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Monograph

Seasonal and site-specific differences in biofouling communities on Pacific oyster Mariculture farms

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ABSTRACT

Artificial substrates are ideal for the settlement of biofouling communities. Oyster cages used in mariculture are known to provide substrate for a diversity of epibiotic organisms to settle and grow. While oyster farmers regularly clean their cages of these epibionts, diverse biofouling communities can still develop and contribute to the composition of the overall ecosystem surrounding mariculture farms. Colonization by biofouling organisms, including algae and animals, can be sudden and have rapid development. Biofouling on cages can have deleterious impacts on the farmed oysters, ultimately increasing operational expenses and decreasing farmer profits. Identifying seasonal and spatial patterns in biofouling community composition and their relationship to environmental conditions is essential for effectively addressing the impact these organisms pose. Here, we examined changes in taxonomic composition of biofouling communities over time at multiple oyster mariculture farms in the Gulf of Alaska with the intent of answering our overarching research question: Does composition of biofouling communities vary seasonally and spatially? To address this question, we took bi-monthly photographs of oyster cages from March to September of 2023 at three farms in Kachemak Bay and one sampling was done in September 2023 in Prince William Sound to assess seasonal and spatial differences in biofouling community composition. A subset of photographs taken at all sites in September were paired with scrape collections for biomass to compare surveying methods. Though there were notable differences in taxonomic resolution between the two sampling methods, both resulted in similar diversity measurements and spatial patterns of composition. Diatom mats and red filamentous algae were predominant contributors to biofouling. Additionally, the spatial differences in community variability and composition were stronger than seasonal differences, and salinity was found to best correlate with patterns in biofouling communities. Altogether, these findings have practical implications for monitoring impacts of biofouling on mariculture, as the methodological approach can be catered to specific research goals or resource constraints.

1. Introduction

Biofouling organisms are found in both natural and artificial habitats and can play roles in ecosystem functioning, such as serving as ecosystem engineers (Nakano and Strayer, 2014) or filtering organic content from the water column (Montalto et al., 2020). Wherever present, biofouling communities progress through natural successional states, beginning with initial colonizers like bacteria and diatoms, with higher trophic levels incorporating over time (Brown et al., 2017; Golinia et al., 2019). Dynamics of biofouling communities can be shaped by propagule supply and interactions among organisms (Cifuentes et al., 2010), which can be influenced by proximity to established local populations and their abundances (Jenkins and Martins, 2010). Invasions of biofouling organisms may also have an impact on local communities when introduced via marine vessels (Lacoursière-Roussel et al., 2016). Biofouling organisms can structure community dynamics as they would in their natural habitats, such as in rocky intertidal shores where there are many compositional similarities between these communities and those utilizing the bare space made available by the introduction of artificial habitats (Connell and Glasby, 1999).

Oysters are farmed globally for both food and also the pearl industry. Historically, they have been farmed in the intertidal and subtidal with nets, stakes, and cages. Cages specifically offer habitat for other non-farmed organisms, which can impact both the farm products and the ecosystem where the farms reside. Common biofouling organisms that settle on or live within cages include pelagic (e.g., fish, shrimp) and

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benthic animals (e.g., other bivalves, sea stars, tunicates, bryozoans, sponges, hydrozoans, crabs) and seaweeds (e.g., kelps, filamentous algae; Rodriguez and Ibarra-Obando, 2008). Many of these organisms are a nuisance to farmers such as colonial tunicates that can smother oyster farm equipment (Cohen et al. 2011) and others that can decrease water flow and inhibit oyster growth (Pit and Southgate, 2003). Biofouling organisms can also be a nuisance to farms by settling on the oysters themselves, which results in increased handling time when processing the oysters (Rodriguez and Ibarra-Obando, 2008). Additionally, biofouling organisms can be invasive species, which can have detrimental impacts to the ecosystem (Arakawa, 1990; Rodriguez and Ibarra-Obando, 2008). Since biofouling organisms can have impacts on the farm equipment and its products, and also on the environment where the farms exist, they are a key consideration in assessing ecosystem health. The mariculture industry in Alaska is expanding across the coastal Gulf of Alaska, as these waters are highly productive and offer cold environmental conditions suitable for oyster farms to produce high quality products year-round (Oliveira et al., 2006). With an increase in oyster production and sales from the Alaskan mariculture industry over the past few decades (Alaska Department of Fish and Game 2021), proposals for establishing oyster farms are indicative of industry growth through community interest and commercial practices. Establishing an oyster farm benefits from an understanding of the ecological setting and potential biofouling community that may develop.

While the ecological and economic impacts of biofouling organisms on oyster farms are broadly understood (Fitridge et al., 2012), the role that spatial and temporal variability plays has been less well studied. Part of what drives this variability is the environmental background that is often site-specific or varies with season. In temperate regions, water temperature can be a driver of temporal variability in biofouling communities (Fragoso and Icely, 2009, Rodriguez and Ibarra Obando 2008). Similarly, ocean conditions such as upwellings and distance to shallow water communities have been shown to influence spatial differences in biofouling communities (Atalah et al., 2016). Turbidity has also been associated with lower species richness, lower overall abundances, and decreased diversities of biofouling macroalgae on buoys (Drakard et al., 2018). Information on drivers of biofouling communities could benefit managers when trying to determine interactions with the natural environment and farming activities.

There are many different approaches to sampling intertidal and subtidal communities that can be applied to assessments of biofouling communities (Peters et al., 2019). Considerations for different methods include logistical constraints and quality or resolution of the data collected. Destructive methods involve physically removing organisms from their substrate and require much post-collection processing (Eleftheriou and Moore, 2005). Photographs or videos are less invasive approaches that have been used to monitor intertidal (Konar and Iken, 2018) and biofouling (First et al., 2021) communities. Comparisons have been made between different types of sampling methods. One study found that point quadrats were a more accurate measure of cover than photo quadrats, except for monolayered assemblages with few species in large patches, or in studies where only the overstory is of interest (Foster et al., 1991). Another comparison between destructive sampling and photographs suggested that although taxonomic resolution was relatively low in the photographs, key habitat-forming taxa were identifiable and the image-derived data were sufficient to infer richness of small epifauna (Beisiegel et al., 2017). Tradeoffs in level of effort, data quality, and logistical feasibility should be weighed when choosing a sampling scheme.

This paper is the first to document and describe biofouling communities associated with oyster (*Crassostrea gigas*) farms in Alaska. We further examine how two surveying methods resulting in different taxonomic resolutions influence spatial patterns in composition. Lastly, we examine spatial and temporal variability patterns in biofouling communities and determine how temperature, salinity, and turbidity might explain these patterns.

2. Methods

2.1. Sites

Kachemak Bay (KB) and Prince William Sound (PWS) are large glacially influenced fjord-type estuaries in the Gulf of Alaska (Fig. 1). Both regions have established oyster farms and new to-be-permitted farms, with KB having the highest density of oyster farms in Alaska. Nearshore areas in protected bays within these regions are favored farm locations. The oyster farms in KB that were surveyed in this study were in Bootleggers Cove, Jakolof Bay, and Peterson Bay. The oyster farm sampled in PWS was located in Simpson Bay. In KB, the study farms are located in bays ranging in bottom depths from approximately 7 m to 11 m at a zero tide, whereas the study farm in PWS was in waters greater than 30 m depth. All of these farms set out growlines from which they hang their cages directly under the water surface that cover between 1 and 2 acres. Cages and lantern nets are both used at these farms and were sampled haphazardly and not treated separately in the analyses (hirthro referred to as cages). Some of the farms have seen some level of operation for over three decades, and others were first seeded as recently as 2019. Farms were in continuous operation for the duration of the present study, with time between cleanings ranging from weeks to months.

2.2. Biological and environmental data collection

Biofouling communities were surveyed at the farm sites in March, May, July, and September in 2023. Note that the Bootleggers Cove farm was not sampled in July, and the Simpson Bay farm was only sampled in September. Divers captured high resolution underwater photographs of biofouling within one 25 cm × 25 cm quadrat that was haphazardly placed on 20 random oyster cages at each farm ($n = 20$ photos/site/month). Biofouling community data were collected by digitally analyzing the photos. Using a standardized point contact method, ten points (each representing 10% of the cover) were randomly superimposed within the quadrat of each photo. Organisms that occupied each point in the photo were identified to the lowest taxonomic level possible and were designated a percent cover.

To ground truth identifications that were made from photos, and to compare different levels of taxonomic resolution from two different surveying methods, a subset of quadrats that were photographed in September were also scraped to collect biofouling organisms for identification in the lab ($n = 6$ photo+scrape pair/site). Organisms collected from the scrapes were identified to the lowest taxonomic level possible using a microscope and were weighed, predominantly resulting in finer taxonomic identifications, relative to the coarser identifications made from photo analysis.

We deployed a conductivity, temperature, and depth sensor (SonTek CastAway) to monitor key environmental parameters, including temperature and salinity, at each site every month. The sensor was submerged at the farms, and point readings at approximately 1 m depth were extracted from the profile measurements and used for analysis. This depth was selected as this is the average depth of the cages. In addition to each sensor measurement, three surface water samples were collected to conduct turbidity measurements. Water samples were processed through a turbidimeter (Hach 2100P) and averaged by site and month. These monthly measurements provided an estimate of environmental conditions at the time of sampling. Altogether, these environmental parameters were selected as they are known to influence the growth and condition of both oysters and biofouling communities.

2.3. Data analysis

Statistical analyses were carried out in the open source R software (R Core Team, 2021). Both percent cover (from photos) and biomass (from scrapes) of biofouling organisms were converted to proportional

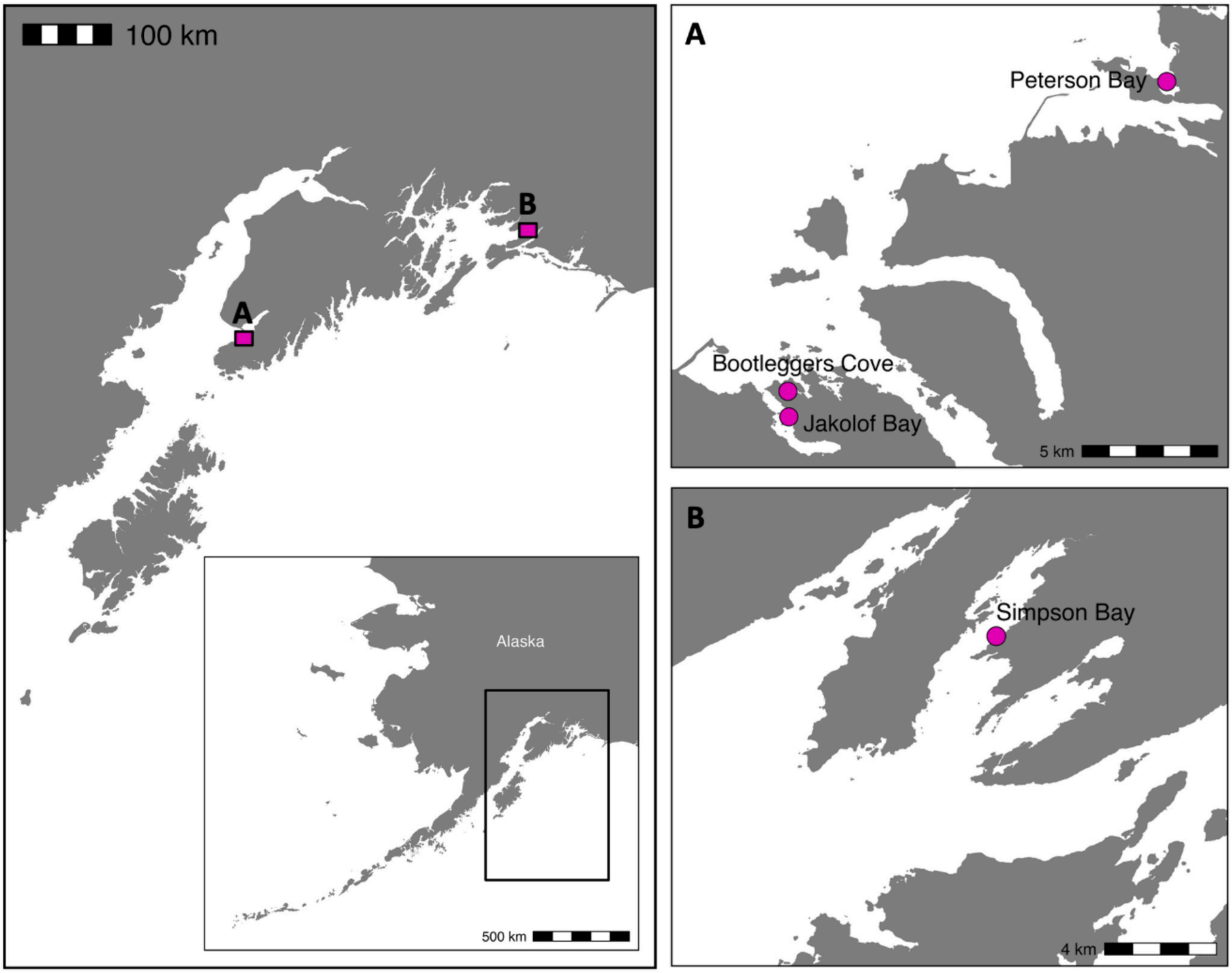

Fig. 1. Map showing locations of oyster mariculture farms (pink circles) surveyed in the Gulf of Alaska within the regions (pink rectangles) of (A) Kachemak Bay and (B) Prince William Sound. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

contributions to the community, bringing both percent cover and biomass to the same datatype of relative abundance. Biomass data were converted to proportions by dividing the biomass of each taxon by the total biomass of the sample. To test how differences in taxonomic resolution resulting from two survey methods influences diversity, Shannon Diversity Index values were calculated from biofouling community data. A combined data frame was generated from the two measures of Shannon Diversity Index values for each sample calculated from both photo (resulting in coarse taxonomic resolution) and scrape (resulting in fine taxonomic resolution) methods. Once combined, a Levene's test indicated equal variance among samples ($F = 0.27$, $p = 0.6$), and a one-way analysis of variance (ANOVA) model was used to test for the effect of surveying method (fixed factor, 2 levels: photo, scrape) on biofouling community diversity.

Multivariate analyses were carried out in the “vegan” package (Oksanen et al., 2019). To test how taxonomic resolution influences spatial patterns in composition, separate resemblance matrices based on pairwise Bray-Curtis dissimilarities from photo and scrape community data were constructed. Only in the month of September were both photos and scrapes collected. Thus, the influence of taxonomic resolution on temporal patterns could not be assessed. Separate non-metric multidimensional scaling (NMDS) plots were constructed from the resemblance matrices to visually examine spatial variability. Separate permutational multivariate analysis of variance (PERMANOVA) models were performed on the resemblance matrices to test the variability among sites (fixed factor, 4 levels: Bootleggers, Jakolof, Peterson, Simpson) based on biofouling community composition determined by photos or scrapes. We then implemented a permutational multivariate analysis of dispersion (PERMDISP) analysis to further test beta diversity of biofouling communities based on the different surveying methods. PERMDISP analyses were implemented to determine if spatial differences were due to dispersion from the multivariate centroids.

To test for spatial and temporal variability in biofouling community composition, coarse taxonomic data were fourth-root transformed to down-weight the highly abundant taxa. Following transformation, a resemblance matrix was constructed based on pairwise Bray-Curtis dissimilarities of biofouling communities. A NMDS plot was constructed from the resemblance matrix to visually examine community variability in ordination space among sites and months. A PERMANOVA model was performed on the resemblance matrix to test the variability in biofouling community composition among sites (fixed factor, 4 levels: Bootleggers, Jakolof, Peterson, Simpson) and months (fixed factor, 4 levels: March, May, July, September) using the *adonis2* function. To further test beta diversity of biofouling communities, PERMDISP was implemented to determine if differences among grouping factors were due to dispersion from the multivariate centroids using the *betadisper* function. Vector-fitting was performed to evaluate relationships between biofouling community composition and predictor environmental variables in ordination space using the *envfit* function. Pearson correlation coefficients indicated temperature and salinity were collinear ($R = -0.8$), so temperature was removed from subsequent analyses because it had a weaker correlation (temperature, $R^2 = 0.59$; salinity, $R^2 = 0.74$) with biofouling community composition according to the *envfit* function. Vectors are overlaid in the direction that shows the strongest correlation between environmental variables (i.e., salinity and turbidity) and biofouling community composition. Additionally, the best correlation between patterns in biofouling community dissimilarities and environmental variables was determined using the *bioenv* function.

3. Results

3.1. *Influence of method and taxonomic resolution on spatial patterns in composition*

Analysis of photographs for percent cover revealed a total of 16 taxonomic groups contributing to the biofouling communities, with bare substrate (13%) on the cages accounting for a relatively high proportion of the cover (Fig. 2). Overall, across all sampled sites and months, biofouling communities were predominantly composed of diatoms (52%), a variety of red filamentous algae (14%), and brown algae that included kelps (8%). All other taxa accounted for 3% or less of the biofouling communities. Less common sessile biofoulers included tube worms, tunicates, hydroids, sponges, mussels, bryozoans, barnacles, and green algae. Mobile biofoulers included filter-feeders, such as anemones and sea cucumbers, and scavengers or predators, such as nudibranchs, sea stars, and crabs.

In September, a finer examination of the farms by scraping all material out of a subset of quadrats and measuring biomass revealed a total of 43 taxonomic groups, opposed to the 16 taxonomic groups at the coarse resolution determined by the photo method (Table 1). Some organisms identified from the scrapes were not observed from the photos, such as smaller annelids, arthropods, and molluscs. However, these “other” taxa altogether accounted for less than 1% of the communities. All biofouling organisms identified in this study were native to the Gulf of Alaska region. Though there were notable differences in taxonomic resolution between the two sampling methods, diversity measurements did not differ significantly (ANOVA, $F = 0.02$, $p = 0.88$; Fig. 3). At the site level, pairwise differences between sampling methods remained similar (Tukey's, Bootleggers coarse vs fine: $p = 0.95$; Jakolof coarse vs fine: $p = 0.98$; Peterson coarse vs fine: $p = 1.0$; Simpson coarse vs fine: $p = 1.0$).

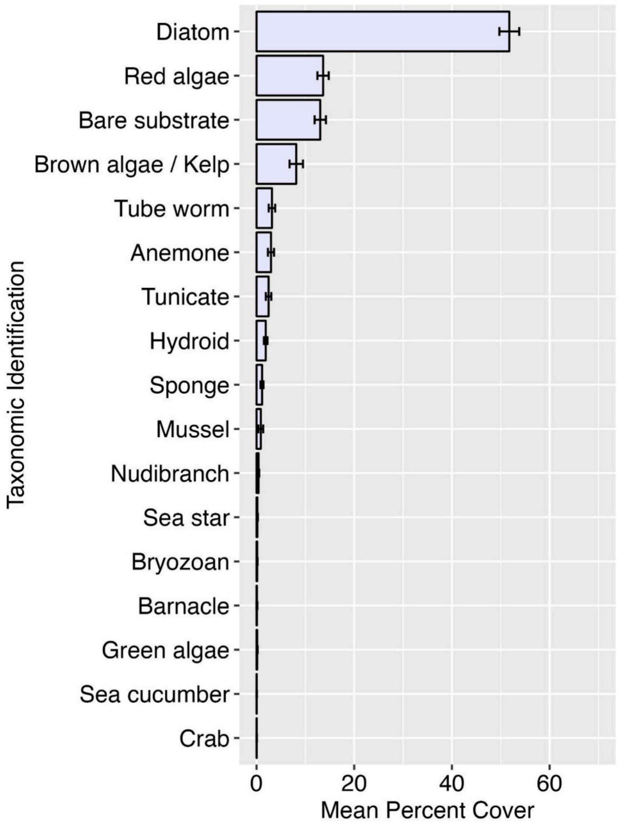

Fig. 2. Overall mean percent cover and standard errors of biofouling organisms at coarse taxonomic resolution and bare substrate based on photo analysis at Pacific oyster farms across all sites and months sampled in Kachemak Bay and Prince William Sound, Alaska in 2023.

A PERMANOVA model indicated that the effect of site on biofouling community variability based on coarse taxonomic resolution was significant ($R^2 = 0.54$, $F = 7.96$, $p = 0.001$; Fig. 4A). A separate PERMANOVA model indicated that the effect of site on biofouling community variability based on finer taxonomic resolution remained significant ($R^2 = 0.49$, $F = 6.35$, $p = 0.001$; Fig. 4B). A PERMDISP analysis indicated that dispersion from the centroid among sites did not differ based on both coarse ($F = 1.53$, $p = 0.23$; Fig. 4A) and fine ($F = 2.7$, $p = 0.08$; Fig. 4B) taxonomic resolution.

3.2. *Spatial and temporal variability patterns in biofouling communities at oyster farms*

Diversity metrics and spatial variability in community structure were similar between coarse and fine taxonomic data sets. As such, we focused on the ecological results at the coarse resolution. Across months, diatoms were the predominant taxa at all sites, but proportions were greatest in Simpson Bay (66%; Fig. 5A). All other taxa showed spatial variability. The proportion of red algae was greatest in Peterson Bay (26%), bare substrate was greatest in Bootleggers Cove (22%), and brown algae (including kelp) was greatest in Jakolof Bay (13%). Across sites, diatom percent cover was greatest in March (64%), decreasing into

Table 1
Taxonomic lists produced from photo and scrape methods resulting in coarse and fine taxonomic resolution of biofouling communities, respectively, at Pacific oyster farms. These lists include all sites and months sampled from Kachemak Bay and Prince William Sound, Alaska in 2023.

Photo identifications (Coarse resolution)	Scrape identifications (Fine resolution)
Diatom	Diatom
Red algae	*Antithamnionella pacifica*, *Ceramium pacificum*, *Pleonosporium* sp., *Polysiphonia* sp., *Savoiea bipinnata*
Brown algae / Kelp	*Desmarestia viridis*, *Saccharina latissima*
Tube worm	*Eudistylia vancouveri*
Anemone	*Metridium* spp.
Tunicate	*Molgula retortiformis*, *Dendrodoa pulchella*, *Corella willmeriana*, *Aplidium* sp., *Ascidia callosa*, *Ritterella pulchra*
Sponge	*Halichondria (Halichondria) panicea*
Mussel	*Mytilus trossulus*
Nudibranch	*Hermissenda crassicornis*, *Diaulula sandiegensis*, *Diaulula* sp.
Barnacle	Barnacle
Sea star	*Evasterias troschelii*
Green algae	*Acrosiphonia* sp., Unidentified filamentous green algae, *Ulva* spp., *Ulva prolifera*
Sea cucumber	*Cucumaria pallida*
Crab	*Oregonia gracilis*
Hydroid	Hydroid
Bryozoan	Bryozoan, Encrusting bryozoan
Other taxa not observed from photos	Amphipoda, Ophiuroidea, Caprellidae, *Pholis laeta*, *Strongylocentrotus droebachiensis*, Polychaeta, Sipuncula, Polynoidae, *Mopalia* sp., Small unidentified clam, *Lacuna vincta*

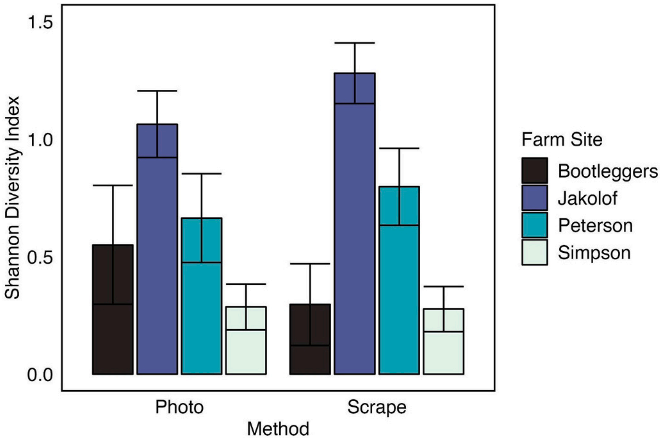

Fig. 3. Mean diversity (Shannon Diversity Index) and standard errors of biofouling communities at Pacific oyster farms in Kachemak Bay and Prince William Sound, Alaska in September 2023. Diversity was calculated from two different datasets with coarse (photos for digital analysis of content within quadrats) and fine (scraped collections of organisms for analysis of content within quadrats) taxonomic resolutions.

September (40%; Fig. 5B). Kelp percent cover peaked in May (17%), while red algae continued to increase and peaked in September (16%).

A PERMANOVA model indicated that the strongest effect on biofouling community variability was observed in differences among sites ($R^2 = 0.22$, $F = 24.78$, $p = 0.001$; Fig. 6A). Weaker effects on biofouling community variability was also significant across months ($R^2 = 0.05$, $F = 5.34$, $p = 0.001$; Fig. 6B) and with the interaction of site and month ($R^2 = 0.07$, $F = 5.18$, $p = 0.001$). A PERMDISP analysis indicated that communities differed in dispersion from the centroid among sites ($F = 16.96$, $p = 0.001$) and months ($F = 10.52$, $p = 0.001$). The subset of environmental variables with the best correlation to biofouling community data was a single variable, that being salinity (BIOENV, $r_s = 0.09$). The set of both salinity and turbidity had a weaker correlation to biofouling community data (BIOENV, $r_s = 0.04$).

4. Discussion

4.1. Influence of method and taxonomic resolution on spatial patterns in composition

Photographs resulted in coarser taxonomic resolution, due to the two-dimensional limitations while finer taxonomic resolution was achieved through scraping quadrats. Identifications made from photographs were often limited to common names given identification uncertainty associated with photos (Foster et al., 1991), whereas scrapes often resulted in identification to genus or species levels. Photo assessments also could not account for layering of organisms, so these layered organisms were only identified in scrapes. However, even with these limitations, we found that both methods resulted in comparable diversity metrics, confirming that either approach resulted in measuring spatial and temporal variability in community dynamics. Photographs offer an efficient approach that can be applied more frequently without logistical challenges or having to deploy trained personnel (Dumas et al., 2009). Photographs also allow for a long-term visual record of the communities. However, if finer taxonomic resolution is needed, scrapes should be considered. Furthermore, coarse taxonomic resolution may be limited in inferring subtle environmental changes reflected in the community (Greffard et al., 2011).

When spatial comparisons were made separately for coarse and fine taxonomic resolutions, the communities based on finer resolution showed sites to be more similar. This result is likely due to the separation of coarser taxonomic groups into multiple finer groups. For example, instead of red filamentous algae accounting for all species in that category, finer resolution differentiated between *A. pacifica* and *S. bipinnata*, which were contributing differently to biofouling communities at each site. Other studies have found similar findings where genus and species level identifications were not needed to determine spatial and temporal trends (Somerfield and Clarke, 1995; Gesteira et al., 2003). In addition, finer taxonomic resolution is typically associated with higher analytical costs (Ferraro and Cole, 1995; Chapman, 1998). Our findings offer implications for a practical approach for researchers and practitioners when considering photographing as a monitoring approach. The choice of methodology could be based on specific research goals or resource constraints.

4.2. Spatial and temporal variability patterns in biofouling communities at oyster farms

At all sites and months, diatoms were the most prevalent taxonomic group growing on oyster farm cages, which is similar to other studies that have found high levels of diatom contributions to biofouling of various artificial structures introduced to the marine environment (e.g., Molino and Wetherbee, 2008; Yang et al., 2015; Kim et al., 2023). Red filamentous algae can also dominate biofouling communities on mussel aquaculture equipment (Watts et al., 2015), similar to the presence of red filamentous algae growing on oyster cages in the present study. Many common biofouling organisms were documented in the present study, and although contributions by amphipods were low, amphipods have been found to be abundant biofoulers on offshore aquaculture equipment (Fernandez-Gonzalez and Sanchez-Jerez, 2017), providing an important source of prey for juvenile salmon in some systems (Cordell

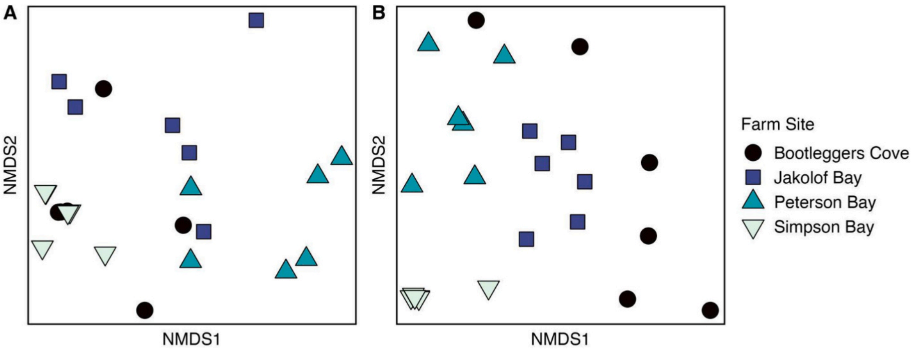

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination plots of biofouling community composition at Pacific oyster farms in Kachemak Bay and Prince William Sound, Alaska in 2023 based on (A) coarse taxonomic resolution from mean proportions derived from percent cover of photos and (B) fine taxonomic resolution from mean proportions derived from biomass of scrapes (2D stress, A = 0.11; B = 0.1). Points represent individual quadrats and are grouped by farm site in both panels.

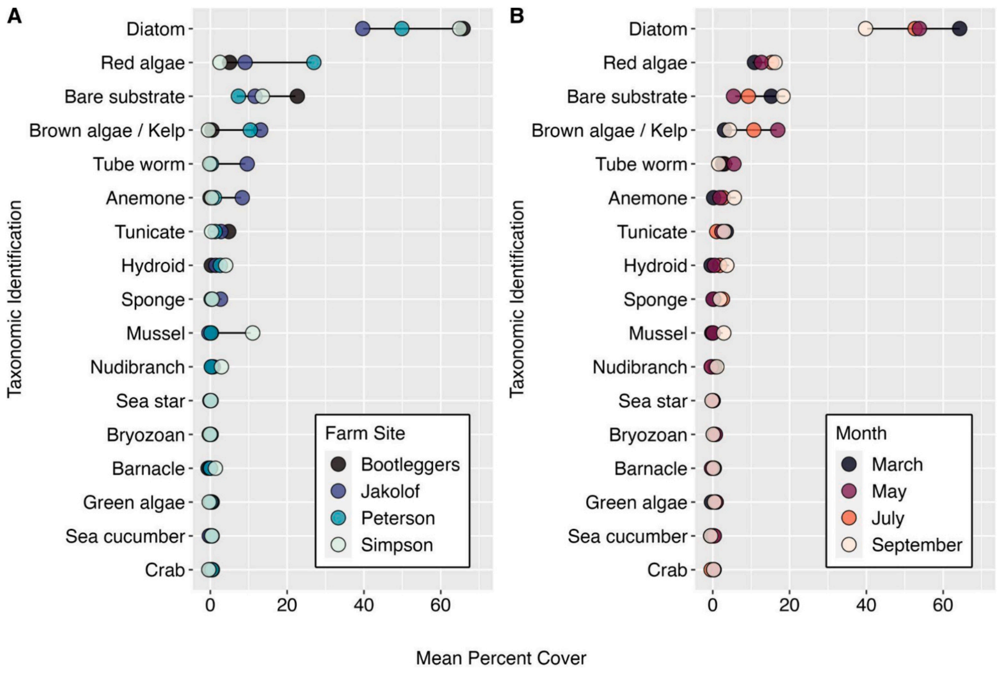

Fig. 5. Mean percent cover of biofouling organisms at coarse taxonomic resolution and bare substrate based on photo analysis by (A) farm site and (B) month at Pacific oyster farms in Kachemak Bay and Prince William Sound, Alaska in 2023.

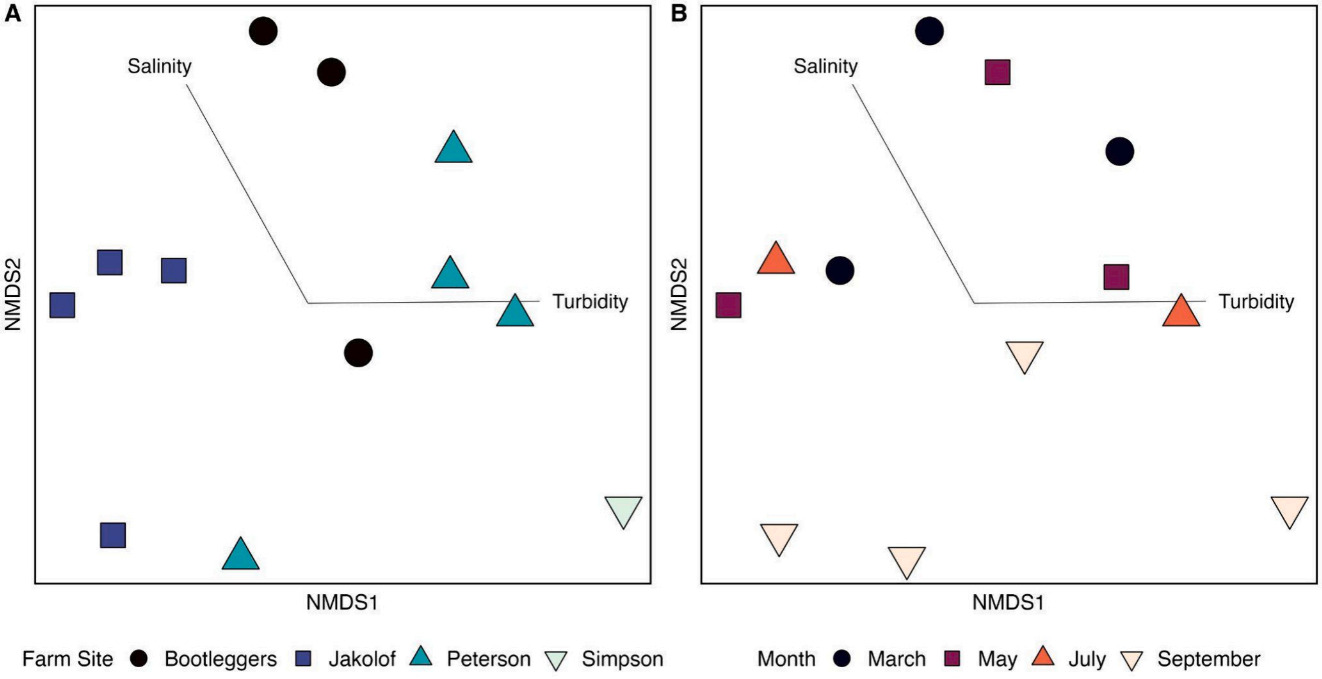

Fig. 6. Non-metric multidimensional scaling (NMDS) ordination plots of biofouling community composition based on mean proportions based on percent cover derived from photo analysis at Pacific oyster farms in Kachemak Bay and Prince William Sound, Alaska in 2023. Points represent a sampling event and are grouped by (A) farm site and (B) month (2D stress, A = 0.11; B = 0.11). Vectors show directional influence of environmental variables.

et al., 2013). Habitat provided by biofouling organisms can have benefits to the ecosystem through enhancement of food availability, but some biofoulers can be invasive (Cordell et al., 2013; Hughes and Ashton, 2017), although none were found in the current study. The presence of non-indigenous species can alter the community and have varying effects on other organisms, like invasive tunicates that can lower abundances of several species within the community or increase abundances of other invasive species (Cordell et al., 2013).

Some ecological interactions among biofoulers and oysters can be negative. Filtering by oysters was shown to effectively alleviate eutrophication and an algal bloom, while significantly increasing phytoplankton diversity and reducing suspended solids and total organic carbon (Jiang et al., 2019). Concern for competitive interactions with cultivated oysters comes from settling filter-feeders, such as mussels, that may compete for food in the water column. This competitive interference may be controlled by settling predators of bivalves on the outside of the cages, such as sea stars that were introduced to fish aquaculture cages (Greene and Grizzle, 2007). However, sea stars that settle on the inside of the cages with the oysters, would have direct negative predatory effects on the oysters, which has been observed as a potential threat in productive oyster farms in Kachemak Bay (W. Bates, pers. comm.). Relatively few mussels and sea stars, each with their own inhibitory effect on oysters, contributed to the biofouling communities in the present study, and likely more detrimental impacts to the oysters comes from inhibition of water flow through the cages from mats of diatoms, kelp, and other algae (Campbell and Hall, 2019).

Through the many interactions that occur within a community, some are beneficial to mariculture farmers if negative impacts on their products are reduced. A positive ecological interaction observed in this study was the co-occurence of nudibranchs (*D. sandiegensis*) and their preferred prey, sponges (such as *H. panicea*) (Penney, 2013). Sponges can have high carbon uptake rates (Gökalp et al., 2021), so the settlement of these filter-feeders on oyster cages can introduce competitive interactions with the farmed oysters. Through ecological interactions among biofouling community members, negative effects of overgrowth and smothering could be remediated by opportunistic consumers. For example, collecting and adding native nudibranchs to farms where sponges are a concern could reduce the abundance of that biofouler. Introduction of small urchins could reduce the biofouling of diatoms and kelp (Sterling et al., 2016). Though the presence of anemones did not decrease diversity of biofouling communities in the present study, even when they accounted for a high proportion of the communities, their prevalence on oyster cages may have potential in aiding minimization of colonizing nuisance species as well (Sedanza et al., 2022). In addition to biocontrol as a means of regulating biofouling in mariculture farms, mechanical and chemical means of biofouling control in bivalve aquaculture are alternative practices (Hunsucker et al., 2019; Cahill et al., 2022). Chemical approaches to keeping artificial structures clean includes application of antifouling coats, though some are toxic and there are environmental concerns associated with this method (Fent, 2006). Non-toxic silicone coatings to farm structures offer another approach to antifouling (Hodson et al., 2000).

The findings of this study showed that farms located in different bays and regions hosted different biofouling communities, with salinity best correlating to these differences. This was to be expected, as natural intertidal communities can also be distributed based on local salinity conditions (Chainho et al., 2006; Iken et al., 2010). Other studies have found that spatial and temporal variability in harbor biofouling communities is also related to patterns in salinity changes, where species diversity increases with increasing salinity (Pati et al., 2015). Temperature may also play an important role in colonization rates and composition of biofouling communities (Lord, 2016). In the current study, the site characterized by lower salinity and higher turbidity was occupied by the least diverse biofouling communities, supporting greater abundances of nudibranchs (*H. crassicornis*) and hydroid prey that can be a dietary preference (Avila et al., 1998). Furthermore, it was found that low salinity conditions can reduce biofouling intensity (de Castro et al., 2018). Spatial variability in communities may have also been explained by nearby natural communities. The site with the most biofouling kelp was located within a bay that supports large abundances of understory kelp, potentially highlighting the influence of proximity to local populations where propagules are sourced to biofouling communities. Additionally, the cages near natural kelp beds may be likely to experience the same environmental conditions (e.g., light, nutrients) that support kelp growth on the cages.

In the present study, variability among samples may be influencing spatial and temporal patterns. This is illustrated through the significant dispersions from the centroid groupings of site and month, meaning that although differences in community composition were significant across sites and months, variability among samples within each of these grouping factors were also significant. Some of this variability may have come from differences in cage material or timing since the cages were last cleaned. The material of lantern nets are soft compared to the more rigid cages, offering variable substrate malleability and texture for biofouling organisms. Other studies have found that substrate type matters for biofouling settlement as some species can distinguish between surface properties (Rosenhahn and Sendra, 2012; Vedaprakash et al., 2013). Further research is needed to elaborate on the effects of specific farming material on attracting various biofouling organisms. Additionally, controlling for cleaning schedules should be incorporated in further studies.

The present study also found temporal variability in the composition of biofouling communities. Diatom cover decreased over time, similar to seasonal trends observed elsewhere when diatom densities decrease in summer and fall due to development of the biofouling community and environmental conditions (Yang et al., 2015). Temporal variability in density of settled biofouling organisms was also found to be correlated with seasonal weather patterns as storms intensify (Swami and Udhayakumar, 2010). In September, when annual kelp was senescing along with the habitat they provide, biofouling community composition started to look more similar across all of the farm sites in the present study. While oyster farmers regularly clean their cages of biofouling, diverse biofouling communities can still develop quickly within days to weeks as is seen in other biofouling environments (Lenz et al., 2004; Cifuentes et al., 2007), and in nature with intermediate disturbances (Bulleri et al., 2016). Cleaning schedules are regular, but the intervals between cleaning individual nets, cages, or sections of the farms are irregular as cleaning the entire farm is spread out over the course of days, weeks, or months. In the present study, samples were collected from multiple lines and randomly selected equipment, likely accounting for some of the variability in cleaning regimens. Thus, spatial and temporal signatures in compositional variability were likely affected by irregular cleaning of cages.

4.3. *Conclusions and future research*

Biofouling communities are diverse and spatially variable, which can be captured through the implementation of different field methods. The initial description here of communities supported by various oyster farms will help inform future research on biofouling communities that may be altered by the northward spread of species incited by warming temperatures, as has already been documented in natural intertidal systems (Jueterbock et al., 2013). Future research at active mariculture farms should further consider cleaning regimes and the influence of this activity on biofouling assessments. Perhaps deploying settling cages that do not undergo cleaning to standardize this factor will improve the ability to decipher successional processes in biofouling community development. This study suggests that current environmental conditions influence spatial and temporal patterns of biofouling communities, and future work can implement these findings to monitor changes in their composition and community dynamics.

CRediT authorship contribution statement

Brian P. Ulaski: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Brenda Konar:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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