduced food availability and feeding with utilisation of food reserves. However, significant variation of condition index was found between sites and between size groups but no distinct pattern of condition index could be discerned between size groups at a given site. Absence of a trend in condition index with increase in size can be attributed to lack of younger year classes in samples.

As the condition index expresses the ratio of flesh weight to shell weight, and shell weight was found to be positively correlated to shell length (see Section 3.7.5), then the condition index should be linked also, to the length-weight relationship. However, regression of condition index with the slope (b) of the length-weight relationship showed no significant correlation. This low correlation could be attributed to the narrow range of sizes, with dominance of large sized individuals.

In general feeding in sublittoral populations may occupy a greater proportion of time resulting in better growth and condition.

A comparison of mean values of body parameters at different sites (Table 3.17) showed that the littoral Mercenaria population at Solent Breezes, had the longest, heaviest widest shells and greater tissue weight in relation to age. In addition, the Gompertz, predicted that the highest shell growth rate would be found in Mercenaria at Solent Breezes. Within Southampton Water it appears that optimum growth conditions for Mercenaria occur at Solent Breezes. This site is characterised by sandy sediments and greater degree of water movement, than sites in the upper parts of Southampton Water.

In conclusion, the results showed that maximum growth rate in length and tissue weight occurred within the first 5 years, and since production is largely affected by growth rate, subsequently maximum production, $P/\bar{B}$ ratio and condition index should occur within the first 5 years, too. However, in estimating various population parameters, individuals less than 6 years of age were virtually absent in samples. Therefore, the expected period of maximum growth rate and production is not represented in the populations sampled. This probably explains the low value of $P/\bar{B}$ recorded in the younger age classes within the samples. An important implication of these results for the clam fisheries in Southampton Water is that fishing should not be permitted on Mercenaria less than 6 years of age, the age before which most growth occurs, and highest production and $P/\bar{B}$ is achieved. Furthermore, it follows that if no recruitment occurs in the near future, the few remaining young individuals will show declining growth rate, production and lower P/$\bar{B}$ ratio with time, ultimately leading to a collapse of the *Mercenaria* population and fishery.

CHAPTER FOUR : REPRODUCTIVE BIOLOGY

4.1 INTRODUCTION

Studies of reproduction are important in ecological investigation, and a thorough knowledge of reproductive cycles is necessary for predicting annual recruitment and interpreting growth and mortality. Considerable research has been carried out on the reproduction of Mercenaria (Loosanoff, 1937a, 1937b; Porter, 1964; Keck et al., 1975, Eversole et al. (1980). A common conclusion derived from those studies is that reproduction in Mercenaria is controlled by environmental factors namely temperature and availability of food, which affect the physiological state and alter the biochemical composition and condition of the animal.

Several methods of assessing the reproductive period of Mercenaria have been followed. Direct methods based on histological study of gonad development and sexual phases have been used by Loosanoff (1937a, 1937b), Keck et al. (1975) and Porter (1964) while Ansell (1964a) measured spawning indirectly by examining the reproductive capacity of experimentally-induced clams, and monitoring the seasonal cycle of biochemical composition and condition of the animal. Mitchell (1974) and Hibbert (1976) monitored the occurrence of clam larvae in the plankton of Southampton Water as a mean of determining the spawning time. The present work takes the study further by examining the different sexual phases of the reproductive cycle, that is the onset and duration of spawning in Mercenaria on a seasonal basis. Counts have been made of oocyte and spermatozoa of clams collected from different parts of Southampton Water, Marchwood and

Lee-on-Solent. These sites differ in their environmental parameters (substrate, salinity, food). In addition preliminary studies (Mitchell, 1974) indicated that Mercenaria living at those sites , showed different growth rates, and probably different reproductive capacity.

4.2 MATERIALS AND METHODS

4.2.1 Collection, Maintenance and Laboratory Treatments

Regular monthly samples of Mercenaria were taken from the shore at Marchwood and Lee-on-Solent from March 1985 to March 1986, in order to monitor the reproductive cycle of Mercenaria. At each site Mercenaria were randomly collected by raking the sediment from the middle to the lower parts of the littoral zones using a garden fork. At each site, the numerical density of the animal was noted, and measurement of air and sediment temperatures were made. In the laboratory the animals were kept in clean sea water for 1 to 2 days at ambient temperature (10 - 20°C). Ten individuals of similar sizes (50 - 70mm) were opened. In order to open the animal, a hacksaw was used to cut a slit through the anterior and posterior parts of the shell and a sharp scalpel was then inserted through the slit and both adductor muscles were cut, allowing the valves to be separated.

4.2.2 Gamete Counts

A standard procedures for obtaining gonad tissue from Mercenaria and counting gametes were adopted. Two portions of the gonadal tissue were dissected from the ventral side of the animal at the middle part of the line connecting the anterior and posterior adductor muscles. The tissue were gently blotted and its wet weight was recorded. Male gonadal tissue was then immediately homogenised with 10mls. of filtered sea water, and few drops of Lugols solution were added to the sperm suspension, and the homogenate was mixed thoroughly. Subsamples of the sperm suspension were then placed in a haemocytometer (Neubauer pattern), and two counts per subsamples were made of the motile spermatozoa. For each male individual, a total of four counts were made. The averages of these counts were used to estimate the number of gametes in diluted suspension. Division of gamete numbers in the sperm suspension by the wet weight of the testicular tissue used, gives an estimate of the number of spermatozoa per gram (wet weight) of the gonad.

Tissue obtained from female individuals, were kept in Gilson fluid which helped to dissociate eggs from the connective tissue. After 2 to 3 days the Gilson fluid was drained, and the tissues were carefully blotted and weighed. Eggs were separated from mantle tissue by teasing the tissue apart using a scalpel followed by careful homogenisation with 10mls. of sea water. One millilitre of ovary homogenate was placed on a Sedgwick Rafter tray and four counts were made. An average of these counts were used to estimate the number of oocytes per gram of ovarian tissue. On each occasion observation of the extent of gonad development was also made.

4.2.3 Measurement of Oocyte Sizes

Attempts were made to assess gonadal developmental stages by following seasonal changes in oocyte sizes. Initially oocyte samples were taken from ventral, dorsal, anterior and posterior parts of the animal, in order to assess the degree of variation in oocyte size throughout the gonad. Thereafter measurement of oocyte sizes were made on tissue dissected from the same area of the gonad used for gamete counting. Thirty randomly selected oocytes were measured from each tissue sample. On each oocyte two axes, perpendicular to each other and passing through the centre of the egg, were measured. A calibrated eye piece micrometer was used for measurement. The mean of the maximum and minimum lengths was used as a measure of oocyte size.

4.2.4 Histology of the Gonad

An attempt was made to describe different stages of the reproductive cycle in *Mercenaria* based on histological thin sections of ovarian tissue. A standard method of preservation, cutting and staining of the tissue was used, similar to the technique used by Lowe *et al*. (1982). The ovarian tissue was dissected from the same location as was tissue for gamete counts. The tissue was fixed in calcium Baker's formal solution and kept at 4°C for 24 hours after which tissue was subsequently dehydrated by immersion in an ascending series of alcohol concentrations (30%, 50%, 70%, 90%) for 1 to 2 hours. Tissue was then placed in 2 changes of absolute alcohol for a further 2 hours. The jars were covered and shaken frequently to speed up dehydration. Tissue was cleared in changes of xylene for 30 to 60 minutes. The process of wax impregnation for the tissue was achieved by immersion in a paraffin wax dissolved in xylene and left overnight, followed by immersion in a wax bath at 70°C. The tissue was finally embedded in fresh molten wax. The block was rapidly cooled, after which it was trimmed and mounted on a Cambridge rocking microtome and serial sections were cut at 10µm and stained by the Papanicolaou technique (Culling, 1963). This procedure, stains various cellular components of the gonad differentially. Male reproductive tissue stains blue and female reproductive tissue blue to mauve. Sections were then dehydrated in absolute alcohol, cleared in xylene and mounted on slides using D.P.X. as mountant.

4.2.5 Induced Spawning

Artificially induced spawning is well documented (Loosanoff and Davis, 1963; Davis and Chanley, 1956; Carriker, 1961; Bricelj, 1979). In the present study a preliminary induced spawning was carried out during October, 1983 on a small scale in the laboratory and under semi-controlled conditions. The experiment aimed to collect data on approximate daily growth and shape / dimensions of different larval stages. Such information was later used for identification of *Mercenaria* larvae collected during field sampling. Apparatus and containers used for the experiment are shown in Fig. 4.1 a. *Mercenaria* were collected from Weston shore and kept in filtered sea water at ambient temperature overnight for acclimation to laboratory conditions. Individuals of similar sizes were selected and divided into 5 groups of 6 individuals and they were kept in separate conditioning tanks which were maintained at 21°C with continuous drip feeding using *Isochrysis galbana* culture. Conditioning of the animal was critical at this stage because the natural season of spawning in Southampton Water was over. On each day 6 clams were removed from the conditioning tanks and placed in fresh filtered sea water at 21°C. Animals were stimulated to spawn by adding heated seawater frequently in order to raise water temperature to 30°C over 1 hour. This was followed by sudden reduction in ambient temperature by changing the water. This procedure was repeated at least 3 times during which water temperature fluctuated from 21 to 31°C. Males were first to respond followed by females, when freshly spawned sperms were pipetted into the containers. The spawning females, were transferred to separate tanks containing fresh filtered sea water, and they were left for 30 minutes until all eggs were shed, and subsamples were taken.

All the eggs were retained on a fine mesh sieve (62µm) and resuspended into 5 litres of filtered sea water maintained at 21°C with continuous aeration. A few drops of sperm suspension were added for fertilisation. Fertilisation was achieved after about 30 minutes. After 24 hours, the water was completely changed, and the developing larvae were caught on nylon mesh (63µm) and resuspended in the rearing tank (Fig. 4.1 b) containing fresh filtered sea water maintained at 21°C and provided with continuous aeration and food (*Isochrysis galbana*).

Growth of the developing larvae was assessed by frequent subsamples during water changes over 14 days. On each occasion, length (anterior-posterior axis), and width (dorsoventral axis) of all the larvae in the subsamples, were measured in the same way as used for measurement of oocyte size (see section 4.2.2).

4.3 RESULTS

4.3.1 Gametes Counts

Results of the oocyte and spermatozoa counts of *Mercenaria* populations at Marchwood and Lee-on-Solent are shown in Fig. 4.2 and 4.3. The graphs clearly demonstrate that there is seasonal changes in counts of both types of gametes.

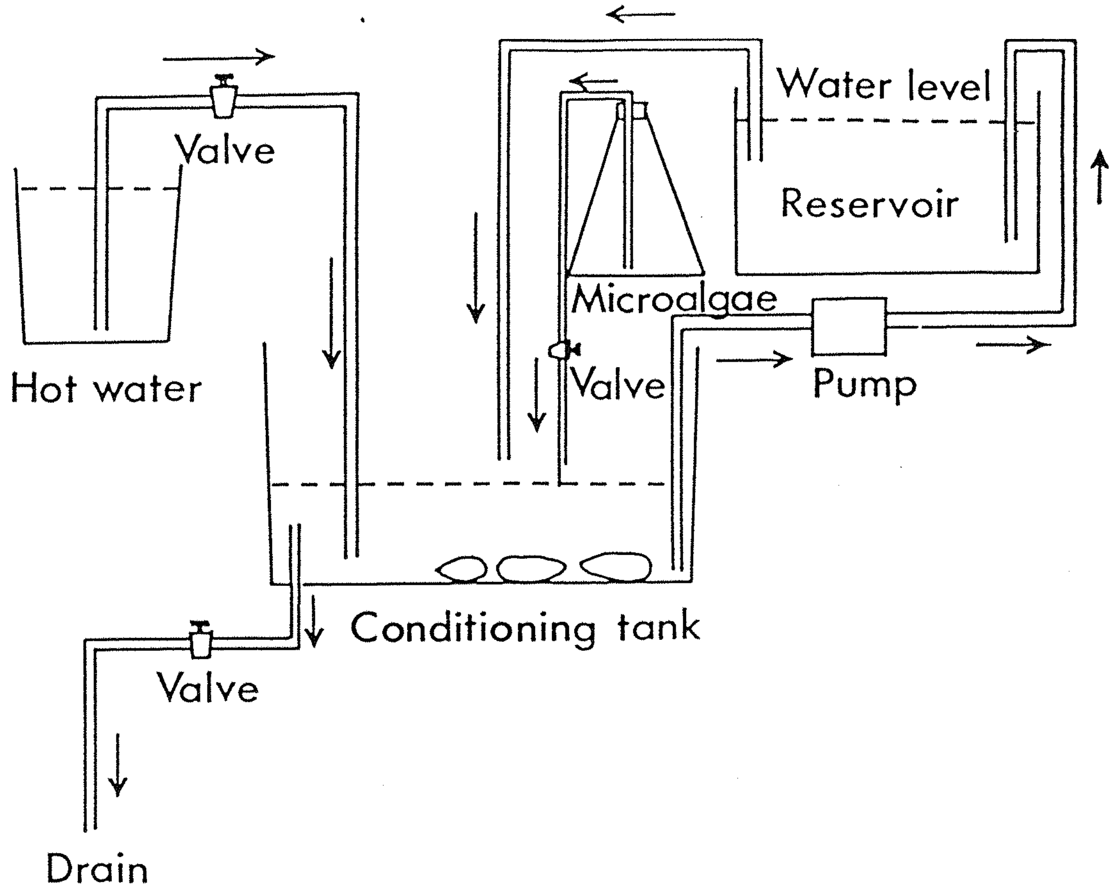


Fig. 4.1a Apparatus for induced spawning of <u>Mercenaria</u>

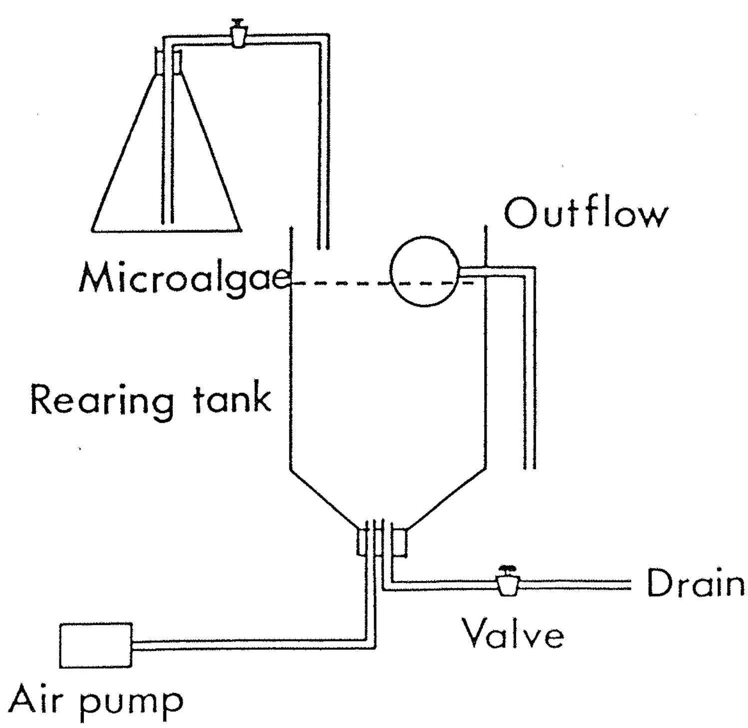
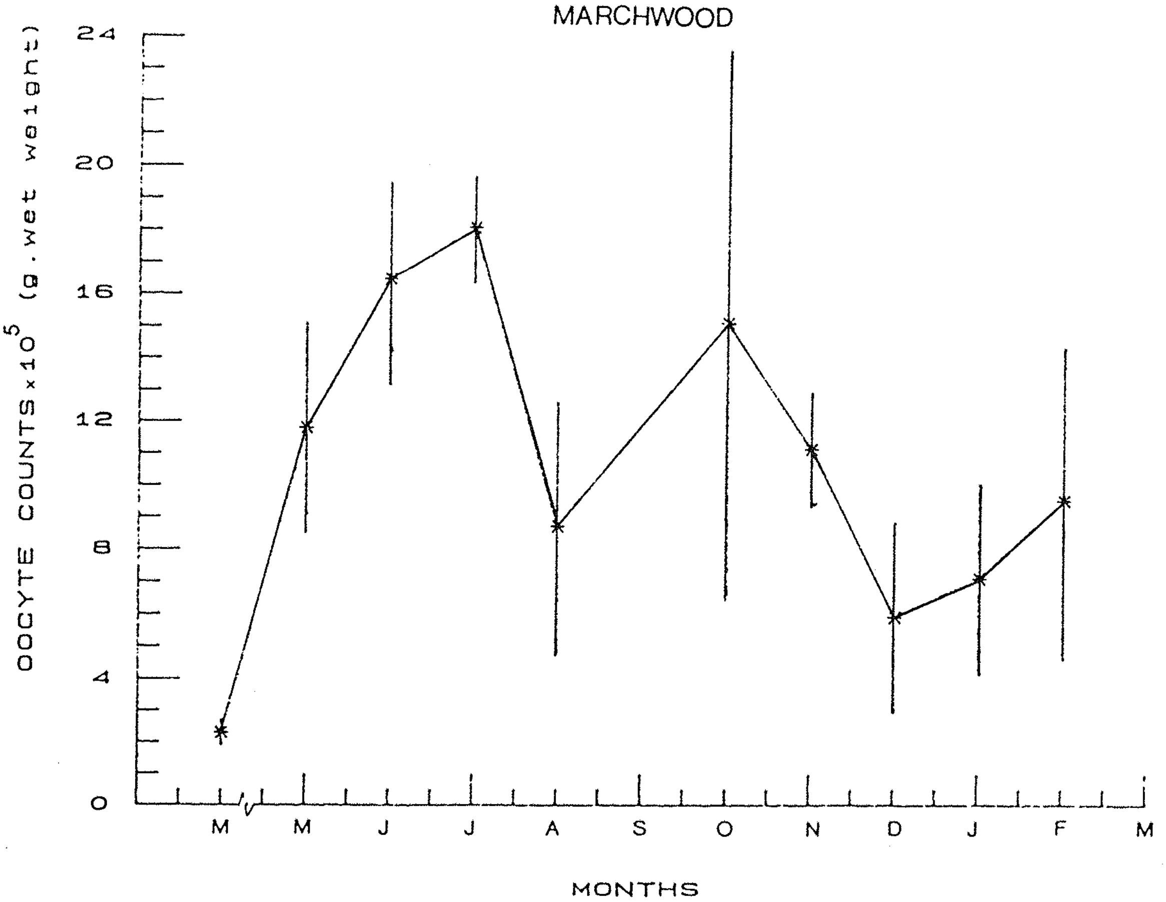


Fig. 4.1b Rearing apparatus for <u>Mercenaria</u> larvae

Oocyte numbers at Marchwood and Lee-on-Solent showed a gradual increase during March and April, followed by a rapid increase in May - June to reach a peak in June and July respectively. A dramatic decline in oocyte counts occurred during August and early September, followed by a second increase in October after which, the counts diminished in Winter months. Graphs of the spermatozoa counts (Fig. 4.3) convey broadly similar pattern to that shown for oocyte counts, with low counts during Spring months, increasing rapidly in June to peak in August followed by gradual diminution in Autumn and Winter months. The results showed that spermatozoa counts were predominantly higher than oocyte counts. Further analysis of female and male gamete counts involved the use of analysis of variance. The results (Table 4.1 and 4.2) revealed that oocyte counts showed significant differences between months and between sites at $P \leq 0.05$. Similarly, spermatozoa counts yielded a significant variation between months, but exhibited no statistical differences between Marchwood and Lee-on-Solent at $P \leq 0.05$.

Records of the monthly sediment temperature measured at both sites for the period 1985 - 1986 are plotted in Fig. 4.4. Temperatures showed wide seasonal fluctuations ranging from -2 to 20°C, and at both sites sediment temperature demonstrated generally similar trend with maximum in July/August and minimum in the Winter months. At Marchwood, spawning of the clam population, as indicated by a drop in gamete concentration in the gonad, appeared to start at the beginning of August when sediment temperature rose to 16°C and continued into September and October until the temperature fell below 16°C. Similarly a dramatic drop in oocyte counts occurred in early August.



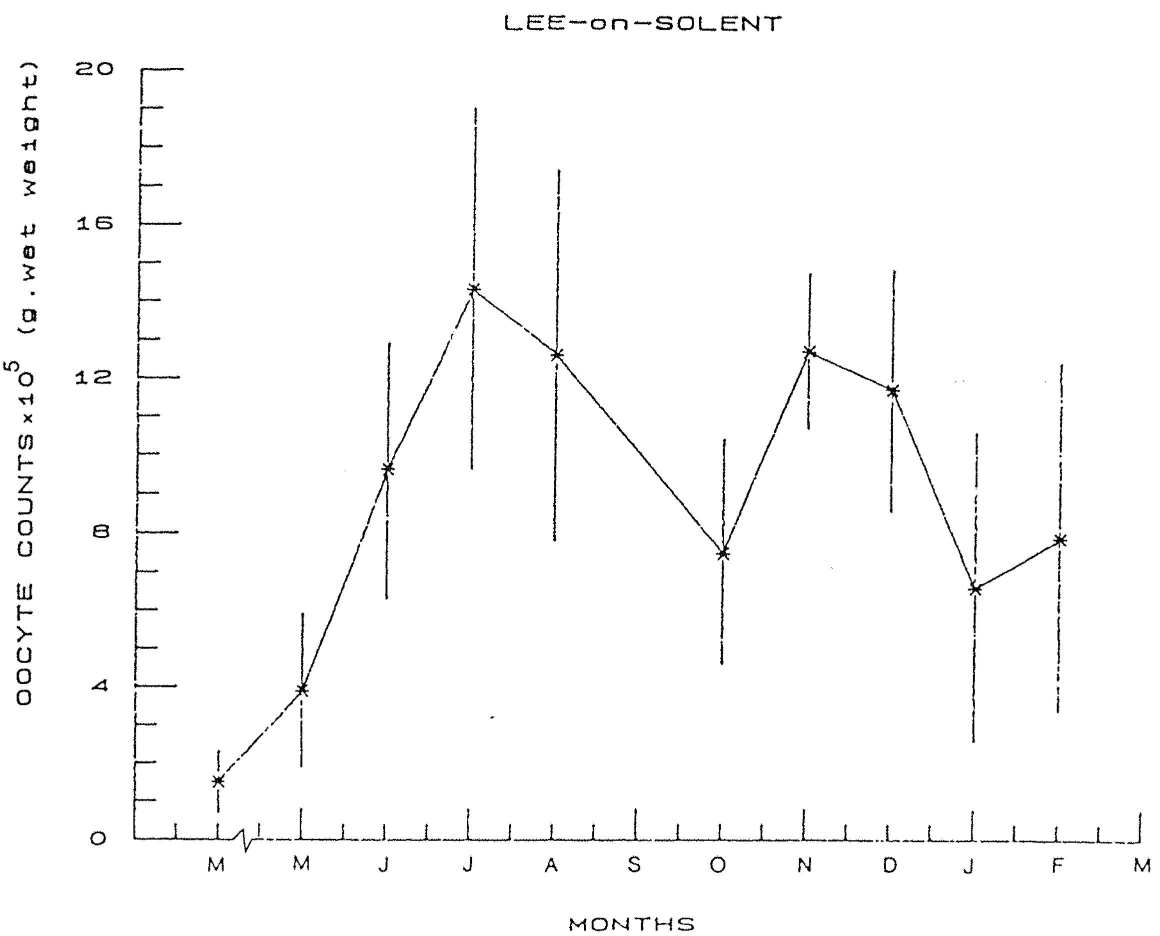
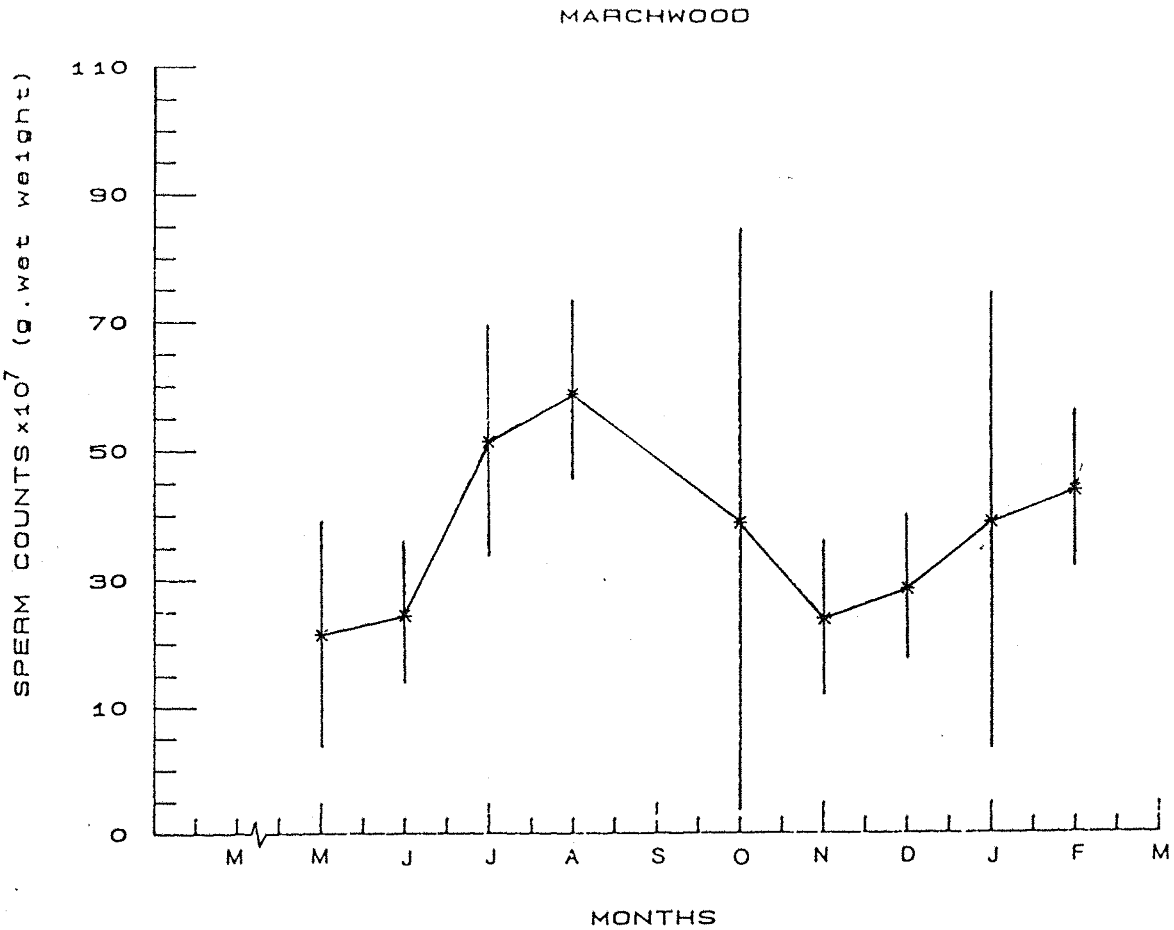


Fig. 4.2 Mean oocyte counts (No. per gram gonad wet weight) in monthly samples of Mercenaria at Marchwood and Lee-on-Solent from March 1985 to March 1986, Mean ± S.E.



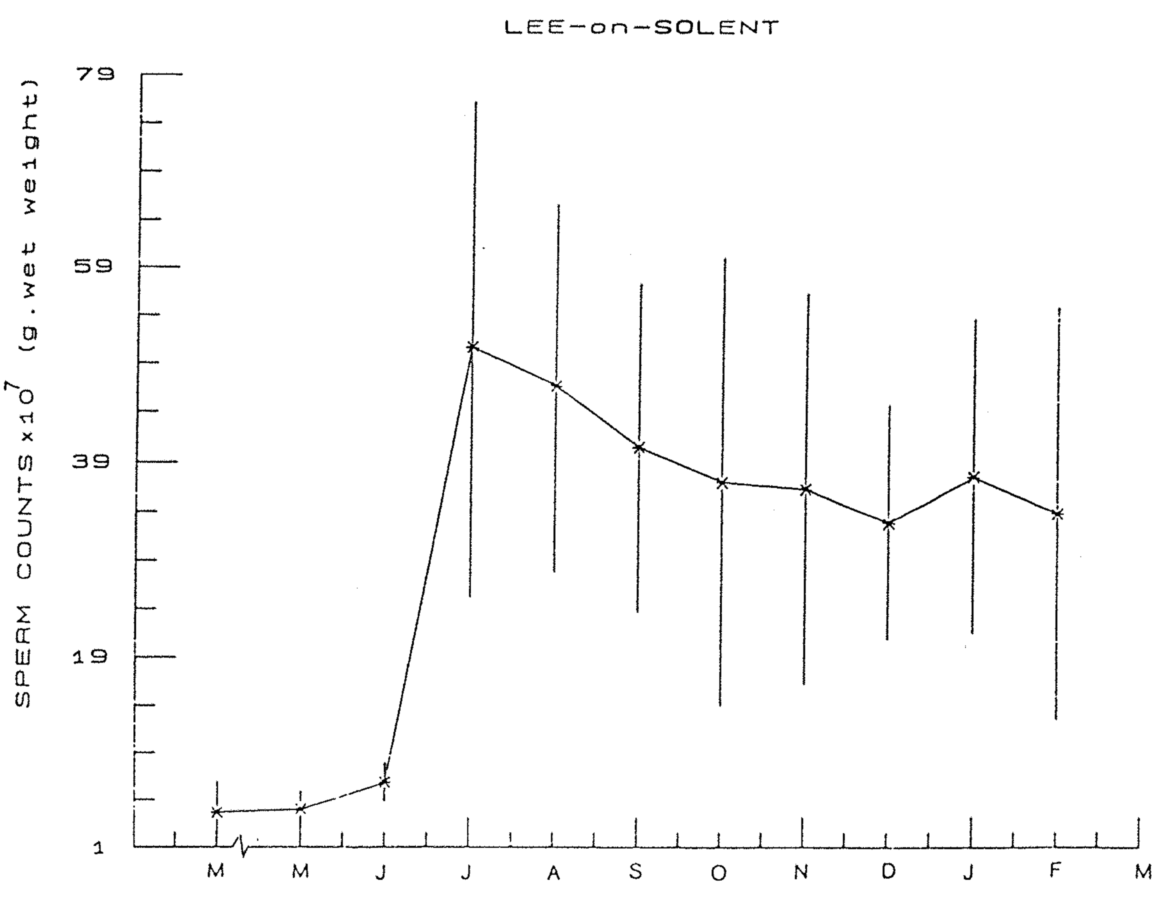


Fig. 4.3 Mean spermatozoa counts (No. per gram gonad wet weight) in monthly samples of <u>Mercenaria</u> at Marchwood and Lee-on-Solent from March 1985 to March 1986, Mean ± S.E.

Table 4.1 : Analysis of variance test on oocyte counts at Marchwood and Lee-on-Solent during March 1985 - March 1986

a. Test of variation of oocyte counts between both sites

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio	Significance level
Among locations	409.434	1	409.43402	3.814	0.0533
Error	12023.418	112	107.35195		

b. Test of monthly variation of oocyte counts

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio	Significance level
Between months	2209.48	10	220.94815	2.226	0.0217
Error	10223.371	103	99.25603		

Table 4.2 : Analysis of variance on spermatozoa counts at Marchwood and Lee-on-Solent during March 1985 - March 1986

a. Test of variation of spermatozoa counts between both sites

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio	Significance level
Among locations	1504.856	1	1504.8560	2.700	0.1033
Error	59073.541	106	557.2976		

b. Test of monthly variation of spermatozoa counts

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio	Significance level
Between months	16084.043	10	1608.4043	3.506	0.0006
Error	44494.354	97	458.7047		

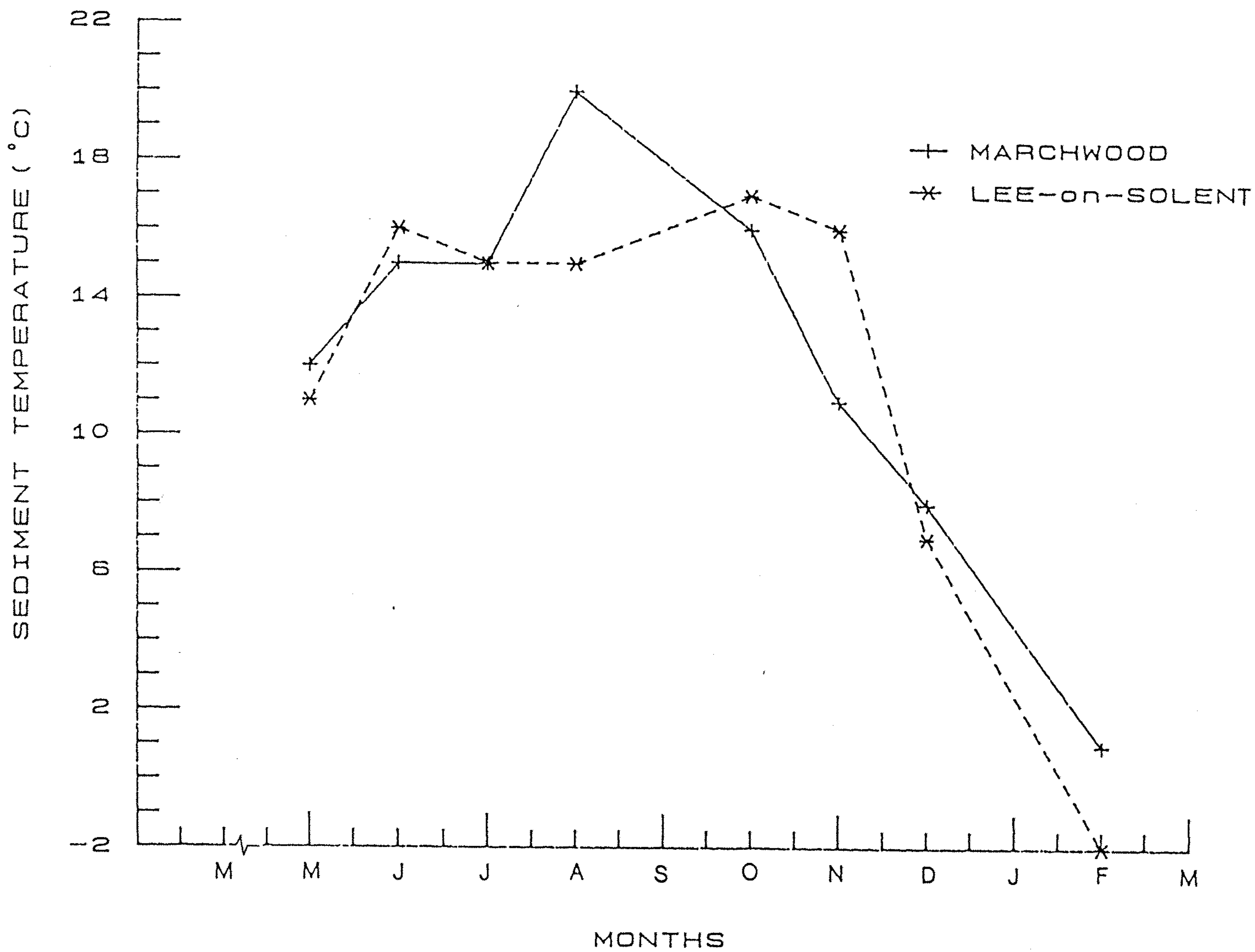


Fig. 4.4 Monthly records of sediment temperature at Marchwood and Lee-on-Solent from March 1985 to March 1986

4.3.2 Oocyte Size Distribution

Ripe spawned oocytes measure about 70 - 73 µm in diameter (Loosanoff and Davis, 1950). But when first released, the oocytes are usually surrounded by a gelatinous membranes which has a thickness of about 25µm, which soon swells and attains a thickness of 95µm, so that the overall diameter of the ovum is approximately 270µm (Carriker, 1961).

Representative results of oocyte measurements are shown in Table 4.3. The results indicated that there was a tendency for little variation in the oocyte sizes measured at different parts of an animal at Lee-on-Solent during June 1984. Although there was variation in the mean oocyte sizes between individuals of one site at any one time, the overall mean showed a seasonal pattern, with large oocytes occurring during March - May and a shift to smaller egg sizes at August and November 1985 which was followed by an increase during January 1986. Moreover, there seem to be relatively little variation in the mean sizes of oocyte found throughout the estuary in summer 1984.

Table 4.3a : Records of the mean oocyte sizes (μm) changes at different parts of the gonad and throughout the year at Lee-on-Solent

Dates	Mean Oocyte sizes (μm)	Standard Deviation	Number of Oocyte measured	Number of animals
13.06.84	59.43	±10.59	20	Tissue A
13.06.84	57.63	±6.47	20	Tissue B
13.06.84	62.99	±4.72	20	Tissue C
13.06.84	62.17	±6.33	20	Tissue D
7.03.85	58.95	±8.45	171	6
5.05.85	56.41	±9.25	90	3
2.08.85	21.11	±2.88	3	126
13.11.85	14.38	±3.87	1	30
27.01.86	17.13	±2.60	1	32

N.B. Tissues A, B, C, and D were taken from one animal but at different parts of the gonad.

Table 4.3 b: Records of the mean oocyte sizes (μm) measured in different clams throughout Southampton Water

Sites	Dates	Mean Oocyte sizes (μm)	Standard Deviation	Number of Oocyte measured	Number of animals
Marchwood	8.6.84	54.9	±9.5	30	1
Weston	18.5.84	58.7	±7.3	30	1
Netley	11.6.84	59.4	±3.6	200	7
Lee-on-Solent	13.6.84	60.0	±2.5	60	1

4.3.3 Histology of the Gonad

Although the Papanicolaou technique (Culling, 1963) has the advantage of differential staining of various cellular components of the gonad, nevertheless no satisfactory histological preparation could be obtained, because the gross anatomy of *Mercenaria* revealed that the gonad was inseparable from the visceral mass and the muscular tissue.

Although the histological preparation of the gonad has been repeatedly used to get detailed cytological information of the gonadal cycle, it requires examination of several hundred sections of *Mercenaria* gonad representing all season of the year. In addition the sectioning and the dehydration which are essential stages in the histological study, are more likely to distort the shape and sizes of the oocytes, giving therefore unsatisfactory results.

4.3.4 Induced Spawning

Results of induced spawning and artificial fertilisation produced normal developmental stages, (early and late straight hinge larvae, followed by the pediveliger stage as described by Carriker (1961). The size range increased with age of the culture as can be seen by comparing the length frequency distribution (Fig. 4.5) of the larvae sampled on each occasion. The mode of the length frequency increased from 59.4 to 156 µm from the first to the 14th day. Observation showed that number of larvae was extremely high at the begining of the experiment but there was high mortality (about 80%) during the 14 days. However, growth of larvae, was regularly monitored by following changes in the mean length of larvae over 14 days, which

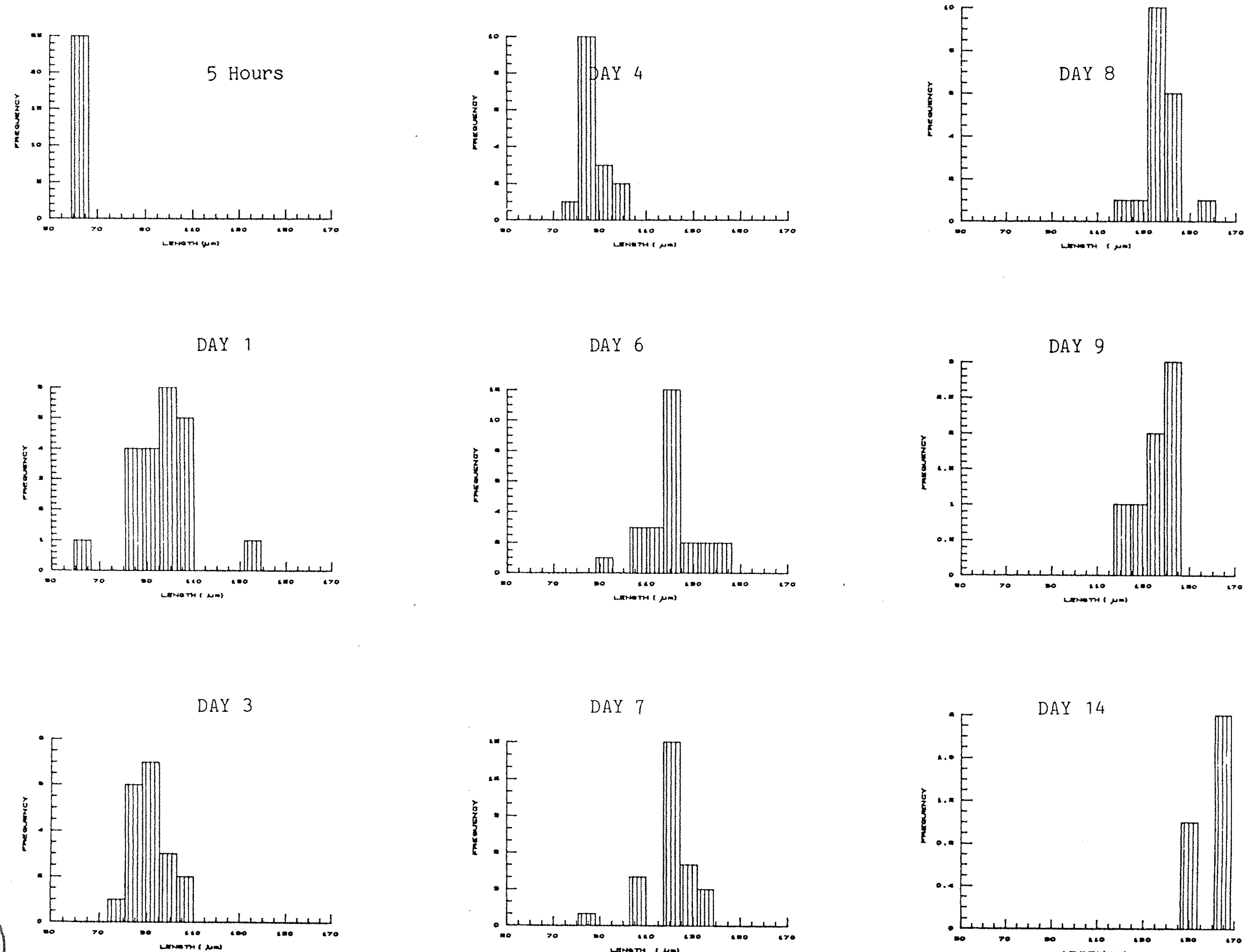


Fig. 4.5 Length frequency distribution of laboratory-spawned Mercenaria larvae over 14 days

is illustrated in Fig. 4.6. Although larvae were grown under identical conditions, there were large individual variation in sizes. However, one way analysis of variance (Table 4.4), revealed that length of larvae exhibit significant variation between days at $P \leq 0.05$ indicating daily growth of larvae.

During the experiment, measurement were also made on height of larvae at different developmental stages (early, late straight hinge and umboned larvae) in order to establish the length-height relationship for Mercenaria larvae. The least square regression analysis, showed that there is a strong and signification positive linear correlation ($r = 0.941$ at $P \leq 0.05$) between length and height of Mercenaria larvae as mentioned in Table 4.5 and Fig. 4.7.

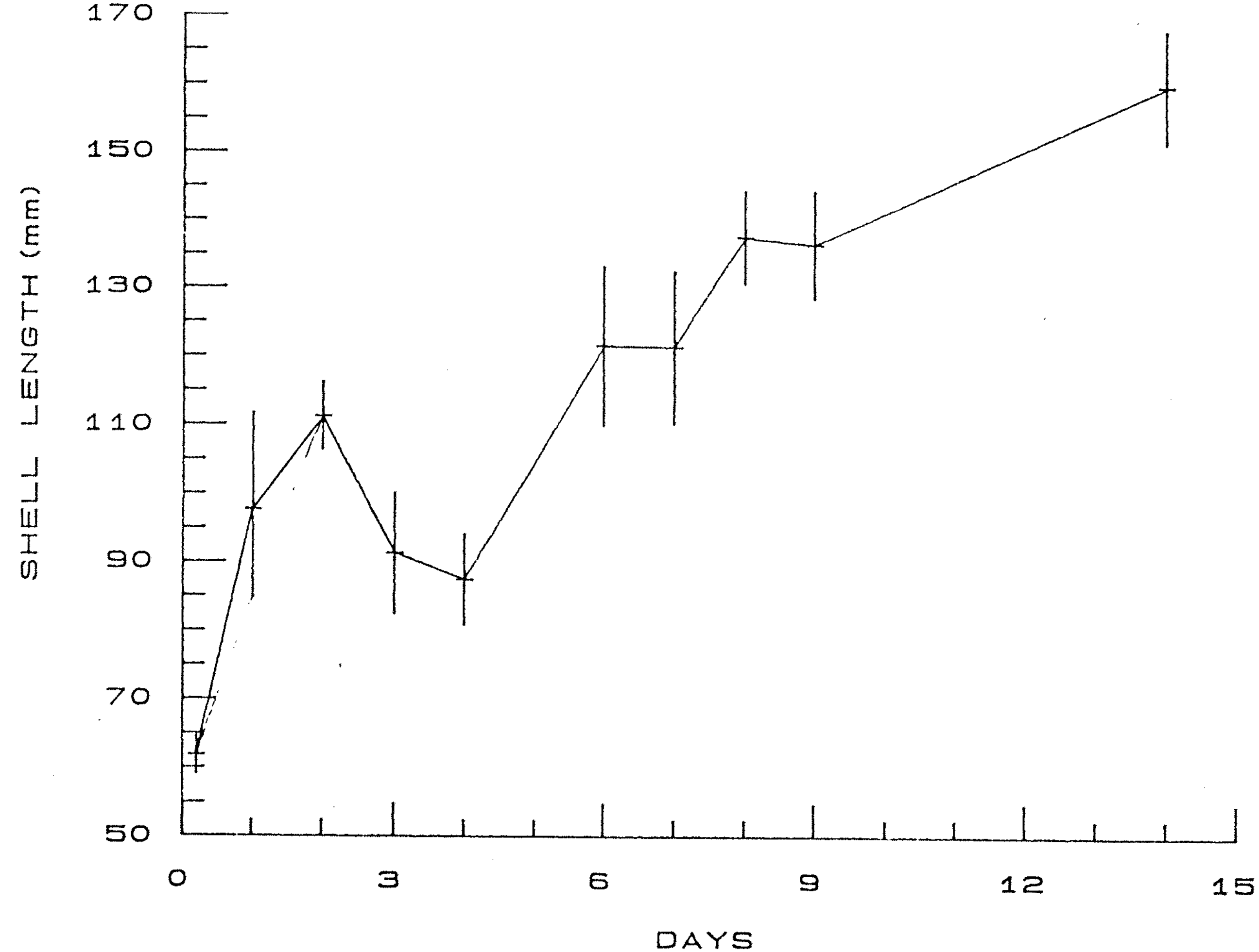


Fig. 4.6 Daily growth of of laboratory-spawned _Mercenaria_ larvae over 14 days, Mean ± S.E.

Table 4.4 : Analysis of variance test for length of laboratory - spawned *Mercenaria* larvae over 14 days

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio	Significance level
Between days	106823.91	9	11869.323	132.962	0.000
Error	14104.41	158	89.268		

Table 4.5 : Linear regression of shell length and shell height (µm) in laboratory-spawned *Mercenaria* larvae

Parameter	Estimate	Standard Error	Correlation Coefficient (r)
Intercept (a)	12.586	39.52	0.941*
Slope (b)	0.084	0.003	

* Significant at $P \leq 0.05$

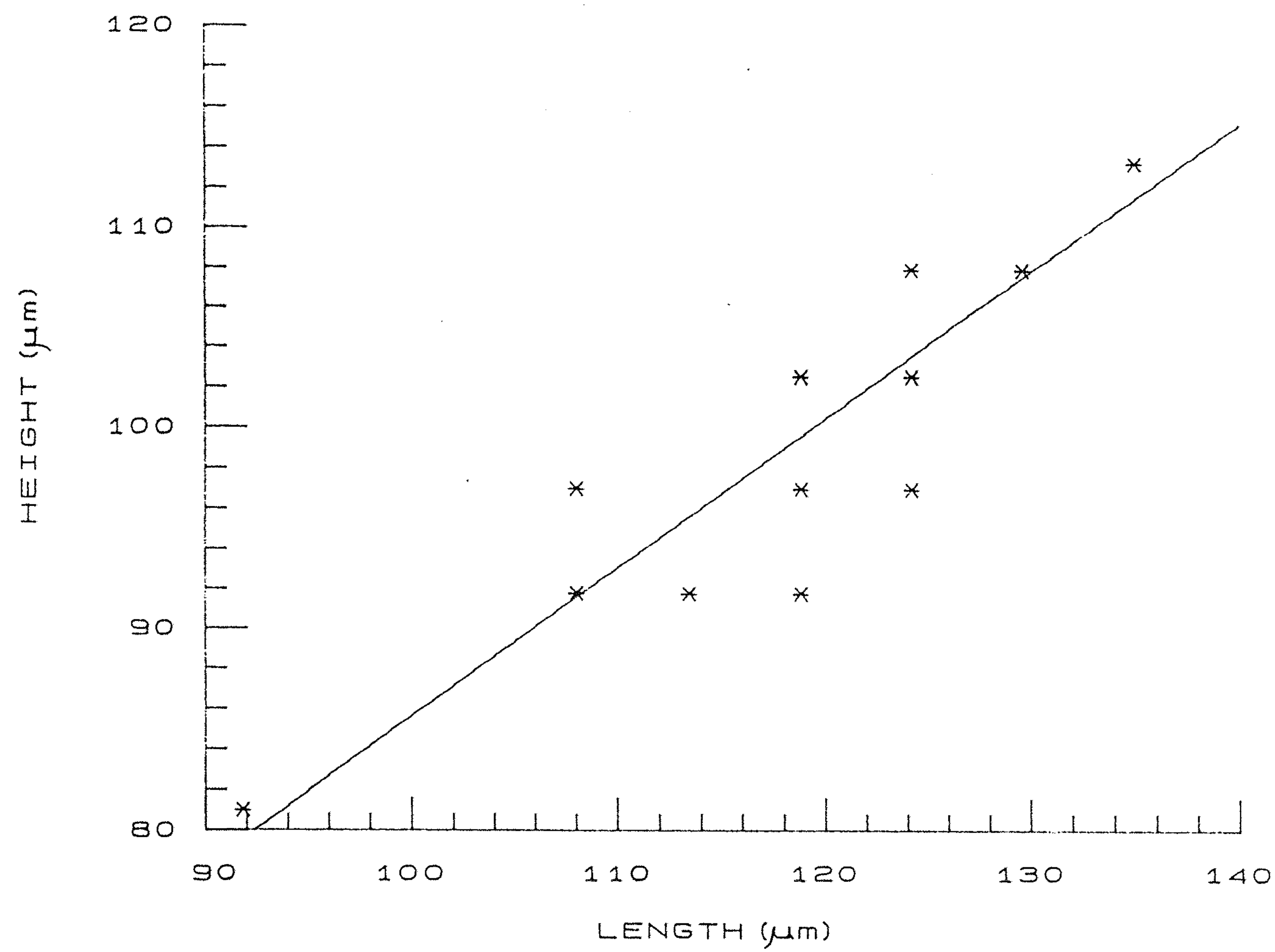


Fig. 4.7 Linear regression of length-height relationship of laboratory-spawned _Mercenaria_ larvae

4.4 DISCUSSION

Study of the reproductive biology of Mercenaria seems to have attracted a great number of works. In the States, Loosanoff (1937a, 1937b) gave the first descriptive account of gonad development in Mercenaria based on histological examinations of the gonad. He noted that spawning occurred in late July in Long Island waters. In North Carolina (Porter, 1964) and Delaware Bay (Keck et al., 1975) clams spawn from June to October. Similarly spawning of clams from a South Carolina estuary was found to start in May / June and continue through October (Eversole et al., 1980). He concluded that Mercenaria had two breeding peaks in South Carolina, confirming the results found by Porter (1964) for clams in North Carolina. In England, few studies designed to investigate spawning in Mercenaria have been carried out. Ansell (1964a) measured spawning indirectly by examining the reproductive capacity of experimentally induced Mercenaria, and monitoring the seasonal cycle of biochemical composition and condition index of the animals. He concluded that spawning occurred twice, once in spring and again in late summer. Mitchell (1974) monitored the occurrence of clam larvae in the plankton and concluded that Mercenaria spawns frequently during the summer months (May to September). Similar conclusions with regard to spawning have been given by Hibbert (1976) who studied the Mercenaria population at Hamble Spit.

In the present study, the seasonal changes in oocyte sizes, the histological thin sections of the gonad, and the gamete counts, were all used to follow the reproductive cycle in Mercenaria. The results showed that there was only a small variation in the mean oocyte sizes throughout different parts of the animal, indicating similar degree of gonad maturity. Although changes in the mean oocyte sizes, were followed for only a few months, a seasonal pattern emerged. The large size of eggs characteristics to March - May 1985 indicate gonad maturation, whereas the shift in sizes during August - November 1985 reflects spawning after which gonad development occurred in Winter.

Bricelj and Malouf (1980) found that spawned eggs had a bimodal size distribution, and the mean egg size decreased as the spawning season progressed. Other bivalves such as Mya arenaria have been reported as showing a significant seasonal differences in the size of ripe eggs (Brousseau, 1978) as a result of a biannual spawning cycle (Spring and Summer). The method of gamete counting developed in the present work, to determine different phases of the reproductive cycle, has several advantages in comparison to the examination of thin sections of the gonad. It is rapid and avoids the inherent error that arise due to tissue dehydration and sectioning artefacts. In addition it provides a quantitative mean for describing the gonadal development. The method showed that gonads contained gametes throughout the year although there were seasonal changes in gamete numbers. Both, spermatozoa and oocytes exhibit a similar trend. A gradual increase in the oocyte counts during spring indicates gonad development. The ripe and mature gonad is represented by a peak in number of oocytes between June and July. A dramatic decrease in oocyte numbers occurs during August, representing a spawning period, followed by a period of gonad regeneration. In October the female gonad has regenerated as evidenced by the increase in number of oocytes, which thereafter exhibit progressive reduction, as a result of a second spawning. The graph of seasonal changes in spermatozoa counts reveals a broadly similar pattern to that shown by the oocyte counts with the exception of the marked reduction in spermatozoa counts during August, September and October reflecting continuous spawning. Male gonad regeneration occurs during winter months. In general, the results therefore show that, the Mercenaria population in Southampton Water during 1985 had two spawning periods, in mid Summer and Autumn. Such trends probably indicate that Mercenaria does not discharge all its eggs and sperms at one spawning, but spawns frequently over extended periods. Similar result was reported by Loosanoff (1937a) who stimulated conditioned clams in the laboratory to produce gametes for 5 to 6 weeks before the majority of the clams become spent. Loosanoff (1937b) concluded that the sexual cycle of Mercenaria is not in phase with other bivalve molluscs and he reported that the major period of redevelopment was in Autumn as water temperature decreased. Unpublished study by Keck et al. suggests that the glycogen cycle in the clams is greatly different from that of the oyster. A spent oyster is devoid of gametes and generally in poor condition. Whereas Mercenaria retains a comparatively high proportion of glycogen and high condition index even after spawning. The maintenance of high condition index allows immediate gonadal redevelopment and spawning in Autumn.

Results of the seasonal changes in water, ash , dry weight, calorific content, condition index and major biochemical compounds, which were repeatedly used to trace the reproductive cycle (Ansell, 1964a; Mitchell, 1974; Hibbert, 1976) seem to coincide with different stages of the gametogenic cycle, found in the present study.

The gonadal development that took place in Spring (March /

May) can be related to the increase in condition index, high water content and increase in major biochemical compounds (Ansell, 1964a; Mitchell, 1974) as result of the spring increase in phytoplankton. Ripe and mature gonads in June / July were associated with maximum values of ash free dry weight and the peak in lipid and minimum water level found by Mitchell (1974). The dramatic fall in gametes in August defined the onset of spawning. At this stage, lipid fell to half its level in June and there was a marked fall in ash free dry weight, as gametes were released (Mitchell, 1974). Ansell (1961) showed that 50% of total organic production of the animal may be released as spawn, accounting for a drop in condition after spawning. The subsequent increase in gamete numbers during September reflects gonad regeneration, which probably accounts for the second peak in the condition index, and increase in calorific level reported by Ansell (1964a) and Hibbert (1976) respectively.

Spawning in Mercenaria resembles the biannual spawning pattern reported for Mya arenaria where the first spawning occurred in response to the spring phytoplankton bloom, whereas the second spawning results from an increase in temperature (Brousseau, 1978).

Temperature is an important factor affecting the regulation of the gonadal cycle in bivalves. Critical spawning temperature for Mercenaria vary in different geographical areas. Loosanoff (1937c) and Loosanoff and Davies (1950) suggested that spawning in the field probably occurs at a temperature not more than 24°C. Porter (1964) in North Carolina and Eversole et al. (1980) in South Carolina found that spawning occurred when temperature rose above 20 - 23°C. Carriker in New Jersey waters, (USA) concluded that maximum spawning occurred within a range of 24°C to 26°C. Keck et al. (1975) reported that Mercenaria population in Delware Bay (USA) spawn at temperature of 25 to 27°C. However, Ansell (1963a) observed that Mercenaria taken from Southampton Water during May, spawned at 18°C in the laboratory. Mitchell (1974) concluded that critical spawning temperature was 18 to 19°C. However, examination of monthly records of sediment temperature, in addition to water temperature during monitoring of larvae in the field (see Chapter 5) suggest that Mercenaria spawn at 16°C which is lower than the temperatures previously reported. This perhaps indicates an adaptation to local conditions over the period since its introduction, permitting spawning at a lower temperature.

In conclusion, the analysis showed that there is statistically significant monthly variations in spermatozoa counts between Marchwood and Lee-on-Solent ($p \leq 0.05$). However, the monthly variation in oocyte counts did not show statistically significant differences between both sites. Nevertheless the graph showed a tendency for higher oocyte counts at Marchwood than at Lee-on-Solent. This result can be explained according to Mitchell's (1974) hypothesis that clams at Marchwood direct a greater proportion of energy to gonadal growth and less energy towards somatic growth, in comparison to clams at Lee-on-Solent, where the reverse situation occurs. Furthermore, the onset of spawning at Lee-on-Solent occurred one month earlier than spawning at Marchwood. The Marchwood clam population consist predominantly of old individuals (see Chapter 1). Hibbert (1976) suggests that older individuals may spawn later in the season.

CHAPTER FIVE : LARVAL ECOLOGY

5.1 INTRODUCTION

During development clam larvae pass through distinct stages. According to Carriker (1961) fertilisation of gametes is external and produces a non-shelled trochophore, followed by a straight hinge veliger, which develops into an umboned veliger (pedivelliger). Final metamorphosis leads to formation of the plantigrade stage, at which the larva affixes itself to the substratum by means of a byssus thread, and assumes a benthic mode of life. *Mercenaria* is an estuarine animal and produces planktotrophic larvae in large numbers in order to counterbalance the many sources of mortality during the larval stage. For example, in estuaries the net flow of water is seaward and estuarine plankton are continuously at risk of being lost in the seaward flow. The risk is especially severe among larvae of benthic invertebrates. Survival of the larvae depends upon being retained in the estuary long enough to permit settlement on suitable substrates in the vicinity of the parent organism.

There have been several studies dealing with mechanisms of retention of different larval groups of estuarine invertebrates (Carriker, 1951; Wood and Hargis 1971 on oysters; Bousfield, 1955, and de Wolf, 1974 on barnacle and Cronin, 1979, on decapod crustacean). All such studies relate retention in two layer estuaries to the ability of the larvae to regulate their position in the water column, in order to exploit the net landward flow in the bottom layer. In the present work, different aspects of larval ecology were monitored to provide confirmation of the time of onset and duration of spawning and to determine horizontal and vertical distribution, as well as growth and survival of the larvae in the field. In addition the role of environmental factors, namely water circulation in dispersal and retention of larvae will be discussed.

5.2 MATERIAL AND METHODS

5.2.1 Sampling and Preservation of Plankton Samples

Planktonic larvae were retrieved from samples collected at different sites in Southampton Water using a hose and pump method modified from the Wickstead (1961) technique. The pump was an automatic multifixture (model ITT JABASCO) water pump driven by a 12 volt battery. A length of PVC tubing marked in 1m. intervals was connected to the inlet of the pump. The inlet hose, weighted with a 4kg. weight, was lowered to the required depth. The outlet hose from the pump was held in a perspex cylinder (50cm in diameter) at the end of which a nylon mesh (62μm) was attached with a clamp. The cylinder was lowered inside a 50 litres dustbin, which was filled twice at each depth. On each occasion 3 to 4 depths were sampled during standing high water. The nylon meshes with their contents, were stored in separate jars containing 4% formalin in seawater, in order to avoid contamination and expedite sampling at each site.

5.2.2 General Surveys of Planktonic Larvae

General surveys of planktonic larvae were carried out on 3 occasions, using the method described above. In July 1983, larvae were sampled at 1 metre below the surface during standing high water at various sites along Southampton Water, from Marchwood to Lee-on-Solent

(Figs. 5.1a and Fig. 5.2a). Water temperature and salinity were measured at each site. The general survey of larvae was repeated in June and August 1984. In addition, measurement of water temperature, salinity and chlorophyll "a", were made.

5.2.3 Weekly Surveys of Larvae

The planktonic larvae were sampled at weekly intervals from May until the beginning of October 1983. Samples representing the whole water column (1, 2, 3 and 4 metres) were collected during the high water stand nearest to midday from 5 separate sites, Itchen Bridge, Royal Pier, Marchwood, Hythe Pier and Netley (see Table 5.2 and Fig. 5.1). Samples were collected using the method outlined above and each site was sampled 15 times from May to October 1983. On each sampling occasion, the salinity and water temperature were measured of water pumped from each depth, and any observation on water and weather conditions were noted.

5.2.4 Daily Changes in Larval Vertical Distribution

Plankton samples were taken at daily intervals from 17 to 24 July, 1984, at Town Quay during approximately the same daily tidal phase. Sampling was carried out at Town Quay which is a semi-enclosed area, providing easy access to the water. Larvae were sampled using a hose and pump method as described earlier. Several depths were sampled every day at 0, 1, 2, 3m below the surface and 1 metre above bottom. In addition daily measurement of water temperature, salinity and chlorophyll "a", at each depth were made.

5.2.5 Hourly Changes in Larval Vertical Distribution

Ability of *Mercenaria* larvae to regulate their position in relation to the tidal cycle was investigated during the spring tide of 4 July, 1985 at Ealing Buoy which lies at the edge of the dredge channel in the Test estuary. Plankton samples were collected at hourly intervals at 1, 4, 7m. below the surface and 1m. above the bottom sediment, over a 12 hour period using a hose and pump method which is described before.

Some environmental parameters were concurrently measured with the hourly monitoring of larvae at each depth. Salinity and water temperature were measured (see Section 5.2.6). Speed and direction of water current at each depth were measured using a NBA current meter.

5.2.6 Measurement of Environmental Parameters

During the larval surveys certain environmental parameters were measured using the following procedures. For chlorophyll "a" determination, 100ml samples of sea water taken from each depth were used. The water was immediately filtered in the field through a plastic funnel fitted with a filter paper (Whatman GF/F, 47mm. in diameter) using a hand operated pump. Two samples of 100ml were filtered from each depth every day. The filter paper were folded and wrapped in aluminium foil and stored under ice to reduce bacterial activity. In the laboratory chlorophyll content was measured using a fluorometric technique which is more sensitive for small concentrations of chlorophyll than the spectrophotometric analysis (Parson *et al.*, 1984). The chlorophyll retained on the filter paper was extracted by homogenising in 10ml of 90% acetone (v/v) for 5 - 10 minutes using a mechanical homogeniser. The homogenate was poured into a 15ml polypropylene centrifuge tube and contents of the homogeniser rinsed with 90% acetone into the centrifuge tubes, which were centrifuged at 7000 rpm for 5 minutes. The acetone extract was carefully transferred into a 25ml volumetric flasks and made up to volume with 90% acetone. The relative fluorescence of the extracts was measured using a fluorometer (Aminco Fluoro calorimeter). The fluorometer was set to zero against 90% acetone and calibrated with a standard concentration of chlorophyll "a" ($1 mgl^{-1}$). A few drops of 10% HCl were added after which all solution was mixed and the relative fluorescence was measured to determine the phaeophytin pigment. The concentration of chlorophyll "a" and phaeo-pigment were calculated using the following equations (Parson, Maita and Lalli, 1984):

$$\text{chlor.a } (mgm^{-3}) = F_D X 1.83\ (R_B - R_A)\ X\ \nu/v$$

$$\text{and Phaeo-pigment } (mgm^{-3}) = F_D X 1.83\ (2.2\ R_A - R_B)\ X\ \nu/v$$

where R_B and R_A are fluoresence reading before and after acidification

F_D = calibration factor and is calculated as $F_D = C_a / R$ where

C_a = concentration of chlorophyll "a" in the standard solution, and R is the fluorometer reading, ν is the volume of acetone extract in ml, and v = the volume of seawater in litres.

Water temperature and salinity, during the daily sampling of larvae at Town Quay were measured using a digital field salinometer (model MK-1) accurate to within $\pm$ 0.2%. Temperature and salinity sensors are incorporated into one probe and attached to a cable which can be lowered to the required depth. Water temperature and salinity were recorded at 0, 1, 3m below the surface and just above the bottom sediment whenever it was possible.

Water current was measured using a Seahorse propeller current meter, which gives direct current speed in knots and current direction in degrees.

5.2.7 Identification of Mercenaria Larvae

Plankton samples were examined alive under the microscope, to distinguish different types of larvae and they were subsequently removed and compared with different stages of *Mercenaria* larvae obtained from the induced spawning in the laboratory. Identification of *Mercenaria* larvae was easier at the umbone stage, where characteristic features of *Mercenaria* larvae became clear. Most of the difficulty however were encountered in distinguishing *Mercenaria* straight hinge stage which was similar in shape and appearance to the straight hinge stage of other bivalve species.

From monthly gamete counts (see Chapter 4) and larvae obtained from induced spawning, in addition to photomicrographs and descriptions of bivalvae larvae in the literature (Carriker, 1961, Chanley and Andrews, 1971, Mitchell, 1974 and Gallager *et al*., 1986), the identification of larvae found in samples was confirmed. Furthermore measurement on field samples revealed that length and height relationship was identical for both the field and laboratory spawned larvae.

The other bivalve larvae found in the plankton samples were tentatively identified as *Cerastoderma edule* which has a comparatively smaller larvae than *Mercenaria*, according to the photomicrographs given by Kingston (1972). Plankton samples taken in the lower parts of Southampton Water contained larvae of the oyster (*Ostrea edulis*) identical to specimens obtained from the Shellfish Culture Unit at Conway.

Photomicrographs of bivalve larvae identified as Mercenaria larvae are shown in Plate I.

5.2.8 Counting and Measurement of Larvae

In the laboratory, plankton retained on the nylon mesh (63µm) were washed down using filtered seawater, and all the sample was poured into a measuring cylinder, and the total volume was recorded (approximately 100 - 400mls). Samples were preserved by addition of 5% neutral formalin. The diluted sample was thoroughly mixed using a perforated plastic disc which was moved up and down in the cylinder. Subsamples of 30mls were removed with a small Stempel type pipette and transferred to a Bogorov counting tray. All Mercenaria larvae were recorded and transferred to a separate container. Subsamples representing more than half of the total volume of each plankton samples were examined. Occasionally, when the number of larvae was small, large numbers of subsamples were examined.

Mercenaria larvae obtained every day from Town Quay were concentrated by filtration and 1ml of aliquot was pipetted into a Sidgewick Rafter cell and examined under a binocular microscope fitted with an eye piece reticule previously calibrated against a stage micrometer. On each occasion, 30 larvae were measured for length (largest anterior-posterior axis parallel to the hinge line) and height (largest dorso-ventral axis).

PLATE 1 A,B,C & D.

PLATE 1 Photomicrograph of some developmental stages of *Mercenaria* larvae in plankton samples

A : Straight-hinged larva.
Length = 90 - 110µm. Magnification = 500x

B : Late straight-hinged larva.
Length = 110 - 140µm. Magnification = 300x

C : Early umboned larva.
Length = 140 - 180µm. Magnification = 600x

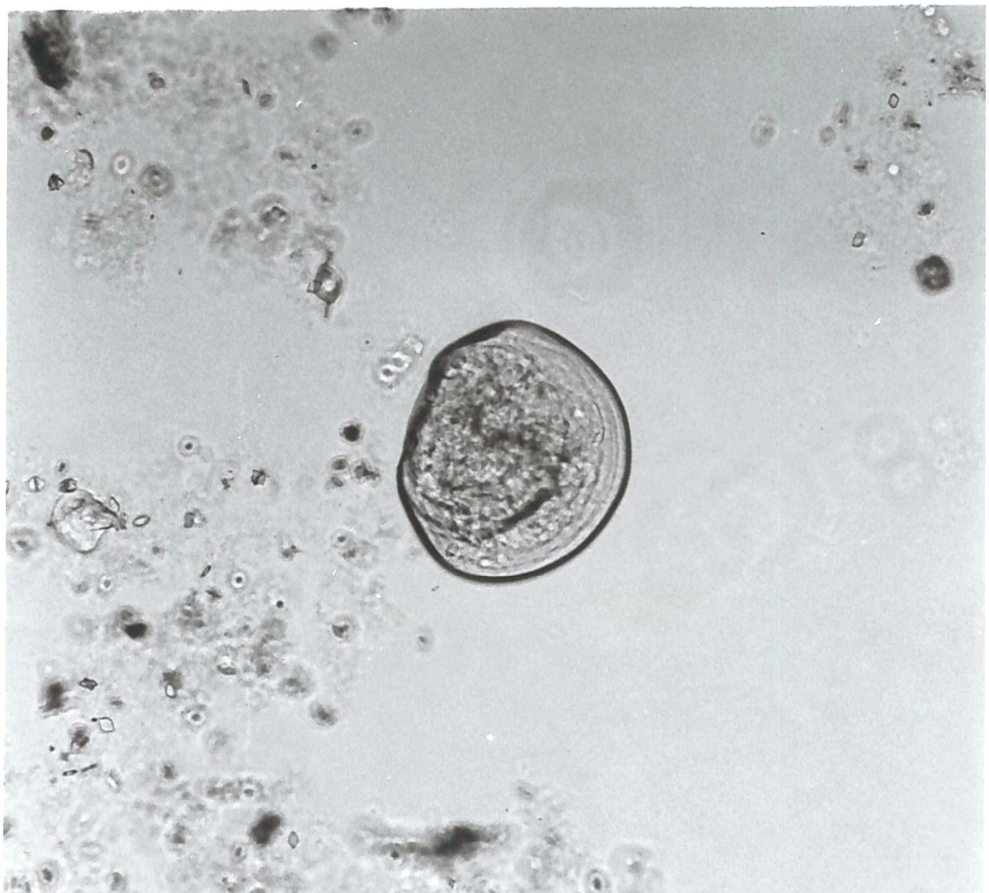
D : Late umboned larva.
Length = 180 - 200µm. Magnification = 300x

Lengths and magnification are approximate

PLATE 1

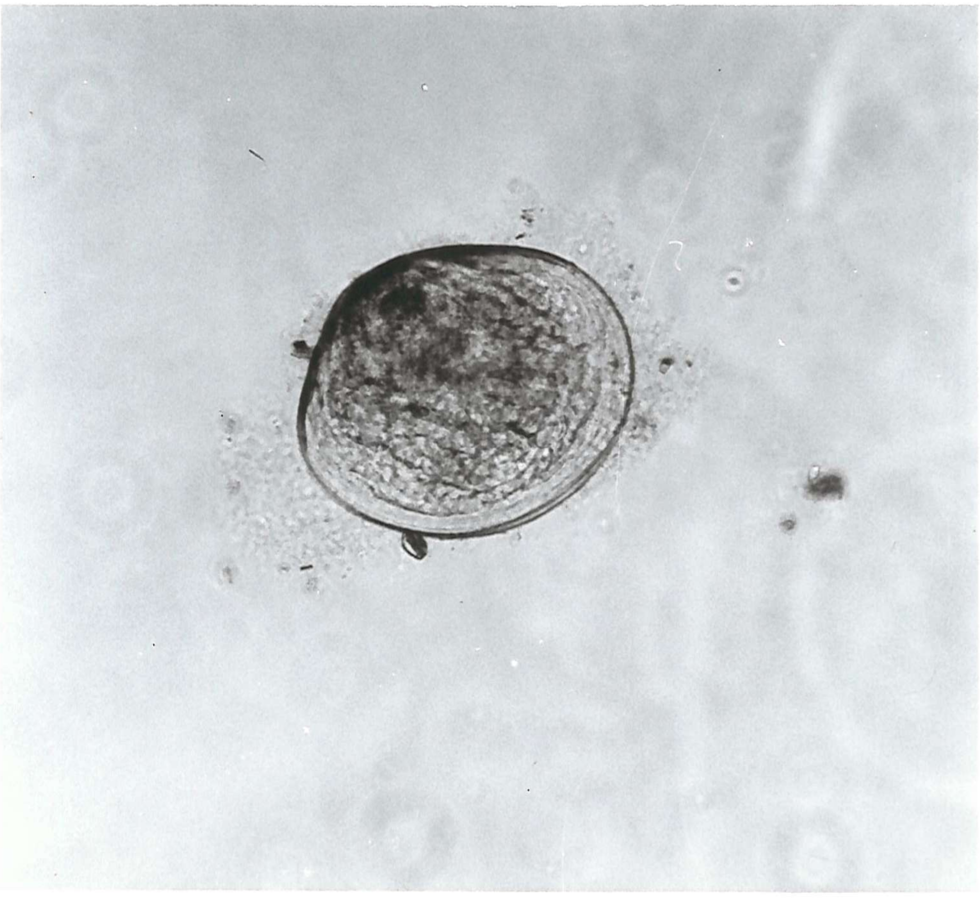
A

B



C

D



5.3 RESULTS

5.3.1 Horizontal Distribution

The abundance of clam larvae at 1m below the surface in different parts of Southampton Water during flooding and ebbing tides on June and August 1984 are illustrated in Fig. 5.1a and 5.2a. All stages of the larvae were present over a large part of Southampton Water during flooding tide. The total number of larvae from upper section (Marchwood, Royal Pier and Hythe Pier) were 3 to 5 times greater than from the lower part of the estuary. In both surveys the maximum number of all stages occurred at Hythe Pier, and the lowest concentration of larvae was in areas of high salinity and low chlorophyll level at the seaward and of the estuary (with the exception of Clipper Buoy).

The spatial variation in salinity, temperature and chlorophyll "a" for all sites are shown in Figs. 5.1b and 5.2b. Water temperature and chlorophyll "a" decreased seaward. Water temperature fluctuated from a maximum of 20.5°C during ebbing tide to 16.9°C at the flooding tide. Chlorophyll "a" showed great variation between stations during flooding water, where the highest concentration ($47.16 \mu g l^{-1}$) was found at Marchwood and lowest ($1.74 \mu g l^{-1}$) at Solent Breezes.

Measurement of water current revealed that the minimum speed (0.05 knots/hr.) at 1m below the surface was recorded at Hythe Pier whereas maximum speed was found at Fawley (2.5 knots/hr.). Data of both surveys were used to calculate correlation coefficients between larval abundance and environmental parameters (Table 5.1). Chlorophyll

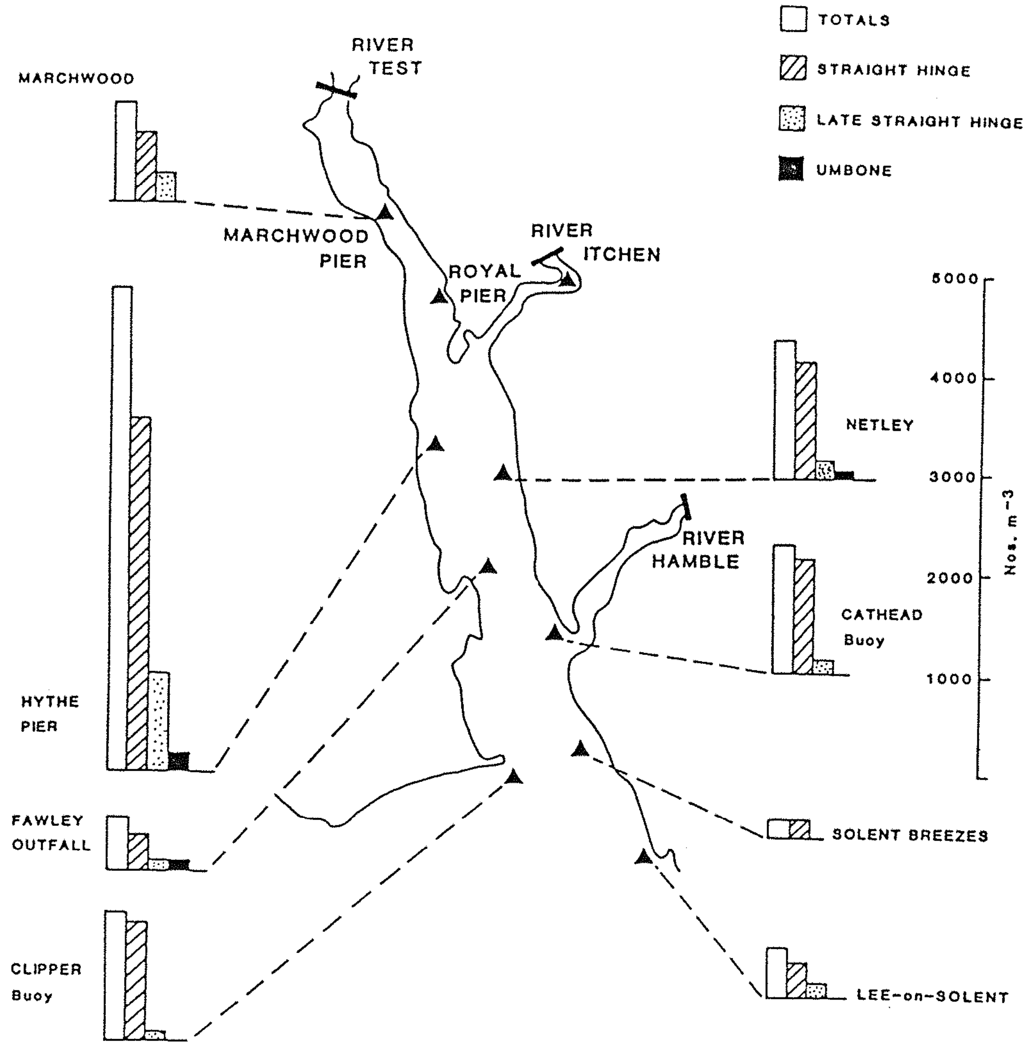


Fig. 5.1a Horizontal distribution of planktonic larvae throughout Southampton Water during flood tide on 18th June, 1984 (1m below surface)

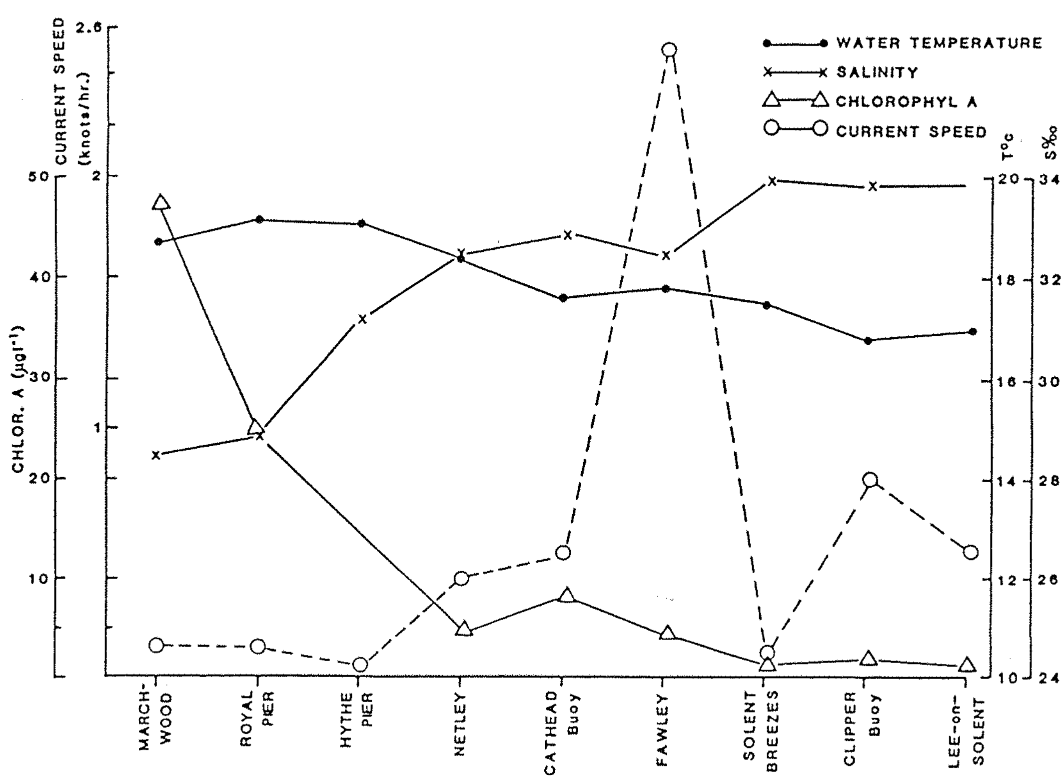


Fig. 5.1b Water temperature, salinity, chlorophyll "a" and current speed during flood tide on 18th June, 1984 (1m below surface)

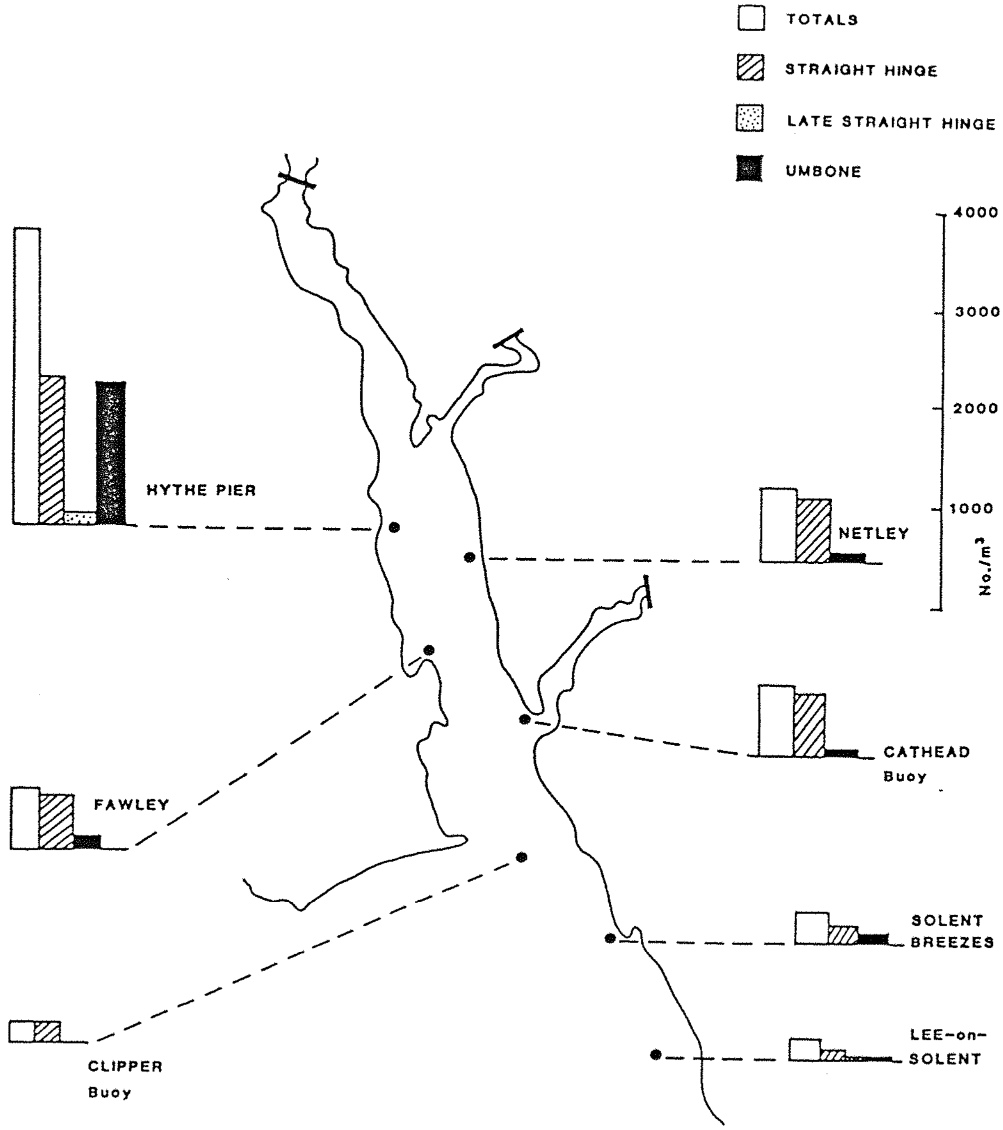


Fig. 5.2a Horizontal distribution of planktonic larvae ($no.m^{-2}$) throughout Southampton Water during ebb tide on 14th August, 1984 (1m below surface)

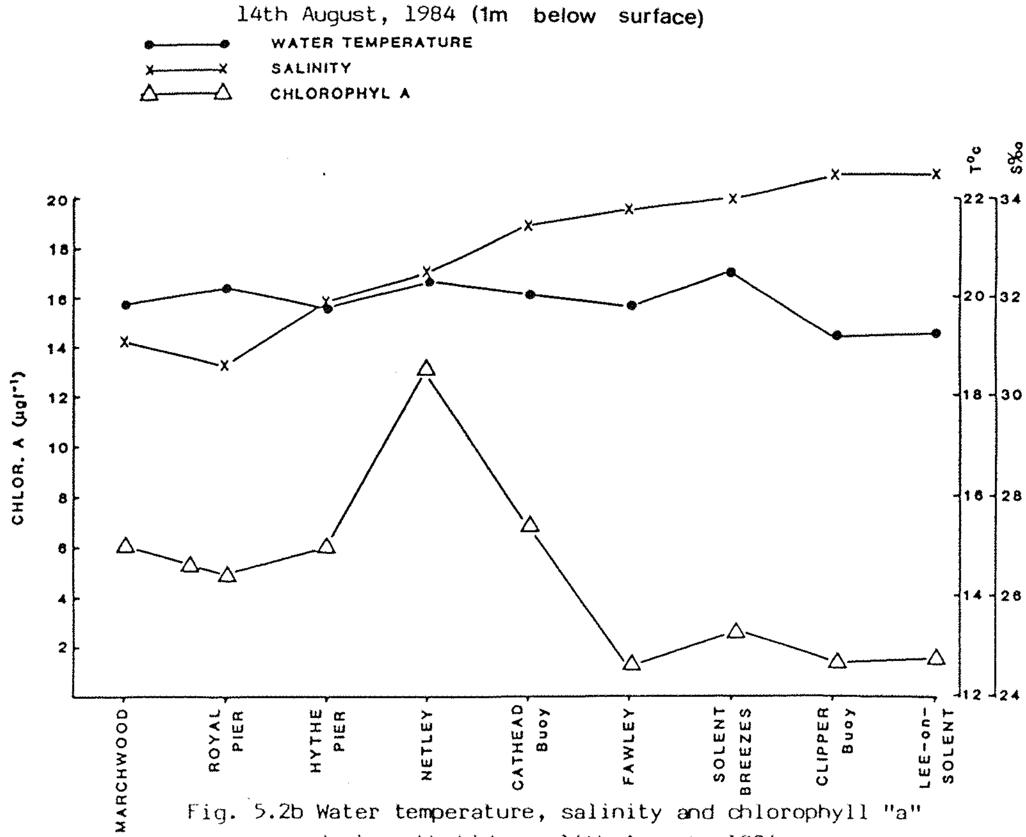


Fig. 5.2b Water temperature, salinity and chlorophyll "a" during ebb tide on 14th August, 1984 (1m below surface)

Table 5.1 : Correlation of larval density (No./m^3) and environmental parameters at ebb and flood tides throughout Southampton Water in June and August 1984

	Density	chlorophyll "a"	Salinity	Water temperature
Density	-	0.430	0.452	0.204
Chlorophyll "a"		-	0.927*	0.128
Salinity			-	- 0.097
Water temperature				-

* indicates statistical significance at $P < 0.05$

"a" gave a significant negative correlation with the increase in salinity in the seaward direction.

5.3.2 Weekly Larval Abundance

Results of weekly monitoring of larvae in the whole water column at 5 sites during Summer 1983 are given in Table 5.2. Plots of mean number of larvae in the water column at various sites in Southampton Water are shown in Fig. 5.3.

Fig. 5.3 shows that larvae during 1983 were produced from the end of May and tailed off at the beginning of October. A simultaneous swarm of larvae appeared at Itchen Bridge, Royal Pier and Marchwood stations in the beginning of August, although earlier swarms were recorded at Royal Pier and Itchen Bridge at the end of June and beginning of July, respectively. The highest number of larvae were encountered at Itchen Bridge and lowest numbers were recorded at Netley.

Sampling at Hythe Pier and Netley was started towards the end of June. However comparing the number of larvae obtained at both sites during the same period, revealed that larvae were more numerous at Hythe Pier than at Netley, despite the higher water temperature recorded at Netley. During the survey, water temperature rose from 15°c at the beginning of May to 23°C in mid Summer then dropped towards the end of September to 16°C. Water temperature varied narrowly between sites ranging from 15°C to 23.5°C. Data on chlorophyll "a" levels measured at Cracknore Hard by Rees and Williams (1982) showed that maximum level occurred in June.

Table 5.2 : Density of *Mercenaria* larvae (No./m^3) in the weekly plankton sampling at Marchwood, Royal Pier, Hythe Pier and Netley in Summer 1983

Date	Marchwood	Royal Pier	Itchen Bridge	Netley	Hythe Pier
24.05.83	733.3	1873	1146	N.S.	N.S.
09.06.83	N.S.	N.S.	N.S.	N.S.	N.S.
14.06.83	342	478.3	433	N.S.	N.S.
20.06.83	494	2373	7937	N.S.	N.S.
01.07.83	253	172	300	361	948
06.07.83	309	N.S.	342	N.S.	N.S.
12.07.83	3322	6726	3267	2454	N.S.
27.07.83	1525.5	2007	2980	N.S.	655
05.08.83	6764	7465	20603	2260	7797
10.08.83	1381	689	2803	N.S.	1766
17.08.83	2789	7523	3898	890	1964
07.09.83	4180	3688	313	1521	667
19.09.83	493	N.S.	1603	459	2783
26.09.83	467	145	346	250	125
10.10.83	5	0	110	25	10

N.S. indicates not sampled

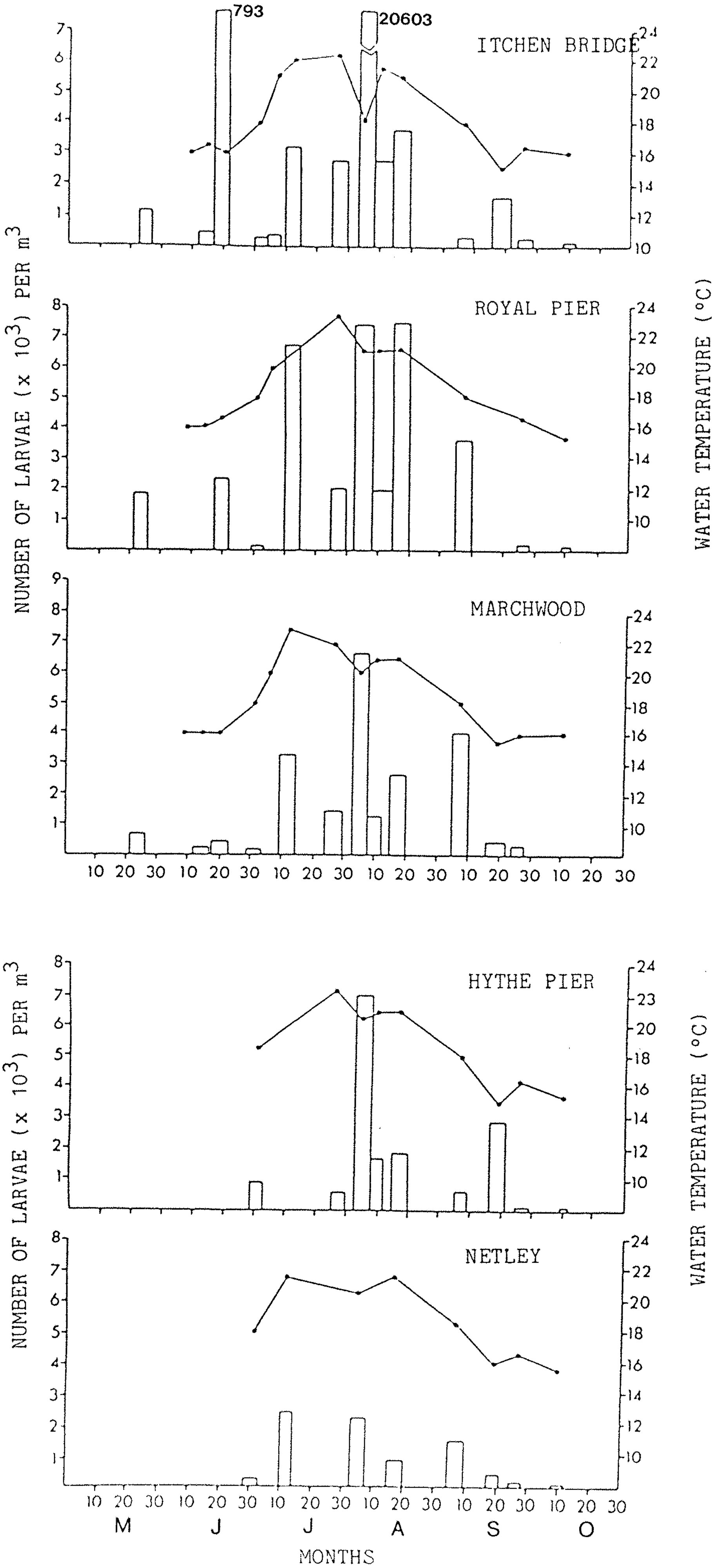


Fig. 5.3 Histograms of weekly abundance of larvae (no.m.$^{-3}$) and water temperature at 5 sites in Southampton Water during summer 1983

5.3.3 Daily Larval Abundance

During the daily surveys, bivalve larvae were separated into straight hinge, late straight hinge and umbone larvae as illustrated in Plate I.

Table 5.3 lists daily changes in abundance of different stages of larvae at each depth at Town Quay over 8 days. All stages were present during the survey with straight hinge larvae dominating the catch forming 60 - 80% of the daily samples, whereas umbone larvae were least abundant. Numerical density of different stages of larvae however showed great variation at $P \leq 0.05$ (see Table 5.4a). In addition there was significant variation in the vertical distribution of larvae with depth, as clear from analysis of variance on distribution of larvae at each depth on the first day (Table 5.4b) where umbone stage occurred predominantly in deeper water.

Daily measurements of water temperature, salinity and chlorophyll "a" at each depth over the 8 days are illustrated in Fig. 5.4. Water temperature was predominantly high in water close to the surface (19 - 20°C) and low near the bottom layer (18.4 - 20.3°C). Similarly, very high chlorophyll "a" values were restricted to the top 1 metre layer. The peak of chlorophyll "a" (66 - 68$\mu g l^{-1}$) occurred on the 4th and 5th days, respectively. The daily salinity records revealed a bottom layer of high salinity (31.5 - 33%) and surface water of lower salinity.

The correlation coefficient between numerical density of different stages of larvae and environmental parameters are given in Table 5.5. Daily values of chlorophyll "a" were among environmental

Table 5.3 : Daily abundance of Larvae (no./m^3) at Town Quay during 17- 24 of July 1984

Dates	Larval stages	Depths (m)							Mean number per m^3
		0	1	2	3	4	5	6	
17.7.84	Straight hinge		1167	1347	753	880	767	320	872
	Late straight hinge		180	300	180	160	420	347	262
	Umbone		80	87	80	107	200	160	109
18.7.84	Straight hinge				987		3553		3669
	Late straight hinge				220		800		951
	Umbone	667			233		980		626.7
19.7.84	Straight hinge	11000	15900		8487		3233		9655
	Late straight hinge	833	1200		533		383		737.3
	Umbone	533	1933		533		267		816.5
20.7.84	Straight hinge	29000	6167		23130		6667		16241
	Late straight hinge	3033	967		1367		533		1475
	Umbone	2367	667		700		467		1050
21.7.84	Straight hinge	2153	9100		2367		1400		3755
	Late straight hinge	120	367		100		43		157
	Umbone	400	800		267		133		400
22.7.84	Straight hinge	4400	4133		1953		3330		3454
	Late straight hinge	3530	153		53		153		972
	Umbone	287	67		53		87		123
23.7.84	Straight hinge	2287	3953		253				2917
	Late straight hinge	220	353		133				235
	Umbone	247	287		113				215.7
24.7.84	Straight hinge	22133	1567				5887		9862
	Late straight hinge	2700	287				153		1046.2
	Umbone	900	20				20		313

Table 5.4a : Analysis of variance test on daily abundance of different larval stages of *Mercenaria* at Town Quay during 17 to 24 July 1984

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio
Days	77956000	7	11136507	1.424 NS
larval stages	173840000	2	8691887	11.113 S
Residual	109500000	14	7821311	

NS and S indicate not significant and significant at $P \leq 0.05$

Table 5.4b : Analysis of variance test on length of *Mercenaria* larvae at each depth at Town Quay on 17 July 1984

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio
Day	129.6245	2	64.81224	0.380 NS
Depth	1147.7067	3	382.56890	2.243 S
Residual	56277.166	330	170.53687	

NS = not significant at $P \leq 0.1$, S = significant at $P \leq 0.1$

Table 5.4c : Analysis of variance for length of <u>Mercenaria</u> larvae on each day at Town Quay from 17 to 24 July 1984

Source of Variation	Sum of Squares	Degree of Freedom	Mean Squares	F-ratio
Between days	3668.8052	5	733.76105	2.52746 S
Residual	167802.53	578	290.31579	

S = significant at $P \leq 0.05$

Table 5.5 : Correlations between densities (no./m^3) of different stages of <u>Mercenaria</u> larvae and environmental parameters in daily sampling at Town Quay from 17 to 24 July 1984

	Straight hinge larvae	Late straight hinge larvae	Umbone larvae	Chlorophyll "a"	Salinity	Water temperature
Straight hinge larvae	-	0.626*	0.753*	0.511*	-0.015	0.046
Late straight hinge larvae		-	0.514*	0.402*	-0.170	0.253
Umbone larvae			-	0.490*	-0.020	-0.007
Chlorophyll "a"				-	-0.557*	0.615*
Salinity					-	0.865*
Water temperature						-

* indicates statistical significance at $P \leq 0.05$

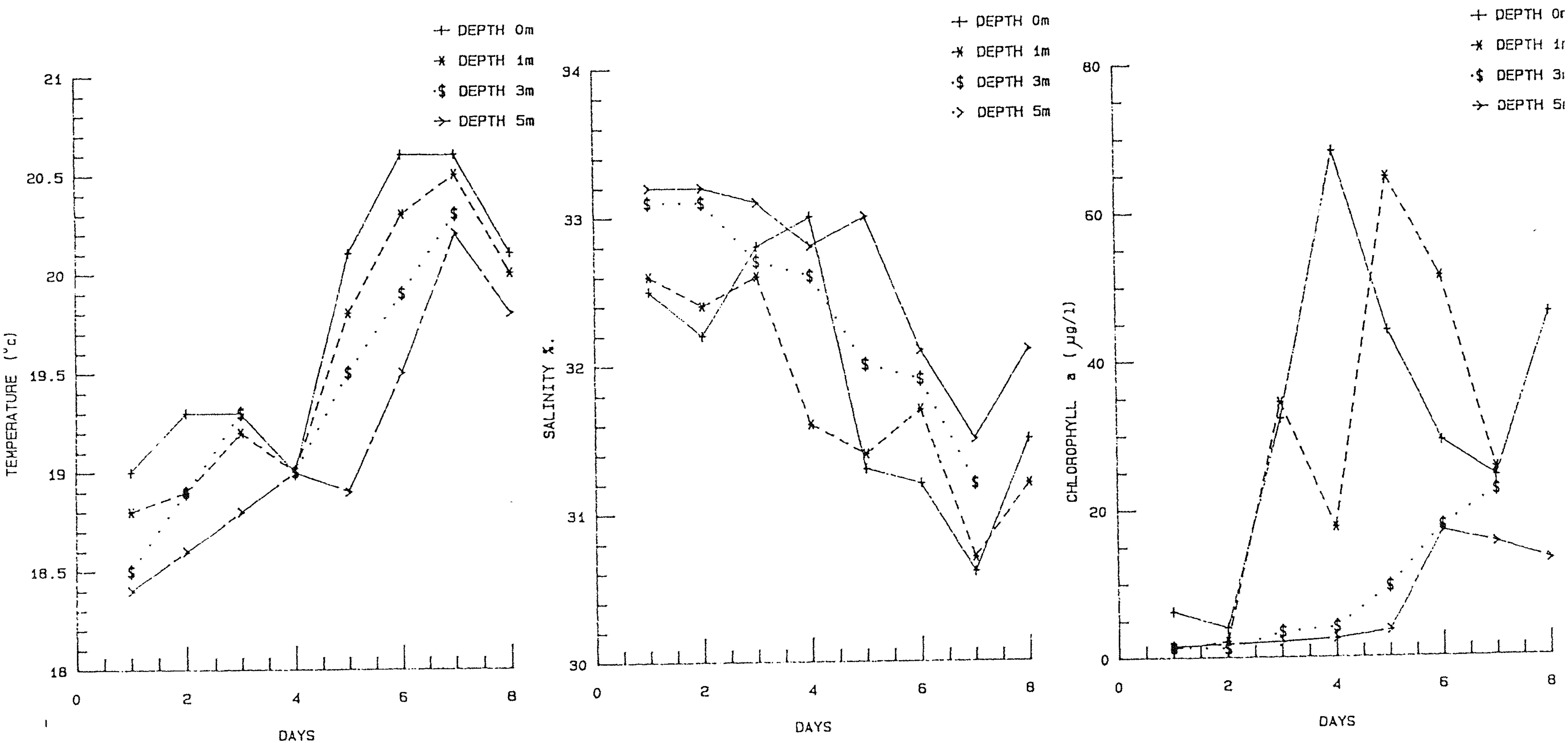


Fig. 5.4 Daily vertical changes of water temperature, salinity and chlorophyll "a" at Town Quay during 17 to 24 July 1984

parameters that gave significant positive correlation especially with the abundance of straight hinge larvae. Swarms of different larval stages coincided with the peak of chlorophyll "a" on the 4th day of sampling (Fig. 5.4).

In this work, changes in length frequency distribution of larvae collected everyday was repeatedly monitored. Although there was significant variation in length of larvae between days (Table 5.4c), and size tended to increase with depth (Table 5.4b), nevertheless dominance of the 120 - 130µm modal classes on most occasions was clear (Fig. 5.5). The largest size of larvae recovered measured 203µm x 187µm and the smallest one was 88µm x 71.5µm. The daily growth of the larval population was approximately estimated by following changes in the length frequency distribution of different size groups during the 8 day period. Plot of daily increase in frequency of different size groups during the study period were compared with Carriker's (1961) results (Fig. 5.6a). Larvae in general grew to 172µm within 8 days. Carriker (1961) on the other hand found that larvae reach 185µm after 7 days. In addition growth of larvae spawned in the laboratory, where the temperature was kept at 20 - 25°C, showed a similar rates of growth to that found by Loosanoff (1951) who reported that larvae grew to 165µm within 14 days at 21°C (Fig. 5.6b).

Measurement of shell length and height were carried out on representative samples of different stages of larvae. The data were analyzed by linear regression in order to determine length-height relationship in naturally occurring larvae and compare it with similar measurements on laboratory spawned larvae (Fig. 5.7). There was significant linear positive relationship between shell length and height of different stages. However, the correlation coefficient was higher at early straight hinge and umbone larvae, $r = 0.93$ and 0.95, respectively, than at late straight hinge larvae ($r = 0.66$, all at $P \leq 0.05$).

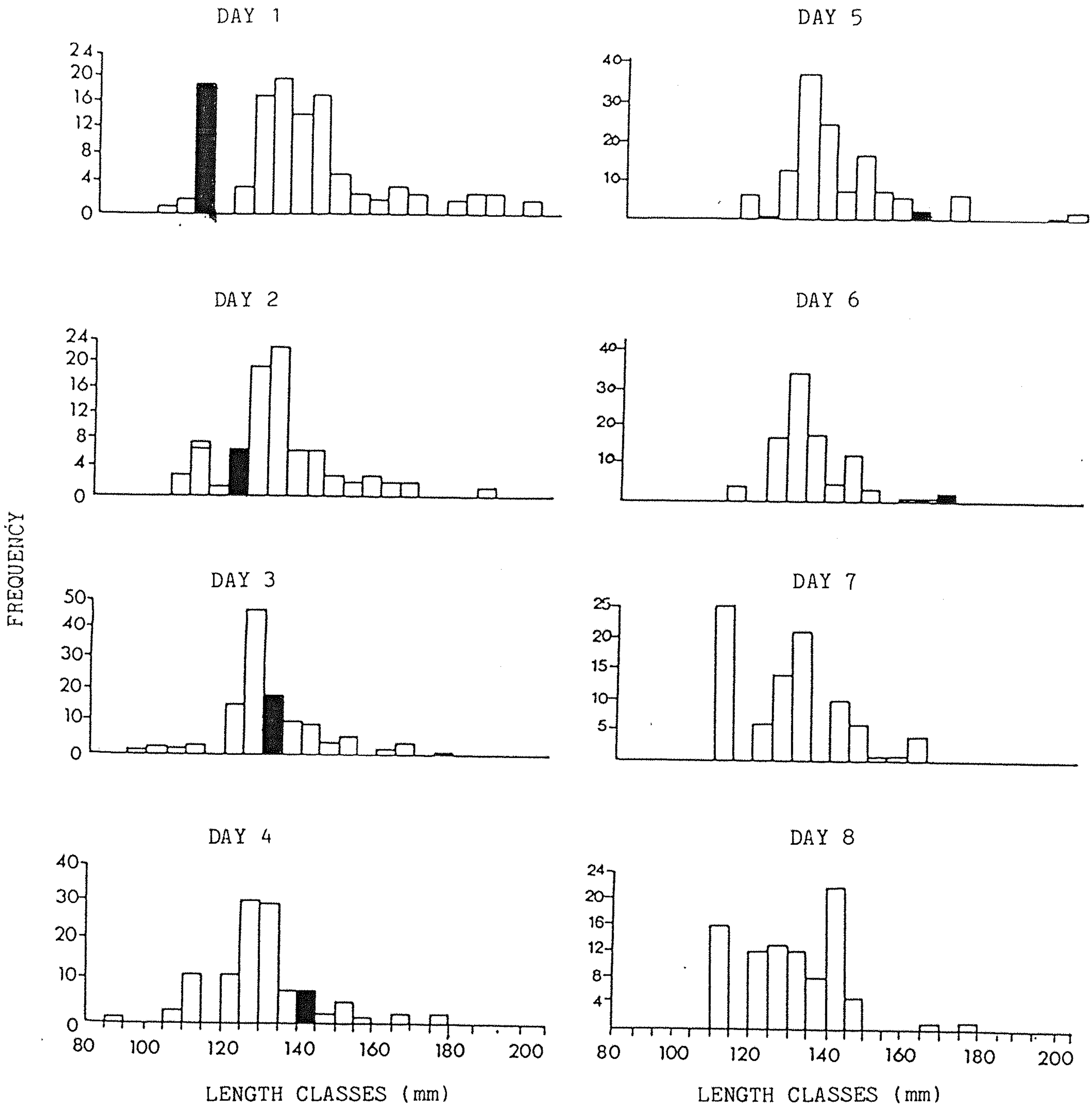


Fig. 5.5 Length frequency distribution of Mercenaria larvae collected at Town Quay from 17 to 24 July, 1984
Black shading represents cohort 2.

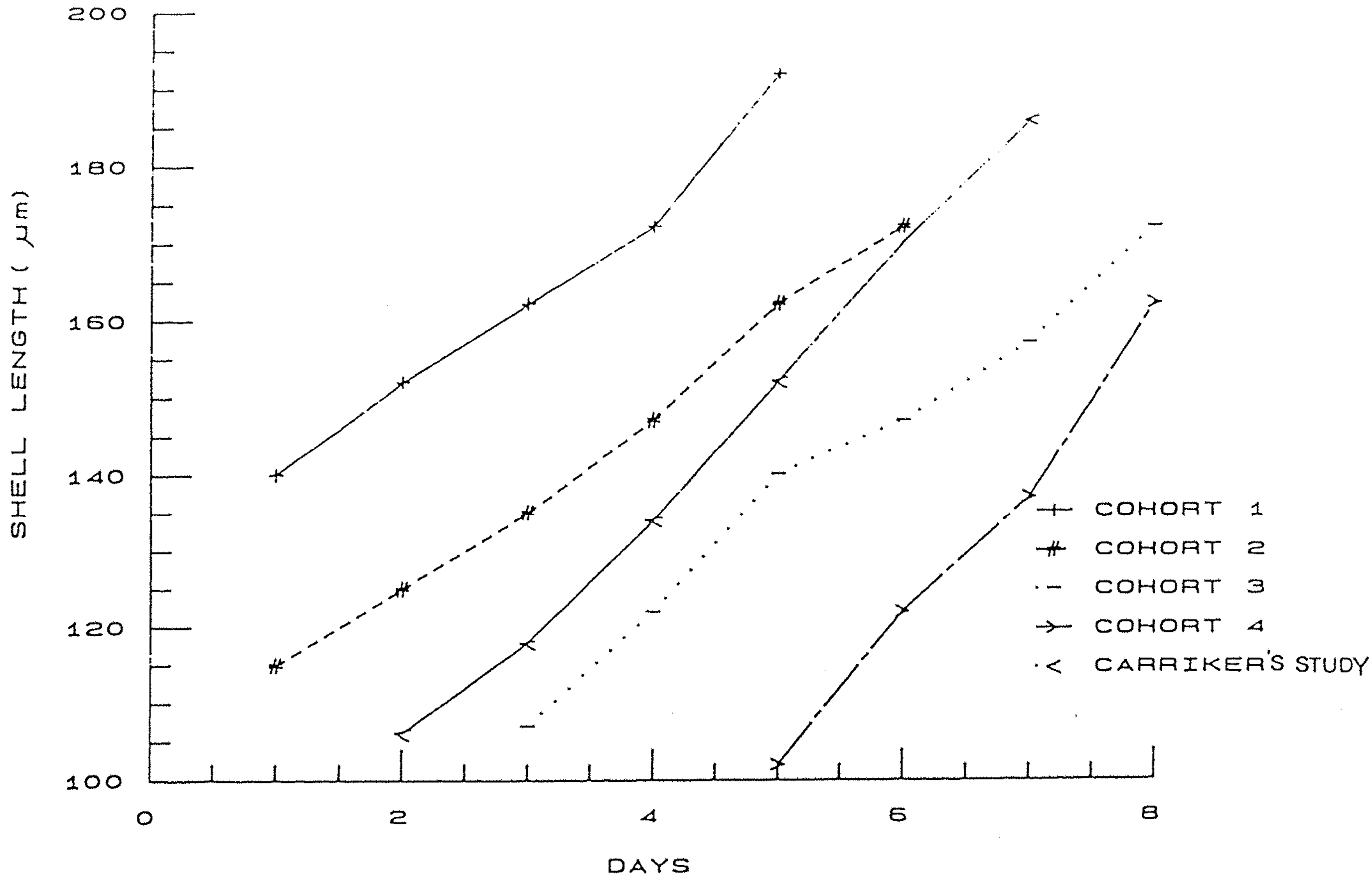


Fig. 5.6a Daily increment in length of different cohorts of larvae sampled at Town Quay compared with Carriker's(1961) data (by interpretation of changes in length frequency shown in Fig. 5.5)

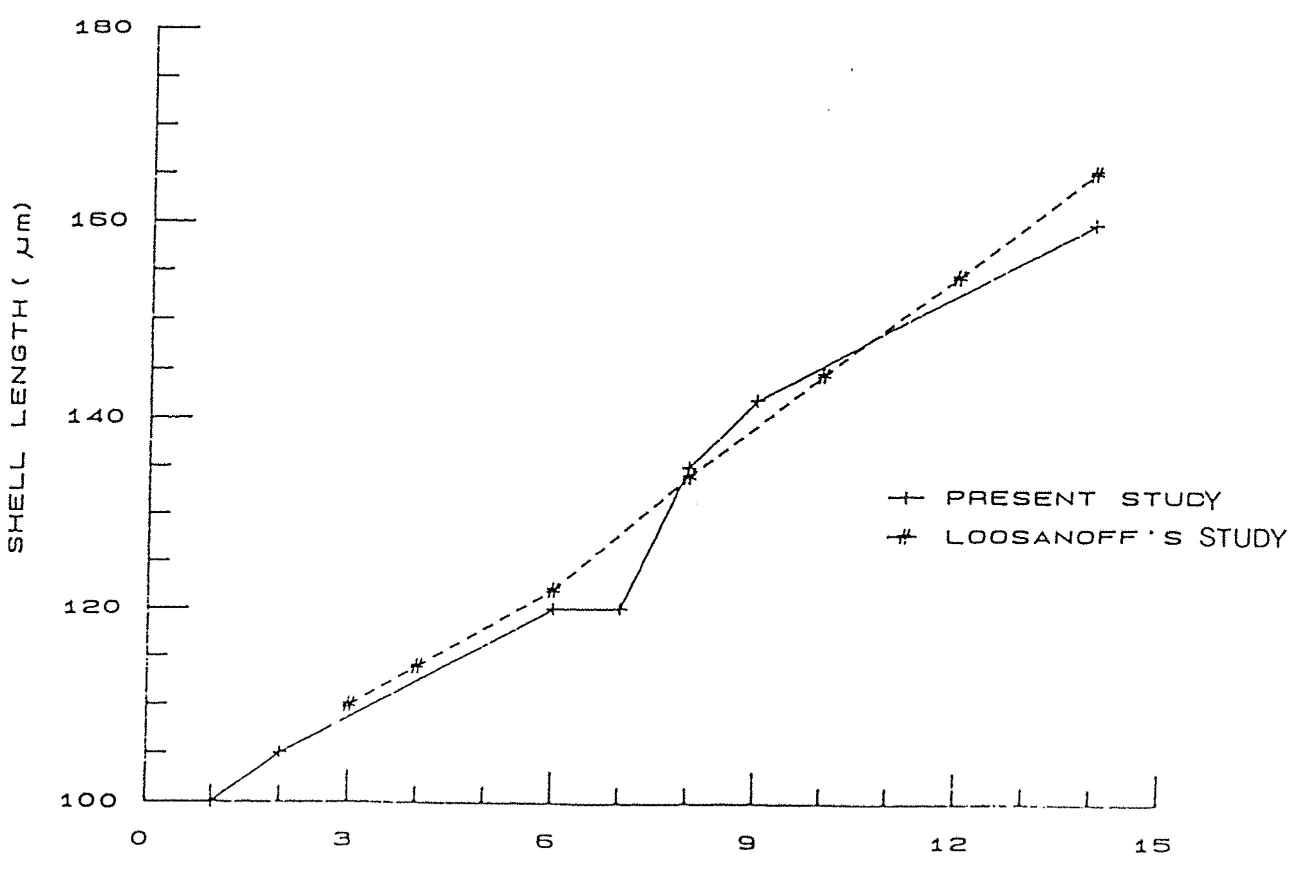


Fig. 5.6b Daily increment of mean length of larvae spawned in the laboratory compared with Loosanoff's(1951) data

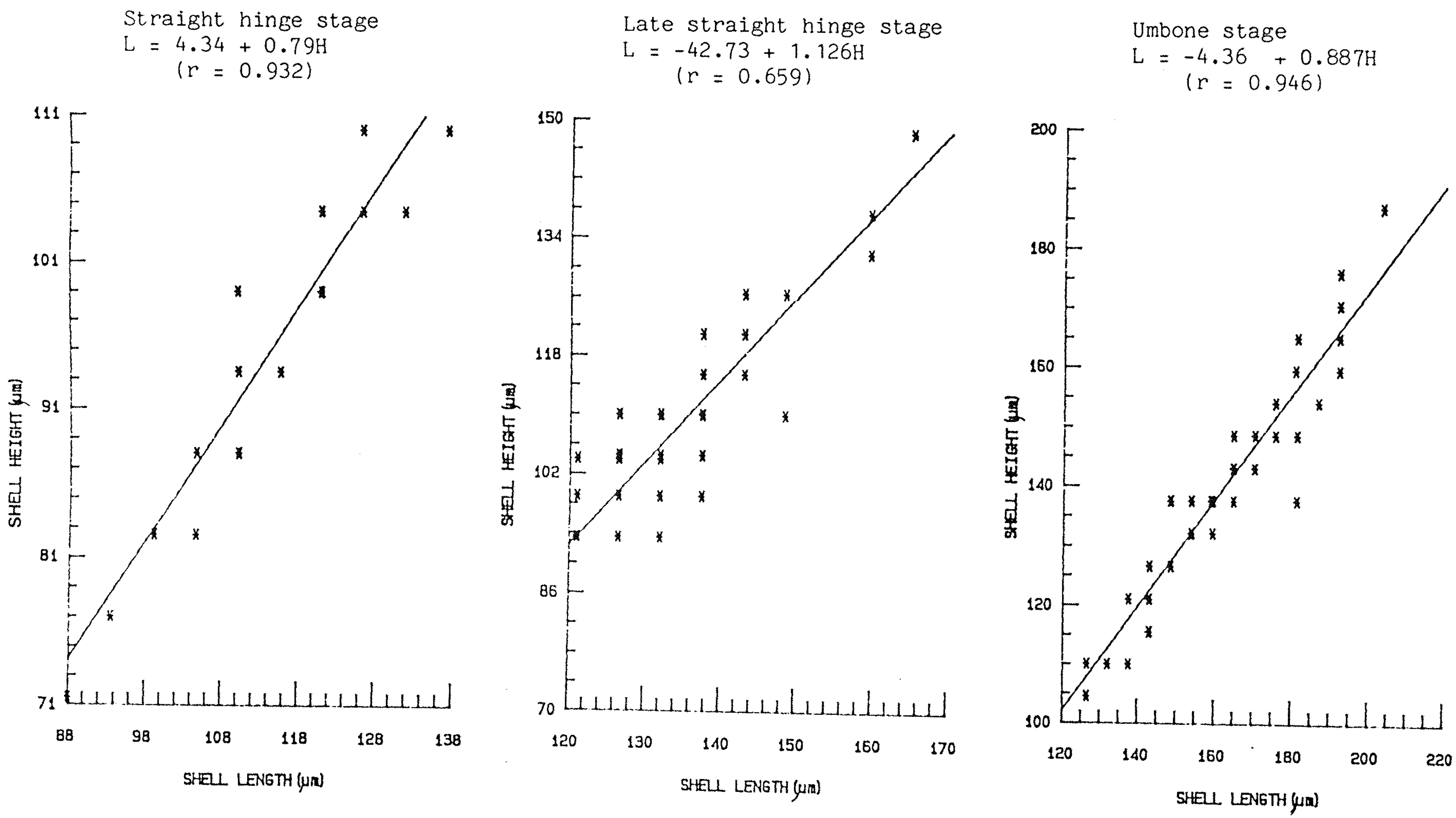


Fig. 5.7 Linear regression of length (L) and height (H) of different stages of Mercenaria larvae at Town Quay during 17 to 24 July 1984

5.3.4 Larval Abundance During A Tidal Cycle

Results of the hourly sampling of different stages of larvae at each depth during a spring tide on 4th July 1985 at Ealing Buoy are given in Table 5.6.

The early and late straight hinge larvae were numerically dominant during the survey and occurred down to the bottom layer. Very few umbone stage larvae were found; a greater number however was recorded towards the ebbing tide. The vertical distribution of different stages does not seem to reflect differences in depth preference among the different larval stages. Furthermore, the numerical density at each depth showed extremely wide variation during the tidal cycle. Therefore, transformation of the data was necessary to avoid the apparent increase of larval abundance caused by tidal advection. On each occasion the numerical density of larvae at each depth were expressed as percentage of the total integrated value for the whole water column. Each percentage was plotted against the depth. Extrapolation of larval density at each 1 metre interval was made, followed by calculation of the cumulative percentage for each depth. The depth corresponding to 25, 50 and 75 cumulative percentage were then read. Those depths were superimposed on a plot of salinity contours at hourly intervals as shown in Fig. 5.8.

Salinity in the top 4 metres showed very wide variation from a minimum of 20‰ to a maximum of 30‰. On the other hand salinity of the deeper layers were significantly higher than the upper layers. Larvae seemed to avoid low salinity areas and were concentrated in the middle and deeper layers, where salinity did not change dramatically. In general larvae during flooding tide and first high water move upward until the second high water. However, the centre of gravity of the vertical population distribution moved downward to deeper water after 15 hours which coincided with start of the ebb during which there was an influx of low salinity water to the site, and greater downstream currents were recorded (Fig. 5.8). Downward movement of the larvae could be interpreted as behavioural adaptation, avoiding strong seaward currents during the ebb tide, and avoiding low surface salinity.

Table 5.6 : Total Larval density (no/m^3) by depths at Ealing Buoy during 12-hours tidal cycle on 4th July 1985

Time (hrs)	Tidal Stage	Depths (m)			
		1	4	7	1m off bottom
8.15 - 9.00	Early flood	284	973	627	630
9.20 - 10.05		567	53	164	130
10.20 - 11.05		57	326	132	70
11.20 - 12.00		70	32	370	470
12.15 - 13.00		220	789	280	220
13.13 - 14.00	High slack	243	130	351	252
14.20 - 14.58		172	550	190	231
15.17 - 15.58		539	352	50	889
16.12 - 16.58		310	867	242	187
17.07 - 17.58		77	110	372	1124
18.13 - 18.58	Maximum ebb	160	549	500	880
19.13 - 19.59		199	679	570	222

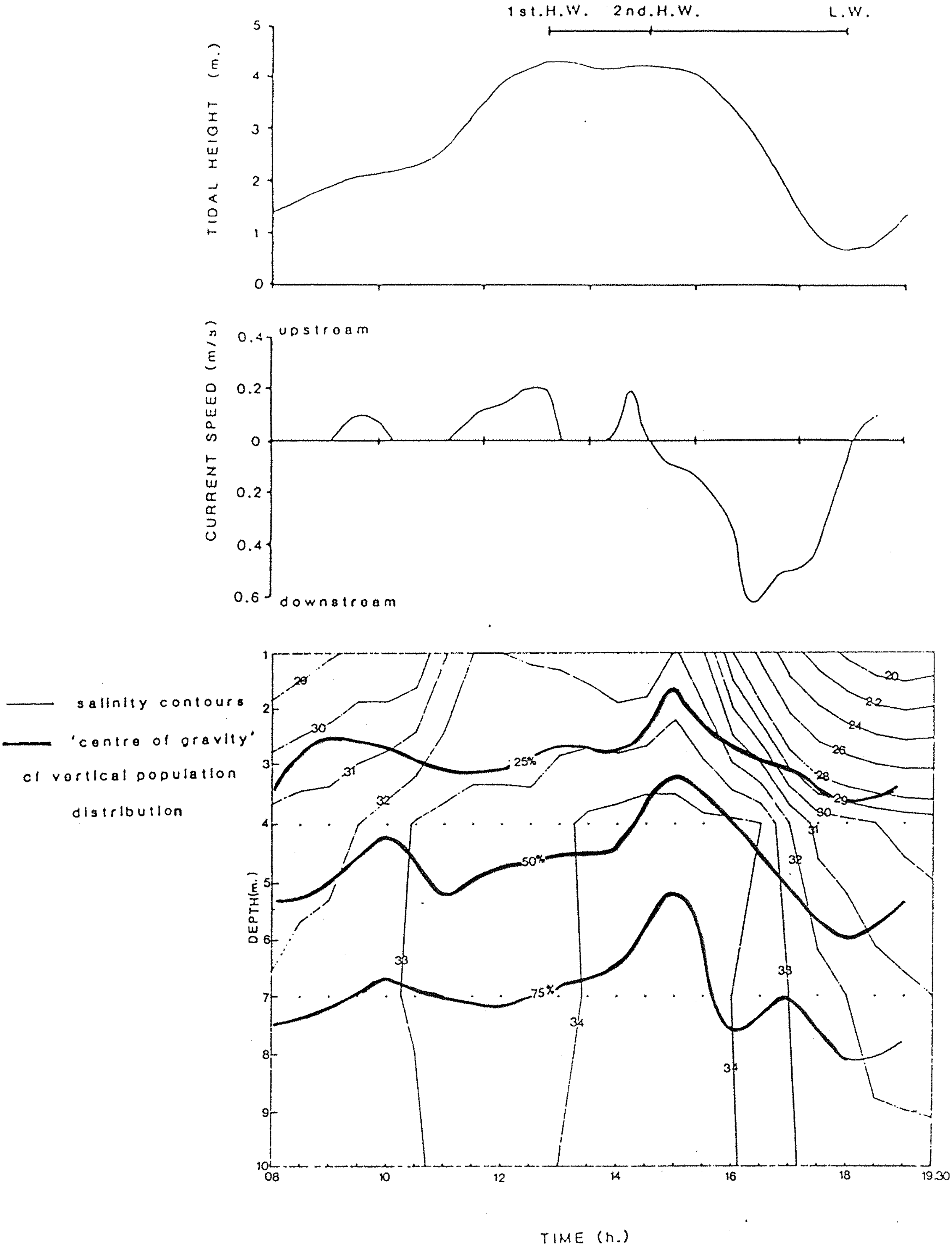


Fig. 5.8 25%, 50% and 75% relative vertical proportion distribution of Mercenaria larvae , and salinity contours with tidal curve and surface current speed.

5.4 DISCUSSION

An investigation of different aspects of larval ecology was carried out in an attempt to understand the mechanism of larval retention within the estuary, daily growth and duration of the planktonic stage, the time of onset and duration of spawning, and the general distribution of larvae throughout Southampton Water.

The regular weekly monitoring of larvae at different sites during the Summer of 1983, revealed that larvae were produced over a long period from May to the beginning of October. Simultaneous swarms of larvae occurred at Marchwood, Royal Pier and Itchen Bridge at the beginning of August. This indicates that August was the main spawning month for *Mercenaria* in Southampton Water, which seems in agreement with results of gamete counts (see Chapter 4). However, earlier smaller larval swarms were recorded at Royal Pier and Itchen Bridge at the end of June and beginning of July indicating that localised spawning can occur whenever the critical spawning temperature is reached. Therefore, spawning in *Mercenaria* takes place when sediment temperature reaches 16°C. Ansell (1961) found in the same area that *Mercenaria* released eggs at a water temperature of 18°C. Furthermore, Mitchell (1974) concluded that *Mercenaria* spawned when water temperature rose to 18 - 19°C.

In the USA, the critical spawning temperature for *Mercenaria* varies at different points in its geographical range. For example, Loosanoff and Davies (1950) concluded that spawning occurs at temperatures below 24°C, whereas Porter (1964) and Eversole *et al.* (1980) in North and South Carolina found that spawning took place at a temperature of 20 - 23°C. Carriker (1961) on the other hand found that maximum frequency of spawning occurred within a temperature range of 24 to 26°C.

Furthermore Keck et al. (1975) concluded that Mercenaria at Delaware Bay spawned at a temperature of 25 to 27°C. The data therefore may indicate a reduction in spawning temperature from above 20°C at introduction, to 18 - 19°C in 1974 and 16°C at present. This may reflect differences in the methods used to determine minimum spawning temperature, but may also indicate physiological adaptation to a new climatic environment.

Larvae not only showed great weekly variation during the Summer months, but they also showed wide daily fluctuations during the 8 days survey at Town Quay. the survey showed great daily variation in larval abundance and the environmental parameters especially within the upper 2m layer. Horizontal dispersion and influx of larvae from surrounding water during daily tidal exchange probably had more effect than loss of larvae by predation and natural mortality. Therefore assessing changes in abundance of larvae during the 8 days and at various depths utilising the present daily sampling results is a difficult task. Nontheless some indication of overall trend in abundance and population growth of larvae could be concluded. Although all stages of larvae were present in the daily sampling, the maximum number were recorded on the 4th day reflecting perhaps a widespread spawning.

The straight hinge larvae dominated the catch, whereas the umbone larvae were the least abundant. Size tended to increase with depth reflecting the movement of larvae towards the bottom during the later developmental stages.

The average numerical density calculated from the overall abundance of each stage and plotted against the average size of each larval stage (Fig. 5.9) showed that a dramatic decline in number occurred as larvae increase in size.

The daily changes of chlorophyll "a" was among environmental parameters that gave the highest correlation especially with abundance of the straight hinge larvae. Although this can be interpreted as that chlorophyll "a" levels affect the larval population, it is possible that such factor may have co-varied with other unmeasured parameters which had a more important effect on larval densities. On the other hand, no apparent relationship was found between larval density and water temperature, probably because temperature changed only by a few degrees during the study period.

During the daily survey, representative samples of larvae (90 individuals) were removed for length and height measurements. The results showed that there was significant variation in length of larvae in the daily samples, and the length tended to increase with depth. However, a dominance of 120 - 130μm modal class in the daily catch was clear. Nevertheless, the decrease in the frequency of remaining size groups indicated that larvae migrated towards the bottom layer as they grow older, or dispersed to other areas.

The dominance of the 120 - 130μm size group could be interpreted in two ways. Firstly, that larvae showed a low rate of growth or secondly that larvae were continuously produced as a result of continuous Mercenaria spawning. The former interpretation seems unrealistic and can be rejected because laboratory-spawned larvae showed daily growth. Therefore the assumption that there was a daily

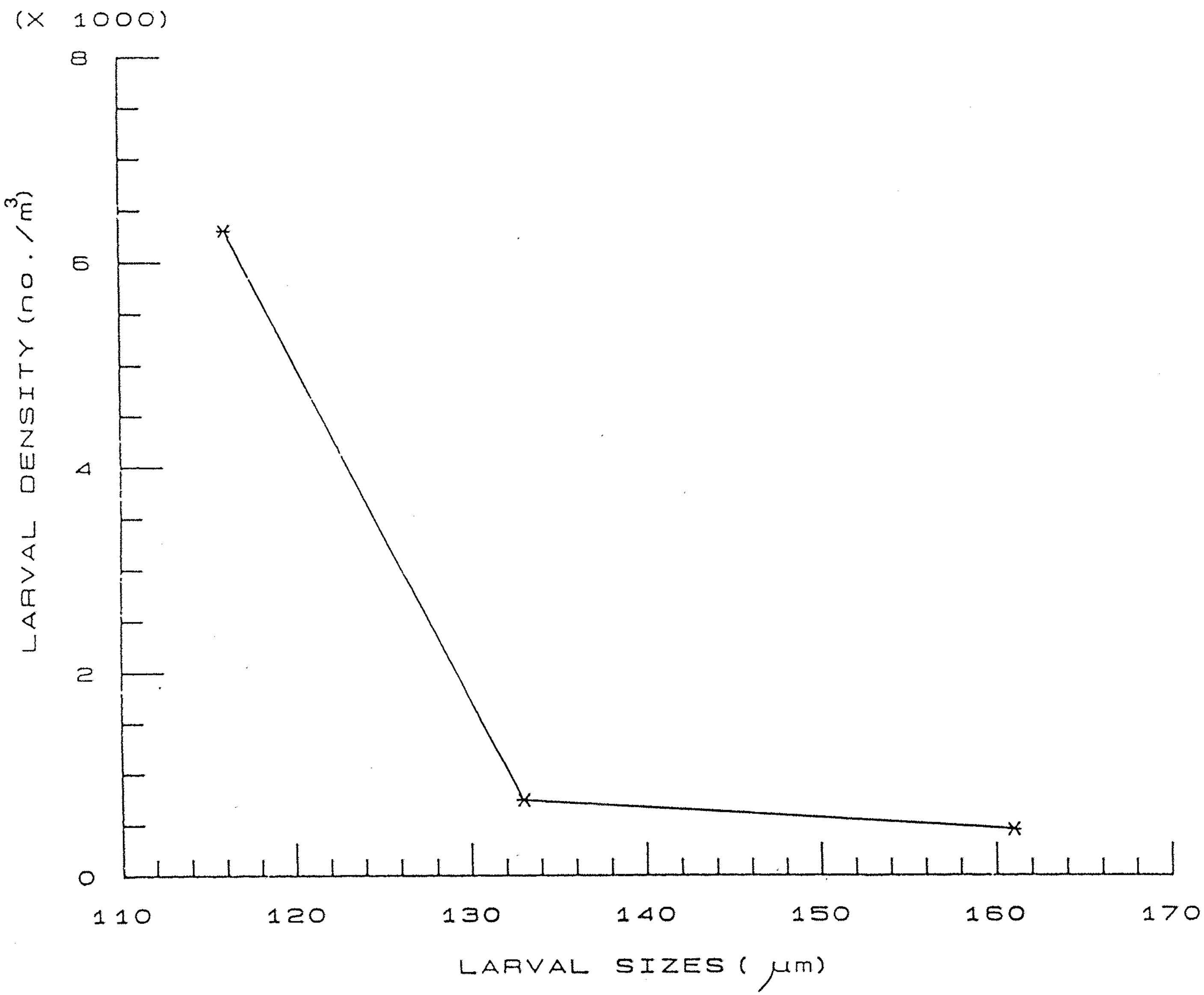


Fig. 5.9 Survival of different larval stages estimated from daily changes in mean number of larvae per m^3 during 17 to 24 July 1984 at Town Quay

progressive increase in length frequency of different size groups could be used to estimate an approximate growth of larvae in the field. Larvae in general grew to 172µm within 8 days which is slightly lower than the results of Carriker (1961), who noted that larvae reached 185µ after 8 days.

The period of pelagic development of Mercenaria is known from laboratory studies to range from 7 to 24 days depending on the water temperature (18 - 30°C) (Loosanoff et al., 1951). Extrapolation based on the field and laboratory data, indicated that larvae grew to a settling size of 200µm in 15 to 20 days at a temperature in the field of (18.6 to 20.4°C).

The general survey showed that larvae were widely distributed in Southampton Water. The maximum number of different stages during ebb and flood tides were recorded around the middle part of the estuary where the lowest current speed was recorded. It is possible that such a distributional pattern occurred as a result of concentration of Mercenaria in those areas. On the other hand, larval densities decreased in a seaward direction. Towards the mouth of the estuary salinity increases and chlorophyll decreases. The apparent decrease in larval densities might be related to the distribution of adult Mercenaria over a large area. In addition the strong current action in the lower parts of Southampton Water would lead to the dispersal of larvae horizontally and loss from the estuary. In general, occurrence of large numbers of larvae in the upper part of the estuary during low water suggests that larvae are able to maintain their position within the estuary by behaviour regulation of vertical distribution during ebbing and flooding tides. A survey was carried out during spring tide on 4th July 1985 in order to investigate changes in the larval population during a 12 hours tidal cycle. In addition, some environmental parameters (salinity, current speed and direction) were concurrently recorded on the hour. The relative proportion of larvae at each depth and hour were plotted against contours of salinity during the same period. Such treatment was necessary in order to reduce wide variation of larval density caused by the tidal movement. The similarity between biological and physical parameters was striking. Concentration of larvae, salinity and current speed followed the tidal curve. Larvae do not cross contours of low salinity and tend to concentrate in areas of high salinity. However, all levels of relative proportion of larvae showed gradual upward movement during flooding tide until the second high water after which rapid downward movement occurred. This coincided with maximum current speed in the down stream direction which indicated an influx of low salinity water. Such behaviour of larvae is necessary in order to maintain their position within the estuary, and avoid the fast ebbing tide (only 4 hours) in Southampton Water.

CHAPTER 6 : SPATFALL AND SETTLEMENT

6.1 INTRODUCTION

As maintenance of adult benthic population depends in part on the input of settling of larvae (Cameron, 1986), the study of density and distribution of post planktonic stages is therefore essential in understanding the population dynamics of a species.

Several works on spat settlement of *Mercenaria* in different habitats have been carried out. Carriker (1961) found abundant clam and oyster spat settlement at certain sites in New Jersey, with maximum settlement occurring on shell bars ($125m^{-2}$). Young clams were found to be concentrated around objects projecting from the bottom.

Several studies have investigated settlement in Southampton Water. Ansell and Lander (1967) concluded that *Mercenaria* probably has two major spawning periods, one in spring and the other in late summer. Ansell (ibid) suggested that successful settlement in Southampton Water resulted only from spawning in August and September, because earlier in the year temperature was assumed to be too low for larval development. Mitchell (1974) found larvae at settling size in the plankton as early as May and June. He attributed settlement success to conditions of river flow during summer months.

The present work is designed to study intensity and duration of settlement, distribution,growth and survival of young clams in Southampton Water.

6.2 MATERIALS AND METHODS

6.2.1 Sampling Sublittoral Spat

In January 1985 quantitative samples were collected from different parts of Southampton Water (Fig. 6.1) using a Baird grab ($0.5m^2$). The survey was repeated in August 1985 using a Van Veen grab ($0.1m^2$); 5 grab samples were collected at each site, and additional samples were collected whenever hard bottom substrates prevented successful grabbing. Following the appearance of a successful settlement of *Mercenaria* spat in October 1984 semi-quantitative samples from 6 sublittoral sites were collected at approximately monthly intervals from October 1984 to November 1985. Samples were collected using an oyster dredge 80cm wide with double mesh bags with the inner one having a 10mm mesh aperture. Two tows were made at each site parallel to the shore for 10 minutes at 1.5 knots. Additional samples were collected whenever animal numbers were low. The catch was sieved on board through a 1mm sieve. All *Mercenaria* spat and juveniles were picked from the sieve surface and taken to the laboratory for further measurement.

6.2.2 Sampling Littoral Spat

Earlier investigations (Rodhouse, 1973; Mitchell, 1974) reported that the use of traps was an inefficient way of sampling the settling larvae, therefore it was decided to adopt quantitative screening of the sediment despite the additional effort and time this required.

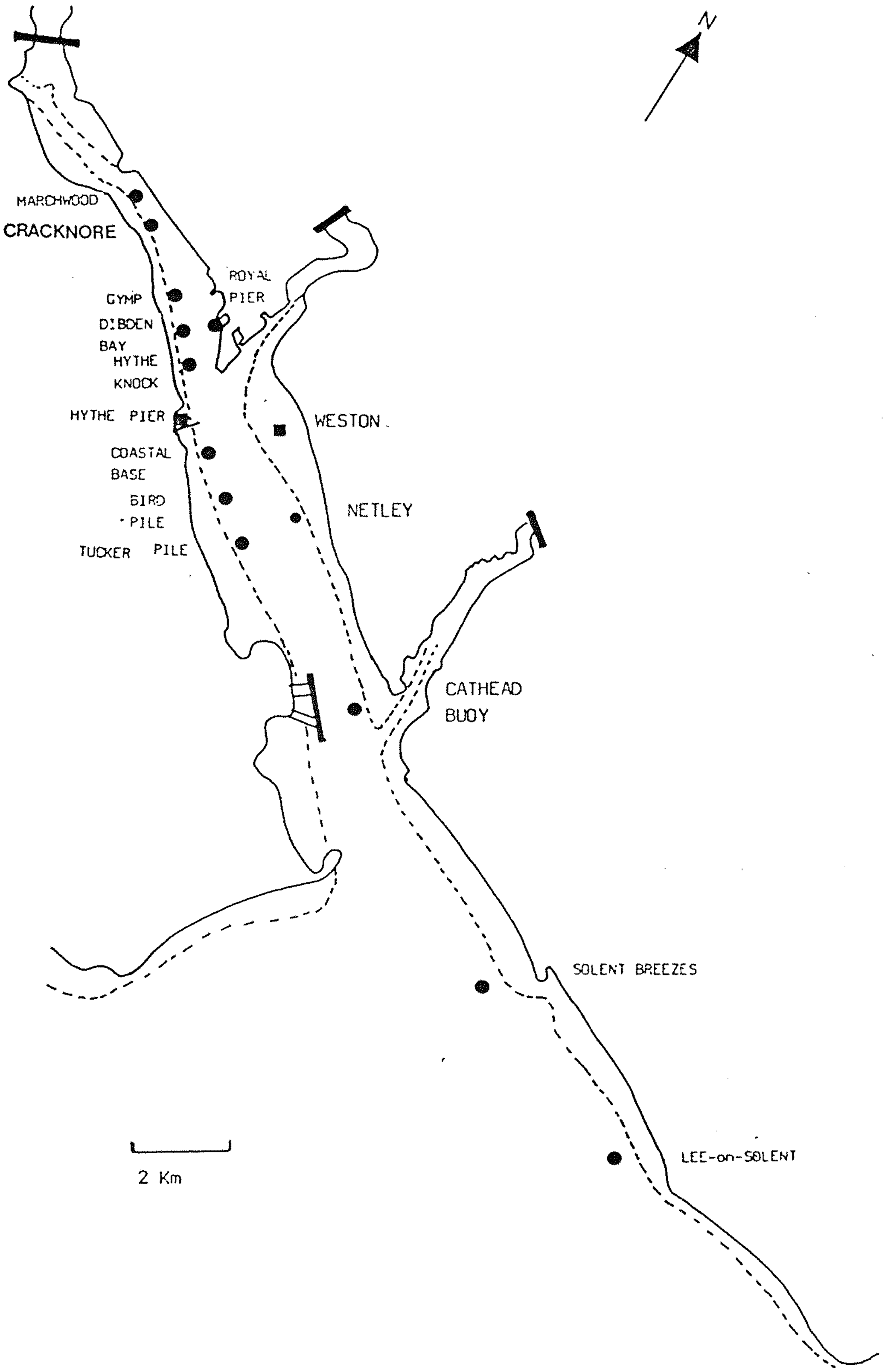


Fig. 6.1 Littoral and sublittoral spat sampling stations

Samples were collected intermittently from February 1984 to March 1986 from the mid-littoral areas at Marchwood, Royal Pier, Woolston, Netley, Hamble Spit and Lee-on-Solent (Fig. 6.1). At each site 10 to 15 samples of undistributed surface sediment was removed to a depth of 5cm using a quadrat ($0.032m^2$), and kept in polythyne bags. In the laboratory each sample was sieved through a 1mm sieve using aquarium water, and the material retained on the sieve examined under a stereo microscope. Any bivalve spat were recorded.

In this study spat is defined as all settled individuals measuring up to 30mm in shell length. Measurement of sediment temperatures were made on each sampling occasion.

6.3 RESULTS AND DISCUSSION

The abundance of Mercenaria spat in various sublittoral areas of Southampton Water for the period October 1984 to November 1985 is given in Tables 6.1 and 6.2. The results suggest that settlement showed temporal and spatial variations. More settlement was recorded in 1984 than 1985 at nearly all the sampling sites though results of the surveys are somewhat patchy. In 1984 Mercenaria spat was recorded at the beginning of October with the main settlement occurring on the western side of Southampton Water, extending below Hythe Pier up to Marchwood. Comparatively lower settlement occurred in other parts of the estuary.

Although there was a widespread settlement during 1984, the spatfall intensity however was relatively low compared to the settlement density of $125m^{-2}$ found by Carriker (1961) in Little Egg harbour

Table 6.1 : Density of sublittoral spat (mean no. m^{-2}) at different sites in Southampton Water in January and August 1985

Station	January 1985	August 1985
Marchwood Channel	12	N.S.
Military Jetty	10	0
Gymp	4	7.5
Dibden Bay	9.4	2.5
Hythe Knock	8.2	6.7
Netley Hard	10	N.S.
Netley Dome	0.7	N.S.

Table 6.2 : Monthly abundance of sublittoral spat (no. per dredge) at different sites in Southampton Water

Station	October 1984	July 1985	September 1985	October 1985	November 1985
Marchwood Channel	N.S.	3	N.S.	N.S.	N.S.
Military Jetty	N.S.	N.S.	N.S.	7	11
Royal Pier	1	N.S.	N.S.	N.S.	N.S.
Dibden Bay	94	7.7	2	2	3
Hythe Knock	N.S.	N.S.	N.S.	N.S.	N.S.
Coastal Base	3	N.S.	N.S.	N.S.	N.S.
Woolston	N.S.	1	1	N.S.	N.S.
Bird Pile	5	3.5	1	13	N.S.
Tucker Pile	4	3	3	5	N.S.
Cathead Buoy	2	N.S.	N.S.	N.S.	N.S.
Itchen Bridge	1	N.S.	N.S.	1	N.S.

N.S. = Not sampled

(New Jersey). Earlier investigations of the Mercenaria population in Southampton Water reported the occurrence of very limited spatfalls during 1969, 1970 and 1973 (Mitchell, 1974). Hibbert (1976) considered 1970 and 1971 as reasonably successful years where a large proportion of larvae reached settlement size.

Many factors have been suggested as important in controlling the settlement of bivalve larvae in estuaries. The most important of these factors are water temperature, food supply, salinity and flushing rate (Thorson, 1966) and these have been discussed in relation to Mercenaria by Mitchell (1974) who concluded that conditions of river flow during summer months together with reasonably high temperature and abundant food supply are essential for the successful settlement of Mercenaria.

In the present work the mean water temperature at the beginning of summer (May and June) was lower in 1983 than 1984 measuring 13.4 and 19.8°C respectively (Table 6.3). The phytoplankton bloom in Southampton Water may appear between May and July and either takes the form of a single peak, a series of peaks scattered over a longer period, or a more protracted bloom. Chlorophyll "a" values vary from about 1 - 2 μgl^{-1} in the winter months to 10 - 20 μgl^{-1} during summer and may exceed 40 μgl^{-1} at the peak of the bloom (Raymont and Carrie, 1964; Savage, 1965; de Souza, Lima and Williams, 1978).

Data on river flow, supplied by the Southern Water Authority, indicate that the mean river flow during the period August, September and October of 1984 was lower than that for the same period in 1983 (Fig. 6.2).

Table 6.3 : Temperature records in Southampton Water during summer months of 1983 and 1984

Year	June		July		August		September		October	
	Air	Water	Air	Water	Air	Water	Air	Water	Air	Water
1983	13.4	16.1	22.8	20.5	19.9	20.7	15.4	16.8	13.2	15.7
1984	19.8	18.8	21.3	19.8	20.7	20.2	-	-	-	-

Table 6.4 : Density (Mean no. m^{-2}) of spat during October 1984 at different littoral sites in Southampton Water

Site	Density
Marchwood	6.4
Hythe Pier	49
Weston Shore	9.6
Lee-on-Solent	9.6

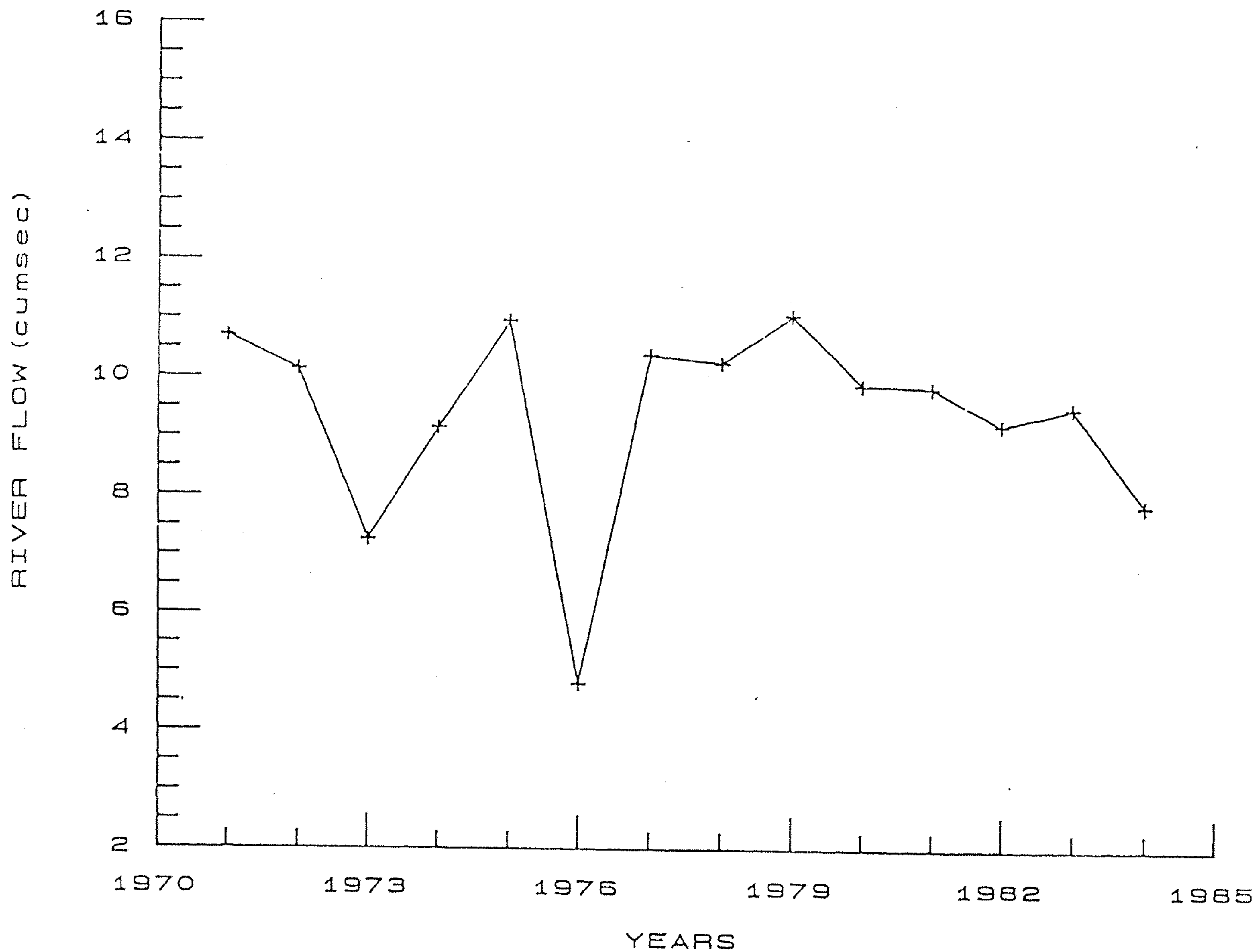


Fig. 6.2 Mean River Test flow (cumsec.) in August, September and October during 1969 - 1984

Therefore, it might well be that a combination of all these factor, low river flow and higher early summer temperature provided good conditions for settlement during the summer of 1984. Similarly, it was found that settlement occurred at several littoral sites in Southampton Water (Table 6.4) during the summer of 1984, but no littoral spat was found from summer 1983, as revealed from results of the survey in February 1984.

The occurrence of the main concentration of spat around Hythe Pier and Dibden Bay could be attributed to a number of factors. Hydrographical characteristics of the area, such as the presence of Langmuir circulation, may trap larvae, moving them towards deeper layers, and settlement achieved whenever a suitable substrate is encountered. In Langmiur circulation, water tend to move in vortices, creating 'micro-zones' of upwelling and downwelling water. This process has been suggested by Stavn (1971) as the main factor in concentrating plankton, especially under high-velocity upwelling current, where plankton move downward in order to avoid surface light.

The presence of a large number of cockles and tube worms, perhaps gives further evidence that the Hythe area is a good place for settlement. Alternatively settlement in the area can be explained using the result of Dyer's study (1982). He reported the presence of a water mass in the middle of Southampton Water that was comparatively less saline, with probably different chemical and biological characteristics and exhibiting gradual mixing as a result of up and down movement during the tidal cycle. Accordingly, it might well be that a similar patch of water occurs around the Hythe-Dibden Bay area, and contains larvae that are able to grow in favourable conditions of

Table 6.5 : Frequency distribution of size structure of sublittoral spat in monthly samples (October 1984 - November 1985) throughout Southampton Water

Size classes (mm)	October 84		January 85		July 85		August 85		September 85		October 85		November 85	
	No	%	No	%	No	%	No	%	No	%	No	%	No	%
3 - 5	-		-											
5 - 7	1	4	1	1.2			1	11.1						
7 - 9	22	21.8	21	25.3					1	14.3	3	8.3	3	14.3
9 - 11	41	40.6	26	31.3	5	13.5			1	14.3	3	8.3	3	14.3
11 - 13	26	25.7	21	25.3	2	5.4					2	5.6	1	4.8
13 - 15	6	5.9	12	14.5	5	32.4					2	5.6	2	9.5
15 - 17	2	2	2	2.4	9	24.3	1	11.1	2	28.6	3	8.3	2	9.5
17 - 19					3	8.1	2	22.2			4	11.1	6	28.6
19 - 21					3	8.1	4	44.4	1	14.3	4	11.1	1	4.8
21 - 23					2	5.4			1	14.3	7	19.4	2	9.5
23 - 25					1	2.7			1	14.3	2	5.6	1	4.8
25 - 27							1	11.1			2	5.6		
27 - 29											1	2.8		
Total Number	101		83		37		9		7		33		21	

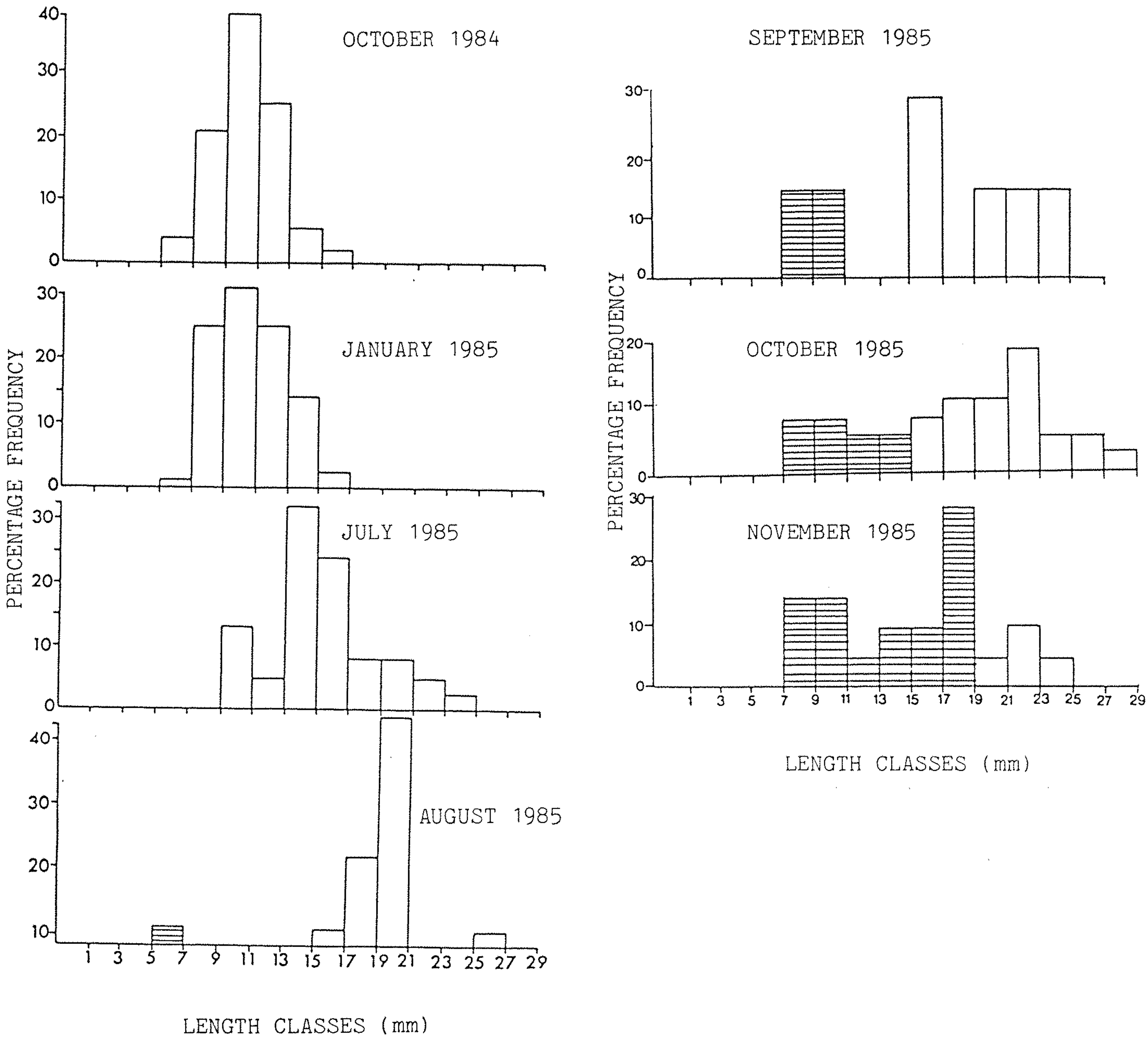


Fig. 6.3 Length frequency of *Mercenaria* spat from all Southampton Water, October 1984 to November 1985, hatched represent settlement in 1985

temperature and food, and can settle whenever a suitable substrate is located.

The size structure of all the spat collected at approximately monthly intervals during the period October 1984 to November 1985 from various sublittoral sites of Southampton Water are shown in Table 6.5 and Fig. 6.3.

From October 1984 to January 1985 most of the individuals were in the size group 9 - 11mm, whereas from January 1985 to October 1985 there was a sharp increase in the modal sizes from the 9 - 11 to the 21 - 23mm size groups. A new and smaller spatfall was evident in the August to November 1985 samples.

Growth of spat spawned in summer 1984 and summer 1985 was estimated by following changes in the mean length of each year classes through consecutive samples (Fig. 6.4). For the 1984 year class, there was a small increase in the mean length between October 1984 to January 1985, indicating a slow growth during this period, as a result of low temperature and scarcity of food. Maximum increment in shell length was found between January to July 1985 (Table 6.6) as a result of increasing temperature and availability of food during the seasonal phytoplankton bloom.

The low increment in shell length of the 1984 year class during September to November 1985 may indicate that spat had low growth efficiency despite the higher temperature and abundant food. The 1985 year class however showed an increase in shell length during September to November 1985 which could be interpreted as a mechanism to allow young spat to outgrow predators rapidly. <u>Carcinus maenus</u> is thought to be the main predator on Mercenaria spat less than 2 years old (Hibbert, 1976).

On the basis of the above measurement and assuming a uniform rate of growth from October 1984 to October 1985, an average daily growth in shell length of Mercenaria spat in Southampton Water amounts to 29 μm per day during the first 12 months. It follows that spat of a mean size of 10.40mm found in October 1984 if average growth were at the same rate, would have settled in mid to late August 1984. This prediction fits with observed patterns of the reproductive cycle and daily monitoring of larvae. Peak of spawning was recorded at the beginning of August, and larvae would have settled towards the end of August after 15 days in the plankton.

Monthly changes in the number of spat collected at Dibden Bay over one year are shown in Fig. 6.4 and were used for tentative estimation of mortality in the post planktonic stages under natural conditions.

A dramatic decline in the number of spat amounting to 92% occurred between October 1984 and July 1985 thereafter levelling off. Moreover, higher mortality is expected on post settlement stages at sizes 200μm to 5mm which the present sampling method is unable to detect. Carcinus maenus has been identified as the main predator of Mercenaria measuring up to 25mm (Walne and Dean, 1972) and on individuals aged less than 2 years (Hibbert, 1976), but other mortality factors may be involved in the decline.

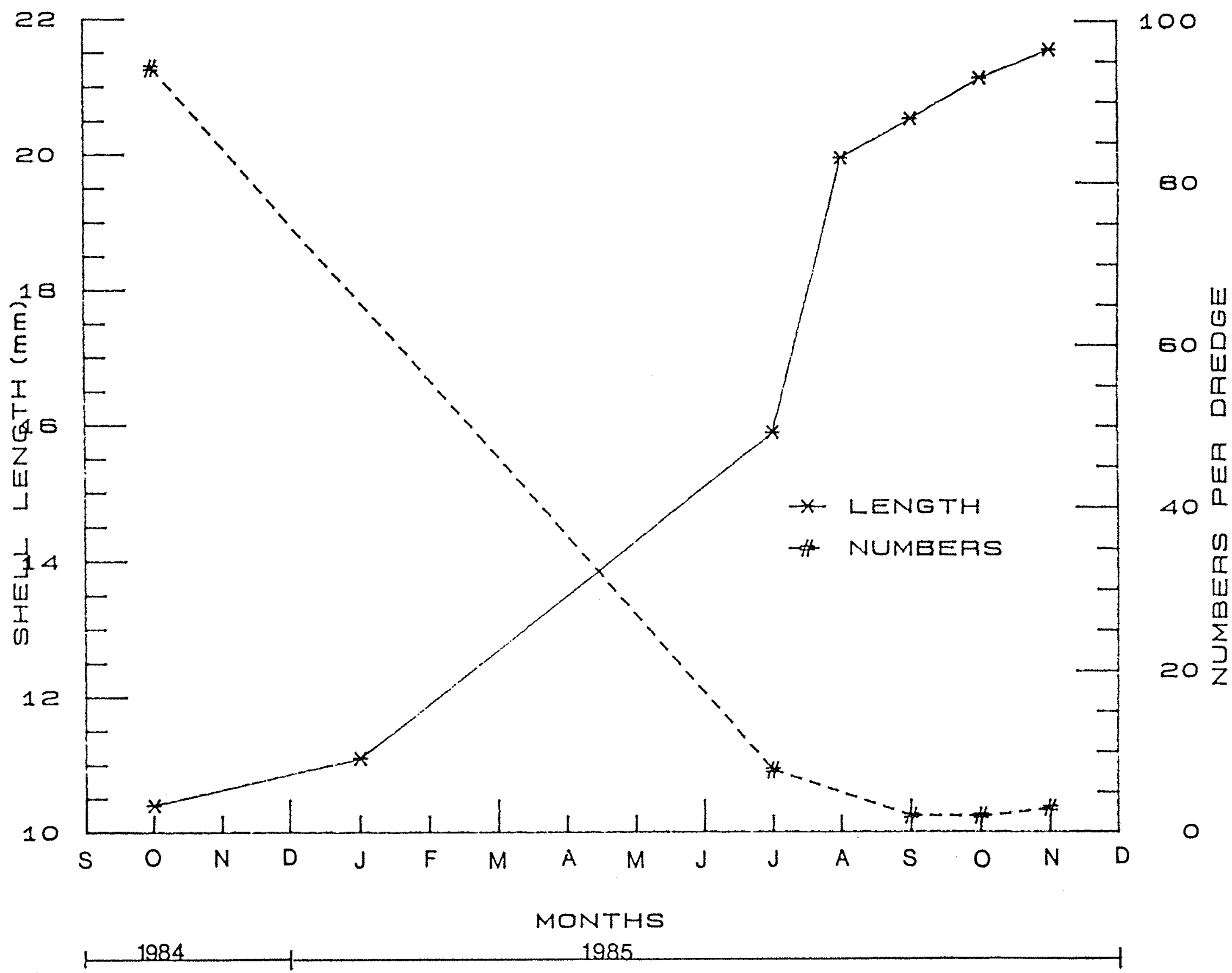


Fig. 6.4 Monthly growth in shell length of _Mercenaria_ spat spawned in summer 1984 with mortality of spat at Dibden Bay

Table 6.6 : Monthly increments in mean sizes (mm) of two year classes spat, 1984 and 1985 in all Southampton Water

	Months						
	October 1984	January 1985	July 1985	August 1985	September 1985	October 1985	November 1985
1984 year class	10.40	11.10	15.90	19.96	20.55	21.16	21.58
increments (mm)	-	0.70	4.80	4.06	0.59	0.61	0.42
1985 year class	-	-	-	6.50	9.90	10.95	13.39
increments (mm)	-	-	-	-	3.40	1.05	2.44

CHAPTER SEVEN : GENERAL DISCUSSION

The ecological study of the American hard shell clam Mercenaria mercenaria revealed interesting facts on different characteristics of the population (density, distribution, age structure, growth rates production, reproductive biology and the onset of sexual maturity). Also different aspects of the larval ecology including growth and mortality of post settlement stages were investigated.

Littoral sites on the eastern and western shores of Southampton Water and the sublittoral sites from the head to the mouth of the estuary have been sampled, showing the absence of Mercenaria from littoral sites above Marchwood power station and sites below Hythe Pier to Calshot Spit. The main occurrence of the clam was on the eastern side of Southampton Water from Northam Bridge in the Itchen river to the Lee-on-Solent at the seaward end of Southampton Water. However, in 1984 a few Mercenaria spat were found sublittorally at the Coastal Forces Base on the western side of Southampton Water. The absence of Mercenaria from the sublittoral sites south of the Coastal Forces Base to Fawley is most probably due to the industrial effluent discharged into the region (Levell, 1978). The occurrence of a few spat at the Coastal Forces Base might represent movement by tidal current from upstream sites.

Abundance of the animal at each sites, showed that littoral sites support a higher number of individuals than do the sublittoral sites. A growing and reproducing colony of Mercenaria seems to be established at the seaward end of Southampton Water, as evident from the large number of gametes in Mercenaria as well as the occurrence of spat at Lee-on-Solent.

The stock size of Mercenaria throughout Southampton Water, was estimated, following a standardised method of calculation. Densities and biomass of the clam reported in the earlier studies (Mitchell, 1974, Hibbert, 1976, Oyenekan, 1980) were used, in order to assess changes in Mercenaria stock size over the years. The littoral areas seem to support comparatively larger numbers of Mercenaria than do the sublittoral areas. Although some littoral sites, such as Weston, Netley and Hamble have shown an increase in stock since 1971 as a result of dominance of individuals spawned in 1971, 1972 and 1973, which are large and were until recently rejected by fishermen as being commercially unmarketable (Mitchell, 1974), but generally speaking the total littoral stock throughout Southampton Water has undergone a 75% and 47% reduction in total numbers and tonnage, respectively since 1971. The Ministry of Agriculture Food and Fisheries (MAFF) reported that between 1979 and 1985, the stock had been reduced to about 12% of the original stock of 1979, but these estimates did not include littoral populations where greater numbers occur (Barnes, 1973).

Although the different methods used in the estimation of the Mercenaria stock, may account in part for the discrepancy in the estimate of the stock between the present work and the MAFF study, nevertheless it might also demonstrate that the Mercenaria stock in littoral areas has not been reduced greatly in comparison to the sublittoral stock which is heavily fished. The number of fishing boats has increased from 10 in 1979 to 40 or more in 1983. Moreover, in recent years, an increase in numbers of boats using hydraulic dredges as opposed to the more traditional dredges has been found to have great impact on the benthic community (Sheader, 1986). A decline in numbers of dominant macrofaunal species, (especially *Mercenaria*) was found in areas of intensive dredging. Dredging might also be expected to have a deleterious effect, by burying spat and changing the nature of the bottom sediment rendering it unsuitable for settlement and growth. In addition to the fishing mortality, several works (Mackenzie, 1979; Bricelj and Malouf, 1980; Walker, 1985) have concluded that a characteristic feature of the clam fishery both here and in the USA is the irregular and infrequent recruitment to the adult stock. Although, the *Mercenaria* stock has been reduced in recent years throughout Southampton Water, dominance of large-sized individuals especially at some littoral sites can still make a substantial contribution to the total spawning potential of the fishery. Several works (Davis and Chanley, 1956; Ansell, 1967; Bricelj and Malouf, 1982) have showed gamete production increases with age and size.

Another effect of the dominance of old and large-sized individuals in the population, is that production was found to be lower than it was in 1971, 1976 and 1981 when the population contained a broad size range of individuals, especially small and young clams. Maximum growth rates in shell length and soft tissues occurs within the first 5 years with high production associated with populations containing large numbers of these rapidly growing individuals. An important implication for the present production tonnage is that it cannot sustain the fishery for a long period, because young individuals which are responsible for most of the production and the high $P/\bar{B}$ ratio, will not be productive as they age, leading therefore to collapse of the fishery in the near future, if successful settlements does not occur.

The age composition of the littoral population of *Mercenaria* in Southampton Water, showed dominance of individuals spawned in 1971, 1972 and 1973, with the year class 1976 dominating the population at Solent Breezes, Hillhead and Lee-on-Solent at the lower end of Southampton Water. There were records of successful settlement years, in earlier surveys. Mitchell (1974) found that 1959, 1961, 1965 and 1968 were the dominant year classes throughout Southampton Water. Hibbert (1976) reported that the year classes 1965, 1968 and 1970 dominated the population at Hamble Spit. Oyenekan (1980) concluded from *Mercenaria* results that no settlement took place in 1978 or in 1979. Irving (1983) reported that most of the *Mercenaria* she found resulted from settlement in 1974 and 1975. In the present study dominance of the year classes 1971, 1972, 1973 and 1976 cannot be explained by temperatures, because mean and maximum temperatures for August, September and October did not vary significantly between years. However, the dominance of the 1973 and 1976 year classes at Marchwood, Royal Pier, Solent Breezes, Hillhead, Lee-on-Solent and the recent settlement recorded in 1984, seem to coincide with times of low river flow during August - October of 1973 and 1976, respectively. The river flow in the summers of 1971 and 1972 was comparatively high suggesting therefore that the relationship between settlement and river flow is not a simple relationship, and other factors may be relevant, namely survival of the larvae in the plankton and their ability to regulate their position in order to avoid dispersal in a seaward direction by the ebb tide. All such factors must play an important role in the recruitment of new individuals to the adult population.

Three of the commonly used models, namely the Logistic, the Gompertz and the Monomolecular, were fitted to growth data of Mercenaria throughout Southampton Water. Mathematical description of the growth according to Preece (1978) has the advantages of reducing a large set of growth data into a few parameters which are interrelated and expressed by an equation, permitting easy comparison of growth of individuals between different sites. In addition, models provide a graphical illustration of the growth history of an animal. The growth seems to conform best to the Gompertz model, which showed the highest correlation coefficient as well as the highest coefficient of determination and the lowest standard error. The Gompertz model demonstrated that growth rates in terms of shell length vary widely between different sites and at differrent ages, with maximum growth rates in terms of shell length occurring during the second year throughout Southampton Water, with the exception of the population at Marchwood and Hythe Pier where maximum growth was achieved in the third year. The growth rates in shell length appear to depend on the locality within the estuary. High growth rates were found in the littoral population at Solent Breezes, Hamble Spit and Weston. Although these sites are characterised by different types of sediment, Mitchell (1974) concluded that there was no simple relationship between growth rates and sediment type, and suggested other factors, such as availability of food, temperature and salinity, might influence growth rates. In addition, Wildish (1985) demonstrated that growth and production in estuarine bivalves (e.g. Mytilus edulis and Mercenaria) are a function of the speed of the bottom current. In areas of strong currents, the animal has greater opportunity for continuous feeding. Such evidence might explain the high growth rates in shell length, tissue weight and shell morphometry found in Mercenaria at Solent Breezes. It has also been established in this study, and was suggested by Mitchell (1974) that the variation in growth at different sites seems to be related to the manner in which the food energy is utilised. At Marchwood where growth was relatively low, the gamete counts were higher than they were at Lee-on-Solent, which is characterised by higher growth. This indicates that at Marchwood a higher proportion of the food energy is directed to the production of gametes, whereas at Lee-on-Solent a greater proportion of the energy is directed towards somatic growth.

The relationship between shell growth and soft tissue growth was investigated on the Mercenaria population at Marchwood and Lee-on-Solent. It seems that Mercenaria directs a greater proportion of the available energy in the first 3 years towards shell formation, more so than it does in older stages. Moreover, the peak of shell growth in terms of shell length occurs two years earlier than the peak in tissue growth. This pattern of early investment in shell growth can be interpretted as advantageous in reducing mortality risks caused by several predators such as Carcinus maenus, wading birds and gulls which are the main predators on young Mercenaria in Southampton Water (Hibbert, 1976). An additional advantage of early shell development, is the avoidance of damage caused by the wave action and sediment abrasion especially on sandy shores, or muddy sandy shores with an admixture of shingle. Mitchell (1974) explained the fall in condition index in young individuals (less than 3 years) as an indication of the greater growth of the shell relative to growth of flesh. Rodhouse (1977) found that production of shell organics in the oyster (Ostrea edulis) is maximized after the first year and exceeds soft tissue production for a short time.

The production and biomass of Mercenaria at Marchwood and Lee-on-Solent, studied over one year revealed important facts on performance of the animal at both sites. The annual production and mean biomass and the calculated $P/\bar{B}$ ratio were similar at both sites amounting to 3 $gm^{-2}yr.^{-1}$, 30 gm^{-2} and 0.1 $yr.^{-1}$ respectively. The present estimates of production, biomass and the $P/\bar{B}$ are low in comparison to the earlier estimates for the littoral population at Hamble Spit (Hibbert, 1976) and for the sublittoral population (Oyenekan, 1980). The reduction in production is largely attributable to the lower density and to the change in the population structure since 1980, with the present dominance of large and old individuals. Mercenaria is a long-lived species and production per unit biomass declines with age. Such pattern of low production suggest that although Mercenaria might dominate biomass of the macrobenthic community, energetically the role of Mercenaria in the ecosystem has diminished in recent years, as a result of the prevalence of old and large individuals with lower growth rates, production and lower $P/\bar{B}$ in comparison to younger individuals. A characteristic feature of the populations sampled, was the lack of individuals less than 6 years old, the period during which maximum growth rates, production and $P/\bar{B}$ ratio would be at its highest. This therefore explains the lower production and $P/\bar{B}$ ratio recorded in the present study. An important implication of such results for the clam fishery, is that no fishing should be permitted for individuals younger than 6 years, in order to allow for maximum growth and production during those years. It can be added that if no recruitment occurs in the near future the few young individuals that presently occur, will show reduced rates of growth and production as well as a decreasing $P/\bar{B}$ ratio as they age, ultimately leading to collapse of the Mercenaria fishery and perhaps eventually loss of the population.

Based on the calculation of $P/\bar{B}$ ratio of 0.1 at the two extreme sites, Marchwood and Lee-on-Solent, it was possible to estimate production of Mercenaria throughout Southampton Water, using the biomass data. The estimated production varied between sites with the highest production recorded was at Netley and the lowest at Royal Pier. Gray (1981) concluded that low temperature, slow growth rates and high predation rates, are all factors which influence production and $P/\bar{B}$ ratio. In the present study, however, estimates of the production were largely determined by the numerical density of clams at each site. Difference in abundance of the animal, therefore might explain the low correlation between production and growth rates.

The condition index of Mercenaria population showed significant variation between sites, with the highest condition index occurring in the sublittoral population, probably as a result of continuous feeding and higher growth rates. However no clear pattern in condition index could be found with increase in size groups at a given site. The absence of a detectable trend is probably due to the lack of younger year classes in the samples.

It seems that within Southampton Water optimum growth conditions in the littoral Mercenaria population occurs at Solent Breezes in which the different morphometric characters mainly the shell length, width, height, breadth and curvature as well as flesh weight and condition index in relation to the age, were the highest in comparison to other parts of the estuary. Furthermore, the highest growth rates in terms of shell length was found at Solent Breezes, which is characterized by sandy sediments and greater degree of water movement than the sites up the estuary.

The study of the spawning in Mercenaria involved the development of a novel method based on gamete counting. The method is simple, rapid and avoids the inherent error that arise due to tissue dehydration and sectioning artefacts. In addition the method allows direct assessment of different phases of the reproductive cycle.

The gonad contained gametes throughout the year although there were seasonal changes in the gamete counts. However, based on the gamete counts, various stages of gonad maturation could be distinguished and were correlated with the seasonal changes in the tissue water content, ash, dry weight, calorific content, condition index and the major biochemical compounds reported in earlier works (Ansell, 1964a; Mitchell, 1974; Hibbert, 1976). In the female Mercenaria, gonad development starts in the spring (March - May) which correspond with the increase in condition index, high water content and increase in the major biochemical compounds (lipid, carbohydrates, proteins) probably resulting from increase in food intake during the spring phytoplankton bloom. The gonads reach maturity in June - July, which is associated with the peak in ash free dry weight and peak in the lipid content of the animal. The dramatic decline in the gamete counts in August, indicates spawning which coincides with the rapid decrease in lipids to about half of the original level at gonad maturation (Mitchell, 1974). In addition, there was a marked fall in ash free dry weight and a drop in condition index after spawning

(Mitchell, 1974). Similarly Ansell (1961) concluded that 50% of the total organic production in Mercenaria could be released as spawn. Gonad regeneration and a second spawning occurred in September. This would account for the second peak in the condition index and the increase in the calorific value reported by Ansell (1964a) and Hibbert (1976).

The seasonal changes in the male gonad development followed a similar pattern to the female gonad, with the exception of the marked reduction in the spermatozoa counts during August to October indicating continuous spawning. Regeneration of the male gonad occurred during the winter months.

The littoral population of Mercenaria in Southampton Water appear to have two major peaks of spawning at the end of summer and during autumn. Such a spawning pattern might indicate that Mercenaria does not discharge all of its gametes in one spawning but releases them over an extended period. Loosanoff (1937b) concluded that the reproductive cycle in Mercenaria is different from many other bivalves, because the major period of gonad development was in autumn. Further evidence was given by Keck et al. (unpublished report) who found that Mercenaria retains a comparatively higher proportion of glycogen and maintains a higher condition index even after summer spawning, whereas a spent oyster is generally in a poor condition and devoid of gametes. Keck (ibid) suggested that maintenance of a high condition index allows immediate gonad development. Spawning in Mercenaria probably resembles the biannual spawning pattern found in Mya arenaria where the first spawning is initiated as a result of the spring phytoplankton bloom and the second spawning occurs n response to the increase in temperature (Brousseau, 1978).

In *Mercenaria* the presence of a reduced breeding stock is unlikely to affect recruitment until numbers fall below a critical levels because gamete counts revealed that each individual contained very large number of potentially active gametes capable of successful fertilisation and larval production during the spawning season as evident from the induced spawning experiment. However, it is the quality of gametes rather than the quantity, have been found to affect survival and growth of the larvae to a great extent. Kraeuter *et al.* (1982) attributed the best larval growth and the highest survival of larvae to those hatching from large-sized eggs, with a greater amount and quality of stored food reserve.

The regular monitoring of *Mercenaria* larvae in the plankton not only served as a check on the breeding data recorded from the gamete counts, but also gave valuable information on the times of larval recruitment to the parent stock. *Mercenaria* larvae occurred in the plankton over a long period from May to October with a peak in August at all the sites studied, indicating that August was the main spawning month in 1983, despite the earlier smaller swarm which demonstrated that a localised spawning can occur whenever the critical spawning temperature is reached. However, the maximum production of larvae may vary between different years presumably depending on the temperature during the summer months.

The critical spawning temperature for *Mercenaria* seem to vary, ranging from 20°C up to 27°C depending on the geographical areas (Loosanoff, 1973; Loosanoff and Davies, 1950; Porter, 1964; Eversole *et al.* 1980). In Southampton Water Ansell (1961) spawned *Mercenaria* in the laboratory at 18°C, whereas Mitchell (1974) found that spawning was achieved when the temperature rose to 18°C - 19°C in the field. In the present study, gamete production and larvae occurred when the temperature rose to 16°C. This may therefore represent a reduction in the spawning temperature from 20°C at introduction around 1925 to 18 - 19°C in 1974 an to 16°C at present. Although this variation of temperature might reflect difference in the method used to determine the spawning temperature, it might also indicate a physiological adaptation to the local conditions, permitting spawning at a lower temperature.

The daily sampling of larvae was designed to provide the necessary data to determine the daily growth, survival and duration of the planktonic stage under natural conditions. The survey revealed great daily variation in larval abundance and the environmental parameters (temperature, salinity and chlorophyll "a") especially within the top 2m layer resulting from daily tidal movement. However, some indication of the overall trend in abundance and growth of the larval population can be concluded. There was variation in abundance, vertical distribution and growth between different larval stages. The straight hinge larval stage was predominant in the samples, but had the greatest mortality risks due to predation and dispersal. Numbers fell greatly at this stage. On the other hand, the umbone larvae were the least abundant stage in the plankton with a relatively low estimated mortality. There was significant changes in the length of larvae in the daily samples. Length tended to increase with depth indicating that larvae move towards the bottom during later stages of development.

The daily growth of larvae in the field was determined by following the daily changes in length frequency of the different size groups. During an 8 day period *Mercenaria* larvae grew from 162µm to 172µm at a temperature of 18.5°C - 20.5°C. Such a growth rate is comparatively lower than that reported by Carriker (1961) who found that *Mercenaria* larvae in the field grew to 185µm after 8 days. In the laboratory the larvae reached a size of 140µm in 14 days at 21°C. Similarly Loosanoff *et al.* (1951) reported that under controlled conditions, larvae of *Mercenaria* reached settlement in 14 days at 21°C and 16 days at 18°C. Ansell (1963a) on the other hand found that larvae from Southampton Water achieved settlement after 13 days at 19 - 21°C. Based on the average growth of the larval population in the field and from the laboratory data, and assuming a settling sized of 200µm, *Mercenaria* larvae, therefore remain in the plankton for about 15 days before settlements.

The general surveys of larvae in relation to environment parameters revealed that *Mercenaria* larvae were widely distributed in Southampton Water with maximum number of different stages during ebb and flood tides occurring around Hythe Pier, where the lowest current speed was recorded. In addition most of the settlement occurred around the Hythe Pier - Dibden Bay area. Such a distributional pattern could be attributed to a number of factors. For example the presence of Langmiur circulation that traps and concentrates the larvae in a descending water movement towards the bottom layer, would serve to concentrate larvae and increase the chances of settlement.

The occurrence of a large number of different larval stages during low water as well as location of most of the settlement in the upper part of Southampton Water, must indicate the ability of Mercenaria larvae to maintain their position within the estuary. The hourly sampling of larvae was carried out in order to investigate the vertical distribution of different stages of Mercenaria larvae and their correlation with the environmental factors over a 12-hour cycle during a spring tide. It seemed there was no depth preference among the different larval stages, because the early and late straight hinge larvae were numerous throughout the 12-hour sampling period and all stages occurred closer to the bottom layer in greater number towards the ebb tide. Moreover, the very few umbone stages were found predominantly during the flood and maximum ebb tide. The total number of larva at each depth revealed great variation during the tidal cycle, probably as a result of tidal advection. One way to overcome the effect of tidal advection was to monitor movement of the 'centre of gravity' of the larval vertical distribution during the sampling period. Although the 'centre of gravity' showed that larvae were concentrated in the middle and deeper layers, where salinity was high and did not change significantly over the period, movement of larvae however, seemed to follow hourly changes in the tidal height, salinity and current speed and direction. The upward movement of the larval population from flooding tide to the second high water water might indicate that larvae rise to the surface layer in order to exploit the upstream flow of seawater. Whereas the rapid downward movement of larvae during the ebb tide could be interpreted as a behavioural adaptation, avoiding the strong seaward current during low water as well as avoiding low surface salinity. This indicates that Mercenaria larvae show similar behaviour to many other invertebrate larvae in estuarine environments, where the water circulation is characterised by the net seaward flow in the surface layer and a landward flow in the bottom layer. In the literature there are several studies dealing with mechanism of retention of different larval groups of estuarine invertebrates. Wood and Hargis (1971) explained the marked differences between the behaviour of coal particles and oyster (Ostrea edulis) larvae in a tidal estuary as providing firm evidence that larvae have the potential to control their vertical position during the tidal cycle. Similar behaviour has also been demonstrated in barnacles larvae (Bousfield, 1955; de Wolf, 1974), and in decapod crustaceans (Cronin, 1979).

Andrews (1983) monitored settling of the oyster Crassostrea virginica in different tributaries in Chesapeake Bay over several years and concluded that estuaries can be classified broadly into 2 categories. The first category is the high-flushing type estuary (e.g. James River) with low to moderate settlement of larvae and a strong river flow, and a wide deep channel bordered by shallow flats. The second category is the trap-type estuary which is characterised by low river flow and the presence of numerous projecting points, and shallow flats. All such characteristics aid in retention of larvae within the estuary, resulting in high rates of settlement.

In Southampton Water, Westwood (1982) concluded that the short duration of the ebb tide (only 4 hours) results in faster currents and greater dispersal and flushing of pollutants and larvae in a seaward direction, than during the corresponding flood. Furthermore, Westwood (1982) added that Southampton Water is characterised by a reasonable degree of tidal flushing, and the tidal excursion during spring tide was estimated at 4.25km on the flood and

5.75km on the ebb. This indicates that unless Mercenaria larvae have the potential to regulate their position, larvae (or pollutants) at the middle part of the estuary at high water will be carried to areas beyond the estuary mouth during the following ebb tide, assuming uniform flow conditions.

One is tempted, given the hydrographical characteristics of Southampton Water and the predominance of a high river flow with the frequent failure and the sporadic nature of settlement, to conclude that Southampton Water approximates to the high-flushing type estuary described by Andrews (1982).

A general survey of spatfall throughout Southampton Water was carried out at monthly intervals from October 1984 to November 1985. The regular monitoring of spatfall permitted calculation of approximate growth and mortality of spat under natural conditions. Individuals spawned in summer 1984 little small growth in shell length over the winter presumably as a result of scarcity of food and low temperature. Maximum increment in shell length occurred in the period between winter and beginning of the following summer, mainly in response to increasing temperature and greater food availability as a result of the seasonal phytoplankton bloom. However, spat in their second summer showed small growth in comparison to growth in the first summer. Such a reduction in growth during the second summer might indicate a lower growth efficiency despite the higher temperature and the abundant food during summer. It was established earlier that maximum growth rate in shell length occurred during the second year, as predicted by the Gompertz model. Furthermore Hibbert (1976) concluded that temperature is a major factor in the growth of

Mercenaria at Hamble Spit, and maximum growth occurs during March - October. Other bivalves such as the cockle *Cerastoderma edule* showed delayed growth during their second summer, and this has been attributed to the commencement of gonad maturation (Seed and Brown, 1975).

The average daily growth rate in shell length of spat, calculated over 12 months approximated to 29µm per day assuming a uniform rate of growth. This means that spat which have a mean shell length of 10.4mm at the beginning of October 1984, if growth rate is uniform, resulted from settlement in mid to late August. This assertion seems to be in agreement with the observed pattern of the reproductive cycle and the daily monitoring of larvae. The peak of spawning was shown to occur at the beginning of August, and as duration of the planktonic life was also known to last for about 13 - 15 days it follows that peak larval settlement should occur towards the end of August.

In *Mercenaria* the spawning season lasts for several months, and during some if not all of this period, environmental factors that stimulate spawning of the animal and support survival, growth and settlement of larvae must exist. Although larvae are present in the water column for much of the spawning period; failure of spatfall and settlement seems to be the general case. In 1984 successful settlement occurred in August but the time of onset of spatfall might vary between summer months in different years.

The daily monitoring of larvae and the monthly sampling of spat revealed that mortality varies with size and stage. The calculated mortality was high in the planktonic stages (90 - 200 µm) amounting to 99% and 98%. There is also likely to be high post settlement mortality, in the size range 0.2 - 5mm, which the sampling methods used in the current study would be unable to detect. However, mortality, though . . . comparatively lower (about 92%) remained high among the settled spat as they grew from 5mm - 15mm.

Predation and dispersal play important roles in the survival of larvae. Raymont and Carrie (1964) reported that the peak in Pleurobrachia and Aurelia coincided with the major spawning of Mercenaria in Southampton Water. Zooplankton (e.g. Pleurobrachia pileus and Aurelia aurita) have been suggested to account for considerable reduction in the number of larvae (Mitchell, 1974). Hibbert (1976) considered that Carcinus maenus is the main predators of juvenile Mercenaria.

The study revealed various aspects of the biology and ecology of the Mercenaria population in Southampton Water. Mercenaria is a long-lived and hardy species tolerating a broad range of environmental variation. The population is capable of tolerating spat failure for many years and natural mortality is low among adult individuals (at an average age of 10 years). However, the hard clam population is heavily fished in Southampton Water and forms a valuable export. If properly managed, the animals could provide a useful renewable fishery resource in Southampton Water. Some suggestions for development of a management strategy to improve the clam fishery could include:

1. Restriction on the size and number of Mercenaria that fisherman can remove from each bed. No fishing should be permitted on individuals younger than 6 years and measuring 50-60 mm in length in order to

allow for a period of maximum growth and production and also to allow several years of spawning.

2. Improvement/changing the existing hydraulic dredging method which alters the nature of the substrate, probably reducing the chances for settlement, survival and growth of *Mercenaria* larvae. Additional research on the effects of hydraulic dredging would be useful.

3. Legal protection of the clam population between Marchwood and Hythe Pier where the largest concentration of *Mercenaria* larvae and spatfall were found. The area might serve as a source of larvae for various parts of the estuary.

4. Transferring adult *Mercenaria* individuals from Solent Breezes where optimum growth conditions were found to the Marchwood area during the breeding season in order to ensure retention of the larvae within Southampton Water.

5. A great possibility for increasing the clam population in Southampton Water is by development of a hatchery for production of larvae, a nursery for production of seed clams and a subsequent relay of the seed clams in the high growth areas of the estuary (e.g. Solent Breezes) until they reach a marketable size.

6. Survival of *Mercenaria* larvae in the plankton could be improved by controlling predators such as *Pleurobrachia pileus* and *Aurelia aurita* with chemical agents immediately before settlement of the clam larvae. This is likely to be impracticable.

7. Recruitment to the adult Mercenaria stock could be increased by controlling predators of clams spat and juveniles. The hard clam normally burrows in the sediment, and apart from several wading birds which are known to prey on the clams, majority of the predaters are mobile and live on surface of the bottom sediment. It is possible to remove those predaters from the bottom without disturbing the clams. Several methods of controlling predaters could be tried such as fencing an area, use of a chemical methods, and a mechanical method in which a dredge is specially designed to catch predaters only. In Southampton Water there are many conflicting uses of the estuarine environment, and the use of these methods would require careful consideration.

8. Removal of predaters once or twice during the post settlement period should lead to greater survival and abundance of clams spat.

9. Other factors that might limit settlement and survival of Mercenaria larvae should be identified, such as changes of the water quality especially during the summer breeding season.

APPENDIX

A computer programme written in basic language for the BBC model B computer is presented, to calculate the parameters and constants of the Logistic, the Gompertz and the Monomolecular equations according to the following steps:

- Load and run the programme "EMAN". The programme prompts you for number of growth rings and maximum number of animals.

- Input raw data on lengths of 1st rings of all the animals, followed by lengths of 2nd rings of all the animals and so on for the remaining growth rings. The programme then converts the original data into arrays of $L_{avg.}$ and $dL/(dt.L_{avg.})$, ln L_{avg} and dL/dt which are needed for each model.

- Store the converted data into separate files.

- Use any regression programme to carry out linear regression of L_{avg} on $dt/(dt.L_{avg})$ and ln $L_{avg.}$ on $dt/(dt.L_{avg})$ and L_{avg} on dL/dt.

- Load the "LOGIS" programme and input values of k (intercept), b (slope) and average length of the 1st growth ring. The programme then calculates predictive shell lengths using the Logistic model.

- Load "GOMPERT" and input values of k and b which are obtained from regression of ln L_{avg} on $dL/(dL/dt.L_{avg})$, as well as values of average length of each growth ring. The programme proceeds to calculate values of P at each growth ring then choose P values that are close to each other and calculate $P_{avg.}$ The programme then calculates predictive shell length at each age according to the Gompertz equation.

- For the Monomolecular model, input values of k and b which are obtained from regression of L_{avg} on dL/dt. Also input values of average length of each growth ring in order to calculate c value at each age after which c_{avg} is calculated. Then predictive shell lengths at each age are calculated according to the Monomolecular model.

The listings of the programme are given overleaf.

```
LOAD"EMAN"
  10 @%=&20309
  20 CLS
  30 REM Program developed for Phd Oceanography
  40 PROCinitials
  50 DIM DAT (N+1,T),ANS(N+1,T),AVE(N+1,T),LAV(N+1,T),Total (N), Average
     (N), Ans1(N+1,T)
  60 PROCdatainput
  70 PROCcalc_and_results
  80 PROCstore_data_1
  90 PROCstore_data_2
 100 PROCstore_data_3
 105 PROCstore_data_4
 110 PROCregress
 120 END
 130 REM-------------------------------------------------------------------
 140 DEFPROCinitials
 150 PRINTTAB(5,8)"Please input the required data.":PRINT:PRINT
 160 INPUTTAB(3,10)"Total length of growth = "N
 170 INPUTTAB(3,12)"Total time             = "T
 180 ENDPROC
 190
 200 REM-------------------------------------------------------------------
 210 DEFPROCdatainput
 220  FOR I=1 TO N
 230 Total (I)=0
 240 NEXT
 250 CLS
 260 INPUTTAB(5,4)"Do you wish to input the data from the keyboard
     (Y/N)?"ans$
 270 IF ans$="N" THEN 290
 280 GOTO 390
 290 FOR J=1 TO N
 300 FOR I=1 TO T
 310     READ DAT(J,I)
 320 Total (J)=Total (J)+DAT(J,I)
 330     NEXT
 340 Average(J)=Total(J)/T
 350   NEXT J
 360 DATA 2,3,4,5,6,5,5,7,8,10,0,9,12,13,0,0
 370 GOTO 470
 380 REM---Data from keyboard
 390 FOR J=1 TO N
 400 FOR I=1 TO T
 410 PRINT"Time = ";I;"  Length = ";"J
 420      PRINT:INPUT"Data = "DAT(J,I)
 430 Total (J)=Total (J)+DAT(J,I)
 440       NEXT I
 450    Average(J)=Total(J)/T
 460       NEXT J
 470 ENDPROC
 480 REM-------------------------------------------------------------------
 490 DEFPROCcalc_and_results
 495 CLS
 500 INPUTTAB(5,6)"Do you wish to view the results on screen (Y/N) ? "opt$
 510 L=0
```

```
520 FOR J=1 TO N
530 FOR I=1 TO T
540 IF DAT(J+1,I)=0 THEN 580
550     AVE(J,I)=(DAT(J+1,I)+DAT(J,I)/2
560 LAV(J,I)=LN(AVE(J,I))
570 L=L+1
580     NEXT I
590   NEXT J
600 FOR X=1 TO N-1
610 FOR Y=1 TO T
620      IF DAT(X+1,Y)=1 THEN 660
630     ANS(X,Y)=(DAT(X+1),Y)-DAT(X,Y))/(AVE(X,Y))
635 Ans1(X,Y)=(DAT(X+1,Y)-DAT(X,Y))
640 IF opt$="N" THEN 660
650 PRINT:PRINT"data";ANS(X,Y);TAB(16);"ave";AVE(X,Y);TAB(30);"LN(ave)"
:LAV(X,Y):ge(X)TAB(63);ave(C)"Average(X)
660     NEXT Y
670   NEXT X
680 ENDPROC
690 REM-------------------------------------------------------------
700 DEFPROCstore_data_1
710   PRINT:PRINT"Type in all the file names as required.":PRINT
712   PRINT"You are need to note all the file name as it will be used
in the later prog.
714 PRINT:INPUT"1) File name for ave vs data       : "F$
715 PRINT:INPUT"2) File name for LN(ave) vs data   : "R$
716 PRINT:INPUT"3) File name for ave vs DI/Dt      : "H$
718  PRINT:INPUT"4) File name for ave(c)            : "G$
760 Z=OPENOUT(F$)
770   PRINT£Z,L
780 FOR J=1 TO N-1
790 FOR I=1 TO T
800 IF ANS(J,I)=0 THEN 820
810  PRINT£Z,AVE(J,I),ANS(J,I)
820 NEXT I
830 NEXT J
840 CLOSE£Z
850 ENDPROC
860 REM-------SKIP TO REGRESS-------
870 DEFPROCregress
880 PRINT:PRINT:
890 PRINT" Do you wish to continue the program uing the REGRESS
program ? "
900 INPUT"(Y/N) "ans$
910 IF ans$="N" THEN ENDPROC
920 CLS:PRINT:PRINT:PRINT:PRINT:PRINT:PRINT
930 PRINT".......LOADING REGRESS......."
940 CHAIN"REGRES1"
950 ENDPROC
960 REM---------------STORE LEN DATA-----------
970 DEFPROCstore_data_2
1030 Z=OPENOUT(R$)
1040  PRINT£Z,L
1050 FOR J=1 TO N-1
1060 FOR I=1 TO T
1070 IF ANS(J,1)=0 THEN 1090
```

```
1080 PRINT£Z,LAV(J,I),ANS(J,I)
1090 NEXT I
1100 NEXT J
1110 CLOSE£Z
1120 ENDPROC
1130 REM-------------DATA FILE------------
1140 DEFPROCstore_data_3
1170 X=OPENOUT(G$)
1180 PRINT£X,N
1190 FOR I=1 TO N
1200 PRINT£X,Average(I)
1210 NEXT I
1220 CLOSE£X
1230 ENDPROC
1240 REM---------------
1250 DEFPROCstore_data_4
1310 Y=OPENOUT(H$)
1320 PRINT£Y,L
1330 FOR J=1 TO N-1
1340 FOR I=1 TO T
1350 IF Ans1(J,I)=0 THEN 1370
1360 PRINT£Y,AVE(J,I),Ans1(J,I)
1370 NEXT I
1380 NEXT J
1390 CLOSE£Y
1400 ENDPROC
```

```
 10 REM--LOGESTIC GROWTH MODEL-----
 20 CLS
 30  DIM Lt(20),DI(20)
 40  PRINT:PRINT"THIS PROGRAM IS TO CALCULATE THE VALUE OF THE
PREDICTED LENGTH":PR
 50 INPUT"The value of b (slope) = "b:PRINT
 60 INPUT"The value of k (intercept) = "k:PRINT
 70 Lmax=k/b
 80 INPUT"How many iteration ? "it
 90  PRINT:INPUT"Type in the value of initial size at age 1 = "LO
100   PRINT:INPUT"Do you wish to view the results on the screen ?
(Y/N) "ans$
110   FOR t=1 TO it
120        Lt(t)=Lmax*(1+EXP(-k*t)*((Lmax-LO))Δ-1
130 IF ans$="N" THEN 150
140 PRINT:PRINTt;TAB(20);Lt(t)
150 NEXT t
160 PRINT
170 INPUT"Do you wish to save the data ? (Y/N) "ans$
180 IF ans$="N" THEN 250
190 PRINT:INPUT"Type in the file name "R$
200 Z=OPENOUT (R$)
210 FOR I=1 TO it
220 PRINT£Z,Lt(I)
230 NEXT
240 CLOSE£Z
250 PRINT:INPUT"Do you wish to continue the program to calculate the
growth rate from Logistic model
```

```
260 IF ans$="N" THEN END
265 PRINT:INPUT"Do you wish to view the results on the screen ? (Y/N)
"ans$
270 FOR t=1 TO it
280 DI(t)=k*Lt(t)-b*(Lt(t)Δ2)
290 IF ans$="N" THEN 310
300 PRINT:PRINTt;TAB(20);DI(t)
310 NEXT
320 PRINT:INPUT"Do you wish to save the data ? (Y/N) "ans$
330 IF ans$="N" THEN END
340 PRINT:INPUT"Type in the file name "R1$
350 Z=OPENOUT (R1$)
360 FOR I=1 TO it
370  PRINT£Z,D1(I)
380 NEXT
390 CLOSE£Z
```

```
LOAD"GOMPERT"
  10 REM-----GOMPERTZ GROWTH MODEL----
  20 @%=&20309
  30 CLS: DIM Average(20)
  40  DIM P(20),Lt(20),E1(20),D1(20),C(20)
  50 PRINT''''''''''"THIS PROGRAM IS TO CALCULATE THE VALUE OF GOMPERTZ
GROWTH MODEL
  60 PRINT:PRINT:INPUT"The value of k (slope) = "k
  70 PRINT:INPUT"The value of c (intercept) = "c
  80 Lmax=EXP(c/k)
  90 PRINT:PRINT:INPUT"Type in the file name from which the value of
Laverage
 100 Y=OPENIN(G$)
 110 INPUT£Y,N
 130 FOR I=1 TO N
 140 INPUT£Y,Average(I)
 160 NEXT I
 170 CLOSE£Y
 175 F=0
 180 Total=0
 190 FOR t=1 TO N
 200 P(t)=-LN(Average(t)/Lmax))*EXP(k*t)
 210      PRINT' "P"(";t;")";TAB(10);P(t)
 212 INPUT"Included ? (Y/N) "ans$
 214 IF ans$="N" THEN 230
 220 Total=Total+P(t)
 225 F=F+1
 230 NEXT t
 240    Paverage=Total/F
 245 PRINT''"Paverage = ";Paverage
 250  FOR t=1 TO N
 260    E1 (t) =-Paverage*EXP(-k*t)
 270      Lt(t) =Lmax*EXP(E1(t)
 280   PRINT'"Lt = ";Lt(t)
 290 NEXT
 300 PRINT'''"Do you wih to continue the program to calculate growth
rate using Gompertz
 310 INPUT"(Y/N) "ans$
```

```
320 IF ans$="N" THEN END
330 FOR I=1 TO N
340 D1(I)=(k*Lt(I)*LN(Lmax))-(k*Lt(I)*LN(Lt(I))
350 PRINT:PRINTI;"  Growth Rate = ";D1(I)
360 NEXT
370 PRINT:INPUT"Do you wish to calculate the predicted length uing
the monomolecular
380 IF ans$="N" THEN END
400 PRINT:PRINT:INPUT"The value of k (slope) = "k
410 PRINT:INPUT"The value of c (intercept) = "c
420 Lmax=c/k
430 F=0
440 Total=0
450 FOR t=1 TO N
460 C(t)=(Lmax-Lt(t)/(Lmax*EXP(-k*t))
470        PRINT'"C = ";C(t)
480   INPUT"Included ? (Y/N) "ans$
490   IF ans$="N" THEN 520
500      Total=Total+C(t)
510   F=F+1
520  NEXT t
525 PRINT"N" = "F;"  TOTAL = "Total
530    Caverage=Total/F
540 PRINT''"Caverage =;Caverage
550 FOR t=1 TO N
560   Lt(t)=Lmax*(1-Caverage*EXP(-k*t))
570 PRINT'"Lt = ";Lt(t)
580 NEXT t
```

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