Damselfish as Keystone Species in Reverse: Intermediate Disturbance and Diversity of Reef Algae

Mark A. Hixon, William N. Brostoff

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Fabry's disease (*4, 5, 25*). Although globotriaosylceramide is present in moderate quantity in normal human erythrocytes (1.6 to 2.0 μg per 100 mg of dried cell residue; 0.08 to 0.10 μmole per 50 ml) (*26*), the quantity is 1/100 that in Burkitt lymphoma cells. Normal erythrocytes were not reactive to antibody 38-13 (*2*) but were weakly reactive to polyclonal antibodies to P absorbed by globoside (*5*). Analyses of the distribution, chemical quantity, and cell surface expression of this glycolipid in cells of other tissues are lacking. It is possible that expression of this glycolipid is cryptic, as it is in normal human erythrocytes and other blood cells. However, a certain strain of *Escherichia coli* causing urinary tract infections had a pili lectin that is known to interact with globoside and globotriaosylceramide (*27*). Whether the globotriaosylceramide of the genitourinary tract epithelia is exposed at the cell surface has not been determined.

The glycolipid associated with Burkitt lymphoma cell lines did not accumulate in other lymphoproliferative or myeloproliferative processes. Because this glycolipid accumulates only in Burkitt lymphoma cells, it could be used for the detection of Burkitt lymphoma cells among various malignant blood cells and lymphoid, erythroid, and myeloid leukemia cells. In a patient with gastric cancer, a rare genotype *pp* was associated with a P-like and P_1-glycolipid antigen. Since the tumor growth in that instance was suppressed by anti-P_1PP^k antibodies (*28*), the effect of monoclonal antibody 38-13 on Burkitt lymphoma growth is of great interest. Globotriaosylceramide accumulation in Burkitt lymphoma could result from a blockage of globoside synthesis or from activation of α-galactosyltransferase. Either mechanism could yield an altered profile in Burkitt lymphoma, analogous to changes generally associated with oncogenic transformation (*29*).

E. NUDELMAN
R. KANNAGI
S. HAKOMORI
M. PARSONS*
Division of Biochemical Oncology, Fred Hutchinson Cancer Research Center, and *Departments of Pathology* and *Microbiology, University of Washington, Seattle 98104*
M. LIPINSKI
J. WIELS
M. FELLOUS†
T. TURSZ
Groupe d'Immuno-Biologie des Tumeurs, Institut Gustave-Roussy, 948000 Villejuif, France

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* Present address: Department of Biochemistry, University of Washington, Seattle 98195.
† Present address: Institut Pasteur, Paris 15, France.

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Damselfish as Keystone Species in Reverse: Intermediate Disturbance and Diversity of Reef Algae

Abstract. *Substrates located within the defended territories of Hawaiian damselfish for 1 year were subjected to intermediate grazing intensity and, as a result, showed greater diversity of algae than substrates either protected within fish-exclusion cages or exposed to intense fish grazing outside territories. Thus, this damselfish enhances local diversity on reefs through "intermediate-disturbance" effects, and is a keystone species that decreases rather than increases overall predation intensity relative to areas where it is absent.*

A major goal of community ecology is to determine what factors allow similar species to coexist in the same habitat without one dominant competitively eliminating most others. One such mechanism is known as the "keystone-species" concept. As described by Paine (*1*), keystone species are predators that keep the population densities of their prey below levels where resources become limiting, thus preventing local competitive exclusions among the prey species. Paine (*1*) found that the controlled removal of a starfish population resulted in mussels excluding most other large invertebrates from a rocky intertidal zone. Thus, a keystone species can maintain high local diversity by increasing the intensity of predation relative to areas where that species is absent. We now describe a fundamentally different kind of keystone species: a damselfish that maintains high diversity of algae on Hawaiian coral reefs by reducing the overall intensity of predation on the algae (*2*). This system and the classic keystone-species concept are reconcilable when examined in the context of what has been called the "intermediate-disturbance" hypothesis (*3*), which predicts that local diversity reaches a peak at moderate levels of disturbance.

Herbivorous fishes affect the local distribution and abundance of algae on tropical reefs (*4–7*). Typically, intense grazing by aggregations of parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) results in most exposed coral rock sur-

faces being covered by crustose coralline algae (*5*). On otherwise identical surfaces in the same area, certain herbivorous damselfishes (Pomacentridae) establish and maintain relatively dense mats of erect filamentous algae by aggressively excluding other fishes from their individual territories (*6, 7*).

Our study site was located along the windward subtidal reef crest at the Coconut Island Marine Refuge (Kaneohe Bay, Oahu, Hawaii). The substrate consisted of a meter-deep bench of dead *Porites* coral rock, upon which the yelloweye damselfish (*Stegastes fasciolatus*) defended territories against numerous parrotfishes (*Scarus* spp.) and surgeonfishes (mostly *Acanthurus* spp.). Sea urchins and other large invertebrate grazers were rare. Settling plates (1152) were mounted on 96 concrete blocks (*8*) and were distributed evenly on 19 September 1980 (i) exposed outside damselfish territories, (ii) exposed inside territories, and (iii) protected within fish-exclusion cages (*9*). Periodically during the next year, a sample of 63 plates (3 treatments × 3 substrate types × 7 replicates) was removed from the field without replacement. Each sample underwent laboratory analyses (*10*). Separate cage-control experiments revealed no substantial secondary effects of caging upon algal diversity, and throughout the main experiment few invertebrate herbivores were found on the settling plates (*10*). Estimates of the proportional relative abundance of each algal species (*11*) were used to calculate seven different species diversity indices (*10*). Because all indices suggested the same patterns, we present here only the Shannon-Wiener index (*12*). Also, the different plate substrate types yielded similar results whether analyzed separately or together, and therefore we report only the pooled results.

During the yearlong course of the main experiment, 17 different samples were analyzed. The successional stages of relative algal diversity among treatments are summarized by considering three of these samples (Fig. 1A). Plates exposed outside damselfish territories showed the lowest diversity and biomass of algae (*10*). Intense grazing by fishes eliminated erect forms, leaving a 14-species assemblage of grazer-resistant prostrate forms dominated by the only crustose coralline alga found in this experiment, *Hydrolithon reinboldii*. Quadrat samples of natural substrates confirmed that diversity and biomass were invariably less outside damselfish territories than inside (*10*).

Algal diversity on caged plates relative to that on plates exposed inside damselfish territories varied through time. Initially (Fig. 1A, 1 week), diversity was greater on the plates inside territories, presumably because these surfaces were closest to a source of colonizing spores provided by the surrounding algal mat (*13*). Midway through the experiment (6 months), diversity was greater on the caged plates, apparently because the algae on these plates were undisturbed but had not reached densities where competitive exclusions were common. By the end of the experiment (1 year), diversity was again greater on the plates inside territories. The caged plates supported the greatest algal biomass of all three treatments (*10*), but by the end of the year many had become overgrown by the red alga *Tolypiocladia glomerulata*. This alga alone had an overall relative abundance of 47.5 percent in an assemblage of 17 mostly filamentous and foliose species. The plates exposed inside damselfish territories for 1 year showed a more diverse assemblage of mostly filamentous forms, such as *Centroceras clavulatum, Taenioma perpusillum,* and *Ectocarpus indicus*, which together had a relative abundance of only 34.4 percent in an assemblage of 20 noncoralline species. *Tolypiocladia* accounted for less than 1 percent of the algae inside territories. Thus, while diversity inside territories had increased during the year, diversity within cages had peaked and then declined (Fig. 1A). The pattern on the caged plates was typical of predicted and observed succession in some forests and algal assemblages, where diversity decreases as an undisturbed "climax" state approaches (*3, 14*).

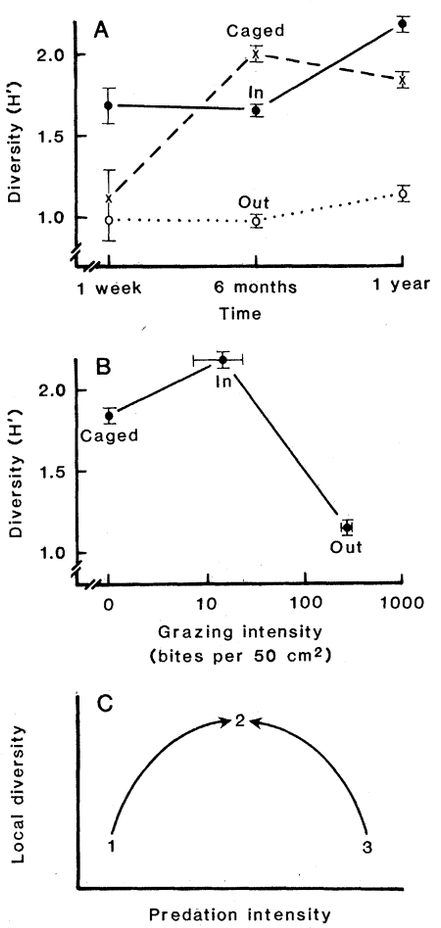

Fig. 1. (A) Diversity, as measured by the Shannon-Wiener index H' (*12*), of noncoralline algae on settling plates as a function of exposure time to three treatments: caged, inside damselfish territories (*In*), and outside territories (*Out*). Each point represents a pooled sample of 21 plates ± 2 standard errors (*12*). (B) Diversity after 1 year [same data as (A)] as a function of the intensity of destructive grazing by fishes [sample mean ±95 percent confidence limits, N = 63 per treatment (*17*)]. The algal assemblages in the cages do not occur naturally on exposed reef surfaces because the fish are always present. (C) Graph of the intermediate-disturbance hypothesis, showing that a keystone species can enhance local diversity either by increasing predation intensity from point 1 toward point 2 (classic type), or by decreasing overall predation intensity from point 3 toward point 2 (reverse type).

The "intermediate-disturbance" hypothesis predicts that as the intensity of physical or biological disturbance (or both) progressively increases from zero, the species diversity of the affected community initially increases and subsequently decreases (*3, 15, 16*). At low levels of disturbance, a few dominant competitors are capable of locally excluding most other species, and at high levels many local extinctions occur. Diversity thus reaches a peak at an intermediate-disturbance level, where the coexistence of many species is maintained because their population densities are kept low enough so that resources do not become limited. When the results of the final 1-year sample from our experiment are plotted as a function of fish grazing intensity (*17*), a pattern typical of intermediate-disturbance systems emerges (Fig. 1B). Algal diversity reached a peak inside damselfish territories, where destructive (holdfast-removing) grazing occurred at intermediate intensity. Grazing by the yelloweye damselfish itself apparently prevents any one algal species from competitively excluding most others, yet is not so intense as to cause many local extinctions. These results suggest that the yelloweye damselfish is a keystone species with respect to the diversity of algae on exposed shallow coral rock substrates in Hawaii. This pattern had been predicted for damselfishes in general by Montgomery (*7*), and also suggested for the effects of these fishes on sea urchins and corals (*18*).

More important, in the context of the

intermediate-disturbance hypothesis, our study provides experimental evidence of a keystone species that enhances local diversity by actually decreasing the overall intensity of predation relative to areas where that species is absent (Fig. 1C). Thus, two general kinds of keystone species exist. The first type enchances diversity directly by increasing disturbance from point 1 toward point 2 in Fig. 1C. Such predators are presumably prevented from normally driving the system close to point 3 by density-dependent factors, although they apparently can do so under certain conditions (*16*). The second type of keystone species enhances diversity not only directly, but also indirectly by decreasing disturbance by other predators from point 3 toward point 2 in Fig. 1C. In the case of the yelloweye damselfish, this indirect effect is a result of defending a feeding territory against more intensive predators.

MARK A. HIXON
Department of Ecology and Evolutionary Biology, University of California, Irvine 92717
WILLIAM N. BROSTOFF
Department of Botany, University of Hawaii, Honolulu 96822

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9. Cages were constructed of 1.3 by 1.3 cm galvanized wire mesh and measured 60 by 60 by 30 cm. One block was placed in each cage, and each settling plate was at least 15 cm from the wall of the cage. Exterior cage surfaces were prevented from fouling by intense grazing of fishes; interior surfaces were periodically cleaned by divers. All cages were placed just outside territories.
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Slow Compressional Wave Propagation in Wet Human and Bovine Cortical Bone

Abstract. *Ultrasonic wave propagation in bovine plexiform and human Haversian bone was studied in the range 0.5 to 15 megahertz. A new longitudinal wave was observed which traveled more slowly than the ordinary longitudinal wave. The slow wave was associated with the dynamics of fluid motion in the pores of bone.*

In two papers (*1*) published in 1956, Biot treated the problem of elastic wave propagation in a fluid-saturated porous medium. He showed that in addition to a shear (transverse) wave, two dilatational (longitudinal) waves were propagated in such media: a higher velocity wave (designated as a wave of the first kind) whose fluid and solid component amplitudes are in phase, and a lower velocity wave (designated as a wave of the second kind) in which these amplitudes are in opposite phase. Waves of the first kind are the usual bulk waves, exhibiting negligible dispersion; waves of the second kind are highly attenuated.

The slow compressional waves have been observed in sintered glass beads at ultrasonic frequencies by Plona (*2*) and in fluid-filled sands and glass beads in the audible frequency range by Paterson (*3*). Plona's results were confirmed analytically by Berryman (*4*). Plona and Johnson (*5*), in a follow-up study, demonstrated the existence of slow compressional waves in three fluid-filled commercially available porous structures as well. The commercial materials included

Table 1. Slow wave amplitudes and velocities.

Specimen	Frequency (Mhz)	A_s/A_f	V_s (km/sec)	V_s/V_f
Bovine longitudinal	0.73	0.50	2.3	0.54
Bovine circumferential	0.73	0.22	1.53	0.43
Bovine longitudinal	1.0	0.32	2.30	0.55
Bovine circumferential	1.0	0.22	1.53	0.44
Human la longitudinal	1.0	0.82	2.34	0.62
Bovine longitudinal	2.0	0.12	2.32	0.54
Human la longitudinal	2.0	0.53	2.34	0.62
Bovine longitudinal	3.0	0.044	2.33	0.55
Human lb longitudinal	3.0	0.058	1.89	0.49
Bovine longitudinal	4.0	0.030	2.32	0.55
Human lb longitudinal	4.0	0.042	1.88	0.49
Bovine longitudinal	5.0	0.064	2.32	0.50
Human lb longitudinal	5.0	0.028	1.90	0.55
Bovine longitudinal	6.0	0.0038		
Human lb longitudinal	6.0			