Title

Behavioral Ecology in the Anthropocene

Author

Guerra, Ana Sofia

Publication Date

2022

UNIVERSITY OF CALIFORNIA

Santa Barbara

Behavioral Ecology in the Anthropocene

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution, and Marine Biology

by

Ana Sofía Guerra

Committee in charge:
Professor Douglas McCauley, Chair
Professor Jennifer Caselle
Professor Steve Gaines
Professor Andrew Berdahl

June 2022

The dissertation of Ana Sofía Guerra is approved.

Andrew Berdahl

Jennifer Caselle

Steve Gaines

Douglas McCauley, Committee Chair

June 2022

Behavioral Ecology in the Anthropocene

ACKNOWLEDGEMENTS

There are so many people who made this work possible, through the guidance and mentorship, support, collaboration, and friendship. I am thankful to every one of you.

First and foremost, thank you to my wonderful advisors, Doug McCauley and Jenn Caselle. Thank you for the unwavering support, for the guidance, mentorship, feedback, and advice throughout this whole process. I lucked out in finding two advisors who are incredible and compassionate human beings in addition to excellent scientists, and I am so grateful for that. Thank you for the laughs in the field and the fun brainstorming sessions. I have come a long way in my scientific career since meeting you both ~10 years ago on Palmyra, and you both played a huge role in that.

I would also like to thank the rest of my committee, Andrew Berdahl and Steve Gaines, as well as Hillary Young who provided mentorship and guidance along the way. None of my work would have been possible without collaborators and peers who assisted with fieldwork and labwork. To those who helped me stalk fish on Palmyra and Moorea (Marisa Morse, Katrina Munsterman, Katie Davis, Peter Carlson, and Tim White, Elizabeth Jahn, Alison Haupt, Nina Schiettekatte, and David Lecchini), and wrangle gulls on the Channel Islands (An Bui, Devyn Orr, Maggie Klope, Caroline Owens), thank you all so much for your help. Thank you to Jacey Van Wert and An Bui for help with lab work. To the McCauley lab (past and present): Erin, Molly, Lacey, Keenan, Francis, Paul, Caroline, Jacob - thank you for being the most supportive, eclectic, and overall best lab group I could have asked for.

This work was made possible by the generous funders and field research station who supported my research. I am grateful to the National Science Foundation, UCSB Faculty Senate, P.E.O International, the Worster Family, and the Sea and Sage Audubon Society. Additionally, thank you to the TNC station staff at Palmyra Atoll and Stefan from USFWS, the staff at CRIOBE, and David Mazurkiewicz and the rest of the CHIS NPS team for making my fieldwork possible.

A huge thank you to all the friends who supported me along the way, for keeping me laughing, keeping me going, and listening to all the venting sessions. To my SB friends – Erin, Kelly, Zoe, Ana, An, Heili, Devyn, Colin, Elizabeth, Ere, Sam, Dawnielle, Karly, Alexa, Ronnie, Lindsay, Paul, Ashley, Julie: thank you for all the hikes, the wine, the laughs, the support, and friendship. Each and every one of you were crucial to me wrapping up this dissertation adventure. To my Monterey family, Chelsea, Alison, Steve, Tim, Kerry, and Elena: thank you for everything throughout these many years. You guys are the ballast that has kept me steady, and there are not enough words I can type out to convey my appreciation for you. To the friends scattered far and wide and my OWUSS fam, thank you all for your support and friendship. There is one friend who has supported me beyond words, and that's my canine sidekick – Salsa. He won't be able to read this, but I'll give him extra treats later for never leaving my side, for reminding me to take work breaks, and to stop and smell every single flower. On that note, to all the friends I met through our awesome pups, you guys provided me with so much joy, motivation, and a way to disengage from constant work by finding a new passion in dog sports and training.

Finally, thank you to my family. You guys have unquestioningly supported me as I swerved through this seemingly random science path of working underwater, chasing fish and stalking birds. I cannot express how grateful I am for you fostering my curiosity in the natural world from an early age and supporting me every step of the way. Gracias.

VITA OF ANA SOFIA GUERRA

June 2022

EDUCATION

2022	Doctor of Philosophy in Ecology, Evolution, and Marine Biology, University of California Santa Barbara
2019	Master of Arts in Ecology, Evolution, and Marine Biology, University of California Santa Barbara
2014	Bachelor of Science with Honors in Biology (Ecology Track), Stanford University

PROFESSIONAL EMPLOYMENT

2016 - 2022	Graduate Researcher. National Science Foundation (NSF) Division of Environmental Biology (DEB) Award #3145-0023. University of California Santa Barbara (UCSB)
2017	Teaching Assistant. Ecology, Evolution, and Marine Biology Department. University of California Santa Barbara (UCSB)
2016	Teaching Assistant. University of California Santa Barbara (UCSB)
2016	Expedition Staff. Lindblad Expeditions
2015 - 2016	Research Technician. Ecology, Evolution, and Marine Biology Department. University of California Santa Barbara (UCSB)
2014 – 2015	North American Rolex Scholar. Our World Underwater Scholarship Society (OWUSS)
2014	Natural Resources Technician. California State Parks
2013	Teaching Assistant. Hopkins Marine Station & SEA Education Association. Stanford University
2011 - 2014	Lab and Field Research Assistant. Hopkins Marine Station. Stanford University
2012	Refuge Technician. U.S. Fish and Wildlife Service, Palmyra Atoll National Wildlife Refuge

PUBLICATIONS

Guerra AS, McCauley DJ, Lecchini D, Caselle JE (2022) Shoaling behavior of coral reef fishes varies between two islands with different predator abundance. *Marine Ecology Progress Series* **690**: 133-145.

Williams MA, Faiad S, Claar DC, French B, Leslie KL, Oven E, **Guerra AS**, Micheli F, Zgliczynski BJ, Haupt AJ, Sandin SA, Wood CL (2022) Life history mediates the association between parasite abundance and geographic features. *Journal of Animal Ecology* **91**: 996–1009.

Guerra AS, Kao AB, McCauley DJ, Berdahl AM (2020) Fisheries-induced selection against schooling behaviour in marine fishes. *Proc Roy Soc B,* 287 (1935).

Bertucci F, Maratrat K, Berthe C, esson M, **Guerra AS**, Raick X, ... & Parmentier E (2020) Local sonic activity reveals potential partitioning in a coral reef fish community. *Oecologia*, **193** (1): 125–134.

Gache C, Bertucci F, **Guerra AS**, Calandra M, Berr T, Lafaye J, Jorissen H, Nugues M, Cossy J, Lecchini D (2019) Effects of *Asparagopsis taxiformis* metabolites on the feeding behavior of post-larval *Acanthurus triostegus*. *Journal of Fish Biology* **95** (5): 1355-1358.

Guerra AS (2019) Wolves of the sea: managing human-wildlife conflict in an increasingly tense ocean. *Marine Policy* **99**: 369-373.

Garnier Y, Jacob H, **Guerra AS**, Bertucci F, Lecchini D (2019) Evaluation of microplastic ingestion by tropical fish from Moorea Island, French Polynesia. *Marine Pollution Bulletin* **140**: 164-170.

Wood CL**,** Zgliczynski BJ, Haupt AJ, **Guerra AS**, Micheli F, Sandin SA (2018) Human impacts decouple a fundamental ecological relationship – The positive association between host diversity and parasite diversity. *Global Change Biology* **24** (8): 3666-3679.

Guerra AS, Madigan DJ, Love M and McCauley DJ. (2017) The worth of giants: The consumptive and non-consumptive use value of the giant sea bass (*Stereolepis gigas). Aquatic Conservation: Marine and Freshwater Ecosystems* **28** (2): 296-304.

Young HS, Parker IM, Gilbert, GS, **Guerra AS,** and Nunn CL. (2016) Introduced species, disease ecology and biodiversity-disease relationships. *Trends in Ecology and Evolution* **32** (1): 41-54.

Guerra AS, Eckerlin RP, Durden LA, Dowling APG, Robbins RG, Dittmar K, Helgen KM, Agwanda B, Allan B, Hedlund T, and Young HS. (2016) Host-parasite associations in small mammal communities in semiarid savanna ecosystems of East Africa. *Journal of Medical Entomology* **53** (4): 851-860.

Guerra AS, Micheli F, and Wood CL. (2016) Ecology of a vulnerable shorebird in an altered habitat: Bristle-thighed Curlews (*Numenius tahitiensis*) on Palmyra Atoll. *Pacific Science* **70** (2): 159-174.

Wood CL, Sandin S, Zgliczynski B, **Guerra AS**, and Micheli F. (2014) Fishing drives declines in fish parasite diversity and has variable effects on parasite abundance. *Ecology* **95** (7): 1929-1946.

AWARDS

P.E.O. Scholar Award, 2021

Worster Award, 2018

NSF Graduate Research Fellowship, 2019-2021

Doctoral Scholars Fellowship, University of California Santa Barbara, 2018, 2022

2014 North American Rolex Scholar of the Our World-Underwater Scholarship Society

ABSTRACT

Behavioral Ecology in the Anthropocene

by

Ana Sofía Guerra

Human-induced environmental change has affected ecosystems on a global scale, altering the ecology and evolutionary trajectories of various species. Animal behavior is highly vulnerable to shifting with human impact and shifts and individual variation in animal behavior can influence functioning of the ecosystems they inhabit. Harvest of predators, for example, can have cascading effects on the behavior of their prey as they experience reduced predation pressure. Alternatively, depletion of food sources can cause wildlife to shift their behavior to access alternative food sources. Here, I explore anthropogenic impact to animal behavior and the knock-on consequences any such changes may have on ecosystems in two different systems: shoaling fish on coral reefs and seabirds that nest on oceanic islands.

On coral reefs, I explored differences in shoaling behavior of coral reef fishes on two islands whose predator populations face differing fishing intensities and shed light on the ecological role of shoaling behavior to coral reefs. Fishing of marine predators and 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. I also specifically characterized movement and foraging-associated behaviors of one of these fishes in this same comparative context. My work suggests that in areas with reduced predator abundance the tendency of some, but not all, fish species to form shoals is reduced. Additionally, I found differences in movement, grazing, and

interactions with heterospecific fish between shoaling and solitary fish. These observations shed some empirical light on how overfishing could affect shoaling behavior and suggests that social behavior of individual may play an important role in mediating their ecological function.

On oceanic islands, I examined the effects of large nesting colonies of Western Gulls (*Larus occidentalis*), which are known to forage on human refuse, on the Channel Islands of California. Specifically, I explored how their foraging on anthropogenic food sources may change nutrient deposition patterns at their relatively remote and protected breeding islands. Mobile animals that traverse ecosystem boundaries can fundamentally reshape environments by providing critical nutrient and energy inputs to the ecosystems they inhabit. In particular, aggregations of seabirds often transform coastal and island ecosystems through large amounts of nutrient-rich guano deposition. Anthropogenically-driven losses of these subsidies can occur through changes in abundance of mobile species, including seabirds, and have been shown to drive whole scale ecosystem state change on islands. However, even though many species that forage on anthropogenic food sources are highly mobile and may thus play important roles in moving nutrients from urban systems to otherwise conserved ecosystems, the impacts of anthropogenic *supplements* to spatial subsidies have been largely ignored. I found high (up to 40%) but site-specific rates of urban foraging, resulting in between 66 and 93 kg of guano per hectare (ha) on these two sites during the breeding season, driving marked seasonal increases in soil nitrogen and phosphorus content comparable to nutrient deposition in industrial agriculture.

By exploring similar facets of animal behavior in two separate systems, my research highlights the footprint that human activity can cast on even remote ecosystems through impacts to animal behavior.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1. INTRODUCTION

1.1 HUMAN IMPACT TO WILDLIFE BEHAVIOR

Humans are affecting ecosystems and wildlife populations on a global scale through harvest, pollution, habitat degradation, and climate change (Dirzo et al., 2014; Halpern et al., 2008; McCauley et al., 2015; Palumbi, 2001). Although much focus of human impact on wildlife populations has been that of reducing abundance through harvest and habitat destruction, humans have also substantially altered wildlife behavior (Arlinghaus et al., 2017; Januchowski-Hartley et al., 2015; Elizabeth M. P. Madin et al., 2010a; Ripple and Beschta, 2003). These shifts in behaviors can not only affect population abundance, but also have important ecosystem effects.

Through behaviors such as movement, heterospecific interactions, and foraging strategies, wildlife can play important roles in shaping the ecosystems they inhabit (Caut et al., 2012; Estes et al., 2016; Graham et al., 2018; Peter J Mumby et al., 2006). The focus of my dissertation is to understand how human impact might be changing animal behavior, and shed light on whether any changes to behavior have the potential to be relevant at the ecosystem scale.

CHAPTER 2. LEAVING MORE THAN FOOTPRINTS: ANTHROPOGENIC NUTRIENT SUBSIDIES TO A PROTECTED AREA

2.1. ABSTRACT

Mobile animals that traverse ecosystem boundaries can fundamentally reshape environments by providing critical nutrient and energy inputs to the ecosystems they inhabit. In particular, aggregations of seabirds often transform coastal and island ecosystems through large amounts of nutrient-rich guano deposition. Anthropogenically-driven losses of these subsidies can occur through changes in abundance of mobile species, including seabirds, and have been shown to drive whole scale ecosystem state change on islands. However, even though many species that forage on anthropogenic food sources are highly mobile and may thus play important roles in moving nutrients from urban systems to otherwise conserved ecosystems, the impacts of anthropogenic *supplements* to spatial subsidies have been largely ignored. Here we examine the effects of large nesting colonies of Western Gulls (*Larus occidentalis*), a generalist carnivore known to forage on human refuse, on the Channel Islands of California.

Specifically, we explore how their foraging on anthropogenic food sources may change nutrient deposition patterns at their relatively remote and protected breeding islands. We equipped gulls with GPS loggers to assess the frequency of urban foraging; we partnered this tracking data with bird density data to estimate the rate of wild and urban-derived guano deposition on the island sites. Consistent with research on other gull species, we found high (up to 40%) but site-specific rates of urban foraging, resulting in between 66 and 93 kg of guano per hectare (ha) on these two sites during the breeding season, driving marked seasonal increases in soil nitrogen and phosphorus content. We estimate that 27 kg of

nutrient-rich guano per ha per year is shuttled to these otherwise isolated islands from anthropogenic sources. This research highlights the footprint that human activity can cast on even remote ecosystems by driving significant nutrient enrichment through impacts to animal behavior and connectivity.

2.2 INTRODUCTION

Nutrient transfer by mobile animals can link many seemingly disparate systems and have significant effects on ecosystem functioning (Subalusky and Post, 2019). For example, bears' movement of salmon-derived nutrients to riparian forests changes forest growth and composition (Helfield and Naiman, 2001; Hilderbrand et al., 1999), hippopotami alter water chemistry and shape biodiversity in rivers through defecation of terrestrially-derived food sources (Stears et al., 2018), and large whales transport of nutrients from ocean depths to the surface may change global patterns of ocean productivity (Roman and McCarthy, 2010). As mobile animals that traverse ecosystem boundaries and form large nesting aggregations, seabirds provide important nutrients to their nesting and roosting grounds by depositing nutrient-rich guano sourced from their distant foraging grounds (Caut et al., 2012; Ellis et al., 2006; Wootton, 1991). In areas where nutrient input from other sources is often minimal, seabird colonies have been found to profoundly influence productivity and community structure via the cascading effects of bird-derived nutrient subsidies (Ellis, 2005; Fukami et al., 2006; Otero et al., 2018; Young et al., 2010). We define these subsidies as resource transfer between ecosystems that alters the dynamics of recipient populations and communities (sensu Subalusky and Post, 2019). In many cases, the impacts of cross ecosystem subsidies can dwarf internal nutrient cycling budgets, such that disruptions of subsidy linkages can even trigger whole system state change (Croll et al., 2005).

It has been well established that human activities, such as introduction of invasive species that prey on seabirds or habitat modification, often disrupt allochthonous nutrient inputs to ecosystems by reducing guano deposition (Croll et al., 2005; Fukami et al., 2006). However, in areas where seabirds have shifted towards readily exploiting anthropogenic food sources, nutrient budgets of surrounding ecosystems may instead become increasingly subsidized by humans, with potentially similar, but largely unexplored ecosystem level consequences.

Humans have influenced and subsidized global nutrient budgets dramatically: nitrogen inputs to terrestrial ecosystems have increased with a rise in fertilizer use and cultivation of nitrogen-fixing crops (Vitousek et al., 1997), a rise in emissions and atmospheric deposition poses threats to biodiversity across the globe (Phoenix et al., 2006), and eutrophication remains an imminent threat to many vulnerable marine and freshwater ecosystems (Deegan et al., 2012; Diaz and Rosenberg, 2008; Peñuelas et al., 2013; Silbiger et al., 2018; Vitousek et al., 1997). In an Anthropocene era of urban expansion and global change (Grimm et al., 2008; Seto et al., 2012), few areas remain protected from direct human pressures (Venter et al., 2016). As far as humans increasing nutrient movement into otherwise protected areas by subsidizing animal diets, this may represent another relatively unexamined eutrophication threat to relatively remote ecosystems.

Seabirds, particularly gulls (*Larus* spp.), readily supplement their diet by visiting human refuse sites and consuming anthropogenically-derived food sources (Ackerman et al., 2018; Blight et al., 2015; Fuirst et al., 2018; Langley et al., 2021; Navarro et al., 2016; Shaffer et al., 2017). As seabirds are a taxa of conservation concern (Croxall et al., 2012), the effects of anthropogenic diet subsidies (i.e., human refuse, fishery discards, and agricultural crops) on seabird populations' reproductive output, body condition, and health have garnered considerable attention (Annett and Pierotti, 1999; Auman et al., 2008; Duhem et al., 2008;

Navarro et al., 2017; Ramírez et al., 2012; Weiser and Powell, 2010). However, the effects of anthropogenic diet subsidies on wildlife and surrounding ecosystems are varied (Oro et al., 2013). For example, food subsidies can often increase reproductive output and elevate population densities of a subsidized species (Plaza and Lambertucci, 2017). These population increases may result in reduced populations of sympatric species through spillover predation or competition (Ripple et al., 2013; Votier et al., 2010; West et al., 2016), a decoupling of standing predator-prey relationships (Rodewald et al., 2011), increases in nutrient outputs to surrounding ecosystems (Wilson et al., 2004), and shifts in plant communities (Vidal et al., 2000; Wal et al., 2008). The importance of seabird nutrient inputs to the ecosystems they nest on is well-documented, as is the increasing reach of urbanization and availability of anthropogenic food sources; however, understanding the effects of the coupling of these two phenomena remains in its infancy.

In the present study, we characterize anthropogenic foraging by a generalist seabird and explore bird-derived nutrient inputs on two uninhabited protected coastal islands found along the North American west coast. Western Gulls (*Larus occidentalis*, WEGU) are large carnivorous gulls found along the North American west coast that readily exploit anthropogenic food sources throughout their range (Pierotti and Annett, 2001, 1995; Shaffer et al., 2017). Many Western Gulls forage in urban areas during the nesting season (Annett and Pierotti, 1989), particularly those that nest on islands that are located closer to urban areas (Shaffer et al., 2017). Santa Barbara Island and Anacapa Island, part of the Channel Islands National Park (California, USA), seasonally support various nesting seabirds, including dense aggregations of nesting Western Gulls (Carter et al., 1992). Using GPS loggers and stable isotope analysis to determine foraging patterns of breeding birds, and collecting soil samples to assess nutrient concentrations, we investigate: 1) the extent to which breeding gulls across both islands feed on anthropogenic food sources, 2) shifts in soil nutrients before and after the gull breeding season, and 3) the proportion of gull-derived nutrient inputs that are likely being subsidized by anthropogenic foraging. We hypothesize that anthropogenic subsidies may be a major component of island nutrient cycles, particularly for islands closer to mainland urban areas. Our study highlights how anthropogenic subsidies may be modulating nutrient inputs to a protected island ecosystem.

2.3 METHODS

Study sites

This study was conducted on Anacapa Island (ANIS) and Santa Barbara Island (SBIS), the two smallest of the Channel Islands off the coast of southern California (USA). Anacapa Island is composed of three islets with a total area of 2.9km^2 and is 20km from the mainland (Schoenherr et al., 2003). Santa Barbara Island has an area of 2.6km^2 and is 61km from the mainland (Schoenherr et al., 2003). Both islands are currently managed as part of the Channel Islands National Park and host large breeding colonies of various seabird species, including Western Gulls (Carter et al., 1992). Anacapa and Santa Barbara Islands are both dominated by nitrogen-limited annual grasslands and island sage scrub; they receive low annual precipitation which occurs primarily during the winter months (non-breeding season of seabirds). As they are both uplifted islands, they receive few marine wrack subsidies to island soil and have no springs or streams that would supply a flow of nutrients (Halvorson, 1992; Halvorson et al., 1988; Schoenherr et al., 2003; Subalusky and Post, 2019; Vitousek et al., 1997). Any allochthonous nutrient inputs that are not animal-derived are thus from a result of rock weathering and in the form of aeolian dust (Lawrence and Neff, 2009; Uhlig and von Blanckenburg, 2019).

Nutrient sources and soil nutrients

We measured seabird density and presence of nitrogen-fixing plants to account for different drivers of nutrient concentrations at each site. For measuring seabird density, we conducted nest counts (five, 10m x 4m belt transects) at each site in August 2019. We conducted five vegetation surveys using quadrats (1m x 1m) at each site to assess presence and percent cover of nitrogen-fixing plant species (family: Fabaceae) that could be driving nitrogen inputs to study site soil. Quadrats were arranged with one quadrat in the center of the survey site, and one quadrat each at 5m north, south, east, and west from the center quadrat.

We sampled soil on ANIS and SBIS in 2019 to test for concentrations of available nitrogen and phosphorus, as these soil characteristics are associated with nutrient deposition in seabird colonies (Ellis, 2005; Young et al., 2010). Sampling locations were evenly distributed across the two islands and were selected based on nesting Western Gull densities from previous breeding seasons (personal communication with National Park Service) to approximate an equal distribution of high and low bird density sites at each island. Eight sites were sampled on East Anacapa Island, with a minimum distance of 100m between sites, and eleven sites were sampled throughout Santa Barbara Island, with a minimum distance of 200m between sites (Fig A1). At each site on each island, we collected four random samples of topsoil (10cm) within a 200m^2 area at two separate time points: early in the nesting season when gulls are establishing territories and starting to build nests ("early breeding season", April 2019) and once most chicks had hatched ("late breeding season", July/August 2019).

Soil samples were dried at the field site, homogenized (by site), and sieved (<2mm) upon return to lab facilities at UC Santa Barbara. Soil samples were then evaluated for concentrations of available nitrogen (NO_3- and NH_4-N) [cadmium reduction method (Dahnke and Johnson, 1990)] and phosphorus (Mehlich, 1984) at Brookside Laboratories (New Bremen, OH, USA).

Statistical analysis

We used linear mixed effects models fit by maximum likelihood to explain variations in phosphorus, ammonia, and nitrate across islands, between sampling period, and with varying gull density. Full models were specified for each soil nutrient using the *lme4* package (Bates et al., 2015) with nutrient concentration as a response variable; island, sampling period (early or late breeding season), nest count, and the interaction of all variables were fixed effects, and site was a random effect (Table A1). Best-fit models were selected according to small-samples corrected AIC (AICc) using the package *MuMIn* (Barton, 2020). All computations were done in R using R Studio and the *tidyverse* package (R Core Team, 2020; RStudio Team, 2020; Wickham et al., 2019).

Foraging behavior

We studied Western gull foraging behavior during the 2016 incubation period (April – May). Feather and blood samples were collected from 137 adult gulls (84 on ANIS and 53 on SBIS) for stable isotope analysis, and a subset of 52 birds were equipped with GPS trackers. All sampled and tracked birds were captured from nests containing 2-3 eggs with a snare carpet or single foot snare. Birds that were sampled but not tracked were only captured once and sampled for feathers (two breast feathers and two underwing coverts) and blood (between 0.5 and 2.0 ml of blood from the brachial vein) for stable isotope analysis. We also measured body mass with a spring balance (± 20 g), and culmen, tarsus, and skull lengths using calipers (±0.1 mm). Nine of the sampled gulls regurgitated when captured, and these opportunistic diet samples were also collected in the field.

A total of 52 gulls (31 on ANIS and 21 on SBIS) were equipped with a GPS logger (igotU GT-120, Mobile Action Technology Inc.) that recorded a GPS location every 30-60s with an accuracy of 2-4m. Upon initial capture, a logger was attached to the bird’s three central tail feathers using Tesa adhesive tape (Tesa Tape Inc, Charlotte NC). The GPS loggers were removed from their original plastic casing to decrease total mass and then encased in waterproof heat shrink tubing. Loggers were deployed for a minimum of 24h before attempting recovery using the capture methods mentioned above. GPS loggers were recovered from 26 gulls on ANIS (83%) and 17 gulls on SBIS (80%). While loggers were recovered as quickly as 24hr later, mean deployment was an average of 60+ hours per bird (total 2,778 hours of tracking data). In addition to removing the GPS logger upon recapture, we conducted the sampling protocol for feathers, blood, and morphometric data described above. All blood samples were kept cold and blood was centrifuged within two hours of collection, then kept frozen in liquid nitrogen until return to the laboratory at UC Santa Barbara.

Tracking data analysis

All tracking data were post-processed and analyzed according to methods described in Shaffer et al. (2017). In brief, erroneous locations were removed using an iterative speed filter and foraging trips were identified as any trip where a gull traveled farther than 1 km from the island for durations that exceeded 30 minutes. Foraging excursions were further characterized by calculating the total distance traveled, maximum range, and duration of each foraging trip. In addition, we determined foraging trip destinations (mainland/urban or pelagic and intertidal) and proportion of time away from the island. All trip destinations were evaluated by comparing whether a gull visited the mainland or remained at sea using high resolution coastline data (Global Self-consistent, Hierarchical, High-resolution Shoreline Database; gshhs v.2.3.5). If a foraging trip crossed over onto land, destinations were further evaluated by plotting tracks over Google Earth (Google Earth Pro v.7.1.7.2600) to pinpoint specific destinations within urban areas and/or shoreline that gulls visited. We also determined the frequency of urban foraging trips as a proportion of the total number of trips conducted by each gull and whether foraging by each bird was mixed (some trips to urban areas, some on to natural areas), wholly urban (all trips to urban areas) or marine (all trips to natural areas). All track analyses were performed using purpose-built routines and functions in the Mapping and Machine Learning and Statistics toolboxes in MATLAB R2016b (MathWorks, Natick MA).

Stable Isotope Analysis

We conducted stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ isotope ratios in feather and blood samples to explore potential foraging differences of birds between the two islands and across the breeding and non-breeding season as stable isotope values can be useful indicators of diet. For seabirds foraging in marine environments, $\delta^{15}N$ values reflect foraging trophic level, where higher $\delta^{15}N$ values indicate a higher trophic level; and $\delta^{13}C$ values indicate food source, where enriched $\delta^{13}C$ indicates inshore food sources, and lower values indicate offshore food sources (Hobson et al., 1994). In the case of seabirds foraging in marine and terrestrial environments, lower $\delta^{15}N$ values have been used to indicate increases in urban foraging (Blight et al., 2015; Lenzi et al., 2019; Osterback et al., 2015). Additionally, $\delta^{13}C$ values can be used to differentiate between anthropogenic diets and natural diets, where higher $\delta^{13}C$ values are indicative of a C_4 photosynthetic pathway, which is common in United States corn-based food systems and distinct from the lower $\delta^{13}C$ values of natural vegetation which primarily have C_3 photosynthetic pathways (Jahren and Kraft, 2008). In cases of wildlife foraging in terrestrial and marine systems, marine foraging $\delta^{13}C$ values are intermediate between those of C_3 and C_4 terrestrial foraging values, making it somewhat more difficult to distinguish between marine vs. anthropogenic foraging via carbon isotope values (Kelly, 2000).

We used isotopic signatures from gull plasma to infer diet during the breeding season, as the integration rate for plasma is high and isotope ratios represent a feeding period of ~3 days (Hobson, 2005). We also used isotopic signatures from feathers to infer longer time periods as feathers have a much slower integration rate and isotopic ratios reflect diet at the time of feather growth after a molting period (Hobson, 2005; Hobson and Clark, 1992). For Western Gulls, molting occurs twice a year in the early fall and late winter and lasts at least two months, thus feather isotopic ratios represent the non-breeding season and the very early and late portion of the breeding season, or a year-round diet (Howell and Corben, 2000; McCaskie, 1983). Prior to isotopic analysis, plasma was freeze-dried, homogenized, and ~0.5 mg were loaded into tin capsules. Feathers from each gull were first cleaned of surface lipids and contaminants using a 2:1 chloroform and methanol solution, followed by two methanol rinses, dried, cut into small fragments, and ~0.5mg were loaded into tin capsules. Tin capsules were sent to the University of California, Davis Stable Isotope Facility for analysis. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). We created isotopic biplots ($\delta^{13}C$ and $\delta^{15}N$) to visualize the differences in isotopic space for the breeding season (plasma) and year-round (feather) diets of the two colonies. Additionally, we compared mean isotopic values of plasma and feather tissue across colonies using a Wilcoxon rank-sum test and generated Bayesian standard ellipses (40% confidence level) for each colony and tissue (feather or plasma) using the SIBER package in R to estimate isotopic niche space (Jackson et al., 2011; R Core Team, 2020). We compared the size of the ellipses by fitting Bayesian models adjusted for small sample sizes (SEAc) and calculated overlap in ellipse area between the two colonies, which can be used to determine overlap in diets and niche space (Eurich et al., 2019). All computations were conducted using R studio and the *tidyverse* package (RStudio Team, 2020; Wickham et al., 2019).

Guano deposition estimates

We estimated the amount of guano being deposited onto the island soil by Western Gulls on ANIS and SBIS during the breeding season using tracking data, known fecal deposition rates, and known breeding population size for the two islands (Table 1).

Table 1. Variables used for estimating guano deposition by Western Gulls on Anacapa Island and Santa Barbara Island.

variable	**definition**	**value**	
		ANIS	SBIS
n_c	number of breeding birds	10,000	14,000
d_i	duration of incubation period	37 days	
t_c	average hours per day spent on island during incubation	20.20h	17.55h
f	defecation rate	34.9g/day*	
d_r	duration of chick rearing period	42 days	
t_r	estimated number of hours per day spent on island during chick rearing	9.6hθ	
a	island area	283ha	260ha

* based on the deposition rate of the congener, *Larus argentatus* (Portnoy 1990)
θ an approximation of 40% of day based on Pierotti and Annett 1995

The time spent by Western Gulls on their nesting grounds varies throughout the breeding season, so we differentiated estimated guano deposition between the incubation period and first five days of brooding (d_i) and the chick-rearing phase (d_r), as adults spend a significant amount of time at the nest during incubation and early brooding (Shaffer et al., 2017), but reduce this time allocation during chick rearing (Pierotti and Annett, 1995). We estimated the average amount of time (t_i) gulls spent on the island over a 24h period during incubation and early brooding using tracking data. Throughout the chick-rearing period, adult Western Gulls are thought to decrease their time at the nest to less than 50% of the day, so we used 40% of the day as the value for time spent on the island during the chick rearing period (t_r). As we were unable to determine the fecal deposition rate (f) for Western Gulls, we used the known fecal deposition rate of *Larus argentatus*, a similarly sized congener to approximate deposition by Western Gulls (Portnoy, 1990). Fecal deposition (*D*) onto each island was then calculated as

$$\boxed{D = \frac{n_c[(d_i \times\ t_c \times f) + (d_r \times\ t_r \times f)]}{a}}$$

where *n* represents the number of breeding adults at each colony (National Park Service, 2016) and *a* represents the area of each island (Table 1). Data from a congener suggests gull guano may be composed of 5.5% nitrogen (Bird et al., 2008), which we used to estimate the amount of nitrogen deposition. Incorporating the tracking data, we estimated what proportion of the estimated nutrient deposition occurring on each island may be subsidized by urban foraging.

2.4 RESULTS

Nutrient sources and soil nutrients

To understand potential drivers of any differences in nutrients across sites we surveyed seabird density and nitrogen fixing plant density. We found a higher density of nests per site at ANIS (mean ± sd: 35.12 ± 17.88 per 200m^2) than at SBIS (9.09 ± 5.87 per 200m^2). We found no nitrogen fixing plants of the family Fabaceae in any of our vegetation survey quadrats on either island.

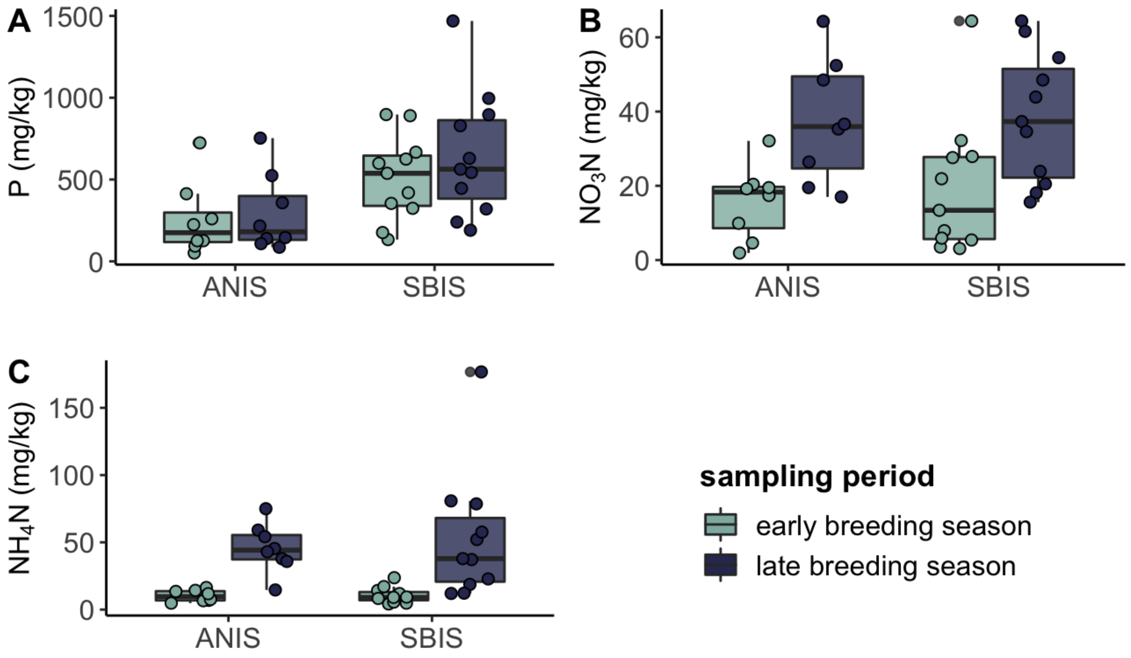

Figure 1. Concentrations of (A) phosphorus, (B) nitrate, and (C) ammonia at Anacapa Island (ANIS) and Santa Barbara Island (SBIS) in the early and late stages of the Western Gull breeding season.

We observed significant differences in soil nutrients between sampling periods and between the two islands (Fig 1). Concentration of NO_3N was best predicted by a model that included sampling period as a fixed effect, with higher concentrations in the late breeding season sampling period (Table 2). The two next best-fit models ($\Delta AIC < 2$) include (1) island and sampling period, and (2) and nest count and sampling period as fixed effects (Table A4). The concentration of NH_4N was best predicted by the full model, including island, sampling period, and nest count as fixed effects as well as their interactions, with small increases in concentration with increased nest density, higher concentrations of NH_4N on SBIS, and increases in concentration in the later sampling period (Table 2). The two next best-fit models ($\Delta AIC < 2$) included (1) all fixed effects, but did not include any fixed effect interactions, and (2) only sampling period as a fixed effect (Table A4). Phosphorus concentration was best predicted by a model that includes island and sampling period as fixed effects, with a higher concentration during the later sampling period and overall higher phosphorus concentrations on SBIS (Table 2). The next best-fit models (ΔAIC <2) include (1) island, sampling period, and the interaction of island and sampling period as fixed effects, and (2) island, nest count, and the interaction of nest count and island as fixed effects (Table A4).

Table 2. Best-fit linear mixed models for predicting pH and concentrations of phosphorus (P), nitrate nitrogen (NO_3N), and ammonium (NH_4N) in soil at two *Larus occidentalis* nesting islands

	NO_3-N			NH_4-N			P		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	17.8	3.66	4.87	6.83	18.29	0.38	223.97	100.28	2.233
nest count	-	-	-	0.1	0.47	0.21	-	-	-
island (SBIS)	-	-	-	3.44	22.32	0.15	307.6	129.78	2.37
sampling period (late)	20.25	4.06	4.99	11.91	25.87	0.46	95.32	34.94	2.73
nest count:island	-	-	-	-0.06	1.29	-0.04	-	-	-
nest count:sampling period	-	-	-	0.67	0.66	1.01	-	-	-
island: sampling period	-	-	-	-15.83	31.56	-0.5	-	-	-
nest count:island: sampling period	-	-	-	4.46	1.82	2.45	-	-	-
Random effect	**variance**	**SD**		**variance**	**SD**		**variance**	**SD**	
site	97.74	9.89		0	0		72207	268.7	

Foraging behavior

We analyzed GPS logger data from 43 gulls and a total of 2,778 hours of tracking data throughout the course of the study. Average tracking duration (the number of hours for which the bird had a tag with operational battery attached) and number of trips logged per bird were 60.36 ± 22.85h and 3.23±1.45 trips on ANIS and 65.09 ± 24.27h and 6.18 ± 4.43 trips on SBIS.

We found variability in foraging behavior (defined as searching behavior for the purpose of this study) across the two colonies and between trips across individual birds (Fig 2A). On ANIS, the mean proportion of foraging trips to urban areas was 0.41 ± 0.36, with 4 (of 26) birds conducting all their foraging in urban areas and 8 conducting all their foraging in pelagic or intertidal habitat of other Channel Islands (Fig 2B). On SBIS, the mean proportion of foraging trips to urban areas was 0.09 ± 0.18, with no birds conducting all their foraging in urban areas and 13 (of 17) conducting all their foraging in pelagic or intertidal habitat of other Channel Islands (Fig 2C). No birds from either island conducted trips to intertidal habitat on the mainland.

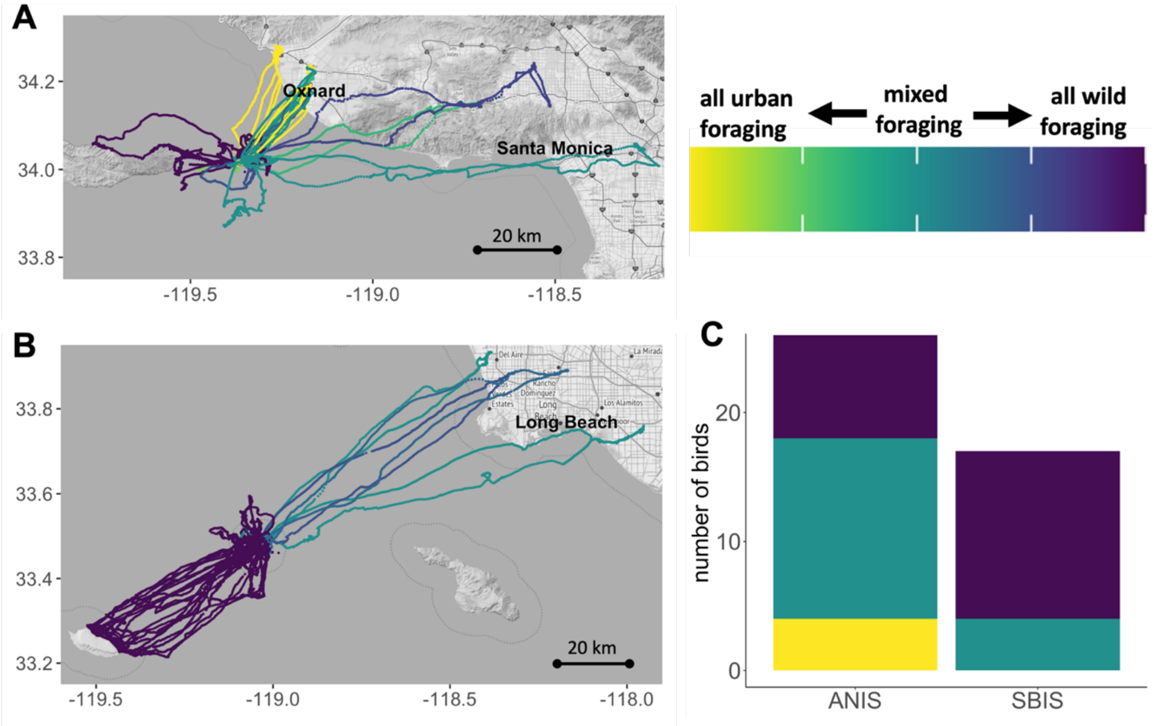

Figure 2. Foraging and movement behavior of 43 *Larus occidentalis* nesting on (A) Anacapa Island (ANIS) and (B) Santa Barbara Island (SBIS). Color of track denotes frequency of anthropogenic foraging (proportion of foraging trips to mainland out of all foraging trips observed) by each individual bird, where yellower lighter tracks denote higher frequency of anthropogenic foraging and darker purple tracks denote a more marine-sourced diet. Individual birds are classified and counted according to their foraging behavior (C): all urban foraging (yellow), a mix of urban and wild foraging (green), and all wild foraging (teal).

Regurgitations that occurred during handling (n = 9) indicated that gulls had consumed a variety of marine food items including barnacles, crabs, fish, squid and kill and anthropogenic items like chicken, hot dogs, tacos, and other processed produce and meats.

Stable isotope analysis

We collected samples for stable isotope analysis from 137 Western Gulls across both colonies (Table A5). There was a significant island population difference between δ^{15}N and δ^{13}C values of plasma samples from ANIS and SBIS (δ^{15}N: W = 380.5, $p < 0.005$; δ^{13}C: W = 1161, $p < 0.005$), but no significant difference between values of feather samples from the two islands (δ^{15}N: W = 1918.5, $p = 0.3$; δ^{13}C: W = 1945, $p < 0.4$). Along the δ^{15}N axis, the mean value for plasma samples from ANIS (13.94 ± 1.82) was 1.28 (‰) lower than plasma samples from SBIS gulls (15.22 ± 1.44), indicative of higher trophic level/marine foraging by nesting SBIS gulls (Table A5, Fig 3A). A similar, although less pronounced pattern was observed along the δ^{13}C axis, where mean value of plasma samples from ANIS gulls (-19.91 ± 0.71), was 0.47 (‰) higher than the plasma samples from SBIS gulls (-20.38 ± 0.80), indicative of more C_4/anthropogenic foraging by nesting ANIS gulls (Table A5, Fig 3A). For feather samples, mean isotope values (δ^{13}C, δ^{15}N) were δ^{13}C: -17.41 ± 0.86, δ^{15}N: 12.92 ± 2.23 for ANIS gulls and δ^{13}C:-17.3 ± 0.68, δ^{15}N:13.25 ± 2.17 for SBIS gulls (Table A5).

Plasma samples from gulls on ANIS had a higher standard ellipse area (4.08) than those on SBIS (3.75) and the area overlap of 1.61 represents 39% of the isotopic niche space occupied by ANIS gulls and 42% of that occupied by SBIS gulls (Fig 3B). For feather samples, gulls from ANIS had higher standard ellipse area (5.71) than those from SBIS (4.65), and had an increased overlap area of 4.52 which accounted for 77% of the isotopic niche space of ANIS gulls and 95% of that of SBIS gulls (Fig 3B).

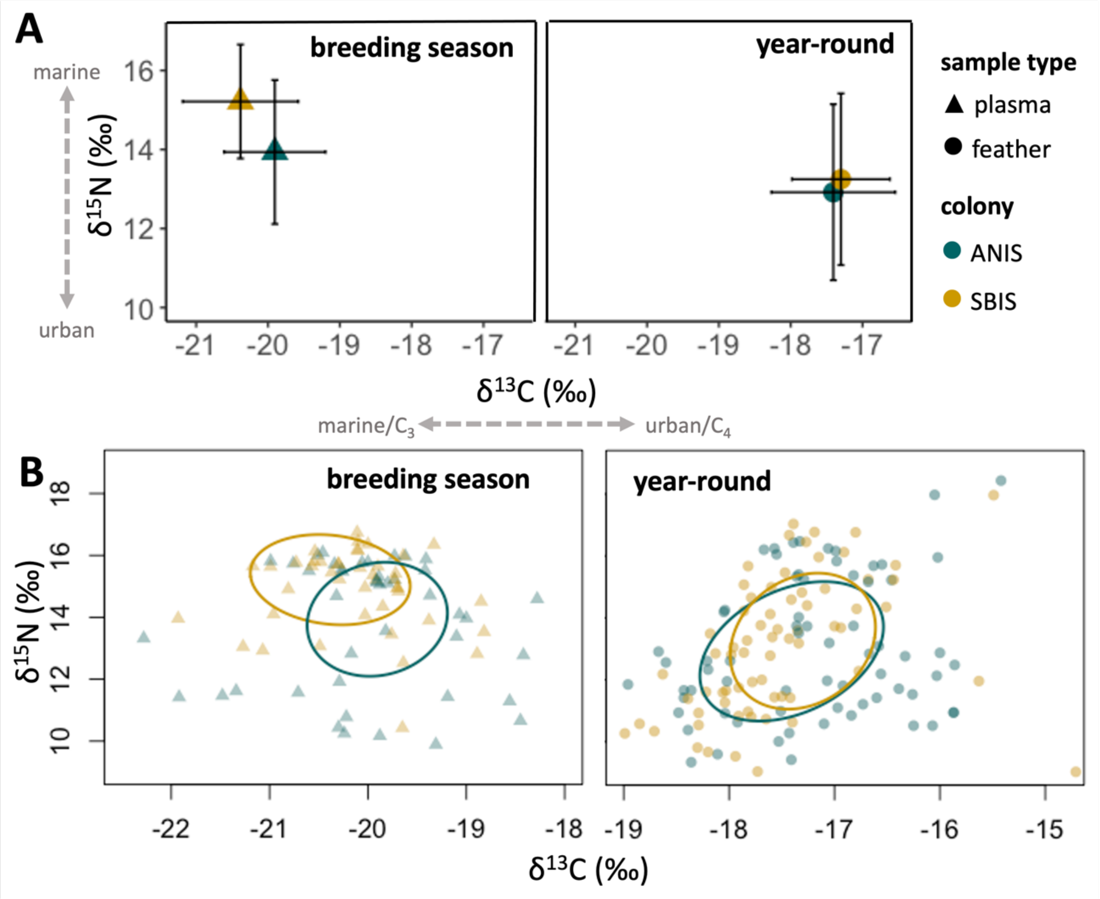

Figure 3. $\delta^{15}N$ and $\delta^{13}C$ (‰) signatures of plasma (triangle) and feather (circle) samples collected from Western Gulls (*Larus occidentalis*) nesting on Anacapa island (green) and Santa Barbara Island (yellow), where feather samples more closely approximate year-round diet and plasma samples approximate breeding season diet. A) Biplot of isotopic signatures where points are group means and error bars represent standard deviation. Dashed grey arrows along x and y axes represented expected directionality of marine and urban foraging. B) Isotopic area overlap of plasma samples and feather samples. Standardized Bayesian Ellipse areas (SEAc) are depicted by solid lines and values for $\delta^{15}N$ and $\delta^{13}C$ are expressed in ‰.

Guano deposition estimate

Based on the tracking data, we calculated the average amount of time per day gulls spent over each island during the incubation period: 20.20 ± 3.32 h on ANIS and 17.69 ± 55 h on SBIS. Using the values referred to above for duration of the incubation and chick-rearing stages, breeding bird population, defecation rates, and island size (Table 1), we estimated a Western Gull breeding season guano deposition of 66.74 kg/ha for ANIS and 93.04kg/ha for SBIS. From these, we estimated nitrogen deposition of 3.67 kg/ha for ANIS and 5.11 kg/ha for SBIS using estimates of nitrogen content found in gull guano. Concomitantly, we estimated that 41% of gull nutrient deposition on ANIS and 9% of gull nutrient deposition on SBIS is likely a human subsidy vectored by urban foraging gulls during the breeding season.

2.5 DISCUSSION

This study provides an exploration into the role anthropogenic subsidies to seabird diet may have in altering the nutrient budgets of two coastal islands. We found an increase in nutrient concentrations, particularly nitrogen, in sampled soil following the Western Gull nesting season, suggesting that breeding gulls are leaving a measurable nutrient footprint on the island soil (Fig 1). Increases in nitrogen and phosphorus concentrations are known to be associated with nutrient deposition by colonial seabirds, and these increased concentrations can be relevant at local and global scales (Baumberger et al., 2012; Otero et al., 2018, 2015). Gull breeding colonies have been found to dramatically increase concentrations of phosphorus and nitrogen in island soils, lakes, and ponds across various continents (García Luis V. et al., 2002; Hogg and Morton, 1983; Martín-Vélez et al., 2019; Otero et al., 2015; Portnoy, 1990; Vidal et al., 1998). Because we found no presence of legumes in any of our sites, and because these high islands have no other sources of marine nutrients, nutrient inputs to the island terrestrial ecosystem are likely only arriving through aeolian dust (small sediment particles suspended in the atmosphere) and vectored by seabirds from their foraging grounds (Halvorson et al., 1988; Lawrence and Neff, 2009; Subalusky and Post, 2019; Vitousek et al., 1997). Aeolian dust is likely small in magnitude compared to estimated inputs from guano and furthermore would be unlikely to vary across these spatially close islets or across these sampling periods. Thus, seabirds are likely to be the dominant source of nutrients to these sites and explain variation in nutrient profiles seen across sites and seasons.

Our estimated quantity of guano deposited on the islands annually by Western Gulls is 66.74 kg/ha for ANIS and 93.04kg/ha for SBIS, which when compared to commercial agriculture, represent about 50% of the average global fertilizer consumption in 2018 (136 kg of fertilizer per hectare of arable land) (FAO, 2020). Additionally, our tracking data analysis revealed that 9-41% of nutrient input is likely derived from anthropogenic food sources (Fig 2A-B), suggesting a significant anthropogenic impact to the fundamental nutrient budget of these fully protected islets that are typically viewed as remote wilderness. This amounts to an estimated 27 kg of anthropogenically subsidized nutrient rich guano per hectare being deposited onto the islands during the breeding season.

Although these estimates are substantial, our estimate of guano deposition by Western Gulls is lower than other estimates of total seabird inputs on nesting islands (Smith and Johnson, 1995; Young et al., 2010). However, these previous estimates included more variation in seabird species and larger nesting populations (Smith and Johnson, 1995; Young et al., 2010). Moreover, as we did not include guano inputs from non-breeding gulls, juveniles, and recently hatched gull chicks in our calculation, nor inputs from gulls that frequent the islands during the non-breeding season, our estimate of guano input likely underestimates total inputs by Western Gulls to these islands. Furthermore, we were unable to determine if any of our tracked gulls foraged on fishery discards while at sea, which is another common source of anthropogenic subsidy for seabirds; therefore inputs of anthropogenically subsidized guano are likely an underestimate as well (Bartumeus et al., 2010).

Interestingly, we found that SBIS had significantly higher concentrations of phosphorus than ANIS during each of the sampling periods (Fig 1, Table A2). Differences in nutrient concentrations across islands could also be a result of dietary differences between the two colonies of Western Gulls, as our tracking data suggest that during the incubation period, gulls on ANIS foraged in urban areas more frequently than those on SBIS (Fig 2). In two additional studies examining the nutrient content of guano in two separate populations of Herring Gulls, *Larus argentatus*, gulls with diets rich in fish had higher concentrations of phosphorus and an order of magnitude less nitrogen than those which frequently consumed human refuse (Gould and Fletcher, 1978; Portnoy, 1990). In a protected island ecosystem such as the Channel Islands National Park, such changes in guano quality could pose conservation challenges as increases in soil nitrogen concentration in similar systems has resulted in increases in exotic and invasive species (Fenn et al., 2010; Vallano et al., 2012).

Population-level differences in foraging strategies between neighboring island colonies during the breeding season have been previously documented for Western Gulls (Clatterbuck et al., 2021; Shaffer et al., 2017). Differences in the prevalence of urban vs. marine foraging is likely explained by the distance to the mainland (Cockerham et al., 2019; Pierotti and Annett, 2001; Shaffer et al., 2017), as distance to the nearest mainland point from ANIS is 20km, compared to 61km from SBIS. We found that some gulls exhibited preferences for wholly marine or wholly urban diets during the tracking period (Fig 2C), although longer tracks would provide stronger support for patterns of individual specialization. Differing foraging strategies between individuals could also be a result of competition among colony members over marine resources near the nesting island (Ashmole, 1963) or a result of behavior learned from parents (Annett and Pierotti, 1999). It is important to note however, that our GPS tracks represent gull foraging only during the incubation period and Western Gulls are known to switch dietary preferences throughout the breeding season, particularly during the chick-rearing period (Annett and Pierotti, 1989). Additionally, as we did not directly collect and analyze fecal samples from tracked individuals to compare nutrient loads in gulls that foraged in each of the environments, we cannot ascertain foraging differences may be driving these differences in soil nutrients.

Isotope analyses of blood plasma, complemented by gull behavior from the tracking data, show a difference in proportion of anthropogenic foraging between colonies (Fig 3). However, the results of feather stable isotope analysis indicate that these differences diminish during the non-breeding season (Fig 3B). Without tracking individuals during the non-breeding period, it is unclear whether the trend we observed of greater urban foraging in gulls from ANIS is maintained after the breeding period when they are not tied to a central place. However, there is evidence of Western Gull numbers increasing around refuse dumps in winter months, suggesting that Western Gulls spend more time foraging in urban environments during the non-breeding season (Spear, 1988). Additionally, the mean feather $\delta^{15}N$ stable isotope values for both islands (SBIS:13.25 ± 2.17, ANIS:12.92 ± 2.23) are lower than those reported for feathers of gulls presumed to be foraging on a mixed diet of anthropogenic and marine sources, further suggesting that our samples reflect a shift towards increased urban foraging by SBIS gulls (Blight et al., 2015; Osterback et al., 2015). If the trend we observed in urban foraging between colonies is the result of colony distance to the mainland, completion of breeding and thus a departure from nesting island allows for a shift towards a more urbanized diet. It is also possible that a diet switch may be triggered by variations in oceanic productivity and marine resource availability (Cimino et al., in press), as the Santa Barbara Channel is most productive during spring and least productive during fall and winter (Brzezinksi and Washburn, 2011; Pierotti and Annett, 2001). Thus, anthropogenic foraging is likely providing important subsidies even to SBIS gulls that primarily forage in marine habitats during the breeding season. The influence of anthropogenic diet subsidies on nesting island soils may therefore reach beyond the direct deposition of guano after an urban foraging trip, but by supplementing diets of these birds during the nonbreeding season.

Our results show that there is a considerable difference in foraging preferences of Western Gulls during the incubation period between ANIS and SBIS, which appear to lead to differences in soil phosphorus concentrations; however, other differences between the islands could also play an important role in shaping soil nutrient profiles. For example, differences in soil types, precipitation, and topography could account for differing soil chemistry across the islands (Sims and Pierzynski, 2005; Tiessen, 2008). Differing influences of humans could also account for these differences in soil chemistry (Tiessen, 2008), as both Anacapa and Santa Barbara Islands were historically inhabited by the

Chumash and Tongva people, respectively (Perry et al., 2019; Rick, 2006), and share a more recent history of livestock ranching (Rick et al., 2014). This latter human presence resulted in overgrazing, and the introduction of non-native species, which led to dramatic vegetation shifts and erosion, both of which can affect soil quality and nutrient retention (Rick et al., 2014; Tiessen, 2008). It is not certain; however, if the histories of human presence of the islands differ enough to result in such drastically different soil profiles. Further, both islands host colonies of other species of nesting seabirds and guano deposition from other seabirds that nest on the islands could contribute to variation in soil chemistry, as excreta from different species can vary in total phosphorus content (Carter et al., 1992; Otero et al., 2015). As Western Gulls are the most abundant nesting seabird on the islands (excluding seabirds that nest on cliff faces and thus do not contribute guano to island soil); it is not likely that other seabirds may be driving these differences in soil nutrient profiles; however, future studies should consider inputs by other seabirds (Carter et al., 1992; National Park Service, 2016).

As in much of conservation biology, this study is limited by lack of baseline knowledge. In this case we lack historical baselines of Western Gull population abundance. Without such data, it is impossible to know whether anthropogenic subsidies are buffering the effects of depleted natural food sources and maintaining historical levels of nutrient inputs to the islands, or whether they are creating an artificially subsidized nutrient budget. However, the implications are clear for other systems where long-term population trends of commensal species are better established. For example, on Mediterranean and Atlantic Islands, substantial increases in seabird populations subsidized by anthropogenic foraging have resulted in a greater influx of nutrients to terrestrial habitats, which has led to plant species turnover and persistence of invasive species (Baumberger et al., 2012; Otero et al., 2015; Vidal et al., 2000). Additionally, anthropogenic diet subsidies may not only alter the amount of bird-derived deposition to an island, but also the quality of the guano itself. As previously described, a shift towards a more urbanized diets could lead to increased nitrogen content and reduced phosphorus in guano deposited on nesting islands. Such shifts towards increased nitrogen content have resulted in increased biomass of invasive plants in other systems (Fenn et al., 2010; Gould and Fletcher, 1978; Portnoy, 1990; Vallano et al., 2012). Restoring native plant communities has been an extensive ongoing effort on the Channel Islands (Adams et al., 2009; Jacques et al., 2005); thus, any dramatic increases in nitrogen inputs will be important for ongoing management efforts.

This study has focused only on the effects of these commensal birds on nutrient budgets; however, it is likely that these birds vector many other potentially dangerous biotic and abiotic items to these protected systems. By frequenting urban areas, and more specifically landfills, gulls can concentrate contaminants, microplastics, and introduce foreign microbes to these protected areas, such as the Channel Islands National Park, in addition to contaminating watersheds and beaches frequented by humans (Cockerham et al., 2019; Converse et al., 2012; Dolejska et al., 2007; Provencher et al., 2018). Finally, all of these effects are likely to extend beyond the island's terrestrial ecosystem. While conducting our work, we observed that many gulls defecate shortly after taking flight, which, in cases where nests are located close to the shoreline, would result in guano deposition along the intertidal and not on the island itself. Like terrestrial ecosystems, bird-derived nutrient inputs can also play an important role in shaping intertidal communities (Wootton, 1991).

Our research highlights the importance of the large shadow that human activity can cast on nutrient dynamics of even seemingly isolated and protected ecosystems. Given whole scale ecosystem change known to occur by loss of animal vectored subsidies, this work argues for more focus on potential ecosystem scale effects of animal vectored anthropogenic subsidies into wild spaces. In areas where generalist animals are foraging in urban areas, future research should explore whether similar impacts due to anthropogenic foraging are already occurring, particularly in areas where considerable effort has been dedicated to conservation. For example, in these study sites – Anacapa and Santa Barbara Islands – restoration and preservation of wilderness is a priority, it is important to clarify how these anthropogenic subsidies are altering these sensitive ecosystems (National Park Service, 2017).

Wildlife that exploit anthropogenic food sources can link urban and human modified areas with even remote and relatively undisturbed areas. As the human footprint continues to expand, it is becoming increasingly clear that no system is out of the reach of human influence. Thus, continuing to understand how urban foraging can affect not only the species feeding on anthropogenic diets, but also the ecosystems they inhabit, is essential for managing ecosystems in the Anthropocene.

Data availability: Data and code for this project are available at: https://datadryad.org/stash/share/bwF3rgUbnbaSVWod8OHlRPzhL6e4V5SLhOs9t_UoM7A.

Acknowledgements: This study was conducted on unceded territories of the Chumash and Tongva people. We thank Jim Howard and David Mazurkiewicz and the rest of the Channel Islands National Park Service staff and crew for their guidance and with their facilitation of fieldwork. Thank you to Andrea Jorgensen who provided help with fieldwork logistics. Caroline Owens, Anna Burrows, and Ben Boyce assisted with fieldwork. Thank you to Douglas McCauley and the McCauley lab for feedback on the manuscript. ASG was supported by the NSF GRFP, the UCSB Doctoral Fellowship, and Audubon Sea & Sage Society. HSY was supported by a UCSB Faculty Grant. All gull sampling and handling was done in accordance with UCSB IACUC protocol #880

Author contributions: Guerra AS[1], Bui A[1], Klope M[1], Orr DA[1,2], Shaffer SA[3], Young HS[1]. ASG and HSY conceived idea and designed methodology, ASG, AB and HSY received funding for this project, ASG, AB, MK, DAO, and HSY collected data for this project, ASG

and SAS analyzed the data, ASG led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

[1] Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93101.
[2] USDA Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR 97720
[3] Department of Biological Sciences, San Jose State University, San Jose, CA 95192-0100

CHAPTER 3. Shoaling behavior of coral reef fishes varies between two islands with different predator abundance

3.1 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 on two islands whose predator populations face differing fishing intensities. We compared the tendency to shoal for three fish species between two 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, two behaviors closely linked with shoaling, could affect the functioning of these vulnerable ecosystems.

3.2 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 (Estes et al., 2011; Heithaus et al., 2008; Pacoureau et al., 2021). Increasingly, there has been interest in documenting not only the direct effects caused by predator removal, but the indirect effects their removal might have on the foraging behavior of their prey (Heithaus et al., 2008; Madin et al., 2016; McCauley et al., 2010). 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 and accessing food sources, and finding potential mates (Foster, 1985; Krause and Ruxton, 2002; Pitcher, 1986). However, this behavior often comes at a cost of increased competition within members of a group (Krause and 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 (Helfman, 1984; Huizinga et al., 2009; Kozak and Boughman, 2012; Magurran et al., 1992; Seghers, 1974). Yet, these shifts in fish schooling and shoaling behavior due to changes in predation pressure remain understudied in natural experiments (Herbert-Read, 2017; Seghers and Magurran, 1994), 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 (Friedlander and DeMartini, 2002; Jackson et al., 2001; Sandin et al., 2008; Stevenson et al., 2006). As a result, lower-trophic level fish are now experiencing relaxed predation pressure by natural predators, altering predation risk (Friedlander and 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 (Davis et al., 2017; Elizabeth M. P. Madin et al., 2010; McCauley et al., 2010). 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; Crook, 1999a, 1999b; Hobson, 1979; Robertson et al., 1976).

In the tropical Pacific Ocean, the islands of Moorea (French Polynesia) and Palmyra Atoll (USA), support different levels of fishing and natural predator abundances (Davis et al., 2017; Sandin et al., 2008) 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 two stages: first by observing the proportion of fish found in shoals for three herbivorous reef fish species, and then by focusing on the movement and grazing behavior of shoaling and solitary fish of one focal species (Table 3). We compared the proportion of fish found in shoals across both islands for *Acanthurus triostegus* (Acanthuridae), an herbivorous surgeonfish that exhibits solitary foraging behavior and also forms roving shoals, and is not fished on either island *Chlorurus spilurus* (Scaridae), an herbivorous parrotfish that exhibits solitary foraging behavior and also forms shoals, and is fished on Moorea; and *Mulloidicthys flavolineatus* (Mullidae), an invertivorous goatfish that forms shoals in addition to being observed engaging in solitary foraging behavior, and is fished on Moorea (Barlow, 1974; Crook, 1999b; Johannes and Hviding, 2000; Kolasinski et al., 2009; Randall, 1961; Rassweiler et al., 2020b; Robertson et al., 1976). For the most frequently encountered of the three species, *A. triostegus,* we investigated differences in distance travelled, area covered, and time spent grazing for shoaling and solitary fish between the two islands.

Table 3. Experimental system framework for observations of shoaling behavior on 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* *Mulloidicthys flavolineatus*	counted every individual observed and noted 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

3.3 METHODS

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 currently supports healthy and stable coral reef predator populations (Bradley et al., 2017; Zgliczynski and Sandin, 2017). Palmyra Atoll is currently protected as a U.S. National Wildlife Refuge. Alternatively, the reefs of Moorea have experienced higher fishing pressures throughout its history (Leenhardt et al., 2012; Rassweiler et al., 2020b; Walker and Robinson, 2009) and host predator populations and have less than a quarter of the biomass found on Palmyra Atoll (Davis et al., 2017). Because these two 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 other biophysical attributes, this well-established, striking contrast in predator abundances has proven valuable to study other direct effects of coral reef predator removal (Davis et al., 2017). Further, we chose particular backreef and lagoonal habitats for this study, that were as similar as possible between the two islands in terms of water depth, benthic habitat, and wave exposure, however, it is impossible to control for all attributes. Thus, 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.

Shoaling behavior

We compared prevalence of shoaling behavior, number of shoals, and shoal sizes for *A. triostegus, C. spilurus,* and *M. flavolineatus* across two islands with differing predator abundances (Table 3).

Surveys

We conducted 30-min roving diver surveys (Rassweiler et al., 2020a; Schmitt et al., 2002) to compare the *prevalence of shoaling behavior* across both islands (11 surveys on

Moorea and 14 surveys on Palmyra Atoll). All surveys were conducted by the same observer (ASG) between the hours of 0930 and 1530. The observer snorkeled in a haphazard, but non-recurring pattern for 30 minutes and recorded any focal species individuals observed. For each of the three species, we counted every individual and assessed whether the fish were in a shoal (and noted shoal size) or solitary. Shoal sizes were measured to 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 below) were conducted at four sites on the backreef of Palmyra Atoll and four sites on the backreef of Moorea (Fig A3). 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 three fish species can differ: *A. triostegus* and *C. spilurus* exhibit polarized group swimming behavior and form roving shoals, whereas *M. flavolineatus* form loose stationary aggregation during the daytime (Pitcher, 1983). For the purpose of this study, *shoaling* refers to three 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 (Norris and Schilt, 1988; Parrish and Turchin, 1997; Pitcher, 1983), 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 (Choat and Bellwood, 1985; Eurich et al., 2018; Foster, 1985). Thus, to control for the potential of variation in the numbers of territorial herbivores to affect shoaling behavior differentially among islands, we also counted the absolute abundance of these territorial herbivores (i.e. *Acanthurus lineatus, Acanthurus nigricans,* and *Stegastes nigricans* on Palmyra Atoll and *Acanthurus nigrofuscus* and *Stegastes nigricans* on Moorea).

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; R Core Team, 2020; RStudio Team, 2020; Wickham et al., 2019) 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 A6). Best-fit models were selected according to small-samples corrected AIC (AICc) 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 three species.

***Acanthurus triostegus* behavioral observations**

For the most frequently encountered of the three 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 3).

Behavioral observations

We conducted 30-60min focal follows on *A. triostegus* to assess the proportion of time spent grazing, the distance traveled, and the area covered via calculation of a 95% kernel utilization distribution (KUD). Snorkeling observers (four observers on Palmyra Atoll, two on Moorea, lead observer (ASG) was present on both islands) followed solitary or shoaling *A. triostegus* while towing a GPS device that recorded location every 60s. Initial follows were conducted at both islands to assess 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 60s, the observer would note shoal size (if applicable) and note fish behavior: whether the focal individual(s) was 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 position at time of observation. Observations on shoals were done by recording behavioral information based on the behavior of 50% or more of the individuals in the shoal (e.g., shoal was recorded as *grazing* if at least half of the shoal was in a nose-down position at the 60s mark). If a shoal was widely dispersed or in a line formation, the observer followed the last 1/3 for 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 were able to search for the fish for up to two minutes. If after two minutes the fish were not located, the focal follow was terminated.

Although it remains to be conclusively determined how fixed the associations are between solitary and shoaling life modes of individuals, our preliminary data suggests that these behavior modes may remain fixed for at least moderate durations. Using natural variation in *A. triostegus* coloration (Fig A4), 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-day observation period (Text A1). 21 months later, two individuals who previously showed fidelity to small groups were resighted exhibiting the same behavior, and two shoaling individuals were also resighted in large shoals (Fig A5, Text A1).

For behavioral follow analysis, we assigned social behavior to focal fish according to the mode of the entire follow duration. We used *mode* (instead of average) of shoal size throughout the follow to assign social behavior throughout a follow since solitary fish occasionally would pair up with another fish for a few minutes before separating; thus, *mode* was determined to be a more accurate descriptor of behavioral follow shoal size than mean shoal size (Fig A3). Fish were thus classified as solitary (mode = 1) or shoaling (mode > 25 fish). The 25 fish cut-off was used as frequent splitting of smaller shoals often resulted in behavioral observations being terminated before 30min.

Analysis

We found a significant difference in time spent in a grazing position and distance travelled in the first five minutes of observation, relative to subsequent five-minute bins, suggesting the presence of an observer effect resulting in increased distance travelled and reduced grazing. Therefore, we removed the first five minutes of every follow. Fish observations had different durations (30-60min), 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 30min (total of 25min excluding initial 5min).

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 within 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 response variables, 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 corrected AIC (AICc) 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* on islands with high and low predator abundance. We specified two full models using the *lme4* package as above, using distance traveled (meters travelled per minute of follow) and 25-min 95% KUD as a response variables. Social status (shoaling or solitary) and predator abundance (island) were included as fixed effects, and site, observer, and time of day were included as random effects. Best-fit models were selected according to AICc, and we did pairwise comparisons of marginal means using the *emmeans* package (Lenth et al., 2021).

3.4 RESULTS

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 *A. triostegus* shoaling behavior was lower at the low predator abundance site, and we found a similar pattern for *M. flavolineatus*, but no significant differences for *C. spilurus*.

Acanthurus triostegus – The prevalence of shoaling behavior for *A. triostegus* was best predicted by a model that includes predator abundance (island), total abundance, and their interaction as a fixed effects, with a higher proportion of fish in shoals occurring on the island with high predator abundance (Fig 4a, Table 4). The model of the interaction of abundance and island suggests this interaction is primarily present on the island with lowest predator abundance. Prevalence of shoaling behavior increases with increasing abundance, but not on the island with high predator abundance (Fig A6). The number of shoals, abundance, and shoal sizes were also significantly different among islands, with more shoals and greater abundance at the high predator abundance island, but larger shoal sizes at the low predator abundance island (Fig 4b-d, Table A7).

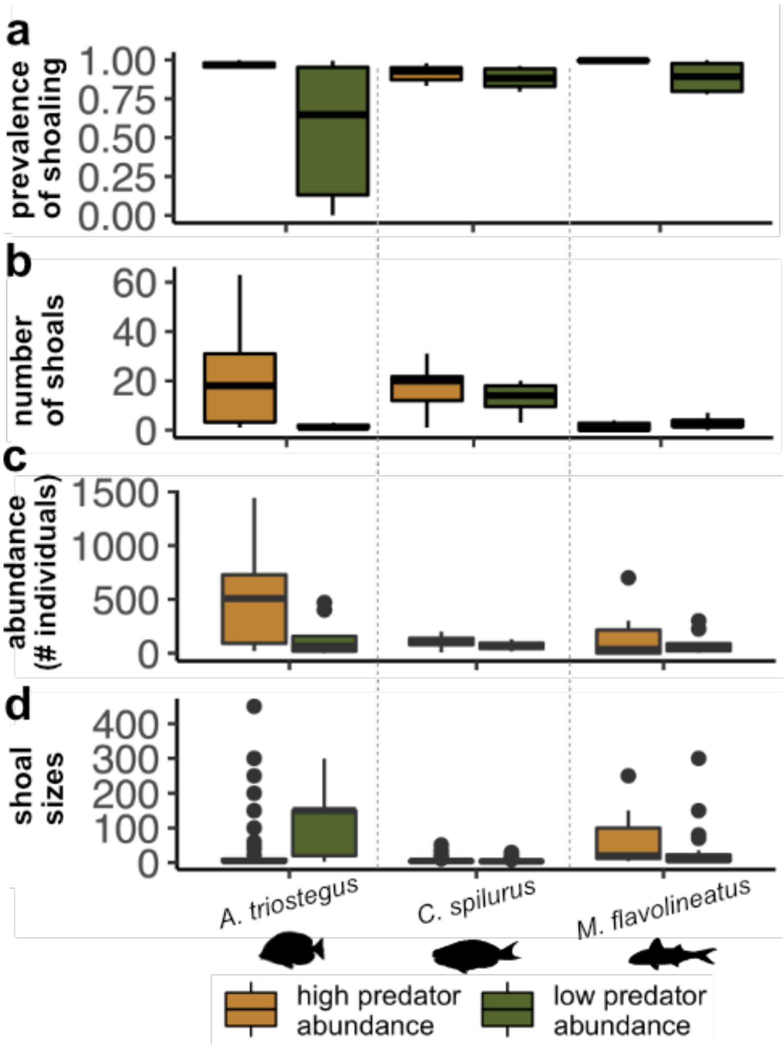

Figure 4. Boxplot of prevalence of shoaling behavior (per survey) (a), number of shoals (b), abundance of individuals per survey (c), and shoal sizes observed (d) for *Acanthurus triostegus, Chlorurus spilurus,* and *Mulloidichthys flavolineatus* on a high predator abundance island (Palmyra Atoll) and low predator abundance island (Moorea).

Chlorurus spilurus – The best fit model for predicting prevalence of *C. spilurus* shoaling behavior included only the total abundance of *C. spilurus* (Fig 4a, Table 4). 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 one fish), and abundance and number of shoals were not significantly different (Table A7).

Mulloidichthys flavolineatus – The prevalence of *M. flavolineatus* shoaling behavior is best predicted by a null model with no fixed effects, suggesting neither social behavior nor island are important predictors of prevalence of shoaling behavior; however, the next two best fit models (ΔAICc < 2) also include total *M. flavolineatus* abundance and predator abundance as fixed effects (Fig 4a, Table 4, Table A8). Average shoal size was significantly different, with larger shoal sizes at the island with highest predator abundances, but abundance and the number of shoals was not significantly different across islands (Fig 4b-d, Table A7).

Table 4. Linear mixed model fit for prevalence of shoaling behavior

	Acanthurus triostegus			*Chlorurus spilurus*			*Mulloidicthys flavolineatus*		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	0.29	0.10	2.85	0.72	0.04	18.27	0.87	0.07	13.33
island (high predator abundance)	0.66	0.15	4.35	-	-	-	-	-	-
abundance	0.00	0	6.32	0.00	0	4.23	-	-	-
island* abundance	-0.00	0	-5.77	-	-	-	-	-	-
territorial herbivore abundance	-	-	-	-	-	-	-	-	-
Random effect	**variance**	**SD**		**variance**	**SD**		**variance**	**SD**	
site (within island)	0.03	0.18		0	0		0.01	0.07	

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. All follows were at least 25min in duration and the majority (69) were 55min in duration. Observations of shoaling fish were distributed across shoal sizes of 25-500 fish (Table A9).

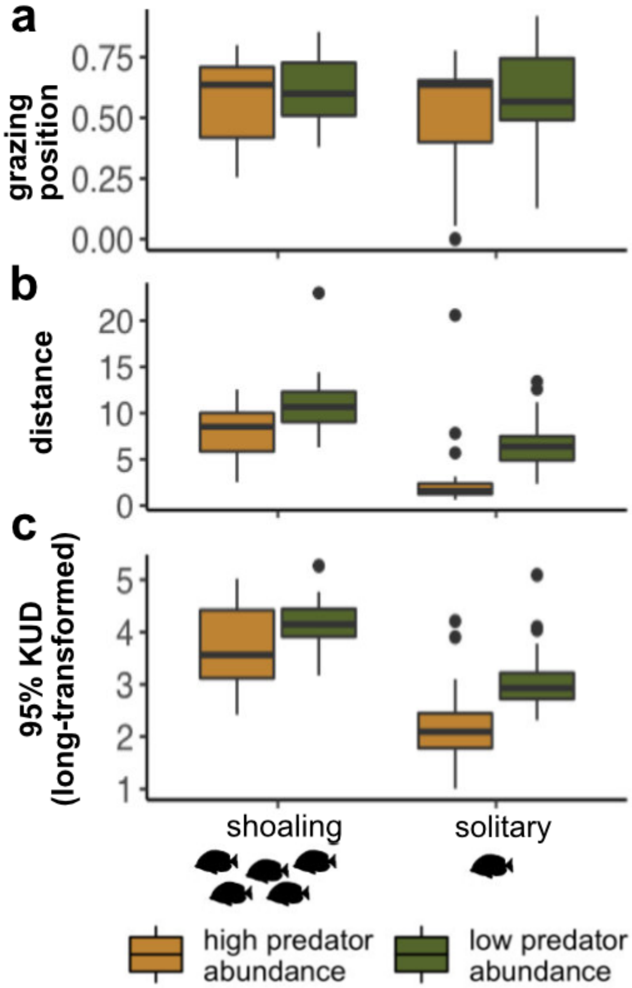

Figure 5. The proportion of time spent in grazing position (a), distance (measured in meters and standardized by minutes of observation) (b), and 25-min 95% kernel utilization distribution (KUD) (c) of solitary and shoaling *Acanthurus triostegus* in a high predator abundance island (Palmyra Atoll) and a low predator abundance island (Moorea)

Time spent grazing for solitary fish is best predicted by a model that includes no fixed effects and only the random effects site and time of day (Fig 5a, Table 5). The next best-fit model (ΔAICc < 2) includes predator abundance (island) as a predictor (Table A10). Similarly, when considering only shoals of *A. triostegus,* the best fit model for time spent in a grazing position includes only the random effects site and time of day (Fig 5a, Table 5). The next best-fit model (ΔAICc < 2) includes shoal size as a predictor (Table A10).

Table 5. Linear mixed model fit for explaining time spent in grazing position for shoaling and solitary *Acanthurus triostegus* on Palmyra Atoll (high predator abundance) and Moorea (low predator abundance)

	solitary			shoals		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	0.54	0.06	8.63	0.48	0.08	5.99
island (high predator abundance)	-	-	-	-	-	-
shoal size†				-	-	-
island*shoal size†				-	-	-
Random effect	**variance**	**SD**		**variance**	**SD**	
time of day	0.01	0.07		0.01	0.07	
site (within island)	0.02	0.14		0.00	0.00	
observer	0.00	0.00		0.02	0.139	

† fit in model for shoals only

Distance traveled (in meters, standardized by observation minute) for shoaling and solitary fish is best predicted by a model that includes both island and social behavior (shoaling or solitary) as fixed effects (Fig 5b, Table 6). This best fit model predicts that in the high predator abundance island, *A. triostegus* travel 3.2m less per minute than those in the low predator abundance island, and that solitary fish travel 4.5m less per minute than shoaling fish (Fig 5b, Table 6). Pairwise comparisons of distance traveled suggest there is a difference between marginal means across all comparisons of shoaling and solitary fish on the high and low predator abundance islands, except for the difference in the marginal means of distance traveled by solitary fish on the low predator abundance island and shoals in the high predator abundance island ($p = 0.67$, Table 7).

Table 6. Linear mixed model fit for shoaling and solitary *Acanthurus triostegus* on Palmyra Atoll (high predator abundance) and Moorea (low predator abundance)

	distance travelled			95% KUD		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	11.06	0.64	17.32	4.28	0.18	23.88
island (high predator abundance)	-4.45	0.72	-6.21	-0.56	0.2	-2.81
social behavior (solitary)	-3.20	0.73	-4.36	-1.29	0.14	-9.13
island*social behavior	-	-	-	-	-	-
Random effect	**variance**	**SD**		**variance**	**SD**	
time of day	0.00	0.00		0.00	0.00	
site (within island)	0.00	0.00		0.56	0.24	
observer	0.00	0.00		0.01	0.10	

95% KUD for 25-min follows is best predicted by a model that includes island and social status (shoaling or solitary) as fixed effects (Fig 5c, Table 6). The next best-fit model (ΔAICc < 2) includes predator abundance and social behavior as predictors (Table A11). The best-fit model suggests fish in 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 on both islands (Fig 5c, Table 6). There is a difference between marginal means across all comparisons of shoaling and solitary fish on the high and low predator abundance islands, except for between shoaling fish on each island ($p = 0.11$, Table 7) and between solitary fish on each island ($p = 0.11$, Table 7).

Table 7. Pairwise marginal means comparisons of distance travelled and 95% KUD

	p - value	
comparisons	**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

if the comparison was significantly different, the subscript indicates which of the compared groups had the highest distance travelled (^{d}) or 95% KUD (^{k})

3.5 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 predators' effects 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 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 *A. triostegus* (surgeonfish) and *M. flavolineatus* (goatfish) in our lower predator abundance sites. Regarding *A. triostegus* behavior specifically, the effect of island predator abundance on shoaling behavior may be two-tiered: a lower predator abundance 1) results in an overall smaller 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 on a high predator abundance island.

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 (Huizinga et al., 2009; Magurran and Pitcher, 1987; Seghers, 1974). Interestingly, we found *A. triostegus* abundance to be a significant predictor of prevalence of shoaling behavior in this species, but this effect was only present on the island with lower predator abundance (Table 4, Fig A6). 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 in the low predator abundance island. Surgeonfish are known to use shoaling to invade and graze down other herbivorous fishes' territories (Foster, 1985; Peter J. 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 4), we hypothesize that in the high predator abundance island, a smaller shoal size may represent a trade-off between predator avoidance and minimizing competition with conspecifics (Buckel and 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, on 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 and Madin, 2011), as well as on *A. triostegus* themselves (pers obs). Thus, predatory attempts by piscivores may split large shoals frequently on 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 and Krause, 2005; Ioannou and 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 two 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 *C. spilurus*. The differing life histories between the species likely explain this difference in shoaling behavior patterns. *Mulloidicthys flavolineatus* shoals are relatively stationary during the day and disperse for nocturnal foraging (Hobson, 1968; Holland et al., 1993; Uiblein, 1991). Thus, with reduced movement, the conspicuous nature of a shoal is reduced (although a shoal still remains more conspicuous than a solitary fish) (Lima and Dill, 2011; Turner and Pitcher, 1986), yet will maintain the added advantage of dilution and confusion effects to reduce predation risk (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 on the low predator abundance island (Moorea), where this species is also a direct target of fishing (Rassweiler et al., 2020b), 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* on 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, Gaines, & Warner, 2010). As such, the strongest drivers for maintaining specific social behavior may not include predator avoidance. The possibility also remains that predation risk affects 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 and 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., 2020b).

Although the two 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 with finding locations where predator differences are large, but resource availability and configuration are similar.

Acanthurus triostegus behavioral observations

Our observations suggest that shoaling *A. triostegus* and solitary individuals spend similar amounts of time grazing on both islands, and both shoaling and solitary fish travel more on the low predator abundance island, with a more pronounced effect on the travel distance of solitary fish (Fig 5, Table 5-7).

We found similar amounts of time spent in grazing positions for both shoaling and solitary fish at both islands despite differing predator abundances (Figure 5, Table 5). Other studies have found differences in feeding rates by herbivores between the two 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 on the high predator abundance island were not captured in our surveys (Hobson, 1973; Lima and 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 on the low predator abundance island relative to their counterparts on the high predator abundance island. A decrease in excursion distance with increasing predation risk has been found for various fish species (Lima and Dill, 2011; Elizabeth M. P. Madin et al., 2010; Orpwood et al., 2008), and has been postulated to result from mechanisms such as moving prey being more easily detected by predators (Dill and Fraser, 1984). This study suggests that similar mechanisms may play a role of movement behavior in shoaling fish. Notably, we found that solitary fish on the low predator abundance island travelled distances similar to shoals on the high predator abundance island, and these distances were much greater than the distances travelled by solitary fish on the high predator abundance island (Fig 5b, Table 6), 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 and 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* on 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 less 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 with 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 area 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 and Dill, 2011), 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 on 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, vigilance, and escape responses (Goetze et al., 2017; Januchowski-Hartley et al., 2011). In other systems and theoretical studies, fishing has been found to alter shoaling behavior (Guerra et al., 2020; Sbragaglia et al., 2021a, 2021b) and shoaling behavior has been found to play an important role in mediating the effects of fishing on vigilance and escape behavior (Samia et al., 2019; Stankowich and Blumstein, 2005). As previously discussed, *C. spilurus* and *M. flavolineatus* experience targeted fishing on Moorea (Rassweiler et al., 2020b). Although *A. triostegus* is not directly targeted by fisheries on Moorea, similar species on Moorea have been observed to shift their behavior despite not facing direct fishing pressure (Rassweiler et al., 2020b; Tran et al., 2016). 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 two 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 predator abundance, comparisons of behavior within island that contain marked gradients in predator abundance (e.g. inside and outside large protected areas), and potentially some manipulative experiments (e.g. increasing fish 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 a 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.

Data availability: Data and code are available at doi: 10.6073/pasta/678b0008e9906e402bcccde906fbbf25

Acknowledgements: We thank the Palmyra Atoll National Wildlife Refuge, Palmyra Atoll Research Station, and CRIOBE staff for their invaluable support. Thank you to K Davis, P Carlson, K Munsterman, M Morse, E Jahn, F Bertucci, and T White for fieldwork assistance. Thanks to the McCauley Lab, Caselle Lab, and Gaines Lab for support and feedback. ASG was funded by the NSF GRFP, UC Santa Barbara, and UCSB Worster Award. We are grateful for the support of the Marisla Foundation for funding the Palmyra research. This is Palmyra Atoll Research Consortium publication #PARC-160.

Author contributions: Ana Sofia Guerra[1], Douglas J. McCauley[1,2], David Lecchini[3,4], Jennifer E. Caselle[2]

ASG conceived idea. ASG, DJM and JEC developed methodology. ASG, DJM, JEC and DL acquired funding for the study. ASG and JEC collected data. ASG analyzed data. ASG led writing of the manuscript. All authors contributed to drafts and approved final draft for publication.

[1] Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93101.
[2] Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93101
[3] PSL University, EPHE-UPVD-CNRS, UAR 3278 CRIOBE, Moorea, French Polynesia
[4] Laboratoire d'Excellence "CORAIL", Paris, France.

CHAPTER 4. Diverse intraspecific differences between a shoaling and solitary coral reef fish

4.1 ABSTRACT

General variation in behavior within species can influence functioning of the ecosystems they inhabit; however, the role social behavior specifically may play in ecosystem function remains under-explored, despite the fact that many aggregating animals that play pivotal ecological roles. As a taxa that inhabits diverse and important marine and freshwater ecosystems, fish ecological function has received significant attention. On coral reefs, for example, considerable effort has been dedicated to understanding the ecological role of heavily fished herbivorous species which create suitable habitat for coral recruitment and mediate coral-macroalgae interactions through their grazing behavior. Many coral reef fish species provide potentially insightful models for exploring how social behavior shapes ecologically function because they exhibit radical intraspecific variation in sociality within a shared habitat.

Here, we provide an empirical exploration on how the ecological function of shoaling surgeonfish (*Acanthurus triostegus*) may differ from that of solitary conspecifics on two Pacific coral reefs using behavioral observations, stable isotope analysis, and macronutrient analysis of gut and fecal matter. We detected important differences in how the social mode of *A. triostegus* affected its spatial and feeding ecology, as well as that of other reef fish species. Specifically, we find increased distance traveled and area covered by shoaling fish relative to solitary *A. triostegus*. Additionally, shoaling *A. triostegus* primarily grazed within territories of other herbivorous fish and had piscivorous and non-piscivorous heterospecific fish associated with the shoal, while solitary did not have any such interactions with heterospecific fish.

Results from stable isotope and macronutrient analysis suggest that these social modes may be persistent and support our observation of grazing differences between shoaling and solitary fish. Our study suggests that social behavior of individuals may play an important and underappreciated role in mediating their ecological function.

4.2 INTRODUCTION

Shifts and individual variation in animal behavior can influence functioning of the ecosystems they inhabit. For example, herbivorous animals may shift their foraging habitat to avoid predation, which alters primary production, distribution of their food sources, and influences nutrient cycling (Dill et al., 2003; Heithaus et al., 2008; Stief and Hölker, 2006). Work exploring ecologically important behaviors has primarily focused on movement and habitat preference (Stief and Hölker, 2006; Wirsing et al., 2007), yet, another candidate behavior that has the potential to influence ecosystems is social behavior; i.e. whether members of a species tend to live and operate in groups or spend all or most of their time alone. Preliminary work suggests these differences in sociality may shape ecological outcomes. For example, seed dispersal by harvester ants varies depending on whether the ants are solitary or social foragers; consequently, plant community patterns differ in the foraging grounds of solitary and social ants (Avgar et al., 2008). Further, in the Great Lakes region of North America, when wolves form larger pack sizes, their moose kill rate increases (Post et al., 1999). This increased kill rate then influences moose abundance and cascades to reduced browsing and greater understory growth (Post et al., 1999).

As a taxa that inhabit many diverse and important marine and freshwater ecosystems, fish ecological function has received significant attention (Peter J. Mumby et al., 2006; Nash et al., 2013). On coral reefs, for example, considerable effort has been dedicated to understanding the ecological role of heavily fished herbivorous species such as parrotfish (Labridae) and surgeonfish (Acanthuridae), which create suitable habitat for coral recruitment and mediate coral-macroalgae interactions through their grazing behavior (Hughes et al., 2007; Peter J. Mumby et al., 2006) and provide nutrients through excretion (Allgeier et al., 2017; Burkepile et al., 2013). One aspect of fish behavior that remains understudied in the context of ecological function is shoaling and schooling behavior, despite many fish forming large roving shoals and that social behavior leads them to forage in ecologically unique ways (Foster, 1985). For example, on Caribbean reefs, solitary blue tang (*Acanthurus coeruleus*) primarily graze in undefended areas while shoaling blue tang often invade and graze down other herbivorous fishes' territories (Foster, 1985; Robertson et al., 1976). Additionally, shoaling parrotfish have been found to graze at faster rates when in shoals, creating more suitable habitat for coral growth (Welsh and Bellwood, 2012). Further, shoals of grunts that shelter around coral heads are important for creating nutrient hotspots of bioavailable nitrogen that can foster coral growth (Meyer et al., 1983; Shantz et al., 2015). Recent evidence suggests that some grouping behavior in fish, such as shoaling, could be vulnerable to change in a heavily fished ocean (Guerra et al., 2022, 2020; Sbragaglia et al., 2021a); thus, heightening the importance of understanding how social behavior shapes ecosystems.

Here, we examine in a field setting how the ecological function of shoaling surgeonfish may differ from that of solitary conspecifics. On two different tropical Pacific reefs, we compared foraging, movement, and interspecific interactions of shoaling and solitary convict surgeonfish (*Acanthurus triostegus*), an abundant herbivore that has a variable tendency to form large shoals (1000 fish), small and medium sized shoals that range from 5-500 individuals, or forage solitarily (Randall 1961, Barlow 1974, pers.obs). Using behavioral focal follows we recorded information on four parameters: 1) distance traveled, 2) area covered, 3) grazing invasions of fish territories, and 4) associations by heterospecific fish. From collected specimens of shoaling and solitary fish we measured data on two parameters: stable isotope values of muscle tissue, and macronutrient amounts present in stomach and fecal contents. This suite of measures provided strong evidence that sociality does indeed control important ecological outcomes.

4.3 METHODS

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 that forms part of the Society Islands archipelago in the South Pacific.

Acanthurus triostegus are abundant and exhibit both shoaling and solitary behavior on both islands (Guerra et al., 2022), providing an excellent opportunity to explore the ecology of shoaling behavior. Fish behavioral follows mentioned below were conducted at four sites on the backreef of Palmyra Atoll and four sites on the backreefs of Moorea, and fish collections were conducted at two backreefs sites on Moorea (Fig A7).

Behavioral observations

In order to measure foraging, distance traveled, 95% KUD (kernel utilization density) and interspecific interactions by shoaling and solitary *A. triostegus*, we conducted 30-60min focal follows on both islands. Snorkeling observers (four observers on Palmyra Atoll, two on Moorea, lead observer ASG was present at both islands to ensure methodological consistency and observer training) followed solitary or shoaling *A. triostegus* while towing a GPS device that recorded location every 60s. Initial follows were conducted at both islands to assess 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

60s, the observer would note shoal size (if applicable), presence or absence of grazing behavior, whether a grazing event constituted a territorial invasion, and associations with heterospecific fish species (Table 8, Table A12 for species list). Interspecific interactions that occurred during each observation minute were recorded, and described as either: "territorial invasions", where grazing behavior by *A. triostegus* elicited territorial defense behavior from heterospecific fish (Foster, 1985), "non-predatory association", where herbivorous heterospecific fish associated with the focal school or fish (Alevizon, 1976), or "predatory association", where the interaction involved a piscivore or invertivore (Madin and Madin, 2011; Ormond, 2009) (Table 8). Predatory and non-predatory associations were defined as a fish of a different species moving in the same direction and in close proximity to *A. triostegus* for five or more consecutive minutes. Observations on shoals were done by recording behavioral information based on the behavior of 50% or more of the individuals in the shoal (e.g., shoal was recorded as "grazing" if at least half of the shoal was in a grazing position at the 60s mark). If a shoal was widely dispersed or in a line formation, the observer followed the last 1/3 for 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 were able to search for the fish for up to two minutes. If after two minutes the fish were not located, the focal follow would be terminated.

Table 8. Experimental system framework for observations of solitary and shoaling behavior of *Acanthurus triostegus*

observation	**description**
distance traveled	Linear distance traveled (standardized per minute of follow)
area covered (95% KUD)	area covered in 25-min follow
grazing	proportion of follow spent in grazing position (measured every 60s)
territorial invasions	proportion of grazing events that were territory invasions
non-predatory fish associations	proportion of time non-predatory fish were associated
predatory fish associations	proportion of time predatory fish were associated

We found a significant difference in time spent in a grazing position and distance traveled in the first five minutes of observation, relative to subsequent five-minute bins, suggesting the presence of an observer effect; therefore, we removed the first five minutes of every follow. As fish observations had different durations (30-60min), distance traveled was standardized per minute (divided over total follow duration), and analysis of KUD was done by capping all follows at 30min (total of 25min excluding initial 5min), as total follow time may affect total space use. The proportion of time spent in grazing position, proportion of territorial invasions out of all grazing events, and associations by heterospecific fish (predatory and non-predatory) were calculated across all follow durations. We computed distance traveled using the *adehabitatLT* package in R and 95% utilization kernel using a biased random bridge method in the *adehabitatHR* package in R (version 4.0.3) (Calenge, 2006; R Core Team, 2020; RStudio Team, 2020).

Analysis

We used linear mixed effects models fit by maximum likelihood (ML) explain variations in distance traveled, 95% KUD, proportion of grazing events that were territorial invasions, and associations with predatory and non-predatory fish for *A. triostegus* on Palmyra Atoll and Moorea. We specified full models using the *nlme* package (Pinheiro et al., 2022) in R, using distance traveled (per min), 25-min 95% KUD, proportion of grazing events that were territorial invasions, associations with predatory fish, and associations with non-predatory fish as responsible variables; social status (shoaling or solitary) as a fixed effect; and site, island, and time of day as random effects, as it is well understood that time of day can affect surgeonfish behavior (Montgomery et al., 1989; Zemke-White et al., 2002). As our behavioral observations were done on shoals of different sizes, we also used linear mixed effects models fit by ML to explain variations in the response variables mentioned above for shoaling *A. triostegus* only. We specified full models as above using the *nlme* package, with the only difference being the inclusion of shoal size as a fixed effect instead of social status (shoaling or solitary). Best-fit models were selected according to small-samples corrected AIC (AICc) using the package *MuMIn* (Barton, 2020). For 95% KUD, the data distribution was non-normal, thus we transformed the data with a log normal transformation as suggested by Zuur, et al. (2009). As time spent in grazing position data were collected differently between shoaling and solitary fish (shoal-scale vs. individual), we did fit models to compare this metric between shoaling and solitary fish. All computations were conducted using R studio and the *tidyverse* package (RStudio Team, 2020; Wickham et al., 2019).

Fish sampling

In order to directly test whether any differences in foraging and movement behavior that were detected between shoaling and solitary *A. triostegus* affected their diet and trophic ecology, we collected 100 individuals (25 shoaling and 25 solitary from two different sites in Moorea only; Fig A7, sites P and H) to compare muscle tissue stable isotope values and assess nutritional quality of stomach contents and fecal matter.

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 moderate durations. Using natural variation in *A. triostegus* coloration (Fig A4 & A5), we found that at least a small number of readily identifiable 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-day observation period (Text A1). Over 21 months later, we resighted two individuals showing fidelity to small groups exhibiting the same behavior, and two shoaling individuals in large shoals (Text A1).

We sampled all shoaling fish from shoals of 50 individuals or larger. All fish were collected between 1000-1600h, to ensure the fish had been feeding for sufficient time to have contents in their stomach (gut throughput time data from congeners in Polunin et al. (1995). Following collection, we kept fish on ice for a maximum of three hours before processing. During processing, we recorded body morphometrics (standard length, wet weight), and sampled muscle tissue for stable isotope analysis. We also removed and weighed the gut, and dissected and stored stomach contents and feces (determined as contents in terminal 1cm of intestine) for each fish.

Stable isotope analysis

We conducted stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ isotope ratios to explore potential foraging differences between shoaling and solitary *A. triostegus*. Stable isotopes can be useful indicators of diet over longer time-periods than those available from stomach content analysis (Matley et al., 2016). Analysis of isotopic signatures have been successfully used to determine differences in dietary and trophic niche between coral reef fish species and individuals within a species (Eurich et al., 2019). We used isotopic signatures from muscle tissue to infer *A. triostegus* diet, as the integration rate for fish muscle tissue is found to be reliable over long periods of time (Matley et al., 2016). Prior to isotopic analysis, muscle tissue was lyophilized for 48h, homogenized, and ~1.3 mg were loaded into tin capsules which were sent to the University of California, Davis Stable Isotope Facility for analysis. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

We created isotopic biplots ($\delta^{13}C$ and $\delta^{15}N$) to visualize the differences in isotopic space and used linear models to explain variations in nitrogen and carbon stable isotope values for shoaling and solitary *A. triostegus* on Moorea. We specified full models using the *nlme* package (Pinheiro et al., 2022) in R, using $\delta^{15}N$ and $\delta^{13}C$ as response variables; and social status (shoaling or solitary), site, and fish size (standard length) as predictors. Best-fit models were selected according to small-samples corrected AIC (AICc) using the package *MuMIn* (Barton, 2020). Additionally, we generated Bayesian standard ellipses (40% confidence level) for each social behavior (shoaling or solitary) and backreef site using the SIBER package in R to estimate isotopic niche space (Jackson et al., 2011; R Core Team, 2020). We compared the size of the ellipses by fitting Bayesian models adjusted for small sample sizes (SEAc) and calculated overlap in ellipse area between the two sites and social behaviors, which can be used to determine overlap in diets and niche space (Eurich et al., 2019). We considered a shared overlap of >60% to be significant shared niche space as described in Schoener (1968) and Eurich et al. (2019).

Macronutrient analysis

We selected a subset of 38 fish based on the results of the stable isotope analysis for analyzing stomach contents and fecal matter macronutrients. As $\delta^{15}N$ values for shoaling and solitary fish were significantly different (as discussed below), we elected to analyze the stomach contents of 19 of the shoaling fish with the lowest $\delta^{15}N$ values and 19 of the solitary fish with the highest $\delta^{15}N$ values. By selecting these most isotopically divergent individuals, we hoped to characterize with greater clarity any macronutrient differences in diet and fecal content that may occur between these behavior modes.

Stomach contents and feces were analyzed for moisture, protein, carbohydrate, lipid, and ash content to the nearest 0.00001 g (Mettler Toledo MS105DU). We first freeze-dried samples in a lyophilizer for 36 h to remove and measure water content. We then manually homogenized each sample with a conical glass homogenizing pestle and measured 10 mg of sample into homogenizing 2 ml screw cap vials for further homogenization for protein analysis. We diluted these aliquots with milliQ water with a dilution factor of 100 and homogenized the samples using 10 mg 0.5 zirconium oxide beads at 6 m/s for four 30 s cycles (Fisher Brand Bead Mill 24). We stored the homogenized aliquots and the remainder of the sample at -20°C until further use. To measure total protein, we thawed the homogenate and precipitated the protein from the sample with bovine albumin serum (BSA) standard and 72% trichloroacetic acid (TCA), removed the supernatant, and then followed a microplate BCA assay protocol (Thermoscientific Pierce BCA Kit) and measured absorbance at 562 nm in triplicate (Mann and Gallager, 1985). We used standard curves with R2 > 0.98. For lipids, we followed a modified micro version of the Folch method (Folch et al., 1957; Johnson et al., 2017; Mann and Gallager, 1985). Briefly, we measured 5 - 20 mg of sample into solvent washed test tubes in duplicate, added 100 ul water and 1.5 ml chloroform : methanol (1:2), incubated at 4°C for 10 min, and centrifuged (4000 rpm, 5 min). We removed the supernatant and re-extracted the remaining sample with 1.5 ml chloroform:methanol (2:1) and pooled the supernatants. Finally, we added 950 ul NaCl (0.7%), incubated the mixture at 4°C for 30 min, centrifuged, quantified the volume in the lower phase, and added 1 ml of the lower phase to a pre-weighed aluminum weigh boat. We dried the sample overnight, re-weighed the remaining lipid, and extrapolated the entire bottom layer volume for lipid content. To measure ash content, we pre-combusted aluminum weigh boats at 450°C for 6 h and pre-heated the samples in an oven at 100°C overnight to ensure full water loss. We then combusted pre-weighed samples in a muffle furnace for 6 h at 450°C and reweighed samples to measure ash content. Finally, we estimated total carbohydrate using a method commonly used for estimating carbohydrate content in food, as carbohydrates = 100 - proteins - lipids - ash, where variables are in % dry weight (Opstvedt et al., 2003; Rempel et al., 2022; Southgate, 1969).

We used linear models to explain variations in macronutrients for *A. triostegus* on Moorea. We specified full models using the *nlme* package (Pinheiro et al., 2022) in R, using percent dry matter of protein, carbohydrates, and lipids in stomach contents and feces as response variables; social status (shoaling or solitary), site, the interaction of social behavior and site, and fish size (standard length) as predictors. We selected best-fit models according to small-samples corrected AIC (AICc) using the package *MuMIn* (Barton 2020).

4.4 RESULTS

Behavioral observations

We conducted a total of 94 behavioral follows across both islands; 17 solitary and 19 shoaling fish follows on Palmyra Atoll, and 37 solitary and 21 shoaling fish follows on Moorea. All follows were at least 25min in duration and the majority (69) were 55min in duration. Observations of shoaling fish were distributed across shoal sizes of 25-500 fish.

Table 9. Best fit linear mixed models for explaining variations in distance traveled and 95% KUD for shoaling and solitary *Acanthurus triostegus*.

	distance traveled			95% KUD		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	9.46	1.66	5.69	3.96	0.30	13.37
social behavior (solitary)	-4.45	0.72	-6.18	-1.25	0.14	-8.88
Random effect	**variance**	**SD**		**variance**	**SD**	
time of day	0.00	0.00		0.00	0.00	
island	4.97	2.23		0.14	0.38	
site (within island)	0.00	0.00		0.06	0.25	

Distance traveled (in meters, standardized by observation minute) is best predicted by a model that includes social behavior (shoaling vs. solitary) as a fixed effect and predicts that solitary *A. triostegus* travel 4.5m less per minute than shoaling fish (Fig. 6a, Table 9). The best-fit model for predicting distance traveled by shoals did not include shoal size (Table A13). Similar to results for distance traveled, the 95% KUD for 25-min follows is best predicted by a model that includes social behavior (shoaling or solitary) as a fixed effect and suggests solitary fish cover less area than shoaling fish (Fig 6b, Table 9). The best-fit model for predicting 95% KUD by shoals did not include any fixed effects, but the next best-fit model included shoal size as a fixed effect (Table A13).

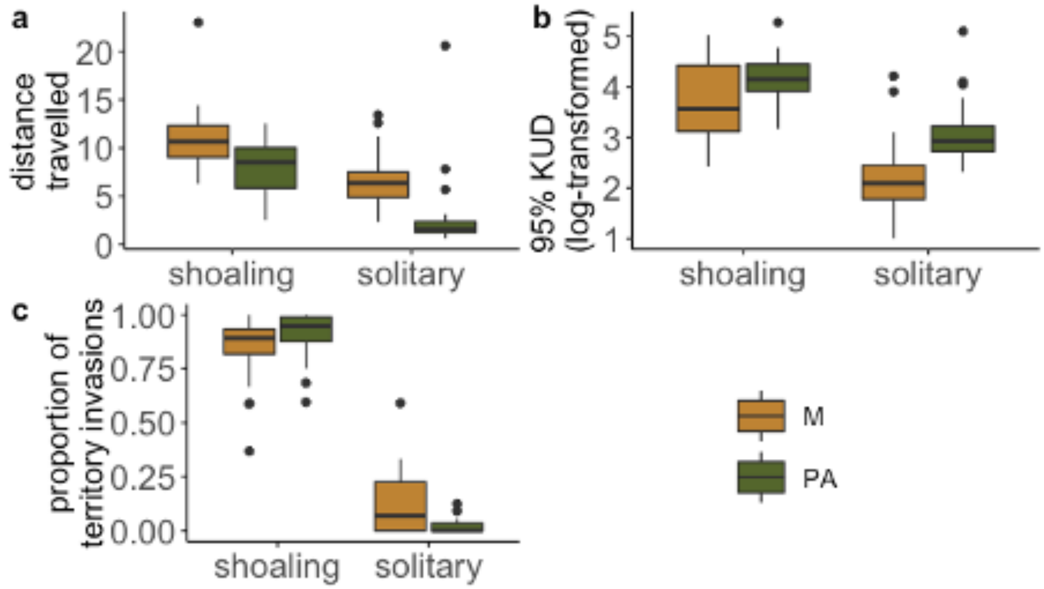

Figure 6. (a) Distance traveled (measured in meters and standardized by minutes of observation), (b) 25-min 95% kernel utilization distribution (KUD), (c) and proportion of grazing events that were territory invasions for solitary and shoaling *Acanthurus triostegus* on Palmyra Atoll (PA) and Moorea (M).

Mean proportion of time *A. triostegus* spent in a grazing position during an observational follow was 0.58 (PA)-0.62 (M) in a shoal and 0.51(PA)-0.60 (M) while solitary (Table A14). The proportion of grazing events that were invasions of a territory were 0.90 ± 0.12 (std. dev.) for shoals on Palmyra Atoll and 0.83 ± 0.16 for shoals on Moorea (Fig 6c, Table A14). For solitary fish, territorial invasions comprised only 0.02 ± 0.04 and 0.13 ± 0.14 of grazing events on Palmyra Atoll and Moorea, respectively (Table A14). The species whose territories were most commonly invaded were *Stegastes nigricans, Acanthurus lineatus, Acanthurus nigricans, Ctenochaetus striatus* on Palmyra Atoll and *Stegastes nigricans, Zebrasoma scopas, Acanthurus nigrofuscus, Ctenochaetus striatus* on Moorea. Invasions to *S. nigricans* algal gardens accounted for 0.49 ± 0.37 and 0.30 ± 0.29 of territorial invasions on Palmyra Atoll and Moorea, respectively. Proportion of grazing events that were territorial invasions is best predicted by a model that includes social behavior as a fixed effect, with invasions being more prevalent with fish in shoals (Table 10, Fig 6c).

Table 10. Best fit linear mixed models for explaining variations in territorial invasions, predatory fish associations, and non-predatory fish associations for shoaling and solitary *Acanthurus triostegus*

	territorial invasions			non-predatory fish			predatory fish		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	0.87	0.21	40.52	0.42	0.06	6.89	0.27	0.09	2.88
social behavior (solitary)	-0.77	0.03	-27.47	-0.41	0.05	-8.45	-0.24	0.04	-5.62
Random effect	**variance**	**SD**		**variance**	**SD**		**variance**	**SD**	
time of day	0.00	0.00		0.00	0.00		0.00	0.06	
island	0.00	0.00		0.00	0.07		0.01	0.11	
site (within island)	0.00	0.01		0.00	0.03		0.01	0.08	

Non-predatory heterospecific fish were associated with 95% (18/19) of all follows of *A. triostegus* shoals on Palmyra Atoll and 71% (15/21) on Moorea (Table A14; Fig 7). Species associated were *Acanthurus blochii, Acanthurus xanthoptherus, Chlorurus spilurus, Kyphosus* sp., *Mellycthis niger,* and *Scarus psittacus* on Palmyra Atoll and *Acanthurus guttatus, Cantherhinis dumerilii, Chlorurus spilurus, Ctenochaetus striatus,* and *Scarus psittacus* on Moorea. Non-predatory fish spent an average of 0.54 ± 0.35 proportion of the follow with shoals on Palmyra Atoll and 0.30 ± 0.32 on Moorea. No solitary fish had non-predatory fish associations on either island. Interspecific associations by non-predatory fish were best predicted by a model that includes social behavior as a fixed effect, with shoaling behavior increasing likelihood of the association (Table 10).

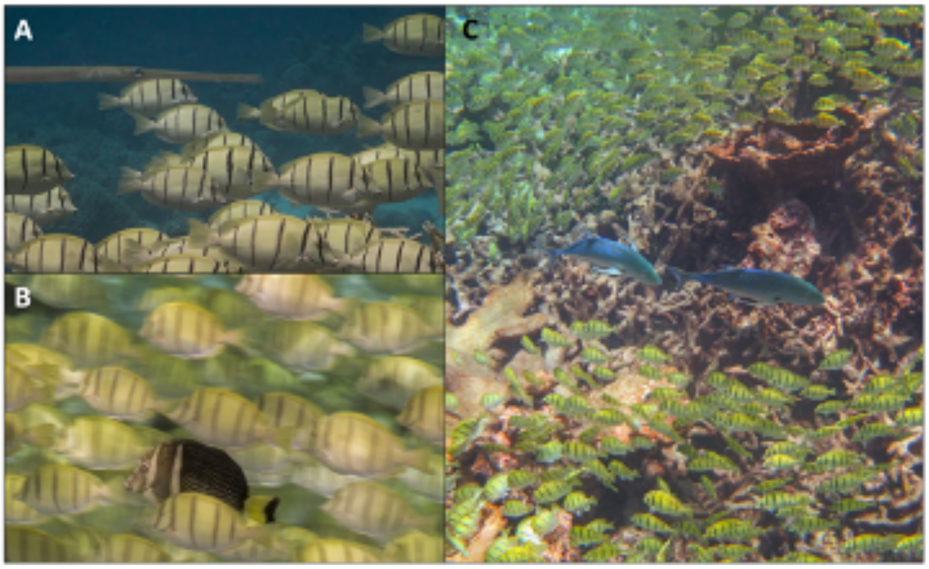

Figure 7. Heterospecific fish associated with *Acanthurus triostegus* shoals: A) *Fistularia commersonii* (carnivore, not predator of adult *A. triostegus*) on Moorea, B) *Acanthurus guttatus* (herbivore) on Moorea, and C) *Caranx melampygus* (carnivore, can predate *A. triostegus*) on Palmyra Atoll. Photographs by ASG.

Predatory fish were associated with all shoals (19/19) on Palmyra Atoll and 24% (5/21) on Moorea had a predatory fish associated with the shoal at some point during the follow (Fig 7). Primary species associated were *Aulostomus chinensis, Carcharhinus melampygus, Cephalopholis argus, Caranx melampygus*, and *Lutjanus bohar* on Palmyra Atoll and *Aulostomus chinensis, Caranx melampygus,* and *Fistularia commersoni* on Moorea. Predatory fish spent an average of 0.47 ± 0.28 proportion of the follow with shoals on Palmyra Atoll and 0.12 ± 0.27 on Moorea (Table A14). No solitary fish had non-predatory fish associations on either island. Interspecific associations by predatory fish were best predicted by a model that includes social behavior as a fixed effect, with shoaling behavior increasing likelihood of the association (Table 10).

Stable isotope analysis

We collected 100 *A. triostegus* for stable isotope analysis from two sites on Moorea (P and H on the map in Fig A7; 25 shoaling and 25 solitary fish from each site). Shoal sizes ranged from 50 – 500 individuals. Average fish size (standard length) was not significantly different across sites and social behavior (Table A15, Fig A8).

The mean value for samples from shoaling fish were δ^{13}C: -12.42 ± 1.19, δ^{15}N: 6.63 ± 0.61 at site H and δ^{13}C: -12.36 ± 0.98, δ^{15}N: 6.63 ± 0.69 at site P (Fig 8a). For solitary fish, the mean value for samples from site H were δ^{13}C: -11.88 ± 0.91, δ^{15}N: 6.94 ± 0.38 and δ^{13}C: -12.48 ± 0.56, δ^{15}N: 7.01 ± 0.43 from site P (Fig 8a). δ^{15}N is best predicted by a model that includes social behavior and fish size (SL) (Table A16); however, this model result was primarily driven by one very small fish (SL<9cm) and one very large fish (SL>13.5cm) that were outliers in our size distribution (Fig A8). Excluding these two outliers, δ^{15}N is best predicted by a model that includes only social behavior (Table 11), with higher δ^{15}N values in solitary *A. triostegus*. δ^{13}C is best predicted by a model that includes site and fish size, and this best-fit model is maintained even with the exclusion of the two fish outliers (Table 11; Table A16). In this best-fit model, δ^{13}C values are lower at site P and decrease with decreasing fish size (Table 11).

Table 11. Best fit linear models for explaining variations in δ^{15}N and δ^{13}C stable isotope values of muscle tissue of shoaling and solitary *Acanthurus triostegus**

	δ^{15}N				**δ^{13}C**			
coefficient	**estimate**	**SE**	**t-value**	**p-value**	**estimate**	**SE**	**t-value**	**p-value**
intercept	6.64	0.07	90.29	0.00	-6.88	1.18	-5.82	0.00
social behavior (solitary)	0.33	0.1	3.23	0.002				
SL (cm)					-0.45	0.10	-4.42	0.00
site (P)					-0.41	0.16	-2.6	0.01

*these models do not include two size outlier fish

Samples from shoaling fish at both sites had a higher standard ellipse area (P:1.85, H: 2.04) than solitary fish (P:0.57, H:0.89). Shoaling fish had a significant overlap (77%) in shared isotopic niche space across the two sites (Fig 8b). Solitary fish had a non-significant overlap of 27% in isotopic niche space across the two sites (Fig 8b). Overlap in isotopic niche space between shoaling and solitary fish was non-significant across the two sites: at site P, shoaling and solitary fish had an overlap in isotopic niche space of 26% and of 16% at site H (Fig 8b).

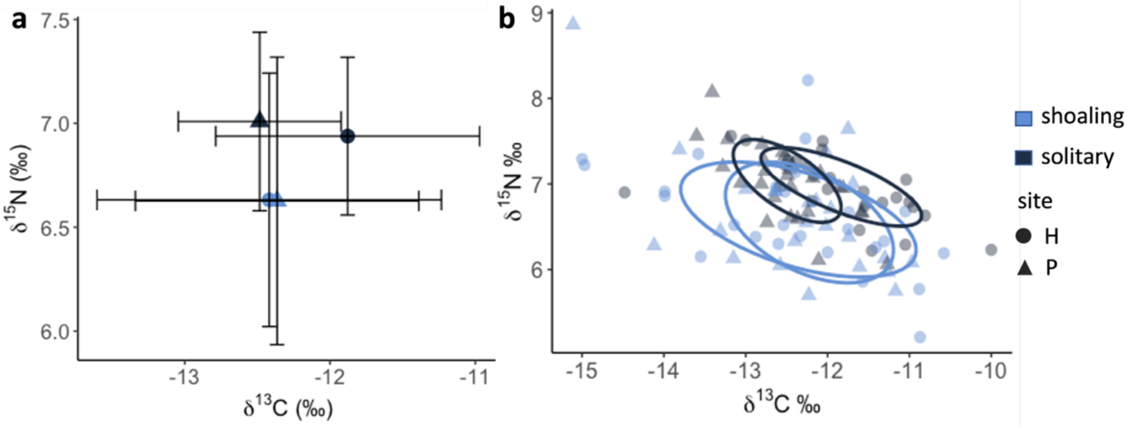

Figure 8. $\delta^{15}N$ and $\delta^{13}C$ (‰) signatures of shoaling and solitary *Acanthurus triostegus* tissue samples collected at two sites on Moorea. (a) Biplot of isotopic signatures where points are group means and error bars represent standard deviation. (b) Isotopic area overlap of shoaling and solitary fish samples. Standardized Bayesian Ellipse areas (SEAc) are depicted by solid lines and values for $\delta^{15}N$ and $\delta^{13}C$ are expressed in ‰.

Macronutrients

Protein (percentage of dry matter) for shoaling and solitary fish stomach contents is best predicted by the full model, which includes social behavior (shoaling or solitary), fish size (SL), site, and the interaction between site and social behavior as predictors (Fig. 9a, Table 12). For the interaction of site with social behavior, this model predicts higher protein percentage for solitary fish at site P (+7.26), as well as higher protein for all fish at site P (+2.28) and larger fish (1.23), but lower protein percentage for just solitary fish (-2.79). The next best-fit model (ΔAICc <2) includes: site, social behavior, and their interaction as predictors (Table A17). The best fit model for protein percentage in shoaling and solitary *A. triostegus* feces is best predicted by a model that includes social behavior, site, and the interaction between site and social behavior as predictors (Fig 9a, Table 12). The next best-fit model (ΔAICc <2) includes site, social behavior, fish size, and the interaction between site and social behavior as predictors (Table A17).

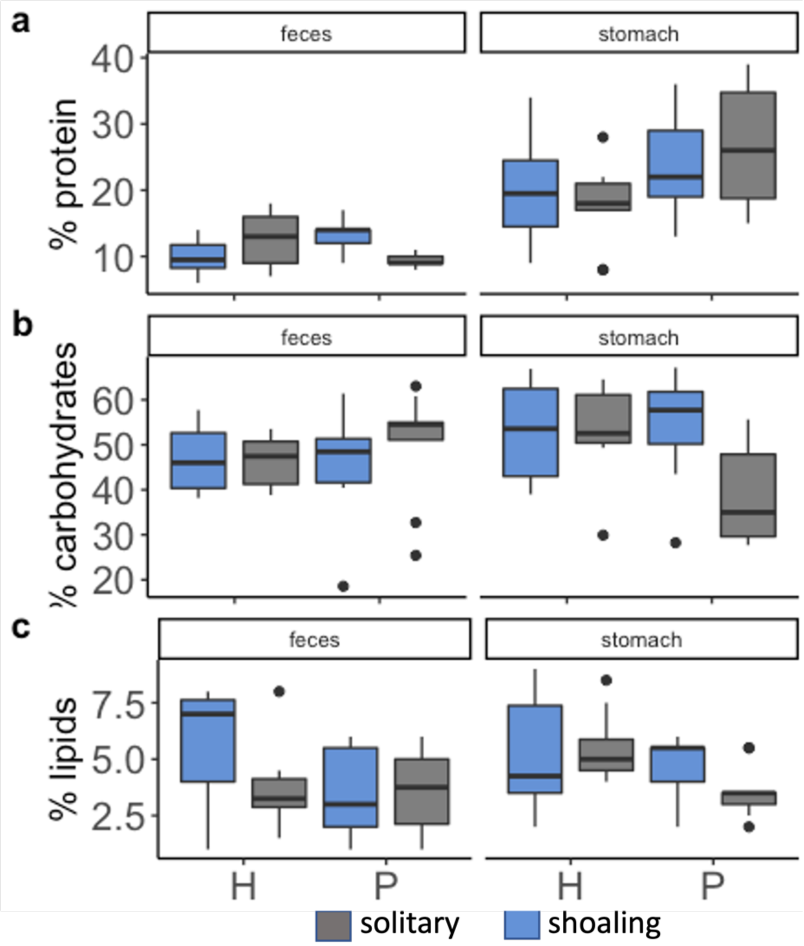

Figure 9. Percent dry matter of (a) proteins, (b) carbohydrates, and (c) lipids in the feces and stomach contents of shoaling and solitary *Acanthurus triostegus* from two backreef sites on Moorea.

Carbohydrate percentage in shoaling and solitary *A. triostegus* stomachs is best predicted by a model that includes social behavior (shoaling or solitary), fish size (SL), site, and the interaction between site and social behavior as predictors (Fig 9b, Table 12). This model predicts lower (-19.17) carbohydrate percentage for solitary fish at site P, as well as lower carbohydrate percentage for larger fish (-4.45), and higher carbohydrate percentage for solitary fish (+1.46) and site P (+1.95). The best fit model for carbohydrate percentage in shoaling and solitary *A. triostegus* feces is best predicted by a model that includes social behavior, site, the interaction between site and social behavior, and fish size as predictors (Fig 9b, Table 12)

Percentage of lipids in shoaling and solitary *A. triostegus* stomachs is best predicted by a model that includes site as a predictor (Fig. 9c, Table 12). This model predicts lower (-1.22) lipid percentage at site P. The next five best-fit models (ΔAICc <2) include: 1) site and fish size, 2) site, social behavior, and their interaction, 3) site and social behavior, 4) the full model (all predictors), and 5) site, social behavior, and fish size and predictors (Table S6). The best fit model for lipid percentage in shoaling and solitary *A. triostegus* feces is best predicted by a model that includes social behavior, site, the interaction between site and social behavior, and fish size as predictors (Fig 9c, Table 12). The next best-fit models include: 1) social behavior, site, the interaction of site and social behavior, and fish size, 2) site and fish size, and 3) site, fish size, and social behavior as predictors (Table A17).

Table 12. Best fit linear models for explaining variations in stomach content and feces macronutrients (proteins, carbohydrates, lipids) for shoaling and solitary *Acanthurus triostegus*

		protein				carbohydrates				lipids			
	coefficien	estimate	SE	t-value	p-value	estimate	SE	t-value	p-value	estimate	SE	t-value	p-value
stomach	Intercept	5.85	22.12	0.26	0.79	105.14	29.82	3.52	0.01	5.33	0.39	13.75	0
	social behavior (solitary)	-2.79	3.68	-0.76	0.45	1.46	4.96	0.29	0.77	-	-	-	-
	SL (cm)	1.23	1.89	0.65	0.52	-4.45	2.54	-1.75	0.09	-	-	-	-
	social:site (solo:P)	7.26	5.37	1.35	0.19	-19.17	7.24	-2.65	0.01	-	-	-	-
	site (P)	2.28	3.69	0.62	0.54	1.95	4.97	0.39	0.06	-1.22	0.55	-2.2	0.03
feces	intercept	10	0.85	11.81	0	88.54	35.5	2.49	0.02	5.81	0.73	7.97	0
	social behavior (solitary)	2.44	1.23	1.99	0.06	1.05	7.01	0.15	0.88	-2.06	1.03	-2.2	0.03
	SL (cm)	-	-			-3.51	2.96	-1.18	0.25				
	social:site (solo:P)	-6.37	1.74	-3.66	<0.01	2.22	9.29	0.24	0.81	2.23	1.4	1.59	0.12
	site (P)	3.22	1.23	2.62	0.01	-1.6	6.86	-0.23	0.82	-2.48	1	-2.48	0.02

4.5 DISCUSSION

This study provides some preliminary evidence that differences in the sociality of *A. triostegus* (i.e. shoaling versus solitary behavior modes) affects important attributes of their behavioral and functional ecology. We found that shoaling fish travel more distance and cover more area than solitary conspecifics on the same reef. Additionally, shoaling fish and solitary fish graze in different areas as shoaling fish primarily graze within territories of herbivores, while solitary fish do not. Further, results from the stable isotope analyses suggest that these differences may be more long-lasting, and results from the stable isotope and macronutrient analyses indicate that the dietary niche of shoaling fish may be more fixed than that of solitary fish.

We observed greater distance traveled and area covered (25-min 95% KUD) by shoaling *A. triostegus* relative to their solitary counterparts (Fig 6a-b). Size of home and foraging ranges that vary with social behavior have been shown for other coral reef fish (Afonso et al., 2008) such as species of parrotfish where social behavior is separated into roving shoals, harems, or solitary territorial modes (Mumby and Wabnitz, 2002; Welsh and Bellwood, 2012). While consistent with our results, some of these other fish species pose more challenging models to purely examine the role of sociality as their movement may be confounded by other complex behavioral interactions such as mating and reproductive behavior drivers. Contrasting results have been observed for the relationship between gregarious behavior and movement. For example, in some parrotfish species, larger harems often have larger foraging ranges and territories than solitary fish that hold territories (Mumby and Wabnitz, 2002). However, *Acanthurus coeruleus*, a surgeonfish found on Caribbean reefs, exhibits similar variation in social behavior as *A. triostegus* in that it is found in solitary foraging modes and in large shoals; yet, solitary wandering *A. coeruleus* were found to traverse more distance and had larger foraging ranges than their shoaling conspecifics (Reinthal and Lewis, 1986). Further, on the Great Barrier Reef, shoaling *Scarus* *rivulatus,* an abundant parrotfish species, has similar home ranges when solitary and in shoals (Welsh and Bellwood, 2012). Our observation of increased movement and larger area covered by shoaling fish could be due to predation risk and resource availability. Predator avoidance can affect movement in fish, with fish at increased risk of predation opting to occupy smaller areas that provide structure for cover (Elizabeth M. P. Madin et al., 2010b; Rooker et al., 2018). As shoaling can reduce predation risk, solitary *A. triostegus* may counter-balance this risk by reducing movement. Further, results from a previous study on *A. triostegus* on Palmyra Atoll and Moorea found that solitary fish travel greater distance on Moorea, where natural predator abundance is lower, suggesting that movement may be influenced by predation (Guerra et al., 2022). Alternatively, if *A. triostegus* primarily use shoaling behavior to gain access to resources guarded by territorial herbivores, as is the case with the congener *A. coeruleus* (Reinthal and Lewis, 1986), movement may be dictated by distribution of damselfish territories.

Heterospecific fish associated with almost all *A. triostegus* shoals on both Palmyra Atoll and Moorea (Table A4). Associations of predatory and non-predatory fish with shoals of *A. triostegus* have been previously documented (Barlow, 1974; Madin and Madin, 2011). We observed more predators associated with shoals on Palmyra Atoll than on Moorea, as well as more higher-trophic level fish on Palmyra Atoll. Moorea hosts a smaller predator biomass than Palmyra Atoll due to a history of commercial and subsistence fishing, which likely explains the observed difference between the two islands (Davis et al., 2017). Piscivores often associate with fish shoals in order to approach prey by using the focal shoaling species as cover (Lukoschek and McCormick, 2002), and may opportunistically prey on the focal shoaling species (Pers. Obs). Species such as *Lutjanus bohar, Caranx melampygus,* and *Aulostomus chinensis*, for example, will associate with shoals of surgeonfish and approach territorial damselfish that may be temporarily preoccupied with defending their territory from shoaling herbivores (Madin and Madin, 2011; Ormond, 2009). Similarly, heterospecific invertivores and herbivores may associate with shoals to accrue benefits such as gaining access to foraging on algae or invertebrates within damselfish territories (Alevizon, 1976; Klumpp and Polunin, 1989; Lukoschek and McCormick, 2002; Montgomery, 1981; Ormond, 2009). Additionally, mixed-species grouping is sometimes thought to provide mutualistic benefits to focal the species involved, such as increased protection through vigilant behavior by associated species (Paijmans et al., 2019). The benefits to the associated herbivores and piscivores are clear; however, without further study it is not possible to conclusively determine whether *A. triostegus* accrue any benefits from these associations.

The high proportion of invasions of herbivorous fish territories by shoaling fish supports the hypothesis that shoals may traverse long distances in search of territories and that heterospecific fish may associate with shoals to gain access to these areas. Territorial invasions by shoaling fish have been documented for other shoaling coral reef species (Catano et al., 2014; Dowdell et al., 2013; Foster, 1985), as well as for *A. triostegus* on other islands (Barlow, 1974). Algal farms maintained by the damselfish (*S. nigricans*), in particular, received a high number of invasions by *A. triostegus* shoals. Damselfish territories are considered zones of high algae productivity, with rates of up to 3.4 higher productivity than algae outside the territories (Blanchette et al., 2019; Klumpp et al., 1987) and includes highly digestible red algae (Klumpp and Polunin, 1989)(Klumpp 1989), providing a desirable food source for shoaling *A. triostegus* and other surgeonfish (Eurich et al., 2018).

The results from isotope and macronutrient analyses reflect our observed differences in the grazing by shoaling and solitary *A. triostegus*. The best-fit model for $\delta^{15}N$ isotope values suggests these behaviors may be more fixed beyond the short duration of our observational follows (Table 11). Differences in $\delta^{15}N$ are usually attributed to differences in trophic level; however, the difference we observed (~0.3) is not large enough to indicate a shift in trophic level (Post, 2002). Furthermore, *A. triostegus* is considered to be an obligate herbivore with a specialist diet (Abitia, 2011). Thus, this difference between solitary and shoaling fish is likely indicative of a different herbivorous dietary niche. A plausible explanation for the difference in $\delta^{15}N$ isotope values is the tendency for shoals of *A. triostegus* to forage in *S. nigricans* territories as damselfish territories. Damselfish territories promote higher epiphytal loads than those found outside of their territories (Ceccarelli et al., 2001; Ceccarelli, 2007; Jones et al., 2006) and $\delta^{15}N$ isotope values signatures of macroalgae and their epiphytes can differ (Hata and Umezawa, 2011; Yamamuro, 1999). Alternatively, $\delta^{13}C$ isotope values were found to vary across sites and fish size, but not between shoaling and solitary *A. triostegus*. Carbon isotopes are known to vary among species of marine plants and across space, supporting our findings of differing foraging locations and area covered by shoaling and solitary *A. triostegus* (Carassou et al., 2008; Fry et al., 1982). Additionally, ontogeny has been shown to affect tissue $\delta^{13}C$ values in *A. triostegus*, which may explain the relationship between fish size and $\delta^{13}C$ (Frédérich et al., 2012). Further, the Bayesian ellipses show high overlap between shoaling fish, but not between solitary fish across the two sites, or between shoaling and solitary fish at either site (Fig 8b). This high overlap between shoaling fish supports our observation of high proportion of foraging on damselfish territories by shoaling fish (Fig 6c), as *S. nigricans* territories are meticulously maintained and thus likely homogenous across sites (Blanchette et al., 2019; Hata and Kato, 2002). Solitary fish, however, are unable to access territories and their foraging may be more sensitive to resource availability variation across sites.

Results from the macronutrient analysis suggest that the observed differences in foraging between shoaling and solitary *A. triostegus* are nutritionally and ecologically consequential (Fig 9, Table 12). Stomach content carbohydrate and protein percentages varied with social behavior and site, suggesting that regardless of differences in activity and metabolism between shoaling and solitary fish that may affect nutrient assimilation (Bailey et al., 2022;

Killen et al., 2012; Metcalfe et al., 2016), their initial nutritional intake is different. Importantly, the interaction between social behavior and site had the strongest effect on the concentration of macronutrients in feces (Fig 9, Table 12). This result aligns with the results from the Bayesian ellipses, suggesting that solitary fish have a more variable diet, and thus higher variation in the nutritional quality of their feces (Fig 9, Table 12). Additionally, as differences in individual fish behavior can affect metabolic processes and nutrient assimilation, the nutrients in the feces of shoaling and solitary fish are also likely to differ even if their diet does not (Bailey et al., 2022). Herbivorous fish can influence their environment by supplying nutrients to corals and macroalgae through excretion and egestion (Allgeier et al., 2017); however, the corals can be sensitive to the ratios of nutrients supplied by fish (Allgeier et al., 2014), as well as the spatial scales of nutrient supply (Meyer et al., 1983). Importantly, because we intentionally sampled macronutrients from individual fish that were most divergent in their stable isotope values, our macronutrient results may be best considered to provide insight into the upper bound differences between solitary and shoaling fish.

Collectively, these results provide an important starting point for better understanding the ecological role of the two social modes of *A. triostegus*. There are important limitations to our study that must be considered. For example, our study explored differences only between two islands, and fish were collected from two sites on a single island, thus it is possible that environmental factors beyond *A. triostegus* social behavior may influence our observations and results. For example, differences in habitat structure and resource availability can influence fish movement (Tootell and Steele, 2016) and diet (Francini-Filho et al., 2010). Additionally, by design, our observational follows took place on the extremes of social behavior – large shoals and individual fish. Future studies should include a range of shoal sizes, to better assess the point at which the differences we observed and measured begin to emerge or whether these differences vary by group size. Finally, our behavioral observations were limited in duration and do not account for the activity or these fish throughout a full day, where behavioral social modes may shift. Although results from the stable isotope analysis and our preliminary fish resighting data (Text A1) suggest these behavioral social modes may be fixed and long-lasting, further investigation is necessary to confirm these observations.

The social behavior of fish may be subject to alteration in a fished ocean (Guerra et al., 2020; Sbragaglia et al., 2021a). We previously showed, for example, that shoaling behavior in *A. triostegus*, in particular, may be shifting on Moorea, where natural predator populations have been depleted through fishing (Guerra et al., 2022). This work extends the significance of those findings by suggesting that the functional role of *A. triostegus* on a coral reef is likely to change as a result of such shifts in social behavior.

We identify three of potentially many possible mechanisms through which a shift in *A. triostegus* social behavior towards fewer shoaling fish (and more solitary fish) may specifically influence the coral reef ecosystems they inhabit:

1) Reduction in grazing within territories

Considering the high (80-90%) proportion of shoaling *A. triostegus* grazing that occurred within the territory of a heterospecific fish, a shift toward more solitary fish would likely reduce the amount of grazing occurring in these areas (Fig 6c). As solitary fish are mostly unable to access these well-defended areas, a decrease in shoaling behavior would correspond to a decrease in total amount of grazing within these territories. Herbivorous fish such as *A. triostegus* can play an important role in preventing shifts from coral to macroalgae dominated systems (Marshell and Mumby, 2015, 2012), and considering the high abundance of *A. triostegus* on these reefs (Hamilton et al., 2014), reduced grazing could be consequential to coral reef health.

In particular, a reduction in grazing within *S. nigricans* territories due to reduction in shoaling behavior may have important outcomes for coral reefs. Whether territorial damselfish algal gardens are beneficial or detrimental to coral reef health remains unresolved and their effect is likely context-dependent, as studies have found that territories can serve as a) serve as refuges for macroalgae, which could facilitate phase shifts towards algae dominated systems (Hoey and Bellwood, 2010), b) cause decreases in coral survival and reduced coral health (Arnold et al., 2010; Casey et al., 2014; Potts, 1977; Vermeij et al., 2015), and c) cause increases in coral survival within damselfish territories (Gochfeld, 2010). Importantly, in areas where damselfish territories are detrimental to reef health by allowing macroalgae to outcompete live coral, a substantial reduction in grazing within territories may promote phase shifts to algae-dominated systems.

2) *Reduced subsidies to heterospecific fish associates*

Heterospecific piscivores and herbivores were found associated with *A. triostegus* shoals on both islands. Although our study did not compare predation success or foraging of these heterospecific fish while associated with shoals and while not associated with shoals, studies suggest that these associations commonly confer benefits to the associated fish (Aronson, 1983; Ormond, 2009). If foraging alongside *A. triostegus* shoals facilitates a high proportion of the diet of associated heterospecifics, a decrease in shoals might lead to a reduction in the survival of individuals, leading to population declines. Notably, these heterospecific fish include species of herbivores that also play important roles in mediating coral-macroalgae interactions (Peter J. Mumby et al., 2006).

3) *Shifts in spatial distribution and composition of bioavailable nutrient supply*

Consumers on coral reefs can influence their environment not just through grazing, but through supplying nutrients via egestion and excretion, providing nutrients to both macroalgae and corals (Allgeier et al., 2017; Burkepile et al., 2013; Munsterman et al., 2021). Nutrient supply from fish can be detrimental to reefs by facilitating macroalgae growth, or beneficial by fostering coral growth (Burkepile et al., 2013; Meyer et al., 1983). In instances where fish nutrient supply facilitates coral growth, coral can be sensitive to ratios of nutrients supplied by fish (Allgeier et al., 2014). Shoaling fish appear to maintain fixed dietary niche across sites, likely because of foraging within *S. nigricans* territories, but solitary fish would appear to shift their diet based on local resource availability at each site (Fig 9). Thus, a shift towards a solitary social mode may increase variability in nutrient supply. Additionally, the spatial scale at which nutrients are supplied can also influence productivity and coral growth. For example, corals that shelter fish schools experience more growth due to the concentrated pulses in nutrients, as opposed to those that only experienced sporadic nutrient supply (Shantz et al., 2015). We did not measure defecation by *A. triostegus* shoals, and whether defecation was "pulsed" by all members of a shoal simultaneously, or whether fish defecated at different times. However, as shoals traverse larger extents of the reef than solitary fish, their effect on nutrient supply will be spread over larger areas.

Our study suggests that social behavior of individuals may play an important role in mediating their ecological function. Aggregating wildlife that play pivotal ecological roles are found across various ecosystems. Some examples include, annual wildebeest migrations that contribute significantly to river nutrient cycling due to mass drownings (Subalusky et al., 2017), colonial nesting seabirds that provide marine-derived nutrients to oceanic islands (Ellis et al., 2006), and herding ungulates that can alter nutrient cycling and plant community composition through grazing, trampling, and defecation (Hobbs, 1996). Given the ubiquity of these social behaviors and that such behaviors may be subject to alteration from human disturbance, more attention and future work should be dedicated to better understanding the relationship between animal sociality and ecological function.

Data availability: Data and code are available at doi: 10.6073/pasta/678b0008e9906e402bcccde906fbbf25

Acknowledgements: We thank the Palmyra Atoll National Wildlife Refuge, Palmyra Atoll Research Station, and CRIOBE staff for their invaluable support. Thank you to K Davis, P Carlson, K Munsterman, M Morse, E Jahn, F Bertucci, S Howlett, N Schiettekatte, B

French, A Mercerie, and C Gache for fieldwork assistance. Thanks to the McCauley Lab and Caselle Lab for support and feedback. ASG was funded by the NSF GRFP, UC Santa Barbara, and UCSB Worster Award. We are grateful for the support of the Marisla Foundation for funding the Palmyra research.

Author contributions: Ana Sofia Guerra[1], Jacey Van Wert[1], Alison J. Haupt[3], Timothy D. White[4], David Lecchini[5,6], Erika J. Eliason[1], Douglas J. McCauley[1,2], Jennifer E. Caselle[2]

ASG conceived idea. ASG, DJM, JEC, and TDW developed field methodology. EJE and JVW developed lab methodology. ASG, DJM, JEC, EJE, and DL acquired funding for the study. ASG, JEC, and AJH collected field data. JVW conducted lab work. ASG analyzed data. ASG led writing of the manuscript. All authors contributed to drafts and approved final draft for publication.

[1] Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93101.
[2] Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93101
[3] Department of Marine Science, California State University Monterey Bay, CA 93955
[4] Global Fishing Watch, Washington, DC, 20036
[5] PSL University, EPHE-UPVD-CNRS, UAR 3278 CRIOBE, Moorea, French Polynesia
[6] Laboratoire d'Excellence "CORAIL", Paris, France.

REFERENCES

Abitia, A., 2011. Feeding habits of the convict surgeonfish Acanthurus triostegus (Teleostei: Acanthuridae) on the Los Frailes reef, Baja California Sur, Mexico. Aqua, International Journal of Ichthyology 17, 121–126.

Ackerman, J.T., Peterson, S.H., Tsao, D.C., Takekawa, J.Y., 2018. California Gull (*Larus californicus*) space use and timing of movements in relation to landfills and breeding colonies. Waterbirds 41, 384–401. https://doi.org/10.1675/063.041.0402

Adams, J., Mazukiewicz, D., Harvey, A.L., 2009. Populaton monitoring and habitat restoration for Cassin's Auklets at Scorpion Rock and Prince Island, Channel Islands National Park, California: 2007-2008. Interim Data Summary Report (Unpublished interim data summary report to the Montrose Trutee Council). U.S. Geological Survey, Western Ecological Research Center, Moss Landing Marine Laboratories, Moss Landing, CA and Channel Islands National Park, Ventura, CA.

Afonso, P., Fontes, J., Holland, K., Santos, R., 2008. Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. Mar. Ecol. Prog. Ser. 359, 215–227. https://doi.org/10.3354/meps07272

Alevizon, W.S., 1976. Mixed schooling and its possible significance in a tropical western Atlantic parrotfish and surgeonfish. Copeia 1976, 796–798. https://doi.org/10.2307/1443464

Allgeier, J.E., Burkepile, D.E., Layman, C.A., 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Global Change Biology 23, 2166–2178. https://doi.org/10.1111/gcb.13625

Allgeier, J.E., Layman, C.A., Mumby, P.J., Rosemond, A.D., 2014. Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. Global Change Biology 20, 2459–2472. https://doi.org/10.1111/gcb.12566

Annett, C., Pierotti, R., 1989. Chick hatching as a trigger for dietary switching in the Western Gull. Colonial Waterbirds 12, 4–11. https://doi.org/10.2307/1521306

Annett, C.A., Pierotti, R., 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. Ecology 80, 288–297. https://doi.org/10.1890/0012-9658(1999)080[0288:LTROIW]2.0.CO;2

Arlinghaus, R., Laskowski, K.L., Alós, J., Klefoth, T., Monk, C.T., Nakayama, S., Schröder, A., 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. Fish Fish 18, 360–373. https://doi.org/10.1111/faf.12176

Arnold, S.N., Steneck, R.S., Mumby, P.J., 2010. Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Marine Ecology Progress Series 414, 91–105. https://doi.org/10.3354/meps08724

Aronson, R., 1983. Foraging behavior of the West Atlantic trumpetfish, *Aulostomus maculatus*: use of large, herbivorous reef fishes as camouflage. Bulletin of Marine Science 33.

Ashmole, N.P., 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b, 458–473. https://doi.org/10.1111/j.1474-919X.1963.tb06766.x

Auman, H.J., Meathrel, C.E., Richardson, A., 2008. Supersize me: does anthropogenic food change the body condition of Silver Gulls? A comparison between urbanized and remote, non-urbanized areas. Waterbirds: The International Journal of Waterbird Biology 31, 122–126.

Avgar, T., Giladi, I., Nathan, R., 2008. Linking traits of foraging animals to spatial patterns of plants: social and solitary ants generate opposing patterns of surviving seeds. Ecology Letters 11, 224–234. https://doi.org/10.1111/j.1461-0248.2007.01140.x

Bailey, L.A., Childs, A.R., James, N.C., Winkler, A., Potts, W.M., 2022. Links between behaviour and metabolic physiology in fishes in the Anthropocene. Rev Fish Biol Fisheries 32, 555–579. https://doi.org/10.1007/s11160-022-09701-2

Barlow, G.W., 1974. Extraspecific imposition of social grouping among surgeonfishes (Pisces: Acanthuridae). Journal of Zoology 174, 333–340. https://doi.org/10.1111/j.1469-7998.1974.tb03161.x

Barton, K., 2020. Mu-MIn: Multi-model inference package in R.

Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D., Levin, S.A., 2010. Fishery discards impact on seabird movement patterns at regional scales. Curr. Biol. 20, 215–222. https://doi.org/10.1016/j.cub.2009.11.073

Bates, D., Machler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models using *lme4*. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Baumberger, T., Affre, L., Torre, F., Vidal, E., Dumas, P.-J., Tatoni, T., 2012. Plant community changes as ecological indicator of seabird colonies' impacts on Mediterranean Islands. Ecological Indicators 15, 76–84. https://doi.org/10.1016/j.ecolind.2011.09.009

Bird, M.I., Tait, E., Wurster, C.M., Furness, R.W., 2008. Stable carbon and nitrogen isotope analysis of avian uric acid. Rapid Communications in Mass Spectrometry 22, 3393–3400. https://doi.org/10.1002/rcm.3739

Blanchette, A., Ely, T., Zeko, A., Sura, S.A., Turba, R., Fong, P., 2019. Damselfish Stegastes nigricans increase algal growth within their territories on shallow coral reefs via enhanced nutrient supplies. Journal of Experimental Marine Biology and Ecology 513, 21–26. https://doi.org/10.1016/j.jembe.2019.02.001

Blight, L.K., Hobson, K.A., Kyser, T.K., Arcese, P., 2015. Changing gull diet in a changing world: A 150-year stable isotope (δ13C, δ15N) record from feathers collected in the Pacific Northwest of North America. Global Change Biology 21, 1497–1507. https://doi.org/10.1111/gcb.12796

Botham, M.S., Krause, J., 2005. Shoals Receive more Attacks from the Wolf-Fish (*Hoplias malabaricus* Bloch, 1794). Ethology 111, 881–890. https://doi.org/10.1111/j.1439-0310.2005.01122.x

Bradley, D., Conklin, E., Papastamatiou, Y.P., McCauley, D.J., Pollock, K., Pollock, A., Kendall, B.E., Gaines, S.D., Caselle, J.E., 2017. Resetting predator baselines in coral reef ecosystems. Scientific Reports 7, srep43131. https://doi.org/10.1038/srep43131

Brzezinksi, Mark.A., Washburn, L., 2011. Phytoplankton primary productivity in the Santa Barbara Channel: Effects of wind-driven upwelling and mesoscale eddies. Journal of Geophysical Research: Oceans 116.

Buckel, J.A., Stoner, A.W., 2004. Negative effects of increasing group size on foraging in two estuarine piscivores. Journal of Experimental Marine Biology and Ecology 307, 183–196. https://doi.org/10.1016/j.jembe.2004.02.003

Buckman, N.S., Ogden, J.C., 1973. Territorial behavior of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54, 1377–1382. https://doi.org/10.2307/1934202

Burkepile, D.E., Allgeier, J.E., Shantz, A.A., Pritchard, C.E., Lemoine, N.P., Bhatti, L.H., Layman, C.A., 2013. Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Scientific Reports 3, 1493. https://doi.org/10.1038/srep01493

Calenge, C., 2006. The package *adehabitat* for the R software: a tool for the analysis of space and habitat use by animals., Ecological Modelling.

Carassou, L., Kulbicki, M., Nicola, T.J.R., Polunin, N.V.C., 2008. Assessment of fish trophic status and relationships by stable isotope data in the coral reef lagoon of New Caledonia, southwest Pacific. Aquatic Living Resources 21, 1–12. https://doi.org/10.1051/alr:2008017

Carter, H.R., McChesney, G.J., Jaques, D.L., Strong, C.S., Parker, M.W., Takekawa, J.E., Jory, D.L., Whitworth, D.L., 1992. Breeding populations of seabirds in California, 1989-1991. Volume I - population estimates (Monograph or Serial Issue). U.S. Fish and Wildlife Service.

Casey, J.M., Ainsworth, T.D., Choat, J.H., Connolly, S.R., 2014. Farming behaviour of reef fishes increases the prevalence of coral disease associated microbes and black band disease. Proc Biol Sci 281. https://doi.org/10.1098/rspb.2014.1032

Catano, L., Shantz, A., Burkepile, D., 2014. Predation risk, competition, and territorial damselfishes as drivers of herbivore foraging on Caribbean coral reefs. Mar. Ecol. Prog. Ser. 511, 193–207. https://doi.org/10.3354/meps10921

Caut, S., Angulo, E., Pisanu, B., Ruffino, L., Faulquier, L., Lorvelec, O., Chapuis, J.-L., Pascal, M., Vidal, E., Courchamp, F., 2012. Seabird modulations of isotopic nitrogen on islands. PLOS ONE 7, e39125. https://doi.org/10.1371/journal.pone.0039125

Ceccarelli, D., Jones, G., LJ, M., 2001. Territorial Damselfish as determinants of the structure of benthic communities on coral reef. Oceanography and Marine Biology: an Annual Review 39, 355–389.

Ceccarelli, D.M., 2007. Modification of benthic communities by territorial damselfish: a multi-species comparison. Coral Reefs 26, 853–866. https://doi.org/10.1007/s00338-007-0275-1

Choat, J.H., Bellwood, D.R., 1985. Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. Mar. Biol. 89, 221–234. https://doi.org/10.1007/BF00393655

Cimino, M.A., Shaffer, S.A., Welch, H., Santora, J.A., Warzybok, P., Jahncke, J., Schroeder, I., Hazen, E.L., Bograd, S.J., in press. Western Gull foraging behavior as an ecosystem state indicator in coastal California. Frontiers in Marine Science.

Clatterbuck, C.A., Lewison, R.L., Orben, R.A., Ackerman, J.T., Torres, L.G., Suryan, R.M., Warzybok, P., Jahncke, J., Shaffer, S.A., 2021. Foraging in marine habitats increases mercury concentrations in a generalist seabird. Chemosphere 279, 130470. https://doi.org/10.1016/j.chemosphere.2021.130470

Clifton, K.E., 1989. Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behaviour. Animal Behaviour 37, 90–103. https://doi.org/10.1016/0003-3472(89)90009-2

Cockerham, S., Lee, B., Orben, R.A., Suryan, R.M., Torres, L.G., Warzybok, P., Bradley, R., Jahncke, J., Young, H.S., Ouverney, C., Shaffer, S.A., 2019. Microbial Ecology of the Western Gull (*Larus occidentalis*). Microb Ecol 78, 665–676. https://doi.org/10.1007/s00248-019-01352-4

Connell, S.D., 2002. Effects of a predator and prey on a foraging reef fish: implications for understanding density-dependent growth. Journal of Fish Biology 60, 1551–1561. https://doi.org/10.1111/j.1095-8649.2002.tb02447.x

Converse, R.R., Kinzelman, J.L., Sams, E.A., Hudgens, E., Dufour, A.P., Ryu, H., Santo-Domingo, J.W., Kelty, C.A., Shanks, O.C., Siefring, S.D., Haugland, R.A., Wade, T.J., 2012. Dramatic improvements in beach water quality following gull removal. Environ. Sci. Technol. 46, 10206–10213. https://doi.org/10.1021/es302306b

Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M., Byrd, G.V., 2005. Introduced predators transform subarctic islands from grassland to tundra. Science 307, 1959–1961. https://doi.org/10.1126/science.1108485

Crook, A.C., 1999a. Quantitative evidence for assortative schooling in a coral reef fish. Marine Ecology Progress Series 176, 17–23.

Crook, A.C., 1999b. A quantitative analysis of the relationship between interspecific encounters, schooling behaviour and colouration in juvenile parrotfish (family scaridae). Marine and Freshwater Behaviour and Physiology 33, 1–19. https://doi.org/10.1080/10236249909387078

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor, P., 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 1–34.

Dahnke, W.C., Johnson, G.V., 1990. Testing soils for available nitrogen, in: Soil Testing and Plant Analysis. John Wiley & Sons, Ltd, pp. 127–139. https://doi.org/10.2136/sssabookser3.3ed.c6

Davis, K., Carlson, P.M., Bradley, D., Warner, R.R., Caselle, J.E., 2017. Predation risk influences feeding rates but competition structures space use for a common Pacific parrotfish. Oecologia 184, 139–149. https://doi.org/10.1007/s00442-017-3857-9

de Girolamo, M., Scaggiante, M., Rasotto, M.B., 1999. Social organization and sexual pattern in the Mediterranean parrotfish *Sparisoma cretense* (Teleostei: Scaridae). Marine Biology 135, 353–360. https://doi.org/10.1007/s002270050634

Deegan, L.A., Johnson, D.S., Warren, R.S., Peterson, B.J., Fleeger, J.W., Fagherazzi, S., Wollheim, W.M., 2012. Coastal eutrophication as a driver of salt marsh loss. Nature 490, 388–392. https://doi.org/10.1038/nature11533

Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–929. https://doi.org/10.1126/science.1156401

Dill, L.M., Fraser, A.H.G., 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behav Ecol Sociobiol 16, 65–71. https://doi.org/10.1007/BF00293105

Dill, L.M., Heithaus, M.R., Walters, C.J., 2003. Behaviorally Mediated Indirect Interactions in Marine Communities and Their Conservation Implications. Ecology 84, 1151–1157. https://doi.org/10.1890/0012-9658(2003)084[1151:BMIIIM]2.0.CO;2

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406. https://doi.org/10.1126/science.1251817

Dolejska, M., Cizek, A., Literak, I., 2007. High prevalence of antimicrobial-resistant genes and integrons in *Escherichia coli* isolates from Black-headed Gulls in the Czech Republic. Journal of Applied Microbiology 103, 11–19. https://doi.org/10.1111/j.1365-2672.2006.03241.x

Dowdell, S.C., Francisco, M.I.R.D., Hull, E.H., Pugh, M.R., 2013. Friends with benefits: does schooling behavior enhance foraging in blue tang, Acanthurus coeruleus, during interactions with territorial damselfish? Dartmouth Studies in Tropical Ecology.

Duhem, C., Roche, P., Vidal, E., Tatoni, T., 2008. Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. Population Ecology 50, 91–100. https://doi.org/10.1007/s10144-007-0059-z

Ellis, J.C., 2005. Marine birds on land: A review of plant biomass, species richness, and community composition in seabird colonies. Plant Ecol 181, 227–241. https://doi.org/10.1007/s11258-005-7147-y

Ellis, J.C., Fariña, J.M., Witman, J.D., 2006. Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. Journal of Animal Ecology 75, 565–574. https://doi.org/10.1111/j.1365-2656.2006.01077.x

Estes, J.A., Heithaus, M., McCauley, D.J., Rasher, D.B., Worm, B., 2016. Megafaunal impacts on structure and function of ocean ecosystems. Annual Review of Environment and Resources 41, 83–116. https://doi.org/10.1146/annurev-environ-110615-085622

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of Planet Earth. Science 333, 301–306. https://doi.org/10.1126/science.1205106

Eurich, J.G., Matley, J.K., Baker, R., McCormick, M.I., Jones, G.P., 2019. Stable isotope analysis reveals trophic diversity and partitioning in territorial damselfishes on a low-latitude coral reef. Mar Biol 166, 17. https://doi.org/10.1007/s00227-018-3463-3

Eurich, J.G., Shomaker, S.M., McCormick, M.I., Jones, G.P., 2018. Experimental evaluation of the effect of a territorial damselfish on foraging behaviour of roving herbivores on coral reefs. Journal of Experimental Marine Biology and Ecology 506, 155–162. https://doi.org/10.1016/j.jembe.2018.06.009

FAO, 2020. Fertilizer consumption (kilograms per hectare of arable land) [WWW Document]. World Bank. URL https://data.worldbank.org/indicator/AG.CON.FERT.ZS?end=2018&start=1961&view=chart (accessed 1.13.22).

Fenn, M.E., Allen, E.B., Weiss, S.B., Jovan, S., Geiser, L.H., Tonnesen, G.S., Johnson, R.F., Rao, L.E., Gimeno, B.S., Yuan, F., Meixner, T., Bytnerowicz, A., 2010. Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. Journal of Environmental Management 91, 2404–2423. https://doi.org/10.1016/j.jenvman.2010.07.034

Folch, J., Lees, M., Sloane Stanley, G.H., 1957. A simple method for the isolation and purification of total lipides from animal tissues. J Biol Chem 226, 497–509.

Foster, S.A., 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. Animal Behaviour 33, 782–792. https://doi.org/10.1016/S0003-3472(85)80011-7

Francini-Filho, R.B., Ferreira, C.M., Coni, E.O.C., Moura, R.L.D., Kaufman, L., 2010. Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition. Journal of the Marine Biological Association of the United Kingdom 90, 481–492. https://doi.org/10.1017/S0025315409991147

Frédérich, B., Colleye, O., Lepoint, G., Lecchini, D., 2012. Mismatch between shape changes and ecological shifts during the post-settlement growth of the surgeonfish, Acanthurus triostegus. Frontiers in Zoology 9, 8. https://doi.org/10.1186/1742-9994-9-8

Friedlander, A.M., DeMartini, E.E., 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Marine Ecology Progress Series 230, e264. https://doi.org/10.3354/meps230253

Froese. R., Pauly, D., 2015. FishBase [WWW Document]. www.fishbase.org.

Fry, B., Lutes, R., Northam, M., Parker, P.L., Ogden, J., 1982. A 13C/12C comparison of food webs in Caribbean seagrass meadows and coral reefs. Aquatic Botany 14, 389–398. https://doi.org/10.1016/0304-3770(82)90112-7

Fuirst, M., Veit, R.R., Hahn, M., Dheilly, N., Thorne, L.H., 2018. Effects of urbanization on the foraging ecology and microbiota of the generalist seabird *Larus argentatus*. PLOS ONE 13, e0209200. https://doi.org/10.1371/journal.pone.0209200

Fukami, T., Wardle, D.A., Bellingham, P.J., Mulder, C.P.H., Towns, D.R., Yeates, G.W., Bonner, K.I., Durrett, M.S., Grant-Hoffman, M.N., Williamson, W.M., 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. Ecology Letters 9, 1299–1307. https://doi.org/10.1111/j.1461-0248.2006.00983.x

García Luis V., Marañón Teodoro, Ojeda Fernando, Clemente Luis, Redondo Ramón, 2002. Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. Oikos 98, 75–86. https://doi.org/10.1034/j.1600-0706.2002.980108.x

Gil, M.A., Zill, J., Ponciano, J.M., 2017. Context-dependent landscape of fear: algal density elicits risky herbivory in a coral reef. Ecology 98, 534–544. https://doi.org/10.1002/ecy.1668

Gochfeld, D.J., 2010. Territorial damselfishes facilitate survival of corals by providing an associational defense against predators. Marine Ecology Progress Series 398, 137–148.

Goetze, J.S., Januchowski-Hartley, F.A., Claudet, J., Langlois, T.J., Wilson, S.K., Jupiter, S.D., 2017. Fish wariness is a more sensitive indicator to changes in fishing pressure than abundance, length or biomass. Ecol Appl 27, 1178–1189. https://doi.org/10.1002/eap.1511

Gotanda, K.M., Turgeon, K., Kramer, D.L., 2009. Body size and reserve protection affect flight initiation distance in parrotfishes. Behav Ecol Sociobiol 63, 1563–1572. https://doi.org/10.1007/s00265-009-0750-5

Gould, D.J., Fletcher, M.R., 1978. Gull droppings and their effects on water quality. Water Research 12, 665–672. https://doi.org/10.1016/0043-1354(78)90176-8

Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S., MacNeil, M.A., 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559, 250. https://doi.org/10.1038/s41586-018-0202-3

Grimm, N.B., Foster, D., Groffman, P., Grove, J.M., Hopkinson, C.S., Nadelhoffer, K.J., Pataki, D.E., Peters, D.P., 2008. The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. Frontiers in Ecology and the Environment 6, 264–272. https://doi.org/10.1890/070147

Guerra, A.S., Kao, A.B., McCauley, D.J., Berdahl, A.M., 2020. Fisheries-induced selection against schooling behaviour in marine fishes. Proceedings of the Royal Society B: Biological Sciences 287, 20201752. https://doi.org/10.1098/rspb.2020.1752

Guerra, A.S., McCauley, D.J., Lecchini, D., Caselle, J.E., 2022. Shoaling behavior of coral reef fishes varies between two islands with different predator abundance. Marine Ecology Progress Series 690, 133–145.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952. https://doi.org/10.1126/science.1149345

Halvorson, W.L., 1992. Alien plants at Channel Islands, in: Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. University of Hawaii, Cooperative National Park Resources Unit, Honolulu, HI, pp. 64–96.

Halvorson, W.L., Fenn, D.B., Allardice, W.R., 1988. Soils and vegetation of Santa Barbara Island, Channel Islands National Park, California, USA. Environmental Management 12, 109–118. https://doi.org/10.1007/BF01867382

Hamilton, S., Smith, J., Price, N., Sandin, S., 2014. Quantifying patterns of fish herbivory on Palmyra Atoll (USA), an uninhabited predator-dominated central Pacific coral reef. Marine Ecology Progress Series 501, 141–155. https://doi.org/10.3354/meps10684

Hata, H., Kato, M., 2002. Weeding by the herbivorous damselfish Stegastes nigricans in nearly monocultural algae farms. Marine Ecology Progress Series 237, 227–231. https://doi.org/10.3354/meps237227

Hata, H., Umezawa, Y., 2011. Food habits of the farmer damselfish Stegastes nigricans inferred by stomach content, stable isotope, and fatty acid composition analyses. Ecol Res 26, 809–818. https://doi.org/10.1007/s11284-011-0840-5

Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L.M., Fourqurean, J.W., Burkholder, D., Thomson, J., Bejder, L., 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. Journal of Animal Ecology 76, 837–844. https://doi.org/10.1111/j.1365-2656.2007.01260.x

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology & Evolution 23, 202–210. https://doi.org/10.1016/j.tree.2008.01.003

Helfield, J.M., Naiman, R.J., 2001. Effects of Salmon-Derived Nitrogen on Riparian Forest Growth and Implications for Stream Productivity. Ecology 82, 2403–2409. https://doi.org/10.1890/0012-9658(2001)082[2403:EOSDNO]2.0.CO;2

Helfman, G.S., 1984. School fidelity in fishes: The yellow perch pattern. Animal Behaviour 32, 663–672. https://doi.org/10.1016/S0003-3472(84)80142-6

Herbert-Read, J.E., 2017. Social behaviour: the personalities of groups. Current Biology 27, R1015–R1017. https://doi.org/10.1016/j.cub.2017.07.042

Hilderbrand, G.V., Hanley, T.A., Robbins, C.T., Schwartz, C.C., 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121, 546–550. https://doi.org/10.1007/s004420050961

Hoare, D.J., Couzin, I.D., Godin, J.-G.J., Krause, J., 2004. Context-dependent group size choice in fish. Animal Behaviour 67, 155–164. https://doi.org/10.1016/j.anbehav.2003.04.004

Hoare, D.J., Krause, J., Peuhkuri, N., Godin, J.-G.J., 2000. Body size and shoaling in fish. Journal of Fish Biology 57, 1351–1366. https://doi.org/10.1111/j.1095-8649.2000.tb02217.x

Hobbs, N.T., 1996. Modification of Ecosystems by Ungulates. The Journal of Wildlife Management 60, 695–713. https://doi.org/10.2307/3802368

Hobson, E.S., 1973. Diel feeding migrations in tropical reef fishes. Helgolander Wiss. Meeresunters 24, 361–370. https://doi.org/10.1007/BF01609526

Hobson, E.S., 1968. Predatory Behavior of Some Shore Fishes in the Gulf of California. Bureau of Sport Fisheries and Wildlife.

Hobson, K.A., 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. Diversity and Distributions 11, 157–164. https://doi.org/10.1111/j.1366-9516.2005.00149.x

Hobson, K.A., Clark, R.G., 1992. Assessing Avian Diets Using Stable Isotopes I: Turnover of 13C in Tissues. The Condor 94, 181–188. https://doi.org/10.2307/1368807

Hobson, K.A., Piatt, J.F., Pitocchelli, J., 1994. Using Stable Isotopes to Determine Seabird Trophic Relationships. Journal of Animal Ecology 63, 786–798. https://doi.org/10.2307/5256

Hobson, S., 1979. Interactions Between Piscivorous Fishes and Their Prey, in: Predator-Prey Systems in Fisheries Management. Sport Fishing Inst., Washington, D. C., pp. 231–242.

Hoey, A.S., Bellwood, D.R., 2010. Damselfish territories as a refuge for macroalgae on coral reefs. Coral Reefs 29, 107–118. https://doi.org/10.1007/s00338-009-0567-8

Hogg, E.H., Morton, J.K., 1983. The effects of nesting gulls on the vegetation and soil of islands in the Great Lakes. Can. J. Bot. 61, 3240–3254. https://doi.org/10.1139/b83-361

Holland, K.N., Peterson, J.D., Lowe, C.G., Wetherbee, B.M., 1993. Movements, distribution and growth rates of the White Goatfish *Mulloides flavolineatus* in a fisheries conservation zone. Bulletin of Marine Science 52, 982–992.

Howell, S.N.G., Corben, C., 2000. Molt cycles and sequences in the Western Gull. Western Birds 38–49.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17, 360–365. https://doi.org/10.1016/j.cub.2006.12.049

Huizinga, M., Ghalambor, C.K., Reznick, D.N., 2009. The genetic and environmental basis of adaptive differences in shoaling behaviour among populations of Trinidadian guppies, *Poecilia reticulata*. Journal of Evolutionary Biology 22, 1860–1866. https://doi.org/10.1111/j.1420-9101.2009.01799.x

Institut national de la satistique et des études économiques, 2017. Populations légales des communes et des communes associées de Polynésie française en 2017.

Ioannou, C.C., Krause, J., 2008. Searching for prey: the effects of group size and number. Animal Behaviour 75, 1383–1388. https://doi.org/10.1016/j.anbehav.2007.09.012

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637. https://doi.org/10.1126/science.1059199

Jacques, M.E., Yamagiwa, A.A., Mazukiewicz, D.M., Harvey, A.L., Little, A., 2005. Seabird habitat restoration on Santa Barbara Island, California: 2007-2014 data report. Unpublished Report. California Institute of Environmental Studies.

Jahren, A.H., Kraft, R.A., 2008. Carbon and nitrogen stable isotopes in fast food: Signatures of corn and confinement. PNAS 105, 17855–17860. https://doi.org/10.1073/pnas.0809870105

Januchowski-Hartley, F.A., Graham, N.A.J., Cinner, J.E., Russ, G.R., 2015. Local fishing influences coral reef fish behavior inside protected areas of the Indo-Pacific. Biological Conservation 182, 8–12. https://doi.org/10.1016/j.biocon.2014.11.024

Januchowski-Hartley, F.A., Graham, N.A.J., Feary, D.A., Morove, T., Cinner, J.E., 2011. Fear of Fishers: Human Predation Explains Behavioral Changes in Coral Reef Fishes. PLOS ONE 6, e22761. https://doi.org/10.1371/journal.pone.0022761

Johannes, R.E., Hviding, E., 2000. Traditional knowledge possessed by the fishers of Marovo Lagoon, Solomon Islands, concerning fish aggregating behaviour. SPC Traditional Marine Resource Management and Knowledge Information Bulletin.

Johnson, J.S., Clements, K.D., Raubenheimer, D., 2017. The nutritional basis of seasonal selective feeding by a marine herbivorous fish. Mar Biol 164, 201. https://doi.org/10.1007/s00227-017-3223-9

Jones, G.P., Santana, L., McCook, L.J., McCormick, M.I., 2006. Resource use and impact of three herbivorous damselfishes on coral reef communities. Marine Ecology Progress Series 328, 215–224. https://doi.org/10.3354/meps328215

Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can. J. Zool. 78, 1–27. https://doi.org/10.1139/z99-165

Killen, S.S., Marras, S., Steffensen, J.F., McKenzie, D.J., 2012. Aerobic capacity influences the spatial position of individuals within fish schools. Proceedings of the Royal Society B: Biological Sciences 279, 357–364. https://doi.org/10.1098/rspb.2011.1006

Klumpp, D., McKinnon, D., Daniel, P., 1987. Damselfish territories: zones of high productivity on coral reefs. Marine Ecology Progress Series 40, 41–51. https://doi.org/10.3354/meps040041

Klumpp, D.W., Polunin, N.V.C., 1989. Partitioning among grazers of food resources within damselfish territories on a coral reef. Journal of Experimental Marine Biology and Ecology 125, 145–169. https://doi.org/10.1016/0022-0981(89)90040-3

Kolasinski, J., Frouin, P., Sallon, A., Rogers, K., Bruggemann, H.J., Potier, M., 2009. Feeding ecology and ontogenetic dietary shift of yellowstripe goatfish Mulloidichthys flavolineatus (Mullidae) at Reunion Island, SW Indian Ocean. Marine Ecology Progress Series 386, 181–195. https://doi.org/10.3354/meps08081

Kozak, G.M., Boughman, J.W., 2012. Plastic responses to parents and predators lead to divergent shoaling behaviour in sticklebacks. Journal of Evolutionary Biology 25, 759–769. https://doi.org/10.1111/j.1420-9101.2012.02471.x

Krause, J., Ruxton, G.D., 2002. Living in Groups. Oxford University Press, New York, NY.

Langley, L.P., Bearhop, S., Burton, N.H.K., Banks, A.N., Frayling, T., Thaxter, C.B., Clewley, G.D., Scragg, E., Votier, S.C., 2021. GPS tracking reveals landfill closures induce higher foraging effort and habitat switching in gulls. Movement Ecology 9, 56. https://doi.org/10.1186/s40462-021-00278-2

Lawrence, C.R., Neff, J.C., 2009. The contemporary physical and chemical flux of aeolian dust: A synthesis of direct measurements of dust deposition. Chemical Geology, Combined Ecological and Geologic Perspectives in Ecosystem Studies 267, 46–63. https://doi.org/10.1016/j.chemgeo.2009.02.005

Leenhardt, P., Moussa, R.M., Galzin, R., 2012. Reef and lagoon fisheries yields in Moorea: A summary of data collected. SPC Fisheries Newsletter.

Lenth, R.V., Buerkner, P., Herve, M., Love, J., Riebl, H., Singmann, H., 2021. *emmeans*: Estimated Marginal Means, aka Least-Squares Means in R.

Lenzi, J., González-Bergonzoni, I., Machín, E., Pijanowski, B., Flaherty, E., 2019. The impact of anthropogenic food subsidies on a generalist seabird during nestling growth. Science of The Total Environment 687, 546–553. https://doi.org/10.1016/j.scitotenv.2019.05.485

Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: the Predation Risk Allocation Hypothesis. The American Naturalist 153, 649–659. https://doi.org/10.1086/303202

Lima, S.L., Dill, L.M., 2011. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology. https://doi.org/10.1139/z90-092

Lukoschek, V., McCormick, M.I., 2002. A review of multi-species foraging associations in fishes and their ecological significance, in: Moosa, M.K., Soemodihardjo, S., Romimohtarto, K., Suharsono, S., Soegiarto, A. (Eds.), Proceeding 9th International Coral Reef Symposium. Bali, Indonesia, pp. 467–474.

Madin, E.M.P., Dill, L.M., Ridlon, A.D., Heithaus, M.R., Warner, R.R., 2016. Human activities change marine ecosystems by altering predation risk. Glob Change Biol 22, 44–60. https://doi.org/10.1111/gcb.13083

Madin, Elizabeth M. P., Gaines, S.D., Madin, J.S., Warner, R.R., 2010. Fishing indirectly structures macroalgal assemblages by altering herbivore behavior. The American Naturalist 176, 785–801. https://doi.org/10.1086/657039

Madin, Elizabeth M. P., Gaines, S.D., Warner, R.R., 2010a. Field evidence for pervasive indirect effects of fishing on prey foraging behavior. Ecology 91, 3563–3571. https://doi.org/10.1890/09-2174.1

Madin, Elizabeth M. P., Gaines, S.D., Warner, R.R., 2010b. Field evidence for pervasive indirect effects of fishing on prey foraging behavior. Ecology 91, 3563–3571. https://doi.org/10.1890/09-2174.1

Madin, E.M.P., Madin, J.S., 2011. Predators, facilitators, or both? Re-evaluating an apparent predator–prey relationship. Marine Ecology Progress Series 431, 299–302. https://doi.org/10.3354/meps09162

Magurran, A.E., Pitcher, T.J., 1987. Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. Proceedings of the Royal Society of London B: Biological Sciences 229, 439–465. https://doi.org/10.1098/rspb.1987.0004

Magurran, A.E., Seghers, B.H., Carvalho, G.R., Shaw, P.W., 1992. Behavioural consequences of an artificial introduction of guppies (*Poecilia reticulata*) in N. Trinidad: evidence for the evolution of anti-predator behaviour in the wild. Proceedings of the Royal Society of London. Series B: Biological Sciences 248, 117–122. https://doi.org/10.1098/rspb.1992.0050

Mann, R., Gallager, S.M., 1985. Physiological and biochemical energetics of larvae of Teredo navalis L. and Bankia gouldi (Bartsch) (Bivalvia : Teredinidae). Journal of

Experimental Marine Biology and Ecology 85, 211–228. https://doi.org/10.1016/0022-0981(85)90159-5

Marshell, A., Mumby, P.J., 2015. The role of surgeonfish (Acanthuridae) in maintaining algal turf biomass on coral reefs. Journal of Experimental Marine Biology and Ecology 473, 152–160. https://doi.org/10.1016/j.jembe.2015.09.002

Marshell, A., Mumby, P.J., 2012. Revisiting the functional roles of the surgeonfish Acanthurus nigrofuscus and Ctenochaetus striatus. Coral Reefs 31, 1093–1101. https://doi.org/10.1007/s00338-012-0931-y

Martín-Vélez, V., Sánchez, M.I., Shamoun-Baranes, J., Thaxter, C.B., Stienen, E.W.M., Camphuysen, K.C.J., Green, A.J., 2019. Quantifying nutrient inputs by gulls to a fluctuating lake, aided by movement ecology methods. Freshwater Biology 64, 1821–1832. https://doi.org/10.1111/fwb.13374

Matley, J.K., Fisk, A.T., Tobin, A.J., Heupel, M.R., Simpfendorfer, C.A., 2016. Diet-tissue discrimination factors and turnover of carbon and nitrogen stable isotopes in tissues of an adult predatory coral reef fish, Plectropomus leopardus. Rapid Communications in Mass Spectrometry 30, 29–44. https://doi.org/10.1002/rcm.7406

McCaskie, G., 1983. Another look at the Western and Yellow-footed gulls. Western Birds 85–107.

McCauley, D.J., Micheli, F., Young, H.S., Tittensor, D.P., Brumbaugh, D.R., Madin, E.M.P., Holmes, K.E., Smith, J.E., Lotze, H.K., DeSalles, P.A., Arnold, S.N., Worm, B., 2010. Acute effects of removing large fish from a near-pristine coral reef. Mar Biol 157, 2739–2750. https://doi.org/10.1007/s00227-010-1533-2

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: Animal loss in the global ocean. Science 347, 1255641. https://doi.org/10.1126/science.1255641

Mehlich, A., 1984. Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis 15, 1409–1416. https://doi.org/10.1080/00103628409367568

Metcalfe, N.B., Van Leeuwen, T.E., Killen, S.S., 2016. Does individual variation in metabolic phenotype predict fish behaviour and performance? Journal of Fish Biology 88, 298–321. https://doi.org/10.1111/jfb.12699

Meyer, J.L., Schultz, E.T., Helfman, G.S., 1983. Fish schools: an asset to corals. Science 220, 1047–1049. https://doi.org/10.1126/science.220.4601.1047

Montgomery, W.L., 1981. Mixed-Species Schools and the Significance of Vertical Territories of Damselfishes. Copeia 1981, 477–481. https://doi.org/10.2307/1444245

Montgomery, W.L., Myrberg, A.A., Fishelson, L., 1989. Feeding ecology of surgeonfishes (Acanthuridae) in the northern Red Sea, with particular reference to *Acanthurus nigrofuscus* (Forsskål). Journal of Experimental Marine Biology & Ecology 132, 179–207. https://doi.org/10.1016/0022-0981(89)90127-5

Mumby, Peter J, Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science (New York, N.Y.) 311, 98–101. https://doi.org/10.1126/science.1121129

Mumby, Peter J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311, 98–101. https://doi.org/10.1126/science.1121129

Mumby, P.J., Wabnitz, C.C.C., 2002. Spatial Patterns of Aggression, Territory Size, and Harem Size in Five Sympatric Caribbean Parrotfish Species. Environmental Biology of Fishes 63, 265–279. https://doi.org/10.1023/A:1014359403167

Munsterman, K.S., Allgeier, J.E., Peters, J.R., Burkepile, D.E., 2021. A View From Both Ends: Shifts in Herbivore Assemblages Impact Top-Down and Bottom-Up Processes on Coral Reefs. Ecosystems 24, 1702–1715. https://doi.org/10.1007/s10021-021-00612-0

Nash, K.L., Graham, N.A.J., Bellwood, D.R., 2013. Fish foraging patterns, vulnerability to fishing, and implications for the management of ecosystem function across scales. Ecological Applications 23, 1632–1644. https://doi.org/10.1890/12-2031.1

National Park Service, 2017. Foundation Document: Channel Islands National Park.

National Park Service, 2016. Western Gull - Channel Islands National Park (U.S. National Park Service) [WWW Document]. Channel Islands National Park: Western Gull. URL https://www.nps.gov/chis/learn/nature/western-gull.htm (accessed 1.14.22).

Navarro, J., Grémillet, D., Afán, I., Ramírez, F., Bouten, W., Forero, M.G., 2016. Feathered Detectives: Real-Time GPS Tracking of Scavenging Gulls Pinpoints Illegal Waste Dumping. PLOS ONE 11, e0159974. https://doi.org/10.1371/journal.pone.0159974

Navarro, J., Grémillet, D., Ramirez, F.J., Afán, I., Bouten, W., Forero, M.G., 2017. Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes. Marine Ecology Progress Series 578, 243–251. https://doi.org/10.3354/meps12124

Norris, K.S., Schilt, C.R., 1988. Cooperative societies in three- dimensional space: On the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. Ethology and Sociobiology 9, 149–179. https://doi.org/10.1016/0162-3095(88)90019-2

Nowicki, R.J., Thomson, J.A., Fourqurean, J.W., Wirsing, A.J., Heithaus, M.R., 2021. Loss of predation risk from apex predators can exacerbate marine tropicalization caused by extreme climatic events. Journal of Animal Ecology n/a. https://doi.org/10.1111/1365-2656.13424

Opstvedt, J., Aksnes, A., Hope, B., Pike, I.H., 2003. Efficiency of feed utilization in Atlantic salmon (Salmo salar L.) fed diets with increasing substitution of fish meal with vegetable proteins. Aquaculture 221, 365–379. https://doi.org/10.1016/S0044-8486(03)00026-7

Ormond, R.F.G., 2009. Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. Journal of Zoology 191, 247–262. https://doi.org/10.1111/j.1469-7998.1980.tb01458.x

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16, 1501–1514. https://doi.org/10.1111/ele.12187

Orpwood, J.E., Magurran, A.E., Armstrong, J.D., Griffiths, S.W., 2008. Minnows and the selfish herd: effects of predation risk on shoaling behaviour are dependent on habitat complexity. Animal Behaviour 76, 143–152. https://doi.org/10.1016/j.anbehav.2008.01.016

Osterback, A.-M.K., Frechette, D.M., Hayes, S.A., Shaffer, S.A., Moore, J.W., 2015. Long-term shifts in anthropogenic subsidies to gulls and implications for an imperiled fish. Biological Conservation 191, 606–613. https://doi.org/10.1016/j.biocon.2015.07.038

Otero, X.L., Peña-Lastra, S.D.L., Pérez-Alberti, A., Ferreira, T.O., Huerta-Diaz, M.A., 2018. Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. Nature Communications 9, 246. https://doi.org/10.1038/s41467-017-02446-8

Otero, X.L., Tejada, O., Martín-Pastor, M., De La Peña, S., Ferreira, T.O., Pérez-Alberti, A., 2015. Phosphorus in seagull colonies and the effect on the habitats. The case of yellow-legged gulls (*Larus michahellis*) in the Atlantic Islands National Park (Galicia-NW Spain). Science of The Total Environment 532, 383–397. https://doi.org/10.1016/j.scitotenv.2015.06.013

Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.-M., Marshall, A.D., Pollom, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J.S., Kindsvater, H.K., Dulvy, N.K., 2021. Half a century of global decline in oceanic sharks and rays. Nature 589, 567–571. https://doi.org/10.1038/s41586-020-03173-9

Paijmans, K.C., Booth, D.J., Wong, M.Y.L., 2019. Towards an ultimate explanation for mixed-species shoaling. Fish and Fisheries 20, 921–933. https://doi.org/10.1111/faf.12384

Palumbi, S.R., 2001. Humans as the world's greatest evolutionary force. Science 293, 1786–1790. https://doi.org/10.1126/science.293.5536.1786

Parrish, J.K., 1991. Do predators shape fish schools: Interactions between predators and their schooling prey. Netherlands Journal of Zoology 42, 358–370. https://doi.org/10.1163/156854291X00388

Parrish, J.K., Turchin, P., 1997. Individual decisions, traffic rules, and emergent pattern in schooling fish, in: Parrish, J.K., Hamner, W.M. (Eds.), Animal Groups in Three Dimensions: How Species Aggregate. Cambridge University Press, Cambridge, pp. 126–142. https://doi.org/10.1017/CBO9780511601156.009

Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., van der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M., Janssens, I.A., 2013. Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. Nature Communications 4, 2934. https://doi.org/10.1038/ncomms3934

Perry, J.E., Glassow, M.A., Neal, M.L., Joslin, T.L., Minas, K.R., 2019. Small islands and marginality: Santa Barbara Island and its role in the prehistory of California's Channel Islands. Journal of Field Archaeology 44, 581–595. https://doi.org/10.1080/00934690.2019.1662262

Phoenix, G.K., Hicks, W.K., Cinderby, S., Kuylenstierna, J.C.I., Stock, W.D., Dentener, F.J., Giller, K.E., Austin, A.T., Lefroy, R.D.B., Gimeno, B.S., Ashmore, M.R., Ineson, P., 2006. Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. Global Change Biology 12, 470–476. https://doi.org/10.1111/j.1365-2486.2006.01104.x

Pierotti, R., Annett, C., 2001. The ecology of Western Gulls in habitats varying in degree of urban influence, in: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Springer US, Boston, MA, pp. 307–329. https://doi.org/10.1007/978-1-4615-1531-9_15

Pierotti, R.J., Annett, C.A., 1995. Western Gull (*Larus occidentalis*), in: The Birds of North America Online (A. Poole Ed.). Cornell Lab of Ornithology, Ithaca.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2022. nlme: Linear and Nonlinear Mixed Effects Models. CRAN R Project.

Pitcher, T.J., 1986. Functions of Shoaling Behaviour in Teleosts, in: The Behaviour of Teleost Fishes. Springer, Boston, MA, pp. 294–337. https://doi.org/10.1007/978-1-4684-8261-4_12

Pitcher, T.J., 1983. Heuristic definitions of fish shoaling behaviour. Animal Behaviour 31, 611–613. https://doi.org/10.1016/S0003-3472(83)80087-6

Plaza, P.I., Lambertucci, S.A., 2017. How are garbage dumps impacting vertebrate demography, health, and conservation? Global Ecology and Conservation 12, 9–20. https://doi.org/10.1016/j.gecco.2017.08.002

Polunin, N.V.C., Harmelin-Vivien, M., Galzin, R., 1995. Contrasts in algal food processing among five herbivorous coral-reef fishes. Journal of Fish Biology 47, 455–465. https://doi.org/10.1111/j.1095-8649.1995.tb01914.x

Portnoy, J.W., 1990. Gull contributions of phosphorus and nitrogen to a Cape Cod kettle pond. Hydrobiologia 202, 61–69. https://doi.org/10.1007/BF00027092

Post, D.M., 2002. Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Post, E., Peterson, R.O., Stenseth, N.C., McLaren, B.E., 1999. Ecosystem consequences of wolf behavioural response to climate. Nature 401, 905–907. https://doi.org/10.1038/44814

Potts, D.C., 1977. Suppression of coral populations by filamentous algae within damselfish territories. Journal of Experimental Marine Biology and Ecology 28, 207–216. https://doi.org/10.1016/0022-0981(77)90092-2

Provencher, J.F., Vermaire, J.C., Avery-Gomm, S., Braune, B.M., Mallory, M.L., 2018. Garbage in guano? Microplastic debris found in faecal precursors of seabirds known to ingest plastics. Science of The Total Environment 644, 1477–1484. https://doi.org/10.1016/j.scitotenv.2018.07.101

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramírez, F., Navarro, J., Afán, I., Hobson, K.A., Delgado, A., Forero, M.G., 2012. Adapting to a changing world: unraveling the role of man-made habitats as alternative feeding areas for Slender-Billed Gull (*Chroicocephalus genei*). PLOS ONE 7, e47551. https://doi.org/10.1371/journal.pone.0047551

Randall, J.E., 1961. Contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. Pacific Science 15, 215–272.

Rassweiler, A., Dubel, A.K., Hernan, G., Kushner, D.J., Caselle, J.E., Sprague, J.L., Kui, L., Lamy, T., Lester, S.E., Miller, R.J., 2020a. Roving divers surveying fish in fixed areas capture similar patterns in biogeography but different estimates of density when compared With belt transects. Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.00272

Rassweiler, A., Lauer, M., Lester, S.E., Holbrook, S.J., Schmitt, R.J., Madi Moussa, R., Munsterman, K.S., Lenihan, H.S., Brooks, A.J., Wencélius, J., Claudet, J., 2020b. Perceptions and responses of Pacific Island fishers to changing coral reefs. Ambio 49, 130–143. https://doi.org/10.1007/s13280-019-01154-5

Reinthal, P.N., Lewis, S.M., 1986. Social behaviour, foraging efficiency and habitat utilization in a group of tropical herbivorous fish. Animal Behaviour 34, 1687–1693. https://doi.org/10.1016/S0003-3472(86)80256-1

Rempel, H.S., Siebert, A.K., Van Wert, J.C., Bodwin, K.N., Ruttenberg, B.I., 2022. Feces consumption by nominally herbivorous fishes in the Caribbean: an underappreciated source of nutrients? Coral Reefs. https://doi.org/10.1007/s00338-022-02228-9

Rick, T.C., 2006. A 5,000-year record of coastal settlement on Anacapa Island, California. Journal of California and Great Basin Anthropology 26, 65–72.

Rick, T.C., Sillett, T.S., Ghalambor, C.K., Hofman, C.A., Ralls, K., Anderson, R.S., Boser, C.L., Braje, T.J., Cayan, D.R., Chesser, R.T., Collins, P.W., Erlandson, J.M., Faulkner, K.R., Fleischer, R., Funk, W.C., Galipeau, R., Huston, A., King, J., Laughrin, L., Maldonado, J., McEachern, K., Muhs, D.R., Newsome, S.D., Reeder-Myers, L., Still, C., Morrison, S.A., 2014. Ecological change on California's Channel Islands from the Pleistocene to the Anthropocene. BioScience 64, 680–692. https://doi.org/10.1093/biosci/biu094

Ripple, W.J., Beschta, R.L., 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184, 299–313. https://doi.org/10.1016/S0378-1127(03)00154-3

Ripple, W.J., Wirsing, A.J., Wilmers, C.C., Letnic, M., 2013. Widespread mesopredator effects after wolf extirpation. Biological Conservation 160, 70–79. https://doi.org/10.1016/j.biocon.2012.12.033

Robertson, D.R., Sweatman, H.P.A., Fletcher, E.A., Cleland, M.G., 1976. Schooling as a Mechanism for Circumventing the Territoriality of Competitors. Ecology 57, 1208–1220. https://doi.org/10.2307/1935045

Rodewald, A.D., Kearns, L.J., Shustack, D.P., 2011. Anthropogenic resource subsidies decouple predator–prey relationships. Ecological Applications 21, 936–943. https://doi.org/10.1890/10-0863.1

Roman, J., McCarthy, J.J., 2010. The whale pump: marine mammals enhance primary productivity in a coastal basin. PLOS ONE 5, e13255. https://doi.org/10.1371/journal.pone.0013255

Rooker, J.R., Dance, M.A., Wells, R.J.D., Quigg, A., Hill, R.L., Appeldoorn, R.S., Padovani Ferreira, B., Boswell, K.M., Sanchez, P.J., Moulton, D.L., Kitchens, L.L., Rooker, G.J., Aschenbrenner, A., 2018. Seascape connectivity and the influence of predation risk on the movement of fishes inhabiting a back-reef ecosystem. Ecosphere 9, e02200. https://doi.org/10.1002/ecs2.2200

RStudio Team, 2020. RStudio: Integrated Development Environment for R. RStudio, PBC., Boston, MA.

Samia, D.S.M., Bessa, E., Blumstein, D.T., Nunes, J.A.C.C., Azzurro, E., Morroni, L., Sbragaglia, V., Januchowski-Hartley, F.A., Geffroy, B., 2019. A meta-analysis of fish behavioural reaction to underwater human presence. Fish and Fisheries 20, 817–829. https://doi.org/10.1111/faf.12378

Sandin, S. a, Smith, J.E., Demartini, E.E., Dinsdale, E. a, Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R.E., Walsh, S., Jackson, J.B.C., Knowlton, N., Sala, E., 2008. Baselines and degradation of coral reefs in the Northern Line Islands. PloS one 3, e1548. https://doi.org/10.1371/journal.pone.0001548

Sandin, S.A., McNamara, D.E., 2012. Spatial dynamics of benthic competition on coral reefs. Oecologia 168, 1079–1090. https://doi.org/10.1007/s00442-011-2156-0

Sbragaglia, V., Jolles, J.W., Coll, M., Arlinghaus, R., 2021a. Fisheries-induced changes of shoaling behaviour: mechanisms and potential consequences. Trends in Ecology & Evolution 36, 885–888. https://doi.org/10.1016/j.tree.2021.06.015

Sbragaglia, V., Klamser, P.P., Romanczuk, P., Arlinghaus, R., 2021b. Evolutionary impact of size-selective harvesting on shoaling behavior: Individual-level mechanisms and possible consequences for natural and fishing mortality. The American Naturalist. https://doi.org/10.1086/718591

Schmitt, E., Sluka, R., Sullivan-Sealey, K., 2002. Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage off southeastern Hispaniola. Coral Reefs 21, 216–223. https://doi.org/10.1007/s00338-002-0216-y

Schoener, T.W., 1968. Sizes of Feeding Territories among Birds. Ecology 49, 123–141. https://doi.org/10.2307/1933567

Schoenherr, A.A., Feldmeth, C.R., Emerson, M.J., 2003. Natural History of the Islands of California. University of California Press.

Seghers, B.H., 1974. Schooling behavior in the guppy (*Poecilia reticulata*): An evolutionary response to predation. Evolution 28, 486–489. https://doi.org/10.2307/2407174

Seghers, B.H., Magurran, A.E., 1994. Predator inspection behaviour covaries with schooling tendency amongst wild guppy, *Poecilia Reticulata*, populations in Trinidad. Behaviour 128, 121–134. https://doi.org/10.1163/156853994X00073

Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. PNAS 109, 16083–16088. https://doi.org/10.1073/pnas.1211658109

Shaffer, S.A., Cockerham, S., Warzybok, P., Bradley, R.W., Jahncke, J., Clatterbuck, C.A., Lucia, M., Jelincic, J.A., Cassell, A.L., Kelsey, E.C., Adams, J., 2017. Population-level plasticity in foraging behavior of western gulls (*Larus occidentalis*). Mov Ecol 5. https://doi.org/10.1186/s40462-017-0118-9

Shantz, A.A., Ladd, M.C., Schrack, E., Burkepile, D.E., 2015. Fish-derived nutrient hotspots shape coral reef benthic communities. Ecological Applications 25, 2142–2152. https://doi.org/10.1890/14-2209.1

Silbiger, N.J., Nelson, C.E., Remple, K., Sevilla, J.K., Quinlan, Z.A., Putnam, H.M., Fox, M.D., Donahue, M.J., 2018. Nutrient pollution disrupts key ecosystem functions on coral reefs. Proceedings of the Royal Society B: Biological Sciences 285, 20172718. https://doi.org/10.1098/rspb.2017.2718

Sims, J.T., Pierzynski, G.M., 2005. Chemistry of phosphorus in soils, in: Chemical Processes in Soils. John Wiley & Sons, Ltd, pp. 151–192. https://doi.org/10.2136/sssabookser8.c2

Smith, J.S., Johnson, C.R., 1995. Nutrient inputs from seabirds and humans on a populated coral cay. Marine Ecology Progress Series 124, 189–200.

Southgate, D. a. T., 1969. Determination of carbohydrates in foods II.—Unavailable carbohydrates. Journal of the Science of Food and Agriculture 20, 331–335. https://doi.org/10.1002/jsfa.2740200603

Spear, L.B., 1988. Dispersal Patterns of Western Gulls from Southeast Farallon Island. The Auk 105, 128–141.

Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society B: Biological Sciences 272, 2627–2634. https://doi.org/10.1098/rspb.2005.3251

Stears, K., McCauley, D.J., Finlay, J.C., Mpemba, J., Warrington, I.T., Mutayoba, B.M., Power, M.E., Dawson, T.E., Brashares, J.S., 2018. Effects of the hippopotamus on the chemistry and ecology of a changing watershed. PNAS 201800407. https://doi.org/10.1073/pnas.1800407115

Stevenson, C., Katz, L.S., Micheli, F., Block, B., Heiman, K.W., Perle, C., Weng, K., Dunbar, R., Witting, J., 2006. High apex predator biomass on remote Pacific islands. Coral Reefs 26, 47–51. https://doi.org/10.1007/s00338-006-0158-x

Stief, P., Hölker, F., 2006. Trait-Mediated Indirect Effects of Predatory Fish on Microbial Mineralization in Aquatic Sediments. Ecology 87, 3152–3159. https://doi.org/10.1890/0012-9658(2006)87[3152:TIEOPF]2.0.CO;2

Subalusky, A.L., Dutton, C.L., Rosi, E.J., Post, D.M., 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. PNAS 114, 7647–7652. https://doi.org/10.1073/pnas.1614778114

Subalusky, A.L., Post, D.M., 2019. Context dependency of animal resource subsidies. Biological Reviews 94, 517–538. https://doi.org/10.1111/brv.12465

Tiessen, H., 2008. Phosphorus in the global environment, in: White, P.J., Hammond, J.P. (Eds.), The Ecophysiology of Plant-Phosphorus Interactions, Plant Ecophysiology. Springer Netherlands, Dordrecht, pp. 1–7. https://doi.org/10.1007/978-1-4020-8435-5_1

Tootell, J.S., Steele, M.A., 2016. Distribution, behavior, and condition of herbivorous fishes on coral reefs track algal resources. Oecologia 181, 13–24. https://doi.org/10.1007/s00442-015-3418-z

Tran, D.S.C., Langel, K.A., Thomas, M.J., Blumstein, D.T., 2016. Spearfishing-induced behavioral changes of an unharvested species inside and outside a marine protected area. Current Zoology 62, 39–44. https://doi.org/10.1093/cz/zov006

Turner, G.F., Pitcher, T.J., 1986. Attack Abatement: a model for group protection by combined avoidance and dilution. The American Naturalist 128, 228–240.

Uhlig, D., von Blanckenburg, F., 2019. How Slow Rock Weathering Balances Nutrient Loss During Fast Forest Floor Turnover in Montane, Temperate Forest Ecosystems. Frontiers in Earth Science 7.

Uiblein, F., 1991. Ontogenetic Shifts in Resource Use and Shoaling Tendency Related to Body Size in Red Sea Goatfish (Parupeneus forsskali, Mullidae). Marine Ecology 12, 153–161. https://doi.org/10.1111/j.1439-0485.1991.tb00249.x

Vallano, D.M., Selmants, P.C., Zavaleta, E.S., 2012. Simulated nitrogen deposition enhances the performance of an exotic grass relative to native serpentine grassland competitors. Plant Ecol 213, 1015–1026. https://doi.org/10.1007/s11258-012-0061-1

van Rooij, J.M., Kroon, F.J., Videler, J.J., 1996. The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. Environ Biol Fish 47, 353–378. https://doi.org/10.1007/BF00005050

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Global terrestrial Human Footprint maps for 1993 and 2009. Sci Data 3, 160067. https://doi.org/10.1038/sdata.2016.67

Vermeij, M.J.A., DeBey, H., Grimsditch, G., Brown, J., Obura, D., DeLeon, R., Sandin, S.A., 2015. Negative effects of gardening damselfish Stegastes planifrons on coral health depend on predator abundance. Marine Ecology Progress Series 528, 289–296. https://doi.org/10.3354/meps11243

Vidal, E., Médail, F., Tatoni, T., Bonnet, V., 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. Oecologia 122, 427–434. https://doi.org/10.1007/s004420050049

Vidal, E., Médail, F., Tatoni, T., Roche, P., Vidal, P., 1998. Impact of gull colonies on the flora of the Riou archipelago (Mediterranean islands of south-east France).

Biological Conservation 84, 235–243. https://doi.org/10.1016/S0006-3207(97)00130-4

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H., Tilman, D.G., 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7, 737–750. https://doi.org/10.1890/1051-0761(1997)007[0737:HAOTGN]2.0.CO;2

Votier, S.C., Bearhop, S., Witt, M.J., Inger, R., Thompson, D., Newton, J., 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. Journal of Applied Ecology 47, 487–497. https://doi.org/10.1111/j.1365-2664.2010.01790.x

Wal, R.V.D., Truscott, A.-M., Pearce, I.S.K., Cole, L., Harris, M.P., Wanless, S., 2008. Multiple anthropogenic changes cause biodiversity loss through plant invasion. Global Change Biology 14, 1428–1436. https://doi.org/10.1111/j.1365-2486.2008.01576.x

Walker, B.L.E., Robinson, M.A., 2009. Economic development, marine protected areas and gendered access to fishing resources in a Polynesian lagoon. Gender, Place & Culture 16, 467–484. https://doi.org/10.1080/09663690903003983

Weiser, E.L., Powell, A.N., 2010. Does garbage in the diet improve reproductive output of Glaucous Gulls? Condor 112, 530–538. https://doi.org/10.1525/cond.2010.100020

Welsh, J.Q., Bellwood, D.R., 2012. How far do schools of roving herbivores rove? A case study using Scarus rivulatus. Coral Reefs 31, 991–1003. https://doi.org/10.1007/s00338-012-0922-z

West, E.H., Henry, W.R., Goldenberg, W., Peery, M.Z., 2016. Influence of food subsidies on the foraging ecology of a synanthropic species in protected areas. Ecosphere 7, e01532. https://doi.org/10.1002/ecs2.1532

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. Journal of Open Source Software 4, 1686. https://doi.org/10.21105/joss.01686

Wilson, L.J., Bacon, P.J., Bull, J., Dragosits, U., Blackall, T.D., Dunn, T.E., Hamer, K.C., Sutton, M.A., Wanless, S., 2004. Modelling the spatial distribution of ammonia emissions from seabirds in the UK. Environ Pollut 131, 173–185. https://doi.org/10.1016/j.envpol.2004.02.008

Wirsing, A.J., Heithaus, M.R., Dill, L.M., 2007. Fear factor: do dugongs (Dugong dugon) trade food for safety from tiger sharks (Galeocerdo cuvier)? Oecologia 153, 1031–1040. https://doi.org/10.1007/s00442-007-0802-3

Wootton, J.T., 1991. Direct and indirect effects of nutrients on intertidal community structure: variable consequences of seabird guano. Journal of Experimental Marine Biology and Ecology 151, 139–153. https://doi.org/10.1016/0022-0981(91)90121-C

Yamamuro, M., 1999. Importance of epiphytic cyanobacteria as food sources for heterotrophs in a tropical seagrass bed. Coral Reefs 18, 263–271. https://doi.org/10.1007/s003380050191

Young, H.S., McCauley, D.J., Dunbar, R.B., Dirzo, R., 2010. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. PNAS 107, 2072–2077. https://doi.org/10.1073/pnas.0914169107

Zemke-White, L.W., Choat, J., Clements, K., 2002. A re-evaluation of the diel feeding hypothesis for marine herbivorous fishes. Marine Biology 141, 571–579. https://doi.org/10.1007/s00227-002-0849-y

Zgliczynski, B.J., Sandin, S.A., 2017. Size-structural shifts reveal intensity of exploitation in coral reef fisheries. Ecological Indicators 73, 411–421. https://doi.org/10.1016/j.ecolind.2016.09.045

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.

APPENDIX

CHAPTER 2 APPENDIX

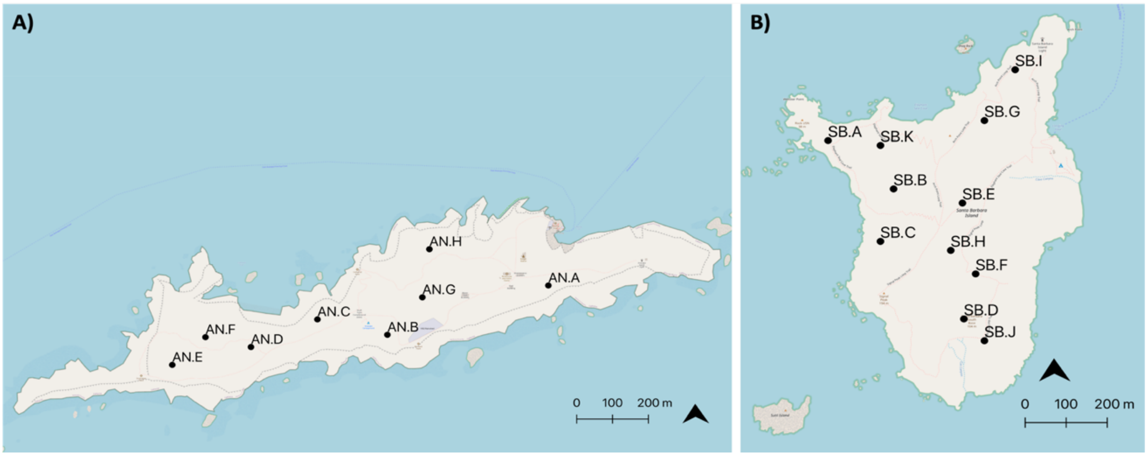

Figure A1. Soil sampling and nest count sites on (A) Anacapa Island (ANIS) and (B) Santa Barbara Island (SBIS), part of the Channel Islands National Park in California (USA).

Table A1. Description of full linear mixed effects models fit by maximum likelihood (ML)

Response	NO_3N, NH_4N, P
Fixed effects	island sampling period nest count
Random effects	site (within island)

Table A2. Mean (± sd) soil nutrient concentrations during early and late breeding season.

Soil nutrient (or characteristic)	**ANIS**		**SBIS**	
	Early season	*Late season*	*Early season*	*Late season*
NH_4-N (mg/kg)	10.24 ± 4.14	45.61 ± 17.30	10.62 ± 5.70	53.33 ± 46.46
NO_3-N (mg/kg)	15.63 ± 9.44	37.5 ± 16.06	19.38 ± 18.00	38.44 ± 17.14
Phosphorus (mg/kg)	252.13 ± 215.09	291.13 ± 230.30	511.10 ± 251.00	647.36 ± 369.38

Table A3. Nest counts

Island	Site	nest count
ANIS	A	35
	B	10
	C	60
	D	44
	E	44
	F	51
	G	15
	H	22
SBIS	A	17
	B	8
	C	2
	D	14
	E	0
	F	16
	G	12
	H	4
	I	14
	J	8
	K	5

Table A4. Next best-fit linear mixed models (AIC<2) for predicting concentrations of P, NO3-N, and NH4-N at two *Larus occidentalis* nesting islands

NO_3-N model 2	*Random effects*	*variance*	*sd*	
	site	106.6	10.32	
	residual	156.6	12.51	
	Fixed effects	*estimate*	*se*	*t-value*
	(intercept)	16.439	5.218	3.15
	island	2.351	6.318	0.372
	sampling period (post)	20.247	4.06	4.987
NO_3-N model 3	*Random effects*	*variance*	*sd*	
	site	108.1	10.4	
	residual	156.6	12.51	
	Fixed effects	*estimate*	*se*	*t-value*
	(intercept)	17.894	5.2	3.442
	nest count	2.351	6.318	0.372
	sampling period (post)	20.247	4.06	4.987
NH_4-N model 2	*Random effects*	*variance*	*sd*	
	site	0	0	
	residual	605.9	24.62	
	Fixed effects	*estimate*	*se*	*t-value*
	(intercept)	-7.027	14.863	-0.473
	nest count	0.431	0.368	1.171
	island (SBIS)	-4.478	17.467	-0.256
	sampling period (post)	39.621	7.989	4.961
	nest.count : island	2.172	1.007	2.157
NH4-N 2 model 3	*Random effects*	*variance*	*sd*	
	site	0	0	
	residual	712.3	26.69	
	Fixed effects	*estimate*	*se*	*t-value*
	(intercept)	10.458	6.124	1.708
	sampling period (post)	39.621	8.661	4.575
P model 2	*Random effects*	*variance*	*sd*	
	site	72511	269.3	
	residual	10990	104.8	
	Fixed effects	*estimate*	*se*	*t-value*
	(intercept)	252.13	102.16	2.468
	island (SBIS)	258.97	134.27	1.929
	sampling period (post)	39	52.42	0.744
	island:sampling period	97.27	68.89	1.412
P model 3	*Random effects*	*variance*	*sd*	
	site	72207	268.7	
	residual	11597	107.7	
	Fixed effects	*estimate*	*se*	*t-value*
	(intercept)	186.816	218.724	0.854
	island (SBIS)	90.542	266.002	0.34
	sampling period (post)	1.058	5.604	0.189
	nest count	95.316	34.939	728
	island:nest count	26.906	15.333	1.755

Table A5. Values of δ_{13}C and δ_{15}N isotope ratios for plasma and feather samples from *Larus occidentalis* nesting on Santa Barbara Island (SBIS) and Anacapa Island (ANIS).

sample type	**colony**	**N**	δ^{13}C (mean ± sd)	δ^{15}N (mean ± sd)
feather	ANIS	87	-17.41 ± 0.86	12.92 ± 2.23
	SBIS	49	-17.3 ± 0.68	13.25 ± 2.17
plasma	ANIS	59	-19.91 ± 0.71	13.94 1.82
	SBIS	27	-20.38 ± 0.80	15.22 ± 1.44

CHAPTER 3 APPENDIX

Figure A2. Field sites on Palmyra Atoll, USA (A) and Moorea, French Polynesia (B). GPS Coordinates for sites can be found in data repository at https://doi.org/10.25349/D94617

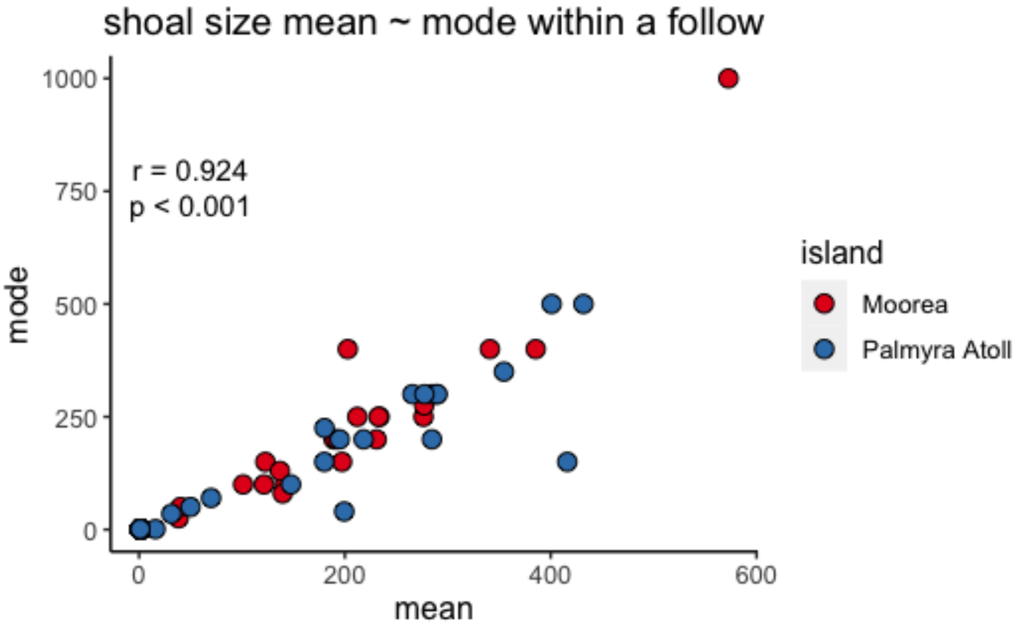

Figure A3. Correlation between mean shoal size and mode of shoal size for Moorea (low predator abundance) and Palmyra Atoll (high predator abundance).

Text A1. Resighting of *A. triostegus*

Acanthurus triostegus resight surveys were conducted at a single site on Moorea, French Polynesia (17°28'47.1"S 149°47'37.1"W). A total of 12 surveys were conducted between 29-September-2019 and 22-October-2019. Any shoals and solitary fish were photographed for later analysis. Towards later surveys, individual solitary and paired fish were easily identifiable by observer and their presence was logged without photographing.

Shoaling and solitary fish in photographs were identified using right-side markings only (Fig. SI3). We identified and re-sighted five solitary fish and seven shoaling fish. Every resighted fish was exhibiting social behavior (shoaling or solitary) across sightings. Average number of resights was 3.5 ± 2.2, with a maximum of 8 resights and a minimum of 2. The mean time span between first and last resight was 14.7 ± 6.5 days, with a maximum of 20 days and a minimum of 1 day. We also photographed putative matches for 2 solitary and 2 shoaling fish in the same location and same behavioral mode 21.5 months later; however, the shoaling fish exhibited some subtle growths to their melanistic patterns, as such without knowledge on how these patterns may change over time, we cannot provide complete certainty that these are the same fish (Fig SI4). Future work can help further substantiate if this behavioral fidelity does indeed persist for long time periods and whether this pattern remains consistent across a wider range of geographic sites.

Figure A4. Examples of the distinguishing markings of *A. triostegus* found on the reefs of Moorea. Top image shows a fish with distinct melanistic facial markings, and bottom image shows a fish with distinguishing spots on the right flank, distinct spotting along the third bar, and an incomplete bar in the caudal peduncle.

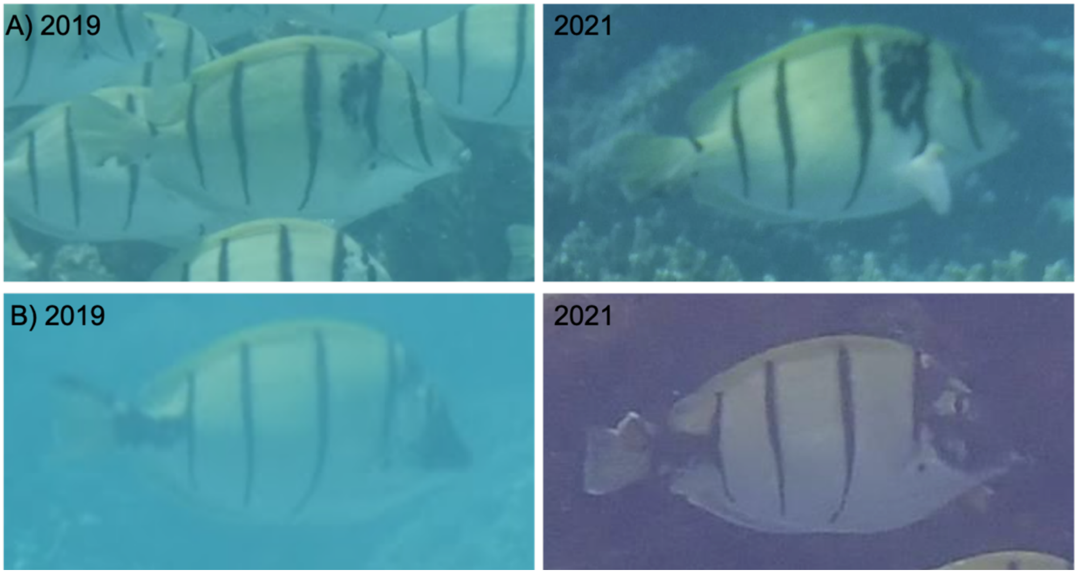

Figure A5. Two shoaling A. triostegus (fish A and B) sighted in 2019 (first column) and their potential resights in 2021 with growth to melanistic patterns. Fish A shows a fish with a dark mottling that contains a light vacuoule after the second bar, a thick third bar, and a notch on the ventral side of the caudal fin in 2019. In 2021 the caudal fin notch is still present, the third bar appears a bit thicker, and the mottling behind the second bar has grown, but the vacuole is still present. Fish B in 2019 has dark patterns along the nose and in the forehead area between the first and second bar, thin bars along the body, and then a thick stripe of mottling between the 5th and 6th bars, extending out into the caudal peduncle. The dorsal side of the caudal fin also has dark mottling. In 2021 the facial markings appear to have grown to almost fully occupy the anterior side of the second bar. The stripe along posterior end appears similar, although the caudal fin has been damaged and it is not possible to assess the markings along the dorsal side of it.

Table A6. Description of full linear mixed effects models fit by maximum likelihood (ML)

Response	**Prevalence of shoaling behavior**	**distance travelled, 95% KUD***	**non-vigilant grazing behavior•**	**Non-vigilant grazing, distance travelled, 95% KUD†**
Fixed effects	island (predator abundance)	island (predator abundance)	island (predator abundance)	island (predator abundance)
	abundance°	social state (shoaling or solitary)		shoal size
	territorial herbivore abundance			
Random effects	site (within island)	site	site	site
		time of day	time of day	time of day

°total abundance of fish for the species of interest

*for both solitary and shoaling *A. triostegus*

• ony for solitary *A. triostegus*

†only for shoals of A. triostegus

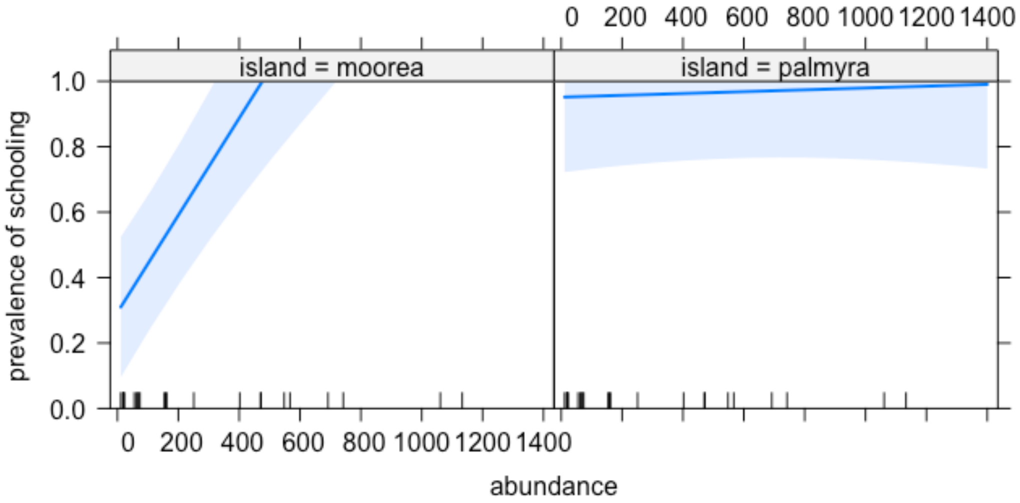

Fig A6. Model of interaction of abundance and island from best fit mixed effects model for predicting prevalence of shoaling behavior in *Acanthurus triostegus,* suggesting prevalence of shoaling increases with fish abundance on the low predator abundance island (Moorea), but not the high predator abundance island (Palmyra Atoll).

Table A7. Means and differences in number of shoals, abundance, and shoal sizes observed per survey between islands for three focal species

		mean (± SD)		**Wilcoxon rank sum**	
		High predator (PA)	*Low predator (M)*	*W*	*p*
A. triostegus	*number of shoals*	20.71 (±13.07)	2 (±2.49)	16.5	0.0
	*abundance**	519.50 (±454.76)	127.45 (±163.36)	31	0.01
	shoal size	38.31 (±101.46)	123.10 (±103.23)	1315	0.01
C. spilurus	*number of shoals*	17.71 (±8.49)	13.36 (±5.54)	47	0.11
	*abundance**	105.57 (±52.78)	70.36 ± (39.37)	46	0.10
	shoal size	6.40 (±5.69)	5.42 (±4.29)	9054	0.00
M. flavolineatus	*number of shoals*	1.57 (±2.10)	3.27 (±2.97)	108	0.09
	*abundance**	128.28 (±196.76)	85.45 (±94.91)	90.5	0.47
	shoal size	85 (±135.10)	32.19 (±62.38)	170	0.02

*abundance of individuals of each species

Table A8. Next best fit linear mixed models (ΔAICc < 2) for prevalence of shoaling behavior for *Mulloidicthys flavolineatus*

	Model 1			*Model 2*		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	0.78	0.08	10.27	0.80	0.07	11.08
island (high predator abundance)	-	-	-	0.20	0.12	1.70
abundance	0.00	0	1.74	-	-	-
island*abundance	-	-	-	-	-	-
territorial herbivore abundance	-	-	-	-	-	-
Random effect	**variance**	**SD**		**variance**	**SD**	
site (within island)	0	0		0	0	

Table A9. Mean (± SD) for shoaling and solitary *A. triostegus* behavior at the high and low predator abundance islands.

Island	**Social behavior**	**Non-vigilant behavior (proportion of follow)**	**Distance travelled per minute (m)**	**95% KUD (m^2 for a 25min follow)**
high predator abundance (PA)	solitary	0.51 (± 0.24)	3.37 (± 4.98)	1706.18 (± 4341)
	shoaling	0.58 (± 0.58)	7.83 (± 3.07)	18139.56 (± 27710)
low predator abundance (M)	solitary	0.60 (± 0.17)	6.59 (± 2.62)	5067.56 (± 20230)
	shoaling	0.62 (± 0.14)	11.09 (± 3.50)	28360 (± 39713)

Table A10 Next best fit (Δ> AICc) linear mixed model fit for explaining time spent in grazing position for shoaling and solitary *Acanthurus triostegus* on Palmyra Atoll (high predator abundance) and Moorea (low predator abundance)

	solitary Model 1			shoals Model 1		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	0.60	0.08	0.55	0.49	0.10	5.04
island (high predator abundance)	-0.12	0.1	1.23	-	-	-
shoal size†				-0.00	0	-1.38
island*shoal size†			-	-	-	
Random effect	**variance**	**SD**	**variance**	**SD**		
time of day	0.01	0.08	0.01	0.10		
site (within island)	0.02	0.13	0.00	0.00		
observer	0.00	0.00	0.02	0.16		

† fit in model for shoals only

Table A11. Next best fit linear mixed models (ΔAICc < 2) for 25-min 95% KUD (log-transformed) for *A. triostegus*.

	Model 1		
Fixed effect	**estimate**	**SE**	**t-value**
intercept	4.22	0.19	22.05
island (high predator abundance)	-0.46	0.25	-1.85
social behavior (solitary)	-1.21	0.18	-6.63
island*sociality	-0.20	0.29	-0.70
Random effect	**variance**	**SD**	
time of day	0.00	0.00	
site (within island)	0.06	0.24	
observer	0.40	0.63	

CHAPTER 4 APPENDIX

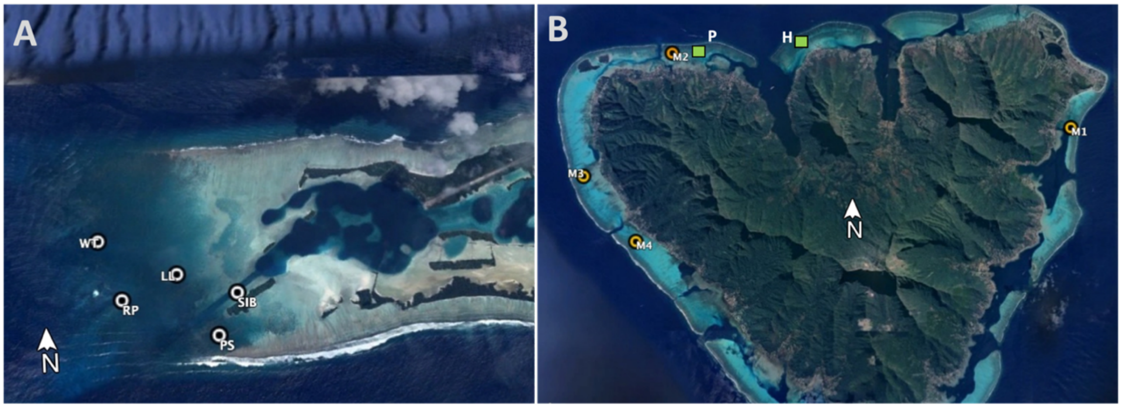

Figure A7. Field sites on (A) Palmyra Atoll, USA and (B) Moorea, French Polynesia. Circles represent behavioral observation sites, and squares (sites P and H, only on Moorea (B), represent sampling sites). GPS Coordinates for sites can be found in data repository at https://doi.org/10.25349/D94617

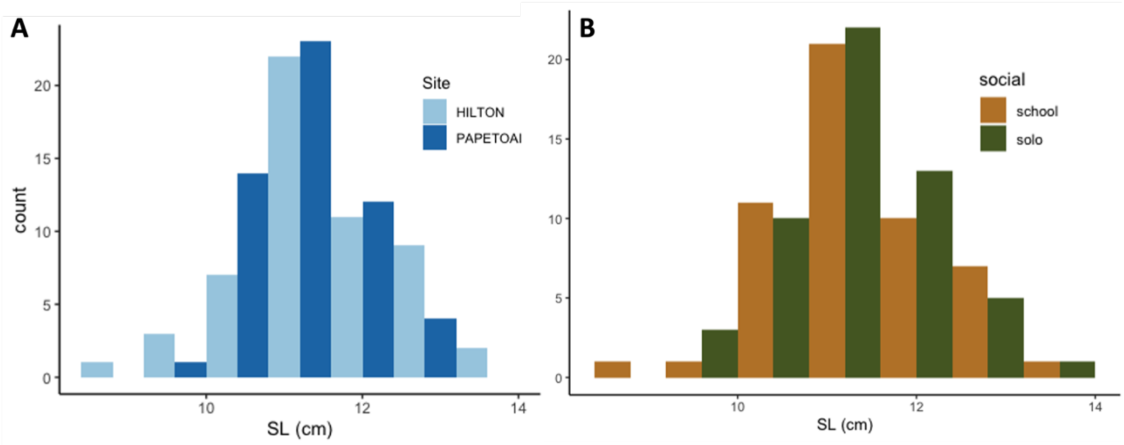

Figure A8. Histograms of sampled fish sizes (standard length in centimeters) across the two sites on Moorea, French Polynesia (A), and distribution across the two social modes: shoaling and solitary (B).

Table A12. Species list for heterospecific fish associated with *A. triostegus* on Palmyra Atoll and Moorea

	Palmyra Atoll	**Moorea**
Predatory	*Aulostomus chinensis* *Caranx melampygus* *Carcharhinus melanopterus* *Cephalopholis argus* *Lutjanus bohar*	*Aulostomus chinensis* *Fistularia commersoni* *Caranx melampygus*
Non-predatory	*Acanthurus blochii* *Acanthurus xanthoptherus* *Chlorurus frontalis* *Chlorurus spilurus* *Kyphosis sp.* *Mellycthis niger* *Scarus altipinnis* *Scarus frenatus* *Scarus oviceps* *Scarus rubroviolaceus*	*Acanthurus guttatus* *Cantherhines dumerilii* *Chlorurus spilurus* *Scarus psittacus* *Siganus argenteus*

Table A13. Best fit linear mixed models for explaining variation in distance traveled and 95% KUD for shoaling *Acanthurus triostegus*.

	distance traveled			95% KUD		
Fixed effect	**estimate**	**SE**	**t-value**	**estimate**	**SE**	**t-value**
intercept	9.35	2.05	4.55	3.95	0.23	17.36
shoal size	-	-	-	-	-	-
Random effect	**variance**	**SD**		**variance**	**SD**	
time of day	1.78	1.33		0.00	0.06	
island	6.42	2.53		0.04	0.21	
site (within island)	0.33	0.57		0.23	0.48	

Table A14. Summary of mean and standard deviation (SD) of proportion of time spent grazing and grazing within heterospecific territories for shoals and solitary *Acanthurus triostegus*, and proportion of all follows during which predatory and non-predatory fish were associated.

observation		**shoals**		**solitary**	
		mean	SD	mean	SD
grazing (proportion of follow)	*Palmyra Atoll*	0.58	0.17	0.51	0.24
	Moorea	0.62	0.14	0.6	0.17
territorial invasions (proportion of grazing events)	*Palmyra Atoll*	0.9	0.12	0.02	0.04
	Moorea	0.83	0.16	0.13	0.14
non-predatory fish associations (proportion of all follows)	*Palmyra Atoll*	0.95	0.23	0	0
	Moorea	0.71	0.46	0	0
predatory fish associations (proportion of all follows)	*Palmyra Atoll*	1	0	0	0
	Moorea	0.24	0.44	0	0

Table A15. Wilcoxon-rank sum test results for comparing *A. triostegus* size between the two collection sites and two social modes (shoaling and solitary)

	W	**p-value**
Sites	1280	0.21
Social behavior	1413.5	0.95

Table A16. Best fit linear models for explaining variation in δ^{15}N and δ^{13}C stable isotope values of muscle tissue of shoaling and solitary *Acanthurus triostegus**

δ^{15}N					δ^{13}C			
coefficient	**estimate**	**SE**	**t-value**	**p-value**	**estimate**	**SE**	**t-value**	**p-value**
intercept	4.87	0.67	7.26	0.00	-5.97	1.08	-5.58	0.00
social behavior (solitary)	0.35	0.1	3.43	0.001				
SL (cm)	0.15	0.06	2.64	0.01	-0.45	0.10	-5.58	0.00
site (P)					-0.54	0.16	-2.24	0.03

*these models include all size fish

Table A17. Next best-fit (dAICc <2) linear models for explaining variations in stomach content and feces macronutrients (proteins and lipids) for shoaling and solitary *Acanthurus triostegus*. Best fit model presented in main text.

		protein				lipids			
	coefficient	**estimate**	**SE**	**t-value**	**p-value**	**estimate**	**SE**	**t-value**	**p-value**
stomach 1	intercept	20.10	2.48	8.11	0.00	-1.66	4.26	-0.39	0.70
	social behavior (solitary)	-2.43	3.61	-0.68	0.5	-	-	-	-
	SL (cm)					0.59	0.36	1.65	0.11
	social:site (solo:P)	6.26	5.1	1.23	0.23	-	-	-	-
	site (P)	2.68	3.6	0.74	0.46	-1.11	0.55	-2.04	0.05
stomach 2	intercept					5.15	0.54	9.46	0.00
	social behavior (solitary)					0.35	0.77	0.45	0.65
	SL (cm)					-	-	-	-
	social:site (solo:P)					-1.52	1.10	-1.38	0.18
	site (P)					-0.43	0.79	-0.54	0.59
stomach 3	intercept					5.52	0.48	11.51	0.00
	social behavior (solitary)					-0.39	0.56	-0.70	0.49
	SL (cm)					-	-	-	-
	social:site (solo:P)					-	-	-	-
	site (P)					-1.21	0.56	-2.70	0.04
stomach 4	intercept					0.35	1.47	-0.08	0.94
	social behavior (solitary)					0.13	0.78	0.17	0.87
	SL (cm)					0.47	0.38	1.24	0.22
	social:site (solo:P)					-1.06	1.16	-0.91	0.37
	site (P)					-0.58	0.80	-0.73	0.47
stomach 5	intercept					1.43	4.30	-0.33	0.74
	social behavior (solitary)					-0.38	0.55	-69.00	0.49

	SL (cm)					0.59	0.36	1.63	0.11
	social:site (solo:P)					-	-	-	-
	site (P)					-1.10	0.55	-2.01	0.05
feces 1	intercept	8.23	7.35	11.12	0.27	13.34	5.68	2.35	0.03
	social behavior (solitary)	2.36	1.3	1.81	0.08	-1.71	1.05	-1.62	0.12
	SL (cm)	0.15	0.63	0.24	0.81	-0.65	0.49	-1.34	0.19
	social:site (solo:P)	-6.19	1.9	-3.27	0.01	1.53	1.48	1.03	0.31
	site (P)	3.17	1.26	2.51	0.02	-2.25	1.01	-2.24	0.03
feces 2	intercept					14.45	5.48	2.64	0.01
	social behavior (solitary)					-	-	-	-
	SL (cm)					-0.81	0.46	-1.77	0.09
	social:site (solo:P)					-	-	-	-
	site (P)					-1.52	0.70	-2.16	0.04
feces 3	intercept					15.04	5.45	2.76	0.01
	social behavior (solitary)					-0.88	0.69	-1.28	0.21
	SL (cm)					-0.83	0.46	-1.82	0.08
	social:site (solo:P)					-	-	-	-
	site (P)					-1.50	0.70	-2.15	0.04