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 mmole 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 expressed 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 glycolipid antigen. Since the tumor growth in that instance was suppressed by anti-P, P 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 a-galactosyltransferase. Either mechanism could yield an altered profile in Burkitt lymphoma, analogous to changes generally associated with oncogenic transformation (29).

References and Notes
12. Glycolipids were designated according to the recommendations of the nomenclature committee of the International Union of Pure and Applied Chemistry Commission on Biochemical Nomenclature, Lipids 12, 455 (1971).
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Damselsh as Keystone Species in Range: Intermediate Disturbance and Diversity of Reef Algae

Abstract. Substrates located within the defended territories of Hawaiian damsels 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 damselsh 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 murrel fish 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 damselsh 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 the seaweed Ceramium rubrum 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 (3). 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 fasciatus) defended territories against numerous parrotfishes (Scaurus 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 pattern, 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). Intensive 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 Tolypodium glomerulatum. 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. Tolypodium glomerulatum 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 observed succession in some forests and algal assemblages, where diversity decreases as an undisturbed "climax" state approaches (3, 14).

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 enhances 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 yellowswallow damselfish, this indirect effect is a result of defending a feeding territory against more intensive predators.

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References and Notes

2. We include both herbivory and carnivory as being predation or biological disturbance.
8. Each support block four of each type of settling plate: flat slabs cut from sun-dried coral rock and squares of roughly sandblasted gray polyvinyl chloride plastic, both of which measured 50 cm², and naturally contoured coral rock slabs, which were approximately the same size but had irregular contours. Each of these three substrates had specific advantages as settling surfaces relative to the others (40). All plates were mounted horizontally with their upper surfaces on the same plane. Each block was sampled four times during the main experiment.
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 protected from fouling by intense grazing of corals; interiors surfaces were periodically cleaned by divers. All cages were placed just outside territories.
11. The algae on the plates grew in mixed-species stands. All erect and prostrate coralline algae were scraped from each plate, spread uniformly within a glass petri dish, and the number of species was counted. Randomly selected points (100) within the dish were then examined under ×100 magnification. The algae in the central point of each ocular field provided data on relative abundances.
17. Grazing intensity was measured as the "standing crop" of visible fish bites (mostly by parrotfish) counted on each polyvinyl chloride settling plate sampled during the first 10 weeks of the experiment. Afterward, bite marks on plates exposed outside territories became too dense to quantify accurately, while those on plates inside territories remained nearly constant. No bite marks were found on caged plates. The flat and natural coral rock plates showed the same relative pattern of grazing intensity, but individual bite marks were not readily countable on these substrates.