


## ARTICLE

# Shellfish aquaculture farms as foraging habitat for nearshore fishes and crabs

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## Abstract

**Objective:** Oyster reefs across North America have declined precipitously over the past 140 years. In Washington State, Olympia oyster *Ostrea lurida* reefs historically provided water filtration and nearshore structural habitat for fishes and invertebrates, but this species is now functionally extinct across its historical range. In place of these naturally occurring reefs, shellfish farms consisting mainly of nonnative Pacific oysters *Magallana gigas* now occupy patches of nearshore habitat across Washington. These farms modify intertidal substrate by adding structural habitat via suspended oyster grow bags, predator exclusion nets, loose oyster beds, and other shellfish grow-out gear. As interest and investment in shellfish aquaculture have expanded both locally and globally, so has interest in how these farms modify intertidal habitat and whether the complex structure created by the shellfish and shellfish growing gear provides ecosystem services that are comparable to those of unfarmed areas, such as mudflats and eelgrass meadows.

**Methods:** In this study, we sought to quantify how shellfish farms are used as foraging habitat for several common nearshore species of fish and crabs in Puget Sound, Washington. We used direct observations of species-specific behaviors from underwater video to model how habitat type affected observed foraging rates.

**Result:** We obtained a total of 393 crab observations, 431 demersal fish observations, and 1856 pelagic fish observations across all seven farm sites. Several common species of pelagic fish (e.g., surfperch [Embiotocidae]) used aquaculture-growing gear more frequently than unfarmed areas as foraging habitat, but *Metacarcinus* spp. crabs displayed higher foraging frequency in unfarmed mudflats. Species groups such as sculpins (Cottidae) and small flatfish (Pleuronectidae) clearly used specific aquaculture-growing gear and mudflats in roughly equal proportion.

**Conclusion:** Our results indicate that shellfish farms within a larger nearshore habitat mosaic of eelgrass meadows, mudflats, bivalve aquaculture gear, and edge habitat can provide foraging habitat for several species of nearshore fish.

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**KEYWORDS**

aquaculture, ecosystem services, feeding, habitat, nearshore marine, oysters, shellfish

**INTRODUCTION**

Oyster reefs are important habitats for many species of fish and invertebrates because they provide foraging opportunities (Shervette and Gelwick 2008) and predator refuge (Hixon and Beets 1993). Oysters provide extensive ecosystem services through habitat formation of oyster reefs and water filtration in estuaries (Coen et al. 2007b). The physical structure created by the mass of shells in reefs creates habitat complexity (Humphries et al. 2011) and provides refuge habitat for small organisms, such as juveniles of the Dungeness crab *Metacarcinus magister* (Holsman et al. 2006), which is a valuable commercial species. Widespread oyster reef restoration efforts have been undertaken in areas such as Chesapeake Bay to protect and restore the important ecosystem services provided by oyster reefs (Beck et al. 2001; Coen et al. 2007a).

Over the past 140 years, oyster reef habitat has declined by about 64% in the United States, and native Olympia oysters *Ostrea lurida* in Washington State have become functionally extinct across most of their historical range (Zu Ermgassen et al. 2012). Some Olympia oyster reefs still exist within limited areas in Washington's Puget Sound, with core historical populations having been reduced by approximately 96% (Horowitz and Hoberecht 2016).

Although native oyster production has declined, shellfish farms located on tide flats along the coast of Washington State are growing enterprises that confer both economic opportunities and high-quality, locally grown food (Horowitz and Hoberecht 2016). Shellfish aquaculture of all farmed bivalves contributes approximately US\$184 million annually to the state's economy (Horowitz and Hoberecht 2016). These farms grow oysters either (1) directly on the tide flat in a method that is analogous to a naturally occurring oyster reef or (2) on a variety of gear types attached to the tide flat substrate. Increasingly, the preferred gear type for growing oysters in Puget Sound consists of oyster flipbags, which are buoyant, oyster-filled mesh bags hanging from wires directly above the tide flat (Figure 1).

A major consideration when permitting and implementing shellfish aquaculture is its impact on nearshore habitats, either through effects from the physical addition of structure or through pulse disturbance from activities such as harvesting or gear installation (Dumbauld et al. 2009). Many studies show that certain shoreline modifications can impair habitat function and structure (Griggs 2005; Munsch et al. 2017). However, the introduction of structured artificial habitats via placement of bivalve aquaculture growing gear on tide flats may enhance

**Impact statement**

Shellfish farms within a larger nearshore habitat mosaic of eelgrass meadows, mudflats, bivalve aquaculture gear, and edge habitat can provide foraging habitat for several species of nearshore fish.

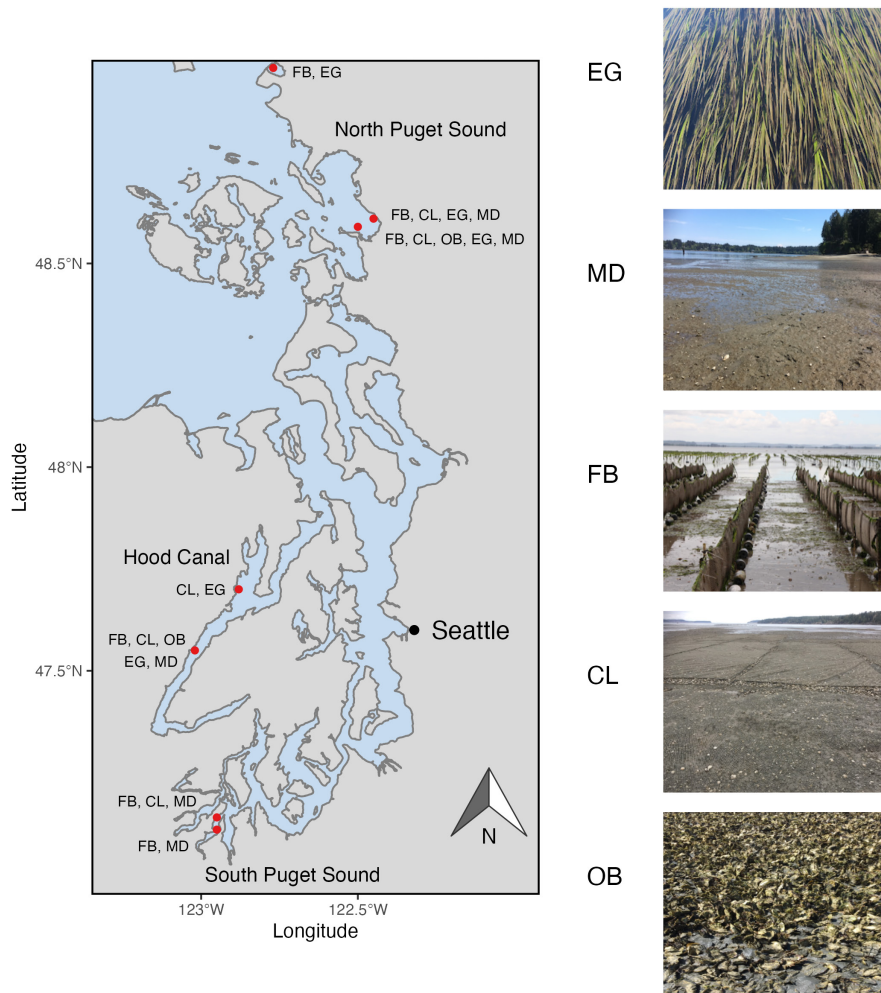
predator feeding opportunities by providing increased prey availability (Hosack et al. 2006) or it may provide predator refuge (Wechsler 1996) for nearshore species, thus mitigating the risks of feeding behavior. Nevertheless, these benefits are probably species and location specific, with different species showing different preferences for structure and habitat (Dumbauld et al. 2009).

There is some evidence that bivalve aquaculture confers some habitat functions (Alleway et al. 2019; Gentry et al. 2020), but how habitat functions at shellfish aquaculture sites compare to those of natural areas is still not well understood (Dumbauld et al. 2011). Thus, an improved understanding of whether aquaculture sites provide foraging and refuge opportunities for commercially, recreationally, and culturally important fish and crab species and the ecosystem value of aquaculture sites relative to natural areas will help to inform decisions about the ecological implications of an expanding shellfish aquaculture industry.

In this study, we analyzed underwater video to compare feeding of nearshore fish and crab species among five different farmed and unfarmed habitat types in Puget Sound, Washington State. We sought to understand (1) how habitat type influenced the observed feeding behavior, (2) how substrate cover (i.e., algae, eelgrass, or bare) influenced the observed feeding behavior, and (3) whether structure-affiliated species used structurally complex habitats for foraging more than structurally simpler habitats.

**METHODS****Study area**

Puget Sound is a complex and highly productive inlet within the Salish Sea ecosystem of Washington State, United States, and British Columbia, Canada, and consists of several large, environmentally distinct subbasins (Ruckelshaus and McClure 2007). Extensive tidal flushing



**FIGURE 1** Map of Puget Sound, Washington, and the locations of the seven study sites. The five different habitat types used in the study are shown in photos on the right: eelgrass meadows (EG), mudflats (MD), oyster flipbags (FB), clam nets (CL), and oysters on bottom (OB). (Photo credits: K. B. Veggerby, B. L. Sanderson, and B. E. Ferriss.)

combined with significant freshwater inputs from rivers creates a complex estuarine ecosystem within the various subbasins (Moore et al. 2008), with salinity levels lower than those in the open ocean. Shellfish aquaculture occurs across most of the major basins of Puget Sound; the largest concentration of farms is present in South Puget Sound, North Puget Sound, and Hood Canal. The shellfish produced are primarily Pacific oysters *Magallana gigas* and Manila clams *Ruditapes philippinarum* by weight (Horowitz and Hoberecht 2016). Farming occurs on tide flats, which, depending on the location, are naturally composed of a combination of eelgrass meadows, mudflats, and naturally recruiting nonnative Pacific oyster beds.

## Data collection

The use of cameras to quantify species and behavior is an increasingly common technique that has been employed in similar studies (Gross et al. 2018; Muething et al. 2020;

Ferriss et al. 2021; Mercaldo-Allen et al. 2021; Shinn et al. 2021), and this method allowed us to capture more observations than would have been possible by using dive or snorkel surveys. We used GoPro video cameras to record several hundred hours of underwater video of shellfish aquaculture habitats and adjacent eelgrass and mudflat habitats (Ferriss et al. 2021). A subset of these data was analyzed to identify the species present in these habitats and to classify the observed behavior.

We collected data in the spring and summer of 2017 and 2018. GoPro cameras were placed at seven shellfish aquaculture sites across North Puget Sound, South Puget Sound, and Hood Canal (Figure 1). We selected sites based on the shellfish species being farmed, the grow gear present, and the accessibility of the site. Our focus was on the three most predominant grow-out gears used in Puget Sound: oyster flipbags (also known as tumble bags), clam nets, and loose oyster bottom culture (hereafter, “oyster-on-bottom culture”). We selected reference sites with a tidal elevation similar to that of the farmed areas.

Reference sites consisted of unfarmed eelgrass meadows and mudflats that were located 30–60 m away from the edge of the shellfish farms. We chose this distance from the farms to minimize potential environmental influences from the shellfish farms while maintaining similarity in environmental conditions between the farmed sites and unfarmed reference sites.

Of the farming methods listed, oyster-on-bottom culture most closely resembles a natural oyster reef, although there are significant differences in rugosity and age structure between cultured and natural reefs as well as between different farms. This habitat type was characterized by oyster-covered mudflats with minimal algae and eelgrass cover, a highly complex benthos, and low vertical structure. Clam net habitats were located on mudflats with varying degrees of algae cover, depending on whether the farmers were actively removing the biofouling. Thick mats of algae formed on clam nets that had been allowed to biofoul, which created a complex benthos and vertical structure. Flipbag habitats most closely resembled mudflats, although with the addition of high vertical structure from the hanging oyster bags. The flipbag habitat benthos ranged from completely bare to dense algae or eelgrass cover.

Within the two types of reference sites, mudflat substrates were generally bare, with no vertical structure and simple benthic surfaces. Eelgrass reference sites had high vertical structure and complex benthic surfaces and were composed of a mixture of native eelgrass *Zostera marina* and invasive Japanese eelgrass *Nanozostera japonica*. Several cryptic species of demersal fish, such as Bay Pipefish *Syngnathus leptorhynchus* and gunnels (Pholidae), often co-occur with eelgrass meadows, while some dorsoventrally compressed fish, such as flatfish (Pleuronectidae) and Pacific Staghorn Sculpin *Leptocottus armatus* (Cottidae), generally are more common in mudflats or clam net habitats (Williams 1994; Able et al. 2005; Ferriss et al. 2021).

We deployed cameras at low tide inside GoPro dive housing cases, with attached time-lapse sequence timers that triggered video collection during high tide on the following day. At each location, we placed GoPro Hero 3+ and GoPro Hero 4 cameras in pairs at the centers of several different aquaculture gear types as well as unfarmed reference areas. Cameras were deployed in pairs so that we would have a backup camera if one camera failed to record properly.

We mounted the cameras on individual pieces of polyvinyl chloride (PVC) pipe approximately 30 cm above the benthos, facing downward at a 20° angle. Two small PVC stakes were placed in front of each pair of cameras to mark a 1-m<sup>2</sup> area of visibility starting from the bottom edge of the camera's frame of view. During summer 2017, four of our sites were sampled once and three sites were not sampled at all. During summer

2018, we sampled all seven sites twice. Not every habitat type was present at every site. For example, our two study sites in South Puget Sound did not have any eelgrass present. Eelgrass reference sites were present at five of seven sites, and mudflat reference sites were present at six of seven sites. Of the three aquaculture gear types sampled, oyster flipbags were present at six of seven sites, clam nets were present at five of seven sites, and oyster-on-bottom culture was present at two of seven sites. Each site had a maximum of two reference types (eelgrass and mudflats) and a maximum of three aquaculture gear types (oyster flipbags, clam nets, and oyster-on-bottom culture).

Preliminary results indicated that visibility was best at or near slack tide. Videos were collected for 2 min every 10 min for 3 h on either side of high tide, when visibility was generally highest. If available, we used morning high tides for analysis due to improved visibility during the morning tides relative to afternoon tides. During tidal cycles in which daylight morning high tides were not available, we used afternoon high tides for analysis instead. The tidal range in Puget Sound varies from 2 to 4 m depending on the location (Mofjeld and Larsen 1984). Data from several tidal cycles were recorded during each camera deployment. Over the course of the two field seasons, we collected several hundred hours of video.

## Data analysis

After camera retrieval, we selected 10 video segments for analysis from each habitat type. Five videos were from time-lapse images that were recorded over the course of 1 h prior to high tide and five videos were from time-lapse images recorded over the course of 1 h directly after high tide for a total of 20 min of video analyzed from each pair of cameras in each habitat type recorded over a 2-h time span. In total, we analyzed 20 h of video for species and behavioral observations, representing approximately 600 videos across five habitat types and seven sites. See Ferriss et al. (2021) for more information on how we collected these data.

Using the video analysis software BORIS (Friard and Gamba 2016), we counted all fish and crabs observed within a 1-m<sup>2</sup> area from each video. Each observation was also assigned a behavioral classification (“feeding” or “not feeding”). Feeding was defined as an individual subjectively observed to be eating or attempting to eat something at any point in the video for any length of time. If no feeding attempts by an individual were observed during the 2-min video, then that individual was classified as not feeding. We used this feeding/not feeding classification as the response variable in our models.

Videos were subjectively ranked as either low, medium, or high visibility to account for potential observer bias resulting from varying water quality conditions across the study sites, which could have obscured observations or behaviors in lower visibility videos (Ferriss et al. 2021). Dense eelgrass or other physical obstructions may have also limited our ability to detect organisms. For example, Gross et al. (2018) found that pelagic fish were undercounted in eelgrass habitat relative to more open habitat, such as mudflats and flipbags; therefore, we assumed that pelagic fish were underrepresented in eelgrass habitat. In an attempt correct for this probable visibility bias resulting from physical obstruction or poor water quality, we included it as a predictor variable in our analysis.

We summed observations from each 2-min video to calculate the sum of each species × behavior combination observed per video segment. In several videos, we observed large schools of fast-moving fish, which were primarily forage fish. We chose to remove these large schools from the data set, as this would cause a few observations to skew the results. Species with fewer than three observations were also removed, along with species that (1) were not in our three vertical functional groups (e.g., jellyfish [Cnidaria], harbor seals *Phoca vitulina*, and diving birds), (2) appeared to be attracted to the camera (e.g., Pacific Spiny Dogfish *Squalus suckleyi*), or (3) were not identifiable. After the data were subset, we obtained a total of 393 crab observations, 431 demersal fish observations, and 1856 pelagic fish observations across all seven farm sites (Table 1; Veggerby et al. 2023). Pelagic fish were defined as fusiform-style fish that were primarily associated with the open water column, and demersal fish were defined

as fish that were primarily associated with the benthos or near the benthos. In general, to prevent misidentification, we chose not to identify organisms to the species level; instead, we kept most observations at the genus or family level. We did not separate crabs into species or other groupings for the analysis due to the difficulty of consistently identifying crabs at the species level using video. The most commonly observed crab taxa were shore crabs *Hemigrapsus* spp., Dungeness crabs, and graceful crabs *Metacarcinus gracilis*.

We used a generalized linear mixed-effects model approach to analyze the probability of foraging activity among species groups and habitat types by using the packages MuMIn (Bartoń 2022), lme4 (Bates et al. 2015), and arm (Gelman and Su 2022). The species observations were separated into pelagic, demersal, and benthic functional groups (Table 1), and analyses were applied to each group. Our goal was to separate species that were clearly morphologically and functionally different into discrete groups for analysis while also maintaining a sufficient sample size to effectively perform the analyses. Species within each vertical functional group were modeled together, so the more abundant species drove the observed trends. For example, surfperch (Embiotocidae) dominated our pelagic fish observations and thus also dominated the pelagic fish model results.

Within the models for each group, we included habitat type, visibility, and cover type (eelgrass, bare mud, or algae) as fixed effects and we included site as a random effect. Inclusion of cover type was important, as there was substantial variability within a given habitat type based on algae cover. Some mudflats and bivalve farming areas had substantial algae and/or biofouling, whereas other areas

**TABLE 1** Numbers of fishes and crabs (organized by vertical functional groups) that were observed in underwater videos taken within coastal areas of Puget Sound, Washington.

Vertical distribution	Species grouping	Count	Percentage observed feeding
Pelagic	Surfperch (Embiotocidae)	1824	36
	Forage fish (Pacific Herring <i>Clupea pallasii</i> , Surf Smelt <i>Hypomesus pretiosus</i> , Pacific Sand Lance <i>Ammodytes hexapterus</i> )	23	57
	Salmonids (Salmonidae)	9	0
Demersal	Threespine Stickleback <i>Gasterosteus aculeatus</i>	184	27
	Sculpins (Cottidae)	141	16
	Flatfish (Pleuronectidae)	82	37
	Gunnels (Pholidae)	12	8
	Snake Prickleback <i>Lumpenus sagitta</i>	5	40
	Bay Pipefish <i>Syngnathus leptorhynchus</i>	4	0
	Greenlings (Hexagrammidae)	3	0
Benthic	Crabs ( <i>Hemigrapsus</i> , <i>Metacarcinus</i> , <i>Pugettia</i> )	393	11

were bare or mostly bare. Classification of an area as algae covered or bare was determined subjectively using our best judgment. During initial camera deployments, we used a quadrat replicated five times to assign the predominant cover type present at each habitat, and we further verified our cover type classification when analyzing the videos.

We did not include the specific subbasin within Puget Sound as a fixed effect (i.e., North versus South Puget Sound) because differences in behavior across the region were captured by the individual farms spread across Puget Sound. For each vertical functional group  $k$ , we modeled the probability  $P$  of foraging at site  $j$  by individual  $i$ :

$$\text{feeding}_{i,j,k} \sim \text{Bernoulli}(P_{i,j,k}),$$

$$\log_e\left(\frac{P_{i,j,k}}{1-P_{i,j,k}}\right) = \alpha_{k[j]} + \beta_0 + \beta_1(\text{habitat}_{j,k}) + \beta_2(\text{substrate}_{j,k}) + \beta_3(\text{visibility}_{j,k}),$$

$$\alpha_{k[j]} \sim N(\mu_{j,k}, \sigma_{j,k}).$$

We first fitted a saturated model that included all covariates with the random effect of site and compared it to a model with no random effects. After determining the appropriate random effect structure via Akaike's information criterion corrected for small sample size ( $AIC_c$ ), we fitted all combinations of models that included habitat type and compared model parsimony using  $AIC_c$  values calculated with the MuMIn package (Bartoń 2022). We did not include model combinations without habitat type as a predictor because we were specifically interested in the effect of habitat type. Models within 2  $AIC_c$  units of each other were considered comparable (Burnham and Anderson 2004). Comparable top models with fewer predictor variables were considered preferential to models with more predictor variables. For models containing both fixed and random effects, we calculated Nakagawa's conditional and marginal  $R^2$  metrics (Nakagawa and Schielzeth 2013). The conditional  $R^2$  takes both fixed and random effects into account, while the marginal  $R^2$  takes only the fixed effects into account. For models without random effects, we calculated a single Cox and Snell pseudo- $R^2$  metric (Cox and Snell 1989). Both Nakagawa's  $R^2$  and Cox and Snell pseudo- $R^2$  metrics are generally comparable to traditional  $R^2$  metrics. However, values that would be considered good are much lower than what would generally be expected from traditional  $R^2$  metrics. For example, a pseudo- $R^2$  of 0.20 would be considered a good fit. We used these alternative metrics for our models because traditional  $R^2$  values cannot be calculated for this class of models.

All statistical analyses were conducted in R version 4.2.2 (R Core Team 2022) and RStudio version 2022.12.0 (RStudio Team 2022). The packages performance (Lüdecke

et al. 2021), here (Müller 2022), tidyverse (Wickham et al. 2019), and RColorBrewer (Neuwirth 2022) were also used. All data and code necessary to reproduce our analyses and results are available on GitHub at [https://github.com/veggerby/Veggerby\\_2023\\_fish-behavior](https://github.com/veggerby/Veggerby_2023_fish-behavior).

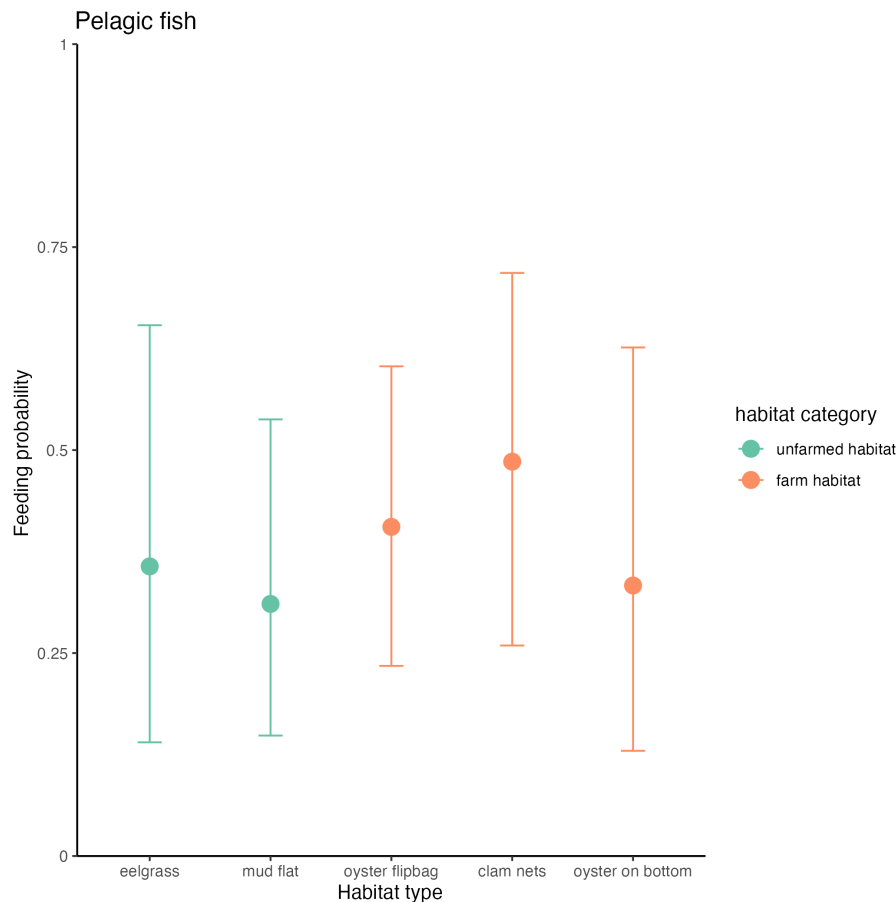
## RESULTS

Of the 393 crabs, 431 demersal fish, and 1856 pelagic fish that were seen on video, 11% of the crabs, 24% of the demersal fish, and 36% of the pelagic fish were observed feeding. There were very large overlaps in feeding probability standard errors (SEs) across habitats for both pelagic fish and crabs, while demersal fish clearly fed at higher rates in mudflat and oyster flipbag habitats compared to the other habitat types. The probability of pelagic fish feeding was highest in clam net habitat (Figure 2; Table 2). However, the large overlap in SEs meant that foraging probabilities were overall similar between habitats. When comparing different cover types, the probability of pelagic fish feeding was highest for algae-covered substrate (Figure 3). This type of substrate cover was most commonly associated with flipbags and clam nets, particularly in South Puget Sound. The SEs for cover types were smaller than those for habitat types. Algae-covered substrate was clearly used by pelagic fish, dominated numerically by surfperch.

The probability of pelagic fish feeding was explained equally well by two models that were within 2  $AIC_c$  units of one another. One model contained the fixed effects of habitat type, cover type, and visibility and the random effect of site. The second contained the fixed effects of habitat type and cover type and the random effect of site (Table 3). Since these models were considered comparable during  $AIC_c$  ranking, the most parsimonious model was chosen as the top model for generating estimates of feeding probability across habitats. The most parsimonious model had a Nakagawa's conditional  $R^2$  value of 0.12 and a Nakagawa's marginal  $R^2$  value of 0.05 (Nakagawa and Schielzeth 2013).

The probability of demersal fish feeding was highest in mudflat and oyster flipbag habitats (Figure 4; Table 2). Unlike pelagic fish, demersal fish had a much higher probability of feeding in these two habitat types than in clam net, oyster-on-bottom, and eelgrass habitats. Standard errors of feeding probability in the mudflat and oyster flipbag habitat types had little or no overlap with SEs for the three other habitat types, indicating a clearly higher feeding probability.

The model that best explained the probability of demersal fish feeding contained a fixed effect of habitat type (Table 3) and had a Cox and Snell pseudo- $R^2$  of 0.09 (Cox and Snell 1989). There were no other competing



**FIGURE 2** Feeding probability for pelagic fish across the five habitat types, as estimated from the most parsimonious model with a  $\Delta AIC_c$  of 2.0 or less (where  $\Delta AIC_c$  is the difference in Akaike's information criterion corrected for small sample size). Lines denote two standard errors above and below each estimate. Light-green color denotes unfarmed habitat types; light-orange color denotes farmed habitat types.

models for the demersal fish functional group, so this model was used to generate estimates of feeding for demersal fish.

The probability of crab feeding was highest in mudflats (Figure 5; Table 2). Crabs also had a higher probability of feeding in either eelgrass or algae-covered substrate (Figure 6). Feeding probability was higher when visibility was better, indicating that water quality had an impact on whether crabs were observed feeding. The model that best explained the probability of crab feeding contained the fixed effects of habitat type, cover type, and visibility (Table 3) and had a Cox and Snell pseudo- $R^2$  of 0.07. There were no other competing models for the crab functional group, so this model was used to generate estimates of feeding probability across habitats for crabs.

## DISCUSSION

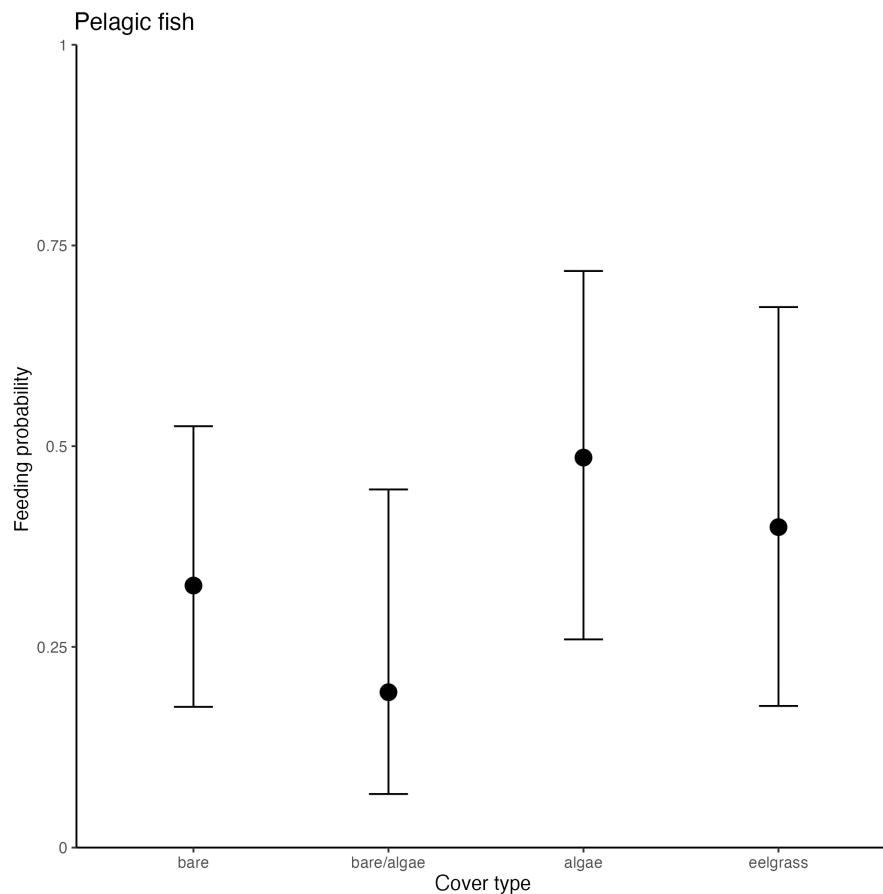
Habitat played an obvious role in the probability that aquatic organisms were observed feeding, yet these

patterns were influenced both by organism functional groupings and by substrate characteristics. There were large overlaps in feeding probability across habitats for both pelagic fish and crabs, indicating more generalist habitat usage compared to demersal fish, which clearly fed in mudflat and flipbag habitats at higher rates. These two habitat types had the least direct benthic structure present since flipbags are suspended in the water above the substrate. Small flatfish have previously been found to prefer open, unstructured benthic habitat, such as mudflats (Williams 1994; Able et al. 2005). The lack of clearly defined differences in foraging probability between cultivated and uncultivated habitat supports the idea that for some species, shellfish aquaculture provides foraging opportunities that are equivalent to those offered by uncultivated reference areas. Since habitat usage is species specific, any cultivated and uncultivated habitat equivalencies are also necessarily species specific.

Demersal fish were much more likely to feed in oyster flipbag and mudflat habitats, but those habitat types encompassed both cultivated and uncultivated areas. Pelagic

**TABLE 2** Coefficients and standard errors (SEs) of parameters in each top foraging behavior model. The best model for each vertical functional group was the model with the fewest parameters and that also had a  $\Delta AIC_c$  of 2.0 or less (where  $\Delta AIC_c$  is the difference in Akaike's information criterion corrected for small sample size).

Parameter	Pelagic fish		Demersal fish		Benthic (crabs)	
	Estimate	2 SEs	Estimate	2 SEs	Estimate	2 SEs
Habitat type						
Eelgrass	0.36	0.14–0.65	0.09	0.04–0.21	0.10	0.006–0.65
Mudflat	0.31	0.15–0.54	0.33	0.22–0.48	0.59	0.13–0.93
Oyster flipbags	0.41	0.23–0.60	0.33	0.23–0.43	0.14	0.01–0.67
Clam net	0.49	0.26–0.72	0.09	0.03–0.22	0.37	0.04–0.89
Oyster on bottom	0.33	0.13–0.63	0.09	0.03–0.25	0.16	0.01–0.75
Cover type						
Eelgrass	0.40	0.18–0.67	NA	NA	0.91	0.50–0.99
Algae	0.49	0.26–0.72	NA	NA	0.37	0.04–0.89
Bare/algae	0.19	0.07–0.45	NA	NA	0.07	0.005–0.54
Bare	0.33	0.18–0.52	NA	NA	0.27	0.14–0.44
Visibility						
High	NA	NA	NA	NA	0.37	0.04–0.89
Medium	NA	NA	NA	NA	0.20	0.03–0.67
Low	NA	NA	NA	NA	0.05	0.003–0.45

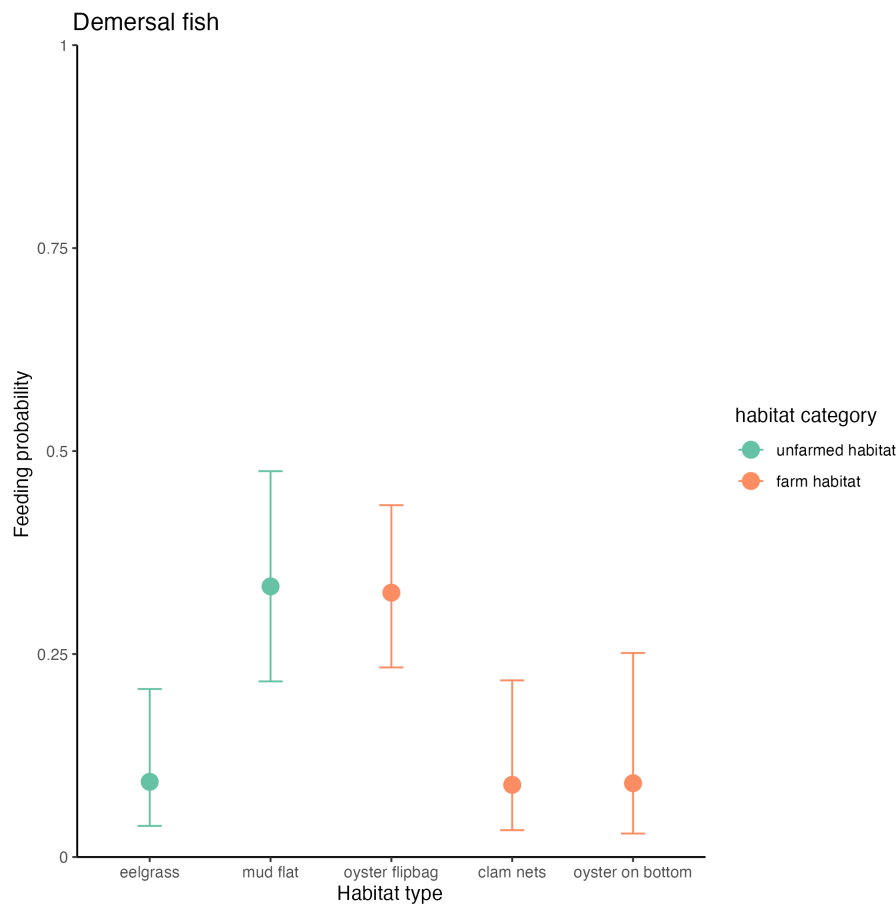


**FIGURE 3** Feeding probability for pelagic fish across the four cover types as estimated from the top-ranked model based on Akaike's information criterion corrected for small sample size. Lines denote two standard errors above and below each estimate.



**TABLE 3** Top models for each functional group based on a  $\Delta AIC_c$  of 2.0 or less (where  $\Delta AIC_c$  is the difference in Akaike's information criterion corrected for small sample size). Habitat type, cover type, and visibility were fixed effects and site was a random effect in the generalized linear mixed-effects models. The best model within a functional group was the model with the fewest parameters and that also had a  $\Delta AIC_c$  of 2.0 or less. There were no competing models for either the demersal fish or the crab vertical functional group.

Functional group	Model covariates	$\Delta AIC_c$	$AIC_c$ weight
Pelagic fish	Habitat type + cover type + site	0.00	0.494
Pelagic fish	Habitat type + cover type + visibility + site	0.28	0.431
Demersal fish	Habitat type	0.00	0.642
Crabs (benthic)	Habitat type + cover type + visibility	0.00	0.977

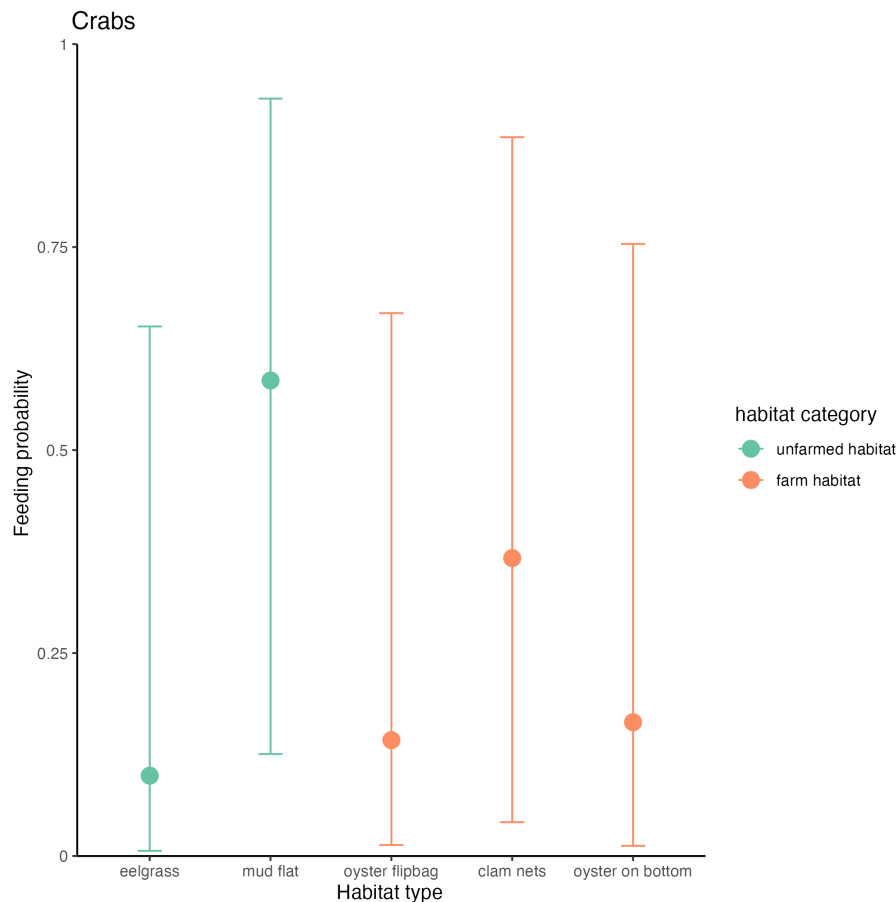


**FIGURE 4** Feeding probability for demersal fish across the five habitat types, as estimated from the top-ranked model based on Akaike's information criterion corrected for small sample size. Lines denote two standard errors above and below each estimate. Light-green color denotes unfarmed habitat types; light-orange color denotes farmed habitat types.

fish and crab feeding probability differed by habitat, but the differences were seemingly insignificant when factoring in the SEs. It might be that species abundance differs due to various species' habitat preferences, but where these fish and crabs are found, they have an equal propensity to forage in shellfish farms relative to eelgrass or mudflat habitat.

Structurally complex habitats, such as eelgrass meadows and oyster reefs, harbor higher densities of epibenthic meiofauna (Bell et al. 1984; Attrill et al. 2000; Jenkins et al. 2002; Hosack et al. 2006). As such, shellfish

aquaculture grow gear may provide increased feeding opportunities for structure-associated species by facilitating the attachment and growth of aquatic epiphytes, which similarly may harbor increased invertebrate prey. In South Puget Sound, we observed higher feeding probabilities for surfperch directly above clam nets, which were covered in thick filamentous algae. These nets likely provided attachment points for algae to adhere and grow, which in turn created beneficial habitat for preferred prey items, such as amphipods (Caine 1991). Algae, as a benthic cover type, was the top foraging cover type for



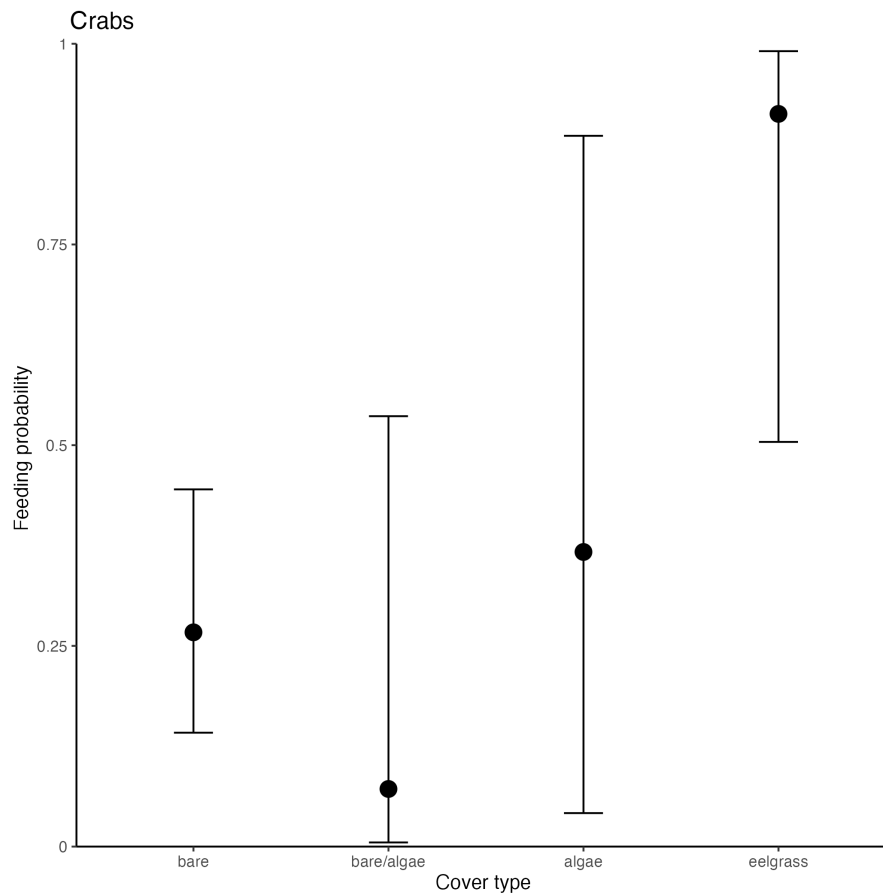
**FIGURE 5** Feeding probability for crabs across the five habitat types as estimated from the top-ranked model based on Akaike's information criterion corrected for small sample size. Lines denote two standard errors above and below each estimate. Light-green color denotes unfarmed habitat types; light-orange color denotes farmed habitat types.

pelagic fish but not for demersal fish or crabs (Table 2). The use of epiphyte-covered clam nets as foraging habitat may be location dependent. South Puget Sound has little or no eelgrass (Washington State Department of Natural Resources 2022), so thick algae mats adhering to natural or artificial structure may play a role similar to that played by eelgrass meadows in Puget Sound regions where such meadows are more abundant and support invertebrate prey species.

Individual species' preferences for the presence or absence of structure likely drove the trends that we observed. Responses to the addition of habitat structure are likely species and/or life stage specific. For example, small crabs have been previously documented to use eelgrass and oyster beds as refuge before moving into open mudflats to forage (Fernandez et al. 1993; Holsman et al. 2006). We documented a similar phenomenon here, with mudflats being the habitat with the highest foraging probability for crabs. However, the large overlap in SEs indicated that foraging habitat usage was highly variable, with a high probability of foraging where eelgrass as a cover type was present.

Oyster-on-bottom habitat was not a top feeding habitat for crabs, but Ferriss et al. (2021) found that the density of small crabs was generally very high in oyster beds, indicating that this is important habitat for crabs, such as young-of-the-year Dungeness crabs (Fernandez et al. 1993). Small crabs, such as shore crabs, were common in video recordings but generally were not assigned to the species level due to difficulty in generating a definitive identification. Behavior from these individuals was challenging to quantify due to their small size as well as physical blockage of the video frame by the scattered oysters that they were in. Thus, the feeding probability of crabs was likely underestimated in oyster beds specifically. Oyster beds may also provide other habitat functions for small crabs, such as nursery habitat or predator refuge, which has been previously documented (Holsman et al. 2006).

Our results were driven by a few numerically dominant species groups, primarily surfperch, sculpins, flatfish, and Threespine Sticklebacks (Table 1). Species that are less common or simply cryptic and difficult to study via video were likely underrepresented. For example,



**FIGURE 6** Feeding probability for crabs across the four cover types as estimated from the top-ranked model based on Akaike's information criterion corrected for small sample size. Lines denote two standard errors above and below each estimate.

Bay Pipefish and gunnels are extremely abundant in eelgrass meadows, but due to their camouflaged and cryptic nature we identified very few of them on video, so their contributions to the data set were too small for us to draw confident conclusions. Additionally, the behavior patterns observed here may not apply to other Puget Sound species that were not part of this study. We also focused only on adults and larger juveniles; small juveniles or larval stages of fish and crabs were excluded, as we could only quantify individuals that were large enough to be seen on video.

Our study adds to the growing body of knowledge on the ecosystem role that bivalve farms play in intertidal and nearshore habitats. We found that structure-associated species, such as surfperch (Hosack et al. 2006), foraged in and around bivalve gear types as well as naturally occurring eelgrass meadows and mudflats. Species that are not associated with structure, such as small flatfish (Williams 1994; Able et al. 2005), foraged in unstructured mudflats and oyster flipbag habitat in approximately equal proportions, indicating that oyster flipbags did not impede feeding for several demersal species. Crabs primarily fed in unfarmed mudflats as

well as eelgrass-covered substrate; however, very small crabs (e.g., shore crabs) inhabited oyster-on-bottom-style farm plots in high densities (Ferriss et al. 2021) and may have utilized these oyster beds in ways that we were not able to accurately quantify based on video observation.

Our results indicate that oyster and clam aquaculture habitat provides foraging opportunities for several common species of nearshore fish, particularly surfperch, sculpins, and small flatfish. The large SEs of feeding probability for pelagic fish and crabs indicated that feeding by these species groups was similar across habitats—that is, they appeared to be generalists. Demersal organisms, dominated by sculpins, Threespine Sticklebacks, and small flatfish, were much more likely to forage in open mudflat and oyster flipbag habitats. Structurally complex habitat usually harbors higher diversity and abundance of nearshore fauna (Orth et al. 1984; Jenkins et al. 1997; Heck et al. 2003). Vertically elevated habitat, such as that created by oyster farm gear or eelgrass meadows, harbors higher densities of organisms compared to unstructured and unvegetated habitat, such as mudflats (Castel et al. 1989; Pinnix et al. 2005; Hosack et al. 2006; Ferraro

and Cole 2007). Habitat structure created by the addition of oyster or clam growing gear also provided attachment points for aquatic epiphytes, which may further enhance feeding by creating ideal habitat for invertebrate prey items (e.g., amphipods). Although some species were observed to forage more in shellfish aquaculture-associated habitat, we do not know whether foraging in these habitats leads to higher growth and survival relative to unfarmed natural areas. Shellfish farms within a larger nearshore habitat mosaic of eelgrass meadows, mudflats, bivalve aquaculture gear, and edge habitat can provide foraging habitat for several species of nearshore fish, including adult and subadult individuals.

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## CONFLICT OF INTEREST STATEMENT

None of the authors has a conflict of interest associated with this study.

## DATA AVAILABILITY STATEMENT

All data used in this study and all R code used for the analysis and figures are available online at [zenodo.org](https://doi.org/10.5281/zenodo.7742785) (<https://doi.org/10.5281/zenodo.7742785>).

## ETHICS STATEMENT

This study meets the ethical guidelines outlined by the American Fisheries Society (AFS 2014).

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