



# To Feed or Not to Feed? Coral Reef Fish Responses to Artificial Feeding and Stakeholder Perceptions in the Aitutaki Lagoon, Cook Islands

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Feeding wild animals is a regular habit in ecotourism worldwide with poorly known consequences for ecosystem functioning. This study investigates how effective bread feeding is at attracting coral reef fish in the South Pacific, which feeding groups of fish are most attracted, and how natural foraging rates of an omnivorous and a grazing-detritivorous fish are affected. Data were collected at sites where fish are regularly fed bread by snorkellers and at comparison sites where bread was only provided for this study, within the Aitutaki lagoon (Cook Islands). The fish community was censused and foraging rates of two model species (*Chaetodon auriga*, *Ctenochaetus striatus*) were quantified one hour before, during, and an hour after feeding events. Twenty-five percent of the species present at all sites (piscivores-invertivores) were effectively attracted to bread. Overall, mean fish density was higher at tourism feeding sites than at the comparison sites. During bread feeding events, taxonomic richness decreased, compared to the hours prior and after feeding across all sites. As piscivore-invertivores were consistently attracted to bread, localized shifts in their dominance over other trophic groups may be expected if bread feeding persists, likely carrying consequences for ecosystem functioning. The effect of bread feeding events on natural foraging rates differed between the model species. *C. auriga* ceased foraging on natural foods to feed on bread. Although *C. striatus* never fed on bread, its foraging rate on epilithic algal matrices decreased during bread feeding events. This indirect non-lethal ecological consequence of bread feeding contributes a previously unanticipated example relevant to the “ecology of fear” in marine fish. Stakeholder interviews revealed that locals favor feeding to sustain tourist satisfaction, whereas tourists appreciate snorkeling regardless of feeding. This indicates an opportunity for restrictions on fish feeding with minimal drawbacks for tourism. Future research on fish metabolism and cascading effects on the reef benthos may reveal further impacts of feeding on coral reef communities.

**Keywords:** coral reef, tourism, ecosystem function, foraging rates, provisioning, supplementary feeding, recreation, conservation evaluation

## INTRODUCTION

Wild animals have always fascinated humans. Procuring encounters with non-captive wildlife is therefore a core motivation for wildlife- and eco-tourism, two booming sectors in the tourism industry (Newsome et al., 2005; Burgin and Hardiman, 2015). Tourists' demand for prolonged encounters with elusive animals encourages tour operators globally to attract these artificially through food (Newsome et al., 2004; Milazzo et al., 2006; Trave et al., 2017). Feeding marine fauna whilst snorkeling and diving is therefore a common, yet poorly regulated practice in marine tourism (Green and Higginbottom, 2000; Moscardo and Saltzer, 2004; Corcoran et al., 2013), with potentially grave implications for the conservation of affected marine ecosystems.

Artificial feeding of marine megafauna by tourists has reportedly led to changes in population size, migration, reproduction, and behavioral patterns, as well as being detrimental to an organism's health (Reynolds and Braithwaite, 2001; Orams, 2002; Hammerschlag et al., 2012). Less well-understood are the consequences of feeding coral reef fish, which are most commonly encountered by tourists visiting tropical oceans (Sweatman, 1996; Bessa et al., 2017a; Mattos and Yeemin, 2018). Resource management agencies in different parts of the world enforce bans on feeding of large mammals but ignore the customary feeding of small species like birds and fish at the same locations (Orams, 2002).

Although concerns have been raised over artificial foods potentially interfering with critical ecosystem functions underpinned by coral reef fish (Cole, 1994; Milazzo et al., 2005; Medeiros et al., 2007; Bessa et al., 2017b), behavioral responses of the latter to artificial feeding events remain understudied. This is of importance, as behavior of reef fish is considered a major determinant of an organism's functional role (Bellwood et al., 2019). Not only may artificial foods prevent fish from interacting naturally with their environment, but food provisioning by tourists may also result in behavioral habituation (Harriott, 2002; Orams, 2002; Newsome and Rodger, 2008; Semeniuk et al., 2009; Brookhouse et al., 2013; Bessa et al., 2017b). Artificial feeding events aggregate predatory fish and exacerbate predatory behaviors, thus resulting in interference competition and elevated predation risk for certain species (Newsome et al., 2004; Milazzo et al., 2006; Semeniuk and Rothley, 2008). Importantly, when large species are attracted and excited through artificial foods, human safety can be compromised (Perrine, 1989; Moribe, 2000; Brookhouse et al., 2013; Trave et al., 2017).

Spatio-temporal alterations in the relative abundance of fish species and structure of the fish community, as well as in habitat use and movement patterns (e.g., diel inversion of activity), are likely to affect the structure of entire populations and communities (Milazzo et al., 2005; Corcoran et al., 2013; Bessa et al., 2017a; Geffroy et al., 2018). Despite evidence from the Mediterranean, Atlantic, and Indian Ocean (Hémery and McClanahan, 2005; Milazzo et al., 2006; Feitosa et al., 2012) indicating that fish feeding can alter the community structure of fish assemblages, only few studies have focused on community-scale effects of artificial feeding with

bread (Hémery and McClanahan, 2005; Ilarri et al., 2008; Sanguansil et al., 2017). It follows that experimental approaches documenting the effect on the habitual foraging rates of species are scarce (e.g., Wen et al., 2018). These knowledge gaps complicate the quantification of the impacts of artificial feeding at the ecosystem level and the sustainability of this practice within the ecotourism industry (reviewed by Newsome et al., 2012; Trave et al., 2017).

In remote island countries surrounded by extensive coral reefs, tourism is an important source of income largely supported by activities on reefs (Mellor, 2003; Spalding et al., 2017). Reduced reef health may change the abundance of reef fish, decreasing the value of the experience for tourists (Jones et al., 2004; Bruno and Selig, 2007) and potentially reducing their interest in the area. This may, in turn, prompt snorkeling and dive operators to attempt maintaining the aesthetic value of the reef environment and customer satisfaction by feeding fish artificially. Customer expectations and satisfaction are fundamental driving forces of the profitability of tourism (Semeniuk et al., 2009). Further, maintaining profitability will guide the attitudes and behaviors of local tour operators (Vaske and Manfreda, 2012). Whether the perceptions of tour operators regarding the added value of artificial fish feeding match the actual levels of satisfaction tourists obtain from such activity, however, remains uncertain (Patroni et al., 2018). As drivers and consequences of food provisioning for wildlife touch the realms of social as well as ecological sciences (Newsome, 2017), approaches that consider both ecological implications of artificial fish feeding and stakeholder perceptions are crucial to guide conservation and management actions (Ziegler et al., 2015; Patroni et al., 2018).

This study investigated for the first time both, temporary changes in fish species composition and disruptions in species foraging rates in response to artificial bread feeding while considering the stakeholder perceptions regarding this practice. Focusing on Aitutaki Lagoon (Cook Islands), where fish are fed bread daily during snorkeling tours, it was hypothesized that: (1) reefs where bread feeding by groups of tourist is a well-established practice will have higher fish density and species richness compared to sites where bread was provisioned experimentally by one researcher, (2) omnivorous fish will be most attracted to bread whereas more specialized feeding functional groups will avoid it, (3) fish species that feed on bread will cease foraging on natural substrata during bread feeding events and display lower-than-usual foraging rates afterward likely due to satiation, and (4) bread feeding is considered essential for tourists' satisfaction during lagoon snorkeling tours by both tourists and local tour operators.

## MATERIALS AND METHODS

### Study Area

This study was conducted from 6<sup>th</sup> December 2016 to 9<sup>th</sup> March 2017 in the near-atoll Aitutaki, located in the South Pacific Ocean, 18°51'28" S, 159°47'7" W. With an area of 18.1 km<sup>2</sup> and ~2000 inhabitants, Aitutaki is surrounded by a triangular carbonate foreereef that encloses an approximately 50-km<sup>2</sup> shallow, sandy

lagoon, spiked with coral pinnacles (Loubersac et al., 1991; Berno, 1999; Hoffmann, 2002; Rankey and Reeder, 2009, **Figure 1**). An estimated 29,261 tourists visited Aitutaki in 2015, thus showing a tourists-to-residents ratio of nearly 15:1 (Cook Islands Tourism, 2019). Fish feeding has been practised regularly for more than 15 years, as a part of lagoon tours to areas where wildlife is naturally abundant and diverse. Two-hour snorkeling tours are offered daily by 10 different operators mostly within the marine protected area around One Foot Island (1–5 tours  $d^{-1}$ ) and at Maina (1–3 tours  $d^{-1}$ ).

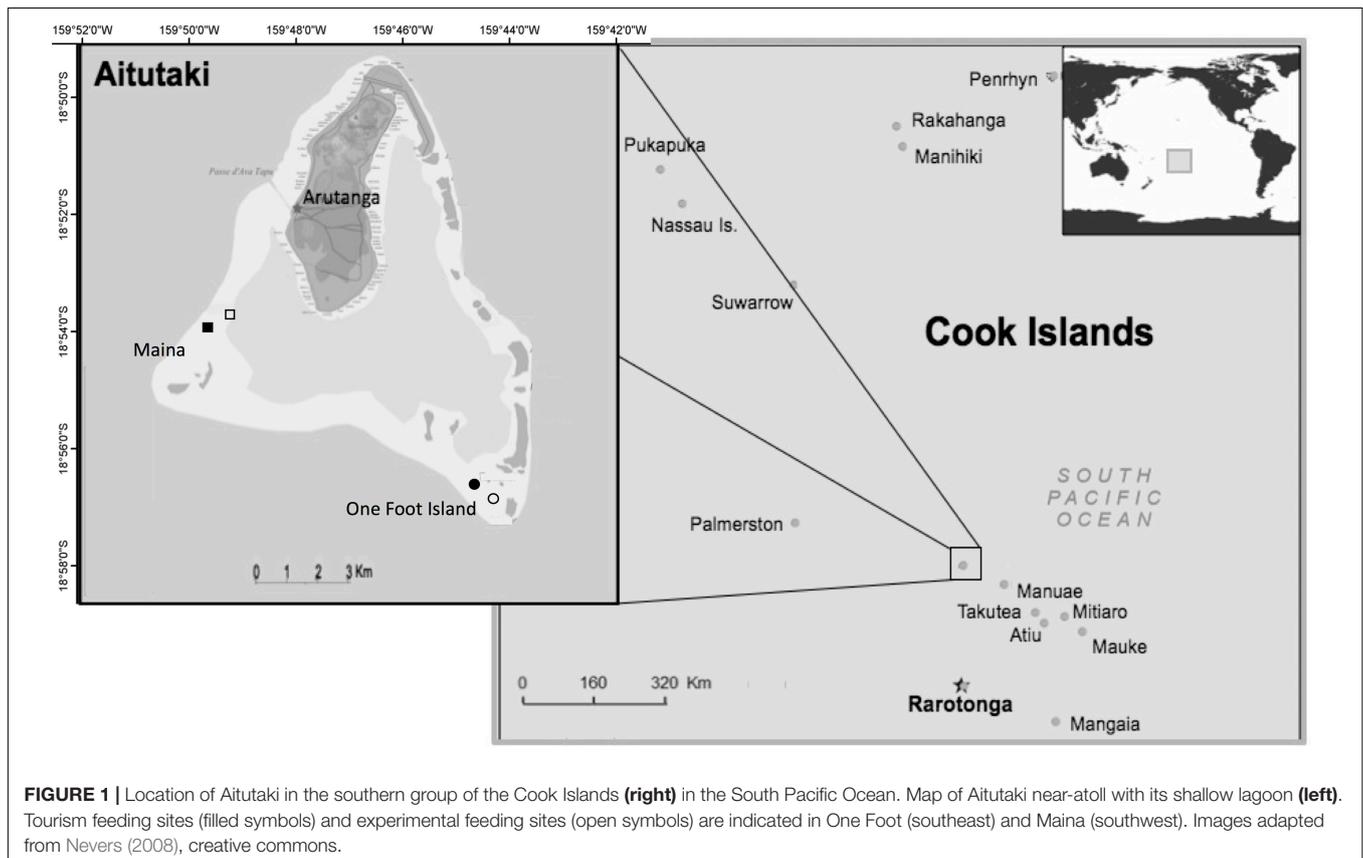
This study was conducted in accordance with the research permit issued by the Foundation of National Research and Office of the Prime Minister (reference number: 24- 16), Ministry of Marine Resources and the Aitutaki Island Council, which covered all underwater surveys and stakeholder interviews. It was carried out in accordance with the regulations of Guideline 2010/63 of the European Commission, and was approved by the local authorities (Secretary, Ministry of Marine Resources, Cook Islands, December 2016).

## Field Experiment

### Effects of Bread Feeding Events on Fish

The field experiment spanned four sites located on lagoonal pinnacles. Two of these sites had been established as bread feeding locations by tourism operators and regularly visited by groups of snorkellers for 15 years and throughout this study. These represented the characteristics of fish communities

habituated to a well-established food provisioning practice (i.e., hereafter referred to as tourism feeding sites). Two comparative adjacent sites that had never been used for food provisioning were also studied. At these sites, experimental bread feeding was conducted by one of the authors (NP) for the duration of the experiment (i.e., experimental feeding sites). Experimental feeding sites would therefore resemble the situation that would emerge immediately following the initiation of an incipient food provision practice. Experimental feeding sites were located between 600 and 850 m apart from the corresponding tourism feeding sites (**Figure 1**). This separation ensured no exchange of individual fish between tourism and experimental feeding sites at least for small species, including the focal species which commonly move over distances  $< 20$  m (Krone et al., 2008; Matis, 2018). Although published home range sizes of large-bodied fish may exceed the separation between sites, in practice, these tend to be constrained by the extensive flat sandy areas separating pinnacles and reef patches in lagoonal habitats (Jordan et al., 2005). It is therefore unlikely that confounding effects would have emerged due to the exchange of fish between tourism and experimental feeding sites. The spacing between sites also avoided competitive foraging halos of snappers (Strelcheck et al., 2007). All sites were similar to each other in substratum composition, mean depth and topographic complexity (Wilson et al., 2007, **Supplementary Material S1**). One loaf of bread (approximately 500 g) was used per feeding treatment across all sites.



To compare the effects of bread feeding events between tourism-established and experimentally-established artificial feeding practices, the 15-min surveys were conducted in tourism and experimental feeding sites at three time points, namely 1 h before, during, and 1 h after bread feeding episodes (Feitosa et al., 2012). Surveys focused on: (a) quantifying changes in fish density, fish community composition (by feeding group), and taxonomic richness in response to bread feeding events, (b) identifying fish species with high and low affinity for bread, and (c) detecting changes in natural foraging rates of two model species attributable to bread feeding. All surveys were conducted  $\pm$  2 h from high tide between 11:00 and 15:00 to capture diurnally active fish (English et al., 1997). No tourists were present at any time when surveys were conducted.

Quantifying the fish density, fish species composition (by feeding groups), and taxonomic richness is important because of the ecological relevance of these metrics, but also because they are important contributors to the aesthetic value of snorkeling tours for tourists. Fish density and taxonomic richness were quantified using stationary underwater visual censuses (Bohnsack and Bannerot, 1986), consistently conducted by the same observer (NP) to avoid inter-observer bias (Albuquerque et al., 2015). A 3 m radius (area of 28.27 m<sup>2</sup>) was observed from a fixed position on the sea surface for 15 min while counting all active, non-cryptic fish. The maximum number of fish per species was recorded. At all sites, five censuses per site per feeding episode (before, during, after) were completed over 5 days. Species were assigned to feeding groups following Green and Bellwood (2009) and Pratchett et al. (2011) (Table 1). Mobile pelagic fish species, cryptic species and large wrasses were excluded from further analysis due to the bias that either their high variability and little attachment to single reef patches.

Species that fed on or avoided bread were identified through direct behavioral observations during the five bread feeding events initiated at both tourism and experimental feeding sites. Species were considered to display a high affinity for bread when more than 10 individuals fed on bread. Species were noted as having low affinity for bread when individuals were indifferent to or tried and rejected it.

### Effects of Bread Feeding on Fish Foraging Rates

Two model species were selected for foraging rates observations given their ubiquity and important ecosystem function. Here, the species' function is defined as the species' role in the movement or storage of energy or material (Bellwood et al., 2019). Functionally, the omnivorous butterflyfish, *Chaetodon*

*auriga* (facultative corallivore), consumes from very little to high amounts of live coral (Harmelin-Vivien, 1989; Pratchett, 2005; Cole et al., 2008), but also feeds on a variety of small invertebrates and algae (Myers, 1991). The detritivorous surgeonfish, *Ctenochaetus striatus*, targets the detritus entrapped within epilithic algal matrices, incidentally ingesting algal turfs and sediments (Crossman et al., 2001; Marshall and Mumby, 2012; Tebbett et al., 2017a). *C. striatus* plays a major role in benthic community composition structure dynamics and is one of the most important detritivorous fish species on Indo-Pacific coral reefs (Tebbett et al., 2017a). Species foraging rates (bites minute<sup>-1</sup>) were considered a valid proxy for ingestion (Choat and Clements, 1993; Bellwood, 1995; Streit et al., 2015; Tebbett et al., 2017b). Gut content analyses were avoided as the study was designed to be minimally intrusive and target species were not found in fish markets. Foraging rates were further considered representative of the animal's ecological trophic function (Bellwood et al., 2006a; Fox and Bellwood, 2007, 2008). The extent to which fish trophic functions were affected by bread feeding was evaluated by quantifying foraging rates via 5-min focal follows of individuals of comparable size (i.e., ~15 cm TL) conducted by a snorkeller from a conservative distance of ~3 m (Lehner, 1996). The observers ensured the selected fish displayed no signs of disturbance, wariness, flight or hiding and continued behaving normally (Bellwood, 1995). As video recordings provide more accurate bite counts than those recorded visually by Scuba divers (Goatley and Bellwood, 2010), visual bite counts were supplemented here by recordings of the 5-min focal follow made with a GoPro video camera. Bouts of rapid consecutive bites that could not be discerned as individual bites were classed as single bites (Bellwood and Choat, 1990). Bites were not counted if dislodged material was ejected (Mantyka and Bellwood, 2007). Fifteen focal follows per species, site, and bread feeding event were completed over 5 days.

### Stakeholder Perceptions

Perceptions regarding bread feeding of fish were investigated through a total of 104 questionnaires distributed among Cook Island nationals (50%,  $n = 52$ ) and overseas-born stakeholders (50%,  $n = 52$ ), including Aitutakian lagoon tour operators ( $n = 4$ ), students ( $n = 28$ ), employees of other sectors ( $n = 20$ ), as well as foreign residents ( $n = 13$ ) and tourists ( $n = 39$ ) after obtaining prior informed consent (Questionnaire layout in **Supplementary Material S2**). The survey was conducted over a period of 2 weeks in March 2017 and respondents were selected

**TABLE 1** | Feeding groups assigned to trophic level and as generalist or specialist feeder.

	Carnivores	Omnivores	Corallivores	Herbivores
Generalist feeding groups	Piscivore- Invertivore Invertivore	Omnivorous Planktivore Omnivore	Facultative Corallivore	
Specialist feeding groups	Ectoparasite feeder		Obligate Corallivore	Grazer-detritivore Scraper-small excavator Macroalgal browser

by opportunity sampling. Questions assessed whether the person agreed or not with feeding bread to fish and why. Tourists were asked to respond whether their level of satisfaction would decrease or remain unchanged if bread was not provided during snorkeling tours.

## Data Processing and Statistical Analysis

To investigate responses in fish density, species composition by feeding group, and taxonomic richness to bread feeding and to determine whether the magnitude of these responses differed between places where the food provisioning is well-established or experimentally initiated, linear mixed-effects models (LMEs) were fitted (Pinheiro et al., 2015). Initial models included treatment (tourism or experimental feeding site) and timing relative to the bread feeding event (before, during, after) as fixed effects, and site as a random effect to account for the repeated observations. Model residuals were plotted against the fitted values to check for homogeneity of variance, and against each explanatory variable to check for violations of independence (Zuur et al., 2007). Stepwise model selection and AIC further identified the best-fit models. Models were followed by Tukey's *post hoc* tests to test for pair-wise differences whenever significant effects of multilevel factors were detected (Day and Quinn, 1989). Fish density was modeled using an LME, a fixed variance structure, and maximum likelihood estimates to account for heteroscedasticity (Zuur et al., 2009). Taxonomic richness was modeled using a generalized linear mixed-effects model (GLMM) with Poisson distribution verifying that the scale parameter  $\varphi$  was not significantly different from that assumed in a Poisson distribution (i.e., 1) (Crawley, 2007). To test the differences in fish species composition by feeding group, the densities were also compared between treatment (tourism or experimental feeding site) and timing relative to the bread feeding events (before, during, after) as fixed effects, and site as a random effect. To assess the degree of a species' affinity toward, or avoidance of bread, the absolute difference between its density during and before, during and after, and before and after bread feeding events were computed in both tourism and experimental feeding sites. This analysis focused on nine species commonly

observed throughout all sites, including four carnivorous fish and five herbivorous fish that are considered to fulfill important functional roles in the reef.

To determine whether bread feeding disrupts fish trophic functions, we tested whether foraging rates of the model species changed before, during, and after bread feeding events, and whether such changes occurred both at sites where bread feeding is well-established or experimentally initiated. As foraging rates did not differ between the location Maina and One Foot, these were pooled together such that 10 feeding observations were available for *C. striatus* and nine for *C. auriga*. LMEs were fitted with treatment (tourism or experimental feeding site) and timing relative to the bread feeding event (before, during, after) as fixed effects, and site as a random effect. After model residual against fitted values were tested for homogeneity of variance, stepwise model selection and AIC further identified the best-fit models (Zuur et al., 2009). To test a *posteriori* pairwise differences, the Tukey's *post hoc* test was performed (Day and Quinn, 1989).

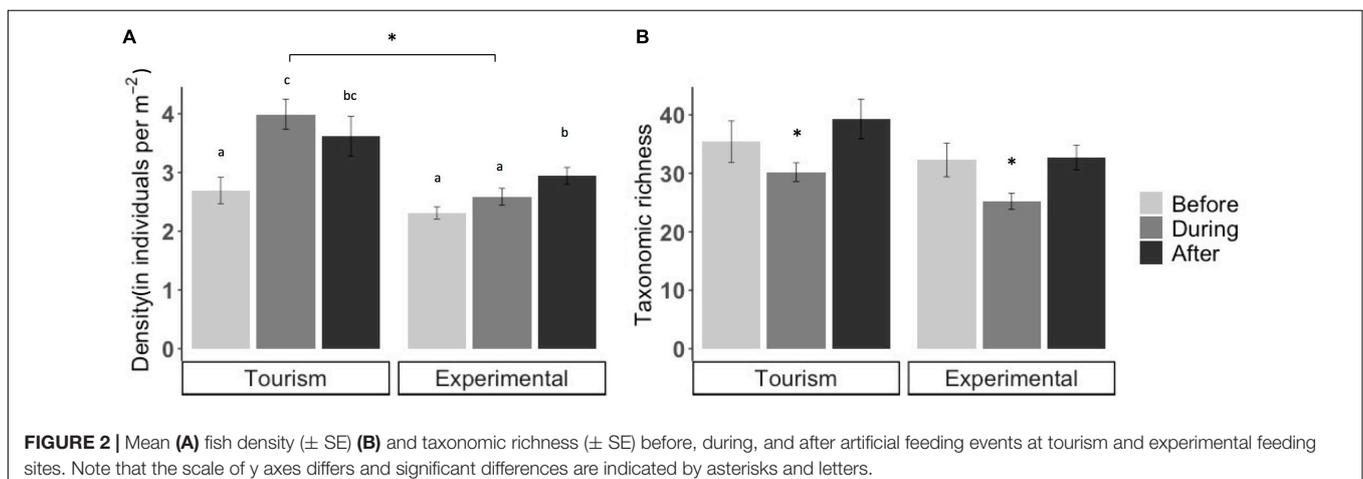
To obtain differences in (Yes/No) answers of stakeholders, questionnaire data were visualized in R-Studio and statistical analysis of frequency of particular responses among stakeholders was performed, using a Chi-square test (expected and observed values in **Supplementary Material S4**, and **Supplementary Table S3**). All statistical tests were performed using R-Studio (R Core Team, 2015).

## RESULTS

A total of 5128 individuals of 71 species, belonging to 14 families, were recorded throughout the study (**Supplementary Material S3**). Overall, carnivores and herbivores were the dominant feeding groups, whereas corallivores were least represented across sites.

### Effects of Bread Feeding on Fish Species Composition

Bread feeding events had significant short-term effects on fish assemblages. Mean fish density was significantly higher at



tourism feeding sites compared to experimental feeding sites (density:  $p = 0.046$ ; **Figure 2**). At tourism feeding sites, fish density increased by 29% during bread feeding events compared to 1 h prior to feeding ( $p = 0.01074$ ). One hour after feeding events, the visible fish density remained high across sites (**Figure 2A**). At experimental feeding sites fish density increased after feeding compared to before ( $p = 0.0136$ ). Taxonomic richness decreased during feeding events by an average of  $\sim 20\%$  compared to 1 h before feeding ( $p = 0.001$ , **Figure 2B**), but recovered 1 h after ( $p < 0.00188$ ). This pattern was consistent through sites and treatments.

Piscivores-invertivores were consistently and strongly attracted to bread during feeding events at tourism feeding sites, but not at experimental feeding sites [ $p < 0.001$ , Tukey *Post hoc* (during Tourism – during Experimental:  $p = 0.00205$ , **Table 2**)]. With the exception of large groups of planktivores (*Abudefduf sexfasciatus*, *A. vaigiensis*), which were consistently attracted to bread during feeding events and remained an hour after in only one of the tourism feeding sites (**Figure 3**), the density of all other groups remained unchanged by bread feeding events.

### Affinity of Fish Species for Bread

During bread feeding events 25% of species fed on bread across sites, whereas 70% of species were indifferent to bread feeding episodes, and 5% tested but subsequently rejected or avoided the bread (**Table 3**). The majority of species that fed on bread were piscivore-invertivores (44%) and omnivores (28%). The relatively more specialized feeding groups, obligate corallivores, scrapers, macroalgal browsers, and grazer-detritivores did not feed on bread. About 40% of all species that fed on bread were non-scarine labrids (wrasses). Labrids ( $p = 0.0486$ ) and lutjanids ( $p < 0.0001$ ) congregated significantly when bread was supplied at tourism but not at experimental feeding sites (**Figure 4** and **Table 2**). For both non-bread-feeding families Acanthuridae and Scaridae the magnitude of the difference in density between before and during bread feeding events was not significantly different between tourism and experimental feeding sites.

### Effects of Bread Feeding on Fish Foraging Rates

Across sites, foraging rates of *C. striatus* on the benthos significantly decreased by 22% during bread feeding events compared to an hour before ( $p = 0.038$ , **Figure 5A**). One hour after bread feeding events *C. striatus* resumed foraging rates similar to those observed prior to bread feeding (**Figure 5A**). *C. striatus* only tested the bread with consistently low rates across sites (**Figure 6**).

Foraging rates of *C. auriga* on natural substrata were significantly different between tourism and experimental feeding sites. The magnitude of the effect of bread feeding events differed between tourism feeding sites and experimental feeding sites ( $p = 0.001$ ). At tourism feeding sites, foraging rates of *C. auriga* were eight times lower during bread feeding events ( $0.46 \pm 0.34$  bites  $\text{min}^{-1}$ ) compared to the hour before ( $4.09 \pm 1.8$  bites  $\text{min}^{-1}$ , **Figure 5B**). This effect remained 1 h after the feeding

episode ( $1.57 \pm 0.5$  bites  $\text{min}^{-1}$ ). At sites where bread feeding was experimentally initiated, the foraging rates of *C. auriga* remained stable before ( $5.72 \pm 1.5$  bites  $\text{min}^{-1}$ ), during ( $4.41 \pm 1.1$  bites  $\text{min}^{-1}$ ), and after ( $4.29 \pm 0.9$  bites  $\text{min}^{-1}$ ) bread feeding events. *C. auriga* fed on bread at very high rates ( $12.46 \pm 1.8$  bites  $\text{min}^{-1}$ ) at tourism feeding sites, whereas it did not feed on bread at experimental feeding sites ( $p < 0.001$ , **Figure 6**).

### Stakeholder Perceptions

Of all respondents ( $n = 104$ ), 54% agreed that feeding may have a negative impact on the marine environment and modify natural fish feeding behaviors. All interviewed tourists that participated in a lagoon cruise declared they would appreciate these tours without bread feeding events, whereas only 54% of local stakeholders conceded that bread feeding was likely non-essential for the satisfaction of their guests ( $p = 0.0003$ , **Table 2**, Chi-squared expected and observed values in **Supplementary Material S4**, and **Supplementary Table S3**). Correspondingly, 75% of all local stakeholders (including tour operators) argued that bread feeding should continue, while 21% of all local stakeholders were in favor of stopping feeding fish artificially ( $p < 0.0001$ ).

## DISCUSSION

This study investigated for the first time both the ecological consequences of artificial feeding for coral reef fish in a Pacific Ocean lagoon, and whether this practice is considered necessary by local and foreign stakeholders. Although feeding fish artificially during recreational activities is commonly regarded as a possible cause for changes in fish behavior this had not yet been tested. Using a controlled field experiment this study demonstrates that bread feeding of coral reef fish influences short-term density and taxonomic richness at sites where bread feeding is a well-established practice, compared to sites where feeding is experimentally initiated. Species with relatively more generalist diets were consistently attracted to bread and drove the observed changes in fish species composition. Species-specific foraging rates were significantly altered by bread feeding events, and the magnitude of these alterations differed between tourism feeding and experimental feeding sites. As a result, the functional role of key species may be incompletely fulfilled in areas where fish are artificially fed. Whether these effects are strong enough to cause long term changes in ecosystem function remains to be tested. Perceptions of local tour operators regarding bread feeding being necessary to enhance tourists' satisfaction were not shared by tourists themselves. This indicates a potential opportunity to implement restrictions on bread feeding practices causing minimal drawbacks for local tourism.

### Fish Density and Richness Are Modified at Well-Established Artificial Feeding Sites

The higher fish density observed at sites where artificial feeding practices are well-established compared to sites where the

**TABLE 2 |** Statistical outputs of mixed-effects models accounting for the temporal correlation among site observations and Tukey's *post hoc* test results for each research question and according models.**Research question 1:** changes in density and taxonomic richness and fish species composition Linear mixed effects model [main factor = Timing (before, during, after), Treatment (tourism, experimental feeding sites) random factor = Site (Maina, One Foot)]

	<b>Model</b>	<b>df</b>	<b>AIC</b>	<b>L-Ratio</b>	<b>p-value</b>
Density	Timing + Treatment	1	121.6709		
	Interaction	2	119.5135	6.157432	0.046*
	<b>Post hoc</b>	<b>Estimate</b>	<b>SE</b>	<b>z-value</b>	<b>Pr(&gt;  z )</b>
	Before tourism – during tourism	-1.2947	0.3921	-3.301	0.01079*
	Before tourism – after tourism	-0.6332	0.1675	-3.780	0.00188*
	During tourism – during experimental	-1.4043	0.3691	-3.805	0.00172*
	During tourism – before experimental	-1.6802	0.3691	-4.553	<0.001*
	During tourism – after experimental	-1.0470	0.3691	-2.837	0.04545*
	After tourism – before experimental	-1.3053	0.3691	-3.537	0.00472*
	Before experimental – after experimental	-0.6332	0.1675	-3.780	0.00185*

Generalized linear mixed effects model [main factor = Timing (before, during after), Treatment (tourism, experimental feeding site) random factor = Site (Maina, One Foot), family = poisson]

	<b>Model</b>	<b>df</b>	<b>AIC</b>	<b>LRT</b>	<b>Pr(Chi)</b>
Richness (S)	Timing	2	429.68	23.32	<0.001*
	<b>Post hoc</b>	<b>Estimate</b>	<b>SE</b>	<b>z-Value</b>	<b>Pr(&gt;  z )</b>
	Before – during	-0.20050	0.05727	-3.501	0.00136*
	During – after	-0.26209	0.05649	-4.639	0.00188*

Linear mixed effects model [main factor = Timing (before, during, after), Treatment (tourism, experimental feeding sites) random factor = Site (Maina, One Foot)]

<b>Feeding group</b>	<b>Model</b>	<b>df</b>	<b>AIC</b>	<b>L-Ratio</b>	<b>p-value</b>
Piscivore-invertivore	Timing + Treatment	1, 11	403.2769		
	Interaction	2,13	392.0574	15.21955	< 0.001*
	<b>Post hoc</b>	<b>Estimate</b>	<b>SE</b>	<b>z-value</b>	<b>Pr(&gt;  z )</b>
	During tourism – before tourism	24.500	4.380	5.593	<0.001*
	During tourism – after tourism	22.300	4.173	5.344	<0.001*
	During tourism – before experimental	27.700	7.106	3.898	<0.001*
	During tourism – during experimental	26.100	7.088	3.682	0.00205*
	During tourism – after experimental	23.900	7.140	3.347	0.00708*

**Research question 2:** species affinity to bread feeding Linear mixed effects model [main factor = Timing (before, during, after), Treatment (tourism, experimental feeding sites) random factor = Site (Maina, One Foot)]

<b>Family</b>	<b>Model</b>	<b>numDF</b>	<b>denDF</b>	<b>F-value</b>	<b>p-value</b>	
Labridae	Interaction	2	173	3.077278	0.0486*	
		<b>Post hoc</b>	<b>Estimate</b>	<b>SE</b>	<b>z-value</b>	<b>Pr(&gt;  z )</b>
		During tourism – before tourism	3.50000	1.07675	3.251	0.01452*
		During tourism – before experimental	4.23333	1.07675	3.932	0.00118*
		During tourism – during experimental	4.20000	1.07675	3.901	0.00134*
Lutjanidae	Interaction	2	53	15.64637	<0.001*	
		<b>Post hoc</b>	<b>Estimate</b>	<b>SE</b>	<b>z-value</b>	<b>Pr(&gt;  z )</b>
		During tourism – before tourism	14.200	1.847	7.686	<0.001*
		During tourism – after tourism	14.700	1.847	7.957	<0.001*
		During tourism – before experimental	13.000	1.847	7.037	<0.001*

(Continued)

TABLE 2 | Continued

During tourism – during experimental	10.400	1.847	5.629	<0.001*
During tourism – after experimental	11.600	1.847	6.279	<0.001*

**Research question 3(1):** species-specific feeding rates, feeding on natural substrate Linear mixed effects model [main factor = Timing (before, during, after), Treatment (tourism, experimental feeding sites) random factor = Site (Maina, One Foot)]

Species	Model	df	AIC	L-Ratio	p-value
<i>Chaetodon auriga</i>	Timing + Treatment	1,8	358.0112		
	Interaction	2,10	346.3495	15.66168	<0.001

Linear model [main factor = Timing (before, during, after), Treatment (tourism, experimental feeding sites)]

Species	Model	numDF	denDF	F-value	p-value
<i>Ctenochaetus striatus</i>	Timing	6,2	7.00		0.0302
	<b>Post hoc</b>	<b>Estimate</b>	<b>SE</b>	<b>z-value</b>	<b>Pr(&gt;  z )</b>
	Before – during	–6.71	2.74	–2.45	0.038*

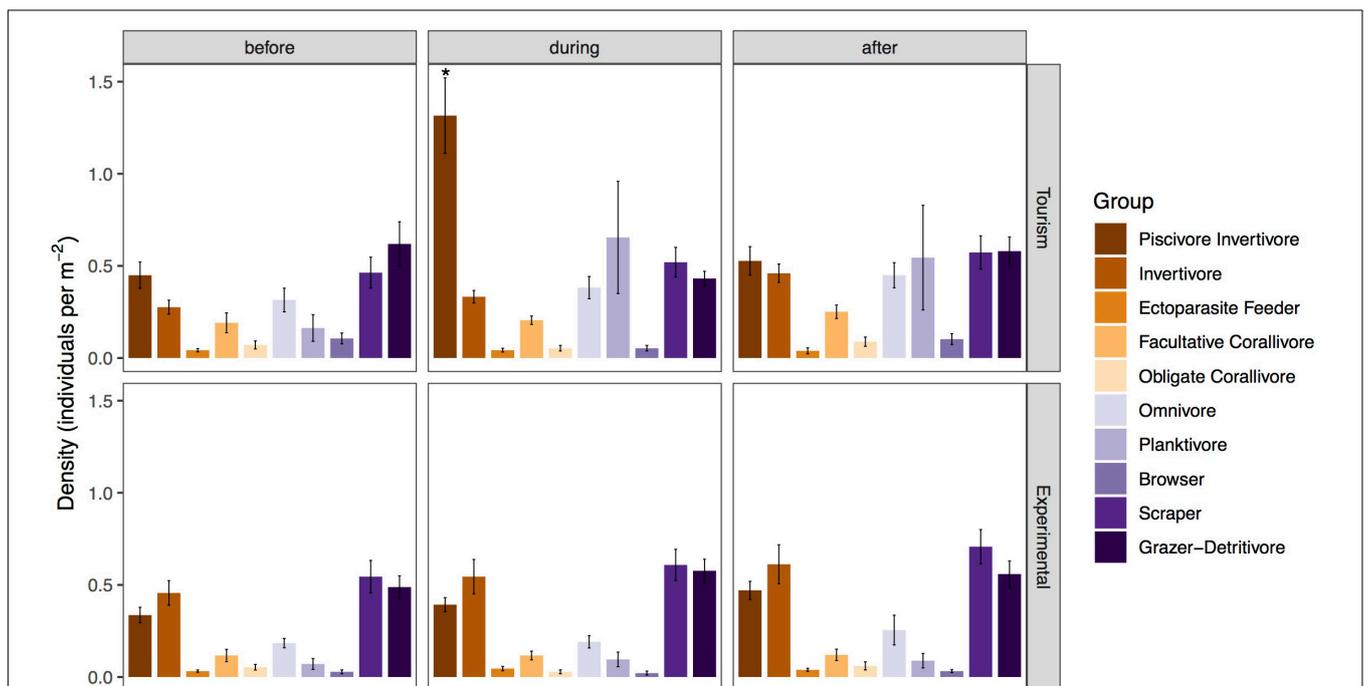
**Research question 3(2):** species-specific feeding rates, feeding on bread Linear mixed effects model [main factor = Treatment (tourism, experimental feeding sites)]

Species	Model	df	Chi-sq.	p-value
<i>Chaetodon auriga</i>	Tourism – experimental	1	14.197	<0.001

**Research question 4:** people's perception about fish feeding Chi-squared test (Cook Island locals, overseas-born)

Question	Chi <sup>2</sup> value	df	p-value
Feeding changes marine environment?	1.479	2	0.48
Like the cruise even without feeding?	16.425	2	0.0003*
Should continue or stop?	30.004	2	<0.0001*

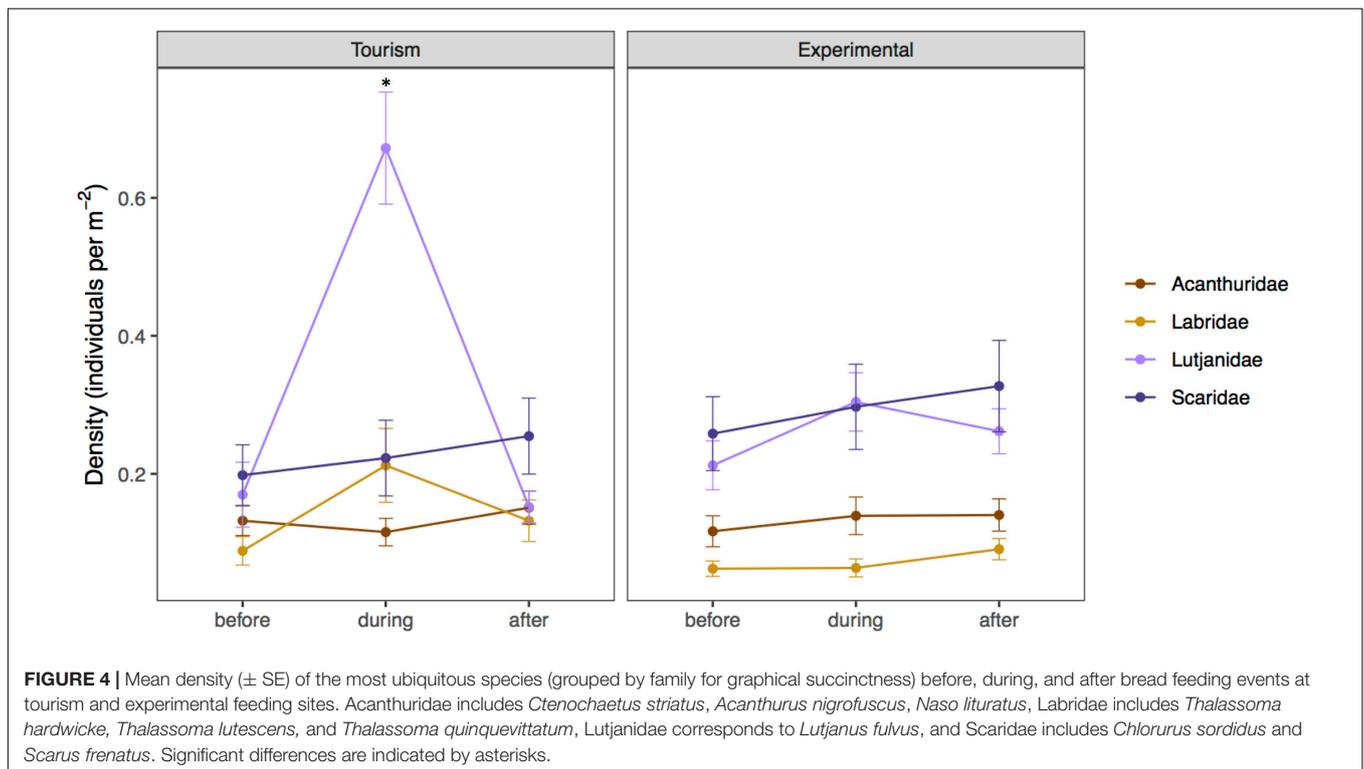
Significant terms and pairwise differences are highlighted with asterisks.



**FIGURE 3 |** Mean density (± SE) of fish classified in feeding groups before, during, and after bread feeding events at tourism and experimental feeding sites. Significant differences are indicated by asterisks.

**TABLE 3** | Fish species feeding on or testing bread when it was provided during artificial feeding event.

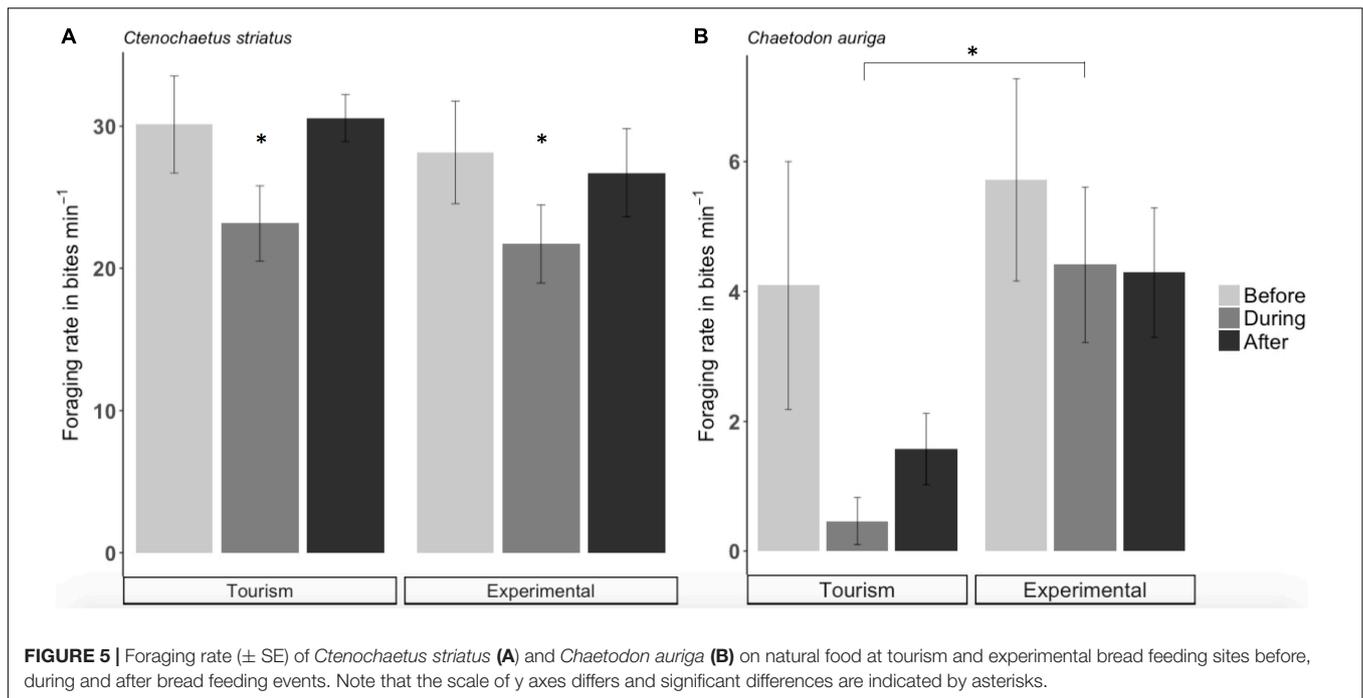
Species	Family	Feeding group	Attraction during bread feeding
<i>Rhinecanthus aculeatus</i>	Balistidae	Omnivore	Feeding
<i>Chaetodon auriga</i>	Chaetodontidae	Facultative Corallivore	Feeding
<i>Chaetodon ulietensis</i>		Omnivore	Feeding
<i>Cheilinus chlorourus</i>	Labridae	Invertivore	Feeding
<i>Gomphosus varius</i>		Piscivore-invertivore	Feeding
<i>Halichoeres trimaculatus</i>		Piscivore-invertivore	Feeding
<i>Labroides dimidiatus</i>		Ectoparasite feeder	Feeding
<i>Thalassoma hardwicke</i>		Piscivore-invertivore	Feeding
<i>Thalassoma lutescens</i>		Invertivore	Feeding
<i>Thalassoma quinquevittatum</i>		Piscivore-invertivore	Feeding
<i>Gnathodentex aureolineatus</i>	Lethrinidae	Piscivore-invertivore	Feeding
<i>Lutjanus fulvus</i>	Lutjanidae	Piscivore-invertivore	Feeding
<i>Abudefduf lorenzi</i>	Pomacentridae	Omnivore	Feeding
<i>Abudefduf sexfasciatus</i>		Planktivore	Feeding
<i>Abudefduf vaigiensis</i>		Omnivore	Feeding
<i>Pomacentrus brachialis</i>		Omnivore	Feeding
<i>Cephalopholis argus</i>	Serranidae	Piscivore-invertivore	Feeding
<i>Epinephelus merra</i>		Piscivore-invertivore	Feeding
<i>Acanthurus nigrofuscus</i>	Acanthuridae	Grazer-detritivore	Testing
<i>Ctenochaetus striatus</i>		Grazer-detritivore	Testing
<i>Chaetodon trifascialis</i>	Chaetodontidae	Obligate corallivore	Testing
<i>Chlorurus sordidus</i>	Scaridae	Scraper	Testing



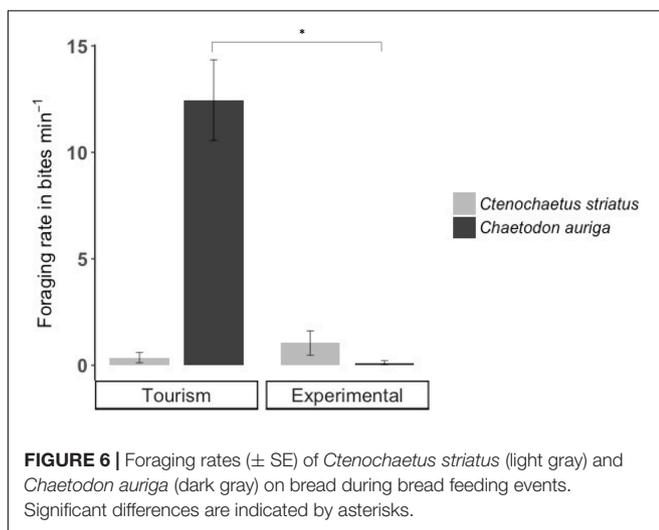
**FIGURE 4** | Mean density ( $\pm$  SE) of the most ubiquitous species (grouped by family for graphical succinctness) before, during, and after bread feeding events at tourism and experimental feeding sites. Acanthuridae includes *Ctenochaetus striatus*, *Acanthurus nigrofuscus*, *Naso lituratus*, Labridae includes *Thalassoma hardwicke*, *Thalassoma lutescens*, and *Thalassoma quinquevittatum*, Lutjanidae corresponds to *Lutjanus fulvus*, and Scaridae includes *Chlorurus sordidus* and *Scarus frenatus*. Significant differences are indicated by asterisks.

practice was experimentally initiated, confirms an influence of bread feeding on the fish community structure, in accordance with previous studies (Hémery and McClanahan, 2005; Milazzo et al., 2006; Medeiros et al., 2007). At tourism feeding

sites fish density peaked during bread feeding events, whereas at experimental feeding sites density was highest on the hour after. This suggests that well-established artificial feeding practices may alter diel cycles of fish abundance that are otherwise driven by



**FIGURE 5** | Foraging rate ( $\pm$  SE) of *Ctenochaetus striatus* (A) and *Chaetodon auriga* (B) on natural food at tourism and experimental bread feeding sites before, during and after bread feeding events. Note that the scale of y axes differs and significant differences are indicated by asterisks.



**FIGURE 6** | Foraging rates ( $\pm$  SE) of *Ctenochaetus striatus* (light gray) and *Chaetodon auriga* (dark gray) on bread during bread feeding events. Significant differences are indicated by asterisks.

tidal changes or time of day (Corcoran et al., 2013). On Brazilian reefs where fishes are regularly fed with bread and crackers by divers, fish abundance and taxonomic richness remained higher than usual 1 h after feeding, indicating that the effect of artificial feeding can last several hours or days (Milazzo et al., 2006; Feitosa et al., 2012). Habituation of fish to artificial feeding can lead to the dominance of a few species and a long-term reduction of taxonomic richness (Medeiros et al., 2007). At several tourism feeding sites, fish also anticipate feeding events and congregate in response to the noise of boat engines (Newsome et al., 2004, reviewed by Whitfield and Becker, 2014). Although arguably possible, it is unlikely that the differences observed here between tourism and experimental feeding sites are confounded by fish

moving across sites. Small-bodied reef fish tend to move over very small home ranges (i.e., <3 m for *C. auriga* and *Abudefduf sexfasciatus*, and <16.4 m *C. striatus*, Krone et al., 2008; Matis, 2018), and wide-ranging lethrinids and lutjanids were repeatedly observed at the same sites (NP, personal observation).

Taxonomic richness of fish assemblages decreased significantly during bread feeding events compared to an hour prior and an hour after at both tourism and experimental feeding sites, consistently with previous studies (Ilarri et al., 2008; Albuquerque et al., 2015). It is therefore argued here, that regular artificial feeding may account at least partially for an overall decrease in species richness at tourism feeding sites here and elsewhere. Although not necessarily permanent, this phenomenon is likely not in the interest of operators or tourists, as speciose fish assemblages are generally preferred over those dominated by a few species (Salim et al., 2015; Tribot et al., 2018). This decrease is also undesired from an ecosystems' perspective, given that decreases in taxonomic richness are usually accompanied by reductions in functional richness thus posing risks to reef health and ecosystem services other than those associated to tourism (Worm et al., 2006; Burkepile and Hay, 2008).

## Carnivorous and Omnivorous Fish Were Consistently Attracted to Bread

Results from this study support the notion that trophic generalists are most attracted to bread compared to relatively more specialist feeding groups (e.g., macroalgal browsers, grazer-detritivores). Bread feeding events favored generalist trophic groups such as carnivores and omnivores, as observed elsewhere (Albuquerque et al., 2015; Bessa et al., 2017b; Mattos and Yeemin, 2018). Fish species composition by trophic groups in Brazil, for instance, was also significantly altered during artificial feeding events

compared to before and after (Feitosa et al., 2012). In the present study, piscivore-invertivores showed the steepest change in response to bread feeding events and fed profusely on bread. This was mainly driven by the immediate congregation of *Lutjanus fulvus*, *Thalassoma hardwicke*, and *Cephalopholis argus*, which dissipated when bread feeding ceased. Almost 40% of all species that fed on bread were non-scarine labrids (wrasses). These, together with Pomacentrids, were also the most representative family of bread feeding fish on reefs in Kenya and Taiwan (Hémery and McClanahan, 2005; Wen et al., 2018). *Labridae* are one of the most speciose, ecologically, and functionally diverse group of fish inhabiting the world's coral reefs feeding opportunistically as generalist predators (Thresher, 1979; Wainwright, 1991; Bellwood et al., 2006b).

Short-term variability in fish community composition is natural (McClanahan et al., 2007). Yet, the prevalence of omnivores (e.g., labrids) above the reef, which peaked during bread feeding events and persisted after feeding ceased, may have long-term consequences on the reef fish community. If repeated bread feeding events lead to a persistent dominance of predatory fish on certain reefs, important changes in the trophic structure of fish assemblages may be expected (Beukers-Stewart and Jones, 2004). The consistent prevalence of high-trophic-level fish at bread-feeding sites may equate to high predation risk for small-bodied fish, but may also lead to higher fish excretion rates, which might cascade into changes in algal productivity and benthic dynamics (Allgeier et al., 2017; Wen et al., 2018).

Artificial feeding events may influence key biological interactions, such as aggressive exclusion, predation pressure, competition for local resources, and grazing (Coker et al., 2009; Brookhouse et al., 2013). Importantly, this is one of the few studies detecting non-lethal ecological consequences of artificial marine fish feeding linked to pulse increases in predator abundance (see also Milazzo et al., 2006). In this present case, snorkelers cause a sudden increase in (artificial) food that congregates predatory fish in a feeding frenzy around the bread. This likely generates a momentary “landscape of fear” where both predation risk and competition levels increase for smaller fish. Although fish may not necessarily feed on bread, their behavior may be indirectly affected by the bread feeding event (Brookhouse et al., 2013; Paula et al., 2018). Wary species that are regularly spear-fished may react solely to the presence of snorkelers. Macroalgal browsers (*Naso lituratus* and *N. unicornis*), for instance, tended to flee during bread feeding events, yet returned to their home reef an hour after. Changes observed in community composition during feeding events can therefore be attributed to both the congregation of opportunistic species habituated to feed on bread, and the departure of specialists that show alarm responses (Geffroy et al., 2017).

## Bread Feeding Events Disrupted Natural Fish Foraging Rates

Foraging rates of both model species changed in response to bread feeding events across sites, yet the nature of these changes differed between species. At tourism feeding sites, the facultative

corallivore *C. auriga* fed on bread whilst substantially decreasing foraging rates on natural prey. An hour after the tourism bread-feeding events, foraging rates of *C. auriga* remained lower than usual, suggesting possible satiation. During the hour prior to bread feeding events at experimental feeding sites, natural foraging rates of *C. auriga* on the benthos resembled those recorded in the Great Barrier Reef (Gregson et al., 2008). At experimental feeding sites, *C. auriga* disregarded bread and foraged on the benthos consistently throughout bread feeding events. This indicates that habituation of *C. auriga* to bread likely occurs beyond the time frame covered by this study (i.e., 12 weeks). This also corroborates previous findings, where none of the fish identified as bread consumers at tourism feeding sites in Thailand fed on bread when supplied by researchers at experimental feeding sites (Sa-nguansil et al., 2017). The ecological implications of the responses of *C. auriga* to bread feeding may not be immediately obvious, given the broad range of food items it consumes. The consumption of bread by *C. auriga* likely reflects its opportunistic feeding behavior and may not strongly affect predator-prey interactions (Pratchett, 2005; Cole et al., 2008). Yet, the high carbohydrate content of bread provokes unhealthy high glucose levels in the blood of carnivorous fish (Moon, 2001). Consequences of artificial feeding on growth, survival or reproductive success of animals feeding on unnatural diets such as bread are still to be evaluated (Rodgers, 2017). Further physiological effects of bread feeding on *C. auriga*, as well as changes in its natural diel foraging rates should be investigated. As a consequence of bread feeding, foraging ranges may be spatially restricted as fish concentrate within a few meters from the usual bread provisioning places. This could lead to artificially-enhanced levels of competition and feeding pressure on prey and other density-dependent processes, such as disease and parasite transmission (Vignon et al., 2010; Brookhouse et al., 2013). It is suggested here that these impacts may however be limited to generalist butterflyfishes, given that several obligate corallivore species observed during this study (e.g., *Chaetodon bennetti*, *Chaetodon lunulatus*, *Chaetodon reticulatus*) were not attracted to bread at all.

Natural foraging rates of the detritivore *C. striatus* were similar to rates recorded previously elsewhere (Bellwood and Choat, 1990). Likely reasons for the indifference of *C. striatus* toward bread may be the specialization of *C. striatus* to feed on benthic detritus of high nutritional value (Crossman et al., 2001). Interestingly, reduced foraging rates of *C. striatus* on the benthos during bread feeding compared to before and after, indicate a form of indirect disruption of its feeding activity. It is suggested here, that the feeding activity of *C. striatus* decreases during the bread feeding frenzy due to an increase in perceived predation risk. This alludes to the concept behind the “ecology of fear” which refers to the family of studies considering the ecosystemic consequences of prey fear responses (Brown, 2019). Previous research indicated that predation risk perceived by coral reef herbivorous fishes increased with distance from refuge habitat and affected herbivory rates (Gil et al., 2017). More generally, a number of studies on escape behavior yielded important implications for the reef fishes' ecology of fear (e.g., the influence of fishing, marine protected areas,

surveyors, prey body size, proximity of refugia, mutualism between preys, and group size) (Madin et al., 2011; Januchowski-Hartley et al., 2012; Lyons, 2013; Nunes et al., 2018). This study therefore contributes the first example linking a coral reef tourism-driven increase in perceived predation risk with potential ecosystemic consequences relevant for the reef fishes' ecology of fear. A similar finding for freshwater fish, which reduced foraging rates in response to tourism visitation and increased them again at the end of the day, was interpreted as a rebound effect of compensatory feeding following disturbance (Wu et al., 2002; Rubio et al., 2010; Bessa et al., 2017a). The bread feeding effect observed here in *C. striatus* may indirectly alter the way it fulfils its ecosystem function as an important detritivore, eroder, and transporter of sediments (Schuhmacher et al., 2008). Short-term alterations of foraging intensity may not drastically influence the functionality of the reef ecosystem, yet long-term effects may include *C. striatus* moving their feeding grounds or even abandoning the site entirely. This effect on the presence of *C. striatus* and its functional role may result in a more profound alteration of reef health through locally-reduced detritivory. Further research into the response of specific feeding groups to bread is required to substantiate that assumption, as a study from Taiwan found no effect on the bite rates of herbivorous fishes (*Acanthurus nigrofuscus* and *Scarus schlegeli*) between provisioned and non-provisioned sites (Wen et al., 2018). Bread feeding of fish may be a short-term intrusion, but where repeated consistently it may have significant implications for the ecosystem function of different feeding groups (Albuquerque et al., 2015). In light of increasing tourist numbers, artificial feeding practices may pose a long-term threat to the lagoon environment through lasting physiological and behavioral changes in fish (Geffroy et al., 2018). Fish may potentially "learn" to feed on bread and this habit may cause chronic satiation, have physiological consequences, and affect their metabolic pathways. This laid beyond the scope of this study and should be further investigated. Arguably, this study would have benefited from comparisons of tourism and experimental feeding sites with sites where no bread feeding was provided. Such comparisons would have disentangled more clearly the effect of well-established artificial feeding practices from those introduced by diurnal variability in fish biodiversity and feeding behavior. However, in this case, preliminary observations (NP) and the knowledge of local tour operators indicated that diurnal variability in fish community structure was low in all sites selected for experimental bread feeding exercises. In the face of logistical limitations preventing from adding more survey sites, preference was given to the establishment of experimental bread feeding sites. This allowed for the fully factorial comparison among before, during, and after artificial feeding episodes, and revealed important information on the process of fish habituation at the onset of artificial feeding practices. Ecological effects of bread feeding practices are likely shaped by multiple mechanisms including changes in fish behavior and community structure, but may also be mediated by the distribution of food, duration of bread artificial feeding events, number of tourists, and their behavior (Feitosa et al., 2012).

## Tourists Did Not Consider Bread Feeding Essential

In order to regulate the frequency and intensity of fish feeding in coral reef systems, understanding the perceptions of stakeholders is essential (Newsome, 2017; Breckwoldt et al., 2018). A stakeholder's perception is largely dependent on their socio-demographic background, cultural context, knowledge, attitudes, norms, and personality (Beyerl et al., 2016). The respondents' perception that "bread feeding can impact fish feeding behavior and the marine environment" shows a relatively high level of awareness of the ecological consequences of this practice. A primary human motivation in the context of ecotourism is to observe nature in as natural a state as possible (Orams, 2002). The question remains whether tourists want to see wild animals completely uninfluenced by humans or "domesticated" by continued feeding over years (Orams, 2002). Orams (1999) cautioned that "fish feeding turns the sub-aquatic world into an aquarium without walls, a zoo without bars." Studies on the perception of whale-shark feeding tourism showed tourists supported the practice despite many being aware of the ethical complications of animal feeding for tourism purposes (Ziegler et al., 2018). In the present study, the question whether to feed or not to feed resulted in significantly different opinions between stakeholder groups. All overseas participants of snorkeling cruises declared that they would have enjoyed the activity with or without bread feeding, whereas local stakeholders highlighted the need for continued bread feeding practices in order to guarantee tourists' satisfaction during snorkeling cruises. This suggests that implementing restrictions on bread feeding practices in Aitutaki may meet some resistance from tour operators, but will likely not harm tourist satisfaction levels. It could be argued that overseas snorkelers regarded bread feeding as superfluous only because they had already been satisfied by the proximity of abundant fish during the cruises. Whether their opinion on banning bread feeding would change if they had encountered less fish when snorkeling remains to be tested in controlled experiments. In practice the link between bread feeding activities and tourism satisfaction is driven by tourists' behaviors and expectations, which are often to see high numbers of fish. Tourists' satisfaction in Australia, Thailand and Malaysia was directly related to fish abundance and taxonomic richness (Moscardo et al., 2001; Topelko, 2007; Salim and Mohamed, 2014). Arguably, sustainable tourism activities provide a high-quality experience for visitors, which encourages them to be concerned about the conservation of the observed animals (Higginbottom et al., 2001). In the Cook Islands, environmental sustainability already constitutes a constraint to tourism growth, which in turn places a high priority on the protection of the environment in order to support tourism (Mellor, 2003).

## Recommendations

In light of these findings, this study suggests regulation of artificial feeding practices, supporting conservation measures to protect fish communities and functions in Aitutaki lagoon or elsewhere, being subject to local management priorities. This study highlights a difference between long-term and short-term

effects of bread feeding on fish assemblages. The following recommendations are given:

Initially, restrictions to bread feeding activities could be issued in the form of guidelines and rules that allow local tour operators to supply bread strictly (i) at designated feeding sites, (ii) using appropriate food types (Murray et al., 2016; Birnie-Gauvin et al., 2017), (iii) providing limited food amounts per person and boat (Great Barrier Reef Marine Park Authority, 1994; Murray et al., 2016), and (iv) at unpredictable times (Murray et al., 2016).

In lieu of a ban, it would be relevant to (1) work on transferring the perceptions of snorkellers to operators of snorkeling tours, (2) inform tour operators and dive guides on how the bread may impact fish behavior and function, and (3) involve education programs for tourists (Wiener et al., 2009; Patroni et al., 2018). Environmental education during tourism activities will result in positive attitudes of visitors toward wildlife conservation (Higginbottom et al., 2001), and may thus assist in a voluntary reduction of feeding (Bessa et al., 2017a). Lastly, pressure to feed wild animals may, in many places, come from tourists rather than from tourism operators. Avenues of non-scientific communication (i.e., tourism magazines, airline magazines, signs, flyers) to educate visitors could be helpful worldwide. On coral reefs, further research should aim to improve the understanding of long-term harmful effects of this previously overlooked activity on ecosystem health and on feeding behaviors of more fish species. In addition, potential indirect cascading effects of unconsumed bread on reef benthos, e.g., in terms of oxygen consumption and nutrient release, should also receive attention (Turner and Ruhl, 2007; Brookhouse et al., 2013).

These recommendations were delivered, and are relevant for, the currently-developed Aitutaki Management Plan. The continuous management of touristic activities in the reef requires active participation of governments, tour operators, scientists, and local communities in order to ensure its long-term ecological sustainability and incentives for conservation (Hawkins et al., 1999; Trave et al., 2017). The results of the current study suggest that no major impacts on tourism-dependent livelihoods are expected if the activity was modified by regulating the artificial feeding of fish. These findings underline the potential for sustainable management interventions in the form of reduced fish feeding activities in the Cook Islands.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

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## AUTHOR CONTRIBUTIONS

NP and SB conceptualized and designed this study with input of SF. NP procured funding and conducted the field experiment and stakeholder interviews with the support of RS and SL. This study took place within the frame of the project Resilience of South Pacific coral reef social-ecological systems in times of global change (REPICORE) led by SF. NP and SB performed the statistical analysis of the data. NP and SB led the writing of the manuscript with input of SF. All authors approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00145/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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