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Parrotfish grazing on coral reefs

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Document Version

Publisher's PDF, also known as Version of record

Publication date:

1995

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Bruggemann, J. H. (1995). *Parrotfish grazing on coral reefs: A trophic novelty*. s.n.

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Abstract

1. Parrotfish (family Scaridae) are grazers that are restricted to shallow tropical marine environments, and form an important component of the herbivore assemblage on Caribbean and Indo-Pacific coral reefs. Most scarid species have fused jaw teeth with which they scrape off algae that grow on and in dead coral substrates. Along with their food, a lot of limestone is ingested. The ingested material is ground with the powerful pharyngeal mill, and processed rapidly in a digestive tract without an acidic stomach. The lack of quantitative data on the feeding ecology of these herbivores inspired a detailed study of the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*. The study was performed at the leeward fringing reef of Bonaire, Netherlands Antilles.

2. This study aimed a) to determine what food resources are consumed by these parrotfish in different reef zones; b) to quantify the amount of nutrients and energy ingested and assimilated by these fish, as well as their allocation to growth and reproduction; c) to estimate the proportion of the daily algal production that is consumed directly by herbivores; and d) to evaluate the effect of parrotfish grazing on the structure and functioning of coral reefs.

3. The two parrotfish species show similar foraging preferences. Preferred food items are turf algae growing on substrates infested with boring (endolithic) algae. Crustose corallines tend to be avoided. Foraging preferences are related to yield, i.e. the amount of biomass, protein and energy that can be harvested per bite. Higher yields are effected by a) higher biomass of turfs growing on substrates with endolithic algae compared to turfs growing on crustose corallines; b) higher protein and energy content in endolithic algae than in crustose corallines; and c) substrates infested with boring algae having a lower density and allowing *Sparisoma viride* to excavate larger amounts of substrate bound algae than from substrates covered with crustose corallines.

4. Foraging behaviour differs between the two species, which results in a certain degree of resource partitioning between these sympatric grazers. Slightly different portions of the primary production are harvested. *Scarus vetula* employs a scraping feeding mode by which mainly epilithic algal turfs are ingested. In contrast, *Sparisoma viride* feeds by excavating the substrate, and derives a large part of its food from endolithic algae and crustose corallines. The scraper selects for substrates with a smooth surface, whereas the excavator prefers to graze on concave and rugose surfaces and on substrates of low skeletal density. These differences in substrate preference result in some spatial segregation on the level of individual bites and substrate types.

5. Food intake per bite, which was determined experimentally using natural dead coral substrates with associated algae, increases linearly with fish body mass and algal standing crop. For the excavator, *Sparisoma viride*, food intake per bite is further determined by the skeletal density of the grazed substrate: low-density substrates (e.g. dead *Montastrea annularis* colonies), that predominate on the deeper reef, enable this species to ingest higher amount of algal biomass than from high-density substrates (e.g. dead *Acropora cervicornis* and *A. palmata* colonies), that predominate on the shallow reef. For the scraper, *Scarus vetula*, food intake per bite was much lower than for the excavator. However, in spite of differences in feeding mode and food intake per bite, the daily amounts of assimilated nutrients and energy are similar for both species, resulting from higher feeding rates and higher assimilation efficiency in *S. vetula*.

6. Food quality is very poor. The material ingested by *Sparisoma viride* contains ca 0.4 to 2.5 % protein, and ca 0.9 to 4.2 KJ g⁻¹ dry mass. In spite of exploiting low quality food resources, growth rates of *S. viride* equal that of other herbivorous and carnivorous fish. Growth rates are flexible and depend on size, reproductive activity and season. Highest growth rates were found for juveniles and non-territorial males that do not partake in reproduction. Lower growth rates of initial phase fish (females) and territorial males are directly linked to increased energy investment in gamete production and territorial defense. Sex change in these protogynous fish can occur over a wide size range. Initial phase fish that change sex and become non-territorial males, trade-off current reproductive output for growth, in order to reach a size at which they can compete for the status of territorial male and have a higher reproductive output.

7. *Scarus vetula* and *Sparisoma viride* are important bioeroders on the reef. Their distribution over different reef zones determines the rate of bioerosion on a large spatial scale. Highest bioerosional rates occur on the shallow reef (ca 7 kg m⁻² y⁻¹), and decrease with depth. Parrotfish foraging preferences and the effects of food type and substrate skeletal density on bite size result in large differences in bioerosional rate on a small spatial scale. Substrates infested with boring algae and of low skeletal density are eroded fastest, while substrates covered with crustose coralline algae are partly protected from grazing bioerosion. On the shallow reef zone, where cover of living coral is presently very low, the rate of bioerosion exceeds carbonate accretion by corals and crustose corallines. On the deeper reef parts, carbonate accretion exceeds removal by grazing parrotfish, resulting from the lower densities of fish and the higher cover of reef building corals.

8. Quantitative comparison of primary production and consumption demonstrated that all algal production is consumed directly, mainly by fish. Scarids, and notably *Scarus vetula* and *Sparisoma viride*, are the main primary consumers on the reef. Herbivore

standing stock is probably limited by food supply. This is indicated by the following observations: a) non-preferred food items are consumed often; b) seasonal shifts occur in habitat use between shallow and deeper reef parts, probably driven by food shortage on the shallow reef in winter; c) fluctuations in consumption of individual species and of different functional groups of consumers compensate each other; and d) total herbivore biomass did not increase any further after initial increases during 1989 to 1990. The initial increase resulted from mass-mortality of the herbivorous sea urchin *Diadema antillarum* in 1983, which was the most important herbivore before this event.

9. The composition of the herbivore assemblage changed over time. These changes followed a predictable pattern after the disturbance caused by *Diadema* mass mortality. This resulted in large increases in algal biomass from which pomacentrids and juvenile fish initially benefited. During the study period (1989 to 1992) the reef was in a later stage of succession, with the scarids as dominant herbivores. These fish are able to exploit food resources that have low biomass and low nutritional quality. They have now reduced the algal biomass to such an extent that density of pomacentrids is decreasing. Thus, competition for food resources structures the pattern of change in the herbivore assemblage.