ARTICLE

Larval fish assemblages in two nearshore areas of the Humboldt Current System during autumn-winter in northern Chile

Ensambles de larvas de peces en dos áreas costeras del Sistema de Corrientes de Humboldt durante otoño-invierno en el norte de Chile

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Resumen.- Se analizaron patrones espaciales y temporales en la composición de larvas de peces en dos áreas costeras pertenecientes al Sistema de la Corriente de Humboldt (HCS), en el norte de Chile. Cinco muestreos fueron realizados en Isla Santa María (ISM) y Punta Coloso (COL), Península de Mejillones. El ictioplancton fue recolectado cada 15 días durante la temporada otoño-invierno austral en 2014 (mayo a agosto). Un total de 412.410 larvas de peces pertenecientes a 36 taxa fueron identificadas, una alta abundancia comparada con otras regiones del HCS. Se registraron similares especies en comparación al centro de Chile, así como diferentes especies respecto del centro de Perú; se compartieron varias familias entre estas regiones del HCS y otros sistemas (por ejemplo, Sistema de Canarias). ISM fue dominado por especies del intermareal-submareal (por ejemplo, *Helcogrammoides cunninghami*), mientras que *Engraulis ringens* fue predominante en COL. Varias especies se correlacionaron positivamente con oxígeno disuelto (por ejemplo, *Auchenionchus microcirrhis*), así como con temperatura y transporte de Ekman (por ejemplo, *Sebastes oculatus*), mientras que otras se correlacionaron negativamente con los mismos parámetros ambientales (por ejemplo, *Graus nigra*). Los resultados sugieren que las larvas de peces podrían utilizar diferencialmente estas áreas, como refugio o zona de alimentación, y que los peces adultos estarían acoplando sus periodos de desove con procesos oceanográficos a corta escala temporal. Este estudio describe por primera vez los ensambles de larvas de peces en áreas costeras del norte de Chile, resaltando su importante rol en los primeros estados de desarrollo de los peces.

Palabras clave: Ictioplancton, peces epipelágicos, peces intermareales-submareales, Sistema de la Corriente de Humboldt

Abstract.- This paper presents an analysis of spatial and temporal patterns in the fish larvae composition of two geographically adjacent nearshore areas within the Humboldt Current System (HCS), northern Chile. Five surveys were performed at Isla Santa María (ISM) and Punta Coloso (COL), Mejillones Peninsula. Ichthyoplankton were collected every 15 days in 2014 during the austral autumn-winter (May to August). A total of 412,410 fish larvae belonging to 36 taxa were identified, a high abundance compared with other HCS regions. Data also revealed similarities in species recorded compared with central Chile as well as differences compared with central Peru; a number of families were shared between these HCS regions and other systems (*e.g.*, Canarias Current System). ISM was dominated by intertidal-subtidal species (*e.g.*, *Helcogrammoides cunninghami*), while *Engraulis ringens* was most abundant at COL. Several species were positively correlated with dissolved oxygen (*e.g.*, *Auchenionchus microcirrhis*), as well as temperature and Ekman transport (*e.g.*, *Sebastes oculatus*), while the presence of others is negatively related to the same environmental parameters (*e.g.*, *Graus nigra*). Results suggest that larvae differently utilize these two areas as a refuge or for feeding, and that adults might be coupling their spawning periods with short-term oceanographic features. Larval fish assemblages of nearshore areas in northern Chile are described here for the first time and highlight the important role of these two areas in the early developmental stages of fish species.

Key words: Ichthyoplankton, epipelagic fishes, intertidal-subtidal fishes, Humboldt Current System

INTRODUCTION

The Humboldt Current System (HCS) in the southeastern Pacific Ocean is a highly productive marine ecosystem that supports one of the largest anchovy and sardine fisheries in the world (Mann & Lazier 1991, Chavez & Messié 2009, Ayon *et al.* 2011). Previous research on the HCS has therefore been focused mainly on the biology of adult fish and the management of this industry; although our knowledge about the early life stages of marine fish species has increased significantly in recent decades, many aspects of the ecology and dynamics of ichthyoplankton assemblages in nearshore areas still remain unknown.

Nearshore zones are characterized as environments that provide high food abundance, refuge against predators and suitable ecophysiological conditions for the development of all fish life history stages (Olivar *et al.* 2010, Pattrick & Strydom 2014, Rabbaniha *et al.* 2015). A number of previous studies have highlighted the importance of shallow nearshore zones as spawning and nursery areas, as well as for the recruitment of larval fish species with offshore and inshore habitats (Strydom 2003, Borges *et al.* 2007, Landaeta *et al.* 2015).

The distribution and abundance of larval fish assemblages are modulated by hydrographic (*e.g.*, temperature, dissolved oxygen, nutrients) (Johnson-Colegrove *et al.* 2015) and hydrodynamic processes (*e.g.*, upwelling shadows, frontal zones, eddies) (Castro *et al.* 2000, Olivar *et al.* 2016). These factors can influence the quantity and quality of food availability as well as reproductive pulses, behavioral adaptations, the duration of pelagic larval stages, and the survival of different developmental stages (Landaeta & Castro 2006, Yannicelli *et al.* 2006, Bustos *et al.* 2008). Coastal geomorphological features are also important for the accumulation and retention of larval fish abundance (Paris & Cowen 2004, Velez *et al.* 2005, Álvarez *et al.* 2015), while bathymetric features as well as distance from the coast can determinate distributions (Hernández-Miranda *et al.* 2003, Adkins *et al.* 2016). Variations in all these characteristics can result in completely different structures and diversities of fish larval assemblages (Smith & Suthers 1999).

The nearshore area around northern Chile is known to be one of the most productive zones within the HCS. This area are largely influenced by a constant upwelling input, which maintain high level of biological productivity (Marín *et al.* 1993, Escribano & Hidalgo 2000, Thiel *et al.* 2007) that sustains a very important pelagic fishery (Escribano *et al.* 2004a) dominated by sardines (*Strangomera bentincki*) and anchovies (*Engraulis ringens*). These fish species utilize nearshore areas around northern Chile for spawning (Rodríguez-Graña & Castro 2003) and as nurseries (Contreras *et al.* 2017). This region is also noteworthy because it is characterized by the presence of a unique topographic structure, the Mejillones Peninsula, which separates the coastlines of Mejillones and Antofagasta Bay, oriented to the north and south, respectively. The presence of this topographical feature, combined with interactions between oceanic and atmospheric regional circulation, has enabled the formation of three upwelling centers and shallow zones within this region (Fonseca & Farías 1987, Escribano & Hidalgo 2001, Marin *et al.* 2003, Thiel *et al.* 2007).

As a result of these particular characteristics, research in this area has emphasized the effects of El Niño events (Rojas *et al.* 2002), feeding ecology (Rodríguez-Graña *et al.* 2005), the vertical and offshore distribution of fish larvae (Angel & Ojeda 2001, Rodríguez-Graña & Castro 2003, Rojas 2014), larval retention (Rojas & Landaeta 2014), and the influence of oceanographic conditions on *E. ringens* larvae (Contreras *et al.* 2017). Information about compositional variations and the abundance of larval fish assemblages in these nearshore areas is currently lacking.

The aim of this study was therefore to evaluate the taxonomic composition and larval fish abundances associated with two nearshore areas in the Mejillones Peninsula during austral autumn-winter season. These data will provide new information about ichthyoplankton community structures in the coastline of northern Chile.

MATERIALS AND METHODS

STUDY AREA

The study was performed in two nearshore areas (50 m offshore) around the Mejillones Peninsula within the Antofagasta region: Isla Santa María (ISM; 23°26'S, 70°36'W) and Punta Coloso (COL; 23º45'S, 70º28'W) (Fig. 1). These nearshore areas are both very shallow (less than 25 m depth), largely influenced by permanent upwelling and characterized by several oceanographic processes that generate high aggregation and retention of phytoplankton and zooplankton (Escribano & Hidalgo 2000, Escribano *et al.* 2004b).

Although the study areas are geographically close to one another, they are markedly different oceanographically. The first, ISM area is a semi-closed

bay with a central island that is characterized by cold waters with high nutrient content and low surface oxygen levels (Piñones *et al.* 2007, Pacheco *et al.* 2011). The ocean bottom in this area includes rocky reefs, barren ground, and kelp forests of *Lessonia trabeculata* and *Macrocystis integrifolia* (Ortiz 2008, Jofré-Madariaga *et al.* 2013, Uribe *et al.* 2015). In contrast, the COL, is an open coastal area that includes an upwelling plume and a cyclonic eddy in front of the bay (Escribano & Hidalgo 2001) and an ocean bottom that mainly comprises sand, gravel, and mud (Carrasco 1997, Ortiz *et al.* 2015) as well as patches of *L. trabeculata* kelp (Villouta & Santelices 1986, Ortiz *et al.* 2010, Jofré-Madariaga *et al.* 2013).

Sample collection

Five surveys were carried out within each area over the 2014 austral autumn-winter season in late-May, mid-June, late-June, mid-July, and at the beginning of August. We collected ichthyoplankton samples using a Bongo net (60 cm mouth diameter, 300 µm mesh size) equipped with a TSK flow meter (The Tsurumi-Seiki Co., Ltd., Tsurumi-ku, Yokohama, Japan) to quantify filtered water. For each survey, a total of eight consecutive oblique tows at a depth of 10 m were performed parallel to the coastline between 07:00 and 10:00. An artisanal boat was used for tows that had durations of between 10 and 15 minutes at speeds of 1-2 knots. All samples were fixed in 5% formalin buffered with sodium borate and then were transferred to 96% ethanol after 24 h.

All fish larvae were separated, counted, and classified to the lowest possible taxonomic level using previous descriptions presented by Balbontín & Pérez (1979, 1980), Pérez (1979, 1981), Herrera (1984), and Herrera *et al.* (2007). Fish larvae were categorized according to the adult habitats as epipelagic, demersal, mesopelagic, intertidal-subtidal, or sandy subtidal.

Values for temperature (T; °C), dissolved oxygen (DO; mg L^{-1}), and the salinity (S) of the water column were obtained at the beginning and end of each survey day from the surface to depths between 15 m and 20 m using a CTD Seabird SBE-19 plus. Mean values were used for statistical analyses in all cases. Daily prevailing wind data were provided by the Cerro Moreno Meteorological Station (23°27'S, 70°26'W), a facility that is supervised by the Dirección Meteorológica de Chile. Datasets were downloaded two days prior to each survey for both areas, and values for Ekman transport (E$_t$) were calculated to assess the effect of wind on the offshore displacement of
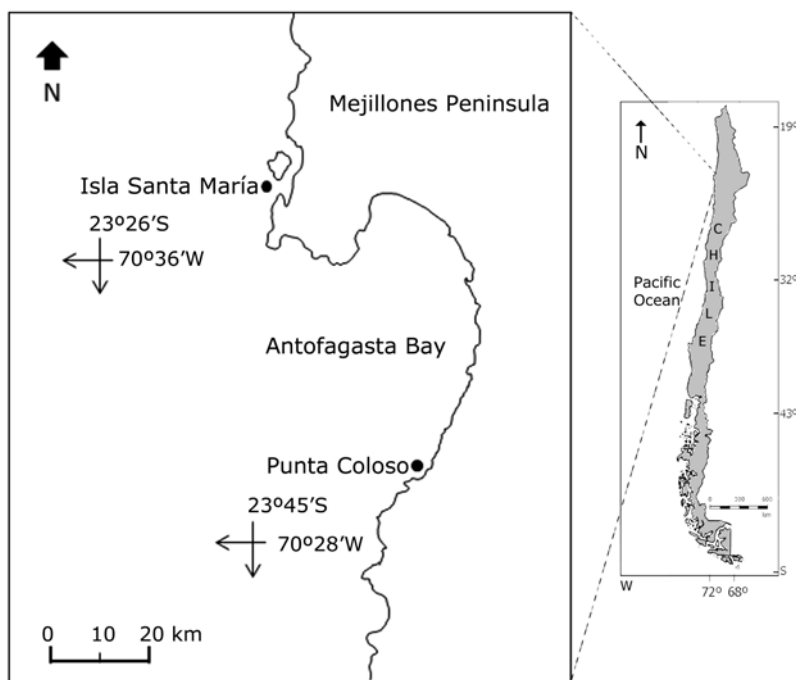

Figure 1. Study area in the northern Chilean coast (southeast Pacific). The black marks on this figure show the surveys areas: Isla Santa María and Punta Coloso / Área de estudio en la costa Norte de Chile (Pacífico Sudeste). Los puntos negros indican las áreas de muestreo: Isla Santa María y Punta Coloso

surface coastal waters (Mann & Lazier 2013). The equation used for this calculation is as follows:

$$M_E = \tau/f \qquad (1)$$

In this expression, M_E denotes E_t (1,000 kg m^{-1} s^{-1}), while f is the Coriolis parameter, and τ is the along-shore wind stress at the water surface (Pond & Pickard 1983). Similarly, tau (τ) was estimated as follows:

$$\tau = \rho_a * C_d * W \qquad (2)$$

In this expression, ρ_a denotes air density (1.2 kg m^{-3}), C_d is the drag coefficient (0.0014), and W refers to along-shore wind speed (m s^{-1}).

DATA ANALYSIS

Larval abundances were standardized to individuals (ind.) per 1000 m^{-3} for each fish species. These data were transformed using the fourth-root to enhance the contribution of less abundant taxa in analyses.

A two-way permutation multivariate analysis of variance (PERMANOVA) was performed using the Bray-Curtis index to assess variations in fish larval abundances between areas (ISM-COL) and surveys (May-August). Several similarity percentage analyses (SIMPER) was carried out to compare the contributions of larval fish species between areas and surveys. All analyses were performed using the software package PRIMER V6.1.16 + PERMANOVA (Clarke & Gorley 2006).

Associations between larval fish abundances and environmental variables were evaluated via canonical redundancy analysis (RDA). A variance inflation factor (VIF) ≤ 10 was used to reduce multicollinearity among predictive variables and statistical significance was tested using Monte Carlo permutations in the software CANOCO 4.5 (ter Braak & Šmilauer 2002) using 9,999 iterations.

RESULTS

FISH LARVAL COMPOSITIONS

A total of 412,410 fish larvae were collected belonging 22 families and 36 taxa (Table 1). The compositions of larval fish species were different between areas; 21 species representing 27.21% of the total larval assemblage were collected from the ISM area, while 31 species representing 72.79% of the total were collected from COL (Table 1). Temporal peaks in species were also different between areas; the species count at ISM was higher in August while that at COL peaked in late-June (Fig. 3).

The results of this study reveal variations in both the abundance and composition of larval fish species belonging to different habitats in both areas. 98.57% of total larval fish abundance within the ISM area corresponded to intertidal-subtidal species while just 1.43% corresponded to epipelagic, demersal, mesopelagic, and sandy subtidal species (Fig. 2, Table 1). The most abundant fish species recorded within this area included the triplefin, *Helcogrammoides cunninghami* (43.9%), and the labrisomid blenny, *Auchenionchus crinitus* (36.6%). Intertidal-subtidal species were also the most dominant group and comprised 57.1% of the total ISM composition. The remaining 42.9% of total species
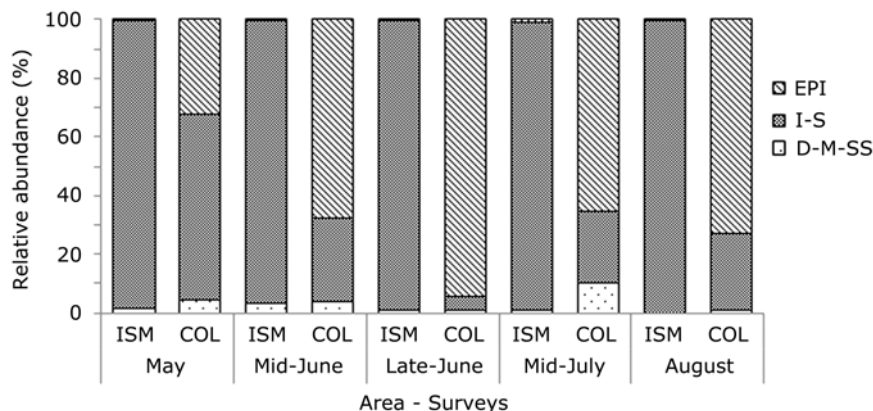

Figure 2. Patterns in fish larvae relative abundances based on adult habitats, including relative abundances per survey (May-August) and area (ISM-COL). Habitats were grouped as: E: epipelagic; I-S: intertidal-subtidal and D-M-S.S.: demersal, mesopelagic and sandy subtidal / Patrones de abundancia relativa de larvas de peces según el hábitat de los peces adultos, incluyendo las abundancias relativas por muestreo (mayo-agosto) y área (ISM-COL). Los hábitats fueron agrupados como: E: epipelágicos, I-S: intermareales-submareales y D-M-S.S.: demersales, mesopelágicos y de fondos submareales

Table 1. Taxonomic composition and abundance (ind. 1000 m⁻³) of fish larvae collected in nearshore Isla Santa María (ISM) and Punta Coloso (COL) areas / Composición taxonómica y abundancias (ind. 1000 m⁻³) de las larvas de peces colectadas en las áreas costeras de Isla Santa María (ISM) y Punta Coloso (COL)

Family	Species	Species code	Habitat	ISM			COL		
				Median	Q1	Q3	Median	Q1	Q3
Engraulidae	*Engraulis ringens*	Er	E	6.09	3.25	11.59	696.95	294.78	3342.05
Clupeidae	*Strangomera bentincki*	Sb	E	-	-	-	11.10	5.96	39.06
Myctophidae	*Hygophum bruuni*	Hb	M	3.56	-	-	20.19	10.42	30.59
	Lampanyctus iselinoides	Li	M	-	-	-	14.29	14.29	16.72
	Lampanyctus parvicauda	Lp	M	-	-	-	5.97	5.42	19.55
	Myctophidae gen.sp1	M	M	-	-	-	6.21	-	-
	Triphoturus oculeus	To	M	-	-	-	13.09	8.30	16.72
Merlucciidae	*Merluccius gayi*	Mg	D	-	-	-	7.99	-	-
Ophidiidae	*Genypterus* sp.	Gs	D	-	-	-	13.94	8.30	25.45
Gobiesocidae	*Gobiesox marmoratus*	Gm	I-S	23.32	13.81	47.69	30.59	11.83	83.59
	Sicyases sanguineus	Ss	I-S	4.14	2.96	13.40	11.93	7.05	20.11
Atherinopsidae	*Odontesthes regia*	Or	E	10.83	3.50	17.08	-	-	-
Sebastidae	*Sebastes oculatus*	So	D	9.56	4.91	20.14	22.48	10.85	30.33
Normanichthyidae	*Normanichthys crockeri*	Nc	E	4.38	-	-	21.48	12.58	42.45
Agonidae	*Agonopsis chiloensis*	Ac	D	3.12	-	-	-	-	-
Sciaenidae	Sciaenidae gen.sp1	S	S.S.	-	-	-	7.16	6.07	11.67
Kyphosidae	*Girella laevifrons*	Gl	I-S	16.29	9.34	30.58	-	-	-
	Graus nigra	Gn	I-S	-	-	-	19.36	14.61	39.51
Pomacentridae	*Chromis crusma*	Cr	I-S	-	-	-	11.83	7.38	48.87
Pinguipedidae	*Pinguipes chilensis*	Pc	D	-	-	-	22.60	6.97	47.15
	Prolatilus jugularis	Pj	D	-	-	-	21.50	15.25	47.03
Tripterygiidae	*Helcogrammoides cunninghami*	Hc	I-S	348.76	99.81	720.47	19.51	9.78	35.45
Dactyloscopidae	*Sindoscopus australis*	Sa	S.S.	9.46	5.09	16.46	11.79	7.70	18.99
Blenniidae	*Hypsoblennius sordidus*	Hs	I-S	12.02	6.42	22.69	21.26	12.42	49.68
	Scartichthys viridis	Sv	I-S	52.62	18.43	112.76	18.50	10.85	36.65
Clinidae	*Myxodes* sp.	Ms	I-S	13.77	7.86	48.76	-	-	-
Labrisomidae	*Auchenionchus crinitus*	Acr	I-S	327.14	118.98	654.93	41.68	13.09	199.18
	Auchenionchus microcirrhis	Am	I-S	26.75	11.03	54.22	154.91	47.31	469.11
	Calliclinus geniguttatus	Cg	I-S	32.50	15.12	70.64	11.92	10.08	22.60
	Labrisomidae gen.sp1	L	I-S	3.83	3.18	5.82	111.78	-	-
Gobiidae	*Ophiogobius jenynsi*	Oj	I-S	27.09	6.68	59.02	35.49	12.28	84.75
Stromateidae	*Stromateus stellatus*	Ss	E	-	-	-	5.96	-	-
Paralichthyidae	*Hippoglossina macrops*	Hm	D	5.42	4.04	6.64	22.48	7.38	39.18
	Paralichthys adspersus	Pa	S.S.	-	-	-	17.19	10.20	29.31
	Paralichthys microps	Pm	S.S.	-	-	-	11.83	4.95	27.94
Syngnathidae	*Leptonotus blainvilleanus*	Lb	I-S	3.83	-	-	-	-	-
	Unidentified larvae			9.66	4.50	16.6	26.12	13.11	97.13

E: epipelagic, D: demersal, M: mesopelagic, I-S: intertidal-subtidal, S.S.: sandy subtidal

composition comprised taxa from epipelagic (19.05%), demersal (14.29%), mesopelagic (4.76%), and sandy subtidal (4.76%) habitats, mainly the anchovy *E. ringens*, the rockfish *S. oculatus*, and the sand stargazer *Sindoscopus australis* alongside some others (Fig. 2, Table 1).

Data show that species of epipelagic fish (85.49% of total larval abundance) were the most abundant group recorded within the COL nearshore area, followed by intertidal-subtidal taxa (12.72%). The remaining 1.79% corresponded to larval species of demersal, mesopelagic, and sandy subtidal habitats. The most abundant species was the anchovy *E. ringens*. Intertidal-subtidal taxa comprised 38.72% of the total composition, dominated by the labrisomid *A. microcirrhis*. The remaining 61.28% of species composition comprised demersal (19.35%), mesopelagic (16.13%), epipelagic (12.9%), and sandy subtidal species (12.9%), a total of 19 taxa including *E. ringens*, *Hygophum bruuni*, *Paralichthys adspersus*, and *Prolatilus jugularis* (Fig. 2, Table 1).

The hydrographic characteristics of the water column (T, S and DO) varied little between surveys in each area (Fig. 3). The water temperature at ISM remained similar between May and June ($14.6 \pm 0.1°C$) but decreased in August ($14.0 \pm 0.1°C$) (Fig. 3b), while the lowest DO value at this area was recorded in late-June (2.82 ± 0.27 mg L^{-1}) and the highest in August (4.33 ± 0.22 mg L^{-1}) (Fig. 3c). Salinity values also varied little between surveys, from 34.83 ± 0.0005 to 34.95 ± 0.049 (Fig. 3d), while E_t decreased temporally between May and August (507.52 and 210.8 m^3 s^{-1} km^{-1}, respectively) (Fig. 3e).

Recorded water temperature at the COL area fluctuated between a minimum of $14.3 \pm 0.1°C$ and a maximum of $15.2 \pm 0.03°C$ (Fig. 3b). The lowest DO value

recorded at this area was in July (1.97 ± 0.20 mg L^{-1}) while the highest was in August (4.34 ± 0.16 mg L^{-1}) (Fig. 3c). Although salinity did not fluctuate much between surveys (34.82 ± 0.02 and 34.88 ± 0.01) (Fig. 3d), E_t peaked during late-Jun (545.48 m^3 s^{-1} km^{-1}) and decreased again in August (210.8 m^3 s^{-2} km^{-1}) (Fig. 3e).

VARIATION IN FISH LARVAL COMPOSITION

The results of PERMANOVA tests revealed significant differences in both, abundances and composition between areas and surveys, as well as their interactions (Table 2). At the same time, the results of our SIMPER analysis show that the species *E. ringens*, *H. cunninghami*, *A. crinitus*, and *A. microcirrhis* contributed the most to average dissimilarities between areas (Table 3a). The
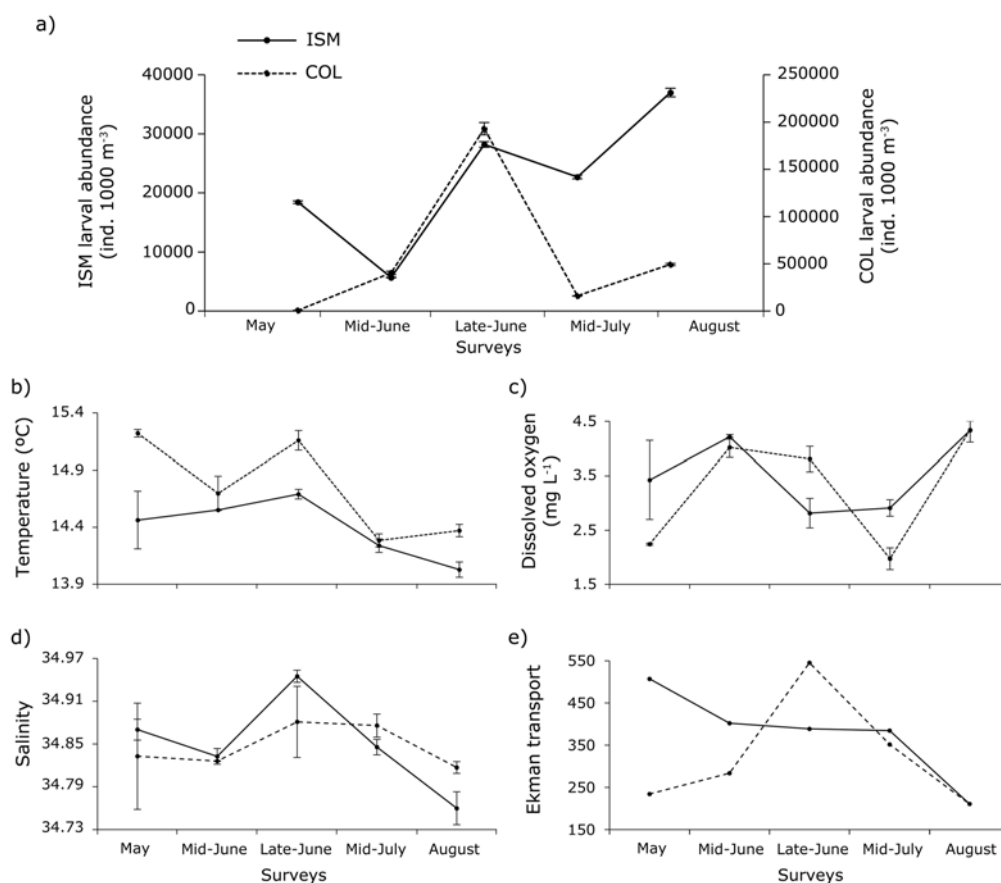

Figure 3. Temporal variations between fish larvae abundances and environmental variables during the study period. The continuous line on this figure marks ISM while the dashed line marks COL for: (a) ISM and COL larval fish abundances, (b) average temperature, (c) average dissolved oxygen, (d) average salinity and (e) Ekman transport per survey (May-August). The vertical lines correspond to standard deviations / Variaciones temporales entre las abundancias de larvas de peces y las variables ambientales durante el periodo de estudio. La línea continua en la figura indica a ISM mientras que la línea discontinua indica a COL, para: (a) abundancias de larvas de peces de ISM y COL, (b) temperatura promedio, (c) oxígeno disuelto promedio (d) salinidad promedio y (e) transporte de Ekman por muestreo (mayo-agosto). Las líneas verticales corresponden a la desviación estándar

Table 2. PERMANOVA results for similarities in fish larvae abundances between areas (Isla Santa María and Punta Coloso), surveys (May-August), and their interactions / Resultados de PERMANOVA por similitud en las abundancias de larvas de peces entre áreas (Isla Santa María y Punta Coloso), muestreos (mayo-agosto) y su interacción

Source	df	SS	MS	Pseudo-F	P
Areas	4	71349	71349	97.77	**0.001**
Surveys	1	32849	8212.4	11.25	**0.001**
Areas x Surveys	4	29245	7311.3	10.02	**0.001**
Residuals	70	51080	729.71		

*df: Degrees of freedom, Pseudo-F: ratios and P: permuted probability values

species *A. crinitus* and *H. cunninghami* contributed the most to dissimilarity within the ISM area (Table 3b), while *E. ringens* and *A. microcirrhis* were the main contributors in the COL area (Table 3c). Additional species that made lower contributions to these areas are also listed in Table 3.

RELATION BETWEEN FISH LARVAL ASSEMBLAGES AND ENVIRONMENTAL VARIABLES

The results of RDA revealed both a good fit and high statistical significance (ISM, $F_{3,21} = 3.605$, $P < 0.005$; COL, $F_{3,31} = 10.38$, $P < 0.001$). Data show that 95.6 and 98.5% of total variance in fish larval composition was explained by environmental parameters at ISM and COL, respectively. However, salinity was excluded for these comparisons because this variable exhibited strong collinearity with DO. Some species were positively correlated with water temperature and E_t at ISM, independent of survey (*e.g.*, *Myxodes* sp., *S. oculatus*), as well as with DO in both May and mid-June (*e.g.*, *C. geniguttatus*, *Hippoglossina macrops*). A number of other species were negatively correlated with temperature and E_t in August (*Sicyases sanguineus*, *E. ringens*, *H. cunninghami*) as well as with DO in mid-July (*e.g.*, *Gobiesox marmoratus*, *Girella laevifrons*) (Fig. 4a).
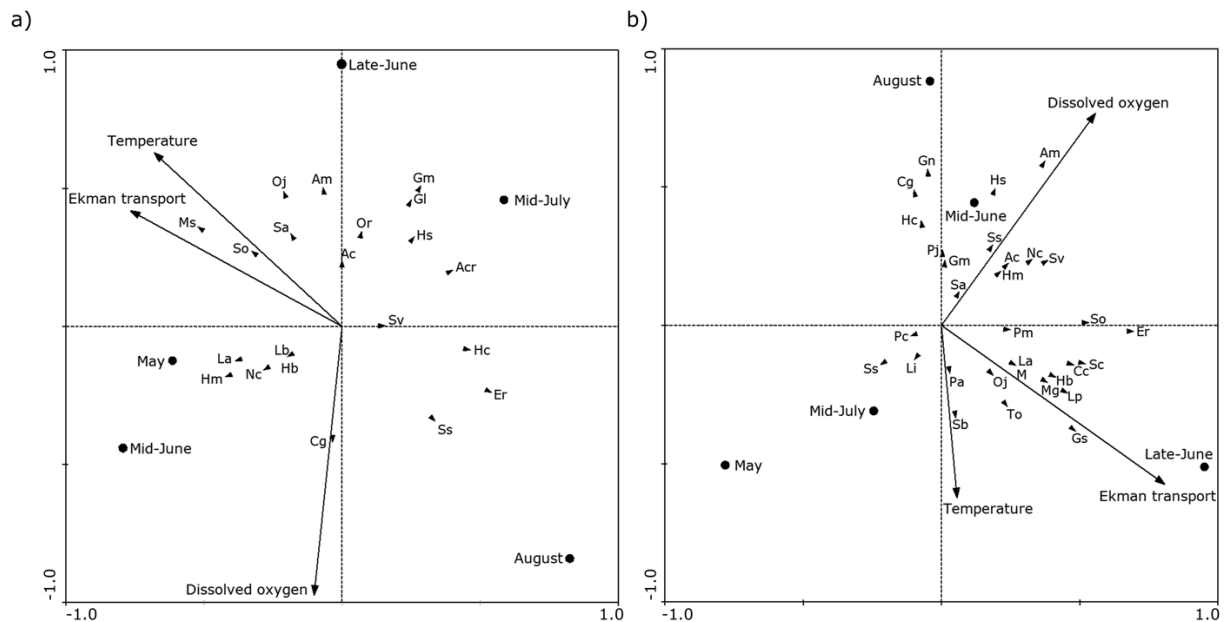

Figure 4. RDA triplot of larval fish assemblages, environmental variables (dissolved oxygen, temperature, and Ekman transport), and surveys at (a) ISM and (b) COL. Fish species are represented by arrows, environmental variables with thick solid arrows, and surveys (May-August) by points. Species codes are given in Table 1 / Triplot del análisis de Redundancia (RDA) del ensamble de larvas de peces, variables ambientales (oxígeno disuelto, temperatura y transporte de Ekman) y muestreos en a) ISM y b) COL. Las especies de peces están representadas por flechas, las variables ambientales por flechas con líneas gruesas, y los muestreos (mayo-agosto) por puntos. Los códigos de las especies se muestran en la Tabla 1

Table 3. SIMPER results for (a) areas (ISM-COL), (b) ISM, and (c) COL based on average fish larvae abundances. Only species contributing 90% to average similarity between areas were included in these analyses / Resultados de SIMPER para (a) áreas (ISM-COL), (b) ISM y (c) COL usando las abundancias promedio de larvas de peces. Sólo se incluyeron aquellas especies que contribuyeron en un 90% de la similitud promedio entre áreas

	Group	Species	ISM	COL			
a)	ISM & COL	AS%: 30.48	AA	AA	AD	%Co	%Cu
		E. ringens	0.97	54.17	22.08	31.76	31.76
		H. cunninghami	30.43	1.9	11.84	17.03	48.79
		A. crinitus	28.76	5.76	9.54	13.73	62.52
		A. microcirrhis	6.94	20.87	5.78	8.32	70.83
		A. variolosus	8.11	0.93	2.98	4.28	75.12
		S. viridis	8.8	3.78	2.09	3.00	78.12
		N. crockeri	0.1	4.00	1.62	2.33	80.44
		Myxodes sp.	3.83	0.00	1.59	2.29	82.73
		O. jenynsi	5.42	1.90	1.46	2.10	84.83
		S. sanguineus	0.21	2.64	1.01	1.45	86.29
		P. jugularis	0.00	2.12	0.88	1.26	87.55
		H. brunni	0.05	2.12	0.86	1.24	88.79
		P. adspersus	0.00	2.07	0.86	1.24	90.02
b)	ISM	AS%: 68.05	AA	AS	%Co	%Cu	
		A. crinitus	28.76	19.67	28.91	28.91	
		H. cunninghami	30.43	19.19	28.2	57.11	
		A. variolosus	8.11	6.19	9.09	66.20	
		S. viridis	8.8	5.13	7.54	73.74	
		G. marmoratus	6.4	3.48	5.11	78.85	
		H. sordidus	4.68	3.18	4.68	83.53	
		A. microcirrhis	6.94	3	4.41	87.94	
		S. australis	3.76	2.7	3.97	91.91	
c)	COL	AS%: 42.95	AA	AS	%Co	%Cu	
		E. ringens	54.17	17.28	40.22	40.22	
		A. microcirrhis	20.87	9.81	22.85	63.07	
		G. marmoratus	5.75	2.63	6.11	69.19	
		A. crinitus	5.76	1.86	4.34	73.53	
		S. viridis	3.78	1.80	4.19	77.72	
		S. sanguineus	2.64	1.32	3.08	80.80	
		N. crockeri	4.00	1.26	2.94	83.73	
		H. sordidus	3.45	1.24	2.88	86.61	
		S. australis	2.94	1.13	2.64	89.25	
		P. adspersus	1.48	0.59	1.38	90.63	

AS%: percentage of average similarity, AA: average abundance, AD: average dissimilarity, AS: average similarity, %Co: percentage of contribution to the average similarity, %Cu: percentage of accumulated contribution to the average similarity

Almost all the species recorded at COL were positively correlated with both E_t and temperature in late-June (*e.g.*, *Genypterus* sp., *Strangomera bentincki*) and with DO in mid-June (*e.g.*, *A. microcirrhis*, *Hypsoblennius sordidus*). At the same time, some species exhibited negative correlations with temperature and E_t in August (*Graus nigra*, *C. geniguttatus*, *H. cunninghami*), as well as with DO in May and mid-July (*Pinguipes chilensis*, *Lampanyctus iselinoides* and *Sicyases sanguineus*) (Fig. 4b).

DISCUSSION

The results of this study highlight a number of important differences in larval abundances within shallow nearshore areas of the HCS during the austral autumn-winter period. The larval abundances reported here for northern Chile (23°S latitude) are higher than those previous recorded during the same season along the central Peruvian coast (14°S latitude) (Vélez *et al.* 2005) and along the central Chilean coast (30°S latitude) (Hernández-Miranda *et al.* 2003, Landaeta *et al.* 2015). The key phenomenon responsible for the higher biological productivity of the HCS is coastal upwelling (Montecino & Lange 2009); indeed, the high ichthyoplankton abundance of nearshore northern Chile compared with other HCS regions could by a consequence of the very narrow continental shelf (less than 20 km wide) in this region. These features enable permanent upwelling within the coastal zone and lead to incremental levels of biomass and productivity throughout the year (Fonseca & Farias 1987, Morales *et al.* 1996, Daneri *et al.* 2000, Escribano *et al.* 2004b, Letelier *et al.* 2012). This also means that changes in upwelling conditions in northern Chile are less pronounced than those at other HCS latitudes where differences in peak fish larvae abundances are strongly coupled to spawning and short-term oceanographic events (Hernández-Miranda *et al.* 2003).

Fish larvae assemblages are very similar between central and northern Chile; 5 species are found just in northern Chile (*Lampanyctus parvicauda*, *Agonopsis chiloensis*, *G. nigra*, *C. geniguttatus*, and *Ophiogobius jenynsi*) and another 13 occur just in the central part of the country (*e.g., Bovichthys chilensis*, *A. variolosus*, *Helcogrammoides chilensis*). At the same time, Peru and northern Chile share just 8 common species (*e.g.*, *E. ringens*, *G. marmoratus*, *Normanichthys crockeri*). Species variation between regions might be the result of biogeographic processes. The HCS is a large marine ecosystem and each distinct regions are influenced by different water masses that predominate at different latitudes with different characteristics; fresh, cooler, and less saline surface water predominates in northern and, principally in central Chile

(sub-Antarctic surface water, Antarctic intermediate water), while warmer and more saline waters are seen around central Peru (subtropical surface water, equatorial subsurface water) (Silva 1977, Silva & Neshyba 1980). These water masses influence the biotic and abiotic characteristics of each region, largely determining the composition of fish larvae in nearshore areas.

Species of Engraulidae, Tripterygiidae, Labrisomidae, Gobiesocidae, Blenniidae, and Gobiidae families were dominant in both sample areas, in agreement with previous studies on the HCS that have demonstrated the presence of similar groups at high abundance in nearshore shallow waters around the central coasts of Peru and Chile (Hernández-Miranda *et al.* 2003, Vélez *et al.* 2005, Landaeta *et al.* 2015, Díaz-Astudillo *et al.* 2017). The families recorded in this study have also been noted in other current systems, including the Canarias Current System (Azeiteiro *et al.* 2006, Beldade *et al.* 2006, Álvarez *et al.* 2015), the Australia East Current System, and the Equatorial North Current System (Leis & Miller 1976, Kingsford & Choat 1989, Gray 1993), as well as in shallow nearshore waters within the Agulhas Current (Rabbaniha *et al.* 2015). These similarities not only result from similar reproductive behaviors, but also suggest that these fish species require the same resources during early life stages (Nonaka *et al.* 2000). Independent of habitat (*e.g.*, epipelagic, intertidal), fish species spawn in, or near to, coastal habitats in order to avail of a suitable food supply, shelter, and favorable ecophysiological conditions for larval development (Blaber & Blaber 1980, Pattrick & Strydom 2014). Indeed, by taking advantage of the optimal conditions offered by these habitats, adults increase the probability of survival and development of their offspring and therefore influence the ichthyoplankton abundance and composition of nearshore areas (Houde & Zastrow 1993, Castro & Hernandez 2000).

The data presented in this study show that larval compositions were different between areas, as well as the presence of a marked difference in the dominance of inshore and offshore larval species. The ISM area was characterized by the highest abundance of intertidal-subtidal fish species (*e.g.*, *H. cunninghami* and *A. crinitus*), those that develop and settle on the seabed; this result suggests that such species permanently utilize this area, independent of seasonal shifts over short time-scales. A high abundance of inshore habitat fish species is also characteristic of other nearshore ecosystems around the world (Borges *et al.* 2007, Álvarez *et al.* 2015, Isari *et al.* 2017), and is indicative of interactions between biophysical mechanisms that cause taxa to remain within their natal areas (Sponaugle *et al.* 2002, Vélez *et al.* 2005). This means that features such as coastal geomorphology, ocean bottom topography,

and the presence of kelp forests might be reducing circulation patterns at ISM. These attributes also decrease the probability of offshore transport and contribute to larval retention, especially for species that develop in nearshore areas (Cowen 2002, Kingsford *et al*. 2002, Largier 2003, Palma *et al.* 2006).

Offshore larval species classified as epipelagic were the most abundant and dominant at the COL area. The fact that the epipelagic anchovy (*E. ringens*), a species with a life cycle that takes place in the water column, was most abundant at this area likely reflects the fact that adult fish use nearshore regions as nursery areas because of high productivity and low offshore transport. A number of previous studies have noted that *E. ringens* preferentially spawns during the austral winter (Bernal *et al*. 1983, Loeb & Rojas 1988, Castro & Hernandez 2000, Hernández & Castro 2000), especially in zones that are characterized by highly variable short-term processes (*e.g.*, upwelling-relaxation) and favorable oceanographic and meteorological conditions (Rojas *et al.* 2002, Rojas & Landaeta 2014). High abundances of *E. ringens* larvae are common in other nearshore areas within the HCS (Hernández-Miranda *et al*. 2003, Vélez *et al*. 2005, Landaeta *et al*. 2015), while larval fish from the Engraulidae occur frequently in other ecosystems of this type (Able *et al*. 2010, Pattrick & Strydom 2014, Giordano *et al*. 2015). Thus, use of the COL nearshore area for spawning might be a tactic to increase larval survival as this region is characterized by the high retention of planktonic organisms and food availability (Escribano & Hidalgo 2000, 2001, Escribano *et al*. 2004b).

The environmental features measured in this study remained relatively constant throughout the austral autumn-winter season. However, our results did reveal association differences between larval assemblages and short-term oceanographic features between both areas. Several species in our dataset were strongly correlated with high DO levels (*e.g.*, *A. microcirrhis*, *C. genigutattus*), warmer temperate waters, and strong E_t values (*e.g.*, *Myxodes* sp., *S. oculatus*); indeed, the fact that rarer species were negatively correlated with the same parameters (*e.g.*, *G. nigra*, *E. ringens*, *S. sanguineus*), suggests aggregation with cooler water temperatures, lower E_t values, and higher oxygen waters.

Temperature is one of the most important environmental factors that influence the metabolism, growth, and development of ichthyoplankton (Munday *et al.* 2008). For example, a high temperature close to the tolerance limit of a species will increase metabolic costs and limit the energy available for growth (Pörtner & Peck 2010),

particularly during periods of short-term temperature variability, where also several biochemical indices (*e.g.*, lipids, protein synthesis) may influence natural coastal fish populations (Duarte *et al.* 2018). In other words, this suggest that species correlated with high or low water temperatures could have different thermal requirements or preferences in both their metabolism and growth during early fish stages (Houde 1989, Pepin 1991).

Similarly, variations in DO influences the growth of larval fish species over the long-term and reduces their probability of survival (Vanderplancke *et al.* 2015). The correlation reported here between larval species and high DO rates might also reflect a strategy of spawning during optimal conditions due to low DO rates can cause conditions of stress for spawning fish and their eggs (Beitinger 1990). This is because are significantly less tolerant to low oxygen levels compared with their adult counterparts (Zeng *et al.* 2010, Gilly *et al.* 2013, Sloterdijk *et al.* 2017).

Favorable E_t conditions are also related to nutrient influx into superficial waters near to coasts (Hernandez-Miranda *et al.* 2003). Plankton accumulation provides a key potential food source and is therefore beneficial for larval survival, another reason why fish species could evolved their spawning behaviors in these areas (Tiedemann & Brehmer 2017). The presence of several species correlated with E_t values suggests a reproductive strategy which might also act as a coupled life history mechanism in several species (Cushing 1990).

Although the HCS is extremely important, surprisingly little information about the ecology of fish larvae in nearshore habitats is currently available. Most research in Chile has focused on the central parts of the country (Hernández-Miranda *et al.* 2003, Landaeta *et al.* 2015, Díaz-Astudillo *et al.* 2017); this study therefore presents the first evidence of spatial and temporal variation in fish larval assemblages in nearshore northern latitudes. We have demonstrated the presence of high abundances of fish larvae in two shallow nearshore areas in north coast of Chile compared with other geographical areas encompassed by the HCS. Irrespective of the processes that underlie these variations, further detailed studies will be required to better understand the ecology of fish larvae across northern Chile. This study highlights a number of intriguing new possibilities that might explain variations in ichthyoplankton abundances in other HCS nearshore areas (Mejillones Peninsula).

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