

The influence of environmental factors on the abundance and recruitment of the sand crab *Emerita analoga* (Stimpson 1857): Source–sink dynamics?



R. Veas^{a,b}, E. Hernández-Miranda^{b,*}, R.A. Quiñones^{a,b,c}, E. Díaz-Cabrera^b, J.M. Rojas^{d,e}, J.M. Fariña^d

^a Programa de Postgrados en Oceanografía, Departamento de Oceanografía, Casilla 160-C, Universidad de Concepción, Concepción, Chile

^b Programa de Investigación Marina de Excelencia (PIMEX), Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

^c Interdisciplinary Center for Aquaculture Research (INCAR), Casilla 160-C, Universidad de Concepción, Concepción, Chile

^d Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile

^e Centro de Investigación e Innovación para el Cambio Climático (CIICC), Universidad Santo Tomás, Santiago, Chile

ARTICLE INFO

Article history:

Received 9 January 2013

Received in revised form

8 April 2013

Accepted 18 April 2013

Keywords:

Sandy beach

Seasonality

Life history

Larval supply

Settlement

Connectivity

ABSTRACT

The sandcrab *Emerita analoga* is the dominant species inhabiting sandy beaches along the Pacific coast of the American continent. In our study, 10 sandy beaches were sampled seasonally from 2006 to 2011, including coastal planktonic sampling from 2006 to 2008. Two major population cores were detected, the first one in the northern part of the study area and the second in the area immediately to the south of the Itata River mouth. Zoel stages were found along the entire coastal zone. Highest densities and recruitment were found during spring and summer of each year. PLS regression indicated that source–sink habitat proxies correlated positively with morphodynamic parameters; while beach slope and total organic matter were negatively correlated. These results agree with the source–sink hypothesis, finding higher densities of adults, recruits and cohort recurrence on open coast beaches with milder physical dynamics. Furthermore, a hypoxic event and a mega-earthquake/tsunami negatively affected recruitment at the inter-annual scale.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Sandy beaches are dynamic environments, whose physical structure has been characterized by the interaction of three principal factors: tides, waves and sand type (McLachlan and Brown, 2006). The interaction between the tide regime, wave regime and sediment type produce morphodynamic gradients ranging from reflective microtidal beaches with narrow and steep slopes to wide and flat macrotidal dissipative beaches (Short, 1996, 1999). The abundance and species composition of macro-invertebrates living on sandy beaches is highly determined by geomorphologic structures, as well as other environmental factors such as the presence of fresh water streams, rivers and effluents reaching the coastal area (Lercari and Defeo, 1999; Celentano et al., 2010). Spatially sandy beaches occur in discrete units along the coast, and even neighboring beaches may be of different

morphodynamic types. This type of heterogeneity may facilitate source–sink dynamics in macroinvertebrate populations inhabiting this kind of environment (Caddy and Defeo, 2003; Defeo and McLachlan, 2005). Kawecki (2008) defined a demographic source as a habitat where emigration on average exceeds immigration, and the number of births exceeds the number of deaths; by contrast, a demographic sink is a habitat in which immigration on average exceeds emigration and the number of deaths exceeds the number of births. According to this conceptual framework, populations living in source habitats (or high quality resource areas) should have reproductive rates that exceed their mortality rate, allowing migration to other habitats, defined in this regards as sinks (or poor quality resource areas). Population persistence in sink habitats depends on – and is determined by – migration from source habitats (Kawecki, 2008).

At the population level, the Habitat Harshness Hypothesis (HHH, Defeo et al., 2003) predicts that the severe environment of reflective beaches will induce organisms to invest more energy in maintenance than in reproduction and growth, resulting in lower abundance, fecundity, growth and survival compared with

* Corresponding author.

E-mail address: eduhernandez@udec.cl (E. Hernández-Miranda).

dissipative beaches. It has been hypothesized that sandy beaches, which are morphodynamically characterized as dissipative, act as source habitats; whereas reflective sandy beaches function as sinks (Caddy and Defeo, 2003; Defeo and McLachlan, 2005). It is expected that a source habitat will show greater adult and recruit densities than sink habitats; also most of the cohorts should be present, in contrast to sink habitats where only a few cohorts should be successful. Recently, in a study of 16 beaches influenced by the saline gradient of the Río de La Plata along a 400 km stretch of the Uruguayan coast, Celentano et al. (2010) found evidence for reflective beaches acting as sinks, and dissipative beaches acting as sources, demonstrated by populations of *Emerita brasiliensis* that were unable to prosper.

The anomuran crustaceans of the genus *Emerita* are one of the most successful macroinvertebrate groups living in sandy intertidal zones around the world (Efford, 1969, 1976). These anomurans live in the swash zone of beaches, reaching the upper subtidal zone (Dugan et al., 1995; Subramoniam and Gunamalai, 2003), and feeding by filtering the water washed by waves (Efford, 1966). Only one species lives along the coast of Chile: *Emerita analoga* (Stimpson 1857). This species is distributed along the west coast of America from the Kodiak Islands in Alaska (57° N) to Bahía Magdalena (24° N) in Baja California, and from Salaverry in Peru (8° S) to the Strait of Magellan (53° S). On the Atlantic coast, it reaches Bahía Falsa, Argentina (55° S) (Efford, 1969, 1976). The sandy beaches of the South Eastern Pacific present highly heterogeneous habitats with beaches with high and/or low abundances (i.e. Jaramillo et al., 1999, 2012; Brazeiro, 2001). In the southeastern Pacific, it is expected that *E. analoga* is distributed in patches, forming spatial mosaics at the scale of tens of kilometers, and therefore it is likely that source–sink *E. analoga* population dynamics occur at this spatial scale. *E. analoga* has a complex life cycle with benthonic (sedentary) adult states and planktonic zoeal and megalopal larvae. Once larvae are liberated they remain in the plankton for about four months, going through 5–8 zoeal stages (Johnson and Lewis, 1942; Efford, 1970). Considering (1) the patchy distribution at a scale of tens of kilometers and (2) the great potential for dispersion of its larvae and the sedentary habits of its adults, *E. analoga* is a good candidate for analyzing the source–sink dynamics of sandy beach macroinvertebrate populations.

In this study we describe the results of a five-year sampling campaign at ten sites along 50 km of the central-south Chilean coast. The aims of the study were: (1) to determine if there are spatial differences in recruitment and adult density of *E. analoga*, and (2) explore whether there is evidence for source–sink population dynamics, and whether these dynamics are correlated with environmental variables such as beach morphodynamics and freshwater inputs to the coast.

2. Materials and methods

2.1. Climate conditions in the study zone

The coastal zone in south-central Chile (35–19°S) has a Mediterranean climate (di Castri and Hajek, 1976). The study zone is characterized by seasonal variability in the wind regime, which is determined by meteorological and oceanographic factors (Saavedra, 1980; Arcos and Navarro, 1986; Montecinos and Gomez, 2010). Climate is mainly determined by the South Pacific Anticyclone (28–31°S), high latitude atmospheric lows, and continental atmospheric lows (Saavedra, 1980; Saavedra and Foppiano, 1992). During the austral spring and summer there is a displacement of the South Pacific Anticyclone toward the south, causing an anticyclonic wind circulation (south-westerly wind),

which favors coastal upwelling (Sobarzo et al., 2007). Moreover, the presence of the South Pacific Anticyclone in south-central Chile reduces precipitation and river runoff. By contrast, during the austral winter the South Pacific Anticyclone moves to the north, producing northerly winds and more precipitation (Sobarzo et al., 2007).

2.2. Sampling design and data analysis

A sampling program was carried out with the aim of describing the *E. analoga* population inhabiting the area adjacent to the mouth of the Itata River in south-central Chile. Ten sandy beaches (sites) were sampled along 50 km of coast (Fig. 1). Six of these were located near the Itata River mouth (A, B, C, D, E and F), while three were approximately 20–30 km north [X (Cobquecura), Z and Y], and the tenth was at Coliumo Bay near the stream Estero Villarrica (G, 20 km south). Because the settlement of *E. analoga* in south-central Chile occurs mainly during the austral spring–summer (Contreras et al., 1999), a series of 17 surveys from November 2006 to February 2011 were carried out seasonally; spring (November 2006, 2007, 2008, 2009 and 2010), summer (February 2007, 2008, 2009 and 2011), autumn (May 2007, 2008, 2009 and 2010) and winter (August 2007, 2008, 2009 and 2010). Only February 2010 (summer) records are missing due to the 8.8 Mw earthquake and tsunami that affected the study area at this time (Vigny et al., 2011; Jaramillo et al., 2012; Sobarzo et al., 2012).

A number of physical variables were measured. A calibrated polarographic YSI-556 MPS Multiprobe System (YSI Inc. USA) was used *in situ* to record sea surface temperature (°C), salinity and dissolved oxygen ($\text{ml O}_2 \text{l}^{-1}$) in the swash zone of each site. Intertidal sediment samples were taken for granulometry and organic matter content determination. The samples were collected in the midpoint between the high and low tidal marks. Sediment grain size was determined in the laboratory using a series of geological

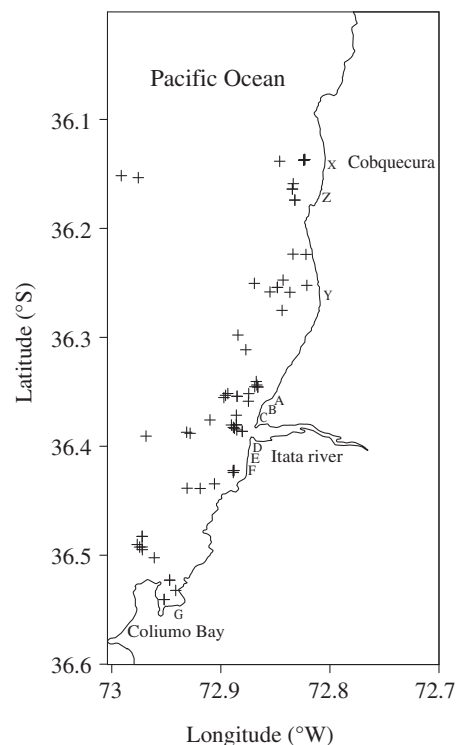


Fig. 1. Map of the study area. Letters X, Z, Y, A, B, C, D, E, F and G correspond to study beaches. Crosses correspond to planktonic sampling stations.

sieves (from 2 mm to 63 μm mesh) (Buchanan, 1971). Mean grain size was calculated by the moment method using the GRADISTAT software (Blott and Pye, 2001), and the results were expressed on a ϕ scale (Folk, 1974). Total organic matter (TOM) was calculated as the percentage loss in dry sediment weight after combustion at 550 °C for 4 h (Byers et al., 1978). Sand fall velocity (W_s) was directly measured using settling tubes (Emery, 1938; Gibbs et al., 1971). In the field, wave period (T_b) was estimated as the time interval between consecutive breaking waves, and breaker height (H_b) was estimated by measuring the height of breaking waves with graduated poles against the horizon (e.g. Contreras et al., 2003; Brazeiro, 2005). Beach slope (S_b) was measured by the Emery method (Emery, 1961); this variable can be used as a proxy of the physical dynamics of beaches. Estimates of breaker height (H_b), wave period (T_b), and sand fall velocity (W_s) were used to calculate Dean's parameter (Ω), an index of the morphodynamic state of the beach, according to:

$$\Omega = \frac{H_b}{W_s \times T_b}$$

The Dean index (Ω) is a measure of how reflective or dissipative a beach is. If $\Omega < 2$ the beach is considered reflective, if $\Omega > 5$ the beach is dissipative, and $2 < \Omega < 5$ describes a wide range of intermediate beach states (Short, 1996; Defeo and McLachlan, 2005). In order to test temporal and spatial differences in the environmental variables mentioned above, a two-way analysis of variance was performed, with sites (beaches) and time (sampling dates) as factors. When significant differences were found a Tukey HSD post hoc comparison was also carried out for testing differences among particular sites and times.

Sampling of *E. analoga* was performed under daylight low tide conditions by sampling at each site using four transects perpendicular to the coastline, separated by 100 m, running from the lower to the higher tide mark. Along each transect, ten samples were taken with a cylindrical PVC corer of 63.6 cm² and 15 cm depth. During each survey a total of 400 samples were collected (40 from each location). Collected samples were sieved at 0.5 mm mesh size, conserved in 8% formaldehyde, and dyed with Rose Bengal solution to facilitate the sorting of the individuals. In the laboratory sampled individuals were sorted, characterized as recruits or adults (using their body sizes, see below) and counted. Density (total, recruits, and adults), standardized as the number of individuals per square meter (ind./m²), was determined by pooling all the samples from each transect and averaging the four transects of each sampling area. To test temporal and spatial differences in recruitment and adult density, a two-way repeated measures analysis of variance (RM ANOVA) was performed using the log ($x + 1$) transformed data (Underwood, 1997; von Ende, 2001). Time was the within-subject factor and "sites" (beaches) the between subject factor, including the time \times site interaction. For ANOVA the four transects sampled at each site in every sampling date were considered as replicates. The assumptions of normality and variance homogeneity were tested by residual plots and sphericity was tested using the Mauchly test. Since in both cases (total and recruit density) the sphericity assumption was not fulfilled, Greenhouse–Geisser, Huynh–Feldt and Lower-bound corrections were applied (Crowder and Hand, 1990; Quinn and Keough, 2002). Tukey HSD post hoc comparisons were also carried out for testing differences among particular sampling areas and dates.

Additionally, cephalothorax length (CL, mm) was measured in all individuals collected. Brazeiro (2005) and Diehl et al. (2007), described that *E. analoga* recruits at 3–4 mm CL. However, during our 3 month inter-sampling period, individuals should have grown near 8 mm on average (Osorio et al., 1967; Fusaro, 1978); we thus

classified individuals under 8 mm as recruits, and individuals larger than 8 mm as adults (juveniles and sexually mature adults). With this information, a global size frequency distribution (SFD) was built for each beach to visualize the size structure representative of the entire study period, grouped into 1 mm size classes and pooling the entire sampling time series together. To identify the cohorts presented in each SFD, the normal components were separated by the NORMSEP routine included in the FISAT software package (Gayano et al., 1996). Also an index of recurrence of size classes (IRSC) was calculated for each beach (Caddy and Defeo, 2003; Celentano et al., 2010), according to:

$$\text{IRSC} = \frac{N_i}{N_T}$$

where N_i represents the i th size class on a beach and N_T the total number of size classes observed on all sampled beaches. This index ranges from 0 to 1 (1 corresponds to all size classes present).

Given that a source habitat is expected to show greater adult and recruit densities than sink habitats, most cohorts should be present. In contrast, in sink habitats only a few cohorts should be successful. Therefore, the negative exponential curve of total density versus size classes should have a greater determination coefficient (r^2) in source than in sink habitats, because of the higher recruitment and number of cohorts in source habitats. For these reasons, to assess whether a particular beach meets the characteristics of a source or sink habitat, four proxies were utilized for each beach: a) total density, b) recruit density, c) index of size class recurrence (IRSC), and d) determination coefficient of the adjusted negative exponential curve of total density, as a function of relative time (size classes).

To assess the relations among the four proxies of source–sink habitat and environmental variables, a partial least squares (PLS) regression model was computed in Minitab v.15. PLS is a statistical analysis technique which is especially suitable for dealing with data in which the number of samples is small compared to the number of variables, and also when data displays co-linearity among variables (Mevik and Wehrens, 2007; Carrascal et al., 2009). PLS regression is adequate for testing our hypothesis because it allows relating multiple dependent variables (source–sink proxies) to multiple independent variables (environmental variables) at the same time. The number of PLS components to be included in the model was determined by a jackknife procedure, running PLS as many times as there were observations in the data set, leaving out one observation at a time for each run. The resulting weights of each PLS component can be utilized as an indicator of how important a variable is for explaining the variance of the PLS component; the higher the weight, the greater the importance of the variable.

Additionally, zooplankton sampling was carried out to obtain an estimation of larval supply in the coastal study area. Seven research cruises were conducted between May 2006 and February 2008 on board RVs "Kay–Kay" or "Kay–Kay II" (Universidad de Concepción, Chile). The surveys were planned to cover both summer and winter conditions, and from Cobquecura to Coliumo Bay, especially three areas; Itata Mouth, North Itata River, and South Itata River (Fig. 1). In each area four sampling stations were allocated at random. Sampling was done in the coastal zone up to five nautical miles offshore. A linear distance of 50 km and a total area of 400 km² were sampled (see also Díaz-Cabrera et al., 2012). The larvae were collected with a bongo net of 60 cm mouth diameter and 300 μm mesh size. To estimate the volume of water filtered, the net was equipped with a calibrated Hydrobios flowmeter. At each sampling station, oblique tows were made throughout the upper 15 m of the water

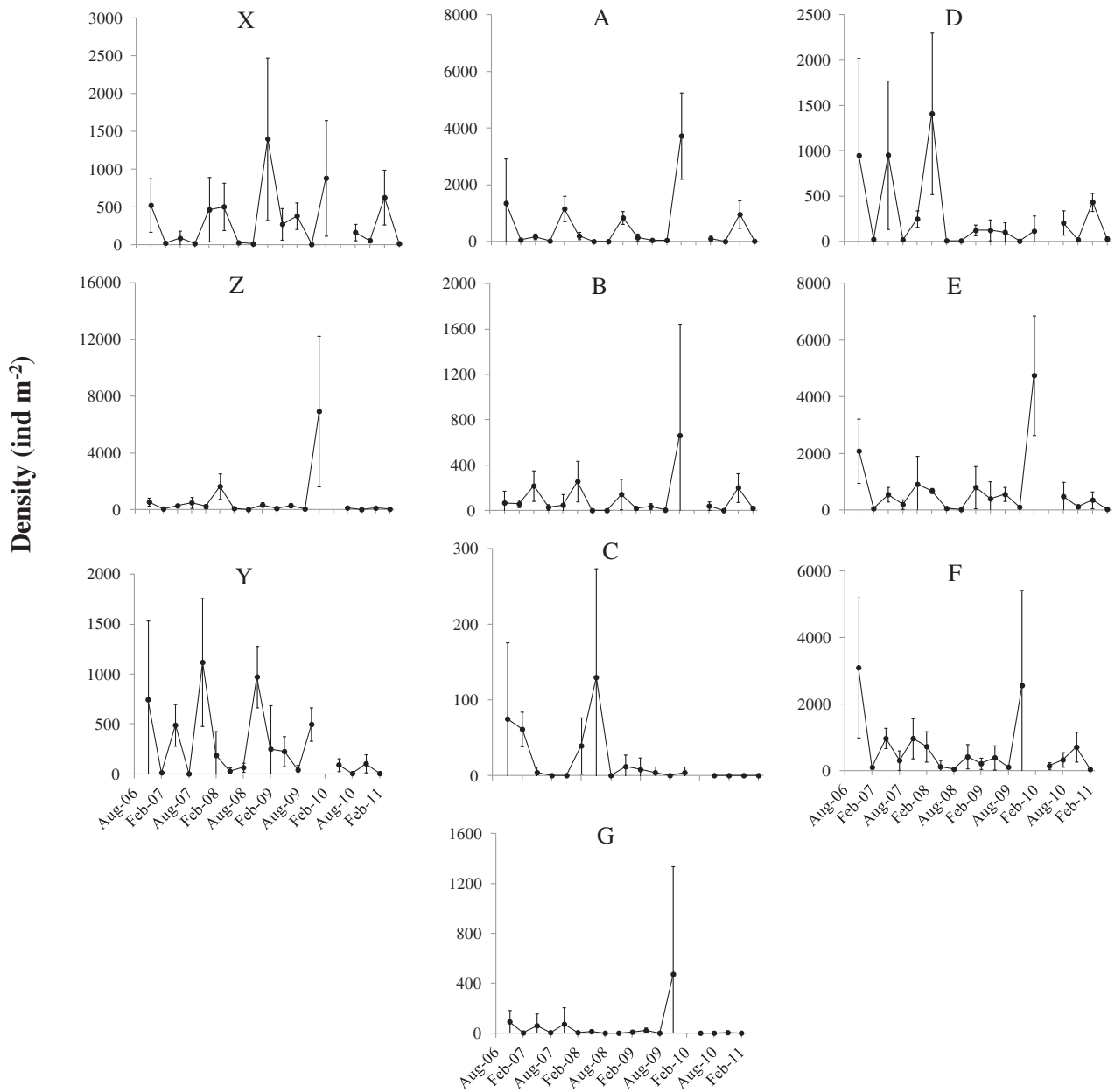


Fig. 2. Time series of density (ind m⁻²) including standard deviation (lines and points with error bars) of *Emerita analoga*, at all sampling sites. Scale of Y-axis is not the same for all sampling areas. Capital letter inside each plot correspond to sampling site.

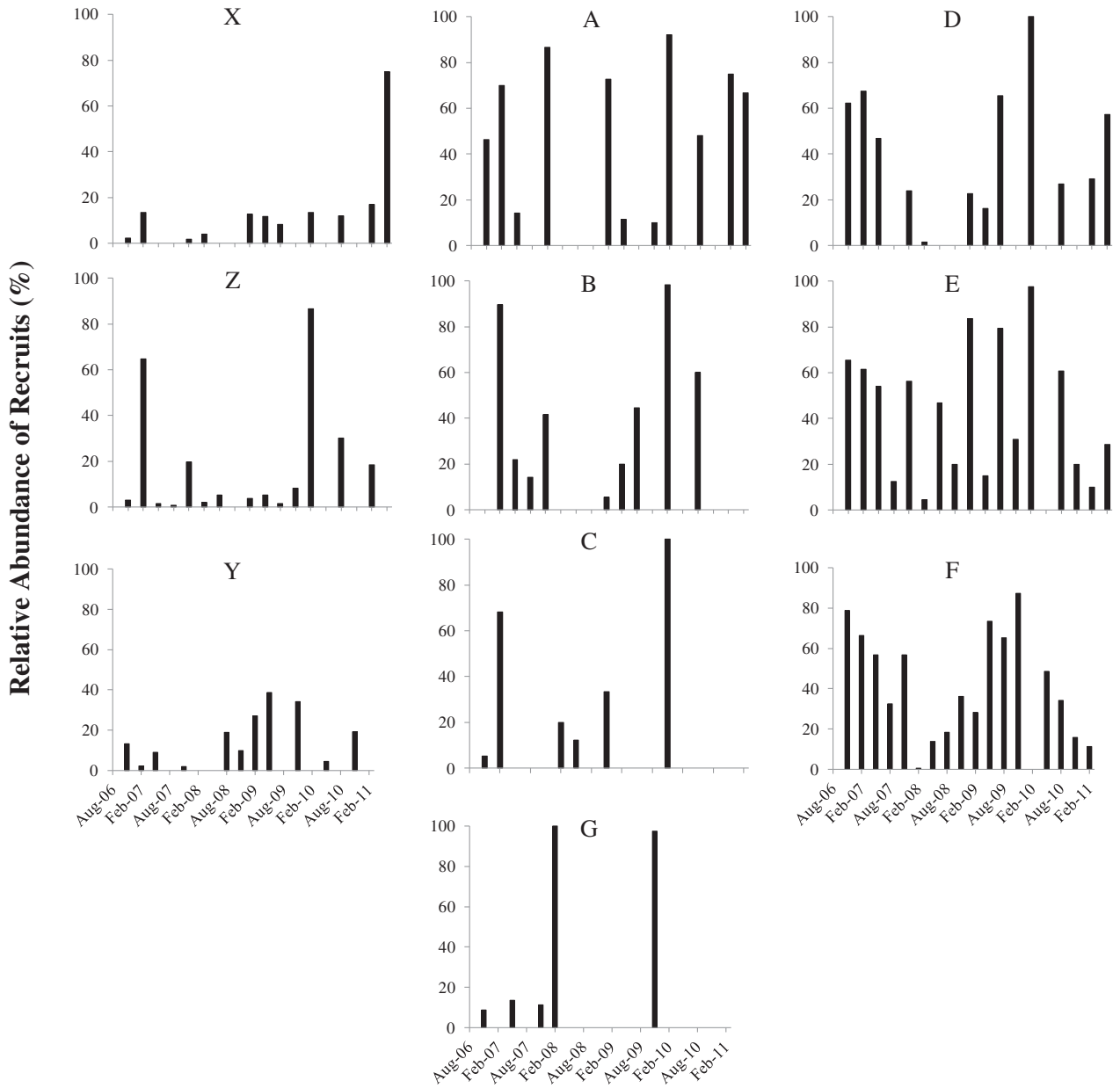


Fig. 3. Time series of relative abundance of recruits (%) of *Emerita analoga*, at all sampling sites. Capital letter inside each plot correspond to sampling site.

column. Samples collected were preserved in 96% ethanol. In the laboratory, *E. analoga* zoea larvae were identified and sorted according to available identification keys in the literature (Johnson and Lewis, 1942). For each cruise, larval density was estimated as ind./1000 m³. Finally, to visualize possible spatial patterns georeferenced density was plotted on a map using Surfer 8.0.

3. Results

3.1. Spatio-temporal dynamics of total density and recruits

The time series of total density and relative recruit abundance of *E. analoga* at all sites (Figs. 2 and 3) showed high variability, both spatially and temporally. The RM ANOVA shows significant differences for these variables within sites and between sampling dates (Time); the interaction site * time was also significant (Table 1a and b). Site C had the lowest significant density; while the highest density was found in sites E and F. Lower densities occurred at sites located close to the mouths of the Itata River (such as site C) and the Estero Villarrica in Coliumo Bay (site G) (Fig. 4). A similar pattern was found for the density of recruits (Fig. 4). However, sites X, Z and Y had lower recruit density than sites A and D (Fig. 4c). Although there was high variability in total density and recruit density, significant differences were mostly associated with seasons. In general: (i) greatest total and recruit densities were found during November (spring) and February (summer) of each year (Fig. 4b and d); (ii) lowest values of both densities were found in August (winter) (Fig. 4b and d); (iii) although there was recruitment throughout the entire year, the greatest recruit densities were recorded mainly in November (spring), and occasionally in February (summer) and May (autumn) (Fig. 4d); and (iv) the greatest recruitment event of the study period was recorded in November (spring) 2009 (Fig. 4d).

3.2. Body size frequency distribution

Small size classes were highly represented (mode approximately 6 mm) at the majority of the sites, except for sites X and Y, where there was a predominance of intermediate size classes (mode approximately 15 mm; Fig. 5). The recurrence index of annual classes was greater at sites Y, D, E and F (IRSC = 0.9), while there were lower values at sites A, B, C, and G (IRSC = 0.6) (Fig. 5).

3.3. Correlations with environmental variables

Average values of environmental variables for each site are shown in Table 2. Table 3 shows the results of the two-way ANOVA for testing temporal (sampling dates) and spatial (sampling sites) differences of environmental variables in the study area. All variables showed significant differences both temporally and spatially, except for dissolved oxygen which only showed temporal differences (Supplementary material Figs. 1 and 2). In terms of spatial variability the sediments from X to C ranged from medium to coarse sand, whereas the sites D, E and F had medium to fine sand, and site G had coarse to very coarse sand. Total organic matter ranged between 0.8 and 1.0%, except in F (0.6% approx.) and G (1.2%). Average H_b was near 1.2 m in all sites, except in G where it was around 0.2 m. Beach slope (S_b) was greater in the sites located in the north (X, Z, Y; 16–20%) of the study zone and decreased in the beaches located south of the Itata River (D, E, F; 10–12%), but near 10% in G. The beaches from X to F were all intermediate, with most of them closer to the reflective limit; G was the only one classified as reflective (Dean = 0.9), while beaches A and D were close to the dissipative limit. The average temperature was

Table 1

Results of univariate repeated measures ANOVA for log transformed values of: a) Total density, and b) Recruit density. Since the sphericity assumption was not fulfilled, three different corrections were estimated (Greenhouse-Geisser, Huynh-Feldt, and Lower-bound). The Mauchly test of sphericity is also included, and the results without correction ("sphericity assumed"). Significant *p*-values are in bold.

a) Total density [log(x + 1) transformed]					
Sphericity test					
	W – Mauchly	Chi-squared	d.f.	<i>p</i>	
Time	0.001	183.065	135	0.007	
Within-subject effect					
Source	SS (type III)	d.f.	MS	<i>F</i>	<i>p</i>
Time					
Sphericity Assumed	293.15	16	18.32	52.43	<0.0001
Greenhouse-Geisser	293.15	8.79	33.34	52.43	<0.0001
Huynh-Feldt	293.15	16	18.32	52.43	<0.0001
Lower-bound	293.15	1	293.15	52.43	<0.0001
Time * sites					
Sphericity assumed	189.72	144	1.32	3.77	<0.0001
Greenhouse-Geisser	189.72	79.13	2.40	3.77	<0.0001
Huynh-Feldt	189.72	144	1.32	3.77	<0.0001
Lower-bound	189.72	9	21.08	3.77	0.0029
Error (time)					
Sphericity assumed	167.74	480	0.35		
Greenhouse-Geisser	167.74	263.76	0.64		
Huynh-Feldt	167.74	480	0.35		
Lower-bound	167.74	30	5.59		
Between subject effect					
Source	SS (type III)	d.f.	MS	<i>F</i>	<i>p</i>
Sites	267.96	9	29.77	76.88	<0.0001
Error	11.62	30	0.39		
b) Recruit density [log(x + 1) transformed]					
Sphericity test					
	W – Mauchly	Chi-squared	d.f.	<i>p</i>	
Time	0.0004	194.520	135	0.001	
Within-subject effect					
Source	SS (type III)	d.f.	MS	<i>F</i>	<i>p</i>
Time					
Sphericity assumed	266.07	16	16.63	41.01	<0.0001
Greenhouse-Geisser	266.07	8.82	30.17	41.01	<0.0001
Huynh-Feldt	266.07	16	16.63	41.01	<0.0001
Lower-bound	266.07	1	266.07	41.01	<0.0001
Time * sites					
Sphericity assumed	216.77	144	1.51	3.71	<0.0001
Greenhouse-Geisser	216.77	79.37	2.73	3.71	<0.0001
Huynh-Feldt	216.77	144	1.51	3.71	<0.0001
Lower-bound	216.77	9	24.09	3.71	0.0032
Error (time)					
Sphericity assumed	194.65	480	0.41		
Greenhouse-Geisser	194.65	264.56	0.74		
Huynh-Feldt	194.65	480	0.41		
Lower-bound	194.65	30	6.49		
Between subject effect					
Source	SS (type III)	d.f.	MS	<i>F</i>	<i>p</i>
Sites	171.00	9	19.00	66.03	<0.0001
Error	8.63	30	0.29		

generally between 12 and 13 °C, except in C, where temperature was around 13.2 °C. Sea water in the swash zone was well oxygenated with dissolved oxygen from 5.7 to 6.0 ml l⁻¹. The salinity was between 32 and 34, except in C, where the riverine influence was detected and the salinity was about 26 (Supplementary material Figs. 1 and 2).

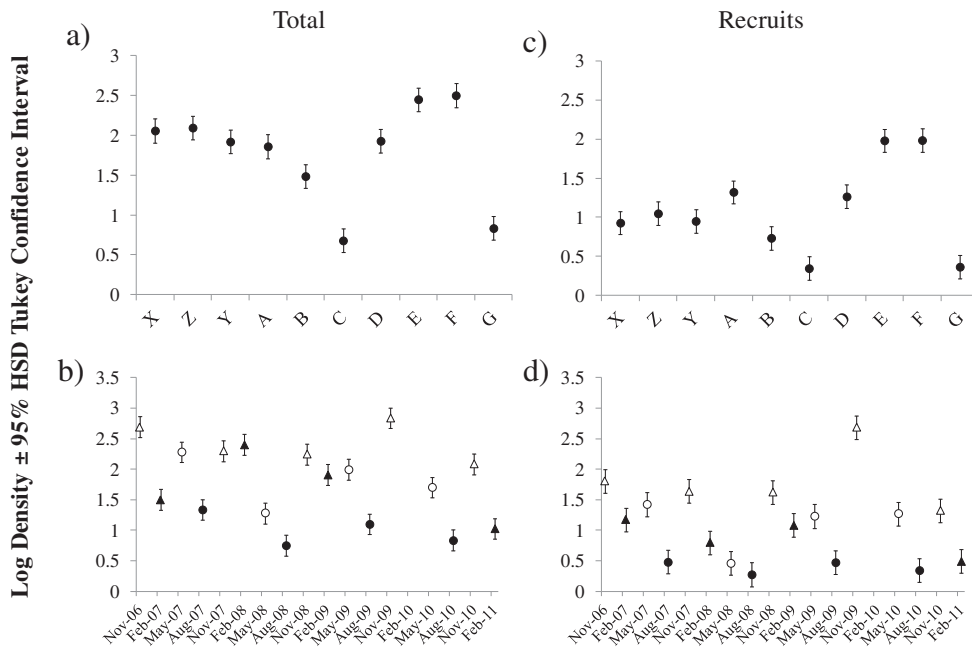


Fig. 4. *Emerita analoga*'s total density for each site (a) and sampling date (b), and *E. analoga*'s recruit density for each site (c) and sampling date (d). HSD Tukey confidence intervals (95%) are also shown. White triangles = November; black triangles = February; white circles = May; black circles = August.

The values of PLS weights are proportional to their importance in the PLS component; the sign indicates whether the variable is positively or negatively related to this PLS component. The results of the PLS regression between the proxies of source–sink habitat and environmental variables are shown in Table 4; only the best model (highest r^2) is shown. In the case where both log density of adults and log density of recruits were considered, the model was improved ($r^2 = 0.59$, $p = 0.010$). In the above mentioned case, mean grain size, Dean and H_b correlated positively with the first PLS component, while beach slope and TOM were negatively correlated with that component. In the case of the PLS regression of log density as a function of the environmental variables (Table 4), only one valid component accounted for 57% of the variance; the most important variables were those which described sediment characteristics (mean grain size and TOM) and beach morphodynamics (Dean, H_b and beach slope). Particularly, Dean, H_b and mean grain size were positively correlated with the first component, while beach slope and TOM were negatively correlated with this component. Body size (CL, mm) was explained by two components (81%), with the first accounting for 69% and the second for 12% of the variance (Fig. 6, Table 4). Salinity and the variables describing beach morphodynamics were directly correlated with the first PLS component; while temperature and dissolved oxygen were negatively correlated.

3.4. Zoel larvae distribution

Zoel larval stages were present during all surveys (Fig. 7), reaching maximum values in May, 2007 (Fig. 7d). Although larvae were collected throughout the entire study area, maximum densities were recorded in the North Zone off Cobquecura (sites X, Z, Y) and around the mouth of the Itata River (sites A, B, C, D, E and F); they were significantly lower in the South Zone (two-way ANOVA, $F_{2,37} = 3.76$, $p = 0.033$). There was also a marginally significant difference both for temporal variability (two-way ANOVA, $F_{5,37} = 2.21$, $p = 0.074$) and for the interaction zone*time (two-way ANOVA, $F_{10,37} = 1.87$, $p = 0.082$), probably associated with the seasonal reproduction of *E. analoga*.

3.5. Mega-perturbations and their effect on the inter-annual population dynamics

It is important to note that during the study period, the coast of south-central Chile was strongly perturbed, on a scale of tens to hundreds of kilometers, by two events of different origin. In this context, in an inter-annual time scale and considering the whole sampling area, a global decrease in the density of recruits was observed following two major perturbations: (i) a January 2008 hypoxic event, and (ii) the February 2010 mega-earthquake 8.8 Mw (Fig. 8).

4. Discussion

4.1. Recruitment and adult density

Our results indicate great temporal (intra- and inter-annual) and spatial variability in the total density and recruitment of *E. analoga*. Recruit density generally presented higher values during November and February, suggesting maximum annual settlement rates in spring and summer. According to the literature, settlement appears to be variable over time along the geographic distribution of *E. analoga*. In the Northern Hemisphere larval settling is always high during summer, although settling events do occur throughout the entire year at lower levels (Efford, 1965; Barnes and Wenner, 1968; Diehl et al., 2007). In other coastal zones of Chile settlement occurs mainly during spring–summer (October to December, Contreras et al., 1999), as found in this study. However, off the coast of Valparaíso, Chile, Conan et al. (1975) reported two settling periods in winter and at the beginning of spring (June and the end of September); Osorio et al. (1967) reported only one settling period during Spring. In south-central Chile larval release occurs mainly during winter (Contreras et al., 1999) and/or at the end of summer (Yannicelli et al., 2006; Díaz-Cabrera et al., 2012). According to Yannicelli et al. (2006), the highest densities of the zoel larvae are found in the coastal zone. However, this zone displays important advection away from the coast. Intermediate larval states (zoea II–IV) had higher densities further from the coast, while the zoea V

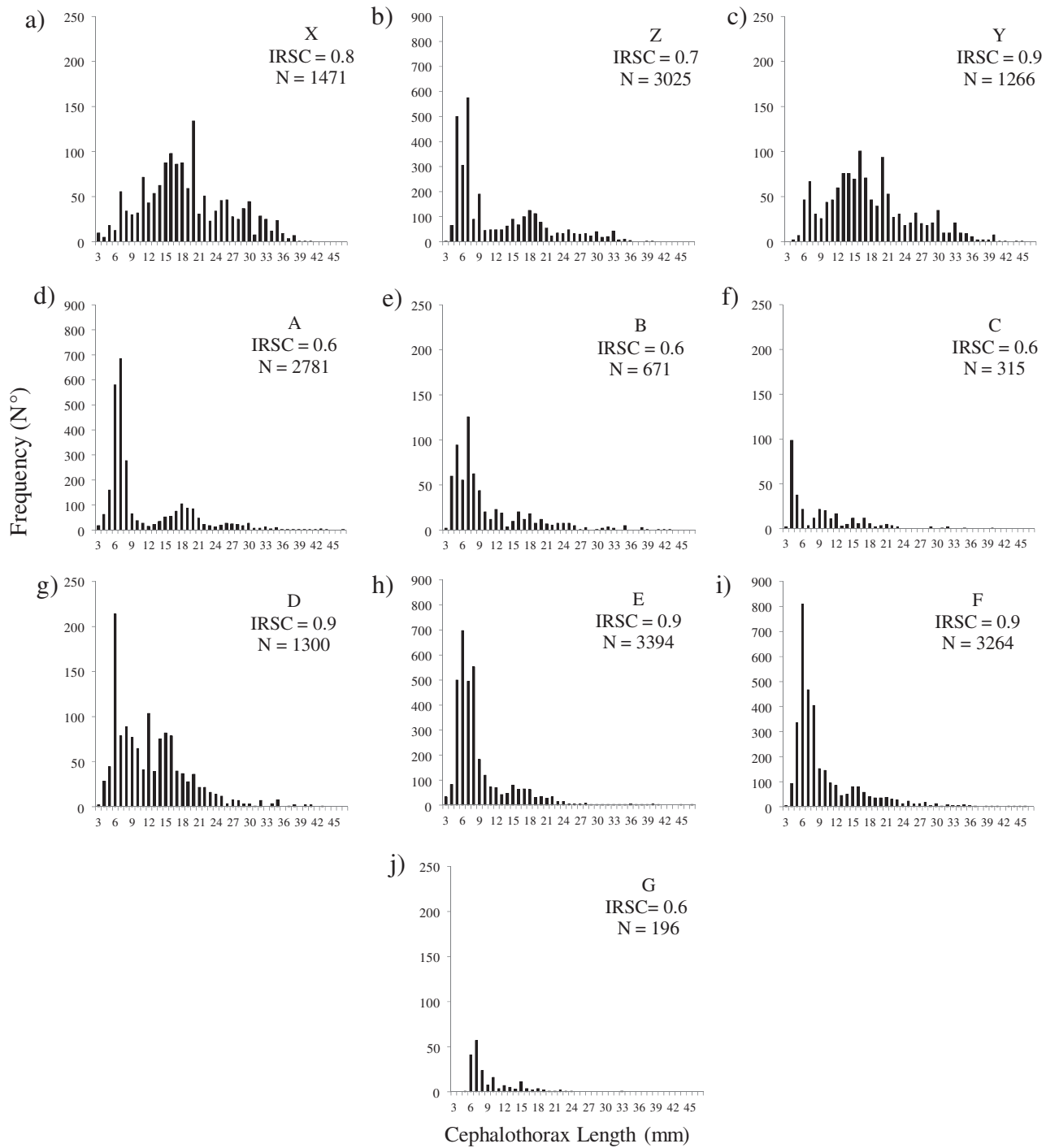


Fig. 5. Body size (Cephalothorax length) frequency distribution of *Emerita analoga* for all sites. Sample size (N) and an index of recurrence of size classes (IRSC) are included into the plot. Capital letter inside each plot correspond to sampling site.

larval state had highest densities near the coast. Yannicelli et al. (2006) suggested that the pattern of larval release of *E. analoga* is linked to the seasonality of the coastal upwelling in south-central Chile which would explain the offshore advection of intermediate developmental stages. The mechanism – or mechanisms – by which larvae return to the coast is not yet clear (Yannicelli et al., 2006). In our study, zoeal stages of *E. analoga* were present in the water column during the entire sampling period (May 2006 to February 2008), but the maximum larval abundance was found during two periods of the year (January and May, see Fig. 7), which

suggests that the recruitment events in November and February are consistent with these larval abundance maxima.

In terms of spatial distribution, the highest adult densities were observed on beaches north of the Itata River, while the highest recruit densities were found on beaches immediately south of this river (Fig. 4). The differences in adult densities were accompanied by differences in body size (*i.e.* cephalothorax length) frequencies among the studied beaches. Two of the beaches north of the Itata River (sites X and Y) had a bell-shaped body size frequency distribution, while the rest were skewed to the left (toward lower body

Table 2

Average values (\pm standard deviation) of environmental variables recorded during the entire sampling period for each sampled site (beach). Mean grain size in phi (ϕ) scale, TOM = total organic matter content in sediments, H_b = breaker height, Sb = beach slope, Ω = dean parameter, DO = dissolved oxygen in swash area. Temperature and salinity were also recorded in the swash area.

Site	Mean grain size (ϕ)	TOM (%)	H_b (m)	Sb (%)	Ω	Temperature ($^{\circ}$ C)	DO ml l $^{-1}$	Salinity
A	1.1 \pm 0.7	0.9 \pm 0.2	1.21 \pm 0.15	14.66 \pm 10.46	3.66 \pm 2.28	12.37 \pm 1.33	5.7 \pm 0.7	33.0 \pm 1.7
B	1.1 \pm 0.5	0.9 \pm 0.1	1.27 \pm 0.21	16.37 \pm 10.73	2.90 \pm 1.47	12.36 \pm 1.33	5.7 \pm 0.5	32.9 \pm 1.5
C	1.0 \pm 0.6	0.8 \pm 0.2	1.26 \pm 0.18	15.29 \pm 10.29	2.67 \pm 1.98	13.19 \pm 2.00	5.9 \pm 0.9	26.6 \pm 9.8
D	1.5 \pm 0.5	1.0 \pm 0.2	1.21 \pm 0.15	11.63 \pm 3.09	3.76 \pm 2.53	12.66 \pm 1.32	5.8 \pm 0.7	31.4 \pm 6.5
E	1.6 \pm 0.4	0.9 \pm 0.3	1.20 \pm 0.14	10.39 \pm 2.99	3.16 \pm 1.66	12.89 \pm 1.53	5.9 \pm 0.9	31.8 \pm 5.3
F	1.9 \pm 0.7	0.6 \pm 0.3	1.16 \pm 0.15	10.71 \pm 2.53	3.15 \pm 1.97	12.94 \pm 1.37	5.8 \pm 0.8	31.4 \pm 4.4
G	0.0 \pm 1.2	1.3 \pm 0.7	0.18 \pm 0.06	10.19 \pm 1.89	0.90 \pm 0.65	12.90 \pm 1.56	5.8 \pm 0.7	33.1 \pm 2.2
X	1.1 \pm 0.7	0.9 \pm 0.2	1.24 \pm 0.13	19.65 \pm 14.09	2.75 \pm 1.75	12.77 \pm 1.31	5.9 \pm 0.9	33.8 \pm 1.1
Y	1.1 \pm 0.5	0.9 \pm 0.2	1.23 \pm 0.12	19.57 \pm 12.69	2.68 \pm 1.48	12.59 \pm 1.40	5.8 \pm 0.6	33.7 \pm 1.3
Z	0.7 \pm 0.8	0.9 \pm 0.2	1.23 \pm 0.13	16.56 \pm 10.98	2.54 \pm 1.18	12.47 \pm 1.20	5.8 \pm 0.8	33.8 \pm 0.9

sizes, Fig. 5). The non-homogeneous structure of size distribution among beaches indicates that in some cases there were marked pulses of recruitment, while in others the larger size classes were more abundant. This means that in spite of having larger-sized individuals in the northern part of the study area, recruitment rate was lower than expected. This may be due to: 1) high mortality in the pre-settling stages (or larval transport away), and/or 2) less success in settling due to the physical dynamics in the swash zone of these beaches. According to Yannicelli et al. (2006) and Díaz-Cabrera et al. (2012) *E. analoga* larvae should be found along all the coastal waters of central-south Chile, and if mortality in pre-settling stages were high, then it would be of the same magnitude throughout the entire study zone (50 km of coast), thus recruit availability would be equally affected on all sampled beaches. In agreement with this hypothesis, we found zoeal larvae all along the study area, although their average density in the south zone was lower than the other two zones located to the north of the study area. This result does not support the hypothesis of higher mortality of the pre-settling stages in the north zone (see Fig. 7). Further, body size frequency distributions with few individuals in smaller size classes at sites X and Y are probably associated with a failure in local settlement. This reduced settlement may be related to reflective-type beaches, or at least to strong physical dynamics in the swash zone. Brazeiro (2005) determined the burrowing velocity of *E. analoga* in two types of sediment (coarse and fine) from reflective and dissipative beaches, respectively, finding that independent of individual size, the burrowing velocity was always

greater in fine sand and slower in coarse sand. This means that on reflective beaches, or those with stronger physical dynamics (e.g. higher beach slope, sites X and Y), the new settlers would have more difficulty in burying to protect themselves from wave wash, which could contribute to a decrease in successful settling.

4.2. Source–sink dynamics

Sandy beaches are harsh environments where numerous physical factors interact to produce a wide variety of morphodynamic states from dissipative to reflective (Short, 1996, 1999). This environmental gradient has important consequences for the resident communities by decreasing species richness, abundance and total biomass from dissipative to reflective beaches or, at least, from high energy to low energy environments (Defeo and McLachlan, 2005). At the population level, the Habitat Harshness Hypothesis (HHH, Defeo et al., 2003) predicts that the severe environment of reflective beaches will induce organisms to invest more energy in maintenance than in reproduction and growth, resulting in lower abundance, fecundity, growth and survival compared to dissipative beaches. Recent evaluations of the HHH show that *E. analoga* off the central coast of Chile displays less growth and burrowing capacity on extremely reflective beaches. A similar result was described for *E. brasiliensis* on the Uruguayan coast; lower abundance, shorter duration of the reproductive and recruitment periods, and smaller size of megalopae larvae and adult females were found. This evidence coincides mostly with our results (PLS regression), since on one hand the mean density of *E. analoga* was negatively correlated

Table 3

Results of two-way analysis of variance for environmental variables as a function of time (sampling dates) and sites (beaches). Significant *p*-values in bold.

Environmental variables	Source	SS	g.l.	MS	F	<i>p</i>
Mean grain size (ϕ)	Time	20.75	17	1.22	3.04	0.0001
	Sites	42.52	9	4.72	11.77	<0.0001
MOT (%)	Time	2.41	17	0.14	1.74	0.0408
	Sites	3.97	9	0.44	5.43	<0.0001
H_b (m)	Time	2.39	16	0.15	19.95	<0.0001
	Sites	16.82	9	1.87	250.09	<0.0001
Sb (%)	Time	3495.24	16	218.45	9.40	<0.0001
	Sites	746.95	9	82.99	3.57	0.0005
Dean	Time	315.30	16	19.71	14.98	<0.0001
	Sites	91.82	9	10.20	7.76	<0.0001
Temperature ($^{\circ}$ C)	Time	260.11	17	15.30	26.01	<0.0001
	Sites	11.53	9	1.28	2.18	0.0266
Dissolved oxygen (ml l $^{-1}$)	Time	70.52	17	4.15	21.21	<0.0001
	Sites	1.25	9	0.14	0.71	0.6996
Salinity	Time	710.80	17	41.81	2.34	0.0033
	Sites	748.60	9	83.18	4.65	<0.0001

Table 4

Results of PLS regression for source–sink proxies as a function of environmental variables. Comp 1 and 2 are weights of each variable in the first and second PLS components respectively; r^2 = proportion of the variance accounted for by the PLS regression. *p* values lower than 0.05 are also in bold, and indicate a significant result. CL = cephalothorax length (body size).

Independent variable	Log adult density	Adult CL	Log recruit density	
	Log recruit density	Total CL	Log total density	
Log total density				
Dependent variable	Comp1	Comp1	Comp2	Comp1
Beach slope (%)	−0.272	0.470	0.452	−0.300
H_b (m)	0.456	0.480	−0.376	0.448
Dean (Ω)	0.513	0.311	−0.523	0.511
Mean grain size (ϕ)	0.520	0.029	−0.568	0.534
TOM (%)	−0.437	−0.238	0.392	−0.441
Temperature ($^{\circ}$ C)	−0.186	−0.578	0.075	−0.149
Salinity	0.037	0.331	0.096	0.002
Dissolved oxygen (ml l $^{-1}$)	−0.204	−0.420	0.152	−0.175
r^2	0.57	0.69	0.12	0.59
<i>p</i>	0.012	0.003	0.010	

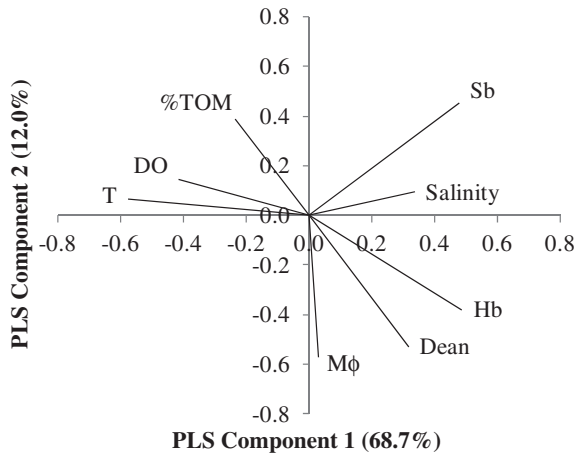


Fig. 6. Partial Least Squares (PLS) regression weights of the first versus second PLS component, for *Emerita analoga* body size (CL, mm) as a function of environmental variables. In brackets the percentages of variance explained by each component are shown. $M\phi$ = mean grain size in phi (ϕ) scale, %TOM = % total organic matter content in sediments, H_b = breaker height, S_b = beach slope, Dean = Dean parameter (Ω), DO = dissolved oxygen in swash area, T = temperature in swash area.

with beach slope (S_b), TOM and temperature, and positively correlated with Dean (Ω), wave height (H_b) and mean grain size ($M\phi$), while on the other hand body size (CL) was positively correlated with H_b , S_b and Ω (Table 4). This implies that the density of *E. analoga* increases as beach slope decreases and when Ω and mean grain size increases (ϕ scale; finest sediment). Also, mean body size increased along with Ω , in agreement with the HHH, but also increased with beach slope, contrary to the predictions of this hypothesis. Taking into account that the analyses were global, the results described above may be masked by low recruitment found on beaches with greater slope, thus increasing the mean size at these sites (see Table 2). Alternatively, larger individuals could be sufficiently strong to dig deep enough to avoid hydrodynamic conditions in the swash. Another factor that also could affect density is the outflow of freshwater (i.e. Lercari and Defeo, 1999). In our study area, two sources of freshwater are present: the Itata River close to site C and the Villarica stream close to site G. The first corresponds to the most important source of fresh water in the study area (Soto-Mendoza et al., 2010), which is consistent with the reduced salinity observed at site C (see Table 2). This is reflected in the low density both of adults and recruits at this location (see Fig. 4). In the particular case of the study site in Coliumo Bay (G, Dichato beach, an important human settlement), in addition to

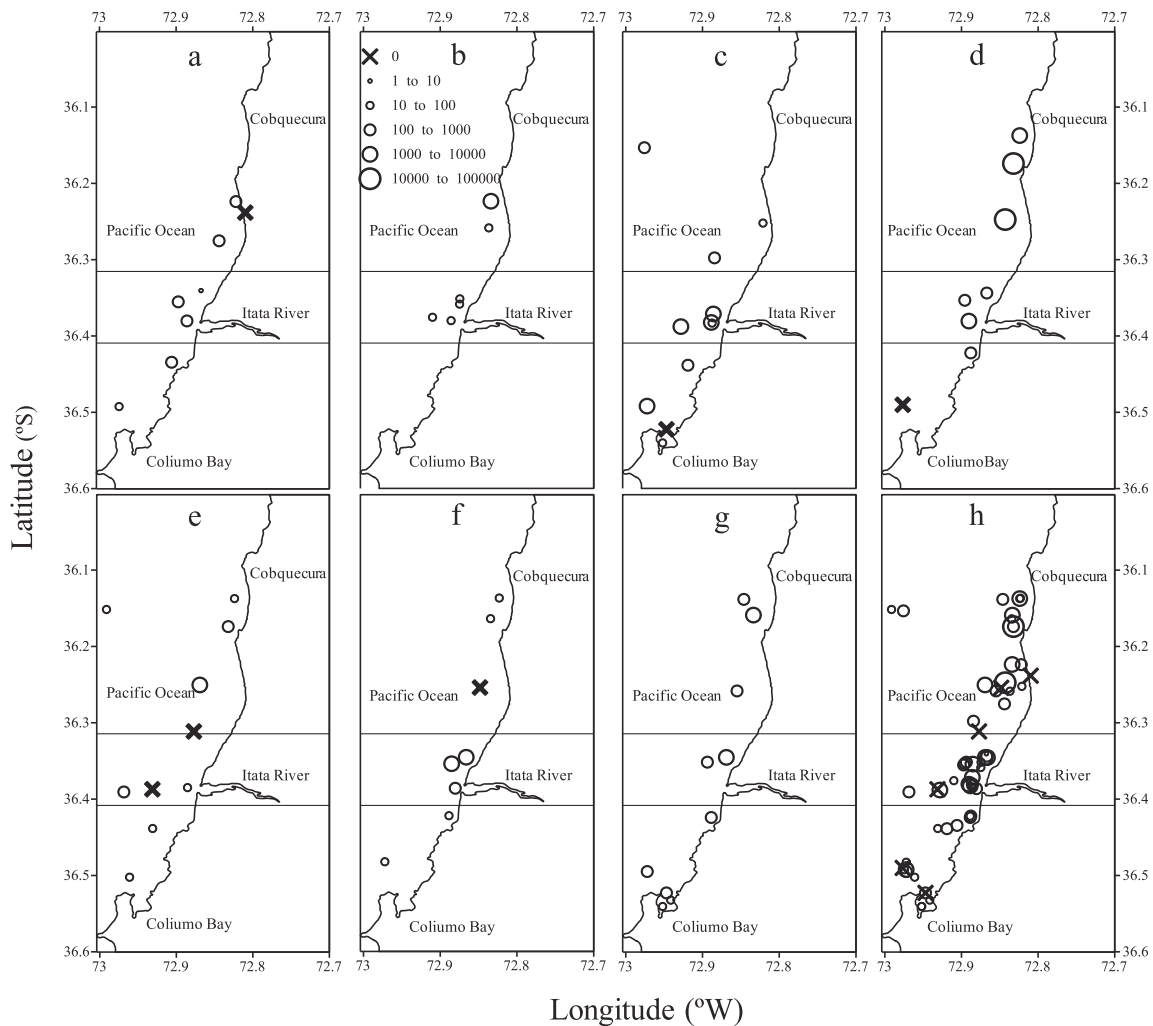


Fig. 7. Larval density (zoea; ind 1000 m^{-3}) of *E. analoga*, for a) May 2006, b) August 2006, c) January 2007, d) May 2007, e) August 2007, f) November 2007 and g) January–February 2008. In panel h) the sampling stations for all cruises are pooled. Density scale is indicated in panel b). For the Southern Hemisphere autumn = May, winter = August, spring = November and summer = January. The zones North, Itata Mouth, and South, are delimited by horizontal solid lines in each map.

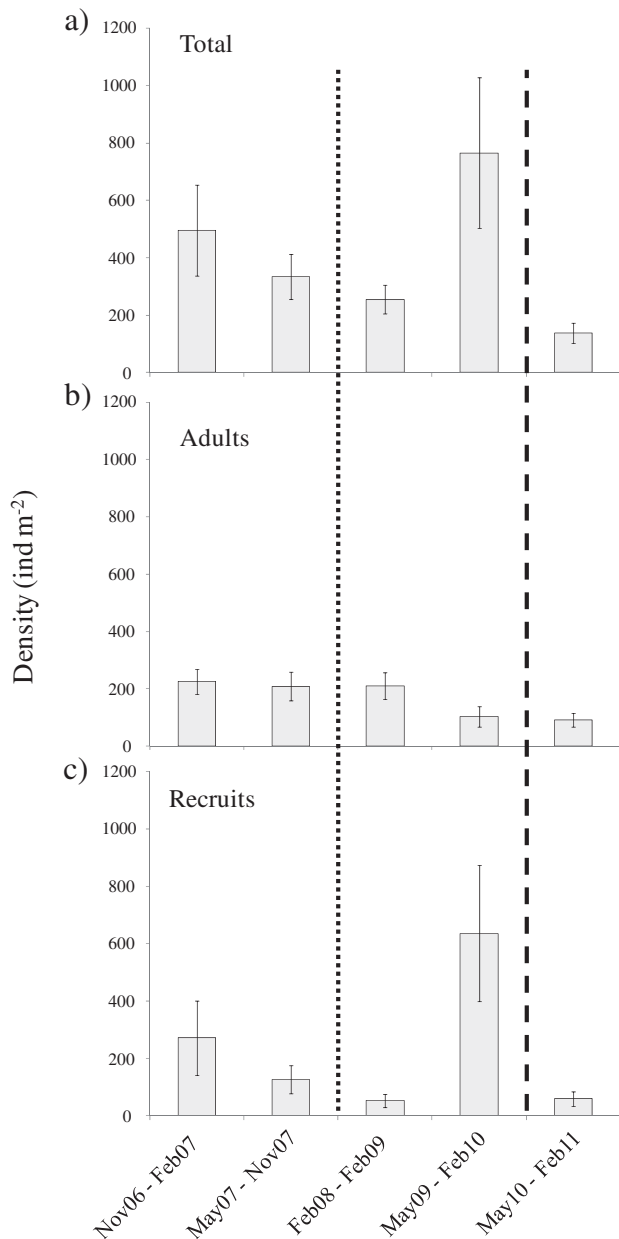


Fig. 8. Total (a), adult (b) and recruit mean density (c) of *Emerita analoga* for the complete study area, and periods of time before and after the two perturbation events: the hypoxic event of January 2008 (dotted line), and the 8.8 Mw earthquake and tsunami of February 2010 (dashed line). Standard error is also included in the bars.

lower densities due to proximity to the Villarrica stream and human activities, it is highly likely that the hypoxic event (Hernández-Miranda et al., 2010, 2012a) and tsunami (Jaramillo et al., 2012) were responsible for the overall low densities found at this site. It should be noted that after the February 2010 earthquake and tsunami, bulldozers have been removing refuse and sand from this beach strongly impacting the sandy intertidal zone.

4.3. Mega-perturbations and their effect on the inter-annual population dynamics

It is important to note that during the study period, the coast of south-central Chile was strongly perturbed by two events of different origin on a scale of tens to hundreds of kilometers. The

first, in January, 2008, was a natural hypoxic event associated with the coastward intrusion of upwelled water low in dissolved oxygen, which produced a massive mortality of benthic and planktonic organisms in Coliumo Bay (Hernández-Miranda et al., 2010, 2012a,b). The second event was the 8.8 Mw earthquake and tsunami that occurred in February 2010 (Castilla et al., 2010; Jaramillo et al., 2012; Sobarzo et al., 2012). Our study zone is located in the middle of the segment of the fault zone which ruptured during the earthquake. It produced the tectonic uplift of the coast along the 700 km of rupture zone, in some areas up to 4 m, and the deposit of important quantities of sediment on beaches along the entire coast caused by the tsunami waves. Burrowing organisms such as *E. analoga* were trapped in the sediments above the swash zone, and consequently, suffered massive mortality (Jaramillo et al., 2012). The tsunami also destroyed human settlements and deposited enormous quantities of sediment onto beaches, which also produced changes in the granulometry of sandy beaches toward coarser grain sizes. On an inter-annual time scale (see Fig. 8), a global decrease in the density of recruits was found following the hypoxic event, a phenomenon apparently associated with massive mortality of larvae, and with recovery during the period prior to the February 2010 earthquake. A similar consequence on recruit density was observed after the earthquake, in this case probably due to massive adult mortality (Jaramillo et al., 2012) associated with the change in the physical characteristics of the substrate produced by the tsunami.

In consideration of our results over different spatial and temporal scales, we found that *E. analoga* displayed source–sink dynamics in the study area. We found that total density, recruit density and number of cohorts present in the zone from Cobquecura to Coliumo Bay suggest that sites E, F, X, Y, and Z act as source areas. These areas have lesser slopes, finer sediment, greater MOT content (indicator of food availability) and greater values of Dean's index (in this case, intermediate beaches far from the reflective extreme). It is important to note that from the population point of view at least two of these source areas are distant from each other, providing important buffer conditions for perturbation events on a local scale. It is also evident that above and beyond these intra- and inter-annual dynamics, perturbations on a scale of hundreds of kilometers (i.e. natural hypoxia and earthquake-tsunami) may influence the population response over larger spatial scales.

Acknowledgments

This study is part of the Programa de Investigación Marina de Excelencia (PIMEX) and the Programa de Monitoreo del Medio Marino del CFI-Nueva Aldea (PROMNA) of the Faculty of Natural and Oceanographic Sciences (University of Concepción, Chile), both funded by Celulosa Arauco y Constitución S.A. This paper is part of the R.V. doctoral thesis. We thank Dr. Lafayette Eaton and three anonymous reviewers for their valuable comments and suggestions.

Appendix A. Supplementary material

Supplementary material related to this article can be found at <http://dx.doi.org/10.1016/j.marenvres.2013.04.004>.

References

- Arcos, D., Navarro, N., 1986. Análisis de un índice de surgencia para la zona de Talcahuano, Chile (Lat. 37°S). Investigaciones Pesqueras 33, 91–98.
- Barnes, N.B., Wenner, A.M., 1968. Seasonal variation in the sand crab *Emerita analoga* (Decapoda, Hippidae) in the Santa Barbara area of California. Limnology and Oceanography 13, 465–475.

- Blott, S.J., Pye, K., 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms* 26, 1237–1248.
- Brazeiro, A., 2001. Relationship between species richness and morphodynamics in sandy beaches: what are the underlying factors? *Marine Ecology Progress Series* 224, 35–44.
- Brazeiro, A., 2005. Geomorphology induces life history changes in invertebrates of sandy beaches: the case of the mole crab *Emerita analoga* in Chile. *Journal of Marine Biological Association United Kingdom* 85, 113–120.
- Buchanan, J.B., 1971. Measurements of the physical and chemical environment. In: Holme, N.A., McIntyre, A.D. (Eds.), *Methods for the Study of Marine Benthos*. IBP Handbook, vol. 16. Blackwell, Oxford, pp. 30–52.
- Byers, S., Mills, E., Stewart, P., 1978. A comparison of methods of determining organic carbon in marine sediments, with suggestion for a standard method. *Hydrobiologia* 58, 43–47.
- Caddy, J.F., Defeo, O., 2003. Enhancing or Restoring the Productivity of Natural Populations of Shellfish and Other Marine Invertebrate Resources. FAO Fisheries Technical Paper 448. FAO, Rome.
- Carrascal, L.M., Galvan, I., Gordo, O., 2009. Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos* 118, 681–690.
- Castilla, J.C., Manriquez, P.H., Camaño, A., 2010. Effects of rocky shore coseismic uplift and the 2010 Chilean mega-earthquake on intertidal biomarker species. *Marine Ecology Progress Series* 418, 17–23.
- Celentano, E., Gutiérrez, N.L., Defeo, O., 2010. Effects of morphodynamic and estuarine gradients on the demography and distribution of a Sandy beach mole crab: implications for source–sink habitat dynamics. *Marine Ecology Progress Series* 398, 193–205.
- Conan, G., Melo, C., Yany, G., 1975. Evaluation de la production d'une population littorale du crabe Hippidae *Emerita analoga* (Stimpson) par intégration des paramètres de croissance et de mortalité. In: 10th European Symposium on Marine Biology, vol. 2, pp. 129–150.
- Contreras, H., Defeo, O., Jaramillo, E., 1999. Life history of *Emerita analoga* (Stimpson) (Anomura, Hippidae) in a sandy beach of south central Chile. *Estuarine, Coastal and Shelf Science* 48, 101–112.
- Contreras, H., Jaramillo, E., Duarte, C., McLachlan, A., 2003. Population abundances, growth and natural mortality of the crustacean macrofauna at two sand beach morphodynamic types in southern Chile. *Revista Chilena de Historia Natural* 76, 543–561.
- Crowder, M.J., Hand, D.J., 1990. *Analysis of Repeated Measures*. Chapman and Hall, London.
- Defeo, O., Lercari, D., Gómez, J., 2003. The role of morphodynamics in structuring sandy beach populations and communities: what should be expected? *Journal of Coastal Research* 35, 352–362.
- Defeo, O., McLachlan, A., 2005. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Marine Ecology Progress Series* 295, 1–20.
- di Castri, F., Hajek, E., 1976. *Bioclimatología de Chile*. Editorial de la Universidad Católica de Chile, p. 163.
- Diehl, J.M., Toonen, R.J., Botsford, L.W., 2007. Spatial variability of recruitment in the sand crab *Emerita analoga* throughout California in relation to wind-driven currents. *Marine Ecology Progress Series* 350, 1–17.
- Díaz-Cabrera, E., Hernández-Miranda, E., Hernández, C.E., Quiñones, R.A., 2012. Mesoscale β diversity and spatial nestedness of crustacean larvae in the coastal zone off central southern Chile: population and community implications. *ICES Journal of Marine Science* 69 (3), 429–438.
- Dugan, J.E., Hubbard, D., Page, H., 1995. Scaling population density to body size: test in two soft sediment intertidal communities. *Journal of Coastal Research* 11, 849–857.
- Efford, I.E., 1965. Aggregation in the sand crab, *Emerita analoga* (Stimpson). *Ecology* 34, 63–75.
- Efford, I.E., 1966. Feeding in the sand crab, *Emerita analoga* (Stimpson) (Decapoda, Anomura). *Crustaceana* 10, 167–182.
- Efford, I.E., 1969. Egg size in the sand crab, *Emerita analoga* (Stimpson) (Decapoda, Anomura). *Crustaceana* 16, 15–26.
- Efford, I.E., 1970. Recruitment to sedentary marine populations as exemplified by the mole crab, *Emerita analoga* (Decapoda, Hippidae). *Crustaceana* 18, 293–308.
- Efford, I.E., 1976. Distribution of the sand crab in the genus *Emerita* (Decapoda, Hippidae). *Crustaceana* 30, 169–183.
- Emery, K., 1938. A rapid method of mechanical analysis of sands. *Journal of Sedimentary Petrology* 8, 105–111.
- Emery, K., 1961. A simple method of measuring beach profiles. *Limnology and Oceanography* 6, 90–93.
- Folk, R., 1974. *Petrology of Sedimentary Rocks*. Hemphills, Publishing Co., Texas.
- Fusaro, C., 1978. Growth rate of the mole crab, *Emerita analoga*, (Hippidae) in two different environments. *Fishery Bulletin* 76, 369–375.
- Gayaniolo Jr., F.C., Sparre, P., Pauly, D., 1996. The FAO-ICLARM Stock Assessment Tools (FISAT) User's Guide. FAO Computerized Information Series (Fisheries) No. 8. FAO, Rome.
- Gibbs, R., Matthews, M., Link, D., 1971. The relationship between sphere size and settling velocity. *Journal of Sedimentary Petrology* 41, 7–18.
- Hernández-Miranda, E., Quiñones, R.A., Aedo, G., Valenzuela, A., Mermoud, N., Román, C., Yañez, F., 2010. A major fish stranding caused by a natural hypoxic event in a shallow bay of the eastern South Pacific Ocean. *Journal of Fish Biology* 76, 1543–1564.
- Hernández-Miranda, E., Veas, R., Labra, F.A., Salamanca, M., Quiñones, R.A., 2012a. Response of the epibenthic macrofaunal community to a strong upwelling-driven hypoxic event in a shallow bay of the southern Humboldt Current System. *Marine Environmental Research* 79, 16–28.
- Hernández-Miranda, E., Quiñones, R.A., Aedo, G., Díaz-Cabrera, E., Cisterna, J., 2012b. The impact of a strong natural hypoxic event on the toadfish *Aphos porosus* in Coliumo Bay, south-central Chile. *Revista de Biología Marina y Oceanografía* 47 (3), 475–487.
- Jaramillo, E., McLachlan, A., Coetzee, P., 1999. Intertidal zonation patterns of macroinfauna over a range of exposed sandy beaches in south-central Chile. *Marine Ecology Progress Series* 101, 105–118.
- Jaramillo, E., Dugan, J.E., Hubbard, D.M., Melnick, D., Manzano, M., Duarte, C., Campos, C., Sanchez, R., 2012. Ecological implications of Extreme events: footprints of the 2010 earthquake along the Chilean coast. *PLoS ONE* 7 (5), e35348.
- Johnson, M.W., Lewis, W.M., 1942. Pelagic larval stages of the sand crabs *Emerita analoga* Stimpson, *Blepharipoda occidentalis* Randall, and *Lepidopa myops* Stimpson. *Biological Bulletin* 83 (1), 67–87.
- Kawecki, T.J., 2008. Adaptations to marginal habitats. *Annual Review in Ecology, Evolution and Systematic* 39, 321–342.
- Lercari, D., Defeo, O., 1999. Effects of freshwater discharge in sandy beach populations: the mole crab *Emerita brasiliensis* in Uruguay. *Estuarine Coastal and Shelf Science* 58, 17–24.
- McLachlan, A., Brown, A.C., 2006. *The Ecology of Sandy Shores*. Elsevier, p. 373.
- Mevik, B.H., Wehrens, R., 2007. The PLS package: principal components and partial least squares regression in R. *Journal of Statistical Software* 18, 1–24.
- Montecinos, A., Gomez, F., 2010. ENSO modulation of the upwelling season off southern-central Chile. *Geophysical Research Letters* 37, L02708.
- Osorio, C., Bahamonde, N., Lopez, M.T., 1967. El Limanche [*Emerita analoga* (Stimpson)] en Chile. *Boletín Museo Nacional de Historia Natural* 29, 60–116.
- Quinn, G., Keough, M., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press.
- Saavedra, N., 1980. La presión y la dirección del viento en Concepción. *Tralka* 1, 153–162.
- Saavedra, N., Foppiano, A.J., 1992. Contribución a la cinemática del anticiclón del Pacífico sur. *Geoaeta* 19, 95–110.
- Short, A.D., 1996. The role of wave height, slope, tide range and embaymentisation in beach classification: a review. *Revista Chilena de Historia Natural* 69, 589–604.
- Short, A.D., 1999. *Handbook of Beach and Shoreface Morphodynamics*. John Wiley, London, p. 379.
- Sobarzo, M., Bravo, L., Donoso, D., Garcés-Vargas, J., Schneider, W., 2007. Coastal upwelling and seasonal cycles that influence the water column over the continental shelf off central Chile. *Progress in Oceanography* 75, 363–382.
- Sobarzo, M., Garcés-Vargas, J., Bravo, L., Tassara, Andrés, Quiñones, R.A., 2012. Observing sea level and current anomalies driven by a megathrust slope shelf tsunami: the event on February 27, 2010 in central Chile. *Continental Shelf Research* 49, 44–55.
- Soto-Mendoza, S., Castro, L.R., Llanos-Rivera, A., 2010. Variabilidad espacial y temporal de huevos y larvas de *Strangomera bentincki* y *Engraulis ringens*, asociados a la desembocadura del río Itata, Chile. *Revista de Biología Marina y Oceanografía* 45 (3), 471–487.
- Subramoniam, T., Gunamalai, V., 2003. Breeding biology of the intertidal sand crab, *Emerita* (Decapoda: Anomura). *Advances in Marine Biology* 46, 91–182.
- Underwood, A.J., 1997. *Experiments in Ecology: Their Logic Design and Interpretation Using Analysis of Variance*. Cambridge University Press.
- Vigny, C., Socquet, A., Peyrat, S., Ruegg, J.-C., Métois, M., Madariaga, R., Morvan, S., Lancieri, M., Lacassin, R., Campos, J., Carrizo, D., Bejar-Pizarro, M., Barrientos, S., Armijo, R., Aranda, C., Valderas-Bermejo, M.-C., Ortega, J., Bondoux, F., Baize, S., Lyon-Caen, H., Pavez, A., Vilotte, J.P., Bevis, M., Brooks, B., Smalley, R., Parra, H., Baez, J.-C., Blanco, M., Cimbaro, S., Kendrick, E., 2011. The 2010 Mw 8.8 Maule Megathrust earthquake of central Chile, monitored by GPS. *Science* 332, 1417–1421.
- von Ende, C.N., 2001. Repeated measures analysis: growth and other time-dependent measures. In: Scheiner, S.M., Gurevitch (Eds.), *Design and Analysis of Ecological Experiments*, second ed. Oxford University Press, pp. 134–157.
- Yannicelli, B., Castro, L.R., Schneider, W., Sobarzo, M., 2006. Crustacean larvae distribution in the coastal upwelling zone off central Chile. *Marine Ecology Progress Series* 319, 175–189.