Shoaling behavior of coral reef fishes varies between two islands with different predator abundance

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ABSTRACT: Human-induced environmental change has affected ecosystems on a global scale, altering the ecology and evolutionary trajectories of various species. Fishing of marine predators, and any cascading effects on marine ecosystems, is of critical concern. Predators are thought to be an important reason for why fish shoal; thus, reducing predator populations could alter shoaling behavior for prey fish, and impact aspects of their behavior or life-histories. Here, we explore differences in shoaling behavior of coral reef fishes at 2 islands whose predator populations face differing fishing intensities. We compared the tendency to shoal for 3 fish species between 2 Pacific coral reefs: Palmyra Atoll (USA), an unfished reef with high predator abundance, and Moorea (French Polynesia), a fished reef with low predator abundance. We also specifically characterize movement and foraging-associated behaviors of one of these fishes, the convict surgeonfish *Acanthurus triostegus*, in this same comparative context. Our work suggests that in areas with reduced predator abundance, the tendency of some, but not all, fish species to form shoals is reduced. Decreased predator abundance also appears to have affected movement of shoaling and solitary *A. triostegus*, with increases in distance travelled and area covered occurring in contexts with low predator abundance. These observations shed some empirical light on how overfishing could affect shoaling behavior. Such insight is specifically valuable in the context of coral reefs, where changes to low-trophic level fish movement and foraging (2 behaviors closely linked with shoaling) could affect the functioning of these vulnerable ecosystems.

KEY WORDS: Shoaling · Fishing effects · Fish behavior · Collective behavior · Indirect effects

1. INTRODUCTION

Top predators include the most targeted and vulnerable species in our oceans, and the effects of their loss on marine ecosystems remains of critical concern (Heithaus et al. 2008, Estes et al. 2011, Pacoureau et al. 2021). Increasingly, there has been interest in documenting not only the direct effects of predator removal, but also the indirect effects their removal might have on the foraging behavior of their prey (Heithaus et al. 2008, McCauley et al. 2010, Madin et al. 2016). For example, on temperate and tropical reefs, the presence of predators reduces grazing on algae by herbivorous prey fish (Connell 2002). In Australia, the fear effects of tiger sharks on grazing sea turtles and dugongs shape the spatial patterns of seagrass patches, and shifts in these tiger shark populations can alter ecosystem resilience through changes to grazer behavior (Heithaus et al. 2007, Nowicki et al. 2021). Another important behavior

that may be indirectly affected by predator removal, and one less well studied in marine systems, is aggregation behavior.

Aggregation behavior is a common behavior observed across various animal taxa that can provide several benefits, including decreased predation risks and increased odds of locating food sources and potential mates (Pitcher 1986, Krause & Ruxton 2002). However, this behavior often comes at a cost of increased competition within members of a group (Krause & Ruxton 2002). In fish, one form of aggregation is shoaling behavior, where a congregation of moving or stationary fish are considered to be in a shoal when they remain together for social reasons (Pitcher 1986). The drivers of shoaling behavior are complex, but in many fish species, this behavior is thought to have arisen primarily as a response to predation (Parrish 1991). Laboratory-based studies on wild and laboratory-raised populations of guppies and sticklebacks have found variation in shoaling behavior of fish exposed to differing predation intensities, where populations of fish from high predator areas show higher shoaling tendency and cohesion than those from low predator areas (Seghers 1974, Helfman 1984, Magurran et al. 1992, Huizinga et al. 2009, Kozak & Boughman 2012). Yet, these shifts in fish schooling and shoaling behavior due to changes in predation pressure remain understudied in natural experiments (Seghers & Magurran 1994, Herbert-Read 2017), particularly in marine systems.

On many coral reefs, multiple generations of commercial and artisanal fisheries that predominantly target high-trophic level fish have severely depleted predator populations (Jackson et al. 2001, Friedlander & DeMartini 2002, Stevenson et al. 2007, Sandin et al. 2008). As a result, lower-trophic level fish are now experiencing relaxed predation pressure by natural predators, altering predation risk (Friedlander & DeMartini 2002). Although intense fishing on some of these same low-trophic level fish (e.g. parrotfish and surgeonfish) has lowered their abundance on reefs, reduced predator abundance can alter predation risk and affect the foraging behavior, space use, and temporal partitioning of lower trophic level fish (Madin et al. 2010a,b, McCauley et al. 2010, Davis et al. 2017). Various species of coral reef fish, in particular herbivorous parrotfish and surgeonfish, are known to form large shoals, although the drivers of this social behavior remain unresolved (Barlow 1974, Robertson et al. 1976, Hobson 1979, Crook 1999a,b).

In the tropical Pacific Ocean, the islands of Moorea (French Polynesia) and Palmyra Atoll (USA) support different levels of fishing and natural predator abun-

dances (Sandin et al. 2008, Davis et al. 2017) and yet host very similar coral reef fish assemblages. These locations provide an insightful opportunity to explore the social behavior of the same fish species under different predator regimes. Across both islands, we asked if predator abundance affects shoaling in 2 stages: first by observing the proportion of fish found in shoals for 3 herbivorous reef fish species, and then by focusing on the movement and grazing behavior of shoaling and solitary fish of 1 focal species (see Table 1). We compared the proportion of fish found in shoals across both islands for *Acanthurus triostegus* (Acanthuridae), a herbivorous surgeonfish that exhibits solitary foraging behavior and also forms roving shoals, and is not fished at either island; *Chlorurus spilurus* (Scaridae), a herbivorous parrotfish that exhibits solitary foraging behavior and also forms shoals, and is fished on Moorea; and *Mulloidichthys flavolineatus* (Mullidae), an invertivorous goatfish that forms shoals in addition to being observed engaging in solitary foraging behavior, and is fished on Moorea (Randall 1961, Barlow 1974, Robertson et al. 1976, Crook 1999a, Johannes & Hviding 2000, Kolasinski et al. 2009, Rassweiler et al. 2020a). For the most frequently encountered of the 3 species, *A. triostegus*, we investigated differences in distance travelled, area covered, and time spent grazing for shoaling and solitary fish between the 2 islands.

2. MATERIALS AND METHODS

2.1. Study sites

The study was conducted on the Pacific coral reefs of Palmyra Atoll (5° 53′ N, 162° 5′ W) and Moorea Island (17° 32′ S, 149° 50′ W). Palmyra Atoll (USA) is a remote uninhabited island that forms part of the northern Line Islands archipelago in the Central Pacific. Moorea (French Polynesia) is an inhabited island (population 17 816 in 2017) that forms part of the Society Islands archipelago in the South Pacific (Institut national de la satistique et des études économiques 2017). Palmyra Atoll has experienced minimal fishing throughout its history, and supports healthy and, to-date, stable coral reef predator populations (Zgliczynski & Sandin 2017, Bradley et al. 2017). It is currently protected as a US National Wildlife Refuge. Alternatively, the reefs of Moorea have experienced higher fishing pressures throughout their history (Walker & Robinson 2009, Leenhardt et al. 2012, Rassweiler et al. 2020a) and host predator populations that are more than 4 to 5 times lower in

biomass compared to those found on Palmyra Atoll (Davis et al. 2017). Because these 2 islands share similar reef fish species assemblages, they confer a useful opportunity to compare how prey fish behavior (i.e. shoaling) is shaped by predator abundance and fishing pressure. Although Moorea and Palmyra Atoll do certainly vary in respect to some of their biophysical attributes, this contrast in predator abundance between these 2 well-studied coral reefs has been utilized previously to study other direct effects of coral reef predator removal (Davis et al. 2017). Further, we chose for this study particular backreef and lagoonal habitats at the 2 islands that were as similar as possible in terms of water depth, benthic habitat, and wave exposure; however, it is impossible to control for all attributes.

Throughout the course of this paper, Palmyra Atoll will also be referred to as the 'high predator abundance' island and Moorea as the 'low predator abundance' island.

2.2. Shoaling behavior

We compared prevalence of shoaling behavior, number of shoals, and shoal sizes for *Acanthurus triostegus*, *Chlorurus spilurus*, and *Mulloidichthys flavolineatus* across 2 islands with differing predator abundances (Table 1).

2.2.1. Surveys

We conducted 30 min roving diver surveys (Schmitt et al. 2002, Rassweiler et al. 2020b) to compare the prevalence of shoaling behavior across both islands (11 surveys at Moorea and 14 surveys at Palmyra Atoll). All surveys were conducted by the same observer (A. S. Guerra) between 09:30 and 15:30 h. The observer snorkeled in a random pattern for 30 min and recorded any focal species individuals observed. For each of the 3 species, we counted every individual and assessed whether the fish were in a shoal (and noted shoal size) or solitary. Shoal sizes were measured as the number of individuals when possible, and approximated in bins of 5, 10, or 50 in larger or fast-moving shoals. Shoaling surveys and focal follows (described in Section 2.3) were conducted at 5 sites on the backreef of Palmyra Atoll and 4 sites on the backreef of Moorea (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m690p133_supp.pdf). We defined 'prevalence of shoaling behavior' as the proportion of fish individuals observed shoaling out of the total number of individuals of that species observed within a survey. The grouping behaviors exhibited by the 3 fish species can differ: *A. triostegus* and *C. spilurus* exhibit polarized group swimming behavior and form roving shoals, and *M. flavolineatus* form loose stationary aggregations during the daytime (Pitcher 1983). For the purpose of this study, shoaling refers to 3 or more fish exhibiting group behavior and can include groups of fish that exhibit polarized swimming behaviors and momentarily slip out of polarization for foraging, and stationary grouping and shoaling (Pitcher 1983, Norris & Schilt 1988, Parrish & Turchin 1997), but excludes any seasonal spawning aggregation behavior.

Some species of herbivorous fish that form shoals are known to use their numbers to overwhelm territorial herbivores to force access into their guarded territories (Foster 1985, Choat & Bellwood 1985, Eurich et al. 2018). Thus, to control for the potential of variation in the numbers of territorial herbivores affecting shoaling behavior differentially among islands, we also counted the absolute abundance of these territorial herbivores (i.e. *Acanthurus lineatus*, *A. nigricans*, and *Stegastes nigricans* on Palmyra Atoll and *A. nigrofuscus* and *S. nigricans* on Moorea).

Table 1. Experimental system framework for observations of shoaling behavior at the islands of Palmyra Atoll (high predator abundance) and Moorea (low predator abundance)

Aim	Survey	Focal species	Data collected
Shoaling behavior Compare prevalence of shoaling behavior, number of shoals, and shoal sizes between islands	30 min roving diver survey	*Acanthurus triostegus* *Chlorurus spilurus* *Mulloidichthys flavolineatus*	Number of individuals observed and shoal size (>3 individuals)
***A. triostegus* behavioral observations** Compare movement and grazing of shoaling and solitary fish between islands	30–60 min focal follows	*Acanthurus triostegus* shoals (>25 individuals) and solitary fish	Behavior: grazing/non-grazing Distance travelled (m) 95% KUD

2.2.2. Analysis

Linear mixed effects models fit by maximum likelihood (ML) were used to explain variation in prevalence of shoaling behavior. Full models were specified for each species using the lme4 package in R (version 4.0.3) (Bates et al. 2015, Wickham et al. 2019, R Core Team 2020, RStudio Team 2020) with proportion of fish in shoals as a response variable; predator abundance (island), territorial herbivore abundance, and total focal species abundance as fixed effects, and site as a random effect (Table S1). Best-fit models were selected according to small-samples corrected Akaike's information criterion (AIC_c) using the package MuMIn (Barton 2020). We used Wilcoxon rank sum tests to test for differences in the average number of shoals, shoal sizes, and fish abundance between high and low predator abundance islands for each of the 3 species.

2.3. *Acanthurus triostegus* behavioral observations

For the most frequently encountered of the 3 species, *A. triostegus*, we conducted focal follows to evaluate movement and time spent grazing for shoaling (>25 fish) and solitary fish subject to different predator abundances (Table 1).

2.3.1. Behavioral observations

We conducted 30 to 60 min focal follows on *A. triostegus* to assess proportion of time spent grazing, distance travelled, and area covered via calculation of a 95 % kernel utilization distribution (KUD). Snorkeling observers (4 observers at Palmyra Atoll, 2 at Moorea, lead observer [A.S.G.] was present at both islands) followed solitary or shoaling *A. triostegus* while towing a GPS device that recorded location every 60 s. Initial follows were conducted at both islands to assess the appropriate distance for following fish that would not impact normal foraging nor initiate a flight response, which we defined as moving away from the observer at an accelerating speed, or quickly changing swimming directions (Gotanda et al. 2009). Every 60 s, the observer noted shoal size (if applicable), and whether the focal individual(s) was (were) exhibiting non-grazing behavior, defined as an upright body orientation whether the fish was swimming or stationary, or grazing behavior, defined as a position in which the fish had their body oriented towards the substrate in a nose-down grazing posi-

tion at time of observation. Observations on shoals were done by recording behavioral information based on the behavior of ≥50 % of the individuals in the shoal (e.g. a shoal was recorded as grazing if at least half of the shoal was in a nose-down position at the 60 s mark). If a shoal was widely dispersed or in a line formation, the observer followed the last 1/3 of the shoal and recorded the information for that subset of the shoal. If an observer lost sight of a solitary fish or shoal of fish, they searched for the fish for up to 2 min. If after 2 min the fish were not located, the focal follow would be terminated.

Although it remains to be conclusively determined how fixed the associations are between solitary and shoaling life modes within individuals, our preliminary data suggests that these behavior modes may remain fixed for at least short durations. Using natural variation in *A. triostegus* coloration (Fig. S3), we found that at least a small number of focal individuals showed fidelity to either small (i.e. ≤3 individuals) groups (n = 5 individual tracked fish) or to large (i.e. >50 individuals) groups (n = 7 individual tracked fish) over the entirety of a 20 d observation period (Text S1). Over 21 mo later, 2 individuals showing fidelity to small groups were resighted exhibiting the same behavior, and 2 shoaling individuals were also putatively resighted in large shoals (Fig. S4, Text S1).

For behavioral follow analysis, we assigned social behavior to focal fish according to the mode of the entire follow duration. As solitary fish would sometimes pair up with another fish for a few minutes before separating again, mode was determined to be a more accurate descriptor of behavioral follow shoal size than mean shoal size (Fig. S2). Fish were thus classified as solitary (mode = 1) or shoaling (mode > 25 fish). The reason for the 25 fish cut-off was that frequent splitting of smaller shoals often resulted in behavioral observations being terminated before 30 min.

2.3.2. Analysis

We found a significant difference in time spent in a grazing position and distance travelled in the first 5 min of observation, relative to subsequent 5 min bins, suggesting the presence of an observer effect resulting in increased distance travelled and reduced grazing; therefore, we removed the first 5 min of every follow. Fish observations had different durations (30 to 60 min), which may affect total space use and travel distance; therefore, total distance travelled was standardized per minute (meters travelled

divided by total follow duration in minutes) and analysis of 95% KUD was done by capping all follows at 30 min (total of 25 min excluding initial 5 min).

The proportion of time spent grazing was calculated across all follow durations, but because observations of grazing behavior for shoaling fish were assessed for most of the shoal at each time period (i.e. not collected for an individual member of the shoal), we only compared grazing between islands and not between shoaling and solitary fish at each island. To explain variation in time spent in grazing position for shoaling and solitary fish separately, we fit a linear mixed effects model using the lme4 package in R with time spent grazing as a response variable, predator abundance (island) as a fixed effect, and site, observer, and time of day as random effects, as it has been documented that time of day can affect surgeonfish behavior (Montgomery et al. 1989, Zemke-White et al. 2002). Best-fit models were selected according to small-samples AIC_c using the package MuMIn (Barton 2020).

We computed distance travelled using the adehabitatLT package in R and 95% utilization kernel using a biased random bridge method in the adehabitatHR package in R (Calenge 2006). For 95% KUD, the data distribution was non-normal, thus we opted to transform the data with a log normal transformation as suggested by Zuur et al. (2009). Linear mixed effects models fit by ML were used to explain variation in distance travelled and 95% KUD for shoaling and solitary *A. triostegus* at islands with high and low predator abundance. We specified 2 full models using the lme4 package as above, using distance travelled (meters travelled per minute of follow) and 25 min 95% KUD as responsible variables; social status (shoaling or solitary) and predator abundance (island) as fixed effects; and site, observer, and time of day as random effects. Best-fit models were selected according to AIC_c, and we did pairwise comparisons of marginal means using the emmeans package (Lenth et al. 2021).

3. RESULTS

3.1. Shoaling behavior

We conducted a total of 11 shoaling behavior surveys on Moorea (low predator abundance) and 14 surveys on Palmyra Atoll (high predator abundance). The prevalence of *Acanthurus triostegus* shoaling behavior was lower at the low predator abundance

site, and we found a similar pattern for *Mulloidichthys flavolineatus*, but no significant differences for *Chlorurus spilurus.*

3.1.1. *Acanthurus triostegus.* The prevalence of shoaling behavior for *A. triostegus* was best predicted by a model that included predator abundance (island), total abundance, and their interaction as fixed effects, with a higher proportion of fish in shoals occurring at the island with high predator abundance (Fig. 1a, Table 2). The model of the interaction of abundance and island suggested this interaction is primarily present at the island with low predator abundance where prevalence of shoaling behavior increases with increasing abundance, but not at the island with high predator abundance (Fig. S5). The number of shoals, abundance, and shoal sizes were also significantly different, with more shoals and greater abundance at the high predator abundance island, but larger shoal sizes at the low predator abundance island (Fig. 1b,c,d, Table S2).

3.1.2. *Chlorurus spilurus.* The best fit model for predicting prevalence of *C. spilurus* shoaling behavior included only the total abundance of *C. spilurus* (Fig. 1a, Table 2). Average shoal size was significantly different between the islands, with larger shoal sizes at the high predator island (although mean shoal size only differed by 1 fish), and abundance and number of shoals were not significantly different (Fig. 1b,c,d, Table S2).

3.1.3. *Mulloidichthys flavolineatus.* The prevalence of *M. flavolineatus* shoaling behavior was best predicted by a null model with no fixed effects; however, the next 2 best fit models ($\Delta AIC_c < 2$) also included total *M. flavolineatus* abundance and predator abundance as fixed effects (Fig. 1a, Tables 2 & S3). Average shoal size was significantly different, with larger shoal sizes at the island with high predator abundance, but abundance and the number of shoals was not significantly different across islands (Fig. 1b,c,d, Table S2).

3.2. *Acanthurus triostegus* behavioral observations

We conducted a total of 94 behavioral follows across both islands; 17 solitary and 19 shoaling fish follows at the high predator abundance island, and 37 solitary and 21 shoaling fish follows at the low predator abundance island (Table S4). All follows were at least 25 min in duration, and the majority (69) were 55 min in duration. Observations of shoaling fish were distributed across shoal sizes of 25 to 500 fish.
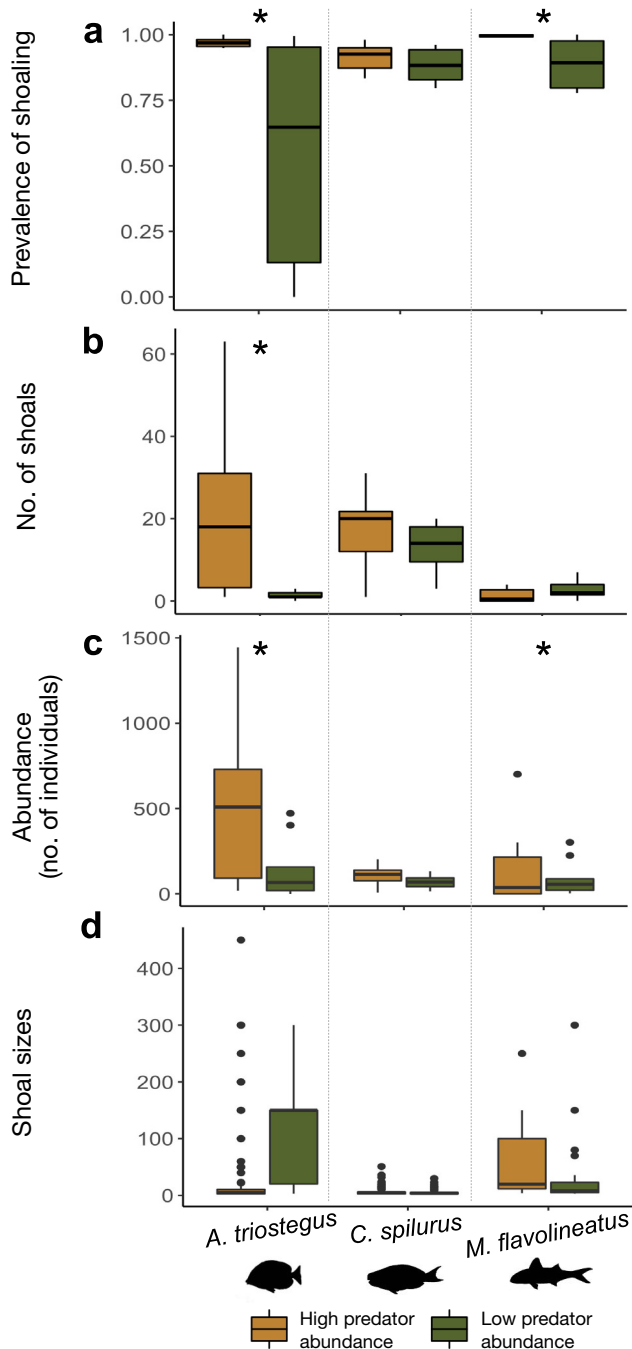
Fig. 1. (a) Prevalence of shoaling behavior (per survey), (b) number of shoals, (c) abundance of individuals per survey, and (d) shoal sizes observed for *Acanthurus triostegus*, *Chlorurus spilurus*, and *Mulloidichthys flavolineatus* at a high predator abundance island (Palmyra Atoll) and low predator abundance island (Moorea). Box: interquartile range; horizontal line: median; whiskers: minimum and maximum values; dots: outliers; asterisks: significant differences between islands

Time spent grazing for solitary fish was best predicted by a model that included no fixed effects and only the random effects site and time of day (Fig. 2a,

Table 3). The next best-fit model ($\Delta AIC_c < 2$) included predator abundance (island) as a predictor (Table S5). Similarly, when considering only shoals of *A. triostegus*, the best fit model for time spent in a grazing position included only the random effects site and time of day (Fig. 2a, Table 3). The next best-fit model ($\Delta AIC_c < 2$) included shoal size as a predictor (Table S5).

Distance travelled (in meters, standardized by observation minute) for shoaling and solitary fish was best predicted by a model that included both island and social behavior (shoaling or solitary) as fixed effects (Fig. 2b, Table 4). This best fit model predicts that at the high predator abundance island, *A. triostegus* travel 3.2 m min^{-1} less than those at the low predator abundance island, and that solitary fish travel 4.5 m min^{-1} less than shoaling fish (Fig. 2b, Table 4). Pairwise comparisons of distance travelled suggest there is a difference between marginal means across all comparisons of shoaling and solitary fish at the high and low predator abundance islands, except for the difference in the marginal means of distance travelled by solitary fish at the low predator abundance island and shoals at the high predator abundance island (p = 0.67, Table 5).
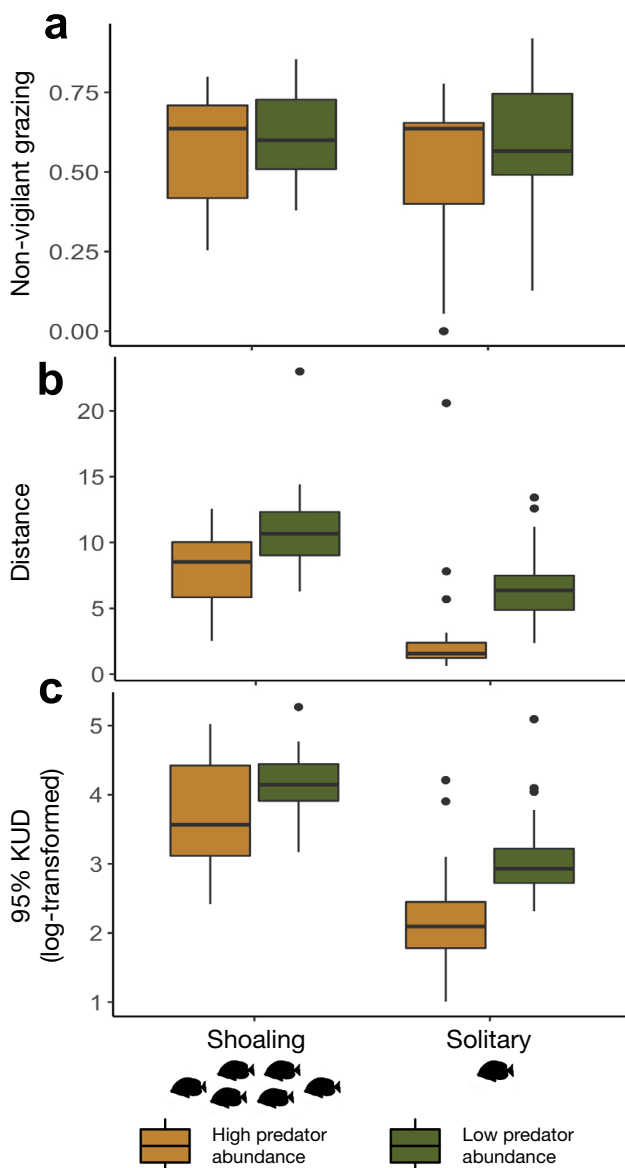
The 95% KUD for 25 min follows was best predicted by a model that included island and social status (shoaling or solitary) as fixed effects (Fig. 2c, Table 4). The next best-fit model ($\Delta AIC_c < 2$) also included the interaction between predator abundance and social behavior as predictors (Table S6). The best-fit model suggests fish at the high predator abundance island cover less area than those in the low predator abundance island, and solitary fish cover less area than shoaling fish at both islands (Fig. 2c, Table 4). There was a difference between marginal means across all comparisons of shoaling and solitary fish at the high and low predator abundance islands, except for between shoaling fish at each island (p = 0.11, Table 5) and between solitary fish at each island (p = 0.11, Table 5).

4. DISCUSSION

This study provides an initial exploration into the effects that predator abundance might have on fish shoaling behavior on coral reefs, a previously understudied area. Understanding the effects of predators on shoaling behavior is consequential, for behaviors like shoaling are tightly linked to foraging, and thus are likely to influence a wide range of ecological functions and dynamics. Our results suggest that

Table 2. Linear mixed model fit for prevalence of shoaling behavior

Fixed effect	*Acanthurus triostegus*			*Chlorurus spilurus*			*Mulloidichthys flavolineatus*		
	Estimate	SE	*t*-value	Estimate	SE	*t*-value	Estimate	SE	*t*-value
Intercept	0.294	0.103	2.847	0.719	0.04	18.27	0.867	0.065	13.33
Island (high predator abundance)	0.658	0.151	4.354	–	–	–	–	–	–
Abundance	0.001	0	6.317	0.002	0	4.225	–	–	–
Island × abundance	−0.001	0	−5.772	–	–	–	–	–	–
Territorial herbivore abundance	–	–	–	–	–	–	–	–	–
Random effect	Variance	SD		Variance	SD		Variance	SD	
Site (within island)	0.034	0.184		0	0		0.005	0.07	

Fig. 2. (a) The proportion of time spent in grazing position, (b) distance travelled (measured in meters and standardized by minutes of observation), and (c) 25 min 95% kernel utilization distribution (KUD) of solitary and shoaling *Acanthurus triostegus* at a high predator abundance island (Palmyra Atoll) and a low predator abundance island (Moorea). Box: interquartile range; horizontal line: median; whiskers: minimum and maximum values; dots: outliers; asterisks: significant differences between islands

lower predator abundance may decrease the prevalence of shoaling behavior in some, but not all reef fish species. Notably, we observed a lower shoaling prevalence in *Acanthurus triostegus* (surgeonfish) and *Mulloidichthys flavolineatus* (goatfish) in our lower predator abundance sites. Regarding *A. triostegus* behavior specifically, the effect of island predator abundance on shoaling behavior may be 2-tiered: a lower predator abundance (1) results in an overall lower prevalence of shoaling behavior (but shoaling behavior is not entirely eliminated as protection from predation is unlikely to be the only potential benefit of this behavior), and (2) increases the movement of shoaling fish and solitary fish relative to conspecifics at a high predator abundance island.

4.1. Shoaling behavior

A decrease in the prevalence of shoaling behavior with decreased predator abundance has been previously demonstrated in freshwater systems for minnows and guppies exposed to differing predation regimes (Seghers 1974, Magurran & Pitcher 1987, Huizinga et al. 2009). Interestingly, we found *A. triostegus* abundance to be a significant predictor of prevalence of shoaling behavior in this species, but

Table 3. Linear mixed model fit for explaining time spent in grazing position for shoaling and solitary *Acanthurus triostegus* at Palmyra Atoll (high predator abundance) and Moorea (low predator abundance)

Fixed effect	Solitary			Shoals		
	Estimate	SE	t-value	Estimate	SE	t-value
Intercept	0.543	0.06	8.626	0.481	0.080	5.986
Island (high predator abundance)	–	–	–	–	–	–
Shoal size[a]				–	–	–
Island × shoal size[a]				–	–	–
Random effect	Variance	SD		Variance	SD	
Time of day	0.005	0.072		0.005	0.069	
Site (within island)	0.018	0.135		0.000	0.000	
Observer	0.000	0.000		0.019	0.139	
[a]Fit in model for shoals only						

Table 4. Linear mixed model fit for shoaling and solitary *Acanthurus triostegus* at Palmyra Atoll (high predator abundance) and Moorea (low predator abundance)

Fixed effect	Distance travelled			95% KUD		
	Estimate	SE	t-value	Estimate	SE	t-value
Intercept	11.058	0.638	17.324	4.276	0.179	23.876
Island (high predator abundance)	−4.452	0.721	−6.214	−0.562	0.2	−2.814
Social behavior (solitary)	−3.196	0.734	−4.355	−1.291	0.141	−9.125
Island × social behavior	–	–	–	–	–	–
Random effect	Variance	SD		Variance	SD	
Time of day	0.000	0.000		0.000	0.000	
Site (within island)	0.000	0.000		0.556	0.236	
Observer	0.000	0.000		0.010	0.099	

Table 5. Pairwise marginal means comparisons of distance travelled and 95% KUD. If the comparison was significantly different, the subscript indicates which of the compared groups had the highest distance travelled ([d]) or 95% KUD ([k])

Comparisons	p-value distance	95% KUD
High predator shoal[d,k] – high predator solitary	<0.0001	<0.0001
High predator shoal – low predator shoal[d]	<0.03	0.11
High predator shoal[k] – low predator solitary	0.67	0.05
Low predator shoal[d,k] – high predator solitary	<0.0001	<0.0001
Low predator shoal[d,k] – low predator solitary	<0.0001	<0.0001
Low predator solitary[d] – high predator solitary	<0.03	0.11

this effect was only present at the island with lower predator abundance (Table 2, Fig. S5). This represents an interesting first observation, as it provisionally suggests that increased fish abundance does not necessarily give rise to a higher prevalence of shoaling in all contexts. Additionally, we found larger *A. triostegus* shoal sizes at the low predator abundance island. Surgeonfish are known to use shoaling to invade and graze down territories of other herbivorous fishes (Foster 1985, Mumby et al. 2006). This behavior has been observed in *A. triostegus*, where shoals primarily invade the algal farm territories of the damselfish *Stegastes nigricans* and other territorial surgeonfish (Barlow 1974). Although we did not find territorial fish abundance to be a predictor for shoaling prevalence in the best fit model (Table 2), we hypothesize that at the high predator abundance island, a smaller shoal size may represent a trade-off between predator avoidance and minimizing competition with conspecifics (Buckel & Stoner 2004, Hoare et al. 2004), but may potentially come at a cost of reduced access to damselfish territories. However, as

we did not conduct focal follows on small shoals (<25 fish), this hypothesis remains to be tested. Additionally, at the high predator abundance island, piscivorous predators such as *Caranx melampygus* and *Lutjanus bohar* are often seen in close association with large shoals and have been observed to prey on the territorial fish displaced by *A. triostegus* (Madin & Madin 2011), as well as on *A. triostegus* themselves (A. S. Guerra pers. obs.). Thus, predatory attempts by piscivores may frequently split large shoals at the high predator abundance island, resulting in smaller shoals. Alternatively, while grouping behavior may decrease per capita predation risk once a predator is encountered, large shoals may become more conspicuous in nature and thus more visible to a predator (Botham & Krause 2005, Ioannou & Krause 2008). Therefore, for fish forming shoals in low predator abundance environments, a larger shoal size may be optimal to gain access to food resources within guarded territories, without the added predation risk. Finally, as smaller fish are more often found in shoals than larger conspecifics for other fish species, a scarcity of predators may result in increased survival of small fish and thus a higher occurrence of large shoal sizes (Hoare et al. 2000). Future studies should consider differences in fish size and prevalence of shoaling behavior and size of shoals.

For the other 2 species, we found lower shoaling behavior prevalence and smaller shoals for *M. flavolineatus* at the low predator abundance island, and no difference between islands in prevalence of shoaling behavior or shoal sizes for *Chlorurus spilurus.* The differing life histories of the species likely explain this difference in shoaling behavior patterns. *M. flavolineatus* shoals are relatively stationary during the day and disperse for nocturnal foraging (Hobson 1968, Uiblein 1991, Holland et al. 1993). Thus, with reduced movement, the conspicuous nature of a shoal is reduced (although a shoal still remains more conspicuous than a solitary fish) (Turner & Pitcher 1986, Lima & Dill 1990), yet the advantages of the dilution and confusion effects that lower predation risk are maintained (Parrish 1991). The model results suggest there is no clear consensus on what predicts prevalence of shoaling behavior for *M. flavolineatus.* The abundance of *M. flavolineatus* was lower at the low predator abundance island (Moorea), where this species is also a direct target of fishing (Rassweiler et al. 2020a), so observed differences in shoaling behavior could be driven by direct fishing pressure lowering abundance. Alternatively, parrotfish such as *C. spilurus* can exhibit extensive behavioral plasticity with regard to social behavior, such as forming shoals or defending territories and harems (Clifton 1989, van Rooij et al. 1996). Previous work on *C. spilurus* at both study islands found that at short time scales (e.g. hours), space use is primarily related to competition and not predation risk (Davis et al. 2017, but see Madin et al. 2010b). As such, the strongest drivers for maintaining specific social behavior may not include predator avoidance. The possibility also remains that predation risks affect behavior at time scales that we were unable to measure. Additionally, we did not note individual fish sex in our surveys, which may account for differences in the tendency to form shoals as social behaviors differ among parrotfish reproductive modes (Buckman & Ogden 1973, de Girolamo et al. 1999). Finally, fishing pressure may account for the different response in prevalence and size of shoals. Parrotfish are among the most targeted fish on Moorea, thus a high predation of *C. spilurus* by humans may compensate for any loss of natural predation and maintain the prevalence of shoals (Rassweiler et al. 2020a).

Although the 2 islands differ substantially in fishing pressure and, as a result, predator abundance (low on Moorea, higher on Palmyra Atoll), other biological and physical differences between the islands, such as food availability and habitat rugosity, could play an important role in shaping patterns of shoaling behavior. Controlling for other important drivers of shoaling behavior in future studies is essential for clarifying the role of predator abundance in the prevalence of shoaling behavior in these coral reef fish species. This will always be challenging when making comparisons at among-island scales, especially finding locations where predator differences are large, but resource availability and configuration are similar.

4.2. *Acanthurus triostegus* behavioral observations

Our observations suggest that shoaling *A. triostegus* and solitary individuals spend similar amounts of time grazing at both islands, and both shoaling and solitary fish travel more at the low predator abundance island, with a more pronounced effect on the travel distance of solitary fish (Fig. 2, Tables 3–5).

We found a similar amount of time spent in grazing positions for both shoaling and solitary fish at both islands despite differing predator abundances (Fig. 2, Table 3). Other studies have found differences in feeding rates of herbivores between the 2 islands; however, as we were not measuring individual bite rates or subtle signs of vigilance, it is possible

we were not able to capture the effects of predator abundance (Davis et al. 2017). Another possible explanation for the differences among studies is that the most acute predation risk occurs outside our observation windows (e.g. dawn or dusk) and thus marked decreases in foraging for fish at the high predator abundance island were not captured in our surveys (Hobson 1973, Lima & Bednekoff 1999). Importantly, we did not measure food resource availability or availability of refuge habitat, which may influence trade-offs in grazing and predation risk (Gil et al. 2017).

Overall, both shoaling and solitary fish travelled greater distances at the low predator abundance island relative to their counterparts at the high predator abundance island. A decrease in excursion distance with increasing predation risk has been found for various fish species (Lima & Dill 1990, Orpwood et al. 2008, Madin et al. 2010a), and has been postulated to result from mechanisms such as moving prey being more easily detected by predators (Dill & Fraser 1984). This study suggests that similar mechanisms may play a role in movement behavior of shoaling fish. Notably, we found that solitary fish at the low predator abundance island travelled distances similar to shoals at the high predator abundance island, and these distances were much greater than the distances travelled by solitary fish at the high predator abundance island (Fig. 2b, Table 4), suggesting an important effect on the behavioral release of solitary fish. On coral reefs, the spatial distribution of grazing by herbivorous fish can affect coral survival, where sparse grazing over large areas, as opposed to intense grazing in small areas, may contribute to phase shifts towards algae-dominated systems (Sandin & McNamara 2012). Thus, a behavioral shift towards increased prevalence and movement of solitary fish could have important consequences for the ecology of coral reefs. It is worth considering; however, that the behavioral follows did not account for smaller shoals of *A. triostegus* at either island (i.e. <25 fish), as these were more prone to splitting and often resulted in prematurely terminated preliminary observational follows. Whether these dynamics for shoals persist for shoal sizes smaller than our 25 fish cut off is a matter deserving of future research. Thus, our work may not capture the entirety of shoaling behavioral differences associated with predator abundance, and future studies should consider capturing the entire range of shoal sizes, as well as variation in resource and habitat availability.

It is critical to note that many factors, other than predation, differ between Moorea and Palmyra Atoll.

It is also evident that the drivers that shape shoaling behavior are complex. As such, while we present with confidence the aforementioned differences in shoaling behavior, we cannot attribute these changes definitively to inter-island differences in predator abundance alone. There are a myriad of non-mutually exclusive alternate hypotheses that may also shape the behaviors we report upon. Two prominent such mechanism are: (1) bottom up effects and resource availability, and (2) differences in fishing pressure. Our study did not account for bottom-up effects such as the abundance of food resources and habitat rugosity, which are likely to influence movement associated with foraging and predation avoidance (Gil et al. 2017). Yet, pairwise comparisons of 95% KUD (area covered) and distance travelled found no significant difference between the core areas covered by shoals or by solitary fish across islands, but did find a significant difference in total distance travelled throughout this core area. This observation would seem to offer stronger support for a response to predator abundance versus differences in resource availability (Lima & Dill 1990), but further work is needed to determine the extent to which predation influences these behaviors.

Further, the same fishing pressure that can reduce predator abundance at Moorea could also directly influence the shoaling behavior of *A. triostegus*, *C. spilurus*, and *M. flavolineatus*. Humans are predators too, and fishing can have important impacts on the behavior of coral reef fish, including vigilance and escape responses (Januchowski-Hartley et al. 2011, Goetze et al. 2017). In other systems and theoretical studies, fishing has been found to alter shoaling behavior (Guerra et al. 2020, Sbragaglia et al. 2021, 2022) and shoaling behavior has been found to play an important role in mediating the effects of fishing on vigilance and escape behavior (Stankowich & Blumstein 2005, Samia et al. 2019). As previously discussed, *C. spilurus* and *M. flavolineatus* experience targeted fishing at Moorea (Rassweiler et al. 2020a). Although *A. triostegus* is not directly targeted by fisheries at Moorea, similar species at Moorea have been observed to shift their behavior despite not facing direct fishing pressure (Tran et al. 2016, Rassweiler et al. 2020a). Thus, fishing pressure could be similarly influencing our observations of shoaling behavior.

The fact that certain of these shoaling behaviors differed in significant ways between these 2 islands is in and of itself interesting. While there appears to be some provisional support for predation as a key driver of these differences, future research conducted between additional islands differing in pred-

ator abundance, comparisons of behavior within islands that contain marked gradients in predator abundance (e.g. inside and outside large protected areas), and potentially some manipulative experiments (e.g. increasing fishing pressure on shoaling fish) are some of the possible future ways to more clearly identify the importance of predation as a driver relative to alternative mechanisms.

This study provides an important starting point for continuing to explore the effects of predator abundance on fish shoaling behavior and potential consequences of fishing down predator populations. Our results suggest that overfishing of predators on coral reefs may decrease the prevalence of shoaling behavior of some prey fish. Our observations that such shifts occur in the case of an abundant herbivorous reef fish may indicate hitherto unrecognized implications of predator loss on the spatial distribution of grazing on coral reefs, as shoaling fish can forage in ecologically unique ways (Foster 1985) and can provide nutrient subsidies to coral colonies (Meyer et al. 1983); however, these ecological effects are unresolved and deserve further direct investigation. As we continue to find new ways to better manage ecosystems, it would be prudent to incorporate shifts in the social behavior of fish into management strategies, as these could have important ecological consequences.

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