Stability of Benthic Coral Reef Communities: Top-down Herbivory Control *versus* Bottom-up Eutrophication

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ABSTRACT

Anthropogenic activities, including pollution and overfishing, threaten the equilibrium of the coral reef ecosystems, which often lead to a shift from coral dominated to macroalgae dominated benthic communities. Several reef sites of Guadeloupe Island (FWI) have been studied in order to estimate the effects of the algal growth boosted by nutrients in eutrophic waters (bottom-up) and of the control exercised by herbivorous fishes (top-down) on the stability of coral communities. Herbivorous fishes were counted on seven reef sites differing by their exposure to coastal sources of nutrients and by their protection status. Sixteen environmental variables were measured. The coverage rate of the bottom by benthic organisms was established and the algal consumption by herbivorous fishes was evaluated.

Analysis of the results showed that reef zones subjected to anthropogenic influence were characterized by high levels of nitrates, phosphates and matters in suspension. In these areas, algal productivity was high and benthic communities were dominated by macroalgae. An exception was constituted by the reef flat of the barrier reef of the Grand Cul-de-Sac Marin, located in a marine protected area (MPA): macroalgae occupied less than 3 %of the bottom, although the nutrient level was important there. In this non-protected zone, herbivores were numerically abundant with a high biomass. Results concerning the herbivory pressure showed that in the MPA the fishes were able to consume the whole algal production. In fished areas, herbivorous fishes were of small size and could not regulate the algal growth enhanced by the nutrient enrichment of the waters.

KEY WORDS: Coral reefs, eutrophication, herbivorous fishes

Estabilidad de las Comunidades Bentónicas Arrecifales: El Control por los Herbívoros ("Top-down") *versus* la Eutroficacion de las Aguas Costeras ("Bottom-up")

Las actividades antropogénicas, incluyendo la polución y la sobre explotación de los recursos marinos, afectan severamente los ecosistemas arrecífales y conducen a menudo a una substitución progresiva de las poblaciones coralinas por comunidades de algas. Un estudio fue realizado sobre arrecifes de Guadalupe (Antillas francesas) para estudiar la influencia del crecimiento de las algas (efecto " bottom-up ") y de su regulación por los peces herbívoros (efecto "top-down") sobre la estabilidad de las comunidades bentónicas. Se realizaron censos de peces herbívoros sobre 7 arrecifes diferentes por su exposición a los nutrimentos de origen costero y por su estatus de protección en cuanto a la pesca. Se midieron dieciséis variables ambientales. Se estableció el recubrimiento del fondo por los organismos bentónicos y se estimó también el consumo de algas por los peces herbívoros.

El análisis de los resultados muestra que las zonas arrecifales más contaminadas están sometidas a tasas elevadas de nitratos, fosfatos y materias en suspensión. En estas zonas, la productividad de algas es elevada y las comunidades bentónicas están dominadas por macroalgas. La meseta de la barrera arrecífal del Grand Cul-de-Sac Marin, situada en una reserva marina, constituye una excepción donde las macroalgas representan menos del 3% de recubrimiento del fondo, aunque la concentración en nutrimentos sea elevada. El estatus de protección de esta zona hace que los peces herbívoros sean abundantes con biomasas elevadas. El estudio de su consumo de algas muestra que, en la reserva, los peces controlan la producción de algas del arrecife, mientras que en las zonas pescadas, los peces, de pequeña talla, no son capaces de regular el crecimiento de algas favorecido por la eutroficacion de las aguas.

PALABRAS CLAVES: Arrecifes coralinos, eutroficacion, peces herbívoros

Stabilite des Communautes Benthques Recifales: Le Contrôle par las Herbivores (« Top-down ») *versus* L'eutrophisation des Eaux Cotieres (« Bottom-up »)

Les activités anthropiques, incluant la pollution et la surexploitation des ressources, affectent sévèrement les écosystèmes récifaux et conduit souvent à un remplacement progressif des peuplements coralliens par des communautés algales. Une étude a été réalisée sur plusieurs récifs de Guadeloupe (Antilles françaises) afin d'étudier l'influence de la croissance algale (effet « bottom-up ») et de sa régulation par les poissons herbivores (effet « top-down») sur la stabilité des peuplements benthiques récifaux. Des comptages de poissons herbivores ont été réalisés sur 7 récifs qui différent par leur exposition aux nutriants d'origine côtière et par leur statut de protection vis-à-vis de la pêche. Seize variables environnementales ont été mesurées. Le recouvrement des fonds par les différents organismes benthiques a été établi. Enfin, la consommation en algues par les poissons herbivores a été évaluée. L'analyse des résultats montre que les zones récifales les plus anthropisées sont soumises à des taux élevés de nitrates, de phosphates et de matières en suspension. La productivité algale y est élevée et les peuplements benthiques dominés par des macroalgues. Le platier de la barrière récifale du Grand Cul-de-Sac Marin, situé dans une réserve marine, constitue une exception dans la mesure où les macroalgues représentent moins de 3% de recouvrement des fonds, bien que la concentration en nutriants soit élevée. Le statut de protection de cette zone fait que les poissons herbivores y sont abondants avec des biomasses élevées. L'étude de la consommation des algues par ces herbivores montre que, dans la réserve, les poissons contrôlent la production algale du récif, alors que dans les zones pêchées, les poissons, de petite taille, ne sont pas capables de réguler la croissance algale favorisée par l'eutrophisation des eaux.

MOTS CLÉS: Récifs coralliens, Caraïbe, Poissons herbivores, habitat

INTRODUCTION

Coral reefs are among the most productive communities in the world. The low algal biomass on coral reefs suggests a rapid growth and high turnover rates of primary producers. The algal turf communities are the major producers on coral reefs (Carpenter 1985), and their growth is nutrient limited on the oligotrophic coral reef waters (Lapointe 1997, Lapointe *et al.* 2004). Nowadays, the increase of coastal pollution lead to a surge of nutrient overloads, allowing an overproduction of algae and destabilizing the competition relationship between corals and algae (Koop *et al.* 2001, Thacker *et al.* 2001, McClanahan *et al.* 2005). At an increasing rate, scleractinian coral-dominated systems are supplanted by macroalgae-dominated ones, the latter being favoured by eutrophication (Miller *et al.* 1999, Costa Jr. *et al.* 2000, Smith *et al.* 2001, Fabricius *et al.* 2005). Additionally to eutrophication, the reduction of herbivores is one of the major threats to coral reefs. On coral reefs, herbivorous organisms consume a large part of algal productivity (Hatcher 1981, Carpenter 1986, Paddack *et al.* 2006). Through their role in algal removal, these herbivores are essential for coral reef recovery towards coral dominated states (Mumby *et al.* 2006). However, the increasing catch of herbivorous fishes has resulted in depletion of grazing pressure and by cascade, increased proliferation of algae (Jackson *et al.* 2001, Mumby 2006).

The concepts of "top-down" and "bottom-up" have been used to understand what occurs actually on coral reefs (Littler *et al.* 2006). Indeed the abundance of macroalgae on coral reefs is controlled by complex interactions of the bottom-up control such as nutrient levels and top-down control such as grazing by herbivorous organisms. Understanding the processes of bottom-up and top-down conjointly is critical to the elucidation of mechanisms that regulate the algal-herbivore balance.

For that purpose, herbivorous fish assemblages and nutrient concentrations were compared across several coral reefs, either protected from fishing or not, located around the Caribbean island of Guadeloupe. The production of algae and the algal consumption by herbivorous fishes were compared, as well as the macroalgal cover observed inside and outside protected areas in order to know whether the top-down effects by herbivores can be cancelled by the bottom-up influence by nutrients.

MATERIALS AND METHODS

Study Area

Guadeloupe is located in the Eastern Caribbean Sea (16°15′N, 61°35′W) and is composed of two islands, Basse-Terre and Grande-Terre (Figure 1) separated by a narrow sea channel called Rivière Salée. Marine protected areas in Guadeloupe are: Ilets Pigeon (400 ha) and the Grand Cul-de-Sac Marin Bay (2135 ha) in the north of the island. Three zones were chosen inside marine protected areas (S1 to S3) (Figure 1). Four non-protected reefs sites (S4 to S7) were studied (Figure 1).

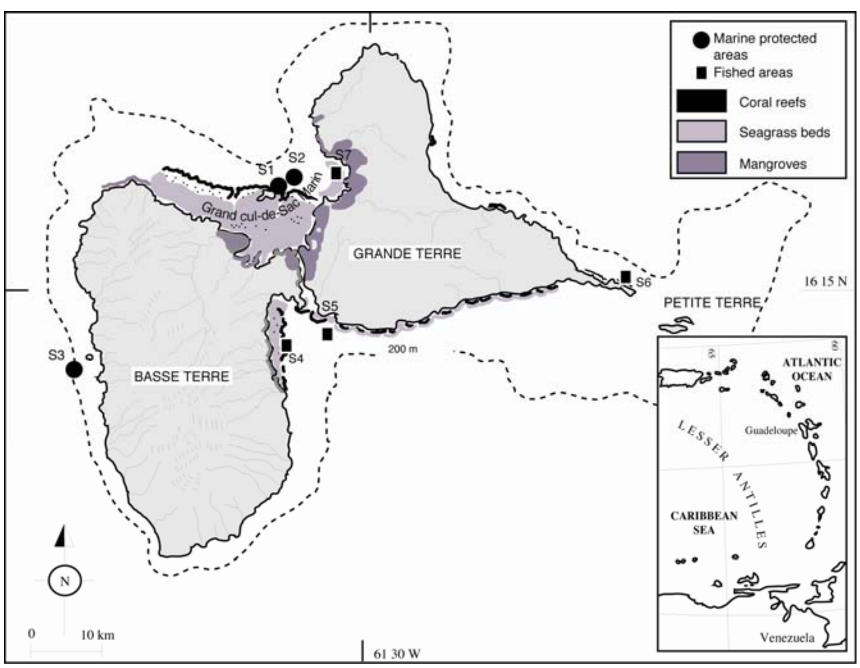

Figure 1. Map of the study area and location of the sampling sites.

Fish Surveys

Estimations of fish density were obtained by visual surveys from 300 m x 2 m band-transects. All species of Scaridae and Acanthuridae present on the band-transects were identified, counted and their size estimated. Fish biomass was then estimated using the median value of each class and weight-length relationships (WLR) available in the literature.

Survey of Benthic Communities

Simultaneously with all fish surveys, the benthic community composition was estimated on each transect (in percentage) by noting the nature of benthic organisms at point intercepts distributed every meter along a 150 meter long transect (Liddell and Ohlhorst 1987). The recorded benthic categories were: Cyanobacteria, algal turf, soft Chlorophyta, calcareous Chlorophyta, Phaeophyta, Rhodophyta, encrusting crustose coralline algae, seagrasses, sponges, gorgonians, corals, actinarians, zoanthids and tunicates.

Algal Consumption

The method used to determine the algal consumption by herbivorous fishes consisted in building a curvilinear regression between the mass of dry organic matter found in the digestive tracts and the fish biomass. Data were available for all species except for *Scarus taeniopterus* and *S. vetula*, as they lived mainly in marine protected areas and could not be captured. These species were assimilated to *S. iserti* and *Sparisoma rubripinne* respectively for they have similar morphologies. The equation of the regression curve allowed calculating the quantity of algae ingested by the fishes according to their biomass (determined with WLR). The daily algal consumption was evaluated taking into account the data of Bardach (1961) who considered that guts are filled thrice daily. This method allowed obtaining a global algal consumption estimation using simultaneously fish density on the reefs and algal consumption per species.

Nutrient Analyses

Water samples were collected every time fish and benthic surveys were realized. The water samples were collected in 500 mL bottles and analyzed for suspended solids, nitrate and soluble phosphates using the cadmium reduction for nitrate and ascorbic acid methods for phosphorus.

Estimation of the Algal Production

The measurements of algal production were carried out in each site. For that purpose, floating plastic ribbons were settled on the bottom. Every month, plastic ribbons were collected from the reef. Back to the laboratory, the algal turf was scrapped from the (known) surface of each ribbon and dried at 80°C until constant weight. Algal turf production was so estimated by dry weight per surface and per month.

Statistical Analyses

i) Principal component analysis (PCA) was used to determine the major patterns of variation within the environmental data.
ii) Cluster analyses were undertaken on the same dataset (Ward's hierarchical cluster analyses) and results of these cluster analyses were superimposed onto the plot of the first two components of the preceding PCA.
iii) Student's t-tests were used to determine if there was a significant difference between the different reef zones in terms of environmental variables.
iv) The Kruskal-Wallis one-way analysis of variance was used to compare the algal consumption between sites.

Whenever a difference was found, multiple pairwise comparison tests were used to go further in the analyses.

RESULTS

Description of the Studied Sites

A correlation biplot of the principal component analysis (PCA) of the environmental variables is shown on Figure 2 with (A): the projection of the sites and (B) the environmental variables. The first two principal components account for 47.3% of the total variance and reflect the main patterns of variations in the environmental data. Results revealed that there was an opposition between degraded reef flats on the one hand and healthy coral reefs on the other hand. The classification as well as the projection of the variables in the first factorial plan confirms these results. On non-protected reefs, high concentration of nitrates, phosphates, and suspended organic matter were noted. The algal production was high and the benthic cover was characterized by the dominance of macrophytes (Chlorophyta, Phaeophyta, Rhodophyta and CCA). These variables are opposed to the sites with high coral cover corresponding mainly to Marine Protected Areas.

As this study focuses on the influence of bottom-up control via nutrient enrichment, we will now focus on the degraded reefs sites that harbour high nutrient and suspended organic matter concentrations. In this group, all the reef sites are reef flats. Among this group, one site is located inside MPA (S1) whereas all the others are non-protected reefs. We will try to understand why this site appeared in this group rather than in the MPA group.

Focus on the Degraded Group of Coral Reef Sites

Nutrients — Fajou island harbour high values of nitrates concentration as well as a high suspended organic matter (SOM) concentration (respectively 0.42 mmol/L and 20.6 g/L). The concentration of phosphates was under the detection limit.

Concerning the nitrate concentration, in the group of degraded reef sites, the mean value (± S.E.) was 0.155 ± 0.054 mmol/L. Inside MPA, the mean nitrate concentration was 0.034 ± 0.021 mmol/L. The difference was significant (*p-value* = 0.032).

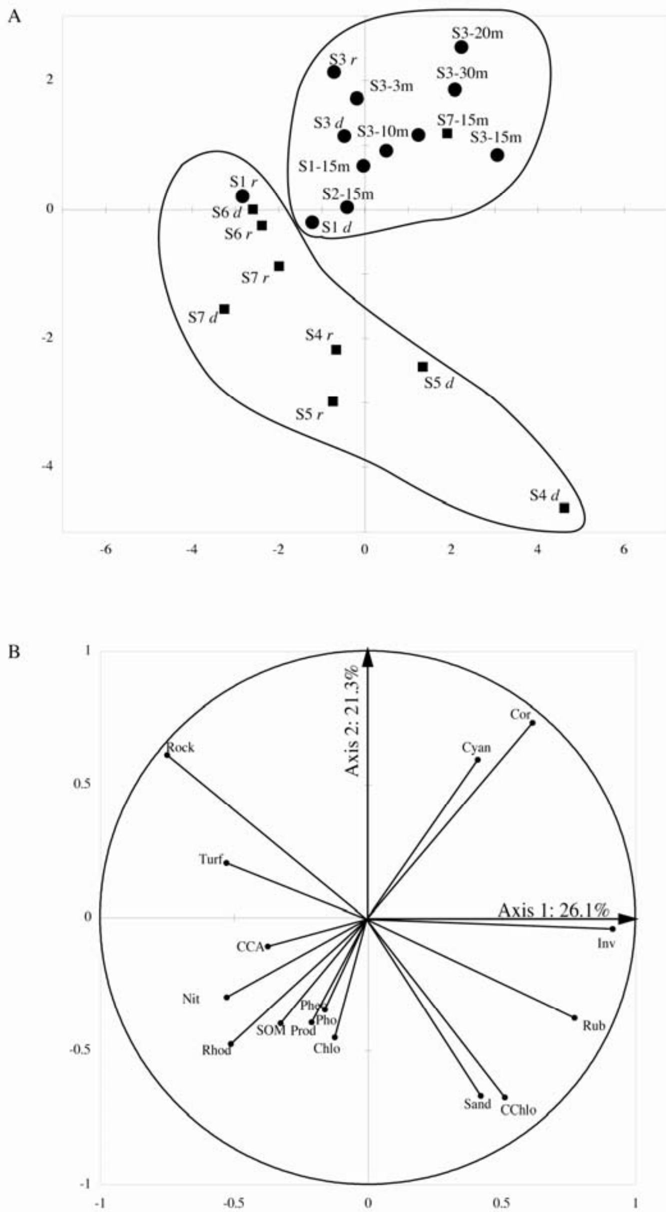

Figure 2. PCA on environmental data with A: projection of the site and B: projection of the environmental variables with *d*: dry season and *r*: rain season, l: MPA,<: non-MPA, Turf: algal turf, Cyan: cyanobacteria, Chlo: soft Chlorophyta, CChlo: calcareous Chlorophyta, Phae: Phaeophyta, Rhod: Rhodophyta, CCA: encrusting crustose coralline algae, Cor: Corals, Inv: Invertebrates, Rock: rock, Rub: coral rubble, Sand: sand, Nit: nitrate, Pho: phosphate, SOM: suspended organic matter, Prod: the algal production.

The mean concentration of SOM inside this group was 16.1 ± 4.9 g/L whereas it was 7.4 ± 1.5 g/L inside the MPA group. The difference between the two groups was close to be significant at the 5% level (*p- value* = 0.074).

Algal production — The algal production varied between 0.1 and 1.5 g/m^2/day among the degraded reefs group. The site located inside the MPA of Fajou (S1) had a production of 0.9 g/m^2/day. The mean value of production inside the degraded reef group was 0.84 ± 0.15 g/m^2/day, whereas it was 0.56 ± 0.16 g/m^2/day inside the MPA group.

Macroalgal cover — The macroalgal cover on Fajou reef flat was 3.6 ± 0.6% whereas it varied between 27.2 and 57.3% on the other reef flats, with a mean of 33.9 ± 5.1%. On protected reefs, the mean macroalgal cover was 15.2 ± 3.6%. The difference between the two groups was significant (p-value = 0.006).

Fish assemblage and algal consumption — The algal consumption was evaluated on the different reef sites whatever the season. A Kruskall-Wallis test showed that algal consumption is significantly different among the different reef flats (p-value = 0.04). A multiple pairwise comparison test revealed that this difference was due to site S1, which presents a high level of algal consumption (2.8 g/m^2/day) compared to S5, S6 and S7 where the consumption values were low (respectively 0.4; 0.7 and 1 g/m^2/day). Algal consumption was more important in S1 as herbivorous fishes were well represented in biomass and were of bigger size.

DISCUSSION

The results of the present study have enhanced the role of nutrients (nitrate, phosphates, and suspended organic matter) on the algal populations of the studied sites. The study focusing on several reef sites spatially distributed, allowed to compare the algal production on different reef sites and the nitrogen, phosphates and suspended organic matter concentration. Results showed that on the reefs sites were the nutrients and the suspended organic matter concentrations were high, the algal cover of Phaeophyta and Rhodophyta was high and that these sites presented the highest algal production rate.

The influence of nutrients on benthic communities has already been pointed out by some authors (i.e. Koop *et al*. 2001, Lapointe *et al*. 2004, McClanahan *et al*. 2005). In particular, Fabricius *et al*. (2005) demonstrated that in Australia, the high nutrient concentration led to an increase in the cover of Rhodophyta and Chlorophyta whereas coral cover decreased. Indeed, as noted by Littler and Littler (1988), nitrates and phosphates are thought to be the nutrients most often limiting tropical marine algal growth rates, and when the waters are eutrophic, it favours large population of frondose macroalgae that can ultimately overgrow. However, for Boyer *et al*. (2004), intact populations of herbivores are able to compensate the increase of nutrient on coral reefs by grazing algae, even if they growth faster with the organic matter inputs and nutrients. Littler *et al.* 2006 agree with this assertion. On Belize coral reefs, where herbivores are numerous, macroalgae development is low, although nutrient concentrations are high. On the other hand, the high nutrient concentrations enhance the growth of frondose macroalgae in areas of scarce herbivores. That was the case for the present study. Inside MPA, even if the nutrient concentration was high, herbivorous fish manage to regulate algal growth as they present high density, biomass, and large individuals.

In conclusion, the present study highlighted how hard it is to know whether, bottom-up or top-down factors exert the most intensive control on coral reefs because the environmental conditions are different on each coral reef, even in the same island. Any factor that contributes to an imbalance between the production and the consumption of algae will result in a coral community structure change (Szmant 2002).

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