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Intertidal and Subtidal Marine Succession Rates on New Rock Armor in Chiniak Bay, Kodiak, Alaska

Running footer: Alaska Marine Succession Rates

2 tables, 6 figures

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Abstract

Alaska has 33,904 miles of coastline and most coastal infrastructure in the state is armored for erosion protection, yet little is known about colonization or recolonization rates post-disturbance in high northern latitudes. This study quantifies the recruitment and colonization of new armor rock at the Kodiak Airport and documents algal and sessile invertebrate species abundance and assemblage (percent cover) at the airport and at reference sites with similar substrates, salinity, wave exposure, and depth. Over four years of annual intertidal and subtidal monitoring, average percent cover by algae and invertebrates at study sites ranged from 13% to 100%. Study sites showed extensive cover by early colonizing algae and invertebrates in both the intertidal and subtidal at 15 months post-construction silt curtain removal (Year 1). Prominent biobanks of monospecies (e.g., bay mussels [*Mytilus trossulus*]) observed in Year 1 largely changed to barnacles (*Balanus* sp.) and algal species by Year 4. Both algal cover and number of species increased over time at study sites; total cover and number of species were similar to reference sites by Year 4. The colonization rate of rock armor and the successional timeframe to develop full ecological functions are important because of the potential effects of rock armor on aquatic habitats, at both local and landscape scales. This study illustrates that colonization of new armor rock in southcentral Alaska can be rapid (can average 80.8% cover of intertidal and subtidal substrates after 1 year) and that interannual variability of species abundance may occur throughout the successional cycle.

Keywords

Kodiak, Succession, Recruitment, Colonization, Alaska

Introduction

Alaska has 33,904 miles of coastline (NOAA 1975) and nearly all coastal infrastructure requires some amount of armor rock for erosion protection. Statewide, 449 miles of shoreline are armored or comprised of impermeable human-made structure (Shorezone 2024). However, in coastal communities that depend on marine infrastructure, the proportion of armoring is higher. In the Kodiak area, 33% of the shoreline in the 21-mile stretch of coast from north of the City of Kodiak to Womens Bay is comprised of armor rock . Yet, little is known regarding algae and invertebrate colonization rates or recolonization rates post-disturbance in high northern latitudes. A study from Prudhoe Bay (latitude 70°N) documented initial recruitment of sessile organisms at less than 1% cover after three years; less than 10% of boulder surfaces were colonized after seven years (Konar 2012). A monitoring study of fill placed at the Sitka Airport (latitude 57°N) documented a faster than anticipated colonization of armor rock (Hart Crowser 2014). That study observed greater than 80% of pre-construction function (defined by primary productivity, habitat complexity, and species diversity) in the construction area after two years. A study from Burrard Inlet and Howe Sound, British Columbia (latitude 49°N) found that mussel beds stripped to bare rock were quickly recolonized by small mussels (Lacroix 2006), though sites varied widely in rate of recolonization. Some sites achieved 75% mussel cover in 2 months post-disturbance, while others achieved only 37% cover in 17 months. Of the parameters analyzed for influencing recolonization rate (disturbance size, intertidal height, exposure and angle), only disturbance size significantly affected recolonization rate (larger mussel beds recolonized quicker than small ones). Generally, after complete depletion, approximately a year was required to recover to over 80% mussel cover.

Recolonization of the intertidal and shallow subtidal following eruption of Kasatochi volcano in the central Aleutian Islands (latitude 52°N) occurred relatively slowly: qualitative observations indicate that sparse barnacles and diatom mats were visible at year 2, canopy forming algae by year 3, and well-defined biobands by year 4 (Jewett and Drew 2014).

Monitoring data regarding recovery from the 1989 Exxon Valdez oil spill in Prince William Sound, Alaska (latitude 60°N), show rapid recovery (within 2 years) in the lower and middle intertidal zones by most algae and invertebrate species, though some species, such as *Fucus* sp., took 8 years or longer to recover, particularly in the upper intertidal (Stekoll and Deysher 1996, Exxon Valdez Oil Spill Trustee Council 2022). In the subtidal, kelps recovered within a year, though seagrass took 4 years (Peterson 2000). However, these data are not entirely analogous to Kodiak Island (and the study area, latitude 58°N) because there may be toxicity factors that influenced recovery of algae and invertebrates.

An understanding of colonization rates can help inform management decisions regarding how infrastructure projects are designed, what level of mitigation for effects to marine resources is warranted, and if or when financial resources should be allocated if a physical disturbance occurs.

This study assesses recruitment and colonization of sessile invertebrates and algae, which informs the associated rate of increase in ecological function post-construction or post-disturbance. The purpose of this study was twofold: 1) to evaluate the length of time for new bare rock to be colonized by algae and invertebrates and 2) to assess the successional differences in the algal and invertebrate species abundance and assemblage (percent cover) over the four years as compared to reference sites with similar substrates, salinity, wave exposure, and depth.

Methods

Study Area

The Buskin River enters Chiniak Bay immediately north of and adjacent to the Kodiak Airport (Figure 1). The river supports the largest subsistence salmon fishery within the Kodiak Archipelago (Witteveen et al. 2018). The nearshore marine area at the river mouth is shallow and mostly sand to cobble-bottomed with varying levels of kelp density. The river mouth is framed to the south by a sand and gravel barrier bar (Figure 2) that has periodically migrated, as evidenced in historical aerial photographs. The barrier bar provides a dynamic gently sloping, soft-bottomed area that is a nursery for a variety of fish species (SWCA 2009). Substrates in the Buskin River nearshore marine area become more large-grained closer to airport runway ends and further offshore (SWCA 2009). The area has moderate wave exposure and shelter in Chiniak Bay (latitude 58°N).

As part of the expansion of the Kodiak Airport runway safety area, new armor rock was placed in the intertidal and subtidal area along the coastal edge of two runways in 2014 and 2015. The fill area was mostly isolated by a silt curtain (a barrier intended to minimize transport of silt and sediment) that was removed in March of 2015. Three study sites and two reference sites (Figure 2) were established in 2016, Year 1 (or 15 months post-construction silt curtain removal), and surveyed annually in June and July for four years. Study sites occurred on the new fill at runway ends 26 and 01. The reference sites were outside of the construction footprint on existing armor rock that extends from the supratidal to subtidal with similar wave exposure, depth, and salinity as those within the construction area. Reference sites were established on either side of the entrance to a small boat basin between runway ends 29 and 01, locally referred to as the crash basin. Though it is unknown when the armor rock at the reference sites was placed, the crash basin was constructed prior to 1985 (Landsat aerial imagery provided in Google Earth Pro). The initial construction of the airport and associated military facilities occurred in the 1940s. Study sites were compared to reference sites that had at least 30 years of succession.

A wastewater treatment outfall is located 324 meters offshore of the crash basin at about 3.4 meters below mean lower low water (Alaska Pollutant Discharge Elimination System permit number: AK0020648). The reference sites were located on the outer jetties of the crash basin, 116 and 147 meters outside of the 5- by 7-meters mixing zone for the outfall (Alaska Department of Environmental Conservation 2016). Though reference sites were located well outside the mixing zone of the wastewater outfall near the crash basin, nutrient levels were not measured at reference sites or study sites. Salinity was measured in Year 1 at both reference and study sites and was similar.

Monitoring

At each study and reference site, a benchmark was established above the high tide line and marked with fluorescent, reflective, marine-grade paint so it could be readily located throughout the four-year study. Global position system (GPS) coordinates were captured at each benchmark. A 10-meter benchmark line was marked from the benchmark down slope into the subtidal area. Sampling at each site consisted of quadrat and band sampling at up to four elevational strata along the benchmark line: two or three in the intertidal strata depending on terrain (upper-, middle-, lower-intertidal) and one upper subtidal strata. Each stratum was marked on the benchmark line and a 20-meter perpendicular transect was run laterally along the elevation contour (Figure 3).

Elevational Strata—Intertidal

Intertidal monitoring occurred during extreme low tides by walking the area between roughly mean higher high water (2.7 meters) and extreme low water (-0.7 meter). At some sites, the new rock armor did not extend into the lower intertidal and two strata were sampled for site representation. The need for two or three intertidal elevational strata was determined in the field. The general characteristics used to distinguish the three intertidal elevational strata were:

1. Upper Intertidal: 2.7 meters to 1.4 meters (mean higher high water to mean sea level), characterized by rockweed (*Fucus* sp.), laver algae (*Porphyra* spp.), and barnacles (*Balanus* sp. and *Chthamalus dalli*); typically with low diversity and moderate productivity (as determined qualitatively in the field)
2. Middle Intertidal: 1.4 meters to 0 meter (mean sea level to mean lower low water), characterized by brown and green algae with moderate diversity and moderate productivity
3. Lower Intertidal: 0 meter to -0.7 meter (mean lower low water to extreme low water), characterized by a matrix of red algae, kelps, and invertebrates

At runway end 01, only the upper- and mid-intertidal were sampled (using the quadrat method described below) because there appeared to be homogeneity in habitat types and species assemblages and access to the lower intertidal was unsafe to traverse by foot. At runway end 26 and at the reference sites, all three intertidal strata were sampled.

Elevational Strata—Subtidal

Subtidal monitoring was completed via scuba and snorkel surveys (using the quadrat method described below) between extreme low water (-0.7 meter) and -1.8 meters (or the deepest extent of the new fill). Because the actual depth of the new fill does not extend into the lower subtidal at either study site, only the upper subtidal (-0.7 meter to -1.8 meters, characterized by kelps) was sampled at runway end 01 and no subtidal transects were sampled at runway end 26. The new fill at runway end 26 extends approximately 0.3 meter into the subtidal zone before the substrate transitioned to sand.

For the subtidal elevational strata, the start and end points of the transects were located using a GPS at the water surface and marked with anchored buoys; a tape measure was strung tightly between them along the bottom for locational reference. The elevation of the transect was located between the lower intertidal and the end of the new fill.

Band Sampling—

Prior to quadrat sampling and as each 20-meter-long elevation contour was marked, larger mobile animals within a 1-meter-wide band next to the tape measure were recorded that might not otherwise be recorded in the quadrat sampling (e.g., crabs, fish, etc.). Along each of these band transects, the number and general size of animals were recorded. To minimize disturbance of mobile species, band transects were completed immediately after establishing the depth benchmark, while laying out the elevation strata line. Band transect species were generally not added to the percent cover of quadrats, but were added to the total number of species observed. If a mobile species remained in the area during quadrat sampling and happened to be in a quadrat, it was counted in the percent cover of that quadrat.

Quadrat Sampling—

In the first year of sampling, five randomly selected 0.25-meter square quadrats centered along each elevation contour were surveyed for percent cover by substrate type, algal species, and invertebrate species. These same quadrats were sampled again in Years 2 through 4. The numbers of motile animals larger than 4 millimeters were documented. Photographs of each quadrat were taken and included a label showing date, transect number, and quadrat number. Photographs were used to verify species and abundance during quality control of data entry post-field work. Very abundant species were subsampled by counting the number within a subset of the quadrat and extrapolating to the remainder of the quadrat.

Percent cover was visually estimated. Species that were less than 1% cover were noted as such. When calculating total percent cover, the total number of species noted as less than 1% were used to back-calculate the actual percent cover. For example, if there were four species that had less than 1% cover, and all the other species and bare rock totaled 98% cover, then those four species were assigned an individual percentage of cover to total 2% based on their relative abundance (e.g., if all species were relatively equal in cover, they were assigned equal percent covers totaling 2% [0.50% in this case]; or, in cases of decreasing abundance, they were assigned decreasing percent covers, such as 0.75%, 0.50%, 0.50%, and 0.25%).

Species that could not be identified in the field were vouchered and identified in the lab. Taxa were identified to species level when possible; the condition of some algae did not allow identification to species and the lowest taxonomic level practicable was noted.

Percent cover of subtidal quadrats was noted at two levels: canopy and substrate. Canopy observations were recorded from above and captured the percent cover within the quadrat without displacing the algae to see what was below. Observations at substrate level were taken below the algae to document encrusting organisms or smaller (non-canopy-forming) algae.

The location of each quadrat was noted by elevational strata and by position on the transect line. Each subsequent year of monitoring attempted to capture the same position of each quadrat from the year before.

Statistical Methods

Quadrats from the middle and upper intertidal areas were used to conduct two sets of analyses: 1) changes in percent cover and total species observed per quadrat over the four years and 2) differences between the study and reference sites during the last year of the study. We focused on the middle and upper intertidal elevations because lower intertidal data were not available from study sites 2 and 3 (runway end 01) and subtidal data were not available for study site 1 (runway end 26). For each analysis, we evaluated four responses: algal percent cover, invertebrate percent cover, total percent cover (sum of algal and invertebrate covers), and the total species observed per quadrat (number of species observed in a single quadrat). To investigate changes over time, we used site and year and their interaction as covariates in separate models for each of the responses. The year term was centered prior to modeling.

〖[Eq.1] y〗_ij =α +β_1 〖site〗_i * β_2 〖year〗_j + β_3 (〖site〗_i* 〖year〗_j) + ε

Where y at site i and year j represents one of the four responses, and site and year are covariates. When the interaction term was not significant, it was removed from the model.

To assess whether study sites had reached reference conditions by the end of the four-year period, we evaluated differences between the sites in Year 4 for each response.

〖[Eq.2] y〗_i =α +β_1 〖site〗_i + ε

Where y at site i represents one of the four responses and site was the only covariate. We used beta regression from the betareg package in R (Cribari-Neto and Zeileis 2010, R Core Team 2023) to model the cover responses since they are proportions on the interval (0,1). We used generalized linear models with a Poisson distribution to model the count of total species using the glm package. We evaluated differences among sites using the emmeans and multcomp packages (Hothorn et al. 2008, Piepho 2018, Lengh 2024).

Results

All study sites showed an average of 62% – 85% cover by early colonizing algae and invertebrates in both the intertidal and subtidal areas in Year 1 (approximately 15 months after the silt curtain was removed post-construction). Table 1 summarizes the average percent cover of reference and study sites for Year 1 through Year 4. Though reference sites consistently had higher species richness, the difference between study sites and reference sites narrowed over the four-year study (Δ = 44 in Year 1 to Δ = 9 in Year 4). Particularly, the number of algal species at reference sites was more than double the number of algal species at study sites in Year 1, but by Year 4 the study sites had only 3 fewer algal species than the reference sites (Table 1, Figure 4).

Table 2 lists species observed with an average percent cover greater than 5%. Intertidal colonization in Year 1 was dominated by bay mussels (*Mytilus trossulus*) at runway end 01, whereas runway end 26 was dominated by barnacles and laver algae. Runway end 26 had more bare rock than runway end 01. Prominent biobands of monospecies were observed at runway end 01.

Several species of fish were observed along the subtidal transects at runway end 01, including juvenile black rockfish (*Sebastes melanops*) and great sculpin (*Myxocephalus polyacanthocephalus*). Crabs were also observed in the lower intertidal and subtidal study sites: Pygmy rock crab (*Cancer oregonensis*), graceful decorator crab (*Oregonia gracilis*), and helmet crab (*Telmessus cheiragonus*). Data and comprehensive species lists are available online: https://www.birchleafconsulting.com/brimsreport.

In the beta regression model of algal percent cover, the interaction term was not significant and increases in percent cover over the four years were larger at the reference sites (~10%) compared to the study sites (~5%, Figure 5). The interaction term was significant for invertebrate percent cover and the largest decreases occurred at the two study sites on runway end 01 (-16% and -24%, Figure 5). The contrasting trends in algal percent cover (increasing) and invertebrate percent cover (decreasing for three sites) resulted in slight decreases in total percent cover that ranged from 4 to 7%. The total number of species increased by 3 to 8 species at the three study sites and had contrasting patterns at the two reference sites (Figure 5).

Data from 2019 indicated minimal differences in algal percent cover, invertebrate percent cover, or total percent cover between sites. Statistically significant differences in the percent cover responses included lower algal cover at Site 2 compared to Site 4 and higher invertebrate cover at Site 2 than Site 5 (Figure 6). The total number of species per quadrat was significantly less at Sites 2 and 3 compared to Site 1 and the reference sites had an intermediate number of species (Figure 6).

Discussion

Succession at the study sites continued throughout the four-year study. The total number of species observed at study sites increased each year, a pattern not consistently observed at the reference sites (Table 1). The small decreases in total cover at the study sites over the four-year study could indicate successional predation of encrusting species (Table 1 and Figure 6).

Bay mussels and barnacles are typical early successional species (Farrell 1991, Lacroix 2006, Peterson 2000), followed by algae, which are later successional species. Early succession favors species with planktonic larval stages that are fast growing. Predators of mussels (e.g., adult sea stars and gastropods) are slower to inhabit new habitats since they are not planktonic, and move into new areas from surrounding habitat. As concentrations of these predators increase, mussels typically experience a sharp decline. This successional progression opens up surface area for more stable community species, such as algae.

The prominent biobands of monospecies (e.g., bay mussels [*Mytilus trossulus*]) that were observed at study sites in Year 1 (especially at runway end 01) largely changed to barnacles (*Balanus* sp.) and algal species by Year 4. The average percent cover of bay mussels at study sites in Year 1 was approximately 34% and fell to approximately 10% in Year 4, as shown in Table 1. These biobands were comprised of bay mussels that were mostly small in size indicating that they were relatively newly settled.

In Year 4, percent cover by predatory snails and sea stars, which had been gradually increasing throughout the study period, was the highest observed for all study sites (1.2%) and reference sites (0.9%) (Table 1). Average percent cover by algae at study sites grew over the four-year study period, from 17% cover in Year 1 to 26.5% cover in Year 4, indicating a maturing of the intertidal and subtidal communities (i.e., mature reference sites ranged from 32 to 48% algal cover).

The successional boom and bust of bay mussels at the study sites was expected and has been observed at other locations in Alaska (NOAA 2018a, 2018b); however, colonization and succession occurred faster than anticipated. Long term monitoring in Prince William Sound after the Exxon Valdez oil spill documented a 4–10-year cycle of intertidal marine life (Driskell et al. 2001, Mearns et al. 2017, NOAA 2018a), including (most dominantly) bay mussels and rockweed (*Fucus* sp.). Sites have been observed to be nearly devoid of mussels and cyclically return to be dominated by mussels. Similarly, intertidal sites have been observed to be rapidly colonized by rockweed and then experience a steep decline of the species (Driskell et al. 2001, Mearns et al. 2017, Hart Crowser 2014). In Prince William Sound, there is evidence that a single cohort of rockweed rapidly recruited soon after the oil spill and monopolized space for several years before declining; there was no evidence that the decline was due to overgrazing by herbivores (Driskell et al. 2001). These studies have also documented high inter-annual variability of species abundance at study sites, which we also observed at our study sites.

Throughout the four-year study, there were species that occurred only in some years, or occurred in higher abundance in some years. For example, *Anisodoris nobilis* (lemon nudibranch) was first documented in Year 3 at study sites and reference sites. It feeds on a variety of sponges, including *Halichondria panicea* (Crumb of bread sponge) and *Haliclona permollis* (Purple encrusting sponge) (Wheeling 2002), both of which were documented at study and reference sites in all years. However, percent cover of these sponge species was low in Year 3 (0–0.2%), when *Anisodoris* was at its highest percent cover (0.02–0.1%). In Year 4, percent cover of sponge species increased and *Anisodoris* notably dropped. This could suggest that *Anisodoris* overgrazed on these sponge species and then moved out of the study area in search of food or starved; in Year 4, the sponges were recovering from overgrazing.

The succession rates that we observed in Kodiak (latitude 58°N) were similar to those observed in Sitka (latitude 57°N). In Kodiak, we observed an average of 80.8 total percent cover of intertidal and subtidal substrates after one year; in Sitka, greater than 80% of pre-construction function was observed in the construction area after two years (Hart Crowser 2014).

This study counted the time to colonization starting from when the silt curtain was removed post-construction. It is possible that the colonization began before that, and the actual time to colonization was longer than the results we recorded. The fill area was mostly isolated by a silt curtain, though weather prevented the curtain from being 100% effective; and at times, storm surge breached the curtain and could have introduced algae or larval invertebrate species. The new rock armor was placed in 2014 and 2015 and the silt curtain was removed in March of 2015. This study began monitoring approximately 15 months after the silt curtain was removed.

Though latitude may be a factor that influences recolonization, this study did not directly evaluate that. Recolonization at the Kodiak airport (latitude 58°N) was similar other latitudes from 49°N to 60°N (Stekoll and Deysher 1996, Lacroix 2006, Hart Crowser 2014, Jewett and Drew 2014, Exxon Valdez Oil Spill Trustee Council 2022). However, it was considerably faster than at 70°N (Konar 2012), though there may be other compounding factors at 70°N (Prudhoe Bay) that would limit recolonization such as ice cover and higher seasonal ambient turbidity.

This study illustrates that colonization of new armor rock in southcentral Alaska can be rapid (average 80.8% cover of intertidal and subtidal substrates after one year) and species abundance may likely continue to experience interannual variability for many years. In Prince William Sound, interannual variability has been documented to be occurring for over 27 years (Mearns et al. 2017) post-oil spill. This type of natural variation complicates defining when a successional cycle is complete. However, increased species richness and percent cover of the armor rock four years post-construction appears to be much higher than when the bare rock was placed.

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Figures

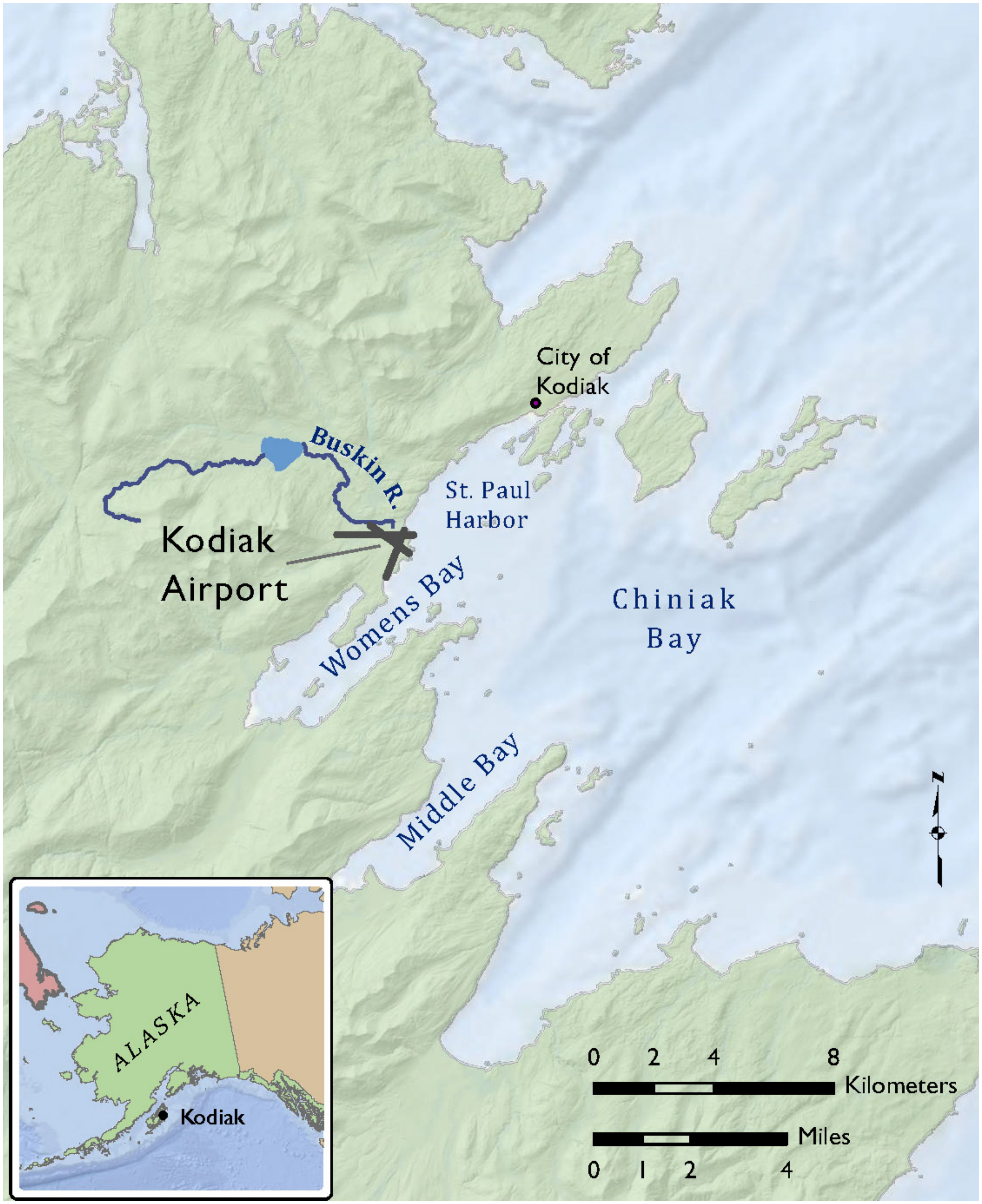
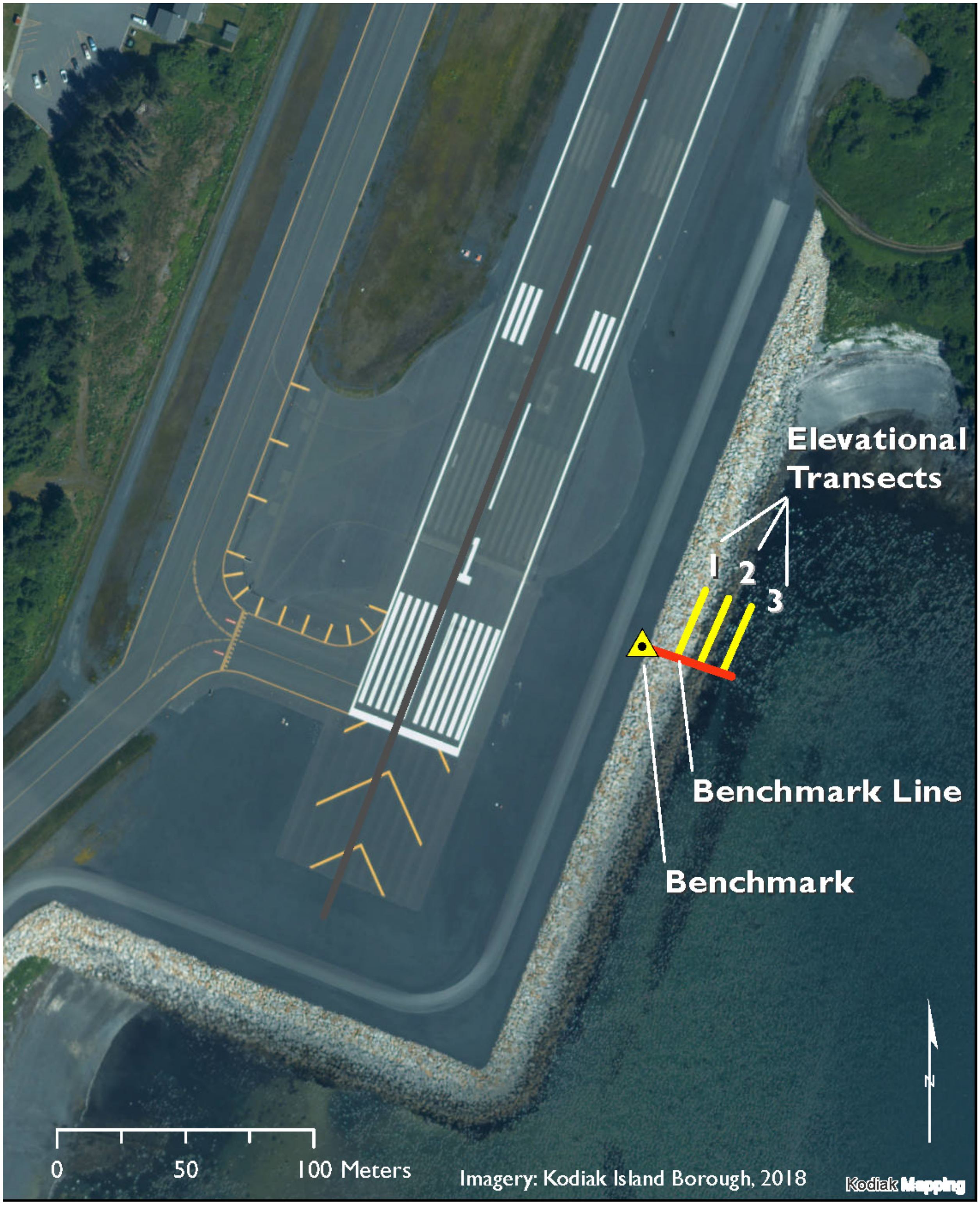


Figure 1. Buskin River Area, Kodiak Island, Alaska

Figure 2. Kodiak Airport and the Buskin River Nearshore Marine Area Study and Reference Sites

Arsan EL, Lance T, Krueger K, Shaftel R. 2025. Intertidal and subtidal marine succession rates on new rock armor in Chiniak Bay, Kodiak, Alaska. Northwest Science 98(2): *in press*.



Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.

Figure 3. Example Sample Site with Benchmark (triangle), Benchmark Line (red line), and Elevational Transects (yellow lines). Not to scale.

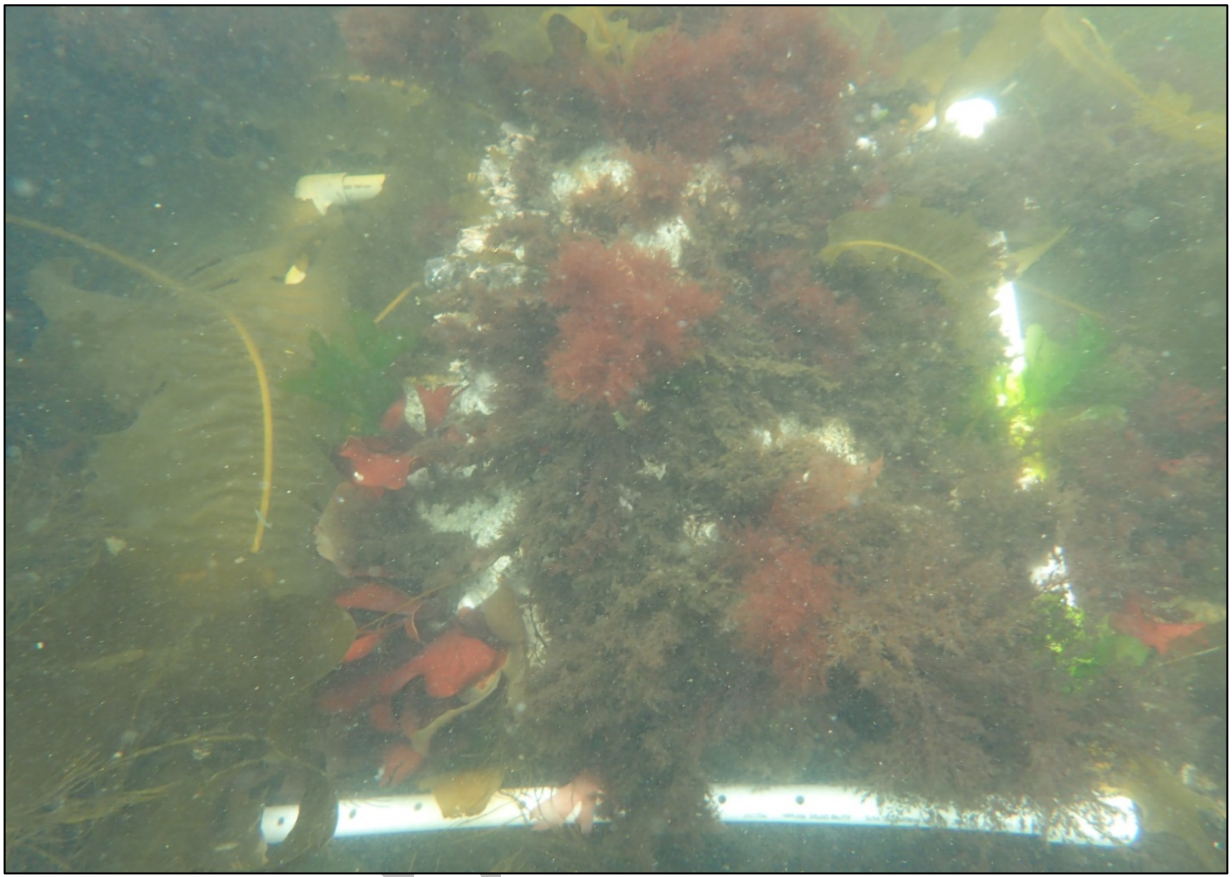


Figure 4. Abundant Algal Cover, Subtidal Study Site 2019 (Year 4, Site 2, Quadrat 231)

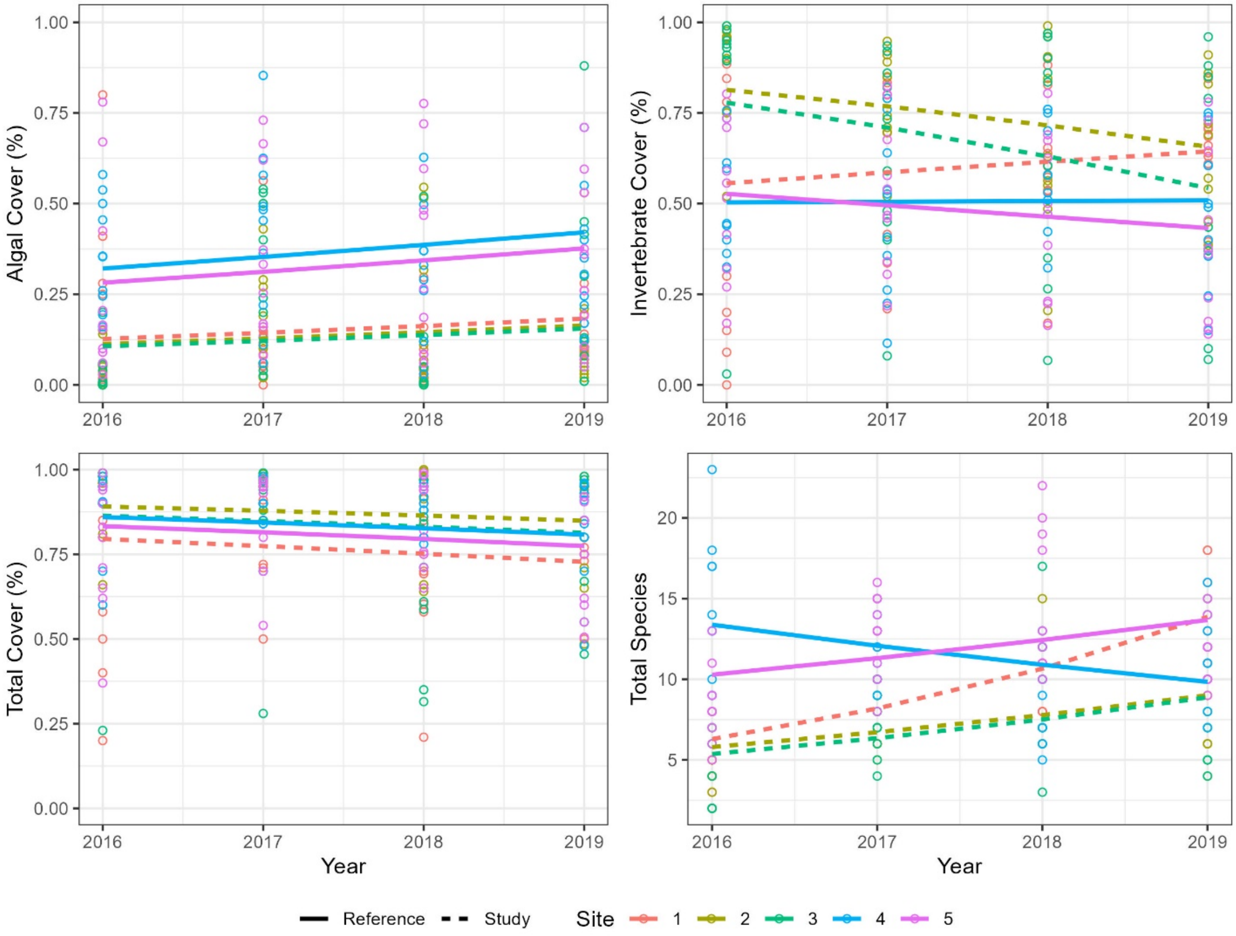


Figure 5. Changes in Algal Percent Cover, Invertebrate Percent Cover, Total Percent Cover, and Total Species per Quadrat in Mid and Upper Intertidal Elevations

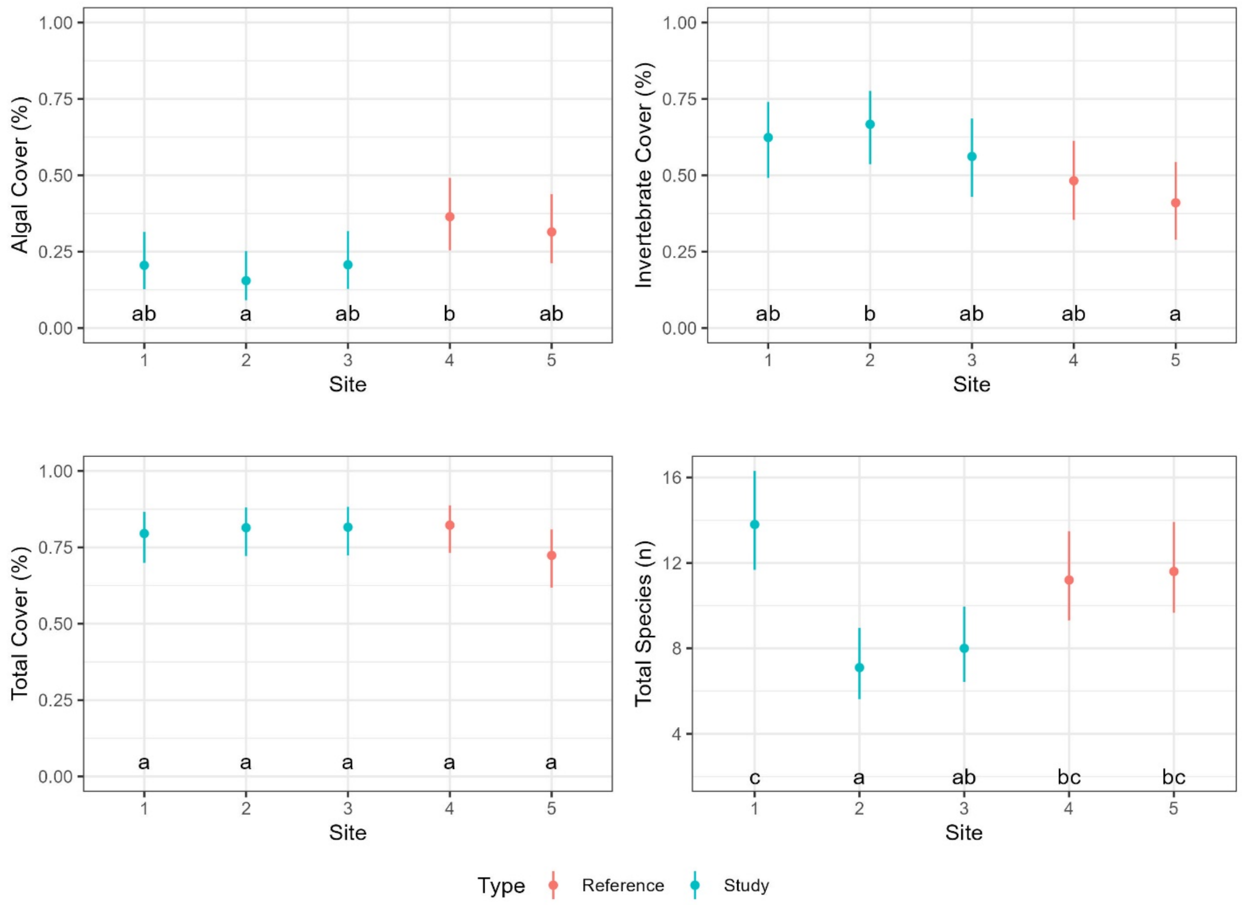


Figure 6. Differences in Algal Percent Cover, Invertebrate Percent Cover, Total Percent Cover, and Total Species per Quadrat Among Reference and Study Sites in Year 4 (2019)

Tables

TABLE 1. Average Percent Cover and Relative Composition, Years 1 through 4

Metric	Year 1 - 2016 Study Sites	Year 1 - 2016 Ref Sites	Year 2 - 2017 Study Sites	Year 2 - 2017 Ref Sites	Year 3 - 2018 Study Sites	Year 3 - 2018 Ref Sites	Year 4 - 2019 Study Sites	Year 4 - 2019 Ref Sites
Total species observed	43	87	65	78	77	95	79	88
Average percent cover intertidal and subtidal[a]	80.8	76	76.5	80.2	79.7	83.0	73.3	81.8
Average intertidal percent cover	84.6	80.7	86.1	88.4	78.2	84.8	80.5	83.3
Average subtidal percent cover substrate level	65.6	61.8	46.2	70.2	80.3	70.5	44.2	77.3
Average subtidal percent cover canopy level	71.2	76.3	64.1	64.8	Not taken	79.5	77.4	81.9
Maximum percent cover by a single species (species)	98.5 (MT)	99 (AM)	89 (AM, CD)	93 (BS)	93.6 (BS)	83.5 (BS)	80.5 (AM)	74.9 (FD)
Minimum total percent cover	20	18	28	25	21	44.7	13	40
Maximum total percent cover	100	100	100	100	100	99	100	100
Number of algal species	19	41	35	44	41	54	48	51
Average percent cover by all algal species (intertidal)[a]	17 (8)	33 (29)	23 (16)	32 (30)	22 (10)	48 (29)	26.4 (18.5)	45.7 (37)
Average percent cover *Mytilus trossulus* (intertidal)[a]	34 (39)	5 (6)	5 (7)	3 (4)	9 (11)	5 (9)	9.6 (13.7)	4.5 (7.5)
Average percent cover *Balanus* sp. (intertidal)[a]	25 (20)	22 (23)	42 (55)	25 (24)	34 (44)	20 (32)	26.5 (35.4)	19.2 (24.2)

Metric	Year 1 - 2016 Study Sites	Year 1 - 2016 Ref Sites	Year 2 - 2017 Study Sites	Year 2 - 2017 Ref Sites	Year 3 - 2018 Study Sites	Year 3 - 2018 Ref Sites	Year 4 - 2019 Study Sites	Year 4 - 2019 Ref Sites
Average percent cover predatory snails and sea stars (intertidal) [a]	< 0.1 (0)	0.25 (0.33)	0.18 (0.23)	0.46 (0.57)	0.64 (0.72)	0.67 (0.88)	1.2 (1.1)	0.9 (0.5)

Note: Ref (reference); MT (*Mytilus trossulus)*; AM *(Alaria marginata)*; CD (*Chthamalus dalli)*; BS (*Balanus* sp.); FD (*Fucus distichus*)

[a] Averages are presented as combined subtidal (substrate and canopy levels) and intertidal; parentheses indicate intertidal average only.

TABLE 2. Average Percent Cover of Observed Species with Five Percent Cover or Greater[a]

Species	Strata	Year 1 - 2016 Study Sites	Year 1 - 2016 Ref Sites	Year 2 - 2017 Study Sites	Year 2 - 2017 Ref Sites	Year 3 - 2018 Study Sites	Year 3 - 2018 Ref Sites	Year 4 - 2019 Study Sites	Year 4 - 2019 Ref Sites
Algae									
Ribbon kelp (*Alaria marginata*)	Sub	23	15.7	39.3	29.1	23.6	17.2	27.9	10.8
Hooked skein (*Antithamnionella pacifica*)	MI	0	0	0	0	0	0.3	6.3	0.3
Enigmatic coral seaweed (*Corallina frondescens*)	Sub	0	1	0	6.6	0	3.5	0.2	7.5
Three-ribbed kelp (*Cymathaere triplicate*)	Sub	0	0	0.1	0.7	0	0	9.5	0
Stringy acid kelp (*Desmarestia viridis*)	Sub	17.3	2.1	2.7	2.5	43.2	11.2	2.3	1.1
Rockweed *(Fucus distichus subsp. Evanescens*)	MI	0	24.4	0	30.3	0	29.6	6.1	29.6
Southern stiff-stiped kelp (*Laminaria setchellii*)	Sub	3	0	0	0.3	0	10.3	0	0
Suction-cup kelp (*Laminaria yezoensis)*	Sub	0	0.4	1	5.5	2.5	6.1	0	0.5
Neorhodomela – Odonthalia complex (Oregon pine,	MI	0	7.4	0.4	9.9	9.9	11.5	1.3	0.1

Species	Strata	Year 1 - 2016		Year 2 - 2017		Year 3 - 2018		Year 4 - 2019	
		Study Sites	Ref Sites	Study Sites	Ref Sites	Study Sites	Ref Sites	Study Sites	Ref Sites
Neorhodomela oregona; Black pine, *Neorhodomela larix;* Sea brush, *Odonthalia floccosa*)									
Red ribbon (*Palmaria mollis*)	LI	0	0.3	0	0.2	3	0	10.8	0
Alternate skein (*Pleonosporium vancouverianum*)	Sub	0	0	0	0	0	0	12.1	1.1
Olive green winter laver (*Porphyra pseudolanceolata*)	AI	0.7	0	9.6	3.5	1.1	0.1	3.4	0.1
Split kelp (*Saccharina groenlandica)*	Sub	0	0	0	0	4.3	5.5	1	0
Sea lettuce (*Ulva lactuca)*	Sub	0.3	0.4	0	0	3.0	5.5	6.0	0.2
Encrusting coralline red algae (Unknown spp.)	Sub	0	17.3	0	11.5	0	16	1.1	22.8
Invertebrates									
Acorn barnacle (*Balanus* sp.)	AI	25.4	23.2	55.3	24.3	43.6	31.7	35.4	31.7
Little brown barnacle (*Chthamalus dalli*)	AI	1.2	7.9	5.5	21.4	8.6	11.7	6.3	11.7
Bay mussel	AI	30.3	5.7	6.9	4.5	11	8.7	13.7	8.7

Species	Strata	Year 1 - 2016		Year 2 - 2017		Year 3 - 2018		Year 4 - 2019	
		Study Sites	Ref Sites	Study Sites	Ref Sites	Study Sites	Ref Sites	Study Sites	Ref Sites
(*Mytilus trossulus*)									

Note: AI (average intertidal: average of upper-, middle-, and lower intertidal); LI (lower intertidal); MI (middle intertidal); Sub (subtidal).

[a] In at least one transect on at least one year.