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Coral reef fish communities of natural habitats and man-made coastal structures in Bora-Bora (French Polynesia)

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Abstract. Coastal habitats have long been recognised to be nurseries and growing grounds for many marine organisms. Worldwide, coastal hardening and urbanisation are leading to the removal of natural ecosystems. The tropical island of Bora-Bora in the South Pacific has undergone extensive coastal changes, with the construction of seawalls along more than half of its coastline since the 1950s. The daytime and night-time juvenile and adult fish communities were surveyed with multiple temporal replicates on a range of lagoon and coastal habitats on Bora-Bora. Over 47% of all fish on coastal habitats were juveniles. Mangroves, traditionally viewed as nurseries, had a high daytime and night-time abundance of juveniles, but less than 1% of the coastline of Bora-Bora consists of mangroves. The manmade seawalls, which are the most common type of coastal habitat on the island, were associated with lower juvenile densities during the day and promoted the presence of predators. The comparison of coastal and lagoon sites also highlighted contrasting life history strategies depending on coral reef fish species: although many favour coastal habitats as juveniles, others do not undergo ontogenetic shifts and thus other habitats must be considered when designing management plans to protect juvenile fish. Overall, our surveys show the importance of natural coastal zones in the lifecycle of numerous coral reef fish species in the lagoon of Bora-Bora and highlight the potential long-term impacts of coastal hardening on fish communities.

Keywords. Urbanisation, coastal habitats, coral reef, fishes, coastal management.

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Introduction

Numerous coral reef fish species have a complex life cycle: after the dispersion of eggs into the open ocean, larvae colonise coral reefs and recruit in specific habitats as juveniles, where they grow until they move into adult populations (Lecchini & Galzin 2005). This juvenile phase is particularly important and conditions individual growth and survival to the adult reproductive stage (Lecchini & Galzin 2005). Identifying and studying habitats where juveniles recruit has been the subject of scientific scrutiny for decades (e.g., Williams 1955; Gasc *et al*. 2021). Fish can sense diverse environmental cues which guide them towards a suitable environment to grow (Lecchini *et al*. 2014, 2017). Each species uses varied and contrasted criteria such as substrate complexity, food availability, but also the presence of predators, hetero- and conspecifics (e.g., Montgomery *et al*. 2001; Lecchini *et al*. 2017), but also may differentially settle on natural *vs.* artificial locations due to different needs and depending on local conditions, with some artificial structures offering more advantages to fish than degraded natural locations. For instance, the southern hulafish *Trachinops caudimaculatus* preferentially settled on custom-designed artificial reefs than on the nearby natural habitats which had less structural complexity (Komyakova & Swearer 2019).

There is a variety of habitats available to settling juveniles, among which some environments stand out. This is the case for nurseries. Beck *et al*. (2001) defined nurseries as habitats with a contribution per unit area to the production of juveniles of a particular species that recruit to adult populations that is greater, on average, than the production from other habitats in which juveniles occur. The destruction of such zones could disproportionately affect fish populations (Hamilton *et al*. 2017). Coastal zones are often referred to as nurseries for marine organisms. Among coastal zones, seagrass beds and mangroves have been identified as nurseries around the world (Nagelkerken 2007, 2009; Whitfield 2017; Lefcheck *et al*. 2019; Madi Moussa *et al*. 2020). These habitats typically provide the resources needed by juvenile fish to grow and survive until adulthood, with shallow and sheltered waters, intricate structures that provide refuge and food, and sufficient substrate space for fish to settle and develop (Chittaro *et al*. 2005; Verweij *et al*. 2006; Nagelkerken 2007, 2009; Grol *et al*. 2014).

Protecting zones which are important in the early life stages of numerous fish species is a crucial step in maintaining sustainable adult fish population levels (Jones 1990). However, in the context of global changes and local urbanisation, intact coastal ecosystems are becoming increasingly rare, with nearly half of all coastal zones worldwide heavily affected by anthropogenic activities (Williams *et al*. 2022). In particular, man-made structures, such as shoreline hardening, jetties, quays, dikes, groins, breakwaters, are being deployed worldwide to gain land over the sea and protect coastal zones from erosion and storms (Cooper & Jackson 2019), and their extent is expected to continue to increase (Bugnot *et al*. 2021). Such structures modify coastal habitats which are often key habitats for juvenile marine organisms (Gasc *et al*. 2021). In this context, the impact of urbanisation and man-made structures of the nursery role of coastal zones must be investigated. There are a few studies about how man-made structures can function as nurseries in the literature (mostly from shipwrecks and artificial reefs, e.g., Love *et al*. 2012; Mercader *et al*. 2017), but even less studies have provided a comparison of various natural habitats with shoreline hardening engineering structures such as seawalls. Recently, CHEMINÉE *et al.* (2021) showed that all shallow coastal zones, natural or artificial, can serve as nurseries for Mediterranean juvenile fish. To address similar questions in a different geographic area, fish surveys were conducted in Bora-Bora, French Polynesia, from February to May 2021 to characterise the fish communities of a range of habitats along its coastline and throughout its lagoon and examine the potential changes in communities linked to artificial seawalls built to stabilise the coastline.

Material and methods

Study sites

Bora-Bora (16°29′ S, 151°44′ W) is a ~20 km² tropical volcanic island encircled by a 70 km² coral reef in French Polynesia (LECCHINI *et al*. 2020). On Bora-Bora, as of 2019, seawalls represented approximately 62% of the coastline, vegetation zones 25%, beaches 11%, mangroves 1%, and grass zones 1% (GAIRIN *et al*. 2021) (Fig. 1).

For this study, five categories of coastal habitats (i.e., habitats within a few meters of the main island of Bora-Bora) were surveyed; they were chosen based on ease of access and on the map of the 2019 coastline classifications of the island by GAIRIN *et al*. (2021): 1) Sand beaches, with white sand and sparse and shallow reef mounds; 2) Mangroves, shallow silty zones with *Rhizophora stylosa* plants; 3) Grass zones, shallow silty zones with coastal rushes and bushes with roots in the water at high tide; 4) Vegetation zones, shallow sandy zones where tall trees have roots directly in or near the water; 5) Man-made seawalls, vertical volcanic rock piles extending into the water column with interstices between the rocks.

Three lagoon habitats (i.e., habitats that were further than 500 meters from the main island of Bora-Bora) were also surveyed (barrier reefs, fringing reefs, pinnacles – isolated reefs in the middle of the

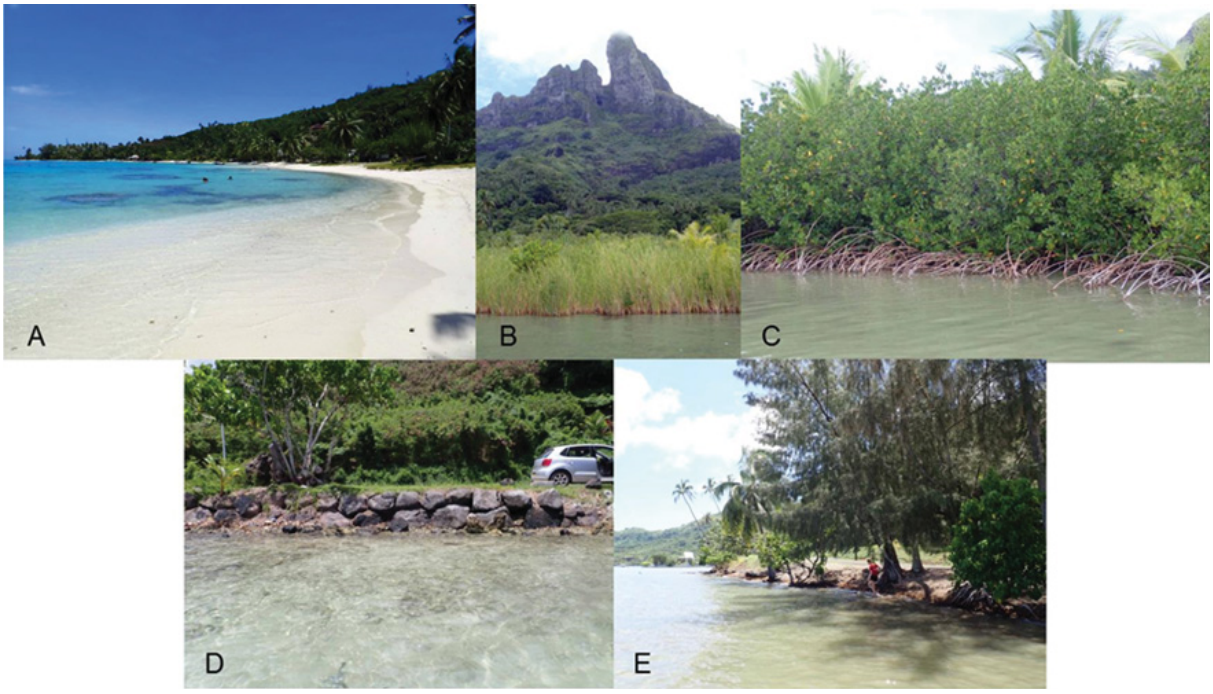

Figure 1 – Field pictures of coastal habitats. A: beach; B: grass; C: mangrove; D: seawall; E: vegetation (trees).

TABLE 1

Summary table of the number of habitat categories, the number of study sites per category, the number of fish surveys at each site as conducted from March to May 2021 during the day and night along the coastline and in the lagoon of the island of Bora-Bora.

Period | Location	**Number of categories (e.g., sandy beach, mangrove, barrier reef)**	**Number of sites per category**	**Number of surveys at each site from March to May 2021**	**Total number of surveys**
Day | Lagoon	3	2	3	18
Day | Coastal	5	2	6	60
Night | Coastal	5	1	5	25

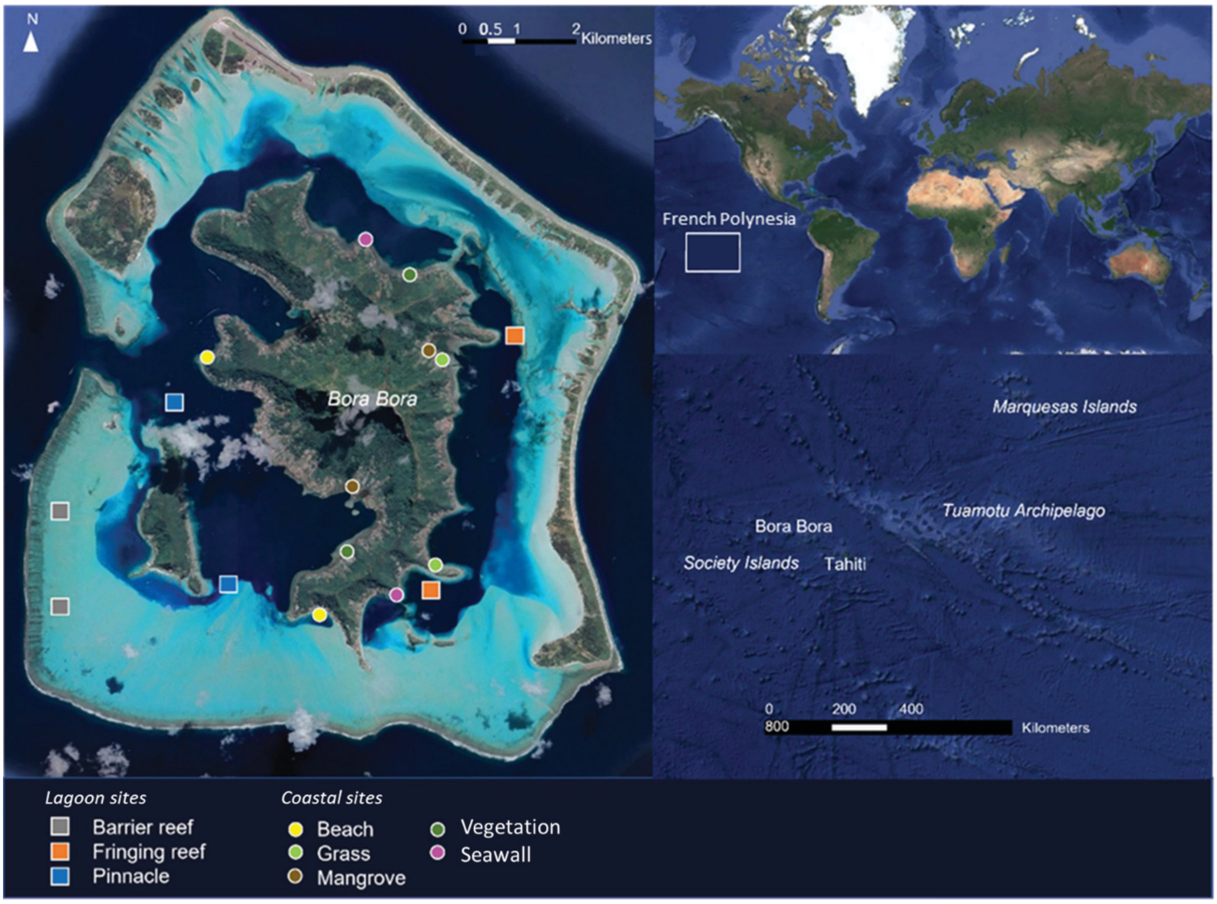

Figure 2 – Geographical location of the island of Bora-Bora in French Polynesia and map of the coastal (circles) and lagoon (squares) study sites across Bora-Bora. The lagoon sites were surveyed three times during the day, every month, from March to May 2021. The coastal sites were surveyed six times during the day, every two weeks, from March to May 2021. The southernmost coastal site for each category (beach, grass, mangrove, vegetation, seawall) was also surveyed five times at night, every two weeks, from March to May 2021. Figure adapted from Google Earth (2023).

lagoon; Figs 1–2). Two study sites were examined for each lagoon and coastal habitat category during the day; one site for each coastal habitat category was also surveyed at night due to logistical constraints.

Coastal sites were surveyed six times during the day, every two weeks, from March to May 2021. At night, they were surveyed five times, every two weeks, from mid-March to May 2021. Lagoon sites were surveyed three times during the day, once a month, from March to May 2021, due to logistical constraints (Table 1).

Survey methodology

At each site, visual surveys by snorkel were performed on three 25 m × 4 m transects (2 m, 12 m, and 32 m from the shore and parallel to it) in the morning (between 0800 hrs and 1200 hrs) every two weeks (full moon/new moon) from February to May 2021 (yielding six temporal replicates) at the coastal sites (water depth < 1.5 meters), and once a month (three replicates) at the lagoon sites (water depth < 2 meters). At night, the southern beach, grass, mangrove, seawall, and vegetation habitats were also surveyed along the three 25 m × 4 m transects (2 m, 12 m, 32 m from the shore and parallel to it) every two weeks between 2100 hrs and 0000 hrs from February to May 2021 (yielding five temporal replicates). The tidal range on Bora-Bora is limited (maximum during spring tides: 0.4 m; PIRAZZOLI *et al*. 1985) and was thus not considered when choosing the day and time of sampling. Fish were recorded to the species-level (with all species recorded except for cryptic Gobiidae and Blenniidae – SIU *et al*. 2017). The size of all individuals was measured with a 2 cm precision at the coastal sites (the sizes and pigmentation patterns were used to differentiate adults and juveniles for each species based on expert knowledge, following LECCHINI & GALZIN 2005). Two passes were performed per transect; mobile, more visible fishes were recorded during the first pass and more cryptic fishes were recorded on the second pass (LECCHINI & GALZIN 2005). At each site, a 25 m gap was left between each transect to ensure the independence of the replicates. All observed individuals were classified with respect to their life stage – juvenile vs. adult (LECCHINI & GALZIN 2005).

Data analysis

The data analysis was performed for day and night surveys separately due to the different fish communities observed during either period, as well as due to the different number of categories, sites, and temporal replicates (Table 1). To characterise each site, the number of species of all juvenile and adult fish and corresponding Shannon diversity indices were calculated (for day and night separately). The density (number of individuals per 100 m²) of all juveniles, all adults, and predator piscivorous adults were assessed for each transect (3 per site), each site (2 per habitat type), and for six temporal replicates.

R version 4.2.0 was used for all statistical analyses. Using the vegan package in R and the Nonmetric Multidimensional Scaling Method with a Bray-Curtis similarity matrix, a NMDS analysis followed by a one-way analysis of similarity (ANOSIM) with 9999 permutations were performed to examine differences in juvenile and adult fish assemblages between each habitat (lagoon and coastal habitats combined). Following this, the species contributing to the dissimilarity between each habitat for juvenile and adult communities during the day and at night were obtained using Similarity Percentage (function simper from the R package vegan).

Linear mixed-effects models (lmerTest and afex packages on R) were used to assess whether juvenile, adult, and predator fish densities (values scaled and centred at 0) were significantly different across the coastal habitats (beach, grass, mangrove, vegetation, seawall). The habitats were taken as fixed effects while the time of sampling, site and transect (transect nested per site) were taken as random effects (density ~ habitat + (1|site/transect) + (1|time) for daytime survey results; density ~ habitat + (1|transect)

+ (1|time) for nigh-time survey results). P-values were estimated by the afex package in combination with the lmerTest package on R.

Lastly, the overall changes in juvenile, adult, and predator densities on Bora-Bora were estimated based on the assumption that fish densities were similar in equivalent habitats in 1955 and 2019. To do so, the density of juveniles, adults, or adult predators from each coastal category was multiplied by the total length of each category along the coastline of the main island of Bora-Bora in 1955 and 2019 (from Gairin *et al*. 2021: fig. 6; Table S11). This estimation provides an overview of the extent to which modifications in coastline typology, excluding numerous other factors, may have impacted the fish communities in the lagoon of Bora-Bora.

Results

Overall, 27212 fish of 133 species were observed, with 21568 fish belonging to 116 species recorded during the day at ten coastal (six temporal replicates) and six lagoon sites (three temporal replicates), and 5644 fish of 52 species recorded at five coastal sites at night (five temporal replicates).

8432 juveniles (69 species) were observed during the day, and 3272 (39 species) at night. During the day, 13136 adults (112 species) were counted, of which 646 were piscivores, i.e., fish predators (with 31 species) – roughly 5% of all adults. Only 76 of those were found in coastal habitats, all others were on the barrier reef, fringing reef, or pinnacle. At night, 1450 of the observed fish (17 species) were predators out of 2372 adults (38 species) – accounting for 61% of adult fish.

Fish density

The average density of fish juvenile (averaged over the three transects performed for each site and temporal replicate) was highest on the barrier habitats (mean±SE = 60.2±12.6 juveniles per 100 m²). Juvenile density was also higher in the beach, grass, and mangrove coastal habitats during the day (52.6±4.3, 40.9±3.3, 42.3±4.6 respectively) (Fig. 3) when compared to the vegetation and seawall during the day (20.6±3.5 and 16.8±2.9 per 100 m²). Based on the linear mixed effect model (Table 2), the presence of seawalls significantly impacted the densities of juvenile fish. Overall, the fixed effects, consisting of the habitat type, represented 36% of the variance, while the transect distance from the shore at each site accounted for most of the remaining variance (64%), and time had a minimal effect (Table 2).

Adult density was highest on the lagoon habitats (135.3±55.4 to 202.9±157.0 adults per 100 m²; Fig. 3); among the coastal sites, during the day, it was on average highest on the beach habitats (32.5±25.2) and lowest on the vegetation (10.2±4.0) and grass habitats (6.8±4.6). Based on the linear mixed effect model, none of the habitats significantly influenced adult densities, although habitat type represented 45% of the variance while distance from the shore accounted for 38% of the variance (Table 2).

The results showed that the density of predators was highest in the lagoon (from 3.3±1.1 to 13.2±10.4 per 100 m² on the pinnacle and fringing habitats; Fig. 3) and on the coastal seawall sites (1.25±0.6). Predator density was significantly lower on the other coastal habitats (e.g., beach, grass, mangrove, vegetation in particular when compared to the lagoon habitats; Tables S1-S4). During the day, density was lowest on mangroves with 0.08±0.06 per 100 m² and grass with 0.14±0.11, and highest on average on seawalls with 1.25±0.65. Across the five coastal habitats, only seawalls led to a significant difference in predator densities based on a linear mixed-effects model (Table 2).

At night, fish juvenile density was on average highest on the mangrove (62.5±5.6 juveniles per 100 m²), followed by the grass, vegetation, and beach habitats (48.6±8.8, 28.3±7.3, 30.3±4.7), and lastly the seawall habitat (Fig. 4). The grass and mangrove habitats led to significantly fixed effects on the juvenile densities; habitat type accounted for 45% of the variance, while the distance of the transect from the shore accounted for 49% (Table 2). Adults were most numerous on the beach (101.5±8.2), followed by seawalls with 23.1±13.4, and other habitats had adult densities below 14.6±9.6. All habitat types had a significant effect on all adult densities and on adult predator densities (Table 2). In addition, adult predators made up most of the adults on beaches (71.7±10.1 individuals per 100 m², significantly higher than in the mangrove and vegetation habitats), with 71% of all observed adults being piscivores.

The overall proportion of juveniles among all observed fish (in terms of average density) was markedly higher on coastal sites than lagoon sites during the day for a number of species, including the very abundant *A. sexfasciatus*, *Acanthurus triostegus*, *Halichoeres trimaculatus*, *Lutjanus fulvus*, *Mulloidichthys flavolineatus*, *Scarus schlegeli*, *Scarus sordidus*, *Siganus spinus*, or *Zanclus cornutus.* In contrast, species such as *C. striatus*, *Dascyllus aruanus*, *Halichoeres margaritaceus*, or *Stegastes nigricans* had relatively similar juvenile-to-adult ratios on the coastal and lagoon sites (Fig. 5).

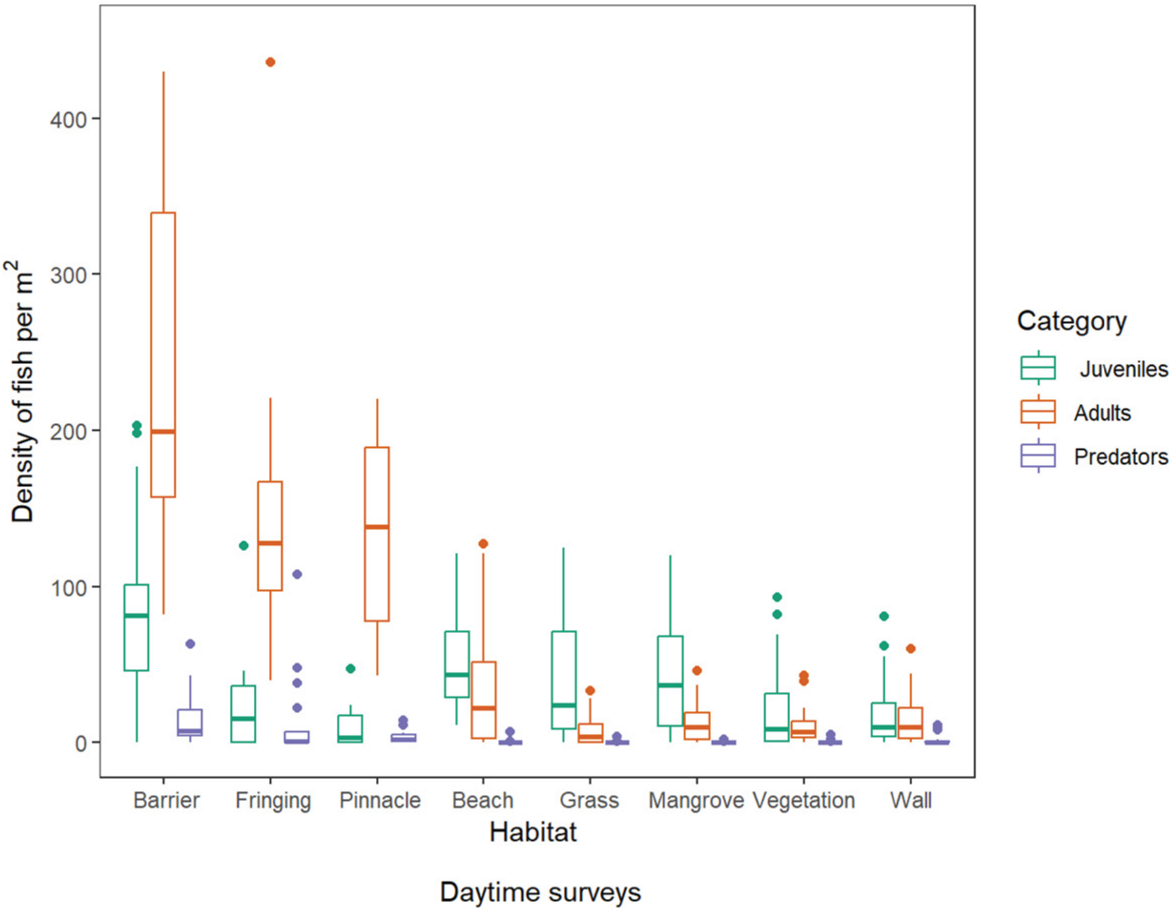

Figure 3 – Summary of juvenile, adult, and predator density (number of fish per 100 m^2) of each habitat during the day. The lower and upper hinges of the boxplot correspond to the 25th and 75th percentiles; the middle line is the median. The upper whisker extends to the largest value which is within 1.5 times the interquartile range; the lower whisker extends to the smallest value within 1.5 times the interquartile range. Large outliers (beyond 450 individuals per 100 m^2 – 2 instances for the barrier reef and one for the fringing reef) are not shown for better visualisation.

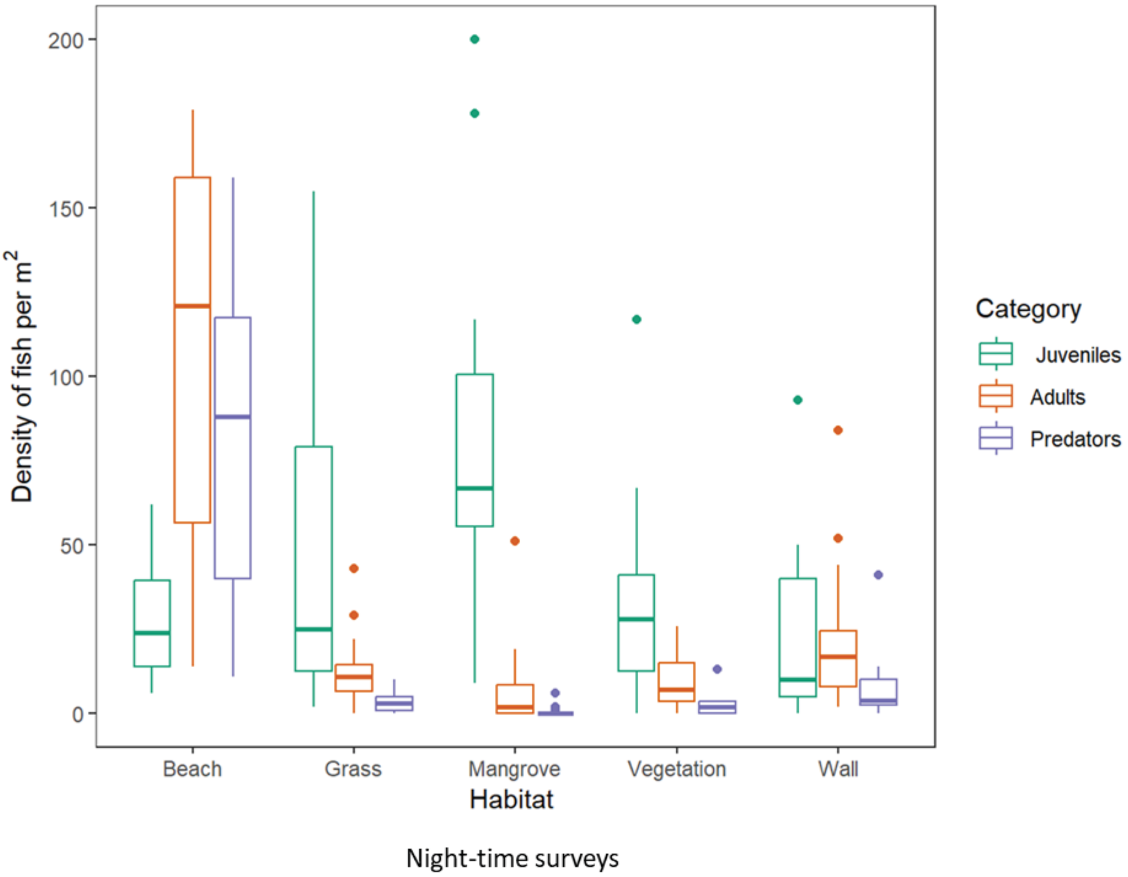

Figure 4 – Summary of juvenile, adult, and predator density (number of fish per 100m^2) on each habitat during the night. The lower and upper hinges of the boxplot correspond to the 25th and 75th percentiles; the middle line is the median. The upper whisker extends to the largest value which is within 1.5 times the interquartile range; the lower whisker extends to the smallest value within 1.5 times the interquartile range.

Since the 1950s, the coastline of Bora-Bora has transitioned from natural to artificial features (from GAIRIN *et al.* 2021: fig. 6). Extrapolating from the average juvenile, adult, and predator densities found with our fish surveys for each type of coastal habitat, coastal modifications (excluding all other sources of variability) could potentially have led to a change of juvenile abundance by +4% during the day (mainly due to a lengthening of the coastline from 37 km to 44 km through artificial structures) and 0% at night, an increase of adult presence by +31% during the day and +44% at night, and of predator presence by +122% during the day and +40% at night. This strong rise in predators is mainly driven by an increase in the proportion of seawalls around the island – predators on seawalls represent 85% of all predators during the day and 51% at night (details of calculations in Table S9).

Fish diversity

Across all sites during the day, the number of species observed (juvenile and adult combined) was highest on the barrier reef sites, with 83 species observed across sites and temporal replicates; this was followed by the beach sites, with 64 species. Inversely, the lowest species number was in mangroves, with 17 species overall during the day. At night, beaches had overall 38 different fish species, grass

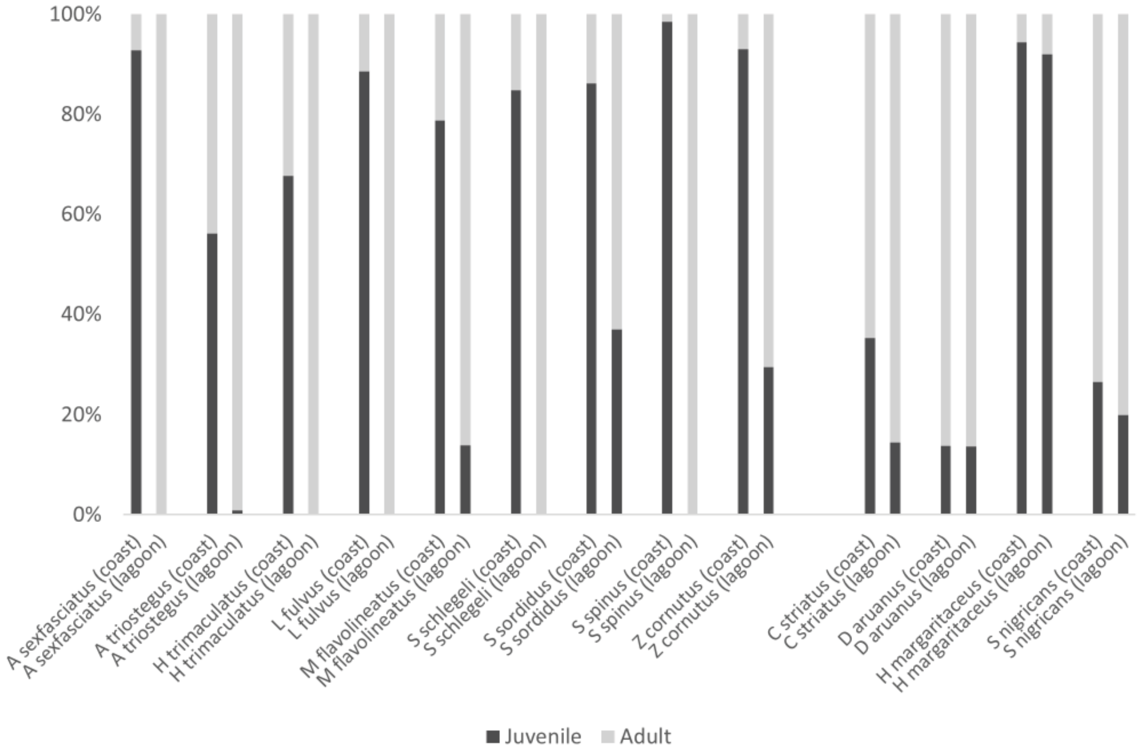

Figure 5 – Average proportion of juveniles and adults of *A. sexfasciatus*, *Acanthurus triostegus*, *Halichoeres trimaculatus*, *Lutjanus fulvus*, *Mulloidichtys flavolineatus*, *Scarus schlegeli*, *Scarus sordidus*, *Siganus spinus*, *Zanclus cornutus*, *C. striatus*, *Dascyllus aruanus*, *Halichoeres margaritaceus*, and *Stegastes nigricans* on the coastal and lagoon sites surveyed during the daytime between March and May 2021 in Bora-Bora. The break in the x-axis separates on the left species that have different proportions of juveniles and adults on coastal and lagoon sites from species that have similar proportions on the right.

zones 22 and the other habitats 17 (for details about juveniles or adults, refer to Tables 3 to 6). Among coastal sites, the Shannon-Wiener index of diversity was consistently highest on beaches among coastal zones for both juveniles and adults, and lowest on mangroves (Tables 3 to 6).

Figure 6 displays the number of species with individuals or adults observed on lagoon or coastal habitats during the surveys. Only adults were observed for 47 species, and only juveniles for 4 species. Of particular importance, 24 species with adults found on the lagoon only had juveniles on coastal habitats.

Non-Metric Dimensional Analyses based on the juvenile and adult fish communities during the day and at night (Fig. 7) separated, along the first dimension, the night and day fish communities from coastal habitats as well as the communities from the coastal habitats from those of the lagoon habitats. The ANOSIM performed to examine differences in juvenile and adult assemblages on each habitat during the day and night using each temporal and spatial replicate highlighted significant dissimilarities (R = 0.596, p = 0.0001). The NMDS plot also shows that the fish communities on the beach during the day were most similar to fish communities from the lagoon habitats (the beaches of Bora-Bora have reef patches – cf. Supplementary Figure S1). Grass and mangrove adult fish communities were highly similar, and so were seawall and vegetation juvenile communities. Lastly, the juvenile and adult fish populations of each habitat tended to cluster closer together than to those of other habitats (with the exception of nighttime mangrove and vegetation fish communities, and mangrove and grass

TABLE 2

Linear mixed-effects model outputs examining the density of juvenile, adult, and adult predator fish on five coastal habitats of Bora-Bora (beach, grass, mangrove, vegetation, seawall) with habitat as a fixed effect, site of sampling (2 sites per category during the day. Not considered at night as only one site per category), time of sampling (6 temporal replicates during the day, 5 at night), and distance of the transect to the shore (2 m, 12 m, 32 m) as random effects.

Day | Juveniles					
REML criterion at convergence: 356					
Scaled residuals					
Min	1Q	Median	3Q	Max	
-2.5506	-0.5248	-0.1306	0.5377	2.7069	
Random effects					
Groups	Name	Variance	% Variance	SD	
transect:site	(Intercept)	0.499284	63.7	0.7066	
site	(Intercept)	0	0	0	
time	(Intercept)	0.000815	0.1	0.02855	
Residual		0.28432	36.2	0.53322	
Fixed effects					
	Estimate	SE	df	t-value	Pr(>|t|)
(Intercept)	0.4186	0.3021	25.0289	1.386	0.178
Grass	-0.3196	0.4269	24.9999	-0.749	0.461
Mangrove	-0.284	0.4269	24.9999	-0.665	0.5119
Vegetation	-0.8733	0.4269	24.9999	-2.046	0.0514
Wall	-0.9779	0.4269	24.9999	-2.291	0.0307
Day | Adults					
REML criterion at convergence: 275.1					
Scaled residuals					
Min	1Q	Median	3Q	Max	
-3.1243	-0.4605	-0.1536	0.3436	4.4193	
Random effects					
Groups	Name	Variance	% Variance	SD	
transect:site	(Intercept)	0.157833	38.0	0.39728	
site	(Intercept)	0.060062	14.5	0.24508	
time	(Intercept)	0.008978	2.2	0.09475	
Residual		0.188369	45.4	0.43402	
Fixed effects					
	Estimate	SE	df	t-value	Pr(>|t|)
(Intercept)	0.3947	0.2511	5.2395	1.572	0.1741
Grass	-0.8116	0.3509	5.0024	-2.313	0.0686
Mangrove	-0.6619	0.3509	5.0024	-1.886	0.1179
Vegetation	-0.7022	0.3509	5.0024	-2.001	0.1018
Wall	-0.563	0.3509	5.0024	-1.604	0.1695

Day | Predators					
REML criterion at convergence: -453					
Scaled residuals					
Min	1Q	Median	3Q	Max	
-1.4918	-0.447	-0.0548	0.1023	6.2869	
Random effects					
Groups	Name	Variance	% Variance	SD	
transect:site	(Intercept)	0	0	0	
site	(Intercept)	0	0	0	
time	(Intercept)	0.000498	11.6	0.02232	
Residual		0.003793	88.4	0.06159	
Fixed effects					
	Estimate	SE	df	t-value	Pr(>|t|)
(Intercept)	-0.248544	0.013725	16.0705	-18.109	4.08^{E}-12
Grass	-0.006049	0.014517	170	-0.417	0.67743
Mangrove	-0.008469	0.014517	170	-0.583	0.56042
Vegetation	0.00363	0.014517	170	0.25	0.80288
Wall	0.042344	0.014517	170	2.917	0.00401
Night | Juveniles					
REML criterion at convergence: 182.3					
Scaled residuals					
Min	1Q	Median	3Q	Max	
-1.7841	-0.5716	-0.143	0.3815	2.8458	
Random effects					
Groups	Name	Variance	% Variance	SD	
transect	(Intercept)	0.07776	6.2	0.2789	
time	(Intercept)	0.61152	49.1	0.782	
Residual		0.55558	44.6	0.7454	
Fixed effects					
	Estimate	SE	df	t-value	Pr(>|t|)
(Intercept)	-0.2361	0.5064	2.9287	-0.466	0.6735
Grass	0.6362	0.2722	64	2.338	0.0225
Mangrove	1.4761	0.2722	64	5.423	9.54^{E}-07
Vegetation	0.1127	0.2722	64	0.414	0.6802
Wall	-0.1763	0.2722	64	-0.648	0.5194
Night | Adults					
REML criterion at convergence: 197.7					
Scaled residuals					
Min	1Q	Median	3Q	Max	
-3.1322	-0.2795	-0.1303	0.2208	2.5112	
Random effects					
Groups	Name	Variance	% Variance	SD	
transect	(Intercept)	0	0	0	
time	(Intercept)	0.017	2.1	0.1304	
Residual		0.8028	97.9	0.896	

Fixed effects					
	Estimate	SE	df	t-value	Pr(>|t|)
(Intercept)	2.7052	0.2433	21.7655	11.12	1.92^{E}-10
Grass	-2.9167	0.3272	68	-8.915	4.81^{E}-13
Mangrove	-3.1142	0.3272	68	-9.519	3.94^{E}-14
Vegetation	-3.0364	0.3272	68	-9.281	1.05^{E}-13
Wall	-2.6225	0.3272	68	-8.016	2.05^{E}-11
Night | Predators					
REML criterion at convergence: 213.1					
Scaled residuals					
Min	1Q	Median	3Q	Max	
-2.8489	-0.252	-0.1221	0.2865	3.266	
Random effects					
Groups	Name	Variance	% Variance	SD	
transect	(Intercept)	1.05^{E}-09	9.8^{E}-08	3.25^{E}-05	
time	(Intercept)	1.04^{E}-01	9.6	3.22^{E}-01	
Residual		9.76^{E}-01	90.4	9.88^{E}-01	
Fixed effects					
	Estimate	SE	df	t-value	Pr(>|t|)
(Intercept)	3.3427	0.3157	8.4745	10.589	3.56^{E}-06
Grass	-3.4669	0.3608	68	-9.609	2.72^{E}-14
Mangrove	-3.5773	0.3608	68	-9.914	7.75^{E}-15
Vegetation	-3.4959	0.3608	68	-9.689	1.95^{E}-14
Wall	-3.2666	0.3608	68	-9.053	2.70^{E}-13

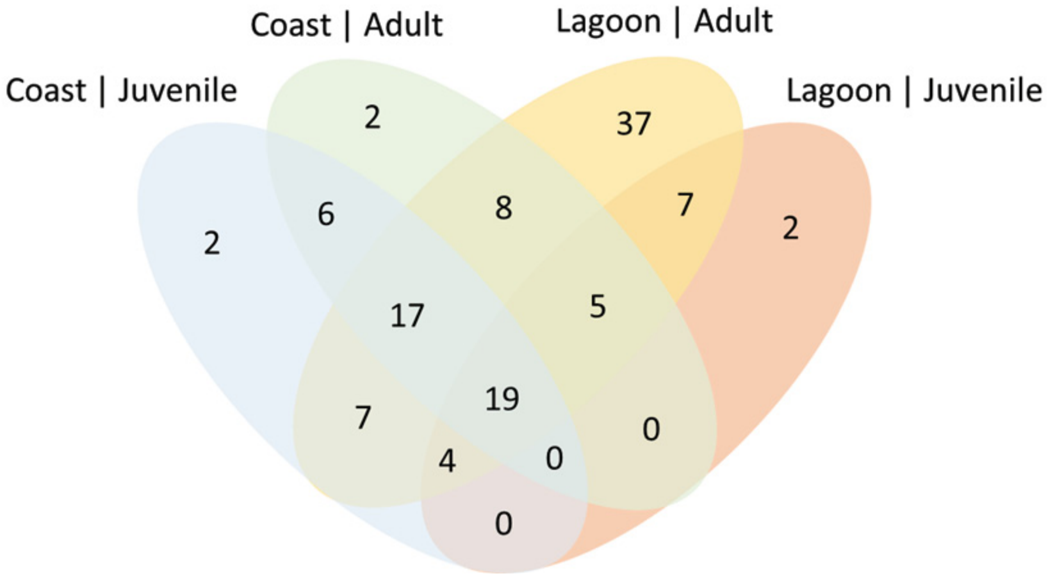

Figure 6 – Venn diagram representing the number of species for which juveniles and/or adults were observed from March to May 2021 on coastal (beach, grass, mangrove, vegetation, seawall) and/or lagoon (barrier reef, fringing reef, pinnacle) sites.

TABLE 3

Shannon-Wiener indices for juveniles on each site across temporal replicates during the day.

Habitat	**Total number of species(sites combined)**	**Shannon-Wiener index (sites combined)**	**Shannon-Wiener index (northern site)**	**Shannon-Wiener index (southern site)**
Barrier reef	61	2.03	1.9	1.89
Fringing reef	45	2.36	1.83	2.2
Pinnacle	29	1.64	1.42	1.05
Beach	73	3.21	2.58	3.07
Grass	25	1.77	1.99	2.75
Mangrove	21	1.68	0.86	1.82
Vegetation	23	2.03	1.14	2.15
Wall	36	2.43	2.49	2.07

TABLE 4

Shannon-Wiener indices for adults on each site across temporal replicates during the day.

Habitat	**Total number of species (sites combined)**	**Shannon-Wiener index (sites combined)**	**Shannon- Wiener index (northern site)**	**Shannon-Wienerindex (southern site)**
Barrier reef	83	1.40	1.38	1.36
Fringing reef	54	1.15	1.16	1.00
Pinnacle	59	1.30	1.17	1.23
Beach	64	0.94	0.92	0.96
Grass	21	0.30	0.38	0.44
Mangrove	17	0.20	0.22	0.33
Vegetation	19	0.59	0.33	0.78
Wall	32	0.99	1.10	0.84

TABLE 5

Total number of species and Shannon- Wiener indices for juveniles on each site across temporal replicates at night.

Habitat	**Number of species**	**Shannon- Wiener index**
Beach	37	1.08
Grass	21	0.77
Mangrove	17	0.77
Vegetation	17	0.89
Wall	17	0.91

TABLE 6

Total number of species and Shannon- Wiener indices for adults on each site across temporal replicates at night.

Habitat	Number of species	Shannon- Wiener index
Beach	30	1.07
Grass	16	0.83
Mangrove	6	0.54
Vegetation	11	0.76
Wall	13	0.97

daytime fish communities). Overall, this indicates that fish species communities are more similar across developmental stages within sites rather than across sites. In particular, Fig. 7 highlights that the adult fish communities of the lagoon may for a large fraction originate from lagoon juvenile communities rather than fish developing along the coastline and then moving to lagoon habitats.

A SIMPER analysis showed that *Crenimugil crenilabis*, *Mulloidichthys flavolineatus*, and *Ellochelon vaigiensis* juveniles and adults were consistently among the top five fish species that drove differences among pairwise comparisons of habitats performed based on the daytime and nighttime composition of juvenile and adult fish communities. The only exceptions were pairwise comparisons between lagoon habitats (i.e., between the barrier, fringing, and pinnacle reefs), for which *Chlorurus sordidus* and *Stegastes nigricans* were the top fish species driving differences in juvenile communities. In addition, for

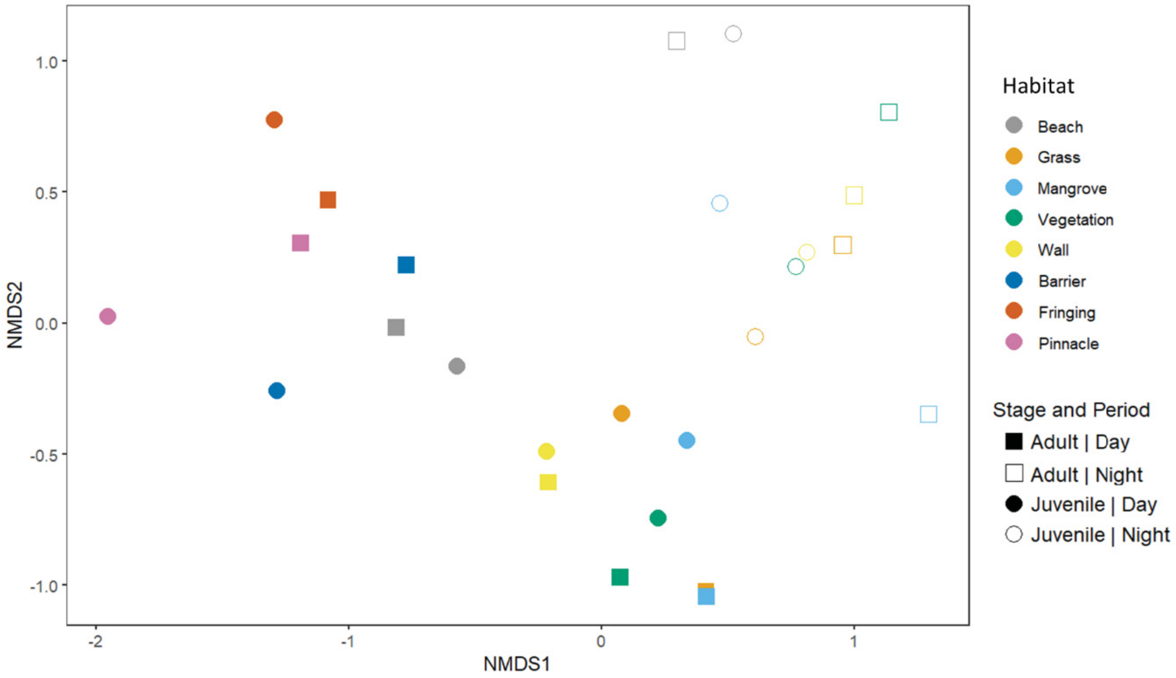

Figure 7 – NMDS plot based on the abundance of all juveniles and adults from the 70 most abundant species on each habitat type (lagoon habitats: barrier, fringing, pinnacle; coastal habitats: beach, grass, mangrove, vegetation, wall) during the day and at night (average of all temporal replicates).

comparisons involving beach habitats, *Myripristis berndti* was the top fish species causing differences in adult communities due to its strong presence along the beach (cf. Table S10-S13).

Discussion

Through all surveys performed on the lagoon sites and along the coast of Bora-Bora (Figs 1–2), coastal sites were found to be important habitats for juveniles. More particularly, 24 species had adults on lagoon sites, but juveniles only on coastal sites (Fig. 6). In addition, coastal sites had a higher proportion of fish juveniles than lagoon sites (Fig. 3): across all coastal sites, 47.6±6.0% of the fish were juveniles. Such high values are similar to those found in nurseries (e.g., GILLANDERS 2002). Furthermore, coastal habitats had lower predator densities than lagoon habitats during the day (on average 2.9±3.0 individuals per 100 m², compared to 35.0±56.8 for lagoon habitats). The density of observed predators on coastal sites was higher at night than during the day as many piscivore species have nocturnal lifestyles (DANILOWICZ & SALE 1999) and move into shallower waters at night (BECKER & SUTHERS 2014). No survey was performed on the lagoon habitats at night for logistical reasons, but we can expect the predator densities to largely exceed those observed during the day in those locations. On coastal sites, the higher proportion of juveniles and lower predator density can be linked to various factors: coastal habitats tend to be sheltered, shallow, with abundant food resources and refuges where small fish can hide from predators (CHITTARO *et al*. 2005).

Among coastal habitats, numerous studies have identified mangroves as nurseries for juvenile fish (e.g., NAGELKERKEN 2007, 2009; GROL *et al*. 2014), where their growth and survival to adulthood are higher than in other coastal zones. These may be attributed to the unique characteristics of mangroves: their dense root network and silty substrate can provide foraging grounds and shelters (VERWEIJ *et al*. 2006). In Bora-Bora, mangroves had the highest juvenile densities of all coastal habitats when combining day and night surveys. However, three factors may limit their overall role as a nursery for reef fish on the island: firstly, the spatial extent of mangroves is low: *Rhizophora stylosa* mangrove trees were introduced in French Polynesia in the 1930s (CAVALOC 1988) and have not expanded beyond a few turbid bays (less than 1% of the coastline; GAIRIN *et al*. 2021); although they have high juvenile densities, their effective contribution to adult fish populations in the lagoon may be limited. In terms of raw abundance rather than absolute densities, they likely contribute only to a small fraction of the adult populations. This has been recognized in the literature and has led to developing the concept of "effective juvenile habitat" (DAHLGREN *et al*. 2006), which considers habitat area in addition to its nursery characteristics to identify key locations to preserve. In many tropical settings throughout the world, mangroves play a crucial role as nursery grounds (e.g., CHITTARO *et al*. 2005; NAGELKERKEN 2007, 2009); in French Polynesia, they are constrained to small areas or completely absent from many islands, and thus may not play as important a role as in other locations. Secondly, when identifying key zones for juvenile fish, juvenile diversity may be one of the most important factors to consider, despite not being formally cited in BECK *et al*.'s (2001) definition of a nursery. In Bora-Bora, juveniles of 23 species only were observed on mangroves (with one species that was only present on mangroves, *Parupeneus ciliatus*), out of the 116 species observed throughout the island. In particular, goatfish such *as Ellochelon vaigiensis*, *Crenimugil crenilabis*, and *Mulloidichthys flavolineatus* represented 84% of all juveniles on mangroves, which had the lowest Shannon indices of diversity (Tables 2 and 4). Figure 7 shows that mangrove juvenile fish communities, although relatively dissimilar to their adult communities (which may indicate an export of species and individuals away from the mangroves after the juvenile stage), are highly different from most other adult communities on different habitats of the lagoon. The role of mangroves as a key habitat may thus be limited to a few fish species. Thirdly, juvenile fish species may use mangroves but not be specialists of such locations. Previously, BARNES *et al*. (2012) noted on Orpheus Island in the Great Barrier reef that non-estuarine Indo-Pacific mangroves such as the one in Bora-Bora, in contrast to those in the Caribbean, may provide foraging grounds for species moving from habitat to habitat but may not be obvious nurseries for reef fishes. In our study, apart from the whitesaddle goatfish *Parupeneus ciliatus*, which was observed on lagoon sites as an adult but only on mangrove sites as a juvenile, most species prominent on mangroves were also common on other habitats, in particular on vegetation and grass habitats (Fig. 7). This highlights that, overall, Bora-Bora's mangroves may not be uniquely important nursing grounds for the island's reef fish.

A main threat to coastal ecosystems in numerous locations worldwide, and in particular in French Polynesia (GITTMAN *et al*. 2016; GASC *et al*. 2021; GAIRIN *et al*. 2021, 2022), is coastal hardening. In Bora-Bora, the most common coastal habitat is artificial seawalls (over 60% of the shoreline). These were put in place from the 1950s to allow for urbanisation and road construction, and mainly replaced vegetation areas which were prominent beforehand (Gairin *et al*. 2021). Based on our surveys and on a linear mixed effects model, seawalls were significantly associated with lower densities of juvenile fish during the day. These results mirror studies highlighting shifts in juvenile fish communities and decreases in abundances in nurseries due to artificial structures (e.g., MUNSCH *et al*. 2014, 2017). However, in our study, both seawalls and vegetation areas had low juvenile fish diversity and density, with similar communities, in particular at night (Fig. 7). In Bora-Bora, in spite of the construction of seawalls, the shallow underwater topography and substrate (sediment, debris) are similar in zones bordering vegetation and seawall habitats (Supplementary Material Figure S1). Besides affecting numbers of juvenile fish, previous studies predicted that the implementation of artificial structures along coastlines could also lead to rises in predator numbers (KORNIS *et al*. 2018). Our study provides a significant contribution to this prediction with the first survey of fish populations confirming this increase based on comparisons with multiple natural sites. In addition to a higher average density of adult fish on artificial structures than on vegetation habitats (43% more than on vegetation habitats during the day, 134% more at night, although this is not statistically significant), seawalls have a higher density of predators than any coastal site during the day, and the second highest after the beach habitat at night (Table 4). The presence of predators along seawalls may be linked to several abiotic features. Firstly, the seawalls in Bora-Bora are not smooth vertical concrete seawalls. Volcanic rocks were used to build them, and there are thus large holes between the rocks from which predators may ambush preys. Indeed, predators are most abundant on seawall habitats, but also on beaches, as the few large coral colonies on the study sites possess cave-like holes, similar to the spaces between rocks in embankments. Another explanation could be that the seawall sites were selected for this study in part for their ease of access, which means that fishermen can also easily use them as locations to scale and prepare fish (pers. observation), thereby attracting predators.

On a historical timescale, by pairing the historical evolution of the coastline (GAIRIN *et al*. 2021) with the fish surveys from March to May 2021, the transformation of the coastline from natural to man-made structures – with 56% of the island's coastline consisting of seawalls in 2019 as compared to 11% in 1955– could by itself have led to an overall increase of the number of fish predators by 122% during the day around the entire island and by 40% at night (Table S9). Although this figure cannot be taken at face value – as numerous other environmental parameters and human pressures changed through time – it can serve as a warning for the potential consequences of coastal hardening on the physical characteristics of potential nursery grounds for fish communities, with particular consequences on the survival of juvenile fish to adulthood. A preventive solution could be to replace seawalls, which are mainly put in place to stabilise coastlines, by alternative features that prevent erosion while being beneficial for juvenile fish. There are numerous options: low-lying vegetation (grass, bushes), strong-rooted trees (local varieties such as aito – *Casuarina equisetifolia*, purau – *Hibiscus tiliaceus*, miki – *Pemphis acidula*), or the promotion of coral growth with adapted artificial frameworks – leading to hard structures that attenuate wave energy (GRACIA *et al*. 2018). In urban settings, putting in place complex substrate frameworks (MERCADER *et al*. 2017; MORRIS *et al*. 2018; USHIAMA *et al*. 2019) instead of smooth quays or simple seawalls with large rock blocks such as in Bora-Bora (Fig. 1) could also provide more resources for juvenile fish, especially refuges from predation.

In addition to modifications of shoreline typology on Bora-Bora, shallow fringing reef flats have been dredged to make way for navigation routes or filled in to gain land over the lagoon since the 1950s. This is notably near the main town of Vaitape on the western side of the island, directly near the only pass in the barrier reef, where more than 100 meters were gained over the lagoon to build infrastructure (GAIRIN *et al*. 2021). This phenomenon also occurred on private lands, with gardens bordering the lagoon being extended by filling in the fringing reef over 5 to 10 m, and consolidating the newly gained land with a seawall. In addition to the direct removal of fringing reef habitats, these considerable modifications may have led to alterations of sedimentation, water circulation and hydrodynamics, and turbidity (GAIRIN *et al*. 2021). There is no historical data on the fish communities of the island, but we can hypothesize that these modifications have also had profound impacts on fish nursery grounds as well as on habitats for adult fish near the main island but also in more distant locations throughout the lagoon.

Beyond coastal habitats, our study also highlights that not all fish species sighted in Bora-Bora may rely on coastal zones for early juvenile development – i.e., not all species are coastal-to-lagoon ontogenetic shifters; there are also many habitat specialists and habitat generalists (ADAMS *et al*. 2006; HONDA *et al*. 2013; KOMYAKOVA *et al*. 2019). This is indicated by the NMDS analysis showing a clustering of juvenile and adult fish communities of the lagoon together and away from coastal sites (Fig. 7; see also Fig. S2 in the Supplementary Material). Although some fish species have markedly higher ratios of juveniles to adults on coastal sites rather than lagoon sites, such as *A. triostegus*, *L. fulvus*, *M. flavolineatus*, which may indicate that they live and grow on coastal sites as juveniles and move onto deeper and more distant sites as adults (thus using coastal sites as nurseries), numerous other species have different life strategies (Fig. 5 and S2 for examples of species). Many fish species have few juveniles on coastal habitats as compared to their high abundances on 'adult' reef habitats – barrier, fringing, and pinnacle habitats. Beyond the habitat-specialist coral-bound damselfish (e.g., *Chromis viridis*, *Pomacentrus pavo*, *Dascyllus aruanus*) that often reside on a specific colony and habitat throughout their life (KOMYAKOVA *et al*. 2019), more mobile species can be cited as examples here: for instance, the surgeonfish *Zebrasoma scopas* is absent from the coastal habitats as juvenile but is the fourth most abundant fish species on fringing reef habitats. Coastal habitats may hence be nurseries for certain fish species, but not all develop on such habitats. This is linked to the debate on the role of mangroves as reef fish nurseries in the Indo-Pacific, where mangroves are nurseries for a few species only, but may still be of high importance for ecosystems and fisheries on the whole (THOLLOT 1992; NAGELKERKEN 2007). Furthermore, there could also be seasonality in the use of a certain habitat as a nursery by a given fish species (MELLIN *et al*. 2007). Performing more surveys and varying methods (e.g., tagging and recapture) over a longer time series throughout Bora-Bora's lagoon, in addition to experiments testing juvenile growth and survival, could be envisaged to examine species-specific life histories.

Lastly, across the world, there are strong drivers to implement marine areas and preserve ecosystems and communities, in order to achieve global targets for conservation and management, help to support fish population maintenance, and promote sustainable fisheries. This study highlighted the importance of coastal habitats for juvenile fish by comparisons with lagoon habitats, and underlined that all types of coastal habitats, both natural and man-made, support juveniles from a variety of fish species in unique and potentially complementary ways. Of particular interest to fishery managers, on Bora-Bora's coastal habitats, 20% of the observed juveniles belonged to 15 commercial species (including the yellowstripe goatfish *Mulloidichthys flavolineatus*, the bigeye trevally *Caranx sexfasciatus*, and the convict surgeonfish *Acanthurus triostegus*). Globally and in particular in tropical settings, the preservation of coastal zones must hence not be forgotten so that juvenile marine organisms can successfully grow, move into adult populations, and participate in population replenishment cycles.

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The datasets generated and analysed during the study are available at: https://figshare.com/articles/dataset/Data_used_in_Gairin_et_al_Role_of_natural_and_man-made_structures_as_nurseries_for_coral_reef_fish/19609464.

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Supplementary material

TABLE S1

Kruskal-Wallis test results to assess significant differences in juvenile density, adult density, and predator density between habitats during the day (all temporal replicates and transects together). There are 78 replicates for coastal and reef sites (2 sites per category of habitat, 3 temporal replicates for reef sites and 6 for coastal sites).

Comparison	n	Kruskal-Wallis rank sum statistic	Df	p value
Juvenile density (coastal and reef sites)	78	44.8	7	<0.01
Adult density (coastal and reef sites)	78	51.9	7	<0.001
Predator density (coastal and reef sites)	78	40.5	7	<0.001
Juvenile density (coastal sites)	60	34.3	4	<0.001
Adult density (coastal sites)	60	18.9	4	<0.001
Predator density (coastal sites)	60	9.35	4	0.053

TABLE S2

Dunn's post-hoc test results (Hochberg correction) with significant differences in juvenile density, adult density, and predator density between each habitat during the day (all temporal replicates and transects together).

Comparison	Z	Adjusted p-value
Juvenile density (coastal and reef sites)		
Barrier - Pinnacle	3.59	0.0041
Barrier - Vegetation	2.94	0.0293
Barrier - Wall	3.35	0.0090
Fringing - Beach	2.95	0.0302
Pinnacle - Beach	4.37	0.0002
Pinnacle - Grass	3.43	0.0070
Pinnacle - Mangrove	3.48	0.0061
Juvenile density (coastal sites)		
Beach - Vegetation	4.18	0.0001
Beach - Wall	4.74	<0.0001
Grass - Vegetation	2.93	0.0084
Grass - Wall	3.50	0.0017
Mangrove - Vegetation	3.00	0.0080
Mangrove - Wall	3.57	0.0015
Adult density (coastal and reef sites)		
Barrier - Grass	4.72	0.0000
Barrier - Mangrove	3.54	0.0044
Barrier - Vegetation	3.99	0.0008
Barrier - Wall	3.35	0.0076
Fringing - Grass	4.55	0.0001
Fringing - Mangrove	3.37	0.0076
Fringing - Vegetation	3.82	0.0016

Comparison	Z	Adjusted p-value
Fringing - Wall	3.18	0.0119
Pinnacle - Grass	4.55	0.0001
Pinnacle - Mangrove	3.72	0.0078
Pinnacle - Vegetation	3.83	0.0016
Pinnacle - Wall	3.19	0.0123
Adult density (coastal sites)		
Beach - Grass	4.18	0.0001
Beach - Vegetation	3.03	0.0109
Predator density (coastal and reef sites)		
Barrier - Beach	3.63	0.0034
Barrier - Grass	3.91	0.0013
Barrier - Mangrove	3.96	0.0011
Barrier - Vegetation	3.30	0.0105
Fringing - Beach	2.94	0.0294
Fringing - Grass	3.22	0.0129
Fringing - Mangrove	3.27	0.0113
Pinnacle - Beach	3.52	0.0050
Pinnacle - Grass	3.80	0.0018
Pinnacle - Mangrove	3.85	0.0016
Pinnacle - Vegetation	3.19	0.0135
Predator density (coastal sites)		
Grass - Wall	2.56	0.0467
Mangrove - Wall	2.62	0.0440

TABLE S3

Kruskal-Wallis test results to assess significant differences in juvenile density, adult density, and predator density between habitats during the night (all temporal replicates and transects together).

Comparison	n	Kruskal-Wallis rank sum statistic	Df	p value
Juvenile density (coastal sites)	25	15.2	4	0.004
Adult density (coastal sites)	25	16.9	4	0.002
Predator density (coastal sites)	25	17.3	4	0.002

TABLE S4

Dunn’s post-hoc test results (Hochberg correction) with significant differences in juvenile density, adult density, and predator density between each habitat during the night (all temporal replicates and transects together).

Comparison	Z	Adjusted p-value
Juvenile density (coastal sites)		
Beach - Mangrove	2.54	0.04
Mangrove - Vegetation	2.66	0.03
Mangrove - Wall	3.57	0.002

Comparison	**Z**	**Adjusted p-value**
Adult density (coastal and reef sites)		
Beach - Mangrove	3.78	0.0007
Beach - Vegetation	3.00	0.01
Predator density (coastal sites)	78	
Beach - Mangrove	4.01	0.0003
Beach - Vegetation	2.76	0.03

TABLE S5

Kruskal-Wallis test results to assess significant differences in the density of juvenile, adult and predatory fish species between temporal replicates during the day and at night (for each habitat).n = total sample size; df = degrees of freedom.

Density of juvenile fish species (day)	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Barrier	6	4.57	2	0.10
Fringing	6	3.6	2	0.17
Pinnacle	6	3.6	2	0.17
Beach	12	5.81	5	0.33
Grass	12	5.08	5	0.41
Mangrove	12	2.08	5	0.84
Vegetation	12	5.92	5	0.31
Wall	12	8.55	5	0.13

Density of adult fish species (day)	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Barrier	6	4.57	2	0.10
Fringing	6	3.71	2	0.16
Pinnacle	6	3.43	2	0.18
Beach	12	2.77	5	0.74
Grass	12	9.54	5	0.09
Mangrove	12	8.97	5	0.11
Vegetation	12	7.02	5	0.22
Wall	12	3	5	0.70

Density of predator fish species (day)	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Barrier	6	4.57	2	0.10
Fringing	6	2.00	2	0.37
Pinnacle	6	0.96	2	0.62
Beach	12	3.70	5	0.59
Grass	12	4.41	5	0.49
Mangrove	12	4.41	5	0.49
Vegetation	12	8.20	5	0.15
Wall	12	8.87	5	0.11

Density of juvenile fish species (night)	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Beach	10	4	4	0.41
Grass	10	4	4	0.41
Mangrove	10	4	4	0.41
Vegetation	10	4	4	0.41
Wall	10	4	4	0.41

Density of adult fish species (night)	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Beach	10	4	4	0.41
Grass	10	4	4	0.41
Mangrove	10	4	4	0.41
Vegetation	10	4	4	0.41
Wall	10	4	4	0.41

Density of predator fish species (night)	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Beach	10	4	4	0.41
Grass	10	4	4	0.41
Mangrove	10	4	4	0.41
Vegetation	10	4	4	0.41
Wall	10	4	4	0.41

TABLE S6

Kruskal-Wallis and Dunn's post-hoc test results to assess significant differences in the density of juvenile fish species between transect positions on coastal sites during the day (3 transects, 2 spatial replicates, 6 temporal replicates for each habitat) and at night (3 transects, 1 spatial replicate, 5 temporal replicates for each habitat). n = total sample size; Df = degrees of freedom.

Density of juvenile fish species	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Beach / Day	36	2.67	2	0.26
Grass / Day	36	23.02	2	<0.001
T2m – T12m Z = 3.98, p = 0.0001				
T2m – T32m Z = 3.98, p < 0.0001				
Mangrove / Day	36	19.64	2	<0.001
T2m – T12m Z = 3.37, p = 0.0008				
T2m – T32m Z = 4.16, p < 0.0001				
Vegetation / Day	36	19.41	2	<0.001
T2m – T12m Z = 2.48, p = 0.01				
T2m – T32m Z = 4.39, p < 0.0001				
Wall / Day	36	9.24	2	0.01
T2m – T12m Z = 2.08, p = 0.04				
T2m – T32m Z = 2.96, p = 0.005				
Beach / Night	15	0.13	2	0.94
Grass / Night	15	9.59	2	0.008
T2m – T32m Z = 3.08, p = 0.003				

Density of juvenile fish species	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Mangrove / Night	15	10.67	2	0.005
T2m – T12m Z = 2.08, p = 0.04				
T2m – T32m Z = 3.22, p = 0.002				
Vegetation / Night	15	7.25	2	0.03
T2m – T32m Z = 2.69, p = 0.01				
Wall / Night	15	12.43	2	0.002
T2m – T12m Z = 3.35, p = 0.001				
T2m – T32m Z = 2.44 p = 0.01				

TABLE S7

Kruskal-Wallis and Dunn's post-hoc test results to assess significant differences in the density of adult fish species between transect positions on coastal sites during the day (3 transects, 2 spatial replicates, 6 temporal replicates for each habitat) and at night (3 transects, 1 spatial replicate, 5 temporal replicates for each habitat). n = total sample size; Df = degrees of freedom.

Density of adult fish species	**n**	**Kruskal-Wallis rank sum statistic**	**Df**	**p value**
Beach / Day	36	15.39	2	<0.001
T2m – T12m Z = 1.70, p = 0.04				
T2m – T32m Z = 3.91, p = 0.0001				
T12m – T32m Z = 2.28, p = 0.02				
Grass / Day	36	7.39	2	0.02
T2m – T32m Z = 2.72, p = 0.01				
Mangrove / Day	36	5.66	2	0.06
Vegetation / Day	36	5.28	2	0.07
Wall / Day	36	2.37	2	0.31
Beach / Night	15	8.98	2	0.01
T2m – T12m Z = 2.26, p = 0.02				
T2m – T32m Z = 2.83, p = 0.01				
Grass / Night	15	2.64	2	0.27
Mangrove / Night	15	0.88	2	0.64
Vegetation / Night	15	0.13	2	0.94
Wall / Night	15	7.97	2	0.02
T2m – T12m Z = 2.37, p = 0.02				
T2m – T32m Z = 2.51, p = 0.02				

TABLE S8

Kruskal-Wallis and Dunn’s post-hoc test results to assess significant differences in the density of predatory fish species between transect positions on coastal sites during the day (3 transects, 2 spatial replicates, 6 temporal replicates for each habitat) and at night (3 transects, 1 spatial replicate, 5 temporal replicates for each habitat). n = total sample size; Df = degrees of freedom.

Density of predator fish species	n	Kruskal-Wallis rank sum statistic	Df	p value
Beach / Day	36	2.19	2	0.34
Grass / Day	36	1.03	2	0.60
Mangrove / Day	36	4.11	2	0.13
Vegetation / Day	36	1.34	2	0.51
Wall / Day	36	4.66	2	0.10
Beach / Night	15	8.70	2	0.01
T2m – T12m Z = 2.48, p = 0.01				
T2m – T32m Z = 2.62, p = 0.01				
Grass / Night	15	3.01	2	0.22
Mangrove / Night	15	2.30	2	0.32
Vegetation / Night	15	3.03	2	0.22
Wall / Night	15	3.55	2	0.17

TABLE S9

Estimation of the potential total abundance of juvenile, adult, and predator fish individuals along the coastline of Bora-Bora in 1955 and 2019, and percentage change between those dates based on aerial imagery information about the coastal typology and extrapolations of the average densities observed on each habitat in 2021.

	Length coastline 1955 (m)	Length coastline 2019 (m)	Juvenile 1955 (total abundance)	Juvenile 2019 (total abundance)	Adult 1955 (total abundance)	Adult 2019 (total abundance)	Predator 1955 (total abundance)	Predator 2019 (total abundance)
Day								
Beach	4411	4918	232067	258741	143358	159835	1225	1366
Grass	438	0	17921	9738	2957	1607	60	33
Mangrove	0	312	0	13190	0	3588	0	26
Vegetation	26956	24542	555593	221981	275490	110069	9734	3889
Wall	4150	24541	69512	411061	60590	358299	5187	30676
Total			875095	914714	482394	633397	16208	35991
% change			+4%		+31%		+122%	
Night								
Beach	4411	4918	133800	149179	447540	498980	316416	352784
Grass	438	0	21287	11567	6395	3475	1372	745
Mangrove	0	312	0	19490	0	3326	0	208
Vegetation	26956	24542	763753	305150	265786	106192	53912	21540
Wall	4150	24541	87427	516997	447540	498980	32093	189784
Total			1006267	1002383	815711	1179607	403793	565062
% change			0%		+45%		+40%	

TABLE S10

List of species contributing to 80% of the differences in the composition of fish communities for daytime observation of juvenile communities. Based on pairwise comparisons between each surveyed category of habitats, using SIMPER.

Barrier Beach	**Barrier Fringing**	**Barrier Grass**	**Barrier Mangrove**	**Barrier Pinnacle**
C. sordidus	*C. sordidus*	*C. sordidus*	*C. sordidus*	*C. sordidus*
M. flavolineatus	*S. nigricans*	*C. crenilabis*	*C. crenilabis*	*S. nigricans*
H. margaritaceus	*S. schlegeli*	*S. nigricans*	*S. nigricans*	*S. schlegeli*
S. nigricans	*T. hardwicke*	*E. vaigiensis*	*T. hardwicke*	*T. hardwicke*
T. hardwicke	*H. margaritaceus*	*T. hardwicke*	*S. schlegeli*	*H. margaritaceus*
S. schlegeli	*C. striatus*	*S. schlegeli*	*E. vaigiensis*	*C. striatus*
E. vaigiensis	*S. psittacus*	*H. margaritaceus*	*H. margaritaceus*	*S. psittacus*
C. crenilabis	*C. trifasciatus*	*S. psittacus*	*M. flavolineatus*	
S. psittacus	*C. viridis*	*C. striatus*		
C. viridis				
C. striatus				

Barrier Vegetation	**Barrier Wall**	**Beach Fringing**	**Beach Grass**	**Beach Mangrove**
C.. sordidus	*C. sordidus*	*M. flavolineatus*	*C. crenilabis*	*C. crenilabis*
S.. nigricans	*S. nigricans*	*E. vaigiensis*	*M. flavolineatus*	*M. flavolineatus*
T. hardwicke	*T. hardwicke*	*C. sordidus*	*E. vaigiensis*	*E. vaigiensis*
S. schlegeli	*S. schlegeli*	*C. crenilabis*	*C. sordidus*	*C. sordidus*
C. crenilabis	*H. margaritaceus*	*C. striatus*	*A. sexfasciatus*	*S. nigricans*
H. margaritaceus	*C. crenilabis*	*C. trifasciatus*	*S. nigricans*	*H. margaritaceus*
E. vaigiensis	*E. vaigiensis*	*S. nigricans*	*H. margaritaceus*	*S. spinus*
S. psittacus	*S. psittacus*	*T. hardwicke*	*C. striatus*	*C. sexfasciatus*
C. striatus		*H. margaritaceus*	*A. triostegus*	*C. striatus*
		Z. scopas	*S. spinus*	*A. triostegus*
		S. psittacus	*C. sexfasciatus*	
		A. triostegus		
		Z. cornutus		
		S. schlegeli		

Beach Pinnacle	**Beach Vegetation**	**Beach Wall**	**Fringing Grass**	**Fringing Mangrove**
M. flavolineatus	*M. flavolineatus*	*M. flavolineatus*	*C. crenilabis*	*C. crenilabis*
E. vaigiensis	*E. vaigiensis*	*E. vaigiensis*	*E. vaigiensis*	*E. vaigiensis*
C. sordidus	*C. crenilabis*	*C. crenilabis*	*C. sordidus*	*M. flavolineatus*
C. crenilabis	*C. sordidus*	*C. sordidus*	*C. trifasciatus*	*C. sordidus*
C. striatus	*S. nigricans*	*H. margaritaceus*	*A. sexfasciatus*	*C. trifasciatus*
S. nigricans	*H. margaritaceus*	*S. nigricans*	*M. flavolineatus*	*C. striatus*
H. margaritaceus	*C. striatus*	*C. striatus*	*C. striatus*	*Z. scopas*
P. pavo	*A. triostegus*	*A. triostegus*	*Z. scopas*	*T. hardwicke*
A. triostegus	*S. spinus*	*Z. cornutus*	*T. hardwicke*	
Z. cornutus	*Z. cornutus*	*T. hardwicke*		
T. hardwicke	*S. schlegeli*	*S. spinus*		
S. schlegeli				

Fringing Pinnacle	**Fringing Vegetation**	**Fringing Wall**	**Grass Mangrove**	**Grass Pinnacle**
C. striatus	*E. vaigiensis*	*C. crenilabis*	*C. crenilabis*	*C. crenilabis*
C. sordidus	*C. crenilabis*	*E. vaigiensis*	*E. vaigiensis*	*E. vaigiensis*
C. trifasciatus	*C. sordidus*	*C. sordidus*	*M. flavolineatus*	*C. striatus*
P. pavo	*C. trifasciatus*	*C. trifasciatus*	*A. sexfasciatus*	*A. sexfasciatus*
T. hardwicke	*M. flavolineatus*	*C. striatus*	*C. sexfasciatus*	*M. flavolineatus*
Z. scopas	*T. hardwicke*	*T. hardwicke*		*P. pavo*
S. nigricans	*C. striatus*	*Z. scopas*		
D. flavicauda	*Z. scopas*	*H. margaritaceus*		
	L gibbus	*M. flavolineatus*		
	S. spinus	*S. nigricans*		
		A. triostegus		
Grass Vegetation	**Grass Wall**	**Mangrove Pinnacle**	**Mangrove Vegetation**	**Mangrove Wall**
C. crenilabis	*C. crenilabis*	*C. crenilabis*	*C. crenilabis*	*C. crenilabis*
E. vaigiensis	*E. vaigiensis*	*E. vaigiensis*	*E. vaigiensis*	*E. vaigiensis*
M. flavolineatus	*M. flavolineatus*	*M. flavolineatus*	*M. flavolineatus*	*M. flavolineatus*
A. sexfasciatus	*A. sexfasciatus*	*C. striatus*	*S. spinus*	*C. sexfasciatus*
C. sexfasciatus	*H. margaritaceus*	*P. pavo*		*S. spinus*
	C. sexfasciatus			
Pinnacle Vegetation	**Pinnacle Wall**	**Vegetation Wall**		
E. vaigiensis	*C. crenilabis*	*C. crenilabis*		
C. crenilabis	*E. vaigiensis*	*E. vaigiensis*		
C. striatus	*C. striatus*	*M. flavolineatus*		
P. pavo	*P. pavo*	*H. margaritaceus*		
M. flavolineatus	*H. margaritaceus*	*A. triostegus*		
D. flavicauda	*D. flavicauda*	*S. spinus*		
C. sordidus	*C. sordidus*	*C. striatus*		
	A. triostegus			
	M. flavolineatus			

TABLE S11

List of species contributing to 80% of the differences in the composition of fish communities for daytime observation of adult communities. Based on pairwise comparisons between each surveyed category of habitats, using SIMPER.

Barrier Beach	**Barrier Fringing**	**Barrier Grass**	**Barrier Mangrove**	**Barrier Pinnacle**
A. triostegus	*C. viridis*	*A. triostegus*	*A. triostegus*	*A. triostegus*
C. sordidus	*A. triostegus*	*S. nigricans*	*S. nigricans*	*S. nigricans*
C. striatus	*S. nigricans*	*C. striatus*	*C. striatus*	*C. viridis*
S. nigricans	*C. striatus*	*C. sordidus*	*C. sordidus*	*C. striatus*
T. hardwicke	*C. sordidus*	*T. hardwicke*	*T. hardwicke*	*C. sordidus*
C. viridis	*T. hardwicke*	*C. viridis*	*C. viridis*	*M. scopas*
S. psittacus	*S. psittacus*	*S. psittacus*	*S. psittacus*	*D. flavicauda*
S. schlegeli	*D. aruanus*	*S. schlegeli*	*C. crenilabis*	*S. psittacus*
C. flavissima	*C. trifasciatus*	*C. flavissima*	*S. schlegeli*	*A. sexfasciatus*
D. aruanus	*M. scopas*	*C. ulietensis*	*C. flavissima*	*T. hardwicke*

C. ulietensis	*P. pavo*	*C. crenilabis*	*C. ulietensis*	*P. pavo*
M. flavolineatus	*S. schlegeli*	*P. multifasciatus*	*P. multifasciatus*	*C. ulietensis*
P. multifasciatus	*G. aurolineatus*	*C. auriga*	*C. auriga*	*S. schlegeli*
C. auriga	*C. ulietensis*	*M. flavolineatus*	*M. flavolineatus*	*M. flavolineatus*
M. scopas	*M. flavolineatus*	*M. scopas*	*M. scopas*	*C. auriga*
H. hortulanus	*L. fulvus*	*H. hortulanus*	*H. hortulanus*	*P. multifasciatus*
S. bandanensis	*C. auriga*			*P. tile*
	M. vanicolensis			*M. vanicolensis*
	C. flavissima			*C. flavissima*
				C. iomelas
				S. bandanensis
Barrier Vegetation	**Barrier Wall**	**Beach Fringing**	**Beach Grass**	**Beach Mangrove**
A. triostegus	*A. triostegus*	*C. viridis*	*S. nigricans*	*S. nigricans*
S. nigricans	*S. nigricans*	*C. striatus*	*C. crenilabis*	*C. crenilabis*
C. striatus	*C. striatus*	*S. nigricans*	*C. striatus*	*C. striatus*
C. sordidus	*C. sordidus*	*C. sordidus*	*E. vaigiensis*	*E. vaigiensis*
T. hardwicke	*T. hardwicke*	*M. scopas*	*D. aruanus*	*D. aruanus*
C. viridis	*C. viridis*	*C. trifasciatus*	*A. triostegus*	*A. triostegus*
S. psittacus	*S. psittacus*	*D. aruanus*	*M. flavolineatus*	*M. flavolineatus*
C. crenilabis	*M. flavolineatus*	*T. hardwicke*	*T. hardwicke*	
S. schlegeli	*S. schlegeli*	*P. pavo*		
C. flavissima	*C. flavissima*	*G. aurolineatus*		
C. ulietensis	*C. ulietensis*	*L. fulvus*		
P. multifasciatus	*P. multifasciatus*			
C. auriga	*C. auriga*			
M. flavolineatus	*C. crenilabis*			
M. scopas	*M. scopas*			
H. hortulanus	*H. hortulanus*			
	S. bandanensis			
Beach Pinnacle	**Beach Vegetation**	**Beach Wall**	**Fringing Grass**	**Fringing Mangrove**
C. striatus	*S. nigricans*	*S. nigricans*	*C. viridis*	*C. viridis*
M. scopas	*C. crenilabis*	*C. striatus*	*C. striatus*	*C. striatus*
T. hardwicke	*C. striatus*	*C. crenilabis*	*C. sordidus*	*C. crenilabis*
C. sordidus	*E. vaigiensis*	*E. vaigiensis*	*M. scopas*	*C. sordidus*
S. nigricans	*D. aruanus*	*M. flavolineatus*	*C. trifasciatus*	*M. scopas*
D. flavicauda	*A. triostegus*	*D. aruanus*	*T. hardwicke*	*C. trifasciatus*
A. sexfasciatus	*M. flavolineatus*	*A. triostegus*	*D. aruanus*	*T. hardwicke*
P. pavo	*T. hardwicke*	*H. trimaculatus*	*C. crenilabis*	*D. aruanus*
S. schlegeli		*C. sordidus*	*S. nigricans*	*S. nigricans*
S. psittacus		*T. hardwicke*	*P. pavo*	*P. pavo*
D. aruanus			*G. aurolineatus*	
P. tile				
C. iomelas				

Fringing Pinnacle	**Fringing Vegetation**	**Fringing Wall**	**Grass Mangrove**	**Grass Pinnacle**
C. viridis	*C. viridis*	*C. viridis*	*C. crenilabis*	*C. striatus*
C. striatus	*C. striatus*	*C. striatus*	*E. vaigiensis*	*M. scopas*
D. flavicauda	*C. sordidus*	*C. sordidus*		*T. hardwicke*
A. sexfasciatus	*M. scopas*	*M. scopas*		*C. sordidus*
C. sordidus	*C. trifasciatus*	*C. trifasciatus*		*S. nigricans*
M. scopas	*C. crenilabis*	*T. hardwicke*		*D. flavicauda*
T. hardwicke	*T. hardwicke*	*D. aruanus*		*A. sexfasciatus*
S. nigricans	*D. aruanus*	*S. nigricans*		*P. pavo*
P. pavo	*S. nigricans*	*C. crenilabis*		*S. schlegeli*
C. trifasciatus	*P. pavo*	*P. pavo*		*C. crenilabis*
D. aruanus	*G. aurolineatus*	*G. aurolineatus*		*S. psittacus*
S. schlegeli		*L. fulvus*		
P. tile		*M. flavolineatus*		
S. psittacus				

Grass Vegetation	**Grass Wall**	**Mangrove Pinnacle**	**Mangrove Vegetation**	**Mangrove Wall**
C. crenilabis	*C. crenilabis*	*C. striatus*	*C. crenilabis*	*C. crenilabis*
E. vaigiensis	*E. vaigiensis*	*M. scopas*	*E. vaigiensis*	*E. vaigiensis*
C. glauca	*A. triostegus*	*T. hardwicke*		*A. triostegus*
	M. flavolineatus	*C. sordidus*		*M. flavolineatus*
	H. trimaculatus	*S. nigricans*		*H. trimaculatus*
	C. striatus	*C. crenilabis*		*C. striatus*
	C. glauca	*D. flavicauda*		*C. glauca*
	A. septemfasciatus	*A. sexfasciatus*		
		P. pavo		
		S. schlegeli		
		S. psittacus		

Pinnacle Vegetation	**Pinnacle Wall**	**Vegetation Wall**		
C. striatus	*C. striatus*	*C. crenilabis*		
M. scopas	*M. scopas*	*E. vaigiensis*		
T. hardwicke	*T. hardwicke*	*H. trimaculatus*		
C. sordidus	*C. sordidus*	*A. triostegus*		
S. nigricans	*S. nigricans*	*M. flavolineatus*		
D. flavicauda	*D. flavicauda*	*C. glauca*		
A. sexfasciatus	*A. sexfasciatus*	*C. striatus*		
C. crenilabis	*P. pavo*	*H. margaritaceus*		
P. pavo	*S. schlegeli*			
S. schlegeli	*S. psittacus*			
S. psittacus	*C. crenilabis*			
P. tile	*P. tile*			
	C. iomelas			

TABLE S12

List of species contributing to 80% of the differences in the composition of fish communities for nighttime observation of juvenile communities. Based on pairwise comparisons between each surveyed category of habitats, using SIMPER.

Beach Grass	Beach Mangrove	Beach Vegetation	Beach Wall	Grass Mangrove
E. vaigiensis	*C. crenilabis*	*M. berndti*	*E. vaigiensis*	*C. crenilabis*
C. crenilabis	*M. flavolineatus*	*M. flavolineatus*	*M. berndti*	*E. vaigiensis*
M. flavolineatus	*S. spinus*	*E. vaigiensis*	*S. punctatissimus*	*M. flavolineatus*
M. berndti	*M. berndti*	*C. crenilabis*	*M. flavolineatus*	*S. spinus*
S. punctatissimus	*L. fulvus*	*S. punctatissimus*	*N. opercularis*	*L. fulvus*
C. sexfasciatus	*C. sexfasciatus*	*C. sexfasciatus*	*M. pralina*	
N. sammara	*S. punctatissimus*	*S. diadema*	*N. sammara*	
M. pralina		*M. pralina*	*N. savayensis*	
		N. sammara	*S. diadema*	
		A. exostigma	*C. sexfasciatus*	
Grass Vegetation	**Grass Wall**	**Mangrove Vegetation**	**Mangrove Wall**	**Vegetation Wall**
C. crenilabis	*C. crenilabis*	*C. crenilabis*	*C. crenilabis*	*M. flavolineatus*
E. vaigiensis	*E. vaigiensis*	*M. flavolineatus*	*M. flavolineatus*	*E. vaigiensis*
M. flavolineatus	*M. flavolineatus*	*S. spinus*	*S. spinus*	*C. crenilabis*
C. sexfasciatus	*N. opercularis*	*E. vaigiensis*	*E. vaigiensis*	*N. opercularis*
S. diadema	*C. sexfasciatus*	*L. fulvus*	*L. fulvus*	*S. diadema*
L. fulvus				*C. sexfasciatus*
				N. sammara
				S. spinus

TABLE S13

List of species contributing to 80% of the differences in the composition of fish communities for nighttime observation of adult communities. Based on pairwise comparisons between each surveyed category of habitats, using SIMPER.

Beach Grass	Beach Mangrove	Beach Vegetation	Beach Wall	Grass Mangrove
M. berndti	*M. berndti*	*M. berndti*	*M. berndti*	*C. crenilabis*
M. pralina	*M. pralina*	*M. pralina*	*M. pralina*	*M. flavolineatus*
N. savayensis	*N. savayensis*	*N. savayensis*	*N. savayensis*	*E. vaigiensis*
M. violacea	*M. violacea*	*M. violacea*	*M. violacea*	*N. sammara*
A. callopterus	*A. callopterus*	*A. callopterus*	*A. callopterus*	
S. punctatissimus	*S. punctatissimus*	*S. punctatissimus*	*S. punctatissimus*	
M. flavolineatus	*M. flavolineatus*	*M. flavolineatus*	*M. flavolineatus*	
C. crenilabis			*C. crenilabis*	
			E. vaigiensis	

Grass Vegetation	Grass Wall	Mangrove Vegetation	Mangrove Wall	Vegetation Wall
C. crenilabis	*C. crenilabis*	*M. flavolineatus*	*C. crenilabis*	*C. crenilabis*
M. flavolineatus	*E. vaigiensis*	*C. crenilabis*	*E. vaigiensis*	*E. vaigiensis*
E. vaigiensis	*A. callopterus*	*N. savayensis*	*M. flavolineatus*	*M. flavolineatus*
N. sammara	*M. flavolineatus*	*E. vaigiensis*	*A. callopterus*	*A. callopterus*
S. diadema	*S. diadema*	*A. callopterus*	*S. diadema*	*S. diadema*
N. savayensis	*N. fusca*		*N. sammara*	*N. sammara*
	N. savayensis		*N. fusca*	*N. savayensis*
	N. sammara			

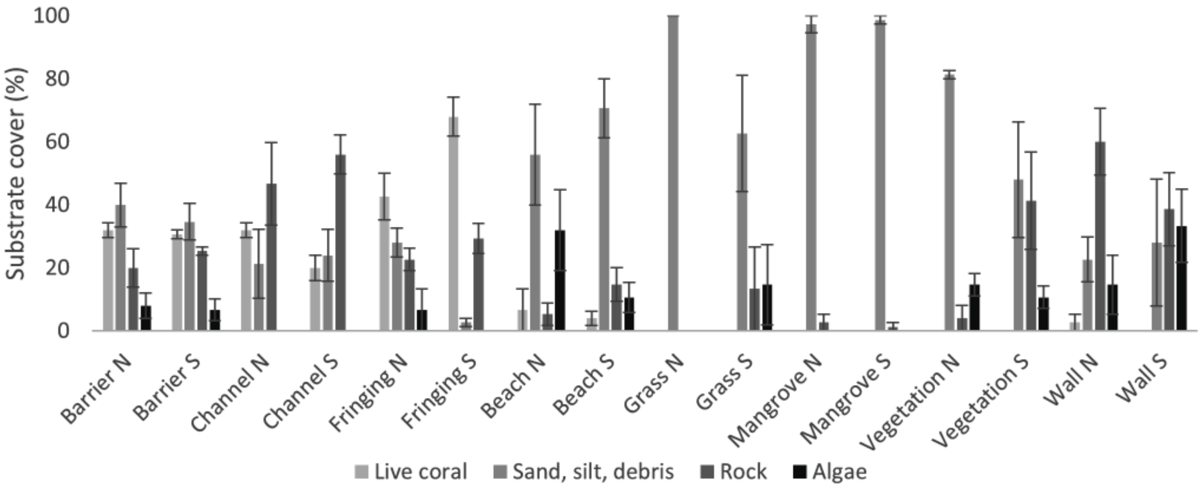

Figure S1 – Average substrate composition of the different study sites in Bora-Bora over the three transects (2 m, 12 m, 32 m away from the shoreline), calculated as percentage cover of live coral, sand/silt/debris, rock, and algae.

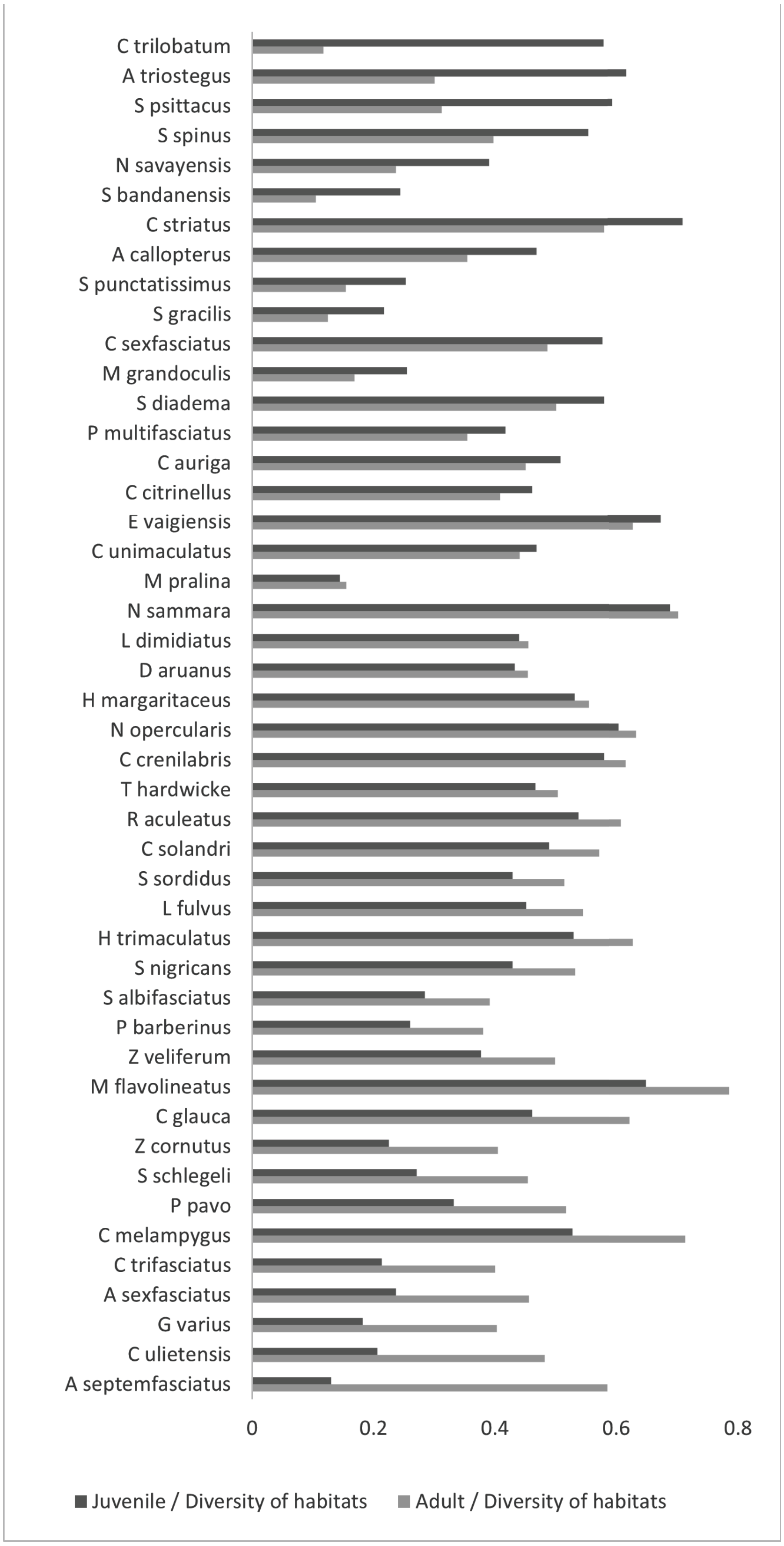

Figure S2 – Shannon index of the diversity of habitats used by juveniles and adults of the most common 47 fish species in Bora-Bora.