Size and wave exposure shape parrotfish distributions and function in shallow coral reefs

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Abstract

Wave exposure is a powerful environmental filter in shallow coral reefs, influencing species distributions and mediating patterns of decline and recovery. How mobile species navigate wave regimes is often mediated by size, morphology and swimming behaviour. How species navigate turbulent wave regimes is especially important in the case of functionally important groups like parrotfish. We explored how wave exposure shapes the distribution, biomass and bioerosional role of parrotfish assemblages in coral reefs using in-water visual surveys in the Lakshadweep Archipelago. Despite being relatively fusiform, we found that parrotfish distribution was strongly influenced by wave exposure, mediated by individual size and body shape. There was a clear decoupling between density, biomass and bioerosion in relation to wave regimes. Parrotfish density was highest in shallow exposed sites, dominated by large shoals of small individuals with low body depth ratios. In contrast, biomass was highest in deeper locations, where larger individuals were most abundant. This differential filtering of species and sizes resulted in considerable heterogeneity in the spatial distribution of bioerosional processes on the reef. Our study highlights the importance of size and shape as critical traits in influencing community assembly and determining the distribution of function in parrotfish.

Introduction

Understanding how species and their abundances vary across spatial and temporal scales is a central theme in community ecology [1]. Theories differ in the relative contributions of biotic influences, abiotic constraints and chance in determining how communities assemble. At environmental extremes, biotic processes like competition and predation are likely masked by the ability of species to withstand harsh conditions as high stress environments present narrow ecological niches that fewer individuals in the assemblage can occupy [2,3]. Negative biotic interactions become increasingly important at gentler ends of environmental gradients, where species' competitive abilities work to structure assemblages [4,5]. The relative role of environmental factors and species interactions is likely dependent on individual species traits within the assemblage and the strength of environmental conditions. What is clear is that biotic, abiotic and chance factors are highly contingent on place and circumstance, varying both spatially and temporally [6,7]. Engaging with this variation is essential to understanding the underlying drivers of community assembly.

While answers to this question are interesting in and of themselves, when linked to ecosystem function, it has profound implications for the integrity of the system and its overall resilience. Some species (or groups of species) are disproportionately important in the functions they perform within ecosystems, and their distribution over space and time can shape the processes they control. In tropical coral reefs, parrotfish (family *Scaridae*) contribute to key ecological processes and are central to reef resilience [8,9]. Parrotfish are a ubiquitous group of herbivores, feeding on both epi and endolithic micro algae off the reef substrate. They perform several critical ecosystem functions including herbivory, corallivory, bioerosion, sediment formation and sediment redistribution [10]. As herbivores, they mediate competition

between turf algae and coral recruits, which becomes particularly critical in post-disturbance recovery trajectories on reefs [11,12]. Parrotfish also play an important role in reef accretion and are among the most important bioeroders on most tropical coral reefs [13,14]. Bioerosion is an essential part of the carbonate cycle, acting as a counterpart to carbonate assimilation or accretion in coral reefs [15]. Parrotfish bioerosion often targets dead corals, creating space for new coral recruits to settle [15], and is closely linked with sedimentation and degradation of dead coral structures [16]. However, they also target live coral and can contribute to coral mortality, particularly of young coral [17]. Parrotfish are a diverse group with widely differing beak structures, musculatures and osteology, leading to significant variation in the ecosystem processes they perform [18]. Depending on their feeding behaviour and amount of coral bioerosion they are responsible for, parrotfish are classified into 3 functional categories —browsers, scrapers and excavators[10]. They are also diverse in their shape, sizes, swimming capabilities and social structures - factors which could determine the impacts of environmental filtering and competition on their function in the reef [19].

Wave exposure is a dominant environmental filter in shallow coral reefs, affecting everything from species growth rates and behaviour to community composition and successional patterns. For instance, turbulent conditions have been shown to influence the growth and mortality rates of sessile intertidal organisms [20]. Many reefs show very different benthic compositions on windward and leeward aspects, and can have divergent post-disturbance recovery trajectories [21,22]. For mobile organisms, wave exposure presents a particular challenge; navigating through the turbulent waters of highly exposed environments can represent significant energetic costs [23,24]. Species that are best able to handle these environments may show a convergence of species traits that reduce drag, or increase swimming efficiency [19]. A study by [25](2020) has shown that wave exposure disproportionately limits flat bodied herbivores to more sheltered, less turbulent locations. Compared with other reef herbivores, parrotfish are much more fusiform in body shape suggesting that they may not be as influenced by wave exposure. However, they show considerable inter and intraspecific variation in body size and swimming traits, which may lead to impacts on individual fish behaviour [26]. While many of these morphometric traits vary with species, they can also vary ontogenically as individuals grow. For one, larger individuals within the same species may have stronger musculature and physiologies, which allow them to counter drag forces that smaller individuals are unable to [24]. In addition, for sex-changing species like parrotfish, a change in sex may also represent changes in body shape, which could translate to shifts in swimming efficiency. Finally, whether individuals travel in shoals or solitarily could also influence their ability to deal with drag [27], and these social behaviours may possibly change ontogenically in several parrotfish species.

We explored how wave exposure influenced parrotfish communities and the distribution of bioerosion in the reefs of Lakshadweep archipelago, northern Indian Ocean. The Lakshadweep atolls are strongly influenced by prevailing south-west monsoon winds, creating strong contrasts in exposure regimes between reefs that can influence species distribution. Working across three atolls in the archipelago, we

explored how exposure regimes influence parrotfish species composition and biomass in reefs, and how this in turn mediated rates of bioerosion on Lakshadweep reefs.

Results

Parrotfish Density and Size Distribution

Parrotfish density was much greater in shallow reef sites compared to deeper locations. In fact, shallow reefs had almost twice the density of parrotfish (Fig. 1a, Table 1). This was mainly driven by the high density of small parrotfish (particularly *Chlorurus sordidus* and *Scarus psittacus*) which made up more than 80% of all parrotfish individuals (Fig S1, Table 1). Further, there were significantly fewer large individuals at shallow depths than in deeper waters (Table 1). Atoll-wide differences were also evident, with the island of Agatti having significantly lower parrotfish density than Kavaratti or Kadmat.

Table 1
Model summary of the model for abundance of parrotfish (M1)

Parrotfish Abundance	Coefficients (95% CI)	Significance
(Intercept)	2.94 (2.38 to 3.5)	*
Depth.ClassShallow	0.77 (0.21 to 1.33)	*
AspectWest	-0.24 (-0.92 to 0.44)	
Size.ClassMedium	-1.81 (-2.40 to -1.23)	*
Size.ClassLarge	-2.99 (-3.64 to -2.34)	*
IslandKadmat	1.03 (0.41 to 1.64)	*
IslandKavaratti	0.88 (0.37 to 1.40)	*
Depth.ClassShallow:AspectWest	-0.57 (-1.36 to 0.22)	
Depth.ClassShallow:Size.ClassMedium	-0.50 (-1.32 to 0.32)	
Depth.ClassShallow:Size.ClassLarge	-2.17 (-3.20 to -1.14)	*
AspectWest:Size.ClassMedium	0.41 (-0.43 to 1.25)	
AspectWest:Size.ClassLarge	-0.20 (-1.11 to 0.72)	
Depth.ClassShallow:AspectWest:Size.ClassMedium	-1.17 (-2.37 o 0.03)	.
Depth.ClassShallow:AspectWest:Size.ClassLarge	0.45 (-1.07 to 1.97)	

Parrotfish Biomass

In contrast with density, parrotfish biomass was significantly lower in the most exposed western shallow sites, where it was less than half of any of the other exposure regimes (Fig. 1b, Table 2). Biomass was

relatively evenly distributed across other exposure regimes, due, in part to an uneven distribution of parrotfish size classes between them. Although deeper locations had fewer individuals, they were considerably larger, and were often terminal phase individuals of species like *Scarus frenatus*, *Scarus prasiognathos* and *Chlorurus strongylocephalus* (Fig S3). Although sheltered shallow reefs had mostly small individuals, their numbers compensated for their size, contributing to high biomass values on these reefs. In contrast, the highly exposed western shallow reefs had fewer individuals, most of which were dominated by small individuals, resulting in significantly lower overall biomass (Fig. 1b, Table 2).

Table 2
Model summary of the model for parrotfish biomass (M2)

log(Biomass + 100)	Coefficients (95% CI)	Significance
(Intercept)	7.13 (6.45 to 7.80)	*
AspectWest	-0.16 (-0.91 to 0.59	
Depth.ClassShallow	0.01 (-0.47 to 0.49)	
IslandKadmat	1.62 (0.69 to 2.56)	*
IslandKavaratti	1.76 (1.00 to 2.52)	*
AspectWest:Depth.ClassShallow	-1.10 (-1.79 to -0.41)	*

Species Richness

Differences in parrotfish species richness were not statistically significant. Species richness followed a similar trend as biomass (Fig. 1c). Exposed sites appeared to have a lower mean species richness than sheltered sites, and shallow exposed reefs had the lowest overall richness (Table 3). Here, the mean richness was less than 6 species per transect, which was roughly 30% less than any of the other exposure classes.

Table 3
Model summary of the model for parrotfish species richness (M3)

Species Richness	Coefficients	Significance
(Intercept)	1.11 (0.79 to 1.44)	*
Depth.ClassShallow	-0.03 (-0.27 to 0.21)	
AspectWest	-0.36 (-0.73 to 0.01)	.
IslandKadmat	0.54 (0.09 to 0.98)	*
IslandKavaratti	0.67 (0.31 to 1.04)	*
Depth.ClassShallow:AspectWest	-0.29 (-0.67 to 0.09)	

Parrotfish Body shape

BDR interacted with body size to determine to what extent species could access wave exposed areas (Fig. 2). While large parrotfish of all species seemed to be at lower densities in high wave exposure sites, BDR seemed to play an important role in determining the strength of the environmental filter for smaller size classes. We found that smaller individuals of more deep bodied species like *C. strongylocephalus, S. russelii, S. niger or S. ghobban* were completely excluded from intermediate and high exposure areas (Fig. 2). However, species with a low BDR like *Scarus psittacus*, *S. scaber* and *Chlorurus sordidus* tended to remain abundant even in high exposure sites.

Parrotfish Bioerosion

Bioerosion rates tracked parrotfish biomass in highly exposed shallow reefs where they were significantly lower than in other areas (Fig. 1d, Table 4). However, unlike parrotfish biomass, bioerosion was highly skewed in its distribution across exposure classes with depth playing an important role in determining bioerosion. The amount of bioerosion caused by a parrotfish increases exponentially with size, with large parrotfish contributing disproportionately more to bioerosion for their biomass compared to small parrotfish. Hence, bioerosion was concentrated in deeper sites which had a higher density of large individuals.

Local species pools played an important role in determining bioerosion rates across reefs (Fig. S4) and the presence or absence of key bioeroding species greatly influenced the overall bioerosion at a site. *Chlorurus enneacanthus*, a significant contributor to bioerosion, was restricted to reefs on the sheltered aspect of Kavaratti. *Chlorurus strongylocephalus* on the other hand, was completely absent from the reefs in Agatti. Since the species was a major driver of bioerosion in Lakshadweep's reefs, bioerosion in Agatti was consequently very low.

Table 4
Model summary of the model for parrotfish bioerosion (M4)

log(Bioerosion + 0.001)	Coefficients (95% CI)	Significance
(Intercept)	-3.07 (-4.18 to -1.96)	*
AspectWest	-0.07 (-1.30 to 1.16)	
Depth.ClassShallow	-0.26 (-1.02 to 0.49)	
IslandKadmat	2.96 (1.42 to 4.51)	*
IslandKavaratti	3.05 (1.78 to 4.31)	*
AspectWest:Depth.ClassShallow	-1.11 (-2.17 to -0.05)	*

Discussion

Population density, biomass and bioerosion represent three related, but very different lenses of the role's parrotfish play in coral reefs. The assumption that number reflects process can be misleading,

particularly when number and biomass are decoupled in their distribution, and when the process in question is linked to species identity, and scales allometrically [28,29]. In Lakshadweep, the distribution of parrotfish across its reefs was influenced by wave exposure regimes and the way species responded to these regimes was mediated by individual size and body shape. As an assemblage, the deep locations had a greater number of large parrotfish individuals, and individuals of key excavating species (like *Chlorurus strongylocephalus* and *Chlorurus enneacanthus*) that accounted for the bulk of parrotfish bioerosion on the reef. In exposed reefs, subject to the highest year-round wave energy, a greater number of small individuals as well as overall higher parrotfish density were found than at sheltered locations. This differential filtering of species and sizes results in considerable heterogeneity in the spatial distribution of bioerosional processes on the reef. This finding is in contrast to other studies which found greater excavator abundance in more exposed conditions [30].

Lakshadweep's reefs are uniquely placed to explore the consequences of wave exposure on community composition and ecosystem processes. The turbulent west and the relatively calm east create strongly contrasting conditions that influence benthic composition and post-disturbance recovery, structural stability regimes, fish assemblages and behaviour [31–33]. It is important to note that the wave exposure contrasts between east and west do not persist year-round. From October to April, western shallow reefs can be as calm as the east. However, for the 6 months of the summer monsoon, the direction of the south-westerly winds represent an environmental forcing large enough to influence the distribution of resident species. This is especially important in the case of species like parrotfish, which hold and patrol territories [34,35]. Wave energy also attenuates with depth and deeper reefs likely represent low wave energy conditions independent of aspect. The shallow leeward reefs of the east lie at the midpoint of this wave exposure gradient. While admittedly coarse, this gradient helps make sense of the distribution of parrotfish in Lakshadweep reefs, showing that exposure is a strong environmental filter for parrotfish communities, driving patterns in species density and biomass, and contributing to an unequal distribution of bioerosional processes on the reef. The high exposure western shallow reefs had lower parrotfish biomass and erosion compared to reefs in low or medium exposures, while the bulk of parrotfish bioerosion was on lower exposure, deeper locations (Fig 1c). These distributional patterns are mediated by size and species-specific differences in their ability to cope with exposure regimes.

Parrotfish biomass was much higher in lower wave energy regimes (Fig 1b). Despite not having as many large parrotfish individuals as deep reefs, sheltered shallow reefs had high densities of small parrotfish from several different species and so their sheer number offset their lower per capita biomass compared to the deeper reefs. This decoupling between density and biomass, mediated through size is important to factor in when considering the overall role that a species plays within an ecosystem.

Swimming through the viscous medium of sea water has a large energetic cost – a cost that varies across the reefscape, with the tide and with the season. In negotiating currents and waves, fish can either be streamlined and small, or larger and invest in robust swimming architecture and musculature[36]. We found that body size was an important factor in determining parrotfish distributions in Lakshadweep.

Large parrotfish individuals were found in much lower numbers at high wave exposure sites. Even though greater musculature in larger parrotfish may allow them to be stronger swimmers, the cost of increased drag appears to outweigh the benefit of increased swimming abilities. In contrast, smaller individuals did better in accessing shallower waters with high wave exposure. Smaller size classes of shoaling *Scarus psittacus* and, to a lesser extent, *Chlorurus sordidus,* which were the dominant parrotfish in terms of numbers (over 65% of mean parrotfish density) were found disproportionately in shallower waters; in fact, *S. psittacus* was a distinct indicator of shallow reefs. Compared with larger parrotfish species, these species have a small cross-sectional area, and likely experience much less hydrodynamic drag in turbulent conditions [37].

Body shape and morphology also play an important role in determining a fish's ability to navigate turbulent conditions. Compared with acanthurids, the other dominant herbivore group in most coral reefs, scarids are more fusiform in shape, which helps them in accessing wave-exposed fronts [19,25]. However, scarids do show intra-guild variation in body depth ratio. Parrotfish BDR seemed to be an important factor in determining how abundant smaller individuals were in conditions of varying wave exposure. Most species with a high BDR were completely absent from regions of high wave exposure. For these species, it is possible that the half-yearly monsoon is strong enough to either limit recruitment or reduce post-settlement survival of these species on shallow western sites resulting in compositional differences between locations. However, species with a low BDR tended to do well in even high exposure sites. More streamlined species like *Scarus psittacus*, *S. scaber* and *Chlorurus sordidus,* with a lower body depth, were likely able to navigate high exposure regimes while escaping competition from deeper bodied and larger parrotfish individuals. The one exception to this trend was *S. prasiognathos*, a relatively deep-bodied species, that was found across exposure regimes, regardless of size class (Fig. 2). However, terminal phase individuals are often much deeper bodied than the initial phase in this species, and the smaller individuals were most often in the initial phase; dimorphic differences in BDR may potentially explain this pattern. Smaller females of *S. prasiognathos* also tended to travel in tight shoals in shallow reefs, potentially reducing individual drag and allowing them to access shallow exposed sites.

Taken together, these patterns indicate that some deep-bodied species may be able to compensate for a less efficient shape with increased muscle power as they grow in size. Therefore, the strength of the environmental filter can vary ontologically, as individuals age and potentially change their shape as well as their ability to manoeuvre strong physical gradients. Body size is a universally powerful proxy of species life history [38]. It acts as an indicator of species age, and in sexually dimorphic species, of its sex [39,40]. These could be indicative of different ontological or physiological states which could drive differences in diet, grouping and other behaviours [41,42]. In addition, size is often a good indicator of an individual's ability to compete with its conspecifics [43,44] or navigate harsh environmental conditions. Another key factor that could cause spatial separation in size classes between individuals of the same species is the distribution of resources across the reef. Without evaluating resource distributions between deep and shallow reefs, it is difficult to unequivocally know if this was a factor in determining parrotfish distribution. Smaller individuals may also be competitively excluded from deeper waters by their larger

conspecifics and congeners. However, algal cover is typically higher in shallower, flushed reefs [45,46], lending support to the idea that environmental filters could be limiting larger individuals from these locations.

The consequences of this size separation are even more stark when considering carbonate removal by parrotfish. The bioerosion potential of parrotfish is strongly linked to their size. The extent of carbonate removal by a parrotfish of a given species may grow disproportionately as they increase in size [47]. Many scraping species of parrotfish contribute very little to total carbonate removal, while large excavators are voracious consumers of coral and other carbonate material [48,49]. Trends in bioerosion track biomass differences across most reefs in Lakshadweep. However, despite having a biomass similar to deeper locations, eastern shallow sites have relatively low bioerosion. As discussed above, these locations were dominated by smaller individuals that contributed significantly to total biomass but very little to bioerosion.

Not all species contribute equally to bioerosion in Lakshadweep. *Chlorurus strongylocephalus* was the key bioeroder in the reef – contributing over 65% to the total carbonate removal by parrotfish in the reefs (Fig 3). This was despite the fact that in terms of biomass it represented only 22% of the assemblage, and only 3% of the total density. Yet, it was a ubiquitous species, found in low numbers in most reefs that we sampled and significantly influenced reef accretion rates across the islands. Previous research has shown that large excavators can contribute much higher rates of bioerosion than scrapers of the same size. In Maldivian reefs, *C. strongylocephalus* was responsible for roughly 130 times the bioerosion function compared to a scraping species of similar size, *Scarus rubroviolaceus*[47]. In low carbonate-producing reefs like Kavaratti, this means that C. *strongylocephalus* distribution and behaviour can tip reefs from being net accreting to net eroding. On the flip side, given the importance of excavating parrotfish to beach dynamics, this species may be critical for island growth and stability. Few other species also contribute to this function including *Scarus rubroviolaceus* and *Chlorurus sordidus*. Many of the large individuals of these carbonate removing species inhabited deeper waters, likely because of the energetic costs of swimming in more exposed conditions. In locations with large populations of *Bolbometopon muricatum* (Green humphead parrot fish, a large fish weighing roughly 75kg), this one species can be overwhelmingly important in carbonate removal, moving over large home ranges transporting material over several kilometres [50]. Although present, *B. muricatum* is rare in Lakshadweep reefs and we did not observe any during our surveys. In contrast, *Chlorurus strongylocephalus* is much more common, and likely to have much smaller home ranges as we know from home range studies on its close congener *Chlorurus microrhinos* [34]. While the total quantity of per capita carbonate removal may not compare to *B. muricatum*, it's much more limited home range means that its overall impact may be more concentrated and more predictable in space.

Our findings contrast with reports from the Great barrier reef or the Maldives, where greater excavator abundance was found in more exposed outer shelf reef habitats[30,51]. However, other studies from Palau and Lakshadweep have shown that wave exposure can significantly limit the function of herbivores

(including parrotfish) on reefs[19,25]. It may be difficult to completely resolve what drives these geographical differences in parrotfish distributional patterns. Given the greater strength of the 5-month long southwest monsoon in the northern Indian Ocean, the exposure contrast in Lakshadweep is likely considerably stronger than further south along the archipelagic ridge[52]. It is possible that in less turbulent conditions, large-bodied parrotfish may seek out the more productive, well aerated environments of shallow exposed reefs. Beyond a threshold however, the costs of navigating these conditions may outweigh any potential resource benefits. In a related behavioural study, we observed that large bodied individuals of key parrotfish species significantly reduced their foraging in high wave exposure conditions (publication in review), indicating why large bodied parrotfish such as *C. strongylocephalus* may avoid high exposure conditions in Lakshadweep reefs. It is important to note that our findings pertaining to parrotfish body depth are exploratory, and further studies are required before strong inferences can be made.

Understanding the variation in functional roles of parrotfish due to various environmental filters is key to understanding the bioerosional capacity of coral reefs, which in turn is a crucial component of reef health. Previous research on the effects of wave exposure on fish has focused largely on the body shape and other measures of swimming performances [19,23,25,53]. Here we show that apart from its underlying traits, exposure mediated body size plays an essential role in shaping the distribution of a species in space, which means that the distribution of functions could also vary as individuals grow. For mobile species that are important mediators of ecosystem processes, a complex set of abiotic and biotic factors could together determine how these functions vary across the reefscape. This depends on how communities are assembled in relation to environmental gradients and how individuals within these communities dynamically respond to their proximate conditions in space and time. Our results highlight that these responses can disproportionately influence the strength of ecosystem processes across the reef.

Methods

Study site and design

The study was conducted in the Lakshadweep Archipelago, a union territory of India, made up of 12 coral atolls in the Indian Ocean, off the west coast of India (Fig. 4). Lakshadweep is the northernmost archipelago of atolls in the extensive Chagos-Lakshadweep ridge. The islands occupy a total land area of 32 km^2, and had a population density of around 65,000 individuals as of 2011, making it among the most highly populated parts of rural India [54]. Although fishing is a mainstay of the Lakshadweep economy, until less than a decade ago fishing mostly targeted pelagic tuna resources, but commercial reef fisheries have recently been growing on the islands [55,56].

The archipelago is strongly influenced by the South-West monsoon winds which influence the region between mid-May and September. Most of the islands in the Lakshadweep have a north-south

orientation, and this creates a stark difference between their eastern and western aspects – while western fronts face strong currents and harsh wave conditions for half the year, the eastern aspects remain relatively sheltered. Although these contrasts in exposure are felt strongly only during the monsoon season, studies in Lakshadweep show that the recovering reef is strongly influenced by differences between wave exposure, with it influencing benthic dynamics as well fish communities [25,31,33,57]. Additionally, wave exposure also attenuates with increasing depth. These clear contrasts make the Lakshadweep a perfect system to study the impacts of wave energy as an environmental constraint on parrotfish communities.

To determine the effects of exposure on the community composition of parrotfish, we sampled fish communities at 10 sites on 3 atolls (Kavaratti, Agatti and Kadmat). At each atoll we sampled two aspects – 5 eastern and 5 western sites (sheltered and exposed), at two depth classes – 10 shallow and 10 deep sites (4-5m and 8-11m respectively). These depths represent where bioerosion is likely to contribute most to overall reef accretion rates[58]. All data collection was completed between December 2019 and March 2020.

Parrotfish distribution and community composition

To examine the effects of wave exposure on the distribution of parrotfish, we used replicate underwater visual transects for fish. The transects were conducted at 2 depth zones – Shallow (4-6m) and Deep (8-11m) on the east (sheltered) and west (exposed) aspects of each island. A total of 4 sites were chosen for each island, with 2 sites on the east and 2 on the west, except for Kadmat, where only 2 sites (one east and one west) were sampled.

At every site, we established 6 randomly laid transects with a 50m transect tape along the depth contour of the reef. We ensured a minimum distance of 15m between transects. Divers swam in a straight line along this transect, recording all parrotfish individuals that were observed within a 5m width of the tape (area of transect: 250m^2). Individuals were identified to the species level. Parrotfish are sequential hermaphrodites and most species go through morphologically distinct phases - an initial and a terminal phase [26]. For every individual encountered the observers also recorded its phase and approximate size (in cm). Sizes of individuals were estimated to the nearest centimetre and later classified into size classes. Before conducting fish transects, the observers familiarised themselves with parrotfish identification and practiced estimating fish sizes using standard reference lengths.

We converted fish lengths into biomass using the formula $W = a.L^b$, where W = Weight in grams, L = Length in centimetres, and a and b are standard, species-specific allometric parameters which we extracted from Perry et al's Reef Budget methodology[59]. When a and b values were not available for the species, we used parameter estimates for sister species or the most closely related, morphologically similar species.

Parrotfish Body Shape

In order to explore how body shape can mediate the effects of wave exposure on parrotfish, we ranked species on a gradient of shallow to deep bodied species based on their body depth ratio (BDR). Deep bodied fish have been associated with increased manoeuvrability in complex reef habitats whereas stronger and more sustained swimming is more easily achieved with more fusiform body plans (Larouche. et. al. 2020). BDR was calculated as the ratio of the maximum body depth at the deepest part of the body to the standard length of the fish in order to make body depth measurements comparable across fish of different sizes [19]. Morphometric parameters were calculated using the software Image-J by measuring multiple images obtained from Fishbase (Froese and Pauly, 2000), I-naturalist (https://www.inaturalist.org) or taken by the authors, and then averaging the values for each species. Only those images where the entire planar view of the individual was clearly visible were used in order to get accurate measurements. We grouped the variables of size and exposure in order to better visualise trends pertaining to body depth ratio. Here individuals were divided into two size classes – small (less than or equal to 20cm), and large (greater than 20cm) and only species for which there were more than 5 separate observations were included. For ease of representation and discussion depth and aspect were also grouped as a single variable. Deep sites face much less wave exposure than shallower sites and so were grouped as low exposure, sheltered shallow sites were medium exposure and shallow exposed sites were classified as high exposure sites.

Bioerosion rates

To assess the role of parrotfish in reef accretion patterns across contrasts of depth and aspect we employed species- and size-specific bioerosion rates from the *Reefbudget* methodology [60]. The *ReefBudget* protocol estimates rates of bioerosion for different species, sizes and phases of parrotfish, based on studies across the Indo-Pacific. We used these published rates to calculate total bioerosion by parrotfish for a reef site based on their density, species composition and size distribution.

Statistical Analysis

Parrotfish density: A generalised linear mixed effects model was constructed to model the effects of wave exposure on parrotfish density. Size class, depth, aspect and their interactions were used as fixed effects along with island, while sites nested within islands were used as random effects. Individuals were assigned to size classes as follows: small: <=20cm; medium: > 20cm < = 35cm; large: > 35cm. A negative binomial error distribution was used in the model due to overdispersion. The model structure (M1) was as follows-

Density ~ Depth.Class*Aspect*Size.Class + Island +(1|Island:Location)

Parrotfish biomass

A linear mixed effects model was constructed to model the effects of wave exposure on parrotfish biomass. A constant of 100 was added to the biomass values before log transforming, in order to meet the assumptions of normality. Depth, aspect, island and the interaction between aspect and depth were

used as fixed effects and sites nested within islands was used as a random effect. The model structure (M2) was as follows −

log(Biomass + 100) ~ Depth.Class*Aspect + Island +(1|Island:Location)

Parrotfish Species richness

A generalised linear mixed effects model was constructed to model the effects of wave exposure on parrotfish species richness. Depth, aspect, island and the interaction between aspect and depth were used as fixed effects and sites nested within islands was used as a random effect. A negative binomial error distribution was used in the model due to overdispersion. The model structure (M3) was as follows -

Species richness ~ Depth.Class*Aspect + Island+(1|Island:Location)

Parrotfish Bioerosion

A linear mixed effects model was constructed to model the effects of wave exposure on parrotfish bioerosion. A constant of 0.001 was added to bioerosion values before log transforming, in order to meet the assumptions of normality. Depth, aspect, island and the interaction between aspect and depth were used as fixed effects and sites nested within islands was used as a random effect. The model structure (M4) was as follows -

log(Bioerosion + 0.001) ~ Depth.Class*Aspect + Island +(1|Island:Location)

The statistical analysis software R version 3.6.0 (2019) was used for conducting all statistical analysis. The r packages glmmTMB, lme4, and vegan were used in the analysis of the data The package ggplot2 was used to plot the data.

All experimental protocols were approved by the Government of India's Department of Science and Technology - Science and Engineering Research Board (DST-SERB); project reference no. - EMR/2017/004014/AS. All methods were carried out in accordance with relevant guidelines and regulations. Informed consent was obtained from all divers prior to their participation the study.

Declarations

Authors Contributions:

W.P, R.A and T.A conceived the ideas and designed methodology; W.P, R.A, F.D.P and M.D collected the data; W.P analysed the data; W.P, R.A and T.A led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publications. Authors declare no conflicts of interest.

Additional Information

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability Statement

Data available from the Zenodo repository. (DOI: 10.5281/zenodo.7464585)

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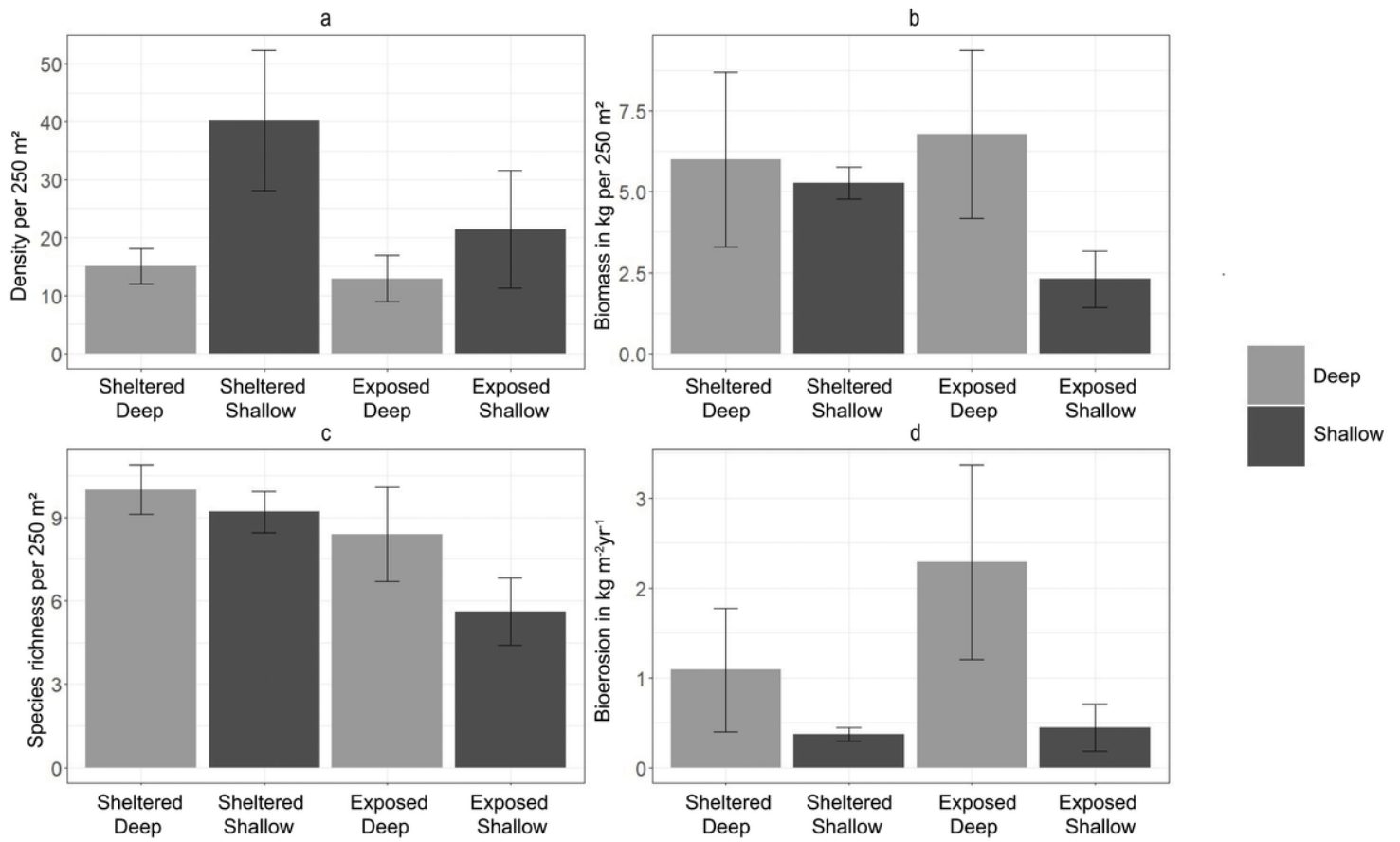
Figures

Figure 1

Parrotfish distributions in Lakshadweep reefs in relation to wave exposure (sheltered and exposed) and depth (deep and shallow): a − Parrotfish density; b − Parrotfish biomass; c-Parrotfish species richness; d-Parrotfish bioerosion rates. Error bars are Standard Errors.
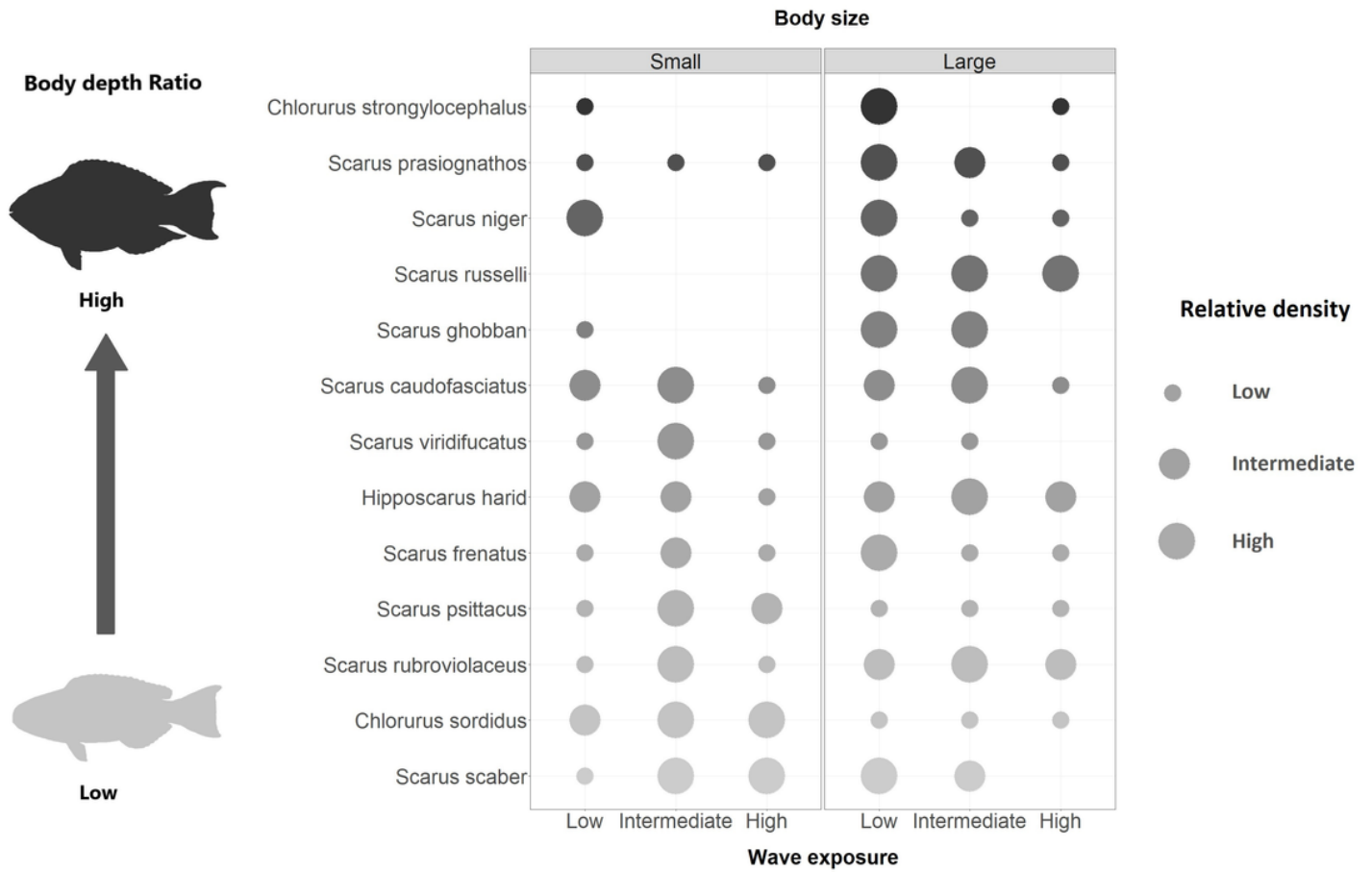
Figure 2

Effects of wave exposure on the density of parrotfish of different body sizes and body shapes. Circle size represent the relative density of individuals across the gradient of wave exposure for each species i.e., the size of the circles for each species are independent of other species.
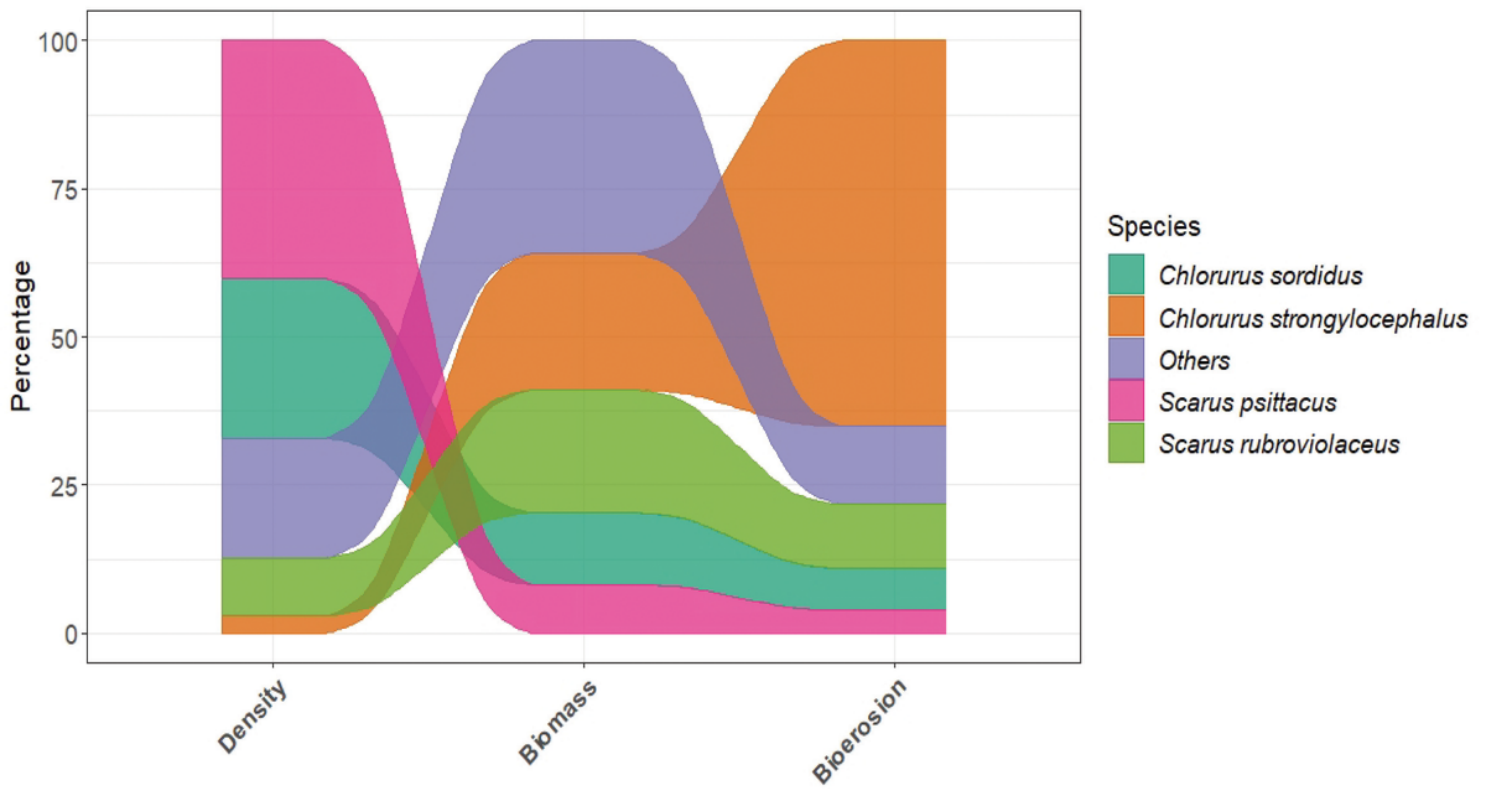
Figure 3

Mean parrotfish density, biomass and bioerosion for key species. Despite contributing only 3% to total density of parrotfish, Chlorurus strongylocephalus contributes over 65% to the total bioerosion.
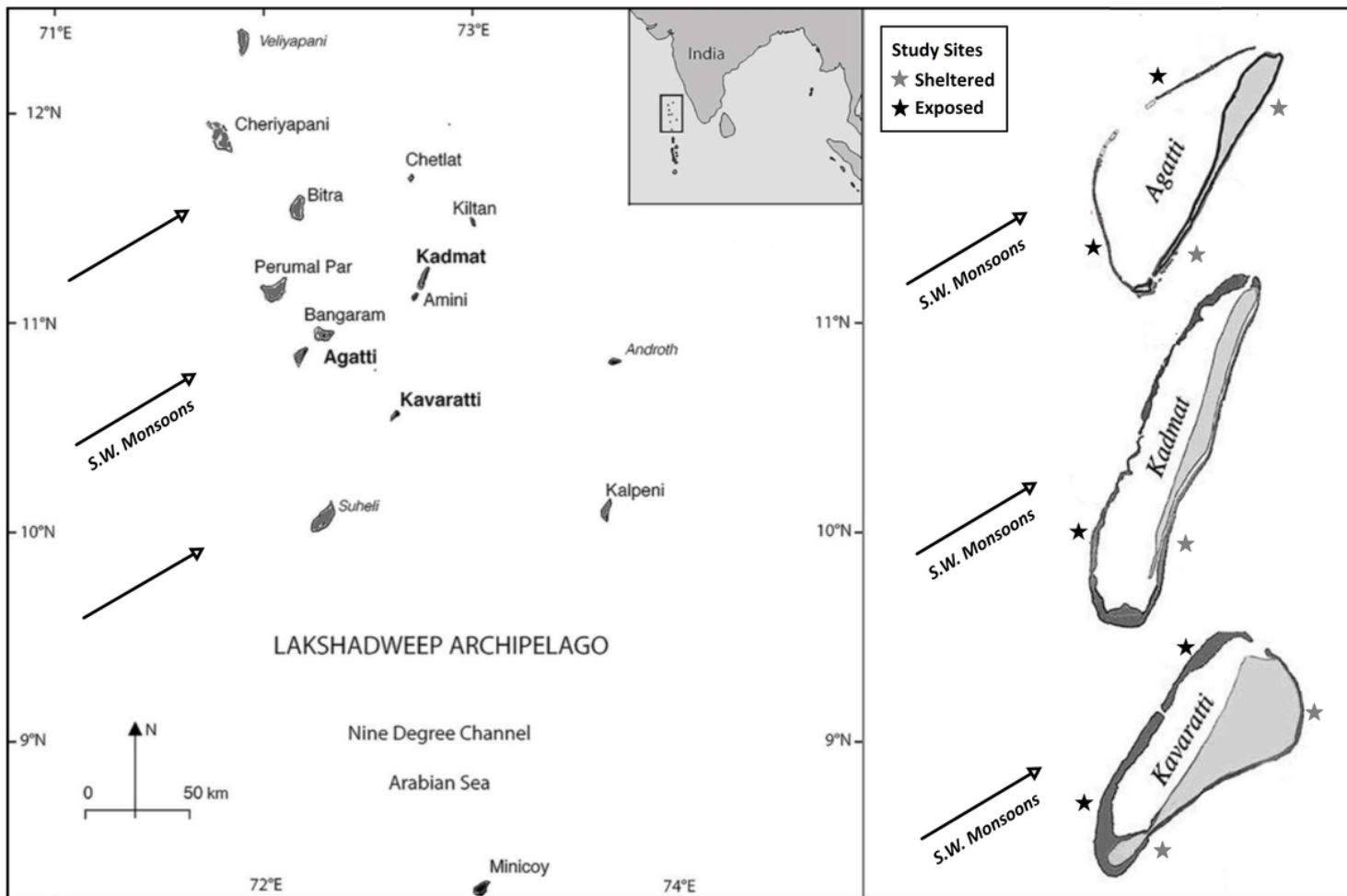
Figure 4

A map of the Lakshadweep Archipelago, with the sampling islands as insets. Map not to scale.

Supplementary Files

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