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Policy analysis

Reduced human activity in shallow reefs during the COVID-19 pandemic increases fish evenness

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ABSTRACT

The COVID-19 pandemic provides a rare opportunity to examine effects of people on natural systems and processes. Here, we collected fish diversity data from coral reefs at the Israeli Gulf of Aqaba during and after the COVID-19 lockdown. We examined beach entrances to the reef, nearby shallow reefs and deeper areas exposed mostly to divers. We found that the lockdown elicited a behavioral response that resulted in elevated species richness at designated reef entrances, predominantly influenced by increased evenness without changes to total abundances. This effect was observed both at the local scale and when several beach entrances were aggregated together. Consequently, non-extractive human activities may have substantial short-term impacts on fish diversity. Our insights could help designate guidelines to manage visitor impacts on coral reefs and aid in their prolonged persistence.

1. Introduction

Measures to control the spread of the COVID-19 pandemic precluded, or significantly reduced, human activity in nature (Rice et al., 2020). These circumstances offered a unique opportunity to test how organisms react to the absence of humans (Bates et al., 2020; Rutz et al., 2020). Several studies provide examples of reduced human pressures on natural ecosystems, cleaner air, and cleaner water (Corlett et al., 2020; Zambrano-Monserrate et al., 2020). Covid-19 lockdowns and travel restrictions have been noted to cause changes to animal behavior, with some animals reclaiming areas that they usually have been precluded from or becoming more diurnal (Manenti et al., 2020; Vardi et al., 2021; Zellmer et al., 2020).

Coral reefs are some of the most diverse ecosystems globally and face multiple threats, including climate change, overfishing, pollution, and physical destruction (Hughes et al., 2017; Munday, 2004; Riegl et al., 2009). Extractive human activities have large effects on fish abundance, diversity and evenness, as seen by the change in fish communities with MPAs compared to fished areas (Blowes et al., 2020; Claudet et al., 2006). Non-extractive recreational activities in coral reefs, such as swimming, snorkeling or scuba diving, promote human-nature interactions, but may also adversely affect biodiversity (Davenport and Davenport, 2006; Hawkins and Roberts, 1993; Zakai and Chadwick-Furman, 2002). To date, effects of such activities have predominantly focused on corals, and research on the impacts of swimmers and divers on fishes are uncommon. Nevertheless, Medeiros et al. (2007) compared two coastal reefs and found indications that recreational activities lead to lower fish assemblage evenness, driven by changes in the abundance of a single species (*Abudefduf saxatilis*). Other effects of recreational activities on fishes include reduced cleaning by cleaner (Titus et al., 2015); shorter latency periods and escape distances (Valerio et al., 2019); increased use of refuge during presence of divers and snorkelers (Benevides et al., 2019). On the other hand, fish feeding based tourism has be shown to boost fish diversity (Brunnschweiler and Earle, 2006; Feitosa et al., 2012) and to expand trophic niches (Drew and McKeon, 2019). These human-induced changes may have cascading effects on

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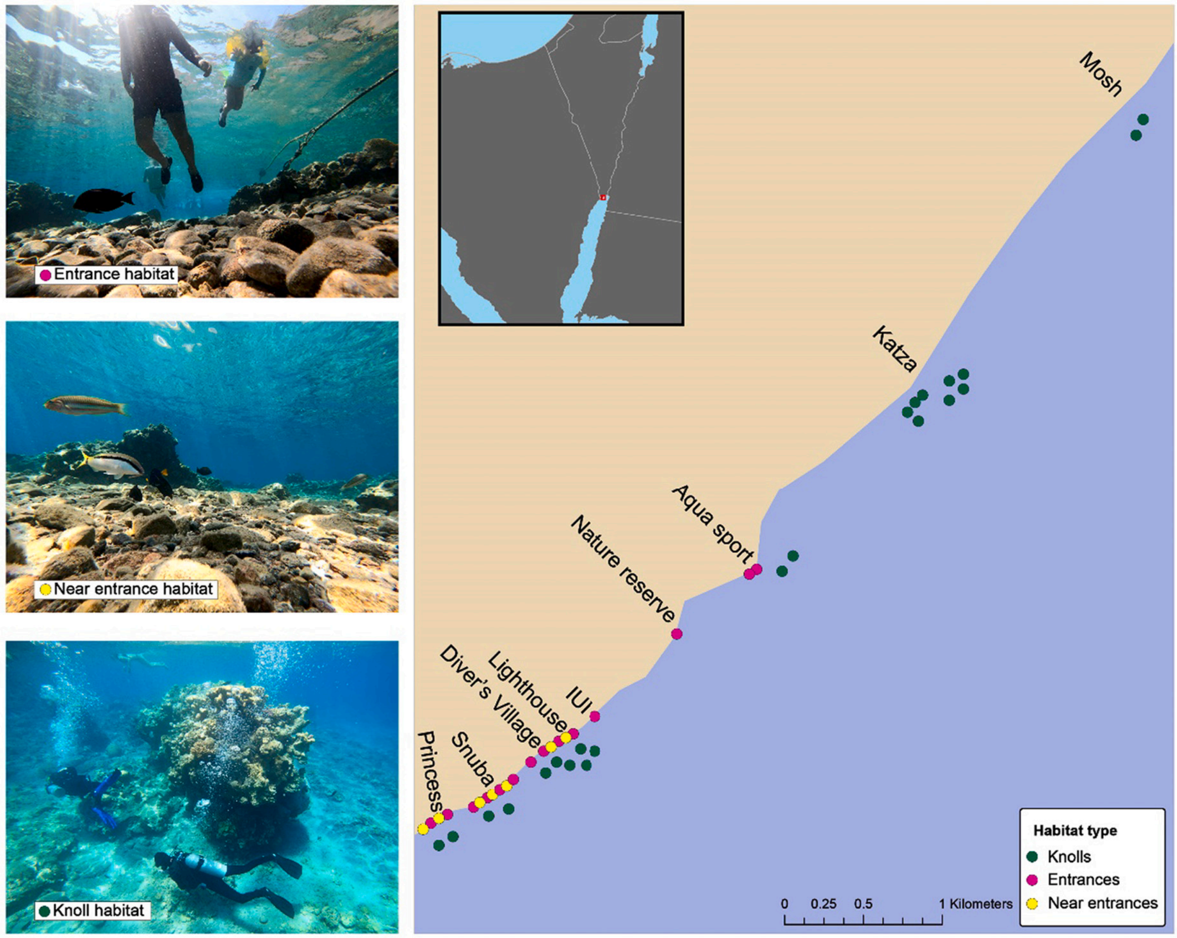

Sampling session	habitat	Mosh	Katza	Aqua sport	Nature reserve	IUI	Lighthouse	Diver's village	Snuba	Princess
Lockdown 14/4-7/5	● Knoll	2	8	2			3	3	2	2
	● Entrance			2	2	2	2	2	2	
Post lockdown 1 16/6–17/7	● Knoll	2	8	2			3	3	2	2
	● Entrance			2	2	2	2	2	2	
Post lockdown 2 8/8–27/8	● Entrance						2		6	2
	● Near entrance						2		6	2

Fig. 1. Map of study area and sampling scheme. Each point represents a site sampled; colors represent habitat type. Insert shows the study area within the larger region. Representative underwater photos of each habitat type are to the left of study area map. Detailed sampling scheme at the bottom of the figure depicts which sites and habitats were sampled during each of the three sampling sessions.

other fish species (Milazzo et al., 2006). Nevertheless, it remains unclear whether recreational activity impacts are chronic or acute and whether they remain local or span spatial scales.

Species richness is one of the most widely-used biodiversity metrics, but is dependent on several distinct mechanisms (McGlinn et al., 2019). To better understand variation in species richness and the mechanisms contributing to it, it should be decomposed to (1) the size of the species pool, (2) the relative abundance of species, with more even communities displaying higher richness, (3) the number of individuals, with denser communities showing higher richness, (4) intraspecific aggregations, with aggregations decreasing richness within a given scale. Such decomposed richness could produce new insights on the effect of humans on fish biodiversity.

COVID-19 lockdowns may help elucidate short- and long-term impacts of humans on coral reefs (Giglio et al., 2020). For example, if human activity causes long-term damage to the habitat, we can expect local reductions in fish density within impacted sites, which is likely to result in lower richness (Wilson et al., 2008). This reduction in diversity will remain during short-term cessation of human activity such as during COVID-19 lockdowns. However, if human activity causes short-term behavioral changes (Albuquerque et al., 2014), we could see changes to richness during COVID-19 lockdowns due to changes in spatial aggregation or evenness of fishes that are either attracted to or repelled by humans. Both long-term and short-term effects may either accumulate across spatial scales or mostly manifest at the local scale.

Here, we tracked changes to coral reef fish diversity across spatial scales from the local site level to the landscape level (5 km stretch of the coral reef reserve in Israel) following the cessation of human activity because of a COVID-19 lockdown. We measured fish diversity at three different coral reef habitats: (1) shallow areas designated as 'entrances' to the reefs with high levels of activity by swimmers, snorkelers, and divers; (2) shallow areas 'near-entrances' with low levels of human activity, and (3) 3–6 m deep 'knolls' which are mostly visited by SCUBA divers and are also exposed to low levels of human activity. Comparing

Table 1
Comparisons made in this study, their corresponding hypotheses, summary of their main findings, and significance.

Comparison between	Hypothesis tested	Summary of findings	Significance
'Knolls' during (14 April–5 July) and after lockdown (16 June −17 July)	Caseation of human activity will result in increased species richness	We found no change in species richness	Lesser visited and deep habitats do not show short term effects of cessation of activity on diversity
'Entrances' during (14 April–5 July) and after lockdown (16 June −17 July)	Caseation of human activity will result in increased species richness	Species richness during lockdown was higher due to increased evenness	Local changes in human activity manifest in changes to diversity
'Entrances' and 'near entrances' post lockdown (8–27 august)	Reduced human activity 'near entrances' relative to 'entrances' will result in increased species richness	Species richness in near entrances was higher due to increased evenness	Local changes in human activity manifest in changes to diversity
'Entrances' during lockdown (14 April–5 July)and 'near entrances' post lockdown (8–27 august)	Habitats with similar low human activity levels will have similar species richness	We found no differences in species richness	Low levels of human activity show similar effects on diversity to complete cessation of human activity

changes to fish richness during and after a lockdown allowed us to understand the mechanisms underpinning potential human impacts on coral reef fishes.

2. Methods

2.1. Study site

We sampled three different coral reef habitats (1) 'entrances', (2) 'near-entrances', and (3) 'knolls' at nine sites across a ~5 km fringing reef along the northern Gulf of Aqaba, in Eilat, Israel (Fig. 1; Note, that not all habitats were available at each site). Due to ease of access, coral reefs in Eilat are among the most heavily visited with ~6 million tourists annually with >300,000 dives per year along a 12 km coastline (Tynyakov et al., 2017). The entire reef area sampled is within a well-enforced marine nature reserve with no fishing. While coral reefs are easily accessible from the shore, entrance to the sea is only allowed at specific marked entrances 4-8 m wide delineated by ropes (there are a total of 19 entrance points along the beach of the nature reserve).

Post lockdown human activity varied between the different habitats we sampled. The highest activity levels were measured at 'entrances' where swimmers, snorkelers and divers enter and exit the water, and bathers are usually abundant. At the 'near entrances' swimmers, snorkelers and divers can swim above the coral reef, but are not allowed to stand or make other contact with the reef. 'knolls' are deeper and access to them is limited mostly to divers, (see Fig. S1 for objective measurements of human activities in each habitat type). We found no significant difference in human activity levels post-lockdown between different entrance sites (Tukey-HSD adjusted p-value>0.074).

2.2. Sampling periods during and after the first COVID-19 lockdown

The first COVID-19 lockdown in Israel (19/03/2020–20/5/2020) was very tight and access to beaches or entering to the sea was prohibited and strictly enforced (we found zero human activity in our lockdown samples; Fig. S1). Touristic activity resumed after the lockdown to levels similar to those measured during 2019 and peaked during July–August (Fig. S2). Beaches were relatively crowded, and diving activity resumed (until a second lockdown started during September 2020). We conducted three sampling sessions. In the first two sessions (during and post lockdown) we tested the effect of the lockdown on 'entrance' and 'knoll' habitats. The third sampling session was added to test for possible temporal changes and test potential movements of fish to adjacent habitats by also examining the 'near-entrances' habitat (see Table 1 and Fig. 1 for all comparisons made and the spatial distribution of sites).

2.3. Sampling method

Data were collected via video surveys. GoPro-8 cameras were deployed randomly within the pre-selected sites to maximize spatial coverage along the nature reserve (see Fig. 1 for sampling design). Cameras were placed without baits in natural light between 11:00 and 14:00 each day and recordings were activated for 45 min (at 4K/24P). From each video we recorded fish species identity and abundance (using "maxN": maximum number of individuals per frame for a given species) (Bacheler and Shertzer, 2015; Campbell et al., 2015). We analyzed 20 min from the middle of each recording (minutes 10–29) to minimize the effect of deployment and collection. A total of 5144 individuals belonging to 111 different fish species were recorded (mean 17.75 species and 58.45 individuals per video). We further quantified human activity levels from these videos (for details see "Human activity" in Supplement; Fig. S2).

2.4. Analyses

The different comparisons we made are summarized in Table 1. For each comparison, we first analyzed changes to local species richness (α-diversity), total species richness across all sites (γ-diversity) and species turnover between sites (β-diversity, the ratio of total to local richness). We then examined changes in species richness across spatial scales using rarefaction curves and thus aggregating an increasing number of sites. We then used the 'Measurement of Biodiversity (MoB)' approach in the R package 'mobr' (McGlinn et al., 2019) to decompose these changes in richness into components attributed to (1) the relative abundance of species (evenness), (2) the number of individuals, (3) spatial autocorrelation due to intraspecific aggregation (see Supplement for details - "The MoB approach").

To gain a deeper understanding of the changes in diversity, we also performed a cross-species analysis. We calculated for each species the bias-corrected log response ratio ('SinglecaseES' R package; James Pustejovsky, 2019), as the logged abundance post-lockdown divided by the abundance during lockdown (Hedges et al., 1999). We further explored the potential effects of fish traits in differentiating between species that increased or decreased their abundance during the lockdown. We obtained the following ecological traits per species (following Belmaker et al., 2013): fish family, diet, home-range, schooling, height in the water column, body size, and trophic level (see Supplement for full details - "Description of the predictors"). To relate these traits to the log response ratio, we adopted an exploratory approach using linear mixed models framework with fish traits as predictors, 'fish family' as a random effect, and the inverse of the variance of the log response ratios as weight (lme4 R package; Bates et al., 2015). All analyses were conducted in R (R Core Team, 2020).

3. Results

The COVID-19 pandemic and consequent lockdown precluded human activity from coral reefs in the Israeli Gulf of Aqaba (Figs. S4, S5).

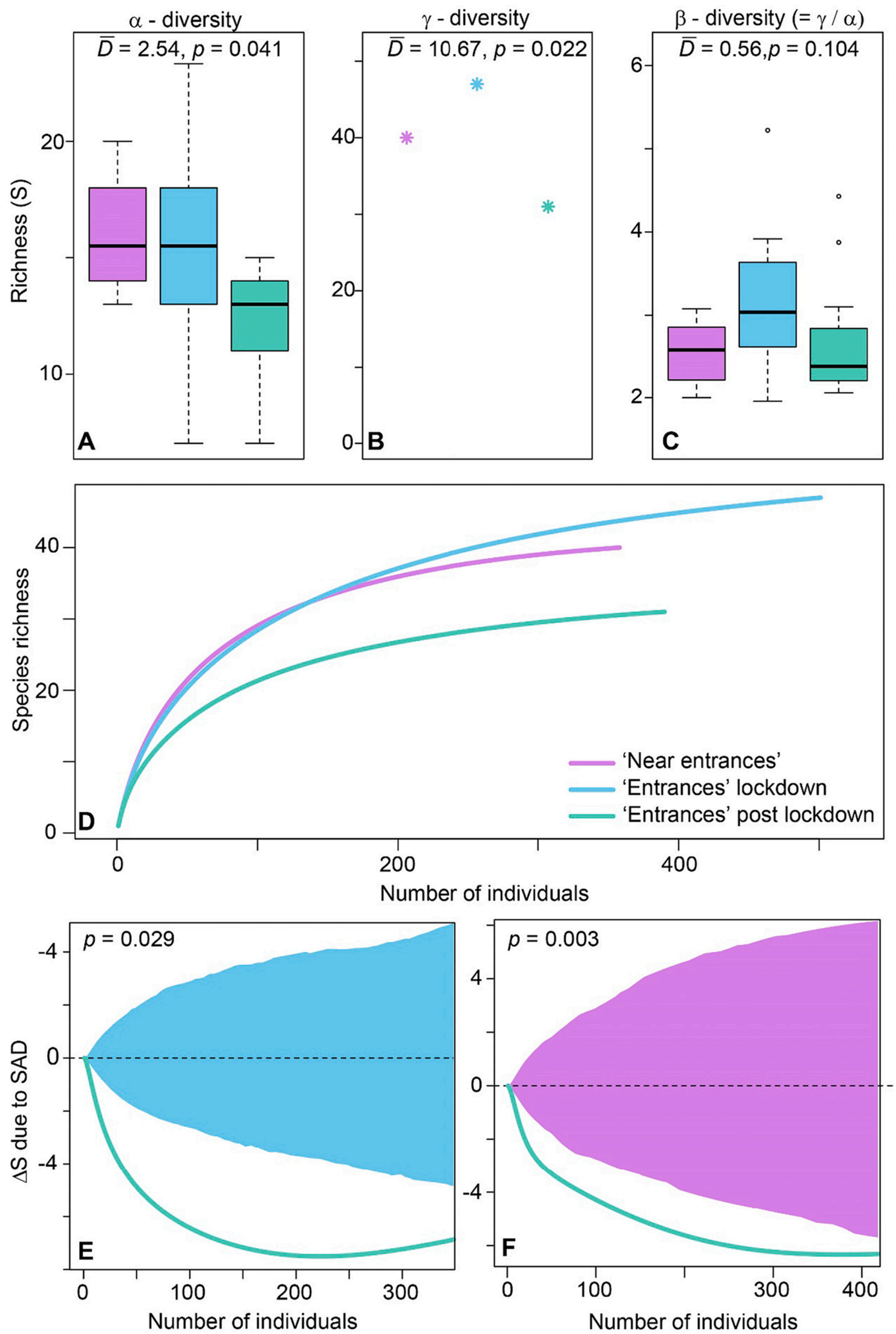

Fig. 2. Comparison of species richness. Panels A, B, C represent a two-scale analysis of species richness; (A) α-diversity sample-level, (B) γ-diversity, (C) β-diversity. p-Values are based on a Monte Carlo permutation procedure applied by the MoB algorithm. Test statistic $\overline{D}$ is average absolute difference in richness between pairwise group comparisons. Dots in figure C represent value two times higher than upper quartile. Panel $\overline{D}$ presents individual-based rarefaction curves for each habitat. Species richness (y-axis) is plotted as a function of the number of individuals (x-axis). Panels E and F represent two pairwise comparisons of a multi-scale analysis comparing pairs of habitats. Panel E compares the expected change in species richness due to differences in species abundance distribution between the 'entrances' during and post lockdown (green line), while the blue shaded area represents 95% acceptance intervals (p-value = 0.029, DCLF significance test). Panel F represents multi scale comparison between 'near entrances' and 'entrances' post lockdown, once again differences are significant (p-value = 0.003, DCLF significance test). Habitats are color coded purple - 'near entrances' post lockdown; blue – 'entrances' during lockdown; green – 'entrances' post lockdown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1. *Two scale analysis*

We did not find significant changes in 'knolls' richness during versus post lockdown, at any scale (Fig. S3, p-value > 0.724, based on Monte Carlo simulations). However, at 'entrances' sites, richness during the lockdown was consistently higher relative to post lockdown (Fig. 2). We found these differences were manifested both at the sample level (Fig. 2A, α-diversity, p-value = 0.041 based on Monte Carlo permutations), and across all samples (Fig. 2B, γ-diversity, p-value = 0.022 based on Monte Carlo permutations). Similarly, post-lockdown richness at the 'entrance' sites was consistently lower than the 'near-entrance' sites post-lockdown (α–diversity: Fig. 2B, p-value = 0.047; γ-diversity: Fig. 2B, p-value = 0.05). In contrast, we found no significant change in richness when we compared 'near entrance' sites post-lockdown to 'entrance' sites during the lockdown nor when we compared 'entrance' sites during the two post-lockdown sessions (Fig. S4 panels C and D, p-value > 0.114).

3.2. *Measurement of Biodiversity*

Next, we used the MobR approach to decompose changes in richness in the 'entrances' as a consequence of the lockdown. We found that differences in richness of 'entrances' were mainly driven by higher evenness in the species abundance distributions during the lockdown (Fig. 2A and E, p-value = 0.029 based on Diggle-Cressie-Loosmore-Ford – DCLF test). Similarly, we found that differences in richness between 'entrances' and 'near entrances' were mainly driven by higher evenness in the species abundance distribution of the 'near entrances' habitat

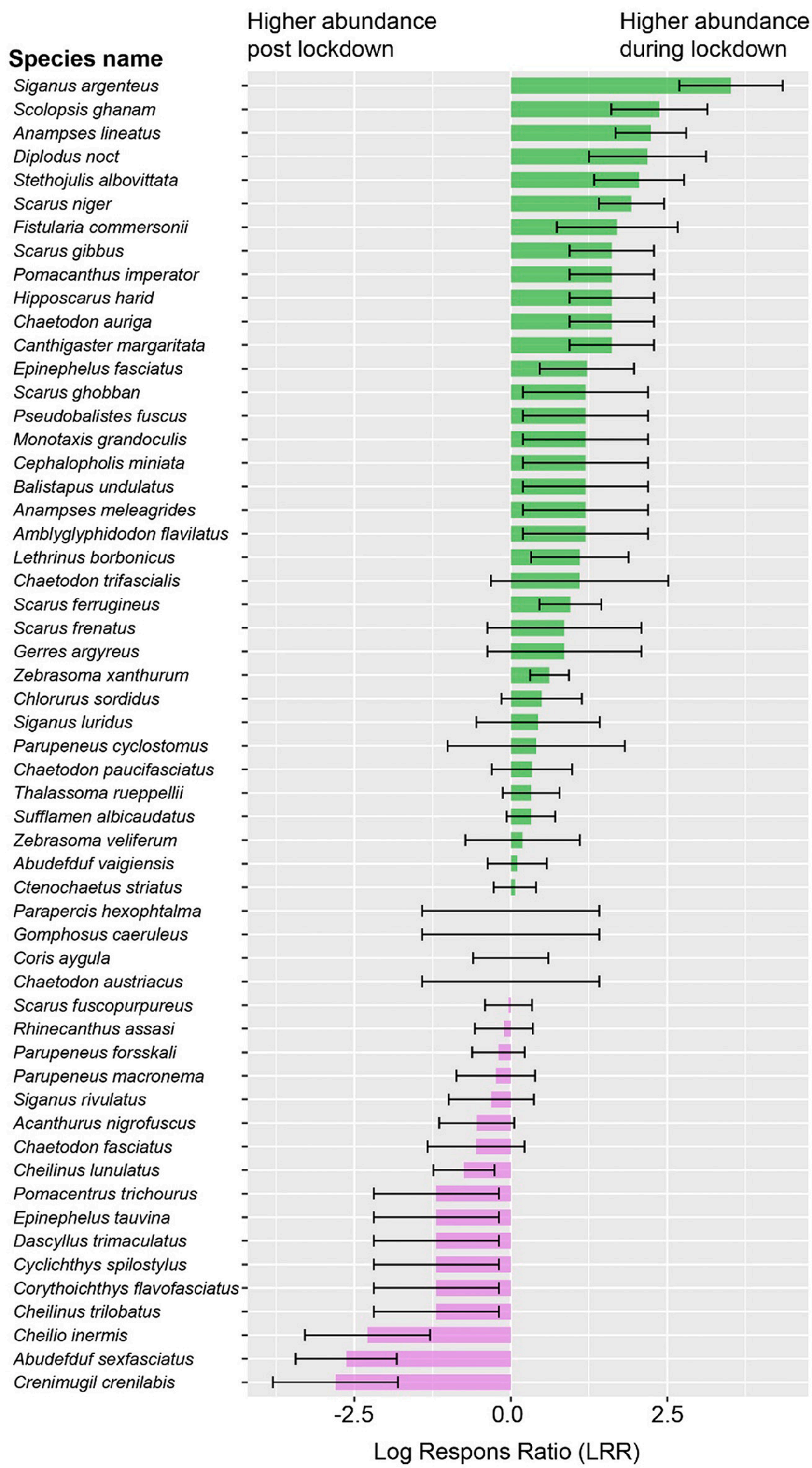

Fig. 3. Changes in species abundance during and after lockdown. The figure shows species level log-ratio of mean abundance during lockdown relative to mean abundance after the lockdown in the 'entrance' sites. Green bars represent species which their abundance was higher during lockdown, red bars represent species which their abundance was lower during lockdown relative to their abundance post lockdown. Error bars represent 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fig. 2A and F, p-value = 0.003 based on DCLF test). The number of individuals and intraspecific aggregation did not have a significant effect on species richness (Fig. S5, p-value > 0.216).

3.3. Species level changes

We found that species showed variable changes to the removal of the lockdown (Fig. 3) *Siganus argentus*, *Scolopsis ghanam* and *Anampses lineatus* showed the highest increase in abundance during lockdown, while *Crenimugil crenilabis*, *Abudefduf sexfasiatus* and *Cheilio inermis* increased in abundance post-lockdown. SIMPER test (Clarke, 1993) based on Bray-Curtis dissimilarity showed that *Abudefduf vaigiensis*, *Siganus rivulatus*, *Acanthurus nigrofuscus*, *Fistularia commersonii* and *Diplodus noct* together contribute about 50% of the dissimilarity between 'entrances' sites during and post lockdown. However, a linear mixed model could not detect traits that explained the change in species abundances due to the lockdown (Table S1).

4. Discussion

The COVID-19 lockdown was associated with a significant rise in reef fish diversity in the habitat that receives most human activity – reef entrances - but not at deeper or less disturbed habitats (Figs. 2, S3 and S4). These differences were associated with an increase in species evenness during lockdown, a phenomenon that was also apparent at 'near-entrances' sites post the COVID-19 lockdown (Fig. 2). While we show an effect of non-extractive human activity on fishes in the reef entrances, these effects are reversible temporally and restricted spatially. Thus, restricting human activities to few designated entrance points can minimize the total effects of human disturbances on reef fishes.

We found that the reduction in human activity during lockdown at the heavily visited 'entrance' habitats had similar effects to restricting human activity year-round at the 'near entrance' habitats (Fig. 2). These findings demonstrate that short-term temporal cessation in human activity has similar effects to long-term spatial restrictions. As the lockdown effect was short-term, we show that at least some of the human impacts to the reef are reversible and are likely related to fish behavior and not habitat alternation. For example, human disturbances at 'entrances' may drive some species to nearby habitats, may shift activity times to periods with less human disturbance (Gaynor et al., 2018), or cause some species to hide or inhibit their movement (Benevides et al., 2019; Côté et al., 2014). However, short term behavioral shifts between high and low disturbance sites may not be enough to mitigate the effect of human disturbance (Albuquerque et al., 2014). Changes to fish assemblages associated with intensive recreational activities lack long term monitoring, and should be better integrated into scientific research and management (Giglio et al., 2020).

In the deeper 'knoll' habitat, accessible mostly to divers, we did not find an effect of the lockdown on species richness (Fig. S3). This can be due to two opposing, yet non-exclusive, mechanisms: (1) divers' impacts on these deeper habitat are mostly associated with physical breakage of the coral (Albuquerque et al., 2014; Zakai and Chadwick-Furman, 2002) cause long –term habitat degradation and thus fish diversity is non-responsive to changes in human activity. (2) Alternatively, fish may perceive divers as a low threat and hence their impact may be lower than those of bathers in shallow reefs. Our data cannot currently differentiate between these two potential mechanisms.

The main driver of changes to species richness in our study was differences in evenness. At the 'entrance' sites communities had more even relative abundances during lockdown (Figs. 2 and S5). The effect of the lockdown on evenness was not limited to the local site scale. Changes in evenness seem to also drive differences in richness across all the spatial scales measured. Hence, while human recreational impacts may be reversible temporally, they may at the same time accumulate across all spatial scales and substantially change diversity. Our findings are consistent with other studies that found declines in evenness due to non-extractive human activities (Medeiros et al., 2007) and are further consistent with the long-term effect of fishing, as MPAs are characterized by higher evenness even when no change in fish abundance is detected (Blowes et al., 2020). It is interesting that the short term behavioral changes associated with the lockdown are similar to the long term impacts of MPAs and may suggest that, at the community level, evenness is more sensitive to human disturbance than richness or total abundance that are more commonly reported.

Interestingly, we did not find an effect of the lockdown on density (number of individuals) or intraspecific aggregation (Fig. S5). In addition, we could not detect traits that explain which species increased or decreased their abundance (Table S1). The similar density values we found could arise from a substitution of individuals of some species by individuals of others (probably occurring at local scales with no consistent spatial pattern). It is less clear why we did not detect the lockdown effect on aggregation, but we believe this could reflect the habitat patchiness across sites which was not affected by the lockdown.

While we found some changes to species diversity, we did not explore many other potential human effects on coral reef fish species. These include the long-term impact of human activity on the permanent degradation of the habitat, and changes to the demography and diet of fishes. We also did not measure direct behavioral changes or the effect of seasonal changes in touristic activity. Future studies could also benefit from exploring stress levels of fish and how they are related to human presence as this may have nontrivial cascading effects.

Although we found that human interference at 'entrance' sites is intensive, their total areas is small (there are a total of only 19 such entry points). Therefore, fishes that are adversely impacted by humans may simply utilize nearby habitats. This suggests that limiting recreational activity from the beach to entrance points is an effective management policy to minimize total recreational human impacts on coral reefs.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109103.

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