Annual cycle of growth and population structure of the estuarine crab *Hemigrapsus crenulatus* (Brachyura: Varunidae) off central Chile

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Abstract

Estuaries and saltmarshes play a fundamental role in the life cycle of many crab species. Diverse studies show that temperature and salinity modulate abundance, size frequency distribution (SFD), sex ratio and growth in crustaceans. These population parameters are usually challenging to estimate due to the high environmental variability of estuaries. Monthly samples of the estuarine crab *Hemigrapsus crenulatus* were taken from October 2003 to October 2004 (except July 2004) in the Tubul estuary, central Chile. We quantified temporal changes in abundance, size distribution, sex ratio and monthly growth through the annual cycle. A total of 1025 individuals were collected. Sizes ranged from 7.72–33.51 mm carapace length (CL) with a growth rate ranging between 2.13–30.5% mm CL mo^{-1}. Size and growth rates were greater in spring-summer, suggesting a faster growth of younger crabs correlated with increasing sea temperatures in the austral summer. Overall, sex ratio was 1.75:1 in favour of males. Modal analysis identified at least seven cohorts cohabiting throughout the annual cycle. Growth parameters for males and females were the following, respectively: $L\infty = 33.6$ and 29.6, $k = 0.69$ and 0.91, $t_0 = -0.39$ and -0.28. Changes in size distribution suggested a recruitment period during autumn and winter seasons when there are lower salinities and temperature fluctuations stresses. Generalized linear models indicated that sea temperature, salinity and chlorophyll were the environmental variables that better predicted the annual patterns in the population structure.

Introduction

Estuaries and saltmarshes have been recognized worldwide as highly productive ecosystems, harbouring a great biodiversity (Kristensen, 2008; Potter *et al.*, 2015; Julian & Osborne, 2018). Estuarine ecosystems are characterized by high variability in environmental parameters (Urbina *et al.*, 2010) over short time scales as a result of changing tidal levels and over long time scales as a result of water inputs from rivers and precipitation (Montagna *et al.*, 2018). Variability in factors such as temperature, salinity and oxygen in substrates and the water column can result in drastic changes in the estuary conditions (Kerner, 2007; Luppi *et al.*, 2013; Montagna *et al.*, 2018; Murrell *et al.*, 2018).

Estuarine systems are especially important habitats for crabs, as many crab species can play key roles in structuring the communities in which they live (Botto & Iribarne, 2000; Kristensen, 2008; Poore *et al.*, 2012). Also, they perform diverse trophic roles from potential prey to higher consumers (Brousseau *et al.*, 2001; Kim & O'Connor, 2007; Grabowski *et al.*, 2008; Hulathduwa *et al.*, 2011). They are also important inter-specific and intra-specific competitors (Brockerhoff & McLay, 2005; Hulathduwa *et al.*, 2011; Cannicci *et al.*, 2018) and can be modulators of ecosystem functions and associated services (Martinetto *et al.*, 2016). Estuarine crabs have high osmoregulatory and physiological plasticity, allowing them to adapt to a wide variety of environmental stressors (Corotto & Holliday, 1996; Bas & Spivak, 2000; Bianchini *et al.*, 2008; Urzua & Urbina, 2017; Urzua *et al.*, 2018; Theuerkauff *et al.*, 2018).

Living systems such as populations and communities are highly dynamic and likely to experience frequent changes in their organization and structure (Datry *et al.*, 2014). As the natural variability of habitats can affect species' fitness, one could expect decapod, and particularly crab life history patterns to respond to environmental (e.g. salinity, temperature and oxygen) and ecological factors (e.g. competition, predation, mortality and food availability) by exhibiting differences in size frequency distributions (SFD), sex ratios, reproductive periods, size of maturity and recruitment (Lardies *et al.*, 2004; Posey *et al.*, 2005; Spivak *et al.*, 2016; Vina *et al.*, 2018), as well as migratory movements, lifespan, physiology and growth rates
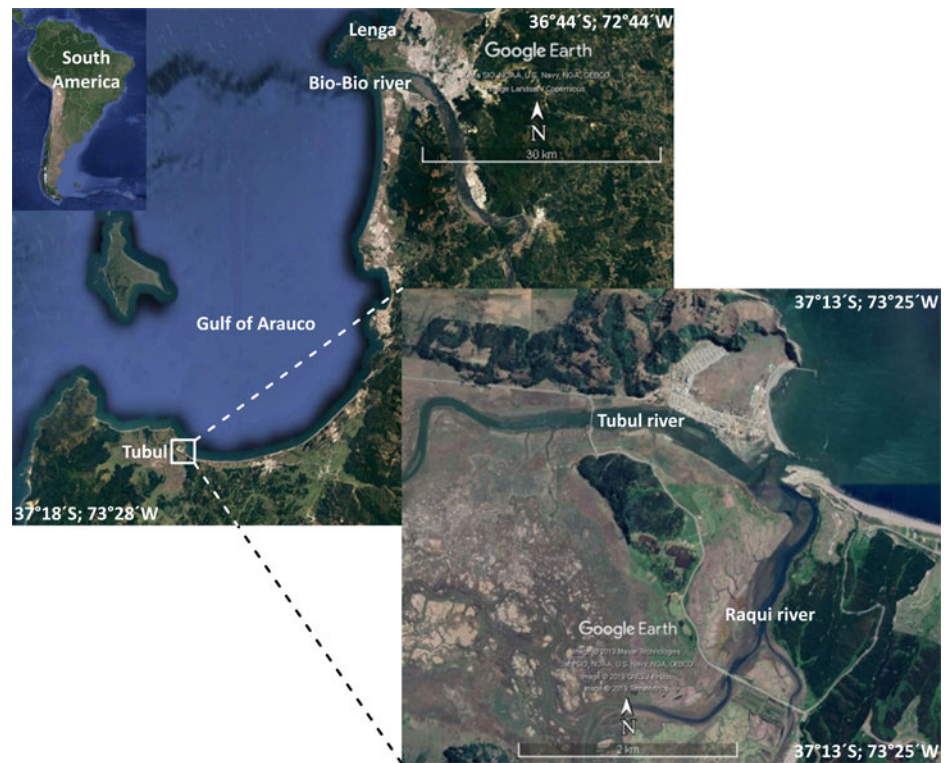
Fig. 1. Map of the study site: Tubul estuary (South America, Chile). Square indicates sampling site.

(Baeta *et al.*, 2005; Posey *et al.*, 2005; Koolkalya *et al.*, 2006; Lagos *et al.*, 2014; Theuerkauff *et al.*, 2018; Bas *et al.*, 2019). Depending on the environment and species, these effects can be expressed equally or differentially in males, females, ovigerous females and juveniles (Bas *et al.*, 2005; Posey *et al.*, 2005; Taylor & Seneviratna, 2005).

Hemigrapsus crenulatus (H. Milne Edwards, 1837) (Brachyura, Varunidae) is among the most conspicuous inhabitants of intertidal and estuarine environments in the SE Pacific, distributed in Chile from 18°–55°S and also in New Zealand (McLay *et al.*, 2011; Vega-Aguayo *et al.*, 2018). While the important ecological and physiological traits of *H. crenulatus* have been well-documented (Retamal, 1981; Stuardo *et al.*, 1993; Haye & Ojeda, 1998; Brockerhoff & McLay, 2005; Taylor & Seneviratna, 2005; Riquelme-Bugueño, 2006; Retamal & Moyano, 2010), few studies have focussed on their population dynamics (i.e. abundance throughout the year and growth). Additionally, there is scant information on the biological processes determining their population structure and productivity.

The Tubul and Raqui rivers form an intertidal marsh-type estuary of coastal origin with a marked seasonal variability coming from the pluvial regime. There is a strong salinity gradient because of the transition between inland and coastal marine waters with mixohaline conditions of high biological productivity (Valdovinos *et al.*, 2017). Between autumn and spring months (i.e. April–September), there is cold and humid weather with precipitation reaching 1300 mm annually. In contrast, during summer periods (i.e. December–March) there is a slight dry season with a strong influence of southern winds which promote coastal upwelling and changes in the sea temperature, salinity and chlorophyll (Valle-Levinson *et al.*, 2003; Landaeta and Castro, 2006; Valdovinos *et al.*, 2017).

The objective of this study was to describe the population dynamics of the dominant estuarine crab *H. crenulatus* in the Tubul estuary. We sought to describe and estimate the following for *H. crenulatus*: (1) the annual pattern in abundance, size structure and sex ratios, (2) the absolute growth pattern, and (3) the relationship of population traits with environmental variation.

We hypothesized that *H. crenulatus* population structure is better explained by the influence of salinity and temperature in the Tubul estuary. In particular, recruitment of crabs is hypothesized to occur during austral autumn and winter seasons when there are lower salinity and temperature fluctuations, while faster growth will occur during austral summer.

Materials and methods

Study area

The Tubul river estuary, located at the southern area of the Gulf of Arauco (37°14′S 73°27′W, Figure 1), is characterized by a highly seasonal and productive embayment, frequently impacted by upwelling waters (Valle-Levinson *et al.*, 2003; Landaeta & Castro, 2006). It is ~17–19 km long, with tidal influence along the first 6 km from the mouth. The river bed is composed of very fine sand with anoxic mud in areas of limited circulation. Gastropods; bivalve shells; algae, mainly *Gracilaria chilensis* (Bird, McLachlan & Oliveira, 1986); and codgrass, mainly *Spartina densiflora* (Brongn, 1829) and *Sarcocornia fruticosa* (L.) (Scott, 1977) are common components of its food web (Alveal, 1988; Stuardo *et al.*, 1993).

The abiotic environment in the Tubul River and adjacent area of the Gulf of Arauco during the study is shown in Figure 2. The temperature pattern in the estuary demonstrated a clear austral summer peak and a winter low. Values above 15°C are typical from November–March. Low temperatures predominated during the rest of the year (Figure 2a). Salinity was far more variable, with multiple peaks over 34, due to the strong marine influence on the estuary. Lower salinities were around 32. Next to the estuary in the Gulf of Arauco, temperature variability presented a clear annual cycle with maximum values during austral spring-summer seasons. Satellite temperature variability during the study period presented a similar pattern to that of *in situ* temperature values inside the estuary. Furthermore, this variability is concordant with long-term climatology (Figure 2b). Chlorophyll variability
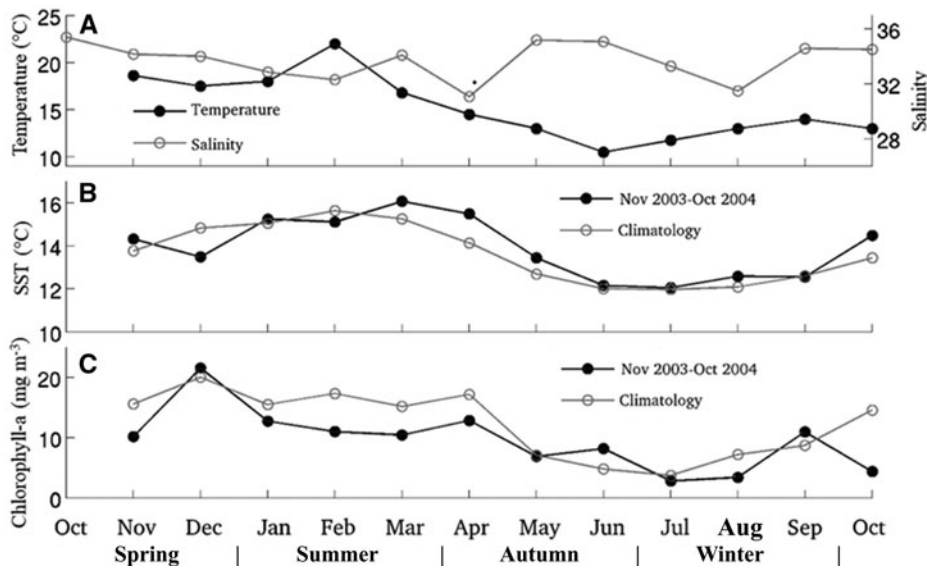
Fig. 2. Annual variations of (a) sea surface temperature (°C) and salinity from October 2003 to October 2004 in the Tubul estuary. (b) MODIS SST during the study period (Nov 2003–Oct 2004) and climatology (2002–2010). (c) MODIS chlorophyll during the sampling period (Nov 2003–Oct 2004) and climatology (2002–2010).
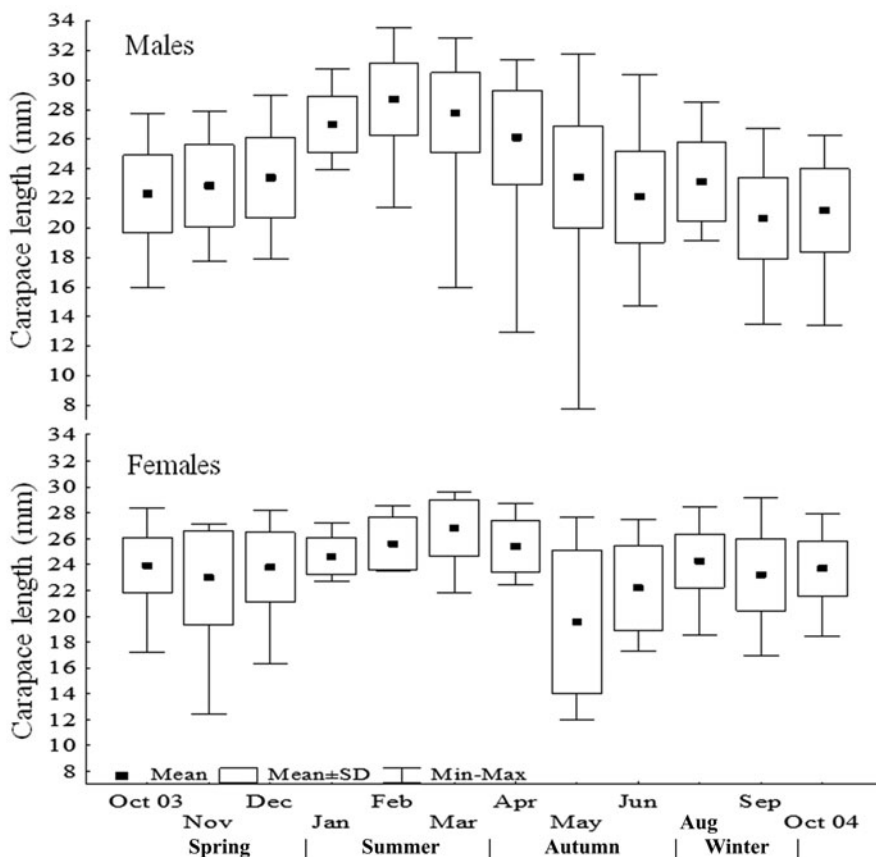

Fig. 3. *Hemigrapsus crenulatus*. Monthly variability in the sizes for males and females from October 2003 to October 2004 (except July 2004) in the Tubul estuary.

followed the temperature trend, with peaks during austral spring-summer time (Figure 2c).

Sampling and statistical analysis

Monthly samples of *H. crenulatus* were taken with a 30 min tow of a 25 cm-diameter, 0.4 cm mesh size net from October 2003 to October 2004 (except July 2004). Sampling was allocated to randomly selected transects parallel to the coastline and performed at low tide. All samplings (N = 12) were carried out at 0.5 m depth on the sandy bottom directly from the mouth of the estuary. The 30 min tow sample was equivalent to 200 m² of bottom surface. Once collected, samples were preserved in alcohol (~70%) for later analysis. Additionally, *in situ* sea surface temperatures were recorded with a thermometer, and 0.5 l water samples were taken from sea surface at the start of tows in order to determine salinity in the laboratory. Further, considering the strong influence of the adjacent Gulf of Arauco on the estuary, the broader climatology including satellite sea surface temperature (SST, °C) and chlorophyll-*a* (Chl-*a*, mg m⁻³) with high-resolution procedures (1 km) were processed and estimated using NASA software SeaDAS 6.0 (http://seadas.gsfc.nasa.gov/). Mean climatology (2002–2010) and seasonal evolution during the sampling period in an area of 10 × 10 km next to the estuary are shown in Figure 2.

In the laboratory, carapace length (CL) of each crab was measured with a digital calliper (to nearest 0.02 mm). Sex was
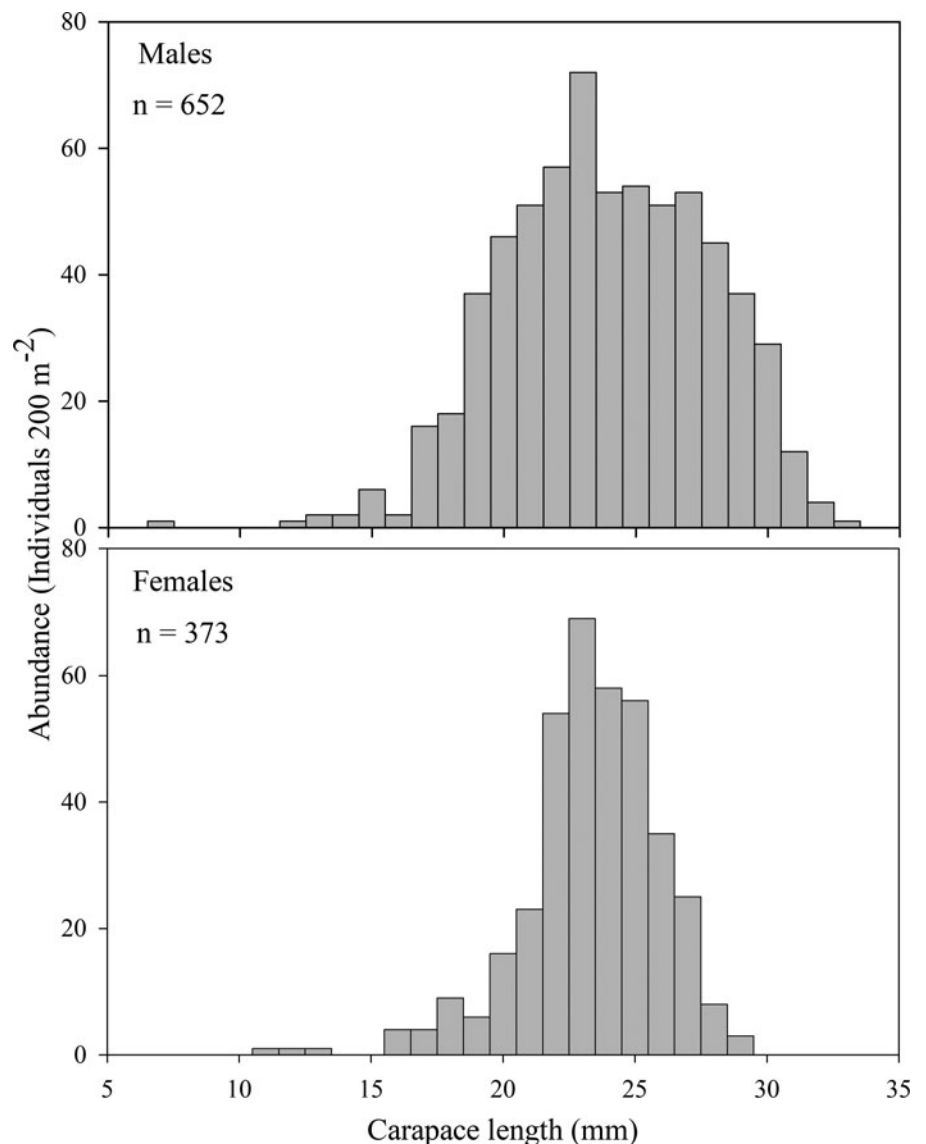
Fig. 4. *Hemigrapsus crenulatus*. Overall size frequency distribution from October 2003 to October 2004 (except July 2004) in the Tubul estuary.

determined by inspection of its secondary sexual characters (abdomen and pleon). All individuals were classified into one of three categories: males, females and ovigerous females (carrying eggs). Differences between mean sizes of males and females for the total period were tested with the Student's *t*-test. The abundance of *H. crenulatus* in the study site was standardized per area (individuals/200 m²).

For SFD analysis, crabs were arranged into 26 size classes (1-mm each class interval), from 7–33 mm CL, according to both minimum and maximum sizes observed. Normality in the size distributions was checked with the Kolmogorov–Smirnov test (KS) (Zar, 1999).

Temporal variations and per-size classes in sex ratio were evaluated by deviations between observed and expected sex ratios (1:1), using the G test to determine their significance (Sokal & Rohlf, 1997).

Monthly length–frequency distributions of collected individuals were plotted, and growth patterns were determined in two ways. The preferred approach was to use a modal progression analysis (MPA), using SFD. Sub-annual individual cohorts were identified from SFD by MPA using the FISAT II software package (Gayanilo *et al.*, 2006) (version 1.2.2.; FAO-ICLARM (Stock Assessment Tools and International Centre for Living Aquatic Resources Management)). Modal distributions were separated from SFD using this method, which assumes that the components are normally distributed (Bhattacharya, 1967). These underlying

distributions can be identified as a series of two or more points defining a regression line with a negative slope when logarithms of the ratios of successive frequencies are plotted against the corresponding midpoints (Gayanilo *et al.*, 2006). Two criteria were used to identify the modes: (a) the separation index (SI), a ratio of the difference between the means of the components and their standard deviations (components showing SI greater or equal to two were considered meaningfully separated); (b) confidence interval of correlation coefficients (r^2) of regression lines. When sufficient degrees of freedom were available, the χ^2 test was performed to indicate how well expected frequencies fitted the observed ones. When small cohorts could not be identified clearly by MPA, we highlighted those on histograms by using the eye fitting method (Chan & Williams, 2004). Sub-annual cohorts were defined when at least two monthly length modes were present and used to provide estimations of instantaneous relative growth rate (IRG), modified from Botter-Carvalho *et al.* (2007), and defined as

$$IRG = \frac{Ln(ML_2) - Ln(ML_1)}{t_2 - t_1} \times 100$$

where, ML_2 and ML_1 are mean length at time 2 and 1, respectively, calculated from MPA and $t_2 - t_1$ = elapsed time in months. IRG is expressed as a percentage of length per time period (%mm mo^{-1}).
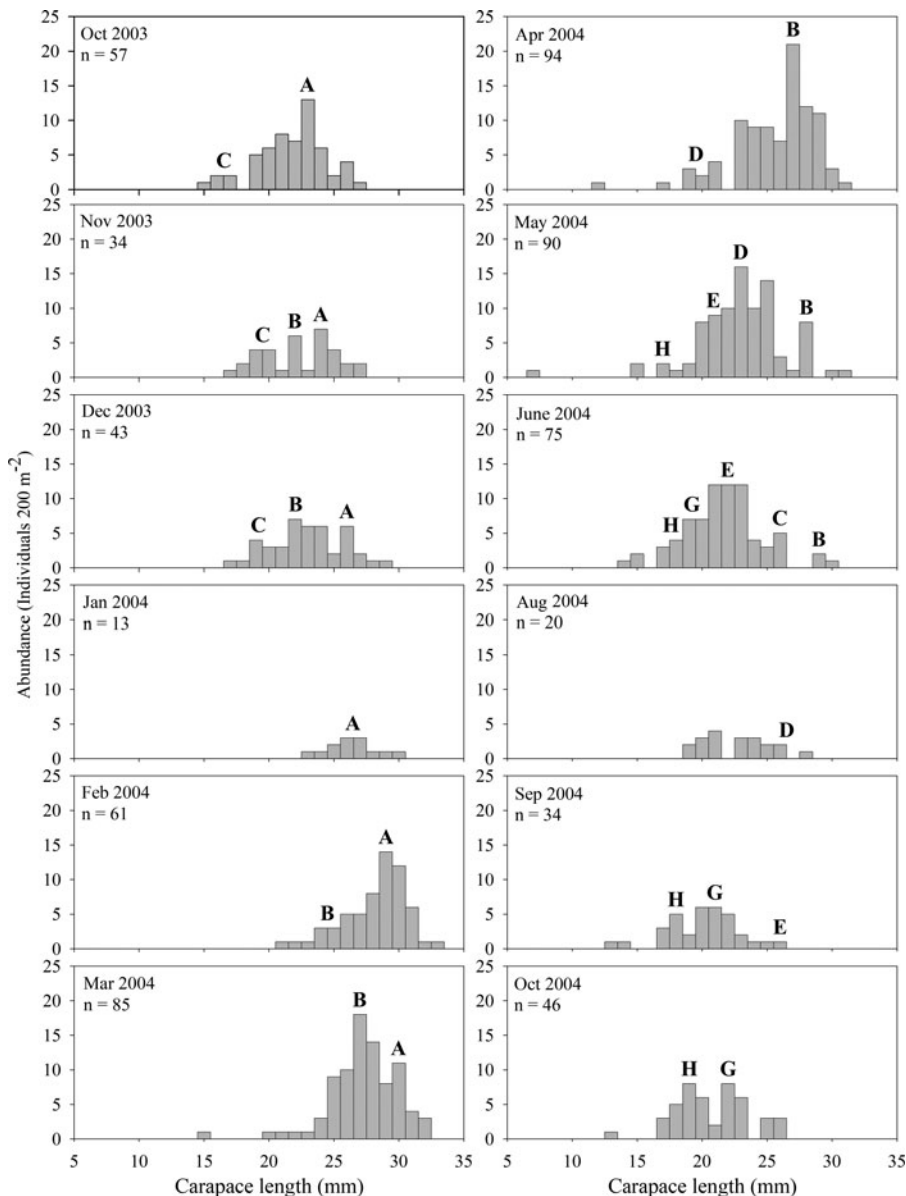
Fig. 5. *Hemigrapsus crenulatus*. Monthly size frequency distribution for males from October 2003 to October 2004 (except July 2004) in the Tubul estuary. Letters indicate the cohorts identified by FISAT.

However, when this was not possible, the von Bertalanffy growth equation was fit to the SFD data. Growth parameters were described with the von Bertalanffy growth model (von Bertalanffy, 1938) for all data sets from SFD using a version of the ELEFAN method (Pauly, 1987) included in the automatic routine of the LFDA software package (Kirkwood *et al.*, 2001) (Length Frequency Distribution Analysis, version 5.0.; MRAG (Marine Resources Assessment Group Ltd)). The von Bertalanffy growth equation is described by,

$$CL_t = CL_\infty \left[1 - e^{-k(t-t_0)} \right]$$

where CL_∞ is the asymptotic size (in mm, that is the mean length a given population would reach if they were to grow indefinitely), k is the constant of annual growth (rate of dimension time^{-1} at which CL_∞ approached), t is the age (in years) and t_0 is the theoretical age at zero length if the population had always grown according to the equation. When it was not possible to estimate some parameter for this method (LFDA), we proceeded to use the routine ELEFAN I included in FISAT II. Furthermore, the growth performance index Φ ($\Phi = 2 \log L\infty + \log k$) (Munro & Pauly, 1983) was employed to compare growth parameters

obtained in the present work with those reported by Retamal (1969) in the Lenga estuary, central Chile.

Generalized linear models (GLM) and linear regressions were applied to statistically test the relationship between growth parameters/patterns with environmental variation. Statistica 12 was used for all calculations with significance level set at 0.05.

Results

Size frequency distributions

A total of 1025 specimens of *H. crenulatus* were collected, of which 652 were males (63.61%), 362 females (35.32%) and only 11 ovigerous females (1.07%). However, ovigerous females were collected all along the year: four specimens in October 2003, two in November 2003, two in December 2003, one in April 2004, one in May 2004 and one in October 2004. All ovigerous females collected were brooding early stage (orange) eggs. Abundance ranged from 30 to 150 individuals 200 m^{-2}.

The monthly size structure for *H. crenulatus* is described in Figure 3. Mean size in males varied from 22.3 mm (October 2003) to 28.71 mm (February 2004), before again decreasing to 21.19 mm CL (September 2004). In females, mean size varied
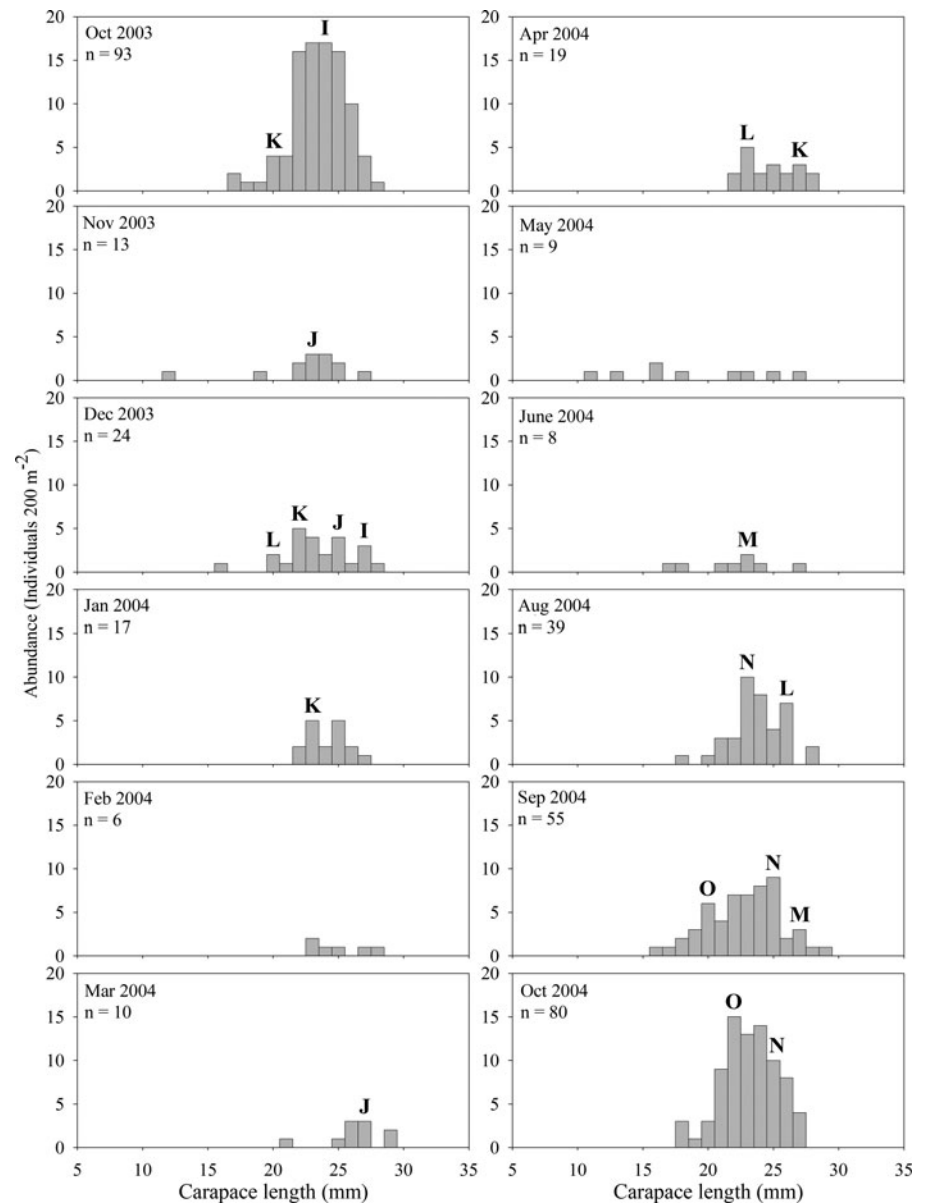
Fig. 6. *Hemigrapsus crenulatus*. Monthly size frequency distribution for females from October 2003 to October 2004 (except July 2004) in the Tubul estuary. Letters indicate the cohorts identified by FISAT.

from 22.97 mm (November 2003) to 26.83 mm (March 2004), decreasing to 19.54 mm CL (May 2004).

Sizes of males ranged from 7.72–33.51 mm CL, with an average of 24.06 ± 2.63 (± SD) mm CL. Sizes of females ranged from 11.97–29.58 mm CL, averaging 23.84 ± 1.85 mm CL. Mean sizes did not differ significantly among sexes (t test; $t_{0.05}$; $1012 = 0.23$; $P = 0.82$). Males attained larger sizes than females did, 33 mm and 29 mm CL, respectively (Figure 4). Normality analysis showed normal distribution in males (KS test; $d = 0.040$; $P > 0.2$), but not in females (KS test; $d = 0.077$; $P < 0.05$). Due to the low number of ovigerous females, the normality analysis was not carried out on this population group.

In males, monthly SFD were mostly polymodal (Figure 5). Multiple modes were observed in the population from November 2003 to January 2004 and from August–October 2004. The monthly pattern in size distribution observed in females contrasts with that found in males (Figure 6). Females were most abundant during the austral spring months (August–October), with few individuals collected at other times of the year. During May 2004, the smallest size was observed for males (i.e. 7.7 mm CL) indicating probably the main recruitment period. A similar pattern was observed when male and female data were combined with subtle differences compared with separate sex histograms (Figure 7).

Sex ratio

Sex ratios are shown in Table 1. The overall sex ratio as a function of time was 1.75:1 favouring males, significantly different from the expected 1:1 (G test; $G_{0.05}$; $1 = 76.43$; $P < 0.05$). The sex ratio was highly variable through the year. It was male-biased, from November to December 2003, and from February to June 2004. In contrast, the sex ratio was female-biased in October 2003, January 2004 and from August to October 2004. However, when examining sex ratios by size classes, it was found that they were significantly male-biased at 17, 19–21 and 27–29 mm size classes (G test; $P < 0.05$).

Growth patterns

The MPA identified the presence of sub-annual cohorts during the study period: seven cohorts in males (A–H, Figure 8a) and seven in females (I–O, Figure 8b). In males, at least two of the identified cohorts (A and B) were based on coherence of six monthly modes. The remaining cohorts (C–H) represent fewer modes (between three and four). Cohorts A, B and C were followed for the longest duration. The number of cohorts identified in any single month varied. For example, in May and June 2004,
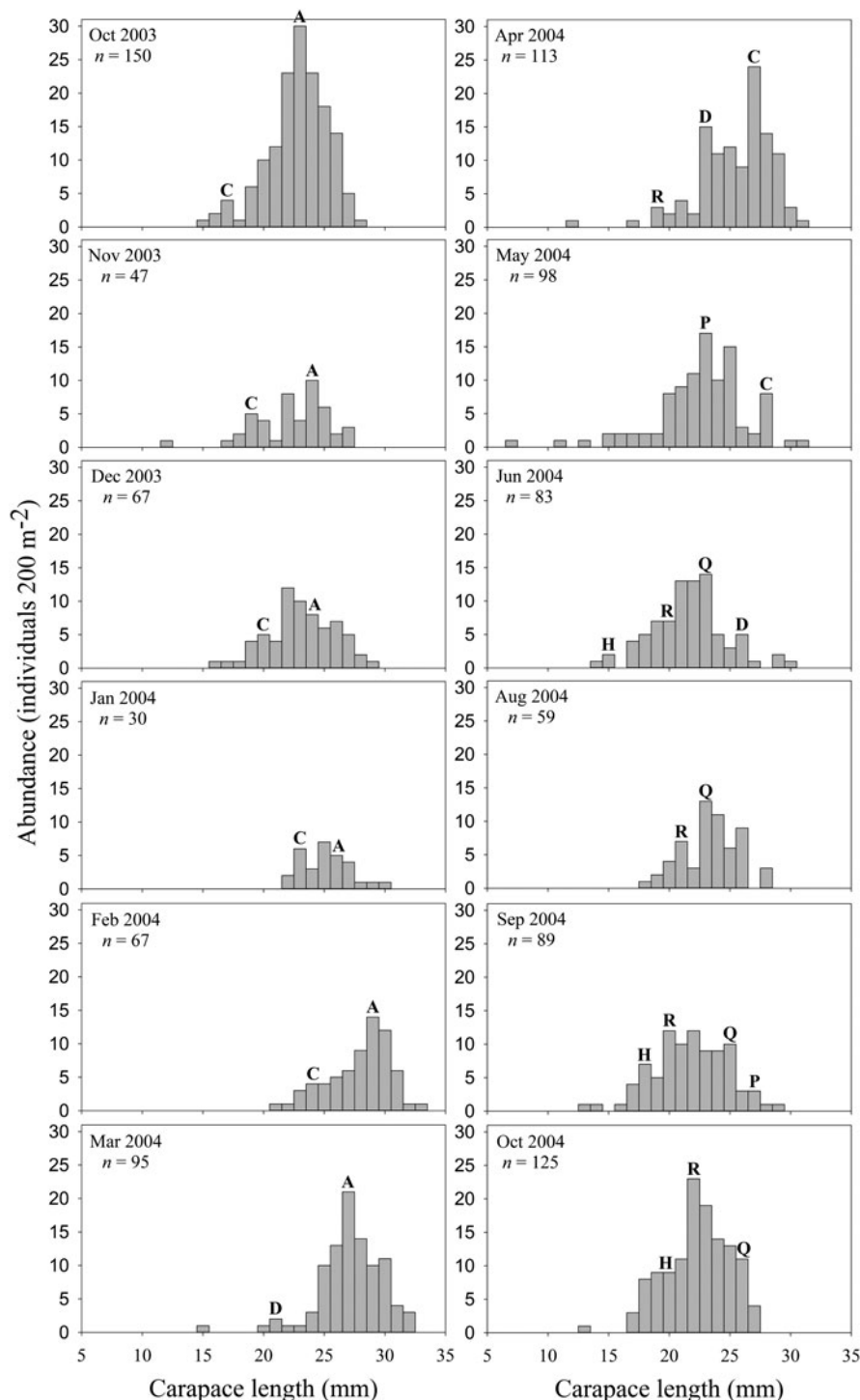
Fig. 7. *Hemigrapsus crenulatus*. Monthly size frequency distribution for males and females (combined) from October 2003 to October 2004 (except July 2004) in the Tubul estuary. Letters indicate the cohorts identified by FISAT.

four cohorts were identified, whereas only two were identified in April 2004. For females, the seven cohorts identified were tracked for only short periods. Cohort K was tracked for the longest time (from October 2003 to April 2004). However, in accordance with the modes identified in December 2003, at least four different groups of age classes coexisting in that month can be inferred. Due to low numbers of small individuals (<7–12 mm CL), it was not possible to determine with precision and confidence the recruitment period of the identified cohorts based on the data presented here. Figure 8c shows seven cohort progressions when male and female data were combined. This consistency in the observed patterns was more evident for the cohorts identified from October 2003 until May 2004 (cohorts A, C and D) whereas

for the remainder of period 3 cohorts were reshaped although keeping a similar trend (Figure 8c).

The observed *vs* expected normal distributions from MPA were neither significantly different in males nor females (χ^2 test; $P > 0.5$) and presented well-separated modal groups (SI > 2), except values found in November 2003, October 2004 and January 2004 (Table 2). Growth estimates for females are less reliable than those for males, as a smaller number of females were sampled (Table 2).

The IRG ranged from 2.13–30.5% mm CL mo^{-1} for males and from 3.45–11% mm CL mo^{-1} for females (Table 3). The IRG estimates varied within cohorts, particularly in males (Table 3). The average IRG values for the study months for males and females

Table 1. Sex ratio (by month and size class) of *Hemigrapsus crenulatus* collected between October 2003 and October 2004 (except July 2004) from Tubul estuary, central Chile

| Months | Carapace length (mm) | | | | | | | | | | | | | Total |
	17	18	19	20	21	22	23	24	25	26	27	28	29	
Oct 03	n.c.	n.c.	2.91	0.4	1.36	3.62	0.53	**5.48**	**12.39**	2.66	1.93	n.c.	n.c.	**0.61**
Nov	n.c.	n.c.	1.92	n.c.	n.c.	2.09	1.05	1.65	0.68	n.c.	0.34	n.c.	n.c.	**2.61**
Dec	n.c.	n.c.	n.c.	0.2	1.05	0.33	0.40	2.09	0.68	**3.96**	0.2	n.c.	n.c.	**1.79**
Jan 04	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	2.91	0.34	1.33	0.2	1.05	n.c.	n.c.	0.76
Feb	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	0.34	1.05	1.05	n.c.	2.91	**6.2**	n.c.	**10.17**
Mar	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	**7.36**	3.98	**11.89**	n.c.	**3.85**	8.5
Apr	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	1.7	**4.82**	3.14	2.94	**15.19**	7.92	n.c.	4.95
May	n.c.	n.c.	n.c.	n.c.	n.c.	**8.55**	**15.96**	n.c.	**13.45**	n.c.	n.c.	n.c.	n.c.	10
Jun	1.05	1.93	n.c.	n.c.	**10.97**	**10.97**	**7.92**	1.93	n.c.	n.c.	n.c.	n.c.	n.c.	9.37
Aug	n.c.	n.c.	n.c.	1.05	0.143	n.c.	**3.98**	2.36	0.68	2.94	n.c.	0.34	n.c.	**0.51**
Sep	1.05	1.33	0.2	n.c.	0.403	0.33	2.94	6.2	**7.36**	0.34	n.c.	n.c.	n.c.	**0.62**
Oct	n.c.	0.50	**6.19**	1.02	**4.82**	2.16	2.64	n.c.	**3.98**	2.36	n.c.	n.c.	n.c.	**0.57**
Overall	**4**	2	**6.16**	**2.87**	**2.22**	1.06	1.04	0.91	0.96	1.46	**2.12**	5.63	12.33	1.75

Numbers in bold are statistically significant and different from 1:1 ratio (test *G*; *P* < 0.05). Values >1 are in favour of males and <1 are in favour of females. n.c., not computed.
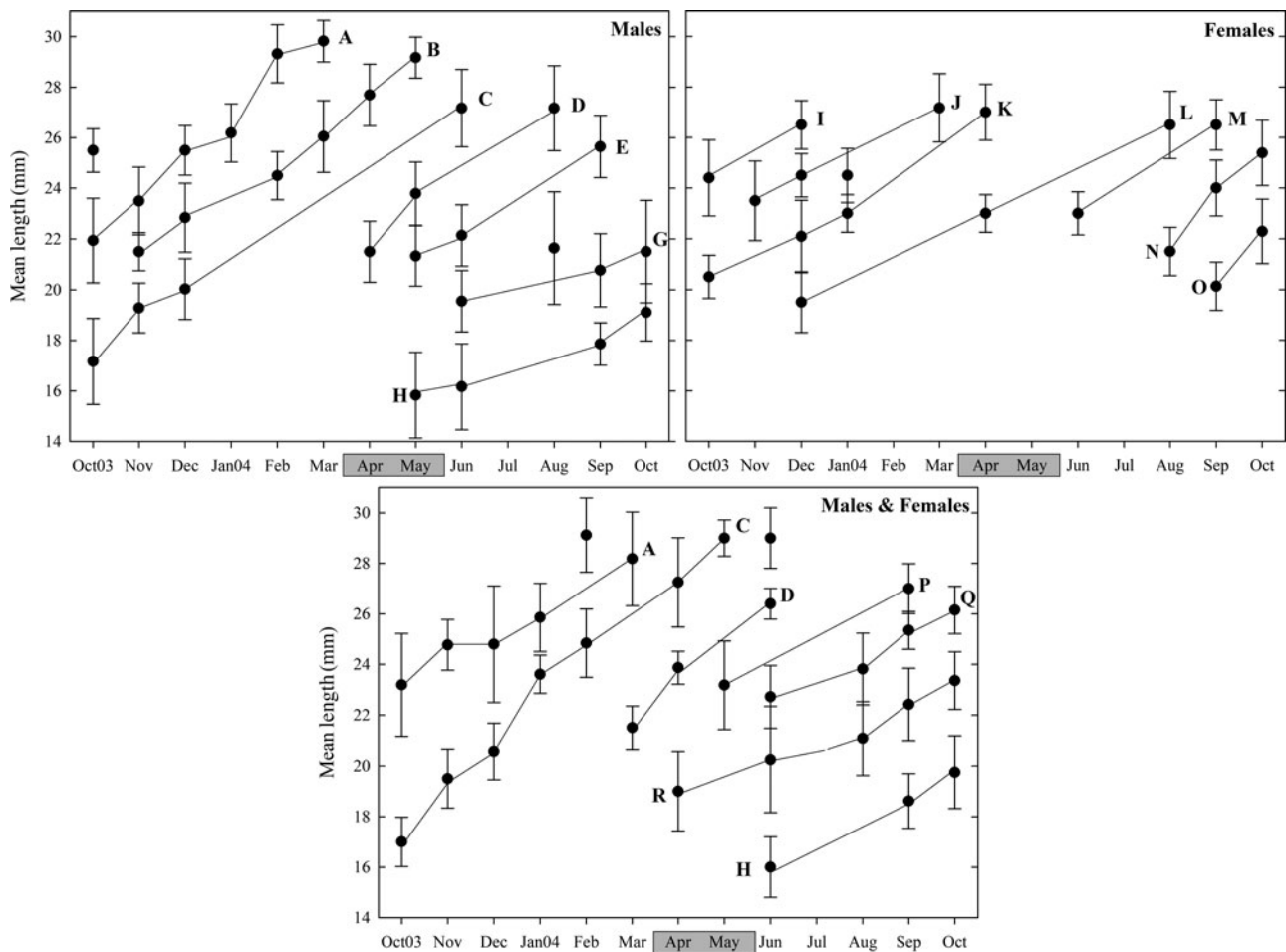
Fig. 8. *Hemigrapsus crenulatus*. Temporal growth patterns of sub-annual cohorts identified for males (A–H) and females (I–O), and males and females combined (lower panel) from October 2003 to October 2004 (except July 2004) in the Tubul estuary. Modes (mean length ± SD) were estimated from SFD using the Bhattacharya method. Grey rectangle indicates probable recruitment period based on this data.

were significantly different, showing a higher growth rate in males than in females during the study period. There were also sex-specific seasonal differences in growth (±3.66 SD for males and ±1.96 SD for females, Table 3).

The asymptotic length (CL∞), growth rates (k) and performance index (Φ) differed based on sex and study area, i.e. Lenga (Retamal, 1969) and Tubul estuaries (this study) (Table 4). The maximum observed lengths (CL$_{max}$) were similar for males but different in females from each study area. The values of t_0 were similar, except those calculated by Retamal (1969) for females (Table 4). The lifespan (t_{max}) was similar between study areas, ranging between 4.16 (50 months) and 4.37 years (52 months) for males and 2.16 (26 months) and 3.29 years (39 months) for females (Retamal, 1969 and this study, respectively).

Annual patterns and environmental relationships

Generalized linear models (GLM) were applied to establish what environmental variables had better predicted the annual structure of *H. crenulatus*. Sea temperature and salinity were correlated with *H. crenulatus* CL, with no difference between sex, and Chl-*a* correlated with per cent increments in *H. crenulatus* IGR (Table 5). Additionally, when analysing the annual cycle of sea temperature, this physical variable showed the same temporal pattern as observed in average carapace lengths (Figure 9a), and both variables revealed a significant correlation ($r^2 = 0.45$; $P < 0.024$; Figure 9b).

Discussion

We have described the dynamics of size structure, sex ratio and growth of the *H. crenulatus* population at the Tubul estuary during a one-year period. The relatively low abundance of ovigerous females and small juveniles (<7 mm CL; Retamal, 1969) limits the scope of inference that can be drawn from this study, likely showing that a portion of the population was missed in the sampling.

Differences in the abundance and sex ratio between Lenga and Tubul estuaries can be explained by the different sampling methodology used by the authors and/or environmental differences of the study sites and consequently, exposure of the crabs to the sampling (e.g. juvenile and ovigerous females) (e.g. Johnson, 2003). However, given the time and frequency of sampling, the data suggest a seasonal pattern in the population structure of this species, in terms of its abundance, SFD, sex ratio and growth parameters in the Tubul estuary. The Lenga and Tubul estuaries present similar physico-chemical characteristics (e.g. sea temperature and salinity) in seawater with predominance of fine sand (Díaz-Jaramillo *et al.*, 2010). On the other hand, the Lenga estuary has a higher content of organic matter than Tubul does, which has been suggested as an enrichment associated with hydrological dynamics (Moscoso *et al.*, 2006; Pozo *et al.*, 2011).

A clear sexual dimorphism was observed in *H. crenulatus*, with males attaining larger sizes than females. Retamal (1969) has previously reported this for this species in the Lenga estuary. In addition, the data trend towards males having greater size than that of females in summer months. Size differences may be a result of

Table 2. Modal progression analysis for males and females of *Hemigrapsus crenulatus* collected between October 2003 and October 2004 (except July 2004) from Tubul estuary, central Chile

Months		Males						Females				
	Ch	CL	SD	*N*	SI	r^2	Ch	CL	SD	*N*	SI	r^2
Oct 2003	1	17.17	1.7	9.62	n.a	0.75	1	20.5	0.85	10.19	n.a	1
	2	21.94	1.67	45.28	2.15	0.6	2	24.4	1.5	66.62	2.14	0.999
	3	25.5	0.86	4.49	2.09	1						
Nov	1	19.28	0.98	11.65	n.a	0.964	1	23.5	1.57	12.57	n.a	1
	2	21.5	0.75	7.18	2.05	1						
	3	23.5	1.34	12.82	**1.99**	1						
Dec	1	20.03	1.2	12.6	n.a	0.6	1	19.5	1.2	3.36	n.a	1
	2	22.84	1.36	24.25	2.02	0.716	2	22.09	1.43	17.74	2	1
	3	25.5	0.98	7.89	2.03	1	3	24.5	0.86	4.42	2.01	1
							4	26.5	0.96	4.19	2.01	1
Jan 2004	1	26.19	1.15	9.99	n.a	0.934	1	23	0.74	9.59	n.a	1
							2	24.5	1.07	7.37	**1.97**	1
Feb	1	24.5	0.95	8.3	n.a	1						
	2	29.32	1.15	43.72	2.21	0.978						
Mar	1	26.05	1.42	37.78	n.a	0.75	1	27.17	1.35	12.21	n.a	0.75
	2	29.82	0.82	23.57	2.11	1						
Apr	1	21.5	1.2	13.27	n.a	1	1	23	0.74	9.59	n.a	1
	2	27.69	1.22	56.97	2.33	0.744	2	27	1.11	8.53	2.18	1
May	1	15.83	1.7	6.45	n.a	0.75						
	2	21.33	1.19	33.91	2.3	0.76						
	3	23.79	1.25	45.25	2	0.407						
	4	29.17	0.81	12.64	2.26	0.75						
Jun	1	16.17	1.7	5.77	n.a	0.75	1	23	0.85	4.39	n.a	1
	2	19.55	1.21	22.56	2.05	1						
	3	22.14	1.21	39.79	2.02	0.857						
	4	27.17	1.53	12.82	2.2	0.75						
Aug	1	21.64	2.22	22.72	n.a	0.945	1	21.5	0.95	8.3	n.a	1
	2	27.17	1.68	3.98	2.14	0.75	2	26.5	1.33	25.39	2.24	1
Sep	1	17.86	0.84	11.02	n.a	1	1	20.13	0.95	14.83	n.a	1
	2	20.77	1.44	24.04	2.07	0.914	2	24	1.1	28.91	2.17	0.763
	3	25.65	1.23	3.19	2.2	1	3	26.5	1	3.92	2.03	1
Oct	1	19.11	1.13	23.35	n.a	1	1	22.29	1.27	48.87	n.a	0.999
	2	21.5	2.02	20.1	**1.93**	1	2	25.39	1.29	28.66	2.05	1

Ch, identified cohorts; CL, carapace length mean (in mm); SD, standard deviation of the mean length; N, number de specimens in each cohort; SI, separation index; r^2, determination coefficient. Numbers in bold represent not representatives distributions (SI < 2). n.a. = data not available. Expected and observed frequencies of the normal distributions were always not significant different (χ^2 test; $P > 0.5$).

sexual selection, which has been proposed in other Grapsidae and Varunidae crabs, where the requirement of males to maximize the probability of success when obtaining a mate has been proposed (Wenner, 1972; Hartnoll, 2001; Miyajima & Wada, 2017). Growth rates in males showed a seasonal pattern, supporting the idea of a temperature-sensitive size increment (see Table 5 and Figure 9); however, data for females do not clearly exhibit such a pattern, because of a probable trade-off between growth and reproduction (Adiyodi, 1988; Nelson, 1991). Several authors have described a lower growth rate in females of several decapod species, and it has been argued to be the result of shorter periods of somatic growth, lower increases in body size, and females not moulting once matured and reducing feeding during ovigerous stages (Schultz & Shirley, 1997; Johnson, 2003; Luppi *et al.*, 2004; Silva *et al.*, 2014). In nature, this lower feeding rate of ovigerous females is the result of an escape behaviour, as they remain hidden to avoid predation (Christy, 2007). Therefore, lower energy consumption and higher metabolic expenditure necessary during reproduction may directly impact the amount of energy available for body growth.

Seasonal migration is a natural process significantly influencing population dynamics (Chen *et al.*, 2014; Sicurella *et al.*,

Table 3. Instantaneous relative growth rate (IRG, in % mm CL mo^{-1}) for each sub-annual cohort for males and females of *Hemigrapsus crenulatus* collected between October 2003 and October 2004 (except July 2004) from Tubul estuary, central Chile

Cohorts	2003 Nov	Dec	2004 Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Oct	Average
Males												Average
A	6.87	8.17	2.67	11.29	1.69							6.14
B		6.05		3.51	6.13	6.12	5.66					5.49
C	11.59	3.82	30.49									15.3
D							10.12		4.43			7.27
E								3.73		4.91		4.32
F									5.08			5.08
G								2.13		8.35	3.45	4.64
H											6.76	6.76
Average	9.23	6.01	16.58	7.40	3.91	6.12	7.89	2.93	4.75	6.63	5.11	
Females												
I		4.13										4.13
J		4.17			3.45							3.81
K		3.74	4.04			5.34						4.37
L						4.13			3.54			3.83
M										4.72		4.72
N										11.00	5.63	8.32
O											10.19	10.19
Average		4.01	4.04		3.45	4.74			3.54	7.86	7.91	

Table 4. Growth parameters and performance index of *Hemigrapsus crenulatus*

	Lenga (36° 45′ S; 73° 10′ W) Retamal (1969)		Tubul (37° 14′ S; 73° 27′ W) This work	
	Males	Females	Males	Females
L_{∞} (mm)	44.40	43.10	33.60	29.60
k (year^{-1})	0.06	0.04	0.69	0.91
t_0 (year)	−0.44	−1.08	−0.39	−0.28
Φ	2.04	1.83	2.89	2.90
L_{max}[a] (mm)	34.2	28.4	33.51	29.58
t_{max}[b] (year)	4.16	2.16	4.37	3.29

In Retamal (1969) calculated from MPA. In this work: $t_{max} = 3/k$ (modified from Botter-Carvalho *et al*., 2007).
[a] Maximum length observed in the sample.
[b] Maximum age (lifespan or longevity) calculated in the sample.

2016). The absence of ovigerous females and spatial segregation of sexes and sizes might be explained by these phenomena. During summer, females and their embryos are exposed to temperature-induced physiological stress. Females try to avoid this stress by migrating towards deeper waters such as the river mouth, outside of the estuary or areas having food available in order to breed and/ or release larvae (Warman *et al*., 1993; Tankersley *et al*., 1998; Eggleston *et al*., 2015). Moreover, monthly SFD shows a polymodal pattern, suggesting the presence of several age groups in the population. The observed pattern of spatial segregation by sex and size with marked seasonality has been attributed in other crabs to migratory movements, associated with food availability and refuge; reproductive biology; and environmental factors (Spivak *et al*., 1994; Bas & Spivak, 2003; Bas *et al*., 2005; Luppi *et al*., 2013).

The lack of juvenile crabs was unusual in our study. Retamal (1969) reported juvenile stages during austral spring, summer and autumn. For Tubul, SFD analyses suggested that juvenile crabs might appear in austral autumn (April–May) when they accumulate, having a higher proportion in the population. Although unlikely, cannibalism has also been frequently observed by Retamal (1969), and it could be a factor here, as cannibals can regulate the recruitment of new cohorts within days of settlement (Moksnes, 2004). The most likely explanation, however, is the spatial segregation of this life history stage with megalopae settling in deeper waters or outside of the estuary and slowly migrating up the estuary as their osmoregulatory ability increases (Urzua & Urbina, 2017). Also, probably settling and growth of these stages occur under more favourable conditions present among algae, mussel beds or codgrass located in the subtidal zone until the juvenile stage to avoid intra- and inter-specific attacks (e.g. *Larus dominicanus* Retamal, 1969; Riquelme-Bugueño, 2006). Such a distribution would limit their vulnerability to the survey gear used here. Ontogenetic changes in habitat use during the species' life cycle of crabs such as nocturnal behaviour patterns or crypsis are alternative explanations (Carvalho-Batista *et al*., 2015).

Retamal (1969) did find significant deviations from a 1:1 sex ratio for populations of *H. crenulatus* (i.e. overall sex ratio of 1.9) from the Lenga estuary. Our study, on a different estuary, is in agreement with a similar overall sex ratio of 1.8. Percentages for males and females were very similar (i.e. 65.5 and 63.6% for males in the Lenga and Tubul estuaries, respectively) although with remarkable differences in abundances. However, our results indicate sex ratios favouring males from

Table 5. Generalized linear models performed on Carapace length (CL) and Instantaneous Growth Rate (IGR) as response variables in *H. crenulatus* and sea temperature (Temp), salinity (Sal) and chlorophyll-*a* (Chl-*a*) as predictor variables

	CL (mm)			IGR (% mm CL mo^{-1})		
Variable	df	Wald test	*P*-value	df	Wald test	*P*-value
Temp	1	5.072	0.024	1	0.956	0.328
Sal	1	7.466	0.006	1	0.449	0.503
Chla	1	2.577	0.108	1	12.904	0.000
Sex[a]	1	0.126	0.722			

For CL, normal distribution and identity-link function were used. For IGR, normal distribution and log-link function were used.
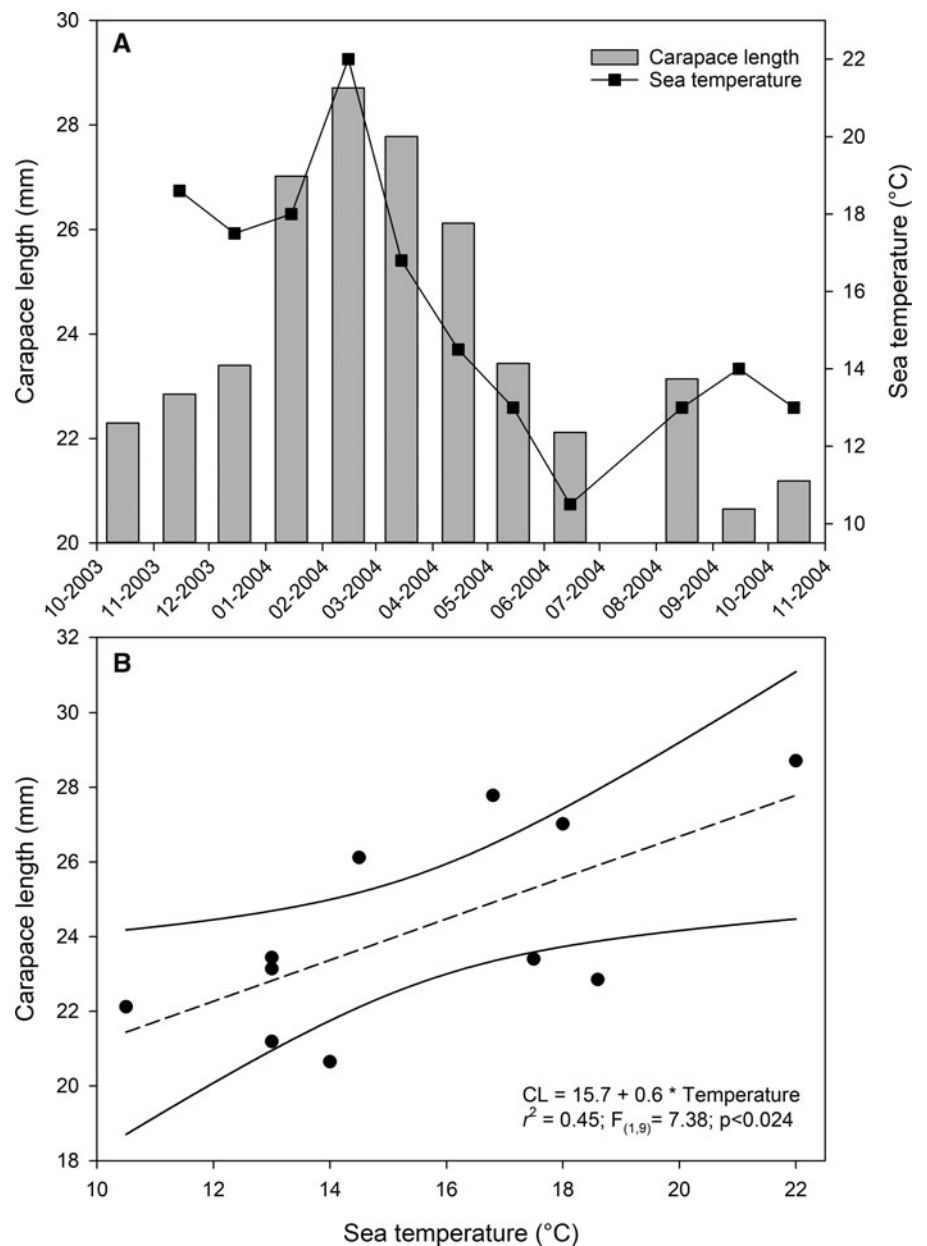[a]Only could be computed for CL as categorical predictor variable.

Fig. 9. (a) Temporal variation in *Hemigrapsus crenulatus* carapace length (CL) and sea temperature from October 2003 to October 2004 (except July 2004) in the Tubul estuary; (b) Linear regression between sea temperature and *H. crenulatus* CL (segmented line) showing 95% confidence intervals (continuous line). Regression equation and statistics are shown.

In the figure (b): CL = 15.7 + 0.6 * Temperature; $r^2 = 0.45$; $F_{(1,9)} = 7.38$; p<0.024

February–June 2004 and favouring females in the remaining period. Retamal (1969) did not find at any time sex ratios <1. Stocking density and the fact that various males court more than one female in the reproductive period can certainly affect the sex ratio in the field (Brockerhoff & McLay, 2005; Waiho *et al.*, 2015). Sex ratio without significant deviations from 1:1 can indicate that such a population is sexually active or has the same probability of finding mates, making that segment of the population more stable (Wenner, 1972; Leme & Negreiros-Fransozo, 1998). In the Lenga estuary, Retamal (1969) sampled 2822

individuals at the mouth of the estuary during low tide. The *H. crenulatus* collection was 2.8 times higher in the Lenga than in our study, and the sampling methodology was also different.

Values of maximum length observed were very similar to those presented by Retamal ([1969](#)). However, different values of L_∞, k and t_0 can be explained by differences in the abundance of individuals found in the study areas and for the methodology used by the authors (see Table 4). Differences in the index Φ can be explained, among other factors, by pollution, mortality, agent stressors and differences in the environmental conditions of the study site (Munro & Pauly, [1983](#)). Despite these differences, the index Φ has been largely accepted to be of great use to compare populations of a particular species from different regions. The Lenga estuary has been historically environmentally polluted (Díaz-Jaramillo *et al.*, [2010](#)), supporting the use and comparison of the index Φ.

Differences in abiotic conditions between the Lenga and Tubul estuaries during sampling were found at the same temporal scale (i.e. annual cycle) of sampling. For example, in the Lenga, sea temperature varied between 12.2–21.7°C (mean: 16.1 ± 3.6°C) while in the Tubul it ranged from 10.5–22°C (mean: 15.5 ± 3.3°C). Salinity ranged from 21–33.6 (mean: 29.6 ± 3.3) and 31.1–35.4 (mean: 33.7 ± 1.5) in the Lenga and Tubul, respectively. Rainfall ranged from 0.1–400.5 mm (mean: 127.5 ± 133.9 mm) in the Lenga and from 0.1–255 mm (mean: 92.5 ± 76.5 mm) in the Tubul. Statistical differences were found between estuaries in paired-records of salinity (*t*-test: 3.4; $P < 0.01$). This difference agrees with the fact that the Tubul estuary receives freshwater inputs only in the rainy season (Constabel, [1993](#)) in contrast to the Lenga estuary.

Hemigrapsus crenulatus is a good osmoregulator, able to regulate and balance water and ions over a wide range of environmental salinities (Urzua & Urbina, [2017](#)). Urzua *et al.* ([2018](#)) pointed out that *H. crenulatus* larvae were larger from eggs incubated at high salinity rather than at intermediate salinity. These authors, among others, suggested that salinity during early ontogeny could strongly influence postsettlement-early growth stages (Bas & Spivak, [2000](#); Bianchini *et al.*, [2008](#); Urzua *et al.*, [2018](#)).

On the other hand, the higher proportion of larger crabs during the austral summer could be correlated with sea temperature and salinity (Brylawski & Miller, [2006](#); Urzua & Urbina, [2017](#)), which may suggest higher capacity to adapt and exploit areas of the estuary than that of smaller crabs. Nevertheless, this correlation of larger crabs (i.e. average size) with sea temperature commonly reflects the proportion of the population sampled in the austral summer, which suggests a faster growth of younger crabs, producing a lower representation of small classes.

Conclusion

Acknowledging that our sampling method might have missed a proportion of the population, we find that our results show a highly dynamic population structure of *H. crenulatus* in the Tubul estuary, with variations in their abundances, SFD, sex ratios and growth patterns. Data suggest at least one recruitment pulse during the austral autumn and probably occurring over the year. Growth patterns showed a correlation with sea temperature, salinity and Chl-*a*, suggesting that these environmental factors directly and indirectly modulate the annual cycle of the population. Other factors such as food availability and refuge need to be studied to understand the influence of biotic factors such as competition and predation on the population.

References

Adiyodi R (1988) Reproduction and development. In Burggren W and McMahon B (eds), *Biology of the Land Crabs*. Cambridge: Cambridge University Press, pp. 139–185.

Alveal K (1988) Gracilaria de Tubul. Historia y significado de un recurso. *Gayana Botánica* **45**, 119–140.

Baeta A, Cabral HN, Neto JM, Marques JC and Pardal MA (2005) Biology, population dynamics and secondary production of the green crab *Carcinus maenas* (L.) in a temperate estuary. *Estuarine Coastal and Shelf Science* **65**, 43–52.

Bas CC and Spivak ED (2000) Effect of salinity on embryos of two Southwestern Atlantic estuarine grapsid crab species cultured in vitro. *Journal of Crustacean Biology* **20**, 647–656.

Bas CC and Spivak ED (2003) Effects of embryonic salinity exposure on larval development in two populations of the estuarine crab *Chasmagnathus granulatus* Dana, 1851 (Crustacea: Brachyura). *Invertebrate Reproduction & Development* **43**, 117–123.

Bas C, Luppi T and Spivak E (2005) Population structure of the South American Estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae) near the southern limit of its geographical distribution: comparison with northern populations. *Hydrobiologia* **537**, 217–228.

Bas C, Nuñez J, Spivak E and Luppi T (2019) Inter-population differences in feeding ecology under nitrogen-limited diets: field growth and the role of cannibalism in limiting/improving reserve accumulation. *Marine Ecology* **40**, e12547. doi: 10.1111/maec.12547.

Bhattacharya CG (1967) A simple method of resolution of a distribution into Gaussian components. *Biometrics* **23**, 115–135.

Bianchini A, Lauer MM, Nery LEM, Colares EP, Monserrat JM and dos Santos Filho EA (2008) Biochemical and physiological adaptations in the estuarine crab *Neohelice granulata* during salinity acclimation. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **151**, 423–436.

Botter-Carvalho M, Santos P and Carvalho P (2007) Population dynamics of *Callichirus major* (Say, 1818) (Crustacea, Thalassinidea) on a beach in northeastern Brazil. *Estuarine, Coastal and Shelf Science* **71**, 508–516.

Botto F and Iribarne O (2000) Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuarine Coastal and Shelf Science* **51**, 141–151.

Brockerhoff AM and McLay CL (2005) Mating behaviour, female receptivity and male-male competition in the intertidal crab *Hemigrapsus sexdentatus* (Brachyura: Grapsidae). *Marine Ecology Progress Series* **290**, 179–191.

Brousseau DJ, Filipowicz A and Baglivo JA (2001) Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus*. *Journal of Experimental Marine Biology and Ecology* **262**, 199–210.

Brylawski BJ and Miller TJ (2006) Temperature-dependent growth of the blue crab (*Callinectes sapidus*): a molt process approach. *Canadian Journal of Fishery and Aquatic Sciences* **63**, 1298–1308.

Cannicci S, Fusi M, Cimo F, Dahdouh-Guebas F and Fratini S (2018) Interference competition as a key determinant for spatial distribution of mangrove crabs. *Bmc Ecology* **18**, 8. doi: 10.1186/s12898-018-0164-1

Carvalho-Batista A, Pescinelli RA, Garcia JR, Guerra PGM, Pardo LM and Mantelatto FL (2015) Crypsis in the mud crab *Panopeus americanus* saussure, 1857 (Decapoda, Panopeidae): relationship to sexual maturity. *Crustaceana* **88**, 963–977.

Chan BKK and Williams GA (2004) Population dynamics of the acorn barnacles, *Tetraclita squamosa* and *Tetraclita japonica* (Cirripedia: Balanomorpha), in Hong Kong. *Marine Biology* **146**, 149–160.

Chen LH, Yang JL and Barnes MD (2014) Effect of natural disturbance on migrations and population dynamics of a catadromous species, *Eriocheir japonicus*, along the Lo-Mei stream in northern Taiwan. *Hydrobiologia* **726**, 179–194.

Christy JH (2007) Predation and the reproductive behavior of fiddler crabs (genus *Uca*). In Emmett Duffy J. and Theil M (eds), *Evolutionary Ecology of Social and Sexual Systems*. New York, NY: Oxford University Press, pp. 211–231.

Constabel SA (1993) *Ambientes sedimentarios de los estuarios Tubul y Raqui, VII región, Chile* (Dissertation). Concepción (Chile): Universidad de Concepción.

Corotto FS and Holliday CW (1996) Branchial Na, K-ATPase and osmoregulation in the purple shore crab, *Hemigrapsus nudus* (Dana). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **113**, 361–368.

Datry T, Larned ST, Fritz KM, Bogan MT, Wood PJ, Meyer EI and Santos AN (2014) Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. *Ecography* **37**, 94–104.

Díaz-Jaramillo M, Ferreira JL, Amado LL, Ventura-Lima J, Martins A, Retamal MR, Urrutia R, Bertran C, Barra R and Monserrat JM (2010) Biomonitoring of antioxidant and oxidative stress responses in *Perinereis gualpensis* (Polychaeta: Nereididae) in Chilean estuarine regions under different anthropogenic pressure. *Ecotoxicology and Environmental Safety* **73**, 515–523.

Eggleston DB, Millstein E and Plaia G (2015) Timing and route of migration of mature female blue crabs in a tidal estuary. *Biology Letters* **115**, 20140936 doi: 10.1098/rsbl.2014.0936

Gayanilo Jr FC, Sparre P and Pauly D (2006) *FAO-ICLARM Stock Assessment Tools II (FiSAT II)*. Revised version. User's guide. FAO Computerized Information Series (Fisheries) No. 8. Rome: FAO.

Grabowski JH, Hughes AR and Kimbro DL (2008) Habitat complexity influences cascading effects of multiple predators. *Ecology* **89**, 3413–3422.

Hartnoll RG (2001) Growth in Crustacea – twenty years on. *Hydrobiologia* **449**, 111–122.

Haye PA and Ojeda FP (1998) Metabolic and behavioral alterations in the crab *Hemigrapsus crenulatus* (Milne-Edwards 1837) induced by its acanthocephalan parasite *Profilicollis antarcticus* (Zdzitowiecki 1985). *Journal of Experimental Marine Biology and Ecology* **228**, 73–82.

Hulathduwa YD, Stickle WB, Aronhime B and Brown KM (2011) Differences in refuge use are related to predation risk in estuarine crabs. *Journal of Shellfish Research* **30**, 949–956.

Johnson PTJ (2003) Biased sex ratios in fiddler crabs (Brachyura, Ocypodidae): a review and evaluation of the influence of sampling method, size class, and sex-specific mortality. *Crustaceana* **76**, 559–580.

Julian P and Osborne TZ (2018) From lake to estuary, the tale of two waters: a study of aquatic continuum biogeochemistry. *Environmental Monitoring and Assessment* **190**, 22.

Kerner M (2007) Effects of deepening the Elbe estuary on sediment regime and water quality. *Estuarine Coastal and Shelf Science* **75**, 492–500.

Kim AKA and O'Connor NJ (2007) Early stages of the Asian shore crab *Hemigrapsus sanguineus* as potential prey for the striped killifish *Fundulus majalis*. *Journal of Experimental Marine Biology and Ecology* **346**, 28–35.

Kirkwood G, Aukland R and Zara S (2001) *Length Frequency Distribution Analysis (LFDA), Version 5.0*. London: MRAG Ltd.

Koolkalya S, Thapanand T, Tunkijjanujij S, Havanont V and Jutagate T (2006) Aspects in spawning biology and migration of the mud crab *Scylla olivacea* in the Andaman Sea, Thailand. *Fisheries Management Ecology* **13**, 391–397.

Kristensen E (2008) Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research* **59**, 30–43.

Lagos M, Caceres CW and Lardies MA (2014) Geographic variation in acid-base balance of the intertidal crustacean *Cyclograpsus cinereus* (Decapoda, Grapsidae) during air exposure. *Journal of the Marine Biological Association of the United Kingdom* **94**, 159–165.

Landaeta MF and Castro LR (2006) Spawning and larval survival of the Chilean hake *Merluccius gayi* under later summer conditions in the Gulf of Arauco, central Chile, *Fisheries Research* **77**, 115–121. doi: 10.1016/j.fishres.2005.08.006.

Lardies MA, Rojas JM and Wehrtmann IS (2004) Breeding biology and population structure of the intertidal crab *Petrolisthes laevigatus* (Anomura: Porcellanidae) in central-southern Chile. *Journal of Natural History* **38**, 375–388.

Leme MHD and Negreiros-Fransozo ML (1998) Reproductive patterns of *Aratus pisonii* (Decapoda: Grapsidae) from an estuarine area of Sao Paulo Northern Coast, Brazil. *Revista de Biologia Tropical* **46**, 673–678.

Luppi TA, Spivak ED, Bas CC and Anger K (2004) Molt and growth of an estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae), in Mar Chiquita coastal lagoon, Argentina. *Journal of Applied Ichthyology* **20**, 333–344.

Luppi T, Bas C, Méndez-Casariego A, Albano M, Lancia J, Kittlein M, Rosenthal A, Farías N, Spivak E and Iribarne O (2013) Variations in activity patterns in the estuarine crab *Neohelice* (= *Chasmagnathus*) *granulata* in different habitats, seasons and tidal regimen. *Helgoland Marine Research* **67**, 1–15.

Martinetto P, Montemayor DI, Alberti J, Costa CSB and Iribarne O (2016) Crab bioturbation and herbivory may account for variability in carbon sequestration and stocks in South West Atlantic salt marshes. *Frontiers in Marine Science* **3**, 122.

McLay CL, Hinnendael F, Lavery S and Riquelme-Bugueno R (2011) Morphological and molecular comparison of *Hemigrapsus crenulatus* (Milne Edwards, 1837) (Brachyura: Varunidae) from New Zealand and Chile: was Miss Rathbun right? *Journal of Crustacean Biology* **31**, 582–589.

Miyajima A and Wada K (2017) Relationships between life history traits and sexual dimorphisms in two varunid crabs, *Hemigrapsus takanoi* Asakura & Watanabe, 2005 and *H. sinensis* Rathbun, 1931 (Brachyura: Varunidae). *Journal of Crustacean Biology* **37**, 21–28.

Moksnes P-O (2004) Self-regulating mechanisms in cannibalistic populations of juvenile shore crabs *Carcinus maenas*. *Ecology* **85**, 1343–1354.

Montagna PA, Hu XP, Palmer TA and Wetz M (2018) Effect of hydrological variability on the biogeochemistry of estuaries across a regional climatic gradient. *Limnology and Oceanography* **63**, 2465–2478.

Moscoso J, Rudolph A, Sepúlveda RD and Suárez C (2006) Effect of temporary closure of the mouth of an estuary on the benthic macroinfauna: Lenga, Chile: a case study. *Bulletin of Environmental Contamination and Toxicology* **77**, 484–491.

Munro JL and Pauly D (1983) A simple method for comparing the growth of fishes and invertebrates. *Fishbyte* **1**, 5–6.

Murrell MC, Caffrey JM, Marcovich DT, Beck MW, Jarvis BM and Hagy JD (2018) Seasonal oxygen dynamics in a warm temperate estuary: effects of hydrologic variability on measurements of primary production, respiration, and net metabolism. *Estuaries and Coasts* **41**, 690–707.

Nelson K (1991) Scheduling of reproduction in relation to moulting and growth in malacostracan crustaceans. In Wenner A and Kuris A (eds), *Crustacean Egg Production*. Rotterdam: A. A. Balkema, pp. 7–116.

Pauly D (1987) A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic vertebrates. In Pauly D and Morgan GR (eds), *Length-based Methods in Fisheries Research*. Safat, Kuwait: ICLARM, Manila, Philippines and KISR, pp. 7–34.

Poore AGB, Campbell AH, Coleman RA, Edgar GJ, Jormalainen V, Reynolds PL, Sotka EE, Stachowicz JJ, Taylor RB, Vanderklift MA and Duffy E (2012) Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters* **15**, 912–922.

Posey MH, Alphin TD, Harwell H and Allen B (2005) Importance of low salinity areas for juvenile blue crabs, *Callinectes sapidus* Rathbun, in river-dominated estuaries of southeastern United States. *Journal of Experimental Marine Biology and Ecology* **319**, 81–100.

Potter IC, Tweedley JR, Elliott M and Whitfield AK (2015) The ways in which fish use estuaries: a refinement and expansion of the guild approach. *Fish and Fishery* **16**, 230–239.

Pozo K, Perra G, Menchi V, Urrutia R, Parra O, Rudolph A and Focardi S (2011) Levels and spatial distribution of polycyclic aromatic hydrocarbons (PAHs) in sediments from Lenga Estuary, central Chile. *Marine Pollution Bulletin* **62**, 1572–1576.

Retamal M (1969) *Hemigrapsus crenulatus* (H. Milne Edwards, 1837) en el estero Lenga (Crustacea, Decapoda, Grapsidae). *Boletín de la Sociedad de Biología de Concepción* **41**, 281–307.

Retamal MA (1981) Catalogo ilustrado de los Crustáceos Decápodos de Chile. *Gayana, (Zool.)* **44**, 1–110.

Retamal MA and Moyano HI (2010) Zoogeografía de los crustáceos decápodos chilenos marinos y dulceacuícola. *Latin American Journal of Aquatic Research* **38**, 302–328.

Riquelme-Bugueño R (2006) Incidence patterns of limb autotomy in the estuarine crab, *Hemigrapsus crenulatus* (H. Milne Edwards, 1837) (Brachyura, Grapsoidea) from a temperate estuary in the eastern South Pacific. *Crustaceana* **79**, 925–932.

Schultz DA and Shirley TC (1997) Feeding, foraging and starvation capability of ovigerous Dungeness crabs in laboratory conditions. *Crustacean Research* **26**, 26–37.

Sicurella B, Musitelli F, Rubolini D, Saino N and Ambrosini R (2016) Environmental conditions at arrival to the wintering grounds and during spring migration affect population dynamics of barn swallows *Hirundo rustica* breeding in Northern Italy. *Population Ecology* **58**, 135–145.

Silva CC, Schwamborn R and Oliveira JEL (2014) Population biology and color patterns of the blue land crab, *Cardisoma guanhumi* (Latreille 1828) (Crustacea: Gecarcinidae) in Northeastern Brazil. *Brazilian Journal of Biology* **74**, 949–958.

Sokal R and Rohlf F (1997) *Biometry. The Principles and Practice of Statistics by Biological Research*, 3rd Edn. New York, NY: W.H. Freeman and Co.

Spivak E, Anger K, Luppi T, Bas C and Ismael D (1994) Distribution and habitat preferences of 2 grapsid crab species in Mar-Chiquita lagoon (province of Buenos-Aires, Argentina). *Helgolander Meeresuntersuchungen* **48**, 59–78.

Spivak E, Bas C and Luppi T (2016) Great unexpected differences between two populations of the intertidal crab *Neohelice granulata* inhabiting close but contrasting habitats (Crustacea: Decapoda: Brachyura). *Zoologia* **33**, e20160020. doi: 10.1590/ s1984–4689z ool-20160020.

Stuardo J, Valdovinos C, Figueroa R and Occhipinti A (1993) Los ambientes costeros del Golfo de Arauco y áreas adyacentes. In Faranda F and Parra O (eds), *Monografía Científica No 9*. EULA. Universidad de Concepción.

Tankersley RA, Wieber MG, Sigala MA and Kachurak KA (1998) Migratory behavior of ovigerous blue crabs *Callinectes sapidus*: evidence for selective tidal-stream transport. *Biological Bulletin* **195**, 168–173.

Taylor HH and Seneviratna D (2005) Ontogeny of salinity tolerance and hyper-osmoregulation by embryos of the intertidal crabs *Hemigrapsus edwardsii* and *Hemigrapsus crenulatus* (Decapoda, Grapsidae): survival of acute hyposaline exposure. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **140**, 495–505.

Theuerkauff D, Rivera-Ingraham GA, Roques JAC, Azzopardi L, Bertini M, Lejeune M, Farcy E, Lignot J and Sucré E (2018) Salinity variation in a mangrove ecosystem: a physiological investigation to assess potential consequences of salinity disturbances on mangrove crabs. *Zoological Studies* **57**, 36.

Urbina M, Paschke K, Gebauer P and Chaparro OR (2010) Physiological energetics of the estuarine crab *Hemigrapsus crenulatus* (Crustacea: Decapoda: Varunidae): responses to different salinity levels. *Journal of the Marine Biological Association of the United Kingdom* **90**, 267–273.

Urzua A and Urbina MA (2017) Ecophysiological adaptations to variable salinity environments in the crab *Hemigrapsus crenulatus* from the Southeastern Pacific coast: sodium regulation, respiration and excretion. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **210**, 35–43.

Urzua A, Bascur M, Guzman F and Urbina M (2018) Carry-over effects modulated by salinity during the early ontogeny of the euryhaline crab *Hemigrapsus crenulatus* from the Southeastern Pacific coast: development time and carbon and energy content of offspring. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **217**, 55–62.

Valdovinos C, Sandoval N, Vasquez D and Olmos V (2017) The Tubul-Raqui coastal wetland: a Chilean ecosystem of high conservation value severely disturbed by the 2010 earthquake. In Fariña J and Camaño A (eds), *The Ecology and Natural History of Chilean Saltmarshes*. Cham: Springer, pp. 293–327.

Valle-Levinson A, Atkinson LP, Figueroa D and Castro L (2003) Flow induced by upwelling winds in an equatorward facing bay: Gulf of Arauco, Chile. *Journal of Geophysical Research-Oceans* **108**, 3054.

Vega-Aguayo R, Figueroa-Munoz G, Retamal MA and De los Rios P (2018) Spatial distribution and abundance of *Hemigrapsus crenulatus* (H. Milne Edwards, 1837) (Decapoda, Varunidae) in the Puerto Cisnes estuary (44°S, Aysen region, Chile). *Crustaceana* **91**, 1465–1482.

Vina N, Bascur M, Guzman F, Riera R, Paschke K and Urzua A (2018) Interspecific variation in the physiological and reproductive parameters of porcelain crabs from the Southeastern Pacific coast: potential adaptation in contrasting marine environments. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **226**, 22–31.

Von Bertalanffy L (1938) A quantitative theory of organic growth. *Human Biology* **10**, 181–213.

Waiho K, Mustaqim M, Fazhan H, Norfaizza WIW, Megat FH and Ikhwanuddin M (2015) Mating behaviour of the orange mud crab, *Scylla olivacea*: the effect of sex ratio and stocking density on mating success. *Aquaculture Report* **2**, 50–57.

Warman CG, Reid DG and Naylor E (1993) Variation in the tidal migratory behavior and rhythmic light-responsiveness in the shore crab, *Carcinus maenas*. *Journal of the Marine Biological Association of the United Kingdom* **73**, 355–364.

Wenner AM (1972) Sex ratio as a function of size in marine crustacea. *American Naturalist* **106**, 321–350.

Zar JH (1999) *Biostatistical Analysis*, 4th Edn. Englewood Cliffs, NJ: Prentice-Hall.