

# THE EFFECT OF THE ENVIRONMENT ON THE MORPHOLOGY OF *MUNIDA GREGARIA* (FABRICIUS) (DECAPODA, ANOMURA)

BY

BARBARA G. WILLIAMS

Department of Zoology and Portobello Marine Biological Station, University of Otago,  
Dunedin, New Zealand

## INTRODUCTION

The relationship of *Munida subrugosa* (White, 1847) and *M. gregaria* (Fabricius, 1793) has been the subject of some discussion in past years. Lagerberg (1906) and Matthews (1932) both consider that *M. gregaria* and *M. subrugosa* are two distinct species but Chilton (1909) and Thomson (1898) conclude that they are in fact two forms of a single species. The features on which the two species can be separated were given by Lagerberg and subsequently confirmed and used by Matthews. These features include the shape of the carapace and the details of the spines at its antero-lateral corners; the shape, size and direction of the rostral spine; the length and shape of the eyestalk and details of the junction of the cornea and the peduncle, and the form of the terminal segments of the endopodite of the third maxilliped.

In *M. gregaria*, the anterior edges of the carapace meet the lateral margins at an angle of approximately  $90^\circ$ , so that the sides of the carapace are more or less parallel, and the anterior lateral corners in the juvenile stages bear several approximately equal-sized spines. Older specimens have some short main spines and several smaller spines. The median rostral spine of the carapace is short and broad and the terminal segment of the endopodite of the third maxilliped is oval and leaf-like. Eyestalks are long and slender, constricted in the middle and the dividing line between the cornea and the peduncle is more or less straight, bearing a few sparse bristles, if any.

*M. subrugosa* has the lateral margins of the carapace converging anteriorly to meet the anterior edge at an obtuse angle, the corners bearing one long fine spine. The median rostral spine is long and slender, the eyestalks short and wide, with a strongly concave line between the cornea and the peduncle. This line is furnished with numerous closely set bristles. The terminal segment of the endopodite of the third maxilliped is more slender than that of *M. gregaria*.

In addition the early post-larval stages of *M. subrugosa* are bottom-living, like the older individuals, while the young adults of *M. gregaria* are pelagic and often swarm at the surface of the sea in vast shoals.

Surface shoals of *Munida* are a common sight in Otago Harbour (New Zealand) during the summer months (November-March). The following study of animals collected from these surface shoals yields further information on the relationship between *M. gregaria* and *M. subrugosa*.

#### METHODS

Samples of *Munida* from surface shoals were collected in Otago Harbour at intervals throughout the shoaling season in the summer of 1969-70. Sample S1 was taken from the first shoal of the season which occurred at the end of November. Samples S2, S3, and S4 were collected from shoals at the beginning and end of December and the end of January respectively, and the last sample, S5, was taken at the beginning of March. No further pelagic animals were seen after this time. Measurements as shown in fig. 1 were made on 12 animals from each sample.

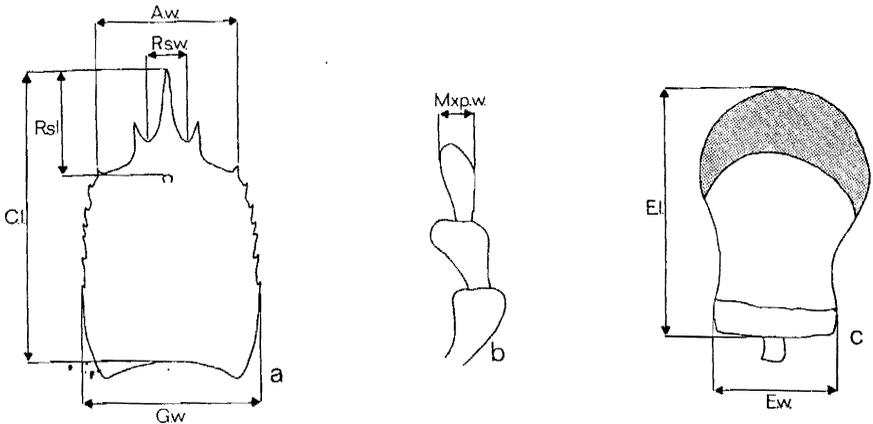


Fig. 1. Measurements made on (a) the carapace, (b) the terminal segment of the endopodite of the third maxilliped and (c) the eyestalk. Cl, carapace length; Aw, anterior width of carapace; Gw, greatest width of carapace; Rsl, rostral spine length; Rsw, rostral spine width; Mxp. w, width of terminal segment; El, eyestalk length; Ew, eyestalk width.

Other animals from samples S2 and S3 (December samples) were placed immediately into an outdoor holding pond, about 2 metres deep with a soft muddy bottom covered with *Ulva*. Within 8 to 9 days of being placed in this pond, the pelagic animals settled to the bottom. Samples of these benthic animals were taken in the following February (B1), and October (B2), and then again in February 1971 (sample B3).

In addition, several pelagic *Munida* were collected in January and maintained in the laboratory for 12 months in individual containers. A comparison of the cast exoskeletons from one animal over a series of moults enabled gradual changes in form to be seen.

#### RESULTS

##### A. Pelagic and benthic samples.

As the shoaling season progresses, the size of the animals in the shoals increases. The mean carapace lengths for each sample are given in table I. Animals

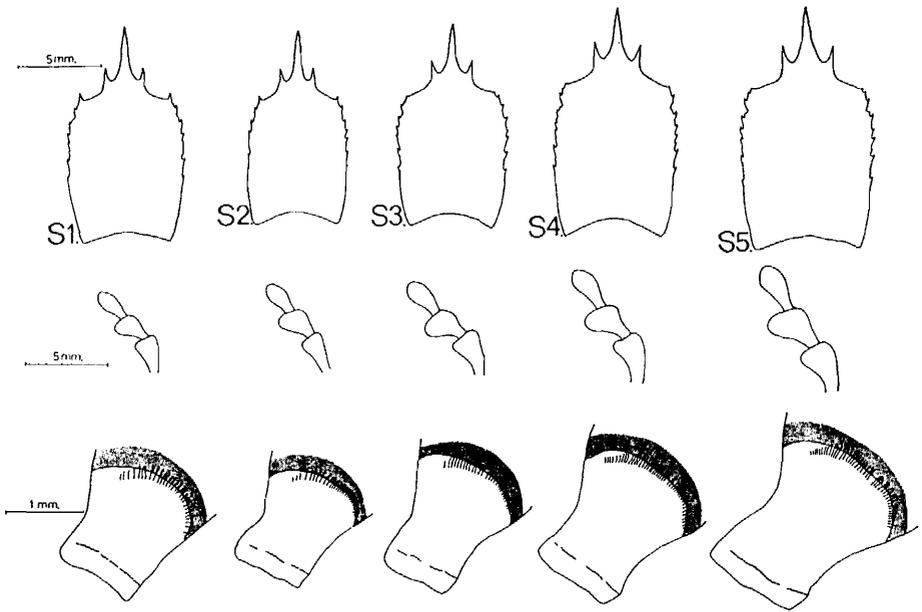


Fig. 2. Outlines of the carapace, terminal segments of the endopodite of the third maxilliped and proximal part of the eyestalk of one animal from each of the pelagic samples, S1-S5.

in the captive benthic population also grew over the 14 month observation period. In both cases, as the animals increased in size, the form and relative proportions of various parts of the body altered, but the changes that occurred in the pelagic animals were quite different from those taking place in the benthic animals. This is seen in plate I, which shows two animals taken from a surface shoal, and two others of approximately the same size from the captive benthic population. Differences in eyestalks, endopodites of the third maxillipeds and details of the carapace are seen, even though the benthic animals had themselves been pelagic only a few months earlier. Diagrams of the carapace, the terminal portion of the maxilliped and part of the eyestalk of one animal from each sample are shown in figs. 2 and 3. Differences between the pelagic and benthic animals and the gradual alteration of the features as growth occurs are evident.

Fig. 4 shows that as growth proceeds in the pelagic animals, there is a tendency for the ratio of the greatest width of the carapace to the anterior width to decrease as the length of the carapace increases. (The mean value for each sample of this and other ratios are given in table I). This indicates an increasing tendency for the lateral margins of the carapace to become parallel to one another. In the captive population, however, the reverse trend is seen (fig. 5), and as the carapace increases in length a narrowing of the anterior edge takes place, shown by the rise in the ratio of greatest width to anterior width when plotted against carapace length.

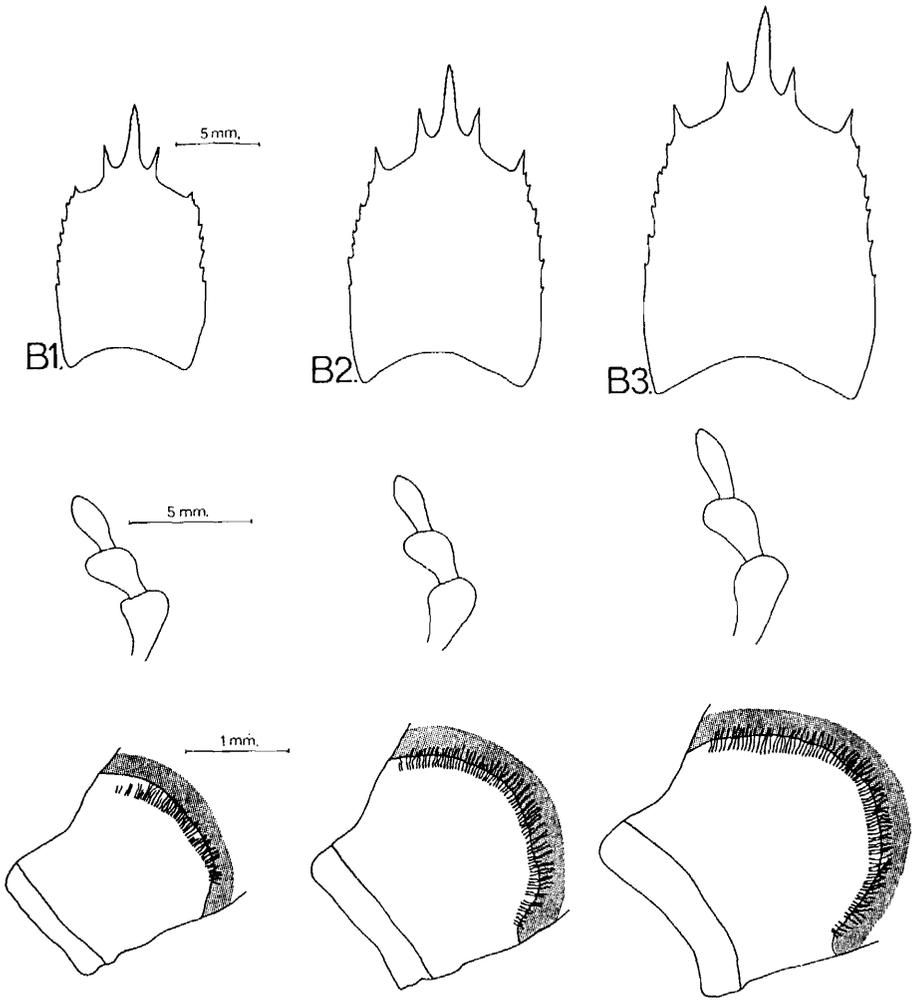


Fig. 3. Outlines of the carapace, terminal segments of the endopodite of the third maxilliped and proximal part of the eyestalk of one animal from each of the benthic samples, B1-B3.

TABLE I

The mean carapace length and means of the ratios of various body measurements in each of the samples (abbreviations as fig. 1)

	Carapace length (in mm)	Gw: Aw	Rsl: Rsw	Cl: Mxp. w.	Cl: El	El: Ew	Cl: Rsl.
S1	10.90	1.25	2.84	12.92	5.19	2.02	2.82
S2	11.08	1.21	2.72	11.22	4.66	2.09	2.83
S3	11.35	1.21	2.46	9.65	4.42	2.22	2.93
S4	12.35	1.17	2.46	9.70	4.25	2.36	2.92
S5	13.77	1.18	2.41	9.56	4.26	2.34	2.90
B1	13.77	1.23	2.70	14.62	4.92	1.99	2.79
B2	17.18	1.31	2.91	19.75	5.51	1.72	2.88
B3	20.49	1.32	3.11	19.99	5.86	1.69	2.89

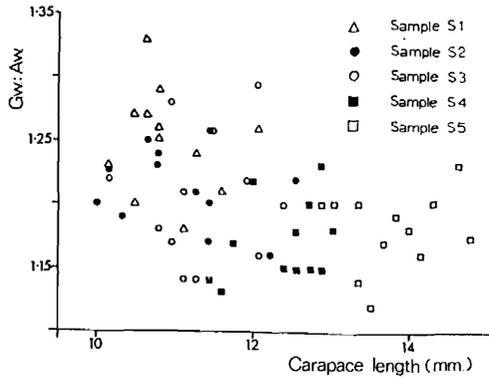


Fig. 4. The ratio greatest width of carapace (Gw) to its anterior width (Aw) in pelagic samples, plotted against carapace length.

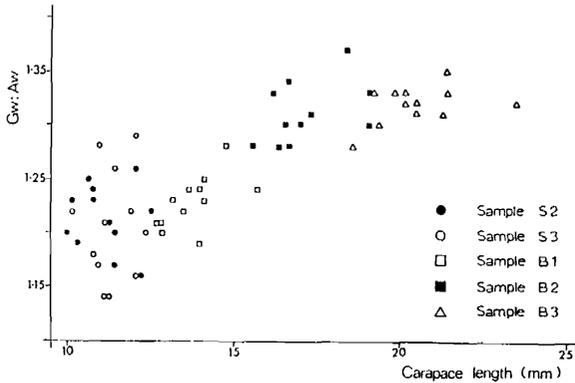


Fig. 5. The ratio of greatest width of carapace (Gw) to its anterior width (Aw) in animals from the outdoor pond, plotted against carapace length.

Figs. 6 and 7 show the ratio of the length of the rostral spine to its width in the various samples. In the pelagic animals (fig. 6), increase in carapace length is accompanied by a decrease in the ratio, whereas in the captive benthic population (fig. 7), there is a tendency for the rostral spine to become narrower as carapace length increases, shown by the increase in the ratio of length to width.

Opposite trends are also seen in the form of the terminal segment of the maxilliped in the pelagic and benthic animals. In the pelagic samples the terminal segment becomes relatively wider as the animals increase in size but in the benthic samples there is a progressive reduction in the width. This is shown by plotting the ratio of the carapace length to the width of the terminal maxilliped segment against carapace length (figs. 8 and 9). A fall in the ratio occurs in the pelagic animals as carapace length increases (fig. 8) in contrast to a marked rise in the benthic population (fig. 9).

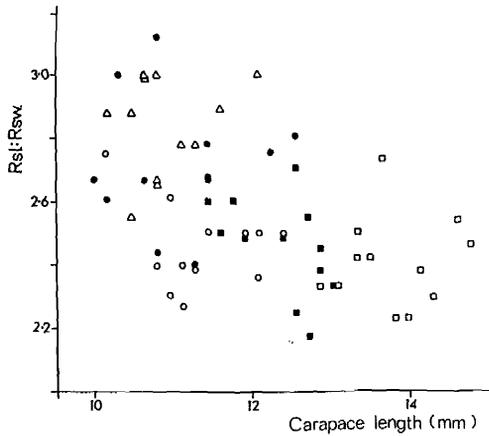


Fig. 6. The ratio of rostral spine length (Rsl) to rostral spine width (Rsw) in pelagic samples, plotted against carapace length. Symbols as in fig. 4.

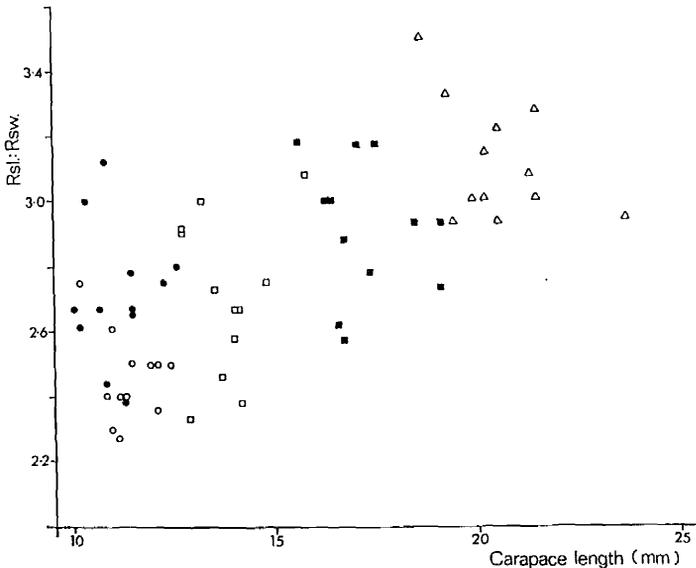


Fig. 7. The ratio of rostral spine length (Rsl) to rostral spine width (Rsw) in animals from the outdoor pond, plotted against carapace length. Symbols as in fig. 5.

Figs. 10-13 illustrate the trends in the form of the eyestalks in pelagic and benthic animals. Although the ratio of carapace length to eyestalk length in the first of the pelagic samples was rather variable, in subsequent samples there was a definite trend to a decrease in this ratio (fig. 10), indicating an increase in eyestalk length relative to carapace length as size increased. As this took place, the shape of the eyestalk altered, the ratio of its length to width increasing with length (fig. 12). The trends in eyestalk morphology of pelagic animals therefore were towards longer and more slender eyestalks as the size of the animals increased.

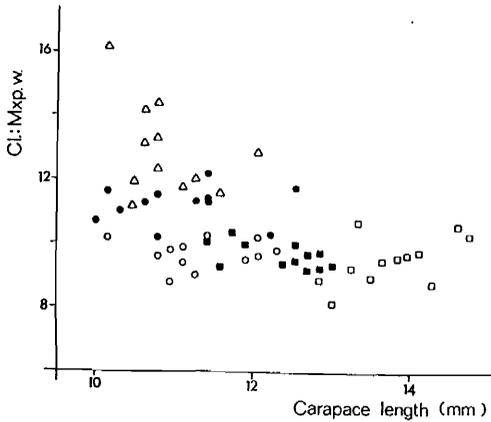


Fig. 8. The ratio of carapace length (Cl) to the width of the terminal segment of the maxilliped (Mxp. w) in pelagic samples, plotted against carapace length. Symbols as in fig. 4.

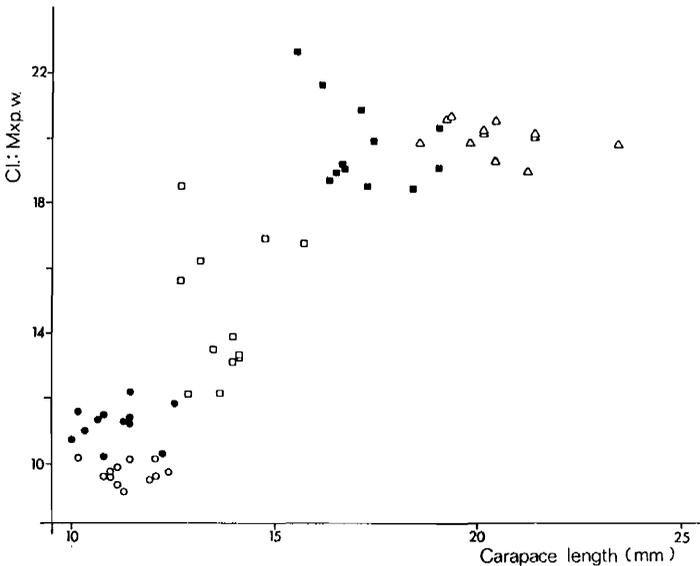


Fig. 9. The ratio of carapace length (Cl) to the width of the terminal segment of the maxilliped (Mxp. w) in animals from the outdoor pond, plotted against carapace length. Symbols as in fig. 5.

In contrast, in the benthic population, the eyestalks became relatively shorter and wider as size increased (figs. 11 and 13).

Changes in the eyestalks also occur at the junction of the peduncle and the cornea. These can be seen in figs. 2 and 3. In the pelagic animals this line is not deeply concave and only a few well-spaced bristles are present. In the benthic animals these features alter as growth proceeds and the line between the peduncle

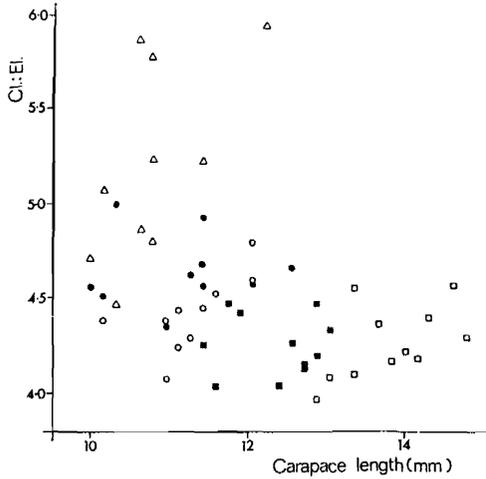


Fig. 10. The ratio of carapace length (Cl) to eyestalk length (El) in pelagic samples, plotted against carapace length. Symbols as in fig. 4.

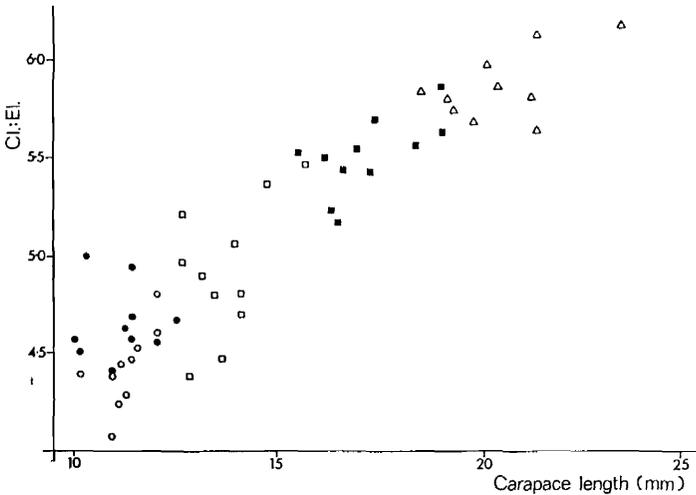


Fig. 11. The ratio of carapace length (Cl) to eyestalk length (El) in animals from the outdoor pond, plotted against carapace length. Symbols as in fig. 5.

and cornea becomes progressively more concave and the bristles associated with it increase in number.

Also seen in figs. 2 and 3 are the changes occurring in the spines of the antero-lateral corners of the carapace. Animals from the first of the pelagic samples had one main spine but this tended to disappear as the surface-shoaling

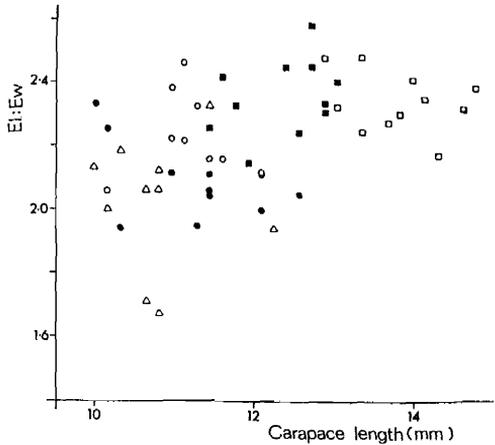


Fig. 12. The ratio of eyestalk length (El) to eyestalk width (Ew) in pelagic samples, plotted against carapace length. Symbols as in fig. 4.

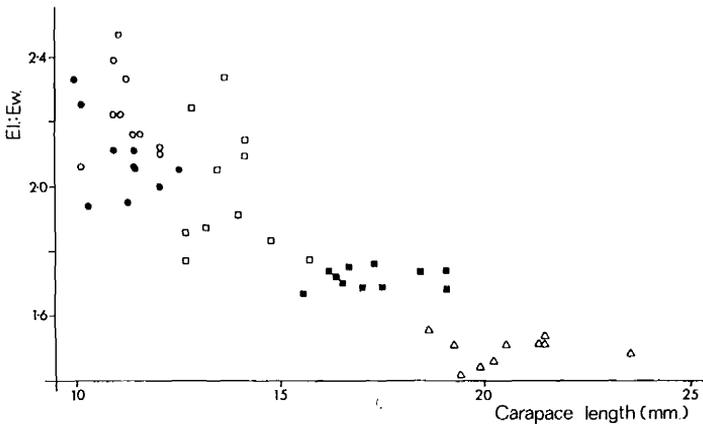


Fig. 13. The ratio of eyestalk length (El) to eyestalk width (Ew) in animals from the outdoor pond, plotted against carapace length. Symbols as in fig. 5.

season progressed. On the other hand, size increase in the benthic animals was accompanied by an increase in the prominence of this spine.

In contrast to the features mentioned so far, no clear trends are evident when the ratio of the rostral spine length to the carapace length is plotted against carapace length. This applies to the pelagic and benthic samples (figs. 14, 15). There is perhaps a slight increase in the ratio in pelagic animals as size increases (fig. 14), although the value of the ratio in the largest pelagic animals is very close to that of the largest benthic ones.

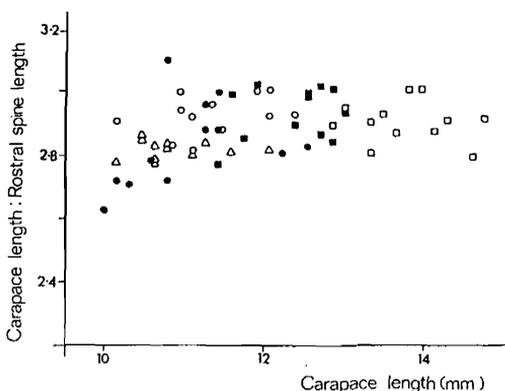


Fig. 14. The ratio of carapace length (Cl) to rostral spine length (Rsl) in pelagic samples, plotted against carapace length. Symbols as in fig. 4.

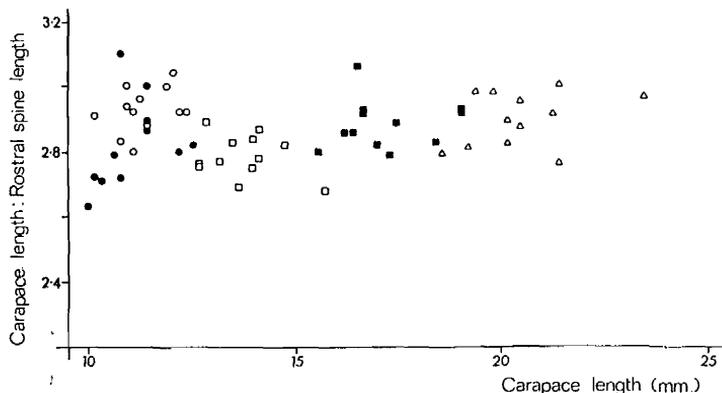


Fig. 15. The ratio of carapace length (Cl) to rostral spine length (Rsl) in animals from the outdoor pond, plotted against carapace length. Symbols as in fig. 5.

#### B. Laboratory-reared *Munida*.

The carapaces of one animal shed at the 1st, 4th and 6th moults in captivity are shown in fig. 16. The exoskeletons of the eyestalk at the 1st and 6th moults are also figured. The gradual development of the spines at the corners of the carapace and the changes in eyestalk morphology are similar to those seen in the growing benthic animals and they illustrate the point that such changes do occur in one animal over a series of moults. The maxillipeds also undergo similar alteration, the ratio of the width of the terminal segment increasing steadily as growth proceeds (table II). Trends in the ratios of the greatest width of the carapace to the anterior width and the rostral spine length to width are by no means as pronounced as in the benthic animals (table II), but are in the same direction (i.e. the ratios are increasing with carapace length not decreasing as in the pelagic samples).

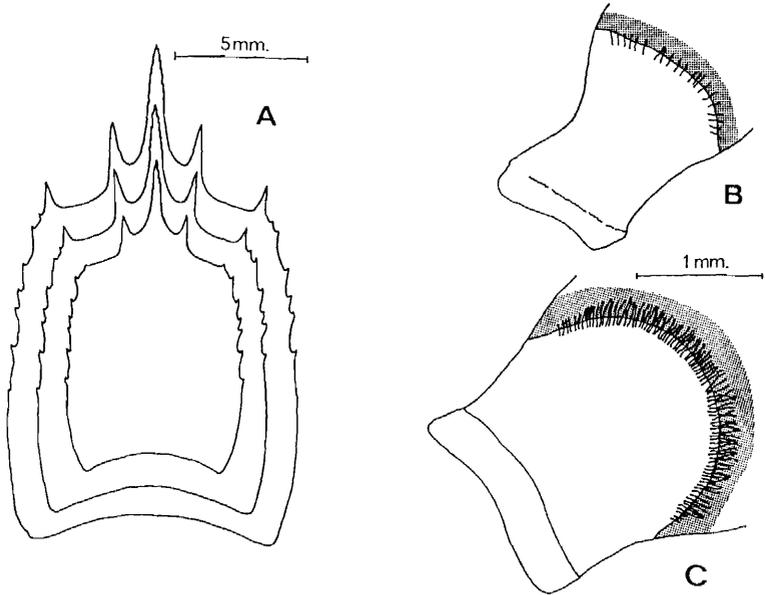


Fig. 16. Carapaces and eyestalks from the cast exoskeletons of one animal over a series of moults. A, outlines of the carapaces shed at 1st, 4th and 6th moults in captivity; B, exoskeleton of the proximal part of the eyestalk shed at the 1st moult; C, as B but from 6th moult.

TABLE II

Ratios of various measurements of cast exoskeletons of 4 animals maintained individually in the laboratory over a series of moults (abbreviations as in fig. 1)

	Animal 1			Animal 2			Animal 3			Animal 4		
	Cl: Mxp. w	Gw: Aw	Rsl: Rsw									
1st moult	9.88	1.21	2.60	10.16	1.18	2.60	8.59	1.14	2.50	8.63	1.15	2.4
2nd moult	10.91	1.22	2.70	11.20	1.22	2.90	9.65	1.16	2.80	9.52	1.19	2.5
3rd moult	15.06	1.23	2.73	14.51	1.24	3.00	11.15	1.21	2.90	11.43	1.21	2.7
4th moult	16.51	1.26	2.83	17.39	1.26	2.91	14.44	1.28	2.91	14.13	1.23	2.6
5th moult	18.32	—	—	17.05	—	—	15.71	—	—	16.33	—	—
6th moult	19.77	1.29	3.08	—	—	—	—	—	—	—	—	—

#### DISCUSSION AND CONCLUSIONS

It is evident that the morphology of the animals in this study depends on the habitat from which they were collected and also on the length of time that they had occupied that habitat. The morphological features affected by the habitat are those on which the two species *M. gregaria* and *M. subrugosa* are distinguished and this leads one to question the validity of the separation.

If *M. gregaria* is the only species with a pelagic stage in its life history, all the animals in this study must be *M. gregaria* as all of them were collected from surface shoals. Yet, of the animals measured, some agree fairly closely with the description of *M. gregaria* given by Lagerberg, others have the characters of *M. subrugosa*, while many seem to fall somewhere between the two.

Considering first the largest of the pelagic animals (those from samples S4 and S5), these agree in most respects with the descriptions of *M. gregaria*. The carapace has more or less parallel sides, prominent main spines at the antero-lateral corners are absent, the eyestalks are long and slender, with the junction between the cornea and peduncle being a straight line. The endopodites of third maxillipeds are large and the terminal segment of each is oval and leaf-like. On the other hand, Lagerberg states that *M. gregaria* has a rather short rostral spine, the ratio of the carapace length to the rostral spine length being 3.16, and that in lateral view, the tips of the lateral spines are level with the dorsal surface of the rostral spine. Animals measured in samples S4 and S5 had a ratio of around 2.9 and of the 24 specimens examined only four had the tips of the lateral spines level with the rostral spine. The other twenty had the rostral spine lying below the tips of the laterals, an arrangement stated by Lagerberg to be characteristic of *M. subrugosa*.

Looking at the complete series of pelagic samples it is obvious that the 'gregaria' features become gradually more pronounced as the animals increase in size. The animals in the first of the pelagic samples (S1), are very different from those in the later samples. The carapace is more tapered and a prominent spine is present at the antero-lateral corners. The rostral spine is broader and the eyestalks shorter and wider; the terminal segment of the third maxilliped is narrower. Their features therefore are tending towards those of *M. subrugosa*, but as the season progresses the characters of *M. gregaria* are gradually established. All of the animals in samples S1, S2, and S3 had the tips of the lateral spines of the carapace above the rostral one.

Once the pelagic animals have settled to the bottom and undergone several moults, they develop characteristics which are, without doubt, those given by Lagerberg for *M. subrugosa*. The animals in samples B2 and B3 have a carapace which tapers at the anterior end, a prominent spine has developed at the corners and the rostral spine has become more slender. The eyestalks and third maxillipeds have also altered to conform with those characteristic of *M. subrugosa*. The ratio of carapace length to rostral spine length, however, does not agree with the figure of 2.42 quoted for *M. subrugosa* by Lagerberg, but neither does it conform to the ratio he gives for *M. gregaria*.

As in the pelagic samples, the animals in the benthic population gradually alter in form as growth occurs, the specimens in the first benthic sample (B1) being at a somewhat intermediate stage.

Animals reared individually in the laboratory developed in much the same way as animals in the outdoor benthic population, though the acquisition of some of the '*subrugosa*' characters was not so pronounced (e.g. the shape of the carapace and rostral spine). This is perhaps due to the highly artificial conditions in which the animals were kept. The most interesting point arising from the individual rearing is the change in eyestalk morphology seen to occur in the animals. The eyestalks shown in fig. 10 clearly show that in six moult cycles, an animal can change from one with typical '*gregaria*' eyestalks to one with equally typical '*subrugosa*' eyestalks.

The results of this study therefore support the conclusions of Chilton (1909) and Thomson (1898) that *M. gregaria* and *M. subrugosa* are not two distinct species. The characters on which the species have previously been distinguished can in fact be altered by a change of environment. A change from a pelagic existence to the benthic one is accompanied by the alteration of existing '*gregaria*' features to '*subrugosa*' features. They cannot therefore be two distinct species but rather two extremes of a range within a single species. By priority, the correct name will be *M. gregaria*.

Chilton considers that the length of time that the animals remain pelagic will depend on the abundance of food at the surface and the availability of a suitable bottom. In this study, the largest pelagic *Munida* caught had a carapace length of 16 mm but off the Patagonian coasts animals with a carapace length of 33 mm were captured at the surface (Matthews, 1932). Details of the behaviour of the pelagic animals are not known at present. The pelagic animals which were placed in the outdoor pond remained at the surface for only a few days before settling to the bottom and they did not appear at the surface again. This, together with the fact that the size of the animals in the surface shoals increases as the season progresses, suggests that the pelagic animals might settle to the bottom intermittently. If the bottom is suitable they remain there, but if not they swim up to the surface again. The morphology of animals trawled from the bottom will then depend on how long they spent as pelagic animals and how long it is since they finally settled out.

#### ACKNOWLEDGEMENTS

I wish to thank Dr J. B. Jillett for his help with this paper.

#### ZUSAMMENFASSUNG

Die untersuchten Tiere besitzen die Charakteristika von *Munida gregaria* während der pelagischen Lebensphase; wenn sie jedoch zum Bodenleben übergehen, ändern sich die Merkmale im Verlaufe einer Serie von Häutungen und gleichen allmählich den für *M. subrugosa* charakteristischen Eigenarten. Diesen Ergebnissen zufolge handelt es sich bei den genannten Formen nicht um selbständige Arten. Eine einzelne Art (*M. gregaria*) existiert vielmehr in einer Serie verschiedener Formen, die vom Habitat abhängen.

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