

# Fish early life stages associated with giant kelp forests in sub-Antarctic coastal waters (Beagle Channel, Argentina)

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Received: 16 March 2017 / Revised: 1 August 2017 / Accepted: 3 August 2017  
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**Abstract** The aim of this study was to assess seasonal and spatial variations in fish larvae abundance between areas with *Macrocystis pyrifera* kelp forests and areas without them off the coast of the Beagle Channel. Monthly plankton sampling at three sites was performed from June 2014 to May 2016 in two areas of each site. One area was defined along the offshore margin (edge of the forests) of *M. pyrifera* kelp forests and the other area parallel to the forests but 200 m offshore (out of the forests). To test for spatial and temporal differences in the abundance of fish larvae, a multiple-hypothesis model approach was adopted by fitting generalized models (GLMs) with the abundance of fishes as the response variable and possible combinations of seasons, sites, areas, and water parameters as

explanatory variables. Ten fish taxa in larval stage were collected of which *Patagonotothen* spp. larvae were the dominant group. Season and area affected most the abundance of fish larvae along the coast of the Beagle Channel. High abundance of fish larvae was collected in spring of both years with a second peak in autumn. *Harpagifer bispinis* and *Patagonotothen* spp. peaked in spring, while *Careproctus pallidus* peaked in autumn. In every season of the two years sampled, the abundance of fish larvae was higher at the edge of the forests than out of them. The importance as nursery ground of *M. pyrifera* kelp forests for early stages of fishes that inhabit the Beagle Channel is discussed.

**Keywords** Ichthyoplankton · *Macrocystis pyrifera* · Sub-Antarctic fishes · Coastal environment · Nursery

**Electronic supplementary material** The online version of this article (doi:10.1007/s00300-017-2196-y) contains supplementary material, which is available to authorized users.

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## Introduction

Nearshore rocky habitats are essential for many fish species for reproduction, feeding, and as nursery grounds (e.g., Adreani et al. 2004; Erisman and Allen 2006; Konar et al. 2015). In temperate, sub-polar, and polar regions, large macrophytes dominate nearshore rocky substrates (Mann 2000). As these macrophytes grow, they conform to a complex three-dimensional structure (similar to land forests), which causes changes in the water column (e.g., light attenuation, flow retardation, enhanced sedimentation, and oxygenated rhizosphere), and in this sense, are considered “ecosystem engineers” (Jones et al. 1994). The large brown algae of the Laminariales and Fucales orders are commonly called “kelps” and groups of related kelps, which grow to extremely large sizes, are collectively

known as the giant kelps, of which *Macrocystis pyrifera* (Linnaeus) Agardh is the best known (Mann 2000).

Kelp forests are especially important for the biological communities associated with them. For instance, it has been established that they are a significant source of food in the trophic webs of coastal marine ecosystems (Dunton and Schell 1987; Duggins et al. 1989). It has also been argued that they contribute to form a complex ecosystem structure that includes various groups of invertebrates (crustaceans, echinoderms, and mollusks), fish, and marine mammals (Steneck et al. 2002). Furthermore, they are regarded as one of the most structurally complex and highly productive components of cold-water marine rocky coastlines. In South America, the species is distributed on the Atlantic coast between the Valdés Peninsula (42°S) and Tierra del Fuego (55°S) (Adami and Gordillo 1999; Ríos et al. 2007), while on the Pacific side, its northern limit reaches Valparaíso (33°S), although it has also been reported off the coast of Peru (Hoffmann and Santelices 1997). Its bathymetric distribution is generally limited to 8–10 m, forming forests of approximately 30–40 m wide (Ríos and Mutschke 2009).

The Beagle Channel is part of the Fuegian system of fjords and canals of the Magellanic region (54–55°S); its waters belong to the sub-Antarctic neritic domain and extend in E–W direction with an approximate length of 200 km, connecting the Atlantic and the Pacific Oceans (Porter et al. 1984). It is characterized by the presence of *M. pyrifera* forests for most of its coasts (Searles et al. 1974; Dayton 1985). Several studies conducted in the area stated that *M. pyrifera* forests offer food and refuge for many species of invertebrates (Santelices and Ojeda 1984; Adami and Gordillo 1999; Ríos et al. 2007) and adult fishes (Vanella et al. 2007), generating a space for trophic interactions between these, as well as with seabirds and marine mammals (Schiavini et al. 1997; Raya Rey and Schiavini 2000, 2001).

The community of adult fishes in the Beagle Channel has been previously assessed by Moreno and Jara (1984), Lloris and Rucabado (1991), López et al. (1996), and Vanella et al. (2007). The authors found that a high percentage of fish species (from a total of 42 described for the area; López et al. 1996) were associated with *M. pyrifera* kelp forests. The reproductive strategy of the fish fauna is very diverse. From the list of species described, some notothenioid fishes (the dominant group in the kelp forest; Vanella et al. 2007) are regarded as “guarders-nest spawners-lithophils” (sensu Balon 1975), spawning in the rocky intertidal in winter and late summer (Rae and Calvo 1995, 1996). However, except for a brief report on the use of *M. pyrifera* forests by juvenile stages of the

notothenioid *Paranotothenia magellanica* (Rae 1991), there are no studies related to the role of *M. pyrifera* forests as nursery ground for larval fishes in the area. Other important species in the Beagle Channel are known to spawn planktonic eggs in spring, like the Fuegian spratt *Sprattus fuegensis* (Ehrlich et al. 1999; Sánchez et al. 1995) and the Patagonian cod *Salilota australis* (Brickle et al. 2011).

Nevertheless, in other areas of the world ocean, there is evidence that giant kelp forests are habitats for juvenile (Bodkin 1988; Nelson 2001) and larval (Holbrook et al. 1990; Koubbi et al. 2001) fishes. Nelson (2001) stated that different stages of the kelp rockfish (*Sebastes atrovirens*) are associated with different parts of the macroalgae *M. pyrifera* along the coast of central California. Moreover, for fishes that are not spawned in the kelp forests, the recruitment process to the forests by larval stages is believed to be mediated by oceanographic features, which have to be stable over time for assured dispersal into this nursery realm (Krug and Steele 2013).

The changes that *M. pyrifera* forests provide to the water column (Jones et al. 1994) generate better environmental conditions for use as nursery grounds by fish larvae, especially in highly energetic environments (e.g., strong currents), which may increase dispersal of fish larvae and their food (Krug and Steele 2013). In the Beagle Channel, the predominant currents are strong along the middle area and run from west to east with maximal speed reported of 15.6 cm s<sup>-1</sup> (Balestrini et al. 1998). Water turbulence is generated by the wind effect. Southwesterly winds are dominant throughout the year with an average speed of 31 km h<sup>-1</sup> (Balestrini et al. 1998). Therefore, although the Beagle Channel seems at first a highly energetic environment, inadequate for the establishment of nursery grounds for fish larvae, it is expected that the giant kelp forests present all along its coasts offer a better nursery ground for fish larvae by, for example, reducing the speed of the water currents allowing larval retention.

The aim of this study is to assess seasonal and spatial variations in fish larvae abundance between areas with *M. pyrifera* kelp forests and areas without them off the coast of the Beagle Channel. We hypothesize that the areas with *M. pyrifera* kelp forests are more suitable to act as nursery grounds for fishes and therefore the abundance of fish larvae differ between areas. We also hypothesize that the abundance of fish larvae varies seasonally according to the specific reproductive seasons of the fish fauna. We expect the abundance of fish larvae to be higher in areas with *M. pyrifera* kelp forests and in late winter-spring months according to the reproductive season of the dominant species.

## Materials and methods

### Study area

The waters that flow through the channels and inner areas of the Fuegian system are the result of intense mixing processes originated in the northern end of the Drake Passage. These mixed waters are formed by waters brought by the Circumpolar Current, diluted by excess precipitation in the South-East Pacific, and by subtropical waters from the Pacific Ocean (Balestrini et al. 1998). In this context, a flow towards the Atlantic Ocean occurs, known as the Cabo de Hornos Current, characterized by salinities of the order of 33.5 (Piola and Rivas 1997). Part of these waters circulate through the Beagle Channel, favored by the preponderance of west-southwesterly winds and in turn, are diluted by the contribution of inland waters originated from the high precipitation and thawing rates that characterize this region. One of the consequences of this process is the low salinity waters (<32.5) flowing eastwards all along the Beagle Channel (Balestrini et al. 1998). In this area, the surface water temperature ranges from 4.2 to 4.3 °C in August to 8.9 to 9.8 °C in January, while salinity ranges from 26.7 in November to December to 31.3 during July (Balestrini et al. 1998).

Three sites (Lapataia Bay, Bridges Island, and Larga Beach) at the Beagle Channel were selected for this study covering a distance of about 25 km along its coast (Fig. 1). Although some differences in oceanographic features, such as coasts with rocky substratum and large giant kelp forests characterize the three sites. Lapataia Bay and the Larga Beach receive discharges of continental waters (from run-off and glacial melting origins), Lapataia Bay from the Ovando and Lapatia streams and the Larga Beach from the Olivia stream. Bridges Island, on the other hand, does not directly receive any continental discharge and is part of the Bridges archipelago in the middle of the Beagle Channel in front of Ushuaia city (Fig. 1).

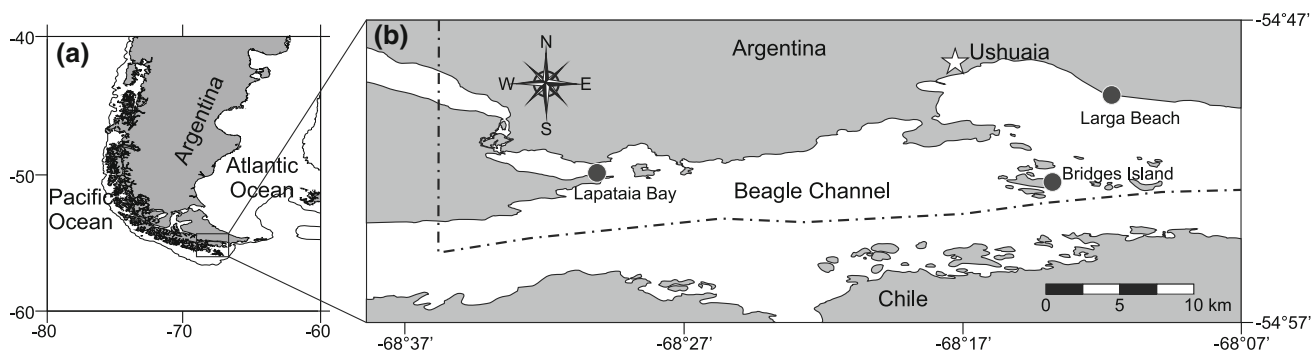
### Sampling design

Monthly plankton samples were collected at the three sites with a 120-HP boat from June 2014 to May 2016, performing oblique tows from near the bottom to the surface using a conical net with 0.28 m<sup>2</sup>-mouth area and 200- $\mu$ m mesh size. Tows were performed against the prevailing current at one knot for 5 min in two areas of each site. One area was defined along the offshore margin (hereafter edge of the forests) of the *M. pyrifera* forests and the other area parallel to the forests but 200-m offshore (hereafter out of the forests). The net was towed twice in each zone at each site. The volume filtered of each tow was about 44 m<sup>3</sup> and depth ranged from 5–10 m (at the edge of the forest) to 10–15 m (out of the forests). Given that samples were collected by performing oblique tows, the slight difference in depth between areas was considered as negligible. After the completion of each tow, nets were washed and the samples stored in plastic bins without using any fixing solution.

Before each tow, water temperature (°C) and salinity were recorded with a Hanna HI 9828 multi-parameter device at the towing depth, while water transparency (m) was recorded with a Secchi disk.

Once in the laboratory, fish larvae (and eggs whenever present) were sorted and identified under a Leica M205 C stereomicroscope to the lowest possible taxon using available literature or diagnostic keys for the area (Kellermann 1990; Ehrlich et al. 1999; Balbontín 2008). Larvae were then counted and measured to the nearest 0.01 mm using the Leica DFC 420 C software. Notochord length (NL) was measured for all yolk sac, preflexion and flexion larvae and total length (TL) for all postflexion larvae (Fuiman 2002). These were termed as ‘body length’ (BL) for all taxa caught. No correction was made for shrinkage (e.g., Kristoffersen and Salvanes 1998) because samples were not fixed in either formaldehyde or ethanol.

An individual of each taxon morphologically identified to the lowest possible level of each sample was stored in



**Fig. 1** Map of the study area. **a** Location of the section of the Beagle Channel under study in South America, and **b** location of the sampling sites (Lapataia Bay, Bridges Island and Larga Beach) along the coast of the Beagle Channel

absolute alcohol at  $-20\text{ }^{\circ}\text{C}$  for subsequent confirmatory identification by molecular techniques. From each harvested tissue, DNA was extracted using the salting-out technique (modified from Miller et al. 1988). The mitochondrial COXI gene was then amplified employing the Polymerase Chain Reaction (PCR) technique using the forward primer COX1L5928D 5'-TCRACYAAY-CAYAAAGAYATYGGCAC-3' and the reverse primer COX1H6664D 5'-TAKACYTCWGGGTGDCCRAAR-AAYCA-3'. PCR were performed using the following cycling conditions: an initial denaturation of 1 min at  $94\text{ }^{\circ}\text{C}$ , 30 cycles of 1 min of denaturation at  $94\text{ }^{\circ}\text{C}$ , 30 s of annealing at  $50\text{ }^{\circ}\text{C}$ , and 1 min of extension at  $72\text{ }^{\circ}\text{C}$ , and a final extension of 7 min at  $72\text{ }^{\circ}\text{C}$  in a 2720 Thermal Cycler (Applied Biosystems). PCR products were sequenced at Macrogen Korea with both PCR primers. The sequences obtained were scored and analyzed using BioEdit (Hall 1999). In the case of the *Patagonotothen* group, identification at species level was confirmed by the preparation of a phylogenetic tree together with a database of previously identified species of the area (Ceballos, unpublished data) using MEGA version 6 (Tamura et al. 2013).

### Data analysis

For statistical comparisons, data were grouped into winter (June, July, and August), spring (September, October, and November), summer (December, January, and February) and autumn (March, April, and May) per year.

Differences in water properties (temperature, salinity and transparency) among seasons by site were evaluated with a Kruskal–Wallis test, followed by Steel–Dwass–Critchlow–Fligner (SDCF) post hoc test. In addition, differences in these parameters between zones (edge of the forests and out of the forests) by season-site interactions were evaluated by a Mann–Whitney *U*-test.

To test for spatial and temporal differences in the abundance of fish larvae, a multiple-hypothesis model approach was adopted (Franklin et al. 2001; Johnson and Omland 2004). Generalized linear models (GLM, Package MASS; Venables and Ripley 2002) were built with the number of fish captured as the response variable. Due to low abundances in the samples, all developmental stages were pooled together (i.e., yolk sac, preflexion and post-flexion). Season (winter 2014, spring 2014, summer 2014, autumn 2015, winter 2015, spring 2015, summer 2015, and autumn 2016), site (Lapataia Bay, Bridges Island, and Larga Beach), area (edge of the forests and out of the forests) and water parameters (temperature, salinity, and transparency) were considered as explanatory variables. Therefore, models with possible combinations of the above-indicated environmental factors were fitted (Table 1). Finally, a model without any of the independent

variables (i.e., null model) was built to test the hypothesis that none of the variables tested had an effect on the fish abundance (Table 1). Since models had large variance-mean relationships and many zero values characterized the samples, a negative binomial error distribution and a log link were specified (Crawley 2005). Model selection was based on Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2002, 2004) and the model with the lowest AICc was selected as the best (Table 1). Models with a  $\Delta\text{AICc}$  value less than 2 were considered to be 'equally good' following Burnham and Anderson (2002). Each model was weighed against the others using AICc weights ( $w_i$ ), which gives an estimation of the likelihood of the model's fit according to the data used (Burnham and Anderson 2002, 2004).

All statistical analysis were done under R 3.3.1 software (R Core Team 2016) and Addin-soft XLSTAT.

## Results

### Physical environment

Water temperature was significantly different among seasons in all three sites (Kruskal–Wallis tests, Table 2). Seasonal trends were observed with high values in summer and in autumn and low values in spring and in winter in both years (SDCF post hoc tests,  $p < 0.05$ , Table S1 in Online Resource 1; Fig. 2a–c). No differences between areas (edge of the forests and out of them) were observed for each season (Mann–Whitney *U*-tests,  $p > 0.05$ , Table S2 in Online Resource 1).

Trends in water salinity among seasons (Kruskal–Wallis tests, Table 2) and areas (Mann–Whitney *U*-tests,  $p < 0.05$ , Table S2 in Online Resource 1) were observed. Lower values were recorded in autumn 2015 at all three sites (SDCF post hoc tests,  $p < 0.05$ , Table S1 in Online Resource 1; Fig. 2d–f). However, the lowest values (median = 24.3; range = 18.9–24.8) were recorded in spring 2015 at Lapataia Bay (SDCF post hoc tests,  $p < 0.05$ , Table S1 in Online Resource 1; Fig. 2d). Water salinity values were higher at the edge of the forests than out of them in spring 2015 at Lapataia Bay (Fig. 2d) and in winter 2014 at the Bridges Island (Fig. 2e), while the opposite result was observed in winter 2014 at Larga Beach (Fig. 2f) (Mann–Whitney *U*-tests,  $p < 0.05$ , Table S2 in Online Resource 1).

Although water transparency was significantly different among seasons at all three sites (Kruskal–Wallis tests, Table 2), there was not a clear trend for this parameter. For instance, water was more transparent in winter 2015 (median = 6.5 m; range = 4.8–8.4 m) and in autumn 2016 (median = 7.4 m; range = 2.4–11.8 m) at Lapataia Bay

**Table 1** Competing models for explaining the importance of giant kelp forests as nursery ground for fish larvae in the Beagle Channel

Model	AICc	df	$\Delta$ AICc	$\omega$
Null	673.0	2	88.3	<0.001
~ season	602.5	9	17.8	<0.001
~ site	666.8	4	82.2	<0.001
~ area	651.9	3	67.3	<0.001
~ season + site	599.2	11	14.6	0.168
<b>~ season + area</b>	<b>584.6</b>	<b>10</b>	<b>0</b>	<b>0.77</b>
~ site + area	650.2	5	65.5	<0.001
~ temperature + salinity + transparency	661.6	5	77	<0.001
~ season + site + area + temperature + salinity + transparency	587	15	2.4	0.23

For each model, Akaike Information Criterion corrected for small sample size (AICc), degrees of freedom (df), the difference between AICc of the current model and the most parsimonious model (in bold) ( $\Delta$ AICc), and the Akaike weight ( $\omega$ ) are given

**Table 2** Kruskal–Wallis rank sum test results among seasons for water parameters recorded at Lapataia Bay, Bridges Island and Larga Beach during the study period

Site	Source	<i>K</i>	df	<i>p</i>
Temperature	Lapataia Bay	65.4	7	<0.0001
	Bridges Island	60.14	7	<0.0001
	Larga Beach	54.72	7	<0.0001
Salinity	Lapataia Bay	42.62	7	<0.0001
	Bridges Island	37.48	7	<0.0001
	Larga Beach	34.12	7	<0.0001
Transparency	Lapataia Bay	24.04	7	0.0011
	Bridges Island	16.58	7	0.0203
	Larga Beach	31.68	7	<0.0001

(SDCF post hoc tests,  $p < 0.05$ , Table S1 in Online Resource 1; Fig. 2g), whereas higher values in water transparency were observed in autumn 2015 (median = 8.8 m; range = 5.6–11.4 m) and in winter 2015 (median = 9.5 m; range = 6–12 m) at Bridges Island (SDCF post hoc tests,  $p < 0.05$ , Table S1 in Online Resource 1; Fig. 2h). Conversely, water transparency was even among all seasons at Larga Beach except in spring 2014 when significant low values (median = 3 m; range = 2.1–4.5 m) were recorded (SDCF post hoc tests,  $p < 0.05$ , Table S1 in Online Resource 1; Fig. 2i). Differences in transparency between areas were only observed at Larga Beach with higher values out of the forests in summer 2014 and in autumn 2015 (Fig. 2i) (Mann–Whitney *U*-tests,  $p < 0.05$ , Table S2 in Online Resource 1).

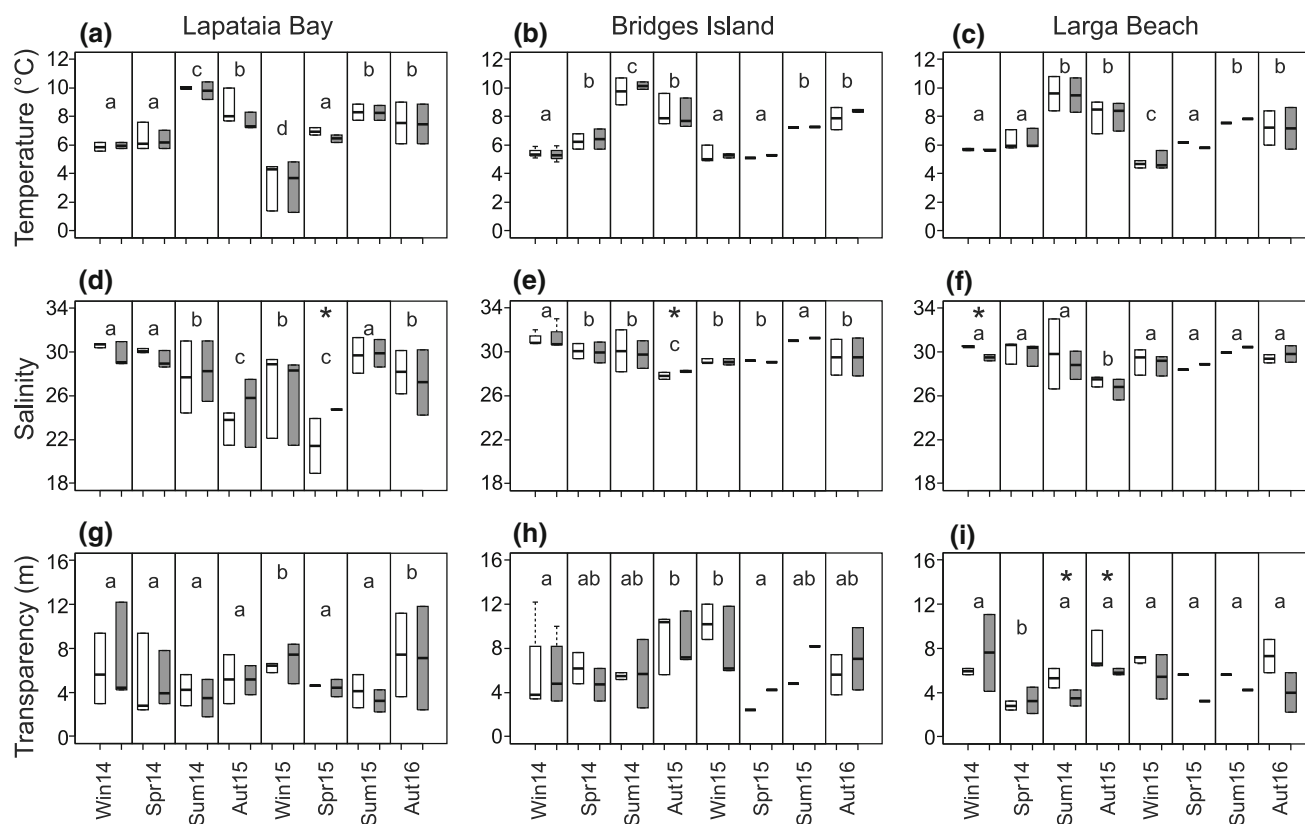
### Composition and abundance of fish larvae and relationships with the environment

Ten fish taxa in larval stage (and eggs from one species) were collected during the study period (Table 3), nine of

which were identified to species level (GenBank accession numbers: KY773205 to KY773221). *Agonopsis chilensis* (Fig. 3a) were found only in preflexion stage and out of the forests. *Careproctus pallidus* (Fig. 3b) and *Harpagifer bispinis* (Fig. 3c), on the other hand, were collected in both areas mostly in pre- and postflexion stages and yolk sac larvae of both species were collected only at the edge of the forests (Table 3). Identification to species level of larvae of the genus *Patagonotothen* (Fig. 3d) by means of morphological or meristic diagnosis was not possible due to a lack of specific dissimilarities. Therefore, identification to the species level of this group was achieved by molecular techniques. Almost 50% of all tissue samples of “*Patagonotothen*” larvae could be sequenced, which evidenced four species (*P. cornucola*, *P. jordani*, *P. tessellata*, and *P. wiltoni*); the other 50% was considered as *Patagonotothen* spp. (Table 3). Nevertheless, larvae from this latter group showed a similar pattern being present in almost all stages at the edge of the forests and only in preflexion stage out of them (Table 3). Eggs and preflexion larvae of *S. australis* (Fig. 3e) were collected in both areas, while *S. fuegensis* (Fig. 3f) larvae in preflexion stage were collected only out of the forests (Table 3). Almost all taxa (except for *A. chilensis*, *S. australis* and *S. fuegensis*) were more abundant at the edge of the forests (Table 3).

Overall, fish larvae in preflexion stage were present throughout the study period (Fig. 4). Postflexion larvae were also present in all seasons except in summer 2015 (Fig. 4). Despite eggs of *S. australis* were collected in both areas, higher densities were observed out of the forests (Table 3) and in spring–summer months of both years (Table 4).

According to the models proposed (Table 1), the season and the area mainly affected fish larvae abundance along the coast of the Beagle Channel. High abundance of fishes in larval stage was collected in spring of both years, although a higher abundance of fishes was collected in 2015 than 2014 (Fig. 5). A second peak was observed in



**Fig. 2** Seasonal variation in water temperature, salinity and transparency at Lapataia Bay, Bridges Island and Larga Beach (line: median; box: 25th–75th percentiles; whiskers: minimum to maximum value range). Gray boxes are for areas at the edge of *Macrocyctis pyrifera* kelp forests and white boxes are for areas out of them. Different letters denotes significant differences in water parameters

by season-site interactions (SDCF post hoc tests,  $p < 0.05$ , Table S1 in Online Resource 1), while asterisk denotes significant differences in water parameters between areas (edge of *M. pyrifera* kelp forests of and out of them) by season-site interactions (Mann–Whitney  $U$ -tests,  $p < 0.05$ , Table S2 in Online resource 1)

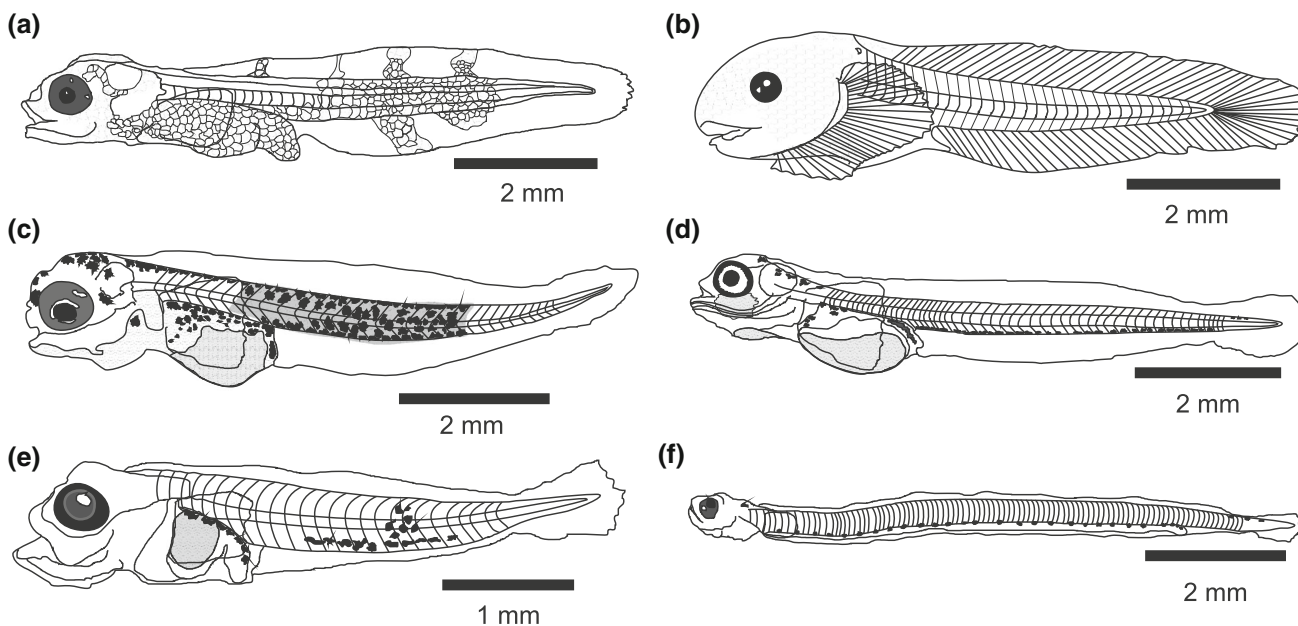
**Table 3** Total density (ind.  $100\text{ m}^{-3}$ ) by developmental stage of larval fish taxa collected from the edge of *Macrocyctis pyrifera* kelp forests and out of them during the study period

Taxa	Edge of the forests					Out of the forests				
	Eggs	Yolk sac	pref.	flex.	postf.	Eggs	Yolk sac	pref.	flex.	postf.
<i>Agonopsis chiloensis</i>	–	–	–	–	–	–	–	2.27	–	–
<i>Careproctus pallidus</i>	–	6.82	2.27	–	109.09	–	–	2.27	–	6.82
<i>Harpagifer bispinis</i>	–	2.27	36.36	4.55	9.09	–	–	11.36	2.27	2.27
<i>Patagonotothen cornucola</i>	–	–	197.73	–	2.27	–	–	34.09	–	–
<i>Patagonotothen jordani</i>	–	–	2.27	–	–	–	–	–	–	–
<i>Patagonotothen</i> spp.	–	22.73	204.55	4.55	4.55	–	–	63.64	–	–
<i>Patagonotothen tessellata</i>	–	–	243.18	–	–	–	–	11.36	–	–
<i>Patagonotothen wiltoni</i>	–	–	18.18	–	2.27	–	–	4.55	–	–
<i>Salilota australis</i>	15.91	–	4.55	–	–	68.18	–	11.36	–	–
<i>Sprattus fuegensis</i>	–	–	–	–	–	–	–	4.55	–	–

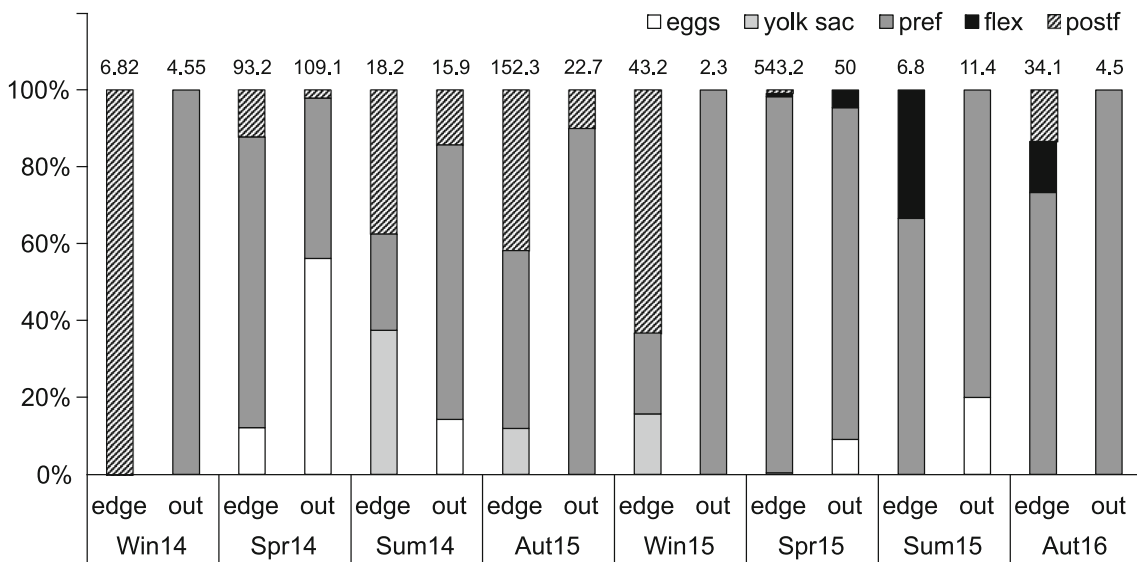
pref. preflexion, flex. flexion, postf. postflexion

autumn of both years. In every season of the two years sampling, the abundance of fish larvae was higher at the edge of the forests compared to that collected out of them

(Fig. 5). Neither the site nor the water parameters were significant for explaining the observed patterns of fish larvae abundance (Table 1).



**Fig. 3** Fish larvae collected during the study period. **a** *Agonopsis chiloensis*, **b** *Careproctus pallidus*, **c** *Harpagifer bispinis*, **d** *Patagonotothen* spp., **e** *Salilota australis* and **f** *Sprattus fuegensis*



**Fig. 4** Seasonal variation of the relative composition of each developmental stage of fishes collected from both areas (edge of *Macrocystis pyrifera* kelp forests and out of them) along the coast of

the Beagle Channel. The total density (ind. 100 m<sup>-3</sup>) collected from each area in each season is indicated along the upper X-axis. *pref.* preflexion, *flex.* flexion, *postf.* postflexion

Seasonal variations in species composition were also evident (Table 4). Larvae of *A. chiloensis* and *S. australis* were more abundant in summer, while eggs of the latter species were more abundant in spring (Table 4). The abundance of *Patagonotothen* spp. and *H. bispinis* peaked in spring, with a second peak in autumn but in lesser extent (Table 4). *Careproctus pallidus* was present from winter 2014 to spring 2015, with a peak in abundance in autumn 2015 (Table 4).

**Discussion**

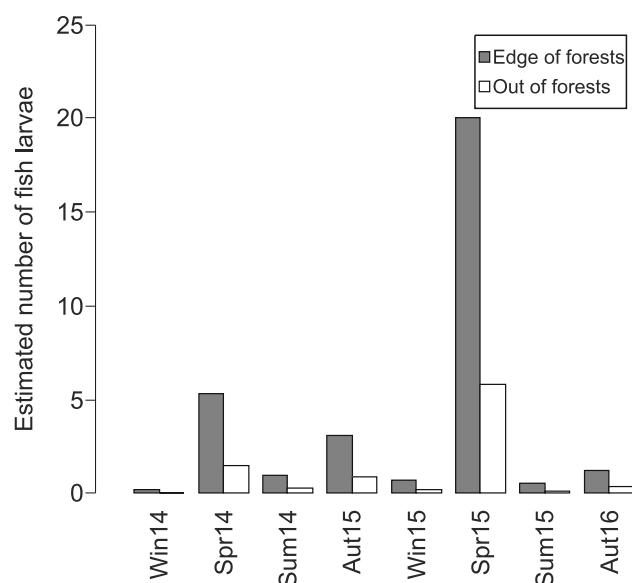
**Water properties at the edge of- and out of the giant kelp forests**

Overall, there were no differences in the water parameters recorded between the area at the edge of *M. pyrifera* kelp forests and the area outside of them, except for some cases

**Table 4** Seasonal total density (ind. 100 m<sup>-3</sup>) of larval fish taxa collected from the three sites (Lapataia Bay, Bridges Island and Larga Beach) and from both areas (edge of *Macrocystis pyrifera* kelp forests and out of them) during the study period

Taxa	Win14	Spr14	Sum14	Aut15	Win15	Spr15	Sum15	Aut16
<i>Agonopsis chiloensis</i>	–	–	2.27	–	–	–	–	–
<i>Careproctus pallidus</i>	6.82	13.64	15.91	61.36	27.27	2.27	–	–
<i>Harpagifer bispinis</i>	4.55	13.64	–	18.18	–	13.64	–	18.18
<i>Patagonotothen cornucola</i>	–	–	–	22.73	9.09	202.27	–	–
<i>Patagonotothen jordani</i>	–	–	–	–	–	2.27	–	–
<i>Patagonotothen</i> spp.	–	100	9.09	52.27	2.27	113.64	4.55	18.18
<i>Patagonotothen tessellata</i>	–	–	–	–	–	252.27	2.27	–
<i>Patagonotothen wiltoni</i>	–	–	–	15.91	4.55	–	4.55	–
<i>Salilota australis</i> larvae	–	2.27	4.55	–	2.27	–	4.55	2.27
<i>S. australis</i> eggs	–	72.73	2.27	–	–	6.82	2.27	–
<i>Sprattus fuegensis</i>	–	–	–	4.55	–	–	–	–

Win winter, Spr spring, Sum summer, Aut autumn



**Fig. 5** Estimated abundance of fish larvae related to seasons and the areas (edge of *Macrocystis pyrifera* kelp forests and out of them) along the coast of the Beagle Channel, estimated by a Generalized Linear Models with a log link and negative binomial error distribution

in water salinity and transparency (Fig. 2). It has been stated that kelp forests are capable of altering local oceanography and ecology by modifying currents (Steneck et al. 2002) and tidal circulation along coasts with damping ratios of 40–80% (Wu et al. 2017). Therefore, it was expected that values of water parameters would be somehow different between areas at the edge of- and out of the *M. pyrifera* forests. Although current velocity was not measured during the study period, there is a large amount of literature that confirm that current patterns and velocity differ within and in the vicinity of kelp forests (e.g., Jones et al. 1994; Steneck et al. 2002; Krug and Steele 2013; Wu et al. 2017). Therefore, we focused on testing other water parameter that may differ between both areas. However, it

seems that the effect that kelp forests have to the water column along the Beagle Channel coast is not related to variations in temperature, salinity or transparency.

### Fish larvae composition and abundance related to the giant kelp forests

Our results revealed that fish larvae are present throughout the year along the coast of the Beagle Channel and that their abundance is higher in areas with *M. pyrifera* kelp forests, not rejecting our hypothesis.

Higher abundance of ichthyoplankton in coastal waters (with large *M. pyrifera* forests) than in offshore waters has been previously observed in the Kerguelen archipelago (Koubbi et al. 1990, 2001). The authors argued that the shallow areas might act as retention zones compared to deeper offshore areas. Such a feature may be closely related to the presence of the complex structures of the kelp forests in the coastal areas (Steneck et al. 2002) as observed by Holbrook et al. (1990) in Californian coasts. In Chilean fjords, on the other hand, the distribution of fish larvae is influenced by the strong horizontal salinity gradients created by melting ice and by tidal currents (Landaeta et al. 2011, 2012; Zenteno et al. 2014). Although innermost areas of fjords are less productive than outer coastal areas (Salvanes et al. 1995), tidal flow advection may cause entrapment of planktonic organisms near fjord heads (Basedow et al. 2004) and subsequently, concentrate them at frontal areas associated with floating kelps (Landaeta et al. 2012).

Holbrook et al. (1990) argued that the higher abundances of reef fish species found in Californian coasts were closely related to the presence of the kelp forests, whether they have a planktonic or live-bearing mode of reproduction. In this regard, fish species collected in this study also present different reproductive strategies, and although all



species have a planktonic larval stage, the mode in which the embryonic stage takes place differs among them. For instance, *P. tessellata* and *P. cornucola* belong to the “guarders-nest spawner-lithophils” guild (sensu Balon 1975), spawning in the rocky intertidal of the Beagle Channel and eggs being guarded by the male until hatching takes place. It is known that the former species has two reproductive events, one in mid-winter and a second in late summer, with juveniles frequently found in *M. pyrifera* forests (Rae and Calvo 1995, 1996). *Patagonotothen cornucola* and *H. bispinis* are supposed to follow the same reproductive strategy, although the latter species is most likely to have a single reproductive event during late autumn-early winter, with a long hatching period mainly in late spring, as observed in the congeneric species *H. antarcticus* (White and Burren 1992; La Mesa et al. 2017). Nevertheless, the present study provides new insights on the distribution of the larval stage of these species, confirming the important role as nursery ground of the giant kelp forests also in early developmental stages of these species. The other *Patagonotothen* species present in the area likely evolved the same reproductive pattern, being more abundant in spring and autumn months, considering a ~28 days embryonic development (like *P. tessellata*; Rae and Calvo 1995, 1996); and also because the abundance of this group was higher at the edge of the forests.

Liparid snailfishes of the genus *Careproctus* are known to extrude eggs through an anteriorly positioned ovipositor into the branchial chambers of large lithodid crabs (Baltontin et al. 1979; Somerton and Donaldson 1998), so that they are considered “nonguarders-brood hiders-ostrophils” (sensu Balon 1975). Despite a hidden embryonic stage, once hatching occurs free-swimming larvae of *C. pallidus* gets out of the king crabs (*Lithodes santolla*) chamber (Bruno, personal observation), which are a common inhabitant of the giant kelp forests in the coasts of the Beagle Channel (Castilla 1985; Lovrich and Vinuesa 1999). Hence, it represents a very advantageous kind of reproductive strategy, as the hosts (in this case the king crab) that protect the embryonic stage inhabit an area (giant kelp forests) suitable for the larval development once hatching occurs.

Fishes with a nonguarder pelagophil strategy are also present in waters of the Beagle Channel. *Salilota australis* and *S. fuegensis* belong to this guild, and the presence of larval stages in summer and autumn evidence for a reproductive season during spring months, like previously stated for the former species in the Falkland Islands (Brickle et al. 2011), coinciding with the higher abundance of eggs collected (Table 4). Leal et al. (2011) stated that *S. fuegensis* is a partial spawner, which spawns between September and October (Austral spring) at southern Chile. Although no eggs were collected during this study, the seasonal pattern

of abundance of larvae coincides with previous studies in the Atlantic Ocean (Sánchez et al. 1995; Ehrlich et al. 1999) and in Chilean fjords (Landaeta et al. 2012).

Almost all species in larval stage were more abundant at the edge of the forests rather than out of them, regardless of their reproductive strategy. Although two species were more abundant out of the forests (*A. chiloensis* and *S. fuegensis*), their abundances were too low to make accurate inferences. Despite the great peak in the estimated abundance on spring months 2014, seasonal abundances of fish larvae were similar between years (Fig. 5). These results demonstrate that fishes in different larval stages are present throughout the year in the Beagle Channel coasts, especially associated with kelp forests, though the abundance and the species composition vary seasonally according to specific reproductive strategies. Carr (1991) also observed this same pattern in rockfishes inhabiting Californian coasts, arguing that temporal differences in species composition could be related to the timing of parturition among species and/or to the length of the planktonic larval period.

Although little is known about the length of the larval period of most of the fish species in the Beagle Channel, the specific differences in timing of egg release seem to be the most plausible explanation, as almost every fish developmental stage was collected throughout the years of sampling (Fig. 4). These specific differences in the timing of egg release might contribute to reduce density-dependent mortality and competition for food resources (compensatory mortality; Houde 2002).

The present study provides evidence of the importance of the giant kelp forests for the early stages of fishes that inhabit the Beagle Channel. These forests seem to fulfill at least one of the requirements of Bakun’s fundamental triad for the establishment of nursery grounds for fish larvae (larval retention) (Bakun 1996). Current velocity and tidal circulation could be damped within the kelp forests and along their edges (e.g., Krug and Steele 2013), minimizing the dispersal of fish larvae and probably allowing the concentration of their preys. Such an environment would be more beneficial for fish larvae compared to the open waters of the Beagle Channel characterized by strong tidal currents (Balestrini et al. 1998). Moreover, in situ primary production and/or terrigenous organic inputs would be enough to sustain a trophic web able to fulfill fish larvae trophic requirements.

Kelp forest ecosystems are finely tuned to natural levels of disturbance (Mann 2000) like deforestation by violent storms or by sea urchin herbivory (Steneck et al. 2002). Unfortunately, there is a growing anthropic disturbance because of harvesting for the algininate industry (as for example in Southern Chile; Gutierrez et al. 2006). *Macrocystis pyrifera* kelp forests in the Beagle Channel are more regularly destroyed by storms than by herbivory

(Dayton 1985) and although there is still no development of commercial harvesting, it is regarded as an important potential resource for Tierra del Fuego (Mendoza and Nizovoy 2000). Therefore, and given that large increases in the level of disturbance inevitably lead to loss of species diversity and degradation of community structure (Mann 2000), baseline information about the role of *M. pyrifera* kelp forests on the dynamics and life history of the associated communities is necessary for assessing management and conservation policies.

**Acknowledgements** We express our gratitude to authorities of “Secretaría de Ambiente, Desarrollo Sostenible y Cambio Climático” (Argentina) and of Administración de Parques Nacionales (Tierra del Fuego, Argentina) for sampling permissions (RSPaYS N° 0298/2016 and 099-CPA-2016, respectively); to M. Pérez, L. Pagnossin, J. Rojo, and T. Chalde for field assistance; and to S.G. Ceballos for assistance with scoring and analyzing DNA sequences. We also acknowledge D. Piepenburg, M. La Mesa, and two anonymous reviewers for their useful comments and suggestions on an early draft, and to F. Sola for helpful revision of grammar style. This study was supported by grants from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET-Argentina) PIP 0321 2014-2016 and Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT-FONCyT, Argentina) PICT 1596 2012-2016; and partially supported by PICT 0900/2015 grant (ANPCyT-FONCyT, Argentina). D.O.B was supported by a postdoctoral fellowship from CONICET (Argentina).

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