

Associations between two species of snapping shrimp, *Alpheus inca* and *Alpheopsis chilensis* (Decapoda: Caridea: Alpheidae)

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This study examined the association pattern of two snapping shrimp species that inhabit burrows at exposed rocky shores of the Chilean Pacific coast. The two species *Alpheus inca* and *Alpheopsis chilensis* were frequently found to share the same burrows. In most burrows an heterosexual pair of each species was found. A strong positive correlation between the body length of female and male conspecifics cohabiting in a burrow was found both for *Alpheus inca* and for *Alpheopsis chilensis*. Similarly, a positive correlation existed between the mean body length of *Alpheus inca* and that of *Alpheopsis chilensis* occurring together in one burrow. Thus, a size-relationship between burrow cohabitants exists both in the intra-specific as well as in the inter-specific association of these shrimps. Most females, regardless of their reproductive stage, were accompanied by males. Within a particular burrow, females of the two species often were in the same reproductive stage, i.e. both were with embryos in a similar developmental stage, or both were without embryos. These data suggest that male and female conspecifics, as well as the pairs of the two species, remain together in the same burrow for relatively long time periods. It is proposed that the intra-specific communication system of snapping shrimp facilitates the development of inter-specific associations, such as the one reported herein.

INTRODUCTION

Selection of habitat and mate are crucial decisions during the life of an organism that affect their survival and reproductive success. These decisions gain increasing importance when either of these resources is temporarily or spatially limited. In order to find or secure such resources, organisms may act as solitary individuals or in association with one (or more) conspecifics.

In the marine environment, associations between conspecifics often develop in shared defence of microhabitats (dwellings). Snapping shrimp, for example, often associate in heterosexual pairs (Nolan & Salmon, 1970; Schein, 1975; Lassig, 1977; Yanagisawa, 1984; Jeng, 1994; Hughes, 1996a) or in large groups (Duffy et al., 2000) that co-operatively occupy and defend small dwellings. These snapping shrimp live in a wide variety of dwellings such as small cavities under shell rubble, gravel and boulders, self-constructed burrows in soft sediments, holes in coral heads, sponges, anemones and ascidians where they find shelter and protection from wave action and predators (e.g. Knowlton, 1980; Vannini, 1985). Many species remain for long time periods in the same dwelling, and they may actively modify and enlarge these (Nolan & Salmon, 1970; Karplus et al., 1974; Yanagisawa, 1984; Kropp, 1987). Successful defence of these microhabitats may only be possible by associating with one or more conspecifics, with which these snapping shrimp may cohabit for long time periods. Long-lasting cohabitation of two (or more) individuals comprising members of the opposite sex may furthermore reduce the need to search

for mating partners and consequently the costs and risks resulting from leaving a dwelling.

Many snapping shrimp possess powerful chelae which they utilize to obtain prey and to fend off aggressors (Versluis et al., 2000). Most snapping shrimp aggressively defend their dwellings similar to reports from stomatopods, which also employ their powerful chelae in defence of their burrows (Steger, 1987; Caldwell, 1991). Individuals that occupy a dwelling may allow access to members of the opposite sex but exclude members of the same sex (Johnson, 1969; Nolan & Salmon, 1970; Huber, 1985; Caldwell, 1991). This will result in the establishment of heterosexual pairs, at least for a short time period. In many crustacean species, formation of heterosexual pairs only occurs during female receptivity, and after successful fertilization in these species, mates separate again. However, if free dwellings are lacking or movements away from them are otherwise risky, it may be favourable for males and females to remain together after fertilization (Salmon, 1983). If these heterosexual pairs persist for long time periods, their members may reproduce repeatedly with the same partner. This has been inferred for many snapping shrimp species, which are commonly found in heterosexual pairs (Nolan & Salmon, 1970; Schein, 1975; Yanagisawa, 1984).

Interestingly, many species of snapping shrimp not only associate with heterosexual partners but also with individuals belonging to other taxa such as xanthid crabs (Vannini, 1985), stomatopods (Frogliola & Atkinson, 1998) and a wide diversity of gobiid fishes (Yanagisawa, 1984; Karplus, 1987). The snapping shrimp may benefit from

the aggressiveness of their partners (Vannini, 1985), and they may feed on material made available by their partners. In many cases it is the snapping shrimp that construct burrows which subsequently attract other species. These inquilines directly benefit from the shelters constructed by the snapping shrimp in environments that otherwise do not offer much protective structure. The members of these inter-specific associations engage in complicated forms of interspecific communication (Karplus, 1979, 1992; Lassig, 1977). In particular, the associations of snapping shrimp with some gobiid fish are long-lasting and may be obligatory to both partners (Karplus, 1987).

Along the Pacific coast of Chile, seven species of snapping shrimp have been reported (Lancellotti & Vásquez, 2000). Most of these inhabit shallow coastal waters where they occur among gravel and shell habitats under boulder fields. Preliminary observations had indicated that the two species *Alpheus inca* and *Alpheopsis chilensis* often occurred together in these habitats, sometimes even in the same burrow. In the present study, we examined the occurrence of these two species in intertidal burrows. We paid particular attention to collect all inhabitants of single burrows in order to document whether or not these species shared the same burrows.

MATERIALS AND METHODS

This study was conducted in Bahía La Herradura and in La Pampilla in Coquimbo, Chile (29°58'S 71°21'W). All samples were taken in the low intertidal zone at fortnightly spring low tides. These two stretches of rocky coast feature large boulders around which small gravel and mollusc shell fragments accumulate. Due to strong wave-action, water circulates deep (tens of centimetres) through the gravel-layer. Gravel fragments are colonized by a diverse community of sponges, hydrozoans, bryozoans, bivalves and ascidians that agglutinate the gravel substrate. Due to the strong water movements, no fine sediment accumulates in these interstitial spaces. The presence of large boulders, however, in combination with clonal organisms and byssal-producing bivalves consolidates the gravel such that burrows built in this substratum probably persist for long-time periods (months). Burrows of snapping shrimp were common in the consolidated gravel substrate, with the species *Alpheus inca* and *Alpheopsis chilensis* being most abundant.

During spring low tides, burrows were opened as carefully as possible. Boulders of manageable size were removed one after the other until the snapping sounds of the shrimp indicated the presence of a burrow. Upon removal of the last stone, all individuals from one burrow were removed as fast as possible and placed in a sampling jar. Often, burrows were difficult to access, and sometimes shrimp may have escaped without the collector becoming aware of their presence. Occasionally shrimp were seen, but could not be collected since they hid in crevices and escaped the 'grip' of the collector. All shrimp that could be collected from one burrow were isolated in a sampling jar, and it was noted whether additional shrimp had been seen escaping or not. Following collection, the shrimp were immediately transferred to the laboratory where they were measured and sexed. The

total body length (BL; from the tip of the rostrum to the base of the telson) of all shrimp was measured with a graduated calliper to the nearest 0.05 mm.

Females were distinguished either based on the presence of embryos under the abdomen or of fully filled ovaries that were visible through the exoskeleton (e.g. Knowlton, 1980; Matthews, personal communication). Individuals without embryos or eggs were examined under the dissecting microscope for the presence of the male's modified 2nd pleopods. Individuals of *Alpheus inca* <15 mm BL and individuals of *Alpheopsis chilensis* <10 mm BL that did not feature any of the above-mentioned characteristics were classified as juveniles. In ovigerous females (with embryos under the abdomen), two embryo stages were distinguished: stage I, embryo with uniformly distributed yolk and absence of eyes; stage II, embryo recognizable with well-developed eyes.

We examined whether a significant correlation existed for the BL of male and female conspecifics found together in one burrow. This analysis was conducted for each of the two shrimp species separately. In a second correlation analysis we examined whether a relationship existed between the BL of *Alpheus inca* and the BL of *Alpheopsis chilensis* found together in one burrow. For this analysis we calculated the average BL of the heterosexual pairs of each species.

RESULTS

A total of 40 burrows were sampled between 13 January and 4 July 2000, four of which only contained juvenile snapping shrimp. The number of juveniles varied between four and 16 individuals per burrow. Of the 36 burrows that contained adult shrimp, 19 (52.8%) contained two *Alpheus inca* and two *Alpheopsis chilensis*, while nine burrows contained three individuals, two from one species and one from the other species (Table 1). In some burrows, additional shrimp individuals were seen during the sampling process, but did escape, while in other cases, no information about other individuals was available. Thus, in the majority of burrows, individuals from both species were found together (Table 1).

Males and females of each species co-occurred in heterosexual pairs in most burrows. While in *Alpheus inca*, all 32 females were found together with a male conspecific, in *Alpheopsis chilensis*, four out of 26 females were found without a male conspecific. Three out of 35 male *Alpheus inca* and four out of 26 male *Alpheopsis chilensis* were found without a female partner in their burrows. Females were associated with male conspecifics irrespective of their reproductive stage (Table 2). For both species, a significant positive relationship existed between the body length of the male and female conspecifics found together in one burrow (Figure 1; $P < 0.05$). In both species, males were slightly smaller than the females with which they cohabited.

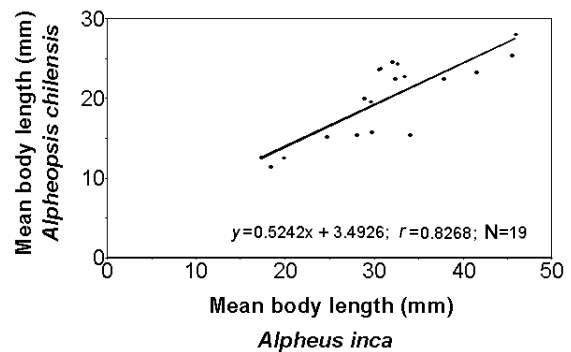
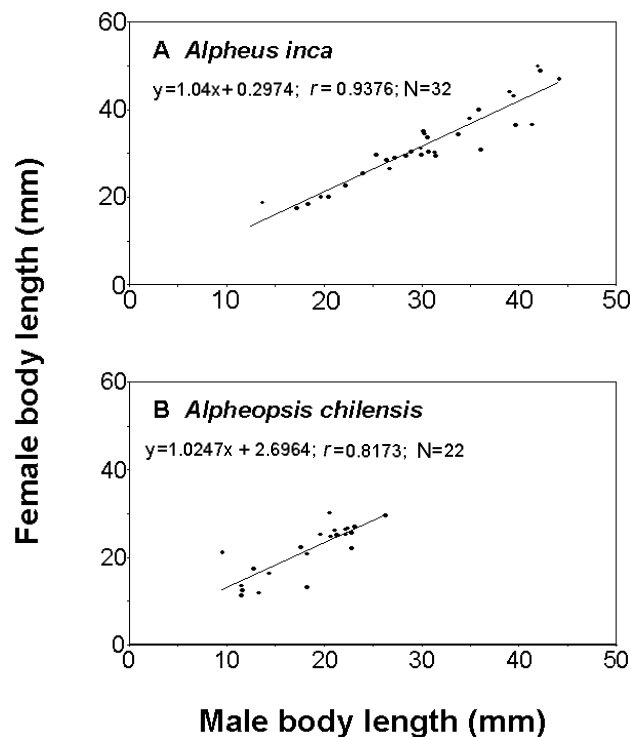
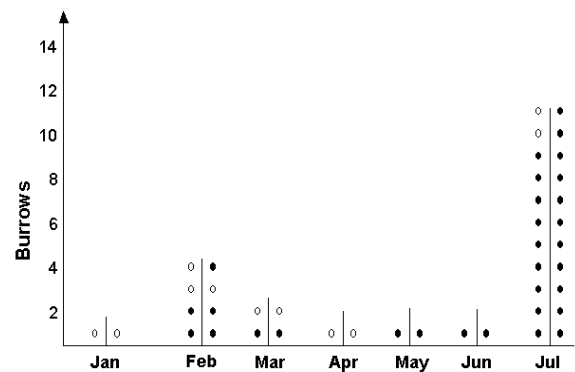
For the 19 burrows, in which two *Alpheus inca* and two *Alpheopsis chilensis* were found together, a positive relationship existed between the average size of *Alpheus inca* (male BL + female BL/2) and the average size of *Alpheopsis chilensis* (Figure 2; $P < 0.05$). The members of *A. chilensis* were always substantially smaller than the members of *Alpheus inca*.

Table 1. Number of snapping shrimp collected from each burrow and number of burrows in which the respective number of shrimp were collected; in some burrows additional shrimp were seen during sampling but could not be collected.

<i>Alpheus inca</i>	<i>Alpheopsis chilensis</i>	Burrows in which no additional shrimp were seen	Burrows in which additional shrimp were seen, but escaped	Total number of burrows collected
2	2	19		19
2	1	6	1	7
2	0	2	4	6
1	2	2		2
1	1	0	1	1
0	2	1		1
		30	6	36

Table 2. Number of female snapping shrimp *Alpheus inca* and *Alpheopsis chilensis* in respective reproductive stages that were found with or without males in the same burrow.

	with males	without males
<i>Alpheus inca</i>		
non-ovigerous	10	0
embryo stage II	17	0
embryo stage I	5	0
Total	32	0
<i>Alpheopsis chilensis</i>		
non-ovigerous	6	2
embryo stage II	11	2
embryo stage I	5	0
Total	22	4

**Figure 2.** Relationships between average body length of male and female *Alpheus inca* and male and female *Alpheopsis chilensis* found together in one burrow; only burrows with two *Alpheus inca* and two *Alpheopsis chilensis* (N=19) are presented; all burrows sampled between 13 January and 7 July 2000 were pooled.**Figure 1.** Relationships between body length of (A) male and female *Alpheus inca* and (B) male and female *Alpheopsis chilensis* found together in one burrow; all burrows with a pair of the respective species that were sampled between 13 January and 7 July 2000 were pooled.**Figure 3.** Relationships between the reproductive stage of female *Alpheus inca* and female *Alpheopsis chilensis* found together in one burrow during each months; shown are all females collected at the respective sampling date; open symbols represent non-ovigerous females, and filled symbols represent ovigerous females; symbols on left side of bars represent *Alpheus inca* and those on right side of bars represent *Alpheopsis chilensis*.

Most females captured during this study were ovigerous (22 out of 32 female *Alpheus inca*; 18 out of 26 female *Alpheopsis chilensis*). Interestingly, females of the two species cohabiting in a burrow appeared to be synchronized in their reproductive stage: often both females from one burrow were ovigerous (or non-ovigerous), irrespective of the sampling date (Figure 3). In 14 burrows (out of a total of 22 burrows in which one

Table 3. Burrows in which one female each of *Alpheus inca* and *Alpheopsis chilensis* were found together and the respective reproductive stages of each female; three different reproductive stages of females were distinguished: non-ovigerous, embryo stage I, and embryo stage II.

<i>Alpheus inca</i>	<i>Alpheopsis chilensis</i>	N	Reproductive synchronization	Total
non-ovigerous	non-ovigerous	4	synchronized	18
embryo I	embryo I	10	synchronized	
embryo II	embryo II	4	synchronized	
non-ovigerous	embryo I	2	non-synchronized	4
non-ovigerous	embryo II	0	non-synchronized	
embryo I	non-ovigerous	2	non-synchronized	
embryo I	embryo II	0	non-synchronized	
embryo II	non-ovigerous	0	non-synchronized	
embryo II	embryo I	0	non-synchronized	
		22		

Table 4. Species of snapping shrimp, associated species, and microhabitat which they share communally.

Species of Alpheid shrimp	Other species	Taxon	Microhabitat	Reference
<i>Alpheus djiboutensis</i>	<i>Cryptocentrotus cryptocentrotus</i>	Teleostei	sB	Karplus et al., 1974
<i>Alpheus purpurilenticularis</i>	<i>Cryptocentrotus steinitzi</i>	Teleostei	sB	Karplus, 1979
<i>Alpheus floridanus</i>	<i>Nes longus</i> , <i>Bathygobius curacao</i>	Teleostei	sB	Karplus, 1992
<i>Alpheus bellulus</i>	<i>Amblyeleotris japonica</i>	Teleostei	sB	Yanagisawa, 1984
<i>Betaeus ensenadensis</i>	<i>Callianassa californiensis</i>	Thalassinoidea	fB	MacGinitie & MacGinitie, 1968
<i>Alpheus dentipes</i>	<i>Upogebia deltaura</i>	Thalassinoidea	fB	Schembri & Jaccarini, 1978
<i>Leptalpheus axianassae</i>	<i>Axianassa australis</i>	Thalassinoidea	fB	Dworschak & Coelho, 1999
<i>Deioneus sandizelli</i>	<i>Corallianassa intesi</i>	Thalassinoidea	fB	Dworschak et al., 2000
	<i>Neocallichirus pachydactylus</i>			
<i>Salmoneus erasimorum</i>	<i>Callianassa tyrrhena</i>	Thalassinoidea	fB	Dworschak et al., 2000
<i>Salmoneus caboverdensis</i>	<i>Neocallichirus pachydactylus</i>	Thalassinoidea	fB	Dworschak et al., 2000
<i>Chelomalpheus crangonus</i>	<i>Upogebia edulis</i>	Thalassinoidea	fB	Anker et al., 2001
<i>Athanas dentiostriis</i>	<i>Upogebia</i> aff. <i>takaoensis</i>	Thalassinoidea	fB	Anker et al., 2001
<i>Athanas amazone</i>	<i>Squilla mantis</i>	Stomatopoda	fB	Froglia & Atkinson, 1998
<i>Alpheus lottini</i>	<i>Trapezia ferruginea</i> , <i>T. cymodoce</i>	Xanthoidea	AC	Lassig, 1977; Vannini, 1985
	<i>Paragobiodon echinocephalus</i>	Teleostei		
<i>Aretopsis amabilis</i>	shells of <i>Dardanus</i> spp.	Coenobitoidea	HS	Vannini et al., 1993
<i>Synalpheus gravieri</i>	<i>Aliaporcellana telestophila</i>	Galattheoidea	AC	Goh et al., 1999
<i>Alpheus inca</i>	<i>Alpheopsis chilensis</i>	Alpheoidea	sB	this study

sB, self-constructed burrow; fB, foreign-constructed burrow; AC, coral colony; HS, hermit crab shell.

female of each species was caught), both females were ovigerous (Figure 3), and the embryos of the two females from one burrow were in the same developmental stage (Table 3).

DISCUSSION

The results presented herein revealed that the two species of snapping shrimp, *Alpheus inca* and *Alpheopsis chilensis*, frequently cohabit in the same burrows. Usually each individual shares a burrow with a conspecific of the opposite sex and a heterosexual pair of the other species. The significant size-relationships found between conspecifics and between the members of the two species cohabiting in one burrow suggests particular intra- and inter-specific interactions and a relatively long-lasting association. In the following discussion, this information will be compared with that of other inter-specific associations, with a particular emphasis on the stability of these associations.

Many marine crustaceans associate with other marine invertebrates in their burrows, tubes and microhabitats (e.g. Schembri & Jaccarini, 1978; Wada et al., 1997), or they simply live on, or in, the body of these hosts. They obtain food and primarily shelter from their hosts. Often, these crustaceans live in pairs or in small aggregations with their hosts. For example, many pinnotherid crabs live as heterosexual pairs in tubes of polychaete or echiurid worms or even within the body cavities of marine invertebrates (e.g. Grove & Woodin, 1996; Baeza, 1999; Hamel et al., 1999), trapezid crabs live as heterosexual pairs on coral hosts (Huber, 1985; Tsuchiya & Yonaha, 1992; Tsuchiya & Taira, 1999), porcellanid crabs as heterosexual pairs or in small aggregations on sea urchins (Werdning, 1983; Baeza & Thiel, 2000). Small shrimp are found in varying numbers on sea urchins or sea anemones (Patton et al., 1985; Omori et al., 1994). Many snapping shrimp also live in heterosexual pairs or in small groups in particular microhabitats or with marine invertebrate hosts (Knowlton, 1980; Kropp, 1987;

Van den Spiegel et al., 1998; Duffy & MacDonald, 1999; Duffy et al., 2000).

In many cases, it is not known how long the cohabitants in a particular microhabitat remain together, but demographic information suggests that some individuals may share home for relatively long-time periods. For example, in the case of snapping shrimp, in which females cohabit with large offspring, these juveniles may require several weeks to reach the sizes which have been measured (Duffy & MacDonald, 1999), similarly as in the mysid *Heteromysis harpax* (Vannini et al., 1993), or in the amphipod *Leucothoe ascidicola* (Thiel, 2000). In some snapping shrimp that live together in heterosexual pairs, identification of individuals has shown that these pairs persist for several months (Knowlton, 1980; Yanagisawa, 1984). In these latter and in other species that live in heterosexual pairs, a linear relationship between the BL of the two heterosexual partners is usually found (Nolan & Salmon, 1970; Schein, 1975; Huber, 1985; Hughes, 1996a). Size-assortative mating is known from many crustacean species with promiscuous mating systems (e.g. Dick & Elwood, 1990), even from symbiotic species. Males of these species only associate with females shortly before these become receptive, but after fertilization of the eggs, males and females separate again (e.g. Wirtz & Diesel, 1983; Diesel, 1988). In contrast, males of *Alpheus inca* and *Alpheopsis chilensis* were always together with females, regardless of the reproductive stage of females. Males are cohabiting with females that will need several weeks before producing another clutch of eggs that can be fertilized. Probably, these heterosexual associations form at an early stage of the reproductive period of these shrimp, and then remain intact unless a mate with a better size-fit appears (e.g. Huber, 1985). It thus appears justified to interpret the size-fit between heterosexual partners as indication for long-lasting cohabitation (e.g. Schein, 1975). In cohabiting pairs of *Alpheus bellulus*, not all pairs fitted this relationship well, which led Yanagisawa (1984) to conclude that possibly one member of these pairs had died and the remaining individual had associated with a new mate. The good size-fit in heterosexual pairs of *Alpheus inca* and *Alpheopsis chilensis* in combination with the observation that most females—regardless of their reproductive stage—were accompanied by male conspecifics also suggests that these pairs remain together for relatively long time periods.

Yanagisawa (1984) also reported a good size-fit and reproductive synchronization for the interspecific association between an alpheid shrimp and a gobiid fish, suggesting that the members of these associations remain together for long time periods (but see Karplus et al., 1974). Similarly, for several symbiotic crustacean species, a significant correlation between the size of the host and the size of the crustacean symbiont has been interpreted as good indication for relatively long-lasting associations between host and symbiont (Christensen & McDermott, 1958; Vannini et al., 1993; Haines et al., 1994; Hamel et al., 1999; Baeza, 1999). Herein, we found significant morphometric relationships for the inter-specific (quartet of the two species) associations of *Alpheus inca* and *Alpheopsis chilensis*. Whether the size-relationship found herein is consequence of long-lasting cohabitation or simply of available space in particular microhabitats (i.e. size of a burrow) cannot be said at present.

Snapping shrimp that share microhabitats with other species may either build the burrows themselves or they may use burrows constructed by others (Table 4). Similarly, the snapping shrimp may or may not be the more aggressive species in these associations. It is therefore not always easy to identify which of the involved species initiated the inter-specific association. However, the complexity of snapping shrimp communication may have been an important precondition for these associations to develop. Most snapping shrimp show sophisticated behaviours towards mates and intruders (Nolan & Salmon, 1970; Schein, 1975). Since the chelae of snapping shrimp are powerful weapons (Versluis et al., 2000), aggressive interactions may result in serious damage to combatants (see e.g. Knowlton & Keller, 1982). Heterosexual partners commonly exhibit behaviours that serve to avoid aggressive interactions between conspecifics (e.g. Knowlton & Keller, 1982; Hughes, 1996a,b). Possibly, this sophisticated intra-specific behaviour has also allowed snapping shrimp to engage in communication with other, often taxonomically unrelated, species (Karplus, 1979; Lassig, 1977; Yanagisawa, 1984; Vannini, 1985; Frogliola & Atkinson, 1998) (Table 4). We therefore propose that the frequent occurrence of snapping shrimp associating with other species is facilitated by the complex intraspecific communication system of snapping shrimp. Whether these associations indeed reflect long-lasting cohabitation or just the capability of snapping shrimp to show (perceive) submissive behaviour towards (by) other burrow inhabitants remains to be investigated in the future.

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