

ASPECTS OF THE BIOLOGY OF THE GALATHEID GENUS *MUNIDA* (CRUSTACEA, DECAPODA) FROM THE PORCUPINE SEABIGHT, NORTHEAST ATLANTIC

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SARSIA



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More than 2000 individuals belonging to four species of the genus *Munida* were collected during a survey of the benthic biology of the Porcupine Seabight. The bulk of the collection consists of *M. sarsi*, which occurs down to a depth of about 800 m in the Seabight. Data are provided on the relative abundance of this species at different depths, the relative growth of its chelae, chelar propodi and eyes, and its reproductive biology. More limited data are provided for *M. tenuimana* which overlaps with the lower part of the bathymetric range of *M. sarsi* and extends to about 1400 m in the Seabight. The new information on *M. sarsi* and *M. tenuimana* is compared with previous data on these species from other regions. The two remaining species, *M. rugosa* from the upper slope and continental shelf and *M. microphthalma* from mid-slope depths were obtained in insufficient numbers to provide significant biological information.

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INTRODUCTION

The galatheid genus *Munida* LEACH has a worldwide distribution, being represented by about 100 species with depth ranges from the sublittoral *M. japonica* STIMPSON (DOFLEIN & BALSS 1913; BABA 1988) to *M. microphthalma* A. MILNE EDWARDS reaching depths of more than 2000 m (HANSEN 1908). Most of the previous literature on the genus has been limited to the taxonomy, nomenclature or distribution (e.g. RICE & SAINT LAURENT 1986; BABA 1988 and references therein; MACPHERSEN & SAINT LAURENT in press). Consequently, little is known about the biology of *Munida* species with the exception of the abundant southern ocean form *Munida gregaria* (FABRICIUS), a species of considerable potential commercial importance (see ZELDIS 1985). Information on other species, including those in the accessible and relatively well-studied areas around Europe, is sparse.

Of the European species, the shallow-living *M. rugosa* (FABRICIUS) has been investigated for its larval development (LEBOUR 1930 as *M. bamffica*, and HUUS 1935 as *M. bamffia*). But although it is the object of an emergent fishery, particularly in Scotland (HOWARD 1981; Scottish Sea Fisheries Statistical Tables 1989), virtually nothing is known of its general biology.

The deeper-living *M. sarsi* HUUS and *M. tenuimana* G.O. SARS have been studied mainly in relation

to their parasites (BRINKMANN 1936; REVERBERI 1942; NEILSEN 1969; ATTRILL 1989), though at the same time population structure, reproductive cycles, burrowing behaviour and diet have also received some attention. INGRAND (1937) also studied the development of the secondary sexual characters in *M. sarsi* (as *M. bamffica*), while BERRILL (1970) investigated the aggressive behaviour of this species and ZAINAL (1990) its relative growth. ZAINAL also pointed out the nomenclatural error in INGRAND's paper which was missed by RICE & SAINT LAURENT (1986) who erroneously listed it within the synonymy of *M. rugosa*.

This study reports limited data on the biology of *Munida* species obtained during an extensive investigation of the benthic biology of the Porcupine Seabight, to the south-west of Ireland, carried out by the Institute of Oceanographic Sciences Deacon Laboratory, Wormley.

MATERIAL AND METHODS

Between 1977 and 1986 a series of more than 400 benthic stations were sampled in the Porcupine Seabight and on the adjacent abyssal plain (49-52° N, 11-14° W), over a depth range from 200 to 4500 m. A general introduction to the study and a description of the area investigated is provided by RICE & al. (1991), while a detailed station list is given in JACKSON & al. (1991).

Fifty four of the stations yielded a total of 2166 specimens of *Munida*. Brief details of these samples and of the

specimens collected are given in Table 1 and their positions are shown in Fig. 1. The samples were collected with three types of gear, the IOS epibenthic sledge (BN), the semi-balloon otter-trawl (OTSB) and the Scottish Marine Biological Association (SMBA) Granton trawl (GT). Calculations of the numerical abundance and biomass were based on estimates of the areas sampled by the sledge and the semi-balloon otter trawl. The distance travelled across the seafloor was determined from an odometer

wheel in the case of the sledge and from the ship's log for the otter trawl. This distance was then multiplied by the effective width of the net in each case (RICE & al. 1991). The failure of such towed gears to produce reliable quantitative data is well documented, but their internal consistency provides a valid basis for comparison (see RICE & al. 1982, 1991; BRATTEGARD & FOSSÅ 1991).

The collected material was fixed in 5 % seawater formalin and later transferred to 70 % alcohol; it is presently

Table 1. Brief details of the Porcupine Seabight samples in which *Munida* species were collected. Further details are available in JACKSON & al. (1991). OTSB = Semi-balloon otter-trawl. BN = IOS epibenthic sledge. GT = SMBA Granton trawl. *M. r.* = *M. rugosa*. *M. s.* = *M. sarsi*. *M. t.* = *M. tenuimana*. *M. m.* = *M. microphthalmma*.

| Station number | Latitude | Longitude | Mean depth (m) | Gear | Specimens in sample | | | |
|----------------|----------|-----------|----------------|------|---------------------|--------------|--------------|--------------|
| | (N) | (W) | | | <i>M. r.</i> | <i>M. s.</i> | <i>M. t.</i> | <i>M. m.</i> |
| 9777#2 | 49°15' | 11°15' | 243 | OTSB | 25 | 208 | | |
| 51813 | 49°24' | 11°16' | 247 | OTSB | 53 | | | |
| 51319 | 49°28' | 11°18' | 265 | OTSB | 29 | 46 | | |
| 51302 | 52°41' | 13°31' | 285 | OTSB | | 37 | | |
| 51401 | 51°08' | 11°25' | 297 | OTSB | | 38 | | |
| 51025 | 49°27' | 11°25' | 470 | OTSB | | 93 | | |
| 50523 | 49°32' | 11°24' | 473 | OTSB | | 831 | | |
| 50806 | 49°27' | 11°27' | 513 | OTSB | | 63 | | |
| 50705 | 49°24' | 11°32' | 743 | OTSB | | | 1 | |
| 50524 | 49°34' | 11°36' | 763 | OTSB | | 26 | | |
| 50702 | 51°17' | 11°38' | 785 | OTSB | | 5 | | |
| 51304 | 51°51' | 13°20' | 790 | OTSB | | | 2 | |
| 50807 | 49°24' | 11°37' | 793 | OTSB | | 2 | | |
| 50601 | 51°19' | 11°41' | 849 | OTSB | | | 3 | |
| 50522 | 49°24' | 11°45' | 983 | OTSB | | | 8 | |
| 51810 | 49°33' | 11°53' | 1016 | OTSB | | | 1 | |
| 50503 | 51°37' | 13°15' | 1017 | OTSB | | | 3 | |
| 9752#1 | 51°16' | 11°43' | 1025 | OTSB | | | 3 | |
| 50606#2 | 50°41' | 14°04' | 1100 | OTSB | | | 4 | |
| 51206 | 51°40' | 13°01' | 1205 | OTSB | | | 17 | |
| 51306 | 51°44' | 12°53' | 1218 | OTSB | | | 11 | |
| 52105 | 51°42' | 13°56' | 1240 | OTSB | | | 12 | |
| 51023 | 49°30' | 12°11' | 1273 | OTSB | | | 1 | |
| 10120#1 | 49°28' | 11°22' | 400 | BN | | 120 | | |
| 50609#1 | 51°40' | 14°17' | 400 | BN | | 5 | | |
| 52404#4 | 51°59' | 13°43' | 450 | BN | | 403 | | |
| 51112#1 | 51°27' | 13°59' | 523 | BN | | 10 | | |
| 50607#2 | 51°01' | 14°06' | 700 | BN | | 11 | | |
| 10110#1 | 49°19' | 11°43' | 925 | BN | | | 6 | |
| 51103#5 | 51°47' | 13°13' | 940 | BN | | | 1 | |
| 50610#1 | 51°26' | 13°24' | 980 | BN | | | 1 | |
| 50606#1 | 50°40' | 14°10' | 1115 | BN | | | 2 | |
| 10109#8 | 49°12' | 12°19' | 1125 | BN | | | 1 | |
| 50606#5 | 50°43' | 13°56' | 1130 | BN | | | 1 | |
| 51707#1 | 51°40' | 13°00' | 1218 | BN | | | 6 | |
| 51403#6 | 51°37' | 12°59' | 1287 | BN | | | 1 | |
| 51403#5 | 51°38' | 12°59' | 1293 | BN | | | 2 | |
| 51402#3 | 51°38' | 12°59' | 1296 | BN | | | 6 | |
| 51403#1 | 51°38' | 13°00' | 1303 | BN | | | 1 | |
| 51403#2 | 51°37' | 12°59' | 1321 | BN | | | 3 | |
| 51402#1 | 51°37' | 12°59' | 1327 | BN | | | 1 | |
| 50611#1 | 51°19' | 13°15' | 1388 | BN | | | 1 | |
| 10111#8 | 49°33' | 13°07' | 1635 | BN | | | | 2 |
| 51312 | 49°27' | 11°37' | 725 | GT | | | 1 | |
| 50716 | 51°53' | 13°26' | 768 | GT | | | 2 | |
| 50707 | 49°54' | 11°16' | 780 | GT | | 1 | | |
| 51315 | 49°33' | 11°52' | 1015 | GT | | | 1 | |
| 50708 | 49°23' | 12°01' | 1058 | GT | | | 1 | |
| 50709 | 49°24' | 12°22' | 1260 | GT | | | 9 | |
| 50713 | 51°22' | 13°18' | 1260 | GT | | | 4 | |

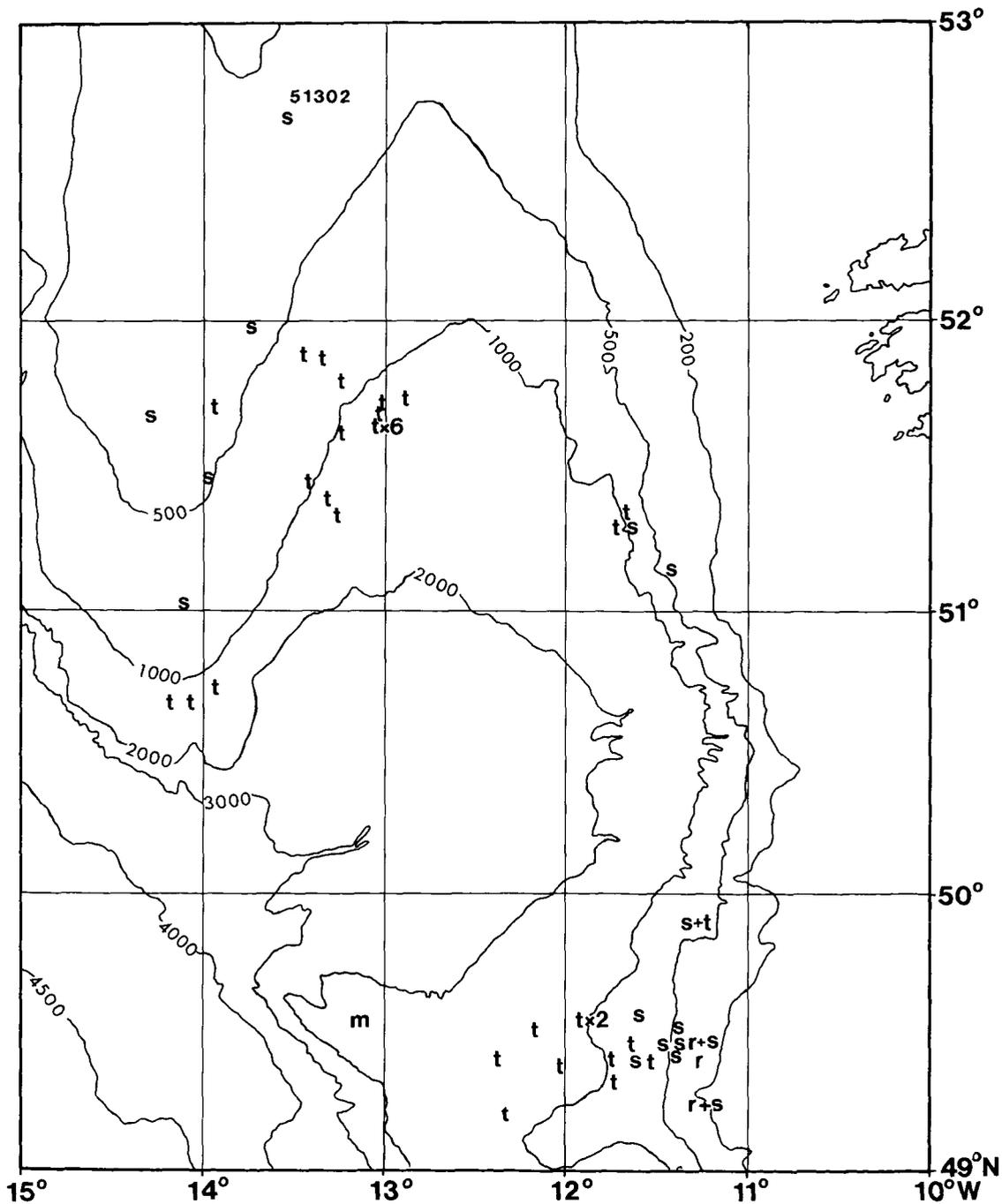


Fig. 1. Chart of the Porcupine Seabight showing the sample positions for the four *Munida* species reported in this paper: r = *rugosa*, s = *sarsi*, t = *tenuimana*, m = *microphthalma*. The position of the exceptional sample of *M. sarsi* (see text) from station 51302 is marked.

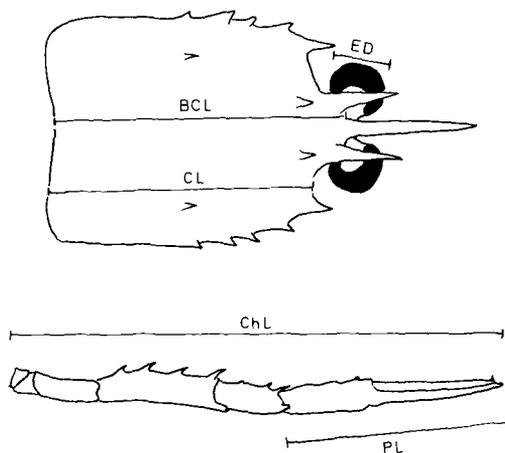


Fig. 2. Generalised *Munida* carapace and chela to show the measurements referred to. BCL = Brinkmann's carapace length; CL = standard carapace length; ED = eye diameter; ChL = chela length; PL = propodus length.

maintained in the Institute of Oceanographic Sciences Deacon Laboratory collections. The measurements taken from each specimen are illustrated in Fig. 2: carapace length (CL) was measured from the posterior margin of the right-hand-side orbit to the posterior border of the carapace; chelar length (ChL) from the tip of the fixed finger of the propodus to the base of the coxa (in specimens with an 'arched' chela (see below) the normal chela was always measured); chelar propodus length (PL) from the tip of the fixed finger to its ventral articulation with the carpus; eye diameter (ED) as shown. All measurements were made with dial callipers to the nearest 0.1 mm. Fig. 2 also shows BRINKMANN'S (1936) unusual measurement of carapace length (BCL) which was also taken in the present study to facilitate comparison. BRINKMANN'S carapace length can be converted to the standard carapace length as follows:

$$CL \text{ (mm)} = 0.96 \text{ BCL (mm)} - 0.51$$

All quotations of carapace length from BRINKMANN'S study are after conversion to standard CL.

Sex was determined from the position of the gonopores and, in juveniles, the presence or absence of the first pair of pleopods. In females the ovaries were classified subjectively as small, medium or large, their colour recorded, and the mean ova diameter determined to the nearest 0.01 mm. If eggs were present on the pleopods the stage was recorded as 'plain' or 'eyed', the number was determined, and the diameter measured under a stereomicroscope to the nearest 0.01 mm.

In both sexes the wet weight of the whole animal was measured to the nearest 0.01 g and any evidence of recent moulting was recorded.

RESULTS

Four *Munida* species, from successively deeper bathymetric ranges, were represented in the Seabight samples: *Munida rugosa*, *M. sarsi*, *M. tenuimana*, and *M. microphthalma*. Of these, the shal-

lowest and deepest species were taken in insufficient numbers for significant biological studies. A fifth species, *M. intermedia* A. MILNE EDWARDS & BOUVIER, which occupies a similar depth range to *M. sarsi*, is also recorded from the southeastern part of the Seabight, but was not taken in the IOSDL collections. The following results therefore concentrate on *M. sarsi* and *M. tenuimana*, but the limited data on *M. rugosa* and *M. microphthalma* are also provided.

Munida rugosa FABRICIUS, 1775

M. rugosa is widely distributed in the eastern Atlantic, having been recorded from Sognefjorden (Norway) in the north (BRINKMANN 1936; CHRISTIANSEN 1972) to Madeira in the south and into the Mediterranean at least as far east as the Adriatic (ZARIQUIEY ALVAREZ 1946, 1952). It is restricted to relatively shallow water less than about 300 m deep. In the Seabight study a total of 108 specimens was taken at three stations on the Goban Spur to a maximum depth of 280 m, two of these samples also containing *M. sarsi*. These samples, all taken with the OTSB, indicate low numerical abundances ranging from about 4 to 12 individuals ha^{-1} .

Munida sarsi HUUS, 1935

M. sarsi is the most northerly of the four species collected, having been recorded in the eastern Atlantic from Iceland (STEPHENSON 1939) and northern Norway (DONS 1915) and the Barents Sea (CHRISTIANSEN 1972) to the southern Bay of Biscay and northern coast of Spain (ZARIQUIEY ALVAREZ 1952). The species has not been recorded from the coast of Portugal or from the Mediterranean.

M. sarsi has been reported from depths ranging from about 100 to 1000 m, and most frequently between about 250 and 400 m. In the Porcupine Seabight study it was taken between 205 and 815 m, overlapping with *M. rugosa* at the shallow end of its range (see above) and with *M. tenuimana* below 740 m. It was the most abundant species in the collection, being represented by 1933 individuals from 17 stations and providing limited biological information.

Length frequency

The 1933 individuals consisted of 1059 (54.8%) males, 863 (44.6%) females and 11 (0.6%) too small to be sexed. Both sexes have a similar length-frequency distribution (Fig. 3), with a single marked peak and a long tail of large individuals. The male peak extends from about 8 to 20 mm CL, with a mode at 13–14 mm, while the females have a some-

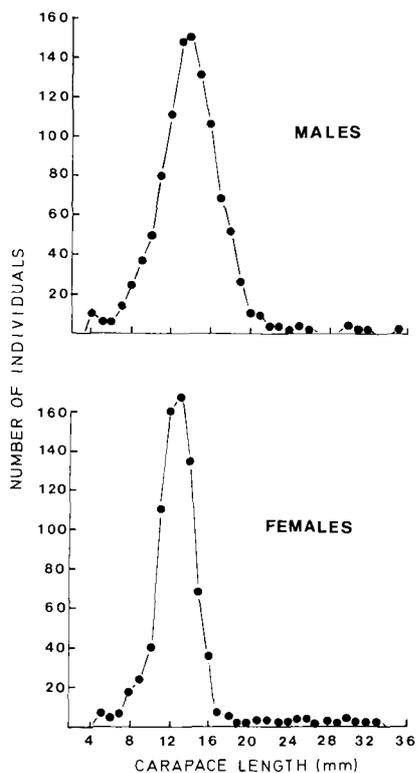


Fig. 3. *Munida sarsi*. Length frequency distribution of all males and females collected during the Porcupine Seabight study.

what sharper peak from about 8 to 17 mm and a mode at 12–13 mm. Most of the large specimens (including all males over 26 mm CL and all females over 23 mm CL) came from a single sample (51302 at a depth of 330 m), which consisted only of these large individuals.

Numerical abundance and biomass

The calculated numerical abundance and biomass data are plotted against depth in Fig. 4. Despite the large discrepancy between the estimates based respectively on the otter trawl and sledge, both gears suggest that *M. sarsi* reaches its maximum abundance in the Seabight at depths between about 400 and 500 m. Apart from sample 51302 which indicates a low abundance (6.1 ha^{-1}) but a high biomass (134 g ha^{-1}), the graphs for density and biomass generally follow similar trends. Moreover, again with the exception of sample 51302, there is no clear relationship between size and depth, with large and small animals being taken throughout the depth range.

Relative growth

Any parasitised specimens (see ATTRILL 1989) were excluded from the relative growth analyses. Specimens with a carapace length ≤ 10 mm were assumed to be immature (see below) and were analysed separately from the larger size classes. All analyses were performed on log-transformed data.

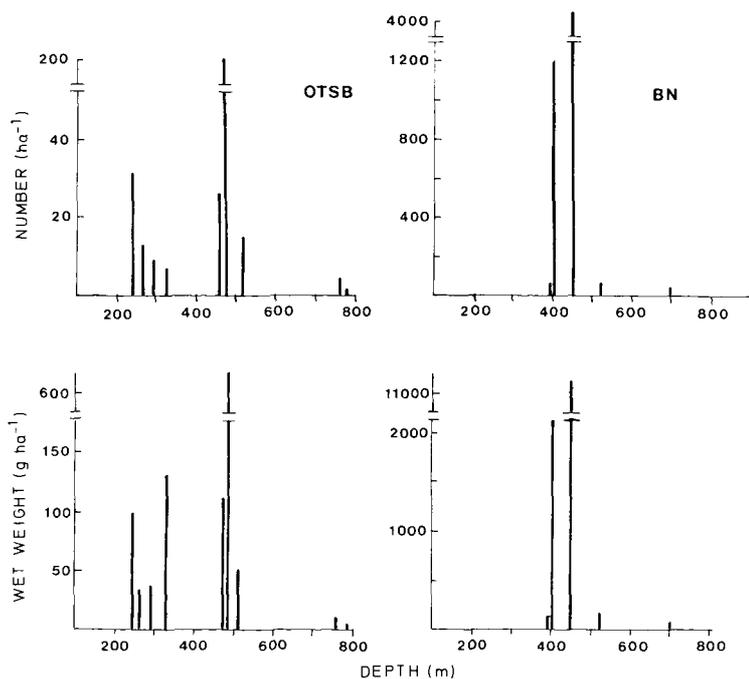


Fig. 4. *Munida sarsi*. Numerical abundance and biomass estimates at different depths, based on OTSB samples (left) and BN samples (right).

Total chelar length was regressed on carapace length giving the following results for males:

| | |
|--------------------------------|--|
| All males | $\ln \text{ChL} = 0.93 + 1.20 \ln \text{CL}$ $r^2 = 0.92 \quad n = 456$ |
| Immature males (CL ≤ 10 mm) | $\ln \text{ChL} = 1.25 + 1.04 \ln \text{CL}$ $r^2 = 0.85 \quad n = 24$ |
| Mature males (CL > 10 mm) | $\ln \text{ChL} = 0.90 + 1.21 \ln \text{CL}$ $r^2 = 0.88 \quad n = 432$ |

This suggests that in males the chelae grow isometrically before maturity, but positively allometrically thereafter. There are very wide confidence limits for the slope for immature males (95 % limits 0.84–1.23), but for mature males growth is positively allometric (95 % limits, 1.17–1.26). The slopes for immature and mature males differ ($t = 3.05$, $n = 454$, $p = 0.005$).

For females the comparable equations are:

| | |
|--------------------|--|
| All females | $\ln \text{ChL} = 1.44 + 0.98 \ln \text{CL}$ $r^2 = 0.91 \quad n = 327$ |
| Females CL ≤ 10 mm | $\ln \text{ChL} = 1.14 + 1.10 \ln \text{CL}$ $r^2 = 0.95 \quad n = 12$ |
| Females CL > 10 mm | $\ln \text{ChL} = 1.49 + 0.95 \ln \text{CL}$ $r^2 = 0.88 \quad n = 315$ |

Thus, for females chelar growth is close to isometric throughout. The slopes for immature and mature females are significantly different ($t = 2.49$, $n = 323$, $p = 0.02$), and that for mature females is significantly less than unity (95 % limits, 0.915–0.992).

Growth of the chelar propodus shows similar trends to that of the entire chela. For males the regression equations are:

| | |
|--------------------------------|--|
| All males | $\ln \text{PL} = -0.17 + 1.31 \ln \text{CL}$ $r^2 = 0.94 \quad n = 358$ |
| Immature males (CL ≤ 10 mm) | $\ln \text{PL} = -0.10 + 1.27 \ln \text{CL}$ $r^2 = 0.96 \quad n = 22$ |
| Mature males (CL > 10 mm) | $\ln \text{PL} = -0.17 + 1.31 \ln \text{CL}$ $r^2 = 0.88 \quad n = 336$ |

The slopes for immature and mature males are not significantly different ($t = 0.57$, $n = 354$, $p > 0.5$). However, for both groups the positive allometry is significant (95 % limits, 1.06–1.48 immature, 1.26–1.36 mature), and at a higher level than that for the whole chela.

For females the equivalent equations are:

| | |
|----------------------------------|---|
| All females | $\ln \text{PL} = 0.42 + 1.05 \ln \text{CL}$ $r^2 = 0.93 \quad n = 245$ |
| Immature females (CL ≤ 10 mm) | $\ln \text{PL} = 0.12 + 1.19 \ln \text{CL}$ $r^2 = 0.96 \quad n = 12$ |
| Mature females (CL > 10 mm) | $\ln \text{PL} = 0.45 + 1.04 \ln \text{CL}$ $r^2 = 0.90 \quad n = 233$ |

For immature females the growth of the propodus is positively allometric (95 % limits, 1.02–1.35), but for mature females it does not differ significantly from isometry (95 % limits, 0.99–1.08). However, the slopes are not significantly different ($t = 1.39$, $n = 241$, $p > 0.2$).

In addition to the changes in the relative size of the chela with growth, there is also a change in the shape of the propodus, as described previously by INGRAND (1937). In smaller specimens the fingers of the chelae are closely apposed along their length, but in some larger specimens the fixed finger is curved, leaving a distinct gap between the basal parts of the fingers and resulting in the so-called 'arched' chela form. Along with this change of shape, there are also changes in the dentition of the dactyl and increased setation. The structure of the two chelar forms is described and figured in detail by INGRAND (1937, plate VI).

In the Seabight material the incipient development of arched chelae is apparent in some specimens without its full expression, indicating that the development of this form can take more than one moult. Usually the arched form is developed on one side only, the tally being 60 specimens with arched left chelae, 34 with arched right chelae, and only three with both chelae arched. The handedness is significant (Chi-squared, $n = 94$, $p < 0.05$).

The occurrence of arched chelae differs markedly between the sexes. Only three females were found with partly arched chelae, all large specimens with carapace lengths of 29–30 mm. Arched chelae are more common among males, but the proportion with such chelae at each size was difficult to determine accurately since a number of specimens had lost one or both chelae. Furthermore, in the partially developed form, the assessment of a chela as arched or not is somewhat arbitrary. Consequently, Table 2 indicates minimal values for partly and fully developed arched chelae in males and suggests an increasing proportion with arched chelae up to a carapace length of about 20 mm, above which almost all specimens have arched chelae.

Table 2. *Munida sarsi*. Percentages of males with arched chelae at different carapace lengths (CL).

| CL range (mm) | Number with chelae | Arched chelae | |
|---------------|--------------------|---------------|------------|
| | | Number | Percentage |
| 12-14 | 258 | 0 | 0 |
| 14-16 | 210 | 8 | 4 |
| 16-18 | 106 | 34 | 32 |
| 18-20 | 39 | 31 | 79 |
| 20-22 | 11 | 10 | 91 |
| 22-24 | 7 | 5 | 71 |
| 24-26 | 2 | 1 | 50 |
| 26-28 | 2 | 0 | 0 |
| 28-30 | 2 | 2 | 100 |
| 30-32 | 6 | 4 | 67 |
| 32-34 | 1 | 1 | 100 |

The relative growth in eye diameter was also investigated since eye size is frequently used in specific identification within the genus *Munida*. The regression equations for the different categories are:

Immature males

$$(CL \leq 10 \text{ mm}) \quad \ln ED = -0.85 + 0.83 \ln CL$$

$$r^2 = 0.89 \quad n = 88$$

Mature males

$$(CL > 10 \text{ mm}) \quad \ln ED = -0.41 + 0.66 \ln CL$$

$$r^2 = 0.92 \quad n = 746$$

Immature females

$$(CL \leq 10 \text{ mm}) \quad \ln ED = -0.79 + 0.80 \ln CL$$

$$r^2 = 0.87 \quad n = 57$$

Mature females

$$(CL > 10 \text{ mm}) \quad \ln ED = -0.38 + 0.64 \ln CL$$

$$r^2 = 0.89 \quad n = 583$$

While there are no significant differences in the level of allometry between the sexes in immature specimens ($t = 0.71$, $n = 143$, $p = 0.2$), the difference is significant for mature individuals ($t = 4.52$, $n = 1323$, $p < 0.001$). In each sex the level of allometry is significantly higher for immature than mature size classes (males, $t = 12.14$, $n = 832$, $p < 0.0001$; females, $t = 5.42$, $n = 636$, $p < 0.0001$).

Reproductive cycle

This part of the study was difficult because of the scarcity of samples during the winter period, though the data were adequate to permit general patterns to be determined. The smallest female collected with eggs attached to the pleopods had a carapace length of 9.6 mm, so that females with a carapace length exceeding 10 mm were all considered to be mature. Some females may not, in fact, mature until they attain a larger size, but the high propor-

Table 3. *Munida sarsi*. Percentage of mature females in each month carrying eggs in various stages of development. No samples were obtained in January.

| | Month | | | | | |
|------------------|-------|---|----|----|-----|-----|
| | D | J | F | M | A | M-O |
| Few plain eggs | 9 | - | 0 | 0 | 0 | 0 |
| Plain eggs | 65 | - | 6 | 0 | 0 | 0 |
| Eggs < 50 % eyed | 0 | - | 41 | 28 | 0 | 0 |
| Eggs > 50 % eyed | 0 | - | 50 | 61 | 4 | 0 |
| No eggs | 25 | - | 3 | 11 | 96 | 100 |
| Total females | 181 | - | 34 | 19 | 123 | 686 |

tion of > 10 mm CL females carrying eggs during the breeding season indicates that this was not a source of serious error.

The occurrence of external eggs, and their developmental stages, on mature females collected at different times of the year are shown in Table 3. None of the large number of females collected between May and October were berried, but in December 75 % of mature females were carrying eggs in an early stage of development, indicating a laying season in November-December. Of the rather small samples obtained in February and March, 90 % or more of the mature females were carrying eggs with an increasing proportion of them eyed. By April almost all of the eggs had hatched, suggesting an incubation period of 4-5 months.

The data on ovarian development (Table 4) support the impression of an annual reproductive cycle in females. In February the ovaries are still very immature after laying the previous November-December. Thereafter, there is a steady maturation, with an increase in size of the ovaries and of the individual ova, and a change of colour from white to peach in May-June and ultimately to orange, the colour of the eggs when first laid, in August-September.

Fecundity

Values for the mean size and number of plain and eyed eggs are also given in Table 4. The small increase in egg size with development is normal, but the great reduction in egg number is not. To examine whether this was simply a result of differing female size, egg number is plotted against female carapace length in Fig. 5. There is a strong correlation between egg number and female size, with the regression of log egg number on log female carapace length for all females carrying plain eggs being:

$$\ln \text{egg number} = 2.89 + 1.52 \ln CL \text{ (mm)}$$

$$r^2 = 0.78$$

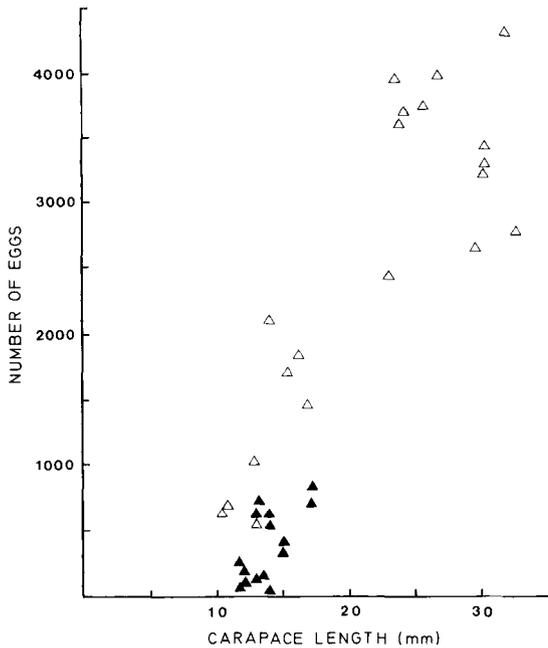


Fig. 5. *Munida sarsi*. Relationship between number of eggs carried and female carapace length. Open symbols = plain eggs; closed symbols = eyed eggs.

Consequently, much of the disparity between the mean numbers of plain and eyed eggs is, indeed, due to the high numbers of plain eggs carried by the very large females from sample 51302. Nevertheless, the number of eyed eggs carried is generally considerably smaller than the number of plain eggs carried by females of a similar size, the difference presumably being due to some having hatched and others having been lost either naturally or during sampling.

Sex ratio and moulting seasonality

The variations in the moulting frequency and sex ratio in the samples throughout the year are shown in Table 5. Males show no obvious seasonality in moulting, but females show a marked peak in April, presumably representing a post-hatching moult. The October sample is too small for any conclusion to be drawn. The sex ratio also varies through the year. The low proportion of females in the May samples is probably a result of cryptic (that is burrowing) behaviour following the April moulting peak, but the relative rarity of females in August seems to be too early to be explained by a similar cryptic behaviour at the onset of egg laying.

Table 4. *Munida sarsi*. Ovarian condition and mean egg size and number in different months.

| Month | Ovary condition | Ovary colour | Mean ova size (mm) (\pm S.D.) | Egg condition | Mean egg size (mm) (\pm S.D.) | Mean egg number |
|--------|-----------------|--------------|----------------------------------|---------------|----------------------------------|-----------------|
| 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) | medium | peach | 0.20 ± 0.03 | none | - | - |
| Jun a) | small | white | 0.15 ± 0.01 | none | - | - |
| b) | medium | peach | 0.21 ± 0.02 | none | - | - |
| Jul | | | No mature females | | | |
| Aug | medium | orange | 0.36 ± 0.08 | none | - | - |
| Sep | large | orange | 0.42 ± 0.07 | none | - | - |

Table 5. *Munida sarsi*. Sex ratio, and proportion for each sex moulting, in each month

| | Month | | | | | | | | | | | | Total |
|----------------------------|-------|----|----|-----|----|-----|----|----|----|----|---|-----|-------|
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| Number of males | - | 50 | 19 | 87 | 70 | 460 | 8 | 81 | 68 | 2 | - | 214 | 1059 |
| Number of females | - | 34 | 19 | 123 | 33 | 395 | 8 | 17 | 49 | 4 | - | 181 | 863 |
| Percent females | - | 41 | 50 | 59 | 32 | 46 | 50 | 17 | 42 | 67 | - | 46 | 45 |
| Number of males moulting | - | 1 | 1 | 2 | 1 | 23 | 0 | 3 | 4 | 0 | - | 1 | |
| Number of females moulting | - | 0 | 0 | 30 | 1 | 33 | 0 | 1 | 4 | 2 | - | 0 | |
| Percent males moulting | - | 2 | 5 | 2 | 1 | 5 | 0 | 4 | 6 | 0 | - | 1 | |
| Percent females moulting | - | 0 | 0 | 24 | 3 | 8 | 0 | 6 | 8 | 50 | - | 0 | |

Munida tenuimana G.O. Sars, 1972

M. tenuimana is distributed in the eastern Atlantic from Iceland (HANSEN 1908), West Greenland (STEPHENSEN 1939), the Barents Sea (CHRISTIANSEN 1972), and Norway (BRINKMANN 1936), and south to the Iberian Peninsula and the Mediterranean (ZARIQUIEY ALVAREZ 1946, 1952). The reported upper bathymetric limit varies geographically, 120–280 m off Iceland, 250–300 m in Norwegian waters and 400 m in the Mediterranean. The deepest record, from 1775 m, is also from the Mediterranean. In the Porcupine Seabight its depth range was 740–1410 m, with 123 specimens being obtained from 34 stations. This range includes that of the hexactinellid sponge *Pheronema carpenteri* which forms dense aggregations particularly at 1100 to 1200 m (see RICE, THURSTON & NEW 1990). Within the sponge range, benthic photographs reveal that *M. tenuimana* may inhabit burrows in the sediment (Fig. 6A), the presumed 'normal' habit of soft-bottom dwelling galatheids. But the species is also frequently photographed in association with the sponge (Fig. 6B), or even using the osculum as an artificial burrow (Fig. 6).

Length frequency

The 123 specimens collected comprised 61 males, 61 females and a single unsexable juvenile. The frequency in each 1 mm CL class is shown in Fig. 7. The two sexes have similar length distributions, each with a peak at about 14 mm CL.

Numerical abundance and biomass

The results of the density and biomass calculations are plotted against depth in Fig. 8. Overall densities and biomasses are low compared with those for *M. sarsi*, but the data from both the OTSB and the BN indicate clear peaks for numerical abundance and, to a lesser extent biomass, in the depth range 1200 to 1300 m.

Relative growth

The data for examining the relative growth of the chelae are rather restricted, and there were insufficient immature specimens (CL < 11.5 mm) to treat them as a separate group. However, the limited data do not indicate any change in relative growth with size. The regression equations for all specimens of each sex are:

| | |
|---------|---|
| males | $\ln \text{ChL} = 1.33 + 1.07 \ln \text{CL}$ $r^2 = 0.97 \quad n = 28$ |
| females | $\ln \text{ChL} = 1.66 + 0.91 \ln \text{CL}$ $r^2 = 0.94 \quad n = 25$ |

The slopes are significantly different ($t = 2.36$, $n = 51$, $p = 0.05$), that for males indicating positive allometry, and that for females negative allometry. For the chelar propodus the comparable equations are:

| | |
|---------|--|
| males | $\ln \text{PL} = 0.25 + 1.14 \ln \text{CL}$ $r^2 = 0.95 \quad n = 28$ |
| females | $\ln \text{PL} = 0.63 + 0.97 \ln \text{CL}$ $r^2 = 0.90 \quad n = 25$ |

Again the slopes for the sexes differ significantly ($t = 2.95$, $n = 51$, $p = 0.005$). For males there is positive allometry (95 % limits, 0.83–1.11), but for females growth was not significantly different from isometry (95 % limits, 0.83–1.11).

For relative eye diameter the regression equations are:

| | |
|---------|---|
| males | $\ln \text{ED} = -1.06 + 0.92 \ln \text{CL}$ $r^2 = 0.98 \quad n = 58$ |
| females | $\ln \text{ED} = -0.91 + 0.85 \ln \text{CL}$ $r^2 = 0.96 \quad n = 59$ |

The slopes are significantly different ($t = 6.96$, $n = 115$, $p < 0.001$), and for both sexes growth is negatively allometric (95 % limits, 0.88–0.95 males, 0.81–0.90 females). The data do not indicate significant differences between immature and mature specimens within either sex, though in each case the slope was greater for immature than for mature classes (as was clear in the much larger samples of *M. sarsi*).

Reproductive cycle

This analysis was carried out as for *M. sarsi*, but was made even more difficult by the much smaller samples. The smallest ovigerous female encountered was 11.5 mm CL, and this was taken as the size of maturity.

The occurrence of different types of eggs throughout the year is detailed in Table 6. Despite the small sample sizes it is apparent that there is not a clear cycle. Plain eggs occur from July to November, suggesting an extended laying period. Predominantly eyed batches of eggs occur from February to July, hatching therefore presumably occurring from March (or later) to July. The lack of any prolonged period without ovigerous females, together with the occurrence of plain eggs as early as July, suggest that external eggs are carried much longer in *M. tenuimana* than in *M. sarsi*, being laid earlier (shortly after hatching the previous batch) and hatched later. The information available on ovarian

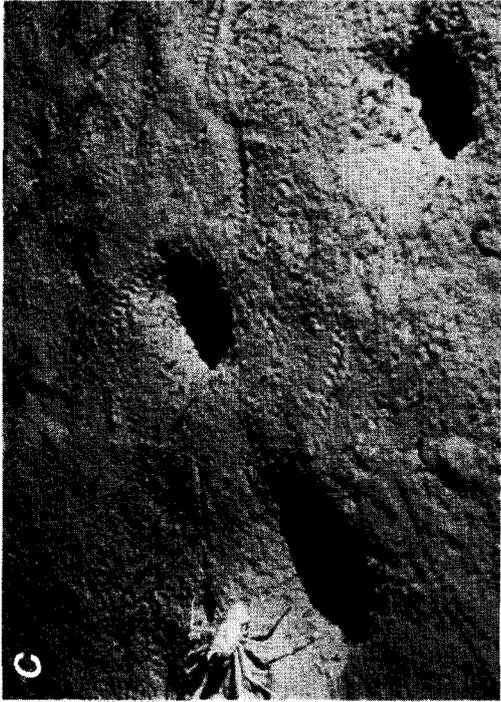


Fig. 6. *Munida tenuimana*. *In situ* photographs from phototranssect 51734 showing *M. tenuimana*, mainly in association with the hexactinellid sponge *Pheronema carpenteri*; depth c. 1100 m. The less obvious galatheids are arrowed. For further explanation see text.

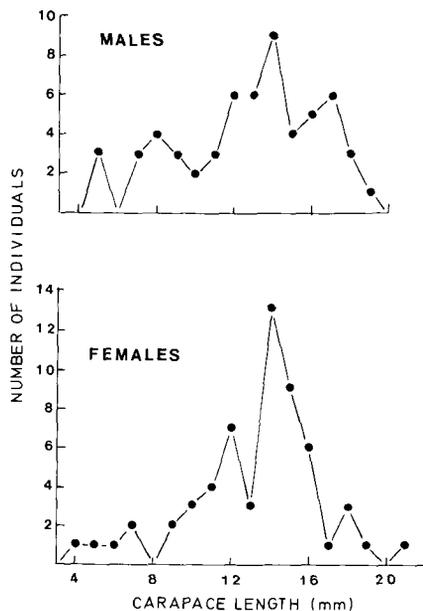


Fig. 7. *Munida tenuimana*. Length-frequency distributions of all males and females in the Porcupine Seabight samples.

condition in *M. tenuimana* does not clarify the picture, since some females with large ovaries occur at all times of the year, while some females carrying plain eggs have large ovaries.

Fecundity

The mean number and size of eggs per female is as follows:

Plain eggs 0.86 ± 0.03 mm 630 \pm 492 eggs n = 7
 Eyed eggs 1.11 ± 0.12 mm 532 \pm 322 eggs n = 5

Within the constraints of the small sample size there is no clear relationship between number of plain eggs carried and the size of the female, unlike in *sarsi*.

Sex ratio and moulting seasonality

The sex ratio values (Table 7) are based on very small samples, but show a consistent trend with the proportion of females being at a minimum during the winter and increasing to a maximum in September–October. Too few moulting specimens were collected to allow any conclusions about moulting periodicity in *M. tenuimana*.

Munida micropthalma A. MILNE EDWARDS, 1880

Widespread in the North Atlantic, from Iceland (HANSEN 1908) to the Cape Verde Islands (HENDERSON 1888) in the east, from the Gulf of Mexico (PEQUEGNAT & PEQUEGNAT 1979) and the West Indies (CHACE 1942) in the west, and from the Mid-Atlantic Bight (WENNER 1982). It has been recorded from as shallow as 194 m (Iceland: HANSEN 1908)

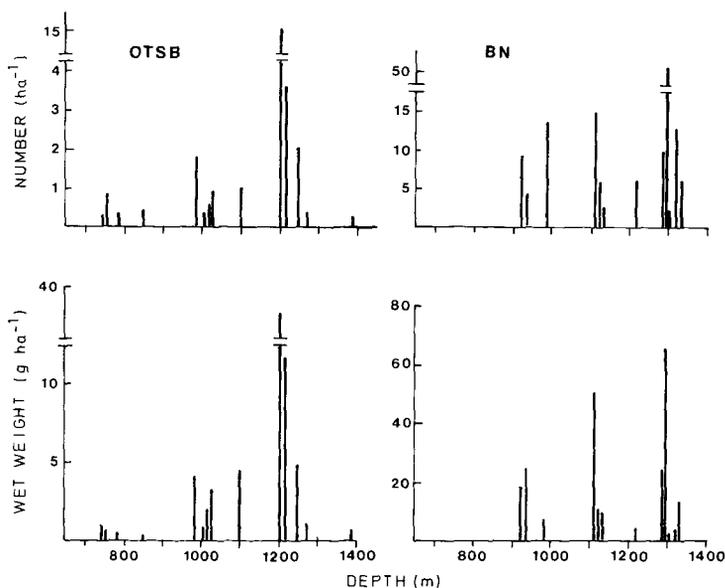


Fig. 8. *Munida tenuimana*. Numerical abundance and biomass estimates at different depths, based on OTSB samples (left) and BN samples (right).

Table 6. *Munida tenuimana*. Percentage of mature females in each month carrying eggs in various stages of development. No samples were collected in December, January and August.

| | Month | | | | | | | | | |
|------------------|-------|----|-----|----|----|----|-----|----|---|----|
| | O | N | D-J | F | M | A | M-J | J | A | S |
| Few plain eggs | 0 | 20 | - | 0 | 0 | 0 | 0 | 0 | - | 13 |
| Plain eggs | 77 | 20 | - | 0 | 0 | 0 | 0 | 20 | - | 40 |
| Eggs < 50 % eyed | 0 | 0 | - | 0 | 0 | 33 | 0 | 0 | - | 0 |
| Eggs > 50 % eyed | 0 | 0 | - | 60 | 33 | 33 | 0 | 20 | - | 0 |
| No eggs | 23 | 60 | - | 40 | 67 | 33 | 100 | 60 | - | 47 |
| Total females | 13 | 5 | - | 5 | 3 | 3 | 6 | 5 | - | 15 |

Table 7. *Munida tenuimana*. Variations in the sex ratio in samples taken at different times of the year.

| | Month | | | | | | | | | | | | Total |
|-------------------|-------|------|------|------|------|------|------|---|------|------|------|---|-------|
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| Number of males | - | 9 | 6 | 9 | 1 | 6 | 8 | - | 10 | 5 | 7 | - | 61 |
| Number of females | - | 5 | 3 | 7 | 1 | 5 | 7 | - | 15 | 13 | 5 | - | 61 |
| Percent females | - | 35.7 | 33.3 | 43.8 | 50.0 | 45.5 | 46.7 | - | 60.0 | 72.2 | 41.7 | - | 50.0 |

to 2129 m (off Ascension: CHACE 1942). In the Seabight study only two specimens of *M. microphthalma* were collected, both from the same station (10111#8) at a depth of 1630-1640 m.

DISCUSSION

Distribution and abundance

The species encountered in this investigation were those which were to be expected from their known geographical distributions and depth ranges. The only other species which might have been expected was *M. intermedia* A. MILNE EDWARDS, a species widespread in the eastern Atlantic and found as far north as the Goban Spur which forms the southern flank of the Porcupine Seabight. (RICE & SAINT LAURENT 1986).

M. rugosa was found in only a few samples, but this was to be expected since it is primarily a continental shelf species extending no deeper than about 300 m and none of the Seabight samples were taken shallower than about 200 m.

The most abundant species in the Seabight study was *M. sarsi*, which occurred over its generally recorded depth range of 200 to 800 m. It was not evenly distributed over this range, but peaked markedly in both numerical abundance and biomass between about 450 and 500 m. In the north-east Atlantic generally the species reaches its maximum abundance between 250 and 400 m (RICE & SAINT LAURENT 1986), so that the peak in the Seabight is somewhat deeper. INGRAND (1937) obtained her samples in the Bay of Biscay at 150-230 m, but the overall depth distribution was not recorded. Although *M. sarsi* is primarily a species of the upper

continental slope, it is one of several upper bathyal species also found in fjord situations. BRINKMANN (1936) found it in large numbers at the unusually shallow depth of 125 m in the Bergen area where, by 500 m, it had become very scarce. More recently, ZAINAL (1990) found *sarsi* in restricted areas within the Firth of Clyde at depths between 95 and 115 m where it occurred together with *M. rugosa*. BRINKMANN suggested that the species settles in the shallower parts of its range and migrates into deeper water as it grows, but there was no evidence for such a behaviour in the Seabight study.

M. tenuimana occurred in the Seabight from 740 to 1400 m, with little overlap with *M. sarsi*. It showed a peak in abundance at depths between 1200 and 1300 m, where the maximum densities indicated by trawl and sledge catches were about 50 individuals ha⁻¹, though photographic evidence indicates densities at least an order of magnitude higher. In other areas *M. tenuimana* occurs both shallower and more abundantly than in the Seabight; BRINKMANN (1936), for instance, collected a sample of some thousands of *tenuimana* at 500 m in the fjords near Bergen, at which depth it was far more abundant than *M. sarsi*.

M. microphthalma appears to be rather rare in the Seabight. Only two specimens were collected, although numerous samples were taken within the species' reported bathymetric range (see RICE & al. 1991).

Size-frequency distributions

The two sexes of *M. sarsi* showed similar size-frequency distributions, both unimodal with pronounced peaks in the 12-14 mm CL range, but with males having a slightly larger modal size than

females. The size-frequencies of both sexes, however, had pronounced tails of large individuals up to carapace lengths of 33–34 mm. All of the largest individuals (males > 26 mm CL and females > 23 mm CL) originated from a single sample which consisted only of these large specimens.

INGRAND (1937) measured 325 males and 187 females from the Bay of Biscay. She reported a maximum carapace length of 23 mm for both sexes, with modes at about 19–20 mm for males and 16–17 mm for females. BRINKMANN'S (1936) much larger samples from his fjord study had a mode of 14–16 mm for both sexes, with males reaching a maximum length of 28 mm and females 26 mm. Thus, both of these populations appear to have had a larger modal length but a much smaller maximum size than the Seabight specimens. ZAINAL'S (1990) selective creel-caught samples from the Firth of Clyde showed maximum carapace lengths for males of 30 mm and for females of 25 mm. Clearly, the anomalous sample of large individuals from the Seabight is unusual by any standards and would repay further study.

Relative growth

The relative growth of both the entire chelae and the propodi alone conformed basically to the usual decapod pattern. Information on the growth in immature specimens was sparse, but in *M. sarsi* the pattern in males was of positive allometry, increasing after maturity, and in females near isometry at all stages. In *M. tenuimana* there was positive allometry in the males, and negative allometry or isometry in the females. INGRAND (1937) also studied the relative growth of the chelae in *M. sarsi*, though not with great statistical rigour. She found positive allometry ($b = 1.24$) in immature specimens of each sex, increasing to 1.40 in males after maturity, but becoming negatively allometric ($b = 0.95$) in mature females. ZAINAL (1990) did not discriminate between immature and mature specimens in her rather small samples of *M. sarsi*: she found positive allometry in males and isometry in females. She also studied the relative growth of the chelae in *M. rugosa*, finding positive allometry for males ($b = 1.20$) and near isometry for females ($b = 0.90$). The general pattern therefore seems to be fairly consistent between species, but further study is required of the changes in relative growth at puberty.

In both *M. sarsi* and *M. tenuimana* growth in eye diameter showed marked negative allometry. This was particularly apparent in *M. sarsi* in which the eye diameter is about 34 % of the carapace length

in males at 4 mm CL, but falls to about 20 % at 30 mm CL. Clearly, eye diameter must be used with caution as an identification aid for both very small and very large specimens.

Arched chelae

The curious development of arched chelae has been reported in a number of galatheid genera including *Galathea* and *Munidopsis* (MILNE EDWARDS & BOUVIER 1894) as well as *Munida*.

The situation with respect to the 'arched' chelae in larger specimens of *M. sarsi* is far from clear. It is apparent from both INGRAND (1937) and from the present study that this chela form does not appear in its complete expression at a single moult and is therefore not comparable with the abrupt chelar change at the puberty moult found in many spider crabs (see HARTNOLL 1963). Instead, the changes take place gradually over several moults and, in the present study, appeared at very different frequencies in the two sexes. In females, the arched form was seen in only three of the largest specimens (29–30 mm CL) and then only partially developed. In males, on the other hand, arched chelae began to appear at a carapace length of about 14 mm (above the size at sexual maturity of around 10 mm CL), and by 20 mm CL almost all specimens had at least one chela of the fully developed arched form. There was a significant bias for left-handedness, and only about 3 % developed two arched chelae. INGRAND (1937) also found that arched chelae were both less common and less well-developed in females. She also found that the arched form appeared in males from about 12–13 mm CL, though the form of her data does not allow the frequency at larger sizes to be assessed. However, there was no evidence of handedness, and in one sample over 40 % of arched males had both chelae affected. ZAINAL (1990) examined only small samples. She found arched chelae in only one large female and in 15 males, the smallest with a carapace length of 16 mm. Of the males, six had the left chela arched, three the right, and six both. Clearly, the development of arched chelae in *M. sarsi* varies considerably in different populations.

Arched chelae also occur in other *Munida* species, with similar inconsistencies with regard to sex, handedness and size at which this form first appears. Thus, ZAINAL (1990) found that in a sample of 25 male *M. rugosa*, six had one arched chela, one had both chelae arched, while the smallest 'arched' male had a carapace length of 27 mm. Eighteen females examined were all unaffected. In a museum collection from the same area there were 65 males,

ten with the left chela arched, ten with the right arched, and 17 with both. One female out of seven had partly developed arched chelae. In the present study there was no evidence of arched chelae in *M. tenuimana*.

The phenomenon of arched chelae resembles the heterochely found in many decapods, which usually occurs in both sexes, though more prominently in males, and is generally assumed to have a feeding rather than a sexual function. However, observations of the feeding behaviour in *M. rugosa* did not indicate any special use being made of the arched chelae (ZAINAL 1990). Moreover, on the basis of scars on the chela of male *M. sarsi* which matched the tooth pattern of arched chelae, INGRAND (1937) suggested that they may be used during fighting between rival males.

Reproduction

There is broad agreement in the literature on the size at sexual maturity in both *M. sarsi* and *M. tenuimana*. In this study the size at maturity in females was based on the development of the ovaries and the existence of external eggs, giving an estimate of 10 mm CL in *sarsi* and 11.5 mm CL in *tenuimana*. Similarly, INGRAND (1937) observed that female *sarsi* developed mature-form pleopods at 11–12 mm CL and that the smallest ovigerous females were at 11.5 mm CL. BRINKMANN (1936) gave 11.5 mm CL as the size of 50 % female sexual maturity in *sarsi* and 12.5 mm CL as the minimum for maturity in *tenuimana*. He also gave 11.5 mm CL as the size at maturity for males of both species.

The Seabight study indicated a fairly distinct seasonal breeding for *M. sarsi*, with egg-laying in November–December, an incubation period of 4–5 months, and hatching in March–April. BRINKMANN (1936) found an equally distinct seasonality in his fjord populations of *M. sarsi*. At a depth of 125 m, eggs were laid in late September–October and hatched in April–May, therefore suggesting an incubation period considerably longer than that in the Seabight. In a deeper population, at 500 m, BRINKMANN reported even earlier egg laying and an incubation period longer by one or two months.

The reproductive pattern for *M. tenuimana* in the Seabight was far less clear, with an extended laying period from July to November and hatching from March (or later) to July. The breeding cycle from BRINKMANN's more comprehensive data was much more definite, with egg laying in June–July and hatching the following March–April. HUUS (1935) also reported hatching of *M. tenuimana* in April. This indicates an incubation period of at least 9–10

months, but is not seriously at variance with the less adequate Seabight data.

The breeding season for *M. rugosa* could not be determined from the Seabight samples, but in the Irish Sea egg-laying occurred in September–October and hatching in March–April (ATTRILL 1988). This agrees generally with the pattern off the west coast of Scotland (COMELY & ANSELL 1989) and in the Firth of Clyde, where ovigerous females were first observed in November and hatching took place from March to May (ZAINAL 1990). It therefore appears that breeding is more clearly seasonal in the shallower species, and in the shallower-living populations of *M. tenuimana*.

Fecundity

Despite the great variability in the number of eggs carried by individual females, it is possible to compare the fecundity in different species by estimating roughly the number of eggs that would be carried by females of the same size. In this way, ZAINAL's (1990) data, based on all egg stages, suggest that a female *M. rugosa* with a carapace length of 20 mm would carry about 3300 eggs. Our own results, on the other hand, suggest that a 20 mm CL female *M. sarsi* would carry about 1700 eggs, while a female *M. tenuimana* of this size would carry less than 1000 eggs. This suggests that fecundity is higher in the shallow-living species, but there is no clear inverse relationship between egg size and fecundity as might be expected. Thus, we found a mean diameter for early eggs of 0.86 mm in *M. tenuimana* and 0.73 mm in *M. sarsi*. ZAINAL (1990) reported a mean diameter of 0.81 mm for *M. rugosa*, but her measurements were based on partly developed eggs in January/February, while early eggs in *rugosa* may be rather smaller.

Moulting

Moulting in decapods is frequently correlated with the reproductive cycle. *M. sarsi* females in the Porcupine Seabight exhibited a post-hatching moulting peak in April, while males showed no obvious moulting seasonality. BRINKMANN (1936) also reported a post-hatching peak in moulting by females in Norwegian populations, but in this case the males also had a distinct moulting season from March to May. Finally, ZAINAL (1990) found newly moulted females in the Firth of Clyde in April and May, whereas males appeared to moult somewhat earlier, from January to March. Our data for *M. tenuimana* were inadequate to investigate moulting periodicity but BRINKMANN (1936) found that Norwegian males

moulted between December and March, and females from April to June, again shortly after hatching. Thus, these species, at least, seem to follow the fairly common moulting pattern in decapods in which males have a rather earlier and less discrete moulting period than the females, so that they are hardened and in a condition to mate with the newly moulted females.

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