UNIVERSITY OF SOUTHAMPTON

LIFE HISTORY BIOLOGY OF DEEP-SEA GAMMARIDEAN AMPHIPODS FROM THE ROCKALL TROUGH NE ATLANTIC

by

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ABSTRACT

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Gammaridean amphipods were examined from collections made during the Scottish Marine Biological Associations time-series sampling programme in the Rockall Trough, NE Atlantic. Twenty three samples were sorted, producing five thousand and thirty four specimens, representing eighty one species. Amphipods comprised 3.56% of the total fauna of the sample site. Multivariate analysis reveal all the samples come from one statistical population, and there was no significant change in composition over the length of sampling programme. There is a seasonal flux of phytodetrital material to the study region, representing a significant input of organic matter to the deep benthic community. Two of the more common species were examined to evaluate any effect of this deposition of phytodetritus on their life history biology. Reproductive studies revealed the ampeliscid *Ampelisca* sp nov to be a quasi-continuous breeder, with a seasonal increase in reproductive intensity. In contrast the lysianassid *Tryphosella biloba* is a seasonal breeder. Both species show a seasonal increase in juvenile recruitment during the summer, coincident with the influx of detrital material. Brood size and embryo diameter were positively correlated with female length for all species examined in this study. Brood sizes were smaller, and embryo diameters larger in deep-sea amphipods than those predicted for a shallow water amphipod of similar size. Studies of the amount and composition of gut contents for *Ampelisca* sp nov reveal it feeds on the phytodetrital flux. Morphological studies on the mandible of this species show it is adapted for a microphagous detritivore diet. The mandible of *T. biloba* reveals morphological adaptions for a scavenging and/or omnivorous diet. Gut content analysis for this species indicates it may supplement its diet with phytodetrital material. Phytodetritus seems to provide amphipods in this study with an energy source for vitellogenesis and/or a food resource for newly released juveniles. Experimental trap studies off the Bahamas attracted scavenging lysianassid amphipods to another important organic input to the deep-sea, macrophyte debris, this attraction was shown to be a feeding, rather than a shelter response.

This study is the first to report seasonality in the reproductive and feeding biology of deep-sea gammaridean Amphipoda. Amphipods form a significant portion of the deep-sea macro-invertebrate fauna, as such their feeding activities may have important structuring effects on the rest of the community.

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None of this would have been possible without the encouragement and support of my parents and this thesis is dedicated to them.

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CHAPTER ONE
GENERAL INTRODUCTION

1.1 HISTORY OF DEEP-SEA BIOLOGY

The voyage of *HMS Challenger* (1872-1876), famous for her collections of deep-sea fauna, is often considered to be the forerunner of modern oceanographic research. The voyage was, however, the climax of several decades of interest in marine biology. Much of the impetus for the expeditions came from biologists eager to discover living fossils, the patterns of distribution of marine animals, and the conditions and evolutionary implications of life in the deep-sea (Mills 1972). The possible origin of the study of deep-sea fauna may be the fortuitous discovery of a deep water basket star made in 1818 by John Ross (Mills 1983, Gage and Tyler 1991). The basket star was recovered from a sounding line in a water depth of more than 1.6 km during a search for the NW Passage. Later in the century, voyages made by the *Erebus* and *Terror* to the Southern Ocean (1839-1843) again discovered animals caught on their sounding lines in depths up to 1.8 km. Gage and Tyler (1991) refer to the descriptions of 'teeming animal life' made by the expedition commander Sir J C Ross and the naturalist J Hooker on these voyages. When Ross (1847) compared these animals with specimens collected on earlier Arctic expeditions, he suggested that the Polar faunas might be continuous with those on the floor of the deep-sea. Around this time another British marine biologist, Edward Forbes, was dredging the Aegean, an area now known to have a depauperate deep-water fauna. The results of his collections led Forbes (1844) to propose an 'azoic zone' below 0.6 km water depth, where he considered conditions were not suitable for life. This concept of a threshold for life was challenged by many scientists of the time, most notably Charles Wyville Thomson. Thomson visited M. Sars in Norway to examine the collections made from the depths of the Lofoten Fjord. These specimens, which included the 'living fossils' or stalked crinoids, stimulated Thomson to organize a cruise to explore deep waters. The first of these cruises was made on board *HMS Lightning* with the help of W B Carpenter, the Royal Society of London and the Royal Navy (Gage and Tyler 1991). The voyage of

the *Lightning* in 1868, between Scotland and the Faroes, was quickly followed by four cruises of the *HMS Porcupine* (1869-1870). The *Porcupine* explored regions to the west and south west of Ireland, between Scotland and the Faroes, off Spain and in the Mediterranean Sea (Mills 1972, Young 1994). The results of these cruises, together with the interest of the Navy in laying submarine cables, helped to stimulate organization of the circumnavigating voyage under taken by *HMS Challenger* between 1872 and 1876. The *Challenger* expedition laid the foundations for the study of deep-sea biology. The thirty four volumes of results, along with the works of Thomson (1878, 1880) and Murray (1885) remain a valuable source of information to this day. Following the voyage of the *Challenger* a period of international exploration of the deep-sea began (reviewed by Menzies *et al* 1973, Mills 1983 and Gage and Tyler 1991). This exploratory phase in the study of the deep fauna of the world's oceans culminated in the voyage of the *Galathea* between 1950 and 1952 (Sparck 1956). It was on these voyages that the ambition of many biologists to recover 'life from the greatest depths' was realized with the collection of animals from the Philippine Trench at 10.19 km depth. An excellent review of the early studies of deep-sea biology, from historical, political and economic viewpoints can be found in Mills (1983).

The early studies of deep-sea fauna suffered from sampling artifacts. For example, the *Challenger's* 'deep-water' samples often contained pelagic species or adventitious animals from shallow water (Mills 1972). The *Challenger* and other early expeditions used the Ball's (or Naturalists') dredge with tangles, or more commonly at greater depths a beam trawl (Thomson 1878). These samplers had large open mouths which resulted in winnowing problems (see Chapter Three for discussion of winnowing effects) and also meant they behaved as low efficiency plankton nets on their return to the surface. Beam trawls with their large mesh sizes would collect only the larger animals, with subsequent over-representation of taxa such as the Asteroidea, Echinoidea and Holothurioidea, and an under-estimate of the proportions of the small light-bodied taxa including Polychaeta, Isopoda, Tanaidacea and Amphipoda (Mills 1972). Such species' sampling problems were prevalent until the mid 1960's,

information on the deep-sea benthos coming from what Hessler *et al* (1978) and Thurston (1979), refer to as 'ponderous samplers' (corers, grabs, dredges and trawls). Hessler *et al* (1978) observe that "*..As a result our interpretation of deep-sea communities has tended to place great importance on a subset of the total fauna, that is, organisms that are small and cannot avoid capture*". The bias of such interpretations has come to light in recent years with the development of new and improved techniques allowing the sampling of organisms previously caught only rarely (Hessler *et al* 1978, Thurston 1979). One such technique, the use of baited traps and cameras (see Chapter Six for a more detailed discussion) has shown the existence of a large and mobile element in the deep-sea fauna (Thurston 1979). Another important development involved the design of more sophisticated nets and trawls, which improved the previous undersampling of small animals. The first modern study incorporating the systematic use of fine meshed samplers, such as the epibenthic sled based on the Woods Hole design (Hessler and Sanders 1967), was on the Gay Head-Bermuda transect, NW Atlantic Ocean (Sanders *et al.* 1965, Hessler and Sanders 1967). These studies have shown that bathyal and abyssal biomass is generally lower by several orders of magnitude than that of the continental shelf and upper slope. The number of species, however, is frequently high, resulting in a greater species diversity at these depths than in other shallower and more productive marine environments (Hessler and Sanders 1967, Thurston 1980, Rex 1983).

A large body of literature exists on the subject of high species diversity in the deep-sea and its possible causes. This work has been reviewed by Gage and Tyler (1991 pp. 201-228), and a full discussion is beyond the scope of this thesis. The main explanations of deep-sea species diversity have been based on ecological interactions within local communities (Stuart and Rex 1994). These include competition (Sanders 1968, Rex *et al* 1988), predation (Dayton and Hessler 1972), physical or biological disturbance (Smith 1986, Grassle 1989), or combinations of the aforementioned mediated by the pattern and rate of nutrient input (Rex 1983). Recent work has proposed that 'patchiness' is the major contributory factor to some of the most characteristic features of deep-benthic communities (Rice and Lambshead 1994).

Grassle and Maciolek (1992) and Grassle (1994) suggest that deep-sea diversity is maintained in part by microhabitat heterogeneity created by a combination of biogenic disturbance and food resources that are divided into patches of varying size. There is also recent evidence of the presence of global scale latitudinal patterns or gradients in deep-sea species diversity (Rex *et al* 1993, Lambshead *et al* 1994). Poore and Wilson (1993) and Poore *et al* (1994) observe that species diversity in mid-latitudes in the Southern Hemisphere is higher than at similar latitudes in the Northern Hemisphere. May (1993) points to the caution needed when extrapolating global estimates from single site studies, and also exactly what is being measured ie. evenness or species richness. Brey *et al* (1994) stress the importance of regional history (geology, oceanography, climatology) when trying to interpret global patterns of species diversity. Interestingly, some workers maintain that species diversity in areas of shallow water are as high as those of the deep-sea (for example Gray's (1993) work off the coast of Norway).

Another large topic of discussion in modern deep-sea biology is the concept of seasonality (reviewed by Tyler 1988). The earliest attempts to address the subject of temporal variation in the deep-sea were studies by George and Menzies (1967) and Schoener (1968). Despite not being designed to address the questions on reproductive biology, these and later studies (Sanders and Hessler 1969, Scheltema 1972) synthesized their data and concluded reproductive periodicity or seasonality was present in some species (Blake and Watling 1994). The validity of these conclusions were challenged by Rokop (1974 and 1977a and b), who designed a seasonal sampling programme in the San Diego Trough. In a five sample, one year study, Rokop showed evidence for seasonality in two of the eleven invertebrate species studied. In 1973 the Scottish Marine Biological Association (SMBA) began a long term deep-sea sampling programme in the Rockall Trough, NE Atlantic (Gage 1977, 1979, Gage *et al* 1980, Gage and Tyler 1991). A Permanent Bottom Station was established at a site close to that first sampled by *HMS Porcupine* (Thomson 1873), at 2900m in the southern Rockall Trough (see Chapter 2 for precise details of location). Regular sampling at this station, at approximately four monthly intervals, took place between June 1976 and

1983, and periodic sampling continues to date. As a result of this programme and the IOSDL 'Deep-Seas' programme, the soft bottom fauna of the NE Atlantic is one of the best documented for a deep-water region anywhere in the world (Tyler and Zibrowius 1992). The samples from the SMBA time series have stimulated much biological research (Mauchline *et al* 1986), especially of the Echinodermata and other megafauna. Work by Gage and Tyler from this time series has shown reproductive seasonality in a number of deep-sea benthic invertebrates in the Rockall Trough (see Gage and Tyler 1991 and references therein), a topic discussed further in Chapter Two.

1.2 CRUSTACEA IN THE DEEP-SEA.

Crustacea were found at depths exceeding 10 000m by the *Galathea* expedition (1950-52) and in terms of number of species constitute one of, if not the, most diverse major animal groups in the deep-sea (Dahl 1954). A dominant component of the deep-sea crustacean fauna is the Peracarida, a superorder of the class Malacostraca. Peracarid species diversity in the deep-sea can often exceed that found on comparable bottoms in shallower water. In many samples 32-51% of total fauna are peracarid crustaceans (Hessler and Wilson 1983). The present study addresses the ecology of a common peracaridean group, the subordinal gammaridean Amphipoda, collected as part of the SMBA sampling programme. Amphipods form a significant part of these SMBA catches. Although amphipods are commonly outnumbered by isopods at abyssal depths, they often have a higher species diversity (Hessler and Sanders 1967, Thurston 1979). Thurston and Bett (1993) report gammaridean diversity is greatest between 0-200m and declines rapidly with increasing depth. Gage and Tyler (1991) report that several authors show amphipods to be rare both at hadal depths and in oligotrophic basins in the Pacific. In contrast, Kamenskaya (1978) reported that the density of amphipods decreases with increasing depth in the bathyal and abyssal zone, but increases in the ultra-abyssal.

The use of baited traps and time-lapse cameras pioneered by Isaacs (1969), has shown the existence of an abundant mobile fauna comprising scavenging predators and

necrophages. In lower abyssal and hadal depths, amphipods are the dominant part of this fauna (Shulenberger and Hessler 1974, Isaacs and Schwartzlose 1975, Hessler *et al* 1978). Barnard and Ingram (1990) report large numbers of amphipods from East Pacific vents, the majority being lysianassids dominated by a single species (*Ventiella sulfuris*). Observations from the submersible *Alvin* (Kaartvedt *et al* 1994), have shown swarms of pardeliscid amphipods in association with mussels, clams and tubeworms in the East Pacific Rise vent field. These swarms are located above, and downstream of cracks emitting hydrothermal fluids (Kaartvedt *et al* 1994). Although this epibenthic fauna does play a significant role in the dynamics of deep benthic communities, research in this area has dominated deep-sea amphipod studies in much the same way research into hydrothermal vents has dominated over other deep-sea community studies.

1.3 AMPHIPODA

The Amphipoda are a diverse group of mainly free-living Crustacea. Amphipods are predominately marine but are well represented in fresh and brackish waters (Schmitz 1992). Marine amphipods occur from the driftline to abyssal depths. Amphipods are known to exploit a wide variety of habitats and include species that are epifaunal free living, infaunal burrowers, epi- and infaunal tube dwellers, pelagic and commensal forms (Nelson 1980). In studying the morphology of amphipods, Steele (1988) concludes that they are basically clinging animals whose primary form of locomotion is to swim forward short distances from the substratum surface. Their success may be a result of their ability to move into diverse habitats with little if any gross morphological change. As swimmers they can become pelagic; as clingers they can live on rock, algae, other animals or sea ice. Using pushing actions of the urosome they can burrow into soft sediments, assisted by flexion and extension of their pereopods which loosens and removes substratum particles. However, amphipods have not been particularly successful on land. This is probably concomitant with their poor walking ability and their respiratory system compared with the crustacean orders Isopoda and Decapoda. Amphipods having exposed branchiae versus the branchial chambers of decapods and

gills protected by pleopod operculum in the oniscoidean isopoda. Their complete embryonic development, with large eggs, limits their reproductive potential but adapts them for life at low temperatures (Steele and Steele 1975).

Amphipods were first recognized as an ordinal group in 1816 by Latreille, based on what are now known to be gammaridean features (Schmitz 1992).The Amphipoda were divided into three suborders, the Gammaridea, Caprellidea and Hyperiidea by Dana (1852). The distinct Ingolfiellidea with their cylindrical bodies and reduced appendages, were established fifty one years later by Hansen (1903). The amphipods and isopods had been considered as a single taxon, the Edriophthalmia, until their separation by Calman (1909) in his classification of Peracarida. This separation was reinforced by Siewing's (1951, 1956 and 1963) interpretations of differences in gut structures and developmental features. However, this separation has been recently challenged by Schram (1981, 1984 and 1986) who considers these features as shared derived characters and as such justify a return to the use of Edriophthalmia (Schmitz 1992). The amphipods are considered to have retained several primitive features (Schram 1986), excepting the uniqueness of three pairs of uropods (lacking in caprellids) and a compact buccal mass (Schram 1986, Schmitz 1992). These primitive features are described by Schram as follows *"...biramous antennules, tendency not to always elaborate coxal plates, prevalence of dicondylic thoracopodal coxa-basis joints, retention of gills on the thoracopods, antennal glands, complete midgut, thoracic circulatory system, complete cleavage of the eggs (to the sixteen cell stage), egg-nauplius stage, and the complete development occurring entirely within egg membranes, the hatchling emerging with a complete set of appendages.'* (Schram 1986, Schmitz 1992). These attempts at phyletic classifications (eg. Schram 1986) have left important phyletic problems unsolved, which has resulted in the alphabetical nature of recent major classification works (for example Barnard and Karaman 1991). A recent publication by Bousfield and Shih (1994) uses a new morphological-behavioural approach to attempt a phyletic classification of amphipods. A summary of these authors conclusions follows. The Amphipoda appear phyletically least remote from the Mysidacea, but more so from the Hemicaridea and the Isopoda. Within the

Amphipoda are two subordinal groups with extant members in both marine and freshwater habitats, the primitive/relict Ingolfiellidea, and the more advanced, dominant Gammaridea. There are two exclusively marine infraorders within the Gammaridea, the Hyperiidea and Caprellidea, which may have arisen from stegocephalid- and podocerid- like ancestors respectively. Bousfield and Shih have used old decapod classification terms to organize the infraorders and superfamilies within the gammaridea into two broad and semi-phyletic categories, Amphipoda Natantia and Amphipoda Reptantia. The Natantia includes reproductively free swimming groups, direct mating occurring in the water column, usually without amplexus. The male is typically has sexually specialized antennal organs (callynophore, calceoli and brush setae), and tail fan, possesses eyes but does not have specialized gnathopods. The male is smaller than the female and is a terminal life stage (non-moulting and often non-feeding). The Reptantia in contrast are mostly benthic or infaunal in all life stages, mating occurring on/in the bottom, with preamplexus (precopulatory grasping of the female and/or antagonistic behaviour toward other males). In the Reptantia the male is often the larger, with sexually specialized gnathopods but not markedly in sensory organs or tail fan, and is indeterminate in growth. Bousfield and Shih (1994) attribute any anomalies within this classification to delayed loss of plesiomorphic structures or to convergent morphology and behaviour in specialized forms.

This thesis concerns the subordinal gammaridean amphipods. Barnard and Karaman (1991) define the Gammaridea as follows, "*...lack a carapace having all but one or two of the thoracic segments freely visible; one thoracic segment carrying maxillipeds fused to head followed by seven visibly articulated thoracic segments, each bearing paired appendages, followed by six abdominal segments, the first three (pleon) bearing paired biramous pleopods, the remaining three (urosome) bearing paired biramous uropods; telson freely articulate though often immovable in primitive and majority of members; head with two pairs of antennae, first occasionally biramous; maxillipeds lacking exopodites; heart mainly thoracic; respiration thoracic with gills attached to coxae of segments 2-7; eyes sessile or rarely borne on unstalked cephalic*

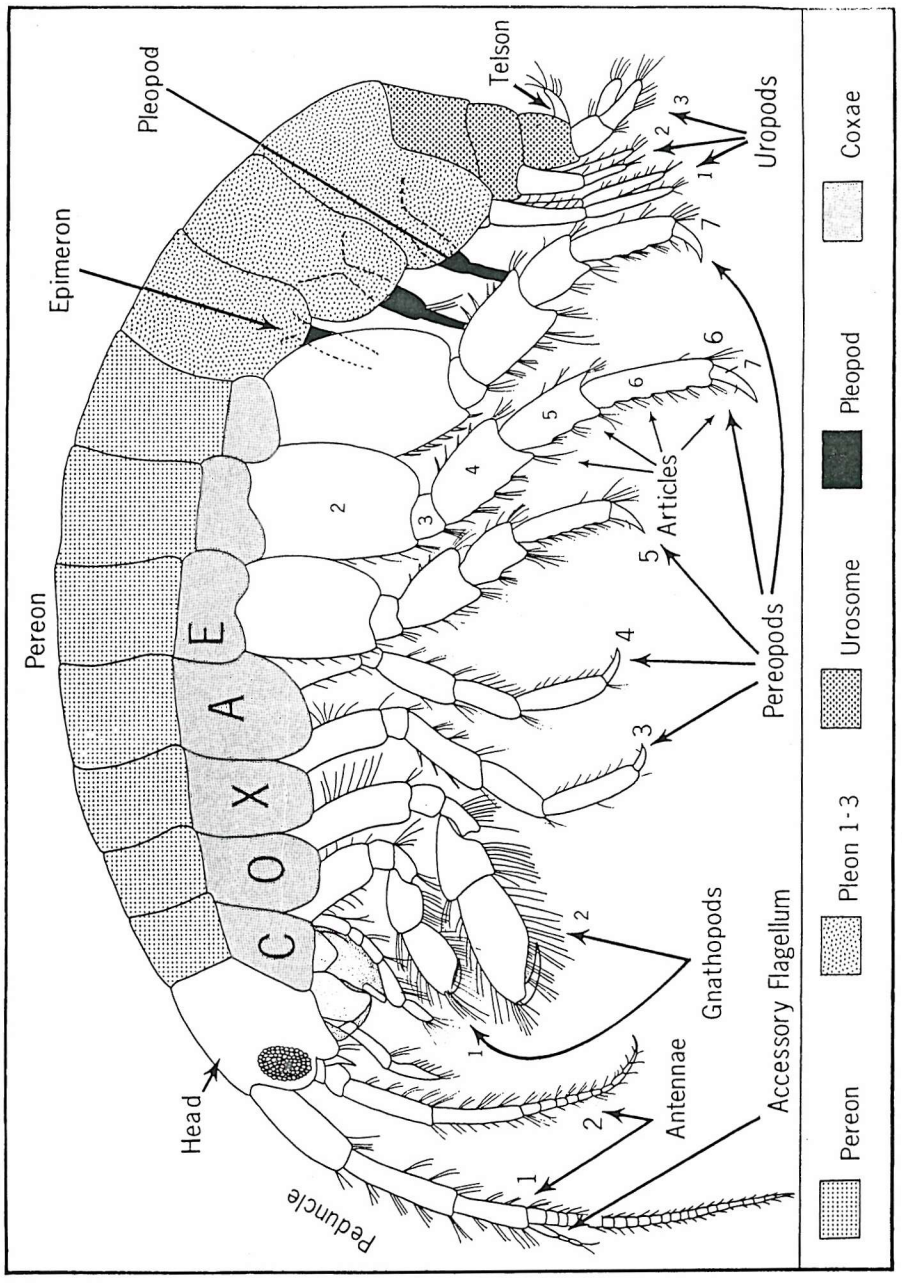
scale; eggs carried in female brood pouch on ventral thorax formed of two to four pairs of lamellae attached to coxae 2-6" (Figure 1).

The Gammaridea are primarily a cool-water group, in terms of their generic diversity, which may account in part for their strong penetration of the deep-sea. Their body sizes are strongly associated with thermal conditions in shallow waters, with larger species occurring in colder water. This does not apply to deep-sea benthic Amphipoda however, for there is a strong indication that body size decreases or remains static with increase of bottom depth, along a latitudinal line (Barnard 1962, Barnard and Karaman 1991).

The deep-sea is now recognised as an important part of the global carbon budget and the repository of a unique and diverse fauna. The summed benthic metabolism over the vast area of the deep ocean may be significant with respect to global-scale carbon equilibria between atmosphere, land, and the oceans (Gage 1992). It would also seem important to study the potential role of deep-sea fauna in redistributing elements naturally present, or added to, the abyss through the disposal of radioactive and other waste materials (Pentreath *et al* 1988. Gage and Tyler 1991, Hargrave *et al* 1992). Amphipods have long been known as sensitive environmental bioindicators through their ecological importance, numerical abundance and sensitivity to a variety of toxicants and pollutants (Hart and Fuller 1979, Thomas 1993, Conlan 1994).

In this thesis I describe the life history biology of the more common amphipod species collected from the Rockall Trough. Following the recent discovery that the deep benthic realm can no longer be considered as an environment lacking variation in physical and biological parameters, I also aim to describe any impact the seasonal input of phytodetritus to the study site may have on the ecology of these amphipods. The concept of seasonality in the deep-sea, a description of the study site and the method of sample collection is described in Chapter Two. The following chapter consists of a faunal analysis of the samples, an introduction to studies of deep-sea amphipods, and the taxonomy of selected species. Chapter Four concerns the population biology of *Ampelisca* sp nov and *Tryphosella biloba*, whilst Chapter Five describes their

FIGURE 1 BASIC GAMMARIDEAN



(from Barnard and Karaman 1991)

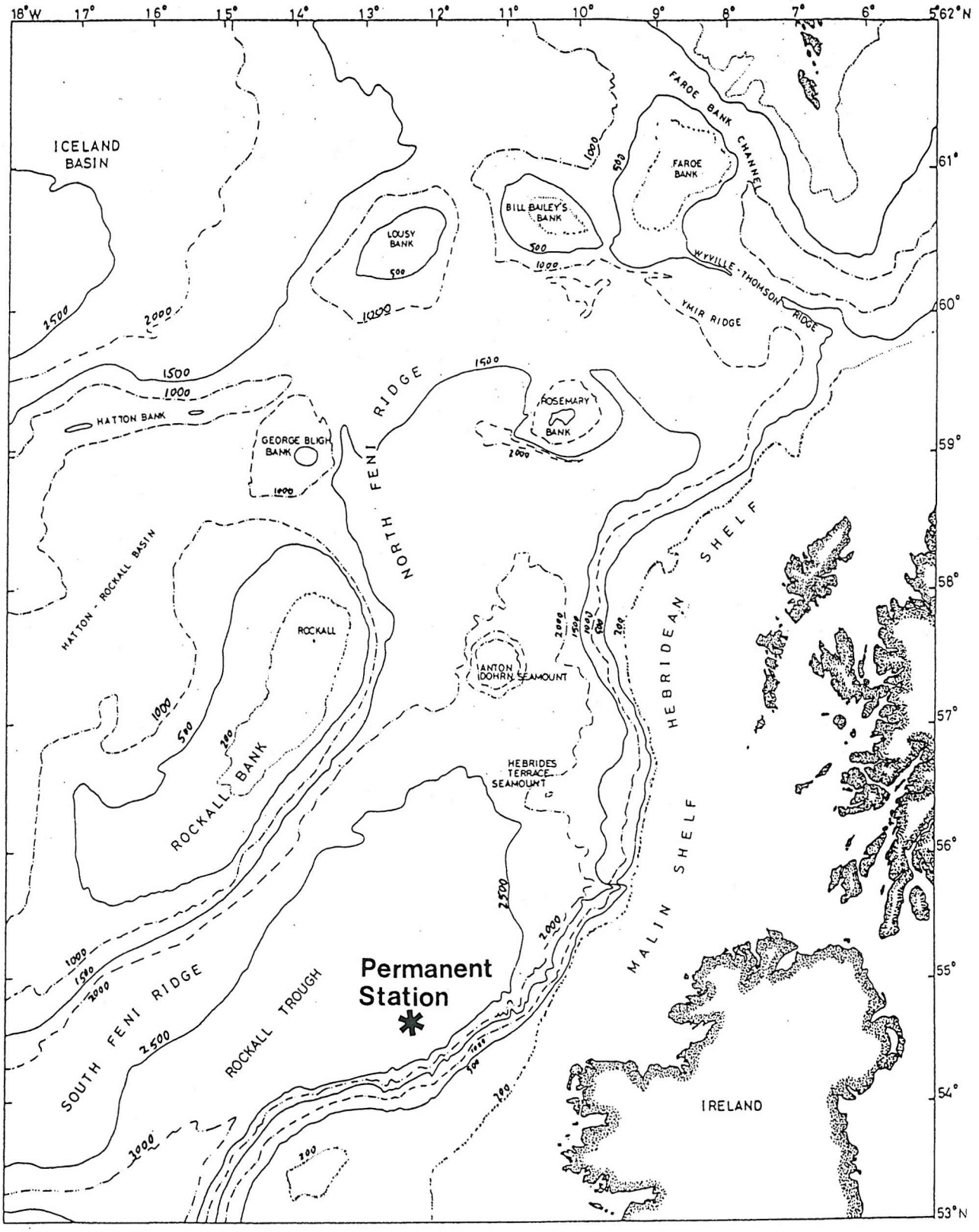
reproductive biology. The feeding biology of amphipods, together with experimental evidence for attraction to macrophyte detritus in bathyal amphipods from the Bahamas is discussed in Chapter Six. This is complemented by studies of gut contents and morphology of mouthparts in the Rockall Trough amphipods. The final chapter is a general discussion of the results and compares them to other known studies on deep-sea strategies and life histories. Here I also answer my question on whether seasonality in the deep-sea affects the life *history* biology of deep-sea amphipods in the Rockall Trough.

CHAPTER TWO
SAMPLE SITE AND SPECIMEN COLLECTION

2.1 MAIN STUDY AREA

The Rockall Trough is 250km in length extending from 53° to 60° N and 10° to 16° W (Figure 2.1). It has an axial depth ranging from 1000 m in the north to 3000 m at its southern end (Lonsdale and Hollister 1979, Scrutton 1986). The Trough was formed during the early Cretaceous period through rifting and seafloor spreading between Greenland and Europe. This was followed by partial sediment infill (Nayler and Shannen 1982, Billett 1988). To the north and northwest the Trough is closed by four banks rising to within 500 m of the surface, namely Rockall, George Bligh, Lousy and Bill Bailey's Banks. To the northeast, the Trough is bounded by the Wyville-Thomson Ridge and adjacent Faroe Bank. North of this ridge lies the deep water connection between the Norwegian Sea and Atlantic Ocean - the Faroe Bank Channel. Forming an eastern boundary are the Porcupine Bank, Malin and Hebridean Shelves. To the west runs the Feni Ridge, a broad sediment drift approximately 600 km long and 500 m thick, that has been forming since the Oligocene period (Roberts 1975). This growth is a result of sedimentation from the intermittent southward overflow of cold Norwegian Sea water across the Wyville-Thomson Ridge (Roberts 1975, Pain 1983).
Ellett and Martin (1973) and Ellett *et al* (1986) have used temperature and salinity variations with depth to describe five distinct water masses in the Rockall Trough. The upper waters, to a depth of 600m, are waters formed from the mixing of eastern N Atlantic water and Sub-polar Mode water flowing northeastwards from the south of the Trough. This mixing occurs in the Bay of Biscay area (McCartney and Talley 1982). High salinity, low oxygen content Gibraltar Water is found between 800m and 1200m, flowing northwards (Pain 1983). Below this (1200-2000m) is Labrador Sea water with its distinct salinity minimum and high oxygen content of 6.0 ml^{-1} (Lee and Ellett 1965, Harvey 1982). NE Atlantic Deep Water, which enters the Trough at high velocity (> 80cm sec^{-1}) between Wyville Thomson Ridge and Ymir Ridge,

FIGURE 2.1 STUDY AREA IN THE NE ATLANTIC



Isobaths in meters.

occurs between 2000 and 2500 m (Roberts 1975). The deepest waters consist of a dense, high silica content layer below 2500 m. This water mass has a probable origin in southern Antarctic waters (Lonsdale and Hollister 1979).

Lonsdale and Hollister (1979) describe a thin (500 m), narrow (10 km), intense current entering the Rockall Trough along the NW margin of the Porcupine Bank. This current follows a loop in the Trough flowing along its southeastern margin, before crossing as a broader slower current to the northwest margin (Pain 1983). This current then leaves the Trough in a southwesterly direction along the Feni Ridge and lower slopes of the Rockall Bank. As the current leaves the Trough it is supplemented by Norwegian Sea Water that has entered over the Wyville-Thomson Ridge and flowed south between the Rockall Bank and Anton Dohrn Seamount (Roberts *et al* 1973). Studies by the SMBA Marine Physics Group at the base of the Hebridean Slope have shown oscillatory tidal currents varying in period from semi-diurnal to diurnal (Booth 1982). Seasonal fluctuations of surface generated kinetic energy (maximum late winter, minimum late summer), have also been observed in the Trough (Dickson *et al* 1982).

The main part of this study is based on samples collected from the Permanent Station, 54° 40' N and 12° 17.5' W, 2900m depth in the Rockall Trough (Figure 2.1). There have been no direct current measurements at the study site but photographs of sediment bedforms suggest diurnal tidal bottom currents between 12 and 15 $cm.s^{-1}$. Also apparent from these photographs is evidence of current smoothing and occasional ripples (Lonsdale and Hollister 1979). The temperature of the bottom water in the Rockall Trough ranges from 2.95 to 3.16°C, and salinity from 34.94 to 34.97 ppt. Dissolved oxygen content is approximately 6 ml l^{-1} (Ellett and Martin 1973). Sediment samples from the permanent station consist of a surface layer of *Globigerina* ooze with a present deposition rate of 2-7 cm per thousand years (Roberts 1975). This is underlain by stiff 'greenish' coloured clay consisting of hemipelagic marls, calcareous oozes, silt and sand (Roberts and Kidd 1979). Analysis of samples show a carbonate ooze, with organic content of 0.47%, (Gage and Tyler 1980), calcium carbonate content of 48% (Gage *et al* 1980) and granulometric analysis of 27.4% by weight of

sand and 57.9% silt/clay (Gage and Tyler 1982).

2.2. SEASONALITY IN THE DEEP-SEA

In the past, both ecological and physio-chemical studies of the deep-sea have shown continuity and lack of variation in the water column and benthic environment below the permanent thermocline. Tyler (1988) reviewed the subject of seasonality in the deep-sea, examining evidence from isolated and time-series studies suggesting a predictable annual periodicity in some deep-sea processes. In his paper, Tyler presents evidence for seasonality in many areas/locations of the world's deep oceans. This seasonality is represented by variation in both physical parameters and the downward flux of detritus. The former can be predictable (seasonal variation in ocean currents, diurnal and semidiurnal tidal variation) and unpredictable (turbidity flows, benthic storms); whilst the latter can be seasonal, (an increase in the intensity of downward flux following increased surface production) or non-seasonal (large food falls, moults, turbidity currents). The following evidence of predictable variability is pertinent to the Rockall Trough area. Semi-diurnal tidal oscillations have been observed in the Rockall Trough (Lonsdale and Hollister 1979). Dickson *et al* (1982) reported a seasonal variation in ocean currents at abyssal depths in the northeastern Atlantic Ocean. In a more detailed study Dickson *et al* (1986) suggested four separate elements of the Trough's circulation pattern show a seasonal variation. These are: i. a summer-autumn maximum overflow of Norwegian Deep-Sea Water ii. an autumn minimum in the upper ocean circulation around the Rockall Bank iii. an autumn-winter maximum in the strength and breadth of the slope current along the European continental margin and iv. a winter-spring maximum in eddy kinetic energy in the open waters and over the full depth range of the Rockall Trough. Through the deployment of a long-term time-lapse camera and current meter in the NE Atlantic, it has proved possible to observe seasonal variations in the vertical flux of surface-derived organic material (Billett *et al* 1983, Lampitt 1985, Rice *et al* 1986 and Thiel *et al* 1991). These data are reviewed in Tyler (1988) and Rice *et al* (1991). From the photographic sequences it is apparent

that the material first arrives at the seabed late May/June, accumulates until late July, and disappears in mid-August. Tyler (1988 pp. 241) refers to the quantification of the data from Lampitt (1985), which seems to indicate substantial resuspension of this material in late July/August and it is no longer visible by mid-September. The seasonal component is recognisable owing to the rapid sinking of this material (Angel 1984, Fowler and Knauer 1986), as faecal pellets (Angel 1986), mucus aggregates/marine snow (Smetacek 1985) and occasionally intact diatoms and other phytoplankton species (Lampitt 1985).

Seasonality in the life-history biology of several invertebrate species has been demonstrated in the NE Atlantic (Tyler 1988). These conclusions came from a long-term study in the Rockall Trough by Tyler, Gage and colleagues, which by the late 1980's had examined mode of reproduction, gametogenesis and life-history biology in twenty nine species of echinoderms and two molluscs (Blake and Watling 1994). The majority of these species showed no evidence of seasonality, but eight species of echinoderms and two mollusc species did (Blake and Watling 1994). These results are more fully discussed in Tyler (1986), (1988) and Gage and Tyler (1991); and the species which exhibit seasonality are as follows : *Ledella pustulosa* and *Yoldiella jeffreysi* (Lightfoot *et al* 1979), *Echinus affinis* (Tyler and Gage 1984); *Ophiura ljungmani* (Tyler *et al* 1982, Tyler 1986); *Ophiocten gracilis* (Gage and Tyler 1981, Tyler and Gage 1982); *Plutonaster bifrons* (Tyler, Pain and Gage 1982, Tyler 1986); *E. alexandri* and *E. acutus* var. *norvegicus* (Tyler and Gage 1984; Gage, Tyler and Nichols 1986), and *Dytaster grandis* (Tyler *et al* 1990). Subsequent studies in the Rockall Trough have also shown evidence of seasonality in the anemone *Amphianthus inornata* (Bronsdon *et al* 1993), isopods (Harrison 1988b) and the cumacean *Leucon profundus* (Bishop and Shalla 1994). It has been suggested (Tyler 1986, 1988) that the seasonal pulse of sinking organic matter may be a selective pressure for larval survival, or an energy source for vitellogenesis. Giese and Pearse (1974) believe there is no firm evidence in the literature of food being a proximal cause in the initiation of gametogenesis and it is thought unlikely to provide a cue for the initiation of spawning. However several authors have reported close coupling between phytoplankton blooms

and gamete release for numerous species in different taxonomic groups (Thorson 1946, Himmelman 1975, 1981, Falk-Petersen 1982). Such a synchronization would mean abundant food resources for planktotrophic larvae, and reduced larval mortality from predation and other environmental factors (Starr *et al* 1990). How reproductive cycles are co-ordinated with environmental conditions is the subject of much speculation (Starr *et al* 1992). Photoperiod has been suggested for echinoderms (Pearse *et al* 1986), but in many invertebrates gonadal maturation is completed before spawning, suggesting an additional signal is required for stimulation of gamete release (Starr *et al* 1992). Physical factors, such as temperature, light, salinity and water movement have been proposed as potential spawning cues (Giese and Kanatani 1987). A lack of experimental studies mean most of these proposed cues are speculative (Starr *et al* 1992). Starr *et al* (1990, 1991), have identified the spring bloom of phytoplankton as a spawning cue, based on correlative and experimental evidence. These authors have shown compounds released by various phytoplankton species stimulate spawning in the mussel *Mytilus edulis* and the urchin *Strongylocentrotus droebachiensis* (Starr *et al* 1990). The release of nauplii in the barnacle *Semibalanus balanoides* is triggered by close contact with phytoplankton cells (Starr *et al* 1991). A substance extracted from the diatom *Phaeodactylum tricornutum* which shows some characteristics of phenolic compounds, has been shown to induce spawning in the urchin *S. droebachiensis* (Starr *et al* 1992). It should also be remembered that although a number of deep-sea species appear to show a degree of seasonality in their life histories, the predominant pattern in the deep-sea is continuous (Tyler 1986). The history of reproductive studies in the deep-sea and work from areas of the world's oceans other than the Rockall Trough are dealt with in the introduction to Chapter Five. The amount, nutritional quality and timing of a downward flux of detritus could be important factors in determining abundance, structure and activity of deep-sea benthos (Billett *et al* 1983). Indeed, Sibuet *et al* 1989, consider the flux of organic carbon to be the first order parameter that controls the biomass distribution in the deep Atlantic Ocean. However, Thurston *et al* (1994) report that carbon burial fluxes show little correlation with surface productivity estimates of Berger (1989). It seems that

fluxes are more dependent on depth, latitude and the physics of the overlying water column. The IOSDL DEEPSEAS programme was initiated to test just such an hypothesis (Rice *et al* 1994), using two main sites with contrasting winter mixed depths. The first site on the Porcupine Abyssal Plain (PAP) was predicted to receive a larger total organic supply than the Madeira Abyssal Plain (MAP) site, be more seasonal and to arrive in the form of aggregated phytodetritus. Preliminary results indicate only the third of these predictions holds true, but faunal differences between stations show a weak link between surface productivity and megafaunal abundance (Thurston *et al* 1994). Although data were inadequate to detect a similar relationship with biomass and surface productivity, biomass values at PAP were 16 - 39 times those at MAP and appear to be explained by the deposition of phytodetritus at the PAP site (Thurston *et al* 1994). The rapid settling of detrital material (Lampitt 1985) might represent a major nutrient input to the deep-sea community, being available for subsequent consumption by the biota (Gooday and Turley 1990, Billett 1991). Svavarsson *et al* (1993), consider it a common notion that deep-sea benthic communities consist primarily of deposit feeding animals, a view also held by Jumars and Gallagher (1982). These workers suggest that as many as 80% of the deep-sea macrofaunal taxa are deposit feeders. As the majority of species in this study are presumed to be benthic deposit feeders, this seasonal deposition of phytodetritus may have an impact on their biology, either through feeding and storage adaptions, or as an energy source for vitellogenesis or juvenile development. This theme is discussed further in Chapter Six. It is hoped that the investigations in this study may shed light on the role of amphipods in the utilization and cycling of organics in the deep-sea.

2.3 SAMPLE COLLECTION

All samples used in this study were collected by an epibenthic sled based on the design developed by the Woods Hole Oceanographic Institution (Hessler and Sanders 1967). This sled consists of a flattened mesh bag mounted in a metal frame that has wide runners to prevent it sinking into the sediment. The sled is designed to work either way

up. Sediment and fauna are collected in a nylon mesh net with a mouth opening of 81 x 30cm, a mesh size of 0.5mm or 1mm and between 1.2 to 2m long. The net extends to a cod end 1.3m behind the sled; an adaption to minimise washing on its return to the surface; and is protected by canvas aprons attached to the rear of the sled (Figure 2.2a). A spring-loaded gate fitted to the sled was used to reduce loss of fauna through the mouth by washing of sample on recovery, and to prevent contamination by pelagic fauna. This gate was closed prior to recovery by a pressure squib electronically activated by a precision timer (Gage *et al* 1982). To obtain a good sample on such a soft surface as encountered in the study area, the sled had to be configured so as not to cut too deeply into the

sediment. This was achieved by setting the hinged biting edges of the sled with leading edges parallel or slightly converging (Gage 1975). This also ensured better samples of the small sized fauna associated with the sediment water interface (Gage 1975, Gage and Tyler 1991). An attempt was made to standardize each haul to a one hour period on the bottom. Variation in actual bottom time is inevitable when the problems of surface currents, waves, bottom currents and ship speed are considered. Weather constraints and strong surface currents also meant a uniform towing direction could not be maintained (Gage and Tyler 1982). Sample numbers, collection dates, mean depth and location of each haul are listed in Table II.I.

Following collection, samples were sieved through a 420 μm sieve using the elutriation technique described by Sanders *et al* (1965). Portions of the muddy sample are placed in a dustbin modified with a spout (Figure 2.2b). A suspension is created with a large volume of filtered seawater, which then overflows onto the sieve. The research vessels non-toxic water supply was used to sieve the samples through a hose fitted with a 40 μm filter to remove plankton contaminants. The sieved residue was fixed in 4% formalin and seawater solution and buffered with borax to pH 7.5. Larger samples were sub-sampled to reduce sorting labour and to render them more easily comparable to the smaller hauls. This was achieved using an aerated sedimentation column fitted with a divided collector bucket (Gage 1982). On return to the SMBA laboratories samples were sorted into different taxa and preserved/stored in 90% ethanol.

FIGURE 2.2a EPIBENTHIC SLED

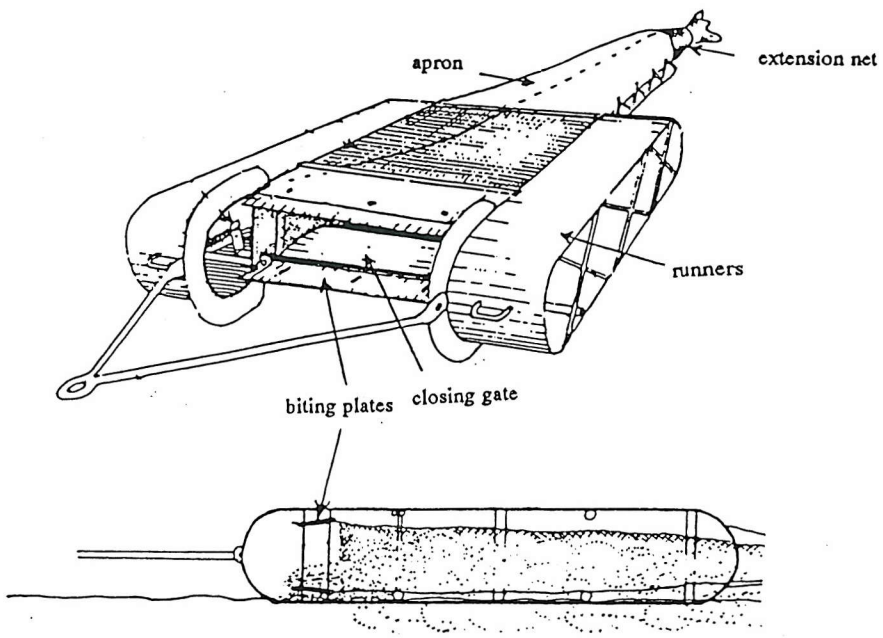
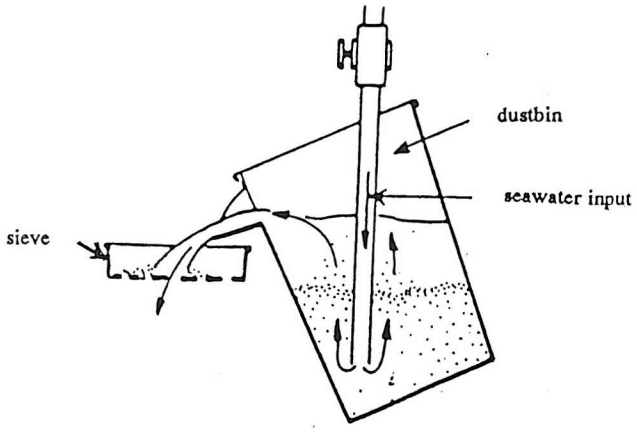


FIGURE 2.2b ELUTRIATION APPARATUS



(adapted from Gage and Tyler 1991)

TABLE II.I SAMPLE NUMBERS AND DETAILS

STATION NO.	DATE	POSITION		MEAN DEPTH m	FRACTION SORTED
		LATITUDE	LONGITUDE		
ES 2	4th JUN 1973	55° 04' N	12° 33' W	2857	WHOLE SAMPLE
ES 6	2nd JUL 1973	55° 03' N	12° 29' W	2900	WHOLE SAMPLE
ES 27	3rd NOV 1973	54° 40' N	12° 16' W	2900	EIGHTH
ES 55	17th NOV 1975	54° 40' N	12° 16' W	2878	WHOLE SAMPLE
ES 56	1st MAR 1976	54° 40' N	12° 16' W	2886	QUARTER
ES 59	21st JUN 1976	54° 40' N	12° 20' W	2900	EIGHTH
ES 111	22nd OCT 1976	54° 40' N	12° 16' W	2886	EIGHTH
ES 118	28th JAN 1977	54° 39' N	12° 14' W	2910	EIGHTH
ES 129	7th APR 1977	54° 39' N	12° 17' W	2900	EIGHTH
ES 135	7th AUG 1977	54° 39' N	12° 16' W	2900	EIGHTH
ES 137	22nd FEB 1978	54° 34' N	12° 19' W	2900	EIGHTH
ES 140	13th APR 1978	54° 40' N	12° 16' W	2912	WHOLE SAMPLE
ES 143	14th APR 1978	54° 41' N	12° 14' W	2892	WHOLE SAMPLE
ES 147	2nd JUN 1978	54° 46' N	12° 19' W	2921	EIGHTH
ES 152	13th JAN 1979	54° 42' N	12° 20' W	2900	EIGHTH
ES 164	11th AUG 1979	54° 37' N	12° 22' W	2925	EIGHTH
ES 169	29th FEB 1980	54° 40' N	12° 17' W	2910	EIGHTH
ES 172	27th MAY 1980	54° 39' N	12° 17' W	2910	EIGHTH
ES 180	15th SEP 1980	54° 42' N	12° 11' W	2886	EIGHTH
ES 185	10th APR 1981	54° 44' N	12° 15' W	2907	EIGHTH
ES 190	16th AUG 1981	54° 40' N	12° 16' W	2898	EIGHTH
ES 204	12th MAY 1982	54° 40' N	12° 20' W	2904	QUARTER
ES 231	17th MAY 1983	54° 42' N	12° 12' W	2898	EIGHTH

CHAPTER THREE
FAUNAL ANALYSIS AND TAXONOMY

3.1 SORTING OF SAMPLES

When collected from the SMBA and Southampton University laboratories, the samples were found to be in poor condition. Of the twenty four samples sorted, nine were found to be completely dehydrated and the remainder partially dried out. These samples were rehydrated using the following solutions and method, used by the British Museum of Natural History (Thurston pers. comm.). The samples are placed in a solution of 0.5 to 1% tri-sodium orthophosphate (Na_3PO_4) for twelve hours. The process works best at relatively high temperatures, so samples were incubated gently on a radiator. Some specimens required manipulation with forceps and a fine needle to remove air bubbles. When rehydrated the specimens were soaked in water to remove the orthophosphate solution prior to transfer to fixative (see below). Following rehydration it was necessary to tease apart the coagulated mass of amphipods. This was achieved using a Wild M5 binocular microscope with fine watch making forceps and tungsten wire. Inevitably because of sieving procedures and damage caused by this dehydration many delicate specimens were badly fragmented. Using morphological characters the samples were separated into putative species. Only whole specimens or anterior fragments were sorted in this manner. Any posterior fragments, limbs *etc* were not used in further analysis, thus preventing an over estimate of numbers present. Specimens were transferred from the rehydrating solution to Steedmans solution - 100ml of which consists of 0.5ml Propylene phenoxetol, 4.5ml Propylene glycol, 5ml 40% Formalin solution and 90ml distilled water (Steedman 1976). This solution is an excellent preservative for crustacean material and also softens the animals for easier manipulation under microscopic examination. Formalin used on its own can leave specimens brittle, but it does retain the amphipod's colour which disappears in alcohol.

3.2 FAUNAL ANALYSIS

3.2.1 Introduction

A large number of specimens can be obtained when using epibenthic sleds for deep-sea research, a distinct advantage for both taxonomic and certain life cycle investigations (Harrison 1988b). However the high variability between samples can undermine the effectiveness of these sleds for general ecological studies. This variety may result from any differences in ground speed, depth of cut, length of haul or winnowing on recovery, and will adversely affect attempts at sample comparisons. For any comparative analysis of sites the samples from each area must be representative of their populations. This must be assessed and not assumed (Harrison 1988a). Despite being collected by an epibenthic sled, the samples in this study suffer from the perennial problems in deep-sea biology of low sample numbers and limited seasonal coverage. This means that samples taken in the same month, but from different years will be pooled to form a representative year. Thus it is important to be sure that each sample is a true reflection of the Permanent station amphipod community. In order to assess if this was indeed the case an analysis along the lines of that used by Harrison (1988a) was attempted. Such an analysis requires an estimate of species richness, concentrating on species absence/presence and on the percentage of each sample comprised by each species (based on numbers of individuals) (Harrison 1988a).

3.2.2 Results

Following subsampling and sorting, the twenty three samples produced five thousand and thirty four identifiable specimens belonging to eighty one species. Three of these species were pelagic contaminants and are not included in the aforementioned analysis. Numbers of amphipods in each sample and their percentage contribution to total fauna are given in Table III.I (Information on total fauna and total crustaceans extracted from Gage *et al* 1980). These results show that the mean percentage of total fauna comprised by Crustacea was 16.9% and by Gammaridea 3.56%, although variation was marked (Table III.I).

TABLE III.I FAUNAL COMPOSITION OF SAMPLES

SAMPLE NUMBER	TOTAL FAUNA NUMBERS	TOTAL CRUSTACEA	TOTAL Amphipoda	TOTAL AMPHIPOD SPECIES	TOTAL FAUNA		No. OF SPECIES PER 100 AMPHIPODS
					% CRUSTACEA	% Amphipoda	
ES 2	1044	44	23	8	4.21	2.2	34.8
ES 6	27136	1965	694	40	7.24	2.56	5.7
ES 27	23984	4680	149	35	19.51	4.97	23.5
ES 55	3800	314	31	11	8.26	0.82	35.5
ES 56	13556	2044	85	27	15.08	2.5	31.8
ES 59	42016	7976	90	20	18.98	1.71	22.2
ES 111	6944	720	23	13	10.37	2.65	56.5
ES 118	12984	1688	59	16	13	3.64	27.1
ES 129	32384	9552	291	27	29.5	7.19	9.3
ES 135	178872	12776	241	38	7.14	1.08	15.8
ES 137	51864	16760	376	26	32.32	5.8	6.9
ES 140	6916	721	156	27	10.43	2.26	17.3
ES 143	2987	367	87	19	12.29	2.91	21.8
ES 147	150816	30080	494	36	19.94	2.62	7.3
ES 152	18448	3584	94	20	19.43	4.08	21.3
ES 164	47536	10072	282	36	21.19	4.75	12.8
ES 169	7792	1096	14	10	14.07	1.44	71.4
ES 172	47536	10264	165	28	21.59	2.78	17
ES 180	37680	7032	214	30	18.66	4.54	14
ES 185		20184	551	39			7.1
ES 190	57904	16120	343	25	27.84	4.74	7.3
ES 204	10408	3486	248	29	33.32	9.53	11.7
ES 231		9408	324	23			7.1
TOTAL	783131	210105	5034				
MEAN				24.3	16.96	3.56	21.1

It has been reported that winnowing of epibenthic sled samples, caused by surge on the wire of the sampling gear as a result of the vessel heaving, will lead to a selective loss of fauna through the mouth of the sled (Hessler and Sanders 1967). The hydrodynamically lightest elements of the fauna would be most affected, a fact demonstrated experimentally by Gage *et al* (1980). They showed that the peracarid crustacea are amongst the 'lighter' elements of the fauna. It is therefore no surprise that the sample with the lowest mean percentage of amphipods was ES 55, taken in a heavy sea with the failure of the mouth-closing gate. However two, of the three samples with the highest mean percentage of amphipods, were samples taken in moderate seas without a closing gate. Whilst a winnowing effect might have been expected, we have an apparent enhancement of amphipod proportions. The variation in other samples similarly cannot be explained simply by performance of the closing gate, or recovery in heavy seas. It could be that such differences in catch may result from differences in towing speed. A slow tow will allow the sled to sink deeper in to the sediment and result in more sediment entering the sled. A faster tow will sample a larger horizontal distance but will capture only those organisms associated with the surface of the sediment. Menzies *et al* (1973) reports that towed sampling gears are very sensitive to changes in towing speed, performance is affected by weather conditions and ship handling/speed. Gage *et al* (1980), performed a correspondence analysis on their data and showed organisms with an apparent epibenthic mode of life were more commonly sampled in faster tows. Conversely those organisms which burrowed into the sediment were more common in slower deeper tows. These data agree with that of this study, two short slow hauls (ES 59 and 56) had low percentages of amphipods, whilst the fastest tows (up to 4 knots for ES 137) have the highest proportions. The low proportion of amphipods in sample ES 135, may be explained by the unusually large number of ophiuroids taken in this haul. These variations in amphipod catch reflect the pattern seen in another peracarid group, the isopods, reported by Harrison (1988a). The average number of species per sample was twenty four (see Table III.I), although variation was high (range from eight to forty). Table III.II orders the species in all

TABLE III.II SPECIES LIST IN ORDER OF NUMERICAL ABUNDANCE

Species	No. of samples	No. of individuals	Cumula-tive %	Species	No. of samples	No. of individuals	Cumula-tive %
23	20	1192	24.8	20	8	11	97.98
7	22	692	39.3	4	6	9	98.16
18	21	385	47.33	48	3	7	98.31
21	18	199	51.48	52	4	5	98.41
17	21	159	54.8	51	3	5	98.52
3	21	157	58.07	39	2	5	98.62
22	20	156	61.33	71	3	5	98.73
10	19	137	64.18	12	4	5	98.83
37	13	130	66.9	15	4	4	98.92
31	15	112	69.23	61	4	4	98.99
2	15	110	71.53	47	3	4	99.08
14	15	103	73.68	70	4	4	99.17
49	15	98	75.72	56	2	4	99.25
11	16	95	77.7	16	2	3	99.31
34	16	88	79.54	32	2	2	99.35
19	19	85	81.31	35	2	2	99.39
6	18	78	82.94	44	2	2	99.44
29	17	69	84.38	40	2	2	99.48
5	17	67	85.77	45	2	2	99.52
42	4	65	87.13	55	2	2	99.56
25	14	64	88.46	66	1	2	99.6
24	10	51	89.53	65	2	2	99.64
36	10	51	90.59	54	1	1	99.67
30	13	40	91.43	57	1	1	99.69
26	12	34	92.14	58	1	1	99.71
33	7	32	92.8	59	1	1	99.73
69	8	30	93.43	60	1	1	99.75
63	6	27	93.99	62	1	1	99.77
50	13	26	94.53	64	1	1	99.79
41	5	25	95.06	67	1	1	99.81
46	9	19	95.45	68	1	1	99.83
43	10	17	95.81	72	1	1	99.85
27	10	16	96.14	73	1	1	99.87
28	6	14	96.43	74	1	1	99.9
13	5	14	96.72	75	1	1	99.92
9	3	13	97	76	1	1	99.94
53	3	12	97.27	77	1	1	99.96
8	5	11	97.52	78	1	1	99.98
38	8	11	97.75	79	1	1	100

twenty three samples by overall abundance. Over 75% of the total collection is accounted for by 13 species, whilst 95% is accounted for by only 30 species - less than half the total number of species found. Conversely 29 species make up only 1% of the collection. A plot of the number of samples in which each species occurs is given in Figure 3.1, data from Table III.II. This graph shows that although many species were found in low numbers, the majority of species are not found in single samples. This would indicate that most species in the areas sampled by the sled are distributed in low densities. An attempt to determine the effect of sample size on species richness, is presented in Figure 3.2. Here an index of number of species per hundred individuals was plotted against the number of individuals for each sample (data from Table III.I). For samples with less than one hundred individuals this index was calculated as follows Index = $No.Sp. \times \frac{100}{No.Ind.}$ and represent extrapolative points on Figure 3.2. Samples which contained more than one hundred individuals were interpolative points calculated as follows Index = $No.Sp. \div \frac{No.Ind.}{100}$.

Figure 3.2. demonstrates that larger samples give smaller numbers of species per hundred individuals, whilst the small samples give an overestimate. For a representative sample to use in ecological studies a consistent value is needed. Consistent values are not reached on Figure 3.2. until the 300 specimen value is exceeded. Thus in the area sampled, any sample containing less than three hundred specimens may not accurately represent species composition. In order to test whether the seventy eight species collected in this study were representative of the Permanent Station population, a cumulative species curve was plotted (Figure 3.3). This should show that as the sample becomes larger, the rate of addition of new species would decrease exponentially (Gleason 1922). After seventeen samples and approximately three thousand individuals the curve is approaching an asymptote. This would seem to indicate that the samples in this study represent the majority of species present in the study area. This approach, although commonly used (*eg.* Hawkins and Hartnoll 1980), is criticised by Gentil and Dauvin (1988). These authors propose modification of the cumulative species curve by removal of the rarer species and construction of a

FIGURE 3.1 SPECIES DISPERSION

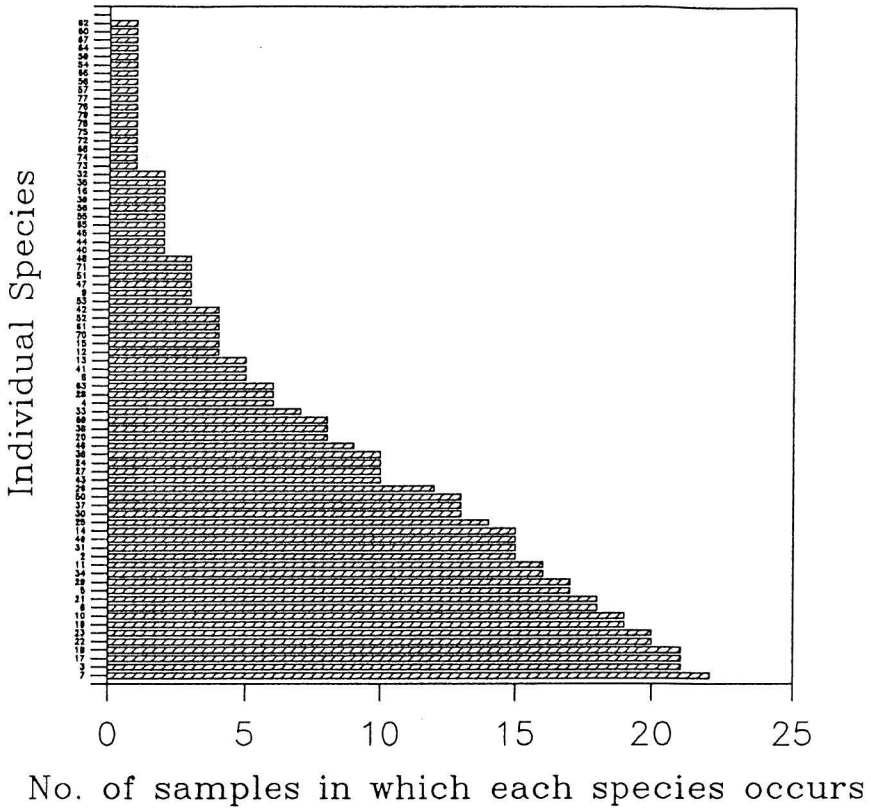


FIGURE 3.2 EFFECT OF SAMPLE SIZE ON INDICATED SPECIES RICHNESS

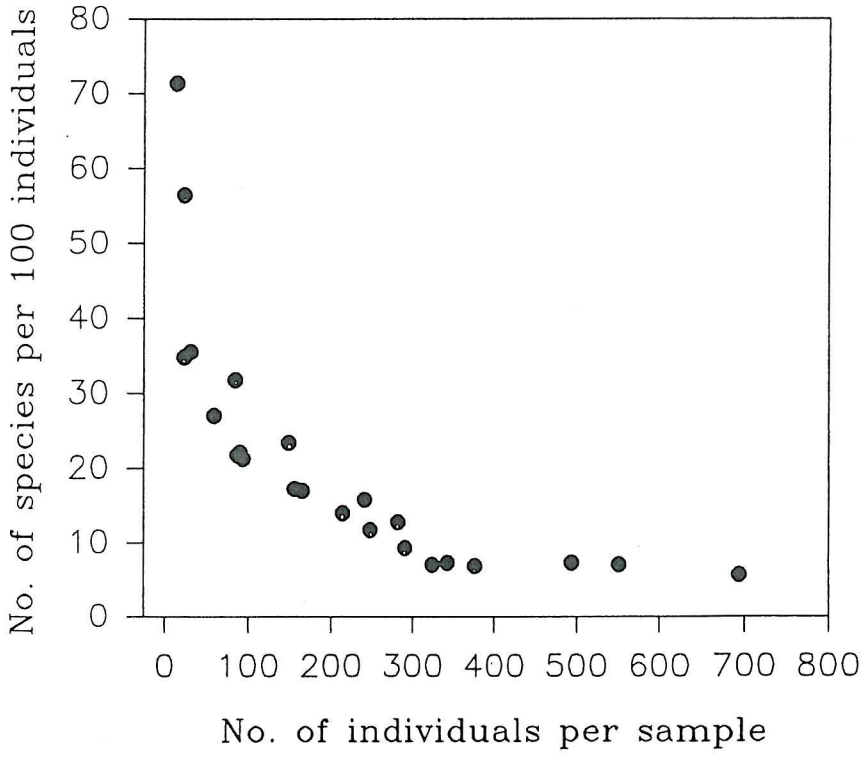
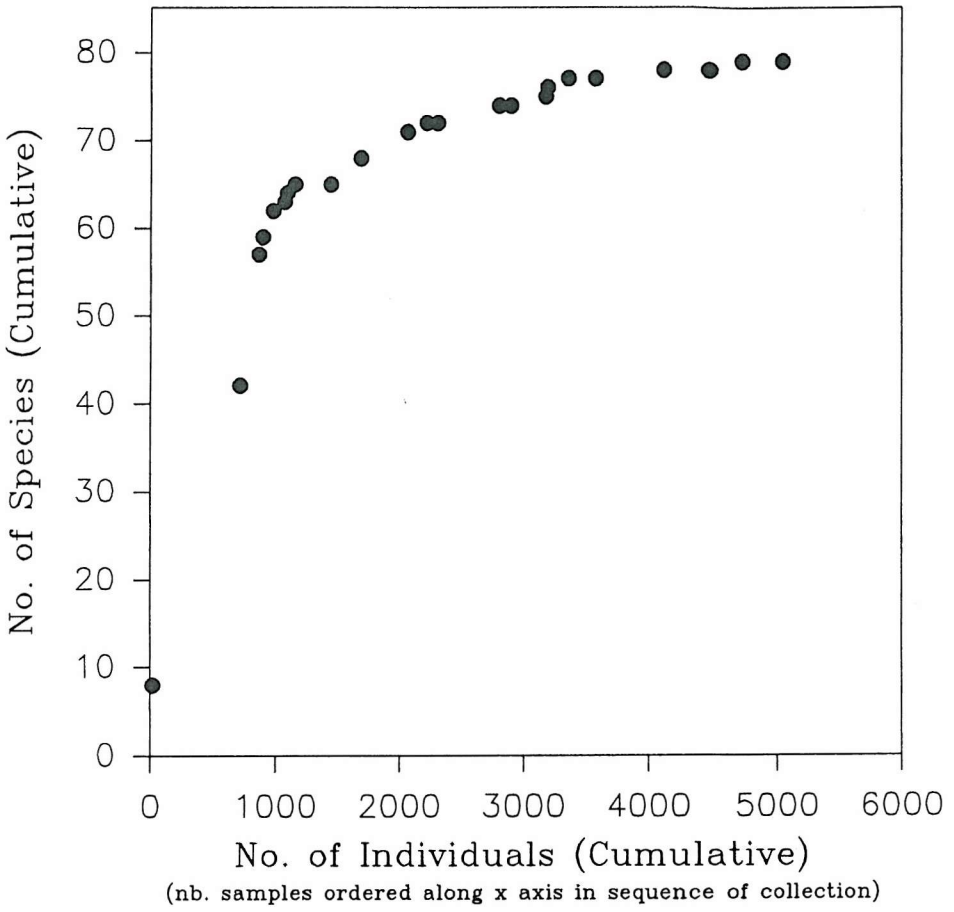
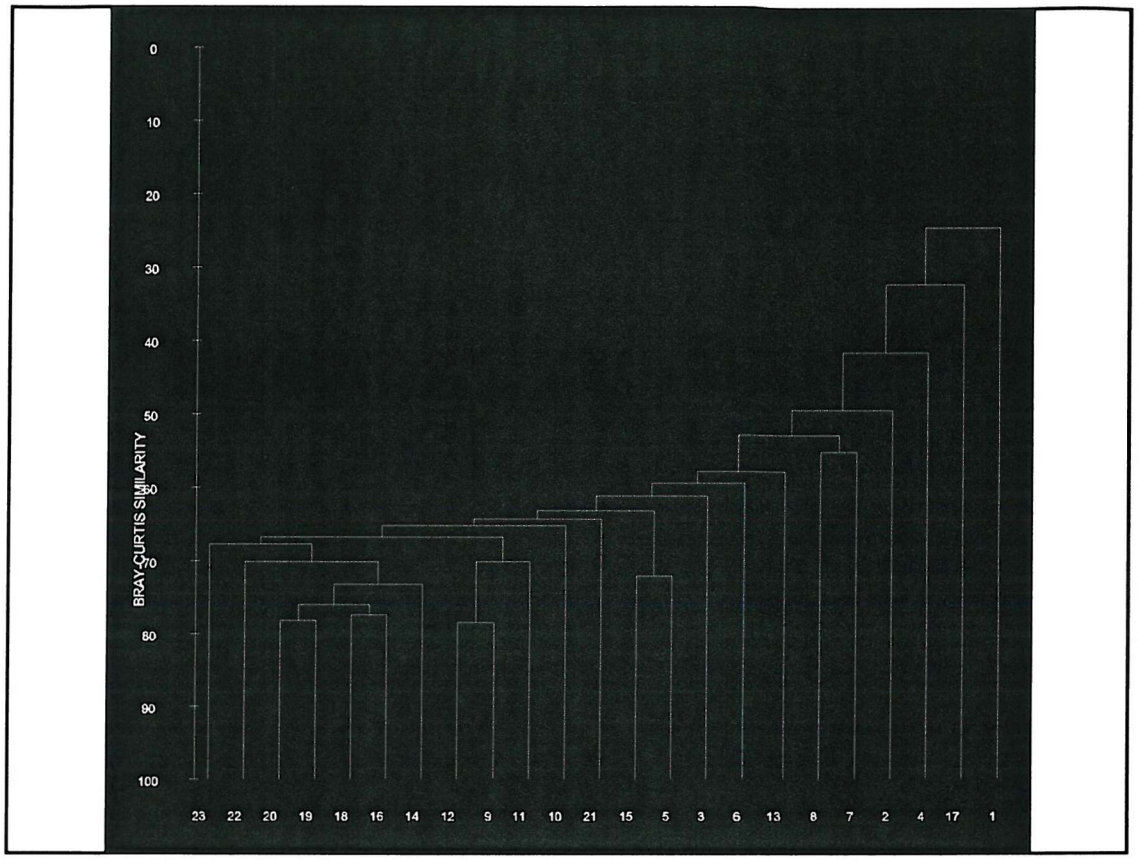


FIGURE 3.3 CUMULATIVE SPECIES TO INDIVIDUALS CURVE



corrected species-area curve. Extrapolations could then be made to predict total number of species present in a community. Such modification was not attempted in this study as the majority of species could be considered 'rare'. As the samples in this study were collected over a ten year period there may be a temporal change in species composition. Harrison (1988a) addressed this problem using correspondence analysis and principal component analysis as forms of indirect gradient analysis. The samples in this study were analysed using the PRIMER (Plymouth Routines in Multivariate Ecological Research), specially designed for multivariate analysis of benthic community data. The data were converted to give the percentage composition of each sample by species (Appendix 3.1) and entered into the PRIMER Cluster program. Cluster performs hierarchial agglomerative clustering to produce a dendrogram plot. The data was transformed using Sqrt(sqrt(x)), then analysed using the Bray-Curtis similarity measure with group average clustering and produced the dendrogram shown in Figure 3.4. The data can also be converted to produce a multi-dimensional scaling (MDS) scatter plot, see Figure 3.5. From these figures we can see that the samples form no distinct or obvious groups or trends. There is a tendency for the samples collected later in the sample program to cluster together. This may reflect improved and more consistent sampling technique as the sampling program progressed. The samples which separate most from the others, both on the dendrogram and MDS plot are ES 2, 6, 55, 111 and 169. These samples have unusually low numbers of individuals and correspondingly high numbers of individuals per 100 species compared to the other samples (excepting ES 2, which has very high individual numbers and low index). When the analysis is repeated using just the twenty most common species, the resulting plots (Figures 3.6a and b) show an even greater separation of samples ES 2, 55 and 169, whilst sample ES 6 now clusters closer to the other samples. This shows the influence of rare species in the 'outlier' samples, samples with a more 'normal' composition now cluster even closer together (Figure 3.6a and b). Interestingly two of the samples which separate from the others are those which have been winnowed (see earlier). This winnowing may have resulted in sample ES 55 because the closing gate

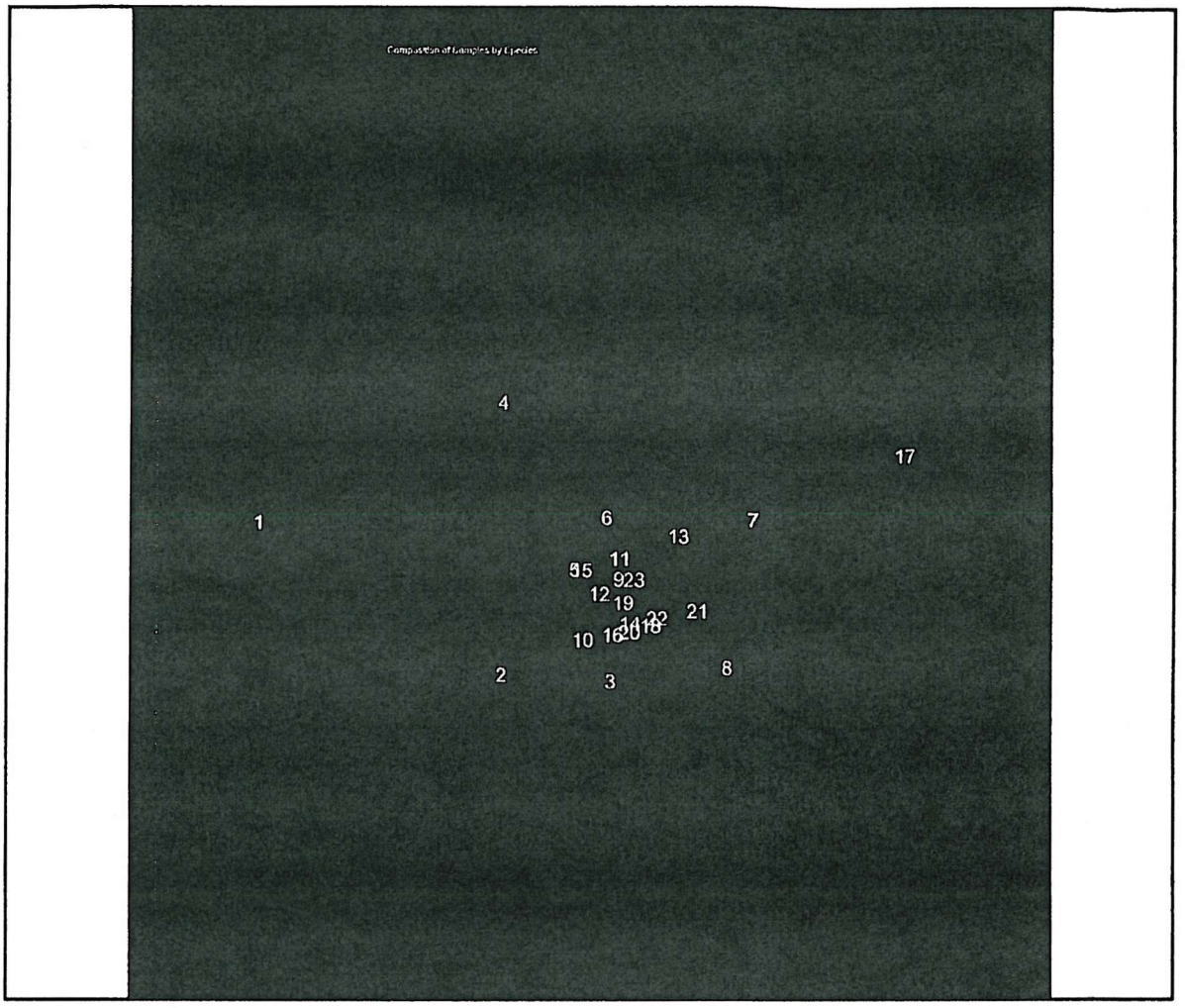
FIGURE 3.4 DENDROGRAM SHOWING RESULTS OF SAMPLE COMPARISON USING CLUSTER ANALYSIS



KEY

SAMPLE																					
23	22	20	19	18	16	14	12	9	11	10	21	15	5	3	6	13	8	7	2	4	17	1
BS 231	BS 204	BS 185	BS 180	BS 172	BS 164	BS 147	BS 140	BS 129	BS 137	BS 135	BS 190	BS 152	BS 56	BS 27	BS 59	BS 143	BS 118	BS 111	BS 6	BS 55	BS 169	BS 2
NUMBER OF AMPHIPODS																						
324	248	551	214	165	282	494	156	291	376	241	343	94	85	149	90	87	59	23	694	31	14	23
NUMBER OF SPECIES																						
23	29	39	30	28	36	36	27	27	26	38	25	20	27	35	20	19	16	13	40	11	10	8
NUMBER OF SPECIES PER 100 INDIVIDUALS																						
7.1	11.7	7.1	14	17	12.8	7.3	17.3	9.3	6.9	15.8	7.3	21.3	31.8	23.5	22.2	21.8	27.1	56.5	5.7	35.5	71.4	34.8

FIGURE 3.5 MULTIDIMENSIONAL SCALING PLOT SHOWING RESULTS OF SAMPLE COMPARISON USING CLUSTER ANALYSIS



KEY

SAMPLE																					
25	22	20	19	18	16	14	12	9	11	10	21	15	5	3	6	13	8	7	2	4	17	1
ES 231	ES 204	ES 185	ES 180	ES 172	ES 164	ES 147	ES 140	ES 129	ES 157	ES 155	ES 190	ES 152	ES 56	ES 27	ES 59	ES 143	ES 118	ES 111	ES 6	ES 55	ES 169	ES 2
NUMBER OF AMPHIPODS																						
324	248	551	214	165	282	494	156	291	376	241	343	94	85	149	90	87	59	23	694	31	14	23
NUMBER OF SPECIES																						
23	29	39	30	28	36	36	27	27	26	38	25	20	27	35	20	19	16	13	40	11	10	8
NUMBER OF SPECIES PER 100 INDIVIDUALS																						
7.1	11.7	7.1	14	17	12.8	7.3	17.3	9.3	6.9	15.8	7.3	21.3	31.8	23.5	22.2	21.8	27.1	56.5	5.7	35.5	71.4	34.8

FIGURE 3.6a DENDROGRAM RESULTS USING 20 MOST ABUNDANT SPECIES

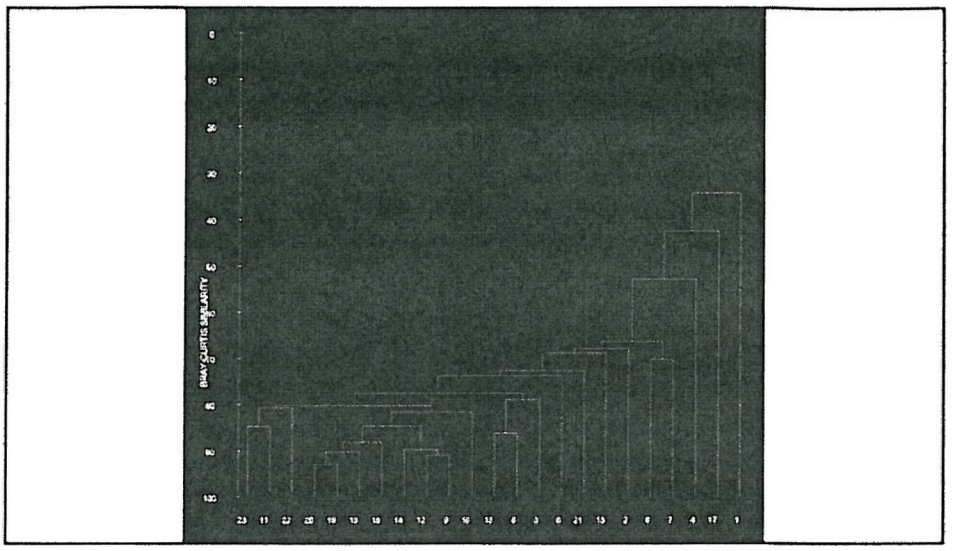
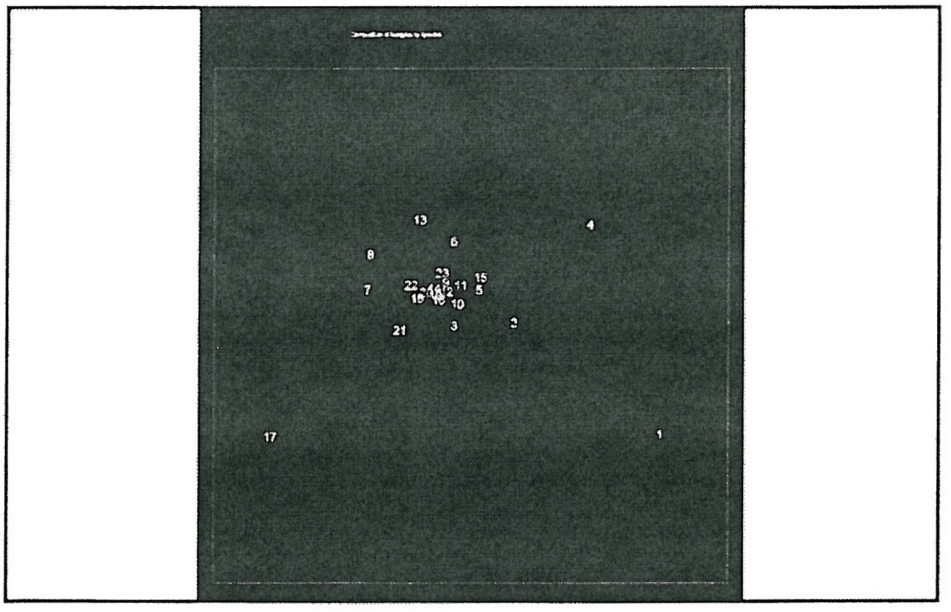


FIGURE 3.6b MULTIDIMENSIONAL SCALING PLOT RESULTS USING 20 MOST ABUNDANT SPECIES



KEY AS PREVIOUS FIGURES

TABLE III.III RESULTS OF DIVERSITY ANALYSIS

SAMPLE	SHANNON-WEINER DIVERSITY INDEX	RICHNESS	EVENNESS
ES 2	1.839	1.520	0.884
ES 6	2.877	8.228	0.785
ES 27	2.696	7.383	0.758
ES 55	1.746	2.171	0.728
ES 56	2.909	5.429	0.893
ES 59	2.489	4.126	0.831
ES 111	2.367	2.606	0.923
ES 118	2.105	3.257	0.759
ES 129	2.415	5.646	0.733
ES 135	3.011	8.034	0.828
ES 137	1.933	5.429	0.593
ES 140	2.789	5.646	0.846
ES 143	2.341	3.909	0.795
ES 147	2.675	7.600	0.746
ES 152	2.595	4.126	0.866
ES 164	2.940	7.600	0.820
ES 169	2.307	2.171	0.962
ES 172	2.657	5.863	0.797
ES 180	2.733	6.297	0.803
ES 185	3.017	8.252	0.823
ES 190	2.056	4.994	0.647
ES 204	2.362	6.080	0.701
ES 231	2.016	4.777	0.643

failed to operate, whilst sample ES 111s' net tore. The PRIMER program was also used to look at the diversity (in terms of amphipod species) of the samples. The results are presented in Table III.III, which shows the Shannon-Weiner diversity index, richness and evenness of each sample. The samples with the lowest diversity are ES 2 and ES 55, whilst those with the lowest richness values are ES 2, 55 and 169. As would be expected these are again the samples which separate most from the others in the previous analysis. The most diverse sample is ES 185, which was also the richest sample. The two most similar samples in terms of diversity are ES 129 and 140, which were collected in April 1977 and April 1988 respectively. They contain the same number of species (27), have identical richness values (5.646) and similar diversity values. The samples were also compared for any significant differences using analysis of variance with the Jandel Scientific SigmaStat computer package. The data failed a normality test ($P<0.001$) so a nonparametric Kruskal-Wallis Analysis of Variance on ranks was performed on the data. The null hypothesis being that there is no difference among the population medians. The results of the test showed a significant difference between the samples $H=53.051$, $df=22$ and $P<0.001$. Such a large H value indicates variability among the average ranks is higher than would be expected from random variability in the population. In order to determine which samples were different from the others a multiple comparison procedure was performed on the data. The Student-Newman-Keuls (SNK) method is an all pairwise comparison of every combination of sample pairs. The results of the SNK test are calculated in the form of a q statistic, presented in Table III.IV. A 'large' value of q indicates a significant difference between the samples, p is a parameter used when calculating q. A large p value requires a correspondingly large q value to be significantly different. Only those results which have a probability (P) of <0.05 are included in Table III.IV. Again the samples which are significantly different from the others are ES 2, 55, 111 and 169. These are the samples which are most removed from the others, grouping to the right on the dendrogram in Figure 3.4. The data in Appendix 3.1 were used to plot Figure 3.7, which shows the percentage composition of each sample by species. From this figure we can see that the majority of species show no great variations over the sample

TABLE III.IV RESULTS OF STUDENT-NEWMAN-KEULS MULTIPLE COMPARISON

COMPARISON	q STATISTIC	p PARAMETER	PROBABILITY
ES 185 v ES 2	5.294	23	P < 0.05
ES 185 v ES 55	4.911	22	P < 0.05
ES 185 v ES 169	4.984	21	P < 0.05
ES 185 v ES 111	4.777	20	P < 0.05
ES 135 v ES 2	5.441	22	P < 0.05
ES 135 v ES 55	5.046	21	P < 0.05
ES 135 v ES 169	5.130	20	P < 0.05
ES 6 v ES 2	5.554	21	P < 0.05
ES 6 v ES 55	5.146	20	P < 0.05
ES 6 v ES 169	5.239	19	P < 0.05
ES 164 v ES 2	5.571	20	P < 0.05
ES 164 v ES 55	5.142	19	P < 0.05
ES 164 v ES 169	5.240	18	P < 0.05
ES 27 v ES 2	5.580	19	P < 0.05
ES 27 v ES 55	5.128	18	P < 0.05
ES 27 v ES 169	5.231	17	P < 0.05
ES 147 v ES 2	5.881	18	P < 0.05
ES 147 v ES 55	5.420	17	P < 0.05
ES 147 v ES 169	5.547	16	P < 0.05
ES 180 v ES 2	5.302	17	P < 0.05
ES 180 v ES 55	4.776	16	P < 0.05
ES 172 v ES 2	5.174	16	P < 0.05
ES 56 v ES 2	5.418	15	P < 0.05
ES 140 v ES 2	5.787	14	P < 0.05
ES 204 v ES 2	6.066	13	P < 0.05
ES 129 v ES 2	6.193	12	P < 0.05
ES 137 v ES 2	5.807	11	P < 0.05
ES 190 v ES 2	5.782	10	P < 0.05
ES 152 v ES 2	6.090	9	P < 0.05
ES 231 v ES 2	6.795	8	P < 0.05
ES 59 v ES 2	7.614	7	P < 0.05
ES 143 v ES 2	7.977	6	P < 0.05
ES 118 v ES 2	6.709	5	P < 0.05
ES 111 v ES 2	6.546	4	P < 0.05
ES 169 v ES 2	5.688	3	P < 0.05
ES 55 v ES 2	6.838	2	P < 0.05

period, and that each sample has a similar percentage composition. The exceptions being species 3, 7, 23, 11 and 14. To enable such variations to be more easily visualized these species, and the ten most abundant species, were plotted on a true temporal scale (Figures 3.8 to 3.12). Of these most abundant species, species 10, 17, 18, 21, 22, 31, and 37 show no significant variations over the sampling period (Figures 3.8a, 3.9c, 3.10a, 3.10b, 3.10c, 3.11b and 3.11c). However species 3 increases its percentage composition of samples from a range of between 1-10% in the majority of samples, to 51.6% in sample ES 55. This sample contains only ten species and the other nine all have very low percentage contributions in comparison with species 3. As mentioned before the closing gate of the sled failed in this sample, leading to a winnowing of its catch. Species 3 is a lysiannassid (see later in chapter), with a compact, hydrodynamically smooth morphology, with a dense integument compared to other species. This may make it less susceptible to the winnowing effect. This possibility is supported by the observation that species 3s' next highest percentage composition of 8.69% is in sample ES 111, this sample's net tore and was again subject to winnowing. Harrison (1988a) refers to the dominance of ES 55 by one species of isopod (*Macrostylis* sp 2), and complete lack of the lightest portion of the amphipod component - the mancae. Harrison views this anomaly as a possible effect of the winnowing of ES 55. However the numbers of species 3 in ES 55 are very much higher than those in any other sample, so it may not be just that less were lost through winnowing, but rather an aggregation or particularly dense patch was sampled by ES 55. Species 7 and 23 have percentage contributions which show a high variability over the sampling period in comparison to other species. Interestingly their variability seems to mirror each other, when percentage composition of species 7 is low, species 23 is high and *vice versa* (Figure 3.8b and 3.11a). This is more apparent when the figures are superimposed (Figure 3.12), the periods Jun 1973-Nov 1975 and Jan 1979-Apr 1981 are dominated by species 7, whilst species 23 is more abundant from Nov 1975-Jun 1978 and Aug 1981-May 1983. Whether this is just a coincidence, or that these species are in some way competing for resources or habitats is impossible to say. Species 11 and species 14 both show a decline in percentage contribution over the

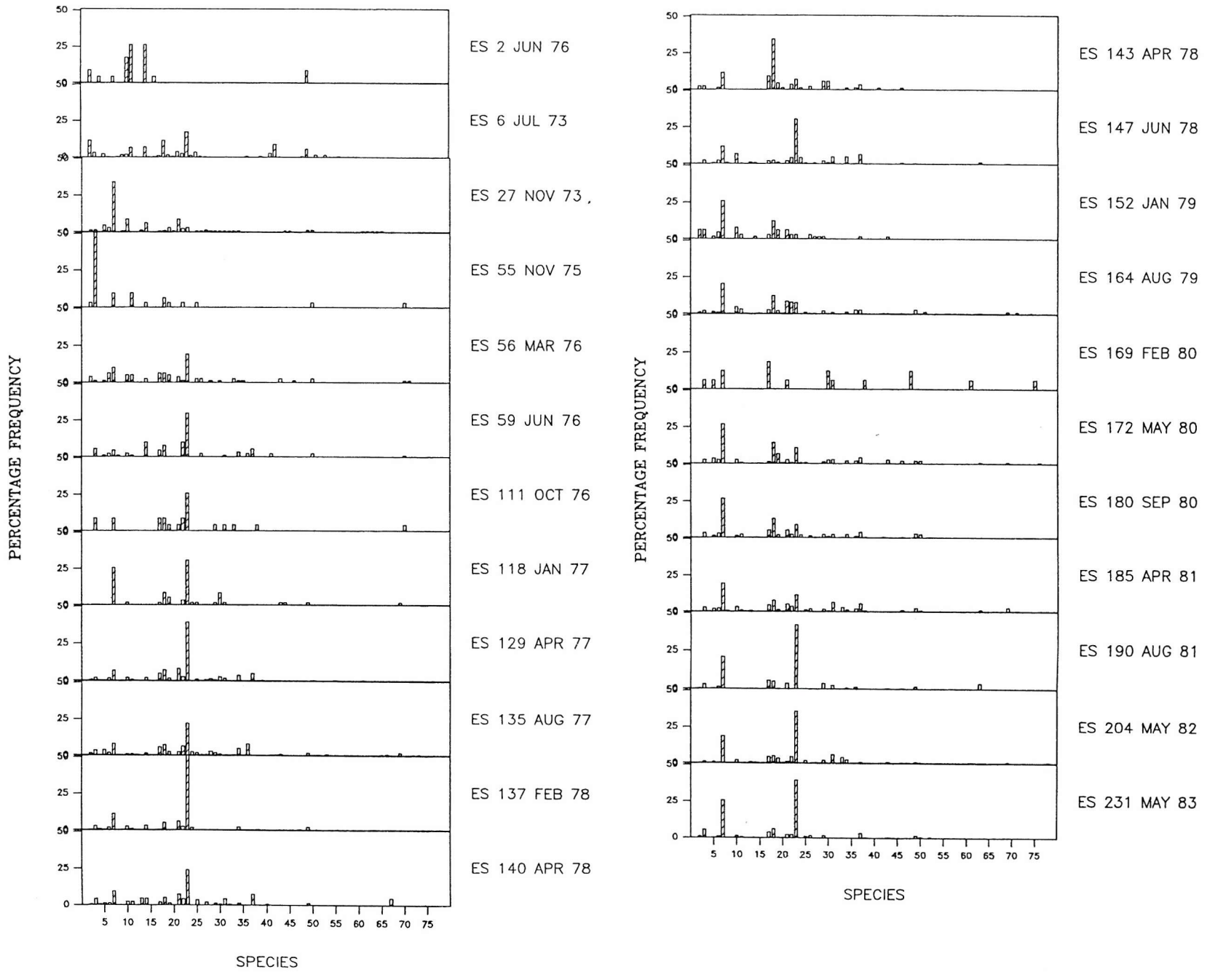


FIGURE 3.7 PERCENTAGE COMPOSITION OF EACH SAMPLE

FIGURE 3.8 PERCENTAGE VARIATION OVER SAMPLING PERIOD

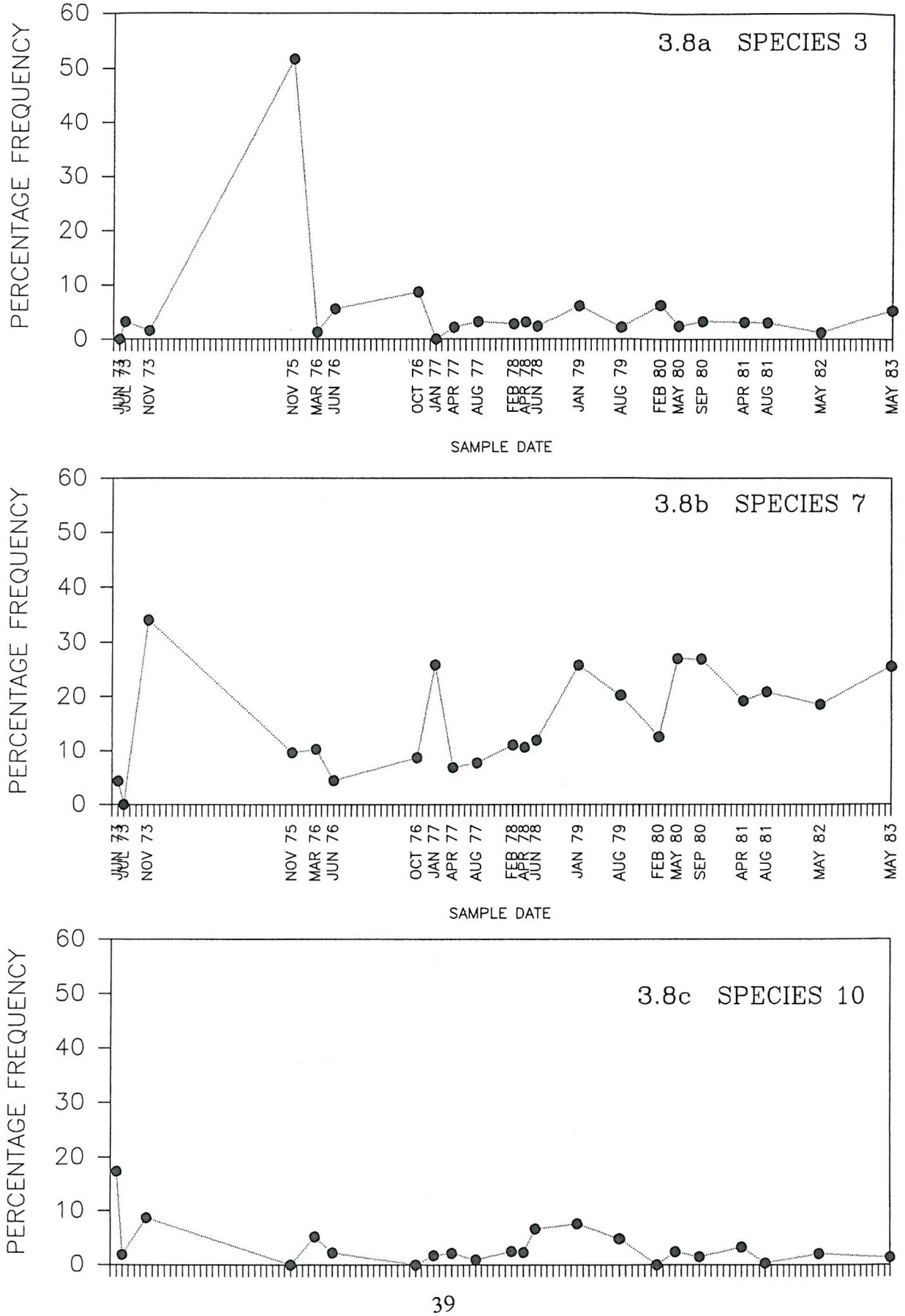


FIGURE 3.9 PERCENTAGE VARIATION OVER SAMPLING PERIOD

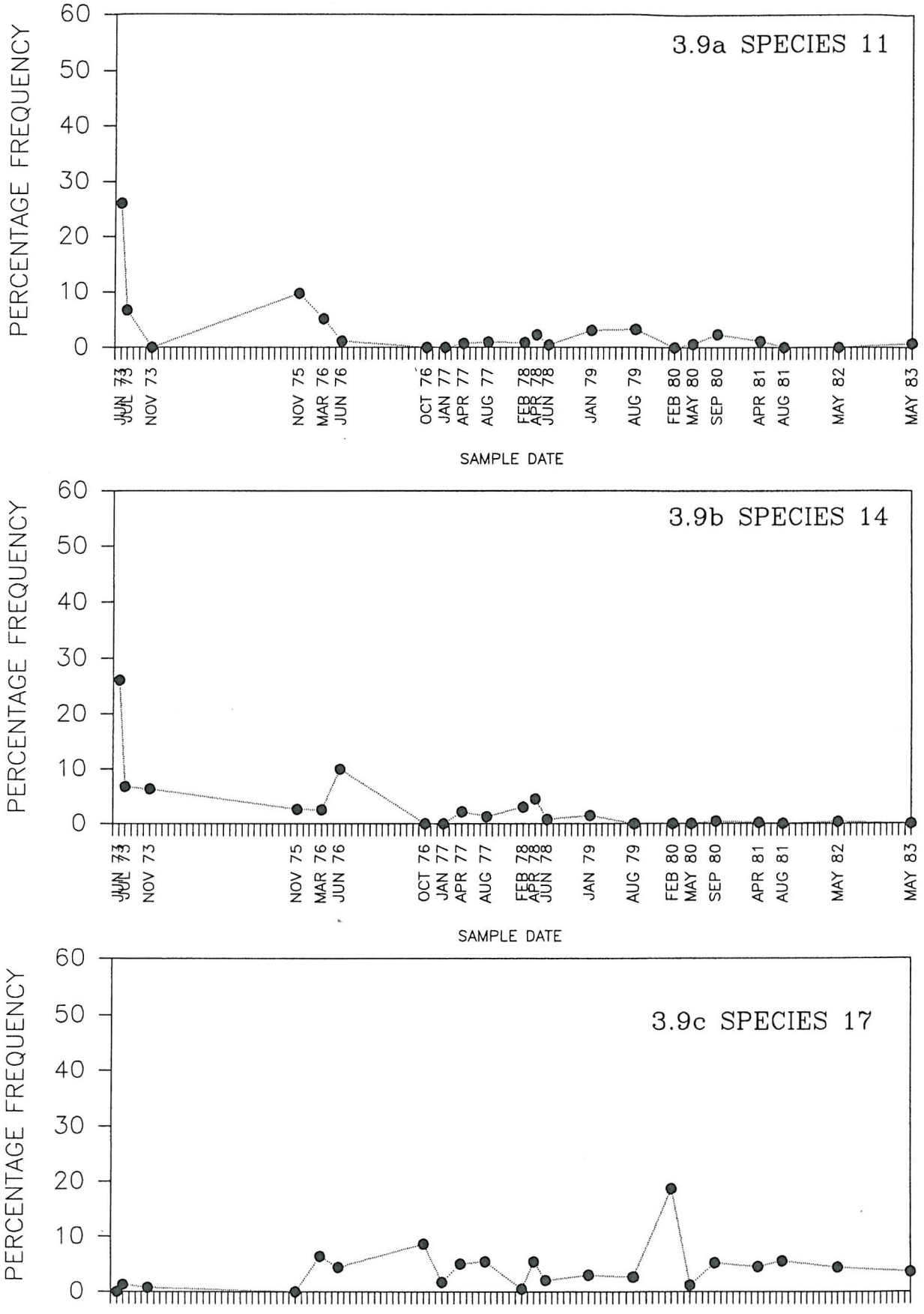
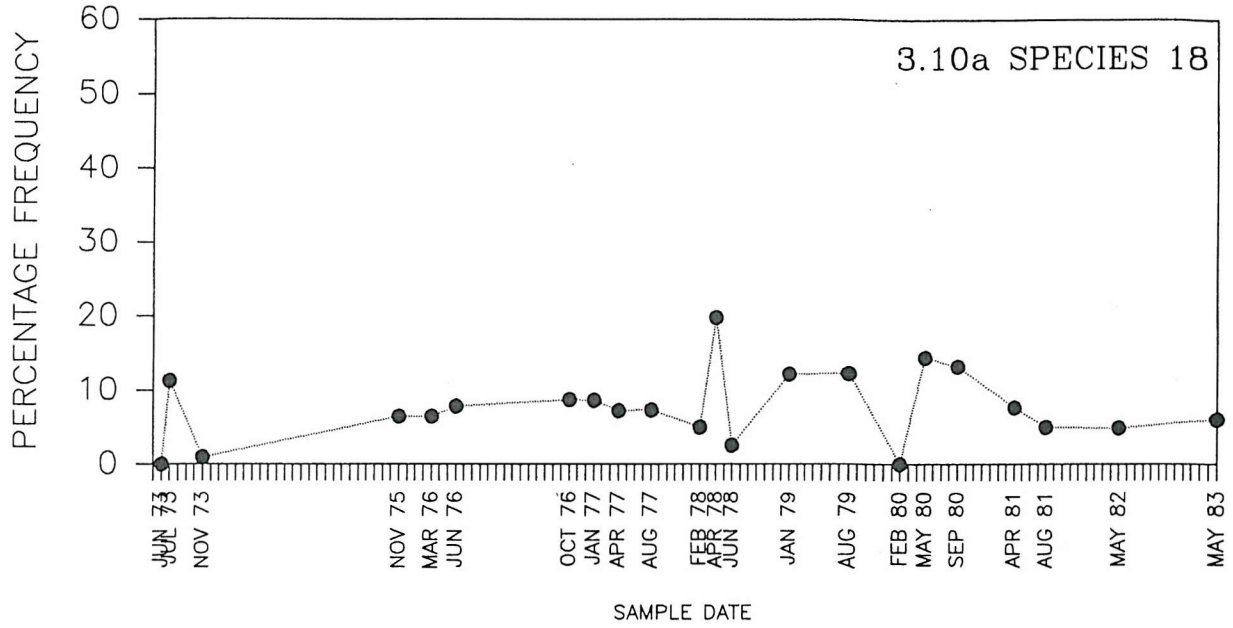
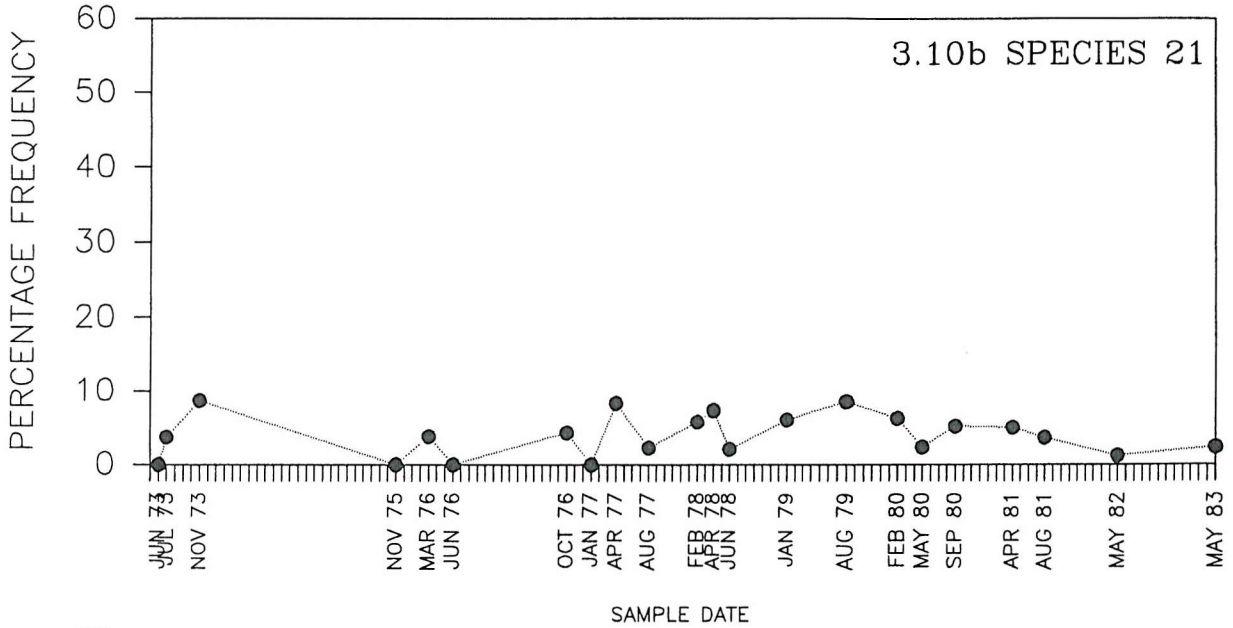


FIGURE 3.10 PERCENTAGE VARIATION OVER SAMPLING PERIOD





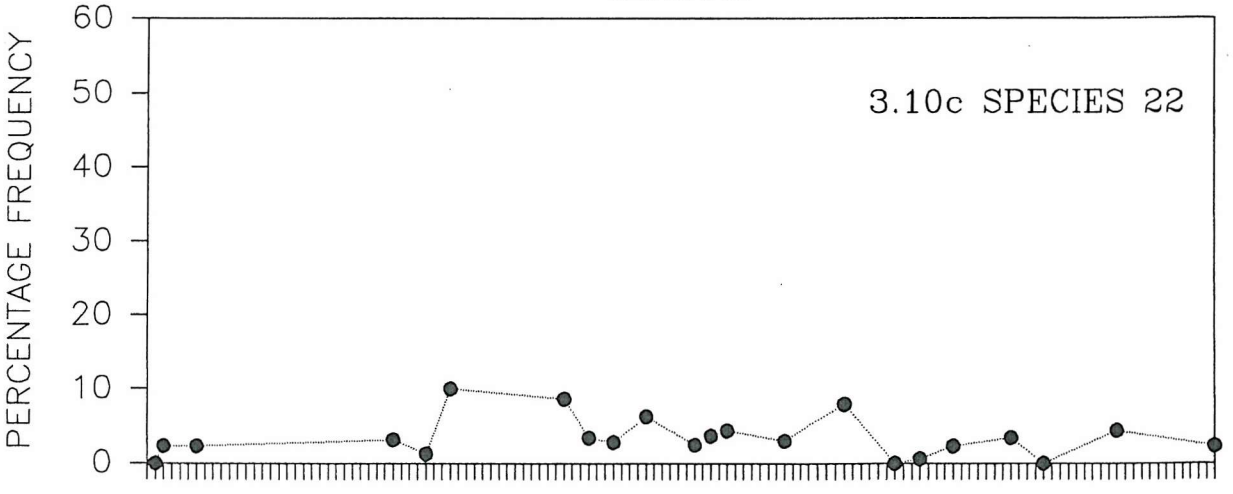
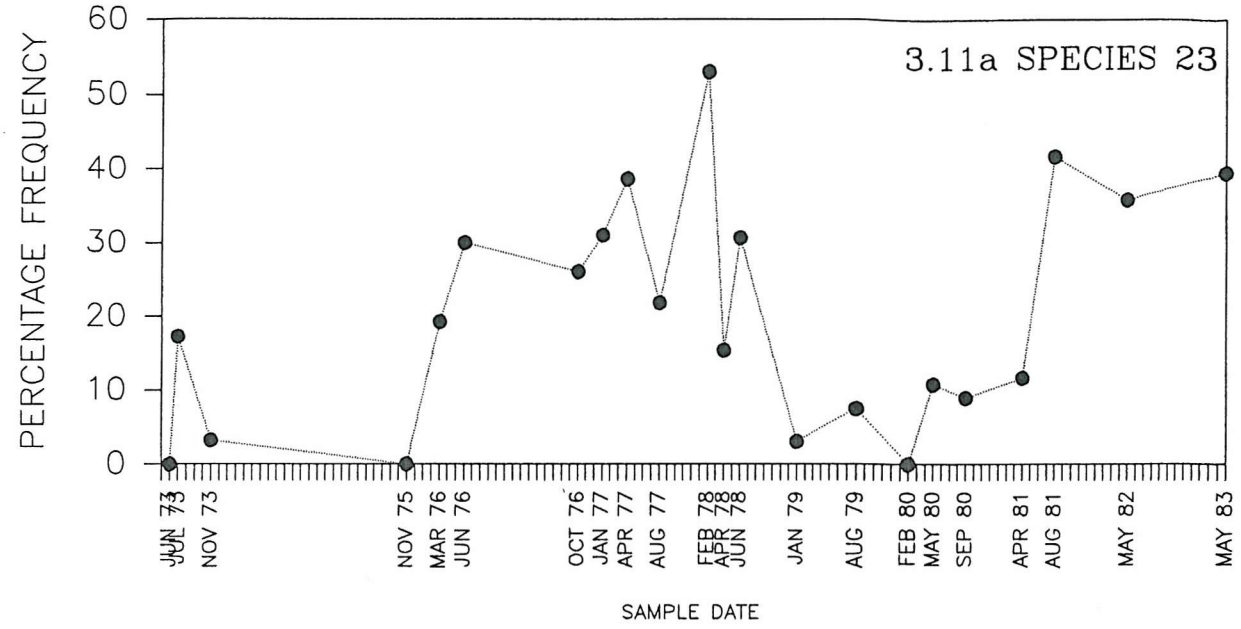
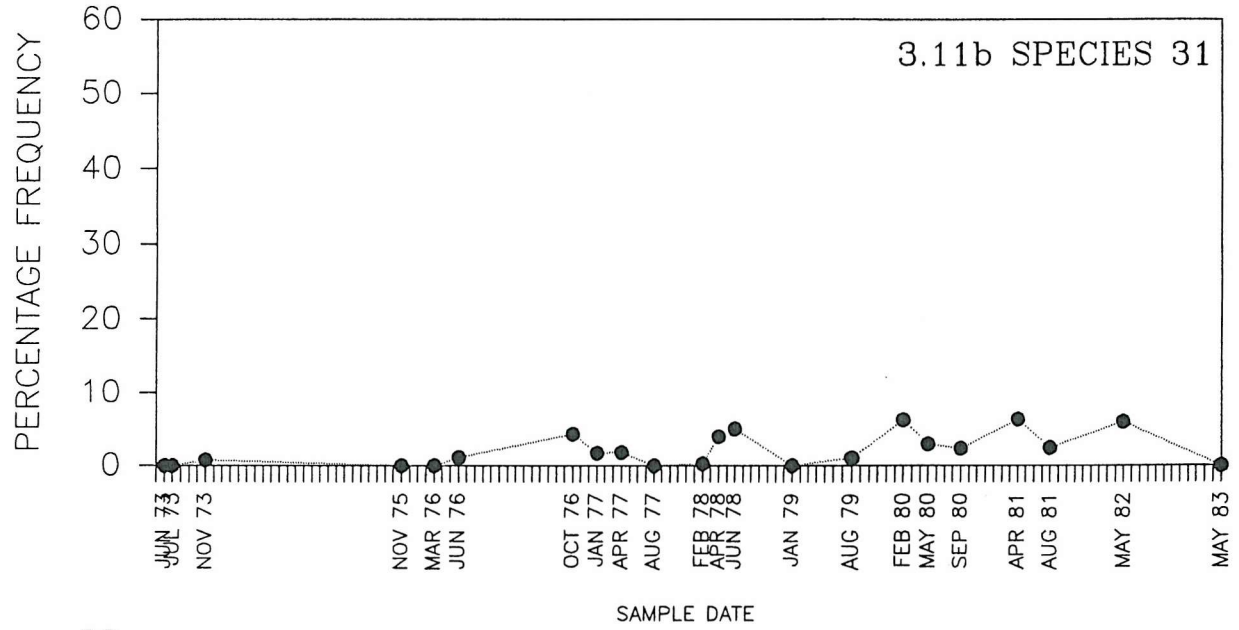


FIGURE 3.11 PERCENTAGE VARIATION OVER SAMPLING PERIOD





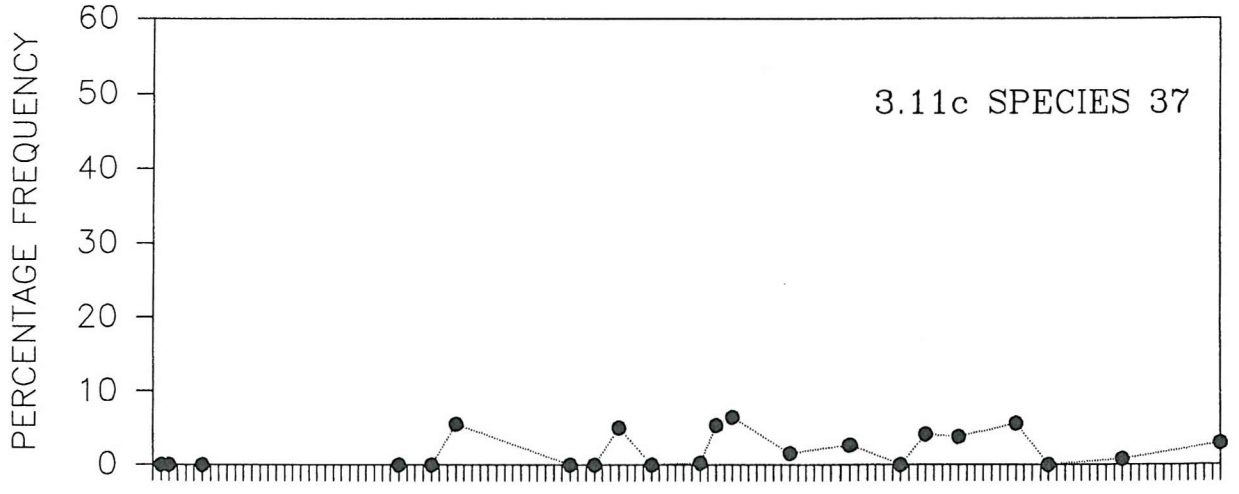
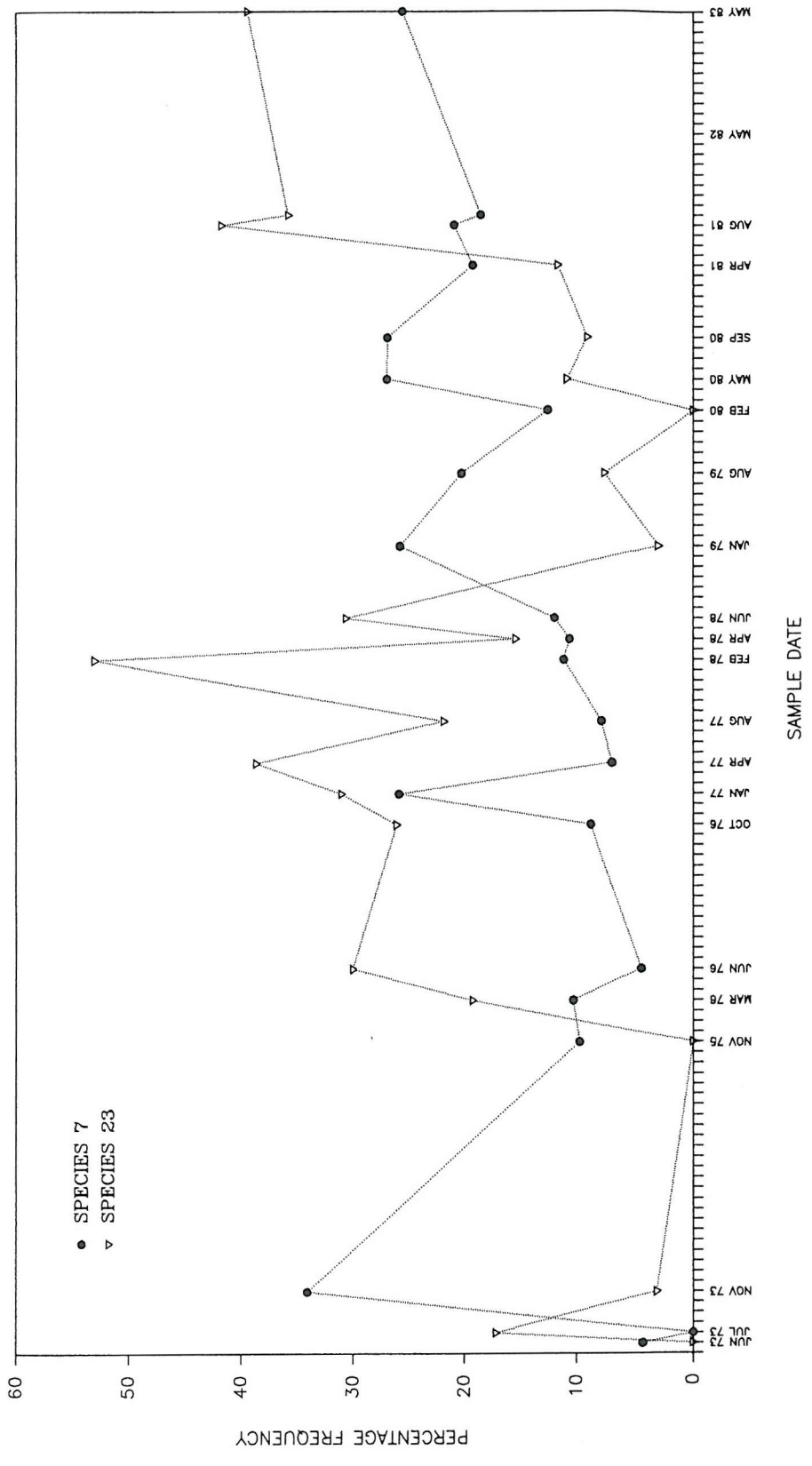


FIGURE 3.12 COMPARISON OF VARIABILTY IN PERCENTAGE COMPOSITION OF SPECIES 7 AND 23.



sampling period (Figures 3.9a and 3.9b). Again this study cannot reveal any possible cause for this decline, excepting perhaps the effect of the sampling programme itself. Although for such a decline to have occurred there must have been a corresponding increase in the percentage contribution of other species. Several species must have increased their contribution slightly as no noticeable trends are apparent.

3.2.3 Discussion

From the results listed above the Permanent Station amphipod population consists of seventy eight species and contributes just over three and a half percent of the total fauna. The plot in Figure 3.3 would seem to be at, or approaching asymptote, indicating that there may be no more than ten to twenty additional species from this area. The percentage of total fauna comprised by amphipods in this study compares well to the value of between 3 and 3.2% in studies reported by Gage (1977, 1978 and 1979). These samples were taken in an area just north of the permanent Station (55^0 03-04' N and 12^0 02-06' W) in 2875m of water using a box-corer. Hessler and Sanders (1967) were the first to design and use an epibenthic sled, the initial trials being on the Gay Head-Bermuda transect. Two of their stations were from a similar depth and length of haul as those in this study, sites 64 and 72. The results of this study compare well with the figures they obtained for amphipods of 3.98 and 1.73% of total fauna. When their results are used to calculate number of species per hundred individuals, St. 72 yields 4.23 and St. 64 a value of 20.6. These figures are comparable to samples of similar sizes from this study and both fall on the curve in Figure 5. Dahl *et al* (1976) carried out a similar study in the Norwegian Sea and found a higher density, lower diversity fauna than the N. Atlantic. Three of their hauls (DS 4, 11 and 17) are in similar depths and of similar length to the Permanent station hauls. However the amphipods in these hauls only contribute 0.5, 1.2 and 1.6% of the total fauna respectively. These figures are lower than most found in this study, despite the mean total numbers of individuals caught being much greater. This is attributed to the anomalous nature of the deep Norwegian Sea compared to other deep-water regions of the worlds oceans. Variation amongst the samples in this study may result from

aggregated patterns in the distribution of the fauna. However Gage *et al* (1980) state that in the Permanent station area, any patchiness will be at a scale small enough to be negated by the length of a typical sled haul. By identifying the effect of sampling process on the variation in samples, other possible sources of variability will be more clearly recognised. We could expect that repeated sampling at the Permanent station will reduce the effect of sample variability and allow environmental patterns to emerge (Harrison 1988a). Multivariate analysis of the samples revealed no obvious groups or trends. Separation of certain samples resulted from sampling artefacts (ES 55, 111) and anomalous samples (in comparison with the majority) with very low numbers of individuals. Thus the twenty three samples all appear to be taken from one statistical population. Analysis of percentage contribution does show some variability in certain species, but the majority of species show no significant increases or decreases. So over the course of the sampling period changes in species presence and percentage contribution to the samples are minimal. If samples used for further ecological studies in this report do not concentrate on samples and species containing small numbers of individuals, such fluctuations can be accommodated. There are sufficient samples to allow coverage of the months affected by such problematic samples. It must be borne in mind that despite the large numbers of individuals obtained from sled hauls, it is rare for a single species to be sufficiently abundant, even in a series of catches, for a population analysis to be practical (Thurston 1979). In addition, as all the samples were collected with a sled, the species caught will be biased by its mode of operation. Thus the samples may not represent the true taxonomic ratios for the environment as a whole (Harrison 1988).

3.3 INTRODUCTION TO DEEP-SEA AMPHIPODS

3.3.1 History of the Deep-Sea Fauna

Palaeotemperature records indicate deep-sea waters were still warm (12 -20^0 C) up to the Palaeocene/Eocene boundary (Fischer and Arthur 1977). A drop to below 10^{0}C by progressive cooling only took place during and after the Miocene. This cooling is correlated with the ventilation of deeper, previously anoxic, layers by relatively dense

well oxygenated waters originating from high altitudes (Berry and Wilde 1978). The major mechanism by which the cooling can be explained is the formation of sea ice. A warm-water deep-sea biota existed before this cooling, that was taxonomically different from that in the present psychrosphere. The major change in the composition of deep-water Ostracoda is placed at about 40 Myr Bp (late Eocene) (Benson 1975). Another event leading to the extinction of the Tethyan deep-water biota was the occurrence of an extended anoxic zone between 200 and 2000m during the Oligocene (Fisher and Arthur 1977). After the progressive cooling and ventilation of the deeper ocean layers, a modern deep-sea fauna evolved from shallow water ancestors (Stock 1986). Without a clear fossil record of deep-sea faunas (excepting the Foraminifera - see below) there have been two opposing theories on the origin of the deep-sea fauna (Gage and Tyler 1991). The first : migration from shallow water, proposes that the deep-sea was populated by emigration from centres of origin in shallow water at high latitudes, where temperature would not pose an environmental barrier between deep and shallow waters (Dahl 1954, Wolff 1960, Kussakin 1973 and Menzies *et al* 1973). The second theory is one of a much earlier invasion of deep water, followed by major radiation and subsequent colonization of cold shallow water at high latitudes. The proponents of this theory argue that groups which are highly diverse in the deep-sea (*eg* members of the isopod superfamily Asellota) have their centres of generic and species diversity in the deep-sea (Hessler and Thistle 1975, Hessler *et al* 1979). Additional support for this argument is the residence of the most primitive species or families in deep water, the complete absence of eyes in deep-sea families, and the absence of eyes in shallow water confamilial species (Hessler *et al* 1979, Hessler and Wilson 1983). A number of authors support the recent origin of the deep Arctic Ocean fauna by reason of its few species, endemism almost solely at the species level and close relationships between the shelf and deep-sea faunas (Dahl 1972, Dahl *et al* 1976, Svavarsson and Stromberg 1987). Lipps and Hickman (1982) believe the faunal histories of the Antarctic and deep-sea are closely linked citing the potential faunal pathways and biological similarities between these two environments. Further contributing to views held earlier that the origin of deep-sea fauna was the shallow

Antarctic (Menzies *et al* 1973), or in the case of deep-sea molluscs, invasions from adjacent shallow water all over the world (Clarke 1962). Conversely, in their examination of the phylogeny of the isopod family Ilyarachnidae, Hessler and Thistle (1975) suggest this family originated and radiated in the deep-sea and then emerged to diversify in the Antarctic. Lipps and Hickman (1982) using Foraminiferan microfossil evidence, conclude that elements of the deep-sea and Antarctic faunas have accumulated by several processes, the majority of species having originated in place. A much smaller proportion of species have migrated between the deep-sea and Antarctic in one direction or another, with fewer still migrating into the deep from other areas (Gage and Tyler 1991). There is every reason to believe that the invasion of the deep-sea by species from the continental shelf is still in process (Dahl 1954). If active immigration is still taking place a taxon will have deep derivatives of many sub-littoral taxa, thus showing a low degree of taxonomic isolation, or conversely a high degree of similarity. In deep-sea gammaridean amphipods this seems to be the case (Barnard 1969, Hessler and Wilson 1983). Indeed, the genus *Ampelisca* seems to be a taxon in full speciation at the moment (Bellan-Santini and Dauvin 1989) which has radiated into deep-waters from pleisiomorphic littoral species (Bellan-Santini and Dauvin 1988a). A full discussion of the importance of *Ampelisca* in the deep NE Atlantic is given in Chapter Four.

3.3.2 Paleohistory of the Amphipoda

The fossil record of the Amphipoda consists of less than two dozen authentic species, from three (possibly four) superfamilies (Cragonyctoidea, Gammaroidea, Corophioidea, possibly Hadzioidea), none of which is older than the Upper Eocene (Bousfield 1983). Despite this, the probable ages of subordinal, superfamily and family groups within the Amphipoda can be deduced from continental geochronology, present geographic distributions and comparative morphology of superfamily groups (Bousfield 1982, Karaman 1984, Bousfield and Shih 1994). Thus, the continental distribution of the primitive gammaridean superfamily Crangoliopsidea parallels that of the Astacura (Decapoda), suggesting an early Gondwanian-Mesozoic ancestry

(Bousfield and Shih 1994). Similarly, the world distribution of the more primitive hypogean ingolfiellid amphipods would suggest a late Palaeozoic origin of the Amphipoda as a whole (Bousfield and Conlan 1990, Bousfield and Shih 1994). This would be consistent with the fossil record of other peracaridean groups (Isopoda, Tanaidacea and Cumacea) that extend back into the Lower Carboniferous. The earliest and most primitive crustacean groups (phyllopods, maxillipods and leptostran malacostracans) were mostly small, filter feeding and deposit feeding marine morphotypes. Their fossil records extend back into the early Palaeozoic and may indicate a Pre-Cambrian origin for the Crustacea *per se*. The abrupt appearance of major new eumalacostracan morphotypes in the Middle to Late Palaeozoic coincides with the contemporaneous evolution and proliferation of new vascular plant groups and attendant invertebrate faunas, which presumably formed a basic and major new food resource for these crustaceans (Bousfield and Shih 1994). The fossil record does seem to indicate however that most amphipod superfamily groups are of recent origin and evolution, probably since mid-Mesozoic (Bousfield 1982). The highly specialized Cyamidae must be more recently evolved than their whale hosts *ie* lower Eocene, whilst the Talitridae are unlikely to be older than their obligatory food and habitat plants which did not evolve until the Middle and Upper Cretaceous (Bousfield 1983, Bousfield and Shih 1994).

3.3.3 Deep-sea Amphipoda

Thurston (1980) examined the abyssal benthic amphipods from the East Iceland basin, and comments on the considerable body of literature and data dealing with the bathyal and abyssal gammaridean amphipods of the temperate north Atlantic Ocean. He cites the more important contributions to be those of Bonnier (1896), Chevreux (1900, 1927, 1935), Stephensen (1915, 1923, 1925, 1931, 1944) and Mills (1967, 1971). The first major work on deep-sea amphipods was that of T.R.R. Stebbing who monographed the *Challenger* Amphipoda. Stebbing received the amphipod material from AM Norman, who was responsible for the distribution of the *Challenger* zoological collections to specialists following the completion of her work in 1876.

Stebbing accepted the amphipod collection in 1882 and six years later published his results as volume 29 of the *Challenger* Report in two parts, of 1737 pages and 210 full-page plates (Stebbing 1888). Stebbing used the volume to review the history of the order Amphipoda and included sections on their phylogeny, nomenclature and distribution (Mills 1971). Stebbings' *Challenger* monograph became the definitive work in English on amphipods and is still useful today for nomenclatural and historical problems (Mills 1971). A similar but less ambitious project was started in Danish by A Boeck, but halted by the author's early death (Boeck 1872). Stebbing described sixty three presumed deep-sea benthic gammaridean amphipods. A reworking by Mills (1971) has since reduced this number to forty four. Mills refers to the inadequate sampling gear of the *Challenger* resulting in contamination of deeper benthic samples by pelagic species. To date, there are no known families of gammaridean amphipods unique to the deep-sea, with the possible exception of the Bathyceradocus-group which is of uncertain status (Thurston and Bett 1993). Barnard and Karaman (1991) report the number of Gammaridean amphipod families to be 91, with 1055 genera and 5733 species. About 40 of the 74 marine families can be classified as cosmopolitan in distribution but the other 34 are strongly confined to specific regions or thermal zones. The geographic distribution of non-cosmopolitan families, or those almost wholly confined to such classification is given in Barnard and Karaman (1991 pg. 25). This shows the following families strongly associated with the deep-sea: Hyperiopsidae, Pardaliscidae, Stegocephalidae, Stilipedidae, Synopiidae and Vitjazianidae. Thurston and Bett (1993) in an analysis of eyelessness in gammaridean Amphipoda, that of the more speciose families only three can be regarded as deep-sea taxa (Pardaliscidae, Stegocephalidae and Synopiidae). All three of these families have a high proportion of eyeless species. The Synopiidae are probably the most diverse of those families primarily confined to the deep-sea. Most deep-sea gammaridean families are adapted to an epibenthic life, with many feeding on the benthos. These adaptations make them successful in the deep-sea but not the hydrodynamically active shallow seas, where wholly nektonic or fossorial amphipods are the norm (Barnard 1972). Table III.V shows the genera of Gammaridea endemic to the deep-sea. *Lepechinella* is considered

TABLE III.V LIST OF ENDEMIC GAMMARIDEAN GENERA IN THE DEEP-SEA (# slightly less than 100%endemic)

ABYSSAL
Alicella, Aristiopsis, Astyroides, # Bathyceradocus, Bathychaderia, Bogenfelsia, # Bruzeliopsis, Bruunosa, # Caleidoscopsis, Cebocaris, Cedrosella, Clepidecrella, Elimedon, Epereopus, Eucallisoma, Galathella, Hopiphoxus, Lepechnelloides, Lepechinellopsis, Lepiduristes, Mesocyphocaris, Metaceradocoides, Necochea, Oedicerina, Paradryope, Parahalice, # Paralicella, Parandaniexis, Pardaliscopsis, Paronesimoides, Parpano, Pleustostenus, # Princaxelia, Steleuthera, Valettia, # Valettietta, # Vemana, Ventiella, Vitjaziana, # Urothoides.
BATHYAL or Deeper
Adeliella, Aficoecetes, Anoediceros, Arculfia, Aristiopsis, Austropleustes, Austrosyrrhoe, Bathyamaryllis, Bathyceradocus, Bathyphotis, Bathystegocephalus, Bonnierella, Bouvierella, Bruzeliopsis, Byblisoides, Caeconynx, Carangolia, Chevreuxiella, Chevreuxius, Clarencia, Cleonardo, Cleonardopsis, Coximedon, Coxophoxus, Cressina, Crybelocephalus, Crybelocyphocaris, Cyclocaris, Cyphocarioides, Cyphocaris, Danaella, Dautzenbergia, Dulichiopsis, Eurythenes, Eursirella, Eusirogenes, Eusiropsis, Eusyrophoxus, Falklandia, Finoculodes, Gainella, Halice, Halicella, Hansenella, Hirondellea, Hyperiopsis, Ileraustroe, Izinkala, Jeddo, Joubinella, Knysmetopa, Koroga, Latacunga, # Lepechinella, Lepidepecreella, Lepidepecreoides, Maeropsis, Megaceradocus, Membrilopus, Mesocyphocaris, Mesopleustes, Metacyclocaris, Metambasia, Metacyphocaris, Meteusiroides, Onesimoides, Palabriophoxus, Paracallisoma, # Paracentromedon, Paracyphocaris, Parahalice, Paralepechinella, Paralicella, Parandania, Parargissa, Pardaliscoides, Pareusirogenes, Pontogeneoides, Priscosyrrhoe, Procyphocaris, Prolaphystiopsis, Pseudamaryllis, Pseudharpinia, Pterunciola, Regalia, Runanga, Scopelocheiropsis, # Scopelocheirus, Stegocephalina, Stegoplax, Stephobruzelia, Stilipes, Thoriella, Tosilus, Valettiella, Valettietta, Valettiopsis.

(Adapted from Barnard and Karaman 1991)

by Barnard (1973) to be the most diverse gammaridean genus confined to the deep-sea. There are twenty nine species, most of which are probably ooze dwellers or weakly epibenthic, many have bizarre ornaments and a few have spinose bodies. Other speciose deep-sea genera include the *Oediceroides* (23 spp), *Syrrhoites* (20), *Harpiniopsis* (27) and *Harpinia* (17) (Thurston and Bett 1993). Barnard (1961, 1962) considers that the broad representation of gammaridean amphipods in the deep-sea, with no special development, is the pattern of a group that has invaded the deep-sea many times. This is a view echoed by Hessler and Wilson (1983), and Thurston and Bett (1993) who suggest the patterns of eyelessness among taxa indicate widespread colonization of the deep-sea, but little evolutionary radiation there. Kamenskaya (1984) proposed an ecological classification of deep-sea amphipods. Based on mode of life, swimming ability and type of feeding she defined two large ecological groups. The first she called 'pelagic' which contain pelago-benthic and purely pelagic amphipods. The second 'bottom and demersal', consisting of purely benthic and nekto-benthic amphipods, which she further subdivided into predators, detritus eaters and seston feeders. Mills, in his work on amphipods from five epibenthic trawl stations on the Gay Head - Bermuda transect (Mills 1971a, 1971b) showed that most families showed a marked change of species with depth. From these data he proposed six faunal groupings as a guide to the pattern of faunal change. These are a. Continental shelf fauna; b. Slope fauna (200-1000m); c. Slope to deep-sea transition (1000-2000m); d. Continental rise fauna (abyssal) (2000-2800m); e. Rise to deep-abyssal transition (2800-4000m) and f. Deep-abyssal fauna (below 4000m) (full details in Mills 1971). Mills observed that very few of the species in his groupings were in common with those of the deep-water collections in the north-eastern Atlantic (made by Stephensen between 1923-44) or those from the shallow-water collections from Arctic North America discussed by Dunbar (1954). From this Mills (1971) concluded that there was little evidence that the amphipod fauna of the North American basin had originated from immigration into deeper water from high northern latitudes. Instead he agreed with the hypothesis of Barnard (1962) that the fauna of each ocean basin is largely derived from the shallower depths on the adjacent continental margin.

Despite the apparent uniform environment of the abyss deep-sea amphipods are not, in general, cosmopolitan but endemic. This endemism seems to be correlated with barriers formed by continental and undersea topography, or distance because of low dispersal rates (Barnard 1961). This is highlighted by Kamenskaya (1981), who showed that amongst 8 species of endemic hadal amphipods there appeared two types of zoogeographical distribution in trenches. Amphipods with weakly developed musculature, legs and pleopods lived only in single trenches, whereas amphipods capable of active swimming occurred in two, three or more trenches. Further evidence supporting regional endemism is the high rate of recovery of new benthic species by each expedition to abyssal depths and low recovery of previously described species (Barnard 1961). Thus abyssal amphipods seem to be regionally endemic and more closely related to 'nearby' shallow water species than to cold-water species and appear therefore to be a product of recent speciation. The subjects of population subdivision and genetic flow in amphipods are rarely reported and limited to the following studies. Bucklin *et al* (1987) detected little genetic subdivision in amphipods over broad geographic areas, although there was significant difference between amphipods collected at different depths in the same area. France *et al* (1992) found significant genetic divergence between populations of hydrothermal vent amphipods inhabiting disjunct ridge axes, and hadal amphipods showed considerable morphological variation in areas separated by topographic highs (France 1993). In a study on necrophagus amphipods in the northeast and tropical Atlantic Ocean, Thurston (1990) reports little evidence to suggest that such species are endemic to particular abyssal plains. Indeed he concluded that in all probability there exists a single faunal entity between 8°N and 50°N. This Thurston attributes to their being highly motile, capable of extensive migrations up into the water column, where they overlap with meso- and bathypelagic species. As such there exists a necrophage/carnivore guild of species with a panoceanic distribution (Thurston 1990). In contrast, France (1994) showed genetic and morphological differentiation between a population of scavenging amphipods living in a deep-sill basin, isolated from a population living in shallow-sill basins off the California Continental Borderland.

3.4 TAXONOMY

Despite the poor condition of the material, eighty one of the eighty two species have been identified to at least family level, and all but two of the sixteen most abundant species (which make up over 80% of the total collection) to species level. Overall twenty four of the species are identified to species level, seven tentatively identified as new species, twenty one identified to genus level, one specimen may represent a new genus and the remaining twenty seven identified to family level. One specimen proved too badly damaged and too small to identify even to family level. The species are listed below in order of abundance, prior to identification each species was given a number when initially sorted, see Table III.I, and these are given in parenthesis.

Podoceridae	*Dulichiopsis abyssi*	(sp.23)
Ampeliscidae	*Ampelisca* sp nov	(sp.7)
Phoxocephalidae	*Pseudharpinia brevirostris*	(sp.18)
Corophioidae	*Autonoe aff longidigitans*	(sp.21)
Phoxocephalidae	*Leptophoxoides molaris*	(sp.17)
Lysianassidae	*Tryphosella biloba*	(sp.3)
Corophioidae	*Aoridae* sp	(sp.22)
Eusiridae	*Rhacotropis gislii*	(sp.10)
Synopiidae	*Lactacunga* sp nov	(sp.37)
Synopiidae	*Syrrhoites* sp nov	(sp.31)
Dexaminidae	*Lepechinella helgii*	(sp.14)
Lysianassidae	*Tryphosella* sp	(sp.49)
Eusiridae	*Cleonardopsis carinata*	(sp.11)
Amphilochoidea	*Amphilocus* sp	(sp.34)
Lysianassidae	*Orchomene pectinatus*	(sp.2)
Phoxocephalidae	*Harpinia plumosa*	(sp.19)
Dexaminidae	*Lepechinella skarphedini*	(sp.60)
Pardaliscidae	gen	(sp.29)

Pleustidae	*Stenopleustes* sp	(sp.5)
Synopidae	*Bruzelia* sp nov	(sp.25)
Isochyoceridae	*Bonnierella* sp	(sp.24)
Oedicerotidae	gen	(sp.36)
Pardaliscidae	*Pardalisca* sp	(sp.30)
Synopidae	*Jeddo simplisyrrhis*	(sp.26)
Synopidae	*Syrrhoites* sp nov	(sp.33)
Melphidippidae	gen	(sp.69)
Oedicerotidae	gen	(sp.63)
Lysianassidae	*Tryphosella* sp	(sp.50)
Pardaliscidae	gen	(sp.41)
Oedicerotidae	*Synchelidium* sp	(sp.46)
Pardaliscidae	*Parpano*	(sp.43)
Pardaliscidae	*Halice*	(sp.27)
Pardaliscidae	gen	(sp.28)
Eusiridae	*Rhachotropis proxima*	(sp.13)
Stenothoidea	*Proboloides* sp	(sp.9)
Liljeborgiidae	*Liljeborgia* sp	(sp.53)
Eusiridae	*Eusiris* sp nov	(sp.8)
Synopiidae	*Pseudotiron golens*	(sp.38)
Phoxocephalidae	*Pseudharpinia brevirostris*	(sp.20)
Stegocephalidae	gen	(sp.4)
Eusiridae	*Rhacotropis rostrata*	(sp.12)
Lysianassidae	*Tryphosella* sp	(sp.52)
Lysianassidae	*Tryphosella* sp	(sp.51)
Lysianassidae	*Cyphocaris challengeri*	(sp.39)
Oedicerotidae	gen nov	(sp.71)
Oedicerotidae	gen	(sp.12)
Dexaminidae	*Lepechinelloides karii*	(sp.15)
Eusiridae	*cf Cleonardopsis*	(sp.61)

Pardaliscidae	gen	(sp.47)
Ampeliscidae	gen	(sp.70)
Pardaliscidae	*Halice* sp	(sp.56)
Ampeliscidae	*Ampelisca* sp	(sp.42)
Pardaliscidae	*Halice macronyx*	(sp.32)
Lysianassidae	*Cyphocaris anonyx*	(sp.35)
Lysianassidae	gen	(sp.44)
Lysianassidae	*Cyphocaris* sp	(sp.40)
Melphidippidae	gen	(sp.45)
Stilipedidae	*Astyra* sp	(sp.55)
Dexaminidae	*Lepechinella* sp nov	(sp.66)
Corophiidae	gen	(sp.88)
Oedicerotidae	gen	(sp.65)
Vibilidae	*Vibilia* sp	(sp.54)
Lysianssidae	*Orchomene* sp	(sp.57)
Lysianassidae	gen	(sp.58)
Lysianassidae	*Ichnopus* sp	(sp.59)
Lysianassidae	*Hippomedon* sp	(sp.62)
Oedicerotidae	gen	(sp.64)
Phoxocephalidae	*Joubinella ciliata*	(sp.67)
Lysianassidae	*Crybelocephalus megalurus*	(sp.68)
Oedicerotidae	sp	(sp.72)
Lysianassidae	gen	(sp.74)
Oedicerotidae	gen	(sp77)
Lysianassidae	*Cyphocaris* sp	(sp.79)
Oedicerotidae	gen	(sp.80)
Oedicerotidae	gen	(sp.81)
Oedicerotidae	gen	(sp.83)
Pardaliscidae	*Halicoides* sp	(sp.84)
Pardaliscidae	gen	(sp.87)

Oedicerotidae *Monoculoides* sp (sp.89)

This species list reveals that the most diverse families found at the Permanent Station are the Lysianassidae, Oedicerotidae and Pardaliscidae, with 17, 13 and 12 species respectively. The Phoxocephalidae, Synopiidae and Dexaminidae also seem important in terms of both number of species and number of individuals. Over twenty five percent of the collection is represented by the single species of Podoceridae, *Dulichiopsis abyssi.*

This collection extends the bathymetric distribution of one species of Phoxocephalid and the geographical range of three species of Lysianassid. These are discussed below along with a description of the adaptions of these two families to the deep-sea habitat. Following this are brief taxonomic notes on some of the more common species not yet identified to species level.

The Phoxocephalidae are represented in this collection by four species, *Pseudharpinia brevirostris, Leptophoxoides molaris, Harpinia plumosa* and *Joubinella ciliata.* Three of these are amongst the most abundant species in the collection, making this family important in both numbers and diversity. This is a family that expresses many fossorial adaptions – powerful antennae, rostra, pereopods and uropods. These appendages are often heavily armed with thin setae (or sparsely armed with heavy elements). Of the two evolutionary lines within this group of amphipods the Phoxocephalinae line is presumed to be the more primitive. They show strong sexual dimorphism, males being strong swimmers with large eyes, longer antennae with sensory armature and stronger pleopods. The more adavanced Harpiniinae show very little sexual dimorphism, some workers have even proposed that some species may be hermaphrodites. Barnard and Karaman (1991) remark that spination and powerful appendages become much reduced (the exception being *Palabriaphoxus*) in the deep-sea, pereopods 5 and 6 become thin and poorly armed. These authors point to the presence of setae on the rami of uropods 1 and 2 as being a feature of deep-sea or cold water phoxocephalids

eg. *Pseudharpinia, Heterophoxus* and *Hopiphoxus*. Another adaption to a deep-sea habitat appears to be loss of setae on the maxilla and maxillipeds, and the reduction of maxillipedal plates in the Phoxocephalinae and Harpiinae. Phoxocephalidae being a dominantly fossorial group of Amphipoda show limited neritic phases, both females and immature males are benthic burrowers in fine grained sediment. The fossorial ecotype has meant a significant descent into the deep-sea (Barnard and Karaman 1991). Here they have radiated into seven genera and fifty species. Barnard and Karaman report that the Phoxocephalid fauna in the North Atlantic is impoverished with only four genera, most species occurring in the blind *Harpinia*. This genus is believed to have followed a bathyal pathway from the deep Austral and emerged into open niches in the North Atlantic onto sublittoral shelves. The Harpiniin group of genera is poorly described, Barnard and Drummond (1978) suggest the seven genera do not adequately express the known diversity. Part of the problem appears to be the lack of descriptions of male specimens. *Harpinia* is a very similar genus to *Pseudharpinia*, differing essentially in the features of the male second antennae. As most males have yet to be described and since it is very difficult to assign females to the correct genus, Barnard and Drummond have suggested that species of *Harpinia* be confined to the North Atlantic. This collection extends the bathyal distribution of one species of this genera, *Harpinia plumosa,* from cold North Atlantic and Artic bathyal (Barnard and Karaman 1991), to abyssal depths.

The Dexaminidae are represented in this collection by four species and two genera, *Lepechinella helgii, Lepechinella skarphedini, Lepechinella* sp and *Lepechinelloides karii. Lepechinella* is said by Barnard (1973) to be the most diverse genera confined to the deep-sea. It is a marine, cosmopolitan, cold water genus, reported from 260-7160m and represented by twenty nine species. *Lepechinelloides* is a marine boreal species, represented by one species. It was found in abyssal hauls between 2663 and 2714 m depth in the East Iceland Basin (Thurston 1980b). Barnard placed the Lepechinellids into the family Dexaminidae along with the Atylidae, Prophliantidae and Anatylidae. He proposed two evolutionary lines within the family, a prophiliantin and

dexaminin line. Thurston (1980b) comments on the recognised similarity between *Atylus* and *Lepechinella*, and the close relationship between the latter genus and *Paralepichinella* and *Lepechinelloides.* He suggests the similarities within this group of genera could imply an atylin line within the Dexaminidae. Barnard (1973) suggests that because no *Atylus* is known to occur in the deep-sea and no *Lepechinella* occur in depths under 1000m, that *Lepechinella* may be cold adapted, substrate adapted and because they lack eyes dark adapted. In contrast *Atylus* is adapted to coarse sediments, it is eurythermic and light adapted. Barnard also suggests that the main advance towards dispersal in the deep-sea involves the loss of eyes and the development of fleshy lobes on the lower lip, rather than any implied thermal adaptions or development of slender appendages. This suggestion is based on the eurytopicity of *Atylus* and the main difference between this genus and the *Lepechinella* of well developed inner lobes of the lower lip. The lepechinellids may have found a habitat in the deep-sea not open to other dexaminids by means of the following adaptions. The extension of appendages, increase in the number and/or size of body processes and the proliferation of articulate spines on the body surface. These features may allow the lepechinellids to live on the soft ooze substrate of the deep-sea without sinking. Barnard (1973) suggests the inner lobes of lepechinellids may increase the 'sucking' capability of the mouthparts by added closure of the buccal channels, and that this may help in the processing of the extremely fine particles of deep-sea sediments.

Lepechinelloides karii, Lepechinella helgii and *Lepechinella skarphedini* have previously only been reported in samples taken from the East Iceland Basin, 60^0 N 20^0 S between 2636 and 2708m (Thurston 1980b). This collection extends their reported geographical range to include the Rockall Trough. *Lepechinella* sp (species 66), proved difficult to identify using the keys in Barnard (1973), and differed markedly from the other *Lepechinella* in the collection. It was represented by two incomplete specimens in one sample. Thurston (1980b) reported that many interspecific characters used in the *Lepechinella* genus are quantitative rather than qualitative. Most species were also known from only a few specimens so the degree of interspecific variation is unknown. The volume of material he collected in the East

Iceland Basin showed a common pattern of sexual dimorphism and allometric growth. The body processes were also shown to increase with increasing body size, there were marked variations in the antennae of terminal males, the rostrum showed gross intraspecific variations as did general body setation and spination. So these specimens could just be immature specimens or specimens showing a marked degree of intraspecific variation. In this collection the four species of Dexaminidae account for 3.9% of the total number of specimens. In contrast in Thurstons' collection in the East Iceland basin the lepechinellids accounted for 12.2% of the total.

Lysianassidae *Tryphosella* sp (sp.49)

Family diagnosis: article 3 of gnathopod 2 elongate, remainder of appendage forming mitten apically, peduncle of antenna one short and stout, articles 2-3 much shorter than 1 and partly telescoped basally.

Family description: body compact, smooth and shiny chitin, accessory flagellum usually present and more than 3 articulate but occasionally vestigial, mouthparts variable, smooth broad incisor bounded by cusp each side in most species, rarely toothed in middle, inner lobes of lower lip absent, gnathopod 1 usually small rarely enlarged, variable, configuration of coxae 1-4 variable, gnathopod 2 always small, pereopods relatively uniform, rarely prehensile, uropods 1-2 ordinary but inner ramus occasionally notched, uropod three generally ordinary, rarely reduced, telson variable.

Genus diagnosis: mouthparts forming quadrate bundle. Labrum and epistome differentially produced, prominent, separate, epistome slightly to strongly dominant in size and projection, blunt. Incisor ordinary, molar simple, small, setulose, palp attached opposite molar. Inner plate of maxilla 1 weakly (2) setose, palp 2-articulate, large. Inner and outer plates of maxilliped well developed, palp strongly exceeding outer plate, dactyl well developed. Coxa 1 slightly shortened, tapering, and partly covered by coxa 2. Gnathopod 1 subchelate, palm oblique, or transverse, articles 5 and 6 subequal or 5 longer than 6, dactyl large, article 6 of gnathopod 2 greatly shorter than article 5, ordinary, propodus minutely subchelate. Inner ramus of uropod 2 without a notch. Uropod 3 ordinary, peduncle ordinary, inner ramus slightly shortened, outer ramus 2-

articulate. Telson ordinary (type) or elongate, deeply cleft.
This species is characterized by its reduced pereopod seven. The merus of pereopod seven is shorter than the merus of pereopod six. Its coxae one is large, broadly expanded distally compared to normal coxae one shape. Coxae one wider than coxae two. No boss on urosome one, just gently rounded.

Oedicerotidae species (sp.36)
Family diagnosis: Pereopods 5-6 equally short, pereopod 7 immensely elongate and of different shape than pereopods 5-6, pereopods weakly fossorial, head large, eyes when present dorsally appressed or fused together, telson short, entire or emarginate, apices of rami on uropods 1-2 naked or bearing immersed nails, no subapical spines.
Family description: Head large, rostrum present or absent, mouthparts basic, coxae large, urosomites 2-3 rarely fused together, uropod 3 with elongate peduncle.
This species's pereopod seven has a relatively slender and pyriform article two. The antenna one is short, less than head and pereonite one combined. The carpus of both gnathopods are strongly lobate, with this lobe at right angles to the axis. The gnathopod propods are elongate and ovate, palms extend for three quarters of the length. The rostrum of this species is obsolescent.

Lysianassidae *Tryphosella* sp (sp.50)
Family and genus decriptions as species 49.
Similar to species 49, differences being: A short vertical posterior margin of urosome one, more angular. The coxae one of this species is distally slightly flat and the pleonite three more humped posteriorly (bossed).

Liljeborgiidae *Liljeborgia* sp (sp.53)
Family diagnosis: accessory flagellum 2+articulate, molar of mandible feeble, not triturative. Gnathopods powerful, carpus of at least 1 pair well produced. Plates of maxilliped only moderately developed. Telson cleft, each apex with spine(s) in notch.

Genus diagnosis: Accessory flagellum 4+articulate. Epistome poorly produced. Article 1 of mandibular palp elongate, molar simple. Coxae 1-4 ordinary. Gnathopod 2 not smaller than 1, propodus and carpus of gnathopods not setose anteriorly, carpus of gnathopods 1-2 strongly produced. Outer ramus of uropod 3 1-articulate. Each lobe of telson with 1 apical spine.

Genus description: Article 2 of peduncle on antenna 1 usually very short, longer than half of article 1. Dactyls of gnathopods usually deeply toothed or serrate.

This species has a mid dorsal tooth on urosomite one, and a broad long telson cleft half way with diverging apices. The maxillipeds have prominent palps, but outer plates are small. The mandibles have a normal incisor, but a strong lacinia mobilis. On the right mandible, molar process is non-existent, just a slight ridged protuberance with a few large setae. There is a small tooth on pleon two.

This species is similar to *Liljeborgia fissicornis* (Sars 1858), except the telson is dissimilar, as is the base of pereopod five, and there is no tooth on epimeron three- its quadrangular.

Lysianassidae *Tryphosella* sp (sp.52)

Family and genus description as species 49.

This is similar to the *Tryphosella* (sp.49), however it differs by having a very upright boss on urosomite one. The gnathopod one is also different, with an enlarged propod five times as long as the carpus and expanded. The carpus is very small and triangular in shape.

Lysianassidae *Tryphosella* sp (sp.51)

Family and genus description as species 49

This species is again similar to species 49, but differs in the following ways:

Gnathopod one is slender and curved, expanded slightly at the distal end. Pereopod five has a tapered article two. There is a low triangular boss on urosome one which is not overhanging. The merus of pereopods five, six and seven all appear approximately the same.

Ampeliscidae *Ampelisca* sp nov (sp.7)

Family diagnosis: Urosomites 2-3 coalesced. Pereopods 5-6 alike but pereopod 7 of distinct structure, article 2 with distinct, usually broad posteroventral lobe, article 2 of pereopods 5-6 rhomboid or diamond shaped and poorly lobed. Eyes when present composed of internal pigment masses served by 2-4 external cuticular lenses. Acessory flagellum absent. Article 4 of pereopods 3-4 elongate, article 6 much shorter than 4 and article 5 much shorter than six, these pereopods glandular. Head very large. Gnathopods feeble. Uropod 3 biramous. Telson laminar.

Genus diagnosis: Flagella of antennae 1-2 with 5 or more articles. Article three of palp unproduced. Article 2 of pereopod 7 with posterior margin oblique and article expanding ventrally, rarely parallel to anterior margin, anterior margin of posteroventral lobe near junction with article 2 not setose. Telson much longer than broad, cleft over half its length.

Genus description: Head generally long and low. Mandibular palp stout, article 3 slender, equal to or shorter than 2. Coxae 1-4 generally elongate, coxa 1 not as prominent, coxae 2-3 usually not tapering, lower part of posterior margin of coxa 4 parallel to anterior margin and usually elongate.

This species has very similar articles of pereopod seven, none are produced or inflated (article five slightly produced distally). Articles three and four are sub equal in length. Pleon four has a very small dorsal process, and epimeron three a tooth.

This species is similar to *Ampelisca odontoplax* described by Sars (1879), except that the pereopod basal to distal posterior expansion is almost a perfect curve from article three to coxae, in *A. odontoplax* it is angular. The antenna one peduncle is less than or equal in length to antenna two peduncle. There are elongate spines on only one rami of uropod two not both, and pereopod seven carpus has three spines. The shape of article two of pereopod seven is also different to that of *A. odontoplax*. The size of this species is also half that reported for *A. odontoplax.*

Corophioidae *Autonoe* sp nov (sp.21)

Family diagnosis: as for species 24.

Genus diagnosis: Article 3 of mandibular palp with posterior margin distally concave, proximally straight, left mandibular molar with complex plates, primary plate triangular, the margins approximately straight, secondary, tertiary and quartenary plates of similar shape or vestigial, anterior margin of maxilliped without wing-like flanges, male gnathopod 1 propodus subequal with carpus or longer, uropod 3 peduncle elongate, not markedly expanded, rami with marginal spines, but no marginal setae, outer ramus with small second article.

This species keys out to the *Autonoe* genus, using diagnostic keys in Barnard and Karaman (1991). It is very similar to *Autonoe longiditans* (Bonnier, 1896) from the Gulf of Gascogne and Myers' Davis Strait material. However this species differs from these authors' descriptions in the following features; there are two strong teeth on the palm of gnathopod one. The lower anterior margin of the head is different. The male has short sternal projections on pereonites three and four. The falcate part of the mandibular article three looks different at fifty three per cent. Coxae one in this species is slightly less acute. Antenna two, article three has a wing. The pereopods three and four of this species are more slender, as is pereopod five. The propod of pereopod five is expanded weakly distally, not tapered as in *A. longiditans*. The distal ventral projection of uropod one is shorter, and the epimeron one is shallower and more drawn out posteriorly. The peduncle of uropod three is distally broadened especially basally and has a distinct medial flange.

So this species is referred to at present as *Autonoe* sp nov aff. *longiditans*.

CHAPTER FOUR
POPULATION BIOLOGY

4.1 INTRODUCTION

Thiel (1992), outlined the importance of understanding the dynamics of deep-sea populations in order to predict their recovery from impacts such as waste dumping or deep-sea mining. The deep-sea however is a remote habitat, inaccessibility and technical difficulties render its study difficult. This has resulted in a very limited knowledge of the rates and energetics of biological processes in the deep-sea biota. The currently known data are reviewed by Gage (1991), who shows that previously held ideas of slow process rates prevailing in the deep-sea are unfounded. There are limited data available on recolonisation experiments (Grassle 1977, Grassle and Morse-Porteous 1987) and direct observations of growth (Lampitt 1990). However the main method available to study population processes in the deep-sea relies on analysis of length-frequency data. This approach was previously deemed unsuitable for studies of deep-sea species, which were thought to breed continuously in the constant temperature regime. As such there would be no variation in recruitment and no detectable changes in population number or biomass. The discovery of seasonality in gametogenesis, recruitment and growth in certain deep-sea invertebrates (see Chapter Two) allows the possibility of separating age classes by length-frequency analysis (Gage 1986, 1992). The majority of deep-sea species however do not reproduce seasonally, but there is increasing evidence for peaks in recruitment of many macrofaunal species in the Rockall Trough (Gage 1986, Harrison 1988, Bishop and Shalla 1994). These recruitment peaks are related to the seasonal input of phytodetritus to the seafloor (see Chapter Two). Using length-frequency analysis and skeletal growth marks, Gage (1986, 1992) studied the growth and secondary production of a number of bivalve and echinoderm species from the Rockall Trough. Unfortunately the majority of invertebrates in the deep-sea are soft bodied or shed their exoskeletons and so have no similar growth marks. This means year classes can only

be separated on the basis of peaks in size frequencies. This requires the measurement of a large number of individuals to minimise random effects, especially if small size intervals are used (Gage 1992). Problems of sample size are thus prevalent in analysis of deep-sea samples which are often small, non-quantitative and suffer from sampler bias. Study of growth in deep-sea crustaceans is further hampered by virtue of their ecdysial growth. Without direct observations of molt frequency, peaks in length-frequency relate to instars rather than age classes. So any growth parameters determined from such peaks lack an absolute time base (Ingram and Hessler 1987, Gage 1992). Ingram and Hessler (1987) used inferences from instar analysis to determine population structure and growth rate in *Eurythenes gryllus*. They followed a shift in size of a distinctive cohort thought to have resulted from increased recruitment following an El Nino event. Difficulties in estimating secondary production and population dynamics also affect studies of shallow water amphipods. Methods of overcoming sampling bias against early life history stages and the difficulty of distinguishing individual cohorts are reviewed by Wildish and Peer (1981).

4.2 MATERIAL AND METHODS

4.2.1 Choice of species

From considerations of the importance of sample size as mentioned in the introduction and as observed by Thurston (1979) that in deep-sea species '*..it is rare for a single species to be sufficiently abundant, even in a series of samples for a population analysis to be practical.*' it is necessary to choose abundant species in terms of number and representation in samples, for further ecological studies. From data in Table III.II we can see that *Dulichiopsis abyssi* (species 23) is the most abundant species in this study. However it was also one of the species most affected by dehydration and sorting damage, and thus unsuitable for further investigations. Thus *Ampelisca* sp nov (species 7) was selected as one of the species for further population-, reproductive- and feeding-biology studies. Not only is this species common in the samples, it belongs to an important genus in the geographic area of this study. The genus *Ampelisca* is

represented in the NE Atlantic by fifty two of the one hundred and fifty known species in the world, thirty four of which are known only from this region (Bellan-Santini and Dauvin 1989). The great diversity of the genus and its relative homogeneity suggest it constitutes a taxon in full speciation at the moment. Analysis of fifty one characters in the genus show highest apomorphic indices for the four bathyal species. This suggests a recent radiation into deep-waters from plesiomorphic littoral species (Bellan-Santini and Dauvin 1988a). The *Ampelisca* genus appears to have radiated in two directions, to the deep-sea and to high latitudes, from a littoral group in temperate and tropical zones (Bellan-Santini and Dauvin 1988a, 1988b and 1989). Bellan-Santini and Dauvin (1988a) regard the ampeliscids as good faunistic material for studies concerning systematics, biology, ecology and biogeography. The biology of ampeliscids renders them easy to model, being essentially sedentary infaunal organisms. Thus, their population structure can be more readily assessed and simulated without the complications of massive emigration or immigration (Coyle and Highsmith 1994). Aspects of the feeding and reproductive biology of ampeliscids that also influenced the choice of this species for study, are discussed further in Chapters Five and Six.
Table III.II reveals a number of species with similar abundances and distribution in the samples from which to choose a second species for study. *Tryphosella biloba* (species 3) was chosen firstly because of its numerical importance, and secondly the presence of a number of brooding females. This condition was rare in other amphipods in this study and thus important in the reproductive analysis of Chapter Six. *Tryphosella biloba* also belongs to a large cosmopolitan family important in cold and deep waters, the Lysianassidae. The family Lysianassidae is also considered to have a feeding biology different to that of *Ampelisca, ie* scavenging as opposed to microphagous detritivore. This theme is discussed further in Chapter Six.

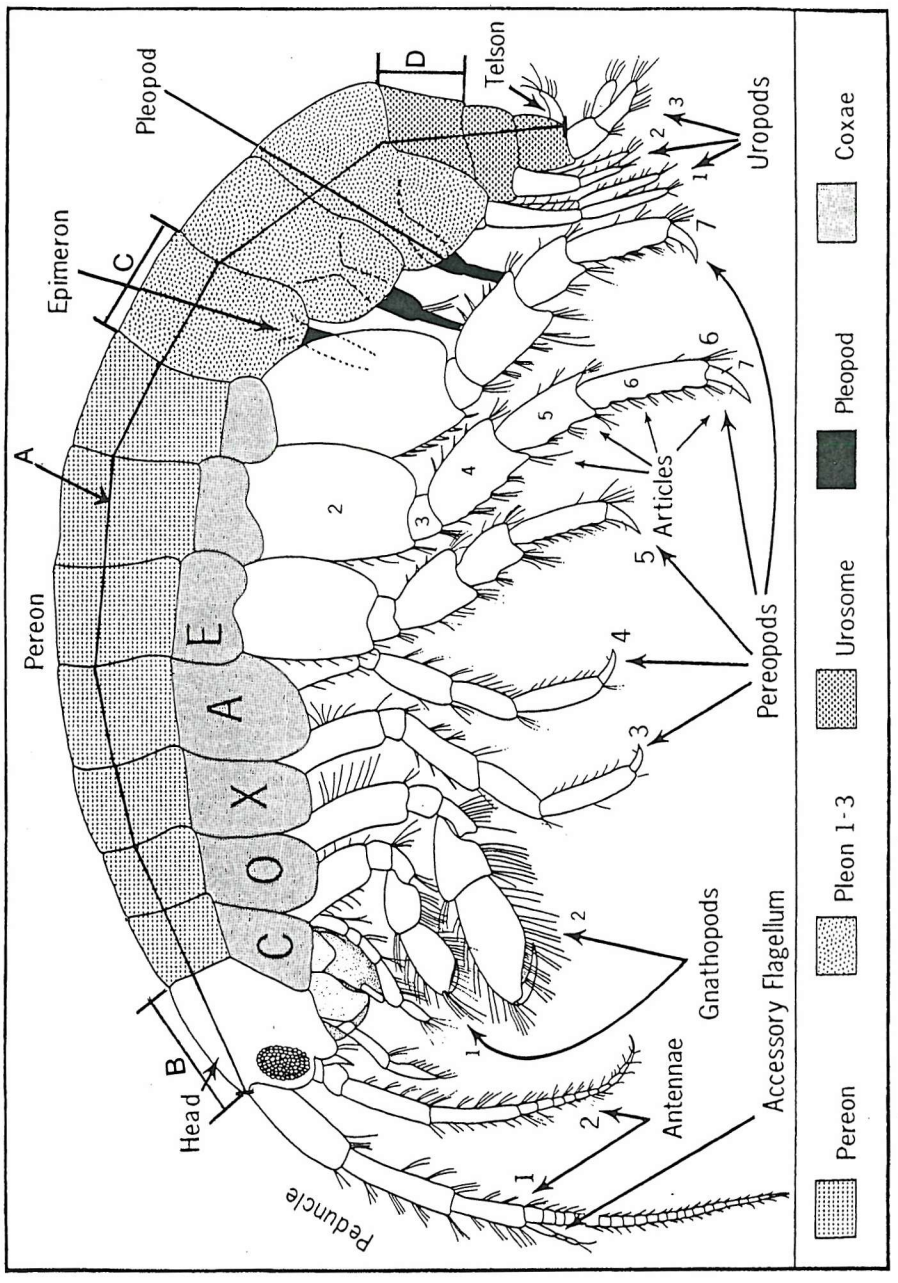
4.2.2 Measurement

Total body length has long been used as a routine method to obtain life history, biomass and production data for amphipod species. Despite the necessity for accurate and precise body length estimates, there has been little technological progress in the

methodology of measuring this parameter. This problem was highlighted by Quigley and Lang (1989) who compared traditional methods, forcep/occular micrometer and map wheel/camera lucida, to a more modern approach using a digitizer and camera lucida. The latter method proved to be more accurate, precise and quicker. Thus in this study length measurement was initially conducted with a Wild M5 microscope fitted with a camera lucida. Amphipods viewed through the microscope were traced on a TDS digitizing tablet coupled to a BBC microcomputer, running software developed by J.D Gage of the SMBA. This system however suffered from technical failures and data loss on a frequent basis. So when a new package from Jandel Scientific software (Sigma-Scan), became available late in this study, measurements were repeated. This system, although still not fully compatible with other software packages, did allow transfer of data onto computer disc for later analysis. In the future it may be possible to use fully automated systems to count, measure and identify zooplankton samples. A basic package has already been developed and tested (Jeffries *et al* 1984). Measurements of total length were made from tip of rostrum to the base of the telson. Traditionally this measurement is made along the dorsal margin of a straightened amphipod. However preserved samples often die in curved postures making such measurement difficult and inaccurate. A more satisfactory measurement is one made from the tip of rostrum, through the head and along a line connecting the points of articulation between body segments, to the base of the telson (Figure 4.1) (M Thurston *pers comm*). Each species had additional measurements made of head length and pleon one length for each specimen. For *Tryphosella biloba* an additional measurement of the length of urus one was made. These lengths were to used to test the best morphological character to predict total length from fragmented specimens. These characters were chosen as they proved easiest to identify and measure in specimens that often lacked limbs and large portions of the main body.

FIGURE 4.1 MEASUREMENTS MADE ON EACH SPECIMEN

KEY A - TOTAL LENGTH B - HEAD LENGTH
C - PLEON 1 LENGTH D - URUS 1 LENGTH



(from Barnard and Karaman 1991)

4.2.3 Regressions

Simple linear regressions, were performed on the data to assess the relationships between total length and length of the morphological characters measured. Analysis of variance (ANOVA) was used to calculate the probability of association between the independent and dependent variables.

4.2.4 Length-frequency and sex ratios

When the best predictor of total length had been determined, length-frequency histograms were plotted from the data obtained using the regression. Size frequencies were determined for the population as a whole, and for monthly variations. Sex ratios for the two species were determined, again for the total population and monthly variations.

4.3 RESULTS

Ampelisca sp nov

The results for the regressions using the independent variables juvenile, male and female length and dependent variables head, and pleon length are given in Table IV.I. This table shows the regression equation, correlation coefficient (r), F statistic from the ANOVA test and probability value (P). Correlation coefficients measure how good a description of the relationship between independent and dependent variable is provided by the regression. Values close to unity indicate a perfect prediction, a value of 0 indicates no prediction can be made. The larger the F statistic, the better the independent variable is at predicting the dependent. The smaller the P value, the better the association is between the two variables. All regressions passed a normality test, indicating the source population is evenly distributed around the regression line.
The results for *Ampelisca* sp nov indicate that all the dependent variables increase as

TABLE IV.I REGRESSION RESULTS FOR *Ampelisca* sp nov

JUVENILE HEAD LENGTH = 0.12291 + (0.12336 x JUVENILE LENGTH)		
r = 0.810	F = 140.79	P <0.001
JUVENILE PLEON LENGTH = -0.0719 + (0.11268 x JUVENILE LENGTH)		
r = 0.836	F = 171.12	P < 0.001
MALE HEAD LENGTH = 0.24499 + (0.09471 x MALE LENGTH)		
r = 0.866	F = 146.388	P < 0.001
MALE PLEON LENGTH = -0.10926 + (0.12483 x MALE LENGTH)		
r = 0.901	F = 210.400	P < 0.001
FEMALE HEAD LENGTH = 0.37767 + (0.07152 x FEMALE LENGTH)		
r = 0.717	F = 57.030	P < 0.001
FEMALE PLEON LENGTH = 0.11103 + (0.06933 x FEMALE LENGTH)		
r = 0.693	F = 49.828	P < 0.001

TABLE IV.II SEX RATIO RESULTS FOR *Ampelisca* sp nov

MONTH	No. of MALES	No. FEMALES	% FEMALES
JAN	9	10	52.63
FEB	5	10	66.6
MAR	0	6	100
APRIL	35	14	28.5
MAY	11	39	78
JUNE	5	11	68.7
AUG	10	26	72
SEPT	4	17	80.1
OCT	0	2	100
NOV	14	15	52
TOTAL	93	145	60.9

the independent variables increase ($P<0.001$). For the juveniles, correlation coefficients and F statistics indicate that pleon one length would be a better predictor for total length than head length. The same is true for the males and females. Prediction of total length using pleon or head length will require the re-arrangement of the regression equations. Interestingly pleon one length would seem to be a better predictor of total length for males than for juveniles and females. The same is true for head length.

Length-frequency histograms were prepared from regressions using pleon one length as the predictor where possible. Unfortunately damaged specimens were more often than not missing tail ends, requiring the use of the head length regression. The length-frequency histogram for the population as a whole (Figure 4.2), shows a bimodal distribution. Juveniles seem to dominate in the population, this is seen more clearly in Figure 4.3. Very few males are caught in relation to females and juveniles, and females appear to reach a larger adult size. There are no clear peaks in the length-frequency distributions for males that could be attributed to instars or cohorts. The irregular shape of the plot is more a function of low numbers than any polymodality. Both male and female histograms seem to demonstrate a normal distribution. Although not distinct peaks, the female histogram does however appear to contain five possible abundance peaks centred on 4.1, 4.6, 5.1, 5.8 and 6.7 mm. There is also an indication in the juvenile histogram of three abundance peaks centred on 2.2, 2.6 and 3.2 mm. The length-frequency histograms showing monthly changes in the population show little variation for adults, but increased juvenile numbers in May, June, August and September. Since there are no clearly separable cohorts, a population analysis would seem impossible for *Ampelisca* sp nov.

Sex ratio results are presented in Table IV.II. The population as a whole shows a female bias, 61% being females. There are clear variations with month, but females dominate in all months (range 52.6 to 100%) except April.

FIGURE 4.2 LENGTH-FREQUENCY HISTOGRAM FOR *Ampelisca* sp nov TOTAL SAMPLE

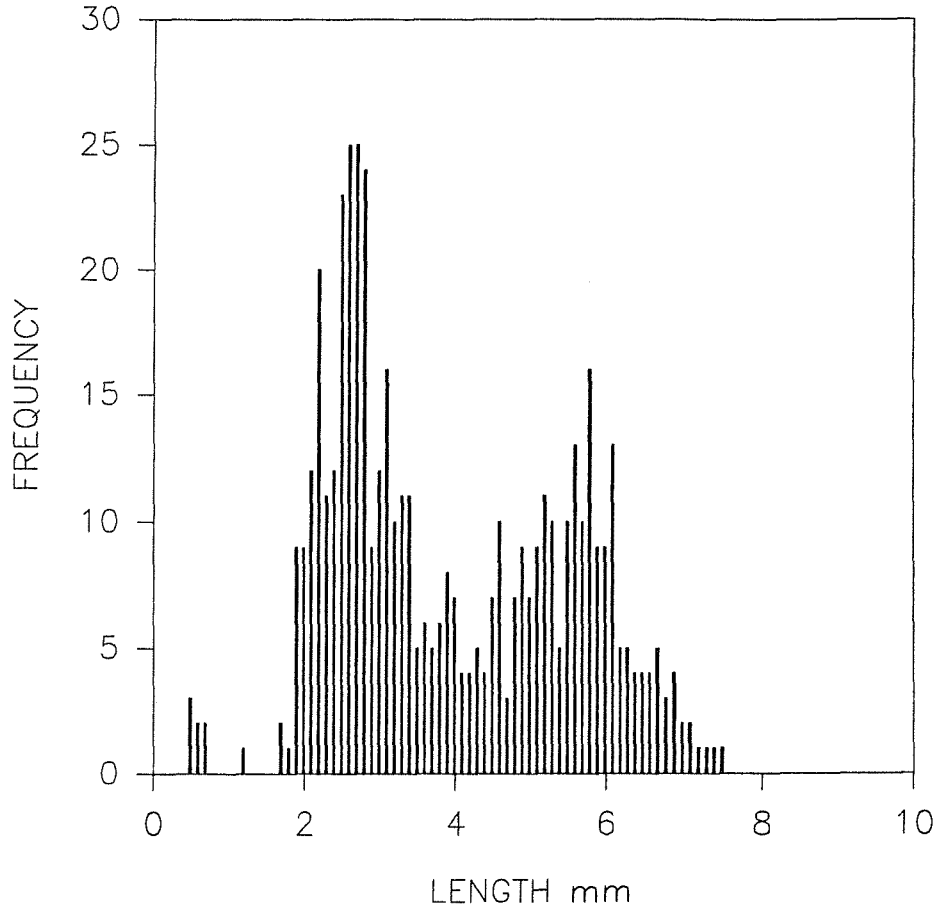
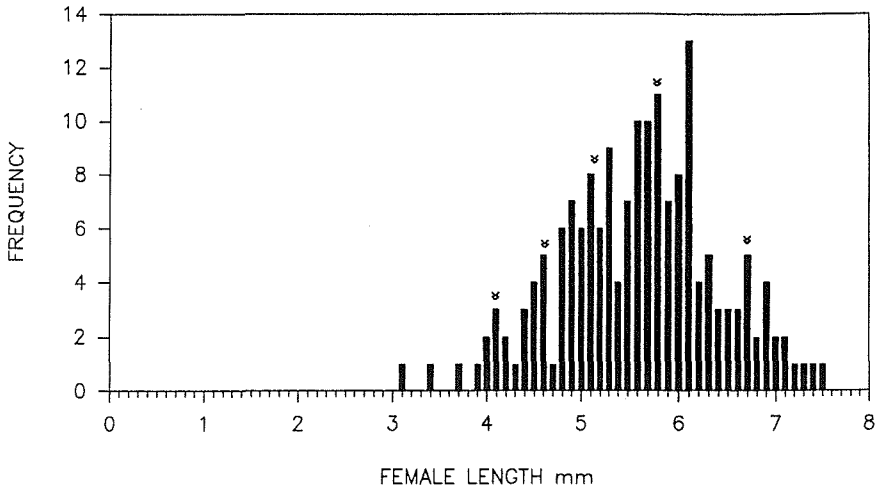
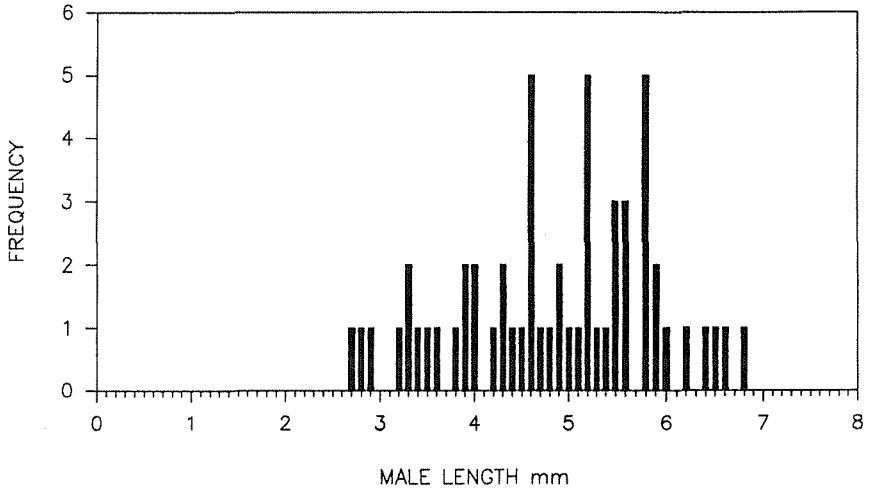
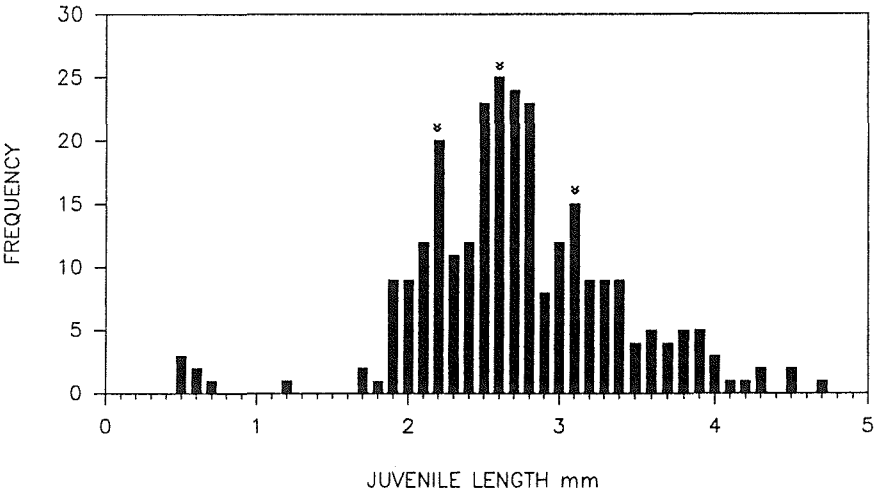


FIGURE 4.3 LENGTH-FREQUENCY HISTOGRAMS FOR *Ampelisca* sp nov FEMALES, MALES AND JUVENILES







In April the population appears to become male dominated, 71.5 % males to 28.5% females.

Tryphosella biloba

Regression results for the females of this species are given in Table IV.III. As can be seen from the correlation coefficients, F statistics and P values, there is no relationship between female length and any dependent variable. This is probably due to the small sample size (N=17), (Dr. E. Free *pers comm*). Poor preservation and damage to specimens prevented analysis of a larger number of female specimens. As there were even fewer male and juvenile specimens to analyse, regression analysis was abandoned for this species.

Length-frequency histograms for *T. biloba* were prepared, Figure 4.4 shows the population data as a whole, whereas Figure 4.5 shows monthly variation. Figure 4.4 demonstrates the domination by females of the population in terms of total numbers and maximum adult size. There appear to be no recognizable peaks in abundance which could be related to cohorts or instars. The size frequencies in Figure 4.5 illustrates the problem of low sample numbers. The only recognizable feature is an increase in the proportion of smaller individuals (juveniles) in the summer months.

Sex ratio results are presented in Table IV.IV., females dominate the population comprising 82.6% of adults captured. There is monthly variation in the percentage dominance of females as reported for *Ampelisca* sp nov. However, there is no dramatic increase in the numbers of *T. biloba* males as seen in April for *Ampelisca* sp nov, although a slight increase is apparent in June.

TABLE IV.III REGRESSION RESULTS FOR *Tryphosella biloba*

HEAD LENGTH = -0.21769 + (0.14244 x TOTAL LENGTH)		
r = 0.351	F = 2.102	P = 0.168
PEREON LENGTH = 0.01694 + (0.04102 x TOTAL LENGTH)		
r = 0.185	F = 0.531	P = 0.477
URUS LENGTH = 0.04206 + (0.02717 x TOTAL LENGTH)		
r = 0.166	F = 0.424	P = 0.525
OOSTEGITE LENGTH = -0.70146 + (0.33904 x TOTAL LENGTH)		
r = 0.303	F = 1.521	P = 0.236

TABLE IV.IV SEX RATIO RESULTS FOR *Tryphosella biloba*

MONTH	No. of MALES	No. FEMALES	% FEMALES
JAN	0	3	100
FEB	2	7	77.7
APRIL	6	19	76
MAY	3	16	84.2
JUNE	5	10	66.6
JULY	0	20	100
AUG	3	12	80
SEPT	1	3	75
OCT	0	1	100
NOV	4	9	69.2
TOTAL	21	100	82.6

FIGURE 4.4 LENGTH-FREQUENCY HISTOGRAMS FOR *T. biloba* TOTAL POPULATION

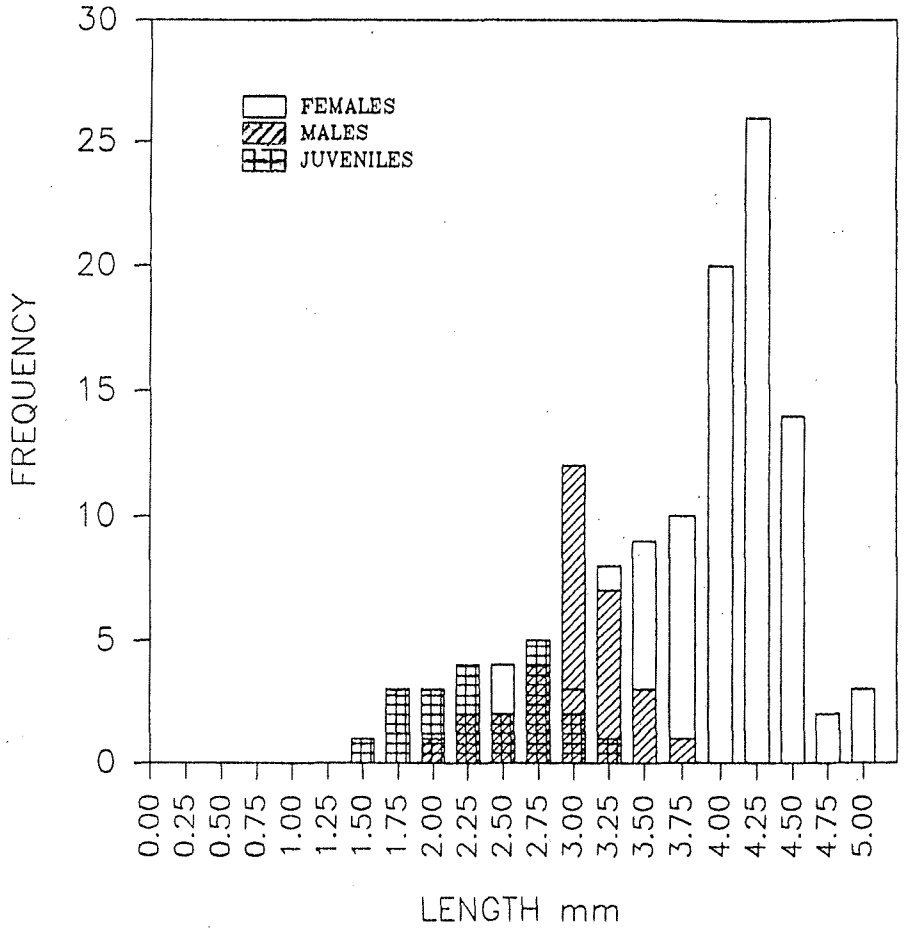
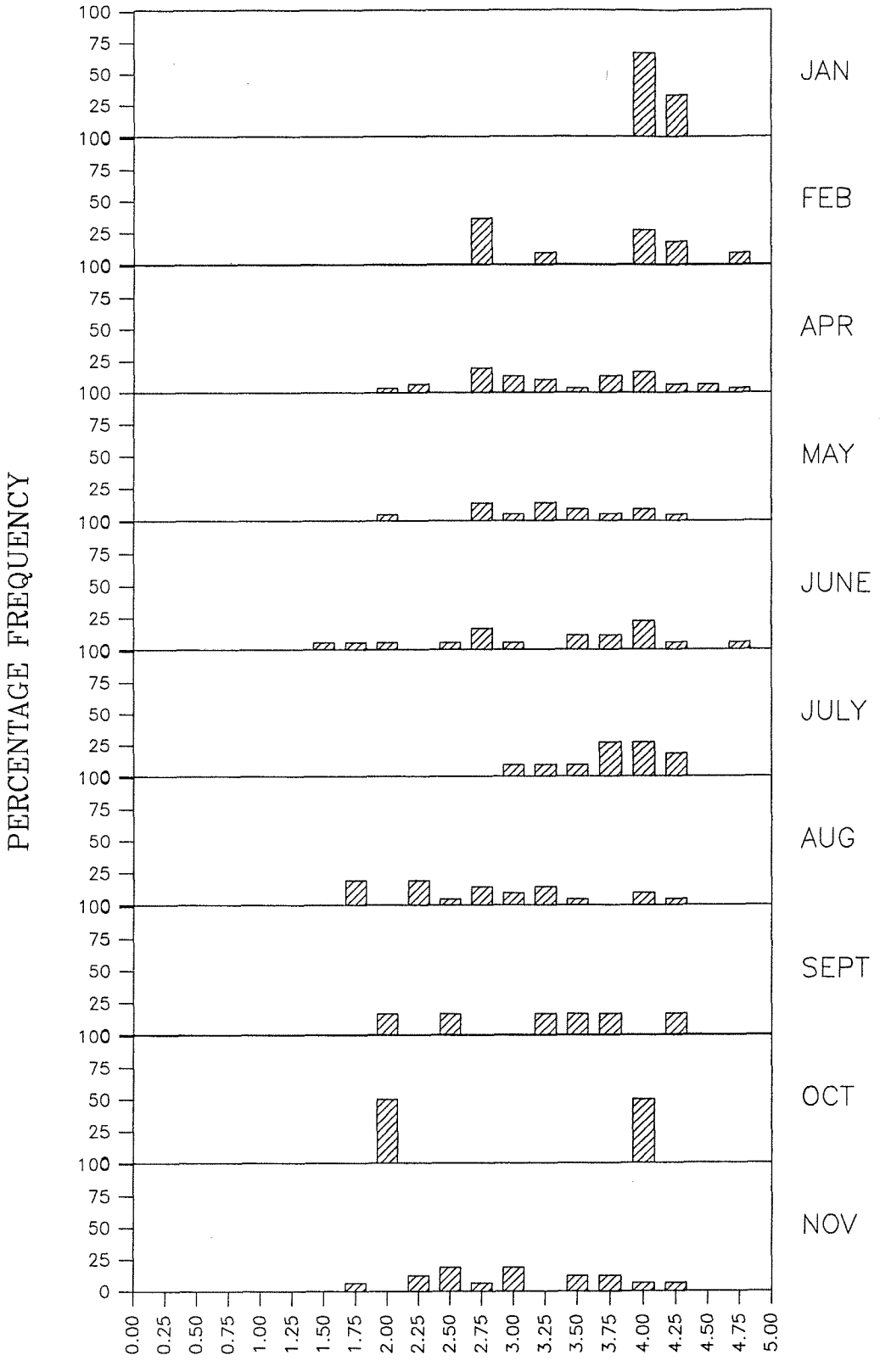


FIGURE 4.5 LENGTH-FREQUENCY HISTOGRAMS FOR *T. biloba* SHOWING MONTHLY VARIATION



4.4 DISCUSSION

Regression results indicate pleon one and head length could be used to predict total length for juvenile, male and female *Ampelisca* sp nov. Interestingly pleon one length was a better predictor than head length, and that the accuracy of prediction varied between males, females and juveniles. In other words pleon one length was a better predictor of total length for males, than it was for juveniles or females. To look at these effects in more detail an Analysis of Covariance was performed on the data. This tests a dependent variable for homogeneity among group means, after adjusting for differences in the independent variable or covariate. The regressions of head and pleon length against total length were compared for male and female *Ampelisca* sp nov. Juvenile regressions were not included in the analysis as juvenile length classes overlapped adult length classes, probably because of difficulties in separating juveniles from immature adults (see length-frequency analysis below).

The results are as follows :

For dependent variable pleon one length, and independent variable total length an analysis of covariance between male and female regressions gave an F statistic of 284.15 at a significance level of less than 1% ($p<0.001$).

For dependent variable head length, an analysis of covariance gave an F statistic of 358.47, $P<0.001$.

For both tests there was a significant heterogeneity of means around their regression slope, indicating a difference between male and female *Ampelisca* sp nov regressions for both pleon one and head length. This would indicate allometric growth of head and pleon lengths. The difference is largest for head length regressions, which explains why pleon length is a better predictor of total length than head length.

Length-frequency histograms for *Ampelisca* sp nov and *T. biloba* suffer from small sample sizes, and this may be the reason that no obvious cohorts or instars could be recognized. Population analysis of *Eurythenes gryllus*, revealed definite peaks in abundance occurring at regular intervals (Ingram and Hessler 1987). These were

attributed to instars (see introduction), and are more readily separable for smaller individuals of *E. gryllus*. There is some indication (Figure 4.2) that this may also be the case for *Ampelisca* sp nov. The histogram which indicates there may be the presence of abundance peaks attributable to growth instars, is that of juvenile *Ampelisca* sp nov. There appear to be three separable peaks in abundance centred on 2.2, 2.6 and 3.1mm. The histogram for female *Ampelisca* sp nov also shows abundance peaks centred on 4.1, 4.6, 5.1, 5.8 and 6.7mm. The ratios between the groups, or linear growth factors (Thurston 1979) are 1.18 and 1.19 for the juveniles, and 1.12, 1.11, 1.14, and 1.15 for females. The ratios between groups for juveniles are very similar, as are those between female groups. This would indicate that growth in total length for *Ampelisca* sp nov is geometric (Thurston 1979). Juvenile linear growth factors are larger than females, indicating juvenile *Ampelisca* sp nov show a relatively greater increase in length between instars than adult females. These size groupings occupy a narrow length range and the between-group ratios are close to a value which would indicate a doubling of body volume (1.26). These features have been used to suggest that such size groupings represent instars rather than year classes (Thurston 1979). Thurston (1979) studied the length-frequency distribution in four scavenging lysianassids, and found that for all four species juveniles formed a distinct size category that did not overlap that of males and females. Both *Ampelisca* sp nov and *T. biloba* had distributions in which juvenile size categories overlapped those of males and females (Figure 4.2 and 4.4). This is likely to be the result of difficulties in distinguishing immature males and females from juveniles. On such small animals the developing oostegite buds and penes are very difficult to discern. The implications of increased juvenile numbers in the summer months for both species are discussed fully in Chapter Five.

Published sex ratio data for deep-sea amphipods is limited to scavenging lysianassids caught in trap studies. The majority of species studied showed no significant difference from unity (Ingram and Hessler 1983, Baldwin and Smith 1987, Bucklin *et al* 1987, Charmasson and Calmet 1987, Lawson *et al* 1993). Thurston (1979) found females dominated in populations of *Paralicella caperesca, Orchomene gerulicorbis* and *O. cavimanus*, and Lawson *et al* (1993) found significantly more females were recovered

in one species recovered by their traps (*Concarnes* sp nov). *T. biloba* and *Ampelisca* sp nov both show female biased sex ratios. Whether this is a true reflection of the population structure for these species, or a sampling artefact is impossible to determine. Amphipod populations may be amphogenous (equal sex ratio), thelygenous (female biased) or arrhenogenous (male biased) (Wildish 1977). Thelygeny, as found in the species in this study, is a means of increasing population numbers (through increased reproductive potential) to the optimum density for a particular environment. Biased sex ratios are therefore considered adaptive as they allow colonization of a wide range of habitats without stress on individual females (Wildish 1977). The mechanisms involved are not clear, but an interpretation given by Wildish (1977), indicates environmental control of the sex ratio which in turn influences the reproductive potential of a population. Jones and Wigham (1993) report a female biased sex ratio for *Orchestia gammarellus* except during the breeding season when it did not deviate from 1:1. In contrast Moore and Francis (1986) report the same species exhibited a 1:1 ratio at all times except the breeding season, when females dominated. The latter study linked the absence of males to selective mortality and/or seasonally labile sex determination hormones. In the food limited deep-sea, a female biased sex ratio may be a more efficient way of utilizing resources to maximize reproductive potential. The normal types of environmental cues being absent in the deep-sea (photoperiod, temperature, lunar cycles). An alternative explanation for the female bias in *Ampelisca* sp nov is that males are not under represented in the population, but that they are not caught. This could result from the sexually dimorphic free swimming behaviour reported for ampeliscids (Borowsky and Aitken-Ander 1989). Members of the genus *Ampelisca* reside in tubes built in the sediment, but adults are often found in the water column. Male ampeliscids enter the water column far more frequently than females. Females only leave their tubes to moult and mate, thus having many males in the water column minimizes the time females are away from the protection of their tubes. Males would thus be more subject to predation, and so their proportion of the population would be lower. In addition, swimming males would be less subject to capture by the epibenthic sled, leading to an under representation in

the samples. The large increase in the proportion of male *Ampelisca* sp nov recorded in April lends support to the theory that males are there, but not being caught. The maximal input of phytodetritus to the sample region occurs in April (see Chapter Two). It may be that the males remain near to their tubes to feed on this food resource, increasing the numbers caught in April. Feeding biology of the amphipods in this study is discussed in detail in Chapter Six of this thesis.

CHAPTER FIVE
REPRODUCTION

5.1 REPRODUCTION IN THE DEEP-SEA

Young (1994) in his review of the history of deep-sea reproductive biology, remarks that early ideas and hypotheses concerning deep-sea reproduction were often based on 'naturalist's intuition' rather than hard facts. Further, such hypotheses became so entrenched in the subsequent literature that preceded today's more rigorous testing of ideas and theories, that they have become in the words of Young (1994) "*...practically canonized by tradition.*" Although ideas about deep-sea reproduction are long standing, there are only two main hypotheses. The first is often referred to as Orton's Rule, first coined as a phrase by Thorson (1946). Put simply, this rule implies that animals living in the isothermal and presumed constant environment of the deep-sea should reproduce continuously. This rule was developed from Orton's (1920) work which showed that seawater temperature controls breeding in marine fauna. In this paper on sea-temperature, breeding and distribution in marine animals, Orton (1920 pg. 340) stated *"..the factor of temperature being of paramount importance in controlling breeding"*. Orton also observed that "*in those parts of the sea where temperature conditions are constant, and where biological conditions do not vary much, that marine animals will breed continuously*" (Orton 1920, pg. 353). Such conditions occur in the deep-sea and Orton remarked on the importance of recording the sexual condition of deep-sea animals, and that his theory should be tested by sampling in various seasons. Such sampling began nearly fifty years later, and these temporal studies showed non-continuous synchronous breeding in several invertebrate phyla (George and Menzies 1967, 1968, Schoener 1968, Rokop 1974, 1977b, Tyler *et al* 1982, Tyler 1986, Harrison 1988, Gage and Tyler 1991). Recent evidence has shown that a variety of seasonal processes exist in isothermal deep-sea environments (Tyler 1988, Scheltema 1994) and that factors other than temperature may be important in entraining reproductive seasonality (Giese and Kanatani 1988). The second hypothesis regarding deep-sea reproduction is the most quoted, pervasive and

long-standing theory which states that deep-sea and polar animals should undergo direct development (Young 1994). This idea was first proposed by Thomson (1878, 1885) and refined and reinforced by the studies of Thorson (1936) in East Greenland. Despite the fact that Thorson's data were all from the Arctic, in 1936 (pp.130) he wrote *"..it is therefore the opinion of biologists that the deep-sea animals complete their reproduction without any pelagic larval stage."* Thorson was to reiterate these ideas so forcefully and so often (see reviews by Thorson 1946, 1950) that it became known as Thorson's Rule (Mileikovsky 1971). Thorson (1961 pp.456) wrote "... *as is well known, nearly all invertebrate species living in the Arctic and Antarctic coastal zones as well as all inhabitants of the deep-sea seem to have non-pelagic larval development.*" This generalization is no longer considered valid, as re-examination of Thorson's and other data has shown examples of pelagic larvae in deep-sea invertebrates (Young 1994, Pearse 1994). Young (1994) concludes his review by stating that there is such a wealth of information in the literature regarding deep-sea reproductive processes, that if it were possible to assemble it all in one place, "...*it would present a mosaic of reproductive diversity rather than a monotonous, general pattern to which all species conform*".

Evidence for seasonality in the life history processes of invertebrates in the Rockall Trough was discussed in Chapter Two. Tyler and Young (1992) maintain there are three reproductive patterns exhibited by the 'megainvertebrates' of the NE (and western) Atlantic. The most dominant pattern being continuous reproduction, which Tyler and Young define as species showing intrapopulation asynchrony of reproduction. The second pattern is shown by a limited number of species that reproduce seasonally and synchronously. Interestingly a higher proportion of seasonal species seem to appear in the western compared to NE Atlantic (Tyler and Young 1992). This is probably related to the depth of sampling, with the driving force for seasonality being stronger in the shallower (~500m) Bahamian samples compared to the deeper (~2900m) NE Atlantic samples. The proposed driving force for this seasonality in reproduction is the seasonal input of organic matter to the deep-sea (Tyler 1988, Tyler and Young 1992, Gage and Tyler 1991). The third reproductive

pattern is displayed by a very limited number of 'opportunistic' species that colonize ephemeral resources in the deep-sea. This pattern is characterized by rapid growth and reproduction, often with a periodicity of less than a year (Tyler and Young 1992). Such a life history has been described for the deep-sea barnacle *Poecilasma kaempferi* (Green *et al* 1994) and the bivalve *Xylophaga* (Tyler *et al* in press), and appears to occur in other transitory deep-sea environments for example hydrothermal vents (Tunnicliffe 1991).

The theory that deep-sea fauna evolved from invasion of shallow water species (Bruun 1957, Menzies *et al* 1973, see also Chapter Three) is the basis of an hypothesis to explain the variable life history patterns found in sympatric bathyal invertebrates in the Rockall Trough (Tyler and Young 1992). Seasonally reproductive species with pelagic larvae may have colonized areas of deep-sea floor at the time of maximum glaciation in the Atlantic, when temperature would not present a barrier between shallow and deep-water (Gage and Tyler 1991). As the ice retreated North these species spread into new areas, where the existing deep-sea fauna with no seasonal gametogenic cycle were present. These non-seasonal species may have been the remnants of a previous invasion that had lost their periodicity, the ice cover removing any seasonal trigger. The seasonally reproductive species may have retained their seasonal cycles, driven by the annual influx of phytodetritus (Tyler and Young 1992). Selective pressures may have led some phyla to evolve lecithotrophic eggs (Tyler and Gage 1984b, Tyler and Young 1992), change from planktotrophy to lecithotrophy being thought to have occurred a number of times in the echinoderms (Strathmann 1974).

5.2 REPRODUCTION IN DEEP-SEA CRUSTACEA

Crustaceans, in particular isopods, amphipods, tanaidaceans and cumaceans, are abundant and diverse in the deep-sea. There is, however, a paucity of detailed studies on their reproductive biology, trends and patterns for the most part inferred from aggregations of data covering widely spaced localities and years (Blake and Watling 1994). George and Menzies (1967, 1968) were the first to suggest seasonality in the reproduction of deep-sea animals using data on isopods and amphipods. Subsequent

studies cast doubt on their conclusions, Sanders and Hessler (1969) finding no evidence of seasonality in the isopod genus *Ilyarachna* from the Gay Head - Bermuda transect. Similarly when Gardener (1975) examined tanaids from this transect, the presence throughout the year of young animals and females with marsupia, indicated quasi-continuous reproduction. The original data of George and Menzies was re-examined by Rokop (1977a), who considered the evidence for seasonal reproduction to be highly tenuous (Gage and Tyler 1991), in all species examined excepting the isopod *Storthyngura birsteini*. A more exacting study was that of Harrison (1988b) who analysed a long-term series of isopod samples from the 2900m deep Permanent Station, Rockall Trough. Harrison found that at the family level, there was a seasonal pattern of breeding intensity (greater percentage of brooding females in the winter, and greater proportion of newly released juveniles in the summer), but no seasonal reproductive cycle. The problem of obtaining sufficient numbers in deep-sea reproductive studies is often a drawback to drawing significant conclusions. Rokop (1977a) sampled two isopod and one amphipod species in large enough numbers from a station at 1240m in the San Diego Trough, to be confident in his results. He found brooding isopods at several times of the year, suggesting continuous reproduction. However, Blake and Watling (1994) considered there was stronger evidence for continuous reproduction in Rokop's data for the amphipod *Pseudharpinia excavata*. Blake and Watling's (1994) study is unusual in that very large numbers of the cumacean *Diastylis stygia* were collected from a single station at several times of the year. Their data, from 2065- 2115m on the Massachusetts continental slope, suggests continuous reproduction (low numbers of sexually mature adults and newly hatched mancae present throughout the year), although there was a seasonally intense recruitment in April 1985 and July 1986 (Blake and Watling 1994). There are few studies that include an assessment of population structure and growth of deep-sea peracarids (Gage and Tyler 1991). Bishop (1982) described the rapid growth of early moult stages (instars) compared to older individuals of the cumacean *Leucon jonesi* from 1.5km depth off Surinam. Females of this cumacean were iteroparous, had a 'resting' instar to allow oocyte development and a brood size of between six and twelve

(Bishop 1982). Polymodal length-frequency distributions of scavenging amphipods in the NE Atlantic have, on the basis of between group ratios of linear growth factors, been ascribed to instars rather than year classes (Thurston 1979). Thurston (1979) concluded that despite examples of seasonality in other taxa, in deep-sea amphipods it is the exception rather than the rule. Baldwin and Smith (1987) carried out an extensive sampling programme of the scavenging amphipod *Eurythenes gryllus* in the Pacific. *E. gryllus* exhibits no trends in recruitment or breeding, the recurrent peaks in size frequency corresponding to successive moult stages (Ingram and Hessler 1987). These authors present data on *E. gryllus* that demonstrate geometric growth increments in successive instars, and that females grow larger and have more instars than males. Until recently, brooding females of deep-sea scavenging amphipods had not been caught, estimates of fecundity were therefore based on oocyte counts. This is an inaccurate method, as in some species of amphipod the oocyte count decreases after the development of secondary sexual characteristics. Resorption of oocytes has been proposed as the reason for temporal variation in oocyte numbers, rather than seasonal effects (Hessler *et al* 1978, Thurston 1979 and Ingram and Hessler 1987). In scavenging amphipods the large amount of stored lipids, slow down in growth of adult stages, and absence of brooding females from traps, has been proposed to optimize reproductive success in an energy poor environment (Hessler *et al* 1978).

Relatively little is known about reproduction in the larger deep-sea crustaceans (Gage and Tyler 1991). The following is a synthesis of the literature reviewed in Gage and Tyler (1991). Ahlfeld (1979) examined seasonally disparate samples of *Parapagurus pilosimanus, Catapaguroides microps, Nematocarcinus ensifer* and *Munidopsis rostrata*, and concluded that all four species reproduce throughout the year - with periodic increases in intensity. One of these species *P. pilosimanus* was studied by George (1981) from samples taken on the Blake Plateau. In this geographic location *P. pilosimanus* had asynchronous year-round breeding activity, but with highly synchronous spawning in winter. In contrast *P. pilosimanus* from the NE Atlantic breeds continuously with no evidence of reproductive seasonality (Tyler *et al* 1985, Gage and Tyler 1991). The bathyal spider crab *Dorhynchus thomsoni* has a distinct

reproductive cycle, similar to its shallow water congeners excepting the longer egg incubation period of eight to nine months (Hartnoll and Rice 1985). The larvae of *D. thomsoni* is one of the few deep-sea decapod larvae to be identified and described (Williamson 1982). Another is the 'typical' larval stage of the deep-sea red crab *Chaecon quinquedens* described by Perkins (1973) and Sulkin and van Heukelem (1980). *Geryon maritae* is a commercially exploited species on the upper continental slope of SW Africa. Studies by Melville-Smith (1987) show *G. maritae* has a gametogenic biology similar to its shallow water congeners, and that it shows no reproductive seasonality. Wenner (1978) found the polychelids *Steromastis nana* and *S. sculpta* to exhibit year round reproduction, whilst the limited data on the penaeid *Benthesicymus bartletti* did not allow her to discern continuous or seasonal reproduction in that species (Wenner 1980).

Since Gage and Tyler's (1991) review the following workers have examined aspects of deep-sea crustacean reproduction. Van Dover and Williams (1991) comment on the lack of a systematic survey of reproductive and distribution patterns among deep-sea decapod species. They attempted to reduce this deficiency with a study on the Galathoidea superfamily. Van Dover and Williams (1991) results showed that for the fifty two species examined there was a significant and positive correlation between egg size and body size and between brood size and body size. Van Dover and Williams also concluded that habitat *per se* does not dictate egg size and mode of larval development, an hypothesis consistent with an earlier study of two *Munidopsis sp* that occur at hydrothermal vents (Van Dover *et al* 1985). Bishop and Shalla (1994) studied time series material of the cumacean *Leucon profundus* from the same station in the NE Atlantic as the gammaridean samples in this study. Through examination of oocyte development in the ovary and development of embryos in the marsupium, seasonal breeding patterns emerged which may have been missed by studying occurrence of brooding females alone. *L. profundus* undergoes vitellogenesis from April to late October, oviposition occurs from February to April with release of young after an inferred brooding period of fourteen months in late spring/ early summer (Bishop and Shalla 1994). Both vitellogenic oocyte growth and release of young therefore coincide

with seasonal peak of phytodetrital flux to the seabed in this region. The gametogenic development of the stalked barnacle *Poecilasma kaempferi* has been examined by Green *et al* (1994), in samples found attached to the lithodid crab *Neolithoides grimaldi* in the Rockall Trough. These studies showed rapid growth and gametogenesis, which Green *et al* suggest could be an evolutionary adaption to the ephemeral nature of their substratum. Thurston and Bett (1994) investigated the scavenging amphipods *Eurythenes gryllus* and *Eurythenes obesus* caught in deep-midwater trawls in the NE Atlantic. These studies revealed the presence of five pairs of oostegites in *E. gryllus*, a character that is very rare in the Amphipoda. This study was also the first to capture brooding females of *E. gryllus* and *E. obesus* in such a trawl. In both females' broods the hatchlings were varied in both size and bodily proportions. Despite this variability the authors could only recognize one instar, which in the case of *E. gryllus* was hitherto unrecorded (Thurston and Bett 1994). There has been an extensive study of the abundance, diversity and feeding habits of decapod crustaceans from the western Mediterranean deep-sea communities (Cartes and Abello 1992, Cartes and Sardia 1992, Cartes 1993). Unfortunately despite mentioning a high proportion of ovigerous females (Cartes 1993), the reproductive data are to date unpublished.

5.3 REPRODUCTION IN AMPHIPODS

Gammaridean amphipods are a diverse and ubiquitous suborder of Crustacea (Bousfield 1973). Yet in comparison to other, generally larger, crustacean groups their biology is relatively little understood. Sainte-Marie (1991) reported that there have been few detailed accounts of the reproductive and brooding behaviour of gammarideans. This is surprising given their ready adaption to laboratory conditions, facilitating observations of their life histories. Amphipods are generally small, allowing their habitats to be closely mimicked, and the maintenance of large numbers of individuals. Many species reproduce repeatedly and frequently in the laboratory, often able to tolerate harsh experimental manipulations (Borowsky 1991).

The majority of gammarideans are dioecious, with external fertilization. Female gammarids ovulate soon after the parturial moult, eggs passing into a ventral brood pouch (oviposition). The brood pouch, or marsupium, is unique to the peracarid crustacea. Female gammaridean amphipods do not store sperm and therefore require the presence of a male at each moult to ensure fertilization. The fertilized eggs remain in the brood pouch for a variable length of time during the females intermoult period. However they must develop and hatch before her next moult. Gammarids exhibit direct development, juveniles hatching with the general adult morphology, excepting the lack of secondary sexual characteristics.

5.3.1 Reproductive anatomy and hormonal control of Gammarideans.

Gammaridean amphipods follow the 'typical' malacostracan pattern of paired tubular gonads. Although their tubular structure is well known, there exist many interpretations of gonadal origin (McLaughlin 1983). Schmitz (1992) believes that in the literature there are two views concerning the origin of amphipod gonopores. The first is that the gonads derive from coelomic pouches continuous with coelomoducts that terminate as adult gonopores (espoused by Siewing 1956, Kaestner 1970, Fretter and Graham 1976). The second view again derives the gonopores from coelomoducts, but the origins of coelomoducts are independent of the coelomic sac. Rather two strands of primary germ cells are surrounded by cells of mesodermal origin from the pericardial septum. These strands then split to form the gonadal cavity, a view supported by Anderson (1979) and Clarke (1979).

Male

Gammaridean testis are paired slender structures that lie ventrolateral to the pericardial septum (Figure 5.1a). They extend from pereiomeres two through to five or six, where they expand to form seminal vesicles (Schmitz 1967). The seminal vesicle structure varies interspecifically, in *Gammarus lacustris lacustris* they extend into pleomere two, whereas in *Orchestia gammarella* they terminate in pereiomere seven where the

vasa deferentia originate (Schmitz 1967). However in *Gammarus fasciatus* the testis narrows from pereiomere five to form vasa differentia which extend into pereiomere seven (Clemens 1950). This apparent lack of seminal vesicles in *Gammarus fasciatus* may be explained by descriptions based on sexually immature/inactive males, with no distension of ducts by spermatozoa (Schmitz 1992). The vasa deferentia of gammarids pass laterally and ventrally around the midgut and ventral caeca (Figure 5.1a). The distal portions of the vasa deferentia join short, muscular, ectodermal ejaculatory ducts opening at the tips of the genital papillae by way of the gonopores. These genital papillae are located on the ventral surface of pereiomere seven (Clemens 1950, Schmitz 1967, Kaestener 1970). Gammarideans do not have copulatory organs *sensu stricto* (Stebbing 1906); however, the genital papillae of *Orchestia agilis* have been reported to enlarge considerably during the breeding season (Kunkel 1918). Clemens (1950) and Schmitz (1967) argue that as the genital papillae are formed by outfoldings of the non-living tissue of the integument (excepting the hypodermal component), they are structurally incapable of enlargement. There have been several descriptions of the histological structure of gammaridean testis, *Gammarus pulex* (Koster 1910), *Gammarus duebeni* (Le Roux 1933), *Orchestia gammarella* (Charniaux-Cotton 1957) and *Gammarus lacustris lacustris* (Schmitz 1967). The testis is bounded by a thin sheath of connective tissue, and the epithelium may be vacuolated (Schmitz 1967) (Figure 5.1b). These epithelial cells are presumed to secrete the mucus that surrounds the spermatozoa (Charniaux-Cotton 1957). These mucus coated spermatozoa are ejaculated in long strings from the genital papillae in the course of being transported to the female during mating (Bousfield 1973). The seminal vesicle wall is formed by rectangular endothelium cells, arranged end to end, surrounded by a fibrous tissue layer (Schmitz 1967) (Figure 5.2a). Within the connective tissue layer are striated muscle fibres emanating from the extrinsic muscle associated with the seminal vesicle (Schmitz 1967)(Figure 5.2a). The vas deferens has a similar structure to the seminal vesicle (Figure 5.2b), except as in the case of *G. lacustris lacustris*, the endothelial cells are cuboidal (~10μm across)(Schmitz 1967). According to Kaestner (1970) the walls of gammaridean vas deferentia are glandular. Located at the distal end of the vas

FIGURE 5.1 GAMMARIDEAN MALE REPRODUCTIVE SYSTEM

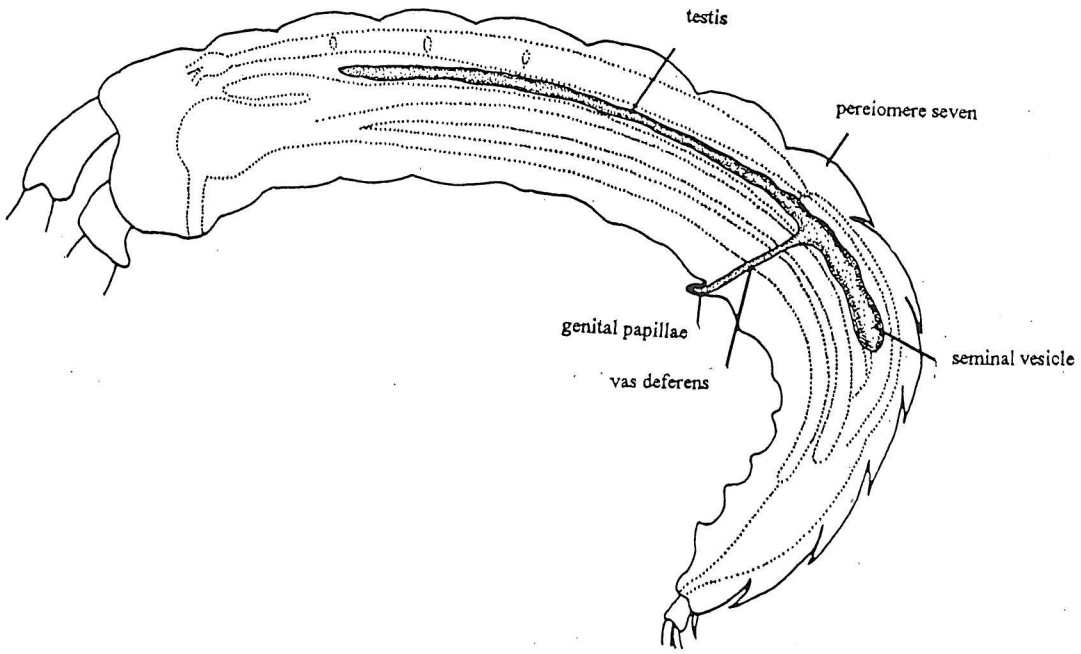


Figure 5.1a. Male reproductive system in relation to other visceral structures.

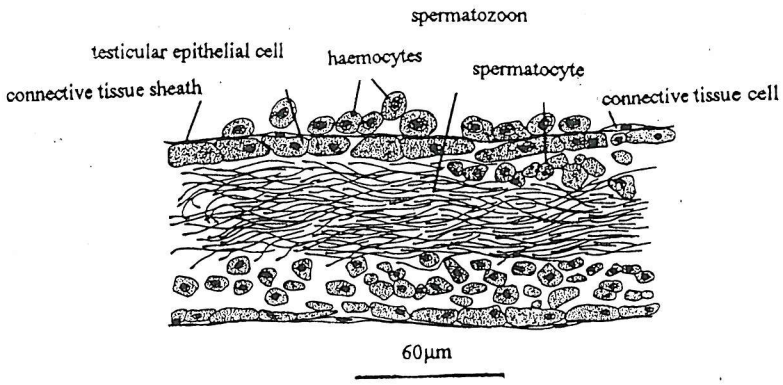


Figure 5.1b. Sagittal section of *Gammarus lacustris lacustris* testis.

Redrawn and modified after Schmitz (1992).

FIGURE 5.2 HISTOLOGY OF MALE REPRODUCTIVE SYSTEM

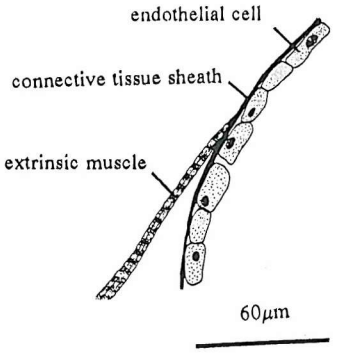


Figure 5.2a. Transverse section of *Gammarus lacustris lacustris* seminal vesicle wall.

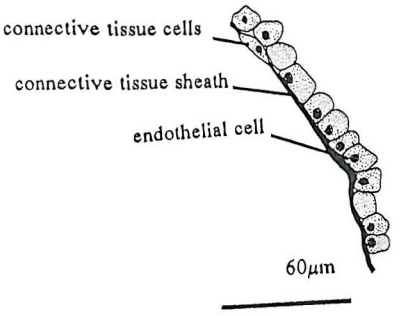


Figure 5.2b. Transverse section of *Gammarus lacustris lacustris* vas deferens wall.

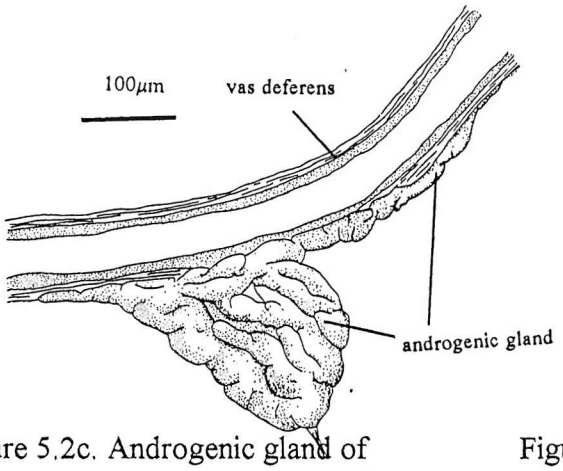


Figure 5.2c. Androgenic gland of *Orchestia gammarella*.

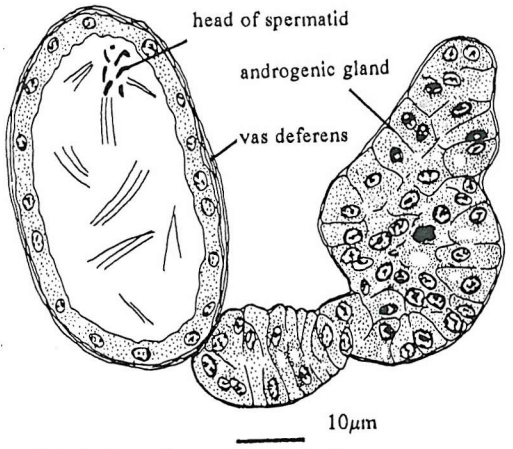


Figure 5.2d. Section of vas deferens and androgenic gland.

Redrawn and modified after Schmitz (1992).

deferens is a small mass of secretory tissue, the androgenic gland (Charniaux-Cotton 1954, 1960). The hormones produced by this gland control development of male sexual characteristics and testis development. Attached to the sub-terminal region of the vas deferens between the coxae muscles of pereiopod seven in *O. gammarella* the gland consists of a solid strand of cells folded back on itself (Charniaux-Cotton 1960)(Figure 5.2c). The length of the strand varies with species and intraspecifically with male size. The strand diameter is relatively constant at ~30μm, as are form and arrangement of cells (Schmitz 1992)(Figure 5.2d). The cells cytoplasm is vacuolated with peripheral nuclei 7-8μm in diameter (Charniaux-Cotton 1960). If the androgenic gland is resected from males, secondary sexual differentiation ceases, and the testis degenerate. Conversely, if an ovary is implanted into a male with the gland intact, the ovary is transformed into a testis (Schmitz 1992).

Female

Gammaridean ovaries, like testes, are slender structures which lie dorsolateral to the midgut, and in *G. lacustris lacustris* extend from periomere two through seven (Schmitz 1967)(Figure 5.3a). However the length of ovaries can also reflect the degree of maturity (*c.f Gammarus faciatus* Clemens 1950, and species in this study, see later in chapter). The paired tubular oviducts arise from the ovaries in pereiomere five, whence they pass around the midgut and ventral cecae to a ventral ectodermal 'vagina' opening into the marsupium (Schmitz 1967, Kaestner 1970). The marsupium or brood pouch, consists of loosely fitting oostegites, the shape and size of which differs interspecifically, which bear fringing setae (Dahl 1977). Typically gammarideans have four pairs of oostegites, occurring on the pereiopods that bear branchiae (*ie.* two to five)(Dahl 1977). Development of these oostegites in gammaridean females is controlled by an ovarian hormone. If a male gammaridean has its androgenic gland resected and is then implanted with an ovary, oostegites will form at the first or second molt following the implant (Charniaux-Cotton 1960). The development of fringing setae on gammaridean oostegites is controlled by an ovarian hormone during yolk

deposition. For example in *O. gammarella* juvenile or sexually inactive females have setae 0.02mm long, whereas females in the molt preceding egg laying bear setae 0.08mm long. Ovariectomy of such reproductively active females results in replacement of ovigerous setae with shorter juvenile setae (Charniaux-Cotton 1960). The gammaridean ovary consists of a follicular layer of connective tissue which sheathes a layer of oogonia, which in turn surrounds a central core of oocytes (Figure 5.3a)(Schmitz 1967). The mature oocytes of *Gammarus lacustris lacustris* range from 70-100μm in diameter, with nuclei up to 50μm in diameter containing conspicuous nucleoli. The oogonia are oblong, with sizes ranging from 10x25 to 10x50μm and have nuclei about 5μm in diameter (Figure 5.3b) (Schmitz 1967). During the reproductive season ecdysterone coordinates the female moult, ovarian and behavioural cycles. The effect of ecdysterone on molt cycles is well documented (Skinner 1985), but it also affects the ovarian cycle in amphipods. Either by directly controlling folliculogenesis (Charniaux-Cotton 1975) or by stimulating the secretion of vitellogen stimulating hormone, that controls vitellogen synthesis (Junera *et al* 1977). In gammarids an ovarian hormone stimulates, whilst a neurohormone inhibits, vitellogenesis. If an additional brain is grafted into a female of *Orchestia gammarella* then yolky oocyte growth is inhibited, and the oocytes undergo lysis (Blanchet-Tournier 1987). In *Gammarus duebeni*, oocytes begin to mature following the female moult and continues during ovulation, the second maturation division being complete about 2hrs after ovulation (Le Roux 1933). In contrast females of *Gammarus limnaeus (=Gammarus lacustris)* and *Gammarus fasciatus*, would not ovulate unless a male was present (Embody 1912). The oviduct of gammarids consists of a thin sheath of connective tissue around the endothelium. Since the oocytes in the ovary are 4-6 times the size of the oviduct, the walls must be quite elastic to permit their passage (Schimtz 1967). Clemens (1950) reported that the eggs of *Gammarus fasciatus* are pressed into an elongated shape whilst passing through the oviduct, but upon extrusion from the gonopores, they return to a spherical shape which swells into an oval in the marsupium.

FIGURE 5.3 GAMMARIDEAN FEMALE REPRODUCTIVE SYSTEM

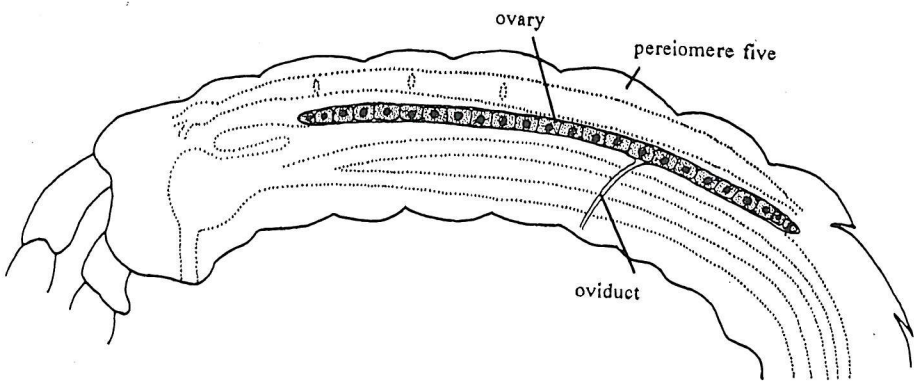


Figure 5.3a. Female reproductive system in relation to other visceral structures.

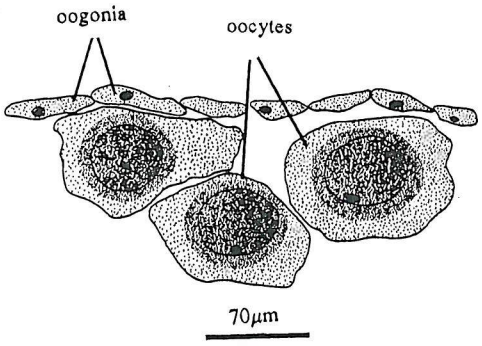


Figure 5.3b Sagittal section of oogonia & oocytes of *Gammarus lacustris lacustris*.

Redrawn and modified after Schmitz (1992).

5.3.2 Reproductive Behaviour in Amphipods

The diversity of crustacean reproductive behaviour, rivals that of the more frequently studied social insects, and many crustacean species have adapted their mating strategies to a wide variety of habitats. Although not mentioned in what are often regarded as classical works on animal social systems *eg* Wilson (1975), Crustacea are regarded by some workers as a valuable group in which to analyse mating systems (Wickler and Seibt 1981, Dunham and Hurshman 1991). In many species of crustacea, males and females pair together for a brief period prior to copulation. In amphipods this precopulatory mate guarding is considered a prototypical behavioural pattern (Dunham and Hurshman 1991). This pattern consisting of a male contacting a female, palpating her, and then physically carrying her until molt and copulation has been observed in a large number of crustacean species (Dunham 1978, Ridley 1983, Salmon 1983). Borowsky (1991) divides this behaviour into distinct stages, at the beginning of the intermoult the female is alone, in stage I a receptive female and male find each other (mate location); stage II involves behaviours designed to initiate pairing (pair formation); stage III is the period during which they remain paired; and stage IV is copulation. There exist many generic assumptions in explanations for precopulatory mate guarding, the two most reported are i. female sex pheromone hypothesis and ii. constant male threshold hypothesis. The first suggests that the female releases a chemical late in her reproductive cycle that attracts a male and elicits mate guarding behaviour. Kittredge and Takahashi (1971) suggested that a primordial crustacea externalized a receptor site and released a moulting hormone into their environment at the same point in their evolution. The reproductive advantage of these two events in terms of finding a mate permitted them to be fixed in the genome with the moulting hormone serving a dual function as a sex hormone (*cf* Hammond, Compte and Ducruet 1975, Dunham 1979, Gleeson, Adams and Smith 1984). In *Microdeutopus gryllotopa*, injections of ecdysterone not only makes females molt earlier, but also express their reproductive behaviours earlier in their intermolt cycles than controls (Borowsky 1980). The second generic assumption, the constant male threshold hypothesis, is seen

as a time investment strategy by Parker (1974) and Ridley (1983). These authors believe precopulatory mate guarding maximizes reproductive success when mating is reduced to a brief period during the females reproductive cycle. Ridley (1983) argues that given such time restraints a randomly searching male will encounter acceptable females at a very low rate, and male competition would be high. Thus sexual selection would favour a male capable of assessing a female's reproductive status and guarding her until copulation. The evidence to date on sex hormones in Amphipoda mirrors the inconsistency encountered in the literature for pheromones in Crustacea in general (Dunham 1978 and 1988). Although it has been demonstrated that males of several amphipod species can make the distinction between a female early and late in her reproductive cycle (*eg* Birkhead and Clarkson 1980, Hartnoll and Smith 1980, Borowsky 1984, Hunte, Myers and Doyle 1985, Dunham, Alexander and Hurshman 1986), the evidence for a pheromone that attracts a male from a distance or on physical contact has not been conclusive. An early study by Dahl, Emanuelsson and Mecklenburg (1970) showed premolt females of *Gammarus duebeni* released a substance that attracted males from a distance. subsequent studies, however, on two different gammarid species *G. pulex* and *G. fossarum* found no evidence that males could be attracted from a distance (Ducruet 1973, Hammond, Compte and Ducruet 1975). In an exacting series of experiments using the same assays employed in the earlier literature, Hartnoll and Smith (1980), failed to replicate the positive results for a sex pheromone using *G. duebeni.* However, Borowsky (1984) demonstrated that males of the tubiculous *Microdeutopus gryllotalpa* selectively chose the arm of an olfactometer containing water from premolt conspecifics over nonreceptive intermolt females. In a second experiment Borowsky (1985) showed that in *Gammarus palustris* there appeared to be an attraction to water from conspecifics regardless of sex and a preference for water that increases the probability of encountering an appropriate mate (*ie* helps the males find a female near molt and the females to find a male). Dunham and Hurshman (1991) attribute the inconsistencies and contradictions to different experiments, employing a variety of species, assays employed, sampling procedures and background laboratory conditions. They used an approach in which several

different behavioural assays were used with the same species (*Gammarus lawrencianus*) and the same background laboratory conditions to test whether premolt females release secretions capable of influencing male reproductive behaviour from a distance. The results of Dunham and Hurshman for *G. lawrencianus* indicated that a chemical substance does alter the behaviour of conspecifics from a distance. However, differential orientation and attraction will be observed only when the stimulus is presented in a water current. According to Dunham and Hurshman the pattern of positive and negative results in the earlier literature is also predictable from this procedural difference. Dunham and Hurshman (1991) and Borowsky (1985) also present evidence that it is not just premolt females that are releasing chemicals, but that both males and females are capable of attracting conspecifics in a choice olfactometer. Similar conclusions can be drawn about other groups of Crustacea (Warner 1976, Atema 1986). Dunham and Hurshmans' work on *G. lawrencianus* has revealed that brood pouch contents may play a role in the mate guarding decision, and consider it unlikely that mating strategy is determined by one line of communication (*ie* a pheromone). They believe several sources of stimulation are involved at several different stages of a behavioral sequence that culminates in copulation. Borowsky (1991) echoes these sentiments and in summarizing her work on *Microdeutopus gryllotalpa* and *Gammarus palustris* suggests that: i. there are two basic types of pheromones, waterborne and contact; ii. there may be two or more types of waterborne pheromones in some species; iii. the same type of pheromone may elicit different behaviours in different species; and iv. other, nonchemical stimuli are also important in eliciting reproductive behaviours. In her experiments Borowsky (1991) found that the principal stimulus for pair formation was a factor associated with the female body. Despite the gross morphology and exoskeletal structure remaining the same throughout intermolt, male responses to it change. The evidence suggested a labile compound associated with the exoskeleton, *ie* a contact pheromone. Many crustacean reproductive displays are preceded by contact, and contact chemoreception has been suggested in the shrimp *Heptacarpus pictus* and several other carideans (Bauer 1976). Seelinger and Schuderer (1985) confirmed the presence of contact

pheromones in the cockroach *Periplaneta americana*, and that airborne pheromones served as attractants and sexual motivators, whilst mate recognition was achieved using contact pheromones. Borowsky (1991) correlates this with her experiments on gammarids, substituting waterborne for airborne pheromone attractants. The site of secretion of water borne pheromones in amphipods is still undetermined, but seems likely to be in the urine (*cf Carcinus maenas* (Eales 1974), *Callinectes sapidus* (Gleeson 1980), *Homarus americanus* (McLeese *et al* 1977). Borowsky believes the site of contact pheromone secretion to be the pore-canals described in amphipods by Halcrow (1978). Halcrow and Bousfield (1987) suggest that the pore-canals could not secrete such chemicals because they are present in both sexes. However, the same could be said of hormones excreted in the urine, a possible explanation is that pore-canals excrete the same substances in both sexes [such as anti-foulants (Halcrow 1978)], but pheromones only in females. Studies on *Gammarus duebeni* (Dahl, Emanuelsson and von Mecklenburg 1970a,b) suggested that the site of water borne pheromone reception was concentrated on the male second antennae, specifically the calceoli. This conclusion was later disproved by Lincoln and Hurley (1981), who examined the microstructure of calceoli and showed them to be pressure sensors, and that the site of pheromone reception was the adjacent aesthetascs. These aesthetascs structures are believed to have a chemosensory function, as do hairlike structures described by Dahl (1973a,b) and the elaborate antennal structure described in amphipods by Lowry (1986). Further evidence for the second antennae of amphipods carrying chemosensors is provided by the work of Ducruet (1973), who ablated these antennae and thereby eliminated the males responses to conspecifics. Finally Dunham and Hurshman (1991) make an interesting comparison between: i. the data that suggest a male *G. lawrencianus* threshold for accepting a female varies with his reproductive history (*ie* the male threshold effect, intermittent contact with an unacceptable female keeps the male threshold high) and ii. the dynamics of intercellular pulsatile hormonal systems in mammals. Although not suggesting these interactions in Crustacea are the precursors of hormonal communication systems, Dunham and Hurshman do propose to further study the effects of increases and decreases in the rate at which the males are

ontogenetically pulsed by females to see how far the parallel can be extended.

5.3.3 Amphipod Life history Traits

There exists in the literature a large body of work on amphipod life history traits. Owing to the lack of a larval stage in the life cycle, and ease of measurement of egg size and numbers, amphipod crustaceans lend themselves to the study of reproductive parameters (Powell 1992). Many authors have attempted to synthesize this literature and Sainte-Marie (1991) categorizes these reviews in terms of taxonomic scope. Those he calls broad taxonomic reviews include the works of Morino (1978), Nelson (1980), Van Dolah and Bird (1980) and Wildish (1982). The 'narrow taxonomic scope' works are those concerning the Talitroidea (Wildish 1988), Gammaridae (Steele and Steele 1975), the genera *Orchestia* (Wildish 1979) and *Ampelisca* (Bellan-Santini and Dauvin 1988). Morino (1978) proposed that gammaridean life history types were distributed according to latitudinal/temperature gradients. As such he predicted semiannual populations for tropical species, annual populations for temperate species and biannual or perennial populations for polar regions. In contrast Wildish (1988) proposed six life history types within the Gammaridea: multivoltine (more than one generation per year) semiannual, univoltine (one generation per year) or multivoltine annual, semelparous (single brooded) biannual, and semelparous or iteroparous (multiple brooded) perennial. Wildish related these six strategies with habitat and rates of predation. Those from warm or tropical habitats, or exposed to high predation rates, Wildish (1988) proposed to be semiannual species that grow rapidly, are very fecund and mature early. Whereas biannual or perennial species grew more slowly, were less fecund and matured later, characteristics of populations in habitats where mortality is influenced by unpredictable physical factors. Sainte-Marie (1991) considered these reviews of limited use, being derived from small data sets with relatively few observations. Nelson (1980) looked at the fecundity of amphipods, comparing average body length of reproductive females with brood size (no. of embryos per brood). He concluded that 'epibenthic' gammarideans had larger females with more embryos per brood than

'endobenthic' gammarideans. This, Nelson maintained, was also true for brackish versus fresh and saltwater gammarideans, and in the family Gammaridae versus the Ampeliscidae and Hausteroiidea. Nelson (1980) also concluded that semelparous species produced more embryos per brood than iteroparous species. Although widely accepted, Sainte-Marie (1991) regards Nelson's conclusions on fecundity as questionable, being based on comparisons of brood size alone, or the ratio of brood size to body size. Sainte-Marie believes the former comparison does not take into account the positive relation between brood size and body size (*eg* Van Dolah and Bird 1980), and that the latter is a statistically incorrect way to account for this relation. A comparison between 'epibenthic' and 'endobenthic' gammarideans was also made by Van Dolah and Bird (1980), who reported the former to have smaller embryos per brood than the latter for a constant female body size. These authors also found a positive correlation between latitude and embryo size for a given species, and hypothesized that adult mortality risk is correlated positively with egg number and inversely with egg size. Although this adaptive hypothesis was supported by Nelson (1980), Fenwick (1984) dismissed it on account of misclassification of epi- and endobenthic categories and a review that was too narrow in taxonomic scope.

The literature contains numerous reports of the effects of habitat on the life history traits of individual species of amphipod. These reports show that body size at maturity, brood size, size of embryos, number of broods per female, age at maturity and breeding season all vary interspecifically with temperature, latitude, depth, salinity or exposure to predators (*eg* Segerstrale 1970, Fish and Preece 1970, Morino 1978, Pinkster and Broodbakker 1980, Kolding and Fenchel 1981, Sainte-Marie and Brunel 1983, Sheader 1983, Skadsheim 1984 and 1989, Clarke *et al* 1985, Bellan-Santini and Dauvin 1988, Naylor *et al* 1988). Sainte-Marie (1991) believed that if these trends are common to all Gammaridea, they should also be obvious at the interspecific level. To answer this question Sainte-Marie considered the previous general reviews too limiting and proposed the following broad ranging approach. Six life history traits were considered in relation to habitat and superfamily : mean and maximum body length of females and males, brood size, embryo diameter, number of broods per female, life

expectancy of females, lifetime potential fecundity (*ie* the number of embryo's produced per female per lifespan) and reproductive potential (*ie* the number of embryo's produced per female per year).In all Sainte-Marie (1991) examined three hundred and two aquatic gammaridean populations, representing two hundred and fourteen species in sixteen superfamilies. Any relationships among life history traits were examined by correlations (simple and partial) and regressions (simple and multiple), whilst variation across habits and superfamilies were quantified by univariate statistics, canonical discriminant analysis, and analysis of covariance.

From these data Sainte-Marie (1991) proposed the division of aquatic gammaridean amphipods into eight categories : semelparous or iteroparous semiannual (both multivoltine), semelparous (univoltine) or iteroparous (multivoltine) annual, semelparous or iteroparous (some multivoltine) biannual, and semelparous or iteroparous perennial (both univoltine). The most common life history category appears to be gammarids of the iteroparous annual type. Sainte-Marie's data seemed to indicate gammarideans from low latitude habitats were characterised by semiannual and annual populations with high reproductive potentials. By contrast, annual and perennial gammarideans, with low reproductive potentials, were more frequent at high latitudes and in the deep-sea. There exist many exceptions and Sainte-Marie believes these may be explained in terms of phylogenetic constraints or selection for a particular ecological habitat. All the aforementioned life history traits covary, however Sainte-Marie's data indicate body size explains most of the variation in brood size and embryo diameter. Brood size may be predicted with simple (using body size) or multiple regression equations (using body size, embryo diameter and number of broods), and these predictive functions are specific to superfamilies and habitat (Sainte-Marie 1991). Reviews prior to that of Sainte-Marie have focused singularly on brood size (excepting Wildish 1982, 1988), which is thought to be adaptive and directly proportional to adult mortality. However, brood size alone is a poor indicator of total reproductive output, as longevity and frequency of breeding are not taken into account. Sainte-Marie (1991) suggests the use of a fecundity rate or more accurately the reproductive potential (Wildish 1982), to infer mortality rates. Reproductive potential varies significantly

across habitats and superfamilies, but any interpretations must be conjectural owing to the almost complete lack of information on amphipod mortality rates.

5.4 REPRODUCTION IN ROCKALL TROUGH AMPHIPODS

5.4.1 Which species and why ?

Ampelisca sp nov (species 7) and *Tryphosella biloba* (species 3) were used for detailed reproductive studies for the reasons given earlier in Chapter Four. In addition, using these species allowed the assessment of ovary condition through their translucent integument. Using the abundance data given in Table III.II (Chapter Three) the ten most common species were also examined for the presence of brooding females and if possible oocyte development stage. A further ten species were also examined as the presence of eggs had been noted during the original sorting of samples. The remaining species occurred in such low numbers as to render any useful analysis of reproductive biology impractical.

5.4.2 Methods

Size at maturity

All lengths were measured as previously described in Chapter Four. As amphipods exhibit indeterminate growth, adult size of a species is difficult to specify. Many workers have used the largest known specimen or the smallest mature female, but these methods mean adult size is determined by the dimensions of a single individual. Steele and Steele (1991) use either the mid point of the range of adult female sizes or the size at which fifty percent of the females are mature. The latter is considered by these authors as the more accurate and was employed in this study. Determination of size of mature females is further complicated by females in ovarian diapause. Where mature females with small oogonia and non-setose oostegites are difficult to distinguish from immature females with the same characteristics. With these difficulties

in mind, adult size for *Ampelisca* sp nov and *Tryphosella biloba* were determined by plotting cumulative percentage of adults against length. 'Adults' were defined as females with developed oostegites, males with visible penile papillae. The size at which fifty percent of females/males were adult was determined from these plots.

Oostegite Development

The structure of oostegites varies considerably between amphipod species (Leite *et al* 1986, Steele 1991) and is mentioned as a taxonomic character by Bousfield (1979). Steele (1991) believes that following the evolution of major amphipod groups, the oostegites were modified in conjunction with the changes in reproductive strategies of these groups. The variation in size and shape of the oostegites and the number and position of their setae were determined for females of *Ampelisca* sp nov. Measurements were made on the oostegite attached to pereopod two of each female. This was for two reasons, firstly this oostegite was the most likely to be present even in damaged specimens and secondly to eliminate the variation between oostegites in an individual amphipod. For example the oostegite of pereopod two is longer and broader than that of pereopod five in *Gammaracanthus loricatus* (Steele 1991).

Histology

Commonly the reproductive biology of deep-sea invertebrates has been studied using histological techniques. Tyler and colleagues have used preparations of the gonads of a variety of invertebrates to determine size, frequency and developmental stage of gametes. Histological investigations of amphipod internal structures are impeded by the difficulty in sectioning the chitinous exoskeleton (which also hinders the embedding process). This problem coupled with the poor preservation of the material resulted in slide preparations of very poor quality. Embedding specimens using a resin/plastic medium as proposed by Howse *et al* (1972), proved no better. Owing to the small number of suitable samples for reproductive studies, the histological approach was

abandoned in favour of a non-destructive method (see below). The histological methods are presented in Appendix 5.1

Oocyte and Embryo development

Amphipods provide ideal subjects for the study of egg production, since developing embryos are held loosely in the ventral brood pouch of the female while they develop. This allows the ready removal of preserved or living embryos. The number and size of eggs/embryos were noted for each female examined. Amphipod eggs are cuboidal in the ovary, almost spherical when deposited in the brood pouch and prolately spheroidal while the embryo develops (Steele and Steele 1991). Beare and Moore (1994) comment on the probable shrinkage of eggs fixed in formalin and preserved in ethanol. As packing in the brood pouch, preservation methods and the effects of rehydration may have significantly affected shape of the eggs in this study, egg size was determined as follows. Longest axis (a), width (b) and depth (c) of egg were measured, and converted to volume using

$V = 4/3\pi \times (a/2) \times (b/2) \times (c/2)$.

Sainte-Marie (1991) reports the use by several authors of long-axis measurements only. Sainte-Marie used the mean of long and short axis and predictive regressions from the long-axis only data for his review. These methods are considered inaccurate when account is taken of the degree of distortion of embryo shape observed in this study, hence all three measurements were taken. Brood volume is simply number of eggs x volume of eggs. Failure to detect distinct reproductive seasonality in deep-sea peracarids may have resulted from using occurrence of brooding females as the main criterion for assessing reproductive activity (Bishop 1994). If development of embryos in the marsupium of brooding peracarids is prolonged by cold temperatures *eg* eight months for the cumacean *Leucon nasica* found at 1.5 °C in the Gulf of Lawrence (Granger *et al* 1979). Then deep-sea species encountering constant cold temperatures may exhibit gravid females throughout most or all of the year even in species with a

single reproductive peak. Using this argument Bishop (1992) suggested it may be possible to better assess presence or absence of reproductive periodicity by recording developmental stage of oocytes in the ovary and embryos in the marsupium. Such an approach was employed in this study. Bishop (1992) assessed ovary condition by splitting the pereon of the cumacean *Leucon profundus* between the first and second pereonites. The specimens were then stained with Rose of Bengal to allow assessment of condition through the translucent body wall. In the present study it proved possible to record the development stage of the ovaries without prior staining. A similar procedure was reported by Steele and Steele (1991), where as the ova became pigmented in the late stages of development, it proved possible to assess their condition through the translucent integument (Plate 5.1). The development stage of oocytes in this study were assessed using the following criteria :

Stage 1. None visible

Stage 2. Oocytes visible in the ovary as a thin short strand

Stage 3. Oocytes clearly visible, obscuring gut

Stage 4. Oocytes large, present through pereon segments 4-7

Stage 5. Oocytes large, present through pereon segments 3-7

Stage 6. As stage 5 but ovaries meeting dorsally above gut

The developmental stage of eggs/embryos were defined as follows :

Stage I. Spheroidal ova/zygote, granular appearance

Stage II. Early embryo, clear embryonic membrane

Stage III. Embryo with dorsal curvature, appendage buds visible

Stage IV. Embryo with ventral curvature, appendages developed, embryonic membrane breaking down

Stage V. Juvenile amphipod, membrane cast off

To overcome the lack of monthly samples from the same year, it proved necessary to pool data for the same month from different years.

PLATE 5.1 ***Ampelisca*** **sp nov WITH DEVELOPING OOCYTES VISIBLE THROUGH INTEGUMENT**

5.1a OOCYTE STAGE 3 Scale Bar 1mm

5.1b OOCYTE STAGE 6 Scale Bar 1mm

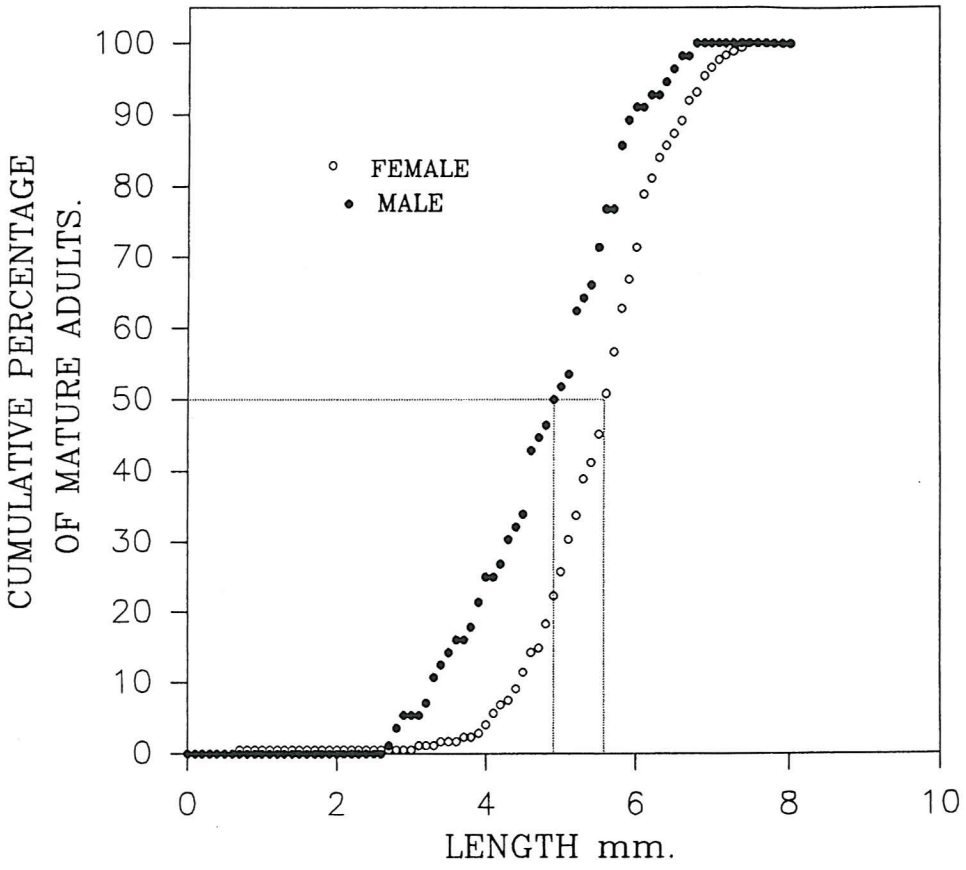
5.4.3 Results

***Ampelisca* sp nov**

Size at Maturity

Using the criteria described in the methods section Figure 5.4 was plotted using data from Appendix 5.2 This figure shows male *Ampelisca* sp nov reach maturity at a smaller size (4.49mm) than do the females (5.57mm). Female *Ampelisca* sp nov appear to reach a greater maximum length than do males (_ max. 6.73mm, _ max 7.41mm). It is not known, however, if there was adequate sampling of both male and female populations. Male ampeliscids tend to venture into the water column more than do females (Borowsky and Aitken Ander 1989), and as such may be undersampled by the epibenthic sled, as indicated by the female biased sex ratio reported in Chapter Four. The Ampeliscoidea superfamily show 62.5% of species have females with equal maximum lengths to males, whilst only 31.3% of females are bigger than males (Sainte-Marie 1991). The adult size of 5.57mm for females falls within the range for the Ampeliscoidea superfamily as a whole of 9.6±3.4 (Sainte-Marie 1991). The half-range of mature female body length ratio (HMFBL) was calculated for *Ampelisca* sp nov. This is a statistic developed to characterise the variability in body length of females at maturity and serve as an index of the number of broods produced by a female, when such information was lacking in a study (HMFBL ratio = (body length max - body length mean) ÷ (body length mean)). Sainte-Marie (1991) found that the HMFBL ratio was significantly correlated with maximum number of broods produced by a female. Thus it is possible to separate semelparous from iteroparous populations using this ratio. For cold water amphipods an HMFBL of <0.1304 indicates they are semelparous, whilst those >0.3478 are iteroparous. *Ampelisca* sp nov has an HMFBL ratio of 0.328 and is therefore in all likely hood iteroparous. *Ampelisca* sp nov has a larger HMFBL ratio than that reported for other Ampeliscoidea species (0.19 ±0.08 Sainte-Marie 1991).

FIGURE 5.4 SIZE AT MATURITY FOR *Ampelisca* sp nov



SIZE AT WHICH 50 % ARE MATURE ADULTS

MALES = 4.49 mm
FEMALES = 5.57 mm

Oostegite development

Using female length and oostegite length data given in Appendix 5.2, Figure 5.5 was plotted. This figure appears to show a linear relationship and when tested with a Pearson product moment correlation the data showed a strong positive correlation ($r=0.622$, $P<0.001$). This test measures the strength of association between pairs of variables regardless of which is dependent or independent. A simple linear regression was also calculated, and plotted on Figure 5.5 with 95% confidence limits. The regression equation was calculated as Female Length = -0.361 + (0.149 x Oostegite Length). Analysis of variance on the regression statistics gave an F statistic of 103.454 at $P<0.001$. From such a large F value it can be concluded that the independent variable (female length) is a good predictor of the dependent variable (oostegite length). The presence or absence of setae on the oostegites was also noted and used to prepare Figure 5.6. Oostegites develop setae as the female matures, and this is clearly shown in this figure, setose oostegites are only present on females greater than 5mm in length. The length of one of these oostegite setae was also measured in relation to female length and oostegite length. The terminal seta was chosen as it was the most easily measured and commonly undamaged. Setae on the margins of overlapping oostegites were often tangled with each other and broke easily on separation. These data (Appendix 5.2) were used to prepare Figure 5.7a and b. There appears to be a relationship between both female length and setae length, and oostegite length and setae length. However, correlation and regression analysis show that for female length and terminal hair length there is no detectable relationship ($P>0.05$). For oostegite length and terminal hair length correlation analysis revealed a positive correlation ($r=0.486$, $P=0.014$) and regression analysis revealed that as the independent variable oostegite length increases, so does the dependent variable terminal hair length ($F=7.119$, $P=0.014$ Terminal hair length= 0.1421 + (0.4535 x oostegite length)). Oostegite development follows the pattern shown in Figure 5.8, which was prepared by drawing the various stages using a microscope and camera lucida. As the female matures the oostegite lengthens and begins to develop setae. The setae develop first

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FIGURE 5.5 RELATIONSHIP BETWEEN FEMALE LENGTH AND OOSTEGITE LENGTH FOR *Ampelisca* sp nov

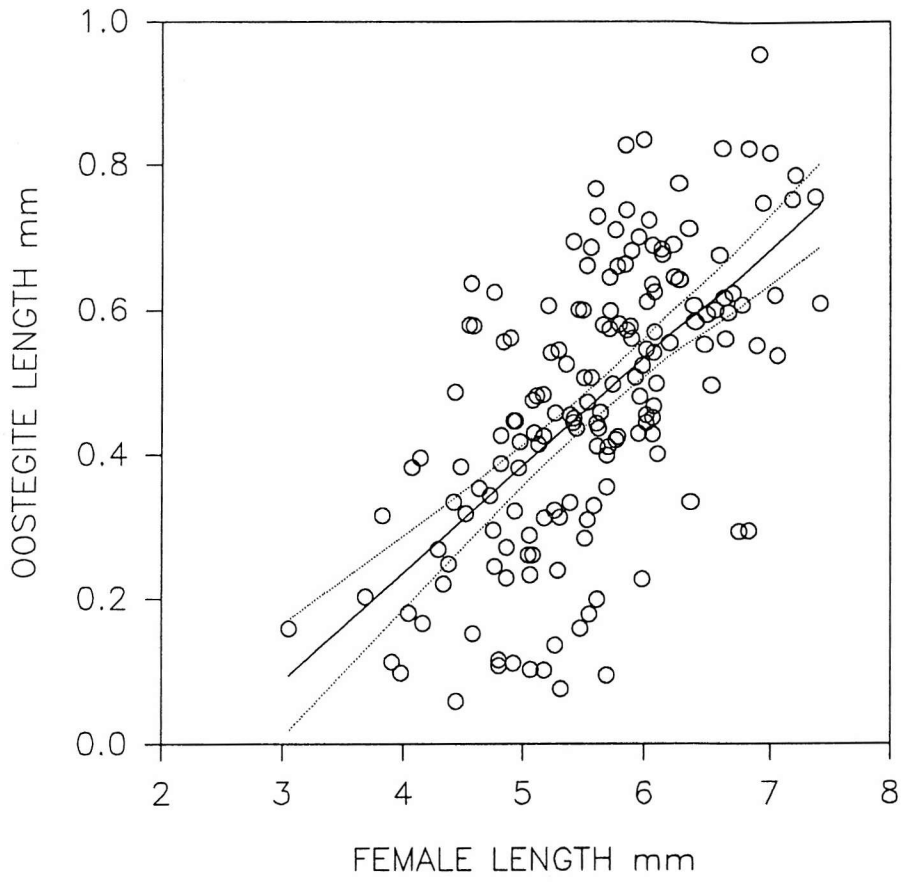


FIGURE 5.6 FEMALE LENGTH AND PRESENCE OF SETAE ON OOSTEGITES FOR *Ampelisca* sp nov

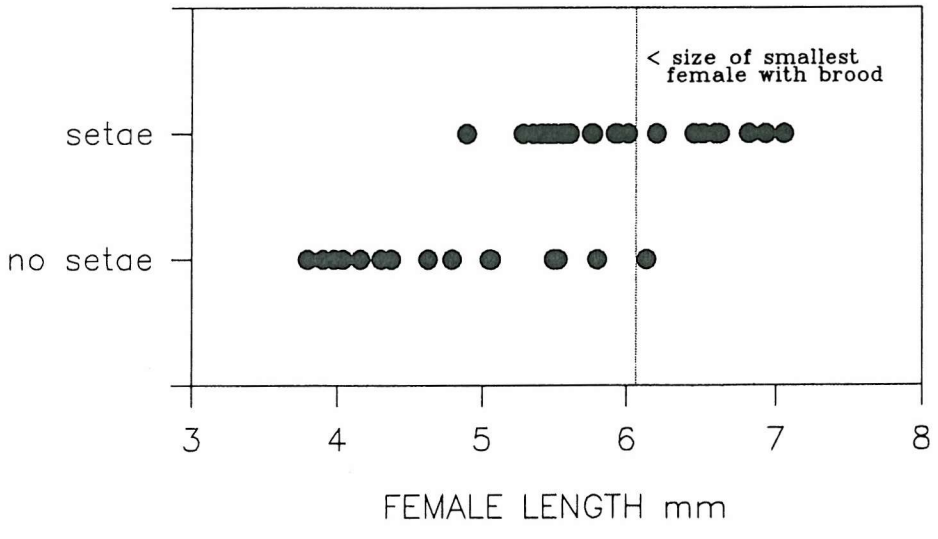


FIGURE 5.7a **RELATIONSHIP BETWEEN FEMALE LENGTH AND OOSTEGITE TERMINAL SETAE LENGTH**

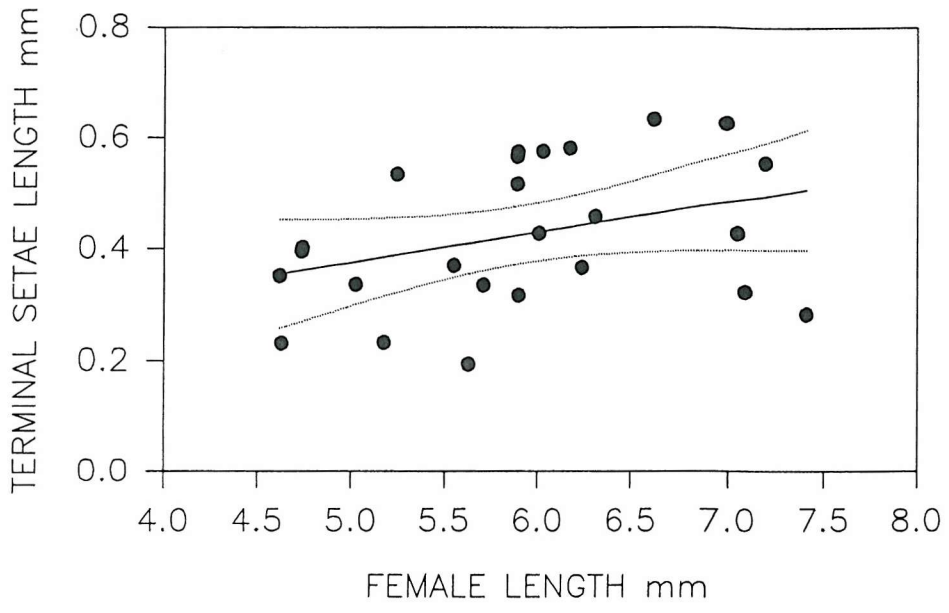


FIGURE 5.7b **RELATIONSHIP BETWEEN OOSTEGITE LENGTH AND TERMINAL SETAE LENGTH**

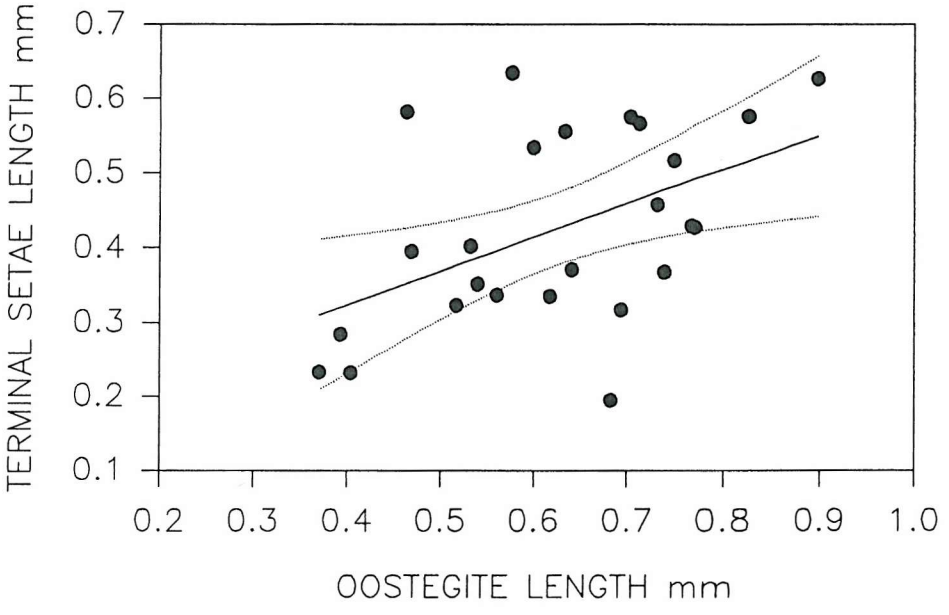
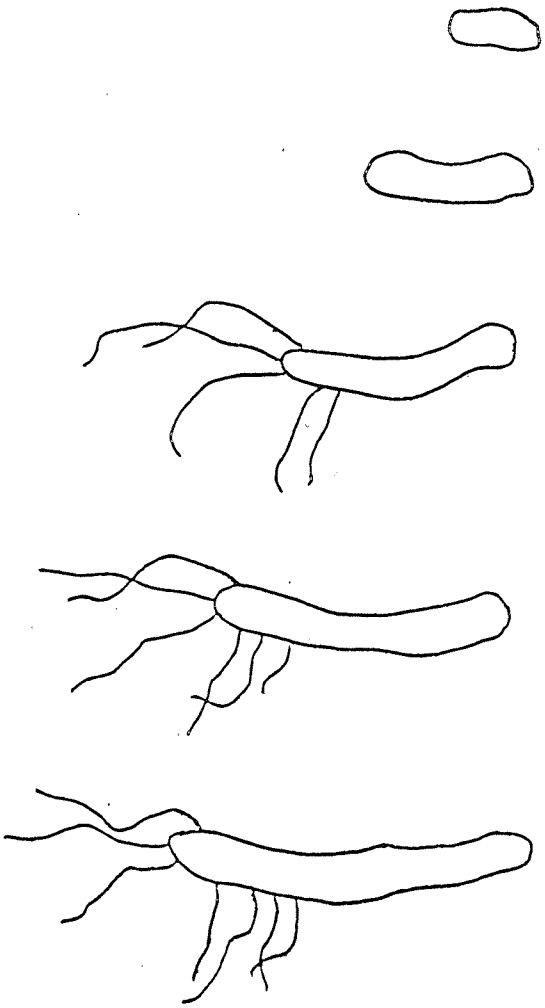


FIGURE 5.8 OOSTEGITE DEVELOPMENT IN *Ampelisca* sp nov

Immature oostegite



Mature oostegite

on the apex of the oostegite (terminal setae) and on one margin only. The developing oostegite does not significantly increase in width, but the number of setae on the margin (side setae) increases with increasing length. The number of 'side setae' in relation to female length and oostegite length was plotted using data in Appendix 5.2. (Figure 5.9a and b). As can be seen in Figure 5.9a there is a clear relationship between female size and number of 'side setae'. The relationship is less clear for increasing oostegite length and number of setae but still appears to be positively correlated (Figure 5.9b). This may be in part a result of the difficulty in measuring accurately oostegite lengths, as they were often damaged in the process. Figure 5.10 shows the relationship between mean oostegite length and month. If there were more mature females at certain times of the year then some variation in mean oostegite length could be expected. There is a slight apparent increase in the early year to a 'maximum' in June, but there is no significant pattern. Similarly, Figure 5.11 shows the variation in number of females with setose (mature) oostegites with month. Again there is some variation in the summer months, but no significant difference.

Penes development

Extreme difficulty in measurement and resulting inaccuracies precluded a detailed analysis. However from the small number of measurements made, Figures 5.13a and b were plotted. Correlation and regression analysis show no relationship between male length and penes length (P=0.090). There was a positive correlation between penes width and male length (r=0.591, P=0.020) and regression analysis revealed an increase in the independent variable male length, resulted in an increase in the dependent variable penes width (F=6.969, P=0.020 penes width = -0.0533 + (0.0405 x male length)). Despite being correlated with male length, penes width alone is not a clear enough indicator of male maturity. Normally secondary sexual characteristics in male amphipods are used as a measure of maturity, for example antennae length and segment number. Unfortunately the extensive damage to specimens and subsequent loss of appendages precluded such an approach in this study.

FIGURE 5.9a **FEMALE LENGTH AND NUMBER OF SIDE SETAE ON OOSTEGITES FOR *Ampelisca* sp nov**

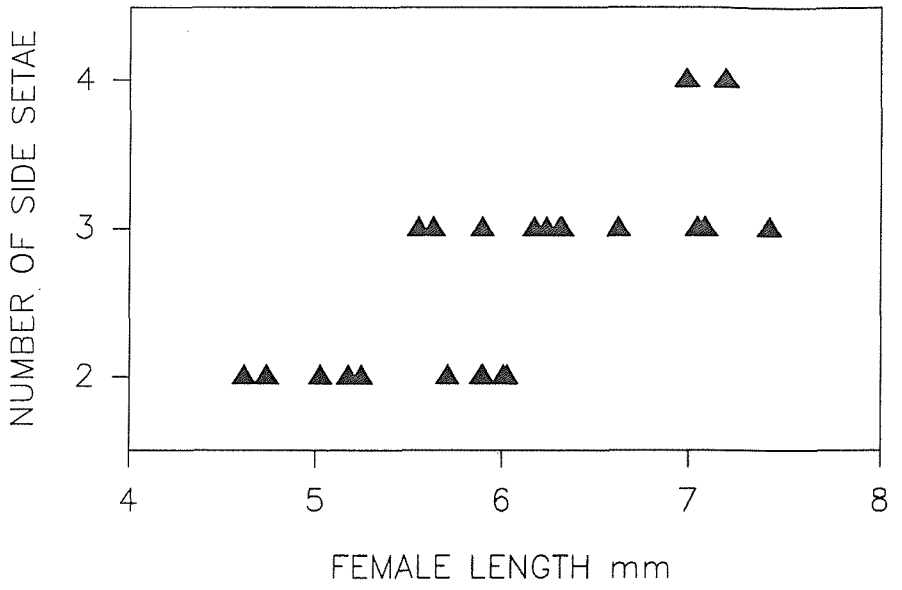


FIGURE 5.9b **OOSTEGITE LENGTH AND NUMBER OF SIDE SETAE FOR *Ampelisca* sp nov**

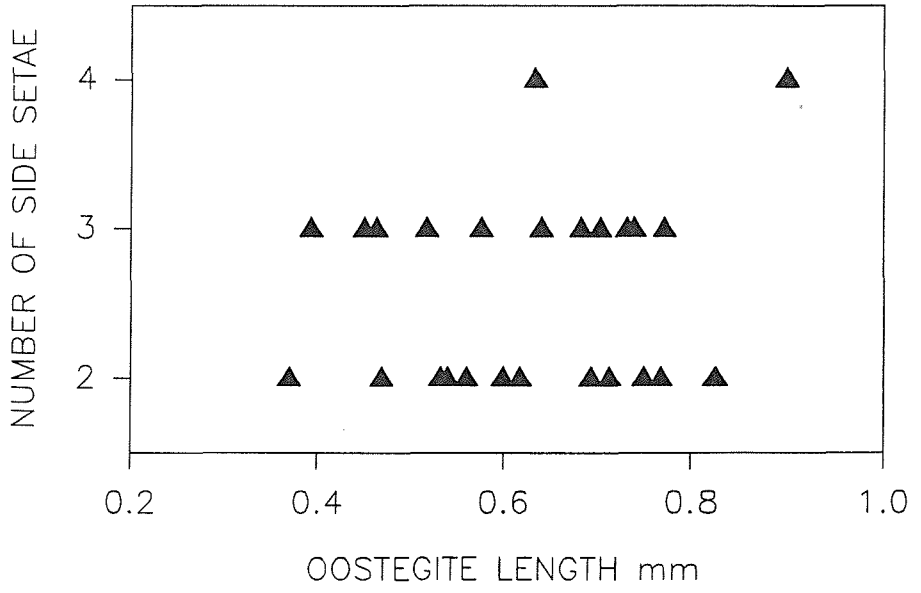


FIGURE 5.10 **VARIATION IN MEAN OOSTEGITE LENGTH WITH MONTH FOR *Ampelisca* sp nov**

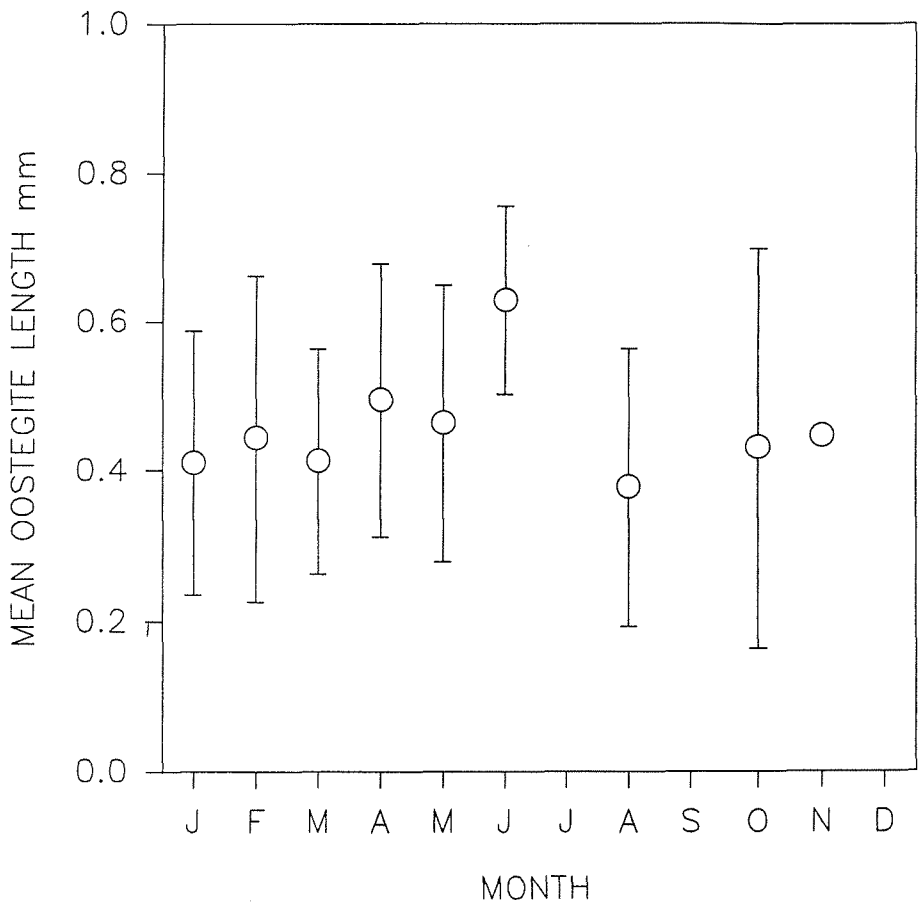


FIGURE 5.11 **VARIATION IN PERCENTAGE OF FEMALE *Ampelisca* sp nov WITH SETOSE OOSTEGITES WITH MONTH**

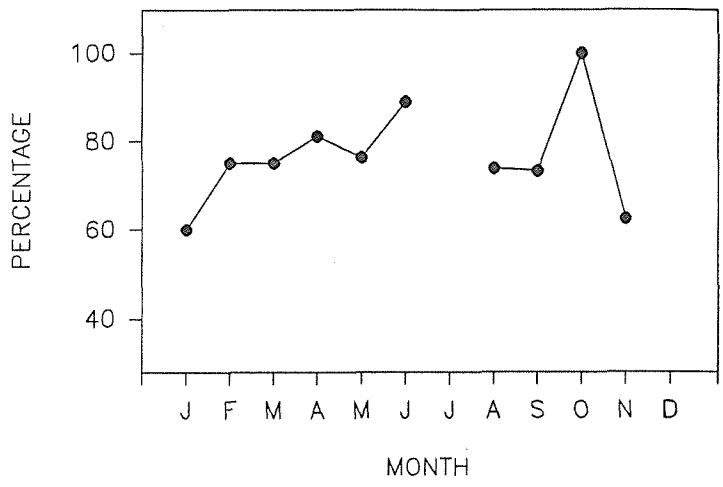


FIGURE 5.12 **VARIATION IN PERCENTAGE OF FEMALE *Ampelisca* sp nov WITH DEVELOPING OOCYTES WITH MONTH**

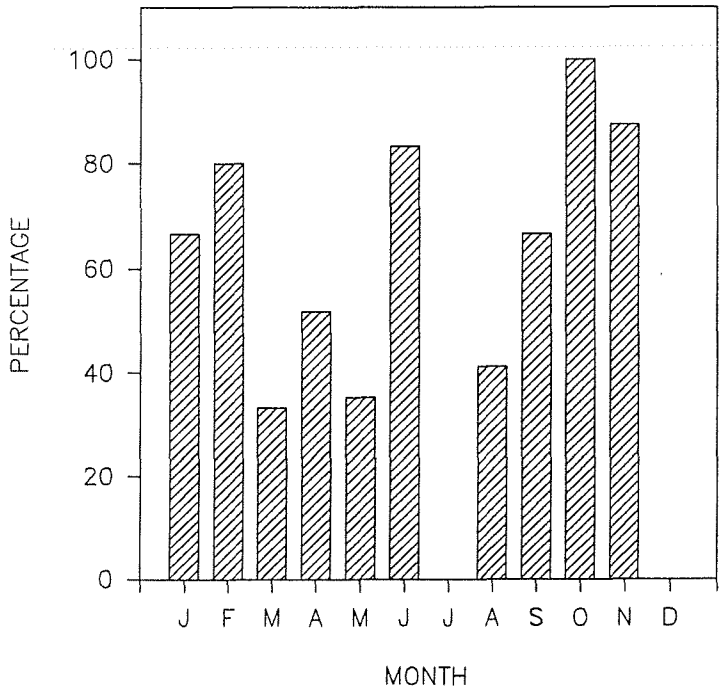


FIGURE 5.13a **RELATIONSHIP BETWEEN *Ampelisca* sp nov MALE LENGTH AND PENES LENGTH**

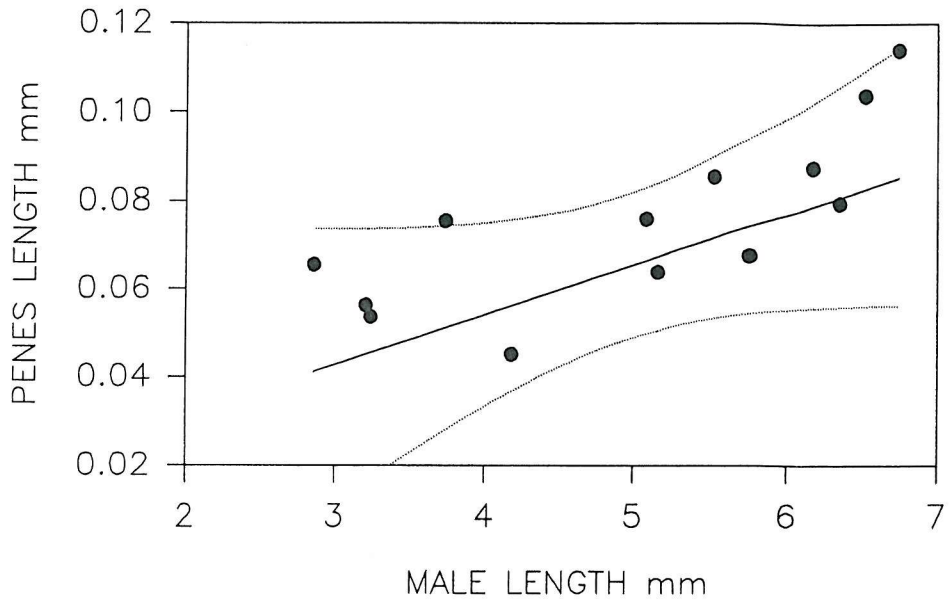
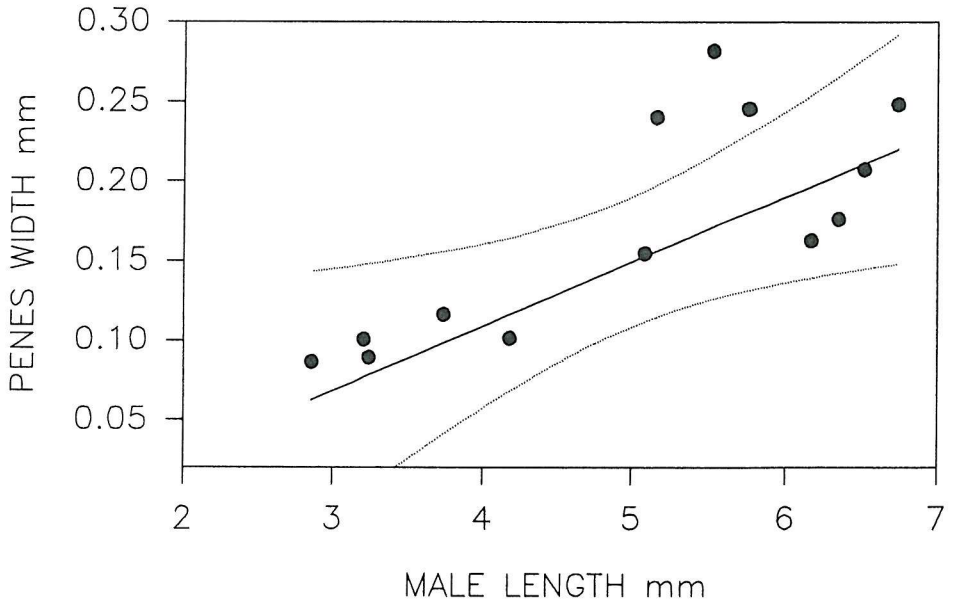


FIGURE 5.13b **RELATIONSHIP BETWEEN *Ampelisca* sp nov MALE LENGTH AND PENES WIDTH**



Oocyte and Embryo development

Females with developing oocytes were found throughout the year, although there was a significant variation in percentage of females with oocytes (Figure 5.12). This figure shows an apparent decrease in the percentage of females with oocytes in March, April and May, a rise to previous levels in June, a fall again in August and a steady rise again between September and November. The figure of 100% of females with developing oocytes in October probably reflects the fact that only two specimens were caught in this month - both with oocytes. This would seem to indicate *Ampelisca* sp nov breeds continually throughout the year. An examination of the developmental stage of the oocytes revealed the presence of stages 0 to 5 throughout the year (Figure 5.14). Stage 6 is only found in the months of February and June, but as it is hard to distinguish between stages 5 and 6, Figure 5.14 would again seem to indicate continuous breeding. A Kruskal-Wallis analysis of variance performed on the data revealed no significant differences between months ($H=2.307$, $P=0.986$). Figure 5.14 shows the percentage frequency of different oocyte stages in the total *Ampelisca* sp nov female population. Figures 5.15 and 5.16 show the percentage frequency distribution for females with non-setose oostegites and those with fully mature/setose oocytes respectively. As would be expected only a small percentage of *Ampelisca* sp nov females with oocytes have non-setose (immature oostegites), and the majority of those that do are of an early developmental stage (Figure 5.15). The percentage composition of developmental stages in females with mature oostegites shown in Figure 5.16 is very similar to that of Figure 5.14. Although *Ampelisca* sp nov appears to breed throughout the year, there is some variation in the 'intensity' of breeding. Figure 5.14 shows a higher percentage of females with late stage oocytes compared to early stages in January, February, June, September and October. Whilst percentages of early stage embryos dominate in March, April, May, August and November. It seems then possible that there are more females capable of oviposition in Spring (Feb) and Summer (June) months.

FIGURE 5.14 VARIATION IN PERCENTAGE FREQUENCY OF *Ampelisca* sp nov OOCYTE STAGES WITH MONTH

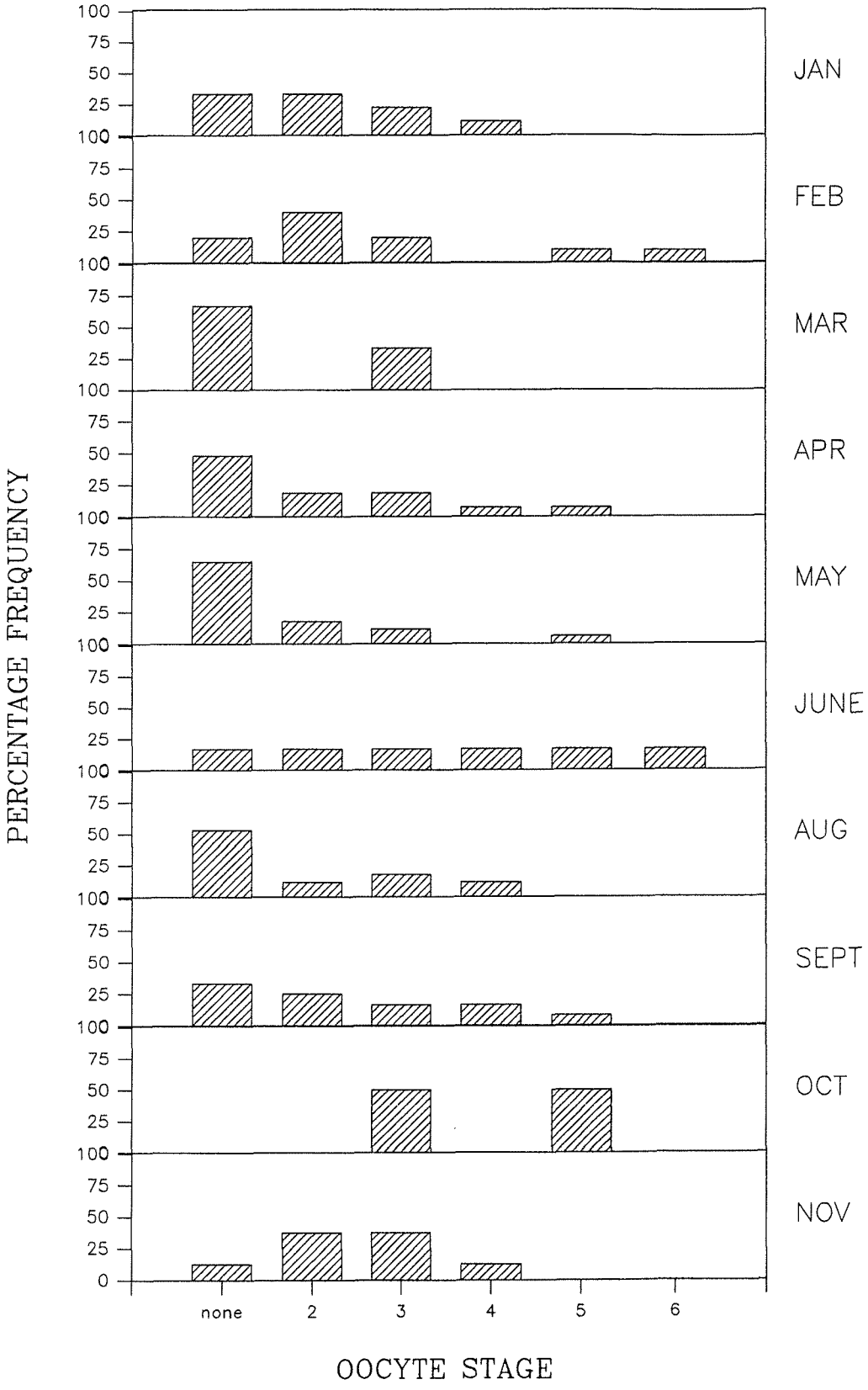


FIGURE 5.15 VARIATION IN OOCYTE STAGE WITH MONTH FOR *Ampelisca* sp nov WITH NON-SETOSE OOSTEGITES

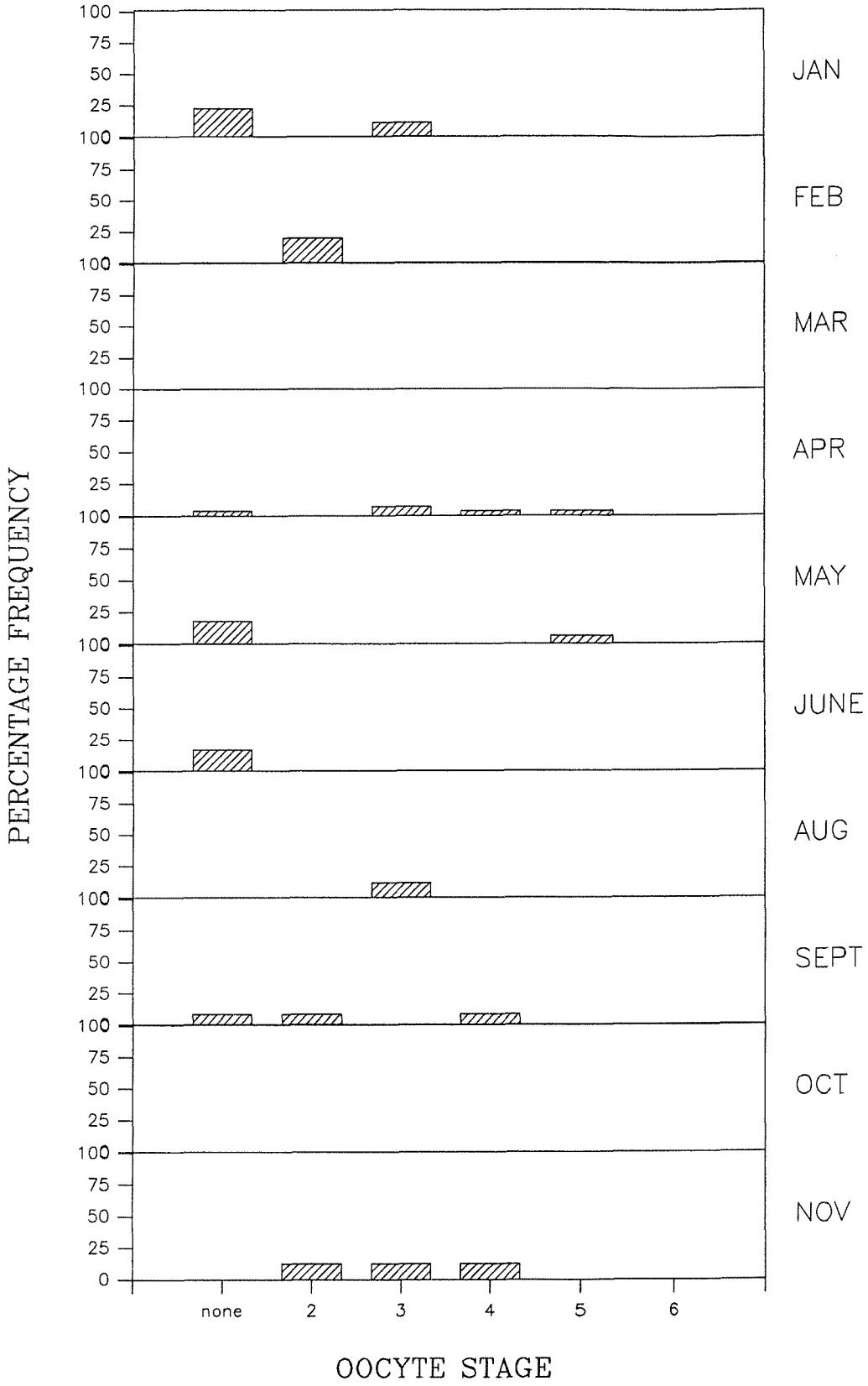
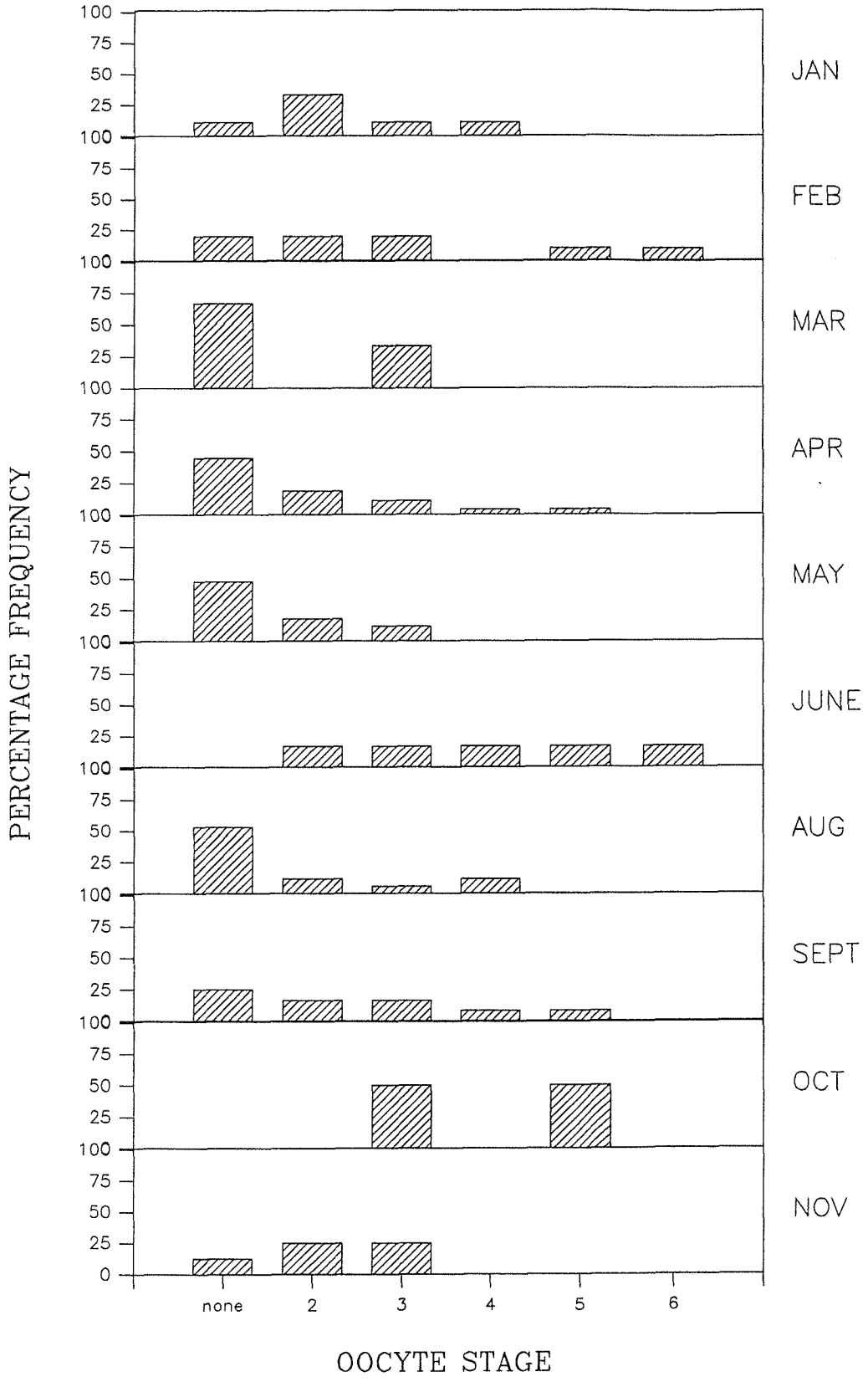


FIGURE 5.16 VARIATION IN OOCYTE STAGE WITH MONTH FOR *Ampelisca* sp nov WITH MATURE OOSTEGITES



Unfortunately only three brooding females of *Ampelisca* sp nov were recovered in the entire sampling programme, precluding any detailed analysis of their temporal distribution. However, one female was caught in each of the months of March, April and May, which ties in with a possible oviposition in February. The female length, plus the developmental stage and volume for each of the embryos were as follows March - Length 6.25mm, Embryo Stage II, Volume 0.049mm^3, April - Length 7.01mm, Embryo Stage I, Volume 0.042mm^3 (Plate 5.2a), May - Length 6.07mm, Embryo Stage III, Volume 0.151mm^3. Although with such low numbers no meaningful analysis of relationship between female size, brood volume and developmental stage can be made, it seems clear that volume increases with developmental stage. The female taken in May which had the most developed embryo of the three (Stage III), also had oocytes in an early developmental stage (Plate 5.2b). This lends support to the theory of *Ampelisca* sp nov being iteroparous. It seems likely that brood size for *Ampelisca* sp nov is greater than one. Indeed examination of oocyte numbers in late developmental stages reveals an average of 8 possible ova. Egg loss is likely to have resulted during sampling, sorting and subsequent handling/transport as has been described for isopods, shrimps and gammaridean amphipods (Fish 1975, Wagele 1987, Sainte-Marie *et al* 1990, Gorny *et al* 1992 and Klages 1993). Gorny *et al* 1992, refer to the added problem of increased loss in samples from deeper waters with correspondingly longer trawling exposure. Coyle and Highsmith 1994 report that fecundity estimates of ampeliscids vary considerably, since eggs are easily lost from the marsupium during collection. *Ampelisca* sp nov, with its long/thin oostegites, relatively exposed marsupium and having been subjected to a long trawl and rough sorting procedures will have undoubtably suffered egg loss. Ideally amphipods should be sorted prior to preservation, and any brooding females isolated in individual vials for an accurate estimate of fecundity (Sainte-Marie *et al* 1990). In his review of reproductive bionomics in gammaridean amphipods, Sainte-Marie (1991) showed that brood size and embryo diameter were positively correlated with body length. Sainte-Marie used these results to produce predictive regressions to calculate brood size and

PLATE 5.2 ***Ampelisca*** **sp nov WITH DEVELOPING EMBRYOS**

5.2a STAGE I EMBRYO IN BROOD POUCH Scale Bar 1mm

5.2b STAGE III EMBRYO REMOVED FROM BROOD POUCH Scale Bar 1mm

embryo diameter from body length. These are as follows, for the Ampeliscoidea superfamily :

log brood size=1.335 log body length + 0.089 (r^2=0.49, F=21.3, P<0.001)

for Deep-Sea gammarids as a whole :

log brood size=0.937 log body length + 0.171 (r^2=0.73, F=24.54, P<0.001)

log embryo dia.=0.695 log body length - 0.919 (r^2=0.57, F=25.33, P<0.01)

for all gammarids surveyed :

log brood size=1.714 log bl - 1.087 log ed - 0.2 log HMFBLr - 0.772

(r^2=0.7, F=94.34, P<0.001)

Using 5.57mm as the size at maturity for females, these regressions give the following results for *Ampelisca* sp nov :

Ampeliscoidea superfamily regression - Brood size=12.1

Deep-Sea gammarid regressions - Brood size=7.4, Embryo diameter=0.4mm

Gammarid regression - Brood size=6.3

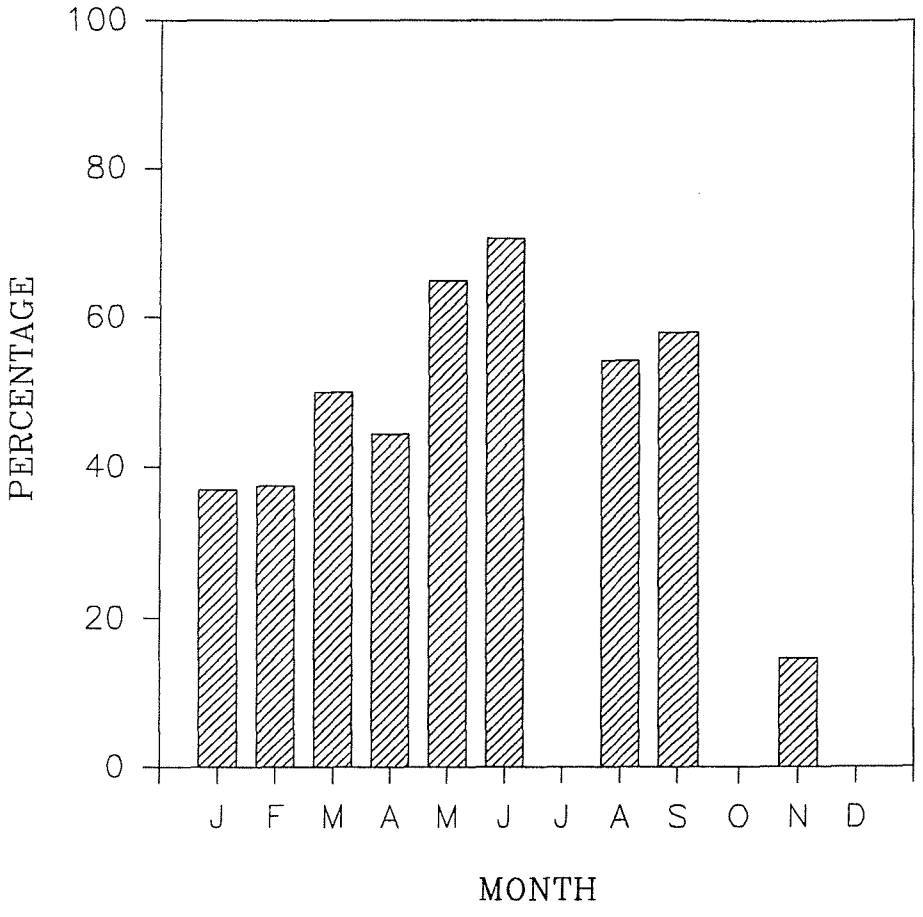
All fall within the ranges given for the Ampeliscoidea superfamily in Sainte-Marie's review, Brood size=27.8±14.8, Embryo diameter=0.51±0.12, and the predicted embryo diameter value is very close to the observed mean of the stage I embryo of 0.435mm. Brood size estimates obtained from the regressions also closely match the number of mature oocytes (8-10), present in *Ampelisca* sp nov ovaries. Such oocyte counts are often used as estimates of fecundity as mentioned in the introduction to this chapter.

Klages (1993) used literature data to develop an empirical relationship between egg diameter and duration of embryonic development :

Development time (days) = 119.4 x Egg diameter + 24.4 (r^2=0.83)

Using the average diameter of a stage I *Ampelisca* sp nov embryo (0.435mm), this gives an estimated development time of 76 days, roughly two and half months. Thus if there is an increase in reproductive effort in early spring and summer as postulated earlier, there should be a corresponding increase in the number of juveniles roughly two and a half months later. Figure 5.17 shows the monthly changes in the percentage of the population comprised by juvenile *Ampelisca* sp nov. This figure clearly shows

FIGURE 5.17 **MONTHLY CHANGES IN THE PERCENTAGE OF POPULATION COMPRISED BY *Ampelisca* sp nov JUVENILES**



the months of May and June, and August and September have a considerably higher percentage of juveniles compared to other months of the year. These 'peaks' in juvenile abundance (May/June and Aug/Sept) are as predicted roughly two and half months after the peaks in oocyte production, and coincide with maximal periods of phytodetrital input to the sampling region.

Tryphosella biloba

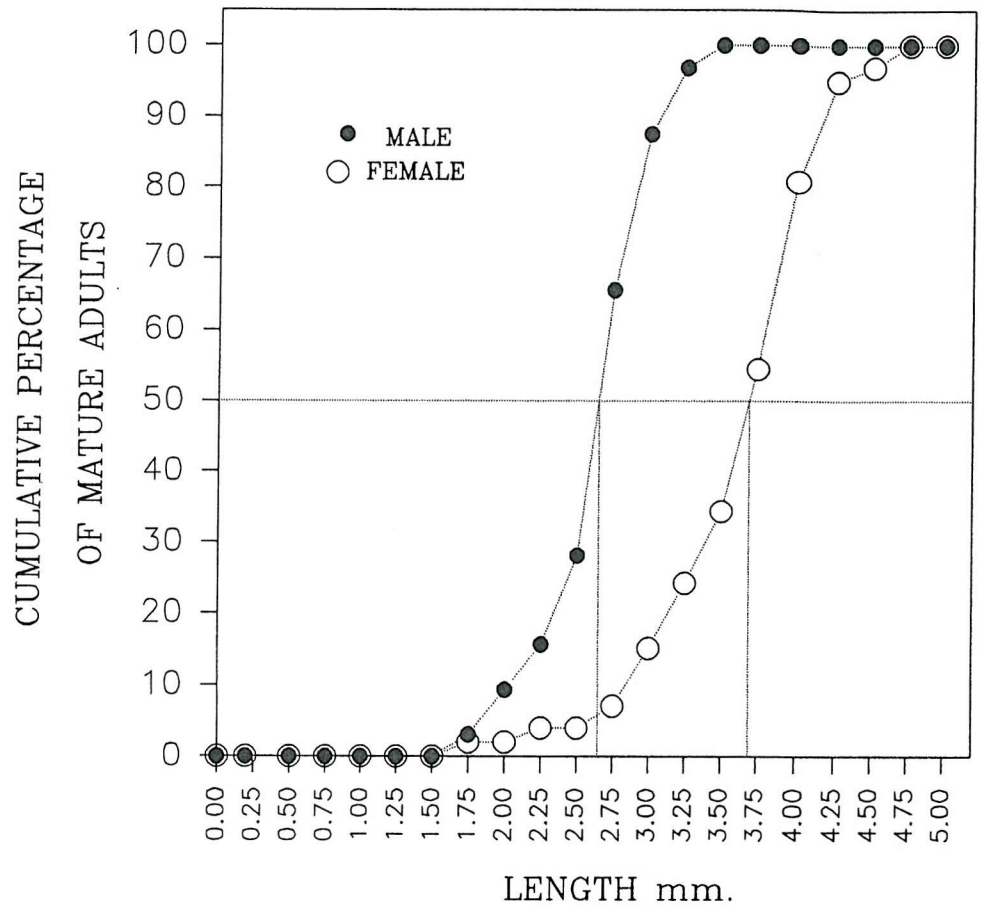
Size at Maturity

Using data from Appendix 5.3, a plot showing size at maturity for *Tryphosella biloba* was prepared (Figure 5.18). As for *Ampelisca* sp nov males reach maturity at a smaller size (2.65mm) than do females (3.69mm). Again as for *Ampelisca* sp nov, *T. biloba* females attain a greater maximum length than their male counterparts (male max. 3.28mm, female max. 4.59mm). However, despite again not knowing if males and females populations have been sampled equally, Sainte-Marie (1991) reports that 88.2% of Lysianassoidea species females have a greater maximum adult body length than males. The HMFBL ratio for *T. biloba* females is 0.2439, which falls within the range given for the Lysianassoidea superfamily of 0.19 ±0.1 (Sainte-Marie 1991). This value falls between the lower limit for species which are definitely iteroparous (0.3478), and the upper limit of semelparous species (0.1304) so cannot be used to indicate how many broods *T. biloba* might produce.

Oostegite and penes development

The small size of *T. biloba* specimens, compounded with their compact morphology (tight overlapping coxae) and a tendency to die curled up in a ball, made manipulation very difficult. Thus it proved virtually impossible to accurately measure oostegite and penes dimensions. This may explain the total lack of correlation and regression between female length and oostegite length (correlation coefficient=0.303 $P>0.05$, regression - no relationship $P=0.236$, $F=1.521$). However this could be related to the

FIGURE 5.18 **SIZE AT MATURITY FOR *Tryphosella biloba***



SIZE AT WHICH 50 % ARE MATURE ADULTS

MALES = 2.65 mm

FEMALES = 3.69 mm

small size of the sample actually measured owing to the difficulties mentioned. Such analysis were therefore abandoned.

Oocyte and Embryo development

Only a small percentage of *T. biloba* females were found with ovaries containing developing oocytes. Such females were found only in April, May and August, and only contained oocytes of stages 3 and 4 (Figure 5.19). The percentage of female *T. biloba* found to be brooding was much higher, over 60% of the female population for much of the year (Figure 5.19). There was a dramatic fall in the percentage of brooding females between June and October, with a minimum in August. As with *Ampelisca* sp nov the figure of 100% for October is misleading, being based on a single female from an anomalous sample (ES 111 see Chapter 3), the real value is likely to fall between the values for September and November. The fall in numbers of *T. biloba* brooding, corresponds with a rise in the numbers with developing oocytes. This would seem to indicate a release of juveniles in summer and an increase in oocyte development leading to oviposition of ova in late summer/autumn. An examination was made of the variation in developmental stage of the brood in different months of the year for *T. biloba.* This revealed an apparent variation in the percentage frequency of different embryo development stages with month (Figure 5.20). These data supports the supposition that *T. biloba* deposits newly fertilized embryos (Stage I) in late summer/autumn (Aug-Oct), which mature through the winter and spring months (Nov-Apr), to late stages IV and V in the summer (May-July)(Plate 5.3). *T. biloba* appears to show seasonal or at least synchronous reproduction. However, a Kruskal-Wallis analysis of variance performed on the data presented in Figure 5.20, reveals no significant difference between the months ($H=2.639$, $P=0.977$). If *T. biloba* is a seasonal breeder, then there should be an influx of juveniles into the population during a given period in the year. Figure 5.21 is a plot of the changes in length frequency data for *T. biloba* with month. This figure does indicate an influx of smaller specimens between June and October. Figure 5.22 is a plot of the percentage of the population

FIGURE 5.19 **MONTHLY VARIATION IN PERCENTAGE OF FEMALE *T. biloba* BROODING OR WITH DEVELOPING OOCYTES**

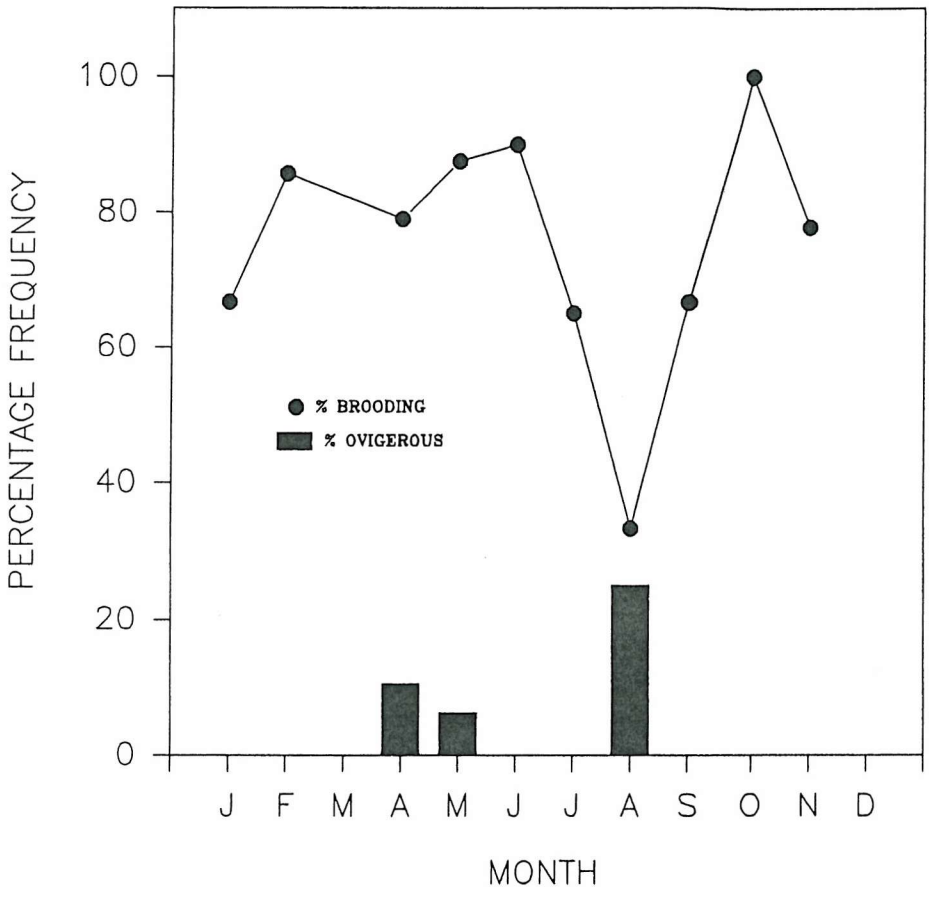


FIGURE 5.20 MONTHLY VARIATION IN PERCENTAGE OF *T. biloba* EMBRYO STAGES

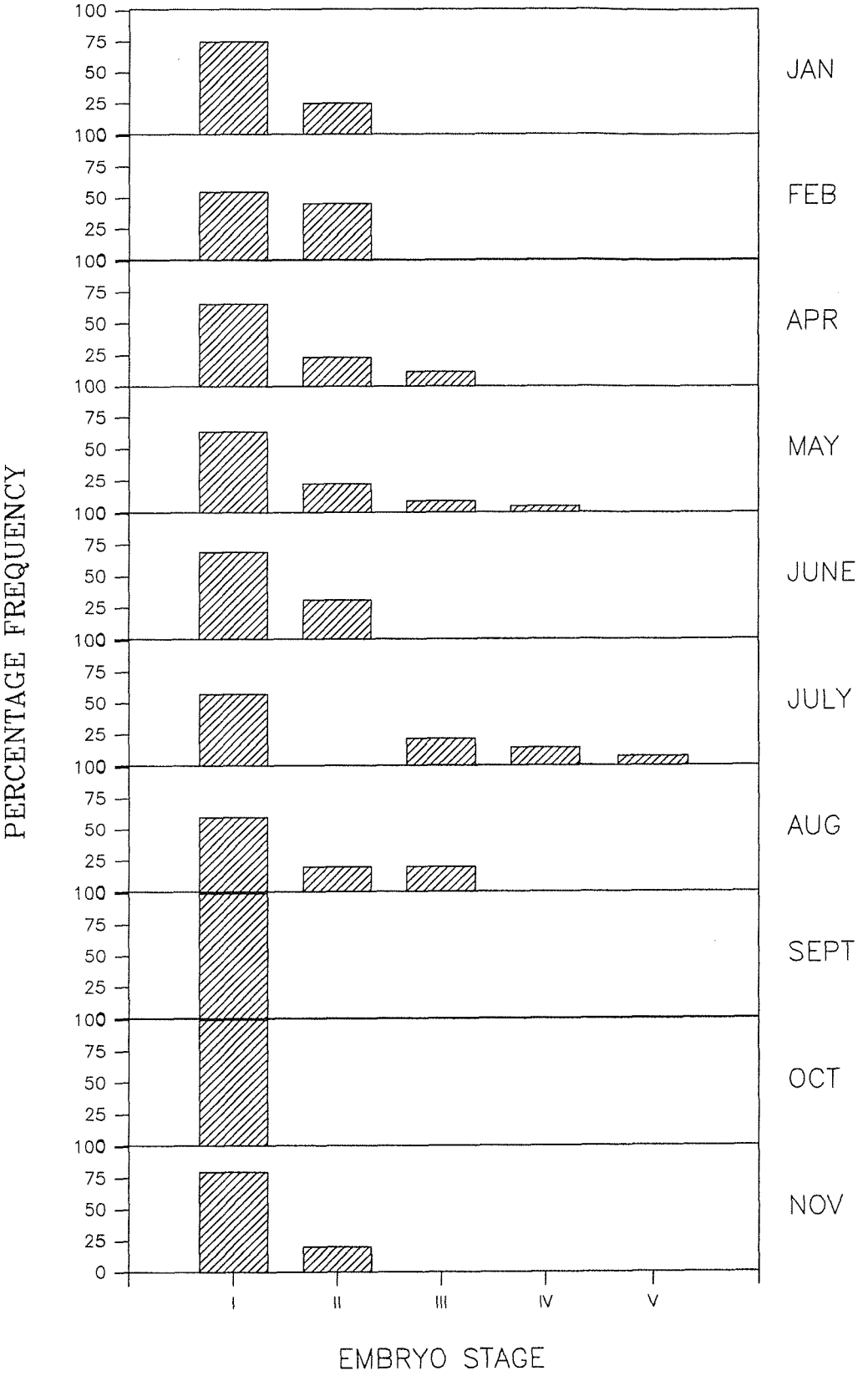
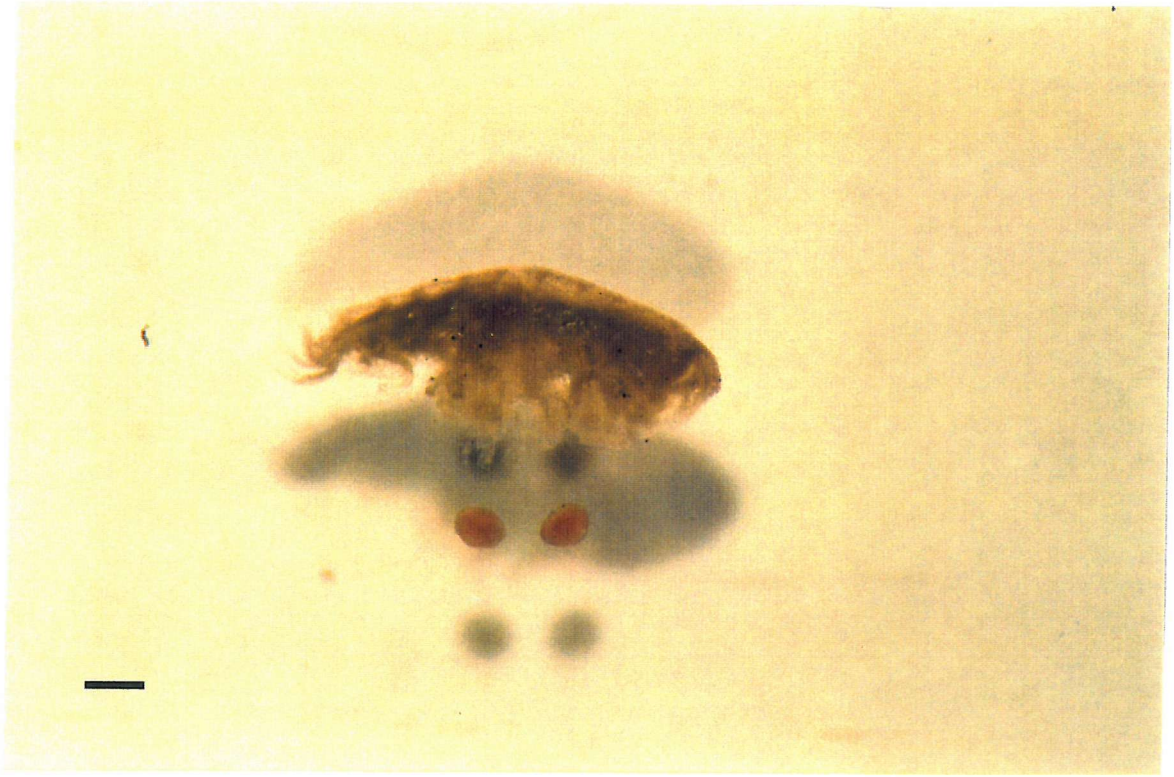
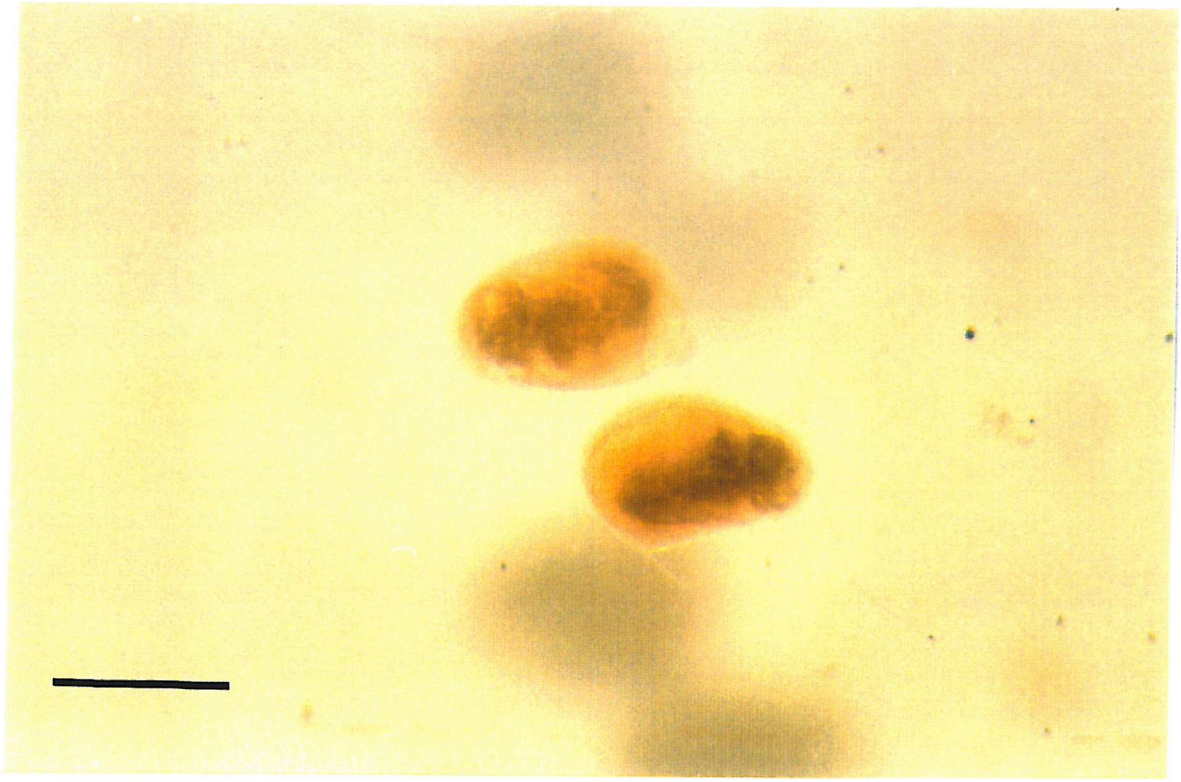


PLATE 5.3 ***Tryphosella biloba*** **WITH DEVELOPING EMBRYOS**



5.3a STAGE I EMBRYOS REMOVED FROM BROOD POUCH Scale Bar 1mm



5.3b STAGE IV EMBRYOS REMOVED FROM BROOD POUCH Scale Bar 0.5mm

FIGURE 5.21 **MONTHLY VARIATION IN *T. biloba* LENGTH - FREQUENCY DISTRIBUTIONS**

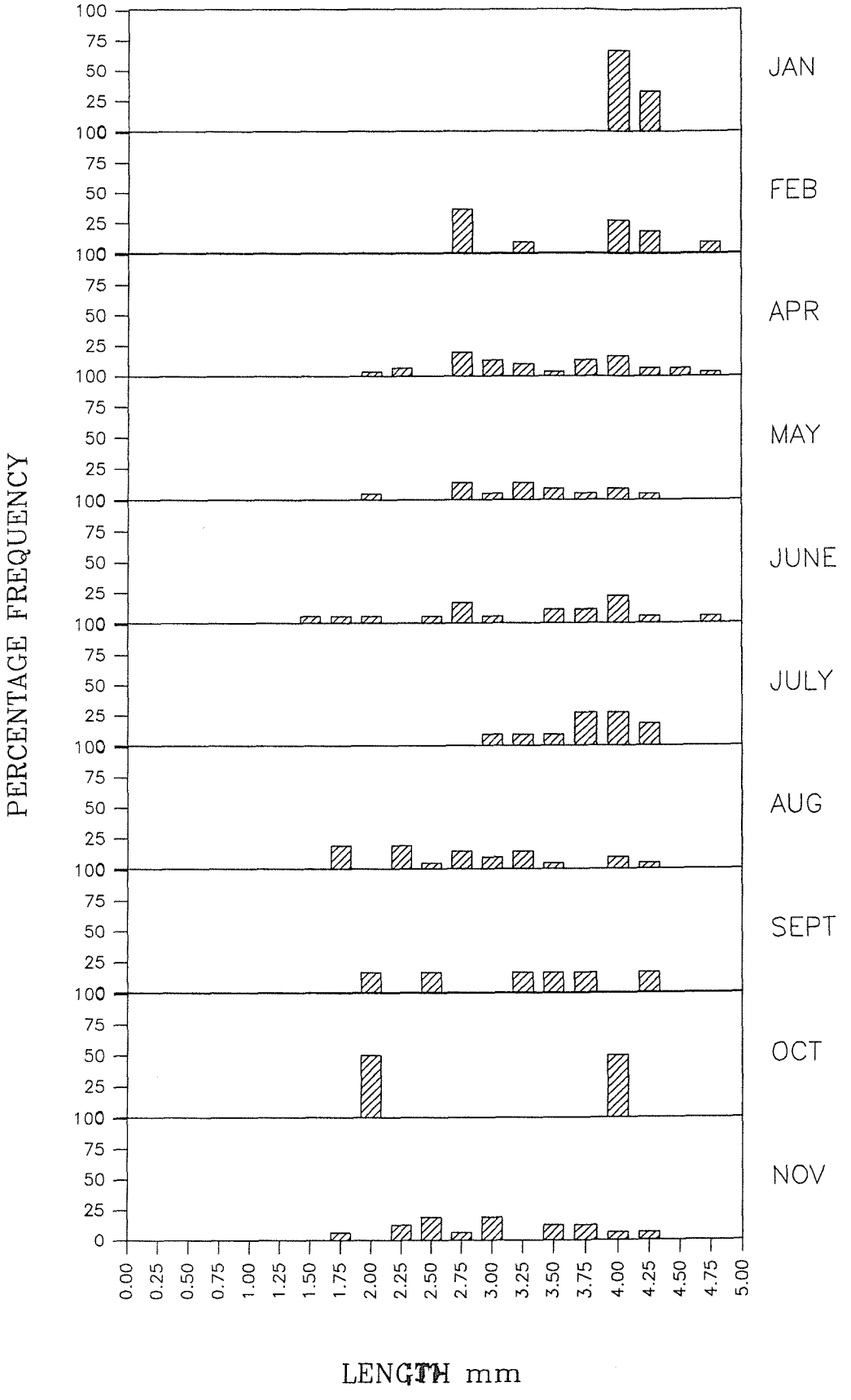
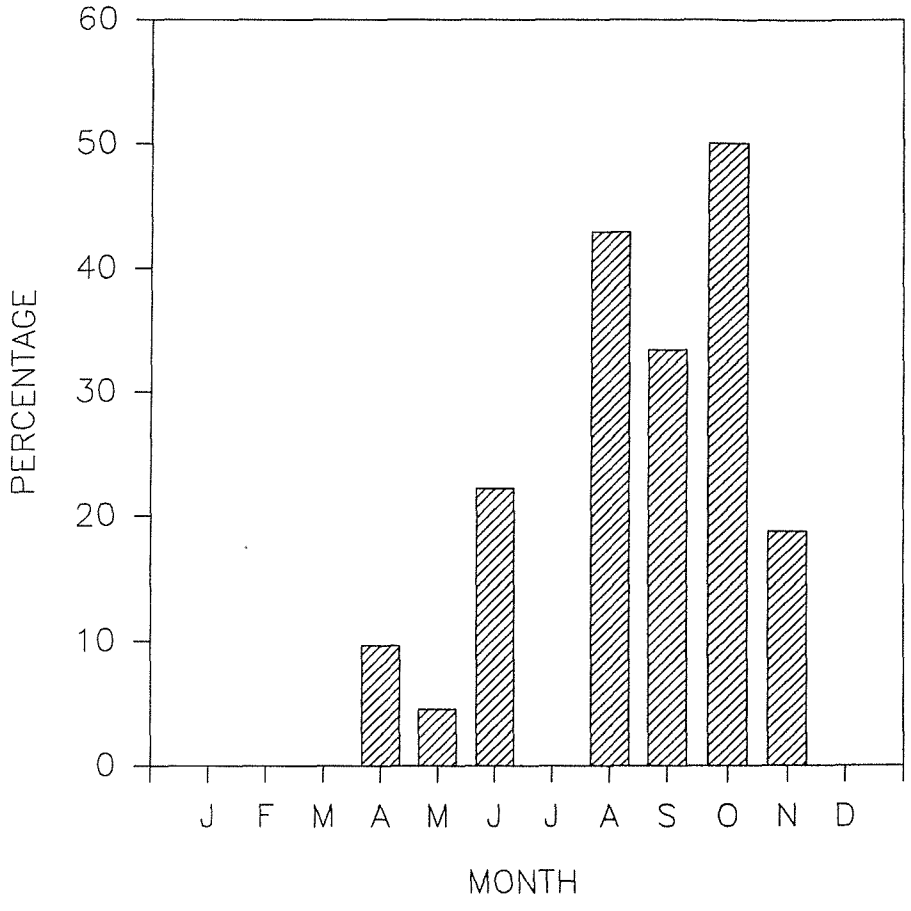


FIGURE 5.22 **MONTHLY VARIATION IN PERCENTAGE OF POPULATION COMPRISED BY JUVENILE *T. biloba***



smaller than 2.65mm (the size at maturity for males) in each month. This clearly shows an influx of juveniles into the population in the late summer. The mean diameter of a stage I, *T. biloba* embryo is 0.41mm. Using Klages (1993) predictive relationship between embryo diameter and development time, this diameter gives an estimated development in the marsupium of 73 days. So the influx of juveniles observed in August and September (Figure 5.22), may be the hatchlings from late stage embryos observed in April and May (Figure 5.20).

The relationship between egg volume and female length for *T. biloba* was investigated (Figure 5.23). There exists a positive correlation between the two variables ($r=0.349$, $P<0.001$), and the regression plotted on Figure 5.23 shows egg volume increases as female length increases (volume=-0.0422+0.0211xlength, $F=14.57$, $P<0.001$).

Brooding *T. biloba* females were found with either one or two embryos, never more. Unlike *Ampelisca* sp nov, the well protected marsupium of *T. biloba*, is likely to have prevented significant egg losses. Using the mature female length of 3.69mm and predictive regressions of Sainte-Marie (1991) mentioned previously, predicted brood size for this species varies between 3 for gammarids as a whole, 5 for deep-sea gammarid regression and 6.4 for the Lysianassid superfamily regression. Predictions of embryo diameter from body length give a value of 0.29mm. This is significantly smaller than the observed mean of 0.41mm. Putting this observed diameter into the regression to obtain mature female length gives a value of 5.8mm, again a much larger value than the actual figure of 3.69mm. Thus it seems *T. biloba* has large embryos in relation to its length when compared to other gammarideans, and the observed brood size of between 1 and 2 embryos may in fact be the true fecundity of this species. There is a relationship between female length and the number of embryos brooded in *T. biloba* (Figure 5.24). A comparison between lengths of females with two embryos compared to those with one, shows the former are larger (Students t-test, $t=4.455$, $P<0.001$).

The failure to detect a relationship between embryo volume and development stage may reflect the small number of late stage embryos recovered (Figure 5.25)(Kruskal-Wallis ANOVA, no significant difference, $H=2.45$, $P=0.654$). A plot of change in embryo volume with month shows some variation (Figure 5.26), and a Kruskal-Wallis

FIGURE 5.23 **RELATIONSHIP BETWEEN FEMALE LENGTH AND EMBRYO VOLUME FOR *T. biloba***

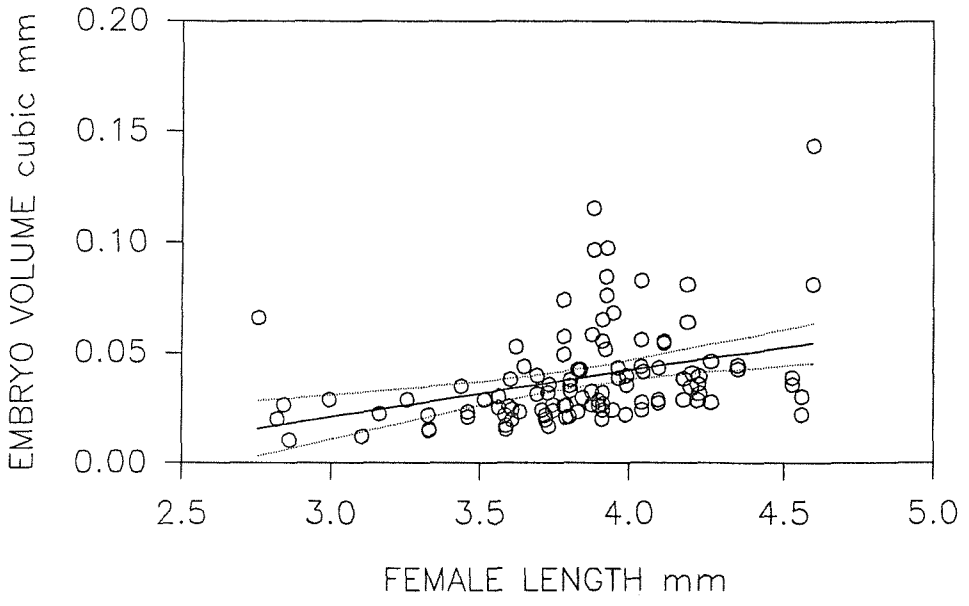


FIGURE 5.24 **RELATIONSHIP BETWEEN FEMALE LENGTH AND BROOD SIZE FOR *T. biloba***

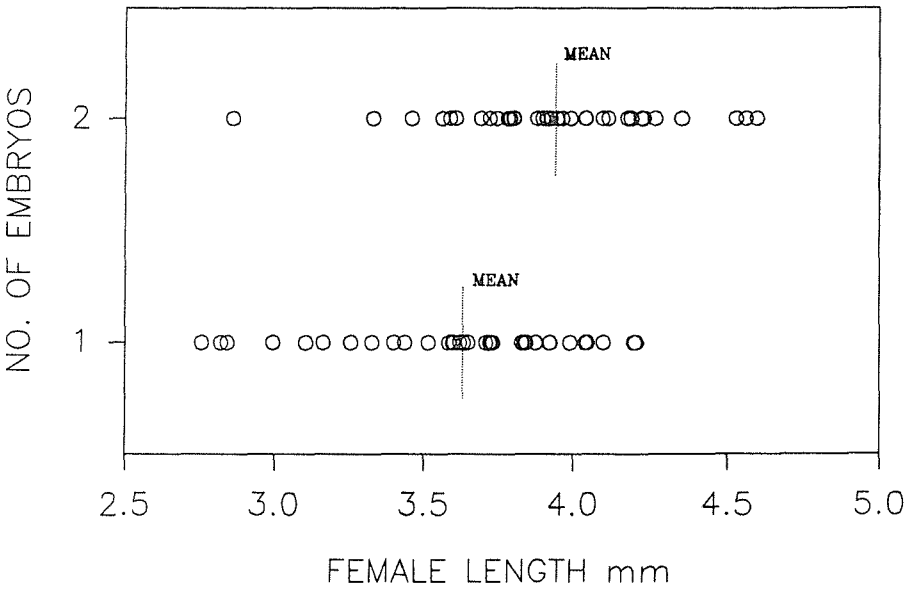


FIGURE 5.25 **VARIATION IN VOLUME WITH DEVELOPMENT STAGE FOR *T. biloba* EMBRYOS**

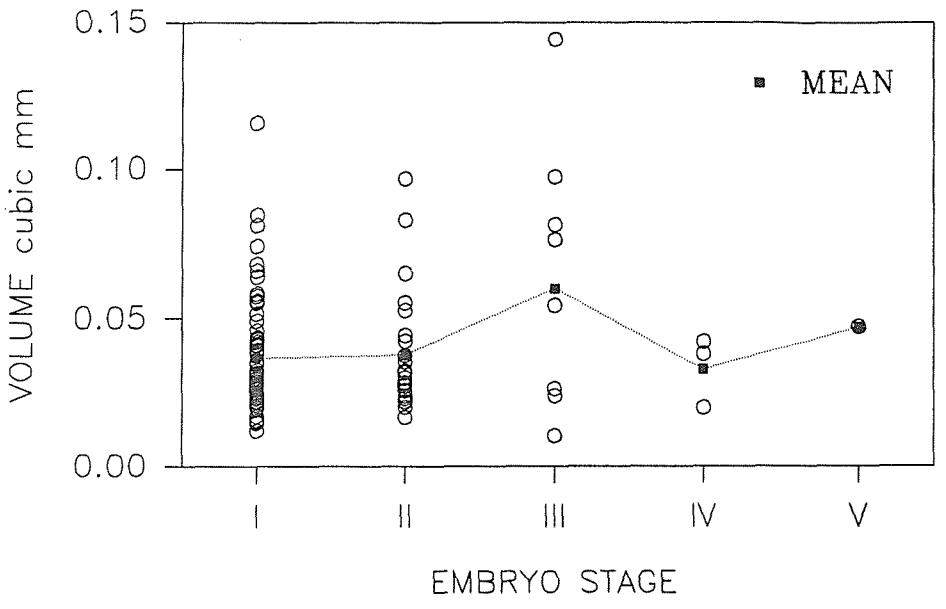
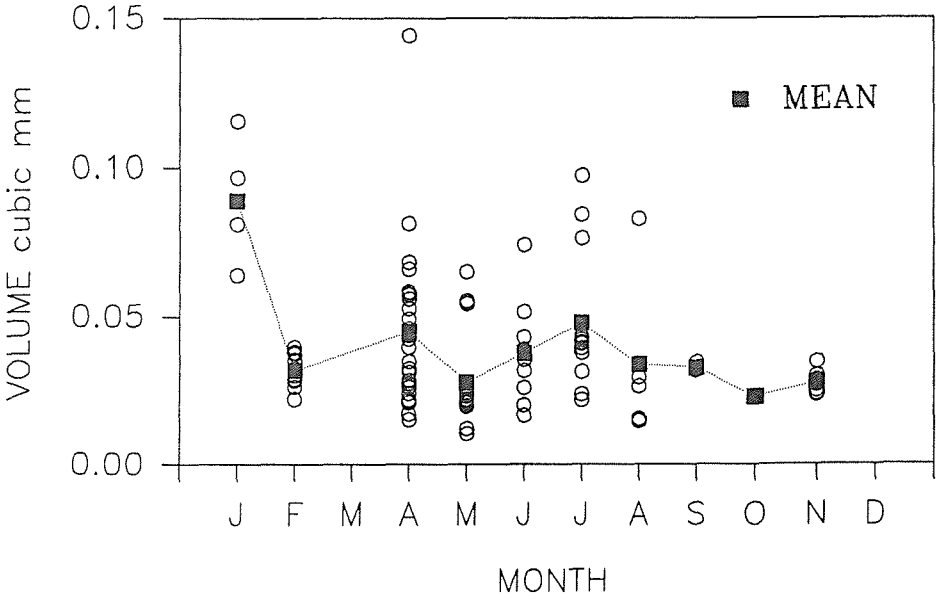


FIGURE 5.26 **VARIATION IN VOLUME WITH MONTH FOR *T. biloba* EMBRYOS**



test suggests there is a significant difference between months ($H=32.451$, $P<0.001$). This result is probably due to the small number of eggs recovered in January which were large in comparison those of other months. A Dunns all pairwise multiple comparison identifies January and October as the most significantly different months ($Q=2.227$, $P<0.05$). When the volumes of the embryos in a female with two embryos were compared with each other (Figure 5.27), one was always bigger than the other. This is not surprising as no two embryos are likely to be exactly the same size, and so there will always be a larger one. However, this plot also shows that one embryo is significantly bigger than the other, by well over 10% in most cases. The small dots on the figure representing a 10% increase in volume of the smaller embryo of the two (nb. the data are treated so only comparisons are made between embryos of similar developmental stages, and from similar months). In a comparison between embryo volumes of single compared to double brood females, no pattern emerges (Figure 5.28). When comparing single brood embryos to both the 'large' and 'small' double brood embryos, the points on this graph fall randomly either side of the line indicating equal volumes. There is also no significant difference between the volumes of different developmental stages for double compared to single brood embryos (Figure 5.29).

The remainder of species are dealt with in order of numerical abundance. As these species were not studied in the same detail as *Ampelisca* sp nov and *T. biloba*, size at maturity has been estimated using the mean length of mature females examined in each species. This value was used in the predictive regressions of Sainte-Marie (1991) to estimate brood size and embryo diameter, as above. Similar regressions were also used to predict what the values would be for a hypothetical shallow water specimen of similar length :

log brood size=1.348 log body length + 0.050 ($r^2=0.62$, $F=464.89$, $P<0.001$)

log embryo dia.=0.449 log body length - 0.717 ($r^2=0.57$, $F=184.47$, $P<0.001$)

These regressions are referred to as deep or shallow predictive regressions respectively for the remainder of the chapter.

FIGURE 5.27 COMPARISON BETWEEN EMBRYO VOLUMES IN 'DOUBLE' BROOD FEMALES

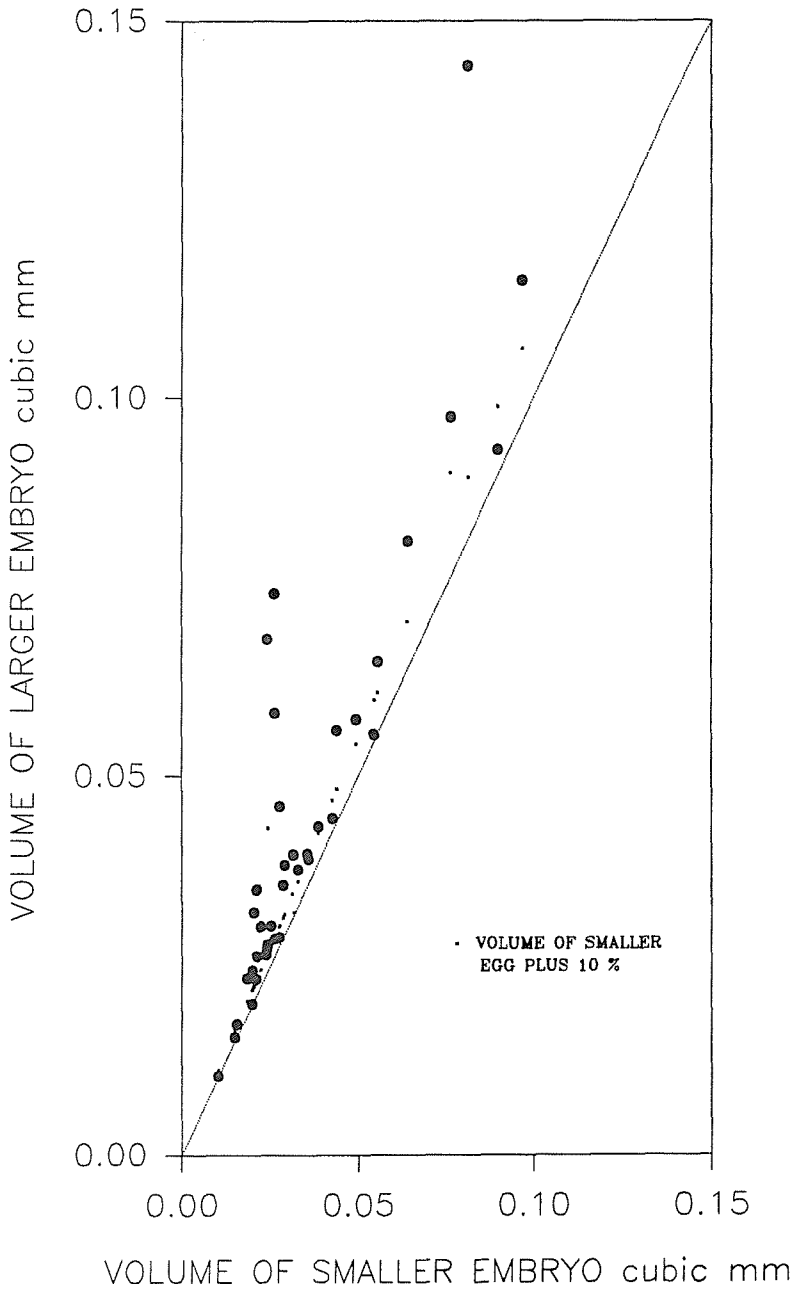


FIGURE 5.28 **COMPARISON OF EMBRYO VOLUMES BETWEEN 'DOUBLE' AND 'SINGLE' BROODS**

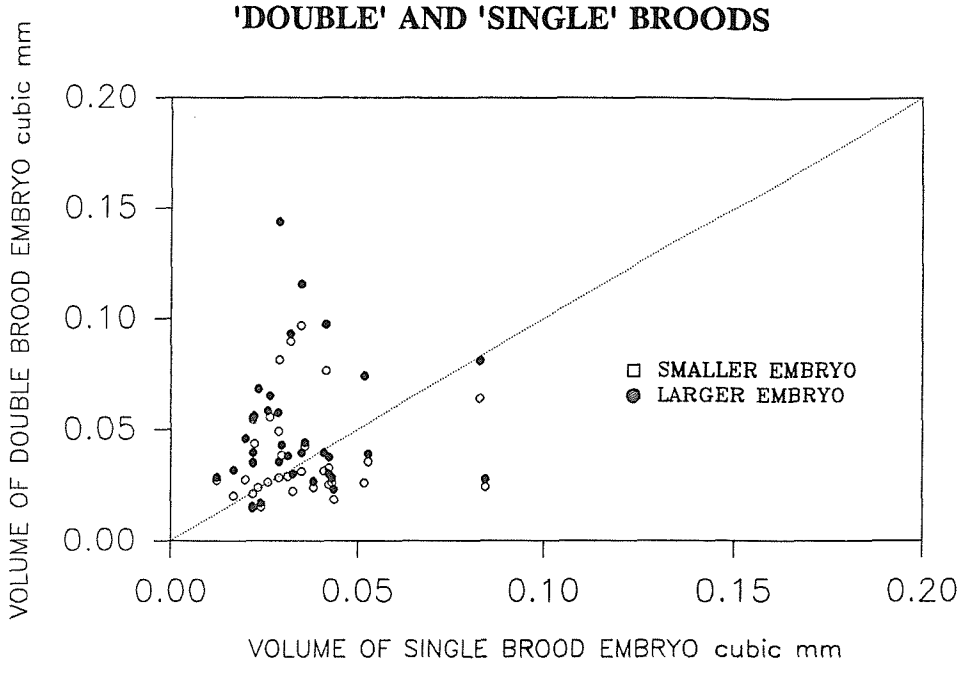
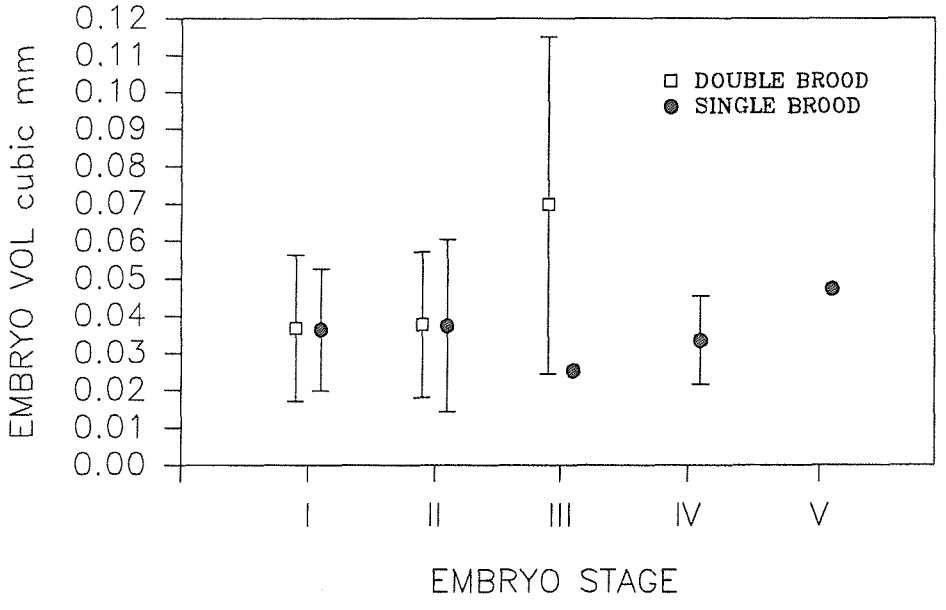


FIGURE 5.29 **COMPARISON OF VOLUME OF EMBRYO'S IN DIFFERENT DEVELOPMENTAL STAGES FOR 'DOUBLE' v 'SINGLE' BROOD EMBRYOS**



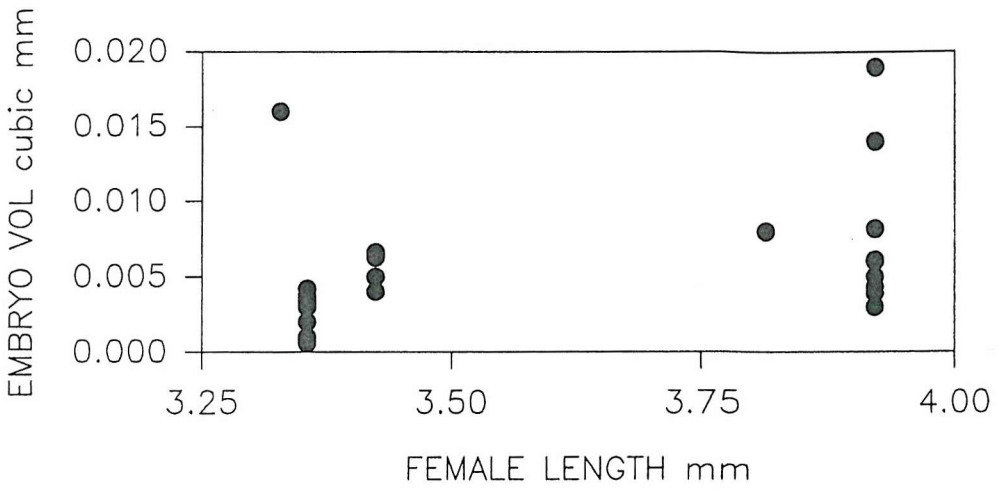
Dulichiopsis abyssi (Species 23)

This species has a mature female mean length of 3.62mm, six brooding females were caught, with brood sizes ranging from 1-11. As mentioned in the introduction to this section *D. abyssi* whilst being the most abundant species (1192 inds.) seems to have suffered the most damage. As such it could be expected that substantial egg loss from the marsupium has occurred, reflecting the low numbers of brooding females recovered and large variation in brood sizes. Brooding and mature females were recovered in May, June and November, the majority of embryos in May were at stage III, June - all stage IV and November - all stage I. Despite indications of mature embryos dominating in the summer, such low sample numbers preclude any definite conclusions as to reproductive mode. Embryo volume seems to increase with female size and developmental stage (Figure 5.30). Mean diameter for stage I embryos is 0.188mm, which gives a predicted development period of 47 days. Mean volume for stage I embryos is 0.0037mm^3, stage III 0.0065mm^3 and stage IV 0.014mm^3. Using mature female length of 3.62mm, 'deep' predictive regressions suggest a brood size of 5 and embryo diameter 0.29mm for this species, both differ markedly from observed values. 'Shallow' predictive regressions estimate a brood size of 6.3 and embryo diameter of 0.34mm.

Pseudharpinia brevirostris (Species 18)

Mean mature female length is 4.04mm, and mature females with oocytes, and brooding females were caught in the spring and summer samples (Figure 5.31). Again small samples numbers prevent any assumptions that this may represent synchronous reproduction. There is no clear relationship between female length and embryo volume, but embryo volume clearly increases with developmental stage (Figure 5.31). Stage I embryos have a mean volume of 0.016mm^3, and diameter of 0.33mm. Stage IV embryos have a mean volume of 0.031mm^3. Diameter of stage I embryos gives a predicted development time of 64 days, whilst predictive regressions using female length suggest a brood size of 5.5, and embryo diameter of 0.32mm. Shallow water predictive regressions suggest a larger brood size of 7.4, and embryo diameter of

FIGURE 5.30 REPRODUCTIVE DATA FOR *Dulichiopsis abyssi*



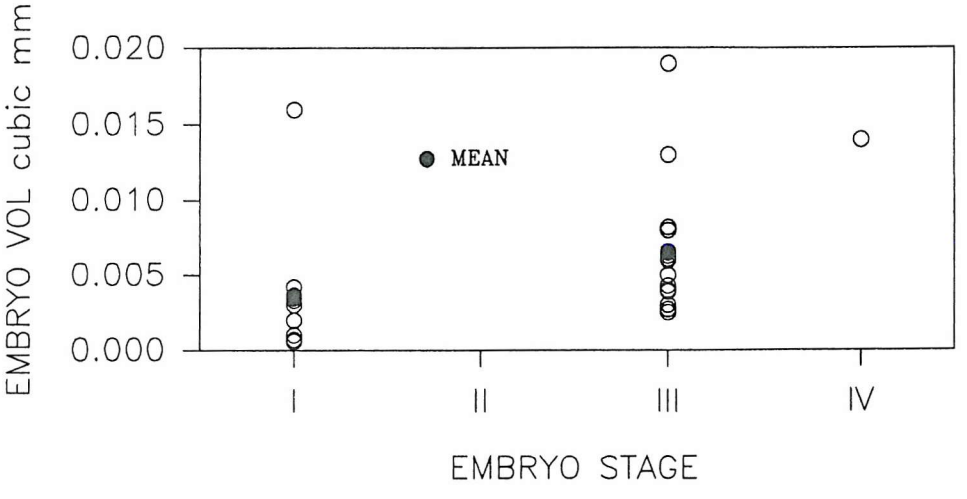
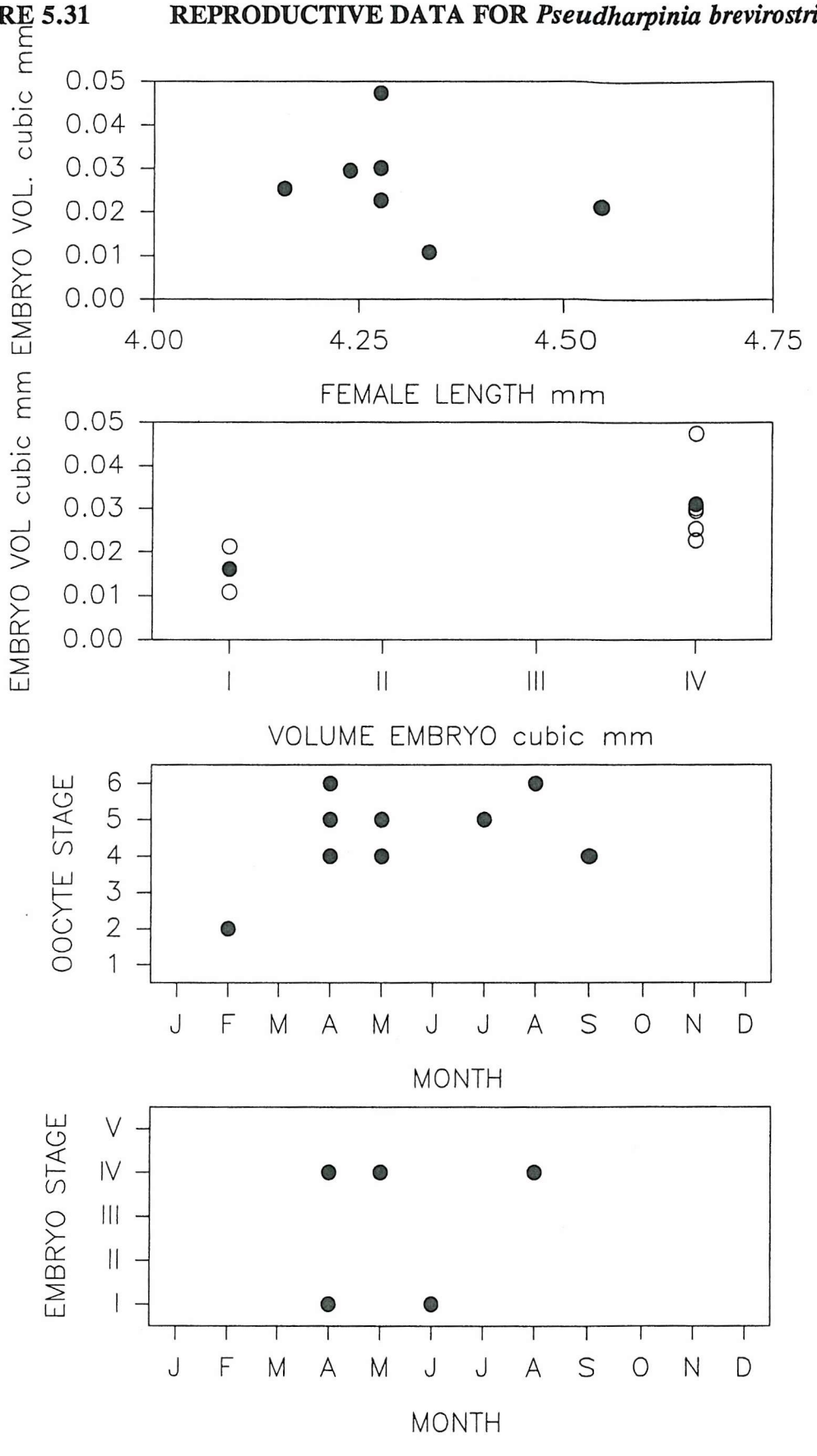


FIGURE 5.31 REPRODUCTIVE DATA FOR *Pseudharpinia brevirostris*



0.36mm. The observed brood size for this species is between 2 and 5, and so closely matches the deep water prediction, as does the observed stage I embryo diameter. However, counts of mature oocytes indicate the
fecundity of this species may be higher, with between 12 and 16 stage 5/6 oocytes present in seven females (Plate 5.4)

Autonoe sp nov (Species 21)

No brooding females were captured of this corophid species, but several mature females with fully developed oostegites and developing oocytes were recovered with a mean length of 6.37mm. Mature females were found in February, April, May, July, August and November, but those containing oocytes were only found in May, July and August. Predictive regressions for deep-sea and Corophioidea superfamily gammarids give brood size estimates between 12.8 and 14.5, an embryo diameter of 0.44mm and development time of 76 days. Whilst shallow water regressions suggest a brood size of 13.6 and embryo diameter of 0.44mm.

Leptophoxoides molaris (Species 17)

Five mature females were collected, with a mean length of 4.54mm. Four contained maturing oocytes in May, August and October and the brooding female was present in a June sample. The brooding female carried a single stage II embryo with mean diameter of 0.4mm and volume of 0.0316mm^3. Predictive regressions suggest a brood size of 6 embryos with a mean diameter of 0.34mm, and development period of 72 days. Shallow water predictive regressions provide estimates of 8.6 for brood size and 0.37mm.

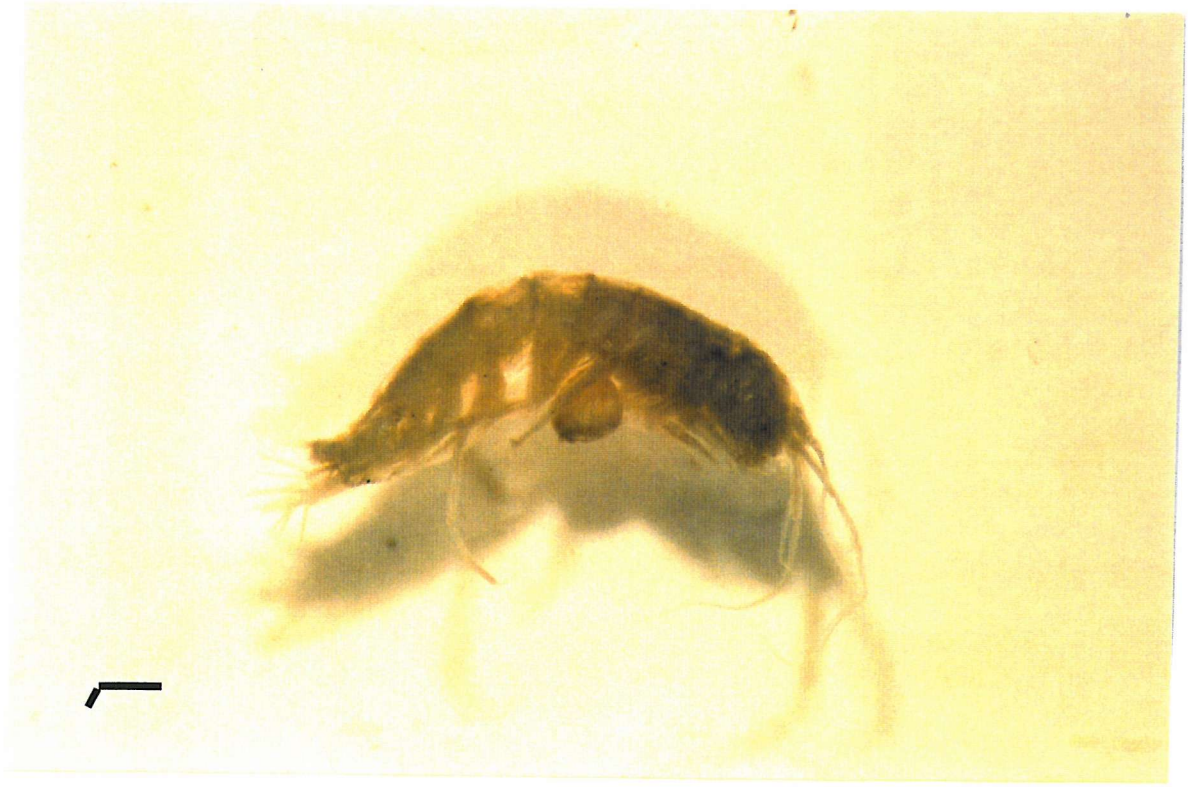
Corophoidae gen (Species 22)

No females brooding or containing developing oocytes were recovered. Only six large/mature females were found, and these were significantly larger than the majority of specimens recovered. Perhaps indicating adults of this species adopt a more epibenthic mode of life than earlier life stages and are not captured by the sled.

PLATE 5.4 ***Psuedharpinia breviostris*** **WITH STAGE 6 OOCYTES DISSECTED OUT**

Scale Bar 1mm

PLATE 5.5 SPECIES 30 WITH COPEPOD PARASITE Scale Bar 1mm



Rhacotropis gislii (Species 10)

Five mature females were recovered, one containing oocytes in development stage 5/6 (July) and one with a brood of 12 embryos (June). These females were 8.1 and 12.4mm in length respectively. Mean embryo volume was 0.074 (range 0.04-0.1), and mean diameter 0.63mm. The embryos ranged in development stage from I to III. Using mean length of 10.2mm, predictive regressions estimate brood size at 13 and embryo diameter 0.61mm, both similar to observed values. In contrast shallow water regressions suggest a much larger brood size of 25.7, but smaller embryo diameter of 0.54mm. A development period of 100 days was estimated from embryo diameters. Thurston (1980), reports female lengths of 8-14mm for *R. gislii* in samples from the East Iceland Basin. He recovered two ovigerous females of 12 and 13mm in length, these lengths are comparable to those found in this study.

Lactacunga sp nov (Species 37)

Two mature females were recovered, one, 5.22mm in length containing 18 stage 5 oocytes, the other 3.35mm long brooding female with one stage I embryo. This embryo has a mean diameter of 0.35mm and volume of $0.02mm^3$. Using these data and mean female length of 4.29mm, give brood size estimates of 6, development period of embryos of 66 days and a predicted embryo mean diameter of 0.33mm. The latter is again a good approximation of the observed figure for mean embryo diameter. Estimates using shallow water predictive regressions suggest a larger brood size, 8 and embryo diameter 0.37mm, whilst estimates from oocyte counts for this species suggest a brood size of 18.

Syrrhoites sp nov (Species 31)

Two females were caught in August with oocytes in development stage 4. Their mean length of 3.91mm was used to estimate brood size at 5.3, embryo diameter of 0.31mm for deep; and 7 and 0.35mm respectively for shallow water regressions. Using the deep water estimate of embryo diameter, a development period of 61 days is suggested for this species. This species had very well developed pleopod basis, indicating they could

be strong swimmers. This may explain why so few adults, and no brooding females were caught.

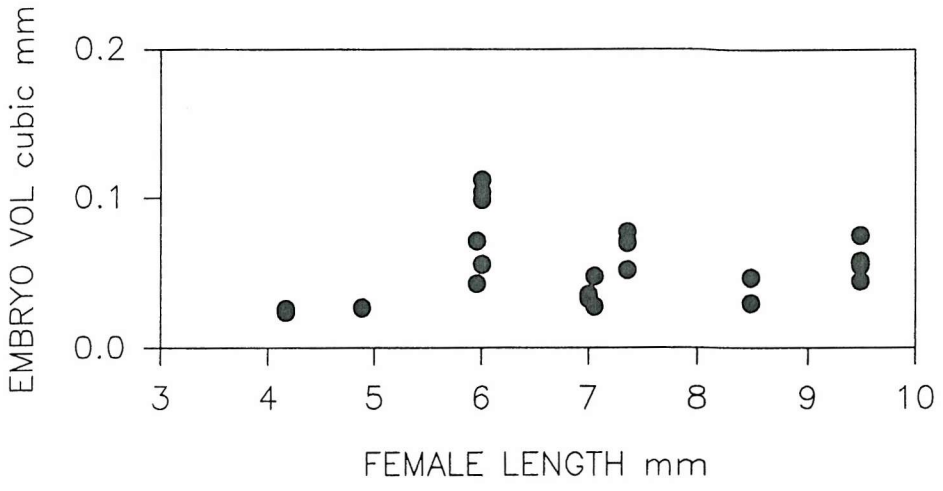
Tryphosella sp (Species 49)

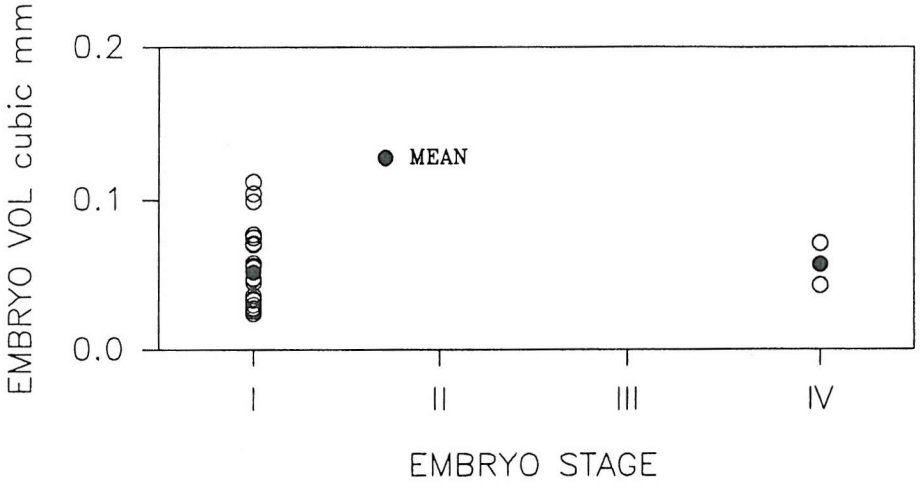
Nine brooding females of this Lysianassid species were caught, with a mean length of 6.71mm. The observed brood size varies between 1 and 6 embryos, with a mean stage I diameter of 0.47mm. There is no clear relationship between female length and embryo volume, but embryo volume does increase with developmental stage (Figure 5.32). Mean volume of stage I embryos is 0.052mm^3, which gives an estimate of 81 days development time. Predictive regressions for deep-sea gammarids estimate this species will have a brood size of 8.8, and mean embryo diameter of 0.88mm. Whilst regressions for the Lysianassoidea superfamily predict a brood size of 12 embryos, and shallow regressions a brood of 14.6 embryos with a mean diameter of 0.45mm. There is no clear pattern in distribution of embryo stages through the year, suggesting continuous reproduction (Figure 5.32)

Cleonardopsis carinata (Species 11)

Again nine brooding females were recovered, but six of these contained what could be termed 'hatchlings' (Plate 5.6). Very late stage V embryos, whose shape precluded volume measurements. Instead mean lengths were determined for each females brood, at 1.22, 1.27, 1.43, 1.49, 1.84 and 1.55mm. There is considerable variation between the means, and do not seem related to female length. The mean length for mature females of *C. carinata* is 9.12mm, with an observed brood size between 19 and 21. Mean diameter was 0.422mm, for a stage I embryo, mean volume being 0.034mm^3, and a predicted development period of 75 days. Embryo volume increases with development stage (Figure 5.33), and appears to increase with female length, although this relationship is not as clear. The majority of developing embryos were recovered in April and June (Figure 5.33). Predictive regressions underestimated brood size at 12 (observed 19-21), and overestimated embryo diameter at 0.6mm. Shallow water regressions also over estimated embryo diameter (0.52mm), but the brood size

FIGURE 5.32 REPRODUCTIVE DATA FOR *Tryphosella* sp (Sp. 49)





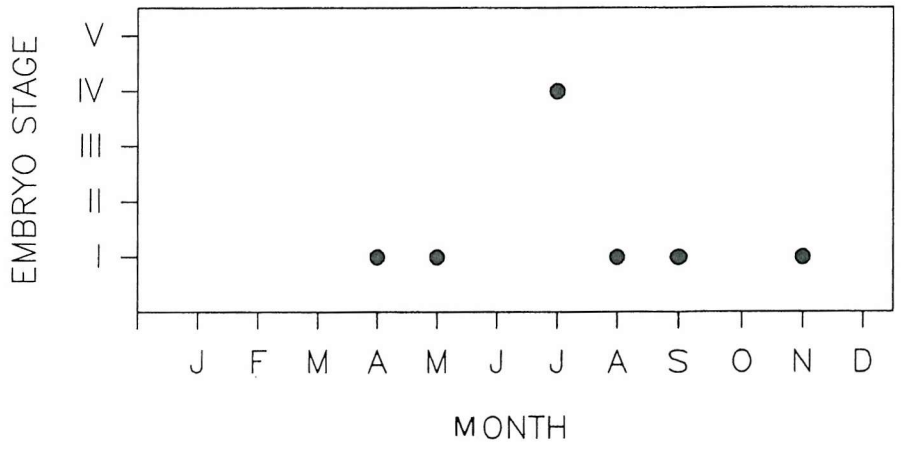
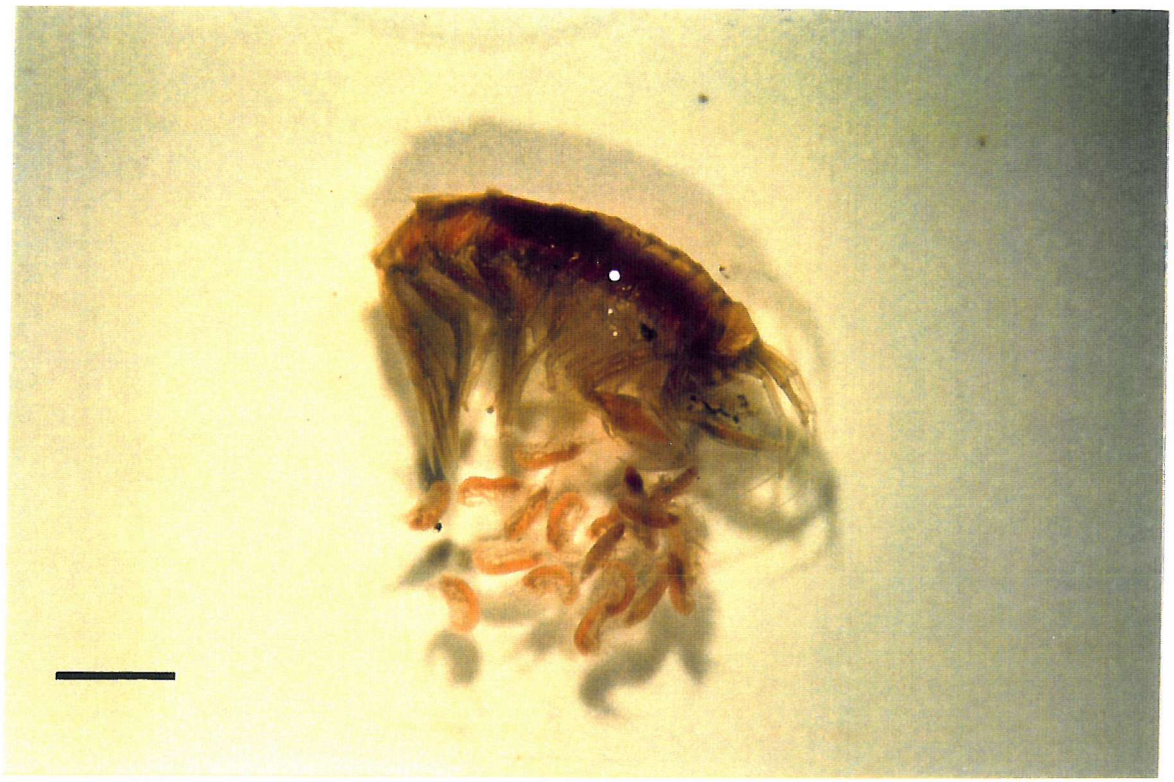
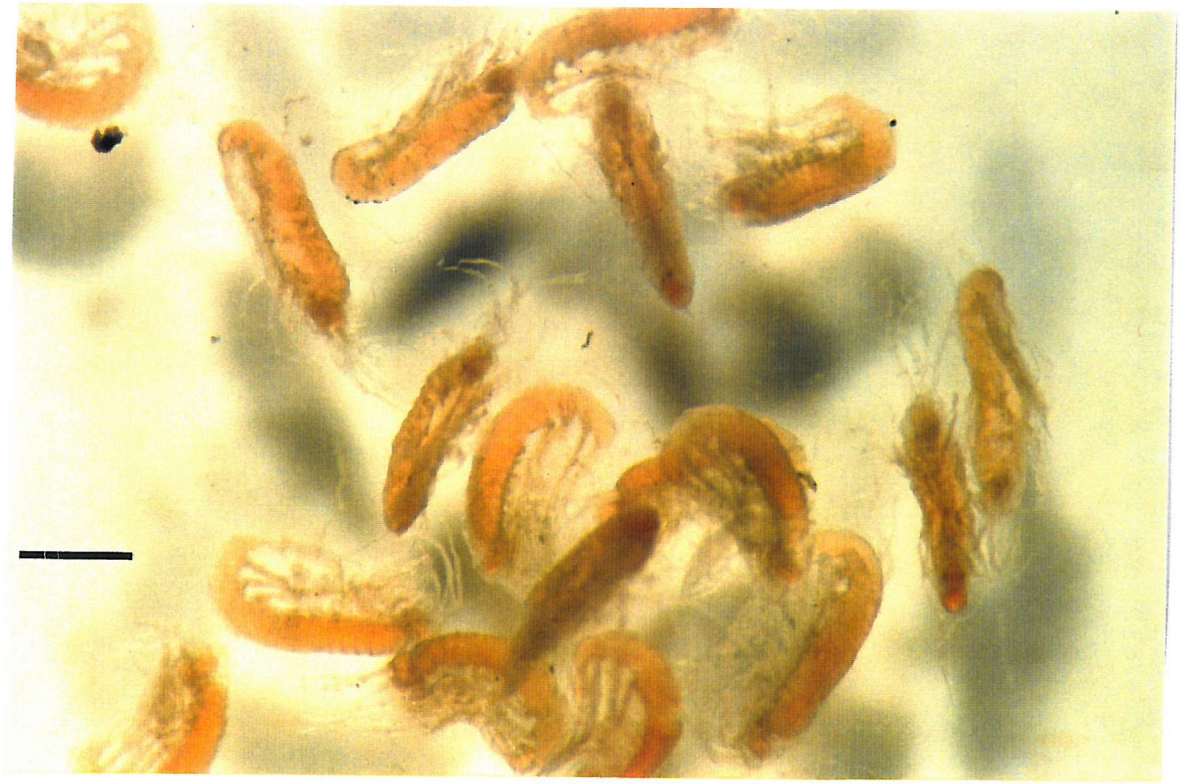


PLATE 5.6 ***Cleonardopsis carinata*** **WITH 'HATCHLINGS'**

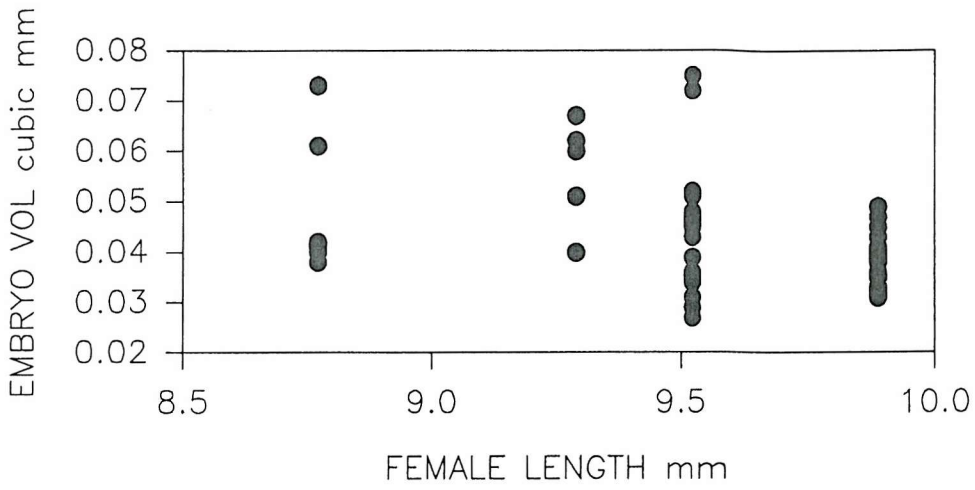


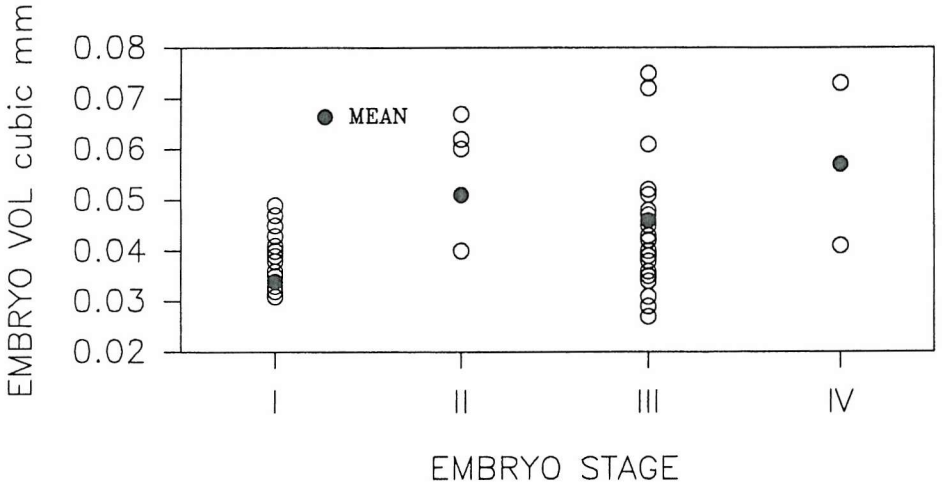
Scale Bar 1mm

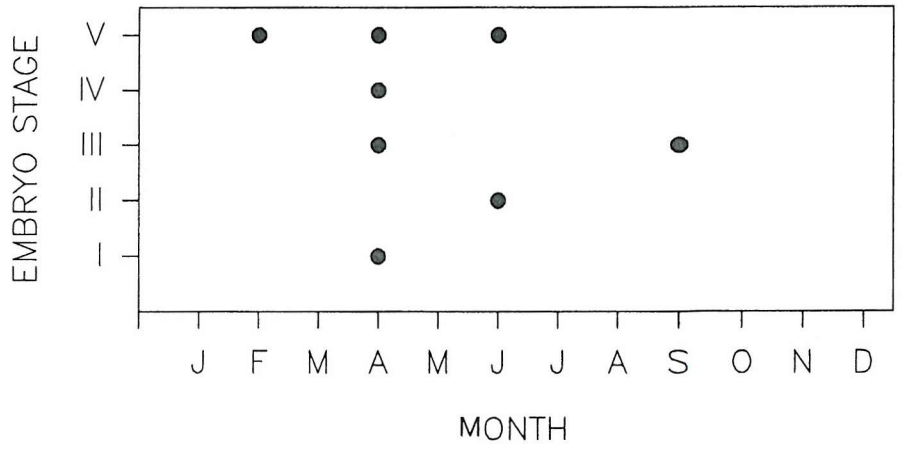


Scale Bar 1mm

FIGURE 5.33 REPRODUCTIVE DATA FOR *Cleonardopsis carinata*







estimate of 22 was similar to the observed value.

Amphilocus sp (Species 34)

Two brooding females and two females with developing oocytes were recovered. Mean mature female length was 3.57mm, observed brood size was between 1 and 2 embryos. The stage I embryo had a mean diameter of 0.28mm and volume of 0.01mm^3, the two stage II embryos had a mean volume of 0.015mm^3. All four mature females were recovered in June. Deep predictive regressions gave brood estimates of 5 embryos, with a diameter of 0.29mm and development time of 58 days. Whilst shallow regressions predicted a brood size of 6.2 and embryo diameter of 0.34mm.

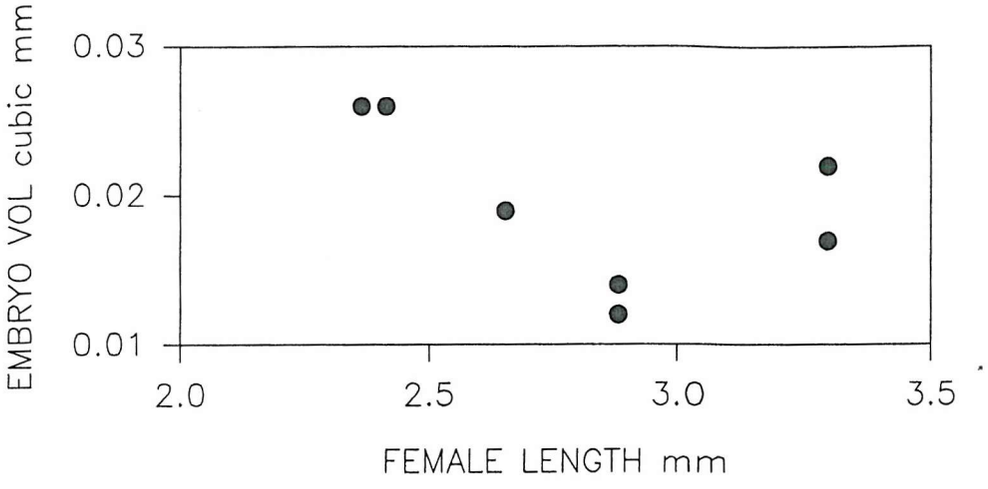
Harpinia plumosa (Species 19)

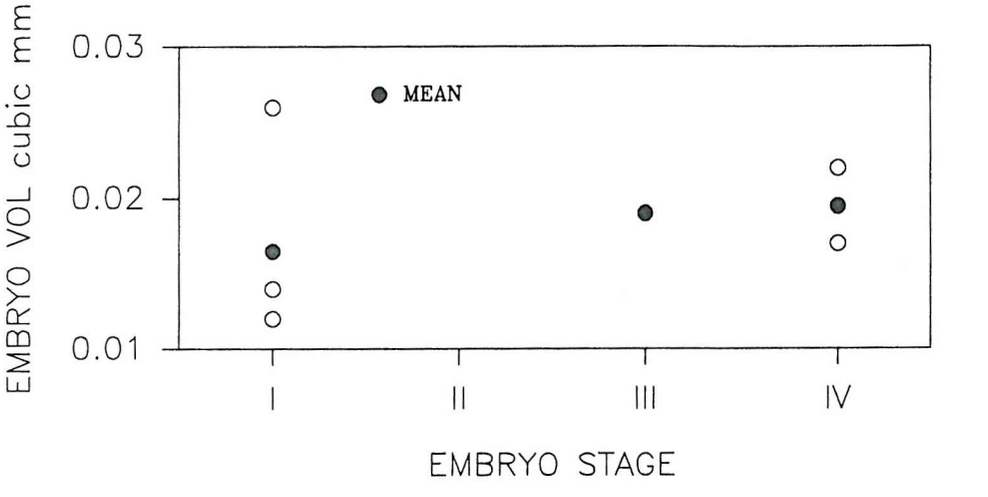
Ten mature females were recovered with a mean length of 4.45mm. Six of these females contained stage 6 developing oocytes, in January, June, July and September. The remaining four females were brooding, between 1 and 3 embryos in Jan, May and April. The mean diameter of stage I embryos was 0.404mm, with a mean volume of 0.032mm^3, and predicted development period of 73 days. The stage III embryos had a mean volume of 0.028mm^3. Predictive regressions give an estimated brood size of 6 embryos with a mean diameter of 0.34mm for deep water, and 8.4 and 0.38mm respectively for shallow water amphipods.

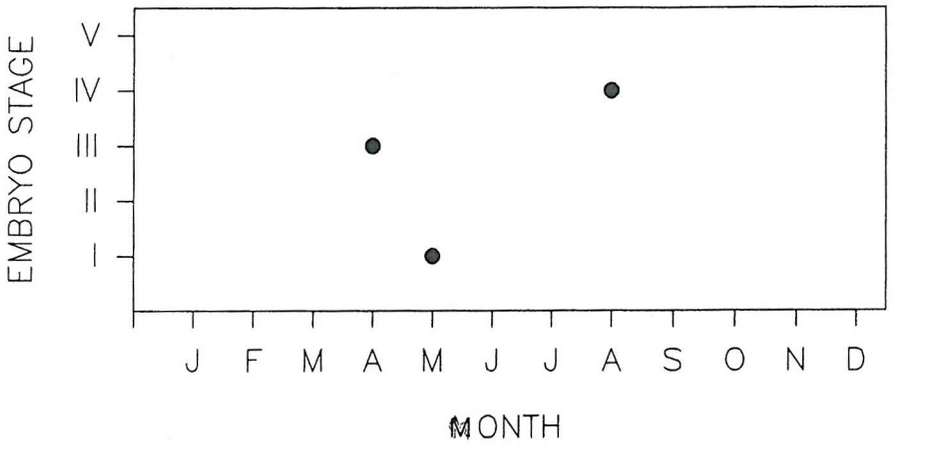
Pardaliscidae gen (Species 29)

Four brooding females of this species were recovered, with a mean length of 2.72mm. Brood size varied from 1-3 embryos, with a mean diameter of 0.34mm and volume of 0.0165mm^3 for stage I embryos. There was no clear relationship between female length and embryo volume, but mean embryo volume shows a clear increase with development stage (Figure 5.34). There were insufficient numbers to determine any periodicity in reproduction, but two females were brooding late stage embryos and contained developing oocytes. This would seem to indicate this species is iteroparous. Predictive regressions suggest a brood size of 3.8 for deep water and 4.3 for shallow

FIGURE 5.34 REPRODUCTIVE DATA FOR SPECIES 29







water amphipods, and embryo diameters of 0.24mm and 0.3mm respectively. The observed mean embryo diameter of 0.34mm for this species suggests a developmental period of 65 days.

Bonnierella sp (Species 24)

Two mature females were recovered, one brooding a single stage II embryo. The mean embryo diameter was 0.23mm and its volume 0.006mm^3. The second female was carrying a parasite in its brood pouch, possibly a copepod. The mean female length of 2.9mm when used in predictive regressions estimates a brood size of 4, mean embryo diameter of 0.25mm and development period of 52 days. Estimates from shallow water regressions suggest a brood size of 4.7 and embryo diameter of 0.31mm.

Oedicerotidae gen (Species 36)

Two mature and brooding females were recovered, the larger carrying three stage V embryos, the other a single stage III embryo. The mean length of 7.4mm provided estimates of 9.7 for brood size and 0.48mm for stage I embryo diameters. The observed mean embryo diameter of stage III eggs in this species (0.38mm) is smaller than this estimate. Using 0.38mm as mean embryo diameter provides a predicted development time of 70 days.

Parparno sp (Species 43)

One mature female 3.32mm in length, carrying six stage 6 oocytes, was recovered. Using deep water predictive regressions estimates of 4.5 for brood size, 0.227mm for embryo diameter and 50 days development time were obtained. Larger estimates of 5.7 for brood size and 0.33mm for embryo diameter were obtained from shallow water regressions.

Rhacotropis proxima (Species 13)

One brooding female, length 16.768mm, carrying 13 stage I embryos was recovered. The mean embryo diameter was 0.65mm, and mean volume 0.13mm^3. Predictive regressions for this species estimate brood size at 20, with a mean diameter of 0.85mm, and development period of 102 days. Whilst values estimated using shallow water regressions are 50.2 for brood size and 0.68mm for embryo diameter. Thurston (1980) reports female lengths for *R. proxima* from the East Iceland Basin of 8 to 19mm. He recovered one ovigerous female of 17mm length, similar in size to that recovered in this study.

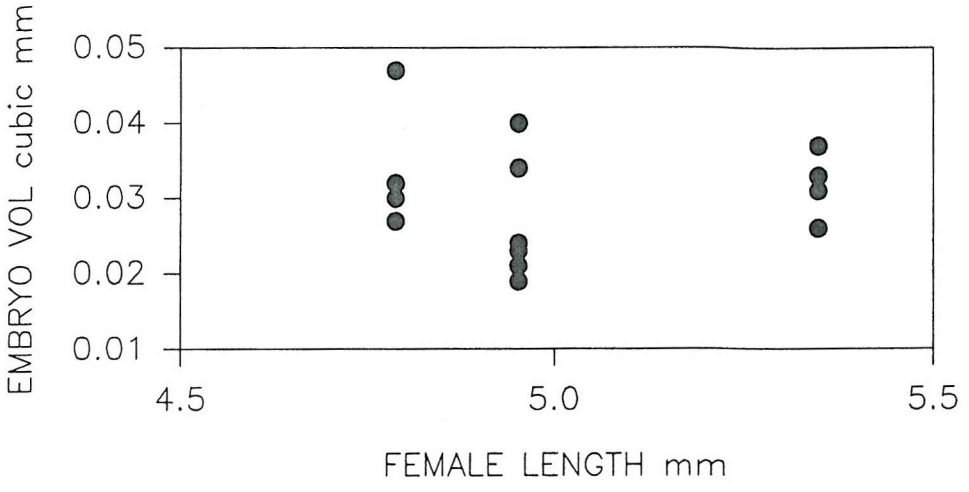
Tryphosella sp (Species 51)

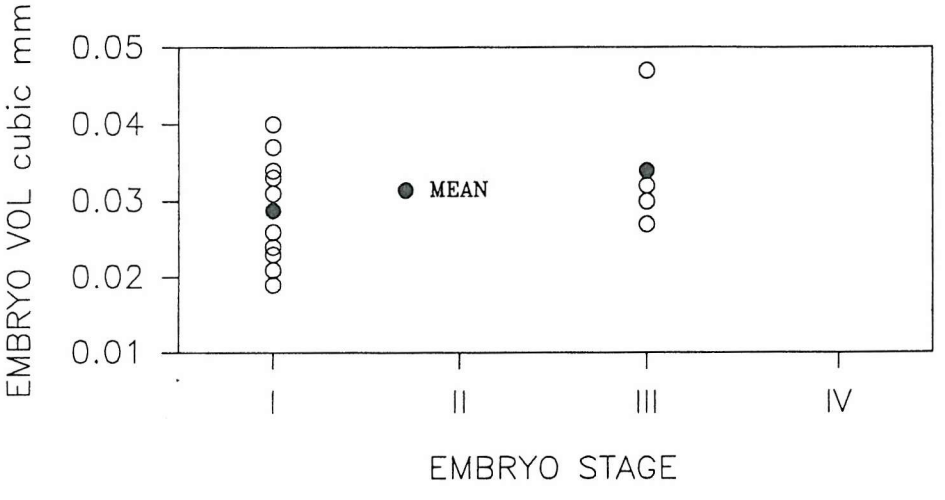
Three mature brooding females were recovered with a mean length of 5.03mm. Brood size varied from 4 to 6, with a mean stage I diameter of 0.41 and mean embryo volume of 0.0288mm^3. Figure 5.35, shows there is no apparent relationship between embryo volume and female length. Mean embryo volume does seem to increase with development stage from 0.0288 for stage I to 0.034 for stage III (Figure 5.35). Estimates from predictive regressions suggest a brood size of 6.7, a mean embryo diameter of 0.41mm and a development period of 73 days. A similar embryo diameter of 0.4mm, but a larger brood size estimate of 10 are obtained using shallow water estimates.

Pardalisca sp (Species 30)

No detailed study, but the presence of an copepod parasite in the brood pouch was noted (Plate 5.5)

FIGURE 5.35 REPRODUCTIVE DATA FOR SPECIES 51





5.4.4 Discussion

There is very little in the literature dealing with life-history traits of deep-sea gammaridean amphipods. In his comprehensive review of the literature on the reproductive bionomics of aquatic gammaridean amphipods, Sainte-Marie (1991) remarked that 96.4% of the reviewed populations were from waters less than 200m deep. To date the majority of work on deep-sea gammarideans has concentrated on the lysianassoids, which have been the focus of research because of their peculiar ecology and presumed importance in the deep-sea (Sainte-Marie *et al* 1990). Since most of the data concern the extremely large scavenging species (for example *Alicella gigantea, Eurythenes gryllus* and *Hirondella gigas*), a size bias has resulted. Such species are not representative of deep-sea gammarideans in general, Barnard (1962) and Steele (1983), compared body size of gammarids across depth and latitude gradients. Their results suggested deep-sea assemblages differ from shallow, cold water assemblages only in the presence of a few extremely large members. Derivation of realistic estimates of reproductive potential for deep-sea lysiannassids suffers from lack of brood size, number and life expectancy data. Capture of brooding deep-sea females is rare, and even for the cosmopolitan and ubiquitous *Eurythenes gryllus*, brooding females were only recently caught for the first time in the N Atlantic (Thurston and Bett 1994). Brood sizes for the majority of deep-sea gammarids are thus based on oocyte counts. As previously mentioned this is an unsatisfactory method, oocyte resorption often preceding oviposition (Bregazzi 1972, Hessler *et al* 1978, Stockton 1982 and Ingram and Hessler 1987). Interestingly Sainte-Marie *et al* (1990) found that despite being on average 4.5 times larger than their shallow water counterparts, deep-sea gammarids had brood sizes which were not significantly greater. Using data for deep- and shallow water lysianassoids, Sainte-Marie *et al* (1990), compared regressions of brood size and embryo diameter on body length. The conclusions they reached are as follows i. the rate of increase of brood size relative to body length was greater in shallow than in deep living lysiannassids, ii. the rate of increase in embryo size was similar for both groups. A broader analysis of all shallow and deep-living gammarideans revealed the

rate of increase of embryo size relative to body length was greater in deep-living species. In other words deep-sea species had smaller relative size of broods than shallow water species, but embryo diameters were larger in comparison to body length in deep- than shallow-living species. This is dramatically highlighted by *Eurythenes gryllus*, brood size for a 120mm female was reported as 237 (Thurston and Bett 1994), a hypothetical lysianassid of this length living in shallow waters would, on the basis of Sainte-Marie *et al* 's (1990) regressions have a brood size of 3677 ! Examination of the reproductive data for the amphipod species in this study lends support to the conclusions of Sainte-Marie. *Ampelisca* sp nov has an estimated brood size of between 8 and 10 from oocyte counts, and 6 to 12 from deep-sea regressions. Both estimates are smaller than the mean for the Ampeliscoidea superfamily of 27.8± 14.8. Embryo diameter for *Ampelisca* sp nov however was not significantly bigger than that for a shallow water ampeliscid of similar length, 0.435mm compared to 0.42mm. As mentioned in the results section the lysianassid *T. biloba* has a smaller observed brood size (2), than estimates for deep-sea gammarids (5), deep-sea lysiannassids (4.3), the lysianassid superfamily (6.4) and a shallow water amphipod of similar length (6.5). *T. biloba* embryo diameters also match the predictions of Sainte-Marie *et al* (1990), by being much larger (0.41mm) than those estimated for similar sized deep-living (0.29mm) and shallow living (0.35mm) amphipods. Even considering the data from the other twenty species examined, only limited information is available on brood size for Rockall Trough amphipods. Despite this some general conclusions can be drawn when comparing observed or predicted brood sizes from the deep-sea gammarids in this study, to predictions for a shallow water amphipods of similar size. The majority of deep-sea gammarids in this study had brood sizes which were smaller than the shallow water predictions (*T. biloba, Ampelisca* sp nov, *Pseudharpinia brevirostris, Rhacotropis gislii, R. proxima,* species 29, 49 and 51). In contrast only two species had larger broods (*Dulichiopsis abyssi* and species 37). When comparing embryo diameters of the gammarids in this study to those predicted for shallow water amphipods of similar size, there are roughly equal numbers of species with larger (*T. biloba, D. abyssi, Leptophoxoides molaris, R. gislii,* species 49 and 29), and similar

sized (*Ampelisca* sp nov, *P. brevirostris, Cleonardopsis carinata, R. proxima,* species 19 and 37) embryos. Only four species had smaller sized embryos (species 24, 34, 36 and 49). Support for Sainte-Marie *et al*'s (1990) theory that embryo size is greater in relation to body size for deep-living species comes from the fact that thirteen species had larger or similar sized embryos compared to hypothetical shallow water predictions. This evidence is however, by no means conclusive.

Previous workers could only speculate on the reproductive potential of deep-living amphipods, because of a lack of information on number of broods and/or lifespan (Sainte-Marie 1991). However using an inferred lifespan of 156 months, and 5 potential brooding instars for the lysianassid *Eurythenes gryllus* from data provided by Ingram and Hessler (1987), and combining it with an observed brood size for this species of 237 (Thurston and Bett 1994), a reproductive potential can be calculated of 91.2 embryos per female per year. This value is similar to the mean for shallow living gammarideans of 91.5 and greater than the mean for shallow living lysianassids of 43.3 (Sainte-Marie 1991). Thus it seems in the case of *Eurythenes gryllus*, reproductive potential is not significantly different to shallow water amphipods. Unfortunately lack of information on lifespan precludes similar calculations for the reproductive potential of amphipods in this study. However, as discussed above, the amphipods in this study have, in general, smaller broods than shallow water amphipods. Thus, in comparison to shallow species, they will have a smaller reproductive effort, unless they compensated with a much larger number of broods. Why should deep-sea amphipods exhibit such characteristics ? Decreased fecundity and reproductive effort may result from food limitation in the deep-sea. Using the habitat templets of Greenslade (1983), Sainte-Marie (1991) suggests that deep-sea amphipods are 'A' selected. The deep-sea being a poorly productive (adverse), but rarely disturbed (predictable) habitat. Animals living in such an environment will show A-selected attributes of great longevity, late maturity and low fecundity (Sainte-Marie 1991). This reduction in brood size seems to be compensated in part by larger embryos of the amphipods in this study. Large eggs have longer development times, because of the relationship between size and metabolic rate (Steele and Steele 1991). The low temperatures in the deep-sea may also increase

development time of eggs, which thus require more investment resulting in a larger egg, as shown for the isopod genus *Ceratoserolis* in the Antarctic (Clarke and Gore 1992). Egg size is an important component of adaptations to environmental conditions, influencing how many broods and generations are possible each year, as well as brood size (Steele and Steele 1991). Egg size, and timing of the onset and termination of ovarian diapause, determine when the young will hatch and be released. The timing of release is critical if there is a short season of food supply suitable for the young. The deep-sea could be equated with high latitudes in having a short season (ie. of phytodetrital input), and iteroparous species with large eggs will be restricted to being annual and univoltine (Steele and Steele 1991). *Ampelisca* sp nov from this study is just such a species. Production of large young would ensure better survival rates in an environment with a scarcity of food, such as the deep-sea. As size of young is correlated with size of egg, in the deep-sea production of large eggs will be an adaptive response (Steele and Steele 1991). Production of large embryos can also cause severe constriction of the gut, as reported for scavenging lysianassids (Sainte-Marie *et al* 1990, and references therein). *T. biloba* has large embryos compared to its body volume, and this seems to have affected its capacity to feed (see Chapter 6 for a more detailed discussion). Cessation of foraging activity in mature females has been proposed as a mechanism to reduce mortality from predators in lysianassids (Bregazzi 1972b, Hessler *et al* 1978 and Thurston 1989). There is a need to distinguish whether this is a result of behavioural constraints or inability to feed because of physical constrictions on the gut (Sainte-Marie *et al* 1990).

The results of this study show an increase in brood size with female length for *T. biloba* (Figure 5.23). Embryo volume also increases with female size in *T. biloba*, *Dulichiopsis abyssi, Cleonardopsis carinata* and species 51 (Figures 5.24, 5.30, 5.33 and 5.35). Gammaridean brood size and embryo diameter are strongly correlated with body length (Sainte-Marie 1991, Powell 1992), as has long been known for other malacostracans (Jensen 1958, Steele and Steele 1975, Mauchline 1988). Nelson (1980) considers increases in brood size with body size to be general throughout the Amphipoda, and Steele and Steele (1991) report brood volume increases with length,

both within and between species. Several species in this study also show a clear relationship between embryo volume and development stage (*T. biloba, D. abyssi, Pseudharpinia breviostris, C. carinata,* species 29, 34, 49 and 51). Jones and Wigham (1993) report on the increase in egg dimensions with development in *Orchestia gammarellus*, noting that embryo volume more than doubled during incubation. Fish (1975) studied the growth of embryos in *Bathyporeia pilosa* and *B. pelagica*, and found in both species the greatest increase in dimensions occurred between stages II and III and stages IV and V. From the limited data available, species 29 and 49 show a 20% and 10% increase in volume during incubation. *P. brevirostris* and *C. carinata* show an approximate doubling in volume, whilst *D. abyssi* shows an almost fourfold increase in volume with development. *Ampelisca* sp nov embryo volumes are only available for stages I, II and III, but volume increases by 3.5x between stages I and III. In contrast to the results of Fish (1975), *D. abyssi* showed greatest increase in volume between development stage III and IV. However, for *Ampleisca* sp nov the data agrees with that of Fish, greatest increase in volume occurring between stages II and III. *Ampelisca* sp nov showed a clear relationship between female size and oostegite development. As females of this species mature, oostegites increase in length, they become more setose, and the setae themselves increase in length. Ingram and Hessler (1987) found oostegite length to be directly related to female length in *E. gryllus*. Similarly, Klages (1993) found oostegite width and length were correlated with female size in the amphipod *Eusirus perdentatus*. The number of setae on the oostegites in this species also increased with female length. Steele (1991) noted the variation in structure of oostegites forming the brood pouch of amphipods, such variation had previously been mentioned as a taxonomic character by Bousfield (1979). Steele distinguished two main types of oostegites, the first are broad with relatively short marginal setae. The broad oostegites essentially form the brood pouch, similar oostegites are found in other peracarids and are probably the primitive type (Steele 1991). The second type are narrow, with long marginal setae, the brood pouch is therefore an open structure formed primarily by the setae. Such oostegites seem to be unique to the Amphipoda. Steele believes oostegites have been modified following the

evolution of the major amphipod groups. This is a response to changes in egg size as part of changing reproductive strategies in amphipods. Amphipods with broad oostegites tend to have smaller eggs than those with narrow oostegites. Steele (1991) gives two reasons for this, if the brood pouch is formed of narrow oostegites and long setae small eggs will tend to fall out more readily than large ones. Secondly as females increase in size, the space between oostegites will increase and eggs will fall out. Therefore small eggs will require broad oostegites to retain them. An open brood pouch formed by setae is also thought to aid in the circulation of water round large eggs, so they have an adequate supply of oxygen for respiration. *Ampelisca* sp nov has oostegites of the narrow type with long setae (Figure 5.8). As female *Ampelisca* sp nov grow, the increase in space between oostegites is compensated for by increases in setal length and the number of setae on the side margins of the oostegites (Figures 5.7 and 5.9).

Mean development time for the amphipods in this study is 66.7 days (range 50-102), which was estimated using the empirical relationship of Klages (1993)(see results section). The development period for shallow water amphipods is much shorter in comparison (eg. 20 days for *B. pilosa* Fish 1975). For Antarctic amphipods however, much longer periods ranging from 4.5 to 12 months are reported (Klages 1993). The maximum estimated development time for an amphipod in this study was 3.5 months. The longer incubation period of deep-sea and Antarctic embryos could result from low temperatures affecting metabolic rates and low rates of diffusion of oxygen and carbon dioxide in large eggs, again affecting metabolic rates. Bishop (1994) reported a prolonged incubation time for the cumacean *Leucon profundus* of 14 months, which he related to the constant low temperatures encountered in the deep-sea.

Seasonal differences in number and size of eggs produced by a variety of amphipod species exploiting a wide range of habitats have been reported (Morino 1978, Sheader 1978, Van Dolah and Bird 1980, Sheader 1983, Kusano and Kusano 1988, Powell 1992, McCabe and Dunn 1994). This has been attributed to variations in reproductive strategy reflecting changes in food availability, and female and offspring mortality (Steele and Steele 1969, Sheader 1978, Kolding and Fenchel 1981, Skadsheim 1984)

and brood sex ratio (Adams 1989). To overcome the lack of monthly samples in this study, data were pooled for the same month from different years. As such any seasonal variations in this study are impossible to ascertain and may have affected brood size and embryo diameter estimates.

Previous workers have demonstrated seasonal patterns in reproductive activity (Bishop and Shalla 1994) and reproductive intensity (Harrison 1988b) in peracarid crustaceans from the Rockall Trough permanent station. Low numbers of specimens is a common problem in deep-sea research, and both these studies reflect such difficulties. Harrison (1988b) was forced to consider the isopod family Asellota as a single unit to obtain statistically convincing results. Bishop and Shalla (1994), despite having low numbers of ovigerous (n=74) and brooding (n=12) females of the cumacean *L. profundus*, clearly demonstrated discrete reproductive seasonality. The amphipods in this study were examined for seasonal variation in reproductive activity. The lysianassid *T. biloba* exhibits a clear seasonal pattern in reproductive activity. Females of this species contain a larger percentage of late stage oocytes between May and August, than other months of the year. There is a dramatic fall in the percentage of brooding females between June and October, with a corresponding increase in percentage of ovigerous females. Release of young during this period results in an influx of juvenile recruits into the population in the late summer. *Ampelisca* sp nov, in contrast, shows no seasonal pattern in breeding activity, ovigerous females present in the population throughout the year. However, there seems to be a seasonal variation in breeding intensity for this species. The percentage of ovigerous females with late stage oocytes being greater in spring and summer months. Again, as in *T. biloba*, *Ampelisca* sp nov juveniles comprise a much larger percentage of the population in May/June and August/September compared to other months of the year. This would seem to reflect increased recruitment following periods of increased reproductive activity. The low number of reproductively mature specimens recovered in the twenty other species examined in this study precluded any firm conclusions as to their reproductive activity. However, brooding and females with late stage oocytes were only caught in the summer months for *D. abyssi, P. breviostris, L. molaris, C. carinata* and species 34.

Whilst mature females were present throughout the year in *Autonoe* sp nov and species 19, and brooding females of species 49 were found throughout the year. The remaining species collected were either devoid of reproductively active females, or present in such low numbers as to make any generalisations impossible. There has been an increase in the study of benthic responses to the temporal input of organic matter to the deep-sea following the realization that deep-sea organisms show a higher frequency of seasonal reproduction than previously imagined (Eckelbarger 1994). Such deposits, either as episodic food falls or seasonal input of phytodetritus, may act as environmental cues to which benthic organisms show a reproductive response (Tyler 1988). The effects of the seasonal input of phytodetritus on the reproductive biology of benthic invertebrates in the Rockall Trough has been discussed previously in Chapter Two and the introduction to this chapter. As has the experimental evidence for the spring bloom of phytoplankton acting as a spawning cue for mussels, urchins and barnacles (Starr *et al* 1990, 1991). The life cycle of the lysianassid *Onisimus litoralis* has been shown to synchronize brood release with early spring blooms in the water column or under ice (Bregazzi 1972, Boudrias and Carey 1988). Sainte-Marie and Lamarche (1985) reported that the juveniles of *Anonyx sarsi*, which are mainly detritivorous, depend on peak seston input to/accumulation in the sediment for survival and rapid growth. The timing of oocyte production in *T. biloba*, and increase in reproductive intensity of *Ampelisca* sp nov, both coincide with the deposition of phytodetritus to the Rockall Trough. Reproductive success in benthic marine communities is influenced by a species' capacity to turn food into egg production (Eckelbarger 1994). Vitellogenesis in amphipods is likely to be an energetically demanding process. However, Cuzin-Roudy and Labat (1992) demonstrated that for krill, vitellogenesis could proceed even in food poor conditions. In contrast, previtellogenesis was not possible under such conditions, so previtellogenesis appears more immediately food dependent than vitellogenesis. Both *Ampelisca* sp nov and *T. biloba* feed on the phytodetrital input (details in Chapter Six), and it may provide the energy source for their reproductive activity. Embryos of *Ampelisca* sp nov show an almost fourfold increase in volume during development from oocyte stage 1 to III.

Such high reproductive energy demands would require the phytodetritus to be a labile and energy rich food source. Rice *et al* (1986) report that phytodetritus does contain short chain molecules and polyunsaturated fatty acids, and will be enriched with colonizing bacteria, flagellates and foraminifera (Lochte and Turley 1988, Gooday 1988 and Gooday and Turley 1990). Campos-Creasey *et al* (1994) present data that support their hypothesis that the seasonal deposition of phytodetritus provides energy for growth and reproduction in the echinoid *Echinus affinis* from the Rockall Trough. Using animals from the same time-series as those in this study, Bishop and Shalla (1994) showed that vitellogenesis was synchronized with the deposition of phytodetritus in the cumacean *L. profundus*. Harrison (1988b) attributed the breeding pattern of asellote isopods in the Rockall Trough to seasonal deposition of organic detritus in the summer in the Northeast Atlantic. An examination of the juvenile settlement of various Northeast Atlantic taxa appears to show a closer synchronization between taxa than does egg release (Harrison 1988b). The amphipods *Ampelisca* sp nov and *T. biloba* from this study both show a seasonal recruitment of juveniles that coincides with the peak availability of phytodetritus (Figures 5.17 and 5.22). The timing and release of young from the marsupium in *L. profundus* in spring and early summer coincides with the maximum availability of food supply from the flux of phytodetritus (Bishop and Shalla 1994). Similarly asellote isopods from the Permanent Station show a peak in the proportion of newly released mancae during the summer months. *Ampelisca* sp nov is a species which exhibits an 'intermediate' life-history pattern as described for the brittle star *Ophiomusium lymani* (Tyler *et al* 1991). *Ampelisca* sp nov does not show seasonal activity in reproduction, but a constant production of oocytes through the year. The linear growth ratios reported for *Ampelisca* sp nov in Chapter Four indicated the peaks in length-frequency distributions were attributable to instars rather than year classes. This supports the view of a quasi-continuous reproductive pattern for this species. However, superimposed on this pattern is a peak in reproductive activity coincident with the flux of phytodetritus. Such continuous but seasonally variable reproduction is not confined to the deep-sea, it is also known for animals living in shallow tropical seas (Giese and Pearse 1974,

Sastry 1985), and seasonal temperate regions in molluscs (Mieleikovsky 1970), mysids (Mauchline 1972) and isopods (Kouwenberg and Pinkster 1985). Tyler *et al* (1991) suggest such a pattern is maintained in the deep-sea by a 'bottleneck' effect (Jumars *et al* 1990). Juveniles or larvae released in the autumn, winter or early spring may starve or fall prey to predators. Any surviving will grow slowly until the arrival of phytodetritus and then develop rapidly and be recruited to the adult population. Those larvae or juveniles whose release coincided with periods of maximum food will stand more chance of successful recruitment. So animals whose reproductively active periods produce young at this time are more likely to pass on this characteristic to the next generation. Caution must be applied when generalizing about the possible effects of phytodetrital input to deep-sea communities. In a study of the reproduction and diet in three dominant deep-sea taxa, Tyler *et al* (1994) compared species pairs of a protobranch bivalve, an echinoid and an asteroid. One of the pair was a quasi-continuous breeder, the other a seasonal breeder. The former as expected showed no seasonal variation in their diet, while in the seasonal breeders, the pattern of reproduction did not vary with the supply of phytodetritus. This study shows that whilst seasonal reproduction has been widely reported in deep-sea invertebrates, control of these cycles is not necessarily related to surface-derived fluxes (Tyler *et al* 1994, Eckelbarger 1994). Data presented in Chapter Four seemed to indicate more *Ampelisca* sp nov males were caught in April, possibly as a result of increased feeding activity. If more males than usual were found on or near the bottom, this would increase the likely hood of encounters with females. This may be an additional factor explaining the increase in reproductive activity for this species in the spring. Although the organic flux to the deep-sea may be an ultimate factor leading to synchronization in many deep-sea invertebrates, the proximate factors (or timing cues) are yet to be determined. Tyler *et al* (1982, 1983) have suggested a possible environmental signal may be the variation in eddy kinetic energy, observed at abyssal depths with changes in current regimes. This energy reaches a maximum between February and March in the Northeast Atlantic (Dickson *et al* 1982). Tyler and colleagues suggest resuspension of the sediment or an increased transmission of chemical signals may stimulate

reproductive events.

5.4.5 Conclusions

1. Brood size and embryo diameter were positively correlated with female length for the deep-sea gammarideans in this study.
2. Oostegite length and number of oostegite setae were positively correlated with female length for *Ampelisca* sp nov.
3. Brood sizes are smaller and embryo diameters larger for deep-sea gammarids from this study compared to predictions for a shallow water amphipod of similar size.
4. Only a small percentage of female amphipods caught were found with broods. This may be a result of egg loss during sampling, low reproductive activity in the population, or behavioural responses and/or gear selectivity resulting in a failure to capture brooding females.
5. *T. biloba* showed seasonal and synchronous reproduction, whilst *Ampelisca* sp nov showed continuous reproduction with a seasonal increase in reproductive intensity.
6. These seasonal reproductive events coincide with periods of phytodetrital input to the study area, which may act as an energy source for vitellogenesis and/or a food resource for newly released juveniles.

CHAPTER SIX
FEEDING BIOLOGY

6.1 INTRODUCTION

6.1.1 Food sources in the deep-sea

One of the most important limiting factors in deep-sea ecology is likely to be food availability (Gage and Tyler 1991). With the exception of hydrothermal vents, production in the deep-sea is reliant on an external input of organic matter, the majority of which sinks from the euphotic zone. The potential sources of, and possible pathways by which this organic material reaches the deep-sea are described by Rowe and Staresinic (1979). This material includes large food falls of animal origin, coastal and terrigenous plant debris, and fine particulate organic matter. The latter consists of the remains of zoo- and phytoplankton, faecal pellets and moults. Large food falls of animal origin, such as marine mammals and fish, are for the most part unpredictable. A seasonal component may exist under the migration routes of some fish species (Tyler 1988). Such food falls have been estimated to provide up to 10% of the energy requirements of the deep-sea benthos (Smith 1985). Animal carcasses are quickly consumed by scavenging species such as amphipods (see below), ophiuroids and fish (Isaacs and Schwarztloze 1975, Thurston 1979, Lampitt *et al* 1983, Hargrave 1985, Smith 1986, Priede *et al* 1990). Large food falls of plant origin are also important sources of organic matter to the deep-sea benthos. Gage and Tyler (1991) report that the presence in the deep-sea of vegetable matter, leaf and fruit debris was reported as early as 1880. Mosely having noted such material in the trawls obtained by *HMS Challenger*. Macroalgae and seagrasses have been commonly observed in deep-sea photographs from the western Atlantic and Caribbean (Menzies and Rowe 1969, Schoener and Rowe 1970). Such plant debris is known to attract specific benthic species (Young *et al* 1993, Lawson *et al* 1993). This form of food fall is known to be ingested by a variety of deep-sea benthos (Wolff 1976, 1979, Suchanek *et al* 1985). A more predictable supply of organic matter to the deep-sea arrives in the form of

phytodetritus and other particulate material from surface waters. The first evidence that such material did not arrive as a slow, constant rain of particles came from trap evidence in the Sargasso Sea (reviewed by Deuser 1986). Evidence obtained from both photographic and trap studies have revealed a marked seasonality in the flux of such material to the NE Atlantic (Billett *et al* 1983, Lampitt 1985, Rice *et al* 1986, Rice *et al* 1991). The transmission of the surface bloom as a recognizable seasonal signal results from the rapid sinking of this material (Angel 1984, Fowler and Knauer 1986). This is caused by the mucus secretions of phytoplankton cells, mainly diatoms, contributing to the formation of aggregates which sink to the bottom. On their descent they scavenge other particles increasing their sinking rates to an average of 100m a day (Smetacek 1985). Organic macroaggregates composed of zoo- and phytoplankton remains are therefore rapidly deposited over a wide bathymetric range following the spring bloom (Billett *et al* 1983, Lampitt 1985, Thiel *et al* 1990, Gooday and Turley 1990, Rice *et al* 1991). After deposition this material is repeatedly resuspended and deposited (Lampitt 1985, Rice *et al* 1986). This detritus may blanket the sea floor, or occur in localized patches in or around structures on the sea bed, such as mounds or hollows (Billett and Hansen 1982). Samples of this detritus taken with the Scottish Marine Biological Association's multiple corer have revealed the main components are diatoms, and gelatinous aggregations of coccolithophorids, dinoflagellates, crustacean eggs, faecal pellets and amorphous organic material (Billett *et al* 1983). The most abundant diatoms in the phytodetritus are *Thalassionema nitzschoides, Nitzschia delicatissima* and *Chaetoceros* spp (Rice *et al* 1986). During its descent and especially after its arrival at the deep-sea bed this material is colonized by bacteria, which in turn are preyed upon by protozoans (Gooday 1988, Lochte and Turley 1988, Gooday and Turley 1990, Thiel *et al* 1990). Chlorophyll derived pigments have been found in the guts of holothurians, which have been found to feed exclusively on phytodetritus when it is deposited (Billett *et al* 1988). Photographic evidence and gut content analysis have shown the deep-sea echinoid *Echinus affinis* feeds on this detritus and the faecal mounds of holothurians (Lampitt and Billett 1988, Campos-Creasey *et al* 1994). The effect of phytodetritus on the ecology of metazoans remains equivocal but has been

postulated to control seasonality in the life history biology of some deep-sea invertebrates (Tyler 1988, Thiel *et al* 1990, Campos-Creasey *et al* 1994). Smith *et al* (1994) have proposed a scenario for the coupling of a pelagically derived food supply and its utilization by benthic communities in the deep-sea. Particulate matter enters the benthic boundary layer, where it is dispersed, raising concentrations of chlorophyll a and organic carbon in surface sediments. This fuels an increase in the sediment community oxygen consumption and increases ATP concentrations. During the summer the sinking organic matter is augmented by lateral advection, and the increased suspended concentration enhances production of larger detrital aggregates. The dispersal and spatial blending of these large aggregates by mobile megafauna creates elevated concentrations of organic carbon across the sediment surface. This permits sustained high rates of sediment community activity into late autumn, even though particulate fluxes are then in decline (Smith *et al* 1994). Food quality, rather than quantity has been proposed as the limiting factor for deposit feeders. The diets of deep-sea deposit feeders are likely to be, on average, of lower quality than nearshore and shelf deposit feeders (Penry and Jumars 1990).

6.1.2 Feeding in deep-sea amphipods

An early attempt to look at the feeding ecology of deep-sea amphipods was made by Barnard (1962). Because the dredge hauls he was studying captured both benthic and bathypelagic amphipods, the habits of the animals could not be determined by the collecting device. He believed that some evidence on their habit might come from examination of gut contents, for example presence of refractory mineral particles may indicate bottom feeding. However his results were inconclusive, mineral particles were sparse even in animals adapted for burrowing and known to be benthic (eg. haustoriids). This suggests deep-sea amphipods show a marked efficiency in locating and utilising detrital/bacterial deposits (Barnard 1962).

Investigations on the ecology of Antarctic amphipods showed them to be mainly omnivorous or necrophagous possibly as an adaption to the discontinuity of the phytoplankton cycle. The constant and predictable environmental conditions of the

Antarctic, as well as its high diversity, lead to an expectation of close niche adaptation and consequently the presence of many specialists (Coleman 1989). It seems likely that similar patterns could be expected in deep-sea amphipods. Feeding studies on deep-sea amphipods have been dominated by those concerning carrion-feeding amphipods attracted to baited traps. All amphipods regularly obtained in such traps belong to the family Lysianassidae (Dahl 1979). Slattery and Oliver (1986) consider lysianassid amphipods may be the most abundant and widespread macro-invertebrate scavengers in the ocean. Morphological studies have demonstrated that their mouthparts are adapted for slicing, biting and chewing, and that their alimentary tracts can accumulate and store large quantities of food (Dahl 1979, Thurston 1979 Sainte-Marie and Lamarche 1985, Barnard and Ingram 1986, Sainte-Marie 1987). These lysianassids may be able to sustain long periods without food, by a combination of gluttonous feeding when carrion is present, long gut retention times, or high assimilation efficiency and low metabolic rates (Dahl 1979, Smith and Baldwin 1982, Hargrave 1985, Sainte-Marie 1986, 1987). There may be an ontogenetic shift in diet from detritus feeding juveniles, to carrion feeding by larger adults capable of metabolic autonomy and environmental probing (Hessler *et al* 1978, Sainte-Marie and Lamarche 1985). There is an apparent cessation of foraging activity in mature brooding females of semelparous species, whilst those of iteroparous species are receptive to bait odour and are still captured in traps. This has been interpreted as a mechanism to minimize mortality from exposure to predators in single-brooded species (Bregazzi 1972, Hessler *et al* 1978, Thurston 1979, Sainte-Marie and Lamarche 1985). It may be that foraging changes in females may not be just behavioural, but related to the physical constraints on the gut by developing ovaries or broods (Sainte-Marie *et al* 1990). Adaptations for carrion feeding in lysianassid genera seem to follow at least three separate lines, the most striking difference being the stomodeal storage of food in *Orchomene* as compared to midgut in other genera (Dahl 1979). Intergeneric comparisons by Thurston (1979) confirm this evolutionary difference among the genera *Paralicella* and *Orchomene*. Thus structural and functional morphological adaptations for deep-sea carrion feeding have evolved independently several times

within the Lysianassidae (Dahl 1979). Two estimates of feeding rate have been obtained for carrion-feeding amphipods one by Hargrave (1985) used *in situ* observations employing time-lapse photography, whilst De Broyer and Thurston (1987) used weight of ingested bait, number of 'bites' of food and residence time in trap. Intestinal microflora from the digestive tracts of trapped abyssal amphipods were studied by Deming *et al* (1981). These bacteria exhibited growth rates unaffected or enhanced by high pressures. Sediment and water samples collected at the same sites as the amphipods consistently yielded no indication of barophilic microbial populations in the environment. Thus it seems abyssal amphipods possess a commensal gut flora capable of responding to increased nutrient levels, via feeding of the host (Wirsen and Jannash 1983, Yayanos *et al* 1979, Deming et al 1981, Nagasawa and Nemoto 1988).

6.1.3 Structure of Chapter Six

This chapter presents the results of a variety of methods utilized to determine the feeding biology of deep-sea amphipods. The first was an experiment designed to test the hypothesis that food falls of macrophyte debris would attract amphipods in a manner similar to animal food falls. The results of this experiment, together with studies on the respiration rates of the trapped amphipods, and an examination of their chemosensory structures are detailed in section 6.2. This is followed by an examination of the feeding biology of two species of amphipods from the Rockall Trough samples, assumed to have different feeding strategies (section 6.3). These studies involve the development of an index to characterise gut 'fullness', and visual examination of gut contents. This is combined with examination of mouthparts and gut contents using electron microscopy to determine any morphological clues to diet, and possible variation of gut content with season.

6.2 EXPERIMENTAL STUDIES USING BAITED TRAPS

6.2.1 Introduction

Baited traps were first used in the deep-sea as long ago as 1888 deployed from the *Hirondelle* (Richard 1934). Between 1892 and 1912, twenty one deployments were made to depths exceeding 3000 m from the Prince of Monaco's subsequent yachts (Richard 1934). Interest in this technique declined until the late 60's when the development of baited traps and time lapse cameras revealed the existence of a highly motile scavenging necrophagous fauna in the deep-sea (Isaacs 1969, Hessler *et al* 1972, Hessler *et al* 1978, Isaacs and Schwartlose 1975, Thurston 1979, Lampitt *et al* 1983). Frequently these catches are dominated in numbers and biomass by amphipods. The most common and best known being the lysianassid *Eurythenes gryllus*, which together with the 'supergiant' *Alicella gigantea* have a worldwide distribution (Barnard and Ingram 1986, De Broyer and Thurston 1987). These and other genera of lysianassid amphipods are attracted in large numbers to traps set under both the oligotrophic central N Pacific and more eutrophic areas in the deep N. Atlantic (Shulenberger and Hessler 1974, Shulenberger and Barnard 1976, Thurston 1979, Hargrave 1985). Traps set in trenches show only crustacean scavengers (mainly amphipods), whilst the 'full range' of natatory forms can be caught at adjacent abyssal depths. Lysianassids are the most common scavengers on the abyssal plain, whilst decapods dominate on the slope (Hessler *et al* 1978, Desbruyeres *et al* 1985). Several observations have shown current direction is important for scavengers locating food. Amphipods photographed approaching a baited camera do so from a down current direction, maximum response occurring during periods of peak tidal current (Thurston 1979, Desbruyeres *et al* 1985), confirming ideas proposed previously (Isaacs and Schwartzlose 1975, Guennegan and Rannou 1979, Lampitt *et al* 1983). A simple Gaussian odour plume model taking into account rate of odour productions by bait, chemosensory threshold of scavengers and satiation time has been developed by Sainte-Marie and Hargrave (1987). This model suggests abundances of scavengers are low, several orders of magnitude lower than in coastal waters. Estimated distances of

attraction to bait suggested a gradient of necrophagy among species, with the pelagic lysianassid *E.gryllus* rallying to bait from greater distances than the fish *Coryphaenoides sp.*, which in turn is attracted from much greater distances than the small demersal amphipods *Orchomene sp.* and *Paralicella caperesca*. These distances of attraction are much greater than those reported for shallow water scavenger species. Between 'meals' it is not certain where these amphipods spend their time. On the basis of optimal foraging theory, Jumars and Gallagher (1982) define two foraging strategies; i. most appropriate for benthic animals is to remain within the viscous sublayer and swim at right angles to the current until the odour is detected; ii. the second involves hovering above the viscous layer where turbulent mixing will widen the extent of the chemical plume of the odour downstream of its source, both horizontally and vertically. These ideas have been tested by means of a trapping program in the abyssal central N. Pacific (Ingram and Hessler 1983, Smith and Baldwin 1984). The results show both a near bottom (demersal) and a more pelagic, off bottom guild exist. The near bottom guild comprises species of *Paralicella* and *Orchomene* which can exploit large and small food falls and bottom-derived organic carrion as a result of their proximity to the sediment. The larger *E.gryllus* belongs to the off-bottom guild, with its greatest abundance 10-20 m from the bottom where it can provide itself with a wide chemosensory 'overview' and use faster background currents in its search for food (Ingram and Hessler 1983, Charmasson and Calmet 1987). Smith *et al* (1992) used acoustic detection methods and trawls to estimate biomass and abundance of *E. gryllus* in the central North Pacific. Biomass of acoustic targets ranged from 0 to 72.3 g wet weight per 10^5 m^3, whilst from trawl catches biomass was reported at 0.2 to 6.7 g wet weight per 10^5 m^3. Abundance data ranged from 0 to 1.6 animals per 10^5 m^3 for acoustic targets, and 1.4 to 11.9 animals per 10^5 m^3 for trawl samples. Recent studies in the west European Basin have revealed an ontogenetic vertical migration in *E.gryllus* : females release their brood near the bottom. The youngest stages stay within a few meters above the sea floor, whereas older stages, especially adult males, migrate into higher water layers (Christiansen *et al* 1990). Large specimens of *E. gryllus* have been caught at depths up to a maximum of

1.8km above bottom in 5.8km of water; the large size of adults probably allows them to forage over a larger area with less risk of predation. The low genetic variability of *E. gryllus* in samples from different basins in the N Pacific indicate high dispersal capabilities and/or uniform selective processes over a wide area. Some differentiation is shown in seamount populations, perhaps resulting from isolation or different selective pressures (Bucklin *et al* 1987). Thurston (1990) gives evidence suggesting that the necrophagous amphipods in the northeast and tropical Atlantic ocean between 8^0N and 50^0N are a single faunal entity.

All trap studies mentioned above have used animal carrion as bait. In marginal deep-seas in low latitude waters marine macrophyte and terrestrial plant debris is often found in abundance on the sea bed. In the subtropical NW Atlantic debris from seagrass beds in shallow water or from the floating seaweed *Sargassum* spp commonly occurs on the seabed. A possible seasonal component in the input of this material may be related to local weather conditions (Johnson and Richardson 1977). This material has been noted in numerous photographs from the western Atlantic and Caribbean (Menzies and Rowe 1969, Schoener and Rowe 1970). It has been reported to act as a substratum, shelter or food source for a variety of deep-sea macroinvertebrates including lysianassid amphipods (Wolff 1976, 1979) and megainvertebrates (Suchanek *et al* 1985). A submersible program looking at the reproduction of deep-sea echinoids in waters off the Bahamas (Young *et al* 1992), noted the clustering of one species (*Stylocidaris lineata*) on patches of *Sargassum* spp, and the presence of fragments of *Thalassia testudinum* in its gut contents. Subsequent experimental studies showed the ability of this species to locate and exploit macrophyte detrital falls (Young *et al* 1993). As part of this program the following experiment was devised to investigate whether traps baited with macrophytes would attract amphipods in a similar manner to those baited with animal carrion (Lawson *et al* 1993).

6.2.2 Materials and Methods

The traps were of a basic cylindrical form, constructed from Nytex 0.5mm nylon mesh, with inverted funnels at each end. The tips of the funnels were cut to provide an entrance aperture of 10mm diameter. To protect the fine mesh, each cylinder was surrounded with 15mm mesh Vexar plastic. Each trap was 22cm long and 9cm in diameter. Traps were weighted with a piece of limestone, to which a buoyant rope was attached to aid deployment by the sub (Plate 6.1). Two traps were filled loosely with *Thallasia testudinum*, two with *Sargassum* spp, two with dead grey mullet, *Mugil cephalus*, and two with inert black plastic bags cut into *Thallasia* sized strips. The *Thallasia* and *Sargassum* used was collected from material which had been uprooted and washed into local bays. The traps were deployed at 09.00hrs on the 21 October 1991 at 503m depth of the SW Reef in the Bahamas by the DSRV *Johnson Sealink*. The traps were deposited on soft mud, bottom temperature was recorded at 13.9 ^{0}C, conductivity 44.25, with no recordable bottom current. The traps were arrayed on the bottom in two randomized block arrangements, with each bait type represented in each block. The traps were monitored 8 hrs later and recovered after 30 hrs, at which point the number of echinoids attracted to each trap was noted. Upon arrival on deck, the traps were immediately placed in cold seawater and stored and processed in the ship's cold room. Each trap was opened individually and the contents washed in filtered seawater. Each blade of *Thalassia* and *Sargassum* was examined for animal colonists and the residual water filtered through a 235μm mesh sieve and the residue examined. The experiment was repeated in water 10m deep off Egg Island, Bahamas on the 24th October 1991. The traps were deployed by scuba divers and recovered 30hrs later, and treated as before. Amphipods and other animals caught were counted and the distribution of numbers and species between each trap elucidated. Individuals of the most common amphipod species caught were transferred to a seawater aquarium in the ships cold room for further experiments. The remaining specimens were preserved in 4% v/v formalin in seawater. Data were compared using ANOVA and Tukey pairwise comparison.

PLATE 6.1 AMPHIPOD TRAP

The amphipods kept alive in seawater aquaria were used for an experiment to determine their respiration rates. This experiment was inspired by the work of Smith and Baldwin (1982), who showed an elevated respiration rate in amphipods exposed to bait odour. Amphipods were placed in 25ml biological oxygen demand bottles, which were filled with filtered seawater, or seawater odourised with fragments of *Sargassum* and again filtered. A 0.22μm mesh filter was used to remove the microbial population. Determination of dissolved oxygen concentration was made using a modified Winkler technique (Parsons *et al* 1984). Odourized and plain water samples were fixed at the start of the experiment to determine original oxygen concentrations. Four replicates of the following treatments were incubated at 14^0C, plain water, odourized water, plain water plus amphipod, odourized water plus amphipod. The oxygen concentrations were determined after 6hrs incubation, and mean wet weights of amphipods determined.

No light penetrates to the bathyal depths, and deep-sea amphipods show a corresponding reduction or loss of eyes. The proportion of eyeless species is correlated positively with depth and latitude (Thurston and Bett 1994). Scavenging lysianassids must rely on chemosensory or mechanosensory receptors to locate food resources and a mate. Kaufmann (1994) reports the largest concentrations of chemoreceptors are located on the first articles of antennular flagella, and widely distributed on the thoracic appendages, particularly the gnathopods. The most common species of lysianassid caught in the trap experiment was examined for the presence of these chemoreceptors. This was attempted using scanning electron microscopy. One of the major problems with such an approach for amphipods is the removal of surface debris. This debris consists of a film of secretions from the integumental glands which are denatured by fixatives, plus epibiotic fauna and sediment particles. Many methods are described for the preparation of crustacean material for scanning electron microscopy (Dahl 1973, Oshel 1985, Felgenhauer 1987, Dittrich 1991, Kaufmann 1994). The following is a synthesis of these methods. Formalin fixed specimens were rehydrated through a graded ethanol series, and washed in three changes of distilled water. They were then

placed in a solution of anionic surfactant (Tween), two drops in 100ml of water for fifteen minutes to help remove surface contaminants. Specimens were again washed in distilled water before dehydration through a graded series of ethanol (25, 30, 50, 70, 80, 90 to 100%) three five minute changes in each. Samples were air dried and mounted onto aluminium stubs with double sided sticky tape. These mounted specimens were coated with 500 Angstroms of gold-palladium, and examined under a Joel-35C scanning electron microscope.

6.2.3 Results

Trap Study

The fish baited traps had disappeared by the time the traps were monitored 8 hrs after deployment. There was no evidence of the traps downslope of the deployment site. It is possible they were taken by a six-gill shark (Family Hexanchidae) that had been observed in the vicinity of the deployment site. The numbers of amphipods caught in each trap type, the species distribution and sex ratios are given in Table VI.I. The traps also attracted the echinoid *Stylocidaris lineata* (Plate 6.2), and galatheid crabs, whose abundance is also recorded in Table VI.I. The shallow water traps attracted a smaller number of amphipods, but a large variety of other invertebrates (Table VI.II). Two-way crossed analysis of variance on the data showed a significant difference between the number of amphipods collected at the deep and shallow water deployment sites, and there was a significant difference among bait types in the total number of amphipods attracted ($F=9.22$, $P=0.0025$). A Tukey HSD pairwise comparison on the deep-water data showed no significant difference between the two types of plant detritus, but both *Thalassia* and *Sargassum* attracted significantly more amphipods than the plastic bags ($Q=4.341$). Traps containing *Thalassia* and *Sargassum* in deep-water collected significantly more amphipods than identical traps in shallow water ($F=24.68$, $P=0.0148$), but there was no difference in the number of amphipods collected in the black plastic traps at the two depths. Four species of amphipod colonized the deep-water traps (Table VI.I). Three species of lysianassids, *Scopelocheirus* sp nov, *Concarnes* sp nov and *Amaryllis* cf *pulchellus*, were attracted

TABLE VI.I NUMBERS OF ANIMALS TRAPPED IN DEEP-WATER TRAPS

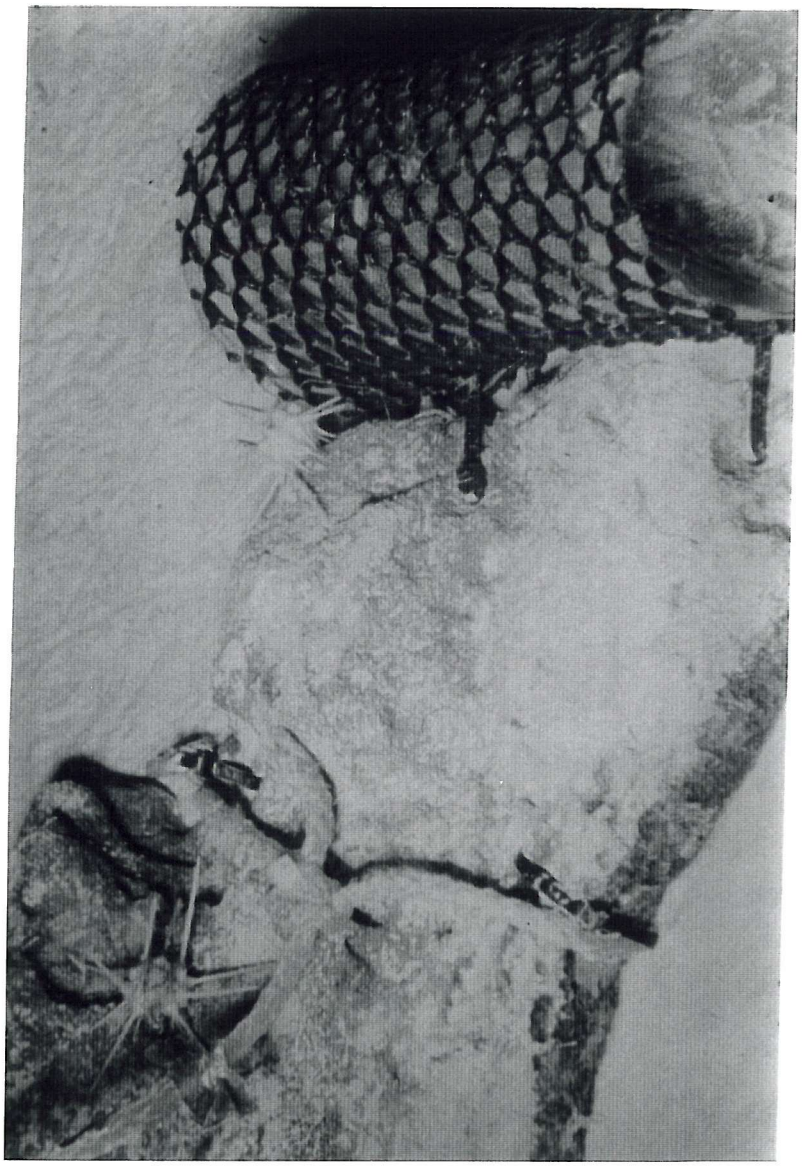
BAIT TYPE	AMPHIPODS	*Scopelocheirus* sp nov		*Concarnes* sp nov		*Amaryllis* cf *pulchellus*		*Rhacotropis* sp nov		ECHINOIDS	CRABS
		MALE	FEMALE	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE		
Sargassum 1	36	10	13	4	8	1	2	0	0	7	1
Sargassum 2	23	0	0	3	13	2	5	0	0	3	0
Thalassia 1	11	0	0	0	8	2	1	0	0	4	2
Thalassia 2	21	2	0	4	10	5	1	0	0	10	1
Bin-Bag 1	1	0	0	0	0	0	0	1 ?	0	3	0
Bin-Bag 2	0	0	0	0	0	0	0	0	0	3	0
Total	92	12	13	11	39	10	9	1	0	23	4

TABLE VI.II NUMBERS OF ANIMALS TRAPPED IN SHALLOW-WATER TRAPS

BAIT	AMPHIPODS	OSTRACODS	COPEPODS	LEPTOSTRACA	STOMATOPODS	CRAB	SHRIMP	WORM	HERMIT CRABS			
									A	B	C	D
Sargassum 1	1	*	*	0	0	1	0	0	0	0	0	0
Sargassum 2	1	*	*	*	1	0	1	2	0	0	0	0
Thalassia 1	2	0	*	*	0	0	0	0	0	0	0	0
Thalassia 2	5	1	*	*	0	0	0	0	0	0	0	0
Bin-Bag 1	1	*	*	*	0	0	0	0	0	0	0	0
Bin-Bag 2	0	*	*	*	0	0	0	0	0	0	0	0
Fish	2	14	3	6	1	1	0	1	52	15	6	1
Fish	0	0	8	1	0	0	1	0	3	2	0	0

KEY *= Too numerous to count, A=*Clibanarius tricolor*, B= *Pagurus brevimanus*, C= *Dardanus fucosus*, D= *Calcinus tibicer*

PLATE 6.2 AMPHIPOD TRAP AT 500m WITH ECHINOID *Stylocidaris lineata*



to both kinds of plant detritus. A single specimen of the eusirid *Rhacotropis* sp nov was the only amphipod found associated with the black plastic bags. The three lysianassid species were distributed heterogeneously among the bait treatments (3x3 contingency table, χ^2=13.41, P=0.0094), although the main cause of this effect was the absence of lysianassids in the plastic bag traps. Sex ratios only varied significantly from unity for *Concarnes* sp nov attracted to the *Thalassia* trap (χ=5.28, P=0.05). Two females of *Concarnes* sp nov attracted to the *Sargassum* trap, and one female of *Amaryllis* cf *pulchellus* attracted to *Thalassia* were found to be carrying broods. The amphipods gut contents were examined for the presence of macrophytes and showed the animals did feed on this material (Plate 6.3).

The respiration experiment was of limited success. The process of odourizing the water reduced initial oxygen concentrations by such a large amount (9.5 ml/l) that the amphipods in those bottles used up all the available oxygen within the incubation period. This may be caused by the alkanoids released by the *Sargassum*, interfering with the Winkler reaction. As such no respiration data are available for this treatment. The non odourized control experienced a rise in initial oxygen concentration of 0.36 ml/l/hr, probably a result of microbial respiration by flora not removed by the filtering process. The mean respiration for the four non-odourized amphipod treatments was calculated as 2.055 µl/l/hr. The mean wet weight for the amphipods used in the experiment was 3.75 mg, so the respiration rate for this species (*Concarnes* sp nov) can be calculated as 0.548 µl O_2 mg^{-1} wwt h^{-1}.

Plate 6.4 shows the scanning electron micrograph of a male *Concarnes* sp nov antennular flagella article one, with an olfactory chemoreceptor or callynophore. Plate 6.5 shows the same for a female specimen, whilst Plate 6.6 reveals the presence of gustatory chemoreceptors on the gnathopods of this species.

PLATE 6.3 ***Concarnes*** **sp nov WITH DISSECTED GUT FULL OF SARGASSUM**

Scale Bar 1mm

PLATE 6.4 *Concarnes* sp nov MALE CALLYNOPHORE

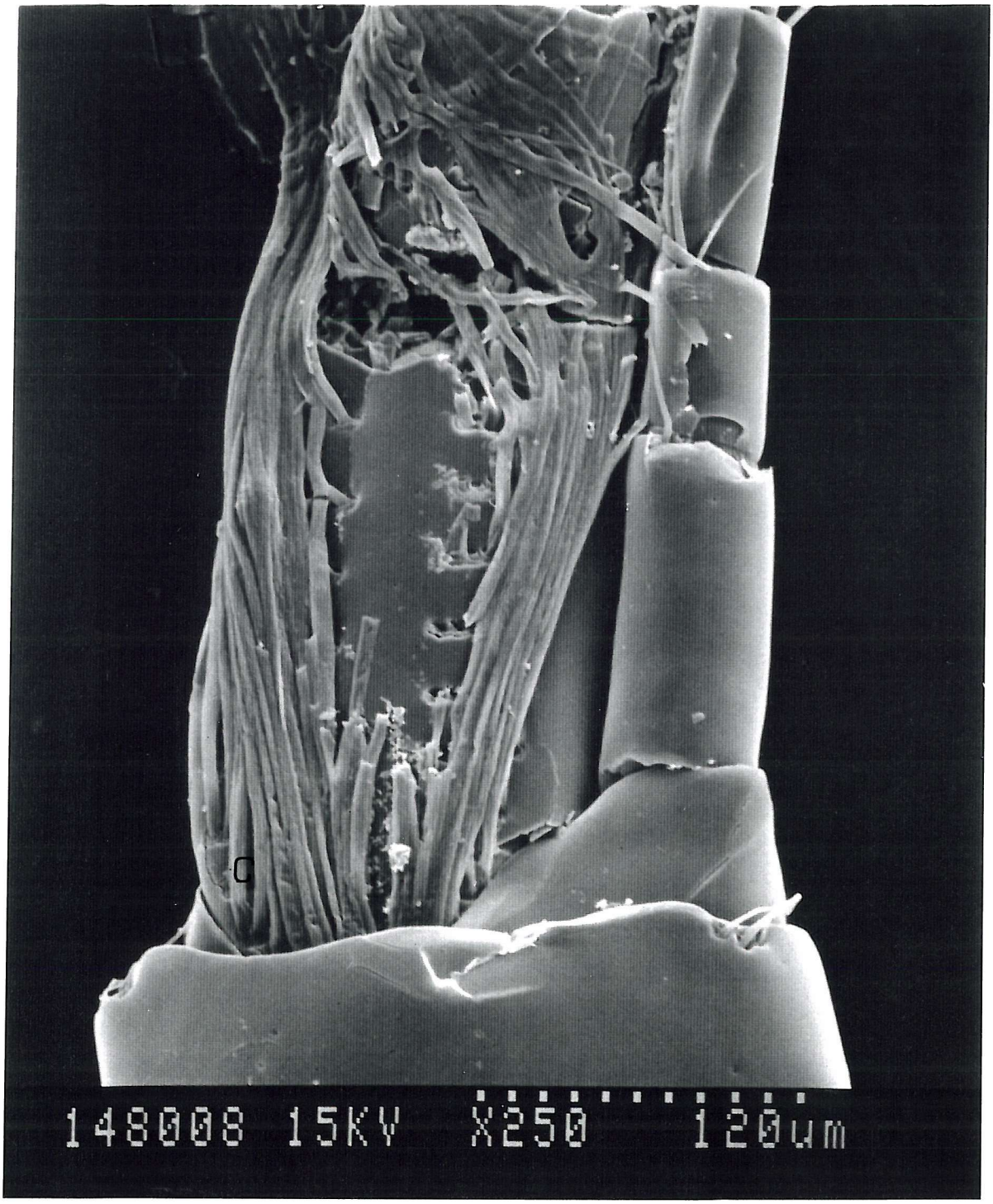


PLATE 6.5 ***Concarnes*** **sp nov FEMALE CALLYNOPHORE**

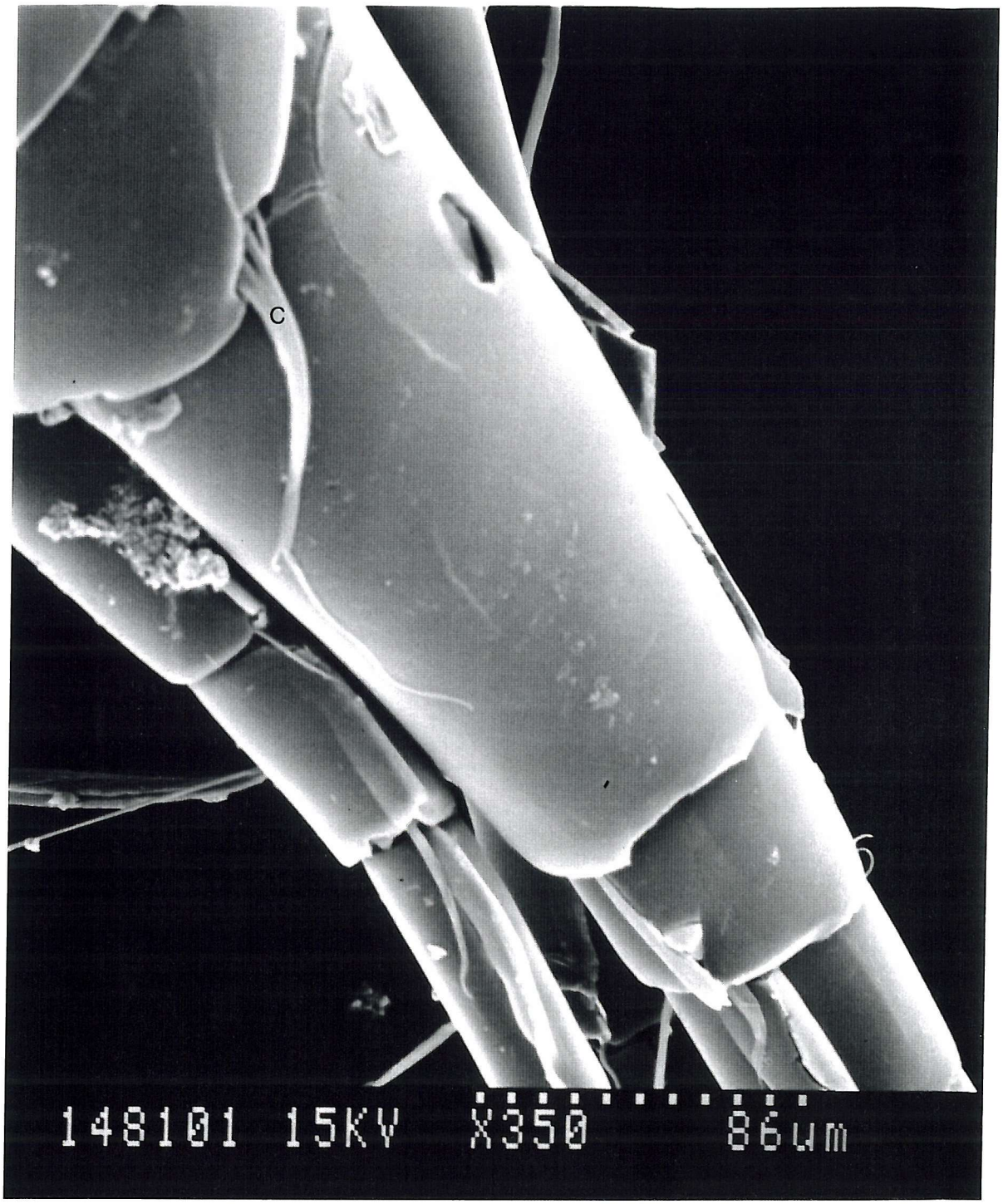
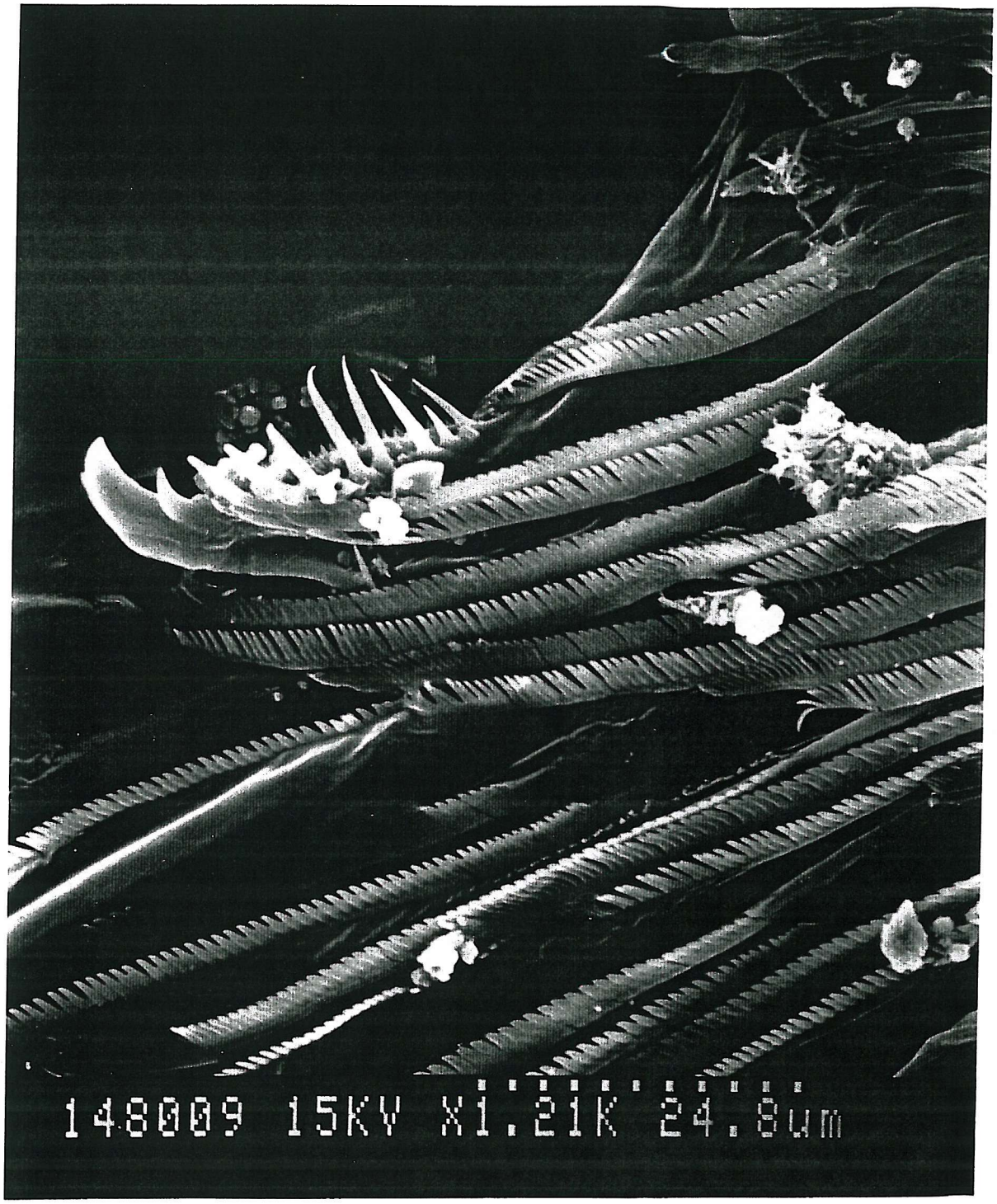


PLATE 6.6 SERRATE SETAE ON GNATHOPOD OF *Concarnes* sp nov



6.2.4 Discussion

Macrophyte debris is known to attract at least one species of deep-sea echinoid *S. lineata* (Young *et al* 1993), and analysis of its stomach contents revealed it did feed on this detritus. However, experimental evidence suggested that *S. lineata* located its food by chance encounter. The experiment outlined in this chapter was designed to test whether macrophyte detritus would attract amphipods as a food substrate or as a refuge. Marine macroalgae commonly have a diverse assemblage of small invertebrates, many of which are herbivores and potentially consume their host plants. Collectively referred to as 'mesograzers', these small herbivores often include amphipods (Duffy 1990). Amphipod densities as high as $6500m^{-2}$ have been reported in beds of seagrass (Nelson 1980). Mesograzers inhabiting macroalgae may feed on the variety of epiphytes that commonly foul macroalgae (reviewed by Brawley 1992). Amphipods are known to consume macroalgae, a large body of literature relating to the grazing of activities of amphipods, and the effects of removing predation pressures are reviewed by Conlan (1994). The importance of the role amphipods play in the fragmentation of eelgrass detritus was demonstrated by Robertson and Mann (1980) with field and experimental studies.

The results of the trap experiment off the Bahamas reveal significantly more amphipods were attracted to packages of macrophytes than to the inert plastic bag controls. This suggests that the amphipods are attracted to the macrophyte as a food resource rather than shelter as has been suggested for other deep-sea species (Wolff 1979). The three species attracted to the macrophyte material all belong to genera known to have a scavenging/necrophagous lifestyle. The single specimen attracted to the plastic bags, *Rhacotropis* sp nov, belongs to a genus thought to have micro-predator/carnivore habits (M. Thurston pers comm). The deep-water traps attracted significantly more amphipods than did the same baited traps in shallow water. This disparity may be a function of food supply. The deep-water amphipods of this study would depend on an influx of organic material from the surface layers. In contrast the amphipods living in the area of shallow water in which the second experiment was carried out, have ready access to areas of high vegetation content. Thus the shallow

water amphipods are unlikely to be food limited. In this study, hermit crabs replaced amphipods as the main colonists in shallow water traps, although all were found in the traps containing dead fish. The significance of sex ratios differing from unity has been discussed previously in Chapter Four. The higher number of *Concarnes* sp nov observed in this study may represent an artefact of sampling rather than a true departure from a 1:1 ratio.

The respiration rate of 0.548 µl O_2 mg^{-1} wwt h^{-1} reported for *Concarnes* sp nov in this study is between five and ten times higher than figures given for deep, midwater and shallow amphipods by Smith and Baldwin (1992). The oxygen consumption values listed by Chapelle and Peck (1995) for Antarctic amphipods are similarly much lower than those of *Concarnes* sp nov. The high oxygen consumption rate of *Concarnes* sp nov is probably related to the stress of recovery from 500m to the surface. Not only has the amphipod to cope with significant pressure changes, but also a rapid water temperature rise. It was then returned immediately to cold *in situ* temperatures in the ships cold room aquaria, and incubation experiment took place at atmospheric pressure. Dramatic lowering of oxygen consumption rates are shown by Antarctic amphipods afforded the opportunity to acclimatize to the respirometer chamber (Chapelle and Peck 1995). The rates were reduced even more by the provision of some sort of substratum, eg. nylon mesh. This paper refutes the concept of metabolic cold adaption in amphipods, elevated metabolic rates probably produced by the effects of stress. No doubt a longer acclimatization period, use of a larger incubation vessel and provision of some sort of shelter or substratum would reduce the abnormally high respiration rates reported for *Concarnes* sp nov.

Putative chemosensory structures of *Concarnes* sp nov were examined using electron microscopy. Amphipods have a variety of sensory structures, the earliest to be recognized was the calceolus. Its prevalence on male gammaridean amphipods, led to the assumption that it was responsible for the detection of sex pheromones. This early conclusion seemed to be confirmed following radioactive tracer experiments by Dahl *et*

al (1970). However, re-evaluation of their procedures and examination of internal structures using electron microscopy, point to a more likely function as phonoreceptors for water borne pressure waves (Lincoln and Hurley 1981, Lincoln 1985). Another sensory organ found on the antennae of amphipods, the aesthetasc, does have a chemosensory function (Lowry 1986). A variety of integumental organs, sensory in nature, appear randomly over the dorsal and lateral surfaces of amphipods (Mauchline and Ballantyne 1975). The comparative morphology and a classification of setae, and microtrich sensilla types, together with inferred chemo- and mechano-sensory function have been described by Oshel and Steele (1988) and Oshel *et al* (1988). These microtrichs appear to form a 'side-line' organ in some amphipods (Platvoet 1985). When looking at the chemosensory structures of *Concarnes* sp nov, a distinction needs to be drawn between those used for olfaction (smell) and gustation (taste). Olfaction is considered purely chemosensory, while gustation is both chemosensory and mechanosensory (Laverak 1989). In lysianassid amphipods, antennular setae are recognized as the principal chemosensory structures. They are termed aesthetascs and are organized into patches called callynophores on the dorsomedial, medial or ventral portion of the first article of the antennular flagellum (Lowry 1986). Examination of the first article of the antennular flagellum in *Concarnes* sp nov revealed the presence of these structures in both male and female specimens (Plates 6.4 and 6.5). Observations of the behaviour of scavenging lysianassids belonging to the genus *Orchomene* are reported by Kaufmann (1994). These show the amphipods orientate the antennular flagellum so that water currents pass over the callynophores. This is aided by sweeping motions of the antennules, and flow visualization experiments indicate entrainment of water in the vicinity of the callynophore. In common with the genus *Orchomene*, the callynophores of *Concarnes* sp nov, show a sexual dimorphism. The number and density of aesthetascs in the male callynophore (Plate 6.4) is far greater than that observed for the female (Plate 6.5). This seems to indicate a possible dual function of sex pheromone detection for the male callynophore. There is behavioural evidence to suggest that scavenging lysianassid amphipods have well developed gustatory systems. When attacking dead or

immobilized prey, lysianassids have been seen to feed selectively on specific tissues, usually the liver or gonads (Shulenberger and Hessler 1974). This suggests an ability to discriminate between food items that differ biochemically and perhaps texturally. The anterior appendages of amphipods bear setae similar to those known to be gustatory in decapods (Kaufmann 1994). Examination of the gnathopods of *Concarnes* sp nov revealed large numbers of serrate setae (Plate 6.6). Serrate setae have been reported in number of crustacean species and have been electrophysiologically identified as gustatory in decapods (Derby 1982). The presence of such setae on the gnathopods of *Concarnes* sp nov may allow it to characterize its food prior to ingestion, and therefore preferentially identify and consume energy rich food.

6.3 FEEDING BIOLOGY OF ROCKALL TROUGH AMPHIPODS

6.3.1 Introduction

The feeding biology of *Ampelisca* sp nov and *Tryphosella biloba* are described in this chapter. These species were chosen for reproductive and population studies for reasons given in previous chapters. *Ampelisca* sp nov was considered particularly suited for feeding studies. Ampeliscids belonging to the genus *Ampelisca* are reported to feed primarily on diatoms in the water column but can also resuspend organic matter from the sediment surface with their second antennae (Highsmith and Coyle 1991). Their sedentary, suspension feeding life style, means ampeliscids depend upon environmental conditions to bring food to them. The amount of food available to the animal is dependent on the flux of organic matter to the bottom within reach of its antennae. Deep-sea ampeliscids from the Rockall Trough would therefore seem likely to be dependent on the seasonal input of phytodetritus. Thus if the seasonal input of this detritus were to have an impact on the life history biology of the amphipods in this study, *Ampelisca* sp nov would be most likely to reflect its effects. *Tryphosella biloba* is a lysianassid, and this family of gammarids is reported to have the most heterogenous spread of life history traits. Species of Lysianassoidea comprise of predators, carrion-feeders, omnivorous scavengers, detritivores, herbivores, as well as typically endobenthic, epibenthic and suprabenthic forms (Sainte-Marie 1991 and references therein). Thus it would be interesting to see what feeding biology could be determined for *T. biloba* which is the most abundant lysianassid present in the samples of this study.

The method of feeding in ampeliscids has been described by Enequist (1949), Mills (1967) Highsmith and Coyle (1991) and Coyle and Highsmith (1994). They position themselves in the tops of their tubes, with the ventral surface turned upward. The long first and second antenna are then used to either passively sift particles from the water column, create a feeding current with a whirling motion in conjunction with beating of the pleopods, or to scrape particles off the sediment surface. *Ampelisca* sp nov exhibits the 'typical' long feeding antenna of ampeliscids (Plate 6.7).

PLATE 6.7 ***Ampelisca*** **sp nov SHOWING 'FEEDING' ANTENNAE**

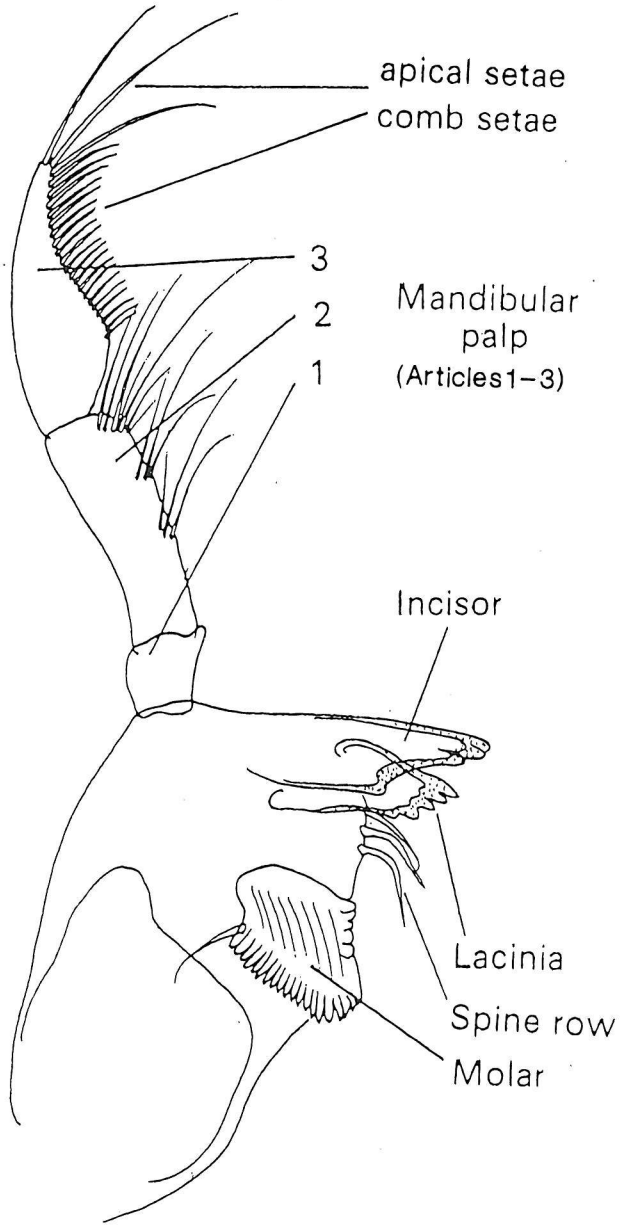
Scale Bar 1mm

The morphology of the digestive tract in amphipods will not be described in detail. This is because the internal structure was not considered in the examination of the feeding biology of amphipods in this report. A detailed review of the digestive system and associated organs of amphipods is given by Schmitz (1992). The amphipod gut can be subdivided into the stomodeal foregut, midgut and hindgut. The gammaridean foregut is lined by a chitinous intima and is differentiated into a buccal cavity, oesophagus and cardiac and pyloric stomach chambers. The midgut is essentially an elongated tube-like structure. A variety of caeca and diverticula arise from the midgut, a dorsal caecum, two pairs of digestive caeca, and a pair of posterior caeca. The hindgut consists of a tubular anterior hindgut that gives way posteriorly to a shorter rectum, opening to form a slit-like anus in the telson.

It is often difficult to identify the gut contents of amphipods through direct observation as the contents may be 'ground up' completely (Sugisaki *et al* 1991). Even more difficult is direct observation of feeding behaviour in the field, especially for deep-sea species ! Gut content analysis is therefore commonly supported with study of the functional morphology of mouthparts and internal organs. This is often complemented by comparisons with related shallow water species or genera. Light microscopy, scanning and transmission electron microscopy have been used by several workers to relate the shape and size of mouthparts, structural morphology of foreguts, stomachs and associated structures; with diet in benthic and pelagic amphipods (Oshel and Steele 1988, Sheader and Evans 1975, Coleman 1989 and Dittrich 1991). Studies of the maxillary setae have been correlated with differences in diet for two co-occurring congeneric amphipods (Wagner and Blinn 1987). Whilst ultrastructural observations on the midgut glands cells of a gammarid have revealed possible functional differences (storage, enzyme production and release) (Musko 1988). The importance of looking at the three-dimensional configuration of the mouthparts using scanning electron microscope techniques is emphasised by Moore and Rainbow (1989). Drawings made from light microscope preparations are of one compressed plane, often hiding functional morphologies.

The variation in size and shape of the amphipod mandible is most often used for studies on functional morphology (Zimmerman 1980, Dittrich 1991, Steele and Steele 1993, Moore *et al* 1994). It has also been proposed as a possible phylogenetic tool (Watling and Holman 1980, 1993). The basic amphipod mandible (Figure 6.1) consists of the mandible body or coxa, which is generally compact and bears : the incisor, a toothed distal projection of the mandible body orientated so that it cuts in the horizontal plane of the body and perpendicular to the long axis of the mandible; the molar, a columnar structure, projecting mediad from the mandible body so that it meets its companion in a rolling crushing action; the lifting spines (or setae row), comprising a row of strong, upwardly curved, coarsely serrate setae which probably function to prevent food particles obtained from the biting action of the incisors from falling away from the molars; the lacinia mobilis, an articulated, broad, flat, often toothed plate, designed to interdigitate with its companion, most likely to keep the mandible from twisting badly out of alignment during biting; and a palp of three articles which projects anterodorsally in front of the head and between the antennae (Watling 1993). The palp is used to clean the base of the antennae and the anterior cephalic space between them. The forward and backward motion of the mandible is generated by abductor-adductor muscles in the transverse plane of the body. On abduction, the coxa of the mandible swings outward, the incisors part, and themolars open slightly ventrally but remain in slight contact dorsally. As adduction occurs, the molars increasingly come together ventrally until the material between them is crushed by the interdigitating ridges, and the incisors gradually close on another piece of the food item. Modifications of the basic mandible plan are numerous and varied. They include the reduction of the incisor, loss of the lifting spines, reduction or loss of the molar, or all of these. Most mandible modifications occur in response to predation and/or scavenging as a feeding strategy.

FIGURE 6.1 BASIC AMPHIPOD MANDIBLE



6.3.2 Materials and Methods

The transparent integument of *Ampelisca* sp nov afforded the opportunity to study the changes in colour of gut contents with season. An estimate of relative gut fullness (gut index) was developed to quantify changes in feeding activity with season. The length of gut containing food particles was divided by the total length of the animal. This index was determined for total sample population, males, females and juveniles respectively. Measurements were made for samples collected in January, April, June, September, October and November. These months were chosen to provide indexes for periods before, during and after the input of phytodetritus to the sample region. The percentage of individuals with full guts were also determined for each sample, a full gut was defined as animal with a gut index of >0.6 . Such an analysis was not possible for *T. biloba*. This was a result of the increased opaqueness of the integument of this species, and the very low numbers of individuals with food in their guts.

The mandibles of *Ampelisca* sp nov, *T. biloba* and *Concarnes* sp nov (from the trap experiment detailed in section 6.2), were examined using scanning electron microscopy. Samples were prepared as described for the study of *Concarnes* sp nov sensory structures. Except that prior to mounting on stubs, mandibles were separated from the other mouthparts and then mounted and coated as before.

The midguts of *Ampelisca* sp nov and *T. biloba* were dissected from adult specimens. For *Ampelisca* sp nov guts were obtained from samples collected in January, April and September. It was hoped these samples would reveal differences between pre- detrital deposition (January), initial influx of detritus (April) and decline in input (September). *T. biloba* specimens were very difficult to dissect, a function of their small size. Coupled with the very low numbers of large (adult) specimens with sufficient gut contents to process. As a result only two gut samples were obtained which were from specimens collected in April. The dissected guts were transferred from Steedmans solution to a 90% steedmans/acetone solution. The guts were then passed through a graded series of this mixture to 100% acetone, with an hours immersion in each concentration. The transfer to 100% acetone was performed to reduce the drying time of the sample, which in turn would reduce the distortion of any delicate structures

present in the gut contents. Guts were transferred to an aluminium stub and opened with a razor blade to allow dispersion of contents onto the stub surface. They were left to air dry, before coating as before. The rapid evaporation of the acetone also aided the adhesion of gut contents to the stub.

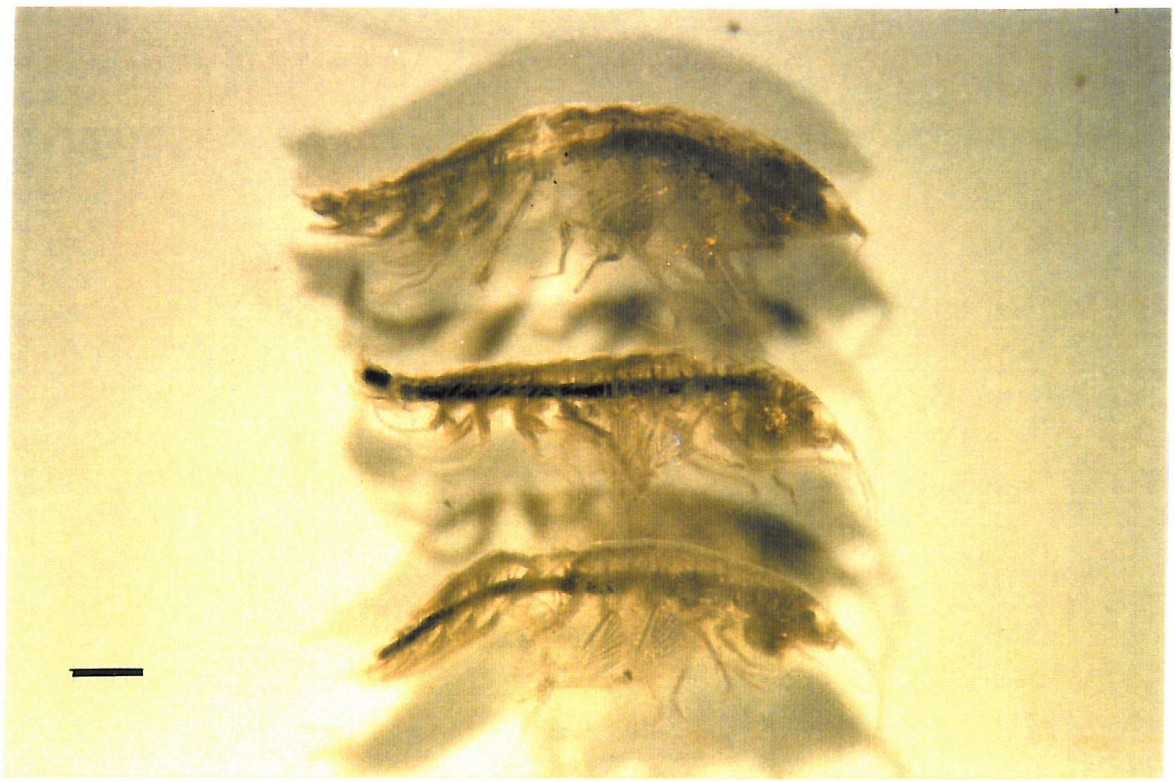
6.3.3 Results

Distinct changes in the appearance of gut contents between months can be seen for *Ampelisca* sp nov. The difference is greatest between individuals from January and April (Plate 6.8a). There is also an apparent difference between January, April and September (Plate 6.8b). Several species in this study had nematodes in their body cavity, two examples are shown in Plate 6.9a and b.

Gut Index values for *Ampelisca* sp nov are presented in Figure 6.2. The mean values show a rise in the relative fullness of the guts for the population as a whole from a minimum in January, to maximum in April, declining in September and October to a minimum in November. The pattern is very similar for female and juvenile *Ampelisca* sp nov, the juvenile plot not showing quite such a sharp decline between June and September. Males seem to have a larger gut index in the early part of the year, compared to juveniles and females, but experience a far more rapid decrease in the relative gut fullness between June and November. Figure 6.3 shows the variation in percentage of total, male, female and juvenile populations which have full guts. The graph shows an increase in percentage of full guts from January to a maximum in June for all categories. Males appear to have a far higher percentage of specimens with full guts than females or juveniles in January and April. No juveniles have full guts in January, but rapidly reach a similar percentage to the females in April. Total, male, female and juveniles populations all show a rapid decline in the percentage with full guts from June to a minimum in October.

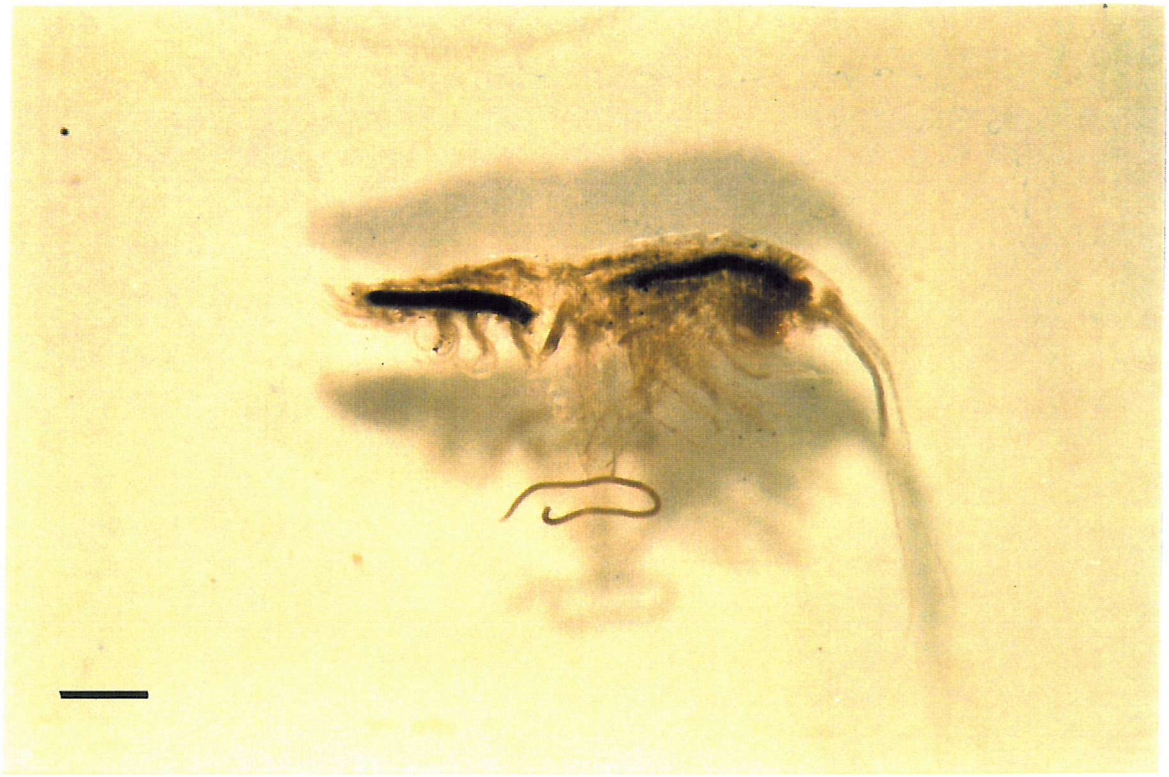
PLATE 6.8 ***Ampelisca*** **sp nov COLOUR OF GUT CONTENTS**

6.8a SPECIMENS FROM JANUARY (top) AND APRIL (bottom)
Scale Bar 1mm



6.8b SPECIMENS FROM JAN. (top), APRIL (middle) AND SEPT. (bottom)
Scale Bar 1mm

PLATE 6.9 NEMATODE PARASITES



6.9a *Ampelisca* sp nov Scale Bar 1mm

6.9b *Leptophoxoides molaris* Scale Bar 1mm

FIGURE 6.2 GUT INDEX FOR *Ampelisca* sp nov

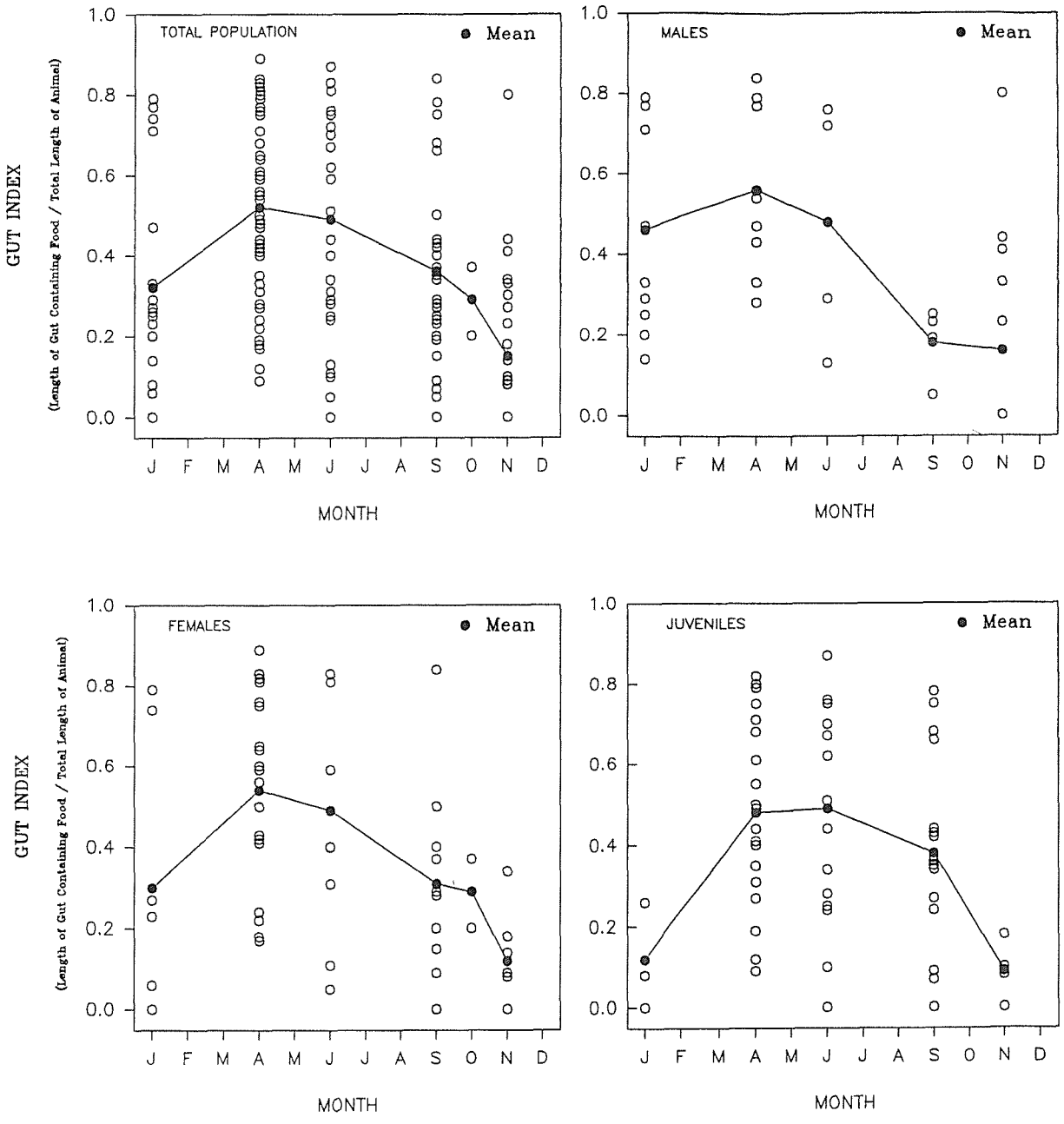


FIGURE 6.3 PERCENTAGE OF *Ampelisca* sp nov WITH FULL GUTS

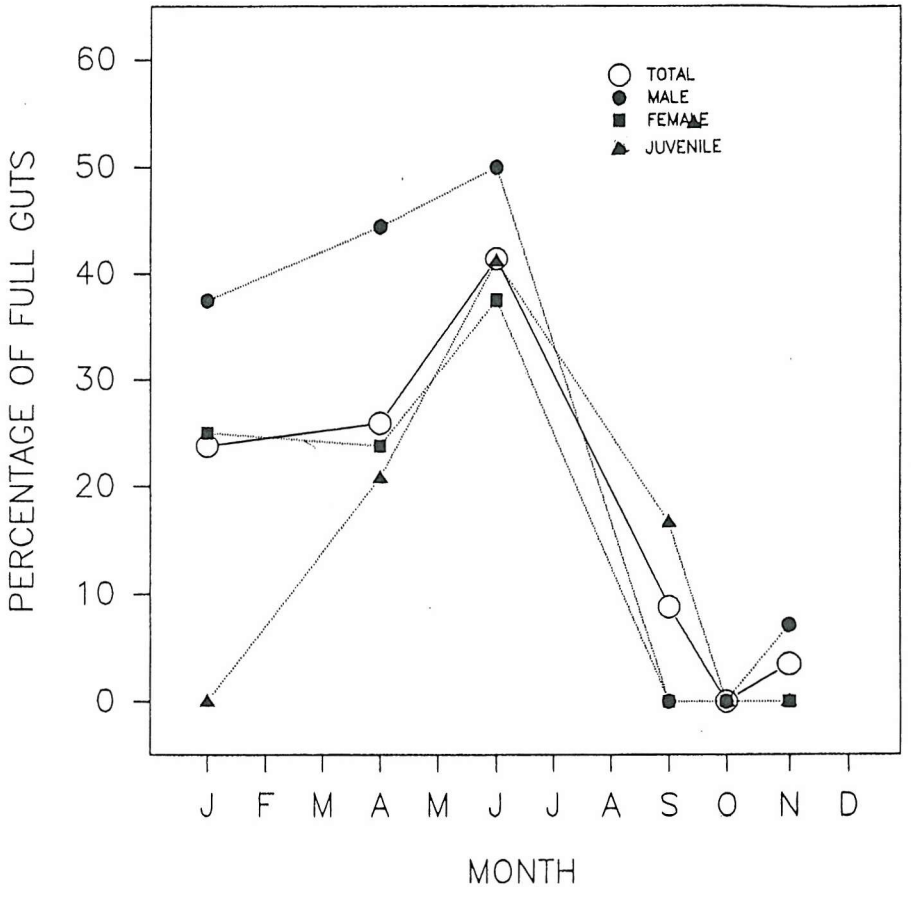


Plate 6.10 shows the scanning electron micrograph of the mandible of *Ampelisca* sp nov. A magnified view of the triturative surface of the molar, together with the incisor and lifting spines can be seen in Plate 6.11. The structure of the mandible in *T. biloba* is presented in Plate 6.12, this is followed by a close up of the molar and incisor (Plate 6.13). This plate reveals the presence of three distinct holes or pores in the molar surface. The scavenging lysianassid *Concarnes* sp nov has a mandible quite distinct in form from the other two species examined (Plate 6.14).

The typical appearance of gut contents from *Ampelisca* sp nov collected in April are shown in Plates 6.15 and 6.16. These plates reveal the presence of numerous pelagic diatom fragments and coccoliths. The diatom fragments are not identifiable to species, but can be identified as belonging to the genus *Thalassiosira* or *Coscinodiscus.* There may also be fragments of *Thalassionema* present in Plate 6.15

Plate 6.17 shows the gut contents of *Ampelisca* sp nov from January, and reveals a very reduced number of ingested items compared to April. Plate 6.17 is approximately the same magnification as Plate 6.15, reinforcing the obvious disparity in gut contents. A closer look at a diatom fragment from January is shown in Plate 6.18. This looks 'degraded' in comparison to those in the April sample. The micrograph for September's gut content sample (Plate 6.19) reveals more diatom fragments than were present in January, but they were not as abundant as in the April sample. A quantitative analysis was not possible for these samples, but qualitative comparison of the replicates for each month show a clear seasonal difference in the number of phytodetrital fragments ingested by *Ampelisca* sp nov.

T. biloba gut contents for April were different in composition and abundance to those of *Ampelisca* sp nov. Very few diatom fragments were observed, but there were a number of coccoliths (Plate 6.20). These liths come from the pelagic coccolithophore *Emiliania huxleyi* (Dr D. Purdie pers comm), which forms part of the spring bloom in the waters overlying the Rockall Trough.

PLATE 6.10 ***Ampelisca*** **sp nov MANDIBLE**

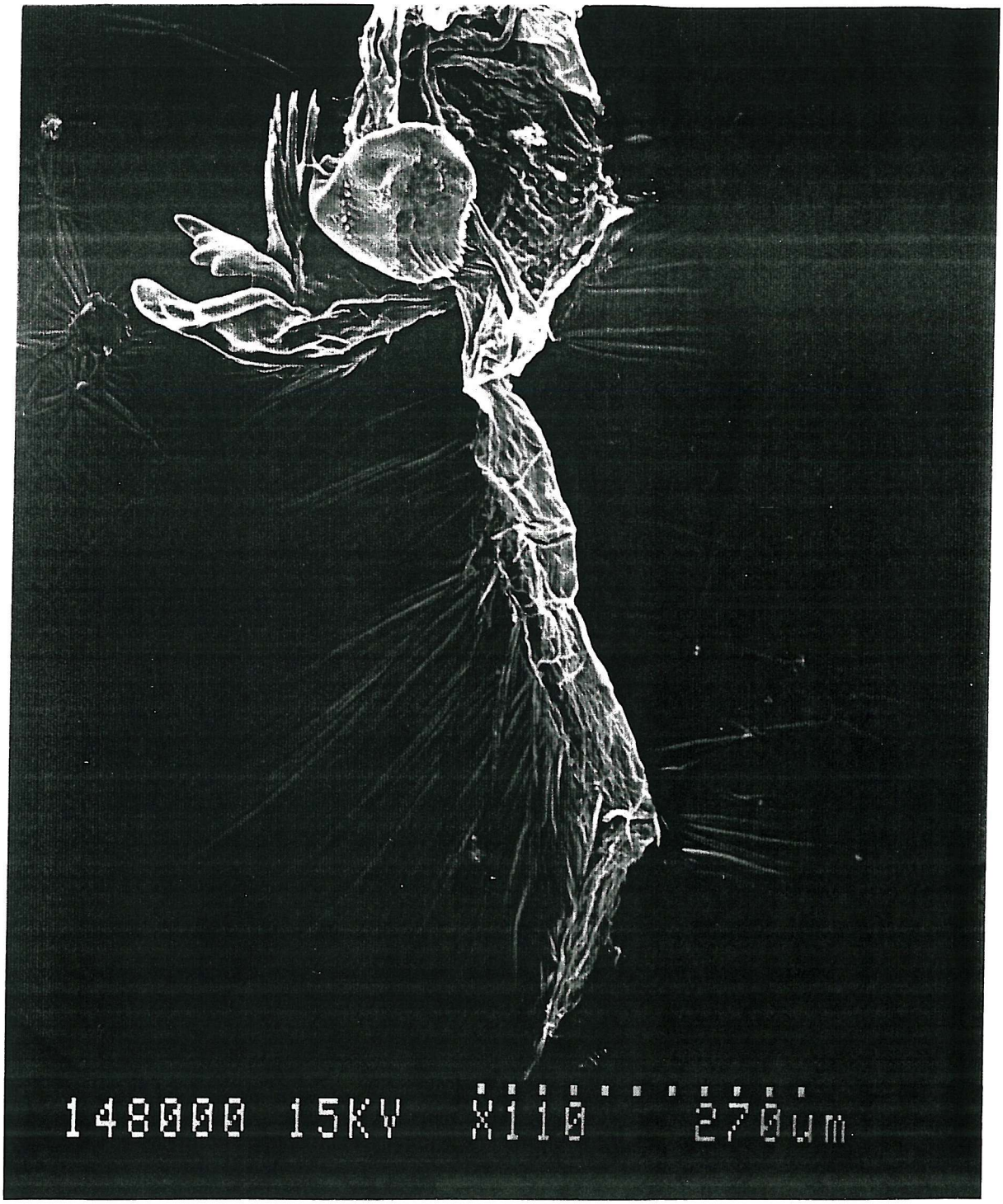


PLATE 6.11 ***Ampelisca*** **sp nov MOLAR AND INCISOR**

PLATE 6.12 ***Tryphosella biloba*** **MANDIBLE**

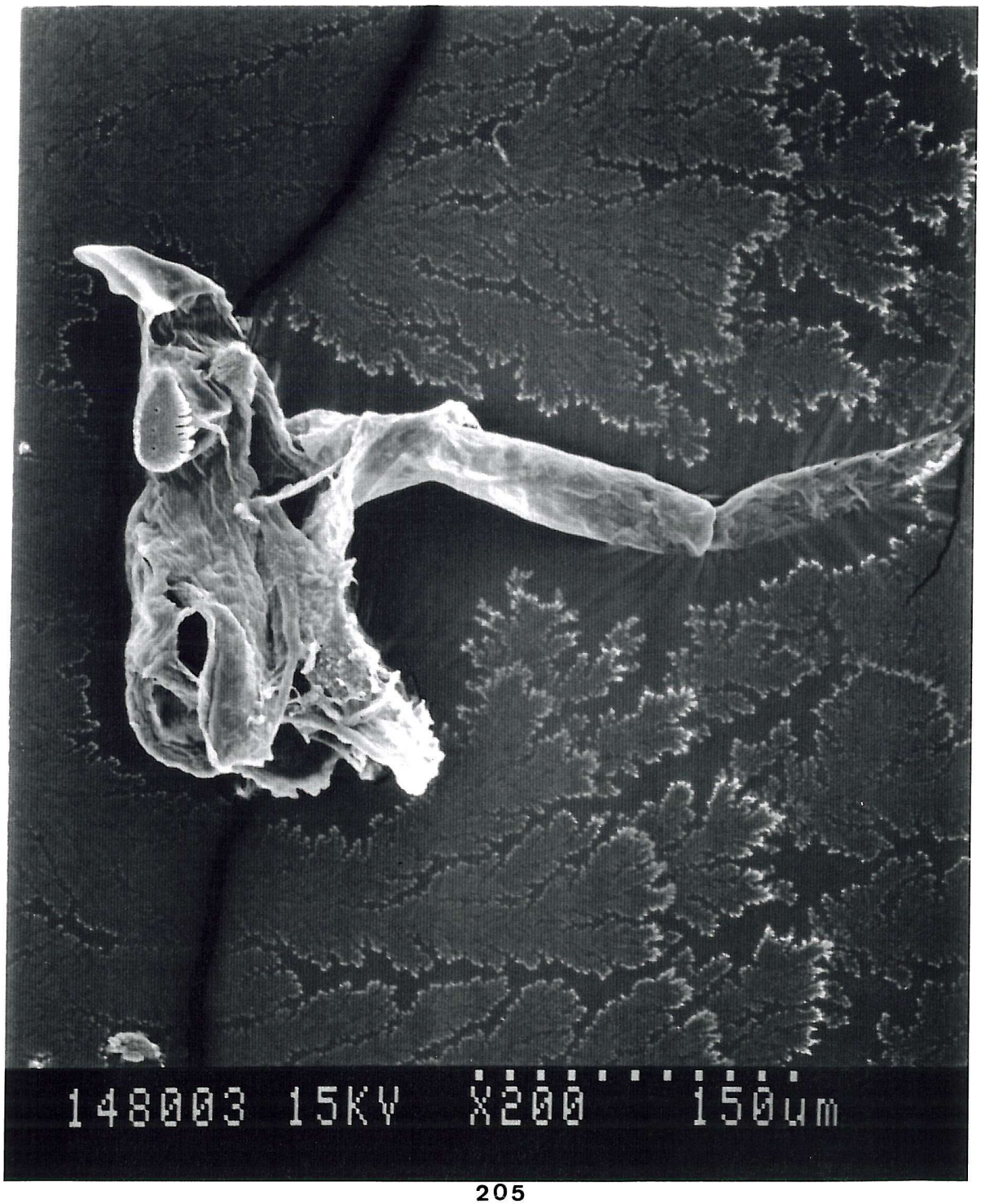


PLATE 6.13 *Tryphosella biloba* MOLAR AND INCISOR

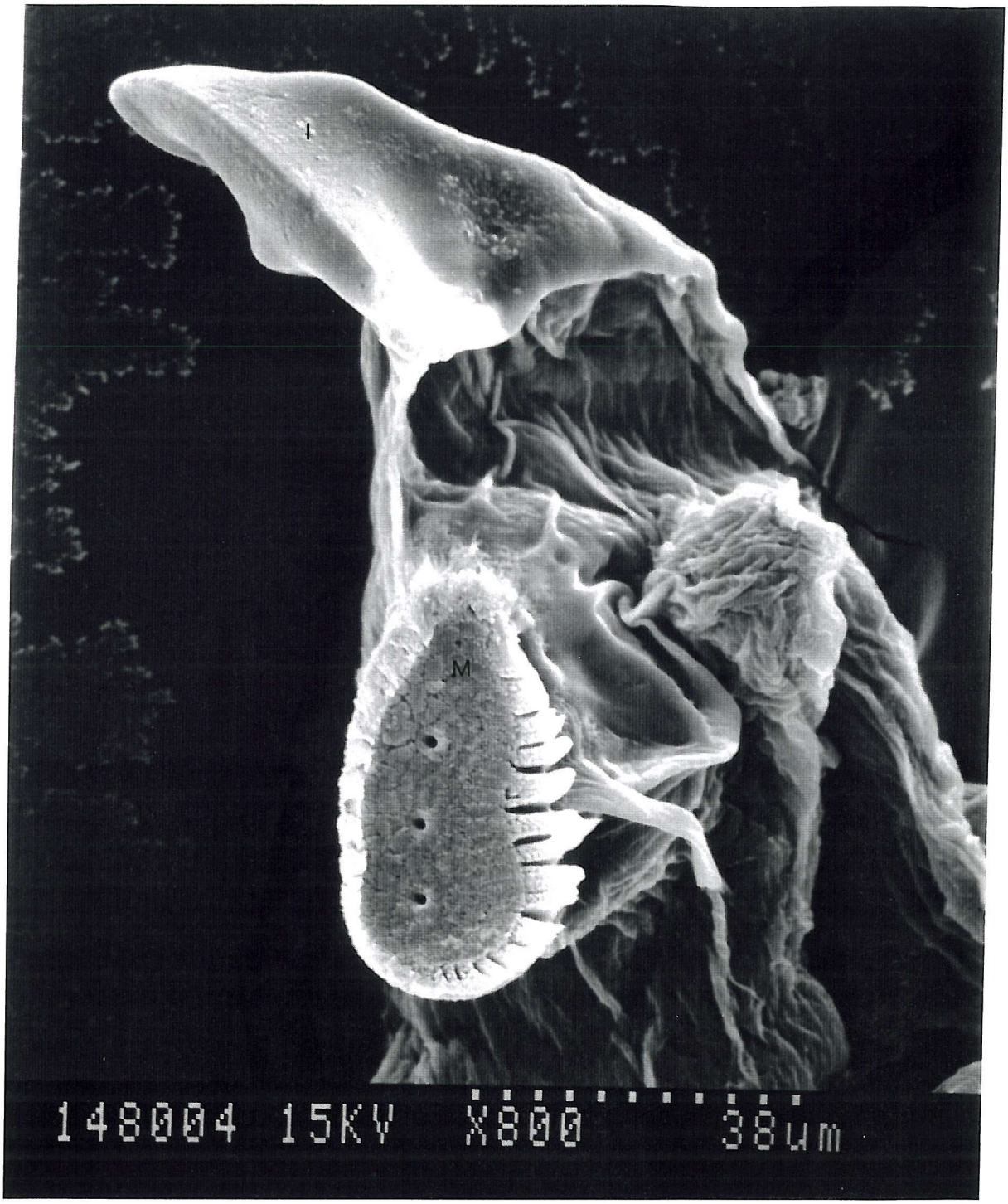


PLATE 6.14 *Concarnes* sp nov MANDIBLE

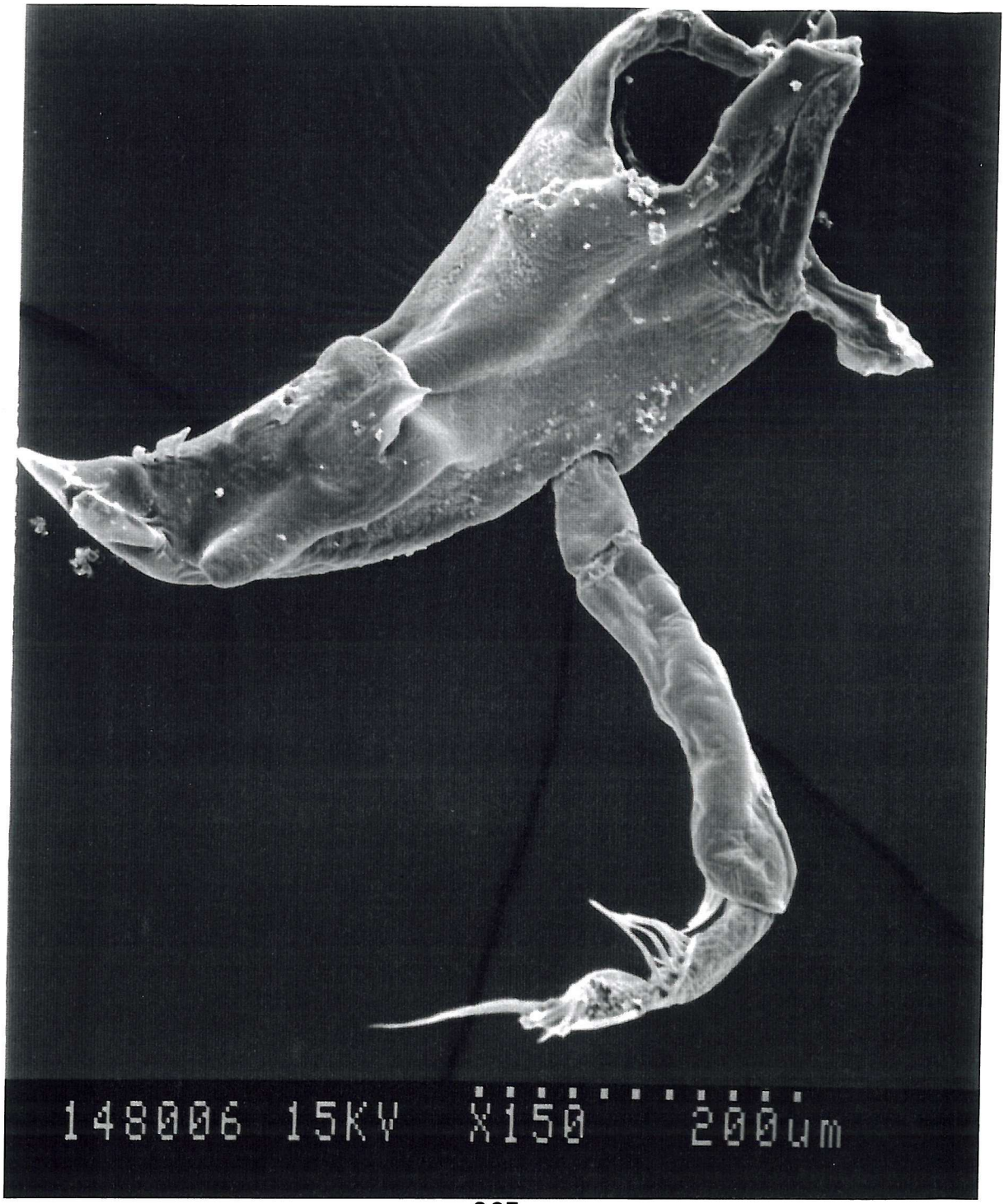


PLATE 6.15 *Ampelisca* sp nov GUT CONTENTS - APRIL

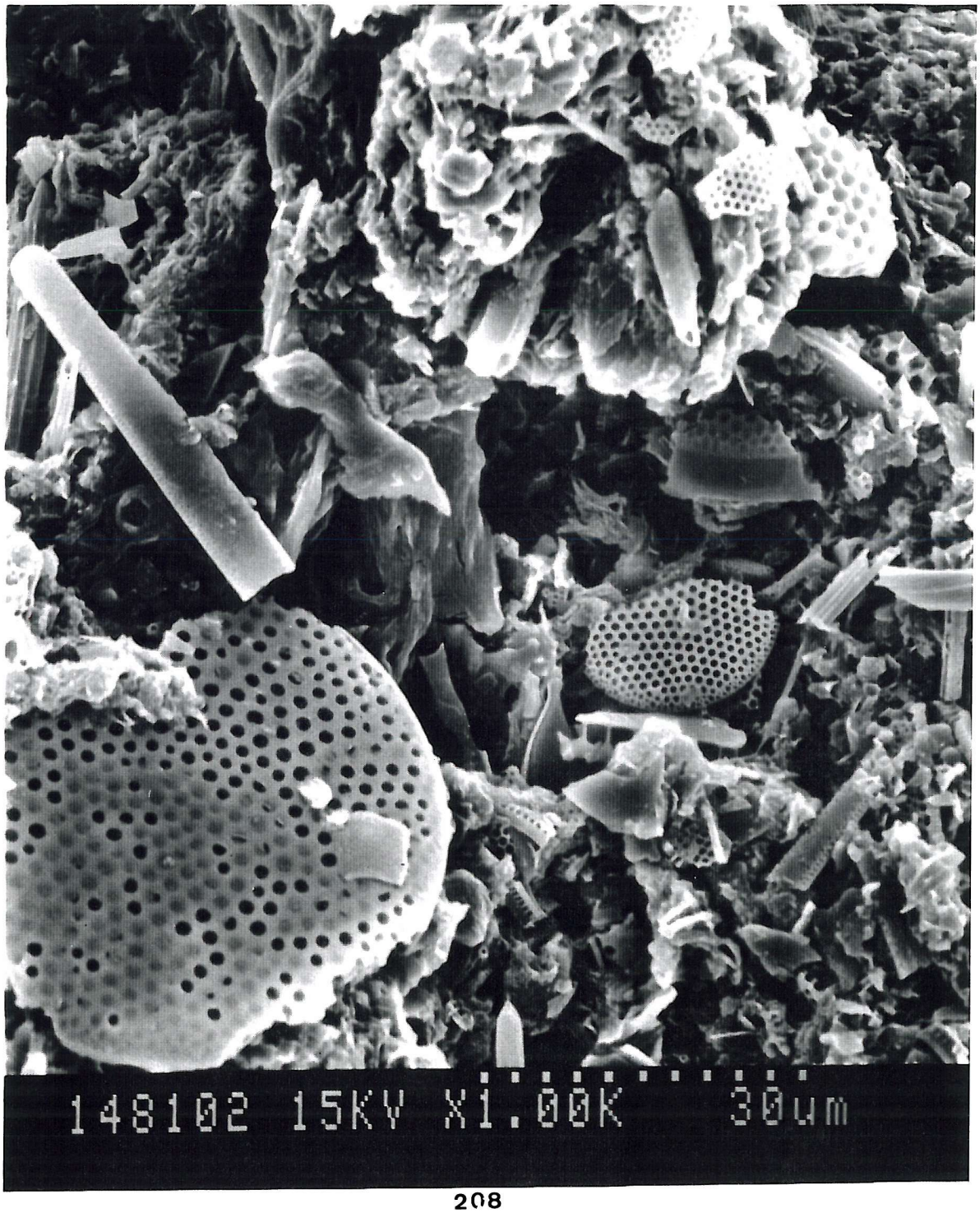


PLATE 6.16 *Ampleisca* sp nov GUT CONTENTS - APRIL

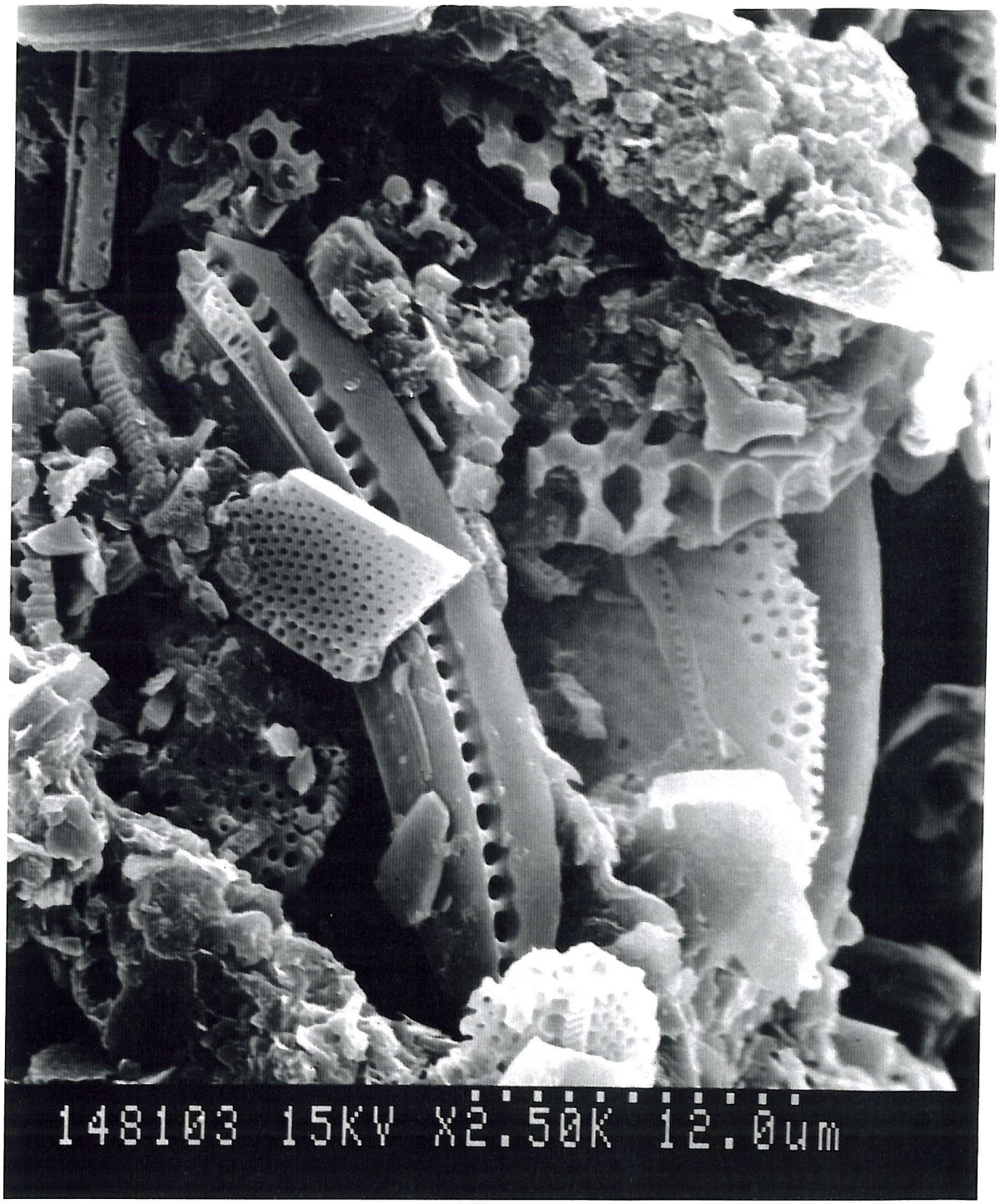


PLATE 6.17 *Ampelisca* sp nov GUT CONTENTS - JANUARY

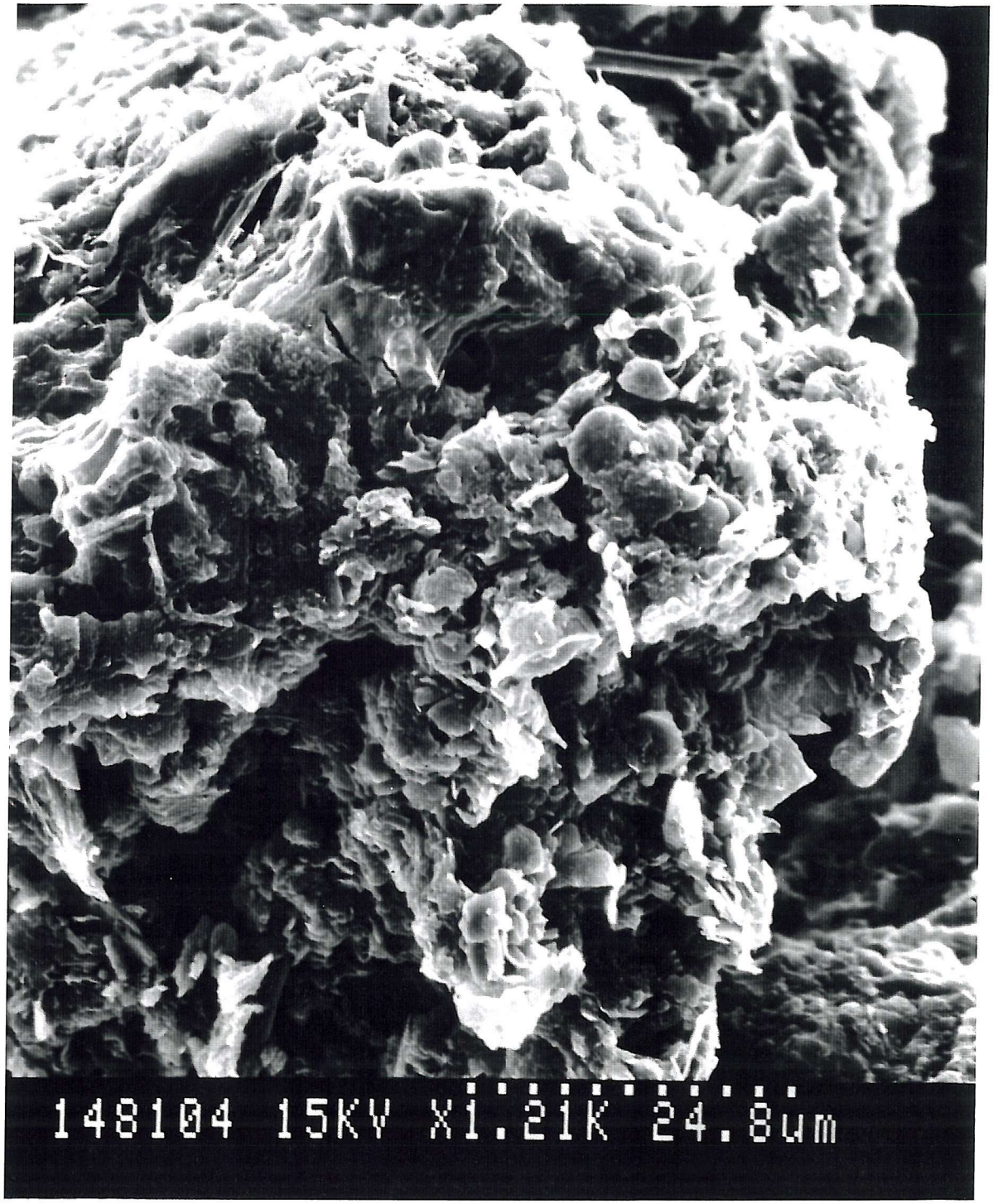


PLATE 6.18 *Ampelisca* sp nov GUT CONTENTS - JANUARY

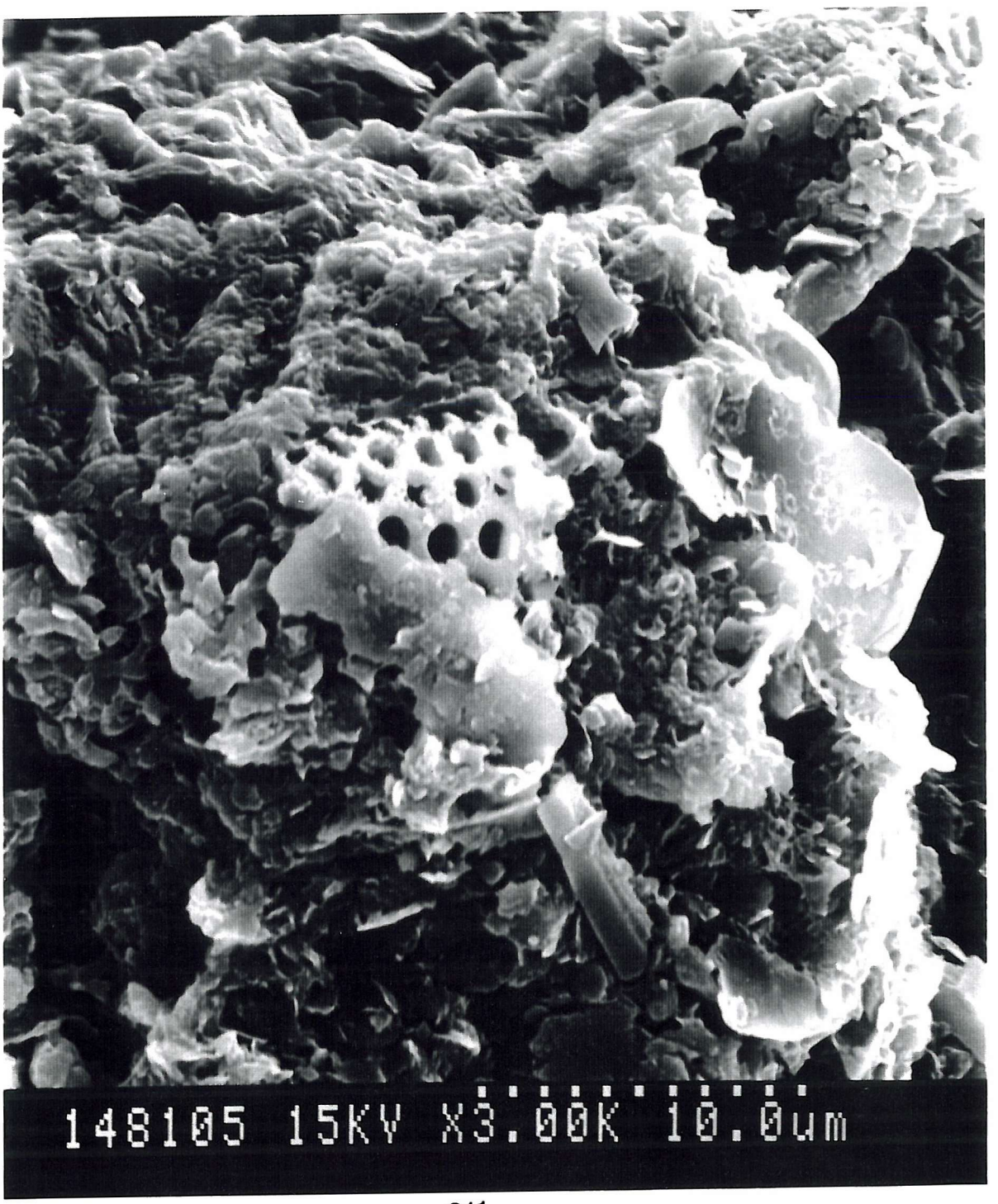


PLATE 6.19 *Ampelisca* sp nov GUT CONTENTS - SEPTEMBER

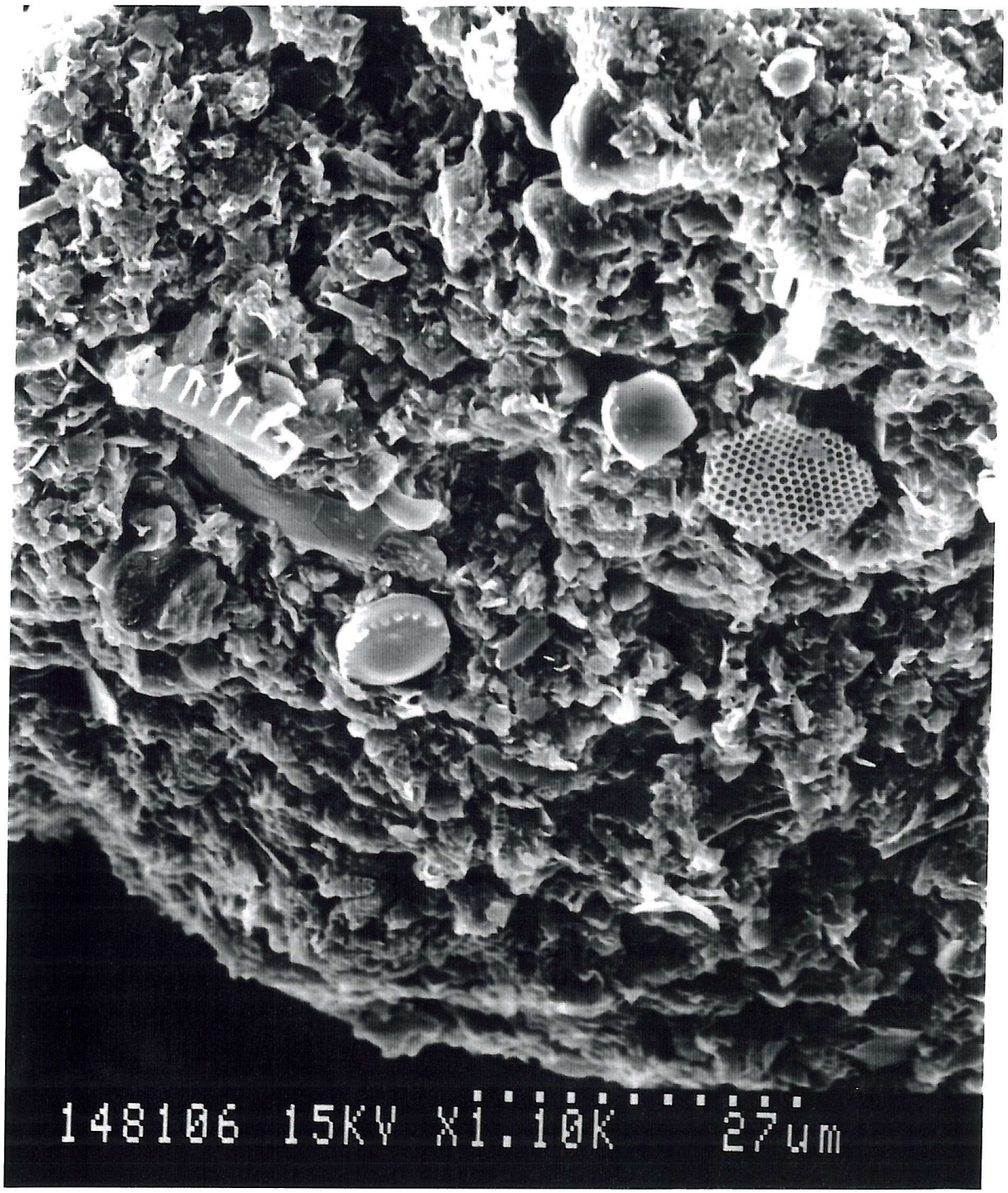
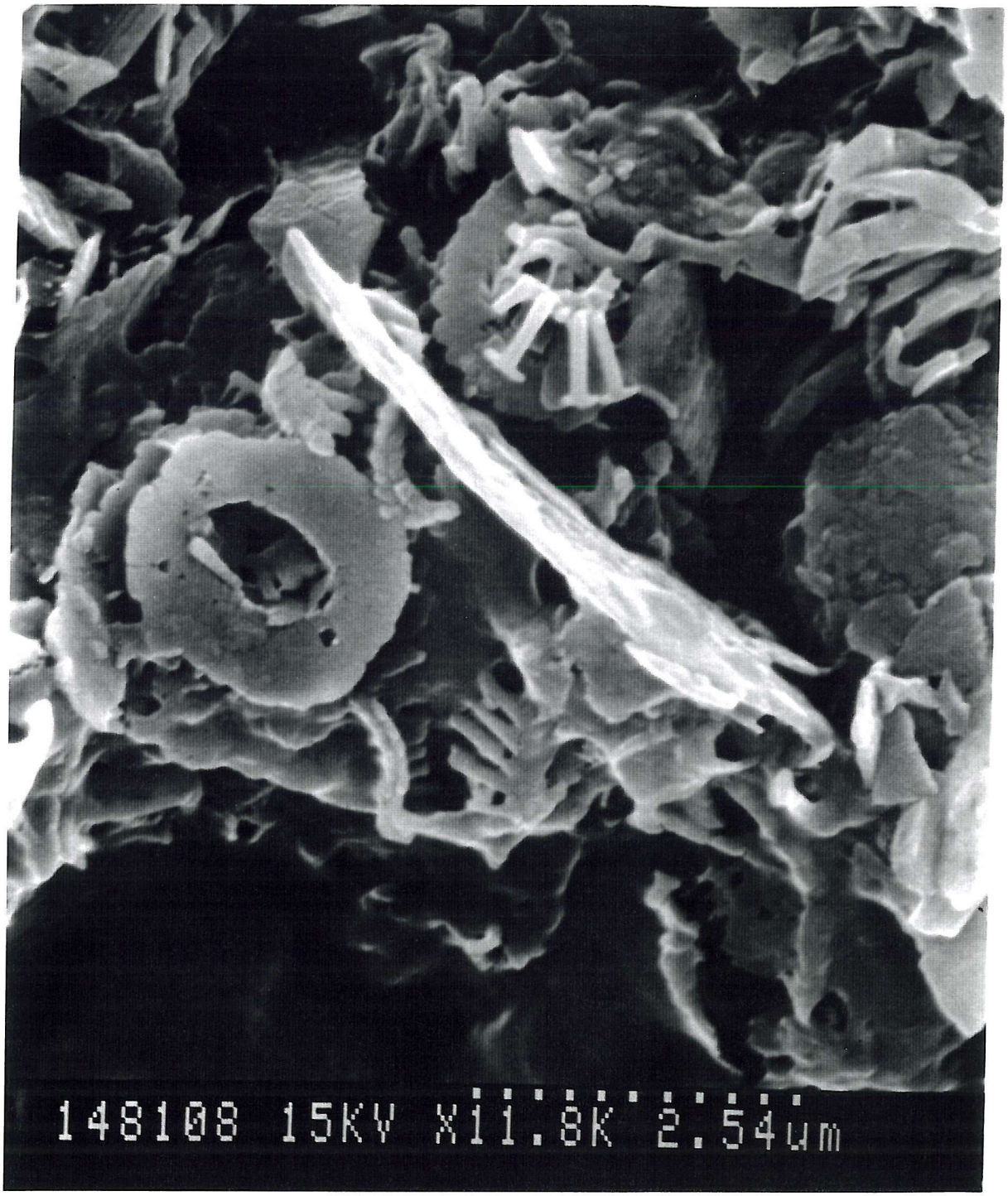


PLATE 6.20 *Tryphosella biloba* GUT CONTENTS - APRIL



6.3.4 Discussion

The link between the seasonal flux of surface derived phytodetritus and seasonal growth and reproductive processes in the NE Atlantic has for the most part been based on circumstantial evidence (Tyler *et al* 1982, Rice *et al* 1986, Tyler 1988). Only two previous studies have undertaken systematic examinations of the gut contents from species in a time series from the deep-sea (Campos-Creasey *et al* 1994). The first of these studies examined gut contents of ophiuroids from various depths in the Rockall Trough, they proved to be unselective omnivores that ingested phytodetritus irrespective of their reproductive mode (Pearson and Gage 1984). The second concerned the echinoid *Echinus affinis*, and showed evidence of a relationship between the echinoderm's diet and deposition of phytodetritus (Campos-Creasey *et al* 1994). Although these data was for a different time-series station to that of this study, both were from the Rockall Trough, and evidence from continuous plankton records indicate the surface production cycle is very similar for both sites (Colebrook 1986). *E. affinis* showed an increase in the total amount of material in the gut coincident with the deposition of phytodetritus (Campos-Creasey *et al* 1994)

Photographs of the stomach contents of *Ampelisca* sp nov reveal a clear difference in the colour between January, April and September (Plate 6.8). The enriched organic content of phytodetritus, coupled with residual photosynthetic pigments is likely to cause the dark colouration observed in the April specimens. This is less pronounced in the September specimen, but is still clearly different in appearance to the January specimen. This would seem to be indirect evidence of the consumption of phytodetrital material. Graphs of the gut index derived for *Ampelisca* sp nov show a clear seasonal variation. An increase in the relative fullness of *Ampelisca* sp nov guts is coincident with the arrival of phytodetritus to the sample region. The index seems to show a decline in the late summer and autumn, reflecting the reduced detrital input to the seabed at this time. The variation in the amount of material in the guts of males appears to show some disparity with that observed for females and juveniles. This is even more evident when the variation in percentage of animals with full guts is examined (Figure 6.2). Males appear to have a greater percentage of full guts earlier in the year, and

reach a higher maximal percentage in June. Possible causes could be as follows : 1. Males are more active swimmers than females and juveniles (Borowsky and Aiken-Ander 1989), this would increase the foraging range, and possibly enhance encounters with concentrated patches of phytodetritus. However, as mentioned in the introduction ampeliscids seem to feed whilst residing in tubes. 2. Females and juveniles rapidly utilise the food to fuel vitellogenesis and growth respectively. 3. Mature males of many amphipods have long antennae compared to females, this is a secondary sexual characteristic. Longer antennae will increase the foraging area around the individuals tube, and trap more suspended material. The small volume of material in the juvenile guts could be a function of reduced foraging efficiency, small effective foraging area (short antennae), competition with adults for food, or the utilization of lecithotropic resources for initial growth. Males, females and juveniles show a rapid decline in the percentage of full guts between June and September (Figure 6.3). The input of detritus to the sea floor is much reduced in late summer/autumn, and a large proportion of the deposited material will have been remineralized or buried. The reduced gut contents evident for the winter months indicate a much reduced feeding rate for *Ampelisca* sp nov. This species therefore seems likely to have some ability to store energy, possibly in the form of lipids as reported for the amphipod *Monoporeia affinis* (Johnson and Wiederholm 1992).

The presence of nematodes was noted in the body cavity of several amphipods in this study. The worms were not found in the gut and so were presumed to be parasitic rather than a prey item. There is an absence in the literature of reports referring to nematodes infecting deep-sea amphipod hosts. The larva of the parasitic nematode *Pseudoterranova decipiens* (sealworm) was reported in the amphipod *Americorchestia megalopthalma* (Marcogliese 1993) and the amphipod *Amphiporeai virginiana* (Marcogliese 1993b). These amphipods form intermediary hosts for this parasite whose definitive hosts (seals) are found in close vicinity to the habit of intertidal amphipods. The larvae of the fish parasite *Cystidicola* sp are carried by the amphipod *Pallisiella quadrispinosa* (Hill *et al* 1990). Whether deep-sea amphipods are intermediary or determinate hosts for the nematodes observed in this study is

impossible to discern without the identification of the species of nematode involved.

Gammaridean amphipods are primarily omnivorous, feeding on debris and detritus, carrion and dead plant fragments. The basic mandible seems to be adapted to biting off chunks with the incisors and grinding those chunks with molarial rasp. The lack of emphasis on herbivorous habits of gammarids in the literature is surprising in view of the properly adapted mandibles and the strong infestation of marine plants by amphipods (Barnard and Karaman 1991). Watling (1993) noted the degree of mandible modification in various amphipod families, and arranged them into four groups I. basic mandible is maintained with only minor modifications in all genera II. most genera possess the basic mandible, but one or two have modified mandibles III. the basic design is maintained in only one or two genera, but several modifications are seen in the others IV. the basic form can no longer be seen in any of the constituent genera. *Ampelisca* sp nov belongs, along with the rest of the Ampeliscidae in group I, whilst *T. biloba* and *Concarnes* sp nov are from families placed in group III. The mandible modifications in ampeliscids are minor, commonly involving change in shape and size of the mandibular palp articles, number of lifting spines, and the strength of the lacinia mobilis on one of the mandibles. The species of group I. families are primarily generalist microphage feeders, whose food source is organic particles in the sediment. The incisors are used in conjunction with the tips of maxilla 1 endites, to capture 'clumps' of particles which are crushed when passed between the molars. The micrograph in Plate 6.11 shows *Ampelisca* sp nov has a mandible similar to the basic mandible design. Typically in the *Ampelisca* genus article two of the palp is thickened compared to articles one and three, this does not appear to be the case for *Ampelisca* sp nov. Plate 6.12 shows the strongly dominant lifting spines and large triturative molar showing a toughened non-setose grinding surface. The morphology would seem to suggest a generalist microphage feeder, with crushing molars and a robust lifting spines to prevent escape of particles. The heavily sclerotized and ridged molar and well developed incisor process will aid in the grinding of particulate material or scraping organic material from sand grains. Similar morphology is reported for the ampeliscid

A. abdita (Mills 1967). The remaining two species belong to the Lysianassidae, a family reported by Watling (1993) to be second only to the Iphimediidae in the changes that have been made to the form of the mandibles. Most mandible modification in this family appears to be a response to a shift in feeding strategy to predation and/or scavenging. The mandibles of both *T. biloba* and *Concarnes* sp nov show such adaptations. Plates 6.12 and 6.13 show the absence of lifting spines, and the change in orientation of the incisor. The incisor is wide in comparison with the basic pattern, and bears no teeth. It seems adapted to a cutting/shearing function, and its orientation would mean such a cutting action would occur obliquely rather than in the horizontal plane. The function of the three clearly defined pores or holes on the molar surface can only be guessed at (Plate 6.13). They may be chemosensory structures to 'taste' the food particles, or perhaps enzyme release sites for pre-ingestion lubrication or digestion of food. The form of the mandible in *T. biloba* would suggest a scavenging or omnivorous lifestyle. *Concarnes* sp nov shows a similar loss of lifting spines but a smaller change in orientation of the incisor. The incisor again lacks teeth, but does not show the same degree of elongation into a cutting 'blade' like form. The molar is, however, different to the previously described species, with a much reduced triturative area. The palp has well developed setae on the third article, possibly with a chemosensory function. The morphology of the mandible in *Concarnes* sp nov would seem to suggest a predatory/scavenging lifestyle, with a molar unsuited to grinding plant material. Trap experiments however show it is attracted to, and feeds on , macrophyte debris. This would suggest this species is an opportunistic omnivore. Scanning electron micrographs of the gut contents of *Ampelisca* sp nov, reinforce the evidence from gut indices, that this species feeds on the seasonal deposition of phytodetritus to the Rockall Trough. Remains of pelagic diatoms are clearly recognizable in the gut contents from April and September. They belong to the *Thalassiosira* and *Chaetoceros* genera, and fragments of *Thalassionema* sp also appear in the April sample. These diatoms were found by Campos-Creasey *et al* (1994) in the guts of *E. affinis*, along with remains of a wide variety of phytoplanktonic and protozoan material. The gut contents of *Ampelisca* sp nov do not exhibit the same

range of material. This would seem to confirm the observation of Coyle and Highsmith (1994), that members of the genus *Ampelisca* feed mainly on diatoms. *Ampelisca* sp nov may feed primarily on settling or re-suspended particulate material, thus the range of protozoans reported by Campos-Creasey *et al* would not be ingested. The diatoms identified in the gut of *Ampelisca* sp nov matches those found in samples of the phytodetritus taken in the Porcupine Seabight (Rice *et al* 1986). The micrographs of September gut contents reveal a similar composition to those of April. However, the abundance of ingested material seems lower, although this cannot be quantified. Examination of the gut contents in January, shows an even greater disparity in the abundance of diatom fragments and ingested material in general. The fragments of diatoms seem 'degraded' in comparison with those from April and September (Plate 6.18). This may indicate the utilization of sparse detrital material in winter months left after the seasonal depositional period, in which the process of remineralization has already started. In contrast to the gut contents of *Ampelisca* sp nov, *T. biloba* contents do not contain any where near the same number of diatom fragments. Ingested phytodetrital material is sparse and consists mainly of liths from the coccolithophore *E. huxleyi* (Plate 6.20) (Dr. D Purdie pers comm). This phytoplankton species is known to form spring blooms in surface waters overlying the study area. *T. biloba* may thus utilize a different fraction of the detrital input than *Ampelisca* sp nov. The lack of adult specimens with gut contents in sufficient quantity to sample is curious. The abundance of *T. biloba* in the samples of this study seem to suggest it is a epibenthic species, and not merely an accidentally sampled pelagic population. So the absence of feeding adults would not be explained by a pelagic feeding guild, as reported for other scavenging lysianassids. The structure of its mandible suggested a scavenging diet, perhaps indicating it supplements its diet with phytodetrital material. The majority of adults caught were females, and lysianassid females are often reported to undergo a severe constriction of the gut by large gonads and invasive brood (Sainte-Marie 1987, Sainte-Marie *et al* 1989) and reduced attraction to bait/food (Bregazzi 1972). This may explain the lack of feeding adults in *T. biloba* which, as reported in Chapter Five, have a large embryo diameter in relation to body length.

6.4 GENERAL SUMMARY OF CHAPTER SIX

Attraction of scavenging lysianassids to traps baited with macroalgae, in preference to inert controls, demonstrate that macrophyte food falls represent an important energy resource to the food-poor deep-sea. The ingestion, and probable fragmentation of this macroalgae material by amphipods will increase rates of leaching and microbial degradation (Harrison and Mann 1975, Robertson and Mann 1980). The action of scavenging lysianassids will therefore play a key role in the supply of particles for detritivores, and help maintain a high efficiency of energy transfer through the deep-benthic community.

Although macrophyte food falls may contribute to the organic carbon input to the Rockall Trough, by far the most important source of energy is the seasonal input of surface-derived phytodetritus. Studies were made of the amount, and composition of ingested material in the guts of *Ampelisca* sp nov, and reinforced by an analysis of the functional morphology of mouthparts. The results revealed that seasonally deposited phytodetritus to the sample site comprised the diet of this deep-sea amphipod. The amount of ingested material showed a seasonal variation, and is the first report of seasonality in the diet of a deep-sea peracarid. Although surface derived material was found in the guts of *T. biloba*, it did not seem to form a major part of the diet of this species. The lack of a seasonal component in the feeding biology of this species may indicate a scavenging and/or omnivorous diet, a conclusion supported by the morphology of its mandible.

Although it is a generally accepted hypothesis that pelagic detrital pulses of autochthonous material drive seasonal growth and reproductive cycles in the deep-sea benthos, evidence is equivocal. Support for this hypothesis came from the coupling of vertical flux in phytodetritus to the diet and seasonal life history of the deep-sea echinoid *E. affinis* (Campos-Creasey *et al* 1994). Johnson and Wiederholm (1992) showed firm evidence that *Monoporeia affinis* populations are intimately coupled with pelagic-diatom production in Lake Vänern, Sweden. They showed for example year class 0 amphipod abundance and total body length were significantly related to the

interannual variability of spring diatom biovolume. Johnson and Wiederholm (1992) predict low metabolism, together with an ability to store energy in the form of lipids are two factors that may be necessary for a strong coupling between the unpredictability of a spring diatom production and invertebrate life history. Hence a strong pelagic-benthic coupling might be expected in a relatively deep (cold), nutrient poor (oxygen rich) system (cf Gardener *et al* 1990). The deep-sea could be described as just such a system, and the low gut index and apparent cessation of feeding by *Ampelisca* sp nov in winter would indicate possible storage mechanisms.

CHAPTER SEVEN
GENERAL DISCUSSION

Two thirds of the earths surface is covered by water, ninety percent of which is two kilometres or more in depth. The deep benthic environment can justifiably be said to comprise the most typical environment, and its inhabitants, the most typical lifeforms on the planet (Gage and Tyler 1991). The deep-sea is recognized as an important part of the global carbon budget and the repository of a unique and diverse fauna. The summed benthic metabolism over the vast area of the deep ocean may be significant with respect to global-scale carbon equilibria between the atmosphere, land and oceans (Gage 1992). It has been suggested (Grassle 1994), that deep-sea communities may be an ideal place to study community dynamics. The relative absence of physical disturbance over vast expanses allowing the persistence of natural or experimentally induced manipulations of structure or food inputs. However, much of the present knowledge about the deep-sea comes from quantitative samples representing less than 0.5 km^2 of the total area of the deep-sea floor below 1000 km depth, estimated at *ca* 3 x 10^8 km^2 (Gage *et al* 1995).

In 1973 the Scottish Marine Biological Association began a long-term sampling programme in the deep NE Atlantic. A permanent bottom station was established at 2900m in the southern Rockall Trough. Regular sampling at this station, at approximately four monthly intervals, took place between June 1976 and 1983, periodic sampling continues to date. This thesis examined the life-history biology of deep-sea gammaridean Amphipoda, these peracarid crustaceans formed a significant part of the collections from this programme. Following sorting, twenty three samples produced five thousand and thirty four specimens representing seventy eight species. Amphipods comprise three and a half percent of the total fauna of the Permanent Station. This figure is very close to that reported for an area just north of the sampling station (Gage 1979). The average number of species per sample was twenty four, over seventy five percent of the collection is accounted for by thirteen species, conversely twenty nine species make up only one percent of the collection.

There is a seasonal influx of surface-derived phytodetritus to the seabed in the Rockall Trough, the nutritional quality and timing of which may be important factors affecting abundance, structure and activity of the benthos (Billett *et al* 1983). There is mounting evidence to suggest that deep-sea invertebrates from the Rockall Trough exhibit seasonal growth and reproductive cycles that show a temporal relationship with this vertical flux (Campos-Creasey *et al* 1994 and references therein). An attempt was made to investigate the impact of this seasonal deposition of phytodetritus on the life-history biology of the amphipods collected from the Rockall Trough. The perennial problems in deep-sea studies of low sample numbers and poor temporal coverage required the pooling of samples from the same month but different years to form a representative year. For any significant conclusions to be drawn from such an approach, each sample must be representative of the Permanent Station amphipod community. A faunal analysis of samples was undertaken in terms of species richness, species absence/presence and percentage composition of each sample. Multivariate analysis performed on the percentage composition of each sample by species revealed the twenty three samples appear to come from one statistical population. Two of the more common species were chosen to study in detail their population, reproductive and feeding biology. The first of these, *Ampelisca* sp nov, belongs to a genus whose species comprise tube dwelling microphagous detritivores. The choice of this species was influenced in part by its assumed feeding method. Ampeliscids are suspension feeders, lying with their ventral side uppermost at the tops of their tubes, creating feeding currents with their antennae and pleopods. They feed on diatoms in the water column or alternatively resuspend organic material from the seabed with their long antennae (Coyle and Highsmith 1994). The amount of food available is thus limited to organic matter within reach of their antennae, and ampeliscids are reliant on environmental conditions to bring food to it. *Ampelisca* sp nov is therefore likely to be affected by the seasonality in the input of phytodetrital material to the seafloor. *T. biloba* was the second species chosen for two reasons, the first was the observation during initial sorting of the presence of brooding females, a rare condition in the other amphipods captured. Secondly it belongs to the lysianassid family, whose members are

strong swimmers with a presumed scavenging feeding strategy and thus a contrasting life style to that of *Ampelisca* sp nov.

Studies on the population biology of *Ampelisca* sp nov revealed allometric growth in adult head and pleon lengths, with differences between males and females. Total length increased geometrically, the observable size groups for this species occupied narrow length ranges and between-group ratio values were similar to those Thurston (1979) took to be indicative of instars rather than year classes. Analysis of oocyte developmental stage for *Ampelisca* sp nov revealed the presence of all six stages throughout the year. This apparent lack of seasonal reproductive activity explaining the absence of year classes in the population data for this species. *Ampelisca* sp nov did, however, exhibit a seasonal increase in reproductive intensity, with a corresponding influx of juvenile recruits to the population in the summer months. *T. biloba* showed a similar increase in the percentage of juveniles recruited to the population in the summer. Reproductive studies for *T. biloba,* in contrast to *Ampelisca* sp nov, showed a clear pattern in reproductive activity. Females of this species contain a larger percentage of late stage oocytes between May and August, than other months of the year. There is a dramatic fall in the percentage of brooding females between June and October, with a corresponding increase in percentage of ovigerous females. The timing of oocyte production in *T. biloba*, the increase in reproductive intensity of *Ampelisca* sp nov, and the release of juveniles by both species, all coincide with the seasonal influx of phytodetritus to the sampling site. Brood size and embryo diameter were both positively correlated with female length for both species. *Ampelisca* sp nov and *T. biloba* have, in common with other species in this study, smaller brood sizes and larger embryo diameters than would be predicted for a shallow water amphipod of similar size. This apparent decrease in fecundity and reproductive effort may result from food limitation in the deep-sea. This may be compensated for in part by production of large embryos. This increased investment of energy may benefit survival of juvenile deep-sea amphipods, larger hatchlings can compete better for limited food resources. The almost fourfold increase of embryo volume during development for *Ampelisca* sp nov, together with the large size of *T. biloba* embryos in relation to its body length/volume

would seem to require a labile and high energy food source. Rice *et al* (1986) analysed samples of phytodetritus from the Rockall Trough and showed it contained short chain molecules and polyunsaturated fatty acids. This detrital material is also enriched as a food source by colonizing bacteria, flagellates and foraminifera (Lochte and Turley 1988, Gooday 1988, Gooday and Turley 1988). Seasonal input of phytodetritus may therefore act as an energy source for previtellogenesis/vitellogenesis and/or a food resource for newly released juveniles. An index of gut fullness for *Ampelisca* sp nov revealed seasonal variations in the amount of ingested material. The pattern reflected that of the input of phytodetritus to the region. Low gut indexes in the winter months, an increase in April as the detrital material first reaches the seabed, followed by a rise to a maximum in June. This is the period of maximal detrital input and the percentage of 'full' guts also shows a maximum in June. A decline in gut indices to minimal values in late autumn and winter reflects the decline in detrital input from surface waters. Scanning electron images of the gut contents in *Ampelisca* sp nov show it is definitely feeding on this detrital material. Identifiable diatom fragments in the guts, match those observed in the phytodetrital samples analysed by Rice *et al* (1986). Gut contents show similar temporal patterns to gut indices, more diatom material is present in pictures from samples collected in April, than September. There is virtually no phytoplankton debris in the January samples, and what is present appears very degraded. There are no gut index data available for *T. biloba,* and very limited gut content information. Samples from April for this species do contain liths from the pelagic coccolithophore *Emiliania huxleyi*. Inferences from morphological studies on the mandible for *T. biloba* suggest a scavenging and/or omnivorous diet. This species may supplement its diet with phytodetrital material but also utilize other food resources which were not revealed by the analyses employed in this study. Reduction in feeding caused by physical constraints on the gut by developing ovaries or broods in adult females may also explain the lack of suitable specimens for study. Morphological studies on the mandible of *Ampelisca* sp nov reveal it is well suited for grinding up phytodetrital material, the strong lifting spines keeping particles in contact with the triturative molar. Experimental studies carried out during a submersible cruise to the Bahamas, looked at

the effect of another important food source to the deep-sea, macrophyte food falls. They were part of an ongoing study of the ecology of deep-sea invertebrates at bathyal depths off the Bahamas (Young *et al* 1989, 1992, Tyler *et al* 1992). Traps designed to attract and retain small mobile invertebrates were baited with macrophyte material and inert controls (Lawson *et al* 1993). On retrieval they were found to contain scavenging lysianassid amphipods. Significantly more amphipods were attracted to the traps baited with macrophyte debris than the inert controls. This observation coupled with the evidence that the amphipods had consumed the bait, indicated the amphipods were attracted to the macrophyte debris as a food resource. Previous studies had described the utilization of this material as a shelter by deep-sea amphipod species (Wolff 1979). The ingestion, and probable fragmentation of this macroalgae material by amphipods will increase rates of microbial degradation. This will increase the number of particles available for other detritivores and help maintain the transfer of nutrients and energy in the deep benthic community.

The traditional view of the deep-sea floor was of a food poor environment, where life proceeded at slow, steady rates. A number of recent discoveries indicate, however, that physical disturbances may be relatively frequent, and that pulses of food reach the seafloor from the upper ocean. The biological processes driven by these events can be highly variable in space and time, exhibiting disequilibrium dynamics (Smith 1994). Despite ignorance of the ecology of the highly diverse, but poorly described fauna of the deep-sea, pressure is mounting for exploitation of its mineral resources and use of its vast areas for waste dumping (Gage 1991). To properly assess the possible impacts of such activity in the deep-sea we need a better understanding of its biological processes. Although it is a generally accepted hypothesis that pelagic detrital pulses of autochthonous material drive seasonal growth and reproductive cycles in the deep-sea benthos, the transfer efficiency and degree of energetic coupling are unclear. The coupling of vertical flux in phytodetritus to the diet of and seasonal life history of the deep-sea echinoid *E. affinis* was reported by Campos-Creasey *et al* (1994). However, whilst seasonal reproduction has been reported in a number of deep-sea invertebrates,

control of these cycles is not necessarily related to surface-derived fluxes (Tyler *et al* 1994). Johnson and Wiederholm (1992) showed firm evidence that the amphipod *Monoporeia affinis* populations in Lake Vänern, Sweden are intimately coupled with pelagic diatom production. These authors predict low metabolism, together with an ability to store energy in the form of lipids are two factors that may be necessary for a strong coupling between the unpredictability of a spring diatom production and invertebrate life history. A strong pelagic-benthic coupling might be expected in a deep, cold, nutrient poor, but oxygen rich system (Johnson and Wiederholm 1992, cf Gardener *et al* 1990). The deep-sea represents just such a system, and Campos-Creasy *et al* (1994) suggest that *E. affinis* may use its stomach wall as a storage organ in addition to the gonads, to supply energy during the winter months. *Ampelisca* sp nov shows a reproductive and feeding response to the flux of detritus in the summer, yet reduced levels of feeding activity during the winter months. This may indicate a possible storage of the energy derived from the summer flux, for maintenance metabolism in the winter.

This study is the first report of convincing evidence for seasonal variations in reproductive and feeding biology of deep-sea gammaridean Amphipoda. The amphipods in this study form a significant portion of the fauna of the Permanent Station. There is an apparent coupling of their life history processes to surface production via a feeding response to the flux of detrital input to this region. The re-suspension and redistribution of this material through feeding activity, its mineralization, and subsequent production of faecal pellets may have an important structuring effect on the benthic community in this region.

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APPENDIX 3.1 PERCENTAGE COMPOSITION OF SAMPLE BY SPECIES

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Sp.	ES2	ES6	ES27	ES55	ES56	ES59	ES111	ES118	ES129	ES135	ES137	ES140	ES143	ES147	ES152	ES164	ES169	ES172	ES180	ES185	ES190	ES204	ES231
1	8.6957	11.4	1.5842	3.226	3.8462	0	0	0	0.72202	1.3636	0.55249	0.56818	2.2989	0.41667	6.0606	1.0638	0	0	0	0	0.6135	0	0.99297
3	0	3.18	1.5842	51.613	1.2821	5.5556	8.6957	0	2.1661	3.1818	2.7624	3.9773	2.2989	2.2917	6.0606	2.1277	6.25	2.3952	3.3019	3.0797	3.0675	1.2048	5.2958
4	4.3478	0	0	0	0	0	0	0	0.36101	0	0.82873	0.56818	0	0.20833	0	0	0	0	0	0.36232	0	0	0
5	0	2.02	4.7525	0	1.2821	1.1111	0	0	0.36101	3.6364	0.55249	1.1364	0	0.83333	1.5152	1.5957	6.25	3.5928	1.4151	1.8116	0.6135	0.80321	0
6	0	0.289	3.1683	0	6.4103	2.2222	0	0	1.8051	1.8182	1.6575	1.1364	1.1494	2.2917	4.5455	1.0638	0	2.3952	2.8302	2.1739	1.5337	0.40161	0.99297
7	4.3478	0	34.059	9.677	10.256	4.4444	8.6957	25.862	6.8592	7.7273	11.05	9.6591	11.494	11.875	25.758	20.213	12.5	26.946	26.887	19.203	20.859	18.474	25.486
8	0	0.289	0	0	0	1.1111	0	0	0	0.45455	0	0	0	0.83333	0	0	0	0	0	0.72464	0	0	0
9	0	1.59	0.79208	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.18116	0	0	0
10	17.391	1.88	8.7129	0	5.1282	2.2222	0	1.7241	2.1661	0.90909	2.4862	2.2727	0	6.6667	7.5758	4.7872	0	2.3952	1.4151	3.2609	0.30675	2.008	1.324
11	26.087	6.65	0	9.677	5.1282	1.1111	0	0	0.72202	0.90909	0.82873	2.2727	0	0.41667	3.0303	3.1915	0	0.5988	2.3585	1.087	0	0	0.66198
12	0	0.145	0	0	0	0	0	0	0	0.45455	0	0	0	0	0	0.53191	0	0	0	0.36232	0	0	0
13	0	0	1.5842	0	0	0	0	0	0	0	0	4.5455	0	1.0417	0	0	0	0	0	0.72464	0	0.80321	0
14	26.087	6.79	6.3366	3.226	2.5641	10	0	0	2.1661	1.3636	3.0387	4.5455	0	0.83333	1.5152	0	0	0	0.4717	0.18116	0	0.40161	0
15	0	0.145	0	0	0	0	0	0	0	0	0.27624	0	0	0	0	0.53191	0	0	0	0.18116	0	0	0
16	4.3478	0.289	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0	1.3	0.79208	0	6.4103	4.4444	8.6957	1.7241	5.0542	5.4545	0.55249	1.7045	9.1954	2.0833	3.0303	2.6596	18.75	1.1976	5.1887	4.529	5.5215	4.4177	3.6409
18	0	11.3	0.9901	6.45	6.4103	7.7778	8.6957	8.6207	7.2202	7.2727	4.9724	5.1136	34.483	2.5	12.121	12.234	0	14.371	13.208	7.6087	4.908	4.8193	5.9578
19	0	1.59	3.1683	3.266	5.1282	0	4.3478	5.1724	1.8051	2.2727	0	1.1364	4.5977	1.0417	6.0606	2.1277	0	6.5868	1.8868	1.2681	0.30675	3.2129	0.33099
20	0	0.434	0.79208	0	0	0	0	0	0	0	0	0	1.1494	0	0	0.53191	0	0.5988	0	0.36232	0	0.40161	0.33099
21	0	3.76	8.7129	0	3.8462	0	4.3478	0	8.3032	2.2727	5.8011	7.3864	0	2.0833	6.0606	8.5106	6.25	2.3952	5.1887	5.0725	3.681	1.2048	2.3169
22	0	2.31	2.3762	3.266	1.2821	10	8.6957	3.4483	2.8881	6.3636	2.4862	3.9773	3.4483	4.375	3.0303	7.9787	0	0.5988	2.3585	3.442	0	4.4177	2.3169
23	0	17.2	3.1683	0	19.231	30	26.087	31.034	38.628	21.818	53.039	23.864	6.8966	30.625	3.0303	7.4468	0	10.778	8.9623	11.594	41.718	35.743	39.388
24	0	1.16	0	0	0	0	0	1.7241	0	2.2727	1.9337	0	1.1494	4.375	0	0	0	0.5988	1.8868	0.36232	0.30675	0	0
25	0	3.47	0.79208	3.226	2.5641	0	0	1.7241	1.083	1.8182	0	3.4091	0	0.83333	0	1.0638	0	0.5988	0	1.4493	0	1.6064	0.99297

26	0	0.578	0.79208	0	2.5641	2.2222	0	0	0	0.45455	0	0	2.2989	0.20833	3.0303	0.53191	0	0	1.4151	1.8116	0	0	1.6549
27	0	0.145	1.5842	0	0	0	0	0	0.72202	0.45455	0	1.7045	0	0.625	1.5152	0.53191	0	0	0.4717	0	0	0.40161	0
28	0	0	0.79208	0	1.2821	0	0	0	1.444	2.7273	0	0	0	0	1.5152	0	0	0	0.4717	0	0	0	0
29	0	0	0.79208	0	0	0	4.3478	1.7241	0.72202	1.8182	0.27624	1.1364	5.7471	1.875	1.5152	2.1277	0	1.1976	2.3585	1.6304	3.681	2.008	1.6549
30	0	0	0.79208	0	1.2821	0	0	8.6207	2.8881	0.90909	0	0.56818	5.7471	1.0417	0	0.53191	12.5	2.3952	0.9434	0.54348	0	0	0
31	0	0	0.79208	0	0	1.1111	4.3478	1.7241	1.8051	0	0.27624	3.9773	0	5	0	1.0638	6.25	2.994	2.3585	6.3406	2.454	6.0241	0
32	0	0	0.79208	0	0	0	0	0	0	0	0	0.56818	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0.79208	0	2.5641	0	4.3478	0	0	0.45455	0	0	0	0	0	0	0	0	0.4717	3.0797	0	4.0161	0
34	0	0	0.79208	0	1.2821	3.3333	0	0	3.6101	4.5455	2.2099	1.1364	1.1494	4.7917	0	1.5957	0	1.7964	2.3585	1.4493	0.92025	2.4096	0.041374
35	0	0	0	0	1.2821	0	0	0	0	0	0	0	0	0.20833	0	0	0	0	0	0	0	0	0
36	0	0.578	0	0	0	2.2222	0	0	0	7.7273	0	0	1.1494	0.41667	0	2.6596	0	1.7964	0.9434	1.8116	1.5337	0	0
37	0	0	0	0	0	5.5556	0	0	5.0542	0	0.27624	7.3864	3.4483	6.4583	1.5152	2.6596	0	4.1916	3.7736	5.6159	0	0.80321	2.9789
38	0	0	0	0	0	0	4.3478	0	0	0	0.55249	0	0	0.20833	0	0	6.25	0	0.4717	0.54348	0.30675	0	0.33099
39	0	0.578	0	0	0	0	0	0	0.36101	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0.27624	0.56818	0	0	0	0	0	0	0	0	0	0	0
41	0	2.89	0	0	0	2.2222	0	0	0	0.45455	0.27624	0	1.1494	0	0	0	0	0	0	0	0	0	0
42	0	8.96	0	0	0	0	0	0	0	0.45455	0	0	0	0	0	0.53191	0	0	0.4717	0	0	0	0
43	0	0.145	0	0	2.5641	0	0	1.7241	0	0.90909	0	0	0	0	1.5152	0.53191	0	2.3952	0	0	0.6135	0.80321	0.33099
44	0	0	0.79208	0	0	0	0	1.7241	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0.79208	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	1.2821	0	0	0	0	0	0	0	1.1494	0.625	0	0.53191	0	1.7964	0.4717	1.087	0.6135	0.40161	0
47	0	0	0	0	0	0	0	0	0	0	0.55249	0	0	0	0	0	0	0	0	0	0.30675	0.40161	0
48	0	0.578	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12.5	0	0	0	0.30675	0	0
49	8.6957	5.49	1.5842	0	0	0	0	1.7241	0	1.8182	2.2099	1.1364	0	0.41667	0	2.6596	0	1.7964	2.8302	2.1739	1.8405	0.80321	1.6549
50	0	0	1.5842	3.226	2.5641	2.2222	0	0	0.36101	0.45455	0	0	0	0	0	0.53191	0	1.7964	2.3585	0.54348	0	0.40161	0.66198

51	0	1.45	0	0	0	0	0	0	0	0.45455	0	0	0	0	0	1.5957	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0.27624	0	0	0	0	0	0	0	0.4717	0.18116	0	0	0.66198
53	0	1.45	0	0	0	0	0	0	0	0.90909	0	0	0	0.20833	0	0	0	0	0	0	0	0	0
54	0	0.145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0.145	0	0	0	0	0	0	0.36101	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0.434	0	0	0	0	0	0	0	0	0	0	0	0	0	0.53191	0	0	0	0	0	0	0
57	0	0.145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0.145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0.145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0.145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	0	0	0.79208	0	0	0	0	0	0.36101	0	0	0	0	0	0	0	6.25	0	0	0	0	0.40161	0
62	0	0	0.79208	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0.79208	0	0	0	0	0	0	0	0	0	0	1.4583	0	0.53191	0	0.5988	0	0.9058	3.681	0	0
64	0	0	0.79208	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0.79208	0	0	0	0	0	0	0.45455	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0.90909	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	4.5455	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0.20833	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	1.7241	0	1.8182	0	0	0	0.41667	0	1.5957	0	0.5988	0	2.7174	0.30675	0.80321	0
70	0	0	0	3.226	1.2821	1.1111	4.3478	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	1.2821	0	0	0	0	0	0	0	0	0	0	1.0638	0	0	0	0.36232	0	0	0
72	0	0	0	0	0	0	0	0	0	0.45455	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0.45455	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.53191	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.25	0	0	0	0	0	0

76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5988	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.18116	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.40161	0
79	0	0	0	0	0	0	0	0	0	0	0	0	0.20833	0	0	0	0	0	0	0	0	0

APPENDIX 4.1 LENGTH DATA FOR *Ampelisca* sp nov and T *biloba*

Ampelisca sp nov

Female Length Data

Female Length Data						
0.682	4.72	5.1	5.47	5.74	6.07	6.62
3.05	4.75	5.11	5.49	5.75	6.07	6.63
3.35	4.76	5.13	5.5	5.76	6.07	6.65
3.69	4.76	5.16	5.51	5.77	6.08	6.69
3.82	4.79	5.17	5.53	5.77	6.08	6.74
3.9	4.79	5.17	5.53	5.78	6.08	6.76
3.98	4.81	5.18	5.53	5.79	6.09	6.81
4.04	4.81	5.2	5.55	5.84	6.1	6.82
4.04	4.83	5.23	5.56	5.84	6.11	6.88
4.07	4.86	5.26	5.56	5.85	6.15	6.9
4.14	4.86	5.27	5.58	5.85	6.15	6.93
4.16	4.89	5.27	5.6	5.89	6.21	6.99
4.29	4.89	5.27	5.61	5.92	6.23	7.03
4.33	4.92	5.29	5.61	5.93	6.25	7.05
4.34	4.92	5.29	5.61	5.95	6.27	7.18
4.37	4.93	5.29	5.61	5.95	6.28	7.2
4.42	4.93	5.3	5.62	5.96	6.35	7.37
4.43	4.96	5.31	5.64	5.98	6.37	7.41
4.44	4.97	5.36	5.66	5.98	6.39	
4.48	5.04	5.38	5.69	5.99	6.4	
4.52	5.05	5.39	5.69	6.01	6.47	
4.55	5.06	5.41	5.69	6.01	6.48	
4.56	5.06	5.42	5.7	6.02	6.52	
4.58	5.08	5.42	5.71	6.02	6.55	
4.58	5.08	5.44	5.71	6.04	6.58	
4.63	5.09	5.46	5.72	6.06	6.6	

Female Size Range Data									
Size	**Percent**	**Size**	**Percent**	**Size**	**Percent**	**Size**	**Percent**	**Size**	**Percent**
0	0	1.8	0	3.6	0	5.4	4	7.2	1
0.1	0	1.9	0	3.7	1	5.5	7	7.3	1
0.2	0	2	0	3.8	0	5.6	10	7.4	1
0.3	0	2.1	0	3.9	1	5.7	10	7.5	1
0.4	0	2.2	0	4	2	5.8	11		
0.5	0	2.3	0	4.1	3	5.9	7		
0.6	0	2.4	0	4.2	2	6	8		
0.7	0	2.5	0	4.3	1	6.1	13		
0.8	0	2.6	0	4.4	3	6.2	4		
0.9	0	2.7	0	4.5	4	6.3	5		
1	0	2.8	0	4.6	5	6.4	3		
1.1	0	2.9	0	4.7	1	6.5	3		
1.2	0	3	0	4.8	6	6.6	3		
1.3	0	3.1	1	4.9	7	6.7	5		
1.4	0	3.2	0	5	6	6.8	2		
1.5	0	3.3	0	5.1	8	6.9	4		
1.6	0	3.4	1	5.2	6	7	2		
1.7	0	3.5	0	5.3	9	7.1	2		

Ampelisca sp nov

Male Length Data

Male Length Data						
2.69	3.74	4.46	4.83	5.36	5.74	6.52
2.79	3.84	4.51	4.91	5.45	5.77	6.74
2.86	3.88	4.51	5.08	5.46	5.79	
3.12	3.95	4.54	5.15	5.48	5.86	
3.2	3.96	4.55	5.16	5.5	5.86	
3.24	4.18	4.55	5.17	5.54	5.92	
3.31	4.2	4.67	5.18	5.56	6.16	
3.49	4.22	4.79	5.19	5.73	6.34	
3.53	4.33	4.82	5.24	5.73	6.41	

Male Size Range Data									
Size	**Percent**	**Size**	**Percent**	**Size**	**Percent**	**Size**	**Percent**	**Size**	**Percent**
0	0	1.8	0	3.6	1	5.4	1	7.2	0
0.1	0	1.9	0	3.7	0	5.5	3	7.3	1
0.2	0	2	0	3.8	1	5.6	3	7.4	1
0.3	0	2.1	0	3.9	2	5.7	0	7.5	1
0.4	0	2.2	0	4	2	5.8	5	7.6	0
0.5	0	2.3	0	4.1	0	5.9	2	7.7	0
0.6	0	2.4	0	4.2	1	6	1	7.8	0
0.7	0	2.5	0	4.3	2	6.1	0	7.9	0
0.8	0	2.6	0	4.4	1	6.2	1	8	0
0.9	0	2.7	1	4.5	1	6.3	0		
1	0	2.8	1	4.6	5	6.4	1		
1.1	0	2.9	1	4.7	1	6.5	1		
1.2	0	3	0	4.8	1	6.6	1		
1.3	0	3.1	0	4.9	2	6.7	0		
1.4	0	3.2	1	5	1	6.8	1		
1.5	0	3.3	2	5.1	1	6.9	0		
1.6	0	3.4	1	5.2	5	7	0		
1.7	0	3.5	1	5.3	1	7.1	0		

Ampelisca sp nov

Juvenile Length Data

Juvenile Size Range Data					
Size	**Percent**	**Size**	**Percent**	**Size**	**Percent**
0	0	1.8	1	3.6	5
0.1	0	1.9	9	3.7	4
0.2	0	2	9	3.8	5
0.3	0	2.1	12	3.9	5
0.4	0	2.2	20	4	3
0.5	3	2.3	11	4.1	1
0.6	2	2.4	12	4.2	1
0.7	1	2.5	23	4.3	2
0.8	0	2.6	25	4.4	0
0.9	0	2.7	24	4.5	2
1	0	2.8	23	4.6	0
1.1	0	2.9	8	4.7	1
1.2	1	3	12	4.8	0
1.3	0	3.1	15	4.9	0
1.4	0	3.2	9		
1.5	0	3.3	9		
1.6	0	3.4	9		
1.7	2	3.5	4		

T. Biloba

Length Data

Length Data							
Month	**Female**	**Male**	**Juvenile**	**Month**	**Female**	**Male**	**Juvenile**
1	3.83			6	3.91		
1	3.88			6	3.92		
1	4.19			6	3.96		
2	3.01	2.69	2.53	6	4.01		
2	3.8	2.71	2.57	6	4.52		
2	3.9			7	3.11	2.83	
2	3.99			7	3.14	2.89	
2	4.18			7	3.38		
2	4.23			7	3.4		
2	4.57			7	3.6		
4	2.64	2.62	1.9	7	3.63		
4	2.75	2.66	2.22	7	3.65		
4	2.87	2.7	2.25	7	3.69		
4	3.07	2.7	2.9	7	3.71		
4	3.45	2.72	2.92	7	3.73		
4	3.58	3.01	3.13	7	3.78		
4	3.59			7	3.83		
4	3.62			7	3.84		
4	3.69			7	3.92		
4	3.78			7	3.93		
4	3.8			7	3.99		
4	3.87			7	4.05		
4	3.88			7	4.1		
4	3.95			7	4.21		
4	4.04			7	4.23		
4	4.1			8	1.6	1.74	1.58
4	4.27			8	1.64	2.2	2.13
4	4.35			8	2.03	2.31	2.56
4	4.59			8	2.18	2.56	
5	2.71	2.79	1.98	8	2.8	2.74	
5	2.82	2.82	2.61	8	2.84	3.13	
5	2.86	2.86	2.62	8	3.14	3.16	
5	3.07			8	3.33		
5	3.1			8	3.83		
5	3.16			8	3.84		
5	3.33			8	4.04		
5	3.46			9	3.04	1.95	2.31
5	3.6			9	3.73	3.28	
5	3.61			9	4.2		
5	3.63			10	3.83	1.96	
5	3.72			11	2.51	2.23	1.75
5	3.74			11	2.91	2.42	2.02
5	3.79			11	2.99	2.43	2.47
5	3.91			11	3.25		2.87
5	4.12			11	3.44		
6	3.28	2.26	1.47	11	3.51		
6	3.43	2.62	1.71	11	3.56		
6	3.73	2.72	1.97	11	3.91		
6	3.73	2.75		11	4.04		
6	3.78	2.76					

T. Biloba

Length Data

Size Range Data			
Size	**Female**	**Male**	**Juvenile**
0	0	0	0
0.25	0	0	0
0.5	0	0	0
0.75	0	0	0
1	0	0	0
1.25	0	0	0
1.5	0	0	1
1.75	0	0	3
2	2	1	3
2.25	0	2	4
2.5	4	2	2
2.75	2	4	5
3	3	12	2
3.25	8	7	1
3.5	9	3	0
3.75	10	1	0
4	20	0	0
4.25	26	0	0
4.5	14	0	0
4.75	2	0	0
5	3	0	0

APPENDIX 5.1 HISTOLOGICAL METHODS

APPENDIX 5.1
HISTOLOGICAL METHODS

WAX EMBEDDING

Samples were removed from Steedman's solution and rinsed in distilled water. Prior to dehydration a small incision was made in the integument to aid penetration of solvents and embedding media. Dehydration was achieved by passing specimens through a graded series of alcohol (50, 70, 90 and 100%), two changes of each, allowing an hour in each concentration.
Samples were cleared and placed in molten wax (56°C) overnight for embedding. Specimens were mounted on plastic blocks for sectioning, both longitudinal and transverse sections 0.7μm thick were obtained. These sections were floated onto slides using a water bath, dried and then cleared with histoclear. Sections were stained using Haemotoxylin and Eosin.

GLYCOL METHACRYLATE EMBEDDING (GMA)

The Sigma chemical company GMA kit for light microscopy was employed. Two solutions were prepared, i. Unpolymerized GMA, 100ml of GMA with 0.15g benzoyl peroxide and 5ml of polyethylene glycol, mixed thoroughly and stored in a brown glass bottle in a freezer. ii. Pre-polymerized GMA, 100ml of GMA with 0.15g benzoyl peroxide, the mixture is poured into an erlenmeyer flask in small amounts, and heated slowly over a bunsen with constant swirling. When solution begins to polymerise, indicated by a change in colour to yellow-orange, it must be immediately plunged into an ice water bath to prevent a violent exothermic reaction. When cooled it is allowed to return to room temperature, then 5ml of polyethylene glycol are added, mix well for an hour using magnetic stirrer and store in freezer.
Samples were washed in 85% aqueous GMA for 30 mins, then dehydrated as above. Tissue is then passed through an ascending series of ethanolic GMA solutions (20, 40, 60 and 80% GMA in ethanol), 30 mins in each. Tissue is then immersed in 100% unpolymerised GMA for 12 hours. Infiltrated tissue is then placed in pre-polymerized GMA in embedding capsules, and left to allow any air bubbles to escape. Capsules are then placed under ultra-violet light for 12-24 hours. Sections are made with a glass knife on an ultramicrotome, and placed on a slide with a drop of distilled water. Sections were cut between 5 and 7 μm thick, and stained as above, no clearing is required.

APPENDIX 5.2 REPRODUCTIVE DATA FOR Ampelisca sp nov

Ampelisca sp nov

Month	% setose	% ovigerous
Jan	60	66.6
Feb	75	80
Mar		
Apr	75	33.3
May	81.1	51.9
Jun	76.3	35.3
Jul	88.9	83.3
Aug	73.9	41.2
Sep	73.3	66.7
Oct	100	100
Nov	62.5	87.5
Dec		

Oocyte Stage	Jan	Feb	Mar	Apr	May	Jun	Aug	Sept	Oct	Nov
1	33.3	20	66.7	48.2	64.7	16.7	52.9	33.3	0	12.5
2	2	33.3	40	0	18.5	17.7	11.8	25	0	37.5
3	22.2	20	33.3	18.5	11.8	16.7	17.7	16.7	50	37.5
4	11.1	0	0	7.41	0	16.7	11.8	16.7	0	12.5
5	0	10	0	7.41	5.88	16.7	0	8.33	50	0
6	0	10	0	0	0	16.7	0	0	0	0

APPENDIX 5.3 REPRODUCTIVE DATA FOR T. *biloba*

sample	month	no. fem	length	no.of egg	area	leng x	leng y
6	7	13	3.93	2	0.174	0.573	0.381
6	7	13	3.93	2	0.152	0.561	0.361
6	7	13	4.05	1	0.195	0.615	0.433
6	7	13	4.21	1	0.158	0.522	0.429
6	7	13	3.92	1	0.352	0.894	0.454
6	7	13	3.4	1	0	0.935	0
6	7	13	3.6	1	0.235	0.671	0.44
6	7	13	3.83	1	0.252	0.626	0.466
6	7	13	3.65	1	0.243	0.72	0.361
6	7	13	3.71	1	0.167	0.517	0.34
6	7	13	3.99	1	0.136	0.488	0.327
6	7	13	4.1	1	0.169	0.537	0.394
6	7	13	4.23	2	0.175	0.65	0.356
6	7	13	4.23	2	0.209	0.599	0.44
6	7	13	3.84	2	0.252	0.626	0.466
27	7	13	3.84	2	0	0.801	0
55	11	1	4.01	1	0.141	0.47	0.398
55	11	7	4.04	2	0.149	0.531	0.343
55	11	7	4.04	2	0.125	0.481	0.34
55	11	7	3.91	2	0.101	0.454	0.362
55	11	7	3.91	2	0.115	0.47	0.353
55	11	7	3.25	1	0.138	0.596	0.339
55	11	7	3.44	1	0.165	0.592	0.383
55	11	7	2.99	1	0.148	0.514	0.388
55	11	7	3.51	1	0.154	0.521	0.387
55	11	7	3.56	2	0.141	0.533	0.309
59	11	7	3.56	2	0.138	0.448	0.319
59	6	2	3.73	1	0.171	0.55	0.406
111	6	2	3.73	1	0.111	0.403	0.283
111	10	1	3.83	2	0.126	0.459	0.345
129	10	1	3.83	2	0.103	0.454	0.237
129	4	1	3.59	2	0.143	0.512	0.349
135	4	1	3.59	2	0.103	0.47	0.255
137	8	1	3.84	1	0.136	0.495	0.339
137	2	5	3.99	2	0.163	0.598	0.353
137	2	5	3.99	2	0.136	0.539	0.403
137	2	5	3.9	2	0.109	0.464	0.355
137	2	5	3.9	2	0.158	0.521	0.43
137	2	5	3.8	2	0.165	0.558	0.461
137	2	5	3.8	2	0.116	0.555	0.326
137	2	5	4.18	2	0.146	0.599	0.328
137	2	5	4.18	2	0.138	0.57	0.328
137	2	5	4.23	2	0.168	0.544	0.392
140	2	5	4.23	2	0.149	0.501	0.413
140	4	3	3.62	1	0.273	0.651	0.409
140	4	3	3.69	2	0.152	0.555	0.383
140	4	3	3.69	2	0.162	0.542	0.379
140	4	3	3.78	2	0.192	0.582	0.4
143	4	3	3.78	2	0.224	0.618	0.428
143	4	2	4.59	2	0.274	0.815	0.443
143	4	2	4.35	2	0.203	0.603	0.4
147	4	2	4.35	2	0.159	0.54	0.371
147	6	5	3.91	2	0.129	0.453	0.319
147	6	5	3.91	2	0.139	0.551	0.356
147	6	5	3.92	1	0.168	0.512	0.453
147	6	5	3.96	2	0.183	0.589	0.359
147	6	5	3.96	2	0.193	0.578	0.356
147	6	5	4.52	2	0.148	0.551	0.321

sample	month	no. fem	length	no.of egg	area	leng x	leng y
147	6	5	4.52	2	0.171	0.701	0.382
147	6	5	3.78	2	0.283	0.566	0.621
152	6	5	3.78	2	0.236	0.823	0.304
152	1	3	4.19	2	0.149	0.647	0.42
152	1	3	4.19	2	0.239	0.715	0.44
152	1	3	3.88	2	0.325	0.626	0.641
152	1	3	3.88	2	0.27	0.602	0.659
152	1	3	3.83	2	0.219	0.664	0.458
164	1	3	3.83	2	0.267	0.652	0.533
169	8	1	4.04	1	0.288	0.642	0.51
169	2	1	4.56	2	0.13	0.386	0.422
172	2	1	4.56	2	0.124	0.379	0.362
172	5	2	4.12	2	0.253	0.456	0.56
172	5	2	4.12	2	0.204	0.513	0.446
172	5	2	3.91	2	0.237	0.657	0.44
180	5	2	3.91	2	0.234	0.705	0.454
180	9	2	4.2	1	0.184	0.542	0.433
185	9	2	3.73	1	0.207	0.581	0.428
185	8	8	4.1	2	0.161	0.458	0.344
185	8	8	4.1	2	0.12	0.443	0.36
185	8	8	4.27	2	0.175	0.523	0.362
185	8	8	4.27	2	0.132	0.456	0.326
185	8	8	3.8	2	0.13	0.589	0.345
185	8	8	3.8	2	0.108	0.51	0.292
185	8	8	3.88	1	0.189	0.556	0.45
185	8	8	3.88	1	0.145	0.428	0.394
185	8	8	4.04	2	0.165	0.509	0.44
185	8	8	4.04	2	0.161	0.517	0.448
185	8	8	3.87	1	0.185	0.552	0.371
185	8	8	3.58	1	0.142	0.468	0.324
185	8	8	3.95	2	0.238	0.612	0.486
190	8	8	3.95	2	0.114	0.419	0.345
190	8	2	2.84	1	0.121	0.37	0.386
190	8	2	3.33	2	0.101	0.437	0.302
204	8	2	3.33	2	0.129	0.445	0.235
204	5	3	3.1	1	0.0745	0.363	0.309
204	5	3	2.82	1	0.105	0.473	0.316
204	5	3	2.86	2	0.0799	0.364	0.295
231	5	3	2.86	2	0.0692	0.371	0.278
231	5	10	3.33	1	0.126	0.493	0.323
231	5	10	3.6	1	0.173	0.496	0.367
231	5	10	3.61	2	0.149	0.493	0.317
231	5	10	3.61	2	0.145	0.46	0.357
231	5	10	3.46	2	0.145	0.577	0.296
231	5	10	3.46	2	0.147	0.498	0.376
231	5	10	3.79	2	0.138	0.472	0.367
231	5	10	3.79	2	0.146	0.521	0.329
231	5	10	3.16	1	0.13	0.448	0.336
231	5	10	3.74	2	0.156	0.53	0.328
231	5	10	3.74	2	0.143	0.569	0.326
231	5	10	3.63	1	0.145	0.466	0.387
231	5	10	3.72	1	0.156	0.41	0.358
231	5	10	3.72	2	0.147	0.504	0.312
	5	10	3.72	2	0.162	0.523	0.322

leng z	volume	length	no of egg	vol big	vol other	volsingb
0.27	0.0974	3.93	2	0.0974	0.0763	0.0415
0.39	0.0763	3.93	2	0.0396	0.0316	0.041
0.294	0.0415	4.05	1	0.0278	0.0243	0.0845
0.27	0.041	4.21	1	0.0271	0.0241	0.0381
0.398	0.0845	3.92	1	0.0303	0.0252	0.0423
0		3.4	1	0.0234	0.0185	0.0437
0.247	0.0381	3.6	1	0.0172	0.0154	0.024
0.277	0.0423	3.83	1	0.0397	0.0353	0.022
0.321	0.0437	3.65	1	0.0285	0.0262	0.0431
0.261	0.024	3.71	1	0.0377	0.0328	0.0423
0.263	0.022	3.99	1	0.0383	0.0289	0.0313
0.389	0.0431	4.1	1	0.0356	0.0285	0.0289
0.261	0.0316	4.23	2	0.0397	0.0313	0.0349
0.287	0.0396	4.23	2	0.0575	0.0493	0.0287
0.277	0.0423	3.84	2	0.144	0.0813	0.0288
0		3.84	2	0.0444	0.0425	0.0357
0.319	0.0313	4.01	1	0.032	0.0202	0.0168
0.291	0.0278	4.04	2	0.0433	0.0386	0.0296
0.284	0.0243	4.04	2	0.039	0.0356	0.0528
0.314	0.0271	3.91	2	0.0742	0.0261	0.0517
0.277	0.0241	3.91	2	0.0811	0.0641	0.0829
0.273	0.0289	3.25	1	0.116	0.0968	0.0347
0.295	0.0349	3.44	1	0.0931	0.0898	0.032
0.275	0.0287	2.99	1	0.0301	0.0222	0.0326
0.273	0.0288	3.51	1	0.0554	0.0545	0.0219
0.35	0.0303	3.56	2	0.0651	0.0554	0.0265
0.336	0.0252	3.56	2	0.0287	0.0274	0.0123
0.305	0.0357	3.73	1	0.046	0.0276	0.02
0.282	0.0168	3.73	1	0.035	0.0211	0.0219
0.282	0.0234	3.83	2	0.0584	0.0263	0.0259
0.328	0.0185	3.83	2	0.0561	0.0439	0.0223
0.184	0.0172	3.59	2	0.0682	0.0241	0.0233
0.245	0.0154	3.59	2	0.0156	0.0148	0.0219
0.336	0.0296	3.84	1	0.0105	0.0103	
0.319	0.0353	3.99	2	0.0244	0.0199	
0.349	0.0397	3.99	2	0.0233	0.0208	
0.304	0.0262	3.9	2	0.0263	0.0211	
0.243	0.0285	3.9	2	0.0264	0.0237	
0.244	0.0328	3.8	2	0.02	0.0198	
0.398	0.0377	3.8	2			
0.373	0.0383	4.18	2			
0.296	0.0289	4.18	2			
0.255	0.0285	4.23	2			
0.329	0.0356	4.23	2			
0.378	0.0528	3.62	1			
0.281	0.0313	3.69	2			
0.369	0.0397	3.69	2			
0.405	0.0493	3.78	2			
0.415	0.0575	3.78	2			
0.43	0.0813	4.59	2			
0.352	0.0444	4.35	2			
0.405	0.0425	4.35	2			
0.268	0.0202	3.91	2			
0.311	0.032	3.91	2			

eng z	volume	length	no of egg	vol big	vol other	volsingb
0.278	0.039	4.52	2			
0.404	0.0742	3.78	2			
0.199	0.0261	3.78	2			
0.451	0.0641	4.19	2			
0.492	0.0811	4.19	2			
0.55	0.116	3.88	2			
0.466	0.0968	3.88	2			
0.564	0.0898	3.83	2			
0.512	0.0931	3.83	2			
0.484	0.0829	4.04	1			
0.353	0.0301	4.56	2			
0.309	0.0222	4.56	2			
0.415	0.0554	4.12	2			
0.455	0.0545	4.12	2			
0.366	0.0554	3.91	2			
0.388	0.0651	3.91	2			
0.282	0.0347	4.2	1			
0.246	0.032	3.73	1			
0.348	0.0287	4.1	2			
0.328	0.0274	4.1	2			
0.464	0.046	4.27	2			
0.354	0.0276	4.27	2			
0.328	0.035	3.8	2			
0.271	0.0211	3.8	2			
0.446	0.0584	3.88	1			
0.298	0.0263	3.88	1			
0.478	0.0561	4.04	2			
0.361	0.0439	4.04	2			
0.304	0.0326	3.87	1			
0.276	0.0219	3.58	1			
0.438	0.0682	3.95	2			
0.318	0.0241	3.95	2			
0.354	0.0265	2.84	1			
0.226	0.0156	3.33	2			
0.271	0.0148	3.33	2			
0.21	0.0123	3.1	1			
0.256	0.02	2.82	1			
0.186	0.0105	2.86	2			
0.19	0.0103	2.86	2			
0.263	0.0219	3.33	1			
0.272	0.0259	3.6	1			
0.243	0.0199	3.61	2			
0.284	0.0244	3.61	2			
0.233	0.0208	3.46	2			
0.237	0.0233	3.46	2			
0.232	0.0211	3.79	2			
0.293	0.0263	3.79	2			
0.283	0.0223	3.16	1			
0.291	0.0264	3.74	2			
0.245	0.0237	3.74	2			
0.247	0.0233	3.63	1			
0.285	0.0219	3.72	1			

MONTH	MEAN VOL
1	0.0901
2	0.032
4	0.0431
5	0.0272
6	0.0376
7	0.0477
8	0.0361
9	0.0334
10	0.021
11	0.0283

month	egg no.	volume	month	clutchv.
7	2	0.0974	7	0.174
7	2	0.0763		
7	1	0.0415		
7	1	0.041		
7	1	0.0845		
7	1			
7	1	0.0381		
7	1	0.0423		
7	1	0.0437		
7	1	0.024		
7	1	0.022		
7	1	0.0431		
7	2	0.0316	7	0.0739
7	2	0.0396		
7	2	0.0423		
7	2			
11	1	0.0313		
11	2	0.0278	11	0.052
11	2	0.0243		
11	2	0.0271	11	0.0512
11	2	0.0241		
11	1	0.0289		
11	1	0.0349		
11	1	0.0287		
11	1	0.0288		
11	2	0.0303	11	0.0555
11	2	0.0252		
6	1	0.0357		
6	1	0.0168		
10	2	0.0234	10	0.0419
10	2	0.0185		
4	2	0.0172	4	0.0326
4	2	0.0154		
8	1	0.0296		
2	2	0.0353	2	0.075
2	2	0.0397		
2	2	0.0262	2	0.0547
2	2	0.0285		
2	2	0.0328	2	0.0705
2	2	0.0377		
2	2	0.0383	2	0.0671
2	2	0.0289		
2	2	0.0285	2	0.0641
2	2	0.0356		
4	1	0.0528		
4	2	0.0313	4	0.071
4	2	0.0397		
4	2	0.0493	4	0.107
4	2	0.0575		
4	2	0.0813	4	0.126

month	egg no.	volume	month	clutchv.
6	2	0.039		
6	2	0.0742	6	0.1
6	2	0.0261		
1	2	0.0641	1	0.145
1	2	0.0811		
1	2	0.116	1	0.212
1	2	0.0968		
1	2	0.0898	1	0.183
1	2	0.0931		
8	1	0.0829		
2	2	0.0301	2	0.0524
2	2	0.0222		
5	2	0.0554	5	0.11
5	2	0.0545		
5	2	0.0554	5	0.121
5	2	0.0651		
9	1	0.0347		
9	1	0.032		
8	2	0.0287	8	0.0561
8	2	0.0274		
8	2	0.046	8	0.0735
8	2	0.0276		
8	2	0.035	8	0.0561
8	2	0.0211		
8	1	0.0584		
8	1	0.0263		
8	2	0.0561	8	0.0999
8	2	0.0439		
8	1	0.0326		
8	1	0.0219		
8	2	0.0682	8	0.0923
8	2	0.0241		
8	1	0.0265		
8	2	0.0156	8	0.0304
8	2	0.0148		
5	1	0.0123		
5	1	0.02		
5	2	0.0105	5	0.0207
5	2	0.0103		
5	1	0.0219		
5	1	0.0259		
5	2	0.0199	5	0.0443
5	2	0.0244		
5	2	0.0208	5	0.0441
5	2	0.0233		
5	2	0.0211	5	0.0474
5	2	0.0263		
5	1	0.0223		