Evidence for a marine molluscan fauna beneath ice shelves in the Lazarev and Weddell seas, Antarctica, from shells of *Adamussium colbecki* and *Nacella* (*Patinigera*) cf. *concinna*

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Abstract: Only one living specimen of *Adamussium colbecki* was found amongst the shells of this species collected in the Lazarev and Weddell Seas, and those of the limpet *Nacella* cf. *concinna* from three locations in the southern Weddell Sea. In order to explain this peculiarity four hypotheses are discussed. The possibility that the shells belong to living deep-water populations is in contradiction to the high number of trawl samples taken in the area and the abundance of empty shell material. ^{14}C dates show the shells are recent, thus excluding the possibility that the shells belong to autochthonous fossil populations exposed on the seafloor. Lateral transport of living specimens or shells over long distances by marine currents or by ice is unlikely due to their state of preservation and the water circulation pattern. The most likely explanation is that the shells are allochthonous, transported only over short distances by marine currents from adjacent areas underneath floating ice shelves where both species have living populations.

Introduction

The Weddell and Lazarev Seas are typical high-Antarctic environments. Most of the coastline is formed by free-floating ice shelves or by ice shelves grounded near the ice edge and forming ice rises such as Berkner Island (Figs 1 & 2). The extensions of the ice shelves vary from several hundred kilometres (Ronne and Filchner Ice Shelves) to a few tenths of kilometres (ice shelves of the eastern Weddell Sea and Lazarev Sea). The continental shelves are characterized by a rough, glacially formed topography and by a general slope towards the continent (Andriashev 1977). The water depths both beneath and in front of the ice shelves are in the order of several hundred metres. The edge of the continental shelf corresponds approximately to the 600m depth contour (Johnson *et al.* 1981).

The Antarctic scallop *Adamussium colbecki* (Smith, 1902) (Bivalvia: Pectinidae, Fig. 3) and the limpet *Nacella cf. concinna* (Strebel, 1908) (Gastropoda: Patellidae, Fig. 4) are common in littoral or shallow Antarctic waters. *A. colbecki* is widely distributed in the Southern Ocean in general (Powell 1960, Nicol 1966, Dell 1972a, 1990), whereas *N. concinna* is more restricted to the Antarctic Peninsula region and the islands of the Scotia Arc (Powell 1960, Dell 1972a, Berry & Rudge 1973, Picken 1980a).

The scallop *A. colbecki* lives attached to stones by a byssus (Stockton 1984) and is reported from hard rock substrata or stones, pebbles and sand (Nicol 1966). Dell (1990) gives a maximum water depth of 2840 m for dead shells and a bathymetric range of 4–1380m for living specimens. *In situ* observations of living *A. colbecki* populations at McMurdo Sound have shown highest densities (up to 85 specimens m^{-2}) in
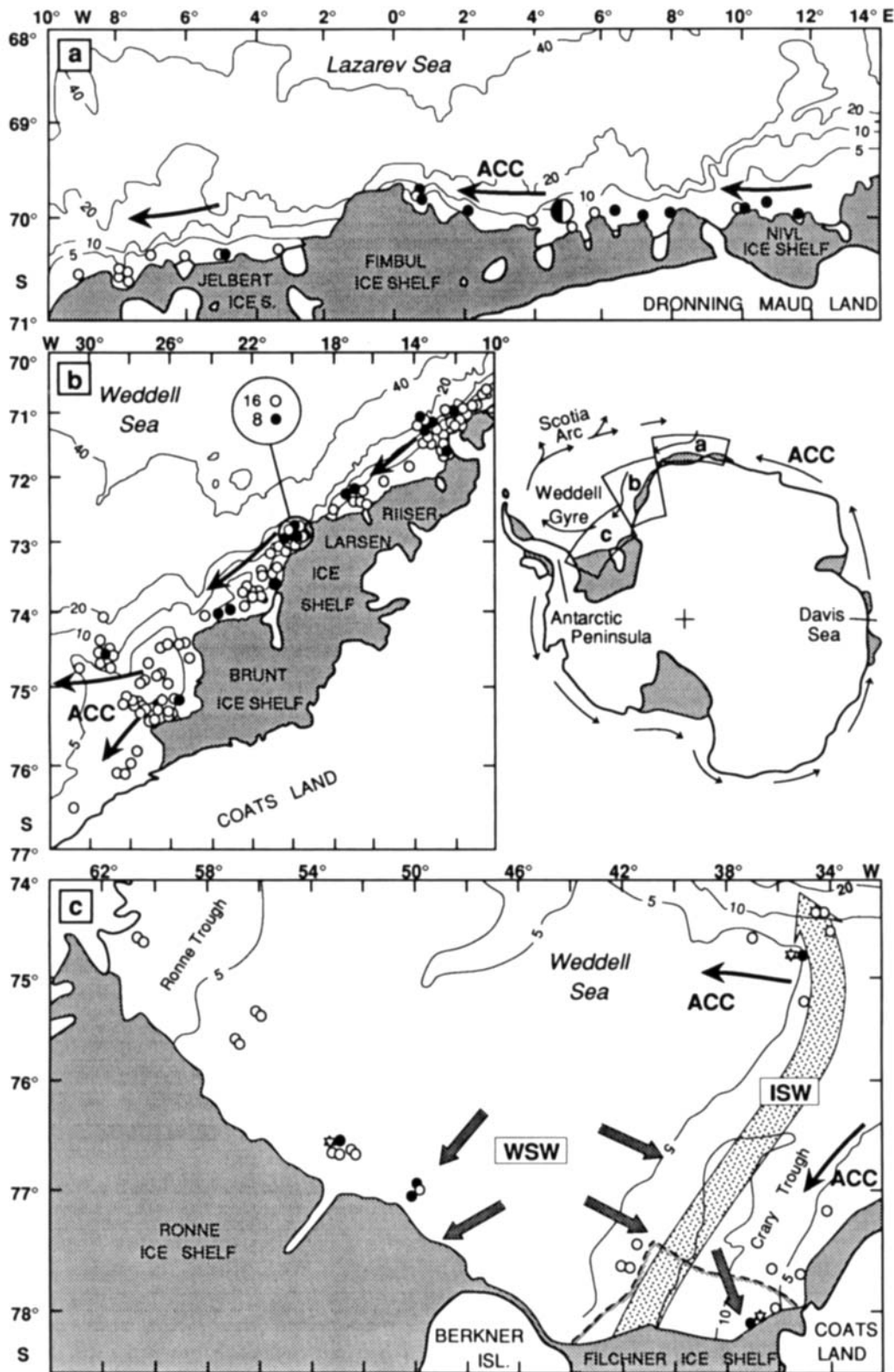
4–6m depth on silty mud benches and near submerged ice cliffs whereas the abundance decreased to 20 specimen m^{-2} at 30m (Stockton 1984, Berkman 1990). Biomass data (wet weight) range between 1600 g m^{-2} in shallow water to 340 g m^{-2} at 30m with the highest biomass values being associated with the bases of ice cliffs (Stockton 1984).

The biology of the limpet *N. concinna* is similar to other subantarctic and Antarctic patellid species, grazing on rocks or macroalgae in littoral areas from the low tide mark to about 60m depth (Dell 1972a, Picken 1984). The maximum depth of occurrence for living *N. concinna* is 110m (Powell 1973). Highest population densities range between 200 and 350 specimens m^{-2} in 1–5m depth at Signy Island (South Orkney Islands) and the Antarctic Peninsula with decreasing densities towards deeper areas (see Picken 1980a for review). Biomass values vary from 8.9 g m^{-2} to 19.7 g m^{-2} dry tissue mass (Picken 1980a).

In 190 benthic trawl samples studied from the Weddell and Lazarev Seas (Fig. 1). *A. colbecki* was found at 37 locations whereas shells of *N.* cf. *concinna* were found exclusively at three locations in the southern Weddell Sea. The problem posed by the shells is that almost all were empty; only one living specimen of *A. colbecki* was obtained (Hain 1992). In this paper we examine four possible explanations for this unusual pattern.

Material and methods

More than 190 benthic Agassiz trawl and bottom trawl samples were recovered in the Weddell and Lazarev Seas during seven cruises of the RV *Polarstern* between 1984 and 1991 (Fig. 1).

Fig. 1. Benthic bottom trawl locations until 1991 of the RV *Polarstern*: **a.** Lazarev Sea, **b.** eastern Weddell Sea, **c.** southern Weddell Sea. Locations containing empty shells of *A. colbecki* = filled circles; living specimen of *A. colbecki* = large, half-filled circle; empty shells of *N.* cf. *concinna* = asterisks. Locations without shells of these species = open circles. Also shown are the general circulation patterns of the Antarctic Coastal Current (ACC), the Western Shelf Water (WSW), and the Ice Shelf Water (ISW). Bathymetric contours are in metres x 100 (after GEBCO 1983). The dashed line in the southern Weddell Sea marks the position of the Filchner Ice Shelf edge until a calving event in austral summer 1986.

Most of the sampling stations are situated on the continental shelf and upper slope, generally close to the ice margins. The mouth openings of the Agassiz and bottom trawls are $3 \times 1m$ and $22 \times 5m$, respectively. Due to the sea ice conditions the employment of the gears could not be standardized; the towing periods varied between 15 and 30 min, the velocities ranged from $1-4$ nm h^{-1}. From these data the areas covered by each of the trawls can be estimated only roughly (Gutt 1988, Voß 1988) and are therefore inappropriate as a basis for calculating average densities of single benthic taxa. More information concerning the sampling procedures can be obtained from the RV *Polarstern* cruise reports of the Antarctic expeditions III/3, V/3, V/4, VII/4, VIII/5 and IX/3 (see Arntz *et al.* 1990, Hain 1992 and references mentioned therein).

The whole trawl samples were roughly sorted and subsamples analysed in more detail aboard RV *Polarstern*. The shells were easily recognised due to their purple-red colour and large size (*A. colbecki*) or because of their limpet shape (*N.* cf. *concinna*). All shells were cleaned mechanically and by use of an ultrasonic water bath to remove epizoic material. The dry weight and the number of shells were determined for each locality.

While the *N.* cf. *concinna* shells were well preserved and hardly damaged the material of *A. colbecki* contained shell fragments. In order to determine the number of *A. colbecki* valves per sample shell fragments with remaining parts of the hinge were counted. Hingeless fragments which obviously (according to shape, size, colour and interlamellar distances of the radial growth increments) did not match with other shell parts from the same sample were also counted as one valve. The original shell heights of fragments were roughly estimated by comparing the sizes of the hinges and auricles, shell thicknesses and convexities of radial growth lines with those of complete valves in order to determine the size range (minimum and maximum height to the nearest 5mm) of valves in the samples.

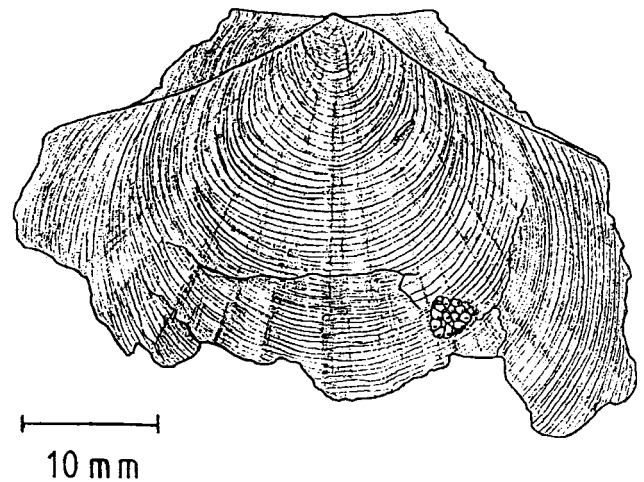All empty shells of *A. colbecki* from the expeditions III/3, V/3,

10 mm

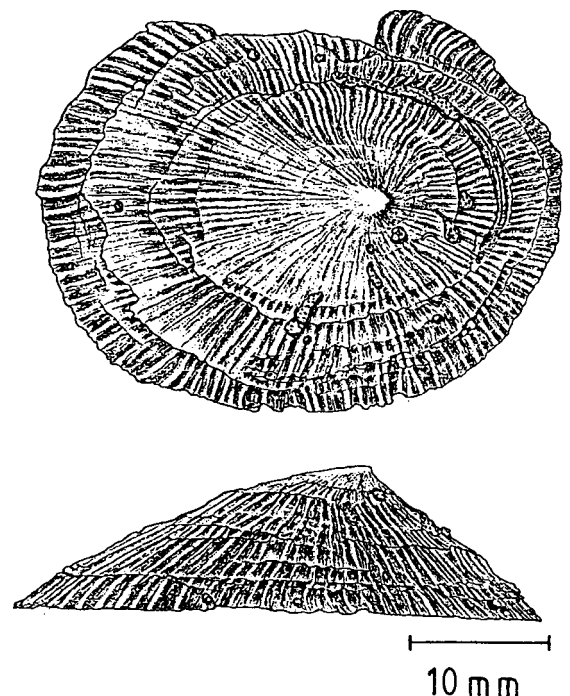**Fig. 3.** Empty valve of *Adamussium colbecki* (Smith,1902) from sampling station 378.

10 mm

Fig. 4. Empty shell of *Nacella* cf. *concinna* (Strebel,1908) from sampling station 738.

V/4, and VI/3 (Table I) were used for ^{14}C age determinations carried out at the ^{14}C laboratory of the University of Kiel. Additionally, preserved material of *A. colbecki* (shells containing tissues) was provided from New Harbor, McMurdo Sound, Ross Sea (coll. J. Lipps) for a reference ^{14}C sample of recent age. For *N.* cf. *concinna* 12 shells from one sampling locality (sta. 738 AGT, Table II) were analysed. To obtain sufficient material (20–25 g) for the analyses, the shells of all localities had to be combined into one sample for each species and ^{14}C-free CO_2 had to be added to the samples to increase the carbon amount analysed. The calculations of the age determination were done with ^{14}C ($^1/_2 = 5568$ years) under consideration of the isotope
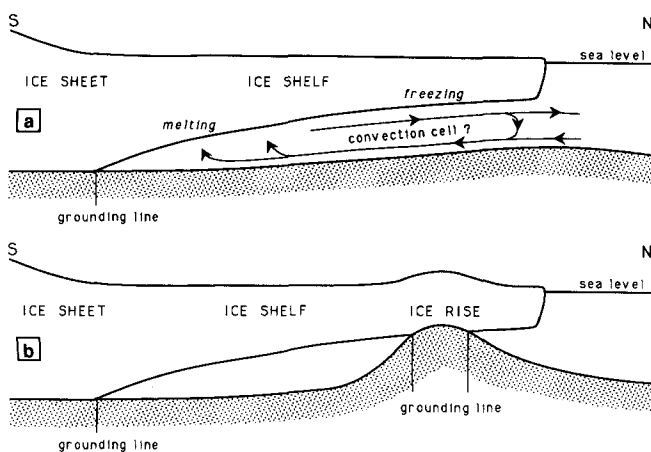

Fig. 2. Schematic S-N sections through ice shelves: **a.** A floating ice shelf with a possible convection cell beneath the ice (after Robin 1979), **b.** An ice shelf grounded at an ice rise near the edge.

Table I. Shell material of *A. colbecki* (AGT = Agassiz trawl, BOT= bottom trawl, EPS = epibenthic sledge).

Station no./ gear	Longitude/latitude	Water depth range (m)	Dry weight (g)	No. of valves	Min/max valve height (mm)	Expedition / ^{14}C analyses (*)
378 AGT	78°12.0'S, 036°54.0'W	843–818	0.2998	3	30–40	VI/3*
403 AGT	76°56.8'S, 049°47.9'W	220–250	0.4145	2	45–50	VIII/5
475 AGT	76°51.4'S, 049°28.3'W	280–281	2.0316	1	75	VIII/5
405 AGT	76°32.0'S, 052°49.4'W	380–390	0.2513	2	40–45	VIII/5
130 BOT	75°16.8'S, 025°53.9'W	600–630	0.3266	1	75	IX/3
226 BOT	75°15.9'S, 025°58.3'W	574–569	0.1654	1	45	VII/4
738 AGT	74°40.6'S, 035°03.8'W	501–500	0.2267	2	35–45	V/4*
250 AGT	74°35.1'S, 029°39.9'W	799–810	1.0093	1	70	VII/4
593 BOT	73°56.3'S, 023°29.3'W	330–340	0.6706	4	20–55	V/3*
592 BOT	73°55.0'S, 022°58.6'W	235–228	0.1614	2	25–40	V/3*
273 AGT	73°43.8'S, 021°03.9'W	197–193	0.6086	3	30–45	VII/4
248 BOT	73°10.0'S, 020°27.0'W	409–410	0.3751	2	35–40	III/3*
247 BOT	73°09.0'S, 020°32.0'W	695–690	0.9686	4	35–75	III/3*
537 BOT	73°05.6'S, 020°14.4'W	430–425	1.0788	2	55–80	V/3*
704 AGT	72°52.6'S, 019°11.9'W	401–402	0.2679	2	40	V/4*
437 EBS	72°51.3'S, 019°21.2'W	390–420	0.2945	3	30–35	VIII/5
615 AGT	72°50.8'S, 019°28.9'W	404–406	0.7877	6	30–65	V/3*
536 BOT	72°50.4'S, 019°36.8'W	551–567	0.2632	1	70	V/3
575 AGT	72°49.6'S, 019°26.7'W	665–573	0.3322	3	40–70	V/3*
271 BOT	72°26.0'S, 017°41.0'W	952–950	0.2382	1	65	III/3*
158 BOT	72°21.8'S, 016°52.1'W	623–539	0.1141	1	70	IX/3
274 AGT	71°38.8'S, 012°09.4'W	196–212	2.7301	14	25–50	VII/4
284 BOT	71°12.0'S, 013°14.0'W	402–412	0.3194	1	60	VII/4
295 AGT	71°08.8'S, 013°48.1'W	2037–2025	0.0911	1	60	VII/4
123 AGT	71°08.8'S, 012°13.4'W	400–405	0.0175	1	65	IX/3
291 BOT	71°06.1'S, 012°33.5'W	499–515	0.1287	1	40	VII/4
162 AGT	70°24.3'S, 004°56.9'W	429–434	2.0824	6	40–80	IX/3
173 AGT	70°00.5'S, 007°08.9'E	228–224	0.2521	1	70	IX/3
179 AGT	69°59.1'S, 008°00.4'E	181–161	0.7433	1	85	IX/3
169 BOT	69°58.9'S, 002°06.3'E	560–450	0.7208	3	45–85	IX/3
211 BOT	69°58.9'S, 005°08.4'E	661–742	3.3564	6	30–75	IX/3
180 AGT	69°57.5'S, 006°19.8'E	282–298	1.3528	1	85	IX/3
207 AGT	69°57.4'S, 011°48.0'E	208–210	0.4580	2	40–50	IX/3
168 AGT	69°47.2'S, 000°52.5'W	447–455	0.0908	1	25	IX/3
206 BOT	69°46.9'S, 010°01.0'E	343–338	7.9005	1	20–90	IX/3
174 BOT	69°43.7'S, 010°44.7'E	432–431	1.9634	3	45–70	IX/3
192 AGT	69°40.3'S, 000°51.1'W	1398–1393	0.2611	2	50–55	IX/3

effect (T_{korr} = T + 16 * δ ^{13}C). The results are corrected to δ^{13}C = 0 $^o/_{oo}$.

Results

For *A. colbecki* 102 shells (= 33.25 g dry weight) were obtained from 11 locations between 160 and 1400m depth in the Lazarev Sea and at 26 locations between 200 and 2000m water depth in the Weddell Sea (Fig. 1; Table I). Seventy percent (n = 26) of all sampling localities (Table I), which provided 78% of the total dry weight and 75 % of the number of valves, were located on the continental shelf. Empty shells of *A. colbecki* were not so common in deeper areas as in the shallower parts. The size of the shells ranged from 20–90mm in height. A single living specimen (height 24.4 mm, wet weight 0.72 g) was obtained at a sampling locality (sta. 211 BOT) in the Lazarev Sea (Fig. 1).

The dating on shell material from both the southern Weddell Sea and McMurdo Sound gave ^{14}C ages between about 300 and 700 years B.P. (Table III).

Shells of *A. colbecki* were also used to identify and classify the Quaternary fossil deposits ('Taylor Formation') at McMurdo Sound, Ross Sea (Speden 1962). The ^{14}C ages obtained on this fossil material ranged between 4620 ± 60 and 6670 ± 220 years B.P. (Stuiver *et al.* 1976). These values were not corrected for the deficiency in ^{14}C in Antarctic waters and hence are between 850 and 1400 years too old (Stuiver *et al.* 1976). Even allowing for this overestimation the ^{14}C ages of the material collected from the Weddell and Lazarev seas are much younger and represent a recent age.

The differences in age between the dead shells of *A. colbecki* and *N.* cf. *concinna* in the Weddell Sea and the fresh shells of *A. colbecki* from McMurdo Sound (Table III) could be explained by incorporation of old CO_2 from glacial melt water in the shells. The natural ^{14}C content of the McMurdo sea-water is in the order of -100 (Δ^{14}C per mil, Michel *et al.* 1979).

Table II. Shell material of *N.* cf. *concinna*.

Station no./ gear	Longitude / latitude	Water depth range (m)	Dry weight (g)	No. of valves	Min /max valve height (mm)	Expedition / [14]C analyses (*)
378 AGT	78°12.0'S, 036°54.0'W	843–818	0.1873	1	22	VI/3
405 AGT	76°32.0'S, 052°49.4'W	380–390	0.8044	1	35	VIII/5
738 AGT	74°40.6'S, 035°03.8'W	501–500	6.3940	13	22–39	V/4*

Nacella cf. *concinna* is less frequent in the samples than *A. colbecki*. Fifteen shells (= 7.39 g dry weight) ranging from 22 to 39 mm length were found exclusively at localities in the southern part of the Weddell Sea (Fig. I). Ten of these showed gastropod (fam. Naticidae or Muricidae) drill holes. The species identification of the dead limpet shells as *N.* cf. *concinna* is not certain because of intraspecific variability of the shell morphology (Berry & Rudge 1973). The shells studied here resemble perfectly the description and figure of *Lepeta depressa* Hedley, 1916. The type specimen of *L. depressa*, a worn dead shell from 240 fathoms off Shackleton Ice Shelf, Davis Sea, was compared by Dell (1972b) with other Antarctic patellid species. He synonymised *L. depressa* with *Patinigera polaris polaris* (Hombron & Jacquinot 1841) known from South Georgia, South Orkney Islands, South Shetland Islands, Paulet Island and Bouvet Island and the Antarctic Peninsula. This name, homonymous to an earlier name, was changed by Powell (1973) to *Nacella concinna* (Strebel, 1908).

Discussion

There are four possible explanations for the origin of the empty shells of the bivalve *A. colbecki* and the gastropod *N.* cf. *concinna* in the Lazarev and Weddell seas:

a) the shells are autochthonous, they belong to populations in the Lazarev and Weddell seas which live on the continental shelf in the areas investigated.

b) the shells are part of fossil marine deposits, e.g. populations of both species had been living in the areas investigated during former glacial/interglacial periods.

c) dead shells (or living individuals) were transported from littoral sites of East Antarctica (*A. colbecki*) or the Antarctic Peninsula/Scotia arc area (*N.* cf. *concinna*) to the Lazarev and Weddell Sea.

d) both species have living populations in areas beneath the adjacent ice shelves that border the Lazarev and Weddell seas and were transported to the open water areas investigated.

The first possible explanation (a), that the shells belong to living, autochthonous populations, is unlikely because of the almost exclusive occurrence of empty shells in the trawl samples. In contrast to the benthic grazer *N.* cf. *concinna*, *A. colbecki* is reported as being a good swimmer (Berkman *et al.* 1991, Stockton 1984). Nevertheless the towing velocities and the mouth openings of the Agassiz and bottom trawls were high or large enough to catch almost all mobile benthic taxa (including demersal fishes) as shown in the general composition of the trawl samples studied (e.g. Arntz *et al.* 1990). Therefore it can be assumed that any living *A. colbecki* would have been sampled when occuring in autochthonous populations in the investigated area.

The autecological information on *N.* cf. *concinna* and *A. colbecki* also argue against hypothesis a. Highest population densities are reported for both species in water depths of 1–6 m (*A. colbecki*; Stockton 1984, Berkman 1990 and *N. concinna*; Picken 1980a for review) with rapidly decreasing densities

towards deeper areas. The shallowest sample containing shells of *N.* cf. *concinna* is situated off the Ronne Ice Shelf in a water depth of 380m which is well below the deepest occurrence reported for living specimens (110m, Powell 1973). In contrast, the depth range covered by the studied shells of *A. colbecki* (161–2037m) coincides approximately with the range given by Dell (1990) for living specimens (4–1380m) and lays well in between that for empty shells (200–2840m). However, for living specimens of *A. colbecki* obtained by benthic trawls, such as the single specimen from sta. 211, it can not be excluded that they were caught during swimming in the upper water column. This behaviour has often been observed for this species (e.g. Berkman *et al.* 1991, M. G.White, personal communication 1992).

The second hypothesis (b) assumes that the shells of *A. colbecki* and *N.* cf. *concinna* represent fossil marine deposits exposed by marine erosion. This suggestion is disapproved by the ^{14}C dates which substantiate a recent age for both species. In addition, geological investigations have shown that since the retreat of the grounded ice masses from the continental shelf edge, which in the southern Weddell Sea started about 14000–13000 years B.P. (Melles 1991), the continental shelves are characterized by accumulation rather than erosion. The sedimentation rates on the Weddell Sea shelf range between 1 and 7 cm ka[-1] (Elverøi & Roaldset 1983, Grobe 1986). On the uppermost continental slope they are even higher and reach 15 cm ky[-1] in the southern Weddell Sea (Melles 1991).

For the third hypothesis (c) large numbers of empty shells or living specimens of *A. colbecki* have to be transported over at

Table III. Results of the ^{14}C age determination on empty shells from the Weddell Sea and on shells taken from living specimens from McMurdo Sound.

Species	Locality	$\delta^{13}C$ (%oo)	[14]C age (BP ± 1SD)
A. colbecki	Weddell Sea	+ 0.7	300 ± 100
N. cf. *concinna*	Weddell Sea	+ 1.5	460 ± 100
A. colbecki	McMurdo Sound	+ 1.8	670 ± 55

least 3500 kilometres from the Davis Sea (Fig. 1), the nearest known place with living littoral populations (Egorova 1972, 1985), into the Lazarev and Weddell Seas. One mechanism of transport could be by anchor ice which can trap benthic living animals as well as sediment and incorporate this material in sea-ice when it detaches from the bottom substrate and floats to the surface (Dayton *et al.* 1969). Dell (1972b) explained the occurrence of empty shells of *N. concinna* far from where they live by transport of shell material via floating ice. However, both multi-year sea ice and sea ice containing sediment was hardly observed in the Weddell Sea (Pfirman *et al.* 1990). The distances between the Davis Sea and the investigated areas, therefore, are so large that ice floes will melt faster than they can be drifted westward with the Antarctic Coastal Current (ACC).

The ACC, which flows along the coastline to the west (Fig. 1), could also transport *A. colbecki* in suspension from the Davis Sea to the area investigated. Current velocities of up to >40cm sec^{-1} (Carmack & Foster 1977) may be high enough to keep the shells in suspension, but, because the ACC reaches the sea bottom, transport over a distance of 3500km seems likely to have resulted in the destruction of the fragile shells due to bottom contacts. Since some of the shells were complete and well preserved, this process can be excluded for most of the shells. Additionally, hypothesis (c) cannot explain the occurrence of *N. cf. concinna* shells off the Ronne Ice Shelf. It has to be assumed that these shells were transported from the Antarctic Peninsula or the Scotia arc area which is contrary to the main, clockwise water circulation of the Weddell Gyre (Fig. 1).

The fourth hypothesis (d) assumes that *A. colbecki* and *N. cf. concinna* have living populations underneath the ice shelves of the Lazarev and Weddell seas and that their shells have been transported to the areas investigated in front of the ice margins.

Schematic sections through ice shelves, freely floating or grounded near the edge, are shown in Fig. 2, respectively. The extensions of the floating ice shelves (grounding line to edge) vary by orders of magnitude (several hundred metres or kilometres) but even large ice shelves such as the Filchner/ Ronne Ice Shelf have areas with relatively shallow water of some tenths or a few hundred metres near the ice edge close to the grounding lines of ice rises such as Berkner Island or smaller ice rumples (Fig. 2b). These water depths are much shallower than the general depths at the ice shelf edges (Fig. 1) and could favour the settlement of *A. colbecki* and *N. cf. concinna*. Additional abiotic factors beneath ice shelves create an environment which resembles shallow water areas. For example, the ice/sediment interface close to the grounding line of ice shelves shows similarities in terms of salinity changes to submerged glacier ice cliffs, a habitat where *A. colbecki* is commonly found (Stockton 1984). In addition, the surface sediment at the grounding line consists of a mixture of poorly sorted fine-grained clay and silt as well as coarse-grained sands, gravels and larger boulders (Anderson *et al.* 1983). Such a substrate could be suitable for both *A. colbecki* and *N. cf. concinna*.

The inaccessibility of the marine environment underneath floating Antarctic ice shelves makes this one of the most unknown biota world-wide. The fauna in these remote areas depend on the primary production of the open water in front of the ice shelf and on lateral currents for transport of nutrients and particulate organic matter beneath the ice. The first samples of the benthic fauna living beneath the ice shelf were collected through natural cracks 22–28 km from the open sea, and demonstrated the existence of a rich invertebrate and fish fauna (Arnaud 1975). In contrast, the benthic fauna observed through an ice hole 450 km inland from the Ross Ice Shelf margin was poor, including unidentified molluscan shells, and resembled oligotrophic deep sea faunal assemblages except that the endobenthos was absent (Lipps *et al.* 1979). Nutrient values and metabolic measurements also indicated low activity rates (Azam *et al.* 1979). Although these observations were carried out at only one location the oligotrophic conditions resemble the oligotrophic habitat of *A. colbecki* at McMurdo Sound mentioned by Stockton (1984), Berkman (1990), and Berkman *et al.* (1991).

In contrast with most Antarctic bivalves and gastropods (Hain & Arnaud 1992) *A. colbecki* and *N. cf. concinna* both reproduce by means of pelagic, planktotrophic larvae (Berkman *et al.* 1991, Picken 1980b) allowing them to colonize or recolonize areas in front of or beneath the ice shelf even during former glacial periods (Clarke & Crame 1989, Clarke 1990) when much of the Antarctic continental shelves were covered by grounded ice. Hence, both species would be able to have colonized areas beneath the ice shelves since the beginning of the postglacial ice retreat from the continental shelf edge. Additionally their populations could survive short-term movements of the grounding lines within the Holocene.

The abiotic and biotic factors mentioned above clearly indicate that *A. colbecki* and *N. cf. concinna* could have living populations in refuges underneath the adjacent ice shelves along the coast. This suggestion requires that all shells found in the investigated areas were transported to the north in front of the ice shelves. The single exception is the occurence of both species at sta. 378 in the southern Crary Trough (Fig. 1c). This locality was covered by the Filchner Ice Shelf until a calving event in austral summer 1986 (Fig. 1c). The shells from sta. 378, obtained two years later, have maximum sizes of 40 mm (*A. colbecki*) and 22 mm (*N. cf. concinna*). Based on external shell growth checks Ralph & Maxwell (1977) indicated an age of 6 to 7 years for a 70mm specimen of *A. colbecki* whereas Stockton (1984) reported up to 13 years for the largest observed specimen (95mm). Picken (1980a) calculated c. 21 years for a 41mm specimen of *Nacella concinna* and estimated 30–40 years for the largest specimens (55 mm). Hence, at least some of the shells found at sta. 378 are older than two years and could have been living autochthonously beneath the Filchner Ice Shelf prior to the calving event.

The empty shells of both species from all other stations could have been transported by marine currents. The occurrence of shells in front of the Ronne Ice Shelf (Fig. 1) could be explained by strong tidal currents at the ice shelf edge north and in the west of Berkner Island. Haase (1986) estimated tidal current velocities

of >20cm sec⁻¹ from the grain-size distribution of surface sediments west of Berkner Island. Measurements of the current velocities directly at the ice shelf edge at the Filchner Station presented velocities up to 40cm sec⁻¹ (Robin *et al.* 1983).

The water circulation beneath ice shelves can also be characterized by convection cells (Fig. 2a, Robin 1979). They produce northward flowing very cold water masses due to melting and cooling at the underside of the ice. In the southern Weddell Sea, modification of Western Shelf Water (WSW), which flows beneath the ice from the shallow shelf area off Berkner Island, into supercooled Ice Shelf Water (ISW) is explained by convection cells beneath the Filchner and Ronne Ice Shelves (Carmack & Foster 1975, Foldvik & Gammelsrød, 1988). The ISW flows to the north along the bathymetric contours at the western side of the Crary Trough until it spills over the shelf break with current velocities exceeding 100 cm sec⁻¹ (Foldvik 1986, Fig. 1c). This high velocity ISW flow may explain the occurrence of *A. colbecki* and *N.* cf. *concinna* shells at sta. 738 near the shelf edge of the southern Weddell Sea (Fig. 1c).

The shells of *A. colbecki* obtained in the Lazarev Sea and eastern Weddell Sea (Fig. 1a,b) could have been transported by smaller convection cells to areas in front of the ice shelf edge and further to the west by the Antarctic Coastal Current (ACC). The shells could either accumulate with allochthonous material in inner shelf depressions (Andriashev 1977, Arnaud & Hain 1992) or may be transported to deeper water areas depending on the current velocities and on the shelf and slope topography. The occurrence of *A. colbecki* at sta. 250 *c.* 150km west of the Brunt Ice Shelf (Fig. 1b) could be due to a reduction of the current velocity of the ACC by 40% in the west of 40°W (Gill 1973), promoting a deposition of suspended material.

Beside current transport, another possible mechanism for transporting shells of *A. colbecki* and *N.* cf. *concinna* into the areas investigated is by icebergs. The shells could have been frozen on the ice in the freezing zone of an ice shelf (Fig. 2a) or could have been incorporated together with terrigenous sediment in the grounded ice during advances of the grounding line (Domack 1982). By calving from the ice shelf they could have been transported over larger distances. Nevertheless, a transport over a distance of some thousand kilometres, e.g. from the Davis Sea, is unlikely because icebergs in Antarctica are believed to stay close to the coast for up to five years, allowing the bulk of the sediment to melt out within a few years (Drewry 1986, Ch. 14). On a single occasion since the beginning of ice observations in 1982 a tabular iceberg at Atka Bay (70°30'S, 008°02'W) has been observed with vertical marine sediment enclosures containing small *A. colbecki* shell fragments (S. Kipfstuhl, personal communication 1992). However, the rarity of these events and the common occurrence of *A. colbecki* in the samples investigated indicates that icebergs play a minor role in the transport of *A. colbecki*.

In summary, the best current explanation for the existence and distribution of empty shells of *Adamussium colbecki* and *Nacella* cf. *concinna* in the Lazarev and Weddell seas is that both species

have living populations in refuges underneath ice shelves along the coast. The survival of benthic invertebrate populations in such refuges beneath the ice shelf during the Miocene is also indicated by phylogenetic and zoogeographical studies for several taxa such as isopods and ostracods (Brandt 1991). *A. colbecki* is found commonly all over the area investigated indicating that this species has at least several living stocks beneath the ice shelves of the Weddell and Lazarev seas. The occurrence of *N.* cf. *concinna* exclusively in the southern Weddell Sea indicates much more restricted refuges, probably around Berkner Island and along the southern coast of Coats Land.

Acknowledgements

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