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Spatiotemporal Variation of an Eastern Tropical Pacific Pelagic Community Assessed With Free-Drifting Bruvs

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Thesis of Tyler Stephen Plum

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Biological Sciences

Nova Southeastern University
Halmos College of Arts and Sciences

December 2021

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

SPATIOTEMPORAL VARIATION OF AN EASTERN TROPICAL PACIFIC
PELAGIC COMMUNITY ASSESSED WITH FREE-DRIFTING BRUVS

By

Tyler Stephen Plum

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Biological Sciences

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Abstract

Information about pelagic community diversity and ecology generally lags far behind that of coastal communities, and largely derives from fisheries data that do not reflect small and non-target species. We describe spatiotemporal vertebrate species diversity and variability over a 3,486 km² area of highly productive pelagic marine ecosystem in Pacific Panama using drifting baited remote underwater video stations (BRUVS), a non-invasive fishery-independent sampling technique. We observed 26 taxa from 17 families, including 1 mammal, 3 reptile, 5 elasmobranch, and 17 teleost species. Community assemblages differed on and off the continental shelf and between wet (April – December) and dry (January – March) seasons but did not vary between sampling depths (10 and 40 m). Seasonal differences were largely driven by the relative abundance of three genera of small zooplanktivorous fish: *Psenes*, *Decapterus*, and *Caranx*. Their abundance was greatest in the wet season, lagging peak plankton production in the dry season, and each species was more abundant off the continental shelf. *Psenes* and juvenile *Caranx* were rare during the dry season, and while *Decapterus* abundance decreased in the dry season, they remained along the edge of the shelf year-round. Despite sampling for ~260 h in a highly productive area known for high fish abundance, we did not fully capture the system's expected vertebrate richness. Differences between expected and observed richness suggest future pelagic BRUVS studies should increase recording time and sample size, especially in less productive systems. Our study demonstrates the practical application of free-drifting BRUVS to detect environmentally driven changes in pelagic communities and fill knowledge gaps in data-limited regions.

Keywords: BRUVS, fishery-independent, forage fish, spatiotemporal

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Introduction

The Eastern Tropical Pacific is a highly productive region comprising the exclusive economic zones of four Central and South American countries (Miloslavich et al. 2011) and heavily fished international waters. The welfare of this seascape is currently of intense international interest, with pledges at the 26th Conference of the Parties to the United Nations Framework Convention on Climate Change (COP26, Oct 31-Nov 12, 2021) made by the governments of Panama, Ecuador, Colombia and Costa Rica to jointly create massive marine protected areas for this biodiverse region that is undergoing a high level of illegal, unreported and unregulated (IUU) fishing (Arias & Pressley 2016). Productivity in the Eastern Tropical Pacific varies seasonally, driven by offshore upwelling of cold, nutrient-rich water that is pushed towards the coast by prevailing winds and subsurface currents combined with rain-driven iron-rich sediment discharge into coastal waters during the wet season (April – December) (Pennington et al. 2006, Fiedler & Lavín 2017, Miloslavich et al. 2011). This combination of factors creates favorable conditions for phytoplankton production, which forms the foundation for complex and diverse coastal and pelagic food webs (Barber & Smith 1983, Barber & Chavez 1986, Johnson et al. 1999, Pennington et al. 2006, Miloslavich et al. 2011).

The pelagic ecosystem off Pacific Panama appears to be especially productive, particularly in the vicinity of Piñas Bay (7.583°, -78.200°) in southern Panama. The area surrounding Piñas Bay boasted the highest catch of yellowfin tuna for Panama's industrial large-body pelagic fishery at its inception during the 1970's (Bullis & Klima 1972). The high abundance and year-round presence of large yellowfin tuna *Thunnus albacares*, dolphinfish *Coryphaena hippurus*, sailfish *Istiophorus platypterus*, blue marlin *Makaira nigricans*, and black marlin *Istiompax indica* near Piñas Bay also led to the establishment of a sportfishing lodge where many recreational angling records have been set (R. White, personal communication, igfa.org/world-records). Currently, the area supports commercial and artisanal longline fisheries for large-bodied pelagic fishes including tuna and dolphinfish, as well as nearshore artisanal fisheries targeting carangids (Mair et al. 2012).

Despite the large amount of fishing that occurs in these waters, little is known about the pelagic ecosystem of this area. Fishery-independent surveys of Pacific Panama have been limited to marine mammals, sea turtles, and planktonic larvae, and no recent fishery-independent surveys of pelagic fish biodiversity exist for the area off Piñas Bay (Olson & Watters 2003,

Vilchis et al. 2009, Martin et al. 2016, Lennert-Cody et al. 2018). Although pelagic fish communities may be partially described through fisheries data, these data are typically biased because of inconsistent reporting procedures and the fishing gear used (Mair et al. 2012, Harper et al. 2014, Cisneros-Montemayor et al. 2018, but also see Lezama-Ochoa et al. 2017). For example, shallow-set longlines, the predominant fishing gear used off Panama, are biased against gape-limited species (e.g., small forage fish), and therefore these species are underrepresented in the catch of Panamanian fisheries. Understanding the dynamics of these small fish species is crucial because they are important prey to the large predatory species that support both recreational and commercial fisheries in the region and are themselves a valuable food source to local communities.

Baited remote underwater video stations (BRUVS) are a fishery-independent, non-extractive sampling method that offers a means to fill biodiversity information gaps that exist in fishery-dependent assessments (Cappo et al. 2004, Espinoza et al. 2014, Whitmarsh et al. 2017; Meeuwig et al. 2021). By passively recording species attracted to both bait plumes and structure, BRUVS can capture the relative abundance of multiple functional groups, including gape-limited, planktivorous, and filter-feeding species for a more comprehensive description of aquatic communities. Additionally, technological improvements in camera technology have made it economically feasible to quickly deploy multiple stations across a large geographic area, increasing both geographic range and spatial resolution of biodiversity data (Mallet & Pelletier 2014). Although stationary, benthic positioned BRUVS are now widely used to characterize biodiversity in coastal habitats, while the use of non-anchored BRUVS to survey biodiversity and community dynamics in the pelagic realm is comparatively sparse (Meeuwig et al. 2021).

Considering the present absence of a fishery-independent, diversity and community assemblage view of large pelagic vertebrates in Pacific Panama, we used drifting midwater BRUVS to survey the pelagic vertebrate community across 3,486 square kilometers of the waters surrounding Piñas Bay, Panama, an area known for high predator abundance. Specifically, our objectives were to: 1) describe the pelagic vertebrate assemblage, 2) describe changes in pelagic assemblages with depth, season, and location relative to the continental shelf, and 3) identify environmental drivers that best explain patterns in pelagic vertebrate biodiversity.

Materials and Methods

Field sampling and video processing

This study was conducted off Pacific Panama near Piñas Bay, ~ 48 km northwest of the Panama-Colombia border (Figure 1). The area is characterized by a continental shelf (50 – 250 m in depth) that narrows in width from north to south, thinning from ~ 42 km off Piñas Bay to ~ 5 km at the Colombian border. Sampling of the pelagic community occurred within a 48-km radius of Piñas Bay, over an area covering 3,486 km², with a ~ 2 km buffer between the sampling area and the coast (Figure 1). Samples were collected in 2019 and 2020 during the region's wet (August – October) and dry (January – March) seasons. Sampling locations were generated using a generalized randomized tessellated sampling design to sample spatial gradients while limiting between-point variance and spatial autocorrelation. This design spatially balances points over an area while maintaining statistical qualities of a random design (Stevens & Olsen 2004, Bouchet & Meeuwig 2015).

At each location the vertebrate assemblage was non-invasively sampled using free-drifting, pelagic baited remote underwater video stations (BRUVS). Each BRUV sampling unit comprised a floating longline with three video stations separated by 200 m to ensure independence. Each video station consisted of a GoPro Hero 4 Black camera in a GoPro Super Suit dive housing affixed to a weighted aluminum frame. Cameras were set to Auto ISO and Auto White Balance, while recording in 1080p at 60 frames a second. A bait-arm filled with ~1 kg of chopped, fresh black skipjack *Euthynnus lineatus* or Pacific sierra *Scomberomorus sierra*, or thawed black skipjack, extended 120 cm in front of each camera. Each sampling unit was set to capture video at a depth of either 10 or 40 m to assess assemblages near the surface or thermocline, respectively, and set adrift for 2 h.

Video footage from each sampling unit was pooled and observed individuals were identified to the lowest possible taxonomic unit. Richness (S), the count of unique taxonomic units, and MaxN, the maximum number of individuals of a taxonomic unit in a video frame at one time, were recorded. MaxN is the most commonly used metric to conservatively estimate relative abundance in BRUVS footage (Cappo et al. 2004, Whitemarsh et al. 2017). Although, MaxN tends to undercount relative abundance, especially when abundance is high in the frame (e.g. a large school of fish), it is weighted towards less abundant (i.e. rare) taxonomic units and reliably avoids over-counting (Whitemarsh et al. 2017). To determine efficacy of sampling effort

for describing assemblages, accumulation curves of taxonomic units identifiable to the species level were generated from 1000 random permutations of the data. Expected species richness was also calculated using the Chao2 estimator in the R package *vegan* (Oksanen et al. 2020).

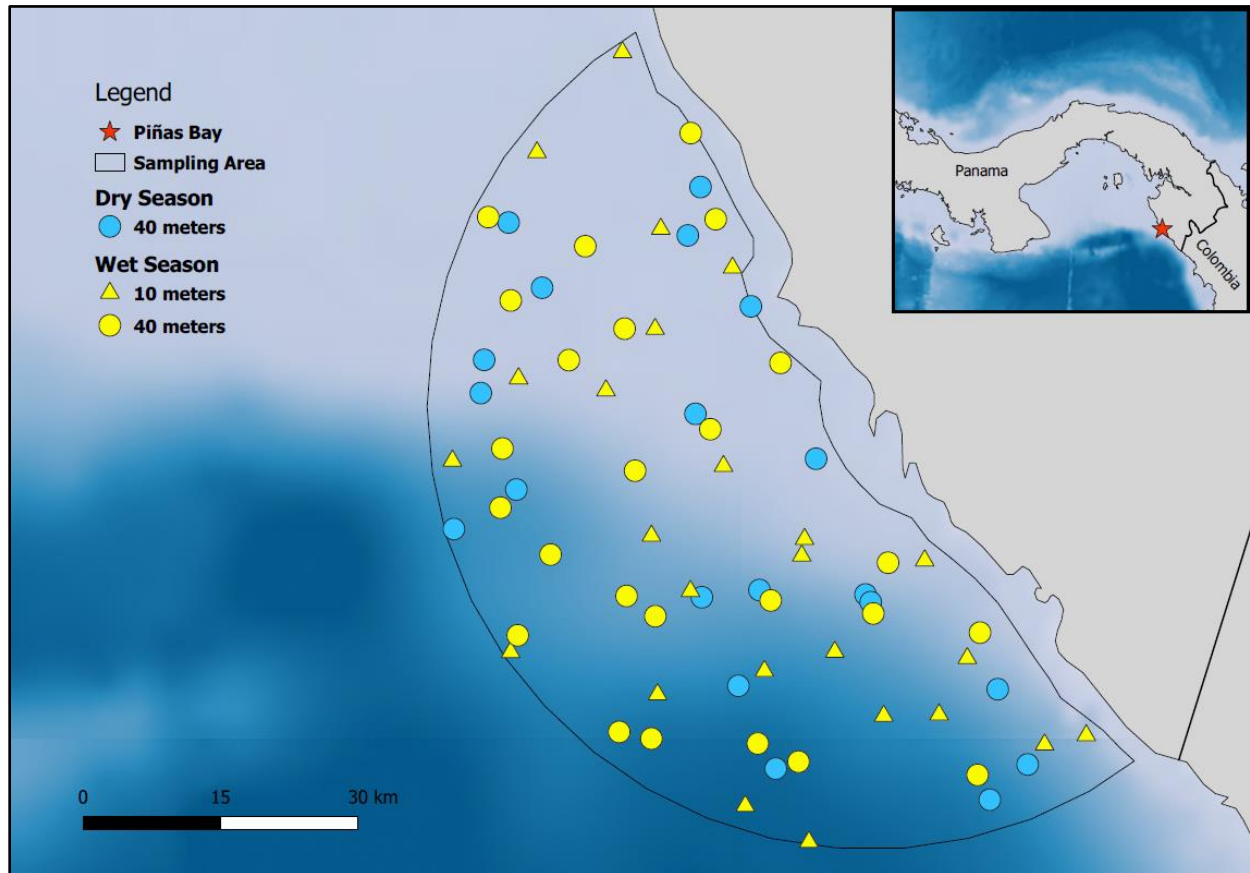


Figure 1. Map of the study area surrounding Piñas Bay, Panama. Circle and triangle symbols show locations for each BRUVS sampling unit by season and deployment depth.

Spatiotemporal environmental patterns

Environmental data for each sampling location was obtained in the field or from remotely sensed or modelled data products. Vertical water clarity was estimated using a secchi disk after each sampling unit was deployed. Seafloor depth was extracted from the ETOPO1 1-arc minute global relief model. Salinity and potential sea water temperature at 10 and 40 m depths were obtained from the daily Copernicus Marine Service Global Ocean 1/12° Physics Analysis and Forecast data product (Copernicus Marine Service 2021). We obtained monthly estimates of sea surface temperature and net primary productivity from the 0.25° Daily Optimum Interpolation Sea

Surface Temperature and Primary Productivity Aqua MODIS NPP Global 2003-present EXPERIMENTAL datasets, respectively (Huang et al. 2020, NOAA NMFS 2020). Gaps in a product's coverage were filled using inverse distance-weighted interpolation in the R package *meteo* (Kilibarda et al. 2014, 2015). Additionally, distance from shore (km) for each sample location was measured in QGIS v3.6.0. To examine relationships between sample locations and normalized environmental characteristics, principal component analysis was performed using the software package PRIMER-e v7.

Vertebrate Assemblage patterns

Taxonomic assemblages were defined by crossing the spatiotemporal factors season (wet or dry), location relative to shelf (on or off), and sampling depth (10 m or 40 m). Due to the high number of indistinguishable, small-bodied teleost congeners observed, all taxonomic units were collapsed to the genus level for the following analyses. Patterns in beta diversity between assemblages were investigated by comparing the relative contributions of genera turnover and nestedness. Beta diversity can be considered a comparison of diversity between two assemblages. Turnover is the replacement of genera between assemblages, whereas nestedness reflects the degree to which one assemblage is a subset of another (Baselga 2010). Turnover was calculated using Simpson's dissimilarity index (β_{SIM}), and because the Sorensen's dissimilarity index (β_{SOR}) represents the sum of nestedness and turnover, nestedness (β_{NES}) was calculated as the difference between the two: $\beta_{NES} = \beta_{SOR} - \beta_{SIM}$ (Baselga 2010).

To compare the composition between assemblages, we used PERMANOVAs. First, MaxN data were square root transformed to down-weight highly abundant genera and reduce heterogeneity of variances. The transformed data were then used to create a Bray-Curtis-Dissimilarity matrix on which two-way PERMANOVAs (9,999 permutations) were used to test for assemblage differences. If differences in assemblages were detected, similarity percentage (SIMPER) analyses were performed to determine the contribution of each genus to the dissimilarities.

Drivers of distribution patterns

The BEST Bio-Env routine was used to identify environmental variables that best explained the patterns in the relative abundance data by linking the Bray-Curtis dissimilarity matrix of

assemblages to a Euclidian matrix of environmental data. Environmental data were normalized prior to constructing the Euclidian distance matrix. BEST Bio-Env models were run using 9,999 permutations.

Generalized linear and additive models (GLMs, GAMs) were used to identify environmental variables associated with presence and relative abundance of the genera identified by SIMPER as contributing the most to dissimilarities between assemblages. Because occurrence and relative abundance of a genus may be driven by different processes, we used a two-step modeling process. First, logistic GLMs using a binomial error distribution with a logit link were used to model genera presence/absence. Then, to identify environmental variables that explained patterns in relative abundance we used vector GAMs with a positive Poisson error distribution with a log link on the zero-truncated dataset. For each set of models, the full model tested included all explanatory variables that were significant when tested in isolation. Logistic models were built within the R package *mgcv* (Wood 2017). To accommodate positive Poisson models, relative abundance GAMs were modeled in the R package *VGAM* (Yee 2021). Statistical significance of categorical predictors in *VGAM* was determined by whether the 95% confidence levels of one or more levels included zero. Residuals of resulting models were examined visually and observed deviations tested non-parametrically using the R package *DHARMA* (Hartig 2020).

Statistical analyses were carried out in the R open-source computing software v4.0.3 (R Core Team 2020) and PRIMER-e v7 with PERMANOVA+ add-on (Clarke & Gorley 2015).

Results

Sampling Effort

Sixty-nine sampling units (each a floating longline of three BRUVS) were deployed over the duration of this study (Table 1). Sampling for the 2020 dry season was prematurely terminated because of the SARS-CoV-2 global pandemic, with only samples at 40 m depth collected. Recording times of individual cameras across sampling depths and seasons were variable, so recording times were standardized by censoring footage to the shortest recording time, 1.25 h, resulting in 3.75 h of footage per sampling unit. Overall, 258.75 h of video were retained for analysis. From this footage 26 vertebrate species from 17 families were observed and one additional species of teleost and family were observed in censored footage (Table 1). While teleost fishes were the most commonly seen vertebrates, 1 mammal, 3 reptile, and 5

elasmobranch species were also observed. Three genera of teleost fishes, *Decapterus*, *Psenes*, and *Caranx*, were the most commonly observed species. *Decapterus* and *Psenes* were mostly adults while the majority of the *Caranx* were determined to be juvenile green jack *Caranx caballus*. Species accumulation curves were generated for each season on the censored data, and neither curve plateaued (Figure 2). Expected species richness in the dry season assemblage ($S_{Chao2} = 27.2$) was greater than the wet season ($S_{Chao2} = 24.94$), though observed richness was greater in the wet season ($S_{Wet} = 22$, $S_{Dry} = 12$). Overall observed richness ($S = 26$) was less than expected ($S_{Chao2} = 32.31$).

Table 1. Occurrence and percent frequency (in parentheses) of vertebrate species by season, deployment depth, and location. Individuals unable to be identified to species level are designated “Unknown.” Species with an * were observed outside the time limit and were not included in analyses. n indicates the number of longline BRUV sets (i.e., sampling units) performed in that category.

Class	Family	Scientific name	Common name	MaxN	Wet				Dry		Total (n=68)
					10 m		40 m		40 m		
					On Shelf (n = 10)	Off Shelf (n = 14)	On Shelf (n = 11)	Off Shelf (n = 13)	On Shelf (n = 9)	Off Shelf (n = 11)	
Mammalia	Delphinidae	<i>Stenella attenuata</i>	Pan-tropical spotted dolphin	34			1 (9.1%)		3 (33.3%)		4 (5.9%)
Reptilia	Chelonidae	<i>Chelonia mydas</i>	Green sea turtle	1		1 (7.1%)		1 (7.7%)			2 (2.9%)
		<i>Lepidochelys olivacea</i>	Olive Ridley sea turtle	1			2 (18.2%)	1 (7.7%)	1 (11.1%)		4 (5.9%)
		Unknown		1		2 (14.3%)	2 (18.2%)			4 (5.9%)	
	Elapidae	<i>Pelamis platura</i>	Yellow-bellied sea snake	1			2 (18.2%)	1 (7.7%)			3 (4.4%)
Actinopterygii	Balistidae	<i>Canthidermis maculata</i>	Rough triggerfish	1	2 (20%)						2 (2.9%)
	Carangidae	<i>Alectis ciliaris</i>	African pompano	1				1 (7.7%)		2 (18.2%)	3 (4.4%)

	<i>Caranx caballus</i>	Green jack	25	3 (30%)	6 (42.9%)	2 (18.18%)	7 (53.9%)			18 (26.5%)
	<i>Decapterus macarellus</i>	Mackerel scad	38		3 (21.4%)		1 (7.7%)			4 (5.9%)
	<i>Decapterus spp.</i>	Scads	71	1 (10%)	8 (57.1%)	1 (9.1%)	6 (46.2%)	4 (44.4%)	2 (18.2%)	22 (32.4%)
	<i>Naucrates ductor</i>	Pilot fish	7				5 (38.5%)			5 (7.4%)
	<i>Selene brevoortii</i>	Mexican lookdown	1					1 (11.1%)		1 (1.5%)
	Unknown		18	4 (40%)	3 (21.4%)	2 (18.2%)	2 (15.4%)	4 (44.4%)	5 (45.5%)	20 (29.4%)
Coryphaenidae	<i>Coryphaena hippurus</i>	Common dolphinfish	1	1 (10%)	2 (14.3%)		1 (7.7%)		1 (9.1%)	5 (7.4%)
Echeneidae	<i>Echeneis naucrates</i>	Sharksucker	1	1 (10%)						1 (1.5%)
Fistulariidae	<i>Fistularia commersonii</i>	Common cornetfish	2		1 (7.1%)		1 (7.7%)		3 (27.3%)	5 (7.4%)
Istiophoridae	<i>Makaira nigricans</i>	Blue marlin	1	1 (10%)			1 (7.7%)			2 (2.9%)
	<i>Istiophorus platypterus</i>	Sailfish	1	1 (10%)	1 (7.1%)	1 (9.1%)	4 (30.8%)		1 (9.1%)	8 (11.8%)
	<i>Istiompax indica</i>	Black marlin	1	2 (20%)						2 (2.9%)
Monacanthidae	<i>Aluterus monoceros*</i>	Unicorn filefish*	1							0 (0%)

Chondrichthyes	Nomeidae	<i>Aluterus scriptus</i>	Scrawled filefish	1	2 (20%)	1 (7.14%)				3 (4.4%)	
		<i>Psenes cyanophrys</i>	Freckled driftfish	49	5 (50%)	6 (42.9%)	1 (9.1%)	9 (69.2%)	1 (11.1%)	1 (9.1%)	23 (33.8%)
	Scombridae	<i>Euthynnus lineatus</i>	Striped bonito	1					1 (11.1%)		1 (1.5%)
		<i>Thunnus albacares</i>	Yellowfin tuna	13		1 (7.1%)	2 (18.2%)		1 (11.1%)		4 (5.9%)
		Tetraodontidae	<i>Arothron hispidus</i>	White-spotted puffer	1			1 (9.1%)			
	Carcharhinidae		<i>Carcharhinus falciformis</i>	Silky shark	1		1 (7.1%)		2 (15.4%)		
		<i>Carcharhinus limbatus</i>	Blacktip shark	1			1 (9.1%)				1 (1.5%)
		Dasyatidae	<i>Pteroplatytrygon violacea</i>	Pelagic ray	1						1 (9.09%)
	Myliobatidae	<i>Rhinoptera steindachneri</i>	Pacific cownose ray	1			1 (9.1%)				1 (1.5%)
		Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead	1	1 (10%)					1 (9.1%)

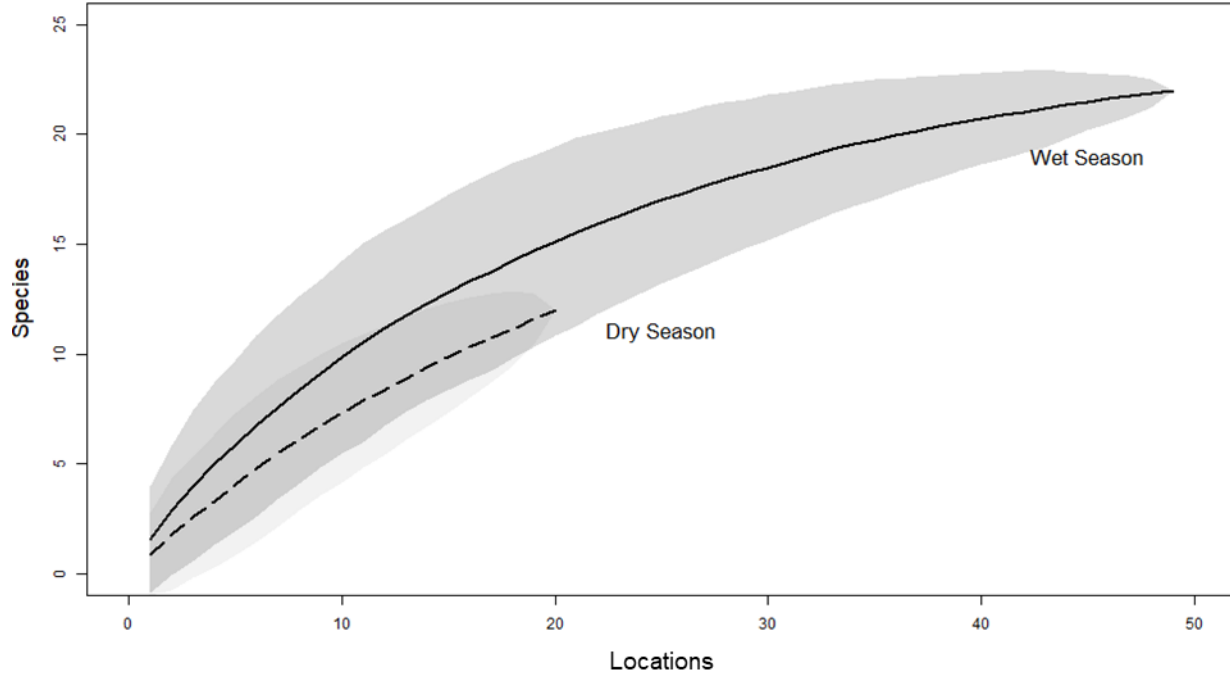


Figure 2. Species accumulation curves for each season. Shaded areas for each curve represent 95% confidence intervals.

Spatiotemporal environmental patterns

Principal components analysis revealed clear separation of sample units into distinct environmental variable-associated, spatiotemporal clusters (Figure 3). PC1 separated samples by sea surface temperature (SST), temperature at sampling depth, log-transformed net primary productivity, and salinity. These variables fluctuate temporally across the year and separated sample units by season and depth. The wet season was characterized by low net primary productivity, low salinity, high temperature at sampling depth and high SST (Table 2).

Conversely, the dry season was characterized by high net primary productivity and salinity and low temperature at depth and SST (Table 2). Along PC2, sites also separated by distance from shore, seafloor depth, and to a lesser extent, vertical water clarity (Figure 3, Table 2).

Table 2. Means and ranges of environmental variables by season.

Environmental Variable	Wet		Dry	
	Mean	Range	Mean	Range
Productivity (log mg C m ⁻² day ⁻¹)	2.69	2.57 – 2.84	3.11	2.89 – 3.42
Salinity (ppt)	32.66	30.40 – 34.78	35.07	34.95 – 35.17
Temperature at Sampling Depth (°C)	26.07	20.96 – 28.50	16.03	15.39 – 16.84
Sea Surface Temperature (°C)	27.86	27.16 – 28.49	24.78	22.42 – 26.68
Distance from Shore (km)	21.38	3.49 – 45.55	19.42	2.30 – 42.66
Seafloor depth (m)	1274.29	63.00 – 3374.00	1139.95	75.00 – 3291.00

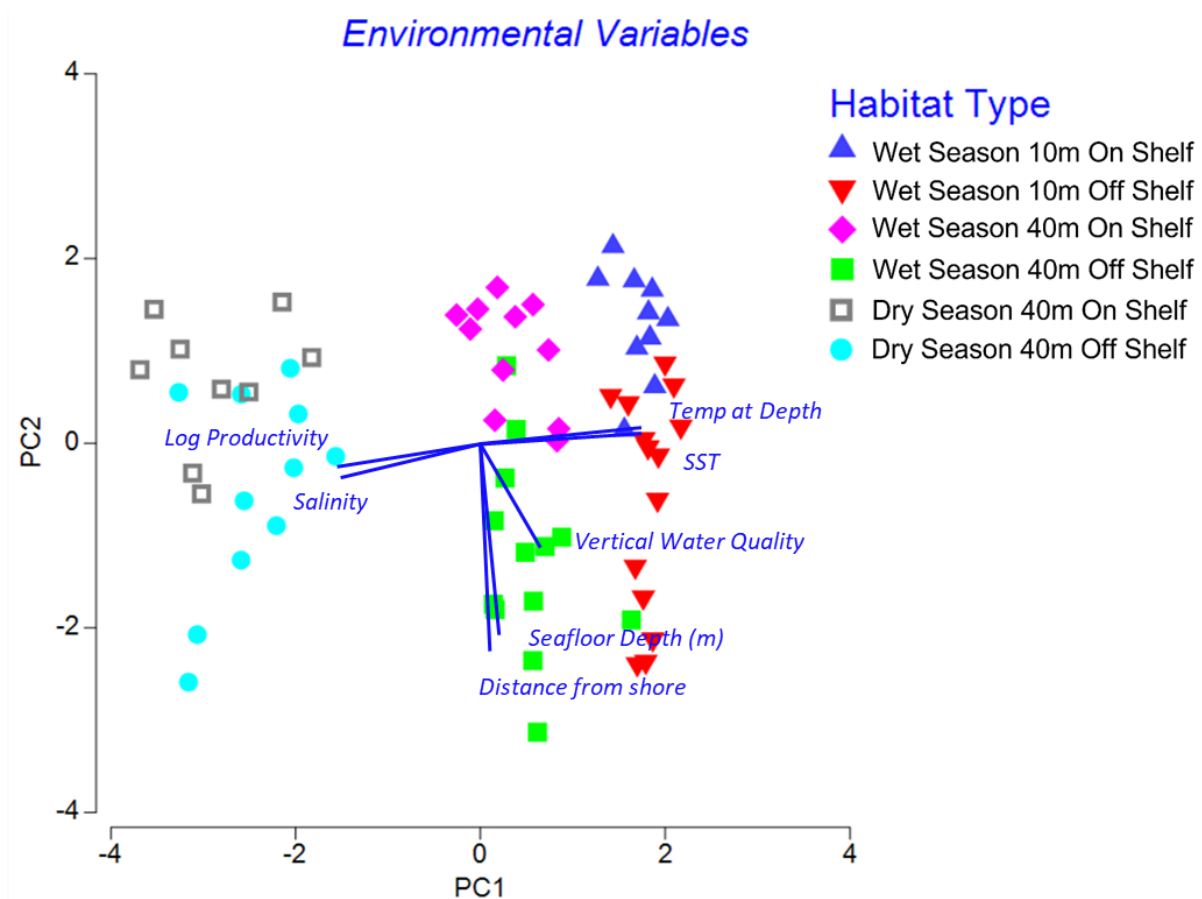


Figure 3. Principal component analysis of normalized Euclidian-treated environmental variables showing clustering by spatiotemporal combination.

Vertebrate Assemblage Patterns

Beta diversity was primarily driven by genera turnover. Beta diversity between sampling depths in the wet season was almost entirely the result of turnover, i.e., almost all genera lost from one depth were replaced in the other ($\beta_{NES} = 0.09$, $\beta_{SIM} = 0.29$). Similarly, beta diversity across seasons at 40 m displayed modest turnover and low nestedness ($\beta_{NES} = 0.13$, $\beta_{SIM} = 0.33$). Beta diversity across shelf locations at 40 m followed a similar pattern, with nearly all lost genera being replaced ($\beta_{NES} = 0.09$, $\beta_{SIM} = 0.60$).

Pelagic vertebrate assemblages at 40 m varied across seasons (Two-way PERMANOVA, $Pseudo-F_{1,35} = 2.4306$, $P < 0.05$) and location relative to the shelf (Two-way PERMANOVA, $Pseudo-F_{1,35} = 2.0765$, $P < 0.05$) (Figure 4). Within the wet season, assemblages on and off the shelf differed (Two-way PERMANOVA, $Pseudo-F_{1,43} = 2.754$, $P < 0.05$), but did not differ between depths (Two-way PERMANOVA, $Pseudo-F_{1,43} = 1.1536$, $P = 0.32$) (Figure 4).

Decapterus, *Psenes*, and *Caranx* were the three most abundant genera contributing ~ 45% of the cumulative total dissimilarities in both SIMPER analyses. The relative abundance of these genera primarily drove the dissimilarity between assemblages for shelf locations and seasons (Table 3). Each of these three genera was consistently more abundant off the shelf within the wet season. In the dry season, *Psenes* and *Caranx* virtually disappeared while *Decapterus* occurrence decreased (Table 1). The BEST analysis indicated that the overall pelagic fish assemblage composition showed a weak correlation with SST ($\rho = 0.246$, $P < 0.05$).

Table 3. Similarity percentage analysis of spatiotemporal factors Season and Shelf location at 40 m. Genera contributions are ordered greatest-to-least. Average square root abundance, percent contribution to dissimilarity, and cumulative percent contribution values are provided for each genus.

Genera	Wet Season	Dry Season	Contrib %	Cum.%
	Av. Sqrt. Abund	Av. Sqrt. Abund		
<i>Decapterus</i>	0.76	1.66	22.74	22.74
<i>Psenes</i>	1.13	0.18	15.47	38.21
<i>Caranx</i>	0.63	0.00	9.42	47.63
Genera	On Shelf	Off Shelf	Contrib %	Cum.%
	Av. Sqrt. Abund	Av. Sqrt. Abund		
<i>Decapterus</i>	1.04	1.20	20.59	20.59
<i>Psenes</i>	0.17	1.18	15.49	36.08
<i>Caranx</i>	0.13	0.57	8.68	44.77

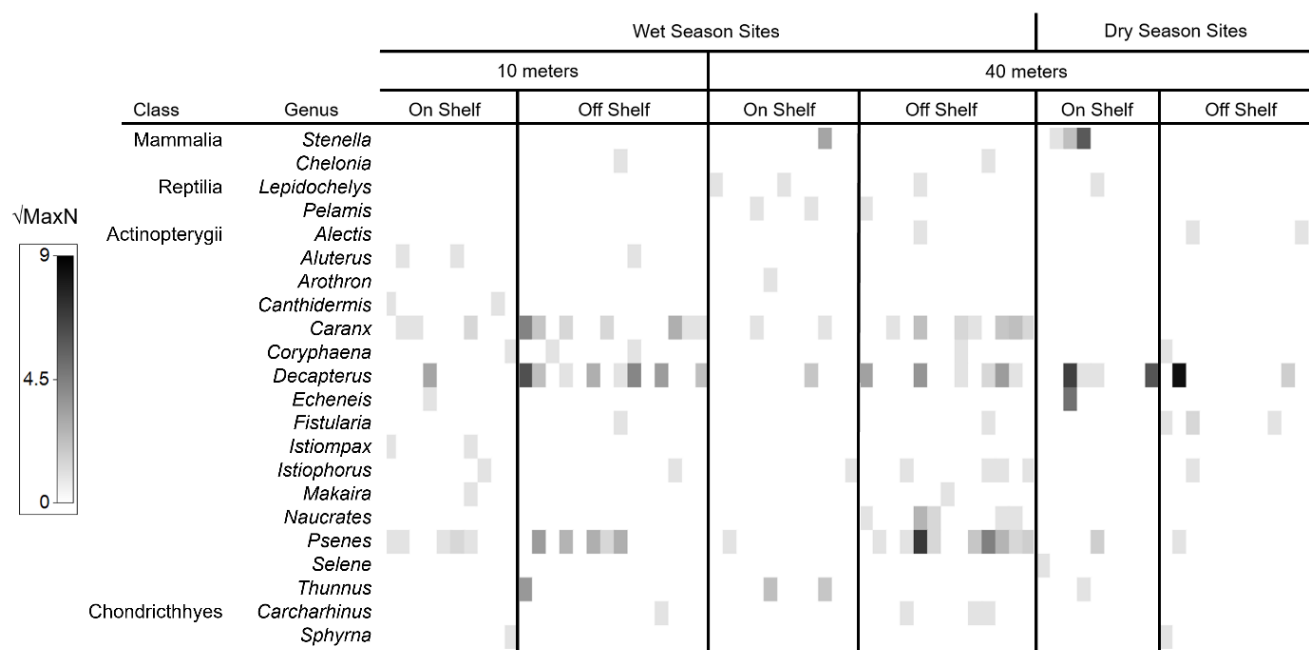


Figure 4. Shade plot showing square root transformed relative abundance (MaxN) of genera, per sampling unit, organized by spatiotemporal combinations of factors.

Drivers of distribution patterns

Because *Psenes*, *Caranx*, and *Decapterus* contributed the most to the dissimilarities between assemblages, their presence and abundance were modeled with environmental variables. *Psenes* were more common in warmer water, as probability of occurrence increased with SST, and few were observed below 26°C SST ($P < 0.05$, adjusted explained deviance = 8.64%) (Figure 5). *Psenes* relative abundance was also related to SST, distance from shore, vertical water clarity, and location relative to the shelf ($P < 0.05$, explained deviance = 69%) (Figure 6, 7). Higher *Psenes* relative abundance was associated with increasing SST above 26.5°C (predictions of increasing abundance below 26°C were based on a single school of fish). Relative abundance decreased with distance from shore until ~20 km and then increased. Increased abundance under 20 km from shore is based on the observation of two large schools close to shore but off the shelf. *Psenes* were most abundant in waters with 6–11 m of vertical clarity. In addition, locations off the continental shelf had higher relative abundances of *Psenes* than those on the shelf (Figure 7). *Caranx* were not observed in the dry season, but they were more common at higher SST in the wet season ($P < 0.05$, adjusted explained deviance = 18.51%) (Figure 5). Location relative to the shelf was the only significant predictor for *Caranx* relative abundance ($P < 0.05$, explained deviance = 59.23%), with relative abundance higher in locations off the continental shelf (Figure 6, 7). *Decapterus* were more common farther from shore ($P < 0.05$, adjusted explained deviance = 12.03%) (Figure 5, 7). *Decapterus* relative abundance was related to SST, distance from shore, and vertical water clarity ($P < 0.05$, explained deviance = 60.84%) (Figure 6). *Decapterus* were most abundant at SST ~25.5°C and decreased sharply until 28°C. *Decapterus* were more abundant inshore and decreased until ~25 km offshore, likely explained by the observation of two large schools inshore. Relative abundance was greatest at vertical clarity <6 m and >10 m.

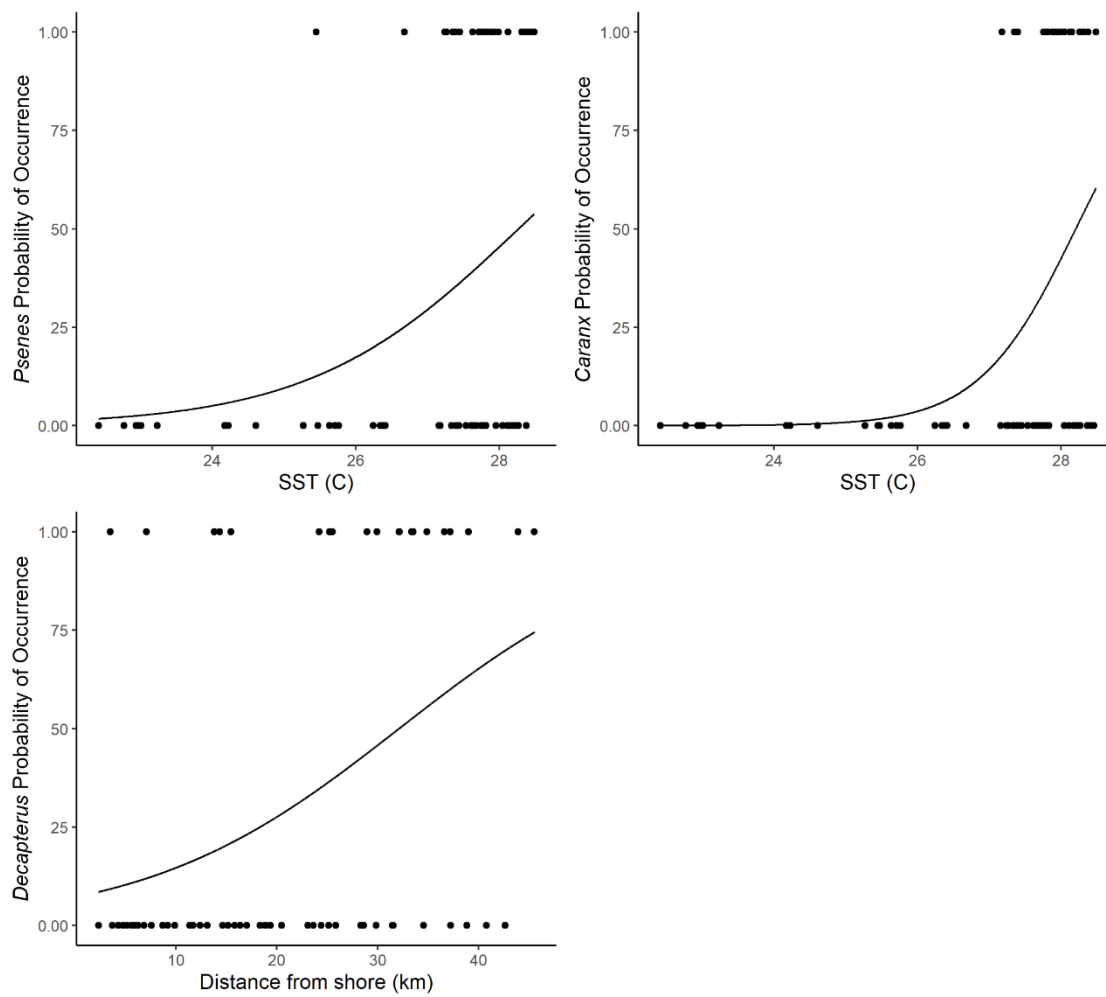


Figure 5. Probability of occurrence plots for environmental predictors with the greatest influence on each genus from logistic regressions.

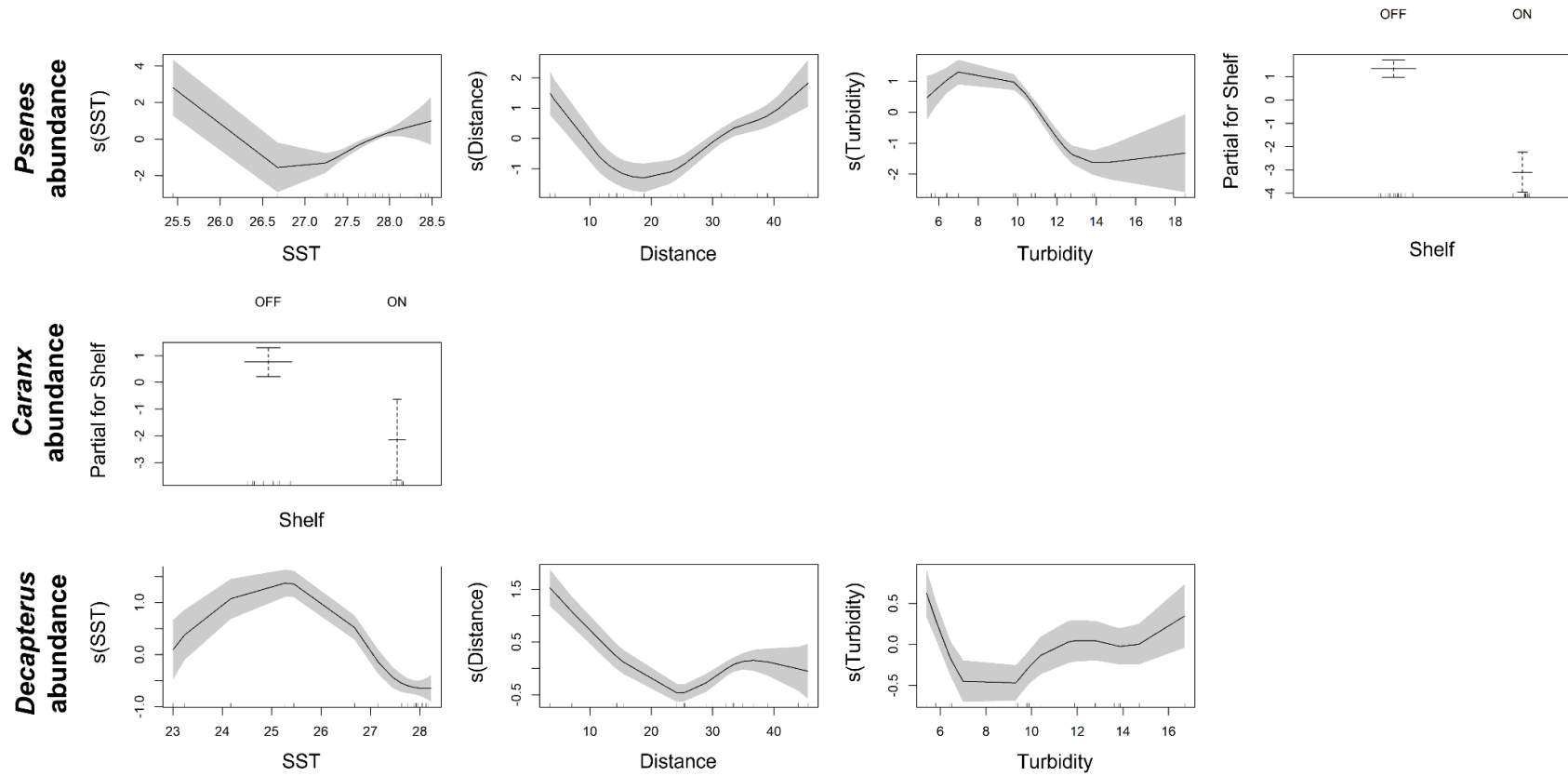
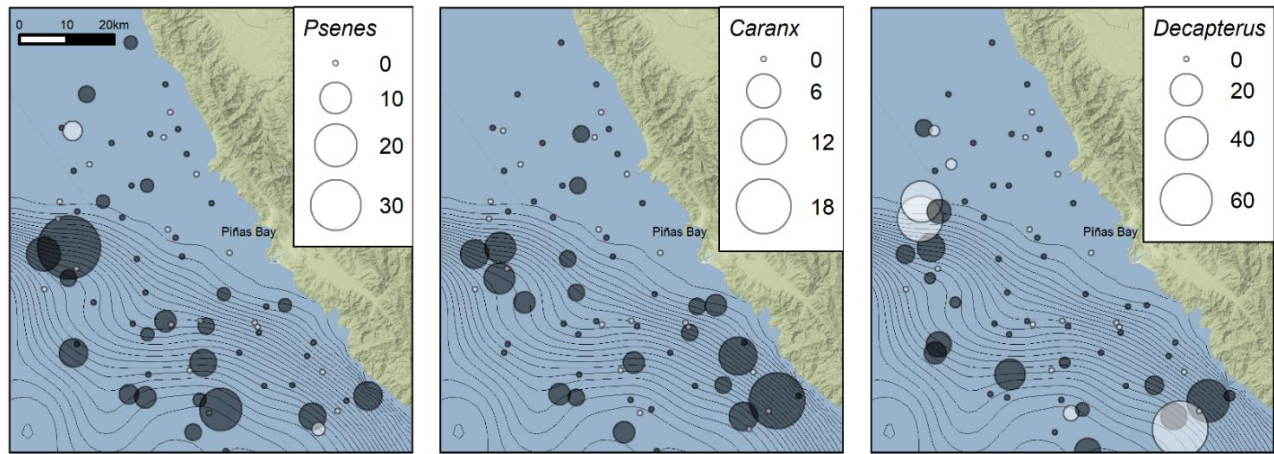


Figure 6. Partial effect plots for environmental predictors of genera abundance from generalized additive models. Solid line indicates smoother estimates, while 95% confidence intervals are represented by shaded polygons and whiskers.

Figure 7. Bubble map of relative abundance and occurrence for *Psenes*, *Decapterus*, and *Caranx* across seasons (white = Dry, dark = Wet). Map contours are 50 m.



Discussion

Our findings add to the very limited fishery-independent knowledge that exists of vertebrate community diversity and spatiotemporal dynamics in the epipelagic ocean - information identified as critical for benchmarking the existing status of these communities and assisting the planning of pelagic marine protected areas (Meeuwig et al. 2021). Additionally, to our knowledge, this study provides only the second analysis of the pelagic ecosystem of the Eastern Tropical Pacific, with the only published study from here (Cambra et al. 2021) focused on large pelagic species at seamount aggregation sites.

Our BRUVS documented that the waters off Piñas Bay, Panama support a wide variety of pelagic vertebrates including reptiles, mammals, elasmobranchs, and teleosts. These taxa included many upper-level predators such as dolphin, sharks, dolphinfish, tunas, and billfish, several of which are important to commercial and recreational fisheries in the region. Despite the area being known, from recreational fisheries data, for an abundance of large teleost predators (Haulsee et al. 2021), we observed fewer large predatory species than pelagic BRUVS studies in other regions (e.g., Santana-Garcon et al. 2014b, Letessier et al. 2019; Bouchet et al. 2020, Forrest et al. 2021, Thompson et al. 2021; but see similarities with Cambra et al. 2021). Compared to many of these studies, we surveyed either fewer total hours or a smaller spatial footprint; furthermore, we sampled a variety of randomly selected habitats rather than focusing on known large vertebrate aggregation topographical features. Our sampling was, however,

conducted at a higher BRUVS deployment density than many pelagic BRUVS studies. Despite the relatively small amount of sampled effort near known species aggregation areas at points along the shelf, we observed nearly as many large predatory species that Cambra et al. (2021) found along the nearby Cocos Islands seamounts which are known aggregation areas, suggesting a greater abundance of large predators in this area. We also observed a diverse array of mid-level and lower-level forage species capable of supporting robust predator populations.

The pelagic assemblage in the area shifted spatially and temporally, varying on and off the shelf and between the wet and dry seasons. Although these assemblages had many species in common, the differences were primarily the result of species replacement as species richness among these assemblages was similar. Assemblages not only differed in composition, but also in relative abundance, with both predator and forage species abundance greatest along the shelf and in the wet season. Predator assemblage patterns appear to be driven by periods of high and low availability of forage fish in the wet and dry season, respectively, while spatial trends likewise seem to be driven by the spatial distribution of forage fish, although likely mediated by other habitat factors and species-specific behaviors.

The structure of the vertebrate community was dominated by three highly abundant genera of small-bodied forage fish (*Decapterus*, *Psenes* and *Caranx*), which also accounted for almost half of the cumulative dissimilarity between assemblages. These fishes are zooplanktivorous and their occurrence and abundance may be influenced by patterns of zooplankton abundance, although they appear to respond differently to the spatiotemporal distribution of zooplankton (Hubbs et al. 1929, Randall & Carlson 1999, Bernal-Ornelas et al. 2008, Mair et al. 2012, Saucedo-Lozano et al. 2012, Metillo & Aspiras-Eya 2014). *Decapterus* occurrence, for example, increased with distance from shore and could indicate that *Decapterus* are following a spatial gradient of increasing productivity from the coastline to past the shelf edge. Satellite imagery shows the productivity gradient in this region is relatively stable throughout the year and with higher maximum productivity compared to other areas along the coast (Copernicus Marine Service 2021). The high productivity past the shelf is the result of nutrient-rich waters from below the thermocline upwelling into iron-rich low-salinity water from the coast at the shelf edge (Hutchins et al. 2002, Bruland 2002, Bruland et al. 2005, Pennington et al. 2006), and likely supports the zooplankton forage base required by *Decapterus*.

The higher occurrence and abundance in the wet season of *Psenes* and *Caranx* corresponded with high SST, but their peak abundance lagged several months behind the peak primary productivity and zooplankton occurrence in the dry season documented in the broader Eastern Tropical Pacific (Legaspi 1956, Bernal-Ornelas et al. 2005, Mair et al. 2012, Saucedo-Lozano et al. 2012). The seasonal patterns we observed in *Psenes* and *Caranx* occurrence may be related to northward current transport. The boundary current tends to transport the debris washed from shore by heavy rainfall north in the wet season. *Psenes* are known to aggregate around floating debris (Gooding & Magnuson 1967), and often aggregated around camera stations in our study. It is possible that *Psenes* associated with the floating debris may passively drift north with the boundary current through our study location, which may account for their higher abundance during the wet season.

Juvenile *Caranx caballus* (the most common *Caranx* species in our data) are likely brought northward by the boundary current during early development. At the Pearl Islands in the Gulf of Panama, *C. caballus* spawn in August – September and develop in mangrove estuaries before moving farther offshore (Mair et al. 2012). However, the area immediately surrounding Piñas Bay consists mainly of rocky coastline, with the nearest southern mangrove estuary system roughly 211 km southeast in Colombia. Northward current transport of *C. caballus* from an August – September spawning event in a southern estuary could account for the abundance of juveniles at our study site from September through October. This timing would also deliver juveniles to the area while zooplankton is still abundant, suggesting reproductive timing to match transport to areas of abundant forage.

Pelagic BRUVS allowed us to gather information on small-bodied species that are often overlooked in typical fishery derived surveys. This high abundance of small pelagic fish in comparison to other large pelagic species has been observed by previous pelagic BRUVS studies, but few have examined the spatiotemporal dynamics of these species on community structure or diversity (Santana-Garcon et al. 2014b, Cambra et al. 2021). The dominant contributions of *Decapterus*, *Psenes*, and *Caranx* in explaining the variability of pelagic assemblages off Piñas Bay illustrates the importance of surveying small-bodied forage fish when describing pelagic ecosystems and demonstrates the limits of fishery-dependent monitoring to achieve a comprehensive view of pelagic systems. Gear used by the dominant industrial fisheries in the area (longlines) passively exclude these genera and other small-bodied fishes from the

catch. Even when bycatch of small-bodied fishes is possible (e.g., purse seines), they are usually condensed into a single category for reporting (e.g., IATTC 2010, but see Lezama-Ochoa et al. 2017). Reliance primarily on catch-reporting has created a distorted picture of many marine ecosystems and has ignored many abundant species of low economic value, regardless of their importance to the system. For instance, despite the considerable seasonal abundance of *Psenes* present in our survey, very little information exists for the genus in Pacific Panama. The three dominant genera observed in our BRUVS are some of the most abundant small-bodied pelagic fish in Pacific Panama, and their occurrence drove the dissimilarity in assemblages between seasons. They also likely form the prey base for a variety of mid-level trophic groups that in turn become forage for large predators. As such, the presence of forage fish is important because it can be used to predict patterns in top predator occurrence and abundance (Similä et al. 1996, Shimose et al. 2008, Vogel et al. 2021).

While the use of pelagic BRUVS in this system was effective at gathering information on species that go unassessed in fishery-dependent surveys, our reported species accumulation curves expose the limits of BRUVS to comprehensively document the vertebrate biodiversity of this and other systems. Underreporting of species richness is a recurring issue in pelagic BRUVS studies, due to the patchiness and sparsity of the open-ocean environment and bias towards large predatory species that actively approach BRUVS (Whitmarsh et al. 2017, Grimm et al. 2020). Despite sampling at a relatively high level (> 250 h) in a productive pelagic system known for an abundance of species, we missed roughly 20% of the expected species richness. However, we were able to determine that local seasonal differences exist in the community assemblage and are likely driven by oceanographic conditions affecting the occurrence and relative abundance of small-bodied zooplanktivorous fishes, which lagged peaks of intense productivity. We were also able to document large marine organisms, including top predators like sailfish and black and blue marlin, that are targeted or caught incidentally by commercial and artisanal fisheries (e.g., longlines). Despite missing a similar percentage of expected richness, previous pelagic BRUVS research in other tropical pelagic systems identified spatial changes in community structure based on seafloor geomorphology (Bouchet et al. 2020). These results suggest that while BRUVS may be unsuccessful at capturing the entirety of a pelagic community's richness, they can still be used to detect changes in the overall community under limited sampling regimes. If the goal of future research and surveys is to detect even gradual community change in pelagic

communities without the need for a complete taxonomic inventory, BRUVS may offer an economical trade-off in effort.

Our findings demonstrate that BRUVS have the capability to survey and document a diverse range of pelagic vertebrates in the Eastern Tropical Pacific, including those species almost entirely missed by locally dominant fishing gear types. However, because even top predators considered abundant in this system were only occasionally observed, we agree with previous recommendations (Santana-Garcon et al. 2014a) that future pelagic BRUVS studies should increase sampling effort by extending recording time and number of deployments, especially in less productive systems, to achieve accurate representations of the community structure. This work provides a first benchmark for the pelagic vertebrate species diversity in a region of strong conservation concern given the high level of IUU fishing occurring here and adds to a steadily growing body of research demonstrating the feasibility and limits of pelagic BRUVS to survey ecosystems with sparsely distributed wildlife and fill knowledge gaps left by fishery-dependent assessments.

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