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PALMA, ÁLVARO T.; CÁCERES-MONTENEGRO, ISMAEL; BENNETT, RICHARD S.;
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RESEARCH ARTICLE

Near-shore distribution of phyllosomas of the two only lobster species (Decapoda: Achelata) present in Robinson Crusoe Island and endemic to the Juan Fernández archipelago

Distribución costera de filosomas de las dos únicas especies de langostas (Decapoda: Achelata) presentes en la Isla Robinson Crusoe y endémicas del archipiélago de Juan Fernández

ÁLVARO T. PALMA*, ISMAEL CÁCERES-MONTENEGRO, RICHARD S. BENNETT, SPARTACO MAGNOLFI, LUIS A. HENRÍQUEZ, JORGE F. GUERRA, KAREN MANRÍQUEZ & R. EDUARDO PALMA

Departamento de Ecología, Pontificia Universidad Católica de Chile and Center for Advanced Studies in Ecology and Biodiversity (CASEB), Alameda 340, Casilla 114-D, Santiago, Chile

*Corresponding author: apalma@bio.puc.cl

ABSTRACT

Two lobster species coexist in the southeast Pacific Juan Fernández archipelago, *Jasus frontalis* (Milne-Edwards, 1837) and *Acantharctus delfini* (Bouvier, 1909). Like most lobster species they undergo a prolonged larval period, which is particularly long for *J. frontalis* (> 16 months). Though typical of Palinurids, this long larval duration is usually not thought to be conducive to local recruitment. While it is known that settlement is confined to the three islands of the archipelago (Robinson Crusoe, Alejandro Selkirk and Santa Clara) and Desventuradas Islands (aprox. 800 km to the north), it remains poorly understood how local larval supply allows such distribution pattern. The goal of this study is twofold. Firstly, we aimed to characterize the distribution and abundance of the larvae of these two species around Robinson Crusoe Island using plankton tows and systematic hydrographic records between October 2008 to March of 2011, thus providing the first systematic and prolonged coupled biophysical observations in the nearshore of the archipelago. We hypothesize that spatial and temporal larval distribution patterns are associated to their retention around the archipelago, thus contributing to our knowledge of the physical and biological processes maintaining their extreme isolation. Secondly, using molecular genetics, we confirm a simple taxonomic criteria to distinguish the larvae of the two species, thus aiding future studies of larval dynamics. Throughout phyllosomas of *A. delfini* were more abundant than that of *J. frontalis*. Both species were more abundant on the northern shores of Robinson Crusoe Island and generally associated with warmer and saltier waters and mostly present in the samples collected during spring and summer months. Phyllosomas of both species were more abundant during night-time tows in the upper layer of the water column surveyed suggesting a diurnal vertical migration behavior which, for coastal dwelling meroplanktonic species, can be related to a nearshore larval retention mechanism. These preliminary results represent a pioneering effort to understand the mechanisms driving the endemism and extreme isolation of the two study species.

Key words: endemism, lobsters, oceanic island, phyllosoma.

RESUMEN

En el archipiélago de Juan Fernández en el Pacífico sur oriental coexisten dos especies de langostas, *Jasus frontalis* (Milne-Edwards, 1837) y *Acantharctus delfini* (Bouvier, 1909). Igual que la mayoría de las especies de langostas estas atraviesan por un prolongado período larval, el cual es particularmente largo para *J. frontalis* (> 16 meses). Aunque típico de los Palinúridos, esta prolongada duración larval por lo general no debiese conducir a un reclutamiento local. Si bien es sabido que el asentamiento se encuentra confinado a las tres islas que componen el archipiélago (Robinson Crusoe, Alejandro Selkirk y Santa Clara) e Islas Desventuradas (aprox. 600 km al norte), el conocimiento acerca de cómo el abastecimiento local, a través del asentamiento y reclutamiento permite tal patrón de distribución, es escaso. El objetivo de este estudio es doble. En primer lugar, caracterizar la distribución y abundancia de las larvas de estas dos especies alrededor de la isla Robinson Crusoe mediante muestreos de plancton y registros hidrográficos entre octubre de 2008 y marzo de 2011, generando de este modo la primera observación sistemática y prolongada en el archipiélago del acople biofísico cercano a la costa. Hipotetizamos que los patrones de distribución espacial y temporal de las larvas están asociados con su retención alrededor del archipiélago, contribuyendo de este modo con el conocimiento de los procesos físicos y biológicos que mantienen su aislamiento extremo. En segundo lugar, mediante el uso de genética molecular, confirmamos un criterio taxonómico simple para distinguir las larvas de ambas especies, contribuyendo así con futuros estudios sobre dinámica de larvas. En general las filosomas de *A. delfini* fueron más abundantes que las de *J. frontalis*. La abundancia de ambas especies fue mayor en los sitios del lado norte de la isla Robinson Crusoe y por lo general asociadas con aguas cálidas y saladas observadas durante los meses de primavera y verano. Las filosomas de ambas especies fueron más abundantes en las capas superiores de la columna de agua y obtenidas durante los muestreos nocturnos, lo que sugiere un comportamiento de migración vertical que, para especies costeras meroplanktonicas, puede relacionarse con un mecanismo de retención larval. Estos resultados preliminares representan un esfuerzo pionero para entender los mecanismos asociados con el endemismo y aislamiento extremo de las dos especies estudiadas.

Palabras clave: endemismo, filosomas, islas oceánicas, langostas.

INTRODUCTION

The duration of the planktonic phase is usually related with the degree of dispersive capabilities and to what extent larvae represent the connection among otherwise isolated benthic stages of many marine invertebrates (Scheltema 1975, Eckert 2003). Despite previous work that has emphasized the extensive dispersal potential of larvae (e.g., Scheltema 1986, Shanks et al. 2003), recent publications also point to the extraordinary extent to which these larvae succeed in returning to their place of origin (Cowen et al. 2000, Cowen 2002, Mora & Sale 2002, Paris & Cowen 2004, Cowen et al. 2006, Steneck 2006). The planktonic larval period of benthic species is highly variable; on the order of minutes for coral species (Carlson & Olson 1993), days for reef fishes (Forrester 1995), weeks for barnacles (Minchinton & Scheibling 1991) and American lobster (Incze et al. 2000), weeks to months for crabs (Wing et al. 1995, Palma et al. 2006), and months to more than one year for some spiny lobsters (Booth & Phillips 1994).

Hence, the study of species with rather long larval duration periods, yet with restricted geographic distribution, represents a rather unique opportunity to understand about the mechanisms responsible for such isolation. This is the case of the Palinurid *Jasus frontalis* (Milne-Edwards, 1837) and the Scyllarid *Acantharctus delfini* (Bouvier, 1909), two lobster species endemic to a small group of islands in the south east Pacific (Robinson Crusoe, Alejandro Selkirk and Desventuradas Islands) off the coast of Chile. Most Palinurids for which data exist have estimated larval duration in nature of 6-12 months (but longer for *Jasus* spp. – up to 24 months, Bruce et al. 2000, Inoue et al. 2001, Phillips et al. 2006). Among Scyllarids, however, there is a wider range of estimated larval lifespan, from one to at least nine months (Inoue et al. 2001, Booth et al. 2005, Phillips et al. 2006). Additionally, it has been suggested that small-size adult Scyllarid species, such as *A. delfini* are likely to have a brief inshore development (Phillips et al. 2006). Such marked difference in larval duration is consistent with differences in the theoretical range of phyllosoma dispersal. While Palinurids have the potential for broad geographic dispersal, Scyllarids are expected to remain within a much more restricted area during their larval phase (Coutures 2000, Inoue et al. 2001).

The series of small islands, inhabited by these lobster species, represent abrupt promontories that emerge from great depths between the west side of the oceanic branch of the Humboldt current system and the subtropical Pacific influence zone along the central-north coast of continental Chile (Vergara & Morales 1985). A large feature affecting this area of the south-east Pacific corresponds to a large anticyclonic system where three main water types can be distinguished; a subtropical surface layer on top of an intermediate Antarctic water and deep Pacific water along the bottom (Parin et al. 1997). The surface layer around this island system is also characterized by the presence of a permanent thermocline between 100 and 300 m (Moraga & Argandoña 2008). The oceanic circulation in this zone is composed by two flows in opposite directions; the northward cold flow influenced by the oceanic branch of the Humboldt system during winter months and the southward warm flow influenced by the subsurface equatorial water during summer months (Fuenzalida et al. 2007).

In addition to being endemic to these few small islands, the spiny lobster *J. frontalis* represents an important economic resource that has been locally exploited since 1893 (Martínez & Boré 1980). This is the main reason that has stimulated numerous studies related to the fishery of this species, which have mainly considered the larger individuals of the population (Arana & Melo 1973, Arana 1985, Yañez et al. 1985, Arana 1987, Arana & Vega 2000). Notwithstanding these studies, it is surprising how little is known about some basic aspects of its ecology. As part of these unknowns, is the lack of information regarding its larval ecology. Fewer, and rather descriptive studies, have documented the presence of some of the larval stages of these species around this island system with presence of a variable number of larvae only from few plankton tows performed near the islands (Rivera & Mujica 2004, Mujica 2006). Like findings from other island settings, the existence of endemic species around isolated oceanic islands suggests successful retention, through the interplay between physical and biological processes (Cowen et al. 2000, Robertson 2001). It is obvious that the highly restricted *J. frontalis* has been able to self-sustain their populations even in the face of historical exploitation pressure. Although *A. delfini*

appears to share the same geographic range and endemism status (Holthuis 2002), much less is known about its ecology, likely due to its lack of commercial value.

The goal of this study is to characterize the distribution and abundance of the larvae of these two species, which we hypothesize are displaying distribution patterns that may lead to their retention within this island system. We addressed this through systematic nearshore plankton collections at different spatial and temporal scales around Robinson Crusoe Island, together with the recordings of basic hydrographic information over the span of several seasons.

METHODS

Study sites and plankton surveys

For this study we performed plankton tows from October 2008 to March of 2011, at different frequencies (depending on weather conditions and logistic feasibilities), along several sites around Robinson Crusoe Island ($33^{\circ}37' S$; $80^{\circ}00' W$) in the Juan Fernández archipelago. At five roughly equidistant sites around the island, transects (ca. 1.5 km long) running parallel to the coast, were surveyed (Fig. 1). These five sites were visited simultaneously only in five occasions (Table 1). On each occasion samples were obtained, on board of R/V Poli, using two types of simultaneously towed plankton nets. Surface samples were collected using a floating epineustonic net with a 1.2×0.5 m rectangular opening and floating frame with a $210 \mu m$ mesh size (see DiSalvo 1988), while 10

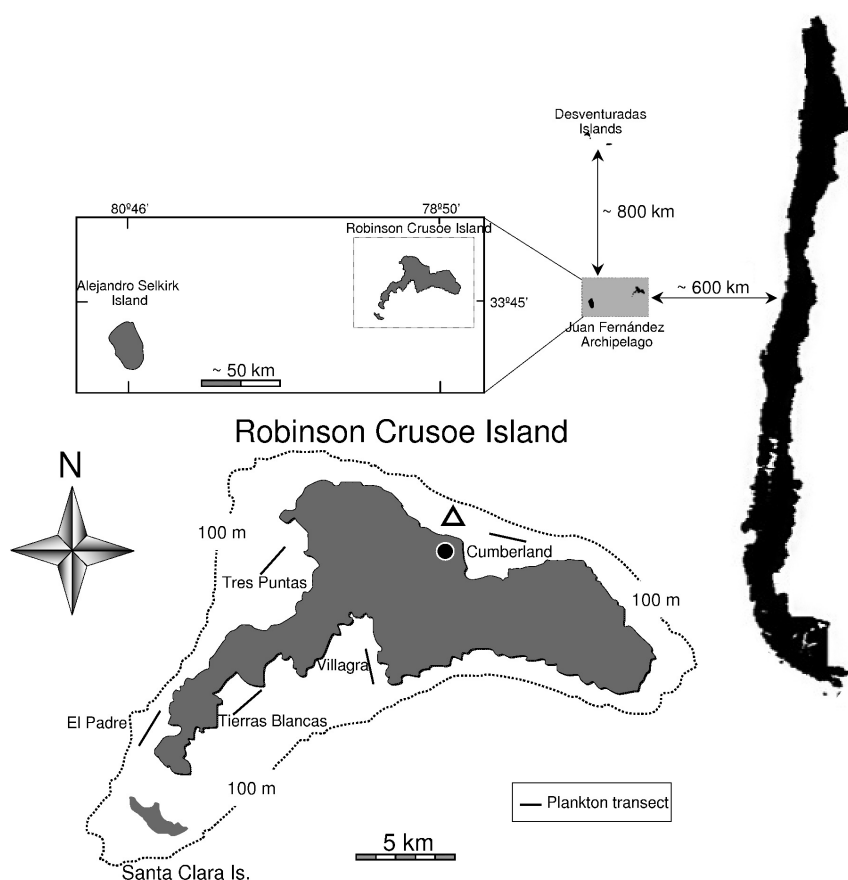


Fig. 1: Map showing the location of the Juan Fernández archipelago (Robinson Crusoe, Santa Clara and Alejandro Selkirk Islands) and the Desventuradas Islands to the north. The position of plankton transects is provided for each site around Robinson Crusoe Island. The triangle signals the location of the mooring system with current meters and the black circle the location of the weather station.

Mapa que muestra la ubicación del archipiélago de Juan Fernández (islas Robinson Crusoe, Santa Clara y Alejandro Selkirk) e Islas Desventuradas hacia el norte. La posición de los transectos de plankton se muestra para cada sitio alrededor de la Isla Robinson Crusoe. El triángulo indica la ubicación del sistema de fondeo con los correntómetros y el círculo negro la ubicación de la estación meteorológica.

m-depth samples were obtained with a bongo circular opening net (60 cm in diameter) with a 210 µm mesh size weighed down by a 2 kg depressor. An angle meter was used to calibrate the towing speed and net depth, which varied depending on the direction and speed of the currents at the time of survey (2-4 km h⁻¹). The volume of water passing through each net was obtained from flowmeters (Hydrobios) attached to each net opening. Plankton samples were preserved in 100 % ethanol for molecular analyses purposes. Larvae were identified, counted and measured under a dissecting scope (Olympus SZX7) with camera (Qimaging Micropublisher CCD). At the end of each transect a probe (HACH HQ 40d) was lowered 20 m and values of temperature and salinity were recorded every 2 m intervals. At most sites and occasions plankton tows were performed during day hours, but off Cumberland bay plankton was also collected at night within the next few hours (11 PM-2AM) of the respective diurnal samples (Table 1). The most general perspective on larval abundance and distribution was achieved when, in five occasions within the same day, all five sites around the island were visited and day-time plankton surveys were performed. A more localized effort, yet more frequent corresponded to the 20 and 13 plankton transects performed during day and night hours, respectively, off Cumberland bay between October 2008 and March 2011 (Table 1).

Near-shore hydrography analyses

We quantified the nearshore currents at different depths as well as wind pattern at fixed points near Cumberland bay during the first months of 2010 (view location of sensors in Fig. 1). Two Falmouth Scientific 3-D acoustic current meters were installed on a mooring system at a place where water depth was 30 m (100 m from shore). One meter was attached to the mooring line below the surface (2-3 m deep)

and the second at 10 m below the surface. Both instruments were programmed to record current direction and speed every 10 min. The weather station (onset microweather station with a Young wind probe) was installed on a nearby summit 400 m above sea level (see Fig. 1), which registered wind speed and direction every 10 min. Wind speed records were re-calculated at 10 m above sea level according with standard methodology following to Large & Pond (1981). We analyzed the wind and current information using progressive vectors, which depict the main flow tendencies for the wind and currents at different depth between February 12 and March 3 of 2010.

Molecular analyses

Nucleotide sequence and phylogenetic analyses

DNA was extracted from ethanol (100 %) preserved samples from 12 adult muscle leg tissues using the Wizard Genomic DNA Purification Kit (<http://www.promega.com/>), whereas for the 18 larvae we used standard phenol/chloroform extraction protocols (Hillis et al. 1990). Two adults were samples from Robinson Crusoe Island, and the other 10 adults were from Desventuradas Islands. All larvae are from Robinson Crusoe Island and for DNA extraction we used the complete specimen. Primers used to amplify the 16s were L2510 and H3080 (Palumbi 1996), and the thermal profile was performed using the following protocol: initial denaturation for 4 min at 94 °C, followed by 30 cycles of 94 °C (30 s), 53 °C (10 s), and 72 °C (30 s). A final extension at 72 °C for 4 min terminated the reaction. Double-stranded PCR products were purified with Qiaquick (<http://www.qiagen.com/>). Cycle sequencing was performed using both PCR primers labeled with the Big Dye Terminator kit (Perkin Elmer, Norwalk, Connecticut). Sequencing reactions were

TABLE 1

Months between 2008 and 2011 when plankton surveys took place at the different sites around Robinson Crusoe Island. (D) correspond to day-time and (N) to night-time surveys. Blank spaces mean that no survey took place. During some months more than one survey was performed which is indicated with numbers in parenthesis.

Meses, entre 2008 y 2011, en los que se realizaron muestreos de plancton en los distintos sitios alrededor de la Isla Robinson Crusoe. (D) corresponde a muestreos diurnos y (N) a muestreos nocturnos. Espacios en blanco significan que no se realizaron muestreos. En algunos meses se realizaron más de un muestreo, lo que se indica con números entre paréntesis.

	2008			2009		2010				2011		
Site	Nov	Dec	Feb	Mar	Dec	Jan	Feb	May	Jun	Nov	Jan	Mar
Cumberland	D(2)	D/N	D(2)	D(3)/N	D(2)/N	D(4)/N(4)	D/N	D/N	D/N	D/N	D/N	D/N
Bahia Padre				D(2)	D	D(2)						
Tres Puntas				D(2)	D	D(2)						
Tierras Blancas				D(2)	D	D(2)						
Villagra				D(2)	D	D(2)						

analyzed on an Applied Biosystems Prism 3100 (<http://www.appliedbiosystems.com/absite/us/>) automated sequencer. Sequences were aligned using the CLUSTAL X program (Thompson et al. 1997) and by eye. All sequences have been deposited in GenBank under accession numbers JN566193-JN566222.

Phylogenetic analyses were conducted using maximum parsimony and maximum likelihood as implemented in PAUP* 4.0 b10 (Swofford 2002), and the tree was rooted with the outgroup criterion using *Jasus edwardsii* and *Jasus lalandii*. For maximum parsimony (MP) we treated all characters as unordered with four possible states (A, C, G, T) using only those characters that were phylogenetically informative. For parsimony, a heuristic search was performed with 100 random additions and branch swapping via tree-bisection-reconnection (TBR; Nei & Kumar 2000). A strict consensus tree was estimated when more than one equally parsimonious tree was obtained, and we obtained the consistency index (CI) and the retention index (RI) for the most parsimonious tree. The reliability of nodes was estimated by nonparametric bootstrapping (Felsenstein 1985) with 1000 pseudoreplications. We selected the best-fitting model of nucleotide substitution using the Akaike Information Criterion (AIC; Akaike 1974) in Modeltest. We evaluated support for the nodes with 1000 bootstrap replicates (Felsenstein 1985). The AIC identified the HKY + Γ model (Hasegawa et al. 1985) as the best model of base substitution. The gamma shape parameter was = 0.1689, and the proportions of nucleotides were A = 0.2980, C = 0.1643, G = 0.2301, and T = 0.3075. For likelihood we performed a heuristic search with 10 random additions and branch swapping via TBR. The reliability of nodes for the likelihood tree was evaluated by 1000 pseudoreplications.

Statistical analysis

In the case of larval abundance, we employed a non-parametric approach because of the nature of the dataset (many zeros but also some values of higher magnitude, which represents an unknown data frequency distribution). These analyses were performed to evaluate differences between samples. The Kruskal-Wallis test was used for comparing the abundance of each species at the five sites around the island. The Mann-Whitney U-test was utilized for the comparisons between the abundance present at night vs. day samples and also for those collected at 10 m vs. at the surface. We examined the use of parametric tools such as zero-inflated Poisson models, but model fits proved poorer than the more simple non-parametric approach (results not shown).

In order to illustrate the association of environmental variables (temperature and salinity) with the abundance of larvae in the water column, Hovmöller plots (time vs. depth) were constructed with Surfer 10 software using Kriging interpolation for environmental variables and overlaying abundance data (ind. 100 m⁻³). In order to explore the association between these environmental factors and larval abundance we utilized the average values of the upper 20 m of the water column. Thus, we studied the relationship between sea surface salinity (SSS) and sea surface temperature (SST) with that of larval abundance through a Spearman rank correlation analysis (r_s). The analysis considered the data obtained from October 2008 to march 2011. A significance level of $P \leq 0.05$ was considered throughout the study.

RESULTS

Larval distribution and abundance

Based on information obtained from cultured individuals (Dupré & Guisado 1996) and larval descriptions (Báez 1973) all phyllosoma found throughout this study (69 and 376 individuals, *J. frontalis* and *A. delfini*, respectively), at least for *J. frontalis*, corresponded to the first four stages, with an average carapace width size of 1.78 ± 0.25 mm (individuals ranged from 1.44 to 2.80 mm). On the other hand, no such referential information is available for *A. delfini*, however, given their small average size (1.36 ± 0.38 mm), yet broader spectrum of size range (0.9 to 5.5 mm), we could infer that our surveys captured a broader range of larval stages.

The distribution and abundance of larvae around the island during day-time surveys exhibited a different pattern for the two species. Phyllosoma of *J. frontalis* were less abundant than those of *A. delfini* collected in the same locations at the same time (Fig. 2A). The former species was significantly more abundant at the two northern sides of the island (Cumberland and Tres Puntas bays) at the two depths considered (surface: $H = 11.58$, $df = 4$, $N = 71$, $P < 0.05$; and 10 m: $H = 15.64$, $df = 4$, $N = 71$, $P < 0.01$). While more abundant than *J. frontalis*, *A. delfini* exhibited comparable numbers at most sites around the island (Fig. 2B) and significant differences among sites were only detected for samples collected at the surface (surface: $H = 9.85$, $df = 4$, $N = 71$, $P < 0.05$ and 10 m: $H = 7.70$, $df = 4$, $N = 71$, $P = 0.1032$). What appears to represent a pattern of higher abundance of larvae at 10 m than those found at the surface (Fig. 2A and 2B) is further investigated with the more frequent surveys off Cumberland bay (see below).

Locally, the distribution and abundance of larvae of the two species, obtained from repeated visits to the same transect off Cumberland bay (the only site visited in repeated occasions between 2008 and 2011, see Table 1), exhibits a pattern of great variability throughout > 2 years of surveys (Fig. 3A and 3C). While the water column between the surface and 20 m exhibited a clear seasonal pattern given the changes in temperature and salinity, it did not show signs of vertical stratification (Fig. 3). Temperature showed a

strong seasonal variability, ranging from 14 °C in the winter (May-June) up to 20 °C during spring-summer (November-March). In the case of salinity it varied between 25 and 34 psu, with lower values during fall-winter months (May-June) and greater during spring-summer months (November-March). Throughout phyllosomas of *J. frontalis* were significantly more abundant at 10m than at the surface ($U = 5$, $P = 0.022$, $N = 6$ and 7 at 10 m and surface, respectively) and also during night-time surveys at both depths ($U = 11$, $P = 0.014$, $N = 6$ and 13 at night and day, respectively) (Fig. 3A). The same pattern was displayed by *A. delfini*, with individuals at 10 m being significantly more abundant ($U = 48$, $P = 0.007$, $N = 21$ and 11 at 10 m and surface, respectively) as well as night

hours compared with day-time surveys ($U = 72$, $P = 0.004$, $N = 11$ and 32 at night and day, respectively) (Fig. 3C).

When correlations between physical variables and the abundance of larvae were explored, we found that in the case of *J. frontalis* neither temperature nor salinity showed a significant relationship with larval abundance (r_s SST = -0.038, $P = 0.874$; r_s SSS = 0.313, $P = 0.191$), although the trend was to find larvae in saltier waters of intermediate temperatures (Fig. 3B). On the other hand, *A. delfini* exhibited a statistically significant preference (r_s SST = 0.336, $P < 0.05$; r_s SSS = 0.511, $P < 0.05$) for warm waters with high salinity (Fig. 3D). A significance value of $P = 0.05$ was considered throughout.

Near-shore hydrography analyses

The progressive vector analysis describes the Eulerian trajectory of wind and currents near the surface and at 10 m depth. Our two week-long window of observation exhibits a fairly steady wind direction to the north-west while currents flow in different directions at each depth (Fig. 4). While water at 10 m follows a south-east direction, that matches the coast line contour at this point, the surface water has an average flow to the south-west, displaying changes in direction at higher frequencies, most likely due to the effect of tides. Even though the current and wind data shown do not pair in time with plankton data they were obtained within one of the same summer field seasons. Results support the presence of distinctive circulation patterns in the upper layers of the water column nearshore.

Molecular analyses and larval identification

Maximum parsimony analysis recovered equal parsimonious trees 106 steps length, consistency index (CI) = 0.9623 and retention index (RI) = 0.9937. Both analyses (parsimony and likelihood) recovered the same topology (Fig. 5) in which a strong differentiation is shown within some of the larvae samples suggesting intraspecific diversification. The bootstrap support for that split was 100 percent. The larval samples from these two branches were carefully examined under the dissecting scope and it was possible to distinguish two

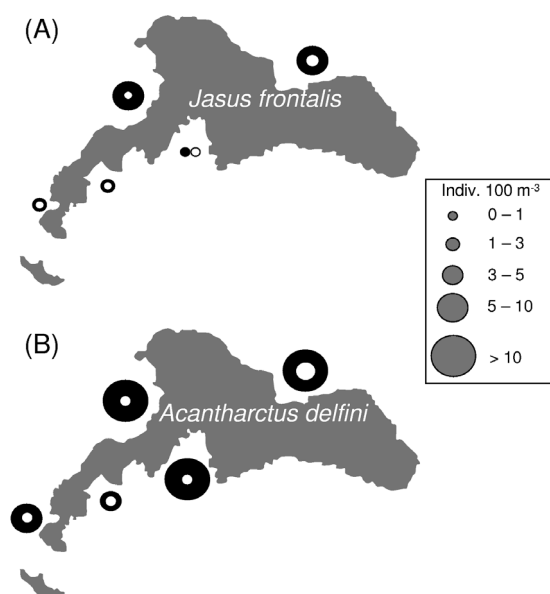


Fig. 2: Average number of phyllosoma 100 m⁻³ of (A) *Jasus frontalis* and (B) *Acantharctus delfini*, at different sites around Robinson Crusoe obtained from 5 replicated plankton tows performed during daytime at each site only during the spring-summer months between December 2008 and January 2010. Black circles correspond to 10 m tows and white circles (within) to surface tows.

Número promedio de filosomas 100 m⁻³ de (A) *Jasus frontalis* and (B) *Acantharctus delfini*, en diferentes sitios alrededor de la isla Robinson Crusoe obtenidos a partir de 5 arrastres replicados de plancton diurnos realizados en cada sitio solo durante los meses de primavera-verano entre diciembre 2008 y enero 2010. Círculos negros corresponden a muestreos a 10 m y círculos blancos (interiores) a muestreos superficiales.

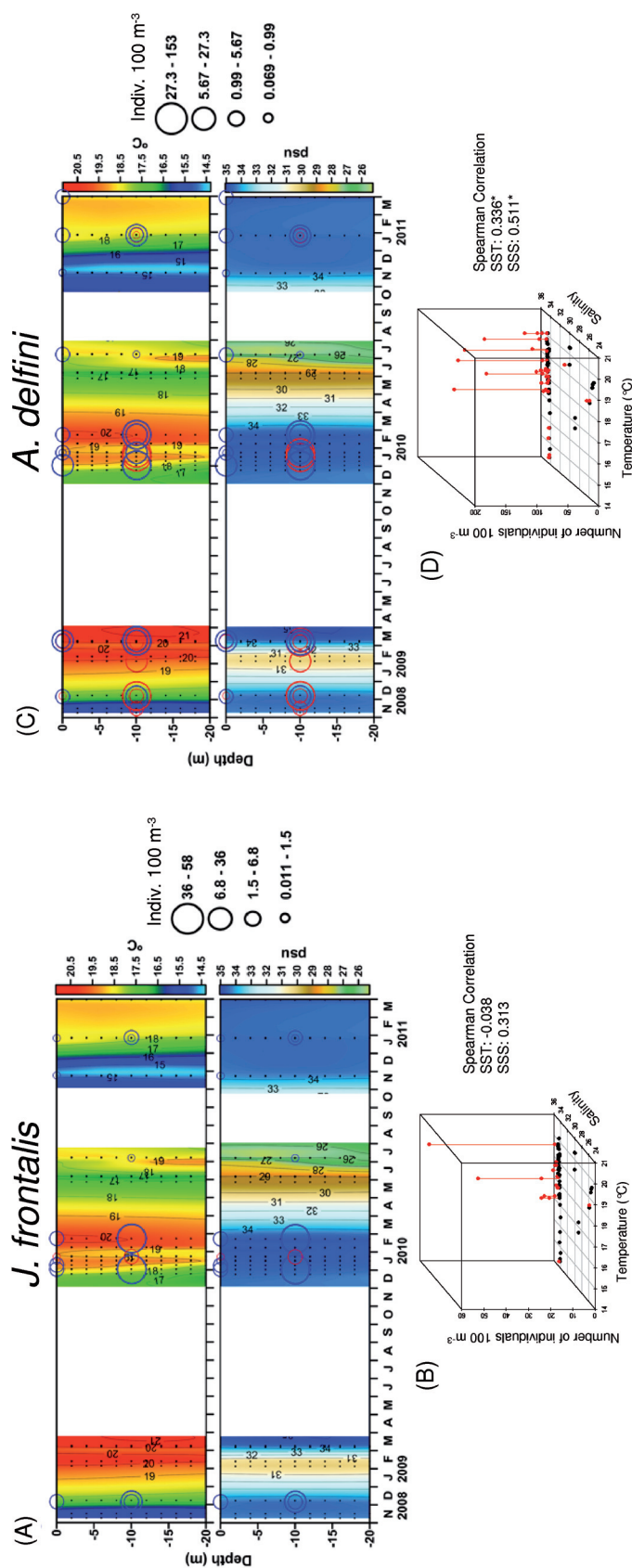


Fig. 3: (A) Hovmöller diagram of temperature (upper panel) and salinity (bottom panel) in association with the *Jasus frontalis* abundance data collected off Cumberland bay during day (red circles) and night (blue circles). Blank sections correspond to periods not quantified. (B) 3D plot and Spearman rank correlations (Rs) between larval abundance and environmental variables (sea surface temperature, SST, and sea surface salinity, SSS) for *Jasus frontalis*. Red circles indicate plankton tows with larvae in them. (*): $P < 0.05$. (C) Hovmöller diagram of temperature (upper panel) and salinity (bottom panel) in association with the *Acantharctus delfini* abundance data collected off Cumberland bay during day (red circles) and night (blue circles). Blank sections correspond to periods not quantified. (D) 3D plot and Spearman rank correlations (Rs) between larval abundance and environmental variables (sea surface temperature, SST, and sea surface salinity, SSS) for *Acantharctus delfini*. Red circles indicate plankton tows with larvae in them. (*): $P < 0.05$.

(A) Diagrama de Hovmöller de temperatura (panel superior) y salinidad (panel inferior) en asociación con los datos de abundancia de *Jasus frontalis* colectadas durante el día (círculos rojos) y durante la noche (círculos azules) frente a bahía Cumberland. Periodos no cuantificados aparecen en blanco. (B) Gráfico 3D y correlación de Spearman (Rs) entre abundancia de larvas y variables ambientales (temperatura superficial del mar, SST, y salinidad superficial del mar, SSS) para *Jasus frontalis*. Círculos rojos indican muestreos de plancton con larvas en ellos. (*): $P < 0.05$. (C) Diagrama de Hovmöller de temperatura (panel superior) y salinidad (panel inferior) en asociación con los datos de abundancia de *Acantharctus delfini* colectadas durante el día (círculos rojos) y durante la noche (círculos azules) frente a bahía Cumberland. Periodos no cuantificados aparecen en blanco. (D) Gráfico 3D y correlación de Spearman (Rs) entre abundancia de larvas y variables ambientales (temperatura superficial del mar, SST, y salinidad superficial del mar, SSS) para *Acantharctus delfini*. Círculos rojos indican muestreos de plancton con larvas en ellos. (*): $P < 0.05$.

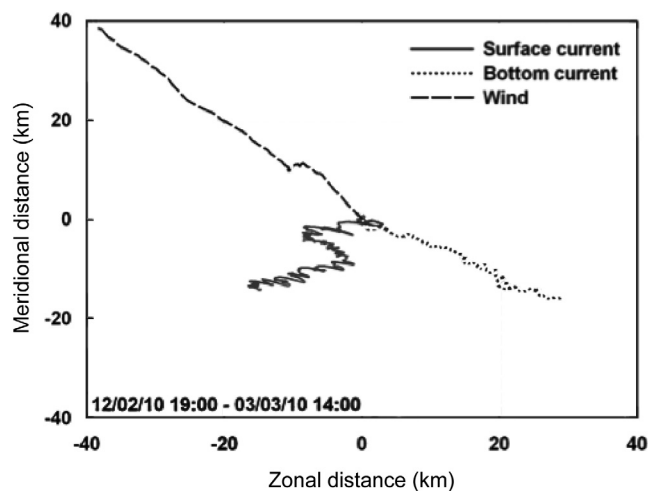


Fig. 4: Progressive vector diagram for the period February 12 and March 3 of 2010 showing the direction of wind and currents (at 2 m and 10 m below the surface) measured with weather station and two acoustic current meters affixed to a mooring located along the shore 2 km west of Cumberland bay.

Diagrama de vector progresivo para el período comprendido entre Febrero 12 y Marzo 3 de 2010 que muestra la dirección del viento y corrientes (a 2 m y 10 m bajo la superficie) medidos mediante una estación meteorológica y dos correntómetros acústicos fijos a un fondeo localizado a lo largo de la costa a 2 km al oeste de la Bahía Cumberland

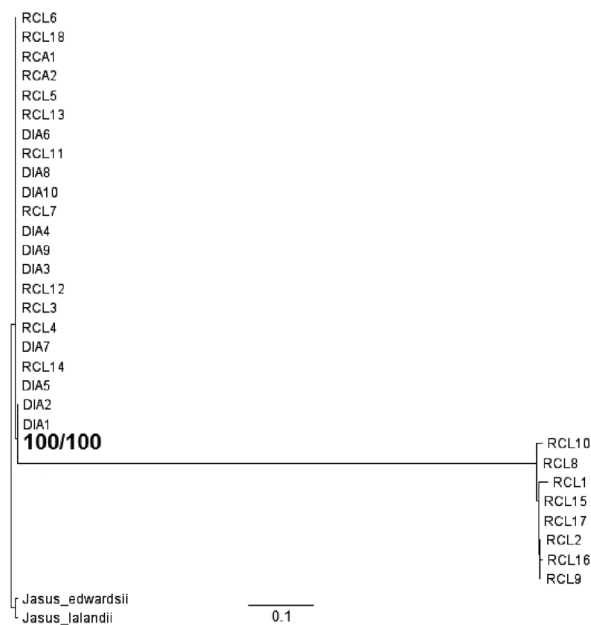


Fig. 5: Maximum parsimony and maximum likelihood tree based on 30 sequences of the 16S rRNA mitochondrial gene on samples originally identified as *Jasus frontalis* according to morphological data. Acronyms of samples in the tree correspond to: RCL (Robinson Crusoe larvae), RCA (Robinson Crusoe adult), DIA (Desventuradas Islands adult). Outgroups correspond to *J. edwardsii* and *J. lalandii*, two congeneric species from the south west Pacific and off the coast of southern Africa, respectively.

Árbol de máxima parsimonia y máxima verosimilitud basado en 30 secuencias de gen mitocondrial 16S rRNA a partir de muestras originalmente identificadas como *Jasus frontalis* de acuerdo a datos morfológicos. Los acrónimos de las muestras en el árbol corresponden a: RCL (larvas Robinson Crusoe), RCA (adultos Robinson Crusoe), DIA (adultos Islas Desventuradas). Los outgroups corresponden a *J. edwardsii* y *J. lalandii*, dos especies congénéricas del Pacífico sur occidental y frente a la costa sur de África, respectivamente.

easy-to-spot anatomical features that separate *J. frontalis* from *A. delfini*. The antenna in the former is as long as the antennule (which presents a bifurcation towards the distal end) while in the later the antenna is much longer than the antennule.

DISCUSSION

Our biologic and geographic system is comparable to others where organisms (i.e. reef fish in the Caribbean) are endemic in spite of having a dispersive larval phase (Robertson 2001). Biophysical models considering larval behavior and ocean currents have been used to show that larvae can stay closer to their places of origination than previously thought (Robertson 2001, Cowen et al. 2000, Cowen et al. 2006). In this study we centered our attention in understanding the distribution and abundance of phyllosoma (*Jasus frontalis* and *Acantharctus delfini*) as a contribution to our understanding of the mechanisms maintaining their endemism in the Juan Fernández archipelago. Most previous initiatives regarding the study of plankton around this island have corresponded to brief visits that collected valuable yet scattered information (i.e. Rivera & Mujica 2004, Mujica 2006). This study is unique in that larval surveys were performed on a frequent basis, over a period of > 2 years, very near the coast and included the simultaneous use of two different nets covering the top 10 m of the water column. In one of the sites around the island (off Cumberland bay) larval tows were also performed during day and night hours. The general justification behind the nearshore sampling scheme obeyed to the fact that adults of these two lobster species only occur along coastal settings of these few islands with steep coastal bathymetry (Báez 1973), therefore the release of larvae and their subsequent return has to be coastal. The close resemblance of the phyllosoma of these species, therefore difficult to identify, was solved thanks to the molecular approach pursued in this study. These results allowed us to unambiguously recognize the two species following specific anatomical features of the antenna and antennule.

Most previous studies regarding the distribution of phyllosomas broadly suggest

that newly-hatched larvae of most species of spiny lobsters first rise to the surface and later migrate vertically between the surface at night and deeper waters during the day as they are carried offshore (Phillips & Sastry 1980). However, it is noticeably that most of those studies (e.g., Booth & Phillips 1994, Chiswell & Roemmich 1998, Chiswell & Booth 2005) focus on large spatial-scale pattern of widely distributed species of lobsters, lacking insight into processes likely to drive the larval ecology of species like *J. frontalis* and *A. delfini*, endemic to a small island system.

After over two years of surveys, with most visits during the spring-summer months, although some additional surveys also covered the remaining seasons, we could draw a generalized pattern in which phyllosomas of the two species were present at all sites around the island. On a closer look, however, *J. frontalis* occurred in greater numbers at the two northernmost sites (Tres Puntas and Cumberland bays) while, in general more abundant, *A. delfini* was evenly distributed along those same sites. At the same island-scale both species were in general more abundant at the deeper strata (10 m). At least for *J. frontalis* all individuals found, corresponded to earlier larval stages; a conspicuous pattern given that phyllosoma of this species can reach a total length 10 times those found in our study (Mujica et al. 2010). On the other hand, the broader size spectrum exhibited throughout by *A. delfini* suggests that we were able to capture more larval stages of this species at nearshore sites around the island. These patterns are similar to those found for several taxa by Morgan & Fisher (2010) further suggesting that larvae (at least of early stages) are being retained near the coast.

The long data set of basic water column features (temperature and salinity) showed a strong seasonal signal that dominated the whole upper 20 m of the water column at any given time. This clearly shows that the island is affected by distinctive water masses at different times, which agrees with the general oceanographic descriptions for this part of the south east Pacific (Fuenzalida et al. 2007, Schneider et al. 2007, Moraga & Argandoña 2008). Some authors have even suggested that these seasonal changes, resulting from alternate northward and

southward circulation conditions, are the way in which larvae are being maintained within the system encompassing the Desventuradas and the Juan Fernández archipelagos (Rivera & Mujica 2004). While the former could be the case, there is no evidence yet on the nature of smaller-scale mechanisms maintaining the larvae within this system. Unfortunately, the sparse nature of our larval collection (we could only visit the island in certain periods) prevented us from exploring their potential seasonality. There is a growing amount of literature, however, showing results wherein larval behavior (mainly vertical migration) is a key aspect keeping larval stages near their adult benthic environment (e.g., Shanks & Eckert 2005, Morgan 2006, Morgan & Fisher 2010).

While both species were significantly more abundant at night at any depth surveyed, they also tended to be more abundant at 10 m at any given time. Although we know that larvae of these species can be found at greater depths (> 10 m, Rivera & Mujica 2004, Mujica 2006) we still were able to capture the signal of their vertical displacement. Such active diurnal vertical migration, novel for *J. frontalis* and *A. delfini*, is common among several other meroplanktonic larvae, and it has been related, for example, to nearshore retention of larvae with coastal adult populations (e.g., Forward et al. 1996, Shanks 1986) and also to the avoidance of predators (e.g., Ohman et al. 1983, Richards et al. 1996). In some cases larvae perform daily vertical migrations that, in combination with contrasting flows at different depths, result in larvae being advected toward the coast (i.e. Poulin et al. 2002a, 2002b) or retained near the coast by staying at layers of the water column that are not advected offshore (Morgan & Fisher 2010). While we cannot rule out any of these hypotheses, and given the endemism status of these species, their ubiquitous short-term spatial and temporal patterns of distribution suggest the possibility of some type of circulation system that would favor nearshore larval retention. For several Scyllaridae species with comparable short larval phase duration, likely to be the case of *A. delfini*, it has been shown how all the larval stages are retained in nearshore waters while only early and final larval stages of Palinuridae remain in the same waters (Inoue et al. 2001). The latter description resembles the broad larval size spectrum

exhibited by *A. delfini* and the narrow one for *J. frontalis* over an extended period of time. Our quantifications of wind and currents at different depths represents additional evidence that the nearshore system of Robinson Crusoe Island presents conditions of contrasting flow at different depths, which linked to the vertical movement displayed by these species, could likely favor the retention near the coast of vertically migrating larvae.

Hence, although further research is necessary, we suggest that these species are capable of coupling their vertical migration behavior with the local circulation dynamics present in the nearshore system off Robinson Crusoe Island. This may be useful to depict the retention conditions, processes and mechanisms behind the endemism of species that have yet, the potential for wide range dispersal.

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