

Coralline algal rhodoliths enhance larval settlement and early growth of the Pacific calico scallop *Argopecten ventricosus*

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ABSTRACT: The features of heterogeneous rhodolith beds (maerl) that contribute to their role as nursery habitats in coastal ecosystems are poorly understood. Rhodoliths are branched, unattached coralline algae that form complex benthic substrates and support diverse communities worldwide. Pacific calico scallops *Argopecten ventricosus* = *circularis* (Sowerby II, 1842) occur in high densities in rhodolith beds in the Gulf of California, México. In this study, we found that *Lithophyllum margaritae* rhodoliths enhanced larval scallop settlement and early post-settlement growth, and examined the settlement cues responsible. In both field and laboratory experiments, larval settlement was significantly higher on (1) rhodolith derived vs. non-coralline sedimentary substrates, (2) living vs. non-living coralline surfaces, and (3) substrates with higher (whole, branching rhodoliths) vs. lower (rhodolith fragments or sediment) structural complexity. In the field, larval settlement (mean \pm SE) onto rhodoliths was 30 to 35 times higher on live rhodoliths (55.0 ± 13.4 and 84.4 ± 8.8 larvae cm^{-2}) than on non-carbonate sediment (1.8 ± 0.8 and 2.4 ± 0.9 larvae cm^{-2}) relative to the surrounding rhodolith or sand habitat, respectively. In a laboratory preference experiment, when comparing live vs. dead coralline surfaces respectively, settlement density was 3.3 times greater (55.8 ± 14.6 vs. 17.0 ± 4.9 larvae cm^{-2}) on whole rhodoliths and 7 times greater (24.2 ± 4.7 vs. 3.4 ± 1.3 larvae cm^{-2}) on fragmented rhodoliths. The strong cueing to live coralline surfaces may have resulted from live coralline algal surfaces or surface biofilms. Growth, presented as post-settlement size, was significantly greater in scallops that settled onto whole vs. fragmented rhodolith substrates for both live (246.6 ± 1.9 vs. 238.9 ± 4.4 μm) and dead (244.2 ± 2.8 vs. 234.7 ± 5.6 μm) coralline surfaces. The structural and coralline cues provided by live, intact rhodoliths and their large-grained sediments contribute to the importance of rhodolith beds as nursery habitats by increasing both scallop settlement and post-settlement growth. Protection of living rhodolith habitats can enhance scallop and other invertebrate populations as well as the sustainability of scallop fisheries by enhancing early life stages.

KEY WORDS: *Argopecten ventricosus* · Coralline · Rhodolith · Scallop · Larval settlement cues · *Lithophyllum margaritae* · Maerl · Bahía Concepción

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INTRODUCTION

Understanding the link between the planktonic and benthic life history phases of marine organisms is a major focus in marine ecology (Caley et al. 1996, Morgan 2001). For marine invertebrates with complex life histories, the process of settlement and metamorphosis

is a critical and typically irreversible transition from planktonic to benthic life-history phases. An increasing number of studies have shown that the settlement process is not random (Crisp 1976, Hadfield 1986, Young 1990), that variation can be an important factor determining the abundance and distribution of organisms (Thorson 1966, Underwood & Denley 1984, Con-

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nell 1985, Raimondi 1990), and thereby strongly influence population and community-level processes (Rodríguez et al. 1993, Connolly & Roughgarden 1999). While hydrodynamic processes are known to strongly influence the delivery of larvae to suitable substrates (Butman et al. 1988, Abelson & Denny 1997), behavior in response to cues is also important in determining settlement patterns (Crisp 1974, Hadfield 1986, Raimondi & Morse 2000).

Settlement cues, often required for metamorphosis of marine invertebrate larvae (Morse & Morse 1984, Pearce & Scheibling 1990), are thought to be indicative of environmental features that enhance survivorship (e.g. habitat, refuge, food or conspecifics). Physical cues include hydrodynamics (Crisp 1955), light (Crisp & Ritz 1973), depth (Knight-Jones & Morgan 1966), surface structural complexity (Harvey et al. 1993, Pearce & Bourget 1996), disturbance events (Woodin et al. 1995) and surface chemistry (Hay 1996, Steinberg & de Nys 2002). Biological cues include presence of conspecifics (Keough 1998) and bacterial or bioorganic films (Maki et al. 1989, Keough & Raimondi 1995, Huggett et al. 2006). In addition, physical and biological cues can act synergistically (Crisp & Meadows 1963, Gee 1965, Le Tourneux & Bourget 1988). Few studies have been conducted in the field to understand *in situ* larval responses (Keough & Raimondi 1995) and how the distribution or magnitude of various cues might influence larval settlement (Underwood & Keough 2000).

Complex seaweed surfaces, such as those found in coralline algae, provide combinations of physical and biological cues that can influence settlement in a range of invertebrates (Walters et al. 1996, Steinberg & de Nys 2002). Species of geniculate and non-geniculate (crustose) forms of coralline red algae occur in most coastal environments (Bosence 1983). A variety of invertebrate larvae are induced to settle on coralline algae by the physical features of the complex surfaces found on attached coralline algae (Daume et al. 1999a), or by the surface chemistry of algal pigments or associated epibionts (Morse 1992, Huggett et al. 2006); therefore, coralline algal distribution can have a strong influence on the distribution of some marine invertebrates (Raimondi & Morse 2000). Understanding the importance of particular coralline surface cues to larval settlement enhances the understanding of the ecological role corallines play in the distribution of some marine species.

Unlike attached corallines, rhodoliths (also known as maerl) are individual, branching, unattached, mobile forms of crustose coralline algae (Fig. 1) that collectively form large heterogeneous beds of biogenic substrates on sedimentary benthos worldwide (Foster 2001). Rhodolith beds support a diverse and abundant

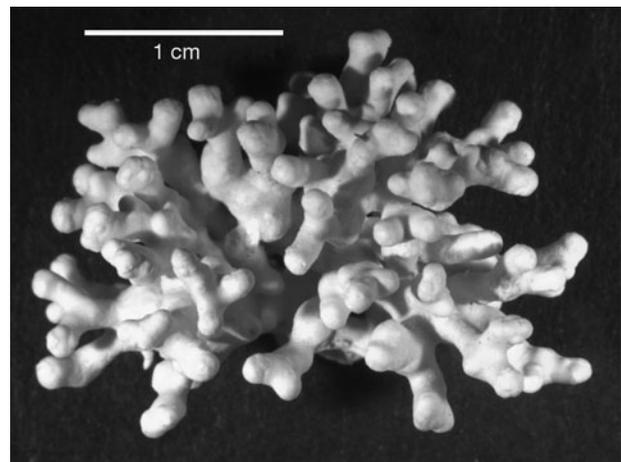


Fig. 1. *Lithophyllum margaritae*. Fruticose branching rhodolith used in all experiments, collected at a 6–8 m depth at the El Requesón rhodolith bed, Bahía Concepción

assemblage of soft and hard bottom organisms (Keegan 1974, Bosence 1979, Steller et al. 2003), including abundant juvenile stages of some invertebrates (Kamenos et al. 2004a, D. Steller pers obs.). However, few studies have examined the processes driving these substrate–species relationships. Scallops are found in rhodolith beds and commercial harvesting of Atlantic species has led to the destruction, and subsequently protection, of numerous European maerl beds due to their fragile nature (Hall-Spencer & Moore 2000b). The trawling for bivalves reduces epifaunal and infaunal diversity through the loss of habitat complexity and through rhodolith thallus fragmentation resulting from the large-scale homogenization of the benthos (Hall-Spencer 1999). Studies have demonstrated that maintaining a high cover of whole, branching rhodolith thalli is essential to the maintenance of high biodiversity (Grall & Glemarec 1997, Grall et al. 2006). Increasing anthropogenic disturbances have motivated recent conservation efforts focused on the protection of fragile rhodolith habitats combined with addressing the need to more clearly understand the ecological role of this benthic habitat in species relationships.

Scallop life histories are fairly well understood and the association of adult populations with rhodoliths (Hily et al. 1992, Hall-Spencer & Moore 2000b) offers a model species with which to examine the ecological interactions and possible benefits from an association with rhodoliths at different life stages. This may provide insight into the high abundance and diversity of other adult species associated with this habitat. High juvenile scallop densities (≥ 18 to 35 mm) in rhodolith beds (Kamenos et al. 2004a) have been associated with greater selection, attachment and growth and indicate that rhodolith habitats are used as nursery grounds or

refuge for some species (Kamenos et al. 2004b,c). Additionally, association with rhodolith beds has been shown to confer a substrate-mediated benefit to adult scallops as a refuge from predators (Kamenos et al. 2006). Less, however, is known about rhodolith substrate relationships with larval stages. One study measured high post-larval scallop recruitment to experimental spat collectors over maerl substrates in the Georges Banks, leading to the suggestion that rhodolith beds may serve as larval 'nursery grounds' (Thouzeau 1991). The reduction of structural complexity and killing of live coralline surfaces of rhodoliths due to anthropogenic disturbances motivates the need to examine the role of rhodolith and rhodolith derived substrates in the induction of larval settlement and subsequent growth of newly settled individuals.

Scallop fisheries are important in bays in the Gulf of California and along the Pacific coast of Baja California, Mexico (Felix Pico 1991). A primary fisheries species is the Pacific calico or catarina scallop *Argopecten ventricosus* = *circularis* (Sowerby II, 1842), a motile, soft bottom species that reaches market size within a year. Extreme population declines due to multiple factors have resulted in efforts in Mexico to increase natural populations through aquaculture and enhanced field recruitment (Ruiz-Martínez & Cáceres-Martínez 1991, Felix-Pico et al. 1997, Maeda-Martínez et al. 1997). Similar population declines in Panamanian fisheries of the same species have been attributed to a lack of suitable habitat for early life stages, predation and changes in oceanographic conditions (Medina et al. 2007). For many scallop species, larval settlement occurs on a variety of substrates, but appears to be enhanced by increased substrate complexity and the degree of bio-fouling (Brand et al. 1980, Pearce & Bourget 1996, Harvey & Bourget 1997). The importance of heterogeneous substrates to recruitment along with the co-occurrence of large populations of scallops and rhodoliths (Steller et al. 2003) suggests the possibility of strong cuing of *A. ventricosus* larvae to rhodolith surfaces for settlement.

Using *Argopecten ventricosus* as a model, we examine the importance of surface cues provided by 2 common benthic substrates in the Gulf of California, the rhodolith *Lithophyllum margaritae* and non-carbonate sediment, in the induction of larval scallop settlement and subsequent early post-settlement growth. We hypothesize that (1) settlement of scallop larvae will be enhanced on rhodolith derived substrates with live coralline surfaces and the high structural complexity of intact branching relative to dead or non-coralline surfaces with fragmented branches or low structural complexity, and (2) larvae selecting substrates with optimal surface cues will gain a benefit of enhanced post-settlement growth. Understanding the relative

importance of rhodolith characteristics in the establishment and enhancement of scallop populations provides a mechanism by which rhodoliths may enhance populations of other species. This information will help identify rhodolith habitat features important to populations of associated species and features that need protection from anthropogenic threats.

MATERIALS AND METHODS

Location. Benthic substrate collections and a field experiment were conducted in Bahía Concepción (45 km in length, 60 m in maximum depth) located in the west central Gulf of California in Baja California Sur (BCS), Mexico (26° 38' 57" N, 111° 49' 82" W). The soft bottom in this bay is dominated by fine grain, non-carbonate volcanic sediments and interspersed with large grain, carbonate sediments derived from the rhodolith beds distributed along the western shore (Steller & Foster 1995). Rhodolith beds in the Gulf of California and Bahía Concepción are dominated by *Lithophyllum margaritae* (Fig. 1), a morphologically variable species (Riosmena-Rodríguez et al. 1999). Historically, the bay has been a major area of scallop production, but the fishery collapsed in the early 1990's and was closed in 1993. Subsequently, intensive efforts have been made to understand the recruitment and growth cycles of the scallops, and to re-establish the fishery (Chavez-Villalba & Cáceres-Martínez 1992, Villalejo-Fuerte 1993, Felix-Pico et al. 1997). Annual surface water temperatures in Bahía Concepción range from ≤ 18 to 30°C. Scallop recruitment generally occurs between January and March, coincident with the spring increase in water temperature from winter temperatures, from ≤ 18 °C to temperatures between 21 to 22°C (Villalejo-Fuerte 1993). Adult scallop densities in rhodolith beds were previously highest in the deeper (11 m) portions of a rhodolith bed that spanned a depth from 4 to 11 m (Steller et al. 2003). The field experiment in this study was conducted in February 2000 when the probability of scallop settlement was optimal.

Substrate preparation. Scallop settlement preferences were measured across benthic substrate types commonly found in and around rhodolith beds using 3 different experiments and with a focus on 2 primary cues (Table 1). The 5 substrate types varied in the level of live coralline surface cue (present/absent) and structural complexity (high/low): (1) live fruticose (branching) *Lithophyllum margaritae* rhodoliths with live coralline surface present and high structural complexity with intact branching (live rhodolith, LR); (2) dead *L. margaritae* rhodoliths with live coralline surface absent and high structural complexity with intact branching (dead rhodolith, DR); (3) live rhodolith fragments with live

Table 1. *Lithophyllum margaritae*. Experimental substrate treatments by code, live coralline cue (presence vs. absence), level of structural complexity (high vs. low) and experiment. x: substrate used in a particular experiment. Pref: preference

Substrate	Stylised illustration	Treatment code	Live coralline cue	Structural complexity	Experiment		
					Field pref.	Lab. pref.	Lab. growth
Live rhodolith		LR	present	high	x	x	x
Dead rhodolith		DR	absent	high	x	x	x
Live rhodolith fragments		LF	present	low		x	x
Dead rhodolith fragments		DF	absent	low	x	x	x
Non-carbonate fine sediment		FS	absent	low	x	x	

coralline surface present and low structural complexity (live rhodolith fragments, LF); (4) dead rhodolith fragments (2 to 4 mm) with live coralline surface absent and low structural complexity (dead rhodolith fragments, DF); and (5) fine grain (<0.5 mm), non-carbonate sediment with live coralline surface absent and low structural complexity (fine sediment, FS).

Substrate treatment preparation was similar among experiments but experimental setup varied relative to the question and logistics. In all experiments, live and dead whole rhodolith treatments and live fragment treatments (LR, DR and LF) were derived from living *Lithophyllum margaritae* rhodoliths (1 to 2 cm diameter) with intact branches that were collected from a depth of 8 m at Manto El Requesón, Bahía Concepción. Associated macroflora and fauna were removed and rhodoliths were lightly scrubbed with a soft plastic brush. Dead coralline rhodolith fragments (DF) were obtained from either (1) a sand flat 20 m outside of the rhodolith bed at 6 to 8 m depth, used in the field and laboratory preference experiments; or (2) from breaking apart whole, dead rhodoliths for the growth experiment. Fine grain, non-carbonate, volcanic sediment (FS, <0.5 mm diameter) was collected 200 m outside of the rhodolith bed at 8 m depth. Fine sediment had the lowest structural complexity of the treatments and lacked any known coralline cue. Material for all treatments void of live surface chemistry (DR, DF, FS) was boiled vigorously for 20 min in deionized water to denature and disrupt surface proteins, pigments and associated organisms. Substrates were either dabbed dry (live material) or air dried (dead or non-living material) prior to preparation into experimental units and subsequently soaked in aerated, filtered seawater for >24 h prior to the experiment.

Effects of substrate on settlement. *Field experiment:*

The field preference experiment was conducted in February 2000 to compare patterns of larval scallop settlement on 4 common benthic substrates relative to the surrounding sediments in 2 locations: a rhodolith bed and a sand flat. The substrate treatments included were those typically found in and around a rhodolith bed (LR, DR, DF, FS; Table 1). The underlying benthic substrate varied with location thus allowing for an examination of the settlement signal of a substrate treatment relative to surrounding dominant benthic cover. For logistical reasons and ease of outplanting, 6 experimental panels were prepared containing a replicate of each of the 4 substrates tested. The panels consisted of clear plastic rectangles (17 × 5 cm) divided longitudinally into 4 equal squares. Each square contained a central 3 × 3 cm region (separated by a 1 cm buffer zone) onto which randomly assigned material for 1 of the 4 treatments was attached with cyanoacrylate glue (Krazy Glue). The effect of glue on scallop settlement was tested in a laboratory experiment and was non-significant (D. Steller unpubl. data), as was previously reported (Miron et al. 1996).

Six experimental panels were deployed into each of the 2 locations supporting adult *Argopecten ventricosus* populations: the El Requesón rhodolith bed and a sand flat ~100 m outside of the bed. In an ~10 m² area in each location, replicate panels were moored ~2 m apart onto the benthos with stakes at a depth of 10 m. To verify that scallop settlement had occurred prior to ending the experiment, one panel from each location was collected after 4 d and examined; however, data were not utilized in the final analysis. Experimental panels were thus deployed for 5 d due to logistics and to allow for settlement, then collected and transported

to the surface where panels were immediately cut up into respective treatment squares and preserved in 80% EtOH. Attached larvae do not release from the substrate when fixed, thus allowing for post-collection density estimates. The density of settled scallop larvae on the surface of a 1 cm² portion of each replicate was subsequently determined through a dissecting microscope (5× power) on the day of collection.

Laboratory experiments: Laboratory experiments were conducted with cultured *Argopecten ventricosus* larvae at the Universidad Autónoma de Baja California Sur (UABCS) aquaculture facility at Pichilingue, La Paz, México during February 1998 and 1999: a time which coincides with the regional spawning and recruitment period of wild scallops (Felix-Pico et al. 1997). Adult scallops were collected from Bahía Magdalena, BCS and fed with high concentrations of diatoms to condition them for spawning under lab conditions. In each year, 12 scallops were induced to spawn and the resulting larvae were divided equally between 2 aerated 1500 l fiberglass tanks filled with 500 l of filtered seawater for 15 d. Feeding stage larvae were fed the microalgae *Isochrysis* spp. and *Chaetoceros gracilis* on a daily basis at concentrations of 30 000 cells ml⁻¹ d⁻¹, from Day 0 to 7; 60 000 cells ml⁻¹ d⁻¹ from Day 8 to 12, and 80 000 cells ml⁻¹ d⁻¹ from Day 13 until the conclusion of the experiments. Water temperature for cultures and experiments ranged from 20.5 to 22.0°C in 1998 and 19.0 to 21.5°C in 1999, reflecting the ambient seawater temperatures. During the early larval development period, the water was drained and changed every 2 d, at which time all larvae were concentrated, counted and measured. Experiments were initiated when ~70% of the larvae were competent to settle (~15 d), corresponding to a larval maximum shell length of 240 to 250 µm. One batch of larvae was used for each laboratory experiment as they were conducted in different years.

The laboratory preference experiment was conducted to test for the strength of settlement cues under controlled conditions and using a wider range of substrates than tested in the field experiment: 5 substrates commonly found in and around rhodolith beds (Table 1). Settlement patterns associated with coralline and structural cues were more thoroughly examined with the additional treatment consisting of LF, allowing for the examination of a live coralline surface under low structural complexity. Rhodoliths and sediments used in the experiment were collected from Bahía Concepción in the same manner as in the field preference experiment and transported and prepared in the Pichilingue laboratory.

Prepared in the same manner as the field panels, 5 experimental panels were constructed, except that these were longer (25 × 5 cm) in order to accommodate

the treatment (LF), divided longitudinally into 5 equal squares, and contained a replicate of each of the 5 substrate treatments in a 3 × 3 cm area. Treatments were randomly assigned to squares, each square separated from adjacent treatments by a 1 cm buffer zone. After preparing the larvae in 1999, the treatment panels were suspended in a single aerated tank containing 500 l of filtered seawater with competent scallop larvae at a density of 5 larvae ml⁻¹. Water was continuously moving due to aeration. After 3 d, panels were removed and examined to determine if settlement had occurred. Settlement was observed on all substrates; thus, the experiment was ended, treatment squares separated, fixed in 80% EtOH and the number of settled larvae cm⁻² immediately counted on each treatment surface using a dissecting microscope (5× power).

Effects of substrate on post-settlement growth. A laboratory growth experiment was conducted to assess patterns of early post-settlement growth relative to the surface cues of rhodolith-derived substrates. An orthogonal design was used to isolate the effects of live coralline surface presence or absence and of high or low structural complexity on both settlement and early post-settlement growth, reported as post-settlement size. Rhodoliths were collected from Bahía Concepción and used to prepare 4 treatments: LR, DR, LF, and DF. All rhodoliths were assessed for wet weight and branching density, determined as number of branch tips within 5 randomly placed 1 cm² quadrats on the rhodolith surface. A standardized amount (1.2 g) of whole rhodolith material of similar size with similar branching density (9 branches cm⁻²) was used in each replicate. Fragmented treatments were produced by breaking branches of intact rhodoliths into fragments of <5 mm. All rhodolith treatment material was attached to separate, individual 5 cm diameter petri dishes with cyanocrylate glue. Four PVC shelves, each containing 4 petri dishes with a replicate of each treatment in randomly assigned locations, were suspended in the tank. In February 1998 a batch of scallop larvae was reared as described above. When 70% of the larvae were competent, they were placed in 1500 l aerated tanks holding 500 l of water at a concentration of 4 larvae ml⁻¹. Experimental duration was 3 d to allow for settlement and growth.

At the end of the experiment, all settled larvae were removed from treatment surfaces using a 5% bleach solution in seawater rinse, concentrated using a 240 µm sieve and preserved in 80% EtOH. All larvae were examined for the presence of a post-settlement growth crest extending beyond the larval shell, which reflects a change in shell morphology and signifies the transition between a swimming veliger (velum present) and a crawling post-larva (velum absent) (Uriarte et al. 2002). Only larvae with a growth crest present were used to

Table 2. *Argopecten ventricosus*. Settlement preferences of larvae in the field. ANOVA results comparing larval settlement (ln settlers cm⁻²) between locations (rhodolith bed and sand flat) and among 4 substrate types with panel nested within location. Values in italics = results of planned general contrast tests comparing substrate types. See Table 1 for substrate codes

Source	SS	df	MS	F	p
Location	3.641	1	3.641	17.936	0.005
Substrate	54.765	3	18.255	98.566	<0.001
<i>Coralline cue: LR (present) vs. DR, DF, FS (absent)</i>	<i>11.34</i>	<i>1</i>	<i>11.344</i>	<i>61.25</i>	<i><0.001</i>
<i>Structure: LR, DR (high) vs. DF, FS (low)</i>	<i>28.512</i>	<i>1</i>	<i>28.512</i>	<i>153.9</i>	<i><0.001</i>
Location × Substrate	0.846	3	0.282	1.523	0.243
Panel (Location)	1.221	6	0.203	1.099	0.401
Error	3.334	18	0.185		

compare treatment-related differences in total settlement and post-settlement size between treatments. Post-settlement size, the maximum shell depth (larval shell + new growth, in μm), was measured from 11 to 50 (average = 35) individuals per replicate.

Data analysis. For the field preference experiment, differences in settlement density (ln settlers cm⁻²) among substrate types and between locations (rhodolith bed vs. sand flat) were examined with a 3-way ANOVA using panel as a nested factor within location. The importance of particular structural and coralline surface cues to larval settlement were assessed via planned general contrast comparisons among the 4 substrate treatments: (1) presence vs. absence of live coralline surface (LR vs. DR, DF, FS), (2) high vs. low structural complexity (LR, DR vs. DF, FS).

In the laboratory preference experiment, differences in larval settlement among 5 substrate treatments (ln [settlers + 1 cm⁻²]) were examined with a 1-way ANOVA comparing substrates. The importance of particular cues on settlement density was assessed via planned general contrast comparisons: (1) presence vs. absence of living coralline tissue (LR, LF vs. DR, DF, FS), (2) high vs. low structural complexity (LR, DR vs. LF, DF, FS).

In the laboratory growth experiment, the effects of live coralline surface cue (presence vs. absence) and structural complexity (high vs. low) on ln (total no. settlers) and ln (post-settlement size) were examined with 2-way ANOVAs. A power analysis was used to determine if sample size was sufficient to capture non-significant results. Data in all analyses were initially evaluated for normality and homoscedasticity using a Cochran's test, transformed if necessary and re-tested.

RESULTS

Effects of substrate on settlement

Field experiment. In the field preference experiment, settlement of wild scallop larvae occurred on all 4 substrate types (LR, DR, DF, FS) in both locations (rhodolith bed, sand flat) after 5 d (Fig. 2). Both location

and substrate type had significant effects on settlement density (Table 2) and density was higher on all substrates deployed on the sand flat relative to those on the rhodolith bed, with the exception of the fine sediment, on which densities were similar. Scallop densities (mean \pm SE) varied across substrate types and were 30 to 35 times higher on live rhodoliths (55.0 ± 13.4 and 84.4 ± 8.8 larvae cm⁻²) than on a non-carbonate sediment (1.8 ± 0.8 and 2.4 ± 0.9 larvae cm⁻²) relative to the surrounding rhodolith or sand habitat. On the sand flat, settlement decreased with the reduction in structural complexity, with no clear effect of the live coralline cue. However, in the rhodolith bed, settlement was greatest in the presence of both live coralline and high structural complexity and declined with decreasing structural complexity in treatments where the live coralline cue was absent. Overall, field settlement was significantly enhanced in the presence of both a live coralline cue and higher structural complexity (post hoc contrast tests; Table 2).

Laboratory experiments. In the laboratory preference experiment, settlement of cultured scallop larvae

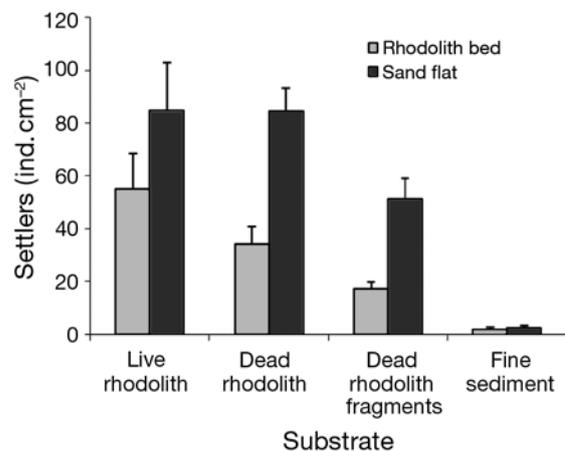


Fig. 2. *Argopecten ventricosus*. Field settlement preferences of larval scallops relative to substrate treatments (*Lithophylum margaritae* whole and fragmented rhodolith substrates) and location (rhodolith bed vs. sand flat) in Bahía Concepción. n = 5; error bars = SE

Table 3. *Argopecten ventricosus*. Settlement preferences of larvae in the laboratory. One-way fixed ANOVA results comparing settlement (\ln [settlers + 1 cm^{-2}]) among 5 substrate types. Values in italics = results of planned general contrast tests comparing substrate types

Source	SS	df	MS	F	p
Substrate	32.229	4	8.057	18.48	<0.001
<i>Coralline cue: LR (present) vs. DR, DF, FS (absent)</i>	<i>21.025</i>	<i>1</i>	<i>21.025</i>	<i>48.22</i>	<i><0.001</i>
<i>Structure: LR, DR (high) vs. DF, FS (low)</i>	<i>14.807</i>	<i>1</i>	<i>14.807</i>	<i>33.97</i>	<i><0.001</i>
Error	8.721	20	0.436		

occurred on all 5 substrates. Selection varied significantly across substrate types after 3 d, decreasing with a decline in structural complexity and loss of the live coralline cue (Fig. 3; Table 3). Settlement was highest on substrates with the live coralline cue present, and when comparing live vs. dead coralline surfaces respectively, settlement density was 3.3 times greater (55.8 ± 14.6 vs. 17.0 ± 4.9 larvae cm^{-2}) on whole rhodoliths and 7 times greater (24.2 ± 4.7 vs. 3.4 ± 1.3 larvae cm^{-2}) on fragmented rhodoliths. Post hoc tests supported the findings that live coralline surfaces and higher structural complexity significantly enhanced settlement (contrast tests; Table 3).

Settlement of crested larvae occurred on all treatments of *Lithophyllum margaritae* in the laboratory growth experiment and ranged from an average (\pm SE) high of 731 ± 111 total number of settlers on live, branching rhodolith material, to a low of 202 ± 37 on dead fragments (Fig. 4A). Settled larvae were generally evenly distributed over the settlement surfaces within each treatment, and no preference for microhabitats such as newly exposed portions of broken branches was apparent. Coralline cue and structural complexity both had separate and significant effects on settlement (Table 4). Settlement was highest on live rhodoliths with the live coralline cue and intact

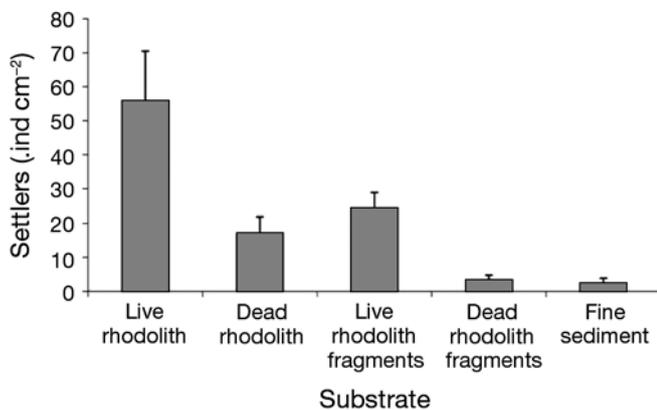


Fig. 3. *Argopecten ventricosus*. Laboratory settlement preferences of larval scallops relative to substrate treatments (*Lithophyllum margaritae* whole and fragmented rhodoliths and non-carbonate fine sediment). $n = 5$; error bars = SE

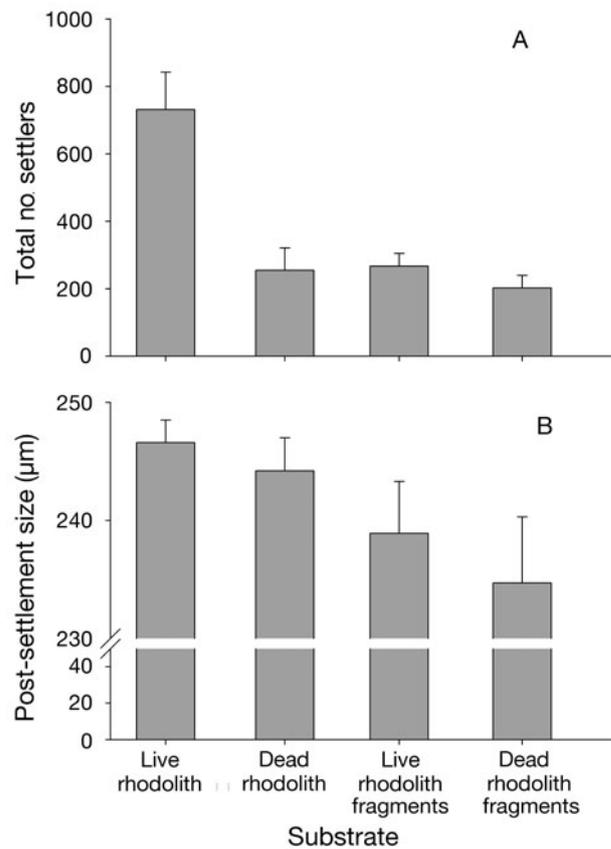


Fig. 4. *Argopecten ventricosus*. Mean \pm SE (A) total number of larval settlers and (B) post-settlement size relative to substrate type in a laboratory settlement and growth experiment

branching. Within comparable levels of structural complexity, settlement was higher in the presence of a live coralline cue, and within comparable levels of live coralline surface treatment (present vs. absent), settlement was higher in the presence of greater complexity.

Effects of substrate on growth

Individuals with post-settlement growth crests occurred on all treatments in the laboratory growth

Table 4. *Argopecten ventricosus*. Effects of live coralline cue (present vs. absent) and rhodolith structural complexity (high vs. low) on the ln-transformed total number of settlers and post-settlement size (maximum shell depth in μm) using a 2-way fixed factor ANOVA

Source	SS	df	MS	F	p
Total no. settlers					
Coralline cue	1.974	1	1.974	13.281	0.003
Structure	1.409	1	1.409	9.479	0.011
Cue \times Structure	0.635	1	0.635	4.269	0.061
Error	1.784	12	0.149		
Post-settlement size					
Coralline cue	0.001	1	0.001	0.741	0.406
Structure	0.005	1	0.005	4.824	0.048
Cue \times Structure	0.000	1	0.000	0.07	0.796
Error	0.013	12	0.001		

experiment and post-settlement size was higher on whole rhodolith treatments with intact structure (LR and DR; Fig. 4B) relative to fragmented treatments. There was a significant and positive effect of high vs. low structural complexity on post-settlement size for both live (246.6 ± 1.9 vs. $238.9 \pm 4.4 \mu\text{m}$) and dead (244.2 ± 2.8 vs. $234.7 \pm 5.6 \mu\text{m}$) coralline surfaces (Table 4). Overall, individuals were $\sim 8.6 \mu\text{m}$ larger on rhodoliths with intact branching structure. Within comparable levels of structural complexity, there was a positive yet non-significant effect of coralline cue on size with larger individuals found in the presence of the live coralline cue. A power analysis revealed that with a sample size of $n = 4$, there was insufficient power ($1 - \beta = 0.498$) to capture a non-significant result for the importance of coralline cue.

DISCUSSION

This study provides the first examination of the proximal settlement factors contributing to the role that rhodolith beds may play as 'nursery grounds' for invertebrate species. We found that both settlement and early post-settlement growth are enhanced on rhodolith-derived substrates. In particular, we found that surface cues of living coralline surfaces and greater surface complexity were important in enhancing scallop larval settlement. Past studies have reported high juvenile scallop densities (≥ 18 to 35 mm) in rhodolith beds (Kamenos et al. 2004a) and attributed this to greater selection, attachment and juvenile growth (Kamenos et al. 2004b, c). The high densities of scallop settlers found on rhodolith derived substrates in this study demonstrates a link between the planktonic stage and enhanced early settlement that may

contribute to the high densities of early juvenile stages and subsequent adult stages reported in other studies. Furthermore, enhanced early growth on rhodolith-derived substrates provides a clear benefit to early life stages for detecting specific settlement cues.

Effects of substrate on settlement

Coralline algal surfaces enhance invertebrate larval settlement and this has been attributed to factors including growth form, surface chemistry, photosynthetic pigments, macroalgal epibionts, biofilms of diatoms or bacteria, and the presence of newly exposed surfaces through sloughing and breakage (Morse & Morse 1984, Stoner et al. 1996, Daume et al. 1999a). While some invertebrates (e.g. abalone and coral spp.) demonstrate a high specificity for coralline algal-associated cues for settlement and metamorphosis (Morse & Morse 1984, Raimondi & Morse 2000), *Argopecten ventricosus* larvae do not require coralline surfaces for settlement. However, our results strongly suggest that features associated with live coralline surfaces (e.g. surface chemistry, proteins and/or mediation by microbial epibionts), regardless of structural integrity, attract scallop larvae and enhance larval settlement. A surface cue associated with live coralline algae that could contribute to enhanced settlement is an unidentified peptide mimic of the common neurotransmitter, γ -amino butyric acid (GABA). While GABA has been shown to induce larval settlement in gastropod species (Morse & Morse 1984, Daume et al. 1999a), similar effects have not been demonstrated for bivalve species and this would require further investigation. There is also evidence that other red algal molecules may promote larval scallop metamorphoses: extracts of some non-coralline red algal species enhanced larval metamorphoses in the scallop *Pecten maximus* (Chevolot et al. 1991). The settlement responses onto live coralline surfaces in this study may be due to a complex synergy of cues that may include the coralline surfaces and surface epibionts.

A potential stimulus for enhanced scallop settlement on living rhodoliths is the presence of biofilms. Biofilms of diatoms and bacteria on various marine substrate surfaces, including live corallines, have also been shown to positively influence larval settlement for some invertebrates (Morse et al. 1988, Daume et al. 1999b, Huggett et al. 2006) including scallops (Parsons et al. 1993, Pearce & Bourget 1996, Prescott et al. 2007, Leyton & Riquelme 2008). Kreft et al. (2001) suggested that substrate texture is one of the determining factors in biofilm formation on surfaces in the marine environment. Rough surfaces present more surface area and a greater diversity of microhabitats than smooth

substrates and thus may provide micro-successional mechanisms favorable to larval settlement (Bourget et al. 1994). It is unclear exactly what role biofilms play in scallop settlement, but it may be related to the transition from feeding with a ciliated velum to the gill filament of the benthic phase (Caddy 1969). This may serve as a mechanism by which complex rhodolith surfaces contribute to enhancing larval settlement and needs further examination.

One of the most obvious features of rhodolith beds is the high surface heterogeneity of rhodoliths relative to most soft-sediment substrates. Increased surface heterogeneity has long been recognized as an important factor enhancing larval settlement of many benthic invertebrates in addition to providing protection from predation and enhancing local availability of food resources (Crisp 1974, 1976, Brand et al. 1980). In contrast to Prescott et al. (2007), who found that substrate complexity alone did not attract *Argopecten ventricosus* scallop larvae, we found enhanced larval settlement on the more complex rhodolith surfaces. Our finding is similar to other settlement studies that found preferential scallop settlement on a wide range of substrates with enhanced structural complexity (Brand et al. 1980, Harvey et al. 1993, Pearce et al. 1996).

Higher settlement onto complex substrates may result from the increased probability of contact between key features of larvae and the substrate. For example, larval mussel attachment to complex substrates under moving water conditions is enhanced by the mucous thread produced by competent swimming larvae that increases the probability of substrate contact (Cáceres-Martínez et al. 1994). Competent swimming larvae of *Argopecten ventricosus* also have a mucous thread that may increase the frequency of contact with the complex substrates. In addition, post-contact discrimination of fine scale differences in substrate complexity has been well documented in bivalve larvae. Some scallop larvae can differentiate between rocks and large fragments vs. sandy sediments (Pearce & Scheibling 1991), and others have shown that larvae have a strong preference for larger grain sediments (Baqueiro-Cardenas et al. 1981, Thouzeau et al. 1991). Enhanced substrate contact combined with a preference for heterogeneous substrates could explain the higher settlement rates we found on rhodolith substrates. It could also explain the significant difference in settlement patterns between locations measured in the field experiment. Higher settlement on substrates introduced into the sand flat relative to those in the rhodolith bed may have been from simple differences in larval supply. Alternatively, larvae over sand flats may contact fewer heterogeneous substrates, thereby locally increasing larval supply to experimental treatments.

Effects of substrate cues on larval growth

Few studies link the cues important for driving settlement choices to increased post-settlement growth. Increased early growth enables newly settled larvae to quickly transition from vulnerable early life history stages. Scallop larvae that settled onto rhodoliths with intact structure in this study, regardless of whether the coralline surface was live or dead, experienced higher post-settlement growth as revealed by increased size. Our results strongly suggest that maintaining beds of rhodoliths with intact structure could contribute to scallop production through enhanced growth. In addition, the trend of larger post-settlement individuals on live coralline substrates likewise suggests that maintaining living rhodoliths could also enhance scallop production through increased growth at small life stages. Further investigation with greater replication could strengthen this argument.

Conservation and management implications

Our studies indicate that the combination of physical and biological cues presented by biogenic rhodolith habitat act to enhance settlement, growth and potentially survival of larval scallops. It is likely that rhodoliths play a similar role for other benthic species. Our study examined the role of *Lithophyllum marginatae* rhodoliths at the scale of individual rhodoliths. The broader scale implications of our results can be better considered by scaling up to the level of rhodolith beds. Within a bed, live rhodolith densities are variable but can range from a few hundred up to 5000 to 10000 thalli m^{-2} (Cabioch 1969, Bosence 1976, Steller et al. 2003), and can cover 10s of km^2 . At these extents and densities, beds likely act to accumulate larvae of many species, resulting in much higher local biodiversity compared to adjacent sandy bottoms (Keegan 1974).

Many commercially harvested species are associated with rhodolith beds. In Europe, there is a large-scale fishery for the scallop species *Pecten maximus*, which often is associated with Scottish maerl beds (Hall-Spencer & Moore 2000a). In Pacific Mexico, commercially important scallops (*Argopecten ventricosus*, *Pecten vogdesi* and *Lyropecten subnodosus*) and other bivalves (*Pinna rugosa* and *Atrina maura*) are associated with rhodolith beds (Steller et al. 2003). Fisheries operations, however, can seriously disrupt coralline algal beds. For example, dredging operations for scallops in the Scottish maerl beds results in the breakage and burial of rhodoliths (Hall-Spencer 1999, Hall-Spencer & Moore 2000a), which, when combined with decades of mining maerl for carbonates used in agriculture, (Blunden et al. 1975) has resulted in wide-

spread destruction. Extreme disturbance can result in reduction of thallus density, size and complexity and ultimately transition to a low-diversity carbonate sand flat, increasing soft sediment suspension-feeders (Grall & Glemarec 1997) and the number of scavengers (Hall-Spencer & Moore 2000a). In Mexican rhodolith beds, damage due to bivalve harvesting with hookah and dragged nets is more localized, but results in significant rhodolith damage through crushing and burial (D. Steller pers. obs.).

In addition to their potential direct role as nursery grounds, natural breakage and degradation of living individual rhodoliths produce large-grain calcareous sediment that serves to increase complexity within and directly adjacent to rhodolith beds. Thus, the maintenance of living rhodolith beds influences heterogeneous biogenic habitat production at 2 levels: the living bed itself and the production of complex soft bottoms over more extensive areas. Unfortunately, wide-spread damage to rhodoliths, combined with slow recovery times predicted from the slow rhodolith growth rates measured on a range of species worldwide (Blake & Maggs 2004, Rivera et al. 2004, Steller et al. 2007), has resulted in significant global degradation of rhodolith biogenic habitat. Given the biodiversity associated with rhodolith beds and the likely importance of these for larval settlement, post-settlement growth, survival and reproduction of commercially important and other associated species—similar to the role of other biogenic habitats such as kelp beds and coral reefs—global conservation of rhodoliths is warranted.

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