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Evaluation of algal regulation by herbivorous fishes on Caribbean coral reefs

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Abstract

The role of herbivorous fishes in maintaining low macroalgal cover was evaluated on coral reefs on several reef sites from Guadeloupe, either protected or not. Grazing by herbivorous fishes was assessed on different algal facies using fish bite counts. Algal consumption by fish was estimated as well as algal production.

Bite counts revealed that herbivorous fishes feed preferentially on algal turf and avoid brown macroalgae. The algal consumption varied between 0.4 and 2.8 $g.m^{-2}.d^{-1}$ and was higher inside marine protected areas than outside. Comparison with algal production revealed that herbivorous fishes did not succeed in regulating algal growth. The insufficient number of grazers may lead to the dominance of stable assemblages of macroalgae on coral reefs, preventing the recovery of reef into previous coral-dominated ecosystems.

Key words Algal consumption; Caribbean region; Coral reefs; Herbivorous fishes; Herbivory pressure

Introduction

The widespread degradation of coral reefs and the shift from scleractinian coral-dominated towards macroalgae-dominated communities have been documented worldwide (Jackson et al. 2001; Gardner et al. 2003; Pandolfi et al. 2003, 2005; Bellwood et al. 2004, 2006; Hughes et al. 2003, 2007). Although Pandolfi et al. (2003) have pointed out that coral reefs have been degraded since the 1900's mainly from overfishing, it is widely accepted that the coral-algal shift has been accelerating in the recent years. The causes are multiple and can be from natural or anthropogenic origins (hurricanes, global warming, eutrophication, overfishing, pollution, increased sedimentation). Crustose coralline algae and algal turfs are a common component of healthy coral reefs, but nowadays, the decline of coral communities is associated to a proliferation in erect macroalgae cover (Pandolfi et al. 2003).

This shift in dominance of benthic organisms affects the Caribbean reefs where benthic communities, originally dominated by invertebrates (corals, sponges, gorgonians) associated with algal turf, are now often replaced by macroalgae (Hughes 1994). According to Gardner et al. (2003), a dramatic drop in coral cover has occurred across the Caribbean from 50% to 10% in the past three decades. In the French West Indies (F.W.I.), remote sensing of marine coastal ecosystems showed that only 15 to 20% of coral reef ecosystems are still flourishing, *i.e.* presenting a high rate of living coral spectral response (Chauvaud et al. 1998, 2001). The degradation of these coral reefs began in the 1950's (Bouchon and Laborel 1986, 1990) and nowadays the percentage of necrosed tissues on coral colonies is varying between 11 and 56% according to reef sites (Bouchon 2008a). Coral cover has declined and algal communities have supplanted coral communities with dominant brown macroalgae such as *Dictyota*, *Lobophora* and *Sargassum* (Bouchon et al. 2008b). In this context there is an urgent need to determine which ecological processes may limit algal pressure on coral reefs and, more particularly, what is the ability of grazing organisms to control this proliferation.

Previous studies have shown that, 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 resilience and 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 hence, by cascade, increased proliferation of algae (Jackson et al. 2001; Mumby

2006). Indeed, in many locations grazers are no longer present in sufficient numbers and biomass to limit and control algal growth, thus leading to the expansion of macroalgae to the detriment of scleractinian corals.

In this study, we propose to quantify algal consumption by fish as well as algal production on different reefs, to test whether herbivorous fishes have an influence on algal communities and how they may influence the stability of coral reefs.

Material and methods

Study area

Guadeloupe Island is located in the Lesser Antilles (Fig. 1). It is composed of two islands, Grande-Terre and Basse-Terre separated by a narrow channel called "Rivière Salée". Eleven reefs sites were studied around the island: six were located on barrier and fringing reef flats at one meter depth and five were situated on reef slopes between 10 to 15 m (Fig. 1). Four reef flats (S1, S2, S3, S4) are submitted to human influence (urban pollution, trap fishing, spear fishing, etc). The two other reef flats are located inside protected areas (S5 and S6) where fishing has been forbidden since 1979 and 1987 respectively. Three of the studied reef slopes are located inside MPA (S7, S8 and S9) and two others (S10 and S11) are submitted to urban pollution and heavy fishing.

Fish surveys

Estimates of fish abundances, both in density and biomass, were carried out on each reef site and obtained from a 150 X 2 meters transect. Each transect was replicated 2 times at each site. All species of Scaridae and Acanthuridae present on the coral reefs of Guadeloupe were studied: *Scarus iserti* Bloch, 1789, *Scarus taeniopterus* Desmarest, 1831, *Scarus vetula* Bloch and Schneider, 1801, *Sparisoma aurofrenatum* (Valenciennes, 1840), *Sparisoma chrysopterum* (Bloch and Schneider, 1801), *Sparisoma rubripinne* (Valenciennes, 1840), *Sparisoma viride* (Bonnaterre, 1788), *Acanthurus bahianus* Castelnau, 1855, *Acanthurus chirurgus* (Bloch,1787) and *Acanthurus coeruleus* Bloch and

Schneider, 1801. Herbivorous fishes present on the band-transects were identified, counted and their size estimated. Lengths were gathered in 5 cm size classes for fish under 20 cm and 10 cm size classes for fish larger than 20 cm. Fish biomass was then estimated using the median value of each class and weight-length relationships (WLR) available in the literature. The parameters *a* and *b* of the WLR used for each species are provided in Table 1.

Gut contents weighing and estimation of organic matter

All scarid and acanthurid species were collected on two reef flats (S2 and S3) by spear fishing, except *Scarus taeniopterus* and *S. vetula*, as they lived mainly in marine protected areas and could not be captured. The ventral cavity of each fish speared was immediately injected with 10% buffered formalin in order to stop the digestion process and the fishes were preserved in 10% formalin. After measuring the total length and weighting the fish, the digestive tract was removed and its content extracted. The gut content was dried to a constant weight at 80°C. The digestive tract contains a ground mixture of sediments and algae. The proportion of organic matter present in the digestive tract was estimated by two different methods. For the Scaridae, the rates previously established by Randall (1967) were retained. For the Acanthuridae, the proportions of algae and sediment contained in the digestive tract were evaluated with a visual estimation derived from that of Jones (1968). Gut contents spread in Petri dishes were photographed with a stereomicroscope. A grid was superposed to the digitized photos and the proportions of algae and sediment were estimated by point-intercept methods. After that, the algal and sediment rates were converted into volume by multiplying the obtained proportions by the densities of the sediment and the algae separately established.

Estimation of algal consumption by fish

Two different methods were used to evaluate the algal consumption by herbivorous reef fishes.

The first method (METHOD 1) consisted of building a curvilinear regression between the mass of dry organic matter found in the digestive tracts and the fish biomass. *Scarus taeniopterus* and *S. vetula* were assimilated to *S.iserti* and *Sparisoma rubripinne* respectively as 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) and Ferreira et al. (1998) who considered that guts are filled thrice daily for herbivorous fishes in the Caribbean. This method allowed obtaining a global algal consumption estimation using simultaneously fish density on the reefs and algal consumption per species.

In order to confirm the values obtained by the previous technique, a second method (METHOD 2) was used. This method used the regression provided by van Rooij et al. (1998) calculating the organic carbon intake (C) as a function of wet body weight (W in g) for herbivorous fishes:

$$\text{daily C intake} = 0.0342 * W^{0.816}$$

with an algae carbon content fit to 40.5% (Bruggemann et al. 1994).

To test whether METHOD 1 and METHOD 2 provide similar results, a regression was carried out with METHOD 1 as a function of METHOD 2. Spearman’ rank correlation test was used to test the correlation between both methods. Then, the proportionality between the two methods has been tested assuming that the regression slope (β) was equal to 1 (H_o: β=1). Because assumptions of normality were not met, non-parametric ANOVAs based on ranks were used to analyse algal consumption. These tests were implemented with R software. The null hypothesis was the absence of effects of *i*) used method to compute the algal consumption *ii*) fish species *iii*) MPA *iv*) sites. After that the Kruskal-Wallis one-way analysis of variance was used to compare the algal consumption between reef flats and reef slopes. Whenever a difference was found, multiple pairwise comparison tests were used to detect which sites were driving the observed differences.

Estimation of the net algal turf production

The measurements of net algal turf production were carried out in each site. For that purpose, floating plastic ribbons were settled on the bottom. A first experiment verified that the algal growth was approximately linear on a one month period. Then, 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. Net algal turf production was so estimated by dry weight per surface and per month. This technique minimized sediment deposition and herbivory from urchins and gastropods but not fishes or crustaceans.

Estimation of grazing rate

The rates of fish grazing were estimated on three reef flats (S2, S3, S6), according to the dominant algal community which was determined using a line intercept method (Lucas and Seber 1977). In S2, fish bites were studied on the two dominant algal facies: turf either growing on coral rubbles or on the reef flat limestone (29.0% of the benthic community) and Phaeophyta (*Dictyota pulchella* ; 28.3%). In S3, fish bites were recorded on algal turf (34.9%), Phaeophyta (*Dictyota pulchella* ; 20.1%) and a facies of *Halimeda* (calcified Chlorophyta ; 12.7%). In S6, fish bites were only evaluated on algal turf (62.5%), as it was the only algal facies to be present.

Grazing rates were estimated from observations made on areas of $1m^2$ (delimited on the bottom by 4 small stones at each corner). Upon arrival at the study site, fish were given a few minutes to acclimatize to the settling of the stones and to the diver before timed observation began. During period of five minutes, the identity of herbivorous fishes, their size and the number of bites taken by each fish feeding in the area were recorded. During episodes of intensive feeding by schools, the number of fishes was recorded and the total number of bites estimated from the observation of a reduced number of individuals. On each site and in each algal facies, the feeding behaviour of fish was recorded during 6 replicated periods of five minutes on five different quadrats, that is a total of 150 minutes of observations for each type of algal facies.

The Kruskal-Wallis one-way analysis of variance was used to compare the grazing pressure between sites. Whenever a difference was found, multiple pairwise comparison tests were used to detect which sites were driving the observed differences. The affinity of the herbivorous fishes with the different algal facies was searched by factorial correspondence analysis (FCA).

Results

Fish consumption of algae

Proportions of organic and inorganic matter in the gut, derived from Randall (1967) for the Scaridae and determined in the present study for Acanthuridae, are given in Table 2. *Acanthurus coeruleus* ingest 100% of organic matter. For *A. bahianus* and *A. chirurgus*, the proportions were found to be respectively of 19.1% and 18.6%. For the Scaridae, the proportions varied between 23.1% and 31.4%. All the correlation coefficients associated with the linear regression (fish weight versus dry organic matter weight in the gut) were statistically significant (Spearman's rank correlation: $p < 0.001$ for all the species; Table 3).

Total algal consumption values obtained using the two methods are presented in Table 4, as well as the algal consumption per species derived from METHOD 1. Values obtained from the two methods are linearly correlated (Fig. 2). Spearman's rank correlation coefficient is statistically significant ($r_s = 0.915$; $p < 0.0001$). Student's *t* statistic showed that the regression slope β was not different from 1 for the values of algal consumption of the global assemblage ($t = 1.81$; $t_{0.05(2),147} = 1.976$) as well as for the consumption by species (t always $< t_{0.05(2),5} = 2.571$). Results from the four-way ANOVA based on ranks showed that the estimation of algal consumption was not influenced by the method used for its computation ($F_{(1,140)} = 2.250$, $p = 0.136$).

Concerning the studied reef sites, results from four-way ANOVA on ranks revealed that, on the whole, the algal consumption was influenced by the protection status of the sites ($F_{(1,140)} = 13.179$, $p < 0.001$) and by the type of sites (reef flats or reef slopes) ($F_{(1,140)} = 4.155$, $p = 0.043$). A Kruskall-Wallis test was used to detail this result between reef flats and reef slopes. Its results 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 mainly due to sites S5 and S6 (MPA), which presented a high level of algal consumption (2.8 and 2.5 $g.m^{-2}.d^{-1}$) compared to S1, S2 and S3 where the consumption values were low (respectively 0.7; 1 and 0.4 $g.m^{-2}.d^{-1}$). These differences were due to fish densities (Table 5) which varied between sites. Algal consumption was more important in S5 and S6 as herbivorous fishes were well represented in biomass (Table 5). Results for S1, S2 and S3 were closer because of their equivalent herbivore assemblages in terms of abundance. A Kruskall-Wallis' test comparing the reef slopes (S7 to S11) showed no significant difference (p-value = 0.88) in the algal consumption that is relatively stable whatever the localization.

Finally, results from four-way ANOVA on ranks pointed out that the algal consumption was different according to the fish species considered ($F_{(9,140)} = 13.514$, $p < 0.001$). Examination of Table 4 shows that *Acanthurus bahianus, A. coeruleus* and *Sparisoma viride* exerted a high consumer pressure (2.6; 3.5 and 2.32 $g.m^{-2}.d^{-1}$ respectively).

Net algal turf production and algal gross production

Net algal turf production was relatively stable between the different reef flats and varied between 0.6 and 1.29 $g.m^{-2}.d^{-1}$ (Table 6). On the reef slopes (S7 to S10), values were lower (0.3 to 0.8 $g.m^{-2}.d^{-1}$). To determine the daily algal gross production on the studied coral reefs, net algal turf production was added to herbivorous fish consumption (Table 6). Algal gross production varied between 1.48 and 3.78 $g.m^{-2}.d^{-1}$ on the reef flats with maximum values observed in S5 and S6. On the reef slopes, algal gross production varied between 1.41 and 1.98 $g.m^{-2}.d^{-1}$.

Estimation of grazing pressure

Preferred algal facies

The grazing pressure of herbivorous fishes was measured on four facies of algae in three sites, S2, S3 and S6.

At S3, three facies of algae were compared. A Kruskall-Wallis test revealed a significant difference between the grazing pressures among the different algal facies when considering the number of bites ($p < 0.0001$). Multiple pairwise comparison tests show that the differences were due to the Phaeophyta facies which is the less grazed. The herbivory pressure was not statistically significant between the other algal facies (algal turf growing on coral rubble and on limestone).

At site S2, four algal facies were present: turf on limestone, turf on rubble, *Dictyota* and *Halimeda*. A Kruskal-Wallis test revealed a significant difference between the grazing pressure among the four algal facies ($p = 0.001$). Pairwise comparison tests showed that this difference could be attributed again to *Dictyota*, less grazed by the fishes.

Figure 3 represent the number of bites counted in the three sites. The rates of fish bites varied between 6936 and 70545 bites.m^{-2}.d^{-1} with the lowest grazing rate recorded on *Dictyota* in S3 and the highest on coral rubble in S2. In S2 and S3 the grazing rate was the greatest on the turf zones and was lower on the macroalgae. In S6 (MPA) only algal turf was present and grazing rate was lower that in the other sites.

Species preferences

In order to highlight peculiar affinities between the herbivorous species and the different facies of algae, a factorial correspondence analysis (FCA) was carried out crossing the number of bites per species and the different algal facies (Fig. 4). The first two axes explain 97% of the variance of the data with 76% on axis 1 and 21% on axis 2. The first axis opposes the algal turf growing on limestone to the three other facies. The species contributing most to this axis are *Acanthurus coeruleus* and *Sparisoma aurofrenatum* which graze preferentially on algal turf. On the other side of the axis, *Sparisoma rubripinne* is more linked to the *Halimeda* facies and to the turf growing on coral rubble. Axis 2 opposes *Dictyota* to *Halimeda*, underlining a preferential distribution of *Acanthurus bahianus* on Phaeophyta and of *Sparisoma viride* on the *Halimeda* facies. The feeding preferences of the other species are more eclectic.

Discussion and conclusions

Algal consumption and production

The algal consumption obtained in the present work (between 0.68 and 2.79 g.m^{-2}.d^{-1}) are in accordance with the values reported by other authors (Table 7) and particularly with the most recent study of Paddack et al. (2006). Contrarily, the values of production estimated in the present study are relatively low compared to those found by other authors. Indeed, when estimating the algal production in the present work, herbivorous fishes, urchins and gastropods were able to graze on the experimental device. The net algal turf production might be consequently under-estimated. When considering fish algal consumption and adding it to the net algal turf production in order to obtain a gross algal production, the values estimated in the present study remain low compared to those found in previous studies (Table 7).

The comparison between algal consumption and production permitted to highlight the quantitative regulation of algae by herbivorous fishes. Thus, on non-protected and heavily fished coral reefs, although the herbivorous fishes are numerically abundant, the small sizes reached by these fishes did not allow them to regulate the algal production. Once epilithic algal turf grows, propagules of macroalgae can develop until their adult size when they become resistant to herbivory.

In marine protected areas, where fishes reach large sizes (Table 5; Hawkins and Roberts 2003), herbivorous fishes consume a larger part of the algal production. On these reefs the herbivorous populations are almost intact and can better ensure their role of regulation on algae than outside marine reserves. On the protected reefs of Bonaire, van Rooij et al. (1998) established that the primary production of algae was completely consumed by herbivores. Carpenter (1986) also observed this phenomenon in the Virgin Islands and argued that herbivores are able to take 100% of the daily algal production. For Hatcher (1981) in Australia, herbivores can consume between 20 and 70% of the algal production on the reefs.

The choice of a stomach repletion rate of 3 times per day food intake may have an influence on the estimated consumption. This value varies among authors. In French Polynesia, Polunin et al. (1995) determined fish food intakes between 1.7 and 13.8 times per day according to the considered species and using stomach repletion rates. Polunin and Klumpp (1992) in Australia determined that herbivorous fishes feed 10.5 times per day in summer and 5.5 times per day in winter using fish feeding rate. For Hatcher (1981) in Australia also, fish daily feeding rate varies between 2.5 and 8.4 with a mean of 5.2 times per day. In the Caribbean, Gygi (1975) determined that *Sparisoma viride* filled up its stomach 1 time per day whereas according to Bruggemann et al. (1996) the same species filled up its stomach 10 times a day based on species feeding rates. Ferreira et al. (1998), based on gut turnover, have determined that Scaridae feed between 2.4 and 2.7 times per day and approximately 3 times per day for the Acanthuridae. Comparison between the results of the present study and those obtained with the estimation of van Rooij et al. (1998) reveals that our estimation was probably appropriate for the Caribbean.

Finally, this study shows that the three species of Acanthuridae (*Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus*) and *Sparisoma viride* are the herbivores ingesting the most important quantity of algae. Two hypotheses can be formulated to explain this fact. First, these four species could have a food digestion lower than the other species and consequently they would have to ingest more food than the other species. A second hypothesis would be that the growth of these species is faster than those of other species and so they have to consume more food to sustain their higher metabolism. Randall (1962) showed that the monthly growth of *Acanthurus bahianus* is 2.7 mm, that of *A. chirurgus* is 2.3 mm, that of *A. coeruleus* 1.3 mm and that of *Sparisoma viride* varies between 3.5 and 7.7 mm. Other scarid species have more important growth rates (for example between 11 and 18 mm per month for *Scarus vetula*) and nevertheless they ingest a lower quantity of organic matter. These results tend to confirm that the first hypothesis would be the most likely.

Feeding rate

The rates of fish bites obtained in the present work (between 6936 and 70545 bites.m^{-2}.d^{-1}) are in accordance with the values reported by other authors. Carpenter (1986) found in St. Croix (U.S. Virgin Islands) that scarid fishes are able to give between 20000 and 156000 bites.m^{-2}.d^{-1} according to the period of the year. For Steneck (1983), the mean number of *bites* on a reef is 5000 bites.m^{-2}.h^{-1}, that is to say, 60000 bites.m^{-2}.d^{-1}.

The results of the present work also revealed that herbivorous fishes feed preferentially on certain type of algae. Algal turf is the favourite food source for herbivorous fishes. Such preferences have already been noted for Caribbean herbivorous fishes (Bruggemann et al. 1994; Paddack et al. 2006) as well as for herbivorous fishes in general (Steneck 1988; Bellwood and Choat 1990). Van Alstyne et al. (1999) reported that algal turf, partly constituted by young shoots of macroalgae, is the most consumed because these shoots contain higher nitrogen concentration in their tissues than old algae. This phenomenon may influence the food choice of herbivorous fishes seeking protidic complements (Mattson 1980). Moreover, algal turf is easily digested and has a higher energetic and proteinic value than macroalgae (Bruggemann et al. 1994).

Conversely, herbivorous fishes avoid brown macroalgae, mainly composed of *Dictyota* spp. in the studied reefs. This phenomenon can be explained in two ways. First, the presence of repulsive or toxic molecules renders macroalgae less palatable and digestive to herbivorous fishes particularly for the *Dictyota* algae that would be the less consumed by herbivorous fishes because they contain diterpenoids that protect them from fish and sea urchins herbivory (Hay et al. 1987; Barbosa et al. 2004). The predominance of this type of algae on the studied non-protected reefs may explain why the herbivory rate is very low. However, some bites have been observed on these macroalgae. Fishes may graze the epiphytic microalgae that grow on the macroalgae thallus. Secondly, the thallus calcification of some algae would prevent fishes from feeding on them (Ochavillo et al. 1992). This hypothesis does not seem to correspond to the results of the present study as the number of bites observed on *Halimeda* spp. is comprised between those observed on algal turf and those on Phaeophyta. According to Schupp and Paul (1994), surgeonfishes avoid grazing on algae containing calcium carbonate like *Halimeda* spp.. Steneck (1988) argue that Acanthuridae are not able to crunch on calcified or incrusting algae because of their dentition, whereas scarids can ingest all algal types. So, the Scaridae would be the only fishes that sometimes consume *Halimeda* spp., such as *Sparisoma viride* in the present study and that of Overholtzer and Motta (1999).

Finally, the grazing rate has been found to be highly correlated with herbivorous fish abundance like in the studies of Lewis and Wainwright (1985) and Carpenter (1986). The reefs presenting the higher grazing pressure harbour the highest abundance of herbivorous fishes but the lowest biomass. Carpenter (1986, 1988, 1990) explained this phenomenon as the majority of herbivores was juvenile scarids that have a small mouth. They produce a high number of bites which only remove small quantities of algae. This can explain why even when herbivorous fishes present high number of individuals, macroalgae can cover large parts of the reef. Algal turf develops into more enduring macroalgae, preventing the recovery of the reef into its previous coral dominated state (Szmant 2002). In marine protected areas, although the rate of fish bites is the lowest, macroalgae are absent. In fact, fishes are of large size in protected areas. They do few bites but efficient ones preventing phase shift by keeping algae cropped down.

This study demonstrated that the role of herbivorous fishes in promoting reef recovery and resilience is likely to depend not only on their feeding preferences but also on their numerical abundance and on their biomass. Fish abundance and mostly fish biomass might be expected to increase when algal production increased in order to control macroalgal proliferation. However, overfishing prevent the establishment of such a feed back control except in MPA where the protection status renders algal regulation possible by maintaining healthy herbivorous fish assemblages.

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Figure and table captions

Fig. 1 Map of the Guadeloupe Island and location of the studied sites (S1 to S11)

Fig. 2 Algal consumption values (g.m^{-2}.d^{-1}) regressed with METHOD 1 versus METHOD 2

Fig. 3 Daily number of fish bites (± S.E.) per 100m^{-2} in S2 (grey bars), in S3 (white bars) and in S6 (dark bar)

Fig. 4 Results of the factorial correspondence analysis crossing the number of bite per species and the different algal facies

Table 1 Parameters of the weight-length relationship with a: coefficient and b: exponent. Values for *Sparisoma viride* were used for *Scarus vetula* as no data is available in the literature

Table 2 Proportions of organic and inorganic matter in digestive tract contents of herbivorous fishes (in %). a: present study; b: Randall, 1967

Table 3 Table 3 Correlation coefficients associated with the linear regression between gut contents *versus* fish biomass, slope and intercept (P value: *** $P \leq 0.001$; ● $P > 0.05$)

Table 4 Daily algal consumption rates ($g.m^{-2}.d^{-1}$) obtained for each species in each site with *METHOD 1* and total algal consumption of the whole herbivorous fish assemblage obtained with both methods. Sites: S1 to S11

Table 5 Mean (± S.E.) number of individuals ($.100m^{-2}$), biomass ($kg.100m^{-2}$) and total length (cm) of herbivorous fishes observed in the different studied sites

Table 6 Algal consumption by herbivorous fishes, algal turf net production, daily algal gross production ($g.m^{-2}.d^{-1}$) and algal consumption as a percentage of gross production (%) in each site

Table 7 Values of algal consumption by different kinds of herbivores and algal production on several reefs

Table 1 Parameters of the weight-length relationship with a: coefficient and b: exponent. Values for *Sparisoma viride* were used for *Scarus vetula* as no data is available in the literature

Species	*a*	*b*	Source
Scarus iserti	0.0166	3.0200	Claro and Garcia-Arteaga 1994
Scarus taeniopterus	0.0176	2.9990	Bouchon-Navaro 1997
Scarus vetula	0.0251	2.9214	cf *Sparisoma viride*
Sparisoma aurofrenatum	0.0301	2.8184	Bouchon-Navaro 1997
Sparisoma chrysopterum	0.0229	2.8801	Bouchon-Navaro 1997
Sparisoma rubripinne	0.0474	2.6824	Bouchon-Navaro 1997
Sparisoma viride	0.0251	2.9214	Bohnsack and Harper 1988
Acanturus bahianus	0.0203	2.9281	Bouchon-Navaro 1997
Acanthurus chirurgus	0.0183	3.0129	Bouchon-Navaro 1997
Acanthurus coeruleus	0.0298	2.8778	Bouchon-Navaro 1997

Table 2 Proportions of organic and inorganic matter in digestive tract contents of herbivorous fishes (in %). a: present study; b: Randall 1967

Species	Organic matter	Inorganic matter	Source
Acanthurus bahianus	19.1	80.9	a
Acanthurus chirurgus	18.6	81.4	a

Acanthurus coeruleus	100		0		a
Scarus iserti	24.6		75.4		b
Scarus taeniopterus	26.4		73.6		b
Scarus vetula	23.1		76.9		b
Sparisoma aurofrenatum	24.5		75.5		b
Sparisoma chrysopterum	30.5		69.5		b
Sparisoma rubripinne	31.4		68.6		b
Sparisoma viride	27.1		72.9		b

Table 3 Correlation coefficients associated with the linear regression between gut contents versus fish biomass, slope and intercept (P value: *** $P \leq 0.001$; $^{\bullet}$ $P > 0.05$)

Species	*r* coefficient	Number of individuals	Slope	Intercept
Acanthurus bahianus	0.6068	23	0.012***	0.565$^{\bullet}$
Acanthurus chirurgus	0.8628	20	0.015***	0.442$^{\bullet}$
Acanthurus coeruleus	0.9111	29	0.015***	-0.101$^{\bullet}$
Scarus iserti	0.8600	27	0.009***	-0.014$^{\bullet}$
Sparisoma aurofrenatum	0.7106	21	0.006***	0.053$^{\bullet}$
Sparisoma chrysopterum	0.8726	20	0.008***	0.062$^{\bullet}$
Sparisoma rubripinne	0.8797	21	0.001***	0.175$^{\bullet}$

Sparisoma viride	0.9018	21	0.011***	-0.313$^{\bullet}$

Table 4 Daily algal consumption rates (g.m^{-2}.d^{-1}) obtained for each species in each site with METHOD 1 and total algal consumption of the whole herbivorous fish assemblage obtained with both methods. Sites: S1 to S11

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	Total per species
Acanthurus bahianus	0.19	0.06	0.14	0.34	0.93	0.43	0.07	0.16	0.11	0.16	0.83	3.43
Acanthurus chirurgus	0.10	0	0.01	0.54	0.25	0.01	0.01	0.01	0	0.33	0.05	1.30
Acanthurus coeruleus	0.25	0.7	0.07	0.45	0.79	0.42	0.07	0.07	0.05	0.60	0.06	3.53
Scarus iserti	0.06	0.12	0.06	0.13	0.51	0.06	0	0.12	0.26	0.11	0.01	1.44
Scarus taeniopterus	0.01	0.02	0.04	0	0.03	0.32	0.08	0.06	0.20	0.04	0	0.80
Scarus vetula	0.02	0	0	0	0.01	0.55	0.12	0.01	0	0.01	0	0.72
Sparisoma aurofrenatum	0.01	0	0.01	0.02	0.03	0.08	0.12	0.19	0.35	0.11	0.14	1.05
Sparisoma chrysopterum	0.01	0.03	0.03	0.05	0.05	0.06	0.01	0	0	0.01	0	0.25
Sparisoma rubripinne	0.01	0.03	0.02	0.17	0.04	0.08	0.07	0.05	0	0	0.15	0.62
Sparisoma viride	0.02	0.02	0.02	0.04	0.16	0.53	0.57	0.51	0.34	0.11	0.01	2.33
Total per site												
METHOD 1	0.68	0.98	0.4	1.75	2.79	2.54	1.11	1.18	1.32	1.49	1.24	
METHOD 2	0.81	1.09	0.67	2.05	3.24	2.77	1.14	1.61	1.77	1.56	1.36	

Table 5 Mean (± S.E.) number of individuals (.100m^{-2}), biomass (kg.100m^{-2}) and total length (cm) of herbivorous fishes observed in the different studied sites

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11
Number	60.3 ± 12.5	56.2 ± 4.5	113.2 ± 15.3	115.0 ± 7.3	167.1 ± 6.1	87.7 ± 11.5	21.8 ± 2.4	97.7 ± 29.2	67.5 ± 16.0	64.4 ± 32.6	144.3 ± 11.4
Biomass	2.1 ± 1.5	2.8 ± 0.5	1.4 ± 0.7	5.3 ± 0.5	8.4 ± 1.3	8.4 ± 1.6	3.8 ± 0.9	4.5 ± 1.3	3.2 ± 0.8	4.8 ± 2.6	2.9 ± 0.4
Length											
Acanthurus bahianus	10.7 ± 0.6	10.5 ± 0.6	8.8 ± 0.5	11.0 ± 0.2	12.5 ± 0.2	11.8 ± 0.3	13.2 ± 0.5	12.1 ± 0.3	13.1 ± 1.1	10.0 ± 0.3	9.8 ± 0.2
Acanthurus chirurgus	16.0 ± 0.8	/	10.0 ± 1.4	15.1 ± 0.2	14.1 ± 0.3	12.5 ± 0	12.5 ± 0	17.5 ± 0	/	21.3 ± 0.6	9.4 ± 0.7
Acanthurus coeruleus	10.7± 0.7	13.4 ± 0.3	9.2 ± 0.7	13.9 ± 0.5	13.4 ± 0.3	13.9 ± 0.3	14.4 ± 0.8	12.5 ± 0.6	10.7 ± 2.1	18.8 ± 0.8	7.8 ± 0.3
Scarus iserti	9.0 ± 0.4	10.9 ± 0.5	6.3 ± 0.2	7.9 ± 0.3	11.6 ± 0.3	17.3 ± 0.8	/	7,5 ± 0.2	9.4 ± 0.3	8.5 ± 0.4	5.5 ± 0.8
Scarus taeniopterus	9.0 ±0.6	12.9 ± 1.1	6.3 ± 0.2	/	12.7 ± 0.2	16.2 ± 0.4	14.6 ± 1.2	8.8 ± 0.7	11.8 ± 1.1	13.8 ± 5.0	/
Scarus vetula	18.1 ± 2.6	/	/	/	17.5 ± 0	24.8 ± 1.1	33.0 ± 3.7	25 ± 0	/	25 ± 0	/
Sparisoma aurofrenatum	7.5 ± 0	/	13.2 ± 1.3	15.0 ± 1.1	15.7 ± 1.0	16.3 ± 0.4	16.3 ± 1.0	14.8 ± 0.6	15.0 ± 0.9	14.5 ± 1.0	10.9 ± 0.4
Sparisoma chrysopterum	10.9 ± 2.5	12.3 ± 1.4	10.0 ± 1.1	17.3 ± 2.1	14.8 ± 2.3	18.9 ± 2.6	17.5 ± 0	/	/	18.3 ± 3.6	/
Sparisoma rubripinne	12.5 ± 1.6	13.8 ± 1.8	16.0 ± 2.9	17.9 ± 1.2	22.0 ± 1.8	24.1 ± 2.8	33.0 ± 2.2	31.7 ± 3.3	/	/	11.0 ± 0.4
Sparisoma viride	7.4 ± 0.8	10.6 ±1.1	7.9 ± 1.0	12.8 ± 1.8	13.5 ± 1.5	24.0 ± 1.4	26.4 ± 2.0	16.3 ± 1.5	14.3 ± 1.3	15.6 ± 1.9	7.8 ± 0.4

Table 6 Algal consumption by herbivorous fishes, algal turf net production, daily algal gross production (g.m^{-2}.d^{-1}) and algal consumption as a percentage of gross production (%) in each site

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11
Algal consumption (g.m^{-2}.d^{-1})	0.68	0.98	0.4	1.75	2.79	2.54	1.11	1.18	1.32	1.49	1.24
Algal turf net production (g.m^{-2}.d^{-1})	0.80	1.15	1.29	0.60	1.00	1.24	0.30	0.80	0.50	0.30	/
Daily algal gross production (g.m^{-2}.d^{-1})	1.48	2.13	1.69	2.35	3.79	3.78	1.41	1.98	1.82	1.79	/
Consumption/gross production (%)	45.9	46	23.7	74.5	73.6	67.2	78.7	59.6	72.5	83	/

Table 7 Values of algal consumption by different kinds of herbivores and algal production on several reefs

Location	Authors	Algal production (g of algae.m^{-2}.d^{-1})	Consumption	
			Species	g of algae.m^{-2}.d^{-1}
Guadeloupe	Present study	1.4 - 3.8	Herbivorous fishes	0.4 - 2.5
Bonaire	van Rooij et al. 1998	4.25	Herbivorous fishes	4.3
			Urchins	0.5
Virgin islands	Carpenter 1986	5.7 - 7.1	Herbivorous fishes	5 - 8.2
	Carpenter 1985	5.2 - 7.7		
Florida	Paddack et al. 2006	2.6	*Sparisoma viride*	0.4
			Herbivorous fishes	1.7
Australia	Polunin and Klumpp 1992	4.4 - 5.3	Amphipod	78.7 - 90.7 (.10^{-3})
			Copepod	1.85 - 2 (.10^{-3})
			Other crustacean	84.6 - 98.5 (.10^{-3})

			Mollusc	41.4 - 47.5 (.10^{-3})
			Polychete	64.4 - 74.1 (.10^{-3})
			Gasteropod	14.9 - 18.1 (.10^{-3})
			Acanthurus lineatus	1.57 - 2.16
	Klumpp and McKinnon 1989	2.75 - 6.2		
	Russ 2003	0.5 - 2.9		
Marshall islands	Bakus 1967	1.6 - 5.3		

Figure1_Kopp_HMR2

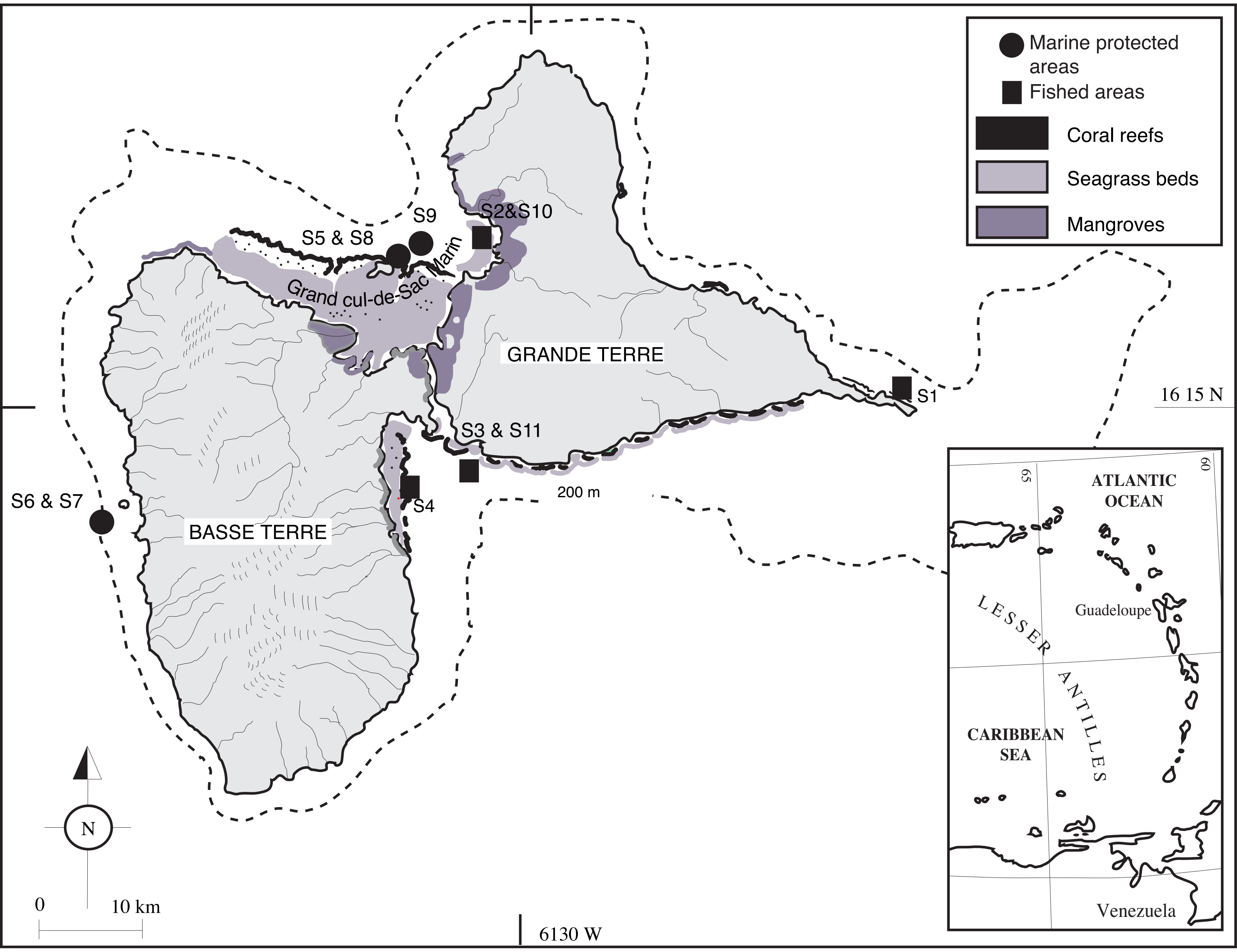

Figure2_Kopp_HMR2

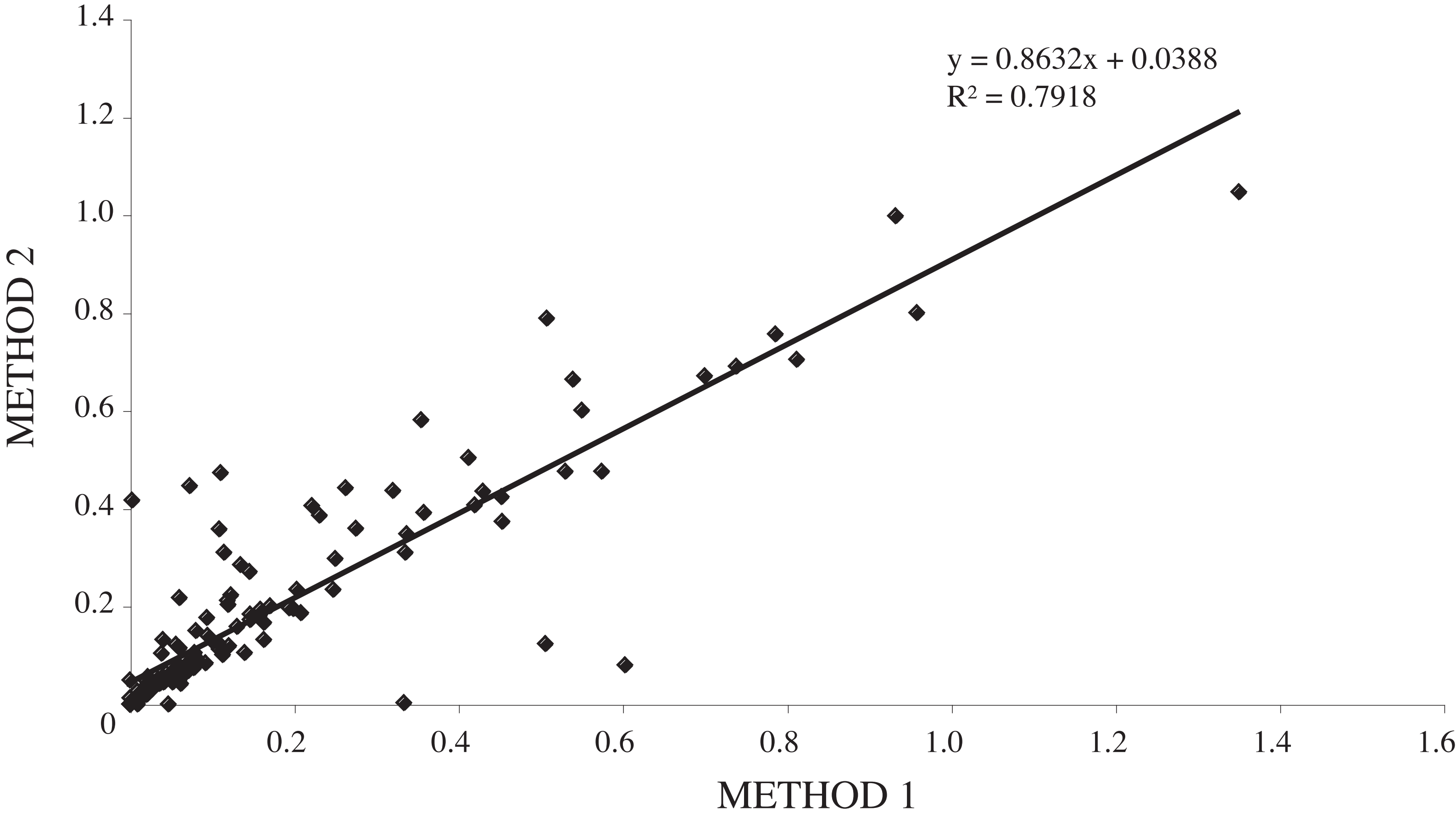

Figure3_Kopp_HMR2

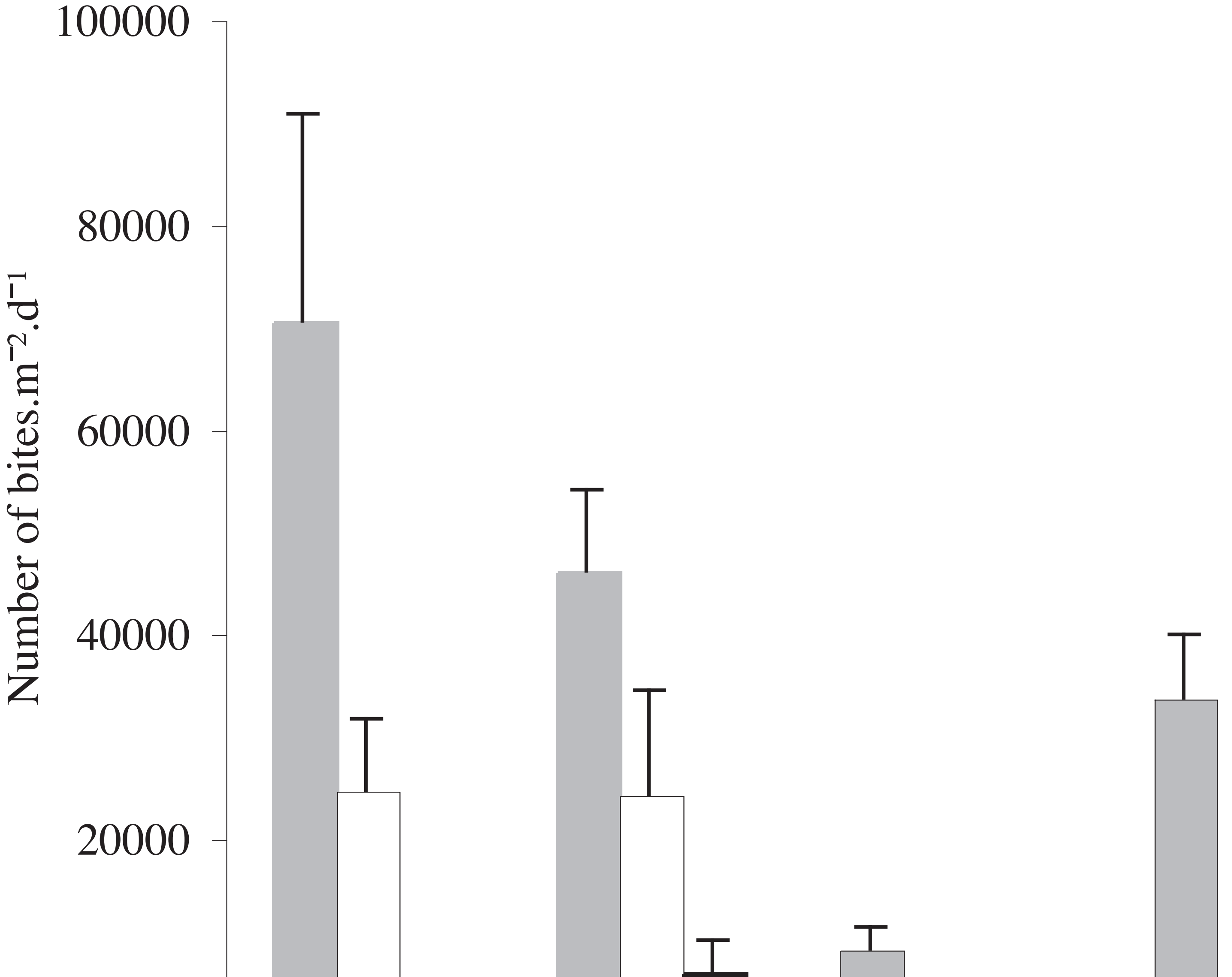

Figure4_Kopp_HMR2