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The cryopelagic meroplankton community in the shallow waters of Gerlache Inlet, Terra Nova Bay, Antarctica

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Abstract: Limited sampling has so far been conducted of the meroplankton community of the high Antarctic, with most research being conducted using vertical hauls in waters > 50 m, and little focused research on the meroplankton community directly under the sea ice (cryopelagic). Here we report the composition of the early summer cryopelagic meroplankton community of the shallow waters of Gerlache Inlet, Terra Nova Bay. A fixed-frame stationary plankton net was deployed *c.* 1 m below the annual sea ice and sampled at *c.* 24 hour intervals over a period of 19 days from mid-November to early December 2006. A total of 173 larvae from the phyla Annelida ($n = 66$), Mollusca ($n = 30$), Nemertea ($n = 4$), Echinodermata ($n = 8$), several *Pleuragramma antarcticum* ($n = 4$) and numerous planulae ($n = 61$) were collected, as well as 265 egg/embryo stages. A mean of 9.1 larvae (SD = 7.3, $n = 19$) and 13.9 eggs/embryos (SD = 20.5, $n = 19$) were found directly below the sea ice in each 24 hour period, and these early life history stages may be subject to the hazards of extensive platelet ice and penetrating ultraviolet radiation. The cryopelagic meroplankton community of shallow water is also compositionally similar to that of deeper waters, suggesting that the 50–0 m plankton tows used in previous research are providing a reliable assessment of the biodiversity of coastal Antarctic meroplankton.

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Key words: embryos, larvae, plankton, Ross Sea, under sea ice

Introduction

In recent years there has been increasing attention paid to the Antarctic meroplankton community, with research conducted in the maritime Antarctic (Stanwell-Smith *et al.* 1999), the Antarctic Peninsula (Shreeve & Peck 1995, Freire *et al.* 2006) and in the Ross Sea (Sewell 2005, 2006, Sewell *et al.* 2006). In contrast to the well studied Antarctic zooplankton (e.g. O'Sullivan & Hosie 1985, Boltovskoy 1999) and ichthyoplankton components (e.g. Efremenko 1985, Kellermann 1989) which can be readily identified to species level, there are few Antarctic invertebrate species whose larvae can be identified using morphological criteria.

A significant step for the identification of Antarctic invertebrate larvae was the production by Stanwell-Smith *et al.* (1997) of "*A field guide to the pelagic invertebrate larvae of the maritime Antarctic*" which described the meroplankton collected during a year-round study at Signy Island (Stanwell-Smith *et al.* 1999). However, unless scientists are using a DNA sequencing approach (Sewell *et al.* 2006, Webb *et al.* 2006), larvae can usually only be identified to higher levels of classification (phyla, class, family) and in quantitative studies are described as morphologically defined operational taxonomic units (OTU, Stanwell-Smith *et al.* 1999) or larval types. DNA bar coding approaches to larval identification are currently limited by cost, the difficulties in achieving consistent amplification from larvae, and the limited availability of adult sequences in the existing DNA databases (Sewell *et al.* 2006, Webb *et al.* 2006). However, with the exception of planula-type larvae which may be derived from several phyla (Cnidarians, Ctenophores or Nemertea, Young 2002) and early developmental stages (eggs/embryos), an experienced invertebrate zoologist can generally assign meroplankton OTUs to a larval type or appropriate taxonomic level to allow quantitative comparisons to be made between locations and/or times.

Quantitative meroplankton studies in Antarctica have generally been conducted using plankton tows that sample over a large depth range, typically 50–0 m, and in the deeper waters of inlets and bays (Shreeve & Peck 1995, Freire *et al.* 2006, Sewell 2005, 2006). With the notable exception of Stanwell-Smith *et al.* (1999), there is little information on the abundance of the meroplankton community in shallow coastal waters or directly under the sea ice. As part of the Latitudinal Gradient Project (LGP, Howard-Williams *et al.* 2006) we have been comparing the meroplankton community at different locations by means of a standard 50–0 m vertically hauled plankton sample (Sewell 2005, 2006, Sewell *et al.* 2006). In the 2006/07 season at the German Gondwana Station in Terra Nova Bay we also deployed a stationary plankton net in the shallow waters of Gerlache Inlet (< 3 m deep). In this paper we had two major aims: firstly, to determine if the shallow water meroplankton community was similar to that seen in the standard 50–0 m vertical plankton samples taken in deeper waters, and secondly to provide a

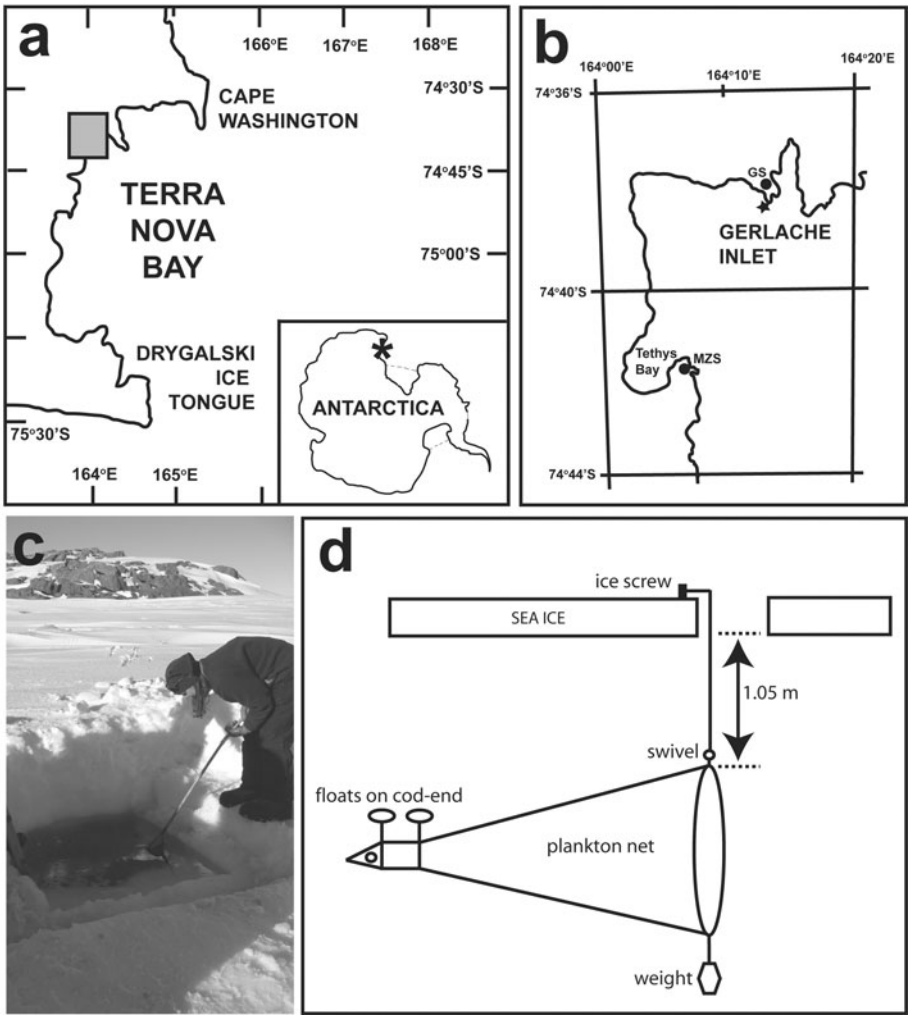

Fig. 1. Location of stationary net for cryopelagic sampling in Gerlache Inlet, Terra Nova Bay. **a.** The Terra Nova Bay region (asterisk) within the Antarctic continent. Shaded square shows location of detailed map of Gerlache Inlet shown in b. **b.** Gerlache Inlet within Terra Nova Bay showing location of Gondwana Station (GS) and Mario Zucchelli Station (MZS) in Gerlache Inlet. Stationary net (star) was located at the end of the point immediately south of Gondwana Station. **c.** Photographic image of sea ice hole excavated for the stationary net, with one of the authors (LS) to the right and the land to the east of Gondwana Station in the background. The excavated hole was initially *c.* 1.5 × 1 m in size. **d.** Schematic of the position of the stationary net under the sea ice. The net was attached to the upper surface of the sea ice with an ice screw and maintained in a vertical orientation with a weight on the bottom of the net and several floats attached to the cod-end. Diagram is not to scale.

qualitative determination of the frequency of eggs/embryos/larvae in the cryopelagic water column of Gerlache Inlet.

The term cryopelagic, which was originally defined for epipelagic fish (Parin 1968, Andriashev 1968, 1970) is now used more generally to describe the community associated with the bottom of the sea ice and the platelet layer; dominant members include copepods, amphipods, polychaetes, adult and larval stages of euphausiids and *Pagothenia borchgrevinki*, other larval and juvenile fish and some benthic invertebrate larvae (Bradford 1978, Knox 2006). In the context of this paper we refer to the cryopelagic meroplankton community as the meroplankton that was collected within 1–2 m of the annual sea ice during a 24 hour period. This is not meant to imply that at other times and/or locations these larval forms are not found at other depths in the water column. Our interest in the cryopelagic meroplankton is because recent experimental studies have shown that early developmental stages can be vulnerable to penetrating ultraviolet radiation (Karentz & Bosch 2001, Karentz *et al.* 2004, Lesser *et al.* 2004, 2006), yet there is currently little information on the prevalence of these stages immediately below the sea ice.

Methods

Cryopelagic plankton samples were collected with a 0.5 m diameter circular fixed-frame plankton net (125 µm mesh) placed in an expanded seal hole on the eastern point of Gondwana Station (74°38.288'S, 164°13.570'E) in Gerlache Inlet, Terra Nova Bay, Antarctica (Fig. 1). The initial seal hole was located at the transition between the annual sea ice adjoining the land and the sea ice proper; expansion of the seal hole to hold the net was achieved using a chainsaw and ice axe (Fig. 1c). The chosen location was in shallow water (2.6 m deep) overlaying a cobble/coarse gravel bottom. The sea ice immediately above the plankton hole was reduced in thickness (0.35 m) in comparison to the adjacent areas where the sea ice was > 2 m thick. Extensive snow cover prevented light penetration under the ice; on sunny days light measurements in the area adjacent to the plankton hole were in the range of 0.3 to 1.1 micro-einsteins (unpublished data).

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Table I. Larval and egg/embryo types from a stationary net collecting cryopelagic meroplankton in the shallow waters of Gerlache Inlet. Numbers represent number of larvae collected over an approximately 24 hour period. Total = number of larvae collected over the 19 days of sampling. No. of days recorded = no. of days when that larval type is present. % days recorded = percentage of the 19 days that larval type is present. Shading shows that larval type was also present in samples collected on that date in the standard 50–0 m sampling (3 vertical tows combined) at > 50 m depth (deep).

		November 2006														December 2006					Cryopelagic summary		
		17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	Total	No. days recorded	% days recorded
Larval types																							
Annelida	Polychaete ≤ 2 setiger*	2	1					1	1	4		5	4	1			4		1		24	10	52.6
	Clear trochophore		2	3	2	1	2		1	1	1	1	3					3	1	1	22	13	68.4
	Yellow trochophore	1	2				1					3	1	1	1			6	2	1	19	10	52.6
	Brown trochophore		1																		1	1	5.3
Mollusca	Nudibranch veliger		2			1				1			1			1		1	1		8	7	36.8
	Tiny molluscan veliger					1					1	3	2	4			2	3	3	1	20	9	47.4
	Green molluscan veliger															1					1	1	5.3
	Nudibranch juvenile																		1		1	1	5.3
Nemertea	Elephant trunk pilidia					1	1	1		1											4	4	21.1
Echinodermata	Bipinnaria	1		1		1		1					2						2		8	6	31.6
Planula**		2			1				4	9	2	3	6	2		5	1	6	15	5	61	13	68.4
Pleuragramma antarcticum																		1	3		4	2	10.5
Total larvae		6	8	4	3	5	4	3	6	16	4	15	19	8	1	7	7	20	29	8	173	19	100
Eggs/embryos	Polychaete embryo	3	4	1			4	7	5	3	1	3	3	4		2		1			41	13	68.4
	Other eggs/embryos	7	10	3	9	93	13	6	3	2	8	9	19	26	5	2	2	4	2	1	224	19	100
Total eggs/embryos		10	14	4	9	93	17	13	8	5	9	12	22	30	5	4	2	5	2	1	265	19	100

* Polychaete ≤ 2 setiger includes metatrochophores; ** Includes numerous forms

The plankton net was deployed 1.05 m below the water surface and attached to the overlaying ice with a rope and ice screw (Fig. 1d). A swivel at the point of attachment of the net to the rope allowed the net to orient to the direction of the prevailing currents, and a diametrically opposed 2 kg weight ensured that the net remained perpendicular to the surface sea ice (Fig. 1d). Net buoyancy of the cod-end was regulated with the addition of three small fishing floats (Fig. 1d). Low current flows were observed at this location, predominantly into Gerlache Inlet from the east (Fig. 1b).

The net was installed on 16 November 2006 and cleared at *c*. 24 hour intervals for 19 consecutive days. The sample collected in the cod-end was transferred to a 600 ml plastic container and, after rinsing any remaining contents into the collection container, the cod-end was reattached and the net redeployed. Plankton samples were sorted live under binocular microscopes using standard Bogorov trays and identified to OTU following the procedures used in previous meroplankton research (Sewell 2005, 2006, Sewell *et al.* 2006). Digital photographs of collected meroplankton were taken in glass depression slides at 40× or 100× with an Olympus 4040 digital camera.

The companion series of 50–0 m vertical tows were conducted with a collapsible plankton net in the deeper waters of Terra Nova Bay (sampling location: 74°38.474'S, 164°12.473'E). A 40.6 cm (16") hole was drilled through the 2.5 m thick sea ice and three replicate meroplankton samples were collected on each sampling day using a vertical haul that sampled from 50 m to the surface (see details in Sewell 2005, 2006).

Results

Over the 19 days during which the stationary net was deployed a total of 173 larvae and 265 eggs or embryos were collected from the cryopelagic water column *c.* 1 m below the sea ice (Table I). An average number of 9.1 larvae (SD = 7.3, $n = 19$) and 13.9 eggs/embryos (SD = 20.5, $n = 19$) were collected per 24 hour period, and there were no days when meroplankton representatives were absent (Table I).

The majority of the larvae could be identified at least to the phylum level, with the exception of the planulae which might

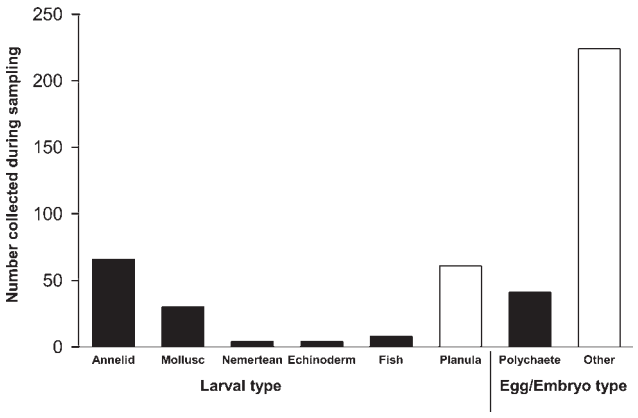

Fig. 2. Frequency of larval and egg/embryo types attributed to phyla (black bars) and to unknown phyla (white bars). A total of 173 larvae and 265 eggs were collected during the 19 days of sampling.

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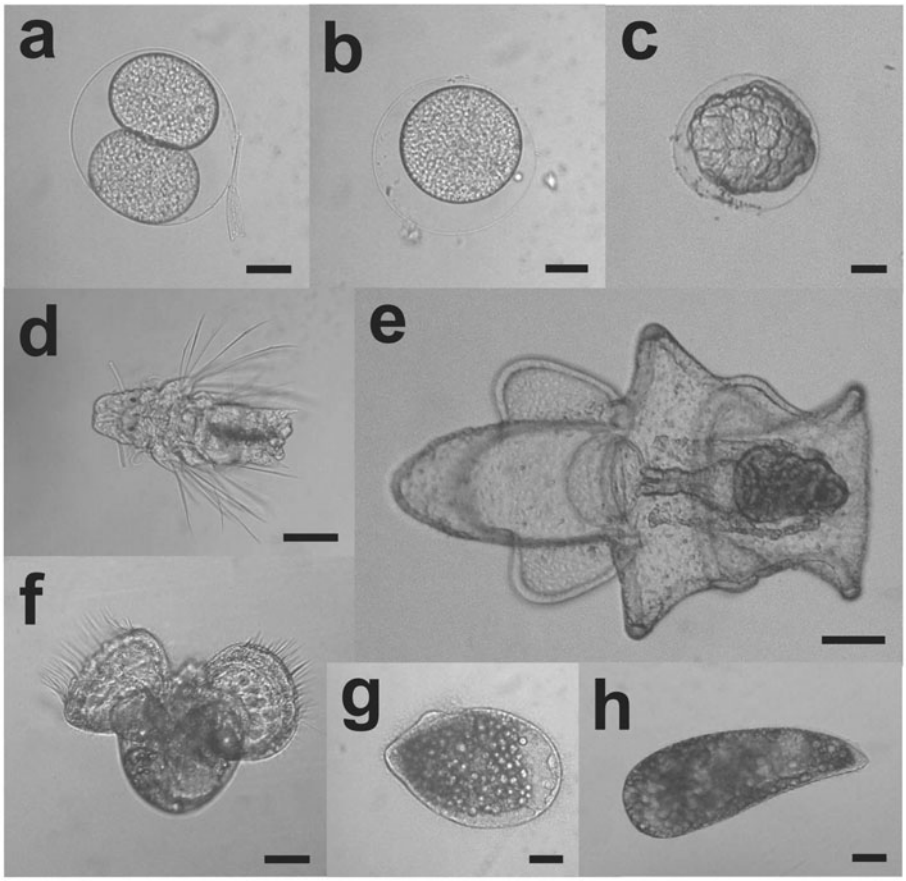

Fig. 3. Photomicrographs of representative cryopelagic meroplankton collected from the shallow water under ice plankton net. **a.** A 2-cell embryo *c.* 180 micron diameter, similar to the sea urchin *Sterechinus neumayeri*. Scale bar = 50 µm. **b.** A 145 micron diameter embryo within a fertilization membrane. Scale bar = 50 µm. **c.** A more advanced embryological stage of b. Scale bar = 50 µm. **d.** A 2-setiger polychaete larva. Scale bar = 100 µm. **e.** A large bipinnaria larva. Scale bar = 100 µm. **f.** Tiny molluscan veliger. Scale bar = 50 µm. **g.** Planula similar to Stanwell-Smith *et al.* (1997) Fig. 7. Scale bar = 50 µm. **h.** Pink speckled planula. Scale bar = 50 µm.

be derived from a number of phyla (Cnidaria, Ctenophora, Nemertea, Young 2002; Table I, Fig. 2). 85% of the eggs/embryos collected could not be assigned to phyla and the OTUs are combined as a category "Other eggs and embryos" (Table I, Fig. 2). The remaining 15% of embryos ($n = 41$) were identified as being polychaete embryos based on their distinctive morphological features (sculptured egg case, green embryo colour) and previous DNA sequencing (Sewell *et al.* 2006).

The larval meroplankton was dominated by representatives of the phylum Annelida (Table I, Fig. 2). These 66 larvae were post-hatch developmental stages, and defined as four OTUs: three trochophore OTUs, and a single OTU (≤ 2 setigers) that combined the rare metatrochophores with the later stage polychaete larvae with < 2 segments (Table I, Fig. 3d). At least one annelid larval form was found on 18/19 days (Table I), with the three dominant forms ($\leq$ 2 setiger, clear and yellow trochophores) being abundant in the standard vertical 50–0 m vertical plankton tows (Table I).

Planulae were the next numerically dominant larval component, comprising 35.3% of the collected larvae (Table I, Fig. 2). Based on colour and size at least 14 different planula OTUs were identified from the cryopelagic water column (Fig. 3g & h). As each OTU was rare, these have all been combined in a single larval type ("Planula") in Table I. Planulae were present on 13/19 sampled days in the stationary net sampling shallow waters, but were less common and diverse in the standard vertical 50–0 m vertical plankton tows (Table I, unpublished data).

Molluscan veligers, representing three OTUs, were present on $>$ 50% of the 19 sampled days, and a single nudibranch juvenile was observed in early December (Table I). Increased numbers of a tiny molluscan veliger (Fig. 3f) were seen in early December at the same time as this larval type increased in the 50–0 m vertical hauls in deeper waters (Table I). Only the rare green molluscan veliger collected on a single occasion (1 December) was absent from the standard vertical 50–0 m vertical plankton tows (Table I).

The remaining larval OTUs were a large nemertean pilidia, found as single individuals on 4/19 sampling days, asteroid bipinnaria (Fig. 3e) found on 6/19 sampling days, and four larval Antarctic silverfish *Pleuragramma antarcticum* found on two days during early December (Table I). All these larval types were commonly collected in the standard vertical 50–0 m vertical plankton tows (Table I).

Eggs and embryo stages of undetermined phyla were numerically dominant in the meroplankton community (224 of 438 = 51.1% of collected meroplankton, Table I, Fig. 2). High day-to-day variability was observed in the

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numbers of these early life stages, often due to large numbers of an OTU appearing in the plankton samples. For example, 84 of the 93 egg/embryos collected on 21 November were recently fertilized 145 µm eggs (Fig. 3b). Large numbers of this egg/embryo stage were also present in the 50–0 m sampling on 21 and 23 November, suggesting a spawning event in Gerlache Inlet. This form was absent from stationary net samples until 27 November when a single embryo of the same colour and size was found (Fig. 3c).

Two-cell and four-cell embryos with a diameter (180 µm) and colour similar to *Sterechinus neumayeri* (based on in-laboratory spawnings and DNA sequencing, MS: unpublished data, Sewell *et al.* 2006) were also collected on 22 November.

In addition to the meroplankton community, the stationary net collected unquantified numbers of copepods and other macrozooplankton (e.g. cnidarian medusae, ctenophores, appendicularians), and amphipods from the cryopelagic community (mean ± s.e.: 54.95 ± 8.64 amphipods per 24 hr period, range 14–135, $n = 19$). The dominant macrozooplankton were two pteropods: the predatory *Clione antarctica* and its prey, the phytoplankton-feeding *Limacina helicina* (Knox 2006). An average of 111.2 *Limacina helicina* (s.e. = 20.8, range 5–325) and 7.1 *Clione antarctica* (s.e. = 2.0, range 0–39) collected over each 24 hour period. There was no correlation between the pteropod numbers and the total no. of larvae (correlation coefficients, $n = 19$: *Limacina* r = 0.155; *Clione* r = -0.264, n.s.) or eggs/embryos collected (correlation coefficients, $n = 19$: *Limacina* r = -0.071; *Clione* r = 0.025, n.s.).

Comparison of shallow and deep water plankton sampling

Detailed statistical comparison of the meroplankton community in the shallow waters of Gerlache Inlet with that in deeper waters is problematic as there are confounding variables in this contrast. Specifically, a shallow versus deep comparison is confounded by sampling method (stationary net, vertical haul), net characteristics (0.5 m diameter, 125 µm mesh; 0.28 × 0.28 m square, 100 µm mesh) and the time over which samples were collected (24 hours, *c*. 15 min).

The approach that we have used to compare the shallow versus deep meroplankton communities is to look at the presence/absence of a particular larval type at the two locations. For this comparison, the three replicate 50–0 m tows were pooled from the deep site and sampling days when the larval types co-occur are shown in Table I by a shaded cell. Three trends are apparent (Table I): firstly, that there are some OTUs that are collected every day at the deep site - clear trochophore, yellow trochophore, elephant trunk pilidia, polychaete embryo, combined eggs/embryos. Secondly, that there is only one OTU, green molluscan veliger, that is found at the shallow site, but absent from the deep site. Thirdly, that the rare larval OTUs - brown trochophore, nudibranch juvenile - are found at both shallow and deep sites, but on different sampling days. The remaining larval OTUs/types are found at both locations in the late November–early December period.

To test for the independence of the presence/absence of larval OTUs/types at the shallow and deep sites, we used a simple χ^2 test. A 2 × 14 frequency table was constructed based on the information in Table I of the number of the 19 days that each larval type was found at the deep and shallow sites respectively. The calculated χ^2 value of 18.85 at 13 df is non-significant. Some of the expected frequencies in this test were, however, < 1 (brown trochophore, green molluscan veliger, nudibranch juvenile). To avoid the frequency of any cell exceeding 19 (the maximum number of sampling days) these frequencies were included in polychaete ≤ 2 setiger, tiny molluscan veliger and nudibranch veliger respectively. The revised χ^2 value of 17.01 at 10 df is also non-significant, showing the compositional similarity of the meroplankton in both the shallow and deep waters of Gerlache Inlet during late November–early December.

Discussion

In this, the first meroplankton study to focus on the cryopelagic environment in the shallow waters of the high Antarctic (*sensu* Hureau 1994) we have shown that there is significant diversity in the embryo and larval forms found immediately below the annual sea ice. Although this is only a semi-quantitative study as no flow-meter was attached to the net, the results are important in two ways: firstly, they indicate that a diverse meroplankton community is found in the cryopelagic environment immediately below the sea ice, and secondly, that the meroplankton community of shallow waters is compositionally similar to that found in deeper waters. This suggests that our standard 50–0 m sampling in deeper waters is generally indicative of the diversity of the Antarctic coastal meroplankton community.

While previous studies have reported advanced larval forms directly below the sea ice (*Odontaster*: Pearse & Bosch 1986, Stanwell-Smith & Clarke 1998; *Sterechinus*: Bosch *et al.* 1987; > 1 larval form: Tanimura *et al.* 1984, Stanwell-Smith *et al.* 1999), this is the first study that directly reports the presence of large numbers of eggs/embryos in the cryopelagic environment. Echinoderm gastrulae were collected by Stanwell-Smith *et al.* (1999) in the under-ice meroplankton at Signy Island; however, as the surface and demersal tows were pooled in the analyses it is unclear where these gastrulae were found in the water column.

The presence of large numbers of larvae and eggs/embryos in the Gerlache Inlet cryopelagic environment during the early summer is particularly interesting in a physiological sense due to the potential dangers posed by extensive platelet ice (personal observation), and penetration of ultraviolet radiation (UVR) through the sea ice (Lesser *et al.* 2004, 2006). Although the extensive snow cover at this location reduced light penetration, and presumably UVR, fertilized eggs and embryos found 1 m

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below the sea ice may, if resident at this depth for extended periods, be subject to DNA damage and developmental abnormalities (Karentz & Bosch 2001, Karentz *et al.* 2004, Lesser *et al.* 2004, 2006). It would, therefore, be of interest to determine the vertical distribution and time that meroplankton spend in the cryopelagic environment/upper water column subject to these environmental conditions.

The second major finding of this study is of procedural importance to our ongoing meroplankton sampling with the LGP. To provide comparative information on the meroplankton communites at different latitudes we have been sampling at sites that are *c.* 1 km from shore, in water depths > 50 m, and with complete sea ice cover (Sewell 2006). While a quantitative comparison between the shallow water stationary net and the standard 50–0 m sampling was not the intention of this study, the similarity of composition between the two locations suggests that the Antarctic coastal meroplankton community is being sampled effectively by our standard methods (Sewell 2005, 2006, Sewell *et al.* 2006).

Interestingly, however, the one component of the meroplankton community that was more diverse in the shallow waters of Gerlache Inlet - the planulae - was also the most diverse OTU in the shallow waters (6–28 m) of Signy Island (Stanwell-Smith *et al.* 1999), but not reported by Freire *et al.* (2006) in sites of 15–60 m depth in Admiralty Bay, King George Island. The higher diversity and numbers of planulae seen in the stationary net sampling reported here is most probably a result of the extended period of time/water volume sampled (24 hours cf. 15 min) which would increase the probability of collecting some of the rarer representatives of the meroplankon. Therefore, to get a complete assessment of patterns in biodiversity of planulae, or other rarer forms in the Antarctic meroplankton, in addition to short-term vertical hauls (Sewell 2005, 2006, Sewell *et al.* 2006), focused long-term sampling may also need to be conducted in nearby shallow waters.

While this study has investigated Antarctic biodiversity using an OTU approach it is recognized that true levels of Antarctic meroplankton biodiversity will only be revealed if we can overcome the considerable constraints of identifying larvae to the species level. Two recent studies have shown that a DNA bar coding approach can be useful in identifying Antarctic larvae to lower levels of classification, and in a few cases to species (Sewell *et al.* 2006, Webb *et al.* 2006). However, DNA bar coding is not a panacea for studies of meroplankton biodiversity, which the Working Group on Zooplankton Ecology (2005) has recognized as being "not well studied either by the zooplankton or the benthic ecologists" (ICES 2005, p. 5). Four major areas of difficulty can be highlighted - some intrinsic to larval studies in general, and others more specifically related to the study of Antarctic meroplankton.

Firstly, many invertebrate larvae show phenotypic plasticity, with differences in larval morphology in relation to environmental conditions (e.g. sea urchins, Sewell *et al.* 2004). Thus, defining morphological criteria for species identification can be difficult. Secondly, as many Antarctic species have long developmental times (e.g. Pearse & Bosch 1986, Bosch *et al.* 1987) numerous larval morphotypes can be present with the same DNA sequence (Sewell *et al.* 2006). Extensive plankton sampling and DNA sequencing is thus required to record all developmental stages of a single species (Sewell *et al.* 2006). Thirdly, larval morphological features are best revealed with formalin fixation, while reliable DNA sequencing generally requires ethanol preservation (but see Kirby & Reid 2001). Fourthly, there are still technical difficulties associated with DNA bar coding of Antarctic larvae, with low rates of amplification and differences in success rates for different gene primers, and a major limitation being the availability of Antarctic adult DNA sequence in the databases (Sewell *et al.* 2006, Webb *et al.* 2006).

Future research on meroplankton will be aided by the Census of Antarctic Marine Life (CAML, www.caml.aq) initiatives in bar coding Antarctic benthic and pelagic biota, and the subsequent development of genetic tools such as "phylochips", species-specific primers and Q-PCR (Webb *et al.* 2006). However, as meroplankton communities reflect the benthic diversity from which they are derived, and both change greatly between Antarctic regions (Sewell 2006), a combination of traditional quantitative studies together with the application of genetic tools will be vital to answer questions such as Thorson's Rule (see Pearse & Lockhart 2004) in non-traditional phyla (i.e. outside the prosobranch gastropods and the echinoderms) and more completely understand bentho-pelagic coupling, recruitment processes and functioning in Antarctic marine ecosystems.

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