

THE PELAGIC AND BENTHIC PHASES OF POST-METAMORPHIC *MUNIDA GREGARIA* (Fabricius) (DECAPODA, ANOMURA)

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Abstract: Some post-metamorphic individuals of *Munida gregaria* (Fabricius) are permanent members of the benthos while others spend at least part of their time in the water column. These two types of individual are distinct, both morphologically and in the composition of the body. Pelagic specimens have a low density throughout the moult cycle, brought about by a high water content, and low ash and calcium contents. Benthic individuals have this low density for only the first few days post-moult. Normally the pelagic habit is retained only during the first summer as post-larvae but on occasions it is extended over the whole year. In captivity specimens collected at the surface quickly settle on the bottom of the tanks and do not reappear at the surface. The strong positive phototactic response, seen when the animals are collected from the surface, is lost in the first few weeks and the low density persists only until they moult.

INTRODUCTION

Animals included in the family Galatheidae (squat lobsters) are typically permanent members of the benthos as adults. Of over 200 species in the family only two, *Pleuroncodes planipes* (Stimpson) and *Munida gregaria* (Fabricius) are sometimes pelagic in the post-metamorphic stages. *Pleuroncodes planipes* occurs off the western coast of Baja California and observations on its pelagic and benthic habits have been reported by Boyd (1967) and Longhurst (1967a, b). *Munida gregaria* is restricted in its occurrence to the southern hemisphere and is the subject of two Discovery Reports (Matthews, 1932; Rayner, 1935).

Lagerburg (1906), Matthews (1932), and Rayner (1935) are all of the opinion that two species of *Munida*, *M. gregaria* and *M. subrugosa* (White) occur in the South Atlantic and Pacific Oceans. All three authors state that *M. gregaria* has early post-larval stages which are pelagic and which differ in appearance from the older benthic individuals, while in *M. subrugosa* the corresponding early post-larval stages are bottom-living and similar to the later stages. Recent work on the development of pelagic individuals off southern New Zealand (Williams, 1973), however, supports the statements of Chilton (1909) and Thompson (1898) that *M. gregaria* and *M. subrugosa* are not distinct species. The characters of the pelagic stages and the characters ascribed to *M. subrugosa* represent extremes of a range of forms within a single species. When a pelagic animal settles to the bottom, its morphology gradually changes over a series of moults until it conforms to the description of '*M. subrugosa*'. *M. gregaria* and *M. subrugosa* are, therefore, the same species (by

priority *M. gregaria*) (Williams, 1973). This being the case, it follows that the post-larval stages of this species may be either pelagic or benthic.

Little is known about the relationship between the pelagic and benthic phases of *M. gregaria*. The morphological differences between animals caught at the surface and those trawled off the bottom mean that the dual habit cannot be accounted for entirely by short-term vertical migration cycles. Rather it would seem that some individuals are adapted for life as permanent members of the benthos while others are modified to spend at least part of the time in the water column. Morphological modifications certainly exist and observations by Matthews (1932) on the extent of calcification of the exoskeleton and Rayner (1935) on 'the degree of heliotropism', suggest other modifications may also be present.

This paper reports observations made on the occurrence and behaviour of pelagic individuals and the results of an investigation into some of the differences in body composition between pelagic and benthic forms.

METHODS

The study is concerned with *M. gregaria* off Otago in southern New Zealand. For many years records have been kept of the presence of pelagic specimens in the vicinity of the wharf at the Portobello Marine Laboratory in the Otago Harbour, at 09.00 h daily.

Pelagic specimens were collected from the surface by dip-net and others were obtained by bottom trawling on the continental shelf. Many hundreds of pelagic individuals were placed in an outdoor holding pond at the laboratory. This 2-m deep pond was supplied with running sea water and had a soft muddy bottom covered with *Ulva* sp. The animals eventually settled to the bottom of the pond and they were used as a source of benthic animals which were known to have had an earlier pelagic habit. They are referred to in this study as the captive benthic population and they were used no earlier than 2 mth after their initial capture.

Other animals were maintained in the laboratory in individual containers with running sea water. They were fed fish every 5-6 days and provided with a piece of *Ulva* for shelter. Records of the times of moulting were kept and regular density measurements were made on some of the animals, starting immediately after capture. Density determinations were made following the method of Denton & Gilpin-Brown (1961). The animal was first weighed immersed and suspended in sea water at 15°C. The weight was recorded to the nearest mg. Variations in the salinity of the water (33.6-35.1‰) used for weighing which would affect the weight recorded, were considered insignificant. The animal was then blotted of excess water and weighed in air. As a measure of density, the weight of the animal in sea water was expressed as a percentage of its weight in air. The volume of an animal was obtained using the expression $(wt \text{ in air} - wt \text{ in sea water})/1.025$.

The length of the carapace was taken as the distance between its posterior border and the tip of the rostral spine. Dry weights were obtained by drying the animal at 90°C to constant weight and ash weight by incinerating at 600°C for 12 h. The ash was taken up in 0.3 N hydrochloric acid and then diluted to 50 ml. The calcium content was determined by titration with ethylenediaminetetra-acetic acid disodium salt at pH 10–12 using murexide as indicator. An 'EEL' titrator was used for the photo-electric assessment of the end-point.

To determine the reaction to light over a period ≈ 100 pelagic animals were collected and placed in a laboratory aquarium provided with running water and weed for shelter in a normal day–night light regime. They were fed every 5–6 days. At weekly intervals, beginning on the day of capture, 20 animals were removed to a clear Perspex tank (90 × 16 cm) with running water at a depth of 13 cm. The only illumination supplied during the experiment was from a 15-W bulb suspended in a shade above one end of the tank. The bottom of the tank was marked off into 12 equal sections, numbered 1 to 12 beginning at the light end of the tank. Water flowed into the tank above the junction of Sections 6 and 7 and left through two outlets, one above Section 11 and the other above Section 2. (In this way a unidirectional current of water in the tank was avoided.) The animals were placed on the bottom of the tank in Sections 6 and 7 and the number in each section was recorded 5, 30, and 90 minutes later. After the experiment the animals were returned to the stock aquarium.

RESULTS

OCCURRENCE

In the Otago area specimens of *M. gregaria* can be obtained throughout the year by bottom trawling in the harbour and offshore in water down to ≈ 100 m, but individuals are normally seen at or near the surface only during the summer months of October–November through to March–April (Fig. 1). Often the pelagic individuals aggregate in dense shoals at the surface (Fig. 2). Although extremely common during both day and night in the summer, they are not present at the surface every day. No regular cycle in their occurrence has been detected. They are not usually seen at the surface in rough weather. Since 1953 there have been two summers when no pelagic individuals were seen and in 1953 and 1977 surface swimming individuals were also recorded during the winter months. In a normal season however, 1969–1970 for example (Fig. 3), the pelagic individuals first appear in October–November and are small, with a carapace length of ≈ 10 mm. These are newly metamorphosed individuals with immature pleopods. Berried females are common in the benthos during the winter months and *Munida* zoeae are abundant in the inshore plankton in August (Jillett, pers. comm.). As the summer progresses the size of the animals caught at the surface increases (Fig. 3) and the morphological characters associated with pelagic individuals become more pronounced (Williams, 1973). The pleopods

soon attain the mature form. In a normal year pelagic animals are not seen later than the end of March or the beginning of April and at this time are 16–17 mm in carapace length. This pattern in the occurrence of surface-swimming animals has been recorded for 22 of the past 26 yr. Animals caught on the bottom have carapace lengths ranging from 10–40 mm. Like the pelagic individuals, they are often encountered in shoals.

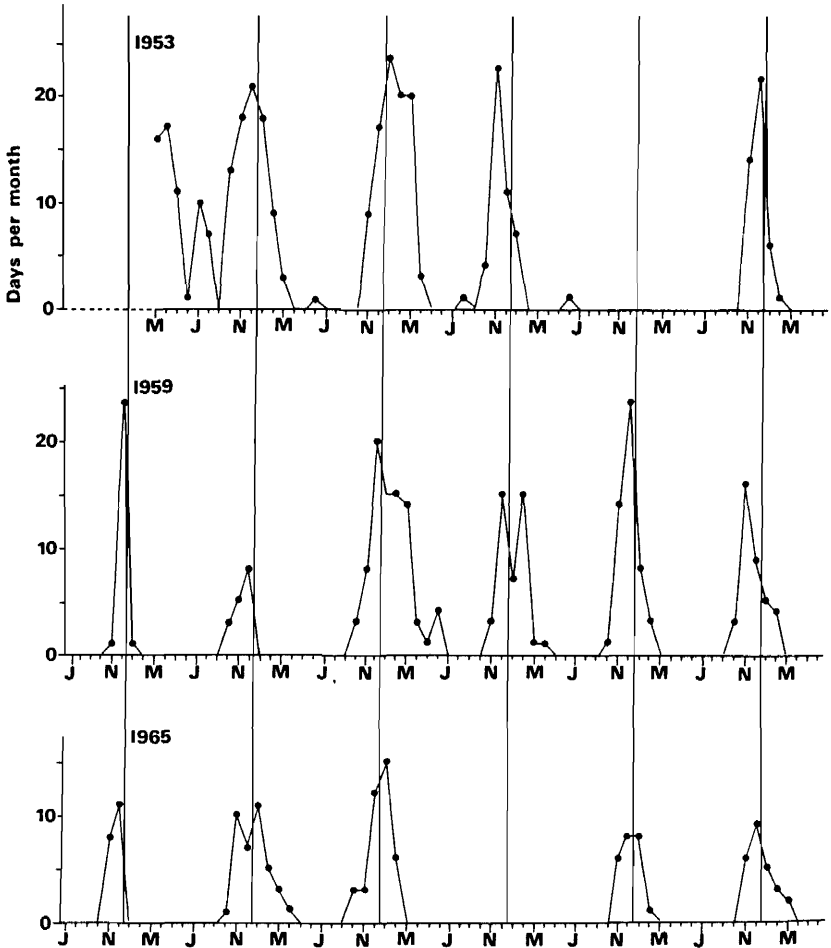


Fig. 1. Number of days per month that *M. gregaria* were seen at or near the surface of the water in the vicinity of the Portobello Marine Laboratory from March 1953 to April 1970: M, March; J, July; N, November.

The pattern of occurrence of *M. gregaria* at the surface in 1977 was unusual. Pelagic individuals were seen throughout the winter and at the beginning of October had reached a carapace length of ≥ 20 mm (Fig. 4). Some were berried females and

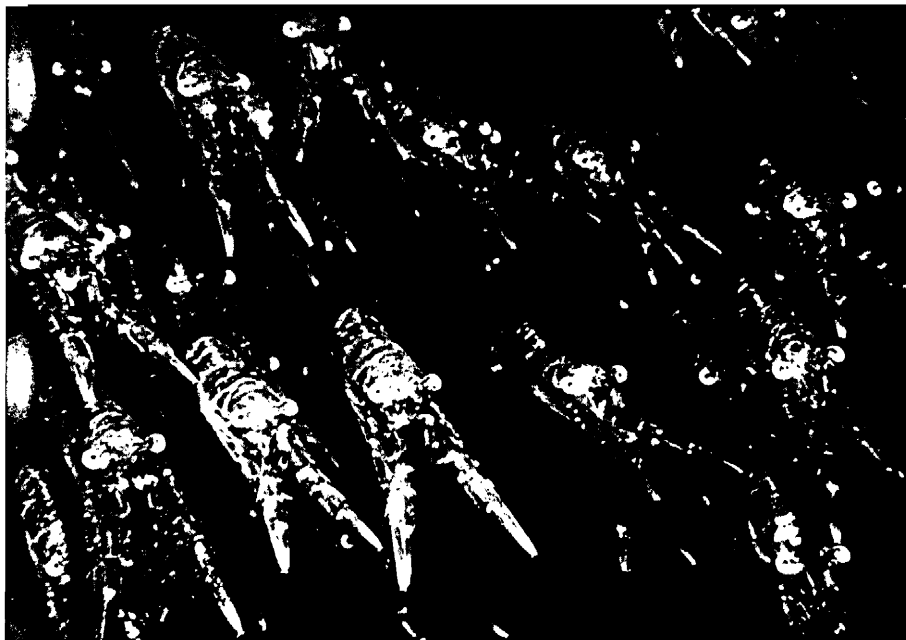


Fig. 2. Underwater view of a shoal of pelagic *M. gregaria* (photograph, K. Westerskov).

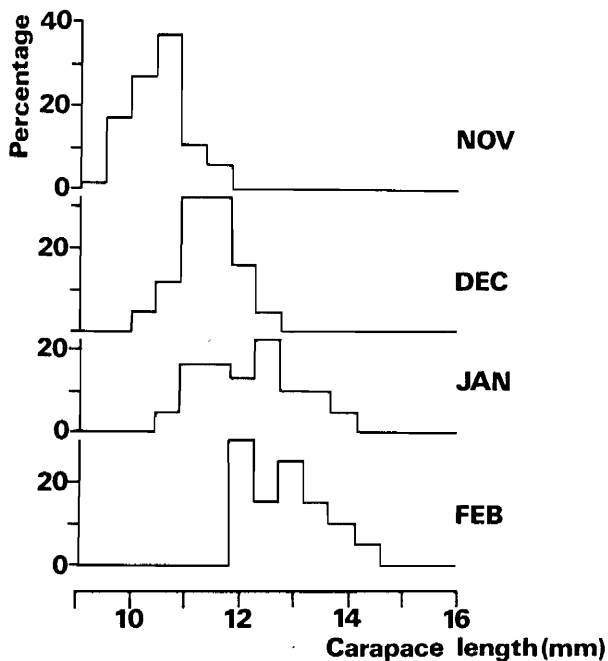


Fig. 3. Size frequency histograms of pelagic *M. gregaria* for the season 1969-1970: Nov. 70 animals; Dec. 25 animals; Jan. 24 animals; Feb. 20 animals.

all had well-developed pelagic morphology. At the same time very small newly metamorphosed individuals were present. By the end of November both age clas-

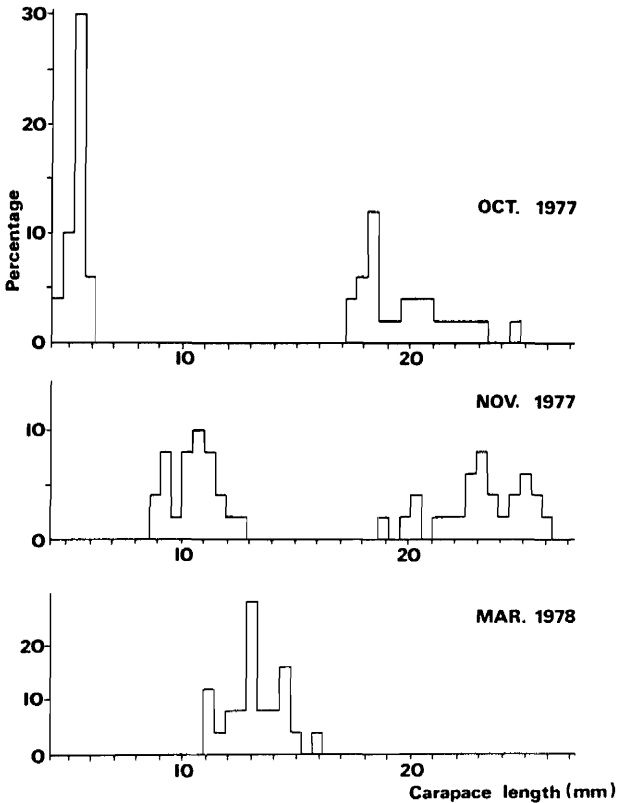


Fig. 4. Size frequency histograms of pelagic *M. gregaria* for the season 1977-1978: Oct. 50 animals; Nov. 50 animals; Mar. 25 animals.

ses were still present and had increased in size (Fig. 4). The large second-year pelagic animals were not seen at the surface after November.

BEHAVIOUR OF CAPTIVE PELAGIC ANIMALS

As was noted by Longhurst (1967a) for the pelagic individuals of *Pleuroncodes planipes*, *Munida gregaria* collected from the surface water do not remain pelagic when placed in laboratory aquaria. They immediately take up residence on the bottom of the container and remain there. On two occasions, several hundred animals were taken from dense pelagic shoals and placed in a large outdoor pond. Subsequent observation showed that once in the pond the majority of the animals reformed into an organized shoal and swam in formation continuously around the

surface of the pond. On the first occasion the animals remained swimming at the surface for 7–8 days. No daily or tidal migrations were observed. After this period more and more animals were seen clinging to the concrete walls of the pond, just below the surface of the water and within another week they had all settled on the bottom, where they remained for the duration of the two-year observation period. Berried females were seen on the bottom of the pond each winter. A second trial gave similar results but with the surface-swimming phase lasting for only 2–3 days.

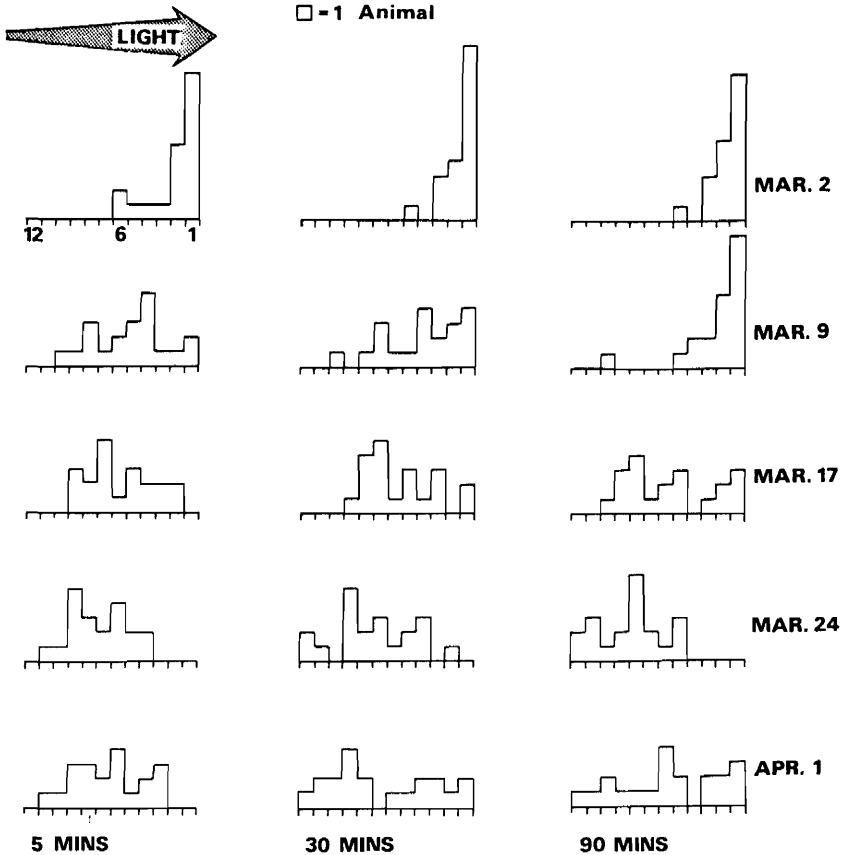


Fig. 5. The response of individuals collected at the surface to a light gradient, on the day of capture and thereafter at weekly intervals: histograms give the distribution of 20 animals on the bottom of the tank after 5, 30, and 90 min; see text for details.

Fig. 5 shows that freshly collected pelagic animals are strongly positively phototactic. Within 5 min of being placed in the experimental tank, 75% were in Sections 1 and 2, where the illumination was strongest. A week later this reaction was still seen but was taking place rather more slowly and by the third week in captivity the positive phototactic response was absent.

DENSITY OF PELAGIC AND BENTHIC INDIVIDUALS

Fig. 6 shows the weight in water of individual animals from a variety of sources plotted against carapace length. All those freshly collected from a pelagic habitat

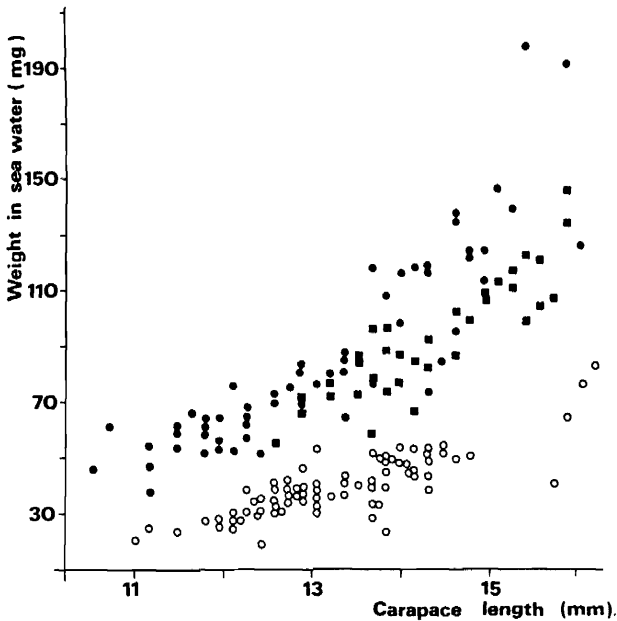


Fig. 6. Weight (mg) in sea water of individuals plotted against carapace length (mm): ○, pelagic individuals; ●, benthic individuals; ■, captive benthic individuals.

had a lower weight than similarly sized animals fresh from a benthic habitat or taken from the captive benthic population, and although still considerably denser than sea water, the pelagic animals are thus closer to neutral buoyancy than the bottom-dwelling groups (Fig. 7). The pelagic animals had a mean density of 1.0927 ($n = 79$, S.D. ± 0.0141), the captive benthic animals 1.1456 ($n = 40$, S.D. ± 0.0114), and the freshly collected benthic animals 1.1652 ($n = 59$, S.D. ± 0.0180), all three groups being significantly different from each other ($P < 0.001$ in all cases, t -test).

On several occasions a number of animals were taken from the three sources and their density, water content, ash weight, and calcium content were determined. In total, data were obtained from 30 fresh pelagic individuals and 25 of each of the freshly caught benthic and captive benthic animals. The results of density and water content measurements are given in Fig. 8. The water content of the pelagic animals was high and significantly greater than that of the two bottom-dwelling groups ($P < 0.001$ in both cases, t -test). Water content of the captive animals was slightly greater than that of the fresh benthic individuals ($P \approx 0.05$, t -test). The ash weight of

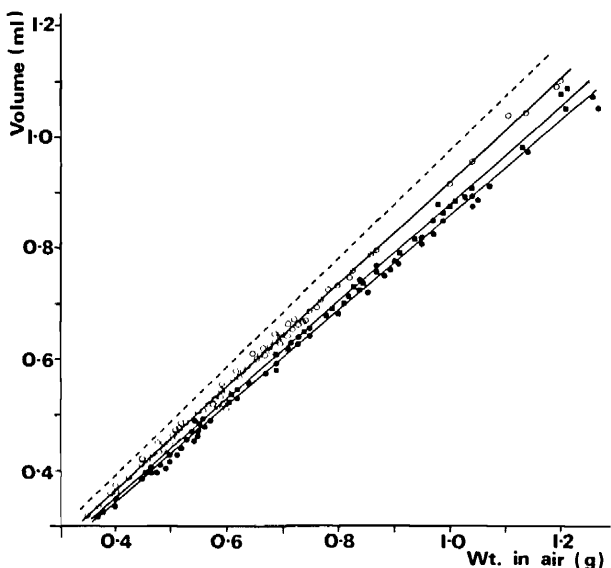


Fig. 7. Volume (ml) of individuals plotted against weight in air (g): symbols as Fig. 6; solid lines fitted by regression analysis; pelagic, $\hat{y} = 0.0032 + 0.9188x$; captive benthic, $\hat{y} = 0.0051 + 0.8794x$; benthic, $\hat{y} = 0.0056 + 0.8506x$; broken line, neutrally buoyant animals.

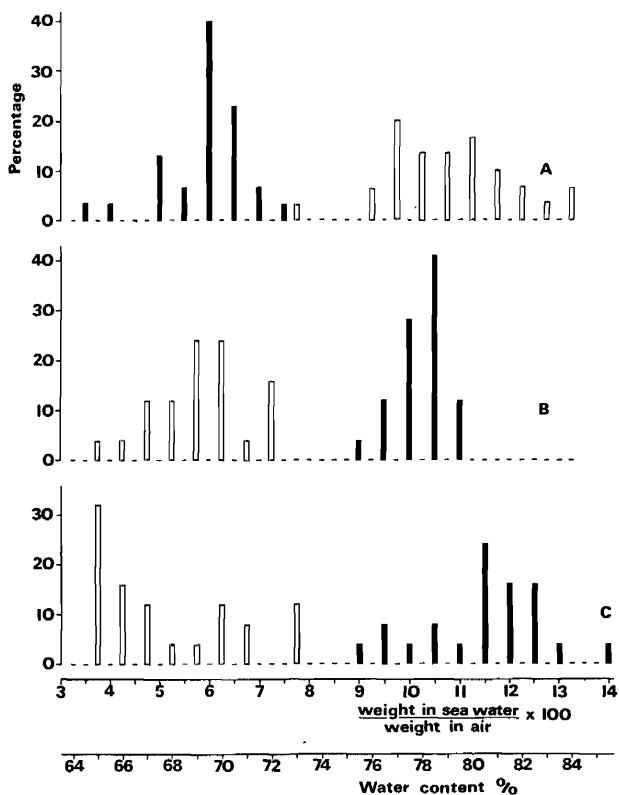


Fig. 8. Histograms giving weight in sea water as a percentage of the weight in air (solid bars) and the water content as a percentage of the wet weight (open bars): A, 30 pelagic animals; B, 25 captive benthic animals; C, 25 benthic animals.

the captive animals expressed as a percentage of the dry weight was, however, identical to that of the pelagic group (Fig. 9). Benthic animals have a significantly higher ash weight ($P < 0.001$, t -test). In contrast (Fig. 9) the calcium content of the

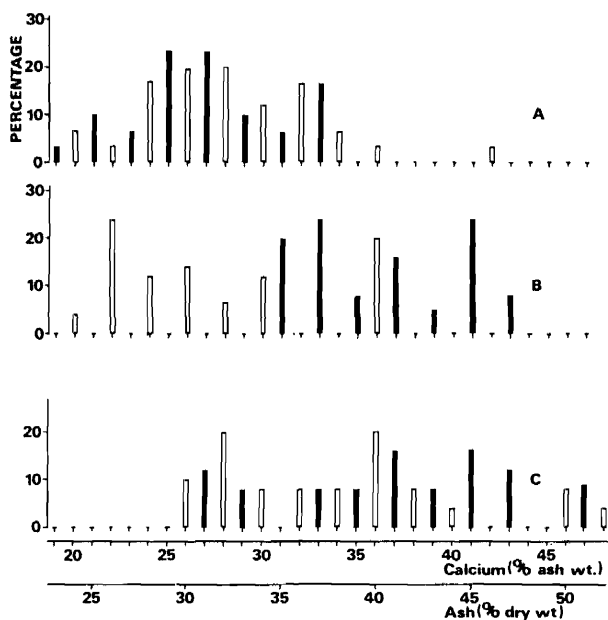


Fig. 9. Histograms giving ash as a percentage of dry weight (open bars) and calcium as a percentage of ash weight (solid bars) for animals as in Fig. 8.

ash from pelagic animals was significantly lower than that of the two bottom-dwelling groups ($P < 0.001$ in both cases, t -test). The calcium content of ash from benthic and captive benthic groups was not significantly different ($P \approx 0.3$, t -test).

DENSITY IN RELATION TO MOULT CYCLE STAGE

Changes in density over the complete moult cycle were followed in several benthic individuals, and a typical record is shown in Fig. 10. This individual moulted twice in the 120-day observation period. Immediately after each moult, the weight in water fell whilst the weight in air increased, as relatively dense material was lost in the cast shell and water was taken into the animal. Fig. 10 and Table 1 show that this situation is short-lived. During the first few days following moulting the weight of the animal in water increases rapidly, due to growth and the deposition of calcium in the new skeleton. Within five days of moulting, the weight in water is $>8\%$ of the weight in air.

Although pelagic animals have a weight in water of $<8\%$ of their air weight they are not, however, exclusively post-moult animals. On two occasions, a number of

animals from pelagic shoals were maintained in isolation in the laboratory and the day on which moulting occurred was noted. In the first trial (Fig. 11A) 50.8% of the animals moulted within 10 days of capture and another 20.5% between 10–20 days.

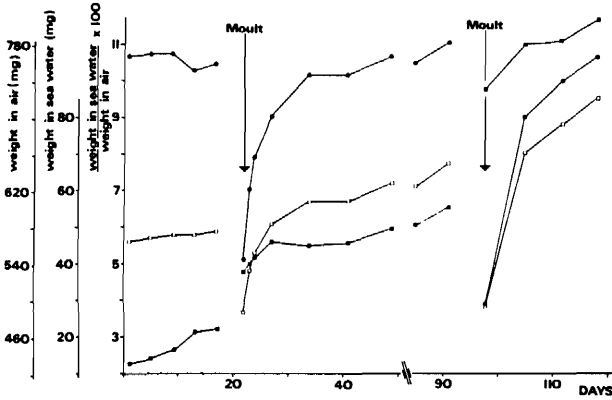


Fig. 10. Weight in sea water as a percentage of weight in air (●), weight in sea water in mg (□) and weight in air in mg (■) of a single benthic specimen over 120 days: vertical arrows, times of moulting.

TABLE I

Weight in sea water as a percentage of the weight in air of *Munida gregaria* at specified times after moulting.

Stage in moult cycle	No. of animals	$\frac{\text{Wt in sw}}{\text{Wt in air}} \times 100$ (mean value)	Range
Immediately post-moult	5	4.63	3.56–5.78
3 days post-moult	5	7.42	6.78–8.40
5 days post-moult	5	8.64	7.98–9.52
10 days post-moult	5	9.07	8.30–9.65
20 days post-moult	4	9.96	9.56–10.45

Frequency of moulting was very low between days 20–40 after capture but increased again between 40–50 days. It was at this time that some of the animals that had moulted in the first few days after capture moulted for a second time. These results suggest that some of the animals in the sample were in pre-moult and some were in the post-moult stage of the cycle when captured. Those in pre-moult moulted soon after capture and took about 40 days to complete the moulting cycle and moult again. The fact that some animals moulted for the first time after a period of ≈ 40 days in captivity indicates that they had recently moulted when captured. Another sample taken from a pelagic shoal 30 days later was quite different (Fig. 11B), the

majority moulting 10–35 days after capture indicating that they were predominantly inter-moult animals when captured.

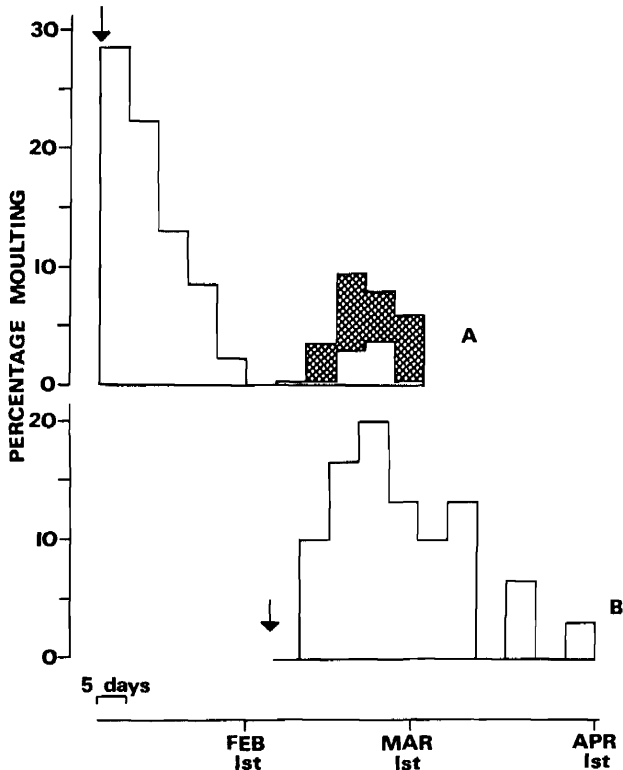


Fig. 11. Histograms showing the percentage of animals moulting per 5-day period: A, sample of 130 individuals collected from a surface shoal in January; B, sample of 30 individuals from a surface shoal in February; hatched area indicates animals moulting in captivity for a second time.

Regular records of the density of a number of pelagic animals were kept for 80 days starting on the day of capture. Three typical records are shown in Fig. 12. The animal in Fig. 12A moulted 11 days after capture and must, therefore, have been in pre-moult when caught. Its weight in water remained around 7% until moulting. At moulting it fell dramatically and then increased steadily over the next 8–9 days to stabilize around 10%. It remained at this level until the next moult and had returned to this figure 12 days after that moult. Fig. 12B shows an animal with a weight in water of $\approx 6\%$ when captured, 21 days before moulting. Here again the density remained more or less steady until the moult. After moulting the weight in water rose rapidly to around the 10% level. The animal in Fig. 12C did not moult for 48 days following capture, indicating that it had recently moulted when captured. An interesting feature here is the rapid rise in density in the first 10 days after capture.

In all, the densities of more than 50 pelagic animals were followed over the first moult in captivity and in no case did a pelagic animal moult in the laboratory and remain in a density of below 8% after the first few days post-moult.

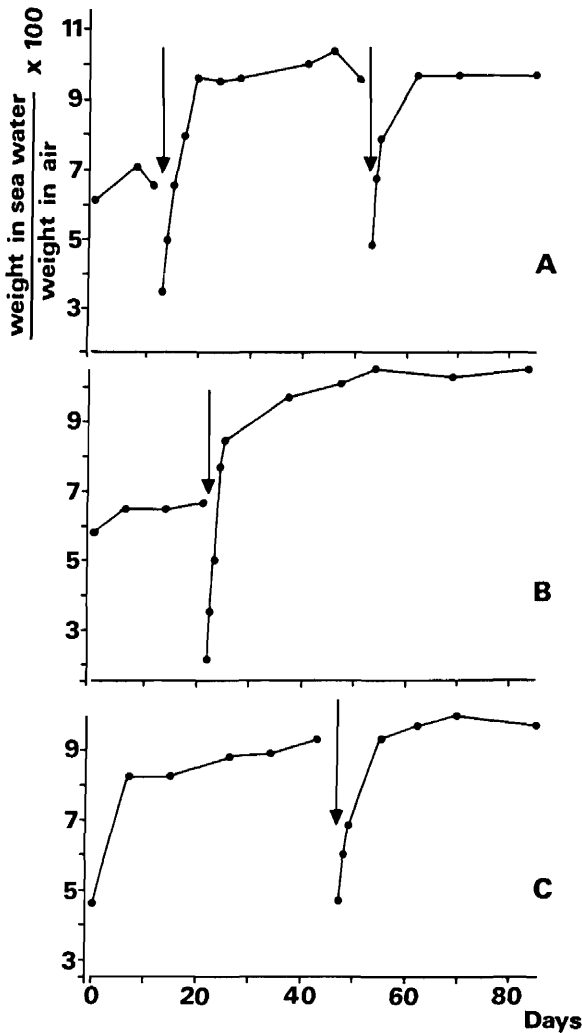


Fig. 12. Weight in sea water as a percentage of the weight in air in three individuals (A, B and C) collected from a surface shoal, over 80 days: vertical arrows, times of moulting.

DISCUSSION

Of hundreds of pelagic specimens weighed during this study, none had a weight in sea water of more than 7.5% of its weight in air and the majority were around

6%. Benthic animals had values up to 13–14%, although they were found to be below 8% in the first few days following moult. Pelagic *M. gregaria*, however, are not exclusively post-moult animals. They have been recorded swimming at the surface in all stages of the moulting cycle. Their lowered density is associated with an increase in water content and a reduction in the ash and calcium contents. Although pelagic specimens are far from being neutrally buoyant, their density is reduced compared with that of benthic specimens and this together with the greater development of setae, will mean a reduction in the amount of energy expended to stay afloat. Following Lowndes (1942) and expressing the density as a sinking factor, benthic *M. gregaria* have a sinking factor of between 1120–1170, which is similar to that of other bottom-dwelling reptantian species. Pelagic specimens have a sinking factor of around 1060–1070 which is of the same order as natantian species examined by Lowndes and also close to that of the mysid, *Hemimysis lamornae*, which spends the daylight hours on the bottom and is pelagic at night, and the rock pool copepod *Tigriopus fulvus*.

In laboratory studies most pelagic individuals retain a lowered density until they moult. Exceptions are pelagic individuals captured immediately after moulting (see Fig. 12C). Such animals increase their density within a few days of capture. Other stages always increase their density after the first moult in captivity. Studies of animals from the captive benthic population, which had presumably moulted 2–3 times since they were initially caught, show their density and associated water, ash, and calcium contents to be at a somewhat intermediate stage between the pelagic and natural benthic stocks (see Fig. 9).

In *Pleuroncodes planipes* pelagic and benthic individuals are thought to be identical. This, together with the data showing that length frequency distribution of benthic animals overlaps with pelagic stocks (Boyd, 1963), has prompted the suggestion that there could be an alternation of individuals between the two habitats. Boyd (1967) concluded that *P. planipes* can be either benthic or pelagic and that there is a diurnal exchange between the two habitats. The animals are in the surface waters at night and settle to greater depths and perhaps the bottom during the day, when a suitable bottom is available. This cannot be the sole explanation of the dual habitats occupied by *Munida gregaria* for although, like *Pleuroncodes planipes*, pelagic and benthic specimens of *Munida gregaria* can be of similar size, in *M. gregaria* there are two types of individual, one occurring at the surface and the other in benthic samples. Individuals trawled from the bottom are distinct both in morphology and body composition from those caught at the surface. Animals with these 'benthic' features are never present in surface samples. The explanation for individuals at the surface is, therefore, not simply that benthic animals undertake regular short-term vertical migration, as suggested for *Pleuroncodes planipes* (Boyd, 1967). Specimens with 'benthic' characters appear to be permanent members of the benthos, a typical life style for adult galatheids.

Considering individuals caught at the surface with 'pelagic' features, benthic

sampling at the present time has not been extensive enough to determine whether they regularly spent part of the time on the bottom. Certainly studies of the behaviour of captive individuals from the surface did not reveal any alternation between the pelagic and benthic habitats. Once the pelagic individuals had settled to the bottom, they did not return to the surface.

In addition, morphological and body composition data suggest that not all post-metamorphic individuals go through a pelagic phase. Very early post-metamorphic animals with a carapace length around 10 mm can be found in the benthos and these possess a very well defined 'benthic' morphology and the body composition of a 'benthic' type. Laboratory studies have shown that complete acquisition of these characteristics by pelagic individuals takes 3-4 moults which suggests that the very small benthic animals settled immediately after metamorphosis. Also, the youngest pelagic individuals have morphological characteristics closer to the 'benthic' type than the 'pelagic' type (Williams, 1973).

Longhurst (1967a, b), too, suggests there could be an alternation between the two habitats in *P. planipes* but of a longer-term nature. He considers that diurnal migration probably consists primarily of a withdrawal from only the upper tens of metres during daylight and that the individual residence times in the pelagic zone must be of the order of weeks or months rather than hours or days.

In Otago waters, shoals of *Munida gregaria* at the surface are an extremely frequent sight during daylight hours and the individuals are strongly positively phototactic at this time (Fig. 5). This does not suggest a behaviour pattern involving a withdrawal from the surface during the day although *Pleuroncodes planipes* too is often sighted at the surface during the day. Boyd (1967) considers that the two habitats are occupied by *P. planipes* during their first two years. Individuals of *Munida gregaria* are normally found at the surface only during the first few months as post-larvae but this is not always the case. Young (1925) records three years between 1904 and 1924 when the 'swimming stage' was present in the Otago Harbour during the winter and in the present study during 1977 animals were seen at the surface throughout the year. In a normal year animals reach a carapace length of 16-17 mm before they abandon the surface-swimming habit in autumn but in 1977 they were seen at the surface during winter and had reached 23-26 mm carapace length when they disappeared from the surface the following spring (Fig. 4). These observations support Chilton's view (1909) that the post-larvae may become bottom living at an early age or may remain pelagic, reaching sexual maturity and breeding at or near the surface. One berried female was also recorded amongst individuals caught at the surface off Argentina by Kawarura (1976). The present study sheds no light, however, on the factors which determine when an individual will leave the surface.

It is of interest that in *Pleuroncodes planipes* (Boyd, 1967) and in *Munida gregaria* some of the benthic animals are larger than has been recorded for pelagic animals, indicating that in both species, individuals settle finally to the bottom.

The advantage of a pelagic post-metamorphic habit in some individuals is not im-

mediately obvious. Presumably dispersal is carried out as efficiently in this species as in other benthic crustaceans, by pelagic larvae. Perhaps relevant to this question is the readiness with which individuals abandon their pelagic habit. In captivity animals do not remain pelagic, The strong positive phototactic behaviour diminishes and is soon lost completely (Fig. 5) and when the animals next moult the morphology and body composition associated with a pelagic existence are modified. In the field too, pelagic animals will settle on any solid surface such as wharf piles and boat hulls they encounter whilst swimming.

Although in laboratory studies no individual has ever moulted and retained its pelagic features, this is obviously not so in the natural environment. Morphological studies have shown that pelagic features become progressively more pronounced as the animals increase in size (Williams, 1973) and such animals must, therefore, have moulted several times and yet retained the pelagic habit. Perhaps in the laboratory the cause of pelagic behaviour in the adult is no longer present. A bottom on which to settle is obviously immediately available in the laboratory although this is not necessarily so in the open sea. Larvae may metamorphose in deep water where a bottom at a depth suitable for settlement is not available. By remaining pelagic such individuals would not be automatically lost to the population. A pelagic post-metamorphic individual has greater swimming powers than the larval stages and might eventually arrive in shallower water. If the pelagic individuals undertook occasional vertical migration through the water column as Longhurst (1976b) suggests for *Pleuroncodes planipes*, once in shallower water they would encounter the sea bed and the behaviour patterns observed in the laboratory and field would cause them to remain there. At the next moult modifications for a benthic existence could commence, as was seen in the present laboratory studies.

ACKNOWLEDGEMENTS

The method for calcium determination used in this study was developed by Dr J. B. Pilkington. The photograph was taken by Mr K. Westerskov. In the course of the work I have had helpful discussions with Professors R. F. H. Freeman, C. Hand, E. Naylor, and Associate Professor J. B. Jillett, and have received willing assistance from the technical staff of the Portobello Marine Laboratory. The late Dr C. R. Boyden offered helpful criticism of the original manuscript. I am most grateful to all these people. Equipment used in this study was purchased in part on Grant No. 136 from the University of Otago Research Committee.

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