Food-limited invertebrate larvae in the Southern Ocean: testing a paradigm

J. Ameneiro[1,*], L. M. Lubián[2], P. Sangrà[3], E. Vázquez[1]

[1]Dpt. Ecoloxía e Bioloxía Animal, Facultade de Ciencias do Mar, Universidade de Vigo, 36200 Vigo, Spain
[2]Instituto de Ciencias Marinas de Andalucía (CSIC), Av. República Saharaui 2, 11510 Puerto Real, Spain
[3]Dpt. Física, Facultad de Ciencias del Mar, Universidad de Las Palmas de Gran Canaria, 35017 Las Palmas de Gran Canaria, Spain

ABSTRACT: A long-standing paradigm of larval ecology is that the high incidence of non-feeding larval development in Antarctic invertebrates is an adaptation to limited availability of algal food. Antarctic plankton communities have a relatively high diversity and abundance of invertebrate larvae, some of which are planktotrophic and synchronize the presence of feeding larval stages to peaks in summer phytoplankton. Among the echinoderm larvae found between 30 December 2002 and 7 January 2003 in the Bransfield Strait, the planktotrophic brachiolaria of *Odontaster* were the most abundant. Although phytoplankton is the main food source for planktotrophic larvae of asteroids in other oceans, previous estimates of the carbon requirements of larvae of the Antarctic asteroid *O. validus* have indicated that these larvae could not survive on natural levels of Antarctic phytoplankton. The main aims of the present study were to establish whether the abundance of *Odontaster* larvae is related to that of palatable phytoplankton and to determine whether the availability of the latter would be sufficient to cover the carbon requirements of the larvae. We found that of all palatable phytoplanktonic groups (Cryptophyceae, picoplankton, nanoplankton and ultraplankton), only Cryptophyceae was a significant predictor of brachiolaria abundance, along with the stratification index. We also found that the carbon content of the total palatable phytoplankton would be sufficient to meet the carbon requirements of *Odontaster* larvae at almost all stations and depths. Although *O. validus* spawns between mid- and late winter when the concentration of phytoplankton is lowest, winter spawning may be one way of meeting the exogenous energetic requirements of larvae.

KEY WORDS: Meroplankton · Phytoplankton · Antarctica · Brachiolaria · Cryptophyceae · Larval starvation · *Odontaster*

INTRODUCTION

Recent studies of Antarctic meroplankton have revealed a relatively high diversity and abundance of larval forms of benthic marine invertebrates (reviewed by Arntz & Gili 2001, Sewell 2005, Vázquez et al. 2007, Bowden et al. 2009, Ameneiro et al. 2012), only some of which are planktotrophic. The paucity of planktotrophic larvae in polar habitats has traditionally been explained by a lack of algae as food (reviewed by Gillespie & McClintock 2007, Pearse et al. 2009). However, research carried out in the Antarctic Ocean and South America has shown no correlation between latitude (in relation to temperature and seasonality) and larval type (Stanwell-Smith et al. 1999, Pearse & Lockhart 2004) and, in fact, some evidence indicates that this may be a consequence of isolation after vicariant events that have led to proliferation of species with non-pelagic development (Poulin et al. 2002, reviewed by Pearse et al. 2009). Nevertheless, some of the most abundant species in these cold-water habitats have planktotrophic larvae

(Pearse & Lockhart 2004). These species reproduce seasonally, usually in late winter and early spring, synchronizing their planktotrophic larvae with the summer phytoplankton bloom (Pearse et al. 1991, Pearse & Bosch 2002, Pearse & Lockhart 2004, Bowden et al. 2009). This has already been shown for echinoderm larvae and nemertean pilidia, which occur in the water column when the flagellate chlorophyll fraction (2–20 µm) exceeds the diatom chlorophyll fraction (Stanwell-Smith et al. 1999), which may be unpalatable (Perissinotto 1992).

In the Bransfield Strait, the meroplankton community is dominated by polychaete and echinoderm larvae (Vázquez et al. 2007), and its distribution depends on water masses, depth and fronts. Thus, polychaete larvae were mainly found close to the South Shetland Islands Slope in Transitional Zonal Water with Bellingshausen influence, below 100 m depth in the central basin in Transitional Zonal Water with Weddell influence, and in upper layers at stations between the Peninsular Front and the Antarctic Peninsula, in Transitional Zonal Water with Weddell influence (Vázquez et al. 2007). By contrast, echinoderm larvae mainly occupied the central basin and were always associated with the upper 100 m in the well-stratified Transitional Zonal Water with Bellingshausen influence, just above the polychaete larvae (Vázquez et al. 2007).

Approximately 98% (n = 3200) of the echinoderm larvae were the planktotrophic brachiolaria of *Odontaster* (Vázquez et al. 2007). Five species of *Odontaster* have been described in the Southern Ocean and southern South America (reviewed by Pearse 2013). *O. meridionalis* (Smith) and *O. validus* Koehler display a circum-Antarctic distribution (McClintock et al. 1988), whereas *O. penicillatus* (Philippi, 1879) shows an almost entirely sub-Antarctic distribution off Argentina, co-occurring with the other 2 species, mainly off South Georgia Island in the Southern Ocean. *O. pearsei* Janosik & Halanych, 2010, inhabits the western side of the Antarctic Peninsula, and *O. roseus* Janosik & Halanych, 2010, inhabits the South Shetland Islands off the northern tip of the Antarctic Peninsula (Pearse 2013). *O. validus* usually occurs at much higher densities (Dayton et al. 1974) and is the most abundant and ubiquitous shallow-water asteroid around the Antarctic continent, especially between 0 and 200 m depth (Pearse 1965, McClintock et al. 1988, Dayton 1990, Chiantore et al. 2002). *O. validus*, *O. meridionalis* and *O. roseus* have long-lived planktotrophic larvae (Bosch & Pearse 1990, Stanwell-Smith & Peck 1998, Janosik et al. 2011) as do the other 2 species (Pearse 2013). *O.*

validus spawns synchronously and seasonally between mid- and late winter (Pearse 1965, Stanwell-Smith & Clarke 1998, Stanwell-Smith & Peck 1998) when the concentration of phytoplankton is very low (Rivkin 1991). However, the free-swimming feeding forms of larvae remain in the plankton for more than 5.5 mo (Pearse & Bosch 1986, Stanwell-Smith & Peck 1998) during the entire period of summer phytoplankton production (Pearse & Bosch 2002).

The availability of food for planktotrophic larvae remains unclear. Phytoplankton is the main source of food for planktotrophic larvae of asteroids in other oceans. However, estimation (from respiration data) of the carbon requirements of larvae of the Antarctic asteroid *O. validus* suggested that these larvae could not survive by feeding only on Antarctic phytoplankton, although larvae held *in situ* in mesh cages did survive (Olson et al. 1987). Consequently, it has been suggested that the larvae can use other sources of nutrition, such as bacteria (Rivkin et al. 1986, Rivkin 1991, but see Pearse et al. 1991), detritus (Strathmann 1971, Rassoulzadegan & Fenaux 1979, Bosch & Rivkin 1988) and directly absorbed dissolved organic matter (DOM) (Manahan et al. 1983, Shilling & Manahan 1991).

The aims of this study were to explore the relationship between the abundance of *Odontaster* larvae and the phytoplankton smaller than 20 µm, which can be ingested by *Odontaster* larvae, and to study whether the abundance of phytoplankton would be sufficient to cover the carbon requirements of *Odontaster* larvae in the Bransfield Strait, Antarctica.

MATERIALS AND METHODS

Plankton sampling was carried out from the RV B.I.O. 'Hespérides' along 4 transects of 60 nautical miles (nmi), each separated by 20 nmi, in the Bransfield Strait (Fig. 1) running from the Antarctic Peninsula to the South Shetland Islands, between 30 December 2002 and 7 January 2003.

Phytoplankton samples were collected every 20 nmi along transect T1 and every 10 nmi along transects T2, T3 and T4 (Fig. 1), with a Neil Brown Mark III conductivity, temperature, depth (CTD)/Rossette Niskin sampler, at the following depths: 5, 10, 25, 50 and 100 m and at the deep chlorophyll maximum. Samples were fixed in 3% formaldehyde and analysed immediately by flow cytometry (FACSCalibur, Becton Dickinson). Acquisition and data analysis were carried out with CELLQuestTM software (Becton Dickinson). Picoplankton (<2 µm), ultraplankton
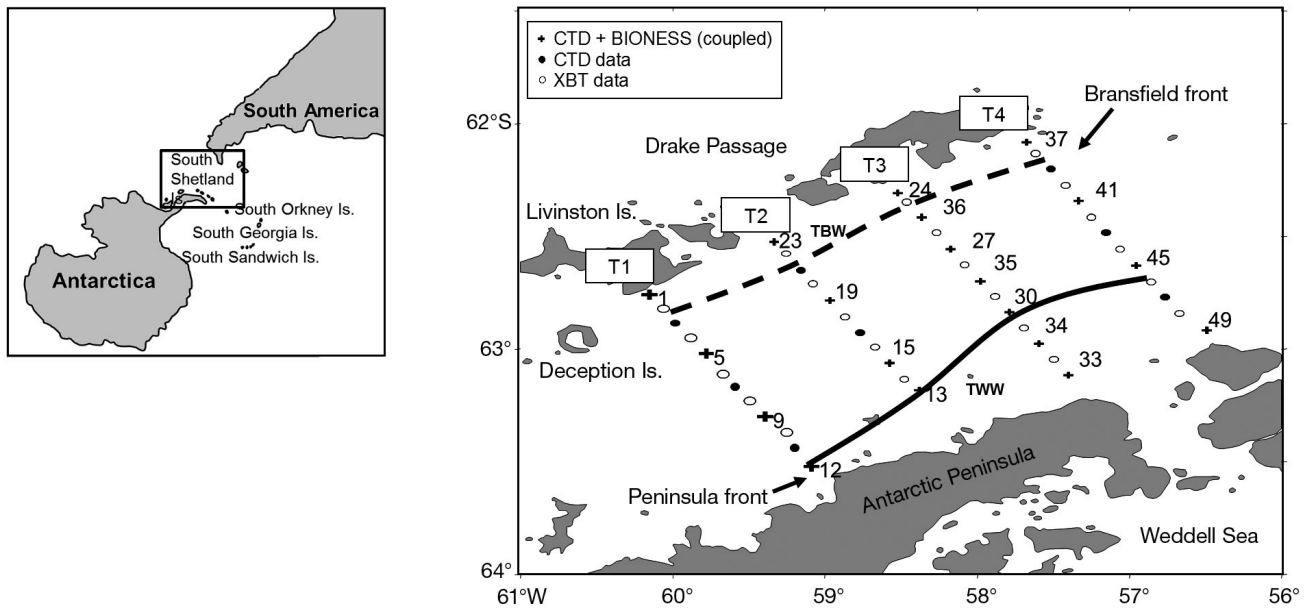
Fig. 1. Location of the sampling stations in the Central Basin of the Bransfield Strait (Antarctica), showing conductivity, temperature and depth (CTD) and expendable bathythermograph (XBT) monitoring points, and the CTD+BIONESS ('coupled') stations (numbered). Dashed line: position of the Bransfield Front; solid line: position of the Peninsular Front that separates the Transitional Zonal Water with Bellingshausen influence (TBW) and the Transitional Zonal Water with Weddell influence (TWW). T1–T4: transects 1–4

(2–8 μm), nanoplankton (8–20 μm) and Cryptophyceae were separated by using combinations of 2-dimensional gates based on orange fluorescence, red fluorescence and side scatter (SSC) signal. The SSC signal was converted to biovolume (BV, in $μm^3$) by applying the empirical relationship shown in Eq. (1) below. The regression equation was obtained by measuring the BV of 4 different cultures of phytoplankton (measured by optic imagery) and comparing the results with the SSC signal. The BV was converted to carbon by applying Eq. (2), proposed by Verity et al. (1992):

$$BV\ (μm^3) = 0.3534 \times SSC + 2.885 \tag{1}$$
$$(r^2 = 0.928;\ n = 4;\ p < 0.01)$$

$$pg\ C = 0.433 \times BV^{0.863} \tag{2}$$
$$(r^2 = 0.984)$$

The data were subsequently depth integrated (surface to 100 m) according to the following equation:

$$B_S = \sum_0^{100} (D_i + D_{i+1})/2(Z_i + Z_{i+1}) \tag{3}$$

where B_S is the phytoplankton biomass (mg C m^{-2}) at Stn S, D_i and D_{i+1} is the amount of carbon measured (mg) at depth i and $i+1$, and Z_i and Z_{i+1} is the depth at which samples are taken (m).

Zooplankton was sampled at 4 stations (separated by 20 nmi) on transects T1, T2 and T4 and at 7 stations

(separated by 10 nm) on transect T3, with a multinet (BIONESS, Open Seas Instrumentation). These stations are designated 'coupled stations' in Fig. 1. The multinet comprises a quadrangular 1 m^2 frame with 5 double nets. The mesh size of the inner net and its cod-end is 250 μm, and the mesh size of the outer net and its cod-end is 80 μm. The standard procedure used was to lower the net to a depth of 300 m (or close to the bottom if the depth was less than 300 m), and to carry out an oblique ascending tow, opening the nets at the desired ranges of depth: 300–200, 199–100, 99–70, 69–40 and 39–10 m. Sampling was not carried out between the surface and 10 m, because the turbulence created by the vessel at this depth could have damaged the delicate nets. The towing speed was approximately 2 knots. The mean tow duration was 5 min 48 s ± 1 min 34 s (SE), and approximately 250 m^3 of seawater were filtered per depth interval (mean swept water volume = 252.72 ± 61.73 [SE] m^3). The larval counts for each tow were therefore corrected to a standard sampling volume of 200 m^3. To analyse the horizontal distribution, the number of larvae m^{-2} integrated over the entire depth was calculated as follows:

$$N_s = \sum_i (b_i \times Z_i/v_i) \tag{4}$$

where N_s is the number of larvae m^{-2} at Stn S, b_i is the number of larvae caught at depth interval i, v_i is

the volume filtered (m^3) for depth interval i, and Z_i is the thickness of the depth interval i (m). Zooplankton was anaesthetised (with menthol crystals in sea water) for 4 h prior to being fixed and preserved in 4 % formaldehyde in seawater solution. All samples (n = 176) were examined under a binocular microscope, and the larvae were counted.

Echinoderm larvae can feed on particles of a wide range of sizes; however, they generally retain 2–20 μm particles most efficiently (Boidron-Métairon 1995) and cannot ingest spheres larger than 65 μm (Strathmann 1971). Therefore, only phytoplankton smaller than 20 μm was considered suitable for larval ingestion and designated 'palatable phytoplankton' in the text. Diatoms such as *Corethron criophilum* and *Proboscia* sp. (diameter around 100 μm), *Thalassiosira* spp. (diameter 65 μm and mainly appearing in long chains) and *Fragilariopsis* sp. (average diameter around 50 μm) were therefore not considered in this study.

Multiple linear regression analysis was used to examine the relationships between total number of brachiolaria larvae of *Odontaster* (expressed as larvae m^{-2}) at each station (dependent variable) and the abundances of nanoplankton, picoplankton, ultraplankton and Cryptophyceae (integrated biomass for each station to a depth of 100 m expressed as mg C m^{-2}) (independent predictors). All variables were previously transformed by applying the expression $Ln(x + 1)$. The potential density anomaly (σ) was added to this set of explanatory variables as a stratification index, as the potential density profiles indicated a stratified water column in the central part of Bransfield Strait where *Odontaster* larvae were found (Vázquez et al. 2007). The index was calculated as the difference between potential density anomaly at 200 m (maximum larvae depth) and at 5 m. The potential density (ρ_θ) of a fluid parcel at pressure P is the density that the parcel would acquire if adiabatically brought to a reference pressure P_0 (often 1 bar, 100 kPa). ρ_θ is especially useful because it is a conserved thermodynamic property. Although density varies with pressure, the potential density of a fluid parcel is conserved as the pressure experienced by the parcel varies. To avoid the difficulties associated with determining absolute density, the density is expressed relative to that of pure water. For simplification, the final 2 digits of the density are often quoted, a quantity named density anomaly or σ. The corresponding potential density anomaly is denoted by

$$\sigma_\theta = \rho_\theta - 1000 \text{ kg m}^{-3} \tag{5}$$

The carbon requirements of *Odontaster* larvae were estimated from all published values of oxygen consumption (pmol O_2 h^{-1} larva^{-1}; Table 1) by using the following equation (Parsons et al. 1984):

$$C = R \times 0.536 \times RQ \tag{6}$$

where C is the carbon requirement (μg C), R is the respiration rate (μl O_2 h^{-1}) and RQ is the respiratory quotient. The RQ of organisms feeding on phytoplankton is usually about 1.

The filtration rates required for an *Odontaster* larva to meet the carbon requirements shown in Table 1 were estimated for each sampling depth and station in the Bransfield Strait, in relation to all palatable phytoplankton, taking into consideration that the highest filtration rate reported for an *Odontaster* larva at −1°C is 0.593 ml h^{-1} (Rivkin et al. 1986).

RESULTS

The size-fractionated measurements of phytoplankton carbon (mg C m^{-2}) suitable for ingestion by brachiolaria larvae and the total abundance of brachiolaria larvae are shown in Fig. 2. In the Bransfield Strait, the Peninsular Front defined the distribution limit of most species of phytoplankton. The Cryptophyceae population was concentrated in the central part of the Bransfield Strait, north of the Peninsular Front, and its distribution appeared to be associated with the transitional waters with Bellingshausen influence (TBW) (Fig. 2B) and with the presence of brachiolaria larvae (Fig. 2A). The distribution of the remaining small groups of phytoplankton was associated with the transitional waters with Weddell Sea

Table 1. Carbon requirements (C; ng C h^{-1} larva^{-1}) based on oxygen consumption values reported in the literature. The V (nl O_2) values were calculated using the Ideal Gas Law ($PV = nRT$, where n is moles (mol), $R = 0.082$ l atm mol^{-1} K^{-1}, T is temperature in K, P is pressure in atm and V is volume)

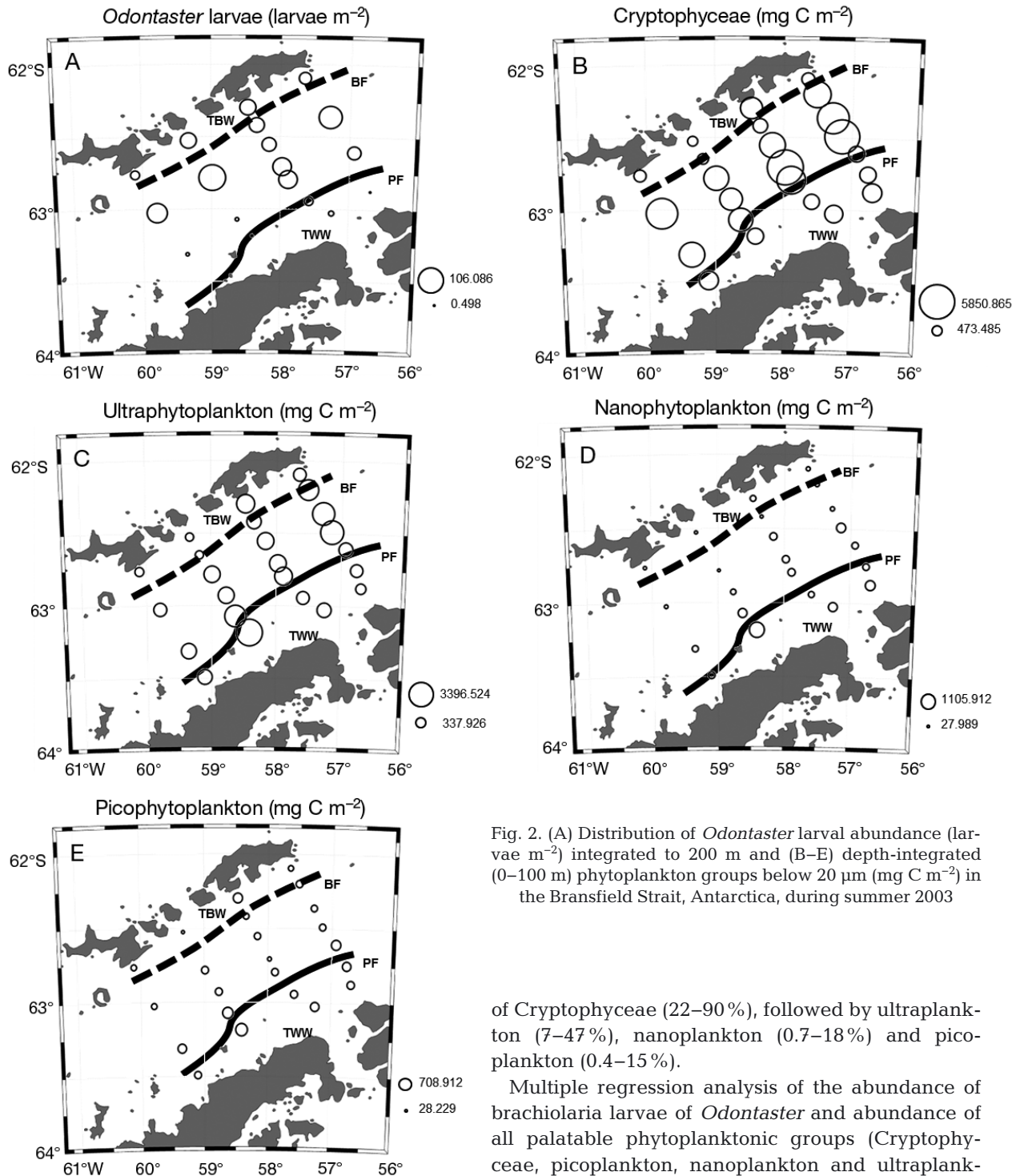| Author	O_2 consumption (pmol O_2 h^{-1} larva^{-1})	V (nl)	°C	$C = R \times 0.536$
Marsh & Manahan (1999)	13	0.29	−1.5	0.16
Shilling & Manahan (1994)	2.22	0.05	−2	0.03
Olson et al. (1987)		1.70	−1.8	0.91
Peck & Prothero-Thomas (2002):				
Mean in 1993	23.8	0.53	−0.5	0.29
Mean in 1997	35.7	0.80	−0.5	0.43
Min. at −0.5°C	7.5	0.17	−0.5	0.09
Max. at −0.5°C	77.68	1.74	−0.5	0.93
Min. at 2°C	18.3	0.41	2	0.22
Max. at 2°C	54.7	1.23	2	0.66

Fig. 2. (A) Distribution of *Odontaster* larval abundance (larvae m^{-2}) integrated to 200 m and (B–E) depth-integrated (0–100 m) phytoplankton groups below 20 μm (mg C m^{-2}) in the Bransfield Strait, Antarctica, during summer 2003

influence (TWW) (Fig. 2C–E). The microplankton constituted a small fraction of phytoplankton biomass, with *Corethron criophilum*, *Thalassosira* spp. and *Proboscia* sp. being the most representative species, with maximum contributions to the total biomass of 9, 7 and 4%, respectively (Lubián et al. 2007). Most of the biomass corresponded to the population

of Cryptophyceae (22–90%), followed by ultraplankton (7–47%), nanoplankton (0.7–18%) and picoplankton (0.4–15%).

Multiple regression analysis of the abundance of brachiolaria larvae of *Odontaster* and abundance of all palatable phytoplanktonic groups (Cryptophyceae, picoplankton, nanoplankton and ultraplankton) at each station, along with the stratification index, showed that only Cryptophyceae was a significant predictor of brachiolaria abundance, and together with the stratification index explained 58.0% (p = 0.001) of the variation in larval abundance in the water column:

$$\Sigma \text{ brachiolaria larvae} \\ = -116.72 + 172.55\sigma + 15.45 \log \text{Cryptophyceae} \tag{7}$$
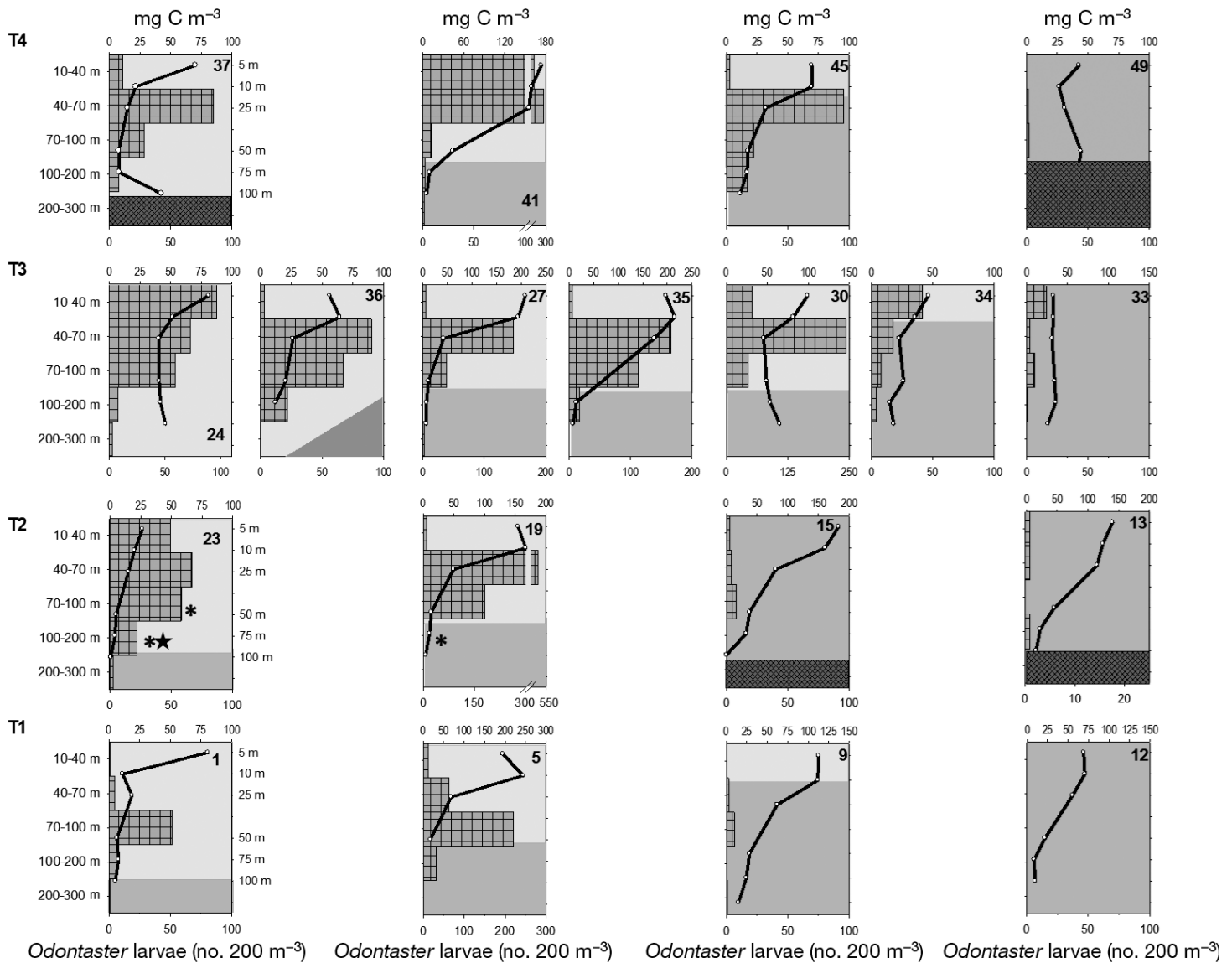
Fig. 3. Distribution of echinoderm larvae (cross-hatched bars) and all palatable phytoplankton (solid line) in the Bransfield Strait. Abundance is expressed as *Odontaster* larvae per 200 m^3 (lower *x*-axis) and mg C m^{-3} (upper *x*-axis). The *y*-axes show depth (left: larvae, right: phytoplankton). The light (dark) grey area in each graph represents Transitional Zonal Water with Bellingshausen influence (Transitional Zonal Water with Weddell influence) and the very dark cross-hatched areas represent the sea floor at shallower stations. The order of the transects (T1–T4) and station numbering follow Fig. 1. Black asterisks indicate those stations/depths where the Cryptophyceae fraction alone would be insufficient to provide the carbon requirements of *Odontaster* larvae. The black star indicates the depth range where all palatable phytoplankton would not be sufficient to meet the carbon needs of *Odontaster* larvae (as these would have to filter more than 0.593 ml h^{-1})

The highest abundance of brachiolaria larvae occurred in the central part of the Bransfield Strait, mainly in the shallowest layers between 40 and 70 m depth in the well-stratified TBW, except at Stn 45, where larvae were found in the TWW below 70 m (Fig. 3). Cryptophyceae with a spherical diameter of 6 µm represented more than 75% of the total phytoplankton biomass at this station.

The estimated carbon requirements of *Odontaster* larvae were very variable, ranging from 0.03 to 0.93 ng C h^{-1} (Table 1), as they depend on the temperature at which the respiration measurements were made as well as on the highly variable oxygen consumption (high temperatures do not necessarily indicate higher oxygen consumption: $R^2 = 0.02$; see Fig. S1 in the Supplement, available at www.int-res.com/articles/suppl/m554p071_supp.pdf). Nonetheless, even considering the highest carbon requirements, in the Bransfield Strait the intake of Cryptophyceae alone would ensure the carbon requirements of the

Odontaster larvae at all stations and depths, except at 3 depths (Fig. 3). Furthermore, the total palatable fraction of phytoplankton would be sufficient, except at 1 station (Fig. 3), where an *Odontaster* larva would have to filter more than 0.593 ml h^{-1}, its maximum filtration rate (Rivkin et al. 1986), to meet its carbon requirements from edible phytoplankton cells (see Table S1 in the Supplement).

DISCUSSION

Water mass distribution is of major importance in determining the spatial variability in the phytoplankton community in the Bransfield Strait. Examination of samples collected during the Bioantar-93 cruise (Mura et al. 1995) revealed that diatoms comprised a small fraction of phytoplankton biomass and were mainly distributed in the colder and saltier TWW (Lubián et al. 2007). Most of the biomass corresponded to Cryptophyceae located in TBW. Similarly, in the austral summer of 1993, the high phytoplankton biomass was clearly dominated by autotrophic nanoflagellates of the Cryptophyceae, represented by *Cryptomonas* indet. associated with a front in the Bransfield Strait (Mura et al. 1995). Kang & Lee (1995) also reported a predominance of nanoflagellates such as *Cryptomonas* indet. and *Phaeocystis antarctica* (motile stage) in the Bransfield Strait, with these species accounting for 83 % of the total phytoplankton carbon. Similarly, in the western region of the Antarctic Peninsula, the phytoplankton community was essentially formed by *Cryptomonas* indet. (Rodríguez et al. 2002, Varela et al. 2002). Greater stabilization of the water column with an initially poor diatom population was indicated as a possible explanation for the proliferation of nanoflagellates (Kopczynska 2008), although the grazing pressure by krill, which are very abundant in both the Peninsular and Bransfield fronts (Hernández-León et al. 2013), may determine the distribution of phytoplankton in this area (Varela et al. 2002).

In the present study, the other phytoplankton groups found made a modest contribution to the community biomass and were associated with the water mass from the Weddell Sea, although Mura et al. (1995) associated them with low-salinity waters from ice melt from the Bellingshausen Sea water mass.

Larval abundance and distribution of asteroid larvae have been poorly quantified. In regions of the Antarctic such as the Ross Sea, McMurdo Sound, Weddell Sea and Bransfield Strait, asteroid larvae

are most abundant in winter and are dominated by *Odontaster validus* (Stanwell-Smith & Clarke 1998, Stanwell-Smith & Peck 1998, Bowden et al. 2009; reviewed by Metaxas 2013). In the Bransfield Strait, brachiolariae represent 23 % (6 larvae m^{-3}) of the meroplankton (Vázquez et al. 2007), in contrast to very low abundance of larvae in the Bellingshausen Sea (0–0.2 larvae m^{-3}; Ameneiro et al. 2012). These spatial differences may reflect temporal variability, although (as for phytoplankton) the larval distribution in the Bransfield Strait is strongly dependent on water masses, depth and fronts (Vázquez et al. 2007).

The position of the larvae in the water column may be determined by their response to various abiotic (light, temperature, salinity, pressure, currents, turbulence) and biotic (predators, food) factors (Young 1995), thus varying their vertical position (Metaxas & Young 1998, Metaxas & Saunders 2009). Larvae of asteroids were mainly found in the upper layers in the Bransfield Strait (Vázquez et al. 2007) characterized by enhanced phytoplankton biomass. This is consistent with the findings of laboratory studies showing that asteroid larvae swim upwards and remain in the upper layers of the water column aggregating around or within areas with high phytoplankton concentrations (Metaxas & Young 1998, Sameoto & Metaxas 2008) to maximize their food intake and hence enhance their opportunities of larval survival and recruitment in the benthos (Metaxas & Young 1998). The relative importance of different food sources is not known, although size-selective feeding occurs (reviewed by Metaxas 2013). Echinoderm larvae can feed on suspended particles of a wide range of sizes, although those of size 4 to 6 μm are captured most efficiently. Echinoderm larvae also preferentially ingest certain species of algae, excluding particles that are too large or unsuitable as food (Strathmann 1971, Okaji et al. 1997). Unsurprisingly, the abundance of brachiolariae was related to the most abundant of the palatable phytoplankton (picoplankton, ultraplankton and nanoplankton), particularly nanoplanktonic Cryptophyceae (spherical diameter 6 μm), which are similar in size to other asteroid larvae (Strathmann 1971, Rassoulzadegan & Fenaux 1979, Ayukai 1994, Basch 1996, Okaji et al. 1997). Moreover, use of this dominant component of phytoplankton is advantageous for the survival of planktotrophic larvae in the field (Rassoulzadegan & Fenaux 1979).

Odontaster larvae must survive for long periods in an environment with low food supply for most of the year, as the concentration of chlorophyll *a* (chl *a*) in Antarctic waters is typically up to 2 orders of magni-

tude lower than the amount considered limiting (Rivkin et al. 1986). Indeed, Olson et al. (1987) concluded that the concentration of carbon in the form of phytoplankton in McMurdo Sound in September and October (1500 ng C l^{-1}, based on chl *a* concentration) was insufficient to support the carbon requirements of bipinnaria larvae of *O. validus*. However, *in situ* experiments did not show any evidence of either larval starvation or food limitation (Olson et al. 1987). Additional nutritional resources such as dissolved organic compounds (Manahan et al. 1983) and bacteria (Rivkin et al. 1986, Bosch et al. 1990, Pearse et al. 1992) have been suggested to be important to *O. validus* survival, as *Odontaster* larvae develop equally well whether fed bacteria or a range of concentrations of algae (Bosch et al. 1990).

However, the carbon requirements of *Odontaster* larvae estimated from oxygen consumption values reported in the literature were very variable, ranging from 0.03 to 0.93 ng C h^{-1} (Table 1). This wide variation can be attributed to the different temperatures at which the respiration measurements were made and to the variability in oxygen consumption itself, as high temperatures do not necessarily indicate higher oxygen consumption (see Fig. S1 in the Supplement; $R^2 = 0.02$). Although a quantitative comparison of oxygen consumption is difficult due to differences in the methods used (Olson et al. 1987, Shilling & Manahan 1994, Marsh & Manahan 1999, Peck & Prothero-Thomas 2002), even the most restrictive estimates indicate that in the Bransfield Strait in January, carbon from total palatable phytoplankton would be sufficient to meet the carbon requirements of *Odontaster* larvae at all stations and depths, except at 1 station. Furthermore, the Cryptophyceae fraction alone would provide enough food, except at 3 depths, at which an *Odontaster* larva would have to filter more than 0.6 ml h^{-1}. The high clearance rate reported for Antarctic bipinnaria larva is similar to that reported for temperate echinoderm larvae (Lucas 1982, Hart 1991, 1996, Ayukai 1994). This may reflect an adaptation for the rapid capture of small particles (Hart 1991), as *Odontaster* larvae have evolved features that partly compensate for the higher viscosity of Antarctic waters, such as characteristics of body shape and ciliary placement or dimensions (Pearse & Pearse 1992, Hart 1996). Thus, surprisingly, the concentrations of both edible phytoplankton and Cryptophyceae would also be sufficient at most depths below 75 m (Table S1 in the Supplement).

The low polar temperatures imply slow metabolic rates and low energetic cost, which may be useful for species with long development times (Peck et al. 2006). The scarce metabolic studies of polar larvae, namely echinoderm larvae (Olson et al. 1987, Hoegh-Guldberg et al. 1991, Shilling & Manahan 1994, Marsh & Manahan 1999, Peck & Prothero-Thomas 2002, Peck et al. 2006, Malanga et al. 2007), have revealed much lower metabolic rates than in temperate larvae (Hoegh-Guldberg & Manahan 1995, Peck et al. 2006). Egg biomass may therefore provide sufficient energy to meet metabolic demands during several months (Shilling & Manahan 1994), until the summer phytoplankton blooms. Furthermore, the larvae could also meet their energy needs and gain biomass by absorbing and metabolizing some components of DOM (Shilling & Bosch 1994). When these energy reserves are consumed, the larvae could cover exogenous carbon requirements by filtering nanophytoplankton, mainly Cryptophyceae, during the summer period of phytoplankton production (December to January), prior to settlement.

In Admiralty Bay, in Bransfield Strait, *O. validus* spawns when the concentration of phytoplankton is low (Freire et al. 2006), and the larvae are very abundant in December and January when phytoplankton biomass increases. The phytoplankton availability would thus enable the larvae to complete their development and would also meet the feeding requirements of the post-metamorphosis juvenile stages (Pearse 1965, Bowden et al. 2009). This may explain the presence of 27 larvae with a rudiment in our study, indicating that they were due to settle within a short period of time. Stanwell-Smith & Clarke (1998) suggested that at Signy Island, *O. validus* spawns in winter to prevent predation by suspension feeders or to avoid the period when the water column is dominated by large diatoms, colonial forms and mucilage from microalgae. However, we suggest that in the Bransfield Strait, *O. validus* may spawn in winter so that the exogenous energetic requirements of larvae hatching in the summer will be covered by the relatively high concentration of palatable phytoplankton available at this time.

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