



Temporal shifts in algal and fish assemblages following the introduction of herbivorous species in coral reef patches (Bora Bora Island)

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ARTICLE INFO

Keywords:

Regulatory invertebrates
Sea urchins
Trochidae
Herbivory
Fish assemblages
French Polynesia

ABSTRACT

Ecological succession (sequential replacement of species following a disruptive event) is critical for understanding ecosystem dynamics. With coral reefs facing increasing threats, comprehending secondary ecological succession is of heightened importance. Coral reef restoration, through techniques such as coral transplantation and herbivore introduction, plays a crucial role in mitigating coral degradation at the local scale. However, the combined effect of these two techniques on ecological succession remains understudied. To determine the impact of herbivory and coral transplantation on ecological succession, four experimental conditions were evaluated on reef patches (Bora Bora, French Polynesia): (i) no-restored control, (ii) restored control, and two conditions with herbivorous invertebrates introduced (sea-urchins and mollusks) alongside restoration: (iii) one site with macroalgae removal and (iv) one without. Macroalgae cover and fish were monitored among the conditions over a 70-day period. Herbivorous invertebrates limited algae cover compared to control. However, no difference in fish assemblages was found in alpha diversity when comparing conditions over time. Changes in fish assemblages were observed in beta diversity, with statistically supported values for juveniles in the restored condition with herbivorous invertebrates present. Understanding the dynamics of ecological succession in so complex environments like coral reefs is essential for designing effective restoration strategies and safeguarding their health.

1. Introduction

An ecological succession is a process that induces a change in a community of organisms over time within an ecosystem. It entails the sequential replacement of species in an ecosystem following a disruptive event, such as coral bleaching in coral reefs (Salvat et al., 2002). Disruptive events can be natural, such as a fire or a flood, or anthropogenic, like deforestation (Payette, 1976). Understanding ecological succession after a disturbance is a major concern for scientists and managers (Jouval, 2019). Indeed, the increasing threat to marine ecosystems calls for further investigation into the extent of predictable and orderly changes in marine communities through the principle of ecological succession (Sandin & Sala, 2012). Despite many coral restoration programs in the world, few studies have been conducted on fish

ecological succession in reef ecosystems (Krimou et al., 2024).

Coral reefs provide a range of ecosystem goods and services: food provision, livelihood opportunities, carbon sequestration, and storm protection (Mellin et al., 2022; Woodhead et al., 2019). Presently, nearly 30 % of coral reefs have been destroyed, while over 60 % are threatened by human activities (Ford et al., 2024; Harris et al., 2018; Reimer et al., 2024). This degradation of coral reefs is attributed to threats associated with human activities, both local, such as overfishing, and global, such as ocean warming and acidification (Knowlton et al., 2021). Include it if they do not directly address the global problem – and that they may fail unless climate change and other global human impacts are urgently reduced (Hughes et al., 2023), solutions are locally implemented to address this coral degradation, such as the establishment of marine protected areas, coral restoration efforts, or awareness and

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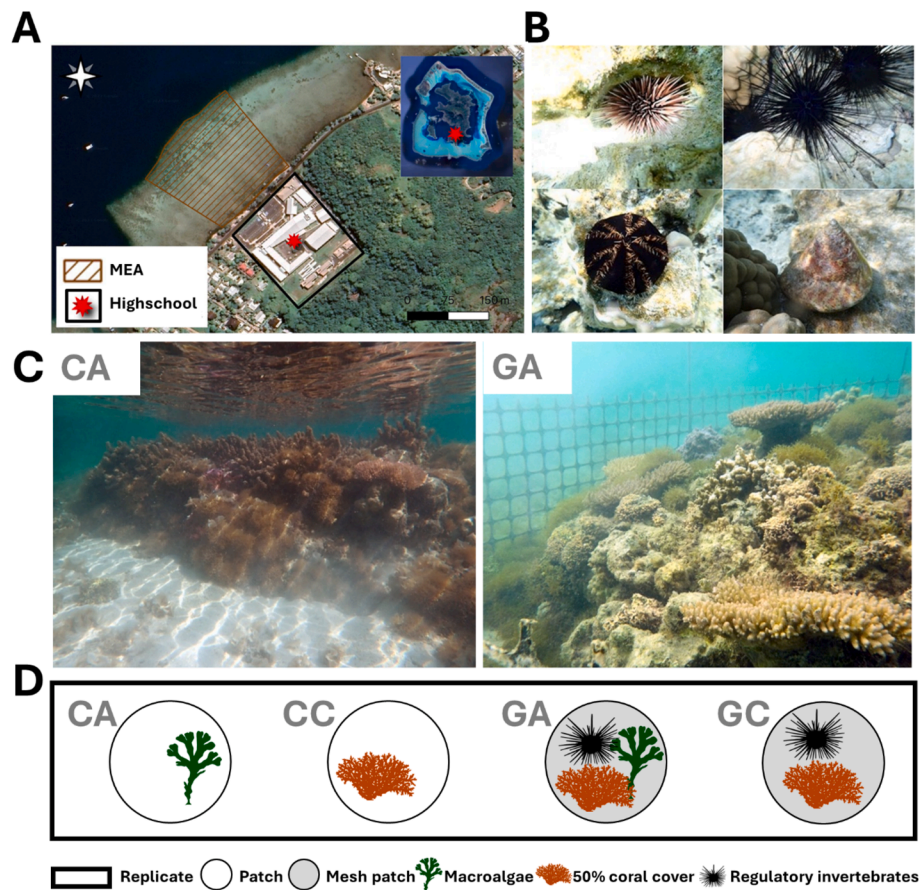


Fig. 1. (A) Map of the study area. The Marine Educational Area (MEA) is situated in the fringing reef adjacent to the high school of Bora Bora (red star). (B) Illustration of the four herbivorous species used in the study: *Diadema savignyi*, *Echinometra mathaei*, *Tripneustes gratilla*, and *Trochus niloticus*. (C) Example of two reef patches (CA and GA). (D) Experimental design of the study. Four experimental conditions were assessed: (1) the algae control (CA), (2) the coral control (CC), (3) the algae experimental group (GA), and (4) the coral experimental group (GC). Macroalgae were initially removed in the CC and GC conditions, whereas herbivorous invertebrates were introduced in the GA and GC conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

communication projects. It is also critical to remember that these actions should not be viewed as substitutes for addressing climate change (Boström-Einarsson et al., 2020). Among these solutions, coral reef restoration is one of the different solutions implemented to counter the threats to marine biodiversity (Chipeaux et al., 2016). The restoration methods are diverse, encompassing techniques such as direct transplantation, coral gardening, micro-fragmentation, larval enhancement, artificial reefs, substratum stabilization, and substratum enhancement.

Measuring the effectiveness of these solutions is not solely based on coral growth. It concerns many other taxa such as fish, sponges, and crustaceans, which are also essential for the overall health of reefs, as well as the ecological interactions and processes among them (Edwards & Gomez, Edgardo, 2007; Odum, 1969). However, to date, there are few studies that have assessed the effectiveness of coral restoration by evaluating the role of ecological succession in fish species. It is known that the effect of coral restoration on fish assemblages varies over time (Fadli et al., 2012; Krimou et al., 2024; Opel et al., 2017) and among trophic groups (Ladd et al., 2019). For example, butterflyfish prefers parts of the reef with a high level of small-scale 3D complexity (Fukunaga et al., 2020) while it is not the case for planktivores (Thresher, 1983). For effective coral restoration, it is also important to understand the interactions between corals and macroalgae. In cases of reduced herbivory or increased nutrient availability, macroalgae often have a competitive advantage over corals (McCook et al., 2001). Some herbivorous species preying on macroalgae, notably sea urchins or some gastropods and fish species (e.g. in *Acanthurus triostegus*), are considered

taxa that reduce this increase in macroalgae and maintain coral colony growth (Brugneaux, 2012; Krimou et al., 2023). Increasing the abundance of these taxa appears as a potential strategy to counteract the increase in macroalgae percentage on the reef (Krimou et al., 2023).

Overall, fish ecological succession and macroalgae cover following coral restoration are two important parameters to consider to better understand the effectiveness of the restoration programs implemented. Our study aims to determine if significant regulation is achieved by herbivorous individuals on coral reefs and to understand the dynamics of fish assemblages in relation to algal dynamic in the presence of regulatory invertebrates. The specific objectives are as follows: (1) to determine the temporal dynamic of algal coverage during restoration in the presence or absence of regulatory individuals, and (2) to determine the temporal dynamic of fish species assemblages under these same conditions.

2. Material and methods

2.1. Study area

Bora Bora (French Polynesia) is an island subject to anthropogenic pressure due to local population growth and luxury tourism since the 1980s (Tinorua & Merceron, 2005). Many initiatives are thus focusing on preserving the reef biodiversity of the island. One such initiative is the Marine Educational Area (MEA – 40,000 m² area). The MEA is a coastal area managed by high school students under the supervision of

their professors and scientists. In the MEA, 20 reef patches, distributed across the whole MEA, were investigated: 3.07 ± 0.68 m in length (mean \pm standard deviation), 2.23 ± 0.41 m in width, and 0.78 ± 0.18 m in height (Fig. 1).

2.2. Experimental design

Four experimental conditions were assessed: (1) the algae control (CA), (2) the coral control (CC), (3) the algae experimental group (GA), and (4) the coral experimental group (GC, Fig. 1C). Each condition consisted of five replicates (i.e., five different reef patches spaced at least 10 m apart). CA sites were designated reef patches where no coral restoration activities were conducted. Within CC sites, macroalgae were removed from reef patches, and a coral restoration effort was implemented to achieve a 50 % coral coverage. To do so, coral colonies representing the three most prevalent genera (*Acropora*, *Montipora*, and *Porites*) were translocated from a nearby fringing reef to the MEA. The proportion of coral genera used was chosen to reflect the one in the fringing reef close to the MEA (Krimou et al., 2024; Lecchini et al., 2021). The colonies were affixed using a mixture of cement, sand, water, and SikalateX during calm sea conditions. The decision to establish a 50 % coral cover was based on its recognized efficacy in restoration endeavors (Krimou et al., 2024). In all experimental sites (GA and GC), herbivorous invertebrates were introduced alongside coral restoration activities. In GA sites, macroalgae were not removed, whereas they were cleared from GC sites. Four herbivorous species were selected and introduced in GC and GA sites: *Diadema savignyi*, *Echinometra mathaei*, *Tripterygion gratilla*, and *Trochus niloticus*. The grazing effects of these species have been evaluated in a separate study (Krimou et al., 2023) (Fig. 1). Their respective mean size was 4.9 ± 1.3 cm, 3.0 ± 0.3 cm, 7.3 ± 0.4 cm, and 9.2 ± 0.7 cm. The herbivorous density was standardized to 1 individual per m², resulting in an average density of 7 individuals per patch (Krimou et al., 2023).

2.3. Biological data

The percentage of macroalgae on the different reef patches was evaluated at the beginning of the experiment and subsequently every 7 days over a period of 70 days. The assessment encompassed the following macroalgal species: *Caulerpa* sp., *Dictyota barataresiana*, *Halimeda* sp., *Padina boryana*, *Turbinaria ornata*, and algal turf. Consistent monitoring was conducted by the same observatory throughout the duration of the study.

The composition of fish assemblages was initially assessed the day prior to the beginning of the study. Subsequently, fish assessments were conducted three days after the beginning of the study and thereafter every 7 days for a total duration of 70 days. The fixed-point method, as described by Mallet (2013), was employed at four designated points positioned 1 m from the reef patch. At each point, all fish species observed within a 1-min interval were recorded. Fish were categorized into the following trophic groups: corallivores, detritivores, herbivores, mobile benthic invertebrate feeders (MBIF), omnivores, planktivores, and piscivores/carnivores. Additionally, the stage of development (juvenile vs. adult) was documented.

2.4. Statistical analyses

A linear mixed-effects model (library *nlme*, function *lme*) evaluated the percentage of algae over time (from day 0 to day 70) across different conditions (CA, CC, GA, or GC), with the patch reef treated as a random factor. The homoscedasticity of variances, normality, and linearity of residuals was assessed graphically, and autocorrelation of the model was examined using the *acf* function. Subsequently, a multiple comparison of means utilizing a Tukey test was used to compare observed trends across plots. Additionally, an ANOVA followed by a Tukey test was used to compare the final algae cover among the four experimental conditions.

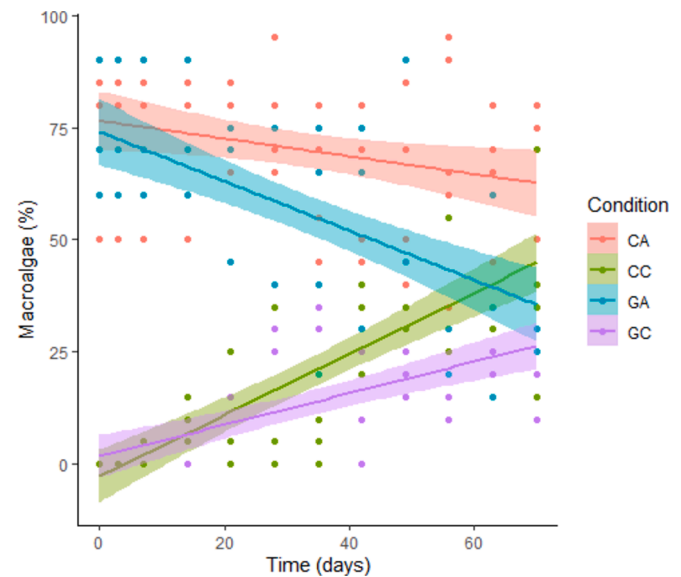


Fig. 2. Temporal dynamics of macroalgae cover (%) for the four experimental conditions (CA, CC, GA, and GC). Lines represent mean values with 95% confidence intervals.

The same statistical approach was applied to assess fish assemblages, separately analyzing adults and juveniles. Three key features were evaluated: abundance, number of species, and Simpson diversity index. To mitigate the influence of reef patch size variations, fish abundance was normalized by the surface area of the reef patch, thereby computing density per square meter rather than raw abundance. Furthermore, the same tests were conducted for various diet groups. Given that the herbivores, MBIF, and omnivores were the most prevalent diet groups among both adults and juveniles, statistical analyses were exclusively performed on these three groups to ensure an adequate number of observations per diet group.

Overall, fish assemblage composition (for adults and juveniles separately) was compared at the beginning of the study (D0) and at the end (D70) for each of the four conditions using analyses of similarities (package *vegan*, function *anosim*). The *anosim* analysis used Bray-Curtis dissimilarities with a fixed number of permutations set to 999. The *anosim* statistic (R) quantified similarities between and within D0 and D70. R values fall within the interval $[-1, 1]$, where values close to 0 indicate random grouping, values close to -1 indicate more similarity between than within groups, and values close to 1 indicate more similarity within groups. Additionally, a canonical correspondence analysis (CCA) (package *vegan*, function *cca*) was performed on the logarithm of the raw data to visually examine the distribution of fish species. CCA was used to identify the best dispersion of fish species. Day (J0 vs. J70) and condition (CA, CC, GA, and GC) were included in the ordination plot to explore their relationships with fish assemblage composition, represented by 95 % confidence interval ellipses. All statistical analyses were conducted using R software version 4.3.0.

3. Results

3.1. Algae cover

The percentage of algae cover varied across the four experimental conditions, time, and their interaction, as determined by a linear mixed-effects model ($F = 37.03, 5.54, \text{ and } 83.41$; $P < 0.0001, 0.019, \text{ and } < 0.0001$; $\text{acf} \leq |0.28|$; Fig. 2). Over time, algae cover displayed a similar decreasing trend in conditions where algae were not removed initially (CA and GA; Tukey test, $z = -0.35, P = 0.98$). Conversely, a similar increasing trend was observed in CC and GC (Tukey test, $z = 0.62, P =$

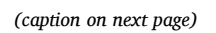


Fig. 3. A-F Temporal dynamics of abundance per m², species richness, and diversity for the four experimental conditions (CA, CC, GA, and GC) for adult (top: A, B, and C) and juvenile (bottom: D, E, and F) fish. A & D: abundance. B & E: Richness. C & F: Diversity (Simpson Index). Lines represent mean values with 95 % confidence intervals. (G) Canonical correspondence analysis ordination plots of the adult fish assemblage composition based on Bray – Curtis dissimilarities. Ellipses are 95 % confidence interval. Pictures of *Acanthurus nigricans*, *Chaetodon citrinellus*, and *Cheilinus chlorourus*: CC BY François Libert. Pictures of *Dascyllus aruanus* and *Heniochus chrysostomus*: CC BY Rickard Zerpe. Pictures of *Acanthurus nigroris* and *Chaetodon lunulatus*: CC BY Arthur Chapman. (H) Canonical correspondence analysis ordination plots of the juvenile fish assemblage composition based on Bray – Curtis dissimilarities. Ellipses are 95 % confidence interval. Pictures of *Cheilinus chlorourus*, *Pomacentrus pavo*, *Chaetodon vagabundus*, and *Stegastes punctatus*: CC BY François Libert. Picture of *Heniochus chrysostomus*: CC BY Rickard Zerpe. Picture of *Acanthurus nigroris*: CC BY Arthur Chapman.

0.93). All other pairwise comparisons yielded statistically significant results (Tukey test, $z \in [-11.26, -10.29]$, all $P < 0.00001$). This pattern persisted when analyzing individual algae species separately (Fig. SP1). At the end of the study (day 70), algae cover differed significantly among the four conditions (Anova, $Df = 3$, $F = 6.43$, $P = 0.0046$). Algae cover was comparable between the two control conditions (CA and CC; Tukey test, $t = -2.27$, $P = 0.15$) and between the two experimental conditions (GA and GC; Tukey test, $t = -1.55$, $P = 0.43$). Notably, algae coverage significantly differed only between GC and CA (Tukey test, $t = -4.33$, $P = 0.0026$, $\Delta = 42\%$).

3.2. Fish

The adult fish abundance showed no significant variation across the four conditions, time, or their interaction, as determined by a linear mixed-effects model ($F = 0.59$, 2.97 , and 1.04 ; $P = 0.63$, 0.086 , and 0.37 ; $acf \leq |0.10|$). However, a decrease over time was observed in both the number of fish species and diversity ($F = 6.89$, $P = 0.009$, $acf \leq |0.11|$; $F = 9.91$, $P = 0.002$, and $acf \leq |0.12|$; Fig. 3), with no significant differences among the conditions ($F = 0.36$ and 0.47 ; $P = 0.78$ and 0.71) or their interaction with time ($F = 0.81$ and 0.20 ; $P = 0.20$ and 0.90).

For juveniles, the abundance did not show significant variation across the four conditions, time intervals, or their interaction (linear mixed effects model, $F = 2.31$, 2.05 , and 1.38 ; $P = 0.12$, 0.15 , and 0.25 ; $acf \leq |0.12|$). Similarly, no significant differences were observed in the number of species ($F = 0.82$, 1.23 , and 2.52 ; $P = 0.50$, 0.27 , and 0.059 ; $acf \leq |0.14|$). Additionally, diversity did not vary significantly among the four conditions ($F = 0.84$, $P = 0.49$, $acf \leq |0.173|$) or their interaction with time ($F = 1.88$, $P = 0.14$). However, there was a notable increase in the diversity of juvenile fish over time ($F = 8.54$, $P = 0.0039$, Fig. 3).

CCA plots showed a displacement of the fish assemblage that tended to occur primarily in sites with coral restoration (CC, GA, and GC) for adults, with less noticeable changes observed in CA ($df = 6$, $\chi^2 = 1.60$, $F = 1.62$, $P = 0.002$, Fig. 3G). Conversely, a degree of displacement in the juvenile fish assemblage was present across all the conditions ($df = 6$, $\chi^2 = 1.67$, $F = 1.48$, $P = 0.04$, Fig. 3H). The anosim statistic (R) between D0 and D70 yielded predominantly low values (Table SP4), associated to non-statistically supported differences, except for GC in juveniles ($R = 0.49$, $P = 0.05$).

At diet level analysis, no significant patterns were observed for adult herbivores fish (Table SP1). Similarly, for juveniles, there was no differences among conditions. However, for herbivores juveniles, there was a statistically supported increase in the number of species over time ($F = 5.69$, $P = 0.019$, $acf \geq |0.21|$, Fig. 4). For MBIF, a statistically supported decline was observed in the number of adult species over time ($F = 4.80$, $P = 0.032$, $acf \leq |0.22|$, Fig. 4), while no significant trend was observed for juveniles (Table SP2). For omnivores, a statistically supported decrease was observed in the abundance of juveniles over time ($F = 7.77$, $P = 0.0062$, $acf \leq |0.18|$, Fig. 4), with no significant trend detected for adults (Table SP3).

4. Discussion

In our study, herbivorous invertebrates limited algae cover compared to control (GA vs. CA and GC vs. CC) while manually removing macroalgae lead to a subsequent increase in algae cover over

time, as newly cleared space became available for macroalgae settlement. Macroalgae are naturally part of reef environments and contribute to their equilibrium when they do not proliferate (Stuart-Smith et al., 2018). However, the proliferation of certain macroalgae species can lead to ecological disturbances, such as when they outcompete live corals (Gaubert, 2018; Hughes et al., 1999). In French Polynesia, an increase in the macroalgae, especially *Turbinaria ornata* has been observed for several decades (Bittick et al., 2010; Stiger & Payri, 1999a). Before the 1980 s, this species was present at low densities in the Society Archipelago (Payri & Naim, 1982). It began appearing in the Tuamotu Archipelago in 1985 (Dellesalle et al., 1985; Stiger & Payri, 1999a, 1999b) and its biomass started increasing in the Society Archipelago (Payri, 1987).

Herbivores play fundamental roles in both terrestrial and marine environments. Consequently, herbivorous species have long been considered a promising solution for regulating some macroalgae species (Coyer et al., 1993) including *Turbinaria*. Include if *T. ornata* is palatable to only a few species of fishes (Davis, 2018; Löffler et al., 2015; Mantyka & Bellwood, 2007), herbivory may prevent the expansion of *T. ornata* (Degregori et al., 2016). In Californian temperate rocky reefs, high densities of sea urchins reduced macroalgae cover, thereby decreasing coral mortality and increasing coral abundance (Coyer et al., 1993). As echinoderms occupy prominent ecological niches in both temperate and tropical marine ecosystems, these findings were not unexpected. Other studies have also demonstrated that herbivorous individuals can help mitigate negative impacts of algae (e.g., *Lobophora*) on coral tissue (e.g., *Porites* sp.) (McCook et al., 2001). It has also been shown that a density of four *T. niloticus* per m² can limit turf cover in the Philippines (Villanueva et al., 2013). Conversely, experimental removal of the sea urchin *Diodema antillarum* in the U.S. Virgin Islands led to macroalgae proliferation (Sammarco et al., 1974). In Bora Bora, *T. gratilla* and *D. baratayresiana* are known to limit macroalgae proliferation at Bora Bora (Krimou et al., 2023). Considering these findings and the current decline in herbivorous populations in Bora Bora (both sea urchins and herbivorous trochid gastropods), mainly due to fishing and collection for tourism purposes, it is essential to regulate fishing/collection practices to protect these regulatory species and ensure a healthy reef ecosystem. In addition, as sea urchins and herbivorous gastropods remove the macroalgae from reef patches, a shift in fish assemblages is expected.

Two types of successions can be described: primary succession, which occurs when organisms colonize an essentially lifeless environment, (Kitayama et al., 1995); and secondary succession, which refers to the sequential replacement of an ecosystem's biocenosis following a less extensive disturbance that does not result in the total loss of biocenosis or the creation of a so-called 'virgin' environment, such as a forest fire (Walker & del Moral, 2003). In our study, we focused on the secondary succession of fish on reef patches, with some changes observed in the juvenile fish assemblages regarding beta diversity in the GC condition. The higher displacement observed in the CCA for juveniles compared to adults appears to underscore a faster modification of this part of the assemblage. This observation aligns with documented differences in habitat responses between juvenile and adult fishes reported in the literature (Fontoura et al., 2020). The close association of many juvenile fish with corals susceptible to disturbances related to global climate change suggests that prioritizing the conservation of resilient reef systems should be emphasized (Wilson et al., 2010). Juveniles may associate with coral skeletons rather than live corals, including herbivorous

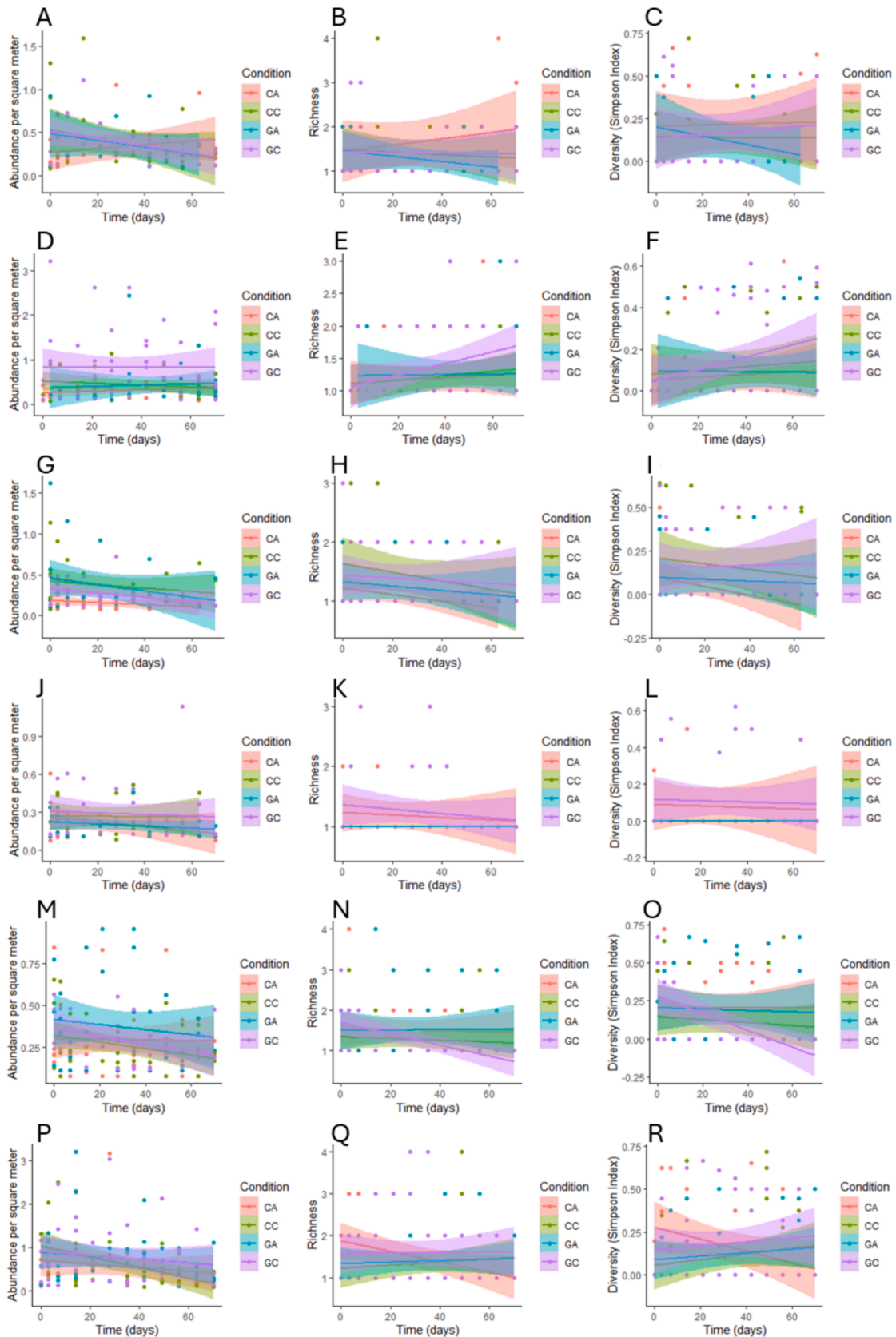


Fig. 4. A-F Evolution of abundance per m^2 , species richness, and diversity over time for adult (top) and juvenile (bottom) herbivorous fish across the four experimental conditions (CA, CC, GA, and GC). Lines represent mean values with 95% confidence intervals. (G-L) Evolution of abundance per m^2 , species richness, and diversity over time for adult (top) and juvenile (bottom) 'Mobile Benthic Invertebrate Feeders' (MBIF) fish across the four experimental conditions (CA, CC, GA, and GC). Lines represent mean values with 95% confidence intervals. (M-R) Evolution of abundance per m^2 , species richness, and diversity over time for adult (top) and juvenile (bottom) omnivorous fish across the four experimental conditions (CA, CC, GA, and GC). Lines represent mean values with 95% confidence intervals.

species that, as adults, feed on epilithic algae, thereby preventing reef overgrowth by macroalgae (Bellwood et al., 2004). Consequently, the recruitment and survival of these fishes are intricately tied to the resilience and recovery of reefs following episodes of extensive coral mortality (Mumby et al., 2007; Nyström et al., 2008; Wilson et al., 2010). Overall, juvenile fish communities are a key component of coral reefs, especially in the current focus on coral reef resilience, as their survival is one of the primary determinants of adult population sizes (Mellin et al., 2007).

Besides the previously stated observations, for the different trophic groups, no differences in alpha diversity were found among conditions. Thus, the relationship between algae biomass in the reef and herbivorous fish is well-established, both at the level of feeding activity, morphometry, and biomass (Russ, 2003). Herbivores regulate algae abundance and promote coral growth by limiting algae's space occupation (Wismer et al., 2009). Therefore, managing fish stocks is a key element in reef resilience management (Hughes et al., 2007), as fishing directly influences herbivory rates, ultimately leading to coral abundance decline, causing feedback via macroalgae abundance (Norström et al., 2009).

The 'top-down' regulation through herbivory complements 'bottom-up' regulation, linked to water nutrient concentrations favoring algae growth over corals (Smith et al., 2001). The relative importance of these two regulation types varies greatly (Carassou et al., 2009), depending on the geographical area (as herbivore diversity varies greatly worldwide) and reef type (with fringing reefs influenced by coastal nutrient inputs) (Carassou et al., 2009). When focusing on top-down regulation, one could examine regulation by benthic invertebrates (e.g., sea urchins and trochids) or herbivorous fish. Theoretically, benthic invertebrates should be better competitors when algal resources are moderate (McClanahan, 1992). However, due to their low biomass production, they are more vulnerable to intense fishing pressure (Carassou et al., 2009; McClanahan, 1992). Conversely, in excessive numbers, they may consume coral juveniles and remove significant amounts of calcium carbonate from both live and dead coral structures (Norström et al., 2009). In extreme cases, this can lead to a rate of bioerosion that surpasses net reef accretion, resulting in a potential shift from a coral-dominated ecosystem to one dominated by invertebrates (e.g., sea urchins) (Eakin, 1996). To monitor the occurrence of such negative changes, longer observation periods than the preliminary 70-day duration in this study are recommended.

Overall, our study highlighted that the fish assemblage change must consider the specific species present and their life stage (adult vs. juvenile), not just the abundance or diversity per trophic group. Moreover, the opportunistic nature of the dietary regime of many species should not be underestimated (Bellwood et al., 2006). This can be problematic when herbivorous fish end up consuming corals, as seen in studies on Scaridae (Alwany et al., 2009) where certain herbivorous species feed on live corals while others do not, with additional variations depending on reef zones. This underscores once again that reef ecosystems are complex, and their modification for regulatory purposes must be extremely cautious. From a management perspective, this study emphasizes the importance of protecting benthic herbivorous species, such as trochids, and highlights the need for monitoring beta diversity.

CRedit authorship contribution statement

Xavier Raick: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Formal analysis, Data curation. **Ethel Mery:** Writing – review & editing, Writing – original draft, Visualization, Investigation. **Camille Carpentier:** Investigation. **Stéphanie Krimou:** Resources. **Jérôme Sowinski:** Resources. **Lucille Sowinski:** Resources. **Natacha Roux:** Resources. **Tehani Maueau:** Resources. **David Lecchini:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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.

Acknowledgements

We would like to thank the staff of 'Polynésienne des Eaux', 'Ia Vai Ma Noa Bora Bora, the 'Commune de Bora Bora' and the private society Espace Bleu for their help. Several funds support this study: Fondation de France (2019-08602), Polynésienne des Eaux, and the French National Research Agency (ANR-19-CE34-0006-Manini and ANR-23-SSRP-0020-01).

Data statement

The data supporting the study are openly available on Zenodo (10.5281/zenodo.11425433).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2024.126761>.

Data availability

The data supporting the study are openly available on Zenodo (10.5281/zenodo.11425433).

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