


The influence of tourism-based provisioning on fish behavior and benthic composition

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Abstract Distribution of non-natural food (provisioning) to attract fish, though popular in coral reef tourism, has often been discouraged due to its assumed adverse effects on fish health and behavior. However, the effects of provisioning on community structure, anti-predator, and foraging behavior of teleost fishes, as well as their potential to indirectly affect benthic organisms, are not yet clear. Here, we compared fish composition, wariness, foraging behavior of herbivorous fishes, and the benthic cover between provisioned and control sites. We found significant differences in fish abundance, species number, and composition at some locations, but not all. Although most provisioned herbivorous fish did not reduce their biting rates of benthic algae, provisioned sites still had higher coverage of green macroalgae. Our results dispute widely held presumptions on the effects of tourism-based provisioning on the ecology and behavior of teleost fishes, as well as the benthic cover. These findings suggest that while regulation of provisioning is necessary to manage and mitigate any deleterious outcomes, when moderated and monitored, it could still provide an educationally beneficial tool for coral reef ecotourism.

Keywords Coral reef · Ecotourism · Fish feeding · Foraging behavior

INTRODUCTION

Coral reefs are one of the most diverse ecosystems in the world. Protecting coral reefs not only maintains high

biodiversity, but increases the socio-economic value of marine resources (via tourism) up to US\$36 billion (Spalding et al. 2017). However, damage caused from poorly managed operations can reduce the health, sustainability, and long-term value of coral reefs. For example, inexperienced divers or snorkelers can damage corals leading to reduced reef complexity (Rouphael and Inglis 2001; Franco et al. 2009). The shade effects from pontoons established by tourism operators can reduce or even prevent the ability of corals to photosynthesize (Glasby 2006). Additionally, the prevalence of coral disease has also been linked to anthropogenic disturbances such as the waste and pollution associated with intense tourism operations (Lamb and Willis 2011; Lamb et al. 2014). Illegal collection of corals by tourists has also been observed near tourism centers that encourage such acts by selling shells and corals for decoration purposes (Huang et al. 2017). Evaluating the influence of tourist activities on coral reef environments should therefore be critical for effective tourism management and sustainable use of coral reefs.

In terrestrial national parks and nature reserves, the influence of tourist activities on animal behavior and health has been well examined. For example, tourists feeding wildlife, also known as provisioning, can lead to malnutrition and the spread of pathogens (Orams 2002). Wildlife habituation of humans can also reduce their vigilance and wariness of predators (reviewed in Higham and Shelton 2011). Although tourist influence can be either positive or negative depending on species, location, and how tourism is managed, wildlife provisioning is often discouraged (Murray and Becker 2016). A well-managed educational whale watching tour, for example, can still satisfy their customers without interfering with the whale's natural behavior (Valentine et al. 2004). However, surveys show that tourists still value wildlife interaction as one of the

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decisive factors in their satisfaction with ecotourism activities (Moscardo and Saltzer 2005; Vaske and Manfredi 2012). Indeed, increased support for conservation efforts resulting from ecotourism should not be overlooked (Zeppel and Muloin 2008; Ballantyne et al. 2009; Brunnschweiler et al. 2013). Seeking a balance between human interference and the positive outcomes that provisioning can provide should therefore be an essential component of effective conservation management.

Studies have shown marine creatures altering their foraging behaviors or habit use as a result of provisioning ecotourism (Orams 2002). Sharks and rays, for example, have been observed to exhibit different home ranges and movement patterns in provisioned areas compared to areas without provisioning (Maljkovic and Cote 2011; Corcoran et al. 2013). The distribution of non-natural food sources is also considered unhealthy or unbalanced in nutrition for marine megafauna (reviewed in Murray and Becker 2016). Although provisioned megafauna altered their foraging or homing behavior, the negative effects from tourism-based provisioning may be over-estimated (Bateman and Fleming 2017; Birnie-Gauvin et al. 2017).

Compared to marine megafauna, the effects of ecotourism provisioning on coral reef fish has not been well studied (but see Albuquerque et al. 2014; reviewed in Prinz 2017). For this reason, restricting or banning fish provisioning in diving tourism is not always based on testable results (Greenfins 2018). Limited work has been done to show that reef fish provisioning would attract certain fish species, thereby leading to changes in the abundance and composition of fish communities on reefs where fish provisioning regularly occurs (Milazzo et al. 2005; Albuquerque et al. 2014; reviewed in Prinz 2017). Speculated impacts from fish provisioning are commonly stressed on different social-media platforms and diving-related articles (Marshall 2015). Many dive shops and dive training organizations (i.e., PADI, Professional Association of Diving Instructors) caution against coral reef fish provisioning as it is thought that non-natural food sources may lead to malnutrition (Denny 2014), although such claims are based solely on studies conducted entirely in captivity (Orams 2002). Fish provisioning can, however, alter the behavior of fishes. The nests of Pomacentrids, for example, may experience increased attacks by unnatural feeding forays of Labrids attracted by fish provisioning (Milazzo et al. 2006), and provisioned fishes may also mistakenly bite divers and snorkelers (Hammerschlag et al. 2012). Although influences from fish provisioning on behavior have been found in coral reef fishes, direct physiological damage from provisioning on bony fishes has yet to be examined (Patroni et al. 2018). In addition, provisioning ecotourism has been proposed on social media (such as Facebook) to alter reef ecosystem food-web dynamics. For

example, fish provisioning has been suggested to decrease herbivory by favoring omnivorous fishes at the expense of herbivorous fishes, thereby leading to algal overgrowth on coral reefs (Greenfins 2018; Marine Ecology Consulting 2018). However, no clear trophic cascades or benthic phase shifts from provisioned herbivorous fishes have been examined. Influences from tourism-based fish provisioning on coral reef ecosystem due to altered herbivorous fish behavior therefore require further investigation.

In this study, we verified the possible influence of provisioning ecotourism on coral reef fishes and ecosystems. According to previous works and speculation from non-peer-reviewed sources, we examined the following hypotheses: (1) fish communities from provisioned reefs are different from other natural reefs; (2) fish communities at provisioned reefs have higher abundance but lower species richness; (3) provisioned reefs support less herbivorous fishes; (4) provisioned fishes display lowered wariness than none fed-fishes; (5) provisioned herbivorous fishes display lower foraging frequency on macroalgae; (6) provisioned sites have higher macroalgae and less coral cover. To examine the hypotheses above, we surveyed the (1) fish community structure, (2) wariness of fishes to divers, (3) foraging behavior of herbivorous fishes, and (4) coverage of coral and macroalgae at popular provisioned and nearby control sites to evaluate the possible consequences of tourism-based provisioning.

MATERIALS AND METHODS

Surveys were conducted during the tourist peak seasons of July and September 2016 and July 2017. Four different locations, each with one control and one provisioned site, were selected for this study within marine reserves of Kenting and Green Island (Fig. 1). The survey sites generally possess a higher diversity of fishes and coral cover than other reefs in the Kenting and Green Island areas (Heatwole in prep.). At each location, a provisioned site and a control site were chosen to examine the effects of fish feeding. Study sites were similar distances from the shore and at similar depths. Provisioned sites were chosen based on their popularity with divers and the regular occurrence of fish provisioning by divers with bread, snacks, or bait (mackerel pike, *Cololabis saira*). Sites that were less popular with divers and where no provisioning activity was observed to occur were selected as control sites. During a pilot study, no attraction behavior of fishes to divers was observed within the control sites, suggesting the fishes at the non-provisioned sites were not used to provisioning and that control sites were largely independent of the provisioned sites that were just 50 m away. Benthic habitats in the provisioned and control sites were similar, with both

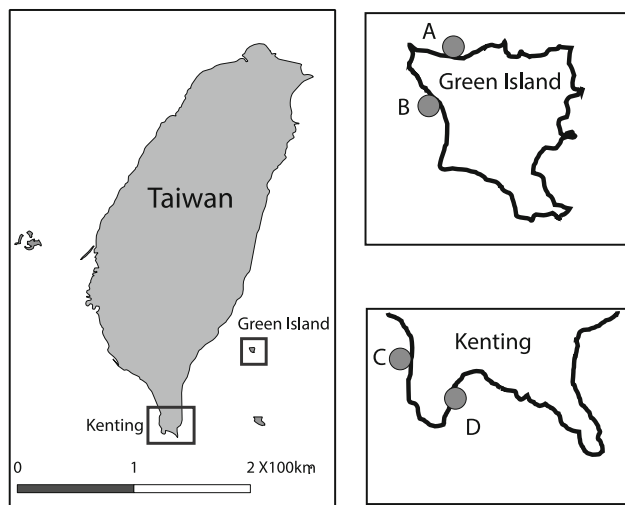


Fig. 1 Four locations with tourism-based provisioning from Kenting and Green Island in Taiwan. A Chaikou, B Shilang, C Wanlitong, D Houbihu

dominated by encrusting and submassive corals surrounded by sandy bottoms ranging from 5 to 10 m in depth. Effects of fishing on fish community and behavior were presumed to be limited as study sites were within protected areas where fishing is prohibited.

Fish community

Fish species and number of individuals were recorded over 5 min by two divers with two-stage stationary point count UVC (underwater visual census). First, divers slowly approached marked reef sites until they could observe fish clearly without disturbing them and began recording mobile species in a 2-m-radius area. After 5 min, divers moved to the reef bottom and searched for reef dwelling species closer to the benthos within a 2-m-radius area. Six replicates for both provisioned and control sites for each location were conducted during our two-year study period. In addition to the composition study, a pilot survey on provisioned fishes was also conducted to establish which fish species were affected for inclusion within the following fish wariness and foraging study.

Fish wariness

Flight initiation distance (FID) was used to examine fish vigilance under predation stress (Januchowski-Hartley et al. 2011; Milazzo 2011). This involved each observer arbitrarily selecting one fish at a time and swimming slowly towards that individual. When the individual started to flee, the observer estimated the distance between themselves and the fish to obtain the FID. Before the survey, observers practiced distance estimation following a

method modified from Januchowski-Hartley et al. (2011) until they were both able to estimate to within a distance of 5 cm or less. Both trained divers collected the FID data during fish wariness surveys. During each survey, the size of each individual fish was also estimated to nearest centimeter.

Fish foraging

Differences in fish foraging behavior were examined at control and provisioned sites by recording the bite rates of herbivorous fishes on benthic algae. Dominant species of Scaridae and Acanthuridae were chosen in each site and their feeding behavior were examined between 1 100 to 1 600 due to constant foraging intensity that been previously observed during this period, (Polunin and Klumpp 1989; Wen et al. 2016). At provisioned sites, divers arbitrarily chose one dominant herbivorous species which had shown signs (i.e., swimming to diver) of previous diver related provisioning. When tourists were present at the site and were provisioning fishes, the researchers waited until provisioning ceased before starting to follow the target individual and recording its bite rate once it resumed feeding on benthic algae. The divers recorded the number of bites in 2 min. At the control sites, the same process for the same species was followed. Size of each individual was also estimated to the nearest centimeter to consider how the size of fishes might affect their bite rates (Gotanda et al. 2009).

Benthic composition

Benthic composition surveys were conducted at the same time with UVC stationary survey for fish communities. In addition to the aforementioned control sites 50 m away, two supplementary sites 100 m away from the provisioned sites were also surveyed three times over two-year study period to compare the possible effects of tourism-based provisioning on the benthic composition at these sites. Photo quadrats were used to determine the major benthic composition (coral, macroalgae, sponge etc.) coverage in control and provisioned sites in Green Island where bottom topography was similar between reefs. The benthic composition in Kenting was not surveyed because the reef structure and topography obviously differed between provisioned and control sites, leaving it unclear whether fish provisioning or topography influenced the benthic cover. Twenty 0.5-m × 0.5-m quadrats were photographed along a 20-m transect line at each site. Photos were analyzed using CPCe with 20 random dots to represent the coverage of different benthic organisms (Kohler and Gill 2006). Each dot from CPCe of the photo was identified as either coral, macroalgae (Phylum level), or other major groups,

such as sponge and sea urchin. The coral and macroalgae coverage were compared between provisioned sites, control sites, and supplementary sites 100 m away.

Data analysis

Fish community

To examine the effects of tourism-based provisioning on fish communities and herbivorous fishes, data were separated into total fishes and herbivorous fishes. Three fish community parameters, (1) total fish abundance, (2) total species number, and (3) herbivorous fish abundance between control and provisioned sites, were analyzed accordingly with a two-way nested ANOVA (site nested in location). All above data were tested for normality (Shapiro–Wilk test) before analysis and then $\log(x + 1)$ transformed. Total fish compositions between control and provisioned sites were analyzed with a two-way nested PERMANOVA. Site (provisioning or not) and locations were used as factors. Data were $\log(x + 1)$ transformed before creating a data matrix using Hellinger distance similarity for further multivariate analysis. Distance-based redundancy analysis (dbRDA) was used to visualize the differences between locations and site. Fish species which had higher correlation (> 0.5) were displayed on the dbRDA plot. Similarity percentage (SIMPER) analysis was also used to indicate which species contributed the most to the differences between provisioned and control sites.

Fish wariness and foraging behavior

The effects of provisioning on fish wariness were examined by analyzing the equality of means of FID of fishes from provisioned and control sites using ANCOVA (analysis of covariance). The relationship between FID and body length of recorded individuals from provisioned and control sites were modeled separately by linear regression and compared between sites. The null hypothesis of ANCOVA is that the regression slope of provisioned and control sites is not significantly different. In addition, the effects of body length on FID were also examined via differences of regression of provisioned or control site and horizon (slope = 0). An ordinary least squares (OLS) regression model was chosen to illustrate the differences between FID of provisioned and control sites with size effects. The effects of provisioning on foraging behavior of fishes were examined by analyzing the bite rate through the same process as FID.

Benthic composition

Significant differences in the benthic composition between provisioned sites, 50-m control sites, and 100-m supplementary sites were examined by ANOVA, and Tukey's pairwise test was used once significant differences were detected. All statistical analyses were performed using PAST v3.16 (Hammer et al. 2001) and PERMANOVA of Primer-E v.7 (Anderson et al. 2008) software packages.

RESULTS

From our pilot survey, we found that 26 (Kenting) and 27 (Green Island) out of a total of 38 fish species were attracted to provisioning at these sites (Table S1). The most common fish families were Pomacentridae and Labridae, with a few other species from Acanthuridae and Chaetodontidae. The most abundant feeding guilds were

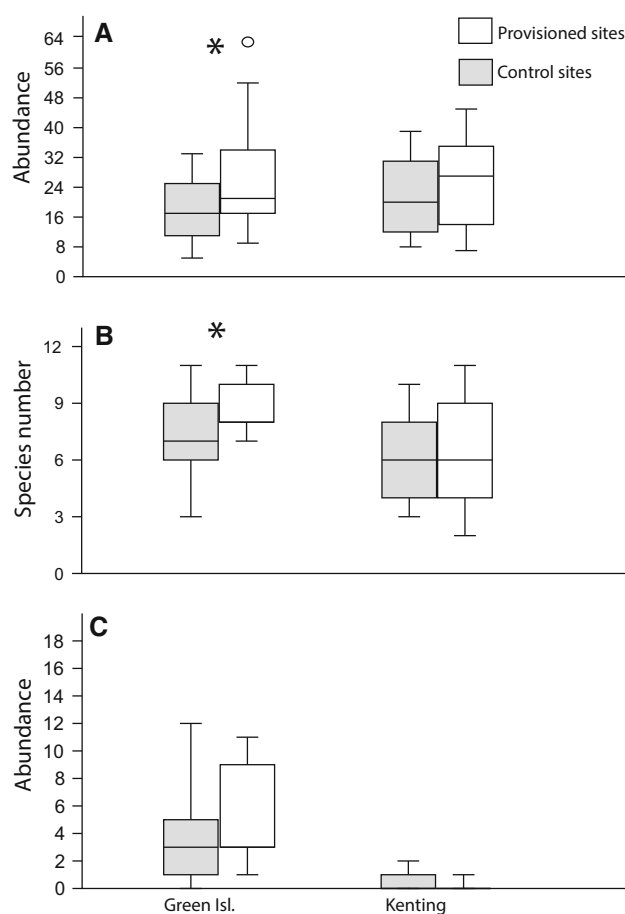


Fig. 2 The **a** abundance, **b** species number of all fishes, and **c** abundance of only herbivorous species at control and provisioned sites in Kenting and Green Island. Asterisk symbols indicate significant differences between control and provisioned sites from two-way ANOVA

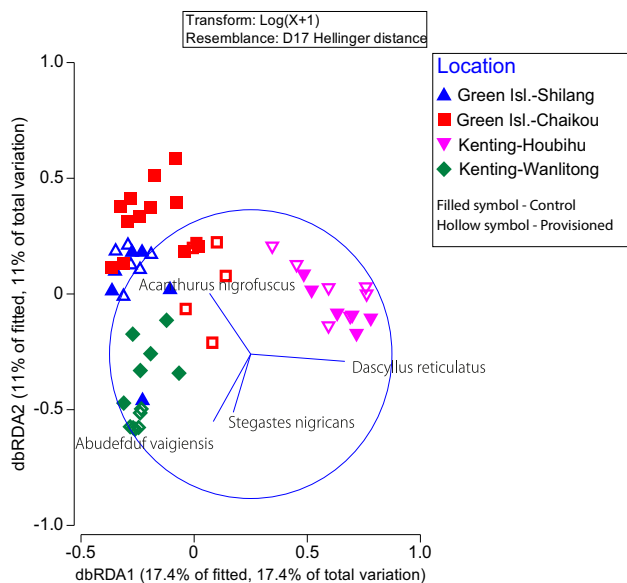


Fig. 3 Distance-based redundancy analysis (dbRDA) showing the species correlated to location and site factors

carnivores (44.7%) and omnivores (34.2%), followed by herbivores (10.5%) and corallivores (10.5%) (Table S1). During the fish composition survey, we recorded 593 individuals and 56 species in Kenting, and 640 individuals and 72 species in Green Island. For the differences between provisioned and control sites, fishes in Kenting did not show any statistically significant differences in abundance or species number ($p > 0.05$; Figs. 2a and 2b), but fishes in Green Island showed significant differences in both species number and abundance ($p < 0.05$; Figs. 2a and 2b). For only herbivorous fishes, there were no differences in abundance between regions (Fig. 2c). For total fish composition, significant differences were found for both site and region factors (Green Island vs Kenting; PERMANOVA, $p < 0.05$, Table S2). Two-stripe damselfish (*Dascyllus reticulatus*), dusky farmerfish (*Stegastes nigricans*)

and sergeant major damselfish (*Abudefduf vaigiensis*) were more abundant within sites at Kenting, while spot-cheeked surgeonfish (*Acanthurus nigrofuscus*) was abundant at the majority of sites at Green Island (Fig. 3). SIMPER analysis revealed higher numbers of bicolor chromis (*Chromis margaritifer*), *Ac. nigrofuscus* and lined surgeonfish (*Ac. lineatus*) at provisioned sites in Green Island, whereas three-spot dascyllus (*D. trimaculatus*) and *A. vaigiensis* were most abundant at the provisioned sites in Kenting (Table 1). However, *Ac. nigrofuscus* also had higher numbers at the control site of one location (Chaikou) in Green Island. Control sites had higher numbers of *D. reticulatus* and six-bar wrasse (*Thalassoma hardwicke*) in Kenting. Most of the different species between control and provisioned sites were those species that displayed attraction behavior towards divers (Table S1).

To examine the effects of tourism-based provisioning on wariness of fishes, we chose to observe several species which were common in provisioned and control sites and that were also observed to respond to divers' provisioning activities (fish ate the food provided by divers). These species were *Ac. nigrofuscus*, *D. trimaculatus*, *D. reticulatus*, *C. margaritifer*, *Chaetodon kleinii*, *P. bankanensis*, and *St. nigricans*. We found provisioned fish's FID was varied by species. For example, *Ac. nigrofuscus*, *Ch. kleinii*, *D. reticulatus*, and *P. bankanensis* have statistically longer FID in control sites than provisioned sites (Figs. 4a, b, d and e), while *D. trimaculatus* and *Stegastes nigricans* did not show any significant differences in FID between sites (Figs. 4g–i). *Chromis margaritifer* did not respond consistently between locations (Fig. 4c and f). In addition, the body length of some fishes did not affect their FID. Some of their FID changes with their size increase, such as *D. reticulatus* (Kenting, provisioning), *St. nigricans* (Green Island, provisioning), *Ch. kleinii* (Green Island, provisioning), and *Ac. nigrofuscus* (Green Island, control) (Table 2A).

Table 1 SIMPER analysis showing the species which contributed most to differences between provisioned and control sites in four different tourism locations (KT for Kenting and GI for Green Island)

Location	Species	Control Av. Abundance	Provisioned Av. Abundance	Contribution (%)
Chaikou (GI)	<i>Acanthurus lineatus</i>	0	1.47	9.73
	<i>Acanthurus nigrofuscus</i>	1.51	0.46	8.02
Shilang (GI)	<i>Chromis margaritifer</i>	1.22	2.03	9.1
	<i>Acanthurus nigrofuscus</i>	0.71	1.41	8.3
Wanlitong (KT)	<i>Abudefduf vaigiensis</i>	0.27	1.99	14.74
	<i>Thalassoma hardwicke</i>	1.13	0.32	9.11
Houbihu (KT)	<i>Dascyllus reticulatus</i>	2.57	2.15	13.98
	<i>Dascyllus trimaculatus</i>	0	0.82	9.98

Bold numbers indicate which of the provisioned and control sites had the higher number of individuals

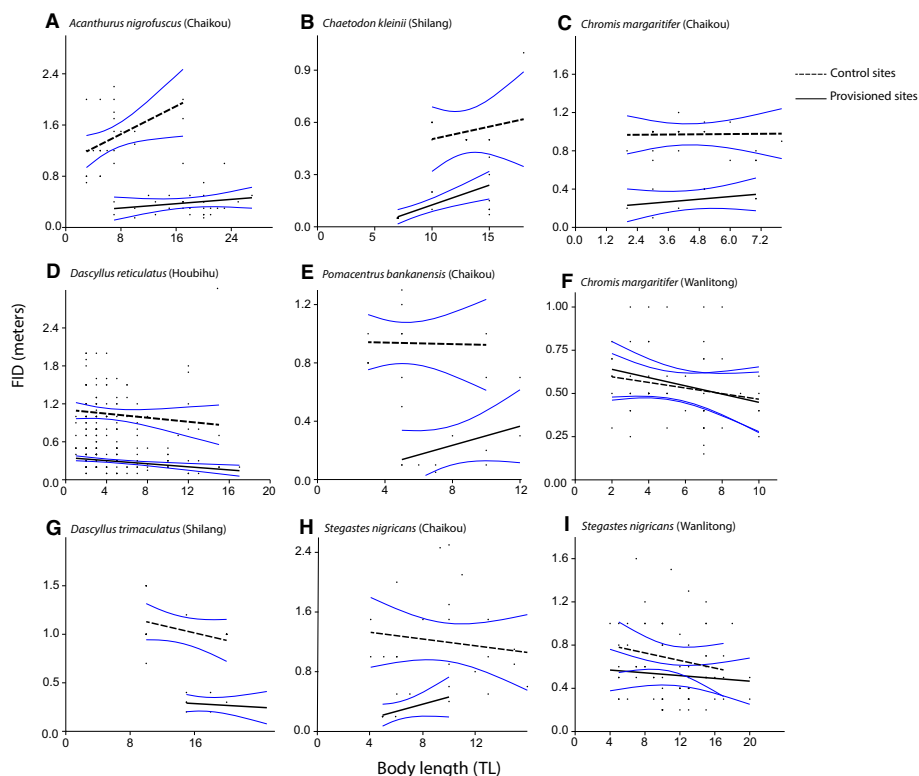


Fig. 4 Linear correlation of flight initiation distances (FID) and body length (cmTL) between provisioned and control sites for fed-fishes. The numbers after the site name represented the sample size of provisioned and control site accordingly. **a** *Acanthurus nigrofuscus* (Chaikou; $n = 33$ and 24), **b** *Chaetodon kleinii* (Shilang; $n = 30$ and 11), **c** *Chromis margaritifer* (Chaikou; $n = 8$ and 25), **d** *Dascyllus reticulatus* (Houbihu; $n = 89$ and 96), **e** *Pomacentrus bankanensis* (Chaikou; $n = 11$ and 11), **f** *Chromis margaritifer* (Wanlitong; $n = 20$ and 34), **g** *Dascyllus trimaculatus* (Shilang; $n = 7$ and 17), **h** *Stegastes nigricans* (Chaikou; $n = 6$ and 21), **i** *Stegastes nigricans* (Wanlitong; $n = 38$ and 37)

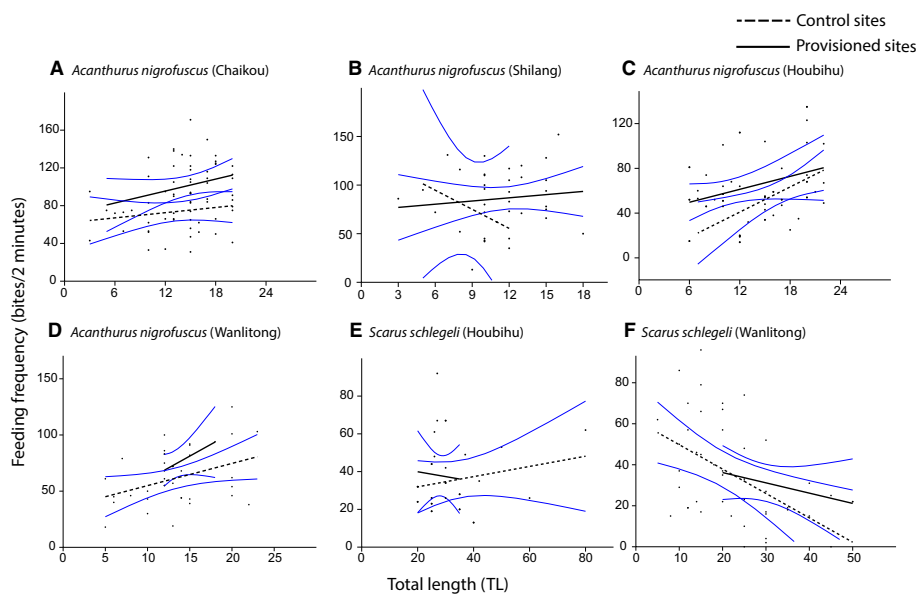


Fig. 5 Linear correlation of foraging frequency (bites per 3 min) and body length (cmTL) between provisioned and control sites for fed-fishes. The numbers after the site name represented the sample size of provisioned and control site accordingly. **a** *Acanthurus nigrofuscus* (Chaikou; $n = 37$ and 28), **b** *Acanthurus nigrofuscus* (Shilang; $n = 30$ and 6), **c** *Acanthurus nigrofuscus* (Houbihu; $n = 30$ and 30), **d** *Acanthurus nigrofuscus* (Wanlitong; $n = 7$ and 31), **e** *Scarus schlegelii* (Houbihu; $n = 17$ and 16), **f** *Scarus schlegelii* (Wanlitong; $n = 14$ and 32)

Table 2 The means and standard error of (A) FID (flight initiation distance) and (B) biting rate with ANCOVA statistical result between provisioned and control sites for dominant species (herbivores for biting rate) in Kenting(KT) and Green Island(GI). *Symbol behind fish species indicates the significant differences ($p < 0.05$). Whether FID or biting rate changes (increase or decrease) significantly with body length in either provisioned or control or both sites were also analyzed to examine the size effects

Family	Species	Location	Provisioned FID (m)	Control	Significant changes with body length
(A)					
Acanthuridae	<i>Acanthurus nigrofuscus</i> *	Chaikou (GI)	0.38 ± 0.04	1.39 ± 0.09	Control
Chaetodontidae	<i>Chaetodon kleinii</i> *	Shilang (GI)	0.10 ± 0.02	0.55 ± 0.05	Provisioned
Pomacentridae	<i>Chromis margaritifer</i> *	Chaikou (GI)	0.29 ± 0.04	0.97 ± 0.05	None
	<i>Pomacentrus bankanensis</i> *	Chaikou (GI)	0.23 ± 0.06	0.94 ± 0.06	None
	<i>Dascyllus reticulatus</i> *	Houbihu (KT)	0.29 ± 0.01	1.04 ± 0.04	Provisioned
	<i>Chromis margaritifer</i>	Wanlitong (KT)	0.55 ± 0.04	0.55 ± 0.04	None
	<i>Dascyllus trimaculatus</i>	Shilang (GI)	0.28 ± 0.03	1.05 ± 0.07	None
	<i>Stegastes nigricans</i>	Chaikou (GI)	0.28 ± 0.05	1.2 ± 0.12	Provisioned
	<i>Stegastes nigricans</i>	Wanlitong (KT)	0.52 ± 0.05	0.68 ± 0.06	None
(B)					
			Biting rate (bites/2 min)		
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Chaikou (GI)	101 ± 5.2	73.8 ± 4.8	None
	<i>Acanthurus nigrofuscus</i>	Shilang (GI)	86.6 ± 5.5	76.2 ± 17.2	None
	<i>Acanthurus nigrofuscus</i>	Houbihu (KT)	59.3 ± 5.4	57.8 ± 5.4	Control
	<i>Acanthurus nigrofuscus</i>	Wanlitong (KT)	73.4 ± 5.5	61.6 ± 4.7	Control
Scaridae	<i>Scarus schlegeli</i>	Houbihu (KT)	37.7 ± 4.9	36.2 ± 4.6	None
	<i>Scarus schlegeli</i>	Wanlitong (KT)	31.3 ± 4.1	37.8 ± 4.8	Control

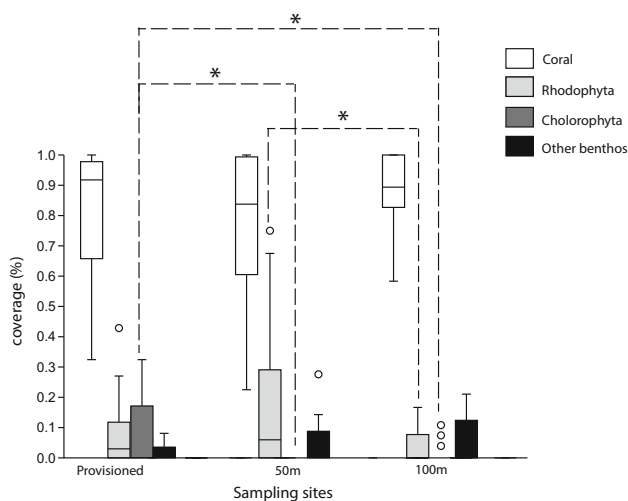


Fig. 6 Boxplot of benthic coverage (coral, macroalgae, others benthos) at provisioned, 50-m, and 100-m control sites. The upper and lower lines of the boxes represent the 25 and 75 percent quartiles. The horizontal line inside the box shows the median. The whiskers represent the largest data point less than 1.5 times the box height. Data outside the whiskers are shown as circles. Significant differences ($p < 0.05$) by Tukey's test are marked as star symbols

Provisioned herbivorous species *Ac. nigrofuscus* and *Scarus schlegeli*, the most common species in our study, were examined for their biting frequency on the benthos

after being fed by divers. No significant differences for biting frequency were found between sites (Table 2B, Fig. 5). There was no relationship between biting frequency and body length for most sites except fishes from three control sites (Table 2B). Coverage by coral, macroalgae, and other benthic organisms (sponges, sea urchins) was examined at provisioned sites, 50-m control sites, and supplementary 100-m control sites (Fig. 6). There was no difference in coral coverage between control and provisioned sites. However, green macroalgae (Chlorophyta) showed significantly higher coverage in provisioned sites than the 50-m and supplementary 100-m control sites (Fig. 6). Although red algae (Rhodophyta) showed higher coverage in the 50-m control sites compared to the provisioned site and supplementary 100-m control sites, this difference was statistically insignificant. There were no other differences in benthic composition among any of the sampling sites.

DISCUSSION

Thirty and forty percent of coral reef fish species in Kenting (26/65) and Green Island (27/90) were attracted to fish provisioning, respectively. These included a variety of functional feeding groups, comprising algal feeders

(herbivores), invertebrate and algal feeders (omnivores), invertebrate and crustacean feeders (carnivores), as well as coral feeders (corallivores). A number of species from the genera *Chromis* (Pomacentridae), *Coris*, and *Thalassoma* (Labridae) were observed to feed on tourists' food, as also noted by Milazzo et al. (2005). The behavioral traits of these species might play an important role in making them more adaptive to provisioning. Tank manipulations using a variety of human food items should be considered in order to further evaluate these responses.

Analysis of coral reef fishes showed, barring a few exceptions, no differences in total fish abundance, herbivorous fish abundance, or species number between most provisioned and control sites. A higher number of individuals were attracted to fish provisioned sites than control sites. Since the nature of control and provisioned sites in this study were identical, it seems feasible that the higher individual numbers of fish in provisioned sites were from tourist provisioning activities. However, higher species numbers were also found in fish provisioned sites, which is inconsistent with previous studies (Milazzo et al. 2005; Ilari et al. 2008). Prinz (2017) suggested that tourism-based provisioning will only attract certain species and that such activities will deter others, thus reducing species richness, although this pattern was not consistently observed across all four of the survey sites within this study. Green Island had more fish species, and showed significantly different fish composition due to fish provisioning. In contrast, Kenting, which is a national park popular for coral reef tourism, did not show statistically significant effects of fish provisioning. This might be because intensive tourism in Kenting has other influences, such as land-sourced runoff, eutrophication, and illegal fishing (Kuo et al. 2012). These impacts may have reduced the fish abundance and species numbers before tourism-related provisioning commenced in Kenting. Therefore, fish-provisioning tourism might be affecting coral reef fishes and ecosystem via other complicated pathways. More specific experimental studies should be considered to clarify this.

The changes in the assemblage structure of coral reef fish communities that were observed in this study due to tourism-based provisioning align with previous works (Milazzo et al. 2005; Albuquerque et al. 2014; Prinz 2017). The number of recorded fish species at the provisioned sites of this study (56, 72 in Kenting and Green Island) were also fewer than at other sites in the same location from a previous survey (65, 90; Heatwole et al. in prep). However, some species that were attracted to provisioned sites such as *A. vaigiensis*, *Ac. lineatus*, and *D. trimaculatus* were uncommon at the control sites. *Abudefduf vaigiensis* and *Ac. lineatus* are mainly shallow water (1–3 m) species (Wen et al. 2005), and they may have been

attracted by the provisioning from shallow areas to the provisioned sites in deeper water. This might therefore explain why they were uncommon at the control sites (5–7 m). Indeed, adult *D. trimaculatus* were observed to be particularly bold and voracious, which might explain why they were most abundant at the provisioned sites (per. observ.).

Fish vigilance and wariness to divers was represented by the distance at which fish started to flee (FID). As expected, several species were found to reduce their wariness of divers after being fed by tourists and were not afraid to approach divers at the provisioned sites. Conversely, species such as *D. trimaculatus*, *St. nigricans*, and *C. margaritifer* maintained similar distances to divers during surveys at (Wanlitong, Kenting and Chaikou, Green Island). This suggests that some species might still maintain the same level of wariness to divers or predators after exposure to tourism-based provisioning. In addition, conspecifics from both areas showing contradictory responses could be attributed to the fact that tourism-based provisioning has been occurring at Kenting for much longer than at Green Island. Titus et al. (2015) and Hawkins et al. (1999) both found that varying intensities of recreational scuba diving activities can affect fish behavior and species composition. Besides, FID was only found to change significantly with body length in few species inside provisioned sites within this study, which was not consistent with the findings of Gotanda et al. (2009) and Albuquerque et al. (2014). Since the relationship of body size and FID were species-specific (Fig. 4), the interaction between provisioning and body length on FID needs further examination. FID was also found strongly correlated to fishing (spearing) pressure (Goetze et al. 2017). Although all the experimental sites at Kenting and Green Island were within marine reserves, illegal fishing has been known to occur in these places. An investigation of the effects from fishing (including illegal) on provisioned fish behavior might need to be conducted to examine differences in behavior between sites within the same fish species.

Provisioned herbivorous fishes *Ac. nigrofuscus* and *Sc. schlegeli* did not reduce or cease their consumption of benthic algae due to an altered diet offered by divers as suggested by others (Orams 2002; Denny 2014; Marshall 2015; Greenfins 2018). These herbivorous fishes resumed foraging benthic algae immediately after divers finished their provisioning activity. We suggest provisioned herbivorous fishes maintained their normal foraging behavior due to two reasons: (1) daily food requirements and (2) absence of predation. Firstly, provisioning ecotourism might not provide adequate food to entirely supplant the need of herbivores for natural food sources. Therefore, it seems feasible to speculate that if divers offered a greater abundance of food that satisfied the daily energy needs of

the fishes, this might lead to different results. Secondly, herbivorous fishes are likely to reduce their bite rates while also increasing their vigilance in response to greater predation threats (Brandl and Bellwood 2015). Low predation pressure due to the relative absence of large predators from Kenting and Green Island due to overfishing is likely to have resulted in lowered vigilance among herbivorous fishes in both the provisioned and control sites. Whether herbivores subjected to higher levels of predation would alter their diet in response to provisioning requires further study.

Higher abundances of Chlorophyta (green macroalgae) were found in fish provisioned sites in comparison to 50-m and supplementary 100-m control sites. Since there were no significant differences in herbivorous fish bite rates or the number of herbivorous fishes between fish provisioned and control sites, the higher green macroalgae coverage in the former is most likely unrelated to herbivory. A possible explanation is that the extra inputs from supplementary feeding and wastes generated from intensive tourism will be increasing nutrient levels, thereby leading to higher abundances of green macroalgae that are able to respond quickly to the resultant nutrient fluctuations (Teichberg et al. 2010; Smetacek and Zingone 2013). Due to a lack of historical data of macroalgae and nutrient levels in the provisioned sites, it is unclear how macroalgal cover may have changed due to the introduction of provision tourism. Long-term monitoring of macroalgae, water quality, and nutrition analysis of fish food are needed to examine possible causes of eutrophication. Other benthic organisms, such as corals and other macroalgae, did not show differences in abundance between sites, which suggests that moderate tourism fish-provisioning activities may only have a minor or non-existent influence on coral reef benthic composition compared to other possible human influences (i.e., land-sourced runoff, sedimentation, destructive fishing practices),

Coral reef ecosystems are highly valuable to the tourism industry. However, intensive tourism can have a number of negative effects on coral reefs such as eutrophication, sedimentation, physical damage from divers, and even the spread of coral diseases (Lamb and Willis 2011). Indeed, in this study, the provisioned sites were also observed to have higher numbers of divers compared to unprovisioned sites. The effects from both provisioning and diver pressure may have therefore confounded the results of this study.

Ecotourism has been recognized as a fundamental approach to educate the public about the importance of coral reefs and their preservation (Spalding et al. 2017). Well-managed ecotourism that can reduce or mitigate the stresses or side effects of tourism on coral reef organisms is essential. Fish provisioning is a common and popular activity in coral reef tourism (Orams 2002). While

provisioning of megafauna elasmobranchii like sharks and rays can alter their home ranges and daily movement (Maljkovic and Cote 2011; Corcoran et al. 2013), conservation and education goals have also been achieved because of well-managed tourism-based provisioning (Brunnschweiler et al. 2013). Coral reef teleosts are the main functional group of animals involved in tourism-based provisioning but have received less attention than elasmobranchs. Our findings did not reiterate all claims from internet sources or previous studies (Orams 2002; Greenfins 2018). However, our results suggest that the behavioral changes of fishes from current intensity of fish provisioning are species-specific. Some fish species appear to be more flexible to human interference, while some are not. These fish species play different ecological roles in coral reefs, suggesting that fish provisioning is likely to be affecting coral reefs in more complex ways than currently thought. As tourist numbers increase, appropriate control for human waste, as well as moderate levels of provisioning with feeds containing limited nitrogen and phosphorus content, that are also non-detrimental to the health of fishes should be considered. Continuous monitoring on provisioning ecotourism under the auspices of the national park (Kenting) and local government (Green Island) will also be necessary in order to maximize conservation efforts.

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