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## The vertical zonation of the deep-sea Antarctic acorn barnacle, *Bathylasma corolliforme* (Hoek): experimental transplants from the shelf into shallow water

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**ABSTRACT.** Eight hypotheses potentially explaining the vertical zonation of *Bathylasma corolliforme* were tested by experimental transfer of barnacles from bathyal depths into shallow oligotrophic and eutrophic habitats of McMurdo Sound. Hypotheses predicated on physiological constraints, or general shallow-water habitat factors including substrata availability, were negated by the successful transfers and by natural history observations. Also negated were hypotheses built on limits to dispersal as we observed nauplii larvae well adapted to planktonic existence and actual larval settlement in shallow McMurdo Sound. We also observed recruitment of complemental males of *Bathylasma*. Tentatively negated were hypotheses of predation on adult barnacles.

Relative lipid contents of the barnacles provide evidence suggesting nutrient limitations in the McMurdo Sound region. Because of the passive feeding of *Bathylasma*, these limitations probably relate to the low velocity currents. It is predicted that *Bathylasma* will be found in the Sound where sufficient currents are found since it apparently occurred there in the past, when ice free and wind driven currents were greater.

### Introduction

Zonal patterns along vertical environmental gradients are well-known biogeographic phenomena in most terrestrial and shallow marine habitats. In many cases the patterns result from reasonably well understood mechanisms including precipitation, temperature and evapotranspiration in terrestrial habitats, and physical and physiological stress and especially biological interactions such as competition and predation in the shallow marine habitats. Zonal patterns also characterize deep-sea benthic habitats (Sanders, Hessler & Hampson, 1965; Haedrich, Rowe & Polloni, 1980), but the mechanisms restricting animals to their deep-sea zones are not understood.

Many facets of biological research in the deep sea are truncated because animals are not readily retrieved alive. Some animals may

be restricted to deep depths because of specialized pressure adaptations (Siebenaller & Somero, 1979), but usually the most important obstacle to the retrieval of healthy animals is bringing them through the surface waters which are usually much warmer than the deep waters.

The temperature restrictions are relaxed in polar latitudes, especially the Antarctic, as the water column is essentially isothermic from top to bottom, and deep-sea species may range into moderate depths – a phenomenon commonly known as ‘high latitude emergence’. Thus, high latitudes offer opportunities to study deep-water organisms that may already occur in shallow water or which may be transplanted there from deep water. Because the Antarctic continent is isolated from other land masses by extensive and deep waters as well as by the west wind drift and attendant

current patterns, the shallow-water fauna that became extinct during Pleistocene glaciations has not been replaced by similar shallow-water species from other shelf habitats. An important question is, then, why do some deep-water species which otherwise appear well adapted to occupying shallow water, fail to do so when their counterparts are absent?

The Antarctic barnacles are a case in point. There are several shallow-water stalked barnacles (Lepadomorpha) but no acorn barnacles (Balanomorpha) known living at depths of less than 100 m. Furthermore, the few Lepadomorpha found are representatives of deep-water fauna which are exhibiting 'high latitude emergence'. Thus, the situation in the Antarctic is just the reverse of what one generally finds elsewhere (Spivey, 1981). Since the fossil record reveals the presence of shallow-water balanomorphs during previous interglacial periods, the present situation must be due to the extinctions of the shallow-water biota during the Pleistocene with a subsequent lack of recolonization (Dayton *et al.*, 1969; Newman & Ross, 1971; Newman, 1979).

This paper addresses possible mechanisms by which the balanomorph, *Bathylasma corolliforme* (Hoek), might be restricted presently to deep water. Specifically, we consider the following hypotheses: (1) physiological constraints restrict the upward distribution; (2) no proper substrata exist in shallow water; or (3) such substrata that exist are fully utilized by competitively superior species; (4) shallow-water predators restrict the barnacles to deeper waters; (5) the annual plankton bloom smothers the barnacles; or (6) there are other factors associated with shallow or eutrophic waters which restrict the barnacles to more oligotrophic areas; (7) barriers to the dispersal of larvae to new areas exist, and finally; (8) there is some other component of the shelf-break habitat which is necessary to the life-cycle of the barnacles.

We took advantage of the relative isothermal condition of the Antarctic waters in the Ross Sea to test some of the above hypotheses by transferring *Bathylasma corolliforme* from relatively oligotrophic deep waters (400 m) to both eutrophic (McMurdo Station) and oligotrophic (New Harbor) shallow-water habitats (Dayton & Oliver, 1977) where a variety of experiments were initiated to test the above

hypotheses. Certain aspects of predation and settlement were further explored by transplanting shallow-water lepadomorphs (*Arcoscalpellum* s.l.) from the relatively oligotrophic South Cape Armitage to the eutrophic McMurdo Station site. Observations of size frequency and settlement allowed deductions about growth rates and dispersal of *Bathylasma corolliforme* and *Arcoscalpellum*. The transplanted *Bathylasma* barnacles, maintained for 2 years in oligotrophic and eutrophic habitats, were examined for trends in tissue/shell ratios, lipids, and reproductive state.

## Methods

In January 1976, approximately 250 barnacles were collected at the shelf-slope break (400 m) in the northwestern Ross Sea (73° S, 176° E) using a modified anchor dredge from the ice breaker, USCG *Burton Island*. Large barnacles were usually attached to well-rounded volcanic rocks, and smaller individuals were commonly attached to the shells of both living and dead barnacles or to large tunicates which were relatively abundant near the barnacle beds. The living barnacles were maintained in a large running seawater aquarium on the deck of the USCG *Burton Island* for the 3-day return trip. Aquarium water temperature was maintained at -1.5°C. Upon returning to McMurdo Sound, half of the barnacles were immediately transported by helicopter to a highly oligotrophic New Harbor study site (Fig. 1) where they were placed on the bottom at 40 m by divers. The other half were placed at the eutrophic McMurdo Station site at a depth of 25 m.

An *in situ* experiment was designed to test both the predation and smothering hypotheses. Barnacles were placed in an array of containers including replicated treatments of open-ended Nitex mesh receptacles which were wrapped with black plastic tape. These precluded a heavy fallout of planktonic algae and by restricting light, prevented the photosynthesis of algae on the barnacles themselves. Transparent containers allowing light but no fallout were used as controls for the dark treatment. Control barnacles were placed on open racks adjacent to the dark containers such that they would be subject to smothering

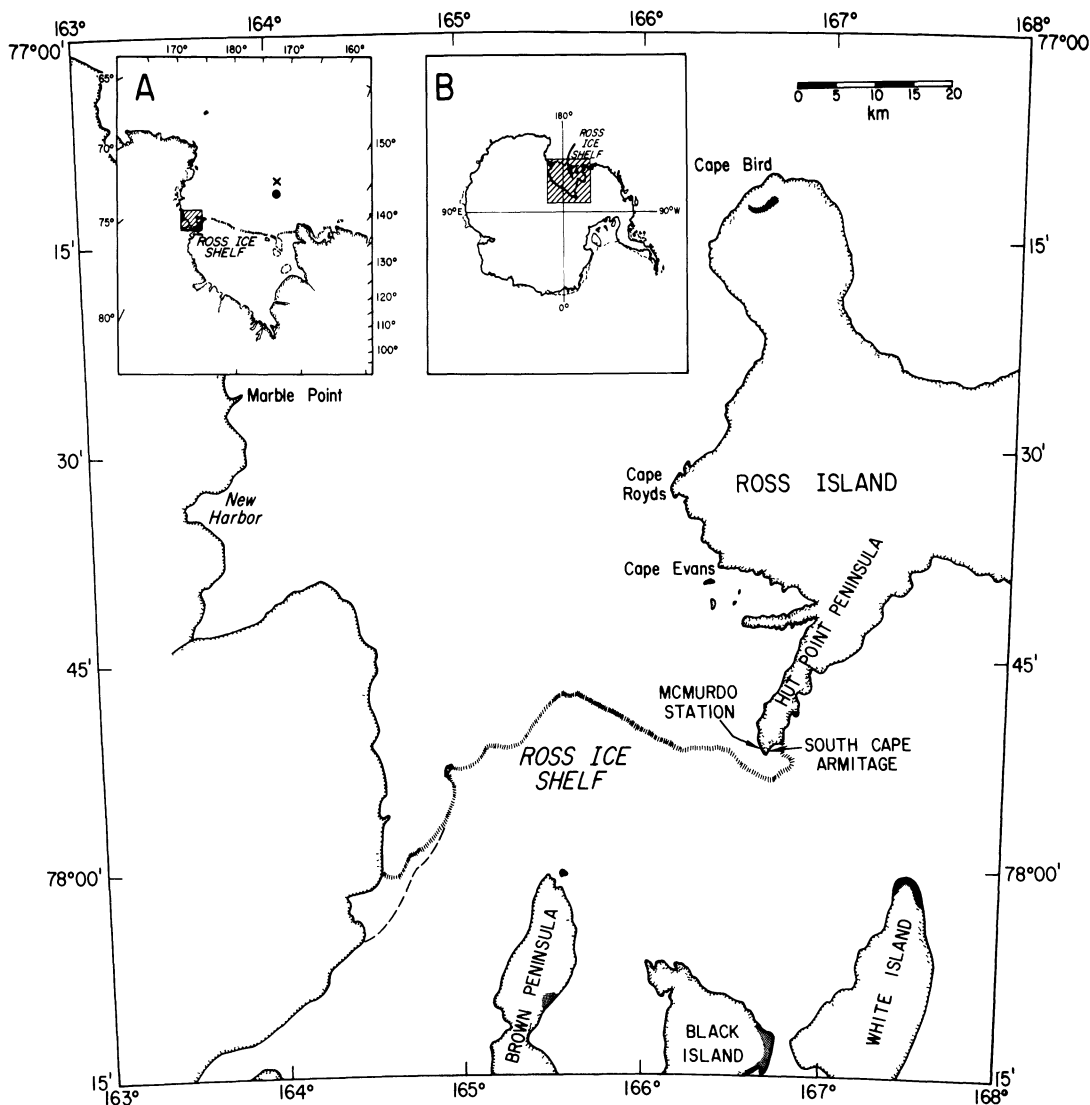


FIG. 1. McMurdo Sound and its relationship to the Ross Sea (A) and Antarctic Continent (B). *Bathylasma corolliforme* (Hoek) specimens were transplanted from site X (in A) to McMurdo Station and New Harbor in McMurdo Sound. Site • (in A) is the location of the *B. corolliforme* contained in the SIO collections and utilized as controls in the lipid analyses. Shaded areas (on Brown Peninsula, Black and White islands and Cape Bird) represent sites of the Scallop Hill Formation of Speden (1962).

by plankton fallout and diatom mats growing on the barnacles. These arrays were then placed on the bottom so that they would be fully accessible to all predators, on racks supported by 1.5 m stilts which precluded benthic but not swimming predators. No swimming predators are known in the area. Finally, barnacles were established in a wire mesh predator exclusion cage allowing light

and sedimentation. This entire experimental design was employed in the New Harbor and McMurdo Station study sites.

At the end of the first year in January 1977 there was no indication of mortality from predation or smothering. At that time the barnacles were removed from the black containers and placed in the open. Some barnacles were transferred from the elevated racks

to the bottom. In addition, three large individuals of *Odontaster validus*, an important shallow-water predator (Dayton *et al.*, 1974), were added to one of the earlier predator exclusion cages. Finally, in order to exaggerate natural conditions, barnacles were transferred to a laboratory with running sea water where some were put under constant illumination, others were kept in a completely dark container, a few more were placed in the presence of several starved *Odontaster validus*, and a number were simply left in a water table so that they could be observed. These experiments were run for an additional year. Most of the barnacles from the field and the laboratory were collected and preserved in formaldehyde in December 1977. These were returned to Scripps Institution of Oceanography for subsequent analyses. A few barnacles were photographed and returned to the field for future observation.

All barnacles were measured and most were dissected, note being taken of reproductive condition and location of small individuals on adults. The tissue to shell ratios and lipid analyses were performed by weighing the adult barnacles and dissecting out the tissue. Wet weight ratios and reproductive data were recorded, and the tissue was subjected to crude lipid analysis performed by calculating the hexane soluble portion of tissue per gram dry weight. The tissue was freeze-dried for 1 day, weighed and extracted three times with distilled hexane which was then filtered and evaporated with a roto-evaporator. The remaining lipid residue was weighed. Thin layer chromatography was performed on the crude lipid extracts in 100% ether, checked for ultraviolet or visible light spots, and treated with 50% sulphuric acid.

## Results

### *Transplant experiments*

All the barnacles survived 2 years in the shallow, relatively eutrophic McMurdo Station habitat (77° 55' S, 166° 40' E; Fig. 1). Thus, the transplant experiment negates hypotheses 1 and 6 that there are biochemical or physiological constraints restricting *Bathylasma corolliforme* adults to deeper water, or that there are other undefined factors associated

with more eutrophic waters which restrict the barnacles to more oligotrophic habitats.

Hypotheses 2 and 3, that the barnacles are restricted to their relatively deep habitats by substrata availability or competition, can be negated by the fact that *B. corolliforme* has a wide circum-Antarctic distribution usually within the depth zone of 100–1500 m, where it has been observed growing on rocks, other barnacles and bivalve remains, and even on large tunicates (Bullivant & Dearborn, 1967; Newman & Ross, 1971; personal observation). These habitats are abundantly available in shallow depths along eutrophic to oligotrophic gradients in the McMurdo South region (personal observation), and appropriate habitats would appear to be available for colonization by *B. corolliforme* in the Davis Sea (Propp, 1970; Gruzov, 1977), the Antarctic Peninsula (Dearborn, 1977), and probably in most Antarctic coastal habitats (Hedgpeth, 1971; Arnaud, 1974). While many encrusting species exist in the shallow water habitats, there is usually much available primary substratum (Dayton *et al.*, 1974). The final observation, which tends to negate the hypothesis that the barnacle distribution is limited by substrata availability, is that the barnacles do live on muddy substrata by virtue of their ability to settle on old barnacle valves, thus effectively building their own reef.

The project was undertaken with the belief that the most likely explanation for restricted deep-water distribution was that predators, which for various reasons are limited to shallow water, consumed those barnacles dispersing into shallow water (hypothesis 4 above). While there are a large number of seemingly appropriate carnivores (Dayton *et al.*, 1970, 1974; Dearborn, 1977; Arnaud, 1977) the asteroid *Odontaster validus* seemed an especially likely candidate as it is widely omnivorous and in eutrophic areas occurs in extremely high densities (Dayton *et al.*, 1974). In addition, most of the *Odontaster* population is restricted to relatively shallow depths (< 50 m), thus fitting the picture of a shallow-water species capable of being an effective barnacle predator. Less restricted to shallow water but equally likely carnivores are *Diplasterias brucei*, an asteroid; *Parborlasia corre-gatus*, a large nemertean; and *Trophon longstaffi* and *Neobuccinum eatoni*, two gastro-

Pods. Complementary to the predation hypothesis is the hypothesis (number 5 above) that the heavy diatom bloom could smother *B. corolliforme* if it has a weak cirral net musculature or feeds passively as does its congener, *B. hirsutum* (Hoek) (Southward & Southward, 1958).

Because no mortalities occurred in either field or laboratory experiments, these experiments convincingly negated the hypotheses that shallow-water predation (number 4) and algal smothering (number 5) restrict adult barnacles to deeper depths. The manipulations made during the second year were especially remarkable in that the *Odontaster* had been starved for a year, yet they never attacked an adult barnacle. Furthermore, the barnacles kept under constant laboratory illumination were quickly covered with a dense (2 cm) mat of diatoms, but they, too, were alive and seemingly healthy at the end of the second year.

It is interesting to note that although the barnacles survived the 2-year transplant, feeding was rarely observed despite the fact that observers spent a great deal of time in the laboratory. In those few cases where feeding was observed, the cirral net was simply extended into the current (cf. Southward & Southward, 1958). Very slow beating was observed only on two or three occasions. We will return to this matter under feeding biology.

#### *Ancillary observations on the pedunculate barnacle, Arcoscalpellum*

Observations ancillary to the predation hypothesis were made of a local pedunculate barnacle, *Arcoscalpellum*, which is found commonly only on the legs and bodies of large pycnogonids at less than 50 m of depth. In 1975 we found dense aggregations of these barnacles growing in hydroid colonies of South Cape Armitage, an area where the sea ice rarely breaks out and heavy snow drifts accumulate. Thus, while still on the relatively eutrophic east side of the Sound (Dayton & Oliver, 1977), this area receives very little light, and presumably most of the primary productivity is advected from the north. The standing stock of benthic chlorophyll *a* is less than 20% of that found at comparable depths a few hundred metres

north where more light penetrates to the bottom (Dayton, unpublished). In the South Cape Armitage area, *Odontaster validus* densities were less than 10% ( $\leq 30$  compared to  $> 300$  per  $100 \text{ m}^2$ ) that of McMurdo Station, and these few *Odontaster* were very much smaller than in the more northern areas. These observations were interpreted as corroborating our original belief in the predation hypothesis because we assumed that in the relative absence of potential predators, the *Arcoscalpellum* were able to settle and survive on substrata other than the refuge of the legs and bodies of large pycnogonids. This belief was also supported by our subsequent discoveries of similarly free-living *Arcoscalpellum* at McMurdo Station in deeper depths ( $> 50 \text{ m}$ ) below where most of the *Odontaster validus* occurred, and on the insides of cages (Dayton *et al.*, 1974), similarly protected from predators.

The predation hypothesis was tested on *Arcoscalpellum* with experiments in which clumps of hydroids (*Halecium arboreum*) laden with pedunculate barnacles were transplanted from the South Cape Armitage area to the McMurdo Station study sites. Here mesh or plexiglass containers were not used because these barnacles are relatively common on pycnogonids in well-lighted habitats thus eliminating the smothering hypothesis. These hydroid clumps were placed in several localities on the bottom, representing various depths and several substrata (mud, rock and sponge spicule mat). They were also attached to sub-surface floats suspended 20–30 m off the bottom. These experiments were set up in early December 1975, and a few *Odontaster* soon crawled into the hydroids and appeared to eat some barnacles. Since we expected the hydroids on the bottom to be cleaned of barnacles, we did not carefully verify what the *Odontaster* were eating. Like the acorn barnacles, however, most of the pedunculate barnacles survived through December 1977. In one case, the hydroid clump with barnacles was placed at 34 m among local barnacle-free hydroids, and by November 1977 the previously 'clean' indigenous hydroids were full of small *Arcoscalpellum*. This species thus appears to exhibit the common pedunculate tendency of gregarious settlement; the predation theory with respect to mortality of adult

barnacles was again negated. The hydroid gives some protection from a number of predators, but this observation tends to negate for *Arcoscalpellum* a subcomponent of the predation hypothesis: that predation on larvae or recently metamorphosed juveniles is sufficient to prevent invasion of a heavily localized settlement. Still viable and supported by the many observations of *Arcoscalpellum* inside cages and below 50 m is the hypothesis that shallow-water predators consume most of the original larvae settling individually and unpredictably. Such settlements must be successful in order to establish the original large clump. Such heavy gregarious settlement of pedunculates might swamp the ability of the predators to over-exploit the barnacle population.

*Distribution and size frequency of small Bathylasma*

A few small barnacles were observed on the transplanted *Bathylasma corolliforme* at the time of their collection, but no records of their sizes, numbers or spatial arrangements were made because it was not realized that they might be important as well as because

logistic constrictions required us to get the barnacles into the field immediately upon the return of the USCG *Burton Island*. Thus, we do not know whether or not all of the larger of the small barnacles observed at the end of the 2-year experimental period (Fig. 2) had been there without appreciable growth for 2 years, or whether some or most had settled on the large barnacles during the experimental period. While we could not rule out the former possibility, one of us (J.O.) was quite certain he had observed recruitment by the end of the first year and there were obviously many more small barnacles on the shells at the termination of the experiments than at the beginning. Hoping to resolve this problem, all of the small barnacles were measured and mapped with respect to the area of the large barnacle where they were found. Because we expected differences between oligotrophic New Harbor and eutrophic McMurdo Station, these data were tabulated separately.

Analysis of the data revealed a trend in which most small barnacles had settled on the plates inside the orifice and on the tergum and scutum of the transplants. Unfortunately, many of these data were destroyed in a fire, thus preventing a full analysis of this unex-

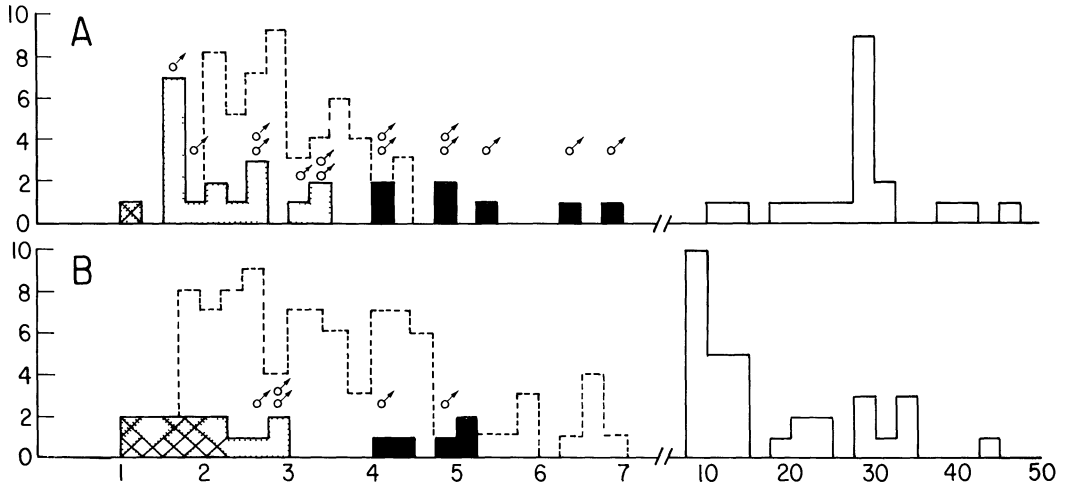


FIG. 2. Size frequency distributions of *Bathylasma corolliforme* (Hoek) from McMurdo Sound: (A) New Harbor; (B) McMurdo Station. Solid bars represent individuals that may have settled on adults (open bars) before transplanted. Stippled bars represent specimens inferred to have settled on adults after they had been transplanted from the Ross Sea shelf. Dotted outlines of bars represent specimens removed, counted and measured, but unusable for other analyses. (Rostro-carinal diameters in millimetres; note change of scale between 9 and 10 mm intervals; male signs indicate number of functional males at each interval; individuals indicated by an 'X' were four-plated.)

pected pattern. The size frequency data are presented in Fig. 2. Note that the sizes range between 1 and 7 mm for both McMurdo Station and New Harbor and that both habitats have relatively large numbers of small (< 3.5 mm) barnacles. In the case of other species for which growth rate data are available, a 1.5 mm barnacle would be from several hours to, at most, 2–3 weeks old (cf. Costlow, 1956). Note that, as noted above, *Arcoscalpellum* sp. settled and grew to normal size within 1 year. This strongly suggests that these small barnacles settled during the 2-year experimental period, especially since some were at the earliest shelled or four-plated stage of development.

### Dispersal

The above observations and interpretation strongly imply that the larvae continuously disperse into the McMurdo Sound region. In addition, we have another experiment demonstrating that larvae are advected into the McMurdo Sound region. A very small (0.7 mm) individual, inferred to be *Bathylasma corolliforme* (Fig. 3), was found attached to a Tuffy scrubber which had been suspended 20 m off the bottom at a depth of 40 m. This floating array, set up for another project, was approximately 200 m from the nearest transferred adult *B. corolliforme*. This barnacle obviously dispersed to this artificial structure as a larva and could not have been more than a day to, at most, a few days old when the tuffy was collected in November 1977. More importantly, it is just slightly smaller than the smallest barnacles in Fig. 2; this constitutes strong evidence that at least the smallest barnacles settled and metamorphosed on the adult during the experimental period.

Another observation helped resolve the question of whether the larvae that settled on the barnacles and Tuffy scrubber came from a pool of larvae within the southern Ross Sea in general or were from very low-dispersing larvae released from the transplants. The life history of bathylasmids is unknown and heretofore the larvae of none has been described. Since bathyabyssal cirripeds commonly pass the nauplius stage in the egg and hatch as non-feeding and

frequently blind cyprid larvae, it was considered that this might be the case in *B. corolliforme*. It was therefore illuminating to find that one large specimen among the sacrificed transplants contained first stage nauplii (Fig. 3A). The first nauplius is neither typically chthamaloïd nor balanoid, and there are a number of important features concerning its capabilities as a planktoner: (1) the setae of the unusually long appendages are mostly setulate, (2) the second antennae and mandibles have extremely well-developed gnathobases and the labrum is remarkably long for a balanomorph, (3) a nauplius eye is present, and (4) the entire nauplius is of a relatively large size. These characteristics indicate a planktotrophic, phototropically responsive form capable of sustained planktonic existence before metamorphosing into the non-feeding cyprid stage.

The cyprid larva of *B. corolliforme* remains unknown, but we have what we believe to be the earliest post-cyprid or youngest juvenile stage (Fig. 3B) from the Tuffy where it had settled on an artificial substratum well removed from the *B. corolliforme* transplants. The shell at this stage is an undivided chitinous annulus with a single hirsute ring, and chitinous terga and scuta guard the aperture, as is commonly the case in balanomorphs at this stage. A special feature may be the two rows of spine-like setae on the terga. Of particular ecological significance is the pair of photoreceptors (separated elements of the nauplius eye) seen rostrally, beneath the cuticle adjacent to the occludent margins of the scuta. The specimen's rostro-carinal (R-C) diameter is approximately 0.7 mm, or just a little smaller than the smallest juveniles with four calcified plates known to be those of *B. corolliforme* discussed below.

Because the McMurdo Station habitat is flushed by tidal currents with a southerly trend (Dayton & Oliver, 1977), it is probable that any larvae released by experimentally transplanted barnacles would be flushed far away from this area before they would be ready to settle. The New Harbor site has a much slower current, but it appears to flow only to the north (Dayton & Oliver, 1977). Thus, larvae released from New Harbor barnacle transplants also would be flushed away, although it is conceivable that larvae



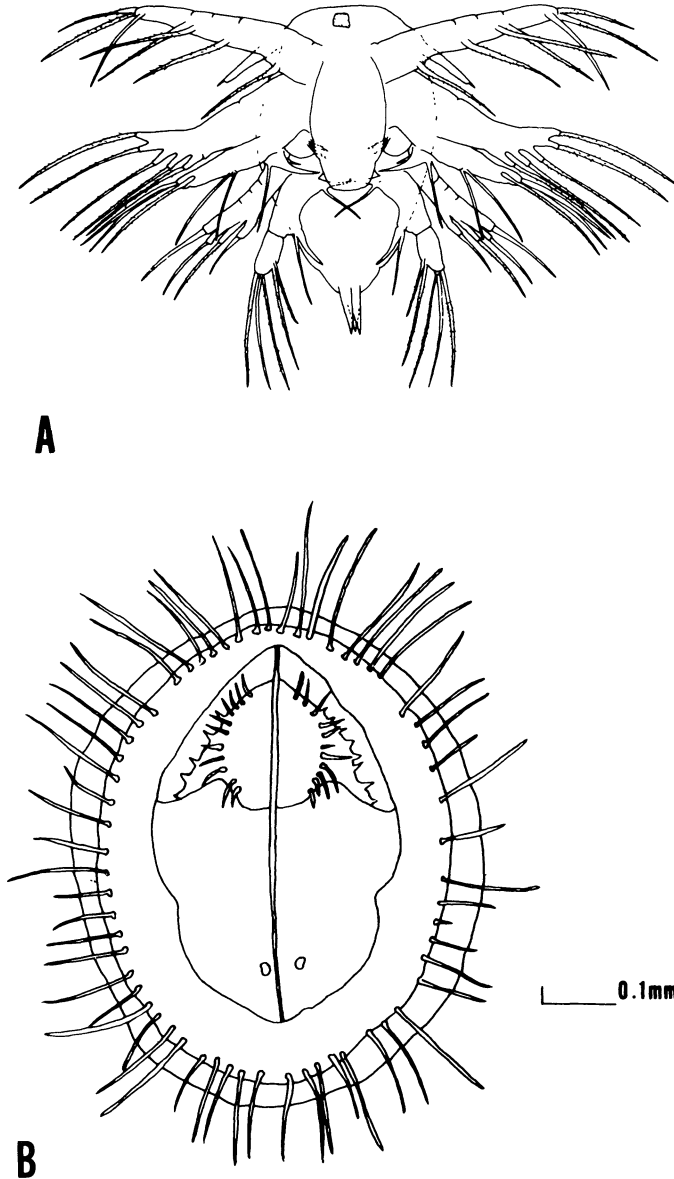


FIG. 3. *Bathylasma corolliforme* (Hoek): (A) Nauplius I removed from the mantle cavity of a hermaphrodite sacrificed 2 years after having been transplanted into McMurdo Sound; (B) juvenile from artificial substratum in McMurdo Sound inferred to be that of *B. corolliforme*; (C) transplanted hermaphrodite (New Harbor) on a cobble and viewed from the right side, with upper portion of carinolateral plate broken exposing six-plated complementary male attached in the articular furrow of the tergum just below the apex; (D) close-up of complementary male illustrated in (C). (A and B to same scale; C, X 1.6.)

from McMurdo Station transplants could be advected to New Harbor. By far the most parsimonious explanation is that there is a pool of *B. corolliforme* larvae throughout the

Ross Sea. Certainly, one consequence of these observations is that it is reasonable to reject hypothesis 7, that the *B. corolliforme* distribution is limited by larval dispersal capabilities.

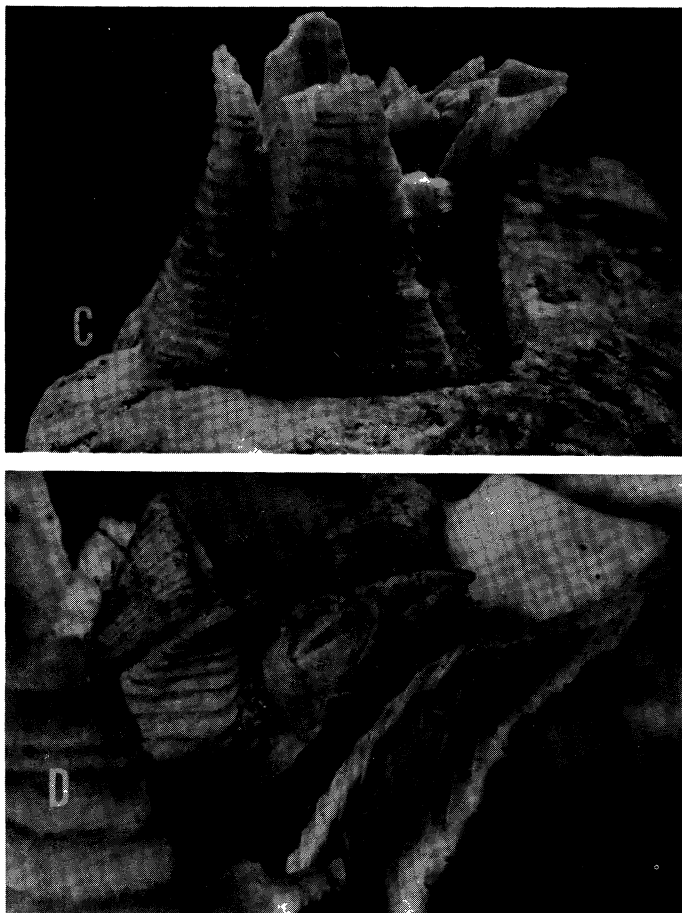


FIG. 3. C, D.

*Natural history: phylogenetic relationships, relict distributions and reproductive biology*

*Bathylasma corolliforme* (Hoek, 1883) is a relatively large, generalized or primitive species with solid plates and membranous basis, and it is the only extant balanomorphan known from south of the Antarctic Convergence (Newman & Ross, 1976). It is bathyal (from 100 to 1500 m) and circumpolar in distribution. There are two other extant species in the genus: *B. hirsutum* (Hoek, 1883) in the northeast Atlantic and *B. alearum* (Foster, 1978) from New Zealand, from comparable depths. Fossil species are known from the Paleocene of North Carolina (Zullo & Baum, 1979) and New Zealand (Buckeridge, 1980), and *B. corolliforme* itself is known from the Pleistocene of Antarctica (Speden, 1962).

*Bathylasma* belongs to the family Bathylasmatidae. The family includes *Tetrachaelasma southwardi* Newman & Ross (1971), a form comparable to *Bathylasma* but found at greater depths (from greater than 1000 to nearly 3000 m) north of the Antarctic Convergence, and the more advanced members, *Aptolasma* and *Hexelasma*, known primarily from the Indo-West Pacific (one species in the western Atlantic) at shelf depths. Representatives of all except *Tetrachaelasma* are known from the Eocene of Tonga (Newman & Schram, 1982). Thus the Bathylasmatidae is not only an ancient family but extant members have relict distributions at shelf depths into the deep sea.

Once we had satisfied ourselves that recruitment had been achieved since the transplant, the answer to the question as to why recruits were settling and growing on the transplants

but apparently not elsewhere in the vicinity might have been simply the gregarious nature of most barnacles; that is, the tendency to settle on or about established individuals. However, the recruitment on established individuals was primarily on the opercular valves; why not as frequently or more frequently on the outside of the shell where there would be less interference with and competition from the established individuals as the juveniles grew? The explanation of this might have been looked for in differential predation on the youngest stages; perhaps those settling on the opercular valves were less susceptible to predation because of the activities of the adults. However, a less pedestrian and in some ways more parsimonious explanation came to light with Foster's discovery (personal communication, 1979) that in the New Zealand species, *B. alearum*, the small individuals on the opercular valves of the hermaphrodite were acting as males. They are apparently not just precocious, protandric individuals, but rather definitive males because they settle in very specific places on the shell, especially on the terga and the exposed sheath of the carina and they remain small (Foster, 1980).

Armed with the knowledge of the presence of males in *B. alearum*, we returned to the supposed juveniles of *B. corolliforme*. While they had already been removed from the hermaphrodites, fortunately their remains had been saved. Re-examination substantiated Foster's findings in *B. alearum*: about half of the six-plated 'juveniles' of *B. corolliforme* were obviously functional males by virtue of having charged seminal vesicles and testes occupying most of the prosoma and a well-developed penis (five out of eleven or 45.5% of those from McMurdo Station and fourteen out of twenty-four or 58% from New Harbor). All of the six-plated 'juveniles' from New Harbor not sexually active were among the smallest individuals, as were half of those from McMurdo Station, and therefore may have been simply immature. The two larger ones from McMurdo Station, on the other hand, may have been spent males and/or were progressing to become hermaphrodites when sacrificed.

As mentioned earlier, nearly all of the 'juveniles' occurred on the opercular parts of

the transplants, but since they had been removed before we were alerted to the possibility of there being males among them, it was not possible for us to say which were actually located near the apices of the terga (Fig. 3C–D) or on the exposed sheath of the carina. No individuals at the four-plated stage had become males. So, while maleness is very precocious it is not actually progenetic (Gould, 1977) with regard to shell structure, as it is in scalpellids and archaeobalanids (Darwin, 1851, 1854; McLaughlin & Henry, 1972).

*Bathylasma corolliforme* hermaphrodites rarely if ever settle and none that may have is known to survive at depths of less than 100 m or so in the Ross Sea under present conditions. But the larvae are available, since they settled on transplanted individuals and the floater. Gregariousness in barnacles has two functions: (1) it increases the likelihood of settling in a situation favourable to reaching a size capable of reproduction, and (2) it ensures that hermaphrodites are close enough together to cross-fertilize. However, the hermaphrodite need not settle where there are established individuals as long as alternative sites selected are favourable (if this were not true, a species' range could only get smaller with time).

A larva destined to become a complementary male must not only settle on an established hermaphrodite, it must also select a site from which it can affect fertilization. This could explain the recruitment of what were apparently for the most part, if not entirely, males on the transplanted *B. corolliforme*. However, under the circumstances of the transplant, the siren song of the hermaphrodite, likely pheromonal, was not only seductive but, as we shall see, likely deceptive.

If sex were genetically determined (Gomez, 1975), it may have been primarily larvae destined to become males that were being attracted out of the plankton to the hermaphrodites. However, if sex were not predetermined, but rather dependent upon the condition of established individuals, it might better explain what we observed. It seems obvious that a larva would be wasting its resources in becoming a precocious male if the hermaphrodite it encountered were close enough to another hermaphrodite to have been or to be readily fertilized. However, a

larva encountering an isolated, receptive hermaphrodite would have a better chance of living long enough to pass its genes on to the next generation if it settled in an appropriate position on the hermaphrodite and became a precocious male, than if it settled beside it and directed its resources into also becoming a hermaphrodite. It is noteworthy therefore that while our transplanted hermaphrodites were in good condition, individuals were frequently too widely spaced for cross-fertilization to occur, no recruitment was observed immediately adjacent to them, only one was brooding young and most were literally swamped with potential or active complementary males when the experiments were terminated. Thus it seems possible that the transplants, effectively virgins, were attracting all comers to attach to the orificial region (an ordinarily unusual place for settlement) to become males.

#### Feeding biology

Little is known about the biology of any bathylasmatid; living material has been observed only in an active state twice before, and then in *Bathylasma hirsutum* from the North Atlantic (cf. Southward & Southward, 1958). The Southwards' observations, made on shipboard and ashore, can be summarized as follows: extension and orientation of the cirral net was strongly influenced by water velocity, direction and temperature. Full extension was induced only by currents in excess of  $1 \text{ cm s}^{-1}$ , and increases to  $5 \text{ cm s}^{-1}$  induced extension in more individuals. Velocities above  $5 \text{ cm s}^{-1}$  appeared to cause little or no increase in the number of individuals reacting, and high currents, to greater than  $30 \text{ cm s}^{-1}$ , had an inhibitory effect. Reducing the current from greater than 10 to less than  $5 \text{ cm s}^{-1}$  resulted in an immediate reduction in the number extending their cirri. The greatest number were active at appropriate currents when water temperatures approximated those of their normal habitat, and it was concluded that currents between 1 and  $5 \text{ cm s}^{-1}$  were not only required for feeding but in keeping hard substrata needed for larval settlement clear of fine sediments. It would seem then, since *B. hirsutum* and *B. corolliforme* are closely related by shell characters

and their cirri and trophi are very similar in structure, that the latter requires comparable currents in order to feed. That such strong currents are not available in our study areas suggests why the adults were not observed to feed. But what about the so-called juveniles? Many had become sexually mature males and therefore must have fed.

The juveniles with calcified plates were all removed from the shells of *B. corolliforme* sacrificed 2 years after transplant (Fig. 2). The smallest measure between 1 and 1.25 mm in R-C diameter, or just a little larger than the uncalcified juvenile discussed above. The earliest calcified shell consists of four plates (rostrum, carina and paired laterals) and some individuals still at this stage, from McMurdo Station, were as large as 2.1–2.5 mm in R-C diameter. All individuals larger than this were, by addition of a pair of carinolateral plates, six-plated, a condition reached in specimens from New Harbor between 1.5 and 1.75 mm in diameter. It appears then that juveniles at McMurdo Station were growing faster and, as we shall see, were maturing at a larger size than those at New Harbor.

The smallest specimens of *Bathylasma hirsutum* from the North Atlantic studies by the Southwards (1958) were also between 1 and 2 mm in diameter, but the one illustrated (1958, Fig. 1), measuring 3 mm in R-C diameter, is apparently still at the four-plated stage and is therefore remarkably large as compared to ours of *B. corolliforme*. But theirs had grown under conditions normally inhabited by the barnacles, and perhaps this and the warmer temperatures found there account for the difference. It is more likely the latter since the six-plated juvenile of *B. corolliforme* dredged from the Ross Sea and illustrated by Foster (1978, Fig. 48a) measured 2 mm in R-C diameter. It seems then that the juveniles found on the transplants were growing normally and certainly the four-plated and smaller six-plated individuals had settled on the adults in the 2 years intervening between transplantation and sacrifice. In contrast to the adults with their delicate cirri which are extended into currents, the juveniles have short cirri capable of beating and therefore feeding in quiet water. An analogous situation has been discovered recently in the stalked barnacle, *Pollicipes*

*polymerus*; while juveniles can beat normally, adults rely on the backwash of waves to provide the feeding current into which they extend their cirri (Lewis, 1981). This would explain why juveniles of *Bathylasma* were apparently growing normally while the adults were barely sustaining themselves.

### Nutrition

The rare and leisurely cirral extension in large *B. corolliforme* and the fact that conspicuous growth was not observed suggest support of hypothesis 8, that there is a component of the shelf-break habitat which is necessary for the barnacle. It could be availability of appropriate food, but since our juveniles grew, a more likely explanation is the higher current velocities experienced at the shelf break. While this hypothesis may be considered unlikely because no mortalities were observed, 2 years may be an insufficient amount of time in which to observe mortalities. This hypothesis could not be negated by observing the reproductive and physiological conditions of barnacles maintained in our two habitats. Unfortunately, no barnacles were preserved immediately after our original Ross Sea collection. Consequently, our comparisons must be based on the barnacles from our two transplant sites plus barnacles from the Ross Sea shelf break in the collections of the Scripps Institution of Oceanography (Fig. 1) which have been preserved in alcohol for many years, thus precluding exact comparison of lipid analyses.

There were no significant differences in the tissue-to-shell ratios between the McMurdo Station and New Harbor barnacles. However, the barnacles maintained for 2 years in the more eutrophic McMurdo Station habitat had a significantly higher lipid content ( $X = 2.268\% \pm 0.217$  s.d.,  $N = 5$ ) than those from the oligotrophic New Harbor site ( $X = 0.68\% \pm 0.585$  s.d.,  $N = 5$ ) where there is usually little or no current. Thus, the hypothesis that barnacles in eutrophic McMurdo Station are slowly smothered by inedible diatoms seems negated by the fact that the McMurdo Station laboratory barnacles which survive beneath a heavy growth of diatoms had a significantly higher lipid content than the New Harbor barnacles. Nevertheless, lipid analyses on *B. corolliforme* specimens dredged from the

same area on the shelf as those transplanted, but in 1961 (Fig. 1), and held in the Scripps Institution of Oceanography collection yielded lipid values higher ( $X = 6.51\%$ ,  $N = 3$ ) than those from either of the experimental sites, despite the barnacles having been preserved in alcohol and thereby losing an unknown amount of lipid. One of the three deep-water barnacles from the Scripps Institution of Oceanography collection had a value of 12% lipid. This value was obtained in spite of the barnacle having been preserved in alcohol for a number of years. It probably represents mature ovaries with yolky ova. Thin layer chromatographic analysis revealed an ultra-violet active portion not found in the other barnacles. This ultraviolet active portion was found to contain mostly phospholipids with a triglyceride backbone. The lipid data indicate that important nutritional and/or habitat differences exist between their native deep-water habitat and the two transplant sites.

The lipid data suggest that the barnacles at the eutrophic McMurdo Station site were somewhat better nourished than were those at the oligotrophic New Harbor site, as did the data on apparent growth rate of the juveniles. Considering the long storage in alcohol, the high lipid values from the Scripps Institution of Oceanography barnacles very well may offer support to hypothesis 8: that the feeding conditions are better in the natural deep-sea habitats. We have no primary productivity data from the areas where the barnacles were collected, but they were taken near the 'shelf break' where the productivity is higher relative to other open sea areas and there are presumably strong local currents. Evaluation of the reproductive condition of twelve barnacles maintained at McMurdo Station and sixteen maintained at New Harbor showed that over half had functional penes, testes and ovaries. One was full of nauplius larvae ready for release. Thus, while the deep-water barnacles appear better nourished, those transplanted to McMurdo Sound were at best only moderately undernourished after 2 years at their respective sites.

### Discussion

In recent years, biogeographers have flocked to support various popular renditions of the

Popperian philosophy that science advances by rigorous falsification of hypotheses (Ball, 1975). Because most biogeographic theories involve a strong component of history and global patterns, hypotheses are tested vicariously, if at all. Here we have negated directly several reasonable hypotheses regarding the boundaries between deep-water and shallow-water assemblages.

The successful translocation of many barnacles from deep to shallow water and their subsequent survival over 2 years negates hypotheses built around physiological constraints or other undefined factors associated with shallow or eutrophic waters. The natural flexibility of these barnacles with regard to acceptable substrata plus abundant observations of appropriate and available substrata in shallow water negate hypotheses relating to availability of, or competition for, substrata. The multifaceted evidence that larvae did settle on the McMurdo Sound transplants plus the direct observation that one settled on an artificial surface negate hypothesized barriers to larval dispersal. Finally, we found no evidence supporting any predator hypothesis.

Our observations of larval dispersal into McMurdo Sound Region are unexpected and exciting as they demonstrate that larval propagules continuously immigrate but seemingly never successfully colonize, at least under present conditions. The fact that living adults have never been found in this region cannot be attributed to lack of sampling effort because, despite the remote location, the benthos has been well sampled (Hodgson, 1907; Bullivant & Dearborn, 1967; Dayton *et al.*, 1974; Lowry, 1976). Thus, despite the fact that larvae are advected into the area, successful colonization has never been observed in natural situations despite reasonably extensive surveys.

There is evidence that *Bathylasma* once lived in southern McMurdo Sound as Speden (1962) has recovered their shells in conglomerates from the Scallop Hill Formation immediately to the south. In addition, John Macdonald and Rufus Wells (personal communication) retrieved a *Bathylasma* shell from 60 m at South Cape Armitage in 1977. Thus, we ask what was different which might have allowed *Bathylasma* to have lived in McMurdo Sound in the past? We note that Southward

& Southward (1958) found that *B. hirsutum* fed only in currents in excess of  $1 \text{ cm s}^{-1}$  and seemingly preferred velocities in the neighbourhood of  $5 \text{ cm s}^{-1}$ . The need for currents has also been noted in shore barnacles (cf. Denley & Underwood, 1979). Such currents are not seen in the present McMurdo Sound habitats we have examined, but one would expect much stronger wind-driven currents were there no permanent ice shelf in the area. Hence, we propose the hypothesis that adult *B. corolliforme* needs stronger currents to maintain itself, and that such currents likely prevailed in the past, as recently as 10 000 years before present, when there was apparently less ice (Sugden & Clapperton, 1980).

The biogeographic implications of the observations of dispersal and the demonstration that adults do survive at least 2 years in the relatively shallow waters of McMurdo Sound suggest that the distribution barriers may also involve the barnacle life history phases of larval settlement through successful metamorphosis and growth to some size refuge at which they become safe from predation. Future hypotheses which should be considered include: (A) larval behaviour patterns tend to preclude settlement without 'arthropodin' from 'seed barnacles' where current velocities are negligible; (B) predators such as the abundant filter feeders (hydroids, alcyonaria, etc.), deposit feeders (*Odontaster*, several ophiuroids and holothurians, etc.) and dense populations of infaunal and epifaunal animals (scale worms, amphipods, isopods, etc.) kill the settled larvae and recently metamorphosed barnacles; (C) various components of the current and nutritional hypothesis discussed earlier.

Hypothesis A receives support from the observation of many recently settled barnacles on the large transplants, but in its extreme form is negated by our observation of a small barnacle on an artificial substratum. Hypothesis B is a variant of the predator hypothesis, but differs as the settled cyprids and very small barnacles are substantially more vulnerable than the very large adults we offered the predators. This hypothesis B will be difficult to test without obtaining cyprid larvae which are about to settle, but hypothesis C can be negated if some of the small barnacles on the large adults which we left at McMurdo show

growth and reproductive activity many years hence. We believe that hypothesis A will be disproven, and that B and C will be modified by the eventual discovery of living *Bathylasma* in the McMurdo Sound Region. We predict that the barnacles will be found on stable outcrops subject to stronger currents than found in the areas we have investigated. Specifically, we suggest looking south of Cape Armitage, at White Island, or on the West Coast north of Marble Point, especially at Granite Harbor.

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