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Research

Resource-to-consumer ratio determines the functional response of an herbivorous fish in a field experiment

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In theoretical ecology, the quantity of resource consumed by a consumer per unit of time, defined as functional response, is of paramount importance. To better understand species interactions over time it is necessary to analyze whether consumer's functional response depends on resource density alone (which is the reference assumption) or on both resource and consumer densities. There are few field studies that, by varying the resource and consumer densities, provide solid empirical evidence to indicate the most suitable model of functional response in complex systems, such as coral reefs. We performed a field experiment with an herbivorous surgeonfish and their resource, a red seaweed, in a near-pristine reef ecosystem. We measured algal consumption while varying densities of consumers and resources. We fit nine alternative functional response models, which either included or excluded consumer-dependence. The model selection and the parameter estimation indicated that the functional response of the herbivorous surgeonfish depended on the ratio of seaweed to herbivorous fish densities. These results imply that, within a given density, surgeonfish can share resources but individual's consumption rate decrease with higher fish densities. These results also suggest that mutual intraspecific interference exists at herbivorous fish densities generally observed in the field and it should be considered in predicting consumption rates by herbivorous reef fishes. Finally, this study indicates that models incorporating consumer-dependence must be considered for understanding herbivorous fish and algae population dynamics when placed in the context of the most biodiverse ecological communities, such as reef ecosystems.

Keywords: *Acanthurus chirurgus*, Bayesian inference, *Digenea simplex*, herbivory, mutual interference, ratio-dependence, reef ecosystem, surgeonfish, Rocas Atoll

Introduction

In consumer–resource interaction theory, resource consumption is quantified by determining the average consumption rate per consumer, known as the consumer's functional response (Solomon 1949, Holling 1959b). Functional response plays an

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important role in consumer–resource interactions because it connects individual behavioral-level processes (e.g. foraging behavior) and community-level processes (e.g. consumers can only be produced from the resources they consume; Pimm 1982, Polis and Winemiller 1996). Mathematical models on functional response have been used since the 1920s (Lotka 1925, Volterra 1926), leading to many new formalizations of ecological processes, such as disease epidemics, food web dynamics and other important biological phenomena (Murray 2002, McCann 2012, Weitz 2015). How ecosystems are structured is directly linked to our ability to define which functional response model adequately captures the observed predation patterns (May 1973, Drossel et al. 2004, Kalinkat et al. 2013).

Since the 1950s, functional response models considered two main ecological factors: 1) the resource density and 2) the density of consumers (but see Turchin 2003). In resource-dependent models, functional response is assumed to be a function of resource density alone (Holling 1959a). On the other hand, consumer-dependent models are based on the assumption that mutual interference among consumers can reduce the per capita consumption rate (Leslie 1948, Park 1954). Ratio-dependent models represent a special case in which the consumption rate depends on the resource-to-consumer ratio (Arditi and Ginzburg 1989). In the last 50 years, more complex models have been proposed to account for the role of interference among consumers by mechanically defining it with further parameters (Ivlev 1961, Hassell and Varley 1969, Arditi and Akçakaya 1990). For the sake of clarity in this study functional response models with more complex dependence on resource and consumer will be termed consumer-dependent. Nowadays, both resource and consumer densities have been used to describe the consumer's functional response, in terrestrial and aquatic ecosystems (Abrams and Ginzburg 2000, Skalski and Gilliam 2001, DeLong and Vasseur 2011).

The comparative functional response approach has only been explored concerning a few herbivore–resource interactions, with no clear empirical evidence supporting either functional response form (Crawley 1997, Fortin et al. 2004, Fussmann et al. 2005). Many empirical herbivore–plant studies used experimental designs that made it impossible to detect anything other than resource dependence because the consumption experiments were carried out with a single herbivore individual (Hobbs et al. 2003, Morozov 2010, Xu et al. 2016). Therefore, a shortcoming remains over which of the two classic functional response forms represents ecosystem dynamics where herbivores interact directly or indirectly while foraging.

Marine herbivorous fishes are critical in determining the structure and dynamics of shallow reef ecosystems and play a key role in carbon and nutrient fluxes (Clements et al. 2009, Bonaldo et al. 2014, Plass-Johnson et al. 2015). Empirical evidence has indicated a negative relationship between herbivore fish per capita energy reserves (i.e. liver mass/total mass index) and total fish density, suggesting that resource availability and consumer density determine individuals' physiological condition (Tootell and Steele 2016). However, social foraging (e.g. a group formed by more than one fish individual) is indicated as a biological mechanism that increases the per capita resource intake by enhancing the ability of herbivorous fish to locate specific food items, especially when resources are either scarce or patchily distributed (Michael et al. 2013). In the southwestern Atlantic Ocean, agonistic interactions were more frequent where herbivorous fish were most abundant but there was no clear relationship between interference competition and foraging patterns (Francini-Filho et al. 2010). It is important to consider that these agonistic interactions can strongly affect the amount of algae consumed by the fish and the resulting rate at which the fish move energy and materials through the reef ecosystem (Gil and Hein 2017). Despite considerable efforts and debate seeking to disentangle how herbivores shape reef marine ecosystems (Steneck et al. 2017), few field experimental studies have quantified the role of intraspecific interactions on the herbivore fish per capita consumption rate (Lewis and Wainwright 1985, Vergés et al. 2009).

We combined field experiments and mathematical modeling to determine whether herbivorous fishes' per capita consumption rate depends on consumer, resource or both in the southwestern Atlantic Ocean's reef ecosystems. We used the herbivorous surgeonfish, *Acanthurus chirurgus* (Perciformes, Acanthuridae), and the red seaweed, *Digenea simplex* (Rhodophyta, Rhodomelaceae), as an experimental consumer–resource pair in the field and tested the alternative hypotheses that the per capita consumption rate depends on either the resource density alone or both the resource and consumer densities. We fitted nine functional response models, which either included or excluded consumer dependence, adopting a Bayesian inference approach (Ellison 2004). Our field experiment and modelling analysis suggest that the ratio of resource to consumer is likely to be an important factor influencing the effects of herbivorous fish on the structure and dynamics of reef ecosystems.

Methods

Model organisms and study location

We measured the per capita consumption rate of the surgeonfish *Acanthurus chirurgus* feeding on the red seaweed *D. simplex*, its primary diet item (Longo et al. 2015), in a tide pool in the Rocas Atoll (32°00′W–34°00′W longitude and 03°30′S–04°30′S latitude, Fig. 1). The area of the pool where the study was conducted was about 595 m^2 (70 × 8.5 m). In this pool, hardly any *Digenea simplex* was available for fish to eat, as it was mostly covered by sand (Longo et al. 2015). The surgeonfish *A. chirurgus* is a diurnal grazer that mostly feeds on algae and organic detritus found on compacted sand and rocky bottoms (Choat et al. 2002, Ferreira and Gonçalves 2006, Longo et al. 2015). Maximum movement distance of 215 m is reported for *A. chirurgus* (Chapman and Kramer 2000). Since its intense feeding activity reduces spatial

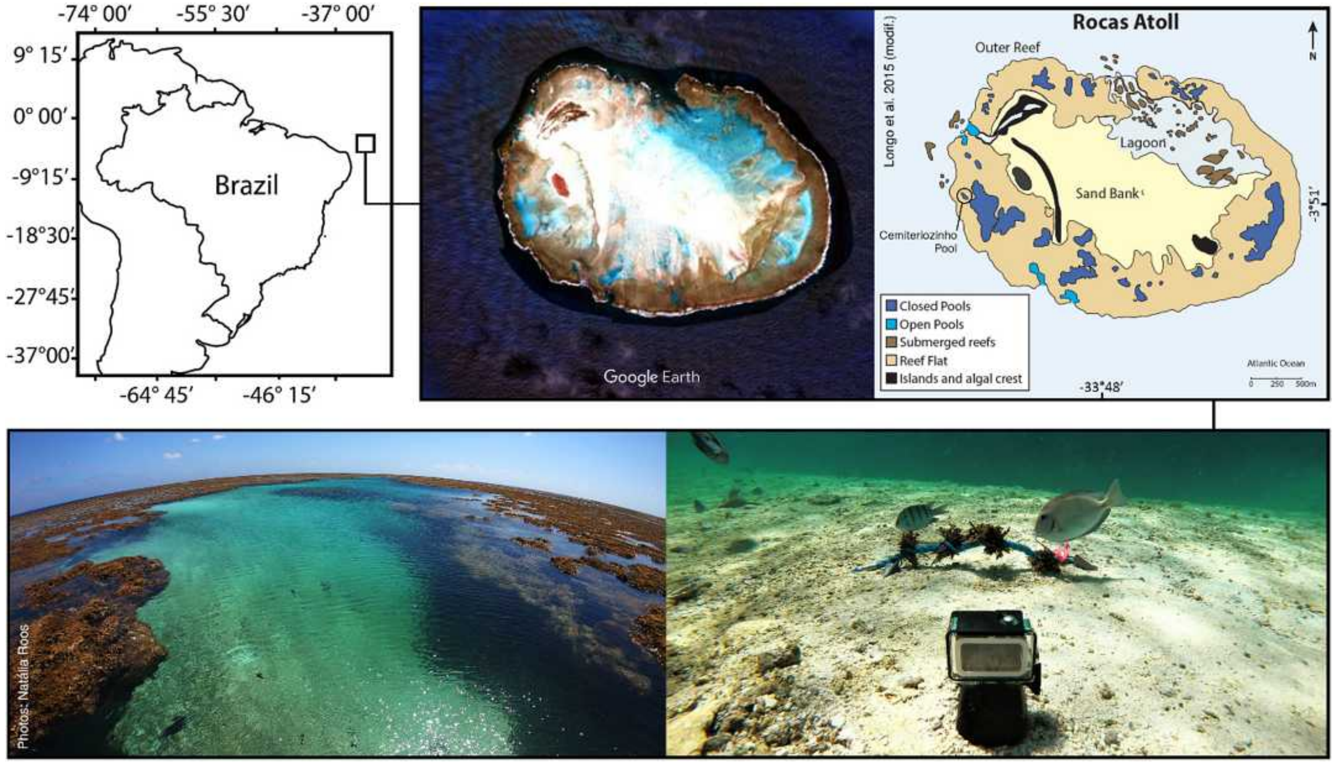

Figure 1. Study area location for the functional response underwater video experiments in the Rocas Atoll, Brazil. Top right panel: exact location of the enclosed pool 'Cemiteriozinho' where experiments were made (area = 595 m^2). Left bottom: photograph shows the emerged part of the 'Cemiteriozinho' pool. Right bottom: photograph shows the experiment setup with GoPro camera and *Acanthurus chirurgus* individual in frame. Photographs credits: Dr. Natalia Roos. Maps of the Rocas Atoll were retrieved and adapted from Google Maps and Longo et al. (2015).

competition between corals and algae, *A. chirurgus* is widely recognized as a critical functional species on reef ecosystems (Marshell and Mumby 2015, Longo et al. 2019). The red seaweed *D. simplex* is a common tropical to warm-temperate species with a disjunct distribution in the tropical to warm-temperate Atlantic and Pacific Oceans (Pakker et al. 1996). In Rocas Atoll, *D. simplex* is the most consumed seaweed by herbivorous fishes, occurring within tide pools and being more abundant in small crevices and ponds in the reef plateau that remain exposed during low tides, hindering herbivore's access (Marques et al. 2006, Longo et al. 2015). Rocas Atoll has a 7.5 km^2 of emerged area and is the only atoll formation in the southwestern Atlantic Ocean (Claudino-Sales 2019). It is considered a near-pristine reef ecosystem because it presents unique environmental and geomorphologic conditions, being the first marine protected area established in Brazil since 1979 where the only human activity allowed on site is scientific research (Amado-Filho et al. 2016). Fieldwork was conducted in May-June 2019 under the federal permit SISBIO 41327-13.

Functional response experiments

The experiments consisted in 15-min single-replicate field trials in which seaweed was offered in five different densities to a constant number of herbivorous fishes in the same tide pool (Fig. 2). Previous experiments (Marques et al. 2006, Longo et al. 2015) and personal observations from the authors demonstrate that seaweed available within these tide pools are covered in sediments that greatly reduce herbivory (Goatley and Bellwood 2012). We conducted twenty trials over four non-consecutive days (i.e. five trials per day) in the same tide pool cited above. Fish density was naturally controlled during low tides, because fishes get trapped in the tide pool with no exchange with the outer side of the Atoll ring (Longo et al. 2015). Such natural dynamic allowed us to avoid artificial manipulation of fish density (fish removal or addition), which could greatly affect their feeding behavior. We assessed the abundance of *A. chirurgus* before the beginning of the trials through underwater visual census using the time-swim method, in which an expert diver counted and estimated the total length of all *A. chirurgus* in the tide pool for three minutes. The *A. chirurgus* densities observed in each day were 0.08, 0.11, 0.13 and 0.15 individuals m^{-2} (50, 63, 79 and 90 individuals $pool^{-1}$ respectively). We collected *D. simplex* from the reef flat, placed in a mesh bag and rotated ten times to remove the excess water before being weighted on a high precision scale (according to Longo et al. 2015). The seaweed densities offered were 0.03, 0.05, 0.08, 0.10 and 0.13 g m^{-2} (15, 30, 45, 60 and 75 g $pool^{-1}$ respectively). Each seaweed density was then attached to 0.5 m length ropes and transported separately inside Ziploc bags to the experiment

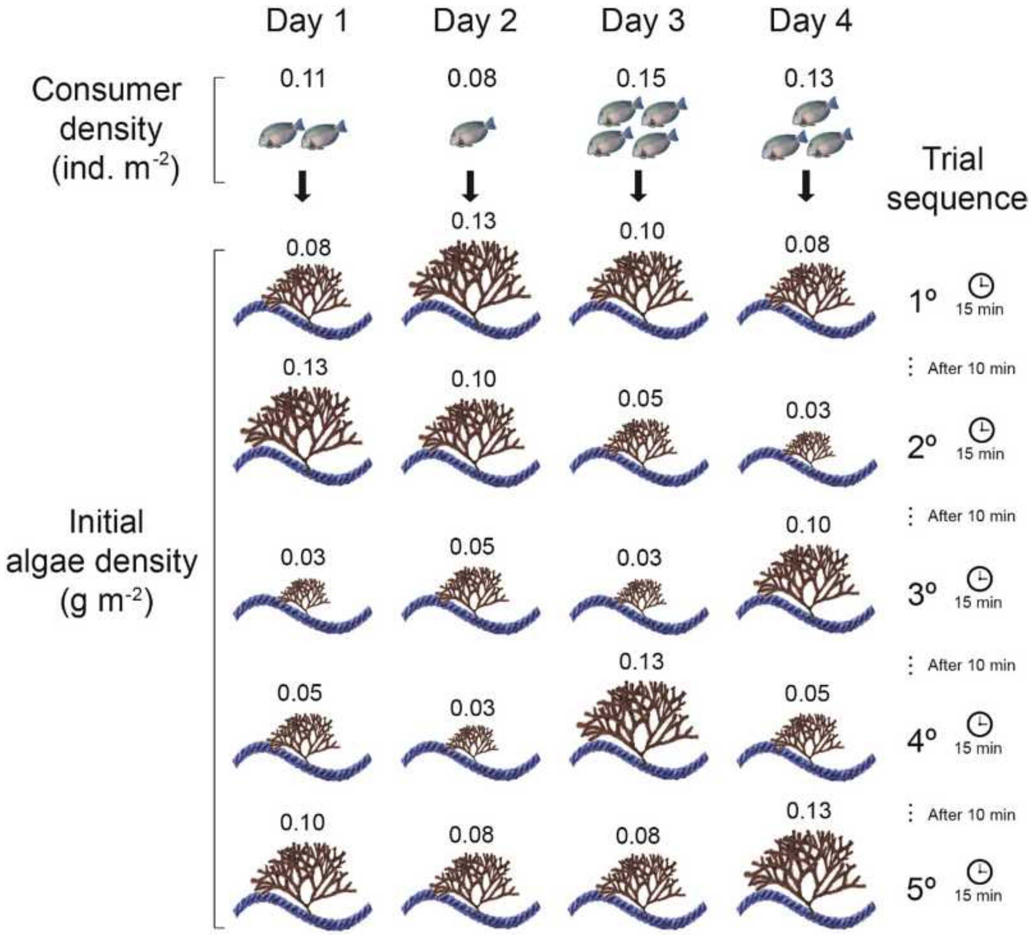

Figure 2. Experimental design used in the present study. Five trials per day were conducted in randomized orders over four different days. Each trial was recorded for 15 min with 10 min intervals between them. Per capita algae consumption rate was measured at factorial combinations of four consumer densities and five resource densities. Fishes and seaweeds are not to scale in this figure.

pool. Each rope had a cage control which was placed at a distance of less than 2 m from the rope not caged. The cage control consisted in a cage of 1 cm mesh size to prevent fish grazing and to control for biomass loss due to hydrodynamics and handling procedures. The number and length of trials reflect the small interval to conduct the experiments during low tide (about 2 h per day), which also restricted our ability to include a wider range of seaweed densities. Therefore, we consider the 4.3 times difference between the lowest and highest seaweed density (0.13 and 0.03 g m^{-2}, respectively) appropriate for the functional response assessment in the field.

We conducted each feeding trial at low tide during the same period of the day (10:00–14:00 h). Each trial was separated by a 10-min break period. An underwater video camera (GoPro Hero model 7, 12 megapixels; 60 frames/s) was positioned in front of each rope, approximately 1 m from the trial, to record the feeding activity of *A. chirurgus* on the seaweed and surrounding substrate (Fig. 1). After this period, the rope and cage control were removed from the pool and stored in the Ziploc bags for posterior weighing after all trials were concluded. We analyzed the videos in slow motion to estimate the number of *A. chirurgus* individuals feeding on *D. simplex* per minute in each trial and the number of bites per minute in each trial.

Data processing

Grazing rates were determined on the basis of two measurements: how much algae was grazed from each rope over the 15-min trials, relative to the amount lost on the control rope (Eq. 1); and the number of grazing bites observed over the same time period counted in 1 min increments using the video recordings (Eq. 2). First, the amount of algae consumed per trial (AC, g) was calculated as:

$$AC = \left(W_i - W_f\right) \times \left(\frac{Wc_f}{Wc_i}\right) \tag{1}$$

where W_i and W_f are the initial and final algae biomass in the trial rope, respectively, while Wc_i and Wc_f are the initial and final algae biomass in the control rope, respectively. Then, we estimated the per capita consumption rate per minute (F_t, g ind^{-1} min^{-1}) as:

$$F_t = AC \times \left(\frac{B_t}{TB \times Z_t} \right) \tag{2}$$

where TB is the total number of bites observed per trial; B is the number of bites observed per minute t (bites min^{-1}) and Z_t is the number of *A. chirurgus* individuals observed feeding on algae in that minute.

Functional response models

Nine functional response models were chosen to explain the observed per capita consumption rates F_t by herbivorous fish (Table 1): (1) a model consisted of a constant, density-independent consumption rate (termed the 'null model'), (2–4) the resource-dependent models (Holling type I, type II and the simplified Ivlev model), (5–7) the consumer ratio-dependent models (Arditi–Ginzburg type I, type II and the Ivlev ratio-dependent model) and (8 and 9) the consumer-dependent models that incorporate mutual interference through the use of an additional parameter (Hassell and Varley 1969, Arditi and Akçakaya 1990).

In these models, we used as predictor variables N and P, which represents the density of the seaweed and herbivorous fish respectively (i.e. grams of algae and number of fish divided by the area of the tide pool, ind. m^{-2}). In addition, to explore the effect of consumer body size, we perform another model fitting using P as the density of herbivorous fish in terms of grams of fish per square meters. On the other hand, the following model parameters were estimated by the data: parameter a is the consumer's searching efficiency and it can be defined as the proportion of the resource encountered per consumer per unit of searching time (Turchin 2003). Parameter h is the handling time, assuming that consumers waste time handling the resource (Turchin 2003). For Ivlev models, c is the maximum consumer intake rate and d is the consumer satiation coefficient (Ivlev 1961). Finally, parameter m is the mutual interference between consumers, it generally designates the fact that increasing consumer density depresses the average individual consumer food intake (Arditi and Ginzburg 1989, 2012).

When a resource is depleted throughout an experiment by consumer feeding, it is relevant to integrate the consumer's instantaneous feeding rate over the duration of the study (Rogers 1972, Juliano 2001). In this study, the experimental duration of the trials was sufficiently short concerning the residency time of the fish in the reef pool (i.e. 15 min versus 4–5 h). Therefore, we assumed constant instantaneous per capita feeding rates (i.e. invariant herbivore fish consumption rates of *D. simplex* during the observation period). To ensure that the results were independent of this assumption, we estimated the difference in means between the first and the last 7 min using a Bayesian parameter estimation probability distribution over the difference (Kruschke 2013). Moreover, we performed an ordinary linear regression for consumption rate against sequence to account the effect of the order of seaweed offered to the herbivorous fish. Both were carried out in R (ver. 4.1.0, <www.r-project.org>) using the BEST (Meredith and Kruschke 2021) and brms (Bürkner 2017, Carpenter et al. 2017) packages, respectively.

Model fitting and selection

We adopted a Bayesian framework to fit the functional response models, where the model parameters were treated as random variables (Ellison 2004). We assigned a prior distribution to the parameters to express our prior knowledge about them. Since consumption rate cannot take negative values, we choose positive half-normal distributions for the full probability model of our experimental data:

Table 1. Equations for the different functional response models: the null, the resource-dependent (Holling type I and type II and Ivlev), the consumer ratio-dependent (Arditi–Ginzburg type I and type II) and the consumer-dependent (Hassell–Varley and Arditi–Akcakaya) models. *N*: seaweed density (g m^{-2}); *P*: herbivorous fish *Acanthurus chirurgus* density (ind. m^{-2}); *a*: searching efficiency, *h*: handling time; *c*: consumer maximum intake rate; *d*: consumer satiation coefficient; *m*: consumer mutual interference coefficient.

Model name	Shape	Equation form (FR)	References
Null model	Constant	$f(N) = \alpha$	–
Resource-dependent models			
Holling type I (H1)	Linear	$f(N) = a \times N$	Holling 1959a
Holling type II (H2)	Hyperbolic	$f(N) = a \times N/(1 + a \times h \times N)$	Holling 1959b
Ivlev (IV)	Hyperbolic	$f(N) = c \times (1 - \exp[-d \times N])$	Ivlev 1961
Ratio-dependent models			
Arditi–Ginzburg type I (R1)	Linear	$f(N, P) = a \times (N/P)$	Arditi and Ginzburg 1989
Arditi–Ginzburg type II (R2)	Hyperbolic	$f(N, P) = a \times N/(1 + a \times h \times N/P)$	Arditi and Ginzburg 1989
Ivlev (IVR)	Hyperbolic	$f(N) = c \times (1 - \exp[-d \times N/P])$	Ivlev 1961
Consumer-dependent models			
Hassell–Varley (P1)	Linear	$f(N, P) = a \times N \times P^{-m}$	Hassell and Varley 1969
Arditi–Akcakaya (P2)	Hyperbolic	$f(N, P) = a \times N/(1 + a \times h \times N \times P^{-m})$	Arditi and Akçakaya 1990

$$f_t \sim \mathrm{Normal}\left(\mu,\sigma^2\right)T\left(0,\right) \tag{3}$$

where the mean (μ) was modelled with the functional response equations of Table 1. The standard deviation (σ) was modelled with a positive Cauchy distribution. Finally, mean and standard deviations of the functional response parameters were chosen to cover only realistic values with enough prior uncertainty to be mostly informed by our data. Prior probability distributions for functional response parameters can be found in the Supporting information.

We fitted the models using the *brm* function in the brms package within R ver. 4.1.0 (<www.r-project.org>). The brms package provides an interface to fit generalized (non-)linear multivariate models using Stan performing full Bayesian inference (Bürkner 2017, Carpenter et al. 2017). Markov chain Monte Carlo sampling (MCMC) was run with 3 chains of 1500 iterations each, of which the first 500 were discarded as the burn-in. The last 1000 were used to generate posterior probability density ranges. The convergence of the MCMC chains was assessed by using the Gelman–Rubin diagnostic (Rhat) which compares the estimated between-chains and within-chain variances for each model parameter, reaching the value 1 at convergence (Gelman and Rubin 1992). Finally, we compared the fit accuracy of the functional response models using Bayesian R^2 in order to estimate the amount of explained variation of each model (Gelman et al. 2019). We identified the best fitted model by the highest R^2 and the lower number of parameters.

Results

Field experiments

The herbivorous fish *Acanthurus chirgurus* was observed feeding on the algae *Digenea simplex* throughout the entire time in all 20 trials and the seaweed was not fully consumed in any trial. The median per capita consumption rate of the 20 trials was 0.18 g ind.$^{-1}$ min^{-1} with a standard deviation of 0.23. The highest per capita consumption rate was 1.5 g ind.$^{-1}$ min^{-1}, found at intermediate seaweed and fish densities (Fig. 3). Higher and dispersed values of per capita consumption rate were detected at intermediate to high seaweed densities (Fig. 3a) and intermediate to low fish densities (Fig. 3b).

The difference of mean per capita consumption rates through time showed a 95% probability of being zero in 19 out of 20 trials, indicating an invariant consumption rates of *D. simplex* by herbivorous fishes as a function of the trial duration (Supporting information). On the other hand, the effect of the order of seaweed offered to the herbivorous fish showed null effect sizes for all the four fish densities tested, indicating it was not a strong determinant of the per capita consumption rate (Supporting information).

Fit of the functional response models

All models converged and we did not detected divergences in the Markov chain Monte Carlo sampling method for all fitted models (Rhat = 1). Both set of models using fish density and fish biomass density showed similar fit accuracy and order in terms of parsimony. Here, we present the fit results from the models fitted with fish density. Results from the

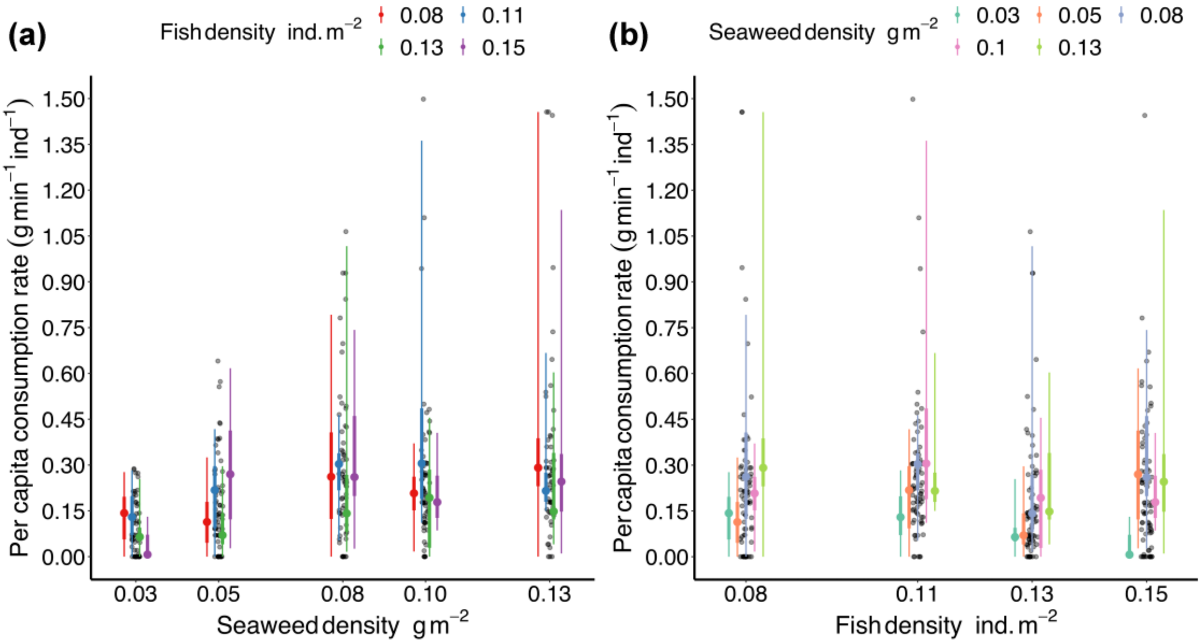

Figure 3. Observed functional response of herbivorous fish *Acanthurus chirurgus* on seaweed *Digenea simplex* in the Rocas Atoll. (a) Per capita consumption rate versus algae density; (b) per capita consumption rate versus fish density. Dots represent raw data and vertical bars represent the median (dot) and 50% and 95% credible intervals, respectively.

Table 2. Performance of herbivorous fish functional response models relative to resource density *Digenea simplex* and consumer density *Acanthurus chirurgus* in the Rocas Atoll. Model: see code in Table 1; *k*: number of estimated parameters in the model; R^2: R-squared estimated as the variance of the predicted values divided by the variance of predicted values plus the expected variance of the errors. Values inside the square brackets represent the 95% credible interval. Boldface type identifies the best-fit model according to R^2 and number of parameters *k*.

Model	k	Form	Variables-dependence	R^2
R1	**1**	**linear**	**Ratio**	**0.62 [0.57; 0.65]**
P1	2	linear	Consumer	0.61 [0.56; 0.65]
IV	2	hyperbolic	Resource	0.56 [0.47; 0.62]
IVR	2	hyperbolic	Ratio	0.53 [0.40; 0.62]
R2	2	hyperbolic	Ratio	0.51 [0.33; 0.63]
P2	3	hyperbolic	Consumer	0.50 [0.27; 0.64]
H1	1	linear	Resource	0.45 [0.20; 0.59]
H2	2	hyperbolic	Resource	0.36 [0.06; 0.55]
Null	1	constant	–	0.00 [0.00; 0.00]

models fitted with fish biomass density can be found in the Supporting information.

From the nine functional response models tested, the Arditi–Ginzburg type I consumer ratio-dependent model (R1) provided the best fit accuracy and parsimony to our data ($R^2 = 0.62$; fitted parameter $a = 0.31$ m^2 $min^{-1} \cdot fish$ [0.26; 0.37]; Table 2 and Fig. 4). The Hassell–Varley consumer-dependent model (P1) also showed good accuracy ($R^2 = 0.61$), with an extra parameter (i.e. *m*: mutual interference), which increases its complexity. The functional response models with the handling time parameter (R2 and P2) showed intermediate accuracy but high complexity (with 1 or 2 extra parameters) (Table 2). The Holling resource-dependent functional response models (H1, H2) and Ivlev functional response models (IV, IVR) showed a less accurate fit to data (Table 2 and Fig. 4). Supporting information for parameter estimates of all nine models.

Finally, we found a clear linear increase of the observed per capita consumption rates as a function of the ratio between seaweed and fish densities (Fig. 5 vertical bars). Accordingly, our best fitting model (R1) predicted higher per capita consumption rates as the amount of algae per fish increases (Fig. 5 solid line). More clearly, with a given density of seaweed, *A. chirgurus* individual's consumption rate is reduced when there are more conspecifics in the tide pool.

Discussion

To our knowledge, this study provides the first manipulative experiment examining the functional response of a marine herbivorous fish in its natural environment. We found that the consumer–resource interaction between the herbivorous fish *Acanthurus chirurgus* and the red seaweed *Digenea simplex* is best described by a ratio-dependent model, indicating that both resource and consumer influence fish per capita consumption rate. According to our best fitting model, the area searched by an individual herbivorous fish is inversely proportional to the density of fishes (*a*/*P* in model R1). We suggest that the ratio dependent functional response detected here relates to the fact that mutual interference of herbivorous fish arises from seaweed spatial clustering rather than aggressive behavior (Cosner et al. 1999). Such mutual interference exists at surgeonfish densities generally observed in the field (Vincent et al. 2011, Morais et al. 2017, Hernández-Landa and Aguilar-Perera 2019). Therefore, mutual interference by consumer should be considered as a biological mechanism by which herbivorous fish density depresses individual consumption performance.

We found that the herbivorous fish per capita consumption rate on seaweed is proportional to their ratio, with herbivorous fish handling time (*h*) playing a minor role in the shape of its functional response. Because of the lack of herbivorous fish handling time in our best fitting models (the linear R1 and P1 models), we infer from our results that time required for *A. chirurgus* to handle seaweed was negligible compared to their active search time (*a*). This result is in agreement with the evidence that the *Acanthurus* genus display higher gut turnover rates, constantly feeding throughout the day (Polunin et al. 1995, Craig 1996). For our best model, the parameter *a* can be interpreted as the rate at which the seaweed is made available to the herbivorous fish population (Arditi and Ginzburg 2012). Therefore, the area searched by an individual consumer is inversely proportional to the density of consumers.

Mutual interference between consumers arises from both behavioural and environmental conditions (Cosner et al. 1999, Abrams and Ginzburg 2000, Francini-Filho et al. 2010). We observed surgeonfish aggregation patterns around the algae during our field experiments, which suggests that surgeonfish density is positively associated with algae density (Lawson et al. 1999). Consumers should compete for resource-rich patches, meaning that resource spatial clustering can further reduce consumption rates by increasing the opportunity for fish–fish interactions (Levin et al. 2000, Osório et al. 2006). Mutual interference also emerges when the consumer's individual home ranges are relatively large compared to the area available for foraging (Ginzburg and Jensen 2008). In our experimental system, fish are constrained to search for patchily distributed algae over a discrete area during a discrete time period (low tide). In such a situation, home ranges tend to overlap, and mutual interference may take place, leading to consumer density dependence in the herbivorous fish' per capita consumption rate (Nash et al. 2012, Welsh and Bellwood 2012).

Overall, our results add to a growing body of evidence supporting the idea that consumer's consumption rate can be modelled by using resource and consumer density as explicative variables in ecosystem functioning (Arditi and Ginzburg 2012, Hossie and Murray 2016, Chan et al. 2017). Since the density of surgeonfish changes daily in our study system, we acknowledge that interference could shift from low to high levels as the herbivorous fish population size increases. This shift in mutual interference strength and, consequently, in consumer dependence may stabilize the biomass dynamics

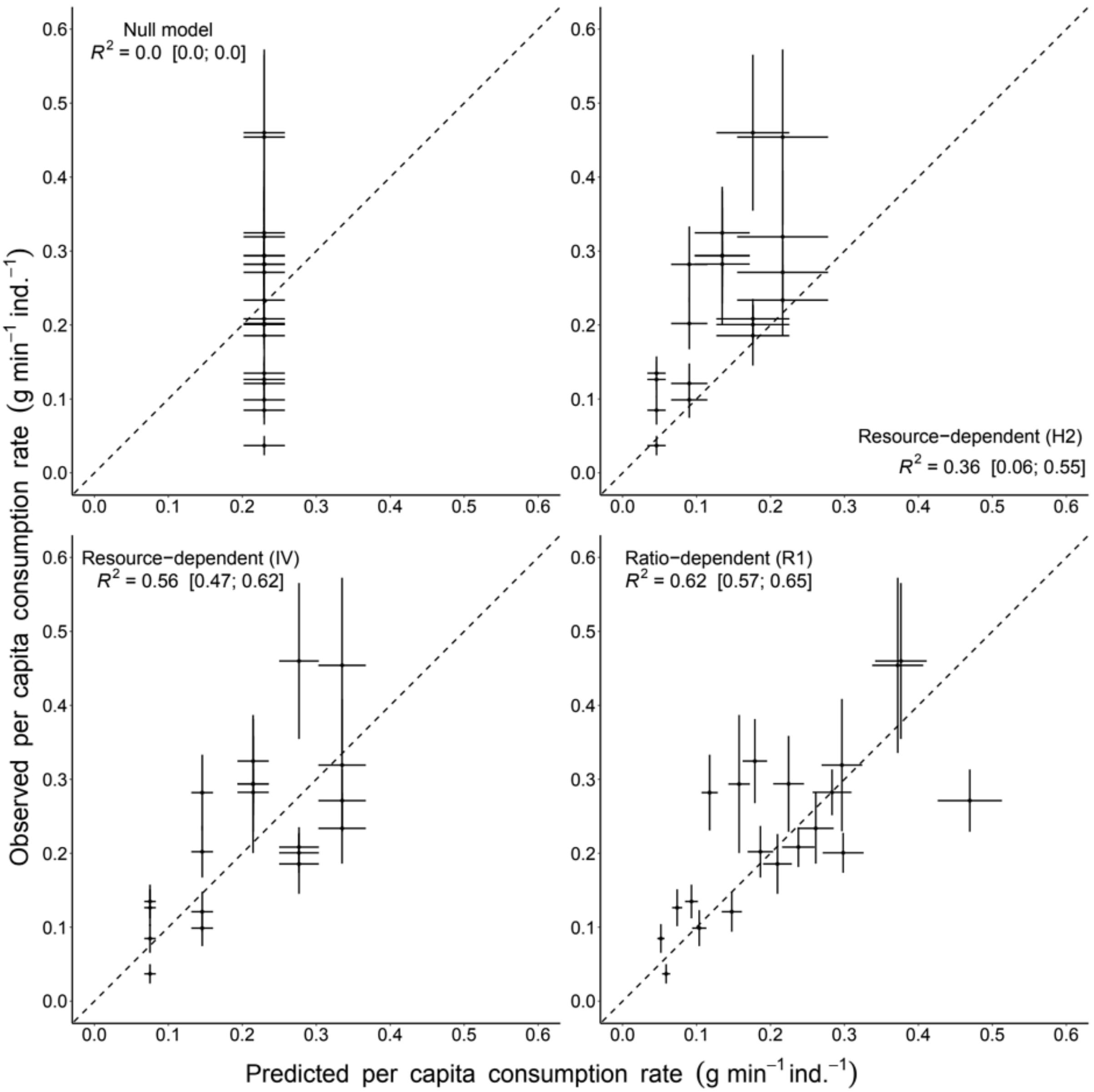

Figure 4. Observed versus predicted scatter plots derived from the functional response models fitted in this study. Vertical and horizontal bar represent standard errors. The functional response models presented here are in ascending order for Bayesian R^2. (a) Null model; (b) Holling type II hyperbolic resource-dependent; (c) Ivlev hyperbolic resource-dependent; (d) Arditi–Ginzburg type I linear ratio dependent. The dashed line represents the 1:1 line. For the five models not presented in this figure we refer the reader to Supporting information.

across trophic levels, consistent with field and theoretical predictions (Arditi et al. 2004, Griffen and Delaney 2008). Our results imply that functional response models that do not consider fish density could mischaracterize the consequent interactions between fish and algae populations.

Speculations

Functional response can be an important tool to understand population dynamics in systems with high spatial and temporal variability, such as reef ecosystems (Gil et al. 2020). During the low-tide period, both consumer and resource densities will depend on the particular pools where fish get trapped. Likewise, during the high-tide period, fish can regroup and exploit a new pool (or open sea) with a different algae density. We found that the consumption rate of the dominant herbivorous fish of our intertidal system depends on the ratio between its food and conspecifics trapped in the same pool. Our results suggest that herbivory (consumer–resource interaction among populations) is not homogenous, varying on spatial (different pools) and temporal (low- versus high-tide periods) scales. Therefore, dynamic models to predict the demography of fish and algae populations, and their interaction (herbivory) in natural systems would benefit from

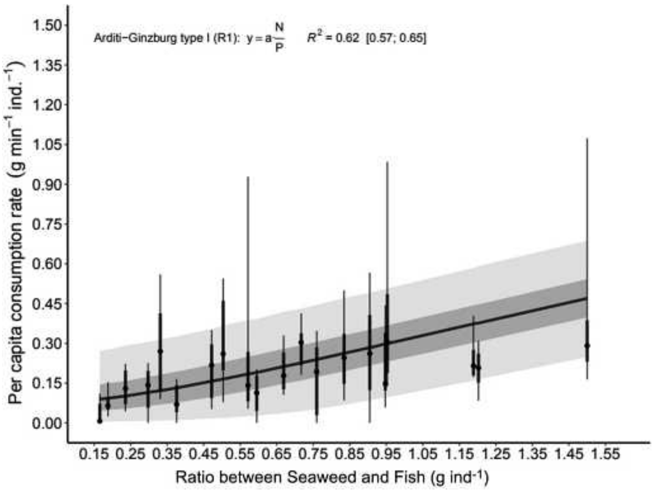

Figure 5. Observed functional response of the herbivorous fish *Acanthurus chirurgus* on seaweed *Digenea simplex* and prediction of the best-fit model R1 (linear ratio-dependent). N: seaweed density (g m^{-2}); P: *Acanthurus chirurgus* density (ind. m^{-2}). Vertical bars represent the observed consumption rates from our field experiments (here, the dot in the middle shows the median, the thin lines are the 75% credible intervals and the thicker lines are the 50% credible intervals). The solid line is the Bayesian posterior mean model prediction and the shaded regions are the 50% and 95% posterior credible intervals.

combining our best functional response model with spatio-temporal variables, instead of assuming spatio-temporal homogeneity in complex marine ecosystems.

Alternative viewpoints

Our results suggest a negative density dependence scenario generated over a low seaweed and herbivorous fish density ranges. However, it is known that some herbivorous fish in the Pacific Ocean benefit from the exchange of information among them (e.g. behavioral coupling) to increase foraging time and protect from predators (Gil and Hein 2017). We expect the negative density dependence scenario to be most important when the seaweed/herbivore abundance ratio is low enough that per capita consumption is limited by the amount of time an individual fish spends searching for the resource. Positive density dependence will likely be important if the resource/herbivore ratio is higher and resource density is not limiting.

Conclusion

The consumption of algae by herbivorous fish and the consequent excretion of essential nutrients such as N and P are fundamental ecological processes for the functioning and health of reef ecosystems around the world (Hughes et al. 2007, Allgeier et al. 2014, Munsterman et al. 2021). By combining field experiments with a modelling approach, we found that the functional response of an herbivorous fish in an Atlantic's reef ecosystem is ratio-dependent and that the final outcome of consumption is constrained by mutual interference. We suggest that future work investigate whether and how other important variables such as resource quality, top-predator presence and water temperature affect herbivorous fish' functional response. The accumulation of evidence will allow clear mechanistic explanations of the effect of herbivory in one of the most complex and biodiverse marine ecosystems on Earth.

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Author contributions

Leonardo Capitani: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Natalia Roos**: Methodology (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Guilherme O. Longo**: Conceptualization (equal); Methodology (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Ronaldo Angelini**: Conceptualization (equal); Methodology (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Luca Schenone**: Data curation (lead); Formal analysis (lead); Investigation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Raw data and the R code for data analysis that support the findings of this study are free available from gitHub repository, <https://github.com/leomarameo7/ FR_herbivore_fish> (Capitanis et al. 2021). Videos footages showing mutual interference behavior in surgeonfish *A. surgus* while eating algae are available from gitHub repository too, https://

github.com/leomarameo7/FR_herbivore_fish. Complete high-quality video of the experimental trials are available on request to corresponding author.

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