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Settlement of the gastropod *Concholepas concholepas* on shells of conspecific adults

Patricio H. Manríquez*, Sergio A. Navarrete*, Armando Rosson† and Juan Carlos Castilla*‡

*Estación Costera de Investigaciones Marinas, Las Cruces and Centro de Estudios Avanzados de Ecología & Biodiversidad, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114–D, Santiago, Chile. †Bitecma Ltda., Valparaíso, Chile. ‡Corresponding author, e-mail: jcastill@genes.bio.puc.cl

Competent larvae of the commercially important marine gastropod *Concholepas concholepas* (Gastropoda: Muricidae) 'loco', were collected in the field and exposed in the laboratory to adult conspecific shells with and without barnacle epibionts. Settlement and metamorphosis was induced by the presence of barnacles on shells of live or dead conspecifics, but not by *C. concholepas* shells without barnacles. Results from laboratory experiments agreed well with field surveys showing the presence of recruits on conspecific shells overgrown with barnacles in shallow subtidal habitats (~3–30 m deep), suggesting the potential importance of barnacles in inducing settlement and metamorphosis of locos under natural conditions. Most loco recruits were found below the *C. concholepas* shell apex, feeding on barnacles, inhabiting crevices among them, and inside dead barnacles. The mean size of recruits on locos' shells increased over four months from the beginning of the settlement season and no individual larger than 1.5 cm was observed, suggesting that they abandon adult loco shells at this size, roughly 5–6 months after settlement.

INTRODUCTION

The muricid gastropod *Concholepas concholepas* (Bruguière 1789), known in Chile as 'loco', is an important component of intertidal and shallow subtidal communities along the Chilean coast (Castilla, 1999), and is one of the main invertebrates targeted by small-scale fisheries in the country (Leiva & Castilla, 2002). Despite the importance for the management of the fishery, direct evaluation of settlement under natural conditions has not been thoroughly studied. Recruits of *C. concholepas* have been found in the rocky intertidal zone (Guisado & Castilla, 1983; Stotz et al., 1991; Moreno et al., 1993; Martínez & Navarrete, 2002), as well as in shallow subtidal habitats (Arias, 1991; Stotz et al., 1991), and seldom on the shells of conspecifics collected subtidally down to depths of 30 m (Arias, 1991). Attempts to quantify abundances of *C. concholepas* settlers in intertidal conditions, using natural and artificial substrata, have shown positive results (Moreno et al., 1993; Martínez & Navarrete, 2002) and encouraged studies of temporal and spatial variation in intertidal settlement for the species. Few studies have, however, quantified *C. concholepas* settlement in subtidal habitats, mainly because of difficulties associated with their detection and quantification in the usually rough nearshore characteristics of the Chilean coast. Nevertheless, the largest portion of the *C. concholepas* population is found in subtidal habitats (between 3–40 m deep), and there, suitable microhabitats and substrata for *C. concholepas* settlement have not been adequately described. An important issue in the design of management strategies for commercially exploited species is to assess when and where settlement and recruitment takes place.

In this study, we tested the hypothesis that settlement and metamorphosis of *C. concholepas* competent larvae is triggered by cues associated with barnacle prey and that conspecific adult loco shells, naturally overgrown with barnacles, in subtidal habitats serve as settlement sites for new recruits.

MATERIALS AND METHODS

Settlement cues and metamorphosis under laboratory conditions

In 1995, 2000 and 2002, we collected competent planktonic larvae of *Concholepas concholepas* during the peak time of larval abundance (August to December, Poulin et al., 2000a), using an epineustonic net (DiSalvo, 1988) at the Management and Exploitation Area of Caleta El Quisco, central Chile (MEA–El Quisco, 33°23′S 71°42′W). Competent larvae were identified by the presence of an upturned lip on the edge of the shell aperture (DiSalvo, 1988). In the laboratory, and within 12–24 hours following sampling, we exposed them to conspecific adult shells with and without barnacles attached to their surface. Experiments were done at the Estación Costera de Investigaciones Marinas (ECIM) in Las Cruces, Chile (32°43′S 71°38′W).

In year 1995 experiments, small fragments (~1 cm^2) of adult *C. concholepas* shells were placed in glass Petri dishes (10×0.15 cm) filled with 5 ml of 0.45 μm UV-treated filtered still seawater (FSW). Before the experiments, all barnacles and other epibionts attached to the shell surface were mechanically removed (Shells-only treatment), or left balanoid barnacles on the shell pieces (Shell–Barnacle treatment). Petri dishes without shell fragments were used as a control. One newly collected larva was transferred, with a soft artist's brush, into each Petri dish and the three treatments were replicated four times with different larvae. Larvae were kept in the Petri dishes for two weeks, and survivorship, settlement and metamorphosis assessed every 24 hours. Petri dishes with covers and semi-immersed in seawater were maintained at 15 ±2°C and 33 psu, changing seawater and cleaning with tap water every second day. Since in the laboratory competent larvae swim mostly at night (P.H. Manríquez, personal observation), settlement evaluations were made every night at about 0100 hours under a dim red light, examining each larva over a 3-min period to determine whether they were: (1) active (larvae with extended velum), or (2) inactive (larvae resting on the bottom or crawling). An index of settlement behaviour was calculated (ranging from 0 to 1) as 1 − [ST/OT], where ST was swimming time and OT was observation time (3 min). The index approaches one when larvae display no swimming activity, indicating that settlement has occurred. Larvae were considered to have metamorphosed when they lost the larval swimming organ, changed protoconch coloration and the posterior new shell or teleoconch was formed (Figure 1).

In year 2000 experiments, we examined the effect of whole shells and live animals of adult *C. concholepas* on metamorphosis of competent larvae using glass aquaria (15×15×25 cm) containing 5 l of FSW. The treatments consisted of live *C. concholepas* adults whose shells either had been completely cleaned or not been cleaned of barnacles (Live Shell-only treatment, Live Shell–Barnacle treatment). We also used empty shells of newly sacrificed *C. concholepas* adults with (Dead Shell–Barnacle treatment) and without live barnacles on them (Dead Shell-only treatment) as treatments. In all cases, locos' shells were carefully cleaned with the aid of a brush to remove epibionts (i.e. barnacles, bryozoans, crustose algae and mussels). As a control for manipulations, we assigned individual larvae to containers filled with 5 l of FSW without adult shells. The four treatments and control were replicated four times with different larvae. Experiments were conducted with still seawater, since bubbling is a known inductor of metamorphosis in competent larvae of *C. concholepas* (DiSalvo & Carriker, 1994). To avoid the potential effect of adult feeding on larval behaviour, adults were fed *ad libitum* with mussels before the experiments, but food-deprived during the experimental period. In year 2002 experiments, we repeated the same basic experiment, but with six replicates of the Shell-only and Shell–Barnacle treatments and a manipulation control. Because of the larger containers, visual estimates of settlement were not conducted during 2000 and 2002 experiments.

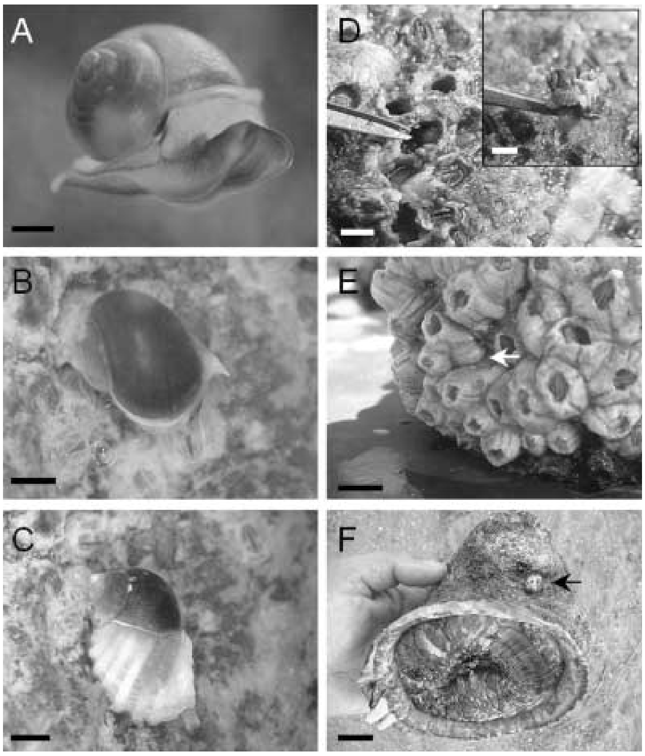

Figure 1. Photographs showing (A) a competent larva of *Concholepas concholepas* caught at MEA–El Quisco; (B) a 24 h old postmetamorphic individual, metamorphosed under laboratory conditions and feeding on a small barnacle; (C) a two-week old postmetamorphic individual raised under laboratory conditions; (D) an early postmetamorphic individual (insert) growing on an adult conspecific shell; (E–F) post settlers individuals growing on adult conspecific shells. Scale bars: A–C, 500 μm; D, 2000 μm; E,F, 1 cm.

Pilot field surveys of recruits on adult shells

To determine whether recruits of *C. concholepas* were present on shells of conspecifics, we sampled juveniles and adults collected subtidally. In this study, we defined *C. concholepas* recruits as individuals with a peristome length (PL, maximum length from the siphonal notch to the posterior edge of the shell) ≤1.5 cm, and further discriminated between early settlers (≤0.20 cm PL) and post-settlers (0.21–1.50 cm PL). To search for recruits on shells, empty loco shells in individual plastic bags were transported to the laboratory within 3 h from collection, or shells were inspected directly in the field. Since larval size at metamorphosis is ~0.16–0.19 cm PL (DiSalvo, 1988; P.H. Manríquez, personal observation), observations were carried out without the aid of magnification. The number of recruits on each shell was recorded, and when transported to the laboratory, recruits were measured to the nearest 0.01 cm under a stereomicroscope.

Since we aimed to develop a methodology that would facilitate monitoring of loco recruitment during the regular *C. concholepas* harvesting conducted by fishers, and which could be applied in different locations throughout the country, most of the surveys were based on adult specimens collected subtidally by divers during the period that the fishery was legally open. Currently, the fishery is closed in Chile for much of the year with an open season of a few days or weeks, which dictated when we conducted the surveys. The minimum extracting legal size is 10 cm PL, which restricted our sampling to adult individuals (summary of shell sizes sampled in Table 1). With these sampling restrictions, we conducted pilot surveys during December 2000, which included a total of 736 adult locos collected by divers from the MEA–EQ, and 130 locos from Caleta Las Conchas, Los Vilos (31°54′S 71°31′W).

Depth distribution survey

To characterize variation in the abundance of *C. concholepas* recruits with depth, a stratified subtidal

Table 1. *Date and depth range of adult specimens of* Concholepas concholepas *collected at each site. Number and size range of inspected specimens is also included.*

Site	Date	Depth range (m)	No. specimens	Size range (cm)
Las Conchas	December 2000	5–30	130	9.9–12.3
Leandro	December 2000	1–5	100	10.1–11.3
	December 2000	5–15	100	10.0–11.0
	December 2000	15–30	100	9.8–10.7
El Quisco	December 2000	5–18	736	9.8–13.3
	October–November 2001	3–30	2880	10.0–14.3
	March 2002	3–12	1272	4.1–14.8
	August 2002	4–17	1078	9.6–13.7
	September 2002	3–15	510	9.9–12.9
La Chimba	January 2002	3–6	146	6.8–11.1
	April 2002	3–8	98	4–10.4
Estaquilla	June 2002	8–20	450	11.4–15.3

survey was conducted in December 2000 in the vicinity of Caleta Leandro (36°38′S 73°06′W). There, 100 adult specimens were collected from three depth ranges (Table 1), visually inspected on-board the boat, registering the number of recruits on each shell and then later measured them in the laboratory. After inspection, adults were returned to their habitat.

Distribution of recruits on shells with different epibionts

In the pilot surveys the presence of small *C. concholepas* changed depending on the epibionts on the shells. Therefore, shells were classified into two to eight different categories according to the composition of epibionts, which varied in the different sampling sites (Table 2), and additional samplings were conducted in years 2001 and 2002 at four different sites (Table 1). In these surveys, 30 adult *C. concholepas* were randomly sampled from each artisanal boat involved in the fishery. When two divers operated from a single boat, the sample size per boat was doubled. The location in the shells where recruits were found was also recorded as either around the loco's apex, or on the rest of the shell. To determine if there was a preference for one of those areas, the number of individuals by surface area (cm^2) was standardized. Shell surface areas were estimated by tightly wrapping the shell with an aluminium sheet and then cutting out the section plastering the apex and the rest of the shell. The surface of each section was then measured with a digital planimeter (Ushikata, Digi-Plan220L). The specific location of recruits was notedc as: (1) inside dead barnacles; (2) among barnacles; (3) on algae; and (4) on bare shell.

Additionally, adult individuals were sampled in March 2002 (N=1272), April 2002 (N=120 poached individuals that had been impounded by police), August (N= 1078), and September 2002 (N=510) at MEA–EQ to determine whether or not recruits were still present on adult shells (roughly 5–10 months after the peak recruitment for this species, Poulin et al., 2002a; Martínez & Navarrete, 2002). Similarly, in January 2002 (N=146) and April

Table 2. *Position of* Concholepas concholepas *recruits in different categories of shells classified according to composition of epibionts at MEA–El Quisco and Caleta La Chimba. Values in the table are the total number of recruits found in the apex or the rest of the shell. Figures in parentheses are the number of recruits in each sector of the shell standardized by area of that sector.*

El Quisco	30 Oct.–2 Nov.		9–10 Nov.		11–13 Dec.		15 Mar.	
Shell category	Apex	Rest	Apex	Rest	Apex	Rest	Apex	Rest
Bare[1]	0	0	0	0	0	0	0	0
Bare–Barnacle[2]	2 (0.119)	3 (0.008)	4 (0.119)	3 (0.008)	1 (0.118)	1 (0.009)	0	0
Barnacle[3]	39 (0.128)	34 (0.011)	29 (0.137)	17 (0.009)	16 (0.132)	13 (0.009)	2 (0.142)	0
Barnacle–*Gelidium*[4]	14 (0.116)	6 (0.008)	6 (0.123)	8 (0.008)	10 (0.129)	5 (0.008)	0	0
Gelidium[5]	1 (0.111)	2 (0.013)	0	0	0	0	0	0
Bare–*Gelidium*[6]	1 (0.230)	1 (0.008)	0	0	0	0	0	0
Coralline algae[7]	0	0	0	0	0	0	0	0
Total	57 (0.129)	46 (0.011)	39 (0.133)	28 (0.009)	27 (0.130)	19 (0.009)	2 (0.142)	0
La Chimba	15 Jan.							
	Umbo	Rest						
Barnacle	3	18						
Barnacle–*Pyura*[8]	0	2						

Categories of shell according to the composition of epibionts: [1], barnacle: 80–100% of the shell covered by barnacles, mostly *Notobalanus flosculus* and *Balanus laevis*; [2], *Gelidium*: 80–100% of the shell covered by *Gelidium chilense*; [3], bare: shell virtually free of epibiont; [4], coralline algae: 80–100% of the shell covered by encrusting coralline lithothamnioid algae; [5], barnacle–*Gelidium*: 80–100% of the shell covered by a mix of balanoid barnacles and *G. chilense*; [6], bare–*Gelidium*, 30–50% of the shell cover by *G. chilense* and the rest basically free of epibiont and barnacles; [7], bare–barnacle, 30–50% of the shell covered by barnacles and the rest free of epibionts; [8], barnacle–*Pyura*: shell covered by a mix of barnacles and *Pyura praeputialis* (Heller, 1878).

2002 (N=98) at Caleta La Chimba (23°32′S 70°22′W) sampling took place.

Accuracy of sampling method

To evaluate the accuracy of the sampling method, the number of recruits found on *C. concholepas* shells by naked eye inspections were compared with the numbers found in the same shells after they had been cleaned of all epibionts and the sample examined under a stereomicroscope. This procedure was repeated with 50 shells of the *Gelidium* and Barnacle categories (see Table 2) from Caleta El Quisco, and 20 shells of the Barnacle and Barnacle–*Pyura* categories from La Chimba. In all shell categories, all recruits were found by naked eye inspection, suggesting that our sampling methodology was adequate.

RESULTS

Settlement cues and metamorphosis under laboratory conditions

In year 1995 experiments, settlement behaviour of *Concholepas concholepas* competent larvae began on the first day after initiating the trials and in the two treatments with shell fragments, crawling was concentrated on the locos' shell surface rather than on the bottom of the Petri dish. In the Shell–Barnacle treatment, the mean settlement behaviour index increased from the first experimental day reaching its maximum six days later, when all larvae metamorphosed (Figure 2A). In the Shell-only treatment, low settlement behaviour was recorded during the first three days, but then increased to about 0.9 until the end of the experiment (14 days later), without larvae actually settling and metamorphosing (Figure 2B). In the control treatment, settlement behaviour fluctuated between 0.6 and 0.9 throughout the first ten days, and then increased to over 0.9 for the remainder of the experiment, without settlement and metamorphosis taking place (Figure 2C).

In year 2000 and 2002 experiments, settlement behaviour began in all treatments two days after initiating the trials. As before, in year 2000 experiment metamorphosis was achieved only when competent larvae were maintained with conspecific locos' shells covered with barnacles, and no difference was observed between Live Shell–Barnacle and Dead Shell–Barnacle treatments. In these treatments, all larvae metamorphosed between four and five days from the beginning of the trials (Figure 3A). No metamorphosis was observed in the control treatment (Figure 3B). In year 2002 experiment, 100% of locos' metamorphosis was achieved by the fifth day in the Shell–Barnacle treatment (Figure 3C). In the Shell-only treatment, only 50% of metamorphosis occurred by the end of the experiment (Figure 3C) and no metamorphosis was observed in the control treatment (Figure 3D).

Pilot field surveys of recruits on adult shells

A total of 48 and 14 recruits were found on equal numbers of adult shells at Caleta El Quisco and Las Conchas respectively in December 2001, representing approximately 6% and 11% of the sampled adult shells at these sites. Adult shell sizes were similar between these sites (Table 1). The small sizes of recruits (0.46 cm PL, SD=0.21, and 0.42 cm, SD=0.08, at El Quisco and Las Conchas, respectively) and morphological characteristics (Figure 1D,E), suggested that they had metamorphosed from the plankton.

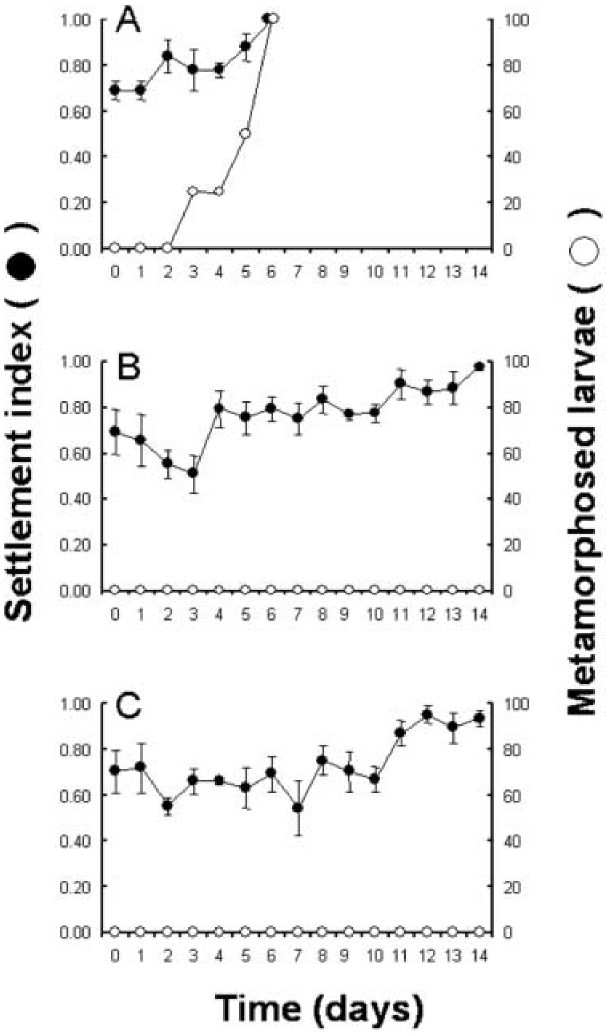

Figure 2. Mean (±SE) settlement behaviour index and percentage of metamorphosed competent larvae of *Concholepas concholepas* (N=4) under different treatment conditions in the 1995 experiment: (A) in the presence of adult *C. concholepas* shell fragments from which all barnacles and other encrusting organisms were removed; (B) in the presence of shell fragments with barnacles; and (C) control without shells.

Depth distribution survey

Post-settlers of *C. concholepas* were found in 10% of the adult shells sampled between 1–5 m depth (mean recruit density=0.11 ind/shell, SD=0.3, N=100), in 8% of those sampled between 5–15 m depth (mean recruit density=0.09 ind/shell, SD= 0.3, N=100) and no recruits were found on shells collected below 15 m.

Distribution of recruits on shells with different epibionts

At Caleta El Quisco, most adult individuals were characterized by shells overgrown by barnacles and *Gelidium chilense* (Barnacle and *Gelidium* categories, Figure 4A). Shells on which barnacles were present represented more than 50% of the total (Figure 4A). During year 2001,

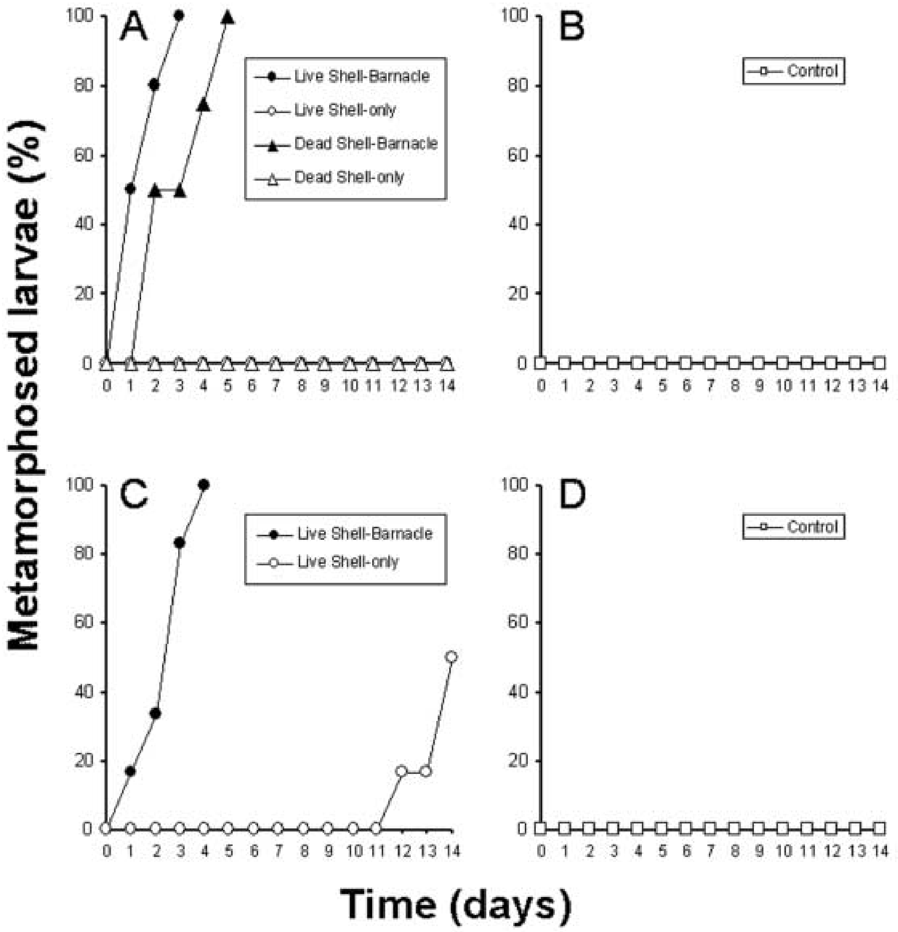

Figure 3. Percentage of metamorphosed competent larvae of *Concholepas concholepas* reared under different treatment conditions in the year 2000 (A and B) and 2002 (C and D) experiments.

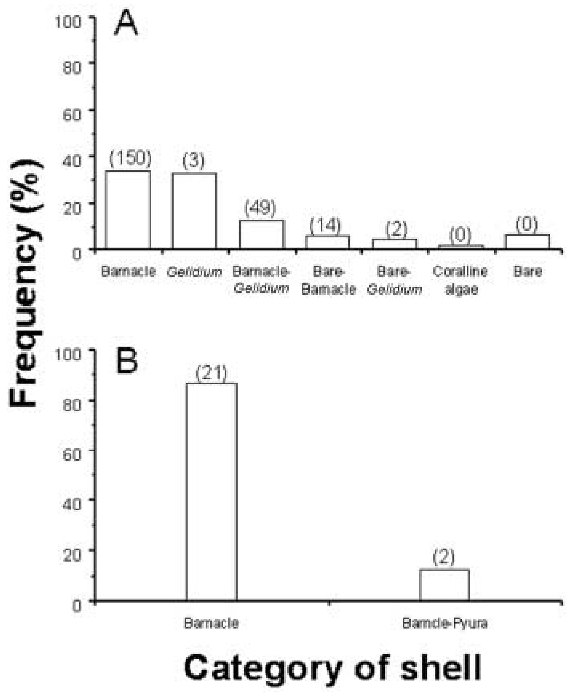

Figure 4. Percentage of different categories of shells of *Concholepas concholepas* adults in four successive samplings at MEA–El Quisco (A: October–December 2001 and March 2002) and in a single sampling episode at Caleta la Chimba (B: January 2002). Values on top of each bar are the number of shells with recruits.

8% of the adult shells collected had at least one recruit at Caleta El Quisco, but in March 2002 only less than 1% of the locos' shells had recruits. The proportion of shells with recruits varied significantly among shell categories type (χ^2=1.54; df=4; $P<0.001$). The highest densities of recruits were found on conspecific shells corresponding to the Barnacle, Bare–Barnacle and *Gelidium*–Barnacle categories (Figure 5A), while on the other shell categories recruit densities were always low or zero (Figure 5A–D). At Caleta La Chimba, between 87% (January) and 96% (April) of the adult shells classified in the barnacle category and the rest corresponded to Barnacle–*Pyura* shells (Figure 5E). No *C. concholepas* early settlers ($\leqslant$0.2 cm of PL) were found on adult shells, but post-settlers were found on the Barnacle and Barnacle–*Pyura* shell categories (Figure 5E, mean recruit densities= 0.16 in both categories). In April and August 2002, neither early settlers nor post-settlers were found on loco shells. At Caleta Estaquilla, Barnacle and Bare–Barnacle shell categories represented 98% and 2% of the total, respectively, and in 3% of them at least one post-settler recruit was found (mean recruit densities=0.03 ind/shell, SD=0.21, N=442, and 0.13 ind/shell, SD=0.37, N=8, respectively). The shells in this locality were so heavily overgrown it was not possible to assign recruits to the apex or rest of the shell area.

Specific location of the 220 recruits of *C. concholepas* on adult conspecific shells collected in four surveys at MEA–El Quisco between October 2001 and March 2002

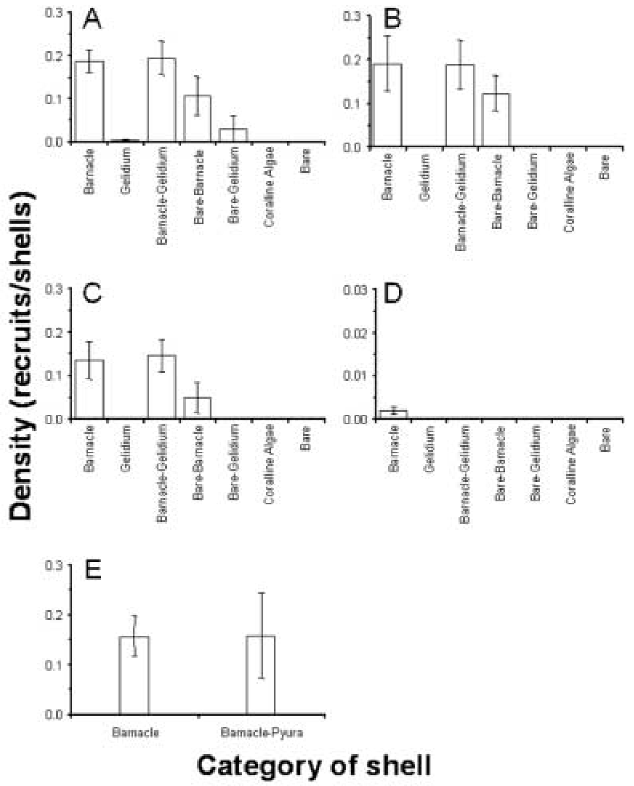

Figure 5. Mean (±SE) density of recruits of *Concholepas concholepas* (recruits/conspecific adult shell) in each shell category found in four successive samplings spanning from October 2001 to March 2002 at MEA–El Quisco A, October–November 2001; B, November 2001; C, December 2001; D, March 2002) and (E) in a single sampling episode at Caleta la Chimba, during January 2002.

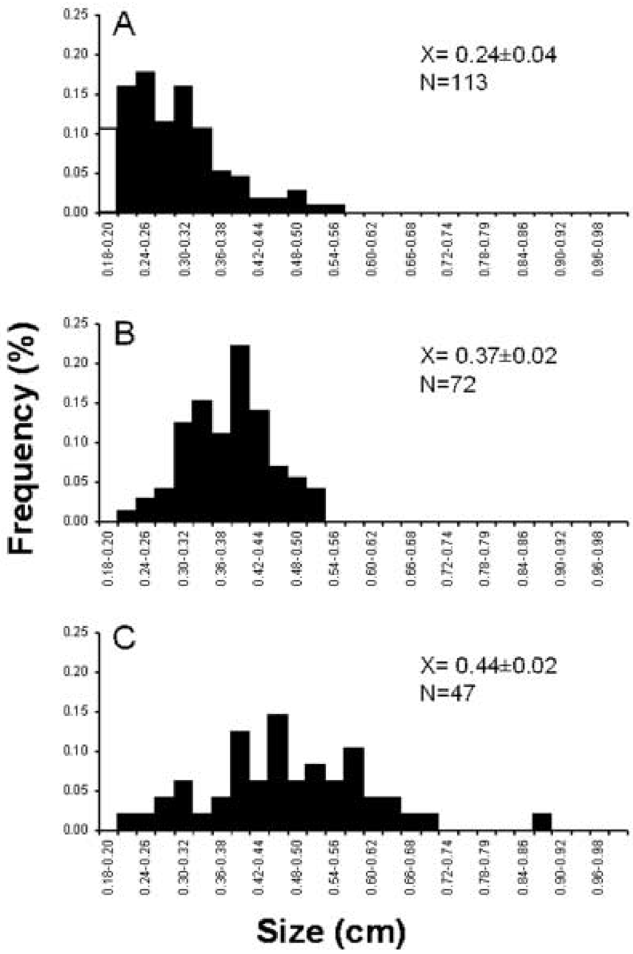

Figure 6. Size distribution (mean peristome length), of *Concholepas concholepas* recruits found in adult conspecific shells. Data correspond to three successive samplings conducted at MEA–El Quisco between October and December 2001. Open and solid bars correspond to early settlers ($\leqslant$0.2 cm of PL) and post-settlers (>0.2 cm of PL), respectively. Values on each panel are mean peristome (±SE) and sample size.

shows that most recruits were found in small openings among adult barnacles (87%), especially in areas with barnacle recruits. Occasionally, recruits of *C. concholepas* were found inside dead adult barnacles (11%, Figure 1D). The rest of the recruits were found on bare shell or on the surface of algae encrusting loco shells (2%). Overall abundances of *C. concholepas* recruits found on the apex and the rest of the shell were similar (Table 2). However, standardizing by shell surface area showed between 15 and 35 times higher densities of recruits on the apex (Table 2). Other mobile invertebrates such as chiton, key-hole limpet, starfish, and crab were also commonly found around the apex. Small mussels, *Brachidontes granulata* (Harley), a common food item of *C. concholepas* (Méndez & Cancino, 1990), were also found in this region of the shell. At Caleta La Chimba, we found the highest abundances of *C. concholepas* recruits on the rest of the shell area (Table 2).

Size distribution of *C. concholepas* recruits found on adult conspecifics at Caleta El Quisco showed that early settlers (mean=0.24 cm PL; SD=0.43; N=113) were found only during the first surveys conducted in October 2001 (Figure 6). Post-settlers showing a mean 0.37 cm PL (SD=0.17; N=72; Figure 6) were found in surveys conducted 7–8 days later, and post-settlers of 0.44 PL (SD=0.14; N=47; Figure 6) were found 39–40 days later. In March 2002, we found only three post-settlers, mean size of 1.36 cm PL (SD=0.17). Neither recruits nor post-settlers were found in the last field surveys done in April and August 2002.

DISCUSSION

Results from laboratory experiments demonstrate that barnacles on shells of *Concholepas concholepas* induce settlement behaviour and metamorphosis of competent loco larvae. The results also provide an explanation for the association between recruits of *C. concholepas* and recruitment of barnacles observed in the field (Martínez & Navarrete, 2002; authors' personal observations). Under natural conditions and throughout the settlement season, we found *C. concholepas* recruits on conspecific adult shells collected at sites between 23° and 36°S, suggesting that this may be a general phenomenon along the Chilean coast. Thus, adult shells overgrown by barnacles may play an important role, mediating larval settlement and metamorphosis for the species under natural conditions. The settlement microhabitat offered by *C. concholepas* shells may also be locally important as natural refugia in areas where barnacle beds on rock surfaces are scarce or have been decimated by predators.

The apparent selectivity of *C. concholepas* recruits to settle on conspecifics, overgrown by barnacles, highlights the important role played by prey on inducing settlement and metamorphosis (see also DiSalvo & Carriker, 1994). It is suggested that larvae of this species respond to chemical cues originated from barnacle prey, by swimming downwards to the bottom and exhibiting exploratory settlement behaviour. Although in several other marine invertebrates induction of settlement and metamorphosis by conspecific-derived cues has been described (Pearce & Scheibling, 1990; Bryan et al., 1997), these results show that there is no such effect in *C. concholepas*. The laboratory experiments also show that when appropriate settlement substratum is not present, competent larvae can delay metamorphosis for periods of at least 14 days. The ability to delay metamorphosis is common in the larvae of many invertebrates (reviewed in Pechenick, 1990). A laboratory artefact produced by the shallow waters of the experimental containers probably triggered the onset of settlement behaviour (either on loco shells with or without barnacles). However, this condition might be similar to those encountered by larvae when approaching shallow waters in the surf zone. Moreover, Poulin et al. (2002b) presented evidence suggesting that competent *C. concholepas* larvae undergo reverse diel vertical migration, which would allow them to explore an appropriate benthic habitat. A long temporal dissociation between settlement and metamorphosis is also possible in this species as all settled larvae in laboratory experiments were able to metamorphose when exposed to barnacles, at the end of the experiments. This suggests that the strategy of delaying metamorphosis may also be advantageous for the loco, allowing competent larvae to crawl longer and search for suitable habitats to metamorphose.

Presence of early loco settlers in adult shells between October–November suggests that settlement is taking place on this substratum. It is not completely clear for how long *C. concholepas* recruits remain on adult shells. However, the data suggest that they may leave the adult shells before the beginning of the following mating season. Indeed, we did not find recruits or small juveniles on adult shells during the April and August 2002 surveys at El Quisco or April 2002 at La Chimba. In central Chile, the intertidal and subtidal mating season of *C. concholepas* takes place between March and June (Manríquez & Castilla, 2001). Mating involves the formation of aggregations in which males climb on top of the females (Castilla, 1974), and therefore, it is expected that recruits may leave conspecific loco shells before being consumed or bulldozed by adults. Mortality of post-settlers caused by pedal smothering by adults has been recorded in other gastropods (Naylor & McShane, 2001) and may be also important in *C. concholepas*. Further studies under natural conditions are needed to determine the fate of recruits on conspecific shells. The results show that recruitment of *C. concholepas* on conspecific adult shells takes place down to 15 m depth. However, in another study recruits of *C. concholepas* have been reported down to 30 m (Arias, 1991). Therefore, further studies are also needed to investigate recruitment in this species at different depths and on alternative microhabitats.

The ornamentation of neogastropods has been reported as providing a wide variety of refuges for small invertebrates (Olabarria, 2000). Specimens of *C. concholepas* lack the distinctive characteristics of other muricid species such as spines and ornamentation. Nevertheless, barnacles can overgrow nearly 100% of the adult shell surface, generating potential refuges for new settlers or small invertebrates, including early settlers and post-settlers of conspecifics. Moreover, adult shells also provide food, free transport and potentially protection against predators. The higher abundance of *C. concholepas* recruits found in the apex area than in the rest of the shell suggest the important role that microhabitats present in the shells as refuges.

If recruitment on adult loco shells represents an important fraction of the total recruitment to local populations, then the potential for post-dispersal Allee effects (*sensu* Quinn et al., 1993) may be considered in the future management of the species. Allee effects due to fertilization success and recruitment refugia associated with adults make populations showing such effects particularly susceptible to collapsing as harvesting pressure drops adult populations below the densities required to ensure adequate recruitment (Karlson & Levitan, 1990). Allee effects (Quinn et al., 1993) predict that harvesting strategies must explicitly consider adult threshold densities and not only bulk population abundances. Thus, quantitative assessment of the importance of adult shells on total *C. concholepas* recruitment should be a focus of future research. Currently, loco cannot legally be removed from the shell before trading, leaving piles of shells in the grounds of canning companies. Therefore, the return of empty shells to the fishing grounds may be a reasonable management strategy to recover refugia and settlers themselves to the adult habitat. Furthermore, since most *C. concholepas* recruits were detected without the need for magnification and on shells collected by divers using the standard extracting methods, we suggest that examination of adult shells during the settlement season may be an easy way to monitor temporal variability in the subtidal recruitment of the loco. The present study also shows that other possible benefits of protected areas for exploited species (see Castilla & Defeo, 2001) may be to improve recruitment when settlement takes place in natural refugia originated by their own protected species.

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