

ARTICLE

Spatial and temporal variations of coastal fish larvae, ectoparasites and oceanographic conditions off central Chile

Variaciones espaciales y temporales de larvas de peces costeros, sus ectoparásitos, y condiciones oceanográficas frente a Chile central

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Resumen. El objetivo de este estudio fue determinar la variación temporal de las condiciones oceanográficas, ictioplancton y sus ectoparásitos en aguas costeras marinas. Se realizaron 30 muestreos de ictioplancton entre el 11 de octubre 2012 y el 5 de junio 2014 a lo largo de una transecta desde 0,25 km hasta 4,5 km de la costa frente a Montemar, Bahía Valparaíso, Chile central. Se identificó un total de 5.553 larvas de peces, pertenecientes a 37 taxa. Las larvas de peces más abundantes originadas de desove pelágico fueron la sardina común *Strangomera bentincki* (abundancia relativa= 26,39%), anchoveta *Engraulis ringens* (8,94%), y el mictóforo *Hygophum bruuni* (7,72%); las especies más abundantes originadas de posturas bentónicas fueron la borrachilla *Scartichthys viridis* (15,77%), el cachudito *Hypsoblennius sordidus* (8,27%) y el pejesapo *Gobiesox marmoratus* (7,06%). Las larvas de peces más parasitadas provinieron de posturas bentónicas, los pejesapos *G. marmoratus* (prevalencia= 9,63%) y *Sicyases sanguineus* (0,54%), el tomollo *Auchenionchus variolosus* (1,72%), y el trombollito de tres aletas *Helcogrammoides cunninghami* (3,28%). La única especie con desove pelágico que presentó ectoparásitos fue el blanquillo *Prolatilus jugularis* (0,57%). Las larvas de peces con ectoparásitos mostraron una disminución en abundancia con la distancia a la costa; *S. bentincki*, *H. bruuni* (desove pelágico) o *S. viridis* (postura bentónica) fueron más abundantes a 2,0 km de la costa. Los ectoparásitos fueron identificados como *Trifur* spp. (Copepoda: Pennellidae) y *Caligus* spp. (Copepoda: Caligidae), siendo los penélidos los más frecuentes (1 a 3 parásitos por larva). El 94 y 88% de los penélidos y calígidos, respectivamente, fue recolectado en la estación más costera. Durante los periodos de mayor prevalencia de ectoparásitos en las larvas de peces, el agua de mar estuvo verticalmente estratificada con una profundización a fines de otoño y un ascenso en verano de la pycnoclina desde mar afuera hacia la costa. Por lo tanto, los resultados sugieren que las larvas de peces originadas de posturas bentónicas son parasitadas más frecuentemente y que las condiciones físicas de la columna de agua pueden favorecer tanto la retención costera como la infestación por ectoparásitos en las aguas más cercanas a la costa.

Palabras clave: *Trifur* sp., *Caligus* sp., pejesapo, gradientes horizontales de densidad, Chile central, Sudamérica

Abstract. The objective of this study is to determine the temporal variation of oceanographic conditions, ichthyoplankton and their ectoparasites in nearshore marine waters. From October 11th 2012 to June 5th 2014, 30 ichthyoplankton surveys were carried out along a cross-shelf transect from 0.25 km of the coastline to 4.50 km offshore off Montemar, Bahía Valparaíso, central Chile. We identified a total of 5,553 fish larvae, belonging to 37 taxa. The most abundant fish larvae with pelagic spawning were the common sardine *Strangomera bentincki* (relative abundance= 26.39%), the anchoveta *Engraulis ringens* (8.94%), and the lanternfish *Hygophum bruuni* (7.72%); whereas the most abundant species with benthic brooding were the blennies *Scartichthys viridis* (15.77%), *Hypsoblennius sordidus* (8.27%) and the clingfish *Gobiesox marmoratus* (7.06%). The most parasitized fish larvae were from benthic brooding origin, namely the clingfishes *G. marmoratus* (prevalence= 9.63%) and *Sicyases sanguineus* (0.54%), the kelpfish *Auchenionchus variolosus* (1.72%), and triplefin blenny *Helcogrammoides cunninghami* (3.28%). Only one species from pelagic spawning origin, the sandperch *Prolatilus jugularis* (0.57%), had ectoparasites. The abundance of some larval fish species with ectoparasite decreased with distance to the shore; *S. bentincki*, *H. bruuni* (pelagic spawning) or *S. viridis* (benthic brooding) were found to be more abundant at 2.0 km offshore. The ectoparasites were identified as *Trifur* spp. (Copepoda: Pennellidae) and *Caligus* spp. (Copepoda: Caligidae), with pennellids being the most frequent (1 to 3 parasites per larva). Ninety-four and 88% of pennellids and caligids, respectively, were collected in the nearshore station. During periods of high ectoparasite prevalence on fish larvae, seawater was vertically stratified with a cross-shelf deepening (late autumn) or shoaling (summer) of the pycnocline from offshore to nearshore. The results suggest that fish larvae with BB were more frequently parasitized and that physical conditions of the water column may contribute both to coastal retention of fish larvae as well as ectoparasite infestation in nearshore waters.

Key words: *Trifur* sp., *Caligus* sp., clingfish, horizontal density gradients, central Chile, South America

INTRODUCTION

The variables that determine the structure of larval fish assemblages at a specific location include environmental features, acting at different spatial and temporal scales, and the behavioral responses of larvae to these factors (Carassou *et al.* 2008, Muhling *et al.* 2013, Flores-Coto *et al.* 2014). Physical processes such as mesoscale eddies (Sánchez-Velasco *et al.* 2013), frontal tide-mixing (Lee *et al.* 2005) and water column stratification (Bustos *et al.* 2008) may affect the composition and abundance of marine fish larvae. Additionally, scales of temporal variation of the ichthyoplankton include monthly (Kent *et al.* 2013), seasonal (Landaeta *et al.* 2008, Su *et al.* 2011), and multiyear fluctuations (*e.g.*, ENSO-related, Landaeta *et al.* 2009). At spatial scales of less than a dozen of kilometers and temporal scales of less than 1 month, however, studies about the response of larval fish assemblages are scarce, particularly in temperate rocky reefs (Hernández-Miranda *et al.* 2003, Sabatés *et al.* 2003, Borges *et al.* 2007).

In nearshore rocky reef environments, larval fish stages of bottom-dwelling species may occur in high abundance and species richness (Hernández-Miranda *et al.* 2003, Kent *et al.* 2013). Given that local scale processes may affect dispersal of reef fish larvae, small-scale studies on larval spatial distributions can give information about possible retention mechanism near the habitat of the adults (Borges *et al.* 2007). Because most of the inshore species lay demersal eggs (*i.e.*, Navarrete-Fernández *et al.* 2014) and their larvae dominate in the nearshore larval fish assemblages (Hernández-Miranda *et al.* 2003, Borges *et al.* 2007), it is expected that larval retention, and therefore self-recruitment, may increase due to locally produced larvae and/or transported from other reefs by alongshore currents.

In central Chile, recent studies have shown that several shallow-dwelling benthic species couple their hatching with the lunar cycle which may be associated with increased larval retention (*e.g.*, the clingfish *Gobiesox marmoratus*, Contreras *et al.* 2013) or favor population connectivity (*e.g.*, the triplefin *Helcogrammoides chilensis*, Palacios-Fuentes *et al.* 2014). These species are characterized for relatively long pelagic larval duration, ranging from 50 to 140 days (Plaza *et al.* 2013, Mansur *et al.* 2014), which pose a complex scenario for survival and nearshore recruitment of postlarvae. During this extended larval planktonic period, a series of ecological interactions take place in the water column, not only as predator-prey interactions, but also in the form of parasite-host

interactions (Palacios-Fuentes *et al.* 2012, 2015). Ectoparasites, mostly copepods of the families Pennellidae and Caligidae (Muñoz *et al.* 2015), are recurrent in larval stages of benthic-brooding marine fishes from central Chile (Herrera 1984a, Palacios-Fuentes *et al.* 2015), causing significant reduction in the larval growth rates (Herrera 1990) and recent condition of fish larvae (Palacios-Fuentes *et al.* 2012). However, it is not clear whether oceanographic processes mediate in the ectoparasite-host interactions in nearshore waters.

The aim of this study was to determine the spatio-temporal distribution patterns of fish larvae and their ectoparasites in a nearshore temperate area off Bahía Valparaíso, central Chile, and the relationship of them to oceanographic conditions and water column structure.

MATERIALS AND METHODS

FIELD AND LABORATORY WORK

From October 11th 2012 to June 5th 2014, a series of 30 surveys were carried out during each season along a cross-shelf transect (Fig. 1) from 0.25 km offshore of the coastline to 4.50 km offshore off Montemar, Bahía de Valparaíso, central Chile. Five stations for CTD deployment and 3 stations for ichthyoplankton collection, were repeated 30 times. A Bongo net (60-cm diameter, 300 µm mesh) with a TSK flow meter, was obliquely towed for 10-15 min from 20 m depth to surface, at around 0.5, 2 and 4 km offshore (Fig. 1). All samples were taken during the morning between 10 and 13 h, at all tidal phases. Samples were preserved in 5% formalin (with sodium borate), and within 24 h they were transferred to 96% ethanol.

All fish larvae were sorted and identified to the lowest possible taxonomic level under a stereomicroscope equipped with a digital camera. Identifications were based on descriptions given by Balbontín & Pérez (1979, 1980), Pérez (1979, 1981), Balbontín & Orellana (1983), Orellana & Balbontín (1983), Herrera (1984b), Zúñiga & Acuña (1992), Landaeta *et al.* (2006), and Herrera *et al.* (2007). Larvae were categorized, according to the reproductive strategy of the adults, either as pelagic spawners (PS), those who release their eggs (or larvae, in the case of rockfish *Sebastes oculatus*), or benthic brooders (BB), species that attach their eggs to benthic substrates (bottom, algae or nests) (Navarrete-Fernández *et al.* 2014). Additionally, all larvae were examined for ectoparasites. Parasitized larvae were placed into individual containers

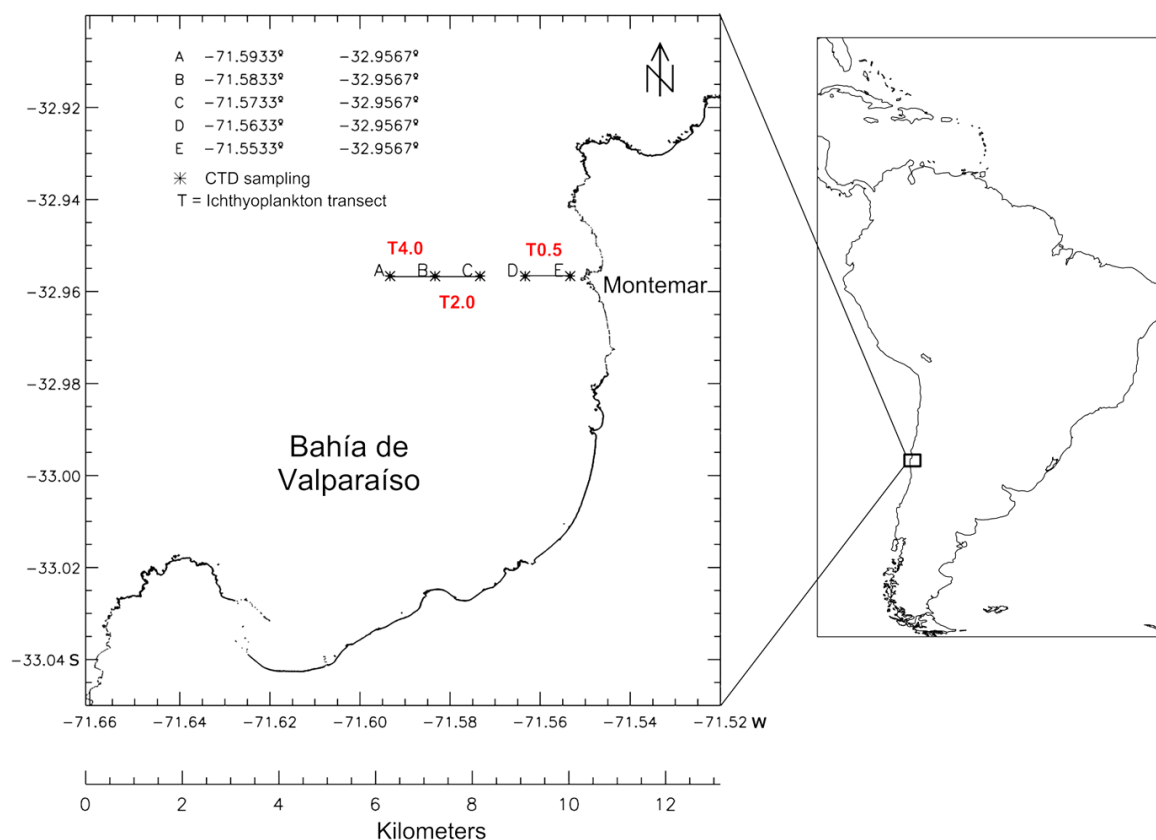


Figure 1. Location of the study site, indicating the position of CTD stations (*) and ichthyoplankton sampling transects (T) at 0.5, 2.0 and 4.0 km offshore Montemar, north Bahía Valparaíso, central Chile / Ubicación del sitio de estudio, indicando la posición de las estaciones de CTD (*) y las transectas de recolección de ictioplancton (T) a 0,5, 2,0 y 4,0 km de distancia de Montemar, al norte de la Bahía Valparaíso, Chile central

for further analysis. Each ectoparasite was identified to the lowest possible taxon based on structure of mouthparts and other appendages (Muñoz *et al.* 2015, Palacios-Fuentes *et al.* 2015).

DATA ANALYSIS

The abundance of each larval fish species was expressed as number of larvae per 1000 m³. Larval abundance from PS and BB were compared utilizing Wilcoxon paired test, taking into account that larvae were extracted from the same sample unit. Moreover, the larval abundances in relation to distance from the shore were compared with Kruskal-Wallis tests for selected species.

To establish the differences in the abundance and composition of larval fish assemblages due to distance to shore and seasonality, a multivariate approach was applied separately for PS and BB larvae. The abundance of fish larvae was log(x+1) transformed to enhance the contribution

of less abundant larvae, and a Bray-Curtis similarity matrix was generated with these data. Similarities between samples were graphically represented by nonmetric multidimensional scaling (NMDS) ordination. The degree of correspondence between the distances among points was measured by a stress function. A two-way analysis of similarities (ANOSIM), which is analogous to a univariate analysis of variance, was utilized to determine the differences in ichthyoplankton composition among stations (0.5, 2 and 4 km from shore) and seasons (Spring 2012, 2013, Summer 2013, 2014, Autumn 2013, 2014 and Winter 2013). Pairwise ANOSIM comparisons were made between groups using 10,000 permutations.

The prevalence and intensity of ectoparasites were calculated separately for each larval fish taxon, based on the methods described by Bush *et al.* (1997). Comparison of the spatial distribution of ectoparasite families was carried out using contingency tables. All statistical analyses were carried out with Statistica 7.0 and Past 3.07.

Table 1. Composition and abundance (ind. 1000 m⁻³) of fish larvae collected in nearshore waters off Montemar, central Chile between October 2012 and January 2014. SD= one standard deviation; PS= pelagic spawning; BB= benthic brooding / Composición y abundancia (ind. 1000 m⁻³) de larvas de peces recolectadas en aguas costeras frente a Montemar, Chile central, entre octubre 2012 y enero 2014. SD= una desviación estándar; PS= desove pelágico; BB= desove bentónico

Family	Species	Type of spawning	Total	%	Mean	SD	Median	Min	Max
Clupeidae	<i>Strangomera bentincki</i>	PS	8800.90	26.39	266.69	623.98	46.85	3.65	2867.30
Engraulidae	<i>Engraulis ringens</i>	PS	2981.25	8.94	72.71	238.24	11.67	4.70	1493.73
	<i>Diaphus</i> sp.	PS	15.54	0.04	5.18	0.78	5.02	4.49	6.03
	<i>Diogenichthys laternatus</i>	PS	25.91	0.07	12.95	2.71	12.95	11.04	14.87
Myctophidae	<i>Hygophum bruuni</i>	PS	2574.93	7.72	42.21	100.21	10.55	3.38	694.36
	<i>Lampanyctus iselinoides</i>	PS	354.25	1.06	11.43	13.32	6.81	3.38	71.22
	<i>Lampanyctus</i> sp.	PS	6.79	0.02	6.79	-	6.79	6.79	6.79
	<i>Triphoturus oculus</i>	PS	169.66	0.50	16.97	15.63	10.97	4.08	51.25
Merlucciidae	<i>Merluccius gayi</i>	PS	296.19	0.88	37.02	39.83	20.73	5.39	120.30
Ophidiidae	<i>Genypterus</i> sp.	BB	36.66	0.11	12.22	4.85	9.85	9.01	17.80
	<i>Gobiesox marmoratus</i>	BB	2353.31	7.05	47.07	124.95	11.73	3.68	780.02
	<i>Sicyases sanguineus</i>	BB	1087.36	3.26	32.95	56.02	11.05	3.89	272.73
Atherinopsidae	<i>Odontesthes regia</i>	BB	12.16	0.03	6.08	0.07	6.08	6.03	6.13
Syngnathidae	<i>Leptonotus blainvillanus</i>	BB	5.25	0.01	5.25	-	5.25	5.25	5.25
Sciaenidae		PS	24.37	0.07	6.09	1.84	5.26	5.02	8.83
Normanichthyidae	<i>Normanichthys crockeri</i>	PS	129.70	0.38	16.21	12.89	12.63	5.02	40.10
Bovichthyidae	<i>Bovichthys chilensis</i>	PS	3.53	0.01	3.53	-	3.53	3.53	3.53
Sebastidae	<i>Sebastes oculatus</i>	PS	1938.93	5.81	27.31	36.69	15.17	3.68	280.70
Kyphosidae	<i>Girella laevifrons</i>	PS	525.92	1.57	30.94	30.08	20.23	3.89	97.15
Pomacentridae	<i>Chromis crusma</i>	BB	521.01	1.56	26.05	39.89	6.96	3.89	140.19
Pinguipedidae	<i>Pinguipes chilensis</i>	PS	12.26	0.03	6.13	0.96	6.13	5.45	6.81
	<i>Prolatilus jugularis</i>	PS	1134.65	3.40	51.57	86.33	21.89	4.96	381.83
	<i>Helcogrammoides chilensis</i>	BB	1027.41	3.08	25.06	41.88	9.23	3.38	202.32
Trypterygiidae	<i>Helcogrammoides cunninghami</i>	BB	363.73	1.09	17.32	20.77	9.68	4.49	89.40
	<i>Auchenionchus variolosus</i>	BB	312.12	0.93	9.75	9.73	6.73	3.34	49.09
Labrisomidae	<i>Auchenionchus microcirris</i>	BB	22.08	0.06	7.36	6.51	3.68	3.53	14.87
	<i>Auchenionchus crinitus</i>	BB	291.47	0.87	11.21	9.98	7.88	3.34	42.19
Clinidae	<i>Myxodes</i> spp.	BB	13.53	0.04	6.76	4.36	6.76	3.68	9.85
Dactyloscopidae	<i>Sindoscopus australis</i>	BB	87.56	0.26	7.96	4.97	6.03	3.53	21.09
	<i>Scartichthys viridis</i>	BB	5259.41	15.77	65.74	143.14	13.59	3.34	952.64
Blenniidae	<i>Hypsoblennius sordidus</i>	BB	2758.09	8.27	30.65	47.73	16.59	3.53	301.13
Stromateidae	<i>Stromateus stellatus</i>	PS	45.88	0.13	6.55	3.40	5.02	3.89	12.31
	<i>Hippoglossina macrops</i>	PS	286.70	0.86	14.33	14.32	9.94	3.89	53.41
Paralichthyidae	<i>Paralichthys adspersus</i>	PS	37.01	0.11	9.25	5.86	7.14	5.06	17.66
	<i>Paralichthys microps</i>	PS	114.65	0.34	16.38	18.36	10.91	5.02	57.66
Unidentified larvae			94.31	0.28	7.25	3.09	5.87	3.65	11.84

RESULTS

LARVAL FISH ASSEMBLAGE IN NEARSHORE WATERS

A total of 5553 fish larvae, belonging to 37 taxa were identified (Table 1). The most abundant fish larvae from pelagic spawning (PS) were the common sardine *Strangomera bentincki* (26.39%), the anchoveta *Engraulis ringens* (8.94%), and the lanternfish *Hygophum bruuni* (7.72%). The larvae of the blennies *Scartichthys viridis* (15.77%), *Hypsoblennius sordidus* (8.27%) and the clingfish *Gobiesox marmoratus* (7.06%) were the most abundant species with benthic brooding (BB).

Figure 2 shows the temporal variation in larvae from PS and BB, at different distances from the shore. In the nearshore stations (0.5 and 2.0 km), BB larvae were dominant almost throughout the sampling period, except late September 2013, when the PS *S. bentincki* larvae increased its abundance (to 70.2%) (Figs. 2a, b). At 4.0 km offshore, BB larvae dominated from early October 2012 to late January 2013; after that, PS larvae dominated until June 2014 (Fig. 2c). However, the differences in the abundance of larvae from PS were not significant compared to those of BB (Wilcoxon test, $T=1576$, $P=0.271$).

The multivariate analyses showed differences in the spatial and temporal variability of PS and BB fish larvae (Fig. 3). Larvae from PS did not show differences along the transect (global $R=0.001$, $P=0.472$), but there were differences among seasons (global $R=0.295$, $P=0.001$) (Table 2). On the other hand, larvae from BB showed significant spatial differences along the transect (global $R=0.069$, $P=0.007$) as well as among seasons (global $R=0.168$, $P=0.001$) (Table 2).

A significant decrease in abundance with distance to the shore was detected for the larvae of clingfish *G. marmoratus* ($H=6.393$, $P=0.041$) and the triplefin blenny *H. cunninghami* ($H=8.647$, $P=0.013$) (Fig. 4). Some fish species, such as clingfish *S. sanguineus*, kelpfish *A. variolosus* (BB) and sandperch *P. jugularis* (PS) were collected mainly in nearshore waters (Fig. 4), whereas *S. bentincki*, *H. bruuni* (PS) and *S. viridis* (BB) were found to be more abundant at 2.0 km offshore (Fig. 4). Due largely to the high variance, no significant differences were recorded among stations for these species (*S. sanguineus*, $H=1.061$, $P=0.588$; *A. variolosus*, $H=1.189$, $P=0.551$; *P. jugularis*, $H=1.624$, $P=0.443$; *S. bentincki*, $H=1.028$, $P=0.597$; *H. bruuni*, $H=1.564$, $P=0.457$; *S. viridis*, $H=1.367$, $P=0.504$).

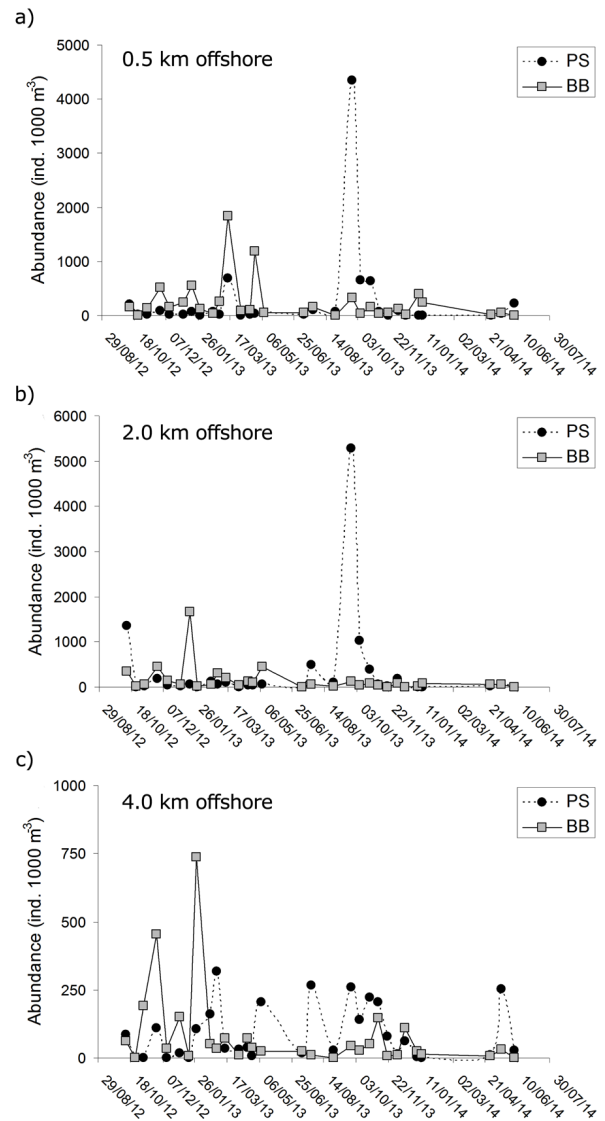


Figure 2. Temporal variation of standardized abundance (ind. 1000 m^{-3}) of fish larvae from pelagic spawning (PS, black dots) and from benthic brooding (BB, grey squares) at different distances from shore, from October 2012 to June 2014 / Variación temporal de la abundancia estandarizada (ind. 1000 m^{-3}) de las larvas de peces provenientes de desoves pelágicos (DP, círculos negros) y desoves bentónicos (DB, cuadrados grises) a diferentes distancias de la costa, desde octubre 2012 a junio 2014

Figure 3. Ordination plots of non-metric multidimensional scaling (NMDS) of ichthyoplankton with pelagic spawning (PS) and benthic brooding (BB). NMDS plots were done taking into account distance from shore (left panel) and sampling season (right panel) / Gráficos de ordenación de escalamiento no métrico multidimensional (NMDS) para el ictioplancton con desove pelágico (DP) y desove bentónico (DB). Los gráficos NMDS fueron realizados de acuerdo a la distancia de la costa (panel izquierdo) y la estación de muestreo (panel derecho)

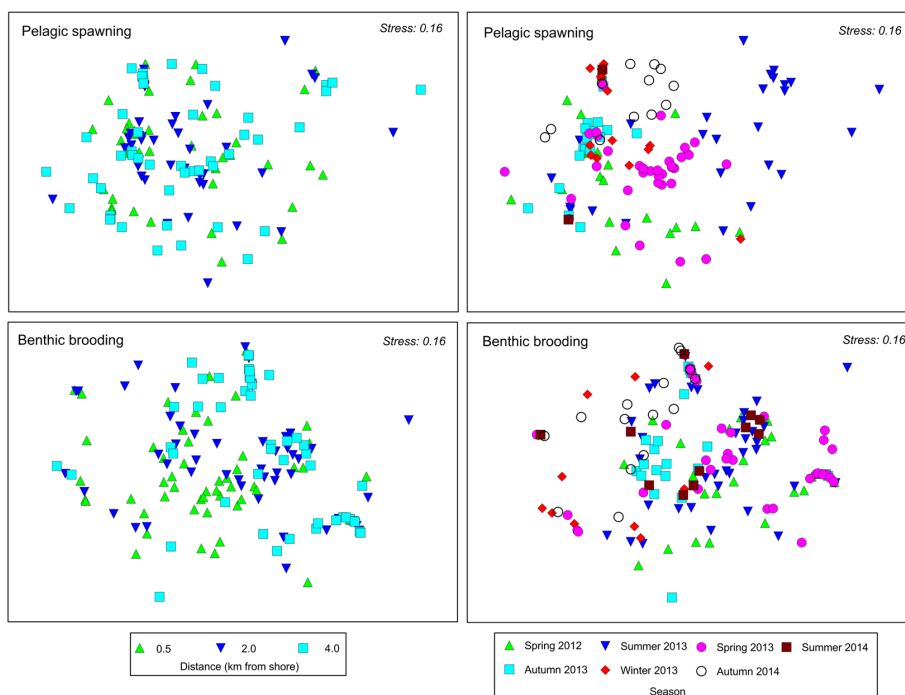


Table 2. Summary of results of two-way ANOSIM carried out with larvae from pelagic spawning (PS) and benthic brooding (BB), according to distance from shore and sampling season. Bold numbers indicate significant differences at $P < 0.05$ / Resumen de los resultados del ANOSIM de dos vías llevado a cabo con larvas originadas de desoves pelágicos (PS) y crianza bentónica (BB), de acuerdo a la distancia a la costa y estación del año del muestreo. Los números en negrita indican diferencias significativas a $P < 0,05$

Groups		Pelagic spawning		Benthic brooding	
		R	P	R	P
By distance	0.5 km, 2.0 km	0.020	0.272	0.064	0.042
	0.5 km, 4.0 km	0.009	0.377	0.165	0.002
	2.0 km, 4.0 km	-0.023	0.704	-0.007	0.550
By season	Spring 2012, Summer 2013	0.313	0.001	0.049	0.127
	Spring 2012, Autumn 2013	0.226	0.001	0.224	0.001
	Spring 2012, Winter 2013	0.239	0.006	0.423	0.001
	Spring 2012, Spring 2013	0.149	0.058	-0.010	0.559
	Spring 2012, Summer 2014	0.501	0.025	0.018	0.362
	Spring 2012, Autumn 2014	0.253	0.016	0.501	0.001
	Summer 2013, Autumn 2013	0.347	0.001	-0.02	0.653
	Summer 2013, Winter 2013	0.370	0.001	0.225	0.017
	Summer 2013, Spring 2013	0.396	0.001	0.064	0.050
	Summer 2013, Summer 2014	0.392	0.042	-0.196	0.991
	Summer 2013, Autumn 2014	0.272	0.003	0.171	0.013
	Autumn 2013, Winter 2013	0.272	0.003	0.244	0.009
	Autumn 2013, Spring 2013	0.275	0.001	0.163	0.009
	Autumn 2013, Summer 2014	0.131	0.321	-0.086	0.816
	Autumn 2013, Autumn 2014	0.445	0.001	0.122	0.067
	Winter 2013, Spring 2013	0.260	0.001	0.193	0.022
	Winter 2013, Summer 2014	0.738	0.024	0.099	0.208
Winter 2013, Autumn 2014	0.173	0.060	0.128	0.089	
Spring 2013, Summer 2014	0.427	0.028	-0.072	0.768	
Spring 2013, Autumn 2014	0.374	0.001	0.281	0.001	
Summer 2014, Autumn 2014	0.982	0.036	0.165	0.075	

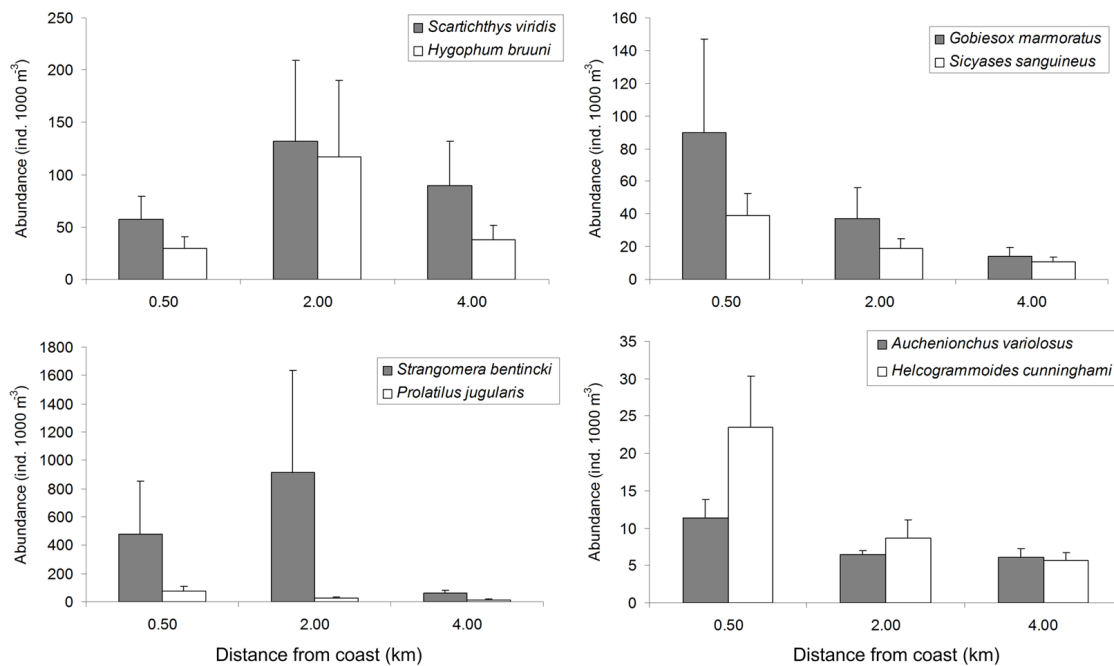


Figure 4. Cross-shelf distribution of fish larvae from Montemar, Bahía Valparaíso, central Chile. Bars correspond to one standard error / Distribución a lo ancho de la plataforma continental de larvas de peces de Montemar, Bahía Valparaíso, Chile central. Las barras corresponden a un error estándar

Table 3. Prevalence and intensity range of the 2 parasite families found on the larvae of 5 different species from nearshore waters of the coasts of Montemar, Bahía Valparaíso, central Chile / Prevalencia y rango de intensidad de las 2 familias de parásitos encontrados en las larvas de 5 diferentes especies de peces de aguas costeras de Montemar, Bahía Valparaíso, Chile central

Taxa	Sample size (n)	Total density (ind. 1000 m ⁻³)	Pennellidae		Caligidae	
			Prevalence	Intensity	Prevalence	Intensity
<i>Auchenionchus variolosus</i>	58	312.12	1.724	[1]	1.724	[1]
<i>Gobiesox marmoratus</i>	405	2353.31	9.630	[1-3]	4.938	[1-2]
<i>Helcogrammoides cunninghami</i>	61	363.73	3.279	[1]		
<i>Sicyases sanguineus</i>	184	1087.36			0.543	[1]
<i>Prolatilus jugularis</i>	176	1134.65	0.568	[1]		

ECTOPARASITES OF FISH LARVAE

The most parasitized fish larvae were from BB origin, particularly the clingfishes *G. marmoratus* (9.63%) and *Sicyases sanguineus* (0.54%), the kelpfish *Auchenionchus variolosus* (1.72%), and the triplefin *Helcogrammoides cunninghami* (3.28%) (Table 3). The larvae of only one species from PS origin, the sandperch *Prolatilus jugularis* (0.57%), had ectoparasites.

A total of 74 ectoparasites were recovered from fish larvae. Seven morpho-species were determined, 2

belonging to families Pennellidae and 5 to Caligidae. They were identified as *Trifur* spp. (Copepoda: Pennellidae) and *Caligus* spp. (Copepoda: Caligidae). The most prevalent ectoparasites were pennellid copepods, with a range of 1 to 3 parasites per larvae (Table 3). Both ectoparasite families showed a similar spatial pattern ($\chi^2=0.815$, $P=0.665$), as they were collected mainly in the nearshore station (94 and 88% for pennellids and caligids, respectively), decreasing exponentially offshore (Fig. 5a). Furthermore, pennellids and caligids on fish larvae

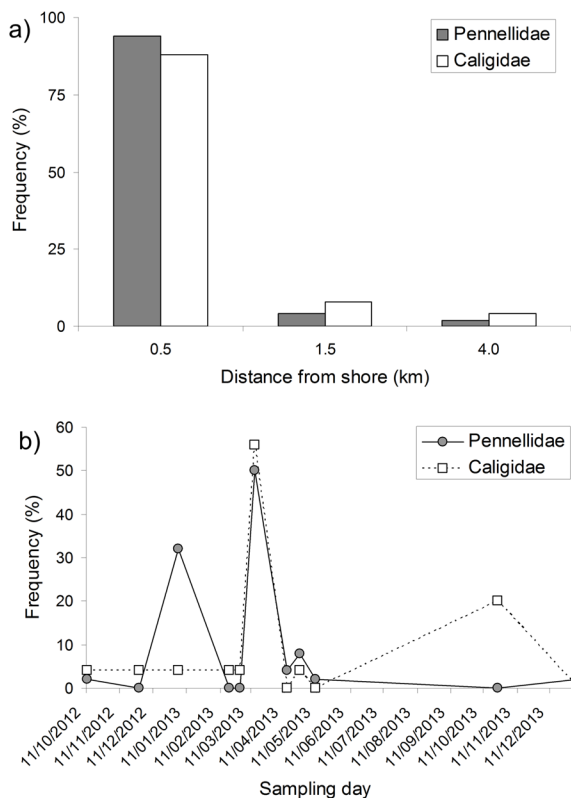


Figure 5. Distributions of ectoparasites of fish larvae from Montemar, Bahía Valparaíso, central Chile. a) Cross-shelf distribution of frequency (%); b) Temporal variation of frequency (%) / Distribución de ectoparásitos de larvas de peces de Montemar, Bahía Valparaíso, Chile central. a) frecuencias (%) a lo ancho de la plataforma; b) variación temporal de las frecuencias (%)

showed significant different temporal variability ($\chi^2=38.1$, $P<0.001$) between them. Pennellids were more frequent during summer and autumn, whereas caligids were more frequent during spring and summer. Specifically, they were found mainly during mid March 2013 (Fig. 5b); pennellids were also frequent during early January 2013, and caligids during late October 2013 (Fig. 5b). In summary, parasitism on fish larvae were more prevalent during summer, autumn and spring, and closer to the coast.

PHYSICAL SETTINGS

Cross-shelf vertical sections of temperature, salinity and density are shown in Figure 6 for selected sampling periods of austral mid- and late-summer, and early winter. During mid-summer, the water column was vertically stratified, with an offshore shoaling of the thermocline, from ~20 m in the nearshore station to ~8 m in the offshore

location (Fig. 6). At around 3 km offshore and in subsurface waters (10 m depth) a tongue of relatively fresher water, probably originated from the Aconcagua River discharges, was evident. Both oceanographic features produced a pycnocline at depths between 10-20 m. On March 14, surface seawater temperature dropped to 13.5°C, showing a weak thermocline at 5 m depth; during this period fresher waters (< 34.3) were found down to 20-30 m depth cross-shelf, causing a shoaling of the pycnocline from 20 m at 2.5 km offshore to 8 m at 0.5 km offshore (Fig. 6). During early winter, the density vertical structure of the water column showed a similar pattern observed during mid-summer, but with lower temperatures and salinities; nearshore waters were dominated by fresher (< 34.3) waters, producing a nearshore deepening of the pycnocline (isopycnal 25.9 units of sigma-t at 20-25 m depth, Fig. 6).

DISCUSSION

The larval fish assemblage from coastal waters off Montemar, central Chile, showed spatial and temporal variability similar to that described by Hernández-Miranda *et al.* (2003), at a location 50 km south to our study site. Cross-shelf distributions of several larval fish taxa and their ectoparasites showed a clear inner-shelf pattern. Intertidal fish species with benthic eggs, like clingfishes and triplefins, are probably not affected by advective processes until they hatch, which reduces the chances of offshore transport. Additionally, hatching events may be synchronized with neap tides (*i.e.*, during first quarter and/or third quarter moon), increasing coastal retention (*i.e.*, *G. marmoratus*, Contreras *et al.* 2013) and potential ectoparasite infestation of fish larvae (Palacios-Fuentes *et al.* 2015). A similar cross-shelf pattern has been reported for larval tripterygiids in the St. Lucia Estuary, southeast Africa (Harris *et al.* 1999), and for larval tripterygiids and blennies in the coast of Portugal (Borges *et al.* 2007).

On the other hand, dispersive events of early larvae from BB can occur. Hatching can take place during spring tides, increasing offshore advection (*i.e.*, *Helcogrammoides chilensis*, Palacios-Fuentes *et al.* 2014), whereas some species have long pelagic larval duration before settlement (up to 100 days in *Hypsoblennius sordidus*, and up to 124 days in *Scartichthys viridis*, Mansur *et al.* 2014). The distributions of Blenniidae and Gobiidae larvae around Medes Islands in the Mediterranean Sea show that they were collected not only inshore but also over the continental shelf at a considerable distance from the habitats of the adults of these species (Sabatés *et al.* 2003). Similarly, larval

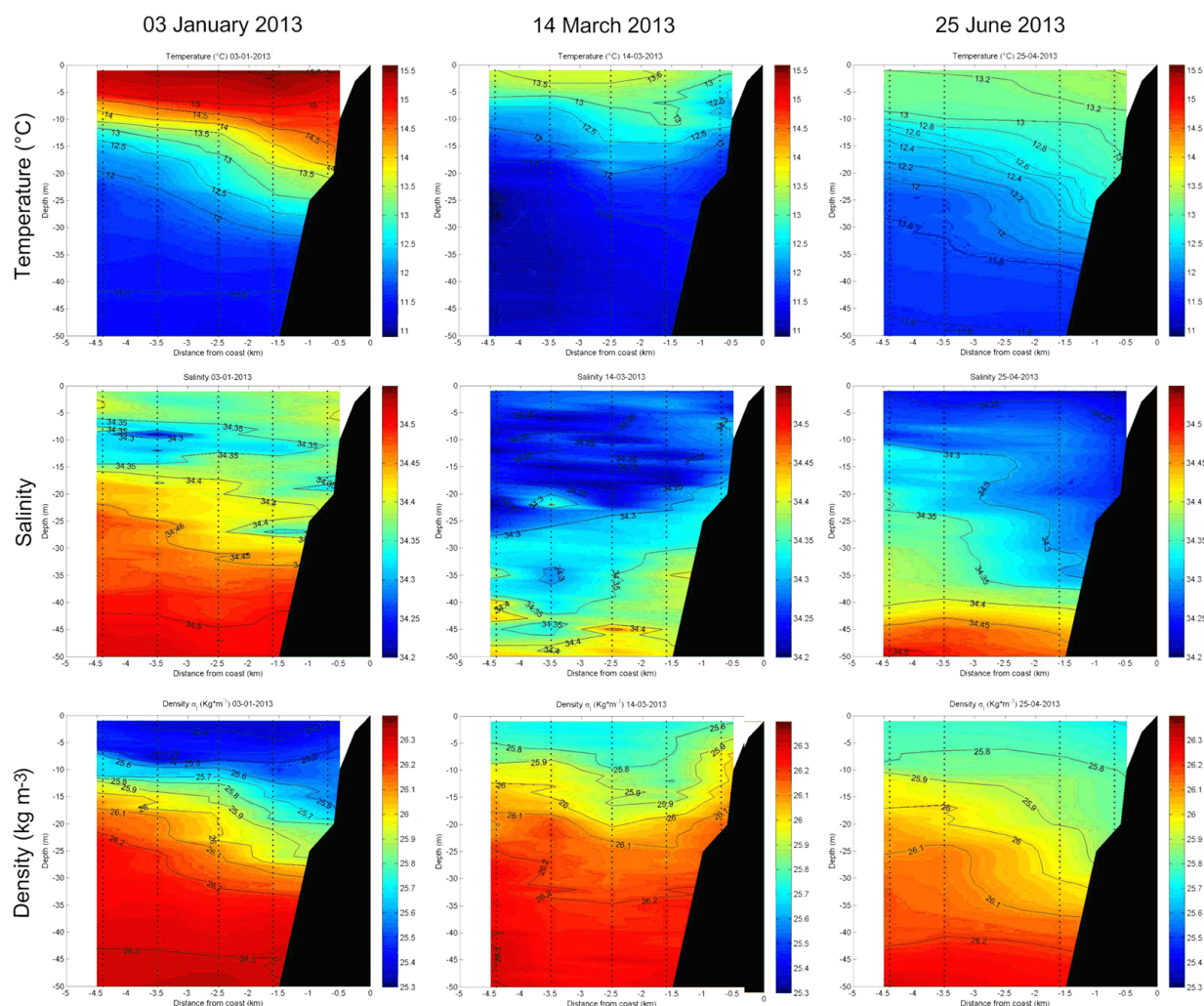


Figure 6. Cross-shelf vertical sections of temperature (°C), salinity and density (units of sigma-t) for periods of high ectoparasite prevalence on fish larvae / Secciones verticales de temperatura (°C), salinidad y densidad (unidades de sigma-t) para periodos de alta prevalencia de ectoparasitos en larvas de peces

H. chilensis and *H. sordidus* can be found in low abundance in slope waters (>10 km offshore) off the Chilean coast during spring and winter (Landaeta *et al.* 2008). In our study, the larvae of some species with BB, such as blenny *S. viridis* and the damselfish *Chromis crusma* were highly abundant; however, they did not have ectoparasites. Most of the larvae of both species were collected as yolk-sac and small reflexion larvae, and they were mostly collected at 2 km offshore. Small larval size and/or development as well as reduced abundance in nearshore waters may preclude copepod infestation in these fish species. From a parasitological perspective, vagrant fish larvae may be lost for the source population and their potential ectoparasites will not be able to attach to their definitive host.

Recently, Palacios-Fuentes *et al.* (2015) described ectoparasites of a larval fish assemblage from El Quisco, central Chile, during late winter-early spring 2010-2012. Similarly to the results in this work, they found that larval clingfish *G. marmoratus* and triplefin *H. cunninghami* had the highest prevalence of pennellid ectoparasites, 12.16 and 5.27%, respectively, and that *G. marmoratus* was the only host species that exhibited positive correlations with pennellid copepod burdens (*i.e.*, prevalence and intensity). Although the larvae of this clingfish were not the most abundant with BB off Montemar during the studied period, their larvae were abundant in nearshore waters were pennellid copepodites may infest fish larvae. Features such as hatching during neap tides, reduced pelagic period (Contreras *et al.*

2013) and nearshore aggregation aided by oceanographic conditions (this study) may enhance the chance of survival of the ectoparasite, and reaching a definitive host (demersal adult fishes from the subtidal zones) (Oliva & González 2004).

Although common sardine larvae, *S. bentincki* were highly abundant from spring 2013 to the end of the study period, they did not have ectoparasites. Herrera (1990) described caligid ectoparasites on larval anchovy *E. ringens*. These ectoparasites are scarcely found in fish larvae with PS, however. This can be explained because it would reduce chances of the completion of the life cycle of ectoparasite copepods, decreasing the probability for the later to find a definitive host (Cribb *et al.* 2000). Larval stages of marine fish species with PS can be found in surface waters over the entire continental shelf off central Chile; this is due to species-specific reproductive tactics (spawning inside embayments, Landaeta & Castro 2006, Landaeta *et al.* 2010), the effect of mesoscale oceanographic features such as upwelling events (Landaeta *et al.* 2008), river plumes (Soto-Mendoza *et al.* 2010) and/or ecophysiological processes (gas bladder inflation, Landaeta & Castro 2013). Furthermore, eggs and larvae from PS may be transported onshore by north wind events during austral winter (Castro *et al.* 2000).

The definitive hosts for pennellids are benthic fish (Muñoz *et al.* 2015, Palacios-Fuentes *et al.* 2015), therefore, fish larvae with BB could be more exposed to larvae of parasitic copepods than fish with PS. In this sense, some oceanographic features may enhance parasite transmission to fish larvae from benthic habitats. For example, a shallow pycnocline might help the aggregation of planktonic organisms in regions where flow often reverses direction, resulting in reduced horizontal transport for the individual (Woodson & McManus 2007). It seems plausible that ectoparasite infestation might increase in locations with these oceanographic conditions.

Nearshore environments of central Chile are characterized by intrusion of river plumes (Soto-Mendoza *et al.* 2010), which produces large turbidity in the system (Saldías *et al.* 2012), affecting the accumulation of meroplankton in the inner shelf (Vargas *et al.* 2006). Additionally, alongshore variation in upwelling intensity and the formation of warm-water pockets or upwelling shadows in sections of the coast (Wieters *et al.* 2003) may increase coastal retention of fish larvae and ectoparasite infestation. However, it is important to continue field-based as well as start laboratory-rearing studies to establish the real importance of oceanographic features in the process of host infestation of pennellid/caligid copepodites on fish larvae and juveniles from rocky shores,

and their impact in the ecology (feeding, growth, survival) of early life stages of marine fishes.

In summary, larval fishes of species with benthic brooding, such as clingfish *Gobiesox marmoratus* and the triplefin *Helcogrammoides cunninghami* showed decreasing abundance with distance from the coast. Similarly, parasitized fish larvae were almost exclusively collected in nearshore waters. The most prevalent ectoparasites were pennellid copepods (*Trifur* spp.), which were found mainly on fish larvae originated from benthic brooding. Finally, during the sampling, the seawater was vertically stratified with a cross-shelf deepening (autumn-winter) or shoaling (summer) of the pycnocline from offshore to nearshore. This might contribute to both larval fish coastal retention as well as ectoparasite infestation in nearshore waters.

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