



Characterizing the habitat function of bivalve aquaculture using underwater video

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ABSTRACT: Bivalve aquaculture is an expanding coastal industry with the potential to modify the habitat of fish and crab species, affecting their refuge, movement, and feeding. The habitat function of shellfish aquaculture is not yet well understood, in part due to difficulties in data collection using traditional methods. Underwater video was used to observe fish and crab species' affiliations with cultured Pacific oyster *Crassostrea gigas* and Manila clam *Venerupis philippinarum* aquaculture sites in comparison to uncultured reference sediment and eelgrass habitats. Sites were monitored in 9 locations across 3 regions of Puget Sound, Washington, USA, in the summers of 2017 and 2018. Of the 3038 fish and crabs observed, 98% were represented by Embiotocidae (surfperch), crabs, three-spined stickleback *Gasterosteus aculeatus*, Cottidae (sculpins), and Pleuronectiformes (flatfish). Overall, the affiliations of fish and crabs with bivalve aquaculture varied by species groups, culture type, and regional environmental and habitat conditions. These interactions varied on a scale of approximately 150 km, highlighting variation of aquaculture–ecological interactions at a scale not previously recorded in Puget Sound. Species composition varied between aquaculture and non-aquaculture habitats in 2 of the 3 regions studied. Species diversity and richness in aquaculture habitats varied regionally, relative to reference habitats. Pelagic species were more abundant in aquaculture and reference sites that had vertical structure, but abundances of demersal and benthic species on aquaculture habitat relative to reference sites varied regionally. The availability of habitats within intertidal regions, including varying types of aquaculture, could determine community structure for marine organisms such as fish and crab.

KEY WORDS: Aquaculture · Shellfish · Video · Habitat · Oyster · Clam · Puget Sound

1. INTRODUCTION

Bivalve aquaculture has the potential to provide social-economic benefits to coastal communities while providing habitat function for nearshore ecosystems (Alleway et al. 2019, Gentry et al. 2020). Through the

addition of structured habitat, bivalve aquaculture may provide ecological functions based on the ecological paradigm that structurally complex habitats support increased species diversity, richness, and abundance (MacArthur & MacArthur 1961). However, the connection between habitat and community

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structure may vary by type of structure (Loke & Todd 2016), latitude (Bracewell et al. 2018), surrounding habitat (Grabowski et al. 2005), scale of habitat relevant to the focal species (Loke et al. 2015), species group (Tews et al. 2004), and types of complexity (Tews et al. 2004), adding to the ongoing discussion of whether artificial habitat has higher abundance of fish due to aggregation or enhanced production (Bohnsack 1989). Because of these uncertainties, questions remain as to whether this habitat complexity paradigm applies to bivalve aquaculture, and if aquaculture provides habitat functions unique or similar to co-occurring, natural habitat structure (e.g. seagrasses) (Dumbauld et al. 2011).

Nearshore marine habitat complexity can support increased species diversity and richness through resource partitioning (Munday 2004), increased survival due to better refuge from predation (Hixon & Beets 1993), and higher abundances of fish and invertebrates (Shervette & Gelwick 2008). Bivalve aquaculture adds structure in the nearshore marine environment in the form of bivalve shells (e.g. oysters growing on the sediment) and grow-out gear (e.g. anti-predation nets and suspended mesh bags). Mobile fish and invertebrates may be attracted to aquaculture structure for protection from predation, or to forage on the cultured bivalves and algae or invertebrates growing on the structure (e.g. Dealteris et al. 2004, Powers et al. 2007, Callier et al. 2018). In contrast, aquaculture structure may also deter species by hiding predators and limiting their mobility or ability to find prey (summarized by Callier et al. 2018) and may result in decreased abundance of taxa associated with unstructured habitats, such as mudflats (Dumbauld et al. 2009). Bivalve aquaculture has been considered in the restoration context via artificial reef production (Mayer-Pinto et al. 2017, Alleway et al. 2019); however, the habitat function of aquaculture is not as well understood when the purpose is primarily economic, and potentially includes gear associated with the shellfish grow-out phase (e.g. anti-predation nets and mesh bags). We also have a poor understanding of the importance of regional context in the assessment of aquaculture habitat function. Do shellfish cultivation sites provide similar habitat functions across scales of 100s of km? Understanding the function of bivalve aquaculture as subtidal habitat in these regional contexts can facilitate the consideration of potential habitat-related changes in the marine community in the sustainable development of aquaculture.

Puget Sound, Washington, USA, supports more than 50 companies and indigenous tribes that commercially produce shellfish, using a variety of shell-

fish and grow-out methods. This 2632 km² estuary contributes to the \$118 million USD mollusk aquaculture industry in Washington State (USDA National Agricultural Statistics Service 2017), largely occurring in the inter-tidal zone, overlapping with mudflats, eelgrass (native *Zostera marina* and non-native *Z. japonica*), and gravelly habitats (Ebbesmeyer et al. 1988, Dethier & Kunze 1997). The industry includes multiple bivalve species and grow-out methods, including Manila clams *Venerupis philippinarum* grown under anti-predation nets and Pacific oysters *Crassostrea gigas* grown directly on the sediment (on-bottom) or suspended in mesh bags (flipbags or tumble bags). To date, oyster and clam aquaculture in the northwest USA has been shown to have mixed effects on species diversity, species richness, and abundance (Dumbauld et al. 2009). Observed ecological responses to on-bottom oyster habitat in this region include increased abundance of sessile benthic organisms, species-specific fish responses, no effect on diversity and abundance of mobile fish and invertebrates, and no effect on salmon (Hosack et al. 2006, Semmens 2008, Dumbauld et al. 2015). Fewer studies have been conducted on the interactions of Manila clam and oyster suspended culture on surrounding marine communities in this region, but research in other geographic locations have shown mixed interaction with clams and oyster suspended culture (Connolly & Colwell 2005, Forrest et al. 2009, Luckenbach et al. 2016).

The purpose of this study was to determine how nearshore fish and crab communities respond to various forms of bivalve aquaculture. We used underwater video to characterize the fish and crab communities observed on 3 types of aquaculture practices: (1) cultured Manila clam, (2) on-bottom Pacific oyster, and (3) Pacific oysters in flipbags (suspended mesh bags), as well as nearby sediment and eelgrass references sites, in 3 regions across 150 km of Puget Sound, WA (see Fig. 1). We tested the following hypotheses: (1) fish and crab community structure varies between aquaculture and non-aquaculture sites, and (2) fish and crab species-specific abundances vary in aquaculture habitats relative to their natural association with structured habitats.

2. MATERIALS AND METHODS

2.1. Study area and site selection

The study was conducted in Puget Sound, a large fjord-like estuary that is 161 km long with a 2143 km

coastline, in the northwest USA (Ebbesmeyer et al. 1988). Puget Sound is comprised of 5 ecologically distinct sub-basins characterized primarily by geomorphology, extent of freshwater influence, oceanographic conditions, and anthropogenic stressors (Ruckelshaus et al. 2007) (Fig. 1, Table 1). Inter-basin differences have been observed for intertidal, subtidal, and nearshore pelagic species in Puget Sound, but with no conclusive mechanisms or defining drivers identified. This study was designed with the knowledge that species' natural distributions and habitat types (including mudflat extent and eelgrass

presence) vary across Puget Sound, and that species' interactions with aquaculture might vary as well (Burns 1985, Rice et al. 2012, Greene et al. 2015, Shelton et al. 2017).

Aquaculture sites were selected based on type of cultured species, grow-out methods, accessibility, and location in Puget Sound. We sampled across 3 basins (hereafter referred to as regions) where aquaculture is most prominent: North Sound, South Sound, and Hood Canal. The types of aquaculture mesohabitats observed in each region included: Pacific oyster grown on the sediment (hereafter referred to as to

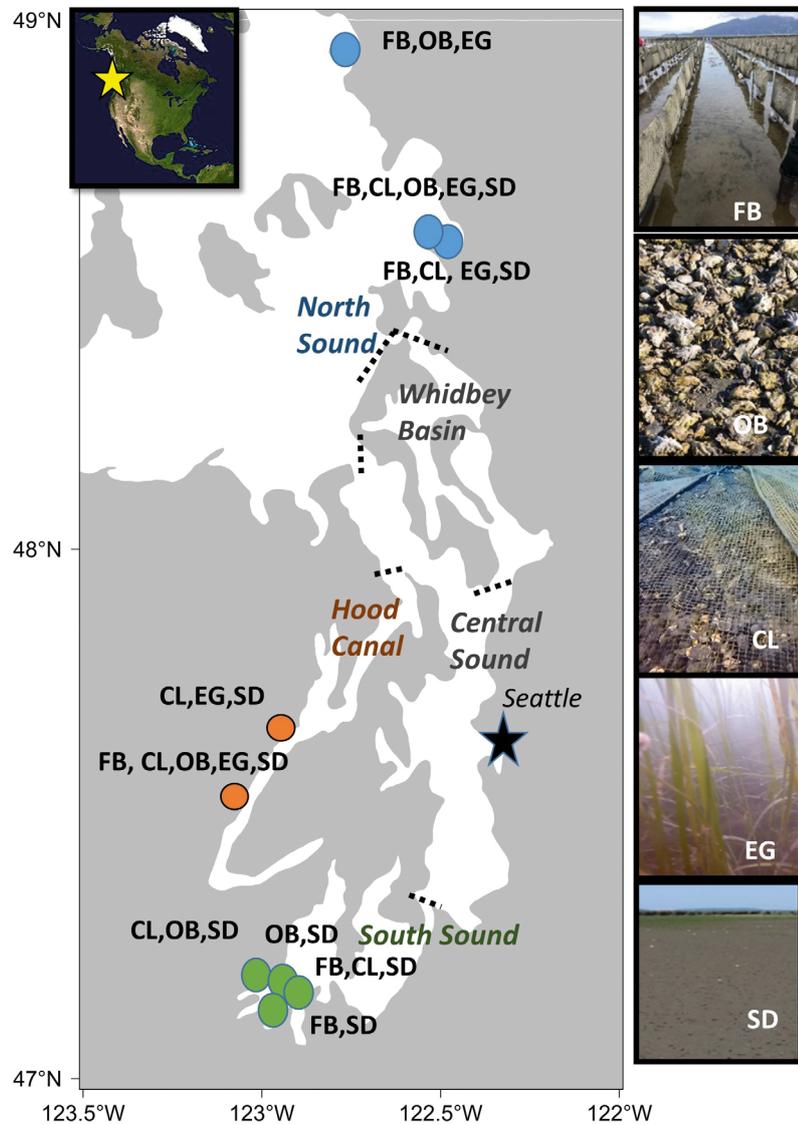


Fig. 1. The 9 sample sites in North Sound (●), South Sound (●), and Hood Canal (●), Puget Sound, Washington, USA. The 5 natural basins are labelled with their boundaries marked by dashed black lines. Photos show the 5 mesohabitat types sampled, including: Pacific oyster in flipbags (FB), Pacific oysters on-bottom (OB), Manila clams (CL), uncultured eelgrass (EG), and uncultured sediment (SD)

as on-bottom), Pacific oyster in suspended flipbags (hereafter referred to as flipbags), and Manila clams (hereafter referred to as clams) grown in the sediment under anti-predation nets (Fig. 1). In addition to the 3 aquaculture mesohabitat types, we sampled 2 types of reference mesohabitats (no aquaculture present) at each farm, where available. Reference sites were generally categorized as eelgrass (*Zostera marina* or *Z. japonica*) or sediment (a range of mudflats to more gravelly beaches, sometimes with low-density eelgrass, *Z. marina* or *Z. japonica*, present), depending on the prominent mesohabitat characteristics. These sites were 30 to 60 m away from existing aquaculture and represented the range of natural habitat in the area. This distance was selected to maximize the similarity in environmental conditions and depth but minimize potential effects from aquaculture sites (Fig. 2). In regions in which eelgrass was present (North Sound and Hood Canal), oyster flipbags were often located at depths in which eelgrass would naturally occur, while clams and oyster on-bottom were often in shallower, more naturally sediment or gravelly habitats.

In total, we collected data from the 5 mesohabitat types (3 aquaculture and 2 reference, with the exception of no eelgrass sites in South Sound), at 6 farm locations (North Sound and South Sound), twice per summer in June to August 2017, and at 9 farm locations (North Sound, South Sound, and Hood Canal) in June to August 2018 (Table 2). The resulting sample

Table 1. Description of the oceanographic and ecological conditions in the 3 focal Puget Sound basins of this study (modified from Ruckelshaus et al. 2007)

Puget Sound basin	Description
Northern basin (focus on eastern part of basin)	<ul style="list-style-type: none"> • Influenced by tidal action and input from the Fraser River • The most heavily used basin for agriculture in Puget Sound • Rosario (in the northern basin) is a relative hotspots for forage fish production (Greene et al. 2015) • Tidal range of 2.4 m (Mofjeld & Larsen 1984)
Southern basin (all waterways south of Tacoma Narrows)	<ul style="list-style-type: none"> • Numerous shallow inlets with extensive shoreline • Shallower and currents are strongly influenced by the tides • No major rivers flow into this area (resulting in less stratified waters compared to other basins) • High water residence times • Higher temperatures in the inlets • Has the least amount of vegetation • Tidal range of 4.6 m (Mofjeld & Larsen 1984)
Hood Canal (focus on central area)	<ul style="list-style-type: none"> • Isolated by a sill at its entrance that limits transport of deep marine waters • Slow currents • Eelgrass found throughout the canal • Central part of Hood Canal is the deepest • Can experience periods of low dissolved oxygen in summer

sizes were North Sound — clams: 8, on-bottom: 6, flip-bag: 10, sediment: 8, eelgrass: 10; South Sound — clams: 5, on-bottom: 8, flipbag: 6, sediment: 14, eelgrass: 0; and Hood Canal — clams: 6, on-bottom: 2, flipbag: 2, sediment: 6, eelgrass: 6. The numbers of aquaculture and reference sites are not equal as we

sampled a maximum of 3 aquaculture mesohabitats on a given farm and 1 to 3 reference sites on a given farm, depending on the footprint of the farm. For example, on a smaller South Sound farm with no naturally occurring eelgrass, we sampled 1 sediment reference site and 2 aquaculture mesohabitats (clam

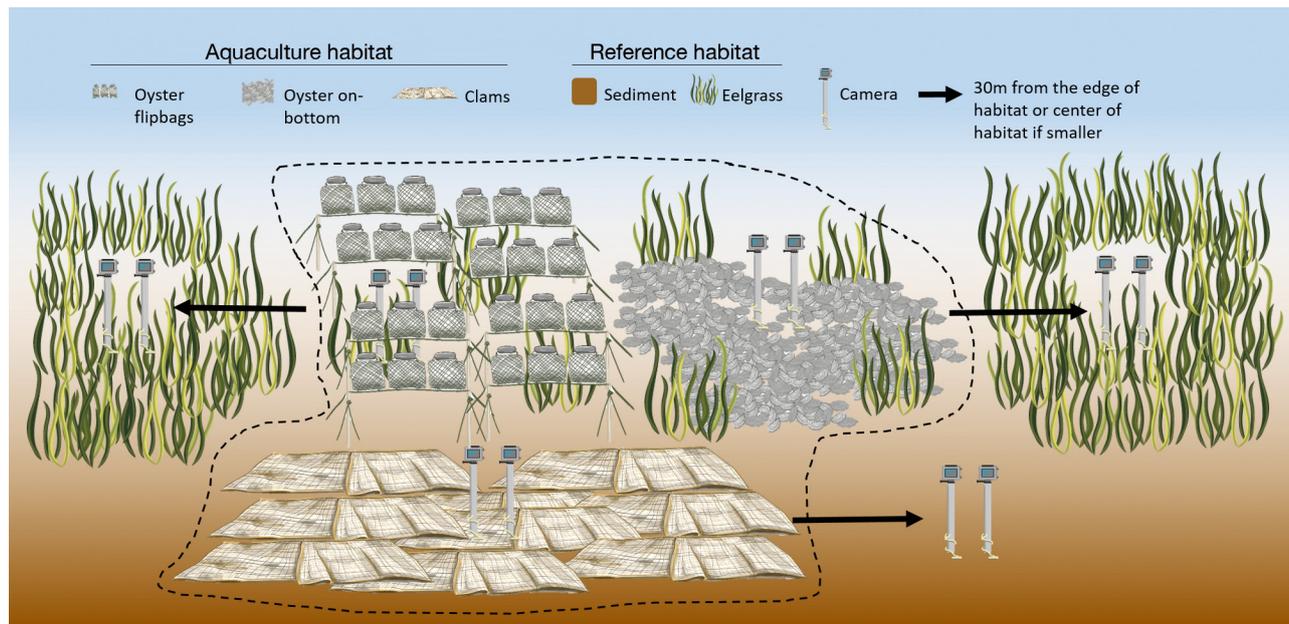


Fig. 2. Camera locations in aquaculture (oyster flipbag, oyster on-bottom, clam) and reference (sediment, eelgrass) mesohabitats for a given aquaculture farm (dashed line) during a single sampling event. Two cameras were set in each mesohabitat for every sampling event. Reference sites were 30 m away from the edge of aquaculture habitat but at similar depth and other environmental conditions. On certain farms, the same site served as a reference for multiple aquaculture sites if available reference areas were limited and the habitats were similar. Drawings by Frances Duncan

Table 2. Number of times each mesohabitat type (aquaculture and reference) was sampled at each site and region, from June to August of 2017 and 2018. One sampling event equates to 2 days of video, of which ten 2 min video segments from 1 day were analyzed to create a unit of analysis. Total number of replicates were 5 to 14 for each mesohabitat–Region combination with the exception of oyster on-bottom and oyster flipbags in Hood Canal (2 replicates). –: no sampling occurred

Region/site	Year	Culture species & grow-out gear			Reference site	
		Manila clam (anti-predation nets)	Pacific oyster on-bottom	Pacific oyster flipbag	Sediment	Eelgrass
North Puget Sound						
Site 1	2017	2	2	2	2	2
	2018	2	2	2	2	2
Site 2	2017	2	–	2	2	2
	2018	2	–	2	2	2
Site 3	2017	–	–	–	–	–
	2018	–	2	2	–	2
No. replicates in region		8	6	10	8	10
South Puget Sound						
Site 1	2017	2	–	2	2	–
	2018	2	–	2	2	–
Site 2	2017	–	2	–	2	–
	2018	–	2	–	2	–
Site 3	2017	–	–	–	–	–
	2018	–	–	2	2	–
Site 4	2017	–	2	–	2	–
	2018	1	2	–	2	–
No. replicates in region		5	8	6	14	0
Hood Canal						
Site 1	2017	2	–	–	2	2
	2018	2	–	–	2	2
Site 2	2017	–	–	–	–	–
	2018	2	2	2	2	2
No. replicates in region		6	2	2	6	6

and oyster flipbags) that were all at similar depths, and separated by approximately 30 m to represent similar environmental conditions. On a larger North Sound farm, we sampled a sediment site close to clam mesohabitat, and 2 separate eelgrass reference sites next to oyster on-bottom and oyster flipbag mesohabitats. We sampled 2 eelgrass reference sites here as the oyster on-bottom and flipbag mesohabitats were separated by a relatively large distance.

Our sampling window of June through August was selected as a relatively stable time in the oceanographic and ecological seasonal cycles of Puget Sound (Strickland 1983, Moore et al. 2008). The spring months (generally March to May) bring increased sunlight and stratification (higher freshwater runoff) resulting in phytoplankton blooms. Zooplankton (e.g. large copepods and euphausiids) rise to the surface to feed on these phytoplankton and release their larvae (March to April). Zooplanktivorous larvae of small

pelagic fish such as herring, smelt, and sand lance arrive, followed by their predators. This cycle reverses in the fall, generally beginning in September.

2.2. Video collection

We used underwater video to quantify abundance and composition of fish and crabs in aquaculture and reference sites while the intertidal habitats were submerged. Benefits of using underwater video include: sampling in complex habitats (i.e. aquaculture farms with structure in the water), passive observations (i.e. removing the bias of sampling disturbance found in beach seines and snorkel/dive surveys), and quality of data (ability to verify species identifications versus snorkel/dive surveys in which there is only one chance for identification and counting). Similar approaches have been used by Gross et al. (2018),

Muething et al. (2020), Mercaldo-Allen et al. (2021), and Shinn et al. (2021). GoPro cameras (Hero 3+ and Hero 4) were set up in pairs, 30.5 cm above the ground, facing down at a 20° angle. Cameras were mounted on PVC pipe (25.4 mm diameter), housed in GoPro Dive casings with an external timer (CamDo Blink) attached. Cameras recorded for 2 min, in 10 min intervals over a period of 3 h around high tide (tides are semi-diurnal). Preliminary trials showed the hours near slack tide had the best visibility. The cameras were angled down to maximize the visibility of fish in the video. All cameras were pointed towards the incoming tide, with the exception of those in flipbag mesohabitat that were directed in parallel with the established line of flipbags (offshore or alongshore depending on the orientation). Cameras were positioned a minimum of 30 m from the edge of a given mesohabitat, or in the approximate center if the mesohabitat had a smaller footprint. Two PVC poles were placed 125 cm from the base of the camera pole and 1 m apart to demark a 1 m² field of view. The 125 cm distance accounted for an extra 25 cm of area off-camera due to the angle of the camera. Redundancy was built into the sampling design to account for camera failure, weather or environmental conditions affecting visibility, or macroalgae obscuring the camera lens, by setting cameras in pairs (approximately 15 cm apart) and recording at high tide over 2 consecutive days. Video with the best visibility was selected for analysis from 1 camera of each pair, and from 1 day of the 2 days recorded. Most recordings were conducted during the morning high tide. Recordings were set for late afternoon high tide if light was limited during the morning high tide. We analyzed the video using a video editing software (BORIS: Behavioral Observation Research Interactive Software accessed from www.boris.unito.it/ on June 14, 2019).

2.3. Video analyses

Fish and crab species were identified to their lowest taxonomic groupings and by vertical distribution (pelagic, demersal, or benthic) (see Table 3 and refer to Text S1 in the Supplement at www.int-res.com/articles/suppl/q013p439_supp.pdf for additional details on species grouping). Abundances of species groups were calculated by totaling the number of each species or species group observed swimming in the 1 m² field of view during a 2 min video clip. We then summed the observations across ten 2 min video clips, recorded closest to high tide, to calculate the

number of fish or crab observed per mesohabitat type and date. We selected our total count metric (total sum of sightings) for its ability to represent species composition and for comparison to other nearshore video studies conducted in the region (Sund 2015, Gross et al. 2017, 2018, Muething et al. 2020). To determine within-mesohabitat variability, we conducted a separate study to determine how well our observations represented species' presence within a given mesohabitat footprint, described in Text S2.

2.4. Data analysis

We first analyzed the video data for similarities and differences in communities and species affiliated with aquaculture at the broader Puget Sound geographic level (combining the 3 regions) and at the individual regional level. Regionally specific trends in community characteristics and species-level mesohabitat affiliations were then analyzed relative to the presence of aquaculture (present: flipbags, on-bottom, and clams or absent: sediment, eelgrass) and the 5 mesohabitat types (flipbags, clam, on-bottom, eelgrass, and sediment). We focus on results with $\alpha < 0.05$. All analyses were done in the R programming environment using R 3.6.1 (R Core Team 2019).

2.4.1. Community structure

We used non-metric multidimensional scaling (NMDS) to analyze the community structure relative to the presence of aquaculture and the 5 mesohabitat types. The NMDS analysis was conducted at an aggregated Puget Sound level (all 3 regions combined) and at a regional level (North Sound, South Sound, and Hood Canal) (using Adonis in the R vegan package; Oksanen et al. 2019). We transformed the data ($\ln + 1$) to reduce the influence of extreme values (Borcard et al. 2011). We created the resemblance matrix using the Bray Curtis similarity measure and computed 2000 permutations. We then used permutational multivariate analysis of variance (PERMANOVA) to determine if observed differences were statistically different ($p < 0.05$). We used SIMPER to determine which species groups had the greatest contributions to observed differences (SIMPER in the R vegan package; Oksanen et al. 2019).

Differences in species richness and species diversity (Shannon-Wiener index) were analyzed using generalized linear mixed models (lme4 package; Bates et al. 2015). To account for the lack of inde-

pendence across replicates, the error structure for each species' group-specific suite of models was assessed using the full model and including random effects of site, year, or a combination of site and year (Zuur et al. 2009). The best-fit model was selected from models with either aquaculture presence or mesohabitat types as fixed effects, determined using Akaike's information criterion corrected for small sample sizes (AIC_c; Akaike 1974). Region was included as a fixed effect in all models as we had previously identified how communities varied by region in the community structure analysis (see Section 3). All species diversity models were run including and excluding surfperch to determine the influence of the most commonly observed species group. We conducted post hoc analysis of pairwise comparisons of the estimated marginal means (least-squares means) from the best-fit model to determine statistical differences (emmeans package; Lenth 2020). The pairwise comparisons used the Tukey method to produce Tukey-adjusted p-values.

2.5. Species and functional group affiliations

We used generalized linear mixed effects models (GLMM) to determine if the presence of aquaculture or the 5 mesohabitat types explained variation in abundance of selected species groups and functional groups (lme4 package; Bates et al. 2015). A subset of species groups was selected based on the highest frequency of occurrence, across all regions, and their importance in ecological and fisheries contexts. The subset of species groups included surfperch, sculpin, crab, unidentified crab, and flatfish. To account for the lack of independence across replicates, the error structure for each species' group-specific suite of models was assessed using the full model and including random effects of site, year, or a combination of site and year (Zuur et al. 2009). Region (North Sound, South Sound, and Hood Canal) was included as an interactive or additive fixed effect in each model acknowledging the regional differences observed in NMDS analysis (see Section 3). We used negative binomial and zero-inflated negative binomial distributions for models except flatfish, as recom-

mended for over-dispersed count data (where the observed variance was greater than the mean) (Zuur et al. 2009). The suite of flatfish models had to be simplified due to the lack of observations in South Sound. The data were analyzed separately by region, using the Poisson distribution (i.e. models only had aquaculture or mesohabitat as fixed effect). We used AIC_c to determine which model best explained variation in species' abundance. The same set of analyses were conducted on all species grouped by their vertical distribution functional group (benthic, demersal, pelagic; see Table 3).

3. RESULTS

We observed 3038 individual fish and crabs in surveys conducted during the summer months of 2017 and 2018 (Table 3, Fig. 3). The 6 species groups representing 98% of the observations included surfperch, unidentified crabs, crabs (*Metacarcinus* spp.) stickleback, sculpin, and flatfish. Overall, we observed differences in abundance of these species groups between aquaculture and reference sites, but these differences were dependent on region, presence/absence of aquaculture and specific mesohabitat types—these complexities are described in the following sections. We observed a low level of within-

Table 3. Total observations of the 13 most common fish and crab species groups summed across farms, months, and years. Data were collected from June to August 2017 and 2018, across 3 regions of Puget Sound, WA, USA

Species/group	Vertical functional group	Hood Canal	North Sound	South Sound
Surfperch (Embiotocidae)	Pelagic	244	406	1451
Unidentified crab (primarily small crabs: including shore crabs <i>Hemigrapsus</i> and juvenile <i>Metacarcinus</i> crabs)	Benthic	224	34	2
Crab (<i>Metacarcinus</i> spp.)	Benthic	80	11	106
Three-spined stickleback <i>Gasterosteus aculeatus</i>	Demersal	1	181	2
Sculpin (Cottidae)	Demersal	42	58	43
Flatfish (Pleuronectiformes)	Demersal	63	19	0
Forage fish (<i>Clupea pallasii</i> , <i>Hypomesus pretiosus</i> , <i>Ammodytes hexapterus</i>)	Pelagic	0	4	20
Snake prickleback <i>Lumpenus sagitta</i>	Demersal	0	0	17
Gunnel (Pholidae)	Demersal	4	7	1
Salmonid (Salmonidae)	Pelagic	0	0	10
Bay pipefish <i>Syngnathus leptorhyncus</i>	Demersal	2	2	1
Greenling (Hexagrammidae)	Demersal	0	3	0

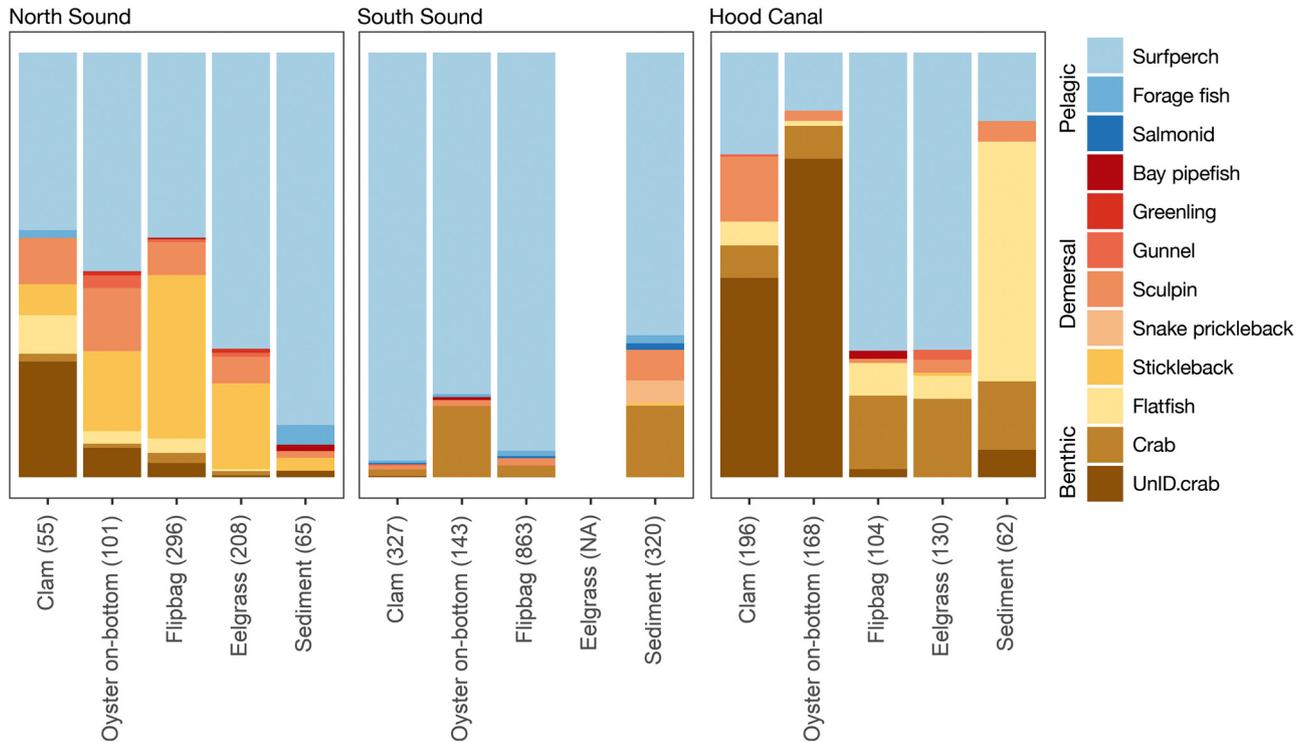


Fig. 3. Proportion of species groups observed in clam, oyster on-bottom, flipbag, eelgrass, and sediment mesohabitat types in North Sound, South Sound, and Hood Canal. Species are ordered by functional groups from top (pelagic: surfperch, forage fish, salmonid) to bottom (benthic: unidentified [UnID.] crabs and crabs), with demersal groups in the middle. The total number of fish and crabs observed is in parentheses after each label along the x-axis

mesohabitat variation between cameras in certain mesohabitat/regions (Text S2) reflecting a certain level of patchiness to species distribution even within a mesohabitat footprint.

3.1. Community structure

3.1.1. Species composition

When data from all regions (North Sound, South Sound, Hood Canal) were analyzed together, species composition of fish and crab communities differed statistically among regions (North Sound, South Sound, and Hood Canal; PERMANOVA, $p < 0.001$; Table 4, Fig. 4a), explaining 22% of the variation. Neither the presence of aquaculture (PERMANOVA, $p = 0.113$; Table 4, Fig. S1), nor mesohabitat type (PERMANOVA, $p = 0.08$; Table 4, Fig. S1), explained statistical differences between the observations, when analyzed all together. When data were analyzed by region, species composition in North Sound was statistically different between aquaculture and reference sites (i.e. eelgrass and sediment) (PERMANOVA, $p = 0.01$; Table 4, Fig. 4b), but not between mesohabitat types (i.e. sediment, eelgrass, flipbags, oyster on-

bottom, clams) (PERMANOVA, $p = 0.4$, Table 4). Surfperch and stickleback explained 43% of the observed variation in the aquaculture model (SIMPER, Table S1). South Sound species composition was not statistically different by aquaculture presence/absence (PERMANOVA, $p = 0.2$, Table 4) or mesohabitat type (PERMANOVA, $p = 0.6$, Table 4), when surfperch were included or excluded from the analysis. In Hood Canal, we found differences in species composition in models that included aquaculture presence/absence (PERMANOVA, $p = 0.02$; Table 4, Fig. 4c), but not in models that evaluated individual mesohabitat types (PERMANOVA, $p = 0.09$, Table 4). Unidentified crabs, surfperch, and flatfish cumulatively explained 67% of the variation in the Hood Canal aquaculture model (SIMPER, Table S1).

3.1.2. Diversity and richness

When all regional data were combined, models that included additive or interacting fixed effects of region and the presence/absence of aquaculture best explained variation in species diversity, given the data, relative to models including individual meso-

Table 4. Summary of PERMANOVA models for all regions combined, North Sound, South Sound, and Hood Canal, which include aquaculture presence (aquaculture) or mesohabitat type (habitat) as variables

Region	Model		df	MS	F	R ²	p
All regions	Region	Region	2	1.117	8.518	0.221	5×10 ⁻⁴
		Residuals	60	0.131		0.779	
		Total	62			1.000	
	Aquaculture	Aquaculture	1	11.020	1.726	0.028	0.113
		Residuals	61	6.385		0.972	
		Total	62			1.000	
	Habitat	Habitat	4	0.237	1.501	0.094	0.076
		Residuals	58	0.158		0.906	
		Total	62			1.000	
North Sound	Aquaculture	Aquaculture	1	0.416	2.893	0.104	0.013
		Residuals	25	0.144		0.896	
		Total	26			1.000	
	Habitat	Habitat	4	0.164	1.074	0.163	0.398
		Residuals	22	0.152		0.837	
		Total	26			1.000	
South Sound	Aquaculture	Aquaculture	1	0.145	1.491	0.077	0.196
		Residuals	18	0.098		0.923	
		Total	19			1.000	
	Habitat	Habitat	3	0.089	0.869	0.140	0.605
		Residuals	16	0.102		0.860	
		Total	19			1.000	
Hood Canal	Aquaculture	Aquaculture	1	0.367	3.222	0.187	0.022
		Residuals	14	0.114		0.813	
		Total	15			1.000	
	Habitat	Habitat	4	0.187	1.697	0.382	0.090
		Residuals	11	0.110		0.618	
		Total	15			1.000	

habitat types ($\Delta AIC_c > 2$) (Tables S2 & S3). These results were true with and without surfperch in the analysis, although the interactive and additive aquaculture models including surfperch tied for lowest AIC_c values. Of these 2 best fit models, we selected the interactive model of region and aquaculture versus the additive model to highlight the previously discovered regional differences in species' responses to aquaculture (NMDS results). We present both the AIC_c /post hoc analysis of significance and the plots of effect size (Fig. 5), in part to show various nuances of these data that would be lost in relying solely on single measures of significance. While SE bars around the mean effect sizes are not overlapping for the North Sound (diversity in aquaculture was greater than that in reference sites when surfperch were included in analysis) and South Sound (diversity in

aquaculture is less than that in reference sites, surfperch included in analysis), post hoc results show neither differences are statistically different ($p = 0.216$) (Fig. 5). The presence of aquaculture in Hood Canal had no predicted statistical effect on diversity, relative to the reference sites ($p = 0.475$) (Fig. 5).

Variation in species richness was best explained by the interaction between region and aquaculture, relative to combinations of region and mesohabitat type ($\Delta AIC_c > 2$) (Table S3). There were no clear trends in richness between aquaculture and non-aquaculture sites in South Sound ($p = 0.915$) and Hood Canal ($p = 0.486$) (Fig. 5).

3.2. Species and functional group affiliations

Among the region-specific analyses, mesohabitat type and aquaculture presence each best explained variation in abundance of 4 species and vertical functional groups; however, some of these trends varied by region ($\Delta AIC_c > 2$, Fig. 6, Tables S4 & S5).

The presence of aquaculture (either additive or interactive with region) best explained trends in sculpin, crab, North Sound flatfish, and the benthic functional group (Fig. 6, Tables S4 & S5;

$\Delta AIC_c > 2$). Trends in sculpin abundance differed by region, however, South Sound sculpin were more abundant in non-aquaculture habitat (sediment only) relative to sites with aquaculture present. North Sound and Hood Canal had the opposite trends, as sculpin were most abundant in habitat with aquaculture present, relative to eelgrass and sediment sites. Flatfish in North Sound were more abundant in aquaculture habitats relative to non-aquaculture habitats. The benthic functional group had higher abundance in aquaculture habitats relative to non-aquaculture habitats in Hood Canal and North Sound, but no difference was observed in South Sound, driven by trends in sculpin abundance (Fig. 6).

Mesohabitat type best explained trends in Hood Canal flatfish, unidentified crabs, and the pelagic

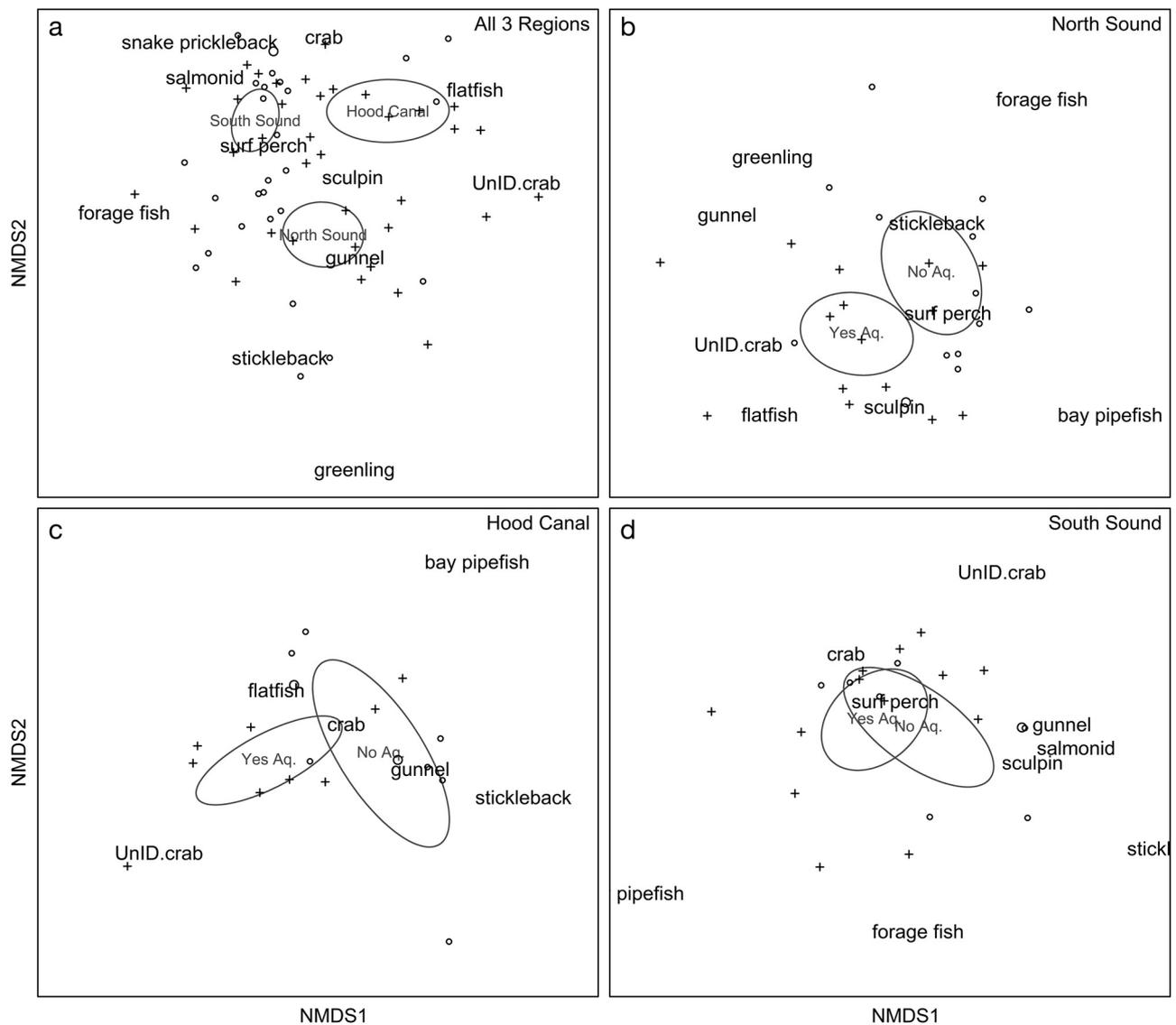


Fig. 4. NMDS results for comparisons that subsequent PERMANOVA tests proved to vary statistically ($p < 0.05$) in species composition across (a) 3 regions of Puget Sound Region, when all data were combined, and between habitat with aquaculture (Yes Aq., +) and habitat without aquaculture (No Aq., O) in (b) North Sound, (c) Hood Canal, and (d) South Sound. The NMDS results for comparisons between habitat with aquaculture present or aquaculture absent in (d) South Sound were not statistically different in subsequent PERMANOVA tests ($p > 0.05$) but are shown here for comparison. The 95% confidence ellipses indicate the uncertainty around the estimate of the centroid, given the data

and demersal functional groups (Fig. 6). Hood Canal flatfish were more common in bare sediment mesohabitats relative to other mesohabitat types. Abundance of unidentified crabs was highly variable, resulting in no variation between mesohabitat types, although abundances in clam and on-bottom mesohabitats were higher. Abundance of the pelagic group (largely driven by surfperch) was greatest in flipbags and eelgrass (or only flipbags in South Sound) in all 3 regions. Demersal species were most abundant in sediment relative to other mesohabitats in

Hood Canal and South Sound. The opposite pattern was observed in North Sound, with lowest abundances of demersal species in non-structured mesohabitats.

The best fit model for surfperch was tied between aquaculture presence and mesohabitat type (Fig. 6). There was little separation in abundance estimates between mesohabitat types or aquaculture presence, although flipbags and eelgrass mesohabitats were higher in all regions (flipbags only in South Sound).

4. DISCUSSION

Overall, while species composition varied between combined aquaculture and non-aquaculture habitats in 2 of 3 regions, we found regionally distinct associations between the fish and crab species and the habitats associated with shellfish aquaculture. Species' affiliations with aquaculture farms varied regionally, on a scale of approximately 150 km. Species diversity and richness did not change with the presence of aquaculture in Hood Canal, was higher in aquaculture sites in North Sound, but lower in South

Sound. Pelagic fish (dominated by surfperch) were more abundant in flipbags and eelgrass. Benthic species had higher abundances in aquaculture sites in North Sound and Hood Canal (influenced by unidentified crabs), but had higher abundance in non-aquaculture sites (sediment) in South Sound. The diverse group of demersal species varied by region and mesohabitat type. Flatfish were more abundant in sediment in Hood Canal, and non-aquaculture sites (including sediment) in North Sound. Sculpin were also found to be more abundant in aquaculture sites in North Sound and Hood Canal, but the reverse was true in South Sound. In part, our results support the application of complex habitat theory to bivalve aquaculture, with higher or neutral abundances, and increased species diversity and richness, in some aquaculture sites, relative to mudflats and eelgrass. However, these effects were context dependent, varying by sample region, aquaculture type, focal species, and vertical position in the water column.

However, these effects were context dependent, varying by sample region, aquaculture type, focal species, and vertical position in the water column.

4.1. Regional variation

The abundance of some species statistically varied between aquaculture and non-aquaculture habitats; however, the responses were not consistent across a spatial scale of approximately 150 km (North Sound, South Sound, and Hood Canal). This trend signifies a biotic response to aquaculture habitat modified by local drivers. No local environmental conditions have been identified that clearly explain these differences in species' use of aquaculture habitat, such as lack of eelgrass in South Sound or increased circulation and water turn over in North Sound (Table 1), and additional environmental drivers were not measured in our study. Natural shellfish populations have historically thrived throughout Puget Sound, and shellfish aquaculture sites are found across a variety of environmental conditions that include tidal mudflats, gravelly sediment, good water quality, and productivity. Previous research in Puget Sound (not related to aquaculture) sug-

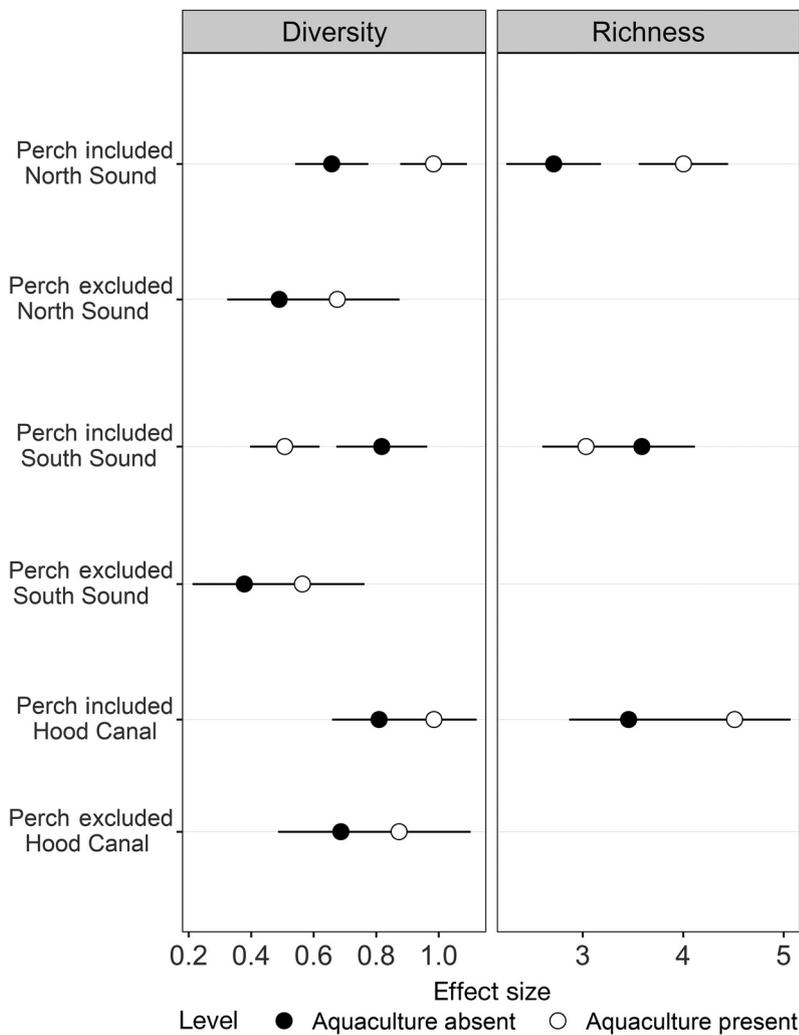


Fig. 5. Predicted Shannon-Wiener diversity index and species richness effect sizes based on general linear mixed models with region and aquaculture presence as fixed, interactive effects, and site as random effect. Models were run including and excluding surfperch. Aquaculture present includes clam, oyster on-bottom, and oyster in flipbags mesohabitats. Aquaculture absent includes sediment and eelgrass mesohabitats. Error bars represent SE. Note only species richness in North Sound (perch included) is statistically different when applying post hoc analysis to the general linear mixed models

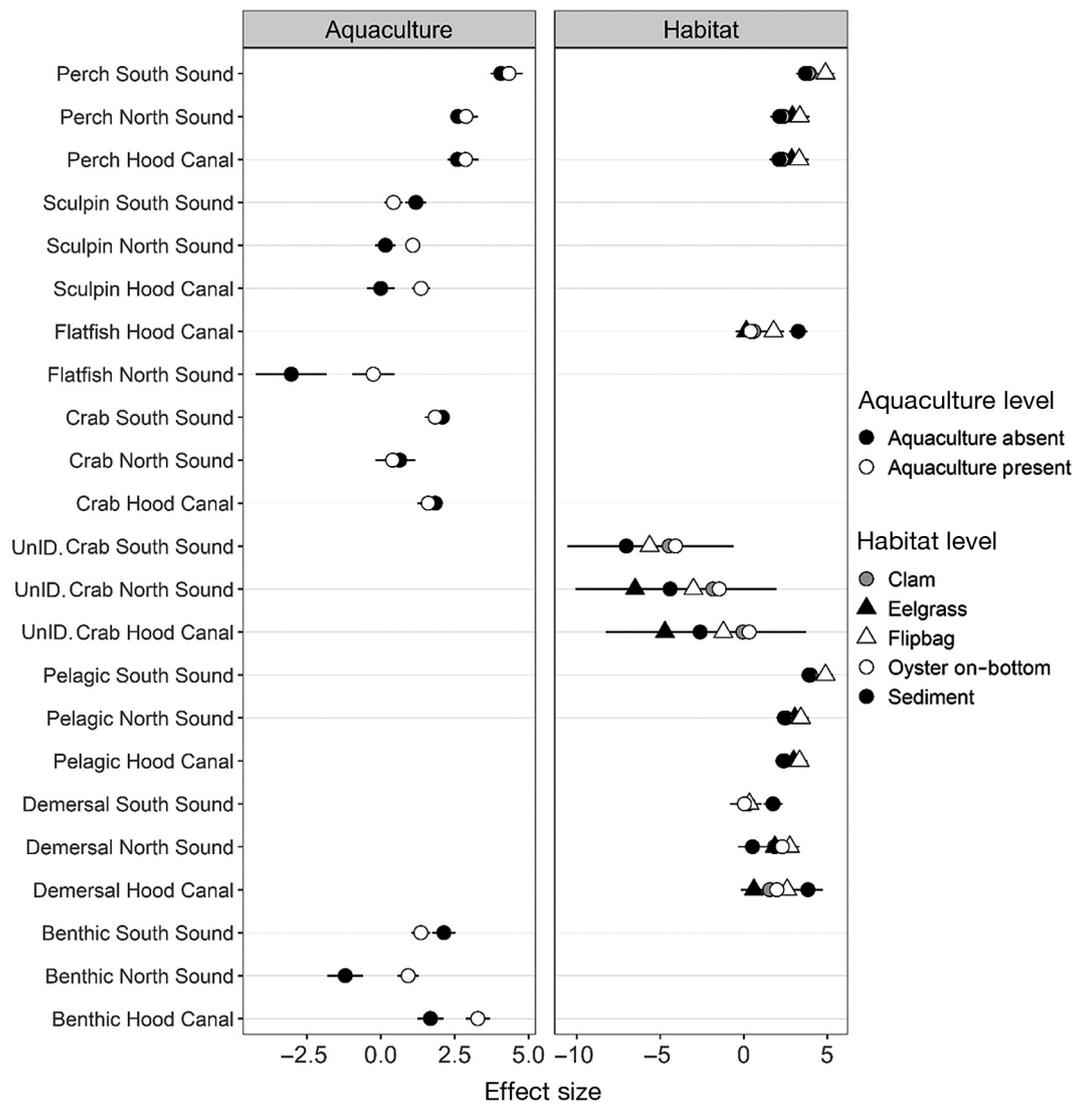


Fig. 6. Estimated effect sizes (SE) from best fit generalized mixed effect linear models that explained observed variation in abundance of surfperch, sculpin, flatfish, crabs, unidentified crabs, and pelagic, demersal, and benthic functional groups. The best fit models include a fixed effect of aquaculture: present (clam, oyster on-bottom, oyster in flipbags) and absent (sediment, eelgrass), or mesohabitat: flipbag, clam, on-bottom, eelgrass, and sediment. All models except flatfish include region (South Sound, North Sound, Hood Canal) as a fixed effect. Flatfish were analyzed separately by region (no model for South Sound. UnID.Crab: unidentified crab species)

gests certain environmental conditions determine trends in species' distribution, but none are conclusive. For example, Llanso (1998) and Rice (2012) observed lower species richness of both benthic infaunal invertebrate and fish communities in the South Sound relative to North Sound locations, which was correlated with lower dissolved oxygen, less water exchange with the continental shelf, and potentially anthropogenic influences. Increased abundance of jellyfish (pelagic cnidarians and ctenophores) and three-spined stickleback (*Gasterosteus aculeatus*) was observed in South Sound over historical abundances (less so in North Sound, and Hood Canal was

not reported), both of which are considered relatively tolerant to reduced water quality (Deegan et al. 1997, Rice et al. 2012, Greene et al. 2015). Rice (2006) and Greene et al. (2015) also found anthropogenic factors better explained variation in forage fish (herring, surf smelt) abundances relative to climate-driven patterns, hypothesized to be linked to the effects of loss of spawning habitat or increased presences of pollutants on juvenile life stages. Accounting for the existing literature on this topic, this study was designed with the knowledge that species' natural distribution and intertidal habitat (including mudflat extent and eelgrass presence) vary across Puget Sound (Burns

1985, Rice et al. 2012, Greene et al. 2015, Shelton et al. 2017). The knowledge that this natural spatial variation potentially influences how nearshore marine species interact with bivalve aquaculture habitat suggests limitations in the ability to extrapolate local studies beyond a given region in Puget Sound. It could also inform the next level of research regarding mechanisms driving this observed variation in interactions (e.g. seascape attributes, nearby/adjacent available habitat, and local predation).

4.2. Community structure

Fish and crab species composition varied between aquaculture and non-aquaculture habitats in 2 of the 3 regions, revealing an effect of aquaculture on species composition in those 2 regions. Species diversity and richness results partially supported the habitat complexity theory that predicts neutral or increased values in aquaculture sites relative to uncultured sites. Species diversity and richness were higher in aquaculture sites in North Sound, while no differences were observed between aquaculture and reference sites in Hood Canal. North Sound and Hood Canal have greater natural habitat complexity due to the presence of eelgrass beds, while the South Sound sites are in areas with primarily sediment habitat. The predicted positive response of diversity and richness to aquaculture habitat in South Sound was not observed (diversity was lower in cultivated sites relative to uncultivated sites). The large numbers and patchy distribution of surfperch observed in South Sound explained the decrease in diversity, as the Shannon Wiener Index accounts for both abundance and evenness in the metric. Other studies in this region have similarly shown variable responses of species diversity and richness to bivalve aquaculture (Dealteris et al. 2004, Dumbauld et al. 2009, Conway-Cranos et al. 2015, McDonald et al. 2015).

4.3. Structure-affiliated species

Surfperch and the pelagic functional group, largely defined by surfperch, were more abundant in vertically structured mesohabitats (flipbags and eelgrass). Surfperch are naturally found in eelgrass and have been observed in some forms of aquaculture (Dumbauld et al. 2015, McDonald et al. 2015, Gross et al. 2017). Shiner perch *Cymatogaster aggregata*, in particular, benefit from foraging and refuge functions in eelgrass, as they feed on epibenthic invertebrates,

such as caprellid amphipods (Caine 1991), and release their live-born young (DeMartini 1988, Moore & Hovel 2010, Love 2011). Our results suggest shellfish aquaculture, particularly with higher vertical structure such as flipbags, may serve some of the habitat functions of eelgrass at this aggregated level, although behavior and ecosystem function were not documented in this study. In addition, caution is advised in interpreting these flipbag–eelgrass mesohabitat comparisons as there is potential for pelagic fish to be undercounted in eelgrass due to limited visibility, as reported by Hosack et al. (2006) and Gross et al. (2018).

4.4. Non-structure affiliated species

Flatfish and large crabs partially followed their hypothesized association with unstructured, sediment mesohabitat. Flatfish had higher abundance in sediment-dominated mesohabitats in Hood Canal, yet were more abundant in aquaculture habitat in North Sound. These conflicting results could indicate multiple ways flatfish associate with aquaculture. Flatfish association with sediment sites in Hood Canal may be explained by the juvenile flatfish preference for sediment (Able et al. 2005). Higher observed abundances of flatfish in aquaculture sites in the North Sound could be influenced by their predation on shellfish (snipping their siphons) or their use of sediment habitat under suspended flipbags (Irlandi 1994, Meyer & Byers 2005). Our results in Hood Canal align with those of McDonald et al. (2015), who found flatfish were more associated with sediment reference areas over cultured geoduck *Panopea generosa* structured habitat in South Sound, although that is a different form of aquaculture-related structure that includes PVC tubes partially submerged in the sediment, covered by anti-predation nets. Crabs had no observed differences between mesohabitat types, although aquaculture presence was the better fit model, indicating they are habitat generalists. Dungeness crabs use mudflats in these regions to move between depths or as foraging grounds (Holsman et al. 2003, 2006). Crabs were observed under the suspended flipbags, indicating they might be using the underlying sediment and are not deterred by the overhanging structure.

4.5. Uncertainty

Underwater video is a research tool that has great utility in aquaculture and other complex habitats, but

is restricted by a limited field of view (Sund 2015, Marini et al. 2018, and references within, Muething et al. 2020). The downward angle of our cameras and timing of our recordings omitted species that swim near the surface and those coming in with the tide. We also acknowledge the potential for aquaculture interactions with additional species not addressed in this study, including seabirds and infauna (e.g. Żydelis et al. 2006, Dumbauld et al. 2009, Faulkner 2013, Liu et al. 2015). The replicate-level variation we observed was potentially due to differences in aquaculture sites, including habitat footprint and the configuration of grow-out gear, local environmental conditions, harvest or disturbance history, and natural variability in species distributions and movement. Importantly, we assume species observations in eelgrass mesohabitats were under-observed due to limited visibility relative to the other mesohabitat sites, a factor previously measured in a similar underwater video study (Gross et al. 2018).

5. CONCLUSION

Local habitat configuration and complexity can alter species abundance and distribution (Godbold et al. 2011). This study demonstrates how local abundances of different species vary between aquaculture and uncultivated areas, as well as among types of bivalve aquaculture. These results also indicate a strong regional signal (approximately 150 km). The next step in understanding habitat function of bivalve aquaculture is to determine the mechanisms that drive these differential trends in habitat use (e.g. foraging, refuge, accessibility). In addition, research is needed to understand the scale of habitat heterogeneity required to support nearshore fish and crab communities. For example, resource managers might not only consider a balance between aquaculture and non-aquaculture habitats in a region, but they might also consider various types of aquaculture within that region, as they provide different forms of habitat. While summaries of the ecological role of shellfish aquaculture help identify emerging trends from the field (Dumbauld et al. 2009, Forrest et al. 2009, Barrett et al. 2019), we highlight the importance of considering species-level interactions with aquaculture, as well as the potential for these interactions to be non-stationary across spatial scales the size of this study area. These factors could ultimately inform the development of a management approach that considers including multiple types of cultivation in a region when developing bivalve aquaculture.

Acknowledgements. This work was funded by an NOAA Office of Aquaculture Grant (NA17OAR4170218) and Washington Sea Grant (UWSC10159). Field assistance was provided by Ellie Mason, Sam Goss, Kirby Bartlett, Mary Brady, Brook Hawkins, Shaun Christean, Sophia Stouse, and Katrina Radach. The manuscript was improved by Kelly Andrews, Greg Williams, and 3 anonymous reviewers. This research was conducted in collaboration with the generous support of shellfish aquaculture farms in WA, USA.

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Editorial responsibility: Pablo Arechavala-Lopez, Esporles, Illes Balears, Spain
Reviewed by: J. Hollarsmith and 2 anonymous referees

Submitted: March 22, 2021
Accepted: August 15, 2021
Proofs received from author(s): November 5, 2021