

Unprotected larval development in the Antarctic scallop *Adamussium colbecki* (Mollusca: Bivalvia: Pectinidae)

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Abstract: Most Antarctic bivalves are small and protect their young by holding fertilized eggs or larvae in their mantle cavities for varying periods. Nourishment for these early growth stages is provided by yolk reserves rather than by planktotrophy. The anomalously large Antarctic scallop, *Adamussium colbecki*, has unprotected planktotrophic larvae that are spawned during the austral spring. Successful recruitment of these larvae, in populations which are most abundant in oligotrophic habitats, may be associated with episodic pulses of organic material. Reasons why planktotrophy persists in *A. colbecki* are suggested by a comparison with another large Antarctic bivalve, *Laternula elliptica*. The latter has protected lecithotrophic larvae that are released at the beginning of the austral winter. This comparison suggests that unprotected larval development persists in *A. colbecki* because of unusual anatomical and ecological adaptations among the adults of the *Adamussium* lineage that have been evolving in the Southern Ocean since the early Oligocene.

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Introduction

It is well known that a very large percentage of Antarctic bivalve species protect the development of their early growth stages (Dell 1972, Picken 1980, Pearse *et al.* 1987, 1990). These protected young are held either within the mantle cavity or gills until they have metamorphosed, or they are released as encapsulated lecithotrophic larvae which may have short planktonic or demersal stages before metamorphosis (Miliekovsky 1971, Jablonski & Lutz 1980, 1983). In fact, of the approximately 65 bivalve species in the Antarctic region (Nicol 1967), only two are even suspected of not having protected early development modes (Pearse *et al.* 1986). The Antarctic bivalve fauna strongly supports the suggestion that the incidence of non-planktonic development among benthic invertebrates increases toward higher latitudes (Thorson 1950).

However, recently the reproductive modes of Antarctic shallow marine invertebrates have been reconsidered and it has been found that there are numerous exceptions to "Thorson's Rule" (Pearse *et al.* 1990). Understanding why protected development modes predominate in the Antarctic benthos (Clarke 1980, Picken 1980, Pearse *et al.* 1987) is only part of the problem. It also is necessary to evaluate why unprotected larval development, as in the echinoderms, persists among certain species (Pearse *et al.* 1990). This latter question is addressed for one of the Antarctic bivalves which has been suspected of having an unprotected early

development mode: the scallop, *Adamussium colbecki* (Smith 1902). Anatomical, ecological and historical comparisons with an Antarctic bivalve which is known to protect its young, *Laternula elliptica* (King & Broderip 1831), provide the basis for this assessment.

Methodology

Aside from direct observations of spawning, larval morphology, and larval feeding behaviour, two indirect methods have been widely used for inferring developmental modes in the Bivalvia. These complementary techniques are based on measurements of growth stages recorded on the larval shell and of egg sizes that differ between protected and unprotected larval development forms.

Larval shells (*prodissoconchs*) of bivalves generally exhibit two stages, designated PI and PII, commonly differing in microsculpture and separated by a more or less distinct growth line (Ockelmann 1965, Jablonski & Lutz 1980, 1983, O' Foighil 1986). The end of the first stage (PI) represents the period during shell development when complete closure of the shell around the larval body is first possible. Hence, PI reflects the size of the larval body and the size of the egg from which it develops (Waller 1981). The fringe of PII around PI is associated with the presence of a fully developed retractable velum, which functions in locomotion and food capture (Strathmann *et al.* 1972, Waller 1981).

It was shown by Thorson (1950, 1961) and Ockelmann

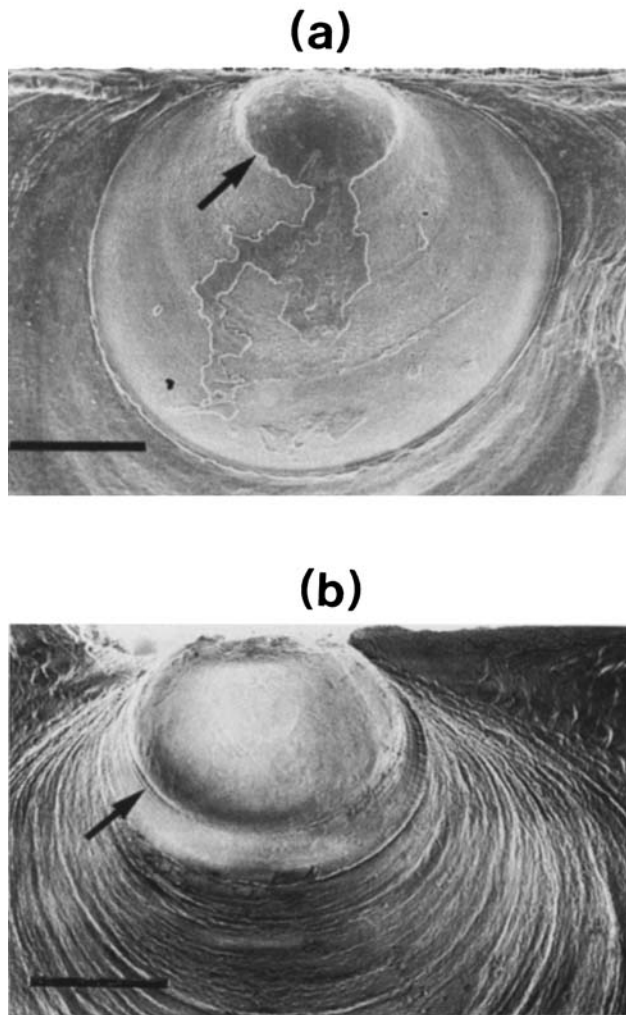


Fig. 1. Scanning electron micrograph (250x magnification at 10 KV) of the right valves of: (a) 11.8 mm *Adamussium colbecki* specimen from Explorers Cove (77°35'S, 163°40'E) and (b) 2.5 mm *Laternula elliptica* specimen from Cape Evans (77° 38'S, 166° 25'E) showing the PI/PII boundary (arrow) and the relative sizes of the larval shell-bands. The scale bars are 100 μ m.

(1965) that planktotrophic bivalve larvae develop from small eggs (40–85 μ m) and have a small PI (70–150 μ m) but a large PII (200 to more than 600 μ m in particular species). In contrast, lecithotrophic larvae develop from large eggs (90–200 μ m) and have large PI stages (135 to more than 500 μ m). The PII fringe peripheral to the PI stage among these lecithotrophic forms is generally very narrow, indicating a short feeding stage before metamorphosis (Ockelmann 1965, Waller 1981). Although the absolute size of PI is the most critical indicator of reproductive mode, the ratio of the length of PI to length of PII is obviously another indicator. Examples given by Ockelmann (1965) and Waller (1981) suggest that unprotected planktotrophic larvae have PI/PII ratios of the order of 0.25 to 0.4, whereas protected lecithotrophic larvae with short planktonic stages have

PI/PII ratios of the order of 0.6 or greater. Many brooded larvae which develop to metamorphosis within the shell of their parent only have a PI stage. In this latter situation, the prodissoconch is commonly cap-shaped and rugose, as in many if not all Antarctic members of the family Philobryidae (Bernard 1897, Dell 1972).

Measurements and observations of the prodissoconch growth stages were taken from scanning electron micrographs and directly from shells examined at 50x magnification with a binocular microscope equipped with an ocular micrometer. These *A. colbecki* and *L. elliptica* samples (which have USNM catalogue numbers) came from the Department of Invertebrate Zoology, Division of Molluscs, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Measurements of *A. colbecki* male and female gonad sizes were derived from histological sections of large adult scallops (80 \pm 10 mm in shell height) collected from Explorers Cove, McMurdo Sound, (77°35'S, 166°25'E). Scallops maintained in 1240 l aquaria under ambient light conditions, with sediment from Explorers Cove and circulating seawater from McMurdo Sound, provided gonad tissues for the 1986 austral winter and scallops from the field provided gonad tissues for the following summer. These tissues were fixed in 10% buffered formalin made in seawater, dehydrated in a graded series of ethanol cleared in xylene, embedded in paraplast+, cut into 2–6 μ m sections with an American Optical Microtome, and finally stained with Harris's hematoxylin and aqueous eosin (Sheehan & Hrapchak 1980). Four male and four female scallops from each time period (May, June, September and January) were used in these analyses, and 15 oocyte measurements were made with a binocular microscope (as above) for each of the female scallops.

Observations

Scanning electron micrographs of the early growth regions of the right valve of a juvenile *A. colbecki* (Fig. 1a) from Explorers Cove show that the PI has a length of 119 μ m and that the larval shell at metamorphosis (PII) is 344 μ m, giving a PI/PII ratio of 0.35. Binocular microscope measurements of *A. colbecki* shells from other localities around West Antarctica further demonstrate the presence of small PI and large PII in this species (Table Ia): PI lengths average 124 μ m, PII lengths average 346 μ m, and PI/PII length ratios average 0.36.

Scanning electron micrographs of the early growth regions of the right valve of a juvenile *L. elliptica* (Fig. 1b) from Cape Evans, McMurdo Sound, (77°38'S, 166°25'E), show that the PI has a length of 190 μ m and that the larval shell at metamorphosis (PII) is 225 μ m, giving a PI/PII ratio of 0.84. Binocular microscope measurements of *L. elliptica* shells from other areas in McMurdo Sound further demonstrate the relatively large PI compared to PII (Table Ib). Mean values from the *L. elliptica* in which the larval shell bands could be

Table I. Prodissoconch measurements

Number	PI	PII	PI/II
	Mean \pm 1 STD (Range) (μm)	Mean \pm 1 STD (Range) (μm)	Mean \pm 1 STD (Range) (μm)
(a) <i>Adamussium colbecki</i>			
22	124.0 \pm 9.8 (110.0 - 144.6)	N/A N/A	N/A N/A
38	N/A N/A	345.7 \pm 19.7 (303.5 - 403.3)	N/A N/A
21	124.6 \pm 9.6 (112.0 - 144.6)	348.0 \pm 19.9 (303.5 - 403.3)	0.36 \pm 0.03 (0.31 - 0.42)
(b) <i>Laternula elliptica</i>			
16	202.4 \pm 9.1 (183.0 - 216.0)	N/A N/A	N/A N/A
13	N/A N/A	242.9 \pm 15.9 (214.0 - 265.0)	N/A N/A
12	201.1 \pm 9.8 (183.0 - 216.0)	242.2 \pm 16.4 (214.0 - 265.0)	0.83 \pm 0.05 (0.76 - 0.92)

distinguished were: PI length 202 μm , PII length 243 μm , and PI/PII length ratio 0.83. The fringe of PII adjacent to the midventral edge of PI is very narrow, measuring between 30–40 μm in width.

Seasonal histological analyses indicate that female and male *A. colbecki* gonads developed synchronously through the austral winter and that gametes were released during the austral spring (Fig. 2). This seasonal gonad cycle is also illustrated by changes in the oocytes from mean sizes of 35 μm in May to 55 μm in September and back down to 15 μm in January (Fig. 3).

Reproductive mode of *Adamussium colbecki*

The data on the size of *A. colbecki* prodissoconchs (Table Ia) and small size of mature oocytes (Fig. 3) are consistent with the known features of bivalve larvae that are planktotrophic (as described above). Based on undefined small egg sizes, Pearse *et al.* (1986) also suggested that the larvae of *A. colbecki* must be planktotrophic. The spring spawning period of these planktotrophic larvae, described in Figs. 2 & 3, also is suggested by observations of “thousands of recently metamorphosed [pinhead size] pectens, *Adamussium colbecki*” in the sediments at Explorers Cove during the austral summer (Dayton & Oliver 1977, Dayton personal communication 1990).

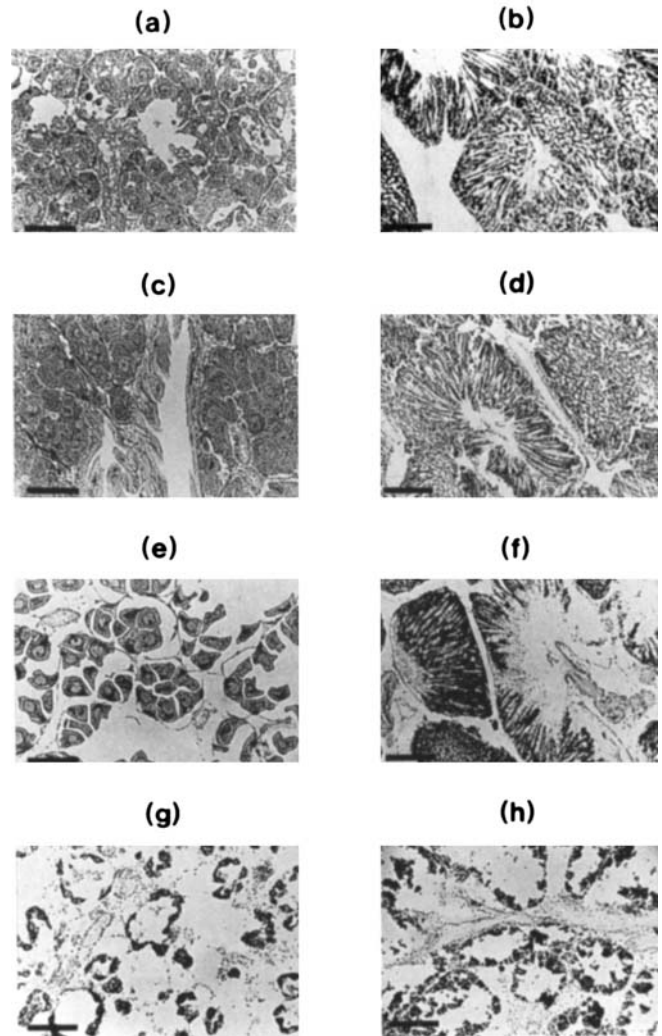


Fig. 2. Gonad histological sections of *Adamussium colbecki* (80 \pm 10 mm in shell height) which were reared in aquaria in May, June and September 1986 and collected directly from Explorers Cove in January 1987. Shown are females (a, c, e, and g) and males (b, d, f, and h) in May, June, September and January, respectively. The scale bar measures 100 μm .

The prodissoconch measurements from *L. elliptica* provide a test for the efficacy of this method. PI and PII measurements for this bivalve species indicate that it has lecithotrophic larval development. This inference is supported by direct observations of large 220 μm eggs and encapsulated lecithotrophic *L. elliptica* larvae which were spawned in the laboratory and field during the early austral winter (Pearse *et al.* 1986, 1990, Bosch & Pearse 1988). The vitelline membrane around these embryos (Burne 1920) may indicate that they develop in a similar fashion to other anomalodesmatan bivalves (Allen 1961).

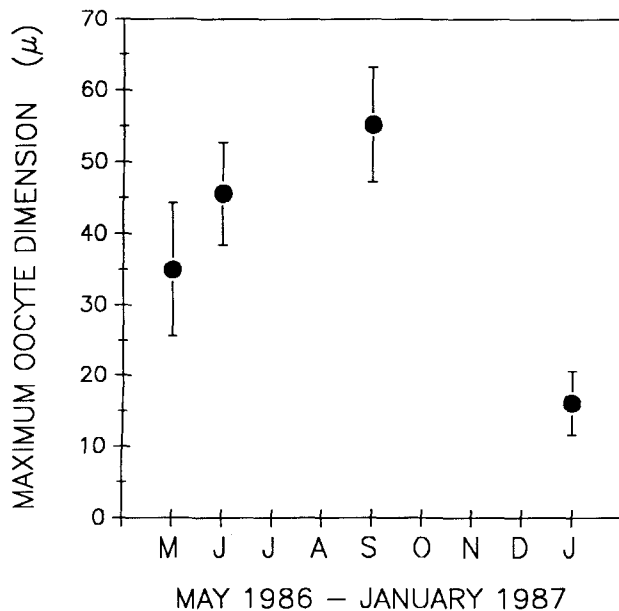


Fig. 3. The maximum oocyte dimensions determined from gonad histological sections of *Adamussium colbecki* (80 ± 10 mm in shell height) which were reared in aquaria in May, June and September 1986 and collected directly from Explorers Cove in January 1987. Shown are the oocyte mean sizes and standard deviations from four scallops for each month ($n = 15$ oocyte measurements per scallop).

Comparisons between *A. colbecki* and *L. elliptica*

Small bivalve size in the Antarctic, as in the deep sea or the Arctic, is influenced by the increased solubility of calcium carbonate at low temperatures (Nicol 1967, Arnaud 1977, Lipps & Hickman 1982). Protected development in bivalves is associated with small adult size (Strathmann & Strathmann 1982), generally less than 10 mm, and indeed about 60% of Antarctic bivalve species are in this size range (Nicol 1970). However, the predominance of lecithotrophy and brooding in the Antarctic fauna also may indicate that protected development is economical under conditions where food may be scarce for much of the year (Chia 1970, Vance 1973, Spight 1976, Picken 1980).

Adamussium colbecki is the largest species in the Antarctic bivalve fauna, with a record maximum length of 120 mm (Berkman 1988, voucher specimen USNM 859341, Explorers Cove). It is approached in size only by *Laternula elliptica*, which has a maximum recorded size of 100 mm (Soot-Ryen 1951). Unprotected planktotrophic or protected lecithotrophic larval development in these species, respectively, clearly is not influenced by adult size alone. Factors influencing the unusual persistence of planktotrophy in *A. colbecki* might be revealed by contrasting the geologic history, anatomy and ecology of these two anomalously large Antarctic bivalve species.

Geologic History

A. colbecki and *L. elliptica* have been considered as members of an "old" Antarctic fauna that had "ancestors from a time of more genial climatic conditions" (Soot-Ryen 1951). There is little information on the history of *L. elliptica* in the Southern Ocean, but it is known that the genus *Laternula* dates from the late Cretaceous (Keen & Cox 1969). Noting the once great diversification of the Anomalodesmata in the Palaeozoic, Morton (1981) referred to the living remnants of this subclass as relics "wonderfully equipped to survive in specialized niches." Today, species of the genus occur in temperate and tropical regions (Dell 1972, Morton 1973a, Bernard 1983) as well as in Antarctica where *L. elliptica* is widely distributed around the continent (Powell 1965) with abundant shallow-water populations (Stout & Shabica 1970, Hardy 1972).

Despite the presence of scallop species in the Southern Ocean since the early Tertiary (Zinsmeister 1982), *A. colbecki* was until recently "without demonstrated derivation from any other pectinid" living or extinct (Dell & Fleming 1975). This absence of any known ancestral connection perhaps caused Habe (1977) to make *A. colbecki* the sole member of a new pectinid subfamily Adamussiinae.

However, the recent discovery of fossil *Adamussium?* n. sp., in the CIROS-1 drill core from McMurdo Sound, provides evidence that the *Adamussium* lineage has been evolving in the Southern Ocean since the early Oligocene (Beu & Dell 1989). Although the ancestral taxon resembles modern *A. colbecki* in certain details, Beu & Dell (1989) also noted that it lacks those features which are associated with well-developed swimming ability in the modern form: wide posteriodorsal shell gapes, projecting V-shaped dorsal margins on the auricles, a broad, flaring umbonal angle, and a wafer thin shell. Because there is no known Miocene record of *Adamussium*, it is not clear when the ancestral taxon became extinct or evolved into the modern *A. colbecki*.

It is known, however, that unrelated scallop species of the genus *Chlamys* were common in the Southern Ocean during the Miocene (Dell & Fleming 1975). From the Pliocene into the middle Pleistocene, *C. patagonica anderssoni* and *C. tuftensis* inhabited shallow-water environments in East and West Antarctica in the absence of *Adamussium* (Beu 1985, Pickard *et al.* 1988). The thick shells of these *Chlamys* species and the taphonomy of associated calcareous foraminifera assemblages (Webb 1972) suggest that warm (5–10° C) sea surface temperatures existed through this latter period (Mercer 1978).

During the early Pleistocene, the sea surface temperatures cooled and the *Chlamys* species became extinct in Antarctica (Speden 1962, Turner 1967) and restricted to southern temperate regions (Beu 1985). It was during this period that *A. colbecki* invaded shallow water environments around Antarctica (Chapman-Smith 1981, Qingsong & Peterson 1984), most likely from deep water habitats which served as

refugia. Such refugia would be well within the three to nearly 1500 m depth range of modern *A. colbecki* (Dell 1972). Interestingly, the highest shallow-water densities of *A. colbecki* (Nakajima *et al.* 1982, Berkman 1988, 1990, Taviani & Amato 1989) occur in areas which share characteristics with the deep sea (Dayton & Oliver 1977).

Anatomy

A. colbecki and *L. elliptica* have strongly contrasting body plans which place constraints on their ability to evolve protected development of early growth stages. Like all members of the family Pectinidae, *A. colbecki* has filibranchiate gill filaments that are held together by ciliary ‘hair brush’ type junctions without strong tissue connections (Morse *et al.* 1982). There is no fusion of the gill lamellae to either the visceral mass or to the mantle, and the mantle cavity is broadly open to the exterior. There are no siphons and the inner folds of the mantle (mantle curtains) are brought into apposition through muscular control, as in the formation of jet openings during the expulsion of water. The violent flushing of the exposed mantle cavity which occurs during swimming (discussed below) and the loose gill structure make it unlikely that *A. colbecki* could protect the development of its early growth stages.

In contrast, like all members of the order Anomalodesmata (except the septibranchiate genera), *L. elliptica* is a eulamelibranch with its gill filaments held firmly together by tissue (Ridewood 1903). The configuration of these gill lamellae and the separation of the gill axis from the posterior part of the visceral mass create a capacious suprabranchial chamber which can be used for brooding or for the storage of large eggs until spawning, as in other anomalodesmatans such as *Pholodomya* (Morton 1980). Moreover, the mantle edges of *L. elliptica* are extensively fused and entry into the mantle cavity is restricted to a pair of narrow and tightly controlled siphonal openings, a narrow pedal opening and a tiny fourth pallial aperture. In *L. elliptica*, the unexposed burrowing habit (discussed below) and restricted access to the suprabranchial chamber are well suited to protecting the development of early growth stages.

Ecology

Both *A. colbecki* and *L. elliptica* live at least 13 years (Ralph & Maxwell 1977, Stockton 1984, Berkman 1990), but they occupy entirely different niches. As with other pectinids (Baird & Gibson 1956, Marshall 1960, Waller 1969), adult *A. colbecki* generally lie free on the bottom in shallow depressions (Stockton 1984, Berkman 1988) which are created by a series of stereotyped movements influenced by the muscular control of water jets through the mantle curtains (Waller 1976). Contrary to the free living habit of *A. colbecki*, adults of *L. elliptica* are deep burrowing (Stout & Shabica 1970, Hardy 1972, Ralph & Maxwell 1977), and like other

species of *Laternula* they are incapable of reburying themselves if dislodged (Runnegar 1972, Morton 1973a, 1973b).

Dissection of *A. colbecki* specimens collected at Explorers Cove revealed benthic foraminifera and sand grains in their digestive tracts (Berkman 1988), which indicated that *A. colbecki* was ingesting detritus from the sediment surface like other scallop species (Shumway *et al.* 1987). Juvenile *A. colbecki*, which commonly were byssally attached to the adults (Stockton 1984, Berkman 1988, 1990), may have benefited from this detrital slurry resuspended by the adults. *A. colbecki* also was highly mobile and has been observed swimming 20 m above the bottom parallel to the underside of the sea ice (Berkman unpublished). This mobility of *A. colbecki* is further suggested by observations of population densities which changed from ‘several hundreds per 10 m² to zero in a few hours’ (Ralph & Maxwell 1977).

Spring spawning in nearshore *A. colbecki* populations would appear to reflect a general tendency among Antarctic benthic invertebrate species with planktotrophic larvae to coordinate their planktonic development with seasonal primary production (Pearse *et al.* 1987, 1990). In contrast, lecithotrophic larval development in *L. elliptica* is known to proceed with nourishment from egg yolk reserves during the winter in the absence of primary production (Pearse *et al.* 1986, 1990, Bosch & Pearse 1988).

However, Explorers Cove is considered to be oligotrophic because of the low summer phytoplankton and bacterial productivity in the overlying water column (Dayton & Oliver 1977, Hodson *et al.* 1981). In this area which generally is covered by multi-year sea ice, recruitment of *A. colbecki* larvae may be episodic (Berkman 1990) and influenced by the higher concentrations of organic matter (Palmisano & Sullivan 1983, Dunbar *et al.* 1989) that would prevail during years when there is first-year sea ice. Alternative food sources, such as bacteria (Rivkin *et al.* 1986), also may enhance the survival of these larvae. Similarly, episodic pulses of organic matter or alternative food sources may account for the successful recruitment of unprotected planktotrophic larvae of *A. colbecki* in the oligotrophic deep sea reaches of its range.

Conclusions

A. colbecki and *L. elliptica* are anomalously large species in the Antarctic bivalve fauna with completely different modes of larval development. *A. colbecki* has rare unprotected planktotrophic larvae which feed in the water column and are spawned during the austral spring. In contrast, *L. elliptica* has common protected lecithotrophic larvae which are nourished by egg yolk reserves and released during the austral winter. Ostensibly, these early development modes and release periods are influenced by the relative dependence of the larvae on seasonally produced food sources.

Curiously, *A. colbecki* most frequently occurs in Antarctic marine habitats that are oligotrophic. Successful larval

recruitment in these populations may be tied to episodic pulses of organic material or alternative food sources. The rare persistence of unprotected larval development in *A. colbecki*, however, appears to be constrained by anatomical and ecological adaptations among the adults of the *Adamussium* lineage that have been evolving in the Southern Ocean since the early Oligocene.

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