Feeding habits of larval *Maurolicus parvipinnis* (Pisces: Sternoptychidae) in Patagonian fjords

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The feeding ecology of larvae of the lightfish *Maurolicus parvipinnis* (Pisces: Sternoptychidae, 2.8–13.4 mm) in fjords and channels of southern Chile (41°–53°S), was analysed during austral spring 2005, 2008 and 2009. Larvae of *M. parvipinnis* begin external feeding at ~3-mm body length (BL). They are carnivorous predators with similar feeding incidence during day and nighttime, but with higher prey numbers in their guts during day than night. Feeding incidence increased after 8-mm BL, coinciding with an increase in the growth rate of the upper jaw length. The diet of *M. parvipinnis* larvae was composed of 22 different prey items, mainly invertebrate eggs, nauplii, calanoid, cyclopoid and poecilostomatoid copepodites, ostracods, cladocerans and amphipods. According to the relative importance index [%index of relative importance (IRI)], the most important prey items were *Paracalanus parvus* copepodites (%IRI = 55.6%), *Oithona* spp. copepodites (%IRI = 16.3%) and copepod eggs (%IRI = 9.2%), indicating that most of the feeding is on copepod early life stages. Trophic niche breadth was ~0.17 and it did not increase with larval length, suggesting that larval *M. parvipinnis* have a high degree of selective foraging. Also, we detected a significant relation between feeding success and vertical stratification of the water column, with higher prey volume per gut found in larvae collected in areas with a Brunt-Väissälä frequency of 0.07–0.2 cycles s^{-1}. We discuss potential effects of the fjord environment on the feeding behavior of this important species along Chilean Patagonia.

KEYWORDS: *Maurolicus parvipinnis*; *Paracalanus parvus*; nocturnal feeding; Chile

INTRODUCTION

Several factors contribute to fish larvae feeding success, such as the concentration and type of food, turbulence, temperature and light conditions (Blaxter, 1986). The response of fish larvae to particular light characteristics is species specific and varies with the age of the larva or development stage (Sabatés *et al.*, 2003). Most fish larvae are visual feeders, both epipelagic (Morote *et al.*, 2008; Sassa *et al.*, 2008) and mesopelagic species (Sabatés and Saiz, 2000; Sassa and Kawaguchi, 2004, 2005), although some fish larvae may have capabilities to predate at night hours, such as the larval myctophid *Myctophum selenops* (Conley and Hopkins, 2004).

Also, larval diet shifts ontogenetically. As larvae grow and develop, their foraging ability improves (e.g. vision and cognitive capacity improve and swimming ability

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increases). Niche breadth is ultimately dependent on changes in the prey that larva are capable of feeding on. Stage-specific variation in feeding habits and prey selectivity in marine fish larvae is consistent with stage-specific differences in the functional morphology of the feeding organs of fish larvae. Mouth gape has been proposed as the main morphological constraint to maximum prey size (González-Quirós and Anadón, 2001). Pearre (Pearre, 1986) formulated the hypothesis that the ratio of prey size to larval size is a constant. However, Pepin and Penney (Pepin and Penney, 1997) suggest that vulnerability to fluctuations in prey availability may be difficult to characterize in general terms, because Pearre's analysis was based on prey lengths in relation to predator lengths rather than measurements of niche breadth relative to mouth size.

The Chilean Patagonia is located on the southeastern border of the Pacific Ocean and covers >1000 km between 41° and 55°S. Fjords therein usually range between 100- and 500-m depth, from 10- to 70-km long, and have a two-layer structure that is vertically limited by a strong halocline between 4- and 20-m depth. The primary production regime is reported to be highly seasonal and may result in the efficient export of carbon to sediments in austral spring (González *et al.*, 2010). During spring, the food web structure of the Patagonian fjords is mainly sustained by large chain-forming diatoms that are favored by increased solar radiation, an extended photoperiod, a constant supply of silicate (input via freshwater discharges) and orthophosphate and nitrogen (provided from below the pycnocline). Crustacean zooplankton is abundant (mostly calanoid copepods and euphausiids, Palma and Silva, 2004) and most marine fish species reproduce during the austral spring season (Landaeta and Castro, 2006a, b; Landaeta *et al.*, 2009). Nanoplankton (both auto- and heterotrophic) largely dominate the system in winter, resulting in the predominance of the microbial loop (González *et al.*, 2010, 2011), high abundance of jellyfish (siphonophores and medusae, Palma *et al.*, 2011) and reduced abundance of fish eggs and larvae (Landaeta and Castro, 2006a; Landaeta *et al.*, 2009).

Lightfish, *Maurolicus parvipinnis* Vaillant 1888, is a small mesopelagic fish which extensively inhabits the southeast Pacific Ocean (Parin and Kobyliansky, 1996), from oceanic islands (Juan Fernandez archipelago, Landaeta and Castro, 2004), to upwelling areas (Landaeta and Castro, 2002) to fjord ecosystems (Balbontín and Bernal, 1997; Bustos *et al.*, 2008, 2011). As for several other mesopelagic fish, *Maurolicus* species have reduced fecundity (between 200 and 1800 eggs ind^{-1} in female *M. muelleri*, Rasmussen and Giske, 1994) and show reproductive tactics to enhance egg and larval transport from oceanic waters to shallower and more productive coastal areas (Landaeta and Castro, 2002). It is the most successful species that spawns in fjord ecosystems of southern Chile, and its early life stages (eggs, larvae) are very abundant along Patagonia (Balbontín and Bernal, 1997; Cordova and Balbontín, 2006; Landaeta and Castro, 2006a; Bustos *et al.*, 2008, 2011). Vertical migration of large larvae at a tidal scale has been suggested in explaining the retention of individuals inside Patagonian fjords (Landaeta *et al.*, 2009), although they can be found in similar proportions both in stratified and well-mixed waters (Bustos *et al.*, 2011). Recently, a study carried out in southern Patagonia (47°–50°S) showed that freshwater input produced by discharge of the Baker river and melting of large glaciers may affect the ecology of larval *M. parvipinnis*, reducing its recent growth and changing diet preferences (Landaeta *et al.*, 2011a).

Taking into account the high variability of the environments along Chilean Patagonia (inner seas, high levels of river discharge, ice melting from glaciers and influx of oceanic waters), we tested the hypothesis that feeding success, measured as the total number of prey items per gut (PIPG) and the total prey volume per gut (TPVG) (Reiss *et al.*, 2002), is not homogeneous and varies on a spatial scale along the Chilean Patagonia. Therefore, the main goal of this work was to determine the feeding habits of *M. parvipinnis* larvae and compare them in zones with different water column structures along Patagonia. Larval morphometrics, feeding incidence (FI), dietary composition, prey size, trophic niche breadth, number and volume of prey per larva were examined for larvae collected throughout Chilean Patagonia during austral spring 2005, 2008 and 2009.

METHOD

Field work

Three bio-oceanographic cruises were carried out along Patagonia in southern Chile during austral spring onboard the AGOR Vidal Gormaz. During the first cruise, carried out between 11 and 21 November 2005, 37 stations located in the inner sea of Chiloé, at 41°30′S and 43°50′S were sampled (Fig. 1). The second cruise comprised 42 stations located between 46°50′S and 50°09′S, sampled during 1–18 November 2008. During the third cruise, a total of 40 stations located from 50°06′S to 52°45′S were sampled from 17 October to 11 November 2009 (Fig. 1). At each

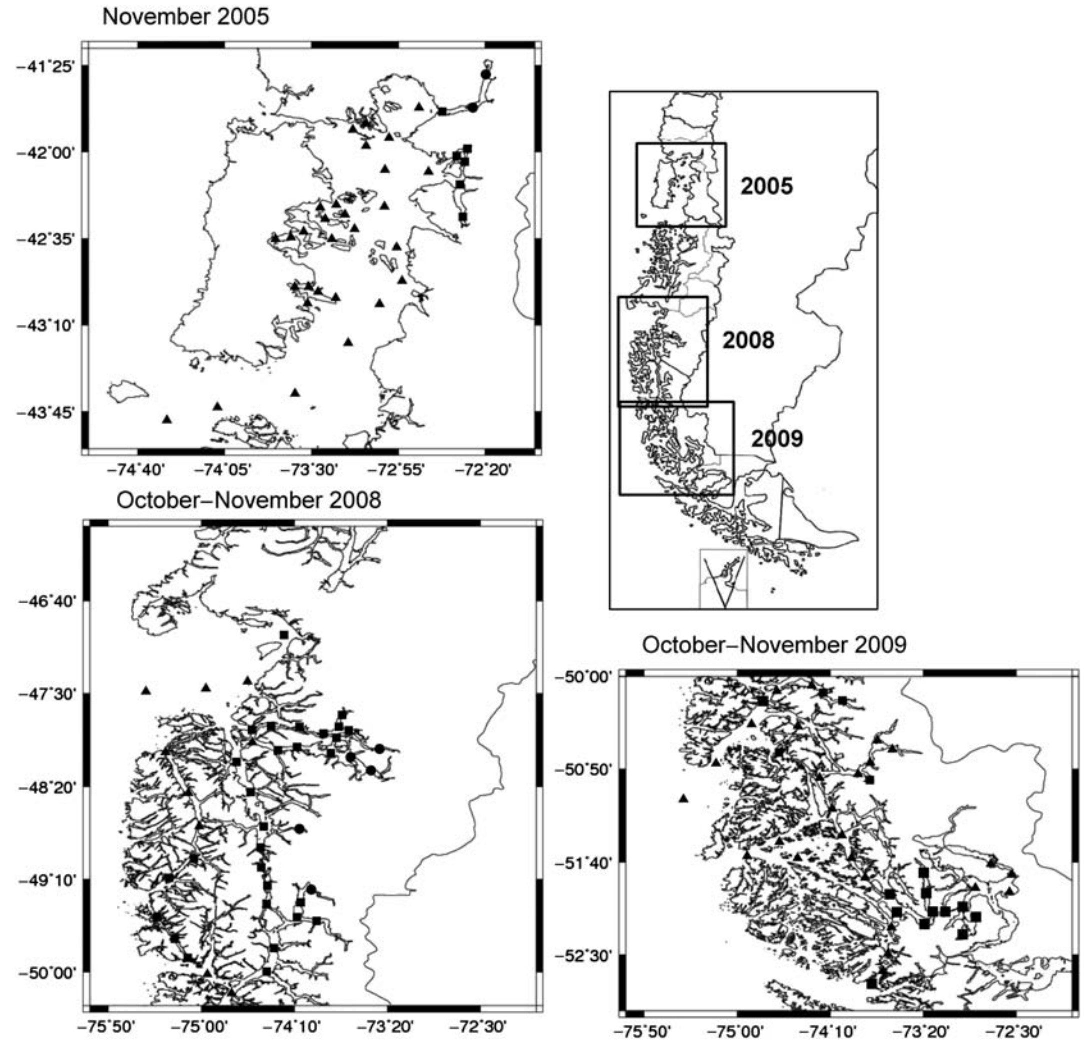

Fig. 1. Sampling localities of fish larvae during the three cruises along Chilean Patagonia. Symbols correspond to stations with high vertical stratification (black circles, $N > 0.2$ cycles s^{-1}), moderate stratification (black squares, $N = 0.07{-}0.2$ cycles s^{-1}) and high vertical mixing (black triangles, $N < 0.07$ cycles s^{-1}).

station, temperature, salinity and dissolved oxygen were measured from surface to 1000-m depth with a Seabird SBE-19 CTD profiler. During austral spring 2005 and 2008, mesozooplankton was collected by oblique tows with a Bongo net (66-cm diameter, 300-μm mesh size), and during 2009 a 1 m^2 Tucker trawl (300-μm mesh size) was utilized, respectively with a General Oceanics flowmeter mounted in the frame of the nets. Volume filtered ranged from 22.8 to 209.3 m^3 (mean $\pm$ 1 standard deviation, SD; 95.5 $\pm$ 45.1 m^3) during 2005, 101.9−881.6 m^3 (419.9 $\pm$ 151.1 m^3) during 2008 and from 22.7 to 897.2 m^3 (221.9 $\pm$ 150.9 m^3) during the 2009 survey. Once onboard, nets were washed and plankton samples were preserved with 5% formalin buffered with sodium borate.

Laboratory work

In the laboratory, all fish larvae from the plankton samples were separated, counted and identified to the lowest taxonomic level. Larval *M. parvipinnis* were identified; BL (notochord length in preflexion larvae; standard length in flexion and post-flexion 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 edge of the maxillae) of all intact larval *M. parvipinnis* ($n = 462$) were measured under a Leica MZ7 stereomicroscope fitted with an micrometer eyepiece. The gut of each larva was dissected from the body and opened lengthwise with fine needles. Prey items were counted and identified to the lowest possible taxon except for indigestible prey remains, such as setae. The maximum BL and width of each prey item were measured to the nearest 0.01 mm, using a microscope with an ocular micrometer, along the maximum cross-section that the larvae had had to ingest (Sassa and Kawaguchi, 2004). The volume of each prey item was estimated using the three-dimensional shape that most closely resembled the item, following Cass-Calay (Cass-Calay, 2003) and Sun and Liu (Sun and Liu, 2003). The prosome length of copepodite prey was measured since the urosome was often missing.

Data and statistical analysis

All larvae with identifiable prey in their guts were used for the analysis. Larval *M. parvipinnis* were separated into five size classes to assess ontogenetic classes in FI, prey composition, and number of prey per gut with growth at 2-mm intervals, i.e. <4, 4–6, 6–8, 8–10 and >10 mm BL. FI was calculated as a percentage of the total number of larvae that had gut contents out of the total number of larvae examined for the day and night samples, and for larval size classes. Following Sassa and Kawaguchi (Sassa and Kawaguchi, 2004), the larvae collected between 1 h after sunrise and 1 h before sunrise, and between 1 h after sunset and 1 h before sunrise, were considered 'daytime' and 'night-time' samples, respectively. Comparisons among size classes and between day and night were carried out with *G*-tests.

The relationships between BL, jaw length and MW of the larvae were determined by linear regression analysis, and comparisons of slopes were done with a multiple slope test (Zar, 1999).

The diet was described using the percent frequency of occurrence (%F) of a diet item in larvae with food in their guts, the percent of the total number (%N) of diet items examined and the percent of volume (%V) of each item out of the total volume of prey items. An index of relative importance (IRI) was calculated as follows: $\text{IRI} = (\%N + \%V) \times \%F$. To readily allow comparisons among prey items, the IRI was then standardized to %IRI for each prey item i (Cortés, 1997).

Changes in prey size were examined through larval development. Pearre's trophic niche width (Pearre, 1986) was adopted to analyse the relationship between prey size (maximum prey width, egg diameter) and predator size. In this analysis, the fish larvae were classified according to BL at 0.1-mm intervals. Only classes with at least three prey items in the gut were further analysed. The mean and SD of the $\log_{10}$-transformed prey width was calculated for each available size class. This model adopts the SD of the $\log_{10}$-transformed prey sizes as a measure of trophic niche width. The relationship between BL and the corresponding raw values, mean and SD of the $\log_{10}$-transformed prey size was examined using linear regression analysis.

The study area is characterized by high variability in the vertical structure of water column, because of freshwater inputs, ice melting and intrusion of oceanic waters (Bustos *et al.*, 2008, 2011). Therefore, as an integrated measure of the water column structure, we utilized the Brunt-Väisälä frequency (N), which is the frequency at which a vertically displaced parcel will oscillate within a statically stable environment, and it is calculated from the CTD data for each oceanographic station. Brunt-Väisälä frequency was calculated as follows: $N = [(g/\rho) \times (\partial\rho/\partial z)]^{1/2}$, where g is the gravity ($9.8\ \text{m}^2\ \text{s}^{-1}$), ρ is the density of the sea water and z the depth (Bustos *et al.*, 2011). We evaluated two measures of feeding success: number of PIPG (number) and TPVG (mm^3) (Reiss *et al.*, 2002), and comparisons were made between levels of vertical stratification. Because data showed no normal distribution (PIPG, Shapiro–Wilks test, $W = 0.52$, $P < 0.001$; TPVG, $W = 0.49$, $P < 0.001$), measurements of feeding success were compared among larvae collected from three levels of N (low level of vertical stratification: $N < 0.07$ cycles s^{-1}; intermediate level of stratification: $0.07 < N < 0.2$ cycles s^{-1}; high level of stratification: $N > 0.2$ cycles s^{-1}; Fig. 1 for location of the stations) with Kruskal–Wallis ANOVA tests and multiple comparisons of mean ranks.

RESULTS

Body and mouth size relationships

M. parvipinnis larvae collected during 2005, 2008 and 2009 ranged from 2.82 to 13.41 mm, BL (mean ± SD, 5.95 ± 1.81 mm) (Table I). Linear regressions were significant ($P < 0.001$) and explained 70.3 and 60.8% of the variability in UJL and MW, respectively (Fig. 2). The jaw length relative to BL ranged from 4.3 to 19.1% (8.8 ± 2.1%) and the MW relative to BL varied from 2.4 to 12.1% (4.8 ± 1.1%). The relationship between MW and UJL was linear (not shown) and explained 63.7% by the regression $\text{MW} = 0.098 + 0.353\text{UJL}$ ($F_{1,460} = 808.9$, $P < 0.001$). Around 8-mm BL there was a significant increase in the proportion of mouth size–BL (ANCOVA, $F_{1,459} = 6.69$, $P < 0.01$), changing from 0.06-mm UJL mm BL^{-1} to 0.14-mm UJL mm BL^{-1}. However, the MW–BL relationship did not change significantly after 8-mm BL (ANCOVA, $F_{1,459} = 3.54$, $P = 0.06$). In addition, during ontogeny

Table I: The number of Maurolicus parvipinnis larvae examined for gut contents and mean body length (BL) (± standard deviation)

Sampling period (gear)	Latitudinal range	Number of individuals	Larval size (mm BL)
November, 2005 (Bongo)	41°30′–43°50′S	180	5.93 ± 1.66
October—November, 2008 (Bongo)	46°50′–50°09′S	75	7.39 ± 2.19
October—November, 2009 (Tucker)	50°07′–52°04′S	207	5.46 ± 1.50

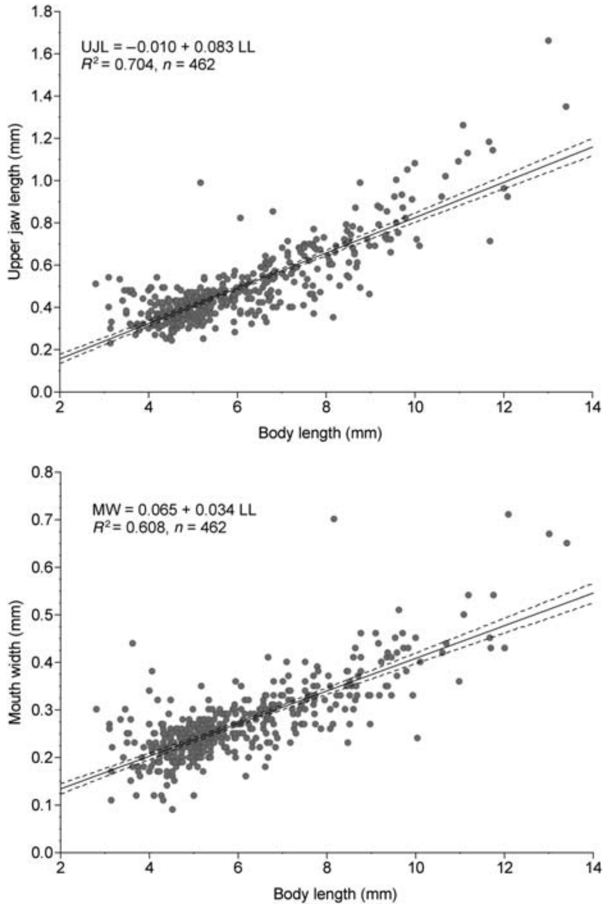

Fig. 2. Relationship between body length (mm) and upper jaw length (mm), and between body length and mouth width (mm). Dashed lines correspond to 95% confidence intervals.

UJL of larval lightfish increased at a faster rate ($0.08\ \text{mm UJL mm BL}^{-1}$) than MW ($0.03\ \text{mm MW mm BL}^{-1}$, multiple slope test, $P < 0.05$). Because of these results, we selected UJL as a measurement of the mouth size.

Feeding incidence

The smallest larva with gut contents was 3.1-mm BL. The FI significantly varied among size classes (*G*-test, $G = 12.803$, $\text{df} = 4$, $P = 0.012$). FI was similar during the preflexion stage (i.e. ~8-mm BL), ranging from 29.41 to 39.13%. At larger size, FI increased up to 88.88% (Fig. 3), coinciding with the larger increase of the UJL relative to BL. However, no differences were noticeable in FI between day and night ($G = 0.246$, $\text{df} = 1$, $P = 0.62$), showing that larval *M. parvipinnis* may predate at low light intensity (Fig. 3).

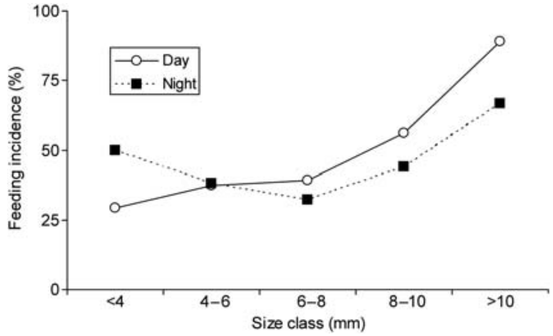

Fig. 3. Feeding incidence (%) of *Maurolicus parvipinnis* larvae collected in the daytime (open circles) and nighttime (black squares) in relation to five size classes of larvae.

Diet composition and trophic ontogeny

The diet of *M. parvipinnis* larvae was composed of 22 different prey items (Table II), mainly invertebrate eggs, nauplii, calanoid, cyclopoid and poecilostomatoid copepodites, ostracods, cladocerans and amphipods. Algae were not observed in the guts of any larvae. Numerically, copepod eggs, other invertebrate eggs and *Paracalanus parvus* copepodites were the most important prey items. The most relevant prey in terms of volume and frequency of occurrence were *Paracalanus parvus* and *Oithona* spp. copepodites (Table II). More than 95% of the %IRI was based on different copepod stages and taxa, and calanoid copepodites were dominant (%IRI = 58.17%).

The main food items of larval *M. parvipinnis* were examined for five larval size categories (Fig. 4). In larvae <4-mm BL, copepod eggs were numerically the most important prey item (87.6%), but volumetrically calanoid and cyclopoid copepodites and digested copepodites (‘others’ in Fig. 4) were more relevant to the diet (39.1 and 25.5%, respectively). With larval growth, the numerical importance of copepod eggs as prey

Table II: Prey composition of Maurolicus parvipinnis larvae

Prey taxon	%*N*	%*V*	%*F*	IRI	%IRI
Cladocera					
Evadne nordmanni	0.16	1.30	0.54	0.79	0.02
Ostracoda	0.95	3.27	2.70	11.41	0.28
Copepoda					
Egg	33.86	0.12	10.81	367.34	9.17
Nauplius	5.06	0.91	11.35	67.77	1.69
Calanoid copepodite					
Acartia tonsa	2.37	5.95	7.03	58.48	1.46
Calanoides patagoniensis	0.79	2.03	2.70	7.62	0.19
Calanus australis	0.32	1.25	1.08	1.69	0.04
Centropages brachiatus	0.16	0.08	0.54	0.13	0.00
Clausocalanus aucucornis	0.16	0.72	0.54	0.48	0.01
Metridia lucens	0.47	0.66	1.62	1.83	0.05
Paracalanus parvus	13.61	49.80	35.14	2227.86	55.63
Paraeuchaeta antarctica	0.16	0.11	0.54	0.15	0.00
Rhincalanus nasutus	1.11	4.14	3.78	19.87	0.50
Unidentified calanoid	1.27	1.35	4.32	11.33	0.28
Cyclopoid copepodite					
Oithona spp.	12.18	11.46	27.57	651.84	16.28
Poecilostomatoid copepodite					
Oncaea spp.	4.43	6.69	9.19	102.17	2.55
Copepoda fragments	9.34	6.17	19.46	301.79	7.54
Bivalvia larva					
Mytilus chilensis	0.79	1.01	2.70	4.87	0.12
Amphipoda	0.16	0.31	0.54	0.25	0.01
Unidentified invertebrate egg	10.92	0.61	12.97	149.54	3.73
Unidentified invertebrate larva	0.16	0.05	0.54	0.12	0.00
Unidentified taxa	1.58	2.00	4.86	17.43	0.44

%*N* corresponds to the percent of the total number of prey items, %*V* corresponds to the percent of the total volume of prey items, and %*F* the percent frequency of the occurrence of a diet item among larvae with food in their guts. IRI and %IRI correspond to the index of relative importance untransformed and as a percentage, respectively.

decreased and was replaced by calanoid copepodites (mainly *Paracalanus parvus*, Table II). Also, at larger sizes *Oithona* spp. and *Oncaea* spp. were both numerically and volumetrically important prey items (Fig. 4). Although few ostracods were found in the diet, their relevance in the prey volume reached 12.2% in larvae of 8–10-mm BL (Fig. 4).

Prey size and trophic niche breadth

The prey size range of larval *M. parvipinnis* was 40–660 μm (Fig. 5). Raw and transformed prey size range showed a slight, but significant increase at larger larval lengths (Table III). The logarithmic average size of prey was significantly related to larval length (Fig. 5, Table III; $F_{(1,56)} = 13.45$, $P < 0.001$). Niche breadth was independent of larval size, and did not change during larval development (regression analysis $P > 0.1$, Table III) with the average niche breadth (SD) of *M. parvipinnis* being 0.17 ± 0.08. Prey size as a percentage of UJL and MW ranged from 4.4 to 68.4% (mean ± SD, 24.9 ± 14.5%) and from 9.3 to 95.6% (43.2 ± 23.1%), respectively.

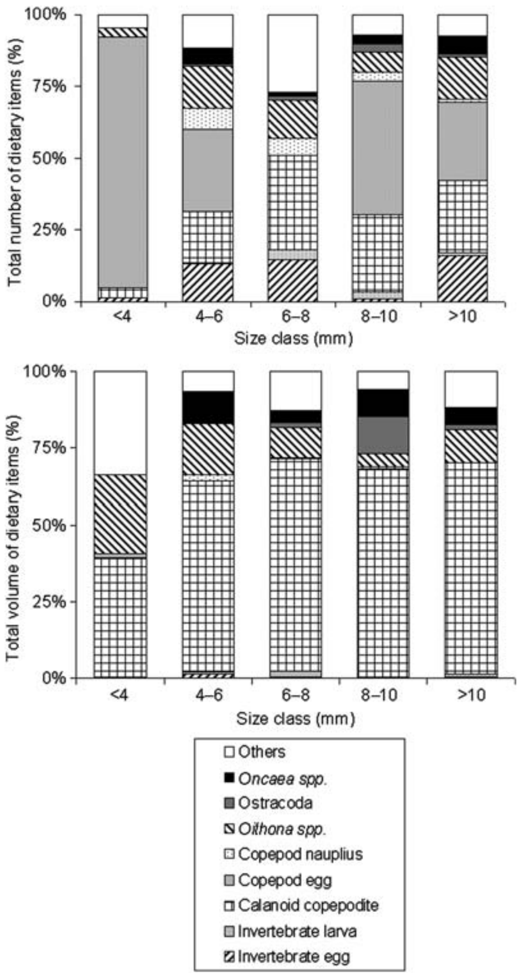

Fig. 4. Ontogenetic variations in the dietary composition of *Maurolicus parvipinnis* larvae, expressed as percent of the total number and volume of major prey taxa.

Number and volume of prey

The number of prey ranged from 0 to 38 (3.42 ± 4.99 prey items, excluding zeros) and showed no positive relationship with larval growth (Fig. 6, $r^2 = 0.007$, $F_{(1,181)} = 1.36$, $P = 0.244$). When the number of prey in larval guts was compared by time of day, larval *M. parvipinnis* captured during daytime showed higher prey number (4.26 ± 6.10 prey per gut, up to 38 prey items) than larvae captured during night (2.32 ± 2.56 prey per gut, up to 15 prey items) ($U = 3235$, $P = 0.015$); these differences cannot be explained in terms of larval size, because there were no significant differences in larval length between day and nighttime ($U = 4027$, $P = 0.848$). Prey volume ranged from 8×10^{-6} mm^3

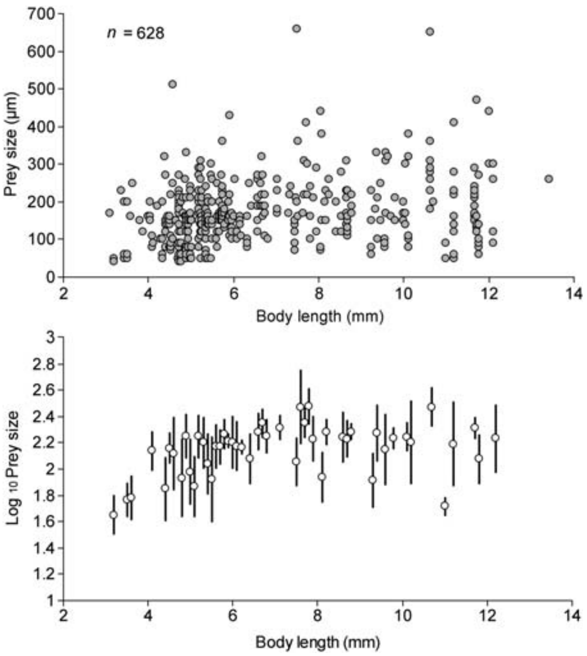

Fig. 5. Prey size-fish body length relationship. Prey size was measured as the maximum prey width. Prey size in upper panel is untransformed raw data, while it is $\log_{10}$-transformed in the lower graph.

Table III: Linear regression analysis of raw (untransformed) and average (log_{10}-transformed) prey width and trophic niche breadth (SD of log_{10}-transformed prey size) as a function of the body length. Intercept, slope, corresponding standard errors (SE) and determination coefficients are shown

	Intercept	SE	Slope	SE	r^2
Raw prey width versus body length	76.497*	9.309	9.819*	1.339	0.079
Average prey width versus body length	1.910*	0.072	0.034*	0.009	0.194
Trophic niche-breadth versus body length	0.182*	0.032	−0.002	0.004	0.004

$*P < 0.001$.

(a copepod egg) to 0.248 mm^3 (a *Paracalanus parvus* copepodite). Prey volume per gut varied between 4.68×10^{-5} mm^3 and 0.49 mm^3 (0.026 ± 0.049 mm^3), and showed a significant positive relationship with larval length (Fig. 6, $r^2 = 0.129$, $F_{(1,178)} = 26.54$, $P < 0.001$).

Relationships between vertical stratification and feeding success

The Brunt-Väisälä frequency (N) estimated for the study area ranged from well-mixed areas (0.004 cycles s^{-1}) to highly stratified zones (0.317 cycles s^{-1}; mean ± one standard deviation: 0.081 ± 0.063 cycles s^{-1}, median = 0.068 cycles s^{-1}), also showing high variability among sampling years (Kruskal–Wallis test, $H = 42.91$, $P < 0.001$). The maximum number of prey items found in one stomach content varied from 22 prey items from stations with reduced vertical stratification ($N <$ 0.07 cycles s^{-1}), to 38 prey items in moderately stratified areas ($0.07 < N < 0.2$ cycles s^{-1}), to 30 prey items at highly stratified stations ($N > 0.2$ cycles s^{-1}). There were no significant differences in the mean prey number per stomach among stations according to the Brunt-Väisälä frequency (Kruskal–Wallis test, $H = 1.95$, $P = 0.37$). However, when feeding success was compared as total prey volume per gut among stations at different levels of vertical stratification, larvae collected in areas with $N = 0.07$–0.2 cycles s^{-1} had larger TPVG (median = 0.017 mm^3) than larvae collected at more stratified (median = 0.003 mm^3) and more mixed stations (median = 0.007 mm^3) (Kruskal–Wallis test, $H = 17.9$, $P < 0.01$).

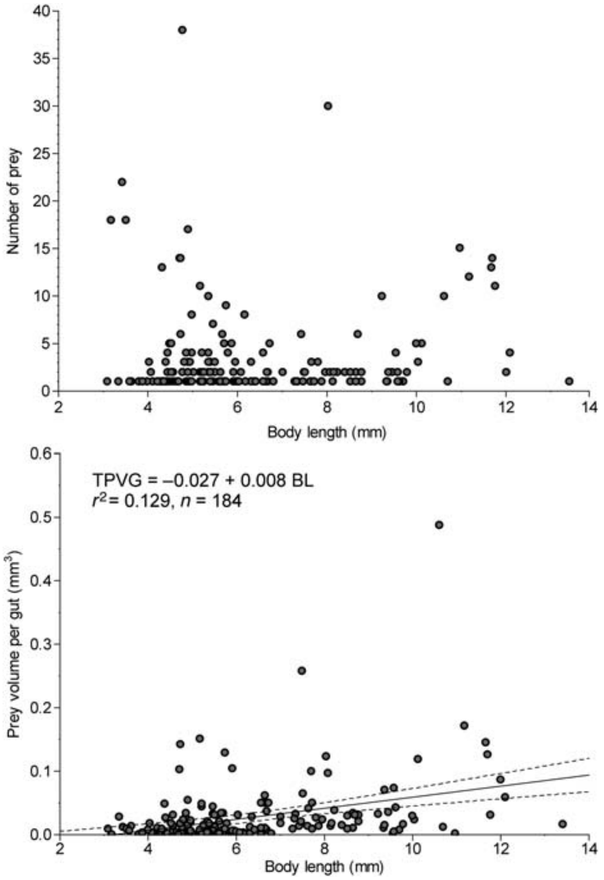

Fig. 6. Simple linear regression between number of prey and total prey volume per gut (mm^3) related to larval size of *Maurolicus parvipinnis*. Dashed lines correspond to 95% confidence intervals.

DISCUSSION

The results of this study show that larval *M. parvipinnis* from fjord areas of southern Chile are carnivorous predators with a wide variety of prey items (i.e. early stages of calanoid and cyclopoid copepods, ostracods, cladocerans, mussel larvae). They initially predate mainly on small invertebrate eggs (larvae <4-mm BL), and then there is an increase in the importance of large calanoid copepodites in the diet. Ontogenetically, ~8-mm BL an increase in the growth of the upper jaw occurred, increasing also the FI. The larvae are able to feed at nighttime, particularly and in higher proportion during the early larval stages, showing also an ontogenetic increase in total prey volume per gut instead of higher prey numbers. However, in terms of niche breadth, this seems to be constant throughout larval development. Finally, the feeding success of larval *M. parvipinnis* measured as total prey volume per gut was higher in zones with moderate vertical stratification, located in the middle of the channels of southern Patagonia.

Compared with other mesopelagic fishes, larvae of *M. parvipinnis* begin to predate at smaller size (3.1-mm BL) than myctophid larvae from the North Pacific, such as *Diaphus garmani*, *Myctophum asperum* (4.1-mm BL, Sassa and Kawaguchi, 2004), *Diaphus tetha* (4.5 mm), *Protomyctophum thompsoni* (4.3 mm), *Tarletonbeania taylori* (5.1 mm) (Sassa and Kawaguchi, 2005), but at similar size compared with myctophid larvae from the upwelling ecosystem of the Southeast Pacific, like *Diogenichthys laternatus* (2.6 mm) and *Triphoturus mexicanus* (3.4 mm) (Rodriguez-Graña *et al.*, 2005). Larvae of epipelagic carnivorous fish species such as albacore *Thunnus alalunga* or bullet tuna *Auxis rochei* start feeding at smaller sizes (2.6 and 2.1 mm, respectively), but feeding is mainly during daylight (Catalán *et al.*, 2007; Morote *et al.*, 2008).

Numeric and volumetric indices showed the dominance of copepods in all life stages (eggs, nauplii, copepodites) in the feeding habits of *M. parvipinnis* larvae, although some typical prey items from brackish waters, such as bivalve larvae, were found in its guts. Probably these prey originate at the head of the fjords, where low salinity waters dominate (Landaeta *et al.*, 2011a). Similarly, juveniles and adults of *Maurolicus muelleri* from Norwegian fjords showed a prey field dominated by bivalve veligers (Rasmussen and Giske, 1994).

The diet of marine fish larvae generally exhibits a shift from copepod eggs and nauplii during the early larval stage towards copepodites during the mid- and late-larval age (Uchikawa *et al.*, 2001; Robert *et al.*, 2008; Sassa, 2010). Copepodites of the medium-sized calanoid species are the preferred prey in the late larval stage of numerous species, as well as larvae of *M. parvipinnis* (Fig. 4) and juvenile *Bathylagichthys parini* (Bathylagidae), which coexist with *M. parvipinnis* in fjords of southern Chile (Landaeta *et al.*, 2011b). In this sense, calanoid copepods, and particularly copepodites stages IV and V, are rich in wax esters (Sargent and Falk-Petersen, 1988). These consist predominantly of 16:0, 20:1 (*n*-9) and 22:1 (*n*-11) fatty alcohols and polyunsaturated fatty acids that are of phytoplankton origin, and are the potential source of lipids of *Maurolicus muelleri* and important in the survival under local environmental conditions (Falk-Petersen *et al.*, 1986). A larval fish diet based on copepodites may increase larval growth rate, development and body pigmentation (Evjemo *et al.*, 2003). Therefore, we suggest that similar benefits may be occurring for larval *M. parvipinnis* which feeds mostly on calanoid copepodites (Table II, Fig. 4).

No significant differences were noticed in FI during day and nighttime, indicating that larvae of this species may predate at low light intensities. High levels of nocturnal feeding have also been described for larval fish inhabiting deep waters such as *Myctophum selenops* from oceanic waters off the Gulf of Mexico (Conley and Hopkins, 2004), post-larval *Protomyctophum thompsoni* (Sassa and Kawaguchi, 2005) and *Merluccius merluccius* (Morote *et al.*, 2011), although the majority of fish larvae are visual predators (Sabatés and Saiz, 2000; Sabatés *et al.*, 2003; Conley and Hopkins, 2004; Sassa and Kawaguchi, 2004, 2005; Rodriguez-Graña *et al.*, 2005; Sassa, 2010). Larvae of *Maurolicus japonicus* (4–20 mm) and juveniles of *Maurolicus muelleri* (23–25 mm) fed more actively at night (Okiyama, 1971; Ikeda *et al.*, 1994; Rasmussen and Giske, 1994; Uchikawa *et al.*, 2001), mostly on calanoid copepods (*Calanus* spp.) and then changed to euphausiids (Uchikawa *et al.*, 2001). Young and Blaber (Young and Blaber, 1986) found a feeding pattern that indicated that most feeding took place in the evening (18:00–24:00 h) and Gorelova and Krasil'nikova (Gorelova and Krasil'nikova, 1990) also found more active feeding in the upper layers of water in the evening. On the other hand, Giske *et al.* (Giske *et al.*, 1990) and Giske and Aksnes (Giske and Aksnes, 1992) found that *M. muelleri* during January in Masfjorden were daytime feeders. Our results indicate that larval *M. parvipinnis* capture a greater proportion of its prey during daytime (i.e. larger number of prey items) than night, but it is also capable of nocturnal predation. A combination of environmental conditions (moon light, water column transparency), visual capabilities (eye morphology) and/or avoidance of visual predators may explain this diel pattern (i.e. Kaartvedt *et al.*, 1998).

Low sea water temperature (3–6°C near glaciers, Landaeta *et al.*, 2011c) may reduce the time of gut evacuation and cause spurious data on night FI; however, prey found during night samples showed a low degree of digestion; additionally, other larval species collected in the same area (particularly larval *Bathylagichthys parini* from the 2009 cruise) have shown a negligible FI during night (Salas-Berrios and Landaeta, unpublished results). Hence, two plausible explanations arise: (i) gut evacuation in larval *M. parvipinnis* is much slower than *B. parini* at the same sea water temperature or (ii) *B. parini* larvae are incapable of capturing prey at low light levels.

As well as *Myctophum* larvae, *M. parvipinnis* initially has eyes that are elongate in the dorsal–ventral plane. The elliptical nature of the eyes would extend its visual field in the elongated axis. If larvae hold their body horizontal with eyes projected upwards, this would presumably provide the possibility for larvae to detect prey passing overhead, silhouetted against the predominantly downwelling sky light (Bozzano *et al.*, 2007). Larval *Myctophum punctatum* fed mostly at twilight (dawn and dusk) and its eyes show a dominance of rods in the retina which supports a visual function predominantly under scotopic (dim light) conditions (Bozzano *et al.*, 2007). More recently, Morote *et al.* (Morote *et al.*, 2011) have suggested that large eyes and lenses provide increased optical sensitivity for nocturnal feeding of hake *Merluccius merluccius*. Although *M. parvipinnis* larvae have smaller eyes than hake larvae, the elongated eye shape in the vertical plane of the former may have an adaptive benefit for predation in the turbid water column of a fjord environment.

Prey size is probably the major determinant of selectivity, and this is intimately related to the mouth size of the fish larvae. During ontogeny, mouth size and prey-searching ability increase; larger larvae are stronger swimmers and can see potential prey at greater distances than smaller stages (Sabatés and Saiz, 2000). The increase of mouth size of larval *M. parvipinnis* after 8-mm BL coincided with an increase in the FI, but not with changes in prey size. Instead, after 8-mm BL the proportion of copepodite prey volume was rather constant, the proportion of other prey changing (Fig. 4). On the other hand, the absence of a significant relationship between niche breadth and larval size indicates a high degree of selective foraging (Young *et al.*, 2010). Therefore, although smaller (<4-mm BL) larvae of *M. parvipinnis* switched from small invertebrate eggs to larger calanoid copepodites, niche breadth was independent of the larval size and did not change ontogenetically. This relationship and the value of Pearre's trophic niche breadth (0.17) is consistent to those observed in other mesopelagic fish larvae (Sabatés and Saiz, 2000; Sassa and Kawaguchi, 2004, 2005). Although the average prey size was not related to larval size (i.e. does not select large prey items), the sum of ingested prey volumes per gut was higher as *M. parvipinnis* larvae grew (Fig. 6).

Effects of environment on feeding success in Chilean Patagonia

The study area shows high environmental variability which contrasts with the low variation and constant niche breadth of feeding habits for larval *M. parvipinnis*. Some areas are dominated by semi-diurnal tides, which are highly correlated, but with a time lag, with larval fish abundance (Castro *et al.*, 2011). Also, the influx of brackish waters at the surface forms important horizontal density fronts, resulting in the aggregation of large amounts of floating kelp (mostly *Macrocystis pyrifera*, Hinojosa *et al.*, 2010) along open waters or more exposed areas, where large larvae may potentially utilize them as feeding grounds.

The entire area acts as a large estuary, with a surface, lighter water moving offshore and a deep, saltier water entering into channels and fjords (Dávila *et al.*, 2002). Some prey items of *M. parvipinnis* are typical of brackish waters, such as mussel larvae and *Acartia tonsa* copepodites; these taxa aggregate along channels associated with density fronts (Rosenberg and Palma, 2003) or are typical of surface waters (Castro *et al.*, 2007). Brackish waters may cause offshore advection of the surface layer (1–15-m depth), with horizontal extension of 100 km, because of the short residence times (~4 day) compared with the deep layer (nearly 1 year, Calvete and Sobarzo, 2011), and also may affect the prey field and therefore feeding selectivity (Landaeta *et al.*, 2011a). Behavioral responses (i.e. vertical migration) of fish larvae might provide them with the benefit of transport to food-rich areas along Chilean Patagonia, inshore (Castro *et al.*, 2011) or offshore (Landaeta and Castro, 2006b). Larval *M. parvipinnis* occurs at similar abundances and size structure in well mixed as well as in highly vertically stratified waters (Bustos *et al.*, 2011). The reduced importance of prey items from brackish waters seems to indicate that most feeding occurs in subsurface waters, where *Paracalanus parvus* and *Oithona* sp. copepods are found (Castro *et al.*, 2007). Alternatively, feeding may occur at the pycnocline, where microplankton may aggregate, favoring predator–prey encounter rates and the reduction of horizontal advection and dispersal (Woodson and McManus, 2007). Our sampling design (vertically integrated plankton sampling) does not allow us to establish where in the water column (mixed layer, pycnocline, deep layer) most of the prey ingestion occurred. Recent studies indicate that water column structure is related to larval fish abundance and composition (Bustos *et al.*, 2008, 2011). Our results indicate that feeding success (measured as total prey volume per gut) was greatest in larvae collected from areas with intermediate N values (between 0.07 and 0.2 cycles s^{-1}). Those stations are located along channels, in contrast to stations with high vertical stratification (i.e. near sources of freshwater and/or ice melting from major glaciers) or high vertical mixing (near the open ocean). The highly stratified areas may affect prey field composition (Landaeta *et al.*, 2011a), and well-mixed areas located offshore, although richer and more diverse in terms of prey field (Landaeta and Castro, 2006b), because of high turbulence, may reduce predator–prey encounter rates. Therefore, those larval *M. parvipinnis* located or retained along channels of south Patagonia may be more successful in terms of ingested prey and increase survival, partially explaining the high abundance of this species along channels of southern Chile. It is important to continue studying these topics and their consequences for growth and survival in the highly variable fjord environment of Patagonia.

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