Temporal succession of reef fish communities on restored reefs of varying ages

A study using fixed-camera SPC methodology in Padangbai, Bali (Indonesia)

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List of abbreviations and acronyms :

α : Statistical significance threshold

ANOVA : Analysis of Variance

df : Degrees of freedom

DOV : Diver Operated Video

H' : Shannon diversity index

J' : Pielou's evenness

JCU : James Cook University

MARRS : Mars Assisted Reef Restoration System

MaxN : Maximum Number (maximum number of individuals simultaneously visible)

N : Total abundance

nMDS : Non-metric Multidimensional Scaling

NUS : National University of Singapore

p : p-value (statistical probability)

R&R : Research & Restoration internship

RUV : Remote Underwater Visual Survey

S : Family richness

S1–S5 : Codes for the five study sites

SPC : Stationary Point Count

SSI : Scuba Schools International

UB : Universitas Brawijaya

UNRAM : Universitas Mataram

UVC : Underwater Visual Census

χ^2 : Chi-square statistic (Kruskal-Wallis test)

σ : Standard deviation

Glossary :

Coral bleaching : A phenomenon involving the expulsion of symbiotic algae (*Symbiodinium* spp.) from coral tissues under thermal stress, resulting in the depigmentation of the reef and potentially leading to the death of coral colonies.

Bray-Curtis (dissimilarity index) : A dissimilarity index used in community ecology to quantify compositional differences between two sites based on relative abundances. Values range from 0 (identical communities) to 1 (no families in common).

Evenness : A measure of the degree to which individuals are evenly distributed among the different families within a community, independent of the total number of families present.

Family (taxonomic rank) : A level of biological classification grouping genera that share common morphological and evolutionary characteristics, situated between order and genus. This is the taxonomic level retained for identification throughout this report.

Herbivore : An organism feeding exclusively or primarily on plants or algae. On coral reefs, herbivores play a key role in controlling algal growth and maintaining coral cover.

Indo-Pacific : A large marine biogeographical region extending from the Indian Ocean to the tropical Pacific Ocean, recognised as the area of highest reef fish diversity in the world.

MaxN : The maximum number of individuals of a given family simultaneously visible in a single video frame. A standard relative abundance metric in fixed-camera monitoring protocols, designed to prevent double-counting of the same individual.

Ordination : A multivariate statistical method that graphically represents the similarity or dissimilarity in composition among communities by reducing a complex dataset to two or three dimensions.

Planktivore : An organism feeding on plankton. On reefs, planktivores often constitute the first trophic levels to recover following a disturbance.

Replicate : The repetition of a measurement under identical conditions in order to assess natural variability and increase the statistical robustness of results. In this report, each site comprises three measurement points (n = 3 replicates).

Taxonomic richness : The number of distinct taxa (here, families) recorded at a site or observation point.

Ecological succession : The process by which the composition of a biological community changes progressively over time, from a pioneer state towards a more stable mature state.

Non-parametric test : A statistical test that does not assume any particular distribution of the data, suited to small sample sizes or data that do not meet the assumptions of classical parametric tests.

Coral Triangle : A marine area encompassing Indonesia, the Philippines, Malaysia, Papua New Guinea, the Solomon Islands, and Timor-Leste, considered the global centre of reef marine biodiversity.

Restoration temporal gradient : A study design consisting of comparing restored sites of different ages in order to reconstruct a recolonisation trajectory over time.

Null hypothesis (H_0) : In a statistical test, the hypothesis that no difference exists between the groups being compared. It is rejected when the p-value falls below the chosen significance threshold.

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I/ Introduction :

Coral reefs are among the most biodiverse ecosystems on the planet, harbouring nearly a quarter of all known marine species despite covering less than 1% of the ocean floor (Bellwood & Wainwright, (2002)). In Indonesia, at the heart of the Coral Triangle (the global centre of marine biodiversity) these ecosystems play a fundamental role at ecological, economic, and social levels. In the Padangbai region, reefs were extensively destroyed by blast fishing practices inherited from the post-war period, compounded today by climate change, coral bleaching, pollution, and overfishing. Reef restoration therefore represents a challenge that extends well beyond conservation alone: by promoting the return of fish communities, it could contribute to revitalising a declining local fishing economy. In response to this situation, active restoration techniques have been developed, consisting of transplanting coral fragments onto artificial structures in order to facilitate the recolonisation of the reef ecosystem.

While the effectiveness of these techniques on coral cover recovery is now relatively well documented, their effects on associated fish communities remain largely unexplored, particularly over the long term (Krimou et al., (2024)). Yet reef fish constitute primary biological indicators for assessing reef health and restoration success (Maire et al. (2018)). The recolonisation trajectory (from pioneer families through to more demanding species dependent on dense coral cover) remains poorly understood, particularly in the Indo-Pacific.

It is within this context that the present internship was carried out, within the scientific team of the LivingSeas Foundation, a marine conservation organisation based in Padangbai, north-east Bali (Indonesia). Since 2020, the foundation has been conducting one of the most ambitious coral restoration projects in Indonesia, with over 432,000 coral fragments transplanted across 8,550 m² of restored substrate (Livingseas Foundation, (2025)). This internship is part of the foundation's scientific mission and aims to contribute to the assessment of the impact of these restoration efforts on reef fish communities.

The primary objective of this study is to describe and analyse the temporal succession of reef fish communities across restored reefs of varying ages, by comparing five sites representing a restoration gradient ranging from 3 months to 3 years, alongside an unrestored reference site. Secondary objectives include identifying pioneer families, quantifying changes in family richness and diversity (Shannon index), and determining whether these changes are statistically significant as a function of site age. The method adopted is the Stationary Point Count (SPC) using a fixed DJI camera, a standardised and validated protocol for reef fish surveys (Samoilys & Carlos (2000)).

This report presents the scientific approach implemented, the results obtained and their interpretation, before concluding with the perspectives opened by this study.

II/ Presentation of the host organisation :

II.a/ The Livingseas Foundation: mission and location

The Livingseas Foundation is a non-profit organisation registered in Indonesia in 2024, headquartered in Padangbai, in the Karangasem regency of Bali. It was founded and is directed by Leon Boey, an active diver and SSI diving instructor since 2005, whose vision is to restore 50,000 m² of coral reef in Padang Bay.

The foundation operates around three main areas of action: the active restoration of coral reefs, environmental education and training for local communities, and marine conservation awareness. On an operational level, restoration is based on the MARRS method (Mars Assisted Reef Restoration System), which consists of deploying hexagonal steel structures coated with resin and sand, known as Reef Stars, onto which coral fragments of approximately 10 cm are attached. These structures are anchored to the seabed at high density in order to maximise colonisation by marine fauna. After approximately two years of maintenance, the metal structure is no longer visible and a functional reef has formed. To date, the foundation's restoration site is the largest in Bali and the second largest in Indonesia, with 8,824 structures deployed, over 432,588 coral fragments planted, and 8,550 m² of seabed restored (LivingSeas Foundation, (2025)).

The field team is composed of young adults from Padangbai, trained in diving and coral restoration directly by the foundation. This approach of integrating local populations is a central aspect of the foundation's philosophy, which seeks to embed marine conservation within a sustainable community development dynamic.

II.b/ The scientific team and its partnerships

II.b.a/ The scientific team :

Within the Livingseas Foundation, a dedicated scientific team is responsible for the ecological monitoring of the restoration site. This team comprises three permanent members: Katrina, Head of Research; Reiss, Education Coordinator and Junior Researcher; and Alex, Research Assistant. These three individuals form the scientific unit of the foundation and also supervise the Research & Restoration internship programme (R&R), within which the present internship was carried out.

II.b.b/ Responsibilities of the scientific team :

The scientific team's responsibilities cover several long-term monitoring objectives: coral growth monitoring, pre-implantation baseline studies, and ecological monitoring of the communities associated with restored reefs. These data are used to assess restoration effectiveness and to document its effects on marine biodiversity over time.

II.b.c/ Partnerships :

The foundation also maintains partnerships with several academic institutions in support of its research activities: the National University of Singapore (NUS), James Cook University (JCU, Australia), Universitas Mataram (UNRAM), and Universitas Brawijaya (UB), both based in Indonesia. These collaborations reflect the foundation's strong scientific commitment, which extends beyond purely operational restoration to encompass a broader approach to data collection on coral reef restoration.

III/ Materials and methods :

III.a/ Study site description

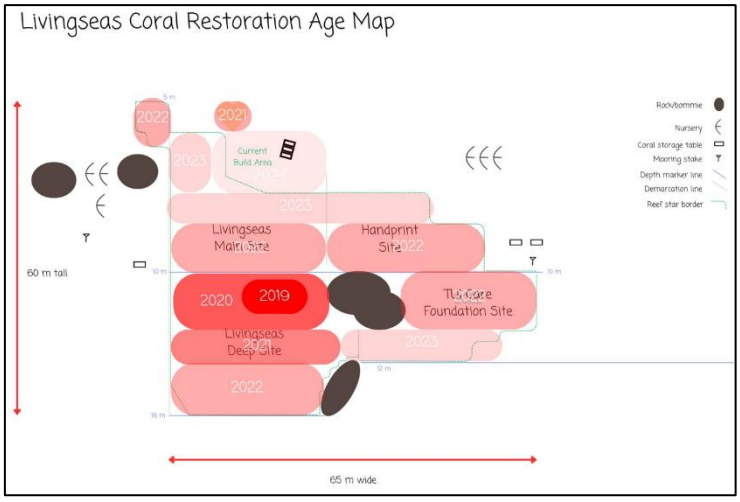

Figure 1 : Location and age of coral restoration zones at the Livingseas Foundation site.

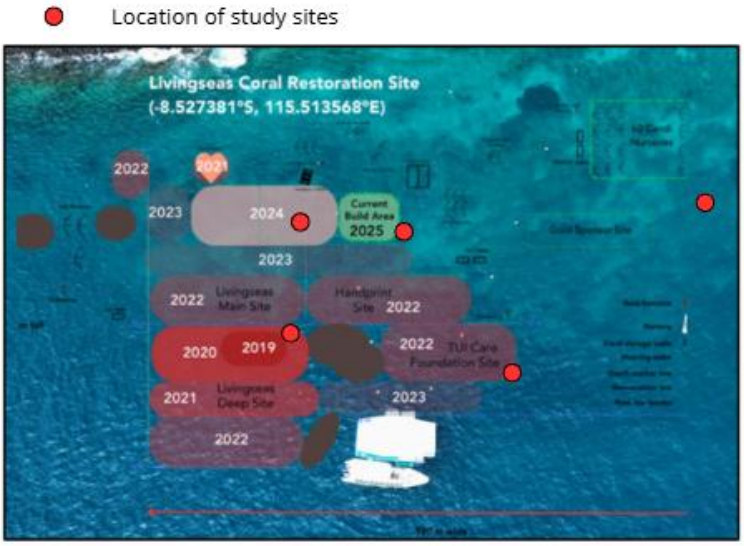

Figure 2 : Satellite image of the Livingseas Foundation coral restoration site indicating the location of the five study sites and the age of the restored zones.

All surveys were conducted within the coral restoration site of the Livingseas Foundation, located in Padang Bai, Bali, Indonesia (coordinates: −8.527381°S; 115.513568°E). The site extends over an area approximately 120 meters wide, directly along a cliff face, at depths ranging from 5 to 16 metres (Figures 1 and 2).

Five study sites were selected to establish a temporal restoration gradient, spanning from a degraded, unrestored reef to a reef restored approximately three years ago. This gradient provides a framework to examining the ecological succession of reef fish communities over time. Site S1 corresponds to a former reef reduced to a mat of dead coral. This site has been incorporated as a low reference representing the baseline state of degradation. Sites S2 through S5 correspond to restoration structures of increasing ages. The depth of each site was verified

during diving sessions and ranges from 5.8 to 9.8 metres, ensuring satisfactory bathymetric homogeneity across sites (Table 1) (Figure 2).

Table 1 : *Characteristics of the five study sites selected for reef fish community monitoring.*

Code	Designation	Age / Status	Depth (m)	Main characteristic
S1	Degraded unrestored reef	Reference	6,8	Dead corals, bare substrate
S2	3-month restoration	3 months	8,3	Pioneer stage
S3	8-month restoration	8 months	9,1	Intermediate stage
S4	18-month restoration	18 months	5,8	Advanced development
S5	3-year restoration	3 years	9,8	Mature stage

III.b/ Survey protocol: fixed-camera DJI SPC methodology

III.b.a/ Overview of survey methods :

Reef fish community monitoring relies on underwater visual survey techniques collectively referred to as Underwater Visual Census (UVC). According to (Caldwell et al. (2016)), 89% of global coral reef monitoring programmes employ one of the following three methods: the belt transect, the Stationary Point Count (SPC), or the timed swim. These approaches are complemented by Diver Operated Video (DOV), which involves manually filming the water column along a transect, and Remote Underwater Visual Surveys (RUVs), based on the deployment of unbaited fixed cameras. However, no universally standardised method currently exists for this type of monitoring (Caldwell et al. (2016)).

III.b.b/ The selected method :

Figure 3 :

Deployment of the DJI camera in a fixed position on the substrate during an SPC survey session.

The choice of method must be guided by the study objectives, the nature of the habitat, and operational constraints. Belt transects and DOV require a confirmed level of diving proficiency as well as solid expertise in species identification under real conditions : sources of operator bias that are difficult to control within the framework of a short-term internship. RUVs, although they record natural fish behaviour without attraction bias, yield lower detection rates

for rare or wary species and may require extended deployment times. The fixed-camera SPC method was therefore selected for this project: it eliminates the operator bias associated with diver skill level, ensures standardised recording conditions across sites, and proves particularly suited to field implementation within a two-month timeframe.

SPC is a standardised survey method widely used in coral reef monitoring. It consists in recording, from a fixed point, all individuals entering a defined observation area over a set period of time. In the present study, the DJI camera was placed on the substrate or attached to the stakes of the restoration structures in a fixed position (Figure 3). The primary metric extracted from these videos is MaxN, defined as the maximum number of individuals of a given family simultaneously visible in a single video frame. This parameter, widely adopted in video-based monitoring protocols, provides an estimate of the relative abundance of each family while avoiding the double-counting of the same individual.

The parameters of the applied protocol are summarised in the table below (Table 2) :

Table 2 : *Parameters of the fixed DJI camera SPC protocol.*

Paramètre	Adopted value	Justification
Video duration	15 min	Allows wary fish to return after diver departure; protocol established by the Living Seas Foundation
Replicates per site	3 points	Statistically significant precision from 3 replicates
Distance between points	> 10 m	Avoid overlap of observation areas
Site depth	5.8 – 9.8 m	Bathymetric homogeneity across sites
Time window	09:00 – 15:00	Peak activity period of diurnal fish

III.b.c/Field protocol :

In the field, each survey session followed an identical sequence across all five sites. The DJI camera was placed on the substrate or attached to the stakes of the restoration structure. The diver then moved several metres away from the deployment point so as not to disturb fish behaviour, and waited for the 15-minute recording to complete. At the end of each video, contextual information was recorded in a waterproof notebook: site code, point number, time, depth, estimated visibility, and hydrodynamic conditions. This information was then shown to the camera prior to retrieval, in order to allow each video to be identified during the analysis phase. The procedure was repeated at the two remaining points of the site, with a minimum distance of 10 metres maintained between each point to avoid filming the same sections of reef.

It should be noted that the first 2 to 3 minutes of each video were excluded from analysis, as the more wary fish required this interval to resume their natural activity following the diver's departure.

III.c/ Video analysis and fish family identification

III.c.a/ Video analysis :
Video analysis constituted the primary work phase outside of field sessions. Each recording was reviewed using VLC Media Player, which allows frame-by-frame navigation and playback pause in order to precisely identify the individuals present within the camera's field of view.

For each video, the MaxN of each family was determined and recorded in an Excel spreadsheet, distinguishing each site and each data acquisition point (Annex 1).

III.c.b/ Fish family identification :
Identification to family level (the taxonomic rank retained for this project given the constraints associated with image quality and internship duration) required the use of several complementary resources: the reference work *Reef Fish Identification: Tropical Pacific*, the online platforms FishIDer, Fishes of Australia, and iNaturalist, as well as identification plates specific to Indo-Pacific reef fauna (Figure 4).

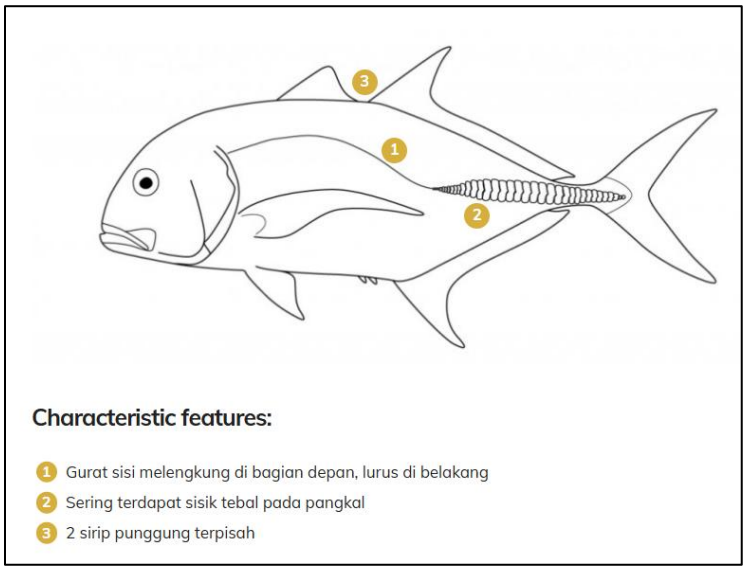

Figure 4 : Example of an identification plate (for the family Carangidae).

Identification was based on four complementary approaches: external morphology, the number and gregarious behaviour of individuals, geographic location, and genetics

- The latter, employed in larger-scale studies, was not used within the scope of this internship.

Each of these approaches targets distinct criteria in order to achieve the most reliable identification possible (Annex 2).

III.d/ Ecological indicators

From the MaxN values extracted for each family and each observation point, five ecological indicators were calculated in order to characterise and compare the structure of fish communities across the five study sites.

III.d.a/ Family richness (S) :

Family richness (S) corresponds to the number of distinct families recorded in a site. It provides a direct measure of the taxonomic diversity of the fish assemblage and reflects the capacity of the reef to support a range of functional fish groups as it develops over time.

III.d.b/ Total abundance (N) :

Total abundance (N) is obtained by summing the MaxN values of all families observed at a given point or site. It provides an indication of the overall density of the fish assemblage, independently of its taxonomic composition.

III.d.c/ Relative abundance by family :

Relative abundance by family is calculated using the formula (MaxN family / N) × 100. It describes the internal structure of the community and allows the identification of dominant families at each stage of restoration, whether pioneer families establishing themselves within the first months or families appearing later and associated with a more structurally developed reef.

III.d.d/ Shannon diversity index (H') :

The Shannon diversity index (H') is calculated using the following formula :

$$H' = -\Sigma\, p_i \times \ln(p_i)$$

where p_i represents the relative proportion of family i within the community.

This index integrates both taxonomic richness and the evenness of family distribution within the assemblage. It equals zero when only a single family is present and increases as the community gains in richness and balance of representation.

However, a high value of H' can result from a large number of families as well as from a very balanced distribution among a few families, making its interpretation ambiguous without a complementary indicator.

III.d.e/ Pielou's evenness (J') :

Pielou's evenness (J') is calculated using the following formula :

$$J' = H' / \ln(S)$$

It ranges between 0 and 1 and quantifies the degree of balance in the distribution of individuals among families, independently of S. A value close to 1 indicates that all families contribute equally to the community, while a low value reflects the marked dominance of a small number of families over the others.

Pielou's evenness (J') thus isolates the equilibrium component of H' by dividing it by the maximum value that this index could reach (ln(S)), for the same number of families. This allows for the comparison of sites independently of their richness.

Taken together, these five indicators allow assessment of whether coral restoration results in a progressive increase in richness and abundance (S, N), a shift in assemblage composition over time (relative abundances), and an increasingly diverse and balanced fish community (H', J').

III.e/ Statistical analysis

The ecological indicators calculated in III.d describe the structure of fish communities at each site, but do not in themselves determine whether the differences observed between sites are statistically significant or simply attributable to natural sampling variability. Two complementary approaches were therefore employed: an inter-site comparison test and a multivariate ordination.

III.e.a/ Inter-site comparison test (Kruskal-Wallis test) :
Family richness (S) and total abundance (N) were compared across the five sites using the Kruskal-Wallis test. This is a non-parametric test equivalent to a one-way ANOVA, applicable when the normality of distributions cannot be verified (which is the case here, as three replicates per site (n = 3) constitutes an insufficient sample size to assume a normal distribution) (Hollander & Wolfe, (1999)). The Kruskal-Wallis test is based on ranking the observed values rather than using their raw values. It tests the null hypothesis that the rank distributions are identical across all groups compared; rejection of this hypothesis, established when the p-value is below 0.05, indicates that at least one site differs significantly from the others. These analyses were performed in RStudio.

III.e.b/ Multivariate ordination (nMDS) :
In order to explore the multivariate structure of the communities (that is, not merely richness or abundance individually, but overall family composition) a non-metric Multidimensional Scaling (nMDS) ordination was applied to the MaxN matrix by family and by site. nMDS is a dimensionality reduction method that projects sites into a two-dimensional space such that the distances between points reflect as faithfully as possible the compositional dissimilarities between communities, calculated here using the Bray-Curtis dissimilarity index (Clarke, (1993)). Two sites positioned close together on the plot therefore exhibit similar family assemblages, whereas two distant sites differ in their composition. The quality of the representation is assessed by the stress value: a value below 0.2 is generally considered acceptable for ecological interpretation (Clarke, (1993)). The nMDS was performed in RStudio using the *vegan* package.

Together, these two approaches allow assessment of whether the age gradient across restoration sites translates into statistically demonstrable differences in the richness and composition of reef fish communities.

IV/ Results :

IV.a/ Composition and abundance of fish communities by site

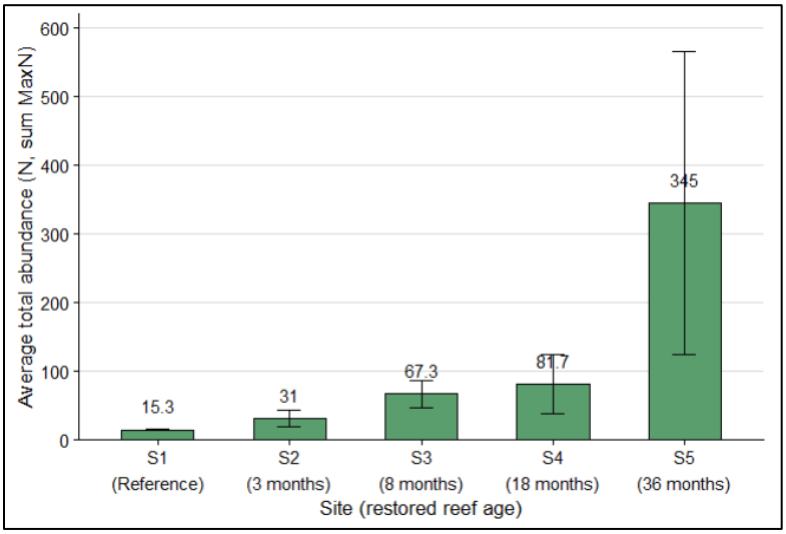

Figure 5: Change in mean total abundance (N) across sites.

Mean total abundance (N, sum of MaxN values across all families) recorded at each of the five study sites. Error bars represent the standard deviation calculated across the three measurement points per site (n = 3).

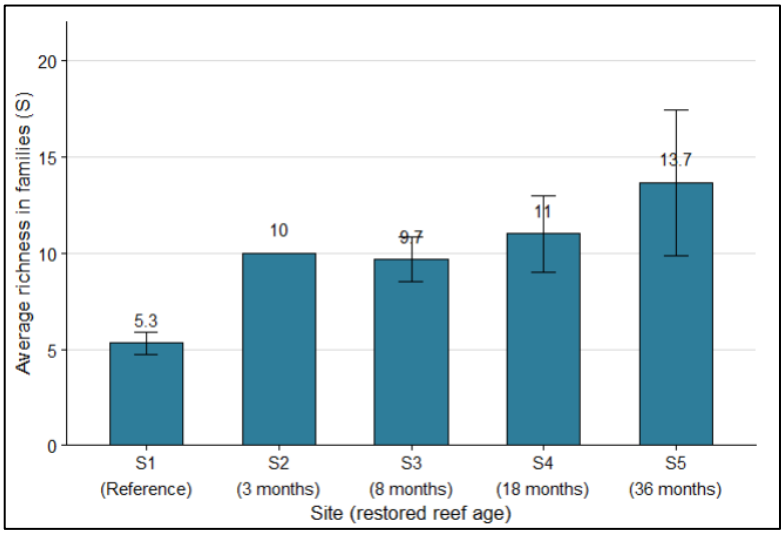

Figure 6 : Change in mean family richness (S) across sites.

Mean family richness (S) recorded at each of the five study sites, from the degraded reference reef (S1) to the 36-month restored reef (S5). Error bars represent the standard deviation calculated across the three measurement points per site (n = 3).

Video analysis of the fifteen observation points (three replicates per site) yielded a total of 20 reef fish families out of the 27 included in the survey grid. Raw data by point and by family are presented in (Annex 1).

At the reference site S1, a mean family richness of 5.3 was recorded alongside a mean total abundance of 15.3 individuals (sum of MaxN values), with a fish assemblage restricted to Pomacentridae, Balistidae, Chaetodontidae, Labridae, Siganidae, Zanclidae, Aulostomidae, and Dasyatidae.

As early as S2 (3 months), richness increased to 10.0 families and abundance to 31.0 individuals, with the appearance of families absent from the degraded reef (notably Acanthuridae, Pomacanthidae, and Scarinae) although the assemblage remained dominated by Pomacentridae, Labridae, and Acanthuridae.

At S3 (8 months), richness remained stable (9.7 families) while abundance increased markedly (67.3 individuals), driven by localised peaks in Mullidae and Carangidae ($\sigma = 20.2$).

At S4 (18 months), richness reached 11.0 families and abundance 81.7 individuals; the appearance of Epinephelidae (MaxN = 1), although limited, signals a more advanced trophic structuring of the assemblage.

Site S5 (36 months) stands out markedly with an abundance of 345.0 individuals (more than four times that of S4) attributable primarily to Pomacentridae (mean MaxN = 238.0). Mullidae (89.0) and Sphyraenidae (82.0) also contributed, but were detected at a single point only, warranting caution in their interpretation. Family richness was highest at this site, with a mean of 13.7 families and 20 families recorded in total.

Table 3 and Figures 5 and 6 summarise all of these trends.

Table 3 : Mean family richness (S) and mean total abundance (N) per study site (n = 3 points per site). σ: standard deviation between points.

Code	Status	Age	Mean S	σ (S)	Mean N	σ (N)
S1	Degraded reef (reference)	—	5,3	0,6	15,3	1,5
S2	Restored	3 months	10	0	31	12,1
S3	Restored	8 months	9,7	1,2	67,3	20,2
S4	Restored	18 months	11	2	81,7	44
S5	Restored	36 months	13,7	3,8	345	216,5

Raw data by family and by measurement point are presented in Annex 1.

IV.b/ Temporal distribution of fish families across sites

The distribution of family presence across sites is presented in Table 4. Of the 27 families included in the survey grid, 23 were recorded at a minimum of one site; 4 families (Haemulidae, Caesionidae, Muraenidae, and Scorpaenidae) returned a MaxN of zero across all five sites and were therefore excluded from this analysis.

Of the 23 families recorded, six were present across all sites, from the degraded reference reef through to the oldest restored site: Pomacentridae, Labridae, Chaetodontidae, Balistidae, Aulostomidae, and Zanclidae. Siganidae, although absent at S2, were recorded at the four remaining sites. Dasyatidae, by contrast, were detected only at S1 and S2, and were absent from the three subsequent sites.

Eight families made their first appearance at S2 : Acanthuridae, Mullidae, Monacanthidae, Pomacanthidae, Lutjanidae, Scarinae, Ostraciidae, and Diodontidae. Of these, three (Acanthuridae, Mullidae, and Monacanthidae) maintained a continuous presence through to S5.

The remaining five showed discontinuous distributions : Pomacanthidae was absent at S3 before reappearing at S4 and S5 ; Lutjanidae was absent from S3 and S4 before being detected at S5 ; Scarinae, Ostracidae, and Diodontidae were recorded at S2 and S3 only.

At S3, Carangidae made their first appearance and remained present through to S5; Tetraodontidae were detected at S3 and S5 but absent at S4. Epinephelidae appeared for the first time at S4 and were also recorded at S5.

Finally, four families were detected exclusively at S5: Holocentridae, Belonidae, Pempheridae, and Sphyraenidae.

Table 4 and the group legends summarise all of these distributions.

Table 4 : Distribution of presence of the 23 reef fish families across the five study sites.

family	S1	S2	S3	S4	S5	family	S1	S2	S3	S4	S5
Pomacentridae	●	●	●	●	●	Lutjanidae	○	●	○	○	●
Labridae	●	●	●	●	●	Scarinae	○	●	●	○	○
Chaetodontidae	●	●	●	●	●	Ostracidae	○	●	●	○	○
Balistidae	●	●	●	●	●	Diodontidae	○	●	●	○	○
Aulostomidae	●	●	●	●	●	Carangidae	○	○	●	●	●
Zanclidae	●	●	●	●	●	Tetraodontidae	○	○	●	○	●
Siganidae	●	○	●	●	●	Epinephelidae	○	○	○	●	●
Dasyatidae	●	●	○	○	○	Holocentridae	○	○	○	○	●
Acanthuridae	○	●	●	●	●	Belonidae	○	○	○	○	●
Mullidae	○	●	●	●	●	Pempheridae	○	○	○	○	●
Monacanthidae	○	●	●	●	●	Sphyraenidae	○	○	○	○	●
Pomacanthidae	○	●	○	●	●						

○ **Absent (MaxN = 0)**

● **Present (MaxN > 0)**

IV.c/ Changes in family richness and diversity

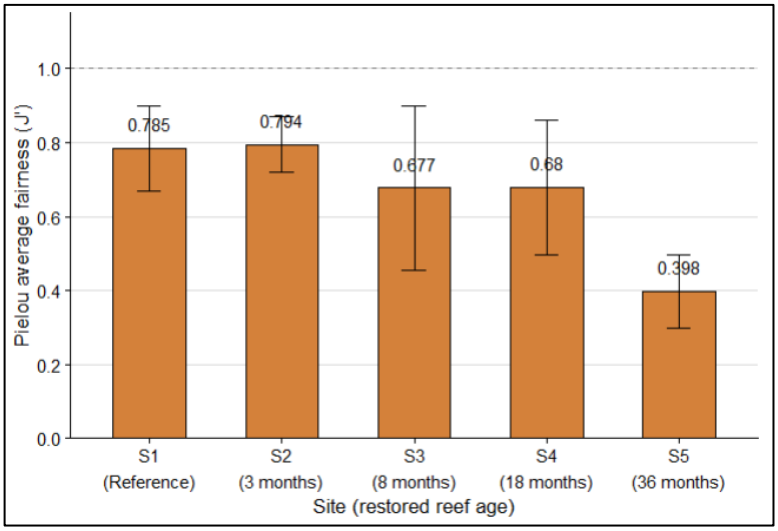

Figure 7 : Change in mean Pielou's evenness (J') across sites.

Mean J' values calculated across the three measurement points per site (n = 3). Error bars represent the standard deviation between points. The dashed line indicates J' = 1 (maximum evenness).

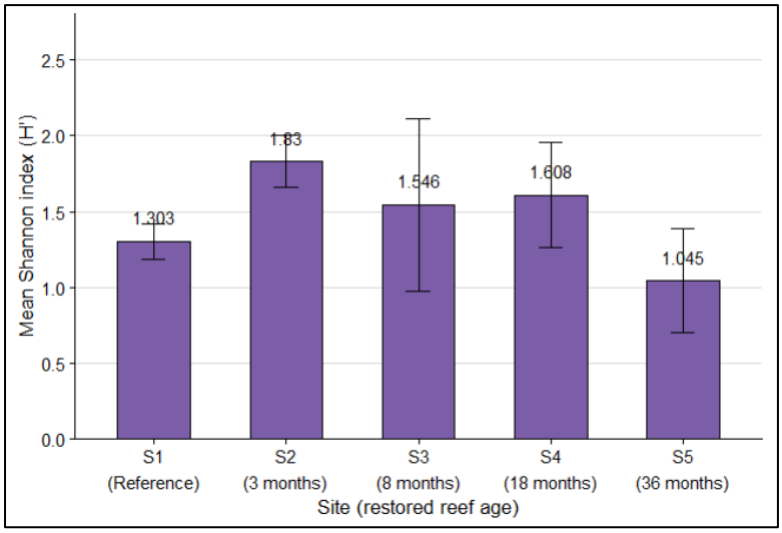

Figure 8 : Change in mean Shannon index (H') across sites.

Mean H' values calculated across the three measurement points per site (n = 3). Error bars represent the standard deviation between points. The dashed line indicates the theoretical maximum value (perfect evenness).

Shannon diversity index (H') and Pielou's evenness (J') values were calculated for each measurement point from the MaxN values per family, then averaged by site (n = 3). Calculations were performed in RStudio; raw values by point are presented in Annex 3. Mean values per site are summarised in Table 5 and illustrated in Figures 7 and 8 (Annex 3) (Figures 7 and 8).

H' was lowest at S1, with a mean of 1.303 (σ = 0.119), and reached its maximum value at S2 (1.830; σ = 0.172), representing a notable increase within the first three months of restoration. It then decreased progressively at S3 (1.546; σ = 0.568) and recovered slightly at S4 (1.608; σ = 0.346), before dropping to its lowest value at S5 (1.045; σ = 0.344). Inter-point variability was particularly high at S3 and S4, reflecting compositional heterogeneity among the three measurement points at these sites.

Pielou's evenness (J') followed a similar trajectory. It was highest at S2 (0.794; σ = 0.075), slightly lower at S1 (0.785; σ = 0.115), then decreased progressively at S3 (0.677; σ = 0.221) and S4 (0.680; σ = 0.182), reaching its minimum value at S5 (0.398; σ = 0.100). This J' value at S5 indicates that the distribution of individuals among families is considerably less balanced than at the other sites.

Table 5 : *Mean values of the Shannon index (H') and Pielou's evenness (J') per site (n = 3 points). σ: standard deviation between points.*

Code	Age	Mean H'	σ (H')	Mean J'	σ (J')
S1	Reference	1,303	0,119	0,785	0,115
S2	3 months	1,83	0,172	0,794	0,075
S3	8 months	1,546	0,568	0,677	0,221
S4	18 months	1,608	0,346	0,68	0,182
S5	36 months	1,045	0,344	0,398	0,1

IV.d/ Results of statistical analyses

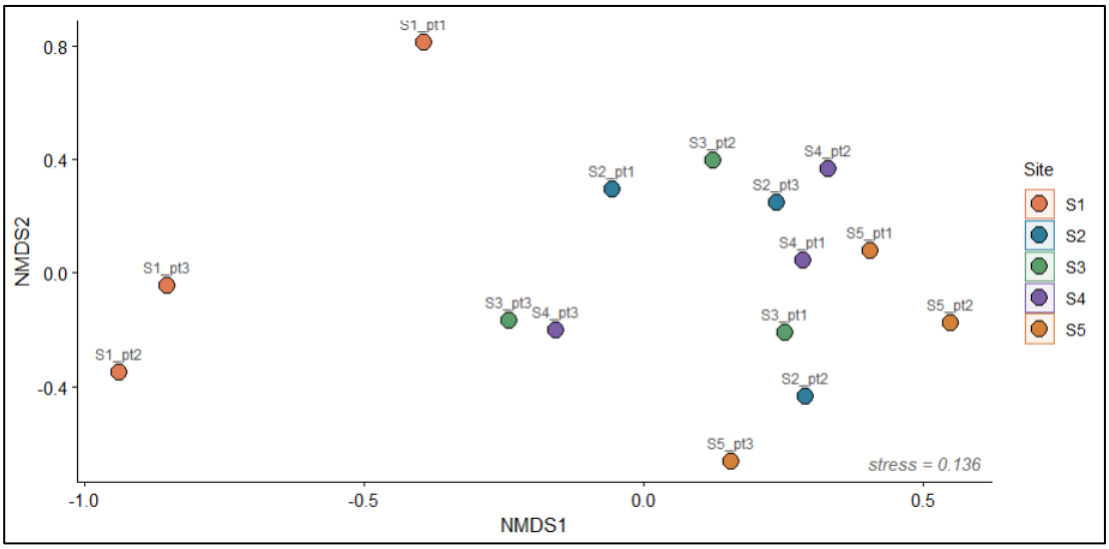

Figure 9 : nMDS ordination of the fifteen measurement points based on fish family composition.

Non-metric Multidimensional Scaling (nMDS) performed on the MaxN matrix by family and by measurement point (n = 15), using the Bray-Curtis dissimilarity index. Each point represents a single measurement point; colour indicates site membership. Stress value = 0.136 (acceptable

The Kruskal-Wallis test applied to family richness (S) revealed a statistically significant difference among the five sites (χ^2 = 10.135; df = 4; p = 0.038). Similarly, total abundance (N) differed significantly across sites (χ^2 = 12.122; df = 4; p = 0.016). In both cases, the null hypothesis of equal rank distributions across sites was rejected at the α = 0.05 threshold, indicating that at least one site differs significantly from the others in terms of

richness or abundance. These results are presented in Table 6. Calculations were performed in RStudio (Annex 4) (Table 6).

The nMDS ordination performed on the MaxN matrix by family and by point (Bray-Curtis dissimilarity) produced a two-dimensional representation with a stress value of 0.136, considered acceptable for ecological interpretation (Clarke, (1993)). The plot (Figure 9) shows that the three points of site S1 are clearly distinct from the other sites, occupying the left-hand portion of the ordination space. The points of sites S2, S3, S4, and S5 are distributed across the central and right-hand portions of the plot, with partial overlap between sites. The dispersion of replicates within certain sites, notably S3 and S4, is consistent with the high inter-point variability observed for the diversity indices in IV.c.

Table 6 : Results of the Kruskal-Wallis test applied to family richness (S) and total abundance (N) across the five sites (n = 3 points per site; df = 4). The significance threshold retained is $\alpha = 0.05$.

Indicator	χ^2	df	p-value	Conclusion
Richness (S)	10,135	4	**0,038**	Significant ($p < 0.05$)
Abundance (N)	12,122	4	**0,016**	Significant ($p < 0.05$)

V/ Discussion :

V.a/ Discussion in relation to the research question

The primary objective of this study was to test whether the age gradient across restoration sites translates into a progressive increase in richness, abundance, and diversity of reef fish communities. The results obtained allow a positive answer to this question, while revealing a more complex underlying dynamic.

The first major observation is the speed of the biological response to restoration. As early as S2 (3 months), richness doubled relative to the degraded reference reef (from 5.3 to 10.0 families on average) and total abundance increased twofold. This early recolonisation indicates that the artificial structure onto which coral fragments are attached (independently of coral development per se) is sufficient to trigger the establishment of new fish families by providing refuge and structural complexity for certain species. The families present as early as S1 (Pomacentridae, Labridae, Chaetodontidae, Balistidae, Aulostomidae, and Zanclidae) form a common baseline assemblage across the entire gradient and cannot be considered indicators of restoration success. The pioneer families in the strict sense (absent from S1 and appearing as early as S2) include notably Acanthuridae, Mullidae, Monacanthidae, and Pomacanthidae.

The appearance of Epinephelidae from S4 onwards (18 months) constitutes a notable ecological signal : these high trophic-level predators require a structurally complex habitat with sufficient resources to sustain them. Their presence indicates that the assemblage has reached a level of trophic maturity not found on a degraded reef.

Mean total abundance at S5 reached 345.0 individuals (more than four times that of S4) but this value is overwhelmingly driven by Pomacentridae (mean MaxN = 238.0), a gregarious, highly fecund family capable of forming dense aggregations on reefs with high coral cover. This phenomenon is directly reflected in the collapse of Pielou's evenness at S5 ($J' = 0.398$): a value approaching 0 indicates that one or a small number of families account for the vast majority of individuals, at the expense of a balanced representation of the others. The numerical dominance of Pomacentridae on mature Indo-Pacific reefs is a well-documented phenomenon and does not in itself constitute a signal of degradation. The Shannon index, which integrates both the number of families present and the balance of their representation, illustrates this point: maximal at S2 ($H' = 1.830$), it reaches its minimum at S5 ($H' = 1.045$), confirming that it is at intermediate restoration stages that the community exhibits the greatest diversity in the strictly mathematical sense. However, this result should not be interpreted as evidence of ecological superiority of intermediate sites: on any mature coral reef in the Indo-Pacific, a small number of gregarious families naturally dominate in terms of abundance. The high density of Pomacentridae at S5 is thus characteristic of a reef whose coral cover is sufficiently developed to support large populations, and as such constitutes an indicator of maturity rather than a deficiency of the community.

The Kruskal-Wallis test reveals significant differences among the five sites for both richness ($\chi^2 = 10.135$; $p = 0.038$) and abundance ($\chi^2 = 12.122$; $p = 0.016$). Both p-values fall below the retained significance threshold ($\alpha = 0.05$), meaning there is less than a 5% probability that the observed differences are attributable to sampling variability alone: the null hypothesis of no effect of restoration age is therefore rejected. The nMDS ordination (stress = 0.136, considered acceptable for ecological interpretation) further corroborates this result at the level of community composition: site S1 is clearly separated from the restored sites in ordination space, reflecting a qualitatively distinct family composition. Sites S2 through S5 show partial overlap, which may reflect genuine ecological continuity between these stages. It should also be noted that the resolution of the analysis is limited by the small number of replicates per site ($n = 3$).

What can therefore be concluded is that coral restoration produces measurable effects on fish communities within the first months, with a rapid doubling of the number of families present and a progressive shift in assemblage structure : that is, the families present and their relative proportions change over time. The observed trajectory is characterised by a phase of high relative diversity at intermediate restoration stages, before S5 reaches a state of maturity defined by high total abundance and the establishment of high trophic-level predators.

Ultimately, the age gradient of the restored reefs is reflected in a temporal succession of reef fish communities, marked by a progressive increase in richness and abundance, an increasing trophic structuring, and a statistically significant evolution in the composition of the population.

V.b/ Comparison with the literature

The rapid response of fish communities to coral restoration observed in this study is consistent with recent work conducted in French Polynesia, which demonstrated that a significant shift in assemblage composition could be detected within less than one month following the implementation of restoration (Krimou et al., 2024). However, those authors did not observe any short-term effect on richness or total abundance, in contrast to what is documented here as early as S2. This difference may be explained by the timescale considered: an interval of three months, as at S2, allows more time for new families to establish, whereas the study by Krimou et al. focused on near-immediate effects.

The numerical dominance of Pomacentridae observed at S5 is a widely documented phenomenon on healthy natural coral reefs in the Indo-Pacific. On the Great Barrier Reef, this family accounts for up to 44% of total benthic fish abundance, with densities closely linked to the availability of healthy branching corals (Emslie et al. (2019)). Similarly, natural coral reef assemblages are frequently dominated by Pomacentridae, which can represent more than 50% of observed individuals, in contrast to artificial reefs where such dominance is absent (Rooker et al., (1997)). These findings support the interpretation that the high density of Pomacentridae at S5 reflects a state of maturity of the restored reef, rather than a dysfunction of the assemblage.

The appearance of Epinephelidae from S4 onwards is also consistent with the existing literature. Studies conducted on the largest coral restoration project in Indonesia show that herbivore, planktivore, and omnivore groups recover to abundances comparable to reference reefs within four to six years, while high trophic-level predators exhibit a slower and incomplete recovery (Lamont et al. (2025)). The early establishment of Epinephelidae at just 18 months in Padang Bai therefore represents an encouraging result, even though their abundance remains low (MaxN = 1 at S4). It is possible that the immediate proximity of the restoration site to more developed reef areas facilitates incursions by predators from these adjacent habitats.

Taken together, these results highlight that the observed recolonisation trajectory is closely linked to the progressive maturation of coral cover. The literature suggests that it is the structural complexity of the habitat (directly conditioned by coral development) that largely determines the functional diversity of reef fish communities (Maire et al. (2018)).

V.c/ Limitations and perspectives

The primary methodological limitation of this study is the low number of replicates per site (n = 3), which reduces the statistical power of the analyses and precludes post hoc testing following the Kruskal-Wallis test, making it impossible to determine precisely which pairs of sites differ significantly from one another. This limited number of replicates is primarily attributable to the time constraints inherent to a two-month internship: while the field phase remained logistically manageable, it was above all the video analysis (conducted frame by frame for each recording) that proved particularly time-consuming and constituted the main

limiting factor. Increasing the number of replicates per site would therefore be the first improvement to consider in order to strengthen the statistical robustness of the results.

Working at the family level rather than the species level represents a second limitation. Within a given family, different species may exhibit distinct ecological requirements, dietary regimes, and behaviours: operating at this taxonomic level therefore entails a loss of information on the fine-scale structure of the assemblage. However, this choice was fully justified in the context of this internship: species-level identification from video requires ichthyological expertise that cannot be acquired in two months, and the available image resolution would not always have permitted reliable identification at that level. Nonetheless, identification to species level remains a relevant perspective for future studies conducted by experienced researchers.

Furthermore, this study is based on a single point-in-time comparison between sites. Ideally, regular monitoring of the same sites over time (for example every three to six months) would allow the ecological succession trajectory of each restoration structure to be documented directly, rather than inferred from a comparison between sites of different ages.

In terms of perspectives, the integration of structural habitat complexity measurements (substrate rugosity, live coral cover, cavities, restoration structure type) would constitute a natural extension of this work. The Livingseas Foundation operates several types of restoration structures (Reef Stars, Octodome, relief grids) whose differing architectures may condition recolonisation in distinct ways. Explicitly testing the relationship between structure type and assemblage composition represents an open research question directly accessible at the Padang Bai site (Maire et al. (2018)).

Finally, replacing or supplementing the fixed-camera SPC with other survey methods would merit consideration. The belt transect would allow broader spatial coverage and density estimation per unit area, while RUVs offer the advantage of recording natural fish behaviour without bias associated with diver presence (Caldwell et al. (2016)). A multi-method approach, combining SPC for standardisation and belt transects for spatial representativeness, would significantly strengthen the comparative value of the data collected by the foundation over the long term.

VI/ General conclusion :

The primary objective of this internship was to describe and analyse the temporal succession of reef fish communities across five sites representing a restoration gradient of 3 to 36 months, in comparison with a degraded reference reef. The results obtained allow the conclusion that coral restoration produces measurable and statistically significant effects on fish communities within the first months following the deployment of restoration structures.

Family richness doubled between S1 and S2 within three months, confirming the speed of the biological response to the creation of artificial structures. The age gradient translated into a progressive increase in richness (from 5.3 to 11.0 families on average between S1 and S4) and total abundance, a trend validated by the Kruskal-Wallis test ($p < 0.05$ for both S and N). The appearance of Epinephelidae from S4 onwards reflects an increasing trophic structuring with site age. The nMDS ordination further confirms that the assemblage of the degraded reef is clearly distinct from all restored sites, whose composition progressively converges. These elements collectively support a positive answer to the research question: the age gradient of restored reefs does indeed translate into a progressive increase in the diversity and complexity of fish assemblages.

However, this progression is not strictly monotonic. The marked numerical dominance of Pomacentridae at S5, which leads to a collapse in evenness ($J' = 0.398$), illustrates that ecological maturity and maximum diversity do not necessarily coincide. This decoupling between richness, abundance, and evenness underscores the necessity of a multi-indicator approach to assess the success of reef restoration.

Beyond the results themselves, this work raises a broader question: to what extent can reefs restored through coral transplantation ultimately converge towards the structure and function of a healthy natural reef? Answering this question would require an undegraded reference site allowing direct comparison, as well as longitudinal monitoring of the same sites at regular intervals. These perspectives naturally extend the efforts undertaken by the LivingSeas Foundation and are part of the broader challenges of coral reef conservation in Indonesia, at the heart of the Coral Triangle.

VII/ Personal reflection :

This internship allowed me to develop technical skills directly relevant to my ambition to pursue a career in marine biology. In terms of practical expertise, I developed my scuba diving practice within a scientific framework, applying a standardised survey protocol (fixed-camera SPC) on coral reefs under real field conditions. Video analysis led me to train in the identification of Indo-Pacific reef fish families, a competency I had not previously acquired through my academic training. I also consolidated my skills in ecological data processing and analysis, notably through the use of RStudio for the calculation of diversity indices and the performance of multivariate ordinations (nMDS).

In terms of professional conduct, working within an international team, in English, and in a demanding field context, taught me to adapt quickly, exercise autonomy, and maintain methodological rigour outside of an academic setting. This internship confirmed my interest in the study of marine organisms and coral reef ecology, a field in which I intend to continue my studies.

My contribution to the host organisation consisted of the collection and analysis of an original dataset on the succession of reef fish communities in Padang Bai, results which are directly integrated into the LivingSeas Foundation's scientific monitoring database.

In terms of skills still to be developed, a stronger prior grounding in tropical ichthyology would have enabled species-level identification, which would have enhanced the taxonomic resolution of the analyses carried out.

VIII/ References :

Bellwood, D.R., Wainwright, P.C. (2002). The History and Biogeography of Fishes on Coral Reefs. In: Sale, P.F. (ed). *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, 5–32.

Caldwell, Z.R., Zgliczynski, B.J., Williams, G.J. et al. (2016). Reef Fish Survey Techniques: Assessing the Potential for Standardizing Methodologies. *PLoS ONE* [online], 11(4), e0153066, accessed 17 June 2026. URL: https://doi.org/10.1371/journal.pone.0153066

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18(1), 117–143.

Emslie, M.J., Logan, M., Cheal, A.J. (2019). The Distribution of Planktivorous Damselfishes (Pomacentridae) on the Great Barrier Reef and the Relative Influences of Habitat and Predation. *Diversity* [online], 11(3), 33, accessed 17 June 2026. URL: https://doi.org/10.3390/d11030033

Hollander, M., Wolfe, D.A. (1999). *Nonparametric Statistical Methods*. 2nd ed. John Wiley & Sons.

Krimou, S., Raick, X., Mery, E. et al. (2024). Restoring the reef: coral restoration yields rapid impacts on certain fish assemblages. *Estuarine, Coastal and Shelf Science* [online], 302, 108734, accessed 15 May 2025. URL: https://www.sciencedirect.com/science/article/abs/pii/S0272771424001227

Lamont, T.A.C., Maulana, P.B., Lange, I.D. et al. (2025). Corallivorous Fish Have Reduced Population Sizes and Altered Foraging Behaviour on a Recently Restored Coral Reef. *Global Change Biology* [online], 31(11), e70590, accessed 17 June 2026. URL: https://doi.org/10.1111/gcb.70590

Livingseas Foundation (2025). Restoring, Conserving & Rebuilding Coastal and Marine Ecosystems [online], accessed 15 May 2025. URL: https://www.livingseasfoundation.org

Maire, E., Villéger, S., Graham, N.A.J. et al. (2018). Community-wide scan identifies fish species associated with coral reef services across the Indo-Pacific. *Proceedings of the Royal Society B* [online], 285(1883), 20181167, accessed 15 May 2025. URL: https://doi.org/10.1098/rspb.2018.1167

Rooker, J.R., Dokken, Q.R., Pattengill, C.V. et al. (1997). Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs*, 16, 83–92.

Samoilys, M.A., Carlos, G. (2000). Determining Methods of Underwater Visual Census for Estimating the Abundance of Coral Reef Fishes. *Environmental Biology of Fishes*, 57, 289–304.

ANNEX :

Table of annexs :

ANNEX 1 :

Annex 1 : Raw video analysis data => example for site S3 (8 months of restoration)

Famille	Point 1 MaxN	Point 2 MaxN	Point 3 MaxN	Moyenne site	Présence (0/1)
Pomacentridae = (Damselfishes / Clownfishes)	7	5	25	12,3	1
Labridae = (Non-Parrotfish Wrasses)	0	2	2	2,0	1
Chaetodontidae = (Butterflyfishes)	3	2	7	4,0	1
Acanthuridae = (Surgeonfishes / Tangs)	9	5	7	7,0	1
Epinephelidae = (Groupers / Sea basses)	0	0	0	0,0	0
Mullidae = (Goatfishes)	10	0	32	21,0	1
Lutjanidae = (Snappers)	0	0	0	0,0	0
Haemulidae = (Grunts / Sweetlips)	0	0	0	0,0	0
Holocentridae = (Squirrelfishes / Soldierfishes)	0	0	0	0,0	0
Pomacanthidae = (Angelfishes)	0	0	0	0,0	0
Caesionidae = (Fusiliers)	0	0	0	0,0	0
Balistidae = (Triggerfishes)	1	0	0	1,0	1
Tetraodontidae = (Pufferfishes)	1	0	0	1,0	1
Labridae subfamily Scarinae = (Parrotfishes)	4	0	0	4,0	1
Siganidae = (Rabbitfishes)	0	0	1	1,0	1
Muraenidae = (Moray eels)	0	0	0	0,0	0
Scorpaenidae = (Scorpionfishes / Lionfishes)	0	0	0	0,0	0
Aulostomidae = (trumpetfish)	1	1	0	1,0	1
Dasyatidae = (stingrayrs)	0	0	0	0,0	0
Zanclidae = (Moorish idols)	4	1	3	2,7	1
Carangidae	0	60	1	30,5	1
Monacanthidae = filefish	3	1	2	2,0	1
Ostracidae	1	0	0	1,0	1
Diodontidae	0	1	0	1,0	1
belonidés	0	0	0	0,0	0
Pempheridae	0	0	0	0,0	0
Sphyraenidae	0	0	0	0,0	0
TOTAUX	44	78	80	67,3	15
S (richesse) =	15	N moyen (abondance) =	67,3		

Annex 2 : Methods and criteria for reef fish family identification

Summary table of the approaches and criteria used during video analysis, based on training provided by the scientific team of the Livingseas Foundation.

Approach	Criteria / Elements used	Notes
External morphology	Anatomy: nape, spines, rays, dorsal fins, tail base, pectoral fins, gill plate cover, pelvic fins, anal fins, caudal fins, finlets, lateral line, barbels, cirri, scutes	Primary approach used in this study
	Tegument markings: lines, stripes, bands, bars, spots, etc.	
	Life stage: morphology differs between juveniles and adults	Taken into account for difficult identifications
	Sexual dimorphism: morphological differences between males and females	
	Environmental conditions: visibility, light intensity, water turbidity	Influence perception of colours and markings
Counting	The number of individuals simultaneously observed can help distinguish certain gregarious families from solitary ones	Complementary approach to morphology
Geographic location	The geographic distribution of species can guide identification when ambiguity remains between morphologically similar families	Useful in the Indo-Pacific context of Padang Bai
Genetics	DNA sequence analysis (molecular barcoding, etc.)	Not used in this study — approach reserved for research programmes with significant analytical resources

Annex 3 : Calculation of Shannon (H') and Pielou (J') indices by site and measurement point => raw results (RStudio)

Results by site and measurement point :

```
--- S1 ---
  Point        S       N      H'     J'
  Point 1      6      15   1.173  0.655
  Point 2      5      17   1.405  0.873
  Point 3      5      14   1.332  0.827
  Moyenne    ---     ---   1.303  0.785  (sd H'= 0.119 ; sd J'= 0.115)

--- S2 ---
  Point        S       N      H'     J'
  Point 1     10      24   1.930  0.838
  Point 2     10      24   1.928  0.837
  Point 3     10      45   1.631  0.708
  Moyenne    ---     ---   1.830  0.794  (sd H'= 0.172 ; sd J'= 0.075)

--- S3 ---
  Point        S       N      H'     J'
  Point 1     11      44   2.100  0.876
  Point 2      9      78   0.965  0.439
  Point 3      9      80   1.573  0.716
  Moyenne    ---     ---   1.546  0.677  (sd H'= 0.568 ; sd J'= 0.221)

--- S4 ---
  Point        S       N      H'     J'
  Point 1     13      82   1.660  0.647
  Point 2      9      38   1.926  0.876
  Point 3     11     125   1.239  0.517
  Moyenne    ---     ---   1.608  0.680  (sd H'= 0.346 ; sd J'= 0.182)

--- S5 ---
  Point        S       N      H'     J'
  Point 1     11     277   0.681  0.284
  Point 2     12     167   1.089  0.438
  Point 3     18     591   1.365  0.472
  Moyenne    ---     ---   1.045  0.398  (sd H'= 0.344 ; sd J'= 0.1)
```

Summary table of results :

```
> cat(sprintf("  %-4s  %8s  %7s  %8s  %7s\n",
+             "Site", "H' moy", "sd(H')", "J' moy", "sd(J')"))
  Site    H' moy   sd(H')    J' moy   sd(J')
> for (i in 1:nrow(resultats_sites)) {
+   r <- resultats_sites[i, ]
+   cat(sprintf("  %-4s  %8.3f  %7.3f  %8.3f  %7.3f\n",
+               r$Site, r$H_moy, r$H_sd, r$J_moy, r$J_sd))
+ }
  S1       1.303    0.119     0.785    0.115
  S2       1.830    0.172     0.794    0.075
  S3       1.546    0.568     0.677    0.221
  S4       1.608    0.346     0.680    0.182
  S5       1.045    0.344     0.398    0.100
```

ANNEX 4 :

Annex 4: Raw results of the Kruskal-Wallis test on family richness (S) and total abundance (N) :

```
cat(sprintf("  Kruskal-Wallis S : chi2 = %.3f, df = %d, p-value = %.4f\n",
            kw_S$statistic, kw_S$parameter, kw_S$p.value))
Kruskal-Wallis S : chi2 = 10.135, df = 4, p-value = 0.0382
cat(sprintf("  Kruskal-Wallis N : chi2 = %.3f, df = %d, p-value = %.4f\n",
            kw_N$statistic, kw_N$parameter, kw_N$p.value))
Kruskal-Wallis N : chi2 = 12.122, df = 4, p-value = 0.0165
if (kw_S$p.value < 0.05) {
  cat("\n  => S : différence significative entre sites (p < 0.05)\n")
} else {
  cat("\n  => S : pas de différence significative entre sites (p >= 0.05)\n")
}

=> S : différence significative entre sites (p < 0.05)
if (kw_N$p.value < 0.05) {
  cat("  => N : différence significative entre sites (p < 0.05)\n")
} else {
  cat("  => N : pas de différence significative entre sites (p >= 0.05)\n")
}
=> N : différence significative entre sites (p < 0.05)
cat("================================================================\n")
```

Solen PERROCHON

Title (EN) : Temporal succession of reef fish communities on restored reefs of different ages: a study using the SPC method with a fixed camera at Padang Bai, Bali (Indonesia)

Abstract (EN) :

This internship, carried out within the Livingseas Foundation in Padang Bai (Bali, Indonesia), aimed to analyse the temporal succession of reef fish communities across coral reefs of varying restoration ages. Five sites were studied, representing a restoration gradient from 3 to 36 months using the MARRS method, alongside a degraded reef used as a reference site. Surveys were conducted using a fixed DJI camera stationary point count (SPC) protocol. Data were analysed using family richness (S), total abundance (N), Shannon diversity index (H') and Pielou evenness (J'). Statistical analyses (Kruskal-Wallis test, nMDS ordination) confirmed significant differences between sites. Results indicate rapid recolonisation within three months, increasing trophic structuring with the appearance of Epinephelidae at 18 months, and strong Pomacentridae numerical dominance at the most mature site, consistent with healthy Indo-Pacific reef communities.

Keywords (EN) : coral restoration, reef fish communities, ecological succession, stationary point count, Indonesia