The intertidal distribution of two algal symbionts hosted by
Anthopleura xanthogrammica (Brandt 1835)

Amanda Bates* a,b, *

a Simon Fraser University, Burnaby, B.C., V5A 1S6, Canada
b Bamfield Marine Station, Bamfield B.C., V0R 1B0, Canada

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Abstract

This paper quantifies the spatial distribution of zooxanthellae (ZX) and zoochlorellae (ZC), two algal symbionts common to the temperate anemone, Anthopleura xanthogrammica, in relation to shore height. Anemones in tidepools and crevices had varying algal proportions: >0.90 ZC (green anemones), 0.10 to 0.90 ZX (mixed), and >0.90 ZX (brown). Brown anemones are primarily found in the high intertidal and the upper region of tidepools. Mixed anemones are most common at intermediate shore heights and green anemones are exclusive to the low shore and at increasing depth in tidepools. Microhabitat was also important to algal proportion, as anemones in crevices had greater proportions of ZC than anemones in tidepools at the same shore height. In a reciprocal transplant experiment, A. xanthogrammica were moved between high and low shallow tidepools. All anemones moved from a low to a high tidepool exhibited a shift from ZC to ZX populations, while the anemones transplanted from high to low tidepools maintained ZX dominance. This is the first documentation that field algal populations can shift from ZC to ZX in Anthopleura. The field survey and transplant study results support the hypothesis that the relative abundance of ZX and ZC in A. xanthogrammica is influenced by the environmental gradient associated with shore height and microhabitat. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The coexistence of multiple algal types within a given host is rare (Muscatine, 1971), and such systems are therefore intriguing. Anthopleura elegantissima and A. xanthogrammica, anemones found on the Pacific northwest coast, commonly host two different

*Correspondence address: Bamfield Marine Station, Bamfield, B.C., V0R 1B0, Canada.
species of algae. One is a symbiotic dinoflagellate, *Symbiodinium californium* (Banaszak and Trench, 1995). Symbiotic dinoflagellates are referred to as zooxanthellae (ZX). The other is an unidentified symbiotic chlorophyte and is commonly known as zoochlorellae (ZC) (Muscatine, 1971; O'Brien, 1980). Anemones with algal populations dominated by ZX are identified as brown, whereas green anemones have primarily ZC (O'Brien and Wytenbach, 1980). Mixed anemones have varying proportions of ZX and ZC that coexist in the endoderm of both *A. elegantissima* and *A. xanthogrammica* (Saunders and Muller-Parker, 1996; Verde and McCloskey, 1996).

Variability in the relative abundance of ZX and ZC becomes more interesting when one considers that brown, green, and mixed anemones occur within single host populations (O'Brien and Wytenbach, 1980; McCloskey et al., 1996; Saunders and Muller-Parker, 1996). Field observations report green anemones to be restricted to subtidal and low shore heights for *A. xanthogrammica*, while brown anemones are found at high shore heights for both *A. elegantissima* (McCloskey et al., 1996; Saunders and Muller-Parker, 1996) and *A. xanthogrammica* (O'Brien and Wytenbach, 1980). Hosting multiple symbiont species may guarantee symbiosis under the varying and extreme conditions characterizing the intertidal zone, and if so, represents an evolutionarily advantageous strategy (Saunders and Muller-Parker, 1996).

Saunders and Muller-Parker (1996) report ZC and ZX to have different responses to temperature and light in *A. elegantissima*, which they attribute to the specific physiological tolerances of each alga to these factors. They suggest that the restriction of ZC from the upper intertidal is due to ZC’s relatively lower growth rate when compared to ZX under prolonged exposure to high temperatures. O'Brien and Wytenbach (1980) also proposed that high temperature is limiting ZC in *A. xanthogrammica* from the high intertidal. However, the distribution of ZX and ZC in field populations of anemones has not been quantified.

This study describes symbiotic algal populations of *Anthopleura xanthogrammica* in relation to shore height and microhabitat on the west coast of Vancouver Island. Shore height of *A. xanthogrammica* found in tidepools and crevices is correlated to the proportion of ZX, following summer exposure in November (1996) and September (1997). A reciprocal transplant experiment exchanged anemones between low and high intertidal tidepools and monitored the algal populations following transplantation from June to September (1997). If shore height plays a significant role in determining the relative abundance of ZX and ZC, then anemones at different shore heights and in different microhabitats are expected to have different algal populations. Anemones that are moved between high and low shore heights are expected to exhibit a subsequent change in their algal population.

2. Methods

2.1. Field sites

Sites in this study were located near Bamfield, British Columbia on the west coast of Vancouver Island (48° 49’ N, 125° 12’ W). Scott’s Bay (Field survey) and Dixon Island
(Transplant study) are moderately wave exposed rocky shorelines (Lewis, 1982) with tidepools. Shore height (distance up the shore from chart datum) was determined with survey equipment (theodolite) and tidepool volumes estimated by multiplying width, length, and average depth measurements for each pool.

2.2. Field survey

*Anthopleura xanthogrammica* in a low-shore tidepool (pool surface 0.8 m up shore; volume of 3.79 m\(^3\)), and in a high-shore pool (pool surface 2.0 m up shore; volume of 1.46 m\(^3\)) were surveyed. Both tidepools had a depth exceeding 0.5 m. *A. xanthogrammica* in a 0.7 m low-shore tidepool were also surveyed. The data is similar to the 0.8 m tidepool and was therefore not included in the results section. Anemones found in crevices were also surveyed. Data were collected in 1997 from September 16–19. These results are pooled with a preliminary survey conducted between October 21 and November 17 (1996) as part of a directed studies project at the Bamfield Marine Station (Bates, 1996).

An attempt was made to sample all anemones in the 2.0 m tidepool. However, all 35 anemones inhabiting the pool were not consistently open during sampling intervals. For the low-shore pool, transects were placed across the pool at random coordinates and the tentacles of all open anemones falling within 5 cm of the transect line sampled.

The shore height for individual anemones found in tidepool was calculated by subtracting the distance from the anemone’s pedal disc to the tidepool’s surface from the shore height of the tidepool’s surface.

Temperature was recorded at a depth of 0.02 m (top) and 0.50 m (bottom) in each tidepool (2.0 and 0.8 m) on 21 random days from June to August, 1997.

All anemones found in crevices and open at low tide were sampled.

2.3. Transplant experiments

To facilitate transplantation, transplant plates were constructed by gluing six petri dishes (5 cm diameter) with fast cure marine adhesive (Sikaflex-241) to a plexiglass sheet (120 cm \(\times\) 25 cm). The petri dishes were prepared by lightly scratching the surface with sandpaper and were immersed in a sea water table for one week (it was thought a diatom layer might encourage attachment).

Six tidepools with populations of *A. xanthogrammica* were located at Dixon Island: three tidepools below 1.0 m, and three above 1.5 m. These tidepools were marked with flagging tape secured in a crevice with a nail and the shore height of each measured, high-shore heights: 2.4 m, 2.3 m, 2.2 m, and low-shore heights: 0.6 m, 0.5 m, 0.4 m. A field survey determined all anemones in the high-shore tidepools to be brown, and all those in low-shore tidepools to be green.

Six anemones were removed from each tidepool with a blunt metal spatula and placed in buckets without seawater to prevent swelling of any damaged pedal disk tissue. They were transported to the lab, with anemones from each of the tidepools in separate containers. Each anemone was labeled with a numbered bead sewn to the base of the pedal foot with suture thread and placed on a transplant plate according to the
experiment design. Of the six anemones removed from each of the tidepools, three were randomly assigned to a control group \((n = 3)\), and the other three formed the transplant group \((n = 3)\). Control anemones were returned to their tidepool of origin. Reciprocal transplants between pairs of low and high tidepools were conducted. Anemones were exchanged between the 0.6 m and 2.4 m tidepool, between the 0.5 m and 2.2 m tidepool, and between the 0.4 m and 2.3 m tidepool.

Attachment to the petri dishes was successful and after 12 h all anemones were fully open. Anemones remained under constant laboratory conditions in a sea water flow table for a total of 36 h, after which the transplant plates were positioned in tidepools, with less than 0.01 m of water above the transplant plate, and secured with two screws into an anchor (May 20, 1997). The anemones were sampled just prior to field placement. This data represents the original (Day 0) algal proportion (as described in Section 2.4 on assessment of algal ratio).

Subsequent algal counts were conducted on June 19, July 21, and September 18 of 1997. The water temperature and salinity was recorded at the plate position in the tidepool from July 25 to August 15 on random days. The treatments were not monitored between August 15 and September 11, 1997.

The transplant plates secured in the 2.3 m and the 0.4 m tidepools were removed by storm activity.

2.4. Assessment of algal ratio

Four tentacles comprised one sample and were removed with dissection scissors. Each of the four tentacles was from a different row, but from the same region of the anemone. Samples were chilled at 4°C on ice during transport to the lab and then frozen at \(-20°C\) until analysis to prevent algal division. Differential degradation of ZX and ZC resulting from freezing and thawing was a potential factor that might influence results. Fresh tentacles were macerated and half the tissue frozen. Algal counts were taken of fresh versus frozen samples and were not significantly different (paired \(t\)-test, \(P < 0.05\)).

To release the algae from the host endoderm tissue, the sample was first macerated between tweezers and then diluted with approximately 1 ml of filtered seawater (0.45 μm). A 1 μl aliquot was withdrawn with a pipetteman and examined at 40× magnification with a compound light microscope on a haemocytometer slide. All ZX and ZC within each of three 1 μl aliquots of each sample were counted.

ZX proportion is \([\text{total number ZX} / \text{the total number of ZX and ZC}]\) for one sample. Following the protocol of Saunders and Muller-Parker (1996), anemones with \(\geq 0.90\) ZX were identified as brown, and anemones with \(\geq 0.90\) ZC were identified as green. Anemones with intermediate proportions of ZX and ZC were identified as mixed.

2.5. Environmental parameters of water

Temperature and salinity was measured with a YSI Model 3 handheld conductivity meter.
2.6. Statistics

The Spearman Rank Order Correlation was used to determine correlation coefficients and significance levels for the field survey. The field survey data for November (1996) and September (1997) was pooled. The Friedman Repeated Measures Analysis of Variance on Ranks was used to determine the significance level of changes in ZX proportion, in field study temperature data, and in transplant study temperature and salinity data.

3. Results

3.1. Field study

ZX were dominant in high tidepool anemones (Fig. 1A). 75% of anemones sampled were brown and no green anemones were observed. The proportion of ZX is significantly positively correlated to increasing shore height ($r = 0.43$, $***P < 0.001$) in the high tidepool. The proportion of ZX in the low tidepool is also positively correlated to shore height ($r = 0.86$, $***P < 0.001$) (Fig. 1B). Anemones in crevices show a similar pattern ($r = 0.79$, $***P < 0.001$), with all anemones below 0.4 m exclusively green. Note that crevice anemones have a greater proportion of ZC than tidepool anemones at the same shore height.

The temperature data for the high (2.0 m) and low (0.8 m) tidepool are summarized in Table 1. The top measurements, at a depth of 0.02 m, were significantly higher (*$P < 0.05$) than the bottom measurements, at a depth of 0.05 m. The top and bottom measurements in the high tidepool were also significantly greater (*$P < 0.05$) than measurements taken at the same positions in the low tidepool.

Based on data received from the Institute of Ocean Sciences, Victoria, Government of Canada, Fig. 2 plots the total hours of exposure to air for the 2.0 m and 0.8 m tidepools between 8:00 and 20:00 from June 15 to August 15, 1997. These were 237 and 11 h (respectively).

3.2. Transplant experiment

Fig. 3A and B shows data collected in the two high transplant tidepools (2.4 and 2.2 m). The three control anemones in each of the high tidepools remained brown throughout the experiment duration. However, transplant anemones removed from low tidepools and placed in high tidepools show a significant change (*$P < 0.05$) from ZC as the dominant algae to ZX.

The proportion of ZX in the low transplant tidepools (0.6 and 0.5 m) is shown in Fig. 3C and D. Control anemones remained predominately zoochlorellate, although the proportion of ZX fluctuated above 0.10 ZX. However, the low tidepools showed a consistent ZX dominance in transplant anemones throughout the experiment’s duration.
Fig. 1. The proportion of ZX as a function of anemone shore height sampled in November (1996) and September (1997). Each point represents one anemone. ($r_\text{c}$ = correlation coefficient, \(*\ast\ast\ast\ast = P < 0.001$). To directly compare algal populations between crevice and tidepool anemones, shore height was calculated for tidepool anemones by subtracting the anemone’s depth in the pool from the pool’s surface shore height.
Table 1
A summary of temperature data for the high (2.0 m) and low (0.8 m) tidepool taken at top (depth of 0.02 m) and bottom (depth of 0.50 m) positions on days from June to August, 1997 (n = 21)

<table>
<thead>
<tr>
<th>Tidepool</th>
<th>Range T (°C)</th>
<th>Mean T (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>High: top</td>
<td>22.8–14.1</td>
<td>18.1</td>
</tr>
<tr>
<td>High: bottom</td>
<td>18.6–13.6</td>
<td>15.7</td>
</tr>
<tr>
<td>Low: top</td>
<td>20.9–13.6</td>
<td>17.2</td>
</tr>
<tr>
<td>Low: bottom</td>
<td>17.4–13.1</td>
<td>15.4</td>
</tr>
</tbody>
</table>

Fig. 2. Total hours exposed to air for the high tidepool and low tidepool with surface shore heights of 2.0 m and 0.8 m (respectively) between June 15 and August 15, 1997.

Fig. 3. The proportion of ZX in transplant (n = 3) and control (n = 3) anemones for reciprocal transplants in tidepools with surface shore heights of 2.4 m (A) and 0.6 m (C) tidepools, and 2.2 m (B) and 0.5 m (D). Sampling was conducted on May 20 (Day 0), June 19, July 21, and Sept 18, 1997 (* = P < 0.05).
Fig. 4. Mean temperature ($n = 21$) for transplant tidepools sampled in the afternoon on days from May to August 1997 ($* = P < 0.05$).

The temperature data for each of the transplant tidepools shows that the mean temperature was significantly greater in the two high tidepools (2.4 and 2.2 m), compared to the two low tidepools (0.6 and 0.5 m) (Fig. 4) ($* P < 0.05$). The 2.4 m tidepool experienced the greatest range in temperatures, with the maximum being 26°C. The maximum temperature was 23°C in the 2.2 m high tidepool. The low tidepools had a moderate temperature range from 13 to 18°C, and were not found to be significantly different for temperature.

Salinity was also measured. The 2.4 m pool had a significantly lower salinity than the sites at 2.2 m, 0.6 m, and 0.5 m ($* P < 0.05$). Further, a greater salinity range was recorded in the 2.4 m tidepool (3–31 ppt). Salinity values for the 2.2 m pool were more extreme (11–29 ppt) and the mean salinity (22 ppt) was lower than for the 0.6 m (17–28 ppt, 24 ppt) and 0.5 m (16–26 ppt, 23 ppt) tidepools. However, no significant difference between salinity data between the 2.2, 0.6, and 0.5 m tidepools was found.

Based on data received from the Institute of Ocean Sciences, Victoria, Government of Canada, Fig. 5 plots the total hours the 2.4, 2.2, 0.6, and 0.5 m tidepools were exposed to air between 8:00 and 20:00 from June 15 to August 15, 1997. These were 304, 269, 3, and 2 h (respectively).
Fig. 5. Total hours exposed to air for each of the 2.4, 2.2, 0.6, and 0.5 m tidepools between June 15 and August 15, 1997.

4. Discussion

The field study documents a spatial distribution of ZX and ZC in *Anthopleura xanthogrammica* inhabiting tidepools and crevices. ZX were dominant in the high-shore and ZC were dominant in the low-shore (Fig. 1). The proportion of ZX represented in the symbiont population significantly increased with shore height. The transplant study documents a shift from ZC to ZX populations in anemones moved from low to high tidepools. These results support the observations of O’Brien and Wyttenbach (1980) who first noticed the restriction of ZC from high-shore *A. xanthogrammica*.

Muscatine (1971) recognized that hosting two algal types is rare. It is possible that the host is regulating the relative abundance of each alga. The spatial distribution of ZX and ZC may be a result of host control mechanisms through preferential expulsion or retention, differential limitation of nutrients, or differential degradation (Muscatine and Pool, 1979). McCloskey et al. (1996) have shown mixed *A. elegantissima* to regulate symbiont density via non-preferential expulsion at varying light intensities. However, host selection of algal type by the above mechanisms has not been observed in *A. elegantissima* or *A. xanthogrammica* to date.

Alternatively, Saunders and Muller-Parker (1996), who worked on the effects of high temperature and varying light levels to the relative abundance of ZX and ZC in *A. elegantissima*, suggest that the reported algal distribution is directly related to environmental gradient. An environmentally determined spatial distribution of ZX and ZC is documented in one other system; in this case the host is a Caribbean coral (*Porites astreoides*). UV radiation was shown to damage brown coral morphs more readily than green morphs when both types were exposed to natural UV wavelengths (Gleason, 1993). ZX may be more susceptible to UV damage than ZC, resulting in a distribution of
ZC nearer the surface and ZX at greater depths (Gleason, 1993). Environmental gradient has also been shown to regulate the distribution of different tropical ZX clades (Rowan and Knowlton, 1995). Further, the bleaching susceptibility of ZX is clade dependent (McField, 1999). There is consequently reason to investigate the role of environment in regulating temperate symbiont distributions.

At increased shore heights exposure to temperature, light intensity, UV wavelengths, and hyposalinity increases. The effects of UV radiation and hyposalinity remain undocumented in Anthopleura (xanthogrammica and elegantissima), whereas the relative effects of high temperature and different light levels to the growth of ZX and ZC in A. elegantissima have been studied (O’Brien and Wytenbach, 1980; McCloskey et al., 1996; Saunders and Muller-Parker, 1996). Based on the research presented by Saunders and Muller-Parker (1996) and O’Brien and Wytenbach (1980), temperature is likely determining the distribution of ZX and ZC by directly affecting algal growth. Prolonged exposure to high temperature (20°C) decreased the density and growth rate of ZC in green and mixed A. elegantissima, while ZX in brown and mixed anemones did not show a similar decrease (Saunders and Muller-Parker, 1996). O’Brien and Wytenbach (1980) also observed a decrease in the division rate of ZC in green A. xanthogrammica in response to elevated temperature and proposed that ZC is restricted from the upper intertidal by temperature.

ZX showed an increase in division rate and density in response to low light in A. elegantissima (Saunders and Muller-Parker, 1996). Low light levels likely contribute to the observed algal distribution by favoring ZX. However, temperature was found to have a greater regulatory effect than light on algal populations of A. elegantissima (Saunders and Muller-Parker, 1996). McCloskey et al. (1996) found algal density and growth rate to be unaffected by light in green and brown A. elegantissima. Based on these studies, temperature is the most parsimonious explanation for the observed algal distribution.

The symbiont distribution follows the summer temperature gradient in tidepools. Anemones near the surface of tidepools experience extreme temperature increases to ambient seawater due to mid-day low tides in summer months (Jensen and Muller-Parker, 1994). Surface tidepool anemones were primarily brown. Although a similar trend was observed for both tidepools (ZX at top, ZC at bottom), the high tidepool was exposed to air for greater duration due to shore height (Fig. 2) and consequently experienced significantly higher surface temperatures for longer intervals than the low tidepool (Table 1). Seventy-five percent of anemones sampled in the high tidepool were brown, and green anemones were not found in this habitat. In comparison, green anemones were observed at depth in the low tidepool, which experienced more moderate temperatures for lesser daily intervals. ZC are only found in habitats which do not experience high temperature.

Anemones in crevices at similar shore heights to anemones in tidepools had algal populations with lesser proportions of ZX (Fig. 1). Crevice anemones are not subject to extreme temperature fluctuations due to shading. Therefore, crevice anemones experience more moderate temperatures than tidepool anemones at similar shore heights. Hence, when the distribution of ZX and ZC in crevice and tidepool anemones is compared, the dominance of ZC reflects exposure to more moderate temperatures.

Crevices receive less light than tidepools that are not shaded by macroalgae.
Anemones at lower shore positions presumably experience lower irradiance than those at higher positions. One would therefore expect to see ZX at lower shore heights, which is not observed. However, the influence of light on the symbiosis is difficult to tease apart from other factors, as anemones are contracted for greater intervals in the upper intertidal in response to high temperature, high light intensity, and UV exposure (Dykens and Shick, 1984), and also attach particles to the body column as a UV shield (Dykens and Shick, 1984). Both behaviors significantly reduce light availability to symbiont populations (Pearse, 1974). These behavioral adaptations complicate interpretation of light's role in determining the algal distribution, as anemones in more exposed habitats and at higher shore heights remain contracted for greater intervals of time than anemones at lower shore heights (Dykens and Shick, 1984). Further, crevice anemones do not fully contract with the receding tide, which decreases contraction-induced algal shading (Dykens and Shick, 1984). However, crevice anemones that are unsupported by rock collapse when the anemone is exposed to air, which might increase algal self-shading. The effect of these differences in behavior between tidepool and crevice anemones to their symbiont populations needs to be considered further.

Data from the transplant study also supports the hypothesis that summer conditions impacting the high intertidal inhibit ZC from upper shore heights. In this study, green anemones were moved from a low to a high tidepool in late May (spring). The initial zoochlorella population was replaced by ZX between mid-July and mid-September. Both temperature and salinity were monitored. The two high tidepools experienced a significantly different salinity regime. Therefore, it is unlikely that salinity caused the shift from ZC to ZX in both of the high tidepools. The temperatures found in the high tidepools were significantly greater than in the low tidepools. The exclusion of ZC from high tidepools is potentially a result of the extreme temperatures experienced in the high tidepools. This research represents the first documentation that the algal population can shift from ZC to ZX.

There are two possible origins to the ZX that replaced the ZC. In the initial algal count, the green anemones had a small ZX population (1–5%). This resident population may have outgrown the ZC following transplantation. Alternatively, the green anemones may have been infected with expelled ZX from brown control anemones. Infection of adult symbiotic Anthopleura has not yet been observed. Weis and Levine (1996) could not infect adult aposymbiotic A. elegantissima with ZX and proposed that there is a window of opportunity for infection during a stage of larval development. Similar studies have not been conducted for A. xanthogrammica. However, aposymbiotic A. xanthogrammica collected in summer 1997 and placed in an aquarium with mixed anemones have remained aposymbiotic to present (personal observations). It is therefore likely that the population of ZX that succeeded ZC originated from resident ZX, and that these cells were able to outgrow the ZC when anemones were exposed to the environment associated with high shore heights.

The reverse transplant did not yield comparable results. Brown anemones removed from high tidepools and transplanted to low tidepools with primarily green anemones maintained their ZX populations for the duration of the study. ZC have a division rate exceeding ZX by eight times, and over time, one would predict that ZC will out compete ZX, simply by growth (Saunders and Muller-Parker, 1996; Verde and McCloskey, 1996).
However, it is unknown how long the succession from ZX to ZC would take. The duration of this study may not have been long enough to allow this succession to occur.

Although lab work shows ZC to be more susceptible to temperature, and field work shows ZC to be limited from environments with extreme temperature exposure, the synergistic role of temperature with high light intensity and UV radiation needs to be considered. The interaction between abiotic factors is most important near the physiological tolerance limits for a given factor (Coles and Jokiel, 1978). Hence, a single factor’s effect on an organism may have limited applicability to natural environments where several abiotic and biotic factors interact (Coles and Jokiel, 1978). In tropical coral–algal symbioses, the synergistic effects of temperature, salinity, light, and UV have been shown to stress algae by increasing the production of oxidating agents (Coles and Jokiel, 1978; Hoegh-Guldberg and Smith, 1989; Lesser et al., 1990). In a tropical zoanthid, the compounding effects of high temperature, light intensity, and UV radiation initiate photosystem damage in ZX by reducing the efficiency of protective enzymes against active oxygen (Lesser et al., 1990). At increased shore heights in the Pacific northwest, the impact of high temperatures during summer months, in combination with high light intensity (Saunders and Muller-Parker, 1996), UV radiation, and hyposalinity may act in concert to differentially impede algal symbionts in high-shore anemones.

Algal growth in corals following exposure to high temperatures, high light intensity, and UV radiation is limited by the following physiological mechanisms: prevention of electron transport in photosystem 2, oxygen toxicity, DNA and protein damage, and reduction in chlorophyll concentrations (Lesser and Shick, 1989; Glynn and Croz, 1990; Lesser et al., 1990). The physiological mechanisms underlying differences in the density and growth rate of ZX and ZC in temperate systems needs to be studied. This information would give insight to how the coexistence of two algal symbionts is sustained and how shifts in algal populations occur (O’Brien and Wyttenbach, 1980; Muller-Parker, 1996; and Verde and McCloskey, 1996).

If algal proportion is determined by environment, the occurrence of *Anthopleura* populations with only ZX, or with both ZX and ZC (McCloskey et al., 1996), may be related to the environmental exposure of the site and shore height the resident population is found at. This would provide broader evidence that environment is key to the relative success of each algal type.

This study is important as it uses a temperature, rather a tropical, field model to describe algal distributions in relation to environmental gradient. The distribution of ZX and ZC in *Anthopleura* populations is likely a consequence of the relative success of each algal type under varying environmental exposures. The *Anthopleura* symbiosis with ZX and ZC represents a unique model in which to study the interaction between two different algal types within one host and the mechanisms maintaining this system (Saunders and Muller-Parker, 1996). It is important to examine the potential role environment plays in other algal symbioses where multiple algal types occur within one host species.

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