Population biology of the burrowing shrimp *Callichirus seilacheri* (Decapoda: Callianassidae) in northern Chile

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Abstract: The life history of ghost shrimps, known for their role in shaping community structures in shallow water habitats, is poorly studied in species occurring along the coasts of the South American Pacific. Here we present ecological information concerning *Callichirus seilacheri* based upon individuals collected from January to December 2003 in Las Machas beach, northern Chile. Burrow densities varied between 1.4 and 20.2 burrows / 0.25 m^2, and was highest during summer (18.2 burrows / 0.25m^2). The sex proportion was 1:1 during most of the study period; however, females outnumbered males in January and September. Males reached a larger maximum size than females (27.1 and 24.0 mm CL, respectively). The presence of juveniles was restricted principally to the time between February and May. Sexual maturity was reached at a size of 20.8 mm (males) and 18.1 mm CL (females). The main breeding period lasted from autumn to winter (May to August, peaking in June), and co-occurred with decreasing water temperatures and the presence of a sediment layer covering the burrows. Rev. Biol. Trop. 55 (Suppl. 1): 141-152. Epub 2007 June, 29.

Key words: burrow density, sexual maturity, reproduction, ghost shrimp, South America, Pacific.

The infraorder Thalassinidea is comprised by the so-called ghost shrimps, which typically occupy intertidal and subtidal marine and estuarine habitats. They are known to construct burrows of different shapes and depths (Suchanek 1983, Griffis and Chávez 1988, Lemaitre and Rodrigues 1991), and play an important role in shaping the community structure in shallow water habitats (e.g. Posey 1986, Posey *et al*. 1991, Nates and Felder 1998). Their burrowing activities contribute considerably to perturbation of the sediments, renovation of the nutrient cycle, and increased food availability among the trophic levels (Ziebis *et al.* 1996, Berkenbusch and Rowden 1999, Felder 2001). Despite of their ecological importance, information about population and reproductive biology of these shrimps is scarce (i.e. Rodrigues and Shimizu 1997, Pezzuto 1998, Nates and Felder 1999, Berkenbusch and Rowden, 2000a), especially concerning those populations occurring along the Chilean coast.

Although the ecology of American thalassinidean shrimps has received growing attention during the last decade (see Coelho *et al*. 2000, Felder 2001, Thatje 2003), the life history of these crustaceans along the South American Pacific coast remains mostly unknown, probably due to their cryptic life style which makes it difficult to capture and study them (Coelho *et al*. 2000). Along the Chilean coast the family Callianassidae (Thalassinidea) is represented by six species which can be found in soft sediments between 0 and 255 m depth (see Thatje and Gerdes 2000, Guzmán and Thatje 2003, Thatje 2003). There are some scattered publications which mention the presence of dense populations of ghost shrimps at Chilean beaches (Aste and Retamal 1983, Soto *et al.* 2002).

In general, however, information concerning biology, population dynamics, and ecology of these shrimps is still lacking.

Callichirus seilacheri Bott 1955 (synonymy of *C. garthi* Retamal 1975; see Sakai 1999) is distributed from El Salvador (12ºN) to Chile (37ºS). The species was observed for the first time on beaches in the extreme northern part of Chile during the ENSO event of 1982-1983 (Soto *et al.* 2002). Existing information is limited to larval development (Aste and Retamal 1983), and the interaction between *C. seilacheri* and the ectosymbiotic copepod *Clausidium* sp. (Marín and George-Nascimento 1993).

The present study aims to provide information regarding the population structure and reproductive aspects of *C. seilacheri*, the most conspicuous intertidal callianassid shrimp in the northern part of Chile (Soto *et al.* 2002). We also present data on habitat use and density changes during the year, which might facilitate a better understanding of the ecological role of this ghost shrimp along the coastal habitats of Chile.

MATERIALS AND METHODS

Specimens were obtained from the intertidal zone in Las Machas beach, northern Chile (Fig. 1) from January to December 2003. The individuals were identified according to

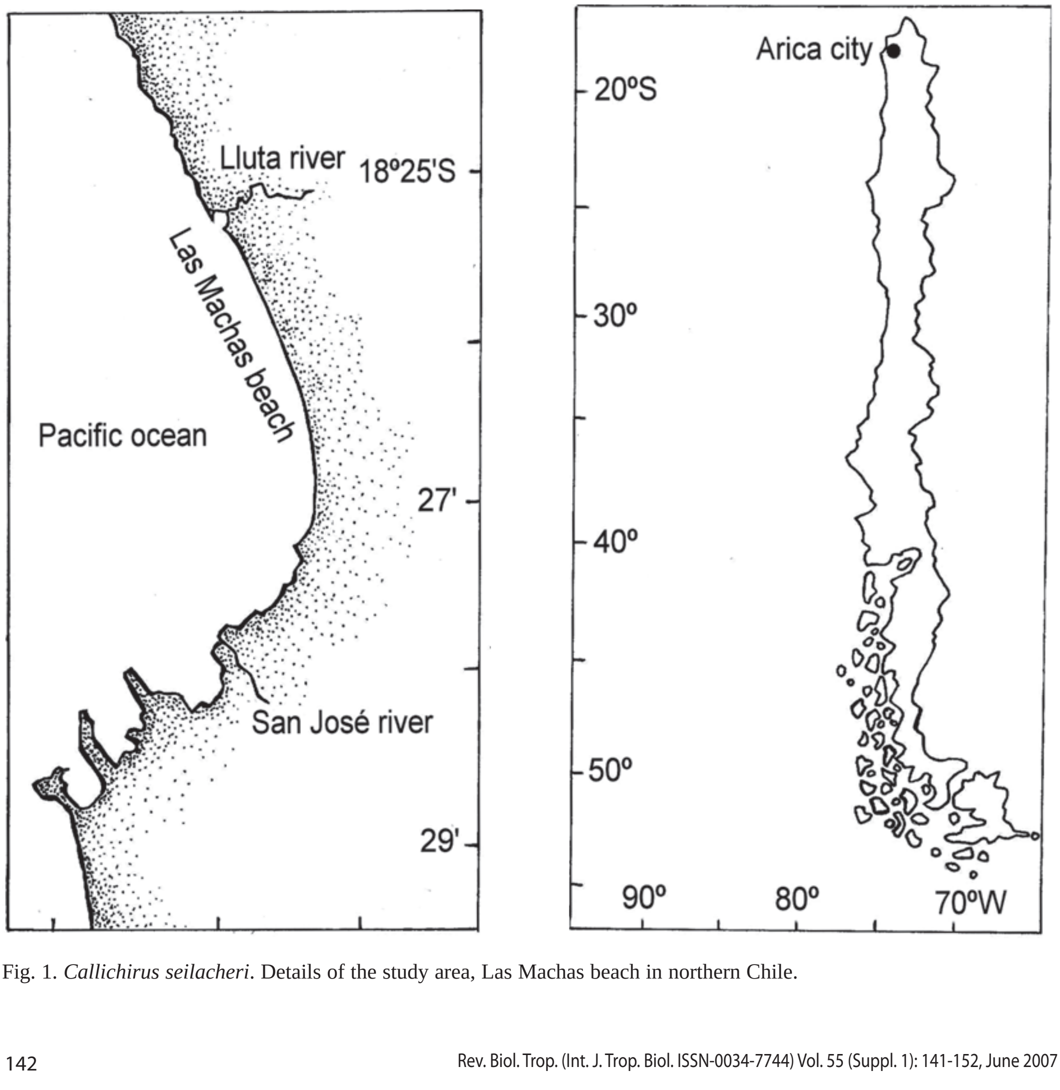

Fig. 1. *Callichirus seilacheri*. Details of the study area, Las Machas beach in northern Chile.

the keys for genera and species, published by Manning and Felder (1991) and Retamal (1975) respectively. In order to get an estimate of the abundance of *C. seilacheri*, we counted the number of holes in an area of 0.5 x 0.5 m, with ten replicates during each monthly sampling (typically between day 15 and 20 of each month). The entrances of each gallery were easily identifiable due to their diameter; however, shrimps might live in interconnected network tunnels, and each gallery was occupied by at least one individual (P. Hernáez, pers. obs.). Individuals were collected with a yabby pump (diameter: 77 mm) after inspecting the area for burrowing holes. However, even when no holes were visible, sediment was searched for ghost shrimps. The physical structure of Las Machas beach changed considerably during the study period making it impossible to determine the number of holes by area between June and August. Therefore, this period was not included when estimating the burrow densities. The following data were also recorded: surface water temperature, number of ghost shrimps per yabby pump suck per burrow opening, associated fauna, and predators present in the burrows.

After extracting the ghost shrimps each individual was sexed and classified into one of the following categories: juvenile (JU), male (MA), non-ovigerous female (NOF), and ovigerous female (OF). The sex determination was based upon macroscopic features such as the clearly elongated carpus of the major chelipeds (males) and the presence of colored gonads in females; when these criteria did not allow a definitive sex determination, the location of the gonopores was revised, too.

The following morphometric measurements ($\pm$ 0.1 mm) were taken: total length (TL: from the anterior margin of the rostrum to the posterior region of the telson), carapace length (CL: from the anterior margin of the rostrum to the posterior margin of the carapace), and length and width of the propodus of the major chelipeds (PL and PW, respectively). The wet weight (WW) of each individual was measured with an analytical balance (Sartorius; $\pm$ 0.1g).

The CL was considered as an independent variable; adjustment of each regression was analyzed by least squares method (Sokal and Rohlf 1981). This procedure was applied for all categories. Specimens of each category were grouped into 1 mm size classes; subsequently data were plotted as length-frequency histograms to analyze the population structure of the juveniles and adult shrimps.

Morphological maturity in *C. seilacheri* was estimated from the biometric relationship between PL x CL in males, and WW x CL in females. The allometric equation ($y= ax^b$) was fitted to each growth phase to obtain the allometric growth constant “b” to determine the growth pattern (see Somerton 1980). Analysis of the allometric growth constant (b) gives information about the increase of one biometric dimension in relation to another; isometric growth was considered when b was between 0.90 and 1.10, negative allometric growth with $b<0.90$, and positive allometry with $b>1.10$ (Kuris *et al*. 1987, Pinheiro and Fransozo 1993). All incomplete individuals were excluded from these analyses and of the determination of size at first sexual maturity.

Our knowledge about mating in ghost shrimps is scarce, principally because mating occurs in cryptic locations (Bilodeau *et al*. 2005). To obtain an indirect estimate of the mating period of *C. seilacheri*, we counted the number of burrows occupied by both a female with mature gonads and an adult male. The percentage of these mature couples (MC) was plotted per month; we considered a month as part of the mating period, when these mature couples comprised $\geq$20 % of all adult individuals collected per month.

According to Connell (1985), recruitment is defined as the entry of individuals into the juvenile and adult benthic population after settlement from a planktonic larval stage. Since *C. seilacheri* has a larval planktonic development (Aste and Retamal 1983), we estimated recruitment through the presence of small individuals (< 9 mm CL), analyzing the size-frequency histograms of each month.

Possible monthly differences concerning the sex proportion were analyzed by means of a χ^2 test (1:1; $p<0.05$). The time of the reproductive period was established by comparing the percentage of ovigerous females to the total number of females collected during the month or the season. The reproduction period was defined as the months where more than 25 % of all collected females carried eggs.

RESULTS

General observations concerning habitat and ecology of *C. seilacheri*. During June, the ocean moved a large amount of sand from the superior zone of the beach towards the intertidal and subtidal areas, covering most of the entrances of the burrows and complicating the count of the burrows per square meter. This situation lasted until end of August, when conditions returned as they were at the beginning of the study. When we removed the upper sediment layer covering the burrow, it became obvious that ghost shrimps were alive and active in the shafts and tunnels. Burrow densities during the year varied between 1.4 and 20.2 burrows/0.25 m^2. High monthly mean values (>19 burrows/0.25 m^2) were recorded in spring and summer, coinciding with reduced accretion intensities in Las Machas beach (Table 1).

Invertebrates associated to the *C. seilacheri* galleries were the carnivorous polychaete *Nepthys ferruginea* Hartman, a very abundant (but unidentified) nemertine worm and the pinnotherid crab *Pinnixa transversalis* Milne Edwards & Lucas. In the sampling area (but not associated with *C. seilacheri* galleries and occurring also outside the collection site), a bivalve of the genus *Donax* sp. was especially abundant during spring when sediment erosion was most intense.

Almost all individuals of *C. seilacheri* hosted the ectosymbiotic copepod *Clausidium* sp. This copepod principally infested the gill region, the insertion area of the thoracic legs, and the egg masses.

Population biology. A total of 716 individuals were analyzed; 37.3 % were males,

TABLE 1

Callichirus seilacheri. *Ecological variables and sex ratio; Las Machas beach, Chile.*

Month	SWT (ºC)	Accretion	Density ($0.25m^2$)	Sex-ratio (M:F)	χ^2
January	18.6 ± 1.66	-	19.6± 3.33	29/48	4.701*
February	20.2 ± 0.72	-	15.2 ± 5.79	11/9	0.250
March	18.0 ± 0.85	-	19.7 ± 3.74	26/21	0.553
April	17.7 ± 1.52	-	16.6 ± 7.49	22/29	0.980
May	17.1 ± 0.77	+	4.7 ± 1.15	26/20	0.804
June	16.2 ± 1.69	+++	2.2 ± 0.32	28/21	1.020
July	15.9 ± 0.98	+++	1.4 ± 0.11	16/18	0.147
August	16.1 ± 1.78	+++	2.3 ± 0.26	11/19	2.167
September	15.8 ± 0.54	+	16.9 ± 2.67	11/29	8.125*
October	17.3 ± 1.44	-	14.7 ± 4.11	19/29	2.104
November	17.3 ± 1.37	-	18.4 ± 3.27	38/30	0.956
December	17.7 ± 1.49	-	20.2 ± 0.49	30/40	1.443

Mean surface water temperature (SWT), intensity of accretion (+++: high; +: medium; -: low) and mean burrow density during of the study period (January to December 2003). Proportion of males and females per month; asterisks indicate significant differences ($p<0.05$; χ^2 test) from the 1:1 ratio.

43.7 % females, and 19.0 % immature individuals. The sex proportion was 1:1 during almost all the year (Table 1), except in January and September when females were significantly more abundant than males (test χ^2, $p < 0.05$).

In all categories, the relation between CL and WW was best described by a potential function which accounted for 97 % of the total variation between these two factors (Fig. 2). The analysis of the relation between PL and CL (Fig. 3) revealed different growth patterns for each of the life cycle stages of *C. sailacheri* (Table 2), indicating isometric growth in juveniles (b=0.90), positive allometric growth in males (b=2.32), and negative allometric growth in females (b=0.86).

The analysis of morphological maturation based on the inflection point of each regression indicates the moment when growth changes from an isometric to an allometric stage. According to this, males and females reached sexual maturity at a size of 20.8 mm CL ($LP= 5.29*10^{-1}CL^{1.11}$, $r^2=0.84$) and 18.1 mm CL ($WW= 2.93*10^{-3}CL^{3.01}$, $r^2=0.94$), respectively.

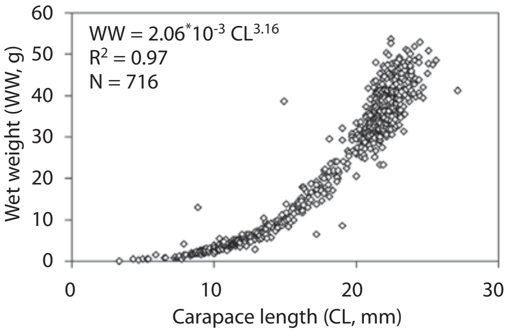

Fig. 2. *Callichirus seilacheri*. Relation between wet weight and carapace length of all individuals collected (N=716) during the study period (January–December 2003) at Las Machas beach, northern Chile.

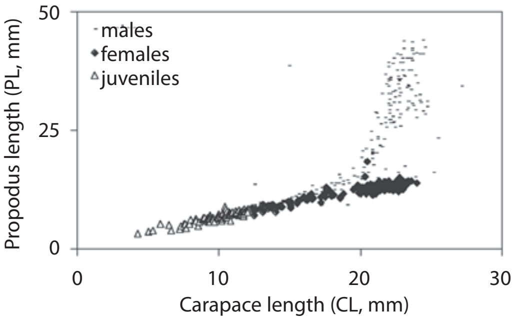

Fig. 3. *Callichirus seilacheri*. Relation between propodus and carapace length of juveniles, males, and females during the study period at Las Machas beach, northern Chile.

Males and females had an average size of 21.4 mm CL (±2.57 mm) and 21.1 mm CL (±1.87 mm), respectively. However, males reached a larger maximum size than females (27.1 and 24.0 mm CL, respectively). All the categories showed significant size differences during the study period (ANOVA; $p < 0.05$).

The presence of mature couples was confined mainly to the period from April to July, with a small percentage present also in November (Fig. 4). Ovigerous females were recorded between March and September, peaking in June with 61.1 % of all collected females during this month (Fig. 4). A second, substantially smaller peak occurred in November and December. The main presence of both mature

TABLE 2

Callichirus seilacheri. *Regression analyses between length of major propodus (PL) and carapace length (CL).*

Variable	Category	n	Equation	r^2	Allometric level
PL	MA	226	$PL=2.00*10^{-2} CL^{2.32}$	0.80	+
	NOF, OF	268	$PL=0.95*CL^{0.86}$	0.88	-
	JU	115	$PL=0.85*CL^{0.90}$	0.82	0
	total	620	$PL=0.33*CL^{1.29}$	0.65	+

MA = males; NOF = non ovigerous females; OF = ovigerous females; JU = juveniles
In all cases, the relation was significant ($p<0.01$). Allometric level refer to isometry (0), negative (-) and positive (+) allometry.

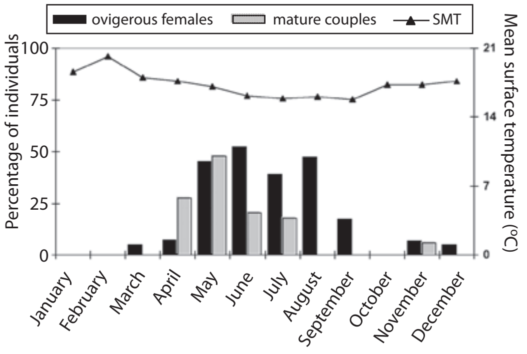

Fig. 4. *Callichirus seilacheri*. Presence (expressed as percentage of all individuals collected during each month) of mature couples and ovigerous females at Las Machas beach, northern Chile, in relation to both the mean water surface temperature (SMT) and the presence of sediments covering the burrows (accretion) during the study period (January–December 2003).

couples and ovigerous females coincided with the period of decreasing temperatures and when accretion was more intense and burrows were covered by sand (Fig. 4).

Sexually mature ghost shrimps (n = 580) varied in size between 12.1 mm CL and 27.1 mm CL; however, a majority of these (55 % of all collected individuals) ranged in size from 20.0 to 24.0 mm CL. Adult shrimps predominated during almost the entire study period with the exception of February when juveniles were more numerous (Fig. 5). The recruitment was more intense during summer. The presence of small individuals (< 9 mm CL) was restricted to the time between February and May (Fig. 6). Their subsequent absence coincided with further decreasing temperatures and the beginning of the main spawning period (see Fig. 5, 6).

DISCUSSION

Physical processes associated with beach morphodynamics may influence the ecology of *C. sailacheri*. Information about distribution and community structure of sandy beach indicates that sediment type, slope and wave characteristics can affect the species richness as well as the abundance and biomass of the macroinfauna (Defeo *et al.* 1992, McLachlan *et al.* 1993, Jaramillo *et al.* 1998). According to Muehe and Tavares-Corrêa (1989), such seasonal movements allow the renovation of nutrients in sandy beaches. This balance is ecologically significant for many benthic populations (Carrasco and Gallardo 1994), especially for those organisms burrowing in the sediment, such as ghost shrimps.

The seasonal movement of sediments along the beaches of northern Chile may be important for the population dynamics of *C. seilacheri*. Our results suggest that recruitment and breeding season in *C. seilacheri* were synchronized with erosion and sedimentation processes, respectively. Erosion may have favored the post-larval settlement during summer, facilitating the encounter of suitable habitats for their development (i.e. open burrows). In winter the accretion was more intense, and numerous burrows were covered by the sediment (see Table 1), which diminished the probability that post-larvae encountered an available refuge.

The main spawning period of *C. seilacheri* coincided with periods of intense sedimentation and low surface water temperatures (winter). During this period we observed reduced sediment expulsion activity of the ghost shrimps, which is in accordance with similar observations regarding *Callianassa subterranea* (see Rowden *et al.* 1998) and *C. filholi* (see Berkenbusch and Rowden 1999). As reported from other callianassids (Coelho and Rodrigues 2001), during winter *C. seilacheri* may be able to shift from filter feeding to a deposit feeding mode, enabling the species to obtain sufficient energy for reproduction.

Callianassid shrimps feed on organic material in the sediment and invest the obtained energy in growth and reproduction (Nickell and Atkinson 1995). In Las Machas, as the result of summer (January and February) rains in the adjacent highlands, two rivers (the San José and Lluta) supplied considerable amounts of fine, nutrient-rich sediments of terrigenous origin to the study area (Soto *et al*. 2002). This apparently favored the establishment of

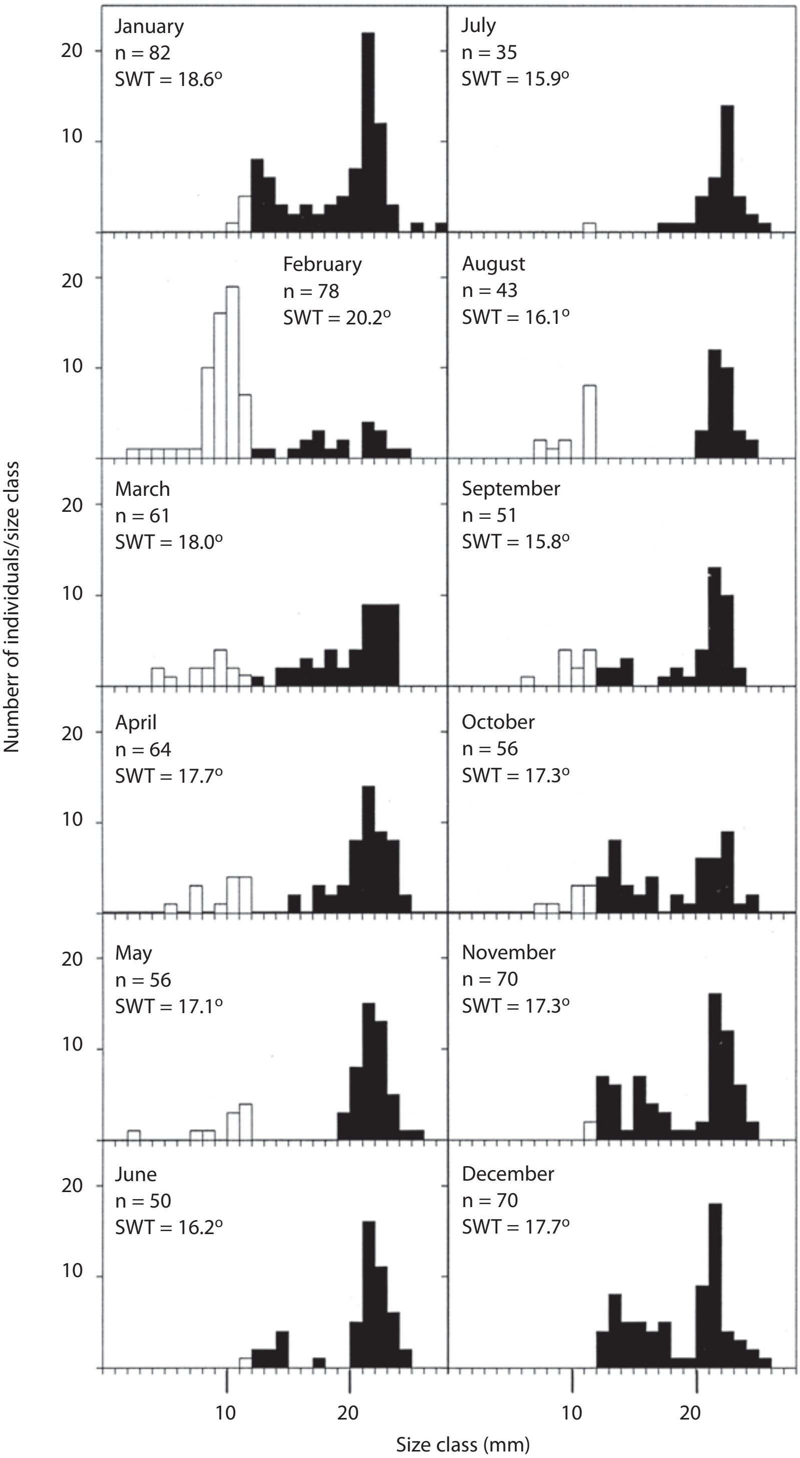

Fig. 5. Monthly length-frequency distribution of *Callichirus seilacheri* collected between January and December 2003 at Las Machas beach, northern Chile. White bars represent juveniles, black bars adults; SWT=surface water temperature.

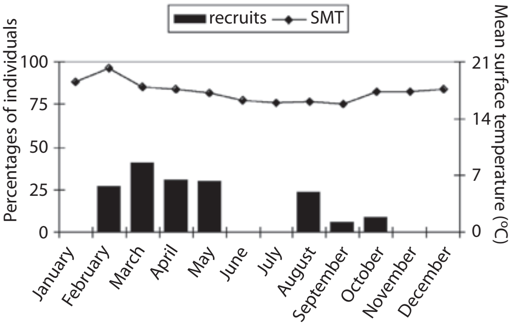

Fig. 6. *Callichirus seilacheri*. Monthly presence of juveniles (expressed as percentage of the total number of collected individuals per month) in relation to the mean water surface temperature (SMT) at Las Machas beach, northern Chile, during the study period (January to December 2003).

the *C. seilacheri* population, which is principally associated with this type of sediment (P. Hernáez, pers. obs.).

Temperature is a dominant factor that governs the population dynamics of many intertidal decapod populations (Kinne 1970, Jones and Simons 1983, Stillman and Somero 2000). This factor has been associated with temporal alterations in the sex ratio, breeding events, size-frequency distributions and sediment turnover activity in natural populations of thalassinidean shrimps (Kevrekidis *et al*. 1997, Rowden *et al*. 1998, Berkenbusch and Rowden 1999, Berkenbusch and Rowden 2000b). Our results confirm these observations and suggest that population dynamics of *C. seilacheri* are strongly influenced by temperatures and annual sediment dynamics in Las Machas beach (i.e. sedimentation and erosion).

The main breeding period of *C. seilacheri* lasted from autumn to winter (May to August), and co-occurred with decreasing water temperatures and the presence of a sediment layer covering the burrows (Fig. 4). Thus, our results corroborate that reproduction in decapods from temperate zones is generally synchronized with cycles of temperature, photoperiod, and food availability (e.g. see Antezana *et al.* 1965, Arana and Tiffou 1970, Bahamonde *et al.* 1986, Wolff and Cerda 1992, Lardies *et al.* 1998, 2004). However, the breeding season of *C. seilacheri* started during a period of diminishing temperatures which contradicts the pattern observed in other thalassinideans from temperate regions where the reproductive season begins when temperatures increased (Leija and Sánchez 1988, Felder and Lovett 1989, Kevrekidis *et al*. 1997, Souza *et al.* 1998).

C. seilacheri seems to have a markedly seasonal breeding period with probably two successive spawnings. The obtained data indicate a second considerably smaller breeding period in November-December (Fig. 4). This interpretation is in accordance with similar observations concerning various decapods from Chile (e.g., Lardies *et al*. 1998, 2004) and other temperate zones (e.g., Beck and Cowell 1976, González-Gurriarán 1985, Haddon and Wear 1993).

The sediment cover seems to reduce the risk of predation, including that by local fisher communities collecting burrowing shrimps at Las Machas. Local people capture these shrimps intensively for bait from October to May, but during the remaining months such activities decrease substantially. The seasonal patterns of the sediment movements regulate human collecting activities, thus indirectly protecting the reproduction of *C. seilacheri*.

Females predominated in January and September (Table 1). In accordance with the present data, predominance of females has been reported also for *Glypturus* (as *Callichirus*) *armatus* (see Vaugelas *et al.* 1986) and *Nihonotrypaea harmandi* (as *Callianassa japonica*) (see Tamaki *et al.* 1997); however, these authors did not provide any explanation for this phenomenon. Burrows of *Callichirus* (for *C. major* see Frey *et al.* 1978) are considered as an interconnected network of shafts and tunnels, which may explain our observation that several females can share a burrow with a male; however, we never found more than one male per burrow. It is speculated that the male due to his polygamist behavior protects his harem during the reproduction period, thus increasing the risk of predation. Such a behavior may explain why females outnumber males during these months.

Recruitment was most conspicuous during the early months of the year, especially February, and to a lesser extent during the period from August to October (Fig. 6). The major recruitment peak in February coincided with the highest water temperatures measured during the study period while the second pulse of recruits occurred during a period characterized by increasing temperatures (Fig. 6). Interestingly, both recruitment events occurred during periods when the burrows were not covered by sediment. Although juveniles may dig their own burrows, frequently we found juveniles inside of occupied burrows. Therefore, such timing may favor the rapid settlement in open burrows, thus reducing predation risk.

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RESUMEN

La historia natural de los camarones fantasma, conocidos por modelar la estructura de las comunidades en hábitats de aguas someras, ha sido poco estudiada en el Pacífico suramericano. Aquí presentamos información ecológica concerniente a *Callichirus seilacheri,* con base en individuos recolectados entre enero y diciembre de 2003 en playa Las Machas, norte de Chile. La densidad de las madrigueras varió entre 1.4 y 20.2 madrigueras / 0.25 m^2, y fue mayor durante el verano (18.2 madrigueras / 0.25 m^2). La proporción de sexos fue 1:1 durante la mayor parte del periodo de estudio; sin embargo, las hembras superaron en número a los machos en enero y setiembre. Los machos presentaron un tamaño máximo mayor al de las hembras (27.1 y 24.0 mm CL, respectivamente). La presencia de juveniles se restringió principalmente al periodo comprendido entre febrero y mayo. La madurez sexual se alcanza a un tamaño de CL de 20.8 mm en los machos y 18.1 mm en las hembras. El periodo reproductivo principal se extendió del otoño al invierno (de mayo a agosto, con un pico en junio), y coincidió con temperaturas decrecientes en el agua y con la presencia de una capa de sedimento sobre las madrigueras.

Palabras clave: densidad de madrigueras, madurez sexual, reproducción, camarón fantasma, Suramérica, Pacífico.

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