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Spatially Explicit Population Dynamics and Viability of Pinto Abalone Across Southeast Alaska

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SPATIALLY EXPLICIT POPULATION DYNAMICS AND VIABILITY OF PINTO ABALONE ACROSS SOUTHEAST ALASKA

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

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SPATIALLY EXPLICIT POPULATION DYNAMICS AND VIABILITY OF PINTO ABALONE ACROSS SOUTHEAST ALASKA

Taylor D. White

ABSTRACT

Pinto abalone (*Haliotis kamtschatkana*) populations in Alaska have faced numerous ecological pressures, including the extirpation of Northern sea otters (*Enhydra lutris kenyoni*) due to the international maritime fur trade, the establishment and later emergency closure of a commercial fishery, the repatriation of sea otters, and ongoing subsistence harvest. Abalone are significant to the region for both ecological and cultural reasons. However, data deficiencies hinder the proper understanding and management of the species across its northernmost range, as no comprehensive surveys of pinto abalone across Southeast Alaska exist. This body of work aims to 1) assess the lasting impacts of fisheries and sea otters on present-day population demographics, 2) explore variations in abalone populations and recruitment and factors promoting recruitment across Southeast Alaska, and 3) assess the indirect and direct effects of repatriating sea otters on abalone populations. In Chapter 1, we assessed the impacts of fisheries and sea otters on current (2016, 2019) population demographics through comparisons of recent resurveys with historical datasets in areas both with and without sea otters. Compared to historical surveys, locations with repatriated sea otters and historically intensive fishery landings had the most significant reductions in abundance and size frequencies. Yet, locations with moderate harvest and no established sea otter populations remained similar to historical surveys. Through a spatially nested design in Chapter 2, we determined the present-day (2018, 2019) population metrics important to management (i.e., abalone densities, recruitment, size structure) and calculated reproductive capacities (i.e., egg mass) and fertilization potential (i.e., aggregation metrics) across Southeast Alaska. We identified distinctly different abalone populations across sites and regions, including Sitka, Prince of Wales Island, and Dixon Entrance, all showing evidence of visible recruitment. We determined adult abalone critical densities of (0.2/m^2) and nearest neighbor distances of (0.2m), beyond which there was a minimal increased benefit of fertilization potential. Finally, with established ecological patterns following sea otter re-establishment, modeled data, and local expertise on sea otters, along with dive surveys of urchins, algal cover, and abalone (see Chapter 3), we identified the indirect benefits of moderate sea otter influence. We found abalone persist with and may likely indirectly benefit from the presence of sea otter populations through their consumption of herbivore competitors like sea urchins, whereby locations where otters remained absent had higher urchin biomasses and lower abalone densities (i.e., Dixon Entrance) than locations with long-established sea otter populations (i.e., Sitka). These findings provide the most comprehensive review of pinto abalone populations throughout Southeast Alaska and suggest effective abalone management must consider complex indirect interactions with sea otters and direct impacts of human harvest at smaller localized scales.

DEDICATION

To the original and ongoing stewards of the place I call home;

my communities, and family

EPIGRAPH

"Our life is an apprenticeship to the truth, that around every circle another can be drawn; that there is no end in nature, but every end is a beginning; that there is always another dawn risen on midnoon, and under every deep a lower deep opens."

— Ralph Waldo Emerson, Circles

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INTRODUCTION

Abalone are marine mollusks (genus *Haliotis*, Linnaeus 1758) that inhabit nearshore rocky reefs and kelp forests (Geiger 2000). There are over 55 known abalone species worldwide, and many are sought after as artisanal food and for traditional, customary, and commercial use (Cox 1962, Ellis and Wilson 1981, Mills 1982, Moss 1993, Campbell 2000, Geiger 2000, Vileisis 2020, Ibarra 2021). Concern over the decline of the abalone population following more intensive harvest and removal of large, fecund abalone is warranted based on notorious histories of overharvest (e.g., Karpov et al., 2000, Rogers-Bennett et al., 2002, Bouma 2007, Rogers-Bennett 2007, Zhang et al., 2007, Rothaus et al., 2008, Chadès et al., 2012, Carson and Ulrich 2019) and have life history traits that do not support commercial or sport fisheries.

Abalone must be aggregated in high enough densities during spawning events, as they broadcast gametes and require proximity to larger, mature individuals of the opposite sex for fertilization success. Hydrodynamic modeling and empirical evidence suggest that one meter is the distance beyond which the fertilization of eggs by sperm is unlikely to occur (Denny and Shibata 1989, Babcock and Keesing 1999). More precise estimates are often species and location-specific, where Rothaus et al. (2008) found pinto abalone (*Haliotis kamtschatkana*) recruitment failure in Washington at neighbor distances below 0.33/m^2 and densities of 0.15 abalone/m^2. At sites in British Columbia, pinto abalone aggregations had recruitment success with densities as low as 0.12/m^2 (Seamone and Boulding 2011). Researchers even found signs of limited recruitment in San Diego at sites with 0.03 individuals/m^2 (Bird 2018). Still, such low densities are likely less resilient to stochastic events (e.g., Catton et al., 2016) and local harvest fluctuations and warrant concern.

Beyond cycles of population decline and reduced reproductive success, abalone are sensitive to additional threats beyond fisheries, including habitat loss (Miner et al., 2006), disease (Melanson, 2018), combinations of multiple environmental fluctuations such as El Niño (Rogers-Bennett and Catton 2019), salinity shifts (Bouma 2007), increased temperatures affecting abalone recruitment (Wootton et al., 2008), and ocean acidification, which increases abalone's energetic demands and affects abalone food availability (Kroeker et al., 2021).

Precipitous abalone population declines have garnered abalone species protections through listing designations. In 2001, following overexploitation by California commercial fisheries, white abalone (*Haliotis sorenseni*) were the first marine invertebrate listed as "Endangered" under the Endangered Species Act (ESA) (66 FR 29046, Hobday et al., 2001). In 2009, another commercially harvested species, black abalone (*H. cracherodii*), were listed as Endangered (74 FR 1937). In 2019, pinto abalone (*H. kamtschatkana*) were added to the Washington State Endangered Species List (Rothaus et al., 2008, Bouma 2012). All species remain at critically low population densities (NMFS 2009, NMFS 2014, Melanson 2018). Recruitment failure was an indicator of population decline for all these listed abalone species (Haaker et al., 1996, Karpov et al., 2000, Rogers-Bennett 2007, Bouma 2012). The criterion for abalone down listing and approaches to determine abalone recovery status often focus on recruitment success, which has been defined in many ways, most with a linkage to fisheries-based stock-recruitment models.

Petitions to list the species central to this research, pinto abalone, as “Endangered” under the Endangered Species Act were denied in 2014 due to the uncertainty in population trends, signs of localized ongoing recruitment, and localized successes of abalone populations that did not warrant immediate listing across the species’ range (Neuman et al., 2018). Pinto abalone (*Haliotis kamtschatkana,* Jonas 1845) have the most extensive range of abalone along the Pacific North America coast, north of Sitka, Alaska, to central Baja, and are found at depths ranging from 0 to 40 meters (Neuman et al., 2018). Pinto abalone populations vary widely across their range, where, as mentioned, the species are listed as “Endangered” in Washington state (Carson and Ulrich 2019), “Endangered” by the International Union for Conservation of Nature (IUCN 2021), yet also experience some recruitment success throughout their range and population growth at select surveys in Southeast Alaska (Bell et al., 2018).

Southeast Alaska is majority Lingít Aaní, Tlingit land, where Tlingit, Haida, and Tsimshian communities have managed resources in diverse and resilient ways with a complex knowledge system built from over 10,000 years subsisting in the region (Goldschmidt and Haas 1998, Thornton 2011, 2015, Turner 2020). Much of the approximately 25,000 miles of coastline of the region consists of remote, irregularly accessible areas, which makes regular surveys of species extremely difficult. In Alaska, pinto abalone are the only abalone species and continue to be a vital subsistence food source (Mills 1982, Ibarra 2021). In Alaska, pinto abalone are most commonly found in nearshore areas and range from the southern international boundary with Canada, Dixon Entrance, to Salisbury Sound, north of Sitka Sound. Still, resident harvesters and resource managers report abalone much farther north, spanning almost all of Southeast Alaska, past Cross Sound, West of Cape Spencer "to the sand beaches of Yakutat" and as far east as Elfin Cove on Chichagof Island (ADFG 1976, see Figure 2 in Bell et al., 2018, J. Dangle personal communication 2021). Three regions on the outer coast of Southeast Alaska that are the focus of surveys herein, Prince of Wales, Dixon Entrance, and Sitka Sound, differ in their histories of commercial and ongoing subsistence abalone harvest, and each is at a distinctly different stage of sea otter repatriation.

Multiple commercial shellfish fisheries (e.g., red sea urchin, geoduck, abalone, and sea cucumber) were established in the mid-1960s during a period of shellfish abundance throughout Southeast Alaska, which was the likely effect of the near total extirpation of sea otters during the maritime fur trade in the late 1800s (Kenyon 1965). The abalone dive fishery began around 1964 and grew as the market price for pinto abalone price per pound increased from $1 in the mid-1970s to upwards of $10 a pound in the early 1990s (ADFG 1976, Hebert 2014). Despite an emergency fishery closure following the peak harvest of abalone during the 1979/1980 season and added restrictions, from a demographic standpoint, pinto abalone were over-harvested through peak fishery years up to the fishery collapse in 1983, when harvestable abalone became extremely rare (Larson and Blankenbeckler 1981, Woodby et al., 2000, Hebert 2014). The decrease in harvest rates, notable stock decline, and fishery-independent concerns for abalone and subsistence use catalyzed the final emergency fishery closure in October 1995 (Mills 1982, Woodby et al., 2000, Chapter 1 Appendix Table A1.1).

Though commercial harvest was closed by 1996, subsistence and personal use harvest continues and has historically varied across Southeast Alaska regions (Mills 1982). Subsistence harvest guidelines were limited to snorkel and hand picking in 1983, and individual abalone possessions changed from 50 abalone per person (20 surrounding the community of Sitka) to five ≥89mm abalone per person by 2013 (Title 5 of the Alaska Administrative Code, Chapter 02, Section 135). No subsistence or personal use reporting is required, and limits are loosely enforced (S. Walker personal communication February 2019). In addition to less certain local impacts of abalone harvest, pinto abalone populations have experienced a changing spatial mosaic of repatriated populations of the northern sea otter (*Enhydra lutris kenyoni*; Tinker et al., 2019), a voracious shellfish predator (Costa 1982, Pitcher 1989, Gill 2013). These populations stemmed from the ADFG translocations of 413 northern sea otters to select sites in Southeast Alaska to conserve individuals from atomic bomb tests by the Atomic Energy Commission in the Aleutians (Bailey 1935, Burris and McKnight 1973, Jerry Deppa personal communication, 2024).

In some locations, subsistence fishers and traditional harvesters of those marine invertebrates targeted by commercial fisheries and sea otters have experienced restricted access to the important resource. In 1981, during subsistence household surveys, abalone harvesters echoed concerns over declining abalone populations (Mills 1982). Unfortunately, due to limited data, determining local trends following sea otter establishment has proven difficult. While significant effects of sea otters on invertebrate populations have been documented across many Southeast Alaska ecosystems

(Weitzman 2013, Hoyt 2015, Lee et al., 2016, LaRoche 2021, Bolwerk 2021, Ibarra 2021, Raymond et al., 2021), little is understood about abalone populations with sea otters and ongoing subsistence harvest.

Until 2015, questions about the status of Southeastern Alaska pinto abalone densities and population viability remained largely unanswered. Since then, multiple agencies have worked to address these data deficiencies, including The Alaska Department of Fish and Game (Donnellan and Hebert 2017), the National Marine Fisheries Service (NMFS AKR-18-0820; White and Raimondi 2020), The Sitka Sound Science Center (Bell et al., 2018), and the University of California Santa Cruz. Eight monitoring sites were established in Sitka Sound in 2015 (Bell et al., 2018), and five were monitored through 2021 and inform research herein. The first resurvey of the few available historical (i.e., 1970s to 1980s) abalone dive sites occurred in the summer of 2016 (Donnellan and Hebert 2017). ADFG researchers reestablished abalone surveys at ten historic sites in Meares Pass, Prince of Wales, and 14 new monitoring sites in Ketchikan (Donnellan and Hebert 2017). In 2019, we reestablished an additional 13 historical sites with the help of NMFS and ADFG in three locations in Prince of Wales, Alaska. As a part of this research and further comparisons, we resurveyed all (n=4) historical sites in Ketchikan in 2020. Additional abalone population surveys in 2018 and 2019 of 32 randomly selected sites around Sitka Sound allowed for comparisons to assess critical metrics on pinto abalone populations across Southeast Alaska.

Chapter 1 focuses on the resurveys of sites with the only available historical records of pinto abalone populations in Southeast Alaska to determine (1) whether abalone populations failed to recover and exhibit demographic artifacts associated with the intensive commercial dive fishery, (2) whether populations exhibit any demographic artifacts associated with the re-establishment of sea otter populations, and (3) whether abalone populations exhibit changes with sea otter presence independent from historic commercial harvest, and if those effects are compounded in areas of current sea otter occupation. **Chapter 2** explores critical densities and nearest neighbor distances that allow for successful reproduction, recorded recruitment, and population growth, specifically at sites nested in Sitka, Prince of Wales Island, and Dixon Entrance regions. Finally, **Chapter 3** investigates sea otter influence on abalone densities through (1) known interactions between sea otters, urchins, and kelp, (2) abalone behavior relative to local refuges and otter influence, and (3) differences in abalone-urchin relationships to explore sea otter-influenced trophic cascades in survey locations and potential impacts to abalone populations in Southeast Alaska.

This research provides the most comprehensive assessment of pinto abalone populations across their Alaska range, where abalone are still harvested, in areas with and without sea otter populations. With historical comparisons and data collected on density, size structure, spatial distribution, and recruitment, we amend data deficiencies critical to understanding current abalone populations. Our scope was intentionally broad, as identifying the abalone status and viability across the expansive and uniformly managed area required assessing an extensive area through strategic sampling.

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CHAPTER ONE

CHANGES TO PINTO ABALONE (*HALIOTIS KAMTSCHATKANA*) POPULATION DYNAMICS IN ALASKA FOLLOWING FISHERY CLOSURE AND SEA OTTER RETURN

CHAPTER 1. Changes to Pinto Abalone (*Haliotis kamtschatkana*) Population Dynamics in Alaska Following Fishery Closure and Sea Otter Return.

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ABSTRACT

Pinto abalone (*Haliotis kamtschatkana*) are harvested by coastal communities in areas recently reoccupied by Northern sea otters (*Enhydra lutris kenyoni*), predators known for their ability to reshape the ecosystems by their eating habits. Disentangling the consequences of humans and sea otters on any species or community can be challenging and often requires historical records to establish population abundance and track changes over time. In Southeast Alaska, pinto abalone were commercially harvested from 1964 to 1996, following a long history of subsistence, customary, and traditional harvest. Historical abalone surveys conducted sporadically from 1978 to 1989 by the Alaska Department of Fish and Game provided an opportunity for comparison to more recent survey data (2016, 2019, 2020) of size frequencies and relative abundance in areas with and without sea otter populations. We investigated demographic shifts in pinto abalone populations and associations with the commercial dive fishery, the re-establishment of sea otter populations, and the compounding effects of both. Pinto abalone abundance and size decreased over time in areas recolonized by sea otters, with additional declines observed in historically heavily harvested locations. In contrast, where sea otters had not yet been established, abalone recent surveys documented shifts towards smaller size classes, yet the overall abundance remained unchanged. Our results suggest pinto abalone populations are vulnerable to both expanding sea otter

populations and commercial fishing and indicate that populations remain inhibited in their recovery following fishery depletion, then closure forty years prior.

INTRODUCTION

Abalone fisheries often lead to rapid population declines (Karpov et al., 2000, Shepherd et al., 2001, Boonstra and Österblom 2014), which remain unresolved by fishery closures alone (Karpov et al., 2000, Tomascik and Holmes 2003, Micheli et al., 2008, Rothaus et al., 2008, Donnellan and Hebert 2017, Sowul et al., 2021). As broadcast spawning, dioecious, and relatively slow-maturing marine snails (*haliotid*), abalone are particularly vulnerable to overharvest (Sloan and Breen 1988). Pinto abalone (*Haliotis kamtschatkana*) are currently the only abalone species for which harvest is allowed in the United States and only in Alaska. However, throughout their range, from Baja California to central Southeast Alaska, pinto abalone have been sport, subsistence, and commercially harvested (Neuman et al., 2018). Like other fished abalone species, pinto abalone did not recover to pre-harvest abundance, and overharvesting resulted in small, patchily distributed populations with a potential for reproductive failure (Neuman et al., 2018). Alaska abalone population decline tracked pinto abalone fisheries in British Columbia by six years (see Figure 1.1), where all forms of abalone harvest were closed by 1990 (Rothaus et al., 2008), and where pinto abalone have been listed on Canada's Species at Risk Act (SARA) since 2003, and later listed “Endangered” under SARA in 2011. In 2019, pinto abalone were declared Endangered in Washington State (Carson and Ulrich 2019) due to critical population declines following the closure of the recreational-only fishery in 1994 (Rothaus et al., 2008, Sowul et al., 2021). In Alaska, the subsistence and personal use harvest of abalone continues following the closure of the commercial fishery after its 1995-96 season.

Pinto abalone remained a vital subsistence, customary, and traditional food source in Alaska (Mills 1982, Ibarra 2021, White and Raimondi 2024). Since time immemorial, Indigenous people have carefully considered and adaptively managed local ecological interactions at specific harvest sites (Thornton 2011 and 2015, Turner 2020). Alaska residents can legally harvest abalone for subsistence, albeit at reduced amounts. In 1963, the first subsistence limits were set at 50 per person per day in study areas via subsistence or personal use harvest. By 2013, harvest was limited to 5 per day per person, following years of apparent and anecdotally noted decline by Alaska Department of Fish and Game (ADFG) dive researchers and subsistence harvesters (Hebert 2014, White and Raimondi 2024; 5 AAC 02.135.). Over time, further restrictions to subsistence included an increase in minimum size limits by half an inch (Chapter 1 Appendix Table A1.1), gear restrictions including limits to subsistence SCUBA and hookah dive harvest, intermittent permit requirements (i.e., 1981 subsistence permits in Sitka and Ketchikan), and reduced bag limits (refer to Table A1.1; Mills 1982, ADFG 1976). Regardless abalone harvest does continue and at precisely unknown amounts, without harvest reporting requirement.

Coinciding with the start of the commercial abalone harvest, sea otters, a voracious predator of shellfish (Estes and Palmisano 1974, Kvitek et al., 1992, Fanshawe et al., 2003), were reintroduced to locations of Southeast Alaska between 1965 and 1969 following their near extirpation in the late 1880s (Kenyon 1969, Jameson et al., 1982).

The reintroduction of sea otters was successful, as they expanded their geographic range and population size (Burris and McKnight 1973, Pitcher 1989, Esslinger and Bodkin 2009, USFWS 2014), into areas they hadn't occupied for over 100 years (Burris and McKnight 1973, Pitcher 1989, Tinker et al., 2019, Schuette et al., 2023). With their understood status as predators of shellfish (Fanshawe 2003), sea otter repatriation and further movement into regions that support abalone populations intensified conflicts between harvesters and tensions between subsistence and commercial fishers, who ventured into areas traditionally reserved for subsistence users due to increasing otter impacts (Hebert 2019).

Abalone populations are likely still impacted by repercussions from the historical dive fisheries and, potentially, by the expanding sea otter populations in Southeast Alaska. It is crucial to better understand any lasting effects of fisheries, and ongoing otter occupation, particularly when considering the importance of the ongoing personal use and subsistence harvest of abalone. Though there are no data on pinto abalone populations before the commercial fishery, historical surveys during the fishery and before sea otter establishment provide a basis for our study comparisons. We investigated whether abalone populations recovered in the forty years following the fishery closure or if populations remained in decline as predicted. We also examined the extent to which re-established sea otter populations correlate with and potentially compound changes. Finally, we examine demographic shifts in abalone size that may be attributable to the intensive commercial fishery, the repatriation of sea otter populations, or some combination of both.

METHODS

Study area

For this study, historical sites originally surveyed sporadically by the Alaska Department of Fish and Game (ADFG) from 1978 to 1989 were resurveyed in 2016, 2019, and 2020 in southern Southeast Alaska, primarily in locations near Prince of Wales Island and Ketchikan (Figure 1.1, Chapter 1 Appendix Table A1.1). Precise site selections at locations were based on the history of commercial harvest and sea otter re-occupation, as well as logistical and safety constraints, such as accessibility, weather restrictions, the likelihood of survey completion, and the quality of the original survey data. Factors considered included dive sampler consistency, completeness of data records, frequency of resurveys, abundance at nearby sites, and the precision of location coordinates provided via nautical charts and LORAN records (ADFG unpublished data; see Appendix 1 in Donnellan and Hebert 2017). Prince of Wales Island sites were re-surveyed in three locations along the outer coast of Dall Island: in Meares Pass (n=10), and 2019 Gooseneck (n=4) and Port Bazan (n=5), and in Cordova Bay (n=5), north of the Barrier Islands and south of Hydaburg (see Figure 1.1). The four (total) historically established sites near Ketchikan, Alaska, were located on Gravina Island (Donnellan and Hebert 2017, White and Raimondi 2020, Table 1.1, Table A1.1).

Location attributes

The characteristics of site locations, including the histories of human harvest and reoccupation by sea otters, as outlined in Table 1.1, were integral to informing our understanding of human and otter impact on abalone populations (see Figure 1.1). Gravina Island location experienced the least commercial harvest with shorter commercial openings and fewer landings (see Table A1.1, ADFG 1975). Similarly, the fishery closed earlier in select areas of Cordova Bay, a Prince of Wales location (see site 85 in Table 1.1). In contrast, all other Prince of Wales locations, Meares Pass, Gooseneck, and Port Bazan, constituted 45% of the total commercial abalone harvest of the Southeast Alaska fishery (see Table A1.1). Sea otters were absent from study sites historically and remained functionally absent from Ketchikan the Gravina Island location (Table 1.1). In Prince of Wales sea otter populations grew slowly initially, expanding from their translocation sites (i.e., the Maurelle Islands N=51 and Barrier Islands N=55; Burris and McKnight 1973) at differing rates into study locations (Figure 1.1, Pitcher and Imamura 1990, Tinker et al., 2019, Eisaguirre et al., 2021, Schutte et al., 2023). By the late 1980s, nearer the end of the commercial fishery, sea otter populations were documented at commercially important abalone harvest locations, including the Cordova Bay location (Woodby et al., 2000, Hebert 2014).

Sea otter populations were not surveyed from 2011 to 2022, during a period of significant population growth, in Southeast Alaska (USFWS 2014, Davis et al., 2019, Schuette et al., 2023). Therefore, when sea otter occupation per study location could not be identified via sea otter population surveys (i.e., Pitcher 1989, Esslinger and Bodkin 2009, Hoyt 2015), sea otter occupation was determined with the best available expert information constituting the first sightings of otters and the year of known sea otter persistence (Table 1.1). Additionally, observations indicating sea otter presence made during ADFG red sea urchin (*Mesocentrotus franciscanus*) dive surveys were used to help identify occupation timing, which included records of large numbers of broken urchin tests, and spines, cracked clam shells and pits (primarily of geoducks), and the precipitous decline in red sea urchin abundance since last observed (Table 1.1; K. Hebert personal communication 2024). Beyond these key indicators of occupation, study locations were considered 'occupied 'following the establishment of viable populations across all survey sites in locations (e.g., otter rafts with pups, individuals that could consistently impact survey sites within locations) (see Table 1.1). Otter abundance during current survey periods were provided by USFWS via modeling of otter populations, applying the diffusion model developed by J. Eisaguirre et al. (2021), calibrated with 2022 otter aerial survey data of local areas of Sitka Sound (Schutte et al., 2023, see Table 1.1).

Sampling approach

Historical field sampling methods

Historical data used in this study were collected by the Alaska Department of Fish and Game (ADFG) through sporadic timed swim surveys twelve or more years into the dive fishery (ADFG unpublished data, Table 1). Divers collected all abalone they encountered, recorded their total underwater search time, and measured individual shell lengths at the surface (see Appendix 1. in Donnellan and Hebert 2017 for detailed method descriptions). These surveys provided information for comparison on size and abalone abundance or "count per minute" and surveys and the only fishery-independent surveys of abalone populations in Southeast Alaska.

Current-day sampling, historical deviations

During resurveys, dive tenders located historical sites and recorded the precise survey start coordinates, indicated by a pelican float deployed by divers. End site coordinates were recorded at the diver ascent location. Two divers partook in surveys and searched for abalone, non-invasively, in a zigzag pattern, shallow to deep, between a band of abalone habitat (depths from 1 to 10 meters) parallel to the shore. The non-sampling dive buddy kept time, pausing a timer during the measurement of abalone (see Donnellan and Hebert 2017). This method allowed for a consistent survey time of 20 minutes in 2019 and 2020 and 30 minutes in 2016. The *in-situ* measures, though different from the historical method of collecting abalone, were employed to avoid risks of cutting and mortally wounding abalone, which may occur with their removal (Cox 1962; Larson and Blankenbeckler 1979). An additional deviation from historical methods was the use of a single diver to survey abalone to reduce observer bias or survey skill bias, which are common issues with timed swim surveys (Andrew et al., 2000).

Abalone categories were examined separately based on survey practicality, harvest, or predation pressures related to distinct abalone sizes. Abalone were categorized by shell length(mm) into distinct classes: juvenile (≤ 41mm), sub-legal adult (> 41mm < legal(mm), identified herein as 'adult' abalone) and legal size (see Chapter 1 Appendix Table A1.1 for yearly minimum legal-size thresholds for both commercial and subsistence harvest). Classification of juvenile abalone is based on a size threshold below which individuals become cryptic or increasingly difficult for divers to identify regularly. The adult abalone size class includes larger individuals that may be the target of sea otters but remain below the minimum size limits set for historical commercial harvest and ongoing subsistence. These size classes do not correspond directly to maturity, though around 50% of pinto abalone mature at 50mm, some may mature at smaller sizes (i.e., 40mm referenced in Campbell et al., 2003). Finally, legally harvestable ('legal') sized abalone have historically been the target of both commercial and subsistence fisheries. However, after repatriation, sea otters may target legal and sub-legal-sized adult abalone, as predicted by optimal foraging theory. This theory suggests that to maximize energetic efficiency, predators may disproportionately target larger and more easily accessible, high-caloric value prey items, such as large abalone (Charnov 1976, Stephens and Krebs 1986, Kleiber 1961, Estes and Palmisano 1974, Ostfeld 1982).

Statistical approach

Our assessment and analyses were based on a combined dataset of newly acquired and historical timed swim data from sites in locations with historically intensive or moderate abalone fishery landings and varied sea otter occupation histories (as detailed in Tables 1.2 and A1.1). This data spread across these locations and survey periods facilitated the experimental structure for this study, wherein locations have both current and historical surveys and either experienced moderate or intensive commercial harvest (Table 1.2). Locations now either host sea otter populations or sea otter populations have yet to establish ecologically impactful populations (Table 1.2).

We used a generalized linear model (GLM with Poisson distribution, unbounded variance components) to assess change in abalone count per minute (CPM) across survey locations and by time periods, current (2016, 2019, and 2020) to historical (select years from 1978 – 1989, refer to Table 1.2). We also tested for combined effects of abalone abundance by time period across southern Southeast Alaska locations.

Initially, we incorporated survey sites as random effects nested within locations in a generalized linear mixed model with comparisons of the same effects. Still, site inclusion did not improve the model's explanatory power. Following GLM tests of total abalone abundance, we examined any significant interactions via contrasts of abalone CPM by size class between time periods (i.e., current and historical). To examine differences in the “shifting baseline” (described by Pauly 1995) of abalone populations originally surveyed during the commercial fishery, prior to sea otter recolonization, and test for shifts in sampled abalone size structures over time, we used Kolmogorov Smirnov (K-S) pairwise tests of shell length frequencies at locations between time periods. We examined size structure shifts across all locations with a focus on reduced legal-size classes of abalone and again for only locations in the current survey period with populations of sea otters. These comparisons tested for similarities in reduced large (not legal) and legal-sized abalone, theoretically more likely targeted by sea otter energy (prey search and size) optimization (see Charnov 1976, Stephens and Krebs 1986).

Since abalone are found to persist with and indirectly benefit from the presence of sea otter populations through their consumption of herbivore competitors like sea urchins (Raimondi et al., 2015, Lee et al., 2016), and given sea otters are shown to diversify target prey over time elsewhere (Estes and Duggins 1995, Tinker et al., 2006, 2008, 2012), otter impacts are likely less linear and more complex following sea otter re-occupation. We, therefore, examined linear and non-linear interactions between abalone and sea otter occupation (as defined in Table A1.1) through GLM models with a Poisson distribution and log link function. Initially, we examined quadratic relationships between abalone abundance (CPM), categorized by size class, and sea otter occupation time. In cases where statistical significance was not achieved with quadratic fits, we used linear fits for the respective size classes.

ArcGIS Online was used for mapping Figure 1.1, and JMP Pro18 was used in analyses and figures.

RESULTS

Changes in Abundance and Size Structure

Abalone abundance (CPM) decreased between time periods (Figure 1.2, Table 1.2) across locations with distinctly different sea otter influences and commercial harvest histories (refer to Table 1.1). Compared with historical survey abundances, current legal and adult abalone abundances were reduced (Figure 1.2, Table 1.2). Adult abalone were the only size class with different abundances across locations and the only size class affected by both time period and location (Table 1.2). When sites where otters remain absent were removed from comparisons (i.e., Gravina Island sites), there were no discernible differences in abalone abundance across locations (Table 1.2). Still, reductions in abalone abundance persisted over time (Table 1.2). As highlighted in Figure 1.2, location-specific contrasts of size class abundances revealed decreased adult abalone abundance at Meares Pass, Port Bazan, and decreased legal abalone at Gooseneck, Meares Pass, and Cordova Bay when compared across sampled time periods (Table A1.2). At Gravina Island, where sea otter populations remained functionally absent, there were insignificant increases in juvenile adult and legal abalone abundances over time (Table A1.2). Of all locations and size classes, the legally harvestable abalone abundance near Ketchikan remained the most unchanged across time periods (Figure 1.2, Table A1.2). Historically, legal abalone at Port Bazan were the lowest in abundance, just below historical levels at Gravina Island (see Figure 1.2). In contrast, current surveys did not record any legally harvestable abalone at Port Bazan (Figure 1.2). Although there is a clear difference in abundance across time periods (see Figure 1.2), contrasts rendered standard errors likely too high to determine significance (Table A1.1).

Size Structure Change

Across locations and time, abalone population size structures showed greater proportions of large and legal abalone during the commercial fishery (Figure 1.3), as indicated by dissimilarities in population size distributions in non-parametric K-S tests (Table 1.3a). The temporal shift towards smaller size classes was the least pronounced at Gravina Island, where sea otters were effectively absent during current survey periods and where abalone populations experienced relatively less commercial harvest (Figures 1.3 and Chapter 1 Appendix A1.1).

Harvestable abalone reductions

Proportions of legally harvestable abalone sizes are far reduced when compared to current locations. Surveys recorded a 58% decrease in abalone ≥89 mm (the current minimum size limit) at Gravina Island (see Table A1.3) and no legal abalone records during the current surveys at Gooseneck and Port Bazan, a 100% decrease from historical surveys (Table A1.3). Historically, half of the surveyed abalone in Cordova Bay would be considered legal by present-day minimum size limits (≥ 89 mm). However, during the current survey period less than 2% of legally-harvestable (≥ 89 mm) abalone were recorded at both Cordova Bay and Meares Pass (Table A1.3).

Sea otter occupation and abalone size structures

Historical abalone population size structures differed across locations prior to the repatriation of sea otters (i.e., Prince of Wales historical size frequencies in Figure 1.3, Table 1.3b). Comparisons of these locations in Prince of Wales surveys determined Meares Pass and Port Bazan had the most similar abalone size structures historically (Table 1.3b). Historical surveys in Cordova Bay, where fishery impact was moderate, documented abalone size frequencies that were least similar to other Prince of Wales locations (Figure 1.3, Table 1.3b).

Relationship between otter occupation time and abalone abundance

Locations with sea otter populations showed decreased adult and legal abalone abundance with increased sea otter occupation time (Figure 1.4, Table 1.4). The best-fit model of the relationships between abalone size class abundance (CPM) and sea otter occupation time, as determined in Table 1.1, revealed that adult and legal abalone CPM showed strong linear negative associations with increasing sea otter occupation time (Figure 1.4, Table 1.4). The model fit was slightly improved when using a quadratic model, particularly for adult abalone sizes as evidenced by a lower AICc value (see Table 1.4). However, juvenile abalone did not notably shift in abundance following years of otter repatriation. Models including all abalone sizes or those individuals ≥ 41 mm (i.e., adult and legal abalone) exhibited negative linear and non-linear responses to sea otter occupation time (Figure A1.1, Table A1.4). In both instances, non-linear models fit slightly better, with lower AICc values (Figure A1.1, Table A1.4).

DISCUSSION

Pinto abalone populations fundamentally changed following the peak of the commercial dive fishery and the later repatriation of sea otters to select locations in Southeastern Alaska. In those locations occupied by sea otters, abalone populations showed disproportionate decreases in size and abundance irrespective of the historical commercial harvest intensity. In contrast, despite the fishery closure four decades prior and significantly reduced personal use harvest limits for abalone, recent surveys of historical sites without sea otter populations (i.e., at Gravina Island location in Ketchikan) remained relatively unchanged from historical surveys (Figures 1.2 and 1.3). Across all resurveyed locations, with and without repatriated otter populations, size frequency comparisons showed fewer and smaller proportions of large and legally-sized abalone than historically recorded (Figure 1.3 and Table 1.3).

This study provides the most comprehensive comparison of historical and current pinto abalone populations in Alaska and, within reasonable bounds given available historical data, defines location-specific effects of commercial fishing and the re-establishment of sea otter populations. These findings underscore historical evidence of abalone population decline related to the commercial fishery in Southeast Alaska (Larson and Blankenbeckler, 1981, Mills 1982, Woodby et al., 2000), a trend associated with the commercial harvest of abalone elsewhere (Shepherd et al., 2001, Rothaus et al., 2008, Donnellan and Hebert 2017). Yet more novel, the study documents a decline in abalone abundance and size following the repatriation of sea otters to commercially harvested areas, a pattern seen with other invertebrate sea otter prey items (e.g., Estes and Duggins 2005, Larson et al., 2013, Hoyt 2015, Raymond et al., 2021).

Abalone populations in the absence of sea otters

Analyses of abalone population changes following the commercial fishery only focused on historical resurveys of sites at Gravina Island, where otters remain absent, as this location provides the best available assessment of the lasting human fishery effect. The distinctly unchanged abundances of legal abalone size classes between historical and current surveys suggest limited recovery despite “moderate” commercial fishery intensity and a shorter commercial harvest history than areas near Prince of Wales Island (Figure 1.2, Figure A1.1, Table A1.1). Notably, legal abalone did not increase in abundance as might be expected following a fishery closure. This may indicate a lasting or limited effect on the fishery or the ongoing impact of local subsistence harvest. Though size frequencies and proportions of recorded juvenile abalone at Gravina Island increased, it was a negligible amount from the historical surveys (Table A1.2), and it is important to note that it is unclear whether, during historical surveys, ADFG divers purposefully recorded small and juvenile abalone. Smaller abalone are often cryptic and likely not fully documented during timed swims. Therefore, juvenile abalone abundance may be a conservative measure, potentially underestimating historical abundances in both Gravina Island and Prince of Wales Island locations. As such, juvenile abalone counts may not accurately reflect historical recruitment limitations.

Otter presence and occupation effects

It is reasonable to anticipate some magnitude of effect on abalone populations following sea otter reoccupation, as is evidenced elsewhere (Hines and Pearse 1982, Watson 2000, Fanshawe et al., 2003). Consistent with this general expectation, measurable differences were found in legal and sub-legal adult abalone abundances between survey periods at locations with established otter populations (see Table 1.3, Figure 1.2). Changes in abalone abundance of this size (41 to 88mm) are important as they may not be legally targeted by commercial or subsistence harvesters, yet they provide sea otters with calorically rich abalone sought after to maximize energy gains (Charnov 1976, Stephens and Krebs 1986). However, there was no difference in adult abalone abundance when sites at sea otter-free Gravina Island were excluded from modeled comparisons (see Prince of Wales comparisons in Table 3), indicating a similarity among sea otter-inhabited Prince of Wales locations of reduced abundances of non-legal sizes. Considering the complexity of regional environmental factors and the diverse predator and competitor dynamics at play across locations, the notably pronounced differences and declines in abalone abundances in areas inhabited by sea otters suggest that their presence may have played a role in further diminishing already depleted abalone populations following the commercial fishery (Figure 1.3, Table 1.3, Table A1.3).

Before the first timed swim surveys were conducted near Prince of Wales Island, subsistence harvesters reported the disappearance of abalone or their decline below harvestable size at traditional sites (Mills 1982). Comparisons of population size structures before sea otter occupation revealed distinct differences, with heavily fished locations being more alike than moderately fished locations (e.g., Cordova Bay; Figure 3). In areas where sea otters were absent, years before the 1979 closure of the fishery, population samples from three undisclosed sites around Ketchikan, without sea otters, showed similar declines in large and legal abalone (Larson and Blankenbeckler 1979). These unpublished data were collected before timed swims were initiated in the area (1976) and described populations with 16% of abalone above 102mm, the commercial harvest limit at the time, and 57% of abalone above 89mm, the subsequent minimum size limit (Larson and Blankenbeckler 1979).

Harvest history and otter occupation

As predicted, we found that abalone abundance declined with increased occupation time of sea otters (Table 1.1, Figure 1.4). Models for non-linear relationships of adult and legal-size classes, both separately and combined (Chapter 1 Appendix Table A1.2), had stronger quadratic responses to increased otter occupation time based on AICc values (Table 1.4). The pattern of decreased adult and legal abalone abundance at sites with the shortest re-establishment time of otters (Figure 1.4), followed by a slight increase in abundance, aligns with findings of otter prey specialization, where otters may diversify and shift target prey items (Tinker et al. 2006; 2008; 2012; Estes and Duggins 1995) and indirectly assist abalone in the removal of herbivorous competitors such as sea urchins (Raimondi et al. 2015; Lee et al. 2016). In both size classes, otter occupation time may help to remove barriers to population growth. However, in this study, the sites with the most recent otter occupation and the greatest reductions in abalone abundance correspond to locations with the most intensive historical fishery landings (see light blue markers indicating historically high harvest in Figure 1.5 and

Figures A1.3 and A1.4). Additionally, historical notes suggest that surveys conducted at commercial harvest sites, some from post-harvest commercial dive vessels, may have been biased toward areas of lower abundance (see Appendix 1 in Donnellan and Hebert 2017).

Inherent limitations of historical comparisons

Given that our survey results were conducted decades after the historical surveys, this study is necessarily limited in its ability to analyze trends following the closure of the abalone fishery. The historical surveys represent an already 'shifted baseline' (e.g., Pauly 1995), and the historical abundances and sizes should be considered a conservative representation of the pre-fishery population level as historical surveys were conducted by ADFG researchers during the periods of most intensive harvest (1978 – 1981) or immediately following (1982 – 1988, Figure 1.1). Historical surveys were not established initially with an experimental design in mind and certainly not with a knowledge of the trajectory of local commercial harvest and the pattern of sea otter expansion. While such comparisons have inherent limitations, they provide insights into understanding trends in abalone populations following sea otter reestablishment and commercial harvest.

Without area estimates, timed swim survey methods are not directly comparable to conventional density measures (Shepherd 1985), and timed swims are more subject to observer bias (Andrew et al., 2000). Timed swims were the historical method; therefore, efforts were made to reduce bias, and one diver dove all surveys. Notably, when compared to sizes recorded along density transects at the same sites (see Chapter 2), we found both methods captured the same location frequencies (Chapter 1 Appendix). This suggests timed swims may be a useful alternative to density transects described in Chapter 2 to document population size structure (Chapter 1 Appendix).

Implications for abalone populations in Alaska

Abalone populations near Ketchikan have not recovered despite the lack of sea otters, closure of the commercial fishery, and reductions to the subsistence, personal use bag limit. These populations do not appear to suffer from "Allee effects" (i.e., a sizable loss of mature individuals that reduces, then prevents population fertilization success), as the current juvenile abundance signifies some reproductive and recruitment successes (Allee et al., 1949, T. White unpublished data). Poaching has been a significant issue elsewhere, such as in British Columbia (Zhang et al., 2007); however, based on the scarceness of State Trooper citations (K. Ferguson personal communication, 2023), it does not appear to be a major concern in the Ketchikan area. Instead, it seems more likely that the abundance and size distribution in the Ketchikan area has been and continues to be driven partly by legal subsistence harvest or personal use harvest. Another possibility is that the scarcity of algae for abalone to consume in the Ketchikan area may contribute to limiting abalone population growth. Less algae may be due to a large red sea urchin population that competes with abalone. In stark contrast, Prince of Wales Island survey sites were in areas with large sea otter rafts and abundant with a diversity of overstory and understory algae. Lee et al. (2016) found that sea otter populations in Haida Gwaii, Canada, facilitate abalone persistence at low densities by indirectly promoting abalone habitat and food (i.e., Macrocystis forests). Similar effects of sea otters on abalone abundance and size have been found in other areas where sea otters and abalone continue to co-exist (Lee et al., 2016, Lowry and Pearse 1973). Further ongoing surveys would be required to understand whether sea otters indirectly support Prince of Wales abalone populations at significantly reduced densities and whether Ketchikan populations remain stagnant due to competition with urchins for food. Though Ketchikan populations show no signs of growth and Prince of Wales current populations have experienced compounded effects of both the fishery and sea otter reestablishment, there has been some recruitment at each area, as juvenile abalone (<41mm) have been recorded in each location. The limited recovery despite fishery management efforts highlights the necessity for a more comprehensive understanding of the factors influencing abalone populations and their capacity to rebound.

Yet unknown otter impact

Though sea otters are known predators of abalone (Fanshawe 2003, White and Raimondi 2024), the extent to which sea otters in Alaska favor abalone remains uncertain, as in Southeast Alaska few observations of sea otters actively eating abalone exist, which may likely be the result of the region's remoteness, and that studies of sea otter prey items were surveyed in areas of low abalone density (Hoyt 2015, LaRoche 2020, same data, recorded no new abalone). Still, sea otters are found to substantially reduce (by 26%) species like sea cucumber, which are < 5% of their known diet (Larson et al. 2013), and are implicated in large impacts on red sea urchin and geoduck populations. Southeast Alaska abalone populations are likely vulnerable to sea otter predation, particularly as the sea otter population is predicted to grow and expand into new areas of Southeast Alaska (Tinker et al., 2019). Growing numbers of sea otters were observed in the Ketchikan area in 2023, marking their return after an absence of over 140 years (K. Hebert, unpublished data). Considering this study's findings, and irrespective of any potential indirect benefits sea otters may offer abalone populations (e.g., Raimondi et al., 2015 Lee et al., 2016), the re-establishment of sea otters in the Ketchikan area is likely to bring about significant changes in abalone populations. This is particularly relevant for populations that continue to provide for human harvest following fishery impacts. Consequently, additional monitoring surveys to document sea otter prey preferences and factors stemming from the rapidly changing environment (i.e., ocean acidification, salinity, and temperature changes), and changes to other mesopredators (e.g., sea stars) over time would significantly enhance our understanding of local effects, especially as sea otters inevitably repopulate areas around Gravina Island and south to Annette Island, where there are additional historical population data (ADFG unpublished data).

In conclusion, this study underscores the legitimacy of concerns regarding declining populations during the commercial fishery (ADFG 1976, Larson and Blankenbeckler 1981, Mills 1982), even before sea otter expansion into these areas. Current abalone populations near Ketchikan, where sea otters have yet to establish, do not appear to have benefitted from over 40 years of fishery closures (i.e., Gravina Island closure in 1979) or subsequent management efforts (i.e., permitting requirements, harvest amount, and harvest technique limitations). Importantly, adult abalone abundance changed over time and differed across otter-occupied locations, which suggests an interplay of commercial harvest (i.e., temporal) and otter (i.e., location) impact.

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TABLES

Table 1.1. Timed swim survey regions, locations, and site survey years later divided for analyses as either historical or current survey time periods. Sea otter occupation range denotes the range of years from “first sign” to “estimated occupation.” Sea otter first sign indicates the first known record of otter presence in a location when otters are present but have negligible or no impact on prey populations, as recorded during urchin and sea cucumber surveys (ADFG unpublished data). Estimated otter occupation is a conservative measure indicating the establishment of viable populations across all survey sites in locations (e.g., otter rafts with pups, individuals that could consistently impact survey sites within locations) and based on aerial surveys, denoting otter occupation (Pitcher 1989, Esslinger and Bodkin 2009, USFWS 2014, Hoyt 2015), or presence with notable prey absence (ADFG unpublished data). Commercial harvest impact is either moderate or high and indicates differences at locations in historical abalone landings (refer to Table A1 for values). Modeled estimated otter abundance (kg^2) based on 2022 aerial surveys (Eisaguirre et al., 2022, Schutte et al., 2023). Study sites at locations are a sample of the 141 sites surveyed from 1977 to 1995, (ADFG unpublished data)

Region	Location	Site ID	Years of Site Survey	First Otter Sign	Re-occup. Range	Est. Occup.	Occupation (yrs)	Est. otter abundance (IQR)	Commercial Harvest Intensity	Tests
Prince of Wales	Meares Pass	16, 18, 20, 23, 24, 102	1981, 1986, 2016	2004[†] (2010[‡])	2004 – 2007[†]	2007	9	0.067 (0.08)	High	ALL
	Meares Pass	17, 19, 21, 22	1981, 2016	2004[†] (2010[‡])	2004 – 2007[†]	2007	9			ALL
	Cordova Bay	42, 51	1981, 2019	2003[§]	2003[§]	2003	16	0.030 (0.033)	Moderate	ALL
	Cordova Bay	54	1979, 1981, 1986, 2019	2003[§]	2003[§]	2003	16			ALL
	Cordova Bay	83	1979, 1983, 2019	2003[§]	2003[§]	2003	16			ALL
	Cordova Bay	85[**]	1979, 1983, 2019	1988[||]	1989[||]	1989	30			K-S, non linear
	Gooseneck	95 ,96, 97	1980, 1986, 2019	2005[†]	2011[†] – 2014[¶]	2011	8	0.042 (0.042)	High	ALL
	Gooseneck	100	1980, 2019	2005[†]	2011[†] – 2014[¶]	2011	8			ALL
	Port Bazan	2, 3, 4, 5, 6	1979, 2016	2005[†]	2011[†]– 2014[¶]	2011	8	0.036 (0.04)	High	ALL
Ketchikan	Gravina Island	1,9,10,14,15,16, 24,26	2016	absent					Moderate	K-S, nonlinear
		105	1978, 1979, 1980, 1981, 1989, 2020							ALL
		106	1980, 2020							ALL
		107*	1979, 2020							K-S
		108	1979, 2020							ALL

* Site #107 was included in KS, but not abalone abundance (CPM) tests, as critical data (survey time) were missing for abundance calculations

†Otter presence and effect notation during area dive rotations (1995 – 2011 of Red Urchin sample sites (K. Hebert pers. comm. or unpublished ADFG data)

‡ First documented by aerial survey (USFWS 2014)

§ Esslinger and Bodkin 2009

|| Pitcher et al.1989

¶Hoyt 2015

Table 1.2. Results for a Generalized Linear Model (GLM) examining the effects of sampled time period (current or historical) and location (see Table 1.2) on abalone "CPM" (Count per Minute) abundance. Tests were done with all abalone and abalone size classes: juvenile (< 41mm), adult (≥ 41 < legal), and legal abalone for harvest (see Table A1.1 for minimum legal subsistence size limit by year). See Table A1.2 for contrasts of size classes per location by time period.

	All Locations				**Prince of Wales Locations**		
Size	**Effects**	**df**	**L-R ChiSquare**	**Prob>ChiSq**	**df**	**L-R ChiSquare**	**Prob>ChiSq**
All	Time Period	1	22.06115	<.0001*	**1**	54.12	<.0001*
	Location	4	15.89476	0.0032*	3	8.6668	0.0341*
	*Time Period*Location*	4	27.14472	<.0001*	3	10.3227	0.0160*
Juvenile	*Time Period*	1	1.72033	0.1897	1	0.6077	0.4356
	Location	4	3.04863	0.5497	3	2.9986	0.3918
	*Time Period*Location*	4	4.51807	0.3404	3	2.2343	0.5252
Adult	*Time Period*	1	21.02066	<.0001*	1	26.9258	<.0001*
	Location	4	16.38559	0.0025*	3	2.2115	0.5297
	*Time Period*Location*	4	23.82959	<.0001*	3	6.1492	0.1046
Legal	*Time Period*	1	9.75766	0.0018*	1	11.6163	0.0007*
	Location	4	3.20305	0.5244	3	0.2321	0.9722
	*Time Period*Location*	4	5.28806	0.259	3	0.0776	0.9944

Table 1.3. Pairwise Kolmogorov-Smirnov (K-S) tests comparing abalone size frequency between historical and current survey periods at southern Southeast Alaska locations, and K-S tests of size frequencies from historical surveys of locations that now host sea otter populations. Refer to Table 1.1 for detailed location characteristics.

(*a*) contrasts of abalone size structures across surveyed time period per location (site 85 included)

Location	**Time Period (F1)**	**Time Period (F2)**	**KS**	**KSa**	**D=max|F1-F2|**	**Prob > D**	**D+=max(F1-F2)**	**Prob > D+**	**D-=max(F2-F1)**	**Prob > D-**	**Count (F1)**	**Count (F2)**	**Edf (F1)**	**Edf (F2)**
Meares Pass	Historical	Current	0.130	6.187	0.545	<.0001*	0	1	0.545	<.0001*	2128	137	0.214	0.759
Gooseneck	Historical	Current	0.153	4.474	0.514	<.0001*	0	1	0.514	<.0001*	767	84	0.248	0.762
Port Bazan	Historical	Current	0.165	3.643	0.544	<.0001*	0	1	0.544	<.0001*	440	50	0.136	0.68
Cordova Bay	Historical	Current	0.277	5.863	0.713	<.0001*	0	1	0.713	<.0001*	365	83	0.203	0.916
Gravina Island	Historical	Current	0.228	9.320	0.461	<.0001*	0	1	0.461	<.0001*	709	966	0.197	0.658

(*b*) KS pairwise tests of abalone size structures between Prince of Wales locations, within the historical survey period. Meares Pass, Gooseneck, and Port Bazan experienced the highest historical harvest across the southeast fishery, and Cordova Bay had less harvest (see Table A1.1)

Time Period	**Location (F1)**	**Location (F2)**	**KS**	**KSa**	**D=max|F1-F2|**	**Prob > D**	**D+=max(F1-F2)**	**Prob > D+**	**D-=max(F2-F1)**	**Prob > D-**	**Count (F1)**	**Count (F2)**	**Edf (F1)**	**Edf (F2)**
Historical	Meares Pass	Gooseneck	0.047	2.509	0.106	<.0001*	0.106	<.0001*	0.014	0.8126	2128	767	0.192	0.086
	Meares Pass	Port Bazan	0.024	1.212	0.063	0.1058	0.034	0.4258	0.063	0.0529	2128	440	0.505	0.568
	Meares Pass	Cordova Bay†	0.086	4.191	0.272	<.0001*	0.272	<.0001*	0.003	0.9962	2128	267	0.537	0.255
	Gooseneck	Port Bazan	0.051	1.786	0.107	**0.0034***	0.002	0.9966	0.107	**0.0017***	767	440	0.248	0.355
	Gooseneck	Cordova Bay†	0.106	3.408	0.242	<.0001*	0.242	<.0001*	0.004	0.9934	767	267	0.587	0.345
	Port Bazan	Cordova Bay†	0.160	4.246	0.329	<.0001*	0.329	<.0001*	0.000	1	440	267	0.584	0.255

*Indicates significant difference between cumulative distribution functions (CDFs), and reduced likelihood of stemming from a similar distribution.

†: Site (#85) removed to maintain historical comparison among sites without otter presence. Inclusion site survey years without otter occupation increase, already significant analysis results.

Table 1.4. Results of linear and non-linear Generalized Linear Model (GLM) analyses both with Poisson distribution and log link functions. Models assess the relationship between sea otter occupation (in years see Table 1.2) and abalone abundance, represented as the count per minute (CPM) by size classes: juvenile (< 41mm), adult (≥ 41mm), and legal (see Table 1.1 for minimum legal size per year)). For quadratic modeling and to reduce multicollinearity, occupation years were corrected via centering transformation by −3.92188 years. See Appendices Table A1.2, Figure A1.2 for adult and legal and total abalone size class comparisons. Parameter estimates of the relationship between sea otter occupation and abalone abundance for each size class and parametric model.

Size Class	Model Type	Predictor	Estimate	Std Error	L-R ChiSquare	Lower CL	Upper CL	Prob>ChiSq
Juvenile	*Linear*	Intercept	-1.390	0.300	34.207	-2.031	-0.849	<.0001*
		Occupation	0.001	0.042	0.001	-0.094	0.072	0.9745
	Non-linear	Intercept	-1.359	0.290	34.779	-1.987	-0.838	<.0001*
		Occupation	-0.038	0.065	0.365	-0.179	0.081	0.5458
		(Occupation corr.)^2	0.003	0.003	0.679	-0.005	0.010	0.4098
Adult	*Linear*	Intercept	1.100	0.091	105.031	0.916	1.273	<.0001*
		Occupation(yrs)	-0.187	0.033	56.613	-0.258	-0.127	<.0001*
	Non-linear	Intercept	0.989	0.093	88.485	0.803	1.170	<.0001*
		Occupation(yrs)	-0.233	0.040	55.684	-0.321	-0.160	<.0001*
		(Occupation corr.)^2	0.008	0.003	6.471	0.002	0.013	0.0110*
Legal	*Linear*	Intercept	-0.482	0.201	6.789	-0.904	-0.112	0.0092*
		Occupation(yrs)	-0.520	0.300	21.570	-2.019	-0.186	<.0001*
	Non-linear	Intercept	-0.774	0.387	0.667	-2.154	3.093	0.4141
		Occupation(yrs)	-0.561	0.342	16.190	-2.475	-0.188	<.0001*
		(Occupation corr.)^2	0.019	0.022	0.226	-0.232	0.107	0.6342

Goodness-of-Fit Statistics for overall model type by size class.

Size Class	Model Type	Predictor	AICc	-LogLikelihood	L-R ChiSquare	df	-2 Log-Likelihood (Prob>Chi Sq)	Model Significance
Juvenile	*Linear*	Occupation(yrs)	79.525	0.001	0.001	1	0.9745	No
	Non-linear	(Occupation corr.)^2	81.049	0.340	0.681	2	0.7116	No
Adult	*Linear*	Occupation(yrs)	231.957	28.307	56.613	1	<.0001*	Yes
	Non-linear	(Occupation corr.)^2	227.689	31.542	63.084	2	<.0001*	Yes
Legal	*Linear*	Occupation(yrs)	86.774	10.785	21.570	1	<.0001*	Yes
	Non-linear	(Occupation corr.)^2	88.751	10.898	21.796	2	<.0001*	Yes

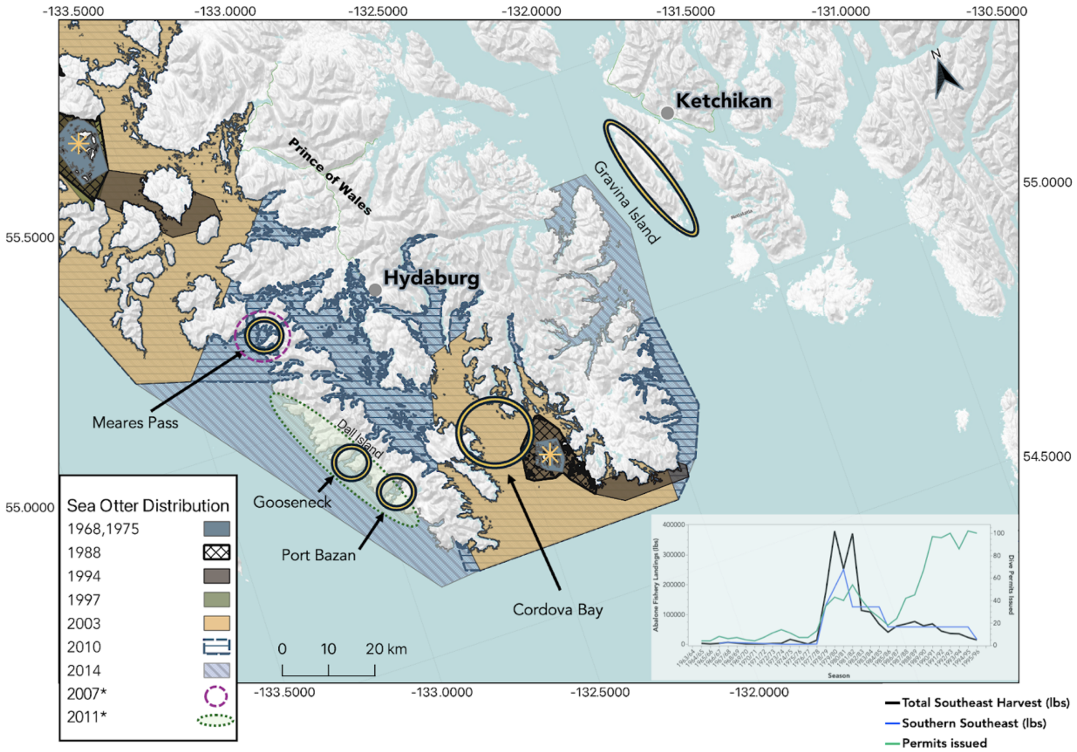

Figure 1.1. Map of southern Southeast Alaska survey locations with regional sea otter distribution, historical commercial fishery harvest, and diver participation. Locations of timed swim re-surveys are labeled and circled (in yellow) in both Prince of Wales (otter occupied) and Ketchikan (otter unoccupied) regions. Sea otter translocation (1968) sites are indicated by yellow asterisks and include the Maurelle Islands to the north (N=51) and the Barrier Islands to the south (N=55). The graph (bottom right) displays abalone fishery landings (as reported in lbs) for the period of commercial abalone harvest in Alaska (1964 to 1996), with harvest from all of Southeast (in black) and southern Southeast Alaska (in green); diver permits are plotted on y-axis in blue (adapted from Woodby et al., 2000). Refer to Table 1.1 for the number of sites and years of site surveys per location, relative historical harvest intensity, and sea otter abundance estimates during years of historical re-survey (2019 or 2016). For additional and updated (from Neuman et al. 2018) commercial harvest metrics, see Table A1. Map created using the Free and Open Source QGIS. Sea otter occupation references: Burris and McKnight 1973; Pitcher 1989; Esslinger and Bodkin 2009; USFWS 2014, Hoyt 2015; K. Hebert personal communication 2024.

*Location-specific years of known sea otter persistence prior to aerial survey confirmation; first sign and occupation periods for all locations are detailed in Table 1.1.

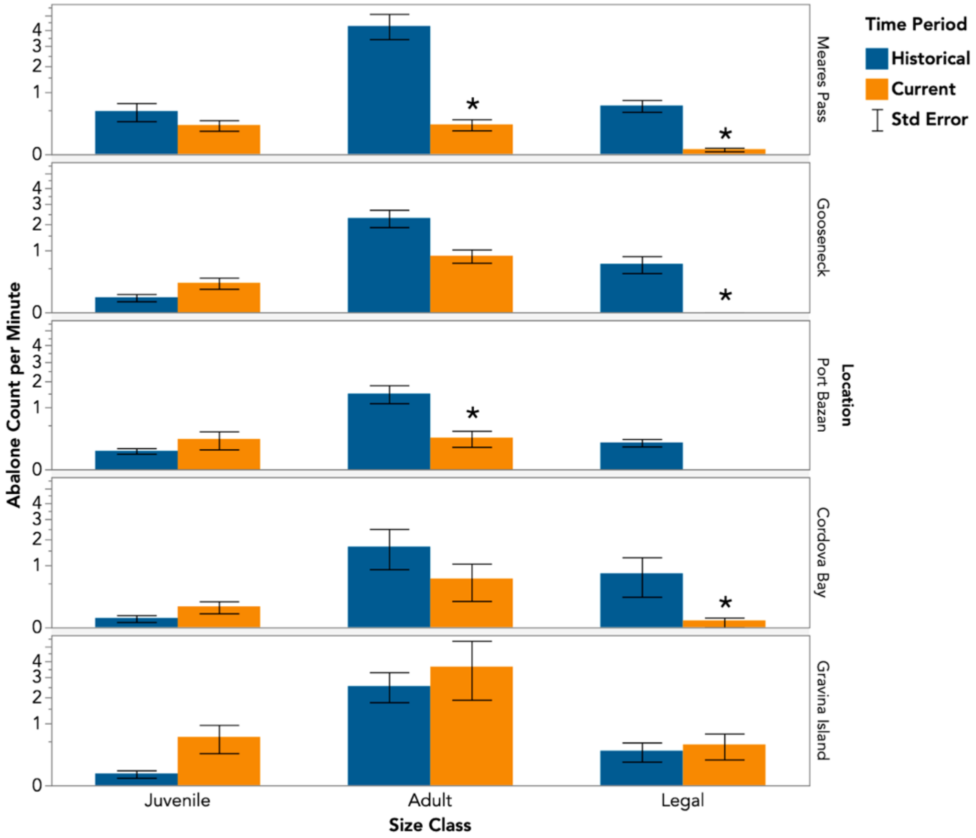

Figure 1.2. Abalone count per minute (CPM), recorded during timed swims across locations: Port Bazan, Gooseneck, Meares Pass, Cordova Bay (Prince of Wales Region), and Gravina Island (Ketchikan Region), and time periods: historic, during the abalone commercial dive fishery (in blue) and current survey, which is a period following fishery closure and sea otter re-establishment in all locations except Gravina Island (in orange), and abalone size classes: juvenile (≤ 41mm), adult (> 41mm < legal size(mm)), and legal size (see Table A1 for minimum legal sizes per survey year). Displayed on square–root scale y-axis.

* Indicates significance between current and historical time periods for location abalone size class abundance. Refer to Table A1.2 for contrasts.

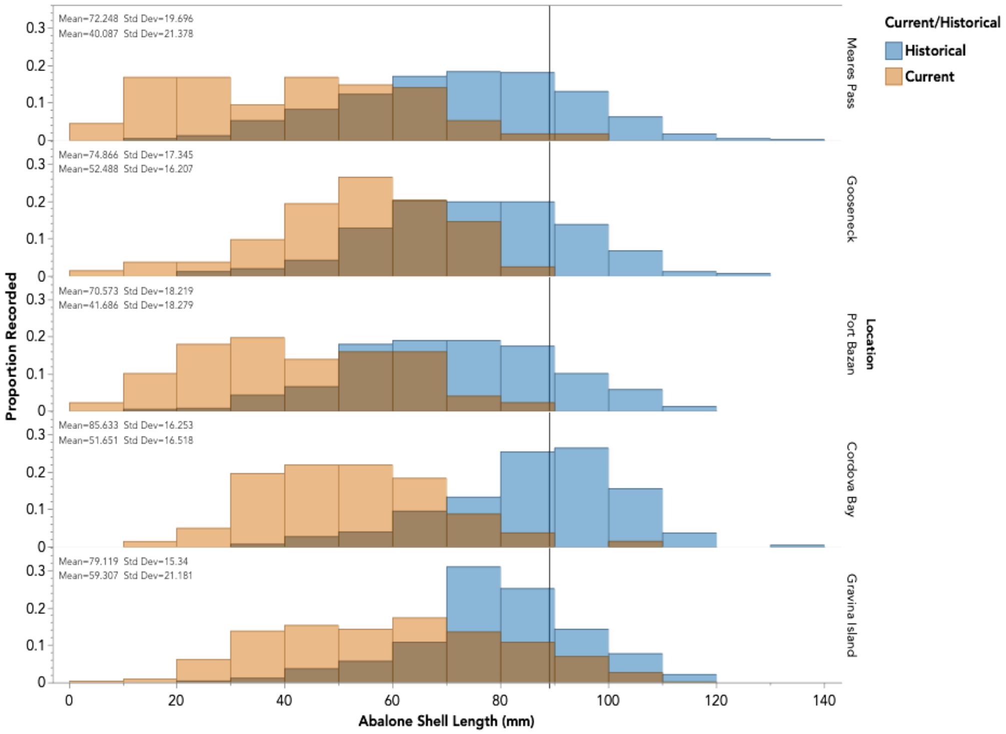

Figure 1.3. Proportions of abalone shell lengths recorded during current (2016, 2019, and 2020; shown in orange) and historical (1978 – 1989; shown in blue) timed swim surveys at select locations in southern Southeast Alaska. The vertical line at 89 mm indicates the current minimum legal size limit for subsistence. The commercial harvest minimum size limit was 95mm for most historical surveys (see Table A1.1). All distributions are distinctly different when compared across time by location, as shown in Kolmogorov-Smirnov (KS) pairwise tests (Table 1.3a).

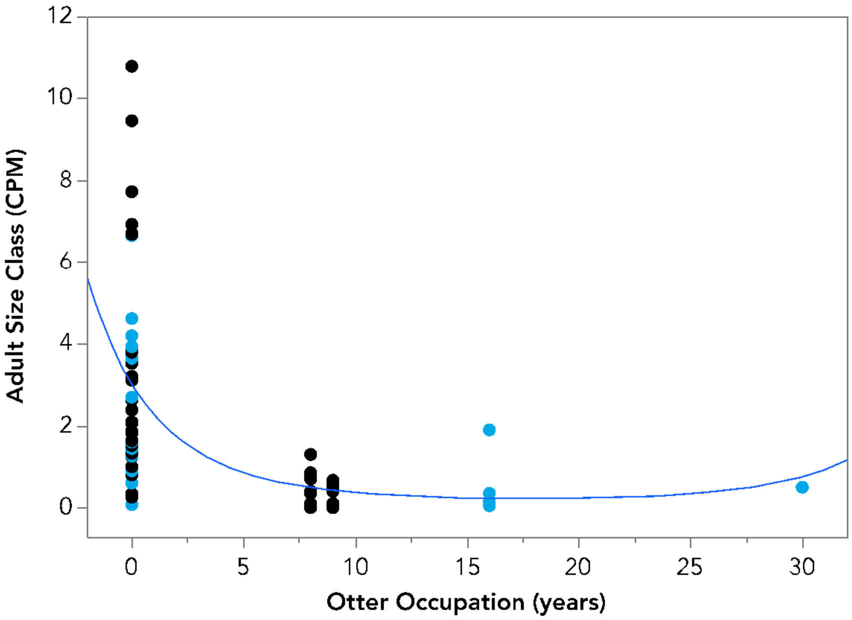

Figure 1.4. Regression of mean adult abalone counts per minute (CPM) recorded at sites during current and historical timed swim surveys as a function of estimated otter occupation (see Table 1.1). Sites with a history of high commercial harvest are marked in grey, and sites with moderate commercial harvest are in blue. Refer to Table 1.4, Table A1.4 for iterations of linear and non-linear GLM model comparisons of additional size classes of abalone CPM abundance as a function of otter occupation.

CHAPTER TWO
REGIONAL AND LOCAL PINTO ABALONE POPULATION DEMOGRAPHY AND REPRODUCTIVE CAPACITY IN SOUTHEAST ALASKA

CHAPTER 2. Regional and Local Pinto Abalone Population Demography and Reproductive Capacity in Southeast Alaska.

ABSTRACT

Abalone have local ecological, cultural, and economic significance worldwide, yet are very vulnerable to overharvest. Closures of abalone fisheries along the Pacific coast of North America due to population depletion reflect this vulnerability. Pinto abalone (Haliotis kamtschatkana) populations in Alaska are unique as they are the only remaining abalone population in the U.S. with allowable subsistence harvest. Following the closure of the commercial abalone dive fishery in Alaska, pinto abalone populations have been uniformly managed but continue to experience differing threats across their northernmost range, including ongoing subsistence harvest and expanding sea otter populations. Our study provides the most comprehensive assessment of pinto abalone population densities, reproductive capacities, and factors associated with visible recruitment at select sites across Sitka, Prince of Wales, and Dixon Entrance regions of Southeast Alaska. Following dive surveys in 2018 and 2019, we recorded dramatic differences among mean regional abalone densities, with the lowest densities recorded at sites in the Prince of Wales region. Still, we recorded recruitment at all three Southeast regions and pre-settlement effects contributing to recruitment variability at local scales. Abalone population densities, not size, were the best predictors of population fecundity, and increased densities corresponded to increased probabilities of being near an abalone of the opposite sex, thereby highlighting the importance of density across Southeast Alaska abalone populations. Irrespective of density, abalone populations were highly aggregated, which suggests an increased probability of successful fertilization during spawning. Sites with adult abalone densities of 0.5 to 0.6

adults/m^2 or higher maintain the highest probabilities of reproductive success. However, adult abalone aggregation significantly affected juvenile recruitment, whereby sites with denser aggregations of adults had fewer recruits. Regional differences in abalone density and local effects on recruitment suggest that identifying spatially specific, local biotic and abiotic effects and managing these at a local scale will support overall abalone population viability in Alaska.

INTRODUCTION

The overexploitation of modern abalone fisheries across the world is often cited as the reason for the precipitous population declines of abalone, including pink (*Haliotis corrugata*), green (*H. fulgens*), black (*H. cracherodii*), and white (*H. sorenseni*) abalone species in California (Karpov et al., 2000 Rogers-Bennett et al., 2002), greenlip (*H. laevigata*) in Australia (Shepherd and Partington 1995), Omani abalone (*H. mariae*; Al Jufaili et al., 2022), and pinto abalone, *H. kamtschatkana*, in British Columbia (Atkins et al., 2004), Washington (Rothaus et al., 2008), and Alaska (Woodby et al., 2000, Hebert 2014). Common approaches to mitigating such decline include fishery closures Yet despite these closures, abalone populations often do not recover, as demonstrated in the sport fishery closure in Washington (Rothaus et al., 2008, Carson and Ulrich 2019) and commercial fisheries in California (Karpov et al., 2000, Rogers-Bennett et al., 2002, Rogers-Bennett 2007).

These fisheries disrupted the two linked abalone life history attributes essential to local abalone population recovery and viability: abalone density and neighbor distance. The declines of fished abalone led to research focused on relationships between adult abalone densities and aggregations promoting population viability (i.e., Shepherd and Partington 1995, Hobday et al., 2000, Karpov et al., 2000, Rogers-Bennett 2007, Seamone and Boulding 2011). As dioecious broadcast spawners, abalone experience increased probabilities of fertilization with increased aggregation (Sloan and Breen 1988). Therefore, local recruitment is typically positively related to the local population density (Prince et al., 1988, McShane 1992). This concept that adult abalone densities determine recruitment densities is most true for "closed" species populations, with little or no dispersal, yet less common for species like abalone with complex bipartite life histories. In the case of abalone, following the successful fertilization of broadcast spawn, recorded planktonic periods are relatively short (5 to 10 days) (McShane 1992, Miner et al., 2006). Planktonic abalone "veliger" are negatively buoyant and poor swimmers, suggesting limited dispersal from abalone spawn sites (Shepherd and Brown 1993, Tegner 1993, Tegner and Butler 1985, Prince et al., 1987, McShane 1992).

Populations with low densities of mature individuals, without individual aggregation, are assumed to have greater distances between potential mates, thereby reducing gamete fertilization successes. Populations at low densities risk reproductive failure and may succumb to the "Allee Effect" past a critical density threshold (Allee 1931). This threshold was originally demonstrated for a different species, a sea urchin, *S. purpuratus*, when eggs of spawning individuals over 1 meter apart had a <10% possibility of fertilization (Pennington 1985), yet the "Allee threshold" (Rothaus et al., 2008) is often applied to abalone. Still, hydrographic modeling (Abelson and Denny 1997) and empirical evidence from other dioecious, broadcast-spawning invertebrates support the idea of density-dependent fertilization success and, more directly, a non-linear negative relationship between fertilization probability and the distance between spawning adults of the opposite sex (Denny et al., 1985, Sloan and Breen 1988).

Potential Allee effects in abalone species are most often inferred through observed recruitment failure. An exception to these anecdotal thresholds involved greenlip abalone (*Haliotis laevigata*) *in situ* fertilization testing (Babcock and Keesing 1999). Researchers found a 50% fertilization success when spawning adults were placed within two meters (Babcock and Keesing 1999). Separate density surveys of previously fished *H. laevigata* populations found recruitment failure between a range of densities below 0.15 to 0.3/m^2 and nearest neighbors between 1 to 2 meters (Shepherd and Partington 1995). The "critical" densities and distances between abalone recorded on *H. laevigata* long-term surveys were comparable to fertilization success densities and distances found through in situ and lab fertilization experiments (see Babcock and Keesing 1999). The 0.2/m^2 threshold used by the California Department of Fish and Wildlife in red abalone management conservatively splits the range of other species' fertilization and recruitment thresholds of 0.15 to 0.30 abalone/m^2 (Tegner et al., 1989, Shepherd and Brown 1993, Shepherd and Partington 1995, Karpov et al., 1998, CDFW 2005). Therefore, such "critical" densities of adults define a foundation for density-dependent recruitment failure and are often a proxy for fertilization probabilities via measures of adult nearest-neighbor distances (NND).

Our focus abalone species, pinto abalone (*H. kamtschatkana*), have the largest latitudinal range of any abalone species, with individuals commonly described as the same species from Baja California to Southeast Alaska (Geiger 2000). Pinto abalone populations exhibit varied demographic, recruitment, and dispersion patterns throughout their range. The species has been under-studied to date, and no density patterns of NND thresholds have been demonstrated across their range. Due to unknown critical densities for pinto abalone, managers have had to adopt fertilization success thresholds from other species. This was true for the Washington Department of Fish and Wildlife (WDFW) abalone recovery plan, which aims for densities of 0.3 abalone/m^2 (see Sowul et al., 2021), borrowing from the upper limit of fertilization threshold determined for *H. laevigata* in Australia (Babcock and Keesing 1999).

Southeast Alaska is a very large region, and pinto abalone populations experience different harvest pressures throughout the area, yet uniform limits for personal use harvest persist. Continued population decline and perceived threats of combined sea otter consumption and human harvest of pinto abalone in areas across their range prompted petitions to shift the definition of pinto abalone from a "Species of Concern" (69 FR 19975) to "Endangered" under the Endangered Species Act (NOAA 2004). This follows the species listing in 2006 as "Endangered" by the IUCN List of Endangered Species (McDougall et al., 2006). The key issue cited by the IUCN in their 2006 review of the species was a lack of current, comprehensive data on the species demography, particularly in Alaska (McDougall et al., 2006).

To remedy the paucity of data concerning pinto abalone populations across Alaska and determine the extent of abalone demographic parameter uniformity implied by spatially uniform harvest regulations, we used a spatially nested design to examine demographic and viability parameters across Southeast Alaska. Specifically, we assess relationships between recruitment, adult density, and neighbor distance. We investigate whether population size structure or density better predicts abalone fecundity density (i.e., number of eggs per meter square) in Southeast regions. Our study provides crucial insights into the current status and trends of pinto abalone at the northernmost extent of their range.

METHODS

Study regions

Southeast Alaska is a dynamic system shaped by complex landscapes and ecology, alongside communities with diverse histories that continue to subsist and adapt to the ever-changing ecosystem (Arland et al., 1974). To address questions on the status and structure of pinto abalone at their northern range limit of Southeast Alaska, we examined populations through a spatially nested design, with regions (Sitka, Prince of Wales, and Dixon Entrance) as the largest scales of comparison (see Figure 2.1). In the three study regions, we established density transects for abalone population surveys in sites of known current and historical abalone populations.

Regional, location histories

These regions differ in their commercial and ongoing abalone harvest histories, and each is at a distinctly different stage of sea otter repatriation (see Figure 2.1; ADFG 2020). The Prince of Wales study region had the most recent (10 to 8 years) established sea otter populations (USFWS 2014, Hoyt 2015, Tinker et al., 2019, K. Hebert personal communication 2023). The two study locations at Prince of Wales, Gooseneck and Port Bazan, small bays on the otherwise exposed outer coastline of Dall Island, were historically the locations of the largest commercial harvest landings (Woodby et al., 2000, Figure 2.1). The Dixon Entrance region encompasses the southernmost islands in Southeast Alaska and is named for the body of water that divides Canada (Haida Gwaii, south) and Alaska (Ketchikan, north) (Figure 2.1). During the 2019 surveys, sea otter populations were not established at Dixon Entrance survey locations (Bee Rocks, Percy Islands, Duke Island). However, dive fisheries managers reported the first otter digs at sites four years following our 2019 surveys signaling active sea otter repatriation of the area (K. Hebert personal communication 2024). The third region, Sitka Sound, on the west coast of Baranof Island (Shee in Lingít), was divided into three locations labeled by proximity to Sitka, North, Inside, and Outside locations The region was initially chosen for ongoing monitoring because sites could be easily accessed from the city of Sitka and were in areas of known pinto abalone aggregations (see Bell et al., 2018). Sites in the Sitka region were in subsistence harvest areas with established sea otter populations (USFWS 2014, White and Raimondi 2024). All surveyed locations were centered around multiple site groupings (see Figure 2.1) and selected and established under parameters that allowed for a stratified sampling approach and ensured divers an increased opportunity to record abalone.

Study Sites

Sampled sites were nested within locations in each region. Two transects were nested within each site. The specific sites in Prince of Wales were established at historical timed swim sites (n=8). Initially, area fisheries managers surveyed these sites via timed swims in 1980, 1981, and 1986 (Larson and Blankenbeckler unpublished data, see Chapter 1). Dixon Entrance sites, 100 km east of Prince of Wales (Figure 2.1), were selected based on recent (2003 and earlier) Alaska Department of Fish and Game dive survey notation of high abalone abundance (K. Hebert personal communication 2019). Sitka sites were approximately 230 km north of Prince of Wales and 330 km northeast of Dixon Entrance (Figure 1) and were selected through the ArcGIS random point generator function. Points were generated at least 100 meters apart within a polygon outlining a study location of Sitka Sound. The Sitka Sound polygon excluded habitat types least associated with pinto abalone populations, including depths below 12 meters and "Fluvial/Estuarine" areas, as determined by the "biological exposure class" function in Alaska ShoreZone© (Lessard and Campbell 2007). Sitka randomly selected sites (n=28) were surveyed over the summers of 2018 and 2019 alongside previously established Sitka abalone monitoring sites. The 2018 and 2019 random site selection methods were similar to those developed by M. Donnellan for 2014 Sitka abalone monitoring site selection (see Bell et al., 2018).

Sampling approach

We examined the general demography of Alaska abalone populations and hypotheses of predicted demographic characteristics through specific comparisons of abalone size classes, densities, aggregation, and other measures of reproductive capacity (i.e., mean Nearest Neighbor distance (NND), an aggregation index (i.e., Clark Evans described below), probability one adult within one-meter, adult density, the mean number of adults within one meter, and mean adult densities).

To identify patterns in abalone density across and within regions, we used variance component models of nested regional scales with respective spatial replicates (Figure

2.1). Survey locations were nested within regions. Sites were nested within locations and transects were nested within sites. This model setup allowed for the determination of the most influential spatial scale for overall abalone density and juvenile recruitment.

At each sampling site, we used strip transects (see Figure 2.2) to provide a sample area to collect location and size information for pinto abalone. We established two 2 x 20-meter transects at each site that followed a depth contour parallel to the shore. One transect was a "shallow" transect at approximately three meters below Mean Lower Low Water (MLLW), and the other was a "deep" transect at six meters MLLW (Figure 2.2).

Adjustments to transects were made if divers found it challenging to establish a lower transect in areas of abalone habitat. The goal of targeting two survey depths was to cover the predominant range of the species as, typically, pinto abalone are found at depths above 8 meters MLLW (Karpov et al., 1998, Zhang 2007, Bell et al., 2018). Comparable surveys have been used successfully across the species' range in British Columbia (Lee et al., 2016), Washington (Abalone Recovery Team 2002, Rothaus et al., 2008), and California (Bird 2018).

Once the transect location was determined, divers would deploy a pelican float to indicate its beginning. The dive tender then recorded the GPS point of the pelican float. Divers recorded the heading of their transect, then searched non-invasively (without turning rocks over or removing algae) for all abalone visible within a 1-meter swath. Aided by a PVC meter bar, divers measured abalone size, depth, distance from transect tape (cm), and distance along transect tape (m). Divers were asked to record every abalone seen. Still, juvenile abalone are often cryptic (Prince et al., 1988, Rogers-Bennett et al., 2004, Zhang et al., 2007, Rogers-Bennett et al., 2016). Therefore, divers may have overlooked some smaller individuals <30mm and densities of juvenile abalone (defined here as > 41mm) are considered minimum estimates.

We calculated the overall density (d), d=N/A, of abalone at the transect level by dividing the number (N) of abalone by the total transect survey area (A). The sample area ($40m^2$) was subsampled if the researcher measured 40 abalone. The subsampled transect area was recorded and used for the transect density measures. To compare densities across size categories, we divided abalone into the following size classes: “juvenile,” abalone with shell lengths <41 mm; “adult,” abalone >40mm, and “legal,” abalone, which were greater than or equal to the current minimum subsistence harvest size of 89mm. Our < 41mm delineation for both juvenile and recruitment aims to exclude those individuals least likely to contribute to aggregation reproductive capacity and include individuals most indicative of future population success.

With measures of abalone density, size, structure, and spatial distribution, we calculated four additional neighborhood metrics: mean number of adults within 1 meter of the focal individual, mean probability of at least one adult of the opposite sex within 1 meter, mean nearest neighbor distances and Clark Evans Aggregation Indices, along with fecundity density, an estimate of egg density.

Assessment of general questions

Densities, recruitment, NND, size structure, and estimated fecundity were assessed through summary statistics to depict patterns at the regional and location scales. Non-parametric Kolmogorov–Smirnov (K-S) pairwise tests were used to make comparisons of regional abalone shell length distributions. Cryptic <10 mm abalone were excluded from size-frequency analyses as they were too small for accurate comparisons. In addition, we used random effects mixed models (variance component models) to examine the variance structure (using REML) for the density variables (adult and juvenile density). This allowed the assessment of the characteristic spatial scaling for each density. The spatial terms included in variance component models were region, location(region), site(location(region)), and transect(site(location(region))). Transects were nested within their sites because there was no effect of depth on the described attributes. Assessment of recruitment was restricted to densities of individuals <41mm, the size category identified as both juvenile abalone and "recruits" (i.e., visible recruitment) throughout our assessment.

Reproductive Measures

The density of mature female abalone is considered an essential factor for population growth and viability because eggs are more limited than sperm for most species, including pinto abalone. Therefore, an increased density of eggs in a sampled population leads to higher reproductive success. To examine the egg density of sampled pinto abalone, we used a model developed from histological surveys in British Columbia (Campbell et al., 2003, Equation 2.1, below). A 50% sex ratio is assumed here for model calculations as it is widely accepted as an evolutionarily stable strategy (Fisher 1930, Hamilton 1967) and has been corroborated by visible gonad score surveys at sites in

Sitka Sound and Prince of Wales (T. White unpublished data). Additionally, researchers in Canada found pinto abalone populations near a 1:1 sex ratio (Breen and Adkins 1982).

Equation 2.1. Pinto abalone egg density calculation (adapted from Campbell et al., 2003)

$$E = \sum_{i=1}^{N} \frac{S_i F_i P}{A}$$

Where E is Egg Density, S_i = size of individual I, F_i is the estimated fecundity for an individual of size i, P is the proportion of females in the population (assumed as 0.5), and A is the sample area. This calculation assumes no sex-based differences in the population size structure.

Nearest Neighbor Distances (NND)

The other key attribute that affects reproduction for broadcast spawners like pinto abalone is the distance between individuals which is assessed by some metric related to nearest neighbor distance.

We assessed whether surveyed pinto abalone were within a critical distance for fertilization success, we used our measurements of abalone along (x) and away from (y) each transect to calculate Euclidian distances between adult (> 40mm) abalone (see Figure 2.1). These data were used to calculate nearest neighbor distances (NND) from each adult abalone at regional and monitoring density transects (PRIMER-e; Clarke et al., 2014).

NND Calculations

The set of NND metrics we used included Euclidean NND, number of adults within 1 meter of focal adult (N_{1m}), probability of an adult of the opposite sex within 1 meter (P_{1m}), and the Clark – Evans Aggregation Index (CEAI, see description below). All NND metrics were derived from the size and spatial data collected along density transects.

Mathematically, areas with increased densities have an inverse relationship to NND, where higher abalone densities are more likely to have closer individual abalone neighbors. Given the relationship between density and NND, we examined whether sampled populations were aggregated more than expected relative to density.

This was done using the Clark-Evans Aggregation Index (Clark and Evans 1954). The CEAI produces a statistic that is calculated as the quotient mean nearest neighbor for a focal individual divided by the expected mean distance, assuming a random distribution of individuals. Equations used for CEAI are shown in Equations 2a and 2b.

Equation 2a. Clark Evans Aggregation Index "R"

$$\text{2a: } R = \frac{\bar{d}_A}{\bar{d}_E}$$

Equation 2b. Calculation of Poisson estimator ($\bar{d}_E$)

$$\text{2b: } \bar{d}_E = \frac{1}{2\sqrt{\lambda}}$$

Where $\bar{d}_A$ = to the average distance to each focal individual, $\bar{d}_E$ = expected average distance to each focal individual based on a Poisson estimator with density λ.

The index R is relative to R = 1, which occurs when the empirical distribution equals the Poisson (random) distribution of neighbor distances based on abalone density. Values below 1 suggest a random aggregated distribution and values above 1 indicate a uniform distribution.

We examined whether, even at low densities, abalone were aggregated by plotting adult abalone density against Clark-Evans Index "R" and mean nearest neighbor distances, as "R" represents a dimensionless index unassociated with density. In addition, we examined differences between NND and Clark-Evans Index as measures of aggregation in abalone in Southeast Alaska by plotting them against one another.

To address whether there was a relationship between recruitment and adult density and NND, we used a mixed model ANCOVA approach using data collected as described above. The response variable was the density of juveniles. The random factors were the spatial scales Region, Location, Site, and Transect. The fixed factors were adult density and the nearest neighbor metrics described above. We used a stepwise approach to sequentially remove unsupported fixed variables from the model using AIC model selection.

To address relationships between fecundity density (number of eggs per meter square) and the density and size structure of resident abalone, we used a mixed model ANCOVA approach using density survey data and calculated egg densities as the response variable. The random factors were the spatial scales Region, Location, and Sites with transects. Sites and transects were linked because not all sites had multiple transects with enough abalone to produce a reliable estimate of median size. The fixed predictor factors were adult density and median size per transect.

RESULTS

We documented size, density, and nearest neighbor distances for 1,735 pinto abalone along 82 transects across three geographic regions, Sitka, Prince of Wales, and Dixon Entrance, in Southeast Alaska.

Regional densities of adult (>40mm), juvenile (<41mm), and combined sizes are shown in Table 2. As discussed above, juvenile abalone were used as a measure of recruitment. By region, adult, juvenile, and combined size densities were highest in Sitka Sound, intermediate in Dixon Entrance, and lowest in the Prince of Wales region. By area of survey, Prince of Wales recorded an order of magnitude lower density than Dixon Entrance, and Sitka had a 75% higher mean abalone density per total meter square (Table 2.1, Table 2.2). There was no difference in the relationship between abalone depth and density among regions.

Spatial Variation in Densities

Variation in abalone density was greatest at the regional and site scales, followed by the smallest spatial scale, transect. No variance was explained by including location in the variance component model (see Table 2.3). Restricting the assessment to juvenile or “recruit” density showed the greatest variance in densities at the smallest spatial scale of a transect, followed by sites and then regions (Table 2.3).

Regional Size Frequency

During 2019 and 2018 surveys, Sitka displayed the most extensive range of shell lengths, with a max size of 104mm (n=33 or 2% total legal, adult abalone; ≥89mm) and a minimum size of 2mm (Table 2.2, Figure 2.3). Dixon Entrance had three 115mm individuals (4% total legal). Prince of Wales had the largest median size, no legal adults, and 35.7% of the total (n=33) surveyed abalone were juvenile “recruits” (n=12). Kolmogorov Smirnov (K-S) tests between regional sizes of abalone (>10mm) only found a difference in the sampled abalone sizes between Sitka and the other regions, Prince of Wales and Dixon Entrance (Table 2.4, Figure 2.3).

Fecundity Density

Fecundity density, measured by estimated eggs per meter square, varied tremendously by region. Sitka Sound (173585 egg/m^2) and Dixon Entrance (191042 eggs/m^2) recorded statistically similar amounts of eggs across sites, and each region had over 30 times more eggs per meter square than Prince of Wales (5677 eggs/m^2) (Figure 2.4). Dixon Entrance had a large spread of sample means, primarily driven by a sampled site outlier (Figure 2.4). All sites are included in analyses. However, following the exploratory removal of the outlier site, Dixon Entrance egg density was reduced by 51.2% (191043 eggs/m^2 to 93294 eggs/m^2), shifting the region’s relationship to Sitka Sound and Prince of Wales egg densities. A Tukey HSD test of egg densities without the outlier indicated that Dixon Entrance fecundity was less distinctly different from both Sitka and Prince of Wales regions (e.g., “AB” in Figure 2.4).

Nearest neighbor metrics

Comparisons of the four nearest neighbor metrics are shown in Figure 2.5. There were differences in two of the four metrics by region. Specifically, Prince of Wales had substantially lower values for the probability of an adult of the opposite sex within one meter and the number of adults within one meter of the focal individual. These measures align with the low adult densities recorded in Prince of Wales (described above). Clark Evans values did not vary by region, and values less than 1 indicate aggregation, or in this instance, that adults are closer together than expected, given the local density. Here the R values for all regions were <0.3, most <0.2, indicating a disproportionate aggregation of adult individuals than would be expected by chance (Figure 2.5).

Overall, sites with densities at or above 0.5 to 0.6 adult abalone/m^2 maintained the highest densities regionally, close neighbor distances, and guaranteed probability of at least one neighbor of the opposite sex (see Figure 2.6).

Relationships between recruitment and adult density

Across regions, recruitment (i.e., juvenile density) was positively related to the Clark Evans Aggregation Index and adult abalone density and negatively associated with mean Nearest Neighbor distance (Table 2.5). These results suggest small-scale spatial relationships determining recruitment. Juvenile density increased with adult density at the transect level yet decreased with decreasing local adult dispersion (NND). The Clark Evans Aggregation Index "R" contributes to the model fit by describing random dispersion, irrespective of surveyed density. The Index suggests that low-density aggregations of adults are positively associated with juvenile density. Still, as the density of adults increases, adult disaggregation becomes increasingly positively related to juvenile density.

Fecundity density and density, abalone size structure

We found that fecundity density increased with both the median size of individuals and the density of individuals (in a transect), indicating that the expected relationship between size structure and density was present for abalone in our surveys (Table 2.6). In addition, using Log-worth values, we determined site size structure to be a better predictor of fecundity density than abalone density. Specifically, Adult abalone density was around 23% (22.76%), more influential than the median size of the estimated egg density for sampled regions (Table 2.6).

All analyses were done with JMP Pro v.16, SAS Institute, Inc, except for neighborhood distances calculated in PRIMER.

DISCUSSION

Spatial patterns in Density, Size Structure, and NND

This study highlights the importance of spatial scales, both large-scale and localized drivers, in understanding the variation in abalone densities across Southeast Alaska.

Specifically, we identified two critical spatial scales, regions, and sites, which accounted for the majority of observed variance (42% and 40%, respectively (Table 2.3). On a regional scale, extending approximately 100 km (Figure 2.1), physical factors such as temperature, wave climate, and circulation patterns (see Eckert et al., 2007, Weingartner et al., 2009) likely influence abalone densities. At more localized scales, biological factors may limit abalone densities, including local subsistence harvest, abundances of repatriated sea otter populations (i.e., Schuette et al., 2023), and herbivorous sea urchins, known to outcompete abalone for food (Rogers-Bennett et al., 2011; see Chapter 3).

Though site-scale differences in abalone densities were apparent, these differences did not translate to location comparisons (see Figure 2.1). Given the dynamic coastlines and systems of Southeast Alaska (see Eckert et al., 2007), it is reasonable to find discrete abalone populations at these location scales. This is further described by the "General "Moran Effect," where populations nearest each other (i.e., sites within locations) likely experience similar spatially specific effects and synchronously shift with local changes to local factors (Hasen et al., 2020). Furthermore, the Effect supports more variability in abalone population density by distance (i.e., regional distances) (see Hasen et al., 2020).

Size Structure

Sitka maintained a distinctly different abalone population size structure compared to other regions (Figure 2.3, Table 2.4). However, Prince of Wales surveys were most notable with the absence or few legally harvestable abalone recorded during surveys (Figure 2.3). In contrast, during the height of the commercial fishery forty years prior, Larson and Blankenbeckler (1980) found that 86% of abalone surveyed near Gooseneck and Port Bazan, Prince of Wales, were of legal, minimum commercial harvest size (≥96mm in 1979). In 2016, researchers recorded a maximum shell length of 96mm and very few large abalone 40km north of the 2019 Prince of Wales survey locations (Donnellan and Hebert 2017). Overall, Prince of Wales surveys document smaller abalone and overall reduced densities than populations sampled historically (White et al., *in prep;* Chapter 1). Based on the scarceness of State Trooper illegal harvest citations (K. Ferguson personal communication 2023), and reported challenges to carrying out illegal harvest activities, with limited access to transportation (e.g., roads, planes) in these remote areas (White and Raimondi 2024), we find it less likely that these trends are driven by poaching, as is a significant issue cited in British Columbia (e.g., Zhang et al. 2007). Instead, it is more likely that the current abundance and size distribution are driven by ecological factors explored in this study and ongoing personal use and subsistence harvest explored in Chapter 1.

Factors Contributing to Regional Variance: Recruitment Dynamics

The variation in recruitment (i.e., juvenile) densities was explained by differences at the regional (23%) and site (31%) scales, yet best explained by the finest survey scale, transects (41% variance; see Table 2.3). Factors operating at these fine scales are likely crucial to local recruitment patterns and include an abundance of algae that support recruitment (i.e., Crustose Coraline Algae, Morse and Morse 1984) and retaining larval abalone (e.g., understory kelp species; Sloan and Breen 1988), along with reef depth, distance from harbor and marina pollutants, substrate types, local temperature, salinity, dissolved oxygen, pH, and hydrodynamics (e.g., local currents, wave shock). Abalone larval duration and local retention are dependent on abiotic factors, such as current and temperatures (14-10 degrees Celsius) (Sloan and Breen 1988, Pearce et al., 2003), which differ across Southeast Alaska (Weingartner et al., 2009, see Figure 2.1). Regardless, pinto abalone populations across their range do not experience reduced genetic diversity (Diamond et al., *in press*), as genetic data show enough gene flow to support a similar genetic population structure within 1000 km (Withler et al., 2001). The physical and biological drivers of spatial variation of the density of recruits at the transect (tens of meter scale) likely also include the amount of refuge available and local densities of adult abalone.

The visual recruitment we compare here consists of individuals <41mm in size who have survived past the planktonic and larval life stages with the highest mortality rates (Leaf et al., 2007) and are reasonably indicative of future population successes under the same ecological and environmental conditions. Still, we acknowledge that as abalone are cryptic at smaller sizes, our visual recruitment measure is more likely to underestimate true recruitment or <41mm population abundance. Surveyor bias and ability to record juvenile abalone along transects differs most significantly across regional surveys (as divers differed at each region), and comparisons across regions are not advised. However, comparisons among the same divers, with similar search images at sites, reinforce the significance of transect-level effects.

Nearest Neighbor Metrics

As a measure of fertilization success, we found that regions generally show similar nearest-neighbor metrics and aggregated populations irrespective of density (see CEAI

Figure 2.5). Abalone populations are likely even more aggregated than described, as the CEAI measure is conservative and underestimates aggregation (Clark and Evans 1954). Without corrections for "edge effects," multiple abalone may be very close to one individual inside the survey transect swath, therefore, only one abalone is documented, and near neighbors are not included in aggregation measures (Clark and Evans 1954, see Figure 2.2). Despite limited adult abalone records at some sites (n=3) and orders of magnitude fewer eggs than the Sitka and Dixon Entrance regions, Prince of Wales experienced some limited recruitment (Figure 2.3, Figure 2.4). This may be because, even with the lowest densities, the Prince of Wales region sites were highly aggregated (Figures 2.5 and 2.6).

Recruitment Dynamics

During our examination of across-region neighborhood attributes, we found a positive relationship between recruitment and aggregation based on the Clark Evans Aggregation Index, which determines aggregation independent of density (Table 2.6). Alternatively, recruitment was negatively affected by increasing Nearest Neighbor Distance, a measure fundamentally linked to survey density (as discussed above). This difference between aggregation metrics suggests small-scale density-dependent effects. In this instance, the CEAI describes abalone dispersion irrespective of density and is, therefore, evidence that as the density of adults increases, disaggregation becomes positively related to increasing juvenile density. This study necessarily focused on recruitment at a post-settlement phase, a proxy for known nearby reproduction, planktonic, and settlement success. Therefore, differences in established recruits' densities suggest deterministic pre-settlement effects at local scales (see Connell 1985), perhaps based on interspecific competition at dense, aggregated adult abalone local scales.

Predictors of Fecundity Estimates

Larger female abalone have higher densities of eggs, irrespective of age and growth rate (Nash 1994). Fecundity density is a function of shell length (Sainsbury 1982, Wells and Keesing 1989, Campbell et al., 2003), and egg volume is a cubic measure. Therefore, this measure should increase exponentially with increasing abalone size or aggregation median size (mm). However, we found an unexpected relationship between adult abalone median sizes, densities, and fecundity density (egg/m^2). Abalone density was a more influential factor in determining local egg abundance (Table 2.6). Pinto abalone size distributions specific to Southeast Alaska likely explain the importance of density for fecundity. Our surveys determined a range in abalone densities much larger than the range of median sizes compared across regions (see Table 2.2). This reflects considerable differences in abalone abundance across regions shown here. Crucially, the variance between site densities, eggs, and sizes is a reminder that local surveys are especially poor representatives of the predictors in areas larger than the "regions" defined here. For example, the Prince of Wales "region" in this study consists of a selection of locations on the outer coast of Dall Island (Figure 2.1), and it cannot be representative of the grouping of islands incorporated in the Prince of Wales-Hyder area. This island grouping includes Prince of Wales Island, the fourth largest U.S. Island, on which there are qualitative reports of areas with higher abalone densities around the large island (Bolwerk 2021).

Population Trajectories and Limitations

Our regional pinto abalone surveys successfully identified three distinctly different populations across regions in Southeast Alaska (Table 2). Population demographic attributes in Sitka Sound suggest a stable or increasing population (Figure 2.3). Additional data show increasing recruitment at annual monitoring sites in the Sitka region (T. White unpublished data, see Chapter 3). In addition, our survey found the threshold for the highest likelihood of population viability beyond 0.5 – 0.6 adult abalone/m^2 (see Figure 2.6). This threshold is larger than those proposed for fertilization successes above (i.e., 0.2 – 0.3). However, beyond the threshold, individuals are nearly guaranteed a 100% chance of an opposite-sex individual within distances of 1 meter, which is considered necessary for stable population size and recruitment (Miner et al., 2006).

Other Southeast Alaska surveys have documented pinto abalone recruitment in low-density areas (see Donnellan and Hebert 2017, Bell et al., 2018) and across the species' range, except Washington. During this study, only three sites in Dixon Entrance and four sites in Sitka fell below the 0.2 abalone/m^2 density threshold, below which other abalone species have experienced recruitment failure (Tegner et al., 1989, Shepherd and Partington 1995, Karpov et al., 1998, CDFW 2005). At all other sites in the Sitka and Dixon Entrance region, divers recorded mean abalone densities above the 0.3 abalone/m^2 threshold (originally 0.33/m^2) determined as the upper limit of recruitment success in greenlip abalone (*H. laevigata*; Babcock and Keesing 1999). Sites with the overall highest densities of adults (individuals >41mm) were in Sitka, except one site in Dixon Entrance with an adult density of 2.64/m^2 (see Figure 2.6). Conversely, all Prince of Wales sites surveyed for this study fell below both $0.3/m^2$ and $0.2/m^2$ established density thresholds, with the highest overall site density at $0.1/m^2$. Despite concerningly low densities, we did record juvenile abalone “recruits” at five of the eight sites in Prince of Wales. Unfortunately, Prince of Wales had a very small adult abalone sample size, which made nearest-neighbor calculations only possible for two sites (see Figure 2.6). Other neighborhood metrics in the region were affected and lowest in the region (i.e., the probability of at least one individual of the opposite sex and the mean number of adults within one meter of a focal adult; see Figure 2.3). Prince of Wales comparisons in nested models were further limited to densities. Other response variables of neighbor attributes, aggregation measures, and estimated fecundity density did not provide enough power at smaller spatial scales for a nested assessment. For example, a zero recorded for density on a transect is informative concerning density but is a missing value for nearest neighbor distance or size structure. Still, our examination isolates the most deterministic spatial scale for overall abalone density and recruitment (juvenile density).

Recruitment theory (see also Connell 1985) and general metapopulation theory suggest that a sole focus on recruitment based on adult density is misguided. In addition, aggregation, often cited as a critical link to fertilization success (e.g., Babcock and Keesing 1999), is independent of local density, as determined here, where very low-density sites can be highly aggregated (see Figure 2.6). We echo a concept initially posited by Prince and Valencia (2009) that concern over Allee effects from reductions of reproductive individuals to the point of fertilization failure (e.g., Gascoigne and Lipcius 2004) is less an issue for such a motile species as pinto abalone that actively aggregate, at times stacking, to spawn (Stekhol and Shirley 1991). The metabolic demands of movement (slime production) alone (see Donovan 1998) during highly aggregated spawning suggests an evolutionary strategy to overcome fertilization constraints. Most concerning are future shifts to aggregation and spawning cues from oceanographic changes that may mismatch local spawning.

Finally, we find fewer juvenile abalone in areas of highly aggregated adults. Though increased adult abalone densities positively correlated with juvenile abalone densities, and adult abalone are generally known to facilitate recruitment (e.g., Richards and Davis 1993, Raimondi et al. 2002), we found highly aggregated adults to have an inverse and adverse effect on juvenile abalone densities (Table 2.5). Indeed, abalone density is essential, particularly to population fecundity in Southeast Alaska (Table 2.6). Though refuge populations may persist at extremely low densities as those recorded in Prince of Wales, it is most important to monitor for changes in recruitment and seek additional information on local abiotic shifts and changes in biotic effects such as algae and sea otter population growth. Management and monitoring of pinto abalone at more local scales to assess local management effectiveness and indirect effects of ongoing harvest and sea otter population expansion across the species' Alaska range will be integral to predicting the ongoing fate of pinto abalone populations in Southeast Alaska.

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TABLES

Table 2.1. Pinto abalone density transect regions, locations, sites, and total area surveyed during 2018 and 2019 in Southeast Alaska. Prince of Wales surveys were done at historical sites via two methods: density transects and timed swims.

Year	Region	Location	Site Count	Transect Count	Abalone Survey Area (m^2)
2018	Sitka	Sitka Inside	5	10	278.83
2018	Sitka	Sitka North	3	6	240
2018	Sitka	Sitka Outside	3	6	240
2019	Sitka	Sitka Inside	4	4	117.62
2019	Sitka	Sitka North	2	4	53.56
2019	Sitka	Sitka Outside	9	18	448.44
2019	Prince of Wales	Gooseneck	4	8	320
2019	Prince of Wales	Port Bazan	4	8	320
2019	Dixon Entrance	Bee Rocks	2	4	140
2019	Dixon Entrance	Duke Island	5	10	374
2019	Dixon Entrance	Percy Islands	2	4	160

Table 2.2. Summary of all 2019, 2018 Southeast Regional Density Surveys. Mean densities (abalone/m^2) with the same letter **A, B, or C** (within columns) are not significantly different (P>0.05, Tukey Kramer test).

Year	**Region**	**Abalone Count**	**Median Shell Length** (mm)	**Mean Density** (All sizes)	**Mean Density** (Adults >40mm)	**Mean Density** (Juveniles <41mm)
2018/2019	Sitka Sound	1337	47	1.57 **A**	0.985 **A**	0.582 **A**
2019	Prince of Wales	33	57	0.045 **C**	0.028 **B**	0.017 **B**
2019	Dixon Entrance	365	54	0.589 **B**	0.507 **A**	0.082 **B**

Table 2.3. Results of variance component model for abalone density treating all spatial scales as random effects. Shown are the percent of variation associated with different spatial scales for all abalone and separately for juvenile ('recruits') abalone (<41 mm). See Table 1 for information about regions, locations, and sites. All densities were transformed ($\log_{x+1}$) for normality assumptions.

Spatial scale	**All abalone % total variance**	**Juveniles % total variance**
Region	41.94	22.83
Location	0.00	5.60
Site	39.52	30.56
Transect	18.54	41.01
Total	100.00	100.00

Table 2.4. Kolmogorov Smirnov (K-S) Tests comparing abalone size frequencies recorded in the Sitka, Prince of Wales, and Dixon Entrance regions during 2018 and 2019 random density transects. Abalone <10mm were removed from these comparisons.

Location 1 (F1)	**Location 2 (F2)**	**Count F1**	**Count F2**	**D max |F1-F2|**	**Prob > D**
Sitka	Dixon Entrance	1302	364	0.241	<.0001
Sitka	Prince of Wales	1302	28	0.080	0.884
Prince of Wales	Dixon Entrance	28	364	0.256	0.671

Table 2.5. Results of ANCOVA for the relationship between Nearest Neighbor metrics and adult density on Juvenile (recruit) density (Log $_{X+1}$). Shown is the final reduced model based on AIC model selection. Estimates are slopes (+ or -) for Clarke Evans (+), Mean NN distance (-), and Log Density per m^2 of adults (+).

Term	Estimate	t Ratio	p-value
Intercept	-0.072	-0.68	0.5245
Clark Evans (adults)	3.794	3.61	0.0007
Mean NN distance	-0.816	-3.0	0.0042
Log[Density per m^2 (adults)+1]	0.243	2.54	0.0138

Table 2.6. Results of ANCOVA for the relationship between egg density (m^2) and density of abalone (m2), both (Log $_{X+1}$) transformed and Median size of abalone in the transect. Estimates (slopes) for the density of adults and median abalone size are both positive. Log worth compares the importance of predictor variables to overall model fit.

Term	Estimate	t Ratio	p-value	log worth
Intercept	5.605	5.42	0.0023	
Log[Density per meter sq+1]	2.473	6.09	<.0001	7.315
Median(mm)	0.063	5.16	<.0001	5.65

FIGURES

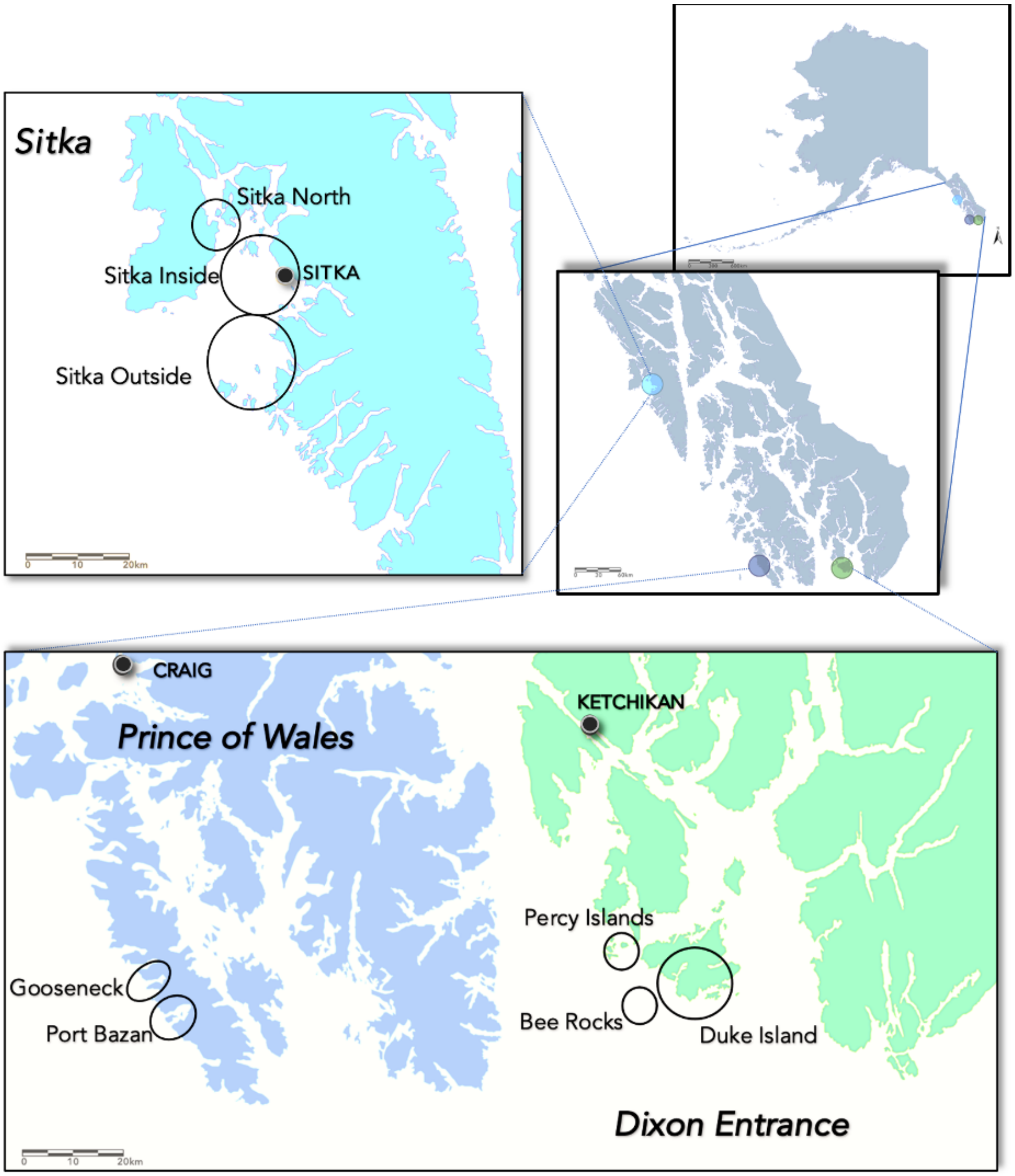

Figure 2.1. A map of regions and locations of 2019 and 2018 abalone survey regional random survey sites. Sites and transects are nested within each location. Within each region, the locations are at least 7 km apart, which is the distance (as the bird flies) between the two locations (i.e., Port Bazan and Gooseneck), in the Prince of Wales region. The Sitka Sound region hosts three locations. The center of the area encompassing the Sitka North sites is 13.5 km from the center of the Sitka Inside location. The center of the Sitka Outside location is 15 km away from the Sitka Inside location center. In the Dixon Entrance region, the center of sites at the Bee Rocks location is 10 km to the west of Duke Island sites and 7 km south of Percy Island location. Percy Island and Duke locations are 12.5 km apart.

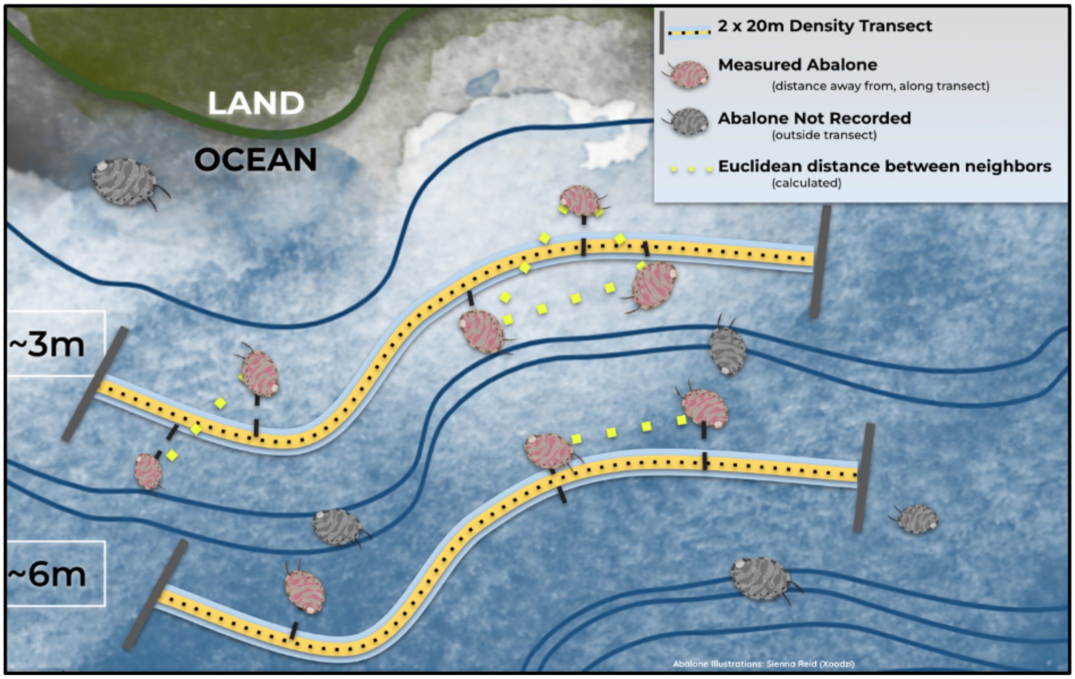

Figure 2.2. Density Transect Layout: abalone density transects that makeup one survey site. Two transects (2 x 20 meters) were placed at a set depth, one shallow (around 3m) and one deep (around 6m) parallel to the shore. For 2019 and 2018 surveys, abalone dive surveyors would begin searching for abalone at the inshore one-meter portion of the two-meter wide transect swath, surveying an inshore meter left to right, followed by an offshore meter swath right to left. Metrics collected and included here were abalone distance away from (y) and along (x) the transect, number of abalone, and the first 40 individual abalone shell lengths measured to the nearest millimeter (abalone artwork by Sienna Reid; Xoodsí).

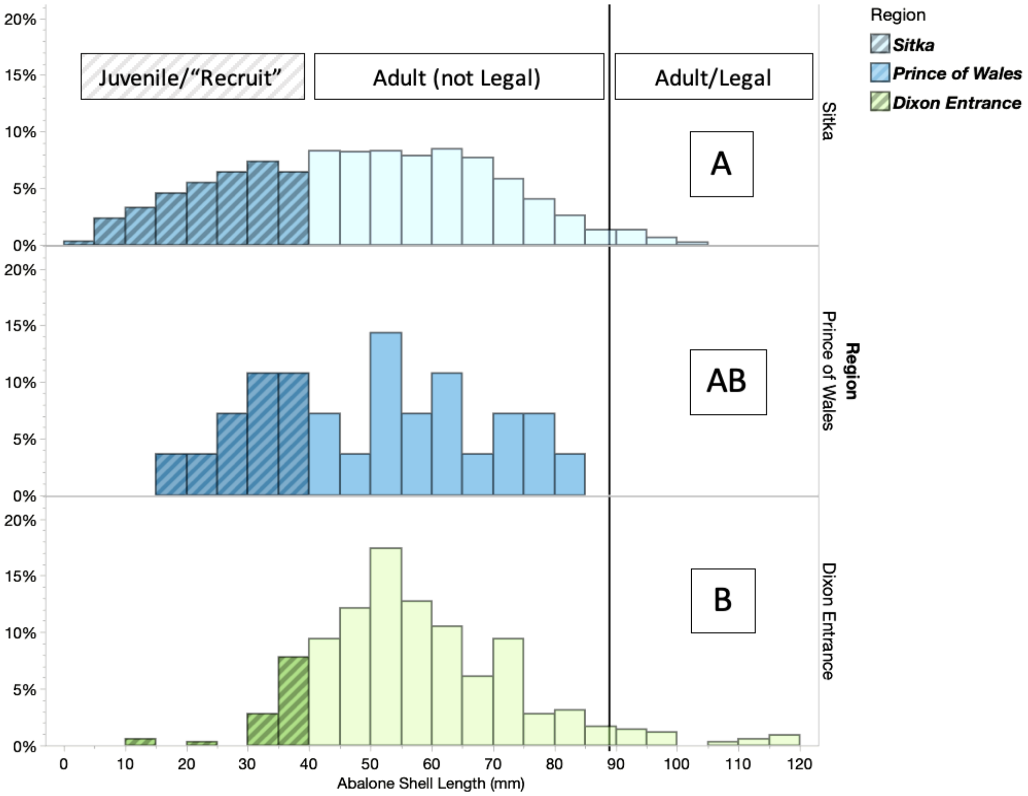

Figure 2.3. Size frequency of pinto abalone shell lengths (mm) recorded during 2018 and 2019 density surveys in Southeast Alaska. Three size categories are delineated: (1) juvenile = recruit <41 mm (2) adult, not legal >40mm and <89 mm, and (3) adult, legal ≥89 mm. A line at 89mm indicates the minimum legal-size limit of subsistence harvest set during the historical fishery in 1977 (Larson and Blankenbeckler 1979). Kolmogorov Smirnov (K-S) Tests results are indicated by letters. Regions with similar letters are not significantly different (P>0.05).

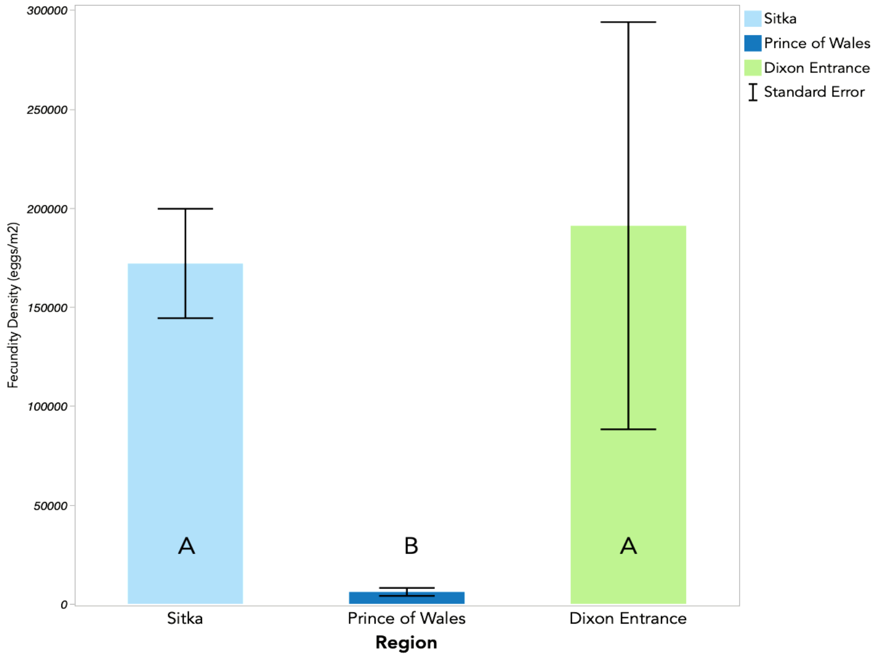

Figure 2.4. Fecundity Density (eggs per meter square) as a function of the region. Bars with the same letter are not significantly different (P >0.05, Tukey Kramer test). Error bars are one standard error from the mean. Refer to Table 6 for analyses with Log(x+1) transformed fecundity and adult density.

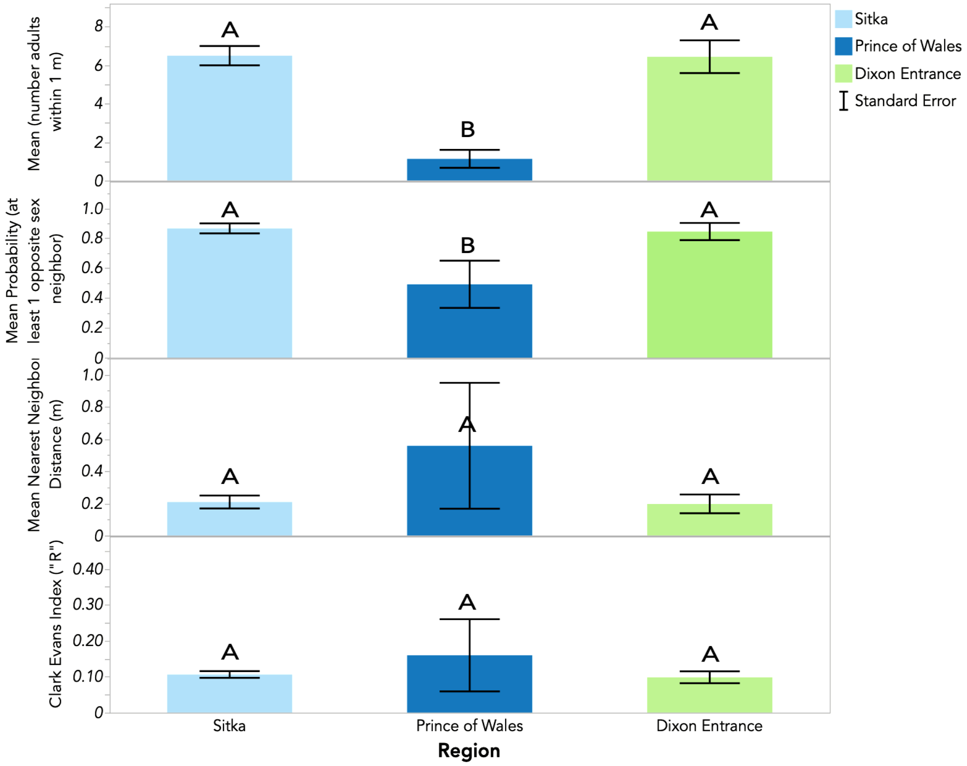

Figure 2.5. Nearest Neighbor metrics by region: mean number of adults within 1 meter of the focal individual, mean probability of at least one adult of the opposite sex within 1 meter, mean nearest neighbor distance to an adult, mean Clark Evans value. Error bars are one standard error. Bars with the same letter are not significantly different (P >0.05, Tukey Kramer test). All sites are included, and all densities modeled from 2019 and 2018 random site density transect surveys were Log_{x+1} transformed for assumptions of normality (see Table 2.5).

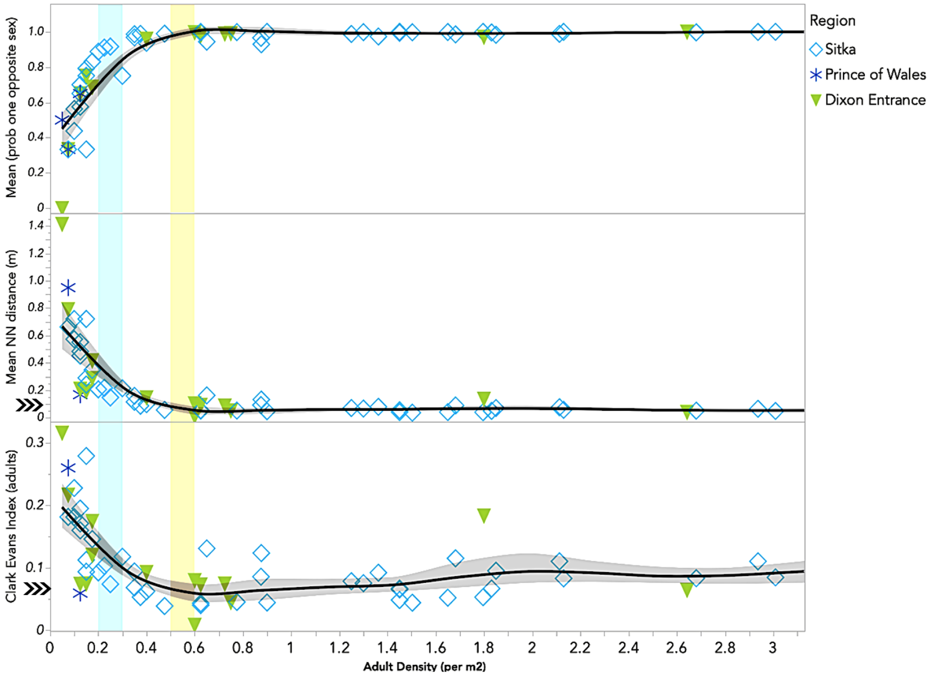

Figure 2.6. Adult abalone density as a function of Clark Evans Aggregation Index (CEAI), Mean Nearest Neighbor Distance (NND), and Mean probability of one opposite sex abalone neighbor from density transect surveys across Southeast Alaska. Regions: Sitka (light blue diamonds), Prince of Wales (navy asterisks), and Dixon Entrance (green triangles). Clark Evans Aggregation Index R < 1 suggests non-random distribution or aggregation. Grey shading is the confidence of line fit (spline method). The blue shaded area indicates the density threshold range of 0.2 to 0.3/m^2 of known recruitment in pinto and other abalone species (e.g., greenlip abalone) used as part of red abalone management in California (i.e., 0.2/m^2; CDFW 2005) and pinto abalone recovery in Washington (0.3/m^2; Sowul et al. 2022). The yellow shaded area suggests the threshold range for pinto abalone population viability in Southeast Alaska. Bolded arrows along the y-axis indicate the asymptote of adult abalone for measured effects of CEAI (R ~0.06) and mean NND (0.1 adult/m^2).

CHAPTER 3

PINTO ABALONE ACROSS PREDATOR, COMPETITOR-SCAPES: SEA OTTERS, URCHINS, AND HABITAT ECOLOGICAL FORECASTING

CHAPTER 3: PINTO ABALONE ACROSS PREDATOR-COMPETITOR-SCAPES: SEA OTTERS, URCHINS, AND HABITAT ECOLOGICAL FORECASTING

Portions of this chapter include or are adapted from: White, T. and P.T. Raimondi. 2024. Diverse knowledge systems for the examination of localized dynamics of sea otters and abalone populations in Sitka Sound, Alaska. NPRB Project 2115 Final report.

ABSTRACT

In Southeast Alaska, Northern sea otter (*Enhydra lutris kenyoni*) populations have reshaped the coastal communities they reoccupy. As an important predator with the ability to regulate invertebrate populations to influence the structure of kelp forests, the ongoing expansion of sea otters into areas where they have been absent for nearly a century offered a unique natural experiment to explore their connections with ecosystems and species essential to local human communities, like pinto abalone (*Haliotis kamtschatkana*). Southeast Alaska is the only place where pinto abalone continue to be harvested. Due to previously scarce area-specific data on abalone and sea otter populations, interactions between the species have yet to be extensively documented throughout Southeast Alaska, a region with varying histories of otter presence and human harvesting practices. This study investigates the impact of sea otter repatriation on abalone populations by examining patterns in sea urchin biomasses, macroalgae, abalone densities, and habitat use behavior. These attributes, in combination with comparisons to direct and indirect effects of sea otters to the well-established otter-urchin-macroalgal trophic cascade. Sea otter influence was determined via spatially specific weighted factors of abundance, occupation time, growth, and harvest. Abalone maintained non-linear relationships with sea otter and sea urchin measures, with the highest abalone densities (1.34/m^2) at locations with moderate otter influence and moderate urchin biomasses (3.18kg/m^2). As predicted,

urchin biomass had an inverse relationship with macroalgal cover and sea otter influence across regions. Overall, this study provides a clearer understanding of mechanisms related to changes in abalone behavior and densities in response to varying amounts of sea otter influence that are integral in effective management and continued community harvest of both species in Alaska.

INTRODUCTION

Large disruptions to ecosystems often produce cascading effects that uncover otherwise invisible community interactions and interaction strengths and allow for research of species' crucial roles in shaping communities (e.g., Paine and Levin 1981, Croll et al., 2005, Travis et al., 2014, Rogers-Bennett and Catton 2019). Large perturbations, like the near extirpation of sea otters in the late 1880s following the intensive maritime fur trade (Kenyon 1969) and the subsequent reintroduction of sea otters to those ecosystems they occupied one hundred years prior (Burris and McKnight 1973) have highlighted profound direct and indirect effects of sea otter predators on lower trophic level species (e.g., Estes and Palmisano 1974, Estes and Duggins 1995, Estes et al.,1998, Watson and Estes 2011, Lee et al., 2016).

Repatriating sea otter populations have well-documented cascades of effects centered around their feeding habits and foraging behavior. These include the consumption of herbivorous invertebrate populations, like sea urchins. Through the removal of urchins from kelp forest ecosystems, sea otters indirectly release algae from urchin herbivory and lend to the growth and increased abundances of macroalgal species (e.g., *Macrocystis* spps., *Laminaria* spps.). In the absence of indirect effects of sea otters, kelp forests are known to become “urchin barren” environments, where sea urchin populations grow, graze kelp, and eliminate algal communities (Konar et al., 2014, Estes et al., 1998). Areas where otters remain absent are also characterized by an abundance of otter prey species, namely invertebrates, including sea urchins, clams, crabs, and sea cucumbers (Estes et al., 1998, Estes and VanBlaricom 1985).

During this urchin barren period in Southeast Alaska, several commercial shellfish fisheries, including abalone, red urchins, geoducks, and sea cucumbers, were established. The first dive fishery was for pinto abalone (Gunxaa – Lingít, *Haliotis kamtschatkana*), with initial landings reported in the mid-1960s (Hebert 2014). The commercial fishery closed in 1996 after fifteen years of precipitous decline, with an 89% decline in catch during peak harvest years from 1978 to 1981 (McDougall et al., 2006, Woodby et al., 2000).

Soon after the first recorded landings of abalone, 413 sea otters were re-introduced to areas of Southeast Alaska (Jameson et al.,1982, Pitcher 1989). Sea otters did not occupy areas of the commercial abalone fishery until near its closure around 1996 (see Chapter 1, Hebert 2014), however, there was an increased conflict between harvesters and those sea otter populations that continued to grow and shape their areas of harvest (Mills 1982, Larson 2014, Hebert 2019). Community subsistence and personal use harvest continued, though at a reduced harvest allowance (i.e., 50 abalone per day to 5 abalone per day in 2013; Title 5 of the Alaska Administrative Code, Chapter 02, Section 135). Though less commonly documented (de la Selva 2016, LaRoche et al., 2021), sea otters do eat pinto abalone in Southeast Alaska (Hoyt 2015, White and Raimondi 2024). This remains a concern since pinto abalone (*Haliotis kamtschatkana*) are the only abalone species in Alaska and have remained a vital subsistence and traditional and customary food source since time immemorial (Mills 1982, Thornton 2011, Turner 2020, Ibarra 2021). Abalone populations in the region have not recovered in many areas following their significant decline (Woodby et al., 2000) and in some areas (e.g., areas of Prince of Wales), population densities remain low (White and Raimondi 2020). Conversely, the first abalone monitoring sites, established in Sitka in 2015 to understand local abalone populations (see Bell et al., 2018), recorded increased densities of abalone populations from 2015 to 2020 (see Figure 3.1, White and Raimondi 2024). These increases occurred at all sites regardless of the perceived effects of sea otters, which had established populations fifteen to thirty years prior in areas of Sitka Sound (Figure 3.1, White and Raimondi 2024).

The most recent modeled estimate of the Southeast sea otter populations derived from 2022 surveys indicated an estimated sea otter abundance of around 22,359 otters (credible interval: 19,595 to 25,290), which comprises over 45% of the estimated carrying capacity in Southeast Alaska (Schuette et al., 2023, Eisaguirre et al., 2024). These recent surveys have been integral in understanding the current abundance of sea otters. Still, population estimates for otters were not conducted in Southeast Alaska between 2011 (USFWS 2014) and 2022 (Schuette et al., 2023), which poses a challenge for our understanding of otter occupation times across the region, especially after 2011, a period of significant expansion and movement of sea otter populations into areas they had not occupied for over a century (USFWS 2014, Hoyt 2015, Davis et al., 2019, Schuette et al., 2023). An understanding of otter abundance and occupation period measures are crucial in determining sea otter population impacts.

Otters may follow an optimal foraging theory (Kleiber 1961; Stephens and Krebs 1986) and initially target disproportionately large (i.e., high caloric value), easy-to-gather prey (Estes and Palmisano 1974, Ostfeld 1982). In addition, following a period of occupation, and a reduction of preferred energetically rich prey, sea otters show a propensity to diversify their diet and eventually specialize on specific species, which widens the breadth of their impact on an ecosystem (Tinker et al., 2008, Hoyt 2015, Weitzman 2013, LaRoche 2021). Even with abundance and occupation measures, sea otters do not always impact ecosystems through the traditional trophic cascades described above. As Smith et al. (2021) found, otters may avoid eating sea urchins and are less likely to initiate kelp forest growth when urchins are starved. Konar (2000) found otters did not impact urchin (density) in the Aleutians after seven years of occupation.

In addition, while sea otters may become re-established in some areas, they may also be removed primarily by hunting, which makes examination of sea otter dynamics and impacts on other species in Southeast Alaska uniquely complex. The Marine Mammal Protection Act (MMPA,1972) permits Alaska Natives to hunt sea otters and sell processed “handicrafts” (50 CFR 18.23). While hunting remains stable at the regional scale of Southeast Alaska, otter harvest rates vary at the sub-regional scale (Raymond et al. 2019). Though hunters report tagged harvest, subsequent information on the cascading effects of local hunting is rarely included in local surveys of invertebrate populations but is likely very significant (see Bolwerk 2021, Ibarra 2021). Finer scale information on sea otter populations is essential as local populations may experience more fluctuations due to hunting, and hunting is found to increase over occupation times, which differ locally (Raymond et al. 2019).

The mosaic of sea otter recovery across Southeast Alaska, a data-poor region for sea otter and abalone interactions, includes variable sea otter repopulation, ongoing legal abalone harvest by residents (5 per person/day, in possession;5AAC 02.135), and sea otter hunting by Alaska Natives is permitted (MMPA 1972 50 CFR 18.23). These location specific effects provided an opportunity to first clarify patterns of most common and predicted trophic cascades following interactions between sea otters, kelp, and sea urchins. Then, assess any direct and indirect impacts sea otter abundance, occupation, and harvest have on patterns of abalone densities, interactions, and abalone behaviors following sea otter establishment.

METHODS

Study Area

This study examines locations nested in three regions of Southeast Alaska, each in different stages of sea otter repatriation and each with characteristically different pinto abalone populations (see Table 1). The spatial mosaic of temporal variation in repatriation provided a unique opportunity to investigate the effects of sea otters on pinto abalone populations and 'proxy' species that otters have known interactions with, such as sea urchins and macroalgae. Study regions included Sitka Sound, Alaska (57.05305° N, -135.33000° W), the Southeast Alaska side of the oceanic barrier between Alaska and British Columbia, defined here as the Dixon Entrance region (54.71667° N, -131.52139° W), and Prince of Wales Island, specifically the incorporated areas, nearby Dall Island (54.94214° N, -133.01363° W).

Regional Characteristics

Study regions were divided into locations representing the diversity of regional habitats, human access, and sea otter repatriation. Where historically, pinto abalone populations across these regions and nested locations were impacted differently by subsistence take and commercial fisheries. Prince of Wales locations had magnitudes greater abalone landings during the historical commercial fishery when compared with surveyed locations in Dixon Entrance (see Chapter 1). Sitka had overall stricter limits for commercial and subsistence harvest (i.e., limit 20 abalone limit per day) compared with other study regions (limit 50 abalone per day; see Hebert 2014, White et al., in prep; aka Chapter 1). In Sitka, the strategic reintroduction of sea otters at various times and locations across the regions of Southeast Alaska resulted in a diverse patchwork of populations with distinct sea otter establishment periods. Otters are functionally absent from sites in Dixon Entrance, more recently established and growing faster in Prince of Wales, and sea otters in Sitka maintain the longest established populations, which experience relatively more hunting, as detailed further below (Table 3.1).

Sites nested in selected locations were surveyed in the summer months of 2018 and 2019 in Sitka (three locations, 24 sites), Prince of Wales (three locations, eight sites), and Dixon Entrance (three locations, nine sites; Table 3.1) regions. Sites were at least 100 meters from each other and were chosen randomly via ArcGIS random point generator in Sitka, chosen from known historical dive survey sites in Prince of Wales and in Dixon Entrance, were selected based on abalone presence noted by ADFG divers surveying urchins and sea cucumbers (further described in White and Raimondi 2020).

Additional abalone density data from sites surveyed in 2016 at the Meares Pass location in the Prince of Wales region and at the Gravina Island location in the Ketchikan region contributed to abalone analyses (surveys detailed in Donnellan and Hebert 2017).

Sampling approach

Pinto abalone densities, sea urchin biomasses, abalone refuge habitat use, and percent algae cover were all determined via metrics collected during dive surveys. Two 2 x 20-meter transects were established at each site and surveyed parallel to shore at 'shallow' (around 3m Mean Low Low Water) and 'deep' (around 6m MLLW) depths within the preferred range of pinto abalone populations (COSEWIC 2009) all < 30 meters deep, well within the mean range of sea otter foraging depths (Riedman and Estes 1990). Similar survey methodologies were used to establish the abalone monitoring sites in Sitka Sound (as in Bell et al., 2018) and to survey pinto abalone in British Columbia (see Lee et al., 2016) and at sites in Prince of Wales (Bolwerk 2021).

During surveys, one diver collected abalone metrics along each 2 x 20-meter transect, while the other surveyed sea urchins and local habitats. The abalone diver measured abalone count, size (mm), depth (m), distance from transect tape (cm), distance along transect tape (cm), habitat (i.e., algae and substrate directly underneath abalone; see Chapter 2 Appendix Table A2.1). and refuge, primarily from predators. In this study, abalone exposure to predators and habitat quality were measured based on perceived human and sea otter access, where "refuge" could be a crack or crevice, and an abalone in a crack or crevice would be documented as using "refuge." At the other end of this scale, "exposed" habitat would apply to a location that would not provide safety to an abalone from predators, such as bare rock, and abalone may be “exposed” to predators in that habitat. “Moderately exposed” habitat is a label for abalone and availed habitats between “exposed” and “refuge” habitats. A similar approach has been used for twenty years by the Multi-Agency Rocky Intertidal Network (MARINe) in the assessment of risks to black abalone, an ESA-endangered species (https://marine.ucsc.edu/; Table A2.1). Refuge metrics were collected as an indicator of sea otter response as abalone have been disproportionately found hidden in refuge following sea otter repatriation to areas in California (Hines and Pearse 1982, Raimondi 2015) and British Columbia (Lee et al. 2016). In addition, abalone refuge use behavior may change based on available macroalgal food, as demonstrated in the cascading effects of a marine heat wave from 2014 to 2016 highlighted complex abalone and urchin interactions in northern California. During the heat wave, an estimated 95% of kelp along a 350 km stretch of coast was lost due to physiological stress (McPherson et al., 2021). Sea urchin populations grew during this period, as did their consumption demands for kelp, which rapidly declined in abundance. This decrease in kelp abundance limited abalone access to drift kelp and forced abalone into more active foraging behaviors, driving them out of their refuge and into more exposed habitats (Rogers-Bennett and Catton 2019).

For insight into local biogenic habitat and potential associations with abalone, urchins, and sea otters, habitat data was collected in two or three layers directly under the transect tape every half meter. Divers recorded the top algal or encrusting invertebrate layer followed by a substrate layer (based on the Wentworth Scale). In high-density algal communities, divers would record the top and bottom algal layer and substrate. Both site refuge quality and habitat data were collected every 0.5 meters for a total of

40 points per transect (i.e., 50% cover of habitat per transect). Finally, habitat divers recorded the widths of *the* first 20 green and first 20 red urchins encountered with transects biomass calculations. Urchin test diameters, excluding spines, were measured to the nearest millimeter within the same 2-meter swath transects (one meter on either side of the transect tape) within the same swath as abalone. Abalone and urchins were sub-sampled along transects. Following the survey of forty individual abalone and twenty green and twenty red urchins, habitat divers recorded the meter mark, then paused the survey to count or tally the number of each urchin species (for detailed dive survey methods, see Appendix in White and Raimondi).

To examine the well-documented trophic cascade among study species, urchin and macroalgal metrics were collected alongside abalone metrics at sites, primarily as indicators of sea otter influence (see Figure 3.2b). Importantly, though seemingly ubiquitous, the urchin–kelp–otter interaction have not been supported throughout Alaska kelp forests (see Konar 2000), the cascade were supported by time-series data comparisons in British Columbia (Lee et al. 2016) and in Southeast Alaska, which showed nearly a 100% decrease in urchin densities and a corresponding near 100% increase in kelp densities in the years following sea otter repatriation (Gorra et al., 2022). Second sea urchins are known to outcompete abalone for food (i.e., macroalgae, Shepherd 1973) and refuge (Lowry and Pearce 1973, Karpov et al., 2001).

We predicted abalone populations at study locations with specific effects of otter re-establishment and abundance would exhibit the artifacts in behavior, size, and abundance in accordance with the well-documented trophic cascades. Specifically, where sea otter influence (described below) increased, sea urchin biomass would decrease, macro-algae would increase, and abalone may have non-linear relationships to otter influence at locations (see Figure 3.1).

We predicted that abalone densities would exhibit a quadratic response to otter influence mediated by a non-linear interaction between abalone and sea urchins. The rationale for this prediction includes: 1) abalone densities will be negatively affected by competition with sea urchins for food, which will manifest in more abalone out of refuge habitat, seeking food in locations where otters are rare or absent, 2) where otter influence is moderate, sea urchins will be relatively rarer as otters will target sea urchins, and abalone densities will increase with fewer food limitations, and 3) where otter influence is highest both urchins and abalone decrease via otter consumption, and abalone may seek refuge from sea otters. The predicted trends across the mosaic of sea otter repatriation are graphically demonstrated in Figure 3.2a, along with the predicted paths of direct and indirect species interactions contributing to plotted trends (Figure 3.2b).

With limited information on sea otter and abalone interactions in Alaska, we further examine urchins and macroalgae interactions as clearer indicators of the presence of location sea otter influence. We predict where otter influence is highest, sea urchin biomass will be lowest, and macroalgal proportions will be greatest, with the opposite response of urchins and macroalgae in low otter influence locations. As determined by Gorra et al. (2022) and shown in Figure 3.2, an inverse relationship between kelp and urchins (3.2a) would further support the direct and indirect local otter interactions at abalone survey locations across Southeast Alaska (3.2b). These interactions, alongside documented refuge-seeking behaviors, are proxies to guide our understanding of abalone and sea otter interactions in data-poor regions of Alaska.

Analytical Approach

To explore differences in abalone populations and potential responses to sea otter repatriation of Southeast Alaska, we identified factors and factor weightings contributing to sea otter influence, including otter presence, absence, general occupation time, predicted growth rates, and loss from hunting. Sea otter influence is used here as a general measure for otter community impacts at regional and at finer local (i.e., location) scales, as sea otter populations have localized effects (Davis et al., 2019, Raymond et al., 2019, Tinker et al., 2019, Gorra et al., 2022). Sea otter influence was determined through the best available local information, including aerial surveys describing otter presence or persistence (Esslinger and Bodkin 2009, USFWS 2014, Hoyt 2015), appearance in ADF&G dive surveys (K. Hebert, pers. comm. 2022), and through input from local experts (Table 3.1; see White and Raimondi 2024). Locations with sea otter populations with a higher estimated otter population abundance and growth rate were weighted positively as these factors added to sea otter influence intensity, while locations with increased otter harvest and increased occupation time were weighted negatively as both harvest and occupation may diminish otter influence on abalone (as outlined below and in Table 3.1).

Occupation influence

The most counterintuitive weighting of a factor contributing to location sea otter influence was otter occupation period. We assign a reduction in overall sea otter influence/impact with increased sea otter presence in locations (Table 1). This is supported by documented and modeled evidence that otters have the most intensive impacts on prey following initial periods of otter occupation (Estes et al., 2003, Hoyt 2015, Coletti et al., 2016, Eisaguirre et al., 2021). An impact reinforced by significant declines in available abalone for local harvest were reported by subsistence abalone harvesters in Sitka (Figures 7 and 8 in White and Raimondi 2024) and other communities in Southeast Alaska (Mills 1982) following the initial occupation of sea otters at sites. As described in the introduction, researchers find that following a period of occupation and reduction of energetically rich prey items, sea otters diversify their diet and, at times, specialize in less calorically rich prey species the breadth of their impact on the ecosystem (Ostfeld 1982, Estes et al., 2003, Ostfeld 2004, Laidre and Jameson 2006, Tinker et al., 2008, Weitzman 2013, Hale et al., 2019). Finally, individual scouts to occupation areas are often identified as males, often generalists, with a larger impact on multiple species than female otters, who are more commonly described as specialists (Smith et al., 2015, Tinker et al., 2008). This study considers survey locations occupied by sea otters following an ongoing persistence of female sea otters, often with pups.

Otter occupation and influence by region

Of regions examined in this study, Prince of Wales locations had the most recent recorded occupation, where aerial surveys documented sea otters in Meares Pass in 2010 (USFWS 2014), yet ADFG dive researchers had noted obvious changes or first signs of otters in the area in 2004, including urchin biomass decline and benthic pits; indicative of otters digging clams (K. Hebert personal communication 2024; Table 3.1). Otter populations were not officially surveyed along the outer coast section of Dall Island (Prince of Wales), where study locations Gooseneck and Port Bazan are located, until 2014 aerial surveys, when Hoyt (2015) recorded established populations. Sea otters were first noted by ADFG divers six years prior, in 2005, in the locations (K. Hebert and Q. Smith personal communication 2019). The otters in Prince of Wales locations are thought to have populated Dall Island via the southward expansion of the Maurelle Islands otter populations (N=51 in 1968; Esslinger and Bodkin 2009, Hoyt 2015). Dixon Entrance was not occupied by sea otter populations during 2019 surveys, however, we noted individual 'scouts' during our 2019 surveys in the Percy Island location, and scouts have been reported in the region, but no rafts or established populations (e.g., Bee Rocks; K. Hebert, personal communication, 2019).

Sitka had the longest-recorded occupation of sea otter populations across regions examined in this study. Aerial surveys and local reports identified established sea otter populations throughout Sitka Sound by 2003, including Sitka North, Inside and Outside locations (Esslinger and Bodkin 2009, White and Raimondi 2024, Table 3.1). Between 1965 and 1969, otters were translocated to areas approximately 70 km north (Khaz Bay, N=164) and 18km south (Biorka Island, N=48) of Sitka (Burris and McKnight 1973). Northern otter populations in Khaz Bay grew and eventually moved south to fully occupy "Sitka North" location by 1987 (Table 3.1). Participants from recent surveys (see White and Raimondi 2024) identified sea otter movement into Sitka Sound from the North, with select sightings of otters inside Sitka Sound in 1993 and established populations by 2000. Though sea otters were reintroduced to Biorka Island, within the Sitka Outside location in 1967 (N= 43; Pitcher 1989), populations were patchy, and otters were not reported to have fully occupied the outside location until 2003 (White and Raimondi 2024, see Table 3.1). The staggered growth of populations on the outer coast of Sitka Sound is an example of the importance of growth rate as a factor contributing to sea otter influence.

Growth rate influence

An added factor important to local sea otter influence, population growth rate, was, by necessity, modeled and substantiated by local experts. There is a general negative relationship between otter population growth and occupation time, where a population grows faster initially, theoretically, when K Carrying Capacity is highest (Tinker et al., 2019). We included “sub-regional” population growth rates (Tinker et al. 2019) in our assessment of regional otter influence (see sub-regions N05 and S04 in Table S4 of Tinker et al. 2019, Table 3.1). As an example, a location with a recently established, large population of sea otters in an area projected to have a higher growth rate was categorized with a relatively high sea otter influence (see Table 3.1).

Otter abundance influence

Information on sea otter abundance measures was provided by the U.S. Fish and Wildlife Service (USFWS). Expected otter abundance measures per area (km^2) in 2019 were derived per survey location using a diffusion model (Eisaguirre et al., 2021) and calibrated with most recent 2022 sea otter surveys of the Southeast otter populations (Schutte et al., 2023). These estimates were not direct counts but provided a theoretical frame for comparisons and were corroborated by local reports and ranking systems of otter abundance in Sitka (see White and Raimondi 2024). Sea otter expected abundance estimates did not include USFWS tag information.

Sea otter harvest influence

Finally, to assess the potential influence of hunting on sea otters, we examined reported harvest figures and behavioral avoidance responses of otters at the location scale. Sitka was the only region in our study with recent, regular harvest reports (USFWS unpublished data, S. Hanchett, B. Benter personal communication). Harvest within Sitka locations displayed considerable variation harvest rates were relatively highest from 2014 to 2017 (USFWS unpublished data). Harvest in Sitka is thought to dampen local population growth and is tied to a deviation between modeled population size and empirically derived population abundancies for Sitka Sound (see sub-region N05 in Raymond et al. 2019, see Table 1). Harvest amount and weight of harvest intensity per Sitka location were determined relative to the mean number of tags per the 2017 to 2019 harvest years (USFWS unpublished data). We focused on the most recent years of location harvest, as sea otter avoidance responses are strongest following recent hunting efforts (Hoyt 2015), and hunters have been documented to slow efforts following a period of initial sea otter repatriation for numerous reasons (Raymond et al. 2019). Otters, fearing being hunted, are found to avoid hunting areas for a period of time, creating what is known as a “halo effect” (Hoyt 2015). Indigenous hunters, who have long-standing relationships with sea otter populations, are familiar with this phenomenon and have historically removed sea otters from specific areas to protect important shellfish (Menzies 2015, Salomon et al. 2018, Moss 2020, Ibarra 2021).

Therefore, the years 2017 to 2019 provided the clearest recorded information on recent harvest dynamics. Sea otter harvest was weighted negatively in the determination of location otter influence. For example, if a location in Sitka experienced recent recolonized by a large population of sea otters in an area projected to have a higher growth rate and experienced high otter harvest in the years preceding the surveys (2017-2019), relatively recent reoccupation and higher projected growth rates would increase otter influence. However, the removal of sea otters and potential fear response related to recent harvest reduces otter influence of the location (i.e., Sitka Outside) to reflect a “moderate” influence (Table 3.1).

In total, these weighted factors contributed to the general categories of sea otter influence per location: high, moderate, low, or no otter influence, and a more specific scale of relative sea otter influence from low (0) to high (7) sea otter influence (see Table 3.1). Given the limited survey data and replications across all locations, we also categorized otter influence at the regional level, where Dixon Entrance had a “low” otter influence, Sitka a “moderate to high” otter influence, and Prince of Wales a “high” otter influence as shown in Table 3.1.

Abalone and urchins by region, otter influence

To determine whether abalone and urchin measures varied across regions and locations with differing levels of otter influence and to assess the potential inverse relationship between otter influence and these measures, we first calculated abalone densities and urchin biomasses. We then conducted separate Analysis of Variance (ANOVA) tests to compare mean sea urchin biomass and mean abalone densities across different locations and regions (fixed effects). We calculated abalone densities (abalone count/m^2), and urchin biomass (kg/m^2) per site provided known relationships of urchin test size (mm) to wet mass (grams) (Estes et al., 1978, Eq. 2.1 in Gorra et al., 2022). We used biomass for urchin comparisons instead of density, as urchin biomass provides the best measure for understanding grazing pressure (Gorra et al., 2022). In this context, urchin biomass provided a more ecologically impactful measure as foraging theory (i.e., Charnov 1976, Stephens and Krebs 1986) suggests larger prey (urchins) would provide greater energic gains to predators (otters) and may be more favored. In addition, species like abalone in locations with higher sea urchin biomass will contend with increased urchin metabolic demands and consumption. Finally, as a measure, urchin biomass has a recorded negative relationship with otter presence (Estes and Duggins 1995, Gorra et al., 2022, Weitzman et al., 2023).

Least square means (LSM) post hoc contrasts uses weighted linear and non-linear functions to test this prediction of non-linear relationship between abalone density and urchin biomass as a response to increased sea otter influence at regions. LSM contrast weighting was determined by relative sea otter influences at ten locations (see Table 3.1), where Prince of Wales had the strongest otter influence and was weighted more negatively than Sitka. Both regions were negatively weighted compared to the positive weights assigned to the Ketchikan and Dixon Entrance regions, which comprised locations with the least relative sea otter influence (see Table 3.1). As urchin biomass data were not available for the same number of regions, with no Ketchikan regional data, linear and non-linear weighting is between three regions for sea urchin comparison. For these comparisons, abalone are examined across four regions. Linear contrasts were ordered -0.75, -0.25, 0.25, 0.75 for abalone and -1, 0, +1 for urchins, and quadratic contrasts of regional abalone densities were -1, 2, 0, -1, and -1, 2, -1 for urchins. We predict sea urchin biomass will have a stronger negative linear relationship across regions and abalone densities and a stronger quadratic relationship to sea otter influence by region, as predicted and illustrated in Figure 3.2a.

Refuge habitat regional comparisons

To understand sea otter impact on abalone populations in Alaska and further corroborate the predicted regional otter influence shown in Figure 3.2, we conducted regional comparisons. We examined whether abalone populations across regions exhibited differing degrees of refuge-seeking behavior, a characteristic typically observed in abalone in otter-occupied areas (Lowry and Pearce 1973, Fanshawe et al., 2003, Raimondi et al., 2015, Lee et al., 2016). We predicted regions with varying levels of sea otter influence would exhibit varied abalone refuge use, and regions like Sitka, characterized by a moderate sea otter influence and over 25 years of sea otter occupation, would have notably higher proportions of abalone in refuge compared to regions in Prince of Wales, with relatively more recent sea otter occupation, and Dixon Entrance, where sea otters remain functionally absent (see predictions Table 3.2a).

We assessed abalone associations with refuge (i.e., cracks or crevices) with the amounts of available refuge habitat (1: good, 2: moderate, and 3: poor) recorded during habitat dive surveys and the observed abalone use of refuge habitat, from abalone surveys across regions. To determine if abalone disproportionately used refuge as a function of local sea otter influence (i.e., by spatial scales of location or region, see Table 3.1), the observed abalone habitat use was the number of pinto abalone (N_i) recorded in the same refuge habitat (i = 1: good= abalone in refuge, 2: moderate = in moderate exposure, and 3: poor = abalone exposed). We then calculated the proportion of available refuge per each available refuge habitat category (P_{hi}) at survey sites. Finally, using habitat and abalone habitat category proportions, we calculated the "Expected" abalone habitat use (E_i ; Equation 3.1).

Equation 3.1.

$$E_i = P_{hi} \times \sum(N_i)$$

'i' = refuge habitat (1: good, 2: moderate, 3: poor)

P_{hi}=*proportion of available refuge habitat per category 'i'*

N_i = number of abalone recorded in refuge habitat category *'i' (1, 2, or 3)*

$\sum (N_i)$ *= total number of abalone across all abalone refuge habitat categories (1, 2, and 3)*

E_i *= expected number of abalone in refuge habitat category per 'i' (1, 2, or 3)*

Finally, we compared distributions of observed (N_i) and expected (E_i) habitat category values across regions with varied otter influence through a generalized linear mixed model (GLMM), Poisson distribution log-link function with fixed effects of regions: Sitka, Prince of Wales, and Dixon Entrance, refuge habitat category (1: good, 2: moderate, or 3: poor), and observed and expected habitat use. Locations were nested in regions both as fixed effects. Sites, included as random effects, were nested in locations and regions. Specific focus was given to GLMM interactions between the differences in available and expected use per habitat category by either fixed effects of regions or fixed effects of locations nested in regions. These interactions were further examined by plotting expected and observed abalone refuge habitat use proportions across regions.

Refuge use a function of abalone size

Smaller abalone are more 'cryptic,' or difficult to record reliably, and may seek refuge as a general life history function of preservation compared with larger abalone. Therefore, to determine if refuge use was at all biased by size, we tested for abalone refuge use by abalone size. We calculated the observed (N_i) and expected (E_i) refuge habitat category values per abalone size category: "juvenile" (individuals ≤ 40mm shell length) and "adult" (individuals >41mm) and plotted proportions. We tested differences in the observed abalone refuge habitat use (N_i) by size across regions via a GLMM (Poisson distribution, log-link function), where abalone refuge habitat use (N_i) was examined as a function of fixed effects: size category ("juvenile" or "adult"), refuge habitat categories: in refuge, moderately exposed or exposed, region and location nested in regions, with sites nested in location, region, as random effects. Special attention was paid to size category per refuge habitat (Refuge Habitat x Size Category) and whether this relationship differed across spatial scales (Location[Region] x Refuge Habitat x Size Category or Region x Refuge Habitat x Size Category).

Refuge, size as a function of local habitat

For a general overview of how habitat compares across regions, and in relation to abalone size class, we examined the biogenic (algae and substrate) community composition at both the regional and Sitka location scales in ordination space through non-metric multidimensional scaling (nMDS). We used PERMANOVA analyses to determine statistical differences in available biogenic habitat among sites across regions and overlaid environmental vectors onto the nMDS ordination to examine the relationships between abalone densities by size class (juvenile or adult). Both the Bray-Curtis dissimilarity matrix and vector fit significance were assessed with a permutation test of 999 iterations.

Abalone, otters, and indicators: macroalgae, urchins, and abalone behavior

We also explored a final potential indirect effect of local sea otter influence on macroalgae, where otters may positively influence these populations via consumption of sea urchins and other grazers, as shown in Figure 3.2b. Mean proportions of macroalgal kelps recorded at sites were used for general comparisons across locations and otter influence. Proportions were calculated via the sum of *Macrocystis spps.*, and understory species of *Saccarina*, *Laminaria*, *Agarum spps.* recorded during habitat surveys, divided by the total number of habitat points recorded, which included algae and substrate (i.e., points of cobble, bedrock), if no algae were documented on the layer above the substrate along transects (see Appendix in White and Raimondi for habitat types surveyed).

Proportions were included in a larger comparison, which focused on the responses of macroalgae, abalone refuge habitat use, and abalone density to predictors of urchin biomass and sea otter influence across locations, with respective sea otter influence values (see Table 3.1). We used regression analysis to examine relationships between macroalgae, refuge habitat use, and abalone density to urchins and sea otter influence. Urchin biomass and sea otter influence were included as separate predictors to assess

1) whether relationships follow predicted otter-urchin-kelp cascading interactions outlined in Figure 3.2), and the efficacy of urchin biomass as an indicator for sea otter influence. For urchin biomass to serve as a proxy of otter influence, we predict that urchin relationships with abalone densities, proportions of macroalgal cover, and refuge habitat use will mirror those relationships with sea otter influence. For instance, locations with relatively low urchin biomass might correlate with higher amounts of macroalgae cover and greater proportions of abalone in good refuge, where abalone may remain sheltered with more abundant macroalgal drift (kelp). Whereas locations with higher sea otter influence were predicted to have increased macroalgal proportions and increased proportions of abalone in refuge habitats as a potential response to predator sea otter presence

Abalone and urchins, urchins and otters

We also predicted similar non-linear responses of abalone densities to urchin biomass as that for densities with sea otter influence and ran model comparisons for best non-linear fits for the relationship of abalone densities as a function of the urchin biomass at locations. Importantly, we tested our prediction that sea urchins would demonstrate a negative relationship with increased sea otter influence in the otter-urchin-kelp trophic cascade (Figure 3.2) and examined urchin biomass as a function of sea otter influence through regression analysis across locations.

For statistical assessment, square root transformations of abalone densities were used to stabilize variance and heteroscedasticity, urchin biomass was transformed by log(x+1) to meet assumptions of normality and proportional refuge habitat, and macroalgae data (proportion cover) were transformed using an arcsine square root transformation. nMDS ordination plots were created in R 4.3.1 “Beagle Scouts” with the metaMDS function and accompanying PERMANOVA analyses were done with the Adonis function in the R vegan package, abalone size class vectors were included and fitted using the envfit function (R Development Core Team, 2023-06-16). All other figures and analyses were run in JMP Pro18.

RESULTS

Abalone and urchins by region, otter influence

Analysis of Variance ANOVA tests revealed differences in mean abalone density (F(3, 3) = 15.646, $p < .0001$) and mean urchin biomass (F(2, 2) = 31.70, $p < .0001$; see Table 2) among regions with varying degrees of sea otter influence (see Table 1). Surveys documented the highest abalone densities in Sitka (0.67/m^2 ± 0.47), a region with relatively moderate sea otter influence, and lowest densities in Prince of Wales (1.61 ± 1.52), a region with the highest sea otter influence. There was a range of abalone densities regions with the lowest otter influence, Dixon Entrance and Ketchikan (0.67/m^2 ± 0.47 and 0.29/m^2 ± 0.30, respectively, Figure A3.1). Urchin biomasses varied widely across regions, increasing with decreasing regional otter influence, with 6.62 per kg^2 (± 7.65) in Prince of Wales, 11.45 per kg^2 (± 12.10) in Sitka, and a notably higher 131.87 per kg^2 (± 51.93) in Dixon Entrance (see Figure A3.1).

Refuge habitat regional comparisons

When examined against expected, exposed, and moderately exposed habitat use, abalone disproportionately occupy refuge habitat types ($p<.0001$ Figure 3.3, Table 3.3).

This observed habitat use is influenced by both the exposure habitat type (1: refuge, 2: moderately exposed, or 3: exposed) and by spatial scales (i.e., interactions with location and region) with respective spatial sea otter influence (see sea otter influence based on factors at locations and regions in Table 1 and the three-way bolded interactions terms: Region x Refuge Habitat x Observed/Expected p<.0001 and Location[Region] x Refuge Habitat x Observed/Expected; p=0.0019 in Table 3.3). Regional effects were the most significant predictors of disproportionate abalone refuge use (per refuge habitat category, see Figure 3.3), where the difference between expected and used refuge in Sitka was greatest, with 93 percent of abalone in refuge in Sitka (Figure 3.3). Fewer abalone were in refuge in areas with relatively more available good refuge habitat in Prince of Wales (87%) and Dixon Entrance (84%), both regions had relatively more refuge habitat (Figure 3.3). Moderately exposed habitat was most available in the Prince of Wales yet the least occupied in the region, whereas abalone in Dixon Entrance appeared more often in the moderate refuge. Notably, Sitka abalone were least often found in exposed, poor refuge habitats, while Prince of Wales abalone occupied exposed habitats more often than expected across regions (Figure 3.3).

Refuge use a function of abalone size

Small (juvenile) and large (adults) abalone used refuge differently across locations (Prob > F = 0.0233) and regions (Prob > F <.0001) scales (Table 3.4). In Sitka and Prince of Wales, adult abalone were more often recorded in good refuge habitat, and higher proportions of juvenile abalone were in exposed habitat (Figure A3.2). Conversely, in Dixon Entrance, there were higher proportions of juvenile abalone in good refuge habitat and more adults exposed in poor refuge habitat (Figure A3.2).

Refuge as a function of local habitat

Ordination plots of regional biogenic habitat show clear differences in biogenic habitat and substrate available across regions PERMANOVA F (2,29) = 7.9378, $R^2 = 0.31916$, p = 0.01 (see nMDS plot Figure 3.4). This difference is reinforced by the clear separation of 95% CI ordination ellipse, each in a separate quadrant (see Figure 3.4). The plot stress value of 0.159 indicates a reasonable fit of data displayed in nMDs format. Compared to other regions, Prince of Wales was more dominant in macroalgal species, found less commonly in other regions. Other key differences in biogenic habitat were found in Dixon Entrance, which had the highest records of Crustose Coralline Algae (CCA), and higher amounts of bedrock that might support ongoing CCA communities (Figure 3.4). Abalone size class densities compared via vectors overlain across regional biogenic habitat did not share significant relationships with plotted habitat (adults: $r^2 = 0.0143$, p = 0.804; juveniles $r^2 = 0.0224$, p = 0.659).

Abalone, otters, and indicators: macroalgae, urchins, and abalone behavior

Otter influence across study locations followed distinct trends (Figure 3.5 panels b, d, f). Higher otter influence was strongly associated with increased proportions of macroalgae, increased records of abalone 'hidden' in good refuge habitats, and lower proportions in poor or exposed habitats (Figure 3.5 panels f and d). Abalone densities had a non-linear association with otter influence, with the highest densities recorded in the Sitka region, with a 'moderate to high' otter influence (also see Figure A3.1). The lowest densities were recorded in areas with the highest otter influence, Prince of Wales (Figure 3.5b; see also Figure A3.1 and Table 3.2). Non-linear trends in abalone density are the same, yet linear trends in the proportions of macroalgal cover, abalone refuge, and exposure habitat use associated with sea urchin biomass were inverse to those associated with sea otter influence (Figure 3.5).

Abalone and urchins, urchins and otters

At regional scale contrasts, abalone densities demonstrated a non-linear relationship with increased urchin biomass at locations where both species were measured across Southeast Alaska (Figure 3.5a). Figure 3.5 panel 'a' showed a significant quadratic relationship between abalone and urchins across locations with varied otter influence. However, a Gaussian Peak model best fit the non-linear relationship between abalone and urchin abundance measures, with a lower AICc (52.78) and a higher AICc weight (0.62), when compared with the quadratic model (Quadratic: AICc:53.72; AICc weight 0.38, SSE = 58.61, MSE = 0.23, $R^2 = 0.31$; Gaussian Peak: SSE = 57.66, MSE = 0.22, $R^2 = 0.33$). The significant peak abalone density value estimated by the Gaussian model was 1.34/m^2 (SE = 0.14, 95% CI [1.06, 1.61], $p < .0001$), at the critical point of 3.18kg/m^2 urchin biomass (SE = 0.22, 95% CI [2.75, 3.61], $p < .0001$), with a growth rate of 1.72 (SE = 0.28, 95% CI [1.17, 2.28], $p < .0001$).

Finally, in a separate regression, we found urchin biomasses were notably reduced at locations with increased otter influence ($p < .0001$) (see Discussion Figure 3.6).

DISCUSSION

Patterns of interactions, trophic cascades

Comparisons across measures of sea otter influence at Southeast Alaska locations showed abundance patterns of abalone, urchins, and macroalgae consistent with traditional urchin-kelp-otter cascades predicted in Figure 3.2 and plotted using non-transformed data in Figure 3.6. Locations with low or no sea otter influence, such as those in Dixon Entrance, documented fundamentally different abalone behaviors (Figure 3.3) and habitats (Figure 3.4) than those with increased otter influence (Table 3.3, Table A3.2). There was a strong negative response of mean urchin biomass at locations as a function of sea otter influence (see Figure 3.6; Log (urchin biomass + 1): $R^2 = 0.63$, $F(1,35) = 68.79$, $p < 0.0001$). Negative direct interactions between sea urchins and otters highlighted in Figure 3.2b were demonstrated in linear LSM tests, which indicate an inverse relationship between urchin biomass and otter influence by regional scales (Figure A3.1, Table 3.2). Increased otter influence was also associated with decreased urchin biomass at a location (Table A3.1) scale and increased overall macroalgal cover (Figure 3.5e, Figure 3.4). As predicted by indirect interactions of otters and kelp in Figure 3.2b, study locations with greater sea otter influence had relatively reduced urchin biomasses and higher macroalgal cover (i.e., Prince of Wales, Figure 3.5, Figure 3.4, Table A3.2). This relationship was also supported by modeled macroalgal-otter relationships ($\sqrt{}$arcsine(macroalgal proportion): $R^2 = 0.43$, $F(2,34) = 12.83$, $p < 0.0001$) from data from Figure 3.6. Finally, non-linear trends shown in abalone densities across regions (Figure A3.1, Table 3.2) and locations (Figure 3.5b) are explained by sea otter influence as shown in Figure 5 (modeled $\sqrt{}$(abalone density): $R^2 = 0.24$, $F(2,34) = 5.47$, $p = 0.0087$).

Urchins also exhibit a non-linear, parabolic relationship with abalone across locations of varied otter influence (Figure 3.5a). This pattern mirrors the non-linear relationships observed in abalone densities when comparing regions with different levels of sea otter influence (Figure A3.1, Table 3.2) and the linear relationships between abalone densities and otter influence by location (Figure 3.5b, Figure 3.6). Positive relationships between abalone, otters, and urchins were limited to moderate degrees of sea otter influence (Figure 3.5b, Figure 3.6) and relatively moderate biomasses of sea urchins (Figure 3.5a). These moderate measures compared across study regions correlated with the highest records of abalone, which were in Sitka locations of the longest otter occupation, least otter population growth, and where harvest of both abalone and sea otters is ongoing (see Sitka in Figure 3.5a,b; Table 3.1).

Urchin indicators

Importantly, sea otter influence maintained a strong, predicted inverse relationship with urchin biomass (Figure 3.6). Since urchin biomass may vary by measurement across locations, yet sea otter influence is fixed, assigned by location factors (Table 3.1), the mirrored or similar patterns observed in both urchin (Figure 3.5a,c,d) and sea otter comparisons (Figure 3.5b,e,f) suggest that sea urchins are reliable indicators of otter influence. This is particularly evident as trends in abalone density, refuge use behavior, and macroalgal cover related to sea otter influence are inversely mirrored by trends related to urchin biomass (see sites by regional color plotted in Figure 3.5). These consistent patterns across surveys and the relationship between otter influence and urchin biomass as predictors suggest urchin biomass may further indicate the indirect impacts of sea otters on abalone populations. Urchin biomass may also help predict the impact of sea otters on habitat and food important to abalone, particularly given the relationship between urchins and abalone (Figure 3.5a) and competition between urchins and abalone (explored below).

Abalone habitat use and behavior

Individual abalone use of refuge habitat may be linked to food (algal) availability, sea otter presence, potential otter predation, and environmental conditions, all varying across spatial scales examined in this study. Abalone occupied different refuge habitat types when compared spatially (Table 3.3). Yet abalone were more often in good refuge habitats than was expected across study regions and locations (Figure 3.3), regardless of the regional biogenic habitat types (Figure 3.4) and respective sea otter influences (Table 1). In the absence of spatial effects of location and region, large (adult) and small (juvenile) cryptic abalone were not overall observed in different refuge habitats, eliminating possible bias of surveyed size per refuge type (see 'Refuge Habitat x Size Category' in Table 3.4).

Dynamics in the absence of otters

Where otter populations were functionally absent, we recorded the highest urchin biomasses, despite an ongoing modest dive fishery for red urchins (see Dixon Entrance Figure A3.1, Table A3.1). However, abalone densities recorded in relatively low otter influence locations were reduced compared to locations with moderate sea otter influences (i.e., Sitka Region, Figure A3.1). In the absence of top-down pressures of sea otter consumption (e.g., Figure 3.2), local abiotic factors are more influential in shaping otter prey populations like urchins (Weitzman et al., 2023), in turn, urchin populations attaining large biomasses in these areas may negatively impact abalone populations, as demonstrated in Figure 3.5a.

The amount of good refuge used by abalone in low otter-influence locations may assist in abalone protection from exposed marine environments. These locations in Dixon Entrance experience particularly extreme oceanic environmental factors as they are exposed to the open ocean. Though not measured, the dynamic system likely translates to limited drift kelp retention and little benefit for abalone and urchins to expose themselves to wave shock in poor refuge habitats. In addition, there were *limited* records of macroalgal cover at low otter-influence sites that may have drawn abalone out of refuge to seek algae, as described by Rogers-Bennett and Catton (2019) (see Dixon Entrance, green markers in Figure 3.5c). However, the most common macroalgae species in the region, Laminaria (green markers in Figure 3.4), is a poor food source, with chemical defenses induced by herbivory (Ritter et al., 2017) and thick blades and long stipes resistant to breakage (Krumhansl et al., 2011; Figure 3.4). Therefore, those abalone observed in poor habitat, and abalone populations overall in the region, may be limited by available food and refuge (i.e., cracks and crevices) found in the bedrock substrate most common in Dixon Entrance, low otter influence locations (Figure 3.4). This pattern supports findings by Lee et al. (2016), which suggest that available substrate and exposure play a larger role in refuge use by abalone at otter-free locations (Figure 3.3).

Dynamics across variable otter influence

In areas of nearby British Columbia, otters had three times more impact on the amounts of exposed abalone than environmental factors (Lee et al., 2016). Similarly, our study location with the longest overall otter occupation, Sitka, had the fewest records of observed poor refuge use and most abalone documented in good refuge (Table 3.1, Table 3.3). Abalone use of good refuge following a period of sea otter re-establishment is observed in other abalone species in areas of California (Lowry and Pearse 1973, Fanshawe 2003, Raimondi et al., 2015) and even in urchin species (Estes et al.,1998, Tegner and Levin 1983), with which abalone may compete for refuge. Contrary to findings in Sitka, where sea otter influence was determined at its highest, in Prince of Wales, abalone were more exposed in poor habitats than expected (Figure 3.3). This region also had the lowest mean densities of abalone and biomasses of urchins (see Prince of Wales locations in Figure A3.1, Table A3.1). This finding supported strong otter influence as initially determined and assigned (Table 3.1). Exposed abalone in the region may not have adjusted to sea otter predator presence. However, otter populations recovered nearly ten years prior, and abalone were recorded more often in refuge following an otter occupation of six years or less (Lee et al., 2016).

Poor habitat use may be an artifact of abalone movement to refuge habitat, as they are one of the more motile abalone species (Neuman et al. 2018, M. Fujioka unpublished data). The amount of moderate refuge in the abundance of algal cover sheltering much of the benthic species in the Prince of Wales region (see Figure 3.4) may also be facilitating more moderate refuge use (Figure 3.3). Prince of Wales abalone were, on average, smaller than other regions (Table A3.1), and most individuals in poor habitat were juvenile abalone (Figure 3.4). In addition, mesopredators were documented at higher densities at high otter influence sites (T. White unpublished data), including voracious sea star species like Pycnopodia, known to consume and play a significant role in abalone populations (Lee et al., 2016, Hofmeister et al., 2018). These mesopredators may influence abalone's use of cracks and crevices (Lee et al., 2016) as abalone may be trapped and consumed in good refuge habitat by *Pycnopodia* (Lee et al., 2016). Finally, abalone in high otter influence locations still used good refuge habitat 73% more than expected, but not as much as Sitka with 86% individuals in good refuge microhabitats (Figure 3.3)

Dynamics in complex systems (Sitka)

Though a suitable habitat may protect abalone from predators like sea otters, developing a learned response to otter presence requires time. Research indicates that otters exert the most intensive ecological impacts during the initial periods of their occupation (Estes et al., 2003, Hoyt 2015, Coletti et al., 2016, Eisaguirre et al., 2021). Initial impacts following sea otter sightings at local harvest sites in Sitka suggest early effects on abalone populations (e.g., White and Raimondi 2024). However, it appears that long-established sea otter populations do not exert the same level of impact on local abalone populations. Despite the initial effects and ongoing perceptions of sea otter impacts on abalone (see White and Raimondi 2024), we observed recruitment of young abalone and increased densities at monitoring sites (Figure 3.1). Notably, the sites in Sitka included in this study continued to exhibit higher overall abalone densities in the region (Figure A3.1, Table A3.1).

Factors contributing to high abalone density

Sitka Sound hosts the longest-established reintroduced sea otter populations in proximity to the community of Sitka. Community members continue to harvest abalone, yet, abalone at locations in Sitka are at relatively higher densities than other regions (Table A3.1). Additionally, following the reoccupation and population expansion of sea otters, local Alaska Natives have re-engaged with historical customary and traditional marine mammal hunting and handicraft practices in Sitka locations, with minimal reports in other study locations (see Table 3.1, USFWS unpublished data). Considering these characteristics, we categorized Sitka as experiencing a moderate otter influence, with the longest occupation of otter populations that are minimally growing or limited by hunting (Table 3.1). This moderate influence was ranked positively (for lower trophic species) as a factor in determining sea otter influence (Table 3.1). The positive weight given to longer otter influence assumes findings elsewhere that following a period of occupation, energetically favorable (large, accessible) prey are reduced, and otters may shift to wider varieties of, often smaller prey items (Estes et al.,1981, Kvitek et al., 1993, Laidre and Jameson 2006, Tinker et al., 2008, Hale et al., 2019).

Accurately determining the effects of local sea otter presence in complex ecosystems is challenging, given factors like available prey and otter behavior (e.g., Honka 2014). Recent surveys of stable isotopes in Prince of Wales showed that otters consumed less calorically rich prey initially, shifting to more lipid-rich urchins with increased occupation time (LaRoche 2023). Though this may not directly apply to abalone, the growth of abalone populations following a period of otter occupation in Sitka supports our initial assumption and the positive weighting of increased otter occupation, suggesting that over time, any initial impacts of otters may be ameliorated by dietary specialization or, potentially in the case of Sitka study locations, by hunting (see Table 3.1). Additionally, researchers found a significant effect of otter occupation in 2009, with reduced sea urchin populations leading to a resurgence of kelp forests (see Gorra et al., 2022). This further supports influence weighting and established trophic cascades (e.g., Figure 3.1(a, b)). In contrast to their herbivorous urchin competitors, pinto abalone populations have recently shown signs of recovery in Sitka (Figure 3.1, Bell et al., 2018). Sitka's dense abalone populations may have been indirectly supported by the impact of sea otters on urchins at more localized scales like those interactions established at regional scales (Figure 3.6). An additional study using the same data found that abalone densities increased with distance from the town (Figure 3.6), where most of the abalone harvesting was reported in recent surveys (White and Raimondi 2024).

Importantly, otters were more abundant in areas farther from the community of Sitka (Table 3.1, Gorra et al., 2022, White and Raimondi 2024), abalone were found in greater densities at sites away from the community of Sitka, towards areas of higher otter abundance (Figure 3.7, Gorra et al., 2022, White and Raimondi 2024). Abalone populations recorded in these 2018 and 2019 surveys appeared to be more supported by the indirect interactions of sea otters (White and Raimondi 2024). Other local environmental processes or the increase in sea otter harvest (USFWS unpublished data) around the sea star wasting event and die-off in 2014 (Miner et al., 2018) likely significantly contributed to these anomalous and high densities of abalone observed in the Sitka region.

The local removal of sea otters through harvesting influences both the ecosystems they occupy and the behavior of neighboring sea otters, leading to their movement away from hunted locations (Hoyt 2015). However, otter hunting was not a likely cause of decreased abundance near a town, as reported otter tags, which indicated areas of take, were most often reported away from Sitka during abalone surveys and not concentrated town (White and Raimondi 2024, USFWS unpublished data). Additionally, hunters reported only short periods of avoidance behavior (i.e., months), which would not likely contribute to a lasting 'halo' of otter avoidance around the community of Sitka during the years of this study (described in White and Raimondi 2024; see Table 3.1). Furthermore, Sitka abalone densities did not show a clear increase in response to otter hunting at local scales (White and Raimondi 2024). Still, as outlined in Sitka (Figure 3.5b) and regionally, moderate otter influence has a clear benefit for abalone (Figure 3.6), and the appropriate practice and harvest of otters via traditional and customary means may mitigate the deleterious effects abalone populations experience at 'high otter influence sites' after an initial period of otter reoccupation (Figure 3.6).

More accurate local assessments of sea otter impact at smaller scales would benefit the spatially specific identification and weighting of the factors determining sea otter influence in this study. Additional information on occupation period, abundance, harvest, and added measures of local or sea otter and abalone harvest (as outlined in White and Raimondi 2024) would help inform local spatial scale changes to abalone populations. More accurate prey choice assessment and specialization over occupation periods are especially important for predicting local sea otter effects (e.g., Tinker et al., 2008). As of 2024, there are opportunities to study sea otter reoccupation in real-time, particularly in areas like Ketchikan, where sea otter activity has been recently reported (K. Hebert pers. comm., 2023). Incorporating Indigenous Knowledge and local expert observations, such as harvester notes and samples of otter stomach contents, otter behavior, and dynamics at abalone harvest sites, could enhance the spatial efficacy of these assessments.

This study identifies a classic otter-kelp-urchin relationship (Figure 3.2, 3.5) across locations in Southeast Alaska and, importantly, provides a foundation for understanding the direct and indirect impacts that pinto abalone populations likely experience across degrees of otter influence. While sea otters are often seen as predators with negative impacts on shellfish (Larson et al., 2014; White and Raimondi 2024), this study reinforces the more nuanced role of sea otters where, via control of species like urchins, otters may indirectly benefit abalone populations (Figure 3.2b). In addition, urchin biomass indicated an inverse relationship with sea otters and acted as a general indicator of the indirect and direct effects on abalone across Southeast Alaska. Given study factors and their weighting (Table 3.1), moderate sea otter influence at locations is most beneficial for pinto abalone populations, even in areas with human abalone harvesting and long-standing otter populations (i.e., Sitka Table 3.1, Table A3.1). Important local dynamics occur at local scales (see random effect of sites included in analyses; Tables 3.2, 3.3, A3.2). Understanding these ecosystem-based interactions is likely crucial for effective management instead of focusing on separate species assemblages or direct species interactions. Identifying and adapting the management of these interactions at local scales is essential for the ongoing harvest of important species like pinto abalone in Alaska.

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TABLES

Table 3.1. Study Regions, Locations, and Factors Used to Assess Sea Otter Influence. Sea otter "re-occupation range" spans from the first sea otter sighting to estimated sea otter population persistence (i.e., otter rafts with pups). Sea otter "occupation" per location is based on available survey data (Pitcher 1989, Esslinger and Bodkin 2009, USFWS 2014, Hoyt 2015) and local expert reports (Prince of Wales, K. Hebert personal communication, Sitka: see White and Raimondi 2024). Estimated occupation year is a conservative measure indicating the establishment of viable populations across all survey sites per location. Factors used to determine sea otter influence per study location included years of occupation, occupation category, harvest, estimated sea otter abundance, and relative growth rate. Influence is based on the weight of these factors as either [+]: a factor that when high increased sea otter influence on prey species, or [-]: a factor that when high decreased sea otter influence on prey species. Otter harvest intensity per location is relative to regional harvest from 2017 – 2019 (USFWS unpublished tag data). Expected otter abundance data included for 2019 (2016 for Meares Pass) per general location area (km2) provided by USFWS via a diffusion model developed by J. Eisaguirre et al., (2021), calibrated with 2022 Southeast Alaska otter aerial survey data (Schuette et al., 2023). Estimates do not include USFWS tag information. Sub-regional population growth rates were ordered and categorized based on Tinker et al. (2019) model (sub-regions N05 and S04 in Table S4). Sea otter influence is relative to locations and survey year, as otter factors (i.e., harvest data, expected sea otter information) are based on 2019 data. Only regional-scale comparisons were made with data collected in 2016 (i.e., Gravina Island and Meares Pass locations). Regions and locations surveyed in 2019 were assigned four general levels of sea otter influence and relative sea otter influence values, from low otter influence (0) to high otter influence (7).

Spatial Scale		Re-occupation timeframe			Otter Factors: Occupation, Growth, Harvest, Expected Abundance						Relative Sea Otter Influence		
Region	Location	First sightings	Re-Occupation Range	Est. Occupation	[-]	[-]	[-]	[+]	[+]	[+]	By Region	By Location	Relative Influence
					Years of Occupation	**Occup. Category**	**Otter Harvest**	**Otter Abundance Ordered**	**Exp. otter abund. per km²**	**Growth Rate Category‖**			
Sitka	Sitka North	1979	1979-1995	1996 (1983)	25 to 36	Moderate	Mod.§	**4**	0.042 (SD: 0.71)	Negative	Mod. - High	Mod.	**4**
Sitka	Sitka Inside	1994	1995 - 2001	2002	15 to 24	Moderate	Low§	**3**	0.053 (SD: 0.08)	Negative	Mod. - High	Mod.	**3**
Sitka	Sitka Outside	1985 (1967**)	1986 - 2002	2003	15	High	High§	**2**	0.057 (SD: 0.08)	Negative to Low	Mod.- High	High	**5**
Prince of Wales	Meares Pass*	2004 - 2007†	2004 – 2007† , 2010‡	2007	9 to 10	High	Low	**1**	0.067 (IQR: 0.08)	High	High	High	/
Prince of Wales	Gooseneck	2005– 2007†	2011† - 2014¶	2011	10 to 8	High	None	**5**	0.042 (IQR:0.04)	High	High	High	**6**
Prince of Wales	Port Bazan	2005†	2011† - 2014¶	2011	10 to 8	High	None	**6**	0.036 (IQR: 0.041)	High	High	High	**7**
Ketchikan	*Gravina Island**	*Sightings in 2015*	*2015 - ongoing*	/	/	Low	None	/	/	Unknown	Absent - Low	*Low*	/
Dixon Entrance	Percy Islands	Sightings in 2017	2017 - ongoing	/	/	Low	None	/	/	Unknown	Absent - Low	Low	**2**
Dixon Entrance	Duke Island	No otter reports	/	/	/	Absent	None	/	/	/	Absent	Absent	1
Dixon Entrance	Bee Rocks	No otter reports	/	/	/	Absent	None	/	/	/	Absent	Absent	0

*2016 surveys (Donnellan and Hebert 2017)
**Burris and McKnight translocation location (Biorka Island)
† Otter presence and effect notation during area dive rotations (1995 – 2011) of Red Urchin sample sites (K. Hebert pers. comm. or unpublished ADFG data).
‡ USFWS 2014
¶Hoyt 2015
§ sea otter tag data (USFWS unpublished data)
||: Sitka growth rate,before a period of harvest (1995-2012) (log(l): -0.022; 95% CI -0.108 to 0.073), and Prince of Wales, Dall Island growth rate (2003-2012; 7.78, log(l): 0.228, 95% CI 0.134 – 0.318) (see sub-regions N05 and S04 in Table S4 of Tinker et al. 2019).
'/' no value or missing value

Table 3.2. Analysis of Variance (ANOVA) Least Squares Means Contrasts (LSM) of regional abalone densities (abalone/m^2) and urchin biomasses (kg/m^2) by weighted regional otter influence (see Table 3.1). Regions (fixed effects) included in order of negative to positive weight for contrasts Prince of Wales, Sitka, Dixon Entrance, and Ketchikan (in abalone density comparisons). Abalone densities from Ketchikan and the location Meares Pass (Prince of Wales) were from 2016 surveys (see Donnellan and Hebert 2017). Urchin biomasses were not available for the 2016 surveys. Abalone densities were square root transformed, and urchin biomasses were log(x+1) transformed to meet assumptions of normality and heteroscedasticity.

LSM CONTRASTS [Weights]

Abalone Density LSM Contrast	**SS**	**NumDF**	**DenDF**	**F Ratio**	**Prob > F**
Linear [-0.75, -0.25, 0.25, 0.75]	0.02	1	57	0.1336	0.7161
Quadratic [-1, 2, 0, -1]	6.814	1	57	45.2143	<.0001

Urchin Biomass LSM Contrast	**SS**	**NumDF**	**DenDF**	**F Ratio**	**Prob > F**
Linear [-1, 0, +1]	30.04	1	32	35.1434	<.0001
Quadratic [-1, 2, -1]	8.688	1	32	10.1643	0.0003

Table 3.3. Generalized Linear Mixed Model (GLMM) analysis of observed and expected abalone refuge habitat use across spatial scales of Southeast Alaska (outlined in Table 3.1). Model log-linear link function, Poisson distribution. Abalone observed and expected refuge habitat (good, moderate, poor) use calculated from habitat surveys. Bolded interactions address study questions on deviations from expected refuge use by the spatial scale and corresponding otter influence. See Figure 3.3 for plotted proportions of observed and expected refuge habitat (good, moderate, poor) use per region (Sitka, Prince of Wales, Dixon Entrance).

Variance Component	Estimate	Std Error	95% Lower	95% Upper	Wald p-Value
Site Label[Region,Location]	0.327	0.116	0.100	0.554	0.0047*

Source	Nparm	DFNum	DFDen	F Ratio	Prob > F
Region	2	2	28.8	37.087	<.0001*
Location[Region]	5	5	24.4	0.493	0.7785
Refuge Habitat	2	2	324	38.019	<.0001*
Observed/Expected	1	1	324	11.676	0.0007*
Region x Refuge Habitat	4	4	324	31.736	<.0001*
Region x Observed/Expected	2	2	324	0.583	0.5587
Refuge Habitat x Observed/Expected	2	2	324	15.947	<.0001*
Region x Refuge Habitat x Observed/Expected	**4**	**4**	**324**	**6.237**	**<.0001***
Location[Region] x Refuge Habitat	10	10	324	3.250	0.0005*
Location[Region] x Observed/Expected	5	5	324	1.157	0.3302
Location[Region] x Refuge Habitat x Observed/Expected	**10**	**10**	**324**	**2.872**	**0.0019***

Table 3.4. Generalized Linear Mixed Model (GLMM) analysis of observed abalone refuge habitat use by size class across scales. Size categories cryptic, 'juvenile' ≤ 41mm, and 'adult' abalone (> 41mm) were recorded in either good (in refuge), moderate (moderately exposed abalone), or poor (exposed abalone). Interactions in bold are the focus of study questions of difference in size class use of refuge habitat across spatial scales. Regions and locations with respective sea otter influences are outlined in Table 3.1. Percent of total refuge habitat use observed per size class is plotted in Figure A3.2.

Variance Component	Estimate	Std Error	95% Lower	95% Upper	Wald p-Value
Site Label[Region,Location]	0.266	0.100	0.070	0.462	0.0077*

Source	Nparm	DFNum	DFDen	F Ratio	Prob > F
Region	2	2	140.0	0.019	0.9816
Location[Region]	5	5	49.2	0.369	0.8675
Habitat	2	2	140.0	0.000	0.9997
Region x Refuge Habitat	4	4	140.0	6.389	<.0001*
Location x Refuge Habitat [Region]	10	10	140.0	3.432	0.0005*
Size Category	1	1	140.0	74.902	<.0001*
Region x Refuge Habitat x Size Category	**4**	**4**	**140.0**	**10.071**	**<.0001***
Location[Region] x Refuge Habitat x Size Category	**10**	**10**	**140.0**	**2.166**	**0.0233***
Refuge Habitat x Size Category	**2**	**2**	**140.0**	**0.006**	**0.9944**
Location[Region] x Size Category	5	5	140.0	2.236	0.0540

FIGURES

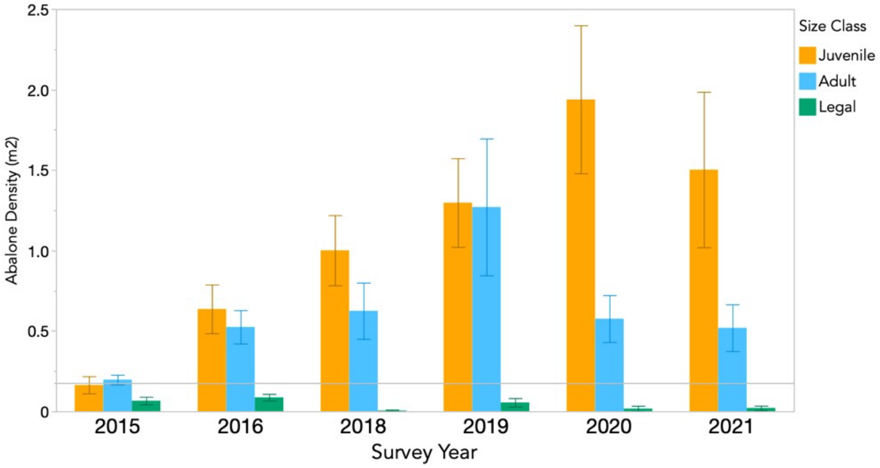
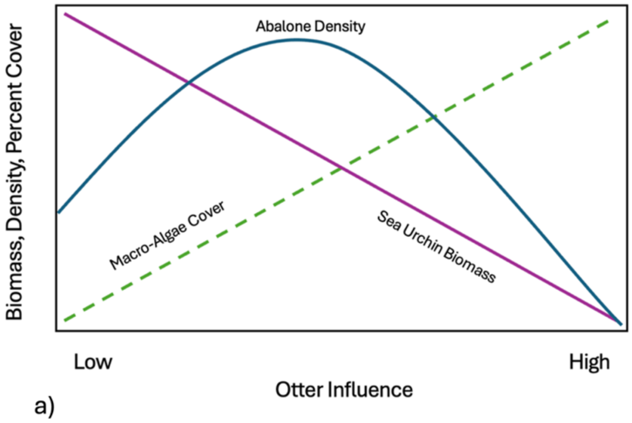


Figure 3.1. Pinto abalone size class densities recorded across Sitka monitoring sites by survey year (2015 – 2021). In yellow: juveniles < 41mm, in blue: adults > 40mm, and in green: legally harvestable ≥ 89mm abalone. Bars represent standard deviations from the mean of the ten transects sampled (at five sites). Abalone < 20mm in length were tallied by divers during 2015 and 2016 dive surveys but included with all sizes in the following survey years. A grey line at 0.2/m^2 indicates the adult abalone density threshold determined for local pinto abalone population viability (see Chapter 2 Figure 2.6). Error bars represent ±1 Standard Error. Original figure from NPRB Report #2115 (White and Raimondi 2024).



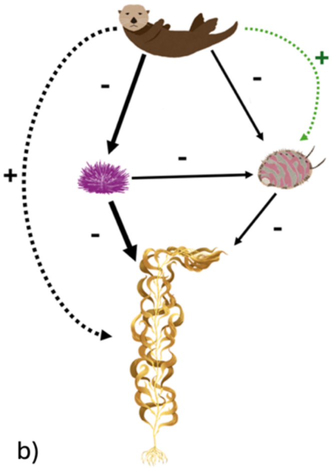


Figure 3.2a. Predicted non-linear relationship between abalone density (per m^2) and sea otter influence with linear trends of co-variant effects of sea urchin biomass (kg/m^2) and proportion of macroalgae (i.e., *Saccarina, Laminaria, Agarum, and Macrocystis*) species presence at locations across Southeast Alaska. As otter influence increases, there is a decline in abalone density (blue curve) after a certain point, a decrease in sea urchin biomass (purple line), and an increase in macro-algae cover (green dashed line). Factors used to inform sea otter influence are in Table 3.1.

Figure 3.2b. Diagram of predicted northern sea otter (*Enhydra lutris kenyoni*), urchin (*Strongylocentrotus spps.*) macroalgae, and pinto abalone (*Haliotis kamtschatkana*) interactions across abalone survey sites in Southeast Alaska. Interactions contributing to relationships plotted by the outcomes predicted by sea otter influence, as outlined in Figure 3.2a. Direct (negative, solid lines) and indirect (positive, dotted lines) species interactions. Line weight suggests the strength of interactions. Art by: Jessica Kendall-Bar (kelp, urchin), Sienna Reid (abalone, otter). Adapted from Figure 2.1 in Estes 2015.

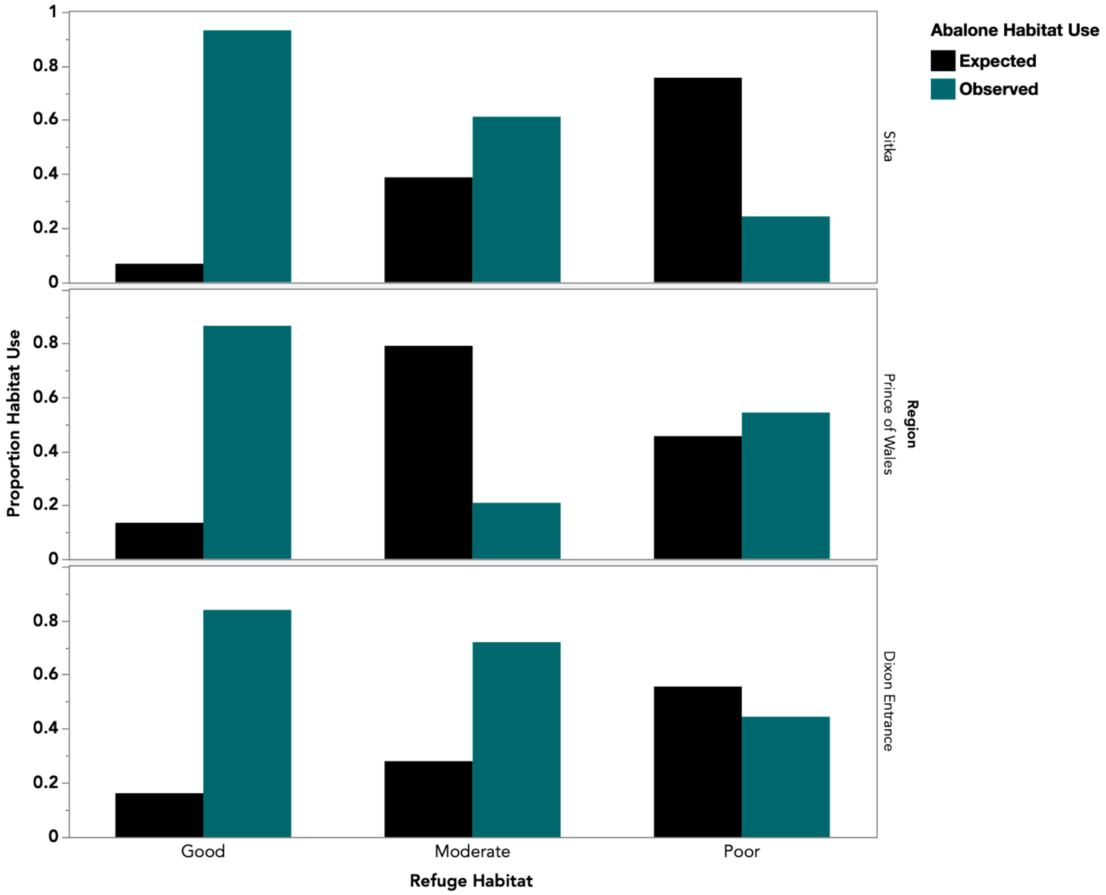


Figure 3.3. The proportion of observed and expected pinto abalone refuge habitat use (good, moderate, or poor) across regions: Dixon Entrance, Prince of Wales, and Sitka. Calculated expected refuge habitat use (in black) from surveys of available habitat refuge and observed refuge habitat use (in teal) in parallel for comparison. See Table 3.3 for modeled interactions and significance. Equation 1. explains calculations of expected and observed refuge habitat use.

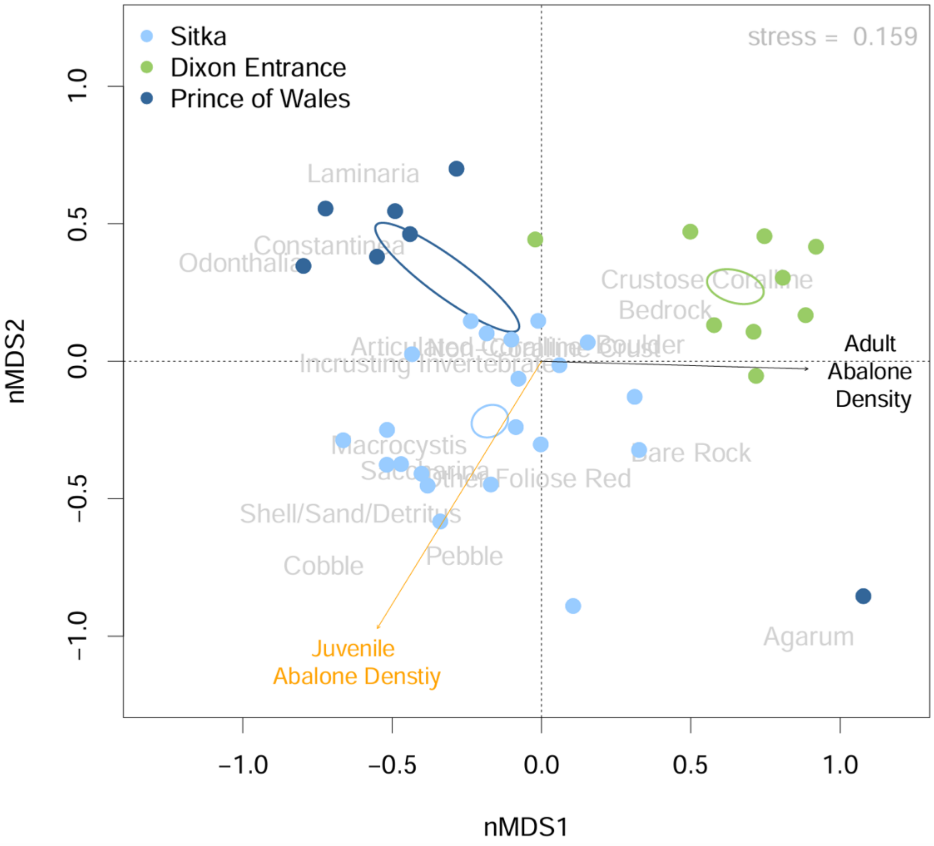


Figure 3.4. nMDS (non-metric multidimensional scaling) plot of biogenic habitat displayed by site habitat characteristics across regions: Sitka (light blue), Dixon Entrance (green), and Prince of Wales (dark blue). Ordination ellipses indicate distinct regional biogenic habitats. Size class densities overlaid as vectors, 'juvenile' abalone (≤ 41mm) in gold and 'adult' abalone (> 41mm) in black. Included are biogenic habitats (i.e., alga and substrate) that primarily influence the distribution of sites (i.e., points) within the plot. See Chapter 2 Appendix Table A2.1 for a species list.

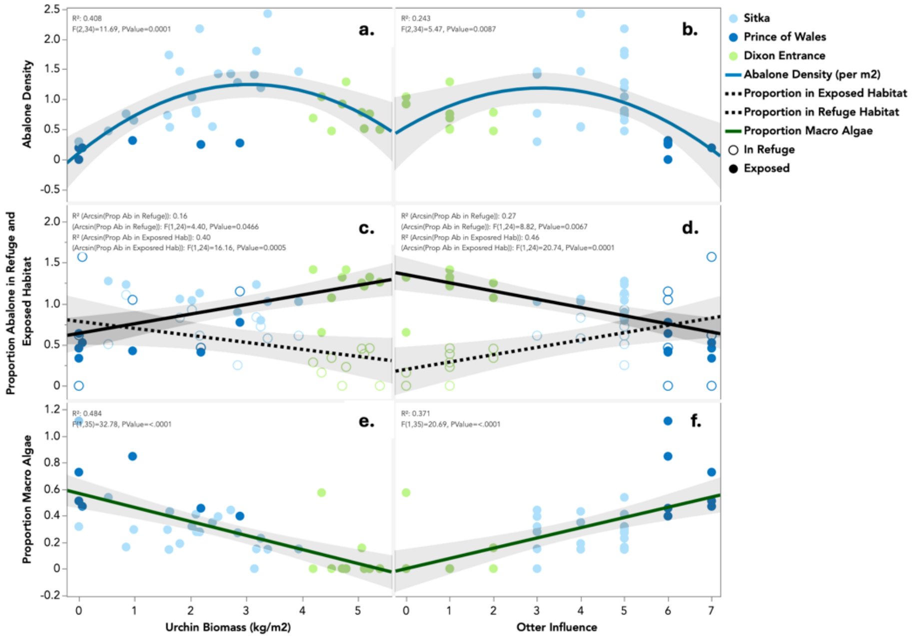


Figure 3.5. Interactions between otter influence, urchin biomass, abalone density, and macroalgae and habitat use across regions. Panels examine relationships between abalone density (a and b), proportions of abalone recorded in habitat considered refuge (i.e., cracks, crevices) or exposed (to predators; c and d), and proportion of macroalgae (e and f) and site urchin biomass (a) and otter influence (b). Factors used to determine otter influence per location are outlined in Table 1. Transformed data used for analyses are also plotted. Abalone densities are square root transformed and proportions of macroalgae and refuge or exposure habitat use are arcsine square root transformed. Urchin biomass was transformed by log(urchin biomass+1). (Non-transformed data are plotted in Figure A3.3).

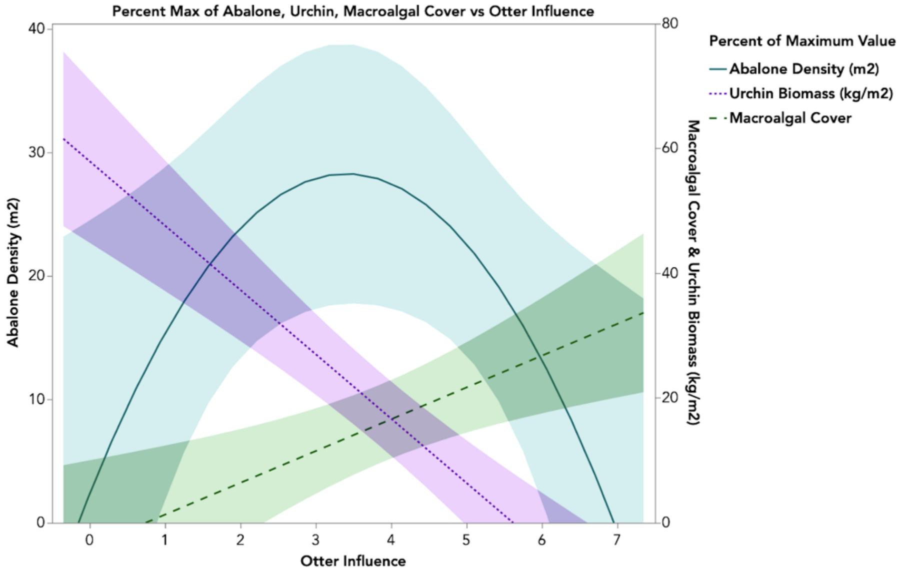


Figure 3.6. Relationships between abalone density (per m^2), urchin biomass(kg/m^2), and macroalgae proportion with sea otter influence across locations in Southeast Alaska. Percent of maximum values used to plot linear and non-linear relationships across locations with varying degrees of sea otter influence in Southeast Alaska (see Table 3.1). Modeled significance used transformed values (square root (abalone density), log (urchin biomass+1), and square root arcsine (macroalgal proportion)). Compare to predicted relationships between study species and otter influence in Figure 3.2a. Shaded areas represent confidence intervals for each trend.

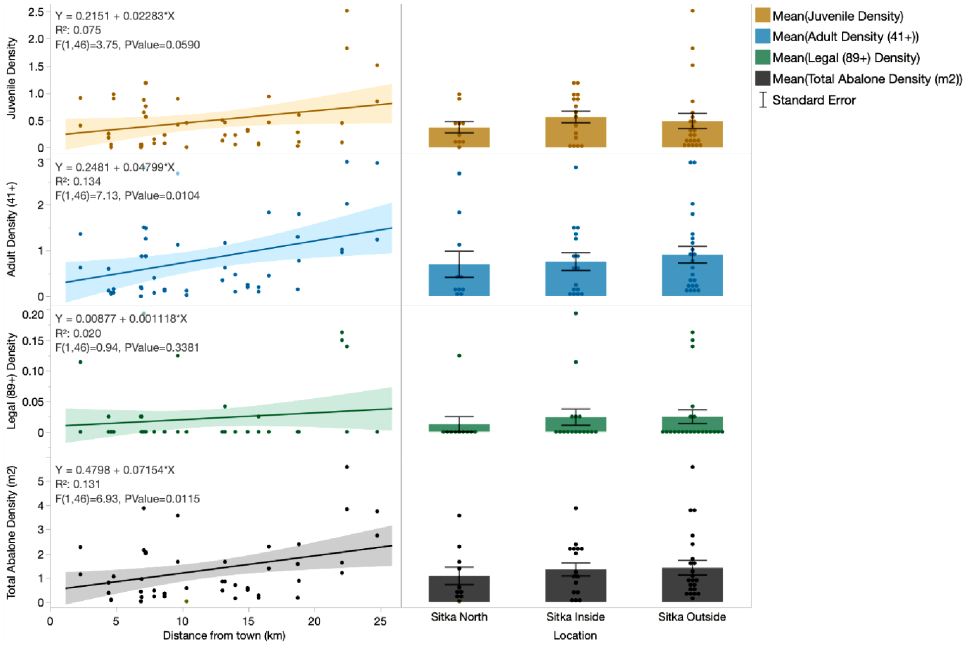


Figure 3.7. Abalone size class densities (count/m^2) distance away from town and among locations in Sitka Sound from randomly selected sites in Sitka Sound (surveyed 2018 and 2019). Abalone densities are categorized by size class categories: juvenile (< 41mm), adult (≤41mm), and legally harvestable (≥89mm) individually measured abalone. See Table 6 for densities by Sitka 'Location' (i.e., Large Polygon). Error bars represent ±1 Standard Error. Figure from White and Raimondi 2024. Table A3.1 outlines the mean total urchin biomasses at Sitka locations.

SYNTHESIS

This work enhances our understanding of pinto abalone populations at their northernmost range. It includes the most comprehensive surveys to date, assessing historical and spatial comparisons, population viability, critical densities, and the impacts of repatriated sea otter populations. Until now, limited and conflicting data on declining and growing pinto abalone populations have made it difficult to accurately determine their population status. The lack of comprehensive data on abalone in their northernmost range motivated the establishment of initial pinto abalone monitoring sites in Sitka Sound in 2015 (Bell et al., 2018). Though an integral first step, Sitka monitoring sites were limited in scope and could not represent all abalone aggregations throughout Southeast Alaska. In comparisons, monitoring sites also did not represent the range of densities at randomly selected site surveys in Sitka Sound revealed (see Chapter 2, White and Raimondi 2024). The expansion of surveys beyond Sitka South to Prince of Wales and Dixon Entrance (see White and Raimondi 2020) made it possible to assess more diverse community interactions and contrast areas with and without sea otters. Surveys of abalone densities across these scales reveal local (e.g., specific sites, see Table 2.3), and regional environmental and ecological drivers likely play significant roles in shaping abalone populations (Table 2.3, Chapter 2). Importantly, we identified distinct populations of abalone across southeast Alaska (see Chapter 2), that were impacted differently by historical commercial fisheries, sea otter populations, and ongoing subsistence (see Chapter 1). These differences manifest in present-day variability in pinto abalone populations across regions examined in this study and warrant spatially specific reviews by local harvesters and managers, particularly since the species is managed uniformly across Alaska.

At local scales, we identified potential interspecific pre-abalone settlement factors, such as the aggregation of adult abalone, which may limit local recruitment (see Table in Chapter 2). The local biogenic habitat and availability of refuge are also likely contributors to the success of abalone populations. These local scales are especially important to abalone harvesters with the most intimate knowledge of these systems. As local and Indigenous knowledge, paired with available data, enhances our understanding of ecosystems, it benefits everyone to include harvesters in needed discussions on the management of local harvest (e.g., Lee et al., 2018, Armitage et al., 2019, Reid et al., 2020, White and Raimondi 2024).

Across regional scales, abalone likely indirectly benefit from sea otter presence via their removal of herbivores like sea urchins (Figure 3.6, Chapter 3). These and similar findings elsewhere (e.g., Raimondi et al., 2015, Lee et al., 2016), challenge concerns for abalone populations following the re-establishment of sea otters in Southeast Alaska. Though negative impacts following the re-occupation of sea otter populations are apparent and described by many in Sitka Sound (in White and Raimondi 2024), there is "no case of local extinction of any abalone population as a result of predation by sea otters" (NMFS 2014). Hope for increased abalone abundance in the presence of sea otters is evident in relatively high abalone densities in Sika Sound, which has the longest-established sea otter populations, experiences a "moderate sea otter influence" (see Table 3.1, Chapter 3) and has relatively higher sea otter harvest compared to other study regions. However, legal abalone densities are not increasing in Sitka Sound (Figure 3.1), and any increase in harvest may raise concerns for subsistence harvesters. Of added concern, abalone populations in areas without sea otters (i.e., Ketchikan) have not shown significant growth following the closure of the historic fishery in other Southeast regions (see Chapter 1).

In the 1950s, researchers recommended avoiding commercial harvest of abalone populations in Southeast Alaska (Livingstone et al., 1952), and this recommendation is even more relevant today. However, ongoing subsistence harvest remains an important and meaningful practice for many. This practice may be best preserved by monitoring populations for viability, considering complex interactions between sea otter presence and hunting, and managing populations at smaller scales in collaboration with harvesting communities.

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CHAPTER 1 APPENDIX

A1. Supplementary Assessment

Density and Timed Swim Measure Comparisons

Size Frequency

Similar abalone size distributions were documented during both abalone survey methods, run sequentially, at the same sites in Prince of Wales Gooseneck and Port Bazan locations K-S; $p = 0.915$). However, density transects recorded fewer overall abalone ($n = 31$), when compared to timed swims ($n = 97$).

CPM as a function of density

Abalone densities ($\log_{x+1}$ transformed for normality) collected along transects were (poor) predictors of CPM (Figure 7). A linear regression fit of the sites surveyed ($n=7$) with the two methods in Prince of Wales fit poorly ($R^2 = 0.1$, RMSE = .093, $P < .0037$, AICc = -1.69). However, the non-linear regression Michaelis Menten model ($R^2= 0.19$, RMSE= .089 $P < .0001$, AICc = 2.42) did predict a slightly stronger relationship between abalone abundance measures. An Exponential 2P regression predicted a weaker fit between the two abalone metrics ($R^2 = 0.086$, RMSE = .094, $P < .0010$, AICc = 2.42)

Density and Timed Swim Measure Comparisons

We examined the future application of timed swim re-survey of historical sites through comparisons to density transect metrics. As noted, timed swim methods are fraught with issues surrounding repeatability and precision (Andrew et al. 2000). To understand how different current populations were from those sampled during the commercial fishery's height, and allow direct comparison, we re-surveyed sites via similar methods. Following 2016 surveys in Prince of Wales, researchers discovered time swims to be faster than absolute density measures along transects oriented perpendicular to shoreline (Donnellan and Hebert 2017). However, we found time swims took equal if not more time than our relatively shorter parallel density transects, and generally, areas with more abalone required longer timed swims *(see* Donnellan and Hebert 2017).

Though density transects and timed swims produce no difference in estimated population size structures (K-S; $p = 0.915$), density transects surveyed at these Southeast locations provide more valuable information for understanding population viability (see Figure 5a for density size structure). Still, timed swim methods documented more abalone overall (56 more individuals were documented in Gooseneck and ten more in Port Bazan). Similarly, timed swims in Meares Pass, Prince of Wales, documented more abalone than other methods (Donnellan and Hebert 2017).

Density is a crucial metric to understand the status of abalone populations, and measuring changes over time is ideal. However, we found a poor relationship between abalone count per minute and density and cannot make reliable comparisons between the two methods. We additionally describe the fit between our nonlinear regression as poor based on a low sample size comparison ($n=7$). Similarly, Donnellan and Hebert

(2017) note a near-significant relationship, but not robust enough to claim a relationship between absolute density measures (different from those used here) and abalone CPM (same methods, same diver). More comparisons of the density and timed swims may provide power to this relationship; however, timed swims are limited by precision between divers and repeatability (McShane 1998). Unlike Donnellan and Hebert (2017), timed swim methods took at times longer than density transects and were more variable (*ranging from 35 to 73 minutes),* whereas high-density sites required more time to record abalone in situ to keep the search time similar to historic swims.

A1. TABLES

Table A1.1. Total Southeast Alaska abalone fishery harvest (pounds), harvest guidelines (pounds), permits, ex-vessel (abalone product) value, catch per unit effort (CPUE = lbs*diver^{-1} *day^{-1}), area-specific minimum legal-size limits (mm), regional minimum subsistence size limits (mm), and season length per year of the commercial fishery (1964 – 1996). Southern Southeast (SSE) harvest includes landings from the Prince of Wales and Ketchikan regions. Northern Southeast (NSE) harvest includes landings just north and south of Sitka Sound. The subsistence harvest limit was 50 abalone per day per person (20 in Sitka Sound) until 2013 when 5 abalone per day were permitted (Hebert 2014). Historically, timed swim surveys were during the most intensive commercial harvest (1978 – 1981) or the years following (1982 – 1989). Values in paratheses are cited elsewhere and not included in the graph in Figure 1.1.

Season	Upper Guideline Harvest	Lower Guideline Harvest	SSE Harvest	NSE Harvest	Total Southeast Harvest	Permits Issued (=number divers?)	Ex-vessel Value	Season Length (days)	CPUE lbs*diver^{-1}*day^{-1}	SSE Min Size Limit (mm)	NSE Min Size Limit (mm)	Subsistence Min. Size Limit (mm)
1963/64				-	-	-		365		76	76	76
1964/65				3000 [a]	3000	> 4 [b]		365		76	76	76
1965/66			-	1000 [a]	1000	4 [b]		365		76	76	76
1966/67			3000[a] (2,500) [b]	-	3000	8 [b]		365	###	76	76	76
1967/68			6511 (5239) [b]	-	6511	6 [b]		365	###	76	76	76
1968/69			-	-	-	7 [b]		365		102[d]	89	76
1969/70			-	1100[b]	1100	5 [b]		365		102 [d]	89	76
1970/71			-	1100[c]	1100	4 [b]		365		102	89	76
1971/72			-	923 [c]	923	7 [b]	-	365	-	102	89	76
1972/73			-	2610 [c]	2610	6 (11)[b]	$2,675	365	1.19	102	89	76
1973/74			144 [a,c]	2699[a] (3897) [c]	2843	3 (14)[b]	$4,500	365	2.60	102	89	76
1974/75			-	16339 [c]	16339	3 (11) [c]	$20,739	365	14.92	102	89	76
1975/76			-	8497 [c]	8497	8 (7) [c]	$17,104	365	2.91	102	89	76
1976/77			55 [a,c]	546 [a]	601	7	-	365	-	102	89	76
1977/78			955 [a,c]	12939 [a]	13894	10 (13) [b]	$14,816	365	3.81	89	89	89
1978/79			130369 [a,c]	43083 [a] (50659) [c]	173452	35	$253,697	365	13.58	89	89	89
1979/80	-		316952	61733	378685	43	$408,980	287	30.69	95	95	89
1980/81	250000	-	233589	18382	251971	40	$420,792	273	23.07	95	95	89
1981/82	125000	100000	338305	32589	370894	54	$445,073	59	116.41	95	95	89
1982/83	125000	100000	100458	12826	113284	41	$240,162	36	76.75	95	95	89
1983/84	125000	100000	99294	8735	108029	31	$302,481	126	27.66	95	95	89

1984/85	125000	100000	59237	8379	67616	25	$165,659	151	17.91	95	95	89
1985/86	58000	25000	32817	7720	40537	18	$117,963	71	31.72	95	95	89
1986/87	58000	25000	47404	13820	61224	24	$168,366	146	17.47	95	95	89
1987/88	58000	25000	57784	10406	68190	42	$208,930	36	45.10	95	95	89
1988/89	58000	25000	65928	10172	76100	45	$307,444	33	51.25	95	95	89
1989/90	58000	25000	57784	4020	61804	67	$330,651	40	23.06	95	95	89
1990/91	58000	25000	62779	5607	68386	97	$374,071	9	78.33	95	95	89
1991/92	58000	25000	35987	8095	44082	96	$267,578	35	13.12	95	95	89
1992/93	58000	25000	26905	9083	35988	100	$386,151	19	18.94	95	95	89
1993/94	58000	25000	27680	7172	34852	86	$487,928	7	57.89	102	102	89
1994/95	58000	25000	15055	7824	22879	102	$330,373	8	28.04	102	102	89
1995/96	16000	0	8524	5828	14352	100	$126,526	7	20.50	102	102	89
1996/97	-	-	-	-	-	-	-	-	-	-	-	89
Harvest[**] Totals			**1,727,516**	**282,044**	**2,052,643**	**Total Fishery Value: $5,402,659**						

a ADFG unpublished data 1980

b Sitka Area Manager Note 1976 (number of permits issued 1964 – 74), and Southeast commercial harvest in lbs

c Sitka Area Manager Note (1978): Commercial catch rates for Sitka (included in NSE) were converted to "round" (whole) abalone pounds using 45% meat recovery, not wet weight.

Note: Harvest denoted by “c” is likely an underestimate of harvest (round) weight reported during other years.

d ADFG increased the size limit for SSE (1968), effectively closing the fishery in SSE for three years.

e SSE area closures at Gravina Island (Ketchikan) and Cordova Bay (Prince of Wales) ahead of the 1996 Southern Southeast Alaska regional fishery closure. These locations are removed from the harvest area in SSE

Table A1.2. Contrast of abalone size class abundance (Count per Minute) by time period (historical vs current) for study locations. Size classes are defined as juvenile (≤ 41mm), adult (> 41mm < legal size(mm)), and legal size (see Table A1 for minimum legal sizes per survey year). Refer to Figure 2 for comparisons of size class differences between time periods and Table 2 for a detailed model fit of the full GLM (Poisson distribution and Maximum Likelihood estimation).

Location	**Size Class**	**Std Error**	**L-R ChiSquare**	**-LogLikelihood**	**Prob>ChiSq**
Cordova Bay	*Juvenile*	3.629	0.259	31.997	0.611
	Adult	0.746	2.064	98.412	0.151
	Legal	4.509	3.735	34.973	0.053
Meares Pass	*Juvenile*	0.778	1.175	32.454	0.278
	Adult	0.670	50.011	122.386	<.0001*
	Legal	**3.886**	**8.784**	**37.498**	0.003
Gooseneck	*Juvenile*	1.881	0.561	32.147	0.454
	Adult	0.605	3.492	99.126	0.062
	Legal	4265.886	3.825	-0.339	0.050
Port Bazan	*Juvenile*	1.755	0.359	32.047	0.549
	Adult	0.950	4.792	99.776	0.029
	Legal	**3815.524**	**1.295**	**33.753**	**0.255**
Gravina Island	*Juvenile*	2.715	2.200	32.967	0.138
	Adult	0.436	0.674	97.717	0.412
	Legal	1.255	0.071	33.141	0.791

Table A1.3. Proportion of abalone recorded at current time period minimum legal size limit (>= 89mm) across current and historical survey time periods at study locations with variable sea otter occupation. See Table 1, Table A1 for more detailed commercial fishery metrics.

Location	Time Period	Historical Harvest Intensity	Otter Occupation	Proportion abalone ≥89mm
Cordova Bay	Historical	Moderate	Absent	48.49
Cordova Bay	Current	Moderate	High	1.19
Meares Pass	Historical	High	Absent	22.46
Meares Pass	Current	High	High	1.45
Gooseneck	Historical	High	Absent	23.08
Gooseneck	Current	High	Moderate	0
Port Bazan	Historical	High	Absent	17.05
Port Bazan	Current	High	Moderate	0
Gravina Island	Historical	Moderate	Absent	25.53
Gravina Island	Current	Moderate	Absent	10.56

Table A1.4 Results of linear and non-linear Generalized Linear Model (GLM) analyses with a Poisson distribution and a log link function for all abalone size classes and adult and legal abalone size classes or individuals 41mm and larger (for related analyses, see Table 1.4, Figure 1.4)

Sizes	**Model Type**	**Predictor**	**Estimate**	**Std Error**	**L-R ChiSquare**	**Lower CL**	**Upper CL**	**Prob>ChiSq**
All Abalone	*Linear*	Intercept	0.247	0.080	8.742	0.086	0.401	0.0031*
		Occupation	-0.163	0.026	63.163	-0.219	-0.114	<.0001*
	Non-linear	Intercept	0.147	0.081	3.227	-0.014	0.303	0.073
		Occupation	-0.216	0.033	68.077	-0.286	-0.155	<.0001*
		(Occupation corr.)^2	0.008	0.002	11.088	0.004	0.012	0.0009*
Adult and Legal	*Linear*	Intercept	0.577	0.083	40.641	0.410	0.734	<.0001*
		Occupation	-0.204	0.033	73.384	-0.276	-0.145	<.0001*
	Non-linear	Intercept	0.458	0.086	25.832	0.287	0.625	<.0001*
		Occupation	-0.252	0.040	69.707	-0.339	-0.180	<.0001*
		(Occupation corr.)^2	0.009	0.003	7.302	0.003	0.014	0.0069*

Size Class	**Model Type**	**Predictor**	**AICc**	**-LogLikelihood**	**L-R ChiSquare**	**df**	**-2 Log-Likelihood (Prob>ChiSq)**	**Model Significance**
ALL Abalone	*Linear*	Occupation(yrs)	542.590	31.582	63.164	1	<.0001*	Yes
	Non-Linear	(Occupation corr.)^2	533.560	37.126	74.252	2	<.0001*	Yes
Adult and Legal	*Linear*	Occupation(yrs)	404.810	36.692	73.384	1	<.0001*	Yes
	Non-Linear	(Occupation corr.)^2	399.611	40.343	80.686	2	<.0001*	Yes

A1. FIGURES

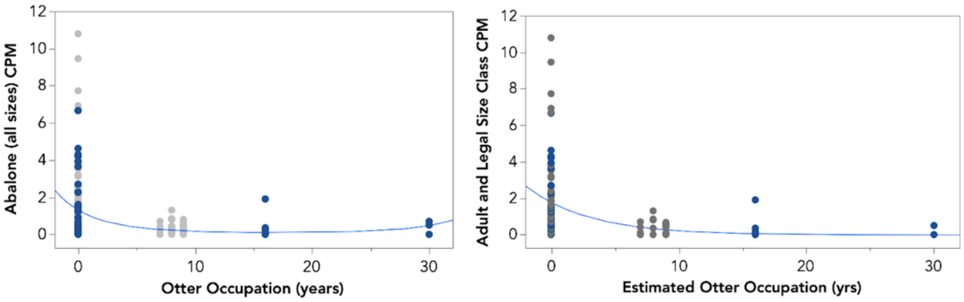


Figure A1.1. Regressions following the GLM model of total abalone counts or filtered adult and abalone counts per minute (CPM) as a function of sea otter occupation period. See Table A1.2 for model relationships. Sites with a history of high commercial harvest are marked in grey, and sites with moderate commercial harvest are in blue.

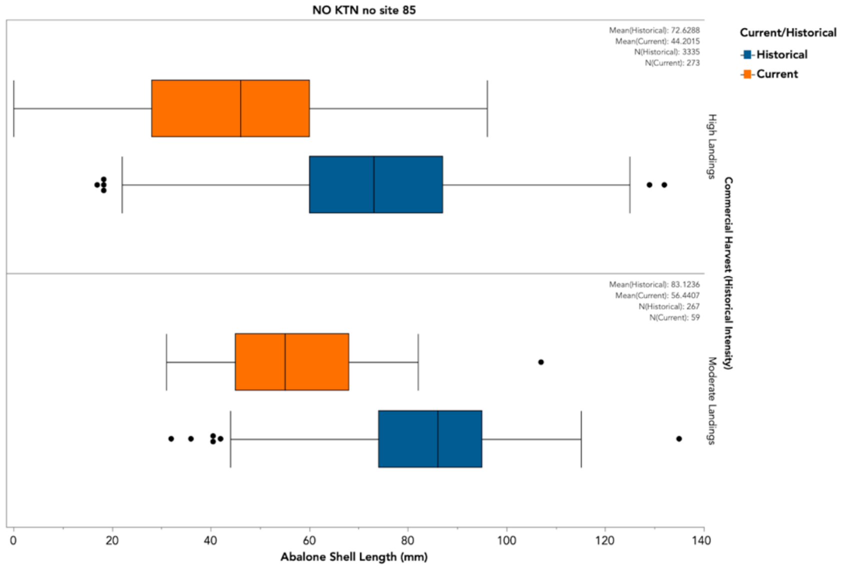
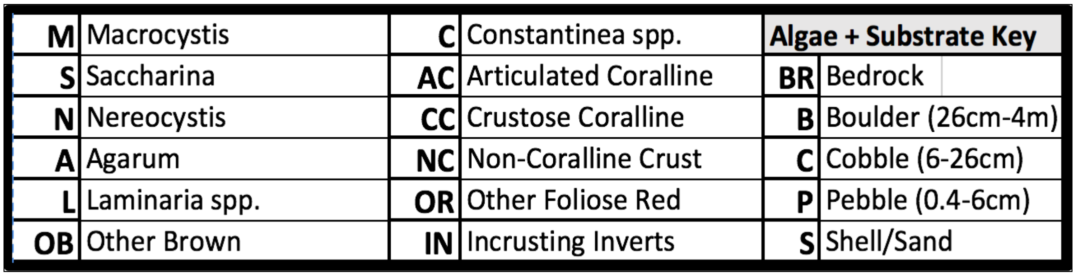


Figure A1.2. Box plots of sizes recorded at sites with current otter occupation. Prince of Wales, historical (during a period of sea otter absence) and current (during occupation of sea otters). Note: sites and locations have various occupation times of sea otters and are only grouped by fishery intensity.

CHAPTER 2 APPENDIX

A2 TABLE

Table A2.1. Species list and codes of algae and substrate used for point contact macroalgal data collection during dive surveys. For additional details on habitat point contact and photo plot methods from dive surveys, refer to Appendix B in White and Raimondi (2020).



M	Macrocystis	**C**	Constantinea spp.	**Algae + Substrate Key**	
S	Saccharina	**AC**	Articulated Coralline	**BR**	Bedrock
N	Nereocystis	**CC**	Crustose Coralline	**B**	Boulder (26cm-4m)
A	Agarum	**NC**	Non-Coralline Crust	**C**	Cobble (6-26cm)
L	Laminaria spp.	**OR**	Other Foliose Red	**P**	Pebble (0.4-6cm)
OB	Other Brown	**IN**	Incrusting Inverts	**S**	Shell/Sand

CHAPTER 3 APPENDIX

A3 TABLES

Table A3.1. Summary of Abalone Density (per m2), Median Shell Length (mm), and Urchin Biomass (kg/m^2) per study location, region

Region	Location	Sites (Transects)	Abalone Density ± SD	Median Abalone Shell Length	Total Mean Urchin Biomass
Sitka	Sitka North	5 (10)	1.08 ±1.15	53	11.90 ±11.32
Sitka	Sitka Inside	8 (16)	1.35 ±1.07	44	17.50 ±17.66
Sitka	Sitka Outside	11 (22)	1.42 ±1.43	49	8.85 ±8.65
Prince of Wales	Meares Pass*	*	0.17	44	-
Prince of Wales	Gooseneck	4 (8)	0.08 ±0.02	44	6.61 ±7.67
Prince of Wales	Port Bazan	4 (8)	0.03 ±0.02	42	0.02 ±0.04
Ketchikan	Gravina Island*	*	0.28	44	-
Dixon Entrance	Percy Islands	2 (4)	0.42 ±0.27	59	124.75 ±47.05
Dixon Entrance	Duke Island	5 (10)	0.64 ±0.59	54	150.04 ±59.33
Dixon Entrance	Bee Rocks	2 (4)	0.97 ±0.67	51	93.58 ±24.39

*Data from Gravina Island and Meares Pass were surveyed during separate 2016 surveys and did not include urchin biomass measures (see Donnellan and Hebert 2017)

Table A3.2. PERMANOVA Results for Biogenic Habitat Point Contact Comparisons and vectors applied to data shown in Figure 3.4.

Source	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Region	2	2.1413	1.07065	7.9378	0.31916	0.01
Location	5	0.6563	0.13127	0.9732	0.09783	0.53
Residual	29	3.9115	0.13488		0.58301	
Total	36	6.7091			1.00000	

Abalone Density and Corresponding NMDS Vector Correlations

Abalone Vector (number per m2)	NMDS1	NMDS2	r2	Pr(>r)
Adult Abalone Density	1.000	-0.031	0.014	0.804
Juvenile' Abalone A	-0.492	-0.870	0.022	0.659

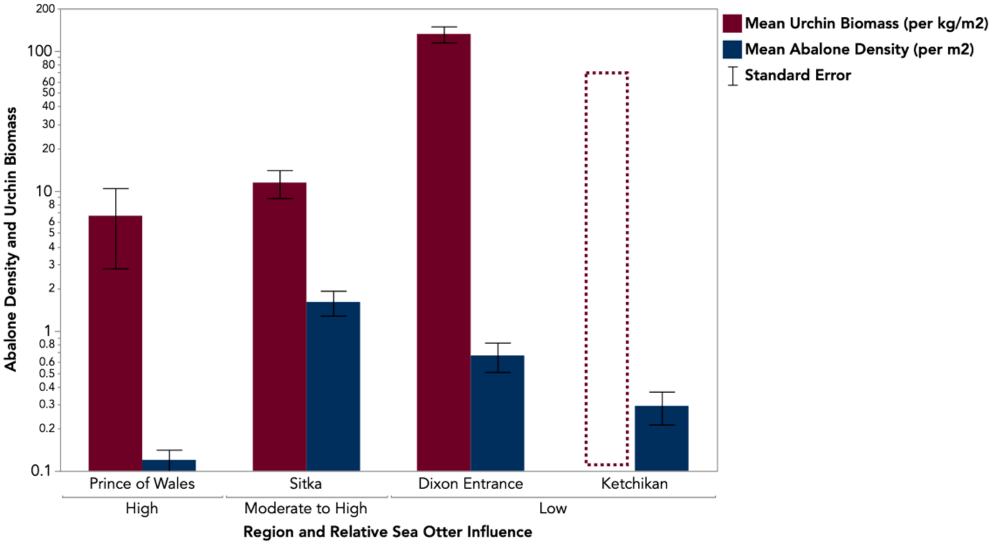


Figure A3.1. Mean abalone densities (per m^2) and urchin biomasses per kg/m^2 per Southeast Alaska Region and assigned otter influence: High, Moderate to High, and Low. Abalone data from Ketchikan, Gravina Island location, and the Prince of Wales location Meares Pass, were collected during a separate survey in 2016 and do not include urchin biomass measures (see Donnellan and Hebert 2017). All other locations in regions shown in this figure were surveyed during the summer of 2019 (see White and Raimondi 2020, NMFS AKR-18-0820). There are large abundances of urchins in Ketchikan; however, biomass data were unavailable and were estimated (see red bar in the outline) for this graph. Displayed with a log-transformed y-axis. Bars indicate one standard error from the mean. See Table 3.1 for factors used to determine region otter influence.

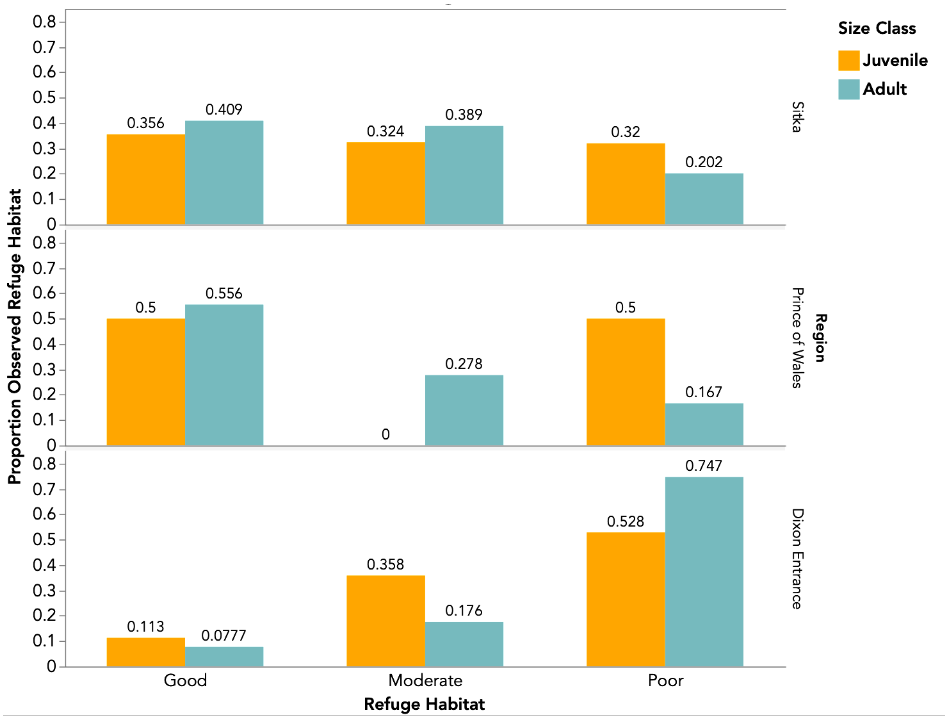


Figure A3.2. Observed proportions of abalone size class refuge habitat use. The refuge was classified as either good, moderate, or poor, displayed by the percent of total refuge type used by small 'juvenile' abalone (≤ 41mm) in gold and 'adult' abalone (> 41mm) in teal. Numbers on bars indicate proportions per refuge habitat category. See Table 3.4 for GLMM for analyses of ‘observed’ abalone per refuge habitat, region, and location percent of the total).

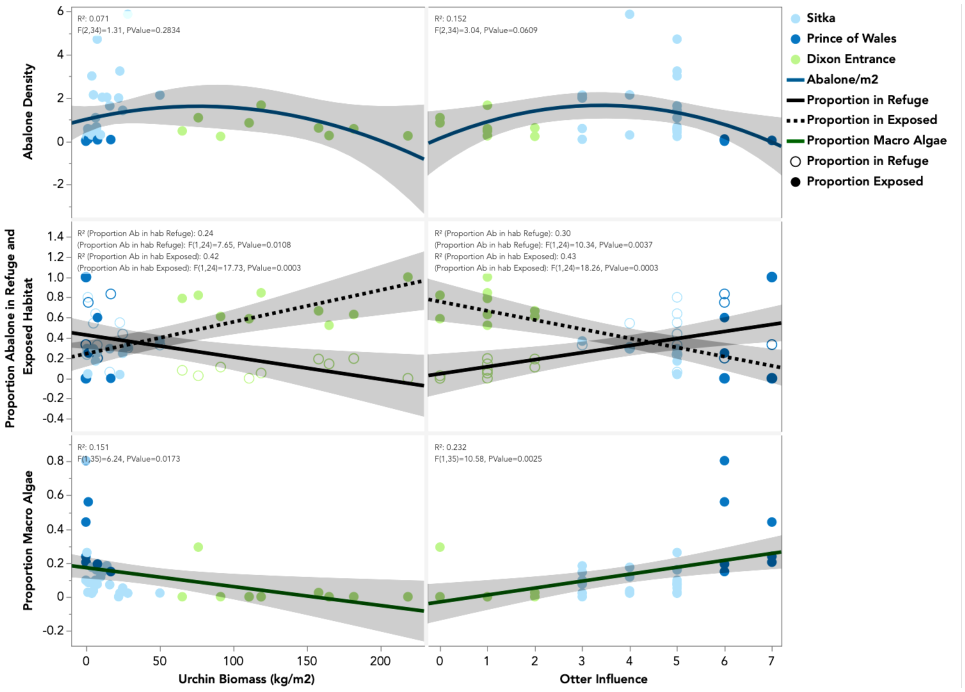


Figure A3.3. Non-transformed Figure 3.4 data plots.