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Symbiont distribution along a light gradient within an intertidal cave

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Abstract

The potentially lethal bleaching of invertebrates through loss of their algal symbionts is a major global conservation issue; cnidarians in such interactions could potentially withstand environmental change by having multiple symbiotic partners whose physiologies vary with critical field parameters such as temperature and light. Spatial variation in symbiont distributions in the field is a strong indicator of such potential. We show that, in an association between an abundant temperate sea anemone and its two endosymbionts, the dinophyte *Symbiodinium muscatinei* (zooxanthellae) and an unidentified green alga (zoochlorellae), densities and ratios of anemones' symbionts change along a light gradient generated by intertidal caves in Washington state. In the laboratory, the photosynthetic performance of zooxanthellate anemones exceeded that of zoochlorellate anemones under high irradiance levels (>100 μmol quanta m^{-2} s^{-1}). Further, field sampling revealed that caves are divided into three distinct regions based on anemones' algal complements: a brown region of zooxanthellate anemones near the mouth of the cave, a green region of zoochlorellate anemones in the middle of the cave, and a white region of algae-free anemones near the back of the cave. These data, together with field reciprocal transplant experiments showing algae-free anemones' ability to regrow algae consistent with local physical conditions, suggest that algal performance (vs. host selection) determines observed variation in these symbioses. Our results support the idea that temperate, as well as tropical, host–symbiont associations can respond plastically to environmental change. Our data also suggest that intact symbioses in adult hosts are surprisingly stable; bleaching may be required in rearranging host–symbiont associations.

Symbiotic interactions between invertebrates, especially corals, and unicellular algal endosymbionts drive much primary productivity and structural complexity in tropical marine habitats. Disruption of these interactions produces coral reef bleaching, a major pantropical threat to coral reefs (Glynn 1993; Knowlton 2001). Recent empirical data and theoretical developments suggest that cnidarians involved in such symbiotic associations could potentially withstand environmental change (on global, regional, or local scales) by having multiple symbiotic partners with different physiological attributes (Buddemeier and Fautin 1993; Baker 2001; Toller et al. 2001). A prerequisite to understanding whether having multiple symbionts benefits hosts under shifting physical conditions is determining the baseline distribution of symbionts in nature with respect to key environmental parameters, such as temperature and light (Rowan and Knowlton 1995; Baker 2003; Knowlton and Rohwer 2003).

Symbioses are also common in temperate environments, where they differ from their tropical counterparts in critical ways, but may still have large ecological impacts (Muller-Parker and Davy 2001; Secord 2002). Specifically, *Anthopleura elegantissima* is the most abundant intertidal sea anemone in the Northeastern Pacific Ocean and, as a host for endosymbiotic algae, it contributes to primary productivity on a par with macroalgae (Fitt et al. 1982; Sebens 1982). It has become a model system for the analysis of the physiology, ecology, and molecular biology of temperate cnidarian–algal symbioses (Muller-Parker and Davy 2001; Mitchelmore et al. 2002; Secord 2002). Moreover, the genus *Anthopleura* is unique among cnidarians in that some of its species harbor phyletically distinct algal symbionts: two zooxanthellae (brown-colored dinophytes, *Symbiodinium californium* and *Symbiodinium muscatinei*; LaJeunesse and Trench 2000) and at least one zoochlorella (green cells in the phylum Chlorophyta; Muscatine 1971; O'Brien and Wyttenbach 1980).

Evidence suggests that the three symbiont species differ in their field distributions according to biogeographic- and microhabitat-scale physical environments (Bates 2000; LaJeunesse and Trench 2000; Secord and Augustine 2000). The body size of individual anemones may even produce microhabitat differences relevant to the distribution and abundance of these two algal symbiont taxa (Secord and Augustine 2000). These environmental gradients most likely reflect the

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biologically influential physical parameters of light and temperature (Verde and McCloskey 2001, 2002). Moreover, unlike the multiple taxa of zooxanthellae found in corals and other tropical and temperate invertebrates (Rowan et al. 1997; LaJeunesse 2001; Baker 2003), at northern latitudes, there is only one zooxanthella (*S. muscatinei*; LaJeunesse and Trench 2000), and zooxanthellae and zoochlorellae are distinguished visually. Thus, the *Anthopleura* system is particularly amenable to field experimentation with anemones in Washington and Oregon because its two known North Pacific algal species can be distinguished in the field by gross visual examination of entire animals, with subsequent verification by light microscopy (Muscatine 1971; O'Brien and Wyttenbach 1980; Saunders and Muller-Parker 1997).

The wave-swept rocky intertidal cave network at Tatoosh Island, Washington state (48°24′N, 122°44′W) affords a unique field opportunity to examine in detail the distribution of these two kinds of symbiotic algae along a long-established environmental gradient. While aspects of the physical biology (Norton et al. 1971) and community ecology (Corriero et al. 2000; Bell 2002) of temperate semisubmerged caves in Ireland and in the Mediterranean have been studied, to our knowledge, this is the first study of the dynamics of algal symbiosis under such novel conditions. We studied two caves that featured suitable anemone habitats at a relatively uniform tidal height (mean lower low water + 1.2 m) with bidirectional tidal flux. This study is among the first mechanistic analyses of the physiology of a dual symbiosis (relative photosynthetic performance of the two algae hosted by *A. elegantissima*) integrated with its field ecology (natural distributions and reciprocal transplant experiments) along a naturally occurring gradient affecting relatively few physical parameters. Along this natural gradient, we measured ambient light and quantified densities and ratios of each alga symbiotic with *A. elegantissima*. We then related these patterns to data on the photophysiological performance of anemones containing these two algae in the laboratory and to the acquisition of symbionts by anemone hosts transplanted to different positions along the natural gradient in the cave.

Methods

Photosynthesis-irradiance curves for *A. elegantissima* were generated as follows. Oxygen flux measurements with green (zoochlorellate) and brown (zooxanthellate) anemones collected from Eagle Point, San Juan Island, Washington, followed procedures in Muller-Parker (1984), except that anemones were incubated in a 165-ml Plexiglas chamber in 0.45-μm filtered seawater (salinity = 31) kept at ambient seawater temperature (11.5–14°C) with a flow-through seawater bath. Irradiance provided by an overhead tungsten-halogen lamp was varied using Kodak neutral-density filters. Each irradiance level was provided for a period ranging from 0.25 to 0.5 h. The incubation seawater was replaced between measurements at each irradiance level. At the end of the measurements, each anemone was homogenized and processed for biomass parameters as described below. Oxygen-flux measurements were standardized to weight of anemone protein. For each anemone, photosynthetic efficiency was determined from a linear regression of the oxygen fluxes from 0 to 93 μmol quanta m^{-2} s^{-1}, respiration rate was obtained as the y-intercept of the regressions, and I_c was the irradiance where the net oxygen flux was zero. P_{max}net of zoochlorellate anemones was obtained by averaging the light-saturated oxygen fluxes above 200 μmol quanta m^{-2} s^{-1}.

To measure light and temperature experienced by anemones in the field during low tides, we established transects along the length of two of the Tatoosh caves (North Cave and Central Cave) by placing a survey tape along the midchannel of each cave, measuring irradiance at 1-m intervals with a quantum sensor (cosine collector, 400–700 nm) connected to a datalogger (LI-1000; LI-COR). We repeated this procedure three times for each cave during morning and evening low tides of a single low-tide series (30 July–3 August 1993). In July 1995, we measured polyps' internal body temperatures along the same cave gradients by inserting a YSI 400 series temperature probe, connected to a YSI telethermometer, through the mouth into the gastrovascular cavities of individual anemones.

We sampled anemones for symbiotic algal populations at 2-m intervals along the intertidal cave transects described above. Five anemones were collected at random from a 0.25-m^2 quadrat centered at each sampling point along the transect. Anemones from each station were removed from the rock, placed alive into individually labeled plastic bags, and frozen within 24 h. In the laboratory, we measured blotted wet weights of each polyp, and algal densities were determined by homogenizing them in filtered seawater using a Wheaton overhead tissue grinder. Homogenate was assayed for protein content using bovine serum albumin as a protein standard (Lowry et al. 1951; Saunders and Muller-Parker 1997). Zooxanthellae and zoochlorellae in each anemone were censused separately by averaging six hemocytometer fields, and densities of each alga subsequently calculated on a per-gram-anemone-protein basis.

Field transplant experiments were conducted by haphazardly collecting green, brown, and white (=visibly algae-free) anemones from their natural habitats in the Central and North caves. Once collected, these animals were randomly assigned to replicated, blocked enclosures at each of three sites in the North cave (n = 9 enclosures at each site: three per initial algal type [green, brown, or white], with three polyps of each type per enclosure; thus, n = 27 anemones per site, n = 81 total experimental anemones). These sites were positioned within the brown-, green-, and white-anemone regions of the cave (see Results), approximately corresponding to the cave positions with 100%, 10%, and 1% of ambient light levels (the 0-m, 9-m, and 18-m points on the North Cave transect), respectively (Fig. 2). To rule out possible biological effects of the transplantation procedure itself (described below), each site included a transplant control treatment of anemones moved within their home light region (e.g., initially green anemones transplanted to their own green region of the cave, and so on). Overall, then, one third of experimental animals were transplant controls.

Field anemone enclosures were constructed as follows. We prepared each site for enclosure installation by using a

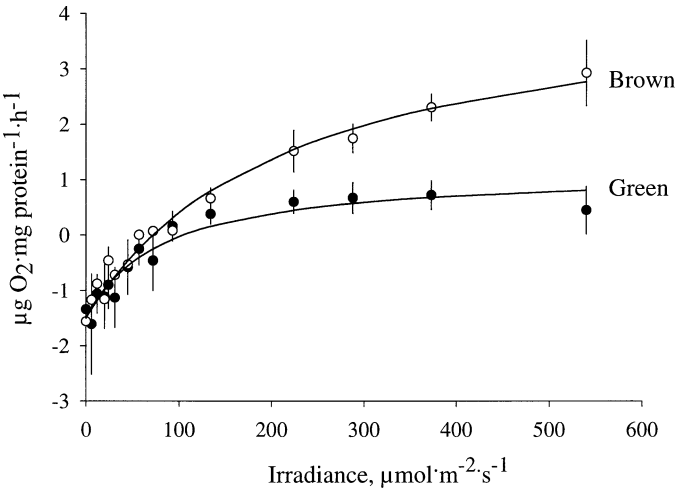

Fig. 1. Photosynthesis-irradiance curves for zooxanthellate (brown) and zoochlorellate (green) *Anthopleura elegantissima* in the laboratory (n = 3 anemones, ±1 SD).

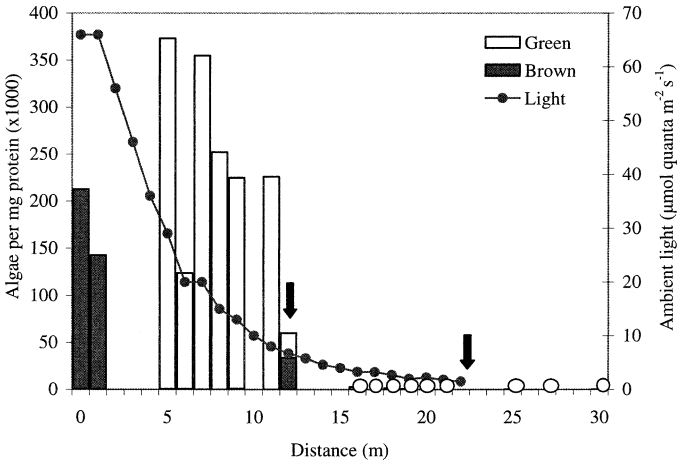

Fig. 2. Natural algal distributions with depth in the North Cave at Tatoosh Island (shown on left y-axis). Average density (number of algal cells per mg protein biomass; n = 5 anemones per transect point) and identity of symbiotic algae as a function of distance along the light gradient created by Tatoosh caves. Circles indicate anemones were sampled at that transect point, but lacked visible algae (although a few zoochlorellae, well below the resolution of this graph, occur as deep as 19 m into the cave). The right y-axis shows light decline with depth into the North Cave at Tatoosh Island. Over distances of 20–30 m, light declines by 99% compared with full ambient light outside the caves. Arrows indicate the points along the gradient corresponding to 90% and 99% light attenuation compared with full ambient light outside of caves.

rock hammer to create nine divots (~5–7 cm across and ~2–3 cm deep) in the bedrock substratum of the cave. Each divot was then surrounded by heavy-duty green artificial turf strips (Ernst Home Center) to create a corral designed to prevent anemone escapes (anemones are reluctant to crawl across artificial turf; pers. obs.). Turf strips (~2 cm × ~20 cm) were cut with a utility knife and seared along the edges with a blowtorch to minimize fraying during wave exposure. They were then tightly screwed to the intertidal with their corners overlapping to create patches of natural substrate circumscribed by a square of turf, each with inside dimensions ~18 cm per side. The corners of each enclosure were fastened with stainless steel hardware (37.5 mm #12 lag screws and fender washers; Tacoma Screw) secured within well-reamed power-drilled holes with plastic wall anchors. To prevent anemones' escape underneath turf enclosure sides, we secured all enclosure-substrate margins with a border of two-part marine epoxy putty (Sea Goin' Poxy Putty 1350; Permalite Plastics). To ensure complete diffusion of any toxins away from setting putty and to remove debris generated by drilling and divot excavation, we always allowed at least one high-tide cycle to pass to cleanse the area before transplanting experimental anemones.

After enclosure installation at all sites, we randomly assigned enclosures within each block of nine anemone corrals per site, to the three treatments (initially brown, green, and white anemones). In April 1994, anemones were installed into their assigned spaces. At low tide, undamaged polyps with their pedal disks cleaned of all adhering debris were placed tentacle-side-up in groups of three into each enclosure's divot. These were then covered with flexible rubber mesh (Neotex fiber-core neoprene antiskid counter liner; Doc Freeman's) secured at the four corners of each enclosure by stretching it over the steel screws, producing gentle downward pressure on each group of anemones. After 1–2 high-tide intervals (24–48 h), we removed all Neotex mesh, leaving anemones of known algal complement in assigned enclosures at each site. These enclosures not only established transplanted animals of known initial algal complement on natural substrates within the cave, but they also excluded other anemones in the area from entering experimental areas.

To assess temporal trends in algal populations, anemones were sampled as described below in May 1994, November 1994, and May 1995. Anemones were also measured monthly (basal diameter in two dimensions) throughout this period and scored for presence and binary fission. Algal complement of anemones was assessed by repeatedly removing a small amount of crown or tentacle tissue using fine, curved iris scissors. Tissues were placed in individually labeled vials and transported on ice to the lab for subsequent processing. Algal cell counts and densities were determined as described above for naturally occurring cave anemones.

Results

Net oxygen fluxes are shown for zooxanthellate and zoochlorellate anemones at a series of irradiance levels (Fig. 1). Under low irradiances and in the dark, no significant differences in the photosynthetic parameters I_c, α, and respiration of zooxanthellate and zoochlorellate anemones were obtained ($p > 0.05$, *t*-test comparisons). The compensation irradiance I_c averaged 73 μmol quanta m^{-2} s^{-1} for both anemone types. Photosynthetic efficiency (α) of zooxanthellate anemones averaged 0.0211 (±0.0075 SD) μg O_2 h^{-1} mg protein^{-1}(μmol quanta m^{-2} s^{-1})$^{-1}$, and α of zoochlorellate anemones averaged 0.0168 (±0.0079 SD) μg O_2 h^{-1} mg protein^{-1}(μmol quanta m^{-2} s^{-1})$^{-1}$. Dark respiration rate of anemones was independent of algal complement; respiration

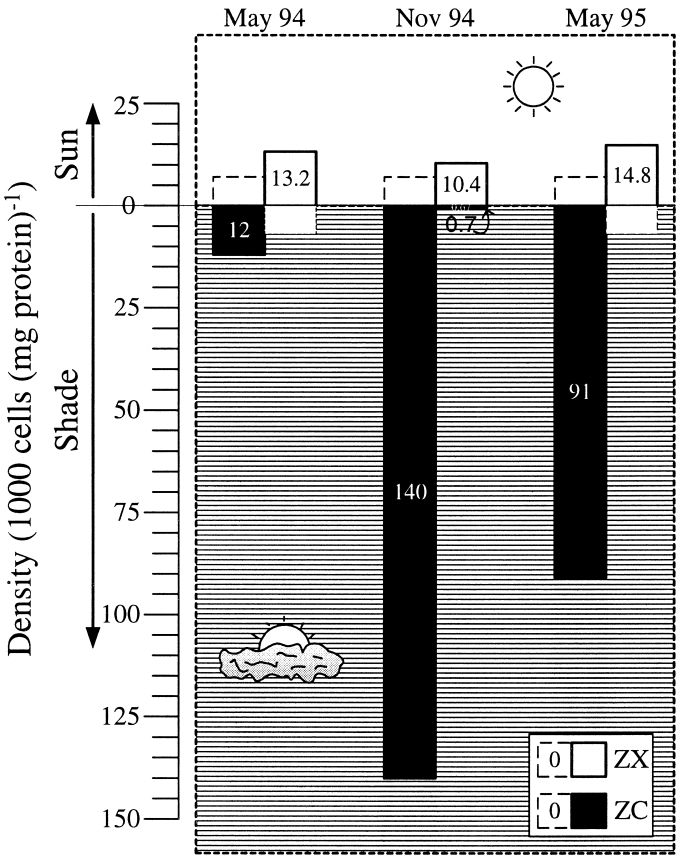

Fig. 3. Algal responses to reciprocal transplant experiments in cave. The figure shows change over a 1-yr period in the algal densities of initially algae-free anemones (time zero = April 1994) transplanted to two positions in the cave (sunny and shady sites, corresponding to natural regions of brown and green anemones, respectively). Values above the zero line show changes at the sunny transplant site and those below the zero line show changes in animals transplanted to the shady site. For each of the three time points, the left bars show density of zoochlorellae and the right bars show density of zooxanthellae. Dotted (ZC) or nondotted (ZX) bars without numbers indicate no visible symbionts of a particular type occurred in that location at that time point. Anemones that began green or brown remained so throughout the experiment, regardless of the position within the cave to which they were transplanted.

rates of the zooxanthellate and zoochlorellate anemones averaged 1.34 (±0.36 SD) and 1.43 (±1.09 SD) μg O_2 h^{-1} mg protein^{-1} for zooxanthellate and zoochlorellate anemones, respectively. However, at irradiances greater than 100 μmol quanta m^{-2} s^{-1}, the productivity of zooxanthellate anemones exceeded that of zoochlorellate anemones. The average P_{max}-net of zoochlorellate anemones was 0.61 μg O_2 h^{-1} mg protein^{-1}, while net photosynthesis of zooxanthellate anemones at the highest irradiance level tested (540 μmol quanta m^{-2} s^{-1}) was almost fivefold higher, averaging 3.0 μg O_2 h^{-1} mg protein^{-1} (Fig. 1). Light-saturated photosynthetic rates of zooxanthellate anemones were not attained at the experimental irradiances.

Photosynthetically active radiation (PAR) declined exponentially with distance into each of the two caves (Fig. 2). PAR declined to about 10% of ambient light halfway into each cave and to about 1% at the rear of the caves. Light-attenuation coefficients (k) derived from distance into the cave were 0.15–0.17 m^{-1}, comparable with light attenuation with depth in adjacent coastal waters. Specifically, nearby clear coastal waters have vertical light attenuation coefficients (k) averaging 0.15 m^{-1} (Kirk 1994), while in the Strait of Georgia, k averages 0.11 m^{-1} in the winter (Harrison et al. 1983).

The caves can each be divided into three zones of symbiosis based on algal complements of anemones (Fig. 2). The first zone near the entrance to each cave received ≥50% full ambient PAR, and zooxanthellate anemones predominated. This first zone also received occasional pulses of higher PAR in the form of direct sunlight at certain times of day, not shown in Fig. 2, which reflects the more typical cloudy or foggy conditions of the Washington coast. The second zone (exposed to between 10% and 50% ambient light) contains mainly zoochlorellate anemones. Although algae in the second group occur at twice the density of those in the first, total algal volumes are equivalent due to the smaller size of zoochlorellae. Within the green zone, the density of zoochlorellae declines by three orders of magnitude over a lateral cave distance of about 15 m (vestigial populations of algae occur as deep as 19 m, with absolutely no algae visible beyond that). There was not a clear transitional zone between brown and green anemones, but this was confounded by the fact that no anemones occurred along our transect between 2 m and 5 m. The third zone at the rear of the cave (<10% PAR) contains white anemones lacking any pigments associated with the presence of algae. Both caves showed qualitatively and quantitatively similar results for both light and algal complement of anemones.

There was no significant relationship between the body size (blotted wet weight, protein biomass, or basal diameter) of anemones and their positions along the cave gradient ($n = 81$; $p > 0.05$). Several series of additional measurements revealed that anemones exposed to sunlight nearer the mouths of the caves were up to 5°C warmer than surrounding air and seawater. All anemones deeper within the caves were the same temperature as the surrounding air, which remained constant (11–13°C) with cave depth. Therefore, only zooxanthellate anemones at the mouth of the caves were subjected to marked increases in temperature or irradiance during summer midday emersion periods.

Experimentally transplanted animals varied in their responses after 1 yr. Anemones that began green or brown did not display significant changes in the densities or ratios of their algal populations, at least within the body regions sampled; initially algae-free animals, however, did experience significant growth in their algae. Anemones transplanted to the lowest light, white region, of the cave remained symbiont-free. Algae-free animals transplanted to the moderate-light green region of the cave acquired predominantly zoochlorellae. Algae-free animals transplanted to the highest light, brown region, of the cave grew populations of zooxanthellae. The densities of these algae after 6 months and 1 yr were approximately an order of magnitude higher for zoochlorellae than for zooxanthellae (Fig. 3).

Discussion

Our results show a clear relationship between an environmental gradient and the participants in symbiotic interactions, suggesting that hosts are not necessarily loyal to a particular symbiont; algae-free anemones acquired symbionts typical of the site into which they were transplanted. Mechanistically, population densities of these symbionts likely depend on physical parameters along the cave gradient that determine algal productivity and growth. Data presented here and elsewhere suggest that the most likely factors influencing algal growth are light and temperature (Verde and McCloskey 1996, 2001, 2002). At least three possible hypotheses could explain the distributional patterns reported here. First, each alga may simply photosynthesize and grow best under the conditions in the zones of the caves where it occurs (Fig. 1; Verde and McCloskey 1996; Saunders and Muller-Parker 1997). According to this scenario, zooxanthellae are the only algae found in the outer region of the cave due solely to locally higher light or temperature. In the middle reaches of the cave, then, light would be adequate for zoochlorella growth but not so high that the superior photosynthetic performance of zooxanthellae at higher temperatures or irradiances allows this symbiont to dominate. Second, anemones display phototactic behavior and may move to regions of the cave that produce the best physiological fit between host and symbiont species (Pearse 1974). Third, anemones may be subject to differential predation based on the symbionts they contain (Augustine and Muller-Parker 1998). While any or all of these mechanisms may be responsible for the distributional patterns observed here, the most parsimonious explanation is based on the different physiological performances of zooxanthellate and zoochlorellate anemones and growth rates of the algae themselves.

Observed distributions of algae reported here probably depend both on the initial establishment of their associations with anemone hosts as well as on subsequent change in symbiont populations, assuming environmental availability of both symbionts. While this study does not address establishment of symbiotic associations, it does suggest that (assuming equal availability of symbionts) algal complement will be associated with environmental parameters related to the photosynthetic performance of the symbiotic association. Demonstration that *Anthopleura* can change its complement of symbionts as environmental conditions change—using field transplants (this study, Bates 2000) or laboratory manipulations (Saunders and Muller-Parker 1997)—suggests a mechanism underlying observed field distributions of hosts and symbionts. Many cnidarians can persist genotypically for centuries or millennia, and thus, symbiont distributions at one time represent an integrated measure of past environmental conditions. If these temperate anemone hosts can respond to local or regional environmental change (Gleason and Wellington 1993; Glynn 1993) (e.g., increasing seawater temperatures, ultraviolet light) by shifting their symbiont complements, then long-lived, locally adapted hosts may substantially expand their phenotypic plasticity. Such plasticity of symbiotic interactions may also be critical as conditions change in tropical marine communities that depend on cnidarian-algal symbioses for their high productivity and diversity (Baker 2001). Geographic variation in intimate species interactions may be equally important in the basic and applied biology of temperate systems as well, both in the sea and on land (Secord and Augustine 2000; Secord 2002). Indeed, disruption of symbioses frequently has profound ecological and economic consequences, the implications of which, for applied conservation, pathology, and control of exotic pests, are often underappreciated (Douglas 1995; Secord and Kareiva 1996; Secord 2002, 2003).

The decline of light within the intertidal caves parallels that with depth in coastal waters. Other parameters notwithstanding, the critical qualitative difference between light decline in a water column versus that in a cave is the elimination of certain wavelengths with depth. We cannot address this difference with our data, but it could be addressed explicitly with future experiments. Current evidence, though, suggests that the quantity rather than the quality of light is a prime determinant of algal densities and ratios (Verde and McCloskey 1996, 2002). Temperature could also be the key parameter influencing these distributions because anemones nearer the entrance to the cave receive pulses of sunlight making them several degrees warmer than animals deeper into the cave ever experience. Light intensity and temperature may act together to influence algal growth in the cave anemones.

Our field data are consistent with those of Secord and Augustine (2000), who showed consistent differences in algal distributions based on several proxies for light and temperature, including latitude (Washington State to Mexico), intertidal height (high and low), and host species (*A. elegantissima*, *Anthopleura xanthogrammica*, and *Anthopleura sola*). They are also consistent with field experimental data for the large solitary *A. xanthogrammica* in Canadian tidepools (Bates 2000). The effects of latitude on midday intertidal temperatures during emersion may, however, be confounded by seasonal variation in the timing of low tides (Helmuth et al. 2002). A temporal component to sampling along such spatial gradients would help in determining the roles of diurnal, seasonal, El Niño-related, and long-term directional variation in mean and extreme conditions influencing symbionts. While only one species of zooxanthella has been detected in Washington (*S. muscatinei*), at least one other is present in *Anthopleura* hosts on the Pacific coast of North America (LaJeunesse and Trench 2000). We do not know whether there are multiple strains or species of visibly similar but genetically different zoochlorellae. This symbiosis, then, may be considerably more complex than currently recognized, with many symbiont taxa belonging to two algal phyla inhabiting at least three species in the genus *Anthopleura* in the northeast Pacific Ocean (McFadden et al. 1997; Pearse and Francis 2000; Secord and Augustine 2000).

Our results differ from those documented in tropical systems in several respects. The symbiosis here is facultative rather than obligate; cnidarian hosts in temperate environments do not depend on photosynthate like their tropical coral counterparts (Muller-Parker and Davy 2001). This is supported by our data suggesting that algae-free anemones at the back of the caves are not smaller than anemones elsewhere, implying a successful heterotrophic lifestyle. Also,

the symbionts are of completely different evolutionary origin and may have substantially different physiologies compared with the different species of zooxanthellae typical even over very fine spatial scales on coral reefs (Rowan et al. 1997; LaJeunesse 2002; Baker 2003; Knowlton and Rohwer 2003). However, in the past, we may have underestimated the physiological variation within the genus *Symbiodinium* (e.g., Iglesias-Prieto and Trench 1997).

Proliferation of zoochlorellae in transplanted algae-free anemones occurred much more rapidly than that of zooxanthellae (Fig. 3). This is consistent with higher observed division rates (mitotic index) of zoochlorellae compared with zooxanthellae (Verde and McCloskey 1996). Zoochlorellae are also smaller than zooxanthellae, but the biomass of zoochlorellae exceeded that predicted simply by their smaller cell volumes. The source of the algae that populated anemones is unknown, though it is clear from our transplant experiments that algae are available, either in the environment or as vestigial bleached populations, to reinhabit anemones. Possible sources of algae include those free-living in the water column (or in the feces of predators on anemones; Augustine and Muller-Parker 1998; Seavy and Muller-Parker 2002), vestigial populations of symbionts inhabiting anemones but undetected by us, or substantial populations of algae inhabiting anemones but with bleached chloroplasts, rendering them invisible by light microscopy. In the latter case, the prediction might be made that algae in near-total darkness are parasitizing their hosts, but our failure to detect smaller mean anemone body sizes at the rear of the caves argues against this (higher rates of binary fission by anemones in the light, however, might reduce their average size). In any case, growth rates would likely be a better indicator of host fitness than body size. Staining of tissue from algae-free anemones for the presence of algal cell walls could help to resolve this issue. Overall, the roles of (at least) two algal symbionts, belonging to different phyla, in the sexual and asexual life-history biology of these anemones remain to be elucidated. However, the stability of intact symbioses in adult hosts is a striking feature of this system; in temperate as well as tropical systems, disturbance-induced bleaching may be the driving factor in rearranging host–symbiont associations.

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