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UNDERSTANDING FISH AND FISHER BEHAVIOR IN CORAL REEF ECOSYSTEMS

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UNDERSTANDING FISH AND FISHER BEHAVIOR IN CORAL REEF ECOSYSTEMS

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Environmental Science and Management

by

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December 2020

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December 2020

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VITA OF MARGARET WATTS WILSON
December 2020

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In Press or Published

Wilson, M., J. Lawson, M. I. Rivera, J. C. Villaseñor-Derbez, S. Gaines. 2020. Status & Trends of moored fish aggregating device (MFAD) fisheries in the Caribbean and Bermuda. *Marine Policy*

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McDonald, G., **M. Wilson**, D. Verissimo, R. Twohey, M. Clemence, D. Apistar, S. Box, P. Butler, Fl Cadiz, S. Campbell, C. Cox, M. Effron, S. Gaines, R. Jakub, R. Mancao, P. Rojas, R. Tirona, G. Vianna. 2020. Catalyzing sustainable fisheries management though behavior change interventions. *Conservation Biology*.

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Liu, O., R. Molina, **M. Wilson**, and B. Halpern. Global opportunities for mariculture development to promote human nutrition. 2018. *PeerJ* e4733: 1-18.

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Cox, M., **M. Wilson**, and T. Pavlowich. 2016. The challenges of local governance: gear-based fragmentation in the Dominican fishery of Buen Hombre. *Marine Policy* 63: 109-117.

Wilson, M., T. Pavlowich, and M. Cox. 2015. Studying Common-Pool Resources over Time: a Longitudinal Case Study of the Buen Hombre Fishery in the Dominican Republic. *Ambio*: 1-15.

In Review or Revision

Wilson, M., A. Stier, B. Halpern, and S. Gaines. Variation in scarid gazing behavior across Caribbean reef sites. *In review at Marine Biology*.

Wilson, M., J. Lawson, M. I. Rivera, J. C. Villaseñor-Derbez, S. Gaines. Optimal conditions for sustainable moored fish aggregating device (MFAD) fisheries. *In prep.*

Tapia-Lewin, S., A. Fredston-Hermann, C. O'Hara, **M. Wilson**, E. Finkbeiner, F. Micheli, R. Molina, and B. S. Halpern. Sustainability in small-scale fisheries through the lens of rights-based management and adaptive capacity. *In prep.*

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ABSTRACT

UNDERSTANDING FISH AND FISHER BEHAVIOR IN CORAL REEF ECOSYSTEMS

by

Margaret Watts Wilson

Human activities are increasing in intensity, duration, and spatial extent. As a result, humans play an increasingly influential role in nearly all of the planet's ecosystems. In order to maintain ecosystem function alongside growing human impacts, we must first understand the nature and drivers of these impacts, and, just as importantly, understand how to manage them. Behavior is a critical consideration in addressing this two-part challenge. Animal behaviors that underlie ecosystem function can be affected by human activities, and human behaviors determine human impacts and management outcomes. This thesis integrates ecological and social approaches to improve our understanding of both animal and human behavior in the context of ecosystem management, with a particular focus on Caribbean coral reef systems. I begin with a comprehensive assessment of the potential pathways in which human activities may influence ecosystem outcomes through impacts on animal behavior across aquatic and terrestrial ecosystems. While such impacts have been increasingly documented, the implications of these behavior changes for ecosystem function remain understudied. Through synthesis of empirical evidence and ecological theory, I find that human-induced animal behavior change has the potential to alter ecosystems through numerous pathways. Whether or not these pathways are realized will depend on several factors, primarily the nature and distribution of human activities and the ecological role of an altered species' behavior. To better understand potential variations in ecologically critical animal behaviors, in my second chapter I examine the feeding behaviors of herbivorous fish in coral reef ecosystems experiencing different human disturbance. Herbivory on coral reefs is a keystone driver of ecosystem health through facilitation of coral survival, growth, and recruitment by suppressing otherwise dominant algal competitors. Across thirteen reef sites in three Caribbean islands with varying levels of coral reef health and anthropogenic impacts, I find that the grazing behavior of herbivorous fish varies significantly. Feeding rates, or the number of bites taken per minute, varied as much as nine-fold across sites, while the grazing intensity, or number of consecutive bites taken while feeding, varied as much as six-fold. I present several hypotheses for these trends and discuss theoretical links to human impacts such as fishing that can guide future studies. In my third chapter, I evaluate the outcomes of efforts to shift human fishing behavior off of coral reefs and onto less exploited pelagic resources through a case study of the Guadeloupe fishery, a mixed-gear small-scale fishery in the Caribbean. I find that these efforts, namely the introduction of moored fish aggregating devices (MFADs), have allowed more vessels to specialize in exclusively offshore fishing and likely facilitated an increasing proportion of landings coming from pelagic species, but that they have also made offshore fishing less accessible to certain portions of the fleet. These findings suggest the importance of understanding human behavior in modifying human impacts on threatened ecosystems.

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I. Introduction

Human activities are increasing in intensity, duration, and spatial extent (Venter *et al.* 2016; Watson *et al.* 2016; Halpern *et al.* 2019). In addition to our growing population and continuing development, technological advances enable us to access and modify previously remote environments, and increased participation in outdoor recreation expands our anthropogenic footprint in natural areas (Gonson *et al.* 2016; Watson *et al.* 2016). Even when not directly present, humans permeate ecosystems through chemical and sensory pollution, habitat modification, trash deposition, and human-facilitated invasive species (Longcore & Rich 2004; Dobson *et al.* 2011; Shannon *et al.* 2016).

As our global human footprint expands, so do our interactions with other species and our potential impacts on ecosystems. Ecosystem management in an increasingly human-impacted world is a two-part challenge. First, we must understand the mechanisms through which human activities affect ecosystems and the ultimate ecological consequences of these impacts. Second, we must understand how human activities can be altered when their impacts on ecosystems are detrimental. Both human behavior and the behavior of other species play an important role in addressing this two-part challenge. Animal behaviors that drive critical ecosystem processes can be altered by human activities, while managing these human activities requires shaping human behaviors.

My dissertation work takes an interdisciplinary approach to enhance our understanding of both animal and human behavior in the context of ecosystem management, with a particular focus on Caribbean coral reef ecosystems. My first chapter expands our broader comprehension of human impacts on ecosystems by examining the ecological consequences of human impacts on animal behavior across both aquatic and terrestrial ecosystems. An increasing number of studies have documented the effects of diverse human activities on animal behaviors, spanning terrestrial and aquatic ecosystems (Wong & Candolin 2015; Larson *et al.* 2016; Shannon *et al.* 2016; Gaynor *et al.* 2018; Tucker *et al.* 2018; Samia *et al.* 2019; Suraci *et al.* 2019). While animal behaviors serve numerous critical ecological functions, including nutrient cycling, primary productivity, pathogen transfer, and habitat provision (Gribben *et al.* 2009; Barber & Dingemanse 2010; Palkovacs & Dalton 2012), we know little about whether the type or magnitude of human-induced shifts in animal behavior drive ecological change. I integrate previously disparate literature from numerous fields to categorize the numerous pathways in which humans can impact the behaviors of other species, and how these behavioral shifts may ultimately impact ecological outcomes. I examine the strength of evidence for each of these pathways and also identify numerous factors known or theorized to impact pathway strength. I discuss the importance of potential nonlinear dynamics among human activity levels, animal behavior changes, and ecosystem consequences that should be considered in designing management approaches. I highlight challenges faced in documenting complete pathways from human impacts to ecosystem consequences, and propose numerous questions and strategies for future research. One knowledge gap I identify is a lack of quantitative information documenting human impacts on keystone behaviors, or the ecologically critical behaviors that can be inferably translated to ecosystem consequences.

In my second chapter, I bring my focus to Caribbean coral reef ecosystems and use a field study to examine the extent to which keystone behaviors can vary across different reef environments. Herbivory on coral reefs promotes a positive feedback loop in which grazers suppress algae and facilitate the survival, growth, and recruitment of corals (Box & Mumby 2007; Rasher & Hay 2010; Steneck *et al.* 2014). Coral growth then increases reef structure, providing habitat for fish and invertebrates including herbivorous species (Nyström *et al.* 2012). In this chapter, I test whether the keystone grazing behaviors of two herbivorous scarid species, *Scarus vetula* and *Sparisoma viride*, vary across different reef settings. I find that both the rates of grazing and the spatiotemporal concentration of grazing differ substantially across reefs, with typically lower grazing activity in characteristically degraded reefs as compared to characteristically healthy reef environments. I propose several hypotheses for these trends and highlight the important implications of these inter-reef variations for restoring coral reef function in areas that have been degraded by human activities such as fishing and habitat destruction.

In my third chapter, I shift to the second challenge of how human behaviors can be altered when they are negatively impacting ecosystems. Specifically, I evaluate the outcome of efforts to shift fishing activities off of over-exploited Caribbean coral reefs and onto less exploited offshore fisheries in Guadeloupe, a French overseas territory in the Eastern Caribbean. Like many small-scale fisheries in the region and around the world, Guadeloupe has introduced the use of moored fish aggregating devices (MFADs) to make offshore pelagic fisheries more accessible and profitable (Beverly *et al.* 2012; Albert *et al.* 2014; Bell *et al.* 2015; Wilson *et al.* 2020a), but the implications of these fisheries for shifts in inshore fishing activity remain poorly studied (Mathieu *et al.* 2014; Wilson *et al.* 2020a). Here I find that while MFADs likely enable more vessels to specialize in exclusively offshore fishing and for pelagic species to make up an increasing proportion of total landings, they may also make offshore fishing less accessible as a part-time fishing activity.

This body of work furthers our understanding of potential human impacts on ecosystems and how they can be managed. In addition to the findings presented, each chapter also generates important questions for future research. As our human footprint continues to expand, incorporating human impacts into ecosystem management through interdisciplinary approaches is critical to enable diverse ecosystems to persist.

II. Ecological impacts of human-induced animal behavior change

A. Abstract

A growing body of literature has documented myriad effects of human activities on animal behavior, yet the ultimate ecological consequences of these behavioral shifts remain largely uninvestigated. While it is understood that, in the absence of humans, variation in animal behavior can have cascading effects on species interactions, community structure, and ecosystem function, we know little about whether the type or magnitude of human-induced behavioral shifts translate into detectable ecological change. Here we synthesize empirical literature and theory to create a novel framework for examining the range of behaviorally mediated pathways through which human activities may affect different ecosystem functions. We highlight the few empirical studies that show the potential realization of some of these pathways, but also identify numerous factors that can dampen or prevent ultimate ecosystem consequences. Without a deeper understanding of these pathways, we risk wasting valuable resources on mitigating behavioral effects with little ecological relevance, or conversely mismanaging situations in which behavioral effects do drive ecosystem change. The framework presented here can be used to anticipate the nature and likelihood of ecological outcomes and prioritize management among widespread human-induced behavioral shifts, while also suggesting key priorities for future research linking humans, animal behavior, and ecology. the ultimate ecological consequences of these behavioral shifts remain largely uninvestigated. While it is understood that, in the absence of humans, variation in animal behavior can have cascading effects on species interactions, community structure, and ecosystem function, we know little about whether the type or magnitude of human-induced behavioral shifts translate into detectable ecological

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B. Introduction

As human activities continue to expand in magnitude, number, and extent (Venter *et al.* 2016; Watson *et al.* 2016; Halpern *et al.* 2019), a growing body of literature has documented widespread human impacts on animal behavior across aquatic and terrestrial ecosystems (Wong & Candolin 2015; Larson *et al.* 2016; Shannon *et al.* 2016; Gaynor *et al.* 2018; Tucker *et al.* 2018; Samia *et al.* 2019; Suraci *et al.* 2019). Animal behavior underlies many critical ecological functions, including nutrient cycling, primary productivity, pathogen transfer, and habitat provision (Gribben *et al.* 2009; Barber & Dingemanse 2010; Palkovacs & Dalton 2012). By affecting both interspecific and intraspecific interactions, behavioral trait variation can alter population and community dynamics (Bolnick *et al.* 2011) and wildlife conservation outcomes (Festa-Bianchet & Apollonio 2003; Blumstein & Fernández-Juricic 2010; Berger-tal & Saltz 2019), yet we know little about whether the type or magnitude of human-induced behavioral shifts translate into ecological change. While many behavioral effect studies allude to the implications of their findings for populations, communities, and ecosystems, limited empirical and theoretical investigation as well as a lack of synthesis across existing literature spheres preclude us from knowing where and to what degree these impacts occur, limiting our ability to guide and prioritize management efforts. Without an enhanced understanding of the ecological consequences of human induced behavioral effects, we risk both overlooking important drivers of ecological change that are not addressed through traditional management strategies, and misallocating management resources to mitigating behavioral impacts that ultimately have little ecological relevance.

While recent frameworks and case studies have linked numerical declines of animal populations to ecological consequences (Estes *et al.* 2011; Dirzo *et al.* 2014), we lack a similar understanding of the behaviorally mediated pathways through which humans impact ecosystems. Here, we present a novel framework outlining the pathways through which human activities may modify ecosystems via changes in animal behavior. We begin by categorizing the mechanisms through which human activities affect animal behavior, synthesizing a broad literature on human-induced behavior change that previous reviews have segregated by ecosystem [e.g., forests (Marzano & Dandy 2012)], behavior [e.g., flight (Stankowich 2008)], or human disturbance [e.g., noise (Williams *et al.* 2015; Shannon *et al.* 2016)]. We then present detailed pathways linking documented animal behavior changes to established or hypothesized ecosystem consequences. While our integrative framework illustrates the potential for human-impacted behaviors to affect population dynamics, community interactions, and ecosystem functions, we identify numerous factors likely to dampen these various pathways and discuss the relevance of these factors for anticipating and managing the ecological consequences of behavior change. While much remains to be learned about the drivers of animal behavior change, we highlight comparatively large knowledge gaps around the actualized ecological impacts of many human-impacted animal behaviors that prevent us from drawing management recommendations from many existing studies. As this body of literature continues to grow, we advocate for an increase in empirical and modelling studies that go beyond documenting behavioral impacts to examine the potential for realized ecological implications of human-induced animal behavior change.

C. Mechanisms for human-induced animal behavior change

Human activities are increasingly impacting the aquatic and terrestrial environments in which wildlife persist. In addition to our growing population and rising urban and agricultural development, technological advances enable us to access and modify previously remote environments (Ramirez-Llodra *et al.* 2011; Pertierra *et al.* 2017), and increased participation in outdoor recreation expands our anthropogenic footprint in natural areas once thought of as protected and pristine (Gonson *et al.* 2016; Watson *et al.* 2016). Even when not directly present, human disturbance permeates ecosystems through chemical and sensory pollution (Longcore & Rich 2004; Williams *et al.* 2015), habitat modification (Torres *et al.* 2016), trash deposition (Newsome & van Eeden 2017), human-facilitated invasive species (Murphy & Romanuk 2013), and anthropogenic climate change (Rosenzweig *et al.* 2008; Hoegh-Guldberg & Bruno 2010).

These diverse human impacts can induce changes in animal behavior by altering the conditions under which animals make behavioral decisions. Direct human presence and indirect impacts on an animal's surroundings can alter behavior via changes in population densities, top-down effects, bottom-up effects, and changes in the physical environment (Fig. 1). We introduce these four mechanisms here, integrating previously disparate literature to establish a foundation for assessing human-induced behavior change pathways more coherently. Selected examples for each empirically documented pathway are provided in Table S1 in Supporting Information.

Population density effects

By changing the density of a given population, humans can alter numerous behaviors that are sensitive to population size. For example, reducing local wildlife abundances through culling has been shown to alter territorial behaviors and increase mixing between social units in *Meles meles* (Eurasian badger) populations (Carter *et al.* 2007). Reduced male to female ratios due to selective hunting of male *Saiga tatarica* (Saiga antelope) led to disruptions of harem breeding dynamics in which older females aggressively prevented subdominant females from mating (Milner-Gulland *et al.* 2003). Other social behaviors such as group foraging (MacNulty *et al.* 2012; Gil & Hein 2017) and shared vigilance (Beauchamp *et al.* 2012; Gil *et al.* 2017) have been established as sensitive to group size and could inferably be impacted by human-induced changes in population density, though these potential links have not been documented empirically.

Top-down effects

Humans can have top-down impacts on animal behavior by directly or indirectly altering how and where animals perceive risk [i.e., risk assessment (Stankowich & Blumstein 2005) and “landscapes of fear” (Laundre *et al.* 2010; Gaynor *et al.* 2019; Suraci *et al.* 2019)]. Animals adjust their behaviors when they perceive direct human presence as a threat, even in response to benign activities such as hiking or boating (Larson *et al.* 2016). Humans play the ecological role of ‘super predators’ in many systems and can shift the behavior of even the highest trophic level species (Darimont *et al.* 2015), triggering fear effects that can differ from and exceed those of natural predators (Proffitt *et al.* 2009; Ciuti *et al.* 2012; Clinchy *et al.* 2016). Humans can also indirectly affect a prey's perception of risk by modifying the populations of their natural predators, either increasing or decreasing risk of predation. For example, exploitation and habitat conversion have led to global predator losses (Estes *et al.* 2011), while predator restoration programs [e.g., *Canis lupus* (gray wolves) in Yellowstone (Ripple & Beschta 2004)] and human-facilitated invasive species [e.g., *Carcinus maenas* (green crabs; Bertness & Coverdale 2013)] have increased predator abundances in some systems. Risk assessments and associated behavioral responses can change dramatically as a result of these human-induced changes in predator densities (Ripple & Beschta 2003; Madin *et al.* 2010b). Top-down effects may be particularly prevalent in aquatic systems, where fluid environments enhance the transmission of chemical cues among species (Preisser *et al.* 2005; Mitchell & Harborne 2020).

Bottom-up effects

Human activity can also have bottom-up impacts on animal behavior by changing the availability and distribution of prey or resources (Monk *et al.* 2018). Intentional and unintentional anthropogenic food subsidies (e.g., provisioning wildlife for tourism purposes, trash availability in residential or recreational areas) can increase resource availability and modify resource distributions (Ditchkoff *et al.* 2006; Burgin & Hardiman 2015; Soulsbury & White 2015). Alternatively, hunting, fishing, land use change, pollution, and climate change can alter resource availability and drive changes in consumer foraging behaviors (Estes *et al.* 1998; Gutierrez *et al.* 2008; Tinker *et al.* 2008). While altering resource availability can of course have numeric effects on consumer populations, it also impacts the conditions determining animal behavior, including risk-foraging trade-offs, movement patterns, and habitat selection.

Physical environment effects

Anthropogenic activities that modify habitat structure or generate chemical or sensory pollution can alter animal behavior by changing environmental conditions and habitat suitability, and by altering sensory cues that inform animal decision-making. Noise and light pollution, for example, influence patterns of animal movement (Tuxbury & Salmon 2005; Castellote *et al.* 2012; Davies *et al.* 2013), feeding (Bird *et al.* 2004; Pirotta *et al.* 2014), and communication (Parks *et al.* 2010; Vargas-Salinas *et al.* 2014). Structural habitat modifications such as those associated with land or coastal development can have large-scale impacts on animal movement and distribution patterns (Leblond *et al.* 2013; Skarin & Alam 2017; Wang *et al.* 2017). Many aquatic organisms are sensitive to anthropogenic changes in water clarity and chemical concentrations, which have been shown to interrupt communication, mating, and schooling behaviors (Seehausen *et al.* 1997; Ward *et al.* 2008; Brodin *et al.* 2013). Changing climate is also reshaping the physical environment in unprecedented ways, many of which are likely to alter animal behavior, as explored more explicitly in other reviews (Wuethrich 2000; Knowlton & Graham 2010; Harmon & Barton 2013; Beever *et al.* 2017).

D. Linking human-induced behavior change to ecological functions

Animal behavior underlies many critical ecosystem functions by shaping interactions with conspecifics, other species, and the abiotic environment (Sih *et al.* 2010; Start & Gilbert 2017). These functions include nutrient cycling, primary production and carbon sequestration, habitat provision and regulation, pollination and seed dispersal, disturbance regulation, and pathogen transfer (Table 1). Humans can alter these functions by changing animal behaviors that directly facilitate them (e.g., altering animal movement may affect seed dispersal). Humans may also indirectly impact these functions by inducing behavior changes that alter individual fitness, population dynamics, and/or interspecific interactions that cascade to affect ultimate functions (e.g., changes in breeding behaviors of a seed disperser may indirectly affect dispersal through changes in population abundances). While human-induced behavior change has the potential to disrupt ecosystem functions, it can also enable functions to persist through adaptations to human-impacted conditions. We outline both documented and hypothesized pathways (Fig. 1, Table S2) that illuminate the potential implications of human-induced animal behavior change and illustrate a needed shift in research priorities to evaluate ecosystem consequences and address numerous links that have not yet been investigated in human-impacted systems. We discuss existing evidence for various pathways through a novel synthesis of existing literature, highlighting pathways with both stronger and weaker empirical and theoretical links to ultimate ecological impacts. We end by outlining open questions for future research.

Foraging

The best evidence for ecosystem consequences of human-induced animal behavior changes come from systems where humans have directly and indirectly altered animal foraging behaviors. By modifying risk environments, top-down human disturbances can initiate behaviorally mediated trophic cascades in which changes in predator or prey behavior cascade to affect downstream trophic interactions (Schmitz *et al.* 1997). For example, Hebblewhite and colleagues (2005) showed how changes in *C. lupus* distribution patterns to avoid human activity on hiking trails led to changes in *Cervus elaphus* (elk) grazing patterns and plant community composition, altering habitat suitability for other species and resulting in changes in *Castor canadensis* (beaver) lodge density and riparian songbird diversity and abundance. Fishing-depleted piscivore populations have been shown to modify the foraging behaviors of herbivorous fish, contributing to seascape-level differences in algal distribution patterns (Madin *et al.* 2010b; DiFiore *et al.* 2019; Madin *et al.* 2019). Direct human presence has also been linked to nutrient cycling in coral reef systems via models, where suppressed herbivore grazing observed in the presence of a spearfisher alters carbon and nitrogen flux in a corresponding simulation model (Gil & Hein 2017).

Beyond implications for habitat suitability and nutrient cycling, the potential ecological impacts of altered animal foraging behaviors are numerous and can be induced by a wide range of human impacts (Fig. 1). Changes in the quantity, type, or location of resources consumed can alter seed dispersal (Beaune *et al.* 2013; Morán-López *et al.* 2020), while consumptive behaviors that alter plant or algal communities can drive changes in primary production and carbon storage (Silliman & Bertness 2002; Atwood *et al.* 2018), habitat suitability (Seabloom & Richards 2003; De Knegt *et al.* 2008), and disturbance regulation such as wildfire and flooding dynamics (Schmitz *et al.* 2008; Cherry *et al.* 2016). Changes in foraging behaviors that alter the type or quantity of resources consumed can also have impacts on body condition (Votier *et al.* 2010) that could potentially cascade up to population and ecosystem consequences, though evidence for these latter links is limited.

Movement

Another pathway through which humans can have ecologically-significant impacts on animal behavior is by altering movement (Spiegel *et al.* 2017). Top-down, bottom-up, and physical environment disturbances have driven widespread changes in animal movement patterns (Tucker *et al.* 2018), which have the potential to modify the transport of nutrients, pathogens, seeds, and pollen within and among ecosystems (Dougherty *et al.* 2018). Changes in *Bycanistes bucinator* (trumpeter hornbill) movement patterns due to habitat fragmentation have been linked to changes in seed dispersal ranges (Lenz *et al.* 2011), while changes in movement and aggregation patterns driven by anthropogenic food subsidies have been shown to increase disease transmission in both aquatic (Semeniuk & Rothley 2008; Burgin & Hardiman 2015) and terrestrial (Carter *et al.* 2007; Becker & Hall 2014; Forbes *et al.* 2015; Moyers *et al.* 2018) systems. Our framework points out the potential link between animal movement and nutrient dynamics, which has been well established in natural systems literature but not yet empirically linked to human impacts. For example, *C. lupus* movements while hunting can drive soil and foliar nutrient patterns by determining the distribution of *Alces alces* (moose) carcasses, leading to increased macronutrient content, microbial abundances, and leaf nitrogen that can persist for more than two years after a kill (Bump *et al.* 2009). Human disturbance can alter movement patterns of numerous predators that have been linked to nutrient transfer in separate natural systems studies, including *C. lupus* (Ashenafi *et al.* 2005; Hebblewhite *et al.* 2005), *Puma concolor* [pumas (Smith *et al.* 2016; Barry *et al.* 2019)], *Ursus spp.* [bears (Schindler *et al.* 2003; Nevin & Gilbert 2005; Zeller *et al.* 2019)], and *Carcharhinus spp.* [sharks (Brunnschweiler & Barnett 2013; Williams *et al.* 2018)], yet no studies have investigated the resulting links between human-induced changes in movement patterns and ecosystem nutrient dynamics.

Communication

By altering animal communication through top-down effects as well as impacts on the physical environment and population densities, humans have the potential to drive changes in population dynamics, interspecific interactions, and ultimate ecosystem functions. The transfer of information among individuals can play a critical role in determining mating success (Schmidt *et al.* 2015), foraging decisions (Gil & Hein 2017), competitive outcomes (Gil *et al.* 2019), and susceptibility to predation (Gil *et al.* 2017). Because animals often glean information from communication among heterospecifics (Magrath *et al.* 2015), impacts on communication can also alter information available to other species. While human impacts on animal communication have been documented for numerous species and systems, the ecosystem consequences of altered communication have been less investigated. Gil and Hein (2017) demonstrated the role of communication about fear and food in determining foraging behaviors of herbivorous fish, with modeled implications for algal consumption and nutrient flux. Altered environmental conditions can also negatively impact breeding via suppressed communication (Habib *et al.* 2007), while many other studies document the ability of individuals and species to adapt communication strategies to account for changing sensory environments (Parris & McCarthy 2013; Vargas-Salinas *et al.* 2014).

Timing and distribution of activities

Top-down, bottom-up, and physical environment effects of human activities may also alter ecosystem dynamics through shifts in the timing and distribution of animal activities, such as increasing nocturnality (Benítez-López 2018; Gaynor *et al.* 2018) and avoidance of or attraction to developed areas (Leblond *et al.* 2013; Soulsbury & White 2015). Because some species are more spatially or temporally displaced by or attracted to human activities than others (George & Crooks 2006; De Knegt *et al.* 2008; Erb *et al.* 2012; Ladle *et al.* 2018; Moll *et al.* 2018; Smith *et al.* 2018), human disturbance can impact community dynamics by altering co-occurrence and interactions among species. Predators, for example, are often more displaced than prey species (Reed & Merenlender 2008; Muhly *et al.* 2011; Wang *et al.* 2017), and prey may actively seek human disturbance as a shield against natural predators (Berger 2007). Disproportionate predator and prey displacement can in some cases lead to changes in predator diets and subsequent trophic interactions (Smith *et al.* 2018). Spatial or temporal displacement may also alter competitive relationships by disproportionately displacing competitor species (Ladle *et al.* 2018; Moll *et al.* 2018) or by increasing niche overlap between species previously occupying separate niches (Smith *et al.* 2018). While changes in species co-occurrence could potentially impact various ecosystem functions, these ecological consequences have not been documented empirically beyond implications for individual species' survival (Vinne *et al.* 2019). Existing studies have largely measured shifts in activity levels but not in ecologically transferable behaviors (e.g., feeding), making it challenging to infer the ecological impacts of some of these spatial and temporal shifts (but see Smith *et al.* 2018).

Vigilance and flight

A large number of studies on human-induced behavior change have focused on human impacts on vigilance and flight behaviors (Stankowich 2008; Weston *et al.* 2012). Changes in flight or vigilance can impact individual fitness via changes in physiological stress (Arlettaz *et al.* 2007; Tarjuelo *et al.* 2015) and susceptibility to predation (Arroyo *et al.* 2017). Human-induced stress has in some cases been linked to lower reproductive output (Pauli & Buskirk 2007; French *et al.* 2011; Arroyo *et al.* 2017) and reduced offspring survival (Mann *et al.* 2000; Phillips & Alldredge 2000), while other studies have documented population stability in spite of increased flight and vigilance behaviors (Reimers *et al.* 2009). Even if the costs of these anti-predator behaviors do add up to influence individual fitness and drive changes in population growth rates (Gomes & Sarrazin 2016), links to broader ecological consequences beyond the affected species remain unstudied (Fig. 1). Changes in flight and vigilance may also indicate tradeoffs with other behaviors [e.g., foraging (Cooper (Jr.) *et al.* 2015; Tarjuelo *et al.* 2015)] that could potentially alter ecosystem function, but these tradeoffs should not be assumed and instead measured explicitly (see "Measuring ecological outcomes of human-induced animal behavior change").

Rest and hygiene

Human activities can also affect rest (Naylor *et al.* 2009; Barnett *et al.* 2016; Déaux *et al.* 2018) and hygienic behaviors (Titus *et al.* 2015; Nedelec *et al.* 2017) through top-down, bottom-up, and physical environment effects. Hygienic behaviors such as personal, conspecific, or heterospecific grooming or the cleaning of an animal's habitat have been shown to affect pathogen transmission in natural systems (Spivak & Reuter 2001; MacIntosh *et al.* 2012; Duboscq *et al.* 2016), though these links have not been established in human-impacted systems. Human impacts on rest have been linked to physiological changes (Barnett *et al.* 2016), but population and ecosystem consequences have not been investigated.

Breeding and parental care

Human impacts on breeding and parental care behaviors can lead to changes in population dynamics with uninvestigated impacts on ecosystem functions. Through top-down effects, perceived risk from human nest visits increased incubation breaks and reduced the probability of nest survival in *Anser albifrons* [greater white-fronted geese (Meixell & Flint 2017)]. Through bottom-up effects, provisioning from *Tursiops truncatus* (bottlenose dolphin) tour boats reduced the amount of time that mothers spent with their calves, which was associated with lower calf survival rates (Mann *et al.* 2000; Foroughirad & Mann 2013). By changing the physical environment, noise from road traffic had negative impacts on *Parus major* (great tit) clutch size (Halfwerk *et al.* 2011). Changes in population densities can also alter breeding behaviors, such as the *S. tatarica* example in which smaller herd size and skewed sex ratios lead to increased aggression among females, thought to have contributed to observed declines in reproductive rates (Milner-Gulland *et al.* 2003). Despite widely documented impacts on breeding and parental care behaviors and implications for population dynamics and single-species conservation goals, links to broader ecosystem functions have not been established.

E. Factors influencing expected pathway outcomes

As described above, human activities have the potential to alter numerous ecosystem functions through diverse behaviorally mediated pathways. However, not all human disturbances will translate into changes in animal behavior, let alone ecological consequences. Human disturbances can also induce behavior changes that serve to maintain ecosystem functions. As demonstrated in Fig. 1, investigation of these complete pathways is extremely limited, giving us little information on the prevalence or strength of these pathways and the conditions under which they are realized. Here we draw on synthesized literature and theory to highlight several factors likely to affect the strength of these pathways (Fig. 2, Table 2), which may contribute to the overall lack of evidence for many ultimate links to ecosystem functions. These factors of interest can also be used as management intervention points and focal areas for future research.

1. Behavioral responses to human disturbance

Spatial and temporal distribution of human disturbance

The degree to which human activities modify animal behaviors – and the likelihood that these behavioral shifts could go on to affect ecosystem functions - will depend in part on the spatial and temporal distribution of human disturbance. Infrequent or highly localized disturbances can at times have dramatic immediate effects on animal behavior, but may not be persistent enough to affect larger ecosystem processes if animals resume behaviors during undisturbed periods (see *'Magnitude and persistence of behavior change'* below).

Chronic and spatially pervasive human disturbances – such as those caused by changes in population densities, top-down or bottom-up effects of altered predator or resource abundances, or changes to the physical environment – may have more persistent and widespread impacts on animal behavior. Indeed, some of the best evidence we have for ecosystem consequences of human-induced animal behavior change comes from systems in which human activities have had chronic impacts via alterations of natural predator abundance that persist beyond direct human presence (Ripple & Beschta 2004; Madin *et al.* 2010b). In cases where animals perceive human disturbances as negative (e.g., hunter or fisher presence, increase in predator abundance) or positive (e.g., provisioning from wildlife tourism, human trash), increased exposure may increase sensitization to disturbance cues (Blumstein 2016). Conversely, when a human disturbance is perceived as non-threatening, chronic or repeated disturbance can facilitate habituation and tolerance (Rees *et al.* 2005; Rodríguez-Prieto *et al.* 2010).

Many human activities are restricted to or peak in intensity at certain temporal cycles (e.g., diurnal human activity cycles, hunting or recreation seasons) or locations (e.g., roads, recreational trails), often allowing animals to shift activities into less disturbed times or places (Rode *et al.* 2006; Leblond *et al.* 2013; Bateman & Fleming 2017; Gaynor *et al.* 2018). These shifts can alter species co-occurrence, as discussed in the previous section, but can also enable other behavioral functions to persist alongside human disturbance (Sih *et al.* 2011). Some behaviors, however, may be more sensitive to spatial and temporal displacement (Wilmers *et al.* 2013). Because the condition of an animal likely varies in time and space, the timing and location of human disturbances may also have differing effects on behaviors that are state-dependent. For example, *Ursus americanus* (black bears) have been shown to forage most heavily on anthropogenic food sources during seasons when natural food production is low and individuals are presumably hungrier (Lewis *et al.* 2015). Disturbances at critical times or locations such as breeding events, along migration routes, or at key resource locations may have elevated population or ecosystem impacts relative to equal disturbance levels occurring at different locations or times of day or year. While many species conservation efforts already include restrictions on human activity at sensitive times or locations (e.g., breeding grounds), we recommend adapting this approach for ecosystem management based on ecologically critical behaviors likely to be sensitive to the timing or location of human disturbances.

Intensity of human disturbance

The intensity of human disturbance also likely plays a role in determining if and to what extent animals alter behavior (Leblond *et al.* 2013). However, these relationships can exhibit numerous nonlinear forms [Fig. 3 (Tablado & Jenni 2017; Gaynor *et al.* 2019)]. Behavioral alterations often come at a cost for animals (Frid & Dill 2002; Eldegard *et al.* 2012; Lamanna & Martin 2016), and may only occur if human disturbance reaches a certain threshold level (Bejder *et al.* 2006; Scillitani *et al.* 2010; Beyer *et al.* 2013; Tablado & Jenni 2017; Smith *et al.* 2019). For example, *Sus scrofa* (wild boars) maintained relatively constant social dynamics and movement patterns as hunter presence increased from low levels, but abandoned former territoriality and dramatically altered mobility across the landscape when hunter presence surpassed a certain threshold (Scillitani *et al.* 2010). Similarly, Smith and colleagues (Smith *et al.* 2019) identified a threshold in housing density that creates barriers for *P. concolor* movement. Threshold effects relative to human disturbance levels may also occur when animals learn positive associations with human activities, such as anthropogenic food subsidies. When the availability of food from humans reaches a certain level or consistency, animals may abandon prior foraging behaviors and adopt strategies centered around anthropogenic food sources (Yirga *et al.* 2012; Lewis *et al.* 2015). Conversely, habituation to human activities may dampen or decelerate impacts on animal behavior as human activities intensify when animals perceive these activities as neither threatening nor beneficial (Higham & Shelton 2011; Jiménez *et al.* 2011; Soldatini *et al.* 2015; Titus *et al.* 2015).

Interacting human disturbances

Given the vast global human footprint, animals are likely experiencing not one, but many forms of direct and indirect anthropogenic impacts that might have additive or interactive effects on animal behavior. For example, hunting pressure has been shown to exacerbate the behavioral impacts of road traffic on migrating elk (Paton *et al.* 2017). Environments where threatening and nonthreatening human activities mix - such as areas used by both hunters and hikers, spearfishers and recreational divers, etc. - may be of particular concern as they can prevent animals from accurately assessing risk and adjusting behavior appropriately (Coleman *et al.* 2008). In cases where animals do habituate to non-threatening human interactions, they may be more susceptible to hunters or poachers (Januchowski-Hartley *et al.* 2013; Geffroy *et al.* 2015). Direct human impacts on animal behavior are likely accompanied by additional indirect effects such as altered predator or resource abundances and changes in habitat suitability, though the behavioral and ecological implications of these overlapping disturbances remain uninvestigated.

2. Ecosystem consequences of animal behavior change

Ecological function of animal behavior

Regardless of the magnitude or persistence of animal behavior change, resulting ecological outcomes will ultimately depend on the ecological importance of a given behavior. While every species is inherently linked to ecosystem function, the behaviors of some - such as keystone species or ecosystem engineers - are far more critical than others for overall ecosystem function. For example, changes in beaver foraging behaviors could have disproportionately large consequences for ecosystem function by changing local water distributions, while changes in foraging behaviors of other rodent species may not trigger any detectable ecological changes. While human-induced behavior change often has a negative connotation, changes in some behaviors may actually be acting to preserve behaviors with direct ecosystem functions. For example, changes in the timing of activities to avoid human interactions may allow beavers to maintain foraging impacts despite human disturbances. Monitoring behaviors that are directly transferable to ecosystem function (e.g., foraging) as opposed to or in addition to those that could have indirect implications (e.g., flight behaviors, which may or may not impact foraging) will be more valuable in anticipating ecosystem impacts. Ecosystem managers can prioritize management efforts by identifying ecologically foundational or keystone behaviors in a given ecosystem context. The pathways illustrated in this framework can guide the mitigation of human disturbances likely to alter these critical behaviors as well as the monitoring of downstream ecological effects.

Population impacts of behavior change

As introduced above, behaviorally mediated changes in species abundances also have the potential to impact ecosystem function. While population impacts for any species will be important from a conservation perspective, those with unique ecological roles will be more relevant to ecosystem function than others. By altering the contexts in which animals make decisions, human impacts can uncouple formerly reliable environmental cues from actual outcomes. In these ecological traps, animals elect seemingly adaptive behaviors that actually prove to be maladaptive and can lead to population declines (Schlaepfer *et al.* 2002; Battin 2004). For example, while *Bison bison* (American bison) repeatedly choose to forage on agricultural lands due to bottom-up human impacts on resource distributions, they are subject to increased hunting in these habitats which has contributed to a nearly 50% population decline in less than a decade (Sigaud *et al.* 2017). Conversely, ecological traps can also arise when animals fail to change their behavior in human impacted scenarios. For example, antipredator responses such as grouping or schooling that are effective for natural predators may actually increase susceptibility to hunters or fishers (Proffitt *et al.* 2009; Hamilton *et al.* 2016).

Ecological traps can lead to demographic Allee effects, in which maladaptive behaviors are unconstrained or exasperated at low population densities and lead to further population declines (Kokko & Sutherland 2001). By depleting local species abundances, humans can also induce information-mediated Allee effects where insufficient communication at low densities impede critical processes such as breeding habitat selection (Schmidt *et al.* 2015) or foraging (Gil *et al.* 2017), potentially compounding population declines and increasing extinction risk for already threatened species (Gil *et al.* 2019). Conversely, the communication of social information can also rescue populations from spiraling demographic declines (Kokko & Sutherland 2001; Schmidt *et al.* 2015; Gil *et al.* 2019). While behaviorally-mediated Allee effects can have dramatic consequences for populations, ultimate cascading impacts on ecosystem functions will depend on the role of the species, as well as on current population size.

Magnitude and persistence of animal behavior change

Even when human activities alter animal behaviors, the magnitude or persistence of the resulting changes may not be substantial enough to affect ecosystem functions. Many human-impact studies focus on acute effects, or behavior changes that occur while humans or human disturbances are immediately present, but provide little clarity as to if and how immediate responses translate to more enduring behavioral shifts with consequences for ecosystem function. For example, while coral reef cleaner shrimp *Ancyclomenes pedersoni* reduce cleaning interactions by over 50% in the presence of SCUBA divers, these behavioral shifts likely have little ecological impact if divers are present for only a small fraction of the day and shrimp resume cleaning behaviors during undisturbed periods or habituate to human presence over time (Titus *et al.* 2015). Despite numerous short-term studies documenting acute disruption of shark behavior when SCUBA divers are present (Quiros 2007; Smith *et al.* 2010; Cubero-Pardo *et al.* 2011), a long-term study found no persistent effects of SCUBA diving on sharks (Bradley *et al.* 2017), highlighting a potential disconnect in the implications of some acute and chronic effects studies. Many animals resume normal behaviors relatively quickly when human disturbance ceases or diminishes (Neumann *et al.* 2010; Higham & Shelton 2011; Titus *et al.* 2015), though lag effects in systems exposed to hunting or provisioning can sustain behavioral shifts for up to months or even years after hunting or provisioning stops (Kitchen *et al.* 2000; Pauli & Buskirk 2007; Sandin *et al.* 2008; Foroughirad & Mann 2013; Januchowski-Hartley *et al.* 2013). Some animals have been shown to compensate for behavioral shifts during low-disturbance periods, such as birds that reduce feeding during weekends when human activity is highest but compensate with increased foraging on subsequent mornings (Tarjuelo *et al.* 2015). Explicitly documenting animal behavior beyond just periods of acute or novel human disturbance is needed to determine ultimate implications for individuals, populations, and ecosystems.

One mechanism through which human impacts can induce persistent behavioral change is by selecting for certain behavioral traits that ultimately alter behavioral phenotypes within a given population. For example, a long-term study of *Circus pygargus* (Montagu’s harrier) populations found increases in boldness towards humans and a gradual disappearance of shy individuals, with an observed negative relationship between human disturbance levels and nest success for shy parents but not bold ones (Arroyo *et al.* 2017). By selecting for certain behaviors that are adaptive in response to human disturbance, humans can drive broader shifts in behavior that may extend beyond just human-impacted scenarios. These behavioral syndromes, or groups of correlated behaviors, can be adaptive in some situations but maladaptive in others [e.g., boldness in response to human vs. natural predators (Geffroy *et al.* 2015)] and may affect intra- and interspecific interactions as well as ecosystem functions (Sih *et al.* 2004).

While increasing the magnitude of animal behavior change would arguably increase associated ecological impacts, these relationships are not necessarily linear and can take a variety of forms (Fig. 3). Many ecosystems exhibit tipping points or thresholds beyond which small increases in a disturbance lead to rapid shifts in ecological condition (Holling 1973; Estes *et al.* 2011). In these systems, behavioral shifts – or population changes that alter the number of individuals performing an ecological function - would have to reach a certain threshold level before having any substantial impact on ecological function. For example, herbivory on coral reefs is thought to have nonlinear impacts on coral health and recruitment, driving a shift between coral- and algal-dominated states (Knowlton 1992; Karr *et al.* 2015). Changes in herbivore feeding behavior may therefore have little effect on coral reef ecosystems until grazing is driven below a certain threshold level at which algae is not sufficiently controlled (Karr *et al.* 2015). Potential threshold dynamics may mask the ecological relevance of some human-induced animal behavior changes and make them more challenging to detect at low disturbance levels.

F. Shifting objectives for future research

As the human footprint expands, human activity will likely have a growing impact on animal behavior, increasing the likelihood of cascading ecosystem consequences and the need to understand and anticipate them. However, our review of existing literature highlights significant knowledge gaps around the prevalence of these pathways and their underlying dynamics, which hinder our ability to prioritize management efforts among ever-increasing human-wildlife interactions and mitigate negative consequences of human activity on ecosystems where applicable. Here we discuss key objectives for future research, challenges faced, and approaches to address them.

Measuring ecological outcomes of human-induced animal behavior change

As shown in Figure 1, the central gap in our understanding of human-induced behavioral effect pathways is centered around the ecological outcomes of human-induced animal behavior changes. A key hurdle in linking altered behaviors to downstream ecological consequences is the implicit challenge in isolating the effects of behavior on complex, larger-scale ecological dynamics. Distinguishing behaviorally mediated effects from density-mediated effects can be especially tricky as they often occur in tandem (Bolker *et al.* 2003; Schmitz *et al.* 2004; Trussell *et al.* 2006). For example, changes in predator abundance, resource availability, and habitat quality will likely impact both the behavior and the overall abundance of a given species, while direct impacts on a species' abundance can have additional behavioral consequences, making it difficult to determine the relative ecological importance of these different mechanisms and to anticipate ecological outcomes. The behaviorally mediated nature of the iconicized Yellowstone wolf cascade has been challenged for this reason, with some researchers questioning the relative effects of changes in *C. elaphus* behavior as opposed to simply changes in *C. elaphus* density as a consequence of wolf reintroduction (Kauffman *et al.* 2010). Furthermore, ecological responses generally occur over much longer time scales than immediate behavioral responses to human activity. For example, Cherry and colleagues (Cherry *et al.* 2016) could readily measure the effects of *Canis latrans* (coyote) exclusion on deer grazing behaviors, but impacts on plant community dynamics were only apparent over the course of ten years. As our anthropogenic footprint expands, it also becomes harder to find adequate control sites that are not impacted by some sort of human activity, especially as humans become more drawn to 'wilderness' areas (Gonson *et al.* 2016).

Predicting ecological outcomes of human-induced animal behavior change

The challenges associated with measuring ecological outcomes empirically call for further incorporation of modelling approaches into behavioral effects literature. While the behavioral effect pathways linking human activities to ecosystem consequences may seem overwhelmingly complex, we provide a theory-supported framework for forecasting ecological outcomes that can be directly adapted into models (Fig. 1). Several studies have used models to infer the consequences of behavior change for populations (Christiansen & Lusseau 2015; Pauli *et al.* 2017; Gil *et al.* 2019; Smith *et al.* 2019) and, to a lesser extent, ecosystem functions (Becker & Hall 2014; Gil & Hein 2017). While models can help predict the ecological outcomes of human-induced behavior changes, they still require empirical data on how human activities affect behaviors with inferable ecological functions. This is a significant limitation in existing literature, which often measures human impacts on behaviors that are not easily translated into ecological outcomes. For example, a large number of human-induced behavioral effects studies have focused on measuring flight initiation distances (Stankowich 2008; McLeod *et al.* 2013), which are a useful indicator of risk assessment (Stankowich & Coss 2007) and tolerance to human disturbance (Blumstein 2016) but are less informative for models predicting ecosystem consequences. Even when a species plays an established ecological role, measurement of the wrong behavioral responses will limit our ability to estimate ecological implications. For example, herbivory can affect numerous ecological functions, including primary productivity and habitat provision, yet many studies measuring human impacts on herbivores have monitored flight or timing of activities instead of actual foraging behaviors (e.g., grazing amount, distribution, selectivity) that could inform models of downstream implications (see Gil & Hein 2017). A key step in progressing the behavioral effects field is to broaden the range of behaviors that are monitored and prioritize those hypothesized to be most relevant to ecosystem function. Particular opportunity exists around pathways linked to foraging and movement, which have myriad potential consequences including nutrient cycling, primary production, and habitat modification that have not been sufficiently investigated but have substantial support from natural systems theory. Future studies may consider specifically investigating the ecological consequences of human impacts on keystone species behaviors as these are more likely to result in detectable ecological change and could provide an upper bound in terms of anticipated outcomes of other behavioral effects pathways.

Another current limitation in existing literature is a lack of information on the persistence of human-induced behavioral effects. Many existing studies only measure acute behavioral shifts while human disturbances are present but do not investigate whether or not these behavioral impacts are sustained over time, limiting the utility of these data for models of ecosystem consequences. Additionally, some behavioral impact studies measure responses to novel anthropogenic stimuli, which risk overestimating behavioral impacts as they do not allow for animals to process and adapt to these disturbances as they would in situ (Peers *et al.* 2018). Increased studies monitoring behavioral responses over time would be extremely beneficial in inferring the actual ecosystem consequences of human-induced behavioral effects.

Differentiating impacts among human disturbance scenarios

As introduced above, nonlinearities between human activity levels, animal behavior change, and ecosystem processes can greatly impact the ultimate outcomes of behavioral effect pathways. In particular, initial studies have demonstrated both accelerating and dampening relationships between levels of human activity and resulting animal behavior change in different contexts. To better understand these relationships, more studies are needed that move beyond solely comparing behavioral responses in disturbed and undisturbed scenarios and instead quantify gradients of human activity levels against which behavioral responses are measured. More information is also needed on potential interactions between concurrent human activities in terms of impacts on animal behavior, specifically with regards to overlapping lethal and non-lethal human activities. Eliminating human disturbance in most ecosystems is unrealistic if not impossible, leaving managers with options to restrict certain types or levels of activities based on anticipated implications for animal behavior and ecosystem function. While our framework provides a foundation for connecting different human activity categories to behavioral effect pathways, effective management decisions will require an enhanced understanding of the effects of different activity levels, types, and combinations, which can also inform models predicting ecological outcomes of different human disturbance scenarios.

G. Concluding remarks

As human and wildlife activities increasingly overlap in space and time, it is critical that we evaluate and quantify the potential for human-induced changes in animal behavior to impact ecosystem structure and function. While investigation of these behavioral effect pathways has been limited, some existing studies have demonstrated that human impacts on animal behavior can drive or contribute to substantial ecological consequences, making our ignorance of behavior change outcomes in other scenarios concerning. Other studies documenting human-induced animal behavior change allude to ecosystem implications despite contextual factors likely to dampen their ultimate ecological effects.

Our proposed framework provides a novel foundation for examining and anticipating the ecological impacts of human-induced behavioral effects and outlines priorities for future research. While it is valuable to document behavioral shifts in response to human activities, incorporating this information into ecosystem management requires an understanding of whether or not these shifts are likely to drive detrimental ecosystem change. Without untangling the ecological consequences of human-induced animal behavior change, we risk situations in which ecologically important behavior changes go unrecognized and traditional management efforts are ineffective in controlling ecological outcomes. Conversely, we also risk wasting valuable management resources on mitigating behavior changes with little ecological relevance. While human impacts on animal behavior often have a negative connotation, behavioral shifts may in many cases be helping animals adapt to unavoidably human-dominated landscapes (Sih *et al.* 2011; Soldatini *et al.* 2015; Wheat & Wilmers 2016; Bateman & Fleming 2017; Vinne *et al.* 2019). In cases where behavioral changes are negatively impacting populations, communities, or ecosystems, we should strive to mitigate these impacts through effective management that addresses behavioral effects. In other cases, behavior change that allows an animal to persist in our increasingly human-impacted world may be something to allow for, if not encourage. As the human-induced behavior change literature continues to grow, our framework calls for an increase in studies that go beyond documenting human-induced animal behavior change to investigate ecological impacts and the factors that influence these ultimate outcomes.

H. Tables

Table 1. Ecosystem functions affected by animal behaviors, with select examples from natural systems. While these impacts are well established in natural systems, only links to habitat modification, pollination and seed dispersal, and pathogen transfer have been empirically documented in human-impacted systems.

Ecosystem function	**Example**	**Reference**
Primary production	Herbivore grazing alters plant communities, primary production, and carbon storage.	(Silliman & Bertness 2002; Schmitz *et al.* 2008)
Nutrient cycling	Predators distribute carcasses throughout a landscape, with consequences for soil nutrient composition.	(Palkovacs & Dalton 2012; Leroux & Schmitz 2015)
Habitat modification	Woodpecker foraging provides nest holes for other species.	(Cockle *et al.* 2011)
Pollination & seed dispersal	Animal movement affects seed dispersal ranges.	(Russo *et al.* 2006; Beaune *et al.* 2013)
Disturbance regulation	Herbivore foraging moderates wildfire potential by altering groundcover composition.	(Cherry *et al.* 2016)
Pathogen transfer	Animal movement and interactions facilitate disease transfer.	(Hawley *et al.* 2011)

Table 2. Factors hypothesized to influence the strength of pathways linking human impacts, animal behavior, and ecological implications. These hypotheses can be tested in future studies across systems with varying degrees of disturbance to better understand when human impacts are likely to impact animal behavior and/or ecosystems. Many relationships may also exhibit nonlinearities, which could be further illuminated through future studies.

Mediating factor	**Traits expected to strengthen pathway**	**Traits expected to weaken pathway**
Human disturbance → Behavioral responses		
Temporal distribution of human disturbance	• Chronic • Unpredictable	• Infrequent • Predictable
Spatial distribution of human disturbance	• Widespread • Continuous • Unpredictable	• Localized • Noncontinuous • Predictable
Intensity of human disturbance	• High intensity	• Low intensity
Behavioral responses → Ecosystem consequences		
Ecological function of animal behavior	• Critical ecological function of impacted behavior (e.g., keystone species, ecosystem engineers)	• Functional redundancy of impacted behavior
Population impacts of behavior change	• Ecological traps and maladaptive behavior change • Behaviorally mediated Allee effects • Overlapping threatening and non-threatening human activities	• Adaptive behavior change • Habituation and tolerance
Magnitude of animal behavior change	• Large behavioral shifts	• Small behavioral shifts
Persistence of animal behavior change	• Lag effects • Behavioral adaptations	• Behavioral recovery • Compensatory behaviors

I. Figures

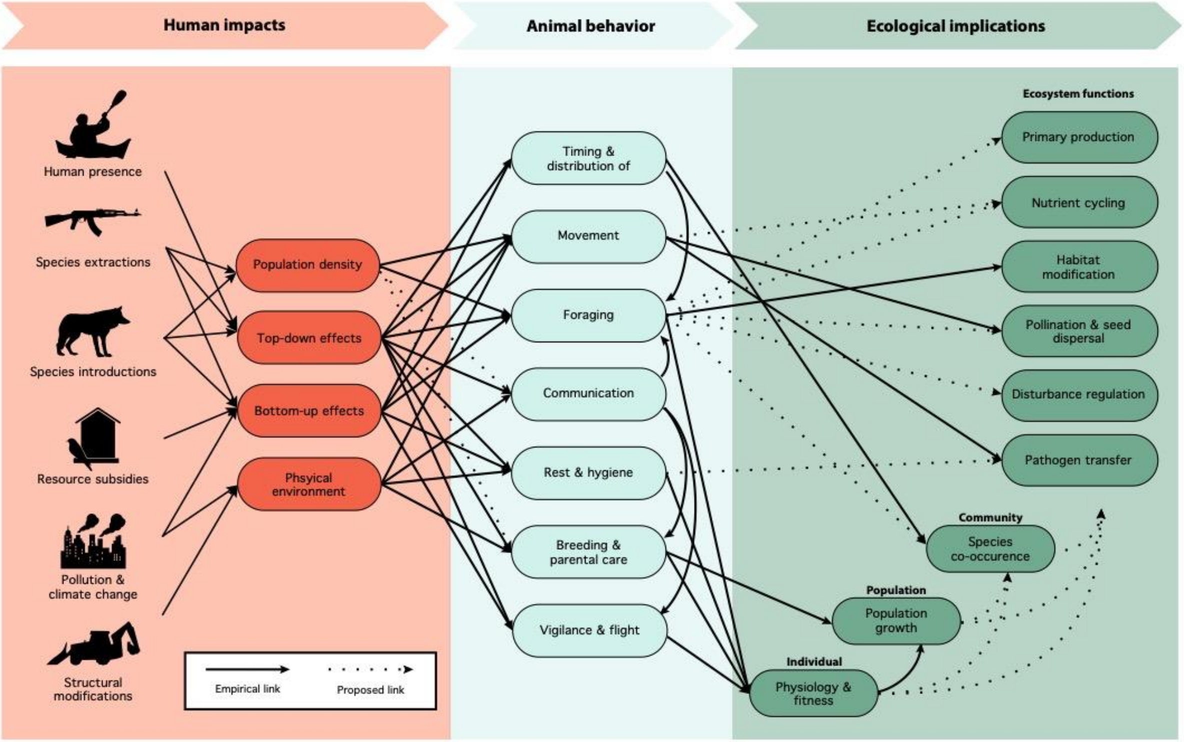

Figure 1. Diverse pathways in which human impacts may affect ecosystem functions through animal behavior change. Solid arrows indicate links supported by one or more empirical studies explicitly linked to human impacts (see Table S2 for supporting examples). Dashed arrows indicate proposed links that have not been empirically documented in human impacted systems but are supported by models and/or by our understanding of the role of animal behavior in natural systems. While human impacts on animal behavior are relatively well documented, many prospective links between animal behavior change and ecosystem functions have not been investigated in human-impacted systems - likely in part due to the complexity of many of these pathways. Studies have documented the effects of human-induced animal behavior change on individuals, populations, and communities, though cascading effects on ecosystem functions remain relatively unexplored. Potential links from individual, population, and community dynamics to numerous ecosystem functions are consolidated into single arrows here for clarity. While nearly all of an individual animal's behaviors will be interrelated due to tradeoffs in time budgets, links among behaviors here represent behavior changes that directly induce changes in subsequent behaviors of the same individual, conspecifics, or heterospecifics.

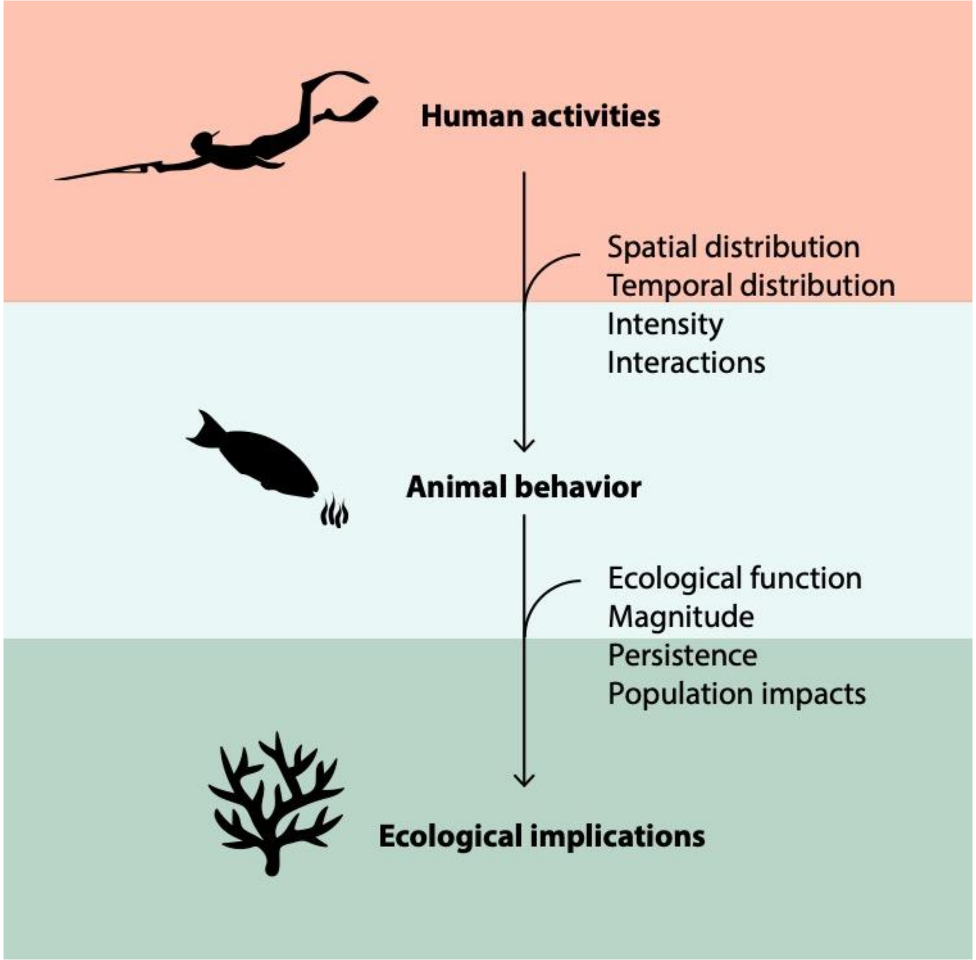

Figure 2. Factors influencing links among human impacts, animal behavior, and ecological implications. Linking human activities to ecosystem impacts via changes in animal behavior. Human impacts on animal behavior will depend on the spatial and temporal distribution and the intensity of human activities. Depending on the ecological function of a given animal behavior, functional redundancy within a community, and the magnitude and persistence of behavior change, human-impacted animal behavior may ultimately drive changes in ecosystem functions.

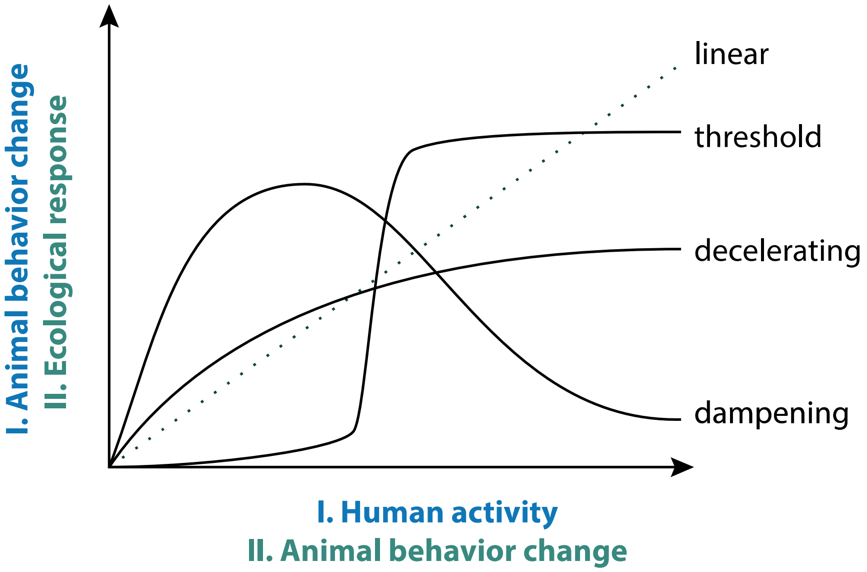

Figure 3. Examples of potential nonlinear relationships between human activity levels and animal behavior change (I) and animal behavior change and ecological responses (II). In relationships between human activities and animal behavior (I), threshold effects can occur when behavior change is costly and may not be induced until human disturbance reaches a certain intensity, after which behavior shifts relatively dramatically. Threshold dynamics have also been documented in cases when animals perceive a human disturbance as beneficial but can only shift behavior once this disturbance is sufficiently consistent or substantial, such as the switching of animal foraging behavior in response to anthropogenic food subsidies. Dampening trends may be exhibited when a human disturbance is initially perceived as threatening or bothersome but is eventually habituated to. Deceleration of behavioral responses may occur when behavior change becomes increasingly costly relative to actual disturbance from human activities, but some level of altered behavior is still perceived as beneficial. Threshold dynamics are relatively common in ecosystem responses to disturbance, suggesting that many relationships between animal behavior change and ecosystem change (II) may exhibit similar patterns.

J. Supplementary Information

Table S1. Selected evidence for links between human activities and animal behavior change.

Human impact	Behavioral effect	Example	Reference
Population density effects	Movement	Culling-reduced badger populations increase migration rates and mixing between social groups, with changes in movement and social interactions persisting for up to 8 years.	(Carter *et al.* 2007)
	Breeding & parental care	Reduced male:female ratios due to hunting trigger behavioral shifts in older haremic females that exclude younger females from mating, thought to drive observed declines in reproductive rates.	(Milner-Gulland *et al.* 2003)
Top-down effects	Timing & distribution of activities	Daytime culls induce nocturnality in lionfish.	(Côté *et al.* 2014)
	Timing & distribution of activities → foraging	Bears avoid preferred foraging but high-risk areas during hunting season, foraging instead on lower quality food.	(Hertel *et al.* 2016)
	Movement	Wild boar increase spatial range size and distance between resting sites during hunting season.	(Scillitani *et al.* 2010)
	Foraging	Exposure to human voices reduces foraging of mesopredators and increases foraging of prey species.	(Suraci *et al.* 2019)
	Communication	Gibbons reduce communicative singing when humans are present.	(Dooley & Judge 2015)
	Communication → foraging	Social cues lead herbivorous fish to cease grazing in the presence of spearfishers.	(Gil & Hein 2017)
	Communication → vigilance & flight	Social cues lead herbivorous to flee in the presence of spearfishers.	(Gil & Hein 2017)
	Rest & hygiene	Cleaning activity of cleaner shrimp is suppressed by >50% during SCUBA diver presence.	(Titus *et al.* 2015)
	Breeding & parental care	Arctic geese increase incubation breaks when observers are present, which lead to 7-35% reductions in nest survival probability.	(Meixell & Flint 2017)
	Vigilance & flight	Reef fish exposed to spearfishing have reduced flight initiation distances in response to divers.	(Januchowski-Hartley *et al.* 2011)
Bottom-up effects	Timing & distribution of activities	Stingrays shift from nocturnal to diurnal foraging in response to provisioning from tourism operations.	(Corcoran *et al.* 2013)
	Movement	Sharks change residency patterns in response to provisioning from tourism operations.	(Clua *et al.* 2010)
	Foraging	Stingray diet composition changes in areas where provisioning from humans occurs.	(Semeniuk & Rothley 2008)
	Rest & hygiene	Dingoes spend 23% of their time resting when employing 'sit and wait' tactics to obtain discards from human fishermen, as opposed to 0.3% in undisturbed environments.	(Déaux *et al.* 2018)
	Breeding & parental care	Provisioned dolphin mothers exhibit reduced parental care, with calves born to	(Mann *et al.* 2000; Foroughirad &

		provisioned mothers spending less time with their mothers, less time resting, and more time foraging than calves born to non-provisioned mothers. Reduction in provisioning activities were associated with an increase in calf survival rate from 23% to 87%.	Mann 2013)
	Vigilance & flight	Birds have reduced flight initiation distances in areas with bird feeders.	(Møller *et al.* 2015)
Physical environment effects	Timing & distribution of activities	Caribou change distribution of activities to avoid developed road areas.	(Leblond *et al.* 2013)
	Movement	Pumas increase nighttime movement ranges in residential development areas.	(Wang *et al.* 2017)
	Foraging	Anthropogenic light pollution alters foraging behaviors of intertidal dogwhelks.	(Underwood *et al.* 2017)
	Rest & hygiene	Cooperation and efficiency of cleaner fish declines during periods of motorboat noise.	(Nedelec *et al.* 2017)
	Communication	Water turbidity associated with anthropogenic impacts reduces predator recognition of minnows.	(Chivers *et al.* 2013)
	Communication → breeding & parental care	Pesticides impair pheromonal communication among newts and impede mate selection behaviors	(Park D *et al.* 2001)
	Rest & hygiene	Dolphins decrease time resting and increase time spent travelling when boats are present.	(Lusseau 2003)
	Breeding & parental care	Noise from road traffic decreases songbird clutch size.	(Halfwerk *et al.* 2011)

Table S2. Examples of human-induced behavioral effect pathways linked to ecosystem functions or individual, population, or community consequences.

Human impact	**Animal behavior**	**Ecological implications**	**Example**	**Reference**
Ecosystem functions				
Bottom-up effects	Movement	Pathogen transfer	Provisioning-induced aggregations alter movement patterns and facilitate disease transfer in moles.	(Forbes *et al.* 2015)
Top-down effects	Timing & distribution of activities → foraging	Habitat modification	Human presence on trails changes wolf distribution patterns, which alters elk foraging and affects plant communities, beaver den distribution, and songbird abundance.	(Hebblewhite *et al.* 2005)
Top-down effects	Timing & distribution of activities → foraging	Habitat modification	Fishing-reduced predator populations increase foraging ranges of herbivorous fish, which contributes to seascape-level changes in algal distribution.	(Madin *et al.* 2010a, 2019; DiFiore *et al.* 2019)
Physical environment effects	Movement	Pollination & seed dispersal	Habitat fragmentation leads to altered movement of hornbills, which changes seed dispersal range.	(Lenz *et al.* 2011)
Individual, population, and community consequences				
Top-down effects	Timing & distribution of activities	Species co-occurrence	Human trail use spatially and temporally displaces bobcats and, to a lesser degree, coyotes, but not deer.	(George & Crooks 2006)
Bottom-up effects	Breeding & parental care	Population growth	Provisioning of dolphins is associated with reduced parental care and lower calf survivorship than non-provisioned periods.	(Foroughirad & Mann 2013)
Top-down effects	Vigilance & flight	Physiology & fitness → population growth	Prairie dogs exposed to hunting activity have elevated fecal cortisone concentrations, associated with 50% reductions in pregnancy rates and 80% reductions in reproductive output.	(Pauli & Buskirk 2007)
Bottom-up effects	Foraging	Physiology & fitness	Higher consumption of fisheries discards by gannets are associated with reduced body condition.	(Votier *et al.* 2010)
Bottom-up effects	Rest & hygiene	Physiology & fitness	Sharks increase metabolic expenditure on provisioning days because they increase activity at times when they would otherwise be resting.	(Barnett *et al.* 2016)
Top-down effects	Vigilance & flight	Physiology & fitness	Increased flight during periods of high human traffic is associated with increased stress hormone levels in birds.	(Tarjuelo *et al.* 2015)

III. Variation in herbivore grazing behavior across Caribbean reef sites

A. Abstract

Herbivorous fish can increase coral growth and survival by grazing down algal competitors. With coral reefs in global decline, maintaining adequate herbivory has become a primary goal for many managers. However, herbivore biomass targets assume grazing behavior is consistent across different reef systems, even though relatively few have been studied. We document grazing behavior of two scarid species in Antigua, Barbuda, and Bonaire. Our analyses show significant differences in intraspecific feeding rates, time spent grazing, and intensity of grazing across sites, which may alter the ecological impact of a given scarid population. We suggest several hypothesized mechanisms for these behavioral variations that would benefit from explicit testing in future research. As managers set targets to enhance herbivory on reefs, it is critical that we understand potential differences in the scarid grazing impact. Our findings demonstrate the variability of grazing behavior across different reef sites and call for further investigation of the drivers and ecological implications of these inconsistencies.

B. Introduction

Herbivorous fishes can play a critical role in coral reef ecosystems by suppressing algae and thereby facilitating coral growth, recruitment, and survival (Box & Mumby 2007; Rasher & Hay 2010; Steneck *et al.* 2014). In recent decades, coral reefs have become increasingly threatened by diverse anthropogenic impacts, including overfishing of herbivorous fish populations (Hughes *et al.* 2007; Edwards *et al.* 2014). Insufficient herbivory can allow algae to outcompete corals for space, ultimately driving shifts from coral to algal dominance that have occurred in much of the Caribbean region (Jackson *et al.* 2014). Coral reef fisheries thus cannot simply manage for sustainable yields as in traditional fisheries, but must also consider the levels of persistent herbivory required to maintain critical ecosystem functions. Increasing attention has been given to understanding how much herbivory is needed to sustain coral reef health and to identify thresholds of herbivore biomass that can be used to guide fisheries management targets (McClanahan *et al.* 2011; Adam *et al.* 2015; Karr *et al.* 2015).

However, all herbivorous fish are not the same in terms of their grazing impact on reefs, and variation can occur both among and within species. Studies have highlighted functional differences across species and size classes in terms of feeding morphology, selectivity, and foraging distribution within a reefscape (Bruggemann *et al.* 1994, 1996; Bonaldo & Bellwood 2008; Lokrantz *et al.* 2008; Ong & Holland 2010; Burkepile & Hay 2011; Afeworki *et al.* 2013; Rasher *et al.* 2013; Adam *et al.* 2015, 2018; Hoey 2018). Selective exclusions of different herbivorous fish species result in distinct algal communities (Burkepile & Hay 2011), highlighting the ecological significance of interspecific differences in functional roles among herbivores and suggesting that simple targets for total herbivore populations may be inadequate in managing for coral reef health.

In addition to established interspecific and size-specific differences, environmental contexts can also drive variability in herbivore behavior. Several empirical studies have demonstrated the sensitivity of behaviors such as foraging and movement to predator presence (Madin et al. 2010b; Davis et al. 2017); reef rugosity (Catano *et al.* 2014); grazing behaviors of proximate herbivores (Gil & Hein 2017); and the abundance, distribution, and nutritional content of algal resources (Tootell & Steele 2016; Davis *et al.* 2017). In some cases these behavioral variations have been explicitly linked to larger ecosystem impacts. For example, fishing-induced declines in predatory fish abundances can increase grazing ranges of herbivorous fish and alter seascape-level algal distribution patterns (Madin *et al.* 2010a; DiFiore *et al.* 2019).

Despite a growing understanding of the ecological importance of herbivore behavior and its sensitivity to environmental conditions, many efforts to predict herbivore impact on reefs assume species- and size-specific feeding rates that remain constant across different reef environments, overlooking factors such as fishing pressure and habitat shifts that, as noted above, have the potential to dramatically alter grazing behaviors. For example, many reef models use grazing behavior data from one or two locations (e.g., Mumby et al. 2006; Bozec et al. 2016; Perry et al. 2018) which – while still valuable - may not accurately represent dynamics on other reefs. Other studies have struggled to establish links between herbivore biomass and reef health (e.g., McClanahan et al. 2011; Karr et al. 2015; Bruno et al. 2019), which could reflect variation in herbivore behavior that makes biomass an incomplete metric of herbivory. If herbivore feeding activity is suppressed under degraded reef conditions, such as low reef structural complexity or low fish populations, the biomass of herbivorous fish identified as capable of maintaining reef function in pristine systems may be insufficient in degraded environments. Insufficient herbivory may of course further reef degradation, potentially forming a reinforcing feedback loop (Mumby & Steneck 2008; Nyström *et al.* 2012; Bozec *et al.* 2013; Adam *et al.* 2015). Knowledge gaps around herbivore grazing behaviors are particularly important as we seek to manage individual reef ecosystems that vary greatly in terms of reef context and condition.

Here we assess both interspecific and intraspecific variability in multiple components of feeding behavior for two scarid (parrotfish) species across reef sites around three Caribbean islands and discuss potential underlying mechanisms, ecological consequences, and management implications. We provide a framework of hypothesized pathways in which human activities may alter reef function through impacts on herbivore behavior that motivate future research and can be used to guide management.

C. Materials and methods

Study sites

Caribbean reefs vary greatly in terms of anthropogenic impacts and reef condition. Our study focused on 13 reef sites off the islands of Bonaire, Antigua, and Barbuda (Fig. 1) that encompass a range of benthic and fish community conditions. Bonaire has among the highest live coral cover and herbivorous fish biomass in the Caribbean region (Jackson *et al.* 2014), likely a result of longstanding fishing restrictions that include the prohibition of parrotfish harvest (Steneck & Arnold 2015). Antiguan and Barbudan reefs are more representative of many Caribbean reefs today (Jackson *et al.* 2014), with relatively low coral cover and high algal abundances, as well as reduced fish stocks due to substantial local fishing pressure. All three islands receive regular wave and wind exposure from the east and northeast, and sites were selected on relatively sheltered western- and southwestern-facing shores for dive feasibility.

Surveys

All data were collected between March and August of 2017. Reef characteristics were assessed at 10 m depth to control for the influence of depth on algal growth rates, with behavioral observations of fish initiated between 8 and 12 m depths. Behavioral data were discarded if focal fish left a 5 to 15 m depth range during the observation period.

Behavioral observations

We observed grazing behavior of two dominant scarid species, *Sparisoma viride* and *Scarus vetula*, at each of our 13 study sites. We targeted these species because of their relative abundance as well as their contrasting grazing mechanisms. *S. vetula* takes relatively shallow, scraping bites and ingests mostly epilithic algae, or algae growing on a substrate's surface. *S. viride* is an excavating grazer, taking deeper bites containing large amounts of both endolithic algae, which grow within the skeleton of a substrate such as dead coral or porous rock, and crustose algae, which form a thin crust on a substrate's surface (Bruggemann *et al.* 1994). This analysis focuses only on initial phase (female) individuals due to their relatively high abundance and to eliminate potential interactions between territorial male behavior and feeding patterns. A size window of 15 – 30 cm forklength was used to reduce the potentially confounding effects of fish size on feeding behaviors.

Prior to data collection, three divers conducted underwater size calibrations with marked PVC reference pipes to ensure consistency and accuracy of fish forklength estimates. PVC dive sleeves (tubes on which data were recorded) were marked at 5 cm increments to provide size references during data collection. Practice dives were completed at the onset of the Bonaire, Antigua, and Barbuda data collection periods, during which divers took turns observing each other's fish follows to ensure consistency in diver behavior and data notation.

Divers quantified grazing behavior by following individual fish for a two-minute observation period. Once a target fish was identified, we estimated fish size and allowed for a 15 second calibration period. We initiated all follows from a distance of at least 3.5 m based on previously established flight initiation distances (*S. viride* = 2.4 ± 0.4 m, *S. vetula* = 2.8 ± 0.4 m; Table S2) at spearfished sites in Antigua. Fish in Bonaire were assumed to have smaller flight initiation distances because of the longstanding and heavily enforced spearfishing ban, but we still initiated follows from a conservative 3.5 m distance. Divers maintained this distance unless the focal fish approached, in which case divers maintained their positioning. We discarded data from any incomplete follows (e.g., where visual contact could not be maintained for a full two-minute period) or follows where fish hid or fled from the observing diver. After each two-minute observation, divers moved slowly in a preestablished direction along the reef and identified a subsequent focal individual of a different species and/or estimated forklength to avoid repeated observations of the same individual (Nash *et al.* 2016).

During each follow period, divers recorded the commencement and cessation of grazing forays and the number of bites taken during each foray. Grazing forays were defined as a cluster of consecutive bites and were distinguished from a preceding foray by an elevation of the fish's head > 45° above the substrate and active swimming to another location (Nash *et al.* 2012). We used these grazing data to quantify several components of feeding behavior: active bite rate, time spent grazing, feeding rate, and grazing intensity (Table 1). Active bite rate refers to the frequency of bites taken during periods of active feeding, while feeding rate refers to the frequency of bites taken during the entire duration of a follow, including time not spent feeding. Time spent grazing is reported as the fraction of the total observation period during which a fish was actively feeding. Grazing intensity refers to the average number of consecutive bites taken in a feeding foray before feeding ceases.

Reef community data

At each site we conducted fish, benthic, and rugosity surveys to quantify various components of reef condition (Table 2). We used a modified Atlantic Gulf Rapid Reef Assessment (AGRRA; Lang et al. 2010) protocol with 30 m by 4 m belt transects and 10 m point-intercept transects for fish and benthic surveys, respectively. We recorded all herbivorous and piscivorous fish encountered that were larger than 5 cm forklength. On benthic surveys, we assessed percent cover of live and dead coral, epilithic turf algae, macroalgae, and other benthic organisms by identifying the substrate under transect points at 10 cm intervals. In cases where multiple substrate types overlapped (e.g., dead coral covered by algae or other benthic organisms), we identified the substrate based on the uppermost layer. We measured the canopy height of turf and macroalgae at each point where it was present to a precision of 1 mm. To assess reef rugosity, we measured the length of a line run molded to the reef contour directly below each meter of the taut 10m benthic transect tape (sensu Alvarez-Filip et al. 2009). We carried out between five and seven fish transects and between four and five benthic and rugosity transects per site.

Analysis

To estimate fish biomass at each site, we calculated the weight of individual fish encountered on underwater surveys using published length-weight relationships (Bohnsack

& Harper 1988). We classified potential predators as piscivores above 30 cm forklength based on approximations of predator gape size relative to the body depth of the smallest (15 cm forklength) *S. viride* and *S. vetula* individuals observed in this study (details provided in supplementary material). While optimal prey size is likely smaller than a predator's full gape (Mumby *et al.* 2006), consumption of prey up to gape size has been observed (Wainwright & Richard 1995; Nash *et al.* 2012). We used benthic point-intercept data to calculate the proportion of each transect composed of each benthic substrate type. To calculate rugosity, we generated a ratio of contoured to taut transect lines where 1 is a flat surface and increasing values indicate increasing complexity (Alvarez-Filip *et al.* 2009). Mean fish, benthic, and rugosity characteristics across transects for each site were integrated via principal component analysis (PCA) to characterize differences across our 13 study sites. All analyses were conducted in R 4.0.2 (R Core Team 2020).

When analyzing behavioral data, we excluded one site in Barbuda (Pallaster West) from *S. viride* analyses and two sites in Antigua (Rendezvous and Turtle Bay) and one in Barbuda (Pallaster East) from *S. vetula* analyses due to a low abundance of initial phase individuals at these sites. Thus, results are based on a total sample size of n = 194 and n = 163 individuals for *S. viride* and *S. vetula*, respectively, with means of 16.2 ± 1.6 and 16.3 ± 3.2 individuals observed per site (see Table S3). Grazing intensity was calculated by averaging the number of bites in a complete feeding foray for each individual fish followed. Site-level summary statistics were calculated using mean values of bite rates, time spent grazing, feeding rates, and grazing intensity. Variation among sites was quantified via Kruskall-Wallis analysis of variance, because heteroscedasticity of behavioral response variables violated parametric assumptions.

To evaluate the effects of reef condition, species, and fish size on grazing behaviors across sites, we used generalized additive mixed models (GAMMs) with Gaussian distributions (Wood 2020). GAMMs allow for detection of nonlinear relationships among variables as well as the distinction among fixed and random effects (Zuur 2009). Because explanatory fish and benthic community variables of interest exhibited collinearities (VIF (variable inflation factor) > 3; Zuur et al. 2007), PC1 and PC2 from our PCA were used to summarize variations in reef condition. Species and average size (forklength) of focal fish for each species at each site were included as explanatory variables, with island included as a random effect. Mean feeding rates and grazing intensities were calculated for each species and site and included as the two behavioral response variables for our GAMMs. The number of knots, which correlates with the complexity of a GAMM's fitted spline, was set to 3 to prevent overfitting while still accommodating potential nonlinear relationships (Zuur 2009). We evaluated models using Akaike's information criteria adjusted for small sample sizes (AICc) using the MuMIn package in R (Bartón 2020). Estimated degrees of freedom (edf) are reported to quantify nonlinearities among continuous predictor and response variables (Hunsicker *et al.* 2016).

D. Results

Reef community composition

Reef characteristics varied substantially among sites (Fig. 2). PC1 and PC2 accounted for 55.6% and 24.6% of variation among sites, respectively. High PC1 values reflect primarily low coral cover, reef rugosity, and scarid biomass and high macroalgal cover and canopy height (Table 2), essentially indicating poor reef health. High PC2 values, on the other hand, primarily indicate high scarid density and low turf algal cover. Large predator biomass and density were highly correlated ($R^2 = 0.99$), so only biomass was used to represent predator presence in the PCA. Bonaire sites were characterized by higher scarid and predator biomass and lower turf and macroalgal canopy height and macroalgal percent cover than Antiguan and Barbudan sites. Barbudan sites typically had higher scarid densities and reef rugosity and lower percent cover of turf algae than Antiguan sites, with both islands having similar levels of coral cover and scarid and predator biomasses.

Feeding behavior

Feeding rates, time spent grazing, and grazing intensity varied significantly ($p < 0.001$) across sites for both *S. vetula* and *S. viride* populations (Fig. 3). For *S. vetula*, feeding rates differed almost nine-fold and grazing intensity differed nearly five-fold between the highest and lowest sites, while *S. viride* feeding rates and grazing intensities varied over five-fold and six-fold, respectively. Differences in site-level feeding rates reflected differences in the fraction of time that fish spent grazing as opposed to differences in bite rates while actively feeding, which did not differ significantly among sites ($p > 0.5$).

To investigate potential drivers of these documented behavioral differences, we compared GAMMs with different combinations of reef condition and fish species and size predictors. We focused on drivers of feeding rate and grazing intensity, omitting time spent grazing because of its inherent link with overall feeding rate. Species and PC1 were included in the best models predicting both feeding rate and grazing intensity (Table 3). The role of species in driving feeding behaviors reflects known differences in grazing morphologies between *S. viride* and *S. vetula*, with *S. vetula* taking more frequent bites. PC1 had a negative effect on both feeding rate and grazing intensity, suggesting that scarids take fewer total bites and fewer bites per individual grazing foray on reefs characterized by low scarid and predator abundances, low coral cover and rugosity, and high turf and macroalgal cover. In the succeeding models for both feeding rate and grazing intensity, PC1 had a stronger negative effect for *S. vetula* than *S. viride*. Continuous predictor variables had linear relationships (edf = 1) in all selected models except for the second-best model predicting grazing intensity, in which the species and PC1 interaction term was slightly nonlinear (edf = 1.46 and 1.43 for *S. vetula* and *S. viride*, respectively).

E. Discussion

Several underlying mechanisms linking environmental conditions to herbivore behavior may be driving observed differences among sites. Covariation among linked reef characteristics restrict us to using PCA indicators as opposed to specific reef traits in our GAMM analyses, and our correlational results do not allow us to determine causality (e.g., algal abundance may be causing differences in herbivore behavior, or vice versa). Despite these limitations, we present hypotheses for potential underlying mechanisms here (Fig. 4) and discuss relevant theory and ecological and management implications. While we cannot conclusively test these hypotheses within the scope of this study, we discuss preliminary evidence for each and highlight priorities for further research.

Social feeding or shared vigilance hypothesis. Shared vigilance theory describes the benefits to prey of grouping together (e.g., schools, herds), as each individual can spend less time looking out for predators and more time carrying out other behaviors such as feeding (Pulliam *et al.* 1982; Roberts 1996; Lima & Bednekoff 1999). Assuming constant predator populations, as group size decreases, vigilance becomes more concentrated on each individual group member. A recent empirical study demonstrated that herbivorous reef fish use social cues from the density and behavior of other herbivores to determine whether or not to feed (Gil & Hein 2017). Individual fish were more likely to commence grazing as the presence of other feeding individuals increased. This 'behavioral coupling' may drive a potential reinforcing feedback loop in which higher herbivore abundances increase the feeding activity of each individual fish, further increasing the grazing impact of a given school (Fig. 4). While we cannot distinguish among correlated reef characteristics here, scarid biomass was one of the strongest contributors to PC1 (Table 2), a significant predictor of feeding rate and grazing intensity in all best performing GAMMs (Table 3). Scarid density contributed moderately to PC1 and strongly to PC2, which was not a significant predictor in any of the selected models. More data and dedicated studies are needed to distinguish the exact effects of herbivore abundance in determining feeding behaviors.

Predation risk hypothesis. As introduced above, predation risk can be an important driver of feeding behavior. While collective vigilance can moderate predation risk, predator presence is an ultimate determinant. Previous work has documented the suppressive effect of acute predator presence (typically simulated with large piscivore decoys) on herbivore feeding rates (Madin *et al.* 2010b; Rizzari & Frisch 2014; Catano *et al.* 2017; DiFiore *et al.* 2019). Reef rugosity may also impact predation risk by modifying prey refuge availability and visibility to predators (Alvarez-Filip *et al.* 2009). While predator biomass was a moderate driver of PC1, rugosity was among the strongest (Table 2), suggesting it may have played a role in predicting feeding rate and grazing intensity in our top performing models.

While not explicitly investigated here, risk of predation from spearfishers may play a substantial role in determining scarid grazing behavior. The larger *S. vetula* and *S. viride* individuals observed in our behavioral observations are approaching size refuge from most natural predators, but they would be likely targets for spearfishers in both Antigua and

Barbuda, but not in Bonaire where long standing regulations prohibit spearfishing. We did not quantify spearfisher presence across sites (beyond its enforced absence in Bonaire), so we cannot assess this potential effect here, but point out that it may have important implications for herbivore behavior. While declines in herbivorous fish abundances that could alter perceived risk and social feeding behaviors may be countered by simultaneous declines in natural predator abundance, spearfishing can have the effect of both reducing group size and increasing predation risk (Fig. 4). Similar to the social feeding hypothesis, spearfishing could have a double impact of both reducing herbivorous fish biomass and reducing the grazing impact of remaining fish by altering perceived risk environments. While several studies have documented the effects of spearfishing on fish flight behavior (e.g., Gotanda et al. 2009; Januchowski-Hartley et al. 2011, 2015), further work is needed to investigate the potential chronic effects of spearfishing on herbivore feeding behaviors.

Bite content hypothesis. Differences in feeding rates could also reflect differences in the content or quality of an individual bite. Significant negative relationships between PC1 and feeding rates and grazing intensity in all top models reflect negative associations with the cover and canopy height of both turf and macroalgae (Table 2). In sites with higher algal canopies, scarids may be obtaining more biomass of food per bite than in areas with heavily cropped algae, requiring them to take fewer bites to obtain the same nutritional intake. However, previous empirical work done on the bite volume of both *S. viride* and *S. vetula* showed that bite content (biomass of algae removed) did not vary significantly with algal canopy height (Bruggemann *et al.* 1994). It is also possible that scarids need to employ more rapid feeding rates if forced to graze on material with lower nutritional quality. This could be the case in Bonaire, where higher parrotfish densities and lower algal cover may make high quality resources more limited. While actual bite content was not assessed here in terms of biomass nor nutritional quality, it would be valuable to investigate potential differences across sites as these could have implications for both fish growth and benthic dynamics.

Variation in herbivore feeding rates and grazing intensity may have important ecological consequences and management implications for coral reef systems. Feeding rates can directly influence the amount of algae removed from a given reef, while grazing intensity can influence the effectiveness of grazing in cropping algae. Grazing forays with more consecutive bites suggests more concentrated grazing, which are likely more effective in maintaining sufficiently low algal canopy heights and clearing substrate for growing or newly recruiting corals than bites dispersed throughout the reefscape. Experimental evidence has shown that more spatially concentrated grazing results in persistently suppressed algal canopy heights, suggesting that a given herbivore population's ability to maintain algae in a cropped state depends on the distribution of grazing efforts (Williams *et al.* 2001).

Because of these ecological implications, behavioral variations may be important in guiding effective coral reef management. If feeding rate data from one area are used to predict the impact of a given species in other parts of the region, we may be overlooking important behavioral differences and misrepresenting grazing levels of different scarid populations. Feeding rates are used in herbivory models to calculate the grazing impact by a given fish community (usually expressed as the amount of reef surface area grazed per unit time). Studies examining relationships between herbivore biomass and reef health have had difficulty finding clear relationships (McClanahan *et al.* 2011; Karr *et al.* 2015; Bruno *et al.* 2019), possibly because these relationships are being distorted by differences in feeding behavior in different reef environments. Several hypothesized mechanisms predict lower feeding rates in more degraded reef conditions, implying that models using feeding rates from exemplary reefs may overestimate herbivory when applied to other systems. While these exact mechanisms are not tested here, we document some supporting trends and pose important questions for future research. Specifically, the relative roles of scarid abundance and scarid behavior, and the potentially reinforcing effects of these two factors, are critical areas for future empirical and modelling work.

While our study investigates the relationships between various reef traits and herbivore grazing behaviors, it is also important to note that we cannot establish causality here and that many of these relationships may be bidirectional or cyclical. For example, correlations between high algal abundances and low feeding rates may mean algal abundance is driving reduced feeding rates or that reduced feeding rates are increasing algal abundances, or that both relationships drive a reinforcing feedback loop. If mechanisms such as social feeding are responsible for variations in herbivore behavior, then links to algal communities could indicate the ecological implications of these behavioral impacts. Because algal variables were expectedly correlated with other reef characteristics such as rugosity and herbivore populations, we could not examine them here as potential response variables. Further investigation of these exact drivers is required to determine causality and investigate potential feedback loops in which grazing reductions attributed to more degraded reef conditions would further compound reef deterioration (Fig. 4). While additional experimental work is needed to distinguish underlying behavioral triggers, it is also likely that multiple mechanisms are acting in tandem as fishing, fish, and benthic characteristics are tightly linked in most reef systems.

Human activities are driving widespread changes in wildlife behaviors across marine and terrestrial ecosystems (Madin *et al.* 2015; Larson *et al.* 2016), which have the potential to affect critical ecological processes (Hebblewhite *et al.* 2005; Madin *et al.* 2010a; Ripple & Beschta 2012; Wilson *et al.* 2020b). This study documents differences in multiple scarid feeding behaviors across various Caribbean reef systems and suggests possible sensitivity of these critical feeding behaviors to reef condition. Coral reef managers should be aware of pathways in which human activities may reduce herbivore grazing impacts and be conservative in setting targets for herbivorous fish biomass in areas where feeding behaviors may be suppressed. If behavioral variation among reef environments is ignored, managers of characteristically degraded areas may overestimate the grazing impact of a given herbivore population when using behavioral data from more ‘pristine’ systems, thereby underestimating the herbivore biomass needed to sufficiently suppress algae and insufficiently restricting fisheries. Managers may also inaccurately assume that increasing herbivore biomass will linearly increase herbivory, while in fact these relationships may be moderated by other environmental conditions. If social feeding dynamics are in fact a strong driver of herbivory behaviors, cessation of spearfishing in reef areas would have disproportionately positive effects on herbivory, in that herbivore biomass would increase as would the grazing impact of each individual. However, further investigation of these specific drivers is needed before conclusive management recommendations can be made. Initial insights from this study suggest a need for increased incorporation of behavioral effects into ecosystem management and highlight critical areas for future research.

F. Tables

Table 1. Behavioral variables measured during fish follows.

Variable	**Definition**	**Unit**
Bite rate	Bite rate during active grazing forays	bites sec^{-1}
Time spent grazing	Fraction of time spent grazing during follow	fraction
Feeding rate	Overall bite rate during total follow	bites min^{-1}
Grazing intensity	Average number of bites per grazing foray	bites $foray^{-1}$

Table 2. Factor loadings of nine reef characteristic variables for PC1 and PC2.

Factor	**PC1 Loading**	**PC2 Loading**
Rugosity	-0.37	0.34
Macroalgal cover	0.36	0.29
Macroalgal canopy height	0.35	0.33
Turf cover	0.25	-0.54
Turf canopy height	0.31	0.20
Coral cover	-0.41	-0.06
Scarid biomass	-0.37	-0.04
Scarid density	-0.21	0.56
Predator biomass	-0.32	-0.17

Table 3. GAMM results predicting feeding rate and grazing intensity by site. Only top three models based on AICc values are reported here.

Model	Adj. R^2	AICc	ΔAICc
A) Feeding rate			
1. Species + PC1	0.59	150.42	0.00
2. Species + PC1~Species	0.64	155.95	5.53
3. Species + Size + PC1	0.57	159.84	9.42
B) Grazing intensity			
1. Species + PC1	0.64	119.87	0.00
2. Species + PC1~Species	0.70	125.19	5.32
3. Species + Size + PC1	0.63	129.19	9.32

G. Figures

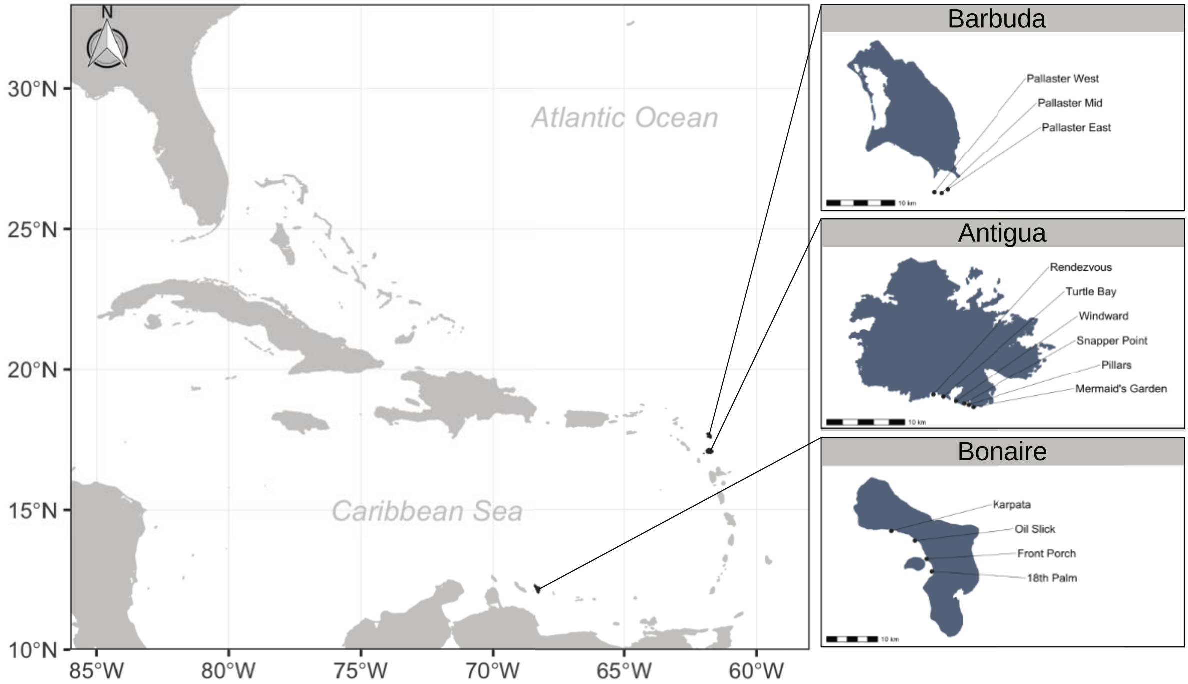

Figure 1. Map of the Caribbean region highlighting Barbuda, Antigua, and Bonaire, the three islands included in this study. Inset maps show the locations of each study site within these three islands.

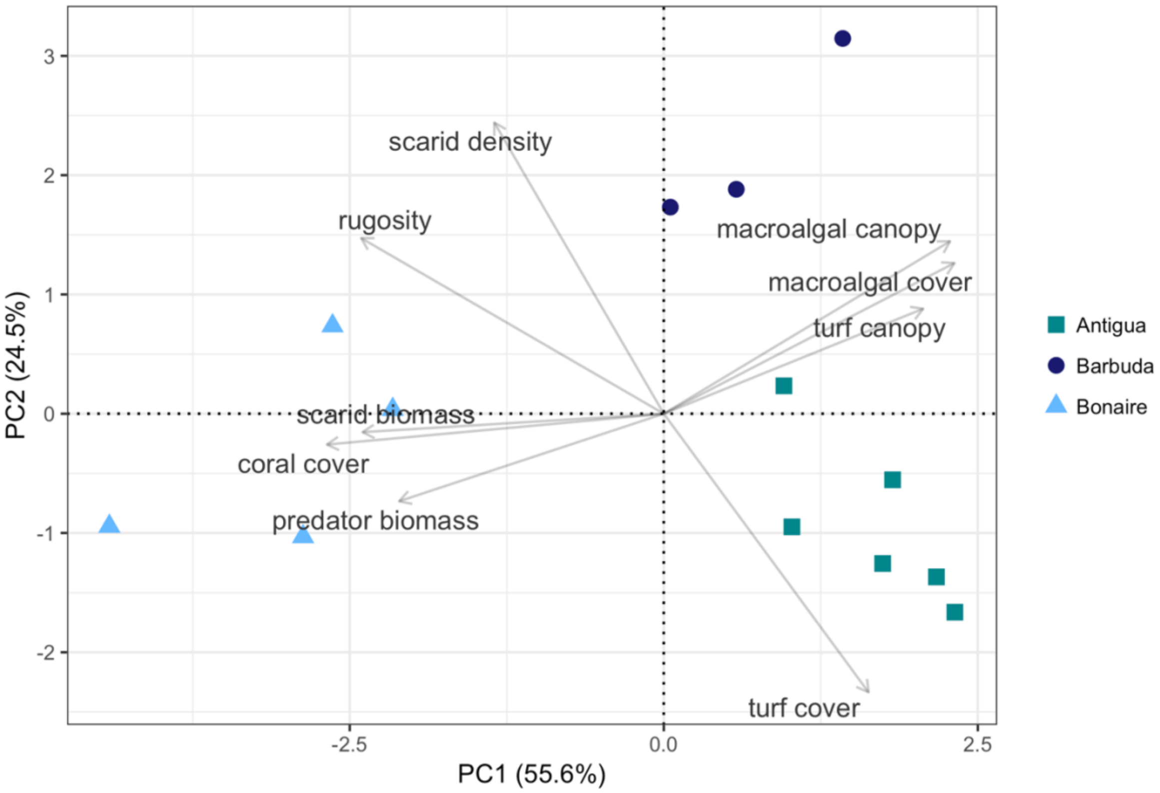

Figure 2. Principal component analysis (PCA) of reef characteristics at 13 assessed sites across Antigua Barbuda, and Bonaire. Arrows represent the contributions of nine reef variables to the first and second principal components (PC1 and PC2). PC1 and PC2 account for 55.6% and 24.5% of variance in reef characteristics, respectively.

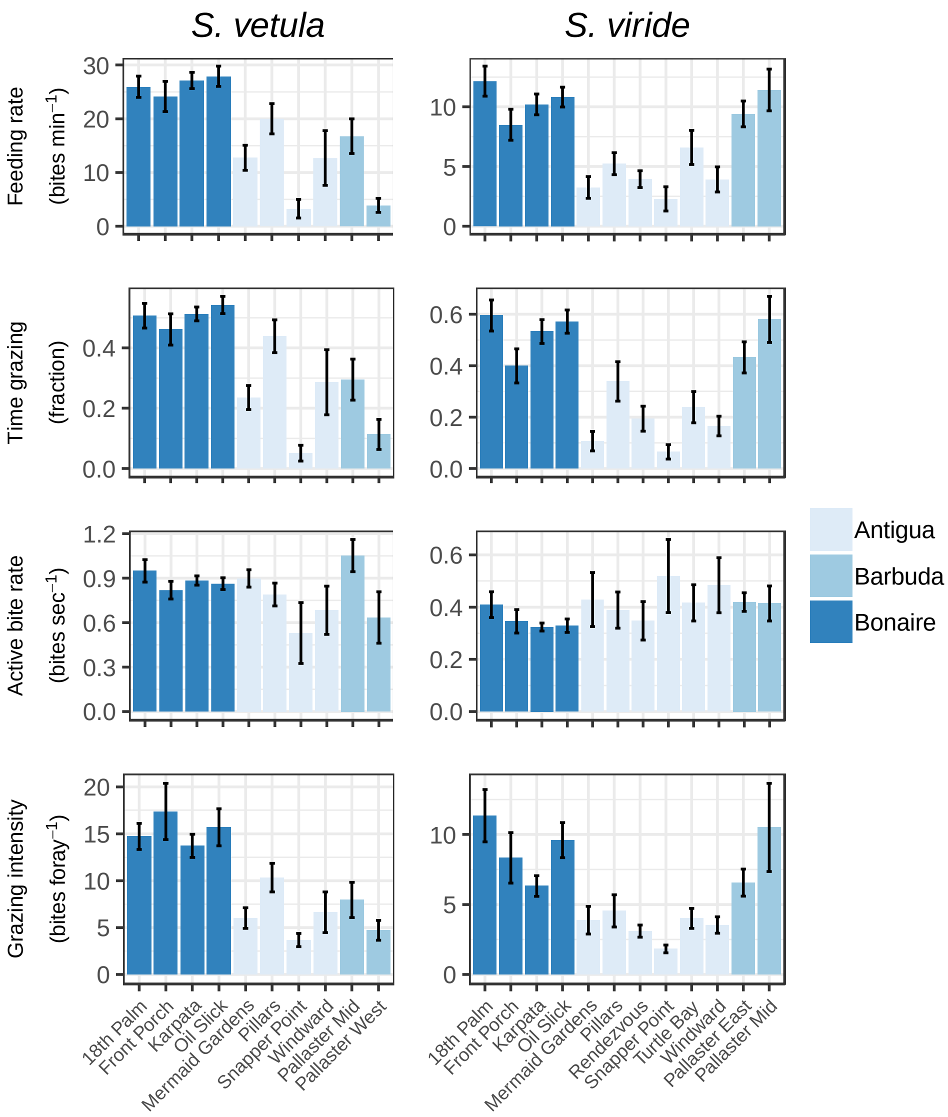

Figure 3. Mean feeding rates, fraction of time spent grazing, bite rate, and grazing intensity across sites for initial phase *S. viride* and *S. vetula* between 15 and 30 cm forklength. Error bars represent +/- standard error.

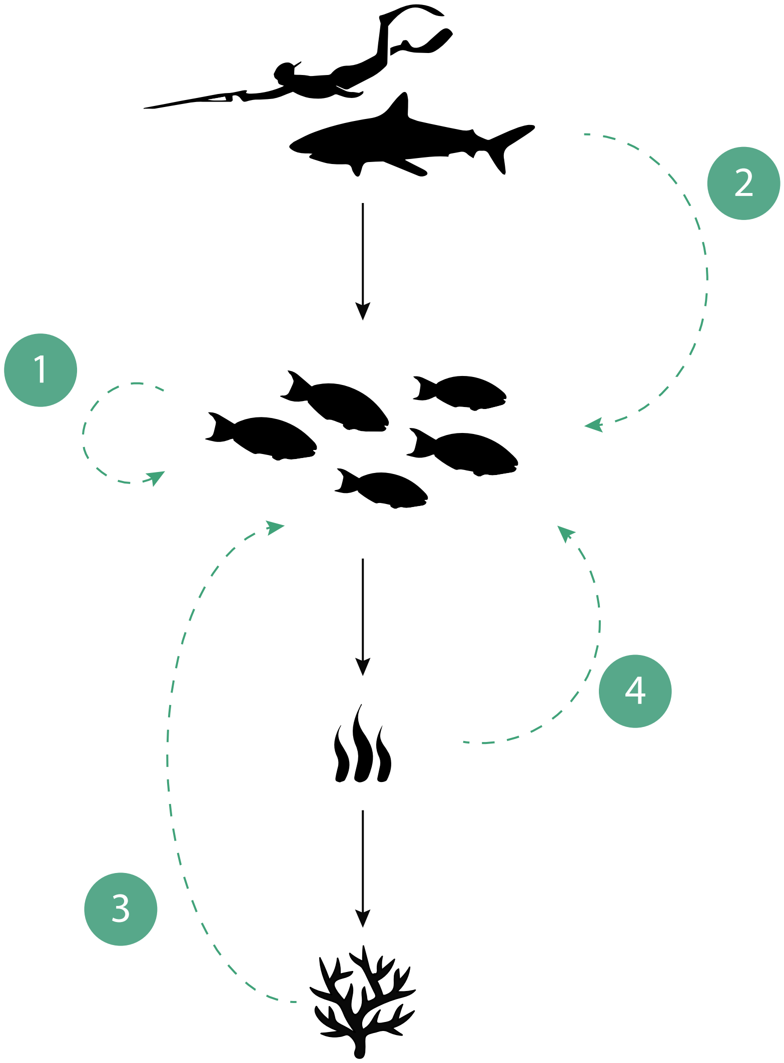

Figure 4. Hypothesized pathways in which various environmental factors may impact herbivore feeding behaviors, and potential feedback loops affecting overall grazing impact and coral health. Dashed lines indicate behaviorally mediated effects while solid lines represent density-mediated effects. Proposed mechanisms include social feeding dynamics (1), risk effects driven by predator presence (2) or reef rugosity (3), and bite content (4).

H. Supplementary Information

Table S1. Reef characteristics measured at each site

Category	Variable
Fish community	Scarid biomass (g $100m^{-2}$)
	Scarid density (indv. $100m^{-2}$)
	Predator biomass (piscivorous fish species greater than 30cm; g $100m^{-2}$)
Benthic community	Live coral percent cover
	Algal turf percent cover
	Algal turf canopy height (cm)
	Macroalgal percent cover
	Macroalgal canopy height (cm)
	CCA percent cover
	Rugosity

Flight initiation distance (FID) calculations

Grazing *Sparisoma viride* (n = 14) and *Scarus vetula* (n = 18) individuals of at least 15 cm forklength were approached by single divers swimming at about 0.5 m/s. A marked weight was dropped at the diver's location when the target fish moved location in response from the approaching diver (typically preceded by eye contact with the diver. A second weight was then placed at the location of the target fish prior to flight. The distance between the fish's location and the first weight was used to calculate the flight initiation distance (FID). Mean FID values are presented in Table S1. FID measurements were taken at an Antiguan site frequented by spearfishers, and was used to represent conservatively large FID for sites where spearfishing is prohibited.

Table S2. Flight initiation distances for *S. viride* and *S. vetula* individuals at spearfished sites in Antigua

Species	Mean FID (± SE)
Sparisoma viride	2.37 ± 0.40 m
Scarus vetula	2.81 ± 0.37 m

Table S3. Behavioral observation sample size by site

Island	Site	Species	N

Bonaire	18th Palm	*Scarus vetula*	26
Bonaire	18th Palm	*Sparisoma viride*	19
Bonaire	Front Porch	*Scarus vetula*	18
Bonaire	Front Porch	*Sparisoma viride*	20
Bonaire	Karpata	*Scarus vetula*	32
Bonaire	Karpata	*Sparisoma viride*	20
Bonaire	Oil Slick	*Scarus vetula*	32
Bonaire	Oil Slick	*Sparisoma viride*	30
Antigua	Mermaid Gardens	*Scarus vetula*	13
Antigua	Mermaid Gardens	*Sparisoma viride*	12
Antigua	Pillars	*Scarus vetula*	9
Antigua	Pillars	*Sparisoma viride*	15
Antigua	Rendezvous	*Sparisoma viride*	17
Antigua	Snapper Point	*Scarus vetula*	8
Antigua	Snapper Point	*Sparisoma viride*	10
Antigua	Turtle Bay	*Sparisoma viride*	11
Antigua	Windward	*Scarus vetula*	7
Antigua	Windward	*Sparisoma viride*	11
Barbuda	Pallaster East	*Sparisoma viride*	17
Barbuda	Pallaster Mid	*Scarus vetula*	8
Barbuda	Pallaster Mid	*Sparisoma viride*	12
Barbuda	Pallaster West	*Scarus vetula*	10

Calculations of predator gape size

To approximate the minimum size of piscivores capable of consuming focal scarid species, we used morphological relationships determined by Rakitin & Kramer (1996) and Mumby et al. (2006). Raktin and Kramer document that *Scarus spp.* and *Sparisoma spp.* of 15 cm forklength (the minimum size of scarids observed in our behavioral study) have a body depth of approximately 4.5 cm. Using the following equation found by Mumby et al. (2006) for a dominant predator *E. striatus*,

$$G = -0.5998 + (0.167 \times TL) \tag{1}$$

where G is predator gape width and TL is the total length of the predator, we find that an *E. striatus* individual of 30 cm has a gape width of 4.5 cm.

IV. Inshore versus offshore fishing activity in a Caribbean small-scale fishery

A. Abstract

Many small-scale fisheries are threatened globally by multiple challenges, including overfishing, habitat degradation, and pollution. These declines are particularly evident in many inshore coastal environments, such as coral reef systems. One posited solution is to move some of the current inshore fishing effort to offshore, pelagic fisheries, in particular through the use of moored fish aggregating devices (MFADs). While MFADs could increase fisher resilience in the face of fluctuating resources and facilitate recovery of degraded inshore areas, the net effects of MFADs on inshore habitats have not been sufficiently investigated. Here we examine gear use, landings, and effort trends across inshore and offshore fisheries in the eastern islands of Guadeloupe, one of the largest and earliest established MFAD fisheries in the Caribbean, from 2006 (gear use) and 2008 (landings and effort) to 2018. We find that the number of vessels fishing exclusively offshore gears has increased since MFAD introduction, despite recent declines in total fleet size. Total landings, combining inshore and offshore fleets, have remained relatively consistent between 2008 and 2018, but an increasing proportion has come from pelagic species in recent years. These trends suggest an overall decline in inshore fishing since the introduction of MFADs. While MFADs may enable more vessels to target offshore fisheries, other vessels that previously used a combination of both inshore and offshore gears have now specialized on inshore fishing. Declines in mixed inshore-offshore gear use are largely due to a substantial decline in offshore trolling, which fishers report to be less efficient as the

density of MFADs increases. The drop in offshore trolling, as well as a more recent decline in inshore line fishing, have resulted in a decrease in the number of gears used per vessel. MFAD and overall offshore gear use is most prevalent in La Désirade, an island situated with favorable currents and depths for FAD fishing relative to other ports. These findings suggest that MFADs have likely enabled certain vessels to specialize in offshore fishing and contributed to an increased proportion of landings from pelagic species. However, MFADs may also reduce the viability of offshore fishing to other portions of the fleet, potentially increasing inshore fishing pressure and reducing resource diversity for some vessels. Improved management of the MFAD fishery could increase access to offshore fisheries to a larger portion of the fleet. As inshore resources become increasingly degraded in small-scale fisheries around the globe and efforts to encourage offshore transitions continue, insights from established MFAD fisheries provide key lessons for evaluating the potential performance of these strategies and identifying factors that may influence their success.

B. Introduction

Many of the world's small-scale fisheries are threatened by declining marine resources (Sadovy 2005; Teh & Sumaila 2013). Coastal inshore environments are particularly at risk, because the proximity of inshore environments to humans can increase exposure to anthropogenic stressors such as overfishing, pollution, and habitat degradation (Cinner *et al.* 2013). Shallow environments may also be more vulnerable to certain consequences of climate change, such as increased irradiance, temperature changes, and storm events (Hoegh-Guldberg & Bruno 2010; Baird *et al.* 2018), with potential interactive effects among coastal nutrient inputs and thermal stress (Donovan *et al.* 2020). These various human impacts have contributed to dramatic declines in coral reef health in recent decades, making reef-based fisheries particularly threatened (Hughes *et al.* 2017).

Diversification of assets and flexibility through alternative livelihoods (e.g., tourism, aquaculture) are often promoted as paths to relieve fishing pressure on these degraded ecosystems and increase fishers' resilience (Allison & Ellis 2001; Cinner 2014; Cinner *et al.* 2018), although these programs have had limited success as fishers often show reluctance to exit a fishery even as their resource declines (Cinner *et al.* 2009; Daw *et al.* 2012; Cinner 2014; Macusi *et al.* 2017). Other strategies encourage fishers to shift inshore fishing pressure onto less heavily exploited offshore species instead of exiting a fishery altogether. However, pelagic fisheries can be less accessible to small-scale fishers due to increased travel distances, the need for more seaworthy vessels, and the often less predictable fish distributions relative to inshore fisheries. One method for reducing these barriers to effort redistribution is the use of moored fish aggregating devices (MFADs). Consisting of surface and/or subsurface buoys anchored in depths of 300 to over 5000 m (Bell *et al.* 2015; Guyader *et al.* 2017), MFADs can be used to aggregate pelagic species such as tunas (e.g., *Thunnus albacares, Thunnus atlanticus*), dolphinfish or mahi mahi (*Coryphaena hippurus*), wahoo (Acanthocybium solandri), and billfish (e.g., *Makaira nigricans*). By aggregating fish at known locations, MFADs can substantially reduce search costs and increase catch per unit effort to fishers (Buckley 1986; Cabral *et al.* 2014; Bell *et al.* 2015; Tilley *et al.* 2019).

As such, MFADs are frequently touted as a mechanism for shifting fishing pressure off of degraded inshore resources by increasing the accessibility and profitability of offshore fisheries to small-scale fishers (Sharp 2011; Beverly *et al.* 2012; Taquet 2013; Bell *et al.* 2017). MFADs may be deployed by governments or non-profit organizations for fishers to use, or MFAD construction techniques and materials may be provided to encourage fishers to set MFADs themselves. However, despite the ongoing promotion of MFADs in many small-scale fisheries, the implications of MFADs for other inshore and offshore gears has not been evaluated empirically. Here we document trends in gear use, landings, and fleet effort in the mixed-gear MFAD fishery of Guadeloupe, including trends in relative inshore and offshore resource use. Guadeloupe, a French overseas territory in the southern Caribbean, was one of the earliest adopters of MFADs in the Caribbean and now has among the largest MFAD fisheries in the region in terms of the number of MFADs deployed and the number of vessels utilizing them (Wilson *et al.* 2020a). Prior to MFAD introduction, offshore fishing in Guadeloupe was a supplementary, and highly seasonal, fishing activity for fishers otherwise focused on inshore gears (Diaz *et al.* 2002). Here we show that while MFAD use has likely enabled a substantial number of fishers to specialize in offshore fishing, it may also have reduced the viability of offshore fishing to other portions of the fleet that do not target MFADs. Drawing on our findings, we suggest several factors that likely affect inshore vs. offshore gear use in small-scale fisheries that have adopted MFADs. As the use and promotion of MFADs continues to grow in small-scale fisheries around the globe, the insights generated from this study can help anticipate MFAD outcomes and inform strategies to best facilitate offshore transitions.

C. Materials and methods

Study area - eastern Guadeloupe

Guadeloupe is an archipelago of six islands in the Lesser Antilles that together form a French overseas region. This study focuses on four fishing ports on Grand-Terre, the eastern of Guadeloupe’s two central islands, and one port on La Désirade, a smaller island off the east coast of Grand-Terre (Fig. 1). Exposed to the predominantly east-southeastern Antilles current and the greater depths of the Atlantic, this eastern region has access to notable pelagic resources.

The Guadeloupe fishery consists almost entirely of undecked, artisanal vessels between five and ten meters. Historically, the use of multiple gears per vessel has been the norm (Diaz *et al.* 2002). Prior to the use of MFADs, most vessels used a combination of nets, pots, lines, and freediving to target a variety of demersal fish and invertebrates, with many vessels trolling offshore during the winter months to target larger pelagics (primarily *Coryphaena hippurus*) (Diaz *et al.* 2002). The first MFAD was introduced in Guadeloupe in 1988, just as MFADs were beginning to be promoted and gaining popularity in the Caribbean region (Diaz *et al.* 2002; Wilson *et al.* 2020a). By 1992, as many as 30 MFADs were estimated to be deployed around Guadeloupe, and by 2000 this number had risen to roughly 200, with many fishers having adopted MFAD construction techniques and beginning to deploy MFADs themselves (Diaz *et al.* 2002). A 2012 aerial survey estimated over 400 MFADs to be deployed in the waters surrounding Guadeloupe (Guyader *et al.* 2017), with estimates exceeding 600 MFADs as of 2019 (Wilson *et al.* 2020a). The vast majority of Guadeloupe's MFADs are privately owned, meaning individual vessels or small groups of cooperative vessels construct and deploy MFADs for their own exclusive use. Fishers are required to obtain authorization before deploying an MFAD, but these regulations are not enforced and most MFADs are deployed illegally (Guyader *et al.* 2015). Because of this the MFAD fishery remains largely unmanaged with the exception of some informal use rights among fishers. MFAD fishers use informal territories, vigilance, and social pressure to enforce exclusive rights to fish on private MFADs, although poaching of other fishers' MFADs does occur (Guyader *et al.* 2018). As of 2019 Guadeloupe had eight public MFADs, or MFADs deployed for the use of all eligible vessels, with the remainder being privately deployed (Wilson *et al.* 2020a).

Data and analysis

This study utilizes two datasets collected by the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) in Guadeloupe. The first dataset comes from annually conducted fishing activity calendars, in which every vessel owner reports the various gears used during each month of the preceding year (Berthou *et al.* 2008). We investigated data collected between 2006 (the first year the calendars were collected) and 2018 in the five eastern ports. For the purposes of this study, we categorize reported fishing gears here as nets, pots, freediving, inshore line fishing, offshore line fishing, or MFAD fishing. See Table 1 for details on the specific gears and target species encompassed within each category.

The second dataset comes from IFREMER's Système d'Informations Halieutiques (IFREMER 2020) and provides estimated landings in terms of both weight and value for the five eastern ports from 2008 to 2018 as well as annual fleet effort in terms of days at sea for both inshore and offshore activities (Weiss *et al.* 2018). We estimated catch per unit effort by dividing annual landings of inshore, offshore, and all species by annual days at sea of inshore, offshore, and all vessels, respectively. All data analyses and visualization were conducted in R version 4.0.2 (R Core Team 2020).

D. Results

In 2006, over half of all vessels used a combination of inshore and offshore gears (Fig. 2A), with more of these mixed inshore-offshore vessels using offshore lines (here referred to simply as trolling, even though occasionally handlines and buoy lines are also used) than MFADs. Eighteen of 206 vessels were engaged exclusively in offshore fishing (Fig. 2A), with nearly 14 of these vessels using MFADs and only four vessels using exclusively trolling lines. Across the fleet, pots, trolling, and nets were the most common gears (Fig. 2B). Vessels used an average of 2.5 ± 0.03 gears over the course of the year, with particularly high overlap between pots and offshore line fishing, but common overlap among all gears except freediving (Fig. 3).

Over the data collection period, the proportion of vessels combining both inshore and offshore gears declined from 57% to 32%, with increasing proportions of vessels fishing exclusively inshore or exclusively offshore gears as of 2018 (Fig. 2A). This stems from a dramatic decline in trolling lines, which had previously been the primary link between inshore gear users and offshore resources (Figs. 2B, 3). By 2018 the use of multiple gears had become much less common (Fig. 3), and average gear diversity per vessel had dropped to 1.7 ± 0.03. Most overlap remaining was between nets and pots and between pots and MFADs, with these combination pot and MFAD vessels making up the majority of vessels utilizing both inshore and offshore resources. Inshore line fishing also declined in the latter half of the data collection period, with particularly sharp declines in both inshore and offshore line fishing between 2017 and 2018. The relative use of nets, pots, MFADs, and freediving remained somewhat consistent over the data collection period (Fig. 2B). Accompanying these trends is an overall decline in the total number of vessels in the fishery (Fig. 2A).

The use of inshore and offshore gears also varies substantially by port (Fig. 4). In La Désirade, half of all vessels combine inshore and offshore gears with an additional 17% fishing exclusively offshore. Sixty-six percent of all vessels in La Désirade use MFADs either part or full time. In the remaining ports, exclusively inshore vessels dominate, comprising at least two thirds of each subfleet, with MFAD use ranging from 0 to 33% of all vessels. Le Moule has a comparable percentage of exclusively offshore vessels (17%) as La Désirade, but a much smaller proportion of vessels combining inshore and offshore gears.

As total fleet size has declined from 2008 to 2018 (Fig. 2A), so has the total fleet effort in terms of annual days at sea (Fig. S1A, Appendix A). Over the same period, catch per unit effort (CPUE) in terms of weight has increased across the fleet ($p < 0.01$). CPUE for offshore fisheries has exceeded that of inshore fisheries and increased significantly ($p < 0.05$) throughout the data collection period, while CPUE for inshore fisheries show no statistically significant trends. Increases in overall CPUE have contributed to sustained landings despite declines in fleet size and effort (Fig. S1B, C, Appendix A). Offshore species surpassed inshore species in terms of the proportion of total landings by weight in 2009 and continued to exceed inshore species over the data collection period, nearly doubling that of inshore species as of 2018 (Fig. 5B). Higher average value of inshore species by weight (due to several high-value inshore species such as conch and lobster) attributes to more comparable landings and CPUE when assessed by value (Fig. S1C-D).

E. Discussion

MFADs have been promoted as tools for shifting fishing pressure onto offshore resources in small-scale fisheries. Our findings support the idea that MFADs allow for increased specialization in offshore fisheries, but that they may also make offshore fishing less feasible for certain portions of the fleet. While prior to MFAD introduction offshore fishing was merely a supplementary and highly seasonal activity (Diaz *et al.* 2002), 9% and 14% of the fleet were fishing exclusively offshore by 2006 and 2018, respectively. With the exception of two vessels that only use offshore trolling lines, all of the exclusively offshore fleet were utilizing MFADs by 2018. The increasing use of MFADs relative to offshore trolling is likely responsible for the increasing CPUE of offshore fishing vessels (Fig. 5D). While offshore landings can vary substantially from year to year, they make up an increasing proportion of total landings relative to inshore fishing (Fig. 5B), which arguably would not have been possible with previous levels of participation in only trolling. These trends indicate promising shifts towards offshore resources with the continued use of MFADs, but are also accompanied by a decline in the proportion of vessels fishing both inshore and offshore resources (57% to 32%) and an increase in the proportion of vessels fishing exclusively inshore (34% to 54%) from 2006 to 2018 (Fig. 2A), suggesting that other vessels have also shifted away from offshore fishing during the data collection period.

The most notable change in gear use over the data collection period is the substantial decline in the percent of vessels using trolling lines, which went from a peak of 63% in 2007 to 17% in 2018. Many fishers and managers attribute these declines to the increasing density in MFADs and the accompanying increase in territoriality of pelagic fishing zones (Guyader *et al.* 2018). It is also thought that a high density of MFADs can reduce the efficiency of trolling away from MFADs. Designed to aggregate fish in specific locations, MFADs inherently draw fish from other areas (Dagorn *et al.* 2000; Girard *et al.* 2004) and have been shown to alter fish movement patterns within local landscapes (Kleiber & Hampton 1994; Gall *et al.* 2000; Taquet 2013). This redistribution of fish around MFADs would likely make targeting them away from MFADs much more challenging and much less efficient in terms of time and fuel costs.

A 2002 report on MFAD use in Guadeloupe notes that by 2000, many vessels were already discontinuing offshore trolling for fishing around MFADs (Diaz *et al.* 2002). While many vessels that dropped offshore line use over the data collection period switched to or continued MFAD fishing, others dropped offshore fishing altogether with increased focus on nets or pots. This suggests that while MFADs may offer a more efficient alternative to offshore line fishing, offshore fishing may also be becoming less accessible to certain portions of the fleet. The gears that vessels used after dropping offshore line use seem to be primarily determined by what gears vessels were using upon entering the fishery. This suggests potential barriers that deter transitions to MFADs for many vessels despite their cessation of trolling.

Several factors likely limit vessels' adoption of MFAD fishing. First, MFAD use in Guadeloupe can be highly territorial. Unofficial territories are typically established by the spatial zones in which different fishers or groups of fishers deploy their MFADs (Guyader *et al.* 2018). Often these zones consist of a series of MFADs deployed linearly at increasing distances from shore so that owners can fish them sequentially on a given trip while maximizing travel efficiency. MFAD territories are not officially recognized but are often well-accepted among fishers (Guyader *et al.* 2018). While poaching of other fishers' offshore territories can occur, regular fishing of these areas by MFAD owners increases the likelihood of encountering and deterring poachers, and MFADs set within another vessel's territory will typically be cut (Guyader et al. 2018). Around the island of La Désirade, MFAD territories have become increasingly saturated in recent years, with fishers passing down territorial rights to family members or selling them to other fishers (Guyader *et al.* 2018). Territories have expanded into deeper waters, where fishers try to gain priority access to migrating pelagic species by setting MFADs upcurrent of the rest of the fleet, but eventually fuel costs and travel time become limiting factors. Across the eastern Guadeloupe fleet, the 2012 peak and subsequent plateau in MFAD engagement could suggest the fishery is close to its capacity in terms of vessel territories. In La Désirade, where MFAD use is particularly high, conflict among fishers over MFAD territories had reportedly increased between 2012 and 2018 (Guyader *et al.* 2018). While the number of MFAD vessels may be plateauing, the total number of MFADs deployed around Guadeloupe is thought to have increased from 2012 to 2019 (though this number is extremely challenging to quantify;

(Guyader *et al.* 2017; Wilson *et al.* 2020a). Fishers interviewed in La Désirade report an increase in the number of MFADs deployed per vessel, suggesting a dynamic in which vessels compete for increased stock access by deploying more MFADs relative to the rest of the fleet, which then dilutes the effectiveness of each individual MFAD, incentivizing fishers to deploy even more MFADs (Guyader *et al.* 2018). Older fishers in La Désirade report catching more fish on fewer MFADs in the early years of MFAD use.

Port location also likely influences the feasibility of MFAD adoption and offshore resource use. While all ports in eastern Guadeloupe have access to sufficiently deep waters for successful MFADs, port locations relative to one another may affect access to pelagic species. MFADs deployed upcurrent in terms of the dominant Antilles current direction are thought to gain earlier exposure to pelagic populations migrating through the area, potentially disadvantaging downcurrent areas (Guyader *et al.* 2018). Because La Désirade is positioned upcurrent of the other eastern Guadeloupe ports, it is possible that high densities of MFADs there aggregate and facilitate the harvest of many fish before they pass through other areas, reducing the efficiency of both MFADs and offshore trolling in downcurrent areas. Vessels from other ports could travel to compete with La Désiradian fishers, but would face increased travel costs and territorial disputes.

Cost is another factor likely to affect MFAD adoption. While offshore trolling requires relatively little gear investment, MFADs can cost over €4500 to construct in Guadeloupe (Guyader *et al.* 2018). Deployment also requires sufficient vessel capacity and experience. As mentioned above, competition among MFAD fishers has driven MFADs to be set farther and farther offshore, increasing fuel costs and also the need for larger, safer, and more powerful vessels. These elevated costs are likely significant deterrents for vessels previously fishing offshore only seasonally or part-time, leading them to fall back on exclusively inshore resources.

While allowing some vessels to specialize in offshore fishing, MFADs also seem to reduce the accessibility of offshore resources to other vessels. In the context of reducing inshore fishing pressure by facilitating offshore fishing, this implies that MFADs may have mixed effects. By enabling some vessels to fish exclusively offshore, MFADs could arguably reduce the fishing pressure that those vessels otherwise may have exerted in inshore environments. Conversely, by displacing offshore trolling fisheries, MFADs also make offshore fishing less accessible to those not specialized in MFADs, potentially increasing those vessel's pressure on inshore fisheries and also reducing fishers' resilience by decreasing resource diversity (Robinson *et al.* 2020). Prior to MFAD introduction, offshore trolling was just a seasonal activity, suggesting that it may have not substituted a large percentage of inshore fishing pressure. However this seasonal trolling activity was participated in by the majority of the fleet (Diaz *et al.* 2002), making potential implications for total inshore fishing pressure notable. The decline in the number of gears used by individual vessels and the number of vessels utilizing both inshore and offshore resources contrasts with some of the anticipated benefits of MFADs in enhancing fisher resilience.

Improved management of the Guadeloupe MFAD fishery would likely improve the outcomes of these fisheries (Taquet *et al.* 2011). Currently the number of MFADs deployed is effectively unregulated, which incentivizes fishers to deploy more and more MFADs at increasing distances from shore to compete with other fishers. This increases the costs of fishing MFADs and reduces their accessibility to fishers with limited financial and/or vessel capacity. Unregulated MFAD deployment generates territoriality and conflict among fishers, which both deter entry into offshore fisheries. Limiting the total number of MFADs deployed has the potential to make offshore fishing accessible to a broader range of fishers, while also preventing the escalating cycle of competitive private MFAD deployment.

We were not able to quantify the effects of MFADs on inshore fisheries in this study, as the data used here do not date back to before MFADs were introduced, which makes it impossible to confirm the effects of MFADs on inshore fishing pressure. Yet our data span a period of growth in MFAD fisheries and a period of transition in the fishery in terms of gears used and nature of the fleet. It is also important to note that MFADs may also draw additional fishers into the fishery that would otherwise not have been fishing inshore, which cannot be accounted for without supplementary survey data. These additional components would greatly benefit future studies and should be prioritized as MFAD promotion continues in other small-scale fisheries. We cannot conclude that the trends observed here are a consequence of MFADs or of other processes, but we integrate fisher insights and relevant literature to make valuable inferences about the observed dynamics.

F. Conclusions

As many small-scale fisheries continue to face declines in coastal resources, finding alternative sources of income for fishers is imperative both for fishers' livelihoods and the potential recovery of overfished areas. The use of MFADs to shift fishers onto offshore resources is widely promoted but poorly understood in empirical contexts. Here we show that MFADs have likely facilitated specialization in offshore fishing, but that they may have reduced a historical overlap between inshore and offshore fishing gears, contrasting with some of the anticipated benefits of MFADs in promoting fisher resilience. The relative location of fishing ports likely has important implications for MFAD and overall offshore fishing success, especially in a competitive private MFAD system. Improved MFAD management and increased cooperation among fishers could increase the accessibility of

MFAD fisheries to a wider range of vessels. While this study suggests that MFADs can facilitate shifts from inshore to offshore fisheries, ongoing and prospective MFAD projects should consider the potential barriers to MFAD adoption and the potential implications for other offshore fishing gears.

G. Tables

Table 1. Definitions of gear categories.

Classification	**Gear category**	**Gears included**	**Species targeted**
Inshore	Nets	Gillnets, trammel nets, seine nets	Parrotfish, jacks, misc. reef fish, deep water snappers, rays, needlefish and halfbeaks, conch, lobsters
	Pots	Fish pots (or traps)	Misc. reef fish, deep water snappers, lobsters, langoustine
	Freediving	Spearfishing, harvest by hand	Misc. reef fish, conch, lobsters, trunkfish, urchins, octopus
	Inshore line fishing	Rod and reel, handline, longline	Misc. reef fish, deep water snappers, groupers
Offshore	Trolling	Trolling line, handline	Dolphinfish, wahoo, tunas, billfish
	MFADs	Any gear (e.g., trolling line, handline, buoy line) used around moored fish aggregating devices (MFADs)	Tunas, dolphinfish, wahoo, billfish

H. Figures

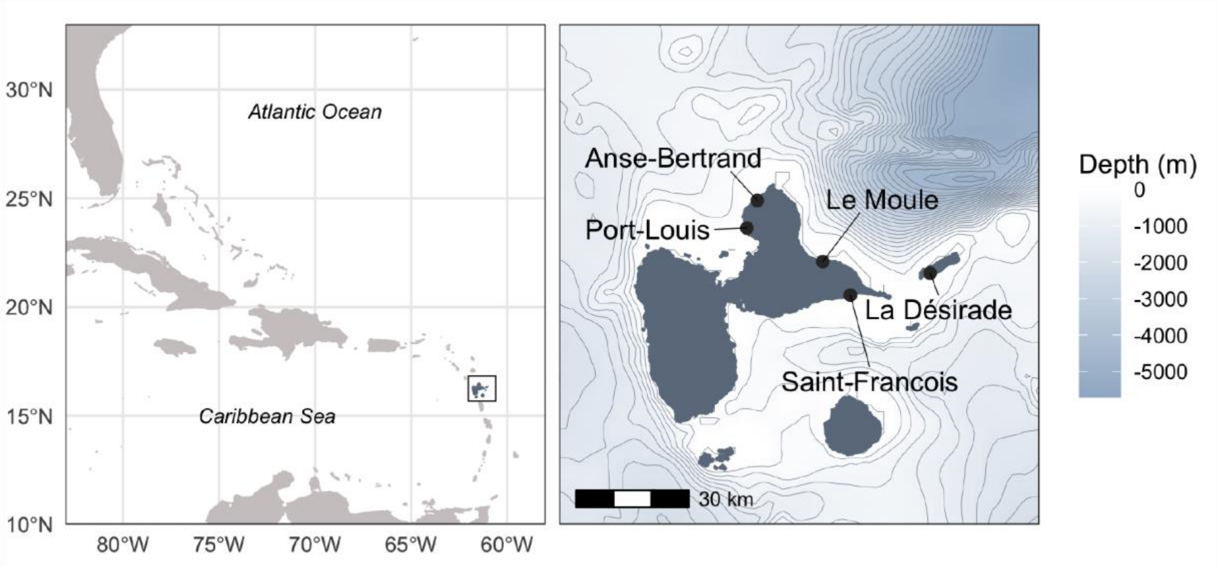

Figure 1. Map of Guadeloupe within the insular Caribbean and location of the five eastern ports included in this study.

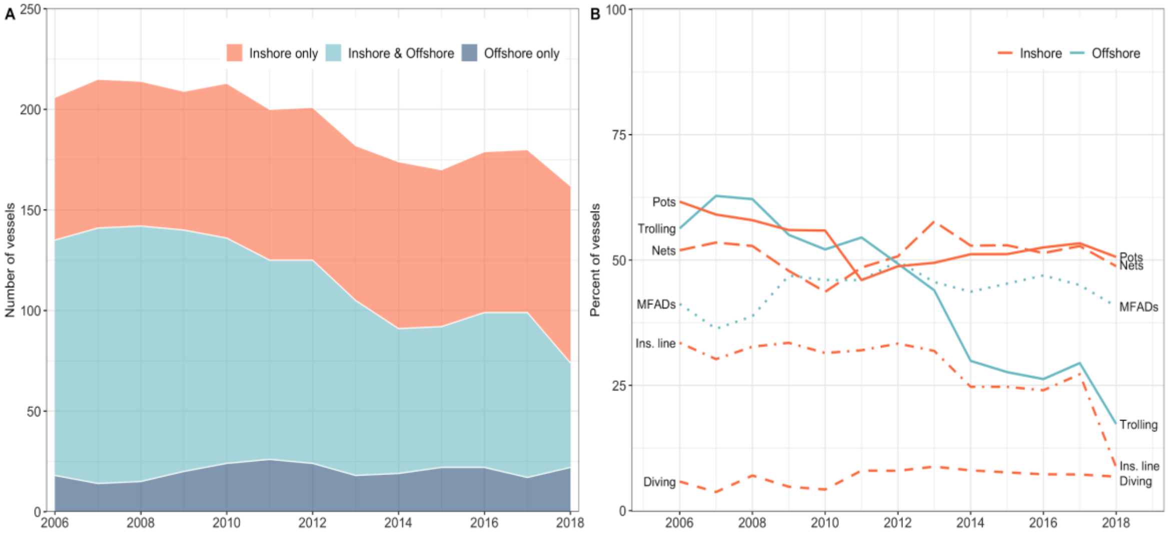

Figure 2. Changes in gear use from 2006 to 2018. A) The total number of vessels has declined over the data collection period. While the number of vessels fishing exclusively inshore or offshore gears has increased (inshore) or remained the same (offshore), the number of vessels utilizing both inshore and offshore gears has declined. B) In 2006 the majority of fishers used some combination of use of pots, offshore line, and nets, followed closely by FAD and inshore line fishing. Over the data collection period, the proportion of the fleet using offshore line declined, with inshore line fishing also showing recent declines.

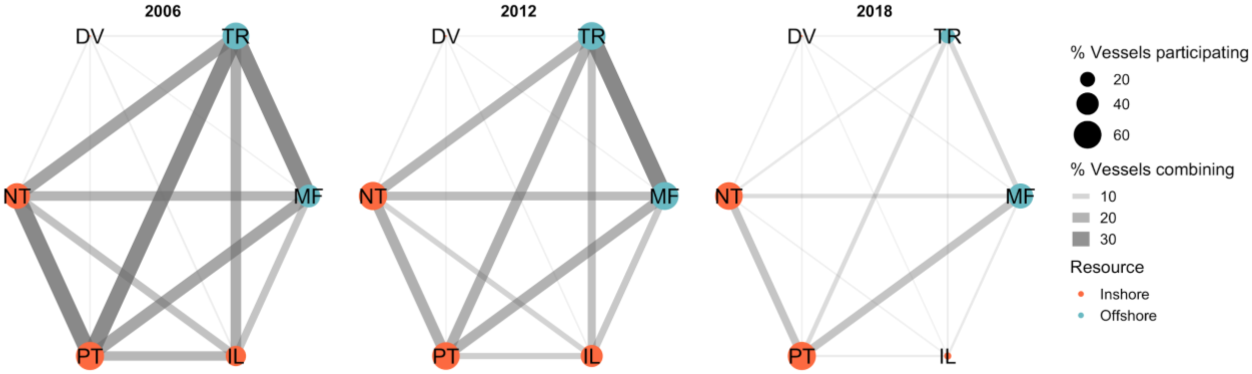

Figure 3. Changes in the use of multiple gears by individual vessels over time. TR = trolling, MF = MFADs, IL = inshore line, PT = pots, NT = nets, DV = diving. In 2006 many fishers utilized multiple gears (indicated by edge width and transparency), with particularly high overlap among trolling, nets, pots, and MFADs. By 2012 the overall proportion of vessels combining gears had declined slightly, with MFADs and offshore line fishing still strongly overlapping. As of 2018, inshore and offshore line fishers are substantially more specialized, with some overlap remaining between nets and pots as well as MFADs and pots.

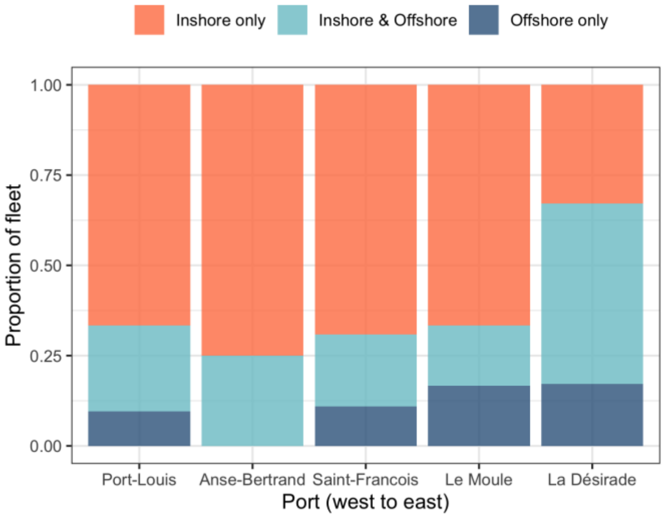

Figure 4. Inshore versus offshore gear use by port. La Désirade, situated upcurrent and near a steep drop off, has the highest proportion of vessels using either only offshore gear or a combination of inshore and offshore gears.

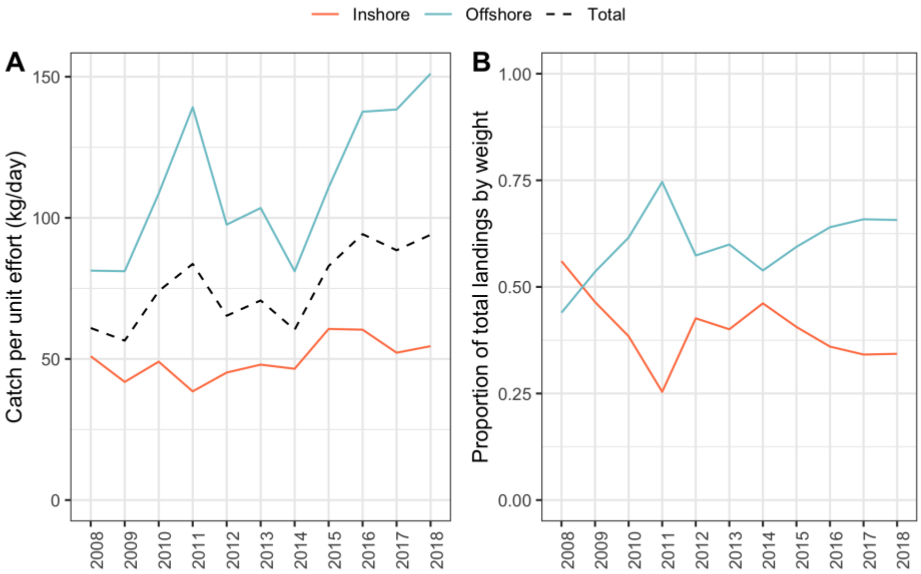

Figure 5. Catch per unit effort (CPUE) proportion of total landings by weight from 2008 to 2018 for inshore and offshore fisheries. Catch per unit effort (CPUE) is higher for offshore than inshore, and has increased across the fleet ($p < 0.01$) and for offshore fishing ($p < 0.05$), with no significant changes for inshore gears (A). Offshore species surpassed inshore species in terms of the proportion of total landings by weight in 2009 and continued to exceed inshore species through 2018 (B).

I. *Supplementary Information*

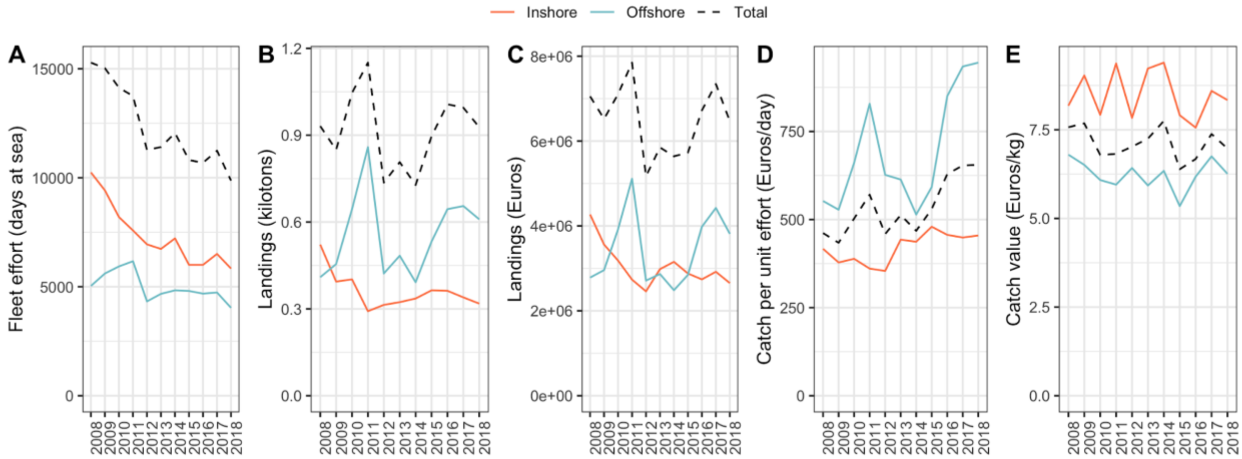

Figure S1. Trends in fleet effort (A), landings by weight (B) and value (C), catch per unit effort in terms of value (D), and relative catch value (E) from 2008 to 2018 for inshore, offshore, and total fleets.

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