EFFECTS OF OYSTER AQUACULTURE ON ELASMOBRANCH ABUNDANCE AND HABITAT USE IN HUMBOLDT BAY, CA

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ABSTRACT

EFFECTS OF OYSTER AQUACULTURE ON ELASMOBRANCH ABUNDANCE AND HABITAT USE IN HUMBOLDT BAY, CA

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Habitat modification from aquaculture can have large effects on natural communities, with the habitat complexity provided by aquaculture structure positively influencing benthic invertebrates and small fish abundance. However, the effects of aquaculture on larger predatory fish like elasmobranchs (i.e., sharks and rays), which use nearshore habitat to forage and provide top-down control of these ecosystems, is largely unknown. Over two years, I deployed baited remote underwater video systems (BRUVS) to examine the effects of oyster aquaculture and environmental variables such as habitat (mudflat or eelgrass), salinity (ppt), turbidity (m), temperature (°C), pH (mV), dissolved oxygen ($mg \cdot L^{-1}$), and tidal height (m) on the presence and abundance of elasmobranchs and their main benthic prey (cancrid crabs) in Humboldt Bay. Humboldt Bay, in Northern California, is a large estuarine embayment that yields ~70% of California's oysters and provides critical habitat for elasmobranchs and crabs. I found significant positive effects of aquaculture and warmer water on bat ray presence in both mudflat and eelgrass habitats. When bat rays were present, they were more abundant on mudflats during periods of high turbidity. In contrast, I found no effect of aquaculture on leopard shark presence, which was better predicted by increasing turbidity. Surprisingly, I also found no effect of aquaculture on abundance of cancrid crabs, however, aquaculture had interactive effects with crab abundance on bat ray presence, which was positively associated with crab abundance where aquaculture structure was present, but not when it was absent. Further, aquaculture also had interactive effects with bat ray presence on crab behavior, with crabs taking longer to visit BRUVS when bat rays were present in general, but more so when aquaculture was absent. Taken together, these results suggest that bat rays (1) may be attracted to aquaculture for increased feeding opportunities in a habitat that provides refuge from larger predators; and (2) that their presence affects crab activity. Based on these findings, I hypothesize that the increased presence of bat rays in and around aquaculture could intensify their top-down effects on crabs, through both consumptive and non-consumptive pathways, thus decreasing the abundance of crabs in aquaculture-modified habitats. Future field experiments should directly test the hypothesis that aquaculture presence increases bat ray consumptive and non-consumptive effects on crab prey in aquaculture-modified coastal habitats.

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INTRODUCTION

Predators are found in virtually all ecosystems (Sinclair *et al.*, 2003; Lafferty, 2004; Croll *et al.*, 2005; Estes *et al.*, 2011; Frank, 2008) and occupy high levels of the food chain while largely influencing lower levels through consumptive and non-consumptive effects (Estes *et al.*, 1998; Lima, 1998; Halpern *et al.*, 2005; Myers *et al.*, 2007). Because predators influence prey populations and their associated communities through both direct consumption (i.e., inflicting mortality) and indirectly through non-consumptive effects where prey species change their behavior (i.e., distribution, feeding activity, habitat use etc.) in response to the risk of predation (Heithaus *et al.*, 2008; Creel and Christianson, 2008), their persistent decline worldwide is anticipated to have large impacts on mid-trophic level consumers and the resources that they consume (i.e., resource species such as primary producers, small invertebrates, etc.; Heithaus *et al.*, 2008). For example, in Shark Bay, Western Australia, AUS meso-grazers (i.e., sea turtles and dugongs) deplete important seagrass habitat by foraging in shallow habitats, resulting in potential shifts in the structure, nutrient content, and detrital cycling of seagrass meadows (Heithaus *et al.*, 2002; Aragones *et al.*, 2006). Seagrass meadows are indirectly, and positively, impacted when tiger sharks (*Galeocerdo cuvier*) are present in the shallower waters of Shark Bay because meso-grazers will retreat to deeper areas to avoid predation by tiger sharks, allowing for seagrass to grow and provide critical diverse habitat for fish and invertebrate communities (Heithaus, 2004; Wirsing *et al.*, 2007).

The effects of predators are well-documented and studied in terrestrial, freshwater, and marine systems, but more recently, researchers have become interested in how humans' impact or alter top predator influence (Rosenblatt *et al.*, 2013; Madin *et al.*, 2015; Hazen *et al.*, 2019). Predatory elasmobranchs (i.e., sharks and rays) are known for their slow growth, late maturation, extended gestation periods, and limited offspring production, and are particularly vulnerable to anthropogenic stressors, including fishing pressure and habitat loss (Hoenig and Gruber, 1990; Frisk *et al*., 2001; Hopkins and Cech, 2003). These stressors are amplified in productive nearshore coastal ecosystems (seagrass beds and mangroves), which are affected disproportionately from habitat modification and resource exploitation (Luypaert *et al*., 2020; Jones *et al*., 2018; Halpern *et al*., 2015; Lotze *et al*., 2006). For example, in Morro Bay, California, USA estuary-wide collapse of eelgrass (*Zostera marina*) beds since the early-2000s has been linked to large-scale erosion and accelerated sedimentation from over a century of human habitat modification (since the early 1990s; Walter *et al.*, 2020). Coastal areas harbor important foundation species, like eelgrass (Bos *et al.*, 2007), which provide critical habitat for many elasmobranchs but also stand out as highly susceptible zones to anthropogenic pressure, because most are in proximity to human populations along nearshore areas (Stevens *et al*., 2000; Last and Stevens, 2009; Yon *et al*., 2020). Thus, understanding how human modification and disruption of nearshore coastal habitat affects the abundance, distribution, and behavior of coastal elasmobranchs is crucial to determining effective management and conservation strategies (Jabado *et al*., 2018).

One way in which humans have impacted coastal marine habitats is through intertidal shellfish cultivation – one of the most important aquaculture industries globally (Forrest *et al*., 2009; FAO, 2006a). Methods of shellfish cultivation may interfere with a range of ecological processes, due to the pre-emption of natural habitat by artificial infrastructure and the added or modified structural complexity of farmed habitats (Forrest *et al*., 2009). Oysters, for example are cultivated primarily in the shallow waters of estuaries using a variety of techniques, including elevated culture where oysters are suspended above the benthos in mesh cages, baskets, or trays (Forrest *et al*., 2009), and longline culture where oyster shells with attached spat (i.e., oyster larvae) are inserted through strands of rope that is then suspended above the benthos and supported by PVC or wooden pegs. Each cultivation technique introduces artificial, hard, physical structure into an ecosystem where such structure may largely be absent (Moroney and Walker, 1999; McKindsey *et al*., 2011; Callier *et al*., 2018) or disrupts and displaces habitat that already naturally provides structure such as seagrass meadows, which are also in decline worldwide (Orth *et al*., 2006).

The refuge provided by natural habitat complexity is an important component of food web dynamics (Pace *et al*., 1999), and refuge availability plays a role in structuring communities within many highly productive coastal habitats, including shallow estuarine habitats (Grabowski, 2004). For example, seagrass beds, salt marshes, and natural oyster reefs harbor high densities of benthic organisms in part because the habitat complexity they create provides refuge from predation for small prey species (Grabowski, 2004; Summerson and Peterson, 1984; Callier *et al*., 2018). The physical complexity of oyster farms (e.g., buoys, ropes, cages, anchors) provides substrate for a variety of fouling organisms, which in turn add biological components to the artificial reef-like structures of elevated culture, attracting additional organisms such as small fish and invertebrates (Costa-Pierce, 2010; Callier *et al*., 2018). Numerous studies have shown that bony fish diversity and abundance increase in areas with physical structure provided by shellfish aquaculture. For example, Brehmer *et al*., (2003) found that the abundance of fish schools was greater within mussel culture sites compared to non-culture sites. Additionally, Dealteris *et al*., (2004) found a greater abundance of juvenile and benthic fish (e.g., flounders, cod, gunnels, pipefish) and mobile invertebrates associated with rack and bag oyster culture than in natural habitats within their study area (i.e., seagrass or sand habitat).

Whereas the positive benefits of shellfish culture are well-documented for small teleost fish and benthic invertebrates, to my knowledge, there are no studies examining the influence of bivalve aquaculture on the abundance and behavior of elasmobranchs, which can act as top predators in nearshore coastal ecosystems where aquaculture is commonly implemented. Thus, it is unclear whether elasmobranchs may be attracted to the physical structure of bivalve farms because of increased prey availability or repelled by them due to risk of entanglement or heightened human activity, or if they are simply incapable of foraging in these complex artificial habitats (Callier *et al*., 2018). Some indirect evidence suggests that the addition of artificial habitat complexity could negatively impact large marine predators, like sharks and rays. For example, Watson-Capps and Mann (2005) showed that bottlenose dolphins (*Tursiops* sp.) were less likely to enter oyster farms than other nearby habitats and suggested that larger-bodied marine predators may avoid shellfish aquaculture structure because the lines and gear associated with the farmed areas interfere with their foraging. Additionally, Byers *et al*., (2017) found that bonnethead shark (*Sphyrna tiburo*) predation on blue crabs was over twofold greater on featureless mudflats compared to structurally complex natural oyster reefs, suggesting that the complexity of oyster habitat weakens the predatory effects of sharks and may impede foraging success. Taken together, these results suggest that artificial habitat complexity associated with oyster aquaculture could negatively affect elasmobranch abundance and weaken their top-down effects in coastal ecosystems.

Fluctuations in environmental variables such as temperature, salinity, pH, dissolved oxygen, turbidity, and tidal flow also have the potential to dictate the abundance and habitat use of elasmobranchs (Schlaff *et al*., 2014), especially in coastal areas like estuaries where environmental conditions are in a constant state of flux from natural and anthropogenic influences (Cloern *et al*., 2016). Elasmobranchs in nearshore habitats prefer warmer temperatures for foraging (Schlaff *et al*., 2014) and will exhibit temperature-mediated seasonal (Dunbrack and Zielinski, 2003; Hopkins and Cech, 2003; Heupel, 2007; Vaudo and Heithaus, 2009) and diel movements (Carey *et al*., 1990; Economakis and Lobel, 1998; Matern *et al.,* 2000; Sims *et al.,* 2006). Nearshore elasmobranchs may also prefer environments with increased turbidity (i.e., decreasing water clarity) as an adaptive strategy to avoid predation (Bethea *et al*., 2015; Yates *et al*., 2015), although there are relatively few studies investigating this claim. Both temperature and turbidity will also be influenced by tidal movements, which themselves strongly influence the movements of coastal elasmobranchs (Carlisle and Starr, 2010) especially in bays and estuaries where shallow mudflats and eelgrass beds are fully exposed and inaccessible at low tide (Whitfield, 2017), and during flood tides elasmobranchs can expand their foraging efforts in shallower habitats (Schlaff *et al.*, 2014). Thus, common coastal elasmobranch species are likely influenced by a myriad of natural and human influenced factors including, artificial habitat complexity, habitat modification, and environmental variability (Schlaff *et al.*, 2014; Madin *et al.*, 2015; Bishop *et al.*, 2017).

Here, I conducted underwater video surveys to assess the effect of oyster aquaculture and abiotic environmental factors on the abundance and behavior of elasmobranchs and their prey in the primary habitat types (eelgrass beds and mudflats) of a large estuary (Humboldt Bay, CA). I hypothesized that habitat type and the presence of aquaculture structure would affect elasmobranch abundance and habitat use, with the expectation of lower elasmobranch and prey abundance on mudflats, a mostly featureless habitat, because there is no artificial or biotic structure that prey can use to hide from predators, and predators may be less abundant in areas with less prey (Chang and Todd, 2023). Conversely, in eelgrass beds – where species abundance and diversity are higher (Hughes *et al*., 2014) and habitat disruption may be less frequent – I anticipated higher abundance of both elasmobranchs and their prey. I also predicted that the presence of oyster aquaculture in both eelgrass and mudflat habitats would inhibit elasmobranch abundance due to the risks associated with frequent human activity and habitat disturbance (Dumbauld *et al*., 2009), but positively impact abundance of their prey (i.e., benthic invertebrates) because of increased refuge availability in these areas (Grabowski, 2004).

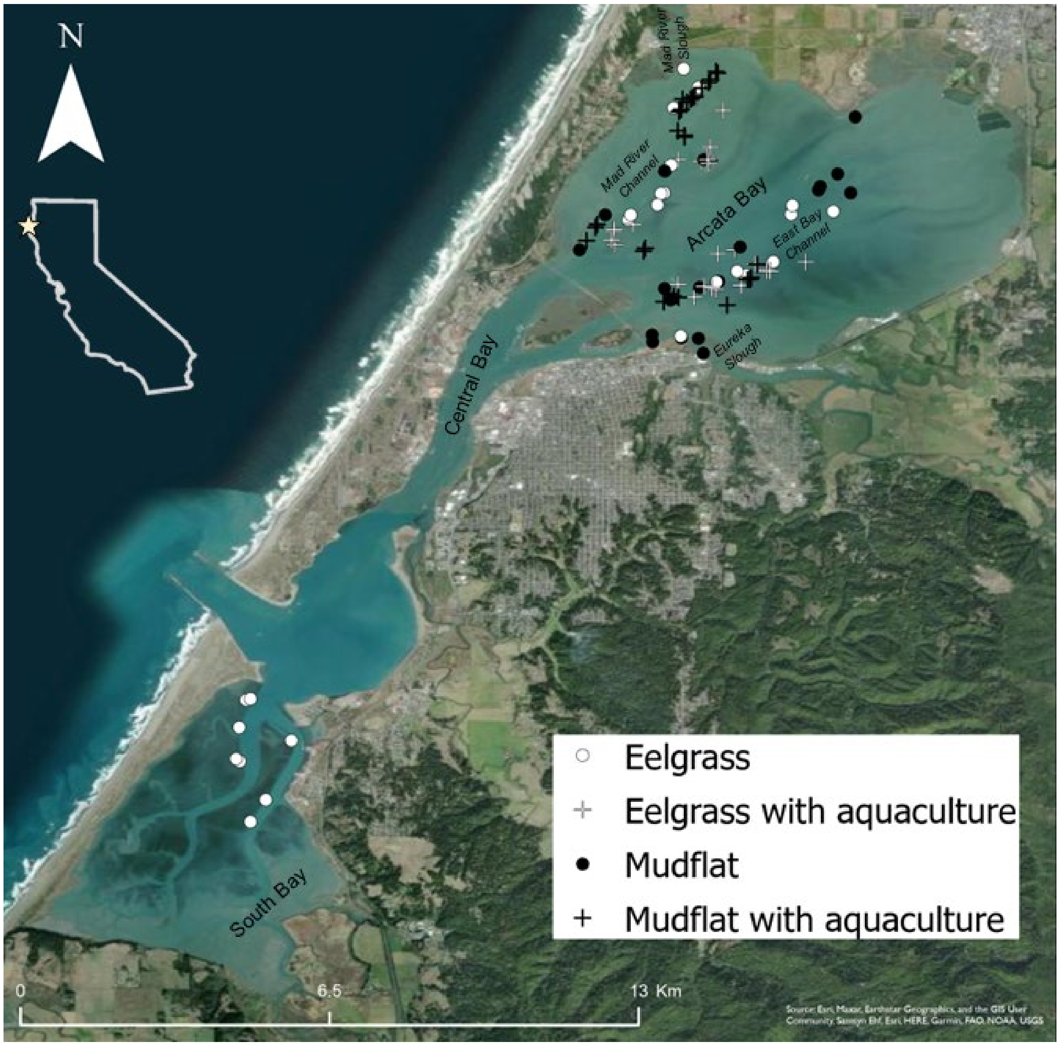
METHODS

Study area

Humboldt Bay is a large marine and estuarine embayment located on the coast of northern California in Humboldt County (40°46′N, 124°14′W) (Gray *et al.*, 1997). It is the second largest bay in California, measuring approximately 106 km^2 (Pacific Marine and Estuarine Partnership, 2017). The bay serves as habitat for a diverse array of invertebrates, fishes, birds, and mammals (Barnhart *et al*., 1992). Eelgrass (*Zostera marina*) beds that grow throughout the bay provide biotically structured habitat and play an important role in the distribution of infaunal organisms and the abundance of fish and birds (Barnhart *et al.*, 1992; Hughes *et al.,* 2014; Toft *et al.*, 2023). Benthic invertebrates, including polychaete worms, molluscs, and crustaceans, including Dungeness crab (*Metacarcinus magister*), Pacific rock crab (*Romaleon antennarium*), red rock crab (*Cancer productus*), striped shore crab (*Pachygrapsus crassipes*), purple shore crab (*Hemigrapsus nudus*), and yellow shore crab (*Hemigrapsus oregonensis*) are commonly found throughout the bay. Many fish, bird, and marine mammal species feed on these invertebrates (Barnhart *et al.*, 1992; Gray *et al.*, 1997; Ebert and Ebert, 2005). Fish in Humboldt Bay belong to two groups, elasmobranchs (cartilaginous fish) and teleosts (bony fish). Common elasmobranchs are the leopard shark (*Triakis semifasciata*), sevengill shark (*Notorynchus cepedianus*), the brown smoothhound (*Mustelus henlei*), and bat ray (*Myliobatis californica*) (Barnhart *et al.*, 1992; Ebert and Ebert, 2005).

Leopard sharks mostly feed on crabs, polychaete worms, and molluscs, while bat rays feed on a combination of crabs, clams, *Crangon* shrimp, and polychaetes (Gray *et al.*, 1997). Cancrid crabs (Dungeness and rock crabs) are one of the most important prey items for both adult leopard sharks and bat rays in Humboldt Bay (Gray *et al*., 1997; Ebert and Ebert, 2005). Sevengill sharks, a larger species, feed on both leopard sharks and bat rays, as well as pinnipeds and bony fish (Ebert, 1989).

Humboldt Bay consists of three main areas: Entrance Bay, South Bay, and Arcata Bay. Arcata Bay and South Bay are broad areas with extensive mudflats and eelgrass beds dispersed throughout. Both eelgrass beds and mudflats in Arcata Bay have the potential to be occupied by oyster aquaculture, while South Bay, which is partially a Marine Recreational Management Area, does not contain any oyster aquaculture. I performed all the sampling procedures described below in Arcata Bay and South Bay (40°50'N, 124°07'W and 40°42'N, 124°14'W) (Fig. 1). I sampled areas adjacent to three of the four large tidal channels (East Bay Channel, Arcata Channel, and the Mad River Channel) in Arcata Bay and in two sloughs (Mad River Slough at the northern end of Arcata Bay and the Eureka Slough at the southeastern end of Arcata Bay). In South Bay, I sampled areas adjacent to two main channels that surrounded a large mudflat on the east and west side of the bay. Sampling sites were selected based on two predefined benthic habitats, eelgrass, and mudflat, and whether oyster aquaculture was present (Fig. 1).



Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community, [illegible], Esri, HERE, Garmin, FAO, NOAA, USGS

Figure 1: Map of Humboldt Bay, CA with 112 total BRUVS deployment sites and 28 individual replicate sites in eelgrass, eelgrass with aquaculture, mudflat, and mudflat with aquaculture. Open (white) circles represent eelgrass habitats, closed (black) circles represent mudflat habitats, white plus (+) signs represent eelgrass habitats with aquaculture, and black plus (+) signs represent mudflat habitats with aquaculture.

At sites where aquaculture was present, I used maps provided by Coast Seafoods Co. denoting the locations of their farmed oyster beds and the type of culture method (NOAA Office for Coastal Management, 2009). There are several different oyster culture methods used in Arcata Bay, including: rack-and-bag culture, where oysters grow in square mesh bags affixed to a steel rebar rack; tray culture, where oysters grow in square trays that are stacked vertically; suspended culture, where oysters grow in baskets that are attached to lines that are raised in the water column and the baskets rise and fall with the tide; and bottom culture, where oyster larvae that is attached to a hard substrate and grows off the bottom in clusters (Forrest *et al*., 2009). I chose non-aquaculture deployment sites using maps of Humboldt Bay from previous studies and habitat assessments (Barnhart *et al*., 1992, Hughes *et al.,* 2014), as well as personal observations from preliminary field surveys.

Estimating elasmobranch and prey abundance

Baited remote underwater video stations (BRUVS) are a useful tool to survey the diversity and abundance of predatory fishes and have been used extensively to compare species abundance in different underwater habitats (Cappo *et al*., 2007; Brooks *et al*., 2011). I used six individual BRUVS units comprised of a 0.5-kg plate affixed to a 1-m pole with a GoPro HERO+ (GoPro®, Inc., San Mateo, CA, USA) at the weighted end of the pole and a mesh bait bag containing between 200-300g of squid at the far end of the pole; Appendix A, Fig. 14) during each sampling day between May – September 2022 and April – August 2023. I deployed these BRUVS at 122 different locations in the bay.

Ten deployments were not used because the camera failed before the 60-minute period or the BRUVS unit tipped over during deployment. As a result, I conducted a total of 28 sampling events for each habitat type/aquaculture presence combination (eelgrass with and without aquaculture, mud with and without aquaculture; Fig. 1).

I used a 6.4 m deep vee aluminum hull center console boat for all sampling procedures. At each sampling site, I deployed BRUVS off the side of the boat (a 2.5-meter rope was attached to the weight with a buoy tied to the opposite end to mark the location of the BRUVS at the surface) and left them submerged for at least 60 minutes to allow for species detection (Currey-Randall *et al.*, 2020). BRUV units were deployed simultaneously with at least 500 m between each unit to reduce the likelihood of non-independence due to individuals being concurrently sampled by adjacent BRUVS (Langlois *et al.*, 2020). The boat was positioned approximately 200 m away from all active deployment sites to reduce the likelihood of boat noise altering species arrival (Roberts *et al.*, 2016), and while recreational and commercial boating is common in Humboldt Bay, many of these vessels stay in deeper channels and I rarely observed any noise disturbance from other vessels when analyzing BRUV footage or on the boat during sampling days.

BRUVS video analysis

I visually identified (to the lowest taxonomic level possible) and counted all elasmobranch, bony fish, and crab species in the video footage from each deployment video. I recorded the total individual counts of each species that entered the field of view and quantified the relative abundance of each species throughout the entire deployment interval using MaxN, the standard metric of abundance that is used when analyzing BRUVS footage. MaxN is defined as the maximum number of individuals of a single species seen in the field of view at any one time per deployment (Cappo *et al.*, 2003a, b). MaxN is commonly used to estimate species abundance in BRUVS because it is a conservative measure in that it ensures that no individual is counted more than once (Schobernd *et al.*, 2014). I also recorded time of arrival (TOA) to understand potential differences in behavior of species observed in deployments – defined as the first time a species was in view during the deployment interval (Gore *et al.*, 2020) – for both crab and elasmobranch species.

Abiotic environmental variables

Fluctuations in abiotic factors can influence movement and changes in behavior and habitat use for many fish and invertebrate species (Brown and Terwilliger, 1999; Schlaff *et al.*, 2014). Thus, I also measured abiotic environmental variables [pH (mV), temperature (°C), dissolved oxygen (DO; mg · L^{-1}), salinity (ppt), and Secchi depth (m)] at each site prior to deploying an individual BRUVS unit. I used a Hach HQ40d portable multi-parameter meter (Hach ®, Co., Loveland, CO, USA) to measure temperature, DO, and pH. I submerged and retrieved a Secchi disc at each deployment site, measuring extinction depth (m) and eruption depth (m), and used transparency depth (m)

$$Secchi\ transparency\ depth\ (m) = \frac{Extinction\ depth\ (m)\ +\ Eruption\ depth\ (m)}{2}$$

as a proxy for turbidity; and to measure salinity I used a handheld refractometer (Sper Scientific Direct, Scottsdale, AZ, USA).

Statistical analysis

To test the effects of habitat type, aquaculture presence, and abiotic variables on MaxN, of elasmobranchs and crabs in BRUVS deployments, I employed a generalized linear model (GLM) approach. Because elasmobranch occurrence on BRUVS deployments was highly zero-inflated (~ 46% zeros), I used a hurdle model to analyze abundance of individual elasmobranch species. Hurdle models account for an excess of zeros via a two-step model structure. The first step fits a binomial probability model to determine whether a zero or non-zero outcome occurs, and the second step fits a separate model for all positive outcomes. Here, I modeled the occurrence of elasmobranchs (presence/absence) across all deployments using a binomial distribution. The next step only included deployments where elasmobranchs were present and modeled elasmobranch abundance ($\text{MaxN} > 0$) using a negative binomial distribution with a log-link function. Including interaction terms in the hurdle model (e.g., habitat type x aquaculture presence) resulted in errors with model complexity and potential overfitting. To improve model performance overall, I only considered additive effects to streamline the model and avoid issues like overfitting. I performed model selection for GLMs on elasmobranch data using an Akaike information criteria (AIC) test on all possible model configurations and a null model. I compared differences between each model by calculating ΔAIC values, and values within less than 4 units (ΔAIC < 4) of the top model (lowest AIC score), were considered equivalent to the top model.

For all cancrid crab species combined, and Dungeness crabs, I used a GLM with a negative binomial distribution and log-link function to model abundance (MaxN) across all deployments. Because rock crab (red rock crabs and Pacific rock crabs combined) abundance was also zero-inflated (~74% zeros), I also used a hurdle model to analyze their abundance. For all models, and in each of the steps in the hurdle models, I included the separate and interactive effects of habitat type and aquaculture presence and the effects of salinity, pH, temperature, dissolved oxygen, Secchi depth, and tidal height. Prior to running the models, I examined variation inflation factors (VIFs) to assess multicollinearity among the predictor variables. To assess potential trophic relationships between elasmobranchs and crabs, I examined the relationship between MaxN of crabs and presence or absence of elasmobranchs across all BRUVS deployments with logistic regression. I also employed a two-way ANOVA to test the separate and interactive effects of aquaculture presence and elasmobranch presence, and the effects of habitat type, on the TOA of crabs. I conducted all analysis using R (R Core Team, 2021) and RStudio (Posit Team, 2023), with the pscl (Zeileis *et al.*, 2008), and MASS (Venables and Ripley, 2002) packages to run the hurdle models.

RESULTS

Elasmobranchs were present in 54% of all BRUVS deployments. Bat rays (present in 40% of all deployments) and leopard sharks (present in 28% of all deployments) were the most commonly observed species (Appendix A, Fig. 8), with sevengill sharks only observed in two (1.7%) of the 112 deployments. Crabs were present in 80% of all deployments. Dungeness crab (present in 70% of all deployments), and rock crab (red rock crab and Pacific rock crab; 26% of all deployments) were the most commonly observed crab taxa (Appendix A, Fig. 9). European green crabs (*Carcinus maenas*), non-native to Humboldt Bay, were observed at only one sampling site (Eureka Slough) on two occasions. Shore crabs (*Hemigrapsus* spp.) were present in only 20% of deployments and were excluded from subsequent analyses because they are not important prey items for leopard sharks or bat rays (Gray *et al.*, 1997; Ebert and Ebert, 2005).

There was one strong and positive relationship between abiotic variables (Appendix A, Fig. 10) including temperature and day of year ($r = 0.85$, $P > 0.0001$); and several significant negative associations including Secchi depth and turbidity ($r = -0.41$, $P > 0.0001$), salinity and dissolved oxygen ($r = -0.45$, $P > 0.0001$), and temperature and dissolved oxygen ($r = -0.63$, $P > 0.0001$). Day of year was removed from the analysis due to its highly positive and significant association with temperature. Despite these correlations, predictor variables had low to moderate collinearity (Appendix B, Table 5) and variance inflation factors (VIFs) for all parameters across all models were low (< 4; Appendix B, Table 6), thus, all variables were included in all models. The best model for leopard sharks and bat rays included all predictor variables (Table 1). The original top model for bat rays did not include Secchi depth (m), however, the ΔAIC score for the second-best performing model – which included all predictor variables – was less than 4 units and so I selected it as the top model (Table 1), and this model was selected for further analyses for both species.

Bat rays were more likely to be present in aquaculture ($\beta = 1.02$, $df = 19$, $P = 0.039$, Fig. 2A) and when water temperatures were higher ($\beta = 0.22$, $df = 19$, $P = 0.040$, Fig. 3; Table 2A). When bat rays were present, they were more abundant on mudflats ($\beta = 1.21$, $df = 19$, $P = 0.015$), at higher salinities ($\beta = 0.63$, $df = 19$, $P = 0.025$), and in more turbid waters ($\beta = -3.67$, $df = 19$, $P = 0.011$; Table 2A). In contrast, leopard shark presence (Table 1B, Fig. 2B) was not influenced by aquaculture, and leopard sharks were more likely to be present in more turbid waters ($\beta = -3.06$, $df = 19$, $P = 0.004$, Fig. 3). Leopard shark abundance was not predicted by any of the variables in the model (Table 2).

Aquaculture presence and habitat type were not significant predictors of crab abundance (Fig. 4). Instead, crab abundance was positively associated with higher salinities ($\beta = 0.24$, $df = 92$, SE = 0.06, $z = 3.65$, $P = 0.003$, Table 3) and water temperatures ($\beta = 0.09$, $df = 92$, SE = 0.04, $z = 2.42$, $P = 0.015$, Fig. 5).

Table 1. Top hurdle models for predicting (A) bat ray and (B) leopard shark presence and abundance. Log-likelihood, Akaike information criterion (AIC), and difference from lowest Akaike information criterion (ΔAIC) are reported. Selected models for both species are indicated in bold. The full model was selected for bat rays because the ΔAIC for the top two models was less than four units and so conservatively, not distinguishable from one another. Variable codes – Habitat: eelgrass or mudflat; Aqua: aquaculture presence; Sal: salinity; Temp: temperature; DO: dissolved oxygen; Secchi: Secchi depth, Tide: tidal height.

(A) Bat ray model	log L	*df*	AIC	ΔAIC
Habitat + Aqua + Sal + pH + Temp + DO	**-67.01**	**15**	**164.02**	**0**
Habitat + Aqua + Sal + pH + Temp + DO + Secchi	**-66.92**	**17**	**167.83**	**3.81**
Habitat + Aqua + Sal + pH + Temp + DO + Secchi + Tide	-65.79	19	169.58	5.56
Habitat + Aqua + Sal + pH + Temp	-72.39	13	170.77	6.75
Habitat + Aqua + Sal + pH	-75.04	11	172.09	8.07
Habitat + Aqua	-85.91	7	185.82	21.8
Habitat + Aqua + Sal	-84.13	9	186.26	22.24
Aqua	-88.54	5	187.09	23.07
Habitat	-96.5	5	202.10	38.08
Intercept	-99.22	3	204.45	40.43
(B) Leopard shark model	log L	df	AIC	ΔAIC
Habitat + Aqua + Sal + pH + Temp + DO + Secchi + Tide	**-54.68**	**19**	**147.36**	**0**
Habitat + Aqua + Sal + pH + Temp + DO + Secchi	**-56.86**	**17**	**147.72**	**0.36**
Habitat + Aqua + Sal + pH + Temp + DO	-63.54	15	157.08	9.36
Habitat + Aqua + Sal + pH	-67.56	11	157.11	9.39
Habitat + Aqua + Sal + pH + Temp	-66.08	13	158.17	10.45
Intercept	-78.34	3	162.68	14.96
Habitat	-77.43	5	164.86	17.14
Aqua	-77.73	5	165.46	17.74
Habitat + Aqua	-76.77	7	167.53	19.81
Habitat + Aqua + Sal	-75.43	9	168.86	21.14

Table 2. Summary of the hurdle model results for predictors of (A) bat ray and (B) leopard shark presence and abundance. The first part of the model (zero hurdle) predicts the likelihood of observing an elasmobranch as a binary (0, 1) response, and the second part of the model (count model) shows what response variables influence the abundance or count (1, 2, 3, 4) of elasmobranchs using a negative binomial distribution. The estimate represents the strength of the relationship of significant predictors and whether the relationship is positive or negative. Bold text indicates statistical significance at $\alpha = 0.05$.

(A) Zero hurdle model			Count model	
Variable	*β*	*P*	*β*	*P*
Intercept	-0.46	0.985	-21.78	0.598
Habitat	-0.39	0.430	1.21	**0.015**
Aquaculture presence	1.02	**0.039**	0.01	0.987
Salinity (ppt)	0.31	0.080	0.63	**0.025**
pH	-2.65	0.439	-2.00	0.732
Temperature (°C)	0.22	**0.040**	-0.04	0.894
Dissolved oxygen (mg · L^{-1})	0.65	0.227	1.69	0.080
Secchi depth (m)	-0.16	0.857	-3.67	**0.011**

(B) Zero hurdle model			Count model	
Variable	*β*	*P*	*β*	*P*
Intercept	-9.57	0.706	-3.84	0.879
Habitat	-0.58	0.261	5.32	0.249
Aquaculture presence	0.53	0.331	-3.78	0.187
Salinity (ppt)	0.02	0.928	0.37	0.716
pH	0.59	0.862	-6.04	0.521
Temperature (°C)	0.18	0.141	0.35	0.498
Dissolved oxygen (mg · L^{-1})	0.33	0.567	4.31	0.292
Secchi depth (m)	-3.06	**0.004**	-20.58	0.216

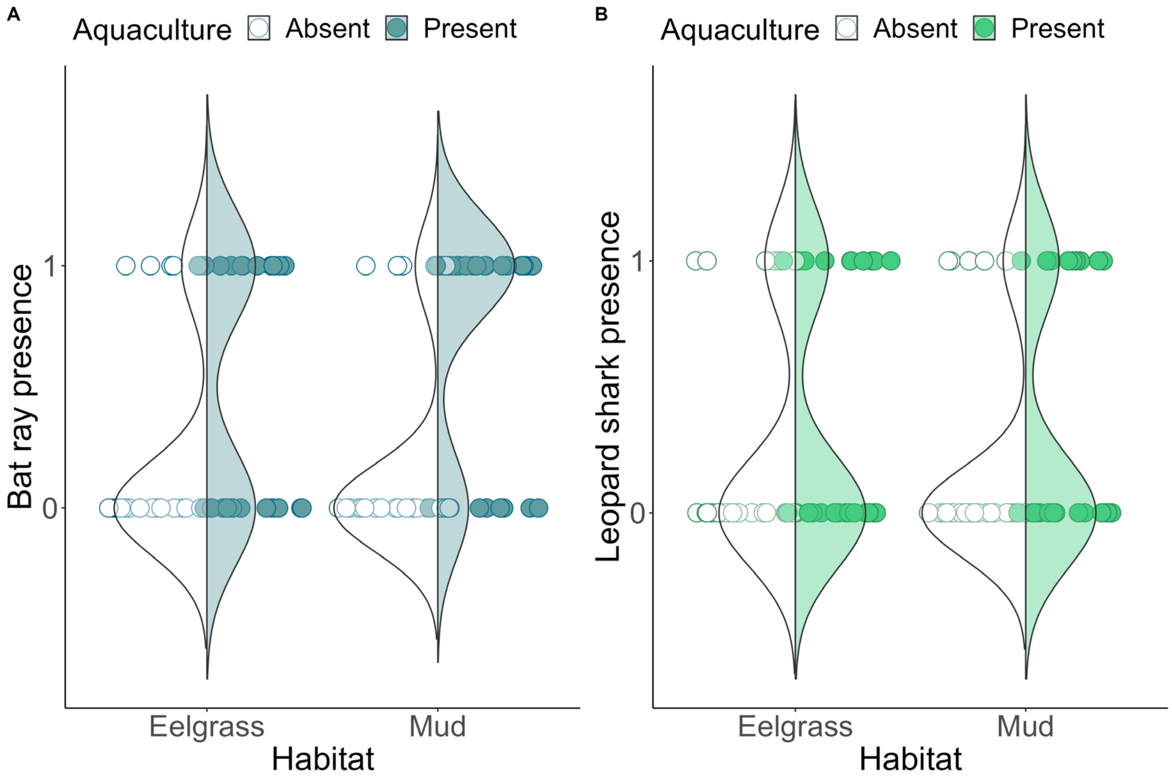


Figure 2. The presence and absence (MaxN) of (A) bat rays, and (B) leopard sharks in mud and eelgrass habitats, with and without the presence of aquaculture structure. Smaller filled circles represent overlapping individual data points from deployments in habitats with aquaculture, and smaller open circles represent overlapping individual data points from deployments in habitats with no aquaculture.

Table 3. Summary of generalized linear model analyzing the effects of aquaculture presence, habitat, and abiotic environmental variables on the abundance of all (A) cancrid crabs (Dungeness and rock crab), and (B) Dungeness crabs. The estimate represents the strength of the relationship of significant predictors and whether the relationship is positive or negative. Bold text indicates statistical significance at $\alpha = 0.05$.

(A) Variable	*β*	*P*
Intercept	-20.43	**0.013**
Habitat	0.09	0.588
Aquaculture presence	0.21	0.240
Salinity (ppt)	0.24	**< 0.001**
pH (mV)	1.15	0.283
Temperature (°C)	0.09	**0.015**
Dissolved oxygen (mg · L^{-1})	0.15	0.408
Secchi depth (m)	0.35	0.269
	AIC	337.4
	No. Iterations	1
	Theta	10.74
	2 x log L	-319.40

(B) Variable	*B*	*P*
Intercept	-23.34	**0.016**
Habitat	0.12	0.550
Aquaculture presence	0.17	0.421
Salinity (ppt)	0.27	**0.0004**
pH (mV)	1.34	0.29
Temperature (°C)	0.12	**0.012**
Dissolved oxygen (mg · L^{-1})	0.14	0.520
Secchi depth (m)	0.15	0.677
	AIC	311.9
	No. iterations	1
	Theta	6.55
	2 x log L	-293.91

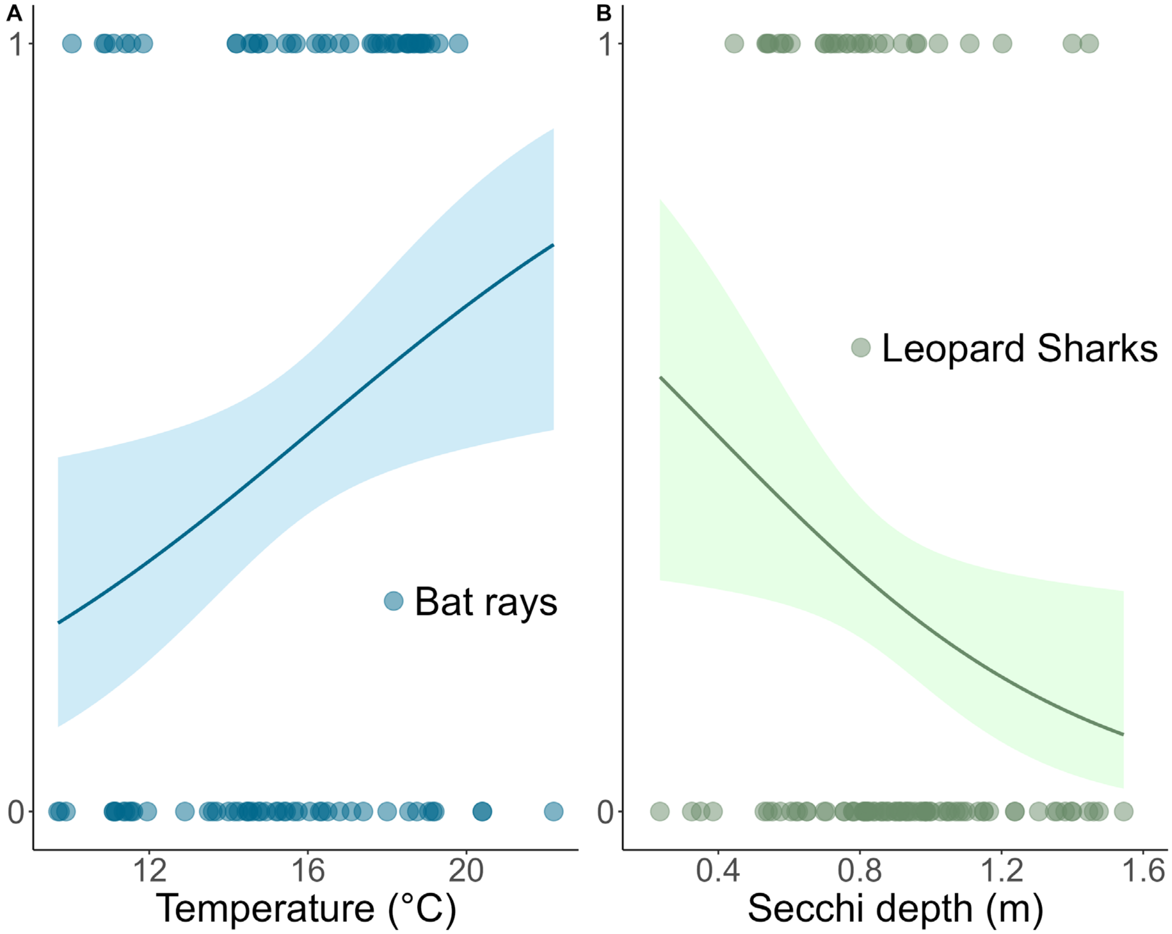


Figure 3. Relationship between presence of (A) bat rays and temperature (°C); and between presence of (C) leopard sharks and Secchi depth (m). Decreasing Secchi depths (m) indicate decreasing levels of water clarity. The fitted logistic curves represent the probability of elasmobranch presence as a binary response (0, 1), and shaded confidence bands represent ± 1 SE. Points represent actual observations.

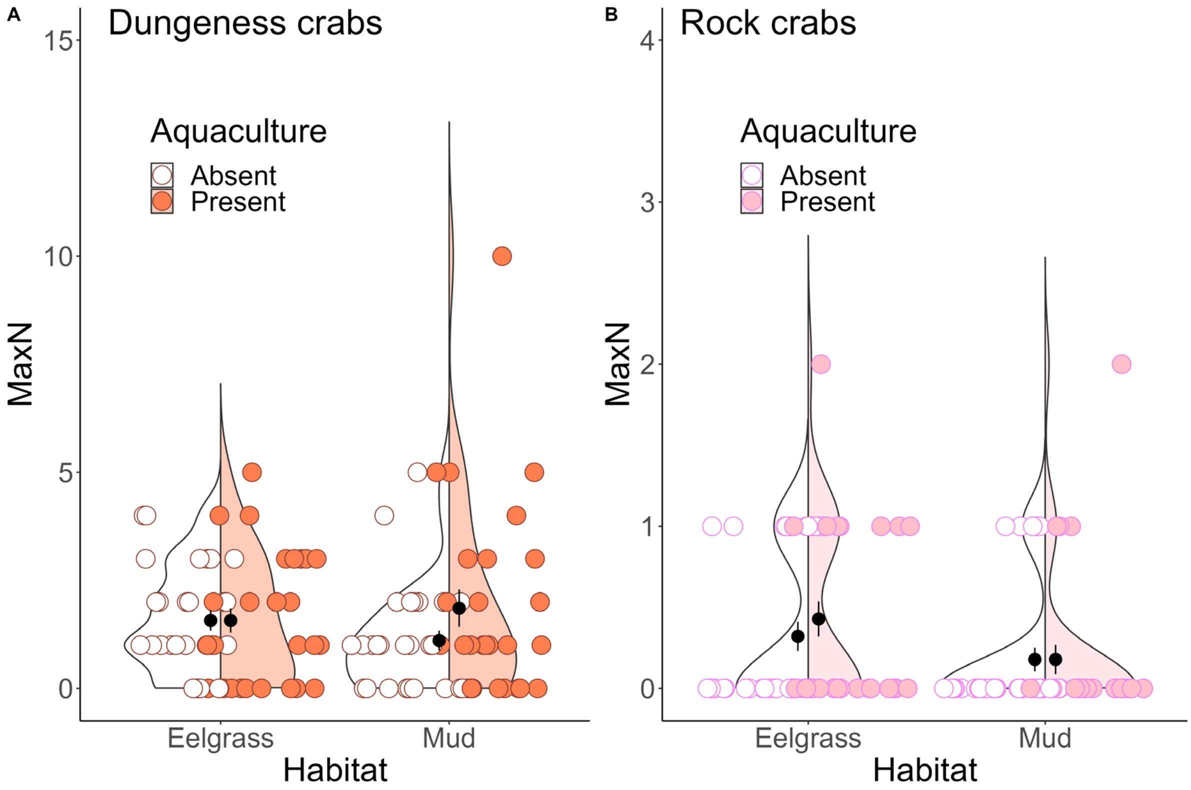


Figure 4. The abundance (MaxN) of (A) Dungeness crabs, and (B) Rock crabs in mud and eelgrass habitats, with and without the presence of aquaculture structure. Smaller filled circles represent individual data points from deployments in aquaculture habitats, and smaller open circles represent individual data points from deployments in non-aquaculture habitats, and larger, black circles represent means ± 1 SE.

Neither aquaculture presence nor habitat type influenced Dungeness crab abundance, but these crabs were significantly more abundant when salinities ($\beta = 0.27$, $df = 92$, SE = 0.08, $z = 3.58$, $P < 0.001$, Table 3) and temperatures ($\beta = 0.11$, $df = 92$, SE = 0.05, $z = 2.37$, $P = 0.018$, Figure 5) were higher. Similarly, aquaculture presence did not predict rock crab presence, but rock crabs were more likely to be present in eelgrass habitats (β = -1.39, *df* = 92, SE = 0.63, *z* = -2.18, *P* = 0.029, Table 4) compared to mudflats, and under higher pH conditions (β = 10.81, *df* = 92, SE = 4.67, *z* = 2.31, *P* = 0.021). When rock crabs were present, their abundance was not predicted by aquaculture, habitat, or any of the environmental variables.

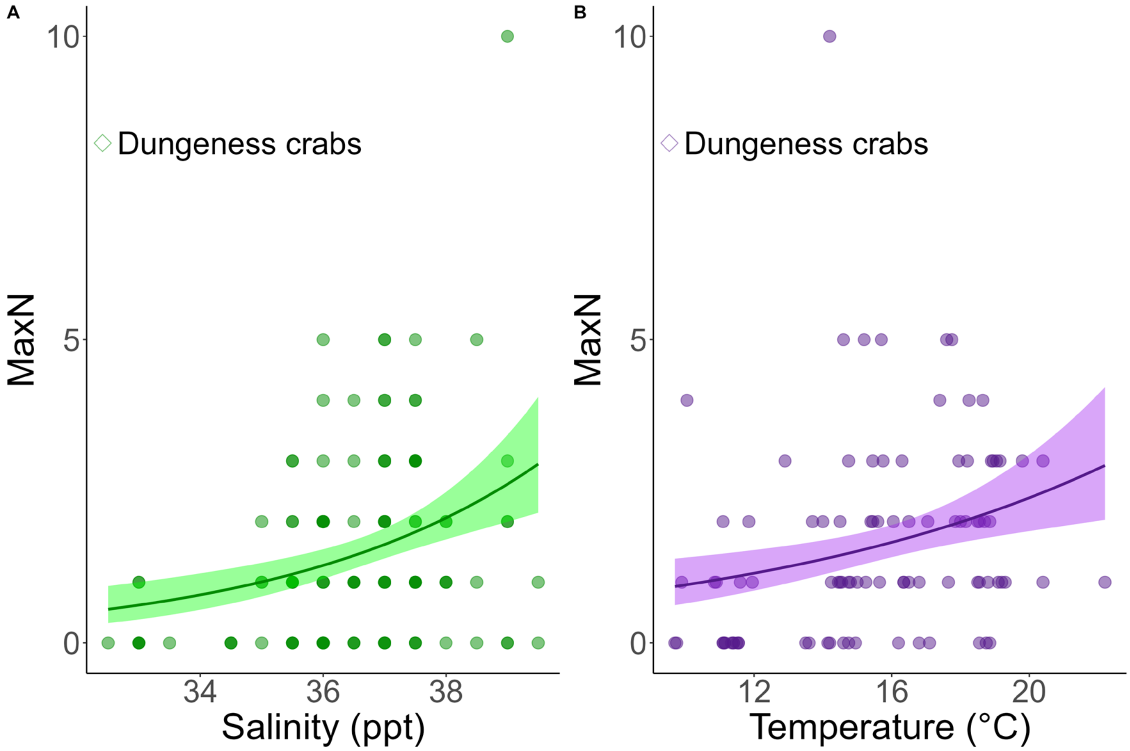


Figure 5. Relationship between abundance of Dungeness crabs and (A) salinity (ppt), and (B) temperature (°C). Increasing salinities (ppt) indicates higher levels of saltwater. The fitted logistic curves represent increasing crab abundance, with shaded ± 1 SE. Points represent actual observations.

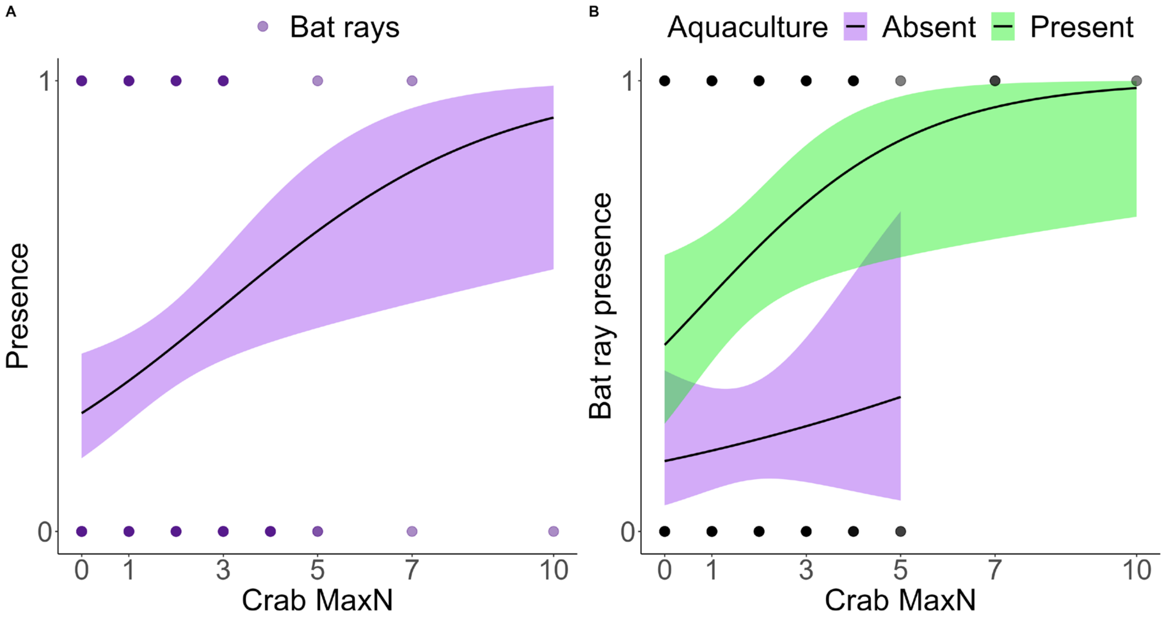


Figure 6. Relationship between bat ray presence and abundance (MaxN) of all cancrid crabs (Dungeness and rock crabs) (A) across all deployments, and (B) in habitats with and without the presence of aquaculture. The fitted logistic curves represent the probability of bat ray presence as a binary response (0, 1) with and without the presence of aquaculture. Shaded confidence bands represent 1 ± SE and points represent actual observations.

Crab abundance (Appendix B, Table 7) was a significant predictor of bat ray presence (Fig. 6a), and this was mainly due to the significant and positive relationship between crab abundance and bat ray presence in habitats with aquaculture ($\beta = 0.366$, *df* = 92, SE = 0.14, $z = 2.63$, $P = 0.009$, Fig. 6b). There was no relationship between the likelihood of observing a leopard shark and increasing crab abundance ($\beta = -0.08$, *df* = 92, SE = 0.13, $z = -0.640$, $P = 0.522$). Rock crab abundance was not a significant predictor of elasmobranch presence in general (β = -0.11, df = 92, SE = 0.443, z = -0.252, P = 0.801). Aquaculture presence and bat ray presence had significant interactive effects on Dungeness crab TOA (ANOVA; $F_{1,34}$ = 4.34, P = 0.044) with bat ray presence increasing the TOA of crabs in general (ANOVA; $F_{1,34}$ = 4.85, P = 0.034, Fig. 7), but more so in the absence of aquaculture.

Table 4. Summary of the hurdle model results for predictors of rock crab (Pacific rock crab and red rock crab) presence and abundance. The first part of the model (zero hurdle) predicts the likelihood of observing a rock crab as a binary (0, 1) response, and the second part of the model (count model) shows what response variables influence the abundance or count (1, 2, 3, 4) of rock crabs using a negative binomial distribution. The estimate represents the strength of the relationship of significant predictors and whether the relationship is positive or negative.

Zero hurdle model			Count model	
Variable	β	P	β	P
Intercept	-86.59	**0.011**	-46.72	0.826
Habitat	-1.39	**0.029**	1.50	0.644
Aquaculture presence	1.05	0.106	18.77	0.830
Salinity (ppt)	0.20	0.347	1.24	0.546
pH	10.81	**0.021**	-6.27	0.853
Temperature (°C)	-0.13	0.300	0.16	0.923
Dissolved oxygen (mg · L^{-1})	-0.75	0.240	2.78	0.642
Secchi depth (m)	1.94	0.060	-0.00	0.999
		Log (theta)	7.80	

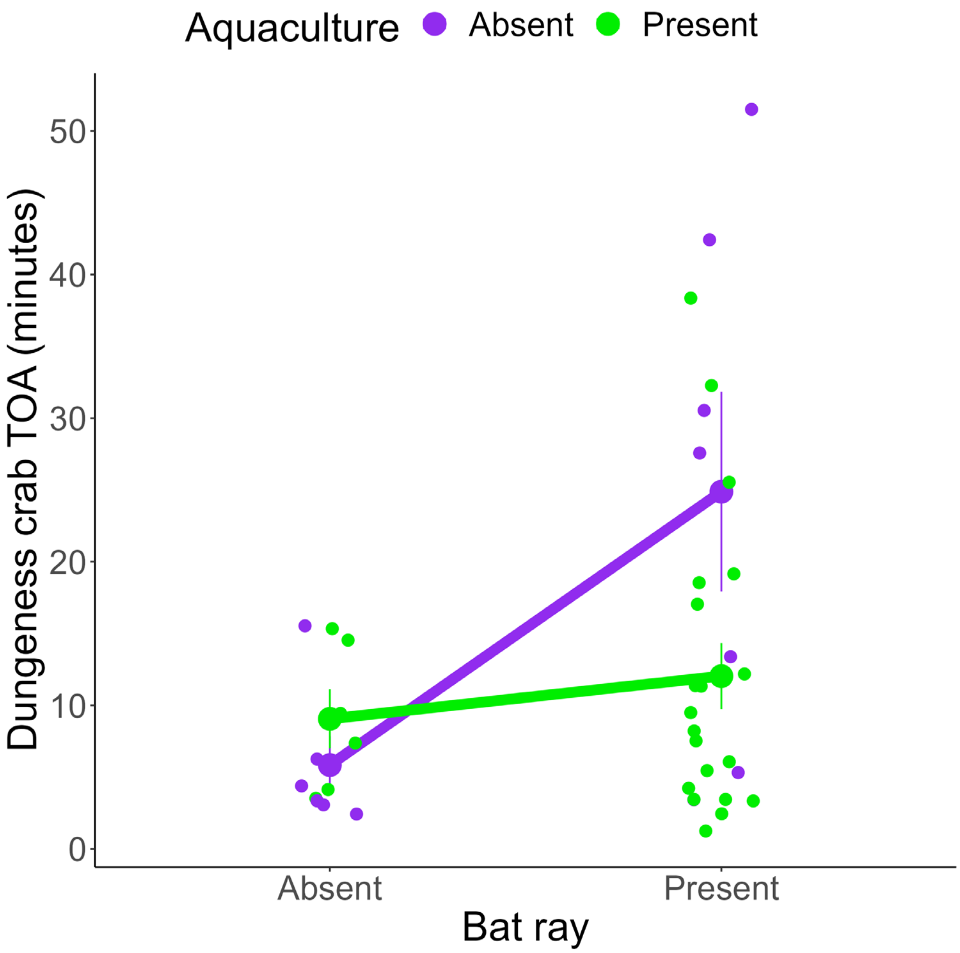


Figure 7. The relationship between Dungeness crab TOA (time of arrival, in minutes) and bat ray presence or absence in and out of aquaculture habitats. The trendlines represent increasing Dungeness crab TOA as a continuous response. Points represent actual observations, larger points at the ends of each trendline represent means, error bars represent 1 ± SE, and color distinguishes between the presence or absence of aquaculture.

DISCUSSION

Based on the analyses of BRUV deployments, bat rays are more likely to be present in habitats with aquaculture structure, while leopard sharks had not significant or positive associations in habitats with and without aquaculture structure. The compressed, discoid body of bat rays may be well-suited to foraging in and around these various types of aquaculture structures, and the increased likelihood of observing this species in and around aquaculture could be attributed to increased prey availability and predator avoidance (Forrest *et al.* 2009). In contrast, aquaculture structure does not appear to be an important factor influencing leopard shark habitat use, and higher degrees of fidelity to turbid waters, likely due to advantages hunting prey and/or the avoidance of predators, appear to be more important (Carlisle and Starr, 2010). Nevertheless, the positive effect of oyster aquaculture on the presence of bat rays in Humboldt Bay indicates that oyster aquaculture can be an important factor influencing elasmobranch habitat use and provides a new understanding of how oyster aquaculture can influence the behavior of mobile predators in nearshore marine systems.

There are two main hypothesized mechanisms through which bivalve aquaculture operations might attract mobile predatory species like bat rays. The first is the addition of physical structure to the environment. This includes physical farming structures as well as the biotic structure provided by the bivalves themselves. The physical structure of the farm and the fouling that concentrates on bivalves and structures create an attraction for a variety of species (e.g., Costa-Pierce and Bridger 2002). Second, the farmed bivalves, the organisms growing on or otherwise associated with the farm infrastructure, and those organisms impacted by organic loading related to farming, may be important food resources for mobile predators. For example, crabs and other crustaceans, molluscs, and demersal fish appear to benefit from increased food availability under bivalve suspended culture (e.g., McKindsey *et al.*, 2011). Thus, for mobile predatory species like rays, complex structure formed by oyster culture is likely to provide a place both to search for prey and to avoid becoming prey to larger predators.

Several studies in U.S. West Coast estuaries have documented abundant, highly diverse infaunal communities associated with on-bottom oyster culture. In Humboldt Bay, where bat rays feed on infaunal invertebrates in addition to crabs (Gray *et al.,* 1997), the diversity and abundance of infauna in on-bottom oyster culture were found to be higher than in open mudflat, but lower than that in eelgrass (Trianni, 1995). In another study in Humboldt Bay, the diversity and abundance of infaunal invertebrates around long line oyster culture were also similar to those observed at eelgrass reference areas (Rumrill and Poulton, 2004). Although I did not sample infauna in our study, the fact that bat rays were more likely to be present in and around aquaculture independent of habitat (mudflat vs eelgrass) suggests that variation in infaunal food resources specifically, were not driving this pattern. In contrast, oyster longlines in Humboldt Bay have been shown to harbor more small fish (Pinnix *et al.,* 2005) than eelgrass or open mud habitats, and more staghorn sculpin (*Leptocottus armatus*) and caridean shrimp (*Crangon franciscorum*) in high-density oyster long-line plots compared to lower-density oyster plots (Rumrill and Poulton, 2004), suggesting that food availability in aquaculture may in part be driving bat ray presence there (see below).

Predator avoidance by bat rays in aquaculture habitats could explain why bat rays were observed in close to half of all deployments in aquaculture while their main predator, sevengill sharks, were observed in only two deployments, and never in aquaculture-modified habitats. In southeast Tasmania, adult sevengill sharks are abundant in shallow coastal regions in the summer and prey on gummy sharks (Williams and Schaap, 1992; Stevens and West, 1997; Barnett *et al.*, 2010), a smaller mesopredator like bat rays. It has been hypothesized that gummy sharks likely use coastal habitats based on trade-offs between predation risk from sevengill sharks and food availability (Heupel *et al.*, 2007). The high abundances of both sevengill sharks and the common occurrence of gummy sharks found in their diets (Barnett *et al.* 2010) indicates that gummy sharks are exposed to high predation risks and that coastal habitats may not provide protection from predation, but increased food availability could be the main reason for the gummy sharks continued use of these areas. A similar scenario may be playing out in Humboldt Bay with sevengills and bat rays. While shallow coastal habitats provide important foraging grounds for sevengills (Ebert, 1991), aquaculture structure may inhibit the foraging capabilities of these larger predators, thereby providing an added benefit of protection (Theuerkauf *et al.,* 2022) for bat rays. Regardless of the precise mechanism driving increased bat ray presence in oyster aquaculture in Humboldt Bay, my findings are consistent with the limited amount of information for the effects of elevated culture systems on mobile fish species, which describe effects best viewed as neutral or positive (rather than adverse) (McKindsey *et al.*, 2006, Dealteris *et al.,* 2004, Leguerrier *et al.* 2004, Laffargue *et al.*, 2006, Erbland and Ozbay, 2008).

In addition to aquaculture presence, elevated water temperature was a significant predictor of bat ray presence. Consistent with the idea that temperature is an important driver of elasmobranch foraging, was my observation that bat ray presence in Humboldt Bay was positively associated with increasing water temperature. Diel movement to locate a preferred temperature range (i.e., behavioral thermoregulation) may be particularly important to the foraging success of many sharks and rays (Carey *et al.*, 1990; Matern *et al.,* 2000; Sims *et al.,* 2006; Thums *et al.,* 2013). This is because thermoregulatory behavior may provide physiological and/or metabolic benefits to the individual that offset movement costs (i.e., energy savings that could be allocated to growth or reproduction). Bat rays in Tomales Bay, CA have been shown to display strong diel movements (Matern *et al.,* 2000) and a combination of telemetry data, foraging patterns, and respiratory temperature-sensitivity in this species, strongly suggest behavioral thermoregulation as the primary driver of this movement pattern (Matern *et al.,* 2000). Specifically, bat rays swim toward the warmer, shallower feeding grounds of the inner bay from 2:50–14:50h where they forage vigorously from approximately 12:00–20:00 h, as indicated by elevated body temperature. Their movements back toward the outer bay from 14:50–2:50h eventually take them to cooler water where digestion and assimilation can take place more efficiently. Bat rays in Humboldt Bay may be employing this same strategy and forage in warmer, shallow, habitats during the day at incoming tides and return to the deeper, cooler, channels as the outgoing tide leaves these areas exposed. A similar ‘‘hunt warm, rest cool’’ strategy has been observed in male dogfish, *Scyliorhinus canicula*, and is thought to lower their daily energetic costs by ~ 4 % (Sims *et al.,* 2006).

The use of turbid coastal environments like estuaries is considered to be an anti-predator strategy employed by young sharks (Yates *et al.,* 2015), although relatively few studies have investigated this relationship empirically. Thus, the increased presence of leopard sharks and increased abundance of bat rays in more turbid water in Humboldt Bay could be attributed to predator avoidance (Bethea *et al*., 2015), especially for leopard sharks, which use turbid estuaries as nursery areas (Ebert and Ebert, 2005). More specifically, the preferential use of turbid environments by leopard sharks and bat rays could be an adaptive strategy for avoiding predation by sevengill sharks (*Notorynchus cepedianus*), their main predator in Humboldt Bay (Ebert, 1991). However, sevengill sharks have been observed to be most active on shallow-water mudflats under conditions of poor light and prefer water that is very turbid (Ebert, 1991). It has therefore been suggested that many of the sevengill’s fast-swimming prey species are more vulnerable in water of poor visibility – suggesting against the use of turbid environments by bat rays and leopard sharks as an anti-predator strategy.

In contrast, turbid environments may provide abundant prey for small sharks and rays (Clarke, 1971; Blaber and Blaber, 1980; Yates *et al.,* 2015) or facilitate stealthy hunting strategies (Heithaus, 2001; Yates *et al.,* 2015). Leopard sharks are strongly influenced by tidal movements and will swim with or against tidal currents to remain in certain intertidal regions (Carlisle and Starr, 2010). Tidal flow can disrupt sediment, making underwater conditions more turbid (Uncles *et al.,* 2002), and turbid conditions are thought to provide abundant prey (Bethea *et al*., 2014). Thus, leopard sharks could be more abundant in areas with increased turbidity to forage. The observed greater number of bat rays on mudflats could be connected to the observed increase in turbidity, where conditions on mudflats are presumably more turbid because resuspension of bottom sediments are more frequent when eelgrass is absent (Ros *et al*., 2014). Given the above prediction, it is worth noting that turbidity measurements taken from mudflat habitats were significantly greater than measurements taken from eelgrass habitats.

Higher temperatures and salinities were significant factors influencing the abundance of Dungeness crabs. Warmer temperatures are an important factor influencing Dungeness crab distribution (McLean and Todgham, 2015) and the average temperatures (~ 15 °C) I observed during sampling are considered optimal for Dungeness crab activity and increase metabolic rates (Appendix A, Fig. 11) (Curtis and McGaw, 2012). Similarly, warmer temperatures increase the activity of bat rays (Schlaff *et al*., 2014). Since there is an increased likelihood of observing bat rays in aquaculture habitats at warmer temperatures, Dungeness crabs might be more vulnerable to predation because their activity also increases during warmer periods (Curtis and McGaw, 2012). Thus, Dungeness crab abundance might be lower than anticipated in habitats where temperatures are warmer and there is an increased likelihood of observing bat rays. Dungeness crabs will reduce activity and exhibit behaviors indicative of stress at low salinity (< 24 ppt) and prefer more saline conditions (Curtis and McGaw, 2012). However, the lowest salinity observed during sampling was 32 ppt (Appendix A, Fig. 12) and so it was unlikely that salinity played any role in Dungeness crab activity and vulnerability to predation in aquaculture habitats.

Prey density and availability (Heithaus *et al.,* 2002; Shepard *et al.,* 2006; Torres *et al.,* 2006; Jaine *et al.,* 2012) and predator avoidance (Heupel and Hueter, 2002; Collins *et al.,* 2007; Heithaus *et al.* 2009) are thought to influence movement patterns and habitat choice for many elasmobranch species. Prey species, or the predators themselves must balance trade-offs between the benefits of hunting prey and the costs of avoiding predators (Schmitz *et al.*, 1997; Heithaus and Dill, 2002; Preisser *et al.*, 2005; Ripple and Beschta, 2007). Further, habitat complexity, like that provided by oyster aquaculture, can shift the balance of this tradeoff and shape predator-prey interactions by influencing encounter rates between predators and prey, the likelihood of an attack, and the probability that prey will escape (Lima and Dill, 1990). Based on my findings, I hypothesize that the positive effect of aquaculture presence on bat ray presence mediates bat ray-Dungeness crab interactions in two ways.

First, the lack of a relationship between crab abundance and aquaculture presence could be attributed to increased predation pressure (i.e., consumptive effects) by bat rays on cancrid crabs in aquaculture habitats. Structured estuarine habitats including seagrass and oyster reefs are widely recognized to provide valuable refuge and food to a wide variety of organisms including commercially important fish and invertebrates (Heck *et al.,* 2003, Boström *et al.,* 2006, Stunz *et al.,* 2010, Whitlow and Grabowski, 2012, Grabowski *et al.,* 2012, Theuerkauf *et al*., 2022), including Dungeness crab. On the U.S. West Coast, and including Humboldt Bay, complex oyster habitat is now mainly provided by the commercially cultured oysters. The effects of complex oyster habitat on juvenile Dungeness crab abundance have been studied extensively, and results indicate that oyster habitats, including oyster aquaculture contribute more to juvenile crab production than eelgrass or open unstructured mud (e.g., Dumbauld *et al.,* 2021). Further, predation on juvenile *M. magister* has been found to be highest in open mud habitat and lowest in structurally complex habitats such as that provided by oyster culture (e.g., Fernandez *et al.,* 1993). It is therefore surprising that I did not observe more Dungeness crabs in structurally complex aquaculture habitats. Higher crab abundances in oyster aquaculture habitats have been attributed to the structure they provide that serves as refuge from predators (Lefcheck *et al.,* 2019). However, as noted earlier, the compressed body of bat rays may be well-suited to foraging in and around elevated oyster aquaculture. Further, bat rays may use the habitat complexity provided by oyster aquaculture as a ‘safe place’ to forage freely in the absence of seven-gill shark predation, as has been observed in other mesopredatory ray species (e.g., Sherman *et al.,* 2020). As Dungeness crabs are an important prey species for bat rays (Gray *et al.,* 1997; Hughes *et al.,* 2014), their abundance around oyster aquaculture in Humboldt Bay may therefore be lower than expected because of the increased presence of bat rays in and around aquaculture. This hypothesis is supported by my finding that increasing crab abundance strongly predicted the presence of bat rays in, but not outside of, aquaculture-modified habitats. The increased presence of bat rays in and around aquaculture could result in increased predation pressure on crabs in the modified habitats. Indeed, certain types of aquaculture operations have been shown to support comparable or greater consumption rates than natural reefs, suggesting an important role for this novel structured habitat in maintaining coastal food webs (Lefcheck *et al.,* 2019).

Second, the lack of a relationship between crab abundance and aquaculture presence could be attributed to increased predation risk (i.e., non-consumptive effects) by bat rays on cancrid crabs in aquaculture habitats. Predators not only consume prey, but also exert non-consumptive effects by eliciting behavioral changes in their prey that increase prey survival but come at the cost of reduced feeding, growth and/or reproduction (Wirsing *et al*., 2021). Studies examining the influence of habitat complexity on predator-prey interactions have found a decrease in prey activity levels in habitats with added structure, indicating that prey may spend more time taking shelter, possibly because the structural elements of the habitat provide shelter and places to hide (e.g., Chang and Todd, 2023). When bat rays are present, crabs may decrease their activity levels and opt to hide in habitats where increased structure provides shelter. Thus, crab abundance observed in BRUVS deployments may be under-represented in habitats with aquaculture, due to the non-consumptive influence bat rays exert in these habitats. Dungeness crabs may initiate behavioral changes when they sense predators to attempt to reduce their risk of predation (Lima and Dill, 1990), as was evidenced by the increased TOA of crabs to the BRUVS when bat rays were present, even when a food source was nearby (i.e., squid bait). Further support for this hypothesis is provided by the finding that crab TOA was even longer in the absence of aquaculture because increased activity should be less risky in habitats where there is the perception of structural refuge from predators. (Theuerkauf *et al.,* 2022). Crabs present in habitats with aquaculture may increase their activity in response to decreased perceived predation risk (i.e., the individual's assessment of the likelihood of a predator's attack; Lima, 1998; Verdolin, 2006; Eccard *et al.*, 2020), even when bat rays are present. Under perceived predator threat, crabs should respond with behaviors that maximize immediate survival (Stein and Magnuson, 1976), such as retreating to refuge structure or reducing their activity (Stein and Magnuson, 1976; Laurel and Brown, 2006). Crabs may perceive aquaculture (habitats with more structure) as less risky habitat because of the proximity of refugia (i.e., structure) and respond by increasing their activity to maximize foraging success. Future field manipulation is needed to directly test the hypothesis of non-consumptive effects on crabs in aquaculture-modified habitats. Future field studies (e.g., measuring the loss rates and behaviors of crabs tethered in an out of habitats with oyster aquaculture) are needed to directly test the hypothesis of increased bat ray presence on crab mortality (i.e., consumptive bat ray effects) and crab activity/sheltering (i.e., non-consumptive bat ray effects) in aquaculture-modified habitats.

Although BRUVS have been shown to generate relative abundance estimates similar to those generated by other survey methods (e.g., scientific longline surveys; Brooks *et al.*, 2011), their use does come with limitations. For instance, MaxN estimates from BRUVS surveys can be sensitive to both density-dependent (i.e., species abundance) and density-independent (e.g., swimming speed, attraction to bait plume, and visibility) factors (Kilfoil *et al.*, 2021), thus care should be taken in interpreting my survey results, as well as potential management decisions based on these data. Regarding density-dependent factors, previous research has indicated that the assumed linear relationship between MaxN and true abundance is likely violated under certain conditions (Campbell *et al.*, 2015; Kilfoil *et al.*, 2017; Sherman *et al.*, 2018). However, this deviation from linearity has only been observed under high densities (~ 10 sharks km^{-2} Kilfoil *et al.*, 2017) and so should be of little concern to my study as deployments never exceed a MaxN of 4 sharks. With regard to density-independent factors, both aspects of species behavior and environmental conditions and can influence MaxN. For example, species-specific movement characteristics could influence relative abundance data (e.g., Ward-Paige *et al.*, 2010), with faster-swimming species appearing more abundant. Differences in swimming speeds are unlikely to have influenced differences in the relative abundances of the most common elasmobranchs in my study as both bat rays (Klimley *et al.*, 2005) and leopard sharks (Gruber and Dickson, 1997) have similar maximum speeds (~0.5 m · s^{-1}). Species may also differ in their relative attraction towards the bait, which may bias relative abundance estimates. Attraction towards bait is known to vary by the amount of bait used (e.g., Heagney *et al.*, 2007), and although I standardized the amount of bait used in this study, the type of bait selected (e.g., Dorman *et al.*, 2012) can also influence relative abundance in species-specific ways (e.g., Harvey *et al.*, 2007). Bat rays and leopard sharks overlap considerably in their food habits in Humboldt Bay (Ebert and Ebert, 2005; Gray *et al.*, 1997), but the relative importance of molluscan prey is much higher in bat rays (Gray *et al.,* 1997) than leopard sharks (Ebert and Ebert, 2005), and so the two species could differ in their relative attraction to the squid bait used my study. Perhaps most importantly, most of the footage recorded by the cameras in my study had less than ideal visibility (~ 1.5 m on average), which means that all individuals of each species in the area were unlikely to be captured by cameras; thus, the results likely represent a conservative estimate of relative abundance. It is also possible that visibility and the limited number of deployments may have contributed to the apparent absence of the larger, roaming sevengill sharks. Many larger sharks are cautious when approaching baited cameras and often maintain a greater distance from the bait bag than smaller species (Yon *et al.,* 2020) and, as such, sevengill sharks may have been underestimated in my surveys because of limited visibility. Despite these limitations, the use of BRUVS in my study provided a viable survey method that detected habitat- and species-specific variation in shark abundance with minimal impact to the species or the habitats sampled.

CONCLUSIONS

I found strong evidence that bat ray presence is significantly and positively associated with oyster aquaculture habitats in Humboldt Bay. Although the mechanisms of preference for oyster aquaculture habitat by bat rays might reflect predator avoidance, I found that abundances of cancrid crabs, a common prey item for bat rays, predicted bat ray presence in habitats with aquaculture; suggesting that prey availability was an important driver of bat ray use of aquaculture habitats. Thus, bat rays – a species that has been historically vilified as the main cause of oyster loss by the aquaculture industry (Gray *et al.*, 1997) – may have reciprocal positive effects on oyster aquaculture by removing a common predator of oysters and deterring their activity in the vicinity of cultured oysters. Although environmental variables including temperature, turbidity, and salinity are also likely to dictate the movement and habitat use of both elasmobranchs and their prey, my research highlights the importance of considering how oyster aquaculture may contribute to changes in the distribution and abundance of elasmobranch species in modified coastal habitats. Future research in the form of predation intensity experiments (e.g., prey tethering) should aim to understand the specific mechanisms of attraction to oyster aquaculture structure by bat rays in coastal environments as the industry continues to expand and subsequently cause structural habitat to change and modification in nearshore marine ecosystems.

REFERENCES

Aragones, L. V., Lawler, I. R., Foley, W. J., & Marsh, H. (2006). Dugong grazing and turtle cropping: grazing optimization in tropical seagrass systems? *Oecologia*, *149*(4), 635–647. https://doi.org/10.1007/s00442-006-0477-1

Barnett, A., Abrantes, K., Stevens, J. D., Yick, J. L., Frusher, S. D., & Semmens, J. M. (2010). Predator–prey relationships and foraging ecology of a marine apex predator with a wide temperate distribution. *Marine Ecology Progress Series*, *416*, 189–200. https://doi.org/10.3354/meps08778

Barnett, Adam, Abrantes, K. G., Stevens, J. D., Bruce, B. D., & Semmens, J. M. (2010). Fine-scale movements of the broadnose sevengill shark and its main prey, the gummy shark. *PLoS One*, *5*(12), e15464. https://doi.org/10.1371/journal.pone.0015464

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., & Doherty, P. A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, *299*(5605), 389–392. https://doi.org/10.1126/science.1079777

Bethea, D. M., Ajemian, M. J., Carlson, J. K., Hoffmayer, E. R., Imhoff, J. L., Grubbs, R. D., Peterson, C. T., & Burgess, G. H. (2015). Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico. *Environmental Biology of Fishes*, *98*(5), 1233–1254. https://doi.org/10.1007/s10641-014-0355-3

Bishop, M. J., Mayer-Pinto, M., Airoldi, L., Firth, L. B., Morris, R. L., Loke, L. H. L., Hawkins, S. J., Naylor, L. A., Coleman, R. A., Chee, S. Y., & Dafforn, K. A. (2017). Effects of ocean sprawl on ecological connectivity: impacts and solutions. *Journal of Experimental Marine Biology and Ecology*, *492*, 7–30. https://doi.org/10.1016/j.jembe.2017.01.021

Blaber, S. J. M., & Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology*, *17*(2), 143–162. https://doi.org/10.1111/j.1095-8649.1980.tb02749.x

Bos, A. R., Bouma, T. J., de Kort, G. L. J., & van Katwijk, M. M. (2007). Ecosystem engineering by annual intertidal seagrass beds: Sediment accretion and modification. *Estuarine, Coastal and Shelf Science*, *74*(1–2), 344–348. https://doi.org/10.1016/j.ecss.2007.04.006

Boström, C., Jackson, E. L., & Simenstad, C. A. (2006). Seagrass landscapes and their effects on associated fauna: A review. *Estuarine, Coastal and Shelf Science*, *68*(3–4), 383–403. https://doi.org/10.1016/j.ecss.2006.01.026

Brehmer, P. (2003). New applications of hydroacoustic methods for monitoring shallow water aquatic ecosystems: the case of mussel culture grounds. *Aquatic Living Resources*, *16*(3), 333–338. https://doi.org/10.1016/s0990-7440(03)00042-1

Brooks, E. J., Sloman, K. A., Sims, D. W., & Danylchuk, A. J. (2011). Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. *Endangered Species Research*, *13*(3), 231–243. https://doi.org/10.3354/esr00331

Brown, A. C., & Terwilliger, N. B. (1999). Developmental changes in oxygen uptake in *Cancer magister* (Dana) in response to changes in salinity and temperature. *Journal of Experimental Marine Biology and Ecology*, *241*(2), 179–192. https://doi.org/10.1016/s0022-0981(99)00071-4

Byers, J. E., Holmes, Z. C., & Malek, J. C. (2017). Contrasting complexity of adjacent habitats influences the strength of cascading predatory effects. *Oecologia*, *185*(1), 107–117. https://doi.org/10.1007/s00442-017-3928-y

Callier, M. D., Byron, C. J., Bengtson, D. A., Cranford, P. J., Cross, S. F., Focken, U., Jansen, H. M., Kamermans, P., Kiessling, A., Landry, T., O'Beirn, F., Petersson, E., Rheault, R. B., Strand, Ø., Sundell, K., Svåsand, T., Wikfors, G. H., & McKindsey, C. W. (2018). Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. *Reviews in Aquaculture*, *10*(4), 924–949. https://doi.org/10.1111/raq.12208

Campbell, M. D., Pollack, A. G., Gledhill, C. T., Switzer, T. S., & DeVries, D. A. (2015). Comparison of relative abundance indices calculated from two methods of generating video count data. *Fisheries Research*, *170*, 125–133. https://doi.org/10.1016/j.fishres.2015.05.011

Cappo, M., Harvey, E., Malcolm, H., & Speare, P. (2003a). *Potential of video techniques to monitordiversity, abundance and size of fish in studies of Marine Protected Areas*.

Cappo, M., Harvey, E. S., Malcolm, H., & Speare, P. (2003b). Advantages and applications of novel "video-fishing" techniques to design and monitor Marine

Protected Areas. In J. P. Beumer, A. Grant, & D. C. Smith (Eds.), *World Congress on Aquatic Protected Areas* (pp. 455–464).

Cappo, M. & Harvey, Euan & Shortis, Mark. (2007). Counting and measuring fish with baited video techniques -an overview. In: Lyle JM, Furlani DM, Buxton CD, editors. Cutting-edge technologies in fish and fisheries science. 2006 AFSB Conference and Workshop, Hobart, Tasmania: Australian Society for Fish Biology, 101-114.

Carey, F. G., Scharold, J. V., & Kalmijn, A. J. (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, *106*(3), 329–342. https://doi.org/10.1007/bf01344309

Carlisle, A. B., & Starr, R. M. (2010). Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. *Environmental Biology of Fishes*, *89*(1), 31–45. https://doi.org/10.1007/s10641-010-9667-0

Chang, C.-C., & Todd, P. A. (2023). Reduced predation pressure as a potential driver of prey diversity and abundance in complex habitats. *Npj Biodiversity*, *2*(1), 1–5. https://doi.org/10.1038/s44185-022-00007-x

Clarke, T. A. (1971). The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. *Pacific Science*, *25*, 133–144.

Cloern, J. E., Abreu, P. C., Carstensen, J., Chauvaud, L., Elmgren, R., Grall, J., Greening, H., Johansson, J. O. R., Kahru, M., Sherwood, E. T., Xu, J., & Yin, K. (2016). Human activities and climate variability drive fast-paced change across the world's estuarine–coastal ecosystems. *Global Change Biology*, *22*(2), 513–529. https://doi.org/10.1111/gcb.13059

Collins, A. B., Heupel, M. R., Hueter, R. E., & Motta, P. J. (2007). Hard prey specialists or opportunistic generalists? An examination of the diet of the cownose ray, *Rhinoptera bonasus*. *Marine & Freshwater Research*, *58*(1), 135. https://doi.org/10.1071/mf05227

Costa-Pierce, B. A. (2010). Sustainable ecological aquaculture systems: The need for a new social contract for aquaculture development. *Marine Technology Society Journal*, *44*(3), 88–112. https://doi.org/10.4031/mtsj.44.3.3

Costa-Pierce, B. A., & Bridger, C. J. (2002). Aquaculture facilities as habitats and ecosystems. Responsible marine aquaculture. CABI Publishing, Cambridge, 105-144.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, *23*(4), 194–201. https://doi.org/10.1016/j.tree.2007.12.004.

Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., & Byrd, G. V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science*, *307*(5717), 1959–1961. https://doi.org/10.1126/science.1108485

Currey-Randall, L. M., Cappo, M., Simpfendorfer, C. A., Farabaugh, N. F., & Heupel, M. R. (2020). Optimal soak times for Baited Remote Underwater Video Station surveys of reef-associated elasmobranchs. *PLoS One*, *15*(5), e0231688. https://doi.org/10.1371/journal.pone.0231688

Curtis, D. L., & McGaw, I. J. (2012). Salinity and thermal preference of Dungeness crabs in the lab and in the field: Effects of food availability and starvation. *Journal of Experimental Marine Biology and Ecology*, *413*, 113–120. https://doi.org/10.1016/j.jembe.2011.12.005

Dealteris, J. T., Kilpatrick, B. D., & Rheault, R. B. (2004). A comparative evaluation of the habitat value of shellfish aquaculture gear, submerged aquatic vegetation and a non-vegetated seabed. *Journal of Shellfish Research*, *23*, 867–874.

de la Haye, K. L., Spicer, J. I., Widdicombe, S., & Briffa, M. (2012). Reduced pH sea water disrupts chemo-responsive behaviour in an intertidal crustacean. *Journal of Experimental Marine Biology and Ecology*, *412*, 134–140. https://doi.org/10.1016/j.jembe.2011.11.013

Díaz López, B., & Methion, S. (2017). The impact of shellfish farming on common bottlenose dolphins' use of habitat. *Marine Biology*, *164*(4). https://doi.org/10.1007/s00227-017-3125-x

Dorman, S. R., Harvey, E. S., & Newman, S. J. (2012). Bait effects in sampling coral reef fish assemblages with stereo-BRUVs. *PloS One*, *7*(7), e41538. https://doi.org/10.1371/journal.pone.0041538

Dumbauld, B. R., Murphy, J. R., McCoy, L., & Lewis, N. S. (2021). A comparison of the juvenile Dungeness crab *Metacarcinus magister* habitat provided by contemporary oyster aquaculture versus historical native oysters in a U.S. west coast estuary. *Journal of Shellfish Research*, *40*(1). https://doi.org/10.2983/035.040.0116

Dumbauld, B. R., Ruesink, J. L., & Rumrill, S. S. (2009). The ecological role of bivalve shellfish aquaculture in the estuarine environment: A review with application to oyster and clam culture in West Coast (USA) estuaries. *Aquaculture*, *290*(3–4), 196–223. https://doi.org/10.1016/j.aquaculture.2009.02.033

Dunbrack, R., & Zielinski, R. (2003). Seasonal and diurnal activity of sixgill sharks (*Hexanchus griseus*) on a shallow water reef in the Strait of Georgia, British Columbia. *Canadian Journal of Zoology*, *81*(6), 1107–1111. https://doi.org/10.1139/z03-087

Ebert, D. A. (1989). Life history of the sevengill shark, *Notorynchus cepedianus*, in two northern California Bays. *California Fish and Game*, *75*, 102–112.

Ebert, D. A. (1991). Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. *South African Journal of Marine Science/Suid-Afrikaanse Tydskrif Vir Seewetenskap*, *11*(1), 455–465. https://doi.org/10.2989/025776191784287637

Ebert, David A. (2002). Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). *Marine & Freshwater Research*, *53*(2), 517. https://doi.org/10.1071/mf01143

Ebert, David A., & Ebert, T. B. (2005). Reproduction, diet and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California, USA. *Marine & Freshwater Research*, *56*(8), 1089. https://doi.org/10.1071/mf05069

Eccard, J. A., Liesenjohann, T., & Dammhahn, M. (2020). Among-individual differences in foraging modulate resource exploitation under perceived predation risk. *Oecologia*, *194*(4), 621–634. https://doi.org/10.1007/s00442-020-04773-y

Economakis, A. E., & Lobel, P. S. (1998). Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes*, *51*(2), 129–139. https://doi.org/10.1023/a:1007416813214

Erbland, P. J., & Ozbay, G. (2008). A comparison of the macrofaunal communities inhabiting a *Crassostrea virginica* oyster reef and oyster aquaculture gear in Indian River Bay, Delaware. *Journal of Shellfish Research*, *27*(4), 757–768. https://doi.org/10.2983/0730-8000(2008)27[757:acotmc]2.0.co;2

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fernandez, M., Iribame, O., & Armstrong, D. (1993). Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Marine Ecology Progress Series*, *92*, 171–177. https://doi.org/10.3354/meps092171

Forrest, B. M., Keeley, N. B., Hopkins, G. A., Webb, S. C., & Clement, D. M. (2009). Bivalve aquaculture in estuaries: Review and synthesis of oyster cultivation effects. *Aquaculture*, *298*(1–2), 1–15. https://doi.org/10.1016/j.aquaculture.2009.09.032

Frank, D. A. (2008). Evidence for top predator control of a grazing ecosystem. *Oikos*, *117*(11), 1718–1724. https://doi.org/10.1111/j.1600-0706.2008.16846.x

Frisk, M. G., Miller, T. J., & Fogarty, M. J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(5), 969–981. https://doi.org/10.1139/f01-051

Gore, M., Ormond, R., Clarke, C., Kohler, J., Millar, C., & Brooks, E. (2020). Application of photo-identification and lengthened deployment periods to baited Remote Underwater Video Stations (BRUVS) abundance estimates of coral reef sharks. *Oceans*, *1*(4), 274–299. https://doi.org/10.3390/oceans1040019

Grabowski, J. H. (2004). Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. *Ecology*, *85*(4), 995–1004. https://doi.org/10.1890/03-0067

Grabowski, J. H., Brumbaugh, R. D., Conrad, R. F., Keeler, A. G., Opaluch, J. J., Peterson, C. H., Piehler, M. F., Powers, S. P., & Smyth, A. R. (2012). Economic valuation of ecosystem services provided by oyster reefs. *Bioscience*, *62*(10), 900–909. https://doi.org/10.1525/bio.2012.62.10.10

Gray, A. E., Mulligan, T. J., & Hannah, R. W. (1997). Food habits, occurrence, and population structure of the bat ray, *Myliobatis californica*, in Humboldt Bay, California. *Environmental Biology of Fishes*, *49*(2), 227–238. https://doi.org/10.1023/a:1007379606233

Gruber, S. J., & Dickson, K. A. (1997). Effects of endurance training in the leopard shark, Triakis semifasciata. *Physiological Zoology*, *70*(4), 481–492. https://doi.org/10.1086/515851

Halpern, B. S., Borer, E. T., Seabloom, E. W., & Shurin, J. B. (2005). Predator effects on herbivore and plant stability. *Ecology Letters*, *8*(2), 189–194. https://doi.org/10.1111/j.1461-0248.2004.00712.x

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., Lowndes, J. S., Rockwood, R. C., Selig, E. R., Selkoe, K. A., & Walbridge, S. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications*, *6*(1), 7615. https://doi.org/10.1038/ncomms8615

Harvey, E. S., Cappo, M., Butler, J. J., Hall, N., & Kendrick, G. A. (2007). Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. *Marine Ecology Progress Series*, *350*, 245–254. https://doi.org/10.3354/meps07192

Harvey, E. S., McLean, D. L., Goetze, J. S., Saunders, B. J., Langlois, T. J., Monk, J., Barrett, N., Wilson, S. K., Holmes, T. H., Ierodiaconou, D., Jordan, A. R., Meekan, M. G., Malcolm, H. A., Heupel, M. R., Harasti, D., Huveneers, C., Knott, N. A., Fairclough, D. V., Currey-Randall, L. M., Newman, S. J. (2021).

The BRUVs workshop – An Australia-wide synthesis of baited remote underwater video data to answer broad-scale ecological questions about fish, sharks and rays. *Marine Policy*, *127*(104430), 104430. https://doi.org/10.1016/j.marpol.2021.104430

Heagney, E. C., Lynch, T. P., Babcock, R. C., & Suthers, I. M. (2007). Pelagic fish assemblages assessed using mid-water baited video: standardising fish counts using bait plume size. *Marine Ecology Progress Series*, *350*, 255–266. https://doi.org/10.3354/meps07193

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., Scales, K. L., Sydeman, W. J., & Bograd, S. J. (2019). Marine top predators as climate and ecosystem sentinels. *Frontiers in Ecology and the Environment*, *17*(10), 565–574. https://doi.org/10.1002/fee.2125

Heck Hay, K. L., Jr, Hays, G., & Orth, R. J. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series*, *253*, 123–136. https://doi.org/10.3354/meps253123

Heithaus, M. R. (2004). Fish communities of subtropical seagrass meadows and associated habitats in Shark Bay, western Australia. *Bulletin of Marine Science*, *75*(1), 79–99. https://www.ingentaconnect.com/content/umrsmas/bullmar/2004/00000075/00000001/art00007

Heithaus, M. R. (2001). Predator–prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *Journal of Zoology (London, England: 1987)*, *253*(1), 53–68.

Heithaus, M. R., Delius, B. K., Wirsing, A. J., & Dunphy-Daly, M. M. (2009). Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary. *Limnology and Oceanography*, *54*(2), 472–482. https://doi.org/10.4319/lo.2009.54.2.0472

Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence Bottlenose dolphin habitat use. *Ecology*, *83*(2), 480–491. https://doi.org/10.1890/0012-9658(2002)083[0480:faatsp]2.0.co;2

Heithaus, M.R., Dill, L.M., Marshall, G.J., & Buhleier, B. (2002). Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology*, *140*(2), 237–248. https://doi.org/10.1007/s00227-001-0711-7

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, *23*(4), 202–210. https://doi.org/10.1016/j.tree.2008.01.003

Heupel, M. (2007). Exiting Terra Ceia Bay: Examination of cues stimulating migration from a summer nursery area. *American Fisheries Society Symposium*, *50*, 265–280.

Heupel, M. R., Carlson, J. K., & Simpfendorfer, C. A. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, *337*, 287–297. https://doi.org/10.3354/meps337287

Heupel, M. R., & Hueter, R. E. (2002). Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Marine & Freshwater Research*, *53*(2), 543. https://doi.org/10.1071/mf01132

Heupel, M. R., & Simpfendorfer, C. A. (2008). Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology*, *1*, 277–289. https://doi.org/10.3354/ab00030

Hoenig, J.M., & Gruber, S.H. (1990). Life-history patterns in the elasmobranchs: Implications for fisheries management. *NOAA Tech. Rep, NMFS, 90,* 1–16.

Hopkins, T. E., & Cech, J. J., Jr. (2003). The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales bay, California. *Environmental Biology of Fishes*, *66*(3), 279–291. https://doi.org/10.1023/a:1023907121605

Hughes, B. B., Levey, M. D., Brown, J. A., Fountain, M. C., Carlisle, A. B., Litvin, S. Y., Greene, C. M., Heady, W. N., & Gleason, M. G. (2014). *Nursery Functions of U.S. West Coast Estuaries: The State of Knowledge for Juveniles of Focal Invertebrate and Fish Species. The Nature Conservancy*.

Jabado, R. W., Al Hameli, S. M., Grandcourt, E. M., & Al Dhaheri, S. S. (2018). Low abundance of sharks and rays in baited remote underwater video surveys in the

Arabian Gulf. *Scientific Reports*, *8*(1), 15597. https://doi.org/10.1038/s41598-018-33611-8

Jaine, F. R. A., Couturier, L. I. E., Weeks, S. J., Townsend, K. A., Bennett, M. B., Fiora, K., & Richardson, A. J. (2012). When giants turn up: Sighting trends, environmental influences and habitat use of the manta ray *Manta alfredi* at a coral reef. *PLoS One*, *7*(10), e46170. https://doi.org/10.1371/journal.pone.0046170

Jones, K. R., Klein, C. J., Halpern, B. S., Venter, O., Grantham, H., Kuempel, C. D., Shumway, N., Friedlander, A. M., Possingham, H. P., & Watson, J. E. M. (2018). The location and protection status of earth's diminishing marine wilderness. *Current Biology*, *28*(15), 2506-2512.e3. https://doi.org/10.1016/j.cub.2018.06.010.

Juan-Jordá, M. J., Murua, H., Arrizabalaga, H., Merino, G., Pacoureau, N., & Dulvy, N. K. (2022). Seventy years of tunas, billfishes, and sharks as sentinels of global ocean health. *Science*, *378*(6620). https://doi.org/10.1126/science.abj0211

Kilfoil, J. P., Wirsing, A. J., Campbell, M. D., Kiszka, J. J., Gastrich, K. R., Heithaus, M. R., Zhang, Y., & Bond, M. E. (2017). Baited Remote Underwater Video surveys undercount sharks at high densities: insights from full-spherical camera technologies. *Marine Ecology Progress Series*, *585*, 113–121. https://doi.org/10.3354/meps12395

Kilfoil, James P., Campbell, M. D., Heithaus, M. R., & Zhang, Y. (2021). The influence of shark behavior and environmental conditions on baited remote underwater video survey results. *Ecological Modelling*, *447*(109507), 109507. https://doi.org/10.1016/j.ecolmodel.2021.109507

Klimley, A. P., Kihslinger, R. L., & Kelly, J. T. (2005). Directional and non-directional movements of bat rays, Myliobatis californica, in Tomales bay, California. *Environmental Biology of Fishes*, *74*(1), 79–88. https://doi.org/10.1007/s10641-005-3997-3

Laffargue, P., Bégout, M.-L., & Lagardère, F. (2006). Testing the potential effects of shellfish farming on swimming activity and spatial distribution of sole (*Solea solea*) in a mesocosm. *ICES Journal of Marine Science: Journal Du Conseil*, *63*(6), 1014–1028. https://doi.org/10.1016/j.icesjms.2006.03.018

Lafferty, K. D. (2004). Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecological Applications: A Publication of the Ecological Society of America*, *14*(5), 1566–1573. https://doi.org/10.1890/03-5088

Langlois, T., Goetze, J., Bond, T., Monk, J., Abesamis, R. A., Asher, J., Barrett, N., Bernard, A. T. F., Bouchet, P. J., Birt, M. J., Cappo, M., Currey-Randall, L. M., Driessen, D., Fairclough, D. V., Fullwood, L. A. F., Gibbons, B. A., Harasti, D., Heupel, M. R., Hicks, J., Harvey, E. S. (2020). A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. *Methods in Ecology and Evolution*, *11*(11), 1401–1409. https://doi.org/10.1111/2041-210x.13470

Last, P. R., & Stevens, J. D. (2009). *Sharks and rays of Australia: Second edition* (2nd ed.). Harvard University Press.

Laurel, B. J., & Brown, J. A. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. *Journal of Experimental Marine Biology and Ecology*, *329*(1), 34–46. https://doi.org/10.1016/j.jembe.2005.08.003

Lefcheck, J. S., Hughes, B. B., Johnson, A. J., Pfirrmann, B. W., Rasher, D. B., Smyth, A. R., Williams, B. L., Beck, M. W., & Orth, R. J. (2019). Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters*, *12*(4), e12645. https://doi.org/10.1111/conl.12645

Leguerrier, D., Niquil, N., Petiau, A., & Bodoy, A. (2004). Modeling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France). *Marine Ecology Progress Series*, *273*, 147–162. https://doi.org/10.3354/meps273147

Lester, E., Langlois, T., Lindgren, I., Birt, M., Bond, T., McLean, D., Vaughan, B., Holmes, T. H., & Meekan, M. (2022). Drivers of variation in occurrence, abundance, and behaviour of sharks on coral reefs. *Scientific Reports*, *12*(1). https://doi.org/10.1038/s41598-021-04024-x

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, *48*(1), 25–34. https://doi.org/10.2307/1313225

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., Kirby, M. X., Peterson, C. H., & Jackson, J. B. C. (2006).

Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, *312*(5781), 1806–1809. https://doi.org/10.1126/science.1128035

Lucifora, L. O., Menni, R. C., & Escalante, A. H. (2005). Reproduction, abundance and feeding habits of the broadnose sevengill shark *Notorynchus cepedianus* in north Patagonia, Argentina. *Marine Ecology Progress Series*, *289*, 237–244.

Luypaert, T., Hagan, J. G., McCarthy, M. L., & Poti, M. (2020). Status of marine biodiversity in the anthropocene. In *YOUMARES 9 - The Oceans: Our Research, Our Future* (pp. 57–82). Springer International Publishing.

Madin, E. M. P., Dill, L. M., Ridlon, A. D., Heithaus, M. R., & Warner, R. R. (2016). Human activities change marine ecosystems by altering predation risk. *Global Change Biology*, *22*(1), 44–60. https://doi.org/10.1111/gcb.13083

Matern, Scott A., Cech, J. J., & Hopkins, T. E. (2000). Diel movements of bat rays, *Myliobatis californica*, in Tomales bay, California: Evidence for behavioral thermoregulation? *Environmental Biology of Fishes*, *58*(2), 173–182. https://doi.org/10.1023/a:1007625212099

McKindsey, C. W., Archambault, P., Callier, M. D., & Olivier, F. (2011). Influence of suspended and off-bottom mussel culture on the sea bottom and benthic habitats: a review. *Canadian Journal of Zoology*, *89*(7), 622–646. https://doi.org/10.1139/z11-037

McLean, K. M., & Todgham, A. E. (2015). Effect of food availability on the growth and thermal physiology of juvenile Dungeness crabs (*Metacarcinus* *magister*). *Conservation Physiology*, *3*(1), cov013. https://doi.org/10.1093/conphys/cov013

Meese, E. N., & Lowe, C. G. (2019). Finding a resting place: How environmental conditions influence the habitat selection of resting batoids. *Bulletin of the Southern California Academy of Sciences*, *118*(2), 87. https://doi.org/10.3160/0038-3872-118.2.87

Michael, S. W. (1993). *Reef sharks and rays of the world: A guide to their identification, behavior and ecology*. Sea Challengers.

Moroney, D. A., & Walker, R. L. (1999). The effects of tidal and bottom placement on the growth, survival and fouling of the Eastern oyster *Crassostrea virginica*. *Journal of the World Aquaculture Society*, *30*(4), 433–442. https://doi.org/10.1111/j.1749-7345.1999.tb00991.x

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, *315*(5820), 1846–1850. https://doi.org/10.1126/science.1138657

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, *423*(6937), 280–283. https://doi.org/10.1038/nature01610

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., & Williams, S. L. (2006). A global crisis for seagrass ecosystems. *Bioscience*, *56*(12), 987. https://doi.org/10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2

Pace, M. L., Cole, J. J., Carpenter, S. R., & Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution*, *14*(12), 483–488. https://doi.org/10.1016/s0169-5347(99)01723-1

Pauly, D., Christensen, V., V., Dalsgaard, J., Froese, R., & Torres, F., Jr. (1998). Fishing down marine food webs. *Science, 279*(5352), 860–863. https://doi.org/10.1126/science.279.5352.860

Pinnix, W., Shaw, T., Acker, K., & Hetrick, N. (2023). Fish Communities in Eelgrass, Oyster Culture, and Mudflat Habitats of North Humboldt Bay. *California Final Report*.

Posit team (2023). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL, http://www.posit.co/.

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, *86*(2), 501–509. https://doi.org/10.1890/04-0719

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ricart, A. M., Ward, M., Hill, T. M., Sanford, E., Kroeker, K. J., Takeshita, Y., Merolla, S., Shukla, P., Ninokawa, A. T., Elsmore, K., & Gaylord, B. (2021). Coast-wide evidence of low pH amelioration by seagrass ecosystems. *Global Change Biology*, *27*(11), 2580–2591. https://doi.org/10.1111/gcb.15594

Ripple, W. J., & Beschta, R. L. (2007). Restoring Yellowstone's aspen with wolves. *Biological Conservation*, *138*(3–4), 514–519. https://doi.org/10.1016/j.biocon.2007.05.006

Roberts, L., Pérez-Domínguez, R., & Elliott, M. (2016). Use of baited remote underwater video (BRUV) and motion analysis for studying the impacts of underwater noise upon free ranging fish and implications for marine energy management. *Marine Pollution Bulletin*, *112*(1–2), 75–85. https://doi.org/10.1016/j.marpolbul.2016.08.039

Ros, À., Colomer, J., Serra, T., Pujol, D., Soler, M., & Casamitjana, X. (2014). Experimental observations on sediment resuspension within submerged model canopies under oscillatory flow. *Continental Shelf Research*, *91*, 220–231. https://doi.org/10.1016/j.csr.2014.10.004

Rosenblatt, A., Heithaus, M., Mather, M., Matich, P., Nifong, J., Ripple, W., & Silliman, B. (2013). The roles of large top predators in coastal ecosystems: New insights from long term ecological research. *Oceanography (Washington, D.C.)*, *26*(3), 156–167. https://doi.org/10.5670/oceanog.2013.59

Rumrill, S.S., & Poulton, V.K. (2004). Ecological role and potential impacts of molluscan shellfish culture in the estuarine environment of Humboldt Bay, CA.

Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2014). Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. *Reviews in Fish Biology and Fisheries*, *24*(4), 1089–1103. https://doi.org/10.1007/s11160-014-9364-8

Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology*, *78*(5), 1388–1399. https://doi.org/10.1890/0012-9658(1997)078[1388:bmtceo]2.0.co;2

Schobernd, Z. H., Bacheler, N. M., & Conn, P. B. (2014). Examining the utility of alternative video monitoring metrics for indexing reef fish abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(3), 464–471. https://doi.org/10.1139/cjfas-2013-0086

Shepard, E. L. C., Ahmed, M. Z., Southall, E. J., Witt, M. J., Metcalfe, J. D., & Sims, D. W. (2006). Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology Progress Series*, *328*, 205–213. https://doi.org/10.3354/meps328205

Sherman, C. Samantha, Chin, A., Heupel, M. R., & Simpfendorfer, C. A. (2018). Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? *Journal of Experimental Marine Biology and Ecology*, *503*, 80–85. https://doi.org/10.1016/j.jembe.2018.03.002

Sherman, C. S., Heupel, M. R., Moore, S. K., Chin, A., & Simpfendorfer, C. A. (2020). When sharks are away, rays will play: effects of top predator removal in coral reef ecosystems. *Marine Ecology Progress Series*, *641*, 145–157. https://doi.org/10.3354/meps13307

Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G. C., Righton, D., Metcalfe, J. D., Nash, J. P., & Morritt,

D. (2006). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *The Journal of Animal Ecology*, *75*(1), 176–190. https://doi.org/10.1111/j.1365-2656.2005.01033.x

Sinclair, A. R. E., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator–prey system. *Nature*, *425*(6955), 288–290. https://doi.org/10.1038/nature01934

State of world aquaculture 2006. FAO Fisheries Technical Paper 500. (2006). Food and Agriculture Organization of the United Nations.

Stein, R. A., & Magnuson, J. J. (1976). Behavioral response of crayfish to a fish predator. *Ecology*, *57*(4), 751–761. https://doi.org/10.2307/1936188

Stevens, J. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science: Journal Du Conseil*, *57*(3), 476–494. https://doi.org/10.1006/jmsc.2000.0724

Stevens, J. D., & West, G. J. (1997). *Investigation of school and Gummy shark nursery areas in southeastern Australia. Australia: Fisheries Research and Development Corporation Project 93/061 final report. 76.*

Stunz, G. W., Minello, T. J., & Rozas, L. P. (2010). Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Marine Ecology Progress Series*, *406*, 147–159. https://doi.org/10.3354/meps08556

Summerson, H. C., & Peterson, C. H. (1984). Role of predation in organizing benthic communities of a temperate zone seagrass bed. *Marine Ecology Progress Series*, *15*, 63–77. https://www.jstor.org/stable/24815922

Barnhart, R.A. (1992). The ecology of Humboldt Bay, California, an estuarine profile. (1994). *Biological Conservation*, *67*(2), 190. https://doi.org/10.1016/0006-3207(94)90388-3.

Theuerkauf, S. J., Barrett, L. T., Alleway, H. K., Costa-Pierce, B. A., St. Gelais, A., & Jones, R. C. (2022). Habitat value of bivalve shellfish and seaweed aquaculture for fish and invertebrates: Pathways, synthesis and next steps. *Reviews in Aquaculture*, *14*(1), 54–72. https://doi.org/10.1111/raq.12584

Thums, M., Meekan, M., Stevens, J., Wilson, S., & Polovina, J. (2013). Evidence for behavioural thermoregulation by the world's largest fish. *Journal of the Royal Society, Interface*, *10*(78), 20120477. https://doi.org/10.1098/rsif.2012.0477

Toft, J. D., Munsch, S. H., Je, Cordell, R., Siitari, K., Hare, V. C., Holycross, B., Debruyckere, L. A., & Greene, C. M. (2023). *Nursery functions of west coast estuaries: Data assessment for juveniles of 15 focal fish and crustacean species*. https://doi.org/10.13140/RG.2.2.13638.75841

Torres, L. G., Heithaus, M. R., & Delius, B. (2006). Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. *Hydrobiologia*, *569*(1), 449–455. https://doi.org/10.1007/s10750-006-0148-6

Trianni, M.S. (1996). The influence of commercial oyster culture activities on the benthic infauna of Arcata Bay. M.S. Thesis, Cal Poly Humboldt Univ., Arcata, CA, 94 pp.

Uncles, R. J., Stephens, J. A., & Smith, R. E. (2002). The dependence of estuarine turbidity on tidal intrusion length, tidal range and residence time. *Continental Shelf Research*, *22*(11–13), 1835–1856. https://doi.org/10.1016/s0278-4343(02)00041-9

Vaudo, J. J., & Heithaus, M. R. (2009). Spatiotemporal variability in a sandflat elasmobranch fauna in Shark Bay, Australia. *Marine Biology*, *156*(12), 2579–2590. https://doi.org/10.1007/s00227-009-1282-2

Venables WN, Ripley BD (2002). *Modern Applied Statistics with S*, Fourth edition. Springer, New York. ISBN 0-387-95457-0, https://www.stats.ox.ac.uk/pub/MASS4/

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, *60*(4), 457–464. https://doi.org/10.1007/s00265-006-0172-6

Walter, R. K., O'Leary, J. K., Vitousek, S., Taherkhani, M., Geraghty, C., & Kitajima, A. (2020). Large-scale erosion driven by intertidal eelgrass loss in an estuarine environment. *Estuarine, Coastal and Shelf Science*, *243*(106910), 106910. https://doi.org/10.1016/j.ecss.2020.106910

Ward, P., & Myers, R. A. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology*, *86*(4), 835–847. https://doi.org/10.1890/03-0746

Ward-Paige, C., Mills Flemming, J., & Lotze, H. K. (2010). Overestimating fish counts by non-instantaneous visual censuses: Consequences for population and community descriptions. *PloS One*, *5*(7), e11722. https://doi.org/10.1371/journal.pone.0011722

Watson-Capps, J. J., & Mann, J. (2005). The effects of aquaculture on bottlenose dolphin (*Tursiops* sp.) ranging in Shark Bay, Western Australia. *Biological Conservation*, *124*(4), 519–526. https://doi.org/10.1016/j.biocon.2005.03.001

Whitfield, A. K. (2017). The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries*, *27*(1), 75–110. https://doi.org/10.1007/s11160-016-9454-x

Whitlow, W. L., & Grabowski, J. H. (2012). Examining how landscapes influence benthic community assemblages in seagrass and mudflat habitats in southern Maine. *Journal of Experimental Marine Biology and Ecology*, *411*, 1–6. https://doi.org/10.1016/j.jembe.2011.10.024

Williams, H., & Schaap, A. H. (1992). Preliminary results of a study into the incidental mortality of sharks in gill-nets in two Tasmanian Shark Nursery Areas. *Marine & Freshwater Research*, *43*(1), 237. https://doi.org/10.1071/mf9920237

Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P., & Schmitz, O. J. (2021). The context dependence of non-consumptive predator effects. *Ecology Letters*, *24*(1), 113–129. https://doi.org/10.1111/ele.13614

Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007). Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? *Oecologia*, *153*(4), 1031–1040. https://doi.org/10.1007/s00442-007-0802-3

Yates, P. M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2015). Ecological drivers of shark distributions along a tropical coastline. *PLoS One*, *10*(4), e0121346. https://doi.org/10.1371/journal.pone.0121346

Yon, A., Meekan, M. G., Andrzejaczek, S., Martinez, S., & Speed, C. W. (2020). Shark and ray community structure in a turbid, nearshore coral reef habitat. *Marine & Freshwater Research*, *71*(9), 1194. https://doi.org/10.1071/MF19301

Zeileis A, Kleiber C, Jackman S (2008). Regression Models for Count Data in R. *Journal of Statistical Software*, **27**(8). https://doi.org/10.18637/jss.v027.i08

APPENDICES

Appendix A

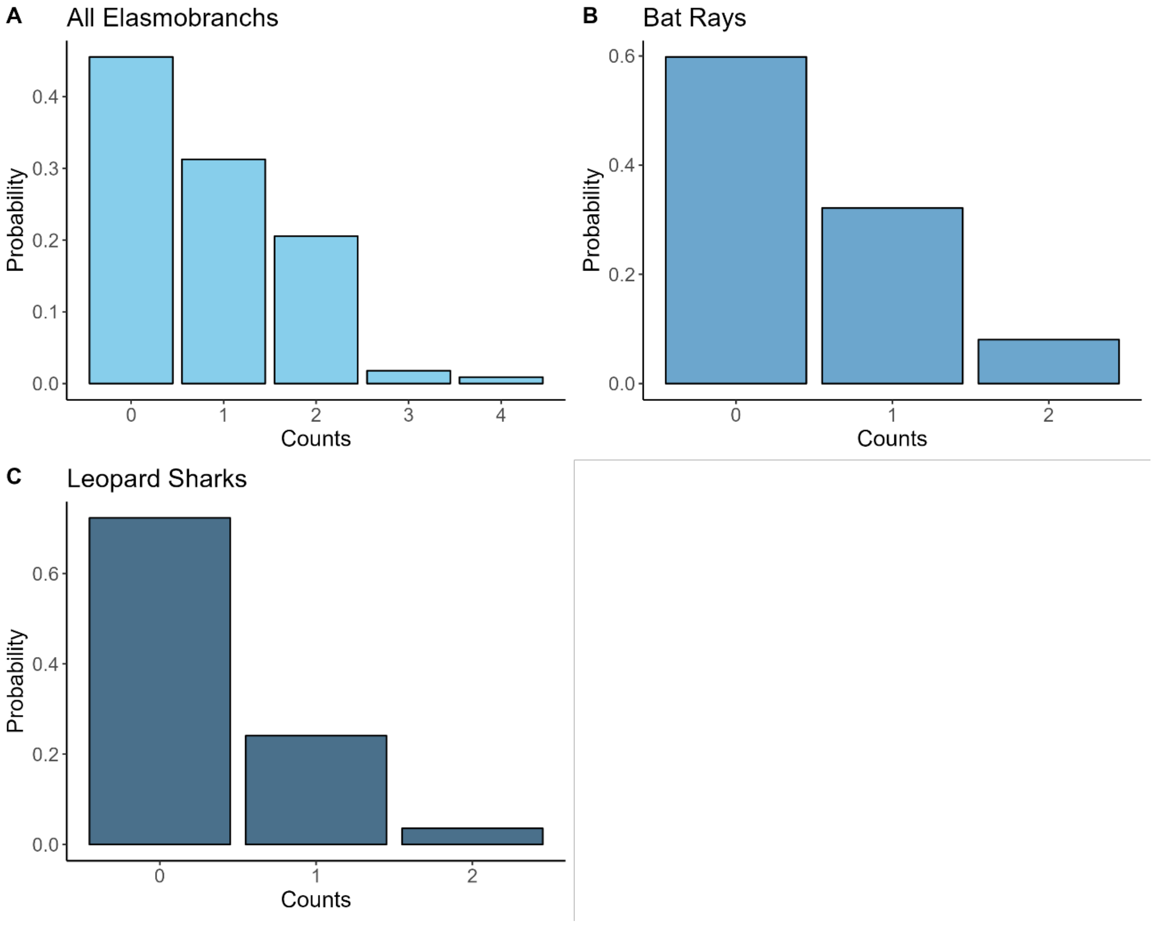


Figure 8. Probability mass function (PMF) plots for (A) all elasmobranchs, (B) bat rays (*Myliobatis californica*), and (C) leopard sharks (*Triakis semifasciata*). Counts represent MaxN for each group, and probability represents the proportion of individuals observed at each count across all BRUVS deployments.

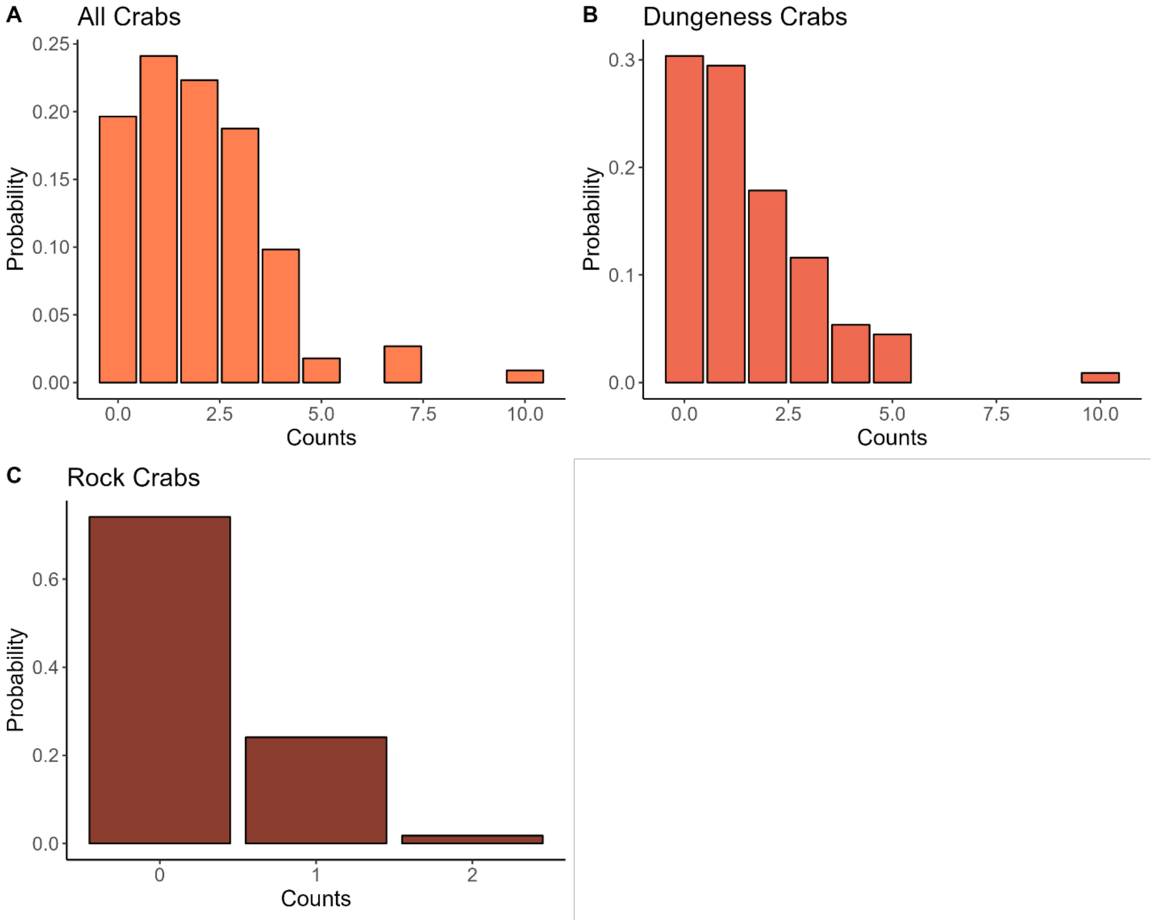
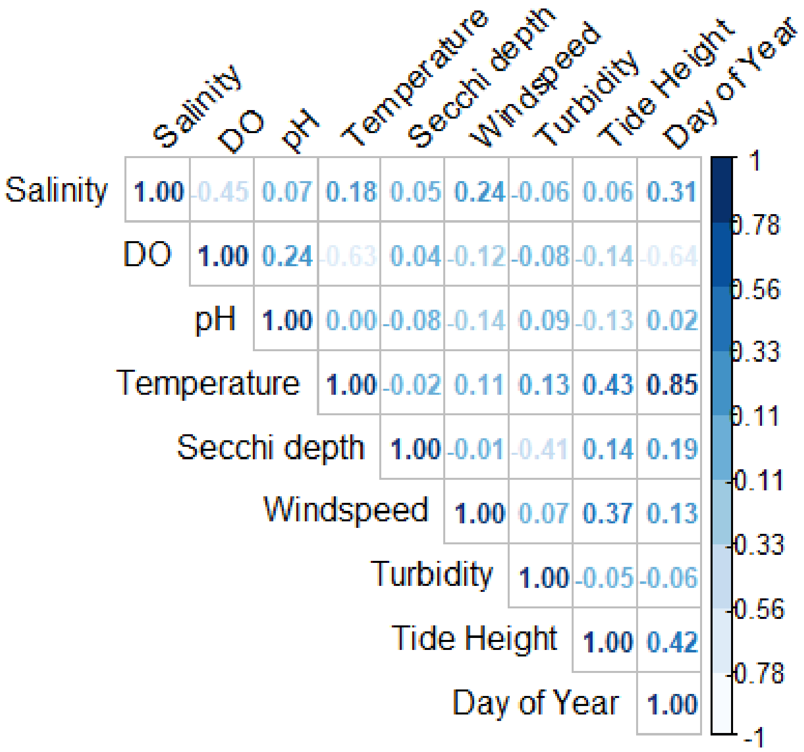


Figure 9. Probability mass function (PMF) plots for (A) all cancrid crabs, (B) Dungeness crabs (*Metacarcinus magister*), and (C) rock crabs (*Romaleon antennarium* and *Cancer productus*). Counts represent MaxN for each group, and probability represents the proportion of individuals observed at each count across all BRUVS deployments.



	Salinity	DO	pH	Temperature	Secchi depth	Windspeed	Turbidity	Tide Height	Day of Year
Salinity	1.00	-0.45	0.07	0.18	0.05	0.24	-0.06	0.06	0.31
DO		1.00	0.24	-0.63	0.04	-0.12	-0.08	-0.14	-0.64
pH			1.00	0.00	-0.08	-0.14	0.09	-0.13	0.02
Temperature				1.00	-0.02	0.11	0.13	0.43	0.85
Secchi depth					1.00	-0.01	-0.41	0.14	0.19
Windspeed						1.00	0.07	0.37	0.13
Turbidity							1.00	-0.05	-0.06
Tide Height								1.00	0.42
Day of Year									1.00

Figure 10. Correlation matrix representing pairwise correlations between abiotic variables including salinity, dissolved oxygen (mg · L^{-1}), pH, temperature (°C), Secchi depth (m), windspeed (km · h^{-1}), turbidity (NTU), and tide height (MLLW), and day of year. Each cell in the matrix displays a correlation coefficient (Pearson's $r = -1 \leq 0 \geq 1$) quantifying the strength and direction of the relationship. Values closer to 1 or -1 suggest a stronger linear relationship, while values closer to 0 suggest a weaker or no linear relationship.

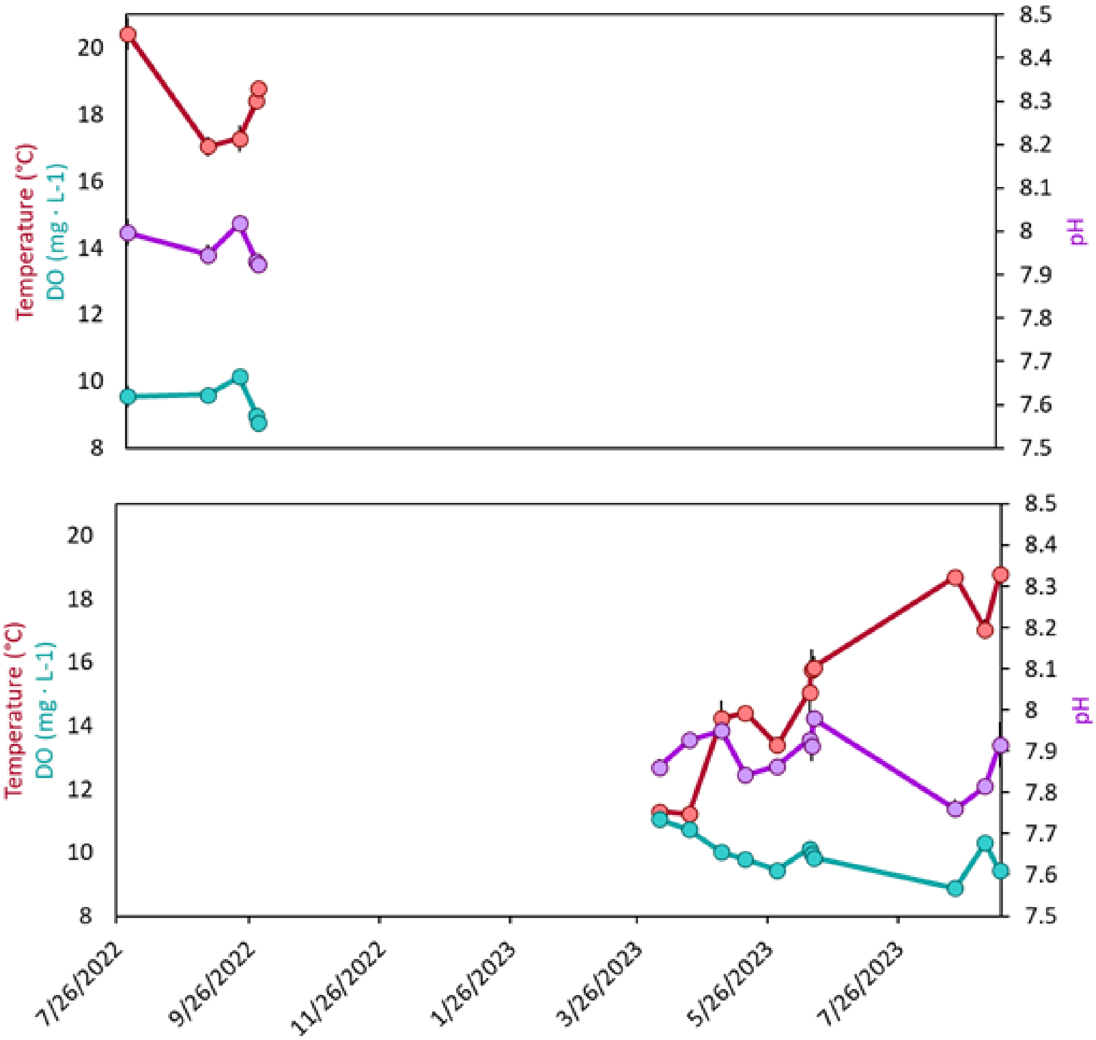


Figure 11. Average (± SD) measurements for temperature (°C), dissolved oxygen (mg · L^{-1}), and pH (mV) between June – September 2022 and April – September 2023 for each BRUVS deployment day. Gaps in the timeline represent periods when no measurements were taken. Error bars are sometimes obscured by symbols.

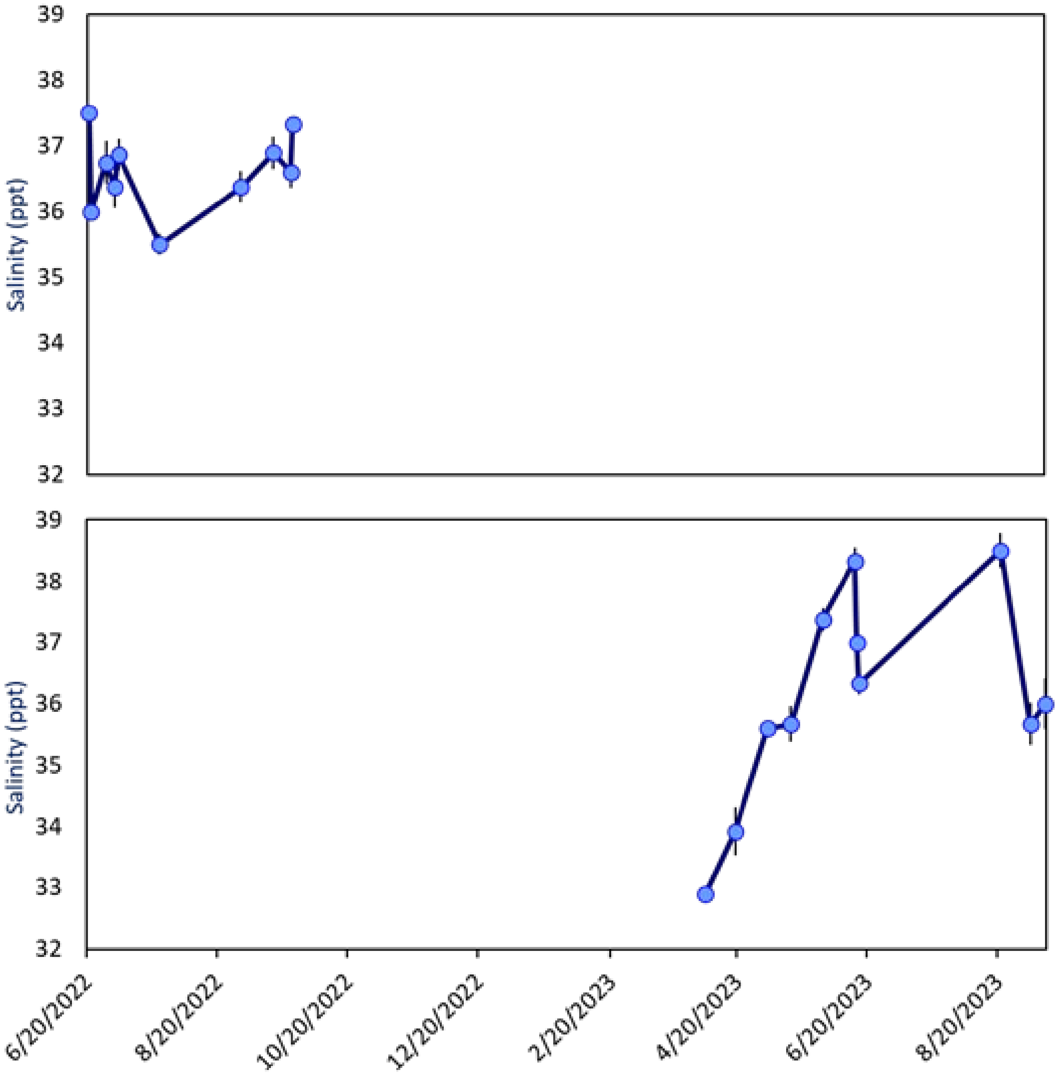


Figure 12. Average (± SD) measurements for salinity (ppt) between July – September 2022 and April – September 2023 for each BRUVS deployment day. Gaps in the timeline represent periods when no measurements were taken. Error bars are sometimes obscured by symbols.

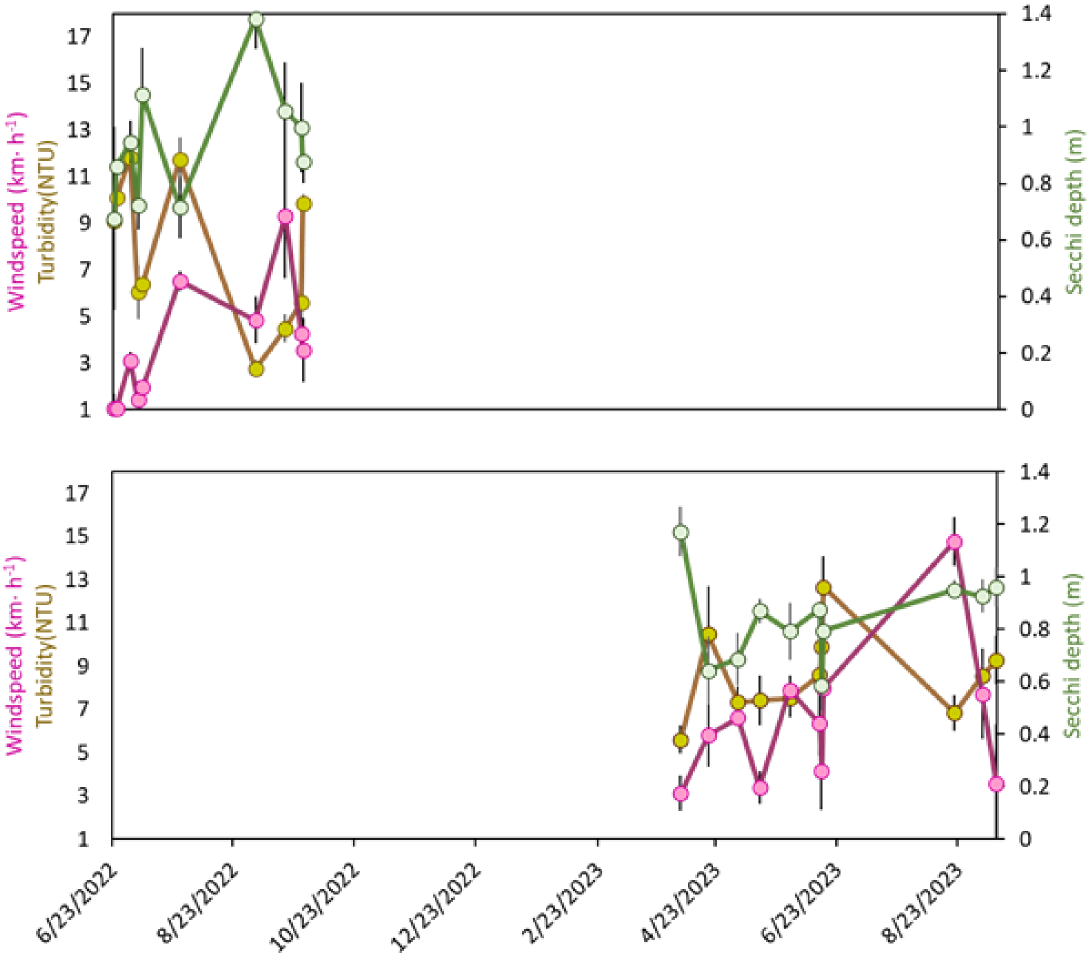


Figure 13. Average (± SD) measurements for windspeed (km · h^{-1}), turbidity (NTU), and Secchi depth (m) between July – September 2022 and April – September 2023 for each BRUVS deployment day. Gaps in the timeline represent periods when no measurements were taken. Error bars are sometimes obscured by symbols.

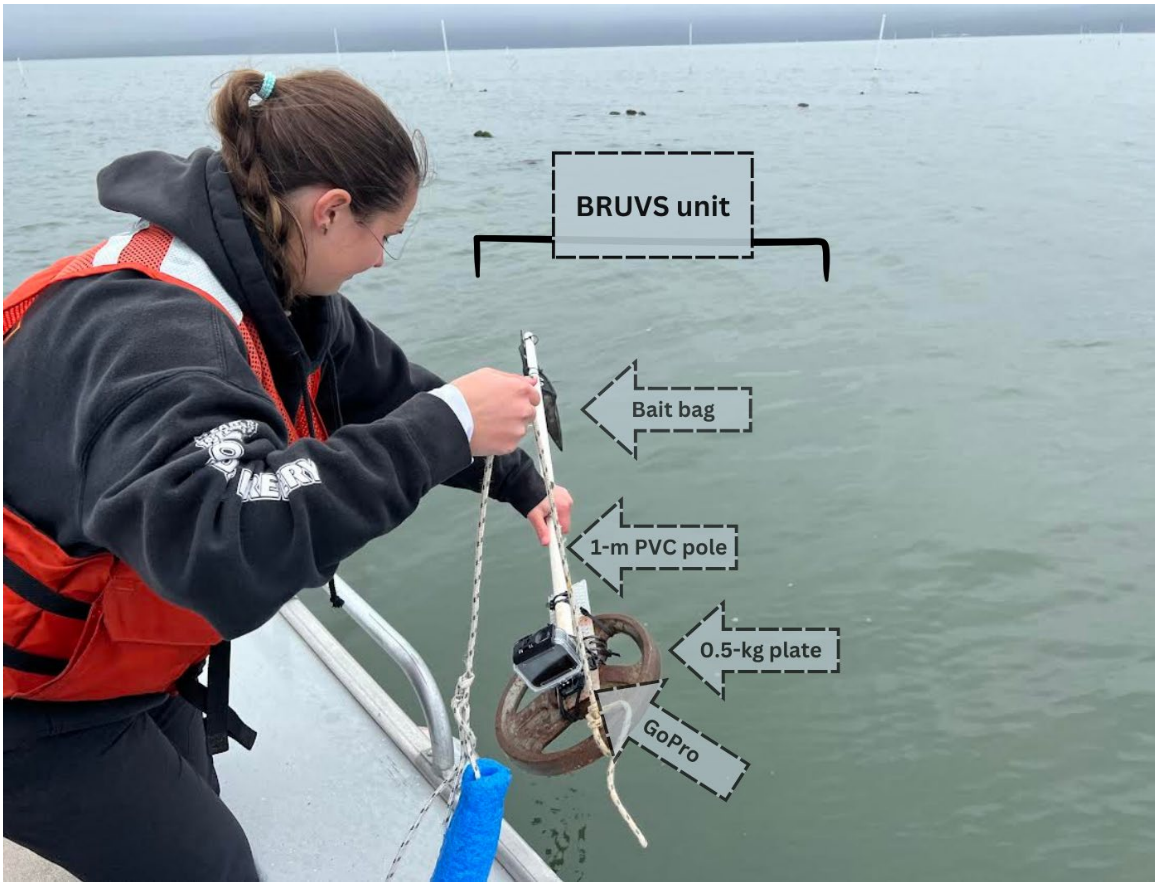


Figure 14. Individual BRUVS unit composed of a 0.5-kg plate attached (with zipties) to a 1-m PVC pole. A GoPro is manually inserted to the weighted end of the BRUVS unit before a deployment, and a ~ 3-m braided polyester rope is tied to the weighted end and a small buoy is tied at the end of the rope and serves as a surface marker. The mesh bait bag is attached to the opposite (non weighted) end of the BRUVS unit and is keeps the 200-300 g of squid bait enclosed with velcro.

Appendix B

Table 5. Summary of the correlation statistics for the nine abiotic variables: salinity (ppt), dissolved oxygen (mg · L^{-1}), pH (mV), temperature (°C), Secchi depth (m), day of year, tidal height (m), windspeed (km · h^{-1}), turbidity (NTU). The mean correlation shows the average values of the correlation coefficients, and standard deviation is the amount of variation in the correlation values. The minimum correlation (Min) represents the smallest correlation coefficient among the variables and the maximum correlation (Max) shows the largest correlation coefficient of the variables, indicating the highest degree of linear association observed.

Statistic	N	Mean	St. Dev.	Min	Max
Correlation	8	0.42	0.40	-0.01	0.85

Table 6. Variance inflation factors (VIF) for each predictor variable. Values indicate the extent to which the variance of the estimated regression coefficients is increased due to multicollinearity. VIF values of 1 indicate no multicollinearity (perfectly uncorrelated predictors) while higher values indicate increasing levels of multicollinearity. The values in the table have low (< 4) VIFs indicating low levels of multicollinearity among predictor variables, and range from 1.09 – 2.46.

Variable	Value
Tide height (MMLW)	1.09
Secchi depth (m)	1.10
Habitat	1.16
Aquaculture presence	1.18
pH (mV)	1.28
Salinity (ppt)	1.48
Temperature (°C)	1.95
Dissolved oxygen (mg · L^{-1})	2.46

Table 7. Results of logistic regression analyzing the relationship between crab abundance (MaxN) and (A) bat ray, and (C) leopard shark presence. Coefficients represent the strength and direction (positive or negative) of relationships. *P*-values for statistically significant relationships at $\alpha = 0.05$, in bold text.

Variable	*df*	*B*	SE	*z*	*P*
(A)					
Intercept	111	-1.10	0.33	-3.33	**<0.001**
Crab MaxN	111	0.34	0.13	2.66	**0.008**
(B)					
Intercept	111	-0.72	0.32	-2.48	**0.013**
Crab MaxN	111	-0.08	0.13	-0.64	0.522