

# Density of herbivorous fish and intensity of herbivory are influenced by proximity to coral reefs

Ryan A. Downie<sup>1,3,\*</sup>, Russell C. Babcock<sup>1,2</sup>, Damian P. Thomson<sup>1</sup>,  
Mathew A. Vanderklift<sup>1</sup>

<sup>1</sup>CSIRO Wealth from Oceans Flagship, Centre for Environment and Life Sciences, Western Australia 6014, Australia

<sup>2</sup>CSIRO Wealth from Oceans Flagship, Ecosciences Precinct, Queensland 4001, Australia

<sup>3</sup>CSIRO Wealth from Oceans Flagship, Hobart Laboratories, Tasmania 7000, Australia

**ABSTRACT:** Ecosystems can be profoundly influenced by consumers, sometimes to the extent that the entire appearance of the ecosystem is altered. We used remotely sensed images to identify distinctive halos around patch reefs in the lagoon of Ningaloo Reef, the world's largest fringing coral reef. Thirty-four halos were identified along the length of Ningaloo Reef. Five halos located within a 122 km tract of the reef were investigated. The halos extended >90 m from each central patch reef and were found to be associated with a high biomass of, and intensive grazing by, herbivorous fish, especially the large-bodied *Kyphosus sydneyanus*. Large brown algae mainly of the genera *Sargassum*, *Dictyopteris* and *Lobophora* were the dominant macroalgae, but were almost absent immediately adjacent to the patch reefs. Other taxa of herbivorous fish were present near the patch reefs, including *Naso* spp., *Siganus* spp. and *Scarus* spp., but the biomass of each was low and none were significant contributors to grazing. The sizes of the halos reported here are tenfold larger than those previously reported in coral reef systems and are likely to be the result of intensive herbivory by *K. sydneyanus*.

**KEY WORDS:** Ningaloo · Macroalgae · Halo · Patch reefs · *Kyphosus sydneyanus*

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## INTRODUCTION

Fish assemblages of shallow coastal marine habitats are strongly influenced by the nature of the surrounding seascape (Steele & Forrester 2002, Vanderklift et al. 2007, Hitt et al. 2011). The arrangement of these habitats (i.e. their spatial extent and how they are juxtaposed) influences the abundance of individuals and composition of species, and the rates of important processes such as grazing, predation and settlement of larvae (Almany & Webster 2006, Rilov & Schiel 2006, Wernberg et al. 2006, Grol et al. 2008). For example, the proximity between coral reefs where adult fish reside and those habitats that juveniles inhabit, such as seagrass beds, mangrove forests and sand flats, has been shown to have a significant influence on species composition (Milchunas

& Noy-Meir 2002, Nagelkerken et al. 2002, Steele & Forrester 2002, Grol et al. 2011), while proximity to reefs can influence the rates of processes, such as herbivory, that are important for maintaining the integrity of coral reefs (Valentine et al. 2008).

Trophic interactions can in turn affect the landscape within which they occur. For example, some terrestrial ecosystems that have experienced an increase in predator abundance have shifted from herbivore-dominated states with low plant biomass to states with a much higher biomass of plants (Ripple & Beschta 2004). Similarly, in temperate rocky reefs trophic interactions can result in changes in the abundance of habitat-forming macroalgae (Babcock et al. 1999), although such changes can be context-specific (Shears et al. 2008, Cook & Vanderklift 2011).

\*Email: ryan.downie@csiro.au

The extent of foraging excursions into adjacent habitats depends on a number of influences, including proximity and extent of juxtaposed habitats, predator density and the size and mobility of individuals. Species exploit adjacent habitats via 2 broad strategies: from a central place of refuge or through flexible foraging behaviour (Lima 1998, Brown et al. 1999). The term 'central place foraging' describes a behaviour in which individuals reside in habitats that provide shelter to which they can retreat in the event of encountering a predator (Lessells & Stephens 1983, Lima 1998). Central place foraging can decrease the abundance of food resources in the immediate vicinity of a refuge (Lessells & Stephens 1983, Festa-Bianchet 1988), necessitating foraging at increasingly greater distances from shelter. The theory predicts that the trade-off between the benefits of foraging further afield and predation risk will even out at a maximum safe foraging distance. Flexible foraging behaviour can minimise the risk of encountering a predator, and can include passing through non-preferred habitat and only foraging in specific areas at times where an individual perceives the risk of predation to be relatively low (Festa-Bianchet 1988, Lima 1998). For example, in tropical coral reef systems some species of fishes display diel variation in foraging habitat, foraging in seagrass beds or low-relief habitat at night and in habitats with relatively high relief such as mangroves and coral reefs during the day (Grol et al. 2008, 2011, Valentine et al. 2008, Luo et al. 2009).

Herbivorous coral reef fish and invertebrates often forage in seagrass- or macroalgae-dominated habitat surrounding reefs. Randall (1965) described a pattern in the Caribbean where seagrass biomass was low up to 30 ft (9.1 m) from the edge of coral reefs and patch reefs, because of grazing by herbivorous fish. Similar patterns were described by Ogden et al. (1973) and found to be due to grazing by sea urchins. This pattern has also been observed in the Florida Keys (USA) and on the Great Barrier Reef (Australia), where grazing halos with a maximum extent of 10 m corresponded to increased grazing pressure adjacent to coral habitat (Valentine et al. 2007, Madin et al. 2011).

Because grazing halos can be detected in clear water by satellite and airborne remote sensing (Andréfouët et al. 2001), it has been suggested that they may provide a rapid and cost-effective means of surveying reefs and detecting changes in the intensity of grazing (Madin et al. 2011). However, interpreting such patterns may be complex (Andréfouët et al. 2003, Brock et al. 2006). Factors such as local

hydrodynamic forces around patch reef structures, related sediment grain size sorting, shading and local availability of nutrients are also potentially important and are likely to act at similar spatial scales to previously observed patterns (Randall 1965, Ogden et al. 1973, DeFelice & Parrish 2001).

This study was initiated to investigate large ( $\geq 90$  m radius) halos observed in aerial photographs and images derived from a hyperspectral survey of Ningaloo Reef (Kobryn et al. 2012). Here, we quantify patterns in the biomass and composition of herbivorous fish, invertebrates and macroalgae, and species-specific rates of grazing around 6 halos. Our main objective was to determine the rates of herbivory, and the identity of the main herbivores, associated with these halos.

## MATERIALS AND METHODS

We conducted our study in the Ningaloo Marine Park between 2008 and 2009. Ningaloo Reef is a fringing reef that extends for 300 km off the Western Australian coast. The reef is typically <3 km wide with a maximum width of just over 6 km and has a characteristic fringing reef structure composed of a lagoon, reef flat, reef crest and forereef (Stoddart 1969). The lagoon is dominated by unconsolidated sand, often overlying low-relief limestone pavement, with occasional patch reefs. Extensive stands of macroalgae dominated by *Sargassum* spp. and *Dictyopteria* spp. are present in parts of the lagoon where limestone pavement is exposed.

Large circular features characterised by lighter colouration within algae-dominated lagoon habitat (3 to 8 m water depth) were identified from hyperspectral images derived from a HyVista airborne hyperspectral survey of Ningaloo Reef conducted in April 2006 (Fig. 1A) (Kobryn et al. 2012). These features appeared to have small dark-coloured features at their centre; when investigated by divers these were found to be *Porites*-dominated patch reefs (~4 m high and 10 m in diameter). Areas immediately adjacent to these patch reefs were virtually devoid of macroalgae (Fig. 1B), while further away the substratum hosted dense stands of brown macroalgae (Fig. 1C). Large schools of fish, notably *Kyphosus sydneyanus*, were observed at most of these patch reefs (Fig. 1D).

After the preliminary investigation, images were further inspected and halos were identified along the entire reef tract. Features were identified as halos if they were in lagoon habitat, had a clearly defined

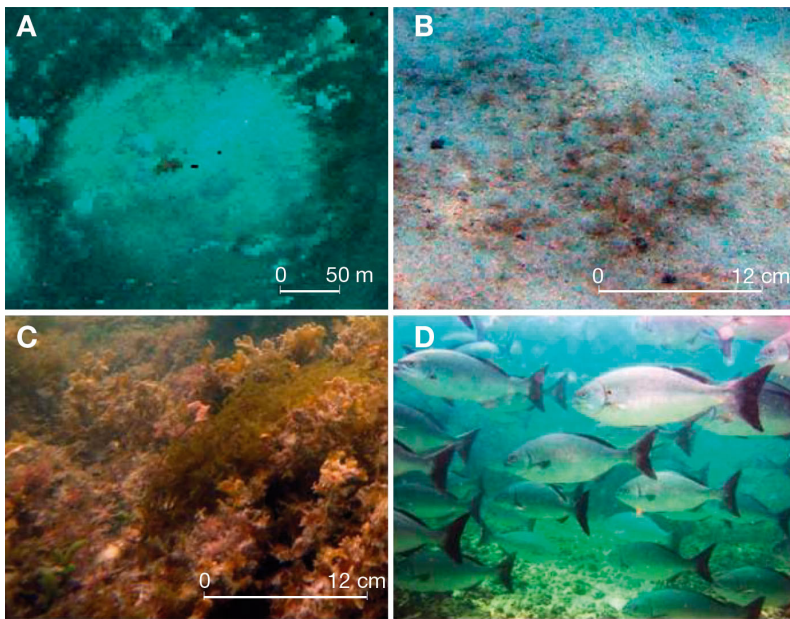


Fig. 1. General features of halos: (A) aerial view of halo, note central patch reef; (B) substrate inside halo, dominated by pavement with coralline and turf algae and sand veneer; (C) substrate outside halo, dominated by macroalgae; (D) school of *Kyphosus sydneyanus*, average length ~50 cm

edge with a single central patch reef and were >20 m in radius. Based on these criteria, we identified 34 halos.

Of the 34 halos, 5 were included in subsequent detailed surveys; these were all located within a 122 km section of the reef from Tantibiddi (21° 53.09' S, 113° 57.2' E) to Coral Bay (22° 54.25' S, 113° 47.09' E). At each of the 5 halos the biomass and species composition of macroalgae, herbivorous fish and large invertebrates and rates of herbivory were quantified at 5 distances relative to the central patch reef: 0 (immediately adjacent to the patch reef), 30, 60, 90 and 120 m.

The density estimates of all fish and invertebrates were measured by underwater visual census using a single transect, swum parallel to the edge of the central patch reef. Each transect was conducted by a single diver. Fish were recorded within a 30 × 5 m transect on the first leg and macro-invertebrates were recorded within a 30 × 2 m transect on the return. Fish, excluding juveniles (<5 cm), and invertebrates were identified to species level and sizes of fish were estimated to the nearest 5 cm. Density and size of fish were used to estimate biomass using length–mass relationships (Kulbicki et al. 2005, Froese & Pauly 2011). Maximum dimensions of invertebrates (diameter, length) were estimated to the nearest centimetre. Benthic macroalgae were harvested by hand

from three 0.25 m<sup>2</sup> quadrats at each distance. Algae were sorted, weighed (wet) and identified to species level (possible for all but 1 species).

Rates of herbivory were measured via 2 methods: measurement of consumption of tethered algae, and video observations of tethered algae. *Cystoseira trinodis*, a species known to be consumed by herbivorous fish at Ningaloo (Steinberg & Paul 1990), was used in all tethering experiments. *Cystoseira* thalli were collected from adjacent algal beds, rinsed in seawater, dried with a paper towel and measured (to the nearest mm). Five thalli were then attached to a 2 m piece of nylon rope by a numbered clothes peg and the rope was secured to the substrate by 3 tent pegs. To estimate consumption of tethered algae, 1 rope was deployed at each of the 5 sampling distances at each site for 12 h, on each of 2 d; ropes were deployed at 17:00 h and collected at

05:00 h the following morning. Thalli were retrieved and lengths were measured. Because tethered algae might erode (thus confounding estimates of consumption), an additional test was conducted in which we deployed 3 pieces of rope, each containing 5 thalli in one 2.5 × 2.5 m steel-framed cage, enclosed by nylon fishing net with a 30 mm mesh size. This was deployed adjacent to one patch reef for a 12 h period, after which thalli were retrieved and lengths were re-measured. There was no significant change in length of the tethered algae between caged and uncaged treatments (df = 2,  $F = 7.81$ ,  $p = 0.26$ ), indicating that inferences about rates of consumption were robust.

Species-specific grazing (bite) rates were obtained by remote video observations using Panasonic NV-GS330 video cameras in SeaGIS underwater housings. Cameras were deployed and focused on the 5 tethered *Cystoseira trinodis* at each of the sampling distances described above. Two 1 h deployments were conducted on each of 2 d at each distance; filming occurred between 14:00 and 16:00 h. Video was observed using EventMeasure (SeaGIS) software, and observers identified species and counted the number of bites taken by individual fish. Bite rates at 0 m underestimated the intensity of herbivory because tethered algae were typically grazed to the stipe or totally consumed within 10 min.

Analyses of the biomass of macroalgae, thallus length and bite rates focused on testing for differences among distances (5 levels; fixed) and sites (5 levels; random). Analyses of biomass of herbivorous fish focused on distance alone, because there were single observations for each distance at each patch reef. Permutational analysis of variance (PERMANOVA) was used for analyses; in this method statistical significance is determined by permutation, and there are no *a priori* assumptions about the distribution of the data (Anderson et al. 2008). Analyses were based on Euclidean distances. Where a statistically significant effect of distance was detected, pair-wise comparisons were used to resolve the nature of differences among distances.

## RESULTS

The biomass of macroalgae was significantly higher with increasing distance from the central patch reefs (Fig. 2A, Table 1). *Hydroclathrus clathratus* and *Lobophora variegata* were the only large macroalgae found within 30 m of patch reefs, but both occurred in relatively low biomass (Fig. 2B). *Dictyopterus serrata* and *Sargassum* sp. were the dominant macroalgae found at distances >90 m from patch reefs, with *Cystoseira trinodis*, *Sargassum decurrens* and *Lobophora variegata* co-occurring at lower densities (Fig. 2B). A statistically significant interaction between distance and site ( $F = 13.0$ ,  $p < 0.001$ ; Table 1) was detected, indicating that the magnitude of the difference was not consistent at all 5 reefs, although the direction of the difference was (Table A1 in the Appendix provides a summary of pairwise comparisons for each site  $\times$  distance combination).

Herbivorous fish assemblages associated with the central patch reef were comprised predominantly of *Kyphosus sydneyanus*, *Naso fageni*, *Siganus fuscescens*, *Acanthurus dussumieri*, *A. grammoptilus* and *Scarus ghobban*. The majority of individuals were found immediately adjacent to the patch reefs (0 m), with no herbivorous fish observed beyond 30 m from patch reefs (Fig. 3A, Table 2). Herbivorous fish assemblages were dominated by *K. sydneyanus*, which accounted for more than half of the total biomass (Fig. 3B).

Individual *Kyphosus sydneyanus* were generally large (40–60 cm total length [TL],  $2.2 \pm 1.3$  kg) and were commonly observed in schools of >50 ind. The similarly sized *Naso unicornis* (40–60 cm TL,  $3.2 \pm 0.8$  kg) were usually observed as single individuals or

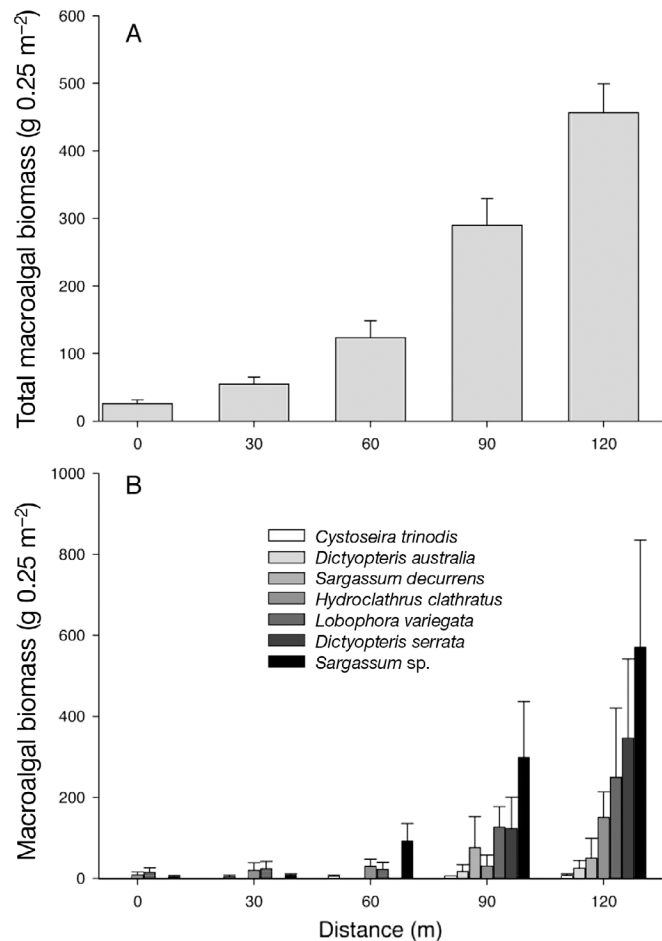


Fig. 2. Patterns of macroalgae biomass at 5 distances from the patch reefs. (A) Total biomass combined; (B) biomass of the 7 most abundant macroalgae species. Data are means + SE

Table 1. Permutational analysis of variance (PERMANOVA) testing for differences in macroalgae biomass among distances and sites

Source	df	MS	F	p
Site	4	52 969	13.269	<0.001
Distance	4	533 160	10.251	<0.001
Site $\times$ Distance	16	52 013	13.029	<0.001
Residuals	50	3992		

occasionally in small groups. *Naso fageni*, *Siganus fuscescens* and *Acanthurus dussumieri* were smaller (20–30 cm TL, <0.5 kg) and occurred in small schools of 5–10 ind.

Large invertebrates, comprising mainly echinoids (*Echinometra mathaei*, *Echinostrephus* sp.) and gastropods (*Tectus pyramis* and *Turbo chrysostomus*) were recorded at very low densities (0.08 ind. m<sup>-2</sup>)

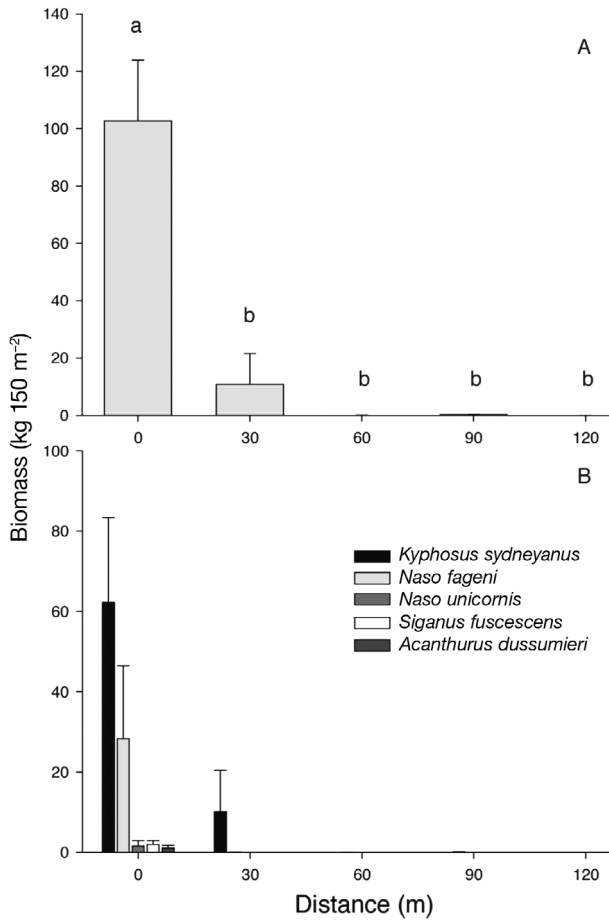


Fig. 3. Biomass of herbivorous fish at each distance from the patch reefs. (A) Total herbivorous fish biomass. Lowercase lettering indicates significantly different groups (PERMANOVA pairwise comparisons). (B) Biomass of each of the 5 most abundant herbivorous fish species. Data are means + SE

Table 2. Permutational analysis of variance (PERMANOVA) testing for differences in the biomass of herbivorous fish among distances

Source	df	MS	F	p
Distance	4	8340.4	11.644	<0.001
Residuals	20	716.28		

and showed no consistent pattern with distance from central patch reefs (Table 3).

Rates of consumption of tethered algae were highest adjacent to the central patch reef (Fig. 4A) and algae were consumed at a mean rate of  $5.2 \pm 1.5$  cm  $12 \text{ h}^{-1}$ , dropping significantly to  $2.9 \pm 1.6$  cm  $12 \text{ h}^{-1}$  at 30 m (Fig. 4A, Table 4). There was also a statistically significant distance  $\times$  site interaction, indicating that the magnitude of the difference was not consistent at

Table 3. Total abundance (total number of individuals observed) of herbivorous macro-invertebrate grazers relative to distance from patch reef. Combined data for totals at all halos

Species	Abundance at				
	0 m	30 m	60 m	90 m	120 m
<i>Echinometra mathaei</i>	0	0	0	47	0
<i>Echinostrephus</i> sp.	4	0	0	8	0
<i>Tectus pyramis</i>	0	3	3	18	0
<i>Turbo chrysostoma</i>	6	0	0	0	0

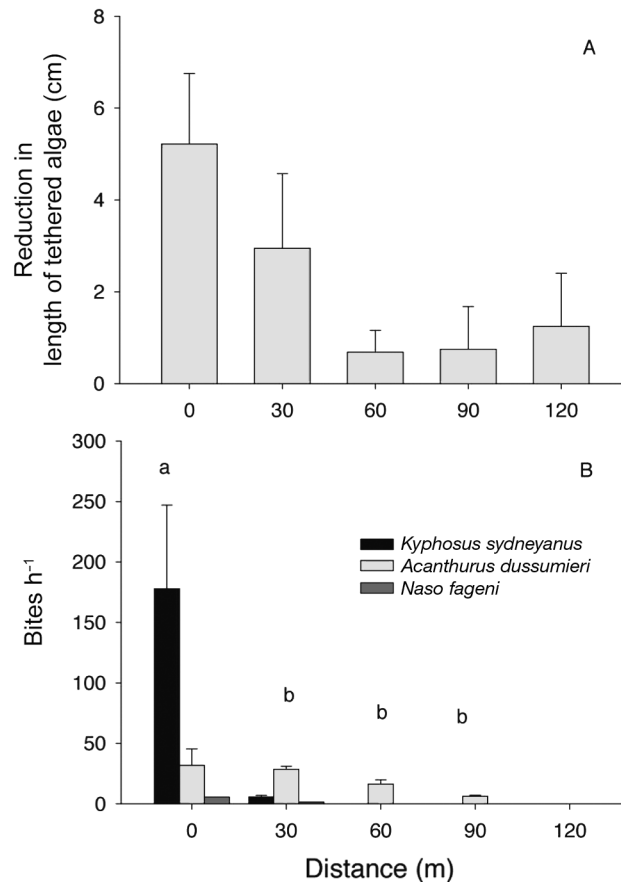


Fig. 4. (A) Rates of consumption of tethered algae at each distance from the patch reefs. (B) Species-specific bite rate at each distance from the patch reefs. Data are means + SE. Lowercase lettering indicates significantly different groups at  $p < 0.1$  (pairwise PERMANOVA comparisons)

Table 4. Permutational analysis of variance (PERMANOVA) testing for differences in the reduction in length of tethered algae among distances and sites

Source	df	MS	F	p
Site	4	1914.1	13.059	<0.001
Distance	4	5175.5	4.1962	0.016
Site $\times$ Distance	16	1233.4	8.4148	<0.001
Residuals	100	146.57		

Table 5. Multivariate permutational analysis of variance (PERMANOVA) analysing species-specific bite rate by site and distance

Source	df	SS	MS	F	P
Site	5	52296	10459	0.74286	0.611
Distance	4	217430	54357	4.7397	0.004
Site × Distance	20	224080	11204	0.79577	0.613
Residuals	20	281590	14080		

all 5 reefs, although the direction of the difference was consistent, showing less consumption with increasing distance from patch reef.

Species-specific bite rates determined from video observations were highest ( $177.8 \pm 69$  bites  $\text{h}^{-1}$ ) for *Kyphosus sydneyanus* immediately adjacent to the patch reefs (0 m; Fig. 4B). Bite rates for *Acanthurus dussumieri* and *Naso fageni* were considerably lower (32 and 6 bites  $\text{h}^{-1}$ , respectively) than for *K. sydneyanus*. *Acanthurus dussumieri* was observed to feed at greater distances from the patch reefs (60 and 90 m) than either *K. sydneyanus* or *N. fageni*. Other commonly observed species of herbivorous fish, such as *Siganus fuscescens*, *Acanthurus grammoptilus* and *Scarus ghobban*, were not recorded grazing on tethered algae. Analysis of the species-specific bite rates (Table 5) indicated that bite rates varied significantly with distance from patch reef; pairwise comparisons revealed that bite rates were highest immediately adjacent to the reefs (0 m). Most bites were taken by *K. sydneyanus* (Fig. 4B).

## DISCUSSION

The strong relationships between the distance from patch reefs, the biomass of macroalgae and herbivorous fish (especially *Kyphosus sydneyanus*), and the rates of consumption of tethered algae support the inference that grazing by *K. sydneyanus* maintains the low biomass of macroalgae we observed close to patch reefs. *Kyphosus sydneyanus* was present in greater abundance and higher biomass than any other species of herbivorous fish at all sites; its biomass was more than twice that of *N. fageni*, and tenfold greater than siganids, acanthurids and scarids (Fig. 3), and most of the bites observed on tethered algae were by *K. sydneyanus*.

Video observations, consumption of tethered algae and estimates of fish biomass provided little indication as to why the 60 and 90 m sampling distances were consistently observed to be devoid of macro-

algae. The biomasses of herbivorous invertebrates were consistently low at all distances and invertebrates were not observed consuming tethered macroalgae. However, *Acanthurus dussumieri* was recorded grazing at greater distances from patch reefs than *Kyphosus sydneyanus*, suggesting that halos may be maintained by multiple species. While *K. sydneyanus* was not observed beyond 30 m during censuses or in video footage, it was observed by divers 60 to 80 m from patch reefs on other occasions, suggesting that infrequent foraging at greater distances (not detected by our methods) might occur.

The large scale and symmetry of the features we have described further support the inference that grazing, rather than hydrodynamic features, maintains these halos. Factors such as wave energy and tidal flow around reef features generate turbulence, and have been demonstrated to influence benthic algal communities (Hurd 2000, Toohey 2007). Taebi et al. (2011) demonstrated that hydrodynamic flow in lagoon waters of Ningaloo is parallel to the shore and exits through reef passes. Should these processes influence the patterning of macroalgal beds around patch reefs, one would expect axes to align with dominant currents, while the halos we have described are largely symmetrical.

Significant grazing by *Kyphosus vaigiensis* has been observed on the Great Barrier Reef (Choat et al. 2004, Hoey & Bellwood 2008, Bennett & Bellwood 2011); however, it was the dominant grazer only in the southern Great Barrier Reef ( $>21^\circ\text{S}$ ) (Bennet et al. 2010). Similarly, large schools of *Kyphosus* are common at Ningaloo Reef (Babcock et al. 2009), most likely due to its high-latitude location ( $21^\circ\text{--}23^\circ\text{S}$ ). *Kyphosids* are reported to be relatively more abundant at higher latitudes in other coral reef bioregions (Floeter et al. 2005), and it is possible that large halo features such as those we have described ( $>10$  m) may be restricted to high-latitude coral reefs. Patterns are also likely to be species-specific. *Kyphosus sydneyanus* and *K. vaigiensis* feed primarily on brown algae (Moran & Clements 2002, Choat et al. 2002), but other species such as *K. cornelii* prefer red algae (Rimmer 1986) and may also display other behaviours such as territoriality that result in different spatial patterns in benthic macroalgae (Berry & Playford 1992).

The processes driving halo development are known to vary, although these do not necessarily lead to visible differences in halo dimensions. Randall (1965) demonstrated that halos in the British Virgin Islands were maintained by acanthurids and scarids and had a maximum extent of 10 m. Ogden et al. (1973) de-

scribed similar patterns in the American Virgin Islands that, while similar in size to those reported by Randall (maximum extent of 10 m), were maintained by the sea urchin *Diadema antillarum*. The findings of these 2 studies raise an important point that halos of similar extent are found throughout the Caribbean, but are driven by different herbivores.

It is therefore important to understand the variability in patterns observed and in the processes that lead to these patterns. All halos described to date are from coral reef lagoon habitats and to that extent are comparable. Halos reported here are  $\geq 90$  m in radius and attributed to herbivorous fish grazing, while those reported elsewhere are have been  $< 10$  m in radius and found to be maintained by herbivorous fish and sea urchins (Randall 1963, Ogden et al. 1973, Valentine et al. 2007, Madin et al. 2011). This suggests that the underlying properties of ecosystem components in the Ningaloo lagoon, and processes constraining central place foraging there, differ from those elsewhere. The differences may relate to the herbivore guild, attractiveness of the food resource available to grazers, as well as the risks posed to grazers by predation.

Low density populations of predators and decreased risk of predation may provide an alternative explanation for unusually large dimensions of halos at Ningaloo. The main predators of large grazers such as kyphosids, acanthurids and scarids on Ningaloo are likely to be sharks; however, populations of sharks on the reefs of Ningaloo are abundant (20 to 50 kg ha<sup>-1</sup>; R.C.B. unpubl. data) due to relatively low fishing pressure. The entire region is protected from commercial fishing and recreational fishing pressure is relatively low. The southernmost halos documented in the study were located in the centre of a large no-take zone that has been in place since 1988 and halos there were of a size similar to those on other parts of the reef (Fig. 5). Furthermore, *K. sydneyanus* is one of the largest of the kyphosids, its size potentially affording relative protection from predators. The schooling behaviour of this species is also likely to enable it to range further from shelter than would be possible for isolated individuals.

At Ningaloo, gradients in the intensity of herbivory in relation to coral

reef structure (reef flat–lagoon transition) have been reported (Verges et al. 2011); however, high levels of unexplained variability in this trend were observed. The distribution of habitats may influence such variability; for example, when patch reefs are close enough together, their halos may merge. In this way the provision of relatively small amounts of shelter can determine the characteristics of much larger areas of reef habitat (Fig. 5).

The large extent of these features means that they are not obvious from the sea surface and can only be viewed from significant elevations. Remote sensing methods are capable of identifying and delineating change in shallow-water coral reef habitats (Mumby et al. 2004, Habeeb et al. 2007, Scopéltis et al. 2009). Remotely sensed imagery coupled with extensive *in situ* observational data has the potential to inform the scientific community on the temporal and spatial variability of benthic habitats. Understanding how these benthic habitats link to higher trophic processes remains a crucial step for the effective use of remotely sensed imagery as a tool for ecosystem-based management.

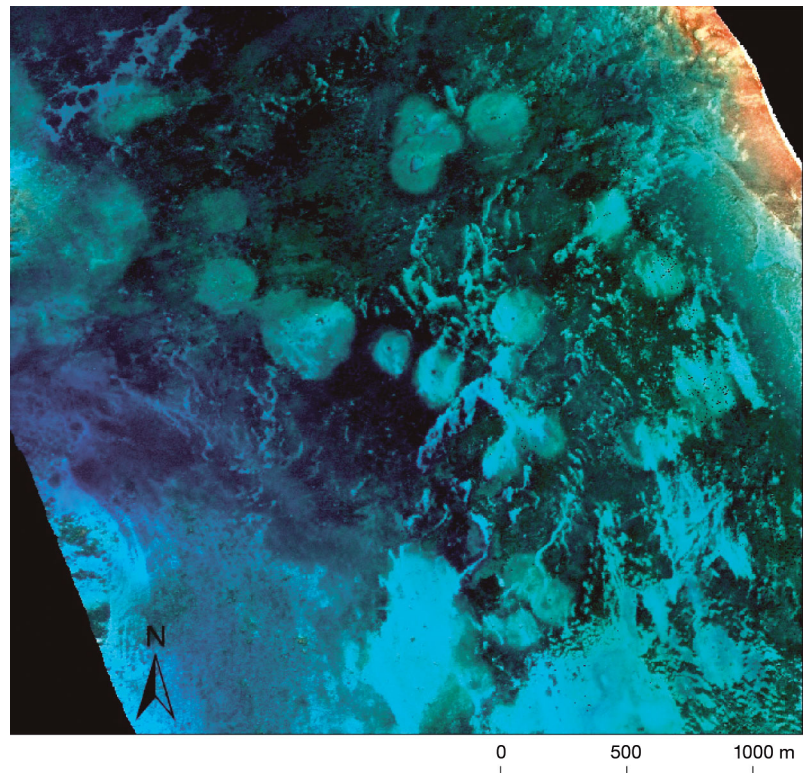


Fig. 5. A false colour image derived from the Ningaloo airborne Hyperspectral survey. Multiple grazing halos in close proximity begin to merge and macroalgal beds can be transformed into coral reef substrata. These halos include the southernmost of the bommies we studied, and were located in the centre of a large no-take area

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#### Appendix. Post hoc test outputs for significant interaction effects

Table A1. Algal biomass analysis, pairwise comparison of site × distance interaction. Group states the comparison for distance from patch reef. Numbers and percentage of significant sites are also shown

Group	Number of sites	Percentage
0 > 30	2	40
0 > 60	2	40
0 > 90	4	80
0 > 120	5	100
30 > 60	2	40
30 > 90	4	80
30 > 120	5	100
60 > 90	4	80
60 > 120	5	100
90 > 120	2	40