

Fish mesograzers as gatekeepers of the species composition of coral reefs

P.M. Yoshioka

Department of Marine Sciences; University of Puerto Rico, Mayagüez

Abstract. I present preliminary evidence that intermediate-sized (~15 cm long) fish mesograzers, principally parrotfish (scarids), play a critical role in controlling the species composition of coral reefs. I describe these mesograzers as gatekeepers because they control the entry of small (newly recruited) prey individuals into coral reef communities. The gatekeeper role of fish mesograzers is based on several well-recognized features of coral reefs: (1) Fish grazing has a major impact on abundances of benthic organisms; (2) Many species have a refuge in size from grazers; and (3) Artificial substrates in offshore habitats lacking fish mesograzers are often characterized by 'fouling' species that are absent in coral reefs. I hypothesize that only small individuals of fouling (and other) species are vulnerable to fish grazers because large prey individuals are protected by structural/chemical defenses. Because of their role as gatekeepers, the reduction of fish mesograzer populations by overfishing may have profound effects on the structure of coral reef communities.

Keywords: Gatekeeper, fish mesograzers, refuge in size, structural/chemical defenses

Introduction

In this report I propose that intermediate-sized (~15 cm long) fish mesograzers have a major impact on the structure of coral reef communities by feeding on small prey individuals. I describe fish mesograzers, principally parrotfish (scarids) and possibly surgeonfish (acanthurids) and other fish taxa, as 'gatekeepers' in the sense that they control the 'entry' (survival) of newly recruited prey into coral reef communities. This hypothesis is based on several well-recognized features of coral reefs.

First, numerous studies spanning several decades (e.g. Randall 1961; Valentine et al. 2007) have demonstrated that fish grazers can control abundances of prey species. In general, previous studies have focused on herbivory by fish grazers. For instance, Randall (1965) attributed the 'halos' surrounding Caribbean reefs largely to parrotfish grazing on seagrasses. Hay (1981) found that algal species such as *Botryocadia occidentalis* and *Spyridia aculeata* are excluded from Caribbean reefs by fish grazers. Hixon and Brostoff (1996) documented the effects of fish grazing on the succession of algal species. With some exceptions (Choat et al. 2004), parrotfish grazing on invertebrates have been largely ignored except for the direct effects on corals (e.g. Rotjan and Lewis 2006) or indirect effects involving overgrowth of corals by algae (e.g. Mumby et al. 2006).

Second, it is well known that many coral reef species possess a 'refuge in size' (Dayton 1971) from

grazers and predators (Hughes and Connell 1987) due to structural and chemical defenses (Jackson and Buss 1975; Harvell and Fenical 1989). However, structural and chemical defenses may be ineffective against grazers when prey individuals are small and inconspicuous. Because macrograzers (large grazers) feed on larger prey (e.g. Bellwood et al. 2006), prey species with structural/chemical defenses may be grazed upon by mesograzers but not macrograzers.

Third, artificial substrates (buoy lines, mariculture cages etc.) are often heavily colonized by so-called fouling species, such as the octocoral *Carijoa (Telesto) riisei*, that are rare or absent in coral reefs (Humann 1993). Sutherland (1974) and others have previously demonstrated that fish grazing influences the structure of the fouling community on artificial substrates in marine systems. Thus, the presence of a coral reef fouling community suggests that fish grazing has a major impact on coral reef systems.

In this report I present preliminary evidence supporting the contention that the gatekeeper role of fish mesograzers structures coral reef communities. I focus on invertebrate fouling species to exemplify the effects of fish mesograzers. I also present results of pilot experiments that indicate small individuals of such species are especially vulnerable to fish mesograzers because they do not benefit from a refuge in size.

Methods and Results

This study was largely instigated by casual observations that the invertebrate epibiota on buoy lines used to locate benthic transects in nearshore, midshelf and shelf edge coral reefs off the southwest coast of Puerto Rico (18° N, 67° W) differed from species occurring on the reefs themselves. To confirm these impressions we surveyed the invertebrates on the buoy lines. Sessile invertebrates found on the buoy lines are listed in Table 1. Several species as the octocoral *Carijoa (Telesto) riisei*, the tunicate *Ascidea nigra*, and the anemone *Aiptasia tagetes* are regarded as coral reef fouling species, and are generally restricted to artificial substrates in coral reef habitats. Other species as the sponge *Dysidea janiae* and the wing oyster *Pteria colymbus* occur frequently in reefs but were more abundant on the buoy lines.

Table 1. Sessile invertebrate species found on buoy lines in nearshore, midshelf and shelf edge reefs near La Parguera, Puerto Rico. * generally absent in reef habitats.

SPONGES	
	<i>Desmapsamma anchorata</i>
	<i>Dysidea janiae</i>
	<i>Monanchora barbadensis(?)</i>
	<i>Mycale laevis</i>
	<i>Mycale microsigmatosa</i>
	<i>Tedania ignis</i>
CNIDARIANS	
	<i>Aiptasia tagetes*</i>
	<i>Carijoa riisei*</i>
	<i>Halocordyle disticha</i>
MOLLUSCS	
	<i>Pinctada radiata</i>
	<i>Pteria colymbus</i>
	<i>Dendrosta frons</i>
TUNICATES	
	<i>Ascidea nigra*</i>
	<i>Botrylloides nigrum</i>
	<i>Didemnum sp</i>
	<i>Polycarpa spongiabilis</i>
	<i>Symplegma viride(?)</i>

Vertical patterns of distribution indicated that fish grazing was responsible for the presence and abundance of the epibiotic species occurring on the buoy lines. At the nearshore and midshelf reefs, only portions of buoy lines more than ~1.5 m above the substratum were colonized by sessile organisms. In contrast, epibiotic cover was low on all portions of the buoy lines at the shelf edge reefs. These vertical patterns coincided with the distribution of fish grazers. The black durgon, *Melichthys niger*, was

restricted to the shelf edge reefs, and was observed feeding throughout the water column. Alternatively, parrotfish mesograzers, principally the redband parrotfish *Sparisoma aurofrenatum*, striped parrotfish *Scarus croicensis* and stoplight parrotfish *Sparisoma viride* occurred at all sites but always remained close to the bottom presumably because of the cover provided from piscivores.

As pilot experiments to test whether fish grazers were responsible for the vertical patterns of the epibiota, we lowered the upper portions of buoy lines to within about a meter of the bottom at two midshelf reefs. Almost immediately, parrotfish, wrasses, surgeonfish and butterfly fish began grazing on the buoy lines (Fig 1a). After about a week, abundances of most epibiota, especially algae, were severely reduced on the lowered portions of the buoy lines except for a colony of the sponge *Dysidea* (Fig. 1b). *Dysidea* is evidently defended chemically because a redband parrotfish *Sparisoma aurofrenatum* spit out *Dysidea* fragments soon after grazing it (Fig 1c). Hay (1991) noted that parrotfish often taste an unfamiliar item before rejecting it. Interestingly, *Sparisoma aurofrenatum* and other Caribbean parrotfish mesograzers are generally regarded as herbivores (e.g. Bruggemann et al. 1994) based on gut contents (e.g. Randall 1967). These observations indicate that various invertebrate species may be grazed upon, but not ingested, by meso-sized parrotfish. Thus, these parrotfish are probably more appropriately regarded as omnivores rather than herbivores in terms of their grazing activities.

An analogous situation with *Dysidea* occurred with a *Carijoa* colony on another lowered buoy line (Fig. 2). These results indicate that the *Dysidea* and *Carijoa* colonies had reached a refuge in size from grazers. By extension, other species occurring on the buoy lines may also benefit from a refuge in size from fish grazers.

Discussion

The maximum time that the buoy lines were on the reefs was about 3 years. This raises the alternative interpretation that the species observed in this study simply represent the initial colonizing stages of species succession, which over time will develop into a climax community dominated by scleractinian corals and other taxa. However, species such as *Carijoa* have not colonized reefs in the study area following hurricanes (Yoshioka and Yoshioka 1987) or other disturbances (pers. obs.). Additional considerations indicate that the short time span of this study is not necessarily the critical factor. For example scleractinian corals are absent on >40 year-old pier pilings locate in a sand plain habitat near Aguadilla, Puerto Rico where fish mesograzers are

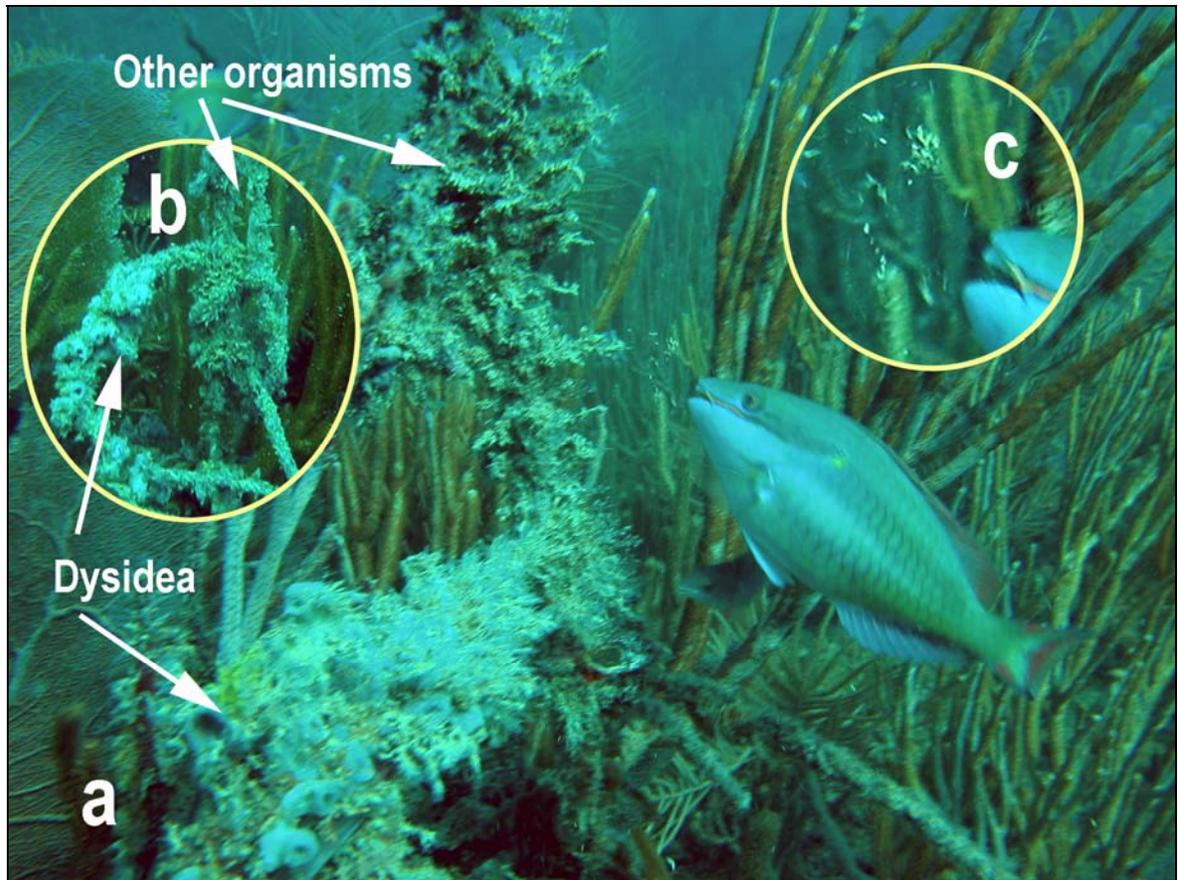


Figure 1. Fish grazing on a lowered buoy line. (a) Grazing by a redband parrotfish (*Sparisoma aurofrenatum*). (b) A *Dysidea janiae* sponge colony and other biota a week later. (c) The *S. aurofrenatum* rejecting fragments of the *Dysidea* colony.

absent (pers. obs.). Alternatively scleractinians are relatively abundant on 30 year-old metal bars in a shelf edge reef site in the study area where fish mesograzers are abundant (pers. obs.). These observations concur with the Inhibition Model of succession (Connell and Slayter 1977) wherein grazing may alter the course of succession.

With respect to terms used to describe ecologically important species, gatekeepers can be viewed as a modification of the keystone species concept emphasizing prey size. Paine (1966) introduced the keystone species concept with the starfish *Pisaster ochraceus*, which controls 'post entry' abundances of the mussel *Mytilus californianus* by feeding on large (mature) individuals. In contrast gatekeepers prevent the 'entry' of prey populations into communities by feeding on small (newly settled) individuals. The emphasis on prey size is especially important if prey individuals enjoy an escape in size from grazers and predators. Paine (1976) recognized the importance of prey size by demonstrating that some *Mytilus* may grow too large for consumption by *Pisaster*.

In terms of fundamental issues in population dynamics, the gatekeeper scenario is consistent with

results indicating that mortality during the early benthic life stage may be the key factor controlling variations in abundances of coral reef organisms (e.g. Yoshioka 1997). Because newly recruited prey individuals are small, the biomass of such individuals is a poor indicator of the ability of gatekeepers to control prey populations. Mumby et al. (2006) concluded that large parrotfish are more effective than meso-sized parrotfish in controlling macroalgae because of the disproportionately greater amount of biomass consumed. The gatekeeper scenario presents the alternative argument that grazing by meso-sized parrotfish may be more effective in controlling macroalgae by grazing on large numbers of small plants.

To my knowledge the gatekeeper role of fish mesograzers has received little attention in coral reef systems. In contrast, gatekeeper effects are relatively well documented in terrestrial systems. Tansley and Adamson (1925) showed that grazing by rabbits prevents the entry of shrubs and trees in grasslands of England. Ripple and Beschta (2008) demonstrated that deer grazing has prevented the successful recruitment of black oak trees for over 80 years in



Figure 2. A *Carijoa riisei* colony on a lowered buoy line. (a) Before gatekeeper grazing. (b) A week after gatekeeper grazing.

some areas of Yosemite Park. The gatekeeper scenario is reminiscent of the hypotheses of Janzen (1970) and Connell (1971) that grazing on seeds or seedlings in the vicinity of parent trees is a major factor in the maintenance of biodiversity in tropical rain forests. However, Janzen (1970) and Connell (1971) emphasize the species-specific preferences of grazers. In contrast the gatekeeper scenario proposed for coral reefs emphasizes nonselective grazing by fish mesograzers. Because the effects on nonselective grazing are more widely distributed among many prey species, relatively high levels of nonselective grazing are probably required for equivalent effects on a given prey species compared to selective grazing. This is evidently the case. Randall (1961) concluded that fish can 'overgraze' reefs, as exemplified by bare sand halos surrounding patch reefs (Randall 1965). Hay (1991) asserted that fish grazing on coral reefs equals or exceeds grazing rates for any other marine or terrestrial system. Fox and Bellwood (2008) estimated that the parrotfish *Scarus rivulatus* grazes >50% of the reef substratum on a monthly basis.

It must be emphasized that the gatekeeper scenario outlined in this report is a simplified overview of the role of fish mesograzers in coral reef systems. Many species-specific features of grazer and prey species merit attention. For example, depending upon the species involved, there is probably a sequential series of refuges in sizes from grazers (Paine 1976) rather than a single threshold in size. Assuming that structural/chemical defenses are equally effective against grazers, faster growing prey species may reach a refuge in size more quickly. Alternatively, faster growth may occur at a cost of allocating less

metabolic resources to structural and chemical defenses (Paine 1977). Gatekeeper effects are probably also contingent on prey morphology. Grazing is more likely to be fatal for solitary compared to colonial organisms since damage often results in 'partial mortality' of the latter and 'complete mortality' for the former (e.g. Harvell and Suchanek 1987). Hay's (1991) observation that parrotfish taste defended prey before rejecting it is noteworthy in this regard because such taste tests may be fatal for solitary, but not colonial, organisms. Also, encrusting forms are less vulnerable than erect forms because substrate scraping by fish mesograzers is more likely to remove erect organisms. Similarly, multi-stemmed erect organisms are less vulnerable than single stemmed individuals.

Finally, I stress that, in addition to grazer-prey interactions, the gatekeeper scenario outlined herein also overlooks grazing by invertebrates and competition among prey species. Anthropogenic influences cannot be ignored because the tendency of 'fishing down the food chain' (Pauly et al. 1998) may severely reduce fish mesograzer abundances in many areas. Because the direct and indirect effects of gatekeeper grazing are largely unknown, the over harvesting of fish mesograzers may result in unforeseen and profound changes in the structure of coral reef systems.

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