ORIGINAL PAPER

Feeding habits and diet overlap of marine fish larvae from the peri-Antarctic Magellan region

Franco Salas-Berrios · Javiera Valdés-Aguilera ·
Mauricio F. Landaeta · Claudia A. Bustos ·
Alfredo Pérez-Vargas · Fernando Balbontín

Abstract The Magellan region is a unique peri-Antarctic ecosystem due to its geographical position. However, the knowledge about the distribution and feeding ecology of fish larvae is scarce. Since this area is characterized by low phytoplankton biomass, we hypothesize that marine fish larvae display different foraging tactics in order to reduce diet overlap. During austral spring 2009–2010, two oceanographic cruises were carried out along southern Patagonia (50–56°S). Larval fish distribution and feeding of the two most widely distributed species were studied, the smelt *Bathylagichthys parini* (Bathylagidae) and black southern cod *Patagonotothen tessellata* (Nototheniidae). Larvae of *B. parini* showed a lower increase in the mouth gape at size, primarily feeding during daytime (higher feeding incidence during the day) mostly on nonmotile prey (invertebrate and copepod eggs, appendicularian fecal pellets, diatoms). They showed no increase in feeding success (number, total volume of prey per gut and prey width) with increasing larval size, and the niche breadth was independent of larval size. Larvae of *P. tessellata* showed a large mouth gape at size, which may partially explain the predation on motile prey like large calanoid copepods (*C. simillimus*) and copepodites. They are nocturnal feeders (higher feeding incidence during night) and are exclusively carnivorous, feeding on larger prey as the larvae grow. Nonetheless, niche breadth was independent of larval size. Diet overlap was important only in individuals with smaller mouth gape (<890 μm) and diminished as larvae (and correspondingly their jaw) grow. In conclusion, in the peri-Antarctic Magellan region, fish larvae of two species display different foraging tactics, reducing their trophic overlap throughout their development.

Keywords Southern Patagonia Ice Fields · Magellan strait · *Bathylagichthys parini* · *Patagonotothen tessellata*

F. Salas-Berrios · J. Valdés-Aguilera · M. F. Landaeta (✉) ·
C. A. Bustos
Laboratorio de Ictioplancton (LABITI), Facultad de Ciencias del
Mar y de Recursos Naturales, Universidad de Valparaíso,
Avenida Borgoña 16344, Reñaca, Viña del Mar, Chile
e-mail: mauricio.landaeta@uv.cl

C. A. Bustos
Programa Doctorado en Acuicultura, Universidad Católica del
Norte, Campus Guayacán, Larrondo 1281, Coquimbo, Chile

A. Pérez-Vargas
Programa Doctorado en Ciencias mención Recursos Naturales
Acuáticos, Universidad de Valparaíso, Avenida Borgoña 16344,
Reñaca, Viña del Mar, Chile

F. Balbontín
Laboratorio de Peces, Facultad de Ciencias del Mar y de
Recursos Naturales, Universidad de Valparaíso, Avenida
Borgoño 16344, Reñaca, Viña del Mar, Chile

Introduction

Food availability is one of several potential factors controlling larval survival, particularly in those fish species with pelagic spawning (Sassa and Tsukamoto 2012). Newly hatched individuals of many fish species prey mainly upon small zooplankters and phytoplankton, partly because of their inability to handle larger prey. Additionally, larvae of the majority of fish species initially have poorly developed alimentary tracts, typically characterized by short length, narrow width, simple structure, weak digestive enzymes and, thus, limited digestive capacity. On the other hand, interspecific interactions can have important implications on growth, survival and recruitment success of fishes. For example, fishes may alter their diets and have lower growth rates, in the presence of competing species (Nunn et al. 2012).

Since fish larvae are visual predators, their feeding depends not only on prey density but also on the amount of light available to perceive prey (Gilbert et al. 1992). For example, the shading effect of higher phytoplankton concentration may reduce predation rates of fish larvae substantially (Fiksen et al. 2002). Turbidity may be caused not only by particulate organic matter in river plumes, but also by ice melting, especially in polar regions during spring and winter, potentially reducing prey perception, feeding and growth of fish larvae (Bailey et al. 1995; Fortier et al. 1996).

A subpolar region where the knowledge of the distribution and feeding ecology of fish larvae is scarce is southern Patagonia, an area comprised of the Southern Patagonia Ice Field (SPIF) and the Magellan Strait (from 50 to 56°S). The Magellan region is a unique peri-Antarctic ecosystem due to its geographical position. It is north of the polar front but closer to the Antarctic than any other large land mass, and it is also linked to the West Wind Drift (Saggiomo et al. 2011). The shallow eastern entrance opening to the Atlantic Ocean is dominated by strong tides (Medeiros and Kjerfve 1988), which cause turbulent and mixed conditions and a homogeneous water column. Physiographic and bathymetric features such as sills, shallow shelves and deep basins affect the intrusion of water and plankton. Microbasins delimited by bathymetric features are consistent with the distribution of oceanographic variables (Panella et al. 1991), copepods (Marín and Delgado 2001), meso/macrozooplankton (Hamame and Antezana 2010; Zagami et al. 2011) and ichthyoplankton (Bernal and Balbontín 1999; Balbontín and Bernal 2005).

The most abundant and widely distributed fish species in this variable environment are the black southern cod *Patagonotothen tessellata* (Richardson, 1844) and the deep-sea smelt *Bathylagichthys parini* Kobyliansky, 1990. *P. tessellata* is a small nototheniid fish (up to 22 cm body length, BL) that inhabits shallow subtidal zones (<15 m depth) along the southern tip of South America and Falkland Islands (Pequeño 2000; Sielfeld et al. 2006; Hüne and Ojeda 2012). This species is distributed in sandy areas throughout the water column, occurs in schools along the periphery of the kelp belts. It can also be found in open areas within the kelp belts but is rarely seen within the kelp belt itself (Moreno and Jara 1984). Adults are omnivorous, feeding mostly on amphipods, calanoid copepods (Moreno and Jara 1984) and nereidid polychaetes (Hüne and Rivera 2010). Females are total spawners and spawn twice a year, during the austral winter and summer (Rae and Calvo 1995a, 1996). Embryonic development lasts around 28 days, during which the males do not ingest food (Rae and Calvo 1995b). Larvae hatch with pigmented eyes and a yolk sac which is absorbed 5–7 days after hatching (Rae et al. 1999). There is no information about the distribution or feeding habits of the larval stages.

Bathylagichthys parini (Bathylagidae) was originally described based on the individuals collected in surface waters (20–70 m depth) of the open sea of Southeast Pacific (42°59′S, 80°15′W) (Kobyliansky 1990), but its larvae, juveniles and adults are frequent along the channels of Chilean Patagonia (Pequeño and Matallanas 2003; Uribe and Balbontin 2005; Landaeta et al. 2011a). Juveniles feed mostly on calanoid copepods and copepodites of *Acartia tonsa* and *Rhincalanus nasutus*, but also on ostracods (Landaeta et al. 2011a), while adults prey on decapod crustaceans (Pequeño and Matallanas 2003). Although larval *B. parini* are recurrently collected in plankton samples taken off Chilean Patagonia (Balbontín and Bernal 1997; Bernal and Balbontín 1999; Balbontín and Bernal 2005; Bustos et al. 2008, 2011), there is no information about the distribution patterns and larval fish feeding of this species.

Both *P. tessellata* and *B. parini* inhabit different bathymetric zones as adults; however, their larvae coexist in the water column during the austral spring season. The main objective of this study is to examine the feeding habits of the larval stages of these two marine fish species, as well as their niche breadth and overlap in southern Patagonia during the austral spring season. We hypothesize that both larval species prey on different prey items to minimize diet overlap.

Materials and methods

Study area

The Southern Patagonia Ice Field (SPIF) is the biggest extension of continental ice from the Southern Hemisphere, extending more than 330 km across three degrees of latitude between the watersheds of Lago San Martín, Argentina, on the east and the fjords of the Pacific Ocean on the west. Its total area (including 1,500 km² of contiguous glaciers) is about 13,000 km² (Aniya 1996). Glaciation and deglaciation processes produced a series of deep fjords (>800 m depth), connected to the shallower adjacent continental shelf (100–200 m depth) by a series of channels. Melting during austral spring and summer decreases seawater temperature and salinity, creating pronounced horizontal and vertical density gradients (Dávila et al. 2002).

The Magellan Strait is a 550-km-long channel (Fig. 1) that represents a boundary area between the southern temperate and the Antarctic regions, as well as between the Atlantic and Pacific oceans, all of which have markedly different climatic and biological features. Due to the high variety of geographical features, the Magellan Strait has distinctive characteristics when compared to the other peri-Antarctic areas, among which it is the only one having a continental nature (Zingone et al. 2011).

Fig. 1 Map of the station locations in the Magellan zone, southern tip of South America. *Black dots* correspond to oceanographic stations carried out during October–November 2009 (CIMAR 15 cruise, northern region), and *black triangles* correspond to locations studied during October–November 2010 (CIMAR 16 cruise, southern region). *Letters A* and *B* correspond to transects showed in Fig. 2
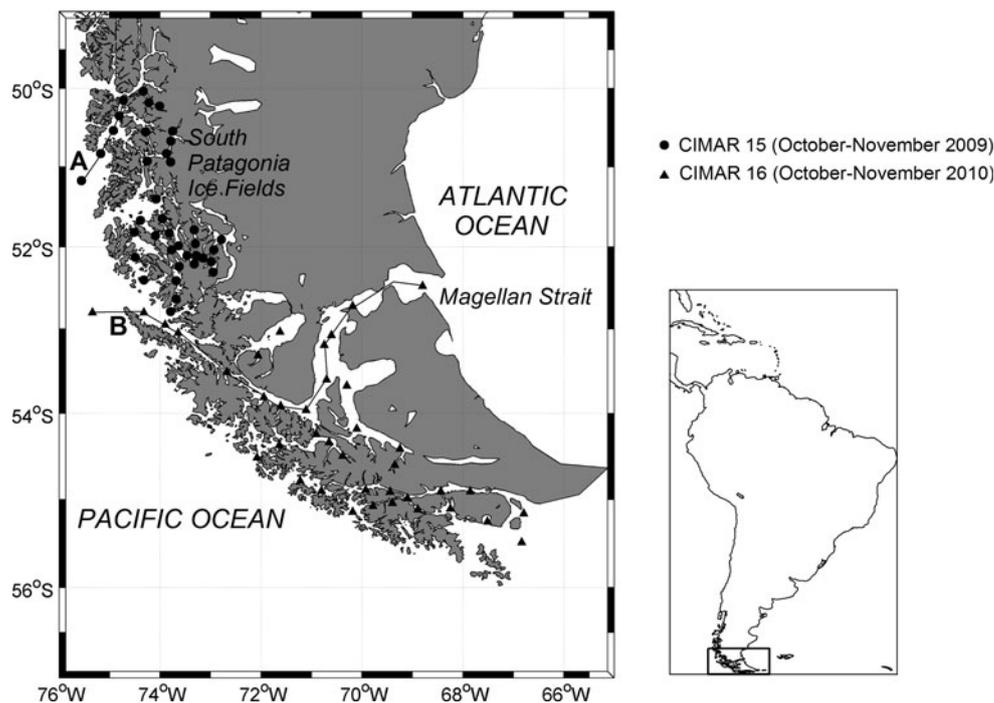
Field sampling

During October–November 2009 and 2010, two bio-oceanographic cruises were carried out between 50°07′–52°45′ S (northern area) and 52°26′–55°23′ S (southern area) (Fig. 1; Table 1). At each station the hydrographic features of the water column were measured with vertical casts of a CTD Seabird SB-19 from the surface to 500 m depth or to 10 m above the floor (at station depths <500 m). Zooplankton was captured using oblique tows from 200 m depth to surface or from 10 m above the bottom to surface (in shallower stations) with a 1-m² mouth Tucker trawl (300 μm mesh size) equipped with a General Oceanics flow meter mounted in the frame of the net to estimate the filtered seawater. Filtered seawater fluctuated from 22.71 to 897.23 m³ tow⁻¹ (mean ± standard deviation 221.94 ± 150.94 m³ tow⁻¹) during 2009, and from 32.63 to 631.60 m³ tow⁻¹ (264.04 ± 132.09 m³ tow⁻¹) during 2010. Once onboard, nets were washed and plankton samples were initially fixed in 5 % formalin buffered with sodium borate and then preserved in 96 % ethanol.

Laboratory work

All fish larvae from plankton samples were picked out from the net samples, counted and identified to the lowest taxonomic level. Larval *B. parini* and *P. tessellata* were identified following descriptions of Uribe and Balbontin (2005) and Poliglieddu and Saccullo (1997). Abundance values were standardized to individuals (ind.) 10 m⁻², taking into account the number of larvae captured and volume of the seawater filtered by the net. Body length (BL, notochord length in preflexion larvae; standard length in flexion and postflexion larvae), upper jaw length (UJL, from the tip of the snout to the posterior end of the maxilla) and mouth width (MW, in the ventral view, the width between the posterior edges of the maxillae) of all intact larval *B. parini* ($n = 300$) and *P. tessellata* ($n = 62$) were measured under an Olympus SZ61 stereomicroscope attached to a camera (Motic moticam 2500, resolution 5.0 MPixel) using Motic Image Plus 2.0 software. The gut of each larva was dissected and opened lengthwise with fine needles. Under a Motic BA310 microscope, prey items were counted and identified

Table 1 Summary of the information about the two oceanographic cruises carried out in southern Patagonia during austral spring 2009–2010

Cruise	CIMAR 15 (northern region)	CIMAR 16 (southern region)
Date	10/11/2009–10/19/2009	10/11/2010–10/19/2010
Range	50°07″S–52°45″S	52°26″S–55°23″S
Stations	38	39
Temperature (°C)	8.26 ± 0.86 (1.42–9.47)	7.06 ± 0.66 (5.27–8.28)
Salinity	31.59 ± 3.15 (14.63–33.48)	31.49 ± 1.13 (26.73–33.29)

to the lowest possible taxon, except for indigestible prey remains such as setae. The maximum BL and width of each prey item (maximum prey width, MPW) were measured with the microscope and a Motic moticam 2500 camera (resolution 5.0 MPixel) using the Motic Image Plus 2.0 software. The volume of each prey item was estimated using the three-dimensional shape that most closely resembled the item, following Cass-Calay (2003) and Sun and Liu (2003). Only the prosome length of copepodite prey was measured, since the urosome was often missing.

Data analysis

The relationships between the variables BL, UJL and MW and UJL and MPW were determined separately for each species by linear regression analyses. Comparisons of slopes were performed with one-way ANCOVA (Zar 1999).

All larvae with identifiable prey in their guts were used for the analysis. The diet was described using the percentage frequency of occurrence of each diet item in the guts examined (%F, i.e., the percentage of guts in which a certain prey taxon occurred), the percentage of the number of each diet item in the total number of diet items found in the guts examined (%N) and the percentage of the volume of each diet item in the total volume of all prey items found in the guts examined (%V). An index of relative importance (IRI) was calculated for each prey item as follows: $IRI = (\%N + \%V) \times \%F$. To readily allow comparisons among prey items, the IRI values were standardized to percentages (%IRI) in the sum of the IRI values across all prey items (Cortés 1997).

Feeding incidence (FI) was calculated as the percentage of the number of larvae that had gut contents in the total number of larvae examined for each species and for the daytime and nighttime samples. Following Sassa and Kawaguchi (2004), the larvae collected between 1 h after sunrise and 1 h before sunset were considered 'daytime' samples, while those gathered between 1 h after sunset and 1 h before sunrise were considered 'nighttime' samples. Comparisons between daytime and nighttime samples were carried out with contingency tables.

To estimate the feeding success of larvae during their development, three measures were compared: number of prey items per gut (PIPG, number), maximum prey width (MPW, mm) and total prey volume per gut (TPVG, mm^3) (Reiss et al. 2002; Landaeta et al. 2011b). To determine whether these indicators of feeding success were related to the growth of larvae, simple linear regressions were carried out between indicators (PIPG, MPW and TPVG) and body length of both larval species. If the slope of the regression (β) was significantly different from zero ($P < 0.05$), feeding success was assumed to be related to larval size. The comparison of the feeding success between the two

species was carried out by using Mann–Whitney U tests, because the feeding success in one species was independent of the larval size (see 'Results').

Intraspecific differences in prey size were examined throughout larval development. Pearre's trophic niche breadth (Pearre 1986) was adopted to analyze the relationship between prey size and predator size. This model uses the standard deviation (SD) of the $\log_{10}$-transformed prey size as a measure of trophic niche breadth. In this analysis, fish larvae were classified according to body length at 1-mm intervals. Only classes with >2 prey item in the gut were used for further analysis. The mean and SD of the $\log_{10}$-transformed prey width were calculated for each available size class of larval fish. The relationship between body length and the corresponding mean and SD of the $\log_{10}$-transformed prey size was examined using linear regression analysis to determine any shifts in niche breadth with growth.

Diet overlap was measured using a variety of similarity indices: Baroni-Urbani and Buser, Czekanowski, Mountford, Dice, percentage similarity (PS) and Bray–Curtis (for equations see Wolda 1981). Because the mouth gape at size differs between species (see 'Results'), comparisons of diet overlap between larval B. parini and P. tessellata were carried out for four mouth gape classes (instead of larval size classes): <890, 891–1,400, 1,401–1,800 and >1,800 μm.

Results

Physical setting

Oceanographic conditions showed important differences in the spatial structure of the water column of southern Patagonia during austral spring (Fig. 2). A slight decrease in temperature was observed between CIMAR 15 (northern region) and CIMAR 16 (southern region) cruises (Table 1), with the southernmost area being colder than the northern zone. However, areas near the South Patagonia Ice Fields (SPIF) showed the influence of very cold water (1.42 °C) because of ice melting. These influences are noticeable in transect A (Fig. 1), where the stations near the SPIF showed a surface (down to 30 m depth, Fig. 2a) tongue of cold water (less than 5 °C). Salinity also showed a similar spatial pattern, with the melted water reducing the salinity of the seawater, producing a surface layer (less than 15 m depth) of brackish water (less than 25) and salinity fronts along the transect (Fig. 2b). These features produce an important vertical stratification near the SPIF and along the channels, and vertical mixing was observed over the shelf.

The Magellan Strait, on the other hand, showed a vertically homogeneous water column, because tidal mixing exceeds freshwater inputs, resulting in a well-mixed water column and the disappearance of the vertical gradient
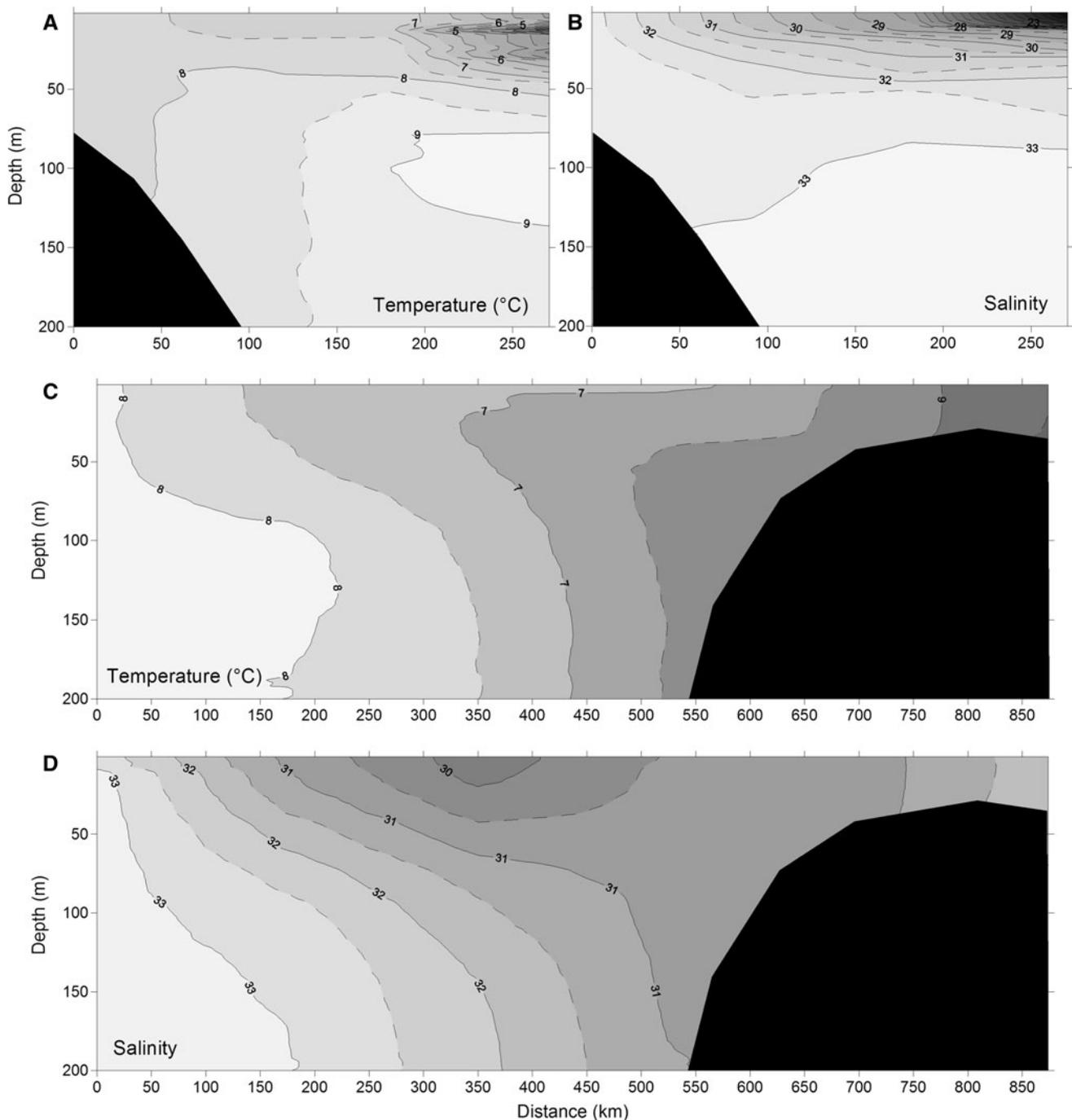
Fig. 2 Oceanographic conditions during 2009 and 2010. Water column conditions off Southern Patagonia Ice Field (SPIF). **a** Temperature (°C) section. **b** Salinity section. Water column conditions along the Magellan Strait. **c** Temperature (°C) section. **d** Salinity section

(Fig. 2c). The snow and ice melting did not affect the surface salinity much, with values around 30–33 in the first 50 m depth (Fig. 2d).

Distribution and abundance of fish larvae

In general, the abundance of fish larvae was low (Fig. 3). Larval *B. parini* showed an important aggregation north and south of SPIF and over the Pacific-influenced waters of the Magellan Strait (Fig. 3). Larval *P. tessellata* coincided spatially in its distribution in the northern area with *B. parini*, but in the southern area, larvae were collected in the middle of the Magellan Strait and in the Atlantic-influenced waters (Fig. 3). In the north zone, larvae of *B. parini* varied in abundance from 5.68 to 222.79 ind. 10 m^{-2} (53.91 ± 75.41 ind. 10 m^{-2}); larval *P. tessellata* abundance

Fig. 3 Larval abundance (individuals 10 m^{-2}) of *B. parini* (*upper panel*) and *P. tessellata* (*lower panel*) during the spring 2009 (*black dots*) and 2010 (*black triangles*)
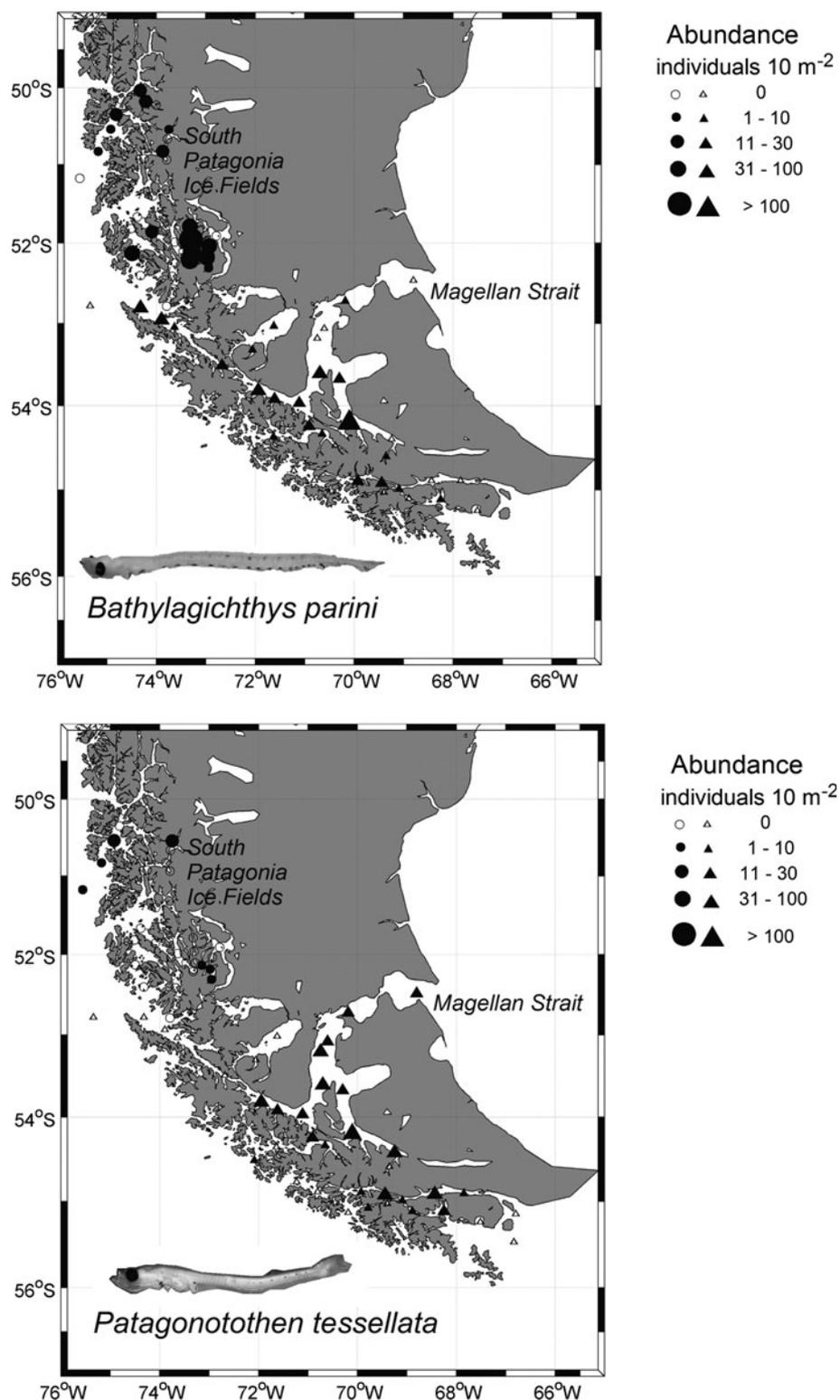
was from 3.78 to 17.03 ind. 10 m^{-2} (9.49 ± 5.43 ind. 10 m^{-2}). In the south zone, abundance of larval *B. parini* ranged from 1.56 to 315.87 ind. 10 m^{-2} (36.91 ± 70.16 ind. 10 m^{-2}), while abundance of *P. tessellata* varied from 3.27 to 154.71 ind. 10 m^{-2} (33.05 ± 37.39 ind. 10 m^{-2}).

Body length and mouth gape relationships

A total of 300 larval *B. parini* were measured, ranging from 4.12 to 17.14 mm BL (7.61 ± 1.98 mm BL). Upper jaw length (UJL) and mouth width (MW) varied from 320.9 to

1,349.5 μm (624.17 ± 164.36 μm) and from 186.8 to 1,029.8 μm (436.25 ± 107.65 μm), respectively (Fig. 4). UJL and MW of *B. parini* corresponded to 3.60–15.31 %BL (8.28 ± 1.20 %BL) and 3.10–10.97 %BL (5.80 ± 0.91 %BL), respectively. UJL was larger at size than MW (one-way ANCOVA, $F = 795.2$, $P < 0.001$), and during ontogeny, UJL of larval *B. parini* increased at a faster rate (70.24 μm UJL mm BL^{-1}) than MW (44.80 μm UJL mm BL^{-1}, homogeneity of slopes, $F = 62.79$, $P < 0.001$) (Fig. 4; Table 2).

Only 62 larval *P. tessellata* were collected, varying from 3.79 to 17.07 mm BL (7.48 ± 2.96 mm BL). UJL varied from 344.0 to 2,804.8 μm (879.94 ± 492.85 μm), and MW varied from 97.80 to 1,897.70 μm (553.31 ± 370.46 μm). UJL and MW of *P. tessellata* corresponded to 5.84–18.72 %BL (11.47 ± 3.11 %BL) and 1.71–22.11 %BL (7.15 ± 3.08 %BL), respectively. Similarly, UJL was larger at size than MW (one-way ANCOVA, $F = 42.7$, $P < 0.001$), and during ontogeny, UJL of larval *P. tessellata* increased at a faster rate (140.22 μm UJL mm BL^{-1}) than MW (86.83 μm UJL mm BL^{-1}, homogeneity of slopes, $F = 10.38$, $P = 0.0016$) (Fig. 4; Table 2).

When mouth gape relationships were compared between species, *P. tessellata* showed larger mouth gape at size compared to those of *B. parini* (for UJL: one-way ANCOVA, $F = 147.1$, $P < 0.001$; for MW: one-way ANCOVA, $F = 89.9$, $P < 0.001$) (Fig. 4). Also, the growth rate of mouth gape in relation to body length was also faster for *P. tessellata* than for *B. parini* (Table 2, homogeneity of slopes, for UJL: $F = 98.01$, $P < 0.001$; for MW: $F = 41.11$, $P < 0.001$). However, the relationship between UJL and MW did not vary between species (one-way ANCOVA, $F = 1.68$, $P = 0.194$, Table 2; Fig. 4).

Dietary composition

A total of 11 and 14 different prey items were detected in the guts of *B. parini* and *P. tessellata*, respectively, in the northern and southern zone (Table 3). *B. parini* larvae showed a high percentage of largely digested prey items (unidentified and chitinous remains, 54.24 and 13.35 % of %IRI, respectively), suggesting that digestion occurs fast. Also, during the larval development, feeding was on the basis of phytoplankton (diatoms of the genus *Fragilaria*), zooplankton (several life stages of copepods, invertebrate eggs, ostracods) and even fecal pellets (from appendicularians), showing an omnivorous tactic. Numerically, invertebrate eggs and fecal pellets were the most important items in the diet (Table 3). Volumetric and most frequent prey items were unidentified (highly digested) and chitinous remains, explaining the high percentage of IRI% (67.6 %) in the gut contents. Most of the identified prey are static (eggs, 15.35 %; fecal pellets, 4.82 %; diatoms, 3.12 %) or show slow movements in the water column (copepod nauplii, 4.86 %).

Larval *P. tessellata* showed a diet based exclusively on zooplankton, being carnivorous in its feeding (Table 3). Numerically, the most important prey taxa were calanoid copepodites (25.11 %) and *Calanus simillimus* (23.81 %), being also the most frequent prey in the guts (93.55 and 85.48 %, respectively). Volumetrically, chitinous remains and *C. simillimus* were dominant (Table 3). Diet of larval *P. tessellata* was largely dominated by different life stages of copepods (74.25 %IRI), mostly adult copepods (41.36 %).

Feeding incidence and feeding success

The feeding incidence (FI) of all larval *B. parini* examined was low ($FI = 26.67$ %). It did not differ between locations (northern vs southern areas, $\chi^2 = 0.338$, $df = 1$, $P = 0.561$), but it was higher in larvae collected during day compared to those captured at night ($FI = 46.96$ and 14.05 %, respectively; $\chi^2 = 39.3$, $df = 1$, $P < 0.001$), suggesting that feeding occurs mostly during daylight. On the other hand, FI of larval *P. tessellata* was high ($FI = 70.97$ %) and significantly greater than that of *B. parini* ($\chi^2 = 44.8$, $df = 1$, $P < 0.001$). FI of *P. tessellata* differs between day and night, with more feeding at night (84.21 % at night, 50 % at day, $\chi^2 = 8.36$, $df = 1$, $P = 0.004$). This result suggests that larval *P. tessellata* are able to feed with low light intensities and/or it is a nocturnal feeder.

Total prey items identified in the guts of larval *B. parini* ranged from 0 to 12 preys (3.25 ± 2.88 prey, excluding zeros, median = 2). There was no significant relationship between the number of prey per gut (NPPG) and the body length ($r^2 = 0.0006$, $F = 0.047$, $P = 0.828$, Fig. 5), nor between the total volume of prey per gut (TVPG) and the body length ($r^2 = 0.002$, $F = 0.142$, $P = 0.707$, Fig. 5), indicating that *B. parini* does not increase the feeding success throughout their larval development. There was no relationship between maximum prey width (MPW) and body length ($r^2 = 0.0059$, $F = 1.479$, $P = 0.224$, Fig. 5); therefore, larger larvae do not prey over larger or bigger prey.

For larval *P. tessellata*, total prey items ranged from 0 to 20 preys (6.13 ± 5.07 prey, median = 4). There was a significant increase in the number of prey per gut and total volume of prey per gut with increasing body length (NPPG: $r^2 = 0.397$, $F = 27.69$, $P < 0.001$; TVPG: $r^2 = 0.356$, $F = 23.25$, $P < 0.001$) (Fig. 5). Also, the MPW was positively and significantly related to BL ($F = 28.33$, $P < 0.001$), although the model explained only the 10.8 % of the variability in the data (Fig. 5).

Trophic niche breadth

Niche breadth was independent of larval size and did not change during larval development (regression analysis,
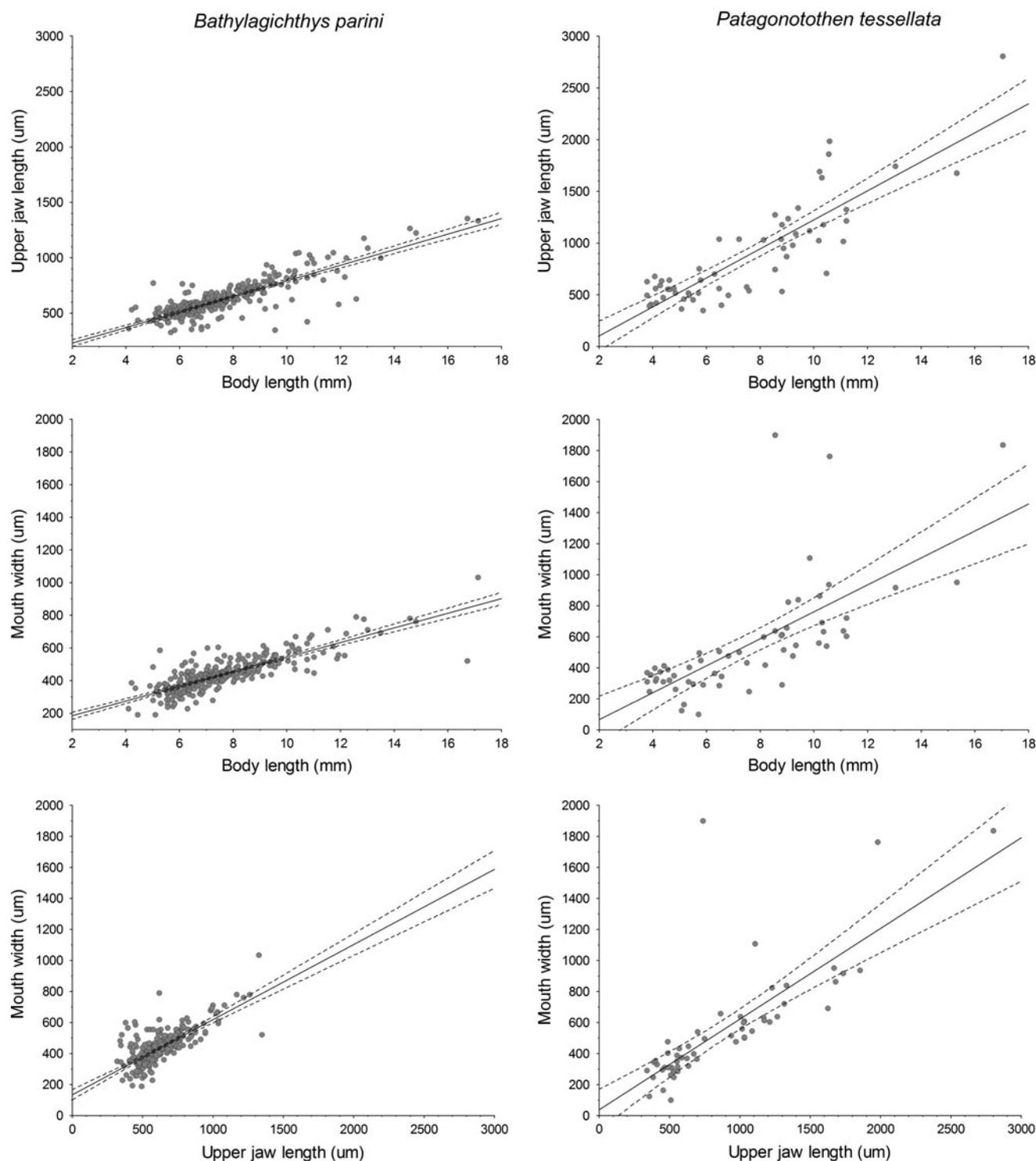
Fig. 4 Comparison of morphometric relationships of mouth gape (upper jaw length, mouth width, in μm) and body length (in mm) for larval *B. parini* (*left panel*) and *P. tessellata* (*right panel*)

$P > 0.1$, Table 4; Fig. 6), nor for larval *B. parini* or for *P. tessellata*. The average niche breadth (SD) of *B. parini* and *P. tessellata* were 0.26 ± 0.12 and 0.21 ± 0.05, respectively.

Diet overlap

All measured similarity indices showed a similar trend throughout the variation in the mouth gape between larval

Table 2 Linear regression models of the morphometric relationships between body length (BL, mm) and mouth gape (upper jaw length, UJL; mouth width, MW) of larval *B. parini* and *P. tessellata* collected in the Magellan region during austral spring 2009–2010

α intercept, β slope, *SE* standard error

Model	α	SE	β	SE	r^2	F	P
B. parini							
BL versus UJL	89.71	20.71	70.24	2.63	0.71	710.53	<0.001
BL versus MW	95.32	14.41	44.80	1.83	0.68	597.42	<0.001
UJL versus MW	133.79	16.81	0.48	0.02	0.55	345.81	<0.001
P. tessellata							
BL versus UJL	−177.63	93.01	140.22	11.48	0.72	149.09	<0.001
BL versus MW	−106.96	97.47	86.83	11.95	0.49	52.78	<0.001
UJL versus MW	37.92	66.11	0.58	0.06	0.60	81.02	<0.001

Table 3 Diet composition of larval *B. parini* and *P. tessellata* from the Magellan region, austral spring 2009–2010

Prey taxa	*B. parini*				*P. tessellata*			
	% N	% V	% F	% IRI	% N	% V	% F	% IRI
Fragilaria sp.	12.06	1.24	10	3.121	–	–	–	–
Bivalvia D larva	1.56	0.90	5	0.288	0.43	0.03	1.61	0.006
Invertebrate egg	17.51	1.02	18.75	8.151	–	–	–	–
Pluteus larva	–	–	–	–	0.43	0.10	1.61	0.007
Copepod egg	14.01	1.33	20	7.200	4.76	0.06	17.74	0.722
Copepod nauplius	6.23	6.98	12.5	3.873	12.99	1.35	48.39	5.858
Calanoid copepodite	7.39	11.06	11.25	4.871	25.11	8.19	93.55	26.303
Aetideus arcuatus	–	–	–	–	7.79	9.44	29.03	4.225
Calanoides patagoniensis	–	–	–	–	1.30	10.60	4.84	0.486
Calanus simillimus	–	–	–	–	23.81	25.57	85.48	35.639
Paracalanus indicus	–	–	–	–	3.90	4.03	14.52	0.971
Phaenna spinifera	–	–	–	–	0.43	0.01	1.61	0.006
Rhincalanus nasutus	–	–	–	–	0.87	0.64	3.23	0.041
Zoea	–	–	–	–	1.30	0.19	4.84	0.061
Mysis	–	–	–	–	1.30	1.19	4.84	0.102
Ostracoda	0.39	0.02	1.25	0.012	–	–	–	–
Salp	0.39	0.00	1.25	0.012	–	–	–	–
Fecal pellet Appendicularia	16.34	1.94	11.25	4.826	–	–	–	–
Chitinous remains	8.95	21.41	18.75	13.359	15.15	38.48	56.45	25.565
Unidentified	14.40	54.10	33.75	54.242	0.43	0.13	1.61	0.008
Setae	0.78	–	2.5	0.046	–	–	–	–

species (Fig. 7; Table 5). Dice, Mountford and Bray–Curtis indices showed a decreasing trend in the diet overlap as mouth gape increases, while Baroni, Czekanowski and PS indices showed a slight increase in the diet overlap from individuals with the smallest upper jaw length to the second size class (891–1,400 µm) and then a steep decrease in the similarity (Fig. 7). Therefore, as larvae of both species grow, their diet overlap diminishes.

Discussion

Marine fish larvae inhabiting the peri-Antarctic region of Magellan and Fuegian zones of South America showed

different tactics in their feeding, during the austral spring. Both species were collected along the southern tip of South America in low abundance during austral spring 2009 and 2010. Larvae of the bathylagid fish *B. parini* showed a lower increase in the mouth gape at size, predates during day hours mostly over nonmotile prey from different types (phytoplankton, zooplankton and fecal pellets). There is no increase in its feeding success with increasing larval size, and the niche breadth is independent of larval size. On the other hand, larvae of the nototheniid fish *P. tessellata* showed a large mouth gape at size, which may partially explain the predation on motile prey like large calanoid copepods (*C. simillimus*). They are nocturnal feeders whose diet is exclusively carnivorous, feeding over more
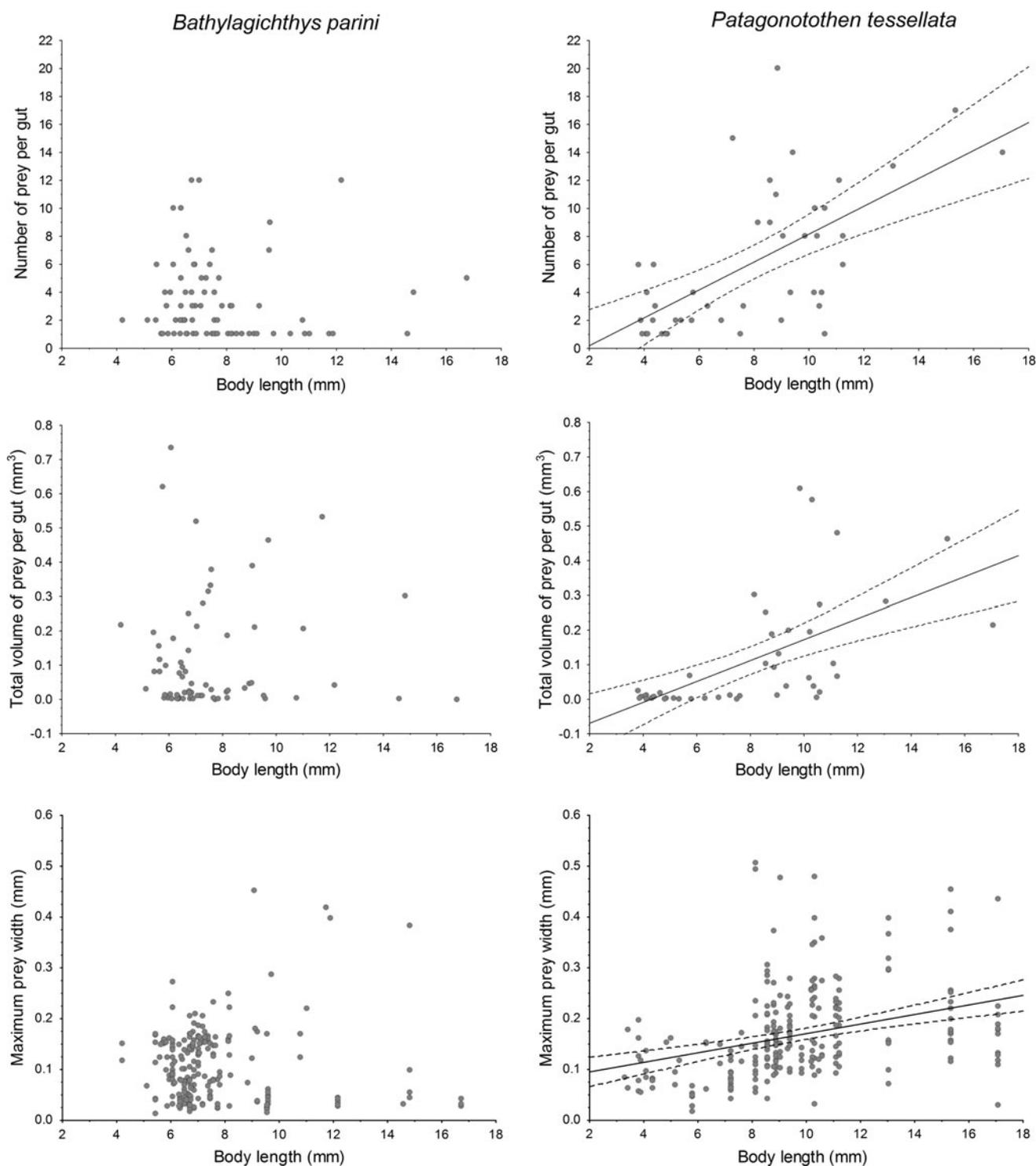
Fig. 5 Variation in feeding success (number of prey per gut, total volume of prey per gut, maximum prey width) throughout larval development of larval *B. parini* (*left panel*) and *P. tessellata* (*right panel*)

and large prey during their larval development; nonetheless, niche breadth is also independent of larval size. Finally, diet overlap was important only in individuals with smaller mouth gape and diminished as larvae (and their jaw) grow.

Larvae of *B. parini* have been collected throughout the fjord zone of Chilean Patagonia (41°30′S–56°00′S), although they have been found in low mean abundance (41°30′–46°S, 13.31 larvae 10 m^{-2}, Bustos et al. 2008; 46°48′–50°S, 14.04–19.81 larvae 10 m^{-2}, Bustos et al.

Table 4 Linear regression analysis of trophic niche breadth (SD of $\log_{10}$-transformed prey size) as a function of the body length

	Bathylagichthys parini	*Patagonotothen tessellata*
Intercept	0.383	0.154
SE	0.124	0.041
Slope	−0.012	0.005
SE	0.011	0.003
r^2	0.149	0.163
F	1.05	1.95
P	0.344	0.192

SE standard error
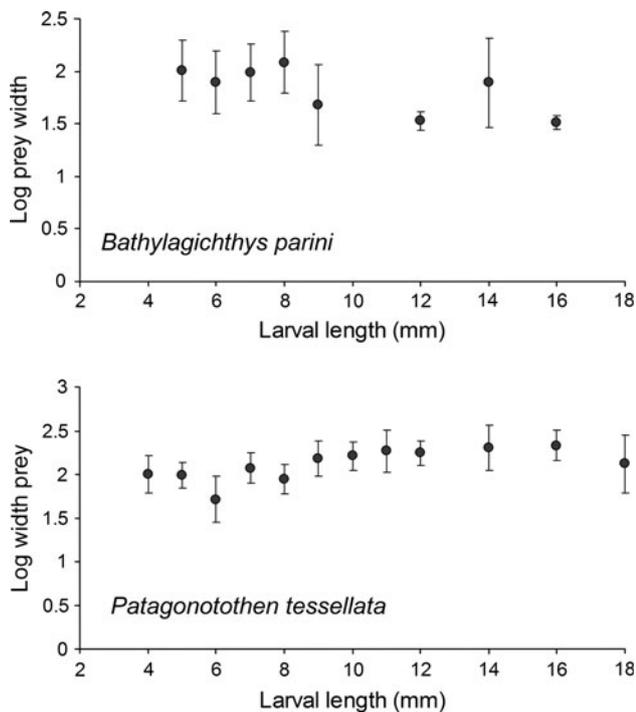
Fig. 6 Variation in trophic niche breadth throughout larval development of larval *B. parini* (*upper panel*) and *P. tessellata* (*lower panel*)

2011). Our results indicate a two- to threefold increase in larval abundance of this species along southern Patagonia (50°–56°S, 36.91–53.91 larvae 10 m^{-2}). Similarly, larvae of nototheniid fish are scarcely collected in coastal waters north of 53°S (Bustos et al. 2011), suggesting that the area around the Magellan Strait is the preferred zone for reproduction (Bernal and Balbontín 2003, this study). Therefore, larval stages of both species are likely to co-occur in the water column of the Magellan region during the austral spring and summer seasons.

Morphological differences were evident among both larval species. Larval *B. parini* showed a low increase in the jaw length with respect to body length ($\sim$70 μm UJL
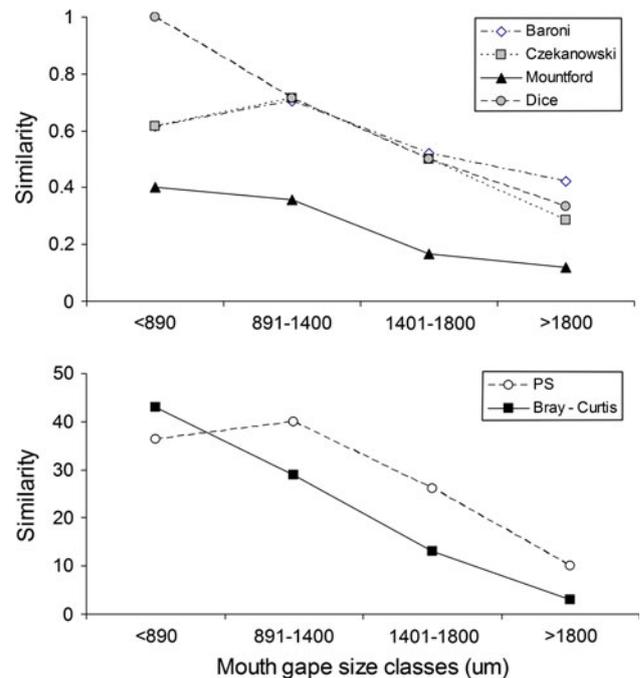
Fig. 7 Diet overlap between larval *B. parini* and *P. tessellata* compared by mouth gape size classes, by using a series of similarity indices

mm BL^{-1}), because of its elongated body and relatively small mouth size (Uribe and Balbontin 2005); this is similar to those described for larval *Notolepis rissoi* (64 μm UJL mm BL^{-1}, Sabatés and Saiz 2000). This contrasts with the relationship observed in larval *P. tessellata*, which is two times larger than *B. parini* ($\sim$140 μm UJL mm BL^{-1}) and similar to myctophid larvae (Sabatés and Saiz 2000; Rodríguez-Graña et al. 2005). Large mouth gape at size can be related to an increase in prey size and number, relationships not evidenced in larval *B. parini*.

Alexander (1967) stated that fishes with smaller mouths can better suck in their prey, whereas fishes with larger mouths can better grasps prey from the side. Therefore, larval *B. parini* would be better at sucking in nonmotile prey, and *P. tessellata* would be better at grasping a greater diversity of large and more elusive prey (mostly copepods). Observations of *Leuroglossus stilbius* (Bathylagidae) suggest that they can slowly approach larvaceans in their houses and locate the animal either by the beating of its tail or from their bioluminescence created by organisms living on or in contact with its houses. They can then suck the larvacean out, ingest the whole complex, or scare the animal away from its house and then catch it and suck it in (Cailliet and Ebeling 1990).

A mechanism like that may explain the large amount of fecal pellets found in the gut content of larval *B. parini*. Feeding over fecal pellets has been observed in larval myctophid (*Diaphus garmani*, Sassa and Kawaguchi

Table 5 Diet overlap between larvae of *B. parini* and *P. tessellata* estimated by several similarity indices

UJL (μm)	Baroni	Czekanowski	Mountford	Dice	PS	Bray–Curtis
<890	0.615	0.615	0.400	1.000	36.32	43
891–1,400	0.703	0.714	0.357	0.714	39.91	29
1,401–1,800	0.519	0.500	0.167	0.500	26.11	13
>1,800	0.422	0.286	0.118	0.333	10	3

PS percentage similarity

2004), pleuronectid (*Parphrys vetulus*, Gadomski and Boehlert 1984) and leptocephali (Congridae, Muraenidae, Muraenesocidae, Nettastomatidae and Ophichthidae, Mochioka and Iwamizu 1996) from oceanic waters, and scombrid larvae (*Euthynnus lineatus*, Sánchez-Velasco et al. 1999) from the Gulf of California. This is the first report of fish larvae feeding on appendicularian houses and their fecal pellets in a peri-Antarctic region. The houses contain large amount of organic material, such as phytoplankters, protozoans and appendicularian fecal pellets, and are of fundamental dietary importance in leptocephali larvae (Riemann et al. 2010).

Differences were also detected in the feeding incidence of larvae collected during daytime and nighttime, with larval *B. parini* being a daytime feeder while larval *P. tessellata* is a night/crepuscular feeder. Because of the small size and generally low mobility of the prey items of *B. parini*, it is plausible that *B. parini* larvae need sunlight for the detection of prey, as it has been reported for most fish larvae (Sabatés and Saiz 2000; Sabatés et al. 2003; Conley and Hopkins 2004; Sassa and Kawaguchi 2004, 2005; Rodríguez-Graña et al. 2005; Sassa 2010). Predation on large, motile prey may increase the chance to capture prey at low light intensities, as known for larval fish inhabiting deep waters such as *Myctophum selenops* (Conley and Hopkins 2004), postlarval *Protomyctophum thompsoni* (Sassa and Kawaguchi 2005), *Merluccius merluccius* (Morote et al. 2011) and *Maurolicus parvipinnis* from Chilean Patagonia (Landaeta et al. 2011b). Differences in the timing when FI increases among larval species from the Magellan zone potentially may reduce any competition for food during early life stages, when diet overlap is largest.

In addition, a larger FI was observed in larval *P. tessellata* compared with larval *B. parini*. Larval fish with straight intestinal tract, such as clupeoids and bathylagids, show low feeding incidence because they tend to evacuate food in response to the trauma of conventional sampling (Munuera Fernández and González-Quirós 2006). Fish larvae with coiled gut (such as *P. tessellata*) have a limited distribution of cholecystokinin (CCK), a major regulatory hormone of digestion (Rønnestad et al. 2003), that may account for digestion time.

The Magellan region is an area with low chlorophyll *a* (Chl*a*) concentration (0.01–1.01 mg m^{-3}), and primary productivity (0.24–4.74 mg C m^{-3} h^{-1}) is performed mainly by pico–nano-fractions of the phytoplankton assemblages during the majority of the year (Saggiomo et al. 2011). In this environment, *Calanus simillimus* overwinters at late copepodite stages at depths >250 m and rises to spawn the following spring (Miralto et al. 1998), temporally matching with larval *P. tessellata*, being their most preferred prey. Several studies (Miralto et al. 1998; Antezana et al. 2002; Zagami et al. 2011) have detected aggregations of calanoid copepods in semi-enclosed areas (e.g., Paso Ancho, in the middle of the Magellan Strait), at similar locations where large abundance of larval *P. tessellata* was found. Antezana et al. (2002) showed important differences in abundance of copepods in surface waters during daytime and nighttime, with values being larger during night. This finding suggests that calanoid copepods are particularly abundant in surface waters during crepuscular times and nighttimes, being available for the feeding of larval *P. tessellata*.

In conclusion, in the peri-Antarctic Magellan region, larvae of two fish species display different foraging tactics, one preferring nonmotile prey in the water column during daytime and the other feeding primarily on motile prey in the nighttime, thus reducing their trophic overlap throughout their development in a region characterized by low biological productivity. This study highlights the importance of the trophic interactions between phyto-, zoo- and ichthyoplankton. In a scarcely investigated area, our data can be utilized as a baseline for evaluating the environmental threats of large-scale open-pit coal mining activities started at Isla Riesco, Magellan Strait, in 2012.

References

Alexander RM (1967) Functional design in fishes. Hutchingson and Co., London, p 164

Aniya M (1996) Holocene variations of Ameghino Glacier, southern Patagonia. Holocene 6:247–252

Antezana T, Giraldo A, Hamamé M (2002) Chlorophyll and size-fractionated zooplankton feeding, within basins of the Magellan and Fuegian fjord system during spring 1998. Cienc Tecnol Mar 25:109–130

Bailey KM, Canino MF, Napp JM, Spring SM, Brown AL (1995) Contrasting years of prey levels, feeding conditions and mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. Mar Ecol Prog Ser 119:11–23

Balbontín F, Bernal R (1997) Distribución y abundancia del ictioplancton en la zona austral de Chile. Cienc Tecnol Mar 20:155–163

Balbontín F, Bernal R (2005) Cambios estacionales en la composición y abundancia del ictioplancton de los canales australes entre el Golfo de Corcovado y Golfo Elefantes, Chile. Cienc Tecnol Mar 28:99–111

Bernal R, Balbontín F (1999) Ictioplancton de los fiordos entre el Golfo de Penas y Estrecho de Magallanes y factores ambientales asociados. Cienc Tecnol Mar 22:143–154

Bernal R, Balbontín F (2003) Distribution and abundance of fish larvae from the Strait of Magellan to the Cape Horn, Chile. Cienc Tecnol Mar 26:85–92

Bustos CA, Landaeta MF, Balbontín F (2008) Environmental effects on the spatial variability of the ichthyoplankton from southern Chile during November 2005. Rev Chil Hist Nat 81:205–219

Bustos CA, Landaeta MF, Balbontín F (2011) Ichthyoplankton spatial distribution and its relation with water column stratification in fjords of southern Chile (46°48′S–50°09′S) in austral spring 1996 and 2008. Continent Shelf Res 31:293–303

Cailliet GM, Ebeling AW (1990) The vertical distribution and feeding habits of two common midwater fishes (*Leuroglossus stilbius* and *Stenobrachius leucopsarus*) off Santa Barbara. CalCOFI Rep 31:106–123

Cass-Calay SL (2003) The feeding ecology of larval Pacific hake (*Merluccius productus*) in the California Current region: an updated approach using a combined OPC/MOCNESS to estimate prey biovolume. Fish Oceanogr 12:34–48

Conley WJ, Hopkins TL (2004) Feeding ecology of lanternfish (Pisces: Myctophidae) larvae: prey preferences as a reflection of morphology. Bull Mar Sci 75:361–379

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Fish Aquat Sci 54:726–738

Dávila PM, Figueroa D, Müller E (2002) Freshwater input into the coastal ocean and its relation with the salinity distribution off austral Chile (35–55°S). Continent Shelf Res 22:521–534

Fiksen Ø, Aksnes DL, Flyum MH, Giske J (2002) The influence of turbidity on growth and survival of fish larvae: a numerical analysis. Hydrobiologia 484:49–59

Fortier L, Gilbert M, Ponton D, Ingram RG, Robienau B, Legendre L (1996) Impact of freshwater on a subarctic coastal ecosystem under seasonal sea ice (southeastern Hudson Bay, Canada). III. Feeding success of marine fish larvae. J Mar Sys 7:251–265

Gadomski DM, Boehlert GW (1984) Feeding ecology of pelagic larvae of English sole *Parophrys vetulus* and butter sole *Isopsetta isolepis* off the Oregon coast. Mar Ecol Prog Ser 20:1–20

Gilbert M, Fortier L, Ponton D, Drolet R (1992) Feeding ecology of marine fish larvae across the Great Whale River plume in seasonally ice-covered southeastern Hudson Bay. Mar Ecol Prog Ser 84:19–30

Hamame M, Antezana T (2010) Vertical diel migration and feeding of *E. valentini* within southern Chilean fjords. Deep Sea Res II 57:642–651

Hüne M, Ojeda J (2012) Structure of the coastal fish assemblage from the channels and fjords of central Chilean Patagonia (48°–52°S). Rev Biol Mar Oceanogr 47:451–460

Hüne M, Rivera G (2010) Contribution of polychaetes (Annelida: Polychaeta) in the diet of three Notothenioids species (Perciformes: Notothenioidei) from the Magellan region. An Inst Patagonia 38:39–46

Kobyliansky SG (1990) Two new species of the genus *Bathylagichthys* Kobyliansky (Bathylagidae: Salmoniformes) from Southern Hemisphere subpolar waters. J Ichthyol 30:21–27

Landaeta MF, Contreras J, Bustos CA (2011a) Chilean fjords: potential nursery ground of *Bathylagichthys parini* (Pisces: Osmeriformes: Bathylagidae). Rev Biol Mar Oceanogr 46:67–71

Landaeta MF, Suárez-Donoso N, Bustos CA, Balbontín F (2011b) Feeding habits of larval *Maurolicus parvipinnis* (Pises: Sternoptychidae) in Patagonian fjords. J Plankton Res 33:1813–1824

Marín VH, Delgado LE (2001) The taxocenosis of calanoid copepods in the Magellan inlets: a nested patterns. Cienc Tecnol Mar 24:81–89

Medeiros C, Kjerfve B (1988) Tidal characteristics of the strait of Magellan. Boll Oceanol Teor Appl 9(2–3):261–271

Miralto A, Ianora A, Guglielmo L, Zagami G, Buttino I (1998) Egg production and hatching success in the peri-Antarctic copepod *Calanus simillimus*. J Plankton Res 20:2369–2378

Mochioka N, Iwamizu M (1996) Diet of anguilloid larvae: leptocephali feed selectively on larvacean houses and fecal pellets. Mar Biol 125:447–452

Moreno CA, Jara HF (1984) Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fueguian Islands, Chile. Mar Ecol Prog Ser 15:99–107

Morote E, Olivar MP, Bozzano A, Villate F, Uriarte I (2011) Feeding selectivity in larvae of the European hake (*Merluccius merluccius*) in relation to ontogeny and visual capabilities. Mar Biol 158:1349–1361

Munuera Fernández I, González-Quirós R (2006) Analysis of feeding of *Sardina pilchardus* (Walbaum, 1792) larval stages in the central Cantabrian Sea. Sci Mar 70(S1):131–139

Nunn AD, Tewson LH, Cowx IG (2012) The foraging ecology of larval and juvenile fishes. Rev Fish Biol Fisheries 22:377–408

Panella S, Michelato A, Perdicaro R, Magazzù G, Decembrini F, Scarazzato P (1991) A preliminary contribution to understanding the hydrological characteristics of the Strait of Magellan: austral spring 1989. Boll Oceanol Teor Appl 9(2–3):107–126

Pearre S Jr (1986) Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. Mar Ecol Prog Ser 24:299–314

Pequeño G (2000) Fishes of the Cimar-fiordo 3 cruise to the channels of the south Magellan region (ca. 55°S), Chile. Cienc Tecnol Mar 23:83–94

Pequeño G, Matallanas J (2003) *Bathylagichthys parini* (Osmeriformes: Bathylagidae) from Chilean fjords: new morphological data. Cybium 27:242–244

Poliglieddu ML, Saccullo FH (1997) Identificación de larvas y juveniles de *Patagonotothen ramsayi* y *Patagonotothen tessellata* (Pisces, Nototheniidae). Seminario de Oceanografía Biológical, Universidad de Buenos Aires, Argentina. p 41. http://www.oceandocs.net/bitstream/1834/3127/1/Poliglieddu_1997.pdf

Rae GA, Calvo J (1995a) Annual gonadal cycle and reproduction in *Patagonotothen tessellata* (Richardson, 1845) (Nototheniidae: Pisces) from the Beagle Channel, Argentina. J Appl Ichthyol 11:60–70

Rae GA, Calvo J (1995b) Fecundity and reproductive habits in *Patagonotothen tessellata* (Richardson, 1845) from the Beagle Channel, Argentina. Antarct Sci 7:235–240

Rae GA, Calvo J (1996) Histological analysis of gonadal development in *Patagonotothen tessellata* (Richardson 1845) (Nototheniidae: Pisces) from the Beagle Channel, Argentina. J Appl Ichthyol 12:31–38

Rae GA, San Roman NA, Spinoglio DE (1999) Age validation and growth of yolked larvae of *Patagonotothen tessellata* (Richardson, 1845) (Pisces: Nototheniidae) from the rocky littoral of the Beagle Channel, Argentina. Sci Mar 63(suppl 1):469–476

Reiss CS, Anis A, Taggart CT, Dower JF, Ruddick B (2002) Relationships among vertically structured in situ measures of turbulence, larval fish abundance and feeding success and copepods on Western Bank, Scotian Shelf. Fish Oceanogr 11:156–174

Riemann L, Alfredsson H, Hansen MM, Als TD, Nielsen TG, Munk P, Aarestrup K, Maes GE, Sparholt H, Petersen MI, Bachler M, Castonguay M (2010) Qualitative assessment of the diet of European eel larvae in the Sargasso Sea resolved by DNA barcoding. Biol Lett 2010: rsbl.2010.0411v1-rsbl20100411

Rodríguez-Graña L, Castro L, Loureiro M, González HE, Calliari D (2005) Feeding ecology of dominant larval myctophids in an upwelling area of the Humboldt Current. Mar Ecol Prog Ser 290:119–134

Rønnestad I, Tonheim SK, Fyhn HJ, Rojas-García CR, Kamisaya Y, Koven W, Finn RN, Terjesen BF, Barr Y, Conceição LEC (2003) The supply of amino acids during early feeding stages of marine fish larvae: a review of recent findings. Aquaculture 227:147–164

Sabatés A, Saiz E (2000) Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. Mar Ecol Prog Ser 201:261–271

Sabatés A, Bozzano A, Vallvey I (2003) Feeding pattern and the visual light environment in myctophid fish larvae. J Fish Biol 63:1476–1490

Saggiomo V, Santarpia I, Saggiomo M, Margiotta F, Mangoni O (2011) Primary production processes and photosynthetic performance of a unique periantarctic ecosystem: the Strait of Magellan. Polar Biol 34:1255–1267

Sánchez-Velasco L, Contreras-Arredondo I, Esqueda-Escárcega G (1999) Diet composition of *Euthynnus lineatus* and *Auxis* sp. larvae (Pisces: Scombridae) in the Gulf of California. Bull Mar Sci 65:687–698

Sassa C (2010) Feeding ecology of *Symbolophorus californiensis* larvae (Teleostei: Myctophidae) in the southern transition region of the western North Pacific. J Mar Biol Ass UK 90:1249–1256

Sassa C, Kawaguchi K (2004) Larval feeding habits of *Diaphus garmani* and *Myctophum asperum* (Pisces: Myctophidae) in the transition region of the western North Pacific. Mar Ecol Prog Ser 278:279–290

Sassa C, Kawaguchi K (2005) Larval feeding habits of *Diaphus tetha*, *Protomyctophum thompsoni*, and *Tartelonbeania taylori* (Pisces: Myctophidae) in the transition region of the western North Pacific. Mar Ecol Prog Ser 298:261–276

Sassa C, Tsukamoto Y (2012) Inter-annual comparison of diet and daily ration of larval jack mackerel *Trachurus japonicus* in the southern East China Sea. J Plankton Res 34:173–187

Sielfeld W, Guzman G, Amado N (2006) Distribution of rocky shore fishes of the west Patagonian channels (48°37′S–53°34′S). An Inst Patagonia 34:21–32

Sun J, Liu D (2003) Geometric models for calculating cell biovolume and surface area for phytoplankton. J Plankton Res 25:1331–1346

Uribe F, Balbontin F (2005) First description of larvae of *Bathylagichthys parini* (Pisces: Bathylagidae) from the southeastern Pacific. Bull Mar Sci 77:201–207

Wolda H (1981) Similarity indices, sample size and diversity. Oecologia 50:296–302

Zagami G, Antezana T, Ferrari I, Granata A, Sitran R, Minutoli R, Guglielmo L (2011) Species diversity, spatial distribution, and assemblages of zooplankton within the strait of Magellan in austral summer. Polar Biol 34:1319–1333

Zar JH (1999) Biostatistical analysis. Prentice Hall, Upper Saddle River

Zingone A, Sarno D, Siano R, Marino D (2011) The importance and distinctiveness of small-sized phytoplankton in the Magellan Straits. Polar Biol 34:1269–1284