Distribution of meroplankton communities in the Bransfield Strait, Antarctica

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ABSTRACT: The spatial distribution of meroplankton in Bransfield Strait, Antarctica, and its relationships with hydrographical conditions are described. Biological sampling was carried out with BIONESS sampling gear at 19 stations and at 5 depths between 10 and 300 m. The main hydrographic features were a shallow hydrographic front in the southern part of the strait that separates Transitional Zonal Water with Bellingshausen influence (TBW) from Transitional Zonal Water with Weddell influence (TWW) and a slope front, the so-called Bransfield front, along the South Shetland Islands Slope (SSI). A northeastward baroclinic jet known as the Bransfield Current (BC) originates from this slope front. The meroplankton community was very diverse and included 12 types of larvae, dominated by polychaete and echinoderm larvae. The meroplankton were more abundant closer to the SSI in the BC and decreased in number towards the Antarctic Peninsula. Polychaete larvae were found close to both shores but mainly close to the SSI in TBW; they were very sparse in the central basin, appeared again below 100 m depth in TWW, and increased in abundance in upper layers at stations between the hydrographic front and the Antarctic Peninsula, in TWW. By contrast, echinoderm larvae mainly occupied the central basin and were always associated with the upper 100 m in TBW, just above the polychaete larvae; they were almost absent from TWW. In summary, meroplanktonic larval exhibit a strong dependence on water masses, depth, and fronts.

KEY WORDS: Meroplankton · Bransfield Strait · Antarctica · Invertebrate larvae · Distribution · Hydrography

INTRODUCTION

Different views of Antarctic marine invertebrate biology have been proposed since the end of the 19th century (reviewed in Arntz & Gili 2001). It was believed that Antarctic marine invertebrates developed adaptations in response to low temperatures and strong seasonality in an area where primary production is reduced to a short period during the austral summer. Low metabolic rate, slow growth rate, longevity and gigantism were among the strategies proposed. In terms of reproduction, strong seasonality with delayed first maturity, low fecundity, large eggs and non-pelagic larval development were considered as adaptations to Antarctic environmental conditions (Arntz & Gili 2001, Poulin et al. 2002). However recent studies of Antarctic meroplankton have revealed a relatively high diversity and abundance of larval forms of benthic marine invertebrates (Arntz & Gili 2001, Sewell 2005).

Despite the general acceptance that, at least in some phyla, there exists a high proportion of Antarctic marine invertebrates with pelagic development, few studies have focused on the distribution of meroplankton in the Southern Ocean. Exceptions are: a 2 yr study by Stanwell-Smith et al. (1999) at Signy Island, where 131 morphologically distinct larval forms were collected throughout the year, and a study of the distribution of pelagic larvae of benthic marine invertebrates.
in the Bellingshausen Sea, by Shreeve & Peck (1995), in which 16 larval and juvenile types, representing 7 phyla, were reported. Very recently, Freire et al. (2006) reported seasonal variation in invertebrate larvae in Admiralty Bay in King George Island.

In addition, some other authors have described or quantified the meroplankton community—Ross Sea: Foster (1987, 1989a,b, 1991), Sewell (2005); Antarctic Peninsula, Ross Sea and Terre Adélie: Bhaud et al. (1999); eastern Antarctica: Tanimura et al. (1986); Ellis Fjord near Davis station: Kirkwood (1993).

The Bransfield Strait is a semi-enclosed Antarctic sea located between the South Shetlands Archipelago and the Antarctic Peninsula (see Fig. 1). It can be divided into 3 major basins—western, central, and eastern—separated from each other by sills shallower than 1000 m. The basic circulation pattern consists of a western inflow of relatively warm and fresh water from the Bellingshausen Sea, the Gerlache Strait and the Circumpolar Current, and an eastern inflow of relatively cold and salty water from the Weddell Sea (Grelowski et al. 1986, Hoffmann et al. 1996, García et al. 2002, Zhou et al. 2006). Following Tokarczyk (1987), Garcia et al. (1994) named these water masses as Transitional Zonal Water with Bellingshausen influence (TBW), and Transitional Zonal Water with Weddell Sea influence (TWW). TBW flows northeastwards along the northern half of the Strait whereas TWW circulates southwestwards along the southern half of the Strait. Both water masses are separated by a shallow hydrographic front. This front has also been observed in both the Western Basin (Garcia et al. 2002) and in the Eastern Basin of the Bransfield Strait (López et al. 1999). A second front, the so-called Bransfield front, has also been observed in this region. This is a slope front that is located along the southern South Shetland Island slope and that separates TBW from the waters on the shelf of the archipelago (García et al. 1994). There is a baroclinic jet associated with this slope front, which is known as the Bransfield Current (BC) (Niiler et al. 1991, Zhou et al. 2002, Zhou et al. 2006), and which circulates northeastwards along the southern South Shetland Island slope. Zhou et al. (2006) suggested that this current could be viewed as a narrow western boundary current where a southwestward wind-induced flow would return northeastwards as a consequence of the blockage in the topography.

The present study describes the vertical and horizontal distribution of the pelagic larvae of benthic marine invertebrates at 19 stations along the Bransfield Strait, Antarctica, and their relationships with hydrographical conditions. Meroplanktonic organisms are subject to passive transport processes and therefore knowledge of the hydrography of the area is required to enable interpretation of the observed distribution patterns.

**MATERIALS AND METHODS**

Plankton sampling. Plankton sampling was carried out along 4 transects (T), each separated by 20 nautical miles, in the Bransfield Strait (Fig. 1), between the Antarctic Peninsula and the South Shetland Islands. Sampling was carried out between 30 December 2002 and 7 January 2003, from the RV B.I.O. (Buque de Investigación Oceanográfica) ‘Hespérides’, as part of a project in which the mesoscale vortices in the central basin of Bransfield Strait and the physical–biological coupling were studied. T1, T2 and T4 included 4 stations each separated by 20 nautical miles. T3 was sampled at a finer spatial scale, with 7 stations each separated by 10 nautical miles (n miles).
The sampling gear was a multinet (BIONESS, Open Seas Instrumentation), which consists of a quadrangular 1 m² frame with 5 double nets. Mesh sizes for the inner and outer nets (including cod ends) were 250 µm and 80 µm, respectively. Standard procedure was to lower the net below the maximum sampling depth for the station, and to make an oblique ascending tow, opening the nets at the desired depth ranges: 300–200, 199–100, 99–70, 69–40, 39–10 m. Samples were not collected between the surface and 10 m because the turbulence created by the vessel could have damaged the delicate nets. Towing speed was approximately 2 knots. The mean tow duration was 5 min 48 s ± 1 min 34 s (SE), thus approximately 250 m³ of seawater were filtered per depth interval (mean swept water volume = 252.72 ± 61.73 m³ SE). The larval counts for each tow were therefore corrected to a standard sampling volume of 200 m³.

Hydrographic sampling. Along each transect CTD stations were combined with XBT (expendable bathythermograph) stations to obtain a 5 n mile resolution in the temperature field and hence to resolve the spatial variability close to mesoscale, since the mesoscale in the Southern Ocean is smaller than 10 n miles (Huntley & Niiler 1995, Zhou et al. 2006).

The mean distance between CTD stations was 10 n miles. At every 2nd CTD station in T1, T2, T4, and each CTD station in T3, plankton were sampled with a BIONESS multinet. These station were designated coupled stations (Fig. 1).

A Neil Brown Mark III CTD was used. Temperature and salinity were calibrated with readings from a digital reversible thermometer and with water samples in which salinity was measured with a Portasal salinometer. Temperature was accurate to 0.001°C and salinity to 0.003‰. Prior to the launching of each XBT, temperature was calibrated with the temperature reading on a digital thermometer held in a bucket of water. Several joint profiles of CTD and XBT were constructed to verify the readings registered by the XBT. The relative geostrophic velocities to 500 dbar for the BC ranged from 0.17 m s⁻¹ at T4 to 0.26 m s⁻¹ at T3. These values are of the same order of those reported by Grewloski et al.

RESULTS

Hydrography

The vertical distributions of potential temperature, salinity and density anomalies along T3 are shown in Fig. 2. The TBW was easily recognised by the well stratified, warmer and saltier water mass that lies over the homogeneous colder and saltier TWW. These water masses are separated by a 0.3°C isotherm, a 34.4 psu isohaline and a 27.65 kg m⁻³ isopycnal. At the southern part of the transect, the TWW reaches the surface and defines a shallow hydrographic front (100 m depth) at Stn 34, which separates TBW and TWW. In the northern part of the transect at the South Shetland Islands slope, isotherms, isohalines and isopycnals show significant tilting that defines a slope front—the so-called Bransfield Front—between Stns 24 and 26, to a depth of 400 m.

The distributions of hydrographic properties along T1, T2, and T4 are similar to those in T3 (Fig. 2). A plot of the position of both the slope front and the hydrographic front for the 4 transects is shown in Fig. 1. In T1, TWW does not reach the surface and in T4 the hydrographic front is further north. Other studies carried out in this region have shown that TBW narrows to the northeast, with the hydrographic front closer to the South Shetland Islands in a northeast direction (Garcia et al. 1994, Basterretxea & Aristegui 1999).

The geostrophic transport along the 4 transects from 500 dbar to the surface is shown in Fig. 3. The main feature of the transport distribution is the relatively strong and narrow transport flowing northeastswards along the South Shetlands Island slope, which gives rise to the BC. This current originated as a baroclinic jet associated with the slope front. Surface geostrophic velocity relative to 500 dbar for the BC ranged from 0.17 m s⁻¹ at T4 to 0.26 m s⁻¹ at T3. These values are of the same order of those reported by Grewloski et al.
However, the values registered by direct current acoustic Doppler current profiler (ADCP) measurement were approximately twice as high (0.5 m s⁻¹) (Zhou et al. 2006). Geostrophic velocity vertical sections (not shown here) show strong vertical shears that may favour the development of mixed regions associated with the baroclinic jet. Outside the BC, transport and current are very diffuse and weak, with mean surface values as low as 0.02 m s⁻¹.

**Larval abundance and composition**

A total of 59,521 larvae were collected during the survey. Highest larval abundances were recorded at Stn 23 on T2, with almost 30 larvae m⁻³ in layers from 40–70, 70–100 and 100–200 m depth (Fig. 4). In contrast, larvae were very scarce at Stns 9, 12, 13 and 15, close to the Antarctica Peninsula. Larval abundance was low in the 200 to 300 m layers, except at Stn 19 (Fig. 4).

Holoplanktonic larvae (mainly copepod nauplii, 64.9% of the total number of larvae collected, n = 38,542) were more abundant than benthic invertebrate larvae. Never-
theless meroplankton represented 28.4% (17,211 larvae) of the total, and were very abundant at stations close to the South Shetland Islands (Stns 1, 23, and 37).

The summer meroplankton community was dominated by polychaete larvae (mainly nectochaetes) and echinoderm larvae (mainly asteroid brachiolaria), which represented 67.4% (n = 11,607) and 23% (n = 3,947) respectively of the total meroplankton. Nemertean pilidium larvae represented 2.5% (n = 424) of all larvae. A total of 361 (2.1%) cypris larvae were collected. Sipunculid pelagosphaerae (n = 203), molluscan veligers (n = 185), decapod zoea (n = 109), enteropneustan tornariae (n = 102), planulae (n = 93), pycnogonidan protonymphons (n = 90), ascidian tadpole larvae (n = 85) and bryozoan cyphonaute larvae (n = 5) were considerably less abundant. The description of all these types of larvae will be published elsewhere (E. Vázquez & J. Ameneiro unpubl.).

Meroplankton distribution

Benthic invertebrate larvae were more abundant close to the South Shetlands Islands and decreased in abundance towards the Antarctic Peninsula between the South Shetland Islands and the slope front in the TBW (Fig. 5). An increment in larval abundance with depth was observed at Stns 1, 23 and 37, and was maximal just above the end of the slope front situated between 150 and 230 m depth. Distribution was uniform at Stns 24 and 36, where strong mixing processes in the upper 300 m of the water masses occurred.

Polychaete larvae were found close to both shores but mainly near the South Shetland Islands in TBW, and reached densities of almost 10 m⁻³ in the 100 to 200 m layer at Stn 23 (Fig. 5). Polychaete larvae were very sparse in the central part of the Bransfield Strait and appeared below 100 m depth in TWW (Fig. 5). A
Fig. 5. Distribution of major meroplankton at Bransfield Strait. Abundances expressed as larvae 200 m$^{-3}$. South Shetland Islands are to the left of panels and Antarctic Peninsula to the right (not shown).
slight increase in abundance in the upper layers at stations between the hydrographic front and the Antarctic Peninsula, in TWW, was observed.

Echinoderm larvae were the second most abundant type of larvae. They mainly occupied the central part of the Bransfield Strait and reached densities of 6 m\(^{-3}\) between 40 and 70 m depth at Stn 19. The larvae always appeared in the upper 100 m of the water column in TBW, just above the polychaete larvae (Fig. 5). They were almost absent at stations and depths characterized by TWW.

The MDS ordination analysis of abundances of echinoderm and polychaete larvae (Fig. 6) revealed 6 major assemblages. The first (Fig. 6a) comprised the upper layers that corresponded to TBW of stations located in the central basin of the Bransfield Strait and were characterized by high abundances of echinoderm larvae. The second group (Fig. 6b) was formed by layers in TBW of the 4 stations located in the BC close to the South Shetland Islands defined by a high abundance of polychaete larvae; in addition the TWW layers of Stns 5 and 34 were also included here because of the large number of polychaete larvae that they contained. The other 4 groups (Fig. 6c–f) included stations and layers of stations in TWW characterized by a gradient from high (Fig. 6c) to low (Fig. 6f) polychaete abundance.

Although larvae of other benthic animals were less abundant, their distributions were very distinctive (Fig. 7). Ascidian larvae were mainly found in TWW in the stations between the hydrographic front and Antarctic Peninsula, and reached maximal density (38.1 larvae 200 m\(^{-3}\); n = 48 out of 85 found in the whole survey) between 40 and 70 m depth at Stn 49 close to d’Urville Island. Decapod crustacean zoea larvae reached highest densities at Stn 30 and inhabited the entire water column; this station was situated close to the hydrographic front. Zoeae were also found, in lower numbers, at Stns 34 and 33 in the TWW in T3. Nemertean and cirrhipeda larvae were concentrated in the central southern part of Bransfield Strait. In contrast, sipunculida pelagosphaera larvae were very uniformly distributed throughout the Bransfield Strait below 100 m depth. Gastropod veligers were also uniformly distributed, mainly in the central part of the Bransfield Strait and were very sparse close to the South Shetlands Islands.

**DISCUSSION**

As far as we know this is the first study of invertebrate larval distribution in Antarctic waters with a 80 µm mesh plankton net with high vertical (5 depth layers from 10 to 300 m) and horizontal (19 stations in 120 square n miles) resolution. In previous studies (Shreeve & Peck 1995, Bhaud et al. 1999, Stanwell-Smith et al. 1999, Absher et al. 2003) nets of 100 to 200 µm mesh size were used at a maximum of 3 depth horizons.

**Meroplankton abundance and composition**

References to the scarcity of marine invertebrate larvae in Antarctic waters date from the first expeditions to the Southern Ocean (reviewed in Arntz & Gili 2001) and were confirmed recently (Shreeve & Peck 1995, Stanwell-Smith et al. 1999, Sewell 2005). Although quantitative comparison of larval numbers is difficult due to differences in the sampling gear used, depth of sampling, and particularly in relation to plankton and mesh size, the present results corroborate the paucity of invertebrate larvae in Antarctica.

The abundance of meroplankton in the Bransfield Strait was very variable, and depended on depth and geographical location. Maximum abundance was 8.43 benthic invertebrate larvae m\(^{-3}\) in the 100 to 200 m layer at Stn 23. This is within the range of densities reported by other authors in other Antarctic locations, although far from figures given for fjord systems and enclosed bays where retention of larvae can occur (Sewell 2005) (Table 1). Timing of sampling is also important. Studies carried out throughout the entire year showed larval peaks between mid and late January (Tanimura et al. 1986, Kirkwood 1993) and in Feb-
ruary–March (Stanwell-Smith et al. 1999, Freire et al. 2006) (Table 1). The present study and those by Shreeve & Peck (1995) and Sewell (2005) (Table 1) were undertaken before the peak levels were reached.

However the scarcity of benthic marine invertebrate larvae in the Southern Ocean refers to abundances rather than to species/larval type richness, as has been demonstrated in recent years (Stanwell-Smith et al. 1999, Sewell 2005, present study). Several explanations for the paucity of benthic invertebrate larvae have been proposed. One such idea is that direct development is the predominant reproductive strategy in deep waters, because of the limited availability of food (e.g. Thorson 1950, Mileikovsky 1971). Nevertheless, the validity of this hypothesis, known as ‘Thorson’s rule’, has been questioned as more Antarctic investigations are carried out (see Arntz & Gili 2001).

The reduction in intertidal and shallow subtidal species due to effects exerted by ice has also been postulated as a major factor explaining the lower larval numbers relative to temperate latitudes (Shreeve & Peck 1995). These authors also pointed out the long distances offshore (300 and 600 km) of their survey to explain the low larval numbers and suggested that similar investigations closer inshore may reveal higher numbers of larvae. We have found similar larval abundances in the Bransfield Strait at stations close to shore in the South Shetland Islands and much lower abun-

Fig. 7. Distribution of minor meroplankton at Bransfield Strait. Abundances expressed as larvae 200 m$^{-3}$. South Shetland Islands are to the left and Antarctic Peninsula to the right (not shown).
Table 1. Meroplankton abundance in different locations in Antarctica with the maximum peak of abundance in year-round surveys

<table>
<thead>
<tr>
<th>Location</th>
<th>Abundance (m$^{-3}$)</th>
<th>Max. peak</th>
<th>Survey period</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Signy Island, South Orkney Islands</td>
<td>2.74</td>
<td>Feb–Mar Jul–Sep</td>
<td>2 yr</td>
<td>Stanwell-Smith et al. (1999)</td>
</tr>
<tr>
<td>Bransfield Strait</td>
<td>8.43</td>
<td>Early January</td>
<td>Present study</td>
<td></td>
</tr>
<tr>
<td>Admiralty Bay, King George Island</td>
<td>15</td>
<td>Dec–May</td>
<td>Freire et al. (2006)</td>
<td></td>
</tr>
<tr>
<td>Syowa Station, Ongul Island</td>
<td>228</td>
<td>Late Jan</td>
<td>1 yr</td>
<td>Tanimura et al. (1986)</td>
</tr>
<tr>
<td>Ellis Fjord</td>
<td>889</td>
<td>Mid Jan</td>
<td>1 yr</td>
<td>Kirkwood (1993)</td>
</tr>
</tbody>
</table>

Contrary to the findings of Stanwell-Smith et al. (1999) for Signy Island, i.e. that most of the variability in the larval abundance was attributable to seasonality rather than to site or depth effects because the long larval life ensured mixing within sites, we found that the presence of meroplanktonic larvae was closely related to depth, water masses and fronts. Currents may generally enhance larval dispersal but also create physical barriers such as density gradients or mixing zones, which restrict the spread of larvae (Scheltema 1986).

Meroplankton were more abundant in TBW and decreased towards the continent where cold water of Weddell origin (TWW) runs parallel to the Antarctic Peninsula. Larval abundance increased with depth to the discontinuity between TBW and TWW at approximately 200 m, and then decreased. Stns 24 and 36 were exceptions to this finding as larvae were uniformly distributed, probably because of strong mixing processes related to the strong shear associated with the BC.

Polychaete larvae were mainly found between the South Shetland Islands and the Bransfield Strait in warm water of Bellingshausen origin (TBW). They were sparse in the central part of the Bransfield Strait, where they appeared below 100 m depth, and increased in abundance again between the hydrographic front and the Antarctic Peninsula, in TWW. Meroplanktonic larvae are generally weak swimmers and their dispersal depends on the distribution of adults and the prevailing hydrodynamics (Pedotti & Fenaux 1992). We speculated 2 different origins for these polychaete larvae. Those in TBW may originate from the abundant adult populations of sedentary
local hydrographic conditions may determine larval distribution of eggs and larvae, but the field Strait appears to be the product of adult spawning. Adult populations dominate, i.e. above 100 m depth where the benthos is inhabited by the benthic fauna. Preliminary results revealed that these larvae may be associated with maximum fluorescence (E. Vázquez & L. Lubián unpubl.).

Ascending larvae were mainly found in TWW, reaching the highest densities at 40 and 70 m depth closest to the shore and at the shallowest station close to habitats where adult populations dominate, i.e. above 100 m depth with strong glacier influence as in the shores of the Antarctic Peninsula (Sáiz-Salinas et al. 1997, Sahade et al. 1998). The low transport (0.001 Sv) recorded at the Antarctic Peninsula (Sáiz-Salinas et al. 1997, Sahade et al. 1998) indicates that these larvae may originate from the large biomass of Astroidea, Echinoidea Regularia and Ophiuroidea (Arnaud et al. 1998) that inhabit the benthos in this region. Preliminary results revealed that these larvae may be associated with maximum fluorescence (E. Vázquez & L. Lubián unpubl.).

In summary, meroplankton distribution in the Bransfield Strait appears to be the product of adult spawning and hydrography. Spawning by adults establishes the initial distribution of eggs and larvae, but the local hydrographic conditions may determine larval dispersal.

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LITERATURE CITED


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