The Biology and Ecology of the Major Deep-sea Benthic Decapod Crustacea From the Porcupine Sea-bight.

Thesis submitted in accordance with the requirements of the University of
Liverpool for the degree of Doctor of Philosophy

by

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Contents.

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See you all in London.

Chapter 1:

An Introduction to the Physical Environment of the Porcupine Sea-bight.

An Introduction to the Porcupine Sea-bight.

The Porcupine Sea-bight is an indented portion of the continental shelf located off the SW coast of Ireland between the latitudes 50-52 °N and 11-15 °W (Fig. 1). The feature represents the trough of an ancient rift system, caused by stress during a period of sea-floor spreading between Greenland and Europe (Naylor & Mounteney, 1975; Roberts *et al.*, 1979). The Sea-bight narrows as it gets deeper, and the mouth is bordered to the north by the Porcupine Bank, and to the south by the Goban Spur. At the shallow end to the east, the trough meets the Celtic shelf.During the Mesozoic and Tertiary periods, extensive sedimentation in the area has produced gentle slopes within the actual Sea-bight area down to the mouth at 3000 m. Here the gradient increases, the sea bed sloping relatively steeply down to the Porcupine Abyssal Plain below 4000 m. The Sea-bight's east slope is characterised by the presence of apparently still active submarine canyons, known as the Gollum Channel System (GCS on Fig. 1), which traverses the mouth of the Sea-bight and widens out into the Abyssal Plain.

Handley (1971) noted an interesting feature of this canyon system using seismic reflection data, concluding that the level of sediment dipped significantly in the GCS. Submersible observations have noted large amounts of detrital material collecting in the channels, so it would appear that any sediments are being constantly eroded from the canyons into the Abyssal Plain, despite the apparent lack of any sediment fan. However, it is likely that this continuous erosion causes a distribution of detrital material to the Abyssal Plain, including the transport of upper and middle slope hard-shelled foraminiferans (Weston, 1985), an added bonus to the fauna of the area. Roberts *et al* (1979) inferred that the limited sediment supply to the equivalent Porcupine Bank area was due to the absence of canyons.

Samples of the Porcupine Sea-bight sediment have been analysed down a transect at 500 m intervals by teams at the Institute of Oceanographic Sciences Deacon Laboratory (IOSDL),

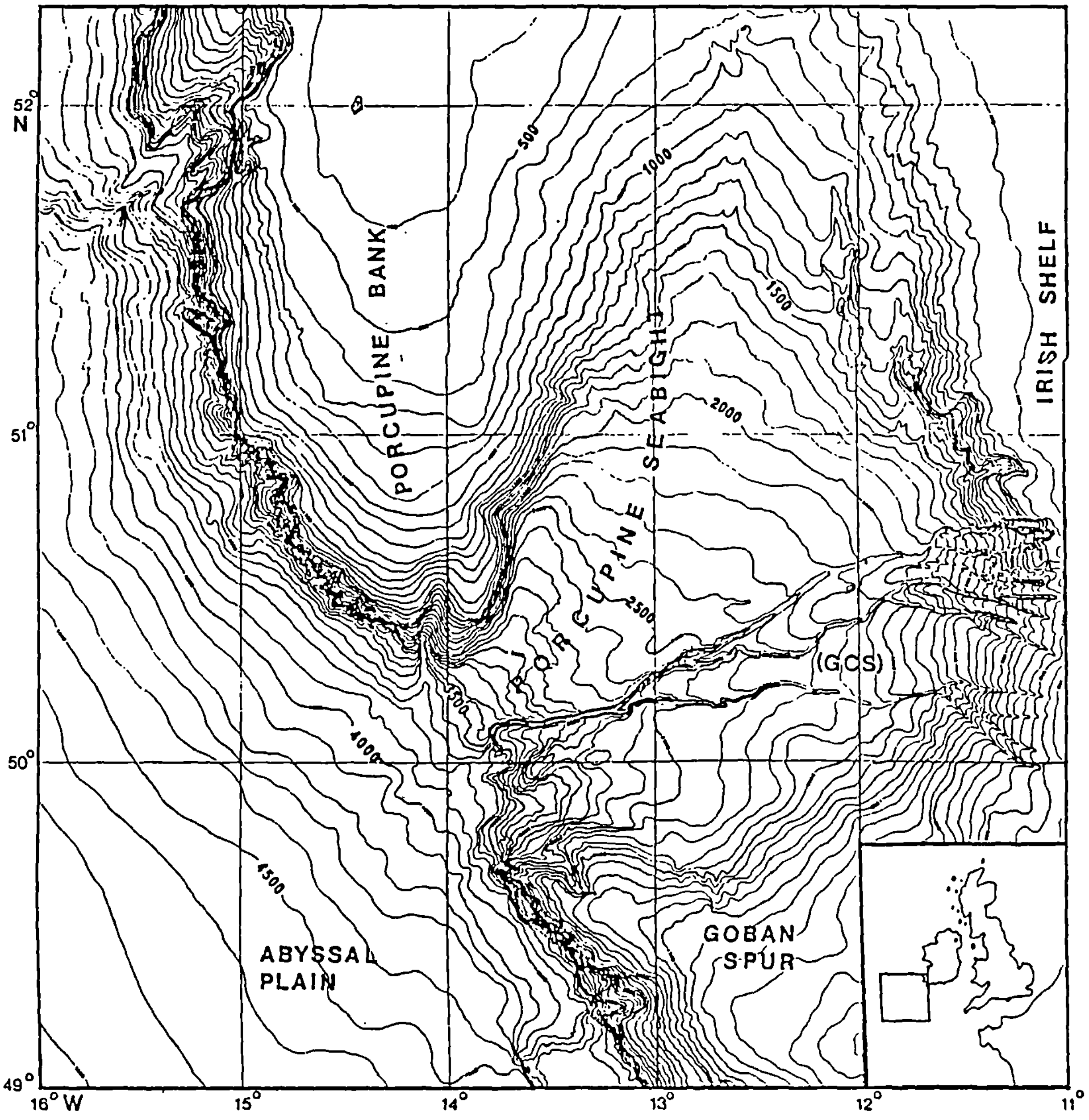


Fig. 1: The topography of the Porcupine Sea-bight area.

Surrey. Generally, the sediments are a coccolith-foraminifera marl with a carbonate content of 45-67 % dry weight (Lampitt *et al.*, 1986). There is a gradient in sediment particle size, the coarsest being found at the top of the slope (median phi = 4·4 at 510 m) and becoming finer with an increase in depth (e.g. median phi = 7·4 at 960 m) (Lampitt *et al.*, 1986). Below 1500 m, the sediment particle size is comparatively constant, with phi values ranging from 8·0-8·6. Rock debris is present in most samples, with a predominance of clinker (including coal and coal shale), the refuse from steam vessels. This collects particularly at the mouth of the Sea-bight (Kidd & Huggett, 1981). Most of this debris is less than 6 cm, but large boulders are occasionally taken. The non-clinker material, i.e. igneous, metamorphic and sedimentary rock, are glacial erratics which have probably been dropped in the past from floating ice (Kidd & Huggett, 1981). In addition to the clinker, a depressingly large amount of general refuse, such as plastic bags, bottles, biscuit tins and drink cans, is often taken in hauls across the Sea-bight.

Sedimentation rates have been calculated to reach 10 cm per 1000 years in the Porcupine Sea-bight (Kidd & Huggett, 1981), the sediment colour indicating oxidation of the top 9 cm, the colour change from brown to a greenish-brown being more acute at depth. The assessment of organic content of marine sediments is often hindered by high carbonate levels (Weliky *et al.*, 1983), but CHN analysis of Sea-bight sediments after acid digestion have shown that they vary little from a figure of 0·5 % of the sediment's dry weight, with no apparent relationship between % organic carbon and depth (Lampitt *et al.*, 1986).

The main features of the water column found in the Porcupine Sea-bight can be illustrated by a standard temperature-salinity plot (fig. 2), and reflect the general water mass structure described by previous studies (e.g. Lee & Ellett, 1965; Harvey, 1982; Ellett *et al.*, 1986). Eastern North Atlantic water forms the surface layer down to about 750 m, and overlays a band of Mediterranean Water, a mass characterised by the peak in salinity at around 980 m. The oxygen content minimum for the water column also occurs in the Mediterranean Water. Beneath 1000 m, this Mediterranean Water becomes mixed with the underlying Labrador Sea Water, this body forming the salinity minimum at around 1700 m. Below this depth there is

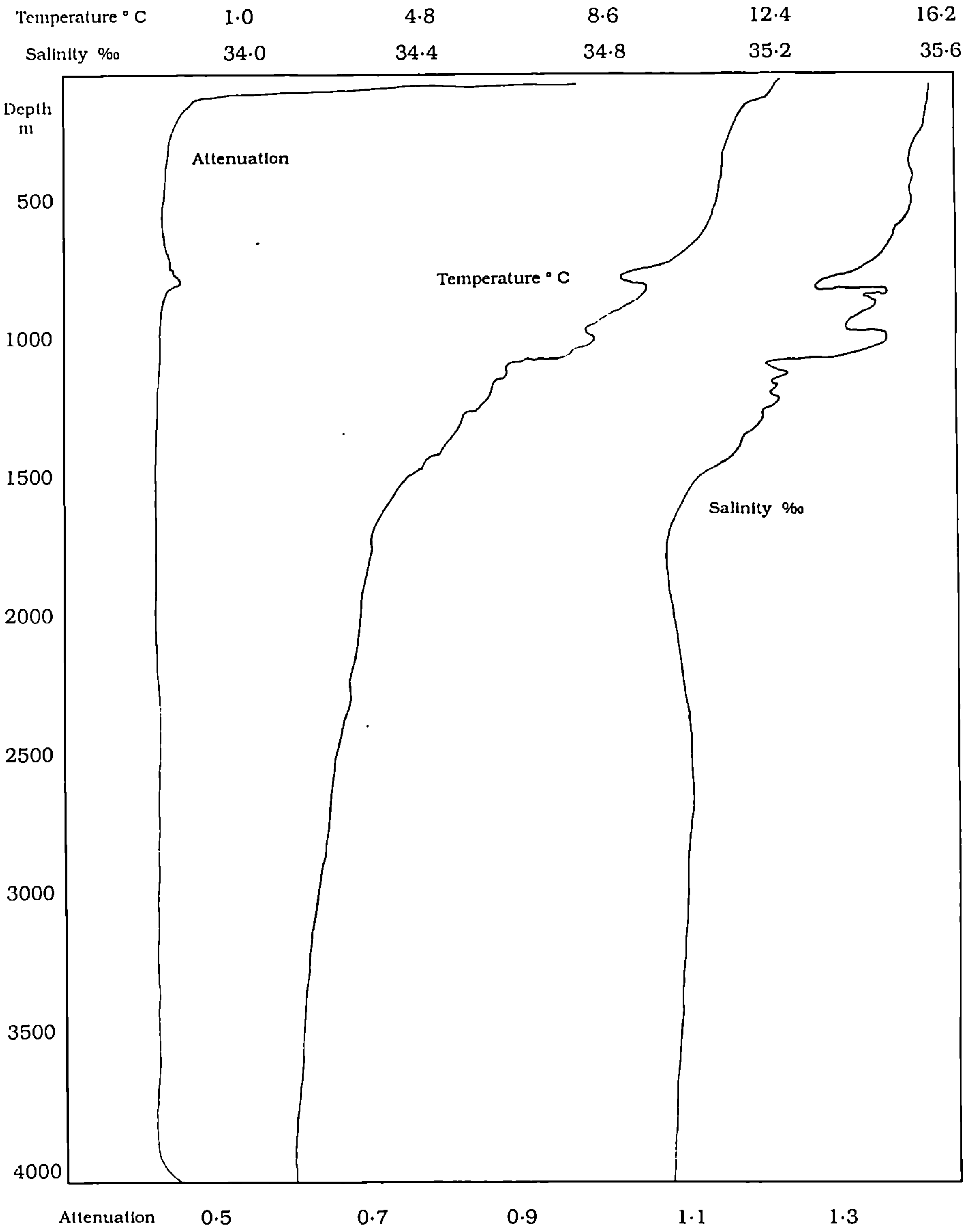


Fig. 2: Temperature/Salinity profile for the water column in the Porcupine Sea-bight (Station 11106).

very little variation in temperature and salinity, though the small increase in salinity at around 2500 m indicates the influx of Norwegian Sea Water. The abyssal water below 4000 m has a southern origin, derived to some degree from Antarctic water (Vanagriesham, 1985).

A permanent thermocline is apparent at 600 m, which is the limit of winter mixing (Ellett & Martin, 1973), the temperature decreasing from 10-4 °C over a depth range of less than 800 m. A surface summer thermocline forms in the top 50 m.

Near-bed currents in the Porcupine Sea-bight tend to be of tidal origin and rarely exceed a flow speed of 15 $cm.sec^{-1}$ (1 m above the sea bed) (Lampitt, 1985; Lampitt *et al.*, 1986). A residual current is apparent, and runs parallel to the contours at all depths, being part of the large northbound boundary current that runs along the margin of the European continent (Swallow *et al.*, 1977; Huthnance, 1986). This current occurs throughout the year (Huthnance, 1986), but may vary seasonally in velocity, with a maximum flow around November (Dickson *et al.*, 1986). Currents over the Goban Spur have been measured at 2·2 $cm.sec^{-1}$(Huthnance, 1986), and will therefore be a major factor influencing the deep circulation of the Porcupine Sea-bight. To the west of the Porcupine Bank, the residual current from the south has been measured at 9 $cm.sec^{-1}$ (Dickson *et al.*, 1985). Out on the Abyssal Plain, currents are generally slow, flowing northwards at 1-2 $cm.sec^{-1}$. In addition to the slope and tidal currents, the upper slope of the Sea-bight will be influenced in winter by water cascading off the continental shelf and Porcupine Bank (Cooper & Vaux, 1949), internal waves and tides inducing near-bottom motion (Huthnance, 1986), which is bound to increase the sediment load of the water.

The deep-sea has in the past been regarded as an environment totally free from the effects of seasonality. However, it is becoming clear that this is not the case in the Porcupine Sea-bight, and most likely in deep-sea areas elsewhere. Dense coccolithophorid blooms occur along the shelf break and Porcupine Bank during the summer (Dickson *et al.*, 1980; Holligan & Groom, 1986), these blooms being maintained by vertical nutrient fluxes due to tidal mixing associated with the activity of shelf break internal waves (Holligan *et al.*, 1985). Most of these blooms occur on the borders of the Sea-bight, but 'streamers' from the blooms will be carried out across the Sea-bight area (Holligan & Groom, 1986) and form an important source of benthically deposited detrital material.

In addition to the coccolithophorids, there is marked seasonal fluctuation in the general deposition of detrital matter to the benthos (Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986). Large amounts of this material accumulates on the sea bed, particularly around mounds and in depressions, during the months of May-July and so provides a valuable organic input to the benthic faunal community. The specific composition of the phytoplankton in these deposits varies over this period, the primary flux being dominated by diatoms, with dinoflagellates and coccolithophorids important in the summer (Billett *et al.*, 1983). This material is resuspended by near bottom currents and distributed over the sea-bed (Lampitt, 1985).

The Porcupine Sea-bight therefore is a prime location for the study of the deep-sea faunal community due to its relatively convenient location, the shallow slopes allowing comparatively easy, accurate sampling and the relatively high degree of knowledge about the physical parameters affecting the organisms living in this area.

Chapter 2:

General Materials and Methods: Sampling Details.

Materials and Methods.

Sampling Details.

The specimens used for this study have all been taken for the "Discovery" collection stored at the IOSDL, Surrey. Those species covered here have been sampled from the Porcupine Sea-bight using either an IOSDL epibenthic sledge (BN) (Aldred *et al*, 1976; Rice *et al*, 1982), a semi-balloon otter trawl (OTSB) (Merrett & Marshall, 1981) or occasionally an IOS Rectangular Midwater Trawl (RMT) (Roe & Shale, 1979), for pelagic juveniles. Details of these pieces of sampling gear follow. In addition, some samples have been taken by the SMBA during investigations on benthic fish communities using either a single warp trawl (SWT) or a Granton trawl (GT) (Gordon & Duncan, 1983, 1985).

Photographic investigations of the benthic community were undertaken using a camera mounted on the IOS benthic sled, either with or without the presence of nets.

All gear was worked off the NERC research vessels RRS "Challenger" and "Discovery", all samples obtained being placed in the "Discovery" collection at the IOSDL.

a). IOS Epibenthic Sled (BN).

The BN is basically a frame formed from scaffolding tubes connecting two lateral skids (Fig. 1), which allows the sled to be used as the basis for a variety of investigations. Along the back, between the skids, can be mounted one large or several small nets up to a total width of 2·29 m and a height of 0·61 m. The single large net has a mouth width of 2·29 m, a mouth area of 1·4 m^2 and a mesh size of 4·5 mm. Alternatively, this net can be swapped for a 'multi-net' system, consisting of three nets strapped together across the mouth of the sledge. The centre net has a mouth width of 0·68 m, a mouth area of 0·42 m^2 and a small mesh size of 1·0 mm. The flanking nets are of the same mesh size as the large net, with a mouth width of 0·8 m and an area of 0·49 m^2. For the quantification of abundance, the total mesh mouth widths are considered equal. Models of the BN since 1979 have been fitted with a suprabenthic

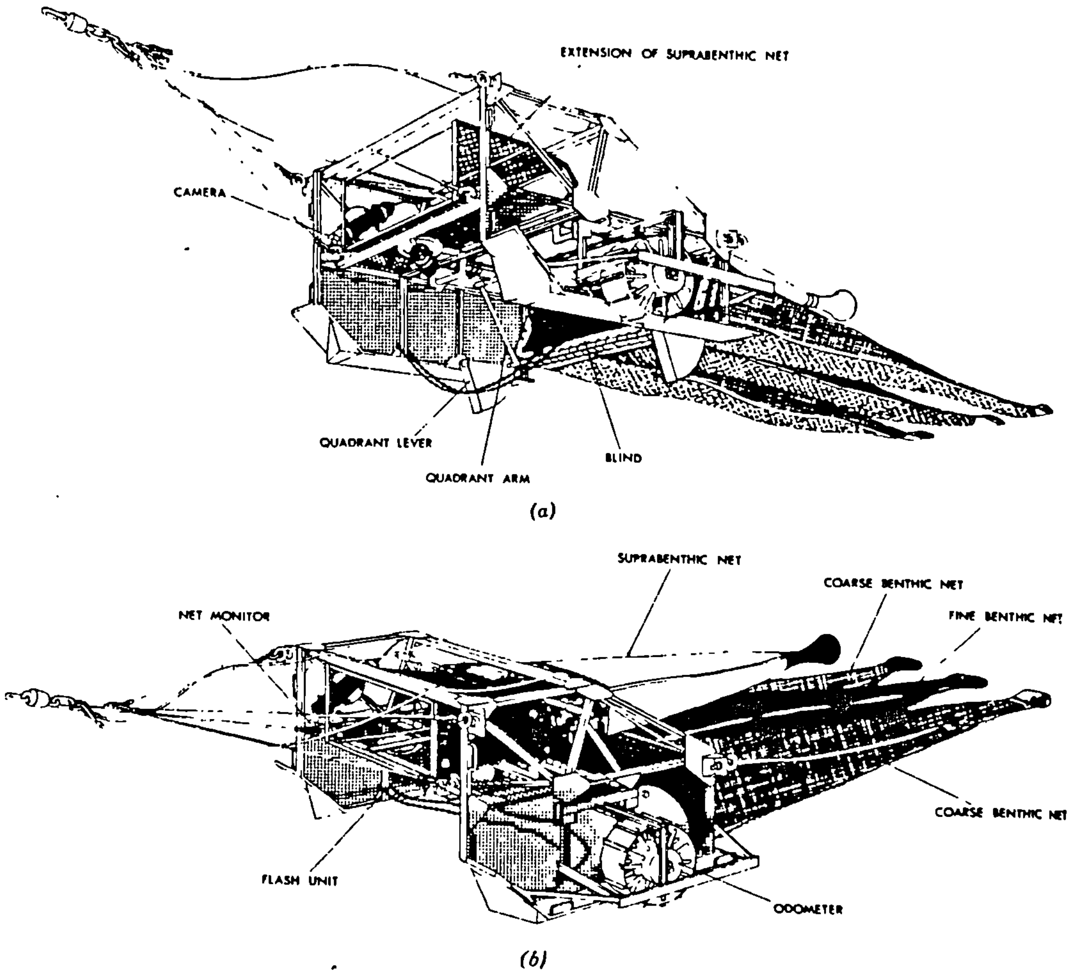


Fig. 1: Diagram of the IOS Epibenthic Sled (from Rice *et al*, 1982).

net in addition to the standard nets, mounted on the top of the superstructure (Fig. 1). This is used to catch off-bottom plankton and to trap animals attempting to swim up in front of the BN. It has a fine mesh of 0·33 mm.

The sledge is monitored by means of an 10 kHz acoustic beacon (IOS type H) mounted on the sledge (Fig. 1 as net monitor), sending signals to a receiver aboard the ship, and all nets are fitted with opening and closing devices to prevent off-bottom contamination. Distance is recorded using the odometer, which starts to run on contact with the sea bed.

The camera system comprises a camera with a constantly open shutter, mounted above the mouth of the benthic net, and a flash unit, mounted separately, which delivers a pulse of light at a set interval and is activated on reaching the sea bed. Occasionally, photosleds are run, with the bare sled and camera only. These give a quantitative photorecord of the sea bed, with a photograph being taken every 15 seconds. The gear is towed at an average speed of 1·5 knots, resulting in a distance of about 12 m between pictures.

b). Semi-balloon Otter Trawl (OTSB).

The semi-balloon trawl (OTSB 14), complete with "V" doors is the standard net used for deep-sea sampling, and was obtained from the Marinovich Trawl Co., Mississippi, USA. It is constructed of 4·4 cm stretch mesh body and 3·7 cm mesh intermediate and codend, with a 1·3 cm inner liner in the codend. Buoyancy is provided by three evenly spaced 25 cm CORNING glass spheres on the headline, each giving a positive buoyancy of 5·7 kg. Along the 17 m footrope are spaced 23 plastic mud rollers (13 x 15 cm), with three loops of 6 mm chain in between each set. The "V" doors are separated from the wing ends of the net by a pair of sweeplines on each side, the height of the wing ends between headline and footrope being 1·5 m. The doors each weigh 180 kg and measure 1·5 x 1 m, and are connected by bridles, 50 m in length, through a swivel to the single trawl warp.

The OTSB is monitored using an 10 kHz acoustic beacon mounted on one of the two trawl doors, and the area sampled by each haul is estimated using the distance travelled by the ship while the net is on the sea bed. As a result, values can not be regarded as being as accurate as the odometer measured BN.

c). Rectangular Midwater Trawl (RMT).

Two versions of the RMT have been used, the original RMT 1+8 and the multiple RMT 1+8M (Fig. 2). The RMT 1+8 uses two nets of differing mesh sizes (0·32 mm, 1 m^2 mouth area and 4·5 mm, 8 m^2 mouth area) simultaneously, the nets being opened and closed by a mechanical release that is triggered using acoustic signals. It is generally used to sample the pelagic community over a specific depth horizon, and the depth, temperature and velocity of the net through the water (from which estimates of volume of water sampled are made) are continuously monitored. A small echo sounder mounted on the net allows distance from the sea bed to be monitored and as a result the net can be accurately fished, in good conditions, 5 m from the bottom.

The RMT 1+8M is a modification of this basic RMT form, with three 1 m^2 nets and three 8 m^2 mouth area nets combined on the same frame. This has the advantage of sampling successive depth horizons without any contamination or temporal separation. Like the RMT 1+8, it is acoustically operated, as one net is closed, the next opens until all have been fished. This is then closed, so sealing all the nets and the gear can be retrieved.

Benthic sampling intensity has not been homogeneous across the whole bathymetric range of the Porcupine Sea-bight. Fig. 3 shows the total number of samples of the decapods covered in this study taken over each 200 m depth interval. As can be seen, sampling peaks are evident each side of 1000 m, at about 2800 m and again at 4000 m. The upper slope peaks are due to the plethora of hauls taken in shallow water, and especially a series of BN hauls taken at 1300 m as part of a study into the sampling repeatability of the sledge within a single small

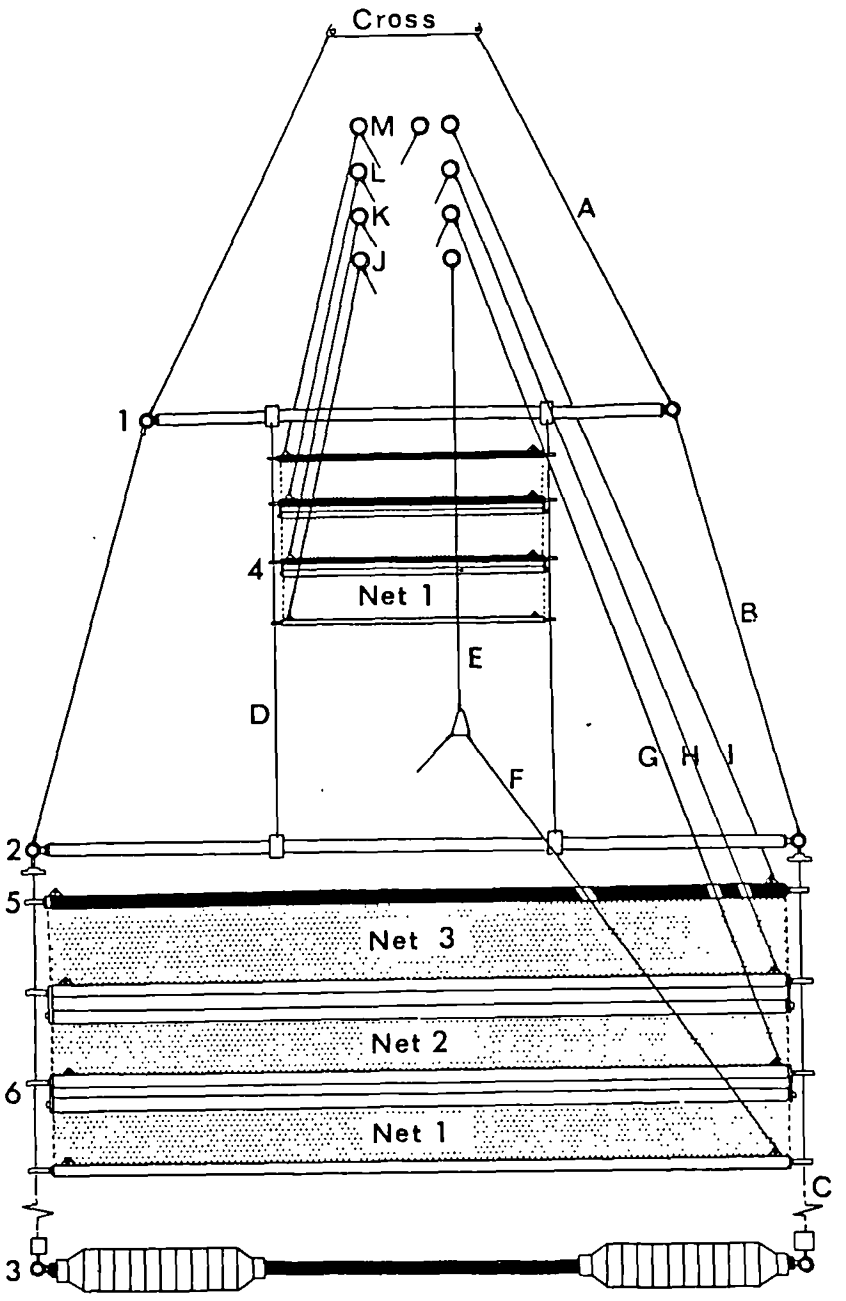


Fig. 2: Diagramatic representation of the RMT 1+8M. (from Roe & Shale, 1979).

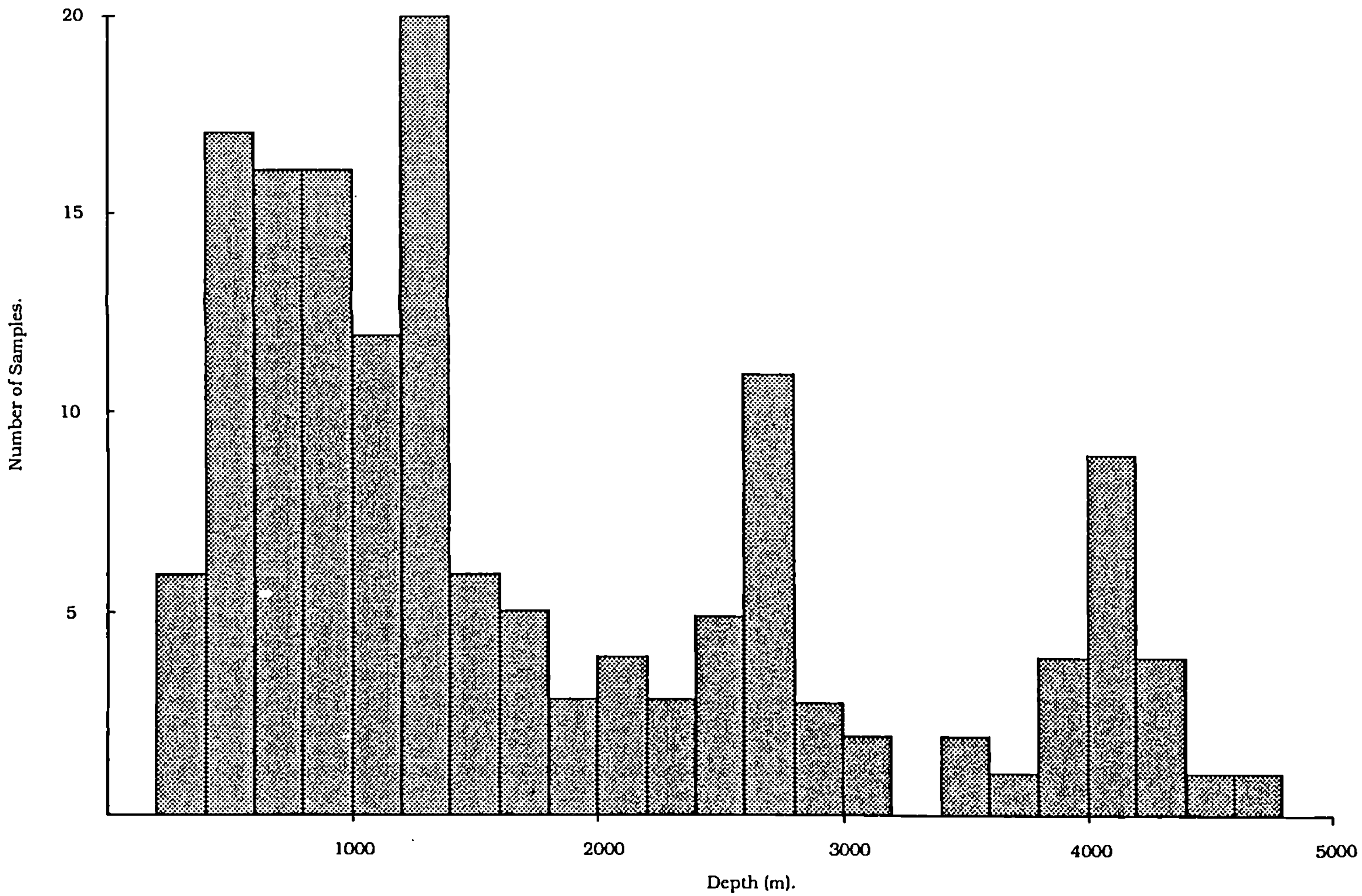


Fig. 3: Sampling profile for samples of the benthic decapods covered by this study.

area (2 km diameter). A similar repeat sampling programme has occurred at 4000 m - hence the peak at this depth. The peak at around 2800 m is probably due to decapod by-catches from attempts to catch the elusive holothurian *Kolga hyalina* (Billett & Hansen, 1982), which has been noted in vast quantities at these depths from long-term photography using the "Bathysnap" system (Lampitt & Burnham, 1983). There is a noticeable lack of samples at around 3200 m on the sampling profile which corresponds to the area of rough terrain at the mouth of the Sea-bight, where sampling is difficult.

Bathymetric ranges of species are given in two forms. The possible range incorporates all of the area sampled where the species in question was taken, i.e the shallowest depth of the shallowest sample to the deepest depth of the deepest sample. The distribution of each species is not known within a sample, so it may only possibly extend to these extremes. The calculated range is the minimum range over which the species is definitely to be found in the Sea-bight, and relates to the range from the deepest depth in the shallowest sample to the shallowest depth of the deepest sample. An example is given below:

Species.	Depth Range of shallowest sample.	Depth range of deepest sample.	Possible Range.	Calculated Range.
Sp. A.	1024-1213 m.	2315-2435 m.	1024-2435 m.	1213-2315 m.

Details of exact sample sites, preservation methods, biomass calculations, measurements and observations taken during the study of the benthic decapods in this study are to be found under the Materials and Methods section for each particular chapter. A more detailed listing of the station data, including dates, can be found in Appendix 2. All wet weight values are for preserved wet weight (Rowe *et al*, 1974; Carey, 1981), the specimen being removed from its preservative, being extensively washed in water and then excess surface water removed with absorbent paper before weighing.

Compared to the BN, the OTSB provides relatively inaccurate samples, due to factors relating to its function, such as bow waves disturbing fast moving animals, variations in mouth width and the net leaving the sea bed undetected. As a result, biomass and density calculations obtained from OTSB samples cannot be regarded as being as accurate as those taken using the BN, but are worthwhile as they provide a comparison between populations taken at different depths using the same piece of equipment.

Chapter 3:

The Biology and Ecology of the Porcupine Sea-bight species of the galatheid genus *Munida* (Decapoda, Anomura).

Introduction.

The galatheid genus *Munida* has representatives worldwide and is recorded from depths ranging from the littoral (*M. japonica*, Doflein & Balss, 1913) to below 2000 m (*M. micropthalama*, Hansen, 1908). Most publications on members of the genus have dealt with either the nomenclature and systematics (e.g. Zariquey Alvarez, 1952; Rice & St Laurent, 1986) or records of their distribution (e.g. Miyake & Baba, 1970; Pequegnat & Pequegnat, 1970). Comparatively little is known about the biology and ecology of *Munida* species, including those found in the Northeast Atlantic. This chapter therefore reports the results of a study into the biology and ecology of *Munida* species from the Porcupine Sea-bight, particularly the reproductive cycles and fecundity and the population structure in relation to biomass and density.

The most studied *Munida* species up to the present has been *M. gregaria* found in the southern temperate oceans, due to the spectacular aggregations of a red pelagic stage at the surface. This was noted by many early explorers, such as Dampier and Cook and Darwin reported the phenomenon in "The Voyage of the Beagle" around Tierra del Fuego noting, "I have seen narrow lines of water of a bright red colour, from the number of Crustacea which somewhat resemble large prawns. The sealers call them 'whale-feed'. Whether whales feed on them I do not know, but terns, cormorants and immense herds of great unwieldy seals derive, on some parts of the coast, their chief substance from these swimming crabs." Longhurst (1968) later qualified the sealers' name, reporting pelagic shoals of *M. gregaria* as the food of southern right, humpback, sei and blue whales. Matthews (1932) noted that "...the blubber oil obtained from Sei whales on the Patagonian and Mexican coasts was always of a definitely yellowish colour, quite unlike that obtained from the species elsewhere." This difference in colour he believed was produced by feeding on the pelagic *M. gregaria*. The shoals soon provided fishery/economic interest. Thomson & Thomson (1923) investigated their economic value as a fertilizer, stating that sometimes these munidids were beached in their millions on New Zealand shores and would be a good manure even if "for weeks they fill the air with an offensive smell." However, after studying the chemical fertilizer value of the whale-feed, Thomson & Thomson had to conclude that due to the cost of the treatment there was "very little commercial value in whale-feed under present conditions." This did not deter interest in a fishery. Longhurst (1968) reported a definite potential for exploitation of the swarms in Chile while Zeldis (1985) stated that fishing for the pelagic *M. gregaria* could provide a food for cultured salmon.

The existence of the spectacular pelagic aggregations and consequent fishery interest inevitably led to investigations into the biology of *M. gregaria*. Thomson & Thomson (1923) stated that the eggs were laid in May-June and hatched in Sept-Oct., the larval stages leading to the swarming juveniles. This was backed up by observations made by Young (1925). Rayner (1935) investigated populations of *M. gregaria* and *M. subrugosa* around the Falklands, confirming the hatching times and describing the *M. gregaria* larval stages, though the picture for *M. subrugosa* appeared much more confused. He also did some work on growth and parasitisation as well as describing the *M. gregaria* swarming 'grimothea' stage (this was originally classed as a separate genus, *Grimothea* Leach).

Williams (1973) explained the reason for Rayner's confusion over *M. subrugosa* and *M. gregaria* as she declared them the same species (*M. gregaria*) whose morphology is influenced by environmental variation. This she concluded from a detailed study of the development of both pelagic and benthic stages, identifying 'gregaria' and 'subrugosa' features at different stages of development. Armed with the knowledge that they were only studying a single species, Zeldis & Jillett (1982) utilised the latest advances in remote sensing technology to study the *M. gregaria* pelagic swarms from satellite observations. They noted aggregations at fronts and mid-shelf internal waves, the grimotheae resisting downward displacement by swimming back to the surface and so aggregating in such areas. They estimated swimming speeds of 16 cm s^{-1}.

Zeldis (1985) undertook a definitive study on *M. gregaria* ecology in New Zealand. The larvae once released pass through five zoeal stages before forming the juvenile swarms. These can persist from six weeks to a year before settling out on the bottom, the length of the pelagic stage depending on bottom adult densities. Benthic recruitment only occurs where adult populations are in low densities, and where such low densities occur, the pelagic stage is short. The absence of benthic settlement in areas of high adult density is attributed to cannibalism and non-lethal agonistic behaviour.

Compared with *M. gregaria*, work on other *Munida* species is sparse, particularly the more accessible species in the highly studied area around Europe, which is somewhat surprising. Lebour (1930) and Huus (1934) both looked in some detail at *Munida* larvae, Lebour describing four planktonic larval stages for *M. rugosa* (as *M. bamffica*) before the juvenile settles. Nicol (1932) studied the feeding habits of *M. rondeletii* (together with *Galathea* spp. and *Porcellana* spp.), describing different methods of feeding for large 'prey' items and material from the substrate. Brinkmann (1936) undertook an investigation into *M. sarsi* and *M. tenuimana* populations in Norwegian fjords, studying large numbers of each species. Although he was basically interested in the rhizocephalan parasites, he also looked at reproductive cycles, burrowing behaviour, diet and some details of growth (the oldest individuals being estimated as at least 14 years old).

Ingrand (1937) studied the development of *M. rugosa* (as *M. bamffica*), concentrating on the chela and pleopod development. Reverberi (1942), while studying crustacean parasites, made some brief references to *M. sarsi* and *M. tenuimana* population structure, while Berrill (1970) investigated *M. sarsi* aggressive behaviour. Williams & Brown (1972) looked at *M. iris*, but they were attempting to describe aspects of its reproductive biology from samples taken over only a short period in June. Roberts (1977), working in the Gulf of Mexico, made the only attempts to quantitatively estimate the densities of *Munida* species, including *M. forceps* (29 ind.ha^{-1}) and *M. valida* (3 ind.ha^{-1}). *M. valida* is the largest member of the genus, growing to a carapace length of over 40 mm. Wenner (1982) undertook a survey of galatheids from the Middle Atlantic Bight (including *M. iris iris, M. longipes, M. valida* and *M. micropthalama*) and made some notes on their biology, particularly presence of eggs, fecundity and parasitism.

Materials and Methods.

During the period 1978 to 1986, a total of 2166 individuals of the genus *Munida* Leach were collected from the Porcupine Sea-bight (49-52°N, 11-14°W). The positions and depths of the stations where *Munida* were taken and the specific composition of each catch can be seen in Table 1 and Fig. 1. Three types of sampling gear were used: the semi-balloon otter trawl (OTSB) complete with "V" doors (see Merrett & Marshall, 1981), the IOS epibenthic sled (BN) (see Rice *et al*, 1982) and the SMBA Granton Trawl (GT) (see Gordon & Duncan, 1983). The ships used were the RRS "Challenger" and "Discovery". The specimens were fixed in 5% formalin solution and later transferred to 70% alcohol for preservation. They have been stored in the "Discovery" collection at the Institute of Oceanographic Sciences Deacon Laboratories, Wormley, Surrey.

Measurements were taken as follows (Fig. 2): carapace length (CL) from the posterior margin of the right orbit to the posterior carapace margin; chela length (ChL) from the tip of the propodus fixed finger to the base of the coxa; eye diameter as Fig. 2. All measurements were taken using dial calipers to the nearest 0·1 mm. Details of egg number and condition were obtained using a Wild stereoscopic microscope. All measurements of egg and ova size utilised the graduated eyepiece of the microscope and were made to the nearest 0·01 mm. Wet weight of whole animals was measured to the nearest 0·01 g. Sex of *Munida* was determined by the position of the gonopores and the structure of the pleopods, particularly the presence or absence of the first pair.

Details of the areas sampled used to calculate biomass and density figures were obtained from either the ship's log (distance travelled) for OTSB or, more accurately, from odometer reading when on the bottom for BN. These were multiplied by width of net to give figures for area sampled in hectares. Details were not available for trawls made using the GT, so density

Station N^o.	Latitude. (N).	Longitude. (W).	Mean Depth (m).	Gear Used.	Number of each species in sample: *M. rugosa*	*M. sarsi.*	*M. tenuimana*	*M. micropth*
CW01			280	'Trawl'		33		
9752#1	51° 37'	11° 43'	1025	OTSB			3	
9777#2	49° 15'	11° 15'	243	OTSB	25	208		
**9778#1*	*49° 15'*	*12° 7'*	*1036*	*OTSB*		*1* *		
**9779#1*	*49° 22'*	*12° 49'*	*1401*	*BN*	*1* *			
10109#8	49° 12'	12° 19'	1125	BN			1	
10110#1	49° 19'	11° 43'	925	BN			6	
10111#8	49° 33'	13° 7'	1635	BN				2
10120#1	49° 28'	11° 22'	400	BN		120		
50503	51° 37'	13° 15'	1017	OTSB			3	
50522	49° 24'	11° 45'	983	OTSB			8	
50523	49° 32'	11° 24'	473	OTSB		831		
50524	49° 34'	11° 36'	763	OTSB		26		
50601	51° 19'	11° 41'	849	OTSB			3	
50606#1	50° 40'	14° 10'	1115	BN			2	
50606#2	50° 41'	14° 10'	1100	OTSB			4	
50606#5	50° 43'	13° 56'	1130	BN			1	
50607#2	51° 2'	14° 6'	700	BN		11		
50609#1	51° 40'	14° 17'	400	BN		5		
50610#1	51° 26'	13° 24'	980	BN			1	
50611#1	51° 19'	13° 15'	1388	BN			1	
50702	51° 17'	11° 38'	785	OTSB		5		
50705	49° 24'	11° 32'	743	OTSB			1	
50707	49° 54'	11° 16'	*780*	*GT*		*1*	*1*	
50708	49° 23'	12° 1'	1058	GT			1	
50709	49° 24'	12° 22'	1260	GT			9	
50713	51° 22'	13° 18'	1260	GT			4	
50716	51° 53'	13° 26'	748	GT			2	
50806	49° 27'	11° 27'	513	OTSB		63		
50807	49° 24'	11° 34'	793	OTSB		2		
51023	49° 30'	12° 11'	1273	OTSB			1	
51025	49° 27'	11° 25'	470	OTSB		93		
51103#5	51° 47'	13° 13'	940	BN			1	
51112#1	51° 27'	13° 59'	523	BN		10		
51206	51° 40'	13° 1'	1205	OTSB			17	
51302	52° 41'	13° 31'	330	OTSB		37		
51304	51° 51'	13° 20'	790	OTSB			2	
51306	51° 44'	12° 53'	1218	OTSB			11	
51312	49° 27'	11° 37'	725	GT			1	
51315	49° 33'	11° 52'	1015	GT			1	
51319	49° 28'	11° 18'	265	OTSB	29	46		
51401	51° 8'	11° 25'	297	OTSB		38		
51403#1	51° 38'	13° 00'	1303	BN			1	
51403#2	51° 37'	12° 59'	1321	BN			3	
51403#5	51° 38'	12° 59'	1293	BN			2	
51403#6	51° 37'	12° 59'	1287	BN			1	
51420#1	51° 37'	12° 59'	1327	BN			1	
51420#3	51° 38'	12° 59'	1296	BN			6	
51610#1	50° 1'	13° 58'	980	OTSB			3	
51707#1	51° 40'	13° 00'	1218	BN			6	
51810	49° 33'	11° 53'	1016	OTSB			1	
51813	49° 24'	11° 16'	247	OTSB	53			
52105			1250	OTSB			12	
52404#4	51° 59'	13° 43'	450	BN		403		
Total					108	1933	123	2

* incongruous samples, possible contamination from previous hauls or error in sorting.

Table 1: Data for those stations where *Munida* spp. were caught, plus the number of each species caught at each station.

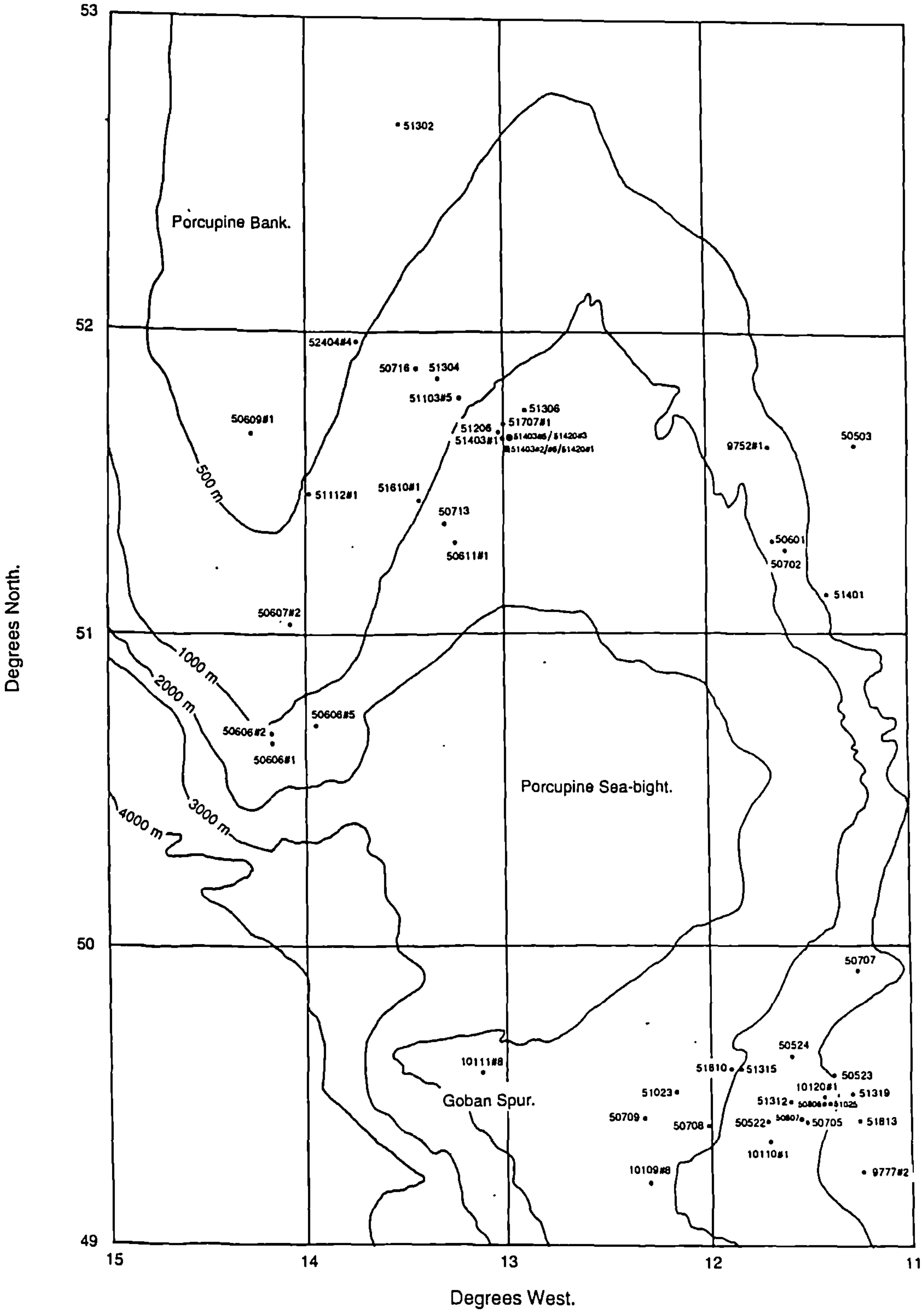


Fig. 1: Map of the Porcupine Sea-bight area indicating the position of stations where *Munida* species were caught.

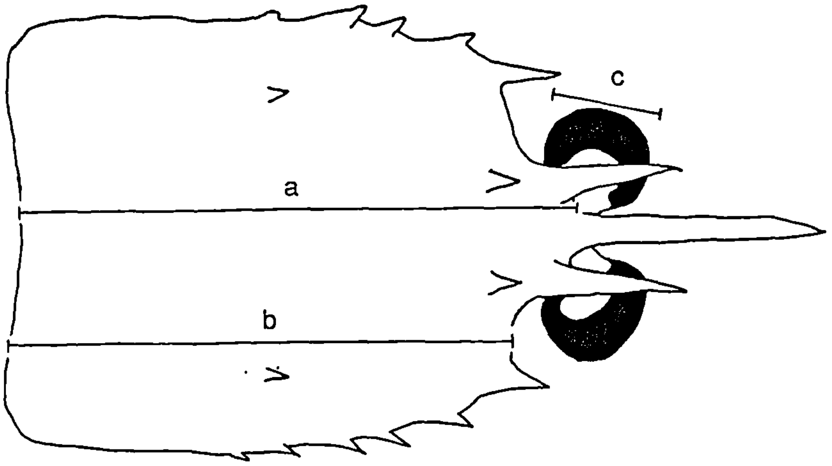


Fig. 2a: Generalized *Munida* carapace indicating: a). Brinkmann's CL., b). Standard CL. measured in this study, c). Eye diameter.

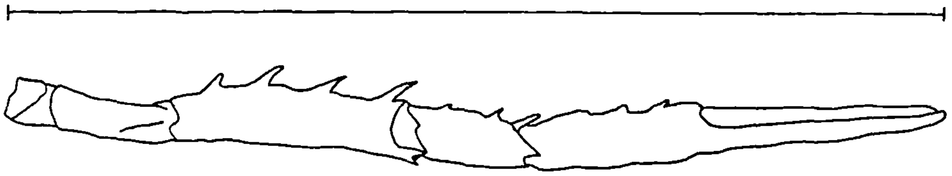


Fig. 2b: Generalized *Munida* chela indicating ChL measured in this study.

and biomass data could not be obtained for these samples.

For comparison, 40 subtidal *M. rugosa* from the Irish Sea were kept in captivity. All individuals were kept in 60x30x30 cm tanks at ambient temperature with circulating sea water. Males were kept at a density of six to a tank purely for observation, while only two ovigerous females were kept in each tank to study egg development. There was no flow-through of sea water between tanks.

For comparative purposes, the peculiar measurement of CL used by Brinkmann (1936) was also taken, this being from the notch between the main and right lateral rostral spine to the posterior edge of the carapace. A relationship to convert Brinkmann's carapace length (BCL) to the standard carapace length (CL) was obtained as: **$CL = 0{\cdot}96\ BCL - 0{\cdot}51$**. Both measurements are in mm. Wherever figures from Brinkmann's study are quoted, they are the converted measurements, not the original, to allow direct comparison.

Results and Discussion.

Four species of Galatheidae constituting 2166 individuals were collected from the Porcupine Sea-bight area between 1978 and 1987: *Munida rugosa, Munida sarsi, Munida tenuimana* and *Munida micropthalama,* with *Munida sarsi* being by far the most abundant species comprising 89 % of the total number of galatheids collected. Details of the numbers of each species caught together with their geographic and depth distributions are presented below. In addition, the numbers of each species caught in each sample are provided in Table 1, together with station data. For details of the complex history of nomenclature of the three main species studied here see Rice & Saint Laurent (1986) where also can be found more details on the diagnostic characters of these species.

Munida rugosa Fabricius, 1775. (Fig. 3).

Distinguishing Features: *M. rugosa* has relatively small eyes when compared with the similar species *M. tenuimana* and *M. sarsi,* the setae that arise from the corneal margin being short and never reaching the outer edge of the eye. The chelae are long and broad and generally setose rather than spiny, with a large amount of setae between the dactyl and the propodus, especially in larger individuals. Spines are always absent from the fourth abdominal tergite, the whole appearance of the animal being less spinose than the other species. Two smaller anatomical details distinguish *M. rugosa:* the merus of the third maxilliped bears a distinct spine on the distal external angle and the striae on the sternal plastron are long and straight compared to *M. sarsi.*

Distribution: Found in most European waters from Norway (Brinkmann, 1936) round the British Isles south to Madiera and the Mediterranean (Zariquiey Alvarez, 1946, 1952). Restricted to relatively shallow water (above 300 m), so only found at the edge of the Porcupine

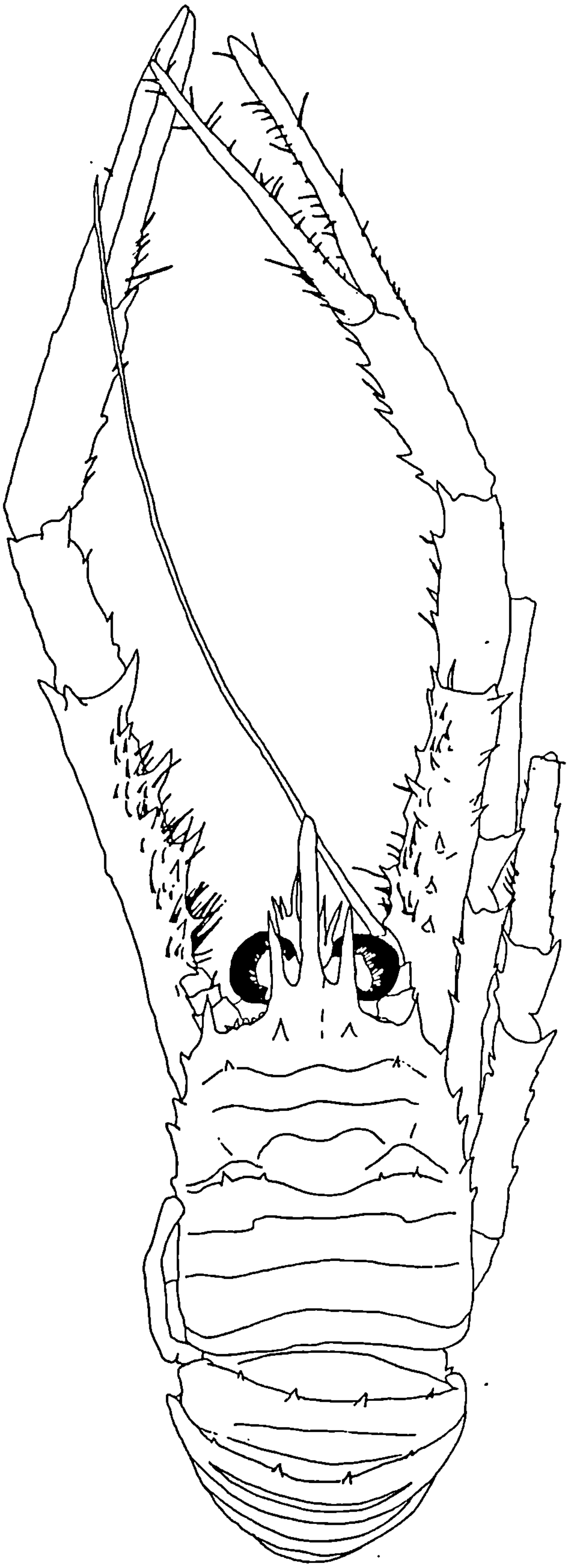


Fig. 3: Female *Munida rugosa*, CL. 13·2 mm.

Sea-bight. In this study its maximum depth was found to be 280 m, where it overlaps in range slightly with *M. sarsi*. A total of 108 specimens have been taken (5 % of the total galatheids caught).

Munida sarsi Huus, 1935. (Fig. 4, Plate 1).

Distinguishing Features: Larger eyes than *M. rugosa*, the setae arising from the corneal margin often reaching beyond the outer edge of the eye. Chelae less setose and with more spines, especially on the propodus and carpus. Adults always have a pair of spines on the fourth abdominal tergite, which may be small or indeed absent in juveniles. No spine on the merus of the third maxilliped. Numerous, short, curved striae on the sternal plastron, especially on the posterior sternites, where they are practically absent in both *M. rugosa* and *M. tenuimana*.

Distribution: The most northern of the species studied here, extending south only as far as the north coast of Spain (Zariquiey Alvarez, 1952). Limited to the Eastern Atlantic north to Iceland (Stephensen, 1939) and Norway (Dons, 1915) and appears to be absent from the Mediterranean. It has been reported mainly between 200 and 800 m, the bathymetric range in this study being a maximum of 205-815 m, overlapping with *M. rugosa* at the shallow end and *M. tenuimana* only below 740 m in the Porcupine Sea-bight. By far the most abundant galatheid in the area, with 1933 individuals taken (89 %).

Munida tenuimana G. O. Sars, 1872. (Fig. 5).

Distinguishing Features: A more delicate, spinose galatheid than the other species, with thin chelae bearing many spines, including a diagnostic row along the ventral border of the merus, a feature absent in the other species. The eyes are very large, but the setae arising from the corneal margins are not elongated to any degree. *M. tenuimana* often has a pair of spines on the cardiac region of the carapace and a row of pronounced spines along its posterior edge.

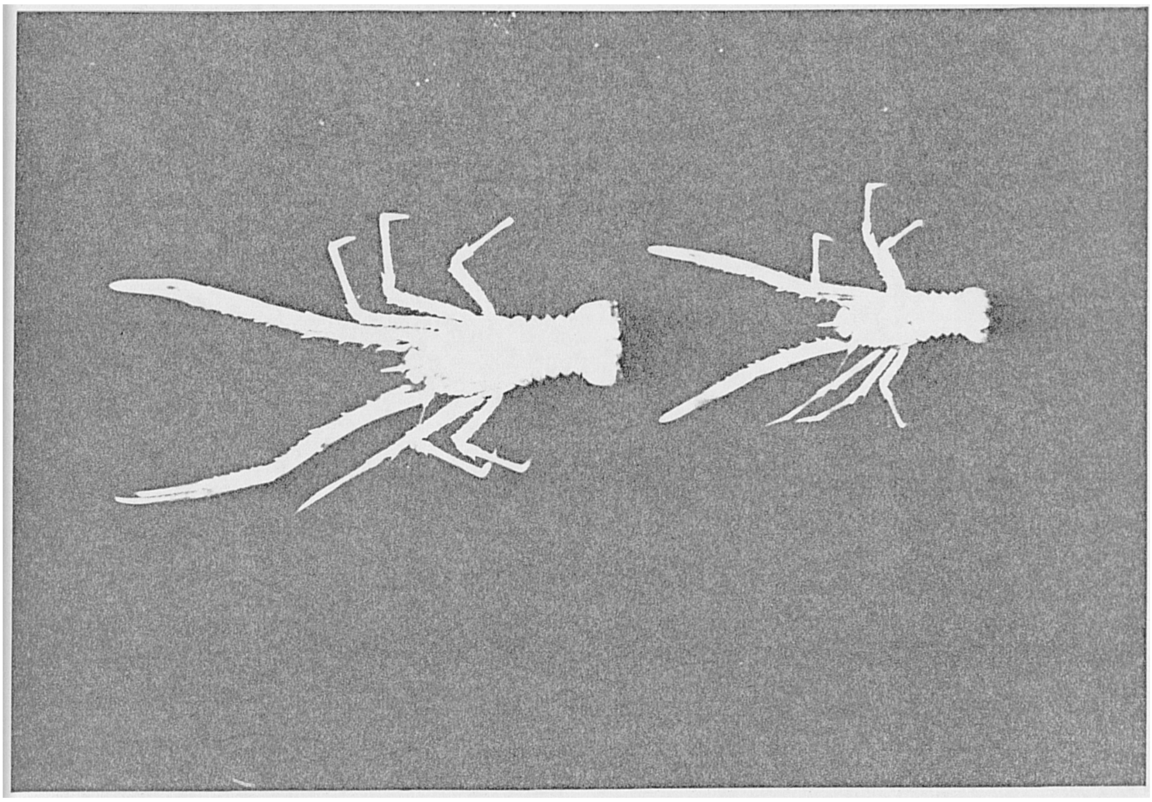


Plate 1: Fresh *Munida sarsi* taken from 450 m (Station 52404#4).

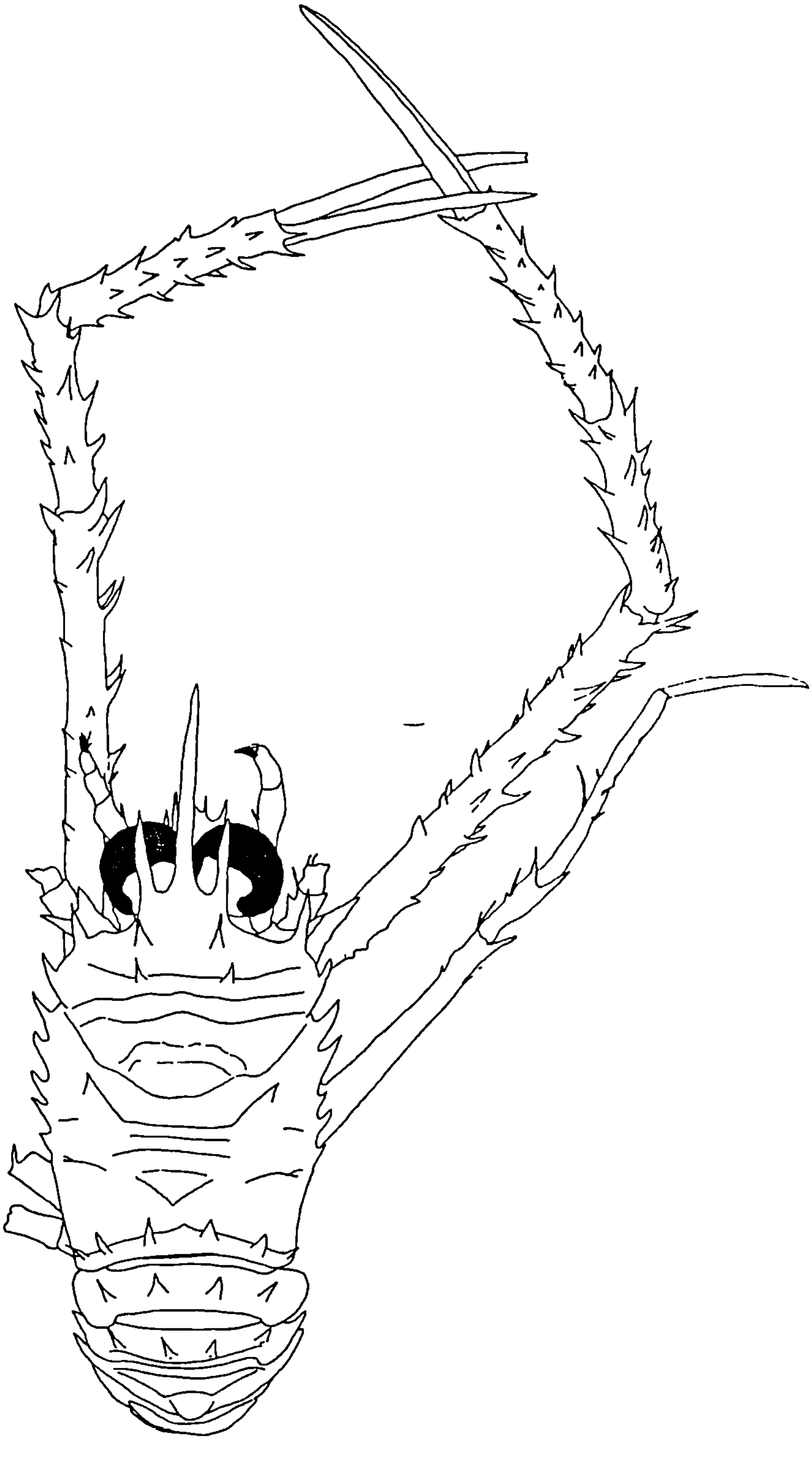


Fig. 5: Male *Munida tenuimana,* CL. 10·3 mm.

Generally, all spines on the carapace, abdomen and limbs are more pronounced than the other species. Like *M. sarsi* there is no spine on the merus of the third maxilliped, but in contrast there are very few sternal plastron striae indeed, giving the sternal plates a smooth appearance.

Distribution: Eastern Atlantic from Iceland (Hansen, 1908), West Greenland (Stephensen, 1939) and Norway (Brinkmann, 1936) south to Portugal/Spain and the Mediterranean (Zariquiey Alvarez, 1946, 1952). The upper limit of the depth range appears to vary geographically, being reported shallow (120-280 m) off Iceland by Stephensen, 1939, 250-300 m by Brinkmann (1936) in Norway and 400 m in the Mediterranean (Zariquiey Alvarez, 1946). In the Porcupine Sea-bight it appears to be limited to deeper water, the depth range found in this study being 740-1410 m. *M. tenuimana* has been found as deep as 1775 m in the Mediterranean. A total of 123 individuals were caught (≈6 %).

Munida micropthalama A. Milne Edwards, 1880. (Fig. 6).

Distinguishing Features: Distinctly different in general appearance from the other three species, seeming very squat with short, broad extremely setose chelae. The eyes are tiny, with the cornea being no wider than the eyestalk. There is a row of 6-8 protuberances across the gastric region of the carapace. The merus of the third maxilliped bears two spines on the inner margin.

Distribution: *M. micropthalama* is the most widespread of the four species considered here, though it is by far the least common in the Porcupine Sea-bight samples, being represented by only two specimens (0·1 % of the total sample). It has been recorded from regions across the whole of the North Atlantic from Iceland (Hansen, 1908) to the Cape Verde Islands (Henderson, 1888) in the east, the Gulf of Mexico (Pequegnat & Pequegnat, 1970) and the West Indies (Chace, 1942) in the West and the Mid-Atlantic Bight (Wenner, 1982). It is by far the deepest of these munidids reported between 194 m (Iceland: Hansen, 1908) and 2129 m off Ascension Island (Chace, 1942). Both specimens in this study were caught in sample 10111#8

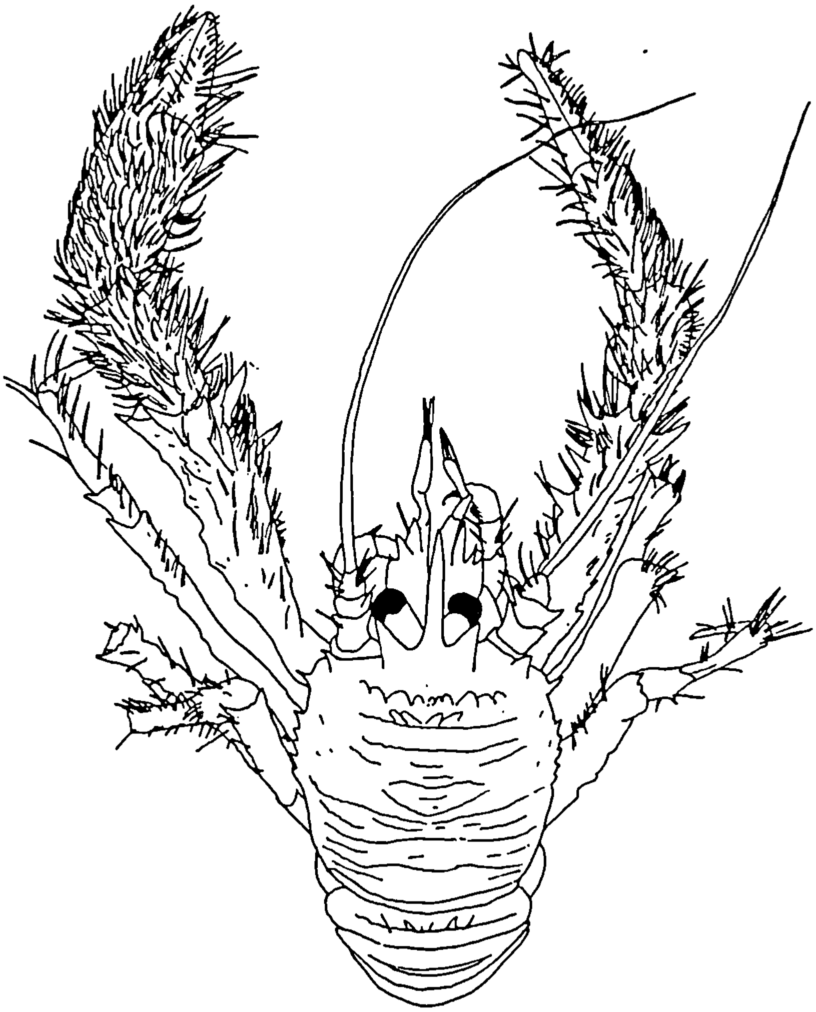


Fig. 6: Male *Munida micropthalama*, CL. 8·1 mm.

between 1630-1640 m.

Details of the biology of *Munida sarsi* and *Munida tenuimana*.

This study has concentrated on the two main deep-sea galatheids represented in sufficient numbers, *Munida sarsi* and *Munida tenuimana*. *Munida rugosa* is basically a continental shelf anomuran, extending to the edge of the continental slope in the Porcupine Sea-bight and will be used where appropriate as a comparison. For this purpose, *M. rugosa* from the Irish Sea were collected and studied. *M. micropthalama* is represented by too small a number of specimens for further analysis.

Length frequency analysis.

The 1933 *M. sarsi* were represented by 863 females (44·65 %) and 1059 males (54·75 %) with 11 individuals too small to be sexed. These were termed "immature". The sample of 123 *M. tenuimana* was composed of 61 females and 61 males, with a single immature.

The CL of all mature *M. sarsi* and *M. tenuimana* were measured and divided into 1 mm CL size intervals for both males and females. The results form Tables 2 and 3. These data are represented graphically in Figs. 7 and 8. The general form of the curves for *M. sarsi* corresponds well with the graphs constructed by Brinkmann (1936) for his study on the populations of galatheids in Norwegian fjords, with the fairly narrow peak representing the majority of the population skewed to the left leaving a long tail of larger individuals. Brinkmann's peak for males stretched from 12-18 mm CL, extremely similar to the Sea-bight population studied here, the peak for females being more acute and at a slightly smaller size. However, despite examining over 18,000 specimens, Brinkmann's tail of large individuals did not extend beyond 28 mm, the population from the Sea-bight being represented by individuals

Carapace Size Interval (mm)	Frequency Females	Males
4	1	0
5	1	3
6	1	0
7	2	3
8	0	4
9	2	3
10	3	2
11	4	3
12	7	6
13	3	6
14	13	9
15	9	4
16	6	5
17	1	6
18	2	3
19	1	1
20	0	0
21	1	0
No Carapace:	3	3
TOTAL	61	61

Table 3: Length frequencies for both sexes of *Munida tenuimana* when divided into 1 mm size classes.

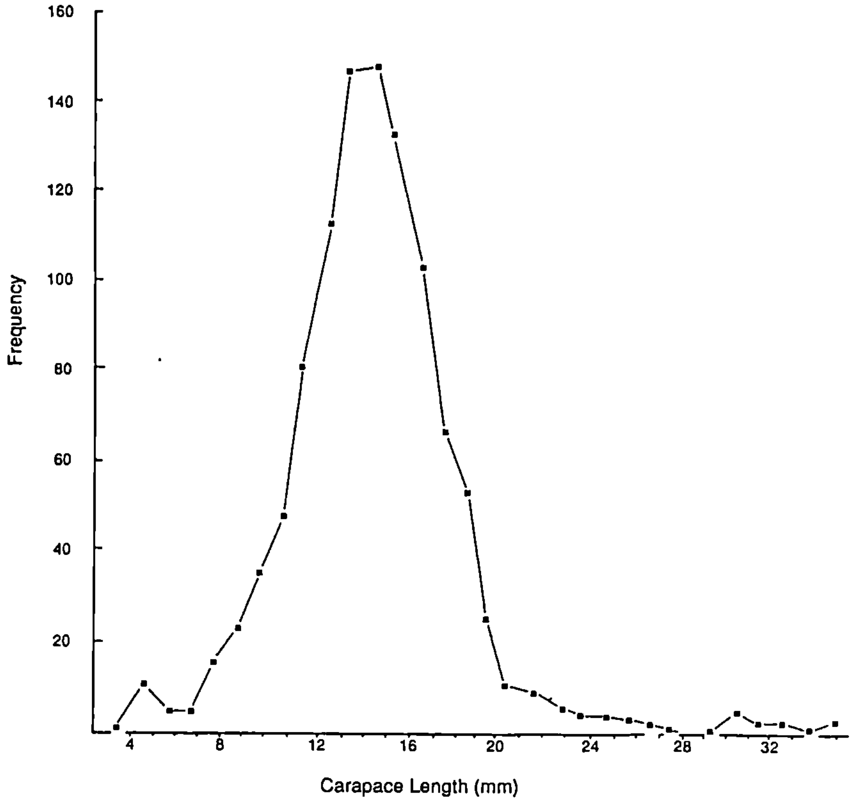


Fig. 7a: Length frequency polygon for 1 mm size classes of male *Munida sarsi.*

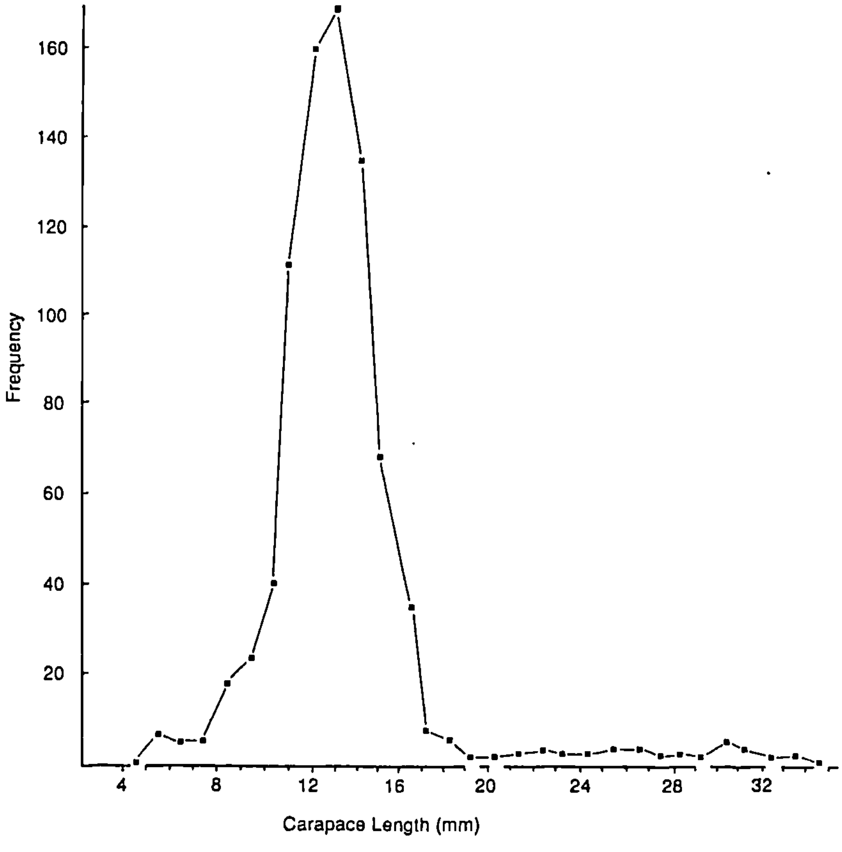


Fig. 7b: Length frequency polygon for 1 mm size classes of female *Munida sarsi.*

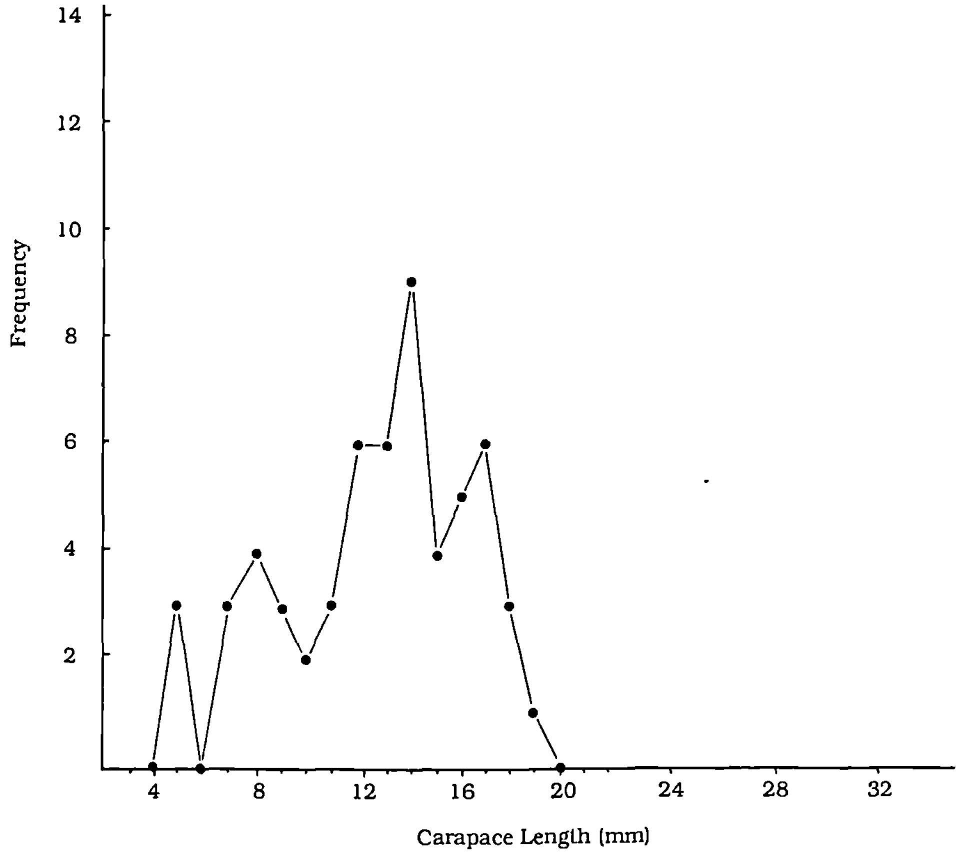


Fig. 8a: Length frequency polygon for 1 mm size classes of male *Munida tenuimana.*

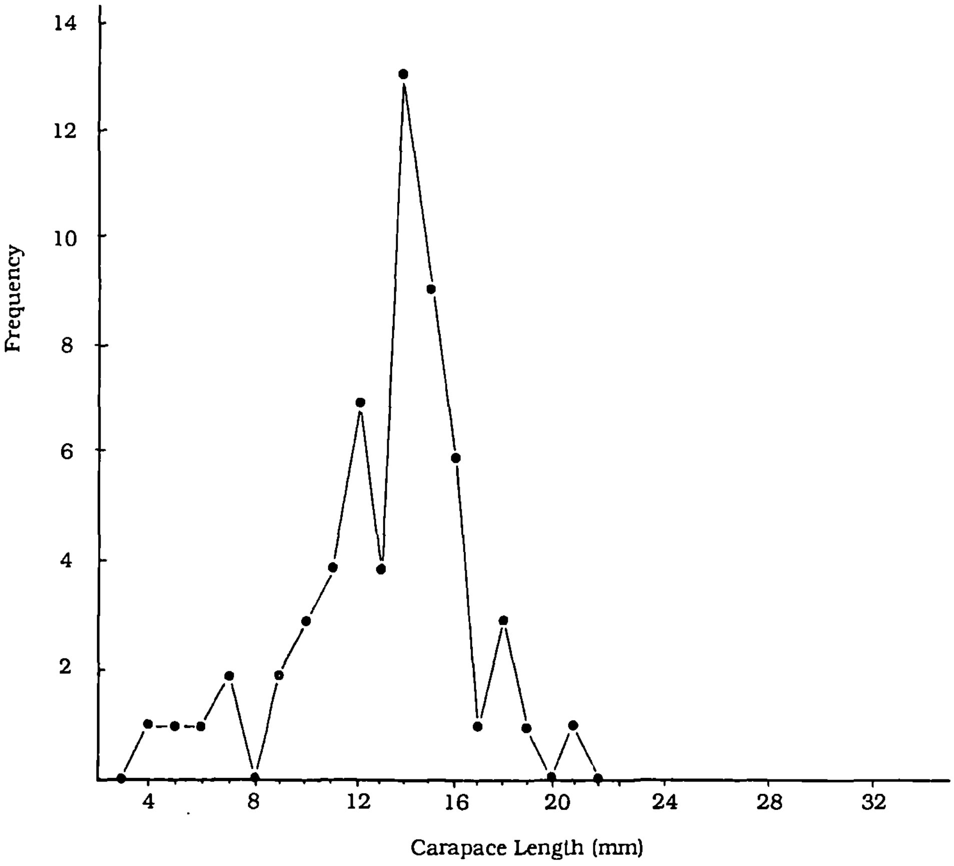


Fig 8b: Length frequency polygon for 1 mm size classes of female *Munida tenuimana.*

up to 34 mm CL. All the large specimens were collected at one station, namely 51302. This incongruous sample will be discussed later.

The graphs for *M. tenuimana* show a slightly different pattern, with a less prevalent peak, especially for males, and no individuals larger than 22 mm. The lack of real peak is probably a function of the smaller sample size.

Brinkmann attempted to discriminate different year classes in his population from observations on growth rates made in the laboratory, and defined the first three year classes as the following sizes of CL:

1 year old	3·8-4·8 mm.
2 years old	6·7-7·7 mm.
3 years old	10·5-11·5 mm.

After 3 years, the animals become mature (at c. 12·5 mm CL) and most live for about another three years. The main peak in the size frequency graphs (Figs. 6 & 7) would therefore correspond to this three year band of mature animals, the tail being those that live longer than six years. Estimating from Brinkmann's figures for laboratory determined average moult increment, the largest individuals must be at least 14 years old if they have lived under the same growth regime.

Biomass and density.

Density (No. Individuals ha^{-1}) and biomass (g. wet weight ha^{-1}) were calculated, using the methods described earlier, for each sample of *M. sarsi* and *M. tenuimana* where the data available made such computations possible. The figures obtained (Tables 4 and 5) were related to the mean depth of the sample and plotted out to give a clearer indication of the population structure in relation to depth (Figs. 9 and 10).

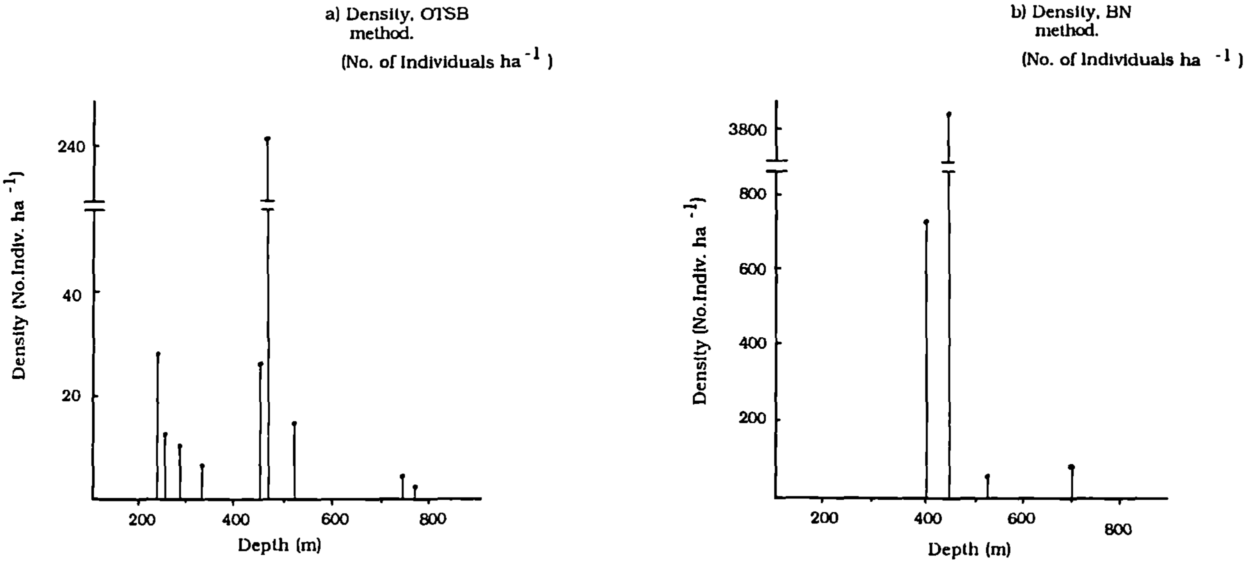
From these graphs it can be seen that both *M.sarsi* and *M. tenuimana* have a certain small

Station Number	Gear Used	Mean Depth (m)	Area Sampled (ha)	Number of Individuals ha^{-1}	Wet weight ha^{-1}
9777#2	OTSB	243	6.70	27.3	85.1
50523	OTSB	473	3.34	242.6	756.3
50524	OTSB	763	6.06	4.1	10.1
50607#2	BN	700	0.15	74.8	23.7
50609#1/ 10120#1	BN	400	0.17	721.9	1430.3
50702	OTSB	785	2.55	2.0	0.6
50806	OTSB	513	4.46	14.1	50.9
51025	OTSB	470	3.50	25.4	108.2
51112#1	BN	523	0.20	50.0	144.1
51302	OTSB	330	5.89	6.3	138.9
51319	OTSB	265	3.67	12.6	33.0
51401	OTSB	297	3.67	10.4	46.2
52404#4	BN	450	0.10	3843.1	10536.1

Table 4: Biomass data. Biomass (g Wet Weight ha^{-1}) and Density (Number individuals ha^{-1}) of *Munida sarsi* at each sample station calculated using either semi-balloon otter trawl or benthic net attatched to an epibenthic sled. (50609#1 and 10120#1 have been combined, having the same mean depths).

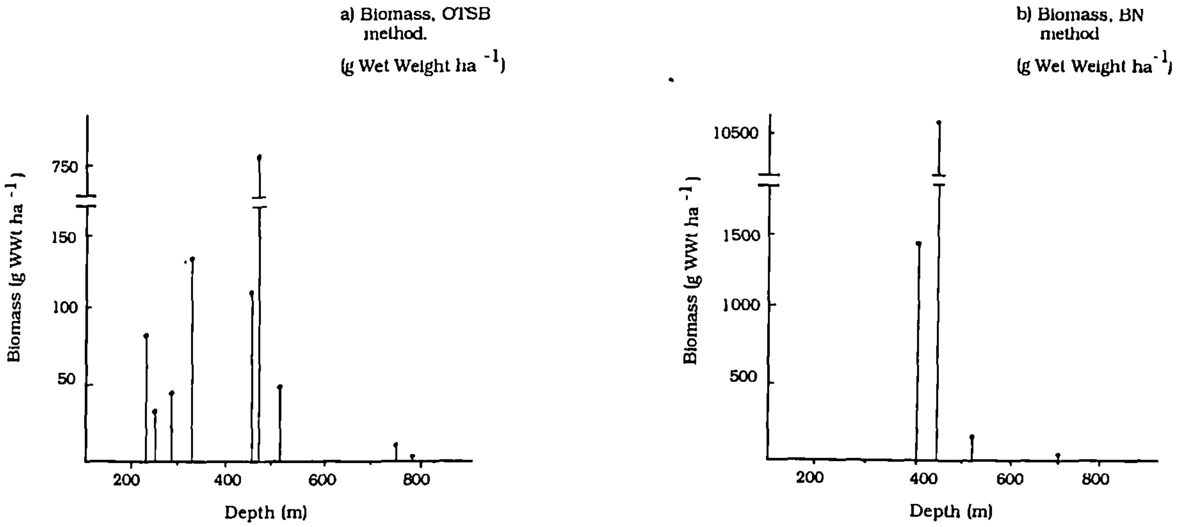
Station N^{o}.	Gear Used.	Mean Depth (m).	Area Sampled (ha).	N^{o}. indiv. ha^{-1}.	WWt (g) ha^{-1}
9752 #1	OTSB	1025	3·352	0·9	3·4
10109#8	BN	1125	0·816	1·2	11·2
10110#1	BN	925	0·552	9·1	18·8
50503	OTSB	1017	3·666	0·6	1·9
50522	OTSB	983	3·826	1·8	4·0
50601	OTSB	849	5·100	0·4	0·1
50606#1	BN	1115	0·137	14·6	51·5
50606#2	OTSB	1100	4·140	1·0	4·3
50606#5	BN	1130	0·419	2·4	10·1
50610#1	BN	980	0·076	13·1	7·9
50611#1	OTSB	1388	6·217	0·2	0·6
50705	OTSB	743	3·347	0·3	0·9
51023	OTSB	1273	3·190	0·3	1·0
51103#5	BN	940	0·247	4·1	24·6
51206	OTSB	1205	1·136	15·0	38·6
51304	OTSB	790	6·539	0·3	0·4
51306	OTSB	1218	3·029	3·6	11·2
51403#1	BN	1303	0·448	2·2	2·2
51403#2	BN	1321	0·236	12·7	1·5
51403#5	BN	1293	0·203	9·8	23·5
51404	OTSB	750	4·140	0·5	0·9
51420#1	BN	1327	0·172	5·8	14·7
51420#3	BN	1296	0·117	51·3	64·4
51707#1	BN	1218	0·951	6·3	3·5
51810	OTSB	1016	3·990	0·3	0·6
52105	OTSB	1240	4·944	2·0	4·9

Table 5:<u>Biomass data:</u> Biomass (g Wet Weight ha^{-1}) and density (Number of Individuals ha^{-1}) of *Munida tenuimana* at each sample station, calculated using either semi-balloon otter trawl or benthic net mounted on an epibenthic sled.


a) Density, OTSB method. (No. of Individuals ha^{-1})

b) Density, BN method. (No. of Individuals ha $^{-1}$)

Fig. 9a: *Munida sarsi:* Density at each sample station in relation to depth.


a) Biomass, OTSB method. (g Wet Weight ha $^{-1}$)

b) Biomass, BN method (g Wet Weight ha^{-1})

Fig. 9b: *Munida sarsi:* Biomass at each sample station in relation to depth.

depth range where they are most abundant. For *Munida sarsi* this lies between 450-480 m, with both of the extremely large peaks for BN and OTSB being at 450 and 473 m respectively. More *M. sarsi* were caught between this narrow depth range than over the whole of the rest of its range between 200-800 m. Rice & Saint Laurent (1986) noted that in the NE Atlantic generally *M. sarsi* seemed to be most abundant between 250-400 m, so in the Porcupine Sea-bight this depth band of peak abundance is deeper and much narrower. As would be expected, the graphs for biomass and density are similar with one notable anomaly-sample 51302 at 330 m, which has a low density (6·3 Ind. ha^{-1}) but high biomass (138·9 g. WWt. ha^{-1}). This is the peculiar sample composed entirely of very large individuals which will be dealt with separately later.

Munida tenuimana also has a distinct peak in abundance, in this case lying between 1200-1300 m, the overall densities being much lower than *M. sarsi.*

Figs. 9 and 10, when taken together, give an indication of the population structure of the two most abundant species of galatheid found in the Porcupine Sea-bight, *M. sarsi* succeeding *M. rugosa* at around 200 m, with some overlap, and becoming more abundant between 450-480 m. The abundance then drops markedly as the extreme of its bathymetric range is reached towards 800 m. Here it overlaps with *M. tenuimana,* which at these depths is in extremely low numbers and doesn't reach its peak of abundance until after 1200 m. The difference in the maximum abundance between the two species is quite striking, *M. sarsi* having a density at 450 m around 75 times as great as the *M. tenuimana* peak at 1296 m and a biomass over 160 times as large.

It was mentioned earlier that the upper limit of *M. tenuimana* is much deeper in the Porcupine Sea-bight than that reported from other areas, so could it be that *M. tenuimana* is forced lower on the slope due to competition with the extremely abundant *M. sarsi* here, the aggressive behaviour of *M. sarsi* when defending feeding territory having been reported by Berrill (1970). In many other areas the two species co-exist over a large part of the range, but in the Porcupine Sea-bight there is very little overlap. Unfortunately, there are no other data for biomass or density in the few similar studies. However Brinkmann (1936) caught 18,500 *M. sarsi* and 10,000 *M. tenuimana* over the many years of his study, all from above 500 m - a much more even distribution of numbers between the two species than the 15:1 ratio of *M. sarsi* to *M. tenuimana* observed in this study. It could therefore be the case that the *M. tenuimana* in the Porcupine Sea-bight are prevented from extending their range upwards by the presence of high densities of the more competitive *M. sarsi* in this region.

Brinkmann also believed that small *Munida sarsi* settle in shallow water and migrate down to deeper regions when they become sexually mature after 3 years. If this is the case, then the shallowest samples should be composed of many small immature individuals and there should be an increase in the average size of each individual in the population with an increase in depth. To investigate whether this pattern existed in the Porcupine Sea-bight, the mean wet weight for each sample was calculated and plotted (Table 6, Fig. 11.), the result expected for Brinkmann's hypothesis being an increase in the mean wet weight with depth. As can be seen from Fig. 11 this is not the case, the mean sizes being very consistent across the depth range with, if anything, a decrease in the mean wet weight below 700 m. Small *M. sarsi* were also found across the whole depth range, including two samples of post-larval settling individuals, caught using a Multiple Rectangular Midwater Trawl (RMT 1+8M) (see Roe & Shale, 1979). Both samples were taken 20 m off the sea bed, the first composed of 50 individuals from 388 m and the second 86 specimens from 668 m. Brinkmann's pattern of size distribution does therefore not occur in the Porcupine Sea-bight population.

The points at 330 m are for the sample 51302, highlighting once again the difference in the size of the individuals between this sample and the rest of the population, which will be dealt with later.

Station Number.	Mean Depth (m)	No. of Males.	Mean Wet Weight (g)	± 95% Confidence	No. of Females	Mean Wet Weight (g)	± 95% Confidence
CW01	280	27	4.32	1.16	6	1.53	1.03
9777#2	243	85	3.54	0.54	98	2.75	0.22
50523	473	443	3.64	0.18	369	2.48	0.20
50524	763	14	2.57	0.95	11	2.29	0.58
50607#2	700	4	0.18	0.05	7	0.40	0.19
50609#1/ 10120#1	400	72	1.91	0.58	50	2.08	0.63
50702	785	1	0.46	—	4	0.26	0.14
50806	513	53	3.69	0.79	10	3.17	1.14
51025	470	61	4.84	0.57	28	2.97	0.33
51112#1	523	6	3.88	2.09	4	1.39	1.35
51302	330	14	24.12	6.84	23	20.89	2.98
51319	265	35	2.69	0.79	11	2.43	0.83
51401	297	19	5.75	1.67	19	3.17	0.64
52404#4	450	213	3.07	0.21	179	2.35	0.14

Table 6: Biomass data. Mean wet weight of *Munida sarsi* at each sample station. (50609#1 and 10120#1have been combined, having the same mean depths.)

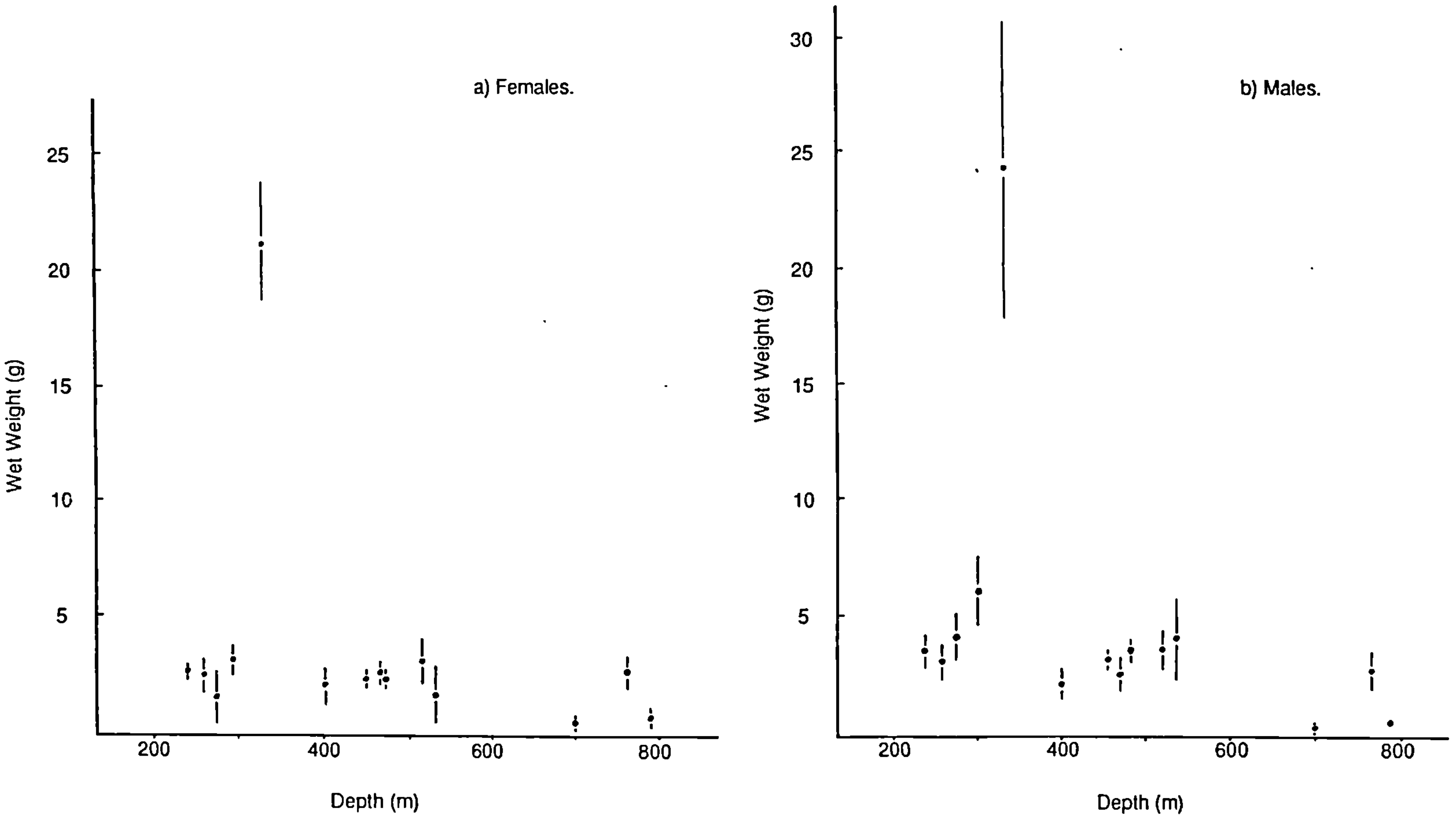


Fig. 11: *Munida sarsi:* mean wet weight at each sample station in relation to depth.

Relative Growth Data.

For both male and female *M. sarsi* and *M. tenuimana*, the values for $\log_{10}$ChL were plotted against $\log_{10}$CL to investigate the relationship between the growth of the chelae and that of the carapace (Table 7; Figs. 12-15.). Ingrand (1937) investigated the chela development of *M. rugosa* (as *M. bamffica*) and found an increase in the relative rate of male chela growth at a CL of around 11·5, which she correlated to the moult of sexual maturity. There is no evidence for this occurring in *M. sarsi* (Fig. 12), but it is noted that the group of points represented by the smallest individuals fall some way from the line. To investigate this further more samples of small male *M. sarsi* with intact chelae would have to be taken. However, two interesting points do arise from these graphs. Firstly, the relative rate of chela growth is greater for both sexes of *M. sarsi* than for *M. tenuimana*, the thin chelae of *M. tenuimana* obviously looking deceptively long. Secondly, the two different regressions for female *M. sarsi*, the largest specimens (>19 mm) have signs of a lower relative growth figure than the bulk of the population, though this is not particularly distinct. Males may also show a different rate, but there were too few large males with chelae still attached to demonstrate this. The large specimens demonstrating the different growth rate belong to the sample 51302.

Another interesting feature of the chela morphology was the development of a different propodus form in some of the larger specimens. The fixed finger develops an arch, so creating a space between the fixed finger and the dactyl (Fig. 16 a, Plate 2), with an accompanying change in the dentition of the dactyl and an increase in the number of setae. This chela form is not restricted to the sample 51302, but is found in some larger specimens (> 17 mm) from the general population. However, it is not a constant feature as some of the largest individuals have no trace of this structure. Generally this chela form is restricted to males, only being present on the largest females from 51302.

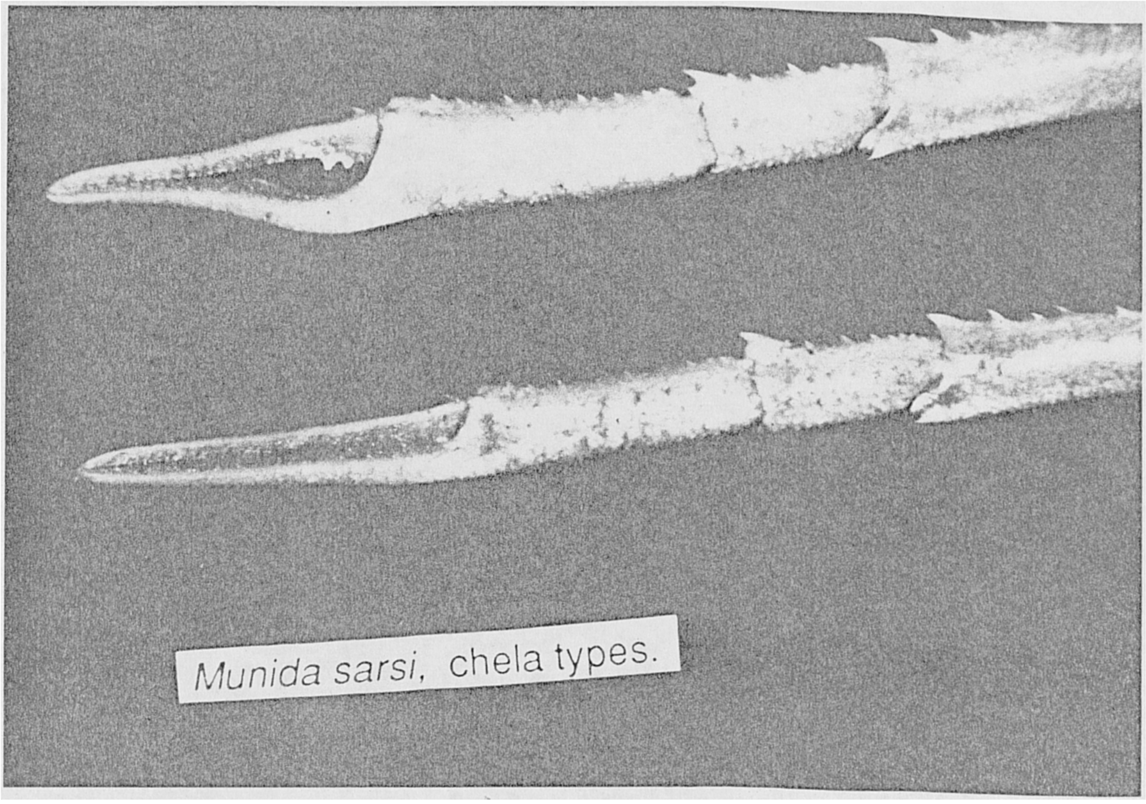


Plate 2: *Munida sarsi* chela types. Above: the 'arched' type, below: the standard form.

Species.	Sex.	Fig. N^{o}.	Correlation.	R-squared.	Slope (b).	Intercept (a).	n-val
Munida	Male.	12	0·97	0·94	**1·20**	0·40	319
sarsi.	Female a).	13	0·93	0·87	**1·00**	0·59	208
	b).	13	0·89	0·80	**0·83**	0·82	11
Munida	Male.	14	0·98	0·97	**1·06**	0·57	28
tenuimana	Female.	15	0·97	0·94	**0·91**	0·72	25

Table 7: Statistics relating to the Chela length (ChL) against Carapace Length (CL) regression (Figs. 12-15) for both sexes of *Munida sarsi* and *Munida tenuimana,* where $\log_{10}ChL = b.\log_{10}CL + a$.

Symbols used on regression figures.

- ∘ 1 datum point.
- o 2-5 data points.
- ○ 6-10 data points.

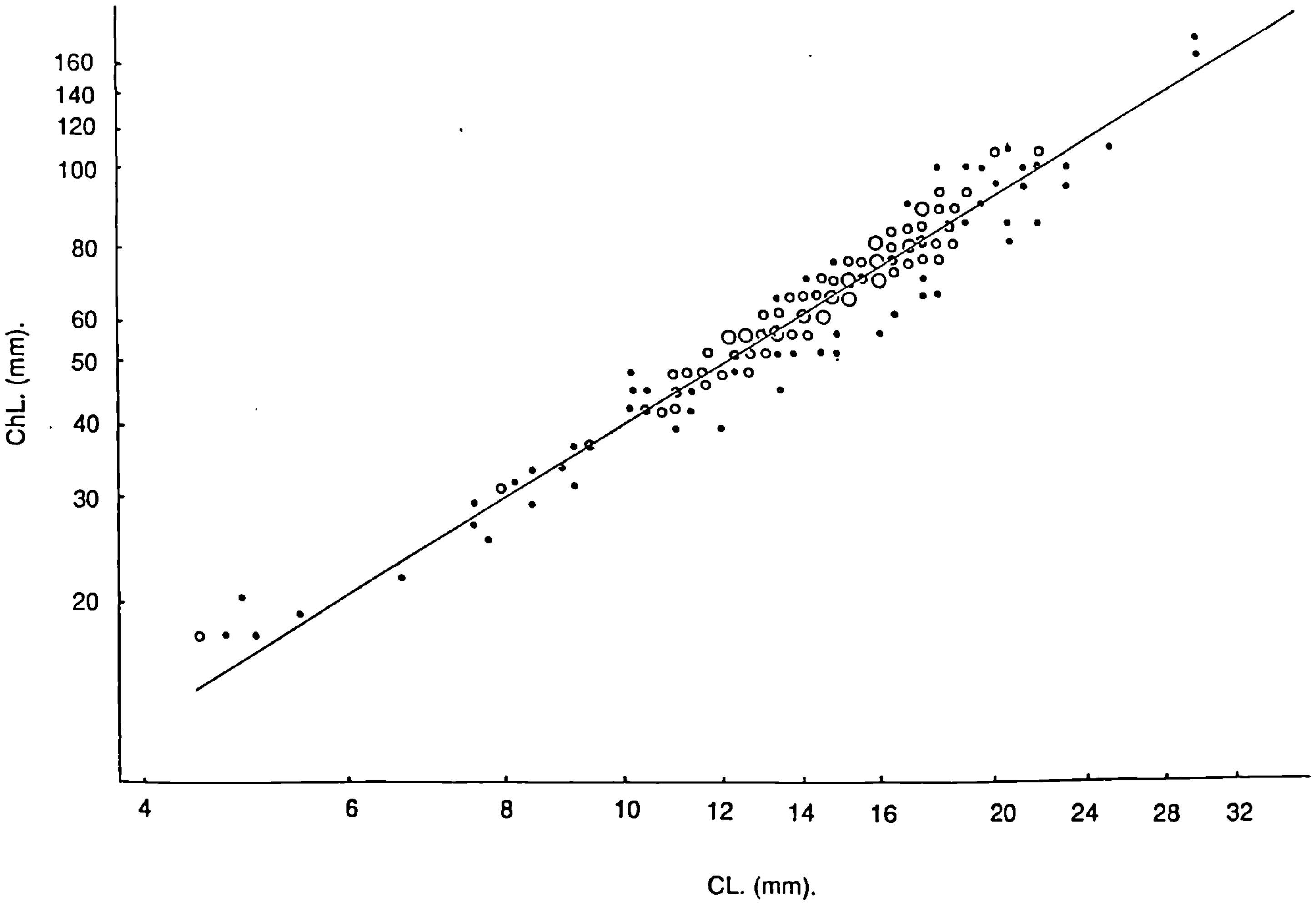


Fig. 12: Regression of $\log_{10}$ChL. against $\log_{10}$CL. for male *Munida sarsi.*

$\log_{10}ChL=1{\cdot}20 \log_{10}CL+ 0{\cdot}40.$

n=319.

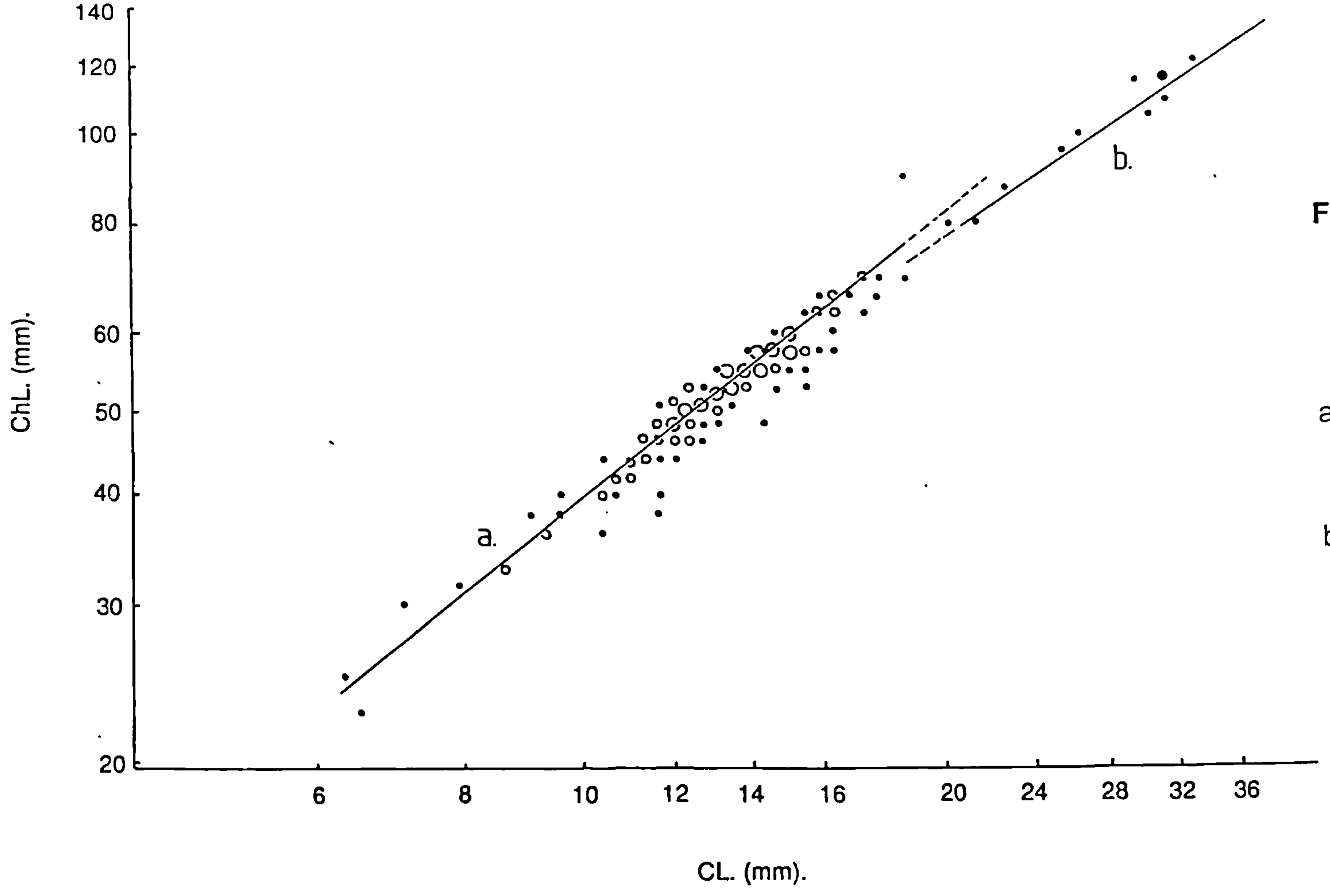


Fig. 13: Regression of $\log_{10}$ChL. against $\log_{10}$CL. for female *Munida sarsi.*

a). $\log_{10}ChL = 1{\cdot}00 \log_{10}CL + 0{\cdot}59$. n=208.

b). $\log_{10}ChL = 0{\cdot}83 \log_{10}CL + 0{\cdot}82$. n= 11.

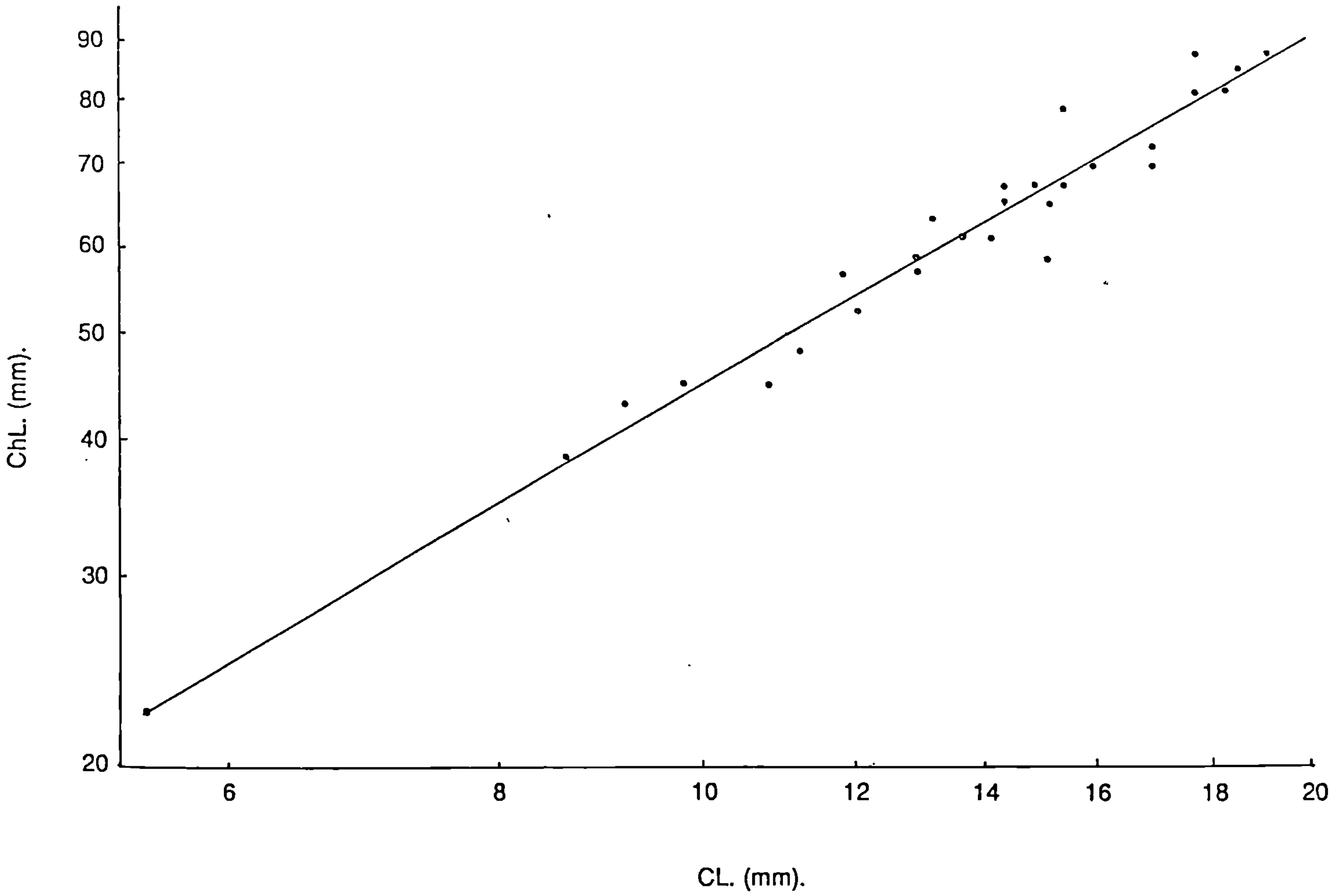


Fig. 14: Regression of $\log_{10}$ChL. against $\log_{10}$CL. for male *Munida tenuimana.*

$\log_{10}ChL=1{\cdot}06 \log_{10}CL+ 0{\cdot}57.$

n=28.

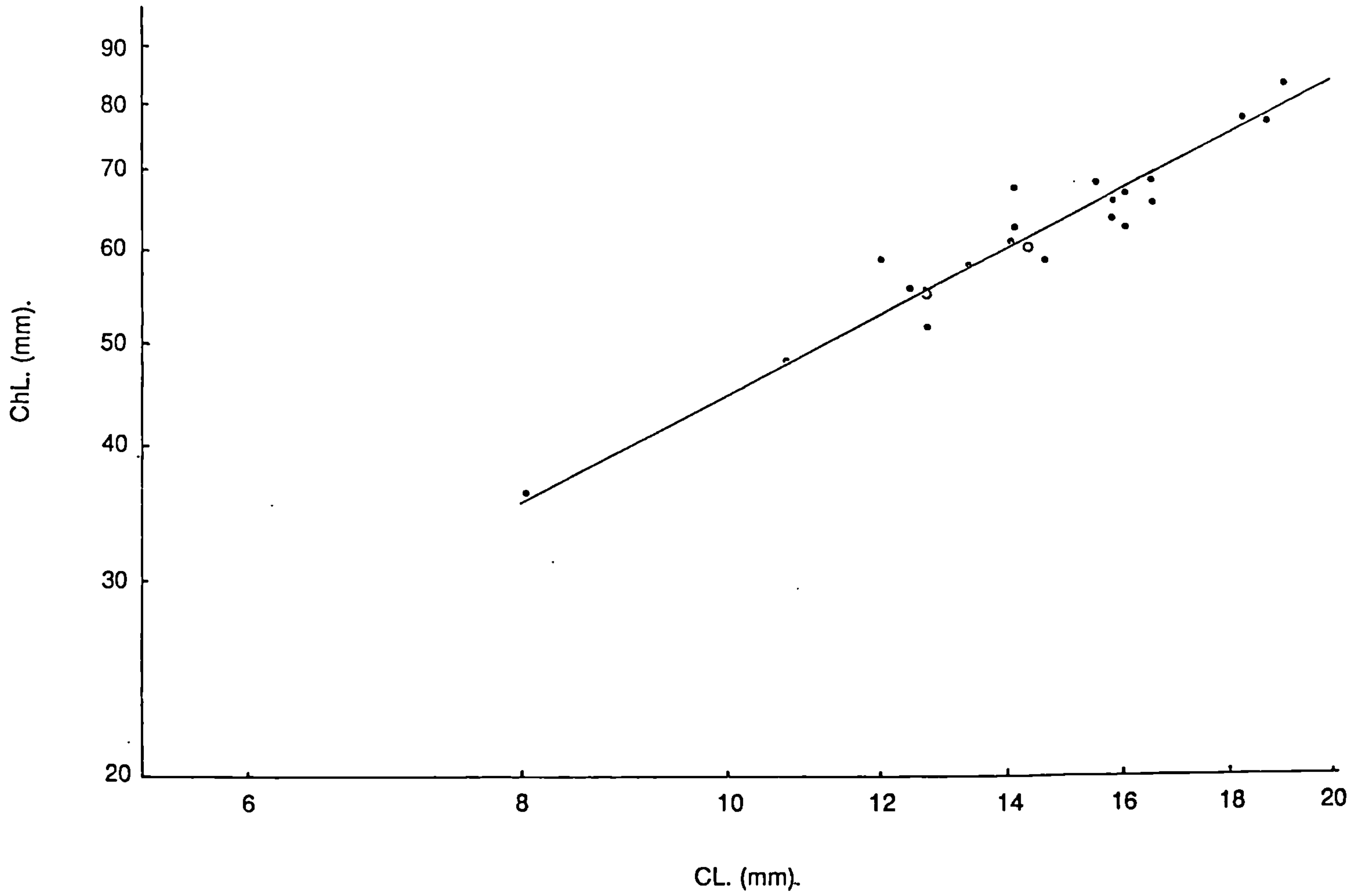


Fig. 15: Regression of $\log_{10}$ChL. against $\log_{10}$CL. for female *Munida tenuimana*.

$\log_{10}ChL = 0{\cdot}91 \log_{10}CL + 0{\cdot}72$.

n=25.

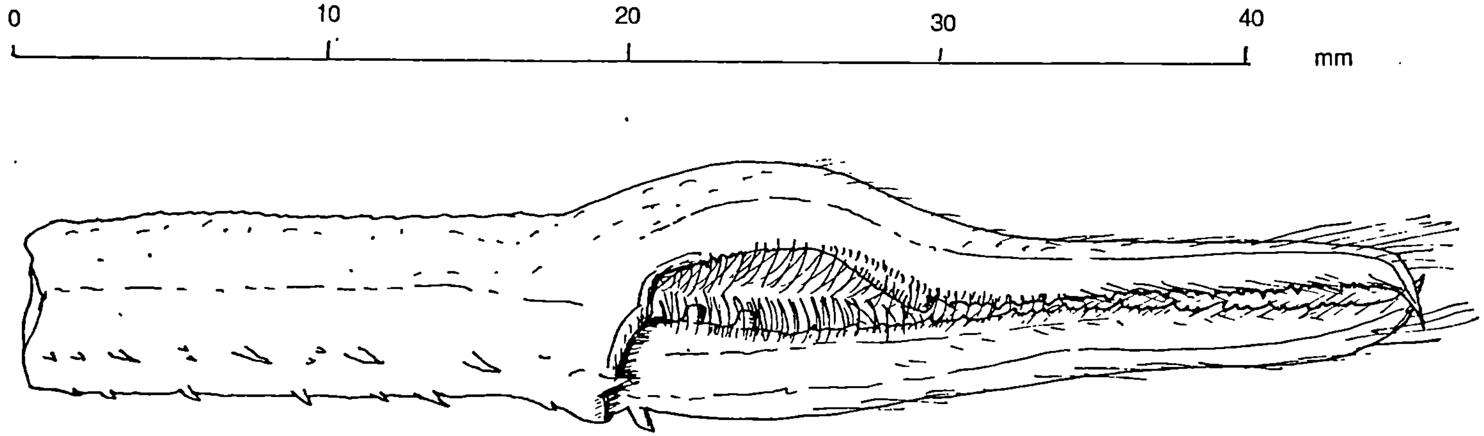


Fig. 16: 'Arched' chela of male *Munida sarsi*, CL. 19·3 mm.

Generally, morphological changes occur when a crustacean undergoes its moult of sexual maturity as seen in many Brachyura (Hartnoll, 1963, 1982). As mentioned earlier, Brinkmann suggested that *M. sarsi* becomes mature at a CL of at the most 11·5 mm, this figure being supported by this study. However, the change in chela morphology does not occur until an appreciably larger size, as can be seen from Fig. 17. Ingrand (1937) noted a similar chela development in *M. rugosa* (as *M. bamffica*), but in this case the development of the arched form related to sexual maturity at a CL of around 11·5 mm. Arching of the fixed finger can be observed in *M. sarsi* of around 15-16 mm CL, though this is much less acute than the final form. It would appear, therefore, that the change from the standard chela form (Plate 1b.) to the arched form takes more than one moult. There also appears to be a significant (Chi-squared, n=94, P<0.05) degree of handedness in the arched chela form, with 60 individuals demonstrating the form on the left chela and only 34 on the right. Three individuals have both chelae developed towards the arched form.

The benefits of this change in chela form are unclear, as are the cues that trigger the development, especially as not all individuals living in the same area undergo these changes. Males are sexually mature a long time before this change occurs, so it would appear unlikely that this development is related to mating or reproductive behaviour. Similarly, if the development was a successful anti-predator adaptation, which appears unlikely, then it would be expected that more, if not all, of the individuals in the population would have this chela form. A possible explanation is a change in diet, the larger individuals being able to handle food objects excluded due to their handling size from the smaller munidids. The chela morphology change may therefore be in response to this food availability and the development of the arched "crusher" claw enables the owner to exploit this food source, such as bivalves, more effectively. However, analysis of the stomach contents of individuals with and without the arched chelae show no evidence of any new food item. Why this modification is not a feature of all the individuals of the same size in one area is a mystery.

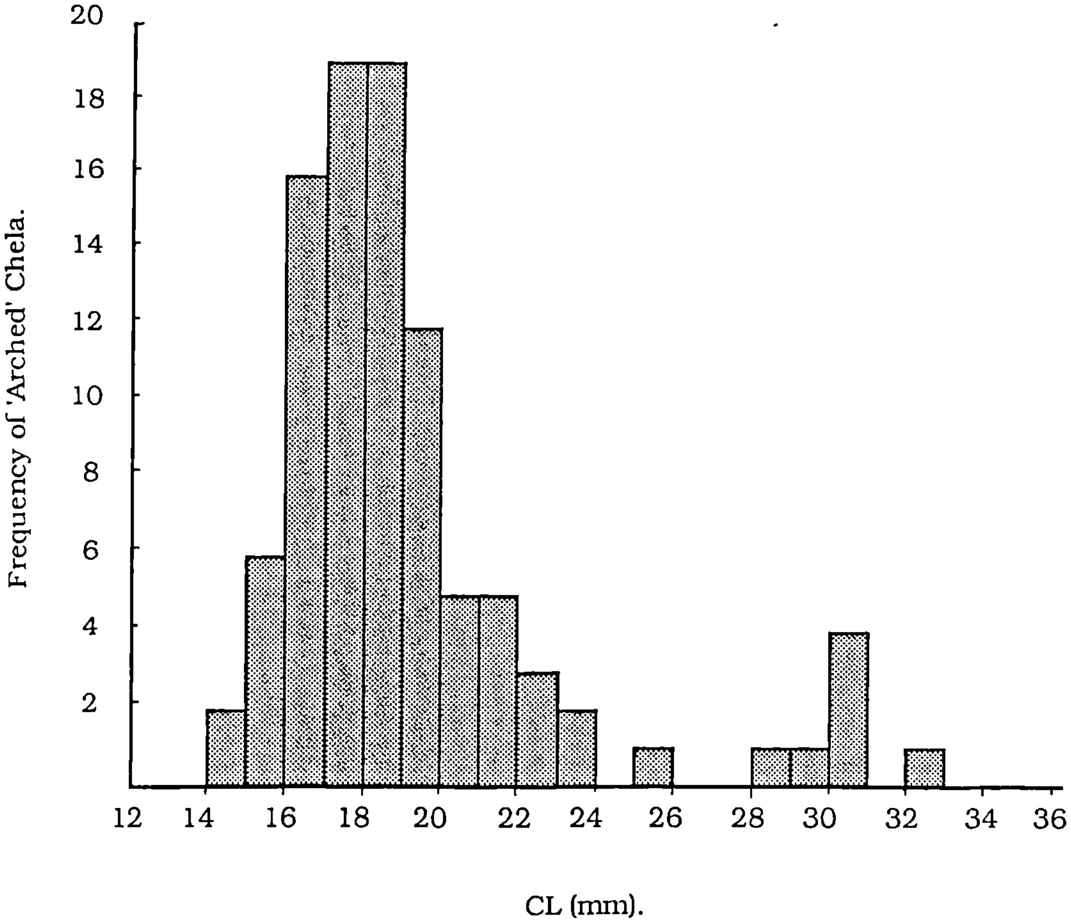


Fig. 17: Frequency of the 'arched' chela form in each mm size class of *Munida sarsi.* (Figures of percentage arched chelae in each size class are not valuable due to the many individuals that have lost one or more chelae during sampling and preservation).

Reproductive Cycles.

To investigate egg development, each individual mature munidid was classed under one of the following headings: No eggs present on the abdominal pleopods, very few (<50) plain eggs present, plain eggs present, eggs present <50% eyed and eggs present >50% eyed. These results allowed data for the proportion of the mature female population in each calender month to be obtained for *M. sarsi* and *M. tenuimana* from the Porcupine Sea-bight (Tables 8a, 8b.) and *M. rugosa* from the Irish Sea as comparison (Table 8c). From these data, graphs were constructed to demonstrate the egg development pattern for each species over the year (Figs. 18-20). Unfortunately, very few samples have been taken in the Sea-bight over the winter period, so some gaps exist in the data for the two deep-sea species. However, this does not totally obscure the general egg development patterns.

It can be seen from Figs. 18 & 20 that the annual egg development cycles of *M. sarsi* and *M. rugosa* are very similar, the eggs being laid in Autumn, developing over the winter period and hatching in March-April. The hatching of *M. rugosa* eggs in the aquarium was remarkably synchronised, all eggs hatching over a two day period 7-8 April 1987, despite the fact that females were kept in separate tanks with no interconnecting water supply. The pattern for *Munida tenuimana* is rather less distinct, with no definite cyclical egg production, though the data are patchy for this species and the sample sizes for each month are comparatively small. However, the patterns for both *M. tenuimana* and *M. sarsi* correspond well with those found by Brinkmann (1936), *M. sarsi* in that study laying in Sept-Oct and hatching in May while *M. tenuimana* eggs hatched in April-May and the females laid again in June/July. This pattern for *M. tenuimana* is corroborated by Fig. 19, the only period when none of the mature females were carrying eggs being May-June. However, the presence of well developed eyed eggs in July (Fig. 19c) suggests that Brinkmann's cycle is not so well defined in the Porcupine Sea-bight.

To investigate the reproductive cycles further, the state of the female ovaries was studied.

			Month			
% Females with:	D	J	F	M	A	M-O
Few small plain eggs	9.4	*	0.0	0.0	0.0	0.0
Plain eggs	65.2	*	6.3	0.0	0.0	0.0
Eggs <50% eyed	0.0	*	40.6	27.8	0.0	0.0
Eggs >50% eyed	0.0	*	50.0	61.1	4.3	0.0
No eggs	25.4	*	3.1	11.1	95.7	100.0
Total Females	181	*	34	19	123	686

Table 8a: Distribution of eggs over the year for mature *Munida sarsi:* percentage of females in each month carrying the different stages of egg development.

							Month			
% Females with:	O	N	D-J	F	M	A	M-J	J	A	S
Few small plain eggs	0.0	20.0	*	0.0	0.0	0.0	0.0	0.0	*	13.3
Plain eggs	76.0	20.0	*	0.0	0.0	0.0	0.0	20.0	*	40.0
Eggs <50% eyed	0.0	0.0	*	0.0	0.0	33.3	0.0	0.0	*	0.0
Eggs >50% eyed	0.0	0.0	*	60.0	33.3	33.3	0.0	20.0	*	0.0
No eggs	24.0	60.0	*	40.0	66.7	33.3	100.0	60.0	*	47.7
Total Females	13	5	*	6	3	7	6	7	*	15

Table 8b: Distribution of eggs over the year for mature *Munida tenuimana:* percentage of females in each month carrying the different stages of egg development.

				Month					
% Females with:	O	N	D	J	F	M	A*	M-A	S
Few small plain eggs	9.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8
Plain eggs	71.4	100.0	100.0	76.2	14.3	0.0	0.0	0.0	0.0
Eggs <50% eyed	0.0	0.0	0.0	23.8	47.6	9.5	0.0	0.0	0.0
Eggs >50% eyed	0.0	0.0	0.0	0.0	38.1	90.5	0.0	0.0	0.0
No eggs.	19.1	0.0	0.0	0.0	0.0	0.0	100.0	100.0	95.2

Table 8c: Distribution of eggs over the year for mature *Munida rugosa:* Percentage of females in each month carrying the different stages of egg development.

* = All eggs hatched 7-8 April. Most of April had no eggs.

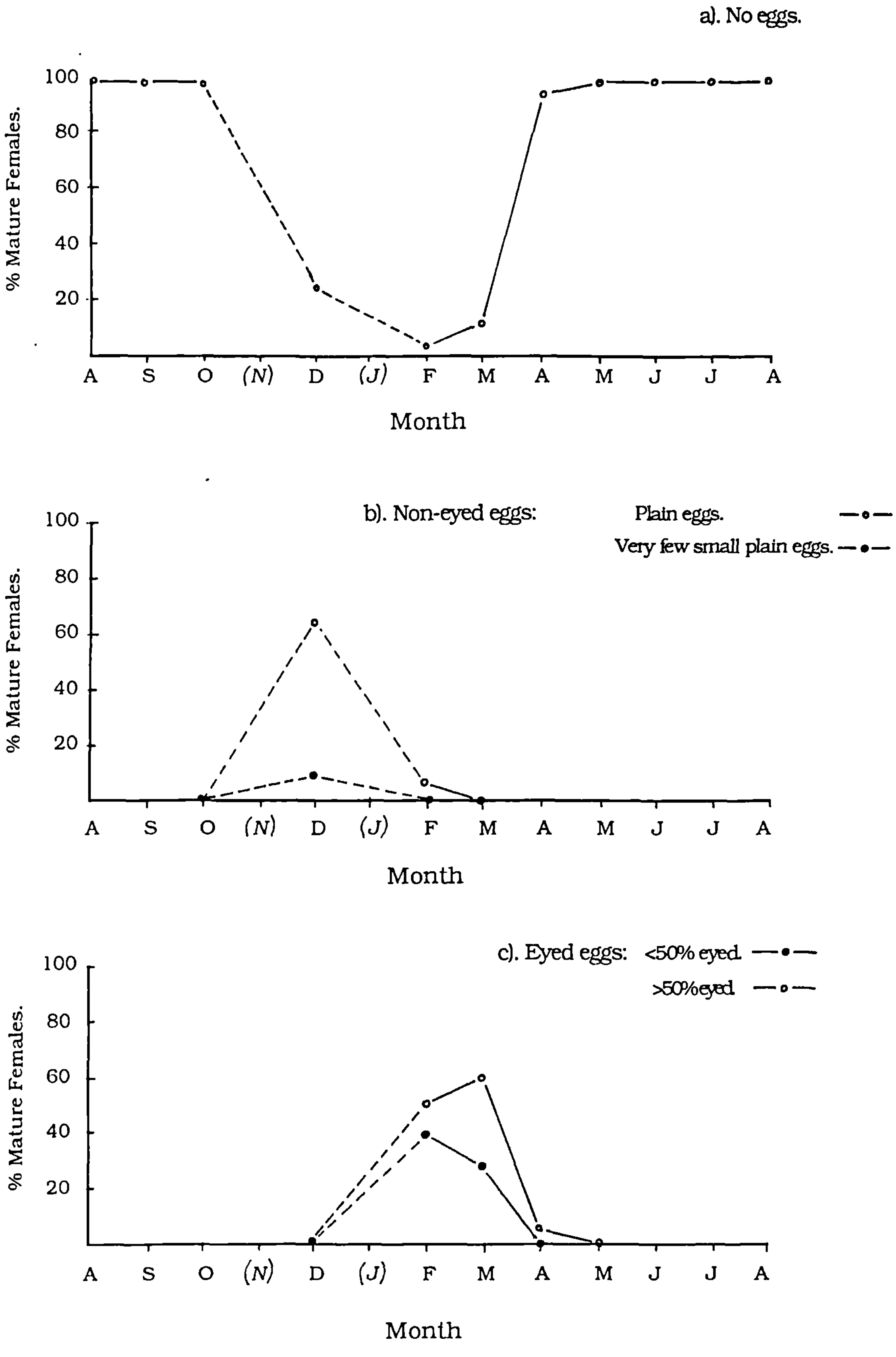


Fig 18: *Munida sarsi:* Egg development (months in parentheses = No data).

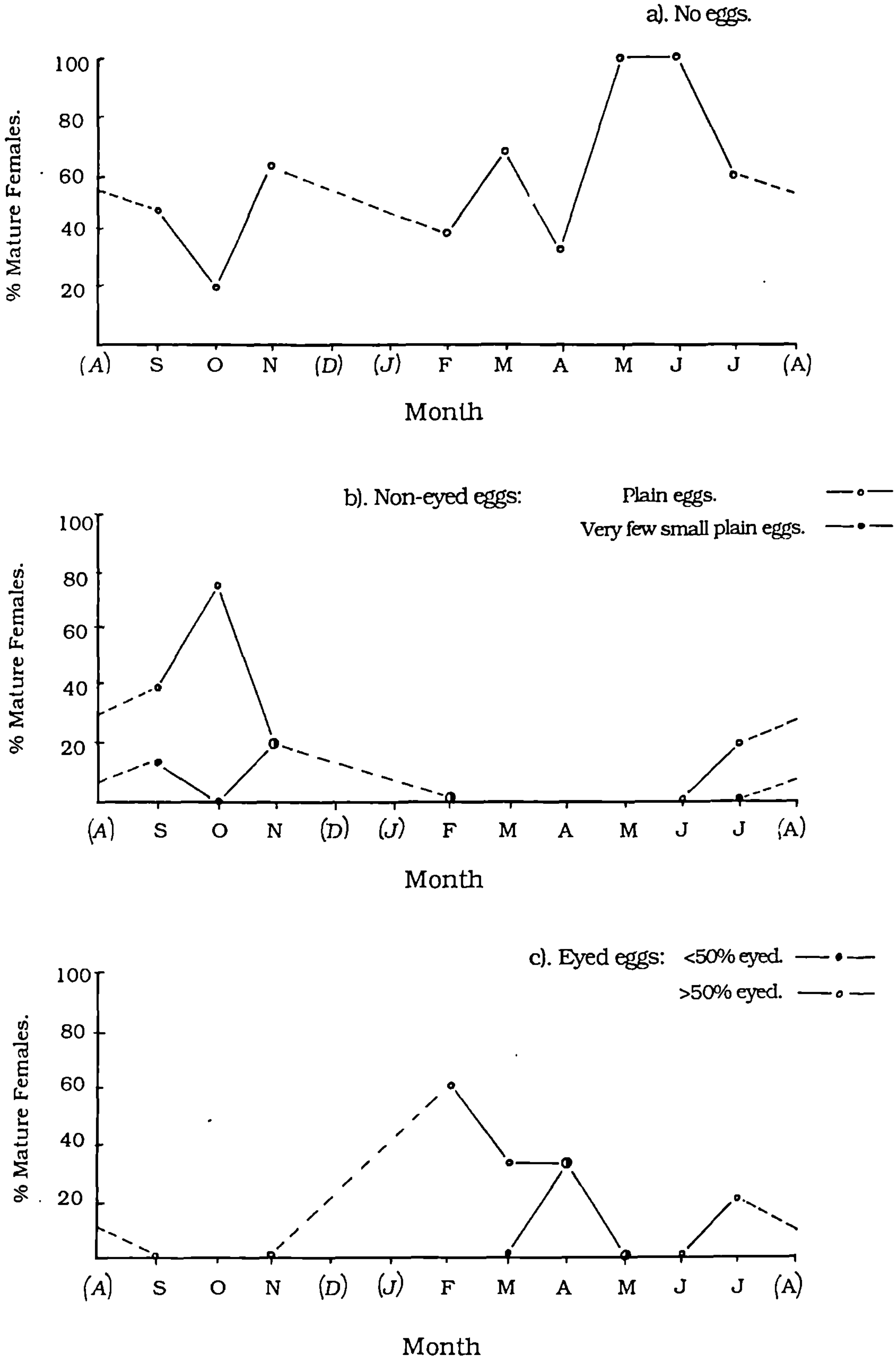


Fig 19: *Munida tenuimana:* Egg development (months in parentheses = No data).

a). No eggs.

b). Non-eyed eggs:

c). Eyed eggs:

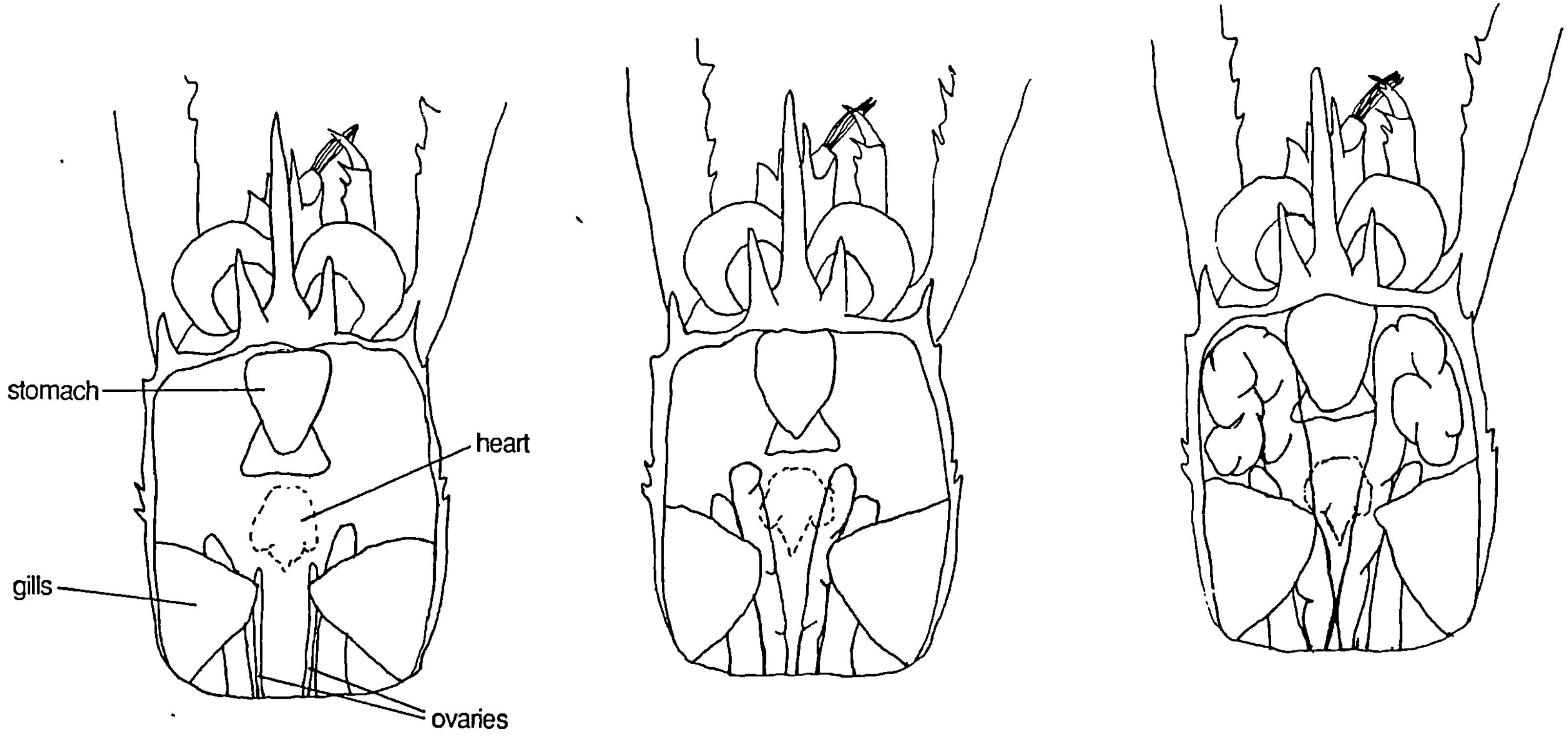
Fig. 20: *Munida rugosa* (Irish Sea): Egg development.

* = Eggs hatched 7-8 April (1987).

An unequivocal sign of female maturity is the presence of laid eggs on the abdomen, as used by Brinkmann. His findings for the smallest mature females using this method are shown below, together with those found in this study:

	Smallest CL size at maturity (mm).	
Species.	Brinkmann.	This study.
M. sarsi.	11·5	9·6
M. tenuimana.	12·5	11·4

M. sarsi >10 mm and *M. tenuimana* >11·5 mm CL were therefore used for the ovary study. The state of development of the ovaries was classed as follows: Small, Large and Extensive (see Fig. 21). The colour of the ovaries was also noted, together with the mean ova size. The results for *M. sarsi* form Table 9 and *M. tenuimana* Table 10. It can be seen that the pattern of development of the ovaries for *M. sarsi* follows the same pattern as the cycle for egg development. After the eggs hatch in April, the ovaries start to develop from the small white form through the larger peach form in May-June reaching the extensive orange ovary in September. The ova by this stage are large and are soon laid onto the pleopods, emptying the ovaries back to the small form at the start of the cycle. *M. tenuimana*, however, shows no real pattern of ovary development, with extensive ovaries being found throughout the year, even when plain eggs are present on the pleopods. It would appear, therefore, that the reproductive cycle for *M. tenuimana* in the Porcupine Sea-bight is not clearly seasonal, unlike the population studied in Norwegian fjords by Brinkmann (1936). This could be due to the differences in the bathymetric distribution of the species in the two studies. Brinkmann's samples all came from above 500 m, whereas no *M. tenuimana* were taken for this study above 740 m. The shallower population could therefore take the same cues for the timing of its reproductive cycle as *M. sarsi*, the two species co-inhabiting, whereas these cues are absent, or less distinct, in the deeper water of the Porcupine Sea-bight. The cues concerned are most



Small

Large

Extensive

Fig. 21: *Munida* ovary size classes.

Month.	Ovary Cond^{n}.	Ovary Colour.	Mean Ova Size.(mm)	Egg. Cond^{n}.	Mean Egg Size (mm).	Mean Egg N^{o}.
Feb.	Small.	White.	0·08 ± 0·01	Plain.	0·73 ± 0·05	2780 ± 1166
Mar.	Small.	White.	0·10 ± 0·01	Eyed.	0·80 ± 0·04	400 ± 258
Apr.	Small.	White.	0·12 ± 0·01	None.	—	—
May. a).	Small.	White.	0·15 ± 0·01	None.	—	—
b).	Large.	Peach.	0·20 ± 0·03	None.	—	—
Jun. a).	Small.	White.	0·15 ± 0·01	None.	—	—
b).	Large.	Peach.	0·21 ± 0·02	None.	—	—
Jul.	NO MATURE FEMALES.					
Aug.	Large.	Orange.	0·36 ± 0·08	None.	—	—
Sep.	Extensive.	Orange.	0·42 ± 0·07	None.	—	—

Table 9: *Munida sarsi* reproduction: size and condition of ovaries, ova and, where present, eggs. For May, ovary type a). was more common than type b). For June, the reverse was true.

Month.	CL	Ovary Cond^{n}.	Ovary Colour.	Ova Size.(mm)	Egg. Cond^{n}.	Egg Size (mm).	Egg N^{o}.
Feb. a).	15·7	Extensive.	Orange.	0·70 - 0·84	None.	—	—
b).	15·5	Large.	Peach.	0·56 - 0·64	Eyed >50%	1·02 - 1·46	540
c).	14.6	Extensive.	Orange.	0·66 - 0·80	Eyed <50%	0·80 - 1·04	680
Mar. a).	14·6	Small.	White.	0·22 - 0·34	None.	—	—
b).	13·2	Extensive.	Orange.	0·20 - 0·44	Eyed >50%*	1·16 - 1·24	210
Apr. a).	15·3	Extensive.	Orange.	0·64 - 0·80	None.	—	—
b).	18·2	Small.	White.	0·12 - 0·28	Eyed <50%	1·00 - 1·20	180
c).	15·8	Large.	Orange.	0·12 - 0·20	Eyed >50%	0·80 - 1·00	1050
May.	14·9	Extensive.	Orange.	0·64 - 0·80	None.	—	—
Jun. a).‡	16·6	Extensive.	Orange.	0·30 - 0·44	None.	—	—
b).‡	16·2	Large.	Peach.	0·16 - 0·28	None.	—	—
Jul. a).	18·2	Small.	White.	0·14 - 0·24	Plain.	0·68 - 0·84	220
b).‡	19·4	Extensive.	Orange.	0·24 - 0·50	None.	—	—
c).	14·6	Large.	Peach.	0·16 - 0·40	None.	—	—
Aug.	NO DATA						
Sep. a).	12·8	Extensive.	Orange.	0·22 - 0·68	None.	—	—
b).	21·7	Large.	Orange.	0·64 - 0·80	Plain.	0·76 - 0·98	1680
Oct. a).	14·2	Small.	White.	0·16 - 0·26	Plain.	0·74 - 1·00	540
b).	12·6	Small.	White.	0·22 - 0·28	Plain.	0·76 - 1·00	570
c).	16·0	Extensive.	Orange.	0·36 - 0·52	Plain.	0·70 - 0·92	480
Nov. a).	14·4	Extensive.	Orange.	0·42 - 0·64	Plain.	0·80 - 0·96	390
b).	12·4	Extensive.	Orange.	0·44 - 0·64	Plain.	0·74 - 0·90	120

* Some Eggs Hatching.

‡ Individual Moulted.

Table 10: *Munida tenuimana* reproduction: size and condition of ovaries, ova and, where present, eggs.

likely the cyclical influx of organic material from surface phytoplankton to the deep-sea benthos (Billett *et al.*, 1983). Sedimentation in the Porcupine Sea-bight occurs soon after the spring bloom arriving at the sea bed around the end of April and extending through the summer. The hatching of *M. sarsi* eggs in April could therefore correspond to this major input of organic carbon to the benthos.

Whether all *M. tenuimana* larvae spend time in the surface plankton is unclear. The larvae hatching from an individual at below 1200 m would have to make an immense vertical migration just to dwell in the surface plankton for a short period before making the difficult return to the bathymetrically small band of sea bed inhabited by the adults, though the use of deeper-water currents is a possibility. This planktotrophic strategy is known to occur in other decapods found below 1000 m, such as *Neolithodes gruinaldii*, *Nephropsis atlantica* (A. L. Rice, pers. comm.), though none of these species are particularly abundant. Huus (1934), again working on shallower *M. tenuimana*, reported that the larvae which hatch in April settle again as young adults in Aug-Sept (when there would still be plenty of sedimented organic material on the bed), giving a larval life from hatching to settlement of around 4 months. This would in theory allow time for a larva to reach the plankton and return to depth, though this would seem very inefficient. But this very fact could explain the low densities of *M. tenuimana* in the Porcupine Sea-bight. It would seem that *M. tenuimana* is basically a shallow water animal, as is *M. sarsi*, but has been forced deeper due to competition between the two. However, it still has a shallow water reproductive strategy, the larvae utilising the plankton. This would not be so successful in the deeper areas due to the vast distances involved, few larvae returning to the adult area compared to the shallower *M. sarsi*, and so contributes to the comparatively small size of the *M. tenuimana* population in the Porcupine Sea-bight.

Fecundity.

To measure fecundity in the munidid species, the number and size of the eggs being carried on the female's pleopods were recorded, though it must be noted that some eggs may be lost during the sampling process. The results for *M. sarsi* and *M. tenuimana* can be seen in Tables 9 and 10. For *M. sarsi,* the mean values are given for plain eggs in February and eyed eggs in March. Due to the smaller sample size, the figures for *M. tenuimana* are presented for the individual specimens. If these figures are meaned to allow comparison with *M. sarsi,* the results are as follows for plain and eyed eggs:

Egg Type.	Mean Size (mm)	Mean N^{o}.
Plain	0·86 ± 0·03	630 ± 492
Eyed	1·11 ± 0·12	532 ± 322

Comparing these means with those for *M. sarsi* in Table 9, it can be seen that the eggs for *M. tenuimana* tend to be a little larger, for both plain and eyed eggs. Lebour (1930) studied the eggs of *M. rugosa* (as *M. bamffica*) and found them to be 0·64-0·80 mm, a similar size to the *M. sarsi* eggs measured in this study. The figure for mean number of plain eggs is considerably less than that for *M. sarsi,* but that for eyed eggs is not. The main feature of the figures for egg number is the great variability. This could be merely a function of size of the individual munidid, especially as the high mean number of plain eggs for *M. sarsi* was influenced by the ovigerous females from sample 51302. The mean number of plain *M. sarsi* eggs when this sample is removed is only 1277 ± 556. So to investigate this size relationship, the plain and eyed egg number was plotted out against CL for both *M. sarsi* and *M. tenuimana..* The resulting graphs form Fig. 22. For *M. sarsi* it can be seen that there is a general, but fairly well

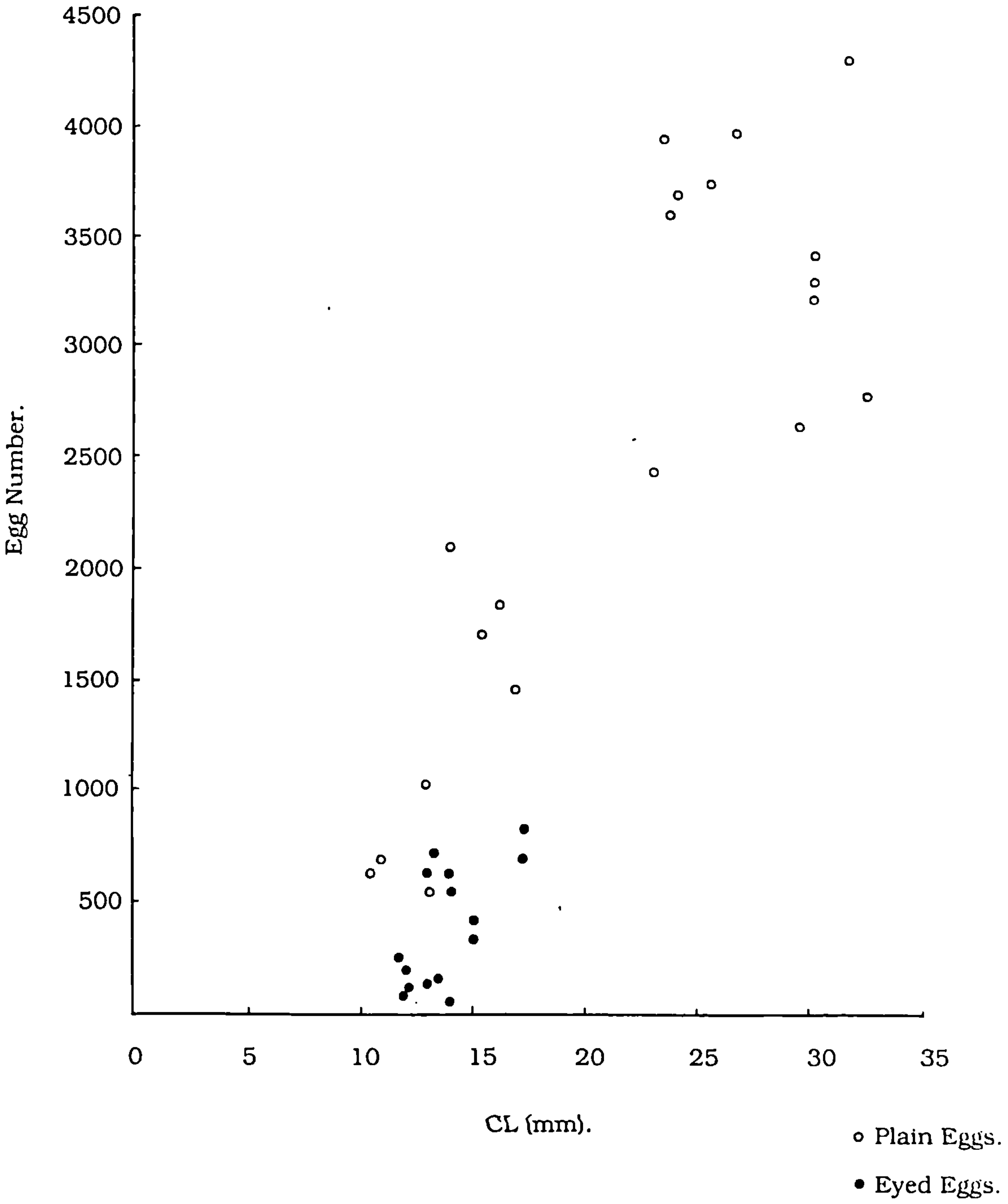


Fig. 22a: *Munida sarsi:* Fecundity. Number of eggs carried against CL.

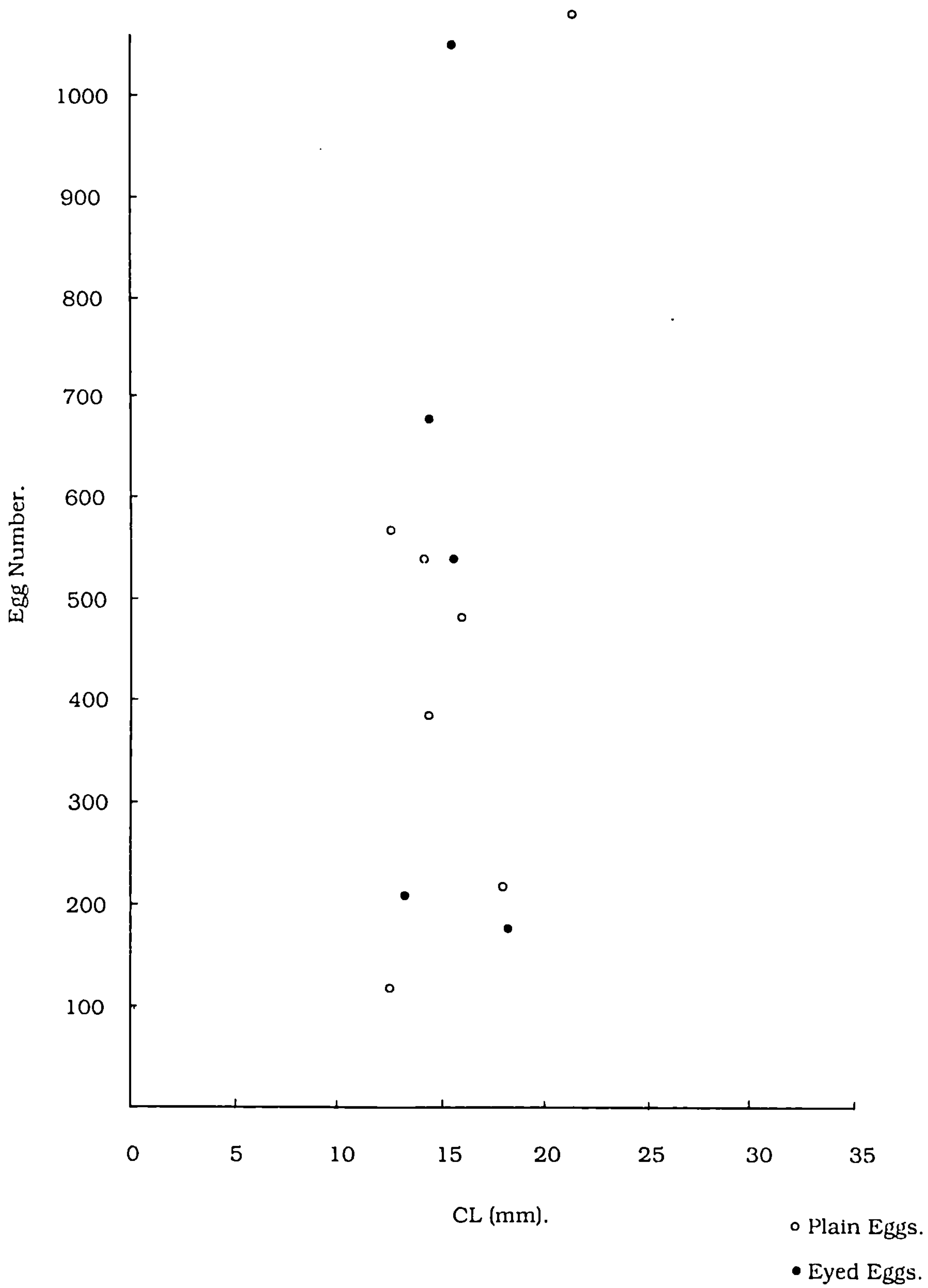


Fig. 22b: *Munida tenuimana:* Fecundity. Number of eggs carried against CL.

spread, increase in plain egg number with an increase in CL. It appears that the relationship with CL therefore gives a good indication of the fecundity of the species. The points for eyed eggs show a similar pattern, but with a general decrease in the number of eggs present. This would be expected as these eggs have been carried longer than the plain eggs, so allowing degeneration, loss and hatching to occur, all of which reduce the egg number present. The scatter for *M. tenuimana* is great, probably due to the small number of ovigerous individuals available, so no real conclusions can be drawn.

Brinkmann (1936) reported that both *M. sarsi* and *M. tenuimana* from deeper water laid their eggs earlier and held them longer before hatching than specimens from shallower areas. This he attributed to the lower temperatures at depth. There is no evidence from this study that this is the case in the Porcupine Sea-bight, but few samples have been taken from the same station at different times of the year. However, it has to be pointed out that Brinkmann's deep (only 500 m) and shallow samples were taken from geographically separated fjords, so other factors may influence the development of the eggs. The Porcupine Sea-bight samples are all from the same basic slope area, there being no land barriers separating the populations.

Moulting and Sex Ratio.

In the decapods generally, both the timing of moults and the sex ratio over the year are often influenced by the reproductive cycle. Brinkmann (1936) reported that both male and female *M. sarsi* and *M. tenuimana* demonstrated a moulting season, each individual moulting once a year. For *M. sarsi* this was from Feb-June for males and Apr-June for females, the females moulting after the eggs have hatched. In this study, the percentage of both males and females having just moulted in each calender month was recorded and the results form Table 11 and Fig. 23. It can be seen that a post-hatching moult is also apparent in females from the Porcupine

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
No. Males Moulting	*	1	1	2	1	23	0	3	4	0	*	1
No. Females Moulting	*	0	0	30	1	33	0	1	4	2†	*	0
% Males Moulting	*	2.0	5.3	2.3	1.4	5.0	0.0	3.7	5.9	0.0	*	0.5
% Females Moulting	*	0.0	0.0	24.4	3.0	8.4	0.0	5.9	8.2	50.0†	*	0.0

* No Data
† Very Small Sample

Table 11: Percentage of each sex of *Munida sarsi* moulting in each calender month.

	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	**Total**
No. Males	*	50	19	87	70	460	8	81	68	2	*	214	**1059**
No. Females	*	34	19	123	33	395	8	17	49	4	*	181	**863**
% Females	*	40.5	50.0	58.6	32.0	46.2	50.0	17.3	41.9	66.7	*	45.8	**44.9**

* No Data.

a) *Munida sarsi.*

	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	**Total**
No. Males	*	9	6	9	1	6	8	*	10	5	7	*	**61**
No. Females	*	5	3	7	1	5	7	*	15	13	5	*	**61**
% Females	*	35.7	33.3	43.8	50.0	45.5	46.7	*	60.0	72.2	41.7	*	**50.0**

* No Data

b) *Munida tenuimana.*

Table 12: Sex ratio over the year for *Munida sarsi* and *Munida tenuimana* combining all catches in each calender month.

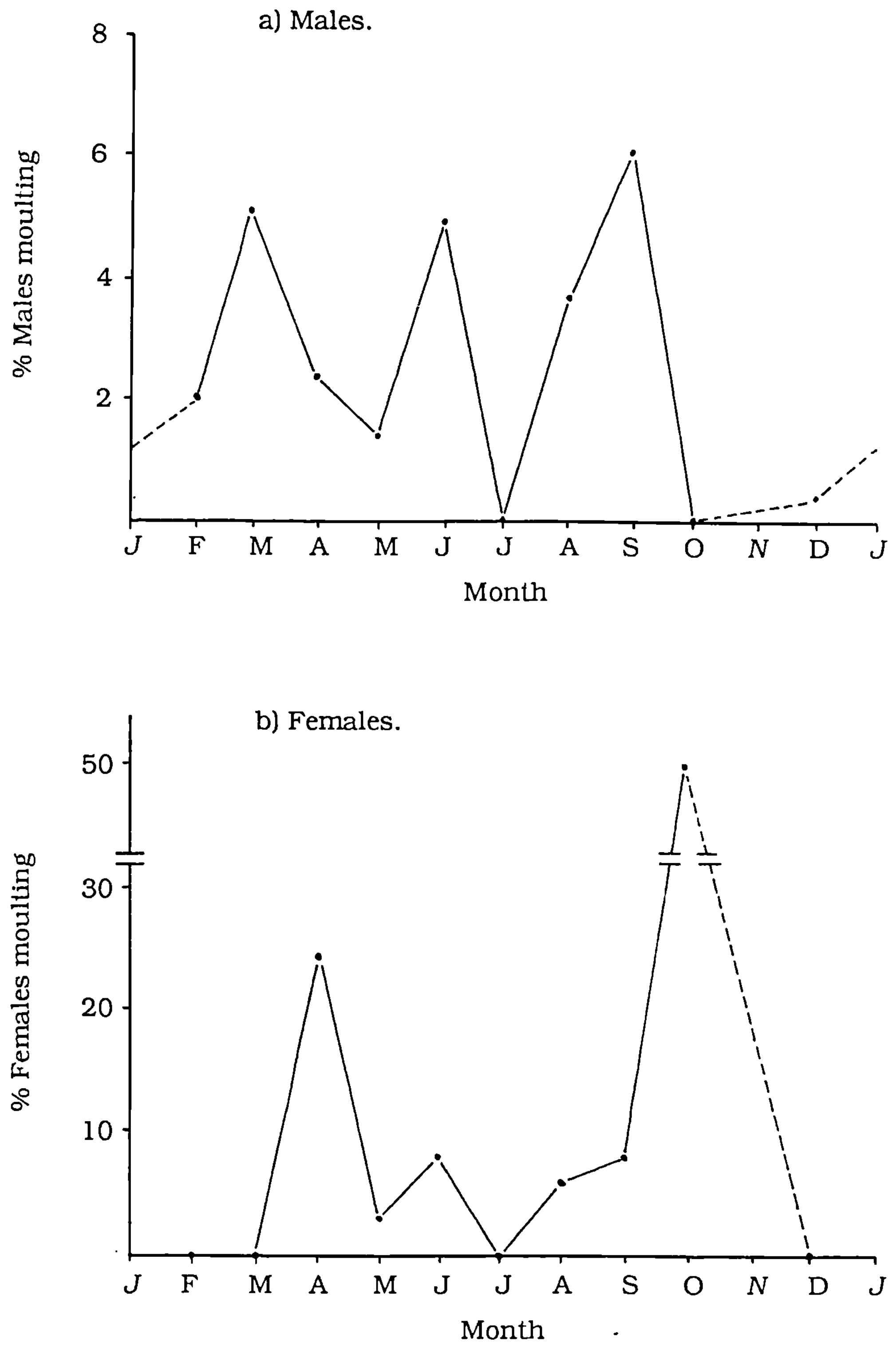


Fig. 23: *Munida sarsi:* percentage of each sex moulting over the year.

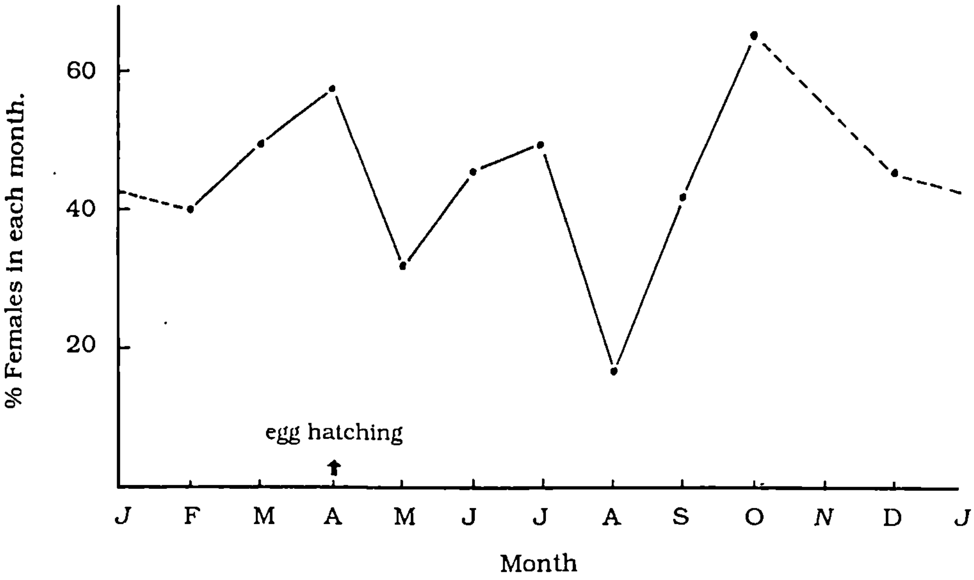
Sea-bight (Fig. 23b), with a peak in percentage females moulting in April. The second large peak in October (pre-laying?) is possibly exaggerated due to the small sample size in this month, but Brinkmann reported no sign of such a second moulting period. There appears to be no moulting season for males (Fig. 23b) with a general low level of moulting frequency during most of the non-winter months.

Very few of the comparatively small sample of *M. tenuimana* were found to be moulting: for females, 4 in June (80%) and 2 in Nov (40%), for males one each in Feb (11·1%), June (16·7%), July (12·5%) and Sept (10%). Brinkmann in his large sample also found moulting seasons for his shallow *M. tenuimana,* these being Dec-Mar/Apr for males and, as for *M. sarsi,* Apr-June for females. None of the observations made above fit into these patterns, the numbers involved being very small, though the proportion of females moulting in June is worth noting.

The sex ratio for both species over the year was investigated by determining what proportion of the catches in each month was made up of females. The results form Table 12 and Fig. 24 and are interesting if not entirely conclusive. The graph for *M. sarsi* shows two troughs where the proportion of females falls dramatically. The first trough corresponds to the post-hatching moult, where many of the females perhaps remain in their burrows until the cuticle has hardened. The second trough for August is highly unexpected and far more difficult to explain as the sample numbers involved are high (a total of 98 individuals), the proportion of females in the catches falling below 20%. It is possible that this trough could be the result of post-laying behaviour, the females remaining in their burrows for a short period after having laid a new batch of eggs.

The graph for *M. tenuimana* (Fig. 24b) is quite different, with no troughs of female low abundance. There is a steady increase in the proportion of females being caught from March onwards, reaching a peak in October and then falling again over the winter. The decrease corresponds to the time when the majority of *M. tenuimana* are laying and carrying their eggs

a) *Munida sarsi*



b) *Munida tenuimana*

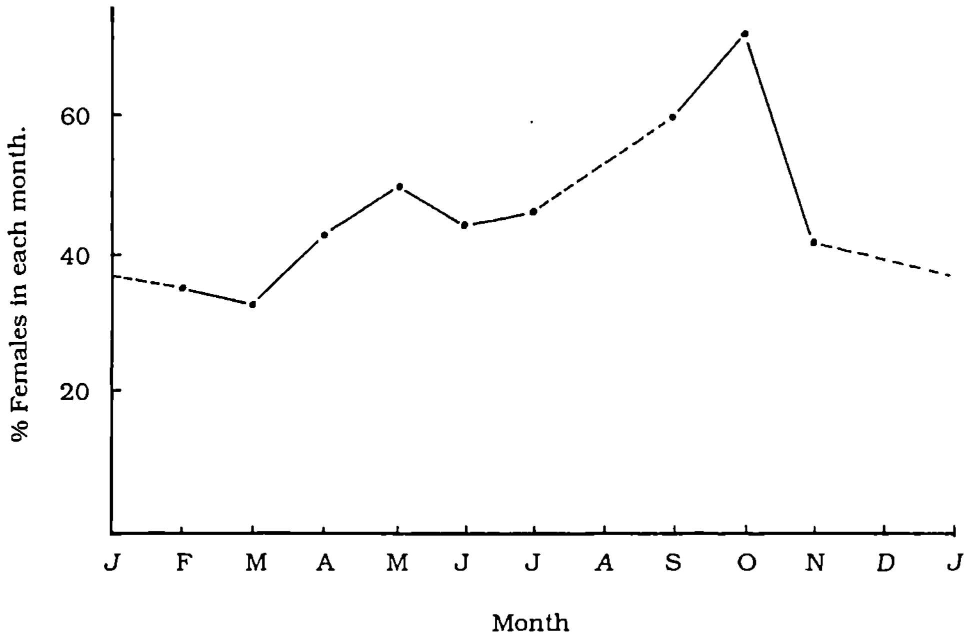


Fig. 24: Sex ratio over the year. Percentage of females caught in each month for both *Munida sarsi* and *Munida tenuimana*.

(Oct-March), so the ovigerous females may become more cryptic during these months and so harder to catch. The lack of a post egg-hatching moult in this *M. tenuimana* population is supported by this graph, as there is no evidence of a decrease in the proportion of females around May.

From the data obtained for a variety of factors it would appear that the cycles for *M. tenuimana* in the Porcupine Sea-bight are less clear-cut than for the population studied by Brinkmann, the patterns of egg development being present, but not uniform for the whole sample. This highlights the difference between the depths of the two populations. Brinkmann's was shallower than 500 m and showed cyclic phenomenon similar to *M. sarsi* whilst the population in the Sea-bight extends from a minimum depth of 740 m down to below 1500. These data reinforce the idea that *M. tenuimana* is more suited to shallower depths than it is found in the Porcupine Sea-bight, and is existing deeper with the reproductive patterns of an upper slope organism.

Behavioural Aspects of *Munida tenuimana* from photographs.

Around the position 51°22'N, 13°18'W at a mean depth of 1260 m is an extensive bed of the glass sponge *Pheronema*. This sponge bed falls into the depth band inhabited by *Munida tenuimana*, and analysis of photographs taken using the IOS benthic photosled indicates a behavioural trait of *M. tenuimana* when associated with *Pheronema*. *M. tenuimana*, like most munidids, tends to form shallow burrows in the sediment and occupy these with the chelae protruding from the entrance (Plate 2, A). However, it can be seen from Plate 3 that when available *M. tenuimana* often utilise the oscula of *Pheronema* as burrows instead of having to make their own. This behaviour could, however, have beneficial consequences:

1. The sponge is a more stable substrate than the fine sediment of the sea bed and so

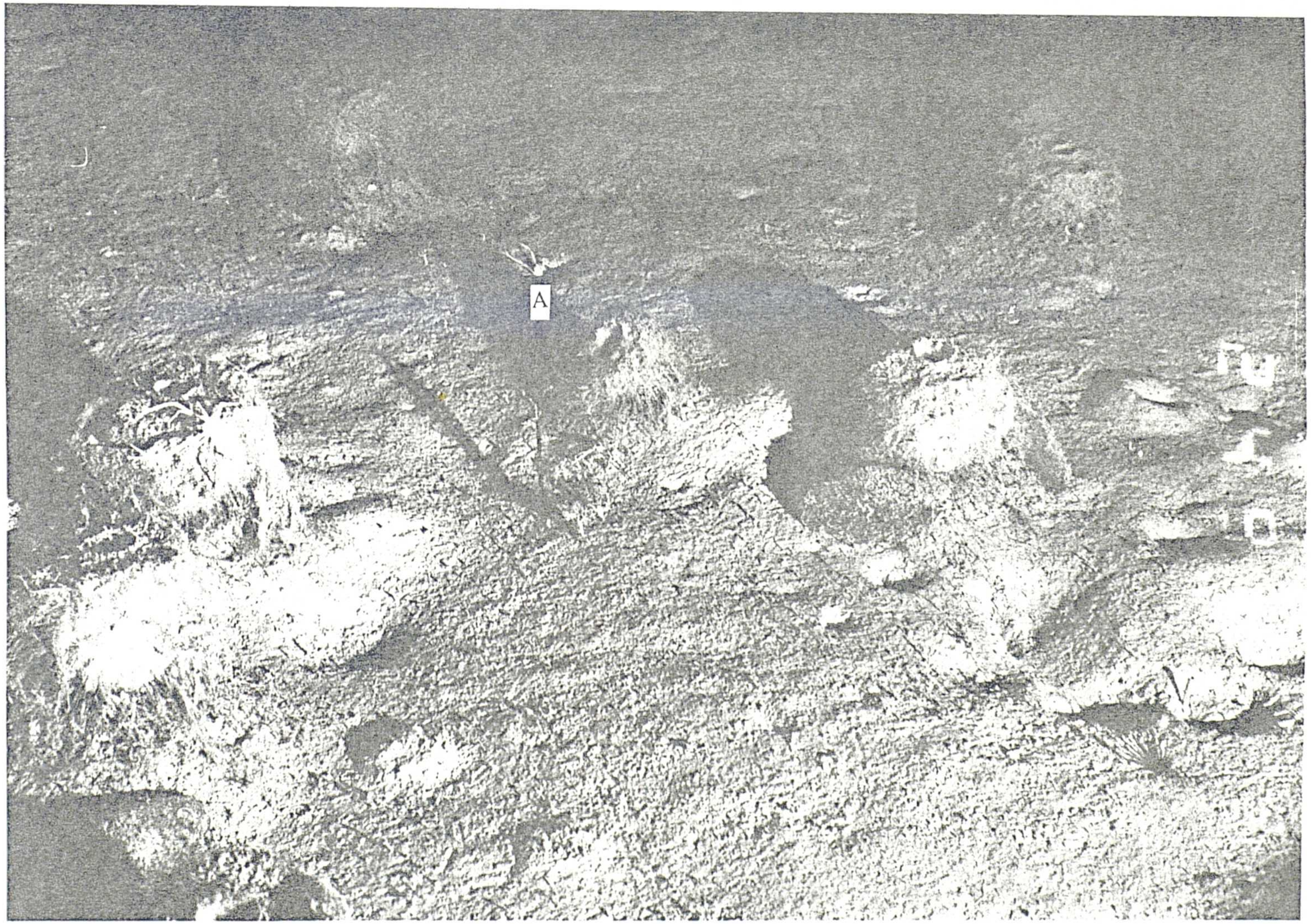


Plate 3: Photograph of
the *Pheronema* bed at 1097 m,
indicating (at A) a *Munida*
tenuimana in a standard
burrow. (station 51734).

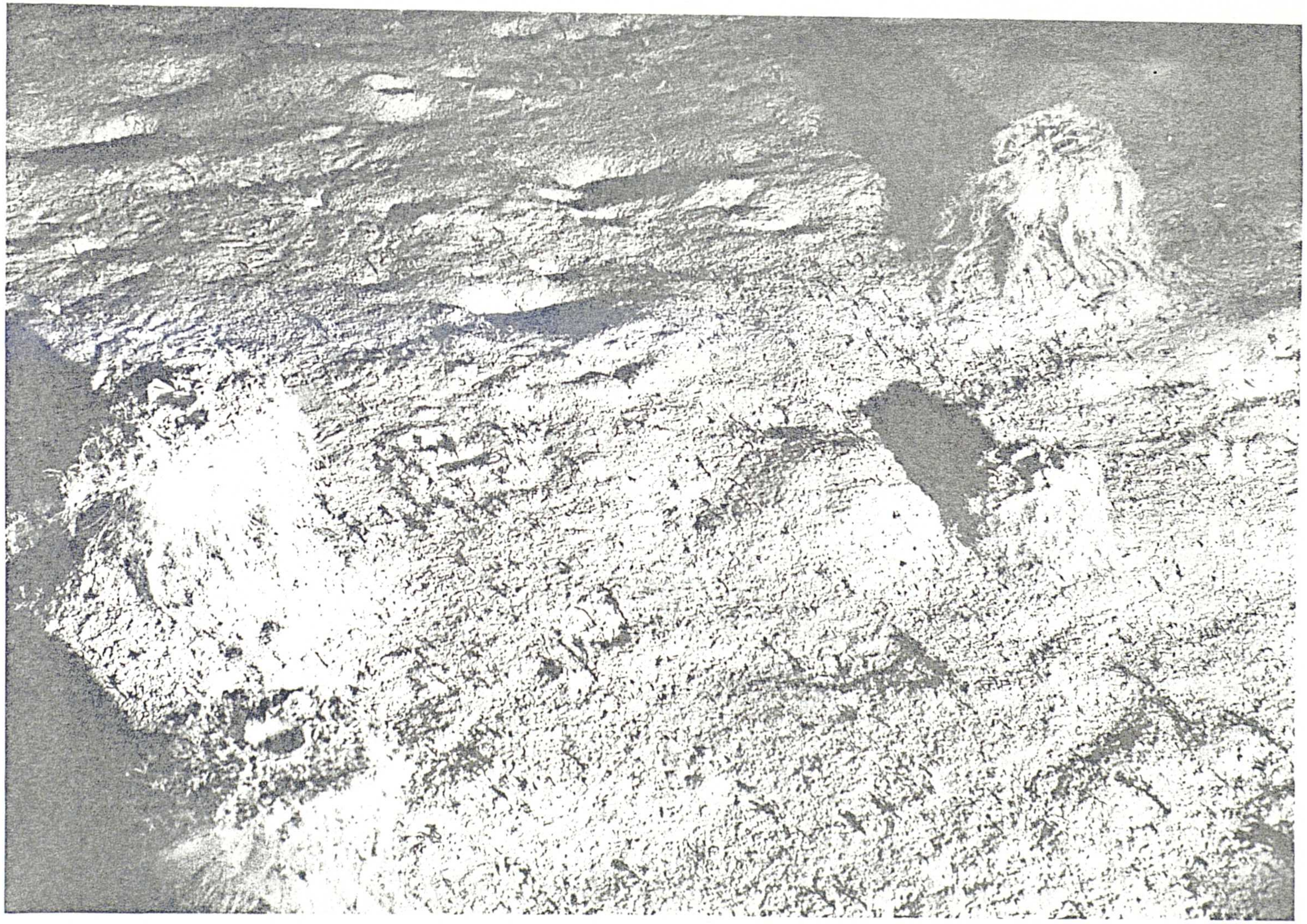
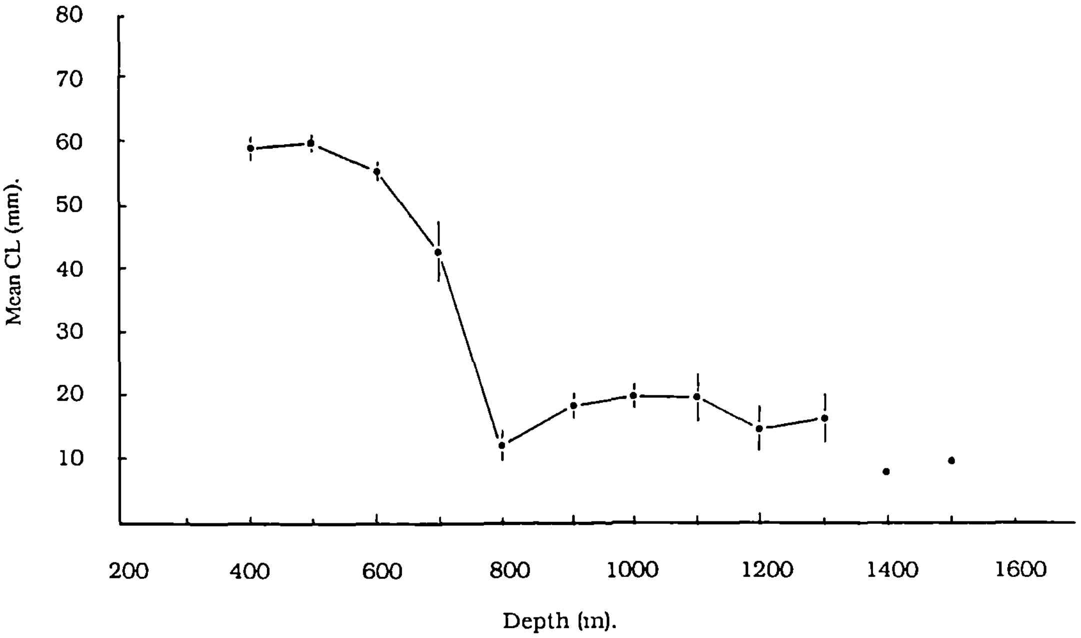


Plate 4: The *Pheronema* bed at 1097 m, illustrating the use by *Munida tenuimana* of the sponge osculae for shelter. (station 51734).

a). Males.



b) Females.

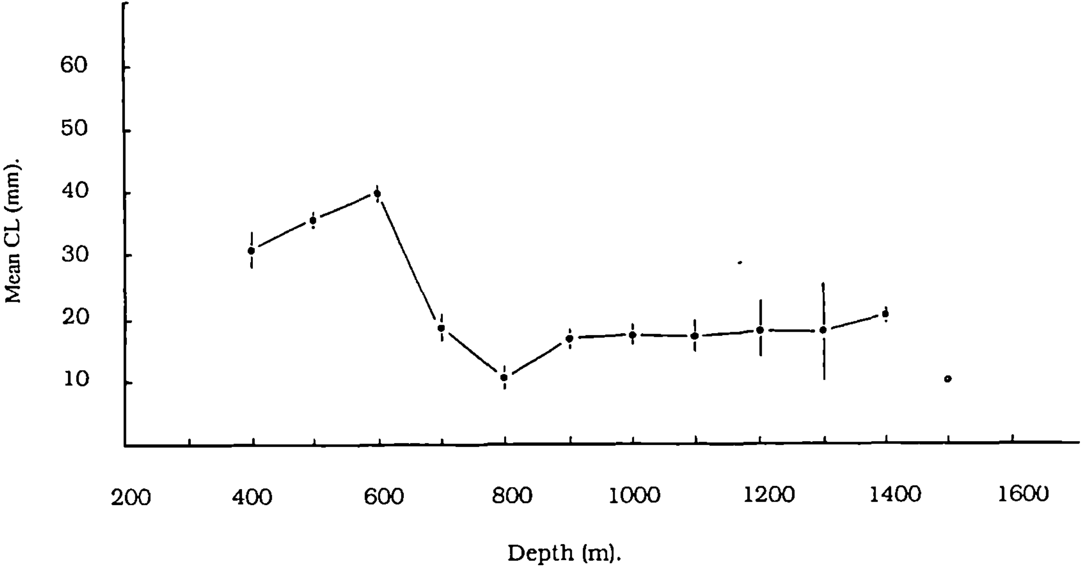
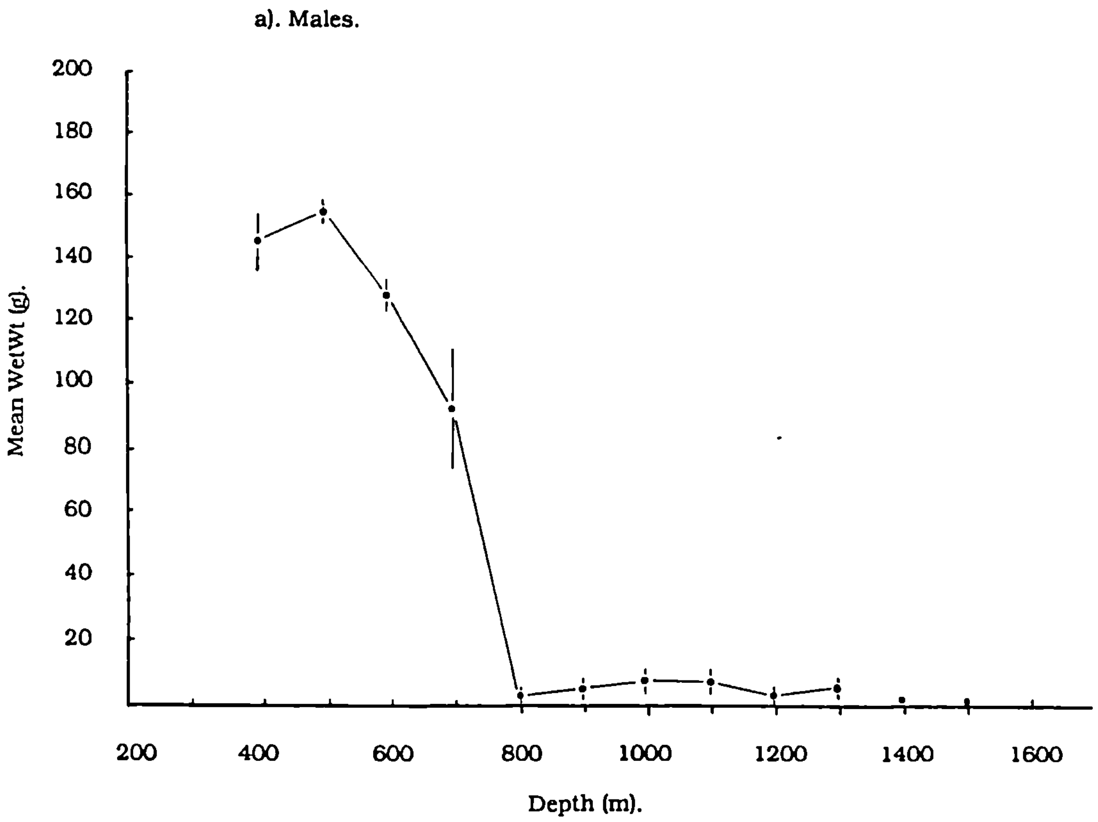
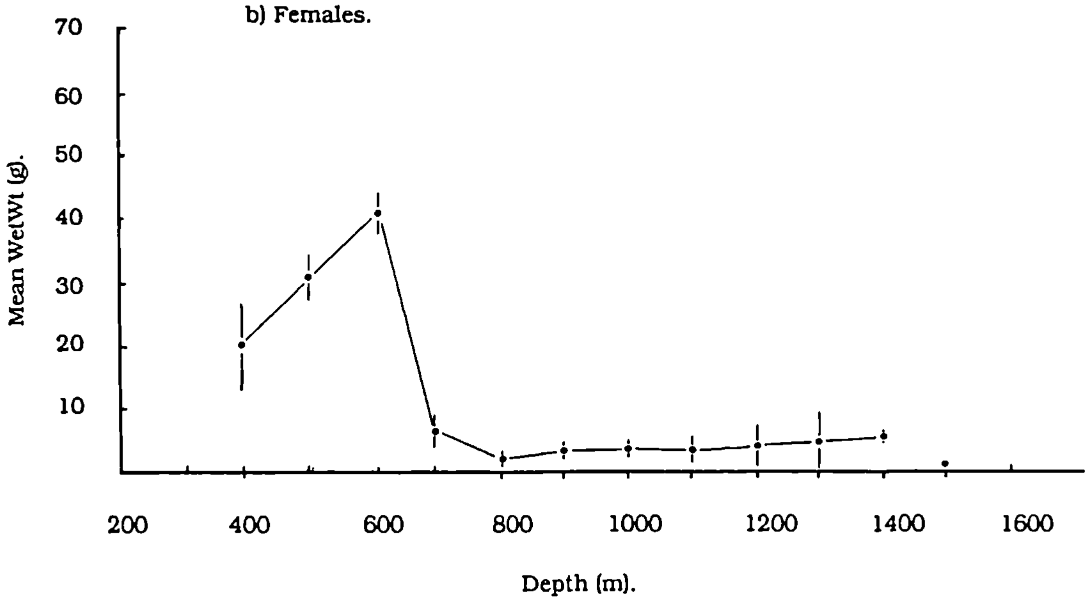


Fig. 7: Mean CL at depth for both sexes of *Geryon trispinosus*.



a). Males.



b) Females.

Fig. 8: Mean Wet Weight at depth for both sexes of *Geryon trispinosus*.

using the osculum as a burrow may be mechanically advantageous.

2. The sponge provides increased protection from predation, the *Munida* being harder to detect against the sponge than the bare sediment. The deep-sea spider crab *Dorhynchus thomsoni* has been recorded using the sponge surface as camouflage, though it does not utilise the oscula (Rice & Hartnoll, 1983).

3. The sponge may indirectly supply a source of food, both through material being discharged by the osculum and, more likely, detrital matter depositing on the tangled exterior of the sponge. Its mesh of spicules would act as an efficient 'net' to catch particles.

4. The exhalant current of the sponge arising from the osculum may aid ventilation of egg masses carried by ovigerous females. The sponge also provides protection for the eggs. A sample of *M. tenuimana* was taken from this area (Station N^{O}. 50713) and all the ovigerous females had many long glass sponge spicules entwined with the pleopods, giving a larger and very secure base on which to lay the eggs. Some eggs were attached directly on to the sponge spicules.

Whatever the reasons for this behaviour, the *Pheronema* beds provide a valuable firm substratum for many species, the diversity and biomass of the community in this area seems high. *M. tenuimana* and *D. thomsoni* are two of the most common decapods at these depths and both gain benefits from utilising the sponge.

The Parasitic Fauna of *Munida*.

Two main groups of parasites were found infesting *M. sarsi* and *M. tenuimana*.

1. Rhizocephala. Three species of rhizocephalan barnacle infesting *M. sarsi: Triangulus munidae*, *Lernaeodiscus ingolfi* and *Tortugaster boschmai*, forming a significant and interesting

sample of 297 individual hosts. The details of the infestation structure and the effects on the host by the parasites are dealt with in the next chapter (also as Attrill, in press).

Lernaeodiscus ingolfi was also found infesting two specimens of *Munida rugosa* caught in the Irish Sea for the comparative egg production study. One externa was in turn infested by two individuals of the parasitic isopod *Liriopsis* sp.

None of the sample of *M. tenuimana* was found to be infested by any of the rhizocephalan species.

The two specimens of *M. micropthalama* were not infested.

2. Bopyrid Isopods. The Bopyridae is a family of parasitic epicaridean isopods living in the branchial cavity of decapod Crustacea, or on the abdomen of hermit crabs (Reinhard, 1949). The family is composed of more than 50 genera, separated into six groups according to external features. Shiino (1965) attempted to sort out the phylogeny of the family using morphological features of the adult parasites, but his evolutionary tree has been disputed by Strömberg (1971), who dealt with the bopyrid's embryology.

Details of the highly adapted and extremely interesting life cycle of bopyrids, together with noted effects on their hosts, can be found in Appendix 1.

Of the six groups of bopyrids described by Shiino (1965), practically all of those infesting *Munida* species fall into the *Pseudione* group. Details of species reported infesting *Munida* can be seen in Table 13. In this study, one species was found to be infesting the munidids in the Porcupine Sea-bight: *Pseudione crenulata* (Fig. 25). This was observed on four female *M. sarsi* and one female *M. tenuimana.* These are the first records of any bopyrid infesting *M. sarsi* (J. C. Markham, pers. comm.) and so adds to the lists of hosts for the *Pseudione* genus (Table 14). *P. crenulata* has previously been observed on *M. tenuimana* (Sars, 1899; Nielsen, 1969; Strömberg, 1971), *M. rugosa* (Sars, 1899), *M. iris rutllanti* and *M.*

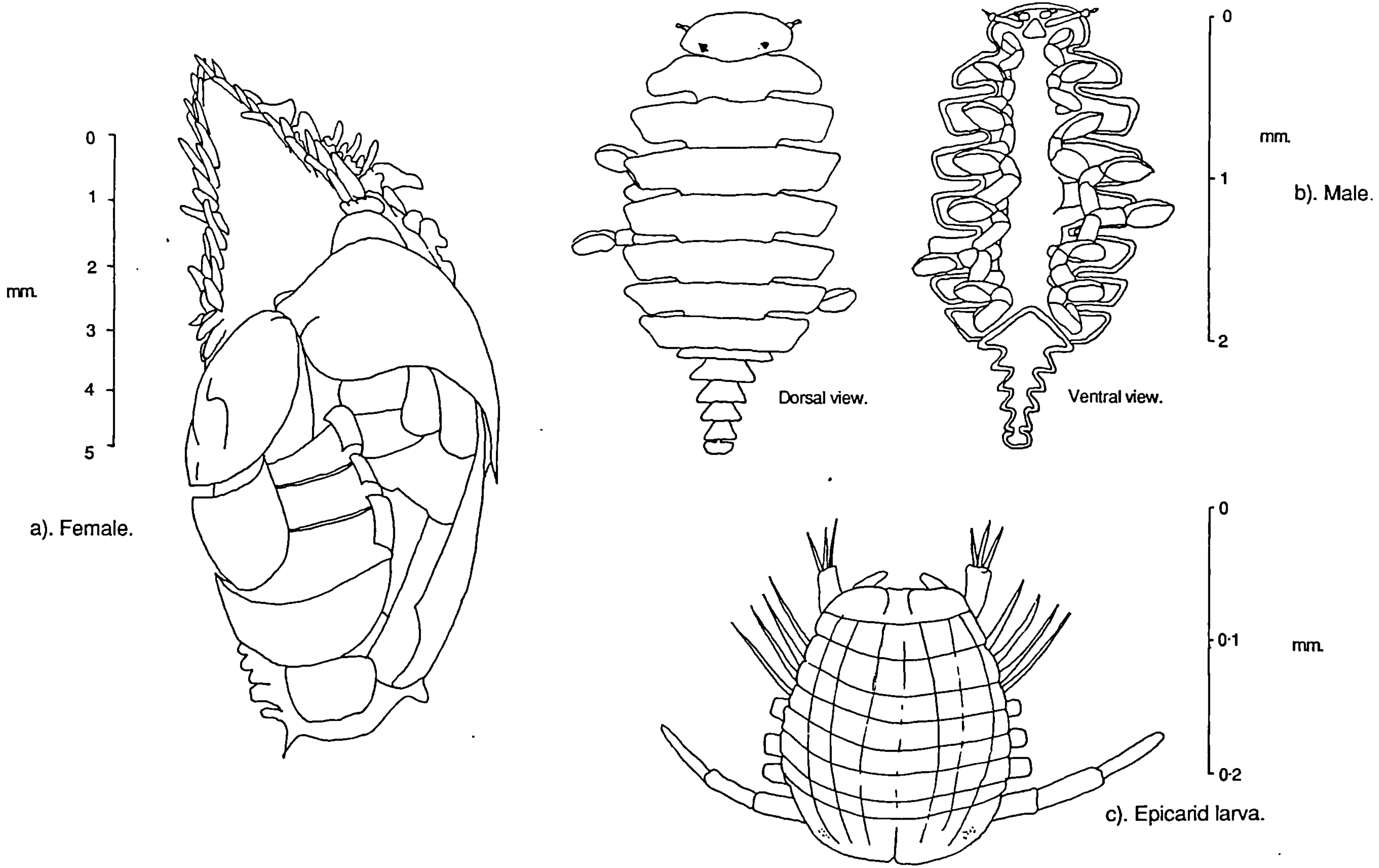


Fig. 25: Bopyrid isopod *Pseudione crenulata* found in branchial cavity of *Munida sarsi* and *Munida tenuimana.* (b. and c. found on a.).

Bopyrid species.	*Munida* species.	Reference.
Anuropodione carolinensis.	*M. iris iris.*	Williams & Brown, 1972; Markham, 1973.
Anuropodione megacephalan.	*M. pusilla.*	Markham, 1973.
Anuropodione senegalensis.	*M. speciosa.*	Bourdon, 1967,
Aporobopyrina anomala.	*M. valida.*	Markham, 1973.
Aporobopyrina javaensis.	*M. andananica.*	Bourdon, 1972a.
Balanopleon tortuganus.	*M. simplex.*	Markham, 1973.
Bonnieria americana.	*M. microphthalama.*	Markham, 1973.
Bonnieria indica.	*M. militaris.*	Nz. & B à B., 1923.*
Entophilus omnitectus.	*M. incerta.*	Bourdon, 1976.
	M. normani.	Bourdon, 1976.
	M. sanctipauli.	Bourdon, 1979a.
Munidion cubense.	*M. stimpsoni.*	Markham, 1975.
	M. flinti.	Markham, 1975.
Munidion irritans.	*M. irrasa.*	Markham, 1975.
	M. irsi iris.	Bursey, 1978.
Munidion laterale.	*M. scabra.*	Bourdon, 1972a.
Munidion longipedis.	*M. longipes.*	Markham, 1975.
	M. schroederi.	Markham, 1975.
Munidion parvum.	*M. quadrispina.*	Markham, 1975.
Munidion parvum cubensis.	*M. stimpsoni.*	Bourdon, 1972b.
Munidion princeps.	*M. refulgens.*	Hansen, 1897.
Paragigantione papillosa.	*M. sanctipauli.*	Bourdon, 1972b.
Parionella elegans.	*M. japonica.*	Nz. & B à B., 1923.*
Parioninella obouata.	*M. japonica japonica.*	Shiino, 1958.
Pleurocrypta keiensis.	*Munida* sp.	Nz. & B à B., 1931*
Pleurocryptella fimbriata.	*M. constricta.*	Markham, 1973.
Pleurocryptella infecta.	*M. militaris.*	Nz. & B à B., 1923.*
	M. japonica.	Shiino, 1937.
Pleurocryptella infecta tuberculata.	*M. tricarinata.*	Bourdon, 1976.
Pseudionine indetermine.	*M. sanctipauli.*	Bourdon, 1979a.

* Nierstrasz & Brender-à-Brandis, 1923.

Table 13: List of known bopyrids infesting *Munida* species.

Pseudione species.	Host species.	Reference.
P. affinis.	*Plesionika antiguai.*	Bourdon, 1979a.
	P. martia.	Bourdon, 1972a.
	Pandalus bonnieri.	Pike, 1960.
	P. leptorhynchus.	Sars, 1899.
	P. montagui.	Sars, 1899.
P. andamanicae.	*Munida andamanica.*	Bourdon, 1976.
P asymmetrica.	*Clibanarius bimaculatus.*	Shiino, 1958.
P biacuta.	*Paguristes robustus.*	Bourdon, 1979b.
P. borealis.	*Callianassa subterranea.*	Stephensen, 1948.
P. calcinii.	*Calcinus latens.*	Shiino, 1958.
P. callianassae.	*Callianassa subterranea.*	Catalano & Restivo, 1965.
P chapini.	*Upogebia furcata.*	Van Name, 1920.
P compressa.	*Callianassa jouseaux*	Shiino, 1964.
P. confusa	*Munida squamosa.*	Bourdon, 1967a,
	Galathea dispersa.	Pike, 1953.
P. c maxillipedis.	*Munida stimpsoni.*	Bourdon 1972b.
P convergens.	*Porcellana longicornis.*	Stock, 1960.
P crenulata.	*M. rugosa.*	Sars, 1899
	M sarsi.	This study.
	M. tenuimana.	Sars, 1899; Nielsen, 1969.
	M. iris rutllanti.	Markham, pers comm.
	M. perarmata.	Markham, pers. comm.
P diogeni.	*Diogenes pugilator.*	Bourdon, 1963.
P dohrini.	*Callianassa truncata.*	Giard & Bonnier, 1887.
P. dubia.	*Eupagurus pubescens.*	Bonnier, 1900.
P elongata.	*Nematocarcinus agassizi.*	Nz. & B à B., 1923.*
P. euxinica.	*Upogebia pusilla.*	Bourdon, 1964.
	U. deltaura.	Bourdon, 1967b.
	U. littoralis.	Caroli, 1948.
P. filicaudata.	*Upogebia issaeffi.*	Shiino, 1958.
P. fimbriata.	*Munida* sp.	Nz. & B à B., 1923.*
P. fraissei.	*Clibanarius erythropus.*	Bourdon, 1964.
P. galacanthae.	*Munida subrugosa.*	Richardson, 1908.
	M. gregaria.	Rayner, 1935.
	M. quadrispina.	Strömberg, 1971.
	Munidopsis diomediae.	Bonnier, 1900.
P. giardi.	*Pagurus hirsutiusculus.*	Strömberg, 1971.
	Eupagurus ochotensis.	Nz. & B à B., 1923.*
P hanseni.	*Axiopsis brocki.*	Nz. & B à B., 1923 *
P. hayi.	*Munida subrugosa.*	Nz. & B à B., 1931.*
P. hoylei.	Unknown.	Giard & Bonnier, 1887.
P. hyndmanni.	*Eupagurus bernhardus.*	Sars, 1899.
	E. pubescens.	Sars, 1899.
	Anapagurus laevis.	Bourdon, 1967b.
P. incerta.	Unknown.	Nz. & B à B., 1923.*
P insignis.	*Munida rugosa.*	Giard & Bonnier, 1890.
P itsindrae.	*Munidopsis trifida.*	Bourdon, 1976.
P japanensis.	*Galathea* sp.	Nz. & B à B., 1931.*
P kossmanni.	*Munida militaris.*	Nz. & B à B., 1923.*
P laevis.	Unknown.	Nz. & B à B., 1923.*
P latilamellans.	*Munida* sp.	Nz. & B à B., 1931.*
P. lenticeps.	*Munida japonica heteracantha.*	Shiino, 1958.
P. longicauda.	*Callianassa japonica.*	Shiino, 1958.
P magna.	*Heterocarpus sibogae.*	Shiino, 1950.
P minimocrenulata.	*Munida incerta.*	Bourdon, 1976.
P munidae.	*Munida sanctipauli.*	Nz. & B à B., 1923.*
P. nephropsi.	*Nephrops japonicus.*	Shiino, 1950.
P. nobilii.	*Mixtopagurus spinosus.*	Nz. & B à B., 1923.
P proxima.	*Eupagurus* sp.	Catalano & Restivo, 1965.
P. retrosa	Unidentified galatheid	Nz & B à B., 1923.*
P subcrenulata.	*Munida scabra.*	Nz. & B à B., 1923.*
P. tattersalli.	*Plesionika ensis.*	Bourdon, 1972a
P tuberculata.	*Callianassa subterranea.*	Stephensen, 1948.
P upogebiae.	*Upogebia* sp.	Lemos de Castro, 1966.
P urogebiae.	*Urogebia affinis.*	Popov, 1929
P. villosa	*Upogebia pugnax.*	Shiino, 1964.
Pseudione sp	*Munida longipedes.*	Markham, 1975.

* Nierstrasz & Brender-à-Brandis

Table 14: List of known *Pseudione* species, together with the hosts on which they were reported.

perarmata (J. C. Markham, pers. comm.).

The parasites had no obvious effect on the internal or external morphology of the hosts, except for the conspicuous deformity of the carapace region covering the parasite, forming a distended bulge to accommodate the large female in the branchial region. All the parasites were found on the right hand side. Pike (1953) studying *P. crenulata* on *Munida rugosa* (as *M. bamffica*) found seven out of his ten specimens on the left hand side.

Sample 51302.

The 37 *Munida sarsi* comprising sample 51302 were taken further North than the rest of the samples (Fig. 1) on the Porcupine Bank at a position of 52°41'N 13°31'W from a depth of 330 m. This sample was strikingly different from the rest of the population, being composed entirely of large individuals, most of which are bigger than any found in the rest of the Sea-bight population (Plate 3).

The size frequency distribution can be seen in Table 15 (compare with Table 2), and almost entirely composes the 'tail' of large individuals as seen on Fig. 7. It is interesting to note that the two smallest individuals in the sample are both parasitised by rhizocephalans, one by a single large *Tortugaster boschmai* and the other with a double infestation of *Lernaeodiscus ingolfi*.. As a result, both individuals may have ceased growth due the action of the parasite (see this study, Ch. 4), hence their smaller size in relation to the rest of the sample. The general differences between this sample and the rest of the population in the Sea-bight are summarised below.

1. Length Frequency. Sample 51302 is composed of individuals of larger size than the majority of the Sea-bight population (Table 15).

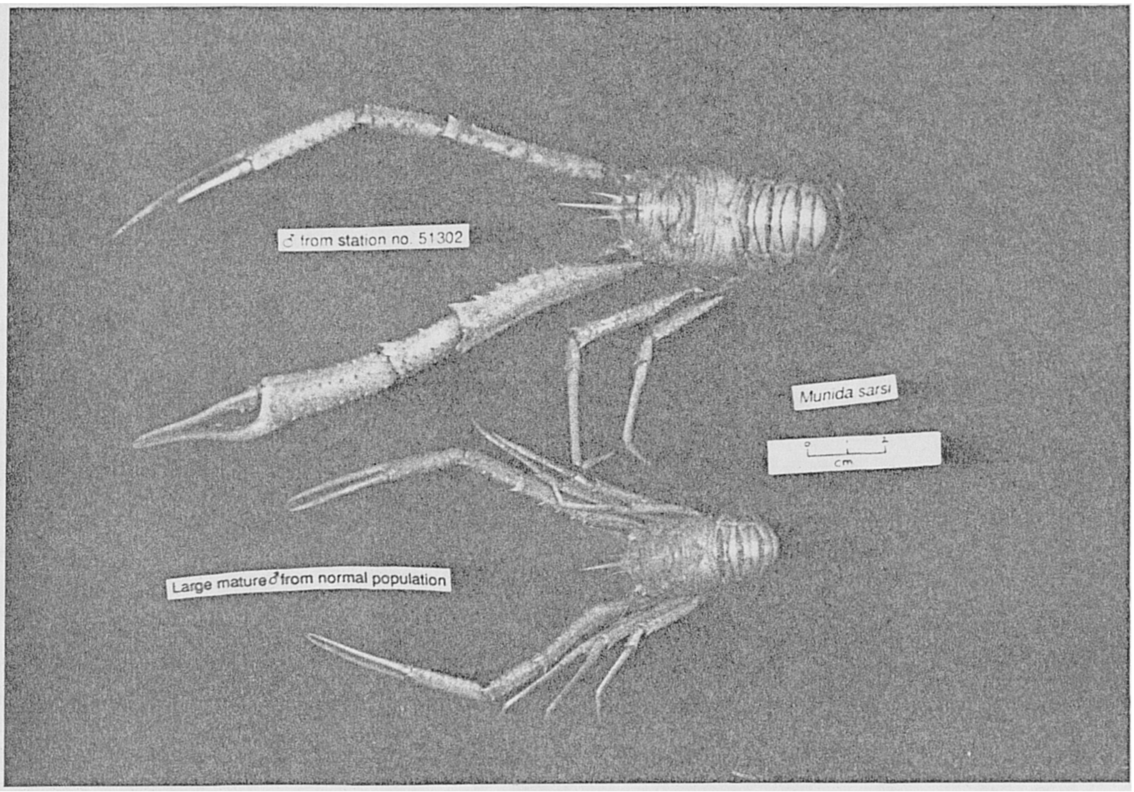


Plate 5: A male from station 51302 (above), together with a male *Munida sarsi* from the Sea-bight population, illustrating the size difference.

Carapace Size Interval (mm).	Frequency		% of all Samples.	
	Females	Males	Females	Males
13	0	1*	0·00	0·68
19	0	1*	0·00	4·00
20	0	1	0·00	10·00
21	1	0	50·00	0·00
22	1	0	33·33	0·00
23	1	1	50·00	33.33
24	2	1	100·00	50·00
25	3	2	100.00	66·67
26	3	0	100.00	0·00
27	1	0	100.00	No Males
28	2	0	100.00	No Males
29	1	0	100.00	No Males
30	4	4	100.00	100.00
31	2	1	100.00	100.00
32	1	1	100.00	100.00
33	1	0	100.00	No Males
34	0	1	No Females	100.00

Table 15: Length frequency data for sample 51302, together with the percentage of the whole sample that size class of 51302 represents.
* = specimen parasitised by rhizocephalan.

2. Mean Wet Weight. The mean wet weight of sample 51302 is far greater than any other sample, being 24·12 g for males and 20·89 for females (Table 6, Fig. 11).

3. Relative Growth of Chelae. Where enough data is available, the individuals from sample 51302 seem to have a different growth rate than the rest of the population, e.g. for female chelae (Fig. 13). This sample is the only one with some females demonstrating the arched chela form (Fig. 16a).

4. Eye Size. The individuals from sample 51302 have smaller eyes in proportion to CL than those from the Porcupine Sea-bight (Fig. 26). This may just be a function of the larger size, though log transforming the values gives a similar pattern.

So basically, sample 51302 is anomalous with the rest of the population, being

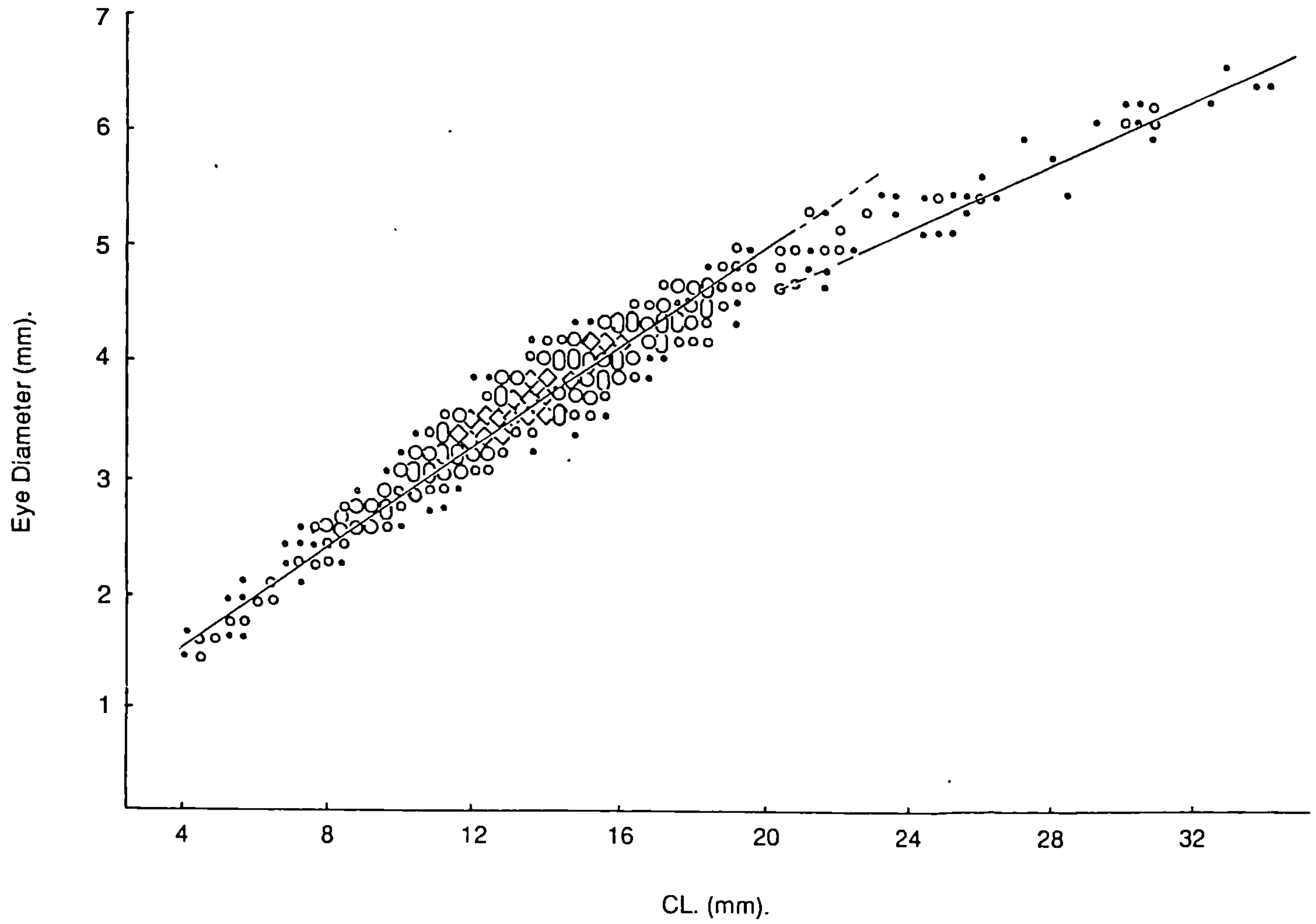


Fig. 26: Eye diameter against CL for *Munida sarsi*. Symbols = ● 1 datum point, ○ 2-5 points, ○ 6-10 points, 0 10-20 points, ◇ >20 points.

composed entirely of very large individuals, with a total absence of the smaller munidids that form the bulk of the Sea-bight population. The sample was taken using an OTSB, which is the same piece of equipment that was used to catch the majority of smaller munidids from the Sea-bight, so there is no size selectivity in respect to the sample gear causing the distribution seen in sample 51302. This results in three main explanations for this sample:

1. The conditions encountered on the Porcupine Bank are much more favourable than those in the Sea-bight, so the *M. sarsi* living in this region either grow much faster and reach a larger size at the same age than those in the Sea-bight, or live longer and so attain a greater size. This has been noted for other crustaceans, such as *Hyas coarctatus* at different sites in the Isle of Man (Hartnoll, 1963). However, in the areas where the animals grow larger, there would still be smaller younger individuals present. This is not the case in sample 51302.

2. The largest members of the *M. sarsi* sea-bight population migrate to this area on the Porcupine Bank. Size related migrations of other deep-sea decapods have been noted, as with the red crabs *Geryon quinquidens* (Wigley *et al.*, 1975) and *Geryon trispinosus* (this study, Ch. 6). However, these migrations are also depth related, but sample 51302 was taken from 330 m. *M. sarsi* of all standard sizes were taken both shallower and deeper than this sample, so using depth as a cue would not cause migrating individuals to necessarily end up in the region of 51302. In addition, there are no apparent reasons for such a migration. The *Geryon* migrations are related to sexual maturity, the main breeding population being found in the shallower water. The large individuals found in sample 51302 are well above the minimum size of sexual maturity, this being around 12·5 mm CL, so any migration would not be correlated to the animals becoming sexually mature.

3. The individuals from sample 51302 represent a new species or a subspecies of *M. sarsi*. However, a study of the diagnostic morphological characteristics shows no significant differences between the specimens from 51302 and standard *M. sarsi*, apart from the eye size

which may be purely a function of size. In addition, if these specimens were indeed a sub-species smaller examples of the younger age groups would be expected. These are not apparent.

Sample 51302 remains something of a mystery, and few conclusions can be drawn without more samples being taken from the area. However, the lack of smaller individuals in a well represented sample is still puzzling.

Chapter 4:

A Rhizocephalan (Crustacea, Cirrepedia) infestation of the galatheid *Munida sarsi* (Decapoda, Anomura), the effects on the host and the influence of depth on the host-parasite relationship.

Introduction.

Munida sarsi Huus is the most northerly species of the galatheid genus *Munida* found in the North-East Atlantic, extending from the North Cape of Norway to the northern coast of Spain (Rice & Saint Laurent, 1986) and has been recorded mainly from depths between 200 and 800 m.

Three species of rhizocephalan parasite have been described infesting *Munida sarsi: Triangulus munidae* (Smith, 1906), *Lernaeodiscus ingolfi* (Boschma, 1928) and *Tortugaster boschmai* (Brinkmann, 1936). All three have also been found infesting *M. tenuimana* G.O.Sars and *M. rugosa* Fabricius (Høeg & Lützen, 1985).

Rhizocephalans have evoked interest for many years due to their amazing adaptations to their parasitic mode of life. They are only recognisable as barnacles during the diagnostic nauplius and cypris larval stages. After these follow highly modified stages unique to the order. There is sexual dimorphism in relation to size in the cypris stage, the females being discernibly smaller (Høeg, 1984). The female cypris invades the host within 6-7 days and attaches using cement glands. This is followed by the formation of a kentrogon larval stage within the cypris (Høeg, 1985), which when fully formed injects, via a special stylet, a 'primordial parasite' into the host. In the studied case of *Lernaeodiscus porcellanae* on *Petrolisthes cabrilloi,* the cypris settlement and resulting kentrogon formation occurs on the gills (Ritchie & Høeg, 1981).

The parasite then enters the vegetative 'interna' stage of its life cycle, when the primordial parasite ramifies and migrates posteriorly inside the host forming an extensive rooting system that intrudes into many of the host's organs (Brinkmann, 1936; Lützen, 1981a). The interna eventually produces an abdominal nucleus between the nerve cord and the epidermis (Lützen, 1981a, 1984), which when complete breaks through the host's skin and changes into a virgin externa. The duration of the interna phase from kentrogon to virgin externa ranges from 3 months to 2 years (Høeg & Lützen, 1985). The resulting virgin externa can only grow and mature if settled upon by male cyprids (Yanagimachi, 1961; Lützen, 1984; Høeg & Ritchie, 1985) which undergo a similar metamorphosis to that of the female cyprids, forming in this case a trichogon larva (Høeg, 1987). These migrate through the externa mantle cavity to the receptacle ducts, two sac-like structures in the basal region of the externa visceral sac. The cuticle of the trichogon is shed and the male cells are implanted next to female receptacle cells.

Once the male cyprids have settled, the externa enters the immature growth phase, extending until the first oviposition (Høeg & Ritchie, 1985). The moults shed the mantle cavity lining and vasa deferentia in addition to the exterior cuticle, the externa increasing rapidly in size. Now mature and with spermatogenesis commencing 5-6 days after the trichogon cells have become embedded in the receptacle cells (Høeg, 1987), egg production begins.

The life span of externae varies from species to species, from 1 year in the case of *Sacculina carcini* (Lützen, 1984), when the externa becomes noticeably old and drops off, to at least 4 years for *Triangulus munidae* (Brinkmann, 1936). When removed either by the death of the parasite or dislodgement by some physical factor, a scar is left on the abdomen of the host. In some cases of removal of externae, regeneration of a new externa has been noted, though this is not at all common (Hartnoll, 1967: Lützen, 1981b).

In the majority of cases, the rhizocephalan causes modifications to the host, often termed rather inaccurately 'parasitic castration', and are generally developments causing the host to tend and protect the externa as if it were an egg mass. Most changes are presumably caused by influence of the parasite's interna on the host's endocrine system and include: degeneration of organs, especially the gonads, changes in the size of the male abdomen towards the female state and particularly alterations to the structure of the pleopods. The effects vary between host and rhizocephalan species and have been reviewed by Reinhard (1956), Hartnoll (1967) and Nielsen (1970). This chapter discusses the effects of rhizocephalans on their hosts in light of more recent developments in crustacean endocrinology.

The relationship between *Munida sarsi* and its three rhizocephalan parasites was studied by

Brinkmann (1936) as part of a general study on the *Munida* from Norwegian fjords. He reported that each rhizocephalan species has a particular, discreet effect on the secondary sexual characters of the host munidid, namely a certain degree of modification of the pleopods of both male and female hosts. This chapter reports on a detailed investigation into the effects that the parasites, in particular *Triangulus munidae,* have on *M. sarsi,* with descriptions of the series of pleopod Types caused by this particular parasite, rather than the single effect as reported by Brinkmann. The endocrine mechanisms behind these structural changes are proposed and discussed, as is the influence of depth on the whole host-parasite relationship.

Materials and Methods.

During the period 1978 to 1986, a total of 1933 *Munida sarsi* have been collected from the Porcupine Sea-bight (49-52°N, 11-14°W) between the depths of 205 and 815 m. Two types of sampling gear were used: the semi-balloon otter trawl (OTSB) complete with "V" doors (see Merrett & Marshall, 1981) and the IOS epibenthic sled (BN) (see Rice *et al*, 1982). The specimens were fixed in 5% formalin solution and later transferred to 70% alcohol for preservation. They have been stored in the 'Discovery' collection at the Institute of Oceanographic Sciences Deacon Laboratories, Wormley, Surrey.

From the main sample, 293 specimens infested by rhizocephalans were removed for further study. The following measurements were taken using either dial calipers or the graduated eyepiece of a Wild stereoscopic microscope. On *M. sarsi:* carapace length (CL) from the posterior margin of the right orbit to the posterior carapace margin. On Rhizocephala: maximum externa width from left to right. All measurements were made to the nearest 0·1 mm. Sex of the *M. sarsi* was determined by the position of the gonopores and the presence or absence of the first pair of pleopods. General pleopod structure could not be used reliably due to the modifications of their form caused by the action of the parasite. In addition, the abdominal segment (AS) position of the externa or scar on the host's abdomen and the state of modification of the pleopods by the parasitic infestation were noted.

For comparative purposes, the peculiar measurement of CL used by Brinkmann (1936) was also taken, this being from the notch between the main and right lateral rostral spine to the posterior edge of the carapace. A relationship to convert Brinkmann's carapace length (BCL) to the standard carapace length (CL) was obtained as: **CL = 0·96 BCL - 0·51.** Both measurements are in mm.

Results.

Three rhizocephalan species were found to be infesting *Munida sarsi* in the Porcupine Sea-bight: *Triangulus munidae* (Smith), *Lernaeodiscus ingolfi* (Boschma) and *Tortugaster boschmai* (Brinkmann). All these species were found on the *M. sarsi* population of Western Norway studied by Brinkmann (1936). The individual species and their effects on the external morphology of the host are detailed later.

In addition to the three species, 43 specimens bore scars from a previous infestation. The position of the scar and the pleopod structure was recorded as for the individuals carrying externae. These scars are left behind when the externa either drops off after completing its life history, or is knocked off, especially during the sampling process or the resulting preservation. Several loose externae were found in the specimen jars, all of which were *Triangulus munidae*. From this, the frequency data for infestation, together with other observations (detailed below) on the effects caused by the now departed parasite to the host, it can safely be assumed that the great majority of the *M. sarsi* now bearing scars were once the hosts of *Triangulus munidae*. However, these squat lobsters with scars were dealt with separately for the purpose of analysis.

Degree of infestation by each species on *Munida sarsi*.

The number of individual *Munida sarsi* of each sex that were infested by each species of rhizocephalan was recorded and using the total figures for each sex in the sample, a figure for percentage infestation could be calculated. The whole sample was composed of 1059 males and 863 females, plus 11 individuals too small to sex which were therefore recorded as immature. A total of 293 *M. sarsi* were found to be infested (15·16 %) and the breakdown of the infestation can be seen in Table 1.

Species	Sex	Total	No. Infested	% Infestation
Triangulus munidae	M	1059	113	10.67
	F	863	121	14.02
Lernaeodiscus ingolfi	M	1059	4	0.38
	F	863	1	0.12
Tortugaster boschmai	M	1059	7	0.66
	F	863	4	0.46
Scars	M	1059	20	1.89
	F	863	23	2.67

Table 1: Infestation of each sex of *Munida sarsi* by each species of rhizocephalan, plus scarred individuals.

It is obvious from these results that by far the most common rhizocephalan on *M. sarsi* in the area studied is *Triangulus munidae*, forming 93·6 % of the non-scar infestations,with *Lernaeodiscus ingolfi* and *Tortugaster boschmai* being represented by only a few cases, 5 and 11 respectively.

Overall, females were infested significantly more than males (Chi-squared, $P<0{\cdot}05$), with a total of 17·3 % of females being parasitised, compared to only 13·6 % of males. This is a reflection of the difference between the infestation of the sexes by the dominant species, *T. munidae*, which Brinkmann (1936) found also to infest females to a greater degree.

Degree of infestation of each host size class.

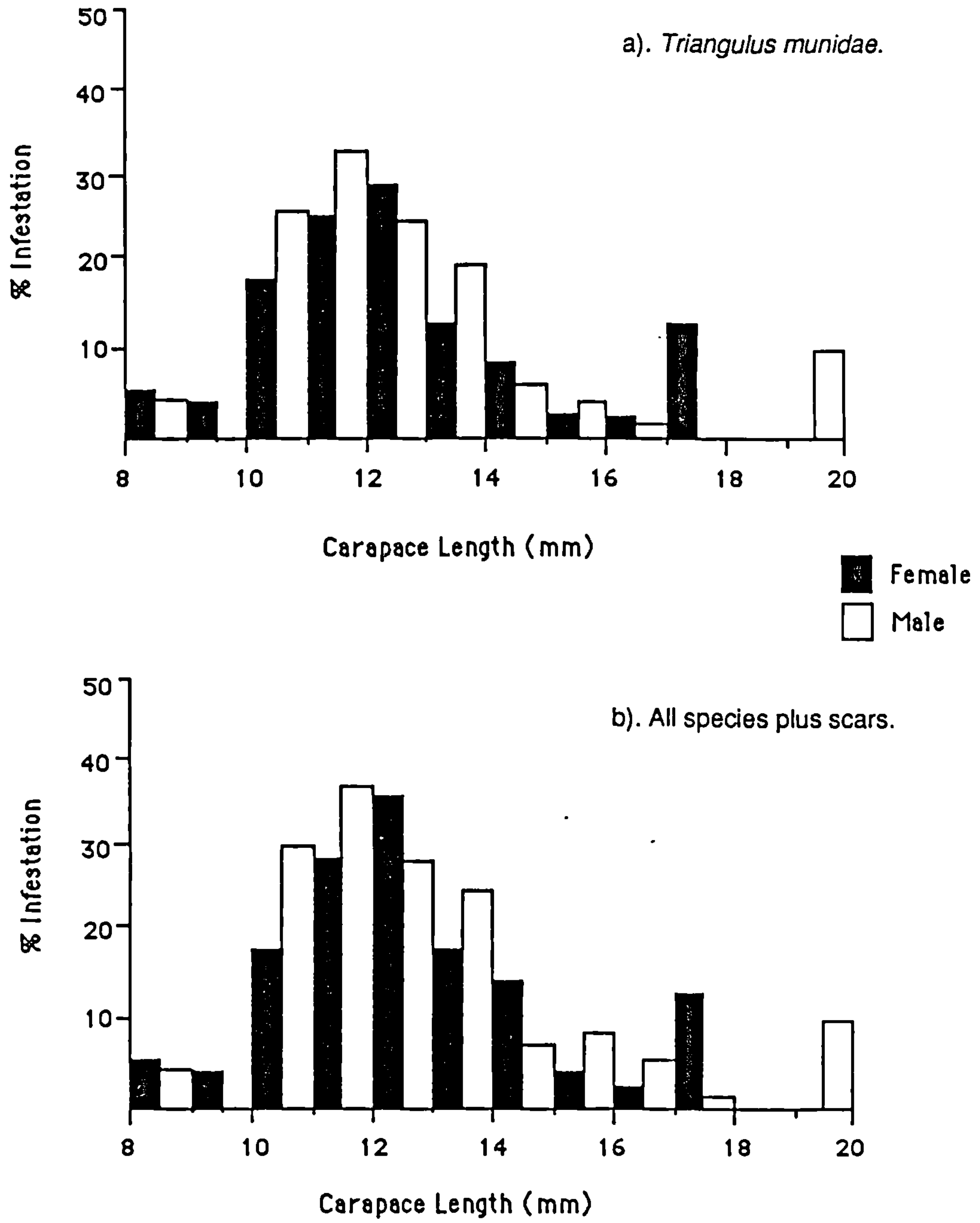
To investigate whether there was a differential infestation in respect to the size of host, the percentage infestation for each millimetre carapace length size interval was determined for both *Triangulus munidae* and for all species plus scars, the sample sizes being too small to obtain valuable results for the less common of the rhizocephalans if treated singly. The results (Table 2, Fig. 1) show that there is indeed a range of host size (11·0-13·0 mm) that is infested in higher proportions than the sizes both smaller and larger than this range. There is also some difference between the graphs for the sexes, the peak for females being more pronounced than that for males, falling quite rapidly after 13·0 mm, while the males remain relatively highly infested up to 14·0 mm.

The range of CL found over the whole sample was 4·0-34·0 mm, whereas the range of infestation was only 8·0-19·0 mm, suggesting a minimum and a maximum size when infestation can occur, as in the total sample individuals up to 34 mm CL were found, but none larger than 19 mm was parasitised. This suggests that there is in fact a size when *M. sarsi* does not become infested by the rhizocephalans studied here.

		CL. Size Class (mm)-% Infestation.											
	Sex	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	14.0-14.9	15.0-15.9	16.0-16.9	17.0-17.9	18.0-18.9	19.0-19.9
Triangulus munidae	F	5.6	4.3	17.5	24.3	28.1	13.6	9.6	2.9	2.8	12.5	0.0	0.0
	M	4.2	0.0	25.0	32.5	23.4	19.0	6.0	4.6	1.9	0.0	0.0	8.0
Total-All Species and Scars.	F	5.6	4.3	17.5	27.9	35.6	17.2	13.2	4.3	2.8	12.5	0.0	0.0
	M	4.2	0.0	29.2	36.3	28.9	24.5	7.4	8.4	5.7	1.5	0.0	8.0
Number of Individuals.	F	18	23	40	111	160	169	138	69	35	8	5	1
	M	24	36	48	80	111	147	149	131	105	67	52	25

Table 2: Percentage infestation of each mm size class of *Munida sarsi* by *Triangulus munidae*, together with all infested individuals.

Fig. 1: Percentage infestation of each mm size class of *Munida sarsi.*



Change in infestation levels at depth.

The specimens were divided into 100 m depth classes to study the effect, if any, of depth on the degree of infestation of *M. sarsi*. However, no samples of this species have thus far been taken between 600-699 m, so unfortunately the data is not continuous.

The proportion of hosts at each depth that was infested by any of the three species, or bore the scars of infestation, was calculated (Table 3 and Fig. 2a). In addition, figures were obtained for the percentage infestation for each species and scarred individuals at each depth (Table 4, Fig. 2, b-e) to give some indication of the depth range of each species. As can be seen from Table 3 and the resulting graph, there is an unexpected gradient in degree of infestation with depth, the shallower samples (200-399 m) demonstrating a much lower percentage infestation than those deeper, this corresponding, as would be expected, with the equivalent data and graph for *T. munidae* (Fig. 2b), the dominant species. All *L. ingolfi* were found between 400-499 m and the examples of *T. boschmai* encountered were all from the shallower depths (<500m).

From the data, depth ranges for each rhizocephalan species in the Porcupine Sea-bight can be stated:

Triangulus munidae:	243-793 m.
Lernaeodiscus ingolfi:	455-490 m
Tortugaster boschmai:	243-490 m
Scars:	243-763 m (c.f. *T. munidae*.)

Multiple infestations.

For each rhizocephalan species, there were hosts demonstrating multiple infestations, although three

Depth (m)	Total No.	No. Infested	%Infestation
200-299	325	6	1.85
300-399	37	2	5.41
400-499	1452	256	17.70
500-599	73	18	24.66
600-699	No data	No Data	No Data
700-799	45	11	24.44
Total *	**1933**	**293**	**15.16**

* Plus one non-infested specimen from 1100-1199 m.

Table 3: Total number of individual *Munida sarsi* infested at each depth interval.

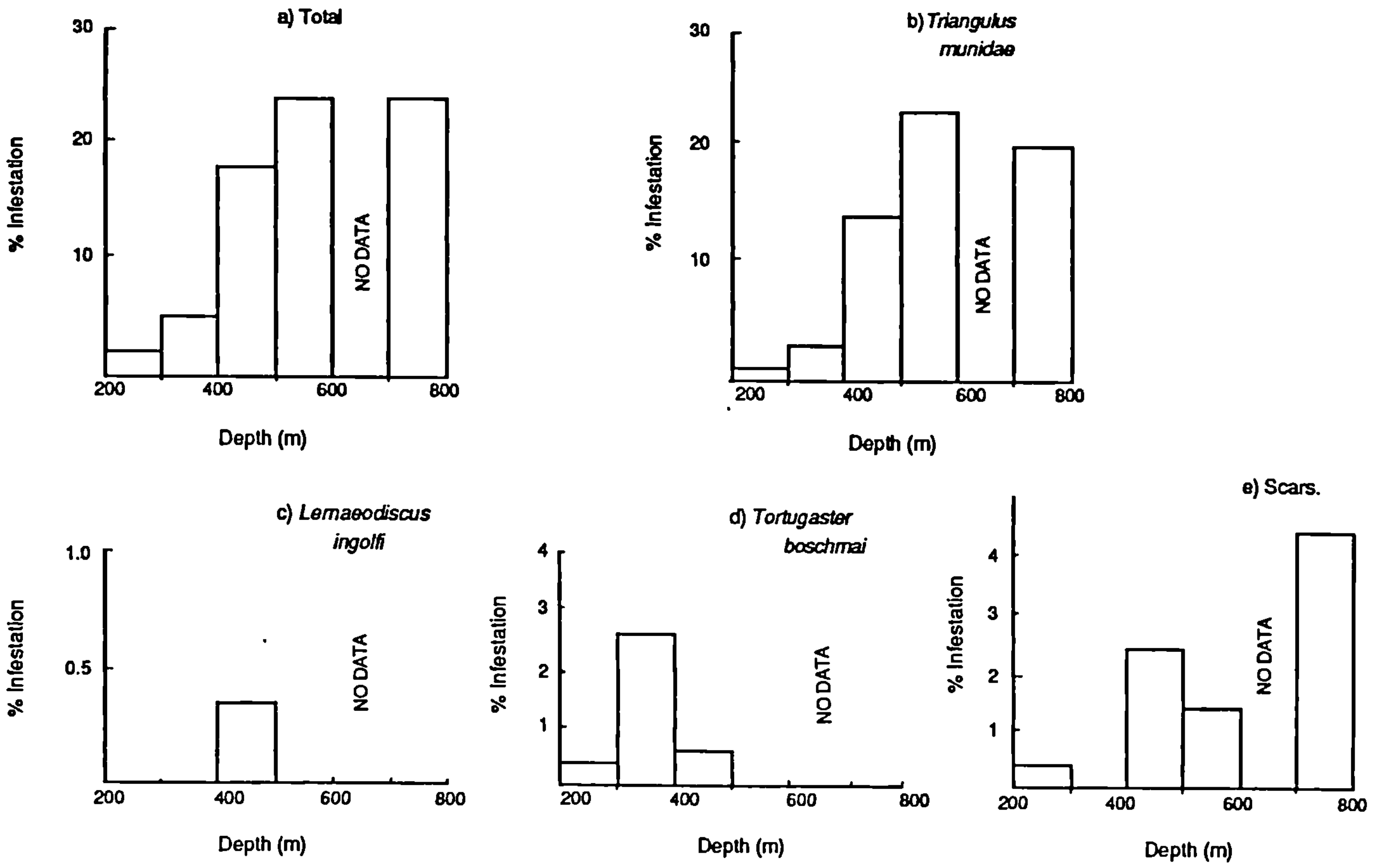


Fig. 2: Percentage infestation at each 100 m depth interval.

	Triangulus munidae		*Lernaeodiscus ingolfi*		*Tortugaster boschmai*		Scars	
Depth (m)	No.Infested	% infestn.	No.Infested	% Infestn.	No.Infested	% Infestn.	No.Infested	% Infestn
200-299	4	1.23	0	0.00	1	0.31	1	0.31
300-399	1	2.70	0	0.00	1	2.70	0	0.00
400-499	203	13.98	5	0.34	9	0.62	39	2.48
500-599	17	23.29	0	0.00	0	0.00	1	1.36
600-699	NO DATA							
700-799	9	20.00	0	0.00	0	0.00	2	4.44

Table 4: Infestation at depth for each rhizocephalen species on *Munida sarsi,* plus scarred individuals.

externae, for *T. munidae*, was the maximum observed. The other cases were of double externae and the number of these double infestations for each species can be seen in Table 5.

The more interesting multiple infestations are detailed below under 'Details of each rhizocephalan species.'

Site of externa emergence: preferential abdominal segment.

The frequency of emergence of each parasite species from each abdominal segment was recorded, the results forming Table 6. From this, Fig. 3 was constructed showing the most common segment of emergence for each species, plus scarred individuals.

By far the most common segment for *T. munidae* was AS3 and for *T. boschmai* this was AS6, as would be expected for this species (Høeg and Lützen, 1985). More details on the abdominal segment preference for each species can be found under the individual heading for the separate rhizocephalan species.

Details of each rhizocephalan species and their effect on the pleopod structure of the host.

The rhizocephalans were identified using Høeg and Lützen (1985) and the basic features peculiar to each species are noted below, together with any new observations.

a) *Tortugaster boschmai* Brinkmann, 1936.

Asymmetrical, left side larger than right side, so the mantle opening, which is relatively small and thin, is displaced to the right hand side. Externa body generally flat and often the edges are folded.

Size range observed: 1·2-11·9 mm (the latter undergoing ecdysis).

Originally reported emerging only from the sixth abdominal segment (Høeg and Lützen, 1985), but

No. Hosts With:	*Tortugaster boschmai*	*Lernaeodiscus ingolfi*	*Triangulus munidae*	Poisson Distribution Expected	Chi-sq.
0 Externae	1922	1928	1699	1695	0.01
1 Externa	9	3	216	222	0.07
2 Externae	2	2	17	15	0.27
3 Externae	0	0	1	1	0.00
				Total =	0.35

Table 5: Number of single and multiple infestations of each rhizocephalen species on *Munida sarsi*, together with the expected number of multiple infestations of *Triangulus munidae* calculated using the poisson distribution. The total Chi-squared value obtained is not significant (P>0·9), the distribution of the externae being as expected.

	Abdominal Segment.					
Species	1	2	3	4	5	6
Triangulus munidae	0	9	227	13	2	1
Lernaeodiscus ingolfi	0	2	2	3	0	0
Tortugaster boschmai	0	0	0	0	2	11
Scars.	0	8	36	2	1	0

Table 6: Abdominal segment site of emergence: number of externae of each rhizocephalan species observed on the abdominal segments of *Munida sarsi*.

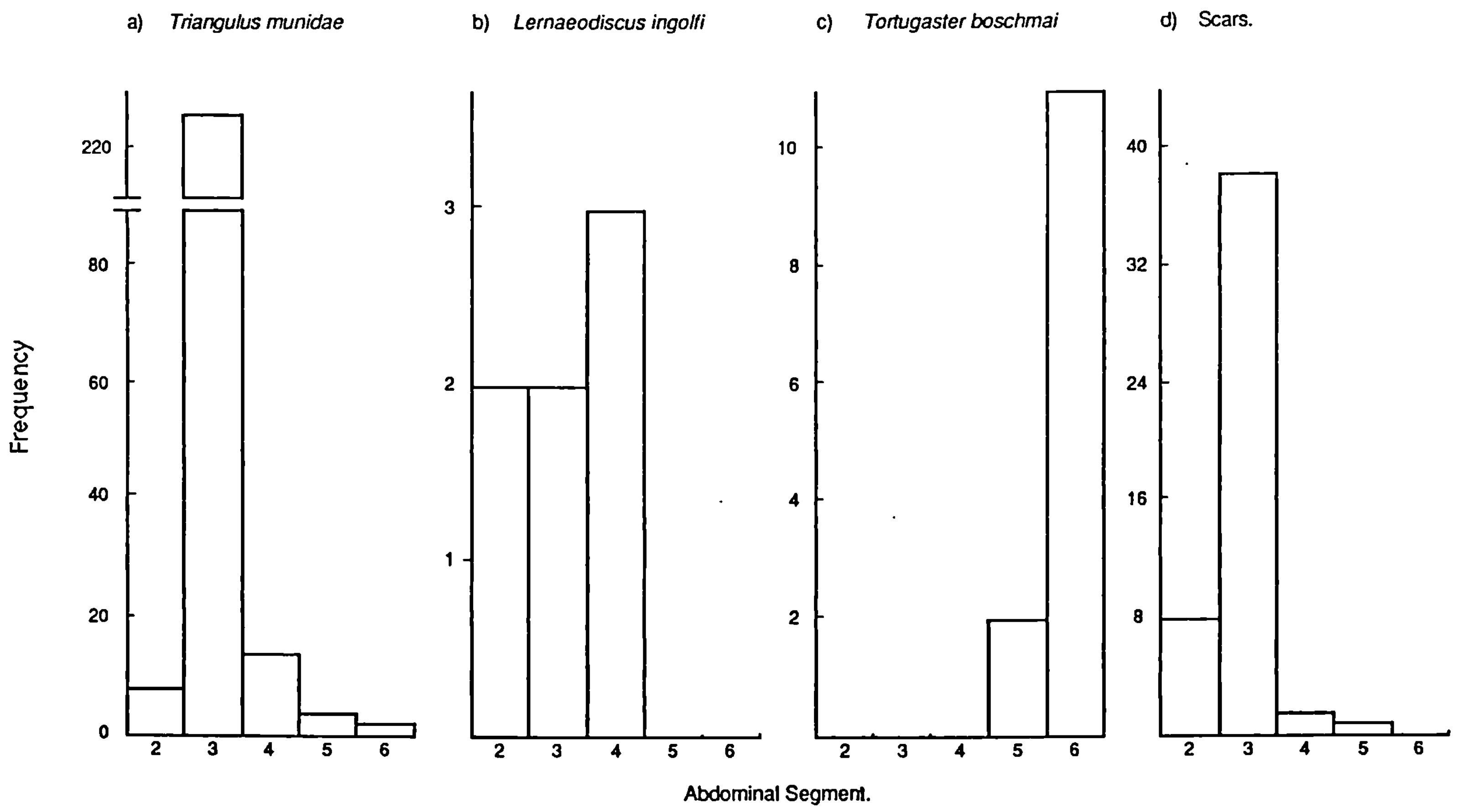


Fig. 3: Frequency of externae of each species on the abdominal segments of *Munida sarsi.*

in this study one host was found to be carrying a single externa on AS5 and another bore a double infestation of *T. boschmai*, with a small externa (2·2 mm) on AS6, together with a larger body (5·7 mm) on AS5.

The parasite has no effect on the pleopod structure of either male or female hosts, both sexes show 100 % normal pleopod structure (Fig. 4: a.i, b.i, c.i, d.i. Fig. 5: a.i-iii.), supporting the observations of Brinkmann (1936).

Found only in shallower samples (<500 m), as did Høeg and Lützen (1985) and not common in the Porcupine Sea-bight (a new recorded locality for this species), with only 11 individual *Munida sarsi* being found infested (0·57 %), 7 males (0·66 %) and 4 females (0·46 %).

b) *Lernaeodiscus ingolfi* (Boschma, 1928).

Perfectly symmetrical. The large mantle opening is central, with a protruding, swollen lip which is always open to some degree, usually extremely wide.

Size range observed: 1·5-9·6 mm.

Høeg and Lützen (1985) reported only single occurrences, but two out of the five infestations were doubles. The single externae emerged one from AS3 and two from AS4, while the double infestations had externae on AS2+3 and AS2+4.

The effect on the pleopods of the host was constant, as was that of *T. boschmai*. However, in the male host, *L. ingolfi* induced a feminisation of pleopods 3-5, the usual swimmeret Type developing into a more elongate and far more setose form (Fig. 4: c.ii, iii. d.ii.). This form is very similar to the effect produced on the sole female found parasitised by *L. ingolfi* (Fig. 5: b.i-iii.), all the pleopods being slightly degenerate and much less setose than those of a non-infested individual. The male copulatory appendages (pleopods 1 and 2) remained unaffected, as with *T. boschmai*.

Brinkmann (1936) found between 0·2 and 0·5 % infestation of *L. ingolfi* on *M. sarsi* off the Norwegian coast and this compares favourably with the 0·26 % infestation of the *M. sarsi* examined in

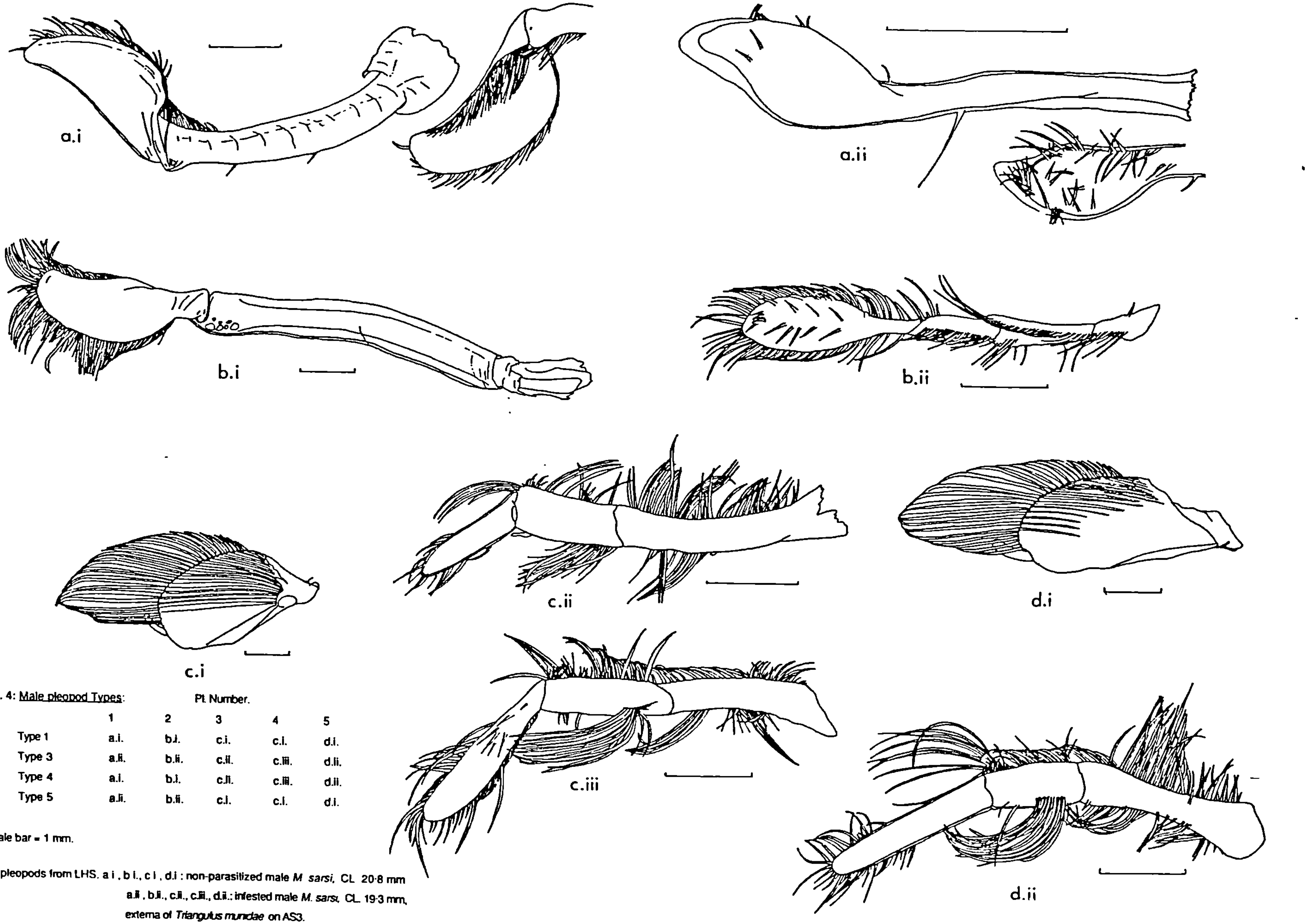


Fig. 4: Male pleopod Types:

	Pl. Number.				
	1	2	3	4	5
Type 1	a.i.	b.i.	c.i.	c.i.	d.i.
Type 3	a.ii.	b.ii.	c.ii.	c.iii.	d.ii.
Type 4	a.i.	b.i.	c.ii.	c.iii.	d.ii.
Type 5	a.ii.	b.ii.	c.i.	c.i.	d.i.

Scale bar = 1 mm.

All pleopods from LHS. a.i., b.i., c.i., d.i : non-parasitized male *M. sarsi*, CL 20·8 mm
a.ii., b.ii., c.ii., c.iii., d.ii.: infested male *M. sarsi*, CL 19·3 mm,
externa of *Triangulus munidae* on AS3.

this study from the Porcupine Sea-bight (a newly recorded locality for this species) and so suggests that *L. ingolfi* is not a particularly common parasite on this munidid.

All specimens of *L. ingolfi* were found in the one large sample taken over a depth range of 455-490 m.

c) *Triangulus munidae* (Smith, 1906).

Asymmetrical body of externa, the right hand side being larger than the left, causing the mantle opening to be displaced to the left hand side. This opening is narrow and longitudinal, resembling a gash on the usually smooth externa surface.

Size range observed: 0·6-11·9 mm.

By far the most frequent rhizocephalan found on *M. sarsi* in the Porcupine Sea-bight (again a new locality for this particular species), with a total of 234 cases of infestation. This was composed of a 10·67 % infestation in males and a 14·02 % figure in females, confirming Brinkmann's (1936) statement that it occurs more frequently on female hosts, although the infestation in this study was considerably higher than that found by Brinkmann, that being between 1·4 and 8·6 %.

The depth range for *T. munidae* was 205-795 m, increasing the depth range (70-600 m) noted by Høeg and Lützen (1985) for this species.

Externae were found on all abdominal segments from 2-6, adding segments 5 and 6 to those described as sites of emergence by Høeg and Lützen (1985). However, by far the most common site of emergence was AS3, especially the posterior part of the segment where it meets AS4, 90 % of all externae being found on this segment. There were 216 cases with a single externa, 17 with two and only one triple infestation, all three being on AS3. This distribution does not deviate from the expected Poisson distribution (Table 5), indicating no clumping or attractant factors influencing the settlement of *T. munidae* larvae on prospective hosts.

Brinkmann (1936) stated that the effect on the male hosts by *T. munidae* was a total degeneration of the copulatory appendages (pleopods 1 and 2) and a feminisation of pleopods 3-5. However, the effect of the parasite on these secondary sexual characteristics seems to be more varied, with different pleopod structures for both male and female hosts being noted. The whole range of pleopod Types is described below.

Pleopod Types observed on infested *Munida sarsi.*

a) Males.

Type 1.

All pleopods unchanged by the presence of the parasite. The copulatory appendages 1 and 2 are relatively non-setose (Fig 4: a.i, b.i.) and the pleopods 3-5 are the standard swimmeret Type found on unparasitised males (Fig. 4: c.i, d.i.)

Type 2.

All pleopods are slightly affected, resulting in structures falling between Types 1 and 3. Pleopods 1 and 2 have diverged from the unparasitised form, with some reduction in size and change in the setae pattern, though considerably less degenerate than Type 3. Pleopods 3-5 show some elongation away from the swimmeret Type, but are small and lacking in setae compared to Type 3.

Type 3.

All pleopods are severely affected. Pleopod 1 is reduced and markedly degenerate (Fig. 4: a.ii.), becoming even less setose in the process, though retaining its basic shape. Pleopod 2 is also reduced (Fig. 4: b.ii.), though more setose and morphologically developed towards the female form. However, the endopodite retains some resemblance of the original shaped male form. Pleopods 3-5 are feminised

(Fig. 4: c.ii, iii, d.ii.), becoming elongate and setose with no trace of the swimmeret structure. However this resembles the parasitised female state (Fig 5: b.ii,iii) rather than the more setose unparasitised mature female form (Fig. 5: a.ii, iii.).

Type 4.

Pleopods 1 and 2 are unchanged, as in Type 1, but the pleopods 3-5 are feminised, as in Type 3.

Type 5.

Pleopods 1 and 2 are totally affected, as Type 3, but no change from the normal male swimmeret form of pleopods 3-5.

b) Females.

Type 7.

Pleopods all represent the forms of a mature unparasitised female, large and extremely setose (Fig. 5: a.i-iii.), unchanged by the presence of the parasite (only observed when infested by *Tortugaster boschmai*).

Type 8.

All pleopods show a reduction in size and are considerably less setose than the unaffected form (Fig 5: b.i-iii.). Pleopod 2 is greatly reduced and is practically free from setae (Fig. 5: b.i.).

Type 9.

A development towards the male unparasitised form of pleopods 3-5, the swimmeret structure emerging from the most proximal segment and the remainder of the original female pleopod form

Species	Pleopod Type of Host (male) 1	2	3	4	5	Pleopod Type of Host (female) 7	8	9
Triangulus munidae	9	20	73	10	1	0	110	11
Lernaeodiscus ingolfi	0	0	0	4	0	0	1	0
Tortugaster boschmai	7	0	0	0	0	4	0	0
Scars	3	1	12	3	1	1	17	5

Table 7: Pleopod types induced by each rhizocephalen species on the host *Munida sarsi*, plus pleopod types found on scarred individuals.

Depth (m)	% of each pleopod type (male) 1	2	3	4	5	% of each pleopod type (female) 8	9
200-299	0.0	0.0	100.0	0.0	0.0	100.0	0.0
300-399	0.0	0.0	100.0	0.0	0.0	No Infested females	
400-499	6.1	19.2	67.2	7.1	0.0	92.3	7.7
500-599	12.5	12.5	25.0	37.5	12.5	77.8	22.2
600-699	NO DATA						
700-799	50.0	0.0	50.0	0.0	0.0	80.0	20.0

Table 8: Percentage of the infested population of *Munida sarsi* at each depth interval with the pleopod types induced by *Triangulus munidae*.

degenerating (Fig 5: c.i-iii.). There is a decrease in masculinisation posteriorly from pleopod 3. Pleopod 2 demonstrates the form of Type 8 (Fig 2: b.i.).

The frequency distribution of the above pleopod Types for each rhizocephalan species, on both male and female hosts, can be seen in Table 7 and the resulting Fig. 6. This gives some indication of the main pleopod structures induced by each species of parasite, as outlined above as well as the comparative frequencies of the effects caused by *Triangulus munidae*. Fig. 4 highlights the single effects on each sex by both *Lernaeodiscus ingolfi* and *Tortugaster boschmai*, compared to the range of pleopod Types caused by *T. munidae*.

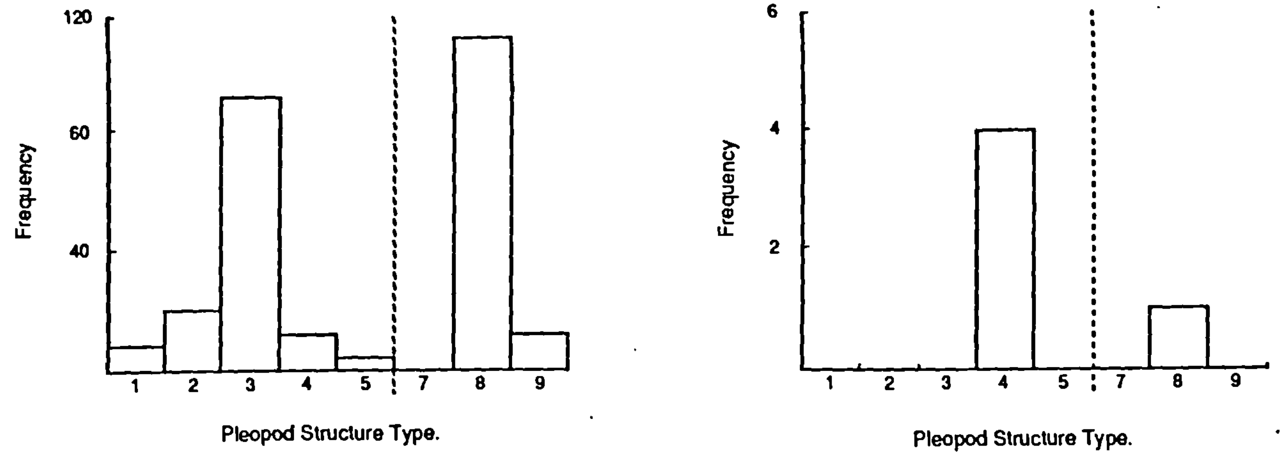
Influence of other factors on host pleopod structure.

The variety of effects produced by *Triangulus munidae* on the pleopod structure of *Munida sarsi* may be influenced by other factors, such as size of the host, externa size, abdominal segment from where the externa erupts and depth.

a) Depth.

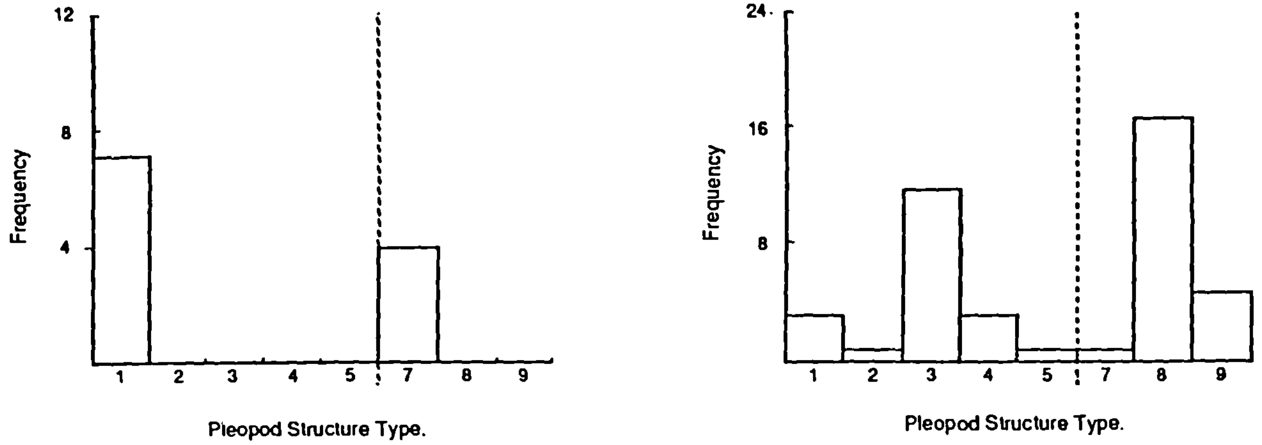
The frequency of each pleopod structure Type of *M. sarsi* infested with *T. munidae* at each depth interval was noted and converted to a percentage of all the parasitised individuals of each sex at that depth (Table 8). From these data, Fig. 7 was constructed and this indicates a change in the composition of the pleopod Types from the form noted by Brinkmann (1936) caused by this rhizocephalan, Type 3, which is dominant in the shallower water (<400m), Fig. 7. c, to the unaffected Type 1 structure in the deepest samples (Fig. 7. a.), moving through examples of Types 2, 4 and 5, the "intermediate" Types, in the mid-depths (Fig 7. b, d, e.).

In respect to the females, the unusual 'male-type' pleopods (Type 9) were only found in the deeper



a) *Triangulus munidae.*

b) *Lernaeodiscus ingolfi*



c) *Tortugaster boschmai.*

d) Scars.

Fig. 6: Frequency of *Munida sarsi* pleopod structure Types induced by each rhizocephalan species, plus scars.

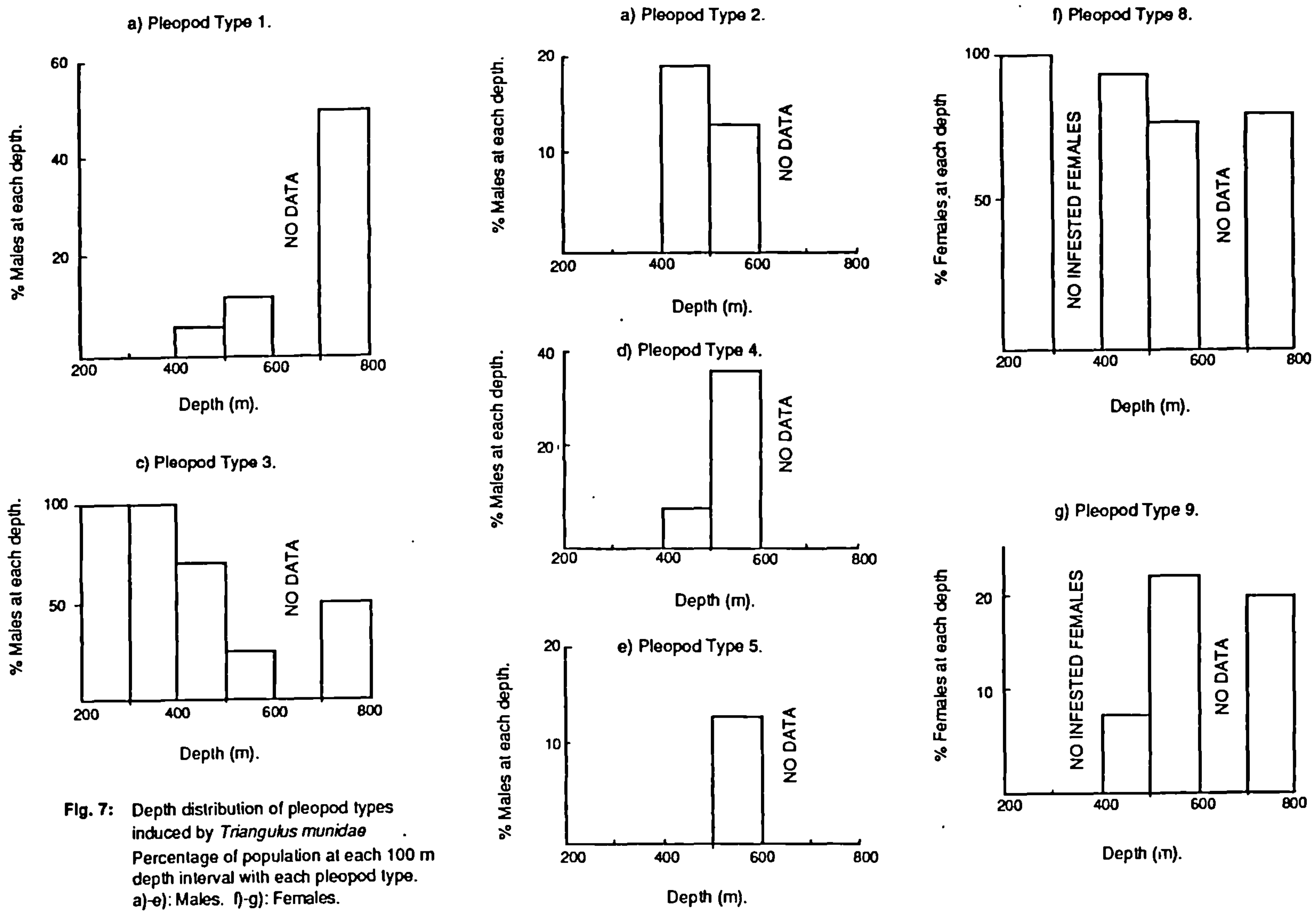


Fig. 7: Depth distribution of pleopod types induced by *Triangulus munidae*. Percentage of population at each 100 m depth interval with each pleopod type. a)-e): Males. f)-g): Females.

Discussion.

The form of the pleopods resulting from infestation by *Triangulus munidae*.

Triangulus munidae, on infestation of *Munida sarsi*, influences the development of the host's pleopods and has the effect of producing a variety of pleopod Types (see above). However, some of these structures are not the expected forms usually induced by a rhizocephalan parasitising large decapods, such as anomurans and brachyurans.

The general pattern is a modification of males towards the ovigerous female form, such as the broadening of the abdomen in a variety of Brachyura (Veillet, 1945; Reinhard, 1950; Hartnoll, 1967) and a development of the pleopods 3-5 to the setose female condition (Reinhard, 1956). In this study, this was demonstrated by the Type 3 pleopods of the infested males, which have been modified as expected, though there is some variation as discussed above.

It is the effect on the female pleopods by the parasite that is particularly interesting, in relation to the actual structures resulting, the mechanisms by which these effects are induced, and the benefit of these pleopod forms to the parasite.

The result of an infestation of a female is usually hyper-feminisation, but a reduction in the size and number of setae of the pleopods of parasitised females is not unknown, as in *Inachus dorsettensis* (Smith, 1906, as *I. mauretanicus*), such reduced females resembling parasitised males, but not normal males (Reinhard, 1956). In this study, the majority of the females infested by *T. munidae* were of this reduced Type. Not one case of hyper-feminisation was found. However, some of the parasitised females resembled normal males, pleopods 3-5 developing into the standard swimmeret form (Type 9). This Type, which was noted by Brinkmann (1936) in just one individual (he was sampling only above 500 m), raises questions about the control of the development of the secondary sexual characters when under the influence of a rhizocephalan.

Various theories have been postulated to explain the effects on the host of sacculinidisation, but it would seem that Goldschmidt's (1931) theory of intersexuality is the most fitting in respect to the observations made in this study, The male and female sex substances produced as a result of the action of the gene in each individual decapod are delicately balanced, so Goldschmidt suggested that this balance between the M-gene's substance and the F-gene's substance is disrupted by the action of the parasite. The male form is the actively maintained state, the dominant M-genes activating the genes responsible for male morphogenesis, which in turn suppress those for the female state (Ginsburger-Vogel and Charniaux-Cotton, 1982). When the M-genes are absent, inactive or in small numbers, the genes for female morphogenesis can be expressed. However, if the dominant M-genes are in these small numbers, or their effect has been reduced due to some extraneous factor, such as parasitism, then this could lead to a state of intersexuality. A result of this would be the distinctive modifications of the secondary sexual characteristics seen in such infested Crustacea. The individual which up to the point of infestation was, for instance, male with dominant M-genes, would then have this balance destabilised, the amount of difference between the levels of the two sex substances then being insufficient to maintain the male state and the F-genes would start to have an influence. The result could be a feminisation of the pleopods, the degree of modification depending on the level of influence of the F-substance, i.e. the amplitude of the difference between the levels of M- and F-substances in the body.

The mechanics of how exactly these levels are influenced by the rhizocephalan itself are more difficult to explain. Basically, either the parasite itself produces the substances and introduces them to the host's body, as conjectured by Reverberi (1944-45), or perhaps more likely the interna of the sacculinid causes the organs of the host to modify in such a way that either substances are prevented from being produced or are generated at a greater rate or the genes themselves are affected.

In Malacostraca, the male sex-determining genes are known to be responsible for the development of the androgenic gland, the organ close to the vas deferens which has been shown to regulate male morphogenesis and spermatogenetic activity (Charniaux-Cotton *et al.*, 1966; Hoffman, 1968), i.e. the production site of the M-substances. So, in some species, the parasite has the effect of diminishing the influence of the M-genes by inhibiting the development of the androgenic gland. Therefore, the balance between the two types of sex-determining substances is affected, the F-genes become influential and the external result, as seen, can be the feminisation of the pleopods of the male host.

However, the effect on the pleopods is not constant, neither in respect of each individual's pleopod Type, nor in respect of the actual modification of the pairs of pleopods on one specimen. The general, Type 3, condition is for the first pair of pleopods to degenerate, while the other four pairs become more setose, elongate and diverge towards the female state. The reason that the first pair does not also follow such a pattern is that it does not come under the influence of the F-genes once the dominance of the M-genes has been diminished, this pair of gonopods being exclusively male. Once there is no control from the M-genes on their structure, these appendages just degenerate, towards the female form where they are not present.

So, for males, the feminisation appears to be caused by an inhibition of the androgenic gland by the ramifying interna of the rhizocephalan, allowing the F-genes to be expressed and so influencing the structures of those pleopods under the control of these female genes, the degree of modification depending on the extent of inhibition of the androgenic gland. This extent of inhibition can be used to explain the main Types of male pleopods observed:

Type 1: No degeneration of the androgenic gland at this stage, all pleopods are therefore unaffected due to the continual domination of the M-genes. There is no expression of the F-genes and so no feminisation.

Type 2: Some influence from the parasite causing partial degeneration of the androgenic gland. M-genes have a decreased effect, allowing the F-genes to be expressed to some degree. The result is partial intersexuality, all pleopods showing some signs of feminisation. Will probably lead to further degeneration of the androgenic gland and so to Type 3. A transition phase in the process of feminisation.

Type 3: Androgenic gland degenerated, dominance of the M-genes lost and expression of the F-genes possible. Pleopods 2-5 come under the control of the F-genes, so becoming feminised. Pleopod 1 has no female control and so degenerates. The culmination of the parasitic feminisation process.

These are the three main Types in the process of feminisation of the pleopods of male *Munida sarsi* by *Triangulus munidae*, though Type 1 is also the effect caused consistently by *Tortugaster boschmai*. However, two other pleopod Types were recorded:

Type 4: Partial disruption of the functions of the androgenic gland by the rhizocephalan causes an upset in the balance of the two sex substances. The F-genes have some expression causing feminisation of pleopods 3-5, though the influence of the M-substance is still sufficient to regulate the structure of the gonopods, pleopods 1 and 2. This, like Type 2, may be a transition stage, though the fact that this is the effect observed consistently on the pleopods by the other of the three rhizocephalans, *Lernaeodiscus ingolfi*, suggests that this may be an end result. It is feasible that the gonopods are under greater control by the M-genes, considering that they are the male copulatory appendages, and so in some cases would be affected by the parasitism at a further stage than the other three pairs of pleopods. These would in turn be under a high level of control by the F-gene, seeing that they are the egg bearing appendages of the female munidid.

Type 5: A Type represented by only two examples in the whole sample. The peculiar degeneration of the gonopods without change of the other three pairs of pleopods seems to be incongruous in the context of what is known, which would suggest that, seeing only two were found, another factor outside of the rhizocephalan may be involved. The pleopods may have been damaged in some way, or, more likely, development of the individual *M. sarsi* may have been retarded. Both individuals were very small and perhaps not fully mature before the infestation occurred.

If Goldschmidt's theory is applied to the infested females then the same type of parasitic activity should increase, in a similar way to the males, the relative amount of the F-substance, as concluded by Reinhard (1950). This would explain the other phenomenon associated with sacculinidised females: the precocious development of the immature female abdomen into the mature adult structure in Brachyura. Examples of such observations are by Smith (1906) on *Inachus dorsettensis* (as *I. mauretanicus*), Perez (1933) on *Pachygrapsus marmoratus* and Hartnoll (1967) on *Geograpsus lividus*. However, if this is the case, why do the pleopods of some such crabs and the pleopods of female infested *Munida sarsi* also become reduced to the form observed? Studies by a variety of workers on ovarian hormones, such as Le Roux (1931a, 1931b), Callan (1940) and Charniaux-Cotton (1952, 1953) have established that the sex substance that stimulates the abdomen to enlarge does not influence the development of the pleopods, these structures being under the control of another sex substance. Therefore, Reinhard (1950) suggested that the development of the pleopods is retarded due to the parasite disrupting the functioning of the ovary and so affecting the development of these specialised structures. This would therefore explain the 'normal' Type 8 parasitised female *Munida* pleopods observed in this study, the ovary being disturbed by the action of the ramifying interna, the control over the pleopods breaking down and the appendages degenerating to the Type 8 form. This leaves the unusual Type 9 structures, the masculinised pleopods of some infested females. This basic lack of ovarian control does not explain why the pleopods should develop towards the standard male swimmeret form, a process which suggests an influence of the M-genes or the resulting M-substance. The idea that perhaps these individuals are in fact males that have lost their first pair of pleopods and developed female genital openings without major changes to the pleopods 3-5, those most affected by the F-substance, is extremely unlikely and there is no evidence that this has occurred from a study of the internal structure.

As mentioned above, the androgenic gland is the site of production of the M-substance. Experiments have shown that implantation of this gland into juvenile, puberal or overiectomised females results in some degree of masculinisation, this first being demonstrated by Charniaux-Cotton (1954). Young *Orchestia gammarella* implanted with one or two androgenic glands become completely masculinised, their development and behaviour being that of a normal male. In decapods, the effect of implantation has not been so great, but external masculinisation has been obtained in *Palaemontes varians* (Charniaux-Cotton and Cazes, 1979) and *Pandalus borealis* (Berreur-Bonnenfent & Charniaux-Cotton, 1965). Also, some effects have been noted in female *Carcinus maenas* and *Rhithropanopeus harrisii*, with a partial masculinisation of their pleon (Charniaux-Cotton, 1958; Payen, 1969, 1975). In reference to these decapods, grafts were only successful on young females, so could it be more than coincidence that the majority of *Triangulus munidae* were found on the young adult munidids of CL between 11-14 mm, whereas no parasites were to be found on the larger specimens of greater than 20 mm CL. Reverberi (1944-45) suggested that the parasite itself may introduce a substance similar to the F-substance in order to initiate the feminisation process observed in infested males, so the manufacture of an M-substance similar to that produced by the androgenic gland is not beyond the realms of possibility.

Success in masculinisation has been achieved by injection of an extract of the androgenic gland. Katakura *et al.* (1975) obtained a partial purification of a protein from 3000 pairs of male sexual organs (including the androgenic gland) from *Armadillidium vulgare*. This was injected into sexually active female *A. vulgare* which were externally masculinised at the ensuing moult. A later study with a more concentrated extract caused the development of testes, seminal vesicles and vasa deferentia in the injected females (Katakura & Hasegawa, 1983). In addition, Reinhard (1949) worked on the differentiation of sex in a bopyrid isopod parasite. He came to the conclusion that any female bopyrid already present on the host influenced the development of any further settling larvae by producing a masculinising substance, so causing these larvae to develop into the dwarf males. Despite this, however, the introduction of such an M-substance by the rhizocephalan seems unlikely as the benefit to the parasite of this action is unclear. All the same, this very fact suggests that this modification of the females is not an effect actively produced by the parasite, but rather an occasional by-product of the rhizocephalan's action. However, if this equivalent M-substance, or a substance that happens to influence the product of the F-genes and so may shift the character of the F-substance to that of the M-substance, were to be produced then a young host may be necessary for the changes to actually occur.

By their nature, sex hormones tend to have similar chemical configurations, so a conversion of the F-substance by a chemical inadvertently released by the parasite is quite possible. If for some reason, such as an external factor, e.g. depth, the general workings and effect of the parasite on its host has to some degree broken down, then this could be the result, hence the fact that all the Type 9 females were found at the extreme end of *Triangulus munidae*'s depth range.

The Influence of Depth.

It was seen earlier that the distribution of the different pleopod Types was aligned with the bathymetric gradient, for males there being a decrease in the proportion of the Type 3 with depth. This involved an increase in the non-affected Type 1 pleopods in the deepest samples, with the intermediate stages becoming apparent in between the two (Fig. 7, a-e.). Likewise for the females, the Type 9 structures were absent in the shallower water (Fig. 7, g.). In addition to this change in pleopod structure with depth, Fig. 2 indicated an increase in the percentage infestation of *Triangulus munidae* with depth. So, in the deeper water, the rhizocephalan has a decreased effect on its host, but a greater proportion of the hosts are infested. This could be due to both *T. munidae* and *M. sarsi* being at the extremes of their depth ranges. Clearly, when an organism is at the limits of any physical range, the stress involved with the environmental parameters encountered, extremes of temperature, salinity, pressure, etc., will prevent the organism from achieving its optimum physiological state. This physiological weakness will in turn make them more susceptible to infections and generally make them less effective than individuals occupying more favourable conditions.

In the case of *Triangulus munidae* on *Munida sarsi*, both organisms are at the extremes of their ranges at below 700 m and so both become affected by the physical stresses of living in such an environment. *Munida sarsi*, being physiologically weakened, becomes more susceptible to infestation, hence the higher percentage of individuals found parasitised here than in the fitter populations at shallower depths. However, despite infesting their hosts to a greater degree, *T. munidae* is also influenced by being at the extreme of its bathymetric range, the result being that at depth it is unable to influence the development of its host as severely as it would if it were shallower. The Type 3 pleopod structure of males, the sign of the feminisation required by the rhizocephalan for the munidid to protect the externa as if it were an egg mass, is therefore not achieved.

The Effect of Externa Size.

Fig. 8 illustrated how the distribution of the pleopod Types was not spread evenly over the range of externa sizes, there being a development from the unaffected Type 1 to the feminised Type 3 as the externa grew in size. At first this would seem peculiar, as it is known that in Brachyura once the rhizocephalan becomes external, the crab ceases to moult (Reinhard, 1956; Hartnoll, 1967; Phillips & Cannon, 1978). However, the situation is different for anomurans as it is possible for them to undergo ecdysis despite the presence of an externa on the abdomen (Brinkmann, 1936; Veillet, 1945; Høeg, 1982; Bower & Sloan, 1985) and so the modification of the pleopods could take place after the externa has emerged. This is backed up by the fact that no examples were found of an individual *M. sarsi* with parasitised Type pleopods, but neither externa nor scar.

If, as in brachyurans, the eventual inability to moult is due to mechanical rather than physiological factors (Brinkmann, 1936), then it is suggested that in galatheids it takes a certain size of externa before moulting is inhibited, if at all, and the development of the pleopods takes place when the externa has emerged, but is still in the immature growth phase.

The parasitisation of *Munida sarsi* by *Triangulus munidae* demonstrates how an increase in depth, and so an increase in pressure and decrease in temperature, can affect the physiology and so the compatibility of deep-sea Crustacea, though how these factors, especially pressure, actually influence the internal workings of the crustacean, is not yet clear.

Chapter 5:

The Depth Related Migration of the Red Crab *Geryon trispinosus* (Herbst) (= *G. tridens* Krøyer), With Notes on Other Aspects of its Biology.

Introduction.

The family Geryonidae was established by Colosi (1923) to incorporate the genera of the deep-sea red crab *Geryon* and the fossil *Archaeogeryon.* Since this time, the family has aroused some discussion from carcinologists as to its exact relationship with other families, its position in the brachyuran family tree, and the genera subsequently assigned to the Geryonidae. Guinot (1971) included in the Geryonidae four east Atlantic genera: *Geryon, Paragalene, Progeryon* and *Platychelonion,* which caused Manning & Holthuis (1981) some concern. They suggested that *Platychelonion* would be better placed in the Xanthidae, and had their doubts about the position of *Paragalene* and *Progeryon,* but stated "as we have not had the opportunity to study this question in detail, we follow Guinot, at least for the time being."

An early attempt to place the Geryonidae in the scheme of classification was made by Balss (1957) who put the family between the Xanthidae and the Goneplacidae. Brattegard & Sankarankutty (1967) studied the larval characteristics of *Geryon tridens* and concluded that the larvae resembled *Macropipus, Polybius* and *Bathynectes.* Ingle (1979) took this study further and stated *Geryon* larvae to be similar to the Portunididae and to have affinities to the sub-family Polybiinae, with features similar to the Xanthidae and Goneplacidae. However, he remained firmly planted on the fence and concluded that the Geryonidae are "derived from the same phylogenetic stock as the Portunididae, Xanthidae and perhaps a part of the heterogeneous Goneplacidae."

The genus *Geryon* has also undergone significant changes, with revision of species names and addition of new species, particularly as new deep-sea areas have been explored over the past decade. In 1980 there were nine described *Geryon* species: *G. trispinosus* (Herbst, 1803) - East Indies, *G. tridens* Krøyer, 1837 - NE Atlantic, *G. quinquedens* Smith, 1879 - NW Atlantic, *G. longipes* A. Milne-Edwards, 1882 - NE Atlantic & Mediterranean, *G. incertus* Miers, 1886 -

Bermuda, *G. affinis* A.Milne-Edwards & Bouvier, 1894 - NE Atlantic, *G. paulensis* Chun, 1903 - Indian Ocean, *G. ischurodous* Stebbing, 1923 - South Africa and *G. granulatus* Sakai, 1978 - Japan. Since then, there has been a flux of new species and revision of some of the older ones. The following six have been described since 1980: *G. maritae* Manning & Holthuis (1981, West Africa), *G. chuni* Macpherson (1983, Namibia), *G. erytheiae* Macpherson (1984, South Atlantic), *G. fenneri* Manning & Holthuis (1984, SE USA), *G. gordonae* Ingle (1985, Bay of Biscay and surrounding localities) and *G. inghami* Manning & Holthuis (1986, Bermuda).

Manning & Holthuis have reexamined some early classified *Geryon* material and in 1986 concluded that the dubious *G. incertus* was a junior synonym of the portunid *Bathynectes longispina*. This was followed by the sad demise of *G. tridens*, Manning & Holthuis (1987) showing that *G. trispinosus* was a senior synonym for this species. In the same paper they cast doubt on the validity of *G. ischurodous*, though for the while this species survives. As a consequence, in 1988 the current list of 13 *Geryon* species is as follows: *G. trispinosus* (Herbst), *G. quinquedens* Smith, *G. longipes* A.Milne-Edwards, *G. affinis* A.Milne-Edwards & Bouvier, *G. paulensis* Chun, (*G. ischurodous*, Stebbing), *G. granulatus* Sakai, *G. maritae* Manning & Holthuis, *G. chuni* Macpherson, *G. erytheiae* Macpherson, *G. fenneri* Manning & Holthuis, *G. gordonae* Ingle and *G. inghami* Manning & Holthuis.

Up until 1970 practically all publications on *Geryon* ecology were involved solely with the distribution of the genus (e.g. Hansen, 1908; Kjennerud, 1967; Sankarankutty, 1968; Pequegnat, 1970), but as sampling methods improved the exploitation of the larger *Geryon* species (*G. quinquedens, G. maritae, G. fenneri*) as a fisheries resource became possible, with work concentrating on the population and reproductive biology of these species. The first set of studies were limited to surveys of the fishery potential of certain areas, generally using baited crab traps (Haefner & Musick, 1974 and McElman & Elner, 1982 (NW Atlantic); Melville-Smith, 1983 (SW Africa)) but these generalised surveys were soon followed by more detailed ecological studies. The major species studied thus far has been *G. quinquedens*, a species fished off NE USA. Wigley *et al.*, (1975) undertook a detailed study of this species using traps, trawls and photography and discovered a depth-related size structure in the population, which they attributed to an up-slope migration. They also found varying sex ratios with depth and a remarkable lack of ovigerous females and made preliminary estimates of biomass and density. Lux *et al.*, (1982) took this study further by using tagging as a method of investigating crab movement, while Haefner (1978) concentrated on the seasonal aspects of the biology of *G. quinquedens*. Recently other studies of this species not directly associated with the fishery have been carried out. Sulkin & van Heukelem (1980) looked into the significance of nutritional flexibility in *G. quinquedens* larvae, which was followed by Kelly *et al.*, (1982) who attempted to construct a larval dispersal model. Meanwhile, Elner *et al.*, (1987) were watching the mating of consenting adult *G. quinquedens* and describing the patterns observed. Intes & LeLoeuff (1976) and Beyers & Wilke (1980) undertook surveys of *G. quinquedens* off the coast of Africa, though it is most likely that they were studying the as then undescribed *G. maritae*. As a result, these were the first surveys carried out on that species, Beyers & Wilke finding a depth related size distribution in their population. Most work on *G. maritae* has been undertaken by Melville-Smith, including studies of density (1985, 1986), tagging and movement of individuals (1987a, 1987b) and reproductive biology (1987c).

The third main *Geryon* fishery is for the golden crab, recently described as *G. fenneri* (Manning & Holthuis, 1984), and found off the SE USA. Otwell *et al.*, (1984) undertook an extensive study of the golden crab fishery in the Gulf of Mexico without them having a scientific name for it (they realised that it was not *G. quinquedens*). This investigation was followed by a study of the population structure of the species by Wenner *et al.*, (1987), who noted variation in sex ratio with depth, made estimates of biomass, and were surprised to find no ovigerous females. Hinsch (1988a) attempted to deduce a reproductive cycle in the face of this lack of females with eggs by undertaking a histological study of *G. fenneri* gonads, following this work with ultrastructure examination of the spermatophores of both *G. fenneri* and *G. quinquedens* (1988b). Erdman & Blake (1988) extended these studies, investigating the reproductive ecology of *G. fenneri* and concluded an annual reproductive cycle

Work on the biology of other *Geryon* species is sparse to say the least. Mori & Relini (1982) investigated the mating behaviour of *G. longipes* in the Mediterranean, and Mori (1982) studied the alimentary rhythms of the same species. Hansen (1908) and Manning & Holthuis (1981) have made passing reference to ovigerous *G. affinis* while concentrating on its distribution.

Little is known about the biology and ecology of *G. trispinosus.* Hepper (1971) made preliminary notes on the then *G. tridens* off Ireland, perhaps originally to investigate fishery potential, with no real conclusive results. Brattegard & Sankarankutty (1967) and Ingle (1979) have investigated fully the development of *G. trispinosus* larvae in the laboratory, Ingle detailing each stage. This chapter is therefore an attempt to make a full study of the biology and ecology of *G. trispinosus* comparable with the more widely studied fisheries species.

Materials and Methods.

During the period 1978 to 1986, a total of 690 individuals of the genus *Geryon* Krøyer have been collected from the Porcupine Sea-bight (49-52°N, 11-14°W). The positions and depths of the stations where *Geryon* were taken, and the species composition of *Geryon* can be seen in Table 1 and Fig. 1. Four types of sampling gear were used: the semi-balloon otter trawl (OTSB) complete with "V" doors (see Merrett & Marshall, 1981), the IOS epibenthic sled (BN) (see Rice *et al,* 1982), the SMBA Granton Trawl (GT) (see Gordon & Duncan, 1983) and the IOS Rectangular Midwater Trawl 1+8M (RMT 1+8M) (see Roe & Shale, 1979). The ships used were the RRS "Challenger" and "Discovery". The specimens were fixed in 5% formalin solution and later transferred to 70% alcohol for preservation. They have been stored in the 'Discovery' collection at the Institute of Oceanographic Sciences Deacon Laboratories, Wormley, Surrey. In addition, 1368 individuals were taken and sized by Dr. A. L. Rice whilst on the "Geryon 2" cruise aboard the "Thalassa". Details of these samples appear in Table 2.

Measurements were taken as follows: carapace length (CL) from the frontal margin of the carapace to the posterior carapace margin (Fig. 2a); chela length (ChL) from the tip of the propodus fixed finger to the base of the propodus; chela width (ChW) across the widest region of the cheliped palm (Fig. 2b); fifth abdominal segment width (AS5) across the midline of this segment (Fig. 2c) . All measurements were taken using dial calipers to the nearest 0·1 mm. Details of egg number and condition were obtained using a Wild stereoscopic microscope. All measurements of egg and ova size utilised the graduated eyepiece of the microscope and were made to the nearest 0·01 mm. Wet weight of whole animals was measured to the nearest 0·01 g. Sex of *Geryon* was determined by the position of the gonopores and the structure of the pleopods, particularly the presence or absence of the first pair.

Data used to calculate biomass and density figures were obtained from either the ship's log

Station Nº	Latitude (N)	Longitude (W)	Mean Depth (m)	Gear Used	Number of each species in sample	
					Geryon trispinosus	*Geryon gordonae*
9776#1	49° 29'	11° 38'	804	OTSB	2	
9778#1	49° 15'	12° 7'	1036	OTSB	1	
9779#1	49° 22'	12° 49'	1401	BN	2	
10109#5	49° 13'	12° 41'	1227	RMT*	2	
10109#8	49° 12'	12° 19'	1125	BN	147	
10110#1	49° 19'	11° 43'	925	BN	8	
50502	51° 56'	13° 34'	500	OTSB	9	
50503	51° 37'	13° 15'	1017	OTSB	2	
50504	51° 54'	12° 54'	973	GT	9	
50506	51° 58'	13° 36'	490	GT	6	
50507	51° 51'	13° 18'	783	GT	2	
50508	51° 34'	13° 18'	980	SWT	1	
50520	49° 34'	12° 8'	1238	GT	1	
50522	49° 24'	11° 45'	983	OTSB	22	
50606#1	50° 40'	14° 10'	1115	BN	1	
50606#2	50° 41'	14° 4'	1100	OTSB	9	
50606#5	50° 43'	13° 56'	1130	BN	3	
50607#1	51° 2'	14° 12'	706	OTSB	19	
50607#2	51° 2'	14° 6'	700	BN	2	
50608#2	51° 19'	14° 22'	510	BN	16	
50610#1	51° 26'	13° 24'	980	BN	2	
50704	49° 40'	12° 7'	1263	OTSB	2	
50705	49° 24'	11° 32'	743	OTSB	2	
50708	49° 23'	12° 1'	1058	GT	5	
50714	51° 45'	13° 15'	943	GT	1	
50716	51° 53'	13° 26'	748	GT	12	
50717	52° 0'	13° 33'	505	GT	67	
50801	49° 35'	12° 11'	1265	OTSB	4	
50807	49° 24'	11° 37'	793	OTSB	3	
50808	49° 35'	11° 49'	960	OTSB	3	
50815	51° 36'	13° 4'	1312	OTSB	8	
50818	52° 0'	13° 31'	518	GT	66	
50819	52° 5'	13° 29'	506	OTSB	41	
50820	51° 55'	13° 19'	720	OTSB	8	
50821	51° 48'	13° 5'	986	OTSB	17	
50824#3	49° 26'	11° 36'	858	BN	32	
50904	51° 22'	13° 27'	1028	OTSB	1	
51003	52° 1'	13° 2'	750	OTSB	2	
51004	52° 10'	13° 25'	515	GT	18	
51007	51° 46'	13° 6'	1025	OTSB	1	
51008	51° 36'	13° 2'	1360	OTSB	2	
51022	49° 33'	12° 39'	1588	OTSB		2
51023	49° 30'	12° 11'	1273	OTSB	1	
51026	49° 25'	11° 34'	740	OTSB	11	
51027	49° 32'	11° 51'	978	OTSB	3	
51103#5	51° 47'	13° 13'	940	BN	7	
51112#1	51° 27'	13° 59'	523	BN	8	
51206#1	51° 40'	13° 1'	1205	OTSB	2	
51303	52° 9'	13° 21'	545	OTSB	17	
51304	51° 51'	13° 20'	790	OTSB	5	
51305	51° 50'	13° 5'	985	OTSB	2	
51306	51° 44'	12° 53'	1218	OTSB	2	
51312	49° 27'	11° 37'	725	OTSB	2	
51315	49° 33'	11° 52'	1015	OTSB	1	
51318	49° 23'	11° 34'	685	OTSB	1	
51403#1	51° 38'	13° 0'	1303	BN	2	
51403#2	51° 37'	12° 50'	1321	BN	1	
51403#5	51° 38'	12° 59'	1293	BN	1	
51404	51° 53'	13° 19'	750	OTSB	8	
51420#1	51° 37'	12° 59'	1327	BN	2	
51402#3	51° 38'	12° 59'	1296	BN	2	
51619#1	51° 33'	12° 54'	1518	BN	1	
51707#1	51° 40'	13° 0'	1218	BN	2	
51715#2	51° 29'	12° 59'	1493	BN	1	
51801	51° 21'	12° 31'	1720	BN		1
51810	49° 33'	11° 53'	1016	OTSB	11	
52013#1	52° 5'	13° 29'	525	BN	5	
52404#1	51° 59'	13° 42'	450	BN	29	
TOTAL					687	3

* RMT 200-310 m off bottom.

Table 1: Station data for the samples where *Geryon* spp. were taken.

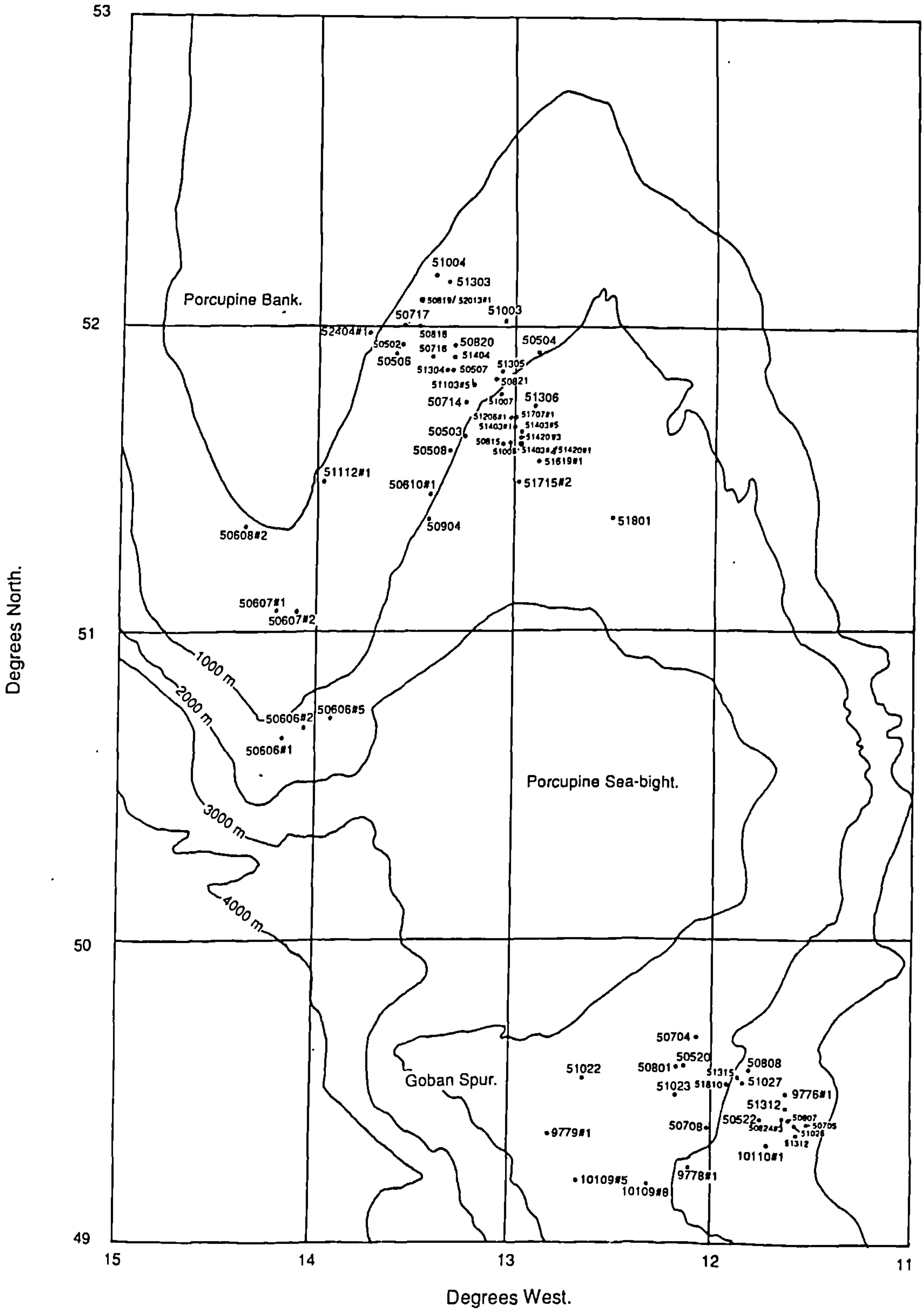


Fig. 1: Map of the Porcupine Sea-bight area, indicating the positions of stations where *Geryon* spp. were taken.

Station.	L201	L202	L203	L204	L205	L206	L209	L210
Depth (m).	600	500	400	500	600	700	500	600
N^{o}. Males								
mm CL class:								
22·0-23·9					1	1		
24·0-25·9								
28·0-29·9		1						
36·0-37·9		1						5
38·0-39·9								2
40·0-41·9								8
42·0-43·9								9
44·0-45·9		2						13
46·0-47·9		1						15
48·0-49·9	1	3			1			12
50·0-51·9	2	6						14
52·0-53·9	7	13		3			2	4
54·0-55·9	29	20	1	5	4	1	2	8
56·0-57·9	24	36	2	11		1	6	10
58·0-59·9	35	64	6	22		1	5	16
60·0-61·9	35	58	6	25	6	4	11	22
62·0-63·9	28	61	3	25	13	3	21	24
64·0-65·9	10	88	6	38	10	2	17	13
66·0-67·9	12	48	2	29	3		6	8
68·0-69·9	3	23	2	6	3	1	8	2
70·0-71·9	1	8	1	4	1		1	1
72·0-73·9		3					1	
74·0-75·9		1		1	1			
Total Males:	197	435	29	169	43	14	80	186

Station.	L201	L202	L203	L204	L205	L206	L209	L210
Depth (m).	600	500	400	500	600	700	500	600
N^{o}. Females								
mm CL class.								
22·0-23·9				1		1		
26·0-27·9					1			
28·0-29·9		3		1			3	1
30·0-31·9		7		1	1			3
32·0-33·9	1	11	1	1				4
34·0 35·9		10		1				6
36·0-37·9	1	6		1			1	11
38·0-39·9		6		3	1	1		16
40·0-41·9		4		4			1	14
42·0-43·9	1	5	2	3	1			23
44·0-45·9		5		3	2			15
46·0-47·9	1	4		5	2			6
48·0-49·9		1		2				5
50·0-51·9								1
Total Females:	4	62	3	26	8	2	5	105

Table 2: Summary of data collected on the 'Thalassa' cruise by Dr. A. L. Rice.

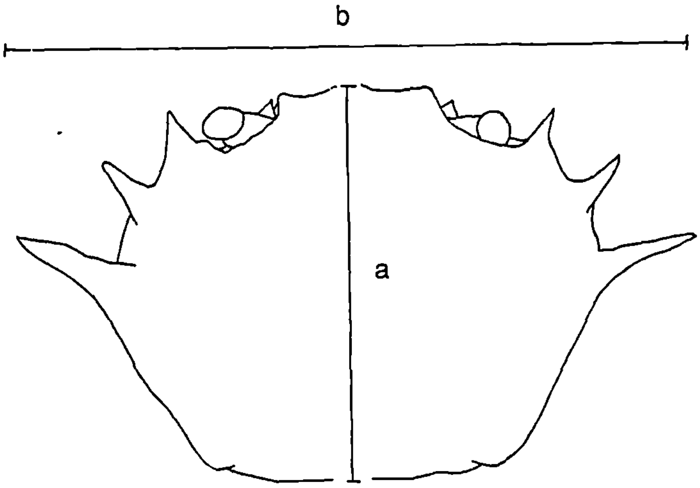


Fig. 2a: Generalized *Geryon* carapace, indicating a). the CL measurement used in this study, and b). the CW measurement used in some other *Geryon* studies.

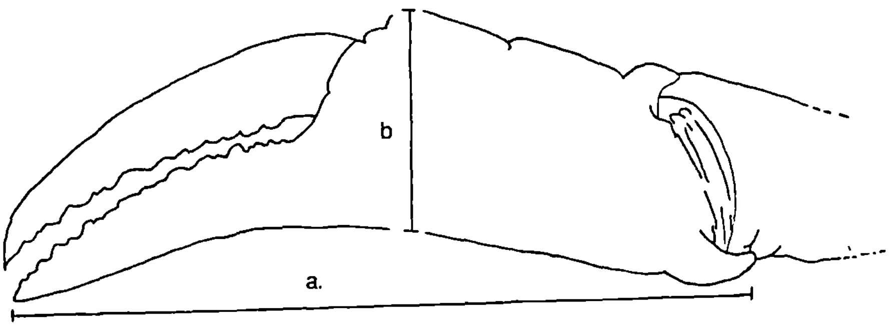


Fig. 2b: Generalized *Geryon* propodus, indicating the measurements of a). ChL and b). ChW used in this study.

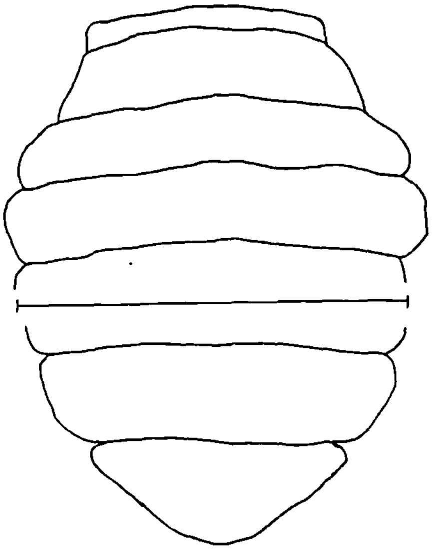


Fig. 2c: Generalized *Geryon* abdomen, indicating the measurement of abdomen width across the fifth abdominal segment.

(distance travelled) for OTSB or, more accurately, from odometer readings when on the bottom for BN. These were multiplied by width of net to give figures for area sampled in hectares. Details were not available for trawls made using the GT, so density and biomass data could not be obtained for these samples.

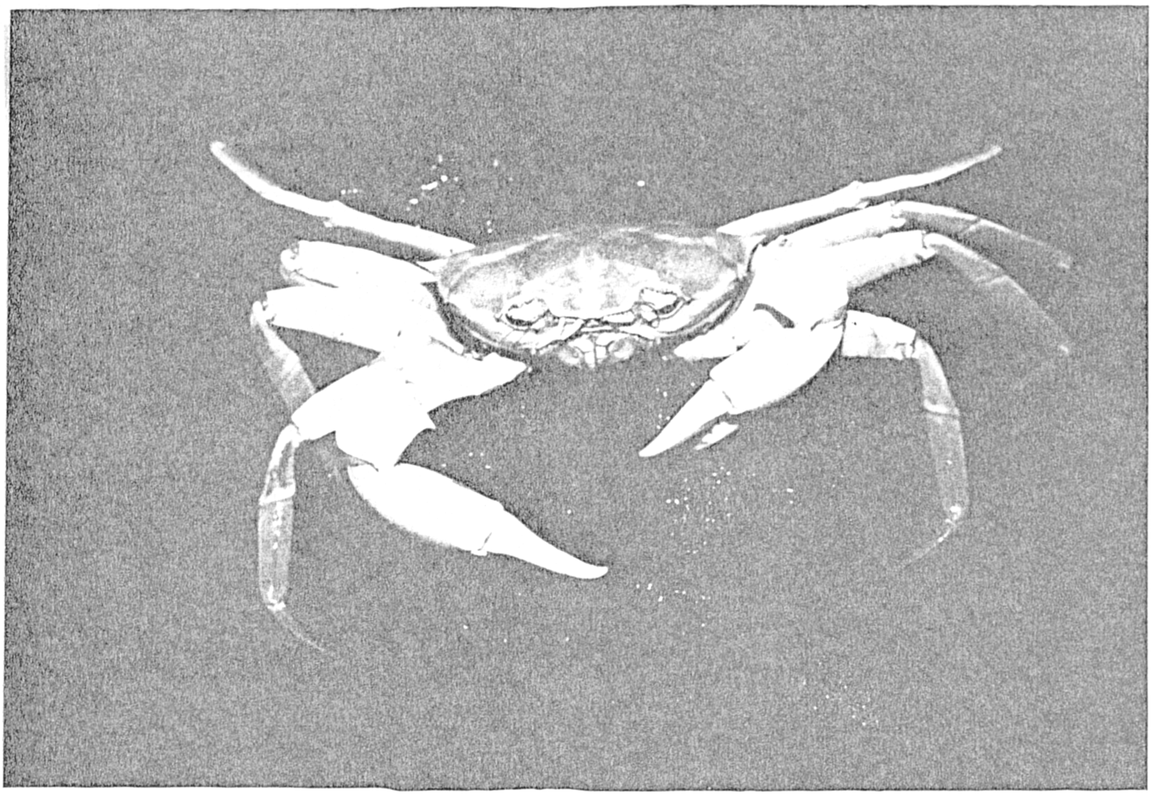
Results and Discussion.

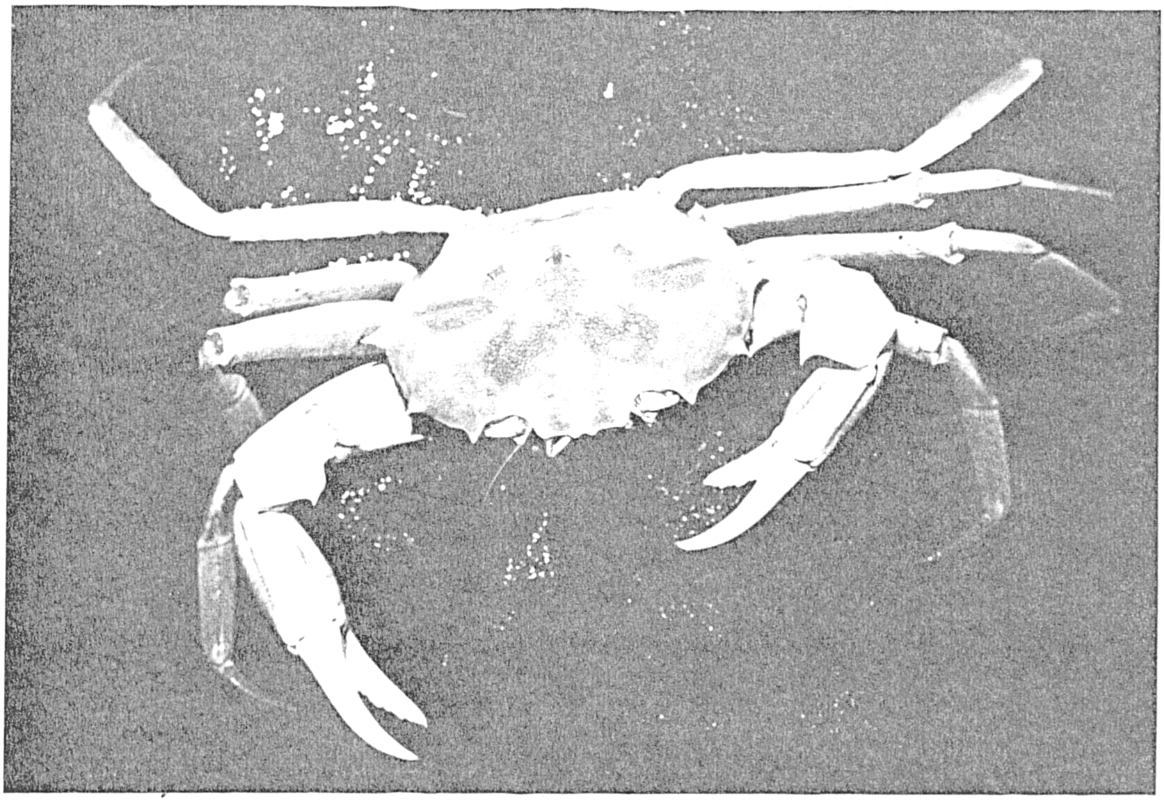
Two species of the red crab genus *Geryon* were collected from the Porcupine Sea-bight area between 1978 and 1987: *Geryon trispinosus* and *Geryon gordonae*, together comprising a total of 690 specimens. Since *G. gordonae* was represented by only three small individuals, the study centred on *G. trispinosus*. The numbers of each species caught in each sample are provided in Table 1. In addition, 1368 mature *G. trispinosus* were caught and measured (CL) by Dr. A. L. Rice whilst aboard a "Thalassa" cruise. These data are summarised in Table 2. Details of the distinguishing features and distribution of the two *Geryon* species found in the Porcupine Sea-bight follow:

Geryon trispinosus Herbst, 1803 (Plates 1-5).

Distinguishing Features: *G. trispinosus* differs from most other *Geryon* species by having only three pairs of anterio-lateral spines on the carapace. The majority of other species have five. The only other species with three pairs of spines is *G. longipes*, which is also found in the N.E. Atlantic region. The two species are distinguished only by a number of minor morphological features, as listed by Ingle (1985):

Feature.	*Geryon trispinosus.*	*Geryon longipes.*
Breadth of orbit.	< width of frontal margin.	= or slightly < frontal margin.
Upper margin of cheliped palm.	without a tooth.	without a distal tooth.
Length/breadth merus pereiopod 5.	4 - 4·25.	5·33.
" " propodus " "	slightly > 4.	5·50.
L/b 3rd maxilliped exopod.	4.	3·67.





Plates 1 & 2: Live adult male *Geryon trispinosus* taken from 450 m. Note the interesting pattern of grey patches on the carapace, an unusual feature common to all the specimens in this particular sample (52404#4).

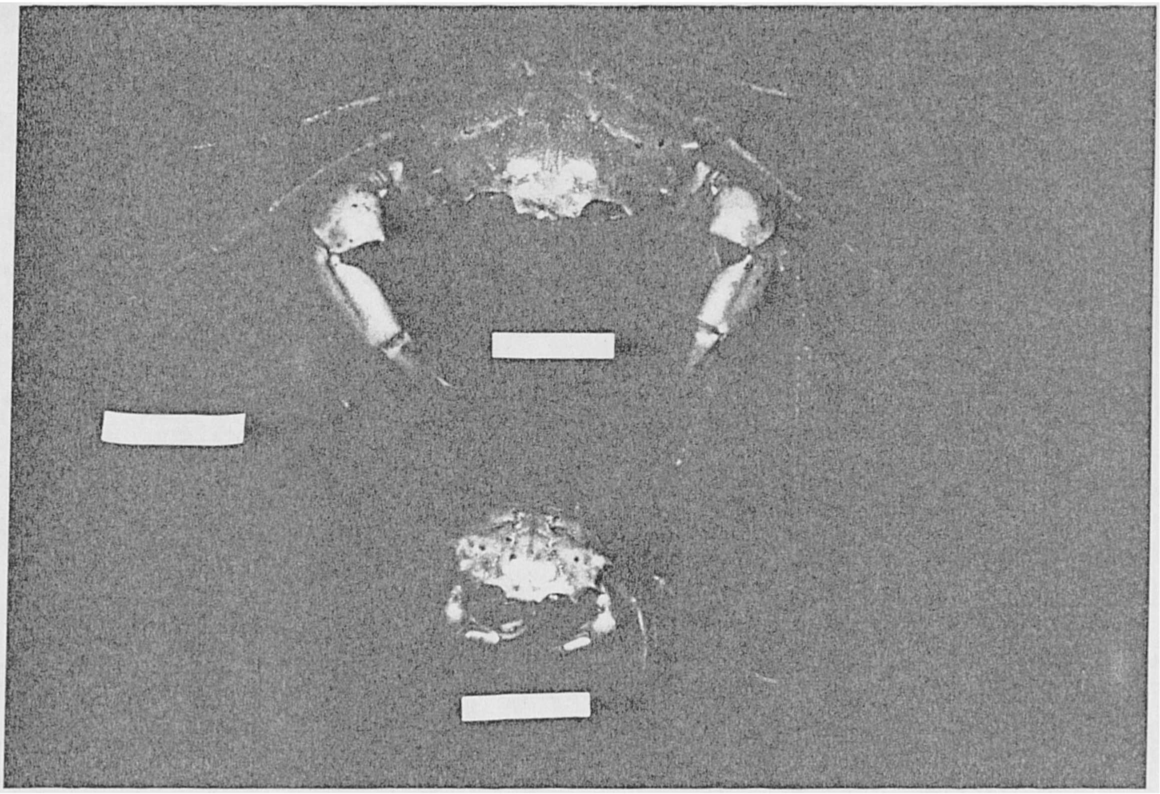


Plate 3: Mature male and female *Geryon trispinosus* illustrating the sexual dimorphism in respect to size.

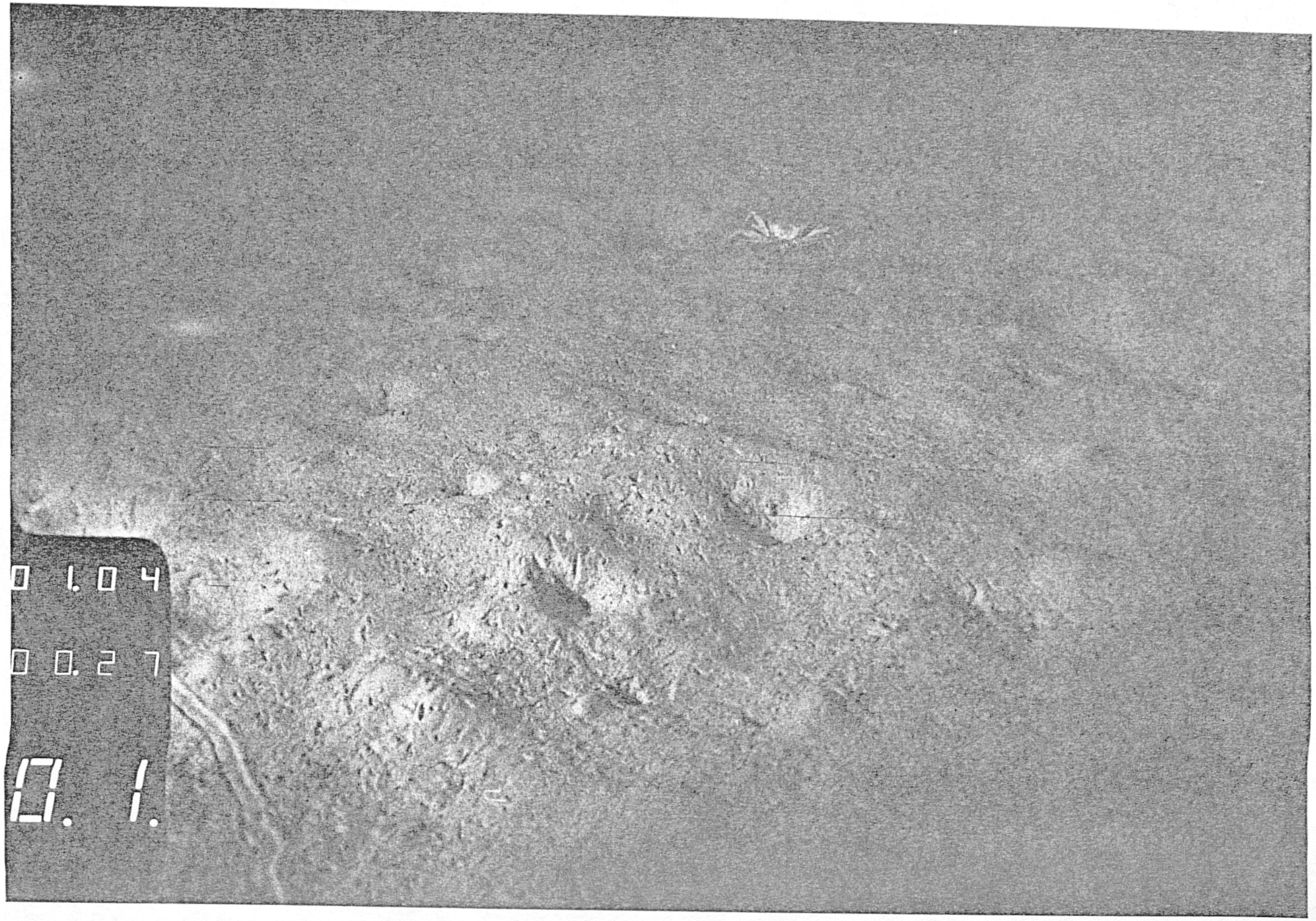


Plate 4: Photosled picture from 498 m, with a male *Geryon trispinosus* on a typical sediment to be found at this depth, overlain by depressions, mounds and animal trails.
(Station 51405).

Plate 5: Large male
Geryon trispinosus in
defensive position against
the oncoming benthic
sled. (station 51112#4
at 555 m)

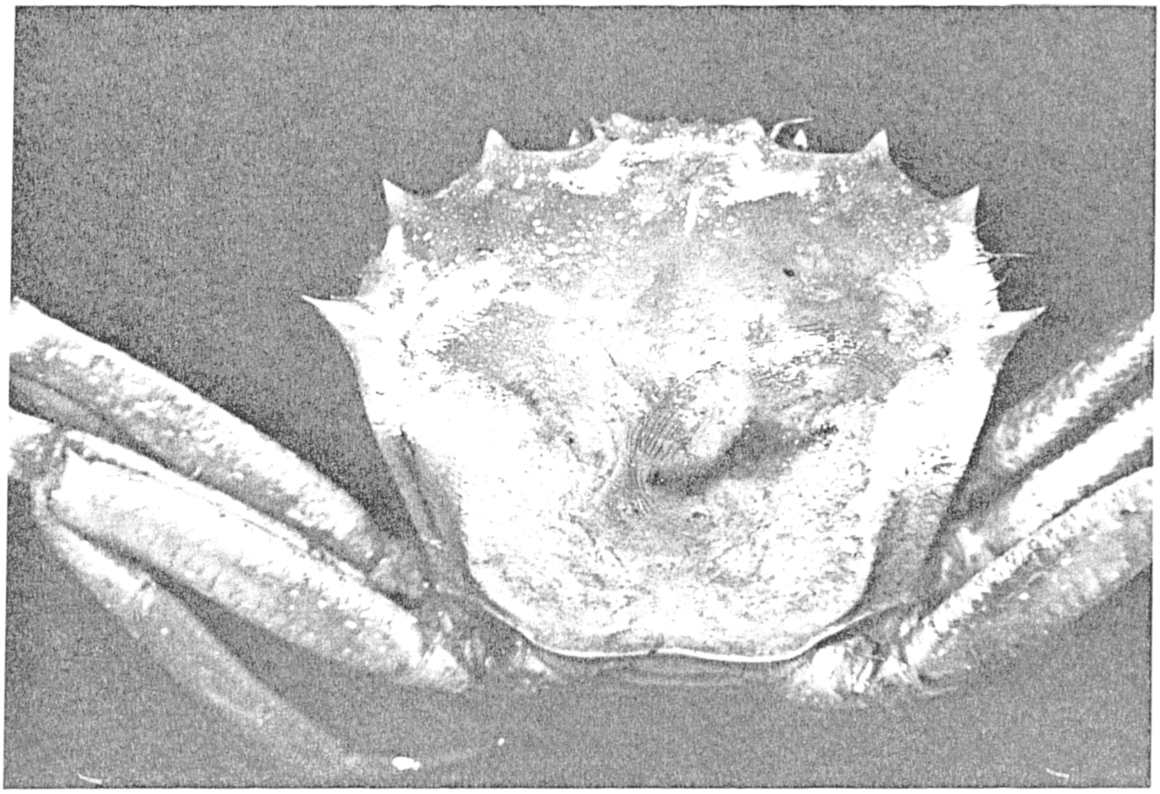


Plate 6: Carapace of male *Geryon trispinosus* illustrating the effects of chitinolytic bacteria.

Distribution: Confined to the N.E. Atlantic, particularly from N. France (Bouvier, 1940) north round the British Isles to the Faroes (Hansen, 1908), Norway (Sankarankutty, 1968) and Denmark (Poulson, 1949). South of Britanny, the distribution becomes confused with *G. longipes*, and old records of *G. trispinosus* in areas such as the Mediterranean are probably *G. longipes*. Reported over a depth range of 82 m (Thomson, 1873) to at least 1857 m (Ingle, 1985). In this study, the depth range of *G. trispinosus* in the Porcupine Sea-bight was 490-1530 m.

Geryon gordonae Ingle, 1985 (Fig. 3).

Distinguishing Features: Adult *G. gordonae* have five anterio-lateral spines (Fig. 4) and so can be instantly distinguished from the three-spined *G. trispinosus*. Younger crab stages have four spines (Fig. 5), a spine developing between the pronounced 3rd and 4th spines of the immature crab at about 22·0 mm CL (Dr. R. Ingle, pers. comm.). This forms the small fourth spine of the adult. There is a gradual reduction in the size and sharpness of the carapace spines with growth (Ingle,1985). *G. gordonae* is harder to separate from other five-spined geryonids occurring in the Atlantic. However, *G. gordonae, G. affinis* and *G. chuni* are distinguishable by the presence of laterally compressed dactyls of the walking legs, compared with the dorso-ventrally flattened dactyls found in species such as *G. maritae* and *G. quinquedens*. These three species can only be separated using minor morphological features as listed by Ingle (1985):

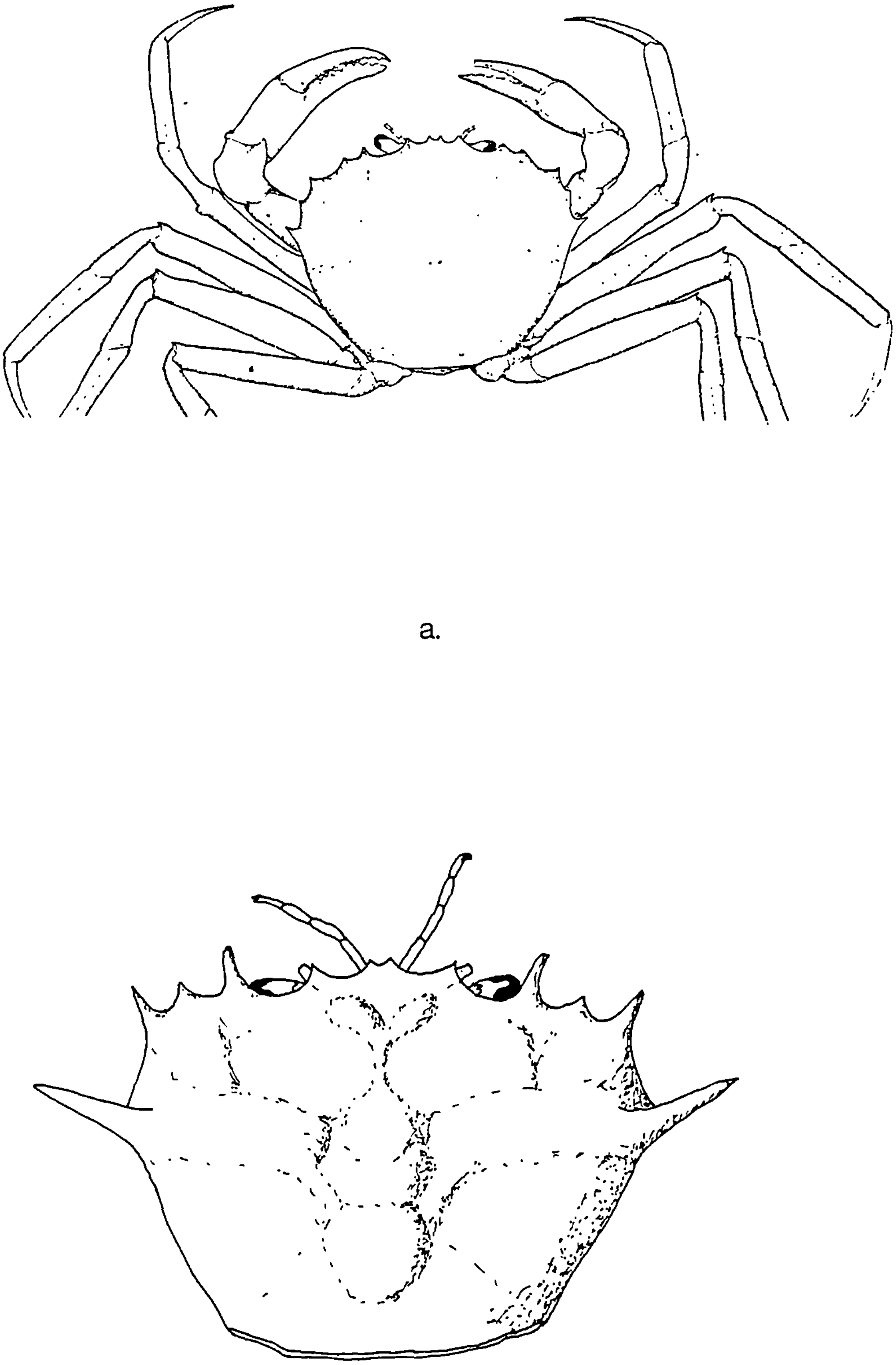


Fig. 3: Geryon gordonae: a). mature male (from Ingle, 1985). b). carapace shape of immature individual examined during this study, indicating the presence of only four spines (CL = 18.3 mm).

Feature.	*G. gordonae.*	*G. affinis.*	*G. chuni.*
First anterio-lateral tooth.	produced.	not produced.	produced.
Inner infra-orbital tooth c.f. antennal 3rd peduncular segment.	beyond middle.	not beyond middle.	beyond middle.
Inner orbital teeth.	spinose.	rounded.	relatively acute.
Breadth of orbit.	< width frontal margin.	variable.	= width frontal margin.
Upper margin cheliped palm.	with distal tooth.	without distal tooth.	
Dorsal margin of cheliped merus.	with distal and sub-distal teeth.	without teeth.	with distal and sub-distal teeth.
length/breadth propodus perieopod 5.	5·5.	< 4.	4·5.

Distribution: N.E. Atlantic. Locations include Rockall Trough, Porcupine Sea-bight and Sierra Leone Ridge (Ingle, 1985). Confined to deeper water, succeeding *G. trispinosus* in the Porcupine Sea-bight, the depth range reported by Ingle being 1153-2110 m. In this study, *G. gordonae* was found in two samples at mean depths of 1588 and 1720 m.

Due to the insufficient number of *G. gordonae* caught in the samples, the study concentrated on *G. trispinosus* and was divided into two sections:

1. The depth related distribution and population structure of *G. trispinosus.*
2. Other aspects of the biology of *G. trispinosus.*

Where possible, the raw data collected by Dr. A. L. Rice was incorporated into the data analysis.

The depth related distribution and population structure of *Geryon trispinosus*.

Length Frequency Analysis.

The Porcupine Sea-bight sample of 687 *G. trispinosus* comprised 156 females (22·7 %), 379 males (55·2 %) and 152 individuals too small to be sexed. These were termed "young" and represented 22·1% of the total sample. If the "Thalassa" data is included, a total of 2055 crabs were caught, comprising 74·5 % males, 18·1 % females and 7·4 % young. The low proportion of females in the population is particularly striking, and is discussed later.

The CL of all mature *G. trispinosus* from the Sea-bight sample were measured and divided into 2 mm CL size intervals for both males and females. The results form Table 3. Details of the CL composition of the "Thalassa" data can be seen in Table 2, but these data were not utilised in the length frequency analysis as only large individuals from shallow depths were caught and this would unfavourably bias the graphs. The data from Table 3 are represented graphically in Fig. 4. As can be seen, males grow considerably larger than females. This sexual dimorphism with respect to size is a feature of the genus *Geryon*, the reason for the size differential becoming apparent during mating. The large male crabs form a "cage" around the female to give protection while she moults (Mori & Relini, 1982; Elner *et al.*, 1987). While subsequently soft, the female is turned over by the male and mating occurs.

Another point of note from the length frequency analysis is the maximum size attained by the crabs, which can be compared to that of other *Geryon* species. To facilitate this, Hepper's (1971) conversion equation for *G. trispinosus* CL to Carapace Width (CW) can be used to allow comparison with other studies using CW. The conversion factor for measurements in mm is:

Carapace Length Interval (mm).	N^o. Females.	N^o. Males.
6·0-7·9	1	12
8·0-9·9	7	11
10·0-11·9	7	8
12·0-13·9	13	9
14·0-15·9	9	10
16·0-17·9	25	13
18·0-19·9	16	17
20·0-21·9	15	13
22·0-23·9	11	12
24·0-25·9	6	9
26·0-27·9	7	6
28·0-29·9	6	4
30·0-31·9	7	1
32·0-33·9	7	3
34·0-35·9	3	0
36·0-37·9	4	0
38·0-39·9	4	2
40·0-41·9	4	1
42·0-43·9	1	3
44·0-45·9	0	2
46·0-47·9	0	2
48·0-49·9	0	4
50·0-51·9	0	8
52·0-53·9	0	5
54·0-55·9	0	12
56·0-57·9	0	27
58·0-59·9	0	36
60·0-61·9	0	43
62.0-63·9	0	55
64·0-65·9	0	30
66·0-67·9	0	14
68·0-69·9	0	4
No Carapace	3	3
TOTAL	156	379

Table 3: Length frequency data for male and female *Geryon trispinosus.*

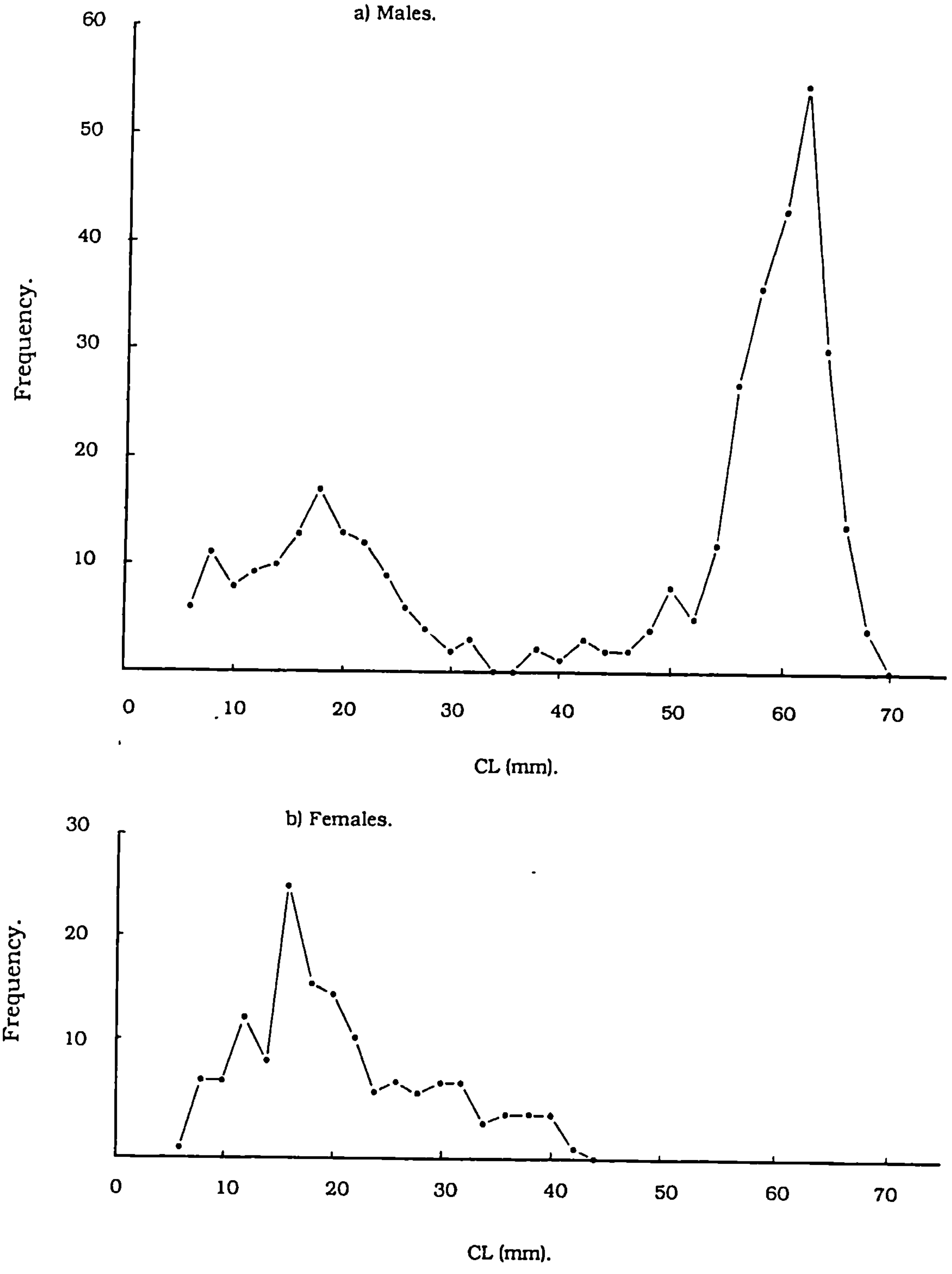


Fig. 4: Length frequency polygons for both sexes of *Geryon trispinosus.*

Males: $CL = 0{\cdot}814\ CW + 1{\cdot}78$.

Females: $CL = 0{\cdot}857\ CW - 0{\cdot}75$.

From these equations, the maximum CW sizes for *G. trispinosus* can be calculated and compared with maximum sizes of other species (Table 4). As can be seen, *G. trispinosus*, together with *G. longipes*, are much smaller than other members of the genus. This would somewhat restrict any potential *G. trispinosus* fishery, unless regulations are lowered for this species, as the minimum landing size for red crabs (96 mm CW (Haefner, 1978)) is greater than the largest known *G. trispinosus*, even though this species is extremely palatable! (pers. comm., personnel of the "RRS Challenger".). Ingle (1985) suggested that two groups of sibling species exist in the Eastern Atlantic, namely *G. affinis - gordonae - chuni* and *G. trispinosus - longipes*, and the results of maximum size and the comparative morphological features bear this out.

Biomass and Density.

Density (N^{o}. Individuals ha^{-1}) and biomass (g WWt ha^{-1}) were calculated for each sample of *Geryon trispinosus* using the methods described earlier where the data available made such computations possible. The data obtained (Table 5) was plotted against the mean depth of the sample to give an indication of the population structure in relation to depth (Figs. 5 and 6).

The highest density found using the BN method was 75 ind.ha^{-1} in sample 50608#2 from 510 m, this sample also having the highest biomass of 9662 g.WWt.ha^{-1}. For the OTSB method, the highest density calculated was 12 ind.ha^{-1} with a biomass of 1603 g.WWt.ha^{-1} (sample 50819 from 506 m). The maximum density figures are much lower than those for *Munida sarsi* (Chapter 3) inhabiting similar depths (maximums: BN: 3843·1 ind.ha^{-1}, OTSB: 242·6 ind.ha^{-1}) but due to the large size of mature *G. trispinosus*, the maximum biomass figures are of a similar magnitude (for *M.sarsi:* BN: 10536·1 g.WWt.ha^{-1}, OTSB: 756·3

Species.	Sex.	CL (max) mm.	CW (max) mm.	Area.	Reference.
G. trispinosus.	M	69	83·0	Porc. Sea-bight.	This study.
	F	42	50·0		
G. trispinosus.	M	74	89·1	"Thalassa"	This study.
	F	50	59·1		
G. trispinosus ‡	M	77	92·0	W. of Ireland.	Hepper, 1971.
	F	48	57·0		
G. fenneri *	M	---	180·0	Gulf of Mexico.	Hinsch, 1988a.
	F	---	140·5		
G. fenneri *	M	---	193·0	S. Atlantic Bight.	Wenner *et al.,* 1987.
	F	---	170·0		
G. fenneri *	M	139	185·0	Florida.	Manning & Holthuis, 1984.
	F	114	147·0		
G. quinquedens *	M	---	142·0	N.E. USA.	Wigley *et al.*, 1975.
	F	---	121·0		
G. quinquedens *	M	---	172·0	S.W. Africa.	Beyers & Wilke, 1980.
	F	---	102·0		
G. quinquedens *	M	143	164·6	N.W. Atlantic.	Haefner, 1978.
	F	116	134·0		
G. inghami	M	82	----	Bermuda.	Manning & Holthuis, 1986.
	F	---	----		
G. affinis.	M	---	210·0	W. Africa.	Manning & Holthuis, 1981.
	F	---	145·0		
G. maritae *	M	---	123·0	S.W. Africa.	Melville-Smith, 1983.
	F	---	> 110		
G. maritae *	M	---	164·0	Senegal.	Gaertner & Laloé, 1986.
	F	---	≥ 109		
G. gordonae	M	119	----	N.E. Atlantic.	Ingle, 1985.
	F	96	----		
G. longipes	M	---	79·0	Mediterranean.	Mori & Relini, 1982.
	F	---	44·0		

* Species of commercial importance.

‡ as *G. tridens*.

Table 4: Maximum size reported for *Geryon* species.

Station N^{O}.	Gear Used	Mean Depth (m).	Area Sampled (ha).	N^{O}. Indiv. ha^{-1}.	WWt (g) ha^{-1}.
10109#8	BN	1125	0·816	1·22	13·14
10110#1	BN	925	0·552	7·24	20·91
50502/51303	OTSB	500	9·699	2·68	292·27
50506	OTSB	490	2·390	2·51	350·96
50522	OTSB	983	3·826	4·97	13·30
50606#2	OTSB	1100	4·140	1·93	12·22
50606#5	BN	1130	0·419	4·77	4·75
50607#1	OTSB	706	4·460	4·04	232·10
50608#2	BN	510	0·213	75·12	9662·86
50610#1	BN	980	0·076	26·32	63·03
50801	OTSB	1265	4·780	0·84	3·50
50808	OTSB	960	3·188	0·94	4·84
50819	OTSB	506	3·188	12·86	1602·87
50820	OTSB	720	5·420	1·48	85·08
50821	OTSB	986	5·260	3·23	21·75
51026	OTSB	740	3·657	3·46	8·39
51103#5	BN	940	0·248	28·23	184·44
51112#1	BN	523	0·200	40·00	2450·35
51206#1	OTSB	1205	1·133	1·77	15·19
51304	OTSB	790	6·678	0·77	26·75
51403#2	BN	1321	0·236	4·24	7·03
51404	OTSB	750	4·140	1·93	10·30
51707#1	BN	1218	0·951	1·20	2·10
51810	OTSB	1016	3·985	2·76	11·43

Table 5: Biomass data; Density (No. of individuals ha^{-1}) and Biomass (g.Wet Weight ha^{-1})of *Geryon trispinosus* at each sample station. (Station N^{os}. 50502 and 51303 have been combined due to having the same mean depths).

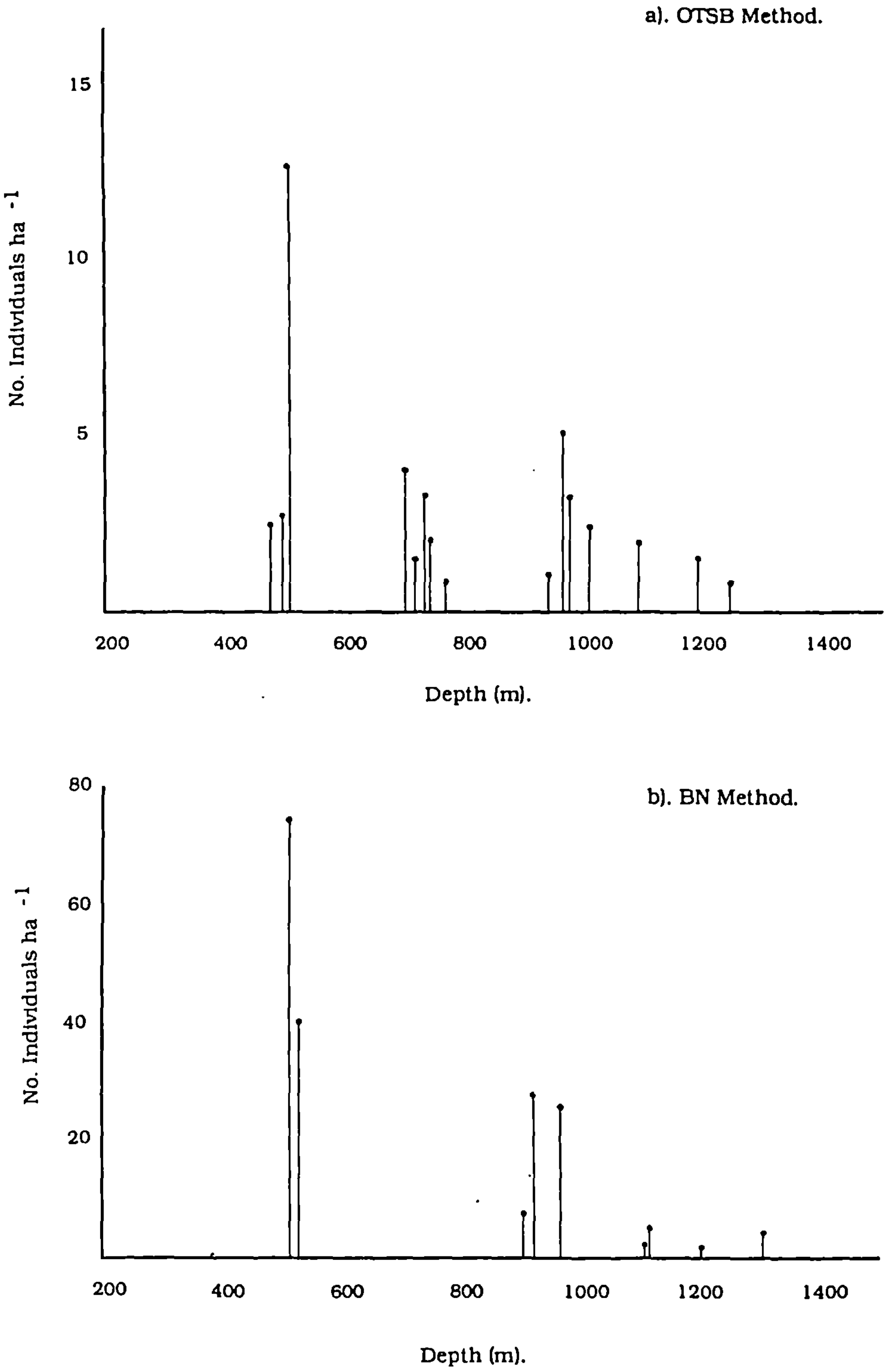


Fig. 5: Density of *Geryon trispsinosus* at each sample station in relation to depth.

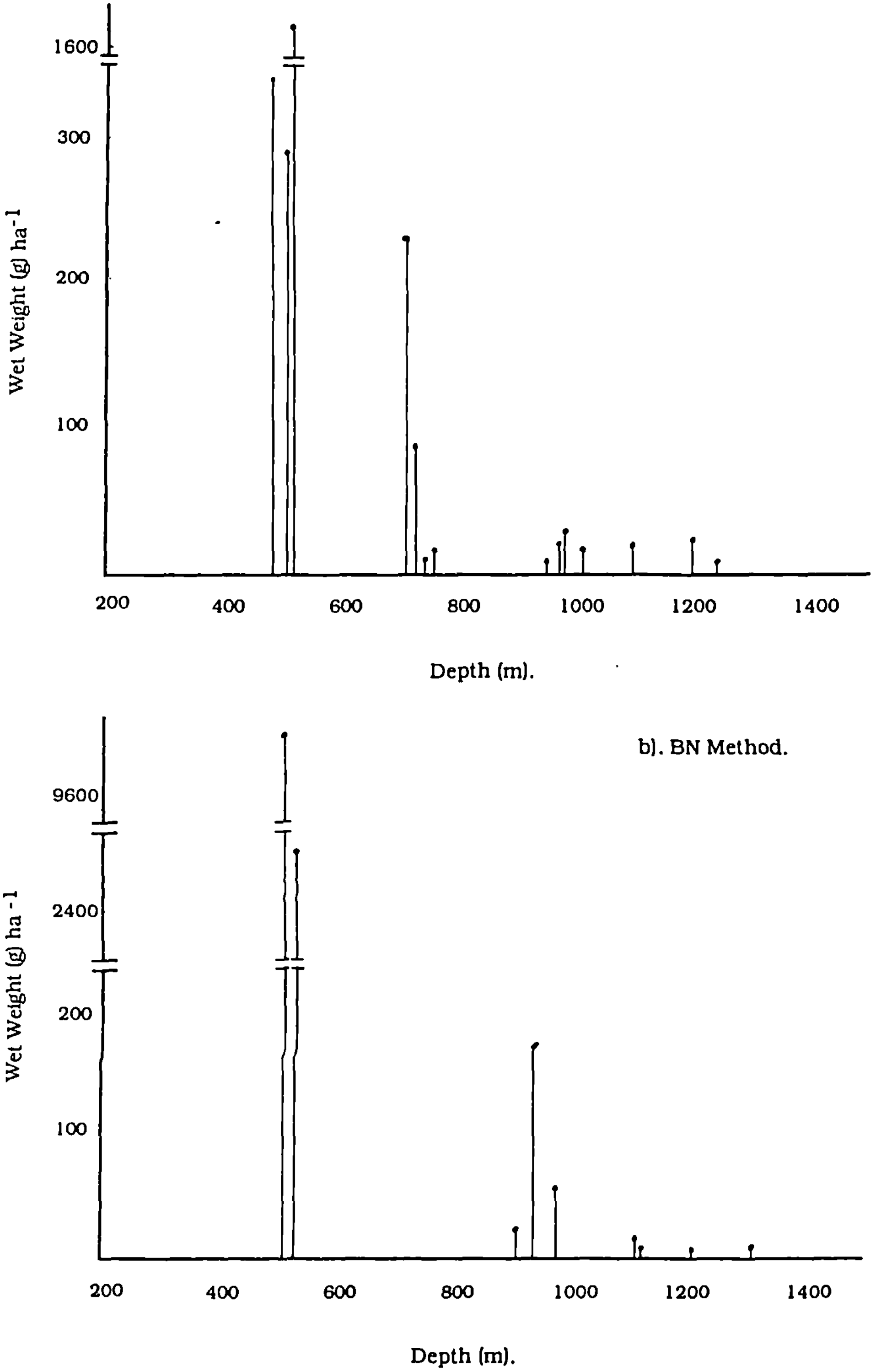


Fig. 6: Biomass of *Geryon trispinosus* at each sample station in relation to depth.

g.WWt.ha^{-1}). Comparing the *G. trispinosus* values with the few studies of other *Geryon* species where density and biomass calculations have been carried out (Table 6) it can be seen that compared with these fisheries species both the density and biomass of *G. trispinosus* are low, the biomass being further reduced by the smaller size of *G. trispinosus.*

From Fig. 5a it can be seen that, barring the one large sample (50819), the density of *G. trispinosus* is fairly constant with depth. However, the two shallow samples from Fig. 5b and the large shallow sample from Fig. 5a suggest an aggregation of numbers in some shallow areas. The distribution of biomass (Fig. 6), however, shows a spectacular decrease in wet weight of the samples with an increase in depth. The difference between the biomass of samples above 700 m and those below 800 m is far greater than that for density (Fig. 5). Indeed, the shallowest two OTSB samples have a density less than many deeper samples, but a far higher biomass. This would suggest that the individual *G. trispinosus* are larger in these shallow samples than in the samples from deeper.

To investigate this further, mean CL and WWt figures were calculated for both sexes at each depth interval (Tables 7 and 8). These data are represented graphically in Figs. 7 and 8. As can be seen from Fig. 7 and more emphatically from the graph for mean WWt (Fig. 8) there is a dramatic drop in size of the crabs below 600 m. This is most obvious for the males; the initial increase in size of the females with depth will be discussed later.

Figs. 5-8 therefore demonstrate a depth related size distribution of *G. trispinosus* in the Porcupine Sea-bight, the largest individuals being found in the shallowest samples and there being a gradation in size down to the smallest crabs below 800 m. Beneath this depth, the sizes are fairly constant. This distribution is highlighted further by the lack of small individuals in the shallow water, as demonstrated by the narrow confidence limits, and the fact that the majority of settling young (1st crab stage) were caught in the deeper samples (see Table 11). The results therefore suggest an up-slope migration of *G. trispinosus,* the young settling in water below 900 m and then migrating up into the shallower water above 600 m,

Species.	Sample method.	Max. Density (ind.ha^{-1})	Max. biomass (g.wwt.ha^{-1})	Area.	Reference.
G. trispinosus.	Trawl	12·9	1602·9	Porc. Sea-bight.	This study.
	BN	75·1	9662·9	Porc. Sea-bight.	This study.
G. fenneri.	Trap	(22·3/trap)	(18040/trap)	S. Atlantic bight.	Wenner *et al.,* 1987.
G. quinquedens.	Trawl	23·0	------	SW Africa.	Beyers & Wilke, 1980.
	Photo.	381·6	157300·0	NE USA.	Wigley *et al.,* 1975.
	Trawl	(218/30 mins)	(78900/30 mins)	NE USA.	Wigley *et al.,* 1975.
	Trap	------	83400·0	S. Angola.	Cayré *et al.,* 1979.
	Trawl	125·4	------	NW Atlantic.	Haefner, 1978.
	Trap	215·5	99280·0	NW Atlantic.	McElman & Elner, 1982.
G. maritae.	Photo.	350·2	55500·0	SW Africa.	Melville-Smith, 1985.
	Trap	510·0	------	SW Africa.	Melville-Smith, 1986.

Table 6: Maximum densities (N^{O}. individuals ha^{-1}) and biomass (g. wet weight ha^{-1}) reported for *Geryon* species.

Depth Interval (m)	N^{O}. Males.	Mean CL (mm).	95% Confid.	N^{O}. Females.	Mean CL (mm).	95% Confid.
400-499.	47	59·9	± 1·4	14	31·0	± 3·2
500-599.	901	61·1	± 0·4	132	35·9	± 1·1
600-699*.	438	56·9	± 0·7	106	40·2	± 0·9
700-799.	63	43·4	± 5·5	28	19·1	± 2·4
800-899.	18	12·4	± 2·3	14	11·4	± 1·9
900-999.	27	19·0	± 2·2	35	17·1	± 1·1
1000-1099.	17	20·6	± 2·1	14	17·5	± 1·1
1100-1199.	10	20·5	± 4·2	4	17·1	± 2·6
1200-1299.	13	15·1	± 3·7	4	17·9	± 4·5
1300-1399.	10	17·4	± 3·8	2	18·0	± 8·6
1400-1499.	1	7·9	-------	2	20·8	± 0·3
1500-1599.	1	9·4	-------	1	10·3	--------

Table 7: Mean CL at each depth interval for male and female *Geryon trispinosus*, including data from the 'Thalassa' cruise. (* 'Thalassa' data only.)

Depth Interval (m)	N^{O}. Males.	Mean WWt (g).	95% Confid.	N^{O}. Females.	Mean WWt (g).	95% Confid.
400-499.	47	146·47	± 9·68	14	20·61	± 6·95
500-599.	901	156·22	± 2·39	132	31·38	± 2·70
600-699*.	438	129·31	± 4·20	106	41·49	± 2·70
700-799.	63	93·90	± 19·40	28	6·01	± 2·50
800-899.	18	1·99	± 1·07	14	1·28	± 0·63
900-999.	27	6·13	± 2·32	35	3·57	± 0·63
1000-1099.	17	6·85	± 1·79	14	3·63	± 0·70
1100-1199.	10	7·59	± 3·36	4	3·43	± 1·48
1200-1299.	13	3·69	± 1·88	4	4·21	± 3·82
1300-1399.	10	4·71	± 2·02	2	4·43	± 5·41
1400-1499.	1	0·35	--------	2	5·74	± 0·24
1500-1599.	1	0·59	--------	1	0·74	--------

Table 8: Mean wet weight at each depth interval for male and female *Geryon trispinosus*, including data from the 'Thalassa' cruise. (* 'Thalassa' data only).

	Externa size (mm)									
% Male hosts with:	0.0-0.9	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9	9.0+
Pl. Type 3	0.0	30.0	40.0	44.4	75.0	68.4	68.2	62.5	62.5	33.3
Pl. Type 2	33.3	10.0	20.0	33.3	18.8	21.1	9.1	6.3	0.0	16.7
Pl. Type 1	33.3	40.0	40.0	11.1	6.3	5.3	18.8	12.5	0.0	0.0
Total numbers	3	10	5	9	16	19	22	16	8	6

Table 9: The effect of externa size: percentage of male hosts demonstrating types 1-3 pleopod structure for each mm size class of *Triangulus munidae* externa.

by which time they have become mature and so comprise the breeding population. This pattern of a depth related distribution has also been noted in *G. quinquedens* by Haefner (1978) and Beyers & Wilke (1980), whilst Pequegnat (1970) found only juveniles below 4000 m. Wigley *et al.* (1975) attributed this pattern to an up-slope migration. An up-slope migration of *G. maritae* was also alluded to by Melville-Smith (1987a) during a tagging survey ("there is a preferred size at depth"), though his crabs tagged were large individuals. Other species appear to show no depth related distribution, such as *G. fenneri* (Wenner *et al.,* 1987). Some authors have noted movements of *Geryon* apparently unrelated to depth, such as Melville-Smith (1987a, 1987b) in *G. maritae,* who suggested crabs were moving north to reach a favourable area off North Namibia. Lux *et al.* (1982) tagged *G. quinquedens* off New England and noted random movements along the slope and limited motion up and down the slope. However, it must be stressed that all tagging studies have involved large mature crabs that may not be migrating anyway. Hepper (1971) worked on *G. trispinosus* (as *G. tridens*) from west of Ireland and noted a size distribution related to longitude. He suggested a westward movement of crabs to a hypothetical main population outside his sample area. However, in his study, only the larger crabs from shallower than 790 m were sampled and Hepper stated that even though there was no correlation between depth and size, the shallowest samples had the largest crabs.

The distances required for young *G. trispinosus* settling in the Porcupine Sea-bight below 1000 m to reach the breeding areas above 600 m are considerable. A vertical movement of up to 900 m is involved, but when the horizontal distances from the sample site to the breeding area are calculated, the scale of the movement becomes apparent. Table 9 shows the minimum horizontal distances from some samples where young or small *G. trispinosus* were caught to both the 700 m and 500 m depth contour. As can be seen, these distances can be up to 60 km. Obviously young settling in the deepest samples may never reach the shallow water, the breeding population recruiting from the depths around 1000 m. However, even the distances travelled by small crabs from these areas are extensive.

Station N^{O}.	Mean Depth (m).	Minimum Distance in km to reach:	
		700 m Depth Contour.	500 m Depth Contour.
10109#8	1125	49·3	60·3
50520	1238	39·7	50·7
50704	1263	41·1	52·1
50708	1058	31·5	41·1
50801	1265	43·8	54·8
50815	1312	38·4	52·1
51008	1360	27·4	43·8
51306	1218	43·8	57·5
51715#2	1493	46·6	60·3
51810	1016	23·3	32·8

Table 9: Minimum distances that migrating *Geryon trispinosus* from below 1000 m would have to cover to reach adult populations at above 700 and 500 m.

Tagging surveys of large adult *Geryon* have shown that 'nomadic' individuals can travel great distances, the greatest reported being an impressive 380 km for a female *G. maritae* (Melville-Smith, 1987a) and 90 km for *G. quinquedens* (Lux *et al.*, 1982), so distances of 60 km for a smaller crab are not impossible.

The question arises of why such a depth related migration should occur. It would seem, from the adult distribution, that the optimum depth for *G. trispinosus* to breed is less than 700 m. Brattegard & Sankarankutty (1967) and Ingle (1979) described the larvae of *G. trispinosus* (as *G. tridens*) and showed that the pre-zoeal, zoeal and megalopa stages are planktonic, the settling stage being the first crab stage. This settling of the first crab stage, as demonstrated by sample 10109#5 caught 200 m above the bottom by RMT, instead of the megalopa is unusual for Brachyura and parallels the situation found in another deep-sea species the spider crab *Dorhynchus thomsoni* (Hartnoll *et al.*, 1987), though the first crab stage of *Dorhynchus* is rather more specialised. It would therefore be beneficial for a deep-sea organism with planktonic larvae to breed in as shallow water as possible, hence shortening the larval journey from hatching to the surface plankton environment. This would increase the chances of more larvae reaching the plankton and therefore reduce the mortality of offspring. The Brachyura are rather infamous for not having representatives in the abyssal and lower slope regions of the deep-sea, despite being such a successful group, and it may be that they are limited by the inflexibility of their shallow water planktonic larval strategy.

If the area above 700 m is the ideal breeding area for *G. trispinosus*, then it would be valuable for young crabs settling deeper to move up to these areas. However, there is a distinct lack of young crabs in the shallow regions, which would appear the ideal area of settlement to avoid the need of an extensive migration. So there appears to be some factor limiting either the settlement or, more likely, the survival of small *Geryon* in these regions.

Biomass and density work on the species of the squat lobster *Munida* found in the Porcupine Sea-bight (Chapter 3), when compared with the findings for this *G. trispinosus* study, shows that *M. sarsi* is by far the most numerous benthic decapod above 800 m, with a maximum density of 3843 ind.ha^{-1} compared with 75 ind.ha^{-1} for *G. trispinosus*. These munidids are of a similar size to the small *G. trispinosus* and are also burrow occupiers (Brinkmann, 1936; this study, Ch. 3) and are noted for their aggressive behaviour when defending burrows (Berrill, 1970). It is therefore suggested that the abundant *M. sarsi* outcompetes the small *G. trispinosus* for the same niche, and so few young crabs survive in the shallower areas. In the deeper water below 800 m, small *G. trispinosus* would co-habit with the much less numerous *M. tenuimana* (max. density: 51·28 ind.ha^{-1}) and the even more scarce *Munidopsis* species (max. density: 6 ind.ha^{-1}) and so competitive stresses would be lessened. The crabs settling here (e.g. all the first stage crabs caught in this study) would have more chance of survival and later migrate up to above 700 m, by which time they would have attained such a size that the now smaller *M. sarsi* would not pose such a threat.

The cues and mechanisms behind the *G. trispinosus* migration are puzzling, as the movement is not directly vertical, as are planktonic migrations, but rather up the continental slope, which has over most of its area a shallow gradient (1-2 %). It would appear to be extremely difficult for a crab to detect this slope without moving great distances. It may well be the case that movement is totally random, as for *G. maritae* (Melville-Smith, 1987a), and crabs wandering down or across the slope simply do not survive. It seems unlikely that no crabs remaining at these depths survive beyond the initial small size, yet no large mature individuals were found in the samples below 800 m. It would seem, therefore, that the migration is directional and so the crab must have some environmental cues. There are several possibilities, acting singly or in combination:

1. Pressure. Detecting significant changes in pressure would involve moving extensive horizontal distances, but this is a distinct possibility considering the large distances that *Geryon* have been reported covering. Crabs might wander nomadically, but on detecting an increase in pressure change direction ("negative barotaxis"). If movement was directed away

from the pressure increase/towards a pressure decrease, then it would lead the crabs to shallower areas. Kelly *et al.* (1982) reported that planktonic larval *G. quinquedens* can detect increases in pressure and increase their swimming rates accordingly. It is therefore possible that adult *Geryon* also have means of detecting pressure changes.

2. Gradient. Crabs may be able to detect the actual slope on which they are living, and so move up it to the shallow areas (negative geotaxis). This phenomenon is well documented in intertidal animals returning to their appropriate level on the shore after being displaced, e.g. species of the gastropod *Littorina* (Fraenkel, 1927; Barkman, 1955). Kelly *et al.* (1982) also reported negative geotaxic movement in larval *G. quinquedens,* so as in the case with pressure, adult *Geryon* may also possess the sensory ability to utilise geotaxism to reach the adult areas. However, to achieve this the crabs would have to be able to discriminate the large scale slope gradient from local fluctuations in sea-bed topography, a feat which would seem unlikely.

3. Light. The major cue used by vertically migrating pelagic Crustacea is light intensity (Ringleberg, 1964; Roe, 1983, 1984), the amount of down-welling light decreasing with an increase in depth. Herring & Roe (In press) state that diel migrations utilising light intensity occur down to around 1500 m, well in the range of *G. trispinosus.* It is therefore possible that migrating benthic *Geryon* demonstrate positive phototaxis, enabling them to move up the slope to the shallow areas. The amount of light reaching 1500 m is minimal, so to use isolumes *G. trispinosus* would require an extremely sensitive optical system. Brachyura, however, possess the simplest form of decapod eye (apposition optics) (Fincham, 1980), while the other successful deep-sea decapods, such as galatheids and natants, including some which are known to use light cues in migrations, have complex superposition reflecting optics, often modified to make full use of minimal light levels and bioluminescence. Whether *G. trispinosus* possesses adequate optical mechanisms to use the light levels found below 1000 m as a cue for migration is therefore debatable and would require further study. However, the very

fact that Brachyura possess apposition optics adds weight to the argument that they are basically a shallow water group ill adapted to deep-sea life. The eye structure may therefore be another reason for their lack of extension into the truly deep-sea abyssal areas.

4. Temperature. Although temperatures at any specific depth in the deep-sea remain fairly constant, there is a gradual temperature decrease with an increase in depth down the continental slope, reaching a minimum of around 2·0-2·5°C only when the abyssal plain is reached below 4000 m (Table 10). This gradient in temperature correlated with depth could therefore provide a cue for migrating *G. trispinosus*, the crabs moving up the isotherms in a similar way to the suggested movement in relation to pressure. However, the crabs would have to possess the ability to detect small changes in temperature of less than a degree, or else cover large horizontal distances before any significant change could be registered, It seems doubtful that *G. trispinosus* would possess such sensitive temperature-sensory apparatus and so the use of temperature as the major cue to the migration would appear unlikely.

5. Current. Herrnkind & McLean (1971) reported that offshore movements of the spiny lobster *Panulirus argus* are mainly directed by orientation into the current or surge. A northward residual boundary current, moving parallel to the depth contours, occurs throughout the year in the Porcupine Sea-bight (Dickson *et al.*, 1986; Huthnance, 1986), with a mean speed of 2·2-9 cm sec^{-1} (Dickson *et al.*, 1986). It is feasible, therefore, that *Geryon* use the residual current as a cue to the migration, moving perpendicular to the current flow, with up slope direction maintained by reference to variations in other environmental factors, such as pressure, temperature and light intensity. Perhaps even more likely is the use of the tidal currents ebbing and flowing along the direction of the slope of the Sea-bight. Crabs could utilise some form of circadian rhythm to induce activity on a tidal cycle, moving into the current when flowing down the slope and then becoming quiescent during the second part of the tidal cycle.

It is most likely that migrating young *G. trispinosus* use a combination of the above cues, relying on one main factor, possibly pressure or current direction, and modify the general

Station N^{O}.	Depth Range (m).	Mean Temp. ° C.
51813	240-255	11·3
51302	270-300	10·1
51002	490-490	9·9
50608	510-515	9·9
50824#5	632-660	9·5
50824#7	725-730	9·3
50807	790-795	9·2
50808	955-964	8·3
51007	1020-1025	7·5
51008	1290-1335	5·9
51009	1475-1485	5·0
51022	1575-1600	4·0
50810	1605-1694	3·9
51011	2180-2165	3·3
51803	3920-3990	2·6
50811	4400-4350	2·2

Table 10: Bottom temperatures for station numbers over a range of depths, obtained using sensors mounted on the gear used.

movement towards the required direction by utilising other environmental gradients, such as those for light intensity and temperature.

Sex ratio at depth.

To investigate further the marked paucity of females in the total sample, the proportion of females at each depth interval was calculated (Table 11). The data for percentage females is represented graphically as Fig. 9. It can be seen that there is a low proportion of females in the samples from the shallowest depths, this proportion increasing down to 900 m and then falling again. However, sample numbers are small below 1000 m and these deeper samples also include a large number of young crabs yet to be externally sexually differentiated.

In the literature, the distribution of female *Geryon* in respect to both total numbers and depth varies considerably. Wigley *et al.* (1975), working on *G. quinquedens,* found overall more females than males (1·24:1 ratio), but that males were more common in the shallow samples (4:1 male: female). In total contrast, Beyers & Wilke (1980) working on the same species found more males than females and that females were more abundant in the shallow samples. Melville-Smith (1987c) found a similar depth distribution of females in *G. maritae.* Wenner *et al.* (1987) working on *G. fenneri* found similar results to this study on *G. trispinosus,* males being generally more numerous than females, but this differential being greatest in the shallowest samples with a 30: 1 ratio of males to females in these areas.

As discussed earlier, there is a size-related depth distribution of both sexes of *G. trispinosus,* the large mature individuals being found in the shallow water. To attempt to explain the sex ratio variations at these depths, the presence of ovigerous females in the samples has to be considered. Details of reproductive cycles will be discussed later and only the number of ovigerous females caught is of relevance here. In this study, out of 372 females caught, only two were carrying eggs (0·54 %) and four individuals had empty egg cases on the

Depth Interval (m).	N^{o}. Males.	N^{o}. Females.	% Female	N^{o}. Young.
400-499.	47	14	22·9	0
500-599.	901	132	12·8	0
600-699.	438	106	19·5	0
700-799.	64	28	30·1	1
800-899.	18	15	45·5	1
900-999.	27	35	56·5	4
1000-1099.	17	14	45·2	0
1100-1199.	11	6	35·3	145
1200-1299.	13	4	23·5	1
1300-1399.	11	2	15·4	0
1400-1499.	1	2	66·7	0
1500-1599.	1	1	50·0	0

Table 11: Sex ratio at each depth interval for *Geryon trispinosus,* together with number of young caught at each depth interval. 'Thalassa' data included.

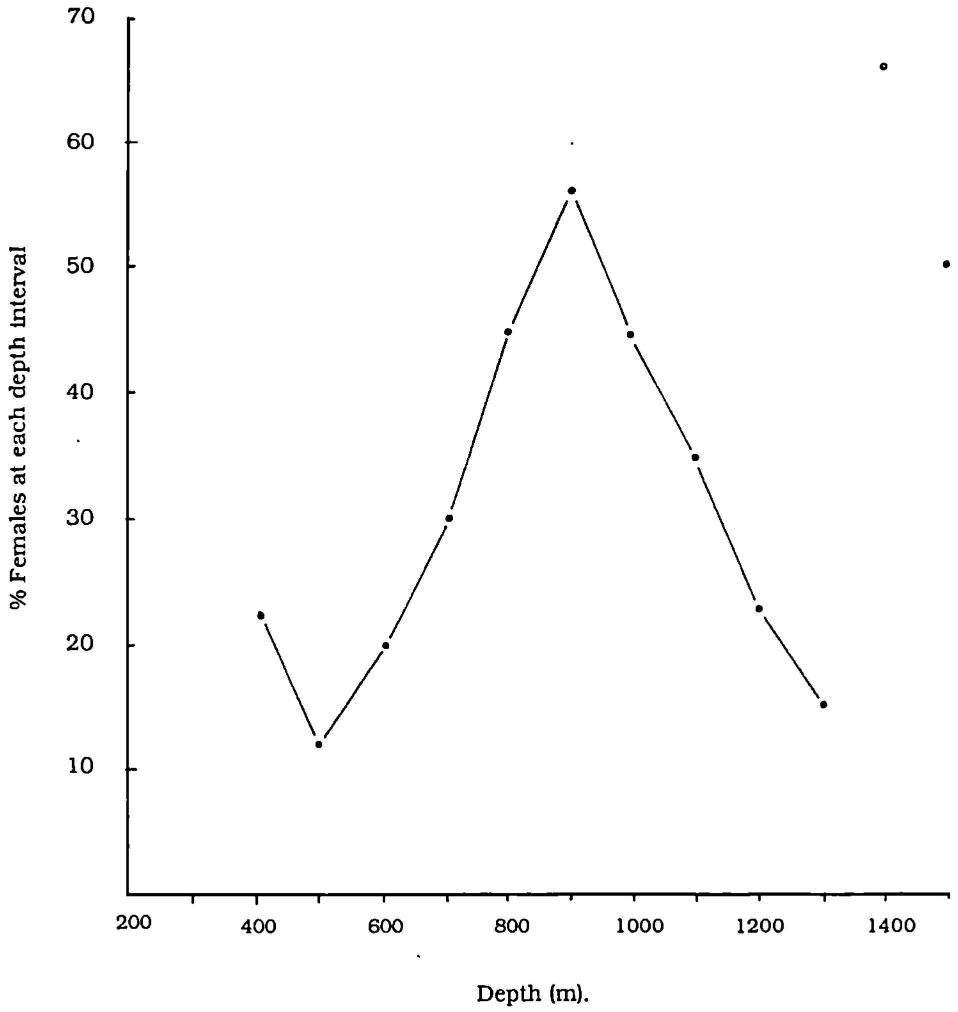


Fig. 9: Sex ratio at depth for *Geryon trispinosus* ('Thalassa' data included).

pleopods (1·08 %). This almost total lack of ovigerous females in the catches is a feature of other *Geryon* studies. Melville-Smith (1987c) found 12 ovigerous *G. maritae* out of 9293 females caught (0·13 %). Wenner *et al.* (1987) had no ovigerous females in their sample of 142 *G. fenneri*, neither did Hepper (1971) in his sample of *G. trispinosus* (as *G. tridens*). Even though Wigley *et al.* (1975) caught more females than males, only 6 % of their sample were ovigerous.

It is therefore suggested that the lack of ovigerous *G. trispinosus* and the low proportion of females in the shallow (mature) samples is due to the ovigerous females remaining in their burrows during the development of their eggs. At this time they stop emerging to feed. These females would therefore be excluded from catches using standard sampling gear, such as benthic sleds, trawls and traps. This behaviour is not unknown in decapod Crustacea and has been reported in *Nephrops norvegicus* (Chapman & Rice, 1971), the catches of females decreasing markedly over the winter months due to berried females remaining in their burrows.

Other Aspects of the Biology of *Geryon trispinosus*.

Relative Growth.

For both male and female *Geryon trispinosus* the values for the natural log of both chela lengths (LChL, RChL) and widths (LChW, RChW), and fifth abdominal segment width (AS5), were plotted against log of the carapace length (CL) to investigate the relationship between these dimensions and the standard CL as the crab increases in size. The results form Figs, 10-19, with data relating to the regression lines in Table 12. It can be seen from the maximum values of the figures for chela dimensions (Figs. 10-17) that there is a slight difference in size between the two chelae, the right chela generally being larger than the left, especially in respect of propodal width. This heterochely is highlighted further if the mean ratios (+ 95% confidence.) between the RCh and LCh dimensions are calculated:

Y axis	Sex.	Fig. N^{o}.	Correlation.	R-squared.	Slope (b).	Intercept (a).
LnLChL	M	10a.	0·99	0·98	**1·05**	0·75
		10b.	0·95	0·90	**1·08**	0·67
	F	11.	0·99	0·98	**0·92**	1·77
LnLChW	M	12a.	0·98	0·96	**1·09**	0·22
		12b.	0·91	0·83	**1·18**	0·17
	F	13.	0·99	0·98	**1·01**	0·26
LnRChL	M	14a.	0·99	0·97	**1·07**	0·84
		14b.	0·93	0·87	**1·20**	0·45
	F	15.	0·97	0·94	**0·81**	1·63
LnRChW	M	16a.	0·97	0·94	**1·12**	0·28
		16b.	0·83	0·70	**1·36**	0·09
	F	17.	0·95	0·91	**0·85**	0·53
LnAS5	M	18a.	0·95	0·91	**1·44**	0·10
		18b.	0·99	0·99	**1·00**	0·30
	F	19a.	0·84	0·70	**1·08**	0·25
		19b.	0·98	0·97	**1·14**	0·35

Table 12: Data relating to the regression plots, Figs. 10-19, where original relationship fits the equation $y = ax^{b}$. This is log-transformed to give $\log_e y = \log_e a + b.\log_e x$. X-axis in all Figures is LnCL.

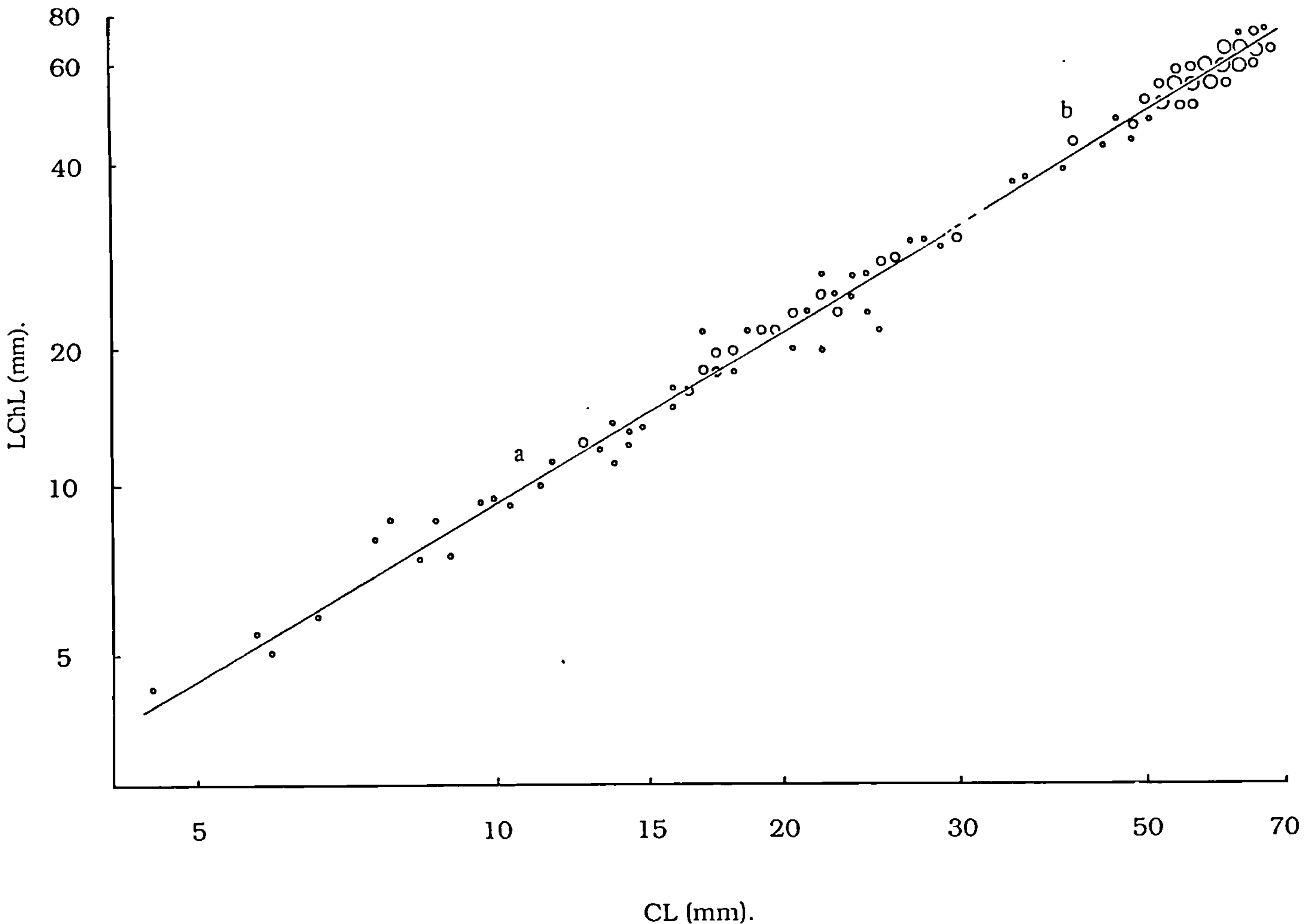


Fig. 10: Regression of LnLChL against LnCL for male *Geryon trispinosus*. n = 271.

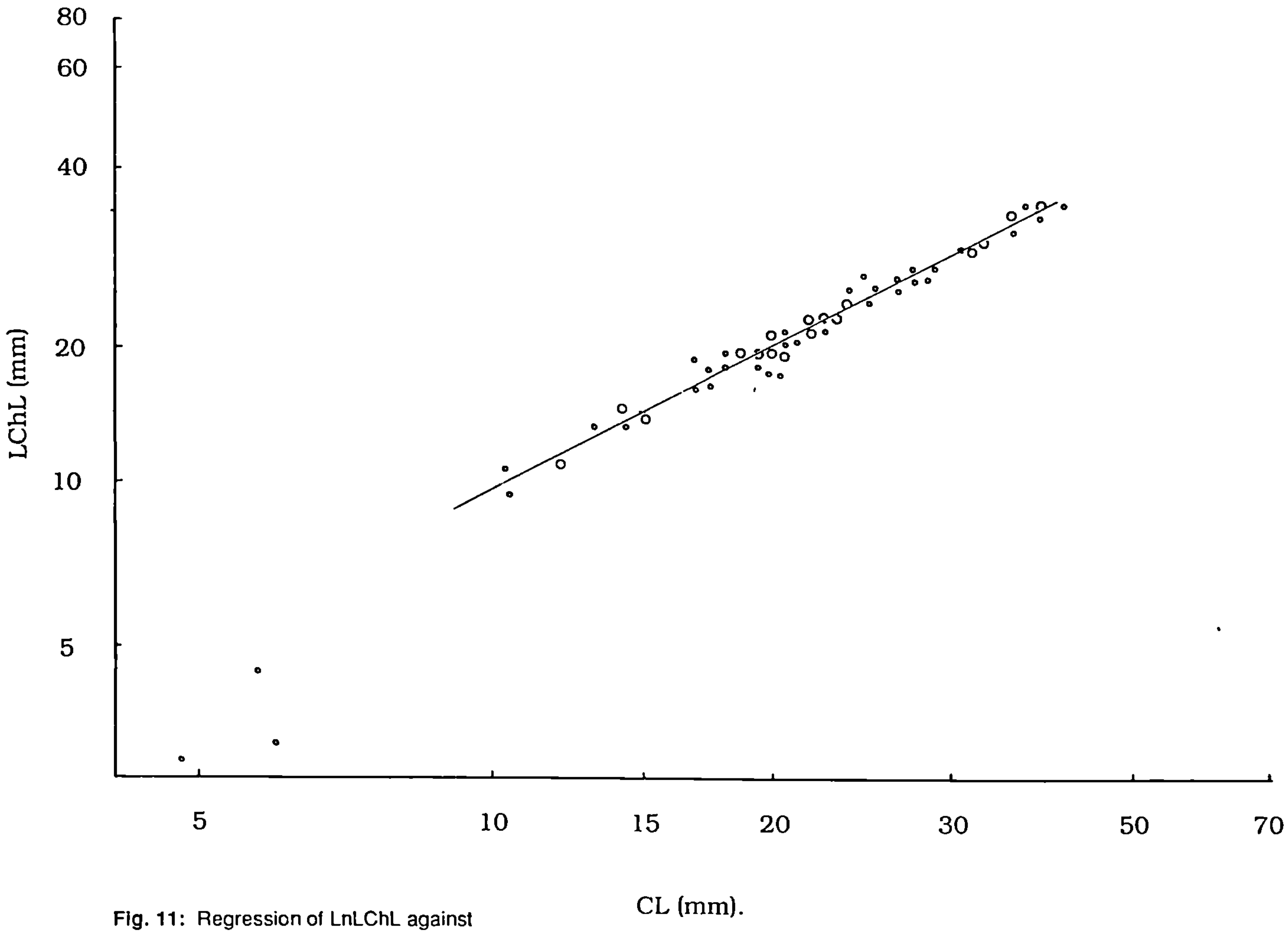


Fig. 11: Regression of LnLChL against LnCL for female *Geryon trispinosus*. n = 80.

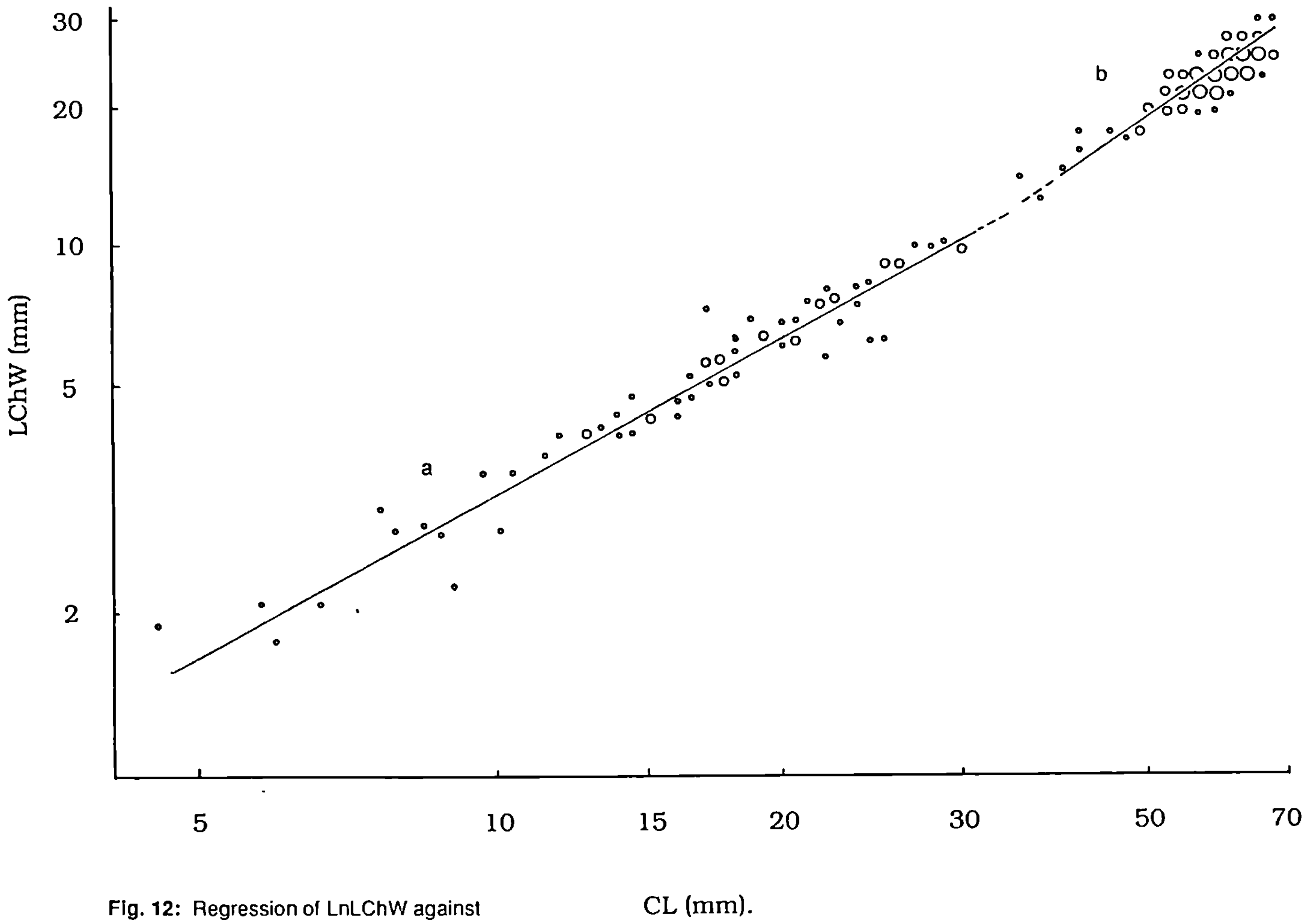


Fig. 12: Regression of LnLChW against LnCL for male *Geryon trispinosus*. n = 271.

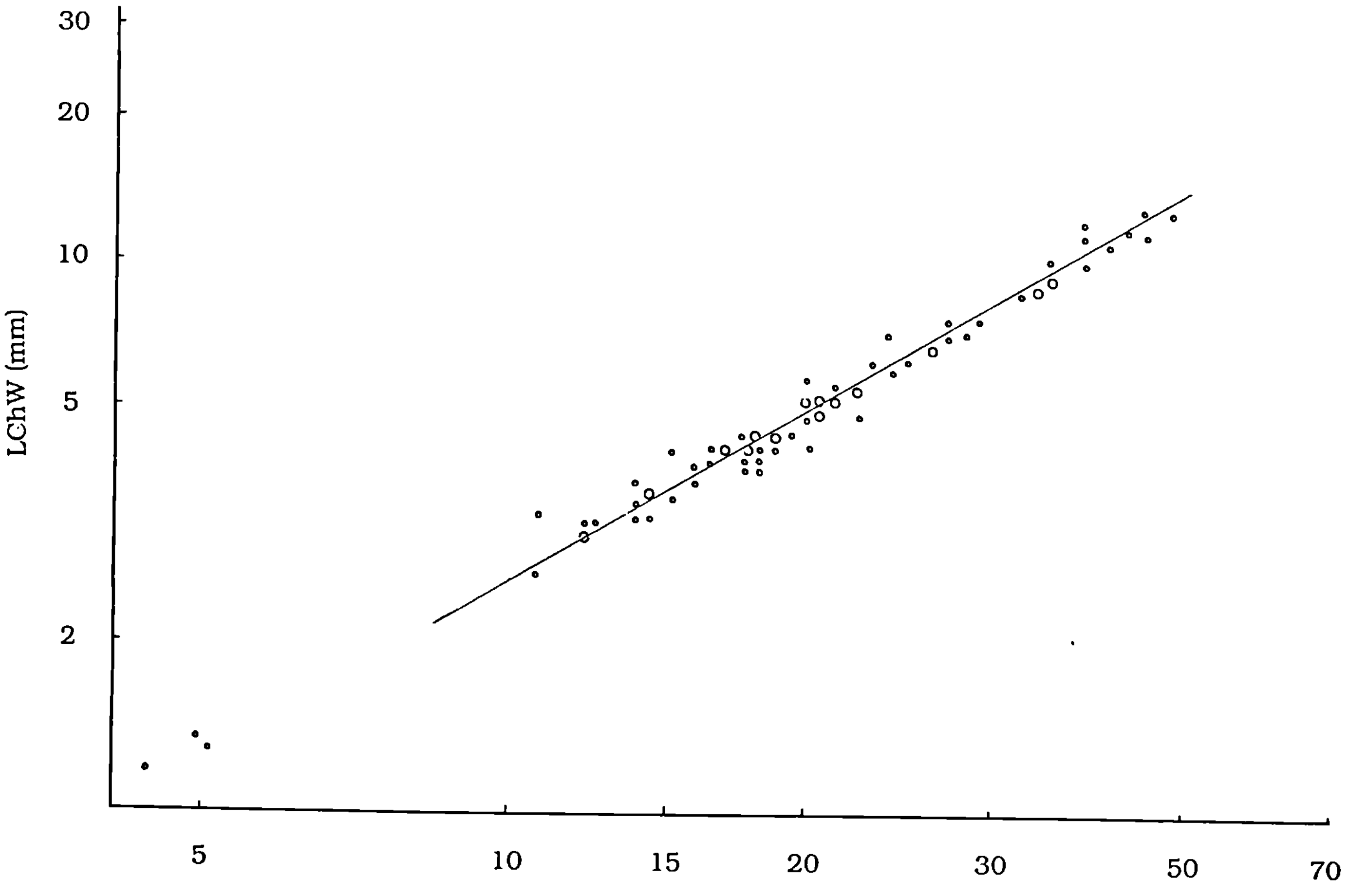


Fig. 13: Regression of LnLChW against LnCL for female *Geryon trispinosus*. n = 80.

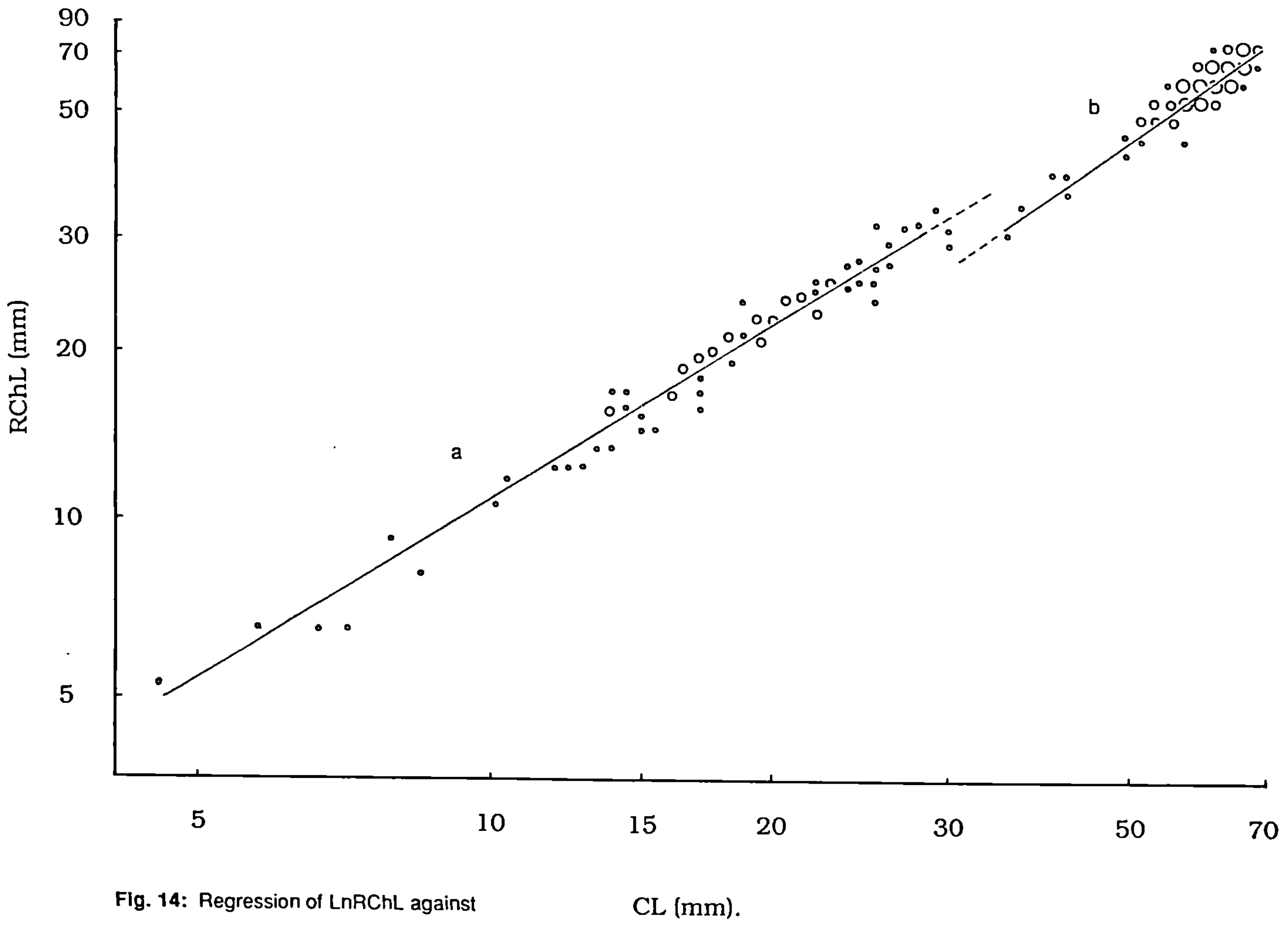


Fig. 14: Regression of LnRChL against LnCL for male *Geryon trispinosus*. n = 278.

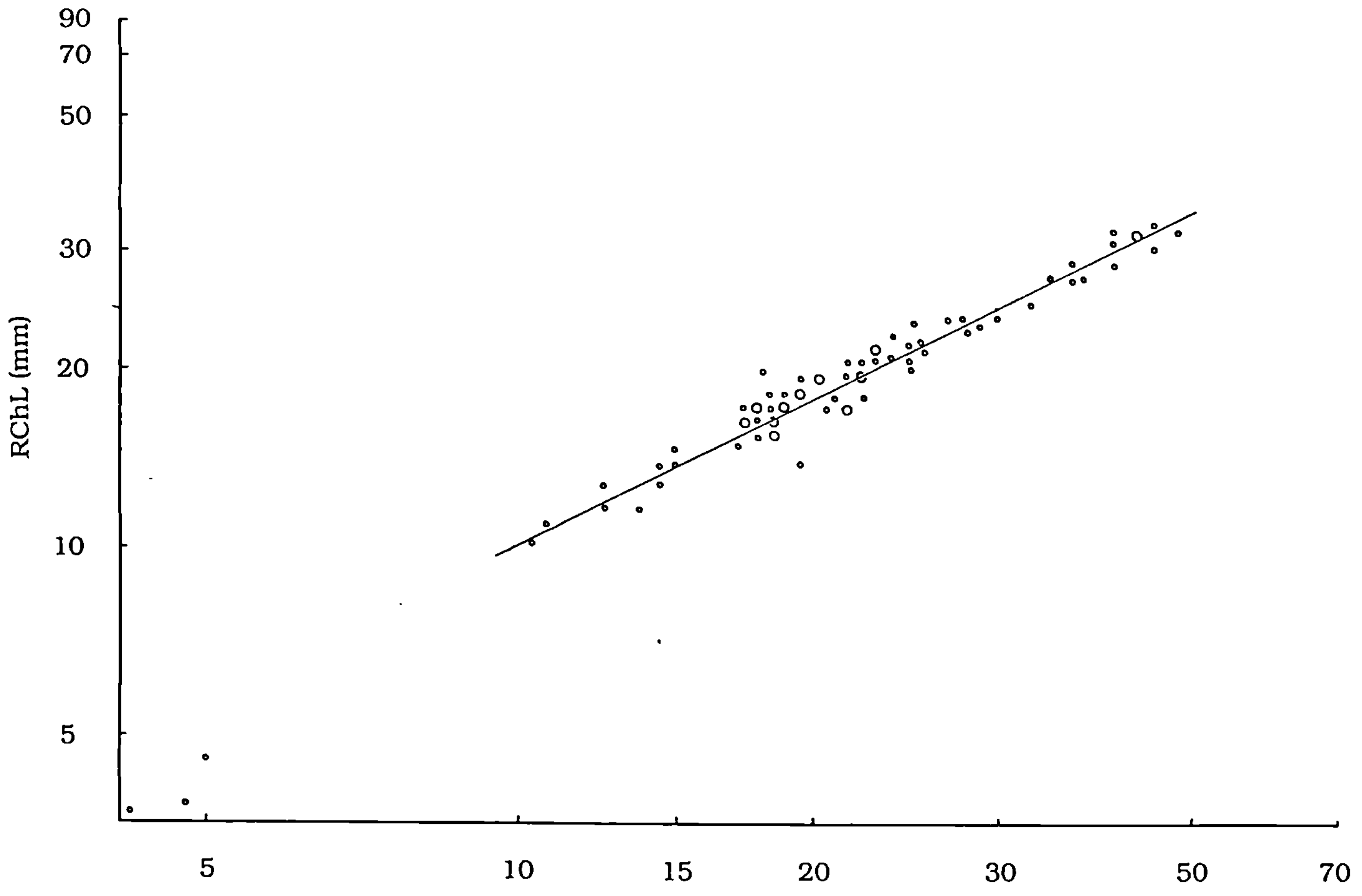


Fig. 15: Regression of LnRChL against LnCL for female *Geryon trispinosus*. n = 83.

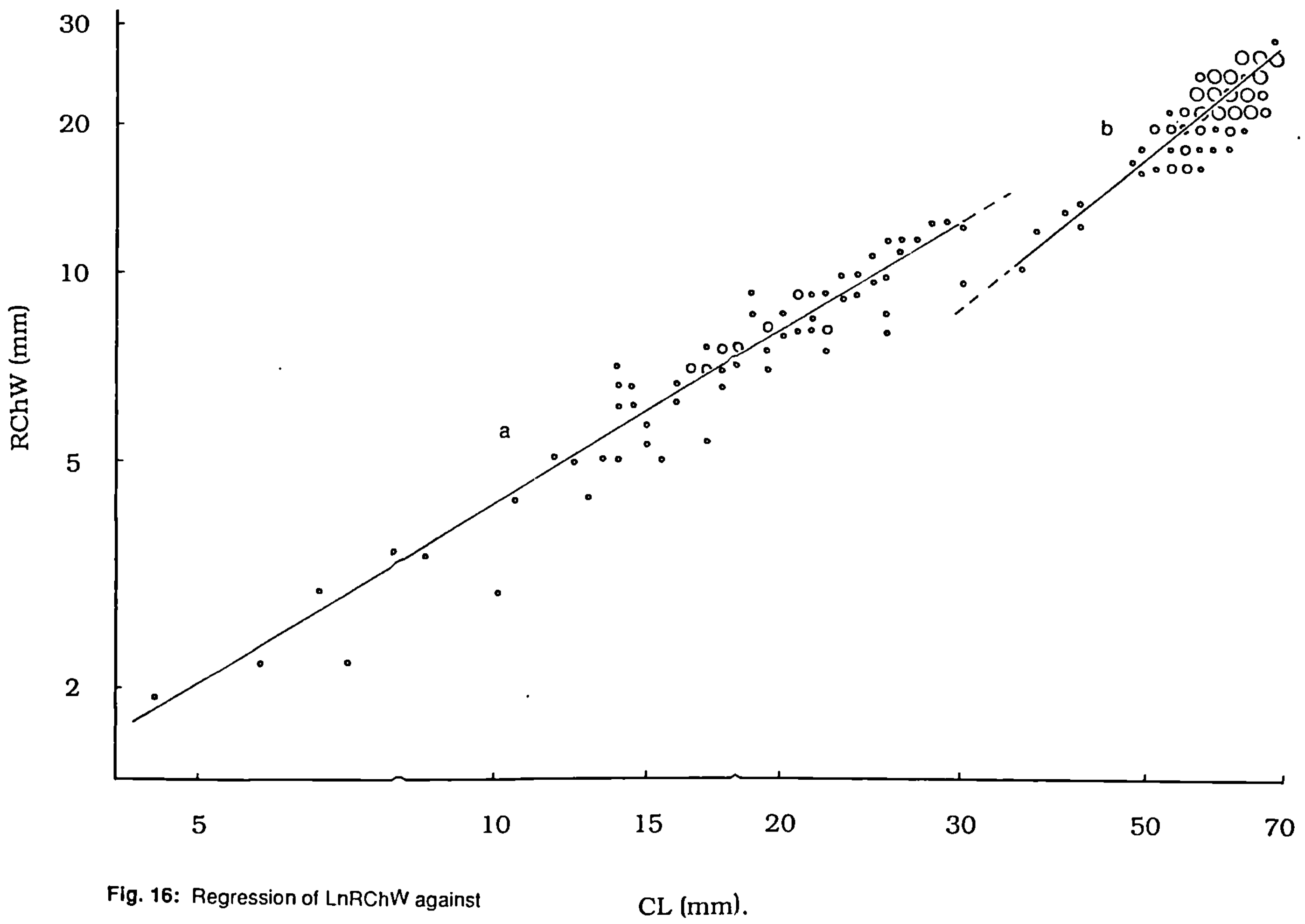


Fig. 16: Regression of LnRChW against LnCL for male *Geryon trispinosus*.
n = 278.

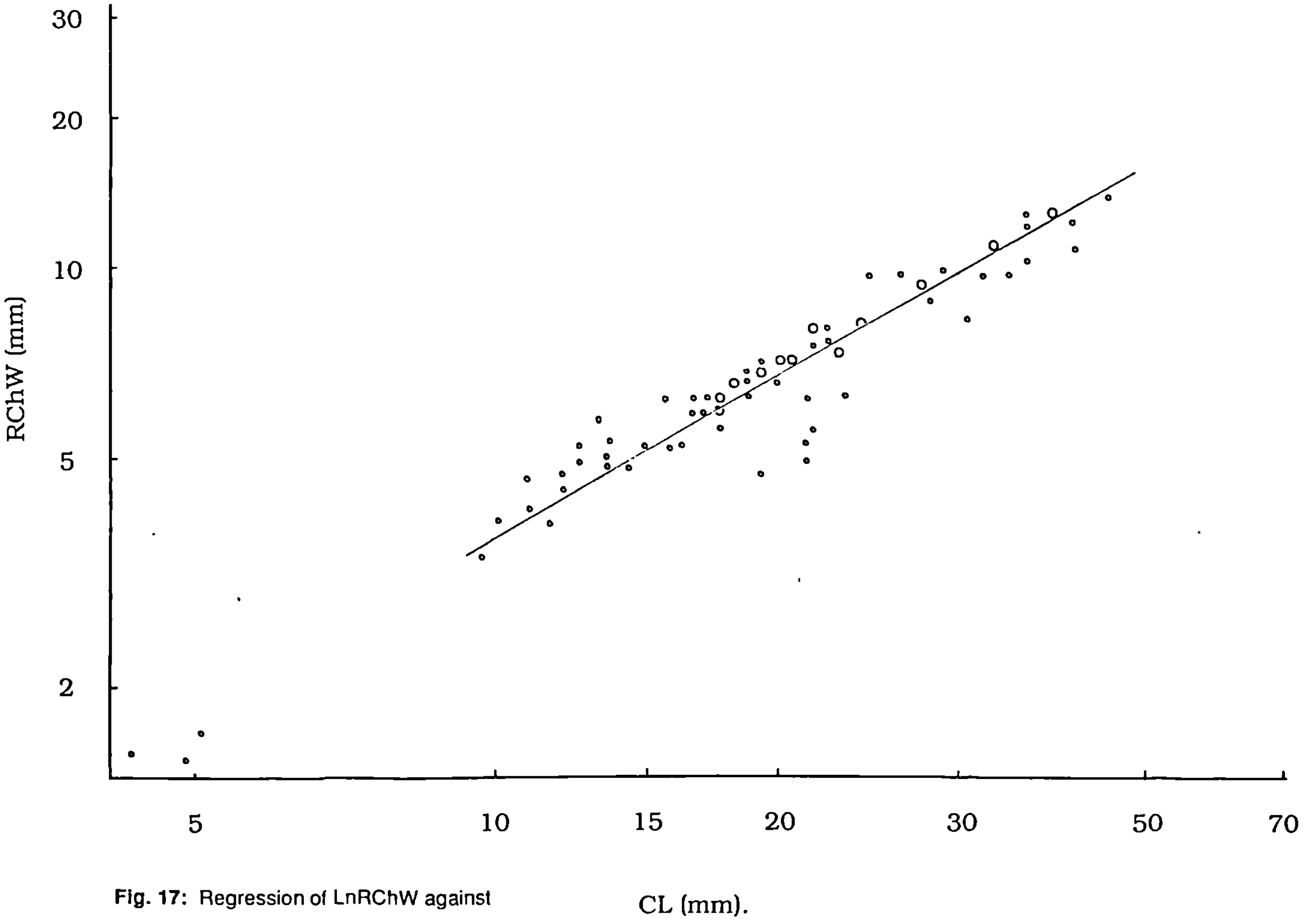


Fig. 17: Regression of LnRChW against LnCL for female *Geryon trispinosus*. n = 83.

	RChl/LChL	RChW/LChW	N
males	1·01 ± 0·01	1·20 ± 0·02	251
females	1·12 ± 0·02	1·28 ± 0·05	63

It is interesting to note that the differential between the two chelae is most pronounced in the females. The dominance of right-handedness is highly significant (Chi-squared; $P< 0{\cdot}05$), with 224 males (89·2 %) and 55 females (87·3 %) having the larger chela on the right, though it has to be stressed that the difference in size between the chelae is not great. However, such distinct handedness is comparatively uncommon, most species demonstrating heterochely being ambidextrous (Hartnoll, 1982). The following examples of handedness in Brachyura have been recorded: *Heterozius rotundifrons* - Right handed (Jones, 1978); *Heteropanope glabra*- 99:33 RH:LH; *Sphaerozius nitidus* - 59:4 RH:LH (both Tweedie, 1950); *Uca tetragonon* - 96·8 % RH and *Uca vocans* - 97·3 % RH (both Barnwell, 1982).

The observation that the right chela of *G. trispinosus* is generally the larger is interesting when considering the unusual relative growth patterns demonstrated by this appendage in males (Figs. 14 & 16). These patterns, together with those for the other dimensions studied, are discussed below.

Relative growth of specific appendages.

a) Left Chela (Figs 10-13). As mentioned above, the left chela is generally the minor chela, though the size difference is slight. The relative growth plots demonstrate a classic pattern of chela development in both sexes, as outlined by Hartnoll (1978, 1982). The male chela (Figs. 10 & 12) shows two phases of growth, the initial development close to isometry up to around 30 mm CL, followed by a slight increase in growth rate after this size, an increase most distinct for LCHW (Fig. 12). There is no rapid increase in chela size at a particular moult, solely an increase in allometry. In this respect, the growth of *G. trispinosus* left chela is similar to that recorded in *Aratus pisoni* (Hartnoll, 1965a).

The female chela shows no change in allometry above 10 mm CL (Figs. 11 & 13), though the three small females with LCh still attached do not appear to fit this relationship. Small females may therefore show a different rate of chela growth, but this can not be concluded from the few specimens obtained. Brachyuran females generally show little or no variation in chela allometry (Hartnoll, 1982).

b) Right Chela (Figs. 14-17). The female right chela shows a pattern similar to that of the left chela, except for the fact that it grows a little larger. However, the degree of allometry is less for both RChL and RChW than the left chela (Table 12). It may therefore be the case that the extra growth occurs at the smaller immature sizes, represented by only three specimens with chelae, but this cannot be concluded due to the paucity of complete small females.

The growth patterns of the male right chela are highly interesting and unusual (Figs. 14 & 16). For both RChL and RChW there is a negative percentage size increment of chela at the critical moult, coupled with a marked increase in growth rate. This is contrary to the usual patterns of male chela development, where either there is a direct change in allometry with no jump in size (e.g. *Aratus pisoni* (Hartnoll, 1965a), *Portunus pelagicus* (Prasad & Tampi, 1954) and *Geryon trispinosus* left chela (this study)) or, more commonly, both a significantly positive % chela size increment and an increase in allometry (e.g. *Corystes cassivelaunus* (Hartnoll, 1972), *Eurynone aspera* (Hartnoll, 1963) and *Maia squinado* (Tessier, 1935)). The only recorded case of a negative % size increment coupled with an increase in allometry is for female *Hyas coarctatus* (Hartnoll, 1963), whilst some other females demonstrated a negative % size increment but no increase in chela growth rate (e.g. *Carcinus maenas* (Veillet, 1945), *Macrocoeloma trispinosum* and *Microphrys* (Hartnoll, 1965b). However, all decreases were small and can be regarded as practically unimportant as females do not require especially large chelae, these being developed in males for a variety of defensive and reproductive uses, such as display, combat and carrying females during courtship (Crane, 1957; Hartnoll, 1968, 1974). It would therefore seem a detrimental growth strategy to have a chela that decreases in size at a moult and then subsequently grows at a faster rate to attain a large size. A decrease in RCh size at this transition therefore seems unlikely, especially as it is the larger chela, so this would not appear to be the explanation for these growth patterns.

Large chelae for display and combat purposes would appear relatively pointless for a crab such as *G. trispinosus* inhabiting a relatively dark and sparsely populated environment such as the deep-sea. Large chelae would not be beneficial in this respect. The most important factor controlling the pattern of male *G. trispinosus* growth would therefore appear to be courtship and mating behaviour. As discussed earlier, the mating of *Geryon* species is a relatively long process, the male forming a protective cage round the female while she moults and then manipulating her into the position for mating with the chelae (Mori & Relini, 1982; Elner *et al.*, 1987). For this process, two basic male morphometric characters are required: chelae large enough to carry the female but mobile enough to allow delicate manipulation, and a large overall size to surround and protect the female prior to mating. Therefore, the required outcome for a male *G. trispinosus* at the moult initiating sexual activity would be to increase in size to allow successful courtship (the greater the size the larger the female it is possible to mate with and hence the greater number of resulting eggs) and to possess chelae of the right size - not necessarily particularly large as there would appear to be few selective pressures from display and male competition.

It may therefore be the case that the break observed in Figs. 14 and 16 are not indicative of a decrease in chela size, but of a large increase in CL, representing an increase in total size. There is no change up or down in the relative size of the chela, only an increase in the degree of allometry. If this were indeed the case, then male crabs at this stage would have to undergo a

CL increase of some 10 mm, a moult increment of around 30 %. However, this phenomenon is not unknown, and has been reported for other Brachyura, such as *Callinectes sapidus* and *Cancer magister* (Hartnoll, 1982).

Other aspects of the biology of *G. trispinosus* already covered support this argument. Firstly, there is an unexplainable absence of males in the sample of a size corresponding to the hypothetical jump in CL at this moult (c.a. 32-42 mm), as illustrated in Fig. 4 (length frequency), though there are relatively large numbers of captured specimens on either side of this range. Perhaps most individuals skip this CL range completely in one moult, so very few crabs of this size ever exist. Secondly, the data representing the migration of small *G. trispinosus* (e.g. mean WWt and CL, Figs. 7 and 8) indicate a rapid increase in size over a small depth range (at around 700 m) with either small or large male crabs being caught here. It would be beneficial, even essential, for small crabs reaching the mature area to quickly achieve a viable reproductive size, and a size to prevent competition with *Munida sarsi,* so as to become successful in this population. Crabs with the greatest increase in size at this point may therefore be favoured. It can also be noted from Figs. 7 and 8 that below 800 m the mean sizes of the crabs are fairly constant. It is possible, therefore, that small crabs migrating up the slope curtail maximum growth at early moults and maintain a large energy store to prepare for the large critical moult before entering the adult population.

c) Abdomen (Figs. 18-19). The general pattern for development of the abdomen, represented by the width of the fifth segment (AS5) (see Hartnoll, 1974, 1978), is the development of an enlarged abdomen in females in order to encompass the egg mass, and practically isometric growth in males paralleled to the first pleopod development. As a result, the reverse of the pattern for chela allometry is often observed, with the female abdomen displaying the greater changes in allometry, and of increase in size at the puberty moult. The figures for *G. trispinosus* AS5 generally follow this format. The males show two phases, with a decrease in

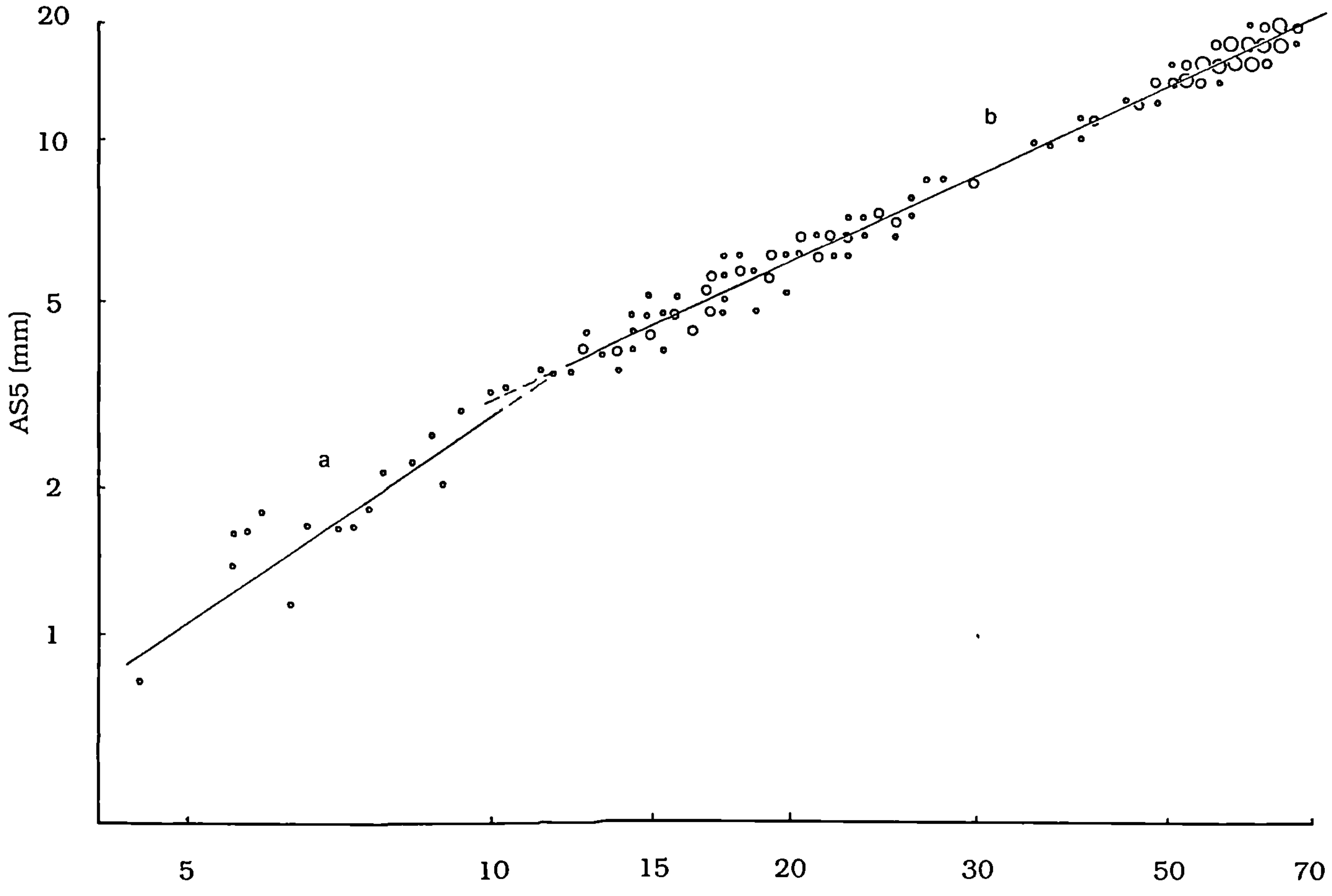


Fig. 18: Regression of LnAS5 against LnCL for male *Geryon trispinosus*. n = 317.

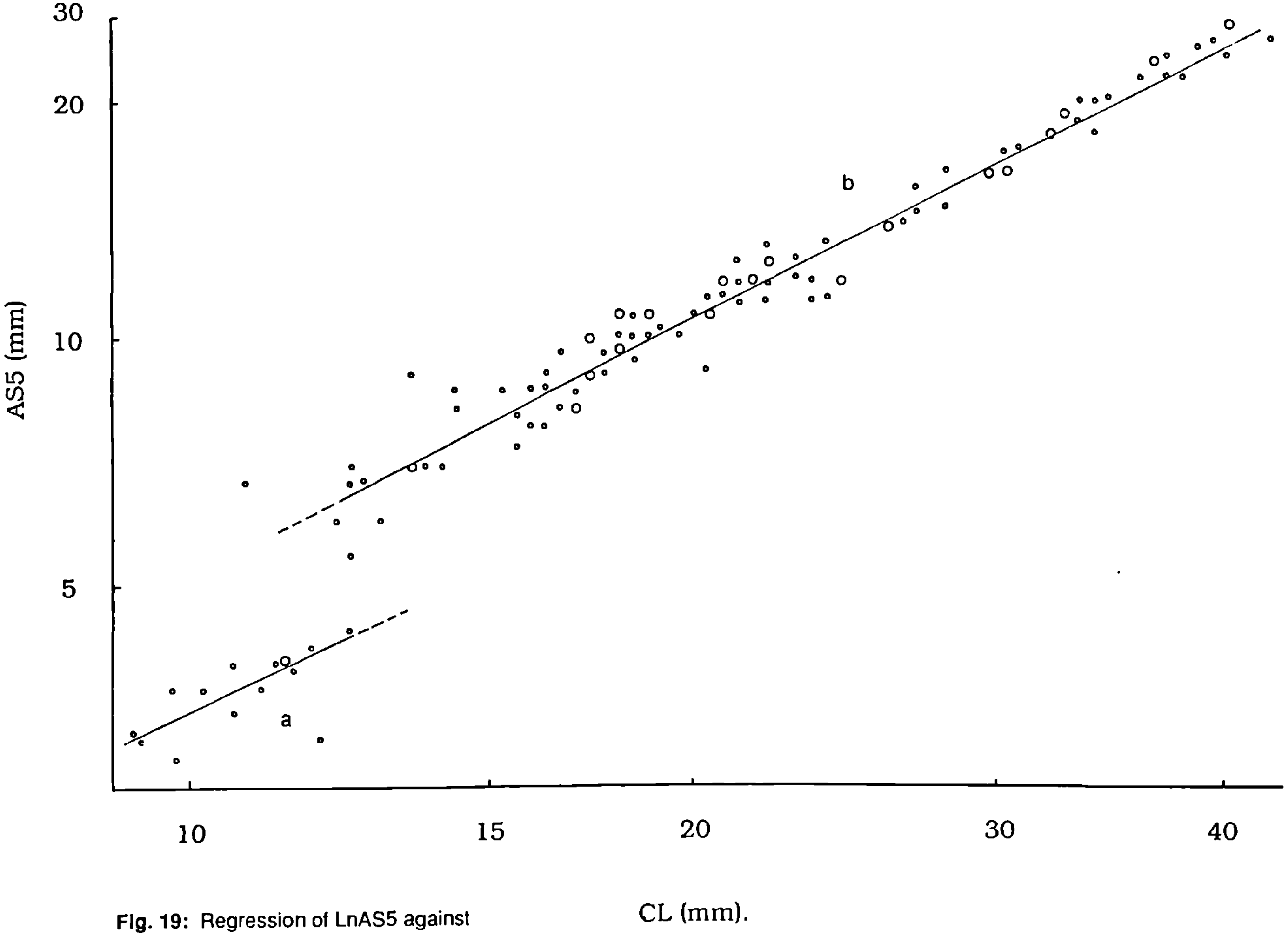


Fig. 19: Regression of LnAS5 against LnCL for female *Geryon trispinosus* n = 115.

allometry at phase 2 and no change in the size of the segment at the transition (Fig. 18). This is similar to *Cancer pagurus* (McKay, 1943) and *Sesarma dehaani* (Hamai & Hirai, 1940). However, it must be noted that the transition point for male AS5 relative growth does not correspond to the point for any of the chela measurements, occurring at a much smaller size of 10-12 mm CL. Females demonstrate a transition moult at a similar size (Fig. 19), with a large jump from one phase to the next and a small increase in allometry. This corresponds to many brachyurans, such as *Portunus pelagicus* (Prasad & Tampi, 1954), *Cancer pagurus* (McKay, 1943) and *Ocypode quadrata* (Haley, 1969).

Size of sexual maturity.

The figures for relative growth (Figs. 10-19) would seem to indicate the size of sexual maturity for both males and females, represented by the critical moult which produces the changes in allometry and chela size. In Brachyura, such changes generally correspond to the puberty moult (Hartnoll, 1974) and can be used to determine sexual maturity (Hartnoll, 1969). Using this method, the approximate ranges of CL where the moult of sexual maturity occurs are:

Males.	30-35 mm.
Females.	10-14 mm.

This range for females is supported by studies of the pleopod setation, ovary structure and the presence of full spermathecae. Presence of eggs on the pleopods is the only infallible sign of female sexual maturity, but it was not possible to utilise this observation due to the lack of ovigerous females caught in the samples. No mature ovaries were found in crabs below 15 mm, whilst the smallest crab with full spermathecae, indicating the occurrence of mating, was 10 mm CL, with 83·3 % of females above 14 mm CL having full spermathecae. Pleopod structure was analysed and classed into degree of setation, an indication of sexual maturity being the presence of fully setose pleopods capable of carrying eggs. The percentage of each size class of females possessing these fully setose pleopods can be seen in Table 13, supporting the size range proposed above for the start of sexual maturity.

It would appear, therefore, that females become mature around a minimum size of 14-15 mm CL, but are capable of mating before this size, perhaps at the puberty moult, and storing sperm while the ovary and pleopods develop fully.

The size range for male sexual maturity (30-35 mm CL) is deduced from the dramatic changes in allometry observed for the chelae. However, an examination of male internal reproductive structure revealed that advanced vas deferentia are found in crabs as small as 12-15 mm CL. This range ties in with the change in allometry seen for male AS5 (Fig. 18). There would thus appear to be two phases of male sexual development, with the pleopods and vas deferens developing at a small size, but the crab not actually becoming sexually viable until the later stage due to the requirement of male size in *Geryon* mating (Mori & Relini, 1982; Elner *et al.,* 1987). Extrapolating from these past studies on larger individuals, a male would have to be of a size of at least 30 mm CL to provide the necessary courtship protection and to be able to achieve the mechanics of *Geryon* copulation with even a small, just mature female of 15 mm. This value correlates well with the size range suggested for male sexual maturity.

Evidence for a terminal ecdysis in *Geryon trispinosus*.

Three basic formats for crustacean absolute growth, as found in the Brachyura, have been listed by Hartnoll (1982):

a). Indeterminate growth, with no terminal ecdysis, e.g. *Cancer pagurus* (Pearson, 1908).

b). Determinate growth, with variable instar number, maturity occurring before the final instar, e.g. *Carcinus maenas* (Carlisle, 1957).

Size Interval. (mm)	N^O. Females.	N^O. with mature pleopods.	% mature pleopods.
6·0-7·9	1	0	0·00
8·0-9·9	7	0	0·00
10·0-11·9	7	0	0·00
12·0-13·9	13	1	7·69
14·0-15·9	9	1	11·11
16·0-17·9	25	11	44·00
18·0-19·9	16	16	100·00
20·0-21·9	15	13	86·67
22·0-23·9	11	8	72·72
24·0-25·9	6	4	66·67
26·0-27·9	7	7	100·00
28·0-29·9	6	6	100·00
30·0-31·9	7	7	100·00
34·0-35·9	3	3	100·00
36·0-37·9	4	4	100·00
38·0-39·9	4	4	100·00
40·0-41·9	4	4	100·00
42·0-43·9	1	1	100·00

Table 13: Proportion of female *Geryon trispinosus* of each 2 mm size class with fully setose mature pleopods.

c). Determinate growth, with variable instar number, maturity delayed until the final instar, e.g. *Maia squinado* (Carlisle, 1957).

Results used to determine such growth patterns have generally been obtained from the observations of successive ecdysis in living crustaceans. However, several features of the study of *G. trispinosus* samples give clues to the nature of its absolute growth pattern. The following observations suggest a terminal moult may occur at a CL of 60-70 mm in males and 45-50 mm in females, though due to the selective nature of the samples of females with comparatively few large mature individuals, the following refer more specifically to males.

1. Length frequency data. As can be seen from Fig. 4 and the relative growth plots (Figs. 10-19), there is a disproportionately large number of males in the size range around 60 mm CL. This peak is also exaggerated in the 'Thalassa' data (Table 2). This clumping of all the large males would suggest a terminal moult resulting in this relatively small size band; a similar graph for indeterminate growth would be expected to have a more normal distribution with a 'tail' of surviving and still moulting larger individuals (e.g. as for *Munida sarsi* (this study, Ch. 3)). The peak on Fig. 4, however, is extremely discrete with no tail.

2. Regeneration of limbs. Crustacea possess the ability to autotomize damaged or trapped appendages and regenerate these at subsequent moults (Bliss, 1960; McVean, 1973, 1975). The first stage of this process is the development of a soft limb-bud from the breakage plain of the basi-ischium of the autotomised limb, which is greatly increased in size and hardened at the ensuing moult. If a crustacean is in terminal anecdysis, the production of limb-buds will therefore not occur as no moult will follow to regenerate the lost limb. Instead a calcified sheath forms over the damaged end of the limb stub. Therefore, if limb-buds are present in large *G. trispinosus* it would suggest that a terminal moult may not occur and that growth is indeterminate. The largest male *G. trispinosus* found with a limb-bud present was only 33 mm CL, around the size of the suggested moult of maturity. Despite the large number of crabs around 60 mm CL none had a limb-bud, while some sealing limb sheaths were apparent. This

supports the existence of a terminal moult.

3. Tagging studies. Studies have been undertaken with other *Geryon* species involving tagging large adults and releasing them in order to investigate movements of such crabs. Results from these studies have provided more evidence for a terminal moult, due to the long time period that crabs have carried tags without moulting. Lux *et al.* (1982) tagged large *G. quinquedens* off New England in 1974 with nylon body tags that are lost at moulting. Three of the largest tagged individuals were recaptured in 1981, so had not moulted in 6-7 years. Either the crabs at this size have an extremely long intermoult period, or more likely moulting has ceased and these crabs, together with those recaptured 4, 5 and 6 years after release, are in terminal anecdysis.

Ovigerous females and ovary condition.

As discussed earlier, there was a striking lack of ovigerous females in the *Geryon trispinosus* samples - a feature of many other *Geryon* studies. It was suggested that female crabs remain in the burrows until the eggs have hatched, so are not available to the sample methods used.

Only two ovigerous female *G. trispinosus* (0·54 %) were caught, with a further four individuals (1·08 %) having egg cases still on the pleopods, indicating the recent release of larvae. Further details relating to egg state, size, number and time of year appear in Table 14. The individual carrying plain eggs was caught in October, while the crab with eyed eggs and the females with the egg cases were from the May sample. It may therefore be the case that a seasonal cycle of egg production occurs, the eggs being laid in Sept/Oct, developing over the winter while the female remains in the burrow, and hatching late spring (Ingle (1979) studied *G. trispinosus* larvae from a hatching during 5-6 May).

To investigate this further, an examination of the ovarian condition of females from each month was undertaken. This involved an assessment of the ovary state, using the classes of small, large and extensive ovary (Fig. 20), the colour also being noted. Portions of the ovary from along its length were removed and studied to investigate ova size. The results form Table 14. Two classes of ova size were noted in some ovaries, suggesting successive batches of eggs being constantly produced. Where large ova were present ready to be laid, small ova were already being formed (e.g. Table 14, Oct. a) & c).). This continuous egg production would be possible due to the storage of sperm from one mating (Elner *et al.*, 1987) which remains viable for several years and can thus fertilise several egg batches (Lux *et al.*, 1982; Melville-Smith, 1987c).

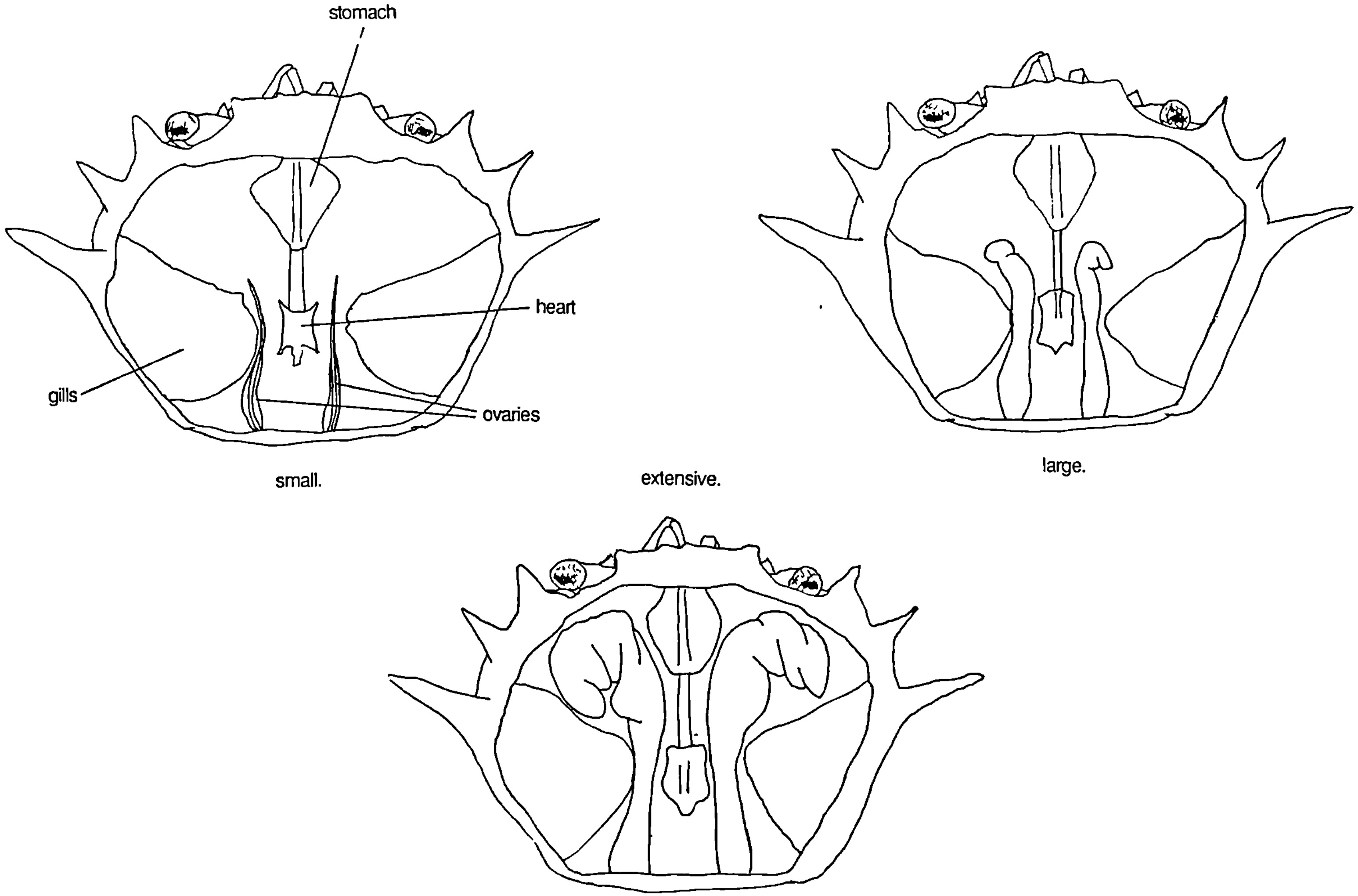
No real cyclic pattern of ovary development can be deduced from the data in Table 14, with large and small ovaries being present over the whole period (Feb-Oct). However, with the successive production of ova this may never be apparent, as the ovaries will always be bearing developing ova rather than starting from initial ova production after the eggs have been laid. It may therefore be the case that ovaries develop at different rates over the year, but once fully ripe delay laying the eggs until the autumn, at which time the eggs are passed to the pleopods and the female moves permanently into the burrow. Here the eggs develop until favourable conditions in late spring, when there is a seasonal input of organic material to the benthos (Billett *et al.*, 1983) signalling a flourishing planktonic community for the emerging larvae to join. However, due to the lack of females, no definite reproductive cycle can be stated - from the evidence *G. trispinosus* could have the suggested cycle, or equally there may be no specific reproductive season.

Other studies reveal both patterns being present in *Geryon* spp. *G. maritae* seems to have no discernible cycle (Melville-Smith, 1987c) whereas *G. quinquedens* (Haefner, 1978) and *G. fenneri* (Hinsch, 1988a) both appear to have reproductive seasons, *G. fenneri* laying in Sept/Oct and the larvae being released during Feb/March, this proposed cycle for *G. fenneri*

Month.	CL	Ovary Cond^{n}.	Ovary Colour.	1° Ova Size (mm).	2° Ova Size (mm).	Egg. Cond^{n}.	Egg Size (mm).	Egg N^{o}.
Feb. a).	33·3	Small.	Cream.	0·09 - 0·12	0·02 - 0·05	None.	---	---
b).	32·2	Large.	Peach.	0·12 - 0·17	None Apparent.	None.	---	---
Mar. a).	22·5	Large.	Peach.	0·12 - 0·15	0·05 - 0·06	None.	---	---
Apr.	---------- NO MATURE FEMALES ----------							
May. a).	31·5	Small.	Cream.	0·03 - 0·06	None Apparent.	None.	---	---
b).	32·5	Large.	Orange.	0·12 - 0·15.	None Apparent.	Eyed >50%.	0·75 - 0·80.	2600
c)- f).	‡‡	Large.	Orange	0·11 - 0·17	None Apparent.	Egg Cases.	0·70 - 0·85	200 - 1000
Jun. a).	37·5	Large.	Peach.	0·15 - 0·24	None Apparent.	None.	---	---
b).	32·6	Large.	Peach.	0·17 - 0·20	0·05 - 0·08	None.	---	---
Jul. a).	27·0	Small.	Cream.	0·12 - 0·15	None Apparent.	None.	---	---
b).	23·5	Small.	Cream.	0·11 - 0·17	None Apparent.	None.	---	---
Aug. a).	38·2	Large.	Peach.	0·11 - 0·18	0·05 - 0·08	None.	---	---
b).	40·2	Extensive.	Orange.	0·35 - 0·45	0·06 - 0·17	None.	---	---
c).	36·5	Large.	Peach.	0·12 - 0·17	0·06 - 0·08	None.	---	---
Sep. a).	21·8	Large.	Peach.	0·05 - 0·09	None Apparent.	None.	---	---
Oct. a).	34·7	Large.	Cream.	0·08 - 0·12	0·03 - 0·05	None.	---	---
b).	23·7	Small.	Cream.	0·06 - 0·09	None Apparent.	None.	---	---
c).	27·9	Large.	Peach.	0·17 - 0·20	0·05 - 0·06	None.	---	---
d).	20·5	Small.	Cream.	0·09 - 0·12	None Apparent.	Plain.	0·53 - 0·57	4200

‡‡ = CL: 34·5, 43·4, 39·7, 26·8.

Table 14: Condition of *Geryon trispinosus* ovaries over the year, together with ova size and egg size, type and number where present.



small.

extensive.

large.

Fig. 20: *Geryon trispinosus* ovary size classes.

being confirmed by Erdman & Blake (1988). The cycle for *G. quinquedens* appears to be less discrete. Haefner (1978) found ovigerous females in all months, with a peak in November which was the culmination of ovary development. *G. trispinosus* could therefore have a similar reproductive pattern to these two NE Atlantic species.

Sex ratio over the year.

To investigate the theory that *G. trispinosus* has a seasonal reproductive cycle, with the females remaining in their burrows over the winter and so not being caught, the sex ratio was calculated for each calender month (Table 15). The values for percentage females were plotted out to give Fig. 21 to indicate whether there was a decrease in the proportion of females in the samples over the winter months. Unfortunately, little can be deduced from this graph because:

a). There is a distinct lack of samples over the important winter period (Oct-Feb) except for a single December sample.

b). The graph includes immature females; so few mature females were caught that a meaningful graph could not be constructed.

The drop in percentage females in October may signal the proposed laying of eggs and movement of the females into the burrows, but more samples would have to be obtained over the winter period to confirm this low value.

A more valuable piece of evidence for the suggested reproductive cycle comes from the number of first crab stage young settling from the plankton that have been caught each month (Table 15, Fig. 22). As can be seen, the vast majority of these young crabs were caught in September on the sea-bed, with a few settling individuals caught using the RMT 200-300 m from the bottom. This distribution over the year fits the theory of larval release around May, the early stages spending summer in the plankton and then the first crab stage settling in late summer/early autumn as seen. Ingle (1979) reared *G. trispinosus* larvae in the laboratory, the development taking 69 days to reach the first crab stage from a hatching on 5-6 May. This

	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	**Total**
No. Males	*	21	8	7	37	29	31	141	12	74	1	18	**379**
No. Females	*	9	3	4	17	25	13	49	10	15	0	11	**156**
% Females	*	30·0	27·3	36·4	31·5	46·3	29·5	25·8	45·5	16·1	0	37·9	**29·2**
N^{O}. Young	*	0	0	1	0	0	2	1	148	0	0	0	**152**

* No Data.

Table 15: Sex ratio of *Geryon trispinosus* over the year, together with the number of settling young caught during each month.

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
N^{O}. Males Moulting.	*	0	0	0	2	2	3	52	1	2	*	*
% Males Moulting.	*	0·0	0·0	0·0	4·5	9·1	9·7	44·4	8·3	2·7	*	*
N^{O}. Females Moulting.	*	3	0	1	3	0	5	10	2	0	*	*
% Females Moulting.	*	33·3	0·0	25·0	17·6	0·0	38·5	29·4	20·0	0	*	*

Table 16: Number and percentage of male and female *Geryon trispinosus* moulting in each calander month.

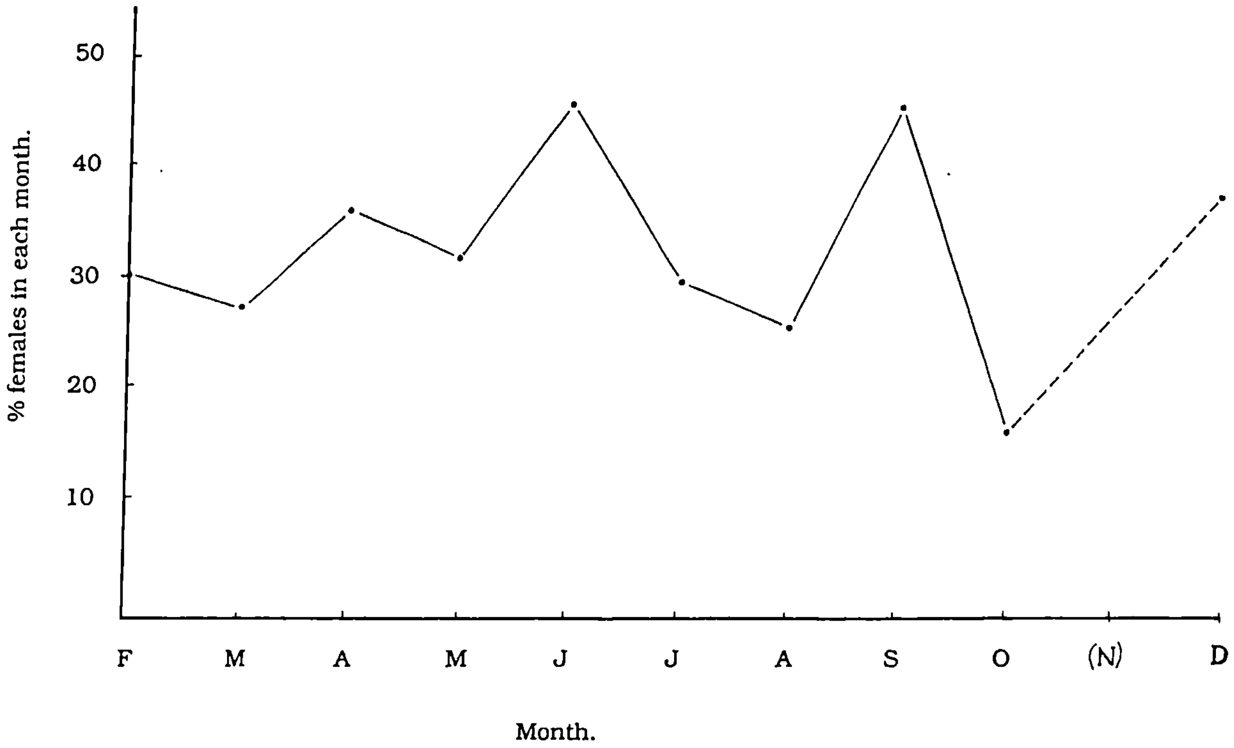


Fig. 21: Sex ratio over the year for *Geryon trispinosus*.

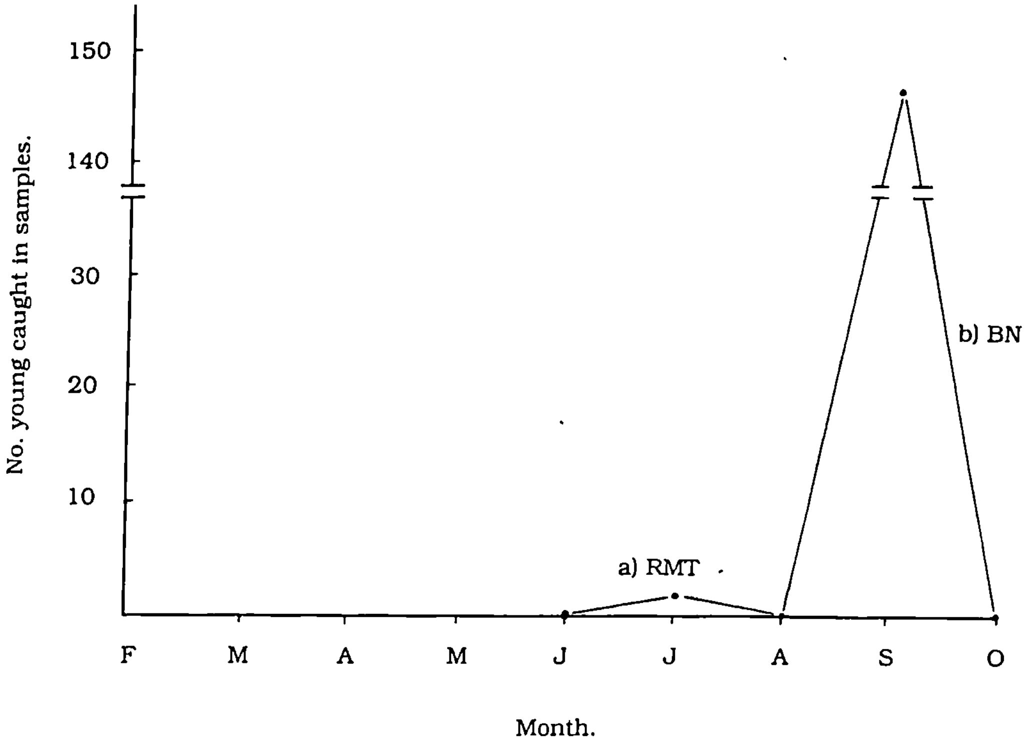


Fig. 22: Catches of young *Geryon trispinosus* settling 1st stage over the year.

admittedly artificial larval length would give a planktonic first crab stage in mid-July (coinciding with the pelagic young caught) and subsequent settlement. The large number of benthic young caught in September, therefore, have probably not been settled much longer than a month, originating from a hatching in May.

Moulting patterns over the year.

The occurrence of a recent moult in *Geryon trispinosus* is apparent from a still soft exoskeleton and the lack of external marks, abrasions or epifauna. The number of individuals of each sex showing evidence of a recent moult was recorded for each calender month (Table 16). These values were converted to the percentage of each sex moulting in each month and plotted out to form Fig. 23. As can be seen, the patterns for males and females are quite different. There is no one peak for females, the moulting rate averaging around 15-20 % with a series of fluctuations.

The graph for males (Fig. 23b) does, however, show a definite single moulting peak in August. When this month's samples are analysed further, two aspects of this moulting peak become apparent:

1. The majority of individuals moulting are large males, perhaps undergoing their terminal moult.

2. There is an amazing synchrony of moulting within each specific sample. In some samples (e.g. the 31 individuals in sample 50819), all the largest males are moulting, whereas in others (e.g. sample 50818) very few males show signs of a recent moult. It would appear that in one small area all the large males are moulting at the same time, yet in other nearby samples from the same month few are, as yet, undergoing ecdysis.

The reasons for this synchronous moulting in crabs from one area are unclear, as are the cues used to trigger all the crabs from one area. A possibility is that this moulting pattern has

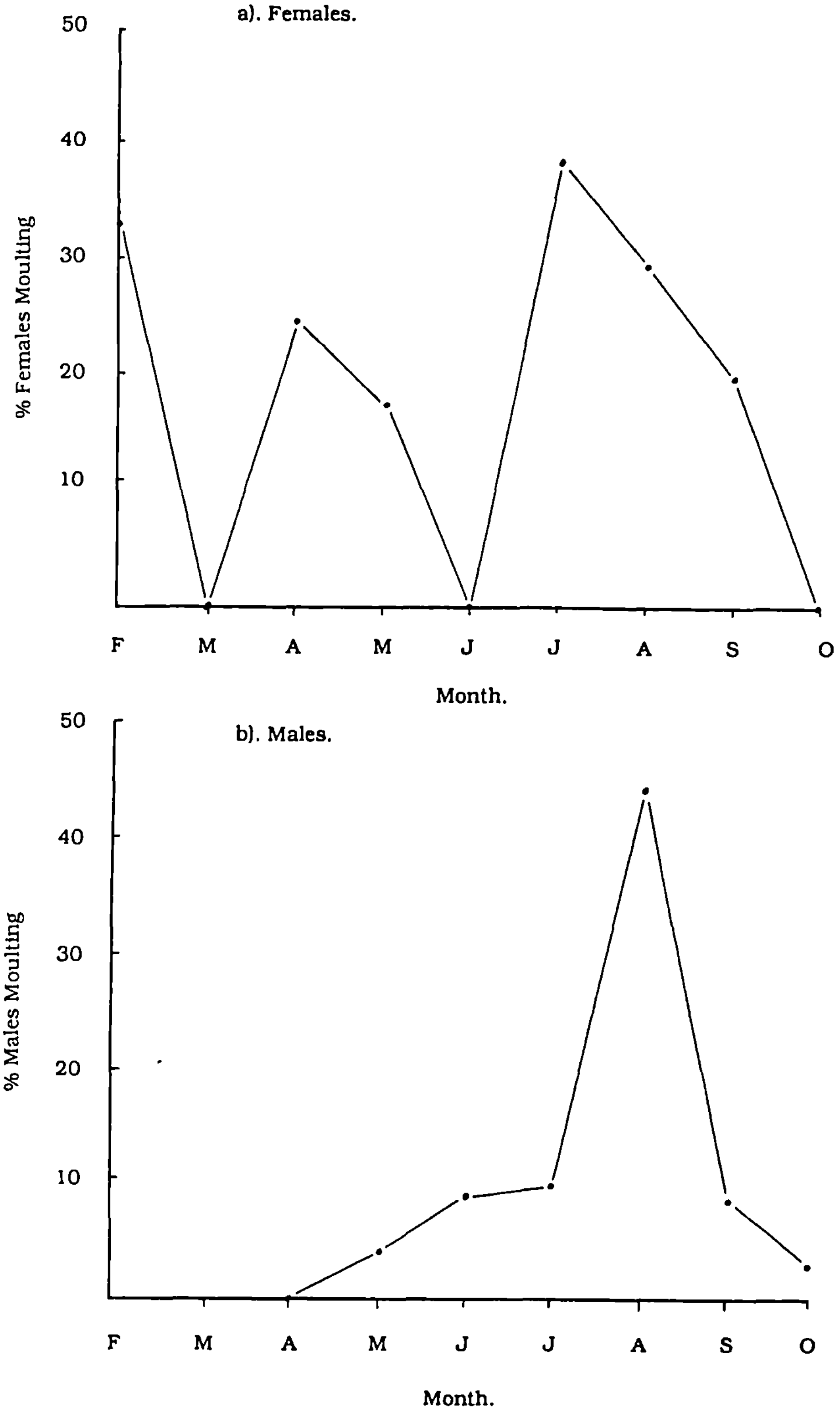


Fig. 23: Percentage of each sex of *Geryon trispsinosus* moulting in each calander month.

developed as a defence against cannibalism - when crabs are all moulting at once there is a lower predation pressure from other individuals during the vulnerable soft post-moult period.

Stomach contents.

An analysis of the material present in the stomachs of *Geryon trispinosus* was undertaken, though most stomachs (78 %) were totally empty. The matter present in the other stomachs was mostly composed of sediment particles and unidentifiable organic tissue and muscle fibres. It was, however, possible to identify the few items listed below.

List of *Geryon trispinosus* stomach contents (closest identification).

Sediment particles.
Unidentified organic tissue and muscle fibres (molluscan?)
Polychaete spicules and parapodia.
Foraminiferans (benthic and pelagic species).
Crustacean setose exoskeleton pieces and gastric teeth.
Ophiuroid calcareous mouth region.
Sponge spicules.
Non-polychaete worm pieces.
Fat masses.
Small stones.
Clinker pieces.
Unidentified animal structures.

The planktonic forams found in the gut show that the crab had been taking in "fluff" material that had been deposited on the sea bed (see Billett *et al.,* 1982).

Mori (1982) undertook an analysis of the alimentary rhythms of *Geryon longipes* and concluded that the crab was a "slow hunter, with rich meals distanced in time". Considering the extremes of full and empty stomachs, it would appear that *G. trispinosus* is a similar feeder, taking macrofaunal organisms that are available in the area, such as polychaetes and crustaceans, and not feeding between these large prey items. The large amount of sediment and related material (stones, clinker, forams) in the stomachs suggest, however, that *G. trispinosus* may also use the sediment as a direct food source if necessary, though it is likely that a lot of this matter is ingested with the infaunal prey items such as polychaetes.

The effects of chitinolytic bacteria.

Wenner *et al.* (1987) noted blackened abraded areas on the exoskeletons of *Geryon fenneri* and attributed these marks to damage caused by chitinolytic bacteria. Similar marks were noted on many large *G. trispinosus,* and in several cases the damage was quite acute (Plate 6). The presence of these marks solely on large crabs of both sexes adds more weight to the suggested terminal moult in *G. trispinosus.*

Epifauna.

In addition to the bacterial abrasions, most of the large *G. trispinosus* in presumptive terminal moult had hydroid colonies growing on the bases of the limbs and the lateral and posterior margins of the carapace (Plate 6 (arrowed), Fig. 24).

Chapter 6:

Notes on the Biology and Ecology of the *Munidopsis* (Anomura, Galatheidae) Species Found in the Porcupine Sea-bight.

Introduction.

Galatheoidean crustaceans of the genus *Munidopsis* constitute a major portion of the continental slope and abyssal decapod fauna worldwide. However, the vast majority of the available literature relating to the genus consists of records of geographic distribution or cruise reports (e.g. A. Milne- Edwards & Bouvier, 1897, 1900; Chace, 1942; Tirmizi, 1964; Laird *et al,* 1976), descriptions of species (e.g. Benedict, 1902; Chace 1939; Miyake & Baba, 1970; Pequegnat & Pequegnat, 1971), and detailed accounts of morphological features (e.g. Gordon, 1955; Sivertsen & Holthuis, 1956; Mayo, 1974; Ambler, 1980). This coverage of the systematics of *Munidopsis* has been extensive, but it would appear that studies on the actual biology of the genus have been somewhat neglected. Up until the 1980s, the only features of the biology studied were records of parasitism (e.g. Guérin-Ganivet, 1911: Boschma, 1962) and mentions of ovigerous females (e.g. Hansen, 1908; Pequegnat & Pequegnat, 1970), usually tagged on to the end of descriptive work.

Wenner (1982) broke the mould of *Munidopsis* reports somewhat with her study on the distribution and biology of the genus from the Middle Atlantic Bight, investigating to some degree reproductive cycles, fecundity, frequency distribution and parasitism as well as giving details of distribution. Gore (1983) undertook a similar study, with notes on rare species of *Munidopsis* found in the Venezuela Basin, commenting on the biology, ecology and in particular parasitism. However, considering Gore had access to the greatest number of specimens of each species so far collected, the biological studies can not be regarded as particularly extensive. Williams & Turner (1986), with the aid of 'Alvin', studied the *Munidopsis* associated with mesh-enclosed wood panels and obtained some interesting results on growth rates from individuals that had become trapped upon moulting. They also made the first attempts at relative growth comparisons, relating carapace length to carapace width. Recent work has also been carried out describing parasitic infestation of *Munidopsis,* including rhizocephalans (Lützen,

1985) and bopyrid isopods (Bourdon, 1972, 1981), though as yet the effects on the hosts have not been fully investigated.

This chapter therefore specifically concentrates on the biology of *Munidopsis*, investigating the distribution, biomass, reproduction, relative growth and parasitism of species caught in the Porcupine Sea-bight. Details of systematics are not covered as they have received adequate coverage in the references quoted.

Materials and Methods.

During the period 1978 to 1986, a total of 317 individuals of the genus *Munidopsis* Whiteaves have been collected from the Porcupine Sea-bight (49-52°N, 11-14°W). The positions and depths of the stations where *Munidopsis* were taken can be seen in Table 1 and Fig. 1. Three types of sampling gear were used: the semi-balloon otter trawl (OTSB) complete with "V" doors (see Merrett & Marshall, 1981), the IOS epibenthic sled (BN) (see Rice *et al*, 1982) and the SMBA Single Warp Trawl (SWT) (see Gordon & Duncan, 1983). The ships used were the RRS "Challenger" and "Discovery". The specimens were fixed in 5% formalin solution and later transferred to 70% alcohol for preservation. They have been stored in the 'Discovery' collection at the Institute of Oceanographic Sciences Deacon Laboratories, Wormley, Surrey.

Measurements were taken as follows: carapace length (CL) from the posterior orbital margin to the posterior carapace margin (Fig. 2a); chela length (ChL) from the tip of the propodus fixed finger to the base of the coxa and chela width (ChW) across the widest region of the cheliped palm (Fig. 2b). All measurements were taken using dial calipers to the nearest 0·1 mm. Details of egg number and condition were obtained using a Wild stereoscopic microscope. All measurements of egg and ova size utilised the graduated eyepiece of the microscope and were made to the nearest 0·01 mm. Wet weight of whole animals was measured to the nearest 0·01 g. Sex was determined by the position of the gonopores and the structure of the pleopods, particularly the presence or absence of the first pair.

Data used to calculate biomass and density figures were obtained from either the ship's log (distance travelled) for OTSB or, more accurately, from odometer readings when on the bottom for BN. These were multiplied by width of net to give figures for area sampled in hectares. Details were not available for trawls made using the SWT, so density and biomass data could not be obtained for these samples.

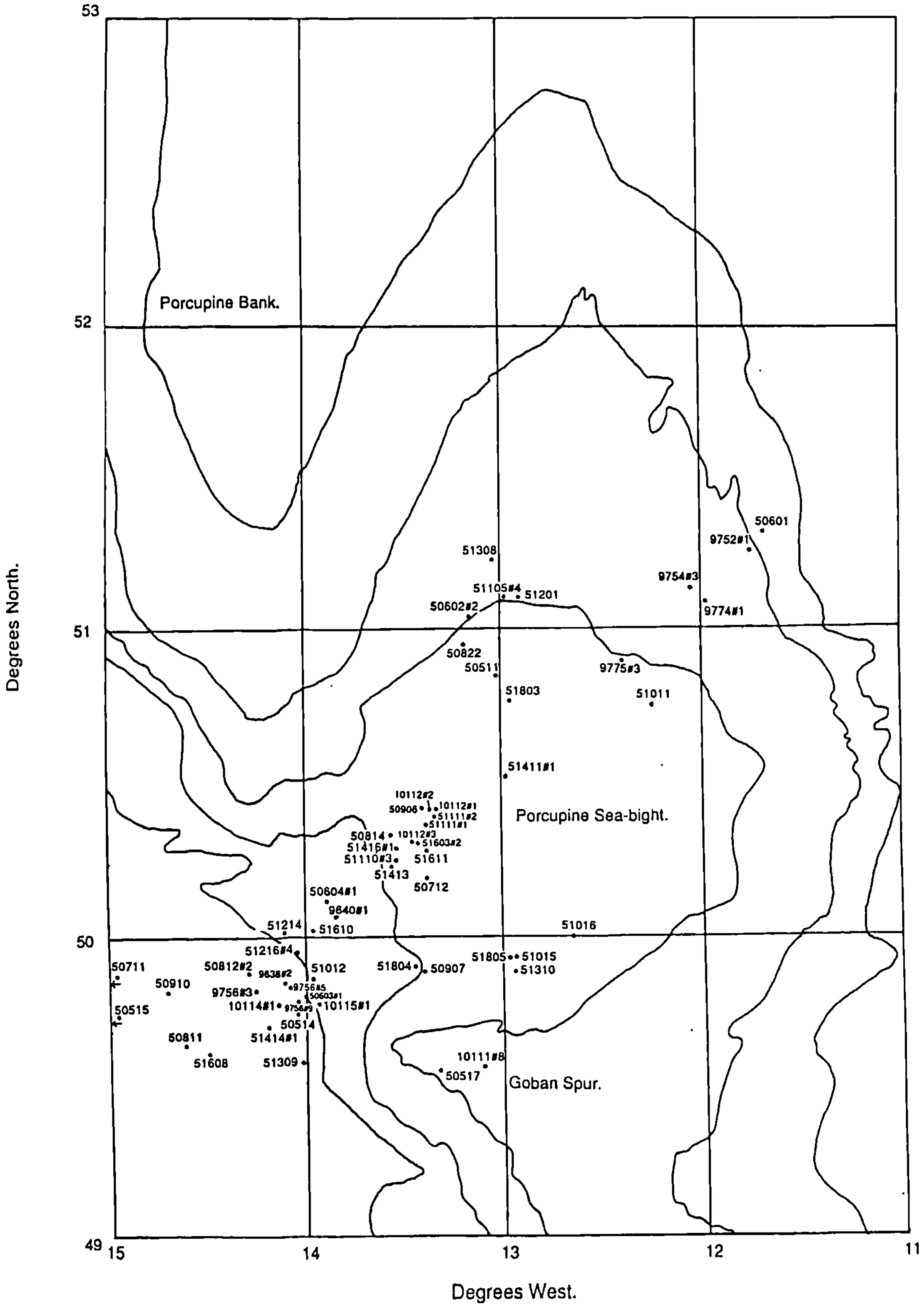


Fig. 1: Map of the Porcupine Sea-bight area indicating the positions of the sample stations where *Munidopsis* spp. were caught.

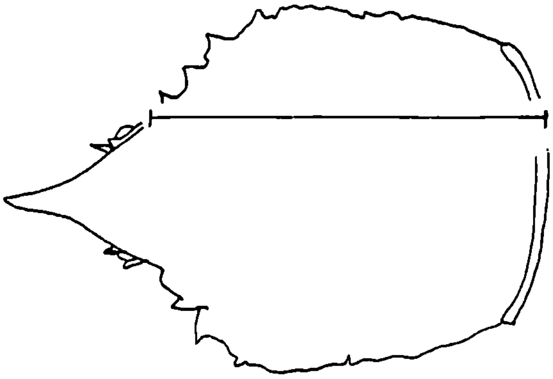


Fig. 2a: Generalized *Munidopsis* carapace indicating the CL measurement used in this study.

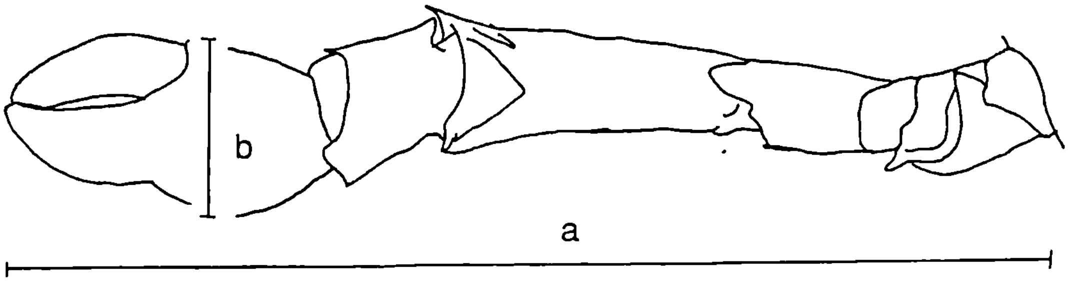


Fig. 2b: Generalized *Munidopsis* chela indicating the measurements of a). ChL and b). ChW used in this study.

Notes on the individual *Munidopsis* species.

This section deals with the nine species of *Munidopsis* represented in the Porcupine Sea-bight samples. Each species is covered separately in alphabetical order, with notes on the nomenclature, distribution and, where samples size allows, biology and ecology. However, to prevent too much repetition, some data have been collated on single tables and figures that refer to all the relevant species. These figures and tables follow and are:

Table 2: Length frequency data for all *Munidopsis* species.

Fig. 3: Distribution of the *Munidopsis* samples over the year.

Table 3: Biomass and density data for all samples where *Munidopsis* was taken.

Fig. 4: Distribution of ovigerous *Munidopsis* females over the year.

Table 4: Details of fecundity for each ovigerous female.

Fig. 5: Female *Munidopsis* pleopod types.

Details of each individual *Munidopsis* species follow:

Munidopsis antonii (Filhol 1884) (Fig. 6).

Galathodes antonii	Filhol 1884: p. 231. Perrier 1886: p. 325.
Munidopsis antoni	A. Milne-Edwards & Bouvier 1894: p. 198.
Munidopsis Antonii	A. Milne-Edwards & Bouvier 1900: p. 321. Hansen 1908: p. 38.
Munidopsis antonii	Henderson 1888: p. 151. Benedict 1902: p. 316. Gordon 1955: p. 244. Baba 1981: Lützen 1985: p. 101.

Occurrence.

9638#2, 4F 14M. 9640#1, 6F 2M. 97563, 2F. 9756#5, 1M. 9756#9, 1F. 10114#1, 1F. 10115#1, 2F 10M. 50514, 3F 7M. 50604#1, 1M. 50811, 1F. 50812#2, 1F 1M. 50910, 2F

CL (mm).	*Munidopsis* species.																			
	aries.		*antonii.*		*bairdii.*		*bermdzi.*		*crassa.*		*curvirost.*		*parfaiti.*		*rostrata.*			*serricorn.*	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	J	F	M	F
3·0-3·9																1		1	
4·0-4·9											1	1							
5·0-5·9															1	1			
6·0-6·9											2								
7·0-7·9			1								4	6			2		1	1	1
8·0-8·9											1	2	1						
9·0-9·9				1								4					2		
10·0-10·9						1									1				
11·0-11·9			1							1					5		1		1
12·0-12·9			1				1										2		
13·0-13·9																			
14·0-14·9								2							1		2		
15·0-15·9							1	1		1					1		1		
16·0-16·9	1		1	1									1		4		3		
17·0-17·9			2					4						1	1		1		
18·0-18·9				1											3		3		
19·0-19·9	1		2	3	1				1				1		1		1		
20·0-20·9			1				1	2		1				1	2		1		
21·0-21·9			5	1									1	2			5		
22·0-22·9			3	1				2							3		2		
23·0-23·9			1					2					4	1	3		3		
24·0-24·9			6										5		3		1		
25·0-25·9			3	1				1		2			5	2			4		
26·0-26·9			3	2									2	1			4		
27·0-27·9			3	2									3	1	1		2		
28·0-28·9			6	2			1						4	6			3		
29·0-29·9			5	2									1	4			2		
30·0-30·9			4	1						1			1	3			1		
31·0-31·9				4			1			1				3					
32·0-32·9			3											1					
33·0-33·9			2	1										1					
34·0-34·9				3			2			1									
35·0-35·9				4			1		1										
36·0-36·9				4						1									
37·0-37·9				2															
38·0-38·9				2															
39·0-39·9				3						2									
40·0-40·9									1	1									
41·0-41·9																			
42·0-42·9										1									
—																			
49·0-49·9									1										
—																			
60·0-61·9	1																		
—																			
71·0-71·9		1																	
72·0-72·9		1																	
No Carapace.			8	2			1				2		1	1	1		1		
Totals:	3	2	61	43	1	1	9	14	4	13	10	13	30	28	33	2	46	2	2
	5		104		2		23		17		23		58		81			4	

bermdzi. = bermudezi.
curvirost. = curvirostra.
serricorn. = serricornis.

Table 2: Length frequency data for all species of *Munidopsis*.

	Month											
Species.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
M. aries.			▨						▨			
M. antonii.				▨	▨	▨		▨	▨		▨	
M. bairdii.											▨	
M. bermudezi.			▨					▨	░	░		
M. crassa.			▨	▨		▨	░	▨		░	▨	
M. curvirostra.		▨		▨	░	▨	▨		▨	░		
M. parfaiti.		▨	▨	▨		▨	▨	▨	▨	▨	▨	
M. rostrata.		▨	▨		▨		▨	▨	▨	▨	▨	
M. serricornis.				▨								

Fig. 3: Distribution of samples of each *Munidopsis* species over the year.

▨	Males and females in sample
░	Females only in sample.
	Males only in sample.
	No sample.

Station No.	Mean Depth. (m)	Gear Used.	Sample Area (ha).	Species.	Number.	Total WetWt. (g)	Density. No.Ind ha^{-1}	Biomass. g WWt.ha^{-1}
9638#2	4074	OTSB	4·79	*M. crassa*	1	2·85	0·2	0·6
				M. antonii	16	137·31	3 3	28·7
				M. parfaiti	6	69·21	1·3	14·5
				M. aries	1	3 51	0·2	0·7
9640#1	3753	OTSB	9 61	*M. antonii*	7	78·96	0·7	8·2
9752#1	1025	OTSB	3·35	*M. serricornis*	2	1·45	0 6	0·4
9754#3	1484	BN	0·48	*M. curvirostra*	3	0·54	6 3	1·1
9756#3	4118	OTSB	5·44	*M. parfaiti*	1	12 54	0·2	2·3
				M. antonii	2	33 93	0·4	6·2
9756#5	4016	OTSB	7·66	*M. crassa*	1	8·18	0·1	1·1
				M. antonii	1	4·46	0·1	0 6
9756#9	4054	BN	0·13	*M. antonii*	1	14·96	7·7	115·0
9774#1	1533	OTSB	4·45	*M. curvirostra*	1	0·36	0·2	0·1
9775#3	2016	BN	1·00	*M. curvirostra*	7	2·24	7·0	2 2
10111#8	1635	BN	0·15	*M. curvirostra*	1	0·68	6·7	4·5
10112#1	2660	BN	0·87	*M. rostrata*	3	28·29	3·4	32·5
10112#2	2645	BN	0 07	*M. rostrata*	1	0·27	14·3	3 8
10112#3	2748	BN	0·13	*M. rostrata*	1	0·10	7·7	0·8
10114#1	4050	BN	0·11	*M. antonii*	1	23 69	9·1	215·4
				M. parfaiti	1	5·88	9·1	53 5
10115#1	3925	BN	0·14	*M. antonii*	4	34·65	28·6	247·1
50511	2420	OTSB	6·54	*M. rostrata*	1	3·36	0·2	0 5
50514	4056	OTSB	8·13	*M. crassa*	1	9·63	0·1	1·2
				M. antonii	10	88·38	1·2	10·9
				M. parfaiti	7	66·51	0·9	8·2
50515	4510	OTSB	6·85	*M. crassa*	2	7·90	0·3	1 2
				M. parfaiti	2	23·94	0 3	3·5
50517	1790	OTSB	4·30	*M. curvirostra*	1	0·41	0·2	0·1
50601	849	OTSB	5·10	*M. serricornis*	2	0·41	0·4	0·1
50602#2	1968	BN	0·60	*M. curvirostra*	4	1·46	6·7	2·4
50603#1	4000	BN	0·78	*M. parfaiti*	1	14·05	1·3	18·0
50604#1	3520	BN	0·85	*M. antonii*	1	2·78	1·2	3·3
50711	4788	OTSB	9·18	*M. crassa*	1	20·66	0·1	2·3
				M. parfaiti	5	54·16	0·5	5·9
50712	2738	OTSB	4 66	*M. bermudezi*	1	23·45	0·2	5·0
				M. rostrata	3	24·03	0 6	5·2
50811	4375	OTSB	7·97	*M. antonii*	1	18·47	0·1	2·3
				M. crassa	4	113·60	0·5	14·2
				M. parfaiti	12	120·38	1·5	15·1
50812#2	4088	OTSB	10·36	*M. antonii*	2	21·01	0·2	2·0
				M. parfaiti	1	11·45	0·1	1·1
50814	2858	OTSB	22·34	*M. bermudezi*	2	17·17	0·1	0·8
				M. rostrata	14	59·79	0 6	2·7
50822	2123	OTSB	10·77	*M. rostrata*	2	18 63	0·2	1·7
50906	2645	OTSB	8·29	*M. bairdii*	1	0·95	0·1	0·1
				M. rostrata	3	17·13	0·4	2·1
50907	2975	OTSB	8·61	*M. rostrata*	2	12·00	0·2	1·4
50910	4312	OTSB	9·25	*M. crassa*	4	63·28	0·4	6 8
				M. antonii	5	12·03	0·5	1·3
				M. parfaiti	5	56·99	0·5	6·2
51011	2173	OTSB	7·17	*M. rostrata*	2	17·65	0·3	2·4
51012	3900	OTSB	9·40	*M. antonii*	2	25·92	0·2	2·8
51015	2530	OTSB	5 90	*M. rostrata*	2	12·04	0·3	2·0
51016	2398	OTSB	5·26	*M. rostrata*	3	30·96	0·6	5 9
51110#3	2793	BN	0·22	*M. bairdii*	1	3·09	4·6	14·1
				M. rostrata	4	5 46	18 2	24 8
51111#1	2665	BN	0·21	*M. rostrata*	3	2·13	14·3	10·2
51111#2	2620	BN	0·21	*M. rostrata*	2	1·52	9·5	7·2
51201	1975	OTSB	3·19	*M. curvirostra*	2	1·33	0·6	0·4
51214	3810	OTSB	5·10	*M. antonii*	5	47·85	1·0	9·4
51216#4	3985	OTSB	6·22	*M. antonii*	4	23·24	0·6	3·7
51308	1743	OTSB	4·62	*M. curvirostra*	1	0·71	0·2	0·2
51309	4223	OTSB	9 88	*M. parfaiti*	2	13 60	0·2	1·4
				M. antonii	1	5·90	0·1	0·6
51310	2478	OTSB	6·53	*M. rostrata*	11	51·15	1·7	7·8
51411#1	2485	OTSB	7·33	*M. rostrata*	7	33 67	1·0	4·6
51413	2855	OTSB	7·81	*M. aries*	1	137·11	0·1	17·6
				M. bermudezi	3	30·49	0 4	3 9
51416#1	2775	BN	0·14	*M. rostrata*	1	0·02	7 1	0·1
51603#2	2735	BN	0·14	*M. rostrata*	1	0·32	7·1	2 3
51608#1	4320	OTSB	7·99	*M. crassa*	1	22 96	0·1	2 9
				M. antonii	1	8·69	0·1	1·1
				M. parfaiti	2	8 80	0·2	1·1
51610#1	3485	OTSB	9·93	*M. antonii*	1	7 63	0·1	1·0
51611#1	2670	OTSB	10·19	*M. rostrata*	2	10·98	0·2	1·1
51613#1	2220	OTSB	8·37	*M. rostrata*	2	3·37	0·2	0·4
51803	3955	OTSB	12·27	*M. antonii*	12	198·48	1·0	16·2
				M. parfaiti	15	206 52	1 2	16 8
51804	3098	OTSB	7·49	*M. aries*	2	178 64	0·3	23 9
				M. bermudezi	1	18·94	0·1	2 5
51805	2488	OTSB	5 58	*M. rostrata*	2	14 20	0·4	2 5

Table 3: Biomass and density data for each station where *Munidopsis* spp. were taken, subdivided into the figures for the individual species.

	Month											
Species.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
M. aries.			▩									
M. antonii.				▩				▩	▩ ░		▩ ░	
M. bairdii.												
M. bermudezi.			░					▩ ░				
M. crassa.											▩	
M. curvirostra.		░		░			▩ ░		░			
M. parfaiti.						░		▩ ░		▩		
M. rostrata.					░			▩ ░	▩ ░	▩	▩	
M. serricornis.				▩ ░								

Fig. 4: Distribution of ovigerous females of each *Munidopsis* species over the year.

▩ Females with >20 eggs present.

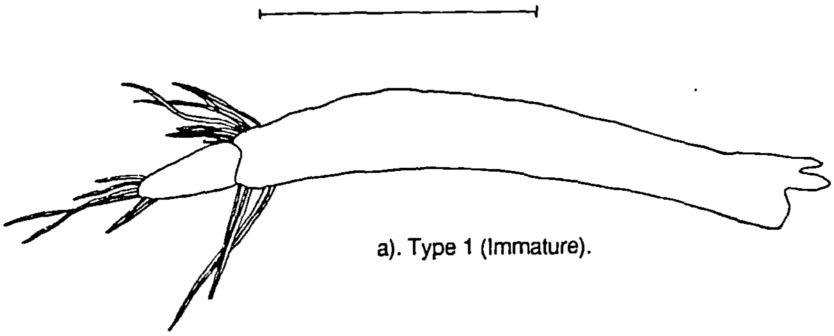
░ Females with < 20 eggs present.

☐ All females have no eggs.

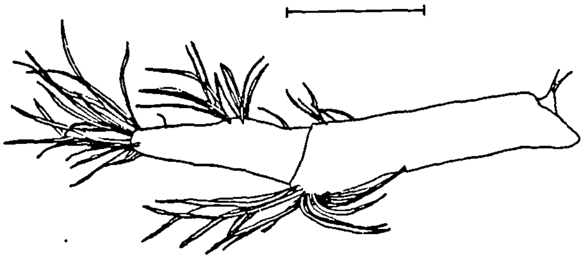
☐ No females caught.

Species.	CL (mm).	Month.	Egg Number.	Egg Size (mm).
M. aries.	71·3	III	106	3·8
M. antonii.	34·2	IV	32	2·4
	36·3	VIII	50	2·5
	37·5	IX	110	2·4
	35·7	IX	1	2·4
	36·4	IX	5	2·5
	36·2	IX	16	2·8
	34·6	IX	3	2·6
	39·8	IX	71	2·2
	36·6	IX	8	2·4
	35·7	XI	28	2·7
	38·3	XI	4	3·0
	31·7	XI	56	2·6
M. bermudezi.	17·6	III	3	1·8
	22·7	VIII	18	1·9
	23·5	VIII	23	1·7
	22·8	VIII	48	1·8
M. crassa.	42·5	XI	32	3·0
M. curvirostra.	9·7	II	11	0·9
	7·8	IV	7	0·9
	8·1	IV	13	0·6
	7·1	IV	13	1·0
	7·3	VII	2	0·9
	9·1	VII	20	0·9
	7·2*	VII	6	0·6
	7·8	VII	5	0·8
	9·8	IX	16	0·9
	9·9	IX	7	Hatching.
M. parfaiti.	26·3	VI	1	3·5
	29·0	VIII	3	3·5
	29·0	VIII	25	2·7
	28·5	X	20	3·1
M. rostrata.	31·4	V	9	2·5
	27·0	VIII	3	2·9
	28·1	VIII	2	2·2
	27·7*	VIII	70	1·7
	28·9	IX	2	2·6
	26·4	IX	43	2·4
	25·2	IX	71	2·7
	28·6	X	108	2·2
	26·8	XI	77	2·6
M. serricornis.	11·2	IV	30	0·8
	7·5	IV	2	0·6

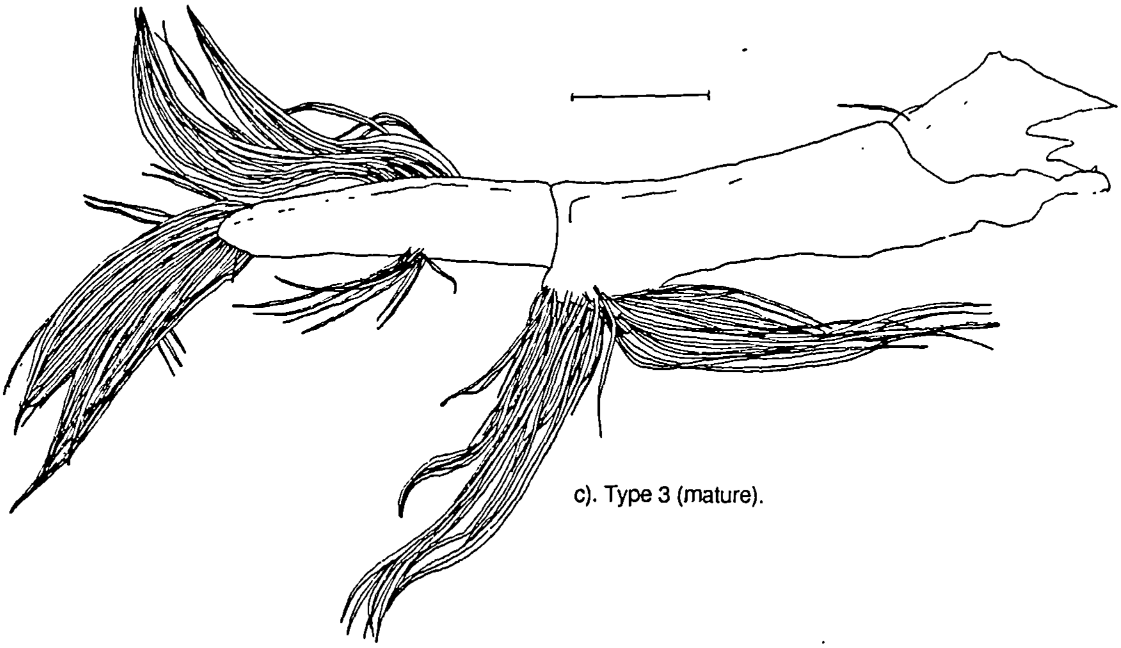
Table 4: Details of egg number and size for the individual *Munidopsis* females found carrying eggs.



a). Type 1 (Immature).



b). Type 2 (Intermediate).



c). Type 3 (mature).

Fig. 5: Female *Munidopsis* pleopod structure types, showing the development of these structures with maturity. (All from *Munidopsis rostrata*.) Scale bar = 1 mm.

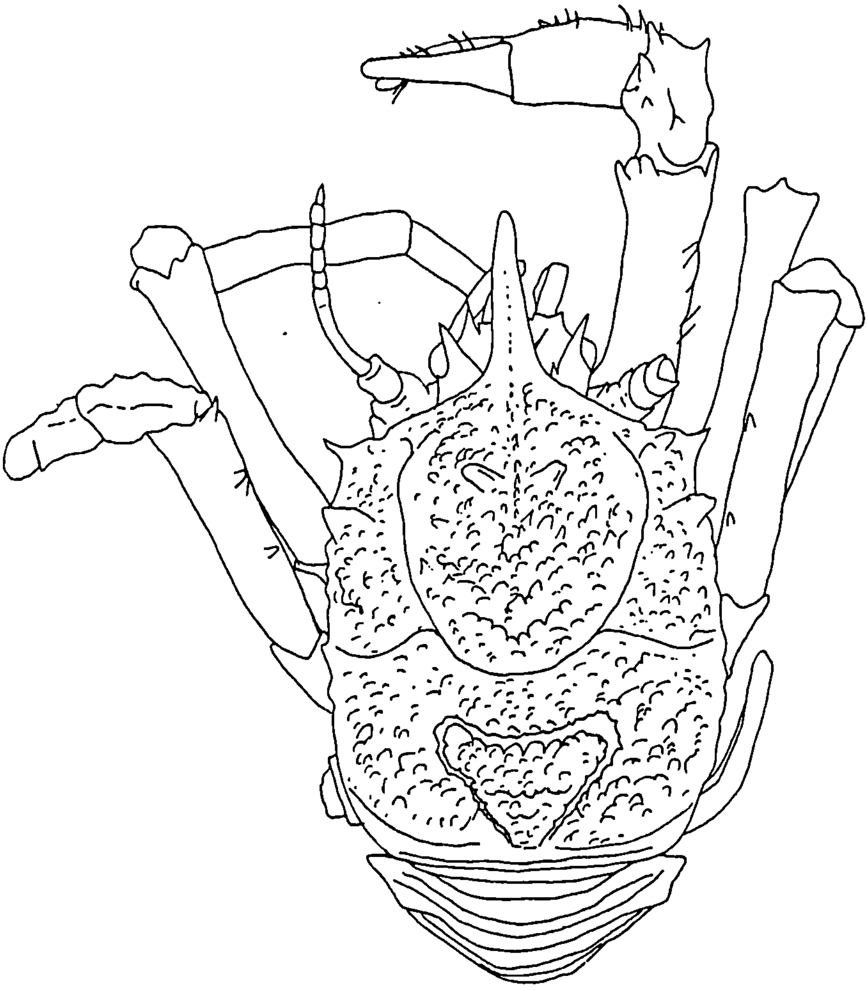


Fig. 6: *Munidopsis antonii.* Male, CL 11·7 mm.

3M. 51012, 1F 2M. 51216#4, 3F 1M. 51309, 1F. 51608#1, 1M. 51610#1, 1M. 51803, 14F 15M.

Distribution.

Geographic: Azores (A. Milne-Edwards & Bouvier, 1899), Valparaiso & SW Australia (Henderson, 1888), Davis Straits (Hansen, 1908), Japan (Baba, 1981).

Bathymetric: 2538 m (Henderson, 1888: Valparaiso) to 3938 m (A. Milne-Edwards & Bouvier, 1899: Azores). In this study, the possible range of *M. antonii* was 3310-4400 m, with a calculated range of 3660-4350 m, so increasing the reported bathymetric range for this species.

Associates.

M. antonii occurred with *M. aries* (Stations 9638#2, 51610#1), *M. crassa* (Stations 9638#2, 9756#5, 50514, 50811, 50910, 51608#1) and *M. parfaiti* (Stations 9638#2, 9756#3, 10112#3, 50514, 50811, 50812#2, 50910, 51309, 51608#1, 51803).

Population Structure.

Size Distribution: *M. antonii* was the most abundant species in the Porcupine Sea-bight samples, represented by 104 specimens (59:41 M:F), ranging in size from 7·6 - 39·8 mm (Table 2, Fig. 7). As can be seen, females grow significantly larger than males. In previous studies (see above), *M. antonii* has only been caught in small numbers. It would therefore appear that the Porcupine Sea-bight region is where the species has been found in the greatest numbers.

Biomass and Density: To investigate the bathymetric distribution of the *M. antonii* population, biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) data were calculated (Table 3, Fig. 8), for both OTSB and BN samples. As can be seen, there is a peak in both biomass and

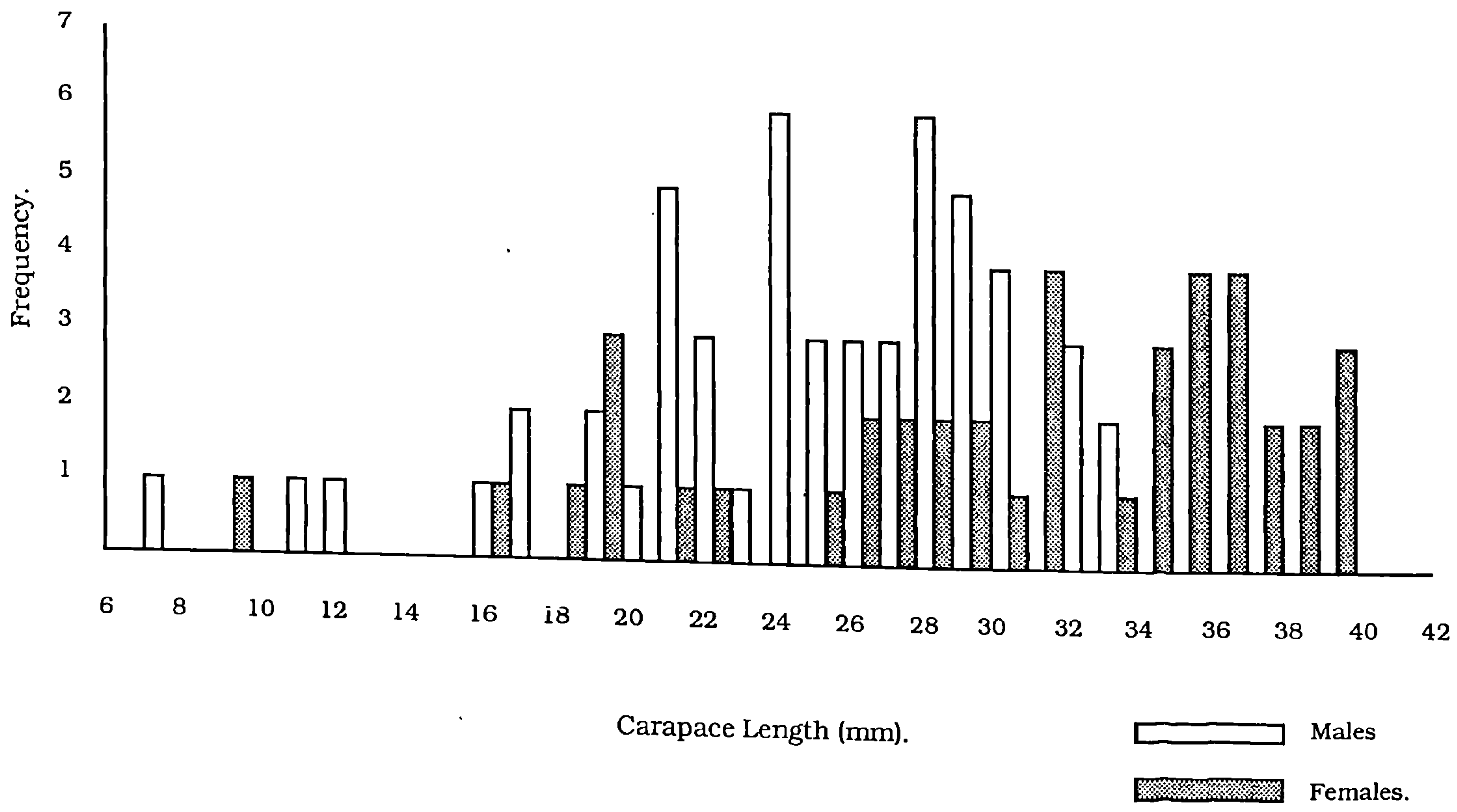
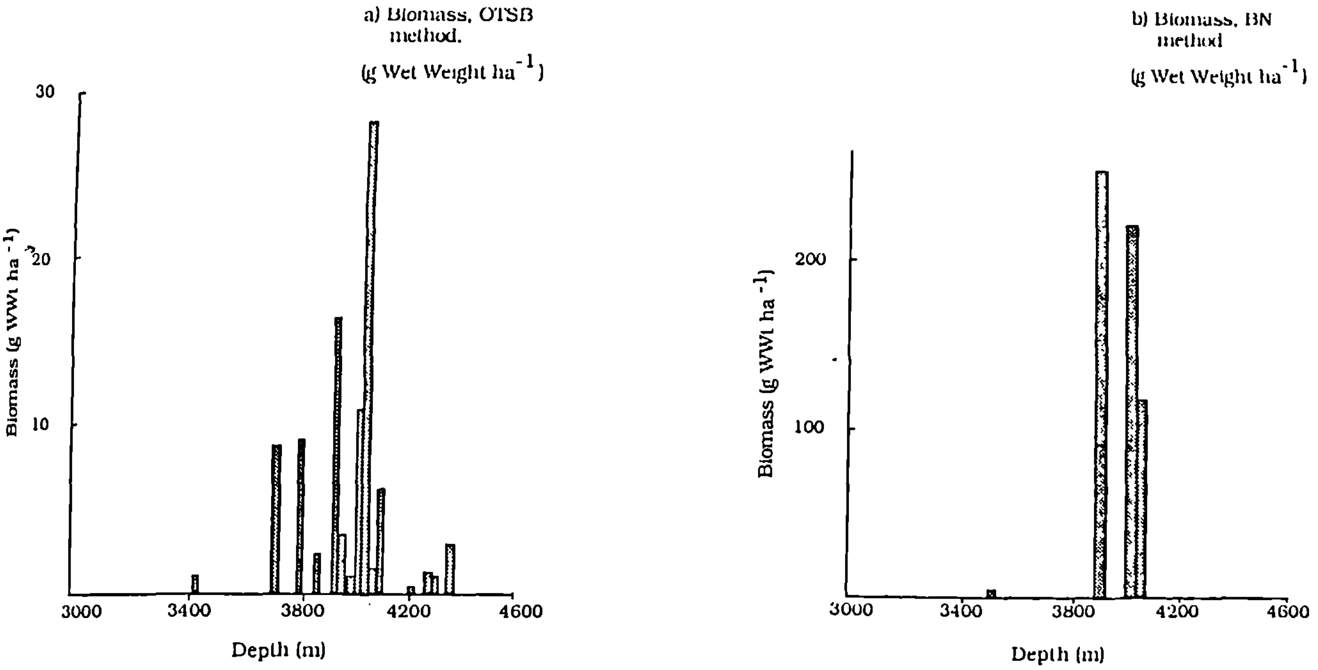
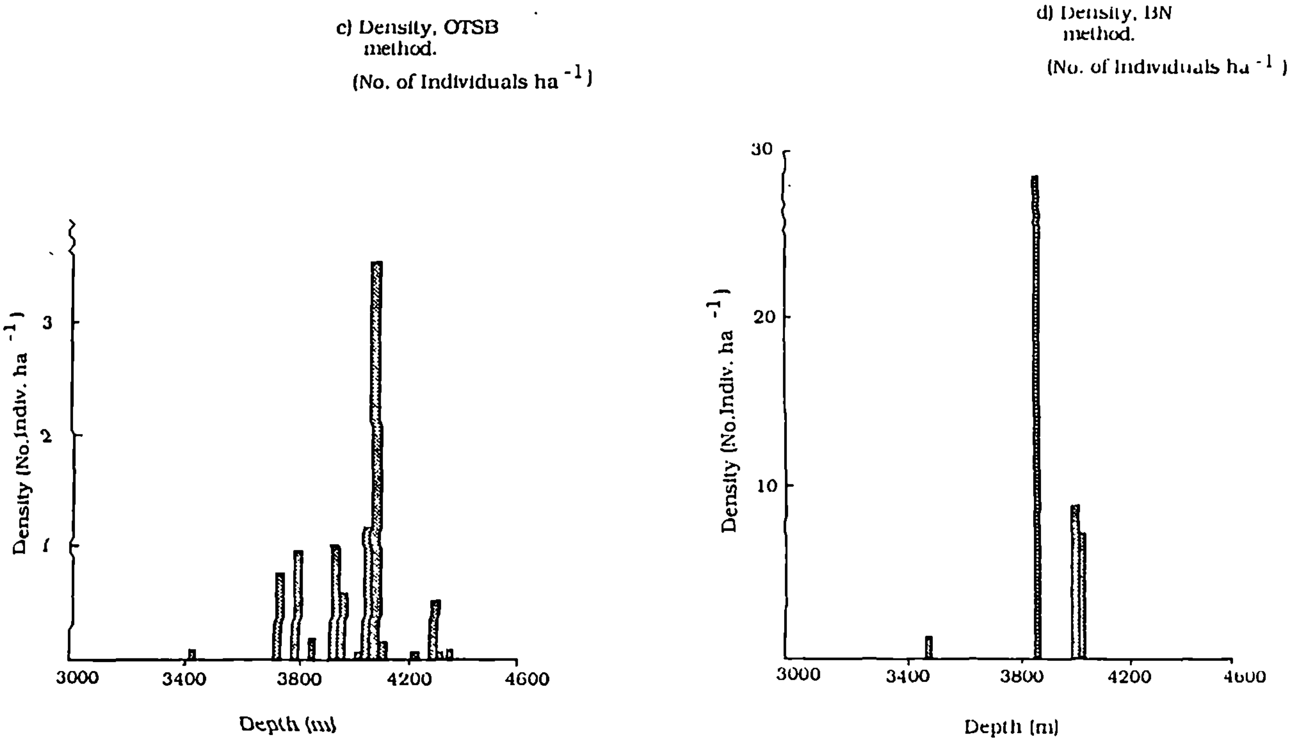


Fig. 7: Length frequency histogram for *Munidopsis antonii*.


a) Biomass, OTSB method. (g Wet Weight ha^{-1})

b) Biomass, BN method (g Wet Weight ha^{-1})


c) Density, OTSB method. (No. of Individuals ha^{-1})

d) Density, BN method. (No. of Individuals ha^{-1})

Fig. 8: Biomass and density for each station where *M. antonii* was taken.

density around 4000 m, the figures displayed by these peaks representing the highest biomass and density of any *Munidopsis* species in the study area, despite *M. antonii* occurring with three other species (see above).

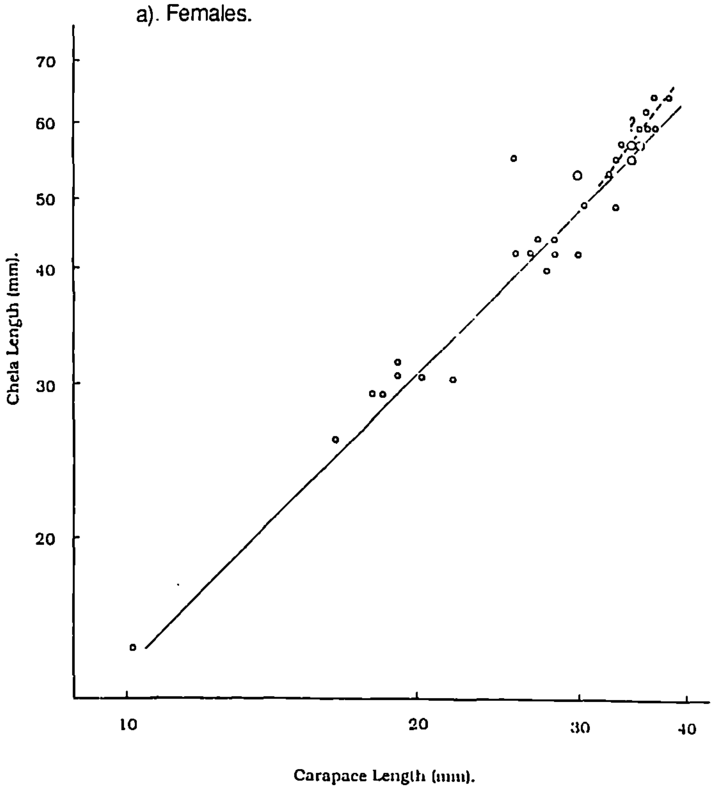
When these biomass and density maxima are compared with those for other shallower decapod species, *Munidopsis* biomass and density are far lower than *Munida sarsi,* but more comparable to the deeper *Munida tenuimana,* and the density to that of the large crab *Geryon trispinosus.*

Species.	Station.	Mean Depth (m)	Max. Biomass ($g.WWt.ha^{-1}$)	Max. Density ($No.Ind.ha^{-1}$)	Chapter.
Munidopsis antonii	10115#1	3925	247	29	6
Total *Munidopsis* spp.	10114#1	4050	269	as above	6
Munida tenuimana	51420#3	1296	64	51	3
Munida sarsi	52404#4	450	10536	3843	3
Geryon trispinosus	50608#2	510	9663	75	5

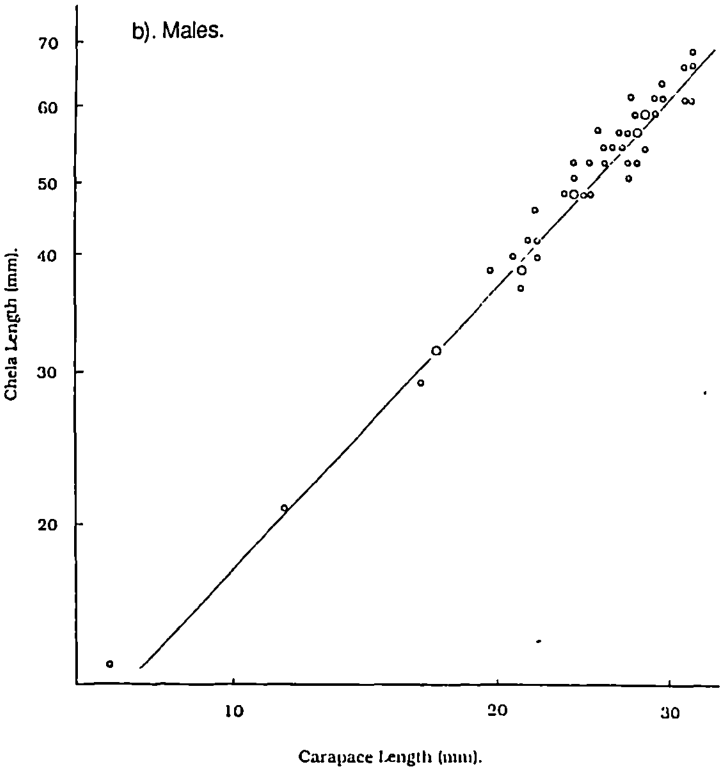
Relative Growth.

The large sample size of *M. antonii* allowed regression lines to be constructed. Ln.ChL against Ln.CL was plotted for both males and females (Fig. 9) giving allometric values of 1·05 and 0·87 respectively. There is a possible change in allometric rate for females at around 30 mm CL (Fig. 9a), which would correspond to sexual maturity (see below). However, this is far from clear and is probably an artifact of the sample size.

To investigate chela shape, ChW was plotted against ChL to obtain a relationship between the two (Fig. 10). The slope values obtained were low (≈0·1) for both sexes, confirming the observation from examination that *M. antonii* possesses long thin 'spear-type' chelae.

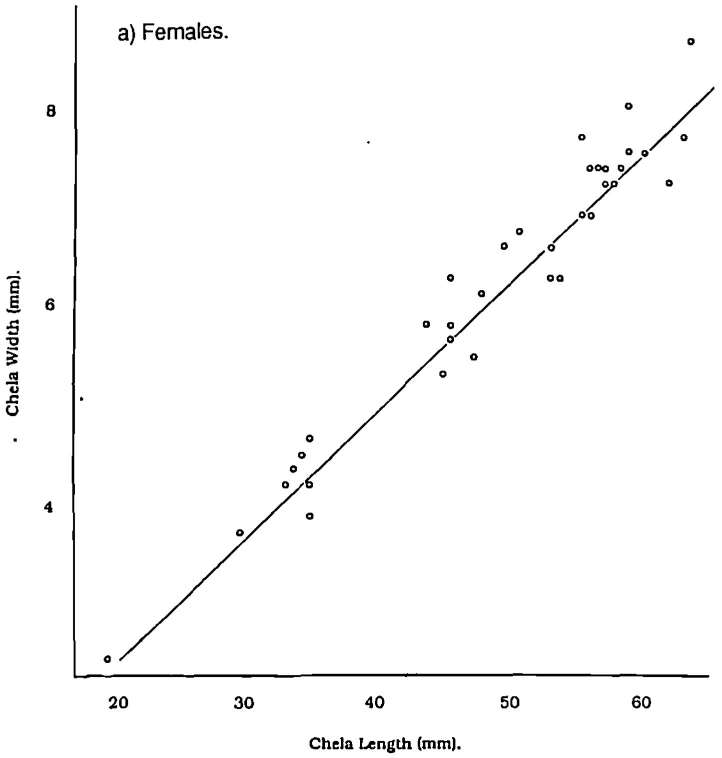


LnChL = 0·866$\overset{\text{Ln}}{\wedge}$CL + 0·950. Correlation = 0·976. R-Squared = 0 952.

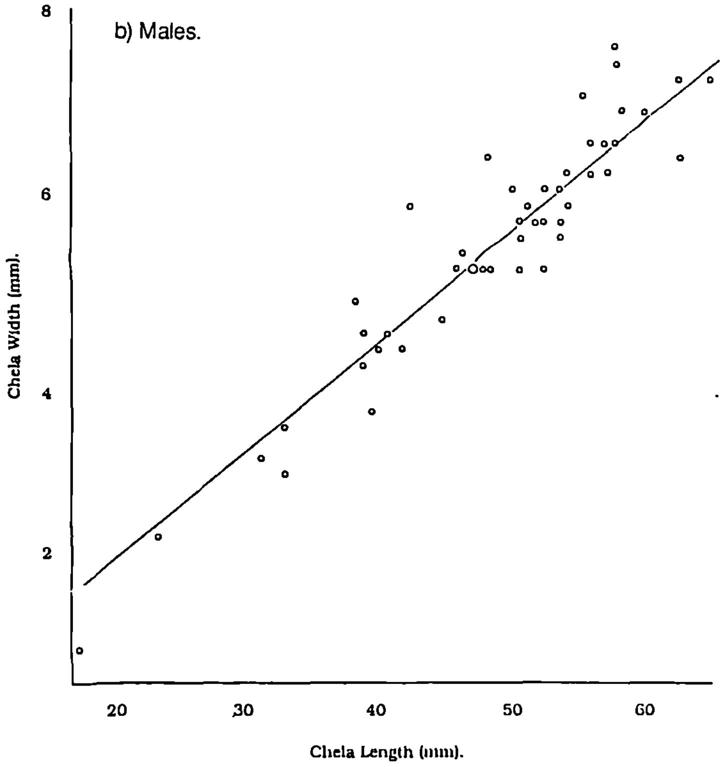


LnChL = 1·052$\overset{\text{Ln}}{\wedge}$CL + 0·469. Correlation = 0·986. R-Squared = 0·973.

Fig. 9: LnChL against LnCL regression plots for both sexes of *M. antonii.*



ChW = 0·125 ChL + 0·003. Correlation = 0·974. R-Squared = 0·950.



ChW = 0·107 ChL + 0·305. Correlation = 0·946. R-Squared = 0 894.

Fig. 10: ChW against ChL regression plots for both sexes of *M. antonii.*

Reproduction.

12 females were ovigerous (46·2 % of mature individuals), caught mainly between August and November (Fig. 4). The number and size of eggs carried is outlined in Table 4, the maximum egg number being 110. This was the largest number of eggs observed on any of the *Munidopsis* studied.

The smallest ovigerous female was 31·7 mm CL, while the smallest female bearing mature Type 3 pleopods (Fig. 5) was 29·5 mm. Sexual maturity would therefore appear to occur by a size of 30 mm (corresponding to the possible shift in chela allometry outlined above). The possibility of a seasonal egg laying and hatching cycle suggested by the distribution of the ovigerous females over the year was investigated by studying the ovary condition of mature females. However, ovary development showed no pattern over the year.

Parasites.

No parasites were found on any of the *M. antonii* examined. Lützen (1985) reported a female *M. antonii* infested with the rhizocephalan (Crustacea: Cirripedia) *Cyphosaccus jensi*, while Bourdon (1972) described an infestation with the bopyrid isopod *Pleurocryptella wolffi*.

Munidopsis aries (A. Milne-Edwards 1880) (Fig. 11).

Orophorynchus aries	A. Milne-Edwards 1880: p. 58. A. Milne-Edwards & Bouvier 1894: p. 209, 1897: p. 111, 1900: p. 340. Faxon 1895: p. 82.
Munidopsis aries	Benedict 1902: p. 316. Doflein & Balss 1913, pl. 75. Chace 1942: p. 50. Pequegnat & Pequegnat 1971: p. 21. Wenner 1982: p. 367. Gore 1983: p. 203.
Munidopsis sundi	Sivertsen & Holthuis 1956: p. 44. Pequegnat & Pequegnat 1971: p. 22. Wenner 1982: p. 271.

Occurrence.

9638#2, 1M. 51413, 1F. 51610#1, 1M. 51804, 1F 1M.

Distribution.

Geographic: Deep Atlantic water, including Azores (Sivertsen & Holthuis, 1956), Gulf of Mexico (A. Milne-Edwards, 1880; Pequegnat & Pequegnat, 1971), Caribbean Sea and West Indies (Chace, 1942; Gore, 1983). East Pacific analog *M. albatrossae* (see Gore, 1983 for details).

Bathymetric: 2615 m (Sivertsen & Holthuis, 1956: Azores) to 4151 m (Pequegnat & Pequegnat, 1971: Colombia Basin). In this study, the possible depth range of *M. aries* was 2770-4104 m, with a calculated range of 2940-4043 m.

Associates.

M. aries occurred with *M. antonii* (Stations 9638#2, 51610#1), *M. bermudezi* (Stations 51413, 51804), *M. crassa* (Station 9638#2) and *M. parfaiti* (Station 9638#2).

Population Structure.

Size Distribution: *M. aries* was represented by only five individuals (60:40 M:F) in the Porcupine Sea-bight samples, ranging in size from 16·3 mm to two females over 70 mm (Table 2). These two specimens were by far the largest *Munidopsis* caught during this study, but are smaller than specimens reported by Gore (1983) and Sivertsen & Holthuis (1956) (as *M. sundi*). As suggested by Sivertsen & Holthuis, this species may well be the largest galatheid known. As with these previous studies, the largest *M. aries* caught were female.

Biomass and Density: Density (No.Ind.ha^{-1}) and biomass (g.WWt.ha^{-1}) figures were calculated for the *M. aries* samples (Table 3, Fig. 12). The biomass figure (Fig. 12a) shows extremes in values, due to the huge size differences of the individuals within the small sample

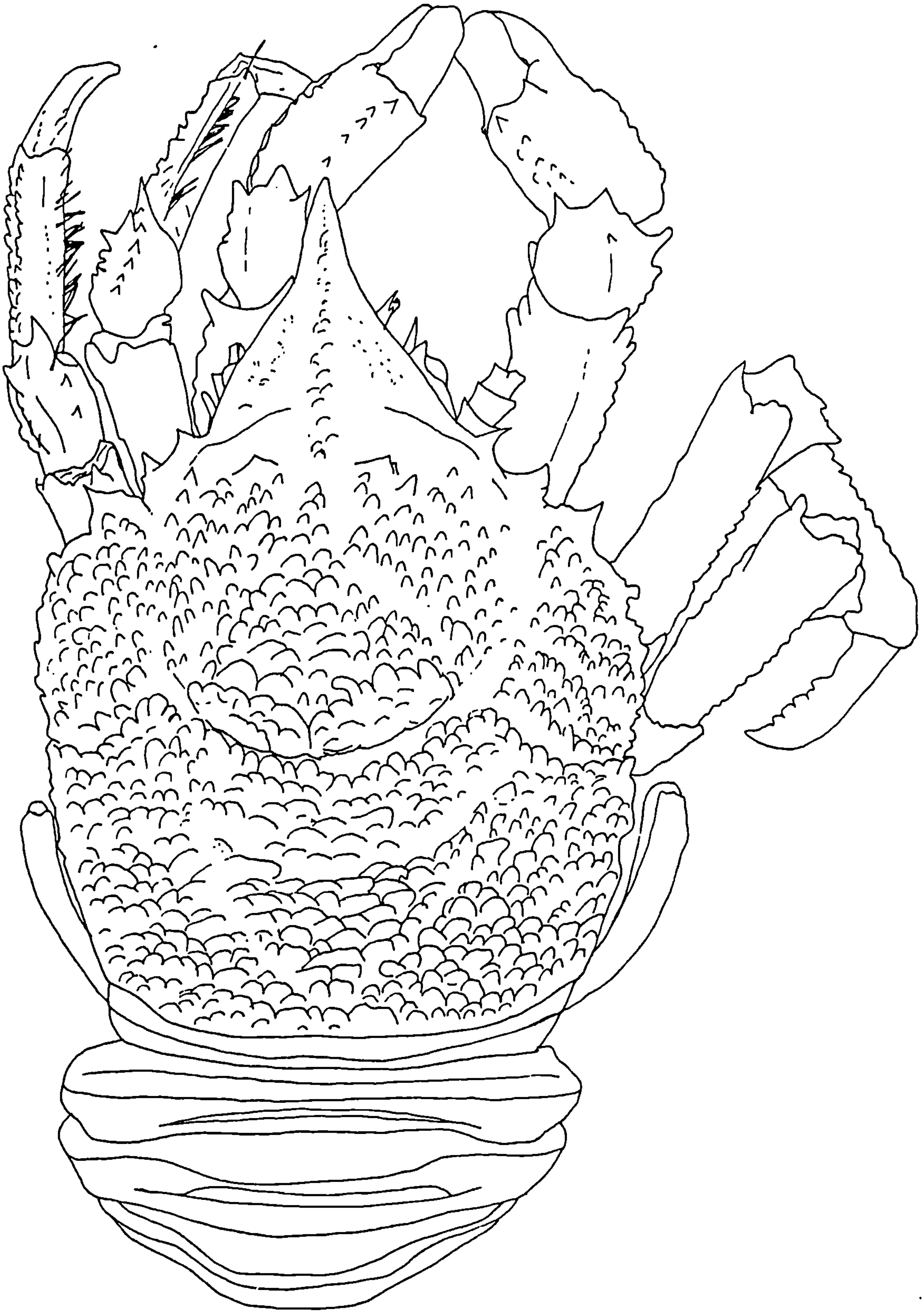


Fig. 11: *Munidopsis aries*. Male, CL 19·5 mm.

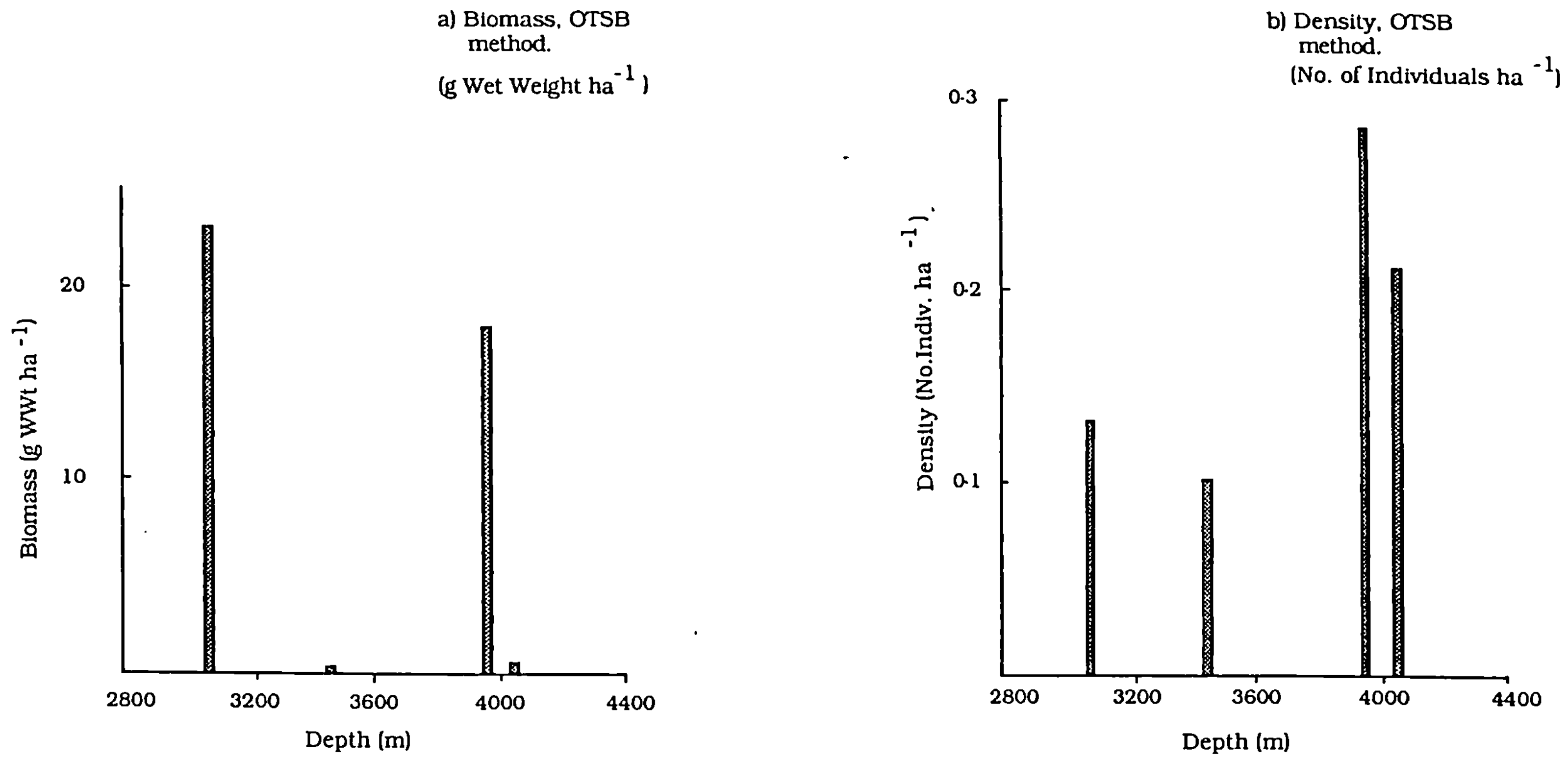


Fig. 12: Biomass and density for each station where *M. aries* was taken.

size. The density graph shows less variation, with the highest density occurring around 4000 m.

Relative Growth.

The sample size for *M. aries* was deemed too small to construct meaningful growth curves. However, chela study showed that *M. aries* possesses short, broad 'spade-type' chelae.

Reproduction.

One female (CL 71·3) was ovigerous (Table 4), carrying over 100 large red eggs. This was also the smallest female with mature pleopods. Gore (1983) lists an immature female of CL 26·7 (including rostrum), so maturity occurs somewhere between this size and 71·3 mm.

Parasites.

No parasites were found on any of the *M. aries* examined and none have as yet been reported.

Munidopsis bairdii (Smith 1884) (Fig. 13).

Galacantha bairdii	Smith 1884: p. 356.
Munidopsis bairdii	Smith 1886: p. 649. Faxon, 1895. Ambler 1980: p. 18. Wenner 1982: p. 367.
Munidopsis chacei	Kensley 1968: p. 288.

Occurrence.

50906, 1F. 51110#3, 1M.

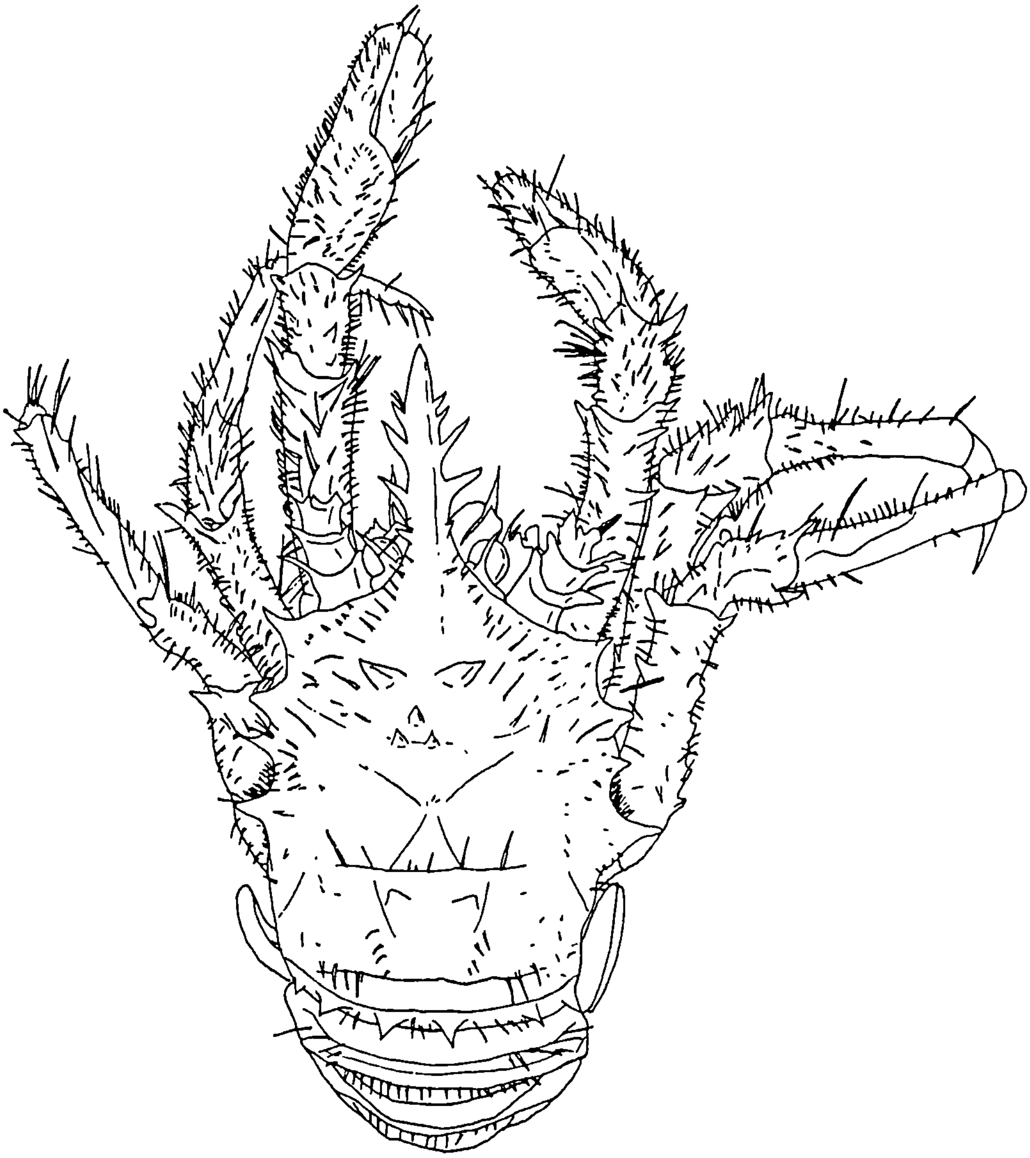


Fig. 13: *Munidopsis bairdii.* Female, CL 10·9 mm.

Distribution.

Geographic: Atlantic and Pacific oceans including Virginia (Smith, 1884), S. Africa (Kensley, 1968), Middle Atlantic Bight and New England (Wenner, 1982), Panama (Faxon, 1895), Cape Sable to Cape May (Smith, 1886), off Oregon (Ambler, 1980).

Bathymetric: 1919 m (Wenner, 1982: New England) to 2940 m (Ambler, 1980: Oregon). In this study, the possible depth range of *M. bairdii* was 2585-2800 m, with a calculated range of 2705-2785 m.

Associates.

M. bairdii occurred with *M. rostrata* at the two stations where it was caught (50906, 51110#3).

Population Structure.

M. bairdii is the rarest species found in the Porcupine Sea-bight samples, represented by only two specimens - an immature female (CL 10·9 mm) and a just moulted male of 19·0 mm CL. Both are small specimens compared to other studies where *M. bairdii* is more common. Ambler (1980) found females up to 45 mm CL (including rostrum) and males up to 48 mm. Wenner's (1982) maxima were males 33 mm and females 35 mm CL.

The sample of two was considered too small to undertake meaningful biomass or relative growth analyses.

Reproduction.

The female caught was immature and possessed Type 1 pleopods (Fig. 5). Wenner (1982) reports the smallest ovigerous females measured being 25 mm CL, whilst in Ambler's (1980) study this value was 43 mm CL (including rostrum).

Parasites.

No parasites were found on either of the *M. bairdii* studied and none have thus far been reported.

Munidopsis bermudezi Chace 1939 (Fig. 14).

Munidopsis bermudezi	Chace 1939: p. 46, 1942: p. 83. Sivertsen & Holthuis 1956: p. 44. Pequegnat & Pequegnat 1970: p. 139, 1971: p. 22. Mayo 1974: p. 83. Türkay 1975: p. 68. Laird *et al.* 1975: p.462. Wenner 1982: p. 367. Gore 1983: p. 204. Lützen 1985: p. 111.

Occurrence.

50712, 1M. 50814, 1F 2M. 51413, 2F 1M. 51804, 1M. + 9041, 11F 4M (Not in Sea-bight area).

Distribution.

Geographic: Widely distributed in Atlantic ocean, including Azores (Sivertsen & Holthuis, 1956), Gulf of Mexico (Pequegnat & Pequegnat, 1970, 1971), Caribbean (Chace, 1942; Gore, 1983), Middle Atlantic Bight (Wenner, 1982), NW Atlantic (Laird *et al.*, 1976). E Pacific analog *M. cascadia* (Ambler, 1980).

Bathymetric: 2434 m (Chace, 1942: Cuba) to 5180 m (Mayo, 1974: Virgin Islands). In this study, the possible depth range of *M. bermudezi* was 2383-3180 m, with a calculated range of 2383-3115 m, so increasing the reported bathymetric range of the species.

Associates.

M. bermudezi occurred with *M. aries* (Stations 51413, 51804) and *M. rostrata* (Stations

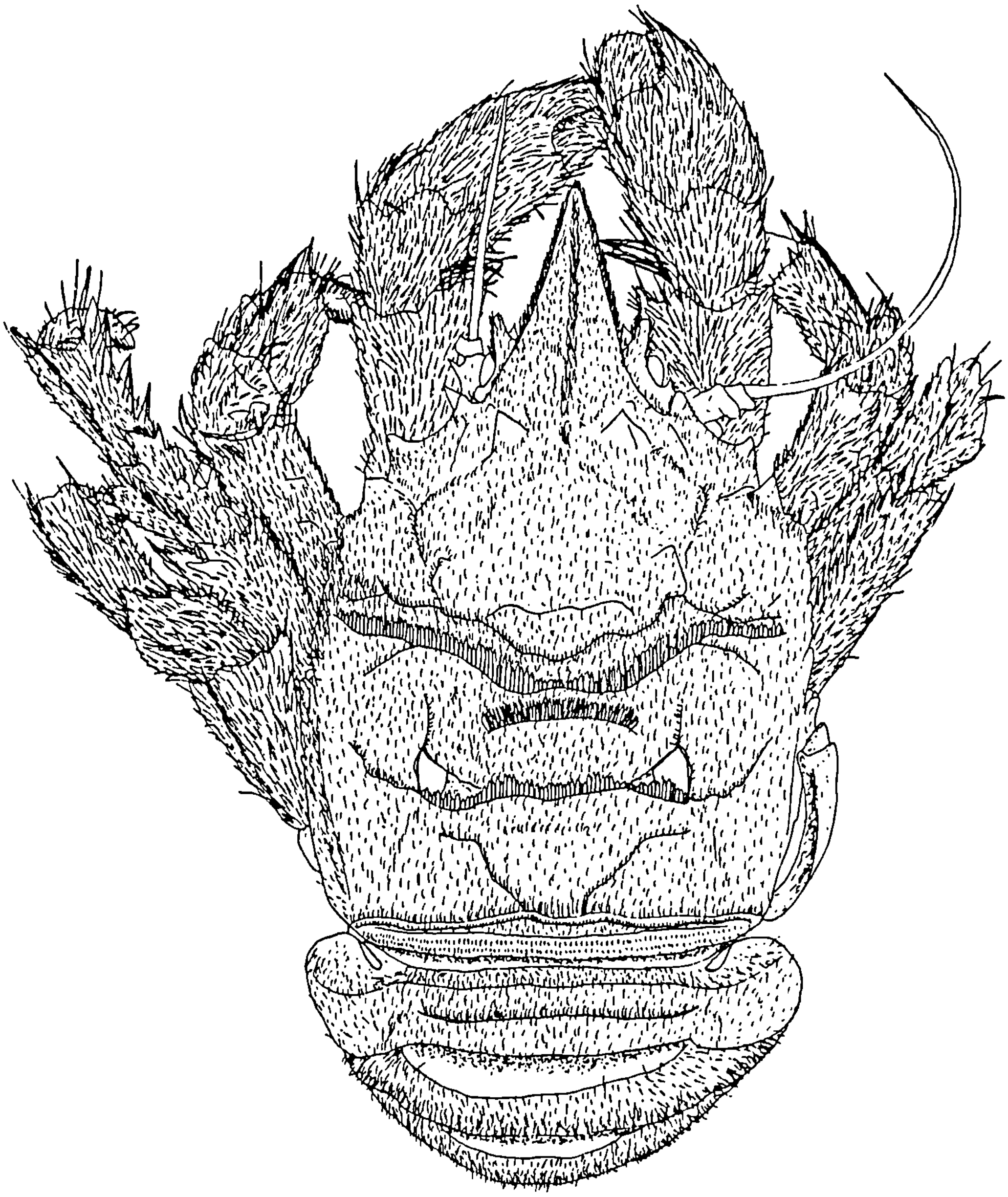


Fig. 14: *Munidopsis bermudezi.* Male, CL 15·0 mm.

9041, 50712, 50814).

Population Structure.

Size Distribution: *M. bermudezi* was represented by 23 specimens (43:57 M:F) in the samples, though only eight individuals came from the Porcupine Sea-bight area. The CL range was 14·2-35·3 mm (Table 2, Fig. 15). Unlike most of the other *Munidopsis* species, the largest *M. bermudezi* were male. *M. bermudezi* has been fairly widely collected, but generally not in particularly large numbers, other total catches include: 1 (Wenner, 1982), 2 (Laird *et al.*, 1976), 2 (Chace, 1939), 1 (Sivertsen & Holthuis, 1956) and 1 (Pequegnat & Pequegnat, 1971). However, Gore (1983) has collected the largest number of specimens, with a total of 47, including ten in one sample. Therefore, sample 9041, with 15 specimens, is the largest single haul of this species so far. This was taken south of the Porcupine Sea-bight off the coast of northern Portugal.

Biomass and Density: Biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) data were calculated for the Porcupine Sea-bight samples of *M. bermudezi* (Table 3, Fig. 16), this species having only been taken using the OTSB. Both biomass and density show peaks at the shallow end of the species' depth range, even though in this region *M. bermudezi* occurs with the comparatively abundant *M. rostrata.*

Relative Growth.

The total sample of *M. bermudezi* was large enough to allow regression lines to be constructed to investigate the relative growth of ChL against CL. Ln.ChL was plotted against Ln.CL for both males and females (Fig. 17), giving allometric values of 1·12 and 0·97 respectively.

To investigate chela shape, ChW was plotted against ChL to obtain a relationship between the two (Fig. 18). The gradient values obtained were high (≈0·2) for both sexes,

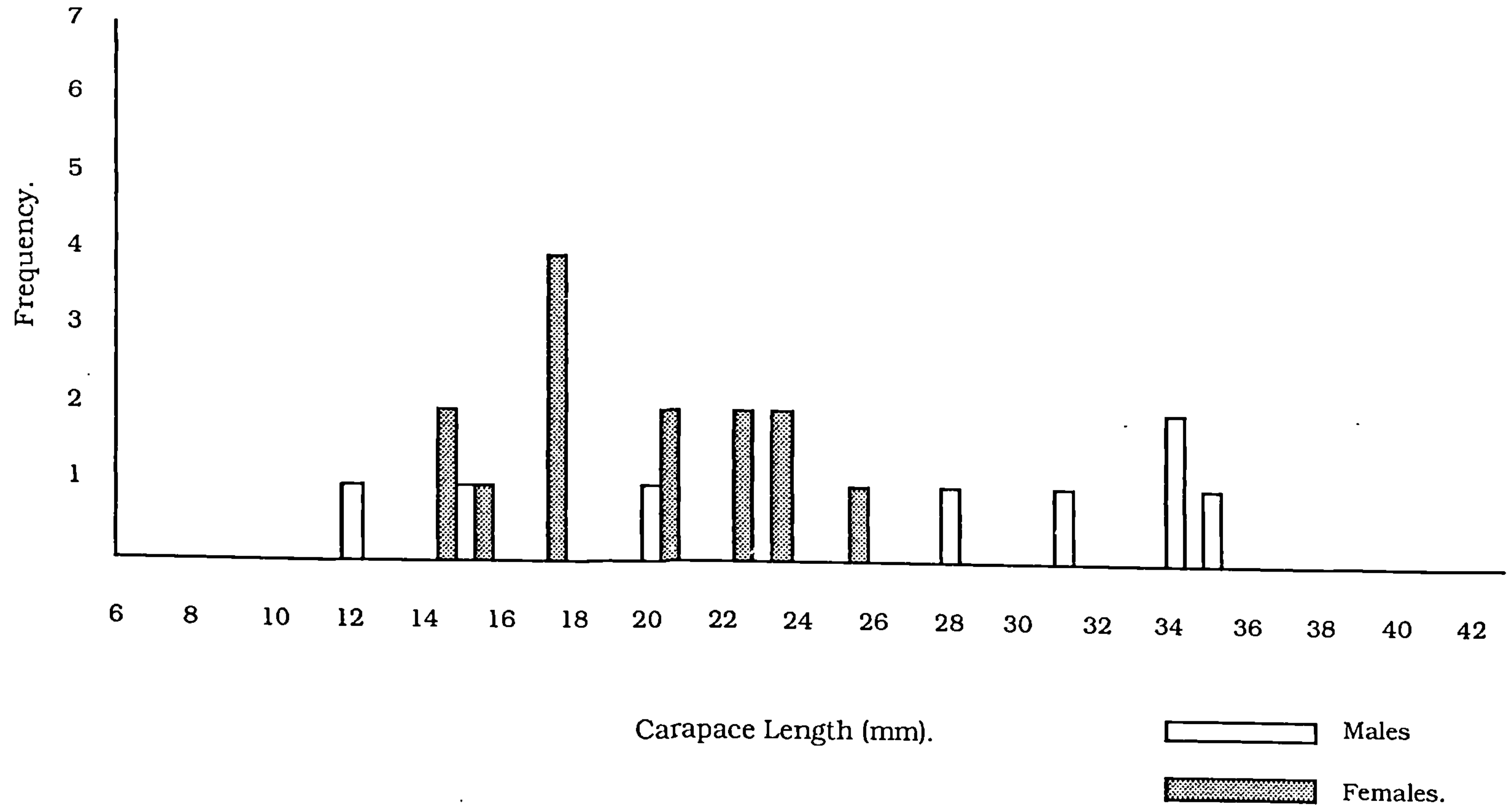
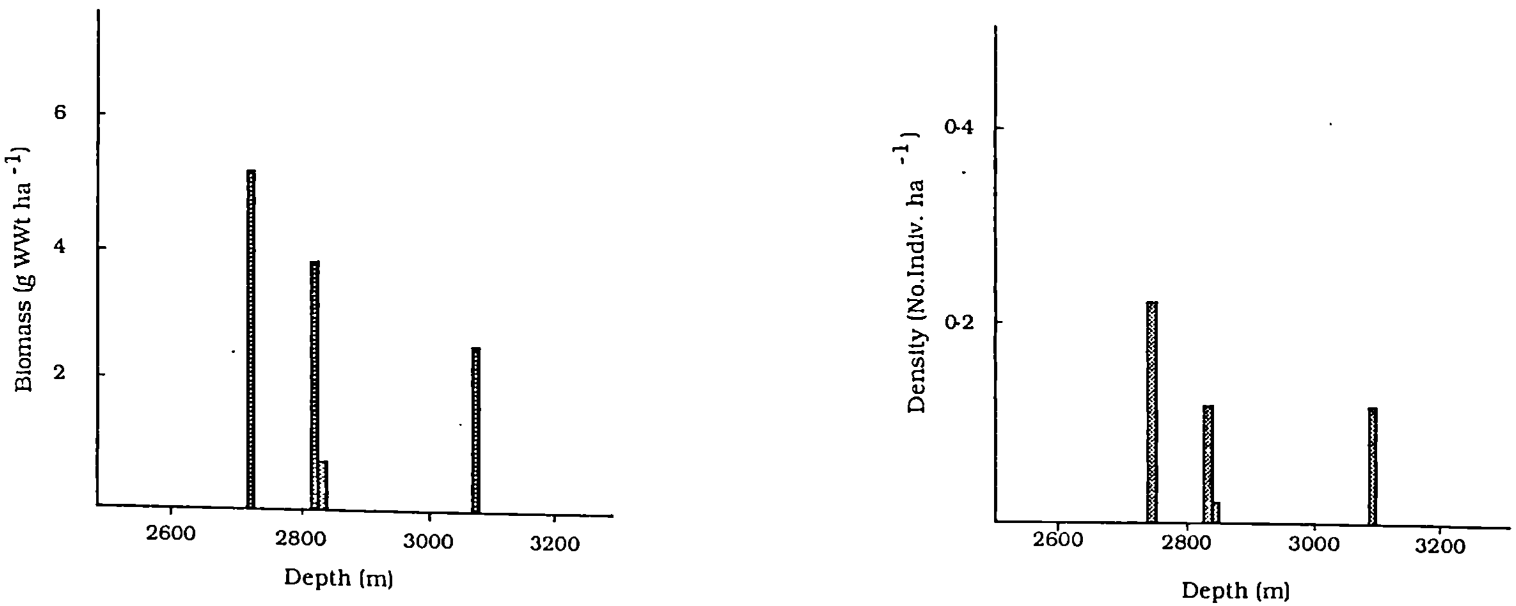


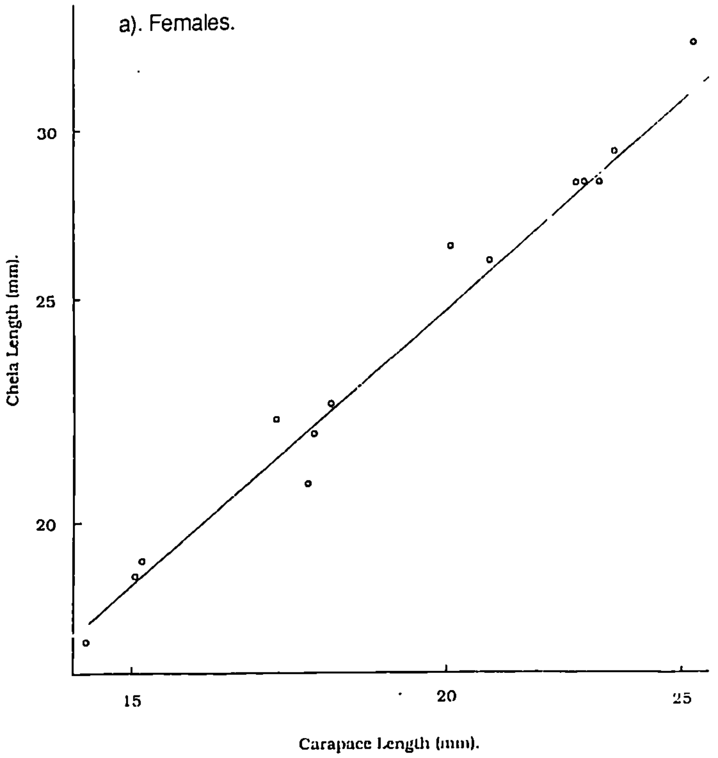
Fig. 15: Length frequency histogram for *Munidopsis bermudezi.*



a) Biomass, OTSB method. (g Wet Weight ha $^{-1}$)

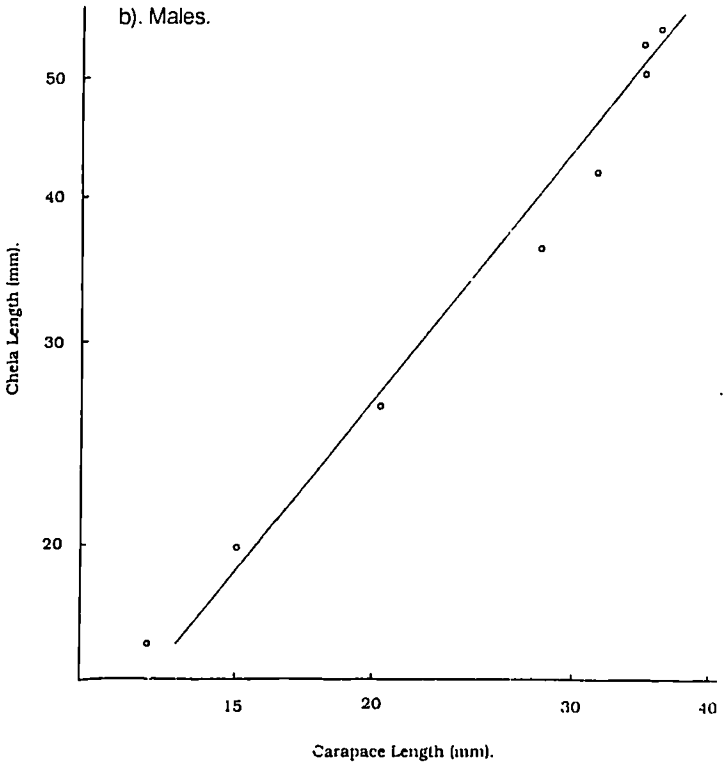
b) Density, OTSB method. (No. of Individuals ha $^{-1}$)

Fig. 16: Biomass and density for each station where *M. bermudezi* was taken.



Ln

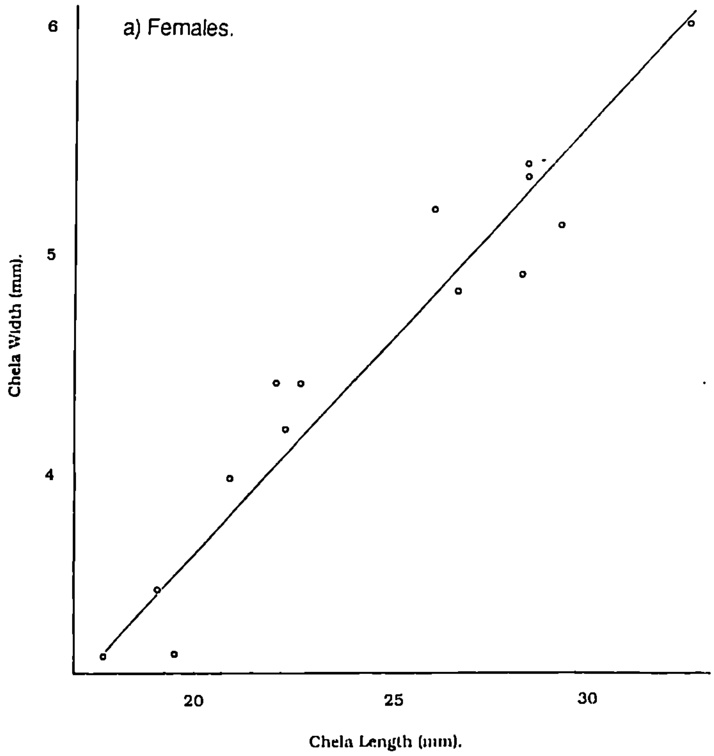
LnChL = 0·974 CL + 0·306. Correlation = 0·988. R-Squared = 0·977.



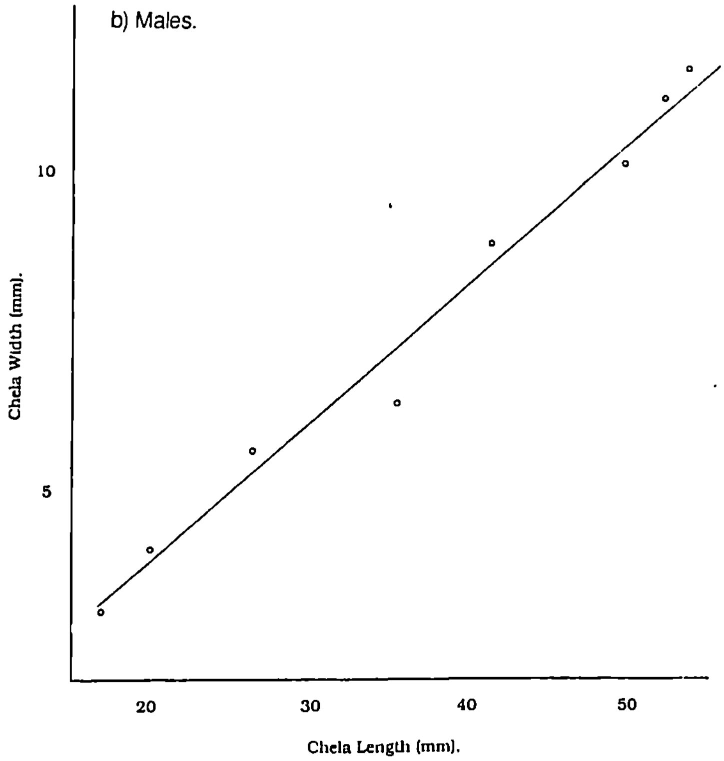
Ln

LnChL = 1·117 CL - 0·054. Correlation = 0·991. R-Squared = 0·981.

Fig. 17: LnChL against LnCL regression plots for both sexes of *M. bermudezi*.



ChW = 0·182 ChL + 0·091. Correlation = 0·961. R-Squared = 0·924.



ChW = 0·218 ChL - 0·539. Correlation = 0·992. R-Squared = 0·984.

Fig. 18: ChW against ChL regression plots for both sexes of *M. bermudezi*.

confirming the appearance from examination of broad 'spade-like' chelae.

Reproduction.

Four females were found to be ovigerous (44·4 % of mature females), three from sample 9041, found in the months of March and August (Fig. 4). The number and size of eggs carried is outlined in Table 4, the maximum number being 48.

The smallest ovigerous female was 17·6 mm CL. This was also the smallest individual bearing mature Type 3 pleopods (Fig. D), so sexual maturity occurs by a size of 17 mm CL.

Parasites.

One male *M. bermudezi* was infested with two rhizocephalan externae emerging from abdominal segments 3 and 4. These were identified as an undescribed species of the genus *Galatheascus* (J. Lützen, pers. comm.). The male pleopods were degenerate, pairs 3-5 showing feminisation towards the mature, setose female form. This form was similar to the Type 3 infested male pleopod described by Attrill (in press) for *Munida sarsi.*

Other parasitised *M. bermudezi* individuals have been reported. Mayo (1974) describes a large female heavily infested with an undescribed species of the rhizocephalan genus *Cyphosaccus*. Lützen (1985) also lists a *Cyphosaccus* sp. on *M. bermudezi.* Gore (1983) reports a female with a "large hydroid-like growth" on the abdomen, together with an anatomically neuter individual that he suggests could be the latent effects of 'parasitic castration'.

Munidopsis crassa Smith 1885 (Fig. 19).

Munidopsis crassa Smith 1885: p. 494, 1886: p. 645. A. Milne-Edwards & Bouvier 1894: p. 275. Benedict 1902: p. 318. Doflein & Balss 1913: p. 176. Bouvier 1922:

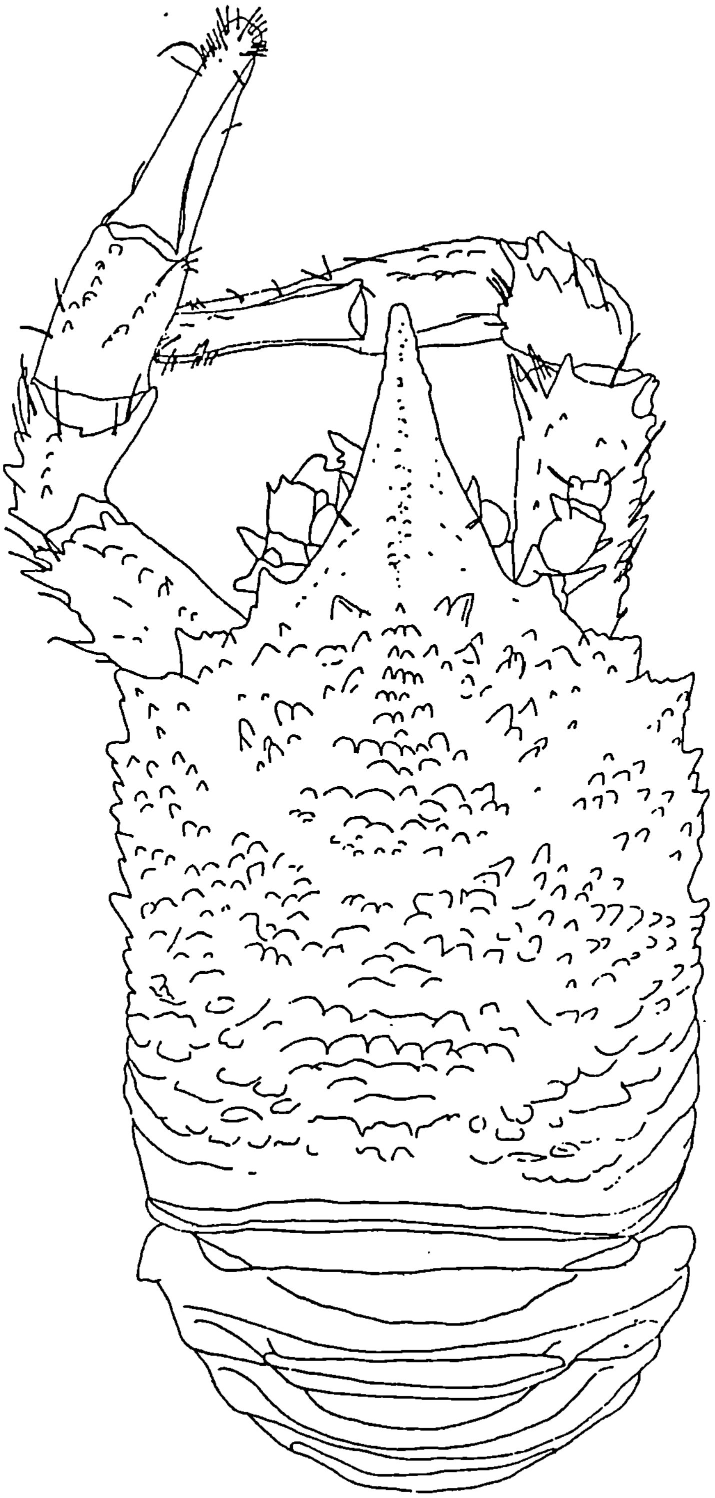


Fig. 19: *Munidopsis crassa*. Female, CL 20·3 mm.

p. 47. Chace 1942: p. 73. Gordon 1955: p. 237. Sivertsen & Holthuis 1956: p. 46. Zariquiey Alvarez 1968: p. 269. Miyake & Baba 1970: p. 89. Pequegnat & Pequegnat 1970: p. 139, 1971: p. 18. Mayo 1974: p. 114. Türkay 1975: p. 67. Wenner 1982: p. 367. Gore 1983: p. 206. Lützen 1985: p. 111. Williams & Turner 1986: p. 618.

Occurrence.

9132#5, 1F. 9638#2, 1M.9756#5, 1F. 50514, 1F. 50515, 2F. 50711, 1M. 50811, 3F 1M. 50910, 4F. 51414#1, 1F. 51608#1, 1M.

Distribution.

Geographic: Widely distributed over Atlantic, including NW Atlantic (Smith, 1885), Azores (A. Milne-Edwards & Bouvier, 1894), Canaries (Gordon, 1955), Biscay (Sivertsen & Holthuis, 1956), Middle N. Atlantic (Bouvier, 1922; Wenner, 1982), Caribbean Sea (Pequegnat & Pequegnat, 1971; Gore, 1983), Iberian deep-sea basin (Türkay, 1975).

Bathymetric: 2532 m (Mayo, 1974: Caribbean) to 5275 m (Türkay, 1975: Iberian deep-sea basin). In this study, the possible depth range of *M. crassa* was 4012-4840 m, with a calculated range of 4020-4840 m.

Associates.

M. crassa occurred with *M. antonii* (Stations 9638#2, 9756#5, 50514, 50811, 50910, 51608#1), *M. parfaiti* (Stations 9638#2, 50514, 50515, 50711, 50811, 50910, 51414#1, 51610#1) and *M. aries* (Station 9638#2).

Population Structure.

Size Distribution: *M. crassa* was represented by 17 specimens (24:76 M:F) in the

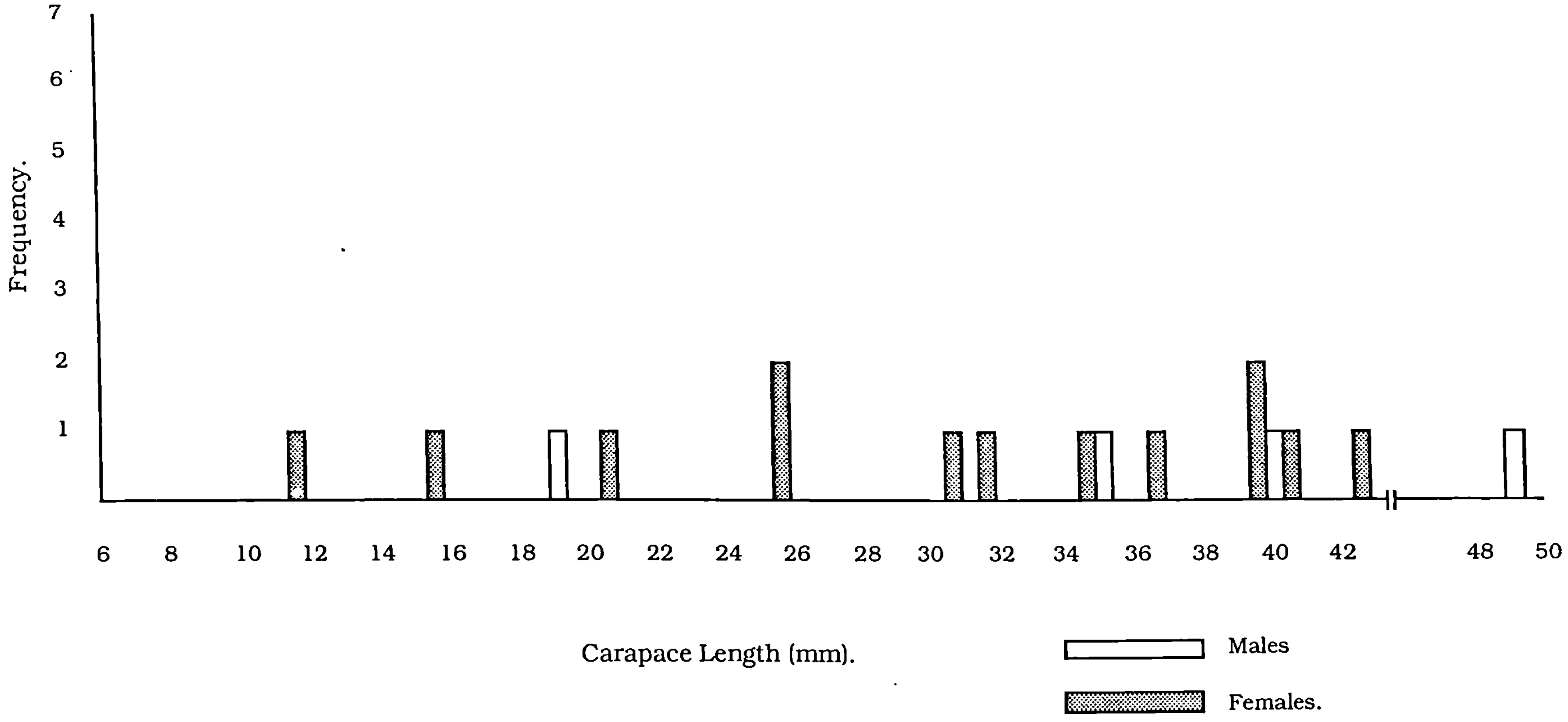
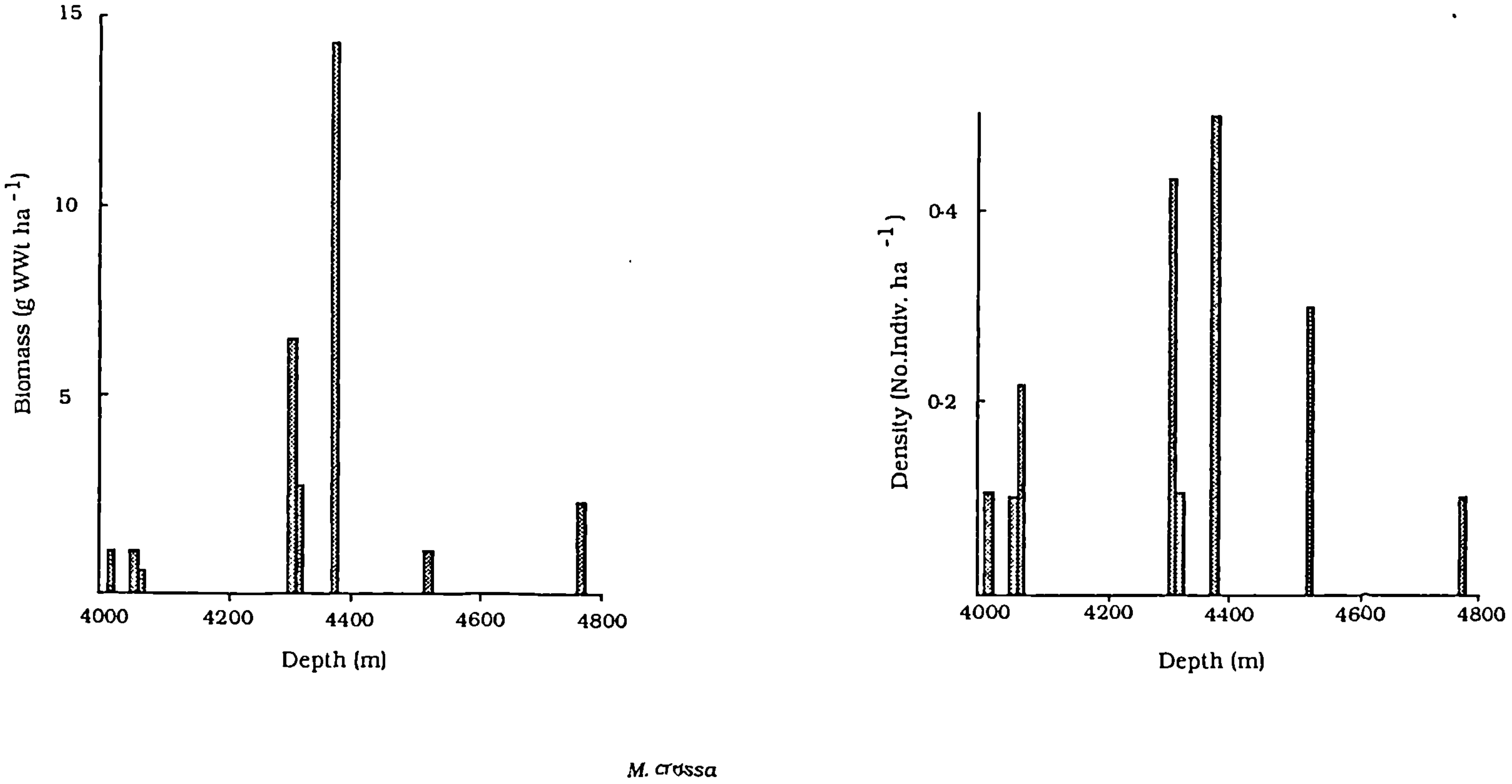


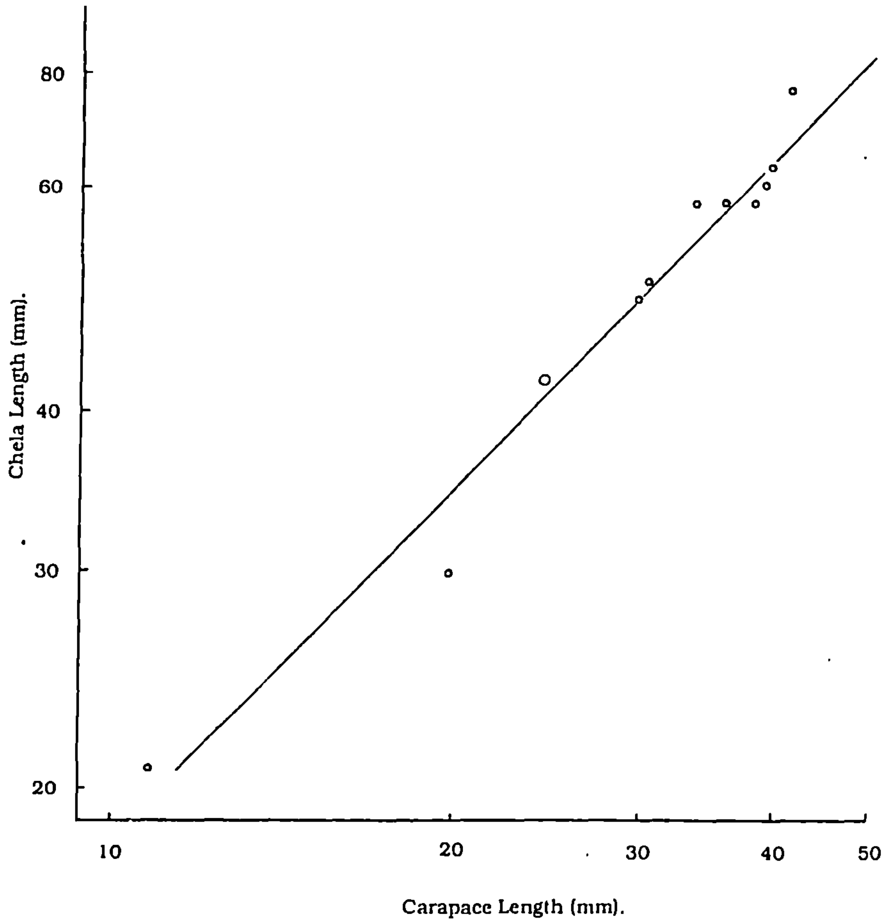
Fig. 20: Length frequency histogram for *Munidopsis crassa*.



a) Biomass, OTSB method. (g Wet Weight ha $^{-1}$)

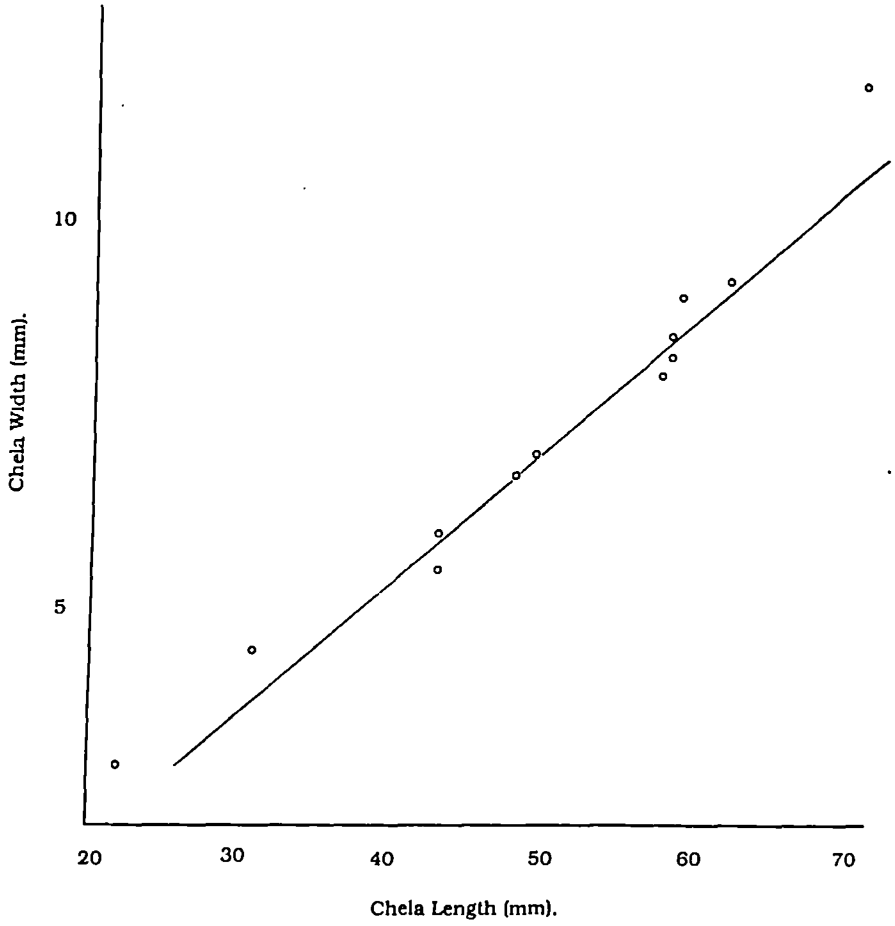
b) Density, OTSB method. (No. of Individuals ha $^{-1}$)

Fig. 21: Biomass and density for each station where *M. crassa* was taken.



LnChL = 0·880 Ln CL + 0·903. Correlation = 0·986. R-Squared = 0·972.

Fig. 22: LnChL against LnCL regression plot for female *M. crassa*.



ChW = 0·163 ChL - 0·887. Correlation = 0·979. R-Squared = 0·959.

Fig. 23: ChW against ChL regression plots for female *M. crassa*.

Porcupine Sea-bight samples. The range of CL was 11·1-49·5 mm (Table 2, Fig. 20), the large male being the largest *M. crassa* reported. Gore's (1983) maximum of 57·1 included the rostrum (the rostral CL (RCL) of the Porcupine Sea-bight specimen was 68·4 mm). Other maxima include: 28 mm CL (Pequegnat & Pequegnat, 1971), 31 mm CL (Williams & Turner, 1986) and 45 mm CL for the holotype (Smith, 1885). Two measurements of total length are given: Gordon (1955) of c.a. 90 mm TL and Sivertsen & Holthuis (1956) of 98 mm TL. The TL of the Porcupine Sea-bight specimen was 122·3 mm.

M. crassa is a widely reported member of the genus, being caught during most studies of the abyssal plain and lower slope region. However, numbers caught have been low, the maximum being eight (Mayo, 1974) until Gore (1983) caught 44 specimens in the Venezuela Basin, including 10 in one haul. This study's total of 17 is therefore the second largest sample of the species.

Biomass and Density: Biomass ($g.WWt.ha^{-1}$) and density ($No.Ind.ha^{-1}$) data were calculated for the samples of *M. crassa* (Table 3, Fig. 21), all of which were taken with the OTSB. Both parameters show a peak between 4300-4400 m, in an area where the species co-habits with *M. antonii* and *M. parfaiti*.

Relative Growth.

To investigate the relationship between ChL and CL, regression lines were constructed. Ln.ChL was plotted against Ln.CL for females (Fig. 22), the sample size for males being too small. An allometric value of 0·88 was obtained.

To investigate chela shape, female ChW was plotted against ChL (Fig. 23), the resulting gradient being 0·16. This falls between the two groups of *Munidopsis* chela type, *M.crassa* possessing fairly broad chelipeds, but the chelae are comparatively longer than 'spade-type' species such as *M. bermudezi* and *M. parfaiti*.

Reproduction.

Only one female *M. crassa* was ovigerous (14·3 % of mature females), caught in November (Fig. 4). This specimen was carrying 32 large eggs (Table 4).

The CL of this specimen was 42·5 mm. However, the smallest female with mature Type 3 pleopods (Fig. 5) was 31·3 mm, suggesting a size of maturity around 30 mm CL. The smallest ovigerous female reported by Gore (1983) was 48·6 mm RCL (≡35·2 mm CL).

Parasites.

No parasites were found on any of the *M. crassa* studies. However, parasites have been recorded on this species. Mayo (1974) found an individual infested with many peltogastrid rhizocephalans of the genus *Cyphosaccus*. Gore's (1983) sample was heavily parasitised, 15 % of specimens having either rhizocephalan or bopyrid isopod parasites, although he does not go into further detail. In addition, one female had "a remarkable isopod parasite (Dajidae?) in the form of a small, sponge-like ball enclosing the distal antennular peduncular and flagellar articles", while another carried "an ?akentrogonid parasite and had the pleura of the second abdominal somite ballooned laterally outward and twisted." Bourdon (1981) reported the bopyrid *Pleurocryptella superba* on *M. crassa*.

Munidopsis curvirostra Whiteaves 1874 (Fig. 24).

Munidopsis curvirostra	Whiteaves 1874: p. 212. Smith 1884: p. 21. Hansen 1908: p. 36. Selbie 1914: p. 84. Sivertsen & Holthuis 1956: p. 47. Squires 1965. Miyake & Baba 1970: p. 94. Brunel 1970. Wenner 1982: p. 368. Williams & Turner 1986: p. 621.
Munidopsis longirostris	A. Milne-Edwards & Bouvier, 1900: p. 314.

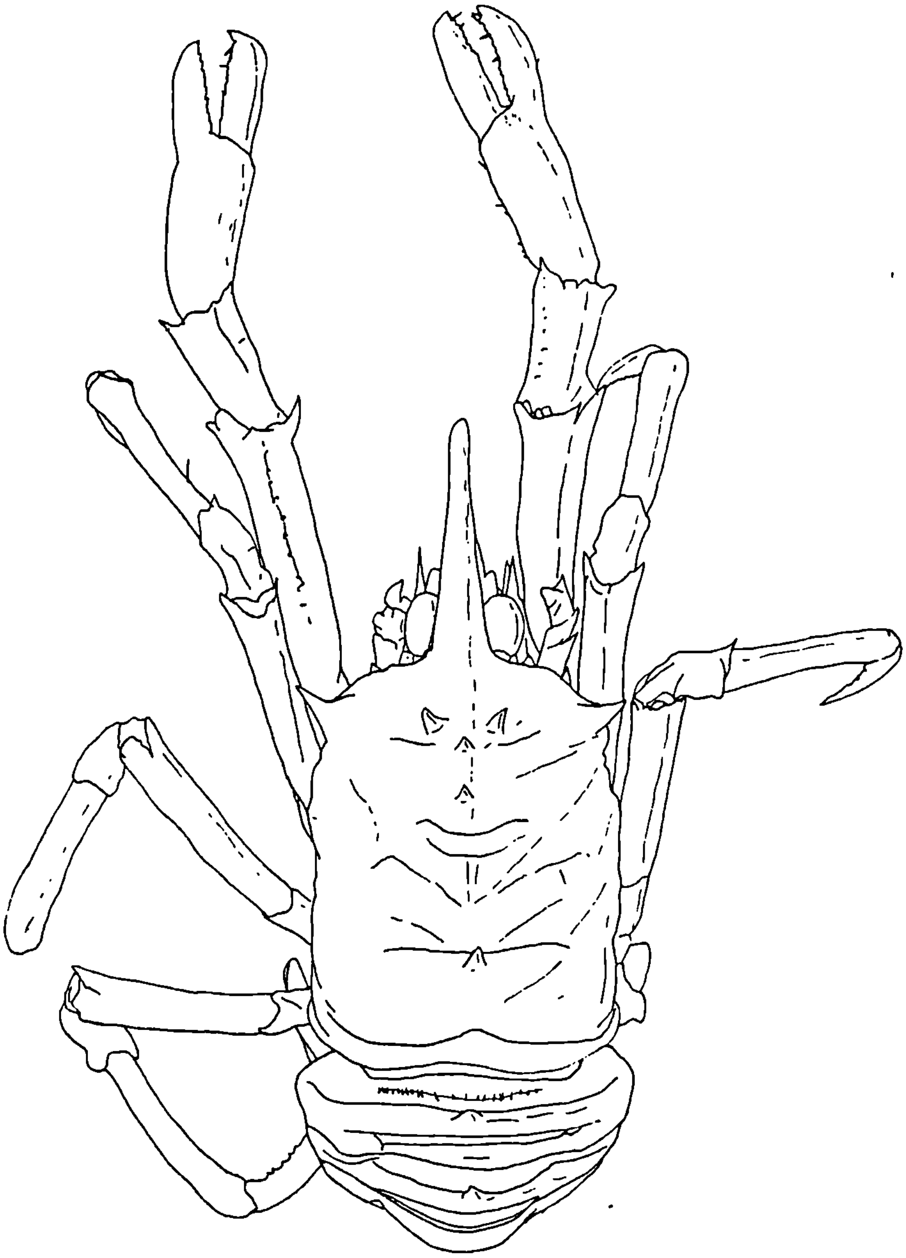


Fig. 24: *Munidopsis curvirostra.* Female, CL 9·8 mm.

Occurrence.

9754#3, 2F 1M. 9774#1, 1F 1M. 9775#3, 2F 5M. 10111#8, 1F. 50303, 1M. 50517, 1F. 50602#2, 4F. 51105#4, 1M. 51201, 1F 1M. 51308, 1F.

Distribution.

Geographic: N. Atlantic, including Newfoundland (A. Milne-Edwards & Bouvier, 1900; Squires, 1965), Davis Straits and Iceland (Hansen, 1908), off Massachusetts (Williams & Turner, 1986), Middle Atlantic Bight (Wenner, 1982), W Africa (Miyake & Baba), British Isles (Selbie, 1914).

Bathymetric: 245 m (Squires, 1965: Newfoundland) to 2212 m (Miyake & Baba, 1970: Morocco). In this study, the possible depth range of *M. curvirostra* was 1484-2019 m, with a calculated range of 1484-2012 m.

Associates.

M. curvirostra was the only representative of the genus at the stations where it occurred.

Population Structure.

Size Distribution: *M. curvirostra* was represented by 23 individuals (43:57 M:F) in the Porcupine Sea-bight samples. Together with *M. serricornis, M. curvirostra* is very different from the other *Munidopsis* species in the study in respect to the generally small size and size of maturity. The range of CL was only 4·3-9·9 mm (Table 2, Fig. 25). As can be seen, the females were generally larger than the males. *M. curvirostra,* perhaps due to its shallow depth, has been collected fairly widely in the N Atlantic, occasionally in some numbers. Wenner (1982) caught 36, Hansen (1908) a total of 101, Sivertsen & Holthuis (1956) 2 and Williams & Turner (1986) a single specimen. The largest specimens found in these studies were 15 mm CL (Hansen, 1908; Wenner, 1982).

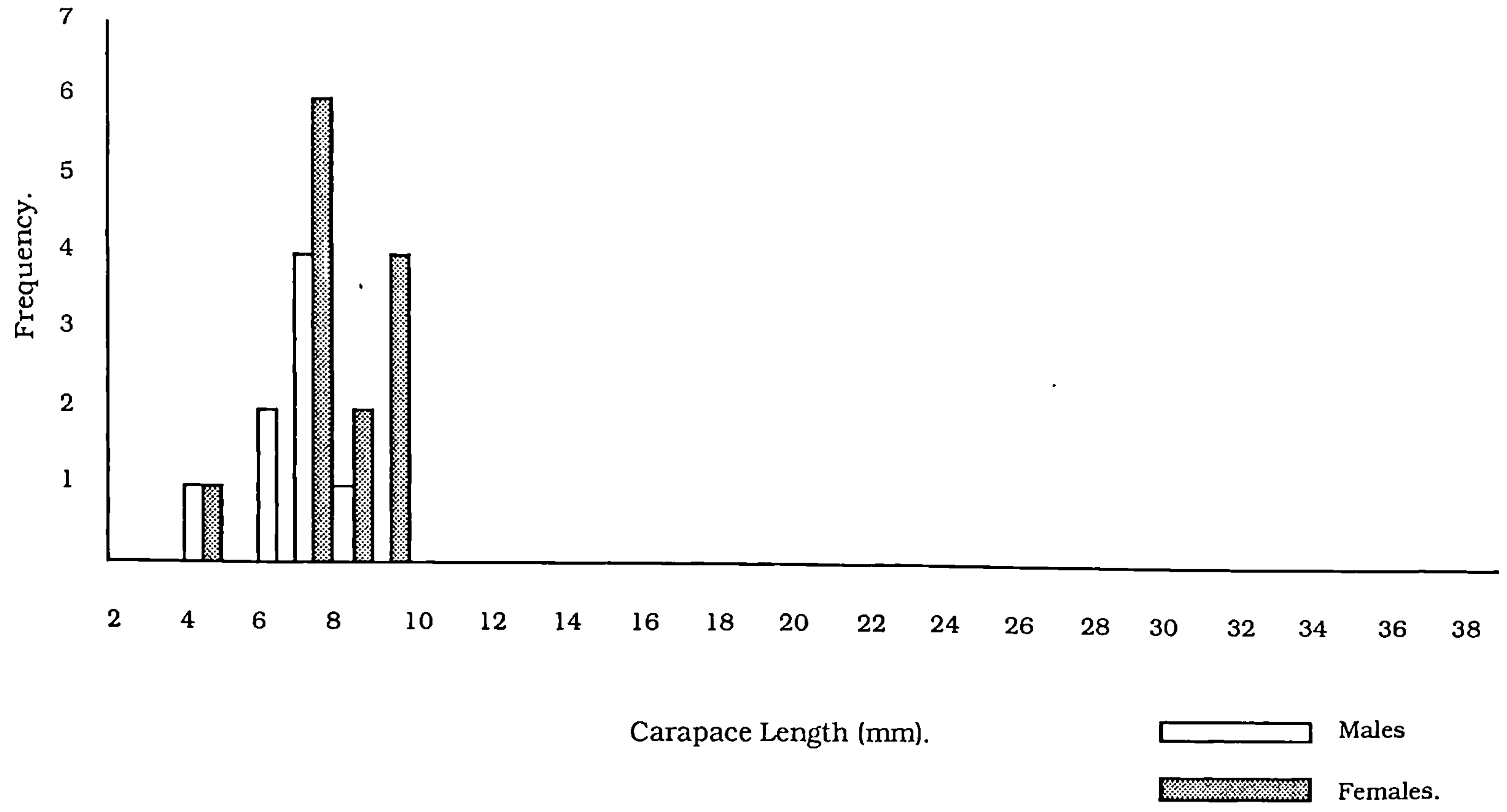


Fig. 25: Length frequency histogram for *Munidopsis curvirostra.*

Biomass and Density: Biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) figures were calculated for the samples of *M. curvirostra* (Table 3, Fig. 26), for both BN and OTSB methods. There is no obvious peak in *M. curvirostra* abundance, in fact the density figures show a high degree of homogeneity across the depth range, particularly for the BN samples at a level around 6 Ind.ha^{-1}. The low biomass figures highlight the small size of the species, this not being counteracted by a proportionally higher density - the density figures are comparable with other *Munidopsis* species.

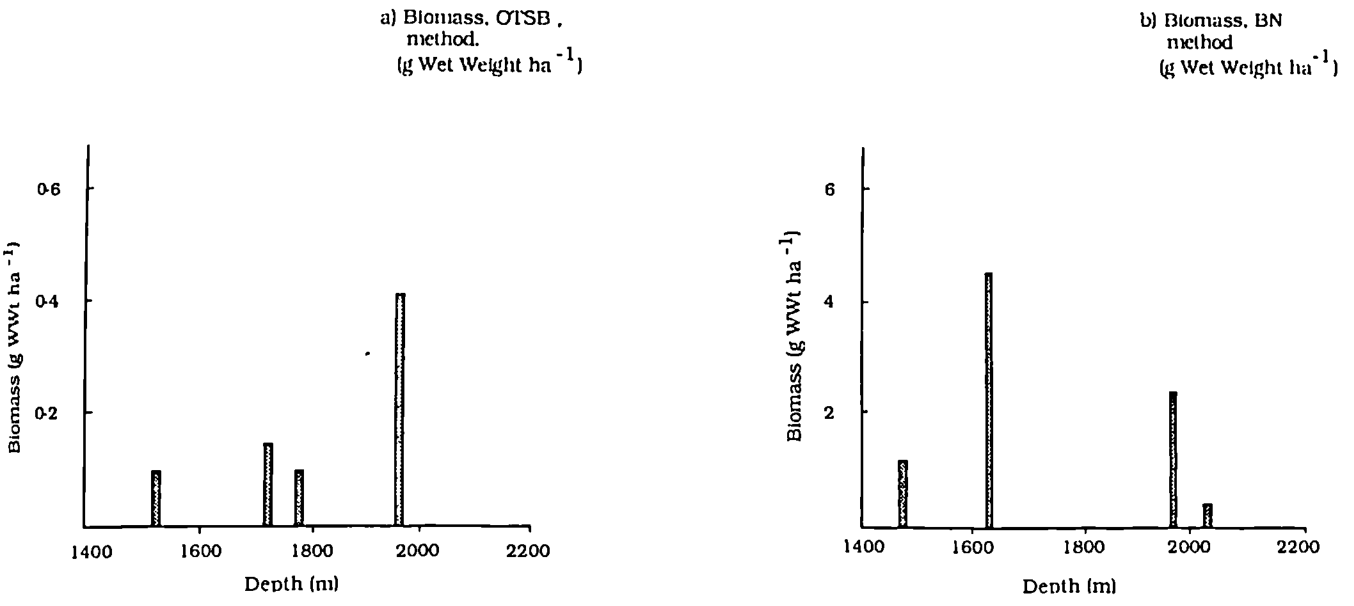
Relative Growth.

Regression lines were constructed to investigate the relationship between ChL and CL. Ln.ChL was plotted against Ln.CL for both males and females (Fig. 27), giving allometric values of 1·14 and 0·80 respectively.

To investigate chela shape, ChW was plotted against ChL to obtain a relationship between the two (Fig. 28). The gradient values obtained were low (<0·1) for both sexes, confirming the appearance from examination of comparatively long, thin 'spear-type' chelae. The data points on the figures are fairly dispersed, this most likely being due to the problems of measuring such small chela widths accurately.

Reproduction.

10 mature females (83·3 %) were ovigerous, spaced over the year from February to September (Fig. 4). The number and size of the eggs carried is outlined in Table 4, the maximum number being 20. The eggs of one female caught in September (CL 9·9 mm) were found to be hatching. The emerging larvae were distorted, probably from preservation and storage, but examination of appendages and particularly the telson showed that the larvae were extremely similar to the advanced first stage zoea of *M. serricornis* as described by Samuelsen



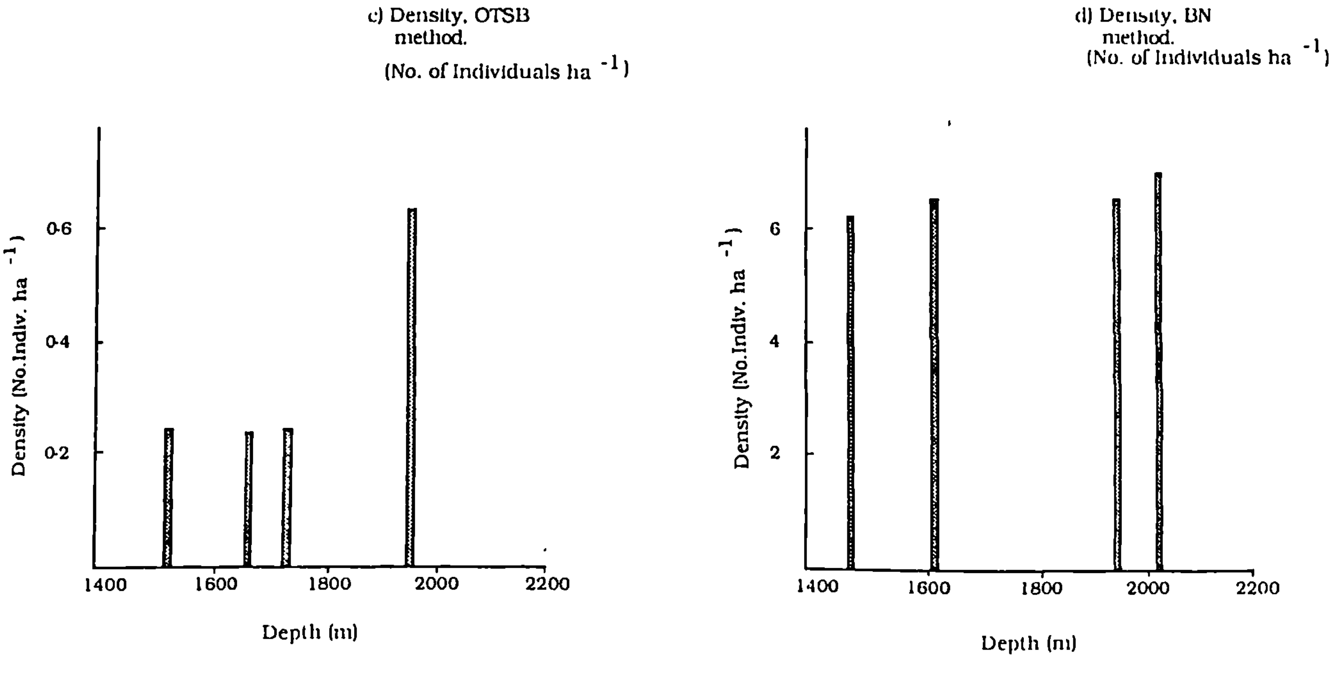
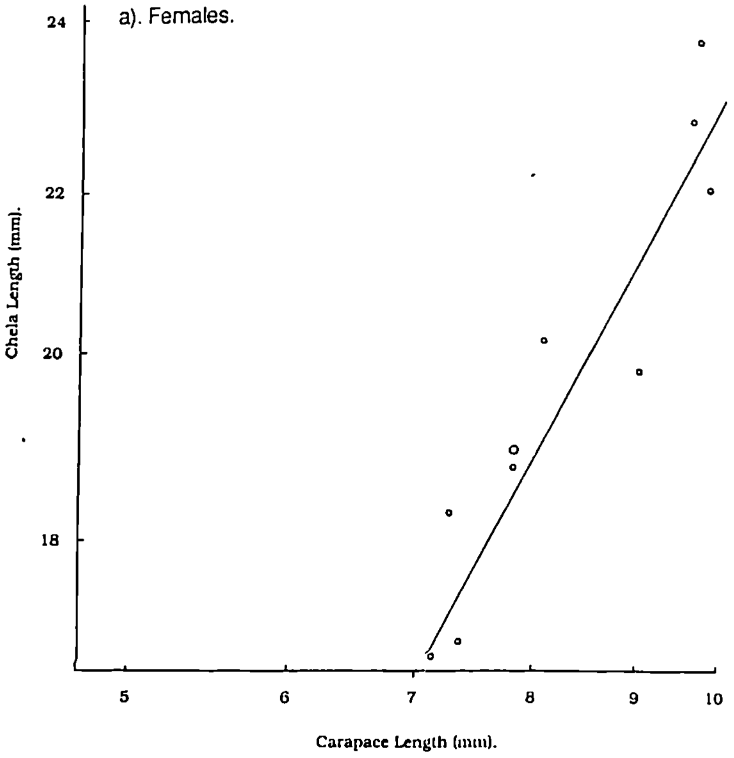
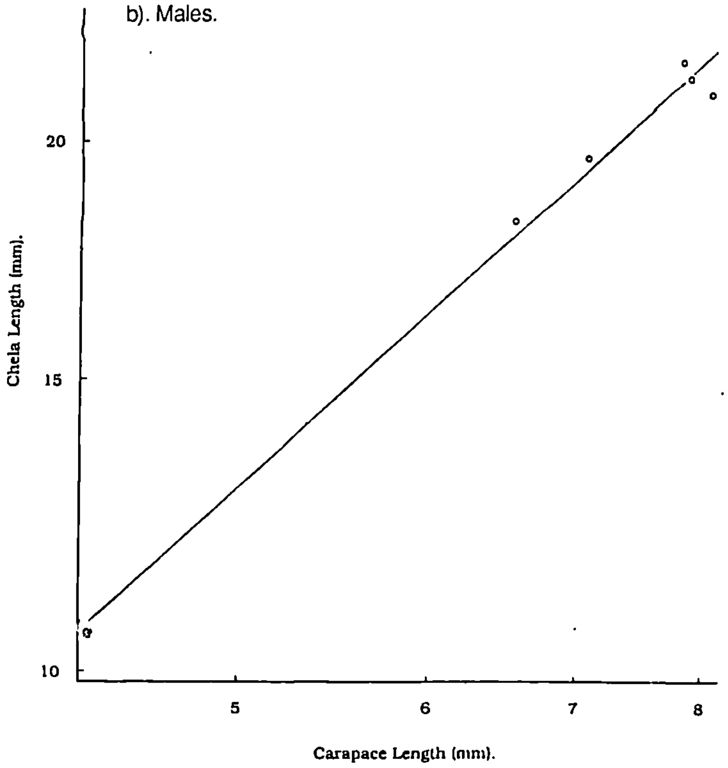


Fig. 26: Biomass and density for each station where *M. curvirostra* was taken.

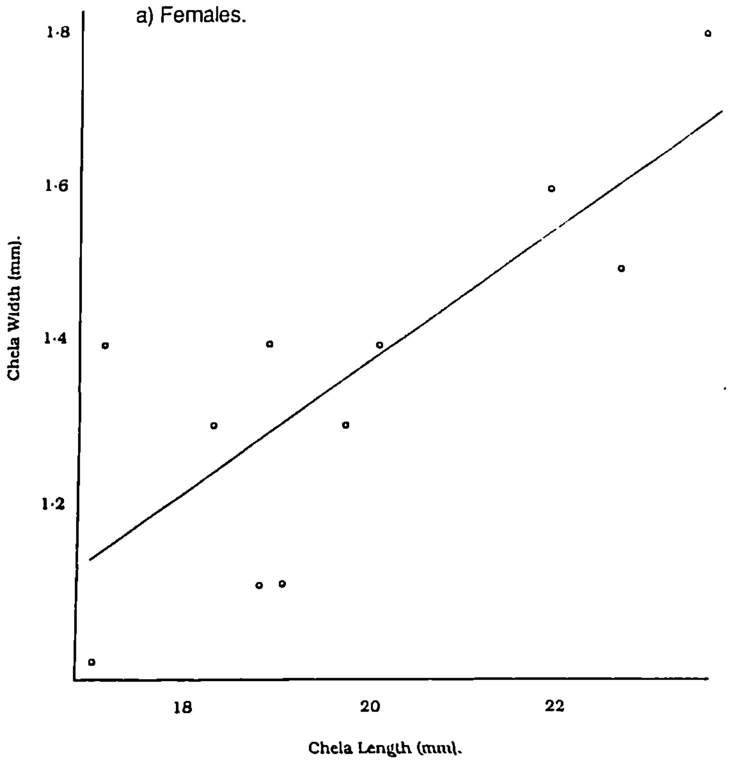


LnChL = 0·797 Ln CL + 1·314. Correlation = 0·935. R-Squared = 0·874.

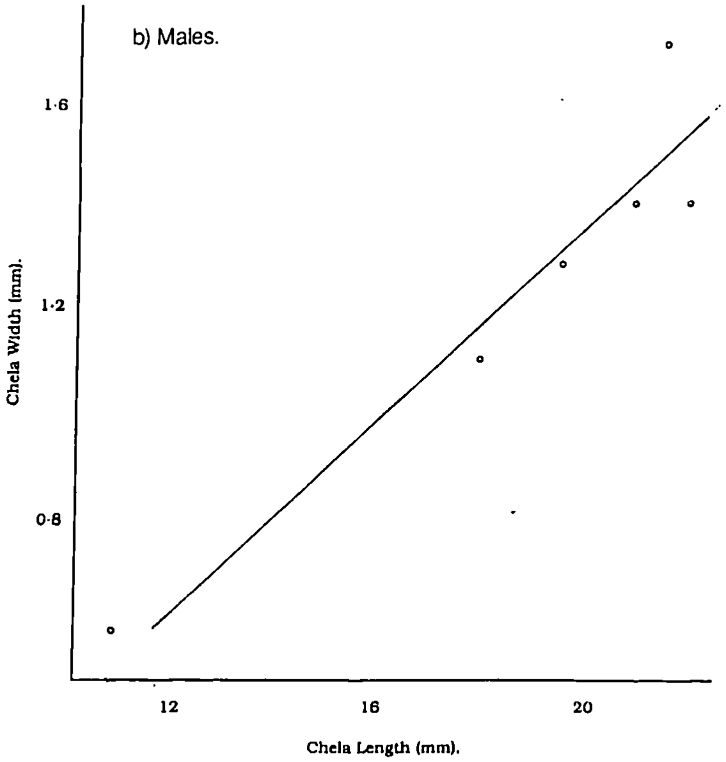


LnChL = 1·135 Ln CL + 0·735. Correlation = 0·993. R-Squared = 0·987.

Fig. 27: LnChL against LnCL regression plots for both sexes of *M. curvirostra*.



ChW = 0·085 ChL - 0·328. Correlation = 0·791. R-Squared = 0·626.



ChW = 0·083 ChL - 0·318. Correlation = 0·948. R-Squared = 0·898.

Fig. 28: ChW against ChL regression plots for both sexes of *M. curvirostra*.

(1972). This indicates some degree of abbreviated development as suggested to be found in *Munidopsis* by Gurney (1942) and implied by Fage & Monod (1936) for the cave-dwelling *M. polymorpha.*

The smallest ovigerous female was of 7·1 mm CL. However, it was interesting to note that no *M. curvirostra* females attained the usual Type 3 mature pleopods (Fig. 5c) as observed in the larger species. The most advanced pleopod Type exhibited by ovigerous females was the less-setose Type 2 (Fig. 5b). Therefore, the smallest female to be definitely mature was the 7·1 mm CL ovigerous individual.

Wenner (1982) found a maximum egg number of 52 on a large 13·0 mm CL female, the smallest ovigerous female being 10·0 mm, larger than any *M. curvirostra* caught in the Porcupine Sea-bight. Wenner also noted ovigerous females from January to November, whereas Squires (1965) found most females with eggs in March.

Parasites.

No parasites were found on any of the *M. curvirostra* studied and none as yet have been reported.

Munidopsis parfaiti (Filhol 1885) (Fig. 29).

Elasmonotus Parfaiti	Filhol 1885: pl. 7. Perrier 1886: p. 295.
Orophorhynchus Parfaiti	A. Milne-Edwards & Bouvier 1894: p. 287, 1899: p. 85, 1900: pl. 3. Nobre 1936: p. 117.
Munidopsis parfaiti	Benedict 1902: p. 324. Guérin-Ganivet 1911: p. ?? Gordon 1955: p. 244. Türkay 1975: p. 67. Lützen 1985: p. 111.

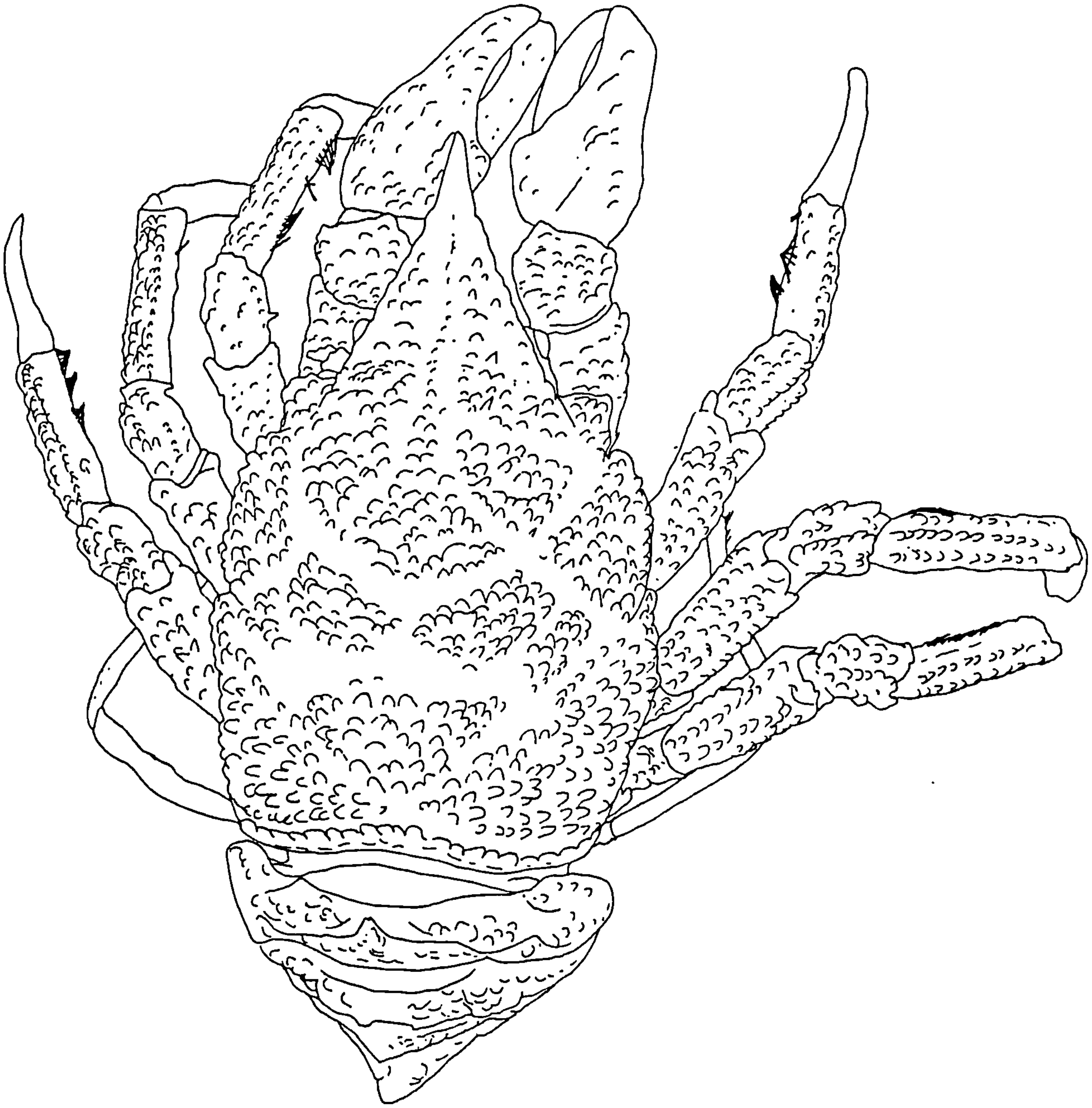


Fig. 29: *Munidopsis parfaiti.* Male, CL 16·8 mm.

Occurrence.

9638#2, 3F 3M. 9756#3, 1F. 10114#1, 1F. 50514, 5F 2M. 50515, 1F 1M. 50603#1, 1F. 50711, 3F 2M. 50811, 6F 7M. 50812#2, 1F 1M. 50910, 1F 4M. 51216#4, 1F 1M. 51309, 1F 1M. 51414#1, 2F 5M. 51608#1, 2M. 51803, 1F 1M.

Distribution.

Geographic: Apparently limited to abyssal regions in the NE Atlantic, including Azores (A. Milne-Edwards & Bouvier, 1900), Iberian Abyssal Plain (Türkay, 1975).

Bathymetric: 4000 m (Nobre, 1936: off Portugal) to 5275 m (Türkay, 1975: Iberian Abyssal Plain). In this study the possible depth range for *M. parfaiti* was 3920-4840 m, with a calculated range of 3990-4840 m, thus slightly increasing the reported range for this species.

Associates.

M. parfaiti occurred with *M. aries* (Station 9638#2), *M. crassa* (Stations 9638#2, 50514, 50515, 50711, 50811, 50910, 51414#1, 51608#1) and *M. antonii* (Stations 9638#2, 9756#3, 10114#1, 50514, 50811, 50812#2, 50910, 51309, 51608#1, 51803).

Population Structure.

Size Distribution: *M. parfaiti* was represented by 58 specimens (52:48 M:F) in the Porcupine Sea-bight samples. The range in CL was 8·4-33·7 mm (Table 2, Fig. 30), the largest individuals being female. The distribution of *M. parfaiti* appears to be limited to a small area of the NE Atlantic, as although it was relatively common in the Porcupine Sea-bight samples it has rarely been reported in other studies, Türkay (1975) only reporting two males from the Iberian deep basin.

Biomass and Density: Biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) data were

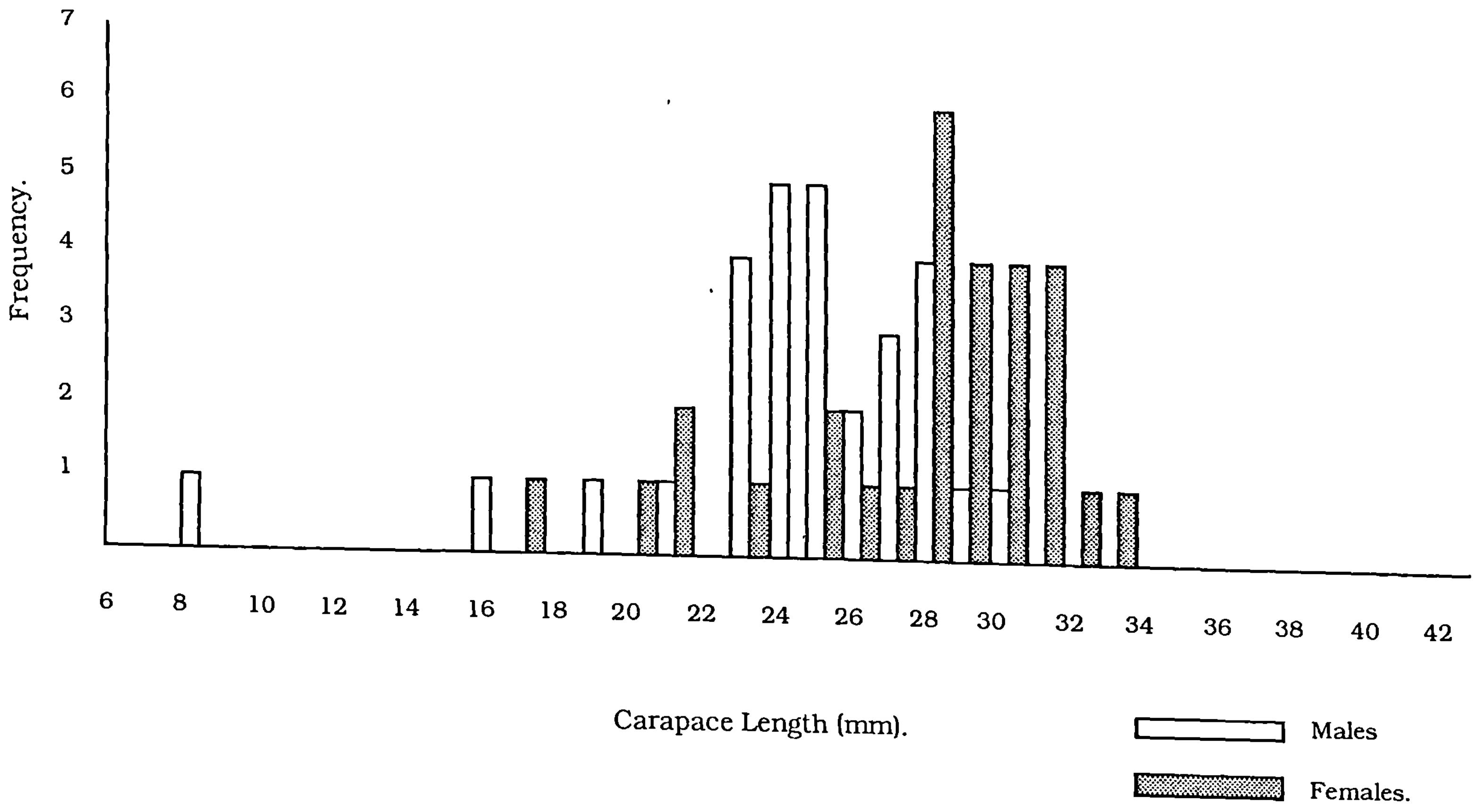
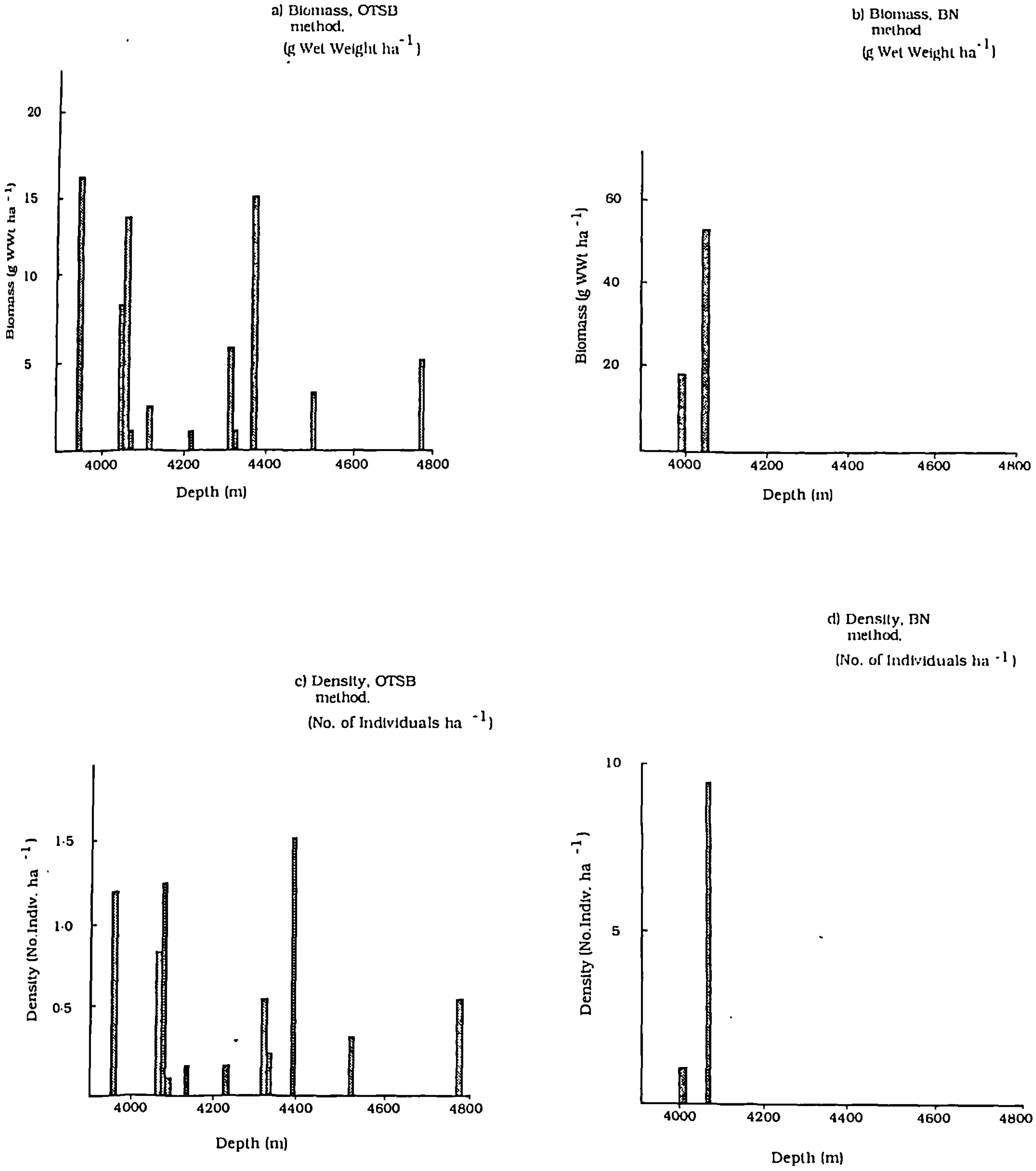


Fig. 30: Length frequency histogram for *Munidopsis parfaiti.*



a) Biomass, OTSB method. (g Wet Weight ha^{-1})

b) Biomass, BN method (g Wet Weight ha^{-1})

c) Density, OTSB method. (No. of Individuals ha $^{-1}$)

d) Density, BN method. (No. of Individuals ha $^{-1}$)

Fig. 31: Biomass and density for each station where *M. parfaiti* was taken.

calculated for the samples of *M. parfaiti* (Table 3, Fig. 31) for both BN and OTSB methods. As can be seen, *M. parfaiti* is most abundant either side of 4000 m, with another peak at 4400 m. At these depths where it is most common, *M. parfaiti* is co-habiting with *M. antonii, M. crassa* and *M. aries*. It would appear that this area at the foot of the slope is capable of supporting a comparatively high biomass of *Munidopsis*.

Relative Growth.

The large sample of *M. parfaiti* allowed regression lines to be constructed to investigate the relative growth of ChL against CL. To achieve this, Ln.ChL was plotted against Ln.CL for both males and females (Fig. 32), giving allometric values of 0·99 and 0·92 respectively.

To investigate chela shape, ChW was plotted against ChL to obtain a relationship between the two (Fig. 33). The slope values obtained were high (≈0·2), especially for males, indicating that *M. parfaiti* possess short, broad 'spade-type' chelae.

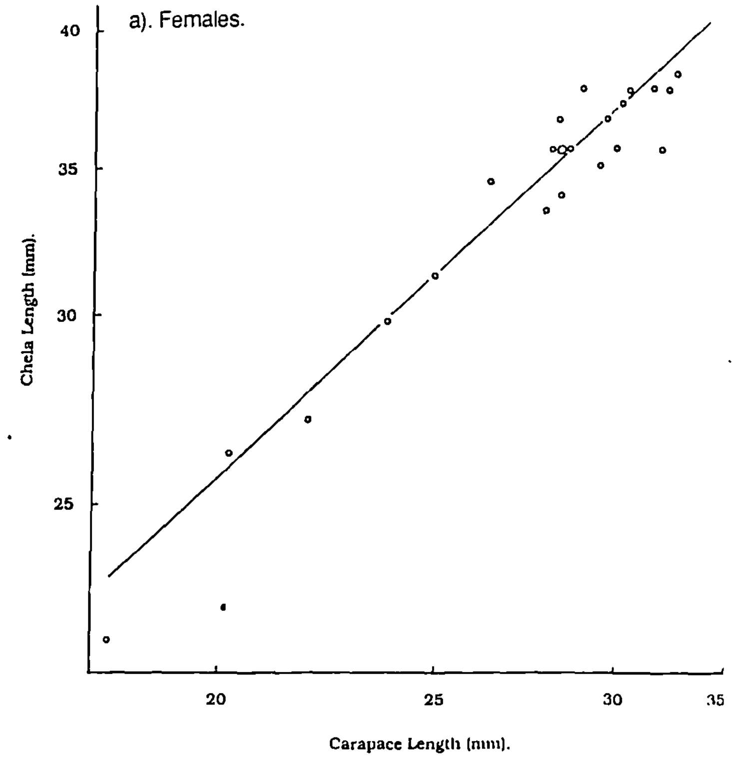
Reproduction.

Four females were found to be ovigerous (18·5 % of mature females) from June, August and October (Fig. 4). The number and size of eggs carried is outlined in Table 4, the maximum egg number being 25 - low for the animal's general size.

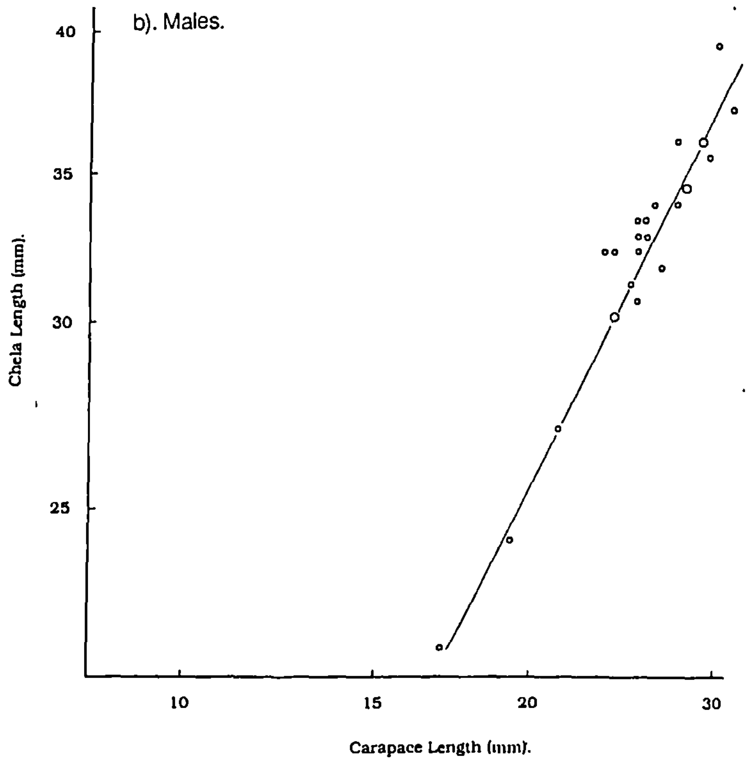
The smallest ovigerous female was 26·3 mm CL, with the smallest female possessing Type 3 pleopods (Fig. 5c) being 23·8 mm CL. Female *M. parfaiti* would therefore appear to become mature at a size of at the most 23 mm.

Parasites.

No parasites were found on any of the *M. parfaiti* studied. However, Guérin-Ganivet (1911) reports a *M. parfaiti* infested by the rhizocephalan barnacle *Triangulopis abyssorum*, this being confirmed in a listing of deep-sea rhizocephala by Lützen (1985).

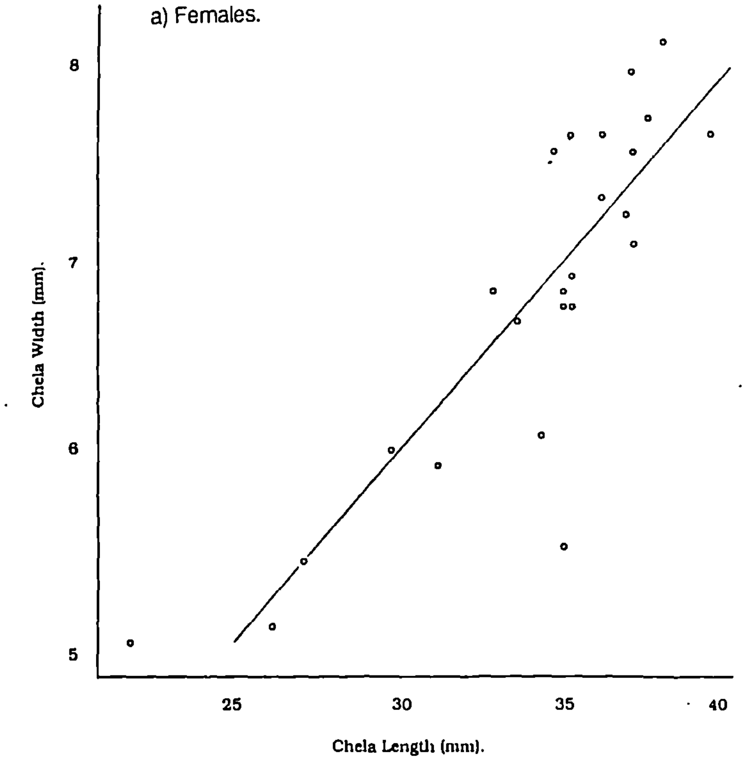


LnChL = 0·921 CL + 0·468. Correlation = 0·971. R-Squared = 0·943.

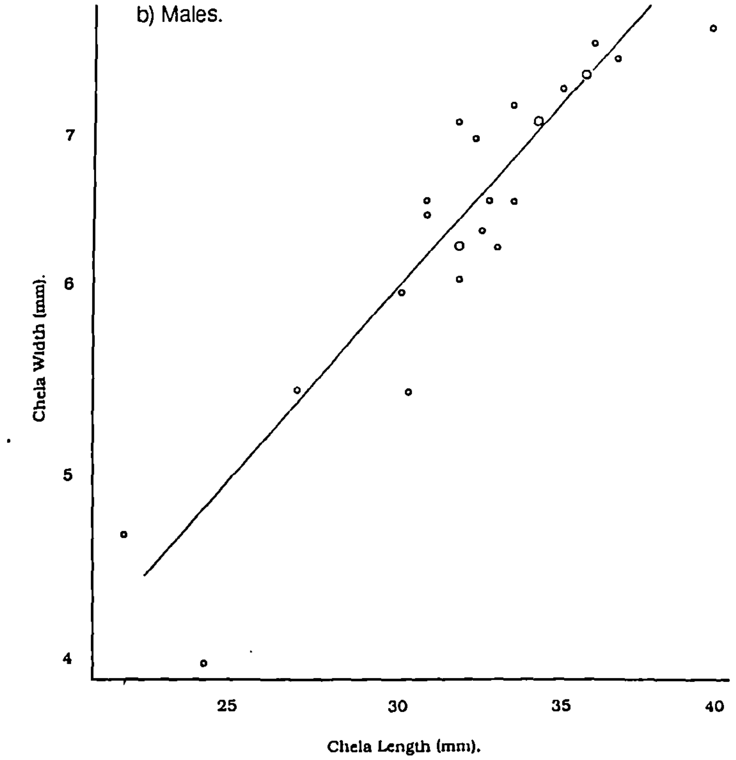


LnChL = 0·993 CL + 0·272. Correlation = 0·970. R-Squared = 0·942.

Fig. 32: LnChL against LnCL regression plots for both sexes of *M. parfaiti.*



ChW = 0·177 ChL + 0·699. Correlation = 0·856. R-Squared = 0·732.



ChW = 0·204 ChL - 0·104. Correlation = 0·924. R-Squared = 0·854.

Fig. 33: ChW against ChL regression plots for both sexes of *M. parfaiti*.

Munidopsis rostrata (A. Milne-Edwards 1880) (Fig. 34).

Galacantha rostrata A. Milne-Edwards 1880: p. 52. Smith 1884: p. 355. A. Milne-Edwards & Bouvier 1894: p. 271, 1897: p. 60, 1900: p. 308. Faxon 1895: p. 78. Benedict 1902: p. 304. Hansen 1908: p. 35. Doflein & Balss 1913: p. 174. Haig 1955: p. 39. Tirmizi 1964: p. 206. Kensley 1968: p. 292.

Munidopsis rostrata Smith 1885: p. 493, 1886: p. 649. Chace 1942: p. 75. Pequegnat & Pequegnat 1970: p. 138, 1971: p. 4. Miyake & Baba 1970: p. 95. Mayo 1974: p. 266: Wenner 1982: p. 370. Lützen 1985: p. 106.

Synonyms.

Galacantha Talismani Filhol 1885: pl. 3.

Galacantha bellis Henderson 1885: p. 418.

Galacantha talismani Henderson 1888: p. 167.

Galacantha areolata Wood-Mason & Alcock 1891: p. 200.

Galacantha investigatoris Alcock & Anderson 1894: p. 173.

Galacantha faxoni Benedict 1902: p. 304.

Occurrence.

10112#1, 2F 1M. 10112#2, 1M. 10112#3, 1I. 50511, 1M. 50712, 1F 2M. 50814, 11F 5M. 50822, 2F. 50906, 3F. 50907, 1F 1M. 51011, 3F. 51015, 1F 1M. 51016, 2F 1M. 51110#3, 2F 2M. 51111#1, 3M. 51111#2, 1F 1M. 51310, 5F 7M. 51411#1, 3F 4M. 51414#1, 1I. 51603#2, 1F. 51611#1, 2F. 51613#1, 2M. 51805, 2F. + 9041, 4F 1M (not in Sea-bight area).

Distribution.

Geographic: Atlantic, Pacific and Indian oceans, including Caribbean (Chace, 1942;

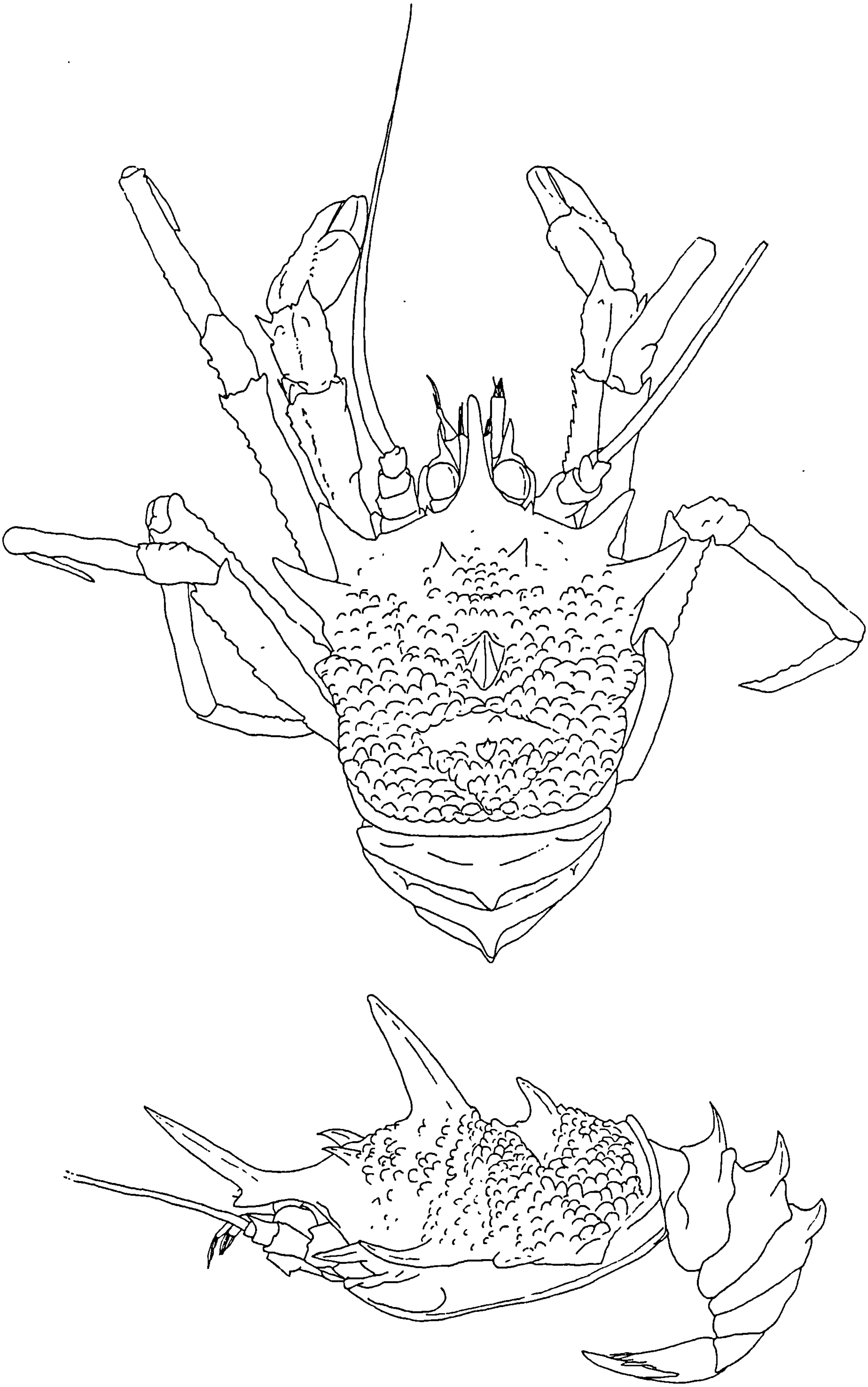


Fig. 34: *Munidopsis rostrata.* Male, CL 11·2 mm.

Mayo, 1974), Middle Atlantic Bight (Wenner, 1982), NW Atlantic (Smith, 1882), Iceland (Hansen, 1908), Canaries (A. Milne-Edwards & Bouvier, 1900), S Africa (Kensley, 1968), Chile (Henderson, 1885), California (Faxon, 1895), W Pacific (Henderson, 1888), Bay of Bengal (Wood-Mason & Alcock, 1891), Arabian Sea (Alcock & Anderson, 1894).

Bathymetric: 1620-3240 m (Wenner, 1982: New England). In this study, the possible depth range of *M. rostrata* was 2095-3100 m, with a calculated range of 2150-2850 m.

Associates.

M. rostrata occurred with *M. bermudezi* (Stations 9041, 50712, 50814) and *M. bairdii* (Stations 50906, 51110#3).

Population Structure.

Size Distribution: *M. rostrata* was represented by 81 specimens (41:57:2 M:F:J) in the Porcupine Sea-bight samples, making it the second most abundant *Munidopsis* species. The range in CL was 3·0-31·4 mm (Table 2, Fig. 35), the largest individuals being female. *M. rostrata,* in its variety of forms (see above) is probably the most widely reported *Munidopsis* species. Mayo (1974) examined four individuals, with a maximum size of 26·3 mm CL. Hansen (1908) took two specimens (max. CL 58 mm including rostrum), Tirmizi (1964) four small individuals and Chace (1942) a single male. However, Wenner (1982) caught 150, the largest being a 36 mm CL female.

Biomass and Density: Biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) data were calculated for the samples where *M. rostrata* was taken (Table 3, Fig. 36) for both OTSB and BN methods. As can be seen, *M. rostrata* is most abundant between 2400 and 2800 m, with several peaks in both biomass and density between these depths. Over its depth range, *M. rostrata* is by far the most abundant *Munidopsis* species and overall second only to *M. antonii.*

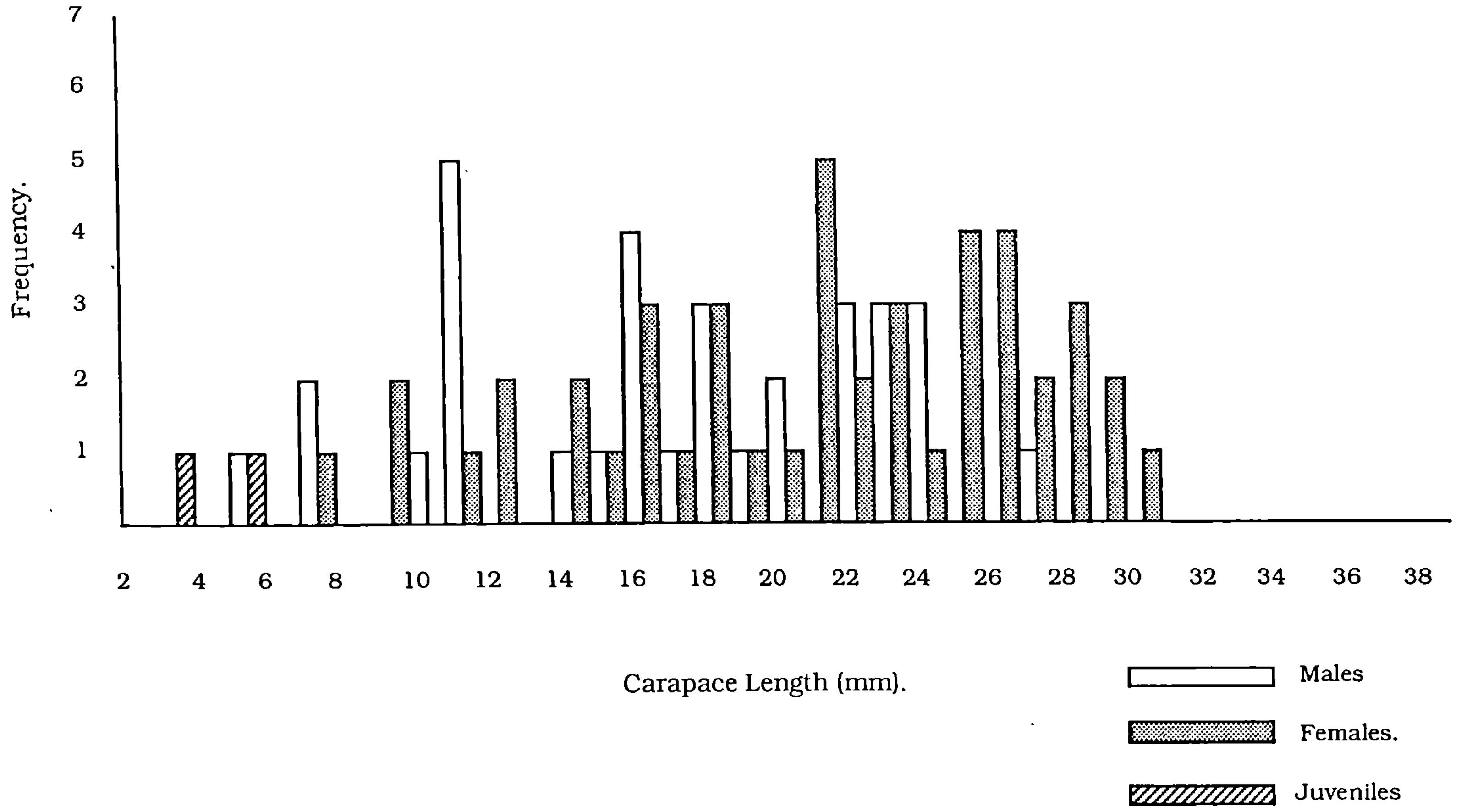
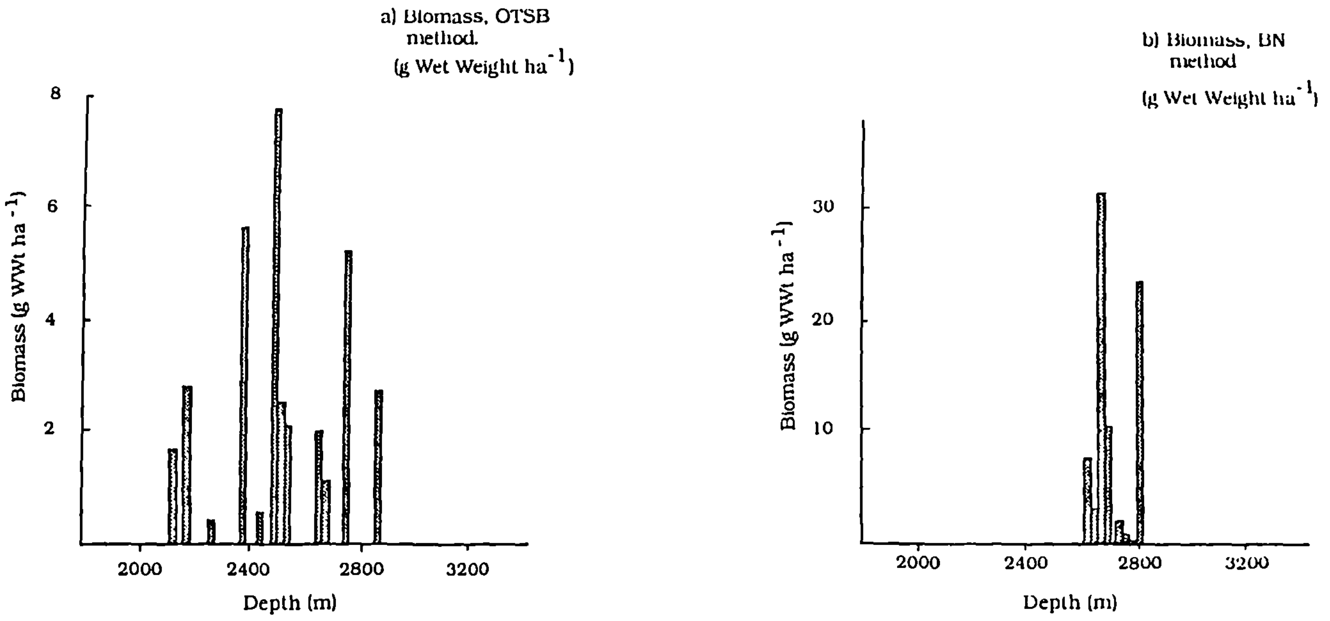


Fig. 35: Length frequency histogram for *Munidopsis rostrata*.



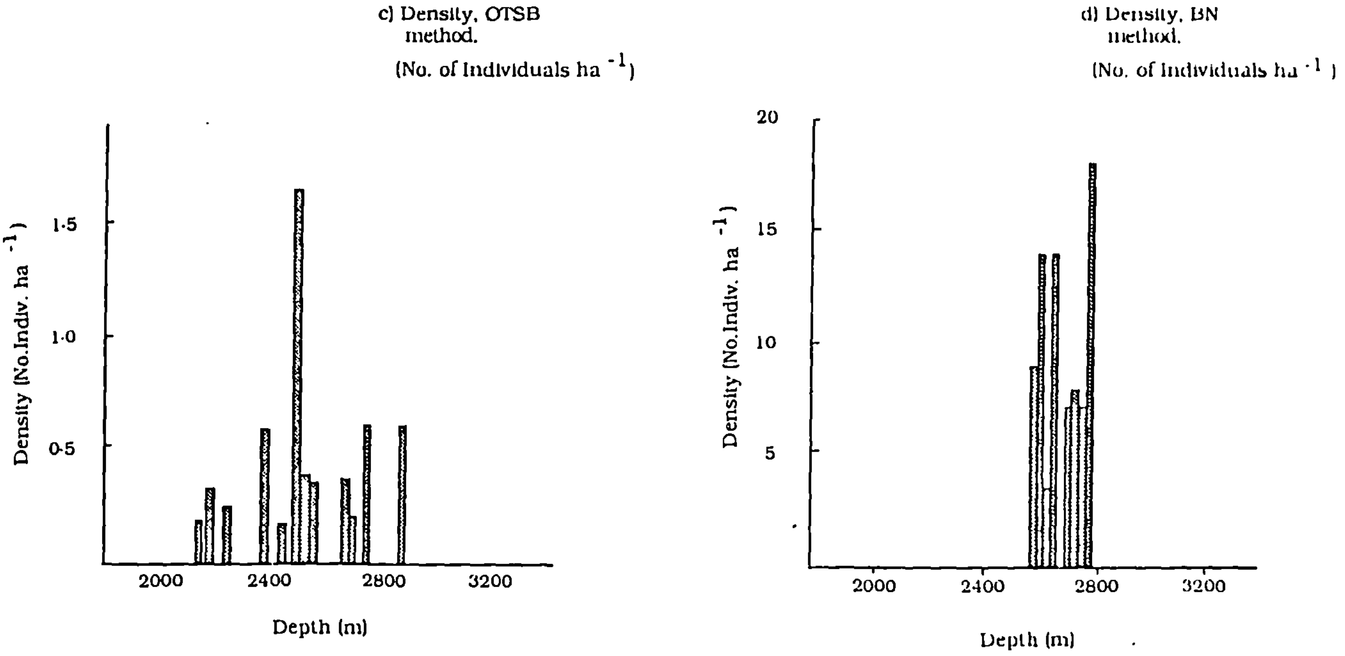


Fig. 36: Biomass and density for each station where *M. rostrata* was taken.

Relative Growth.

The large sample of *M. rostrata* allowed regression lines to be constructed to investigate the relationship between chela length and carapace length. Ln.ChL was plotted against Ln.CL (Fig. 37) for both males and females, giving allometric values of 0·96 and 0·88 respectively.

To investigate chela shape, ChW was plotted against ChL to obtain a relationship between the two (Fig. 38). The gradient values obtained were low (≈0·12), indicating *M. rostrata* possesses comparatively long, thin 'spear-type' chelae, though not as marked as other species such as *M. curvirostra.*

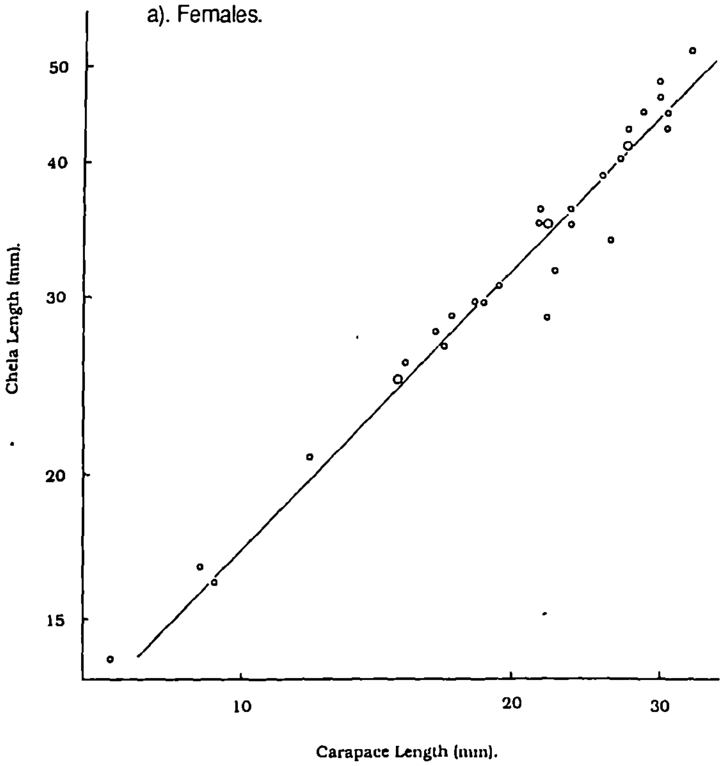
Reproduction.

Nine females were found to be ovigerous (32 % of mature females), mainly from August to November (Fig. 4). However, studies of ovary structure showed no cyclic pattern over the year. The number and size of eggs carried is outlined in Table 4, the maximum number being 108. Wenner (1982) recorded an ovigerous female with 156 eggs, and females with eggs in every month except May and June.

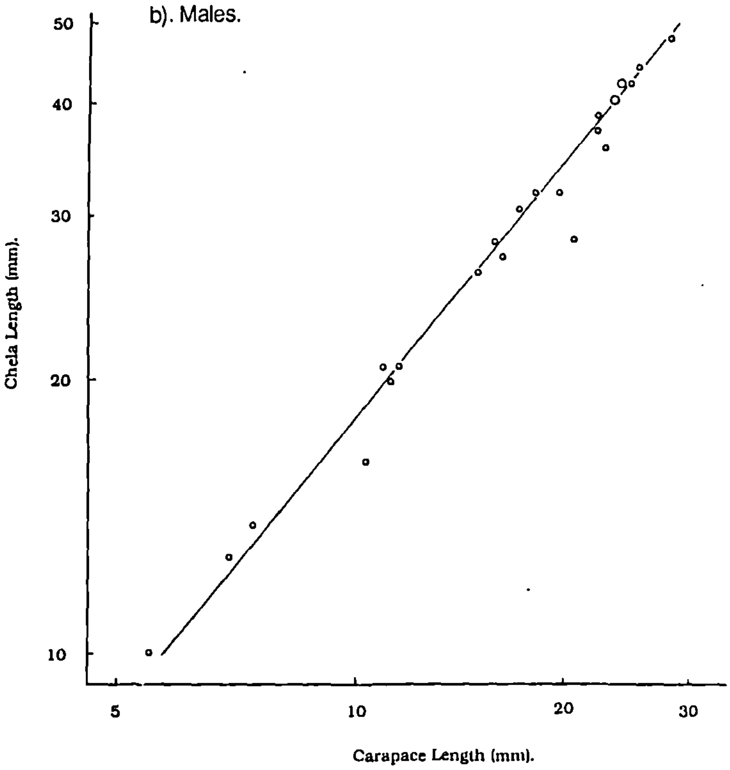
The smallest ovigerous female was of 25·2 mm CL, though an individual of 21·2 mm CL was found with mature Type 3 pleopods (Fig. 5c), suggesting sexual maturity around 20 mm CL.

Parasites.

Two *M. rostrata* were found to be parasitised. One female of CL 25·4 mm was infested with a large rhizocephalan externa of the genus *Lernaeodiscus.* This is probably an undescribed species (J. Lützen, pers. comm.). The externa had emerged from the third abdominal segment and the host's pleopods were slightly degenerate and less setose than the normal Type 3 structure. They appeared similar to the Type 8 pleopods described by Attrill (in press) for the infested *Munida sarsi.*

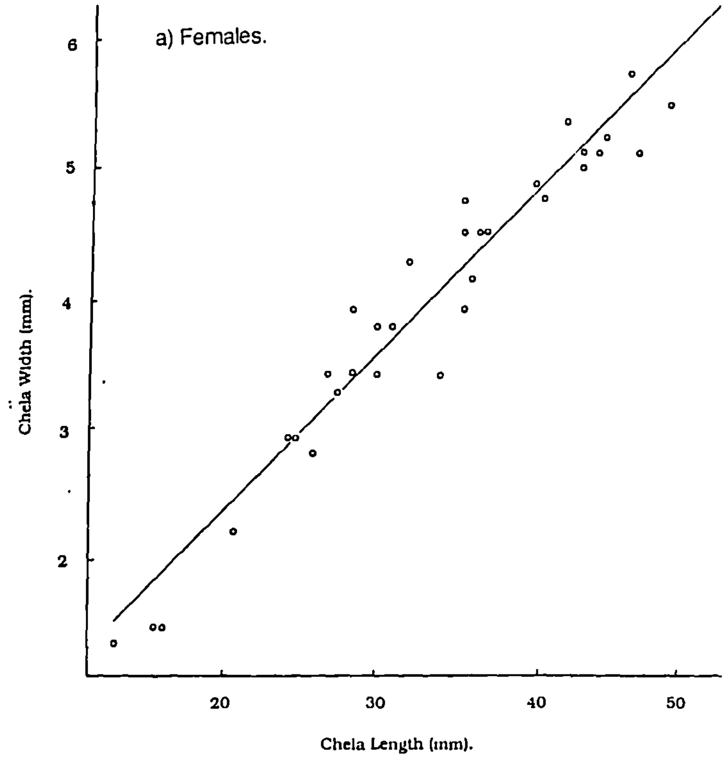


LnChL = 0·883 LnCL + 0·832. Correlation = 0·983. R-Squared = 0·967.

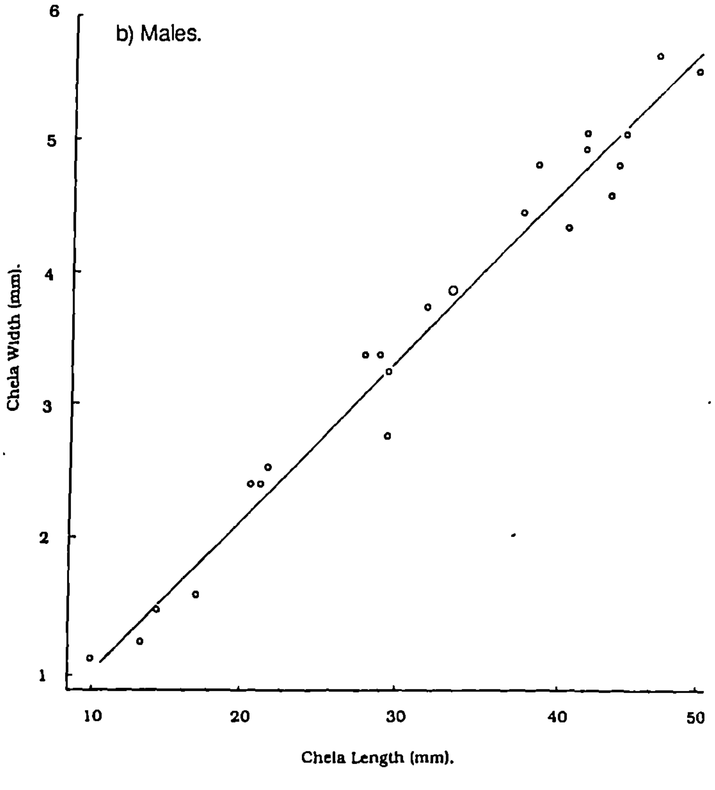


LnChL = 0·964 LnCL + 0·658. Correlation = 0 990. R-Squared = 0·979.

Fig. 37: LnChL against LnCL regression plots for both sexes of *M. rostrata*.



ChW = 0·121 ChL - 0·043. Correlation = 0·974. R-Squared = 0·948.



ChW = 0·122 ChL - 0·211. Correlation = 0·987. R-Squared = 0·974.

Fig. 38: ChW against ChL regression plots for both sexes of *M. rostrata.*

A male *M. rostrata* was found with a bopyrid isopod in the right branchial chamber, causing the carapace to characteristically bulge outwards. This was identified as an immature female belonging to an undescribed species of the primitive genus *Pleurocryptella* (J. Markham, pers. comm.). The pleopods of the host were unaffected.

Other reports of parasitism in *M. rostrata* include rhizocephalans: *Lernaeodiscus* sp., *Cyphosaccus* sp. (Wenner, 1982), *Sacculina* sp. (Mayo, 1974) and *Pirusaccus socialis* (Lützen, 1985). Bopyrids: undescribed genus (Wenner, 1982). It is obvious that there is a lot of taxonomic work to be done on the parasites of *Munidopsis* spp.

Munidopsis serricornis (Lovén 1852) (Fig. 39).

Galathea serricornis Lovén 1852.

Galathea tridentata Esmark 1857: p. 239. M. Sars 1868: p. 19. G. O. Sars 1872: p. 256.

Galathodes tridentata Goës, 1863. A. Milne-Edwards & Bouvier 1894: p. 279, 1900: p. 331.

Munidopsis tridentata Ortmann 1892: p. 256. Benedict 1902: p. 328. Doflein & Balss 1913: p. 175. Gurney 1942. Chace 1942: p. 88. Boschma 1962: p. 76. Zariquey Alvarez 1968. Pequegnat & Pequegnat 1970: p. 158. Miyake & Baba 1970: p. 95. Samuelsen 1972: p. 91.

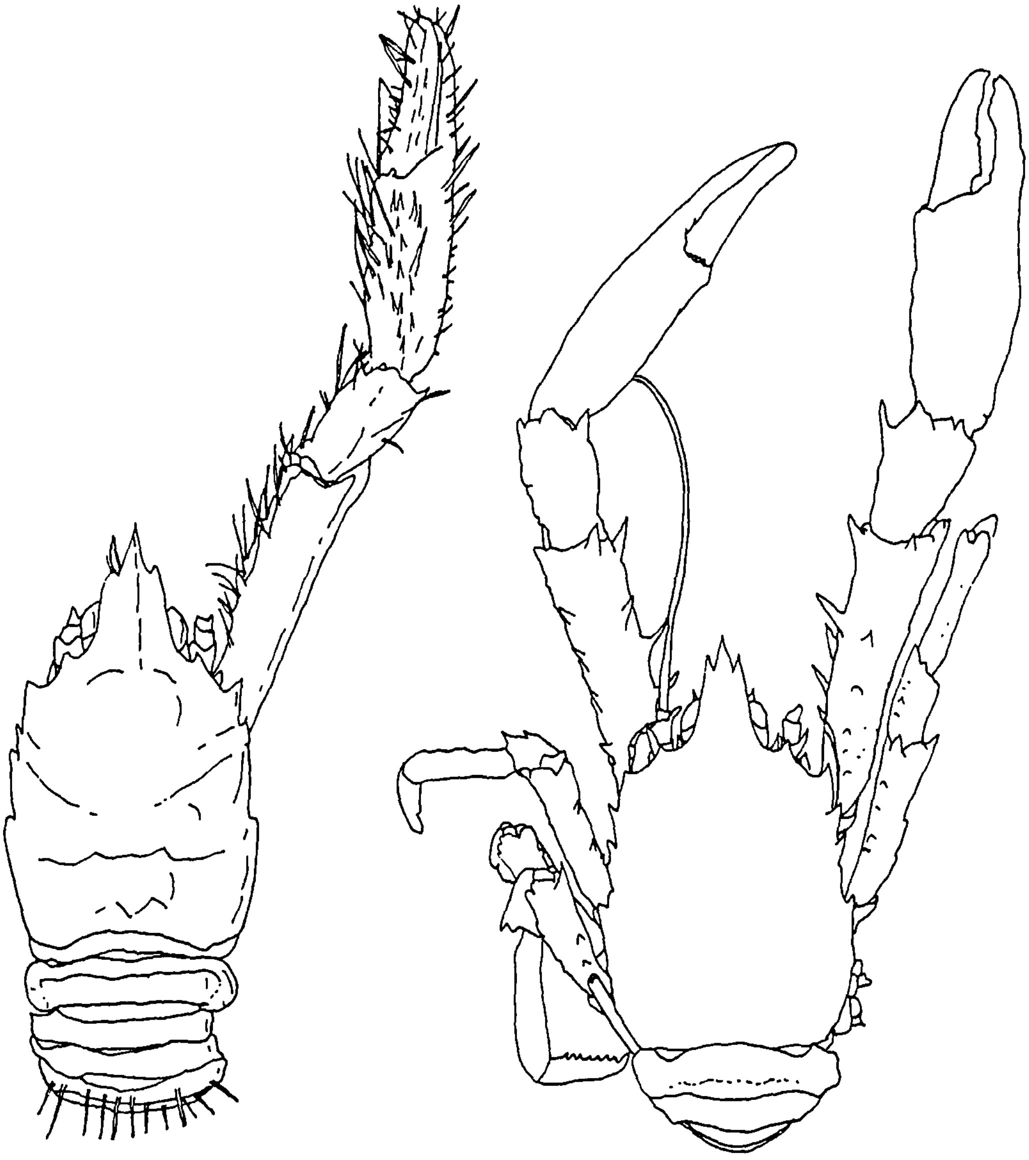
Munidopsis (Galathodes) serricornis Balss 1926: p. 29. Stephensen 1939: p. 26.

Munidopsis serricornis Christiansen 1972: p. 29. Mayo 1974: p. 388. Wenner 1982: p. 373. Lützen 1985: p. 111. Høeg & Lützen 1986: p. 51.

Synonym.

Munidopsis bahamensis Benedict 1902: p. 278. Doflein & Balss 1913: p. 175. Chace 1942: p. 89. Pequegnat & Pequegnat 1970: p. 139, 1971: p. 5.

Munidopsis tenuirostris Benedict 1902: p. 289. Doflein & Balss 1913: p. 176. Chace 1942: p. 74. Pequegnat & Pequegnat 1970: p. 139, 1971: p. 5.



a. b.

Fig. 39: *Munidopsis serricornis.* a) Male, CL 7·1 mm. b) More complete male specimen, CL 11·0 mm (from Mayo, 1974).

Occurrence.

9752#1, 2F. 50601, 2M.

Distribution.

Geographic: N Atlantic and Indian ocean, including Norway (Esmark, 1857), Ireland (Selbie, 1914), Azores (A. Milne-Edwards & Bouvier, 1900), W Africa (A. Milne-Edwards & Bouvier, 1900), Cuba (Chace, 1942), Gulf of Mexico (Pequegnat & Pequegnat, 1970), E Africa and Bay of Bengal (Doflein & Balss, 1913), Maldives (Alcock, 1901).

Bathymetric: 110 m (Selbie, 1914: Ireland) to 2165 m (Miyake & Baba, 1970: W Africa). In this study, the possible depth range of *M. serricornis* was 770-1042 m, with a calculated range of 927-1007 m.

Associates.

M. serricornis was the only representative of the genus at the stations where it occurred.

Population Structure.

Size Distribution: *M. serricornis* was represented by just four specimens (50:50 M:F) in the Porcupine Sea-bight samples. Like *M. curvirostra,* this species is much smaller overall than the other seven species studied, with a Cl range of only 3·3-11·2 mm (Table 2). *M. serricornis* has been widely reported, probably due in part to its shallow depth range, including Pequegnat and Pequegnat (1970), a single female, Samuelsen (1972) one female to study the egg development and Chace (1942), 18 specimens, including nine as *M. bahamensis,* Chace's largest specimen being 18·1 mm CL. Mayo (1974) examined 64 specimens, including a reappraisal of Chace's material. The largest individual in her new material was 13·3 mm CL.

Biomass and Density: Biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) data was calculated for the two samples where *M. serricornis* was taken (Table 3, Fig. 40), both using

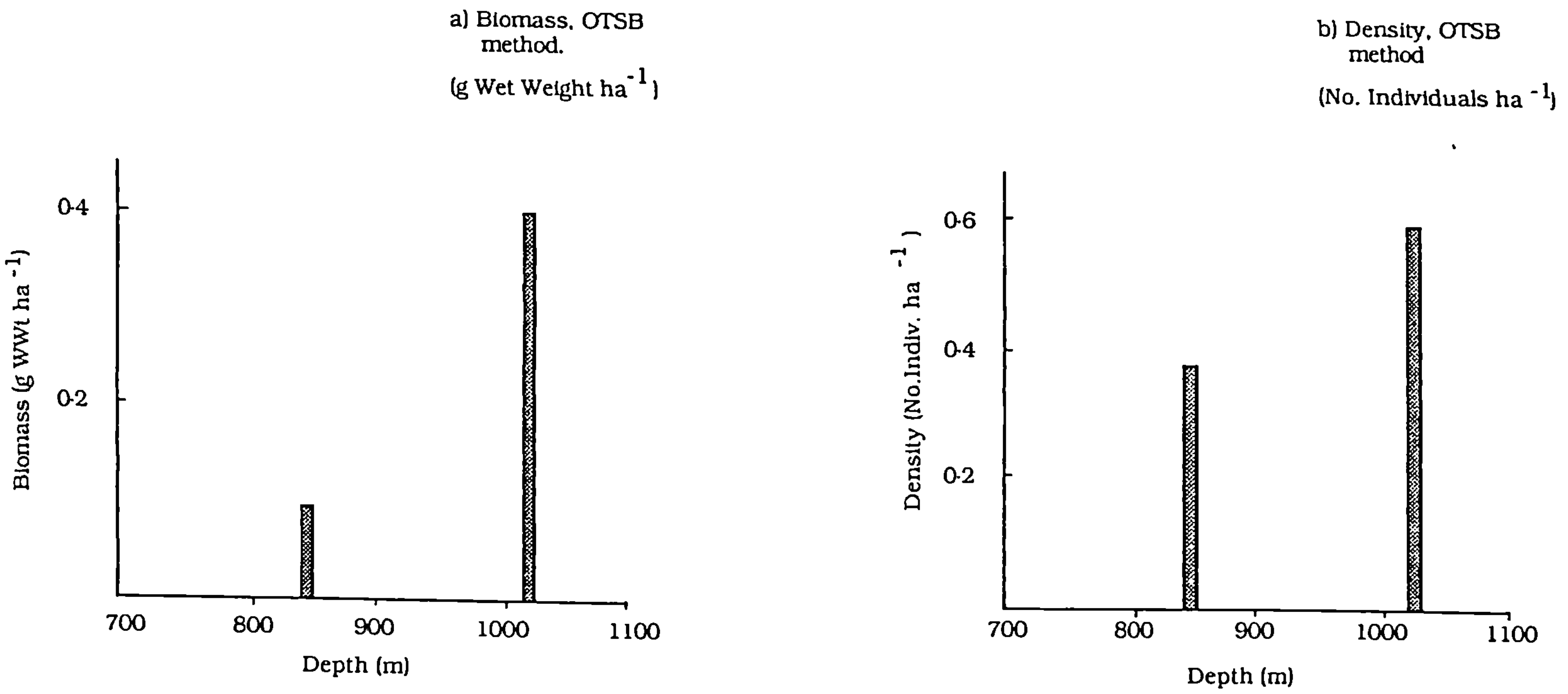


Fig. 40: Biomass and density for each station where *M. serricornis* was taken.

the OTSB. Both density and biomass are low for *M. serricornis*, compared with other decapods found over the same depth range. At around 1000 m, *Munida tenuimana* has a OTSB calculated biomass of 0·5-4·0 $g.WWt.ha^{-1}$ and density of 0·2-1·8 $Ind.ha^{-1}$ (Chapter 3). The small young *Geryon trispinosus* found at 1000 m have OTSB biomass of 11-22 $g.WWt.ha^{-1}$ and density of 2-5 $Ind.ha^{-1}$ (Chapter 5).

Relative Growth.

The sample of *M. serricornis* was considered too small for valuable relative growth analysis.

Reproduction.

Both females caught were ovigerous, taken in April (Fig. 4). The number and size of eggs carried is outlined in Table 4, the maximum number being 30. Samuelsen (1972) reported 30 eggs on his ovigerous female that he was studying in the laboratory, with a mean egg size of 1·65 mm. All the eggs hatched on 20th January.

The smaller of the two ovigerous females was 7·5 mm. However, like *M. curvirostra*, neither of the ovigerous females possessed Type 3 pleopods (Fig. 5c), instead the development only reached Type 2 (Fig. 5b). Female sexual maturity must therefore occur at a size below 7·5 mm. The smallest ovigerous female reported by Mayo (1974) was one of 7·2 mm.

Parasites.

No parasites were found on any of the *M. serricornis* examined. However, parasitism has been noted in this species. Rhizocephalans: Boschma (1962) and Høeg & Lützen (1986) reported *Cyphosaccus norvegicus*, Reinhard (1958) *Tortugaster fistulatus* and Chace (1942) mentioned "an abdominal parasite" on one of his *M. bahamensis*. Mayo (1974) reported infestations of a bopyrid isopod of the genus *Pseudione*.

General Discussion.

Depth Distribution.

The *Munidopsis* species covered by this study show a distinct succession down the slope, from *M. serricornis* at around 800 m to the abyssal plain species of *M. crassa* and *M. parfaiti* below 4000 m (Fig. 41). From this distribution, four bathymetric groups can be defined:

1. Upper slope species - *M. serricornis, M. curvirostra.*
2. Mid slope species - *M. rostrata, M. bermudezi, M. bairdii.*
3. Lower slope species - *M. aries, M. antonii.*
4. Abyssal species - *M. parfaiti, M. crassa.*

The succession is generally continuous except for one obvious gap between *M. serricornis* and *M. curvirostra* of over 400 m. There is no lack of samples taken in this area (see Chapters 3 and 5), so it is interesting that no *Munidopsis* species were caught at these depths. When the density graphs for *Munida tenuimana* are studied (Fig. 42), it can be seen that the peak of *M. tenuimana* density occurs at around 1200 m (see Chapter 3) - corresponding to the gap in *Munidopsis* distribution. Either side of this peak where there are fewer *M. tenuimana, Munidopsis* species are found. It could be that the population of *M. tenuimana* over this depth band is at such a level that the two small *Munidopsis* species are excluded.

The abyssal species probably both extend further out into the deep Atlantic and have indeed been caught in other areas of the NE Atlantic, such as at below 5200 m in the Iberian Basin (Türkay, 1975).

Biomass and Density.

By plotting out biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) data for total *Munidopsis* at each station, some idea can be gained of the abundance of the genus as a whole over its depth range (Figs. 43 and 44). As can be seen, there are two peaks, the first at around

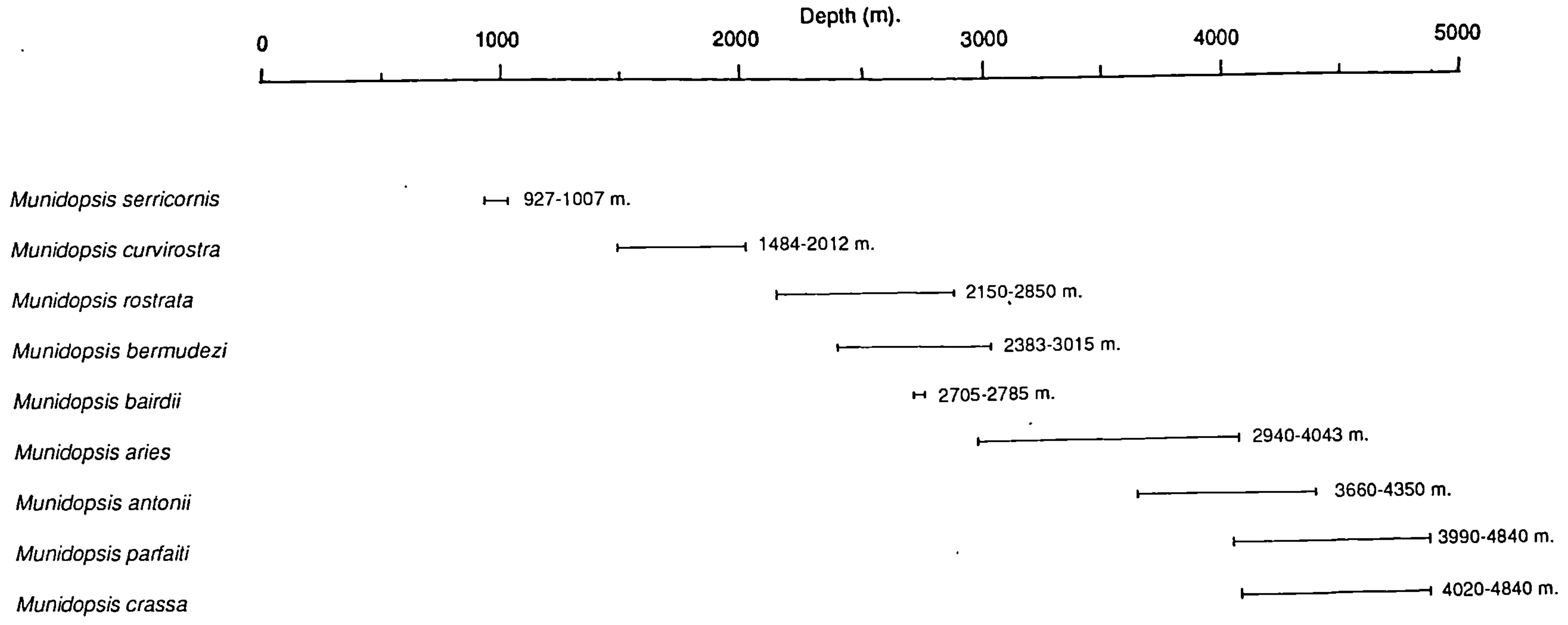


Fig. 41: Bathymetric distribution of *Munidopsis* spp. in the Porcupine Sea-bight. (Calculated ranges).

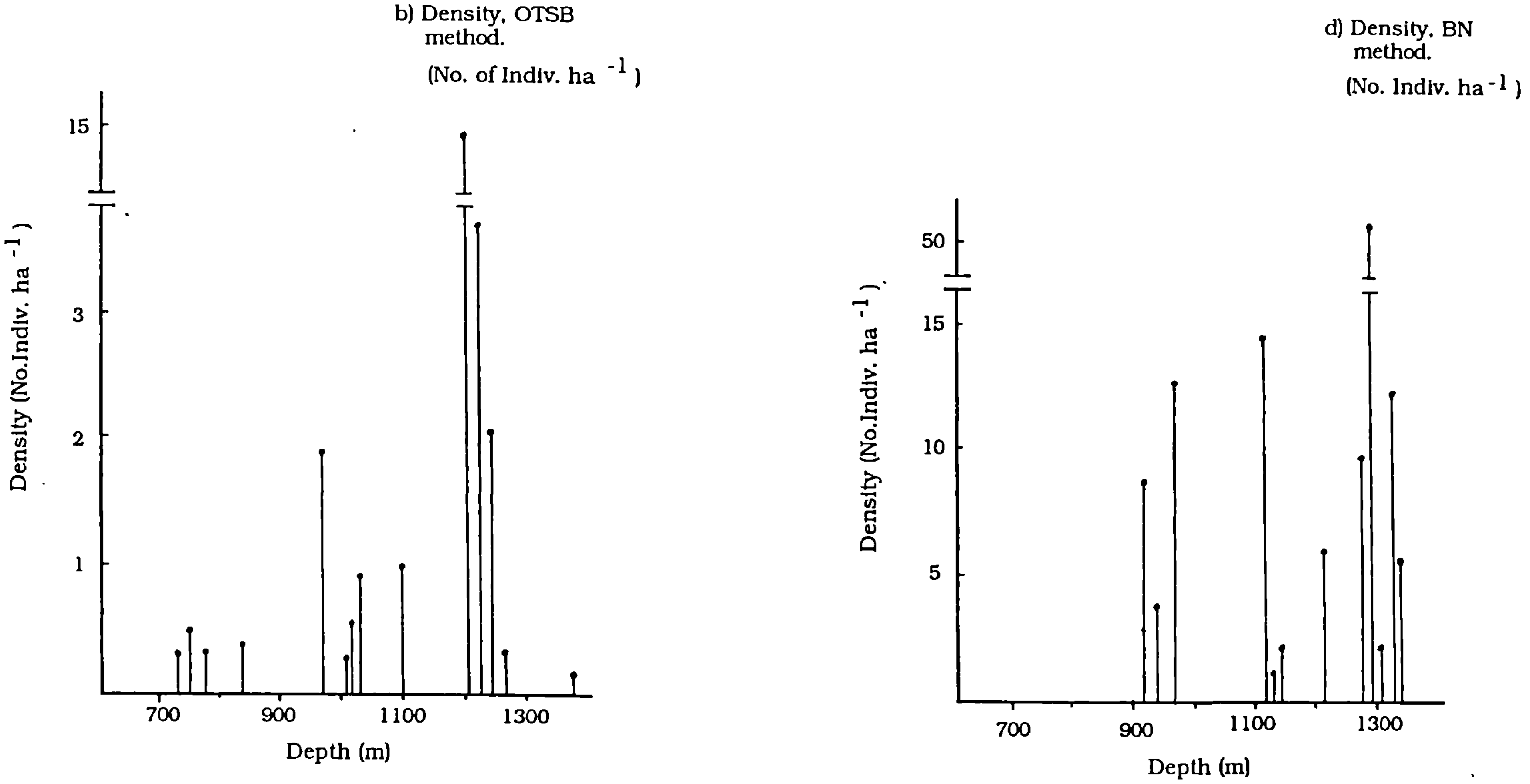


Fig. 42: Density of *Munida tenuimana* at the stations where it was taken.

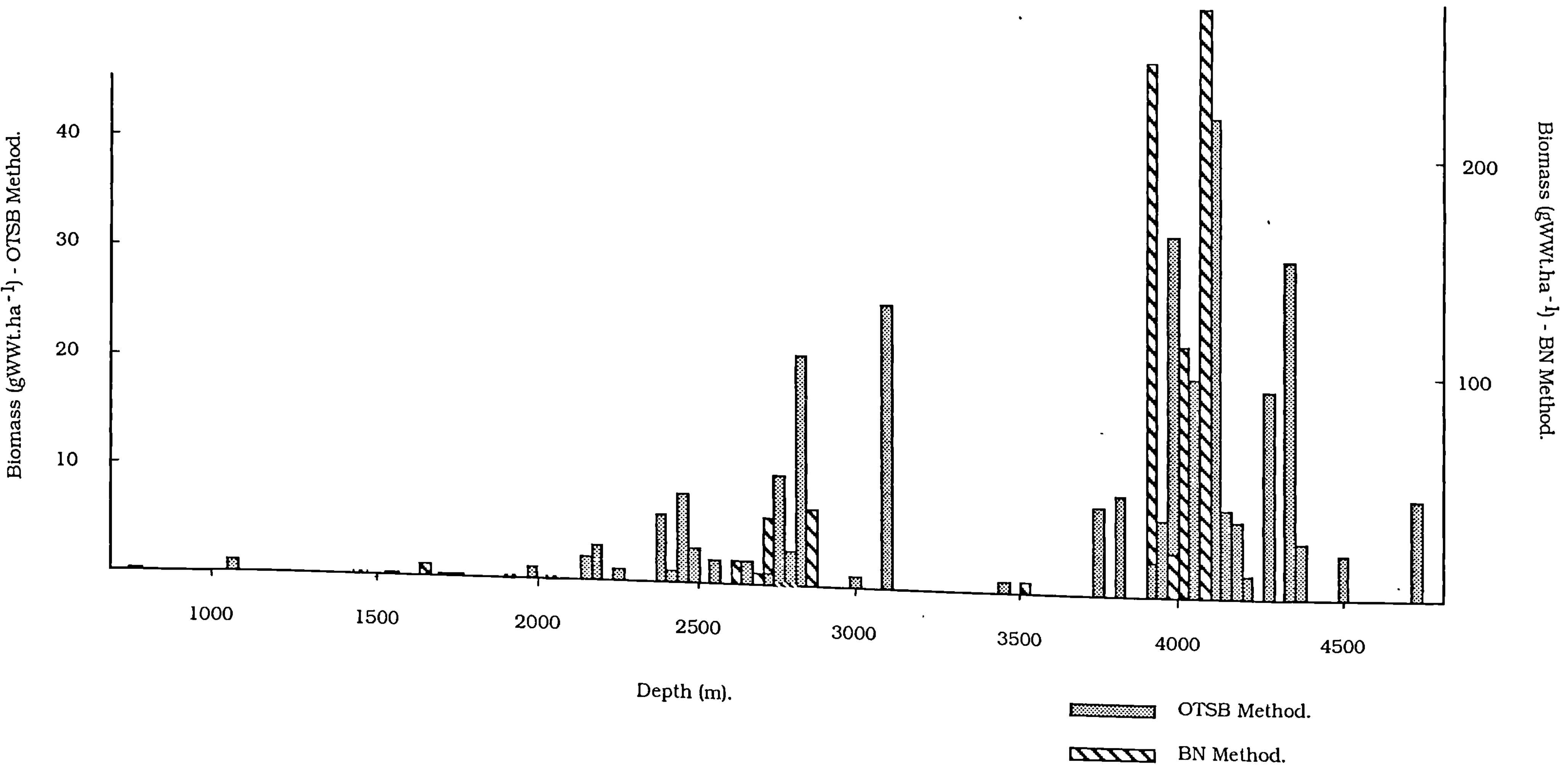


Fig. 43: Total biomass of *Munidopsis* spp. over the depth range of the genus in the Porcupine Sea-bight.

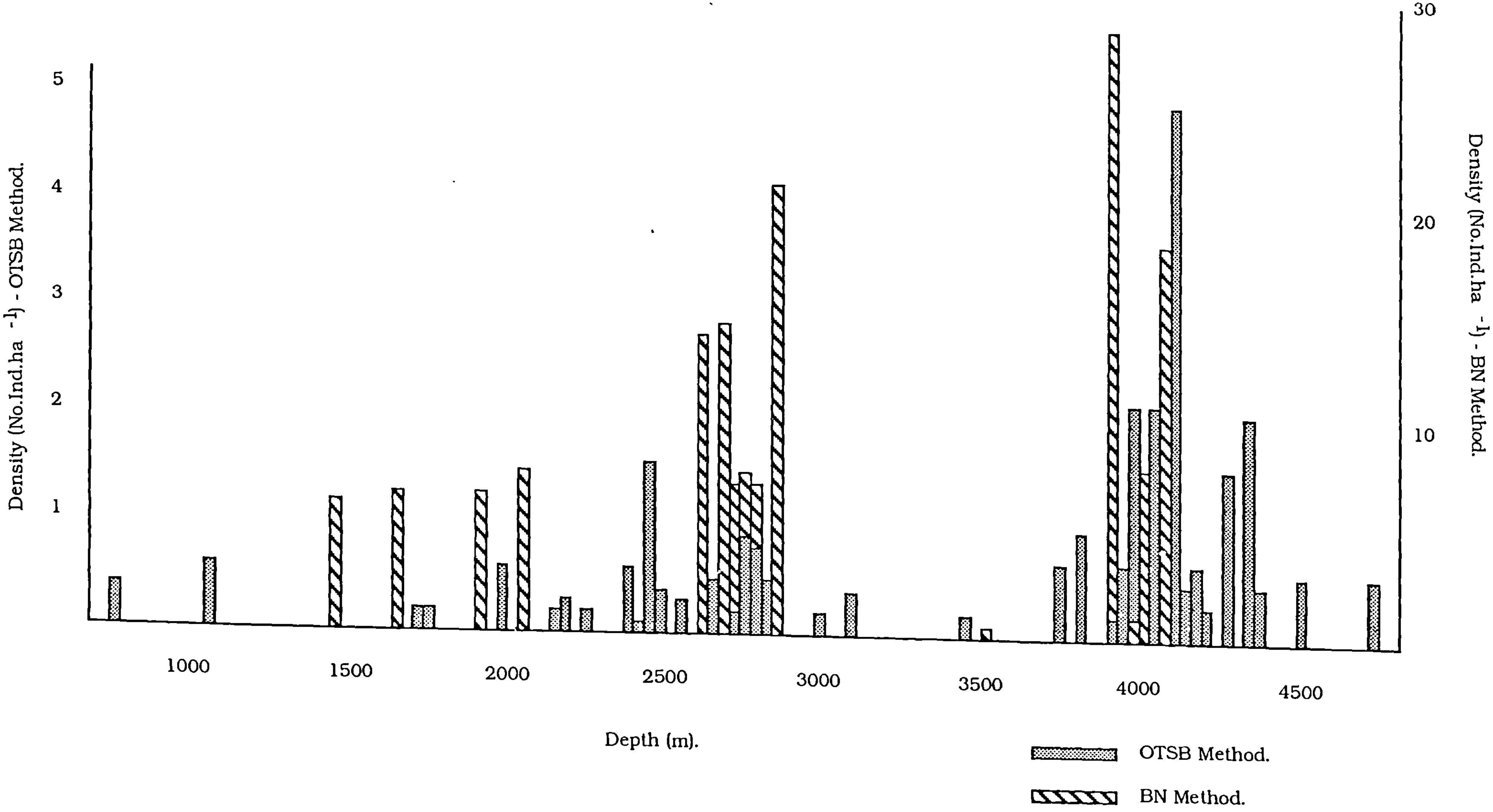


Fig. 44: Total density of *Munidopsis* spp. over the depth range of the genus in the Porcupine Sea-bight.

3000 m, represented by the mid-slope species, in particular *M. rostrata*, and a second greater peak at 4000 m (the base of the slope) representing the overlap between the lower slope species (*M. aries* and particularly *M. antonii*) and the large abyssal species of *M. parfaiti* and *M. crassa*. At one station (9638#2, 4074 m) all four species were taken. This area at the foot of the slope is where the *Munidopsis* genus is both most abundant in the Porcupine Sea-bight and has the highest biomass. This peak may reflect beneficial conditions in the area caused by the congregation of detrital material and other matter at the foot of the slope.

It is interesting to note the low *Munidopsis* abundance between 3000 and 4000 m - the shallow end of the range of the lower slope species. The biomass and density for the two samples taken at around 3500 m are extremely low compared to similar hauls 500 m either side of this depth. Comparatively few hauls have been taken over this depth interval, so more samples are needed to investigate whether there is indeed a low number of *Munidopsis* in this region.

Chela Shape.

From plain observation, it would appear that the *Munidopsis* species covered by this study fall into two groups regarding their physical appearance, characterised by 'spade-type' or 'spear-type' chelae. To investigate this further, the relationship between ChW and ChL was obtained for each species, as outlined under the separate accounts. On initial inspection of morphological features, particularly the claw shape, the species fall into the following groups:

'Spade-type' chelae - *M. bermudezi, M. aries, M. parfaiti.*

Intermediate chelae (Long with broad palms) - *M. crassa.*

'Spear-type' chelae - *M. rostrata, M. antonii, M. bairdii.*

Small type (with elongate chelae) - *M. curvirostra, M. serricornis.*

The mathematical relationships can be compared by plotting each female value (to allow *M. crassa* to be compared) over a hypothetical chela length scale (Fig. 45), though the sample

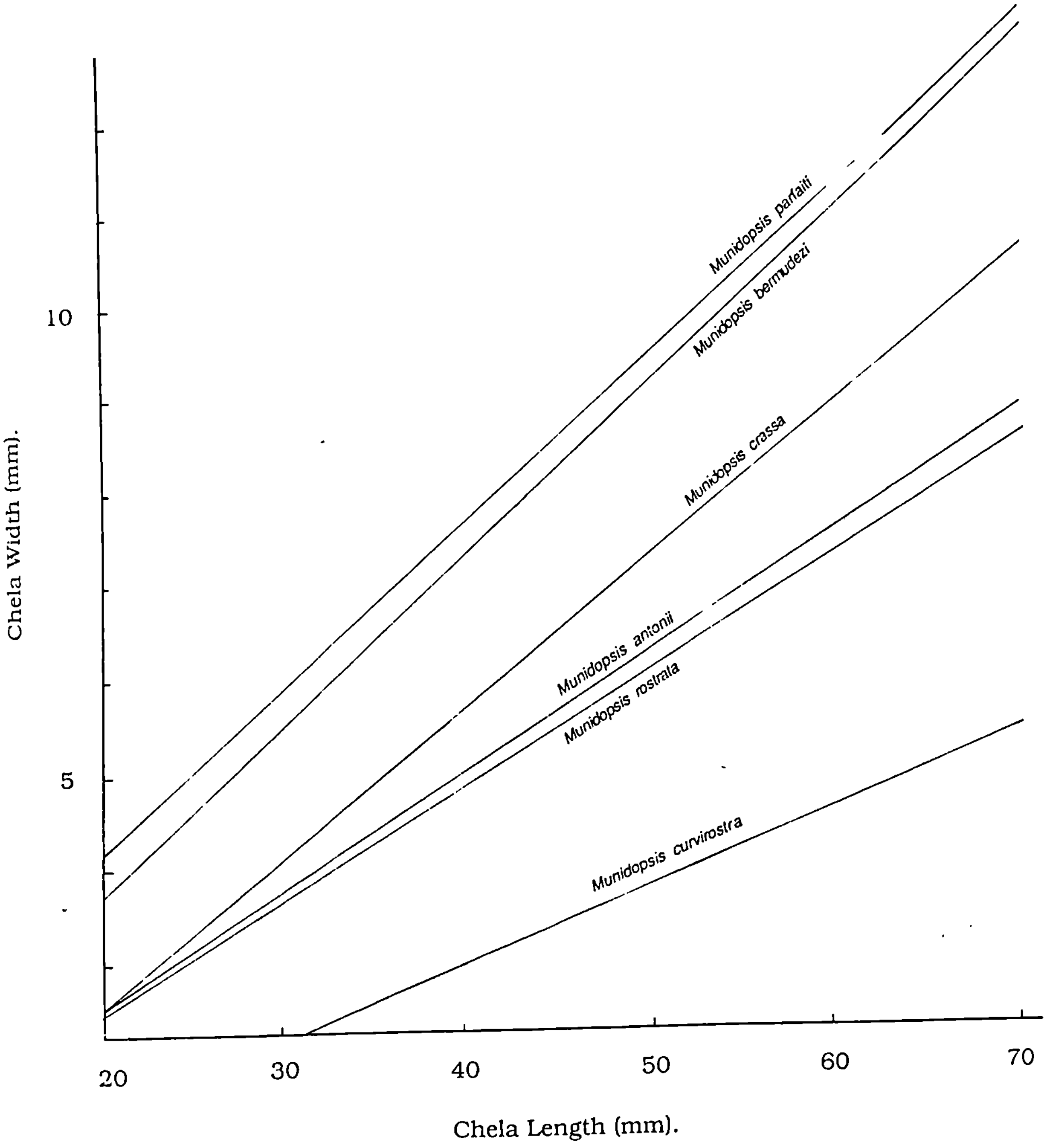


Fig. 45: Comparison of the relationships between ChL and ChW for female *Munidopsis* spp.

sizes for *M. aries, M. serricornis* and *M. bairdii* were too small to allow meaningful analysis. The results support the initial classification, with pairings of *M. parfaiti* with *M. bermudezi* and *M. antonii* with *M. rostrata, M. crassa* falling distinctly between the two pairs with the small *M. curvirostra* quite separate. It is interesting to note that with the exceptions of the very different two small species (which may be adapted to the shallower regions) and the rare *M. bairdii,* none of the species in a particular chela class are found in the same bathymetric distribution group. In addition, the two most abundant species, *M. antonii* and *M. rostrata* both have 'spear-type' chelae. This may indicate niche separation in relation to diet, with the chela types feeding on different food items, though the stomach contents analysis proved inconclusive - stomachs either being empty, distorted due perhaps to preservation or containing unidentifiable detrital and sediment matter. Gore (1983) examined guts of his species and found *M. aries, M. crassa* and *M. bermudezi* with similar detrital material. He suggested the "spatulate" chelae were used as scraping and grasping claws, or in the case of *M. crassa,* used to spoon detritus off the floor. Unfortunately, Gore did not examine any *Munidopsis* species with 'spear-type' chelae. Further evidence for the development of the chela shape to suit diet was provided by the remarkable find of a *Munidopsis* species colonising a piece of wood retrieved by submersible from 2750 m (van Dover, 1988). This species possessed "distinctive rasp-like fingers on its chelipeds that seem ideally suited for scraping up wood." The guts were packed full of "sawdust". The idea that a species of *Munidopsis* has evolved to exploit such an unpredictable and comparatively rare food source is fascinating.

Reproduction.

The fecundity of *Munidopsis* species showed marked differences from the shallower *Munida* species found in the Porcupine Sea-bight (Chapter 3), even *Munidopsis serricornis,* which overlaps with *Munida tenuimana.* The deep-water genus showed the general trend of very few, large eggs, the maximum number found being a mere 110 for *M. antonii* (compared to a

February mean of 1710 for *Munida sarsi*). This difference in fecundity is most likely related to the development and bathymetric distribution of the larvae (Wenner, 1982), *Munidopsis* having a few eggs that reach an advanced stage of development before hatching (Samuelsen, 1972; this study). The larvae released probably remain fairly close to the sea-bed while completing their development, this demersal larval strategy enhancing survival of these deep-living species, as Thorson (1950) suggests for other groups, such as deep-sea shrimps (e.g. *Crytocheles, Bythoceris*) (also Wenner, 1978), prosobranchs (e.g. *Sipho, Acrybia*) and some echinoderms (also Mortensen, 1921).

Fage & Monod (1936) reported that young *Munidopsis polymorpha* were well developed inside the egg, and probably hatched as a form similar to a small adult. This led Wenner (1982) to suggest two possible patterns of *Munidopsis* larval development:

1. Advanced larva, hatching as penultimate/ultimate zoea, which moults to megalopa and settles, e.g. *M. serricornis* (Samuelsen, 1972), *M. curvirostra* (this study).

2. Larvae undergoing direct development, hatching as small adults, e.g. *M. polymorpha* (Fage & Monod, 1936).

Both strategies possibly, if not probably, exist in the deep-sea. It is interesting to note that the species listed with the first pattern of advanced larval development are those found in shallower open water, whereas *M. polymorpha* lives in a restricted cave habitat. It would therefore appear that the reproductive strategy developed by *Munidopsis* is highly adaptive and has enhanced the species' ability to colonise the true deep areas of the oceans. It would not be surprising to find that the abyssal species (*M. parfaiti* and *M. crassa*) have a larval development similar to that of *M. polymorpha.*

Another interesting feature of *Munidopsis* reproduction was the percentage of mature females of each species found to be ovigerous. When a histogram is constructed from these data in order of depth distribution (Fig. 46) an overall pattern of decrease in the proportion of ovigerous females with depth becomes apparent. Whether this is purely coincidental is

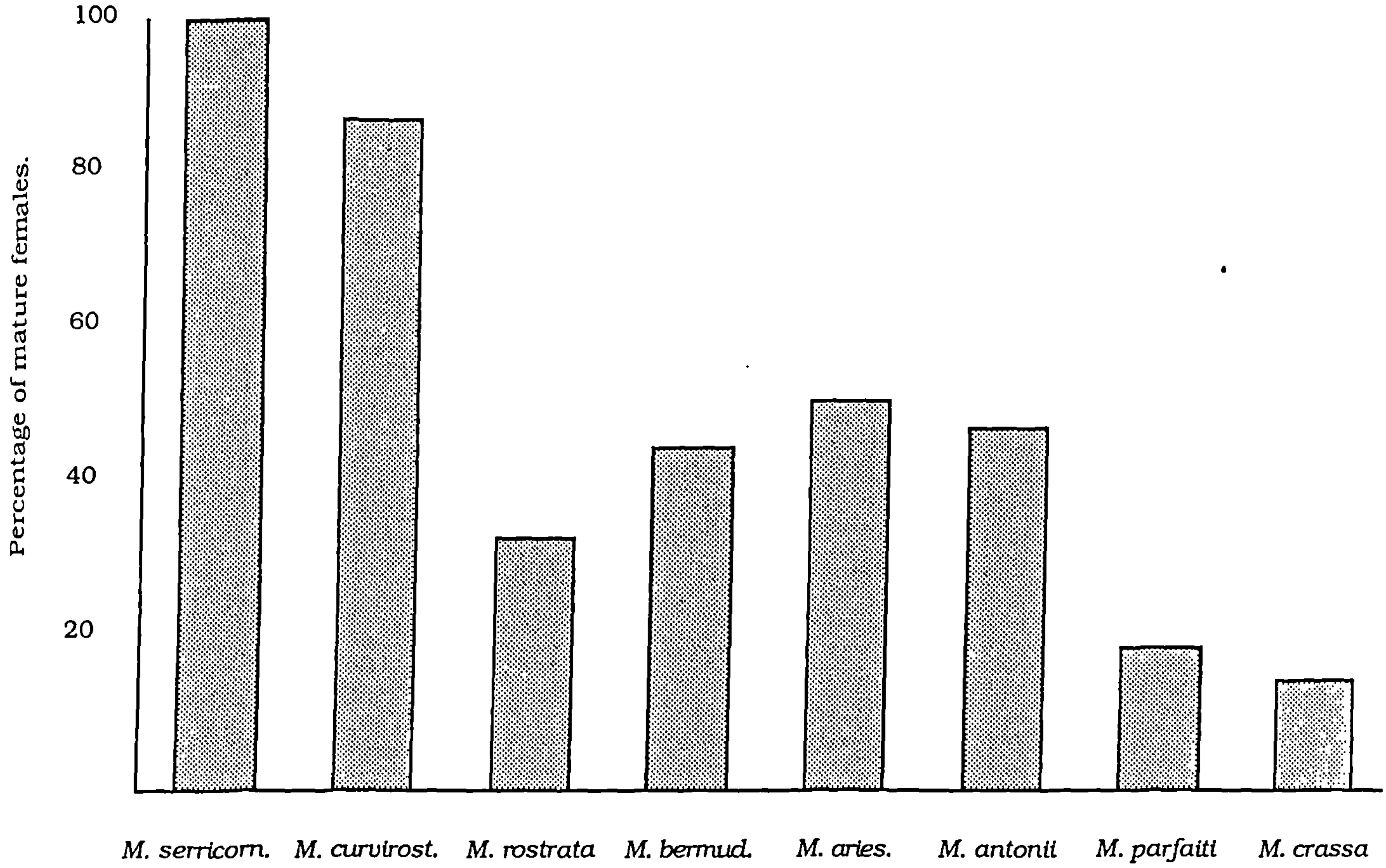


Fig. 46: Proportion of mature females caught carrying eggs for each *Munidopsis* sp.

uncertain, though if not, the reasons behind this pattern are certainly unclear. A possible explanation may be resource limitation, the *Munidopsis* from the abyssal plain having a lower food availability. More time would therefore be needed to accumulate adequate reserves for a batch of eggs, so a longer period of time elapses between broods and consequently a greater proportion of females are non-ovigerous at any one time.

There was no concrete evidence for any seasonal cycles of reproduction for *Munidopsis*, most species having ovigerous females over a wide range of months, with a similar scattering in relation to ovary development. Other studies (e.g. Mayo, 1974; Wenner, 1982) present similar data. The production of young would therefore appear to be a continuous process for each individual, bearing no relationship to the egg production of other members of the species in the same area.

Munidopsis as a genus would appear to be well adapted to life at extremes of depth, being an important constituent of the megafauna in the Porcupine Sea-bight below 2000 m. The genus has developed a reproductive strategy different from other anomurans in having few eggs from which hatch advanced larvae. This would seem beneficial in maintaining and enhancing survival in bathyal and abyssal areas, and in certain regions (e.g. 4000 m) *Munidopsis* comprises a substantial biomass.

Chapter 7:

The Benthic Decapod Crustacea of the Porcupine Sea-bight: a General Overview.

General Overview.

The genera covered by this study (*Munida, Munidopsis, Geryon*) are some of the largest and certainly most abundant benthic decapods to be found in the Porcupine Sea-bight region. They comprise a major part of the megafaunal biomass on the deep-sea bed, along with other important groups such as echinoderms (esp. holothurians, e.g. *Oneirophanta, Stichopus*) (Gage *et al,* 1985), fish (e.g. *Nematomurus, Histiobranchus*) (Merrett & Marshall, 1981; Gordon & Duncan, 1985) and pennatulids (e.g. *Kophobelemnon, Umbellula*) (Marshall, 1979). Most other groups, such as the gastropods and echiurids, are represented, but in smaller numbers (Attrill, *et al,* 1987).

Other less abundant benthic decapods are also to be found in the Sea-bight, especially in the shallower regions, where species such as *Nephrops norvegicus, Nephropsis atlanticus, Pagurus variabilis, Goneplax rhomboides* and *Macropipus tuberculatus* occur, together with natantians such as *Pontophilus* and *Dichelopandalus* (from 'Discovery' collection). On the upper slope, species like *Paramola cuvieri* (Ingle, 1980) and *Dorhynchus thomsoni* (Hartnoll, *et al,* 1987) occur, but on the lower slope and abyssal plain the decapod community is dominated by *Munidopsis* spp. together with deep-water natantians, such as *Plesiopenaeus armatus* and *Glyphocrangon* spp. (Holthuis, 1971). A lot of work is yet to be done on the biology and ecology of these natant and less common reptant decapods.

Despite relatively extensive coverage of the systematics of the three genera covered in this study, the taxonomy of many of the species is still undecided, though the classification of the species covered by this study has been adequately resolved. Of the three genera, the relationships within the genus *Munida* have been most satisfactorily resolved, the major NE Atlantic species being covered by Rice & St Laurent (1986).

The systematics of *Munidopsis* have probably received equal emphasis, yet in some species, such as *M. rostrata, M. aries* and *M. bermudezi,* local variations in morphological features and changes with age have led to the construction of a variety of synonyms and analogs. It is likely that many deep-sea species are reproductively isolated by land masses and oceanic ridges and so may have evolved, or are in the process of evolving, into separate species. The arguments will not be resolved by comparisons of morphological features alone as these are so easily influenced by phenotypic parameters and vary with age, as in the case of *M. aries*/*M. sundi* (Gore, 1983). It would therefore seem that a biochemical/genetic investigation involving electrophoretic or DNA studies is required to try and clarify the situation in respect to these similar species from different localities, and to help determine the relationships between the members of the genus. However, a major hurdle to such an investigation would be the collection of fresh or adequately preserved material of comparatively rare and inaccessible species.

The genus *Geryon* probably poses the most taxonomic problems. Manning & Holthuis (e.g. 1981, 1986, 1987) have started to address the problem of the existing species, though it would appear that this is the tip of the iceberg. Ray Manning, Smithsonian Institute, Washington (pers. comm.) suggests that *Geryon* probably comprises two genera, with the three-spined *G. trispinosus* and *G. longipes* forming a separate genus from the rest of the species, which are five-spined.. He is currently reappraising the material stored in museums worldwide, including that for the NE Atlantic, and it is very likely that many more species will result from these studies. *G. gordonae* for example is probably two species - one from the north of its range and one from the south. Genetic investigation would probably also aid the clarification of *Geryon* classification. This future work will hopefully resolve many of the problems associated with deep-sea decapod taxonomy.

If the taxonomy of the decapods seems a little unsure, that of the parasites infesting these Crustacea is practically non-existent. Most records of both rhizocephalan and bopyrid parasites are listed as, for example, "*Lernaeodiscus* sp." or "an undescribed bopyrid, possibly *Pseudione* sp." There are dozens of records of parasites yet to be properly named and classified, with probably many hundreds yet to be discovered or recognised (J. Lützen, pers. comm.). Jens Høeg and Jørgen Lützen (Copenhagen) are attempting a start at the rhizocephalan part of this material, though the taxonomy of the group practically ground to a halt upon the death of Boschma. John Markham (Oregon) is compiling records of deep-sea bopyrids and resulting partly from material discovered during this study will probably commence a comprehensive attempt at naming and describing these parasites from *Munidopsis*, though the main problem lies with the lack of a series of specimens for each species - most new discoveries being yet more new species or even genera! The parasitic fauna of deep-sea Crustacea is one important area requiring extensive work, both in respect to taxonomy and biology, and hopefully interest in this area will be generated.

The species covered by this study, particularly the galatheids, showed a distinct bathymetric succession, from the subtidal *Munida rugosa* to the abyssal *Munidopsis* species (*M. crassa, M. parfaiti*). The calculated ranges for all these species can be brought together to demonstrate this pattern (Fig. 1). The *Munidopsis* species were classified into four depth zones (Chapter 6, p. 120); the *Munida* species show a more discrete banding, with little overlap in the ranges of the four species. The mechanisms behind this discrete zonation are interesting. Most classic zonation patterns, as found for example on rocky shores (Dayton, 1971; Connell, 1973) infer both some degree of competition and limitation of range due to the extremes of physical tolerance. Could similar phenomena influence the galatheids in the Porcupine Sea-bight? It is likely that excesses of depth, with the increases in pressure, decreases in temperature, etc., exclude species from extending their range further down the slope. For instance *M. sarsi* may not tolerate conditions below 800 m, this being reflected in the decrease in abundance of the species at the lower end of its bathymetric range (Chapter 3, Fig. 9). However, it would be expected that *M. tenuimana* would under normal circumstances colonise the regions above 750 m, where conditions should be more favourable - indeed in other areas, e.g. Norway (Brinkmann, 1936), it is found much shallower. However, there is some factor preventing the

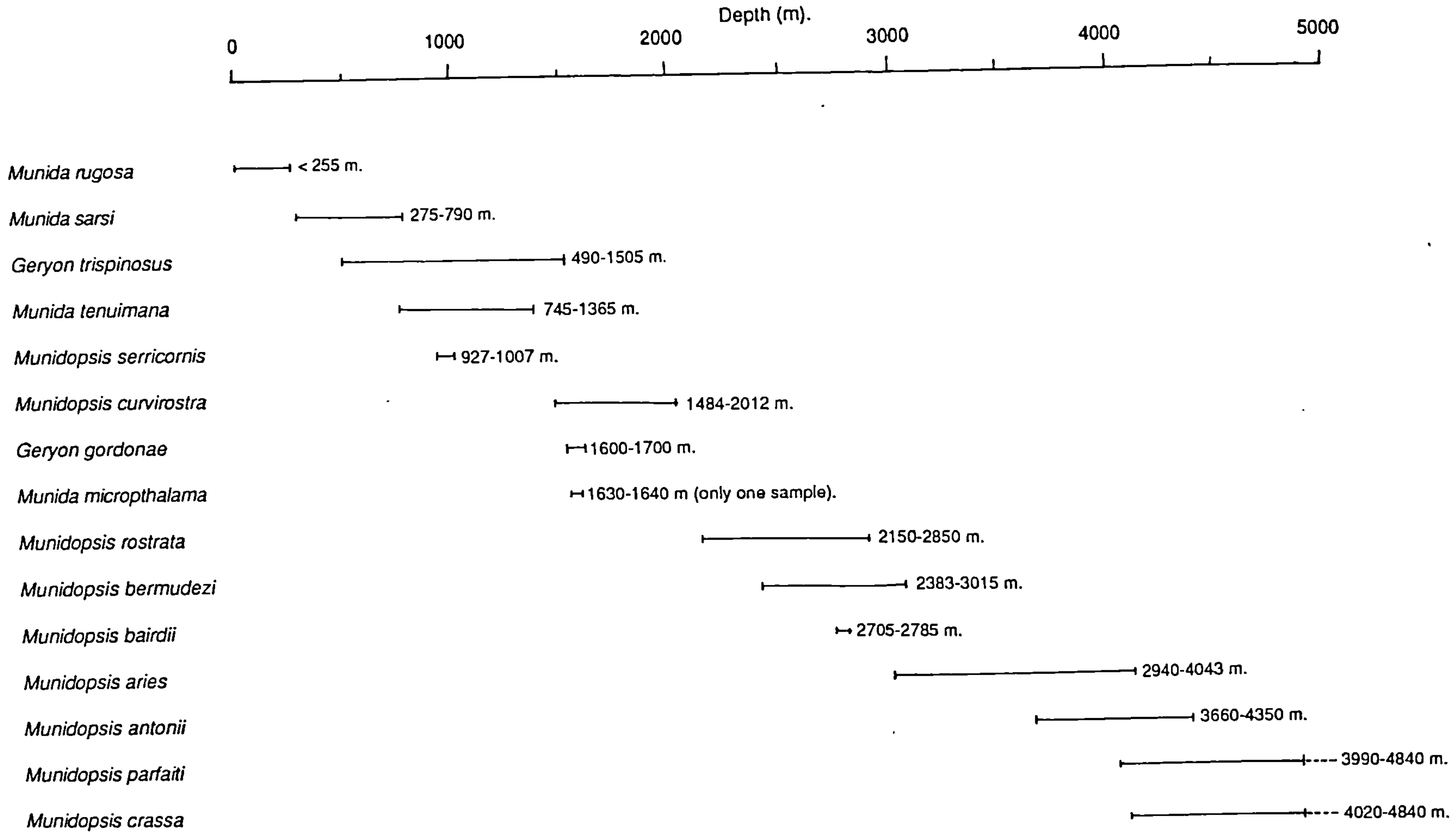


Fig. 1: Bathymetric distribution in the Porcupine Sea-bight of the decapod species studied. (Calculated ranges).

upward spread of *M. tenuimana* in the Porcupine Sea-bight, which could be also affecting other species. The deepest *Munidopsis* may well be prevented from upward range extension by increases in temperature, but this is unlikely for shallower species such as *M. tenuimana* which have survived perfectly well in laboratory conditions. Dayton *et al* (1982) successfully transplanted deep-water barnacles to shallower depths, indicating that at least one species was restricted to a zone smaller than it could potentially fill. Is it possible that *M. tenuimana* is prevented from extending further into the shallows by competitive exclusion by the 'fitter' *M. sarsi?*

Carney *et al* (1983) commented that invoking both competition and predation was "appealing" due to the inability to relate the distribution patterns occurring below 1000 m to purely physiological phenomena. In addition, Menge & Sutherland (1976) reasoned that competition might be expected to play an even greater rôle in the deep-sea than in shallow environments, where physical disturbance is more severe and is therefore a dominant influence.

However, there is a problem in proving the existence of competitive partitioning along the depth gradient due to the lack of a definitive analytical technique for demonstrating such a phenomenon from distributional data. All the same, an adaptation to the deep-sea of the principle outlined by Terborg (1971), for mountain gradients in Peru, stemming from the computation of similarity curves along the gradient, may hold some potential. If species were partitioning some resource along the gradient, with competition at the species interfaces, then the boundaries would be sharp with little overlap. Rex (1977) applied this theory to the deep-sea and found that the rate of faunal change was dependent on the faunal group - megafauna changing the most rapidly. Rex inferred from Menge & Sutherland (1976) that this was due to a lowered predation pressure at the higher trophic levels, more crowding on the gradient and so increased effects of interspecific competition.

The difference between the discrete zonation of *Munida* and the more amorphous succession seen in *Munidopsis* may be due to the development of morphological features in

Munidopsis that allow resource partitioning while co-habiting, namely possible niche separation in feeding methods suggested by the variations in chela morphology. It was noted that below 2000 m, the bathymetric groups of *Munidopsis* species did not contain morphologically similar species, e.g. *M. bermudezi, M. aries* and *M. parfaiti* (spade-type) are separated bathymetrically, as are the successful 'spear-types' of *M. rostrata* and *M. antonii.* As mentioned above, the diversity of reptant decapods is lower in the deep-bathyal and abyssal areas, so it may be the case that *Munidopsis* has been able to diversify as a genus and occupy the available niches unexploited by other genera unable to tolerate the adverse physical conditions.

An important factor of the general bathymetric distribution is the pattern of abundance for each species over that range, represented by biomass (g.WWt.ha^{-1}) and density (No.Ind.ha^{-1}) at the sites where the species in question were taken. These data are available for each species in the previous chapters. However, figures were constructed for total density and biomass at each station for the *Munidopsis* genus as a whole, and these can be extended at the shallow end to incorporate the *Munida* species and *Geryon trispinosus* (Figs. 2 & 3). These figures are important in highlighting the trends in both the biomass and density of the species studied across the whole bathymetric range of the Sea-bight, and it can be seen that there is an initial exponential decrease in both parameters down to 1000 m. From this depth to the abyssal plain the abundance is at a constant low level, with occasional small peaks relating to *Munida tenuimana/Geryon trispinosus* (≈1200 m), *Munidopsis rostrata/M. bermudezi* (≈3000 m) and the lower slope/abyssal *Munidopsis* species (≈4000 m). The difference in levels of biomass between the areas below 1000 m and the highest values in the shallower water is considerable (100-150x), partially explained by the aggregations of large *G. trispinosus* in the shallower regions. However, the highest biomass figures relate to *Munida sarsi* - a decapod smaller than most of the deep *Munidopsis* species, reflected by the equivalent high density figures. Overall,

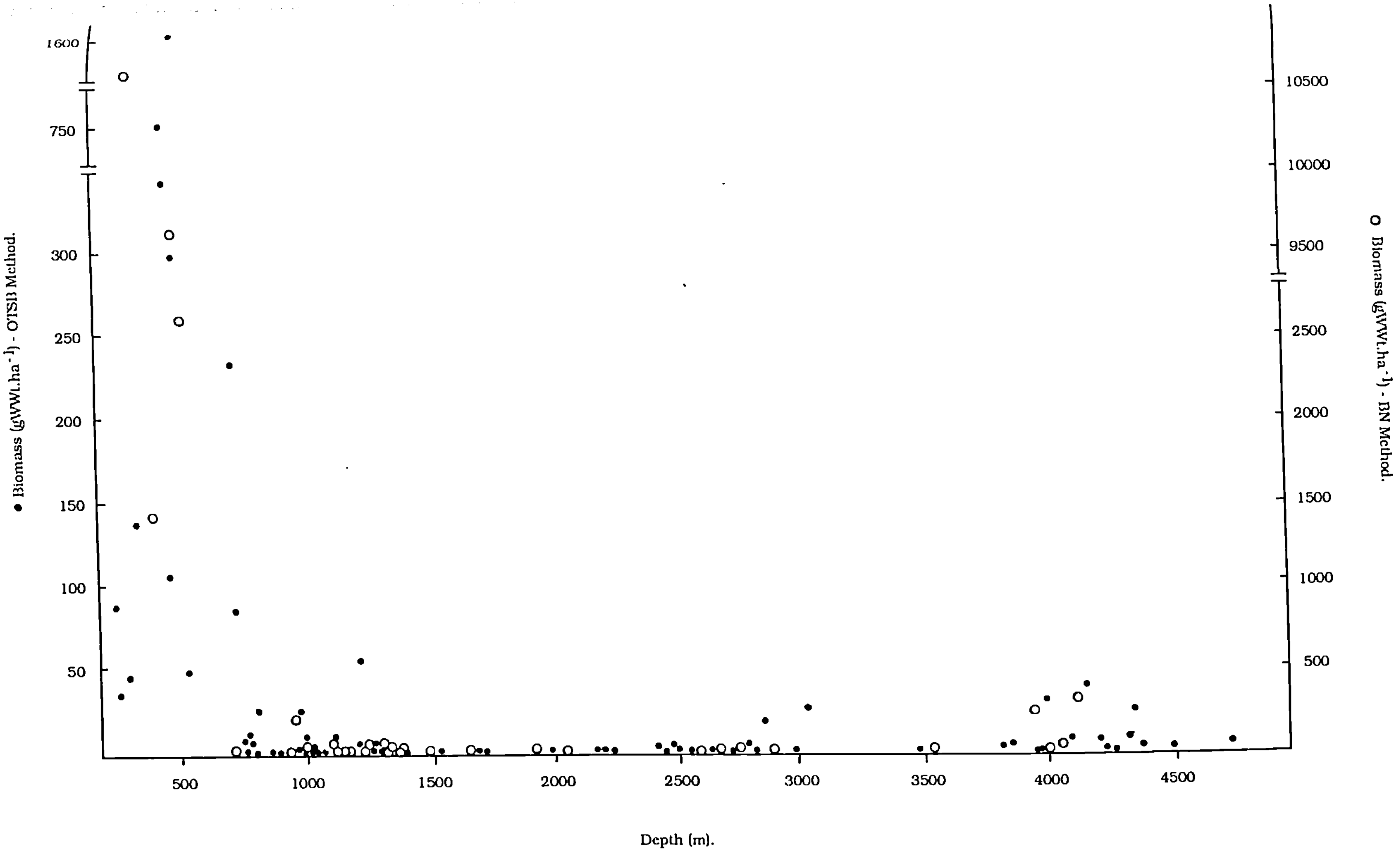


Fig. 2: Total biomass of the decapods studied over the total depth range of the Porcupine Sea-bight.

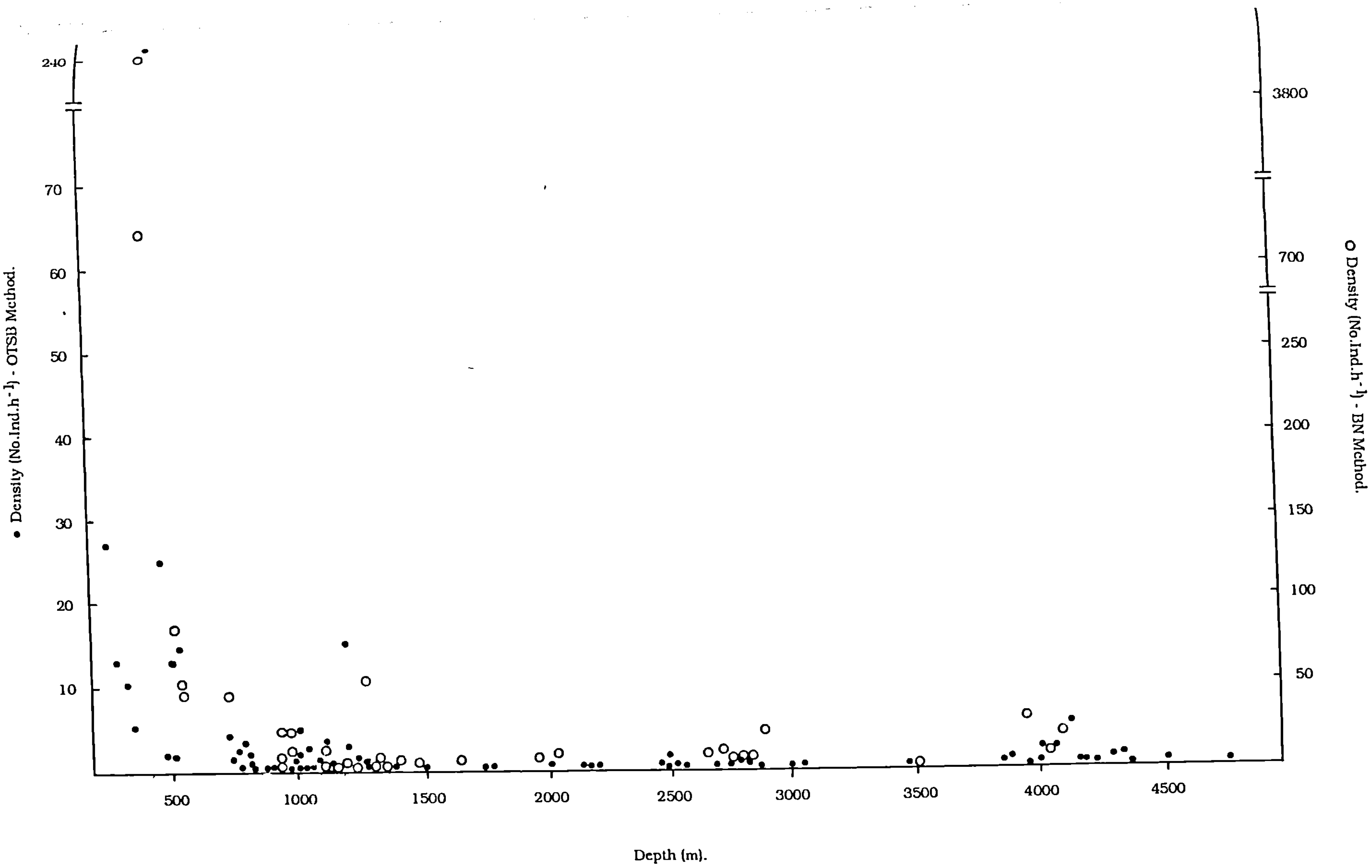


Fig. 3: Total density of the decapods studied over the total depth range of the Porcupine Sea-bight.

the region above 1000 m supports a comparatively high biomass, the species found here being highly successful. These high concentrations of *M. sarsi* and *G. trispinosus* support the theory that these successful species may be competitively excluding the decapods found directly below, such as *Munida tenuimana*, which can survive at depth but do not flourish in the numbers of their shallow water counterparts due to the increasingly adverse conditions. Where *M. tenuimana* has been found at shallow depths, it has thrived in numbers similar to those of *Munida sarsi* (e.g. Brinkmann, 1936). It would appear that conditions overall in the Sea-bight are not as favourable as, for instance, Norwegian fjords, with more limiting factors prevalent. As a result, competition for these resources becomes important, favouring the more competitive species at the expense of less competitive ones - the aggressive behaviour of *M. sarsi* being well documented (Berrill, 1970).

The observed trend in biomass is consistent with worldwide biomass plots for macrobenthos as a whole (see Rowe, 1983 for review), with an initial dramatic decrease followed by a levelling off, this level then being maintained as deep as 10000 m. The decrease in biomass has been attributed to food availability. Zooplankton biomass also decreases in a similar exponential pattern (Vinogradov, 1968), and both deep-sea pelagic and benthic communities have the same basic food source, namely surface-derived organic material (Rowe *et al*, 1974) that sinks, in the Porcupine Sea-bight, seasonally to the sea bed (Billett *et al*, 1982). Therefore, the deeper the water, the greater the utilisation of the organic matter by the pelagic community and the less particulate organic carbon is available to the benthos. Much of the matter arriving on the sea bed is zooplankton faecal pellets, which have had a major portion of the available carbon removed for energy and growth of the planktonic organisms (Rowe, 1983).

Distance from the shore may also be a factor determining resource availability (Bruun, 1957) - the deep-sea regions nearer the coast benefiting from terrestrial runoff and coastal-zone productivity. Whether the comparatively small distances involved down the Porcupine Sea-bight vary in the influence of such inputs is debatable, but again there will probably be utilisation of coastal production by pelagic and upper-slope organisms before such benefits reach the deeper abyssal areas.

Zenkevitch (1961) suggested that one reason for studying deep-sea biomass was to infer levels of heterotrophic production to allow comparison with other marine systems - an extremely low biomass, as seen in the deep Sea-bight, indicating low rates of biological processes compared to shallow water. Evidence of slow growth rates in the deep-sea is contradictory due to the general nature of measuring such parameters under relevant conditions, but recent studies on the megafauna (e.g Tyler & Gage, 1980; Williams & Turner, 1986) suggest rates of growth slower than in shallow water. In Crustacea especially, this may be a function of the cold temperatures of < 5° C (Kurata, 1962; Hartnoll, 1982) as much as anything else.

Living at depth also entails another major problem - the long term maintainance of the population within the depth band that the species inhabits. A reproductive strategy is required that best fits the needs of the species at each particular depth, especially to maintain the population in abyssal regions.

The species covered by this study were divided into two distinct reproductive strategies:

a) Large number of small eggs, usually produced seasonally, with standard planktotrophic larvae spending time in the surface community before descending and settling. Demonstrated by the shallow species *Munida rugosa, M. sarsi, M. tenuimana* and *Geryon trispinosus.*

b) Very few large eggs, with extended development, produced constantly by individuals with no evidence of seasonality. Larvae hatch in an advanced state (lecithotrophic/direct development) and probably remain near the sea bed. Demonstrated by the exclusively deep-sea genus *Munidopsis.*

The first case is the norm for anomurans, so it would appear that the *Munidopsis* species have developed non-planktotrophy as an adaptation to allow extension into the deepest parts of the ocean, as suggested by Thorson (1950) for deep-sea organisms generally. Bouchet (1988) commented that "planktotrophy is a non-adaptive ancestral phylogenetic condition that is maintained throughout evolution, until it is lost to non-planktotrophy as a result of adaptation", which is somewhat contradictory but basically suggests that species with planktonic larvae will keep this state, but may be limited, in relation to the depth distribution, by this strategy unless non-planktotrophy is acquired, as in the case of *Munidopsis*. Bouchet also argues that non-planktotrophy is often a phylogenetic constraint, e.g. for the lower prosobranch gastropods, and the reason such deep-sea representatives have a non-planktonic larval strategy is because all of them possess it anyway, rather than it being an adaptation to deep-sea life. However, this argument can be turned on its head - the reason these prosobranchs are found successfully in the deep-sea is *because* they have the initial benefit of the non-planktotrophic life cycle. Planktotrophic development is occasionally found fairly deep (>1000 m), e.g. in some gastropods (Bouchet, 1988), but rarely below 2000 m.

As outlined in chapter 6, the *Munidopsis* reproductive strategy is divided into two separate classes relating to length of intracapsular development, some larvae hatching as advanced zoeae (*M. serricornis, M. curvirostra*) and others having more-or-less direct development (*M. polymorpha*). Unfortunately, the only larvae described for *Munidopsis* species found in the Porcupine Sea-bight have been for the two shallow species (Samuelsen, 1972; this study, Ch. 6), and it is interesting to note that their strategy falls somewhere between the extremes of *Munida* planktotrophy and *Munidopsis polymorpha* direct development. Where these advanced larvae go upon hatching is unknown - perhaps to midwater areas or utilising near-bottom currents for dispersal. It would be exceedingly interesting to be able to rear the young of deep-water *Munidopsis* (e.g. *M. antonii, M. crassa*), if an ovigerous female can be kept alive, as it would not be surprising to find a direct development to suit the relatively isolated habitat of the abyss, similar to that of the cave-dwelling *M. polymorpha.* This would enable maintainance of position, dispersal perhaps occurring by walking across the sea-bed. Nomadic behaviour such as this, as has been noted by tagging studies for other deep-sea species, e.g. *Geryon maritae*

Species.	Wet Weight (g)	Egg Number.	Total Egg Vol. (mm^3)	Egg Vol./g.WWt.
Munida sarsi	1·4	650	132	94
	2·3	1050	214	93
	2·8	2100	428	153
	4·1	1850	377	91
	11·8*	2400	488	41
	15·1*	3750	764	50
	18·9*	3950	805	43
	30·9*	4350	886	29
Munida tenuimana	1·8	570	203	113
	2·8	540	186	66
	4·1	480	134	33
	5·8	220	43	7
	9·1	1680	579	63
Munidopsis.				
M. serricornis	1·1	30	8	7
M. curvirostra	0·22	13	7	31
	0·38	7	3	7
	0·41	13	2	4
	0·84	20	8	9
M. rosrtata	9·6	71	732	76
	10·7	70	180	17
	11·5	77	709	62
	13·7	108	602	44
M. bermudezi	7·9	48	147	19
	8·3	23	59	7
M. aries	137·1	106	3045	22
M. antonii	13·5	56	515	38
	14·4	32	232	16
	18·5	50	409	22
	20·9	28	289	14
	23·7	110	796	34
	25·6	71	396	15
M. parfaiti	10·5	25	258	25
	11·5	20	312	27
M. crassa	32·8	32	452	14

* sample 51302

Table 1: Total egg volume for size ranges of the *Munida* and *Munidopsis* species with ovigerous female representatives, together with values expressed in terms of body weight.

(Melville-Smith, 1987a), would also aid the location of a mate - a task that would be difficult for strict burrow dwellers living in a low density population as do deep *Munidopsis.*

On initial inspection, it would appear that the *Munida* species have a much greater investment in reproduction with their large number of eggs compared to the few eggs produced by the *Munidopsis* species. However, the two genera can be compared by total egg volume rather than number, and related to the proportional input into reproduction by calculating mm^3 volume of eggs/g wet weight (to equate a volume with a volumetric function). From the resulting Table 1 it can be seen that there is in fact much less of a differential than would at first be expected. The 'standard' *Munida sarsi* do show a greater investment, but *M. tenuimana* and the large *M. sarsi* from sample 51302 have values more comparable to those for the *Munidopsis* species. It is also interesting to note that despite their small size, the shallow water *M. serricornis* and *M. curvirostra* have a low investment - even for *Munidopsis* species. This could relate to the other feature of these two species - the extremely high proportions of mature females found to be carrying eggs. It is possible that both the small, shallow species have practically continuous egg production with lower investment, so get through potentially more broods in a given time period than deeper *Munidopsis* that have more of a gap between hatching and laying. If this were true, useful figures for comparison would be those expressed in mm^3.egg vol./g.WWt./year, if such data could be obtained. Whatever, it would seem that both *M. serricornis* and *M. curvirostra* differ considerably from the other deeper *Munidopsis* in many of the aspects of their biology and morphology covered by this study.

The reproductive strategies demonstrated by the anomurans are an aid to the maintenance of position over relatively narrow depth bands, especially the extended development of the deep *Munidopsis.* A major problem of the planktotrophic larval life of *Munida* spp. and *Geryon trispinosus* is the actual settling process - the settling stage has to locate the small depth band inhabited by the adult population, a small proportion of the sea bed for species like *M. tenuimana.* This larval settlement is most likely passive, i.e. most larvae settle in unfavourable areas such as that inhabited by *M. sarsi* and so do not survive. Only the small proportion surviving their planktonic development and the locating of the sea-bed between 750 and 1500 m sustain the adult population - another factor contributing to the comparatively low abundance of *M. tenuimana*. If the location of the correct site of settlement seems difficult for some of the deep-sea decapods, then the problems of settlement faced by some of their parasites are extreme, especially those infesting the deeper *Munidopsis* species, such as *Pleurocryptella superba* (bopyrid) on *M. crassa* (Bourdon, 1981) and *Cyphosaccus jensi* (rhizocephalan) on *M. antonii* (Lützen, 1985). Not only do the settling cyprids have to locate the depth bands of their hosts, but also locate a potential host specimen within that area, often when the *Munidopsis* species in question, e.g. *M. crassa*, has a low density. Such a feat seems almost beyond the realms of possibility for the already highly specialised life cycles of these two groups (see the summaries of the life cycles in Chapters 3 & 4). For example, a settling female rhizocephalan cyprid has to locate a host, difficult enough, but then to achieve maturity a male cypris has then to locate the host with this virgin female already established. The chances against this randomly happening have to be enormous, so it would seem likely that the deep-sea forms, to have survived this long, have probably adapted an already highly specialised life cycle even further. Chemosensation is probably highly important, especially when many of the deep-sea areas have unidirectional currents, and it is likely that this use of pheromones is coupled with larvae that are comparatively long lived and selective, capable of 'sampling' each potential settling site and then moving on if this site is unsatisfactory. It is possible, judging from the few specimens caught, the apparent rarity of some parasite species, and the logistics involved in deep-sea studies, that the life cycles of such animals may never be fully discovered.

The galatheid genera of *Munida* and *Munidopsis* and the brachyuran *Geryon trispinosus* demonstrate different reproductive strategies reflecting the difference in their bathymetric distribution, *Munidopsis* evolving a non-planktotrophic development to enhance colonisation and survival at the deeper areas, while *Munida* and *Geryon*, with their planktotrophic larvae, are limited to the upper slope and shelf. However, investment in reproduction, when measured in mm^3.egg vol./g.WWt./year, is not too dissimilar. These strategies are important in maintaining the distribution of each species within their specific bathymetric range.

Chapter 8:

Summaries.

Summaries.

1. The *Munida* species of the Porcupine Sea-bight.

1. Four species of *Munida* occur in the Porcupine Sea-bight: *M. rugosa, M.sarsi, M. tenuimana* and *M. micropthalama,* distributed bathymetrically with little overlap of ranges. *M. sarsi* is being by far the most abundant overall. The bathymetric range of *M. tenuimana* is deeper in the Sea-bight than other recorded areas, not being found shallower than 740 m.

2. Both *M. sarsi* and *M. tenuimana* show peaks of density and biomass in their depth ranges: 3843·10 ind.ha^{-1} and 10536·10 g.WWt.ha^{-1} respectively at 450 m for *M. sarsi* and 51·28 ind.ha^{-1} and 64·36 g.WWt.ha^{-1} at 1296 m for *M. tenuimana.*

3. There was no increase in size of *M. sarsi* with depth, contrary to Brinkmann's hypothesis.

4. A development of an arched chela form was noted in some large *M. sarsi* specimens. This was not related to size of maturity.

5. *M. sarsi* was found to have a cyclic annual egg production and gonad development similar to *M. rugosa* studied from the Irish Sea, eggs being laid in Sept-Oct and hatching in Mar-April. Timing of egg hatching is possibly influenced by the influx of organic matter to the benthos from the plankton. All *M. rugosa* eggs kept in the laboratory hatched over a two day period. Patterns for *M. tenuimana* were less distinct. The cause for this is suggested as being one of the deleterious effects of the deeper bathymetric range in the Sea-bight, being forced deeper by competition from the much more abundant *M. sarsi.*

6. *M. sarsi* generally lays a greater number of slightly smaller eggs than *M. tenuimana.* The size of female sexual maturity, determined by the smallest size of munidid carrying eggs, was found to be 9·6 mm CL for *M. sarsi* and 11·4 mm CL for *M. tenuimana.*

7. A post-hatching moult in April was apparent in female *M. sarsi.* There was no apparent moulting peak for males.

8. *M. tenuimana* was found to have a relationship with the glass sponge *Pheronema*, the munidid utilising the osculum of the sponge as shelter.

9. Three species of rhizocephalan barnacle were found infesting *M. sarsi: Tortugaster boschmai, Lernaeodiscus ingolfi* and *Triangulus munidae.* These provided the basis for a separate study.

10. The bopyrid isopod *Pseudione crenulata* was found infesting four *M. sarsi* and one *M. tenuimana.* This is the first record of any bopyrid infesting *M. sarsi.*

11. An incongruous sample of *M. sarsi* was taken from the Porcupine Bank, consisting entirely of individuals larger than most of those found in the Sea-bight. No small individuals were caught and until further samples can be taken from that area the significance of this sample remains a mystery.

2. A rhizocephalan infestation of the deep-sea galatheid *Munida sarsi*, the effects on the host and the influence of depth upon the host-parasite relationship.

1. Three species of rhizocephalan barnacle were found to be infesting 293 specimens of *Munida sarsi* from the Porcupine Sea-bight: *Tortugaster boschmai, Lernaeodiscus ingolfi* and *Triangulus munidae.*

2. *Triangulus munidae* was found to be by far the most common, representing 93·6 % of all infestations.

3. Each species was found to have its own preferred abdominal segment site of emergence.

4. Each species has a particular effect on both male and female host pleopod structure, *Triangulus munidae* causing a series of pleopod forms which led to the definition of a range of

pleopod "Types" for both male and female hosts.

5. Several cases of a peculiar masculinisation of the female host's pleopods were noted, and the hormonal mechanisms behind these modifications are discussed.

6. Depth was found to have an influence upon the host-parasite relationship, there being both an increase in the percentage infestation of *M. sarsi* and a decrease in the effects of *T. munidae* on the host's pleopod structure with an increase in depth. This is related to both organisms being at the extremes of their bathymetric ranges.

3. The depth related migration of the red crab *Geryon trispinosus*, with notes on other aspects of its biology.

1. Two species of *Geryon* were taken from the Porcupine Sea-bight: 687 individual of *Geryon trispinosus* and 3 specimens of the deeper-water *Geryon gordonae.*

2. *G. trispinosus* was collected over a depth range of 490-1505 m, but with a striking depth related distribution, there being a decrease in crab size down the bathymetric gradient.

3. The greatest biomass of *G. trispinosus* was found to be 9662 g.ha^{-1} at a depth of 510 m.

4. An extensive up slope migration is deduced, small crabs settling deep and migrating up to above 700 m, by which time they are sexually mature and join the breeding population. This movement involves distances of up to 60 km.

5. The migration pattern is related to competition between small *G. trispinosus* and the galatheid *Munida sarsi,* which has high densities above 750 m. Possible environmental cues controlling the migration are discussed.

6. There was a notable lack of mature and ovigerous females in the samples, especially in the shallowest samples. It was suggested that this is due to ovigerous females remaining in

their burrows and so are not caught by the sampling gear.

7. Male *G. trispinosus* were considerably larger than mature females. This was related to mating behaviour.

8. Relative growth studies revealed interesting patterns in the development of the chelae, and suggest that male crabs undergo a critical moult accompanied by a large increase in size at around 32-42 mm CL. This was related to the need for males to attain a certain size on reaching the breeding grounds in order to both avoid competition with *Munida sarsi* and to be successful in courtship.

9. Female sexual maturity was found to occur around 10-14 mm CL, but males do not become viable until 30-35 mm.

10. Evidence is given for the existence of a terminal moult in *G. trispinosus*.

11. No definite reproductive cycle could be deduced, mainly due to the lack of mature females in the sample.

12. There appeared to be simultaneous moulting in some samples of mature male crabs. The reasons for this are unclear, but possibilities are discussed.

13. A list of *G. trispinosus* gut contents is presented, together with notes on epifauna and the effect on the exoskeleton of chitinolytic bacteria.

4. The *Munidopsis* species of the Porcupine Sea-bight.

1. Nine species of *Munidopsis* were recorded from the Porcupine Sea-bight samples: *M. antonii* (104 specimens), *M. aries* (5), *M. bairdii* (2), *M. bermudezi* (23), *M. crassa* (17), *M. curvirostra* (23), *M. parfaiti* (58), *M. rostrata* (81), *M. serricornis* (4).

2. The depth range of the genus was from *M. serricornis* at 745 m to *M. parfaiti* and *M.*

crassa, both which are found down to at least 4840 m.

3. Studies were made into the distribution, population structure (biomass, density, size distribution), relative growth, reproduction and parasites of those species represented by sufficient numbers.

4. *M. antonii* was the most abundant species, with a maximum density of 29 $ind.ha^{-1}$ and biomass of 247 $g.ha^{-1}$, both at 3925 m.

5. One *M. curvirostra* was found to be carrying a few hatching eggs. The emerging larvae was of an advanced stage, probably the first zoea.

6. Rhizocephalan parasites were found on *M. bermudezi* and *M. rostrata,* and bopyrid isopods infesting *M. rostrata.* All represent as yet undescribed species.

7. The species of *Munidopsis* were divided into both bathymetric and chela shape groups. It was found that, of the commoner species, none of the species in a particular chela class appeared in the same bathymetric class. It is suggested that this may be a sign of niche separation in relation to diet.

8. Two peaks in biomass/density are apparent for the genus, one at 3000 m and a greater peak at 4000 m, perhaps coinciding with a collection of detrital material at the foot of the continental slope.

9. *Munidopsis* were found to have very few large eggs, and possible reproductive strategies involving advanced development are discussed.

Chapter 9:

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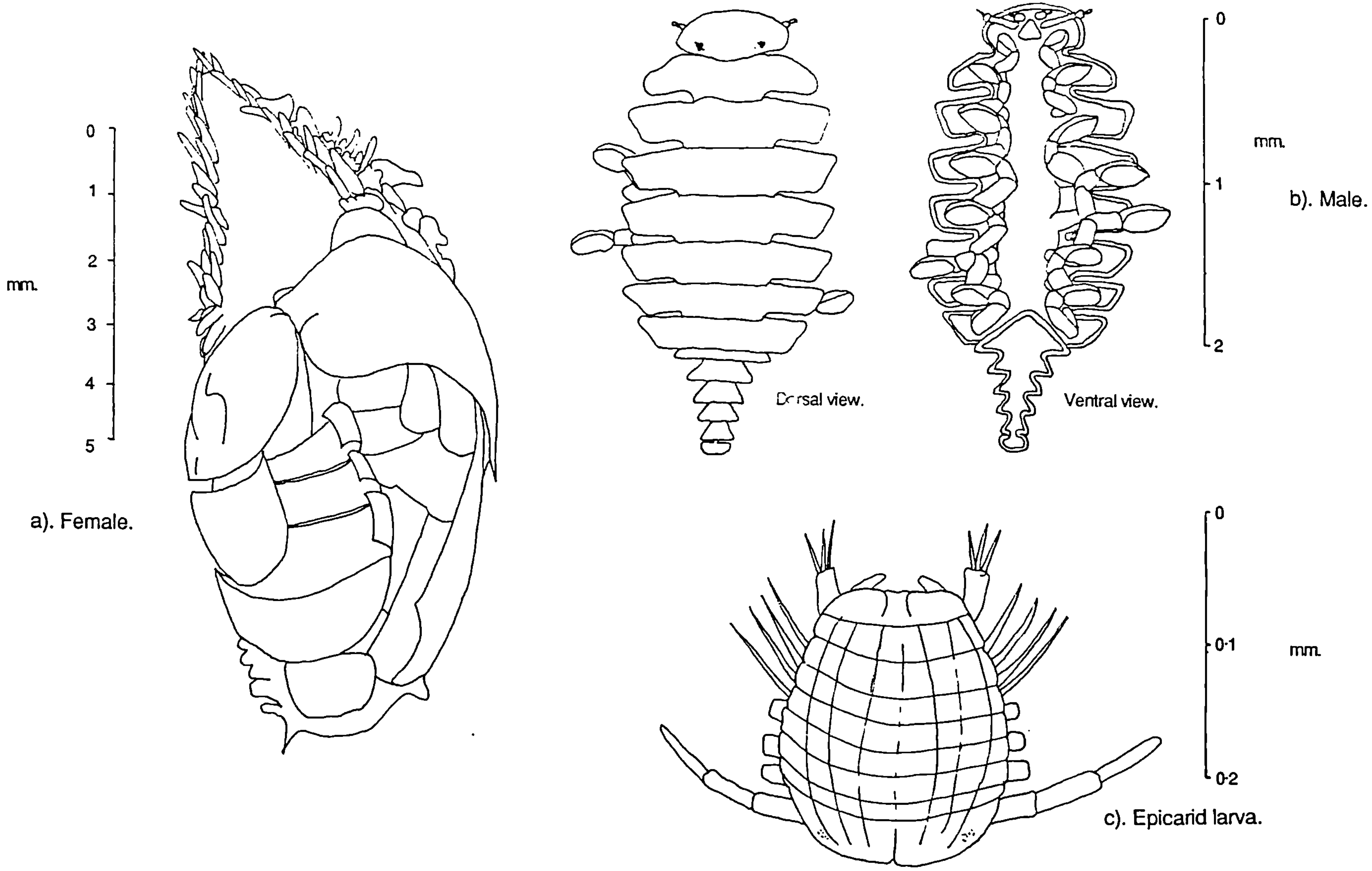
Appendix 1.

The Life Cycle of Bopyrid Isopods.

The Life Cycle of Bopyrid Isopods.

The general pattern of infestation is that of a pair of bopyrids, consisting of a large female (Fig. 1a) and a small male (Fig. 1b) living in the female brood pouch (Reinhard, 1949). Here it remains for the sole purpose of fertilizing successive non-seasonal batches of eggs, Allen (1966) reporting ovigerous female bopyrids throughout the year. The first larval stage is the epicaridium (Fig. 1c), which leaves the brood pouch and enters the plankton. The next stage is the cryptoniscus, which can develop from the epicaridium in either of two ways, depending on the species. The epicaridium may attach to a pelagic copepod, undergo a moult to a microniscus stage and then, after feeding parasitically on the copepod, develop into the cryptoniscus (Caullery, 1907; Reverberi & Pitotti, 1942). Alternatively, the epicaridium may develop directly to the cryptoniscus (Hiraiwa, 1936). The cryptoniscus stage is the settling stage, and is typically isopod in its characteristics (see Reinhard, 1949). Hermit crabs excepted, it settles in the branchial chamber (Pike, 1960) and there metamorphoses into a juvenile female.

The sex determination and differentiation of bopyrid cryptoniscus larvae has provoked a lot of interest in the field, as the first larva to settle becomes the female while any further larvae settling on the same host attach to the female bopyrid and become dwarf males parasitic on the female. Reinhard (1949) removed first settling cryptonisci (presumptive females) and settled them upon mature female parasites. They developed into males, eventually only a single male being left on the female. Similarly, Reverberi (1947) found that presumptive male *Ione thoracica* could be transformed experimentally into females and also changed when placed on a host of a different species. In addition he found that when two females were cultivated together, the younger transformed into a male. Reinhard (1949) therefore hypothesised the production of a masculizing substance by the female bopyrid, cueing further settling larvae



a). Female.

b). Male.

c). Epicarid larva.

Fig. 1: Bopyrid isopod *Pseudione crenulata* found in branchial cavity of *Munida sarsi* and *Munida tenuimana*. (b. and c. found on a.).

towards male development.

Catalano & Restivo (1965) reported an added complication to this life-cycle in the case of *Pseudione euxinica*. This bopyrid infests *Upogebia littoralis*, but only when the host is already parasitized by another bopyrid *Gyge arcassonensis*. The *Pseudione* cryptoniscus settles on the *Gyge*, removing the male and feeding at the expense of the female *Gyge*. The cryptoniscus transforms into a female and the *Gyge* is eliminated. The next settling *Pseudione* becomes the male.

Pike (1960) studied *Pseudione affinis* and found that the female matures nine months from settlement and lives to around 18 months, during which time it produces 3-4 egg broods. Only 18 % of the hosts survived the parasite, but these were able to breed again, the parasite while present causing a cessation of host reproductive activity and some inhibition of the gonad. (Reverberi, 1952; Pike, 1960; Allen, 1966). Pike (1953) noted that *Munida rugosa* outliving the parasite had partially collapsed gill chambers.

Appendix 2.
Full station data.

Appendix 2: Station data for epibenthic sledge, bottom trawl and midwater trawl hauls taken on cruises by IOS and SMBA scientists, including those hauls that contained the decapods covered by this study. Station numbers are preceded by a gear code: BNF- fine mesh epibenthic sledge sample; BNC- coarse mesh epibenthic sledge sample; OT- otter trawl; ST- single warp trawl; GT- Granton trawl; MT8- IOS rectangular midwater trawl. (10,000 m^2 area position = sampled area as calculated from ship's position, 10,000 m^2 Odo = sampled area as calculated from odometer readings on benthic sledges. D = depth (m))

Data kindly supplied by Dr. D. Billett from IOS station data records.

A. Benthic Samples.

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m² Area posn	*10,000m² Area Odo
OT 9638- 2	9:11:77	4043	4104	49 50	14 07	4.788	
OT 9640- 1	11:11:77	3749	3757	50 03	13 51	9.605	
OT 9752- 1	7: 4:78	1007	1042	51 16	11 43	3.352	
OT 9753- 4	7: 4:78	1942	1947	50 55	12 12	5.533	
BNF 9753- 7	8: 4:78	1942	1942	50 55	12 11	0.247	
OT 9753- 8	8: 4:78	1942	1942	50 55	12 11	3.352	
BNF 9754- 3	9: 4:78	1484	1484	51 08	12 02	0.484	
OT 9756- 3	11: 4:78	4080	4156	49 48	14 15	5.442	
OT 9756- 5	12: 4:78	4012	4020	49 49	14 06	7.661	
BNF 9756- 9	13: 4:78	4039	4069	49 47	14 02	0.631	0.125
BNF 9756-14	15: 4:78	3680	3697	50 04	13 56	1.026	0.144
OT 9774- 1	21: 4:78	1494	1572	51 04	11 59	4.448	
BNC 9775- 3	22: 4:78	2012	2019	50 57	12 22	1.003	0.064
OT 9776- 1	23: 4:78	800	808	49 29	11 38	3.671	
BNF 9776- 2	23: 4:78	770	785	49 23	11 36	0.537	0.184
OT 9777- 2	23: 4:78	205	280	49 15	11 15	6.709	
OT 9778- 1	24: 4:78	1016	1055	49 15	12 07	3.463	
BNF 9779- 1	24: 4:78	1398	1404	49 22	12 49	0.700	0.191
BNC 10106- 1	4: 9:79	2300	2315	50 42	12 51	1.020	
BNF 10108- 1	5: 9:79	1385	1390	49 21	12 49	0.474	
BNF 10109- 8	7: 9:79	1120	1130	49 12	12 19	0.816	
BNC 10110- 1	7: 9:79	920	930	49 19	11 43	0.552	
BNF 10111- 8	9: 9:79	1630	1640	49 33	13 07	0.637	0.152
BNF 10112- 1	9: 9:79	2645	2660	50 25	13 19	0.871	
BNF 10112- 2	9: 9:79	2640	2650	50 25	13 20	0.216	0.071
BNF 10112- 3	10: 9:79	2740	2750	50 19	13 26	0.577	0.131
BNF 10113- 1	10: 9:79	2755	2760	50 16	13 32	0.309	0.126
BNF 10114- 1	10: 9:79	4040	4060	49 46	14 08	0.268	0.111
BNF 10115- 1	11: 9:79	3900	3950	49 46	13 56	0.391	0.136
BNC 10120- 1	13: 9:79	400	400	49 28	11 21	0.272	0.101
OT 11116- 1	24: 5:84	4800	4800	47 45	15 25	10.518	
OT 11118- 1	25: 5:84	4450	4680	45 31	18 34	10.358	
OT 50503- 1	1: 6:79	992	1042	51 37	13 15	3.666	
GT 50504- 1	1: 6:79	970	975	51 55	12 53		
GT 50505- 1	1: 6:79	1270	1300	51 44	12 48		
GT 50506- 1	2: 6:79	490	490	51 57	13 35		
GT 50507- 1	2: 6:79	770	795	51 52	13 17		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m² Area posn	*10,000m² Area Odo
ST 50508- 1	3: 6:79	980	980	51 34	13 18		
OT 50509- 1	3: 6:79	1490	1523	51 14	13 17	3.666	
OT 50510- 1	3: 6:79	1925	1960	51 06	13 00	5.579	
OT 50511- 1	4: 6:79	2405	2435	50 32	12 59	6.535	
OT 50512- 1	4: 6:79	3022	3110	50 12	13 35	6.535	
OT 50513- 1	5: 6:79	3400	3600	50 06	14 00	6.693	
OT 50514- 1	5: 6:79	4017	4095	49 42	14 01	8.129	
OT 50515- 1	6: 6:79	4505	4515	49 45	15 06	6.854	
OT 50517- 1	7: 6:79	1785	1794	49 28	13 18	4.304	
OT 50518- 1	7: 6:79	2045	2110	49 27	13 21	6.535	
OT 50519- 1	8: 6:79	1431	1465	49 30	12 46	4.941	
GT 50520- 1	8: 6:79	1230	1245	49 35	12 07		
GT 50521- 1	8: 6:79	965	970	49 30	11 49		
OT 50522- 1	8: 6:79	965	1000	49 25	11 45	3.826	
OT 50523- 1	9: 6:79	455	490	49 30	11 25	3.347	
OT 50524- 1	9: 6:79	736	790	49 36	11 36	6.057	
OT 50601- 1	1: 7:79	770	927	51 20	11 42	5.100	
BNF 50602- 2	1: 7:79	1955	1980	51 01	13 07	0.602	
OT 50602- 3	2: 7:79	1817	1930	51 07	13 21	8.610	
BNF 50603- 1	2: 7:79	4000	4000	49 45	14 01	0.779	
BNF 50604- 1	4: 7:79	3490	3550	50 06	13 52	0.852	
BNF 50605- 1	5: 7:79	2820	2930	50 11	13 30	0.944	
BNC 50606- 1	6: 7:79	1110	1120	50 40	14 10	0.443	0.137
OT 50606- 2	6: 7:79	1080	1120	50 41	14 03	4.140	
BNC 50606- 5	6: 7:79	1120	1140	50 43	13 57	0.417	
OT 50607- 1	7: 7:79	700	712	51 02	14 10	4.460	
BNC 50607- 2	7: 7:79	700	700	51 01	14 07	0.467	0.146
BNC 50608- 2	7: 7:79	510	510	51 19	14 23	0.848	0.212
BNC 50609- 1	8: 7:79	400	400	51 40	14 16	0.085	0.068
OT 50609- 3	8: 7:79	405	410	51 38	14 21	3.826	
BNC 50610- 1	8: 7:79	980	980	51 26	13 24	0.306	0.075
OT 50611- 1	8: 7:79	1365	1410	51 18	13 18	6.217	
BNC 50613- 1	9: 7:79	2440	2440	50 30	13 03	0.474	
OT 50701- 1	11:10:79	2870	2890	54 34	11 54		
OT 50702- 1	13:10:79	755	815	51 17	11 38	2.550	
OT 50703- 1	13:10:79	1575	1625	49 33	12 34		
OT 50704- 1	13:10:79	1260	1265	49 40	12 07		
OT 50705- 1	14:10:79	740	745	49 24	11 32	3.347	
GT 50707- 1	15:10:79	770	790	49 54	11 16		
GT 50708- 1	16:10:79	1050	1065	49 23	12 01		
GT 50709- 1	16:10:79	1260	1260	49 24	12 22		
OT 50710- 1	17:10:79	1800	2000	49 34	13 28		
OT 50711- 1	18:10:79	4780	4795	49 53	15 36	9.177	
OT 50712- 1	19:10:79	2700	2775	50 11	13 21	4.655	
GT 50713- 1	20:10:79	1245	1275	51 22	13 18		
GT 50714- 1	20:10:79	925	960	51 45	13 15		
OT 50715- 1	21:10:79	1635	1720	51 20	12 57	3.990	
GT 50716- 1	21:10:79	745	750	51 53	13 26		
GT 50717- 1	21:10:79	500	510	52 00	13 33		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m^2 Area posn	*10,000m^2 Area Odo
OT 50801- 1	30: 7:80	1245	1285	49 35	12 11	4.782	
OT 50802- 1	30: 7:80	1857	1910	49 40	12 37	3.826	
GT 50803- 1	31: 7:80	450	555	49 26	11 28		
GT 50804- 1	31: 7:80	690	690	49 25	11 33		
GT 50805- 1	31: 7:80	1000	1000	49 36	11 51		
OT 50806- 1	1: 8:80	510	515	49 27	11 27	4.460	
OT 50807- 1	1: 8:80	790	795	49 24	11 37	4.140	
OT 50808- 1	1: 8:80	955	965	49 35	11 49		
GT 50809- 1	1: 8:80	1250	1250	49 32	12 10		
OT 50810- 1	2: 8:80	1605	1694	49 34	12 42	4.460	
OT 50811- 1	2: 8:80	4350	4400	49 39	14 34	7.970	
BNF 50812- 1	3: 8:80	4080	4100	49 45	14 10		0.179
OT 50812- 2	3: 8:80	4035	4140	49 53	14 17	10.361	
OT 50813- 1	4: 8:80	3640	3715	50 14	14 08	8.129	
OT 50814- 1	4: 8:80	2715	3000	50 20	13 32	22.344	
OT 50815- 1	5: 8:80	1280	1344	51 36	13 04		
GT 50816- 1	5: 8:80	1000	1000	51 46	13 05		
GT 50817- 1	6: 8:80	750	750	51 55	13 15		
GT 50818- 1	6: 8:80	515	520	52 00	13 31		
OT 50819- 1	6: 8:80	500	512	52 05	13 29	3.188	
OT 50820- 1	6: 8:80	714	725	51 55	13 19	5.420	
OT 50821- 1	6: 8:80	982	990	51 48	13 05	5.260	
OT 50822- 1	7: 8:80	2095	2150	50 57	13 12	10.773	
BNC 50823- 1	8: 8:80	2830	2830	50 12	13 32		0.208
OT 50902- 1	7:11:80	1825	1865	51 16	12 47	4.941	
OT 50903- 1	7:11:80	1250	1265	51 16	13 24	4.620	
OT 50904- 1	8:11:80	1020	1035	51 20	13 28	5.100	
OT 50905- 1	8:11:80	755	820	51 42	13 24	5.100	
OT 50906- 1	9:11:80	2585	2705	50 25	13 27	8.290	
OT 50907- 1	10:11:80	2820	3120	49 53	13 32	8.610	
OT 50910- 1	10:11:80	4265	4320	49 50	14 45	9.245	
BNF 50913- 1	12:11:80	3000	3040	50 12	13 40		0.373
BNC 50914- 1	12:11:80	2790	2810	50 16	13 30		0.164
OT 51002- 1	1: 5:81	490	490	52 20	13 19		
OT 51003- 1	1: 5:81	740	760	52 01	13 02		
OT 51007- 1	2: 5:81	1020	1030	51 46	13 06		
OT 51008- 1	2: 5:81	1350	1370	51 36	13 02		
OT 51009- 1	2: 5:81	1510	1535	51 34	12 54		
OT 51010- 1	2: 5:81	1780	1800	51 19	12 29		
OT 51011- 1	3: 5:81	2165	2180	50 45	12 15		
OT 51012- 1	5: 5:81	3880	3920	49 51	13 58		
OT 51015- 1	6: 5:81	2520	2540	49 55	12 57		
OT 51021- 1	9: 5:81	1860	1875	49 39	12 41		
OT 51022- 1	9: 5:81	1575	1600	49 33	12 39		
OT 51023- 1	9: 5:81	1270	1275	49 30	12 11		
OT 51025- 1	10: 5:81	460	480	49 27	11 25		
OT 51026- 1	10: 5:81	730	750	49 25	11 34		
OT 51027- 1	10: 5:81	970	985	49 32	11 51		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m² Area posn	*10,000m² Area Odo
BNC 51102- 1	21: 5:81	520	530	52 01	13 27	0.309	0.138
BNC 51103- 4	21: 5:81	950	960	51 48	13 10	0.272	0.145
BNC 51103- 5	21: 5:81	930	950	51 47	13 13	0.391	0.246
BNC 51104- 1	22: 5:81	1370	1390	51 24	13 04	0.391	0.141
BNC 51105- 3	22: 5:81	2020	2030	51 04	12 54	0.511	0.140
BNC 51105- 4	24: 5:81	1985	1993	51 05	12 59	0.300	
BNC 51106- 1	24: 5:81	2510	2520	50 29	13 06	0.342	0.142
BNC 51109- 1	26: 5:81	3940	3960	49 51	14 02	0.459	0.218
BNC 51109- 2	27: 5:81	3980	3990	49 48	14 09	0.649	0.221
BNC 51110- 3	28: 5:81	2785	2800	50 16	13 31	0.443	0.218
BNC 51110- 4	28: 5:81	2718	2755	50 14	13 26	0.711	0.220
BNC 51111- 1	28: 5:81	2660	2670	50 21	13 23	0.631	0.209
BNC 51111- 2	28: 5:81	2620	2620	50 23	13 20	0.212	0.205
BNC 51112- 1	29: 5:81	515	530	51 26	13 59	0.379	0.199
BNC 51112- 4	29: 5:81	550	560	51 25	13 57	0.513	0.141
BNC 51113- 2	30: 5:81	1530	1540	51 15	13 13	0.646	0.223
OT 51201- 1	16: 9:81	1970	1980	51 06	12 54	3.188	
OT 51205- 1	17: 9:81	1373	1394	51 40	12 49		
OT 51206- 1	18: 9:81	1200	1210	51 40	13 00		
BNC 51208- 1	19: 9:81	1170	1200	51 41	13 01	0.523	0.128
BNC 51208- 3	20: 9:81	1170	1185	51 41	13 01	0.241	0.080
OT 51213- 1	26: 9:81	1895	1980	50 44	11 56	1.793	
OT 51214- 1	27: 9:81	3800	3820	49 59	14 05	5.100	
BNC 51216- 1	28: 9:81	4070	4070	49 48	14 10	0.467	0.288
BNC 51216- 3	28: 9:81	4050	4050	49 50	14 07	0.461	0.278
OT 51216- 4	29: 9:81	3970	4000	49 52	14 07	6.217	
BNC 51216- 5	29: 9:81	4030	4040	49 48	14 05	0.621	0.273
BNF 51217- 1	30: 9:81	150	150	50 36	10 18	0.290	0.095
OT 51217- 2	30: 9:81	135	141	50 38	10 08	9.314	
OT 51302- 1	17: 2:82	310	350	52 41	13 31		
OT 51303- 1	18: 2:82	510	580	52 09	13 21		
OT 51304- 1	18: 2:82	760	820	51 51	13 20		
OT 51305- 1	18: 2:82	965	1005	51 50	13 05		
OT 51306- 1	19: 2:82	1205	1230	51 44	12 53	3.029	
OT 51307- 1	19: 2:82	1415	1490	51 26	13 01		
OT 51308- 1	20: 2:82	1715	1770	51 13	13 02		
OT 51309- 1	20: 2:82	4190	4255	49 35	14 01	9.883	
OT 51310- 1	21: 2:82	2455	2500	49 52	12 57		
OT 51311- 1	21: 2:82	1940	2010	49 51	12 23		
GT 51312- 1	22: 2:82	700	750	49 27	11 37		
GT 51313- 1	22: 2:82	1225	1265	49 33	12 12		
OT 51314- 1	22: 2:82	1425	1455	49 32	12 29		
GT 51315- 1	23: 2:82	980	1050	49 33	11 52		
OT 51318- 1	24: 2:82	665	705	49 23	11 34		
OT 51319- 1	24: 2:82	255	275	49 28	11 18		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m² Area posn	*10,000m² Area Odo
OT 51401- 1	24: 3:82	287	307	51 10	11 25	3.666	
BNF 51403- 1	25: 3:82	1292	1314	51 37	13 00	0.448	0.175
BNF 51403- 2	25: 3:82	1317	1325	51 37	12 59	0.236	0.092
BNF 51403- 3	25: 3:82	1319	1325	51 37	12 59	0.156	0.105
BNF 51403- 4	26: 3:82	1319	1333	51 37	13 00	0.332	0.096
BNF 51403- 5	26: 3:82	1289	1297	51 37	12 59	0.203	0.088
BNF 51403- 6	26: 3:82	1278	1295	51 37	12 59		0.094
OT 51403- 7	26: 3:82	1255	1330	51 37	12 59	4.140	
OT 51404- 1	26: 3:82	740	760	51 54	13 18	4.140	
BNC 51405- 1	27: 3:82	492	503	52 01	13 31	0.302	0.127
BNC 51406- 1	27: 3:82	1072	1091	51 23	13 22	0.251	0.150
BNC 51407- 1	27: 3:82	1489	1511	51 20	13 04	0.520	0.144
BNC 51408- 1	27: 3:82	1994	2001	51 04	12 54	0.458	0.183
OT 51409- 1	28: 3:82	1651	1717	51 18	12 58	4.460	
OT 51411- 1	29: 3:82	2470	2500	50 24	13 00	7.332	
BNC 51412- 1	29: 3:82	2760	2790	50 18	13 29	0.749	0.345
OT 51413- 1	30: 3:82	2770	2940	50 10	13 33	7.811	
OT 51414- 1	30: 3:82	4180	4310	49 41	14 13	10.278	
BNC 51414- 2	31: 3:82	4070	4090	49 47	14 09	0.574	0.299
BNC 51415- 1	31: 3:82	3470	3510	50 07	13 53	0.408	0.290
BNF 51416- 1	31: 3:82	2780	2790	50 17	13 31	0.201	0.140
BNC 51417- 1	1: 4:82	2770	2790	50 10	13 22	0.313	0.149
OT 51419- 1	1: 4:82	1488	1529	51 18	13 06	4.460	
BNF 51420- 1	2: 4:82	1326	1328	51 37	12 59	0.172	0.093
BNC 51420- 2	2: 4:82	1304	1309	51 37	12 59	0.163	0.089
BNF 51420- 3	2: 4:82	1293	1298	51 38	12 59	0.117	0.090
BNF 51420- 4	2: 4:82	1279	1287	51 38	13 00	0.163	0.091
BNC 51603- 2	18: 7:82	2730	2740	50 18	13 24	0.198	0.137
BNC 51604- 1	19: 7:82	2890	2920	50 15	13 38	0.291	0.140
OT 51608- 1	19: 7:82	4270	4370	49 38	14 27	7.992	
OT 51610- 1	20: 7:82	3310	3660	50 03	13 53	9.927	
OT 51611- 1	21: 7:82	2640	2700	50 19	13 21	10.185	
OT 51613- 1	21: 7:82	2200	2240	50 48	12 54	8.370	
BNC 51622- 1	24: 7:82	158	158	50 35	10 20	0.265	0.169
BNC 51707- 1	12: 4:83	1205	1230	51 39	13 01	0.951	
BNC 51708- 2	13: 4:83	1430	1470	51 31	12 59	0.513	0.216
BNC 51715- 2	18: 4:83	1450	1535	51 30	12 59	0.664	
BNC 51717- 2	18: 4:83	1970	1980	51 05	12 56	0.228	0.160
OT 51801- 1	24: 9:83	1700	1740	51 21	12 31		
OT 51803- 1	26: 9:83	3920	3990	49 37	13 49		
OT 51804- 1	26: 9:83	3015	3180	49 56	13 26		
OT 51805- 1	27: 9:83	2430	2545	49 55	12 58		
OT 51810- 1	29: 9:83	1011	1021	49 33	11 53		
OT 51811- 1	30: 9:83	685	707	49 34	11 33		
OT 51812- 1	30: 9:83	505	550	49 29	11 26		

Station	Date	min D	max D	Deg. N	Deg. W	*10,000m^2 Area posn	*10,000m^2 Area Odo
BNC 52009- 1	19: 8:84	1206	1236	51 41	12 59	0.311	0.156
BNC 52012- 1	20: 8:84	984	984	51 48	13 07	0.120	0.076
BNC 52013- 1	20: 8:84	515	525	52 05	13 29	0.123	0.068
BNC 52017- 1	21: 8:84	1457	1472	51 32	12 58	0.203	0.071
BNC 52019- 1	22: 8:84	1725	1736	51 25	12 46	0.212	0.199
BNC 52203- 1	16: 6:85	1521	1531	51 26	13 01	0.190	0.148
BNC 52204- 1	16: 6:85	1295	1310	51 37	13 00	0.092	0.071
BNC 52211- 1	18: 6:85	1693	1738	51 11	13 15	0.324	0.141
BNC 52213- 1	20: 6:85	2405	2420	50 33	12 59	0.320	0.136
BNC 52214- 1	21: 6:85	4050	4075	49 52	14 15	1.400	0.453
BNC 52215- 1	22: 6:85	4561	4565	49 30	14 49	0.651	0.350
BNC 52216- 8	25: 6:85	4803	4832	48 48	16 38	0.605	0.405
BNC 52218- 1	26: 6:85	1433	1447	49 25	12 50	0.431	0.232
BNC 52403-14	5:12:86	4850	4860	49 02	16 00		

B. Pelagic samples.

Station	Date	Min D	Max D	m above seabed	Deg N.	Deg W.	*10,000m^3 Vol. filt
RMT8 9756-2	10: 4:79	1000	1500	c. 2750	49 53	14 10	12.007
RMT8 9756-10	14: 4:79	3000	3500	c. 750	49 47	14 04	11.782
RMT8 9756-11	14: 4:79	4000	4012	c. 12	49 50	14 05	10.003
RMT8 50603-2	3: 7:79	3720	3940	c. 160	49 54	14 09	3.865
RMT8 50603-3	3: 7:79	3700	3900	c. 150	49 53	14 04	3.636
RMT8 50605-2	5: 7:79	2640	2750	c. 15	50 07	13 12	4.850
RMT8 52403-21	8:12:86	c.4850	c.4850	0	49 15	16 35	-