



Rapid community change at a tropical upwelling site in the Galápagos Marine Reserve

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Abstract. The high biodiversity of tropical marine communities has attracted considerable interest, yet we still lack a clear understanding of the tempo of diversity change in these systems [Jackson (1991) *BioScience* 41: 475–482; National Research Council (1995) *Understanding Marine Biodiversity*, National Academic Press, Washington, DC]. Knowledge of the conditions associated with fast or slow community assembly in the tropics would enhance our ability to predict recovery from natural and anthropogenic disturbance and to conserve biodiversity. Here we report an unusually rapid doubling of species richness within a year in a tropical, subtidal sessile invertebrate community in a protected (non-extractive) zone of the Galápagos Marine Reserve (GMR). Diversity changes in the rock wall community were accompanied by large increases in the percent cover, density and/or biomass of sponges, barnacles, ascidians, and an ahermatypic coral, *Tubastrea coccinea*, over the 1-year study period (1999–2000). Barnacle (*Megabalanus peninsularis*) and ascidian (*Didemnum cineraceum*) biomasses increased by an order of magnitude from 1999 to 2000. The greater abundance of sessile invertebrate prey was accompanied by significant increases in the abundance of barnacle and *Tubastrea* predators (*Hexaplex princeps*, *Asperiscula billeeana*). An estimated 37% of barnacle tissue biomass production was consumed in 1 year. Temperature monitoring during the study period showed that this site is characterized by strong upwelling, where rapid, 3.0–9.0 °C decreases in temperature occurred at harmonics of the semi-diurnal tidal periodicity during warm (January–February), but not during cool months (June–July). Short-term acoustic current meter measurements revealed strong, highly variable upwelling at the study site, with events ranging from 2–111 min in duration and maximum upwelling velocities of 32.3 cm s⁻¹. These findings suggest that the turnover of diversity and biomass may be unusually rapid at tropical upwelling sites, especially where invertebrate predators are protected from harvesting. Consequently, upwelling sites may warrant special consideration in the planning of marine reserves to ensure the conservation of biodiversity.

Introduction

The species composition of invertebrate communities attached to bedrock or carbonate reefs in the tropics is influenced by biological interactions, disease, disturbance, climatic events and human activities. The time required for tropical communities to re-assemble on vacant, natural hard substrate to a state resembling the diversity of the initial condition commonly exceeds 6 years (Colgan 1987;

Connell 1997) and may require over 50 years in coral reefs (Grigg and Maragos 1974). In some cases, the community may switch to an alternate state characterized by a lower diversity than the initial condition (Knowlton 1992; Hughes 1994), underscoring concerns for the decline of tropical marine diversity. Although less conspicuous than coral reefs, diverse multi-phyletic communities of epifaunal invertebrates commonly encrust the submerged sides of rocky islands throughout tropical and sub-tropical regions (Ayling 1981; Witman 1992; Gili and Coma 1998; Baynes 1999). Little is known about the rate of diversity change in these tropical communities of sponges, corals, anemones, octocorals, gorgonians, bryozoans, molluscs, polychaetes and ascidians.

The Galápagos Marine Reserve (GMR) is one of the largest marine reserves in the world, second only to the Great Barrier Reef Marine Reserve in area (Bustamante et al. 2002). A provisional zonification scheme devised to reduce stakeholder conflicts between tourism, artisanal fishing, and science/conservation was approved in March 2000. Although surveys of the distribution and abundance of benthic invertebrates, algae and fish are being conducted to establish baseline information for the GMR and to evaluate the provisional zonification scheme (R. Bustamante, personal communication), little information is available on temporal variation in biodiversity and community structure of invertebrate species other than corals (Glynn and Wellington 1983; Glynn 1990). As the zonification scheme will be evaluated over the next 2 and 4 years to determine its utility in conserving marine biodiversity, it is important that information on temporal variability of the marine communities is incorporated into the future management of the GMR. To this effect, information on temporal variability in marine biodiversity was underscored as a key research need in a recent workshop on the biodiversity of the Galápagos Archipelago (Branch et al. 2002).

Although the Galápagos Islands are centered on the equator, sea surface temperatures in the Galápagos are unusually cool for a tropical region (Chavez and Brusca 1991). This is primarily a result of the upwelling of cool, nutrient-rich water that is driven by at least three different physical mechanisms that vary in spatial scale, frequency and area of influence. The largest mechanism is wind-driven equatorial upwelling that affects the entire Archipelago and is created as the trade winds blow westward between the Easter Island High and the Indonesian Low Pressure systems (Wyrski 1992). In addition, the westward advection of the cool Peru current causes upwelling that affects the eastern Archipelago in particular (Houvenaghel 1984). On the opposite side of the Archipelago, the equatorial undercurrent (EUC) runs from west to east, creating upwelling as it collides with the principal western islands, Isabela and Fernandina (Houvenaghel 1984; Chavez and Brusca 1991; Wyrski 1992). Topographically induced upwelling also exists on much smaller spatial scales than the EUC in the form of island wakes and other flow-topography interactions on the sides of islands (Houvenaghel 1978; Feldman 1986). The rapid changes in the depth of the thermocline and strong vertical currents commonly observed by scuba divers at many sites in the Galápagos (Glynn and Wellington 1983; J.D. Witman and F. Smith, unpublished observations) may be produced by smaller-scale topographically induced upwelling.

Upwelling influences the structure of marine communities directly by affecting

the recruitment (Roughgarden et al. 1988) and growth of epifaunal invertebrates (Branch and Griffiths 1988; Menge 1992) and algae (Bustamante et al. 1996), and indirectly by changing the intensity of biological interactions (Dayton et al. 1999; Sanford 1999). Menge (1992) and Menge et al. (1997, 1999) have suggested that enhanced levels of nutrients and food in upwelling regimes create a bottom-up effect (i.e. food, nutrient enrichment) on the food web followed by strong predator control (i.e. top-down) in intertidal communities. In the subtidal zone, more is known about population responses to upwelling than about effects on communities. A comparison of coral (*Pocillopora*) growth in upwelling versus non-upwelling regions off the west coast of Panama indicated that growth rates were significantly lower in the upwelling region (Glynn 1977). Off the Florida Keys, Leichter et al. (1998) found that growth of the coral *Madracis* was higher at the depth where upwelling from internal tidal bores was most frequent. Extensive subtidal surveys by Velimirov et al. (1977) showed that filter feeders dominate horizontal rocky areas in the Benguela upwelling system. There is a lack of published information on how upwelling influences the diversity of marine communities. Since upwelling areas are usually characterized by high primary productivity, there is a potential effect of upwelled productivity on species diversity (Rosenzweig 1995). A review by Mittlebach et al. (2001) found that the diversity of aquatic communities may be positively, negatively or parabolically related to various measures of productivity, and that the form of the relationship differed with spatial scale.

Because so little was known about community-level variation in the Galápagos rocky subtidal ecosystem, the first question we attempted to answer was: how fast does invertebrate species richness and abundance change at rock wall sites in the GMR? Secondly, we sought to identify the major biological or physical correlates of community change. Initial observations of rapid temperature fluctuations at several study sites had led us to focus on upwelling as a possible agent of physical forcing. We tracked change in the subtidal communities over a 53-week interval (May 31, 1999–June 6, 2000) on the northeastern side of a collapsed volcano, Rocas Gordon, in the central region of the Galápagos Archipelago (Figure 1). Subtidal topography of this site is characterized by a vertical inclination from the surface to greater than 70 m depth. Although permanent quadrats were established at 6, 12 and 18 m depth, we focus on changes in the 12 m community, which were representative of change at other depths. Sessile invertebrates attached to the rock wall are predominately suspension-feeders on phyto- and zoo-plankton and thus provide an important indicator between production in the water column and consumers at higher trophic levels. The research reported here is part of a larger, ongoing study of community-level variation in subtidal rock wall habitats of the Galápagos.

Methods

Community structure

Permanent transects were established at Rocas Gordon (00°33.953' S; 90°08.493' W) in May 1999 by drilling into the rock wall to emplace stainless steel bolts. A 30

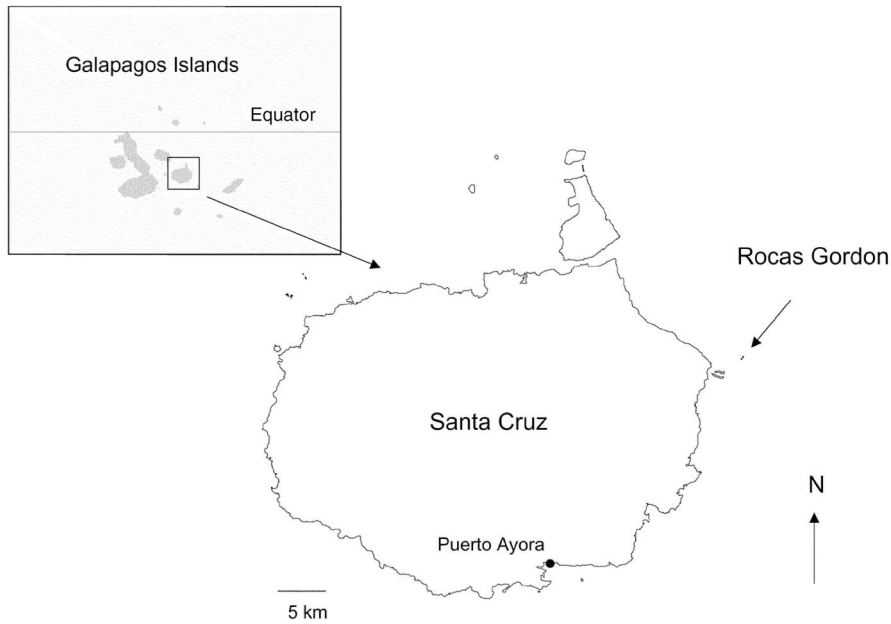


Figure 1. Map of Galápagos Islands (inset) showing the location of Rocas Gordon off the eastern side of Santa Cruz Island.

m transect tape was prepared by randomly marking the locations for two corners of 18 quadrats, each of 0.25 m^2 area. The tape was stretched out across the rock wall along the 12 m depth contour and fixed to the bolts. A 'quadrapod' camera framer holding a Nikonos V underwater camera with a 15 mm lens and two strobes over a 0.25 m^2 quadrat (Witman 1985) was aligned with the marks on the transect. Accurate re-positioning of the quadrapod for the permanent quadrat photos in 2000 was aided by the use of plastic laminated photos of 1999 quadrats. High-resolution quadrat photos were taken with 35 mm slide film. A scale (mm) on the sides of the quadrat allowed measurement of organisms in the images. The lens is corrected for distortion, and the photos were sharp enough to allow identification of encrusting invertebrates down to 0.5 mm body size when the slides were projected. Species richness was determined by counting the number of species in each photo quadrat. Identification of invertebrate species in the quadrats was assisted by collecting voucher specimens and by preparing a photographic library of species from the photo quadrats. Species identifications were made using the following references: sponges, Desqueyroux-Faúndez and Van Soest (1997); Hickman et al. (in preparation); corals, Glynn and Wellington (1983); Cairns (1991); molluscs, Hickman and Finet (1999); anemones and gorgonians, Hickman et al. (in preparation); bryozoans, Banta 1991; Hickman and Humann (in preparation); barnacles, Hickman and Zimmerman (2000); and ascidians, Hickman and Humann (in preparation). When a positive taxonomic identification could not be made, a 'field name' was assigned

Table 1. Comparison of the species richness of epifaunal invertebrates in permanent quadrats at Rocas Gordon between 1999 and 2000.

	1999	2000
Sponges		
<i>Carmia</i> sp.	×	×
<i>Halisarca</i> sp.	×	×
<i>Aplysilla</i> sp. 6	×	×
Unid. white demosponge sp.	×	×
<i>Aplysilla</i> sp. 5		×
<i>Aplysina</i> sp. 7		×
<i>Adocia</i> sp. 2		×
<i>Clathrina</i> sp. 4		×
<i>Tethya aurantia</i>		×
Unid. <i>Cacospongiae</i> sp.		×
Unid. <i>Reneria</i> sp.		×
Unid. <i>Sylotella</i> sp.		×
Corals		
Hermatypic:		
<i>Pocillopora</i> sp.		×
Ahermatypic:		
<i>Tubastrea coccinea</i>	×	×
<i>Rhizopsammia wellingtoni</i>	×	×
<i>Oulangia bradleyi</i>		×
Anemones		
<i>Bunodactis mexicana</i>		×
Zoanthids		
<i>Parazoanthus</i> sp.		×
Antipatharians		
<i>Antipathes galapagensis</i>	×	×
Hydroids		
<i>Pennaria</i> sp.	×	×
<i>Eudendrium</i> sp.	×	×
<i>Macrorhynchia</i> sp.		×
Unid. <i>Obelia</i> sp. (?)		×
Polychaetes		
<i>Filograna</i> sp.	×	×
<i>Spirobranchus giganteus</i>	×	×
<i>Spirorbis</i> sp.	×	×
Parchment tube sabellid	×	×
<i>Salmacina</i> sp.		×
Unid. keeled serpulid		×
Molluscs		
<i>Sepulorbis margaritaceus</i>	×	×
Unid. mytilid mussel	×	×
<i>Lithophaga</i> sp.		×
<i>Arca mutabilis</i>		×
<i>Hytissa solida</i>		×
<i>Chama squamuligera</i>		×
Barnacles		
<i>Megabalanus peninsularis</i>	×	×
Bryozoans		
<i>Crisia</i> sp.	×	×

Table 1. (continued)

	1999	2000
<i>Parasmittina</i> sp.	×	×
Unid. <i>Cabarea</i> sp.	×	×
<i>Bugula californica</i>		×
<i>Bugula</i> sp. 7		×
<i>Cycloperiella rosacea</i>		×
<i>Lichenopora intricata</i>		×
Unid. spotted encrusting bryozoan		×
Ascidians		
<i>Didemnum cineraceum</i>	×	×
<i>Didemnum</i> sp. 1	×	×
<i>Polycarpa ecuadorensis</i>	×	×
<i>Diplosoma listerianum</i>		×
<i>Didemnum perlucidum</i>		×
<i>Pyura haustor</i>		×
<i>Eusynstyela</i> sp.		×
<i>Aplidium solidum</i>		×
Total species richness (observed)	22	52

and referenced to the photo library for consistency, and the abbreviation ‘Unid.’ used as in Table 1.

The Chao 2 index was used to estimate total species richness from the species counts using the computer program EstimateS (Colwell 1997), because it provides the least biased estimator of true species richness for <100 samples (Colwell and Coddington 1995).

$$\text{Chao 2 estimate of species richness} = \frac{S_{\text{obs}} + Q_1^2}{2Q_2}$$

where S_{obs} is the number of species observed in the pooled quadrat samples, Q_1 the number of species occurring in one quadrat, and Q_2 the number of species occurring in two quadrats.

The percent cover of organisms in the photo quadrats was estimated by the random dot method, using 200 random dots per image. Densities of predatory gastropods (*Asperiscula*, *Hexaplex*) were obtained from the permanent quadrats. In addition, three band transects (8.0 m × 0.09 m) were video taped to census *Hexaplex*, which was more dispersed than *Asperiscula*. Numbers of *Hexaplex* in quadrats and transects were pooled and converted to densities per 1.0 m². The mean abundance of organisms in the permanent quadrats was compared by univariate repeated measures ANOVA using Statistica (v. 4.0, StatSoft™, Tulsa, Oklahoma) software. Percent cover data were arcsin square-root transformed and densities and biomass data were log (x+1) transformed prior to ANOVA analyses.

Biomass estimation

The procedure used to estimate the biomass of the encrusting colonial ascidian

Didemnum cineraceum involved photographing colonies in the field, scraping each colony off the substratum and placing them in numbered bags. Colonies were blotted dry on a towel and weighed. The surface area of each colony was measured by digitizing the photographs in Adobe Photoshop^(TM). Least squares linear regression was performed to relate surface area to biomass by the equation:

$$Y = -0.933 + 0.026x, r^2 = 0.83, P < 0.0001, \text{ with } 1, 12 \text{ df}$$

where Y is the wet wt (g) biomass of *Didemnum*, and x is colony surface area (in cm^2).

Per quadrat biomass was predicted by substituting the percent cover of *D. cineraceum* from the random dot analysis into the regression equation. The biomass of *Megabalanus* was estimated by a similar procedure. Barnacles were collected from Rocas Gordon in June 2000 and measured for aperture length (distance from rostrum–carina across the aperture) and basal diameter with calipers. The tissue was dissected out, blotted dry, and weighed as wet weight biomass. Least squares linear regression was performed to relate aperture length to biomass by the equation:

$$Y = -0.168 + 0.06x, r^2 = 0.84, P < 0.0001 \text{ with } 1, 31 \text{ df}$$

where Y is the *Megabalanus* tissue biomass wet wt (g), and x is aperture length (mm).

Aperture lengths of barnacles were measured from the permanent quadrat photos using the scale in the image. This regression equation was also used to predict the amount of barnacle tissue biomass consumed by predators from the size and number of barnacles consumed in the quadrats.

Temperature and current measurements

Waterproof thermistors (Stowaway TidbitTM model data loggers, Onset Computer Corporation, 0.4 °C accuracy) were attached to eyebolts on the rock wall at 3 and 12 m depth to record temperature fluctuations at 16 min intervals throughout the year. Although barnacles settled on the data loggers, the thermistors were not occluded. The rapid temperature decreases recorded by the thermistors motivated a subsequent study of the current regime at Rocas Gordon. Reasoning that vertical currents should be present at the site if the cool water events are caused by upwelling, we deployed a 3000 mhz acoustic doppler current profiler (ADP, SontekTM) at Rocas Gordon in February 2001, when the temperature fluctuations were pronounced. The ADP was set up on a small ledge at 17 m depth, about 5 m out from the rock wall where the permanent quadrats were located. The ledge was a small protrusion on the nearly vertical rock wall, which dropped off immediately below it. The ADP recorded vertical (z) velocity and two components of horizontal velocity (x, y) at 0.5 m depth bins up to 6.2 m above the instrument. Measurements were taken every second, averaged at 1 min intervals for a 6-day period (February 8–13, 2001). For clarity, only the first 28 h of the vertical current velocity data are presented.

Spectral analysis was performed on the temperature time series from the 12 m site

to reveal hidden periodicity in the data related to upwelling using Statistica 4.0TM. Prior to spectral analysis, the data were detrended to subtract any linear trend during January–February and June–July, the months selected for analysis. This was done by fitting a least squares linear regression to the data and entering the resulting intercept, a , and the slope, b , in the equation:

$$x = x - (a + b * t)$$

where t is the temperature datum.

The temperature data were transformed further by subtracting the mean to remove its dominance from the resulting spectrum and smoothing with a Hamming moving average window. The periods corresponding to the 5–6 largest peaks in power spectral density were identified.

Results

Community structure

In May 1999, the community was characterized by low species richness and abundance of invertebrates, with a high percent cover of crustose coralline algae (Figures 2 and 3). Small barnacles, *Megabalanus peninsularis*, accounted for 17%, on average, of the space in the quadrats. The size frequency distribution of barnacles revealed the dominance of a single small size class (1–2 mm aperture length, Figure 4A), indicating that the 1999 sample represented a cohort of newly recruited barnacles. The purplish-black encrusting ascidian, *D. cineraceum*, was also a conspicuous component of the epifaunal community in 1999 (Figure 2).

The site was so transformed by the recruitment and growth of epifaunal invertebrates 1 year later that it was difficult to re-locate the bolts marking the permanent quadrats and thermistors. The surfaces of the thermistors were covered by *Megabalanus* that had settled as larvae and grown to large size in a year. For example, the 10 barnacles on the thermistor placed at 12 m depth ranged from 5 to 31 mm basal diameter with five of them growing to 20–31 mm diameter in 1 year. Clusters of large barnacles also covered, on average, one third of the space on the rock wall in June 2000 (Figure 2). Size frequency distributions of the barnacles showed a striking increase in size with the 2000 mode centered at the 6–7 mm aperture length size class. Due to the large size of the barnacles in 2000, the doubling of barnacle percent cover over the year represented a far greater order of magnitude increase in barnacle tissue biomass (Figure 2B). The percent cover of crustose coralline algae decreased as the epifaunal community developed (Figure 2A). The encrusting sponges, *Carmia* sp. and *Aplysilla* sp. 5 were conspicuous in June 2000, as was *D. cineraceum* that underwent a threefold increase in percent cover and biomass in 1 year. The population size of the non-reef building (ahermatypic) coral *Tubastrea coccinea* increased by 18.8% due to larval recruitment, as indicated by the small size of the new colonies appearing in the year 2000 quadrats.

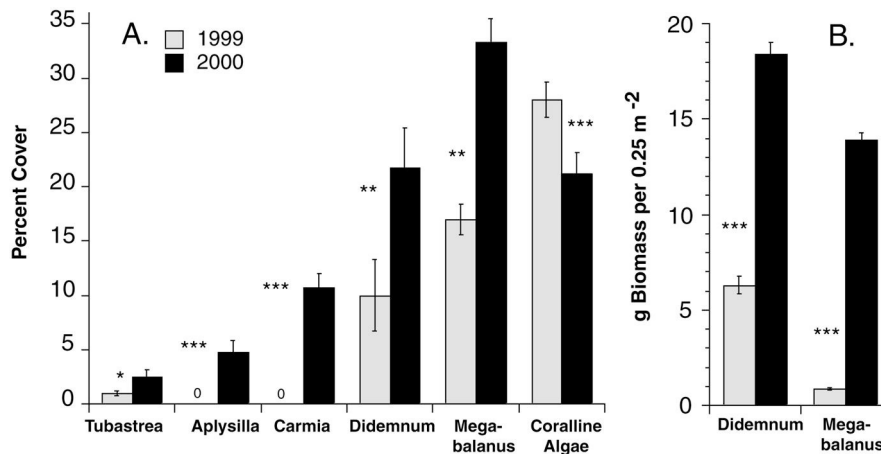


Figure 2. Changes in abundance of major groups of sessile invertebrates and crustose coralline algae in 18 permanent quadrats at 12 m depth. Average percent cover is shown in plot A, with bars indicating ± 1 standard error. *Didemnum* represents *D. cineraceum*, *Aplysilla* indicates *Aplysilla* sp. 5. Average biomasses (blotted dry wet weight) are reported in plot B with standard error bars. Asterisks over bars indicate P values resulting from RM ANOVA comparisons of 1999 vs. 2000 data for each species and coralline algae. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; see Table 2 for more details.

All changes in the percent cover, density and biomass of dominant species between 1999 and 2000 were highly significant (Figure 2, Table 2).

The number of species observed in 1999 and 2000 (observed species richness) was entered into EstimateS to estimate the total species richness of the communities by constructing randomized species accumulation curves. Figure 3 shows that species accumulation curves for the Chao index leveled off by 15 quadrats, indicating that the sampling effort of 18 permanent quadrats was sufficient to characterize the species richness of the community. The curves for the Chao index depict a striking increase from a maximum of 27.5 species in 1999 to 59.1 species in 2000, representing a 111% change in total species richness in 1 year. Accumulation curves for observed species richness more than doubled in a year as well (Figure 3). The largest changes in species richness occurred in the sponges and molluscs that increased threefold between 1999 and 2000 (Table 1). The species richness of bryozoans, ascidians and corals increased by a factor of two or more. Changes in species density (average number of species per quadrat) mirrored overall changes in total species richness (Table 3). We infer that species richness increased primarily by the recruitment of larvae or asexual propagules over the year, since only one of the species counted in the June 2000 quadrats was potentially motile (sea anemone, *Bunodactis mexicana*).

There was evidence that the large increases of sessile invertebrates observed in the quadrats and across the rock wall led to aggregative responses (Hassell and May 1974) in their consumers. For example, two predatory snails, *Asperiscula billeeana* and *Hexaplex princeps*, representing specialist feeders on *Tubastrea* corals and

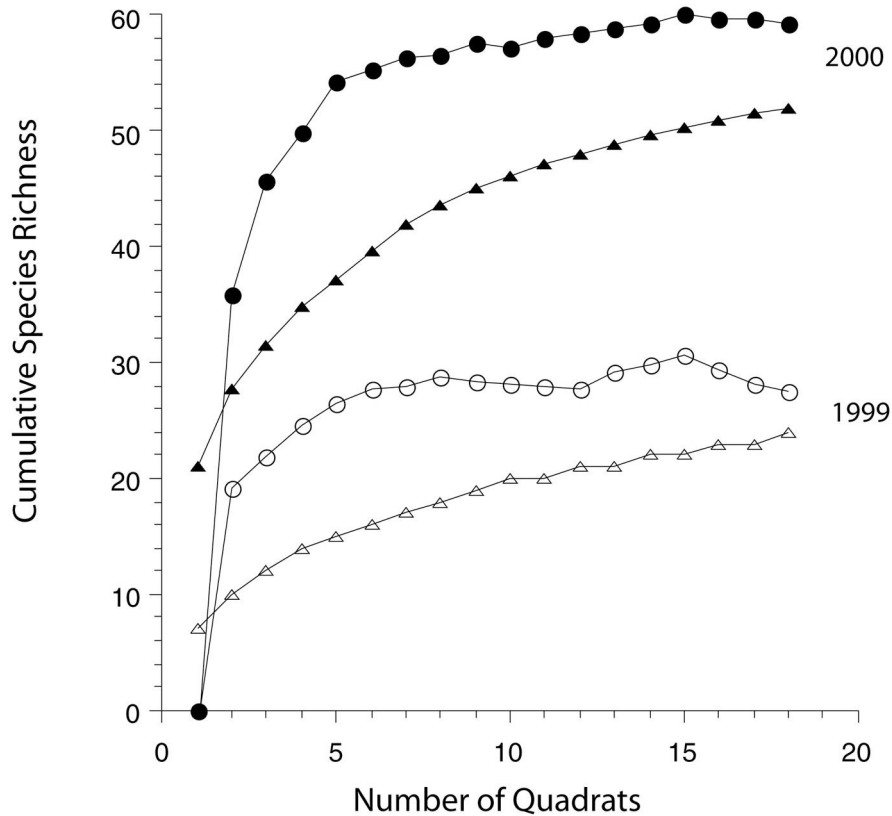


Figure 3. One year change in the total species richness of epifaunal invertebrate communities recorded in permanent quadrats at Roca Gordon (12 m depth). Each point of the species accumulation curves represents the average of 200 estimates of species richness per number of quadrats sampled, calculated by the Chao 2 index (solid circles year 2000, open circles year 1999) and observed species richness (solid triangles year 2000, open triangles year 1999). Note that species richness more than doubled between 1999 and 2000. The effect of sample order on the estimate of species richness was removed by 200 randomizations of sample order.

barnacles, respectively (Hickman and Finet 1999), were significantly more abundant in 2000 than in 1999 (Table 3). All of the snails observed in the quadrats and transects in 2000 were observed feeding on these prey. Counts of the *Megabalanus* in the year 2000 quadrats revealed that 19–57% of the large barnacles in the quadrats were dead, with their tests devoid of viscera, the hallmark of predation by *Hexaplex* (J.D. Witman and F. Smith, unpublished observations). From the barnacle size versus biomass regression analysis, we estimate that *Hexaplex* predation on barnacles could account for an average turnover of 4.9 g of barnacle tissue per 0.25 m² per year, or 37.5% of barnacle biomass production, emphasizing the importance of barnacles in the transfer of water column production to higher trophic levels (Table 3). Although some of the barnacle turnover could be caused by senescence

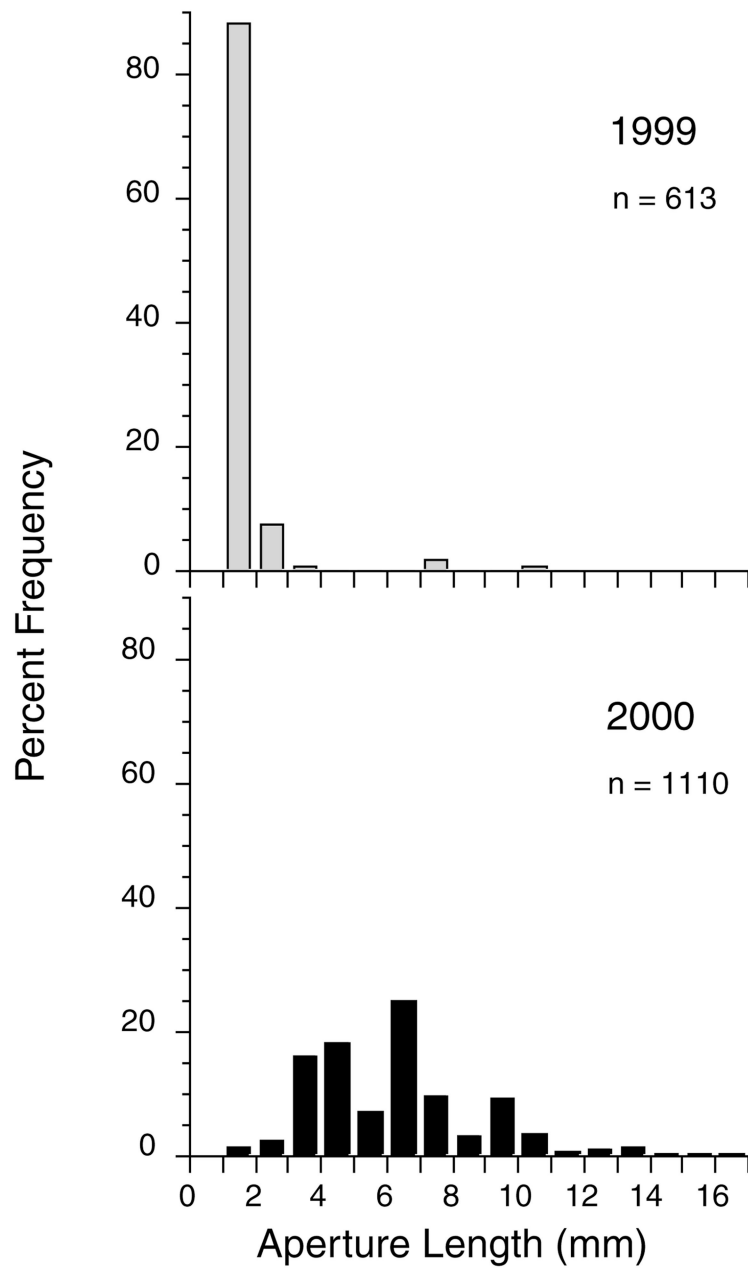


Figure 4. Change in size frequency distributions of aperture lengths of *Megabalanus* barnacles in the permanent quadrats over 1 year. n refers to the number of individual barnacles measured.

Table 2. Changes in average percent cover, biomass, density and species density of epifaunal invertebrates in permanent quadrats and transects at Rocas Gordon between June 1999 and June 2000.

Parameter and taxon compared	MS		F statistic	P
	Effect	Error		
Percent cover				
<i>Tubastrea</i>	0.0716	0.00677	10.5	0.0046
<i>Aplysilla</i> sp. 5	0.359	0.0057	63.0	0.000004
<i>Carmia</i>	0.9776	0.0038	252.4	0.0000001
<i>Didemnum</i>	0.8916	0.0573	15.5	0.001
<i>Megabalanus</i>	0.2285	0.0145	15.7	0.001
Coralline algae	0.2812	0.0048	58.3	0.0000007
Biomass				
<i>Didemnum</i>	20.94	1.079	19.3	0.00038
<i>Megabalanus</i>	40.62	0.214	189.3	0.0000001

Percent cover and biomass values are graphed in Figure 2. Statistical comparisons by repeated measures (RM) ANOVA on arcsin transformed percent cover values and log transformed density and biomass data, all comparisons with 1, 17 df. Data reported as average g/tissue biomass per 0.25 m², average density per 0.25 m². *Didemnum* represents *D. cineraceum*.

Table 3. Changes in average species density, density of predatory snails, barnacle biomass consumed, and total population size (number of colonies) of *Tubastrea* between 1999 and 2000.

Parameter	1999	2000	MS		F statistic	P
			Effect	Error		
Species density	6.7 (2.0)	20.3 (3.2)	11.787	0.0496	237.4	0.0000001
Snail density						
<i>Asperiscula</i>	0.2 (0.7)	1.4 (2.5)	0.0393	0.0069	5.66	0.0293
<i>Hexaplex</i> ^a	0	1.04 (0.5)	0.8167	0.0460	17.7	0.024
Population size						
<i>Tubastrea</i>	165	191				
<i>Megabalanus</i> turnover	4.9 (2.4)					

Comparisons by RM ANOVA on log transformed data with 1, 17 df except for *Hexaplex*, which have 1, 3 df. Species density represents the average number of species per 0.25 m² quadrat, values in parentheses are standard deviations. *Megabalanus* turnover is average tissue biomass consumed per 0.25 m². ^aAverage density/1.0 m².

rather than predation, it is unlikely that the dead *Megabalanus* in the observed size range (1.5–3.5 cm diameter) have only a 1-year lifespan.

Temperature and current regime

Thermistors on the rock wall indicated that temperatures at 12 m ranged from 14.8 to 28.0 °C and were characterized by 20 major, cool water events where temperature decreased abruptly by 3.0–9.0 °C within a 24 h period (Figure 5). Temperature fluctuations at 3 m were positively correlated with those at 12 m (Spearman rank correlation 0.956, $P < 0.00001$), indicating that changes in temperature were highly coherent over a 9 m water column. One potential explanation for the cool water events is that they were caused by tidal flooding, where the flood tide elevates the

thermocline, bringing cold water past the stationary thermistors. Since the tidal amplitude in the Galápagos is only 2.0–2.5 m (Houvenaghel 1978; Glynn and Wellington 1983), tidal flooding alone cannot explain synchronous temperature fluctuations at two locations separated by 9 m vertical distance. Spectral analysis was conducted to discern the periodicity of the temperature fluctuations during cool (June–July) and warm (January–February) seasons. The January–February analysis revealed a major peak in spectral density caused by truncating the time series at 2 months, and five other peaks centered around periods of 45.50, 22.75, 15.17, 11.49 and 9.17 h (numbered in Figure 6). The semi-diurnal tidal period (12.4 h) is included in the fourth peak. In addition, the periods of the first, second and fourth peaks are multiples (i.e. $4\times$, $2\times$), or harmonics, of the fundamental, near-semi-diurnal tidal period. These results strongly suggest that temperature fluctuations during the warm months are influenced by tidal phenomena. The semi-diurnal periodicity of temperature fluctuations was particularly evident during February 25–March 1 (Figure 5B). In contrast, spectral analysis of the June–July record showed little evidence of semi-diurnal periodicity, as the five largest peaks in spectral density occurred at periods of 15.16, 30.30, 8.25, 3.60 and 2.75 days (reported in descending order, not graphed). The short-term (e.g. hourly) variation in temperature that dominated the warm season power spectrum was not evident during the cool (June–July) months.

The ADP current meter deployment revealed strong upwelling at Rocas Gordon (Figure 7), supporting our interpretation from the temperature data that the cold-water events represented upwelling. For instance, upward (positive) velocities dominated the record with maximum velocities of 22.5 cm s^{-1} recorded 3.2 m above the ADP (Figure 7). Temporal variation in vertical velocity consisted of a roughly 12 h period of high and low flow with considerable high frequency fluctuations superimposed on the longer period. Many of the upwelling events were immediately followed by downwelling, suggesting a pulsed flow regime (Figure 7). The complete 28 h velocity record, representing 12 depth bins from 0.7 to 6.2 m above the ADP (not shown), was examined for the number and duration of major upwelling events, defined by positive flow extending to a minimum of 5.7 m of the water column. There were 144 of these major upwelling events, ranging from 2 to 111 min duration for a total of 877 min or 58.4% of the complete record. The average duration of the upwelling events was 6.0 min with a standard deviation of 10.8 min. The maximum upwelling velocity was 32.3 cm s^{-1} .

Discussion

The results of this study suggest that the turnover of the epifaunal invertebrate community at Rocas Gordon was unusually rapid for tropical subtidal communities on natural, hard substrate. The doubling of species richness and species density in a year at this Galápagos upwelling site ranks among the fastest diversity increases in any subtidal epifaunal community (Vance 1979; Colgan 1987; Loya 1990; Witman 1992; Connell 1997; Smith and Witman 1999). In contrast to the rapid rates reported here, a 6 year study of tropical rock wall communities using the same methodology

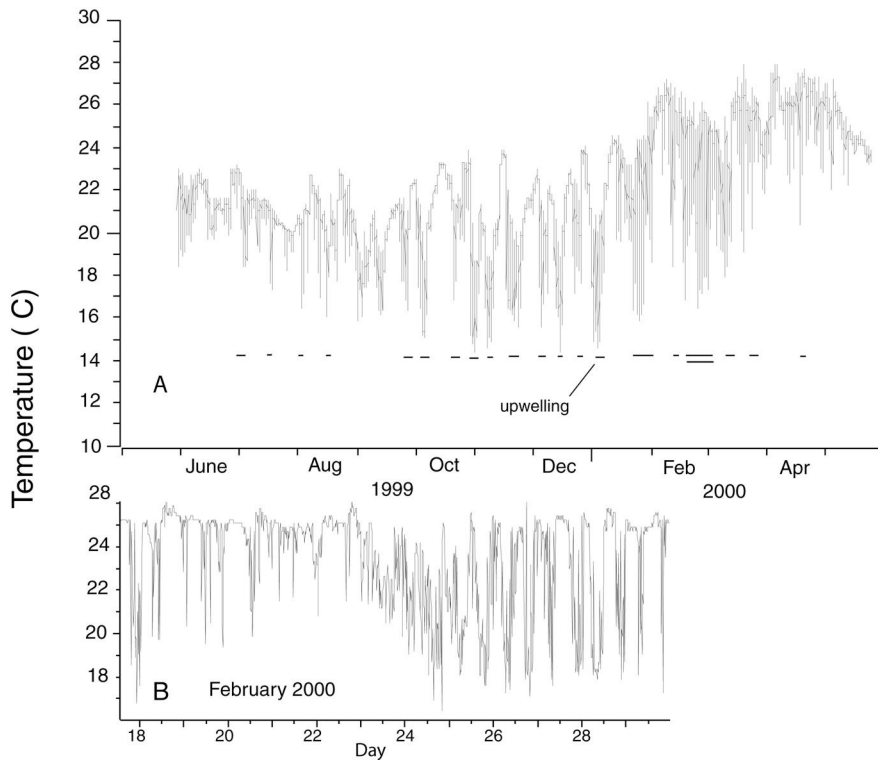


Figure 5. A. Temperature fluctuations at 12 m depth illustrating upwelling events (bars) where temperature decreased by 3.0–8.0 °C in 24 h. Double bars show the section expanded in inset B, illustrating the February 18 to March 1st segment of the record to highlight the magnitude and period of the upwelling. Note the approximate 12 h (semi-diurnal) period of the fluctuations from February 25 to March 1st.

as this study showed no change in species density in St. John, US Virgin Islands (10.3 species per $0.25\text{ m}^2 \pm 4.5$ standard deviation, 1985, vs. 11.5 species ± 4.1 , 1991, RM ANOVA ($F = 1.99$, $P = 0.2$, 1, 7 df, data log transformed, Witman 1992). On coral reefs in the North Pacific and Red Sea, species richness and diversity returned to pre-disturbance levels in 5–6 years (Colgan 1987; Loya 1990). The differences in rates of diversity increase between this study and those conducted on coral reefs could reflect fundamental differences in rates of recruitment of the taxa dominating tropical rock walls versus coral reefs. For example, sponges, ahermatypic corals, hydroids, bryozoans, polychaetes, molluscs, and ascidians may simply recruit faster to natural hard substrate than hermatypic corals (Jackson 1983), but little information is available to evaluate this possibility.

The subtidal community studied here was characterized by high recruitment and growth (percent cover, biomass) of epifaunal invertebrates. High recruitment was evident from abundant barnacle recruits in the permanent quadrats at the beginning of the study, by barnacle recruitment over the year, and by recruitment of all the

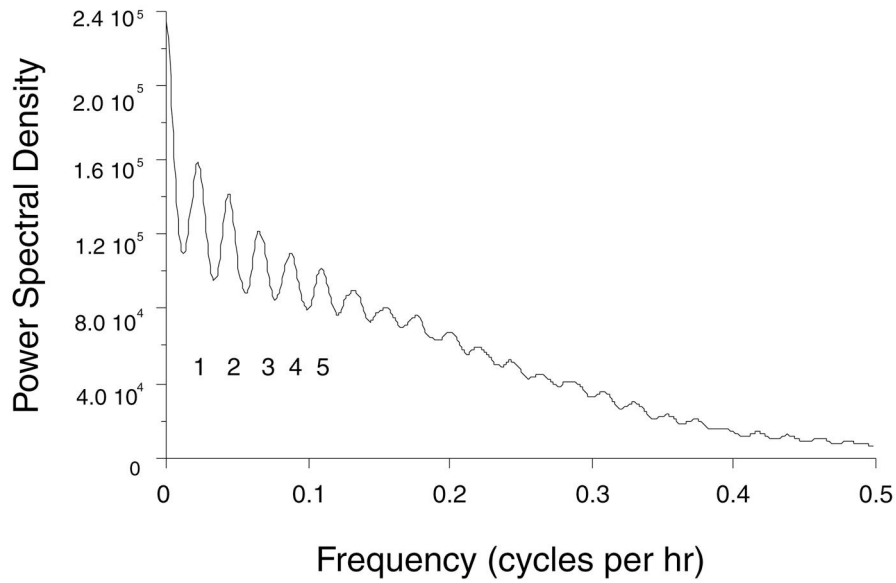


Figure 6. Power spectrum of warm season (January–February) temperature record from 12 m depth, Rocas Gordon. Major peaks in spectral density are labeled with peak 1 at a period of 45.5 h, 2 at 22.75 h, 3 at 15.17 h, 4 at 11.49 h, and 5 at 9.17 h. Peak 4 contains the semi-diurnal tidal period (12.40 h) and peaks 1 and 2 are multiples of the 11.49 h period.

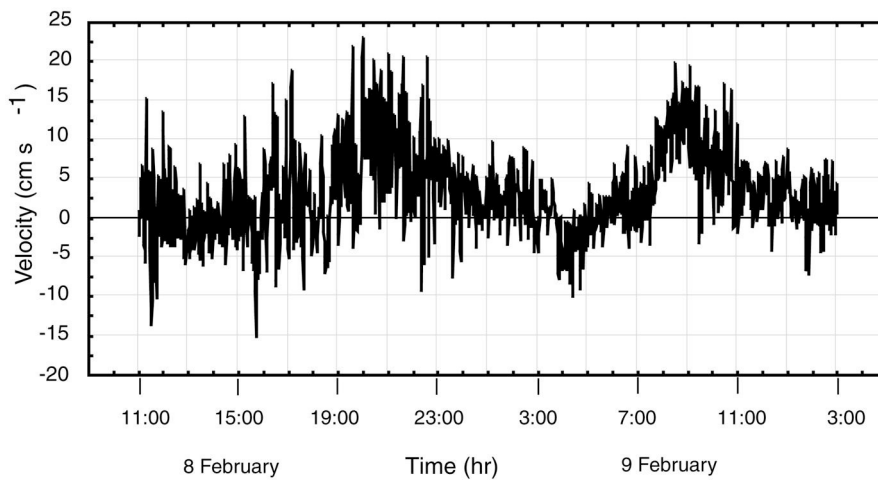


Figure 7. Vertical current velocity at the Rocas Gordon study site over a 28 h time period in February 2001. Data plotted are from 3.2 m above the acoustic current meter which was at 17 m depth, and are representative of the complete record measured from 0.7 to 6.2 m above the instrument. Positive and negative velocities indicate upwelling and downwelling, respectively. Note that the temporal variability in velocity consisted of a roughly 12 h period of high and low flow with considerable high frequency fluctuations superimposed on the longer period.

sessile invertebrate taxa documented in the species richness changes (above). Rapid growth rate of the dominant sessile invertebrates in the community was inferred from the nearly threefold (28–77%) increase in the pooled average cover of invertebrate species in the permanent quadrats (percent) in 1 year. High growth rates of individual barnacles (maximum 31 mm diameter, 17 mm aperture length) were manifested in a 16-fold increase of average tissue biomass of barnacles between 1999 and 2000. Ascidian biomass increased threefold.

When each of the community structure results are considered together in the context of the physical environmental setting, the picture that emerges is one of a rapidly changing epifaunal community in a dynamic oceanographic environment. We suggest that they are causally related and that upwelling underlies the community changes, possibly causing a bottom-up effect on the suspension-feeders and some of their consumers (Menge 1992). Although results of this paper are restricted to one site, large-scale upwelling is known from the Galápagos, and we have recently measured localized upwelling at five other rock wall sites similar to Rocas Gordon (J.D. Witman and F. Smith, in preparation), indicating that upwelling commonly impinges on rocky subtidal communities in the Galápagos. In the bottom-up scenario, nutrients supplied by upwelling would stimulate phytoplankton and subsequent zooplankton production, enhancing food supply to the suspension feeding invertebrates in the rock wall community. A minimal test of this hypothesis requires demonstrating that nutrients and/or food supply is enhanced at upwelling versus non-upwelling rocky subtidal sites in the Galápagos. To this end, we have begun to gather information on subtidal chlorophyll distribution and have found that a subsurface chlorophyll maximum layer was associated with the thermocline at Rocas Gordon and at several other upwelling sites in January–March 2001, and that this layer was absent at several non-upwelling sites during the same time period (J.D. Witman and F. Smith, in preparation). This suggests that phytoplankton production may be enhanced at local upwelling sites. Additionally, Chavez and Brusca (1991) have shown an inverse relation between temperature and nitrate in the Galápagos, with cooler, upwelled water containing higher nitrate than warm water. In other tropical upwelling areas, enhanced growth of suspension-feeders and shifts in epifaunal species composition have been observed in high plankton and nutrient regimes (Birkeland 1988; Taylor 1997).

Spectral analysis of the temperature data showed multiple peaks in spectral density, suggesting that several physical mechanisms are driving upwelling at the site, and that they differ between cool and warm seasons. The semi-diurnal periodicity observed in the warm season temperature and current meter data strongly suggests that upwelling at Rocas Gordon is driven in part by internal tidal bores, which are internal waves that break at tidal frequencies (Winant 1974; Pineda 1991a). The pulsed, upwelling and downwelling currents and high frequency temperature variation documented at Rocas Gordon are also suggestive of breaking internal waves (Pineda 1991a; Leichter et al. 1996). Other potential sources of upwelling at the study site include tidally driven island mixing and wind. The absence of spectral peaks at frequencies near the semi-diurnal tide during June–July implies that the internal tide is less well developed during this period. The maximum

'burst' velocities described from the pulsed upwelling system here (0.32 m s^{-1}) are several orders of magnitude faster than large scale upwelling velocities ($0.000025 \text{ m s}^{-1}$) recorded in the Eastern Equatorial Pacific over longer time periods (Chavez and Brusca 1991). Although both temperature and current records showed semi-diurnal periodicity, the current meter revealed substantially more high frequency variation in upwelling than year-long temperature monitoring. This difference probably results from the higher sampling rate of the current meter that was averaging velocity data taken once per second at 1 min intervals compared to the 16 min interval sampling of the thermistors. By deploying thermistors sampling at the same rate as the current meter, we have recently found that the high frequency (e.g. several minutes–tens of minutes) and the lower frequency (e.g. semi-diurnal) temporal variation is typical of upwelling at rock wall sites in the Galápagos (J. Witman and F. Smith, unpublished data).

High recruitment of invertebrates and large amounts of free space in the rock wall habitat at the beginning of the monitoring period likely contributed to the rapid increases in species richness and species density observed at Rocas Gordon. We found that larval recruitment plays a major role in maintaining species diversity in similar epifaunal communities on rock walls in New Zealand (Smith and Witman 1999). Here, a unique vector may be the vertical transport of passively dispersed larvae of deeper-dwelling invertebrate species to shallow depths. High species richness at upwelling sites would result from a mix of shallow and deep species. In contrast to the large wind-driven upwelling systems that advect flow offshore (Mann and Lazier 1996), the upwelled flow at Rocas Gordon is in direct contact with the subtidal rock wall habitat. The epifaunal invertebrates that colonized the permanent quadrats between 1999 and 2000 (Table 1) represent species with a broad range of larval and/or propagule dispersal distances from short-distance dispersers (ascidians, some sponges and corals) to barnacles that are known to disperse over long distances (Levin and Bridges 1995). This suggests that the internal tidal bores impacting the subtidal walls at Rocas Gordon may have mixed a nearby source pool (i.e. within site) with larvae originating from greater distances, as Pineda (1991a, b) has found for invertebrate larvae off southern California. Since the invertebrates in the Rocas Gordon community can settle on crustose coralline algae that covered most of the substratum in 1999, the developing communities were not likely space-limited as they received recruits from a diverse source pool of larvae and asexual propagules. By the end of the monitoring period, however, rapid growth and recruitment of invertebrates substantially reduced the amount of space available for settlement, so competition for space may have been limiting later on. We speculate that the low invertebrate cover at the beginning of the study may have been caused by high temperature stress and mortality of epifaunal invertebrates during the 1997–1998 El Niño, as reported in the Galápagos after the 1982–1983 El Niño (Glynn 1988) or by severe urchin grazing, which clears space in rock wall habitats (Vance 1979; Sebens 1985). However, no data on the state of the Rocas Gordon community prior to January 1999 are available to evaluate either possibility. At this time, the rock wall community contained low invertebrate cover and low sea urchin densities, averaging 2.1 *Eucidaris thouarsii* and 0.4 *Tripneustes depressus* per 1.0

m², ranking Rocas Gordon 8th out of 11 sites surveyed for sea urchin abundance (J. Witman, R. Etter and F. Smith, unpublished data).

Upwelling at Rocas Gordon may have created a linkage between bottom-up and top-down predatory regulation, where the predators attracted to the site by abundant suspension-feeding prey consume competitively dominant species, opening up space for inferior competitors, thereby increasing diversity (Paine 1966). Barnacles and ascidians are major competitors for space in Galápagos subtidal communities (Glynn and Wellington 1983; authors' personal observations). Barnacles are consumed by many species besides *Hexaplex* such as fish, lobsters and other gastropods in the GMR, so there is potentially a large amount of space opened up by predation. Although additional research is required to fully evaluate the ecological effects of upwelling in the Galápagos, our data provide insight into how upwelling may trigger bottom-up and top-down regulation in subtidal epifaunal communities.

Implications for conservation

The results of this study have several implications for conservation of subtidal communities in the GMR. Firstly, the rapid assembly of the community at Rocas Gordon suggests that certain groups of invertebrate taxa may recover from disturbance quickly at upwelling sites and that the pace of diversity increase is also enhanced at these sites. This applies only to the species of encrusting sponges, barnacles, bryozoans, molluscs, *Tubastrea* coral and ascidians investigated. Other components of the community such as antipatharians, corals, gorgonians and massive sponges that are present in Galápagos rock wall communities, but not abundant in the permanent quadrats studied here, probably take much longer than 1 year to colonize and recover from disturbance (e.g. Grange and Singleton 1988, for antipatharians). Secondly, the rapid growth observed for some of the invertebrate species likely reflects abundant food resources in the upwelling regime. If this is confirmed by future research at other upwelling sites in the Galápagos, then upwelling sites may serve as productive nursery habitats for sessile suspension-feeding invertebrates where they have enhanced reproductive output relative to less productive sites, as suggested by Menge (1992). Since they are apparently sites of rapid prey production, upwelling sites may also be important for the persistence of consumer populations such as gastropods, decapod crustaceans and benthic feeding fish. Finally, we suggest that the greatest turnover in subtidal epifaunal communities, encompassing temporal variation in diversity and abundance, occurs at upwelling sites in fully protected (non-extractive) areas of the GMR. This is possible because there is rapid production of epifaunal invertebrates at upwelling sites and high predation on the primary space occupiers maintained by protecting the predators. We suggest that modifications of the present zonation scheme of the GMR and the design and implementation of other marine protected areas worldwide should consider the interplay of oceanographic processes and biotic interactions to ensure the protection of marine biodiversity.

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