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Research Article

Dispersion of *Emerita analoga* (Stimpson, 1857) larvae in northern coast of Chile (25°-31.5°S)

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ABSTRACT. The larvae of *Emerita analoga*, captured on the northern coast of Chile, during three consecutive years, during the austral summer, were separated by stage of development and their abundance, occurrence, and distribution, was analyzed for its proximity to the coast. The highest abundance was determined in coastal sampling stations and near the main sandy beaches of the study area, where the initial developmental stages were predominantly represented. The intermediate development stages proportionally increased in abundance at sampling stations in remote coastal stations, while more developed individuals had similar distribution than the first zoeae. Statistical analysis established significant differences in abundance, dominance, and occurrence of the different stages with respect to its distance to the coast. The Coquimbo Bay system had the highest concentrations of larvae, which has been associated with adult populations and oceanographic dynamics of the area. Spatial segregation of developmental stages and oceanographic dynamics of the area of greatest abundance would suggest that larval dispersion and retention are associated with water flows and circadian and ontogenetic vertical migration.

Keywords: *Emerita analoga*, larval stages, larval dispersion, distribution, northern Chile.

Dispersión de larvas de *Emerita analoga* (Stimpson, 1857) en la costa norte de Chile (25°-31,5°S)

RESUMEN. Las larvas de *Emerita analoga*, capturadas en la costa norte de Chile en tres años consecutivos, durante el verano austral, se separaron por estado de desarrollo y se analizó su abundancia, ocurrencia y distribución respecto a su proximidad a la costa. La mayor abundancia se determinó en las estaciones costeras y próximas a las principales playas de arena de la zona de estudio, donde predominaron los primeros estados de desarrollo. Los estados intermedios de desarrollo incrementaron su abundancia proporcionalmente en las estaciones más alejadas de la costa, mientras que los más desarrollados tuvieron similar distribución que las primeras zoeas. El análisis estadístico, estableció diferencias significativas entre la abundancia, dominancia y ocurrencia de los distintos estadios, respecto de su distancia a la costa. El sistema de bahías de Coquimbo, tuvo las mayores concentraciones de larvas, lo que ha sido asociado a las poblaciones de adultos y dinámica oceanográfica de la zona. La segregación espacial de los estados de desarrollo y la dinámica oceanográfica de la zona de mayor abundancia, permite postular que la dispersión y retención larval, está asociada a flujos de agua y migración vertical circadiana y ontogénica.

Palabras clave: *Emerita analoga*, estados larvales, dispersión larval, distribución, norte de Chile.

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INTRODUCTION

The sand crab, *Emerita analoga* (Stimpson, 1857), is one of the dominant benthic decapod crustaceans found along the sandy beaches of Chile (Contreras *et al.*, 2000). Its distribution extends from Arica (18°S) to Aysén (46°S), and it has a bathymetric range between 0-3 m depth (Retamal, 2000). Female sand crabs carry eggs on their pleopods for 29-32 days, as observed under laboratory conditions (Barnes & Wenner, 1968; Contreras *et al.*, 1999). Following the hatching period, sand crabs undergo five planktonic larval zoeal stages and one megalopa stage over the course of 3-5 months (Barnes & Wenner, 1968; Sorte *et al.*, 2001). Ovigerous females can be found year round, with molting occurring during the spring and beginning of summer (Contreras *et al.*, 1999).

The successful recruitment of benthic organisms by pelagic larvae depends on a diverse number of factors, such as the time of permanence in plankton (Booth &

Ovenden, 2000; Shanks, 2009) and ocean-dictated transport (Morgan & Fisher, 2010). However, larval developing behavior, such as circadian and ontogenetic vertical migration, allows taking advantage of currents, tides, and other circulation mechanisms. Through these behavior, the larvae are able to remain located at the hatching station, return to their place of origin, or be transported to new recruitment stations (Gil, 1988; Marta-Almeida *et al*., 2006).

Taking into consideration that *E. analoga* larvae only originates in the sandy intertidal zone, studying their distribution and abundance during the different development stages would provide an understanding of the mechanisms behind their dispersion and retention. The present study evaluated the larval dynamics of *E. analoga* along the coast of Chile for three consecutive years (February 2008, 2009, and 2010), using zooplankton surveys performed within the framework of Fondo de Investigación Pesquera (FIP) projects 2007-03, 2008-02, and 2009-03 (Hydroacoustic evaluation of anchovy recruitment between the III and IV Regions) between Paposo (25.0ºS) and Puerto Oscuro (31.5ºS), Chile.

MATERIALS AND METHODS

Three expeditions were taken onboard the RV Abate Molina, belonging to the Instituto de Fomento Pesquero, between the 8-28th of February 2008, the 6-25th of February 2009, and 5-24th of February 2010. Zooplankton samples were taken during each expedition at 80 oceanographic sampling stations distributed along 20 transects perpendicular to the coast, between Paposo (25.0ºS) and Puerto Oscuro (31.5ºS). Sampling stations were located 1, 5, 10, and 20 nm from the coast, and additional 20 sampling stations were located 1 nm from the coast within each transect (Fig. 1).

Zooplankton samples were taken between 0 to 70 m depth, or 10 m above the seabed when the sampling station had a depth less than 70 m. Bongo nets with a diameter of 59 cm, a mesh width of 300 µm, and equipped with a flow meter were used. The samples were preserved in a formalin solution in 5% seawater. *Emerita analoga* larvae were separated according to their development stage (Johnson & Lewis, 1942), and values were standardized by 100 m^3 of filtered seawater.

The following were determined for each sampling station: larvae abundance and development stage; numeric dominance, taken as a ratio of total larvae abundance to the distance from the coast and development stage; and occurrence, taken as a ratio of the total stations where larvae were found and their development stage to the total number of sampling stations.

A statistical analysis of spherical data was used to establish significant correlations between the dependent variables (sampling years, larval stages, and distance from the coast, in relation to abundance and dominance).

The Kolmogorov-Smirnov test was used to determine statistically significant differences for abundance and numerical dominance for each development stage and distribution in relation to coastal proximity (1, 5, 10, and 20 nm). The Levene test was used to verify the homogeneity of variances, and a Box test was used to verify group homoscedasticity ($P < 0.05$).

A multivariate analysis of variance (threeway ANOVA) test was used to establish significant differences for the abundance and dominance of development stages and sampling years, development stages, and distance from the coast. The first factor was the sampling years (2008, 2009, 2010), the second was the developmental stages (five zoeas), and the third was the distance from the coast (1, 5, 10, and 20 nm). The raw data was used for analysis, without considering averages or percentages.

By means of a multiple linear regression analysis it was possible to determine associations between occurrence (dependent variable), and distance from the coast, developmental stage, and sampling years (independent variables). Raw data was used as well for this analysis.

RESULTS

In February 2008, larvae of *E. analoga* were captured at 48% of the sampling stations, with a total of 1,158 larvae 100 m^{-3} (Table 1). These were principally distributed south of Huasco (82% of the stations), and the greatest abundances (>50 larvae 100 m^{-3}) were found south of Punta Choros, with the maximum quantity found at station 78 (175 larvae 100 m^{-3}) (Fig. 2a). North of Huasco, larvae were scarce (20%), whereas the highest abundance was recorded north of Barquito Cove at station 25, which had 34 larvae 100 m^{-3} (Fig. 2a). In February 2009, a total of 2,586 larvae 100 m^{-3} were captured, representing 29% of all sampling stations (Table 1). The greatest densities were found at stations close to and south of Coquimbo (>100 larvae 100 m^{-3}). A maximum density of 1,207 larvae 100 m^{-3} was recorded for station 82 located at the extreme southern end of Tongoy Bay (Fig. 2b). As with the 2008 expedition, larvae distribution was principally found south of Huasco, although there was lesser frequency of occurrence and greater total abundance. In

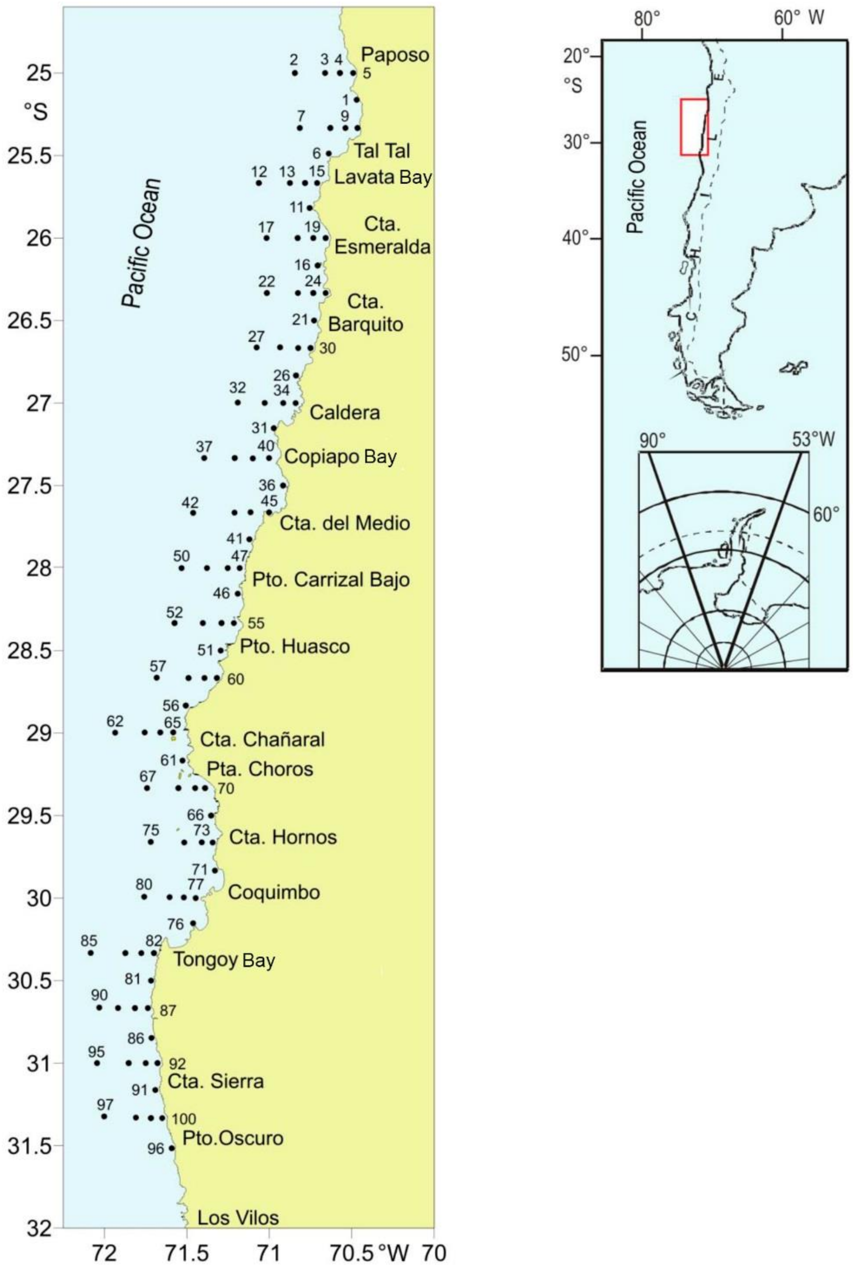

Figure 1. Geographical position of sampling stations along the northern coast of Chile.

contrast to 2008, greater abundance was found in the northern zone of the study. This zone included the stations between Barquito and Caldera, with a maximum abundance of 110 larvae m^{-3} (Fig. 2b).

E. analoga larvae showed a wide distribution along the entire sampling zone in February 2010, although a similar total abundance as the 2009 expedition was found (2,288 larvae 100 m^{-3}), and an occurrence of 46% was recorded (Table 1). The greatest abundances (>100 larvae 100 m^{-3}) were found at sampling stations located near the Coquimbo Bay system, with a maximum of 263 larvae 100 m^{-3}. The frequency of occurrence was generally more homogeneous. Between Paposo and Huasco, the greatest abundance was registered at station 9 with 88 larvae 100 m^{-3} (Fig. 2c).

E. analoga larvae from the three expeditions showed a more coastal distribution, with greater predominance at stations 1 nm from the coast (Fig. 2). In February 2008, 55% of the larvae were captured from sampling stations at 1 nm from the coast, with occurrence decreasing farther from the coast. The same happened with the abundance, where a progressive de-

Table 1. Abundance, dominance, and occurrence by development stage, sampling year, and distance from the coast.

Year	Stage	Abundance (N° 100 m^{-3})					Dominance (%)					Occurrence (%)				
		1	5	10	20	Total	1	5	10	20	Total	1	5	10	20	Total
		nm					nm					nm				
2008	Z I	145	243	9	5	402	36.0	60.5	2.3	1.3	34.7	22.5	20.0	10.0	5.0	16.0
	Z II	47	35	5	28	114	41.2	30.7	4.1	24.1	9.9	15.0	15.0	5.0	15.0	13.0
	Z III	84	28	22	40	173	48.4	16.0	12.5	23.1	14.9	15.0	15.0	15.0	20.0	16.0
	Z IV	108	25	61	24	218	49.7	11.6	27.9	10.8	18.8	27.5	15.0	30.0	15.0	23.0
	Z V	222	17	9	3	251	88.4	6.8	3.4	1.3	21.7	30.0	10.0	10.0	5.0	17.0
	Total	605	348	105	100	1,158	52.3	30.1	9.0	8.6	100	55.0	50.0	35.0	45.0	48.0
2009	Z I	1.024	208	32	166	1,430	71.6	14.5	2.2	11.6	55.3	22.5	25.0	10.0	5.3	17.2
	Z II	0	15	0	0	15	0.0	100.0	0.0	0.0	0.6	0.0	5.0	0.0	0.0	1.0
	Z III	565	88	24	0	676	83.5	12.9	3.5	0.0	26.1	15.0	10.0	5.0	0.0	9.1
	Z IV	160	91	116	39	406	39.4	22.4	28.5	9.7	15.7	10.0	20.0	20.0	10.5	14.1
	Z V	30	10	13	6	59	51.0	17.0	22.4	9.7	2.3	7.5	5.0	5.0	5.3	6.1
	Total	1.779	411	184	211	2,586	68.8	15.9	7.1	8.2	100	35.0	45.0	20.0	10.5	29.3
2010	Z I	545	234	15	44	838	65.1	27.9	1.7	5.2	36.6	20.0	15.0	10.0	10.0	15.2
	Z II	62	102	102	190	457	13.5	22.4	22.4	41.6	20.0	5.0	15.0	25.0	10.0	12.1
	Z III	51	102	88	88	329	15.6	31.1	26.7	26.7	14.4	7.5	15.0	10.0	10.0	10.1
	Z IV	38	66	44	43	190	20.1	34.6	23.0	22.3	8.3	7.5	20.0	10.0	20.0	13.1
	Z V	227	161	85	0	473	48.0	34.0	18.0	0.0	20.7	20.0	30.0	15.0	0.0	17.2
	Total	924	666	334	364	2,288	40.4	29.1	14.6	15.9	100.0	37.5	60.0	55.0	40.0	46.0

crease was observed as the distance from the coast increased (Table 1). This tendency was most evident at Huasco, the area at which the greatest abundance was found (Fig. 2a).

Although the larval abundance from February 2009 showed the same tendency as that from February 2008, occurrence was greater at stations located 5 nm from the coast, but decreased with further increasing distances. This was determined through the longitudinal distribution of stations located near the Coquimbo Bay system, given that from south to north, larvae were mainly captured at stations located between 1 and 5 nm from the coast (Fig. 1b, Table 1).

As with the previous two years, sampling in February 2010 showed the greatest abundances at coastal stations and decreasing abundances for distances farther from the coast. However, the lowest occurrence was detected at stations 1 nm from the coast, while the greatest was detected at stations at 5 nm from the coast, with subsequent occurrence gradually decreasing at farther distances from the coast (Table 1). This lowest occurrence at stations located at 1 nm from

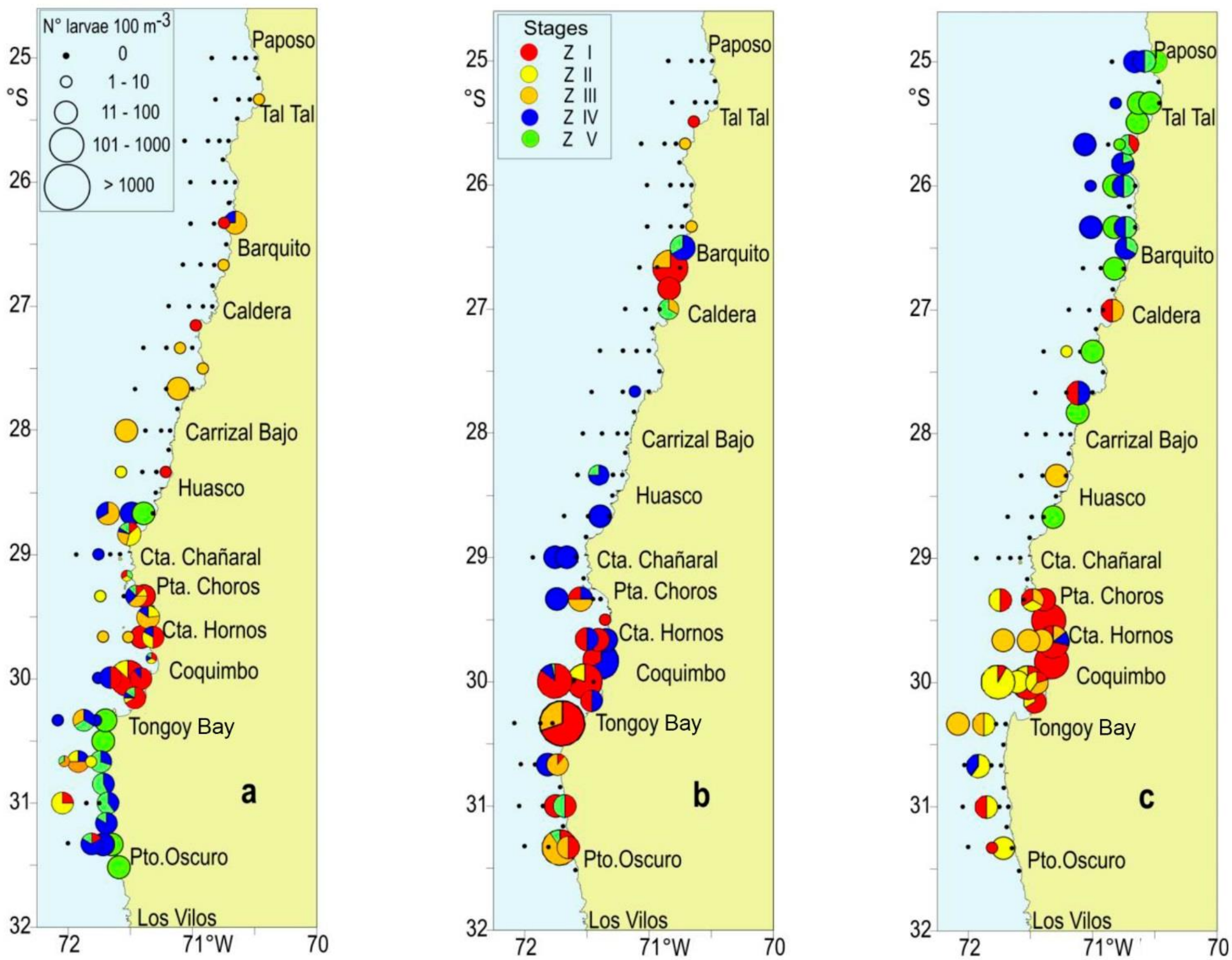

Figure 2. Distribution, abundance, and composition by zoea stage of *Emerita analoga* larvae along the northern coast of Chile. a) February 2008, b) February 2009, and c) February 2010.

the coast was determined on the basis of data obtained south of Tongoy and in the northern zone, where no larvae were captured at coastal sampling stations (Fig. 2c).

The composition by larval zoeal stage in February 2008 was mostly comprised by zoea I larvae, followed by zoea V larvae. The distribution of zoea I larvae was restricted to the coastal stations, and principally to the Coquimbo Bay system. In the case of the more advanced larval stages (zoeas IV and V), these were found mainly at sampling stations located to the south of Tongoy (Fig. 2a). Zoea IV larvae were found with the greatest occurrence at stations located between Huasco and Puerto Oscuro. Zoea III larvae, although rare in occurrence, were predominantly found between Paposa and Huasco, with wide longitudinal distribution along the entire zone studied (Fig. 2a). The least abundance and occurrence was found for zoea II larvae, and this stage was only represented at stations south of Huasco, with similar distribution and occurrence at different coastal distances (Table 1).

In February 2009, the greatest abundance and occurrence of zoea I larvae were found (Table 1). at the more coastal sampling stations located between Barquito and Caldera and at Punta Choros in the south. The greatest abundance (838 larvae 100 m^{-3}) was recorded at the Tongoy station (station 82). Other instances of zoea I larvae were recorded at 10 and 20 nm from the coast at stations 68, 74, and 80, all of which belonged to the Coquimbo Bay system (Fig. 2b). Zoea II larvae were found at station 78, located 5 nm out from Coquimbo, while zoea III larvae were mostly found in stations at 1 nm from the coast between Tal Tal and Caldera and between Caleta Chañaral and Puerto Oscuro (Fig. 2b). Zoea III and IV larvae followed in abundance, although zoea IV larvae were found in a wider spatial distribution, reaching up to 20 nm out from Punta Choros (Fig. 2b). Finally, zoea V larvae had a low abundance and were found at only six stations. This stage was mainly found at coastal sampling stations, but some were found in low numbers at 20 nm out from the coast of Coquimbo.

In February 2010, the first stages of development were predominantly found in the southern sampling zone, with the greatest abundances and occurrences recorded at stations from the Coquimbo Bay system. In contrast, the more advanced development stages were primarily found in the northern sampling zone (Fig. 2c). Zoea I larvae were the most abundant, and the greatest concentrations of this stage were found at the coastal stations located between Punta Choros and Coquimbo. Between Paposo and Huasco, zoea I larvae were only captured at three stations between 1 and 5 nm from the coast. Zoea II and III larvae were mostly captured 5 nm from the coast between Punta Choros and Tongoy Bay. Zoea IV larvae were found in the least abundance. Zoea IV larvae were predominantly found at stations located 5 to 20 nm from the coast, and between Paposo and Barquito, as with other development stages in addition to being found at two stations south of this area (Fig. 2c). Lastly, zoea V larvae were only captured in the northern sampling zone at stations 1 to 10 nm from the coast, with decreasing perceptibility. This larval stage was that with the greatest sample abundance (Table 1).

Three-way ANOVA analysis determined that the abundance and dominance of the distinct developmental stages of *E. analoga* larvae differed statistically in regards to the distance from the coast for the three years analyzed (Table 2).

According to the ANOVA (statistical significance, $P < 0.05$), the occurrence of development stages was highly related to the distance from the coast for all years studied (Table 3). Given the segregated distribution of the different larval stages relative to the distance from the coast, and given the lack of differences in larvae occurrence between years, the bivariate relationship for each of the variables alone with occurrence was not significant. However, when considering the variables together (developmental stage, distance from the coast, and sampling years) with occurrence, a best model fit was achieved, with values of β = 2,024.410 and P = 0.407.

The correlation matrix determined the existence of linear correlations between the pairs of variables: occurrence with development and occurrence with distance from the coast. According to the Pearson correlation, the variables distance from the coast and sampling years had a negative association (inversely proportional) with occurrence (Table 4).

Table 2. Multivariate analysis of variance (three-way ANOVA), for the abundance and dominance of developmental stages, sampling years, and distance from the coast. df: degrees of freedom.

	Wilks λ	F	df	*P*
Years	0.94	2.990	4	0.019
Stages	0.868	3.465	8	0.001
Distance	0.975	0.805	6	0.566

Table 3. Analysis of variance (ANOVA) for the dependent (frequency of occurrence) and independent (distance from the coast, developmental stage, and sampling year) variables. F = 7.351, P = 0.009, df: degrees of freedom.

Model	Sum of squares	df	Root mean square
Total	3,670.081	59	
Regression	412.848	1	412.848
Residual	3,257.233	58	56.159

According to the goodness-of-fit for the analyzed model, a highly significant multiple correlation (34%) was established with an estimated error of 7.5% and a confidence level of 95%.

DISCUSSION

The greatest abundance of *E. analoga* larvae was found in stations at 1 nm from the coast, for the three years analyzed, which is in agreement with the distribution of adults that inhabit the sandy intertidal zone (Lépez *et al*., 2001). Retamal (2000) and Retamal & Moyano (2010) found that populations of *E. analoga* in Chile are most frequently found in sandy beaches located between Arica (18°S) and Aysén (46°S). The larvae recorded in the present study were principally found along the beaches with the greatest extensions of sand, located in the vicinity of Los Vilos and Coquimbo Bay system. Punta Choros northward is predominated by smaller sandy beaches, with the exception of beaches next to Caldera, which coincides with the observed larvae latitudinal distribution. This finding is consistent with the lack of larvae found at the majority of stations in the northern zone of study in February 2008 and 2009.

The distribution of zoea I larvae, which were the most abundant and primarily occupied coastal stations for all three sampling years, coincided with the cursory distribution of adults (Retamal, 2000). While the successive stages of development also generally presented greater densities closer to the coast, the pro-

Table 4. Partial correlation matrix for occurrence (dependent), and distance from the coast, developmental stage, and sampling year (independent variables). In all cases, the number of data was 60.

		Occurrence	Distance	Stage	Year
Pearson correlation	Occurrence	1	-0.335	0.046	-0.104
	Distance	-0.335	1	0	0
	Stage	0.046	0	1	0
	Year	-0.104	0	0	1
Significance (unilateral)	Occurrence	-	0.004	0.364	0.214
	Distance	0.004	-	0.5	0.5
	Stage	0.364	0.5	-	0.5
	Year	0.214	0.5	0.5	-

portional increase in the intermediate stages of development with stations farther from the coast can be related to the dispersion and larval permanence in the plankton. Sorte *et al*. (2001) observed that *E. analoga* larvae can remain in plankton up to 120 days, a time in which great distances can be covered along the California Current (20 km day^{-1}). Moreover, the cumulative mortality of larvae in plankton would explain the greater densities of zoea I larvae found in the three expeditions.

The higher concentrations of larvae found in the three years in the Coquimbo Bay system, and especially of larvae in the earlier stages of development, could be the consequence of adult populations found along the beaches of the sector and of local oceanographic dynamics. Acuña *et al*. (1989) stated that the upwelling that occurs at Punta Lengua de Vaca influences the entire Coquimbo Bay system. This, in addition to the presence of islands close to Punta Choros, allows for a confluence of waters originating from the southeast, generating upwelling zones (Acuña *et al*., 2007), which have been identified by Mujica *et al*. (2011) as areas of larval retention.

In addition, Flores & Mujica (2009) found greater concentrations of larvae in the northern part of the Coquimbo Bay system. This could be the consequence of drifting zooplankton produced through interactions between the Humboldt Current System flowing northward (Escribano *et al*., 2002) and the action of two rotations caused by geostrophic circulation and daytime tides, which permits water originating from Tongoy Bay to move northward (Acuña *et al*., 1989). Moraga *et al*. (1994) indicated that this oceanographic effect, which is seasonal in nature, allows for the existence of two superficial flows towards the north, one which is coastal and one further from the coast. These flows reach up to 50 m in width and up to 100-200 m in depth, separated by a lesser flow towards the south. From this, it is possible to postulate that the planktonic components located at different depths and distances from the coast could have different displacements, which would explain the drifting and retention of larvae in the area.

Differences were observed for the abundance of development stages at stations with distinct distances from the coast, where zoea I larvae were associated with the point of origin (1 nm); zoea II-IV larvae were farther from the coast; and zoea V larvae were found at stations next to the coast. This coincided with other obtained data and with the results from the three-way ANOVA, which established significant differences in abundance and dominance of the development stages in relation to the distance from the coast for the three years studied. Moreover, the analysis of variance of the development stages occurrence determined a high relationship with distance from the coast for the three years studied.

The adult populations along the sandy beaches, the oceanographic dynamic of the studied zone, and the segregated distribution of the different larval stages in adjacent zones suggests a dispersion and subsequent return of larvae to coastal zones apt for settlement, which would be associated with the ontogenetic vertical migration of larval decapod crustaceans (Lindley, 1986; Shanks, 1986; Queiroga, 1998; Yannicelli *et al*., 2006). This indicates that the first stages of development are mainly superficial in distribution while deeper distribution occurs at advanced stages of development.

The predominance of larvae at advanced stages of development in the southern and northern zones in February 2008 and 2009, respectively, could be the product of spawning occurring previous to sampling at Los Vilos and Caldera. It could also be the product of advective processes brought on by the Humboldt Current System (Escribano *et al*., 2002), displacing zooplankton northward. In this sense, Contreras *et al*. (1999) stated that ovigerous females can be found year round, with molting occurring in spring and early summer. Taking this into consideration, the period with the greatest incidence of hatching would have been just prior to the period sampled in the current study.

The oceanographic variations detected in February for the three years of study (Castillo *et al*., 2009a, 2009b, 2010) indicated yearly variations in surface temperature and salinity, upwelling intensity, and depth of the thermocline. These variations are reflected in the Multivariate Equatorial Index, which shows that February 2008 and 2009 corresponded to a cold period, whereas February 2010 corresponded to a warm period (Castillo *et al*., 2010). These yearly environmental variations could influence the reproductive period of *E. analoga*, possibly explaining the observed variations in composition and distribution of the development stages between the three sampling years, which is consistent with results obtained from the Pearson correlation, where the occurrence of larvae had a negative association with the distance from the coast and sampling years.

In general, the abundance and composition by development stage of *E. analoga* larvae is consistent with the existence of sandy beaches from which the larvae originate, with larval permanence in plankton, with the ocean-dictated transport to which larvae are subjected to through predominant currents, and with vertical distribution, which is a product of the ontogenetic and circadian migratory behavior of this species.

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