Demise of monocultural algal farms by exclusion of territorial damselfish

Hiroki Hata*, Makoto Kato

Graduate School of Human and Environmental Studies, Kyoto University, Sakyo, Kyoto 606-8501, Japan

ABSTRACT: Resident herbivorous damselfishes exclude other herbivores from their territories and maintain dense stands of filamentous algae as algal farms. The damselfish *Stegastes nigricans* occupies coral reefs in the Okinawa Islands, southern Japan, and is unique in maintaining monocultural algal farms of the filamentous rhodophyte *Polysiphonia* sp. One of the mechanisms by which *S. nigricans* maintains these unique algal farms is by selective weeding of indigestible algae. This study tested the hypothesis that, were it not for management by *S. nigricans*, monocultures would be taken over by algal succession, even without grazing by other herbivores. We set up *S. nigricans*-exclusion cages inside and grazer-exclusion cages outside the territories of *S. nigricans*, and monitored algal succession. After exclusion of *S. nigricans*, the *Polysiphonia* sp. monoculture deteriorated rapidly and algal biomass decreased simultaneously. Filamentous rhodophytes replaced *Polysiphonia* sp. within 2 wk, and were in turn displaced by corticated macrophytes and calcareous algae (which are usually selectively weeded by *S. nigricans*). Monocultures of *Polysiphonia* sp. did not appear in the grazer-exclusion cages; pioneer *Polysiphonia* sp. colonized the areas just after caging, but thereafter was replaced by other filamentous rhodophytes, corticated macrophytes, and calcareous algae. Our experiments demonstrated that *S. nigricans* maintained monocultures and high biomass of palatable pioneer *Polysiphonia* sp. against algal succession by intensive farm-management, involving selective weeding.

KEY WORDS: Algal farm management · Monoculture · Weeding · *Stegastes nigricans* · *Polysiphonia* sp. · Algal succession · Cage experiment

INTRODUCTION

Plant–herbivore interactions greatly affect the structure and function of ecosystems. In marine ecosystems, only a few host-specific interactions have been reported between algae and algivores (Steneck 1982, Hay et al. 1987, Hay 1991, John et al. 1992), and some unique plant–herbivore interactions have been noted between algae and potentially polyphagous algae-feeding fish. Resident herbivorous damselfishes exclude other herbivores from their territories, and maintain dense stands of filamentous algae (Vine 1974, Brawley & Adey 1977, Lassuy 1980, Lobel 1980, Montgomery 1980a,b, Hixon & Brostoff 1983, 1996, Sammarco 1983, Ruyter van Steveninck 1984, Kamura & Choonhabandit 1986, Hinds & Ballantine 1987, Russ 1987, Klumpp & Polunin 1989,

Ferreira et al. 1998) known as an algal farm (Hata & Nishihira 2002). Dusky farmerfish *Stegastes nigricans* occupies coral reefs in the Okinawa Islands, in southern Japan. This fish is thought to be unique in maintaining a virtual monoculture that is dominated by the filamentous rhodophyte *Polysiphonia* sp. 1, which was treated as *Womersleyella setacea* by Hata & Kato (2002), Hata & Nishihira (2002) and Hata et al. (2002). Other resident herbivorous damselfishes also maintain algal farms, but with high species diversity (Ceccarelli et al. 2001). Since *Polysiphonia* sp. 1 is found almost exclusively in *S. nigricans* territories, occurring quite rarely outside them, *Polysiphonia* sp. 1 and *S. nigricans* have been suggested to be mutualistic (Hata & Kato 2002).

Under natural conditions, nearly monocultural algal communities, or colonial turfs, are formed when algae

*Email: hata@bio.h.kyoto-u.ac.jp

endure physical stress and moderate grazing pressure (Hay 1981, Sousa et al. 1981). These turf-forming algal species possess prostrate and upright branches, and exhibit considerable morphological plasticity in response to grazing. Compared with the algal species in colonial turfs, *Polysiphonia* sp. 1 is softer, has fewer chemical and physical defenses, and is competitively inferior.

One of the mechanisms by which *Stegastes nigricans* maintains these unique algal farms is by selective weeding of less digestible algae (Hata & Kato 2002). Without selective weeding, an algal farm might be displaced by competitively superior algae. The aim of the present study was to verify the role of unique, intensive management used by *S. nigricans* to maintain the monocultural algal farms of *Polysiphonia* sp. 1. To confirm whether *Polysiphonia* sp. 1 monoculture would occur in the absence of *S. nigricans* management, we set up cages to exclude *S. nigricans*, within their territories, and monitored the succession of algal communities that grew inside the cages. We also set up grazer-exclusion cages outside the territories of *S. nigricans*. The substrata outside the territories were exposed to intensive and continuous grazing pressure, and algal recruitment and growth were quite limited (Hata et al. 2002). Algal communities in these grazer-exclusion cages outside the territories were monitored to confirm whether the monoculture of *Polysiphonia* sp. 1 would occur in the absence of grazing and management by *S. nigricans*. By comparing the resulting algal communities in the cages with those observed in the territories of *S. nigricans*, we elucidated how monocultural algal farms are maintained.

MATERIALS AND METHODS

Study area. The study was carried out in the inner flat of a fringing reef on the west coast of Sesoko Island (26° 38′ N, 127° 52′ E), in the NW part of Okinawa. We selected an area of about 50 by 200 m with similar wave action, water flow, and sedimentation (Yamanouchi 1993). In this area, grazers such as scarid fishes (e.g. *Calotomus carolinus*, *Scarus sordidus*, *S. ghobban*), acanthurid fishes (e.g. *Acanthurus nigrofuscus*, *A. triostegus*), siganid fishes (e.g. *Siganus guttatus*, *S. spinus*), and sea urchins (e.g. *Diadema setosum*, *Echinometra* spp., *Tripneustes gratilla*) are common.

***Stegastes nigricans*-exclusion experiment.** Adult *S. nigricans* is about 84 cm in standard length and maintains about 2700 cm^2 algal farm on coral rocks individually (Hata & Kato unpubl.). Within the algal farm, exclusion cages were set on flat horizontal substrata and the succession of algal communities inside them were monitored. These cages were made of 20 × 20 mm plastic mesh, which was sufficient to exclude *S. nigricans*, with a volume of 15 × 15 × 15 cm^3. These cages served mainly for exclusion of the focal fish because within the territories, especially on flat horizontal substrata, all the herbivores are intensively excluded by the fish (Hata & Kato unpubl.). We confirmed that no macroherbivore was found inside these cages and grazer-exclusion cages below. A total of 31 cages were placed within the territories of 31 adult *S. nigricans* on 29 May 2002 using stainless-anchor bolts embedded in holes drilled in the natural substratum on each corner. The cages were cleared of algae and other epibionts by brushing the mesh at least every 4 wk. At each timepoint thereafter (1, 2, 4, 8, 12, and 18 wk), 5 cages (or 6, in some cases) were removed, and quadrats (7 × 7 cm) were immediately established in place of cages. All benthic algae, animals, and sediments in each quadrat were collected using a venturi suction sampler with a 120 μm mesh bag (McShane & Smith 1988, Hata et al. 2002). The mesh bags and their contents were preserved immediately after sampling in a 10% neutralized seawater-formalin mixture. All algae in the samples were identified to species level under a microscope, and the wet weight of each species was measured after removing excess water by blotting with a paper towel.

Grazer-exclusion experiment. We monitored algal succession in grazer-exclusion cages set outside the territories of *Stegastes nigricans*. These cages were made of 2 × 2 mm panels of galvanized wire mesh, with a volume of 15 × 15 × 15 cm^3. Outside the territories, herbivores of various sizes including schooling juvenile siganid fishes were present, and this mesh size was small enough to exclude all of them. Cages were cleared of algae and other epibionts by brushing the mesh at least every 4 wk. A total of 20 grazer-exclusion cages were set outside *S. nigricans* territories on flat horizontal surfaces of randomly selected coral rocks within the study area on 25 July 2002. At each timepoint thereafter (1, 2, 4, and 10 wk), 5 cages were removed, 7 × 7 cm quadrats immediately established, algal samples were collected, and algae were identified and weighed, as described above for the *S. nigricans*-exclusion cages.

Cage controls. We used a shading structure (a roof-only cage without sides) to control for effects of decreased light levels in the cages (Sammarco 1983, Hixon & Brostoff 1996). Roofs were constructed of 20 × 20 mm mesh for the *Stegastes nigricans*-exclusion experiment and of 2 × 2 mm mesh for the grazer-exclusion experiment. The roof-only cages were set on flat horizontal surfaces of randomly selected coral rocks outside the territories on the same day as the respective exclusion cages. At each timepoint of 2, 8,

and 12 wk (for the *S. nigricans*-exclusion controls) or 2, 4, and 10 wk (for the grazer-exclusion controls), 5 roof-only cages were removed, 7 × 7 cm quadrats immediately established, and algal samples were collected, and algae were identified and weighed, as described above for the *S. nigricans*-exclusion cages. At the same time, 5 quadrats were established outside the territories on flat horizontal surfaces of randomly selected coral rocks within the study area; algae within the quadrats were collected, identified, and weighed as described above. Algal communities were then compared between inside and outside the cages.

We also measured light intensity inside and outside both types of exclusion cage *in situ* on calm, cloud-free days at 09:00, 12:00, and 15:00 h (n = 12 paired measurements per timepoint) using a LI-COR LI-1000 Data Logger. Relative water motion inside and outside both types of cage was also examined by measuring the mass loss of 7 pairs of plaster balls set inside and outside each cage (Komatsu & Kawai 1992).

Data analysis. Algal succession was monitored using 4 indices (Hill 1973): (1) biomass; (2) species richness (number of species, S); (3) evenness (Pielou's J; Pielou 1966); and (4) species diversity (Shannon-Wiener index, H'; Shannon & Weaver 1949). Levene's test for homogeneity of variance yielded no significant results for all 4 indices. Therefore, to detect the effect of caging duration on these indices, 1-way analysis of variance (ANOVA) was used for analyses with the period of cage deployment as a fixed factor. Each of the 4 indices was compared among the periods using a multiple comparison test (least significant difference, LSD). Indices for the roof-only cages were compared with those for outside the cages using Mann-Whitney U-test. All analyses were conducted using the computer program SPSS for Windows.

Algal functional groups. Algal species were classified into 6 functional groups after Steneck & Watling (1982): (1) microscopic filaments of cyanophytes (microalgae); (2) delicately branched filamentous algae with no or light cortices (filamentous algae); (3) thin tuber and foliose algae (foliose algae); (4) coarsely branched filamentous algae with cortices (corticated macrophytes); (5) thick blades with thick cortices (leathery macrophytes); and (6) calcified algae (calcareous algae). These functional groups correspond to life history strategies and competitive ability (Littler 1980, Littler et al. 1983a,b).

RESULTS

Cage controls

The *Stegastes nigricans*-exclusion cages decreased total light intensity by an average (±1 SD) of 8.1 ± 12.1 % at 09:00 h, 6.8 ± 4.3 % at 12:00 h, and 5.2 ± 6.6 % at 15:00 h (Table 1). The grazer-exclusion cages also decreased total light intensity by an average (±1 SD) of 15.6 ± 13.7 % at 09:00 h, 13.6 ± 12.9 % at 12:00 h, and 23.3 ± 5.6 % at 15:00 h. Even inside these cages at 09:00 h, however, total light intensity was much greater than the level needed for saturation of the photosynthetic rate of a broad variety of algae (Lüning 1981, Littler & Littler 1992, Kirk 1994). These results indicate that shading by cages was not important to algal succession (Hixson & Brostoff 1996). Water motion differed significantly only inside the grazer-exclusion cages compared with outside, although the cages reduced water motion by an average (±1 SD) of only 8.1 ± 5.1 %. No extra accumulation of sediments was observed inside both cages.

In algal farms, *Polysiphonia* sp. 1 strongly dominated throughout the year (Fig. 1A, Hata et al. 2002). We also conducted cage control experiments outside the territories to examine the secondary effect of caging. Outside cages, *Polysiphonia* sp. 1 was never found (Fig. 1B, Table 2). A mat-forming cyanophyte, *Calothrix aeruginosa*, and filamentous rhodophytes *Herposiphonia obscura* and *Taenioma perpusillum* composed algal communities with much lower biomass than in algal farms (for details, see Hata et al. 2002).

Table 1. Total light intensity inside and outside of *Stegastes nigricans*-exclusion cages (20 × 20 mm mesh) and grazer-exclusion cages (2 × 2 mm mesh). Both n = 12. Comparisons were made using paired *t*-test: *$0.05 \geq$ p 0.01; **$0.01 \geq$ p 0.001; ***p < 0.001

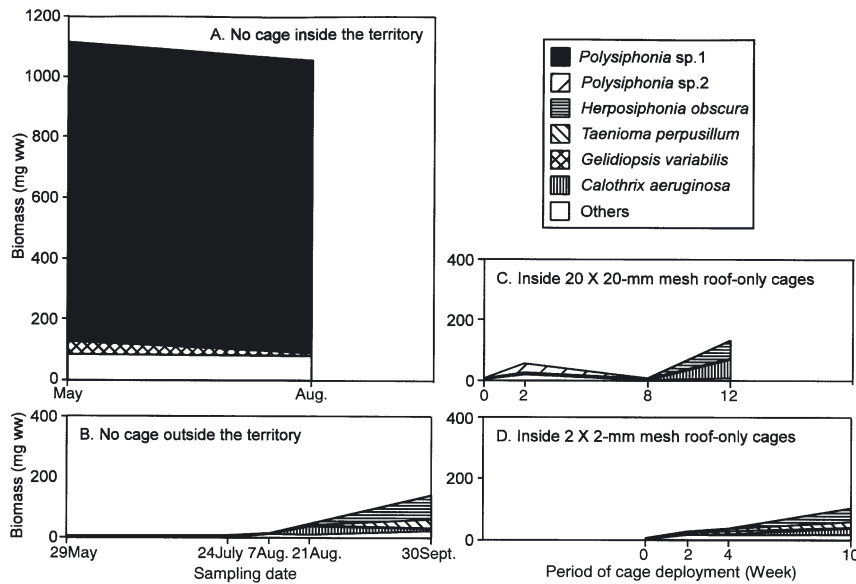| Cage	Time (h)	Inside cage			Outside cage	
		Light intensity (μmol m^{-2} s^{-1})	SD	Significance	Light intensity (μmol m^{-2} s^{-1})	SD
S. nigricans exclusion	09:00	1484.7	170.1	*	1625.6	162.4
	12:00	2560.8	257.5	***	2750.0	281.4
	15:00	1488.9	335.5	*	1568.6	316.6
Grazer exclusion	09:00	1460.1	196.9	**	1742.3	175.2
	12:00	1755.1	158.6	**	2051.4	185.4
	15:00	1483.3	166.1	***	1944.5	250.3

Fig. 1. Algal species composition (A) inside the territory of *Stegastes nigricans* (n = 18, 16 for May, August, respectively; Hata et al. 2002), (B) outside the territory (n = 5), (C) inside 20 × 20 mm mesh roof-only cages (n = 5), and (D) inside 2 × 2 mm mesh roof-only cages (n = 5)

These algae were early-colonizers and also constituted a large proportion of algal communities inside both roof-only cages (Fig. 1C,D, Table 2). Inside one 20 × 20 mm mesh roof-only cage in the second week, *Polysiphonia* sp. 2, which also occurred outside cages, showed high biomass. This occasional increase of *Polysiphonia* sp. 2 resulted in significantly higher biomass and lower evenness in that cage in the second week than those outside the cages (Fig. 2). No other difference in all 4 indices was detected between inside both roof-only cages and outside the cages, and the algal communities inside both roof-only cages showed similar, slight seasonal changes to those outside cages.

These results indicated that the secondary effects of these cages were negligible compared with their primary effect of excluding either *Stegastes nigricans* or other grazers, and that under intensive grazing outside the territories, early-colonizing algae except *Polysiphonia* sp. 1 composed of algal communities with much lower biomass.

Stegastes nigricans-exclusion experiment

Inside *Stegastes nigricans*-exclusion cages, algal communities changed drastically during the study (Fig. 3A, Table 2). Before the cages were put in place, *Polysiphonia* sp. 1 strongly dominated (average relative abundance based on wet biomass ±1 SD = 87.3 ± 10.0%; n = 5), but after the cages were placed, *Polysiphonia* sp. 1 declined quickly and was displaced by

filamentous rhodophytes (*Polysiphonia* sp. 2 and *Neosiphonia savatieri*). Thereafter, a filamentous rhodophyte (*Anotrichium tenue*), corticated macrophytes (*Gelidiella pannosa* and *Chondria* sp.), and calcareous macrophytes (*Jania arborescens* and *Bornetella sphaerica*) increased in biomass. In terms of functional groups, filamentous algae were gradually replaced by corticated macrophytes and calcareous algae (Fig. 3B).

Algal biomass decreased initially, owing to the decrease of *Polysiphonia* sp. 1 biomass, and then increased due to the growth of the later-colonizing algae (Fig. 4A). Species richness increased quickly until the second week, because rare species started to inhabit the cages shortly after they were put in place (Fig. 4B, Table 2). Corresponding to the decline of *Polysiphonia* sp. 1, the evenness of the algal community increased rapidly until the fourth week after the cages started to operate, and then reached a plateau (Fig. 4C), as did species diversity (Fig. 4D).

After exclusion of *Stegastes nigricans*, the *Polysiphonia* sp. 1 monoculture deteriorated and was replaced by many competitively superior late-colonizing algae, and accordingly algal species diversity in the cages increased.

Grazer-exclusion experiment

Without grazing, the *Polysiphonia* sp. 1 monocultures seen in *Stegastes nigricans* algal farms were not present outside the territories of *S. nigricans*. In total, 33 algal species occurred inside the grazer-exclusion cages during the 10 wk of the experiment (Table 2). *Polysiphonia* sp. 1 appeared in the first week and then disappeared (Fig. 5A). In succession, a filamentous rhodophyte (*P. coacta*), a cyanophyte microalga (*Calothrix aeruginosa*), and a calcareous chlorophyte (*Acetabularia parvula*) increased in biomass. By the tenth wk, another filamentous rhodophyte (*Neosiphonia savatieri*), corticated macrophytes (*Gelidiopsis variabilis* and *Padina* sp.), and a calcareous chlorophyte (*Bornetella sphaerica* and *Rhipidosiphon javensis*) had replaced them. From the standpoint of functional groups, filamentous algae colonized first, microalgae partially replaced them, and corticated macrophytes and calcareous algae came thereafter. Therefore, after 10 wk, these 4 algal groups were present in relatively equal amounts (Fig. 5B).

Table 2. List of algal species and their abundance in the first 4 wk (F) and the rest of experimental periods (L) inside *Stegastes nigricans*-exclusion cages and inside grazer-exclusion cages, and cage controls conducted outside the territories, i.e. no cage, inside 20 × 20 mm mesh and 2 × 2 mm mesh roof-only cages. The temporal division was made because in the first 4 wk, caged algal communities changed drastically and were slightly saturated thereafter (see text for details). C: common occurrence more than 10% in relative biomass at least 1 sample; R: rare occurrence — less than 10% in relative biomass at every occurrence; –: no occurrence; Cy: Cyanophyta; Ch: Chlorophyta; He: Heterokontophyta; Rh: Rhodophyta

| Functional groups	Species	Phylum	*S. nigricans* exclusion F	L	Grazer exclusion F	L	No cage F	L	20 × 20 mm roof cages F	L	2 × 2 mm roof cages F	L
Micro-algae	*Calothrix aeruginosa*	Cy	R	R	C	C	R	C	C	C	C	C
	Calothrix sp.	Cy	–	–	C	–	–	C	–	R	C	R
	Lyngbya confervoides	Cy	–	R	R	–	–	–	–	–	–	–
Filamentous algae	*Anotrichium tenue*	Rh	R	C	C	–	–	R	R	–	R	R
	Centroceras clavulatum	Rh	R	R	C	R	–	R	C	R	C	R
	Ceramium sp.	Rh	R	R	–	–	–	–	–	–	–	–
	Corallophila huysmansii	Rh	C	C	R	–	R	R	R	–	–	–
	Herposiphonia obscura	Rh	C	C	R	C	C	C	C	C	C	C
	Neosiphonia savatieri	Rh	C	R	R	C	C	R	C	R	–	R
	Polysiphonia coacta	Rh	–	R	C	C	–	C	–	R	C	C
	Polysiphonia sp. 1	Rh	C	C	C	–	–	–	–	–	–	–
	Polysiphonia sp. 2	Rh	C	–	–	–	–	R	C	R	–	–
	Polysiphonia sp. 3	Rh	R	R	C	R	C	C	C	C	C	R
	Taenioma perpusillum	Rh	C	C	C	C	C	C	C	C	C	C
	Cladophora sp.	Ch	R	R	R	–	C	C	C	R	R	R
	Pseudobryopsis sp.	Ch	–	R	–	–	–	–	–	–	–	–
	Struvea sp.	Ch	R	R	–	–	–	–	–	–	–	–
	Feldmannia indica	He	R	R	C	C	C	C	C	C	C	C
Foliose algae	*Dictyosphaeria versluysii*	Ch	R	–	–	–	–	–	C	–	–	–
	Enteromorpha sp.	Ch	R	R	–	–	C	R	C	R	R	–
	Dictyota friabilis	He	–	–	–	R	–	–	–	–	–	–
Corticated macrophytes	*Champia* sp.	Rh	R	R	R	R	C	R	C	–	R	R
	Chondria sp.	Rh	R	C	R	–	C	–	C	–	R	R
	Gelidiella pannosa	Rh	C	C	C	R	C	C	C	C	R	–
	Gelidiopsis variabilis	Rh	C	C	C	C	C	C	C	C	C	R
	Hypnea sp.	Rh	–	R	–	–	–	R	–	–	R	–
	Wrangelia sp.	Rh	R	C	–	R	–	–	–	–	–	–
	Caulerpa ambigua	Ch	R	–	–	–	–	–	–	–	–	–
	Caulerpa brachypus	Ch	–	–	–	R	–	–	–	–	–	–
	Caulerpa serrulata	Ch	R	R	–	–	–	–	–	–	–	–
	Caulerpa verticillata	Ch	R	R	–	–	–	–	–	–	–	–
	Padina sp.	He	R	R	C	C	–	C	R	R	C	R
Leathery macrophytes	*Sargassum* sp.	He	–	–	R	R	–	R	–	–	–	R
Calcareous algae	*Jania adhaerens*	Rh	R	C	C	R	C	C	C	C	C	–
	Jania arborescens	Rh	R	C	–	R	–	–	–	–	–	–
	Jania sp.	Rh	–	R	–	–	–	–	–	–	–	–
	Acetabularia clavata	Ch	R	R	R	R	–	R	–	R	R	R
	Acetabularia dentata	Ch	R	–	R	–	–	–	R	–	–	–
	Acetabularia exigua	Ch	R	R	C	R	C	R	C	C	R	R
	Acetabularia parvula	Ch	R	R	C	C	–	R	C	C	R	R
	Bornetella sphaerica	Ch	R	R	R	C	–	–	R	R	–	R
	Halimeda discoidea	Ch	–	R	–	–	–	–	–	–	–	–
	Neomeris annulata	Ch	R	R	–	R	–	–	–	–	–	–
	Penicillus sibogae	Ch	R	R	R	R	–	R	R	C	R	–
	Rhipidosiphon javensis	Ch	R	C	–	C	–	R	–	–	–	–
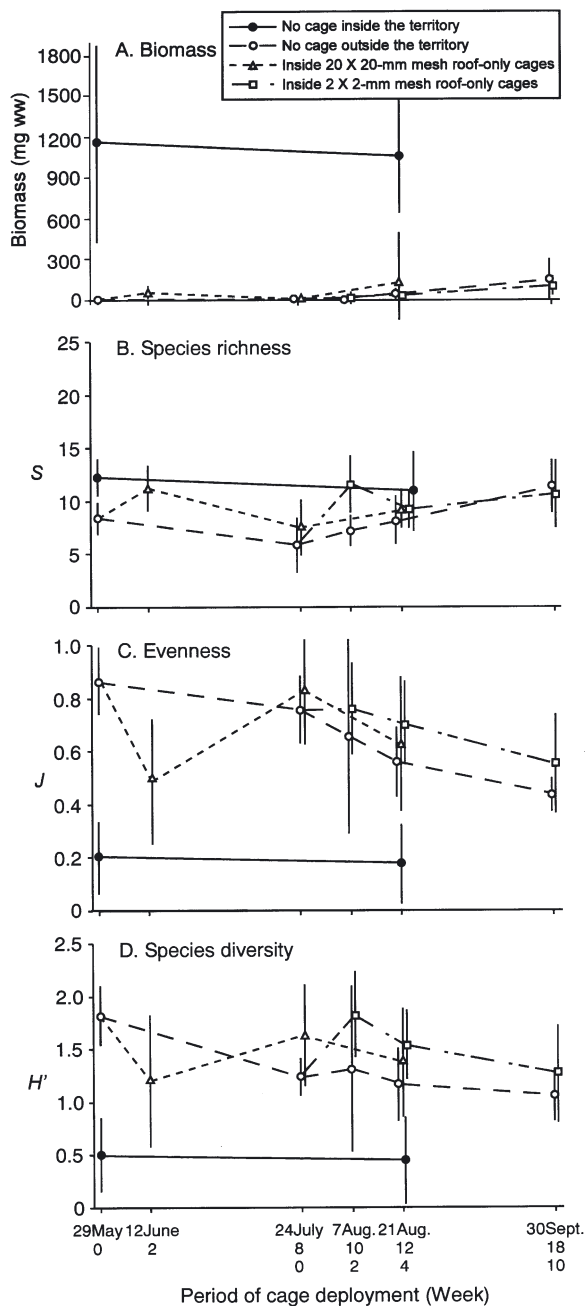
Fig. 2. Temporal patterns of (A) total algal biomass, (B) species richness, (C) evenness, and (D) species diversity for cage controls, i.e. no cage inside the territory (Hata et al. 2002), no cage outside the territory, inside 20 × 20 mm mesh roof-only cages, and inside 2 × 2 mm mesh roof-only cages. Each point represents the average (±1 SD) of 7 × 7 cm quadrat samples. See Fig. 1 for sample sizes

In the grazer-exclusion cages, algal biomass increased quickly until after 4 wk of exclusion (Fig. 6A). Total algal biomass at Week 10 was still much lower than that in the *Stegastes nigricans*-exclusion cages. In the cages, algal species richness

increased abruptly in the first wk and became nearly saturated (Fig. 6B). At Week 10, species richness was 15.0 ± 2.3 (average ±1 SD), and this value was similar to that inside *S. nigricans*-exclusion cages after 18 wk (16.4 ± 3.6; p > 0.05, Mann-Whitney *U*-test). Evenness decreased during the first 4 wk and increased thereafter (Fig. 6C). Because of high species richness and evenness, species diversity after 10 wk was higher in the grazer-exclusion cages (1.78 ± 0.22) than in the algal farms managed by *S. nigricans* (0.52 ± 0.33; p < 0.01, Mann-Whitney *U*-test), and was also higher than inside the *S. nigricans*-exclusion cages at 18 wk (1.22 ± 0.37; p < 0.05, Mann-Whitney *U*-test; Fig. 6D). Compared to the algal assemblages outside cages, evenness and species diversity were higher in the cages at Wk 10 (both p < 0.05, Mann-Whitney *U*-test), although biomass and species richness were not significantly different between inside and outside the cages.

These results indicate that algal communities in the grazer-exclusion cages at Week 10 were composed of both early- and late-colonizing algae, and were in the mid-successional stage with high species diversity.

DISCUSSION

After exclusion of *Stegastes nigricans*, *Polysiphonia* sp. 1 monocultures deteriorated rapidly. Filamentous rhodophytes replaced *Polysiphonia* sp. 1 initially, fol-
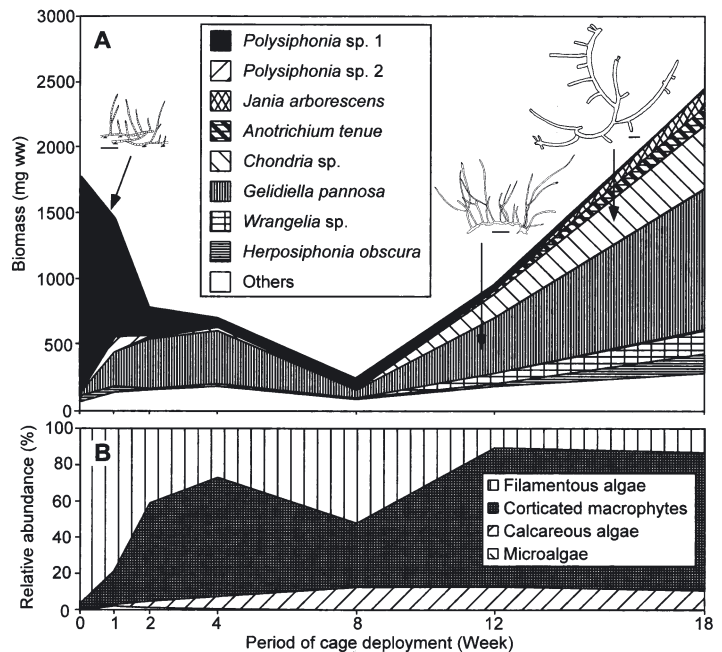

Fig. 3. (A) Algal species composition (scale bar = 1 mm) and (B) relative abundance of wet biomass of algal functional groups inside the *Stegastes nigricans*-exclusion cages. Values are averages of 5 to 6 quadrat samples (7 × 7 cm) per occasion
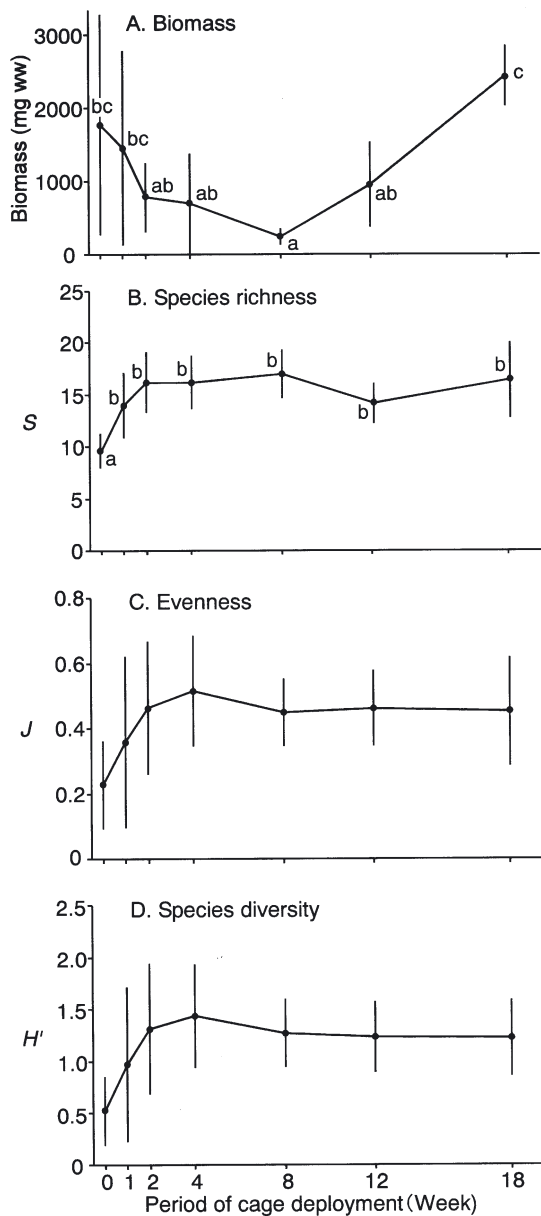
Fig. 4. Temporal patterns of (A) algal biomass, (B) algal species richness, (C) evenness, and (D) species diversity inside the *Stegastes nigricans*-exclusion cages. Each point represents the average (±1 SD) of 5 to 6 quadrat samples (7 × 7 cm). Different letters indicate significant differences at the 5% level by 1-way ANOVA followed by LSD test
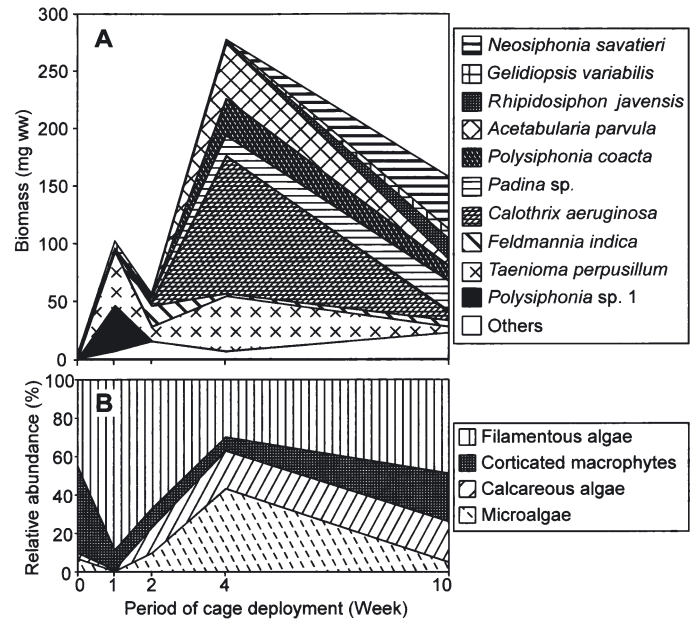

Fig. 5. (A) Algal species composition and (B) relative abundance of algal functional groups based on wet biomass inside the grazer-exclusion cages. Values are averages of 5 to 6 quadrat samples (7 × 7 cm)

lowed by the increase and domination of other filamentous rhodophytes, corticated macrophytes, and calcareous algae. Algal functional groups are strongly related to survival strategies and competitive ability (Littler & Littler 1980, Littler et al. 1983a,b); microalgae and filamentous algae are early colonizers with high growth rates, while corticated macrophytes and calcareous algae are late-successional species with lower growth rates and high competitive ability. Under grazing-free conditions inside the grazer-exclusion cages, the pioneering *Polysiphonia* sp. 1 was replaced by other filamentous rhodophytes, late-colonizing corticated macrophytes and calcareous algae, indicating an inferior competitive ability of *Polysiphonia* sp. 1. Furthermore, late-colonizing corticated macrophytes and calcareous algae that became dominant after 8 wk in the *S. nigricans*-exclusion cages (e.g. corticated *Gelidiella pannosa* and *Chondria* sp., and calcareous *Jania arborescens* and *Bornetella sphaerica*) are not easily digested by *S. nigricans* and are selectively weeded (Hata & Kato 2002). These results demonstrate that by intensive management involving selective weeding, *S. nigricans* manages algal farm monoculture of the palatable alga *Polysiphonia* sp. 1, and this alga may therefore reach high biomass values.

Algal farms of most other damselfishes are characterized by a high species-diversity of mid-successional algal communities, which are composed of both pioneers and late-colonizers (Ceccarelli et al. 2001). Other experiments involving exclusion of other territorial damselfishes (Lassuy 1980, Hinds & Ballantine 1987) found that algal species diversity in cages set inside algal farms decreased because 1 or a few competitively superior alga species outcompeted and dominated algal communities that initially had high species diversity. The reported algal communities resembled those formed inside the grazer-exclusion cages at Wk 10 of
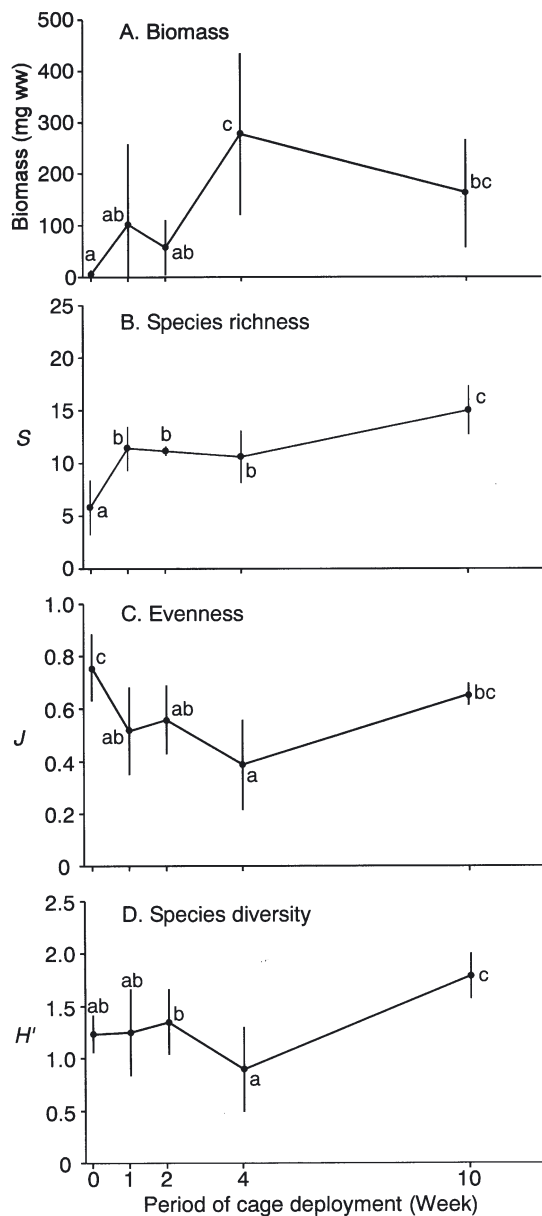
Fig. 6. Temporal patterns of (A) total algal biomass, (B) species richness, (C) evenness, and (D) species diversity inside the grazer-exclusion cages. Each point represents the average (±1 SD) of five 7×7 cm quadrat samples. Different letters indicate significant differences at the 5% level by 1-way ANOVA followed by LSD test

our experiment. In our *Stegastes nigricans*-exclusion experiment, the species-diversity of the algal communities within the cages increased. This discrepancy with the results of previous studies was caused by the initial difference in algal composition and suggests that the *Polysiphonia* sp. 1 monocultures with high biomass are established under conditions of halted succession due to intensive management, i.e. weeding of

later-colonizers strongly prevents them from invading monoculture algal farms. Algal farms of other damselfishes, on the other hand, are maintained by slowed succession due to extensive management, i.e. keeping moderate grazing-pressure prevents later-colonizers from excluding early colonizers competitively (Hixon & Brostoff 1996). In the algal farms of *Hemiglyphidodon plagiometopon*, species diversity increased when the fish were excluded by cages (Lassuy 1980). In these farms, the corticated rhodophyte *Gelidiopsis intricata* and the filamentous rhodophyte *Polysiphonia scopulo-rum* comprised 80% of the biomass; the algal species diversity was intermediate between that of the farms of *S. nigricans* and those of other damselfishes. These data suggest that farm management by *H. plagiometo-pon* may be intermediate, involving only some weeding.

In conclusion, *Stegastes nigricans* directly affects algal succession by its intensive management involving selective weeding on indigestible and late-colonizing algae to maintain highly digestible *Polysiphonia* sp. 1 monocultures in their algal farms. These results suggest that *S. nigricans* manage their algal farms much more intensively than other damselfishes, and that the relationship between *Polysiphonia* sp. 1 and *S. nigricans* is a new example of species-specific mutual interactions between plant and herbivore in marine ecosystems, where such relationships are quite rare.

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