

Trophic cascade facilitates coral recruitment in a marine reserve

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Abstract

Reduced fishing pressure and weak predator-prey interactions within marine reserves can create trophic cascades that increase the number of grazing fishes and reduce the coverage of macroalgae on coral reefs. Here, we show that the impacts of reserves extend beyond trophic cascades and enhance the process of coral recruitment. Increased fish grazing, primarily driven by reduced fishing, was strongly negatively correlated with macroalgal cover and resulted in a two-fold increase in the density of coral recruits within a Bahamian reef system. Our conclusions are robust because four alternative hypotheses that may generate a spurious correlation between grazing and coral recruitment were tested and rejected. Grazing appears to influence the density and community structure of coral recruits but no detectable influence was found on the overall size-frequency distribution, community structure or cover of corals. We interpret this absence of pattern in the adult coral community as symptomatic of the impact of a recent disturbance event that masks the recovery trajectories of individual reefs. Marine reserves are not a panacea for conservation but can facilitate the recovery of corals from disturbance and may help sustain the biodiversity of organisms that depend upon a complex 3-dimensional coral habitat.

Key words: coral reef, grazing, predation, biodiversity, marine reserves

Marine reserves have become one of the most widely-adopted tools for managing commercially important fishes and protecting marine biodiversity (1). Several direct effects of reserves are relatively straightforward to anticipate: reduced fishing mortality usually increases the biomass of target and by-catch species of fishes (2, 3) and reserve status may help prevent acute anthropogenic disturbance such as destructive fishing practices that damage benthic communities (4). However, by enhancing the abundance of fishery species, reserves may also exert indirect impacts on other non-fishery species that naturally interact with fisheries species through processes of predation and competition (5).

Since the indirect effects of reserves on biodiversity arise from species interactions and trophic cascades (6), they are generally complex and may have surprising outcomes (7, 8). We reported such complex outcomes in a study of The Bahamas' Exuma Cays Land and Sea Park (ECLSP), which, at 442 km², is one of the largest and most successful marine reserves in the Caribbean. The ECLSP is a rare example where sustained fisheries exclusion has resulted in a high biomass of predatory fishes (2kg 100 m⁻²). Our *a priori* hypothesis was that high levels of piscivorous fishes such as the Nassau grouper (*Epinephelus striatus*) would exert top-down predatory impacts on grazing fishes (a prey item) and, by reducing the biomass of grazers, promote increases in the cover of macroalgae. However, the hypothesis was not supported because larger-bodied species of grazer (parrotfish) were found to experience a size-escape from predation and therefore the expected negative effects of trophic cascades on grazers were unexpectedly weak (9). In addition, these larger-bodied parrotfishes such as *Sparisoma viride* benefited numerically from a reduction of fishing pressure in the reserve. Since large-bodied individuals are responsible for the majority of algal grazing, the net outcome of the reserve was a doubling of grazing and a four-fold *reduction* in macroalgal cover (9).

Our study of the ECLSP contributes to a growing body of literature that documents conservation-driven trophic cascades within ecosystems, often with fishing pressure at the apex (10, 11). Here, we move beyond trophic cascades and reveal further ecological consequences of reserve implementation. Specifically, since trophic cascades within the ECLSP resulted in an increase in grazing and reduction of macroalgae, we explore the consequences of this shift in benthic community structure on another ecosystem process: the recruitment of corals. Coral recruitment is clearly an essential demographic process for the persistence of coral populations (12). Such processes have received renewed attention because of the great vulnerability of corals to climate change (13).

Corals and macroalgae compete for space on reefs and interact through several mechanisms (14). Coral planulae cannot settle on macroalgae and therefore the space occupied by macroalgae reduces the availability of suitable settlement space for corals (15). Algae can trap sediment that smothers coral recruits (16) and direct contact with macroalgae reduces coral growth rates (17) and may even result in direct overgrowth and coral mortality (18). It is also feasible that macroalgae can negatively influence corals through allelochemicals (19), triggering disease (20) and enhancing microbial activity driven by algal-derived dissolved organic carbon (21). Therefore, any management intervention that reduces macroalgal cover may enhance the recovery of coral populations and resilience of the system (22). We test the hypothesis that increased grazing – largely driven by implementation of marine reserves – can increase the recruitment of corals.

Results

Main hypothesis: Grazing determines macroalgal cover which in turn influences coral recruitment

Parrotfish grazing intensity was strongly negatively correlated to macroalgal cover (Fig. 1, Table 1) which was, in turn, strongly negatively correlated to recruitment. The macroalgal community was dominated by the genera *Halimeda*, *Dictyota*, *Sargassum* and *Lobophora* and whilst their total cover varied with grazing, the overall community composition was conserved among sites (see *Supporting Information*). Overall, grazing intensity was strongly positively correlated to coral recruitment (Fig. 2) and this relationship held for both brooding and spawning species of coral (Table 1). Recruitment was expressed both as raw density and standardised to the availability of colonisable substratum (see methods). However, the results were virtually identical (Table 1) so the standardisation was unimportant albeit theoretically desirable. The highest levels of grazing intensity plotted on figures 1 and 2 were found at sites in the ECLSP and are consistent with our previous conclusion that grazing is significantly higher inside the Park (9). Such variation in grazing intensity was associated with a two-fold difference in coral recruitment.

The community of coral recruits was dominated by brooding taxa (79% of all recruits observed) with strong representation of the genera *Porites* and *Agaricia* (39% and 13% of all colonies; for further details see *Supporting Information*). When the structure of the recruit community was quantified using multivariate methods (23), its spatial pattern was moderately strongly correlated to the level of grazing intensity (Table 1). However, this relationship disappeared when the structure of the entire coral community (recruits to adults) was correlated to grazing ($r=0.07$, $p=0.27$). Furthermore, grazing intensity was not correlated to the total cover of living coral at each site ($r=0.35$, $p=0.35$).

Exploratory analysis of size-frequency distributions

Previous studies have gained useful demographic insight from the size-frequency distribution of corals (24, 25). In our study, the size-frequency distributions of brooding and spawning corals showed no correlation with grazing intensity. For example, the correlations for brooders, which were qualitatively similar to those for spawners, were -0.22 ($p=0.55$, $1-\beta=0.54$), 0.35 ($p=0.34$, $1-\beta=0.34$) and 0.01 ($p=0.96$, $1-\beta=0.90$) for skewness, kurtosis and the mean of successive squared differences respectively.

Alternative hypotheses

An important limitation of using correlation is that cause cannot be inferred directly from statistical pattern. Therefore, to substantiate our inference that grazing reduces macroalgal cover, which then facilitates higher recruitment, we proposed and tested four alternative hypotheses that may plausibly explain all or part of the observed correlation between grazing and recruitment in corals (Table 2). The first three hypotheses identified hidden variables that might account for a spurious correlation. In each case the hidden variable was correlated against both grazing and recruitment and found to be non-significant. The power of several tests was low and therefore the analysis was reinforced using partial correlation that explicitly tests for conditional dependence on hidden variables (Table 2). The fourth hypothesis tested whether the pattern of coral recruitment might be partly explained by differential larval supply among sites such that supply was higher in the ECLSP. Using a high resolution 3-

dimensional simulation model of coral larval dispersal (26), we found no evidence for such pattern (Fig. 3, Table 2). Neither did we find such pattern in the simulated supply of parrotfish larvae that could, in theory, underpin the distribution of grazers (see *Supporting Information*). Moreover, the original rationale for locating the reserve were based on terrestrial considerations and there was no *a priori* evidence that reefs in the Park were any different to those outside its boundaries (27).

Discussion

Although other studies have found positive associations between urchin density and coral recruitment (28), the positive effect of fish grazing on coral recruitment had not previously been documented. We infer that parrotfishes are the primary grazer responsible for this pattern because biomass of the main alternative fish group, Acanthuridae, exhibited a vanishingly weak ($r=-0.05$) non-significant ($p=0.89$) correlation with recruitment. These results have an important implication for coral reef management: maintaining high levels of grazing reef fishes can, in principle, enhance the recovery of Caribbean coral populations from disturbance, as predicted by ecological models (29). Therefore, the results provide empirical support for the notion of managing grazers as part of a strategy to mitigate disturbance on coral reefs and enhance resilience (22). Unfortunately, parrotfishes are rarely protected by fisheries regulations and therefore no-take reserves remain the most common instrument to manage their biomass (29).

The management of grazers is not a panacea for conservation (30). Coral population dynamics are the outcome of processes of colonisation and mortality. Grazing may enhance colonisation rates but its impact on coral mortality is unknown. Possible negative effects of grazing include the predation of parrotfishes on corals (31) whereas possible positive effects include reducing the frequency and duration of coral-algal interactions, which may in turn reduce the incidence of disease and physiological demands on corals for immune response. Indeed, the processes governing the community structure of corals are complex and strongly influenced by the history of disturbance in addition to changes in colonisation rate (32). Such complexity probably explains the absence of a detectable influence of grazing on coral cover, size-frequency distribution, or overall community structure. First, the coral community is dominated by adult colonies whose composition differs dramatically to that of the juvenile community (the former being dominated by spawners and the latter by brooders – see *Supporting Information*). Second, adult corals in the study area experienced extensive mortality from coral bleaching in 1998 (33) and the persistent impact of this event masks differences in the recovery trajectories of reefs. Future studies need to quantify the degree to which grazer-mediated increases in coral recruitment can buffer elevated levels of disturbance.

Our results reveal local-scale impacts of grazing on coral recruitment along a continuous reef system. However, further studies are needed to illuminate the importance of candidate mechanisms such as space occupation by macroalgae and coral-algal competition. Furthermore, additional processes may affect the outcome of grazing on recruitment at larger spatial scales. Harrington et al. (34) described the importance of specific coralline algal species in facilitating the settlement and subsequent early survival of corals. Future studies will need to quantify the availability of such facilitators at various scales and quantify their overall importance in determining large-scale patterns of coral recruitment.

Reserve-driven trophic cascades were found to facilitate the recruitment of corals which should, in theory, enhance the recovery of corals from disturbance and help maintain a complex 3-dimensional reef structure. Many reef organisms depend on such 3-dimensional structure for habitat and shelter from predators (5) and reductions in coral cover and topographic complexity can adversely influence fish density and diversity (35, 36). Therefore, the facilitation of coral recruitment, brought about by marine reserves, may help sustain biodiversity by contributing to the generation of the complex reef habitat required by many organisms. In short, the roles of marine reserves in sustaining biodiversity are complex and extend beyond trophic cascades.

Methods

Study area

The ECLSP was established in 1958 (37) and with a ban on fishing enforced since 1986, maintains higher densities of fish and invertebrates than found outside the reserve (9, 37). Of the large commercial fishing vessels registered as using fish traps in The Bahamas, 40% have sufficient size (>10 m) and are in close enough proximity (Nassau to Exuma Cays) to fish around the reserve (9). In addition, 30 fish traps are deployed locally to the south of the reserve. Though such traps are used to target grouper species, they result in bycatch of parrotfishes (38). All surveys were conducted in the '*Montastraea*-dominated' forereef habitat which has the greatest diversity and density of all fish and invertebrates in The Bahamas (PJM unpub. data). An Ikonos satellite image was used to stratify the location of sampling sites both inside and outside the ECLSP and each site measured approximately 150 m × 150 m. Nine sites were sampled along a continuous stretch of forereef; three sites inside the ECLSP, three to the north (between 5.8 and 18.1 km from the northern boundary), and three sites ~70 km to the south. All surveys were carried out in October 2004 and a full description of study sites is presented in *Supporting Information*.

Coral community structure

At each site, 40 randomly placed 1 m² quadrats were used to quantify benthic species composition and the density of coral recruits. The content of quadrats was filmed in 20 cm swathes, using a high-resolution digital video camera. Following completion of the swathes, cryptic areas such as ledges and regions obscured by overstory macroalgae were filmed in close-up (and if necessary, the algae parted to reveal understory organisms). When viewed on a large TV monitor, the resolution of benthic organisms was greater than that achievable by eye *in situ*. Individual corals were identified to species (or genus in the case of some smaller recruits) and their 2-dimensional horizontal size accurately delineated using the software Vidana*. The smallest corals censused using this technique had a diameter of approximately 1 cm. Each coral was discriminated as being either a new recruit – where its boundaries were inconsistent with the surrounding dead skeleton (39) – or a fragment of a larger colony that had experienced partial mortality. Corals that extended beyond quadrat boundaries were noted and removed from analyses of size distributions. More than 6000 individual corals were sampled. The percentage cover of sand, sponges and functional categories of algae (40) were recorded together with the frequency of occurrence of algal species. Coral recruits were defined as those new individuals whose size was less than 20 cm². Because the cover of sand, sponges and adult corals varied among quadrats and recruits cannot settle on any of these substrata, it would be

* Software freely available from www.ex.ac.uk/msel

inappropriate to report overall density of recruits per quadrat (i.e. 2 recruits in a quadrat of 100% colonisable space constitutes half the density of 2 recruits in a quadrat where only 50% is potentially colonisable and the remaining space is sand). In other words, we standardised recruit density to that per square metre of potentially colonisable space. We assumed macroalgal cover to be relatively ephemeral (41), and treated all algal-covered substratum as potentially colonisable by coral recruits (i.e. macroalgal cover was ignored in the standardisation procedure). In doing this, we avoided the creation of a systematic relationship between macroalgal cover and recruit density. To test for the impact of undertaking standardisation, statistical analyses were carried out with both raw and standardised data on recruit density. The community structure of dominant algal species is given in *Supporting Information*. Rugosity was measured at two scales. At a coarse scale, the maximum vertical relief was measured of each quadrat. This was then converted to a finer scale by calibrating the relationship between maximum vertical relief of a quadrat and fine-scale (millimetre) rugosity measured using the standard and labor-intensive chain-transect method. Rugosity was measured at each scale for 140 quadrats within the *Montastraea* reef habitat and the correlation of the methods was found to be high ($r=0.67$, $p<0.001$). All data reported for rugosity used the converted millimetre scale measures.

Fish census and grazing

Grazing damselfishes exert a strong influence on macroalgal communities by tending and defending territorial “gardens” of algal turf (42). The density of damselfishes by species, life phase and length was sampled using four 30 m × 2 m transects per site. The mean precision (SE/mean) to which their density was sampled was 26%, which is high for such taxa (43). Length was converted into biomass using the allometric coefficients of Bohnsack and Harper (44).

Parrotfish dominate the fish grazing community of most Caribbean reefs (15). The size-frequency of parrotfishes was sampled to the nearest centimetre by the same observer at each site using ten replicate transects of 30 m × 4 m (tests of the surveyor’s accuracy of length estimate in situ yielded a mean discrepancy of 1.3 cm for wire objects of comparable length to fishes, $n=15$). Surveys were carried out in linear site order, thereby avoiding potential bias that could conceivably occur if reserve sites were sampled at either the beginning or end of the study. Parrotfish biomass has limited efficacy as a proxy for grazing because of variation in bite size and rate among fish species and life phases (29). Therefore, the observed size-frequency distributions of individual parrotfishes were converted to an overall measure of grazing intensity using a model that has been tested elsewhere (9, 29). The model uses species-level data on bite rate and genus-level data on the allometric scaling between fish length, sexual phase and bite size, to determine the total area bitten by the parrotfish community. This is then expressed as the maximum percentage of horizontal reef area grazed per hour. The biomass of individual surgeonfish species (Acanthuridae) was sampled simultaneously with that of parrotfishes. The urchin *Diadema antillarum*, an historically important grazer on Caribbean reefs, was not observed in the ECLSP and its density outside the Park never reached functionally-important levels (0.04 m^{-2}).

Modelled larval supply between reserve and non-reserve sites

Coupled biophysical models rich in mechanistic details have become the most efficient tools in larval transport studies (45). A spatially-explicit 3-dimensional

individual-based model developed by Paris et al. (46, 47) and adapted for the wider Caribbean (26) was used to model spatial patterns of larval supply for a typical genus of brooding coral (*Agaricia*) and the dominant parrotfish species, *Sparisoma viride*. An ocean circulation module uses daily outputs of the high-resolution (6-7 km) Atlantic HYbrid Coordinates Ocean Model (HYCOM) forced by real daily winds to represent present-day oceanographic conditions. Vertical resolution is prescribed by the larval vertical behavior and set to 20-m layers (48). The model domain for this extends to the wider Caribbean. The habitat layer of the model was created by satellite remote sensing of the Exuma Cays region. Individual reefs were buffered by a 5 km sensory zone and divided into ca. 10 km segments (i.e. into approximately 50 km² polygons). Initial conditions (i.e. spawning time and frequency) and parameterization (i.e. larval swimming behavior and pelagic larval duration, PLD) of the biological module used the larval traits of *Sparisoma viride* and *Agaricia* spp.. Ontogenetic vertical migration was simulated for *Sparisoma viride* which has a pre-competent period of 47 d and maximum competency or PLD of 80 d (49). Planulae of *Agaricia* stay in the surface layer (0-20 m), their pre-competent period is 48 hours and PLD is 42 days (50). Cohorts of 100 virtual larvae (particles) were released simultaneously into the velocity field at all individual reef sites (93 sites around the Exuma Sound). To simulate reproductive behaviour, releases occurred monthly and year-round for *Sparisoma viride* but only during summer months for *Agaricia* spp.. A total of 27,900 and 111,600 particles were released for the coral and parrotfish species, respectively. Field study sites corresponded to five of the model polygons (2 north of the Park, 2 within the Park, and 1 south of the Park) so recruitment was recorded daily in each of the five relevant model polygons. Further details of the model appear in *Supporting Information*.

Statistical analyses and alternative hypotheses

The relationship between grazing intensity and recruit density (standardised and raw data) was quantified using Pearson Product-Moment correlation. Inferences on the strength of correlation and determination of power followed Cohen (51). Further insight was gained by repeating the analyses separately for those genera that brood their larvae and those that undertake mass spawning. Spatial patterns in the community structure of (i) coral recruits (by density of species or genus) and (ii) the entire coral community (by percentage cover of each species or genus) were explored using non-metric Multidimensional Scaling (MDS) with the Bray-Curtis dissimilarity measure (23). All data were double square-root transformed to allow less common species to influence the analysis. A formal test of the relationship between community structure and grazing was undertaken using the procedure RELATE (52) which correlates the dissimilarity matrices of recruit data (Bray-Curtis dissimilarity among sites) and grazing intensity (Euclidean distance in grazing among sites) using non-parametric Spearman-rank correlation (note, the power of non-significant non-parametric tests is usually not reported). To guard against making Type I error with a total of thirteen statistical tests, alpha was reduced conservatively to 0.0038 using the Dunn-Šidák method (53).

We conducted an exploratory analysis of the impact of grazing on the size-frequency distribution of both brooding and spawning corals. Grazing intensity was correlated with the skewness, kurtosis (53) and half the mean of successive squared differences (MSSD) among size categories. The latter measure is an indicator of heterogeneity among size classes. Size-frequency distributions comprised all individual corals at a

site but excluded fragments. All size data were transformed using natural logarithms prior to the computation of size-frequency distributions (*sensu* 54).

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Table 1. Correlation analyses for the main hypothesis. r is used for parametric correlation and ρ (denoted in rows marked*) is used for multivariate RELATE. p/a denotes use of presence/absence data. p denotes probability that $r=0$. $n=9$.

Scenario	r, ρ	p
Main hypothesis:		
Grazing vs. macroalgal cover	-0.82	0.007
Grazing vs. recruitment (standardised)	0.86	0.002
Grazing vs. recruitment (raw)	0.83	0.005
Macroalgal cover vs. recruitment (std)	-0.82	0.006
Grazing vs. recruit community structure*	0.51	0.005
Grazing vs. brooder recruit density	0.85	0.003
Grazing vs. spawner recruit density	0.86	0.003

Table 2. Alternative hypotheses that may account either partially or fully for the observed correlation between grazing (g) and coral recruitment (r). Other variables are denoted c (coral cover), rg (rugosity), and d (pomacentrid biomass). r denotes Pearson correlation coefficient, r_p = partial correlation coefficient with conditional variables separated by ·, p = probability that coefficient=0, $1-\beta$ = power. GLM = generalised linear model with time (serial autocorrelation, measured using ACF, removed using 5 day aggregate) and site as fixed factors, quasipoisson errors and a log link (55). DP = dispersion parameter for quasipoisson family.

Alternative hypothesis	Tests	Result
1) Since recruitment in the Caribbean is dominated by brooding species whose larvae have short planktonic phases (50), recruitment density may be driven by the local cover of brooding corals. A positive correlation between grazing intensity and recruitment could then be observed because, coincidentally, grazing intensity is also correlated to the adult cover of brooders (and spawners) because such areas have higher rugosity and availability of shelter	$r(r,c)=0.07$, $p=0.84$, $1-\beta=0.07$, $n=9$ $r(c,g)=0.31$, $p=0.37$, $1-\beta=0.26$, $n=9$	Reject
2) Corals recruit in cryptic areas and recruitment density is positively correlated to rugosity. This is particularly true of settling corals although the degree to which it holds for larger recruits, that have survived early post-settlement processes, is unclear. Coincidentally, grazing is also correlated to rugosity of the habitat	$r(r,rg)=0.21$, $p=0.59$, $1-\beta=0.54$, $n=9$ $r(rg,g)=0.4$, $p=0.28$, $1-\beta=0.18$, $n=9$	Reject
3) Increased levels of predation in reserves reduce the biomass and density of territorial damselfish (Pomacentridae). Reduced numbers of damselfish allow enhanced survival of coral recruits since there are fewer territories (56) and/or reduce the amount of macroalgae in territories. In this scenario, the correlation between parrotfish grazing and either coral recruitment or macroalgal cover arises because parrotfish grazing responds to the reserve in the same way as predator abundance, yet it is the latter that influences recruitment and macroalgal cover because of predator impacts on damselfishes	$r(g,d)=0.31^*$, $p=0.43$, $1-\beta=0.33$, $n=9$ $r(r,d)=-0.06^*$, $p=0.89$, $1-\beta=0.07$, $n=9$	Reject
Overall test of hypotheses 1 – 3 seeking evidence for conditional dependence of main effect $r(r,g)$, on other factors $r_p(r,g \cdot c, d, rg)=0.98$, $p=0.0002$, $n=9$. Reject spurious correlation. Also since strongest non-significant relationship is $r(rg,g)$, $r_p(r,g \cdot rg)=0.87$, $p=0.0054$. Reject		
4) Elevated coral recruitment in no-take marine reserve (where fish grazing is greater) is due to exceptionally high larval supply. Whilst this would not disprove the main hypothesis since elevated grazing and larval supply could enhance recruitment together, it could constitute an alternative explanation if larval supply were the only factor involved in determining recruitment. Tested using lagrangian simulation model of larval dispersal	GLM # coral larvae $P_{time}<0.001$ $P_{site}=0.12$ DP=3.9	Reject

*similar result using density of adult damselfishes

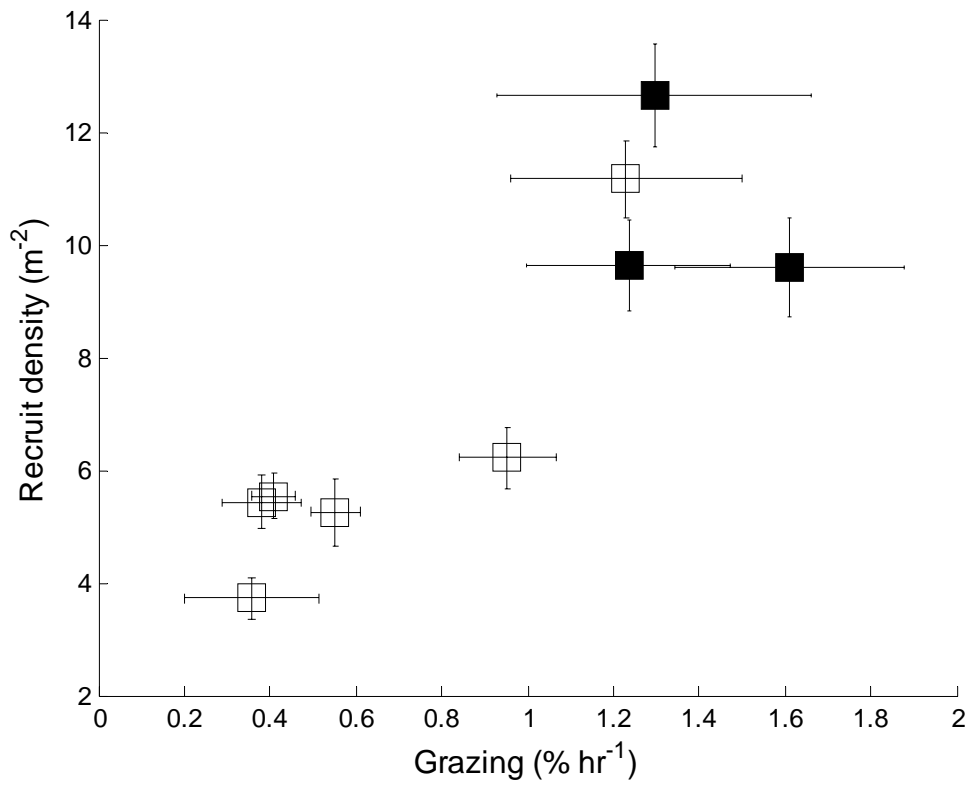


Fig. 1. Relationship between parrotfish grazing intensity and macroalgal cover in the Exuma Cays (\pm SE). Sites in the ECLSP denoted with solid squares.

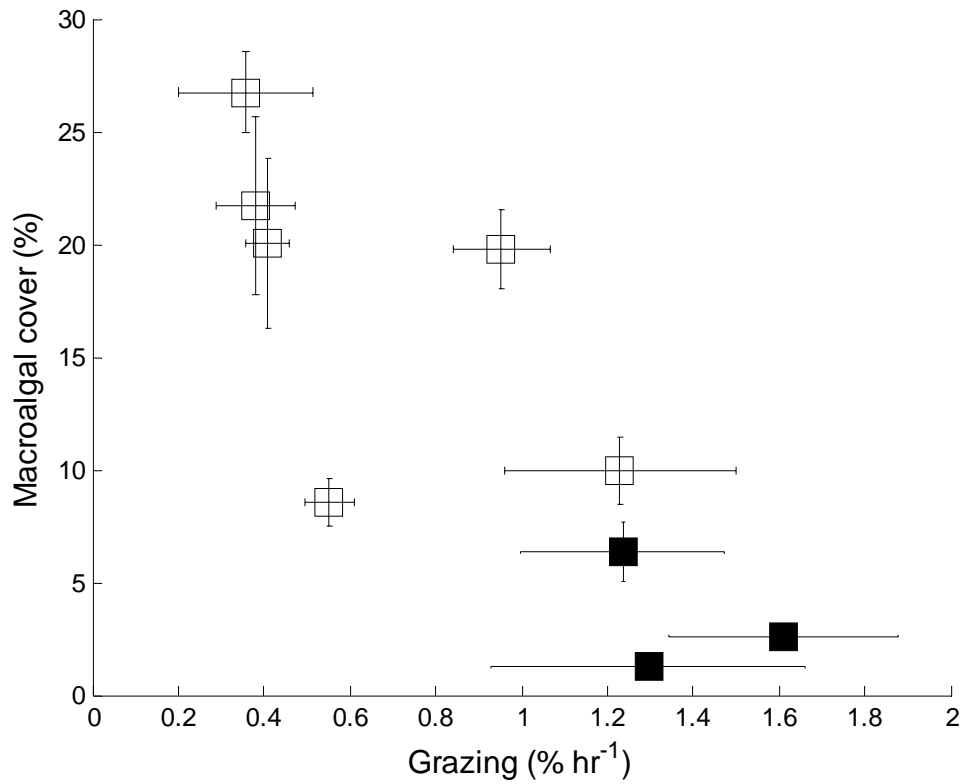


Fig. 2. Relationship between parrotfish grazing and the density of coral recruits (planar area $<20 \text{ cm}^2$) in the Exuma Cays ($\pm \text{SE}$). Sites in the ECLSP denoted with solid squares.

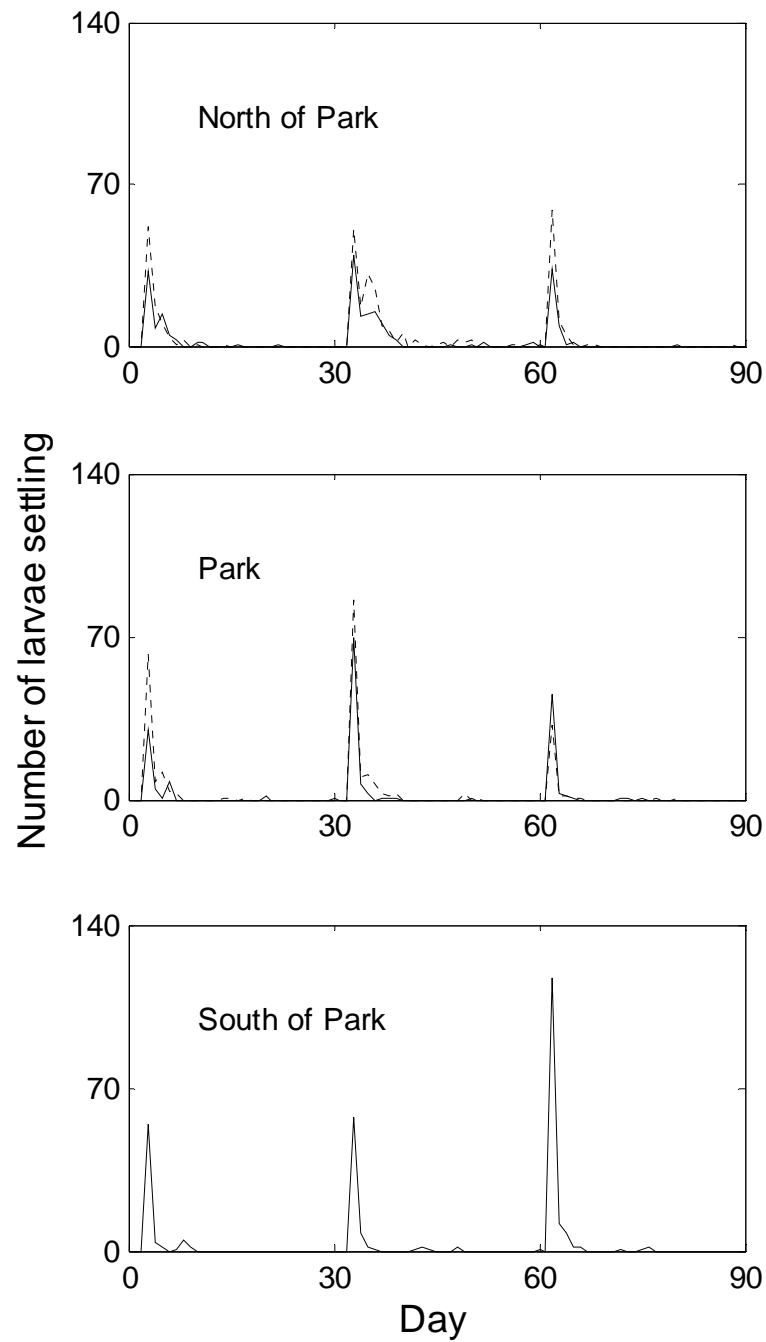


Fig. 3. Daily predicted larval supply of *Agaricia* spp. for the months June – August 2004 for three sectors: North of the ECLSP, the Park itself and South of the Park. Where a sector contained more than one 50 km² polygon with a study site, the results are plotted for each (solid line for the first polygon, dotted for the second).