

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

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**Temporal and spatial patterns influence reef fish
community structure along an upwelling gradient in the
Galápagos Marine Reserve**

Proyecto de Investigación

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RESUMEN

Las Islas Galápagos se encuentran en un sistema complejo de corrientes marinas que varían temporal y espacialmente. Además, eventos de afloramientos, causados por movimientos ascendentes de aguas frías y ricas en nutrientes, aumentan la productividad en sus áreas de incidencia. Por estas razones el Archipiélago consta con aproximadamente 500 especies de peces de arrecife, con afinidades tanto tropicales como templadas. El objetivo de este estudio fue comprender cómo la intensidad de afloramiento entre estaciones influyen en la estructura de la comunidad de peces. Se seleccionaron siete sitios de muestreo: Cabo Ibbetson, Bartolomé y Punta Cormorant (con bajos de afloramiento), y Punta Espinosa, La Botella, Punta Mangle y Cabo Douglas (con alto afloramiento). Estos fueron visitados en las estaciones caliente y fría. Se realizaron censos visuales a 6-8 m de profundidad, consistiendo de ocho transectos de 250m² en cada sitio en ambas estaciones. Las especies de peces registradas fueron clasificadas en grupos funcionales de acuerdo a su nivel trófico y se calculó su biomasa mediante la fórmula de conversión alométrica de longitud y peso $W=aTL^b$. Se compararon varios índices de diversidad y biomasa entre sitios y estaciones. Los resultados revelaron que existe una mayor riqueza y diversidad (Shannon H') de especies en sitios con bajo afloramiento. Por otro lado y contrario a lo esperado, se encontró una mayor biomasa en sitios con bajo afloramiento, pero ésta tendió a ser mayor durante la estación fría. Finalmente, análisis multivariados de la composición de los grupos funcionales sugirieron que la estacionalidad juega un rol importante principalmente en los sitios con alto afloramiento. Concluimos que para predecir cambios en la riqueza, diversidad y biomasa de peces es necesario comprender cómo las comunidades en distintas regiones biogeográficas responden a cambios estacionales y a patrones de afloramiento.

Palabras clave: peces de arrecife, estacionalidad, afloramientos, grupos funcionales, biomasa, diversidad.

ABSTRACT

The Galápagos Islands are immersed in a complex system of marine currents that vary temporally and spatially. Upwelling caused by upward movements of cold nutrient rich waters increase productivity in their areas of incidence. For these reasons, the Archipelago registers approximately 500 species of reef fish with tropical and temperate affinities. This study aimed to understand how seasonality and upwelling intensity influences fish community structure. Seven sampling sites were chosen: Cabo Ibbetson, Bartolomé and Punta Cormorant (with low upwelling), and Punta Espinosa, La Botella, Punta Mangle and Cabo Douglas (with high upwelling). These sites were visited in both warm and cold seasons. Underwater visual censuses were taken at 6-8 m depth, consisting of eight transects of 250m² at each site during both seasons. Fish species were classified into functional groups according to their trophic level; total fish biomass was estimated using the allometric length-weight formula $W=aTLb$. Several diversity and biomass indices were compared between sites and seasons. Results revealed that there was a greater richness and species diversity (Shannon H') in sites with low upwelling. Contrary to our expectations, a higher biomass was found in sites with low upwelling with a tendency to be greater during the cold season. Finally, multivariate analyses suggest that seasonality plays an important role mainly in sites with high upwelling. We conclude that in order to make predictions on how the richness, diversity and biomass of fish change, it is necessary to understand how communities in different biogeographical regions respond to seasonal changes and upwelling patterns.

Keywords: reef fish, seasonality, upwelling, functional groups, biomass, diversity.

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INTRODUCTION

The Galápagos Islands provide a complex dynamic system ideal for understanding how environmental variables and biogeography affects marine community structure. This Archipelago, unlike most tropical islands, is influenced by cool and nutrient-rich waters that vary in frequency and area of influence (Witman and Smith, 2003). Warm and cool water current systems create unique opportunities to study how these currents influence fish communities and functional group composition. Three major currents, the warm south-westerly flowing Panama Current, the cool north-westerly flowing Peru current (Humboldt current), and, the cold eastward-flowing subsurface equatorial undercurrent (Cromwell Current), cause regional variation and changes in community structure (Edgar *et al.*, 2004). As a result, different interactions among consumers and productivity are evident within small spatial scales (Vinueza, 2009).

Species richness varies in the Galápagos Marine Reserve (GMR) between the warm tropical and cool upwelling zones (Edgar *et al.*, 2017). It has been shown that upwelling regimes have a bottom-up effect on Galápagos food webs (Vinueza *et al.*, 2006 & Witman, *et al.*, 2010). Nonetheless, widespread environmental disturbances such as El Niño-Southern oscillation events (ENSO), geographical variables and anthropogenic pressures have a profound impact on the structure of marine communities as well (Okey *et al.*, 2004; Parravicini *et al.*, 2013). On the other hand changes in ocean productivity due to shifts in upwelling intensity can cascade up to higher trophic levels (Vinueza, 2009). While rich, cold waters trigger a bottom-up effect on the food webs, high productivity allows subsequent top-down effects of herbivores such as sea urchins (Witman and Smith, 2003), fishes and whelks (Witman *et al.*, 2010).

Evidence has shown how increasing water temperatures influences trophic interactions by stimulating metabolic activity in ectothermic consumers (Carr *et al.*, 2018). Therefore, invertebrate herbivores tend to have a strong top-down effect by reducing algal biomass in warmer temperatures (Vinueza, 2009, Vinueza *et al.*, 2014). A decrease in predators resulting from changes in water temperatures, habitat destruction/alteration and fishing, will increase herbivory and cause a reduction of primary production (Sonnenholzner, *et al.*, 2009). Hence, predators fulfill a fundamental role through top-down controls in these ecosystems.

Oceanic islands such as the Galápagos are considered plankton sinks due to high primary production (Okey *et al.*, 2004). Localized upwelling favors algal growth, thus sites with strong upwelling regimes in other parts of the world supports higher herbivore fish biomass as a result of a substantial increase in growth, earlier maturation, and increased fecundity (Hixon and Jones, 2017). Diversity and density of planktivores, detritivores and benthic invertivores are also expected to be higher in high upwelling sites (Quimbayo *et al.*, 2019). There are differences in fish species composition across bioregions in the GMR (Edgar *et al.*, 2004), and these species do not contribute equally to the varied ecosystem processes and delivery of services. Therefore, identifying functional group composition and assembly (Stuart-Smith *et al.*, 2013) among sites with high and low upwelling regimes will provide insight of the structure of the food webs, ecosystem dynamics, energy fluxes, and the potential underlying mechanisms for ecosystem stability (Robinson and Baum, 2016). The aim of this study was to understand how changes in ocean productivity within an upwelling gradient determine reef fish community structure and functional group composition.

Hypothesis

- *There is higher fish species richness and lower species diversity in sites with low upwelling.*

Sites characterized by low upwelling intensity, resemble marine tropical ecosystems due to higher sea surface temperature. Warmer tropical waters tend to have higher species richness but lower species diversity (i.e. evenness, Stuart-Smith *et al.*, 2013).

- *High upwelling supports higher fish biomass.*

Western Islands, subject to continuous upwelling, experience higher productivity allowing ecosystems to flourish (Okey *et al.*, 2004). Nutrient-rich sites support more productive fish communities as a result of an increase in plankton and macroalgae biomass (Stuart-Smith *et al.*, 2013) that cascades up into the food web.

- *Fish functional group composition is driven by biogeographic patterns.*

The confluence of tropical and temperate water currents in the Archipelago is responsible for the presence of more than 500 species of fish (Humann & DeLoach, 2003). Connectivity and upwelling regimes across the different bioregions of the GMR give rise to differences in community assemblage along small spatial scales (Edgar *et al.*, 2004; Vinuela, 2009).

METHODS

Study Sites

The Galápagos Islands are located 965 km off the coast of Ecuador and represent a unique place to study how oceanographic processes and biogeography affects specie composition (Edgar *et al.*, 2004 & Witman *et al.*, 2010). During the warm season, which lasts from December to May, trade winds decrease in strength allowing the warm south-westerly flowing Panama Current to reach the Islands, bringing stable warmer waters (Edgar, *et al.*, 2004). During the cold season, lasting from June to November, the dominant westward surface flow South Equatorial Current (SEC) concurs with the Humboldt Current, reinforced as well by the southeast trade winds, carrying cool waters to the islands (Glynn *et al.*, 2018). On the other hand, the Equatorial Undercurrent or Cromwell Current brings constant upwelling to the Islands depending on wind and flow-topography interactions (Witman *et al.*, 2010). This cool underwater current runs from west to east, colliding with the western Islands such as Isabela and Fernandina, as well as with smaller Islands such as Floreana, Santiago, and Santa Cruz in a smaller scale (Witman *et al.*, 2010). According to this, seven sites were chosen following a categorization of upwelling intensity. Cabo Ibbetson, Bartolomé and Punta Cormorant had low levels of upwelling, while Cabo Douglas, Punta Mangle, Punta Espinosa and La Botella had high levels of upwelling (**Table 1**). Punta Mangle and Cabo Douglas in the island of Fernandina where only sampled during the cold season.

Data Collection

Quantitative data was taken during research cruises in the warm and cold seasons in March and in August 2018, respectively. SCUBA Underwater Visual Census

(UVC) were carried out in five different sites throughout the warm season from March 25th-30th, and in seven sites in the cold season from August 11th-17th. Species names and abundances of all fishes were recorded throughout eight transects of 250 m² at each site. Since the study was conducted in a rocky reef substratum, when the bottom became too sandy the direction of the transect was changed to avoid bias-substrate type. In the same manner, the depth was kept constant (6-8 m), if there was a slope the direction of the transect was changed. Average temperature for each site was calculated using a diving computer. All data was collected using waterproof paper, then it was transcribed to paper and finally into an excel database. Species were classified into functional groups depending on their trophic level (**Table 2**).

Data Analysis

Species richness and diversity. Expected local richness was estimated using rarefaction methods and species accumulation curves were produced for the warm and cold seasons with EstimateS. Species diversity was determined by analyzing the relative abundance of species with the Shannon H' index. A two-way-ANOVA was run to identify how the Shannon H' index varied due to upwelling intensity (low and high) or between seasons (warm and cold). Tukey HSD post-hoc tests were run in order to identify where the significant differences were found.

Biomass Estimates. Size for each species was calculated by getting the maximum length of the size range from the book “Reef Fish Identification Galápagos” by Human & DeLoach (2003) and FishBase (2019). Then, fish biomass was estimated using the allometric length-weight formula $W=aTLb$ (Valdiva et al., 2017), where W is biomass in grams, TL is the length obtained as explained above, and a and b are species-specific coefficients (FishBase, 2019). Total biomass was then calculated by multiplying the recorded abundance of each species by W . Additionally, we estimated

the biomass of the most abundant species, by choosing those that had more than 100 individuals in each season. A three-way-ANOVA was ran to see how the biomass of the most abundant species, and of all species together, varied between upwelling regimes (low and high), seasons, and sites (nested in upwelling regimes). Tukey HSD post-hoc tests were run in order to identify where the significant differences were found.

Multivariate Analyses. Multivariate analyses were conducted in PRIMER to have a better understanding of fish community structure (Edgar et al., 2004). ANOSIM, SIMPER, Cluster and Non-metric Multidimensional Scaling (nMDS) analyses were run with Bray-Curtis similarities among sites and seasons. We run ANOSIM tests using 2 factors: season (warm and cold), and sites nested in upwelling category (7 sites). SIMPER provided a more detailed analysis on similarities among fish functional groups between these two factors. Cluster and nMDS analyses gave a visual representation of the community structure and allowed to distinguish how sites aggregate in response to upwelling intensity and season.

RESULTS

A total of 66 species were recorded during the warm and cold seasons with a sum of 15,406 individuals. Nine species of Herbivores, six Planktivores, 10 Omnivores, 29 Invertivores, and 12 Piscivores were identified (**Table 2**).

Species Richness

In general, the expected number of species found in each site was higher at sites with low upwelling in both warm and cold seasons (**Figures 1 & 2**). The species accumulation curves stabilize reaching a maximum estimate of species for some sites. Sample size of eight transects appears to be sufficient, however this is not the case for some sites such as Bartolomé (warm season) and Punta Cormorant (cold season), since the number of species kept increasing with more sampled transects. In the warm season, a maximum of 26 species was estimated for Cabo Ibbetson and Bartolomé (**Figure 1**). For the cold season, a maximum of 30 species was estimated for Punta Cormorant and 28 for Cabo Ibbetson (**Figure 2**). Differing from all the sites where species richness remained similar across seasons, Punta Espinosa (characterized for having high upwelling intensity) varied greatly between seasons. In the warm season it had the least richness of 13 species, whereas in the cold season it was the third site with higher richness with a total estimate of 27 species (**Figures 1 & 2**). Cabo Douglas and La Botella were the least rich, with 17 and 14 species, respectively (**Figure 2**). Overall, species richness was higher in the cold season regardless of upwelling category.

Species Diversity

The Shannon H' index varied between upwelling categories, seasons, and the interaction of the two (**Figure 3, Table 3**). There was a higher diversity in sites with

low upwelling, with a mean value of 2.11 compared to the mean value of 1.74 in sites with high upwelling during the cold season (**Figure 3**). In addition, diversity tended to be lower during the warm season for the low upwelling sites, and it was significantly lower during the warm season in the high upwelling sites (**Figure 3**).

Total Biomass

The total biomass of fish varied between upwelling categories and seasons, but did not vary by site or interaction of upwelling and seasons (**Table 4, Figure 4**). A higher biomass was found in sites with low upwelling, with a mean value of 92,082.97 gr for the cold season and 60,793.83 gr for the warm season compared to the mean value of 27,444.32 gr for the cold season and 15,439.99 gr for the warm season in sites with high upwelling (**Figure 4**). In addition, there was a tendency of a higher biomass during the cold season, however these differences were not significant within upwelling regimes (**Table 4, Figure 4**).

Most Abundant Species Biomass

From a total of 66 species, 19 species had more than 100 individuals in both seasons and 17 significantly varied between upwelling regimes, season or sites (**Table 5**). Most species had higher biomass abundance in low upwelling sites but also during the cold season for both upwelling categories (**Table 6**), such as the The Razor Surgeonfish (*Prionurus laticlavus*), the King Angelfish (*Holocanthus passer*) the Bluechin Parrotfish (*Scarus ghobban*), the Yellowtail Damselfish (*Stegastes arcifrons*), the Cortez Rainbow Wrasse (*Thalassoma lucasanum*), the Burrito Grunt (*Anisotremus interruptus*), and the Blue Gold Snapper (*Lutjanus viridis*). The Mexican Hogfish (*Bodianus diplotaenia*) was most abundant in low upwelling, whereas the Harlequin Wrasse (*Bodianus eclancheri*) biomass was significant higher only in sites with high

upwelling as well as the Peruvian Grunt (*Anisotremus scapularis*) (**Table 6**). The Banded Cleaner Goby (*Elacatinus nesiotus*) was most abundant in sites with high upwelling (**Table 6**). The Dusky Chub (*Girella freminvilli*), the Sabertooth Blenny (*Plagiotremus azaleus*), and the Chameleon Wrasse (*Halichoeres dispilus*) had higher biomass at high upwelling sites and only during the cold season in low upwelling sites (**Table 6**). The Ringtail Damsel (*Stegastes beebei*) and the Bacalao (*Mycteroperca olfax*) had similar biomass in both upwelling sites throughout seasons (**Table 6**).

Multivariate Analyses

Non-metric multidimensional scaling illustrates how the structure and biomass of the fish community of each site differs from each other. There are two main aggregations of sample points that respond to upwelling intensity (**Figures 5 & 6**). Sample points from low upwelling sites remain closer together regardless of the season, suggesting that functional group composition is similar between seasons. Whereas, at sites with high upwelling, the sample points from different seasons are further apart corresponding to different fish community structures. ANOSIM analysis also showed that the sites that were more significantly different were Bartolomé & Punta Mangle ($R= 0.979$), Punta Cormorant & Punta Mangle ($R=0.896$), Bartolomé & Cabo Douglas ($R=0.823$) and Cabo Ibbetson & Punta Mangle ($R=0.813$) (**Table 7**). These results were confirmed as well by Cluster analysis (**Figure 6**) that identified community structure within the data input of each sampled site. Segments show similarities in the community composition for each site depending on the number of ramifications and the distance between them (**Figure 6**). Two main groupings are formed between sites with low and high upwelling. Site comparisons that differed the most (**Table 7**), also have multiple branches that increase the distance between groups representing distinct communities (**Figure 6**).

When we look at comparisons between sites, SIMPER Analyses allowed us to see which particular functional groups contributed the most to sites differences (**Table 8**). Herbivores (58.28%) and Invertivores (28.07%) explained the differences between Bartolomé & Punta Mangle (Av. Diss 83.55%), with a greater biomass in Bartolomé (**Table 8**). Punta Cormorant & Punta Mangle had an average Dissimilarity of 80.17%, and Herbivores (57.34%) and Invertivores (28.81%) again contributed to this difference, with a greater biomass in Punta Cormorant (**Table 8**). Bartolomé & Cabo Douglas had an average Dissimilarity of 75.55% and similarly, Herbivores (66.02%) and Invertivores (30.55%) had a greater biomass in Bartolomé (**Table 8**). Finally, Cabo Ibbetson & Punta Mangle had an average Dissimilarity of 78.98%, and again, Herbivores (58.69%) and Invertivores (26.61%) contributed with a greater biomass in Cabo Ibbetson. In summary, Herbivores and Invertivores are more abundant in low upwelling sites (**Table 8**). On the other hand, the sites with greater similarity were Bartolomé & Cabo Ibbetson, with an average Dissimilarity of 46.2%, with Herbivores (43.98%) and Invertivores (36.61%) being slightly more abundant in Cabo Ibbetson (**Table 8**).

DISCUSSION

Species accumulation curves and Shannon H' index showed that sites with low upwelling were characterized for having higher fish species richness and higher diversity (evenness), thus I partially accept my first hypothesis, because I had originally hypothesized that species diversity would be higher in more productive sites (i.e. high upwelling sites). Global patterns describe that warmer tropical waters have higher number of species than temperate regions, but are lower in evenness (Stuart-Smith *et al.*, 2013), thus the first part of this pattern is consistent with my findings of higher species richness in warmer sites. In addition, higher species richness is expected within short geographical distances between habitats giving way to interconnected meta-communities (Parravicini *et al.*, 2013). During the warm and cold seasons, Cabo Ibbetson in the northern island of Pinta had the highest estimated number of species. Even though not all sites are further north, sites with low upwelling such as Punta Cormorant and Bartolomé had higher species richness as well. Contrary to most sites with high upwelling, which are secluded from the rest of the Archipelago, northern and central bioregions could have greater connectivity and species exchange between these islands and the mainland, and this could be the reason of maintaining high species richness (Vinuela, 2009).

Western islands, by being subject to more constant upwelling, are oceanographically isolated, having less connectivity to the rest of the Archipelago and to the mainland, hence lower species richness is expected there (Edgar *et al.*, 2004). However, my results showed that during the cold season, Punta Espinosa in the Elizabeth bioregion had one of the highest species richness (**Figure 2**). This site is located in Fernandina Island, between Isabela Island and Canal Bolivar. The Elizabeth bioregion is characterized for having the highest endemism in the Galápagos due to its

oceanographic isolation as well as highest productivity of all regions (Edgar *et al.*, 2004). These environmental conditions together with the presence of panamic, endemic, and widespread species found at this western island, could be contributing to a raise in the number of species in Punta Espinosa (Edgar *et al.*, 2004).

Oceanic islands tend to support poor fish fauna and exhibit high functional diversity, nevertheless the Galápagos islands due to their large surface area, high diversity of benthic habitats, varied seasons, and upwelling gradients, are known for having moderate species richness (Stuart-Smith *et al.*, 2013). More than 500 fish species have been identified in the Archipelago (Charles Darwin Foundation, n.d.), but only 66 species were recorded in this study (**Table 2**). Nocturnal, cryptic, and small fish species may not have been quantified properly, leading to a sub-estimation of total species richness across sites and regions (Robinson & Baum, 2016).

The Galápagos stand out from tropical and temperate islands for having the highest functional diversity worldwide (Stuart-Smith *et al.*, 2013), still, the number of species found and their relative abundance in different sites shifts within short distance scales (Edgar *et al.*, 2017). High upwelling sites were expected to support greater number of fish and thus evenness (Okey *et al.*, 2004; Stuart-Smith *et al.*, 2013), however my results showed the contrary (**Table 3, Figure 3**). Species diversity was higher in low upwelling and it was significantly higher during the cold season only for high upwelling sites. Habitat complexity and benthic diversity provide optimal conditions for a rise in species relative abundance (Dominici-Arosemena & Wolff, 2006), thus it is possible that sites of low and high upwelling vary in relation to these factors and influenced my results. On the other hand, Shannon H' indices were relatively low: they reached values of maximum 2.1 (**Figure 3**). This implies that in general diversity is low across all sites, which agrees with what was explained in the previous paragraph. In addition, only a few species like *B. diplotaenia*, *H. passer*, *S.*

ghobban, *L. viridis* and incredible so, *P. laticlavus*, were very abundant (**Table 6**). Consequently, evenness was in general low as a response to the total registered number of individuals their and relative abundances.

High upwelling sites are known for having greater productivity as a result of nutrient availability, which increases plankton and algae biomass, and indirectly influences fish community structure by changing the intensity of biological interactions (Witman & Smith, 2003; Stuart-Smith *et al.*, 2013). These nutrient-rich sites provide hotspots for fish where their ecological functions tend to be proportional to their abundance (Stuart-Smith *et al.*, 2013). Thus, high productivity in sites with continuous upwelling should have had a higher biomass of the different functional groups (Okey *et al.*, 2004; Quimbayo *et al.*, 2018). Contrary to what we expected, we found that total fish biomass was much higher in “less productive sites” and the tendency of being higher during the cold season (**Figure 4**). Biomass estimations using the maximum length of the size range for each species, instead of the real length, might not reflect actual biomass and system productivity. Further studies should take into consideration species real lengths; however, similar results were obtained using only fish abundance (not shown). Consequently the results of low upwelling sites showing higher fish productivity, measured as biomass or number of individuals did not change.

A possible explanation to why total biomass had a tendency to increase during the cold season in high upwelling sites could be driven by a reduction in fishing pressure. Strong currents impact the islands during the cold season, creating rough conditions for navigation and limiting access to shallow rocky habitat as a result of strong wave action (Bucaram & Hearn, 2014). These could reduce fishing efficiency for artisanal fisheries during this time of the year, similar to how lobster fisheries catch-per-unit effort indices are lowered (Bucaram & Hearn, 2014).

Finally, following an upwelling gradient across islands does seem to affect fish community structure as suggested by my third hypothesis (**Figures 5 & 6**). Comparisons between sites without considering seasonality demonstrated that the differences were greatest between sites of low and high upwelling (**Table 7**). Herbivores and Invertivores comprised most of the biomass in the most significantly different sites (**Tables 7 & 8**). Invertivores were one of the most diverse functional groups with the highest number of species (**Table 1**) due to specialized consumption of different invertebrates, which vary in size and feeding mode: hard and soft (Brandt 2012), such as *B. diplotaenia* that feeds on invertebrates, and as lobsters on sea urchins (Sonnenholzner *et al.*, 2009).

The distance between sites and the area of incidence of different current systems leads to differences along the upwelling gradient (**Table 8**). Non-metric Multidimensional Scaling results (**Figure 5**) and Cluster analysis (**Figure 6**) reveal a marked difference between sites with low and high upwelling, yet sites with low upwelling remained fairly consistent between seasons. Temperatures did not vary significantly across seasons for low upwelling sites and for Punta Espinosa (**Table 1**). Interestingly, it did vary for La Botella a high upwelling site, whose communities separated in space in the different seasons. In successional patterns with sessile invertebrate species, a site with high upwelling tended to be more constant between seasons (Krutwa *et al.*, 2014). Since temperature remains stable (or has small variations) during the warm and cold seasons in western islands do to the continual influence of the Cromwell current, species composition tended to remain unchanged (Krutwa *et al.*, 2014). Nonetheless, in my study seasonality seems to play an important role in fish species composition only at high upwelling sites, considering the sample points have a greater distance from each other in the warm and cold seasons (**Figure 5**). Temperatures in high upwelling sites during the cold season were not as cold as expected (**Table 1**).

However, sites such as Punta Mangle and Cabo Douglas cannot be compared since they were only sampled during the cold season. It seems that differences in community structure along sites (**Figures 5 & 6**) are heightened by upwelling intensity and biogeographical position, rather than by changes in seasonality (Parravicini *et al.*, 2013).

CONCLUSION

The vast amount of environmental and geographical variables that influence the Galápagos Archipelago makes it hard to determine how individual factors may affect fish communities. Biogeographical distances that intensify meta-communities connectivity seem to contribute to higher species richness and diversity (Parravicini *et al.*, 2013). More productive islands in the west, submitted to constant upwelling should have had higher fish biomass. Still, environmental factors such as rougher conditions for executing UVCs, lower metabolic rates, cryptic species and anthropogenic pressures could explain why biomass was lower at high upwelling sites (Vinueza, 2009). Response to geographic and historical variables of species distribution in the Tropical Eastern Pacific explains community structure assemblage (Parravicini *et al.*, 2013). Changes in community structure are obvious throughout an upwelling gradient, yet seasonality seems to play an important role in fish community only at high upwelling sites. More extensive sampling will allow us to further comprehend how reef fish communities respond to different variables in this rich and complex marine system.

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TABLES

Table 1. Study sites, temperatures, coordinates and upwelling intensity.

Island	Site	Mean Temperature C°		Coordinates	Upwelling
		Warm	Cold		
Pinta	Cabo Ibbetson	22	24	00°32'38.3"N 90°43'55.2"O	Low
Santiago	Bartolomé	25	24	00°16'47.0"S 90°32'41.5"O	
Floreana	Punta Cormorant	23	22	01°13'14.4"S 90°25'21.4"O	
	La Botella	22	19	01°17'29.2"S 90°29'47.7"O	High
Fernandina	Punta Espinosa	17	17.5	00°16'13.3"S 91°26'09"O	
	Punta Mangle	N/A	19	00°27'10.5"S 91°23'15.2"O	
	Cabo Douglas	N/A	18	00°18'05.9"S 91°39'10.3"O	

Table 2. Species and Functional Group Categorization

	Common Name	Scientific Name
Herbivores	Goldrim surgeonfish	<i>Acanthurus nigricans</i>
	Dusky Chub	<i>Girella freminvillei</i>
	Bumphead damselfish	<i>Microspathodon bairdii</i>
	Lossetooth parrotfish	<i>Nicholsina denticulata</i>
	Razor surgeonfish	<i>Prionurus laticlavus</i>
	Azure parrotfish	<i>Scarus compressus</i>
	Bluechin parrotfish	<i>Scarus ghobban</i>
	Bumphead parrotfish	<i>Scarus perrico</i>
	Bicolor parrotfish	<i>Scarus rubroviolaceus</i>
Planktivores	Guineafowl puffer	<i>Arothron meleagris</i>
	Silverstripe chromis	<i>Chromis alta</i>
	Scissortail chromis	<i>Chromis atrilobata</i>
	Ballonfish	<i>Diodon holocanthus</i>
	Blue banded goby	<i>Lythrypnus gilberti</i>
	Pacific creolefish Gringo	<i>Paranthias colonus</i>

Omnivores	Panamic sergeant major	<i>Abudefduf troschelii</i>
	Harlequin Wrasse	<i>Bodianus eclancheri</i>
	King Angel Fish	<i>Holacanthus passer</i>
	Barberfish	<i>Johnrandallia nigrirostris</i>
	Bravo clinid	<i>Labrisomus dendriticus</i>
	Panamic fanged blenny	<i>Ophioblennius steindachneri</i>
	Pacific beakfish Tigris	<i>Oplegnathus insignis</i>
	Yellowtail damselfish	<i>Stegastes arcifrons</i>
	Galapagos ringtail damselfish	<i>Stegastes beebei</i>
	Cortez rainbow wrasse	<i>Thalassoma lucasanum</i>
Invertivores	Pacific mutton hamlet	<i>Alphestes immaculatus</i>
	Burrito grunt	<i>Anisotremus interruptus</i>
	Peruvian grunt	<i>Anisotremus scapularis</i>
	Mexican Hogfish	<i>Bodianus diplotaenia</i>
	Spotted sharpnose puffer	<i>Canthigaster punctatissima</i>
	Panamic graysby	<i>Cephalopholis panamensis</i>
	Spotfin burrfish	<i>Chilomycterus reticulatus</i>
	Redlight goby	<i>Coryphopterus urospilus</i>
	Diamond stingray	<i>Dasyatis dipterura</i>
	Banded cleaner goby	<i>Elacatinus nesiotes</i>
	Spotted cabrilla	<i>Epinephelus analogus</i>
	Flag cabrilla	<i>Epinephelus labriformis</i>
	Mojarra grunt	<i>Haemulon scudderii</i>
	Chameleon Wrasse	<i>Halichoeres dispilus</i>
	Spinter wrasse	<i>Halichoeres nicholsi</i>
	Bullhead shark	<i>Heterodontus quoyi</i>
	Galapagos Triplefin Blenny	<i>Lepidonectes corallicola</i>
	Blue-and-gold snapper	<i>Lutjanus viridis</i>
	Throatspotted Blenny	<i>Malacoctenus tetranemus</i>
	Mexican goatfish	<i>Mulloidichthys dentatus</i>
	Galapagos Sheepshead	<i>Orthopristis cantharinus</i>
	Galapagos Grunt	<i>Orthopristis forbesi</i>
	Camotillo	<i>Paralabrax albomaculatus</i>
	Goldspot sheepshead	<i>Semicossyphus darwini</i>
	Barred serrano	<i>Serranus psittacinus</i>
	Bullseye Puffer	<i>Sphoeroides annulatus</i>
	Orangeside triggerfish	<i>Sufflamen verres</i>
White tip reef shark	<i>Triaenodon obesus</i>	
Moorish idol	<i>Zanclus cornutus</i>	
Piscivores	Trumpetfish	<i>Aulostomus chinensis</i>
	Coral hawkfish	<i>Cirrhitichthys oxycephalus</i>
	Giant hawkfish (mero chino)	<i>Cirrhitis rivulatus</i>
	Leather bass	<i>Dermatolepis dermatolepis</i>

Rainbow runner	<i>Elagatis bipinnulata</i>
Fine spotted moray ell	<i>Gymnothorax dovii</i>
Jewel Moray	<i>Muraena lentiginosa</i>
Grouper	<i>Mycteroperca olfax</i>
Sabertooth blenny	<i>Plagiotremus azaleus</i>
Almaco jack	<i>Seriola rivoliana</i>
Calico Lizardfish	<i>Synodus lacertinus</i>
Peruvian Torpedo Ray	<i>Torpedo peruana</i>

Table 3. Two-Way-ANOVA for Species Diversity (Factor 1: Upwelling Category, Factor 2: Season)

Effect Test	Sum of Squares	F Ratio	Prob>F
Upwelling Category	7.0652355	125.1847	<0.0001
Season	2.5176532	44.6088	<0.0001
Upwelling*Season	0.7463297	13.2238	0.0005

Table 4. Three-Way-ANOVA for Total Biomass (Factor 1: Upwelling Category, Factor 2: Season, Factor 3: Site nested in Upwelling Category)

Effect Test	Sum of Squares	F Ratio	Prob>F
Upwelling Category	5.8072e+10	26.2457	<0.0001
Season	8996761278	4.0661	0.0468
Site	2.3575e+10	2.1309	0.0692
Upwelling*Season	1785139784	0.8068	0.3715

Table 5. Three-Way-ANOVA for Biomass of Most Abundant Species (Factor 1: Upwelling Category, Factor 2: Season, Factor 3: Site nested in Upwelling Category)

Species	p-Value	p-Upwelling	p-Season	p-Site	p-Up*Season
<i>Abudefduf troschelii</i>	0.8202	0.1177	0.7335	0.871	0.8569
<i>Anisotremus interruptus</i>	0.0113	0.084	0.3219	0.0137	0.3489
<i>Anisotremus scapularis</i>	0.1394	0.9929	0.094	0.1024	0.094
<i>Bodianus diplotaenia</i>	0.0496	0.0022	0.4326	0.7117	0.9749
<i>Bodianus eclancheri</i>	0.0001	0.0002	0.6645	0.0001	0.6645
<i>Elacatinus nesiotus</i>	0.0001	0.0001	0.7577	0.0001	0.8562
<i>Girella freminvilli</i>	0.0001	0.1799	0.1834	0.0001	0.6717
<i>Halichoeres dispilus</i>	0.0001	0.0448	0.0001	0.0005	0.1652
<i>Holacanthus passer</i>	0.0309	0.001	0.4685	0.1169	0.4685
<i>Lutjanus viridis</i>	0.0011	0.0654	0.2751	0.0012	0.7478
<i>Mycteroperca olfax</i>	0.0001	0.879	0.0153	0.0001	0.0153
<i>Ophioblennius steindachneri</i>	0.0001	0.0001	0.0834	0.0005	0.8567
<i>Paranthias colonus</i>	0.0003	0.945	0.0965	0.0001	0.0596
<i>Plagiotremus azaleus</i>	0.0007	0.2053	0.0001	0.1519	0.2777
<i>Prionurus laticlavus</i>	0.003	0.0002	0.1006	0.9389	0.1467
<i>Scarus ghobban</i>	0.0001	0.0001	0.0819	0.398	0.1534
<i>Stegastes arcifrons</i>	0.0006	0.0007	0.3763	0.24	0.6332
<i>Stegastes beebei</i>	0.0001	0.0007	0.5702	0.0002	0.1218
<i>Thalassoma lucasanum</i>	0.0001	0.0006	0.0648	0.0069	0.233

Table 6. Least Square Means Biomass Values of Most Abundant Species.

Species	Least Squares Means (gr)			
	Low Upwelling		High Upwelling	
	Warm	Cold	Warm	Cold
<i>Abudefduf troschelii</i>	91.05	100.80	15.85	15.85
<i>Anisotremus interruptus</i>	929.12	3,241.13	32.41	32.41
<i>Anisotremus scapularis</i>	0.00	0.00	1,099.98	1,111.68
<i>Bodianus diplotaenia</i>	15,578.08	13,167.19	6,189.51	3,964.07
<i>Bodianus eclancheri</i>	0.00	0.00	3,172.49	3,954.75
<i>Elacatinus nesiotus</i>	0.00	0.00	0.14	0.15
<i>Girella freminvilli</i>	0.00	1,446.24	1,463.46	4,252.65
<i>Halichoeres dispilus</i>	0.00	956.48	98.72	423.39
<i>Holacanthus passer</i>	2,022.27	2,022.27	511.89	1,042.73
<i>Lutjanus viridis</i>	3,690.09	2,728.26	1,775.68	13.87
<i>Mycteroperca olfax</i>	1,050.49	1,050.49	1,297.66	3,707.60
<i>Ophioblennius steindachneri</i>	454.52	603.95	21.79	99.62
<i>Paranthias colonus</i>	705.90	533.95	676.49	2,020.41
<i>Plagiotremus azaleus</i>	0.00	46.15	1.62	25.32
<i>Prionurus laticlavus</i>	21,921.00	50,540.08	548.02	1,242.19
<i>Scarus ghobban</i>	1,694.81	3,428.13	28.89	202.22
<i>Stegastes arcifrons</i>	209.30	144.40	19.47	0.00
<i>Stegastes beebei</i>	908.60	1,100.06	1,888.59	1,477.29
<i>Thalassoma lucasanum</i>	124.97	291.36	2.07	34.18

Table 7. Two-Way Analyses of Similarities (ANOSIM). Factor 1: Site (7 levels), Factor 2: Season (2 levels) (Av. R=0.467, p=0.001)

Group Comparison	R	Significance level
Bartolomé & Punta Cormorant	-0.125	0.849
Cabo Ibbetson & Punta Cormorant	0.042	0.319
Cabo Douglas & La Botella	0.167	0.086
Cabo Douglas & Cabo Ibbetson	0.667	0.057
Bartolomé & Cabo Ibbetson	0.266	0.051
Bartolomé & Punta Espinosa	0.297	0.040
Bartolomé & Punta Mangle	0.979	0.029
Punta Cormorant & Punta Mangle	0.896	0.029
Bartolomé & Cabo Douglas	0.823	0.029
Cabo Ibbetson & Punta Mangle	0.813	0.029
Cabo Douglas & Punta Espinosa	0.802	0.029
Punta Espinosa & Punta Mangle	0.750	0.029
Cabo Douglas & Punta Cormorant	0.667	0.029
La Botella & Punta Mangle	0.510	0.029
Punta Cormorant & Punta Espinosa	0.255	0.011
La Botella & Punta Espinosa	0.609	0.005
Cabo Ibbetson & La Botella	0.865	0.003
Cabo Ibbetson & Punta Espinosa	0.578	0.003
Bartolomé & La Botella	0.661	0.001
La Botella & Punta Cormorant	0.620	0.001

Table 8. SIMPER Analyses (Similarity Percentages) for Fish Functional Groups Between Sites.

Bartolomé & Cabo Douglas Av.Diss = 75.55%	Functional Group	Bartolomé	Cabo Douglas		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	35,429.42	260.88	49.88	3.35	66.02	66.02
	Invertivore	21,795.23	11,613.33	23.08	1.6	30.55	96.57
Bartolomé & Cabo Ibbetson Av.Diss = 46.28%	Functional Group	Bartolomé	Cabo Ibbetson		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	35,429.42	44,471.96	20.35	1.46	43.98	43.98
	Invertivore	21,795.23	36,501.06	16.94	1.17	36.61	80.59
Cabo Douglas & Cabo Ibbetson Av.Diss = 76.99%	Functional Group	Cabo Douglas	Cabo Ibbetson		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	260.88	44,471.96	46.91	1.78	60.94	60.94
	Invertivore	11,613.33	36,501.06	19.95	1.96	25.91	86.85
Bartolomé & La Botella Av.Diss = 63.29%	Functional Group	Bartolomé	La Botella		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	35,429.42	560.19	39.99	2.06	63.18	63.18
	Invertivore	21,795.23	9,822.66	17.62	1.48	27.83	91.02
Cabo Douglas & La Botella Av.Diss = 35.41%	Functional Group	Cabo Douglas	La Botella		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Invertivore	11,613.33	9,822.66	25.96	1.21	73.31	73,31
Cabo Ibbetson & La Botella Av.Diss = 69.14%	Functional Group	Cabo Ibbetson	La Botella		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	44,471.96	560.19	32.68	1.3	47.27	47,27
	Invertivore	36,501.06	9,822.66	24.52	1.99	35.46	82,73
Bartolomé & Punta Cormorant Av.Diss = 42.01%	Functional Group	Bartolomé	Punta Cormorant		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	35,429.42	44,382.89	24.96	1.22	59.41	59.41
	Invertivore	21,795.23	22,455.34	13.98	1.2	33.28	92.69
Cabo Douglas & Punta Cormorant Av.Diss = 74.22	Functional Group	Cabo Douglas	Punta Cormorant		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	260.88	44,382.89	46.99	2.44	63.31	63.31
	Invertivore	1,613.33	22,455.34	22.76	1.74	30.66	93.98
Cabo Ibbetson & Punta Cormorant Av.Diss = 46.39%	Functional Group	Cabo Ibbetson	Punta Cormorant		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	44,471.96	44,382.89	25.21	1.48	54.34	54.34
	Invertivore	36,501.06	22,455.34	12.73	1.16	27.43	81.77

La Botella & Punta Cormorant Av.Diss = 64.43%	Functional Group	La Botella	Punta Cormorant		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	560.19	44,382.89	38.5	1.43	59.75	59.75
	Invertivore	9,822.66	22,455.34	20.18	1.45	31.32	91.07
Bartolomé & Punta Espinosa Av.Diss = 45.56%	Functional Group	Bartolomé	Punta Espinosa		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	35,429.42	17,175.59	19.11	1.48	41.95	41.95
	Invertivore	21,795.23	10,898.93	9.73	1.23	21.35	63.31
	Omnivore	3,254.56	9,576.67	6.39	1.06	14.03	77.34
Cabo Douglas & Punta Espinosa Av.Diss = 76.81%	Functional Group	Cabo Douglas	Punta Espinosa		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	260.88	17,175.59	26.9	5.83	35.03	35.03
	Invertivore	11,613.33	10,898.93	14.68	1.76	19.11	54.14
	Piscivore	384.23	7,233.32	13.64	1.24	17.76	71.9
Cabo Ibbetson & Punta Espinosa Av.Diss = 55.74%	Functional Group	Cabo Ibbetson	Punta Espinosa		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	44,471.96	17,175.59	21.19	1.7	38.01	38.01
	Invertivore	36,501.06	10,898.93	19.72	1.41	35.37	73.38
La Botella & Punta Espinosa Av.Diss = 59.77%	Functional Group	La Botella	Punta Espinosa		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	560.19	17,175.59	23.74	1.86	39.71	39.71
	Omnivore	4,598.49	9,576.67	10.25	1.6	17.15	56.86
	Invertivore	9,822.66	10,898.93	9.35	1.35	15.64	72.49
Punta Cormorant & Punta Espinosa Av.Diss = 51.73%	Functional Group	Punta Cormorant	Punta Espinosa		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	44,382.89	17,175.59	22.48	1	43.45	43.45
	Invertivore	22,455.34	10,898.93	13.97	1.18	27	70.44
Bartolomé & Punta Mangle Av.Diss = 83.55%	Functional Group	Bartolomé	Punta Mangle		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	35,429.42	299.98	48.7	3.45	58.28	58.28
	Invertivore	21,795.23	4,015.83	23.45	1.65	28.07	86.35
Cabo Douglas & Punta Mangle Av.Diss = 55.63%	Functional Group	Cabo Douglas	Punta Mangle		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Omnivore	3,034.23	9,547.60	24.3	1.87	43.69	43.69
	Invertivore	11,613.33	4,015.83	22.03	0.95	39.6	83.29
Cabo Ibbetson & Punta Mangle Av.Diss = 78.98%	Functional Group	Cabo Ibbetson	Punta Mangle		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
Herbivore	44,471.96	299.98	46.36	1.79	58.69	58.69	

	Invertivore	36,501.06	4,015.83	21.02	2.46	26.61	85.3
La Botella & Punta Mangle Av.Diss = 48.42%	Functional Group	La Botella	Punta Mangle		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Omnivore	4,598.49	9,547.60	25.09	2.96	51.82	51.82
	Invertivore	9,822.66	4,015.83	13.39	1.4	27.66	79.48
Punta Cormorant & Punta Mangle Av.Diss = 80.17%	Functional Group	Punta Cormorant	Punta Mangle		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	44,382.89	299.98	45.97	2.39	57.34	57.34
	Invertivore	22,455.34	4,015.83	23.09	1.84	28.81	86.14
Punta Espinosa & Punta Mangle Av.Diss = 65.75%	Functional Group	Punta Espinosa	Punta Mangle		Diss/SD	Contrib%	Cum.%
		Av.Biom	Av.Biom	Av.Diss			
	Herbivore	17,175.59	299.98	26.26	6.31	39.94	39.94
	Piscivore	7,233.32	2,564.28	11.89	1.17	18.09	58.03
	Invertivore	10,898.93	4,015.83	11.41	1.36	17.35	75.37

Av.Biom = mean biomass; Av.Dis = mean dissimilarities; SD = standard deviation; Contrib/Cum % = proportional or cumulative contribution of a particular functional group to the average dissimilarity between sites, respectively. All analyses were run by calculating Bray-Curtis similarities and by estimating fish biomass based on the allometric function $W=aTLb$.

FIGURES

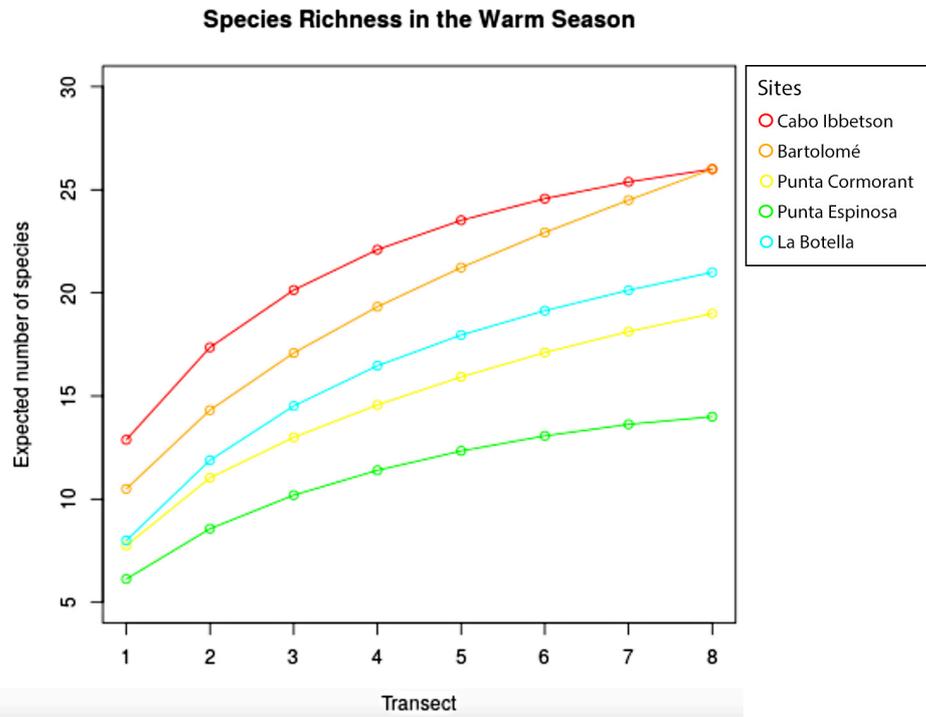


Figure 1. Fish Species Accumulation Curves per Site for the Warm Season using Rarefaction methods.

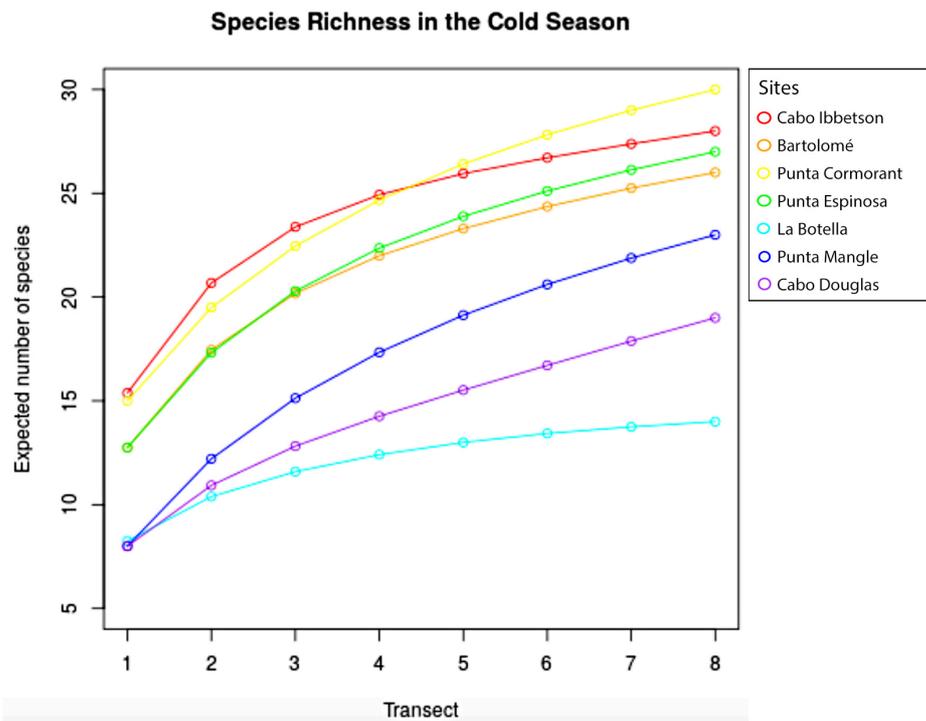


Figure 2. Fish Species Accumulation Curves per Site for the Cold Season using Rarefaction methods.

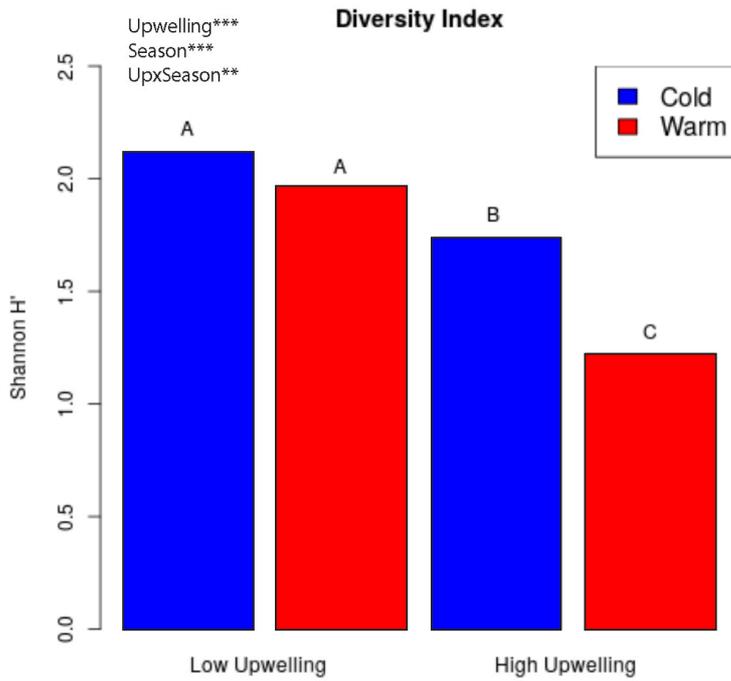


Figure 3. Two-Way ANOVA for Species Diversity Index. The x-axis represent sites with Low and High Upwelling. The * represent the significance for each factor. The letters represent the significant differences between groups ($P < 0.05$, Tukey HSD Test).

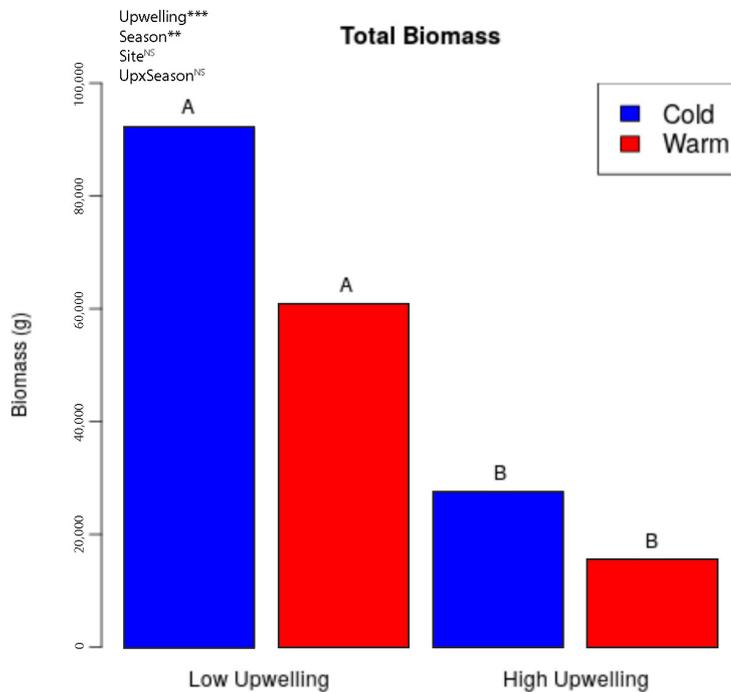


Figure 4. Three-Way ANOVA for Total Biomass. The x-axis represents sites with Low and High Upwelling. The * represent the significance for each factor and ^{NS}= not significant. The letters represent the significant differences between groups ($P < 0.05$, Tukey HSD Test)

Non-metric MDS

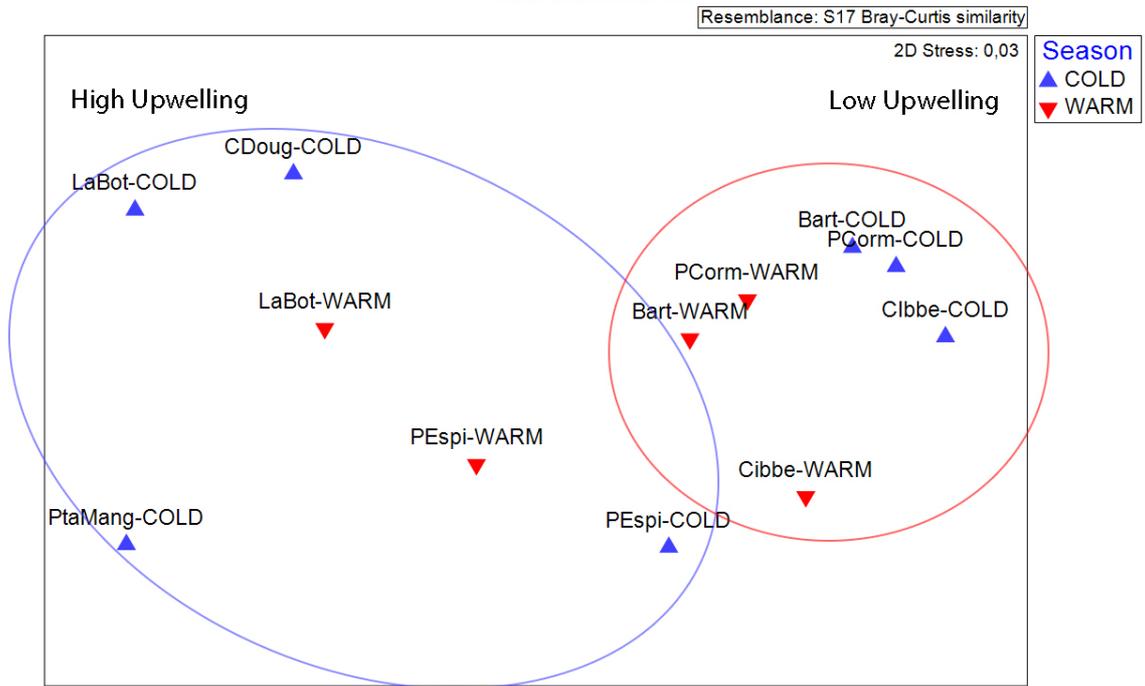


Figure 5. Non-metric Multidimensional Scaling Analysis (nMDS) for fish functional groups across study sites and seasons.

Group average

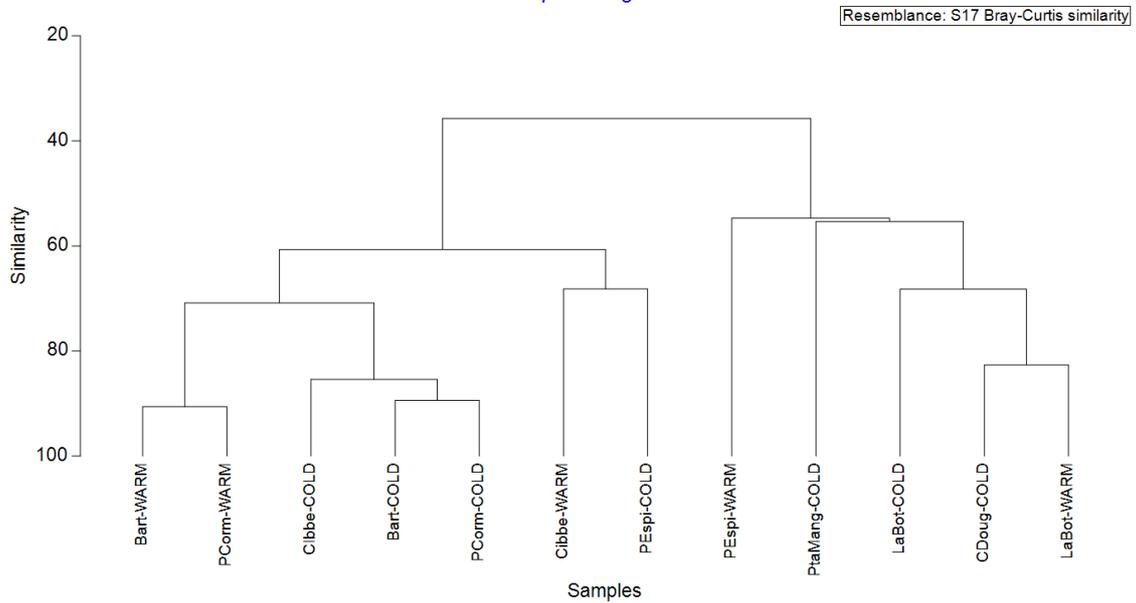


Figure 6. Cluster Analysis for fish functional groups across study sites and seasons.