

# Scraping and grazing herbivorous/detritivorous fish display opposite feeding behaviours under different protection regulations

**Nathan William Price**

Tunghai University

**Kao-Sung Chen**

Fisheries Research Institute

**Chaolun Allen Chen** (✉ [cac@gate.sinica.edu.tw](mailto:cac@gate.sinica.edu.tw))

Fisheries Research Institute, COA, Keelung <https://orcid.org/0000-0003-0452-4226>

**Colin Kuo-Chang Wen**

Tunghai University <https://orcid.org/0000-0002-7684-8820>

---

## Research article

**Keywords:** Bottom-up and Top-down Regulation, Benthic Community, Functional Groups, Marine Reserves, Schooling Behaviour

**Posted Date:** February 24th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-230129/v1>

**License:**   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

**Version of Record:** A version of this preprint was published at Marine Biology Research on April 1st, 2022. See the published version at <https://doi.org/10.1080/17451000.2022.2037002>.

# Abstract

## Background:

Functional groups, especially herbivorous fishes, are important for mediating benthic community structure on coral reefs. Herbivorous and detritivorous fish display complex feeding behaviour, and research into schooling feeding behaviour and feeding rates, and how these change with environmental and social behavioural variables is lacking. Such knowledge is imperative to infer how herbivory/detritivory will change, in light of changing resources and communities, specifically whether reefs can recover from disturbance. Differences in abundance, feeding rate, body length, diet preferences, and schooling size of three major functional groups, scrapers, grazers and browsers were examined across reef habitats under different fishing regulations, such as no-take restricted zones and open-fishing general use zones. Although marine protected areas have been implemented to conserve reef fish species; further precise management based on ecological behaviour of functional groups is necessary.

## Results:

Scrapers and grazers which were mostly parrotfishes and surgeonfishes were more abundant on reef flats and also displayed the highest feeding rates on reef flats. Although scrapers mainly resided inside the restricted zone, more grazers were found in the general use zone where macroalgae abundance was highest, indicating a higher availability of nutritional resources. Browsers, mostly rabbitfishes, were seldom observed and patchily gathered on the reef flat and slope in both zones. Thus, fishing protection did not appear to benefit grazers and browsers, whereas scrapers gathered on shallow reef flats in the protection zone. Lastly, scraper and grazer feeding rates increased from an individual to paired feeding, and increased with body size, these factors led to variations in feeding behaviours on different habitats under different protection regulations.

## Conclusions:

Fishing protection benefits scrapers which subsequently appears to be resulting in a reduction in algal coverage, and variation in feeding rates was largely related to school sizes. The density of these functionally important grazers was influenced more by changes to benthic composition than protection status. The opposite feeding behaviours of two herbivorous/detritivorous functional groups indicates not only protection status, but fishing gear and size limit regulations are needed to help maintain fisheries and diversity on coral reefs in Taiwan.

# Background

Coral reefs provide services such as food, coastal protection and recreation for coastal communities around the world (Harborne et al. 2017; Lau et al. 2018). Reefs are changing as a direct consequence of anthropogenic activities, including intensified fishing and coastal development (Pratchett et al. 2011; Bellwood et al. 2019a). In recent years, it has become evident that climate change-induced ocean

warming, driven by an increase in CO<sub>2</sub> emissions, is leading to more mass coral bleaching events (Graham et al. 2015; Hughes et al. 2018). Reefs have now entered the Anthropocene - an age where humans have become the primary driver of environmental change (Williams & Graham 2019).

Tropical reefs experiencing anthropogenic pressures, including overfishing of herbivores, lessens top-down control, causing phase shifts from coral towards macroalgae (Bellwood et al. 2004; Rasher et al. 2013). A phase-shift occurs when hard coral cover is reduced in favour of algae dominance, and this new state is generally associated with a combination of reduced herbivory and nutrient enrichment (Cheal et al. 2010). Certain functional groups have been recognised as having major functional roles in maintaining reef health and resilience such as herbivorous and detritivorous fishes (Bellwood et al. 2004; Burkepile & Hay 2008; Eggertsen et al. 2019). The former group can be generally divided into four functional groups based on their feeding behaviour and bioerosion of the benthos; bioeroders, grazers, scrapers and territorial gardeners (Bellwood et al. 2004). More in-depth functional roles have been suggested using morphological variation and gut content analysis (i.e., Tebbett et al. 2017), however trait-based functional role classification without empirical evidence might not represent the real energetic material pathways (Bellwood et al. 2019b). Carefully selected groups of herbivores/detritivores have been informative indicators for different studies (i.e., Russ et al. 2018 & Tebbett et al. 2020).

These functional groups play different but complementary roles, performing several critical functions (Rasher et al. 2013; Clements et al. 2016). These functions include controlling algal abundance (Bellwood et al. 2004; Ledlie et al. 2007; Cheal et al. 2010), which mediates the competition between algae and corals for colonising space. Mediating such competition can prevent coral-algal phase shifts (Burkepile & Hay 2008). Herbivorous reef fishes display complex feeding behaviour that can vary between individual species (Burkepile & Hay 2008; Bonaldo et al. 2014; Nash et al. 2016; Tebbett et al. 2017). Research in the Caribbean has shown parrotfish (Labridae: Scarinae) species richness can be crucial for maintaining the structure and function of coral reefs, suggesting certain genera and species are more important for coral reef recovery (Burkepile & Hay 2008). Most parrotfishes, surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae) feed over relatively small areas and often form mixed species feeding schools (Welsh & Bellwood 2012b; Carlson et al. 2017). Feeding behaviour and bite rate reputedly vary between species within a functional group (Bonaldo et al. 2014). Wrasse (*Halichoeres* spp.) significantly increase their foraging rate when group feeding (Nunes et al. 2013). Streit et al. (2019) investigated delivery of herbivory on a reef, rather than assessing the functional potential of the herbivorous fish community and found overlap across functional groups was limited, as functional groups tended to feed next to one another. Whether schooling behaviour is changing the feeding behaviour of herbivorous fishes is unclear (see Brandl & Bellwood 2014). A better understanding of schooling behaviour and the wider ecological implications of such behaviour is needed for effective management.

Herbivorous/detritivorous fish assemblages in the Indo-Pacific are dominated by three clades containing species that intensively graze the surface of coral reefs: surgeonfishes, parrotfishes and rabbitfishes. Despite evolutionary differences, species are generally placed in simplified categories based on general feeding, such as excavators, scrapers and browsers, etc. (Green & Bellwood 2009; Rasher et al. 2013;

Graham et al. 2015; Clements et al. 2016). The relationship between functional groups and benthic communities is not yet clear although research is emerging (see Robinson et al. 2019). Nash et al. (2016) examined variability in density, body size, foraging movements and grazing (feeding) rates of two parrotfish species across reefs exhibiting a range of benthic and fish community compositions. The benthic community was the main driver in foraging movements, and parrotfish densities were influenced by protection status; whereas grazing rates were influenced by management status and individual species. Herbivorous fishes are generally viewed as being critical players in reef recovery following disturbance. Given the increasing frequency and intensity of disturbances, there is a clear need to better understand the feeding behaviour of herbivorous and detritivorous fishes across space and time.

The rapid decline of reef systems has required more rigorous and adaptive management techniques (Bellwood et al. 2004). Marine Protected Areas (MPAs) and zoning have both played roles to help protect and conserve coral reef ecosystems. MPAs, including highly protected no-take areas can only counter a limited subset of threats, primarily those of direct extractive activity (Bellwood et al. 2019a). The logic of using no-take areas for sustaining fisheries is relatively robust (fish grow and reproduce if not extracted), the capacity of no-take areas to protect biodiversity is less clear. Effectively managed MPAs have been shown to increase the density, body size and biomass of targeted fish species in certain regions (Kopp et al. 2010; Russ et al. 2018). Most MPAs fail to achieve conservation goals in response to other anthropogenic impacts such as climate change (Day et al. 2019).

Herbivorous fish stocks and recruitment levels are incredibly difficult to predict, however the effective reaction to conserve an ecosystem when there are crucial gaps in the knowledge, is to install a network of marine reserves (Mellin et al. 2016). Unfortunately, the establishment of MPAs is rarely followed by good management and enforcement, which means the number of MPAs and their coverage can be misleading indicators of effective conservation (Mora et al. 2006). The management of herbivorous fish stocks has been used to assist the regeneration of reefs following disturbance (Bellwood et al. 2004; Graham et al. 2015). When management is focused on particular functional groups, the issues that extend beyond direct impacts are recognised. Despite decades of effort and widely accepted hypotheses, Bruno et al. (2019) found MPAs and the management of herbivorous fish (especially parrotfish) have had little effect on coral reef resilience. The question arises, can we successfully manage herbivorous fish stocks without addressing functional importance, behavioural changes and the wider ecological implications of such behaviour?

Kenting National Park (KNP) is located at the southernmost tip of Taiwan. The coastal region, locally known as Nanwan Bay, supports one of the most diverse coral reefs in Taiwan (Meng et al. 2008; Keshavmurthy et al. 2019). The rich and diversified marine ecology attracts many local and foreign tourists every year (Lee et al. 2019). During high rainfall events, the area is subject to pollution from excessive suspended sediments, which can bury coral and other benthic organisms (Meng et al. 2008). Corals in the region have suffered from six severe typhoons and two major bleaching events from 1985 to 2010 (Kuo et al. 2012), however they are showing signs of resilience and recovery (Keshavmurthy et al. 2019). Cold-water disturbance during spring tides, typhoons, coral disease and overfishing all further

damage the reefs, causing this region to be one of the five most threatened areas in Southeast Asia (Dai et al. 1999; Chen & Dai 2004; Meng et al. 2008). The extent to which these pressures will affect coral reef health around Taiwan in the absence of better management remains unclear.

This paper aims to explore how fish associate with the benthos, examining feeding rates and feeding behaviour of herbivorous/detritivorous fishes, and differences between functional groups, protection status and across reef habitats in KNP. Here, we determined: (1) the abundance and feeding behaviour of scrapers, grazers and browsers across habitats; (2) how group size and fish size influence feeding rates of individual fish; (3) which factors drive benthic community composition and (4) potential correlations between feeding rates, fish size, and schooling behaviour of functional groups with gut contents. These findings will be used as the basis for conserving herbivorous and detritivorous fish functional groups in Southern Taiwan. As the protected areas in KNP fail to address functional groups or feeding behaviour, there is a clear need to better understand such questions and incorporate these findings into further management efforts.

## Results

### Fish abundance by protection status and habitat

Three functional groups were analysed with protection status, habitat type and benthic composition (see Additional file 1: Table S1). The highest abundance of scrapers ( $n = 122$ ) was recorded on the reef flat in the restricted zone (Fig. 1a). Abundance was higher inside the restricted zone, but protection status did not statistically influence abundance, whereas habitat type drove scraper abundance (see Additional file 1: Table S1). Grazers also displayed a significantly higher abundance ( $n = 91$ ) on the reef flat, but only in the general use zone (Fig. 1b; see Additional file 1: Table S1). Browser abundance ( $n = 18$ ) was influenced by protection status or habitat type, but mostly zero-census data made the statistical results less powerful (Fig. 1c; see Additional file 1: Table S1). Habitat type was a significant driver for scrapers, and both scrapers and grazers decreased along the habitat gradient, from reef flat to reef slope (Fig. 1a, 2b). In addition, juvenile scrapers and juvenile grazers were also found mostly gathering on the shallow reef flat rather than other habitats in both restricted and general use areas (see Additional file 1: Fig. S1).

### Feeding rate by size, protection status and habitat

We examined the feeding behaviour of 334 fishes belonging to the functional groups- scrapers ( $n = 141$ ), grazers ( $n = 182$ ) and browsers ( $n = 11$ ). The zero-bite data for scrapers and grazers among different factors were included in the Hurdle analysis (see Additional file 1: Fig. S2). A significant relationship was found between feeding rate and size, as large individuals displayed more non-feeding than feeding behaviour ( $p < 0.05$ ; Additional file 1: Fig. S2). Other factors such as protection status, habitat type and life stage with grazers, and all factors with scrapers showed no significant difference between zero and non-zero data ( $p > 0.5$ ). Therefore, we used a Generalised Additive Model (GAM) with non-zero data to show the correlation of feeding rate and body size for both scrapers (Fig. 2a, 2b) and grazers (Fig. 2c, 2d) between zones. The model selection with the lowest Akaike Information Criterion (AIC) value suggested

protection status drives the feeding rate for both scrapers and grazers. While adult scrapers had higher feeding rates in the restricted zones (Fig. 3a), grazers feed more in the general use zones (Fig. 3b). Both scrapers and grazers exercised an increasing bite rate with increasing body length mostly (Fig. 2), except scrapers in the general use areas (Fig. 2b). The number of recorded herbivores differed across habitats and zones (Fig. 3); with limited individuals recorded at certain sites. Feeding rates of subadult/adult and juvenile fish across different restricted zones and habitat types show similar patterns as the above GAM (Fig. 2, 3). Adult scraper feeding rate was relatively uniform across habitat types in the restricted zones, however in the general use zone, feeding rate was highest on the reef crest (Fig. 3a). Juvenile scraper feeding rate was highest on the reef flat of the general use zone. Adult grazer feeding rate was influenced by both protection status and habitat type, opposite pattern to scrapers. Adult grazer feeding rate was higher on the reef crest of the general use zone and crest of the restricted zone (Fig. 3b; see Additional file 1: Table S2). Finally, juvenile grazers had higher feeding rates in the general use zone (Fig. 3b).

### Schooling feeding behaviour

The restricted zone and the general use zone hosted the highest abundance of adult scrapers and grazers respectively (Fig. 1). These functional groups also had the highest feeding rate on the reefs with highest abundance (Fig. 3). Similarly, the highest juvenile scraper and grazer abundance resulted in higher feeding rates (Fig. 3, see Additional file 1: Fig. S1). The above results implied that possible schooling behaviour increased feeding rate. Therefore, we modelled abundance and feeding rate of schooling fishes (with zero bite data removed). Initial hypotheses were a slope regression (schooling fish increase their feeding rate) and a regression reaching a plateau (feeding rate did not increase with group size). The results suggested a high probability of a non-linear regression showing scraper feeding rate is positively correlated with schooling behaviour (Fig. 4a, 4b). The turning point was around 2 for both scrapers and grazers, indicating these herbivorous fishes show an increase in feeding rate from a single individual to a pair, then no further significant increase after a pair.

### Fish size by protection status, habitat type and correlation with gut contents

The body size (total length, TL) of two major functional groups were examined across protection status and habitat types using a generalised linear model (GLM) (see Additional file 1: Table S3). The habitat drove the size distribution of both scrapers and grazers, and the largest individuals resided on the reef crests in both zones (see Additional file 1: Fig. S3). While the scrapers in the general use zone on reef flat were much smaller than elsewhere, grazers showed the same size distribution across habitats for both zones. Simple linear regression was used to study the relationship between fish size and gut contents. Scraper and browser size were both positively correlated with gut content weight (Fig. 5a, 5c), whereas no relationship was found with grazer size and gut content weight (Fig. 5b).

### Macroalgae coverage with herbivorous fish abundance and environmental factors

The preferred algae were defined from the gut content analysis, which were genera *Gracilaria*, *Dictyopteris*, *Laurencia*, *Ulva*, *Sargassum* and *Dictyota*. Most were filamentous and foliose red algae

(Rhodophyta), brown algae (Ochrophyta) and green algae (Chlorophyta) (see Additional file 1: Fig. S4). Preferred algal coverage was mainly driven by habitat type and fish abundance (see Additional file 1: Table S4). Fish abundance and feeding rate (Fig. 1, 3) were compared with benthic coverage (Fig. 6). Preferred algae types were found to be the most dominant on the reef flat in the general use zone. Less preferred algae types (including turf algae) in the restricted zone hosted a higher abundance of scrapers. In contrast, in the general use zone, Preferred algae coverage was positively correlated with grazer abundance. Although we did not find a clear negative correlation of coral and algae cover, the highest coral cover was found alongside the lowest macroalgae cover (reef slope, restricted area). Our results suggest either macroalgae is being maintained in the restricted zone by the high scraper abundance, or nutritional content is better in the restricted zone leading to a higher abundance. In the general use zone, higher macroalgae coverage appears to attract a higher abundance of grazers.

## Discussion

We investigated the feeding behaviour of two major functional groups under social factors across three habitat types. We found the highest abundance of scrapers and grazers on the coral reef flat. Furthermore, the feeding rate of scrapers was largely affected by protection status and habitat type, whereas grazer feeding rate was influenced only by habitat type. Research investigating specific variabilities of herbivory on reefs is now relatively abundant (Choat & Clements 1993; Russ 2003; Fox & Bellwood 2007; Nash et al. 2016; Bejarano et al. 2017). The highest abundance of scrapers and grazers, along with the highest feeding rates on reef flats, may well be due to the increased macroalgae abundance on this reef habitat (Russ 2003). The reef flats in this study were all at depths of < 5 m. The higher algae abundance observed on the shallow reef habitats may be due to light availability. Consequently, this may be a reason for herbivorous fish congregating in those zones and subjecting the reef to higher levels of grazing (Fox & Bellwood 2007). Fox & Bellwood (2007) also suggest the feeding rate of herbivorous fish is significantly different with depth gradients. Although feeding rate was highest on the reef flats, we also found high levels of feeding on the reef crests.

In this study we found scrapers benefit from protection status whereas grazers are more influenced by benthic habitat, similar to the findings of Robinson et al. (2019). Nash et al. (2016) also conducted extensive research into the foraging movements of two parrotfish species; and found movements were largely influenced by the benthos, densities were driven by management status, and grazing rate was influenced by management status and species. Nash's study partially supports our main findings, highlighting scraper abundance is driven by protection status. Our findings do suggest scraper abundance is mitigating algal abundance in the protected areas but this may not be the case. Russ et al. (2015) found compelling evidence that the benthos exerted strong bottom-up control on parrotfish (both scrapers and excavators) density. Furthermore, Taylor et al. (2019) provided more evidence for this nuanced ecological feedback system - one where disturbance plays a key role in mediating parrotfish-benthos interactions. By influencing the biology of assemblages, disturbance can thereby stimulate change in parrotfish grazing intensity. This suggests benthos (which may be initially driven by disturbance) drives parrotfish density and behaviour and not the other way around. Russ et al. (2018)

investigated decadal-scale response of surgeonfishes to no-take marine reserve protection and changes in benthic habitat and found density of surgeonfish species was influenced more by the changes to benthic cover than marine protection. This highlights the greater importance of bottom-up control than top-down control for surgeonfishes.

Other herbivores such as sea urchins may play an important role in driving macroalgae abundance. Sea urchins have a small habitat range (scale of  $m^2$ ), and when herbivorous fish density decreases (e.g., due to overfishing), sea urchins still create patchy areas of low algal biomass around individuals (Nozawa et al. 2020). Although all the scrapers in our study were in fact parrotfishes, analyses were based on pooled bite rates, further comparisons of bite rate data need to be performed at species-level to investigate further. To expand on this, with species specific analyses we would likely find individual species preferring different benthic habitats, for instance, four species in the genus *Ctenochaetus* have a distinct dentition adapted to detritivory primarily associated with rubble (see Russ et al. 2018).

Our results show that the time of day did not affect fish feeding, however our findings do not reflect the general consensus on this. A strong influence of the time of day on herbivorous fish feeding has been shown across many species in many regions, displaying a pattern of algal nutrients increasing to a midday peak and remaining constant through the afternoon (Polunin & Klumpp 1989; Zemke-White et al. 2002; Yarlett et al. 2018).

Although grazer abundance was highest on the reef flat, there is no clear difference in the feeding rate on the reef flat and reef crest. The reduced feeding rate of grazers on the reef flat in the general use zone was a speculated result of anthropogenic interference. Huang et al. (2017) found fish abundance and diversity were significantly reduced in the presence of many tourists without management. The reef flats of general use zone in this study are subject to snorkelling, swimming and fishing. Although fish generally congregate on reef flats, with so much external disturbance, fish are less likely to display normal behaviour, perhaps leading to reef crest and reef slope feeding.

The reef crests may be preferred by certain species, but hydrodynamic activity is generally higher on the reef crest, meaning the energetic costs of living on the crest is greater than the flat. Traditionally recognised herbivorous functional groups differ in swimming performance, and in their capacity to feed consistently across levels of wave exposure. Species within the same feeding functional group are known to have contrasting responses to wave exposure, emphasising the distinctness of their ecological niche and functional complementarity (Bejarano et al. 2017). Our sampling sites were located on two different sides of Maobitou Cape, which face different monsoon influences between summer and winter. Although we conducted the study between monsoon seasons with no clear wave impact, the long-term influence of wave exposure might also contribute to the different behaviour of herbivorous fishes between sites. Due to our categorisation of functional groups, and failing to investigate individuals within functional groups, it is difficult to investigate how hydrodynamic activity may influence our findings. A change in experimental design is required to investigate further questions regarding swimming abilities of different functional groups.

Grazer and scraper feeding rate and body length were correlated, but the correlation was dependent on protection status. Scrapers displayed correlation in the protected area, while the correlation in grazer feeding and size was found in the general use zone. Large fish inside of protected areas are known to exhibit less but more efficient bites (Kopp et al. 2010). Large parrotfish species (terminal phase, TP) usually spend more time patrolling feeding and breeding territories, which explains large individuals exhibiting slower feeding rates than juveniles (initial phase, IP) (Bonaldo et al. 2006). Our results contrasting with the above research may be due to differences in overall fish assemblages. Most individuals observed on the sites in this study with high abundance also exhibited schooling behaviour.

Several herbivorous fishes have been described moving across areas of reefs in large schools (Choat & Bellwood 1985; Fox & Bellwood 2007). We observed feeding rate increased with school size, but our model revealed feeding rate increased from a single fish to paired feeding, then remaining constant as school size increased. These findings are slightly different to other studies, where the main findings show the larger the group size the higher the feeding rate, as supported by the works of Kopp et al. (2010). Schooling reduces predation risk and allows access to resources which would otherwise be unavailable (Brandl & Bellwood 2014). Welsh & Bellwood (2012a) found the average feeding rate in a school was greater than that of a single individual. They highlighted four rabbitfish species that displayed increases of 50–100% bite rates while feeding in pairs. However, there is still no research on the nonlinear association between the number of schooling trips and feeding rate. Therefore, this study is the first suggesting herbivorous fishes such as parrotfish and surgeonfish schools gradually increase feeding rate. Additional data must be collected and analysed to further support conclusions.

Macroalgae coverage was associated with depth and was also driven by scraper and grazer abundance. Some authors have found herbivores are more abundant in environments rich in algae (Chabanet et al. 1997), whereas others have found no correlation of such (Williams 1986). There are many factors affecting macroalgae coverage, Jessen & Wild (2013) found few herbivorous fish species on a flat reef in the Red Sea, when compared to studies at greater depths and in greater study areas. This indicates larger study areas and greater water depths may host more feeding opportunity and refugia. We also found more scrapers in the restricted zone with low turf algae cover, and more grazers in the general use zone with high turf algae cover. Hoey & Bellwood (2011) have reported grazers, scrapers and browsers tend to avoid high abundances of macroalgae (*Sargassum*) and focus on medium and low-density patches. It might explain grazers in our study gathering at the general use zone hosting 20% macroalgae cover, which is closely related to medium density algae found by Hoey & Bellwood (2011), although comparisons of specific algae types are crucial to confirm this. Although we did not record damselfishes in our study, we noticed more territorial damsels on the reef crest and slope of the general use zone. Herbivorous scrapers in this study were shown to be the main driver for top-down regulation on coral reefs, as in other literature (Smith et al. 2010). The prevalence of top-down or bottom-up regulation on coral reefs in Taiwan requires further research.

The gut content weight from scrapers was consistent with their body length, comparable to Elliott & Persson (1978), who suggested fish gut contents linearly increase with weight. While the gut content and

body length of grazers were not correlated, it was possibly affected by the range of data collection. The anglers mainly targeted the size of grazing fish between 15-20cm TL, unfortunately heavily influencing regression analyses.

The gut contents analysis showed species belonging to the genera *Gracilaria*, *Dictyopteris*, *Laurencia*, *Ulva*, *Sargassum* and *Dictyota*. Preferred macroalgae were consistent with other findings documenting herbivorous fish diet (Tolentino-Pablico et al. 2008). Although contrarily, research in the Caribbean found herbivorous fish avoided brown macroalgae (i.e. *Padina*) favouring turf algae instead (Kopp et al. 2010). Similar results have been found on the Great Barrier Reef (Bellwood & Choat 1990). It has now been recognised that most parrotfishes are microphages that target cyanobacteria and other protein-rich autotrophic microorganisms that live on or within calcareous substrata (Clements et al. 2016). We acknowledge, without the aid of biochemical analyses of diet, the identification of cyanobacteria or microorganism intake poses problems. Although factors affecting food choices of herbivorous fishes in Taiwan are largely unknown, the authors predict a key factor is food availability. Food availability is likely to affect food choices as *Gracilaria* and *Laurencia* are abundant in Southern Taiwan (Tsai et al. 2005). To further investigate food choices, the analysis of functional roles and algal removal rates for specific species would provide much more insight. For instance, Tebbett et al. (2017) compared the gut contents of two surgeonfishes. Gut content analysis revealed *A. nigrofuscus* predominantly ingests algae while *Ctenochaetus striatus* ingests detritus and sediment. In a dietary analysis conducted by Choat et al. (2002), they found a wide range of dietary items were consumed, and dietary groupings do not reflect taxonomic relationships. Finally, Kelly et al. (2016) concluded all surveyed species preferred turf algae, but overall, there were variable foraging portfolios across species. Estimations of algal consumption, grazing rates, additional fish counts and gut content analyses employing a standardised method with DNA barcoding are required to further investigate food choices. This is crucial as knowledge into herbivorous fishes and their food items is important when designing and managing MPAs (Tolentino-Pablico et al. 2008).

Scientists have long advocated for local interventions, such as creating MPAs of varying management levels and implementing fishery restrictions as methods to mitigate local stressors on reef-building corals. However, Bruno et al. (2019) found very little evidence to support the notion of managed reef resilience. They highlighted various reasons why MPAs and the protection of herbivorous fish has had little effect on resilience, which is primarily because the impacts of local stressors are often swamped by the much greater effect of ocean warming. If reefs in KNP cannot be managed properly and saved by local actions alone, then we must face reef degradation by addressing anthropogenic climate change.

## Conclusion

Scraper abundance was largely driven by protection status, whereas grazers gathered in the general use zone at areas with high algal cover. Fish size, reef habitat type and protection status all drove the feeding behaviour of herbivorous/detritivorous fish functional groups. We observed an increasing trend between school size and feeding rate for scrapers and grazers, however our analysis indicated an increase in

feeding rate from an individual to a pair. Further research into the potential roles functionally important detritivorous fish may play in the recovery of degraded reefs is also needed. The restricted zone of KNP is relatively small and management strategies for the protection of functional groups are crucial if we are going to maintain diversity and the structure of coral reefs. These findings can be used to inform fishing regulations, contribute towards efforts in protecting certain reef areas and inform decisions on feeding behaviour and functional groups, thus maintaining coral reef health in KNP.

## Methods

### Study Sites

Kenting is Taiwan's first national park established in 1982, located on the Hengchun Peninsula and is geographically classified as tropical monsoon climate. KNP was designed with limitations on fishing activities. However, with illegal fishing and tourism activities increasing, KNP collaborated with the local tourism industry and announced the Houbihu (Leidashi and Huayuanqu) as a Marine Resources Protection Demonstration Area (MRPDA) in 2005. The MRPDA is a restricted no-take area. Stakeholders and tourists tend to report illegal activities to law enforcement to improve regulation (Yang et al. 2013). Higher fish diversity and large predators are often observed in the MRPDA (Jeng et al. 2015). Illegal angling and spear fishing are often observed in general use areas in KNP (Liu et al. 2012; Wen et al. 2019). This study was conducted between July and September 2015 in KNP (21°56'N 120°47'E). To examine the influence of the regulation levels on the function and behaviour of herbivorous fishes, we surveyed two sites in the general use zone and two sites in the no-take MRPDA (Fig. 7). Wanlitong and Hongchaikeng are in the general use zone and open to regulated coastal angling and subject to more illegal fishing activities (i.e., draft net and gill net). Fish abundance and diversity are lower in the general use zone (Wen, unpublished data). Chu-Shui-Kou and Hou-Hua-Yuan are in the MRPDA restricted zone, where the local tourism industry has acted as a regulatory body, reporting any illegal fishing activities, ensuring the area is managed much more effectively. Although the study sites are situated on different sides of the Maobitou Cape, these sites have similar habitat characteristics (i.e., wave action and currents). The main monsoons in Taiwan are generally north-easterly, meaning the Houbihu is sheltered by the mountains. The fish communities at the Houbihu, Wanlitong and Hongchaikeng are similar (Wen et al 2016).

### Study Species

This study investigated several herbivorous and detritivorous fishes from the tropical region of Taiwan and the Pacific, the subjects were; surgeonfishes (Acanthuridae), parrotfishes (Labridae: Scarinae) and rabbitfish (Siganidae). From previous Underwater Visual Census (UVC) surveys using three 20m transects in this area (Wen et al 2016), the most common surgeonfishes were *Ctenochaetus binotatus* (54%) and *Acanthurus dussumieri* (23%). Surgeonfishes such as *A. nigrofuscus*, *A. xanthopterus* and *Zebrasoma scopas* only represented approximately 5% of the total abundance. The most common parrotfishes were

*Scarus forsteni* (34%), *S. schlegeli* (22%), *S. rubroviolaceus* (15%) and *Chlorurus spilurus* (7%). We only recorded one species of rabbitfish (*Siganus fuscescens*).

We divided these herbivorous/detritivorous fishes into three different functional groups: scrapers, grazers and browsers (Bellwood et al. 2004; Green & Bellwood 2009; Rasher et al. 2013). Scrapers/small excavators are fish that scrape the algae on the surface of the reef consuming algal and detrital material while removing some components of the substratum, such as *Hipposcarus* spp. and *Scarus* spp. Although *Chlorurus* spp. are identified as large excavators/bioeroders (Bellwood & Choat 1990), we did not record any large *Chlorurus* spp., we defined parrotfish from *Scarus* spp. and *Chlorurus* spp. as scrapers in this study. Grazers are species that intensively graze on epilithic algal turf/detritus. All surgeonfishes (*Acanthurus* spp. and *Ctenochaetus* spp.) excluding planktivores were classified as grazers. Browsers are defined as fish that feed directly on large established macroalgae. *S. fuscescens* was the only browser recorded. Choat et al. (2004) indicated the dominant elements in the reef grazing and browsing fauna were consumers of detrital and sedimentary materials. These could not be classified as herbivores. Previous research has shown species composition varies with depth and reef habitat (Hoey & Bellwood 2008), and although depth and habitat type are confounding, we chose three different reef habitat types to investigate feeding behaviour. Three habitats from shallow to deep consisted of the coral reef flat (1-5m), reef crest (5-10m) and reef slope (10-15m).

#### Fish abundance, fish size and feeding behaviour

Fish abundance and body size (cm, TL) were documented using three belt transects (20m) at each site, across habitat types in the general use and restricted zones. The start of the transects were randomly selected and SCUBA divers used UVC to record 2.5m either side of the transect (100m<sup>2</sup>), which took approximately 20 minutes. The transect tapes were laid during the survey to reduce diver effects (Emslie et al. 2018). Feeding behaviour (grazing, scraping and browsing) was documented at the same sampling sites, but not the same area to also reduce diver effects. Feeding rate (bites/minute) and target macroalgae were examined using stationary point count sampling methods (Samoilys & Carlos 2000). Three divers conducted randomly selected stationary point counts (3m radius). Individuals fishes were selected arbitrarily and feeding behaviour was recorded for three minutes. If the subject left the area before three minutes, data were excluded for further analysis. Divers recorded all fishes present for the entire duration of the dives. To determine whether other variables affected feeding behaviour, factors such as time of day, schooling size and benthic composition were taken into consideration. We conducted surveys at three time periods to investigate the effects of the time of day (see Additional file 1: Fig. S5). Data were collected from the morning (8am-10am), noon (11am-1pm) and afternoon (3pm-5pm). There was no significant correlation between the feeding rate of scrapers and grazers with time periods ( $p > 0.05$ ). Data collected throughout the entire day were combined to analyse the effects of habitat type and abundance on feeding behaviour. Divers also recorded group size and feeding rates on the reef flats to determine whether schooling behaviour affects feeding rate. We divided species into solitary or schooling swimming behaviours based on their life stage according to FishBase and literature.

For example, *Scarus schlegeli* and *Scarus ghobban* display schooling behaviour in the juvenile stage, and display solitary behaviour in the adult stage (Welsh & Bellwood 2012a).

## Benthic censuses

Macroalgae and coral coverage data were collected using the same transects as previously mentioned (English et al. 1994). A quadrat frame (30cm x 30cm) was made from plastic pipes with an underwater camera attached 50cm above the quadrat. Divers used this system to take photographs at 1m intervals along the transect. This process was repeated across different habitat types. The 20 photographs from each transect were analysed using Coral Point Count with Excel extensions (CPCe). CPCe was used as it quickly and efficiently calculates statistical coverage over a specified area (Kohler & Gill 2006). A stratified random method was used within CPCe to apply 30 points to each frame. The benthic categories were identified to morphological functional groups (i.e tabular coral, crustose coralline algae and macroalgae). Then data were converted using CPCe to provide a percentage of macroalgae and hard coral coverage.

## Gut contents

Parrotfishes, surgeonfishes and rabbitfish were collected along the coast of the four locations of KNP from local anglers. After measuring weight (g) and fish size (cm, TL), the digestive tract was removed, gut contents extracted and refrigerated to slow digestion. To increase the number of samples, we also collected specimens from the local fish market (only where suppliers could confirm catch locations in confidence). Gut contents were removed *in situ* and refrigerated. In the laboratory, the digestive tract was weighed (wet) with an electronic scale (minimum to 0.01g). Several gut contents were chosen at random, spread in Petri dishes and analysed using a microscope to identify major macroalgae species.

## Data Analyses

### Fish abundance and feeding rate by protection status and habitat

Some of these functional groups were absent during certain surveys. Zero-inflated model (ZIM) and GLM were used to examine the most contributing factors (protection status and habitat type). As some fish observed were not feeding (see Additional file 1: Fig. S2), Hurdle analysis (Poisson with logit link) was used to examine the zero-bite data (i.e., observational periods where the individuals did not bite) between factors prior to the analysis of feeding rate and other factors. GLM and ZIM with negative binomial and Poisson data distribution with multiple factors were used to create different models and to produce the AIC value for each model. If the sample size was small, AIC values were converted into AICc values (AIC with correction). AICc values were compared with different mixing factors, then the Akaike weight was calculated, and the highest Akaike weight indicated the most parsimonious model (Richards 2008; Symonds & Moussalli 2011). The assumptions of models and fitness of the models were diagnosed by using residual plots and the influence of these outliers were explored using Cook's distance (see

Additional file 1: Fig. S6). Models were created using R (v3.1.0; R Development Core Team 2014) with the MASS, pscl and MuMIn packages.

### Schooling feeding behaviour

We first used Hurdle analysis to examine if the zero-bite feeding behaviour was related to solitary or schooling feeding among functional groups and life stages. Then we used a Bayesian model to build a probabilistic exponential growth curve to illustrate the correlation between increasing feeding rate and group size. The model was built in Python (Python Software Foundation 2010) using the PyMC3 module (Salvatier et al. 2016). We used data-driven gradient-based Markov chain Monte Carlo (MCMC) sampling algorithm, No-U-Turn Sampler (NUTS; Hoffman & Gelman 2014) in PyMC3 and Gaussian function to build the Bayesian model. We hypothesized feeding rate increased with group size from a Bayesian GLM model with normal (Gaussian) distribution based on our preliminary observations and literature (Welsh & Bellwood 2012a; Fox et al. 2015). Exponential power regression was used to find the exponential function that fits best for increasing group size in our prior model. Models were fitted with observed bite rate and group size data. Likelihood values were used to estimate 95% confidence intervals.

### Macroalgae coverage with herbivorous fish abundance and environmental factors

GLM with negative binomial and Poisson distribution was used to investigate the correlation between macroalgae coverage and herbivorous fish abundance. Algae coverage was analysed with herbivorous fish abundance as well as protection status (restricted zone, general use zone) and habitat types (reef flat, reef crest and reef slope). AICc was used to find the best explanatory factor. Best goodness-of-fit model indicated the potential drivers (herbivore abundance, protection status and habitat type) of macroalgae coverage.

### Fish size and gut contents

Potential relationships between fish size (TL with log-transformed) and gut content weight were analysed using GLM with AIC selection. The assumptions of above GLMs and fitness of the models were also diagnosed following the previous feeding rate examination (see Additional file 1: Fig. S7). GLM and AIC selection were processed using the `glm` and `step` function with the MASS package in R. The datasets generated and analysed during the study are available in the Figshare repository, <https://doi.org/10.6084/m9.figshare.12362726.v2> (Price et al. 2020).

## Abbreviations

AIC

Akaike Information Criterion

CPCe

Coral Point Count with Excel extensions

GAM

Generalised Additive Model  
GLM  
Generalised Linear Model  
KNP  
Kenting National Park  
MRPDA  
Marine Resources Protection Demonstration Area  
MPA(s)  
Marine Protected Area(s)  
ZIM  
Zero-Inflated Model

## Declarations

### Ethics approval and consent to participate

All data in this study were collected through *in situ* observations and collections from fish markets and fishermen, no fish were killed by us during this study. *In situ* fish observations and fish market sampling did not require animal ethics permits by the animal ethics committee of Tunghai University (Approved by Taichung City, Animal Protection and Health Inspection Office, No. 10500081571).

### Consent for publication

Not applicable

### Availability of data and materials

The data sets supporting the results of this article are available in the *figshare* repository, <https://doi.org/10.6084/m9.figshare.12362726.v2>

### Competing interests

The authors declare they have no competing interests.

### Funding

We thank Kenting National Park Research Program (488-103-02) for initiating this study to monitor Kenting coral reefs (CAC). We also thank the Ministry of Science and Technology Program, Taiwan (103-2313-B-029-004) for financial support during fieldwork (CW).

### Authors' contributions

CW and CAC designed the study, CW and CAC collected the data, CW and KC analysed the data and CW and NP interpreted the data and wrote the manuscript. All authors read and approved the final

manuscript.

## Acknowledgements

We are grateful for the field and laboratory assistance provided by YF Zeng and other researchers, especially Dr. Shaolun Liu for the algal identification. We also thank Derek Ho for statistical analysis advice. Some raw data of this study are based on the collective assignments of Teng-Teng Tan, Yu-Yuan Hsieh and Jia-Hsuan Chen from the Department of Life Science, Tunghai University and a preliminary publication from Wen et al (2016; *Journal of National Park*, in Chinese).

## References

Bejarano S, Jouffray JB, Chollett L, Allen R, Roff G, Marshall A, et al. The shape and success in a turbulent world: wave exposure filtering of coral reef herbivory. *Funct Ecol*. 2017;31:1312-24.

Bellwood DR, Choat JH. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ Biol Fishes*. 1990;28:189-214.

Bellwood DR, Hughes TP, Folke C, Nyström M. Confronting the coral reef crisis. *Nature*. 2004;429:827-33.

Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP, Álvarez-Romero JG, et al. Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. *Biol Conserv*. 2019a;236:604-15.

Bellwood DR, Streit RP, Brandl SJ, Tebbett SB. The meaning of the term 'function' in ecology: A coral reef perspective. *Funct Ecol*. 2019b;33:948–61.

Bonaldo RM, Hoey AS, Bellwood DR. The ecosystem roles of parrotfishes on tropical reefs. *Oceanogr Mar Biol*. 2014;52:81-132.

Bonaldo RM, Krajewski JP, Sazima C, Sazima I. Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. *Mar Biol*. 2006;149:423-33.

Brandl SJ, Bellwood DR. Pair formation in coral reef fishes: an ecological perspective. *Oceanogr Mar Biol*. 2014;52:1–80.

Bruno JF, Côté IM, Toth LT. Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience? *Ann Rev Mar Sci*. 2019;3(11):307-34.

Burkepile DE, Hay ME. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *PNAS*. 2008;105:16201-6.

Carlson PM, Davis K, Warner RR, Caselle JE. Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. *Mar Ecol Prog Ser*. 2017;577:165-76.

- Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R. Relationships between coral reef substrata and fish. *Coral Reefs*. 1997;16:93-102.
- Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, et al. Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs*. 2010;29:1005-15.
- Chen CA, Dai CF. Local phase shift from *Acropora*-dominant to *Condylactis*-dominant community in the Tiao-Shi Reef, Kenting National Park, southern Taiwan. *Coral reefs*. 2004;23(4):508-8.
- Choat J, Bellwood DR. Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. *Mar Biol*. 1985;89:221-34.
- Choat J, Clements K. Daily feeding rates in herbivorous labroid fishes. *Mar Biol*. 1993;117:205-11.
- Choat J, Clements K, Robbins W. The trophic status of herbivorous fishes on coral reefs. 1: Dietary analyses. *Mar Biol*. 2002;140:613-23.
- Choat J, Robbins WD, Clements KD. The trophic status of herbivorous fishes on coral reef. II: Food processing modes and trophodynamics. *Mar Biol*. 2004;145:445-54.
- Clements KD, German DP, Piché J, Tribollet A, Choat JH. Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biol J Linn Soc*. 2016;120(4):729–51.
- Dai CF, Kuo KM, Chen YT, Chuang CH. Changes of coral communities on the east and west coast of Kenting National Park. *J Natl Park*. 1999;9:111-29.
- Day JC, Kenchington RA, Tanzer JM, Cameron DS. Marine zoning revisited: How decades of zoning the Great Barrier Reef has evolved as an effective spatial planning approach for marine ecosystem-based management. *Aquat Conserv: Mar Freshw Ecosyst*. 2019;29(S2):9-32.
- Eggertsen M, Chacin DH, Åkerlund C, Halling C, Berkström C. Contrasting distribution and foraging patterns of herbivorous and detritivorous fishes across multiple habitats in a tropical seascape. *Mar Biol*. 2019. <https://doi.org/10.1007/s00227-019-3498-0>
- Elliott J, Persson L. The estimation of daily rates of food consumption for fish. *J Anim Ecol*. 1978;47:977-91.
- Emslie MJ, Cheal AJ, MacNeil MA, Miller IR, Sweatman HPA. Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ*. 2018. <http://doi.org/10.7717/peerj.4886>
- English SS, Wilkinson CC, Baker VV. Survey manual for tropical marine resources. 2nd ed. The Australian Institute for Marine Science; 1997.

- Fox RJ, Bellwood DR. Quantifying herbivory across a coral reef depth gradient. *Mar Ecol Prog Ser*. 2007;339:49-59.
- Fox RJ, Bellwood DR, Jennions MD. Why pair? Evidence of aggregative mating in a socially monogamous marine fish (*Siganus doliatus*, Siganidae). *Royal Society open science*. 2015;2:50252.
- Froese R, Pauly D, Editors. FishBase. World Wide Web electronic publication. Available at: [www.fishbase.org](http://www.fishbase.org), version (12/2019).
- Graham NAJ, Jennings S, MacNeil A, Mouillot D, Wilson SK. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*. 2015;518:94–7.
- Green AL, Bellwood DR. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience - A practical guide for coral reef managers in the Asia Pacific region. IUCN working group on Climate Change and Coral Reef. 2009; IUNCH. Gland, Switzerland.
- Harborne AR, Rogers A, Bozec YM, Mumby PJ. Multiple Stressors and the Functioning of Coral Reefs. *Ann Rev Mar Sci*. 2017;9:445-68.
- Hoey AS, Bellwood DR. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*. 2008;27:37-47.
- Hoey AS, Bellwood DR. Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? *Ecol*. 2011;14:267-73.
- Hoffman MD, Gelman A. The No-U-Turn Sampler: Adaptively Setting Path Lengths in Hamiltonian Monte Carlo. *JMLR*. 2014;15:1593-623.
- Huang H, Wen CKC, Li X, Tao Y, Lian J, Yang J, et al. Can private management compensate the ineffective marine reserves in China? *Ambio*. 2017;46:73-87.
- Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, et al. Global warming transforms coral reef assemblages. *Nature*. 2018;556:492–6.
- Jeng MS, Wen CKC, Chen JP. Success in the smallest marine reserve of Taiwan: A triumph anchored by effective enforcement, stakeholder support, and replenishment. *MPA News*. 2015;16:7.
- Jessen C, Wild C. Herbivory effects on benthic algal composition and growth on a coral reef flat in the Egyptian Red Sea. *Mar Ecol Prog Ser*. 2013;476:9-21.
- Kelly ELA, Eynaud Y, Clements SM, Gleason M, Sparks RT, Williams ID, et al. Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes. *Oecologia*. 2016;182(4):1151-63.

- Nunes JACC, Sampaio CLS, Barros F. How wave exposure, group size and habitat complexity influence foraging and population densities in fishes of the genus *Halichoeres* (Perciformes: Labridae) on tropical rocky shores. *Mar Biol.* 2013;160:2383-94.
- Keshavmurthy S, Kuo CY, Huang YY, Carballo-Bolaños R, Meng PJ, Wang JT, et al. Coral Reef Resilience in Taiwan: Lessons from Long-Term Ecological Research on the Coral Reefs of Kenting National Park (Taiwan). *J Mar Sci Eng.* 2019;7:388.
- Kohler KE, Gill SM. Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci.* 2006;32:1259-69.
- Kopp D, Bouchon-Navaro Y, Louis M, Mouillot D, Bouchon C. Herbivorous fishes and the potential of Caribbean marine reserves to preserve coral reef ecosystems. *Aquatic Conserv: Mar and Freshw Ecosyst.* 2010;20:516-24
- Kuo CY, Yuen YS, Meng PJ, Ho PH, Wang JT, Liu PJ, et al. Recurrent disturbances and the degradation of hard coral communities in Taiwan. *PLoS ONE.* 2012;7(8):e44364.
- Lau JD, Hicks CC, Gurney G, Cinner JE. Disaggregating ecosystem service values and priorities by wealth, age, and education. *Ecosyst Serv.* 2018;29:91-8.
- Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, et al. Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs.* 2007;26:641-53.
- Lee CH, Chen YJ, Chen CW. Assessment of the Economic Value of Ecological Conservation of the Kenting Coral Reef. *Sustainability.* 2019. <http://doi.org/10.3390/su11205869>
- Liu PJ, Meng PJ, Liu LL, Wang JT, Leu MY. Impacts of human activities on coral reef ecosystems of southern Taiwan: a long-term study. *Mar Pollut Bull.* 2012;64:1129-35.
- Meng PJ, Lee HJ, Wang JT, Chen CC, Lin HJ, Tew KS, et al. A long-term survey on anthropogenic impacts to the water quality of coral reefs, southern Taiwan. *Environ Pollut.* 2008;156:67-75.
- Mellin C, MacNeil AM, Cheal AJ, Emslie MJ, Caley MJ. Marine protected areas increase resilience among coral reef communities. *Ecol.* 2016;19:629-37.
- Mora C, Andréfouët S, Costello MJ, Kranenburg C, Rollo A, Veron J, et al. Coral Reefs and the Global Network of Marine Protected Areas. *Science.* 2006;312:1750-1.
- Nash KL, Abesamis RA, Graham NAJ, McClure EC, Moland E. Drivers of herbivory on coral reefs: species, habitat and management effects. *Mar Ecol Prog Ser.* 2016;553:129-40.

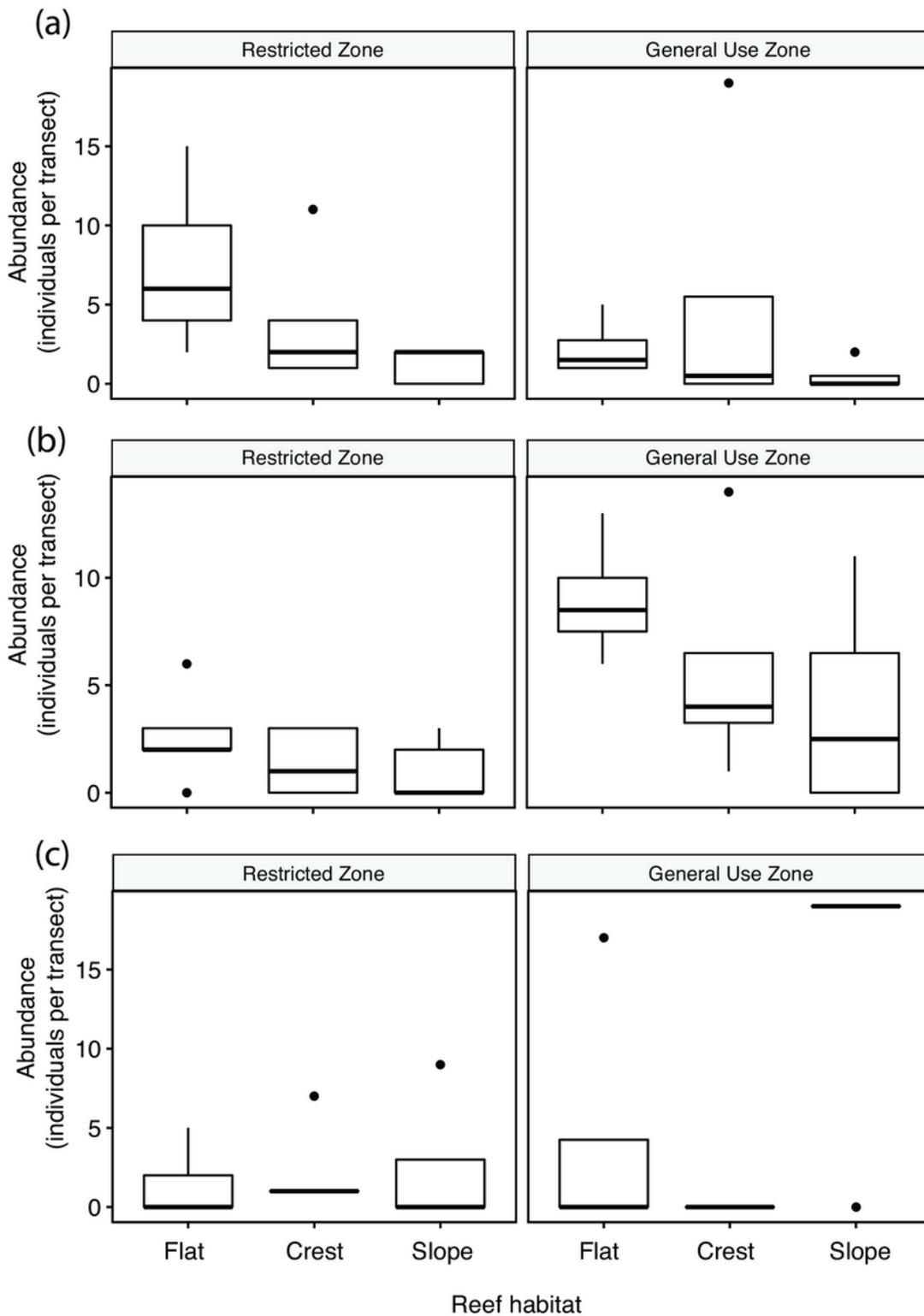
- Nozawa Y, Lin CH, Meng PJ. Sea urchins (diadematids) promote coral recovery via recruitment on Taiwanese reefs. *Coral Reefs*. 2020;39:1199-297.
- Polunin NVC, Klumpp DW. Ecological correlates of foraging periodicity in herbivorous reef fishes of the Coral Sea. *J Exp Mar Biol Ecol*. 1989;126(1):1-20.
- Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ. Changes in Biodiversity and Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss. *Diversity*. 2011;3:424-52.
- Price NW, Chen KS, Chen CA, Wen CKC. Herbivorous fish feeding behaviour. figshare. 2020. <https://doi.org/10.6084/m9.figshare.12362726.v2>
- Python Software Foundation. Python language reference. 2010; Version 2.7. Available at: <http://www.python.org>.
- R Development Core Team. R: A language and environment for statistical computing. 2014; R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org>.
- Rasher DB, Hoey AS, Hay ME. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology*. 2013;94(6):1347-58.
- Richards SA. Dealing with overdispersed count data in applied ecology. *J Appl Ecol*. 2008;45: 218-27.
- Robinson JP, McDevitt-Irwin JM, Dajka JC, Hadj-Hammou J, Howlett S, Graba-Landry A, et al. Habitat and fishing control grazing potential on coral reefs. *Funct Ecol*. 2019. <http://doi.org/10.1111/1365-2435.13457>
- Russ GR. Grazer biomass correlates more strongly with production than biomass of algae turfs on coral reefs. *Coral reefs*. 2003;22:63-7.
- Russ GR, Questel SLA, Rizzari JR, Alcaca AC. The parrotfish-coral relationship: refuting the ubiquity of a prevailing paradigm. *Mar Biol*. 2015;162:2029-45.
- Russ GR, Payne CS, Bergseth BJ, Rizzari JR, Abesamis RA, Alcala AC. Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. *J Fish Biol*. 2018;93:887-900.
- Salvatier J, Wiecki TV, Fonnesbeck C. Probabilistic programming in Python using PyMC3. *PeerJ Comput Sci* 2. 2016. <http://doi.org/10.7717/peerj-cs.55>
- Samoilys MA, Carlos G. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Env Biol Fishes*. 2000;57:289-304.
- Streit RP, Cumming GS, Bellwood DR. Patchy delivery of functions undermines functional redundancy in a high diversity system. *Funct Ecol*. 2019. <http://doi.org/10.1111/1365-2435.13322>

- Smith JE, Hunter CL, Smith CM. The effects of top–down versus bottom–up control on benthic coral reef community structure. *Oecologia*. 2010;163:497-507.
- Symonds MR, Moussalli A. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behav Ecol Sociobiol*. 2011;65:13-21.
- Taylor BM, Benkwitt CE, Choat H, Clements KD, Graham NAJ, Meekan MG. Synchronous biological feedbacks in parrotfishes associated with pantropical coral bleaching. *Glob Chang Biol*. 2019. <http://doi.org/10.1111/gcb.14909>
- Tebbett SB, Goatley CHR, Bellwood DR. The effects of algal turf sediments and organic loads on feeding by coral reef surgeonfishes. *PLoS One*. 2017. <http://doi.org/10.1371/journal.pone.0169479>
- Tebbett SB, Hoey AS, Depczynski M, Wismer S, Bellwood DR. Macroalgae removal on coral reefs: realised ecosystem functions transcend biogeographic locations. *Coral Reefs*. 2020;39:203-14.
- Tolentino-Pablico G, Bailly N, Froese R, Elloran C. Seaweeds preferred by herbivorous fishes. *J Appl Phycol*. 2008;20:933-8.
- Tsai CC, Chang JS, Sheu F, Shyu YT, Yu AYC, Wong SL, et al. Seasonal growth dynamics of *Laurencia papillosa* and *Gracilaria coronopifolia* from a highly eutrophic reef in southern Taiwan: temperature limitation and nutrient availability. *J Exp Mar Biol Ecol*. 2005;315:49-69.
- Yarlett RT, Perry CT, Wilson RW, Philpot KE. Constraining species-size class variability in the rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates. *Mar Ecol Prog Ser*. 2018;590:155-69.
- Welsh JQ, Bellwood DR. How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. *Coral Reefs*. 2012a;31:991-1003.
- Welsh JQ, Bellwood DR. Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral reefs*. 2012b;31:55-65.
- Wen CK, Chen KS, Tung WC, Chao A, Wang CW, Liu SL, Ho MJ. The influence of tourism-based provisioning on fish behavior and benthic composition. *Ambio*. 2019;48:779-89.
- Wen CK-C, Tan TT, Hsieh YY, Chen JH. Marine reserves substantially enhanced herbivorous fish abundance and thereby increased macroalgae removal. *J Nat Park*. 2016; 26:46-60. (In Chinese)
- Williams DMB. Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short-term effect of *Acanthaster planci* infestation. *Mar Ecol Prog Ser*. 1986;28:157-64.
- Williams GJ, Graham NAJ. Rethinking coral reef functional futures. *Funct Ecol*. 2019;33:942–7.

Yang YC, Wang HZ, Chang SK. Social dimensions in the success of a marine protected area: a case in a Taiwan fishing community. *Coast Manage.* 2013;41:161-71.

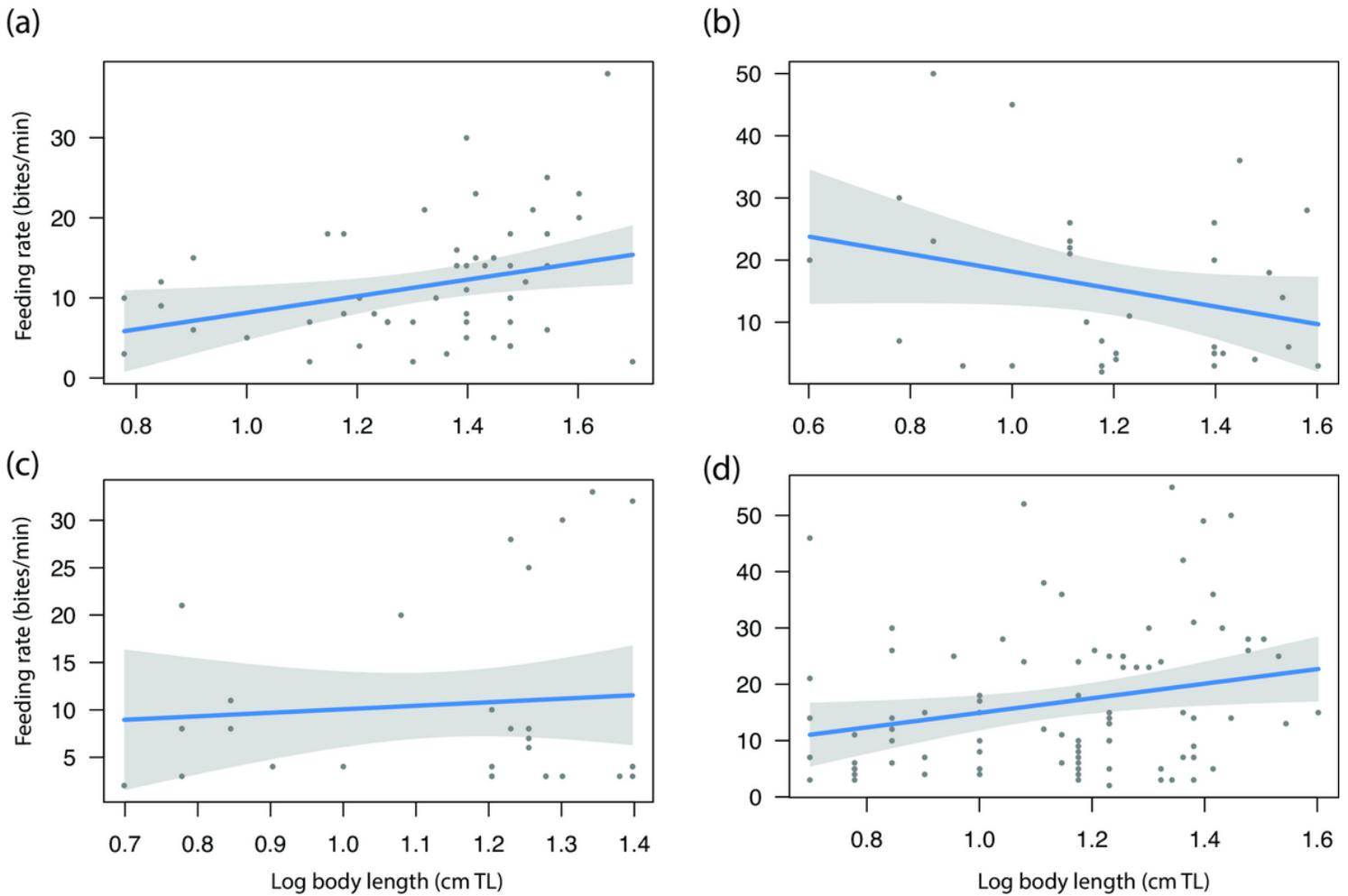
Zemke-White LW, Choat J, Clements K. A re-evaluation of the diel feeding hypothesis for marine herbivorous fishes. *Mar Biol.* 2002;141:571-9.

## Figures



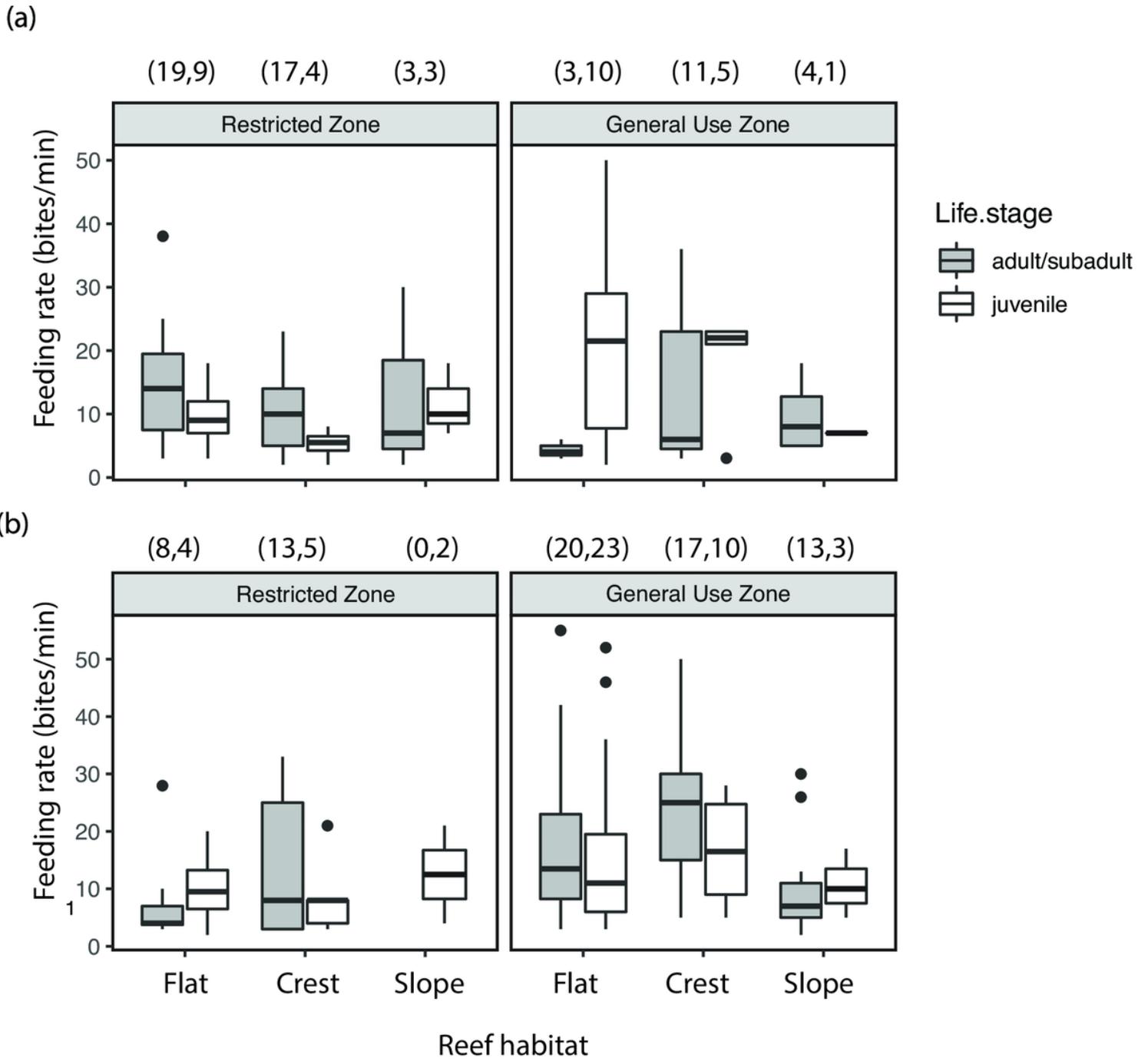
**Figure 1**

Abundance (individual per transect) of subadult/adult (a) scrapers, (b) grazers and (c) browsers across habitat types (reef flat, crest and slope) between the restricted zone and general use zone.



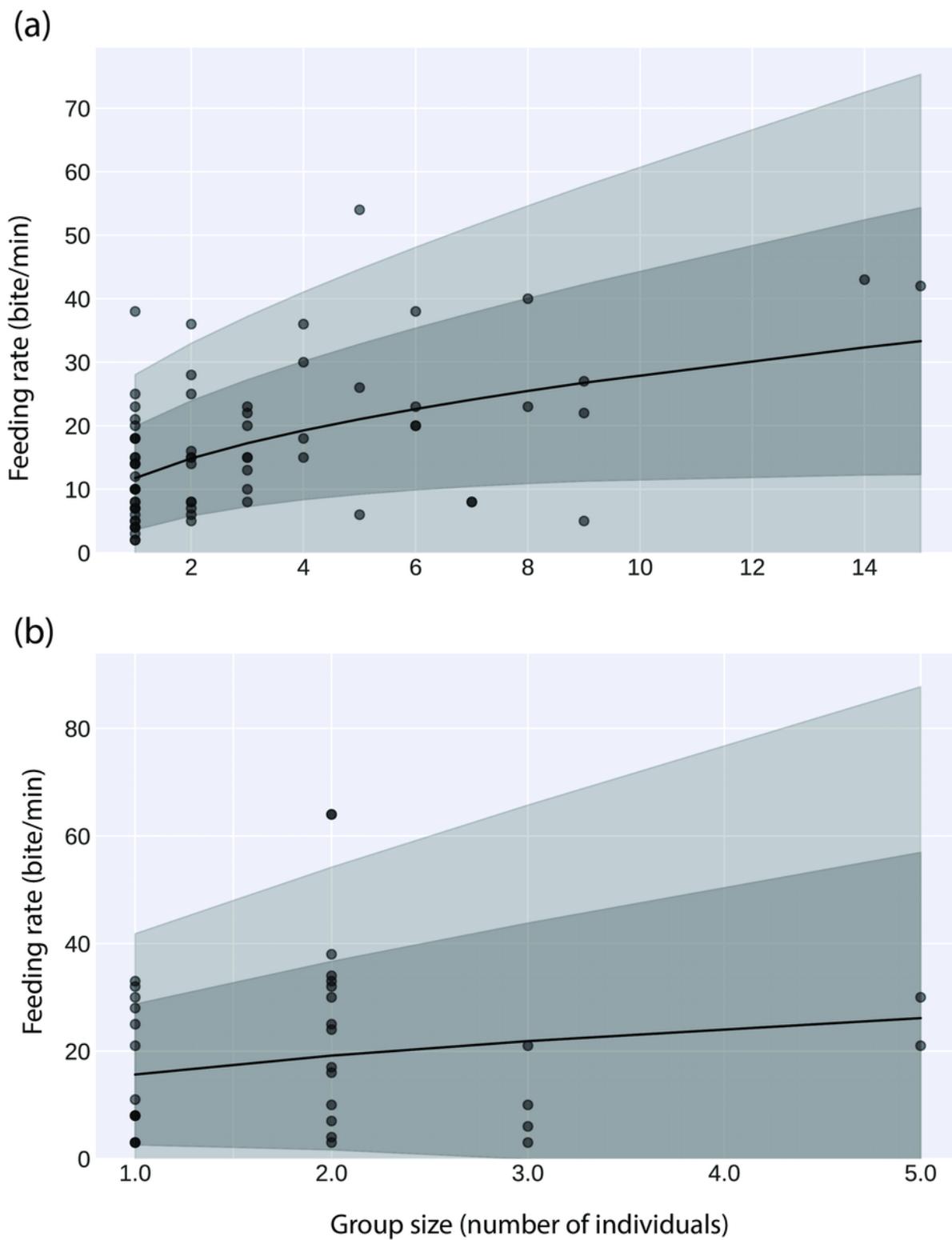
**Figure 2**

Correlation between feeding rate (bites/minute) and body size (cm, TL) of scrapers in the (a) restricted zone and (b) general use zone and grazers in the (c) restricted zone and (d) general use zone, with Generalised Additive Model estimation. The model selection process indicated body size only contributed to grazer feeding rate in the general use zone and scraper in the restricted zone. (AIC values of feeding rate ~ length vs feeding rate~1 is (a) scraper in the restricted zone: 375.31<380.53; (b) scraper in the general use zone: 272.84>272.79; (c) grazer in the restricted zone: 241.62>239.89; (d) grazer in the general use zone: 682.86<686.53).



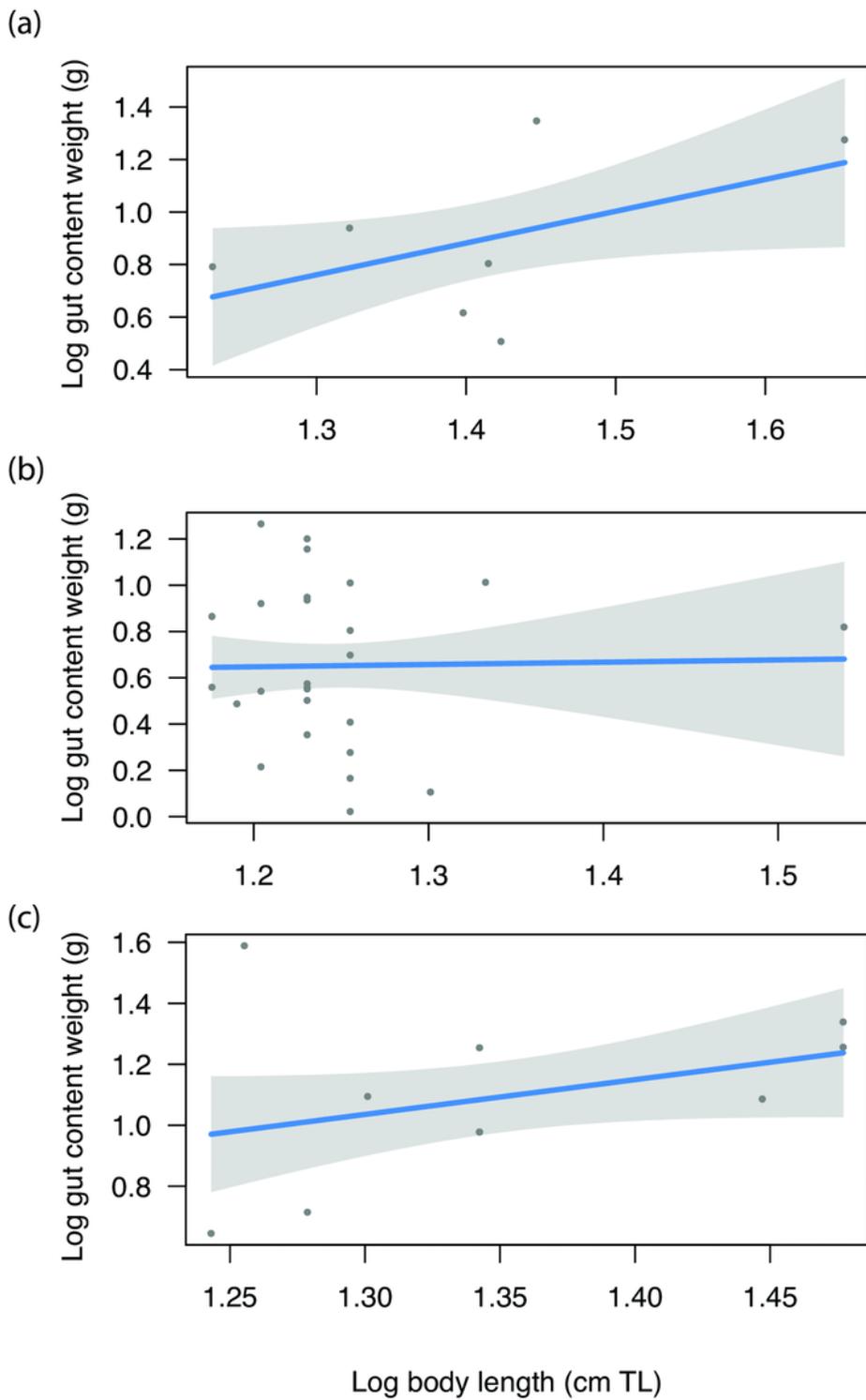
**Figure 3**

Feeding rate (bites/minute) of subadult/adult and juvenile (a) scrapers and (b) grazers across habitat types (reef flat, crest and slope) between the restricted zone and general use zone. The numbers in the brackets indicate the sample size of each group.



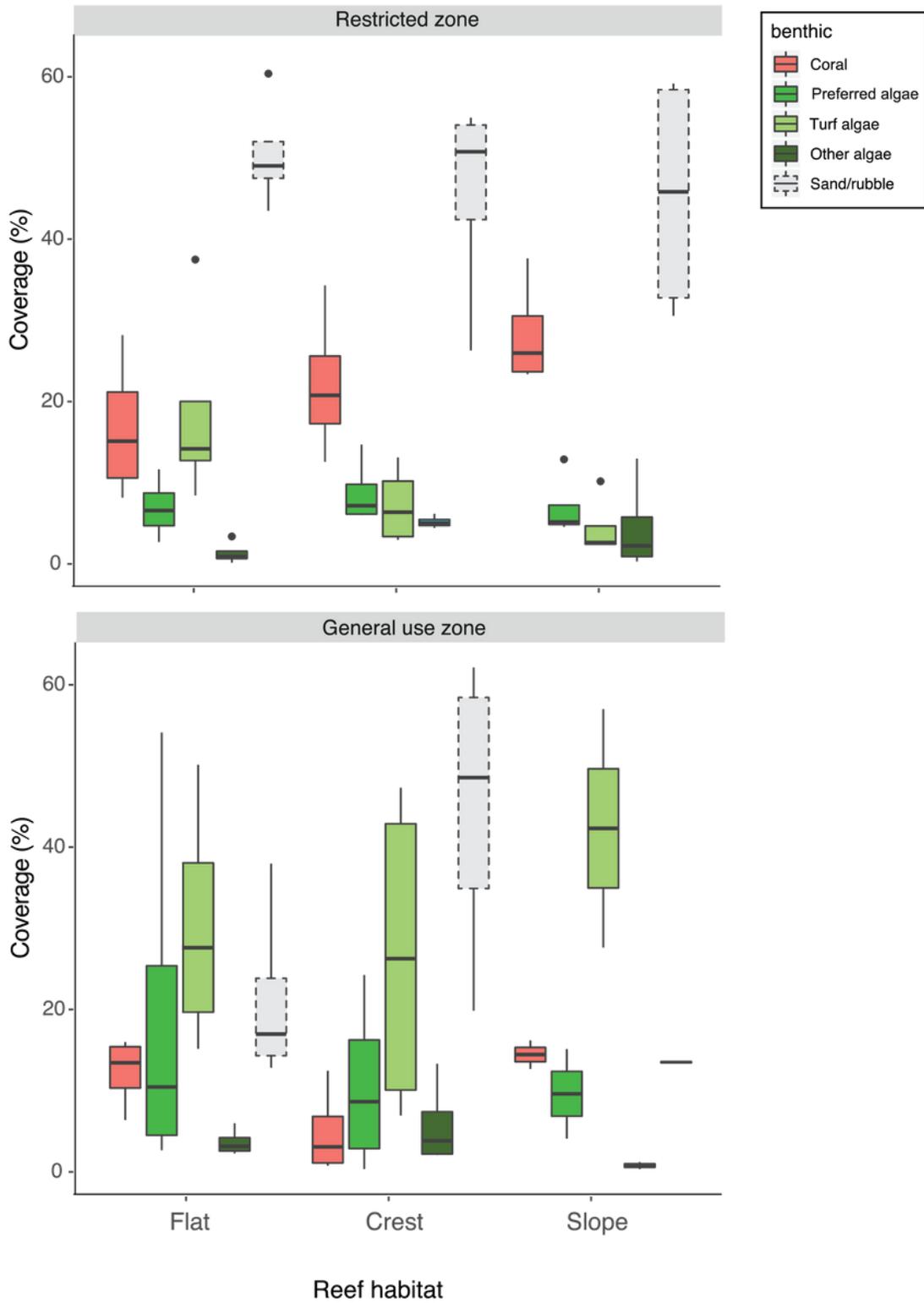
**Figure 4**

Bayesian model for increasing feeding rate (bites/minute) and schooling behaviour of (a) scrapers and (b) grazers, built by observed data with prior hypothesized exponent model. Grey areas represented 95% probability of feeding rate.



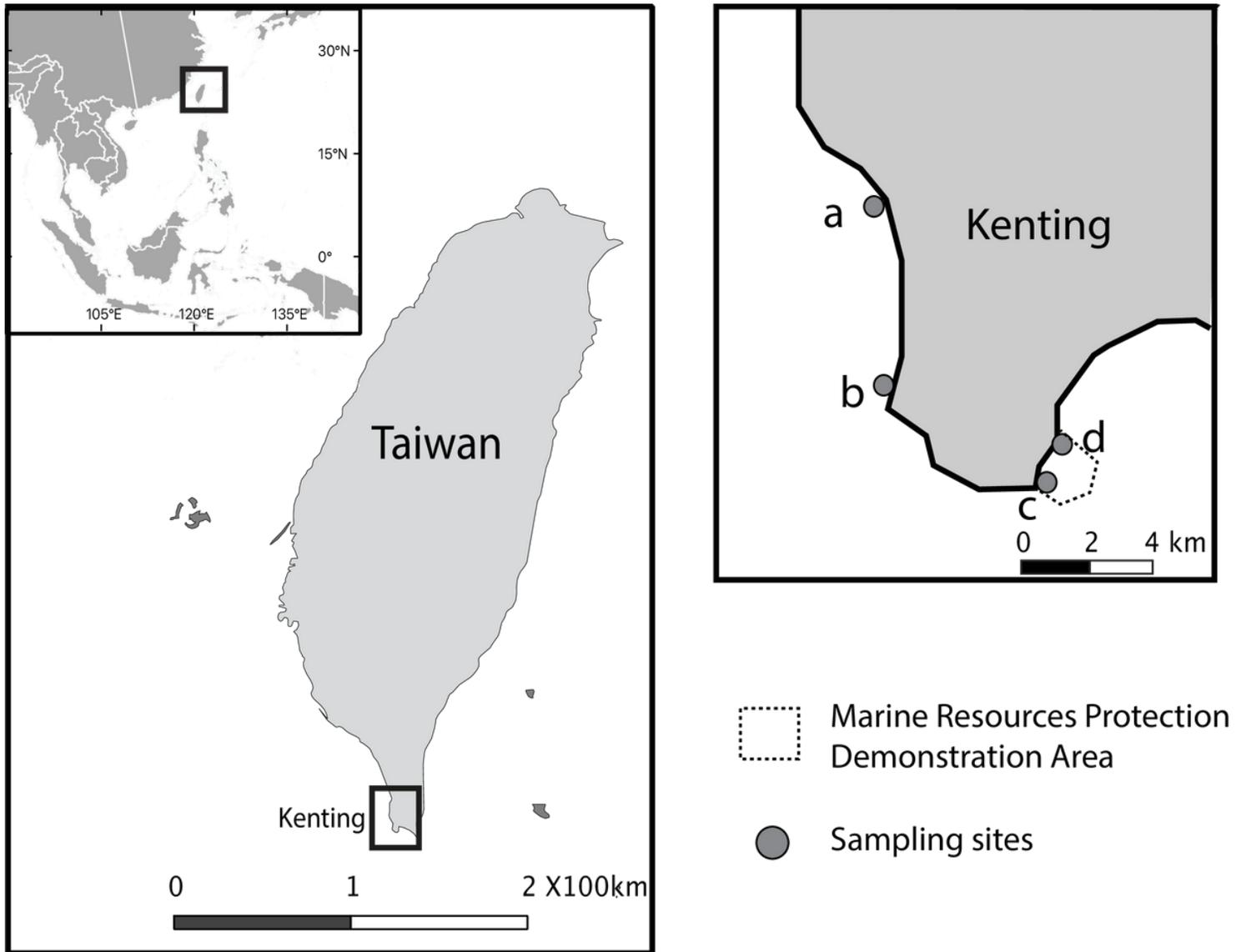
**Figure 5**

Relationship between gut content (g) and body size (cm, TL) for (a) scrapers, (b) grazers and (c) browsers.



**Figure 6**

Dominant benthic coverage across reef habitats between the restricted zone and general use zone.



**Figure 7**

Map of study sites within two different zones inside Kenting National Park. (a) Wanlitong and (b) Hongchaikeng are in the general use zone, (c) Leidashi and (d) Huayuanqu (Houbihu) are in the Marine Resources Protection Demonstration Area (MRPDA). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [ESMR3ScrapingandGrazingHerbivores.docx](#)