

Positive effects of damselfish override negative effects of urchins to prevent an algal habitat switch

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Summary

1. Understanding the factors that influence habitat persistence is a central theme in ecology, particularly for habitats created by terrestrial and aquatic primary producers that are some of the world's most extensive and ecologically important.
2. Many species have positive (e.g. farming) or negative effects (e.g. herbivory) on the abundance of primary producers, potentially causing wholesale switches in habitat structure if the net outcome of effects moves toward one extreme (e.g. over-grazing). Predicting the conditions under which such switches occur remains a key challenge for ecologists.
3. The purpose of this study was to understand how co-habiting species of opposing effect (damselfish as habitat facilitators vs. sea urchins as habitat consumers) can directly and indirectly influence the persistence of algal habitats on a tropical coast, including their potential to initiate switches among habitat types (productive 'turfs' of filamentous algae vs. 'barrens' of encrusting algae).
4. Using a series of five independent experiments, we observed that damselfish facilitated the production of algal turfs both directly, through active farming of selected species, and indirectly, by vigorously attacking and expelling invading urchins from the local area (i.e. preventing herbivory). In contrast, urchins consumed algal turf to directly maintain barrens.
5. The negative effects of urchins on algal turf were strong enough to initiate a habitat switch from turf to barrens, but this was conditional upon the absence of damselfish and the presence of a particular species of urchin.
6. *Synthesis.* These results build upon our understanding of the dynamics of habitat persistence by demonstrating the conditions where biological interactions of opposing direction (positive vs. negative) maintain or switch habitat types. Such knowledge is central to addressing global concerns about habitat loss and predicting the occurrence of switches to less-productive states.

Key-words: algae, alternate states, coralline barrens, filamentous turf, habitat loss, herbivory, indirect effect, Pomacentridae, species interaction

Introduction

Many of the world's most extensive and diverse habitats are created by living organisms, particularly primary producers such as trees, grasses, salt marshes, seagrasses and kelps (Jones *et al.* 1994; Bruno & Bertness 2001). Simply by growing and completing their own life cycle, these organisms create habitats for countless other species by providing living space, food resources and refuge from environmental stress (Dayton 1972; Jones *et al.* 1994; Callaway 1995). Ultimately, such effects can scale up to enhance ecosystem-level properties

such as primary productivity, carbon sequestration, nutrient cycling and maintenance of species diversity (Stachowicz 2001). Globally, biogenic habitats are being fragmented and lost at unprecedented rates (Vitousek *et al.* 1997; Jackson 2001), and given their fundamental ecological roles, it is not surprising that identifying limits to their persistence has become a central theme of ecology (Wilcox & Murphy 1985; Sousa 2001; Hughes *et al.* 2003).

Persistence of biogenic habitat is dependent on processes affecting recruitment, maintenance, fragmentation, local extinction and recovery (Pickett & White 1985; Hutchings *et al.* 2000). Whereas the physical environment can have a strong influence (e.g. temperature gradients, resource availability, severe weather events: Peterson & Pickett 1991), so can biological interactions with other species. Perhaps most obviously, some

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species can have large direct negative effects through processes such as herbivory, which can substantially increase habitat fragmentation while limiting recruitment and recovery (Crawley 1983). Alternatively, some species can have direct positive effects where, for example, fertilization success is enhanced (e.g. insect pollinators: Bronstein *et al.* 2006), or more favourable growth conditions are provided. An obvious example is the process of farming by humans, which enhances productivity of selected plants by increasing availability of required resources (e.g. addition of fertilizers) while reducing consumption and loss of biomass (e.g. use of insecticides and herbicides).

In addition to direct effects, some species can indirectly influence habitat persistence by modifying the effects of an intermediate species (Wootton 1994). One of the most widely cited examples occurs in subtidal kelp forests at temperate latitudes, where over-grazing of kelps by sea urchins exposes pavements of encrusting algae (termed 'coralline barrens' habitat) characterized by low productivity and associated species richness (Witman 1985; Chapman & Johnson 1990; Andrew 1993). However, consumption of urchins by predators, such as sea otters, large fish and even humans, reduces grazing pressure and thereby indirectly facilitates the persistence of kelp forests (Estes & Duggins 1995; Steneck *et al.* 2002); a classic example of Wootton's (1994) 'interaction chain'. More recently, it has been recognized that similar effects on the abundance of primary producers can occur through non-lethal pathways, whereby the behaviour of the intermediate species is altered, rather than its abundance (termed 'trait-mediated indirect interactions': Abrams *et al.* 1996).

From a holistic perspective, habitat persistence can essentially be considered a balance between net production and loss (Grime 1979; Carpenter 1985). When the balance shifts toward one extreme, wholesale switches in habitat structure can occur that are accompanied by large changes in the abundance and biodiversity of associated species. Through over-grazing, animals such as deer on land or sea urchins on rocky coasts are capable of initiating and maintaining a switch from productive and diverse habitats to ones that are comparatively unproductive and/or species-poor (e.g. loss of N-fixers and grasses: Bråthen *et al.* 2007; switching kelp forests to coralline barrens: Steneck *et al.* 2002). While such switches do occur naturally, they can substantially alter the local ecology and are of growing concern given recent increases in their frequency, spatial extent and stability, particularly in urbanized centres (Hughes 1994; Benedetti-Cecchi *et al.* 2001; Connell 2007). Consequently, understanding the conditions that initiate and maintain habitat switches, and ultimately, whether they can be predicted, remain pressing challenges for ecologists.

The purpose of this study was to understand how species of opposing effect on habitat (i.e. facilitators vs. consumers) can directly and indirectly influence the persistence of different benthic algal habitats, including their potential to initiate switches among habitat types. In tropical and temperate seas, damselfish (family Pomacentridae) are small, reef-associated fish that often intensively 'farm' patches of erect filamentous algal 'turf' that they aggressively defend from intruders (see review by Ceccarelli *et al.* 2001). Farming usually involves the

selective weeding of unpalatable algae to create distinct patches and increased biomass of favoured algae upon which damselfish feed (Lassuy 1980). Defending farms requires aggressive chasing and attacking of intruders, particularly herbivorous fish and invertebrates, to repel them from the surrounding area (Wellington 1982; Hourigan 1986).

In contrast, sea urchins are often voracious consumers of algae and produce sizeable effects in marine habitats by removing erect algae to create extensive encrusting coralline barrens (Chapman & Johnson 1990; Andrew 1993). The conditions that allow urchins to switch habitats have received considerable attention (e.g. Foster 1990; Estes & Duggins 1995), particularly on temperate coasts where such switches are associated with large declines in primary productivity and biodiversity (Graham 2004). In general, it appears that the absence of urchin predators (e.g. sea otters), or other factors capable of controlling urchin abundance or foraging behaviour (e.g. physical disturbance from waves), are primary conditions under which urchins can initiate and maintain low-productivity barrens (Estes & Duggins 1995; Steneck *et al.* 2002; Siddon & Witman 2003).

On a shallow subtidal coast of the Galapagos archipelago we quantified interactions among the yellow-tail damselfish *Stegastes arcifrons*, the urchins *Eucidaris galapagensis* (the pencil urchin) and *Lytechinus semituberculatus* (the green urchin), and three common benthic algal habitats (damselfish farms, adjacent algal turfs and coralline barrens) to understand how damselfish and urchins influence the persistence and potential for switches among these three habitat types. Research proceeded in two stages. First, we quantified natural patterns in the abundance and composition of major benthic habitats at the study site: damselfish farms, adjacent algal turfs, coralline barrens and sand. We then tested the hypotheses that (i) damselfish are associated with algal turfs (farms and adjacent patches combined) but not with barrens or sand, while (ii) the pencil urchin and the green urchin are both associated with coralline barrens but not with algal turfs or sand.

Second, we used these natural history observations to design a series of five physically distinct but conceptually linked experiments to identify the direct and indirect effects of damselfish and urchins that may ultimately determine the persistence of algal habitats. We began by identifying interactions between damselfish and algal turfs, testing the hypotheses that established damselfish farms and adjacent algal turfs would (i) be maintained, and (ii) recover from physical disturbance (removal of biomass) only in the presence of damselfish. Next, we identified interactions between urchins and coralline barrens by testing the hypothesis that (iii) established coralline barrens would be maintained only in the presence of urchins. We then focused on interactions between damselfish and urchins, testing the hypothesis that (iv) damselfish prevent urchins and other intruders from establishing in farms and adjacent turfs through aggressive exclusion (i.e. forcefully attacking and removing the intruder). Finally, we linked all three components of the system by testing the hypothesis that (v) urchins are capable of grazing turfs to initiate a habitat switch from algal turf to coralline barrens

(negative effect on turfs), but that such effects are prevented in the presence of damselfish (positive effect on turfs).

Methods

STUDY SITE

All research was done during May and June 2007 on a shallow subtidal rocky coast in Academy Bay, Isla Santa Cruz (0°44' S, 90°18' W), a central island of the Galapagos Archipelago. The study site comprised irregularly-shaped basalt boulders approximately 0.1–1.0 m across, and larger, gently sloping shelves that met the sandy bottom at approximately 2.5 m depth (mean high tide). Damselfish are common, with the yellow-tail damselfish, *S. arcifrons*, accounting for the overwhelming majority (approximately 99%) of individuals farming algal turf. Damselfish farms mostly comprised brown filamentous algal turf (order Ectocarpales: *Giffordia* sp., *Ectocarpus* sp.), and were visually distinct from adjacent turfs of green (order Ulvales: *Ulva* sp., *Enteromorpha* sp.) and red algae (order Ceramiales: *Ceramium* sp., *Polysiphonia* sp.) (see Table 1 in Kendrick 1991 for a comprehensive list of species). Patches of coralline barrens comprising encrusting coralline and non-coralline algae punctuated algal turfs, with pencil urchins, green urchins and yellow-tail damselfish distributed throughout the study site.

While the species and habitats studied occur throughout the archipelago, a combination of limited time and resources, daily maintenance of experimental treatments and the sheer number of experiments carried out made it unfeasible to use replicate sites. However, focusing efforts at one site ensured experiments were thorough and data quality was maximized, negating the risk of gaining an incomplete understanding by spreading resources too thinly.

HABITAT ABUNDANCE, COMPOSITION, AND ASSOCIATIONS

Casual observation identified four major types of benthic habitat, termed herein as 'farm' (algal turf cultivated by damselfish), 'turf' (all algal turf other than damselfish farms), coralline 'barrens' (encrusting algae) and 'sand'. At a coarse scale, farms and turfs appear structurally similar (both filamentous algae), but they were treated as separate habitats because of obvious fine-scale differences in species composition that may respond differently to experimental treatments. The abundance of each habitat was quantified on 10 replicate 10-m-long transects that were oriented randomly along the coast and separated from each other by > 10 m. Observers swam the length of each transect and recorded the distance at which the type of habitat changed, quantifying the extent (length) of each individual patch of habitat, as well as the natural scale of patchiness at the site.

The composition of farms, adjacent turfs and barrens was determined by sampling the percent cover of coarse algal groups using the point-intercept method (25 regularly spaced points within a 0.1 × 0.1-m quadrat, $n = 16$ per habitat). Representative algal samples were harvested to establish taxonomic identities of constituents (see descriptions above), but given the striking differences in composition among habitats, algae were coarsely sampled in the field as brown, green and red filamentous algae, as well as encrusting coralline and encrusting non-coralline algae (e.g. *Ralfsia* sp.) that typically characterize barrens.

To test hypotheses of habitat associations, the abundances of damselfish, pencil urchins and green urchins were quantified within algal turfs (all turfs, including farms), coralline barrens, and over

sand. Damselfish abundance was estimated by counting individuals observed along 10 replicate 10 × 1 m transects placed in each habitat. Urchin abundance was quantified by counting all individuals within haphazardly positioned quadrats (0.5 × 0.5 m, $n = 10$ per habitat). In addition, the test diameter of all sampled urchins was measured because among-habitat differences in urchin size may create variation in grazing intensity (e.g. Freeman 2006), and offer an alternate explanation for the abundance of habitats (particularly barrens).

EXPERIMENTAL MANIPULATIONS

Damselfish and algal turfs

Two separate experiments were performed to test the hypotheses that farms and adjacent turfs would be maintained and recover from disturbance only in the presence of damselfish. For the first experiment (maintenance), established farms and adjacent turfs growing on boulders ($n = 5$ per habitat type) were translocated from areas with resident damselfish to areas where damselfish were locally absent or transitory. Translocation typically involved moving boulders by 2–4 m, usually to an area with fewer boulders and more extensive patches of sand, with care taken to ensure boulders were placed at a similar depth to their original location. A further five boulders supporting each habitat type remained unmoved and served as controls (damselfish present). Daily observation confirmed that treatments were maintained (presence vs. absence of resident damselfish).

A similar design was used to test the role of damselfish for the recovery of farms and adjacent turfs from physical disturbance, except that boulders that either remained unmoved or were translocated were scrubbed with a nylon brush to remove approximately 80% of the algal biomass at the start of the experiment. This treatment was not specifically designed to mimic grazing by urchins, although some comparisons are possible. In addition to these disturbed replicates, five boulders supporting each habitat remained undisturbed and unmoved to indicate the level of recovery among disturbed habitats by the end of the experiment.

The process of translocating boulders is itself a disturbance that may affect algae in ways unrelated to the presence or absence of damselfish. To test for such artefacts, five boulders supporting each habitat type were lifted and placed back in their original position (vertical disturbance), while another five boulders of each habitat type were moved approximately 2–4 m away but placed in the presence of resident damselfish (horizontal disturbance). Any differences between either of these treatments and control (unmoved) boulders would suggest an artefact of translocation that could bias interpretation of the results.

Urchins and coralline barrens

To test the hypothesis that coralline barrens would be maintained only in the presence of urchins, treatments were established in which either pencil urchins, green urchins or both were removed from replicate 1-m²-areas within established barrens ($n = 5$ per treatment). A further five control plots

remained unmanipulated. The number of urchins removed per replicate ranged from 10.88 ± 2.12 (mean \pm SE) for pencil urchins, to 48.96 ± 5.84 for green urchins, corresponding closely to sampled natural densities at the study site (see Results). Treatments were checked daily and were maintained by removing occasional immigrant urchins.

Damselfish and urchins

Urchins were added to damselfish farms and adjacent turfs to test the hypothesis that damselfish prevent intruders from establishing in these habitats through aggressive exclusion. Pencil and green urchins were collected from the local area and a single individual was conspicuously placed either within farms or adjacent turfs. Care was taken to ensure urchins of similar size were added to each habitat. The response of damselfish was measured as the time delay before an attack on the intruder, the time spent attacking the intruder, the number of damselfish involved in the attack, and the final location of the intruder when the attack ceased. Damselfish were allowed 60 s to make an attack, after which the trial was suspended and recorded as 'no attack'. Individual damselfish and urchins were only used once to ensure independence ($n = 10$ trials per habitat).

To test whether damselfish behaviour was specific toward urchins or was typical toward intruders in general, the carnivorous gastropod *Thais melones* and urchin-sized rocks were also placed in farms and turfs, with the response of damselfish quantified as described above.

Habitat switch

A final experiment orthogonally manipulated the presence vs. absence of damselfish, pencil urchins and green urchins to test the hypothesis that damselfish modify the ability of urchins to initiate a habitat switch from algal turf to coralline barrens. It was unknown if urchins would discriminate between farms and adjacent turfs when grazing, so these habitats were not differentiated in this experiment. Consequently, the effect of urchins on the abundance of filamentous algae *per se* was the response of interest, with the relative covers of filamentous vs. encrusting algae in each treatment being the key comparison (i.e. turf vs. barrens habitat).

In the presence and absence of damselfish, either pencil or green urchins were added to boulders at natural densities (approximately 4 per 0.25 m^2 for pencil urchins and approximately 12 per 0.25 m^2 for green urchins; see Results), or were completely absent (2 damselfish \times 3 urchins = 6 treatment groups, $n = 5$). Urchins of similar size were used among treatments to minimize possible bias of size-dependent effects on grazing intensity (mean \pm SE test diameter = 32.04 ± 1.24 mm for pencil urchins and 30.55 ± 0.94 mm for green urchins). Damselfish often immediately attacked urchins added to boulders, so urchins were positioned as cryptically as possible. Easy access to the study site meant that urchin densities could be manually maintained where necessary on a daily basis, eliminating the need for intrusive manipulations such as

inclusion/exclusion cages. After approximately 10 days, maintenance of urchin densities was minimal as they generally remained constant. Furthermore, artefacts due to translocating urchins appeared minimal since urchins were observed to move and forage over boulders where damselfish were absent shortly after translocation.

For this and all experiments testing effects on algae, the percentage cover of broad algal categories described above was sampled after 35 days using the point intercept method (25 points regularly spaced within a 0.1×0.1 -m quadrat). Although this time period was ultimately dictated by the total time available in the Galapagos, it appears adequate to see a response of algae to treatments since a separate experiment showed rapid recruitment of algae to bare surfaces, with approximately 50% cover occurring after 7 days and $94.67 \pm 1.27\%$ cover after 35 days (mean \pm SE across all recruitment plates).

Results

HABITAT ABUNDANCE, COMPOSITION AND ASSOCIATIONS

Among benthic habitats, algal turfs occurred in greatest abundance (approximately 55% of total area sampled), while damselfish farms, coralline barrens and sand occurred in similar amounts (13–18% cover) (ANOVA: $F_{3,36} = 13.38$, $P < 0.0001$, Student–Neumann–Keuls (SNK) tests: turf > farm = barrens = sand). Considerable patchiness of habitat occurred at scales < 1 m, yet patches of algal turf were generally larger than other habitats (approximately 0.65 m in extent vs. approximately 0.18–0.27 m; ANOVA: $F_{3,36} = 11.42$, $P < 0.0001$, SNK tests: turf > farm = barrens = sand).

Habitat composition differed greatly, with damselfish farms comprising mainly brown filamentous algae, adjacent turfs composed of green and red filamentous algae, while coralline barrens supported extensive covers of encrusting algae (Fig. 1a, Table 1). Sand was sampled within farms and algal turfs but not in barrens.

Damselfish were strongly associated with algal turfs (farms and adjacent turf combined), were more sparse within barrens and were rarely observed over sand (Fig. 1b, ANOVA: $F_{2,27} = 589.91$, $P < 0.0001$, SNK tests: turf > barrens > sand). Casual observation suggested both large and small individuals occurred over algal turf habitat, but that mostly small individuals (i.e. approximately 5 cm total length) occurred over barrens.

Pencil and green urchins were sampled throughout the study site but neither species was ever found on sand, so this habitat was excluded from further analyses. Between turf and barrens habitat, pencil urchins were more strongly associated with turf but green urchins with barrens (Fig. 1c, ANOVA: $F_{1,18} = 42.74$, $P < 0.0001$ for pencil urchins, and $F_{1,18} = 131.58$, $P < 0.0001$ for green urchins). No differences in the mean size (test diameter) of either species were observed between turf and barrens habitat (2 sample *t*-test: $P > 0.09$ for both species).

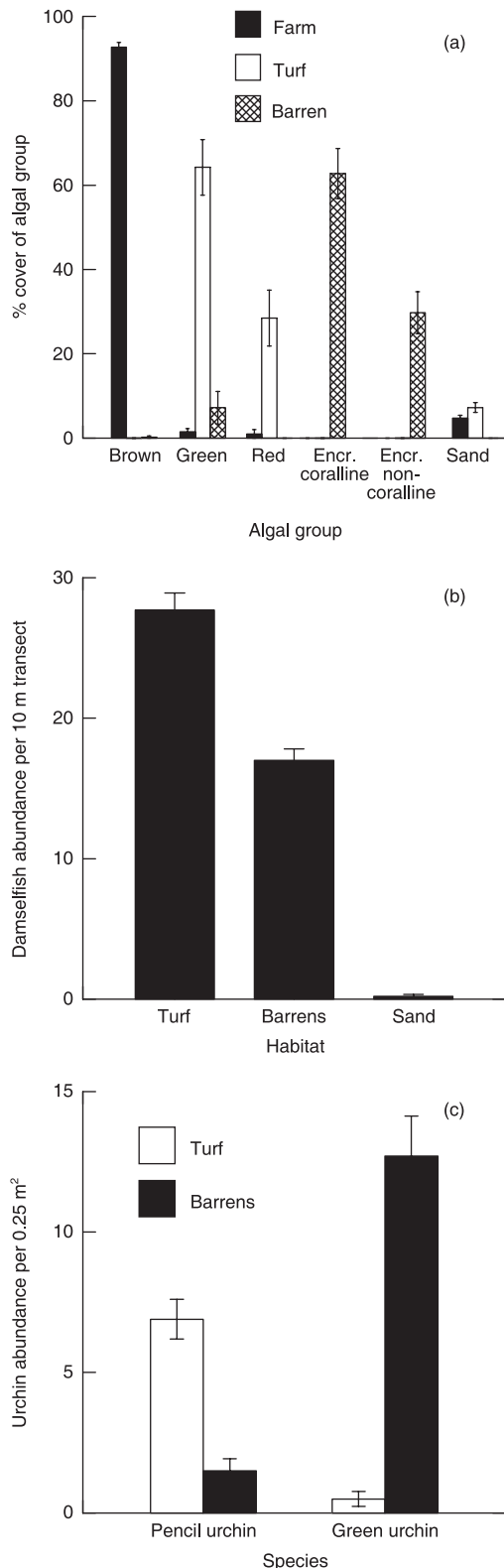


Fig. 1. Natural patterns of algal cover, damselfish abundance and urchin habitat associations. Mean (\pm SE) abundance of (a) broad algal groups within damselfish farms, adjacent algal turfs and coralline barrens, (b) yellow-tail damselfish (*S. arcifrons*) over algal turf, coralline barrens and sand habitat, and (c) pencil urchins (*E. galapagensis*) and green urchins (*L. semituberculatus*) within algal turf and coralline barrens (note: urchins were never sampled on sand habitat).

Table 1. Results of ANOVAs testing for differences in the natural abundance of algal groups among benthic habitats (damselfish farms vs. adjacent algal turfs vs. coralline barrens). EC, encrusting coralline algae; ENC, encrusting non-coralline algae. Student–Newman–Keuls (SNK) tests highlight the location of detected differences (F = farms, T = turfs, B = barrens)

Group	Source	d.f.	MS	F	P	SNK
Brown	Habitat	2	29968.55	2169.42	< 0.0001	F > T = B
	Residual	45	13.81			
Green	Habitat	2	12317.80	66.84	< 0.0001	T > F = B
	Residual	45	184.29			
Red	Habitat	2	4452.72	31.79	< 0.0001	T > F = B
	Residual	45	140.07			
EC	Habitat	2	15389.14	186.76	< 0.0001	F = T < B
	Residual	45	82.35			
ENC	Habitat	2	5370.10	91.03	< 0.0001	F = T < B
	Residual	45	58.99			
Sand	Habitat	2	952.61	46.67	< 0.0001	F = T > B
	Residual	45	20.41			

All data were arcsine (%) transformed before analysis. Cochran's *C*-test of homogeneity of variances: $P > 0.05$ for green algae, $P < 0.05$ for brown, red, EC, ENC algae and sand, and so significance was judged more conservatively for these variables ($\alpha = 0.01$).

EXPERIMENTAL EFFECTS

Damselfish and algal turfs

The maintenance of farms, but not adjacent turfs, was affected when boulders were moved away from resident damselfish (Fig. 2a, Table 2a: Maintenance). In the absence of damselfish, the cover of brown algae in farms declined by approximately 87%, while green and red algae increased markedly until farms became largely indistinguishable from surrounding filamentous turfs. The presence or absence of damselfish produced no qualitative and only minor quantitative effects on turfs (Fig. 2a: Turf with vs. without damselfish).

Following physical disturbance, the presence of damselfish greatly enhanced the recovery of farms but did not affect adjacent turfs (Fig. 2b, Table 2a: Recovery). With damselfish present, disturbed farms regained lost covers of brown algae to levels indistinguishable from undisturbed controls, while disturbed farms in the absence of damselfish did not recover and became identical to adjacent turfs (Fig. 2b). Recovery of disturbed adjacent turf occurred (Fig. 2b: turf treatments), although it was unaffected by damselfish (Table 2a: Recovery).

Importantly, no artefacts associated with the translocation of boulders were detected. For both farms and adjacent turfs, the covers of all groups of algae, as well as sand, remained similar on unmoved controls and boulders subjected to either vertical or horizontal disturbance (e.g. comparison of mean \pm SE % cover among control vs. vertical disturbance vs. horizontal disturbance: brown algae in farms, 89.6 ± 1.6 vs. 86.4 ± 3.7 vs. 85.6 ± 4.3 ; green algae in adjacent turf, 76.8 ± 6.0 vs. 75.2 ± 5.4 vs. 82.4 ± 3.0 ; $P > 0.40$ in all comparisons).

Table 2. Summary of ANOVAs testing the effects of (a) damselfish presence vs. absence on the maintenance and recovery of farms and adjacent algal turfs, and (b) green and pencil urchins on the maintenance of coralline barrens. Only algal groups showing significant responses are reported, with SNK tests showing the direction of differences among treatments. EC = Encrusting coralline algae, +D = damselfish present, -D = damselfish absent, C = undisturbed control, PR = pencil urchins removed, GR = green urchins removed, BR = both pencil and green urchins removed

Experiment	d.f.	Habitat tested	Significant response (<i>P</i> value)	SNK test
(a) Damselfish and Turfs				
– Maintenance	1,8	Farm	Brown (< 0.0001) Green (0.0001) Red (0.0021)	+D > -D +D < -D +D < -D
– Recovery	1,8	Turf	None	+D = -D
	2,12	Farm	Brown (< 0.0001) Green (< 0.0001) Red (0.0008)	C = +D > -D C = +D < -D -D > +D > C
	2,12	Turf	None	C = +D = -D
(b) Urchins and Barrens	3,16	Barrens	Green (< 0.0001) Red (0.0012) EC (< 0.0001)	C = PR < GR = BR C = PR < GR = BR C = PR > GR = BR

All data were arcsine (%) transformed before analysis. Cochran's *C*-test of homogeneity of variances: $P > 0.05$ for all tests except for red algae in the farm maintenance experiment, and so significance was judged more conservatively for this variable ($\alpha = 0.01$).

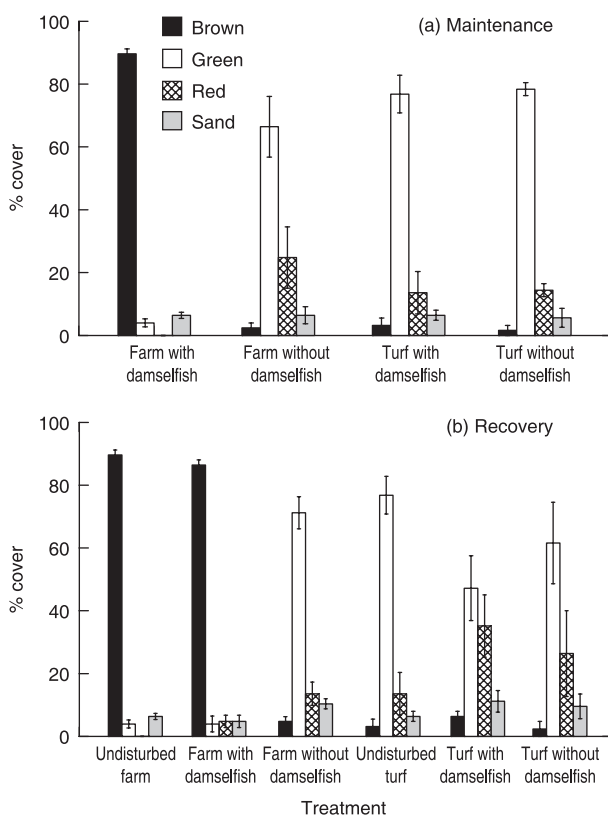


Fig. 2. Mean (\pm SE) % cover of broad algal groups sampled from experiments testing the role of damselfish for the (a) maintenance of farms and adjacent turfs, and (b) their recovery from physical disturbance.

Urchins and coralline barrens

Coralline barrens were maintained on control boulders and where pencil urchins were removed, but not where green urchins or both species were removed (Fig. 3, Table 2b). In these latter treatments,

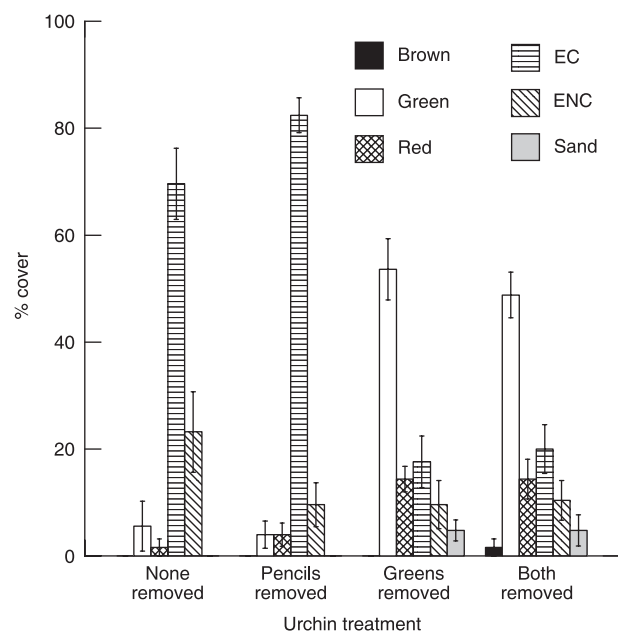


Fig. 3. Mean (\pm SE) % cover of broad algal groups among treatments testing the role of urchins for the maintenance of coralline barrens. Both pencil urchins (*E. galapagensis*) and green urchins (*L. semituberculatus*) were tested.

the cover of green and red algae increased by approximately 46% and 11% respectively, whereas encrusting algae decreased by approximately 57% such that algal assemblages became similar to nearby algal turfs (compare Fig. 3 with Fig. 1a).

Damselfish and urchins

Damselfish attacks on intruding urchins were rapid, occurring from 1.30 ± 0.15 seconds (mean \pm SE) for pencil urchins in farms to 18.20 ± 4.89 seconds for green urchins in adjacent turfs

Table 3. Results of two-way ANOVAs testing the effects of damselfish (presence vs. absence) and urchins (pencil vs. green vs. none) on the % cover of filamentous algae, encrusting algae and sand

Source	d.f.	Filamentous algae			Encrusting algae			Sand		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Damselfish	1	4211.38	69.26	< 0.0001	2473.22	84.45	< 0.0001	606.27	26.64	< 0.0001
Urchin	2	2071.85	34.07	< 0.0001	2473.22	84.45	< 0.0001	106.95	4.70	0.0189
Damselfish × Urchin	2	1567.22	25.77	< 0.0001	2473.22	84.45	< 0.0001	39.34	1.73	0.1989
Residual	24	60.81			29.29			22.76		

All data were arcsine(%) transformed before analysis. Cochran's *C*-test of homogeneity of variances: $P > 0.05$ for sand. $P < 0.05$ for filamentous and encrusting algae, for which significance was judged more conservatively ($\alpha = 0.01$).

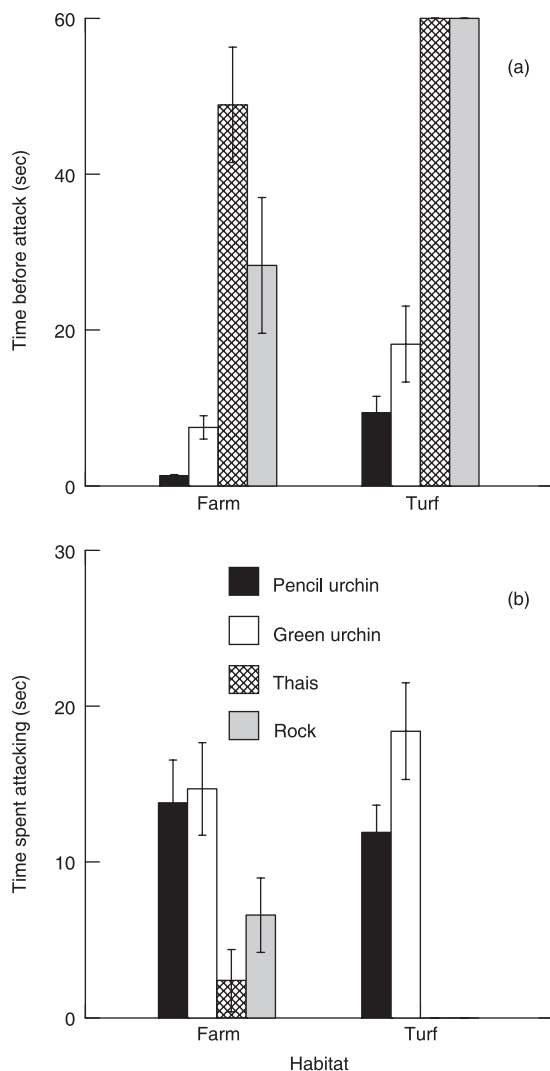


Fig. 4. Summary of damselfish attacks on intruders into farms and adjacent turfs. (a) mean (\pm SE) time before attacking the intruder (note that 60 seconds was the maximum time allowed for each trial), and (b) mean (\pm SE) time spent attacking intruders.

(Fig. 4a). Interestingly, rocks and the gastropod *T. melones* were rarely attacked when placed in farms and were never attacked in adjacent turfs during the 60 s of each trial (Fig. 4a, ANOVA Intruder effect across habitats: $F_{3,72} = 56.17$, $P < 0.0001$;

SNK tests: pencil = green < rock < *Thais*). Overall, damselfish attacked faster when intruders were placed in farms than in adjacent turfs (ANOVA Habitat effect: $F_{1,72} = 23.55$, $P < 0.0001$), and also attacked urchins for longer in both habitats (Fig. 4b, ANOVA Intruder effect: $F_{3,72} = 22.56$, $P < 0.0001$; SNK tests: pencil = green > *Thais* = rock). Damselfish generally attacked intruders individually or in pairs, except for pencil urchins in farms where it was common to see 3–4 damselfish attacking the intruder. When attacked, intruders almost always ended up in rock crevices or on sand, with urchins often left upside-down.

Habitat switch

The ability of urchins to switch habitats by removing algal turf to create coralline barrens was dependent on the absence of damselfish as well as the species of urchin (Fig. 5a, Table 3: Damselfish × Urchin interactions). In the presence of damselfish, neither species of urchin caused any significant change to algal assemblages (Fig. 5a). When damselfish were absent, green urchins, but not pencil urchins, were able to switch the habitat towards greater covers of encrusting algae (i.e. coralline barrens) by grazing filamentous turfs (Fig. 5a, Table 3: interaction SNK tests for filamentous algae: less cover in 'green urchin without damselfish' treatment than all other treatments; for encrusting algae: greater cover in 'green urchin without damselfish' treatment than all other treatments). While ANOVA detected differences among treatments in the cover of sand (Table 3), such differences were minor relative to those observed for filamentous and encrusting algae (Fig. 5a).

Discussion

Understanding factors that affect habitat persistence is a topical issue in ecology, particularly for habitats created by primary producers because their loss can have large consequences not just for associated biodiversity but also for broader ecosystem-level services (e.g. primary productivity, nutrient cycling etc.) (Wilcox & Murphy 1985; Vitousek *et al.* 1997; Stachowicz 2001). On a tropical subtidal rocky coast, we observed that the persistence of different benthic algal habitats was strongly influenced by species of opposing

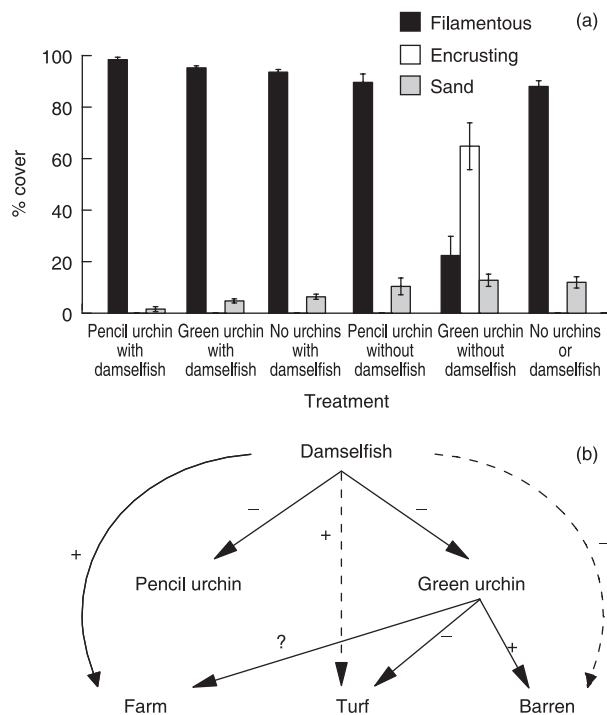


Fig. 5. (a) Mean (\pm SE) % cover of filamentous algae, encrusting algae and sand among presence-vs.-absence manipulations of damselfish (*S. arcifrons*), pencil urchins (*E. galapagensis*) and green urchins (*L. semituberculatus*). (b) Conceptual model of direct and indirect interactions among damselfish, urchins and benthic algal habitats observed from our experiments. Solid lines indicate direct interactions and broken lines indicate indirect interactions, with direction shown (positive vs. negative). For the effect of green urchins on farms, a question mark is shown since this effect could not be tested (see Discussion).

effect (i.e. positive effects of damselfish vs. negative effects of urchins), to the point where switches among habitats could be initiated or prevented. Such outcomes were frequently context-specific, dependent on habitat type and often requiring the presence or absence of particular species. Notably, damselfish had strong direct positive effects on their farms but not on adjacent filamentous turfs, while green urchins, but not pencil urchins, had strong effects on habitats, including the ability to switch them from filamentous turfs to encrusting coralline barrens. This switch, however, required the absence of damselfish.

A conceptual model of the direct and indirect interactions among damselfish, urchins and algal habitats in our experiments is shown in Fig. 5b. Using this model, four key results arise from this research. First, damselfish and green urchins both have strong direct effects on algal habitats that are consistent with their respective ecologies. As farmers of algal turf, damselfish had direct positive effects on the maintenance and recovery of farm habitat. In the absence of resident damselfish, the composition of farms changed or recovered from physical disturbance so as to be indistinguishable from surrounding algal turfs. These results agree with previous exclusions of damselfish that demonstrate rapid deterioration of farms through recruitment of new algal species (Hinds & Ballantine

1987; Hata & Kato 2003). In contrast, green urchins had direct negative effects on algal turfs through grazing, which also produced direct positive effects on the maintenance of coralline barrens by keeping encrusting algae free of overgrowth. Such effects are widely reported around the world (Chapman & Johnson 1990; Andrew 1993; Steneck *et al.* 2002). We were unable to test whether green urchins had negative effects on farms since damselfish prevented urchins from establishing. Nevertheless, we consider it highly probable since farms and adjacent turfs are structurally similar (i.e. composed of filamentous algae), and even though they comprise different species, the diet of a closely related urchin reveals generalist feeding (Cobb & Lawrence 2005).

Second, the effect of urchins on algal habitats was species-specific. Although pencil urchins occurred most abundantly in turf habitat, they did not have any detectable impact on the abundance of either turfs or barrens. In contrast, green urchins were able to effectively graze turfs and maintain barrens as described above. A possible explanation for this difference centres on the dietary requirements of each species. Both species graze benthic primary producers (Brandt 2003; Okey *et al.* 2004), yet pencil urchins are also corallivores (Glynn 2004). It follows that pencil urchins could have lower metabolic demands for algal turfs, and therefore consume less turf per capita than green urchins. Also worth noting is that pencil urchins were maintained at lower experimental densities than green urchins (approximately 4 pencil vs. 12 green per 0.25 m², chosen to represent natural densities at the study site). This may have contributed to observed species-specific effects purely because of differences in absolute potential for grazing. At the very least, therefore, we can conclude that relatively high densities of green urchins impact algal habitats, but relatively low densities of pencil urchins do not, although it is important to remember that such densities represent the natural arrangement at the study site. Nevertheless, further experiments that vary urchin density would yield greater insight into urchin-algae interactions in this system (e.g. possible creation of barrens as pencil urchins shift from corallivory to herbivory at high densities).

Third, damselfish have direct negative effects on urchins by rapidly removing them from farms and adjacent turfs and thereby preventing them from grazing. In this way, damselfish have an indirect positive effect on farms and adjacent turfs by preventing their consumption, and an indirect negative effect on barrens by preventing their creation. Indirect effects can be pervasive in nature (Wootton 1992), and in this system appear most important for the persistence of adjacent turfs since damselfish did not directly enhance this habitat (Fig. 2). In a similar way, sea otters and predatory fish indirectly maintain kelp forests by consuming sea urchins (Estes & Duggins 1995; Steneck *et al.* 2002), although our case involved a non-lethal pathway of behavioural modification of urchins (i.e. prevention of grazing), and therefore may be considered a trait-mediated indirect interaction (Abrams *et al.* 1996). Although the end result was the same (i.e. expulsion of urchins from habitats), it is interesting that pencil urchins were attacked more vigorously than green urchins (i.e. faster, greater number of attackers), even though green urchins pose the greatest threat to damselfish

farms and turfs. We explain this observation in terms of handling efficiency. Pencil urchin spines are large, smooth, and few in number, unlike the short, sharp, and numerous spines of green urchins. When confronted with a pencil urchin, damselfish were observed to attack without hesitation, while they would often stop close to green urchins and examine them before carefully biting down on the spines and pushing the urchin away (authors' personal observation).

The fourth key result from this research was that the presence of resident damselfish prevented a switch of habitat from algal turf to coralline barrens. Only in the absence of damselfish were green urchins able to graze filamentous algae and expose underlying encrusting algae, and thereby switch habitat from turf to barrens (Fig. 5a). This experimental result matches the strong natural positive association of green urchins with barrens, and negative association with turfs (Fig. 1c), and agrees with prior accounts of the consumption of farms by herbivores only after damselfish removal (Brawley & Adey 1977; Hourigan 1986). Somewhat paradoxically, moderate abundances of damselfish were naturally observed in barrens (Fig. 1b), but almost all individuals were small (approximately 5 cm total length) and were probably ineffective at repelling urchins to allow the growth of turfs. Collectively, the mechanism preventing the creation of barrens appears to be the initial attack and expulsion of urchins from farms and adjacent turfs by damselfish, followed, if necessary, by an altered behavioural response of urchins (i.e. reduced foraging, habitat avoidance; Freeman 2006).

Of note in our experiments were the rapid responses of algal habitats to damselfish and urchin manipulations. Large changes were observed after only 35 days, suggesting natural changes can be rapid depending on natural variation in the abundances of damselfish and urchins. Although turfs and barrens could be considered alternate habitat states in this system (Peterson 1984), the potential for such rapid change makes it unfeasible to consider them 'stable' states (Connell & Sousa 1983; Petraitis & Dudgeon 2004). Nevertheless, even short-term changes in turf abundance can impact the ecology of shallow subtidal systems since turfs make substantial contributions to coastal primary productivity (Carpenter 1985) and are exploited by animals as food and habitat (Carpenter 1986). Furthermore, they effectively trap and stabilize sediments (Airoldi 2003), are typically one of the first habitats to develop on bare surfaces (Kendrick 1991; Irving & Connell 2006), and can enhance local biodiversity by comprising numerous fast-growing, opportunistic species (Scott & Russ 1987). Interestingly, turfs are often considered to comprise 'weedy' species (*sensu* Tilman & Lehman 2001) that are undesirable on urbanized coasts where declining water quality appears to facilitate their dominance at the expense of larger canopy-forming macroalgae (e.g. kelp forests: Benedetti-Cecchi *et al.* 2001; Gorgula & Connell 2004). In places that generally lack such forests of macroalgae, such as the Galapagos archipelago, turfs take on greater ecological significance as the major benthic macroalgal habitat and primary producer, and therefore any changes in their abundance and distribution are of significance.

Though our experiments were carried out at one site, it is reasonable to expect similar results throughout the archipelago given the types of habitat sampled (algal turfs and urchin barrens), species tested, substratum type (basalt), and primary habitat configuration (shallow boulders on sand) are widely distributed. While limited research time in remote locations, such as the Galapagos, often precludes tests for temporal consistency of results, we find no *a priori* reason to expect different outcomes if our experiments were repeated. Indeed, there is no evidence that the damselfish or urchins studied undergo seasonal migration to/from the study site (abundances appear consistent throughout the year; authors' personal observation), and the opportunistic nature of filamentous turf-forming algae is well-established (Scott & Russ 1987; Irving & Connell 2006). In short, the observed effects of damselfish and urchins on benthic habitats are consistent with many studies around the world (Lassuy 1980; Hourigan 1986; Chapman & Johnson 1990; Andrew 1993; Steneck *et al.* 2002; Hata & Kato 2003), suggesting that such interactions are the norm rather than the exception. Nevertheless, further work is needed since there has been a noted bias toward study of damselfish species that exhibit strong territorial behaviour (Ceccarelli *et al.* 2001), while there remain many questions about the influence of longer-term oceanographic phenomena on interaction strength (e.g. temperature fluctuations caused by El Niño/La Niña events in the Galapagos may alter recruitment cycles, urchin metabolism, algal growth, etc.).

While we have emphasized biological interactions as key drivers of algal habitats in this system, previous research at the same location has identified an important role of sedimentation for the recruitment of turf habitat and encrusting algae (Kendrick 1991). Variation in the depositional environment (sediment erosion vs. accretion) altered species composition of turfs recruiting to boulders, while encrusting algae could only recruit and persist in reasonable abundance when a physical disturbance designed to simulate sand scour (rubbing boulders with a cloth) periodically removed sediments and turfs. Our results add to this understanding by identifying biological influences on turfs and encrusting algae. Similar to Kendrick's scour treatment, we observed the creation of barrens habitat (encrusting algae) only when turf was removed, in our case through grazing by urchins. In algal turfs, damselfish are clearly adept at maintaining patches with different species composition than on surrounding boulders, similar to the results of Kendrick's test of sediment erosion vs. accretion. Collectively, these results suggest convergent effects of otherwise independent physical and biological factors, adding to our understanding of the ecology of turf and barrens habitats.

Habitat persistence is a perennially topical issue in ecological and environmental research, with many habitats on Earth experiencing unprecedented rates of degradation and loss (Vitousek *et al.* 1997). Even a brief search of the literature reveals substantial concern (and debate) about the causes and consequences of habitat loss and switches to less-productive states (e.g. kelp forests to coralline barrens: Foster 1990; Estes & Duggins 1995; coral reefs to bare rock: Bellwood *et al.* 2004). Therefore, identifying the factors that facilitate habitat

production vs. loss, as well as recognizing the conditions that promote wholesale switches in habitat composition and abundance, are critical steps in addressing such concerns. Such knowledge is particularly necessary for habitats created by primary producers given their substantial ecological roles in carbon sequestration, nutrient cycling, maintaining species diversity and as fuel for most aquatic and terrestrial food webs. While a single biological or physical factor can have a large influence on the persistence of any particular habitat, the challenge remains to integrate the effects of multiple factors, including those of opposing direction (i.e. habitat facilitators vs. consumers). In this way, the conditions where one variable can outweigh another to have a critical effect on habitat abundance, such as initiating a habitat switch, can be best understood.

Acknowledgements

M. Brandt, L. Dee and B. Bar provided steadfast field assistance and it was our pleasure to share truly unique experiences with them. The authors thank the staff and students of BIOMAR and the Charles Darwin Research Station for their continued hospitality and friendship, and for providing access to laboratory space and resources. Helpful comments on an earlier draft of the manuscript were provided by A. Baier, R.L. Jefferies and two anonymous referees. This research was supported by grants from the US National Science Foundation (Biological Oceanography Program) to J.D.W.

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Received 28 August 2008; accepted 18 November 2008

Handling Editor: Bob Jefferies