Shifts in coral reef fish populations linked to human pressure and tourism activities revealed by COVID-19 restrictions

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Shifts in coral reef fish populations linked to human pressure and tourism activities revealed by COVID-19 restrictions

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DL originally formulated the idea, DL and FB developed methodology, DL, LM, CB, FB, VW conducted the formal analysis and investigation, FB and EG wrote the original draft, FB, EG, SCM, NR reviewed and edited the manuscript, DL acquired the funding, TM, VS, GTS provided resources.

Abstract:

Throughout the world, anthropogenic pressure on natural ecosystems is intensifying notably through urbanisation, economic development, and tourism. Coral reef organisms worldwide have become exposed to stressors related to tourism activities. To reveal the impact of human activities, the COVID-19-related social restrictions put in place since 2020 can be used. In French Polynesia, from February to December 2021, there was a series of restrictions of local activities as well as bans of international tourism. These led to variations in the intensity of tourism activities. Here, we aim to determine the consequences of the rapidly changing activity restrictions on the species richness and density of juvenile and adult fish of all species and of harvested species in the lagoon of Bora-Bora (French Polynesia) across sites dedicated to tourism activities, affected by boat traffic, or with low traffic and tourism. Underwater visual surveys demonstrated that the density and species richness of juvenile and adult fish of all species and of harvested species were highest during total lockdowns and lowest when all activities were authorised. Adult and juvenile fish density and species richness increased the most during periods without tourism on sites usually visited by tourists. Fish density and diversity were lowest on sites affected by boat traffic regardless of restriction level, indicating a strong influence of human presence on fish sightings in the lagoon. Overall, COVID-19-related restrictions highlight that human activities are major drivers of fish abundance and species richness on Bora-Bora, calling for a sustainable planning of the lagoon usage.

Keywords: human impacts, fish, coral reef, sound pollution, COVID-19

Introduction

Human activities in natural ecosystems at the global scale are intensifying due to demographic increases, economic development, industrialisation and urbanisation, and the rise in mass tourism. Whilst not minimising or forgetting its considerable human cost, the COVID-19 pandemic provides a unique opportunity to study the impact of human activities on ecosystems. Pandemic-related travel and activity restrictions led to a global 'anthropause' (Rutz et al. 2020b) which, in many areas, translated into a decrease in human pressures on ecosystems and in the exploitation of natural resources. From 2020, studies began to highlight reductions in human activities and improvements in water quality in coastal zones throughout the world (review from Mallik et al. 2021). Among those, lower noise pollution was observed along a ferry lane in Scandinavia (De Clippele and Risch 2021), and higher fish abundances were linked to decreased fishing activities in the Gulf of Mannar, India (Patterson Edward et al. 2021). However, the impacts of tourism on ecosystems, as revealed through the lens of the decrease in tourism associated with the COVID-19 pandemic, have been less studied.

Among the ecosystems affected by tourism that could be studied, coral reefs stand out as particularly important in the context of this anthropause. Coral reefs contain 25% or more of the global marine biodiversity, although they only represent 0.1% of the surface area of the oceans (Reaka 1997; Spalding et al. 2001). Coral reefs provide food and livelihood to a large fraction of the 850 million people worldwide that live within 100 kilometres of a reef (Burke et al. 2011), and are key resources for marine-based tourism in over 100 countries and territories (Spalding et al. 2017). Ocean warming and acidification are two global drivers of coral reef degradation (Pörtner et al. 2019), but tourism can be, at a local scale, a major cause of damage and stress on reefs and the organisms that they shelter (Spalding et al. 2017). These issues notably arise through boat traffic, diving, and snorkelling (Rouphael and Inglis 2001), but also because of indirect activities such as coastal urbanisation and the extraction of resources to accommodate tourists (Tratalos and Austin 2001; Uyarra and Côté 2007; Siriwong et al. 2018; Gairin et al. 2021; Giraud-Renard et al. 2022). Tourism is one of the economy sectors that has been most affected by the COVID-19 pandemic worldwide due to a large decrease in international travel. The direct and indirect tourist generated pressures on ecosystems were thus likely affected by COVID-19. For instance, the fall in tourism and business linked to the pandemic led to an improvement in water quality with reduced turbidity in Vembanad Lake, India (Yunus et al. 2020). With the reduction in noise, frequentation, littering, and activities during two months of lockdown in 2020, burrowing crabs were more numerous on beaches and dunes in Latin America (Soto et al. 2021). On coral reefs in Guadeloupe, lower recreational boat noise pollution during a lockdown led to a reduction in vocalisation sounds produced by fish to communicate, which may indicate that communication was more efficient, with less sound needing to be produced in the absence of boat traffic (Bertucci et al. 2021). Data on coral reef fish communities of Bora-Bora, French Polynesia, before, during, and after the first pandemic-related lockdown in 2020 found that, during the lockdown, fish returned to sites usually frequented by tourists, where total fish abundance more than doubled (Lecchini et al. 2021). However, coral reef fish communities were only monitored over six months in 2020, in response to one lockdown and at a limited number of sites (Lecchini et al. 2021).

Here, we present survey data on coral reef fish communities of Bora-Bora throughout the entire year of 2021, over five different COVID-19 restriction periods associated with various types of lagoon usage, incorporating a three categories of sites. Bora-Bora is a French Polynesian island, famous worldwide for its blue lagoon and coral reefs. More than 95% of tourists visiting the island come from outside Polynesia, among whom many take part in lagoon-based activities and consume local fish. From the start of the pandemic in March 2020 to early 2022, there have been numerous openings and closures of the French Polynesian borders to international tourists, as well as partial and total lockdowns and restrictions on local economic activities. In 2019, 230,000 tourists visited French Polynesia compared to only 70,000 to 80,000 in 2020 and 2021. In 2021, 60% of the tourists travelled between October and December (data from French Polynesia Tourism Department, https://tahititourisme.fr/). On average, 75% of tourists travelling to French Polynesia stay on the island of Bora-Bora for two to four days. During the restrictions on international travel, very few tourists were present in French Polynesia, and almost all tourism vendors in Bora-Bora were closed. As such, Bora-Bora represents an ideal natural setting to characterise how fish communities responded to the changes in lagoon usage due to socio-economic restrictions in 2021 on an island that had been previously and continuously frequented by tourists over the past few decades.

In 2021, there were three social and travel restrictions related to COVID-19 in French Polynesia: (1) a ban on foreign tourists (February to May); (2) total lockdown (August to mid-September); (3) partial lockdown during the weekends with a curfew during the week (mid-September to mid-October). This succession of different social and travel restrictions allowed us to study fish population dynamics over a long timeseries with 10 months of monitoring, in response to complex 2021 pandemic-related restrictions. Furthermore, this study incorporates a wide variety of sites along a gradient of human pressures to determine the relative impacts of prolonged tourist presence and fishing on fish populations. Our sites ranged from control sites, with low tourism activities and boat traffic, through ecotourism sites (locations of coral reef-related tourism; Spalding et al. 2017) with high levels of boat traffic and human presence but no fishing, to intense boat traffic sites along major boat navigation channels where fishing can occur. All sites were located on the fringing and barrier reef of Bora-Bora. We hypothesize that (i) fish populations will be more numerous and diverse in terms of species on sites with less human pressures, and that a succession of periods with varying levels of human pressure will quickly translate into shifts in the distribution of the reef fish community in the lagoon. We predict that the changes in density and diversity of the fish populations observed on the different sites, in terms of juvenile and adult fish of all species and of harvested species in particular, will be (ii) related to the level of socio-economic restrictions – with the greatest changes observed after the most stringent restriction, *i.e,* total lockdown, lesser changes compared to normal conditions during the ban on foreign tourists, and the smallest changes during the partial lockdown (with limited weekend activities). Lastly, we anticipate that (iii) greater restriction-related changes will occur on sites that are usually under stronger human pressures (Boat traffic > Ecosites > Control).

Materials & Methods

Fish community measures

In 2021, we surveyed coral reef fish communities on eight sites over 10 months (February to July and September to December included) on Bora-Bora (16°29’ S, 151°44’ W - French Polynesia) (Fig 1). On each site, three replicate 25m long x 4m wide transects were conducted to record the fish community over seven days centred around the new moon each month. Two passes were performed per transect; more mobile and visible fishes were recorded during the first pass and more cryptic fishes were recorded on the second pass (Lecchini and Galzin 2005). On each site, a 25m gap was left between each transect to ensure independence. All fishes were identified to the species level and according to their ontogenetic stage based on their size and colour pattern (juveniles vs. adults). Fish species targeted by recreational, subsistence, and commercial fishers were categorized as harvested species (Siu et al. 2017). The average fish density (number of fishes per m^2) and species richness (number of species per m^2) for each month were calculated for all adults and juveniles and for adults and juveniles of harvested species.

Sites under varying human pressures

Three control sites (without tourism activities) were surveyed: two on the barrier reef (Control 1 & Control 2) and one on the fringing reef (Control 3; Fig 1). In 2019, the Mayor and the tourism committee designated 14 eco-tourism sites (location of coral reef-related tourism; Spalding et al. 2017) in the lagoon (on the fringing and inner side of the barrier reef) and 1 eco-tourism site on the outer barrier reef (outer slope) (Lecchini et al. 2021). Prior to the pandemic, these eco-tourism sites were visited at least five times a week by tourism operators, with an average of 20 snorkelers per visit/boat (Jossinet 2020). Ecotourism sites are also de facto Marine Protected Areas with no fishing activities (Jossinet 2020). We selected three eco-tourism sites to survey: one on the fringing reef (Ecosite 1) and two on the barrier reef (Ecosite 2 & Ecosite 3; Fig 1). Two sites with high boat traffic (from fishermen and tourism operators on their way to eco-tourism sites), without tourism activities, but where fishing is not restricted, were also surveyed (Boat site 1 & Boat site 2; Fig 1).

Restriction periods

In 2021, coral reef fish populations were exposed to four different periods of restrictions and measured once per month during the following periods: (i) No tourists (low tourism activities due to the absence of international tourists), from February to May (4 surveys), (ii) Open/No restrictions (all tourism operators open due to the return of international tourists) from June to July and November to December (4 surveys), (iii) Partial lockdown (tourism activities only during the week, with a complete lockdown during the weekend), from mid-September to mid-October (1 survey), and (iv) Total lockdown (without human activities in the lagoon), from August to mid-September (1 survey).

Statistics

Fish count data were used to describe differences in species assemblages between the three types of sites under varying human pressures using a Non-metric Multi-Dimensional Scaling analysis (NMDS). This analysis was performed on the Bray-Curtis similarity matrix using the vegan package in R (version 2.6-2, Oksanen et al. 2020). One-way analyses of similarity (ANOSIM) with 9999 permutations were then used to investigate potential differences linked to the month, restriction period, and site. The normality and homogeneity of the variances of density and species richness for both all species and harvested species were verified using Shapiro-Wilk's and Bartlett tests respectively. When normality was not met, the data were square-root transformed, and two-way ANOVAs were used to test the effect of the four restriction periods, sites, and their interaction on density and species richness of adults and juveniles. If significant interactions were found, a contrast analysis was performed (*emmeans* package in R, version 1.8.3) to identify where these differences appear. In the absence of significant interactions, Tukey's HSD post-hoc tests for multiple pairwise comparisons were performed to identify significant differences for each factor. If the raw and transformed data both did not reach normality, non-parametric Kruskal-Wallis tests were used to compare density and richness between the four restriction periods, and between the three categories of sites (no interaction). When a significant effect was found, Dunn's post-hoc tests for multiple pairwise comparisons with Hochberg's correction (FSA package in R, version 0.9.3) were performed in order to identify the differences driving this effect. Species which were most responsible for the differences in fish community composition between groups were identified through an indicator species analysis using the "multipatt" function of the *indicspecies* package (version 1.7.12, De Cáceres et al. 2010) by running 9999 permutations. All statistical analyses were conducted using R-Studio (R version 4.2.0) at the significance level $\alpha = 0.05$.

Results

Fish populations in relation to human pressures

The NMDS analysis revealed graphically that adult fish assemblages (of harvested and non-harvested species) varied most significantly, with the highest R-value, between sites under various human pressures (ANOSIM, $R = 0.59$, $P < 0.001$; Fig 2a) as an R-value closer to 1 suggests a large dissimilarity between groups. An R-value closer to 0 suggests a more even distribution within and between groups, as found between months (ANOSIM, $R = 0.15$, $P < 0.001$) and restriction periods (ANOSIM, $R = 0.13$, $P < 0.001$) (Fig 2a). Similar but weaker results were found for juveniles, with moderate dissimilarities between sampling sites (ANOSIM, $R = 0.33$, $P < 0.001$), and without significant differences between months (ANOSIM, $R = 0.03$, $P = 0.13$) or restriction periods (ANOSIM, $R = 0.008$, $P = 0.39$) (Fig 2c). Out of the total of 133 adult species observed, 50 (38% of all species) were significantly associated to only one or two sites at the adult stage (Table 1). Similar results were found for juveniles, for which the 16 species observed were associated to one or two sites (Table 1). Control sites, with the lowest human pressures, were associated with the highest number of species at both adult and juvenile stages. Control and Ecosites had five times more species associated with them (41) than at boat traffic sites (9) (Table 1). There were overlaps between juveniles and adults associated with the same sites, with four out of seven species on Control sites, one out of two on boat traffic sites, and three out of four on Ecosites.

When considering harvested species, adult densities were more homogenous, with only moderate dissimilarities between sampling sites (ANOSIM, $R = 0.30$, $P < 0.001$), restriction periods (ANOSIM, $R = 0.18$, $P < 0.001$), and months (ANOSIM, $R = 0.22$, $P < 0.001$) (Fig 2b). The lack of harvested species significantly associated with Boat traffic sites likely contributed to this homogeneity between sites (Table 1). Similar but even weaker results were obtained when considering harvested juvenile species, in terms of sampling sites (ANOSIM, $R = 0.18$, $P < 0.001$), and without significant differences between months (ANOSIM, $R = 0.05$, $P = 0.06$) and restriction periods (ANOSIM, $R = 0.002$, $P = 0.50$) (Fig 2d). Out of the total of 49 harvested species observed, 12 (24% of harvested species) were significantly associated to one or two sites at the adult stage (Table 1). Adults and juveniles of harvested species were most associated with Control and Ecosites. No adult harvested species were associated with Boat traffic sites.

Upon testing these differences, we found that the average density of all adult fish (both harvested and non-harvested species) showed significant differences between sites under various human pressures ($F_{2,76} = 38.85$, $P < 0.001$) (Online Resource 1; Fig 3a). Similar results were found for harvested species only (Online Resource 1; Fig 3b). In general, for all fish as well as for harvested fish only, adult density and species richness were significantly lower on Boat traffic sites (Table 2; Fig. 3a,b), while the highest densities were found on both Ecosites and Control sites, and the highest adult species richness were found on Ecosites (Table 2; Fig 3a,b).

Juvenile density and richness were also significantly different between sites under various human pressures (density: $F_{2,76} = 51.54$, $P < 0.001$; species richness: $\chi^2_3 = 51.16$, $P < 0.001$) with the lowest values similar to adult results on Boat traffic sites. The highest juvenile density and richness for all species were observed on the Control sites (Table 3, Fig 4a,c). Similar results were found for harvested juveniles, for which the density and species richness were different across the sites under various human pressures (density: $\chi^2_2 = 25.61$, $P < 0.001$; richness: $\chi^2_2 = 26.09$, $P < 0.001$) (Fig 4b,d) (Online Resource 1), with the lowest levels on Boat traffic sites (Table 3). There was no statistically significant difference in juvenile density and richness for harvested species between Control and Ecosites (Table 3; Fig 4c,d).

Shifts in adult fish population in relation to socio-economic restrictions

The average density and richness of all adult fish (harvested and non-harvested species) showed significant differences between restriction periods (density: $F_{3,76} = 60.76$, $P < 0.001$; richness: $F_{3,76} = 20.64$, $P < 0.001$), but also a significant interaction between restriction periods and site type (density: $F_{6,76} = 6.01$, $P < 0.001$; richness: $F_{6,76} = 2.45$, $P = 0.032$) (Online Resource 1; Fig 3a),. The largest shifts in adult fish densities and species richness were the increases observed from Open to Total lockdown. Indeed, the average adult density and species richness across the sites during Open conditions were 2.7 ± 1.2 individuals per m^2 (mean ± SD) and 0.26 ± 0.07 species per m^2. During the Total lockdown, the values were 7.0 ± 1.6 individuals per m^2 and 0.36 ± 0.09 species per m^2 (Table 4; Figs 3a,b). Considerable increases in adult fish densities and species richness were also observed from the Open to No tourist restriction periods, but only on Ecosites and Boat traffic sites *e.g.,* for Ecosites, with 6.0 ± 1.1 individuals per m^2 and 0.41 ± 0.04 species per m^2 during No tourist periods, and with 2.5 ± 0.4 individuals per m^2 and 0.30 ± 0.04 species per m^2 during Open periods) (Table 4; Figs 3a,b). Smaller but significant increases in adult fish densities across all sites were found from the Open to Partial lockdown periods (from 2.7 ± 1.2 to 4.8 ± 1.4 individuals per m^2) and from No tourists to Total lockdown (from 4.7 ± 1.6 to 7.0 ± 1.6 individuals per m^2; Table 4; Figs 3a,b). In terms of adult species richness, the only significant change from Open to Partial lockdown periods was an increase on Ecosites (0.30 ± 0.04 to 0.38 ± 0.05 species per m^2). The only increases between Partial and Total lockdown were found for adult fish density on Ecosites (from 4.6 ± 1.0 to 8.1 ± 1.6 individuals per m^2) and for species richness on Control sites (0.30 ± 0.02 to 0.39 ± 0.03 species per m^2) (Table 4; Figs 3a,b). Overall, shifts in adult densities in response to restrictions were larger than shifts in species richness.

All sites showed an overall increase in adult fish density (for all species of fish) from Open to Total Lockdown periods, with Ecosites showing significant differences in densities across all periods apart from the No Tourists and Partial Lockdown, while the Boat traffic sites and Control sites showed no significant difference between Partial Lockdown and Total Lockdown (Table 4). Furthermore, on Control sites, the change from an Open period to No tourists did not have an impact on the adult fish populations, and on Boat Traffic sites, there were no significant changes between Partial Lockdowns and No Tourists.

Shifts in harvested adult fish populations in relation to socio-economic restrictions

In terms of harvested fish species, significant interactions between restriction periods and sites were also found for density ($F_{6,76}$ = 3.79, P = 0.002) and richness ($F_{6,76}$ = 4.32, P < 0.001); while there were significant differences across multiple periods among all types of sites in terms of harvested adult density, the different restrictions only impacted the adult species richness of Ecosites (Table 4, Fig 3b, Online Resource 1). Similarly to all adult fish, the largest shifts in adult harvested fish densities and species richness were the increases observed from Open to Total lockdown followed by Open to No tourist restriction periods, but only for Ecosites and Boat traffic sites (for instance, from Open to Total Lockdown on Ecosites: from 1.1 ± 0.3 to 3.7 ± 0.6 Individuals per m^2 and 0.11 ± 0.02 to 0.20 ± 0.03 species per m^2), not Control sites (Table 4; Figs 3b,d). Significant increases in adult fish densities were found from Open to Partial lockdown for Control and Boat traffic sites (on Control sites: from 1.8 ± 0.6 to 3.4 ± 0.7; on Boat traffic sites: from 0.9 ± 0.3 to 1.9 ± 0.6 individuals per m^2) (Table 4; Figs 3b,d). The only increase between No tourists and Partial lockdown was found for harvested fish densities on

Control sites (From 2.0 ± 1.0 to 3.4 ± 0.7 individuals per m^2), from No tourists to Total lockdown only on Boat traffic sites (from 1.6 ± 0.5 to 3.0 ± 0.6 individuals per m^2), and from Partial to Total lockdown only on Ecosites (from 2.0 ± 0.4 to 3.7 ± 0.6 individuals per m^2) (Table 4; Figs 3b,d). Similar shifts in species richness of harvested species occurred for densities but only for Ecosites, notably from Open to No Tourists (from 0.11 ± 0.02 to 0.15 ± 0.02), Open to Total Lock (to 0.20 ± 0.03), and No Tourists to Total Lock (Table 4; Figs 3b,d).

As opposed to all species combined, harvested species showed the largest increases in fish densities with socio-economic restrictions at both Ecosites and Boat traffic, with the smallest changes on Control sites (Table 4; Figs 4b, d). Increases in harvested species richness related to socio-economic restrictions were only observed at Ecosites (Table 4; Figs 3b,d).

Shifts in juvenile fish population in relation to socio-economic restrictions

All juvenile fish (harvested and non-harvested species) showed significant differences in density ($F_{3,76}$ = 5.99, P < 0.001) and in species richness (χ^2 = 8.88, P = 0.031). For both variables, differences were significant only between the Open period (no restrictions) and the ban on foreign tourists when combining all sites (from 0.5 ± 0.4 to 0.9 ± 0.7 individuals per m^2 and 0.04 ± 0.03 to 0.07 ± 0.05 species per m^2) (Table 3). Harvested juvenile fish also showed higher species richness when there were no tourists (0.02 ± 0.02 species per m^2) as opposed to the period with lowest values, *i.e.,* the partial lockdowns s (0.01 ± 0.01 species per m^2) (χ^2 = 10.57, P = 0.014 ; Table 3). Juvenile densities and species richness at all sites were significantly different from each other for all periods combined (Control > Ecosites > Boat traffic), ranging from 1.1 ± 0.5 individuals per m^2 and 0.08 ± 0.04 species per m^2 on Control sites to 0.2 ± 0.3 individuals per m^2 and 0.02 ± 0.01 species per m^2 on boat traffic sites. Juvenile densities and species richness of harvested species on Boat traffic sites were significantly lower (0.2 ± 0.2 individuals per m^2 and 0.01 ± 0.01 species per m^2) than on both Control and Ecosites (above 0.4 ± 0.3 individuals per m^2 and 0.02 ± 0.01 species per m^2). However, as opposed to adult fish and harvested adult fish densities, there were no significant interactions between restriction period and site ($F_{6,76}$ = 1.04, P = 0.41).

Discussion

This study took advantage of the global COVID-19 pandemic-related activity and travel restrictions in 2021 to determine the impact that human activities exert on natural ecosystems (Rutz et al. 2020). In this study, we explored the impact of tourism on fish communities across three sites – Control, Ecosites and Boat traffic sites – in the lagoon of Bora-Bora, a famous tourism destination of French Polynesia. Our results showed that from February to December 2021, a period marked by multiple COVID-19-related travel restrictions and fluctuations in the number of international tourists visiting the island, the abundance and species richness of juvenile and adult fish populations, and notably of harvested species, showed varying increases corresponding to the level of restrictions on travel and tourism activities in the lagoon. Irrespective of restrictions on tourism activities, fish populations were most abundant and diverse on sites where tourists snorkel and scuba-dive, the Ecosites, as well as on sites with limited human presence, the Control sites, while they were least abundant and diverse on the sites most impacted by boat traffic.

Focusing on spatial heterogeneity in fish populations across the restriction periods, we observed stage-specific differences in the abundance and species richness of fish communities depending on the sites. The species richness of adults and harvested adult species were high both on Ecosites and Control sites. For juveniles, they were highest on Control sites followed by Ecosites. Numerous fish species use different habitats as juveniles and adults, and these ontogenetic-related preferences in habitat may lead to the age-related contrasts in fish communities and distributions across the sites (Dahlgren and Eggleston 2000), with juveniles potentially avoiding Ecosites (significantly less juveniles than on Control sites) more than adults (similar densities between Ecosites and Control sites). Interestingly, in the absence of restrictions on activities, Ecosites - which were chosen due to their abundant and rich fish populations - have lower adult and juvenile abundance and richness than the Control sites. When Ecosites were selected, they may have been comparable to or even have had higher abundance and richness than Control sites. The continued presence of tourists could have led to a long-term decrease in abundance and richness, particularly impacting juvenile fish communities.

Overall, our results highlight that adult and juvenile fish abundance as well as species richness remained lowest on sites along the main navigation routes in the lagoon, with intense boat traffic regardless of restriction period. This indicates that boat traffic has a negative impact on fish populations in Bora-Bora. Ecotourism sites are also impacted by boat traffic when tourists arrive and leave, but overall, their fish abundance and species richness were higher than the more heavily used Boat traffic sites, where the intensity of boat noise exposure along the main navigation routes may be higher and more prolonged than on Ecosites. A measurement of the sound intensity across the study sites would provide more information to confirm the cause for lower fish abundance on the Boat traffic sites. Indeed, sound pollution can affect coral reef marine organisms, similarly to terrestrial taxa and across the world's oceans (Barber et al. 2011; Duarte et al. 2021). Anthropogenic noise is one of the characteristic symptoms of human activity in marine ecosystems; it can be used as a proxy of human activity (Ferrier-Pagès et al. 2021). Boat noise represents a major stress for adult and juvenile fish, increasing the levels of stress hormones and interfering with communication and social interactions, disrupting reproduction as well as feeding and/or anti-predatory behaviour (Hanache et al. 2020; Mills et al. 2020; Gairin et al. 2021), which can decrease survival (Simpson et al. 2016; Ferrari et al. 2018; McCormick et al. 2018). Alterations in behaviour and physiology impact inter-species interactions (Nedelec et al. 2017) and are likely to compromise population dynamics, community structure (as highlighted here), and underlying ecological functions (Shafiei Sabet et al. 2016). The observed lower abundance of fish on Boat traffic sites could be due to either direct impacts of boat noise on fish survival (Nedelec et al. 2022) or indirectly through changes in habitat preferences as juveniles (avoidance of noisy areas has notably been observed in coral reef fish larvae, Holles et al. 2013; and pelagic fish, Kok et al. 2021). Few studies have focused on juveniles – which are shown here to be less abundant and diverse on sites impacted by boat traffic. Despite the major potential consequences of sound pollution on coral reef fish, notably as they are key resources for both tourism and fisheries, our knowledge of the impacts of anthropogenic sound stress on juvenile reef fish survival and habitat preference remains limited.

Focusing on temporal variations in fish communities across all study sites, the least abundant and diverse fish communities in terms of adults and juveniles of all species and of harvested species only were observed during periods without restrictions on socio-economical activities. Fish abundance and species richness showed rebounds during periods of restrictions when boat traffic and tourism were reduced. In agreement with our predictions, the changes in density and diversity of fish populations were related to the level of socio-economic restriction, with the greatest increases observed after the most stringent restrictions, *i.e*, from the open to the total lockdown period, with lesser increases occurring from the open period to the ban on foreign tourists, and lastly from the open to the partial lockdown period. Total lockdowns (no lagoon activity every day of the week) and the absence of tourists resulted in the largest increases in adult fish densities and species richness on the study sites (Figure 3). These results are in accordance with surveys performed before, during, and after the lockdown period of 2020 on Bora-Bora, which found that fish abundance more than doubled on ecotourism sites during lockdown periods (Lecchini et al. 2021). This new study confirms that these shifts are directly linked to tourism activities. Indeed, as fishing pressure is absent on ecotourism sites (these are "de-facto" protected areas to preserve the resources used for tourism), the observed changes in fish populations can only be linked to human presence and/or boat noise (Lecchini et al. 2021). We hypothesise that the rebounds in adult fish community abundances and richness in response to the changes in restriction could hint towards avoidance of certain locations; the strong temporal changes in juvenile fish community characteristics, notably on Ecosites, could indicate decreased survival linked to human stressors.

When looking at site-specific changes due to restriction periods, in agreement with our predictions, the largest changes in density and diversity of fish populations occurred on sites that are under stronger human pressure, *i.e.,* on Ecosites and Boat traffic sites – although the Control sites, although not the direct target of human activities, also show differences, highlighting the widespread effect of human presence throughout the lagoon. We observed striking temporal variation in adult densities and species richness on Ecosites and Boat traffic sites, with significantly lower densities when the island was open for tourism, exposed to most boat traffic and human presence, compared to the opposite endpoint, total lockdown, with the highest density and species richness. Beyond adult populations, tourism also impacts juvenile populations, for which the highest densities and species richness on Ecosites were noted on when there were no tourists, notably with a 174% increase in juvenile abundance (Figure 4). This is a large increase, pointing towards the impact of the presence of tourists on developing fish – an impact which can have consequences on their survival to adulthood, and thus on the renewal of reproducing adult fish populations in the lagoon. The only significant temporal increase in juvenile fish density and species richness (for all species and harvested species) across all sites was linked to the ban on international tourists, further confirming that the presence of tourists is a strong driver of changes in fish distribution (Table 3). Interestingly, the absence of tourists was associated with the highest values of juvenile species richness and density, while the total lockdowns led to the highest values for adults. Previous research focused on the impact of various types of human-related noise pollution usually focuses on a single developmental stage; for instance, the comparison of the response of fish to two- and four-stroke outboard engines typically uses juvenile fish (*e.g.,* Ferrari et al. 2018, McCormick et al. 2018). This study shows that human presence in the lagoon differentially impacts fish depending on their developmental stages, opening the door to numerous research avenues that remain underexplored.

The COVID-19 pandemic has had a drastic impact on underwater soundscapes across the world. Studies conducted during a lockdown in Guadeloupe confirmed a significant decrease (-6 to -10dB) in the mean underwater sound level and suggested that the decrease in anthropogenic noise was accompanied by a decrease in animal sound production (Bertucci et al. 2021). In New Zealand, ambient sound levels in a busy coastal navigation zone decreased three-fold within the first twelve hours of the lockdown in March 2020, which was estimated to increase the communication range of fish by 65% (Pine et al. 2021). The COVID-19 pandemic also had a large impact on human presence in natural environments – for instance, on urban beaches across Latin America, multiple indicators of human presence – noise, litter, density of users – decreased while the presence of crabs increased (Soto et al. 2021); the impact of mass tourism and water activities on habitat access by sea turtles was also highlighted by the absence of tourists during a lockdown in 2020 in Greece (Schofield et al. 2021). On coral reefs, fish may acclimate to boat noise when chronically exposed (Nedelec et al. 2016), and may similarly acclimate to regular human presence, as noted in laboratory experiments (Baker et al. 2013) and predicted for wild coral reef fish (Geffroy et al. 2015). This acclimation may also be individual- or species-specific, and context-dependent; a behavioural study examining acclimation to cameras and observers found no acclimation of the fish to the presence of observers (Nanninga et al. 2017). The random alternation between periods of anthropogenic silence and absence and periods of resumed human activity is thus a novel situation with unknown effects on wild organisms. Here, we show that fish which can be presumed to have acclimated to the constant presence of human presence and occurrence of noise pollution in the lagoon of Bora-Bora over the past decades are still being impacted by variations in the presence and/or detectability of humans and noise.

The tight relationship between the intensity of human activities, fish density, and species richness demonstrated by our survey highlights the fast temporal association and strong consistent response of fish to human presence. Restrictions started from March 2020 and their subsequent implementation and removal still led to significant changes in fish presence on habitats in 2021 – whether through the usage of different habitats depending on human activities, or through enhanced recruitment or mortality. In addition to detecting positive responses to reduced human presence (*i.e.,* during restriction periods, which can be referred to as 'anthropauses', Rutz et al. 2020b), we observe subsequent reductions in fish densities and diversity with the return of tourist activities. These reversals in conditions, "anthropulses" - as coined by Rutz (2022) - are scenarios that, before the COVID-19 pandemic, had rarely occurred and been sparsely documented by environmental impact studies. Our study confirms that COVID-19-related restrictions can be used to explore the human-related drivers of fish community distribution in natural settings, such as in a busy coral reef lagoon. In terms of conservation objectives, this study highlights the direct links between human activities and fish communities. Therefore, the creation of no-take zones and restriction of boat access in key parts of the lagoon of Bora-Bora and other marine settings worldwide could rapidly result in fish communities returning to locations they may have previously avoided, which can be beneficial in terms of survival, reproduction, and population maintenance and resilience (Arthington et al. 2016). In addition, regulating boat passage in intensely frequented areas may be a rapid remedial measure to increase fish abundance. In Bora Bora, boat traffic is particularly intense near the only pass of the barrier reef circling the island. However, the pass is a key zone for fish reproduction, notably with reproductive aggregations (Domeier and Colin 1997; Sadovy De Mitcheson et al. 2008). Regulating boat passage during reproduction events may therefore be useful to increase fish stocks. In Bora-Bora, a locally managed Marine Protected Area called 'rahui' will be put in place to restrict access to the southern edge of the lagoon. Through this study, we predict that the rahui will allow fish to rapidly return to the ex-fishing grounds in high numbers and contribute to a long-term increase of the marine biomass and biodiversity of the island.

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Tables

Table 1 – List of species that were identified as significantly associated to one or two sites at the adult and juvenile stages. Species highlighted in grey are harvested species. Species are ranked in decreasing order according to the value of their association statistic. P values are the result of an indicator species analysis run with 9999 permutations.

	Control			Ecosite			Boat traffic			Control + Ecosite			Boat traffic + Ecosite		
	Species	**stat**	**P**	**Species**	**stat**	**P**	**Species**	**stat**	**P**	**Species**	**stat**	**P**	**Species**	**stat**	**P**
Adults	*Chromis viridis*	0.72	< 10-3	*Lutjanus fulvus*	0.64	< 10-3	*Dascyllus flavicaudus*	0.83	< 10-3	*Myripristis pralina*	0.63	< 10-3	*Zebrasoma scopas*	0.48	< 10-3
	Chaetodon trifasciatus	0.61	< 10-3	*Gnathodentex aurolineatus*	0.56	< 10-3	*Centropyge bispinosa*	0.41	< 10-3	*Stegastes nigricans*	0.56	< 10-3	*Pomacentrus pavo*	0.38	< 10-3
	Chrysiptera leucopoma	0.49	< 10-3	*Abudefduf sexfasciatus*	0.54	< 10-3	*Pygoplites diacanthus*	0.35	0.003	*Halichoeres hortulanus*	0.51	< 10-3			
	Chaetodon ephippium	0.49	< 10-3	*Balistapus undulatus*	0.53	< 10-3	*Chromis iomelas*	0.33	0.003	*Labroides dimidiatus*	0.40	< 10-3			
	Acanthurus triostegus	0.48	< 10-3	*Naso lituratus*	0.46	< 10-3	*Forcipiger longirostris*	0.32	0.001	*Heniochus chrysostomus*	0.38	< 10-3			
	Neocirrhites armatus	0.42	< 10-3	*Zebrasoma veliferum*	0.39	< 10-3	*Fistularia commersonii*	0.29	0.011	*Neoniphon sammara*	0.34	0.004			
	Caracanthus maculatus	0.41	< 10-3	*Abudefduf septemfasciatus*	0.39	< 10-3	*Diodon histrix*	0.26	0.04	*Halichoeres trimaculatus*	0.32	0.007			
	Dascyllus aruanus	0.40	< 10-3	*Siganus spinus*	0.38	< 10-3				*Thalassoma hardwicke*	0.31	0.011			
	Coris aygula	0.39	< 10-3	*Thalassoma purpureum*	0.36	< 10-3				*Halichoeres margaritaceus*	0.25	0.036			
	Coris gaimard	0.38	0.004	*Chaetodon ulietensis*	0.34	0.001				*Cheilinus trilobatus*	0.25	0.045			
	Chrysiptera glauca	0.32	0.004	*Chaetodon auriga*	0.34	0.003									
	Sargocentron spiniferum	0.32	0.002	*Acanthurus nigricans*	0.27	< 10-3									
	Stethojulis bandenensis	0.28	0.019	*Aulostomus chinensis*	0.25	0.040									
	Ctenochaetus flavicauda	0.27	0.024												
	Paracirrhites arcatus	0.26	0.032												
	Parupeneus multifasciatus	0.25	0.046												
	Scarus psittacus	0.25	0.045												
	Scarus oviceps	0.24	0.020												

	Control			Ecosite			Boat traffic			Control + Ecosite		
	Species	**stat**	**P**	**Species**	**stat**	**P**	**Species**	**stat**	**P**	**Species**	**stat**	**P**
Juveniles	*Chaetodon trifasciatus*	0.62	< 10-3	*Monotaxis grandoculis*	0.32	0.006	*Pomacentrus pavo*	0.42	< 10-3	*Thalassoma hardwicke*	0.53	< 10-3
	Halichoeres hortulanus	0.47	< 10-3				*Ctenochaetus striatus*	0.26	0.04	*Scarus sordidus*	0.52	< 10-3
	Gomphosus varius	0.47	< 10-3							*Stegastes nigricans*	0.51	< 10-3
	Scarus psittacus	0.32	0.022							*Halichoeres margaritaceus*	0.27	0.041
	Chromis viridis	0.30	0.013									
	Chrysiptera leucopoma	0.29	0.019									
	Chaetodon citrinellus	0.27	0.034									

Table 2 – Summary of all pairwise comparisons performed between restrictions periods and sites in order to identify significant differences in fish density and species richness of overall adults and harvested adults. T and their associate P values are the results of Tukey's HSD post hoc tests following a two-way ANOVA. Significant differences are highlighted in bold.

		Adults	Harvested adults
Fish density	**Restriction Periods**		
	Open *vs.* No tourists	**T = 1.95 ; P < 10^{-3}**	**T = 0.30 ; P < 10^{-3}**
	Partial Lock *vs.* No tourists	T = 0.09 ; P = 0.99	T = 0.12 ; P = 0.51
	Total Lock *vs.* No tourists	**T = 2.27 ; P < 10^{-3}**	**T = 0.38 ; P < 10^{-3}**
	Partial Lock *vs.* Open	**T = 2.04 ; P < 10^{-3}**	**T = 0.42 ; P < 10^{-3}**
	Total Lock *vs.* Open	**T = 4.23 ; P < 10^{-3}**	**T = 0.68 ; P < 10^{-3}**
	Total Lock *vs.* Partial Lock	**T = 2.19 ; P < 10^{-3}**	T = 0.25 ; P = 0.12
	Sites		
	Control *vs.* Boat traffic	**T = 1.96 ; P < 10^{-3}**	**T = 0.27 ; P < 10^{-3}**
	Ecosite *vs.* Boat traffic	**T = 1.71 ; P < 10^{-3}**	**T = 0.20 ; P = 0.005**
	Ecosite *vs.* Control	T = 0.25 ; P = 0.64	T = 0.06 ; P = 0.55
Species richness	**Restriction Periods**		
	Open *vs.* No tourists	**T = 0.06 ; P < 10^{-3}**	T = 0.01 ; P = 0.09
	Partial Lock *vs.* No tourists	T = 0.04 ; P = 0.09	T = 0.01 ; P = 0.88
	Total Lock *vs.* No tourists	T = 0.04 ; P = 0.13	T = 0.02 ; P = 0.07
	Partial Lock *vs.* Open	T = 0.02 ; P = 0.46	T = 0.01 ; P = 0.87
	Total Lock *vs.* Open	**T = 0.09 ; P < 10^{-3}**	**T = 0.03 ; P < 10^{-3}**
	Total Lock *vs.* Partial Lock	**T = 0.08 ; P = 0.003**	T = 0.03 ; P = 0.06
	Sites		
	Control *vs.* Boat traffic	**T = 0.13 ; P < 10^{-3}**	**T = 0.05 ; P < 10^{-3}**
	Ecosite *vs.* Boat traffic	**T = 0.17 ; P < 10^{-3}**	**T = 0.07 ; P < 10^{-3}**
	Ecosite *vs.* Control	**T = 0.04 ; P = 0.005**	**T = 0.02 ; P < 10-3**

Table 3 – Summary of all pairwise comparisons performed between restrictions periods and sites in order to identify significant differences in fish density and species richness of overall juveniles and harvested juveniles. T and their associate P values are the results of Tukey's HSD post hoc tests following a two-way ANOVA. Z and their P values are the results of Dunn's post hoc tests following a Kruskal-Wallis test. Significant differences are highlighted in bold.

		Juveniles	Harvested juveniles
Fish density	**Restriction Periods**		
	Open *vs.* No tourists	**T = 0.25 ; P < 10^{-3}**	**Z = 2.91 ; P = 0.02**
	Partial Lock *vs.* No tourists	T = 0.21 ; P = 0.11	Z = 1.73 ; P = 0.42
	Total Lock *vs.* No tourists	T = 0,11 ; P = 0.65	Z = 0.34 ; P = 1
	Partial Lock *vs.* Open	T = 0.03 ; P = 0.98	Z = 0.12 ; P = 0.90
	Total Lock *vs.* Open	T = 0.14 ; P = 0.46	Z = 1.53 ; P = 0.51
	Total Lock *vs.* Partial Lock	T = 0.10 ; P = 0.81	Z = 1.11 ; P = 0.80
	Sites		
	Control *vs.* Boat traffic	**T = 0.65 ; P < 10^{-3}**	**Z = 5.01 ; P < 10^{-3}**
	Ecosite *vs.* Boat traffic	**T = 0.43 ; P < 10^{-3}**	**Z = 3.13 ; P = 0.004**
	Ecosite *vs.* Control	**T = 0.23 ; P = 0.002**	Z = 1.86 ; P = 0.06
Species richness	**Restriction Periods**		
	Open *vs.* No tourists	**Z = 2.60 ; P = 0.05**	**Z = 2.66 ; P = 0.04**
	Partial Lock *vs.* No tourists	Z = 2.16 ; P = 0.15	**Z = 2.58 ; P = 0.05**
	Total Lock *vs.* No tourists	Z = 1.43 ; P = 0.61	Z = 0.63 ; P = 0.52
	Partial Lock *vs.* Open	Z = 0.50 ; P = 1	Z = 0.89 ; P = 0.75
	Total Lock *vs.* Open	Z = 0.23 ; P = 0.82	Z = 1.07 ; P = 0.85
	Total Lock *vs.* Partial Lock	Z = 0.58 ; P = 1	Z = 1.55 ; P = 0.48
	Sites		
	Control *vs.* Boat traffic	**Z = 7.05 ; P < 10^{-3}**	**Z = 4.86 ; P < 10^{-3}**
	Ecosite *vs.* Boat traffic	**Z = 4.58 ; P < 10^{-3}**	**Z = 3.80 ; P < 10-3**
	Ecosite *vs.* Control	**Z = 2.43 ; P = 0.015**	Z = 1.03 ; P = 0.30

Table 4 – Summary of interactions between restrictions periods and sites in order to identify significant differences in fish density and species richness of overall adults and harvested adults. t and their associate P values are the results of a contrast analysis following a two-way ANOVA. Significant differences are highlighted in bold.

			Adults		Harvested adults	
	Sites	**Restriction Periods**	**t**	P	**t**	P
Fish density	Boat traffic	No tourists *vs.* Open	**4.65**	**<0.001**	**3.59**	**0.003**
		No tourists *vs.* Partial Lock	-0.06	1.00	-0.78	0.87
		No tourists *vs.* Total Lock	**-3.05**	**0.02**	**-3.42**	**0.01**
		Open *vs.* Partial Lock	**-3.07**	**0.02**	**-3.10**	**0.01**
		Open *vs.* Total Lock	**-6.08**	**<0.001**	**-5.77**	**<0.001**
		Partial Lock *vs.* Total Lock	-2.38	0.09	-2.11	0.16
	Control	No tourists *vs.* Open	1.45	0.47	0.49	0.96
		No tourists *vs.* Partial Lock	**-2.71**	**0.04**	**-3.14**	**0.01**
		No tourists *vs.* Total Lock	**-4.88**	**<0.001**	-2.24	0.12
		Open *vs.* Partial Lock	**-3.63**	**0.003**	**-3.45**	**0.01**
		Open *vs.* Total Lock	**-5.80**	**<0.001**	-2.55	0.06
		Partial Lock *vs.* Total Lock	-1.72	0.32	0.71	0.89
	Ecosite	No tourists *vs.* Open	**9.08**	**<0.001**	**5.86**	**<0.001**
		No tourists *vs.* Partial Lock	2.32	0.102	1.28	0.58
		No tourists *vs.* Total Lock	**-3.42**	**0.006**	-2.35	0.10
		Open *vs.* Partial Lock	**-3.53**	**0.004**	-2.50	0.07
		Open *vs.* Total Lock	**-9.32**	**<0.001**	**-6.16**	**<0.001**
		Partial Lock *vs.* Total Lock	**-4.58**	**<0.001**	**-2.89**	**0.03**
	Sites	**Restriction Periods**	**t**	P	**t**	P
Species richness	Boat traffic	No tourists *vs.* Open	**2.97**	**0.02**	0.24	1.00
		No tourists *vs.* Partial Lock	1.54	0.42	0.68	0.90
		No tourists *vs.* Total Lock	-0.90	0.81	-0.96	0.77
		Open *vs.* Partial Lock	-0.37	0.98	0.53	0.95
		Open *vs.* Total Lock	**-2.83**	**0.03**	-1.13	0.67
		Partial Lock *vs.* Total Lock	-1.94	0.22	-1.31	0.56
	Control	No tourists *vs.* Open	1.60	0.38	-0.09	1.00
		No tourists *vs.* Partial Lock	1.54	0.42	0.12	1.00
		No tourists *vs.* Total Lock	-1.78	0.29	-0.36	0.98
		Open *vs.* Partial Lock	0.52	0.95	0.18	1.00
		Open *vs.* Total Lock	**-2.80**	**0.03**	-0.30	0.99
		Partial Lock *vs.* Total Lock	**-2.62**	**0.05**	-0.38	0.98
	Ecosite	No tourists *vs.* Open	**6.18**	**<0.001**	**4.30**	**<0.001**
		No tourists *vs.* Partial Lock	1.16	0.65	0.58	0.94
		No tourists *vs.* Total Lock	-1.40	0.51	**-3.42**	**0.01**
		Open *vs.* Partial Lock	**-2.83**	**0.03**	-2.20	0.13
		Open *vs.* Total Lock	**-5.41**	**<0.001**	**-6.23**	**<0.001**
		Partial Lock *vs.* Total Lock	-2.04	0.18	**-3.19**	**0.01**

Figure captions

Figure 1 – Map of Bora-Bora with the location of the 8 surveyed sites. Black triangles represent control sites, back stars represent eco-tourism sites and black circles represent boat traffic sites. Dark grey represents land areas, light grey represents reef areas. Each site was surveyed throughout five periods with different types of socio-economic restrictions: February-May 2021 with no international tourism, June-July 2021 with no restrictions, September 2021 with a total lockdown, October 2021 with tourism activities on week-days only, November-December 2021 with no restrictions.

Figure 2 – Non-metric multidimensional scaling (NMDS) plots of the similarity of fish assemblages calculated from the Bray–Curtis distances on the number of (a) all adult, (b) harvested adult fish, (c) all juvenile and (d) harvested juvenile fish of all species in the different sites during the four restriction periods.

Figure 3 –Scatter plots of the density (number of individuals per m^2) (top) and species richness (number of species per m^2) (bottom) of adult and harvested species at adult stage observed during the four types of restriction periods in Bora-Bora in Control, Ecosite and Boat traffic sites. Boxes represent the first and third quartiles, thick horizontal bars are the median (second quartile), whiskers correspond to the distribution range (min-max) and dots are all individual observations.

Figure 4 – Scatter plots of the density (number of individuals per m^2) (top) and species richness (number of species per m^2) (bottom) of juveniles and harvested species at juvenile stage observed during the four types of restriction periods in Bora-Bora in Control, Ecosite and Boat traffic sites. Boxes represent the first and third quartiles, thick horizontal bars are the median (second quartile), whiskers correspond to the distribution range (min-max) and dots are all individual observations.

Figure 1

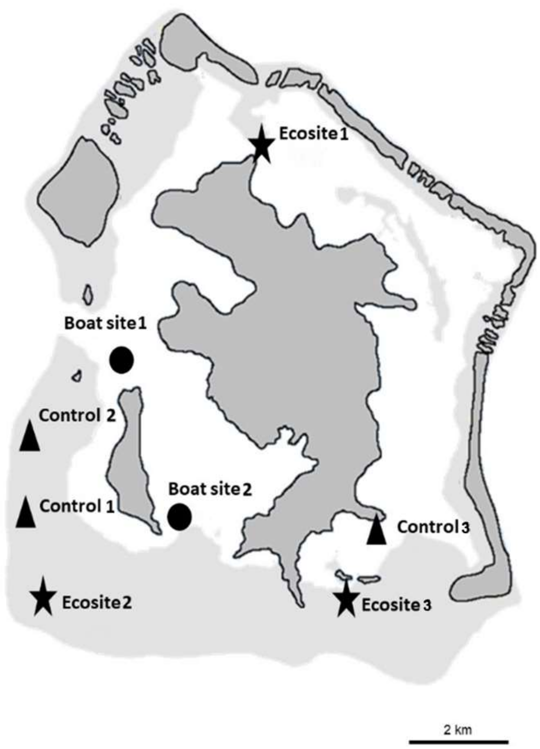

Ecosite 1
Boat site 1
Control 2
Control 1
Boat site 2
Control 3
Ecosite 2
Ecosite 3
2 km

Figure 2

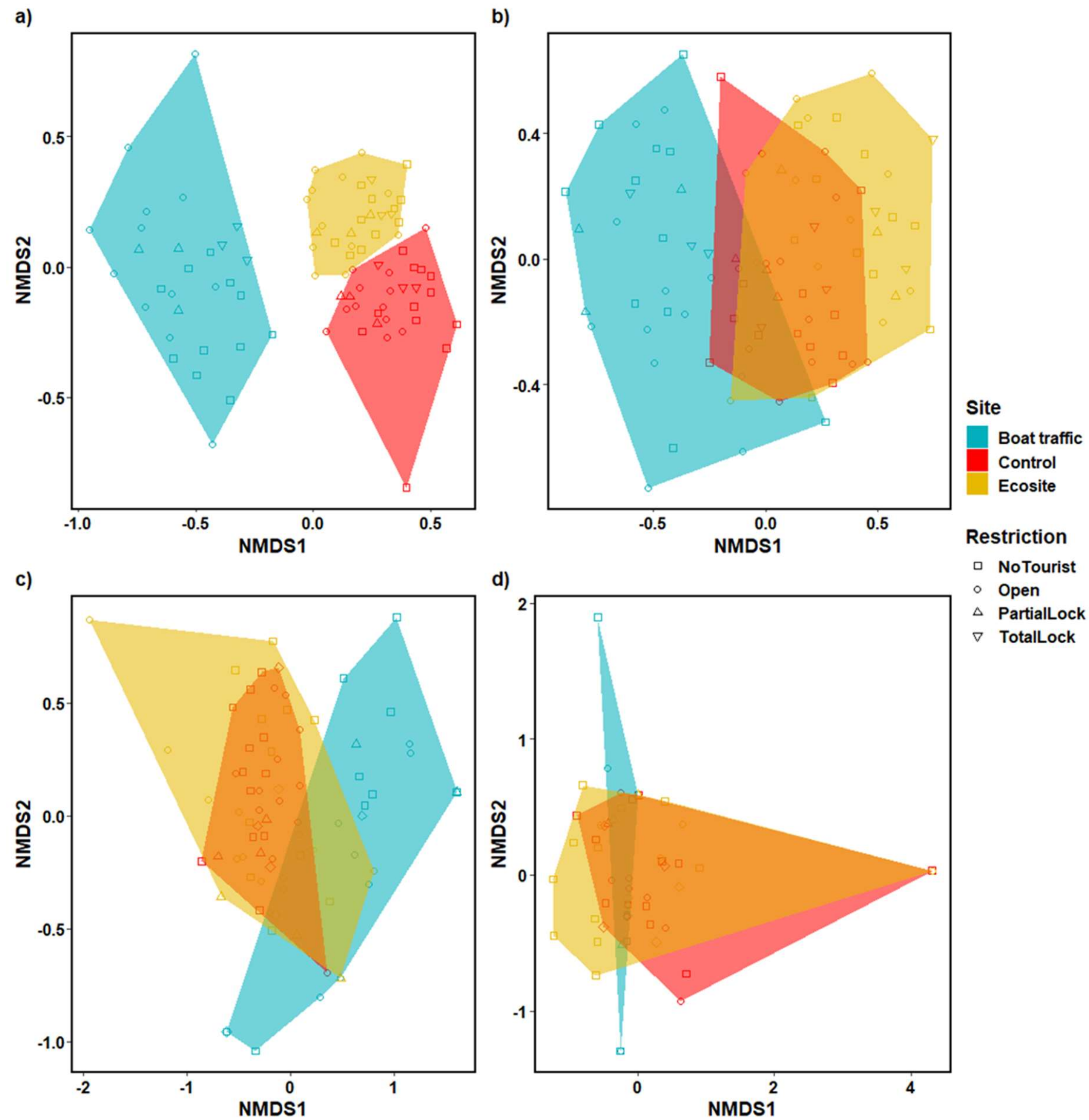
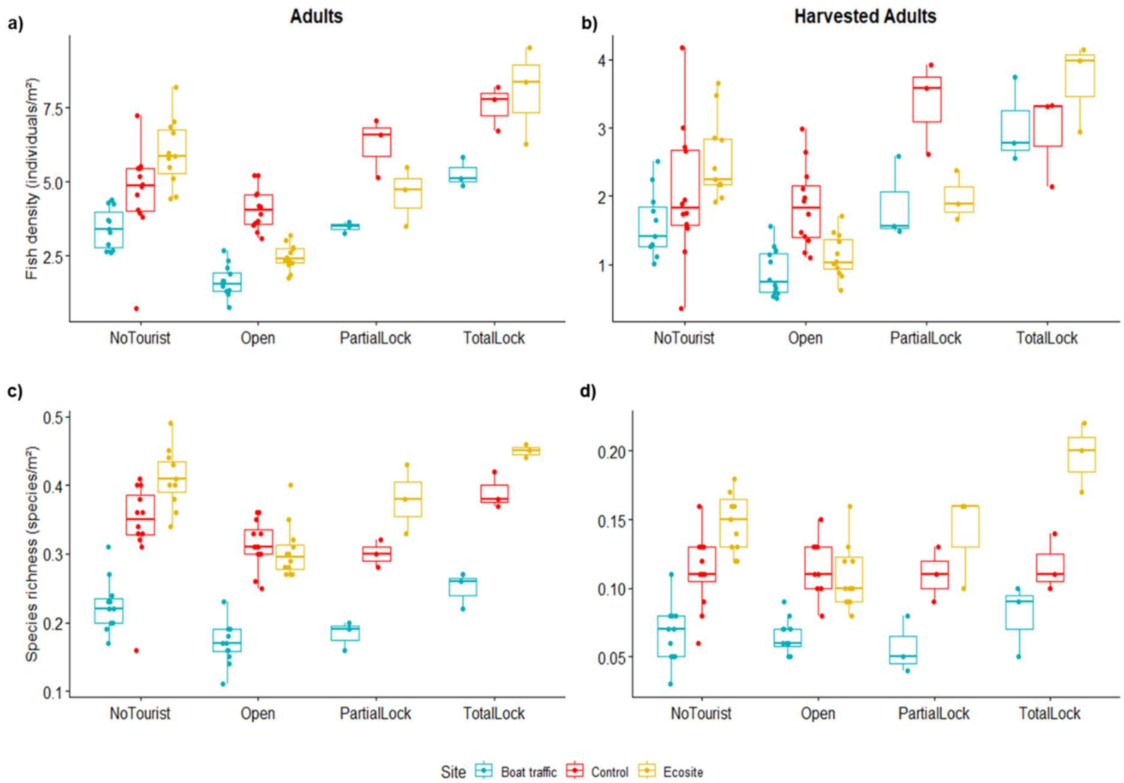
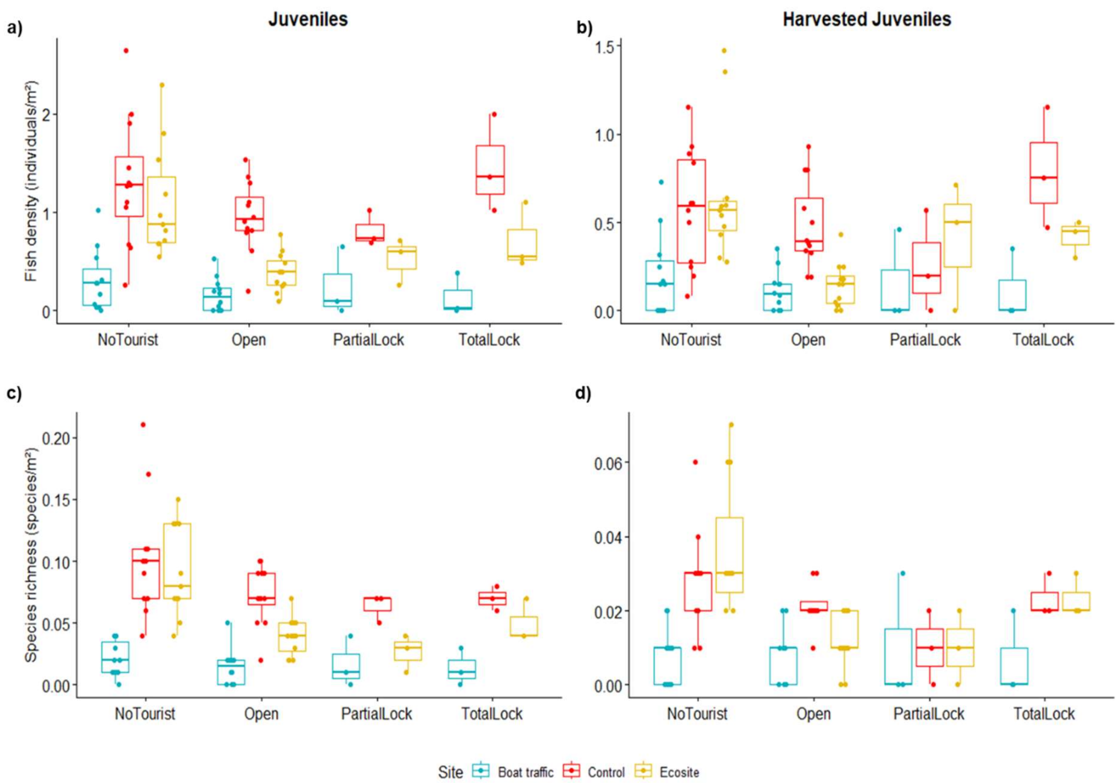

a)
b)
c)
d)
NMDS1
NMDS2
Site
Boat traffic
Control
Ecosite
Restriction
NoTourist
Open
PartialLock
TotalLock

Figure 3



a)
Adults
b)
Harvested Adults
Fish density (individuals/m²)
7.5
5.0
2.5
4
3
2
1
NoTourist
Open
PartialLock
TotalLock
c)
d)
Species richness (species/m²)
0.5
0.4
0.3
0.2
0.1
0.20
0.15
0.10
0.05
Site
Boat traffic
Control
Ecosite

Figure 4



a)
Juveniles
b)
Harvested Juveniles
Fish density (individuals/m²)
0
1
2
0.0
0.5
1.0
1.5
NoTourist
Open
PartialLock
TotalLock
c)
d)
Species richness (species/m²)
0.00
0.05
0.10
0.15
0.20
0.00
0.02
0.04
0.06
Site
Boat traffic
Control
Ecosite