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UNDERSTANDING THE RESPONSE OF GROUPERS (EPINEPHELIDS) TO CLIMATE-CHANGE AND FISHING DISTURBANCES IN THE LAKSHADWEEP ARCHIPELAGO, INDIA

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MANIPAL UNIVERSITY

For Fulfilment of the Requirement for the
Award of the Degree
of

DOCTOR OF PHILOSOPHY

By

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Under the Guidance of

DR ROHAN ARTHUR

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CERTIFICATE

This is to certify that the work incorporated in this thesis **"Understanding the response of groupers (epinephelids) to climate-change and fishing disturbances in the Lakshadweep archipelago, India"** submitted by Ms. Rucha Karkarey was carried out under my supervision. No part of this thesis has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged.

Research Guide

DR ROHAN ARTHUR
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ABSTRACT

Coral reefs in the Anthropocene are increasingly confronted with human induced rapid environmental change (HIREC), that is exposing species to novel circumstances or chronic conditions, above the baseline typical of natural environmental variation. These novel conditions are challenging the evolutionary coping mechanisms of many species, resulting in an unraveling of species assemblages. HIRECs are a vast amalgam of anthropogenic disturbances that span from the local (example fishing, pollution), regional to global (climate-change related habitat degradation, global warming), impacting every level of organisation from individuals to entire ecosystems. To persist in these contemporary disturbances, individuals, populations and species need to be capable of rapid adaptive responses to cope. As a result, HIREC is polarising communities into winners and losers. In this, groups of species with certain functional traits are being favoured over others. Habitat-dependent, benthically-associated predatory fish are particularly vulnerable to HIREC. They play vital functional roles on coral reefs and the consequences of their loss could cascade through the ecosystem. Managing coral reefs under HIRECs requires an understanding of previous disturbance responses of communities – identifying winners and losers and understanding their coping mechanisms and limits.

Through this work, I broadly attempted to understand how groupers (family- Epinephelidae), a community of structure-dependent top predatory fish of high commercial value, are responding to global and local HIRECs on coral reefs. My study was conducted in the Lakshadweep archipelago, Northern Indian Ocean. The archipelago made an ideal laboratory to examine the impacts of global HIREC on fish assemblages as it has been subject to repeated climate-change related mass-bleaching disturbances since 1998. In addition, until 2014, commercial reef fishing was virtually absent on the reef, making it possible to examine climate-change responses in relative isolation. The absence of commercial fishing also allowed me to examine grouper mating behaviour of a newly documented fish spawning aggregation under relatively 'pristine' (unfished) conditions. My study examines the potential impact of local HIREC by comparing these behaviours with typically fished aggregations of the species across the Indo-Pacific.

Community assembly is likely to be strongly influenced by both habitat condition and the durational stability of the habitat. Together these determine the character of the habitat (templet) which can limit the life history strategies of species that can occupy the area. By modifying both structure and disturbance frequency, HIRECs can seriously alter community composition on coral reefs. Climate-change induced mass-bleaching events are bringing about a rapid decline in reef structural complexity across the world, with severe consequences for benthically-associated species. I looked at the impact of rapid structural loss on the distribution of grouper communities across Lakshadweep. Using a long-term (15 years) dataset on changes in benthic coral structure since the 1998 mass-bleaching disturbance, I classified reefs according to their disturbance history (from structurally stable to highly dynamic reefs) and their current structural complexity. Together with an archipelago-wide survey of benthic fish communities, I demonstrated that grouper community composition, diversity and biomass, varies considerably between reefs along a gradient of structural complexity and habitat stability. I found that of the entire grouper community, long-lived (longevity> 15 years) and large-bodied species (maximum size > 60cm), were restricted to structurally stable sites with high structural complexity. Interestingly, these species were not present in sites of comparably high structural complexity but with dynamic disturbance histories. This work shows that it is not just the structural complexity of reefs but also long-term habitat condition that drives the composition of long-lived benthic predators like groupers. Moving forward, stable habitats are going to be critical as climate-change refugia for long-lived and large bodied species, supporting higher diversity and abundances and securing important recruitment and settlement processes.

Rapid structural degradation is generating winners (short-lived, small-bodied species) and losers (long-lived, large-bodied species) in the grouper community. Behavioural plasticity is a key first response to any disturbance that can explain variation in performance. I was keen on exploring the behavioural mechanisms by which some species were successful under habitat degradation. One species in particular, the peacock grouper (*Cephalopholis argus*) appeared to buck the trend of other long-lived and large bodied species, and was ubiquitous and highly abundant in structurally complex and degraded reefs. Using a combination of underwater behavioural observations and stable isotope analysis to characterise diets, I studied foraging plasticity (foraging territory size and use, foraging modes and diet) of the peacock grouper along a gradient of structural complexity. Stable isotope analysis showed that peacock groupers are able to maintain a specialised diet in reefs of high and low structural complexity. However, they show highly flexible foraging modes, varying between structure-dependent 'ambush' and structure-independent 'widely-roving' strategies along the gradient. Further, an incidental competitive release from declining densities of foraging specialist species potentially aided in their success in structurally degraded reefs. This work highlights that plastic species can become important keystone predators in the reefs of the future and help maintain ecosystem functions even in structurally degraded reefs.

While behavioural plasticity enables short-term survival of individuals under HIRECs, it is far from clear whether it can ensure the long-term persistence of individuals and populations. The biological and ecological costs and consequences of plasticity can influence the success of a population under HIREC. I attempted to understand how surviving in degraded reefs impacts the life-history traits of the behaviorally plastic peacock grouper and the population-level consequences of long-term persistence in degraded reefs. I did so by comparing life-history traits (growth, longevity, length-weight relationships) and demographic parameters (size and age-distribution, density) of sub-populations between the structurally healthy and degraded reefs. I used otolith collections and analysis to estimate the age of individuals. Found that on the one hand, peacock groupers were able to achieve a better body condition in structurally degraded reefs, potentially due to their foraging flexibility and competitive release from specialist groupers. On the other hand however, surviving in these sub-optimal habitats came at considerable life-history costs, as the average longevity of peacock groupers declined by twenty percent. In addition, density was halved and there appeared to be high size-specific mortality of juveniles in peacock grouper sub-populations in degraded reefs. This demographic signature indicated a potential bottleneck to the process of recruitment in low structured reefs. The apparently high adaptive capacity of species like the peacock grouper may mask significant life-history consequences with long-term demographic consequences that could add up as habitats degrade further.

In the anthropocene epoch, it is virtually impossible to find undisturbed and unaltered populations of animals in nature. This is particularly true of long-lived predatory fish like groupers because of the highly selective fishing pressures they face in most tropical reefs. As a result, most of our understanding of the behaviours of many species comes from populations that may have historically faced some levels of fishing. Given the low reef fishing pressure in the Lakshadweep, I identified and studied a previously-unfished grouper spawning aggregation of the squaretail grouper (*Plectropomus areolatus*) in the remote island of Bitra in Lakshadweep. I described unique alternative reproductive strategies (ARTs) adopted by individuals in this aggregating population. I then compared this pristine mating system with known aggregations of squaretail groupers across the tropical Indo-Pacific, where fishing is present, to argue that fishing can have potentially significant impacts on rare, density-dependent animal behaviours.

As HIRECs change the dynamics of winning and losing, most long-lived benthic predators get the short end of the stick. Behavioural plasticity in foraging strategies is critical in buffering benthic species from HIREC, but plasticity has its limits, beyond which declines and species extinction seems inevitable. How changing community configurations impacts diverse ecosystem functions is not something I could address in my study, though it is likely to have a strong homogenizing effect. Through my work, structurally stable reefs emerge as critical climate-change refugia, supporting higher species diversity, biomass, and securing important recruitment and settlement processes, particularly for long-lived, benthic predatory fish. Although stemming the impacts of global climate-change may be difficult, managing local impacts like reef fisheries and protecting stable reef habitats, may still be our best bet for bolstering resilience in coral reef systems reeling under contemporary, human-induced disturbances.

List of publications from this thesis

Karkarey, R., Kelkar, N., Lobo, A. S., Alcoverro, T., and Arthur, R. (2014). Long-lived groupers require structurally stable reefs in the face of repeated climate change disturbances. *Coral Reefs*, 33(2), 289-302.

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DECLARATION BY THE CANDIDATE

I declare that this thesis, submitted for the degree of Doctor of Philosophy to Manipal Academy of Higher Education, is my original work, conducted under the supervision of my guide Dr. Rohan Arthur. I also wish to inform that no part of the research has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged

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CHAPTER 1
INTRODUCTION

Taking it from the top: Predators, an essential but vulnerable group

Whitespotted grouper (epinephelus coeruleopunctatus) atop a porites coral

Introduction

Large-bodied predators are perceived as powerful, majestic, elusive, dangerous and have captivated our imaginations for millennia (Kruuk 2002; Sergio et al., 2008). Ecologists and conservation biologists have long capitalized on this appeal, using large-bodied predators as flagship and keystone species in biodiversity conservation, in the restoration of ecosystems, and as indicators of disturbances (Ray et al., 2005). The ecological rationale behind this, backed by ample empirical and theoretical data, is that large-bodied predators can strongly structure communities through direct consumptive effects (Estes and Palmisano 1974) and indirectly through behaviorally mediated effects (Fortin et al., 2005). Top predators can 'engineer ecosystems' by facilitating resources that are otherwise scarce or unavailable to other species (Craighead 1968; Wilmers et al., 2003) and by virtue of being large-bodied, long-lived and long ranging, top predators can connect distant landscapes in space and time. But, despite their importance and allure, large-bodied, top predators are highly imperiled in every ecosystem, owing to historical exploitation of large-bodied animals and continued habitat loss (Estes et al., 2011; Ripple et al., 2014; Berger et al., 2001).

The removal of large-bodied top predators from ecosystems can have cascading consequences on lower trophic levels resulting in mesopredator release, altered ecosystem functioning, and shifted food web dynamics (Estes et al., 2011; Wallach, Ripple, and Carroll 2015). Examples of trophic cascades initiated by the removal top vertebrate predators are rife in aquatic ecosystems (Carpenter and Kitchell 1993; Steneck and Sala 2005; Mumby et al., 2006; Pinnegar et al., 2000). Perhaps the most well known example is that of sea otters (*Enhydra lustris*), sea urchins, and kelp forests along the Pacific coasts of North America (review in Estes, 2005). Estes and colleagues demonstrated how otter predation could limit herbivory by sea urchins, indirectly promoting the existence of widespread and structurally diverse kelp forests. With the removal of otters for fur trade, sea urchins increased to a point where kelp forests were rare or had completely disappeared due to urchin overgrazing. In highly diverse and complex ecosystems like coral reefs however, the ecological impact of the removal of large bodied, top predator is much less straightforward and is highly contested (Shurin et al 2002; Frank et al 2007). A recent review of the ecological role of apex predators on coral reefs (Roff et al., 2016) suggests that most top marine predators are generalist and opportunistic. Because coral reefs support complex food webs with high levels of species diversity, functional trait diversity, and functional redundancy within trophic levels, top predator effects can be dampened by functionally equivalent species, buffering many coral reef ecosystems from catastrophic cascades (Borer et al., 2008). However, coral reefs today have entered a new realm of human-induced rapid environmental change (HIREC), resulting in large-scale habitat degradation and an unraveling of species assemblages (Peters and Lovejoy, 1992; Stork, 2010). This is resulting in a biological and functional homogenization of communities as species with certain functional trait combinations are more negatively affected by HIRECs than others (McKinney and Lockwood, 1999; Julliard et al., 2004; Rooney et al., 2007). A key question in contemporary ecology is whether resilience will be maintained under the newer regimes of human induced rapid environmental change, even in highly diverse systems like coral reefs (Hughes et al., 2017).

Human induced rapid environmental change (HIREC) and benthic top predators

HIREC is a vast amalgam of human-induced disturbances, including habitat change (degradation, fragmentation), exposure to novel species associated with ecological invasions, increased harvesting of natural resources (overfishing), human-induced climate-change and exposure to extreme abiotic conditions (e.g. chemical, light, or noise pollution), varying in extent from being very localized to global., A distinguishing characteristic of HIREC is that it rapidly exposes species to novel circumstances or chronic conditions not encountered in their evolutionary past, i.e. surpassing the baseline typical of natural environmental variation (Palumbi, 2007). These novel conditions often challenge the evolutionary coping mechanisms of most species (Chevin et al., 2010; Hendry et al., 2008). HIRECs is a particular problem for coral reef ecosystems, that make up for less that 1% of the sea floor but provide goods and services to more than 3 billion people worldwide. In addition, most coral reef fish fauna are territorial and may have a limited ability to disperse as adults (Sale, 2002). Of particular concern under HIREC is the fate of habitat-associated, territorial and long-lived, coral reef predators that are susceptible to both habitat loss and overfishing. Large predatory fish have declined by more than 90% from some marine environments (Myers and Worm, 2003). Considering that HIREC is only projected to increase in frequency and intensity in the future on coral reefs, some pressing questions concerning us today are

1. Can we predict or identify, which top predators will fare better than others in the future?
2. What are the mechanisms by which some top predator species survive and thrive under HIRECs?
3. What are the ecosystem consequences of changing predator assemblages?

HIREC: Identifying winners and losers in the community

Traditional approaches: taxonomic diversity-disturbance relationships (DDRs)

Understanding how disturbances shape ecological communities has been one of the central goals in ecology and evolution for decades (Levin and Paine, 1974; Sousa, 1984). Traditionally, ecologists explored the link between the severity of a habitat disturbance and the taxonomic composition of communities, with species richness, evenness, or population abundance often being the sole descriptors (Miller et al, 2011). The effects of disturbance on species diversity can be described graphically with diversity–disturbance relationships (DDRs), which plot a measure of species diversity (e.g., richness) against a dependent variable that is a quantity related to disturbance (e.g., intensity). One of the leading theories the 'intermediate disturbance hypothesis' (IDH, Grime, 1973; Horn, 1975, Connell, 1978) predicts that species diversity reaches its maximum at intermediate levels of disturbances. The underlying mechanistic explanation for this pattern is that competitive exclusion may reduce species richness at low levels of disturbance, whereas high levels of disturbance exclude all but the most disturbance tolerant species. However, the IDH is far from universal and has received much criticism, being challenged by observational, experimental, and theoretical studies (Fox, 2013; Mackey and Currie, 2001; Miller et al., 2011). Taxonomic community descriptors are considered to often be weak quantitative tools in monitoring disturbance responses because processes other than competitive exclusion (biotic interactions, environmental stochasticity, habitat-filtering) may affect species in unpredictable ways, often masking the signal of disturbance in an ecosystem (Mackey and Currie, 2001).

Trait-based approaches: Moving beyond taxonomic diversity

Over the last decade, rather than taxonomic specification, the use of functional traits of organisms to understand community dynamics in response to environmental change, has gained momentum (McGill et al., 2006). Functional traits are well-defined, measurable properties of organisms (life-history, morphological, physiological, or behavioral expressions) that reflect an organism's adaptations to its environment (Goldstein and Meador, 2005). Functional traits are usually measured at the individual level and strongly influence organismal performance (survival, growth, fitness) and function in a habitat (McGill et al., 2006). Further, because functional traits reflect adaptation to, and performance in, different environments (Violle et al., 2007) they can provide mechanistic insights into community composition and ecosystem function under HIREC (Lavorel and Garnier, 2002; McGill et al., 2006). The functional traits-based approach arises from the classical idea of the niche (Hutchinson, 1957); which describes the set of abiotic and biotic conditions where a species is able to persist. Outside the niche, individuals are not expected to leave descendants, nor populations to persist, nor clades to endure and proliferate.

The earliest trait-based theories were based on the concept of habitat filtering – of which Sir Richard Southwood's classical Habitat Template Theory (1969) forms the conceptual underpinning. The HTT proposes that the spatial and temporal features of the habitat are the major determinants of species traits observed in the community. The major premise of Southwood was that trade-offs between traits produce different life-history strategies over ecological time and certain strategies are favoured over others, through their effects on fitness at certain positions along the habitat gradient (Southwood, 1977; Townsend and Hildrew, 1994). Figure 1. Is a simplified conceptual model of the HTT. A habitat can be characterized by two disturbance axes forming the "template"; a temporal axis, which describes the frequency of a disturbance, and a spatial axis, which describes the intensity of the disturbance. Southwood (1977) suggested that the qualitative characters of a habitat (facing a disturbance) can be

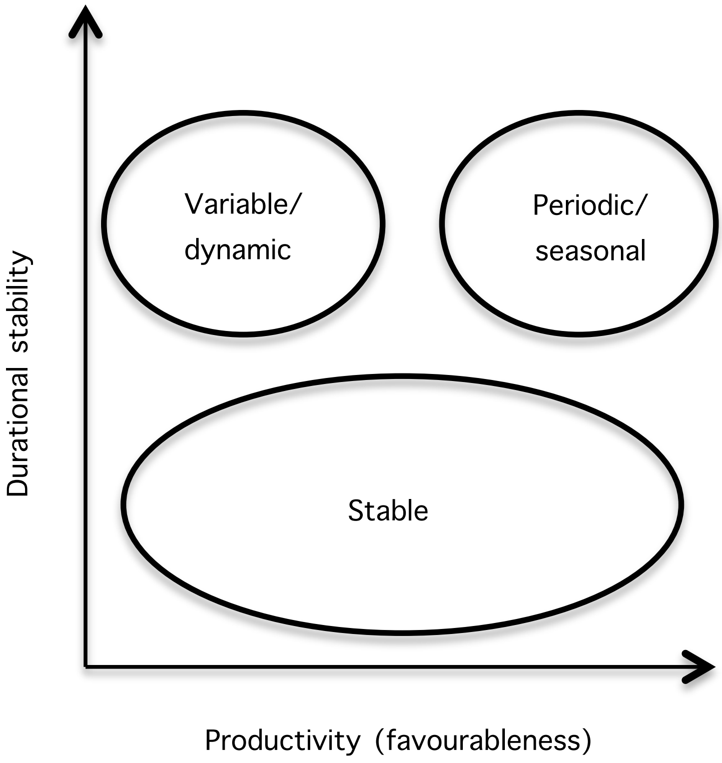

Figure 1. A simplified conceptual diagram of the Habitat Template Theory (Southwood 1977). Habitats responding to a disturbance can be classified along a spatial (productivity) and temporal (durational stability) axis. This two-dimensional classification leads to the identification of three broad habitat types; stable, seasonal/periodic and variable/dynamic. Life-history and ecological traits/strategies are predicted for each of these habitat types.

condensed into two axes: durational stability (long-term habitat condition) and favourableness (resource level and constancy). The theory broadly classifies habitats as being stable (A), seasonal (B) or highly variable (C) in these attributes. It makes certain predictions about the life-history and ecological strategies of species that are likely to be found in different habitats.

Some common predictions of HTT are:

1. Life-history strategies: The r-K continuum model of life history traits, suggested by Macarthur and Wilson (1967) and described by Pianka (1970) is perhaps the most common way of classifying species along the habitat gradient in Figure 1. This model predicts simply that species with r-selected life-histories (example: short lifespan, small body size, rapid growth rates, early maturity) are favoured in dynamic and seasonal habitats while stable habitats favour species with K-selected life histories (example, long lifespan, large body size, slow growth, late maturity). An extension of the r-K continuum is the triangular gradient model proposed for freshwater fishes, based primarily on life-history and reproductive traits of fecundity, age-specific survivorship, and generation time (Winemiller and Rose, 1992). This model splits r strategists further into opportunistic (early maturation, frequent reproduction, short-lived, fast growing, small clutch size and high demographic resilience) and periodic (delayed maturation, large clutch size, synchronous spawning, fast growth of early stages) groups, which together with the equilibrium group (long-lived, low fecundity, slow growing, small clutch size, large egg size, and parental care) define three broad life-history strategies likely to be found in the three kinds of habitats in Figure 1. This model has found wide support across the animal kingdom but especially used in predicting response of aquatic communities to hydrological disturbances (Poff and Ward, 1990; Townsend and Hildrew, 1994).

2. Stress tolerance strategies: Grime (1997) proposed a model of three adaptive strategies for plants, based on traits associated with morphology, resource allocation, phenology and response to stress. This model is known as the Competitive–Stress tolerant–Ruderal model (CSR model). The model predicts that species surviving in stable habitats will have competitive traits (rapid growth rate, high productivity and high capacity for phenotypic plasticity). Species surviving in frequently disturbed and unproductive conditions will show stress-tolerant traits (slow growth rates, long-lifespan, high rates of energy retention, and low phenotypic plasticity), while plants surviving in disturbed but productive habitats show ruderal traits (rapid growth, short lifespan, highly fecundity, low phenotypic plasticity).

3. Ecological strategies: Another common grouping of strategies is based not on life-history or morphological traits but on ecological traits like the degree of specialization or the breadth of feeding niches and habitat preferences. Generally, it is hypothesized that a broad feeding niche can warrant food availability in a range of disturbed environments (Öckinger et al., 2010). Similarly species with high dispersal abilities and broad habitat preferences can migrate to new habitats and easily colonise disturbed landscapes (Tscharntke et al., 2005). From studies of birds (Clavel et al., 2010), butterfly communities in the grasslands of Germany (Börschig et al., 2013), and fish communities on coral reefs in the Great Barrier Reef (Wilson et al., 2009), a common pattern seen is that specialised species are favoured in stable habitats, while generalist species are favoured in frequently disturbed habitats.

The habitat template theory is a useful framework to study broad community-level impacts of HIREC and has found widespread support in aquatic ecosystems. However, although the habitat templet is expected to constrain the kinds of traits present in a community, biotic interactions and individual trait variation can play important roles in further shaping post-disturbance community structure. Because responses to biotic and abiotic disturbances are ultimately realized at the level of the individual, there is an increasing shift in traits-based approaches to study individual trait variation, to better understand the mechanisms underlying community dynamics under HIRECs.

How do individuals respond to HIREC?

To put it simply, when confronted with a novel disturbance an individual organism can respond in three possible ways: spatially (via migration), temporally (i.e. by modifying diel activity patterns, phenology etc.) or by changing itself (ie. phenotypic plasticity). For long-lived, territorial and benthically associated species with a limited potential to migrate as adults, phenotypic plasticity or rapid genetic evolution can be critical in determining their continued survival and success in rapidly degrading habitats. Phenotypic plasticity is the ability for individuals to express context-specific phenotypes of traits under varying environmental conditions (Hendry et al., 2008). Because HIRECs take place repeatedly within the lifespans of individuals, phenotypic plasticity is critical for individual survival and rapid adaptation, as it can circumvent prolonged evolutionary processes (Snell-Rood, 2013). Of the many phenotypic traits (behavioural, physiological, morphological, life history), behavioural responses can be employed fairly instantaneously (Slobodkin, 1964). Behaviour is therefore a key first response to any disturbance that can explain variation in performance relative to HIREC (Mery and Burns, 2010; Tuomainen and Candolin, 2011). Some common behavioural responses to HIREC include: (1) coping with novel enemies (e.g. novel predators, competitors, diseases) and novel abiotic stressors; (2) adopting novel resources (e.g. new habitats, new foods such as crops); and 3) adjusting timing of events (e.g. timing of migration or reproduction), 4) adjusting space use (e.g. movement patterns) to better fit new spatiotemporal conditions and/or 5) modifying intraspecific interactions (e.g. mate choice) (Sih, 2013; Sol et al., 2013; Tuomainen and Candolin, 2011).

Despite the short-term advantages of behavioural plasticity, it is not ubiquitous across the animal kingdom, suggesting that it is a strategy that could incur significant costs (Auld et al., 2010; DeWitt et al.,1998). Costs may arise because of biological limits to plasticity; for instance when the production and maintenance of a plastic response over a longer period of time becomes costly for the individuals. Costs can also arise from ecological limits to plasticity (Valladares et al., 2007) for instance, when interacting individuals impact each other's tolerances and responses to environmental change (through predation, competition etc (Jiang and Morin, 2004; Visser et al., 2006). In the long-term, these costs can effectively reduce individual fitness and survival, by modifying tradeoffs between individual growth, reproduction and mortality (Chevin et al., 2010), with repercussions for the population and community dynamics (Wong and Candolin, 2015).

A Conceptual framework for the thesis

Although functional traits are measured at the scale of individuals, they can vary at all organizational scales in an ecosystem: within a single organism (Pigliucci, 2001), within populations (McGill et al., 2006; Takahashi et al., 2005; Valladares et al., 2007), among species (Westoby et al., 2002) and among communities (Ackerly and Cornwell, 2007). In Figure 2, I present a highly simplified version of how responses to HIREC within individuals, populations and species determine winners and losers in a community. Some anthropogenic disturbances can directly modify species composition and biomass in communities through exploitation (top-down effects), but they can also indirectly affect the community through habitat loss and degradation (bottom-up effects). The three coloured boxes represent three broad levels of organization within the ecosystem; individuals in a population, population of a species and species in a community. A disturbance is presumed to first affect individuals of a population. An individuals' performance will be based on the set of ecological strategies or traits (behavioural, physiological, morphological, life-history) it possesses and the variability or flexibility in these traits which will impact individual fitness. Trade-offs between individual fitness components (growth, reproductions, survival) and the overall density of individuals in the habitat will impact population demographic traits like survival, mortality, fecundity, birth rates and overall density. Similarly, individual behavioural strategies can influence population-level behaviours like mating systems, social structures and dominance hierarchies. Variability in population demographic and behavioural traits will impact the overall rate of population increase and thus influence species composition in the community. The occurrence and frequency of a species in a community will depend not only on the effectiveness of individual and population responses to the disturbance, but will also depend on the outcome of changing inter-species interactions that may arise out of differences in disturbance tolerances between species and random, stochastic effects on species populations. Outcomes at higher-levels can feedback into lower levels within the community and the habitat. To summarize, under HIREC, winning species are ones that have a high variability or flexibility of functional traits within and across scales of organisation.

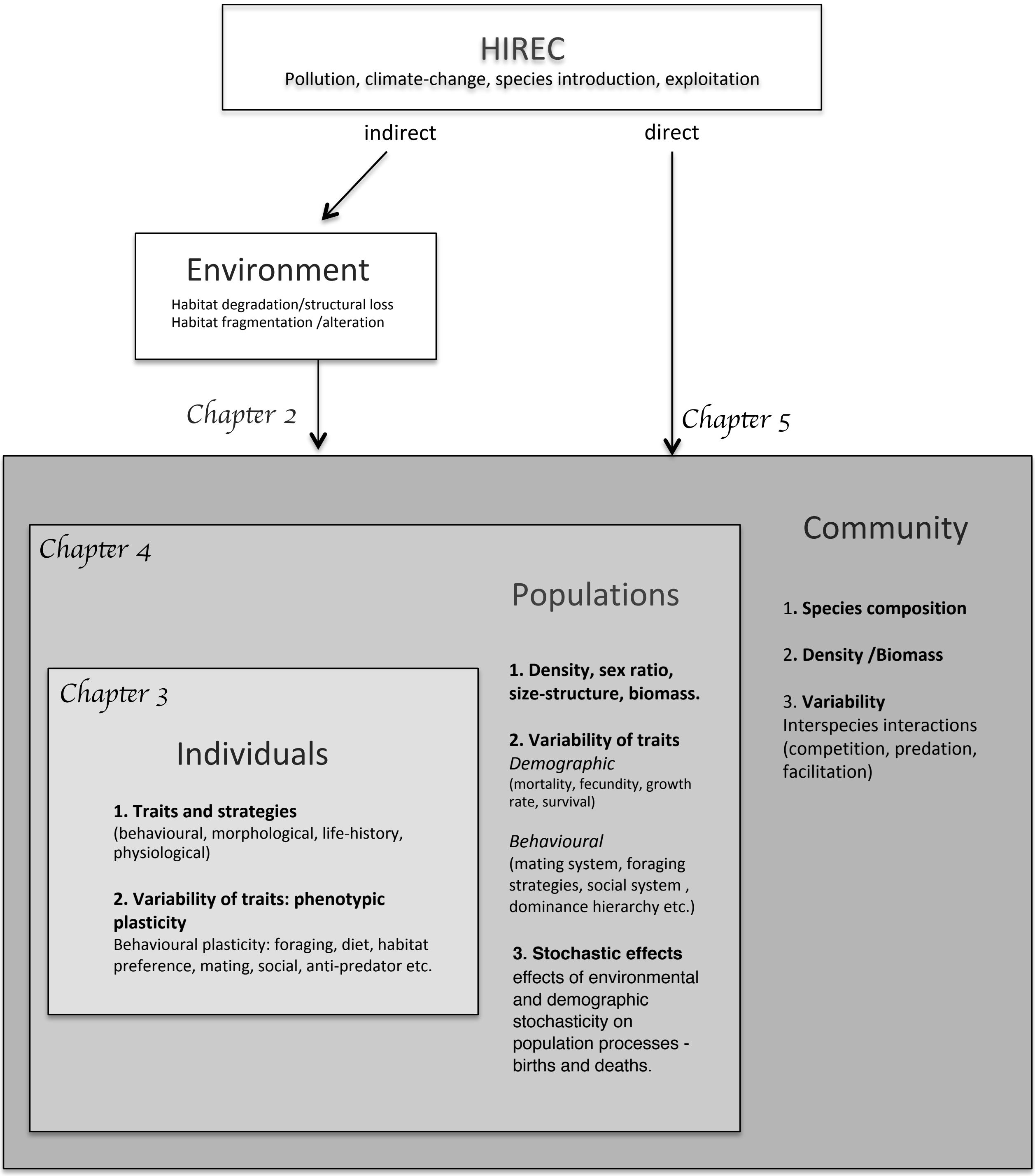

Figure 2. A simplified conceptual diagram depicting the effect of HIREC on communities. HIREC can directly or indirectly influence a community by modifying the environment. The effects of HIREC are generally realized at an individual level and scale up from individuals, population to the community. The performance of species in response to the HIREC (winners and losers) will depend upon ecological traits/ strategies and the variability of traits at different levels of organization, see text. Numbers in the circle indicate the relationships that different chapters in my thesis explore. Chapter two explores the indirect impact of climate-change on the overall grouper community via habitat degradation, Chapter three explores how behavioural flexibility in foraging strategies enables a grouper species (peacock grouper) to survive in rapidly degrading habitats. Chapter four explores the long-term, population-level impacts in peacock groupers of surviving in degraded reefs and Chapter five explores the direct impact of aggregation-based fisheries on the reproductive behaviours of the squaretail grouper. See text for details

In my thesis, I broadly attempt to understand how a community of commercially and ecologically important benthic top predatory fish (groupers, Family Epinephelinae) is responding to HIRECs on coral reefs in the Lakshadweep archipelago, Northern Indian Ocean. I apply the conceptual model of Figure 2 to study how the grouper community has responded to two types of HIRECS; (i) a repeated mass bleaching disturbance since 1998, which brings about catastrophic structural degradation of coral reef habitats and (ii) a recently introduced targeted reef fishery since 2013. I first examine the entire grouper community to determine which species are winning and losing in response to rapid structural degradation (Figure 2, Chapter 2). For one apparently resilient species, the peacock grouper (*Cephalopholis argus*), I study the mechanism of behavioural plasticity (in foraging strategies) by which individuals are coping with habitat degradation (Figure 2, Chapter 3) and the population-level and community-level consequences of surviving in sub-optimal habitats (Figure 2, Chapter 4). For the squaretail grouper (*Plectropomus areolatus*) that is highly vulnerable to targeted fisheries, I first establish population-level baselines of demographic (density, size structure) and behavioural traits (alternative reproductive tactics) in a historically unfished population in the Lakshadweep. I then attempt to compare these baselines against global populations of the squaretail grouper (that are heavily fished) and track changes in the Lakshadweep population against emerging fishing pressures (Figure 2, Chapter 5). In the hope of achieving the larger goal, I have borrowed tools from the disciplines of community ecology, behavioural ecology and population biology.

Study species and site

Groupers (subfamily: Epinephelinae)

I chose to study groupers because this is a fascinating and diverse guild of medium to large–bodied top benthic, marine predatory fish, ubiquitous to coral reefs around the world. I refer to species of the genera Plectropomus, Cephalopholus, Epinephelus, Gracila and Variola, collectively as groupers. Most groupers are piscivores, at the top of the food chain (Craig et al., 2011). However, grouper species show a high amount of variability in their foraging, life-history and reproductive traits (Grandcourt et al., 2005). Most species of groupers are benthic, ambush foragers that are dependent on the structural complexity of habitats for ambush and refuge cover (Kerry and Bellwood, 2012 ; Sluka and Reichenbach, 1996; Lindberg et al., 2006), but some species are also known to be widely-ranging foragers (Samoilys and Carlos, 2000). Species differ in their life-history traits varying in maximum lifespan, body size, fecundity, growth rates etc. Further, groupers possess complex and highly flexible mating modes, ranging from pair-spawning and group-spawning tactics, demersal and broadcast spawning tactics, to gonochorism and hermaphroditism (Erisman el at., 2013). Aspects of the reproductive biology, especially their tendency to form large, spatially and temporally explicit, spawning aggregations, and their life-history characteristics; relatively slow growth rates, late maturity, relatively low fecundity (Domeier and Colin, 1997; Grandcourt et al., 2005; Sadovy de Mitcheson et al., 2013), and territorial nature make them vulnerable to both fishing and habitat disturbances (Munro and Williams, 1985). It is often difficult to independently study the effects of climate-related habitat disturbances and fishing on groupers, because of high selective fishing pressures on benthic top predators in most tropical reefs (Myers and Worm, 2003; Sadovy de Mitcheson et al., 2013). As a result, studies of the effects of habitat degradation on this guild have been limited (Kerry and Bellwood, 2012; 2016).

The Lakshadweep archipelago

My study is based in the Lakshadweep archipelago, a unique group of islands in the northern Indian Ocean. The archipelago, comprises of 13 coral islands and submerged banks with 36 smaller atolls, occupying a total land area of around 32 km^2 between 8°N – 12°N, and 71°E – 74°E (Figure. 3). The Lakshadweep archipelago supports a diverse community of large benthic predatory fish (NCF, unpublished data) with over 35 species of groupers. I chose to conduct my study in the Lakshadweep archipelago in India because the reefs here had been relatively unfished until 2011, after which targeted reef fisheries have rapidly developed in the region (Jaini et al., 2017, NCF unpublished data), and the archipelago has recently been subjected to repeated, high intensity, mass-bleaching disturbances since 1998.

Since the 1998 global mass-bleaching catastrophe, which impacted coral reefs across the world, coral reefs in Lakshadweep have witnessed three subsequent mass-bleaching events in 2010 and 2016. After the 1998 and 2010 events, the region witnessed a 87% and 44% decline in live coral cover respectively and shifts in benthic coral composition (Arthur, 2008, Yadav et al., in progress). Bleached and dead coral is highly susceptible to physical breakage from wave action from storms (Done, 1992). The Lakshadweep region is heavily influenced by strong wave and current conditions during the southwestern monsoon season between mid-May and mid-October, which are said to have impacted coral recovery processes in the region since 1998 (Arthur, 2006). These benthic compositional shifts can have potentially large impacts on habitat structural complexity (Alvarez-Filip et al., 2011) with consequences for associated benthic fauna. This makes Lakshadweep and interesting location to study the responses of benthic predatory fish to rapid habitat degradation.

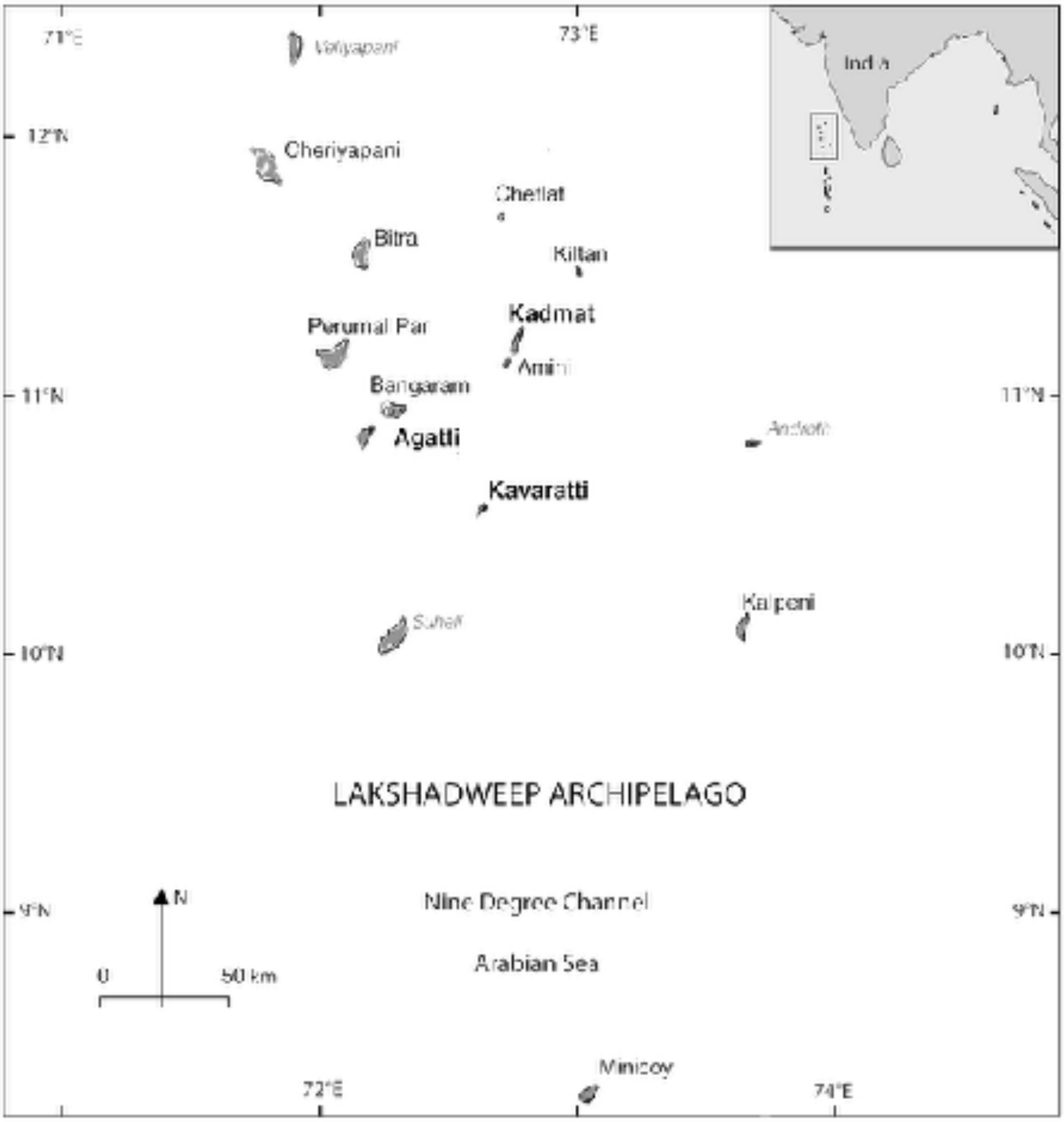

Figure 3: The Lakshadweep archipelago. Islands marked in bold are ones where long-term benthic data exists since the 1998 coral mass-bleaching event. The rest of the islands (in dark grey) have been included in the large-scale study (Chapter 2). Chapter 3 and 4 were conducted in Kadmat and Chapter 5 in Bitra.

The Lakshadweep islands are one of the most densely populated regions of the country, with a human density of 2000/km^2 (sensu 2011 census). Interestingly, despite high human densities, fishing pressure on near-shore coral reefs in Lakshadweep, has been relatively low compared to other systems in the broader region (Jaini et al., 2017). Although fisheries is the main livelihood of the islanders, commercial fishing focuses on pelagic skipjack tuna (*Katsuwonus pelamis*) and amounted to nearly 80% of total fisheries production (Jaini et al., 2017). This pelagic fishery had shifted fishing pressure away from coral reefs in Lakshadweep over the past four decades and aided benthic recovery processes after the 1998 mass bleaching catastrophe (Arthur et al., 2005). However, since 2013, pelagic tuna stocks are undergoing significant fluctuations in availability (Jaini et al., 2017). As a result, commercial nearshore reef fisheries are developing in the region. Earlier, because groupers were not a locally preferred food fish, they were not targeted by even the local artisanal fisheries in Lakshadweep (R.K, unpublished data). However, the recent shifts in commercial and artisanal fisheries are directly threatening grouper populations in the region. Considering that reef fisheries are picking up only in the last three years, Lakshadweep is a unique place to study the impacts of a rapid growth in targeted fisheries on groupers.

Thesis structure, goals and objectives

My primary motivation for my thesis was to understand how iconic reef fish like groupers that are ecologically akin to terrestrial ambush predators like leopards, are adapting to a rapid degradation of coral reef structure in their habitats due to climate-change and introduction of targeted grouper fisheries in the islands.

In my **second chapter**, I attempted to understand the broad community-wide patterns of groupers in response to long-term structural degradation in the reefs of Lakshadweep, using the Habitat Template theory as a guiding concept (Figure 1). I first developed an index of long-term structural stability based on reef depth and degree of exposure to monsoon storms, to classify reefs in Lakshadweep as structurally dynamic, stable and intermediate reefs. For this, I used a long-term (12 year) benthic monitoring dataset collected by the Nature Conservation Foundation from three representative atolls of *Kadmat, Kavaratti* and *Agatti* in Lakshadweep (Figure 3), since the 1998 global mass-bleaching catastrophe. I then conducted an archipelago-wide survey (13 atolls, Figure. 3) of fish communities across a gradient of reefs classified as above to investigate patterns of grouper community composition along this disturbance gradient, with respect to two important functional traits, body-size and longevity.

During the survey, I realized that some species of groupers, like the long-lived peacock grouper (*Cephalopholis argus*), dominated the assemblage even in structurally degraded reefs. I was keen to study the mechanisms by which these species were able to survive rapid environmental degradation. As explained in the section earlier, behavioural responses are among the first that are activated in individuals in response to a disturbance. Using the ubiquitous peacock grouper as a case study, I explored two hypotheses in my **third chapter**; behavioural plasticity in foraging strategies and competitive release from behavioural specialists that potentially gave the peacock grouper a winning edge in degraded reefs. I used focal individual sampling to study territoriality and foraging plasticity in individuals, underwater visual census techniques to estimate population density and laboratory techniques like stable isotope analysis to study individual diets of the peacock grouper. This study was conducted entirely in the atoll of *Kadmat*, which showed a gradient of coral reefs from structurally complex to structurally degraded ones (identified in chapter 2).

Behavioural plasticity can enable short-term survival for individuals under HIRECs, but whether it can ensure long-term persistence of individuals and species populations is far from clear. The biological and ecological costs and consequences of plasticity can influence the success of a species population under HIREC. In the **fourth chapter**, I attempted to understand how surviving in degraded reefs impacts the life-history traits of the behaviorally plastic peacock grouper and the population-level consequences of long-term persistence in degraded reefs. I did so by comparing life-history traits (growth, longevity, length-weight relationships) and demographic parameters (size and age-distribution, density) of sub-populations between the structurally healthy and degraded reefs in *Kadmat*.

In the Anthropocene era, it is virtually impossible to find undisturbed and unaltered populations of animals in nature. This is particularly true of long-lived predatory fish like groupers because of the highly selective fishing pressures they face in most tropical reefs (Myers and Worm, 2003; Sadovy de Mitcheson et al., 2012). As a result, most of our understanding of the behaviours of many species comes from populations that may have historically faced some levels of fishing. During this thesis, I took up a fortuitous opportunity of studying an unfished grouper spawning aggregation in Lakshadweep. In my **fifth chapter,** I attempted to document mating behaviours in the historically unfished and erstwhile undocumented spawning aggregation of the squaretail grouper (*Plectropomus areolatus*) in the remote island of Bitra in Lakshadweep. I describe unique alternative reproductive strategies (ARTs) adopted by individuals in this aggregating population. I then compare the mating system in Bitra with known aggregations of squaretail groupers across the tropical Indo-Pacific, where fishing is present, to illustrate the point that fishing can have potentially significant impacts on rare, density-dependent animal behaviours.

In conclusion, in my **sixth chapter,** I summarize the salient learning from my study of the response of a benthic fish community to HIRECs in the Lakshadweep archipelago. I discuss my findings in relation to the management of coral reef systems in the developing tropics. I stress on understanding past disturbance responses of fish communities to HIRECs, the conservation potential of structurally stable habitats and make a case for identifying behaviorally flexible species as future keystones and conservation targets. I discuss how targeted fishing not only impacts density and size-structure of populations but also can significantly alter population behaviours, which may negatively feedback into population dynamics. As a post-script to chapter five, I provide preliminary results and discuss future directions of an ongoing study, which is tracking the effects of a rapidly growing targeted grouper fishery (which began only towards the end of my study) on the squaretail grouper spawning aggregation in Lakshadweep.

CHAPTER 2

Long-lived groupers require structurally stable reefs in the face of repeated climate change disturbances

Camouflage grouper (epinephelus polyphekadion)

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Abstract

Benthic recovery from climate-related disturbances does not always warrant a commensurate functional recovery for reef-associated fish communities. Here, we examine the distribution of benthic groupers (family Serranidae) in coral reef communities from the Lakshadweep archipelago (Arabian Sea) in response to structural complexity and long-term habitat stability. These coral reefs that have been subject to two major El Nin˜o Southern Oscillation- related coral bleaching events in the last decades (1998 and 2010). First, we employ a long-term (12-yr) benthic monitoring dataset to track habitat structural stability at twelve reef sites in the archipelago. Structural stability of reefs was strongly driven by exposure to monsoon storms and depth, which made deeper and more sheltered reefs on the eastern aspect more stable than the more exposed (western) and shallower reefs. We surveyed groupers (species richness, abundance, biomass) in 60 sites across the entire archipelago, representing both exposures and depths. Sites were selected along a gradient of structural complexity from very low to high. Grouper biomass appeared to vary with habitat stability with significant differences between depth and exposure; sheltered deep reefs had a higher grouper biomass than either sheltered shallow or exposed (deep and shallow) reefs. Species richness and abundance showed similar (though not significant) trends. More interestingly, average grouper biomass increased exponentially with structural complexity, but only at the high stability sites, despite the availability of recovered structure at the lower-stability sites. This trend was especially pronounced for long-lived groupers (life span > 10 yrs). These results suggest that long-lived groupers may prefer temporally stable reefs, independent of the local availability of habitat structure. In reefs subject to repeated disturbances, the presence of structurally stable reefs may be critical as refuges for functionally important, long-lived species like groupers.

Keywords

Coral reefs, Structural change, Habitat stability, Natural refugia, Groupers.

Introduction

Among the most significant long-term impacts of climate change on tropical reefs is the loss of structural complexity (Wilson et al., 2006) due to recurrent ocean warming events like the El Niño Southern Oscillation (ENSO), which are now increasingly frequent (Hoegh-Guldberg et al., 2007). While earlier predictions saw reefs destined for collapse under this repeated disturbance (Pandolfi et al., 2003), a more complex picture of mixed decline and recovery is now emerging (Arthur 2000 ; Arthur et al., 2005 ; McClanahan et al., 2007 ; Sheppard et al., 2008 ; Graham et al., 2011). The ability for rapid benthic recovery suggests that coral reefs may have a greater ability to cope with climate-related disturbances than previously assumed (Halford et al., 2004). Whether this reflects a commensurate functional recovery for reefs and associated fauna is still not clearly understood (Berumen and Pratchett, 2006 ; Bellwood et al., 2012).

Reef architecture, or the structural complexity of reefs, is linked closely with its ecological functioning as it greatly influences fish population densities (Graham and Nash, 2013). Structural complexity is associated with increasing fish diversity through the provision of shelter and diverse physical niches, which mitigate the impacts of predation, competition and physical disturbance (Caley and John, 1996 ; Syms and Jones, 2000 ; Almany, 2004a, b ; Garpe et al., 2006 ; Feary et al., 2007). Although the ability to quickly recover coral structure after disturbance events may be vital to the recovery of coral-associated fish assemblages (Sano, 2000), even short-lived fish, usually in lower trophic groups, have shown a limited ability to recover (Berumen and Pratchett, 2006 ; Bellwood et al., 2012). Additionally, it is still uncertain if longer-lived (K-selected) species that generally belong to higher trophic groups are resilient to such physical disturbances. Given that the generational recovery time for long-lived species may be much longer than disturbance frequencies (Fulton 2011), the effects of repeated disturbances on long-lived species might be multiplicative (Paine et al., 1998), seriously compromising their ability to recover (Bellwood et al., 2012).

As some of the longest-lived top predators, groupers (Serranidae) are among the most important functional species on coral reefs (Grandcourt, 2005). Top predators like groupers often play key roles in regulating communities (Goeden, 1989; Hixon and Beets, 1993) and their reduction has been linked with declines in ecosystem functioning (Bohnsack ,1982 ; Dulvy et al., 2004a ; Heithaus et al., 2008). Groupers are highly dependent on structurally complex reef environments (Sluka and Reichenbach, 1996 ; Lindberg et al., 2006). Reefscape and habitat attributes strongly influence the success of their predatory strategies either directly by changing the effectiveness of ambush strategies (Samoilys, 1997; Auster, 2005) or indirectly by changing resource densities of smaller fish, crustaceans and other prey species (Almany, 2004a). In addition, their slow growth rates, longevity and relatively low fecundity

(Grandcourt, 2005), make them particularly vulnerable to both natural and anthropogenic exploitation (Russ and Alcala, 1998 ; Sadovy de Mitcheson et al., 2012). Taken together, these characteristics make groupers particularly susceptible to declines in reef habitat as a result of climate change and related disturbances.

Separating the effects of fishing from climate-related structural change on grouper communities is often difficult because of high selective fishing pressures on benthic top predators in most tropical reefs (Myers and Worm, 2003; Sadovy de Mitcheson et al., 2012). The Lakshadweep archipelago in India offers a unique opportunity in this context, since the reefs here have had relatively low levels of reef fishing for at least the last four decades (Arthur et al., 2005 ; Spalding et al., 2001). Further, the Lakshadweep reefs suffered two catastrophic bleaching events in the last decade and a half (1998 and 2010), where a total loss of over 90 % (Arthur et al., 2006) and 70 % (RA, personal observations) live-coral cover has been documented, respectively. Smaller-scale bleaching events, related to increased sea-surface temperature have been observed in 2005 and 2007 (~ 10–20 % coral bleaching, RA, personal observations). Local hydrodynamics linked to monsoonal exposure and depth were shown to strongly influence benthic resistance and recovery rates within the archipelago, after the 1998 bleaching event (Arthur et al., 2006).

Wave exposure and depth have long been identified as major controllers of coral zonation and benthic distribution on reefs (Done, 1999 ; Madin and Connolly, 2006 ; Chollett and Mumby, 2012). Exposure and depth work together in mitigating temperature-mediated bleaching responses in corals and in facilitating reef recovery processes (West and Salm ,2003).These physical factors, in addition to reef structural complexity and benthic composition, are known to synergistically affect the distribution of reef-associated fish communities (Gust, 2002 ; Sabetian, 2003 ; Floeter et al., 2007). The long-term interaction between habitat characteristics, physical disturbances that disrupt habitats, and species life-history characters, ‘filters’ unfavourable species from habitats of characteristic disturbance regimes (Southwood, 1977). Thus, understanding the long-term influence of exposure and depth-mediated hydrodynamics on benthic structure may be crucial to predicting the effects of increasing multiple disturbances, not only for corals (Madin and Connolly, 2006) but for reef-associated fish communities as well.

Our primary objective was to determine the effect of local structural complexity and the long-term habitat structural stability on the distribution of grouper communities across the archipelago. We first employ a 12-yr benthic cover data series from three representative atolls to classify reefs across the archipelago according to long-term structural stability based on exposure (either exposed or sheltered from monsoon storms) and depth (shallow and deep reefs). We then use this habitat stability classification (exposure and depth) to test for differences in grouper communities across a gradient of structural complexity by surveying 60 reef sites across the entire archipelago.

Methods

Study area

The Lakshadweep archipelago in the northern Indian Ocean comprises 13 coral islands and submerged banks with 36 smaller atolls (Figure. 1), occupying a total land area of around 32 km^2 between 8°N – 12°N, and 71°E – 74°E. The Lakshadweep region is heavily influenced by strong wave and current conditions during the southwestern monsoon season between mid-May and mid-October during which the currents in the Arabian Sea are known to flow in the southeasterly direction (Shanker et al., 2001). All atolls are oriented in a nearly north–south direction creating a distinct windward or exposed (west) and leeward or sheltered (east) direction during the monsoon months (Figure.1). This difference in exposure to monsoon storms was a key factor affecting benthic recovery processes on these reefs after the 1998 mass-bleaching mortality (Arthur et al., 2006).

Reef fishing pressure in Lakshadweep

Pole and line fishing for Skipjack tuna (*Katsuwonus pelamis*) has been practiced by local fishermen since the early 1900s (Hornell, 1910). Developments in this fishery were facilitated in 1959 by the Fisheries Department and since then the tuna fishery has become the mainstay of local fishermen in Lakshadweep (Jones and Kumaran, 1959 ; James et al., 1986). The pole and line tuna fishery requires the use of bait fish which includes a number of small-sized species including sprats, fusiliers, damselfish and cardinal fish, captured in the lagoons and adjoining reefs of the islands (Pillai et al., 1986). The growth of the tuna fishery requiring a regular supply of bait was closely shadowed by the growth in the reef- and lagoon-based bait fishery in Lakshadweep. This, interestingly, had shifted fishing pressure away from coral reefs in the past four decades (Arthur et al., 2005). Pelagic tuna stocks generate considerable trade revenue (Newton et al., 2007) and have become increasingly important in these regional waters including the neighbouring Maldives. In contrast, the near-shore coral reef and lagoon-associated fisheries remain largely artisanal and subsistence in nature in the northern Indian Ocean region (Spalding et al., 2001). No systematic study on Lakshadweep tuna and reef fisheries has been conducted (but see Tamelander and Hoon (2008) for a study of artisanal fishing in Agatti atoll and more recently by Jaini et al., 2017). The Fisheries Department, however, conducts a voluntary catch-monitoring program of fisheries which estimated a total reef fishery yield for 2011 (from 9 atolls) at 849.3 Metric tons (Mt). These data need to be interpreted with caution, but catch records for 2011 suggest that the pole and line fishery for tuna constitutes 82 % of total landings followed by an 8 %

contribution by a pelagic fishery and a 6.4 % contribution by fish associated with reef and lagoon habitats (see Table 1). We additionally conducted a series of key informant fisher interviews (n = 12) in two of the surveyed islands, Kadmat and Bitra, to get an understanding of patterns of reef access and local preference for reef fish. Key informants reported that the western reefs were completely inaccessible during the monsoon months (May–October) and fishing is focused inside the lagoon and eastern reefs during this lean period. Fishers also reported a low local preference for groupers (Serranidae), while snappers (Lutjanidae), jacks and trevallys (Carrangidae), needlefish (Belonidae), goatfish (Mullidae) and napoleon wrasses (*Cheilinus undulatus*) were the most preferred food fish locally, making up a greater proportion of fish catches from the lagoon and reef.

Table 1. Total fisheries landings (2011): total fisheries landings (metric tons, Mt) in year 2011 from 9 atolls, as documented by the Lakshadweep Fisheries Department from voluntary catch monitoring surveys.

Fishery type	Total annual catch (Mt)	Percent of total annual catch
Pelagic	1,020.984	7.7
Reef associated	411.102	3.1
Reef/lagoon benthic	849.347	6.4
Tuna	10,863.382	82.6

Fisheries catch recorded as : Pelagic - sailfish, seer-fish, barracuda, flying-fish; Reef associated- rainbow runners, reef sharks, carangids, rays; Reef /lagoon benthic- perches, coral fishes, lagoon fishes, goatfish; Tuna- Tuna.

Field methods

Measuring structural complexity (percent standing coral structure)

Structural complexity was estimated at each site by placing five 1-m^2 photo quadrats located at regular intervals on 50m transect lines (total transects n = 5–6 and n = 30–35 quadrates per site). Within each quadrat, the percent areal cover of hard coral was estimated with image processing software (ImageJ version 1.44o) by overlaying a 10 x 10 grid on the photo quadrat. Hard coral cover was further classified into coral forms: branching, massive, tabular and encrusting. We calculated a measure of structural complexity, defined as the percent cover of intact hard coral structure, both living and dead, recorded within the quadrat (loose rubble was excluded from this measure). We conducted a standardization to compare our measure of structural complexity with other commonly used techniques: reef rugosity (chain-link method, see Luckhurst and Luckhurst 1978) and vertical coral canopy height (Wilson et al., 2006 ; Obura and Grimsdith, 2009). For the standardization, we measured structural complexity using all three methods at sites that varied considerably in their structural characteristics from nearly bare platforms to very complex reef sites (n = 9 samples). As our measure of structural complexity correlated positively and significantly with rugosity (Pearson's product–moment correlation, r (7) = 0.72, t = 2.78, P = 0.027) and vertical coral canopy height (Pearson's product–moment correlation, r (7) = 0.79, t = 3.5, P = 0.009), it was therefore used as a proxy for structural complexity in this study.

Classifying sites based on their structural stability (rate of change in structural complexity)

To classify reef sites according to their structural stability through time, we used data from 12 long-term monitored reef sites (hereafter called permanent sites) established in 1998 for long-term monitoring of benthic cover. Permanent sites were established at three representative atolls (Agatti, Kadmat and Kavaratti) at two depths (shallow 5–10 m and deep 11–20 m) and two aspects (hereafter known as exposures; eastern aspect, sheltered from monsoon storms and western aspect, exposed to monsoon storms; total sites n = 12). Sites were sampled by transect surveys using SCUBA. At each site, we tracked changes in structural complexity (see above) over a 12-yr period for the sampled years (from 1999 to 2003, 2007 and 2009, n = 7 yrs). Mean values of structural complexity for each site were regressed against years during the recovery period between the two coral mass mortality events (7 sampled years) and we used the slope of the linear regression (mean slope 2.7 ± 0.62 SE, R^2 = 0.48, $F_{(23,46)}$ = 1.48, P < 0.005) to represent the rate of structural change or turnover in structural complexity (i.e., the loss and recovery of hard coral structure). We use this as an index of structural stability through time for each location.

Archipelago-wide survey of groupers and structural complexity

To determine the relationship between groupers, structural complexity and structural stability we undertook a large-scale survey across the Lakshadweep archipelago between December 2010 to March 2011 at 10 atolls (Agatti, Amini, Bangaram, Bitra, Chetlat, Kiltan, Kadmat, Kavaratti, Kalpeni and Minicoy) and 2 sunken banks (Cheriyapani and Perumal Par, Figure. 1). The sampling was designed to include a gradient of present structural complexity and the two main attributes that determine structural stability, i.e., exposure and depth (see earlier). We sampled 4 sites at each atoll (2 depths and 2 exposures) except for a few large atolls where we sampled multiple sites for better representation. A total of 60 sites were surveyed across the entire archipelago. At each site, we measured present structural complexity in 4–5 random transects located on the reef. Data on structural complexity were collected with the same techniques as the long-term monitoring, using 5–6 photo quadrates per transect (total quadrates per site = 20–25). At each site, we estimated fish abundance using 5–8 random visual belt transects (50 x 10 m = 500 m^2 transect area). Along each transect, we recorded species composition and abundance of groupers (family Serranidae). Species were identified following Lieske and Myers (2002). Individual groupers were visually classified into four size classes (<10, 11–30, 31–50, 51 cm and above). Biomass was estimated using published length–weight relationship data for grouper species from www.fishbase.org (Froese and Pauly, 2012), with the power function $W = aL^b$, where W = weight of the individual (in gm), L = total length of the individual, and a and b are species-specific constants. We used published life-history information to broadly classify grouper species as relatively short lived (<10 yrs) or long lived (>10 yrs). Groupers of the genus Aethaloperca, Anyperodon, Cephalopholis, Epinephelus, Gracila and Plectropomus were classified as long-lived groupers (n = 14 species, Grandcourt 2005; Pears et al., 2006). Smaller coral hinds of the genus Cephalopholis were classified as relatively 'short-lived' groupers (n = 5 species, Cabanban et al., 2008; Liu and Choat, 2008).

Statistical analysis

Patterns in long-term structural stability (structural stability regimes)

We conducted a two-factorial analysis of variance (two-way ANOVA) at the site level with exposure (two levels: sheltered and exposed aspects) and depth (two levels: shallow and deep reefs) as explanatory variables, and the rate of structural change (slope of the regression over a period of 7 yrs, see above, n = 12 sites), as the dependent variable. The results of the ANOVA and Tukey's post hoc comparisons were used to classify sites across the archipelago based on their structural stability.

Archipelago-wide patterns in benthic structural complexity and grouper variables (biomass, abundance and species richness)

We used generalized linear mixed-effects models (GLMMs) to determine how structural complexity (2011), as well as grouper variables: biomass, abundance and species richness, varied between exposure (sheltered, exposed) and depth (deep, shallow). The GLMM families used were based on visual analysis of frequency distributions of the data. We used Poisson, zero-inflated Poisson and negative binomial GLMMs for these response variables either because they were count data or could be effectively treated as count data (no negative values, discretization naturally possible in the case of continuous variables). Exposure (sheltered, exposed) and depth (deep, shallow) were the fixed effects while atolls (n = 10) and sites (n = 60, nested within atolls) were random effects. The general GLMM formulation was represented as follows, for example:

$$\text{structural complexity}_{[ijk]} \sim \text{exposure}_{[i]} + \text{depth}_{[i]} + \text{exposure}_{[i]} \times \text{depth}_{[i]} + \text{random}\left(1 \middle| \frac{\text{atoll}_{[j]}}{\text{site}_{[k]}}\right)$$

where exposure x depth indicates an interaction between exposure and depth category for each site, and the variance term of the random effects (atoll, site) indicate random intercept models, i.e., different intercepts on the response variable for each site, atoll (Zuur et al., 2009). Model selection was undertaken by calculating the Akaike's information criterion (AIC) based on the trade-off between model deviance and parsimony (Crawley 2007). Data were checked for normality by visual inspection of plots of the residuals and fitted values. All data were analyzed with the packages nlme, lme4 and glmmADMB in the statistical software R (R Development Core Team 2011 ; Pinheiro et al., 2012 ; Bates et al., 2012 ; Bolker et al., 2012).

Percentage composition of coral forms and grouper size class distributions at the four structural stability regimes (SD sheltered deep, SS sheltered shallow, ED exposed deep, ES exposed shallow) are reported using dot charts.

Relationship between structural complexity and grouper biomass across structural stability regimes

Relationships between long-lived and short-lived grouper biomass with structural complexity were explored using generalized linear models (GLMs) at locations of different structural stabilities, as identified from our long-term data. Based on the visual analysis of frequency distributions of the data, we used the negative binomial (NB) family for the discretized response variable of grouper biomass. Zeroinflated negative binomial (ZiNB) models were used to account for zero inflation, when present in the dataset. A logarithmic link function was used to link mean biomass to the predictor function as this ensures positive fitted values (Zuur et al., 2009). For each stability regime, the general model formulation for the GLM was:

$$\text{Grouper biomass} \sim e^{\alpha+\beta\times\text{structural complexity}}$$

where a and b are the intercept and slope, respectively. The R packages MASS (Venables and Ripley 2002) and pscl (Zeileis et al., 2008) were used to conduct this GLM analysis.

Results

Structural stability regimes

Our long-term benthic data show that the rate of change in benthic structure (structural stability) was strongly influenced by both exposure and depth (Table 2), structural stability was highest at sheltered, deep reefs (mean slope: 0.37 ± 0.15 SE; Figure. 2). Tukey's post hoc tests showed a sixfold difference in structural stability between sheltered, deep sites (which were highly stable through time) and exposed, shallow sites (which were structurally dynamic through time, mean slope: 5.9 ± 0.15; Figure. 2). Even at the same depth, sheltered deep sites (mean slope 0.37 ± 0.15 SE) were thrice as stable as exposed deep sites (mean slope 1.9 ± 0.40). Sheltered deep locations showed the lowest values of structural change through the sampled years, while exposed shallow locations had the highest values.

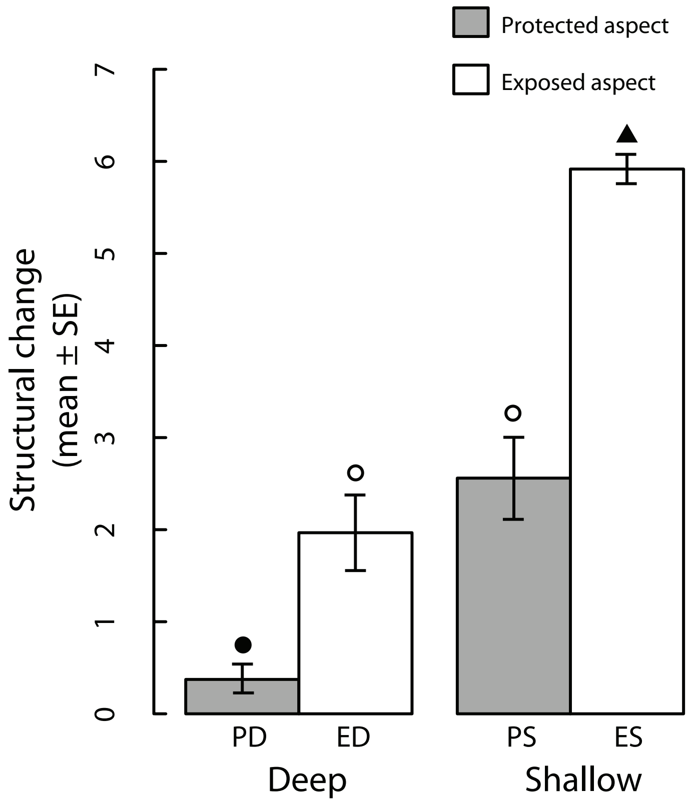

Figure 2. Structural stability (mean slope of structural change ± SE) at 12 permanent monitoring locations (Agatti, Kadmat and Kavaratti atolls, established in 1998), tracked during a recovery period between two major mass-bleaching catastrophes (1999 and 2009, n = 7 yrs). Sites factored by exposure and depth (n = 12). Tukey's HSD indicates three significantly different categories of structural stability at the two depths, represented by high-stability sites filled circle, medium-stability sites open circle, low-stability sites filled triangle. Site code: SD sheltered deep, SS sheltered shallow, ED exposed deep, ES exposed shallow.

Exposed deep (mean slope: 1.9 ± 0.40) and sheltered shallow locations (mean slope: 2.56 ± 0.44 SE) showed intermediate structural stability values (Table 2 ; Figure. 2). These comparisons give rise to a gradient of structural stability in the archipelago; high stability (sheltered deep sites), medium stability (exposed deep and sheltered shallow sites) and low stability (exposed shallow sites).

Patterns in structural complexity

Generalized linear mixed-effects models (GLMMs) showed that structural complexity did not significantly change with exposure but showed a weak positive effect of depth (Table 3). Post-2010 bleaching, the composition of coral forms showed that massive corals dominate the composition of all stability regimes (~70 %, Figure. 3). The percentage contribution of structure-forming tabular and branching corals is low in general throughout the study area, lower than 20 %. Exposed shallow reefs had the highest percentage of branching corals (17.04 %) and the lowest percentage of tabular corals (2.3 %). Sheltered deep reefs had the highest percentage of tabular corals (8 %) among all the reefs (Figure. 3).

Table 2. Structural stability regimes: two-factorial analysis of variance (two-factorial ANOVA) for joint effect of exposure and depth on the rate of change of structural complexity (structural stability) over 7 years (1999–2003, 2007, 2009).

Source of variation	df	Sum of squares	Mean square	F	p value
Exposure	1	18.377	18.376	59.73	<0.01
Depth	1	28.44	28.44	91.81	<0.001
Exposure x Depth	1	2.332	2.33	7.58	<0.001
Model	3	48.95	16.31	53.05	<0.01
Error	8	2.46	0.307		
Total (corrected)	11	51.41			

R2 = 0.65 (adjusted R^2 = 0.63), significant at alpha = 0.01, P < 0.01 **, P< 0.001****

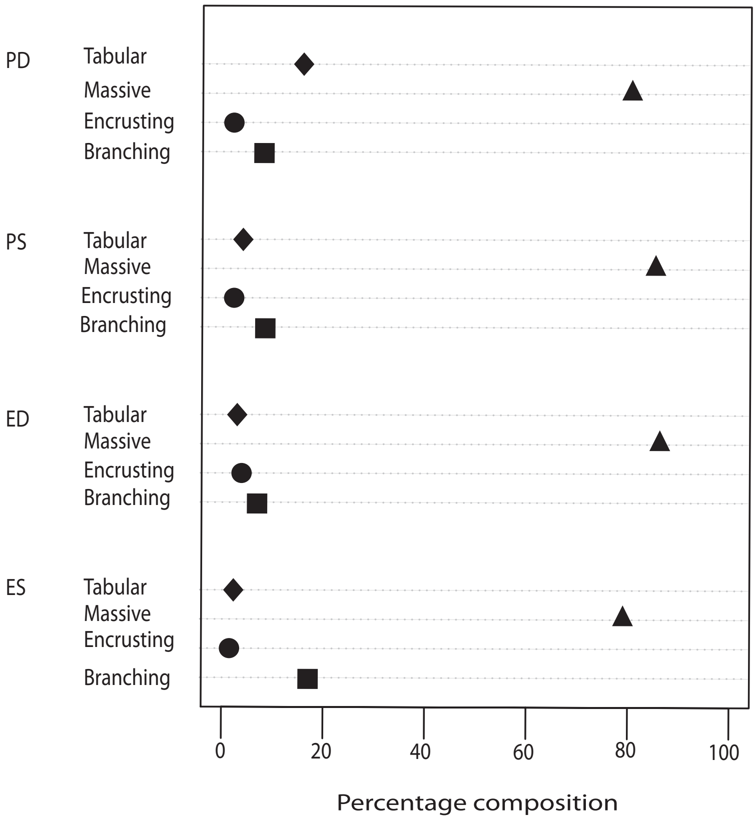

Figure 3. Percentage composition of coral forms: branching, encrusting, massive and tabular in four stability categories. Site code: SD sheltered deep, SS sheltered shallow, ED exposed deep, ES exposed shallow.

Table 3. Summary of Poisson generalized linear mixed effect model (Poisson GLMM) showing the effect of exposure and depth on structural complexity (2011).

Best Model: structural complexity ~ exposure + depth + random (site)

Coefficient	Estimate (SE)	z statistic	Random effects variance term +/- SD
Intercept = exposure (sheltered), depth (deep)	4.35 (0.05)	80.54***	Sites = 0.04 (0.22)
Exposure (exposed)	-0.05 (0.08)	-0.7	
Depth (shallow)	-0.06 (0.02)	-3.35 **	

*The table shows the best-selected model indicating parameter means with standard errors for fixed effects, and variance terms with standard deviation for random effects. Exposure and depth are fixed effects and site represents random effects. Symbols represent significance levels at ** P< 0.001 and *** P< 0.0001.*

Patterns in grouper biomass, diversity and species richness

Mean grouper biomass significantly changed with depth and exposure (Table 4). Within the same depth class, mean grouper biomass was significantly higher at deep sites on the sheltered aspect (Figure.4a), which had, on average, twice the amount of grouper biomass than deep sites on the exposed aspect. Similarly, comparing across depth classes and exposure, sheltered deep sites had six times the biomass of exposed shallow sites (Figure.4a). Grouper abundance (density) and species richness did not change significantly with exposure or depth (Table 4; Figure. 4 b, c). Across the archipelago, 50 % of average grouper biomass was concentrated at merely 10 reef sites (ie. 16 % of sites sampled, Figure.6 a), all of which were sites of high structural stability (sheltered deep, Figure. 2), and were also characterized by high structural complexity (more than 80 % structure, Figure.6 a). The proportion of individuals in large-size classes (31–50 and 51+ cm) was highest in sheltered deep reefs (46.4 and 15 %, respectively; Figure. 5). Sheltered reefs (deep and shallow) were dominated by individuals of length 31–50 cm (~60 %) as compared to exposed reefs (deep and shallow), which were dominated by medium individuals of length 11–30 cm (~50 %). The proportion of very small individuals (< 10 cm) was greater in exposed reefs, both deep and shallow (Figure. 5).

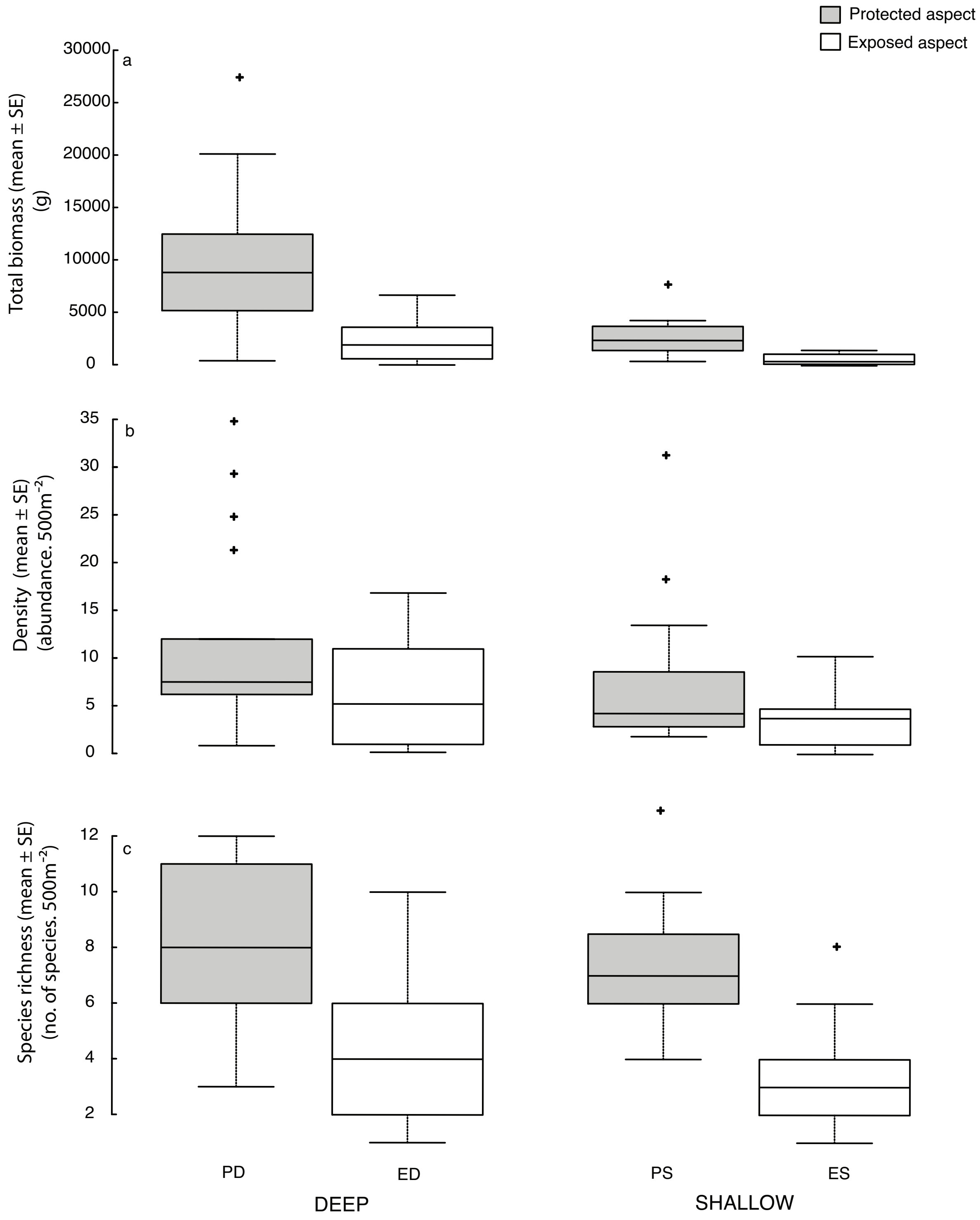

Figure 4. a) Grouper biomass density (mean ± SE), b) abundance density (mean ± SE) and c) species richness (mean ± SE) at exposed and sheltered sites and two depths (deep and shallow). Site code: SD sheltered deep, SS sheltered shallow, ED exposed deep, ES exposed shallow.

Relationship between structural complexity and grouper biomass across stability regimes

Biomass of long-lived grouper species increased significantly and exponentially (with structural complexity but only at the high-stability sites, i.e., deep sites on the sheltered aspect (Table 5 ; Figure. 6a). Further, based on the following estimate:

$$Pseudo\ R^2 = 1 - \frac{\text{residual deviance}}{\text{null deviance}} \times 100$$ (Zuur et al, 2009).

structural complexity predicted about 79 % variation in long-lived species biomass at these high-stability sites. In contrast, long-lived grouper biomass did not show even weakly significant relationships with structure for similar levels of structural complexity at all other locations of medium and low stability (Table 5 ; Figure. 6 b–d). Short-lived species biomass was not significantly influenced by structural complexity at any depth or exposure (Table 5).

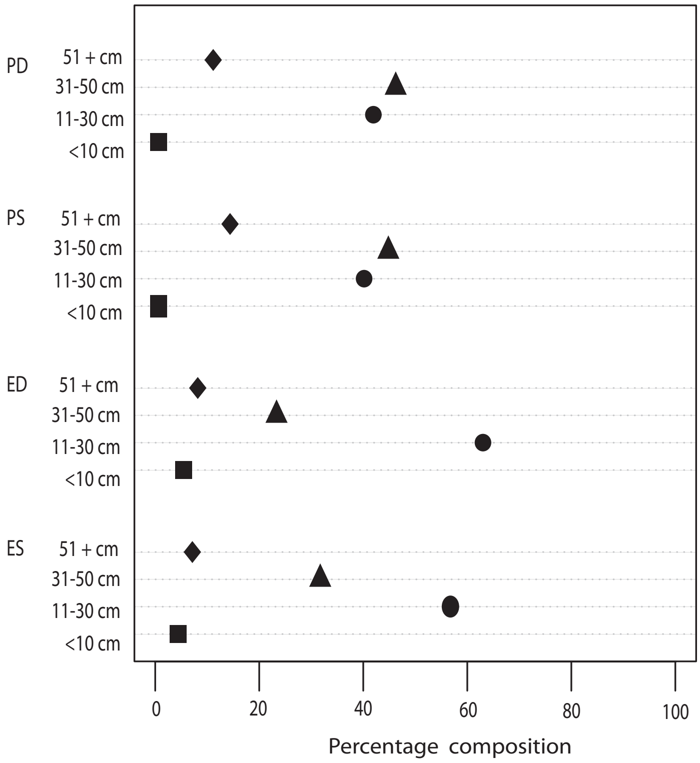

Figure. 5 Percentage composition of grouper size classes: <10, 11–30, 31–50 and 51+ cm at four stability categories. Site code: SD sheltered deep, SS sheltered shallow, ED exposed deep, ES exposed shallow.

Table 4. Generalized linear mixed effect models (GLMMs) showing the effect of exposure, and depth on grouper variables (biomass, abundance and species richness).

best selected models	fixed effects coefficients	estimate (SE)	z statistic	random effects variance term	estimate (SD)
a. Biomass ~ exposure x depth + random (atoll)	intercept - exposure (sheltered), depth (deep)	7.77 (0.20)	36.98 **	Atoll	0.03 (0.17)
	Exposure (exposed)	-0.76 (0.30)	-2.54 *		
	Depth (shallow)	-0.84 (0.31)	-2.67 **		
	Exposure (exposed) x depth (shallow)	-0.14 (0.46)	-0.3		
b. Abundance~exposure x depth + random (atoll/site)	intercept - exposure (sheltered), depth (deep)	1.19 (0.16)	7.18 ***	Atoll	0.08 (0.29)
	Exposure (exposed)	-0.22 (0.21)	-1.04	Atoll x site	0.14 (0.37)
	Depth (shallow)	-0.25 (0.17)	-1.43		
	Exposure (exposed) x depth (shallow)	-0.14 (0.26)	0.54		
c. Species richness ~ exposure + depth + random (atoll)	intercept - exposure (sheltered), depth (deep)	1.12 (0.09)	12.27***	Atoll	0.05 (0.23)
	Exposure (exposed)	-0.14 (0.08)	-1.69		
	Depth (shallow)	-0.49 (0.08)	-5.70		

*Exposure and depth are fixed effects and site (nested within atoll) and/or sites or atolls alone as random effects. Table provides the best-selected top models indicating parameter means with standard errors for fixed effects, and variance terms with standard deviations for random effects * P<0.01, ** P<0.001 and *** P<0.0001. GLMM families used: $_a$ negative binomial (theta = 0.296, SE = 0.024), $_b$ negative binomial (theta = 1.948, SE = 0.317), $_c$ Poisson.*

Discussion

Although the ability of some reefs to rapidly recover their structure after major mortality events is encouraging, our results indicate that long-term stability of habitats and not merely the availability of structure after rapid coral recovery may be far more important for long-lived species such as groupers. Our 12-yr temporal data shows differential rates of structural change (due to degradation and recovery from multiple bleaching events) across Lakshadweep. The structurally stable, sheltered deep sites across the entire archipelago appear to be highly preferred habitats for long-lived groupers. These 'high-stability' sites support about 50 % of grouper biomass recorded in our study. In comparison, even sites with high structural complexity, which have recovered rapidly from bleaching events (exposed deep sites or both shallow sites), do not support the same biomass of groupers as the high-stability sites. Our results suggest that a quick recovery of benthic structure alone may not influence the distribution of long-lived benthic fish associates, especially on reefs subject to recurrent disturbance events.

In many tropical reefs, groupers are highly targeted species, and this off-take pressure can often play a major role in their distribution (Chiappone et al., 2000). The Lakshadweep reef system is fairly unique in this respect because, despite having a dense human population, reef fishing here is a largely artisanal enterprise and contributes little to overall fishing pressure (Table 1). Grouper biomass in our study was, on average, 88 $kg.ha^{-1}$ across the archipelago, comparable with biomass estimates from relatively unfished reefs and well-established marine-protected areas, which can have grouper biomasses of between 20 and 130 $kg.ha^{-1}$ dependent on the location (Chiappone et al., 2000 ; Unsworth et al., 2007 ; McClanahan, 2011). In the absence of robust direct estimates of fishing pressure from the Lakshadweep, these estimates are perhaps the strongest evidence for low grouper fishing from these waters. However, even low levels of fishing can leave a distinct signature on the distribution and size of reef fish, particularly for long-lived species (Dulvy et al., 2004b). Our results, however, show that eastern reefs, despite being open year-round to light to moderate subsistence fishing, consistently show the highest biomass of groupers. The key informants we interviewed also confirmed that groupers were a fairly low-preference food fish locally, and earlier studies indicate that levels of grouper fishing can be low compared with grouper off-take from the nearby Maldives (Tamelander and Hoon, 2008 ; Sattar et al., 2011). Taken together, this suggests that reef fishing pressures do not drive the observed patterns and sheltered deep locations may support higher densities (high-stability habitats) over exposed deep and shallow reefs, potentially even offsetting low to moderate reef fishing pressures. More detailed studies on fishing intensity, access and species selectivity need to be undertaken to confirm the impact of fishing on grouper distributions.

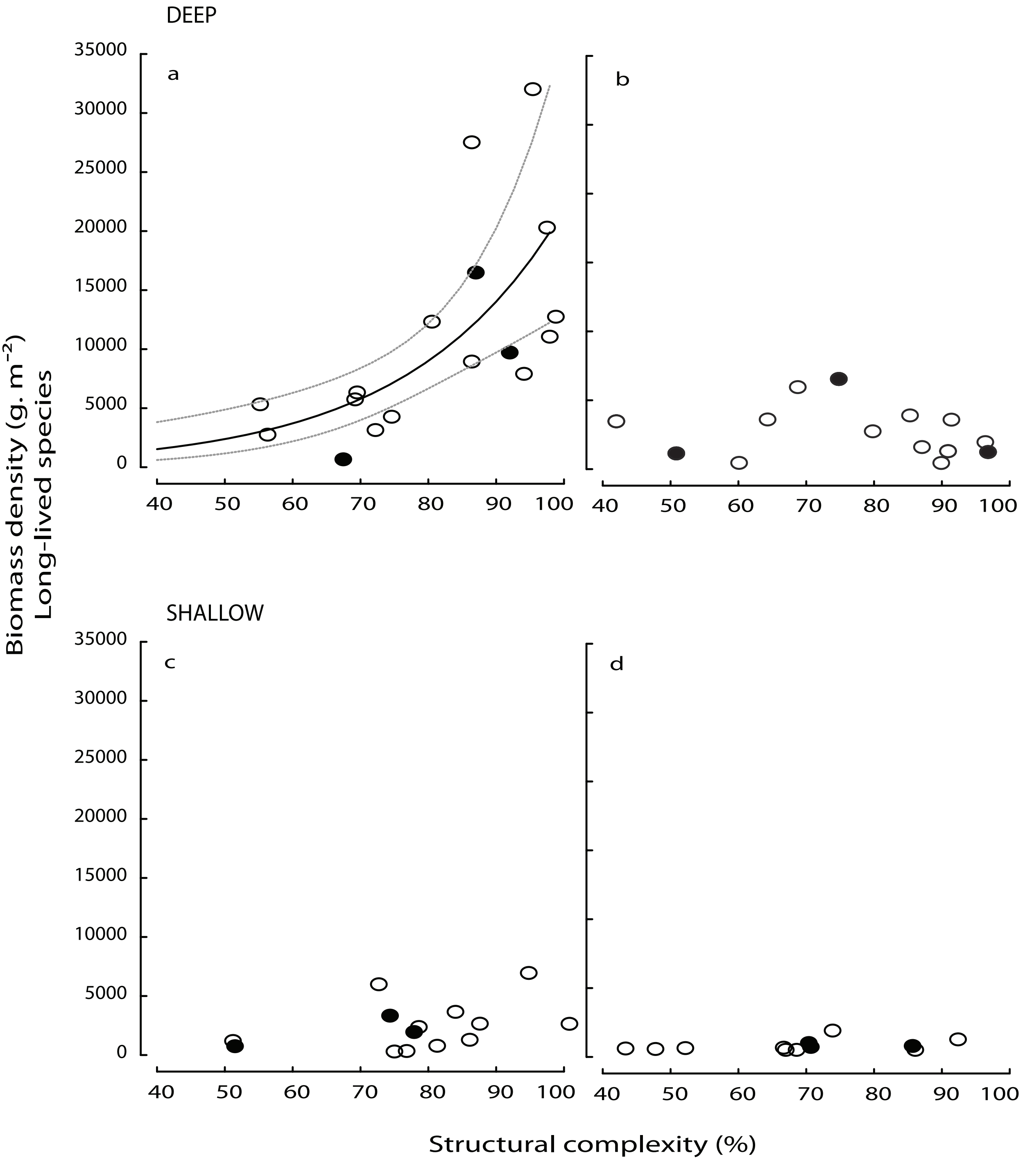

Figure. 6. Effect of increasing structural complexity on mean biomass density of long-lived grouper species (n = 14 species), at exposed and sheltered locations at two depths (deep and shallow) a. SD, n = 17, b. ED, n = 14, c. SS, n = 14, d. ES, n = 14, using GLMs. Relationship between grouper biomass and structural complexity at high-stability locations (a) is fitted by the model: long-lived grouper biomass ~ $e^{(5.46 + \text{structural complexity} \times 0.04)}$ (black solid line), bounded by 95 % confidence intervals (grey dashed lines). Solid circles indicate permanent monitoring sites at three atolls (Agatti, Kadmat and Kavaratti), open circles indicate sites sampled only in 2011. Site code: SD sheltered deep, SS sheltered shallow, ED exposed deep, ES exposed shallow.

Table 5. Generalized linear model (GLM) showing the relationship between grouper biomass (long-lived and short-lived species) and structural complexity at different stability regimes (1) high-stability (SD)-sheltered deep sites, (2) medium-stability (ED)-exposed deep sites (3) medium-stability (SS)-sheltered shallow sites) (4) low- stability (ES)-exposed shallow sites.

Stability regimes	GLM family	Intercept	Structural complexity	z value, df = 15
Long-lived species				
High (SD)	Negative binomial (NB = 2.5, SE = 1.1)	5.56 (0.89)	0.04 (0.01)	4.03*
Medium (ED)	Negative binomial (NB = 1.5, SE = 0.5)	8.49 (0.97)	- 0.009 (0.01)	-0.73
Medium (SS)	Negative binomial (NB = 0.55, SE = 0.18)	4.6 (2)	0.03 (0.02)	1.43
Low (ES)	Zero-inflated negative binomial (ZINB = 0.98, SE = 0.42)	2.28 (0.94)	0.05 (0.01)	1.89
Short lived species				
High (SD)	Negative binomial (NB = 0.30, SE = 0.11)	3.3 (2.3)	0.01 (0.02)	0.57
Medium (ED)	Negative binomial (NB = 0.42, SE = 0.1)	5.4 (1.85)	0.006 (0.02)	0.26
Medium (SS)	Zero-inflated negative binomial (ZINB = 000.9, SE = 0.47)	0.55 (3.92)	0.06 (0.04)	1.3
Low (ES)	Negative binomial (NB = 0.28, SE = 0.107)	4.77 (2.42)	0.009 (0.33)	0.29

* Table gives parameter mean ± SE for the explanatory variable (structural complexity), model intercept and corresponding z statistic for df = 15 * P<0.01 .

Few reefs across the Indo-Pacific (McClanahan et al., 2007; Graham et al., 2011, and our study sites) have shown remarkable ability for benthic recovery after bleaching mass-mortality events. Benthic recovery in the Lakshadweep proceeded rapidly after the 1998 El Nin˜o bleaching event (Arthur et al., 2006), influenced strongly by the interaction of depth and protection from monsoonal storms. Exposed shallow sites incurred the highest amount of coral degradation and recovery from the 1998 mass-bleaching event, being dominated by the fast-growing and fragile Acropora corals (Arthur et al., 2005). As a result, these sites were structurally unstable, going through cycles of very high and very low structural complexity during the 12-yr period we sampled. Sheltered deep sites, on the other hand, appear to have maintained their structure (in spite of coral mortality) since the 1998 mass-bleaching disturbance. Our data support this observation (Figure. 3), and we find that tabular coral forms, which are most susceptible to wave exposure (Madin and Connolly,2006), were highest in sheltered, deep reefs. Similarly, branching coral forms, which contributed largely to the low stability of exposed shallow reefs, were highest in these reefs, despite the recent bleaching disturbance of 2010.

Most atolls in the archipelago are oriented in a north– south direction with a distinct windward and leeward aspect in relation to the annual southwesterly monsoon. The monsoon system has historically played an important role in shaping the geomorphology of the Laccadives— Chagos archipelago (Siddiquie, 1980). Thus, even with a simple binary classification of exposure, our temporal data (12 sites, 3 atolls) is highly representative of archipelago-wide hydrodynamics and we can therefore extrapolate trends in structural stability to the entire archipelago. These results show that structural stability of reefs across the Lakshadweep archipelago increases with depth and degree of protection from the monsoon storms, and sites can be classified, based on their recent history of structural changes as low-stability (exposed shallow), medium-stability (exposed deep, sheltered shallow) or high-stability (sheltered deep) sites.

Independent of structural history, a few years after the last mass-bleaching event, mean structural complexity in Lakshadweep appears to be comparable between sites. Structural complexity is a crucial resource, influencing communities across various ecosystems (MacArthur and MacArthur, 1961 ; Friedlander and Parrish, 1998). Yet, in spite of the availability of structure, we see vast differences in grouper biomass between sites of differing structural stabilities, especially between deeper locations. In the absence of any temporal data on fish abundance across the entire archipelago, it is difficult to ascertain whether patterns in biomass represent the response of long-lived fish communities to multiple mass-bleaching disturbances or if they merely reflect a natural distribution with respect to depth and exposure (Sabetian, 2003). In our survey, depth does emerge as an important factor by itself, positively affecting grouper biomass and structural complexity. It is however, compelling that even at the same depth (deep), sheltered deep sites with very stable structure support twice the amount of grouper biomass as sites with relatively low stability (exposed deep, Figure. 4a). Further, long-lived groupers show an exponential numerical response to increasing structural complexity only in the high stability, sheltered deep sites despite the availability of suitable habitat (80 % structural complexity) at other, less-stable locations (Figure. 6).

Patterns in biomass were driven by a few large-bodied and long-lived species like *Plectropomus laevis, Plectropomus areolatus, Cephalopholis argus, Epinephelus malabaricus, Epinephelus caeruleopunctatus* and *Variola louti* , which were common only in sheltered deep sites at all the atolls we surveyed (Electronic

Supplemental Material, ESM Appendix 1). In contrast, short-lived species like the coral hinds (*Cephalopholis leopardus, Cephalopholis urodeta, Epinephelus fasciatus*) occurred commonly everywhere and did not seem to respond to structural complexity across the stability regimes (ESM Appendix 1). This suggests that unlike their long lived counterparts, shorter-lived species, with faster population turnover rates, may not be limited by structural change or may even benefit from the decline of long-lived top predators in unstable reefs. The breakdown of an important resource-abundance relationship in unstable reefs calls into question the ability of functionally important long-lived fish species to survive and recover from repeated environmental disturbances. Several factors potentially interact to make structurally stable sites in the Lakshadweep critical for long-lived groupers. The observed trends in biomass could largely reflect strong habitat selectivity by grouper species for specific habitat types (Sluka, 2000). Coral morphology, the principle structural element on reefs (Kerry and Bellwood 2012), differs in its functional utility to reef fish (Syms, 1995; Samoilys, 1997; Harmelin and Harmelin-Vivien, 1999; Shibuno et al., 2008; Wilson et al., 2008; Kerry and Bellwood, 2012). Differences in the composition of structural forms between sites may be an essential factor limiting adult groupers from colonizing low-stability reefs. High-stability, sheltered deep sites, with a mix of coral structures, may provide ideal conditions for small and large groupers (Figures. 3, 5).

The pattern of grouper distribution in Lakshadweep, like other species of reef fish, could also have been largely driven by patterns in prey availability (Shpigel and Fishelson,1989; Beukers-Stewart and Jones, 2004), which may fluctuate rapidly in low-stability sites. Species with narrower niche widths in terms of diet, modes of predation and dependence on structure may be unable to survive in low-stability locations where resources are in a state of flux from multiple disturbance events. Similarly, these rapid fluctuations in resources may have created bottlenecks for important population-level processes like reproduction, recruitment, post-recruitment survival, migration, which may only be reflected in the populations after a decadal lag period. The patterns we find suggest the possibility of differential mortality of long-lived species from low-stability sites or adult migrations to high-stability locations. Further studies addressing these various processes are necessary to gain valuable insights into the effects of multiple disturbances on benthic grouper communities. Independent of the specific mechanisms, these structurally stable reef sites may serve as vital refuge areas for fish populations on coral reefs, especially as climate change increases the frequency and intensity of benthic disturbances (Hoegh-Guldberg et al., 2007). Such stable refugia can have important ramifications for overall reef resilience, serving as important insurance locations for functionally important, keystone predators. Reef benthic predators like groupers are highly vulnerable because, apart from the insidious influences of declining reef architecture on their populations, they are often prized fishery targets feeding a growing live fish trade (Sadovy de Mitcheson et al., 2012). Lakshadweep presents a unique situation where the targeted fishing of groupers and reef fish is generally low in comparison to several regions across the tropics, but it is highly vulnerable today to future external market forces.

Our results indicate that even these unexploited populations of benthic predators may be subject to community wide impacts in the wake of climate change even in relatively unfished reefs like the Lakshadweep. Neither a quick benthic recovery nor the relatively low fishing pressure is sufficient to stem these losses to long-lived groupers, making structurally stable habitats all the more critical to the overall resilience of reef systems. Identifying these historically stable refugia should be an important first step in prioritizing reef management initiatives in the face of rapid climate change and expanding reef fisheries.

CHAPTER 3

Coping with catastrophe: foraging plasticity enables a benthic predator to survive in rapidly degrading coral reefs

Peacock grouper (Cephalopholis argus)

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Abstract

Human-induced rapid environmental change (HIREC) disproportionately affects species with specialist traits and long generation times. By circumventing prolonged evolutionary processes, behavioural plasticity is critical in allowing species to cope with rapid environmental changes within their lifetimes. Coral reefs have faced multiple mass mortality events of corals related to climate change in the last two decades. The consequent loss of structural complexity adversely impacts long-lived, structure-dependent fish predators. We attempted to determine how well a guild of groupers (Pisces: Epinephelidae) copes with rapid structural change in the lightly fished Lakshadweep Archipelago, Indian Ocean. Of the 15 species, territorial and site-attached groupers declined exponentially with decreasing structural complexity, while widely ranging species showed no change. However, one site-attached species, the peacock grouper, *Cephalopholis argus*, maintained high densities across the structural gradient. We explored the mechanisms this species employs to cope with declining habitat structure. Our observations indicate that both a potential release from specialist competitors and plasticity in foraging behaviour (foraging territory size, diet and foraging mode) appeared to favour the peacock grouper's survival in sites of high and low structure. While specialist competitors dropped out of the assemblage, the foraging territory size of peacock groupers increased exponentially with structural decline, but remained constant and compact (50 m^2) above a threshold of structural complexity (corresponding to a canopy height of 60 cm). Interestingly, despite significant differences in prey density in sites of high and low structure, gut content and stable isotope analyses indicated that peacock groupers maintained a specialized dietary niche. In-water behavioural observations suggested that diet specialization was maintained by switching foraging modes from a structure-dependent 'ambush' to a structure-independent 'widely foraging' mode. The remarkable foraging plasticity of species such as the peacock grouper will become increasingly critical in separating winners from losers and may help preserve specialist ecosystem functions as habitats collapse as a result of climate change.

Keywords

Ambush and widely foraging modes, behavioural plasticity, coral reefs, diet specialization, HIRECs, site-attached predators, structural degradation.

Introduction

Human-induced rapid environmental change (HIREC) is becoming the new normal for ecosystems (Sih, 2013), resulting in large-scale habitat degradation and an unravelling of species assemblages (Peters and Lovejoy, 1992; Stork, 2010). However, species do not respond equally to rapid environmental change; some species within the assemblage ('winners') are better able to cope with HIREC than others ('losers', McKinney and Lockwood, 1999). The ability of individuals to cope with rapid changes within their lifetimes is critical, especially because evolutionary responses that track environmental change may not necessarily keep pace with the radical rates of current HIREC (Snell-Rood, 2013). Winning species are usually ones in which individuals exhibit phenotypic plasticity, or the ability to express context-specific phenotypes of different traits under varying environmental conditions. Of the many phenotypic traits (behavioural, physiological, morphological, life history), behavioural responses can be employed fairly instantaneously (Slobodkin, 1964). It is therefore not surprising that behavioural plasticity is the most widespread response seen in a range of species surviving under HIREC (Hendry, Farrugia, and Kinnison, 2008; Price, Qvarnström, and Irwin, 2003; Sih, Ferrari, and Harris, 2011; West-Eberhard, 2003).

Repeated climate change disturbances result in a simplification of habitat structure with disproportionate consequences for site-attached species that depend on this structure for prey, refuge and ambush cover. As resource conditions in habitats change, site-attached species need to show strong plasticity in their foraging behaviour by modifying their diet (Layman et al., 2007), habitat use (Kittle et al., 2015) and foraging modes (Helfman, 1990; Huey and Pianka, 1981), in order to continue persisting in degraded habitats. For example, long-lived, site-attached carnivores such as leopards, *Panthera pardus*, cougars, *Puma concolor*, and wolves, *Canis lupus*, have been highly successful at persisting in human-altered and pastoral-dominated landscapes owing to plasticity in their foraging behaviours (Maddox, 2003). These foraging responses involve a complex optimization of resource availability, physiological constraints, predation risk and competition (Delclos and Volker, 2011). How species balance these trade-offs determines their success in suboptimal environments. The general understanding is that generalist species have a winning edge over specialists, since they have broader dietary niches and habitat preferences that enable them to more easily express a plastic phenotypic response (Colles et al., 2009; Gallagher et al., 2015; Spitze and Sadler, 1996). In addition, many winning species could merely be benefiting opportunistically from competitive release, as less plastic, specialist species drop out of the assemblage (Clavel et al, 2011). Competitive release may work together with behavioural plasticity in contributing to the relative success of some species over others in degraded habitats.

The past two decades have seen a wide-scale loss of structural complexity in coral reefs across the globe, associated with repeated episodes of mass bleaching-related mortalities of coral (Alvarez- Filip et al, 2009; Bruno and Selig, 2007). We examined how a guild of long-lived, structure-dependent coral reef predators called groupers (subfamily: Epinephelinae) cope with rapid structural decline in the lightly fished Lakshadweep Archipelago, Indian Ocean. Groupers are a diverse family of long-lived, benthic piscivores (Craig et al., 2011) that play important roles in structuring reef fish communities through direct consumptive and non-consumptive effects (Almany, 2003; 2004). While some groupers are highly territorial and site-attached, others range much more widely (Pears, 2005; Samoilys and Carlos, 2000). Groupers, like most benthic fish, are particularly vulnerable to structural decline (Feary et al., 2007; Karkarey et al., 2014; Pratchett et al., 2008), relying heavily on reef structure for prey, shelter and ambush sites (Kerry and Bellwood, 2012; 2016). To survive reef structural declines, groupers may need to show plasticity in their foraging behaviour. While roving species may have some ability to move to healthier habitats (Ritchie, 2002), site-attached groupers may have to rely much more on foraging plasticity to cope with changing conditions within their adult territories.

We examined the distribution and abundance of a guild of structure-dependent predatory groupers along a gradient of recent structural decline (over the last decade) in the Lakshadweep Archipelago, Indian Ocean. For the single long-lived, site-attached species that was ubiquitously abundant across the gradient, the peacock grouper, *Cephalopholis argus*, we explored its mechanisms of survival., Specifically, we examined whether this species was merely benefiting from the absence of specialist competitors (competitive release) or was, in addition, able to show plasticity in its foraging behaviour, modifying its foraging territory, diet and foraging mode, in degraded reefs.

Methods

Study Area and Site

The Lakshadweep Archipelago, Indian Ocean, comprises 12 coral atolls enclosing 33 small islands (8°N – 12°N, and 71°E – 74°E; Figure.1). The archipelago has witnessed repeated temperature-associated mass bleaching disturbances since 1998 (Arthur et al., 2006), with catastrophic consequences for reef structural complexity which has reduced considerably over the last decade (Karkarey et al., 2014; Yadav et al., 2016). The study was conducted in the centrally located Kadmat atoll, which has a land area of 3.2 km^2 and is surrounded by a large lagoon of 37 m^2 area, with a contiguous fringing reef. We based our study in Kadmat because it supports the lowest levels of commercial and artisanal fisheries in the archipelago (Karkarey, Arthur, and Gangal, 2015) and has suffered heavy reef degradation after the 1998, 2005 and 2010 mass-bleaching disturbances. Still, Kadmat atoll maintains areas that were

Figure 1. Map of Lakshadweep: Kadmat atoll with distribution of sampled sites (black stars).

relatively less affected since 1998 (Arthur et al., 2006), representing a natural gradient of structural complexity from flat barren reefs to reefs of high structural complexity.

Distribution of Species along a Structural Complexity Gradient

Nine reef sites were selected around Kadmat atoll for this study (Figure.1) representing a gradient of structural complexity. We used the mean vertical height (cm) of the coral canopy in the reef as an index of structural complexity. In an earlier study, we found that vertical canopy height was highly correlated with standard measures of coral complexity such as rugosity and density of holes and crevices (Karkarey et al., 2014). Vertical canopy height was measured every 5 m along four 50 m transects, laid randomly at each reef site (N = 40 per site, 10 per transect). Along these transects we estimated the density and diversity of groupers in a belt of 50 x 10 m, collecting information on the abundance and size class (1-15, 15-30, 30-50, 50+ cm) of species belonging to the genera *Cephalopholis, Plectropomus, Gracila, Variola* and *Epinephelus*. We further classified grouper species into two broad behavioural groups (modified from Pears, 2005; Samoilys and Carlos, 2000; see Appendix Table A1) as 'site-attached' and 'roving' species, based on their home range with respect to the area surveyed. The home range of roving species extended beyond the surveyed reef site, while site-attached species maintained a home range within the surveyed reef site.

Peacock Grouper's Response to Structural Decline

Our initial surveys identified the peacock grouper as the only site-attached species that persisted in high numbers across the structure gradient (see Results). This species is known to dominate a range of reef habitats and depths in native and introduced reefs across the Indo-Pacific (Meyer and Dierking, 2011). We explored the potential mechanisms that gave it a winning edge in structurally degraded reefs in Lakshadweep: (1) competitive release due to declining densities of specialist competitors and/or (2) plasticity in foraging behaviour (foraging territory size, diet choice and foraging mode).

Competitive release

To evaluate whether competitive release could potentially benefit the ubiquitous peacock grouper, we compared the relative density of this species with respect to the combined density of other site-attached grouper species (eight species; Appendix Table A1) along the gradient of structural complexity.

Foraging plasticity

We compared changes in three aspects of the foraging behaviour of peacock groupers along a gradient of structural complexity: change in foraging territory size, foraging mode and diet. Additionally, to determine whether potential changes in diet were due to differences in prey availability, we measured prey abundance within territories of peacock groupers. Foraging mode, territory size and prey abundance were measured with in situ observations, while diet was measured using stable isotopes complemented with gut content analyses of collected peacock groupers. To study the foraging behaviour of the peacock grouper we used focal individual sampling. A total of 52 individuals were sampled at the nine selected sites along the structural gradient in Kadmat (Figure.1). At each site, we sampled between four and seven individuals. We targeted the largest individuals (25-30 cm total length, TL) to control for size-related effects, particularly sex, since the largest individuals in peacock grouper harems tend to be males (Shpigel and Fishelson, 1991). We first identified the largest individual at the study site during a 5 min free swim. Every subsequent individual was selected at a minimum distance of 30 m from the limit of the previous individual's territory (see below). Individuals were also selected within a depth range of 10-15 m. Each individual was followed for a total of 30 min. The total sampling interval was identified based on earlier studies of *Cephalopholis* species' home range sizes (Shpigel and Fishelson, 1991), and validated in a pilot survey of three individuals, whose ranging patterns were repeatedly sampled over 2 days. As interspecific aggressive interactions were observed within these home ranges, we assumed that the area represented a defended territory. Individuals were observed at a minimum distance of 5 m from above, after first evaluating the minimum distance at which individuals exhibited a 'flight' response (minimum distance = 1.5 m). All focal-individual sampling was conducted between January and March in 2014 and 2015 and between 0900 and 1200 hours. Focal individual sampling was used to score foraging and other behaviours (Table.1) and to estimate territory size of the groupers. We typically sampled two individuals per dive, marking our position with a GPS to avoid resampling individuals.

Table 1. Peacock grouper behavioural ethogram

State	**Sub-state**
Moving : Individuals were in motion, or in a state which involved movement of dorsal and lateral fins and colour change	1. Patrol - Individuals swam at steady speed around their territory, with head pointed forward, occasionally stopped at 'vantage points' to change direction.
	2. Forage - Individuals either swam with head pointed towards the benthos, or hovered near structure (with movement of fins), and occasionally made attempts at capturing prey. Two broad foraging modes were observed (see methods).
Stationary: Individuals were motionless, no movement in fins or associated colour change	1. Perch - Individuals rested motionless on top of coral structures with no movement in fins and without colour change.
	2. Hide - Individuals rested motionless under structures, in caves or crevices in the structure.

Foraging territory size

We worked with the common assumption that the movement an individual made between foraging bouts was effectively a search behaviour (Stephens and Krebs, 1986). This was supported by our observations since peacock groupers were observed foraging over the entire extent of their territories, and we assumed that the total territory size was a good estimation of its foraging territory size. Focal individuals were followed from above, and a numbered sinker was dropped every 2 min to mark the position of the individual., Foraging territory size was calculated as the rectangular area based on the longest length and breadth distance between the sinkers (territory size = length x breadth). After the territory size was delimited we estimated potential prey density within the foraging territories of 48 of the 52 individuals sampled. We estimated fish prey density (fish/m2) along a timed transect (5 min) of 20 2 m running through the territory. Fish in the families Blenniidae, Labridae, Tripterygiidae , Pomacentridae, Synodontidae, Gobiidae, Apogonidae, Pempheridae, Clupeidae, Pomacanthidae, Microdesmidae Cirrichthidae, Pinguipedidae, Balistidae, Scaridae, Serranidae, Acanthuridae and Holocentridae (all individuals 3-10 cm in TL) were counted as potential prey, based on previous dietary studies and gape limits of large peacock groupers (Dierking and Meyer, 2009). In addition, we estimated invertebrate density (invertebrates/m^2) using 3 min timed searches in 1 m^2 quadrats (N = 3 point searches per territory). Benthic structures were thoroughly searched, with flashlights, for invertebrates. These included molluscs (bivalves, gastropods), crustaceans (diogenid crabs, pocilloporid crabs, trepezid crabs, carid shrimp, alpheid shrimp) and echinoderms. Given the narrow size range of prey, we assumed that prey abundance would serve as a reasonable proxy of prey biomass.

Foraging modes

During the 25 min observation of each focal individual (N = 52) we documented different behavioural states (Table. 1). We observed and scored the frequency of two distinct foraging modes used by peacock groupers during foraging bouts. (1) In the ambush mode, individuals slowly approached prey. The individual often circled coral structures or swam through the holes and crevices of coral colonies while approaching prey. Prior to a predation attempt, the individual became almost motionless (with minimum movement of the caudal fin) changing colour to pale red, before darting out at high speed to capture prey. This sequence (motionless state, colour change and dart) was scored as an ambush attempt. (2) In the widely foraging mode the individual roved swiftly across its territory. During this roving, individuals were seen with their head pointed downwards at the substrate and probed into the structures as they moved along. In this mode, individuals were also observed making occasional rapid linear darts towards prey in the water column. Colour change was not observed in this mode and neither was the use of structure; the individuals were seen roving above the coral canopy. Every probing and linear darting attempt in the water column was scored as a widely foraging attempt.

Diet

We collected 69 random individuals by spearfishing at nine sites across the structural gradient in 2015, using traditional spear guns (see Ethical Note below). Samples varied in TL between 15 and 35 cm. Spearfishing was selected as the least destructive technique for capturing specimens based on fishing and caging trials conducted at our sites. Fishing experiments were conducted with three hook sizes (2, 3, 4) and market-sourced bait (herring and blue-green chromis). Both fishing trials (9 h) and cages (2 nights) led to the bycatch of 22 individuals of red-toothed triggerfish, orange-lined triggerfish, red mouth groupers, honeycomb groupers, scribbled wrasse and moray eels, with no success in catching peacock groupers. Spearfishing success was found to be high (97%) and of the 71 peacock grouper individuals that were speared, only two escaped. We arbitrarily classified captured individuals into 10 cm bins as small (10-20 cm), medium (21-30 cm) and large (31+ cm). Fish were immediately bagged underwater to prevent loss of regurgitated prey (Dierking and Meyer, 2009) and transferred to the boat by a free-diver for anaesthesia and culling (see Ethical Note below). The maximum time delay between spearing of fish underwater and anaesthesia on the boat was under 2 min. Fish were killed immediately after they were anaesthetized, which took between 0.5 and 1.5 min, depending upon their size. Samples were weighed, measured and dissected in the wet laboratory. Guts were opened and inspected for prey items. Prey were broadly classified as fish or invertebrates and identified to the family level wherever possible. We also collected the white muscle tissue (lateral muscle tissue under the dorsal fin) from the samples for stable isotope analysis. The tissue samples were dried at 70◦C for 48 h and ground to a fine powder. The powdered samples were analysed for δ^{15}N and δ^{13}C stable isotopes at the Physical Research Laboratory, Ahmedabad. The carbon and nitrogen isotopic compositions were determined using a MAT 253 Isotope Ratio Mass Spectrometer attached to a FLASH EA 2000 elemental analyser. Carbon and nitrogen isotope ratios are expressed in the delta notation (δ^{15}N and δ^{13}C) relative to Vienna PDB standard and atmospheric nitrogen and expressed in per mille.

Ethical Note

The study was conducted with appropriate research permits and clearances granted by the Department of Science and Technology, Lakshadweep. The peacock grouper is not an endangered species, nor a 'Scheduled' species as per the Wildlife Protection Act of India, 1972. Spearfishing was conducted to effect capture of the target species and size classes of interest, while minimizing harm to non-target species and habitats, which other fishing methods (hook and line and cages) entailed. Identified specimens were speared using locally available, traditional spear guns by experienced personnel. Specimens were rapidly transferred upon capture to a freshwater ice slurry to aid anaesthesia (Blessing et al., 2010), followed by percussive stunning (Roth et al., 2007), considered to be a highly effective and humane technique adopted by industrial-scale fisheries. Percussive stunning was administered by a trained and skilled local fisherman. Whole specimens were processed for stable isotopes, guts (as reported in this study) and for otoliths, physiological parameters and ecomorphology (which forms part of another study).

Statistical Analyses

Distribution of species along a structural complexity gradient

We used generalized linear models (GLMs) to compare mean densities of site-attached (eight species) and roving groupers (seven species) as well as our focal species, peacock grouper, along a gradient of structural complexity (N = 9 reefs, 36 transects). Because density data can be discretised to be considered as count data, we used a quasi-Poisson GLM to account for overdispersion, with density (fish/500 m^2) as the response variable and structural complexity as the explanatory variable.

Peacock Grouper's Response to Structural Decline

Competitive release

We used a quasibinomial GLM to examine the relative difference in proportional density of peacock grouper versus other site-attached groupers (eight species) along the gradient of structural complexity (N = 36 transects, nine reefs).

Foraging plasticity

Foraging territory size

Our preliminary observations suggested that there was an abrupt change in the foraging territory size of individuals at a canopy height of around 60 cm structure. To test whether the relationship between territory size and structural complexity was non-linear, we used a change point detection method in R with the package strucchange (Andersen et al., 2009; Zeileis et al., 2002). The algorithm is based on assessing whether a single set of parameters (mean, variance, trend) can be used to explain different parts of the relationship, or if multiple parameters (regressions) better explain the data series. Further, to assess the significance of every potential change point in the data set, an F statistic (Chow test statistic) was computed. Since these methods require data sets with at least one observation per level of the predictor variable, we pooled structural complexity into 5 cm bins (grouping canopy heights from 0 to 5 cm, from 6 to10 cm, and so on). We used a bootstrapping procedure where the data were sampled with replacement,1000 times. This was used to estimate confidence intervals for the sample mean F statistic and change-point estimator. We then plotted the mean foraging territory size for each interval (N = 52) of structural complexity as estimated by a quasi-Poisson GLM, with the most probable change point and its confidence interval. Based on the identified change point in structure, we classified sites as having either high (> threshold) or low (< threshold) structure. We used this classification to study the effect of structural complexity on foraging mode, prey abundance and diet. The mean densities of fish and invertebrates in each territory (N = 48) were compared between sites of high and low structure using quasi-Poisson GLMs.

Foraging mode

We used a binomial GLM to test for the relative proportion of ambush versus widely foraging attempts made by each individual (N = 52) in sites of high and low structure. To test for differences in the proportion of time spent by an individual in different behavioural substates we conducted a two-factorial ANOVA. The response variable proportion of time was arcsine transformed. Behavioural substate (patrol, forage and perch) and structure (high and low) were the two explanatory variables. Following this, a Tukey's honestly significant difference test (Tukey's HSD) was conducted to test for differences between treatment means.

Diet

Differences in the mean δ^{15}N and δ^{13}C stable isotope of the three size classes (small, medium, large, N . 69) were compared between sites of high and low structure using a one-way ANOVA followed by Tukey's HSD tests.

All data were visually inspected for normality and heteroscedasticity to meet model assumptions.

Results

Distribution of Species along a Structural Complexity Gradient

Site-attached and roving species responded differently to declining structural complexity (Figure. 2). Site-attached groupers declined significantly and exponentially in density by approximately two fish per 500 m2 with a unit decline in structural canopy height (t7=4.53, P= 0.002; residual deviance= 22.85; dispersion parameter = 3.19). At sites with structural complexity less than 60 cm, we recorded no more than one or zero site-attached grouper individuals in our transects. In contrast, roving groupers were found in low densities (6.5 ± 2.19 fish/500 m^2) across the gradient and did not vary significantly in density with structural complexity. Most interestingly, the mean density of the site-attached peacock grouper did not decline with structural complexity, but instead remained three times higher (18.59 ± 1.21 fish/500 m^2) than the mean density of roving species across the gradient, and 16 times higher than other site-attached species in sites below 60 cm structural complexity.

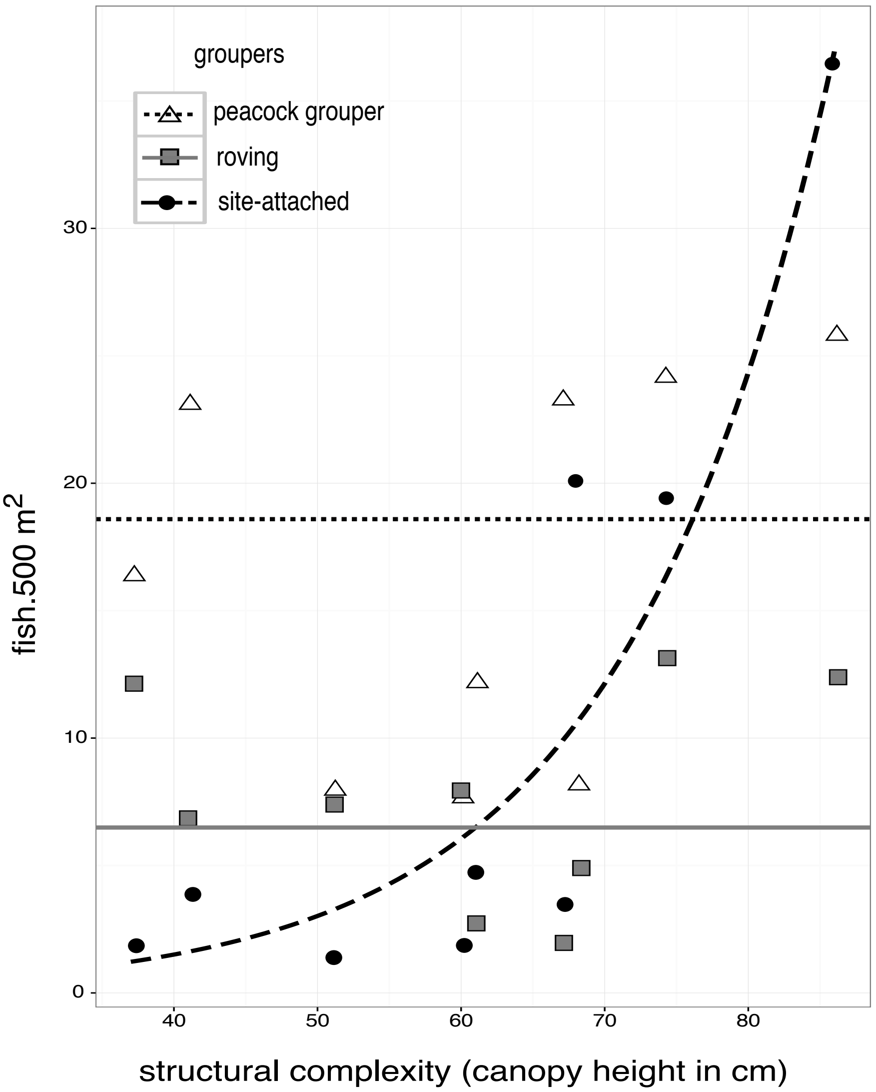

Figure 2. Grouper distribution: relationship between mean density of groupers and structural complexity (measured as mean coral canopy height) in nine reefs. The focal peacock grouper is a site-attached species but is plotted separately from site-attached and roving species for comparison. The black dotted line is a best-fit line from the quasi-Poisson GLM of site-attached species. Black dashed and grey solid lines represent mean densities of peacock grouper and roving species, respectively.

Peacock Grouper's Response to Structural Decline

Competitive release

The relative density of peacock groupers with respect to other site-attached groupers declined with an increase in structural complexity of reefs (t_{33}=3.44, P= 0.002; residual deviance= 81.3; dispersion parameter= 2.116; Figure. 3). In reefs of low structural complexity (< 60 cm structure) mean peacock grouper density represented between 70 and 90% of total guild density while at sites of high structural complexity (>60 cm), peacock groupers represented only 40% of the total guild density of site-attached groupers.

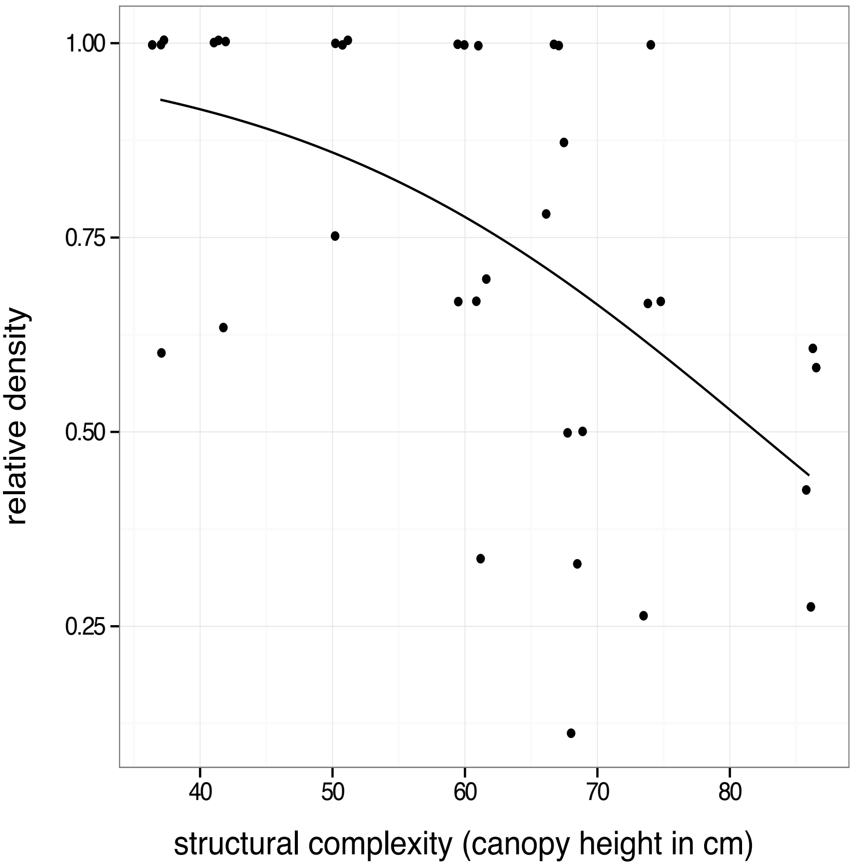

Figure 3. Relative abundance of peacock grouper versus other site-attached species (N = 8) along the gradient of structural complexity (N= 36 transects). The black line represents mean relative abundance of peacock grouper as predicted by a quasibinomial GLM.

Foraging plasticity

Foraging territory size

Territory size increased nonlinearly with decreasing structural complexity, with a potential threshold identified at around 60 cm. The change point analysis confirmed this threshold fit better than a standard regression, showing that there was a clear nonlinearity in peacock grouper territory size with decreasing structural complexity (Figure. 4). The confidence intervals of the threshold estimate spanned from 51 to 65 cm. We used the mean of the two intervals (58 cm) to categorize sites as having 'low' structure (<58 cm) and 'high structure' (>58 cm). In sites having low structure, the mean territory size of peacock groupers increased exponentially by 97%, with every 5 cm decline in structure (t6=3.39, P= 0.001; residual deviance= 96.35; dispersion parameter= 16.13; Figure. 4). In contrast, in sites of high structure, territory size remained relatively constant and small (41.88 ± 7.56 m2), not changing with any further increase in structural complexity. The composition of prey varied between sites of high and low structure. Mean invertebrate density in sites of low structure (12.2 ± 2.01 invertebrates/m2) was nearly three times higher than in sites of high structure (4.7 ± 0.46 invertebrates/m2; t_{44}=4.49, P<0.005; residual deviance= 150.01; dispersion parameter= 3.94). In contrast, mean fish density in sites of high structure (11.6 ± 4.22 fish/m^2)was 11 times higher than that in sites of low structure (1.9 ± 0.30 fish/m^2; t_{44}=2.46, P = 0.02; residual deviance= 623.25; dispersion parameter= 19.68).

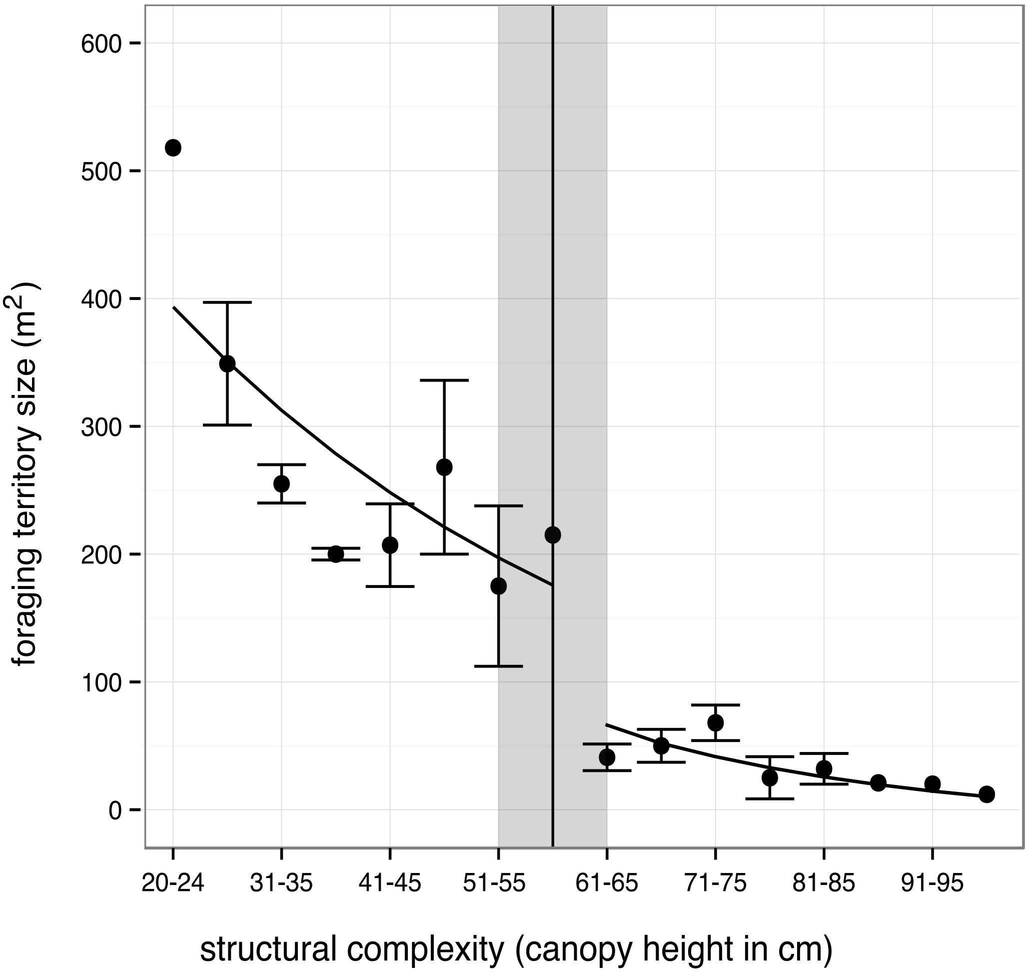

Figure 4. Change in foraging territory size: relationship between mean structural complexity and mean foraging territory size of peacock groupers (N = 52). Structural complexity was binned into 5 cm bins for threshold analysis. The vertical line represents a change point (with 95% confidence interval in shaded rectangle) identified using sequential Chow tests (sup-F = 89.87, P < 0.001). Black lines represent the best fit lines obtained from quasi-Poisson GLMs for the relationship between structural complexity and foraging territory size.

Foraging mode

In sites of high structure individuals used the ambush and widely foraging mode in equal proportions. However, in sites of low structure individuals used the widely foraging mode four times more frequently than the ambush mode (Figure.5; $z_{51} = 2.915$, $P < 0.005$; residual deviance= 38.62). Individuals spent an equal proportion of their time foraging in sites of high and low structure (Figure. 6).

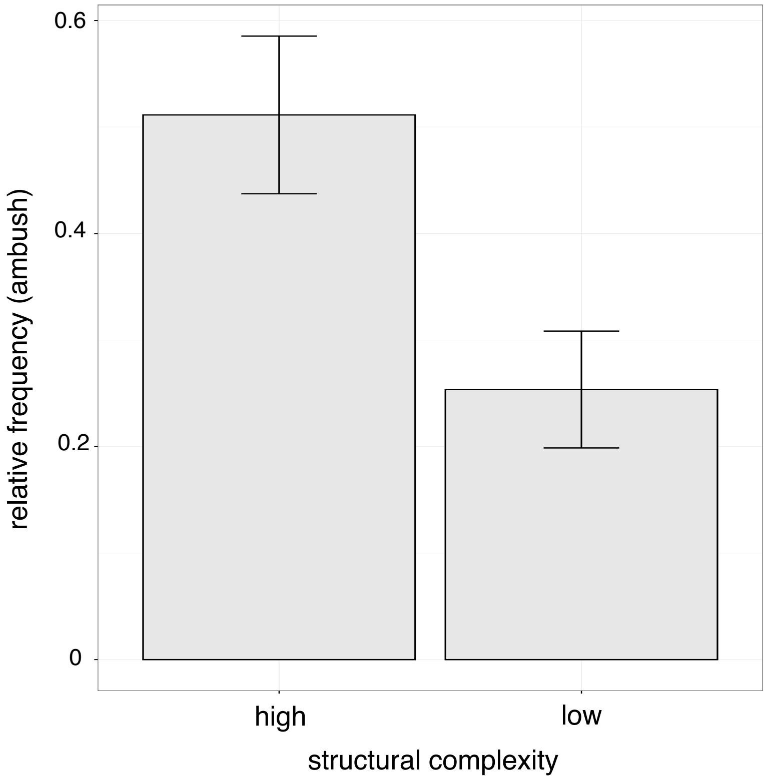

Figure 5. Foraging plasticity: relative proportion of mean and associated SE of ambush versus widely foraging attempts made by each peacock grouper (N = 52) to capture prey in sites of high and low structure as predicted by a binomial GLM.

Diet

Of the 71 individuals, 33 (46%) had empty guts. Of the remaining 38 individuals from sites of high (N =18) and low (N =20) structure, 70% had partially digested or whole acanthurid remains. In addition, prey fish of the families Gobiidae, Labridae, Pomacentridae and crustaceans were represented in diets of small and medium-sized individuals (TL < 30 cm). In contrast, the guts of larger individuals had prey fish of the families Serranidae and Scaridae in sites of both high and low structure. Prey fish found in the guts of the largest individuals were not the most abundant species estimated in their territories (Appendix Figure. A1). During our survey, we encountered a mass recruitment event of acanthurids in early 2015, which disproportionately increased the abundance of juvenile acanthurids on reefs by 200% (R. Karkarey, personal observation). While gut content analysis represents recently

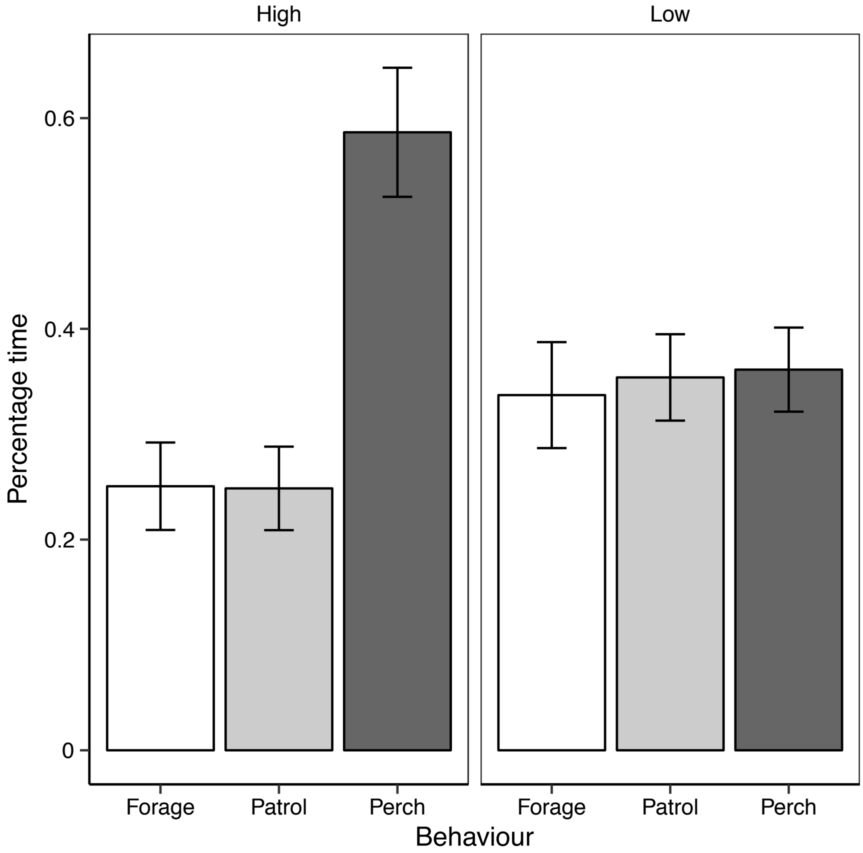

Figure 6. Proportion of time spent in different behavioural substates (forage, patrol, perch) by peacock groupers (N= 52) in sites of high and low structure.

ingested prey by the consumer over the last few hours, stable isotope ratios in animal tissues reflect the diet of a consumer over a period of weeks to months, as they are based on the principles of food assimilation (Post, 2002). We suspect that the unusual mass recruitment event during sampling may have compromised estimation of diet based on gut contents and we therefore consider stable isotopes as a more reliable and representative comparison of diets in our study. Mean δ15N and δ13C values did not vary for large and medium sized individuals in sites of high and low structure (Figure. 7). On the other hand, mean d 15N values for small individuals were significantly lower in sites of low structure (Figure. 7; $F_{3,68} = 4.516$, $P < 0.005$), indicating that small individuals were potentially feeding on prey of lower trophic values such as invertebrates than large and medium-sized individuals. However, all individuals (small, medium and large) in sites of high structure were able to feed on similar prey of a higher trophic value.

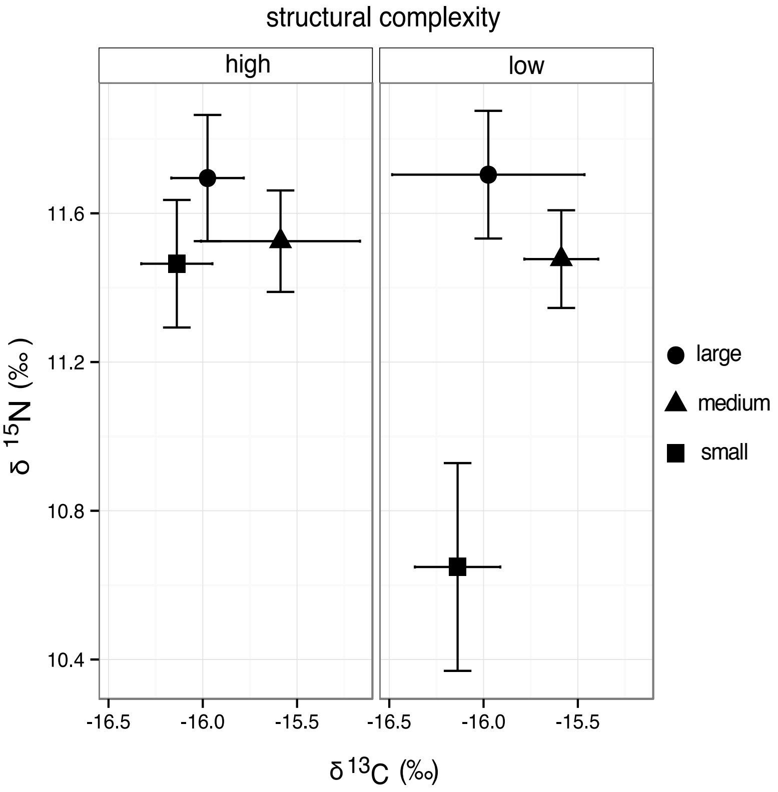

Figure 7. Diet: mean δ^{13}C and δ^{15}N (per mille) ± SE of peacock groupers (N . 69) in sites of (a) high and (b) low structure. Size classes: small: 10-20 cm TL; medium: 21-30 cm TL; large: 30+ cm TL.

Discussion

For most long-lived and structure-dependent predators, the large-scale erosion of structural complexity in the wake of recent climate change can be devastating. In this study, we showed that in coral reefs subject to repeated coral mass mortalities, most long-lived, structure-dependent piscivores (groupers) persisted only in highly structured reefs in the Lakshadweep archipelago. Where reef canopy had degraded below 60 cm in height, site-attached species dropped out of the assemblage, with only roving species found across the reef gradient. The peacock grouper was an unruly exception and did not decline in density with structural complexity as other site-attached species did. Instead, it outnumbered both roving and site-attached species in structurally degraded reefs. Being able to survive in these suboptimal reef environments required peacock groupers to radically modify their foraging behaviour from using an ambush to a widely foraging mode. Foraging mode shifts enabled peacock groupers to rapidly adapt to a structurally homogenized landscape, while maintaining their trophic position and diet specificity. Without such plasticity in foraging modes, long-lived, structure-dependent predators may be placed at a serious disadvantage under regimes of rapidly declining habitat structure.

While a very effective strategy in optimizing resource use in crowded assemblages, specialization results in species using a relatively restricted subset of resources or habitats compared with generalists, putting specialists at a disadvantage in rapidly changing habitats (Irschick et al., 2005). Across a range of taxa such as birds (Julliard et al., 2004), cryptic coral reef fish (Munday, 2004) and mammals (Fisher et al., 2003), greater habitat specialization has negatively impacted species' responses to rapid habitat disturbances and fragmentation. In the context of global change, as ecosystems continue degrading to structurally homogenized states, behavioural inertia, such as site fidelity and foraging inflexibility, is increasingly putting species at risk of local extinctions (Matthiopoulos et al., 2005; Pichegru et al., 2010). Particularly, species with ecological traits that include high trophic levels, resource specialization, low population densities and slow life histories are inherently predisposed to rapid declines under HIRECs (Alonso et al., 2015; Purvis et al., 2000; Roberts and Hawkins, 1999).

In Lakshadweep reefs, it is not surprising that roving groupers were present across the entire range of structural complexity suggesting that they are habitat generalists, while site-attached species dominated the assemblage in less than 50% of sites, all of which had high structural complexity (>60 cm canopy height). However, despite being a relatively long-lived, territorial and site-attached species, the peacock grouper was found in sites across the gradient of structural complexity. Most interestingly though, to sustain this ubiquity, the peacock grouper had to make significant behavioural trade-offs in foraging strategies, while continuing to maintain its diet specialization in degraded reefs. Recent studies highlight the exceptions that some long-lived, structure-dependent, apex predators such as leopards, cougars and wolves can successfully persist in human-altered and structurally homogenized agricultural landscapes owing largely to flexible foraging (Athreya et al., 2013; Valeix et al., 2012). Our study contributes to a growing recognition that behavioural plasticity, more than conventionally used metrics such as life history, population size and resource specialization, may be critical for separating 'winners' from 'losers' in the context of global environmental change.

The clearest response by the peacock grouper to structural decline was in its foraging territory size, which is often the first response of animals to HIRECs as they attempt to adjust to changing environmental conditions (Tuomainen and Candolin, 2010). On the one hand, by increasing territory size with habitat degradation, territorial species significantly improve their chances of encountering prey (Kittle et al., 2015; Mumby and Wabnitz, 2002). For example, the home range size of the spotted sand lizard, *Pedioplanis l. lineoocellata*, increased in degraded Kalahari savannah habitats where prey availability was low, compared with non-degraded habitats (Wasiolka et al., 2010). On the other hand, if habitat disturbance modifies the distribution of predators or superior competitors, inferior competitors may profit by expanding into vacated niches, possibly by increasing their repertoire of resource use (Rosenzweig, 1995). It has been well documented that mesopredators such as racoons, *Procyon lotor*, coyotes, *Canis latrans*, and Eurasian badgers, *Meles meles*, successfully adjust to urbanized landscapes by modifying their ranging behaviours in response to a higher density of human-provisioned food resources as well as the loss of specialized competitors from the community (Davison et al., 2009; Prange et al., 2004; Tigas et al., 2002). The size of peacock grouper territories in this study was strongly influenced by structural complexity only when reef structure declined below 58 cm. Note that other site-attached species were mostly absent beyond this threshold of structure. Large benthic predators are known to use reef structures relative to their body size (Kerry and Bellwood, 2016) and the 58 cm threshold of structural complexity could represent a clear limit to the ability of large benthic piscivores to effectively use the degraded landscape. Thus, while most site-attached predators may be directly limited by the loss of structural complexity and prey resources, smaller, behaviourally flexible species such as the peacock grouper may benefit more from the loss of these specialist competitors than by the loss of physical habitat structure and prey resources (Devictor, et al., 2008; Marvier et al., 2004).

An unusual response by the peacock grouper to habitat degradation was to maintain diet specialization even in highly degraded reefs. Optimality suggests that predators should forage less selectively on prey in degraded habitats to increase prey encounter rates (Stephens and Krebs, 1986). Predators typically broaden their dietary repertoire to incorporate more abundant prey as habitats degrade (Layman et al., 2007). Across taxa, dietary inflexibility has led to drastic post disturbance declines in specialized apex predators such as hammerhead sharks, pinnipeds (Gallagher et al., 2014) and the Cape gannet, *Morus capensis* (Pichegru et al., 2010), to name a few. Most coral reef piscivores show ontogenetic diet shifts from invertebrates to fish, but still maintain a proportion of non-fish prey in their diets at larger sizes (Mittelbach et al., 1988; Scharf et al., 1997). Contrary to our expectations, we did not observe a broadening of diet breadth in peacock groupers in degraded reefs even though fish prey were scarcer than invertebrates. Central to maintaining this diet selectivity was a remarkable plasticity in foraging modes. Our in-water observations showed that large peacock groupers employed very different context-specific foraging modes in sites of high and low structure, essentially becoming much more active and structure-independent foragers in the latter. Predators across trophic groups use either widely foraging or active foraging modes to feed on patchily distributed prey, while employing ambush or passive foraging modes to target highly mobile prey (Manenti et al., 2013). As these strategies require different biomechanical properties, many predators may specialize on a single strategy to feed (Delclos and Rudolf, 2011; Perry and Pianka, 1997; Webb, 1984). However, a few predators such as the lined seahorse, *Hippocampus erectus* (James and Heck,1994), and desert lizards (Huey and Pianka,1981) can efficiently shift from passive to active modes with a decline in prey density (Helfman, 1990; Michel and

Adams, 2009) and habitat structure (Fausch et al., 1997). By switching foraging modes, peacock groupers appear to be able to target specific prey and maintain their trophic position even in highly degraded reefs, unlike in other regions (Hawaii: Dierking et al., 2009; Red Sea: Shpigel and Fishelson, 1989; Madagascar: Harmelin-Vivien and Bouchon, 1976). Peacock groupers in the Lakshadweep probably have a relatively narrow diet because their preferred prey species are still available, albeit at reduced densities across the gradient. It is unclear from our study whether this dietary specialization could change as reefs get degraded still further.

Our results emphasize that, unlike many other site-attached predators, peacock groupers are plastic generalists that can thrive in reefs of varied structural complexity. This ubiquity is made possible by the remarkable context-specific plasticity in foraging modes individuals show, allowing them to maintain a specialized dietary niche. In a recent review, Clavel et al., (2011) proposed a 'functional homogenization' of communities, as specialist species are increasingly replaced by generalists in the context of HIREC. Our study suggests that if habitat generalization does not necessarily imply diet generalization, it means that a larger functional suite of behaviourally plastic species could still persist in degrading habitats. On the one hand, our results show that declines in reef structure can have serious and dramatically nonlinear consequences for inflexible structure dependent piscivores. On the other, it suggests that HIREC may not inevitably mean the loss of all specialists or specialist functions from ecosystems.

An interesting future direction would be to identify the specific suite of biomechanical and physiological traits that allow species such as the peacock grouper to forage flexibly and survive under HIREC compared with species that are unable to cope. While animals may have the capacity to rapidly adjust their behaviour, it is necessary to determine the limits of this plasticity in order to forecast the probable fate of populations in response to both current and projected changes (Wong and Candolin, 2015). These apparently successful species could still suffer considerable longterm consequences to their growth and fitness, which can have demographic consequences. As HIREC continues to inexorably alter ecosystems, foraging plasticity may become increasingly key to maintaining top trophic functioning and fostering resilience in degraded ecosystems.

Acknowledgments

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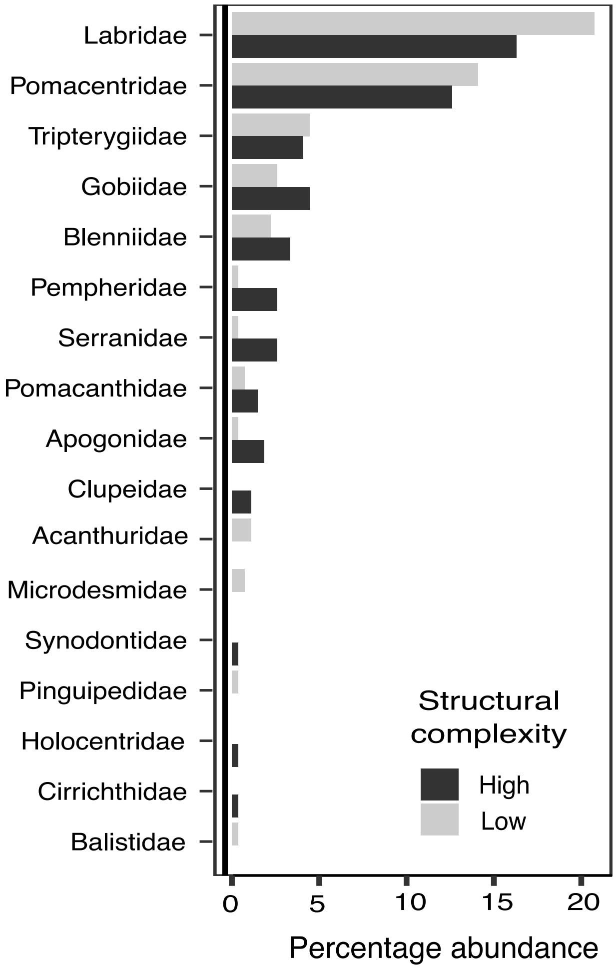
Appendix

Table A1. Grouper species and their behavioural classification, modified from Samoilys and Carlos, 2000 and Pears 2005.

Grouper species	Behavioural guild
Aethaloperca rogaa	site-attached
Cephalopholis argus	site-attached
Cephalopholis miniata	site-attached
Cephalopholis sexmaculata	site-attached
Epinephelis caeruleopunctatus	site-attached
Epinephelus fuscoguttatus	roving
Epinephelus macrospilos	site-attached
Epinephelus malabaricus	roving
Epinephelus polyphekadion	site-attached
Epinephelus spilotoceps	site-attached
Gracila albomarginata	roving
Plectropomus areolatus	roving
Plectropomus laevis	roving
Variola albomarginata	roving
Variola louti	roving



A1.Figure A1. Prey fish composition: Percentage abundance of potential prey fish (family) found in territories of 48 *C.argus* individuals

CHAPTER 4

Live strong, live short: peacock groupers trade-off longevity over body condition to persist in structurally degraded reefs

Juvenile coral hind (Cephalopholis miniata)

Abstract

Behavioural plasticity allows individuals to adjust and survive in rapidly degrading habitats, but can it ensure the long-term persistence of populations in sub-optimal habitats? Both costs and consequences of plasticity may impact population growth through their effects on individual lifespan and fitness. In the Lakshadweep archipelago peacock groupers (*Cephalopholis argus*) are highly widespread along structurally degraded reefs thanks to their flexible foraging behaviors. We studied the life-history and demographic consequences in the peacock grouper of persisting in degraded coral reefs by comparing areas where benthic reef structure has declined drastically since the 1998 bleaching event and areas that maintained their structure. We found that, on an average, peacock grouper growth rates did not differ between sites. Interestingly groupers were in better body condition in degraded reefs, gaining more mass (g) per length. The relative health of these individuals is most likely because of competitive release both from conspecifics and other competitors but could also represent a reallocation of resources linked to supporting a roving foraging strategy. However, surviving in these sub-optimal habitats came at a considerable life-history cost, reflected in a 20% reduction in mean longevity in degraded reefs. In degraded reefs, density was nearly 50% lower than that in high structured sites. In addition, sub populations in degraded reefs were characterized by a relatively lower proportion of juveniles indicative of bottlenecks to recruitment and a truncated age-distribution that is indicative of age-specific mortality. The apparently high adaptive capacity of species like the peacock grouper may mask significant life-history trade-offs with long-term demographic consequences. Although highly plastic species like the peacock grouper may be the only ones able to keep abreast with the contemporary rate of environmental change, the significant life-history costs suggest that there may be a limit to their plasticity. In the long run, high structured, stable reefs are critical in maintaining longer-lived, and potentially more fecund populations to repopulate increasingly degraded benthic habitats.

Keywords

Foraging plasticity, life-history trade-off, longevity, growth, demographic consequences, decline in habitat structure

Introduction

Human induced rapid environmental change (HIREC) is resulting in erratic global climatic irregularities that are modifying the physical structure and composition of ecosystems. Species responses to this change are highly variable, with some disproportionately affected than others (Vitousek et al., 1997;

Walther et al., 2002). HIREC takes place within the lifespans of individuals, subjecting them to novel or extreme environmental conditions. These conditions may challenge the evolutionary coping mechanisms of most species (Chevin et al., 2010; Hendry et al., 2008). In order to survive, phenotypic plasticity – the ability to show alternative phenotypes in response to environmental change – is a critical response buffering species from HIREC (Sih et al., 2011). By increasing fitness in multiple environments, phenotypic plasticity may enable species to widen their geographic range, aid in their dispersal and colonization of novel habitats and acclimatize to changing habitats (Parmesan 2006; Pigliucci et al., 2006; Walther et al., 2002). Thus, plastic species are better able to survive ecological catastrophes and avoid extinctions, owing to their ability to cope with a range of conditions.

Phenotypic plasticity can enable short-term survival for individuals under HIREC, but whether it can ensure long-term persistence of individuals and species populations is far from clear (DeWitt et al., 1998). Animals may show plasticity in a range of phenotypic traits – behaviour, physiology, morphology, life-history etc. Often the very first response a species shows under HIREC is behavioural – modifying foraging, mating, social, dispersal behaviours, among others (Sih et al., 2010). Behavioural responses are labile, instantaneously activated and reversible. Despite these short-term advantages however, behavioural plasticity is not ubiquitous across the animal kingdom, suggesting that it is a strategy that could incur significant costs (Auld et al., 2010; DeWitt et al., 1998). Plastic responses can be costly for the individual in at least two possible ways. Firstly, there can be costs of being plastic such as those associated with the production (the machinery that supports the behavioural response) and maintenance (ie. the physiological mechanisms sustaining a response over a prolonged period of time (DeWitt et al., 1998; Sih et al., 1985) of a behavioural phenotype. Secondly, there can be costs of expressing a suboptimal (or 'wrong') behaviour in a given environment (i.e. phenotype–environment mismatching). These costs may arise when the individual cannot reliably gather cues needed to elicit an appropriate response or is limited in doing so. In the long-term, these costs can effectively reduce individual fitness and survival, by modifying tradeoffs between growth, reproduction and mortality (Chevin et al., 2010), with repercussions for the population and community (Wong and Candolin, 2015). In order to evaluate the persistence of populations of plastic species in rapidly degrading habitats, it is therefore necessary to understand both the immediate and long-term consequences of behavioural plasticity.

Independent of a species' ability to be plastic, the success of a species population under HIREC can be influenced by the changing nature of ecological interactions in the habitat known as the ecological limits of plasticity (Valladares et al., 2007). Differential plasticities and tolerances to HIREC among interacting species may impact their responses to environmental change (Jiang and Morin, 2004; Visser et al., 2006). HIRECs often create ecological release for plastic species that track changing conditions better than their enemies or competitors (Agrawal, 2001). Under such conditions, erstwhile sub-dominant plastic species may become dominant in the community. The absence of natural enemies in a newly colonized region and decline in density-mediated effects, might facilitate enhanced physiological performance under extreme conditions, as has been suggested for invasive plant species (Richards et al., 2006). Therefore, the long-term success of species populations under HIREC depends on both the ability to be plastic but also the ecological context of the changing habitat.

Coral reefs are highly diverse ecosystems that have globally been subjected to dramatic and rapid declines in habitat structure due to multiple mass-bleaching catastrophes (Cheal et al., 2017). This decline in habitat structure has had a disproportionate consequence for long-lived and specialists benthic fish species (Alonso et al., 2015; Darling et al., 2017; Pratchett et al., 2008). The peacock grouper *(Cephalopholis argus)* is an exception, being a benthic grouper with a widespread distribution across the tropical Indo-pacific. It is found in a range of habitats (rocky substrates to coral rich reef), and is a highly competitive species across its native and non-native ranges (where it was introduced to boost local fisheries, Meyer, 2008; Pears, 2005; Shpigel and Fishelson, 1989;1999). More interestingly, under rapid reef structural declines in the Lakshadweep archipelago, this species has shown plasticity in foraging behavior, ie. the ability to switch foraging modes from structure-dependent (ambush) to structure-independent (roving) behaviours (Karkarey et al., 2017). This flexibility in foraging behaviours has potentially led to the species out-competing other less-flexible benthic mesopredators in degraded reefs, remaining one of the only benthic groupers inhabiting degraded reefs in Lakshadweep (Karkarey et al., 2017).

Thus, while this species appears to adapt to changing habitat conditions by foraging flexibly we do not know what (if any) the costs of these mechanisms are to the individuals and populations. In this study, we attempted to understand how surviving in degraded reefs impacts life-history traits of the behaviorally plastic peacock grouper and the population-level consequences of long-term persistence in degraded reefs. We do so by comparing life-history traits (growth, longevity, length-weight relationships) and demographic parameters (density, size and age-distribution) of sub-populations, between recently degraded reefs and reefs that have maintained their structure during the same period in the Lakshadweep archipelago.

Methods

Study species

The peacock grouper is a common benthic mesopredatory fish, found in coral reefs across the tropical Indo-Pacific (Lieske and Myers, 2002). This species is known to dominate a range of reef habitats and depths in native and non-native reefs across the Indo-Pacific (Dierking et al., 2009; Meyer and Dierking, 2011). Peacock groupers are protogynous hermaphrodites, that live in harem groups and maintain permanent territories in reefs after settlement as juveniles (Shpigel and Fishelson, 1999). The peacock grouper is a highly adaptable species, dominating the assemblage in native and introduced reefs in Hawaii, where it has displaced native mesopredators (Donovan et al., 2013; Meyer and Dierking, 2011). It shows high variability in diet, habitat preference and demography within and between populations across small and regional spatial scales (Dierking et al., 2009; Donovan et al., 2013; Hempson et al., 2017; Meyer et al., 2008; Pears, 2005; Schemmel et al., 2016).

Our previous research from the Lakshadweep Archipelago showed that peacock groupers have highly plastic foraging behaviours, with an ability to switch between contrasting ambush and widely-foraging modes as habitat structure declines. Despite differences in prey availability, this flexibility has enabled the peacock groupers to maintain a stable diet in Lakshadweep reefs (Karkarey et al., 2017). In this study, we compare life-history parameters (growth, longevity, length-weight relationships) and demographic parameters (size and age-distribution, density) of sub-populations of peacock groupers, between recently degraded reefs and healthy reefs in the Lakshadweep archipelago, to understand the consequences of surviving in degraded reefs.

Study area and site

The Lakshadweep Archipelago, Indian Ocean, comprises 12 coral atolls enclosing 33 small islands (10.6°N 72.6°E). The archipelago has witnessed repeated temperature-associated mass bleaching disturbances since 1998 (Arthur et al., 2006), with catastrophic consequences for reef structural complexity, which has considerably reduced over the last decade (Karkarey et al., 2014; Yadav et al., 2016). This study was conducted in the centrally located Kadmat atoll, which has a land area of 32 km^2 and is surrounded by a large lagoon of 37 m^2 area, with a contiguous fringing outer reef. This archipelago is characterized by relatively low reef fishing pressure that allows for comparisons mostly based on climate-related effects on fish communities (Alonso et al., 2015). We based our study in Kadmat because the reefs span a large range of reef conditions (Arthur et al., 2006). This allows for a useful comparison of peacock grouper sub-populations between flat-barren reefs to reefs of high structural complexity. The field component of this study was conducted between January-March 2015. Lab and data analysis followed between September 2015- 2016.

Study design

We selected nine reef sites around the Kadmat atoll for this study (see Figure 1, Chapter 3). Sites were classified as having 'high' and 'low' structure, based on a mean coral canopy height of 60cm. In our last Chapters (Chapter 2 and 3), we found this threshold of canopy structure to be critical to support the abundance of long-lived groupers in the region (Karkarey et al., 2014; 2017).

Sample collections and lab analyses

In Chapter 3, we studied the foraging flexibility of peacock grouper in sites of high and low structure by conducting underwater focal video sampling and comparing the frequency of foraging modes (ambush vs widely-foraging models). Similarly 72 individuals were collected to study diets across the sampled sites. The methods of estimating foraging flexibility and diet have been detailed in Chapter 3, Methods sections and are thus not repeated in this Chapter. In this study, we explore the potential costs of persisting in degraded reefs by comparing the life-history traits (size, age, growth, longevity, length-weight relationships) and demographic parameters (age-distribution, density) between sub-populations of peacock groupers, in sites of high and low structural complexity. Most of the variables related to demographics (size-distribution and density) were obtained with *in situ* observations (visual transects). In contrast, the variables related to life-history traits (age, growth, longevity and length-weight ratio) were obtained from collected samples.

In situ observations

At each site, we swam four 5 x 50 m belt transects at a constant and slow speed, collecting information on the abundance and size (cm) of peacock groupers. The first author (R.K.) estimated fish sizes to the nearest cm after considerable prior training with test models in field conditions. We estimated fish density per transect as the number of fish sighted per 500m^2, and we averaged densities across four transects to estimate mean site-level density. A total of 24 transects (low structured sites: n=12, high structure sites n=12) were conducted in February/March 2015. Biomass was estimated by converting individual lengths into biomass (g) based on site-specific length-weight relationships described and estimated in the section below.

Animal Collections

We collected 72 individuals across the nine sites where behavioural sampling reported in Chapter 3 was conducted. Samples were collected using traditional spearguns on snorkel (see ethical note below). We targeted a minimum number of individuals per site (n=8-10), to get a representative sample of the population across their size range (minimum 10cm to maximum 42cm). Fish samples from high and low structured sites (see above) were pooled since sample sizes from each individual sites were too low to permit a demographic study of each subpopulation. Once collected specimens were weighed (g), total body length was measured (mm) and then transferred to the wet laboratory for processing. In the laboratory, otoliths were collected from each individual, dried in the sun and stored in paper envelopes.

Lab analysis

Otolith reading: Otolith processing followed methods described by Choat and Axe (1996) with the exception that sagitta were not embedded but mounted. The left otolith was used for ageing, unless missing or damaged. The sagitta was mounted in thermoplastic glue (CrystalBond) on the edge of a glass microscopy slide. A transverse section containing the nucleus was obtained by grinding down by hand both rostral and distal ends of the otolith using wet lapping film (50 – 30 microns). Each section was then covered with clear Crystalbond thermoplastic and polished down with 12-1 micron before reading. Each otolith was viewed with a transmitted light microscope under 10-100x magnification. One pair of sequential light and dark bands was assumed to form once-yearly; these were counted by one observer (Dr. Nuria Raventos) on three different occasions. In the case where counts were <10% different, the median was used for analysis. In the case of a disputed age (>10%), the annuli were recounted, and if consensus was not possible, the otolith was excluded from analysis.). Analysis of otoliths has been conducted for the peacock grouper previously in the Great Barrier Reef, which satisfied the three criteria for estimating age from otolith microstructure (Pears, 2005): 1. Otoliths displayed an internal structure of increments 2. Otolith increments were predictably related to a regular (annual) period of formation and 3. Otoliths grew throughout the life of individual fish.

Statistical Analysis

1. Life-history traits

a. *Comparing growth rates between reefs of high and low structural complexity*

Growth curves were generated using size-at-age data generated from the otoliths at each location (high and low structure) using a re-parameterized von Bertalanffy growth function (rVBGF, Francis, 1988). The equation represents a logistic growth curve, which estimates growth at three candidate ages. The growth equation is as follows:

$$L(t) = L(\tau) + (L(\mu) - L(\tau)) \times [1 - r^2((t - \tau)/(\mu - \tau))]/(1 - r^2)$$

where , $\boldsymbol{r} = \boldsymbol{L}(\mu) - \boldsymbol{L}(\omega)$ and L(t) is the average size-at age *t* to be predicted by the model.   and

Parameters L(τ), L(ω), and L(μ) are estimated from the average body size at three arbitrary ages τ, ω, and μ. Values for τ and μ were chosen to represent points during in the juvenile and adult growth phases. In this case, τ=2 years and μ=15 were selected, to also make this study comparable to another study from Hawaii (Meyer et al., 2008). Peacock groupers show ontogenetic habitats shifts, where juveniles grow in sheltered back-reef areas for the first few months and typically migrate to fore reef areas ~1 year. We assume that our model represents post-transition growth in the peacock grouper, since we were unable to catch individuals < 1 yr. Since our aim was to compare growth curves between high and low structured sites, we started with a global model varying the three length parameters by the factor of structure (high and low). The global model was simplified using sequential tests, based on evaluation of AICs (Bolker, 2007). We checked for model assumptions by visually inspecting the distribution of residuals.

b. Comparing length-weight relationship between reefs of high and low structural complexity

The allometric length and weight relation of a fish is used by fisheries researchers and managers for two main purposes. First, the relationship is used to predict the weight from the length of a fish and useful for computing the biomass of a sample of fish from the length-frequency of that sample. Second, the parameter estimates of the relationship for a population of fish can be compared to average parameters for the region, previous years, or among populations, to identify the relative condition of the population. We evaluated this relationship to estimate individual biomass and to compare condition of subpopulations between high and low structured sites. The relationship between fish total length (TL) and fish total weight (TW) is described by a power equation, where W is weight of fish in grams, TL is the total length of the fish in cm, a and b are parameters to be estimated. a is considered to be scaling constant characterizing the shape of the individual and b (also known as the allometry coefficient) has an important biological meaning, indicating the rate at which weight increases for a given increase in length. Mean parameter values for the above allometric equation with their corresponding bootstrapped (n=1000 iterations) 95% CI were estimated for groups of fish in high and low structured sites, using an iterative non-linear, least squares method for grouped factors within the R package *nlme* (Pinheiro et al., 2017) and *nlshelper* (Duursma, 2017). We compared models with and without 'structure' as a grouping variable and selected the best model between the two based on a Likelihood Ratio test. We checked for model assumptions by visually inspecting the distribution of residuals.

c. Mean size, age and longevity between reefs of high and low structural complexity

We estimated means of different life-history and demographic variables (Summarized in Table 1) for each subpopulation. We calculated 95% bootstrapped CIs, generated by resampling data with replacement over 1000 iterations to compare group means between high and low structured sites (Bolker, 2007). If the means of one group did not fall within the 95% confidence intervals of the mean of the other, we considered the populations to be significantly different. Bootstrapping was conducted using the R package, *boot* (Canty and Ripley, 2017).

Underwater size and age data from collected samples were used to estimate mean size and age respectively of sub-populations in high and low structured sites. The mean size of the largest 20% of individuals sampled (mean max size) was used as a measure of maximum fish size. Longevity (tmax) and maximum length (lmax) was calculated as the mean age and size of the oldest 20% of individuals for high and low structured sites (Gust, et al., 2002).

2. Demography

a. Comparing demographic variables between high and low structural complexity

A suite of demographic parameters were examined to characterize the subpopulations in both high and low structured sites, summarized in Table 1. Length (N_L) and Age (N_A) richness were used as proxies for size and age frequency distributions of the subpopulations (Pears, 2005), and estimated as the number of length (5 cm) and age (year) groups for sites of high and low structure. Mean density and biomass for high and low structured sites was estimated from in situ transects.

b. Population size and age structure between high and low structured sites.

We plotted age-frequency and length-frequency distributions for visual comparison of populations in high and low structured sites.

Ethical Note

The study was conducted with appropriate research permits and clearances granted by the Department of Science and Technology, Lakshadweep. The peacock grouper is not an endangered species, nor a 'Scheduled' species as per the Wildlife Protection Act of India, 1972. Spearfishing was conducted to effect capture of the target species and size classes of interest, while minimizing harm to non-target species and habitats, which other fishing methods (hook and line and cages) entailed. Identified specimens were speared using locally available, traditional spear guns by experienced personnel. Specimens were rapidly transferred upon capture to a freshwater ice slurry to aid anaesthesia followed by percussive stunning, considered to be a highly effective and humane technique adopted by research and fisheries in Europe and Australia (Blessing et al., 2010; National Health and Medical Research Council, 2008). Percussive stunning was administered by a trained and skilled local fisherman. To avoid additional killings, whole specimens were processed for stable isotopes, guts (as reported in Karkarey et al., 2017, Chapter 3) and for extracting otoliths and other physiological parameters (this Chapter).

Table 1: Demographic and life-history parameters estimated for peacock grouper subpopulations in high and low structured sites.

Demographic and life-history parameters	**Code**
Length richness – number of size classes (5cm bins) represented in underwater samples	N_L
Age richness – number of ages represented in collected samples	N_A
Mean density from underwater visual surveys	Density
Biomass – mean biomass of individuals sampled per site per transect	Biomass
Mean size across all individuals sampled underwater	Mean size underwater
Mean age of collected individuals	Mean age
Mean max size of largest 20% of individuals sampled underwater	Mean max size
Mean age of oldest 20% of collected individuals	Longevity

Results

Life-history traits

Of the 72 samples of peacock groupers collected from high and low structured sites, all were used in size-at-age analysis. Individuals ranged in length from 10 to 39 cm and in age from 1.5 to 27 years.

a. Growth rates

Model simplification showed that the relationship between age and length was consistent across sites of high and low structure (Figure 1, Table 2.a). Growth at the three candidate ages (year 2, 10 and 15), which signifies growth during the fast (juvenile) and slow (adult) phases of the life of the grouper, did not vary between high and low structure sites (Table 2.b).

Figure 1. Growth curves of peacock grouper subpopulations in high (black) and low (blue) structured sites.

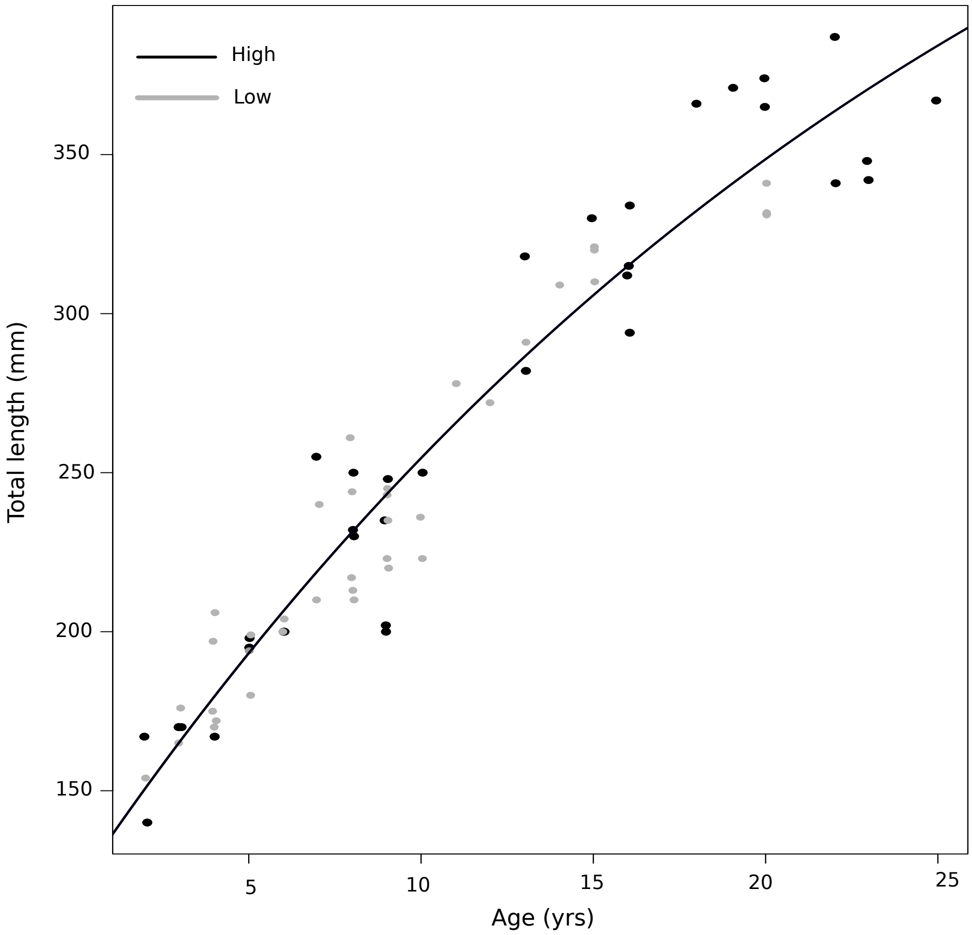


Table 2.a. AIC differences between candidate growth models

Model	**df**	**AIC**	**Delta**	**LL**	**Akaikes.w**
Global	7	620.570	4.664	0.097	0.034
Global vs Common L1	6	619.469	3.564	0.168	0.059
Global vs Common L2	6	619.534	3.628	0.163	0.057
Global vs Common L3	6	618.924	3.019	0.221	0.077
Global vs Common L1L2	5	617.744	1.838	0.399	0.139
Global vs Common L2L3	5	617.581	1.675	0.433	0.151
Global vs Common L1L3	5	617.800	1.894	0.388	0.135
Global vs Model with all parameters in common	4	613.906	0.000	1.000	0.349
Global vs Model with all parameters in common	4	613.906	0.000	1.000	0.349

* **Global model defined as** : Length~L1[structure]+(L3[structure]-L1[structure])*(1-((L3[structure]-L2[structure])/(L2[structure]-L1[structure]))^(2*(Age-t1)/(t3-t1)))/(1-((L3[structure]-L2[structure])/(L2[structure]-L1[structure]))^2), where L1, L2 and L3 is length at age 2,10 and 15 years respectively.

Table 2.b. rVGBF parameters, L1, L2 and L2, estimated at ages= 2, 10 and 15 years for peacock groupers.

Length parameter (age, years)	Estimate (mm)	Standard error	t	Pr(>ltl)	95% bootstrapped CIs	
					Low	High
L1 (2)	150.794	5.617	26.84	<0.005	139.618	160.939
L2 (10)	237.315	2.831	83.82	<0.005	232.08	243.043
L3 (15)	305.782	3.163	96.67	<0.005	299.709	311.938

b. Length-weight relationships

A strong weight-at-length relationship was observed, with significant differences between high and low structured sites (Figure.2, Table 3.a). In low structured sites, fish were of a better body condition than at high structured sites (Table 3.b, Figure.2).

Figure 2. Allometric length x weight relationships of peacock grouper sub populations in high and low structured sites.

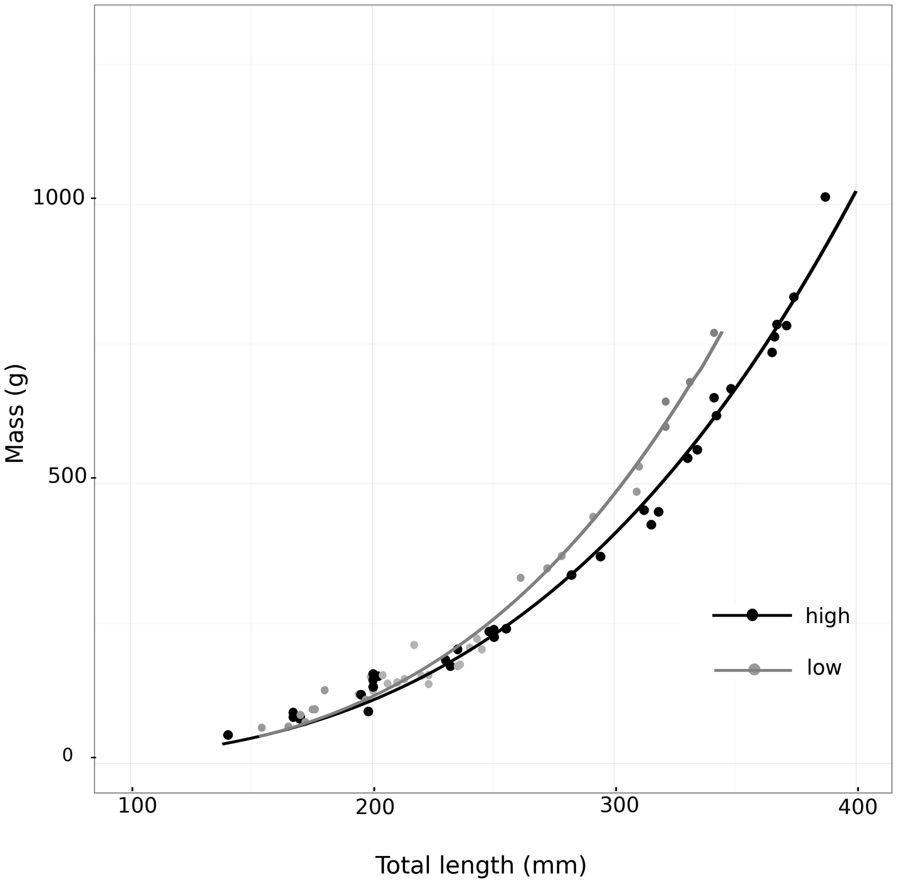


Table 3: a. Likelihood Ratio test between model of length x weight relationship with and without structure as a grouping variable

Model	**Residual sum of squares (RSS)**	**Df**	**Sums of square**	**F-statistic**	**Pr(>F)**
W~ *a* (structure) x L ^ *b* (structure)	98323	69			
W~ *a* x L ^ *b*	45010	67	53314	39.681	<0.0005

Table 3: b. Mean *a* and *b* parameter estimates (95% bootstrapped CI's) of the relationship, in high and low structured sites.

Structure	Parameter	Mean	Standard error	95% bootstrapped CIs	
				Low	High
High	a*	0.0000054	0.0000026	0.0000019	0.0000145
	b	3.1799280	0.0817081	3.0100000	3.3572190
Low	a*	0.0000015	0.0000008	0.0000005	0.0000041
	b	3.4320500	0.0868838	3.2556080	3.6155860

c. Size, age and longevity

Average size and age did not vary between high and low structured sites. However, average longevity declined by 20% in low structured sites. The maximum size of individuals in low structured sites was 10% smaller than in high structured sites (Table 4).

Table 4. Mean demographic and life-history parameters 95% CI of peacock grouper sub populations in high and low structured sites.

Variables	Mean (±95% bootstrapped CI)	
	High structure	Low structure
Mean size	20.18 (18.06 – 22.46)	19.12 (17.142 – 21.28)
Mean age	12 (10 – 14) 9	8 (7 – 10)
Mean max size	38.81 (38.0 – 40.3)	35 (34.428 – 36.714)
Longevity *	22 (21– 23)	16(14 - 18)
NL*	8	7
NA*	6	6
Density	7.367 (5.583 - 9.833)	3.437 (2.8 - 4.39)
Biomass	261.836 (116.647- 451.149)	220.719 (111.039 - 350.789)

Demographic parameters

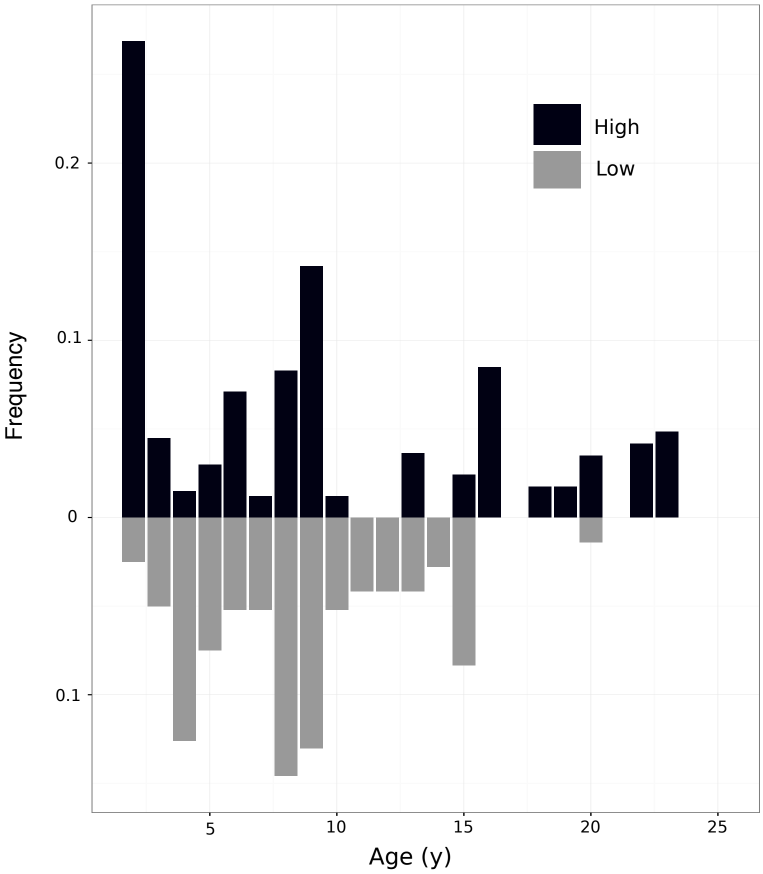
a. Population density and biomass

Population density of peacock groupers in low structured sites was half of that in high structured sites. Average biomass per 500m² did not vary between sites (Table 4). The size and age richness did not vary between high and low structured sites (Table 4)

b. Population age and size-structure

Low structured sites had a higher frequency of individuals between ages 4 – 9 years than high structured sites. Most individuals in low structured sites were <15 years in age, while only a few individuals were aged at 20 years (n=3, Figure 3). High structured sites had a greater proportion of large sized and older (>15 years) individuals compared to low structured sites (Figure 3, 4). The oldest individual we sampled was 26.5 years old found in high structured sites, 7 years older than the oldest in low structured sites. High structured sites were also characterized by a higher frequency of small juveniles (0-5cm, and < 4 year age-classes) compared to low structured sites (Figure 3 and 4).

Figure 3. Age-frequency distributions from sites of high (n=4) and low (n=4) structural complexity. Data from 72 individuals.



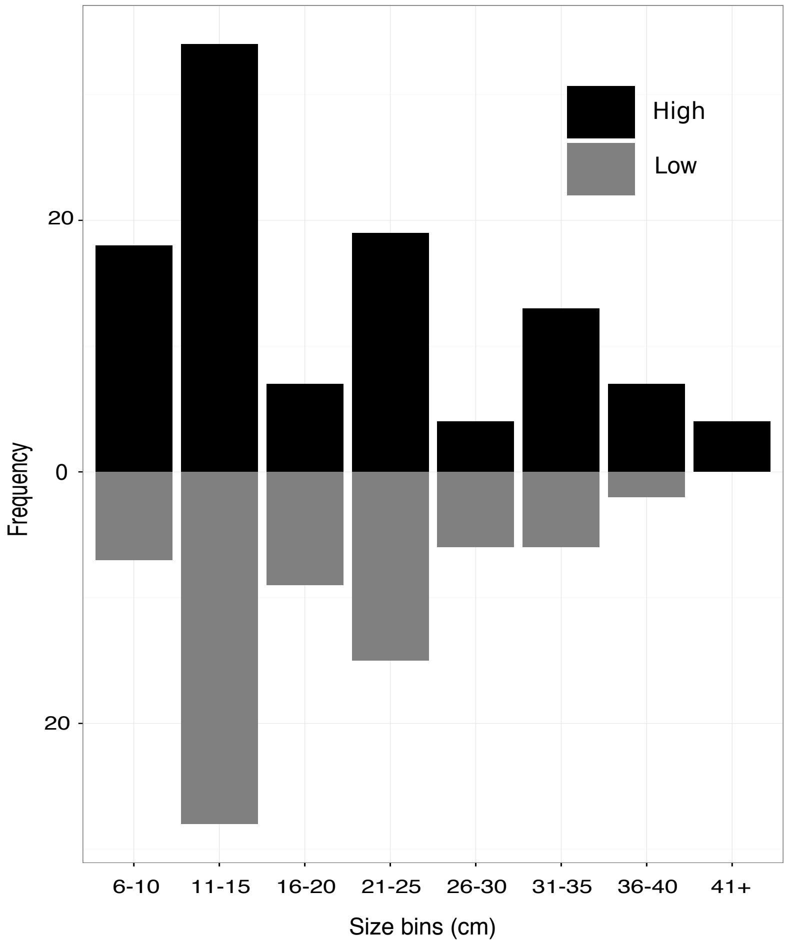


Figure 4. Length-frequency distributions from sites of high (n=4) and low (n=4) structural complexity. Data from a total of 24 transects.

Discussion

Although foraging plasticity enables species like the peacock groupers to survive in rapidly degrading habitats, it may not stave off population declines. Despite habitat degradation, peacock groupers appear to maintain their growth rates. Interestingly, individuals of a given length appear to weigh more in degraded reefs, indicative of a higher body condition. However, surviving in these sub-optimal habitats appears to come at a considerable life-history cost, reflected in nearly a 20% reduction in mean longevity. The maximum size of individuals was also 10% lower in low structured sites. The consequences for population dynamics were observed in the density and age-distribution of sub-populations in high and low structured sites. In degraded sites, the density of peacock grouper was nearly half that in high-structured sites. In particular, high structured sites had a comparatively higher proportion of juveniles less than 2 and adults greater than 15 years of age compared to low structured sites. The latter sites were characterized by a truncated age-distribution, indicative of high mortality of both the smaller and larger size-classes. It appears that the life-history costs of plasticity and bottlenecks to important population processes (recruitment) are likely driving an overall decline in populations of the peacock grouper in reefs under HIRECs in the Lakshadweep.

Behavioural plasticity is often adaptive, generally improving the fitness of individuals compared to non-plastic species in changing habitats as evidenced from a number of urban adapter species and invasive species (Lowry et al., 2013; Sol et al., 2013; Sol et al., 2002). However, even small changes in the environment can have substantial effects on competitive interactions because species differ in their optimal niches, plasticity and tolerance levels (Gherardi, 2013; Valladares et al., 2007; Visser et al., 2006). In the case of the peacock grouper, plasticity in foraging behaviours enables individuals to forage independently of structure in degraded reefs and maintain stable diets (Chapter 3). Thus it appears that foraging plasticity is potentially enabling the species to out-compete other benthic and roving species that have may more restricted foraging repertoires (Karkarey et al., 2017, Chapter 3).

Interestingly we observed a non-intuitive pattern in this study, where peacock groupers that survived to adulthood had a better body condition in low structured sites. Several non-exclusive factors could be operating to produce this counter-intuitive pattern. Firstly, ecological release from competitors as we discuss above could be influencing patterns of resource acquisition, such that peacock groupers are able to maintain stable diets, under lower density-dependent pressures of competition and predation in degraded habitats. Similarly, the higher body mass per unit length in low structured sites could represent a larger investment in musculature, to support a more active foraging strategy to acquire food (Huey and Pianka, 1982; Vanhooydonck et al., 2002; Webb, 1984). Whether this resource allocation comes at the cost of investment in reproduction is not something we could establish in this study. A central understanding in life history theory is that there are essential trade-offs in resource allocation between somatic growth, reproduction and mortality (Stearns, 1992). Fish species with indeterminate growth typically experience a trade-off in resource allocation between reproduction and somatic growth throughout their lives (Roff, 1983). Because fecundity can increase ten-fold with body size in animals showing indeterminate growth, individuals may trade-off current and future reproductive success (Warner, 1984). To complicate this further, the peacock grouper is a protogynous sex-changing and harem-living species, and social dominance hierarchies can strongly impact individual growth rates and fitness (Schemmel et al., 2016). Therefore, to understand fitness-associated costs, we need to evaluate lifetime fitness in individuals, which was beyond the scope of this study.

Plastic behavioural responses can sometimes also be maladaptive when they alter key demographic rates (Van Buskirk and Steiner, 2009). An important life-history trade-off is observed between growth and lifespan, such that faster growing individuals typically have shorter lifespans (Metcalfe and Monaghan, 2003). Often animals show 'catch-up or compensatory growth, where individuals that have experienced a period of poor nutrition and slower growth subsequently exhibit a phase of very rapid growth once conditions improve. Consequently, different individuals can attain similar body sizes that are near or even higher to those of the normally growing conspecifics within the same time frame (Metcalfe and Monaghan, 2001). Compensatory growth is a mechanism that is clearly linked to lowering individual lifespans in fish, through long-term effects on the phenotype (higher metabolism, oxidative stress and senescence (Jennings et al., 2000; Pike et al., 2007) and increased foraging frequency leading to starvation and/or greater exposure to predators (Gotthard, 2000). Our previous study has established clear differences in the diet of juvenile peacock groupers (<10 cm) in structurally degraded and healthy reefs (Chapter 3). Adults on the other hand, appear to maintain stable diets even in degraded reefs. It is likely that individuals beyond a particular size-threshold are able to forage flexibly, and may therefore show compensatory somatic growth as suggested by the elevated body condition in structurally degraded reefs in this study. A larger sample-size from the population, particularly of juveniles with divergent diets could improve our understanding of compensatory growth as a potential mechanism of declining longevity of peacock groupers in degraded reefs. It should be noted that fishing is still a relatively low pressure in Lakshadweep and groupers are rarely targeted as food-fish, thus the effect of fishing on the demographic patterns we observe in Kadmat is likely to be negligible.

While we were unable to address the fitness-related costs of living in sub-optimal habitats, it is likely that reduced longevity and maximum size may be influencing the timing of sex-change in peacock groupers, with consequences for fitness and overall reproductive output. The timing of sex-change in species can be highly variable and depend on ecological factors, social interactions and mortality rates

(Munday et al., 2006). In Hawaii, peacock groupers were found to attain maturity at ~20 cm length (~2 years) and change sex from females to males at ~39 cm (11 years, Schemmel et al., 2016). In our study, low structured sites had a very low frequency of individuals larger than 30 cm compared to high structured sites. In addition, the maximum size of individuals was nearly 10% smaller in low structured sites, suggesting that there could be selective mortality of larger individuals. However, without further studies, we can only speculate of these patterns. Our work aligns with other studies of the peacock grouper from Hawaii, the Great Barrier Reef, Seychelles and the Red Sea (Donovan et al., 2013; Pears, 2005), which show that growth rates and demography of the peacock groupers can be highly variable at small, large and regional spatial scales, within and between populations, in relation to habitat and environmental disturbances.

Our results indicate that structural degradation can have indirect and long-term consequences for behaviorally plastic benthic species like peacock groupers, by modifying trade-offs associated with growth, lifespan and potentially with fitness. However, structure can also have a strong direct impact on populations, by influencing recruitment and settlement processes. Coral structure is used as settlement cues by fish recruits (Coker et al., 2012) and can strongly determine settlement success by mediating predation of early life-stages (Almany and Webster, 2006). In degraded reefs, we see a very low proportion of < 2 year-old juveniles, suggestive of bottlenecks in either recruitment or settlement processes in these habitats. These patterns suggest that foraging behavioural adaptations to structural degradation may not sufficiently be able to buffer species against the direct impacts to population processes.

Taken together, behavioural plasticity can enable species to adjust immediately to degrading habitat structure, but may not necessarily ensure long-term population viability. We concur with several studies that behavioural responses may not always be beneficial, if they come at the cost of lifespan and fitness and may not be adequate enough to buffer direct effects of the environment on population processes. Our study shows that a rapid structural decline of habitats is likely to be a more serious issue than believed, considering it can have insidious consequences for even highly adaptable species like the peacock grouper. As HIREC progressively create mosaics of high and low structured reefs in coral reef ecosystems, high structured reefs appear to be critical refugia for benthic species like the peacock groupers. By supporting individuals that are long-lived, potentially of higher fecundity, and by maintaining vital recruitment and settlement processes, high structured sites are becoming increasingly critical habitats for marine conservation under the influence of contemporary human-induced environmental disturbances

CHAPTER 5

Alternative reproductive tactics and inverse size-assortment in a high-density, unfished fish spawning aggregation

Male Squaretail groupers (Plectropomus areolatus), fighting at the aggregation site

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Abstract

Background: At high densities, terrestrial and marine species often employ alternate reproductive tactics (ARTs) to maximize reproductive benefits. We describe ARTs in a high-density and unfished spawning aggregation of the squaretail grouper (*Plectropomus areolatus*) in Lakshadweep, India.

Results: As previously reported for this species, territorial males engage in pair-courtship, which is associated with a pair-spawning tactic. Here, we document a previously unreported school-courtship tactic; where territorial males court multiple females in mid-water schools, which appears to culminate in a unique 'school-spawning' tactic. Courtship tactics were conditional on body size, local mate density and habitat, likely associated with changing trade-offs between potential mating opportunities and intra-sexual competition. Counter-intuitively, the aggregation showed a habitat-specific inverse size-assortment: large males courted small females on the reef slope while small males courted equal-sized or larger females on the shelf. These patterns remained stable across two years of observation at high, unfished densities.

Conclusions: These unique density-dependent behaviours may disappear from this aggregation as overall densities decline due to increasing commercial fishing pressure, with potentially large consequences for demographics and fitness.

Keywords

Spawning aggregation, High mating density, Alternative reproductive tactics, Shoal and pair courtship tactics, Inverse size-assortment, Squaretail grouper

Introduction

Ensuring reproductive success in competitive high density populations often requires individuals to adopt innovative mating strategies. Reproductive strategies are strongly mediated by density—i.e. the number of potential mates (local mate density) as well as the overall population density (Emlen and Oring, 1977; Koko and Rankin, 2006). High local mate density in a population increases competition for mates. Under these circumstances, if a few individuals are able to monopolize mates, most others will have little success (Shuster and Wade, 2003). This skew in reproductive success often selects for multiple male and female phenotypes or alternative ways of acquiring reproductive benefits, commonly known as alternative reproductive tactics (ARTs, Brockmann, 2001).

Overall population densities may impact alternative reproductive strategies in a population in unpredictable ways (Kokko and Rankin, 2004). For example, high-density conditions could result in significant density-dependent effects such as space limitation and the inability of competitors to fight off multiple intruders (Emlen and Oring, 1977). This may lead to a breakdown in mate monopoly (Reichard et al., 2004), lowering the reproductive skew in a population and consequently suppressing the expression of ARTs (Tomkins and Brown, 2004). However, increasing population density may trigger variations in mate choice (Berglund, 1995; Jennions and Petrie 1997), which may serve to increase reproductive skew and select for costly, novel or elaborate ARTs (Kokko and Rankin, 2004; Mills and Reynolds, 2003; Brockmann et al., 2008). Across multiple taxa, large male size is favoured, either through male-male competition or female choice, with little selection on female size (e.g. fish (Howard et al., 1998); mammals (Charlton et al., 2007; Lindenfors et al., 2007). However, in some taxa (Clutton-Brock, 2009; van den Berghe 1989; Jiang et al., 2013), males also show a preference for large females, resulting in mating pairs where male and female sizes are positively correlated ('size assortment', Jiang at al., 2013). The overall population density can impact the strength of sexual selection on male and female traits through its effects on intra-sexual competition (Crespi 1989).

Animal mating aggregations lie at one extreme of the density spectrum, and can provide valuable insights in understanding size-selection and mating systems in high-density conditions. Fish spawning aggregations are ideal systems to study this relationship because several species spawn in spatially and temporally explicit aggregations that often attain very high densities (Aguilar-Perera, 2006). A rich body of literature dating back to Aristotle (Atz, 1964) has shown that fish have highly variable and flexible mating modes, ranging from pair-spawning and group-spawning tactics, demersal and broadcast spawning tactics, to gonochorism and hermaphroditism (Taborsky, 2008; Oliveira et al., 2008; Johannes, 1978; Petersen, 1990; Henson and Warner, 1997; Taborsky, 1998; de Mitcheson Sadovy, 2008; Choat, 2012). In addition, fish show some of the strongest tendencies for positive size-assortment among animal taxa (Jiang et al., 2013). Fish mating systems can vary considerably between closely related species or even regional populations of the same species (Warner and Hoffman, 1980). These differences are often context (habitat, local density) and condition (body size, age) dependent (Taborsky, 2008; de Mitcheson Sadovy, 2008; Erisman and Hastings, 2011). In the absence of adequate field data for many aggregating fish species, we often rely on generalisations of mating behaviour from closely-related species or populations from better-studied regions. Moreover, 'pristine' or unfished fish spawning aggregations are rare in the wild, and this is particularly true of large-bodied and commercially important marine fish species (Rowe and Hutchings, 2013), impeding our understanding of how many species behave under natural high-density conditions.

Groupers (Teleostei: Epinephelidae: *Epinephelini,* Craig and Hastings, 2007) are large-bodied fish, ubiquitous to coral reefs. They are functionally important predators, and many species form high-density spawning aggregations (de Mitcheson Sadovy, 2001). Groupers possess complex mating systems with several sex-changing species (de Mitcheson Sadovy, 2008; Erisman et al., 2008a; 2008b). Reproductive strategies and sex change patterns in groupers can be strongly mediated by local mate density and overall population density (Erisman et al., 2008b; Liu and Sadovy., 2004). However, because groupers are highly prized food fish (de Mitcheson Sadovy et al., 2008), their spawning aggregations are heavily targeted by commercial fisheries (de Mitcheson Sadovy et al., 2013). Fishing can severely alter population density and the size-structure of a spawning aggregation (Domeier and Colin, 1997; Rowe and Hutchings, 2003; Coleman et al., 1996; de Mitcheson and Erisman, 2012) potentially affecting the mating system. Unfished spawning aggregations, where they still persist, can therefore provide critical baselines and novel insights into grouper mating systems under rare, natural high-density conditions.

The squaretail grouper (*Plectropomus areolatus*) is a common plectropomid species found across the Indo-Pacific region. Previous work observed *P. areolatus* using a pair-spawning tactic where principally large males establish and defend territories at the aggregation site, which are then visited by gravid females (Johannes et al., 1999; Pet et al., 2005). Males court females within their territories and this is associated with pair-spawning just above the male's territory. In 2011, we documented an unfished, high-density aggregation of the squaretail grouper at a remote atoll in Lakshadweep, India. Our observations reveal an additional school-associated courtship tactic, distinct from earlier reports in the literature for this species. We describe this novel courtship tactic as school-courtship, and suggest that this leads to a unique school-spawning tactic in high-density *P. areolatus* spawning aggregations.

Few studies have described ARTs in grouper spawning aggregations (Erisman and Hastings, 2011; Erisman et al., 2009; Johannes et al., 1999; Pet et al., 2005) and to our knowledge, no studies have evaluated ARTs in plectropomid species. Here, in addition to describing a unique spawning tactic, we examine and evaluate ARTs in an unfished, high-density squaretail grouper spawning aggregation over two years (2013 and 2014). Specifically, we evaluate (1) male and female preference for body size (size-assortment) in the two habitats (shelf and slope), by examining their relative spatial distributions. (2) The frequency of two distinct male courtship tactics in the two habitats, and describe how these potentially lead to two alternative spawning tactics and (3) the potential costs and benefits associated with the different courtship tactics.

Methods

Study area and site

The study was conducted in Bitra, a remote atoll in the northern Lakshadweep archipelago. The archipelago lies roughly 400 km off the state of Kerala, along the south-west coast of India. Bitra has a small island (0.105 km^2 area), with a community of less than 200 people. The atoll encloses a large lagoon of 46.51 km^2 surrounded by coral reefs. Until recently, local fishing in Bitra and other atolls has been largely an artisanal enterprise, mainly targeting offshore tuna stocks (Karkarey et al., 2014). Our study was conducted in 2013 and 2014, prior to which there was relatively low reef fishing pressure in Bitra. During the course of our study there was a complete administrative ban on fishing activities on Bitra's reefs during the aggregation period. Due to the remote location of the island and associated logistical challenges, we were able to survey Bitra only opportunistically since 1998 (n = 6 years, 1998, 2011– 2015) between the months of December–April. Based on these opportunistic surveys and local fishermen interviews, the study was conducted in the new moon of January (2013 and 2014), around peak aggregation densities. In 2012, we demarcated the boundaries of the aggregation site based on the presence of territory-holding males, by surveying the area on SCUBA and snorkel. The area of the aggregation was estimated to be approximately 40,000 m^2 comprising a contiguous stretch of reef separated by sand patches. The site can broadly be divided into two habitats, reef shelf and reef slope. The reef shelf starts at a depth of 6 m sloping gently to 11 m where it transitions to a steep reef slope. The reef shelf stretches nearly 170 m in breadth. The reef slope begins at a depth of 11 m descending sharply at an approximately 45° angle, to sand at 20 m. The reef shelf and slope at the aggregation site were very similar in terms of benthic coral structure, dominated by large Porites and Diploastrea boulders.

Study design

Annual aggregation density

Across the Indo-Pacific, densities of *P. areolatus* aggregations peak either on the day of the new moon or full moon (Russell and Muller, 2015). In Bitra, this species appears to spawn over the new moon (RK, RA, AZ, personal observations). We surveyed the aggregation annually for 5 days (2 days of waning crescent, new moon and 2 days of waxing crescent) during the new moon lunar phase in January/February of each year, based on our prior observations of the build-up of numbers and duration of the aggregation. Sampling was focused in a core area of approximately 2500 m^2, which covered 6.5% of the total aggregation area (40,000 m^2). The densest part of the aggregation or the 'core aggregation area' (Rhodes and Sadovy, 2002) was defined as the area within which large female schools roved during the aggregation period (Johannes et al., 1999). In this core area, we established 5 permanent belt transects (50 m x 10 m, 2 slope and 3 shelf transects), following methodology in (Colin et al., 2003). Transects were placed 10 m apart. Transects on the slope and shelf were placed parallel to one another with a minimum distance of 25 m between them. The vertical extent of the sampling area was approximately 5 m, based on movement of fish in the water column. We surveyed these transects every day over the 5 day period in 2013 and 2014, during low tide and compared new moon peak densities from sampling surveys conducted in 2013 (10th February) and 2014 (30th January). Transects were swum by two observers, and a mean of total count of individuals taken by each observer in a volume of 2500 m^3 was used as transect density. Mean (± SE) annual core density was estimated from transect densities (n = 10 transects, 5 transects x 2 years), for surveys conducted on peak days in 2013 (10th February) and 2014 (30th January).

Male and female density distribution: size assortment

We used timed stationary point counts to compare male and female densities on slope and shelf habitats on peak aggregation days in 2013 (30th January) and 2014 (10th February). This additional sampling technique was used to document sex of individuals which was not included in the permanent transect surveys. We randomly established 5–6 survey points in each habitat within the core aggregation area and sampled each point for a total of 5 min (total n = 23). At each point count we noted the abundance, size and sex of individuals within a cylinder of 5 m radius and 5 m height of the survey point (volume ~ 393 m^3). On peak aggregation days (new moon days), we assumed that all individuals with distended bellies were females. We validated this assumption by opportunistically catching and (non-fatally) sexing 24 individuals on peak aggregation days (January 2012 and 2015). All individuals with distended bellies were found to be females (n = 11) and those with flat bellies were found to be males (n = 13). Of these, males and females had overlapping sizes: Male body size ranged between 40 and 74 cm, and female size ranged between 36 and 56 cm. Males and females were binned into fifteen centimetre size classes. We binned individuals post hoc to categorize males that overlapped in size with females and those which did not overlap in size with females. In previous studies (Johannes et al., 1999; Pet et al., 2005), males that overlapped in size with females were often found to be non-territorial and roving with female schools, while larger males held territories at the aggregation site. Males were thus classified as small (40–55) cm and large (56+cm) to study differences in territorial behaviours with body size. Similarly, we used 15 cm bins to classify females as small (35–50 cm) and large (51+cm), based on the size distribution of females observed in mid-water schools in this study. Underwater visual size estimates of a subset of individuals were compared with size-estimates derived from focal videos of the same individuals using a scale reference (n=20, see below). All individuals were correctly assigned to the respective size bins, and sizes were estimated within an error of ± 5 cm. The mean density of males and females and sex ratio was calculated in shelf and slope habitats by pooling point counts conducted in 2013 and 2014, as year did not have a statistically significant effect on mean density (see results). Sex ratio was calculated as the number of females as a proportion of total abundance in each habitat.

Size-assortment: To study the distribution of small and large individuals (of males and females), we used generalised linear models (GLMs). Models were run separately for males and females. Count data from a total of 23 point-counts were used in the analysis. The density of males and females was modelled as a function of body size (large and small), year (2013, 2014), habitat (shelf, slope) and the interactions between habitat, size and year. We used negative-binomial glms to account for overdispersion in the data (Crawley, 2009). Only non-significant interaction terms ($p < 0.05$) were removed from the maximum model, to improve parameter interpretation (Bolker, 2008; Harrell 2015). We used Likelihood ratio test for testing statistical significance of coefficients. Statistical hypothesis tests were not carried out for main effects involved in statistically significant interactions. Statistical analyses were performed with the statistical software R version 2.14.2 (R Core Team, 2016). Negative-binomial glms were performed using *lme4* (Bates et al., 2015). Results were plotted using *ggplot2* (Wickham, 2009).

Courtship tactics

Natural history observations

We observed the courtship behaviour of males and females, specifically the behaviour of female schools and territorial males. Where possible, video recordings were taken by placing GoPro Hero cameras at strategic locations on the reef. Each observed courtship behaviour was classified according to the location where it occurred (benthic or water column) and whether it was a pair courtship (between a single male and female) or a school courtship (single male and multiple females within a school, see results section for complete description). The size of female schools (number of females) was visually estimated underwater before the courtship survey (see below) and later corroborated from videos.

Distribution of male courtship tactics

The frequency of large and small males using pair and school-courtship tactics (see above) in the two habitats (slope, shelf) was estimated from focal individuals ($n = 72$) surveyed during an association-rate survey (see below). We used a contingency table to test if the courtship tactic used by large and small males was associated with the habitat they were found in. Since sample sizes in each cell of the 2 x 4 contingency table were low, we used a Fisher's exact test to test the association (Crawley, 2012).

Costs and benefits of male ARTs

Benefits: association rates (potential mating opportunities)

Courtship took place either with females near the benthos (as in case of pair courtship) or with females within schools in the water column (school-courtship). We estimated association rate as the number of females a male courted per minute. We measured association rates on the peak aggregation day (30th January) in 2014, with focal individual sampling. We sampled randomly identified males in each habitat and observed them for a period of 1 min (total n = 72). For each sampled individual we recorded the size of the male, the type of courtship it engaged in (pair or school) and the number of females it courted within 1 min. It was not possible to record these data blind because our study involved focal animals in the field. We compared mean association rates of large and small males using pair and school courtship tactics on the shelf (n = 42) and slope (n = 30). Sampling with replacement was performed over 1000 iterations to produce 95% bootstrapped confidence intervals around the means. If the mean association rate of one population did not fall within the confidence intervals of the mean of the other, we considered the populations to be significantly different (Crawley, 2008). Bootstrapping was conducted using the R package, *boot* (Canty and Ripley, 2014).

Mating rates are a challenge to measure in *P. areolatus* spawning aggregations because spawning presumably takes place at night or early morning, when surveys are difficult to conduct and because of the difficulties associated with measuring mating in externally fertilizing species. Very few researchers have observed gamete- release in *P. areolatus*, and gamete release has been reported only in male and female pairs after pair-courtship (Johannes et al., 1999; Pet et al., 2005; Russell and Muller, 2015). However, despite the difficulties associated with observing *P. areolatus* spawning, we observed two successful incidences of school-courtship culminating in gamete release. Both observations involved a single male with a group of females in a school. Since access to the number of females appears to differ considerably between courtship tactics, we assume that these would translate into differences in mating opportunities when spawning does take place. We therefore use association rates as a reasonable proxy for potential mating opportunities.

Costs: intra-sexual competition

To determine costs in terms of intra-sexual competition, we measured the proportion of time a male spent in aggressive interactions with other conspecific males. We used focal individual sampling (3 min) to obtain time activity budgets of males in shelf and slope habitats. Male focal individual samples (n = 65) were conducted on peak aggregation days in 2013 (10th February n = 14 slope and n = 14 shelf) and in 2014 (30th January, n = 18 slope, n = 19 shelf). Two observers swam from the northern to the southern edge of the aggregation site. Observers swam parallel to one another, one along the slope and the other along the shelf. During this swim, the observers randomly identified males in the two habitats and video recorded each individual for a 5-min period. Subsequent individuals were identified at a minimum distance of 5 m from the previous. Unique body marking were used to identify individuals in the videos. Individuals were followed at a minimum distance of four meters to minimise observer effects. We used a total sampling period of 5 min after initial observations. Males patrolled their entire territory within a minute on peak aggregation days; a sampling period of 5 min therefore provided us sufficient representation of an individual's behavioural repertoire.

During analyses the first 2 min of the recording were discarded to allow for focal individuals to acclimatize to our presence before we began scoring observations. Video data were recorded blind. From the videos, we broadly classified behavioural states in males as:

Rest: individual stationary in its territory, on top of, or under structures, maintaining its position with slow movements of its lateral and caudal fins. We identified a sub-state within the 'rest' state called 'perching'. Perching: individuals remain completely motionless, perched on top of structures in their territory with no fin movements. Rove: any continuous swimming motion or 'patrols' made by the individual inside or outside its territory boundaries. Defence/aggression: individual chased an intruder from its territory, this state is different from a patrol in that it involved a directed high speed chase, involving flaring of dorsal fins and a colour change to a brown-marbled pattern, and was often followed by biting the intruder. Individuals that were stationary, but which displayed by flaring their dorsal fins and displaying the brown-marbled patterns were also included in this state. Courtship: male courted a female (approaching with quivering motion of its body, followed by a display of his ventral side to the female, with or without body contact, Johannes et al., 1999). A total of n = 32 focal individuals were sampled on the slope and n = 33 on the shelf. Separate models were used for each behavioural state. We modelled the effects of year (2013, 2014), habitat (shelf and slope) and the interaction between year X habitat on the binomial variable— total time spent in a particular behavioural state versus total time not spent in that state. Quasibinomial glms were performed to account for overdispersion (Crawley, 2012). Only non-significant interaction terms ($p < 0.05$) were removed from the maximum model, to improve parameter interpretation (Bolker, 2008; Harrell, 2015). We used Likelihood ratio test for testing statistical significance of coefficients. A summary of sampling tactics used for measuring different variables is provided in the "Appendix " section.

Results

Annual aggregation density

The estimated mean peak annual density of *P. areolatus* was 72.08 ± 27.46 fish per 1000 m^3. At the aggregation site, the mean density of fish on the slope (324 ± 130.58 fish per 1000 m^3) was approximately six times higher than that on the shelf (59.4 ± 11.84 fish per 1000 m^3).

Male and female density distribution: size-assortment

Population sex ratios during peak aggregation days were highly skewed towards females on the slope (0.80), but were much more evenly balanced on the shelf (0.39). The density of small and large males ($\chi_2 = 41.946$, $p < 0.0005$) and females ($\chi_2 = 24.413$, $p < 0.0005$) changed substantially with habitat. The relative density of large males on the slope was approximately three times higher than small males. Conversely, the relative density of small males was 5 times higher than large males on the shelf (Figure. 1; Table 1). Large females were twice as abundant as small females on the shelf (Figure. 1; Table 1). In contrast, small females were 25 times more abundant than large females on the slope (Figure. 1; Table 1).

Table 1. Size-assortment: Negative-binomial GLM testing the relationship between male and female density with habitat (shelf and slope), body-size (large, small), year (2013, 2014) and the interactions between habitat, size and year at the aggregation site (n = 23 points). Maximum model with only the non-significant interaction terms removed to improve parameter interpretation. Statistical hypothesis testing carried out with likelihood ratio tests, except for main effects involved in statistically significant interactions.

Final model	**Coefficients**	**Estimate**	**SE**	**Likelihood ratio tests**	
				χ_2(df)	**p**
Female.density ~ habitat + size + year + habitat x size	**intercept** (habitat:shelf, size:large, year:2013)	1.629	0.395		
theta =0.7819 ± 0.189	**habitat** : slope	-0.576	0.520		
df = 41	**size**: small	-0.946	0.521		
res.deviance= 51.04	**year**: 2014	0.023	0.365	0.003	0.949
	habitat: slope * size: small	4.381	0.732	24.413	<0.0005
male.density ~ habitat + size + year+ habitat x size	**intercept** (habitat:shelf, size:large, year:2013)	0.972	0.237		
theta =5.0346 ± 1.69	**habitat** : slope	2.216	0.269		
df = 41	**size**: small	1.800	0.268		
res.deviance= 52.552	**year**: 2014	-0.115	0.167	0.470	0.49

	habitat: slope * size: small	-2.897	0.352	41.946	<0.0005

Figure. 1 Size-assortment. Mean density ± SE (fish per 1000 m_3) of large and small *P. areolatus* males (TL, 40 55 cm, 56+ cm) and females (TL, 35–50 cm, 51+ cm) in two habitats (shelf and slope) at the aggregation site in Lakshadweep. Y-axis plotted on $\log_{10}$ scale. Values averaged across 2 years 2013 and 2014 (n = 23 points).

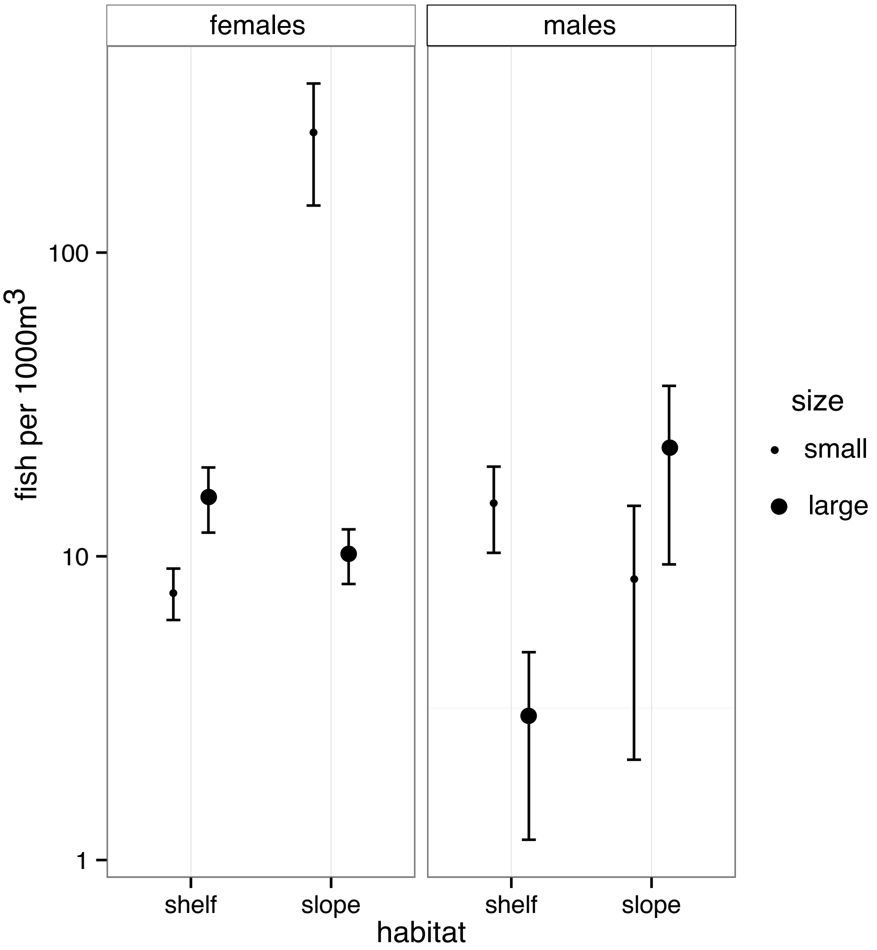
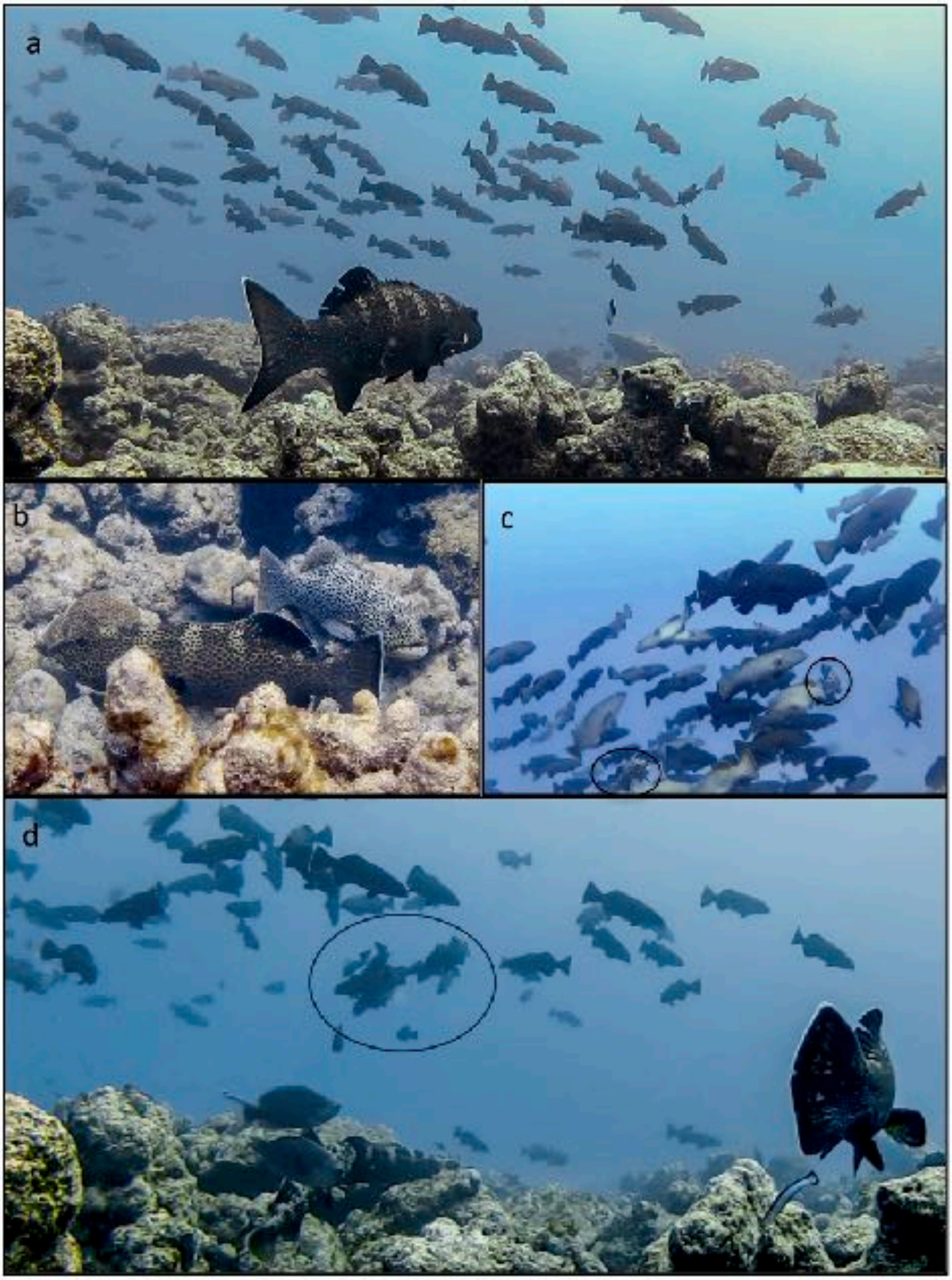


Figure. 2 Courtship tactics. a Female schools: a school of small female squaretail groupers approaches the slope at the aggregation site. b Pair-courtship: a male squaretail grouper courts a female in its territory. This is a typical pair-courtship behaviour observed in *P. areolatus*. c School-courtship: two large territorial male squaretail groupers (encircled) making a foray into a female school >4 m above the benthos on the slope. d School spawning: a novel school-spawning incident (encircled) observed between one large territorial male and a group of female squaretail groupers within a female school in the water column above the slope. This incident was captured on new moon eve, February 2013.


a
b
c
d

Courtship tactics

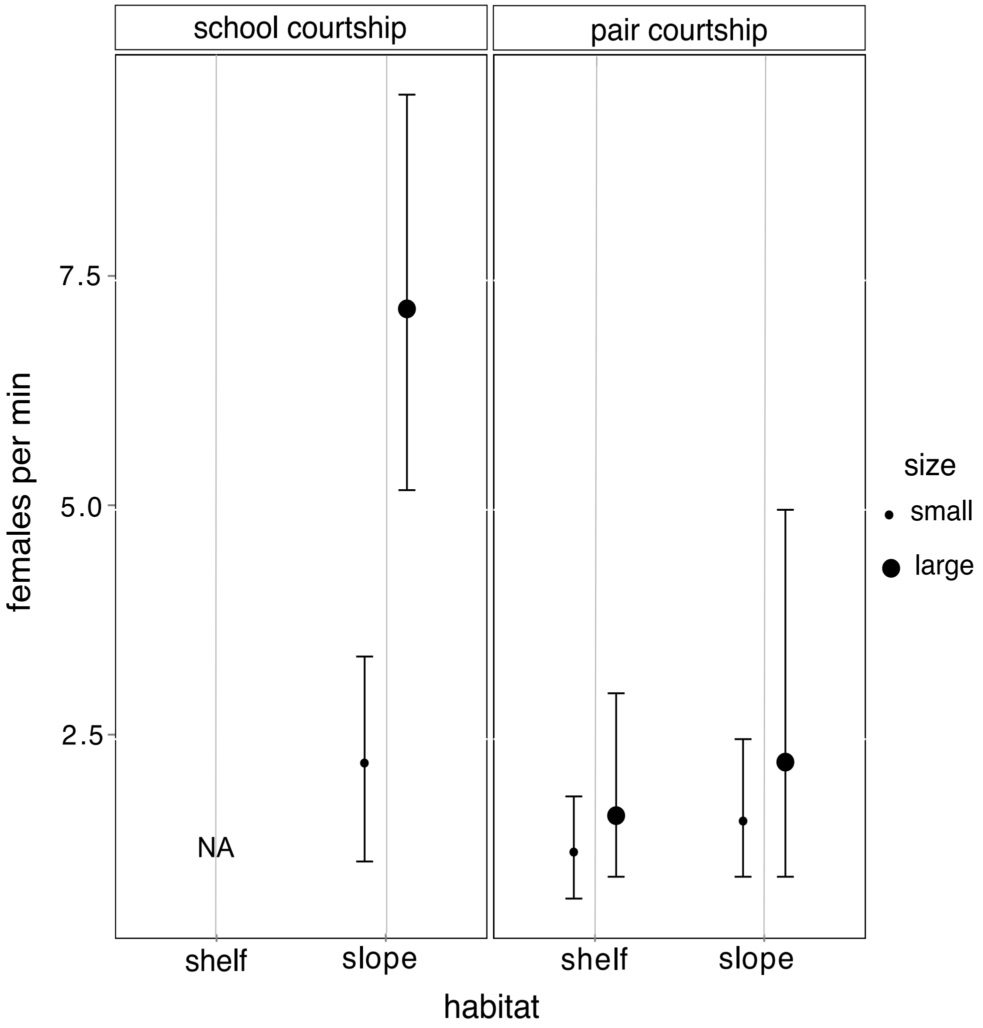
Natural history observations

We observed males arriving at the aggregation site up to 3 days prior to the new moon and establishing small, temporary territories (~5–10 m^2 area) on the reef slope and shelf. Both large and small males established territories at the aggregation site. These territories were maintained up to 2 days after peak spawning over the new moon phase. Females arrived at the aggregation area in large schools along the reef slope, a day prior to the peak aggregation day (Figure. 2a). We observed large schools of females (150–200 fish) moving around the core aggregation area and hovering in the mid-water column (i.e. stationary, with minimum movement of caudal and lateral fins) directly above the male territories. The female schools comprised of smaller individuals (<45 cm TL). Small females from these schools did not leave the school to disperse into male territories on the benthos. In contrast, large females (>45 cm TL) were observed roving independently along the benthos, or within male territories, but never as part of the schools (Additional file 1). We recorded two distinct male courtship behaviours in this aggregation.

Pair–courtship: Pair courtship took place between a territorial male and visiting female within the male's territory. Pair courtship (approach, colour change, quivering motion, ventral side display, quiver, and body contact, Figure. 2b) is often associated with pair-spawning; the latter involves a release of gametes by the pair in a spawning rush just above the male's territory [42]. While we did not directly observe incidents of spawning after pair courtship in our study, this sequence has been previously documented in a study of *P. areolatus* aggregations [42, 43].

School–courtship: School courtship behaviour involved males making regular 'forays' into female schools in the water column, above their territories (Figure. 2c). Males courted multiple females in the school during each foray, before returning rapidly to their territories. Courtship with females in the school was similar to that seen in pair courtship, with the difference that it took place in the mid-water column (3–4 m off the benthos) and simultaneously with multiple females. We documented two distinct incidents of gamete release following this school courtship behaviour in the water column one in 2013 (Figure. 2d) and another incident in 2014. Both events took place between one male and 4–5 females within a larger school. Females partaking in the spawning could be clearly identified based on their distended bellies. The incident involved an upward spawning rush within the school in the water column commonly seen in mass-spawning fish. Spawning took place >5 meters off the benthos (Additional file 2).

Figure. 3 Male association rates: Mean association rates (number of females courted per minute) ± 95% bootstrapped CIs of small (40–55 cm) and large (56+ cm) males (n = 72), using pair and school courtship tactics on the shelf and slope habitat at the aggregation site. The school-courtship tactic was not observed on the shelf despite the presence of female schools. Non-overlapping confidence intervals indicate significant differences in means.



Distribution of male courtship tactics

Courtship tactics used by males varied with size (small and large) and habitat (shelf and slope, Fisher's exact test p <0.005). The school-courtship was more common among large males on the slope and less than a quarter of large males engaged in pair-courtship (Table 2). The frequency of small males using both school and pair courtship on the slope was comparable and low (Table 2). The school-courtship tactic was completely absent on the shelf and all observed males (n = 30) engaged only in pair-courtship on the shelf (Table 2).

Figure. 4 Male activity: Proportional time spent in an activity, by male squaretail groupers (n = 71) on the slope and shelf at the aggregation site. Closed circles and whiskers represent mean ± SE values of shelf males, triangles represent values of slope males.

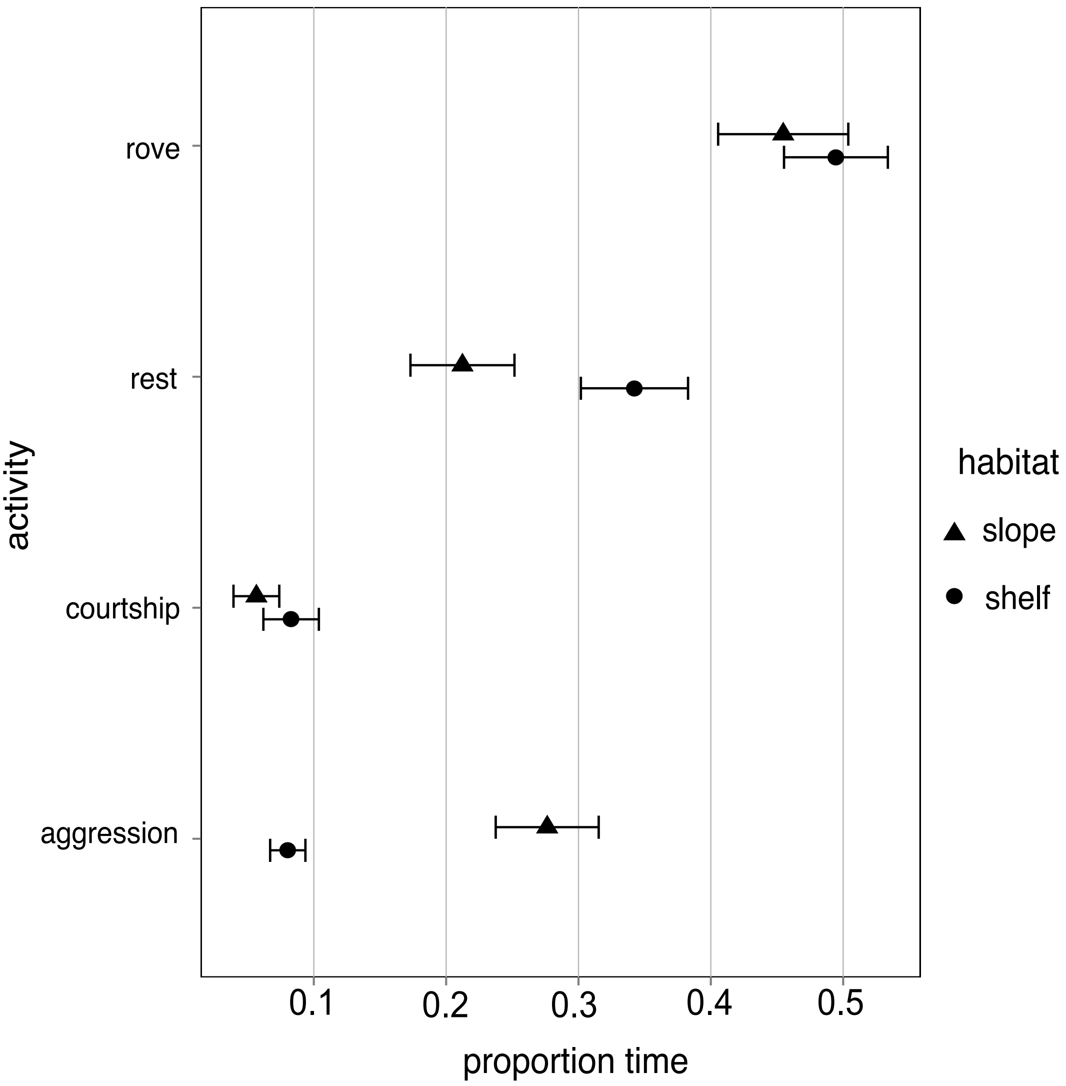


Table 2. Distribution of male courtship tactics: The frequency of small (40–55 cm) and large (56+ cm) males involved in school or pair courtship in shelf and slope habitats (n = 72 males) at the aggregation site.

Habitat	**Male size**	**Courtship tactic**		**Total sampled**
		School	***Pair***	
Slope	Large	20	4	23
	Small	11	8	19
Shelf	Large	0	4	4
	Small	0	26	26

Costs and benefits of male ARTs

Benefits: association rates (potential mating opportunities)

Large males courting schools on the slope, associated with seven times more females per unit time than small males on the slope, and three times more females per unit time than males engaged in pair courtship in both habitats (Figure. 3).

Costs: intra-sexual competition

The proportion of time spent in scored behavioural states did not change significantly between years (Figure. 4; Additional file 3). Time spent by males in aggressive behaviour was considerably higher (up to four times) on the slope than the shelf ($\chi_2 = -845.900$, $p < 0.0005$). Conversely, males spent twice as much time resting on the shelf than slope ($\chi_2 = -347.97$, $p < 0.0005$) Time spent in courtship and roving behaviours did not vary between habitats (Figure. 4 ; Additional file 3).

Discussion

Species often employ unusual reproductive tactics while mating at very high densities (Emlen and Oring, 1977; Kokko and Rankin, 2004; Brockmann, 2001). Fish spawning aggregations can provide unique opportunities to study such unusual, density-dependent mating tactics at high population densities. However, our understanding of natural mating systems of many commercially exploited, aggregating fish species is often obscured by the high anthropogenic pressures their populations sustain. At the time of our observations, the *Plectropomus areolatus* aggregation in Bitra represented one of the few unfished spawning aggregations of a large-bodied marine fish, with the highest recorded densities for this species across the Indo-Pacific (Palau (Johannes et al., 1999); Indonesia (Pet et al., 2005); Western Solomon islands (Hamilton et al., 2011); Papua New Guinea (Hamilton et al., 2011); Pohnpei (Rhodes et al., 2014)). At these unfished densities, we observed two peculiarities in the *P. areolatus* mating system compared to other locations. Firstly, there appeared to be an inverse size-assortment between males and females at the aggregation site in Bitra. Secondly, we observed two distinct male courtship tactics: pair courtship and school courtship— the latter appears to be a novel courtship tactic in this population. Perhaps more interesting than these two distinct courtship tactics were the opportunistic observations of spawning after school courtship, suggesting that the type of courtship tactic (pair or school) may lead to two distinct and alternative reproductive tactics. Of the two ARTs, pair-spawning, is a commonly reported tactic in *P. areoaltus* and is associated with pair-courtship (Coleman et al., 1996; Johannes et al., 1999; Pet et al., 2005). In contrast, school-spawning is a unique tactic in this species, which we describe for the first time in the Bitra spawning aggregation. Given the extremely high densities of individuals observed in this spawning aggregation, we suggest that the unique school-spawning tactic in *P. areolatus* is likely seen only in very high-density populations. This could explain why school-spawning has been previously unreported from studies across the Indo-Pacific. Opportunistic studies from unfished populations such as these can thus provide important baseline information on unique mating strategies of species at naturally high densities.

Inverse size-assortment

Overall the *P. areolatus* aggregation attained its highest density on the slope, as described at other locations across the Indo-Pacific (Hamilton et al., 2011, 2012; Rhodes et al., 2014; Johannes, 1988). Perhaps the most intriguing characteristic of the Bitra spawning aggregation is the inverse size-assortment of males and females, contrary to positive size-assortment, which is commonly seen in fish (Jiang et al., 2013). At first glance, this inverse-size assortment appears counter-intuitive. If female distribution were strongly influenced by the distribution of males alone, we would expect large females to be relatively more abundant in the high-density slope habitat where large males were present, which was contrary to our observation. Typically, females choose larger males as mates for their superior quality and quantity of gametes (Taborsky, 2008; Shuster, 2009). However, size-assortment in individuals can be weak when the costs of mating with a larger partner (asymmetrical exploitation, intra-sexual competition) are not outweighed by size related mating advantages (Taborsky et al., 2008), or simply because body size is not a male trait that directly affects fitness (Warner 1987; Wong, 2004; Wong and Candolin, 2005). Alternatively, females may be indifferent towards male size (Gross, 1984) if they select external environmental cues like predation pressure, or site quality to spawn (Petersen, 1990; Warner and Hoffman, 1980; Petersen et al., 1992). Whether female distribution were a consequence of mate choice, cryptic competition and/or a choice for certain habitat characteristics would require careful manipulative experiments, which were beyond the scope of this opportunistic, observational study. Irrespective of the mechanisms however, it appears that female behaviour may have a strong influence on male distribution in this aggregation.

We observed large males preferentially courting small females within schools on the slope, despite the presence of larger females on the slope. Female schools have been reported at other locations of *P. areolatus* aggregations across the Indo-Pacific, but tend to be much smaller in number (15–45 individuals per school, Johannes et al., 1999; Pet et al., 2005). In comparison, the female schools we observed were an order of magnitude larger (>150 individuals) and unique only to Bitra atoll in Lakshadweep (RA, personal observation, Petersen et al., 1992). While at this juncture we can only speculate on the mechanisms underlying this inverse-size assortment, it appears to be clearly unique to the high-density *P. areolatus* spawning aggregation in Bitra and is currently undocumented in other aggregations.

A unique mating tactic?

An exciting observation in this study is the multiple incidents of a unique mating tactic, school-spawning. The two incidents of school-spawning were remarkably similar in nature, and unique to other tactics in two ways. For one, females within schools simultaneously released gametes as a cohesive unit, and did not disperse into male territories to individually pair spawn after being courted by males (Johannes et al., 1999). For another, the school-spawning tactic differed from traditional observations of 'group spawning' because it involved a single male and multiple females partaking in an upward spawning rush, and not a single female and multiple males, which traditionally defines 'group spawning' (Petersen et al., 1992). It is likely that the school-spawning tactic may be a variation of group spawning, in which multiple males eventually join and simultaneously spawn within the school as seen in mass-spawning fish (Molly et al., 2007).

With these limited observations, we cannot preclude the possibility that school-courtship may also lead to pair spawning or mass-spawning, as has been traditionally explained (Johannes et al., 1999). However, our opportunistic observations clearly suggest that in rare circumstances school-courtship may lead to a unique school-spawning tactic, likely only in very high density *P. areolatus* aggregations.

Male ARTs: patterns and processes

Alternative reproductive tactics are observed in mating populations, when individuals adopt distinct and alternative ways to maximize their reproductive benefits in the context of intra-sexual reproductive competition (Taborsky and Brockmann, 2010). Unpredictability in partner availability, competition and predation risk, often selects for flexible and simultaneous ARTs, which are common in fish (Taborsky and Brockmann, 2010). The two distinct ARTs in the high density *P. areolatus* aggregation appeared to be conditional upon potential mating opportunities and male competitive abilities. The slope habitat appeared to be the preferred habitat at the aggregation site—and this is likely associated with high mate encounter rates (van den Berghe and Warner, 1989; Shuster, 2009) or potential mating opportunities generated by the movement of female schools. In addition, inter-specific competition was found to be four times higher among males on the slope than shelf. Large males had a clear size-related competitive advantage (Taborsky, 2001; Brown and Maurer, 1986) over their smaller counterparts and dominated the slope habitat. The largest males in this population were nearly 1.5 times longer than the smallest males. Further, on the high-density slope, large males engaged in school courtship much more frequently than pair courtship. While it is true that school courtship afforded seven times higher potential mating opportunities to the large males than pair courtship, it appeared to be a highly risky tactic because males had to leave their territories unattended during school forays. Despite higher levels of intra-sexual competition however, it appears that the benefits large males potentially gained by spawning within female schools likely offset these costs, selecting for this unique and costly mating tactic by large males in the high-density slope habitat.

Smaller males in contrast were significantly disadvantaged on the reef slope. We observed large males aggressively chasing away and injuring smaller competitors that attempted school-courtship. With high intra-sexual competition and no significant gains in potential mating opportunities, using the school-courtship tactic offered few benefits for small males on the slope. However, pair-courtship yielded similar potential mating opportunities in both habitats for small males, and these were associated with significantly lower levels of intra-sexual competition especially on the shelf.

Taken together, males in this high-density spawning aggregation appear to adopt two distinct and flexible ARTs: a ‘school-courtship tactic’, which is a high-cost-high-benefit tactic associated with school-spawning, and a ‘pair-courtship tactic’, which is a low-cost-low-benefit tactic associated with pair-spawning.

Conclusion

To our knowledge our observations of two distinct courtship tactics and inverse size-assortment is the first reported for *P. areolatus* . Crucially these properties only occur in Lakshadweep where the aggregation was unfished and aggregating densities were much high than those reported in the rest of the Indo-Pacific. Our study therefore poses an important conservation question; if *P. areolatus* populations in Bitra are exposed to fishing pressures, could it lead to a loss of the rare inverse-size assortment and unique school-courtship tactics from *P. areolatus* spawning aggregation? Commercial fishing of groupers at the aggregation site in Bitra has recently commenced (2013). Our most recent density census from 2015 and 2016 show that the peak aggregation density in January has declined by an alarming 50% compared to 2013.

With an off take pressure estimated at 12–15 tonnes of fish in 2015 (RA, RK unpublished data), the declining density is likely a result of this newly emerging commercial reef fishery. While the impact of the fishery on the unique *P. areolatus* mating system still remains to be evaluated, no female-schools or school-courtship were observed during surveys in 2016. This study raises several questions about the evolution and maintenance of this unusual ‘school spawning’ tactic in high-density *P. areolatus* aggregations. However, we fear that this opportunity may be lost due to the fast declining population densities of the Bitra aggregation. Opportunistic studies from unfished populations such as these can thus provide important baseline information on unique mating strategies of species at naturally high, unfished densities.

Appendix

Table 3. A summary of sampling techniques and sample sizes used for estimating variables.

Variable	Sampling technique	Sample size and factors	tests performed
Annual peak aggregation density	UVC permanent belt transects (transect volume = 50*10*5 m$_3$)	N = 10 transects Year (2013, 2014) Habitat (slope, shelf)	-
Size-assortment: male and female density distribution	UVC points (point volume = π*5*5 m$_3$)	N = 23 points Year (2013, 2014), Habitat (shelf, slope) Size (large, small)	Negative-binomial glm, likelihood ratio tests
Frequency of male courtship tactics	Focal individual sampling, 1 min underwater observations	N = 72 (2014) focal males Habitat (shelf, slope)	2 Å~ 2 Contingency table, Fisher’s exact test
Benefits: association rates (potential mating opportunities)	Focal individual sampling, 1 min underwater observations	N = 72 (2014) focal males Habitat (shelf, slope)	95% Bootstrapped confidence intervals
Costs: intra-sexual competition	Focal individual sampling, Activity budgets, 5 min videos	N = 65 (2014) focal male videos Habitat (shelf, slope)	Quasibinomial glms, likelihood ratio tests

All additional files can be found at this address:
https://bmcecol.biomedcentral.com/articles/10.1186/s12898-017-0120-5

Additional file 1. Female schools: schools of gravid females roving at the aggregation site. Male squaretail groupers (brown-marbled colouration) are seen making forays into the school and courting multiple females.

Additional file 2. School-spawning incident: a school-spawning incident observed in 2013. A male squaretail grouper from the slope males leaves his territory to make a foray into the school. Male is seen courting multiple females in the school. This school-courtship is followed by a sudden upward spawning rush between the male and 4–5 females from the school, proceeded by the release of gametes.

Additional file 3. Male activity. Quasi-binomial GLMs modelling the effect of habitat (slope, shelf), year (2013, 2014) and their interaction on the total time spent by males (n = 65) in an activity (aggression, courtship, rest, rove) versus time not spent in that activity. Maximum model with only the non-significant interaction are terms removed to improve parameter interpretation. Statistical hypothesis testing of coefficients carried out with likelihood ratio tests.

CHAPTER 6
CONCLUSION

A brave new world: embracing human-induced rapid environmental change

Camouflage grouper (epinephelus polyphekadion)

Introduction

In the emerging Anthropocene epoch, coral reefs are beleaguered by Human-induced rapid environmental change (HIREC). While it can be argued that coral reefs have sustained overfishing and pollution for centuries, these are now fast spreading to the remotest of reefs, where local pressures have been largely absent (Heron et al., 2016). But of primary concern is anthropogenic climate-change; a global disturbance that is causing repeated episodes of coral mass bleaching and mass mortality events, resulting in a rapid homogenization of habitat structural complexity all over the world (Alvarez-Filip et al., 2011; Cheal, et al., 2017; Hughes et al., 2017). Under this duress, some groups of species are more affected than others. There is an unraveling of species assemblages on coral reefs, resulting in previously unseen assemblage configurations (Graham et al., 1999). Caught at the cross-section between local fishing, and global climate-related habitat disturbances are benthic top predatory fish like groupers, an ecologically and commercially important but highly vulnerable guild (Craig et al., 2011; Sadovy de Mitcheson et al., 2013).

Managing coral reefs under HIRECs is a big challenge. Multiple disturbances can act simultaneously having additive, antagonistic or synergistic effects on biodiversity and ecosystem function. Further, these multiple disturbances can operate at different scales; from individuals, populations, and communities to entire ecosystems, making it challenging to determine meaningful points of intervention (Bellard et al., 2012). Considering that HIRECs are becoming the new normal for ecosystems, the task now is to understand the ecosystem consequences of rapid, unprecedented changes in assemblage structures. Central to this endeavor is identifying which species are the winners and losers in communities, understanding their coping mechanisms, and the consequent functions they will play in future ecosystem dynamics.

My thesis is an attempt at understanding how a guild of ecologically and commercially important benthic, predatory, coral reef fish (groupers, family: Epinephelidae) are responding to HIRECs in the Lakshadweep archipelago. The main aims of my study were to identify which species in the community are winners and losers under scenarios of rapid habitat degradation and understand the coping mechanism of behavioural plasticity behind the success of winners. My study was based in the Lakshadweep archipelago, which was a unique laboratory to study effects of climate change, in the absence of commercial reef fishing pressures. Under these relatively unfished conditions, I documented mating behaviours at a pristine squaretail grouper (*Plectropomus areolatus*) spawning aggregation to understand how these populations behave in the absence of local fishing pressures. Towards the end of my PhD, there was a sudden growth of a local commercial grouper fishery in the islands, giving me a unique and rare opportunity to study the behavioural and demographic impacts of a local HIREC (targeted fisheries) on a once unfished squaretail grouper spawning aggregation.

In the following two sections, I discuss in detail some of the main findings of my study.

Globally-induced HIREC and its consequences on benthic predators

Globally, coral reefs are steadily declining in structural complexity since 1998 in response to repeated mass-bleaching disturbances (Graham and Nash, 2013). A majority of studies relating fish community composition to structural degradation show that structural complexity is essential to support a diverse group of benthic species (Petren and Case, 1998; Pratchett et al., 2008; Richardson et al., 2017). In my second chapter, based on long-term benthic data (15 years), together with an archipelago-wide survey of grouper communities, I show that long-term habitat condition and not just the availability of structure determines grouper community composition. Community assembly is likely to be strongly influenced by both habitat condition and the durational stability of the habitats (Poff and Ward, 1990; Southwood, 1977). Together these determine the characteristics of the habitat, which limits the life history strategies of species that can occupy the area. By modifying both structure and disturbance frequency, HIRECs can seriously alter community composition on coral reefs (Fisher et al., 2011). On the one hand, I found that of the entire grouper community, long-lived (longevity > 15years) and large-bodied species (maximum size > 60cm) , were restricted to structurally stable sites with high structural complexity. Interestingly, long-lived, large-bodied species were not present in sites that had a dynamic disturbance history but had comparably high structural complexity. On the other hand, short-lived groupers were found in lower densities across all reefs irrespective of long-term habitat condition and structural complexity. My second Chapter suggests that the disturbance history of habitats provides a strong environmental filter limiting benthic species composition in structurally dynamic reefs to a relatively restricted range of life-history and functional characteristics (example, short longevity and small body size).

As seen earlier, HIRECs disproportionately affect species with long generation times (Karkarey et al., 2014). Another general trend seen across taxa confronted with HIRECs is that specialist species, with narrower foraging and habitat repertoires are being driven towards local extinction (Clavel et al., 2011; Vázquez and Simberloff, 2002). By circumventing prolonged evolutionary processes, behavioural plasticity is critical in allowing species to cope with rapid environmental changes within their lifetimes (Chevin et al., 2010; Tuomainen and Candolin, 2011). In my third chapter, I attempted to determine how well the guild of long-lived groupers copes with rapid structural degradation. Of the 15 long-lived species, territorial and site-attached groupers declined exponentially with decreasing structural complexity, while widely-ranging species showed no change. However, one site-attached species, the peacock grouper (*Cephalopholis argus*) maintained high densities across the structural gradient. I explored the mechanisms this species employs to cope with declining habitat structure. Both a potential release from specialist competitors and plasticity in foraging behaviour (foraging territory size, diet and foraging mode) appeared to favour the peacock grouper's survival in sites of high and low structure. While specialist competitors dropped out of the assemblage, the foraging territory size of peacock groupers increased exponentially with structural degradation. Interestingly, despite significant differences in habitat quality, peacock groupers maintained a specialized dietary niche. In-water behavioural observations suggested that diet specialization was maintained by switching foraging modes from a structure-dependent 'ambush' to a structure-independent 'widely foraging' mode. My work demonstrates that foraging plasticity will become increasingly critical in separating winners from losers among benthic predators and may help preserve specialist ecosystem functions as habitats collapse under HIREC.

Behavioural plasticity allows individuals to adjust and survive in rapidly degrading habitats, but can it ensure the long-term persistence of populations in sub-optimal habitats? Both biological and ecological costs and consequences of plasticity may impact population growth of plastic species through their effects on individual growth, mortality and fitness (Auld et al., 2010; DeWitt et al., 1998). In the fourth chapter, I studied the life-history and demographic consequences in the peacock grouper of persisting in degraded coral reefs. I found that, contrary to initial expectations, peacock groupers were in better body condition in degraded reefs, gaining more weight per length compared to reefs with high structural complexity. However, surviving in these sub-optimal habitats came at a considerable life-history cost, reflected in a 20% reduction in longevity. In degraded reefs, density was almost 50% lower than that in high structured sites. In addition, subpopulations in degraded reefs were characterized by a relatively lower proportion of juveniles indicative of bottlenecks to recruitment. My work shows that the apparently high adaptive capacity of species like the peacock grouper may mask significant life-history consequences with long-term demographic effects that could add up as habitats degrade any further.

Locally-induced HIREC and its consequences on benthic predators

Owing to the relatively low local reef fishing pressure in Lakshadweep, it was ideal for me to study the impacts of climate change on groupers without the confounding effects of fishing. Aspects of the life history and reproductive biology of groupers, particularly their tendency to form large spatiotemporally explicit mass spawning aggregations, makes them highly vulnerable to fishing. In the anthropocene epoch, it is virtually impossible to find undisturbed and unaltered spawning aggregations in nature. This is particularly true of long-lived predatory fish like groupers because of the highly selective fishing pressures they face in most tropical reefs (Myers and Worm, 2003; Sadovy de Mitcheson et al., 2012). As a result, most of our understanding of the behaviours of many species comes from populations that may have historically faced some levels of fishing. Groupers possess complex and highly flexible mating modes, ranging from pair-spawning and group-spawning tactics, demersal and broadcast spawning tactics, to gonochorism and hermaphroditism that can vary within and between populations (Erisman et al., 2013). In, Chapter five, I seized a rare opportunity to study mating behaviours in an unfished spawning aggregation of the squaretail grouper (*Plectropomus areolatus*) in Lakshadweep and contrast it with behaviours reported from spawning aggregations across the Indo-Pacific that had been fished. I found a dramatic difference in the mating behavior of this species between the unfished population in Lakshadweep and aggregating populations from across the world. I report unique courtship behaviours in the unfished, high-density spawning aggregation of the squaretail groupers (*Plectropomus areolatus*) in Lakshadweep, that are potentially associated with alternative reproductive tactics (ARTs) – pair spawning and 'shoal spawning'. Aggregating males are typically known to court females in small territories (pair courtship), which is often associated with a pair-spawning tactic in aggregations. However, under high-density conditions, I observed the largest males simultaneously courting several females in mid-water shoals – a unique, high-cost-high-benefit courtship tactic which appears to result in a novel school-spawning tactic. I also observed a counter-intuitive inverse size-assortment among individuals – large males courted smaller females and vice-a-versa, linked to different pay-offs associated with male competitive ability, local mate density and female schooling behaviour.

A post-script: The effects of fishing on a grouper spawning aggregation

While Lakshadweep had been a laboratory of climate-change studies due to low levels of commercial reef fishing, this changed drastically in the last year of my PhD with the rise and expansion of commercial coral reef fisheries. Of specific concern was the rise in targeted grouper fishing which is now putting grouper spawning aggregations under risk of extirpation. In Chapter five, I documented density and rare mating behaviours in an unfished squaretail grouper spawning aggregation. A rapid rise of grouper fisheries in the last two years gave me the opportunity to track how (and how quickly) the density and behaviours in a pristine grouper aggregation can change under the pressures of targeted fishing.

Since 2012, I continued to annually monitor the density and population size-structure of the Bitra spawning aggregation using techniques described in chapter five. In addition, I surveyed reef fish catch and consumption in the islands through structured interviews in 2016. I observed a dramatic 60% decline in the overall density of the aggregating population since we first documented it in 2012 (Figure 1). Particularly, smaller sized individuals (35-45 cm total length) have declined by 80% in the last four years (Figure 2). This size-class presumably represents females that engage in the rare shoal-spawning tactic. In addition to this dramatic population decline, I observed that female shoals were largely absent from the aggregation since 2015, ie. when the aggregation density had declined by a mere 20%. Interestingly, my ongoing fisheries surveys suggest that there is an overall increase in reef fishing pressure in Lakshadweep, which is now targeting groupers in the size range of 38-45 cm. In early 2017, groupers made up for over 22.5% of total reef fish catch of large commercial fishing vessels and the catch per unit effort of groupers has doubled since 2014.

My ongoing work with the grouper spawning aggregation is demonstrating how even a few years of targeted fishing activity can rapidly decimate a population and impact population behaviours. The once unfished, high-density Lakshadweep squaretail grouper aggregation currently matches densities and behavioural characteristics found in aggregations elsewhere in the Indo-Pacific. By drawing comparisons between fished and unfished population behaviours of the squaretail grouper, my work throws light on Daniel Pauly's shifting baselines syndrome, which suggests that we may be managing populations with significantly shifted baselines (Pauly, 1995). When managing populations with shifting baselines, managers often only think of numerical responses of populations but this ongoing work suggests that behavioral baselines may be just as important. Behavioural indicators like density-dependent mating behaviours could be used to predict population crashes even before major demographic shifts appear. This makes documenting behavioural /ethological information from unfished populations like the squaretail grouper spawning aggregation in Lakshadweep all the more urgent.

Figure 1. Annual aggregation density (mean ± 95% CI) of the squaretail grouper spawning aggregation in Lakshadweep. Dashed line indicates years in which large female shoals were observed at the aggregation site. Surveys were conducted during the peak aggregation season in January/February.

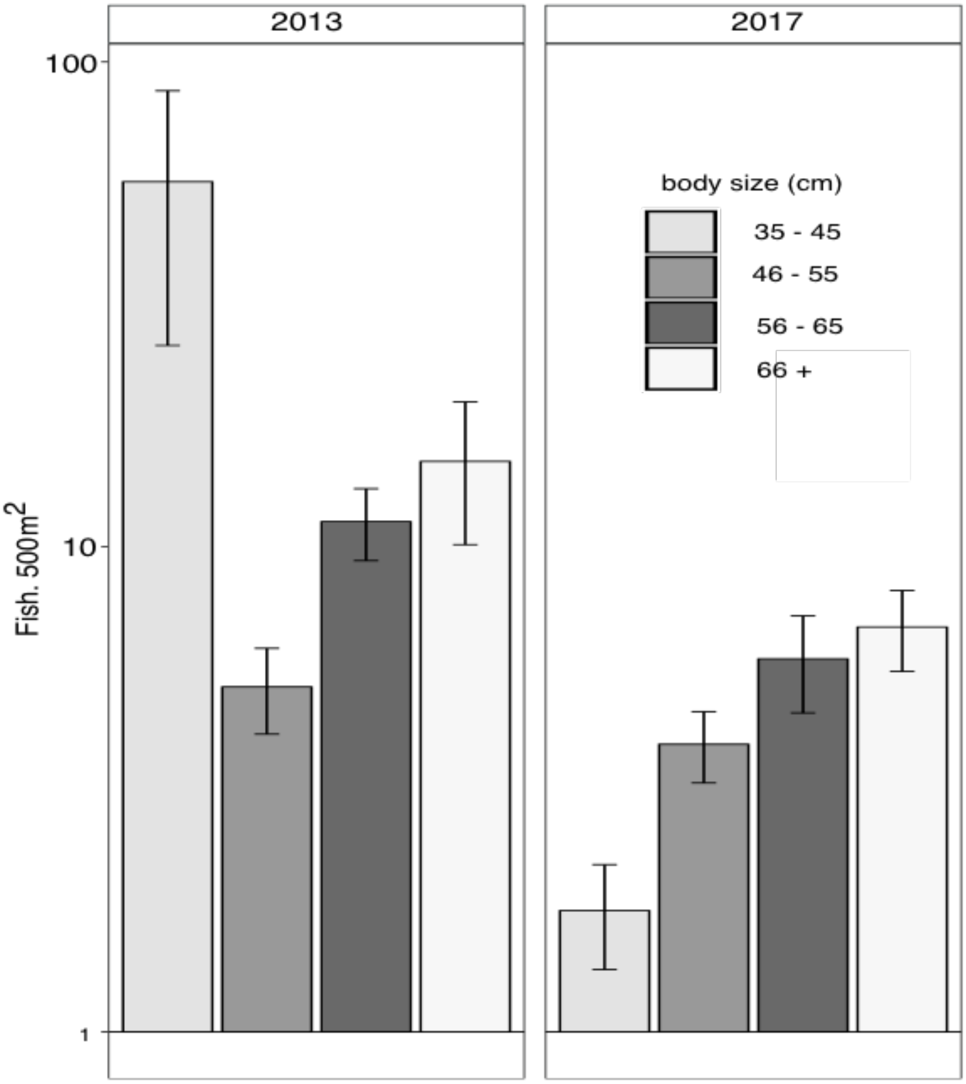
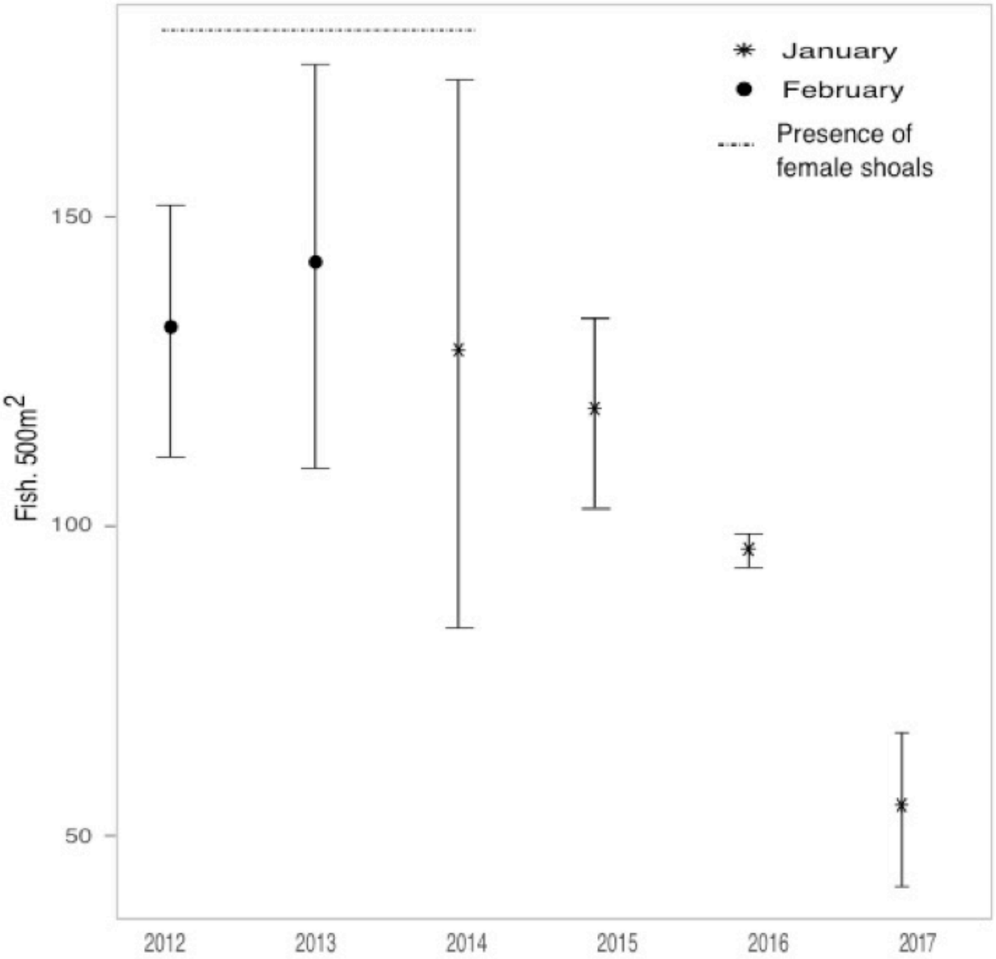

2013
2017
100
10
1
Fish. 500m²
body size (cm)
35 - 45
46 - 55
56 - 65
66 +

Figure 2. A comparison of population size structure (mean ± 95% CI) of the squaretail grouper aggregation between 2013 (pre-fishing) and 2017 (rise of targeted fisheries).



Limitations and avenues for future work

A current challenge in ecology and conservation is to understand how change in trait composition of communities due to HIRECs is translating into a change in ecosystem function. While post-disturbance reefs are strongly driven by herbivory functions played by herbivorous fish (Hughes et al., 2007), the functional role of predators in the recovery and resilience of highly disturbed reefs is largely unresolved (Ritchie and Johnson, 2009; Roff et al., 2016). Several studies have shown that resident ambush predators are often part of complex direct (Almany and Webster, 2006) and indirect interactions (trait-mediated interactions, Catano et al., 2016) which together impact community structure and ecosystem function. From studies conducted in Fiji (Dulvy, et al., 2004) and in East Africa (McClanahan and Muthiga, 1988), we know that the loss of predatory function owing to high fishing pressure on predatory fish can induce a trophic cascade on coral reefs already reeling from climate-change. The functional importance of groupers in coral reefs has been largely assumed in this study. The Lakshadweep archipelago is one of those rare regions where I was able to study the impacts of climate-change on groupers in relative isolation from fishing pressure. However, to fully understand the functional impact of change in grouper composition due to habitat degradation, studies exploring the predatory function of groupers need to be explicitly undertaken in Lakshadweep. In Chapter one, I studied how two functional traits in groupers - long life-span and body size respond to repeated habitat structural degradation. In the functional ecology literature these are called 'response traits', as they respond to a disturbance but their impact on function is unclear. To better understand the impact of HIRECs on predatory functions as raised earlier, it would be useful in the future to study 'effect traits' that directly influence the predatory functions of groupers – example eco-morphological traits and physiological traits.

In my thesis, I focused on understanding the response of groupers to HIREC. However, I expect other benthic predatory fish to show very similar responses. It would be interesting and useful to study patterns and coping mechanisms across a wider taxonomic range of benthic predators.

In Chapter three and four, I focused on understanding foraging plasticity in one ubiquitous and seemingly successful grouper species. A natural question arising from this work is why are some species like the peacock grouper behaviourally plastic and others aren't? Future studies could address the ecomorphological, physiological and evolutionary basis of plasticity in species like the peacock grouper.

In Chapter five, I used behavioural observations to describe ARTs in the high-density squaretail grouper spawning aggregation in Lakshadweep. As discussed in the earlier section, with increasing fishing pressure, there seems to be a significant decline in population densities, change in population size and sex structure and a possible loss of the rare group spawning ART from the aggregation. A comprehensive study of the reproductive biology of the squaretail grouper needs to be undertaken to determine the implications of shifting mating behaviours on population dynamics of the squaretail grouper.

Contribution

This study has made an important contribution towards understanding disturbance responses in benthic predatory fish like groupers to global climate-change and repeated structural degradation in Lakshadweep, one of India's unique coral atoll systems. The archipelago-wide, underwater fish survey conducted as part of this study was one of the first comprehensive fish-species checklists produced for his region based on direct in-water observations in coral reefs. We reported over 500 species of reef fish and 35 species of groupers from Lakshadweep.

Through this study, we documented one of the first grouper spawning aggregations in India. This was found to be one of the largest aggregations of squaretail groupers found across the Indian Ocean. Further, we reported a rare and unique mating tactic and unusual mating system in this high-density aggregation. The discovery and documentation of this unique aggregation lead to a unique collaborative marine conservation initiative between the local Island Panchayat and the Fisheries Department in Lakshadweep. This has lead to the creation of a seasonal fishing closure at the aggregation site during aggregation periods for the last five years. Our data continues to be used in informing the conservation and management of fish spawning aggregations in Lakshadweep.

Implications for management

Information on the historical variability of ecosystem conditions and the natural disturbance regimes that influence such variability is increasingly used in the design of ecosystem management in systems. Coral reef ecosystems are inexorably and increasingly confronted by HIRECs. An improved understanding of changes occurring in these systems can be obtained by relying on the history of ecological systems (their past composition and structure, their spatial and temporal variability, past ecosystem functioning and the principal processes that influenced it (Landres et al., 1999). To put it simply, the past is one of the best means for understanding and predicting impacts to new and novel ecological conditions.

In my thesis, I demonstrated the critical importance of stable, high structured reefs for conserving the entire grouper assemblage, especially long-lived and large bodied species. Stable reefs of high structural complexity appear to be safe havens for long-lived and less-plastic species, but more importantly they support recruitment processes and may potentially serve as 'source' habitats for even plastic species like the peacock grouper that can successfully survive even in degraded reefs. Moving forward, stable reefs need to be protected as climate-change refugia for benthic fish; to prevent local extinction of vulnerable benthic predators and to protect areas that foster recruitment of ubiquitous species.

With respect to the grouper community, I demonstrated that there can be clear winners and losers in response to habitat degradation and the winning species are those that typically show plasticity in foraging behaviours. Identifying and protecting highly plastic species that are now taking on an increasingly keystone role in maintaining predatory function is critical for maintaining functional heterogeneity, as less plastic species drop out. However, it is also just as critical to identify the limits to plasticity in such species. Therefore, while conserving plastic keystone species in the future, habitat protection is still important to prevent them from crossing their thresholds.

Just a few years exposure to commercial fisheries can significantly alter the aggregation densities, population structure and behavioural integrity of a remote grouper spawning aggregation. It is important to identify and strictly protect aggregation sites from fishing. Our work highlights the importance of documenting and monitoring behavioural/ethological baselines to evaluate the success of a management program at its early stages, before population or ecosystem-level responses are evident (e.g., Ikuta and Blumstein, 2003; Lindell 2008). As mentioned earlier, an outcome of my work has lead to the formation of a seasonal fishing closure at the aggregation site, to protect the aggregation from commercial fisheries. There seems to be very high compliance towards the closure, yet significant declines in the aggregation population are being observed. Our ongoing work is suggesting that in addition to complete fishing closures during the aggregating periods, it is urgent to manage targeted fisheries by introducing catch and or gear restrictions during non-aggregation periods as well.

While HIREC appear to affect systems at scales much larger than local management – the resilience of systems to HIREC is strongly dependent on what fishers and managers do at local levels (Graham et al., 2014; Mumby, 2017). HIREC should not engender paralysis – rather it should challenge us to move towards a more resilience management approach which embraces natural variability and disturbance histories. This involves separating local from global drivers of change, understanding past disturbance responses and mechanisms of survival, reducing local disruptors, ameliorating the impacts of global disruptors, and acknowledging that we are managing a system with a constantly changing baseline.

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