

ARTICLE

Higher Aggregation of Key Prey Species Associated with Diet and Abundance of the Steller Sea Lion *Eumetopias jubatus* across the Aleutian Islands

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Abstract

The Aleutian Islands ecosystem is a highly dynamic marine environment that supports commercially important fish species, such as Atka Mackerel *Pleurogrammus monopterygius* and Northern Rockfish *Sebastes polyspinis*, and several large marine mammals, including the Steller sea lion (SSL) *Eumetopias jubatus*. To protect SSL foraging behavior and prey, trawl exclusion zones (TEZs) were established around SSL rookeries and haulouts across the Aleutian Islands and are closed to bottom trawling. The Atka Mackerel fishery is concentrated at small, local patches (~37.04 km [~20 nautical miles]) across the Aleutian Islands, often near and adjacent to TEZs. Food web models and fishery stock assessments predict sufficient prey for both the fishery and foraging SSLs at the level of large management areas (each area is ~463 km [~250 nautical miles] longitudinally), but little is known about local fish distribution (~37.04 km) in proximity to SSL rookeries and haulouts. We used CPUE to examine the spatial distribution of two SSL prey species (Atka Mackerel and Northern Rockfish) and marine invertebrates (as a proxy for habitat quality)

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at large (across the Aleutian Islands) and small (~37.04-km) scales. Although Atka Mackerel abundance estimates were similar across the Aleutian Islands, the density of Atka Mackerel differed. In the eastern Aleutian Islands, where SSL population trends have stabilized, Atka Mackerel aggregations were dense. In contrast, in the far western Aleutian Islands, where SSL populations are still in decline, Atka Mackerel distributions were diffuse and Northern Rockfish exhibited a greater density. Results indicated no significant difference in CPUE between areas open to fishing and closed areas (i.e., TEZs) at all study sites for Atka Mackerel and at all but one study site for Northern Rockfish, whereas invertebrate densities were significantly higher inside of TEZs at all study sites. We discuss how fish distributions across the Aleutian Islands may impact the success and behavior of foraging SSLs.

Fishery stock assessments and food web models may predict sufficient prey abundances for both fisheries and marine predators at the ecosystem scale. However, the distribution of those resources at a scale that is relevant to both fisheries and foraging marine mammals is as important as the quantity available. In addition, fisheries that are concentrated at small spatial scales (~37.04 km [\sim 20 nautical miles]) have the potential to compete with large marine predators for the same resource in time (DeMaster et al. 2001; Casini et al. 2005; Plaganyi and Butterworth 2009; Adams et al. 2018). Such is the case in the Aleutian Islands, Alaska, among fisheries for Atka Mackerel *Pleuragrammus monopterygius* and Northern Rockfish *Sebastes polypinnis*, which occur near and adjacent to Steller sea lion (SSL) *Eumetopias jubatus* rookeries and haulouts. Food web models (Aydin et al. 2007) and fishery stock assessments (Lowe et al. 2018) have predicted sufficient prey for both the foraging SSLs and the Atka Mackerel fishery at the ecosystem level (hundreds of kilometers/nautical miles), but little is known about how the fish are spatially distributed locally in proximity to SSL rookeries and haulouts (tens of kilometers/nautical miles). In the present study, we examine how Atka Mackerel—the dominant prey of SSLs—and Northern Rockfish are distributed at these small spatial scales and we discuss how spatial patterns in prey density may impact the foraging behavior and success of SSLs in the Aleutian Islands.

The Atka Mackerel is a patchily distributed species that is found across the Aleutian Islands and supports a large commercial fishery. Fisheries-independent estimates of their size-structured abundance and distribution come from the National Marine Fisheries Service (NMFS), which has operated a summer (June/July) daytime bottom trawl survey (hereafter, “NMFS survey”) in the Aleutian Islands triennially from 1980 to 2000 and biennially since 2000 (Von Szalay et al. 2017). The Aleutian Islands management area is subdivided into three subareas (Figure 1; NMFS Areas 541, 542, and 543), each approximately 463 km (\sim 250 nautical miles) longitudinally, in which fishing quotas are allocated separately based on NMFS survey biomass estimates (Lowe et al. 2018). Although the Atka Mackerel fishery occurs across the Aleutian Islands, fishery removals within each subarea are concentrated in

small, local patches ($<$ 37.04 km [$<$ 20 nautical miles]), and often near and adjacent to SSL rookeries and haulouts (Figure 1). Atka Mackerel consistently dominate the SSL diet across the Aleutian Islands, with greater percent weight, frequency of occurrence, and percent bioenergetic prey contribution than any other prey species during summer and winter months (Sinclair and Zeppelin 2002; Sinclair et al. 2005, 2013; Aydin et al. 2007; Tollit et al. 2017). Northern Rockfish are patchily distributed and commonly co-occur with Atka Mackerel in NMFS surveys and in the Atka Mackerel fishery (Logerwell et al. 2005; Spencer and Ianelli 2018). Northern Rockfish also occur in the SSL diet, albeit less frequently than Atka Mackerel (percent bioenergetic prey contribution $<$ 15%; grouped with other rockfishes *Sebastes* spp.; Tollit et al. 2017); the occurrence of rockfish species in the SSL diet during winter months did increase by percent weight and frequency of occurrence during 1999–2009 compared to the previous decade.

The decline of SSLs was first recognized in the 1980s, leading to the listing of the SSL in 1990 as threatened under the Endangered Species Act (Fritz et al. 1995; Trites and Larkin 1996; Maschner et al. 2014), which was followed by an uplisting to endangered for the Western Distinct Population Segment (DPS) in 1997 to afford it greater protection (Loughlin and York 2000; Fritz et al. 2016; Zador and Yasumiishi 2016). Since then, several genetically defined regional subpopulations of SSLs within the Western DPS have increased in abundance; however, non-pup and pup counts in the westernmost portion of the Western DPS have continued to decrease (Figure 1; NMFS Area 543). One proposed hypothesis is that fishing vessels either directly or indirectly compete for prey resources used by SSLs (Loughlin 1987; DeMaster et al. 2001; Plaganyi and Butterworth 2009). To offset bottom trawl fishing of SSL prey species (specifically Atka Mackerel, Pacific Cod *Gadus macrocephalus*, and Walleye Pollock *G. chalcogrammus*) and preserve a foraging base for SSLs, trawl exclusion zones (TEZs) were established in the late 1990s around SSL rookeries and haulouts (NMFS 2010). The TEZs were initially drawn to extend 18.52, 27.78, or 37.04 km (10, 15, or 20 nautical miles) in radius from SSL rookeries and haulout locations (Figure 1) but

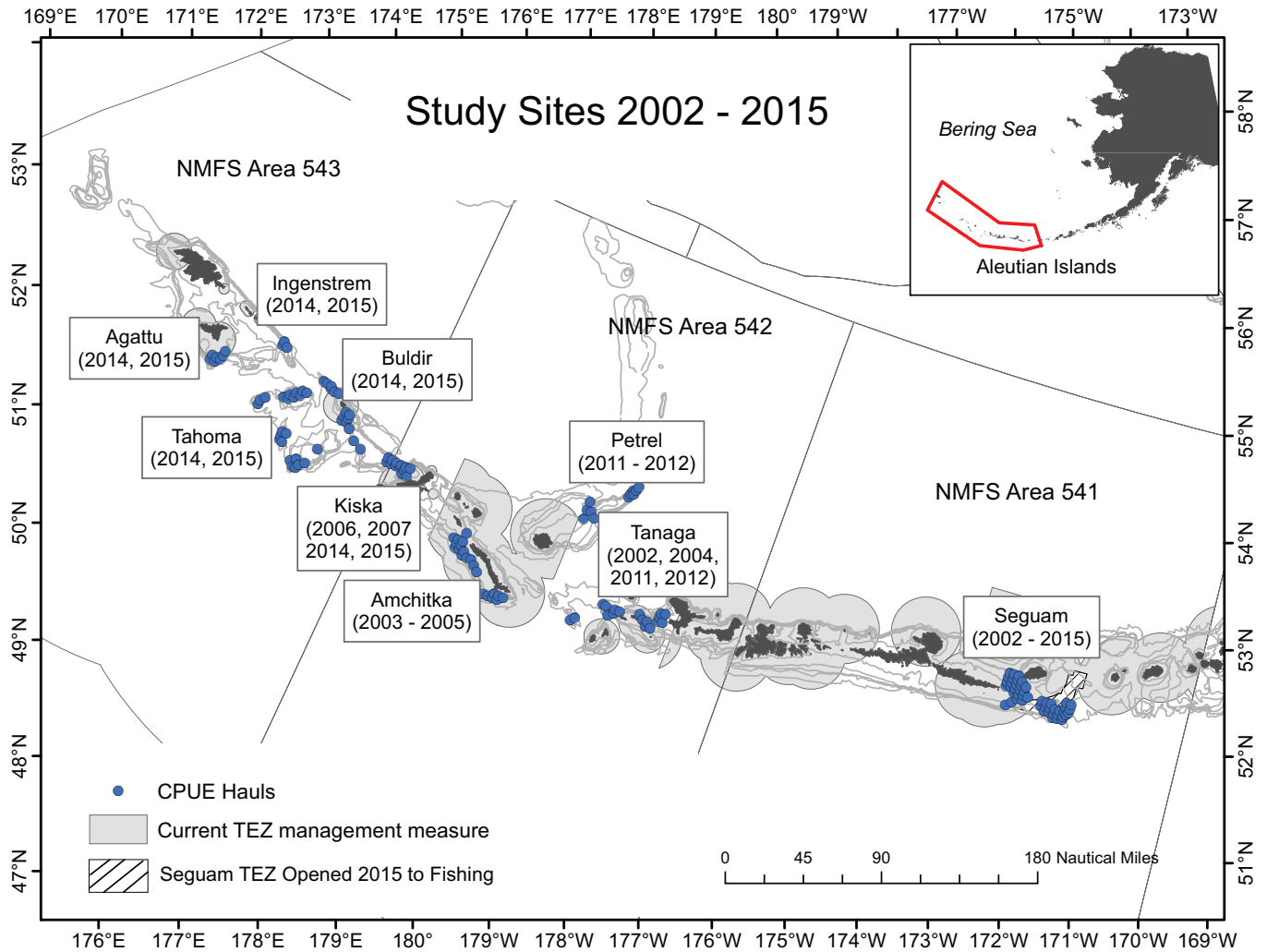


FIGURE 1. Study sites (in boxes) and trawl hauls (blue circles) from 2002 to 2015 across the Aleutian Islands, Alaska; years of sampling are shown in parentheses. Gray areas (current trawl exclusion zone [TEZ] management measure) are closed to bottom trawl fishing. National Marine Fisheries Service (NMFS) Management Areas 541, 542, and 543 are shown as current fisheries management boundaries. Each NMFS area measures approximately 463 km (~250 nautical miles) longitudinally.

have since been adjusted based on estimated fishing exploitation rates reported in small-scale Atka Mackerel mark-recapture studies (McDermott et al. 2016).

Spatial organization of prey likely plays an important role in SSL foraging success. Predators in the marine environment may take advantage of the aggregating behavior of their prey (Pitcher and Parrish 1993). High-density prey aggregations provide foraging opportunities with lower search effort and may allow for the consumption of more than a single prey item (Rieucan et al. 2015). We examined how SSL prey species are spatially organized, and we used CPUE as a proxy for aggregating behavior of Atka Mackerel and Northern Rockfish. Given that the NMFS survey only operates during the daytime in summer, our study examined fish spatial distribution during day/night in the

fall and spring months. The data were collected as part of an Atka Mackerel mark-recapture study that took place from 2002 to 2015 aboard a commercial fishing vessel (McDermott et al. 2005, 2016) and CPUE was used to infer how relative spatial patterns and variability in Atka Mackerel and Northern Rockfish distributions may affect SSL foraging at a small spatial scale (tens of kilometers/nautical miles). Our specific objectives were to (1) determine whether CPUE estimates vary with longitude across the Aleutian Islands (large scale); (2) determine whether CPUE estimates differ between areas inside and outside of TEZs (small scale) across the Aleutian Islands; and (3) identify those variables contributing to the observed spatial patterns in Atka Mackerel and Northern Rockfish CPUEs.

METHODS

The data used in this study were collected from 2002 to 2007 and from 2011 to 2015 (hereafter referred to collectively as “2002–2015”) as part of a larger Atka Mackerel mark–recapture study (McDermott et al. 2005, 2016). During all years, the study was conducted aboard the FV *Seafisher*, a commercial factory trawler that targets Atka Mackerel in the Aleutian Islands. Analyses presented here include data collected during the tag recovery portion of the studies, which primarily occurred in the late fall (October) and spring (April or May). Study sites spanned approximately 14° of longitude, extending from Seguam Pass in the east to Agattu Island in the west (Figure 1; Table 1). Sites were named based on the closest large geographical feature (typically an island or a pass), although names do not indicate that sampling took place at that exact location (e.g., in a pass). From east to west, sites included the following: Seguam (Seguam Pass), Tanaga (Tanaga Pass), Amchitka (Amchitka Island), Petrel (Petrel Bank), Kiska (Kiska Island), Tahoma (includes Tahoma Reef, Tahoma Seamount, Heck Canyon, and Wall's Plateau), Buldir (Buldir Island), Ingenstrem (Ingenstrem Rock), and Agattu (Agattu Island; Figure 1; Table 1). All study sites were adjacent to SSL rookeries and haulouts, were either adjacent to or within TEZs, and also represented the main epicenters of Atka Mackerel commercial fishing-focused locations (outside of TEZs). Seguam is the only study site that occurs in NMFS Area 541, and historically the Atka Mackerel fishery has mainly concentrated on the dense Atka Mackerel aggregations located at Seguam, with little fishing effort occurring elsewhere in NMFS Area 541 (Figure 1; Lowe et al. 2018).

Within each study site, haul locations were not selected randomly but were chosen in fishery-focused locations. The goal of the tag recovery survey was to recover tagged fish; therefore, hauls were set in areas of known high Atka Mackerel abundance (based on historical fishing) and in areas that have not been heavily fished. Once a haul

location was chosen, subsequent haul locations were executed based on a set of guidelines: (1) haul sizes were to be maintained at an average of 25 metric tons (25,000 kg); (2) haul duration was to be maintained for an average of 30 min or 3.704 km (2 nautical miles); and (3) once a haul was completed, the next haul's towing path was at least 1.852 km (1 nautical mile) from or at least 36 h after the previous haul. During towing operations, fishing effort (minutes towed) was defined as the time when the net began fishing on the bottom until net retrieval from the bottom. The vessel's net sounder was used to determine bottom contact and net configuration while towing. Similar net sizes and consistent towing speeds were maintained across all years of sampling. Towing operations occurred during a 24-h period for all study sites, seasons, and years. This “adaptive sampling” design ensured that towing effort was dispersed in space and time.

The primary objective of the Atka Mackerel long-term mark–recapture study was to estimate Atka Mackerel abundance inside and outside of TEZs near and adjacent to SSL rookeries and haulouts. This dictated the number of fish that had to be examined for tags and therefore the number of hauls that occurred either inside of the TEZ (closed to commercial trawling) or outside of the TEZ (open to commercial trawling). The secondary objective was to collect catch composition data describing SSL prey species, including accurate estimates of Atka Mackerel density (i.e., CPUE), the data used in this study. Study sites that did not have a balanced design of hauls that occurred inside and outside of TEZs were excluded from our analyses.

Estimating CPUE.—We did not use CPUE as a measure of abundance but rather as a measure of spatial patchiness of Atka Mackerel and Northern Rockfish. For example, we assumed that given similar biomass estimates, an area with persistently high CPUEs (Figure 2A) near SSL rookeries or haulouts would require less foraging time and energy expended as opposed to those areas with lower

TABLE 1. Study site locations sampled from 2002 to 2015 across the Aleutian Islands, Alaska; the sites are listed longitudinally from east to west, and the latitude and longitude are approximate (TEZ = trawl exclusion zone). Exact locations of the study sites and trawl hauls are shown in Figure 1, and distances listed are in kilometers and nautical miles. National Marine Fisheries Service (NMFS) management areas are also listed.

Study site	Latitude and longitude	NMFS area	TEZ
Seguam	52°26'N, 172°2'W	541	37.04 km (20 nautical miles) (22.224 km [12 nautical miles] in 2015)
Tanaga	51°31'N, 178°32'W	542	18.52 km (10 nautical miles)
Petrel	52°43'N, 179°22'W	542	No TEZ in study area
Amchitka	51°25'N, 178°52'E	542	18.52 km (10 nautical miles) (closed to fishing, 2011–present)
Kiska	52°5'N, 176°52'E	542	18.52 km (10 nautical miles)
Buldir	52°24'N, 175°53'E	543	27.78 km (15 nautical miles) (closed to fishing, 2011–2014)
Tahoma	52°5'N, 175°27'E	543	No TEZ (closed to fishing, 2011–2014)
Ingenstrem	52°40'N, 174°29'E	543	No TEZ (closed to fishing, 2011–2014)
Agattu	52°13'N, 173°51'E	543	18.52 km (10 nautical miles) (closed to fishing, 2011–2014)

CPUEs (Figure 2B). These spatial patterns are difficult to glean from current NMFS bottom trawl survey data, as the sites of tows are randomly chosen within a given grid cell (Figure 2C). This could mean that NMFS surveys do not reflect the level of aggregation present, since they can miss schools altogether (Figure 2C). Indeed, NMFS survey biomass estimates are similar across the Aleutian Islands (Figure 1; Lowe et al. 2016, 2018). Conversely, the mark-recapture study specifically targeted Atka Mackerel, which co-occur with Northern Rockfish. Therefore, CPUE from the mark-recapture study was used only to examine how prey are aggregated at smaller spatial scales within the three large subareas (Figure 1; NMFS Areas 541, 542, and 543) and not as a measure of relative abundance.

Each haul was weighed (kg) and sampled to determine the total weight of each species and the species composition. Total weight of the entire catch was determined using a conveyer-belt flow scale (Marel, Gardabaer, Iceland) that was permanently mounted in the factory vessel. Scale calibrations were performed twice over a 24-h period. Species composition was determined by random sampling of the catch in a manner similar to that described in the Alaska Fisheries Science Center's observer manual (AFSC 2013). Each haul was either sampled in its entirety or subsampled for species composition and extrapolated to the entire catch. For hauls sampled in their entirety (<1,000 kg; approximately 2% of the hauls), all of the catch was collected and sorted by species; each species was enumerated and weighed to the nearest kilogram on a motion-compensated electronic platform scale. The remaining hauls (98%), which ranged in average weight between 14,000 and 28,000 kg (a single cruise had hauls that often exceeded 25,000 kg in a short period of time) were subsampled in the following manner: first, each haul was divided into three sample periods depending on the estimated size of the haul that was dumped into the vessel holding tank. Second, the dominant species in the haul (most frequently Atka Mackerel) was determined, and after passing over the flow scale a sample of approximately 200 individual fish was diverted from the conveyer

belt at a random point, counted, and weighed. Third, within each of the three sample periods, a minimum of 1,000 kg and up to 3,000 kg of unsampled catch was passed across the Marel flow scale and all nondominant species were collected, identified, counted, and weighed to the nearest kilogram. Of the three samples collected from each haul, the proportions of nondominant species and dominant species were estimated for a total subsample weight. These subsample estimates of species proportions and weights were extrapolated to the total weight of each haul.

Total catch weight was estimated for Atka Mackerel, Northern Rockfish, and marine invertebrates. Invertebrates (all phyla combined) were used as a proxy for bottom habitat structure because rockfishes *Sebastes* spp. and greenling species (Hexagrammidae; including Atka Mackerel) may prefer habitats with more substrate, such as those inhabited by invertebrates (Jones et al. 2012). Marine invertebrates were sorted to a coarse taxonomic resolution that included phyla such as Porifera (e.g., sponges; most common), Cnidaria (e.g., coral), Mollusca (e.g., shellfish and gastropods), Bryozoa, Brachiopoda, and unidentified invertebrate taxa. Based on the total estimated catch weight of Atka Mackerel, Northern Rockfish, and invertebrates and based on the time for which the net was fishing on the bottom, CPUE was estimated for each haul in the study and is represented as kilograms per minute fished.

Prior to all statistical analyses, CPUE estimates were cube-root transformed to reduce the effect of outliers. A Kruskal-Wallis test was used to determine whether there was a difference in CPUE across years (TEZ combined and non-TEZ combined) at Seguam (the only location visited during every year of the study; Table 2). Given no difference by year, CPUE was pooled for all years within each study site.

Evaluating effects of trawl exclusion zones on CPUE.— We compared the average CPUE inside of TEZs to that outside of TEZs for Atka Mackerel, Northern Rockfish, and marine invertebrates at most study sites. One-way

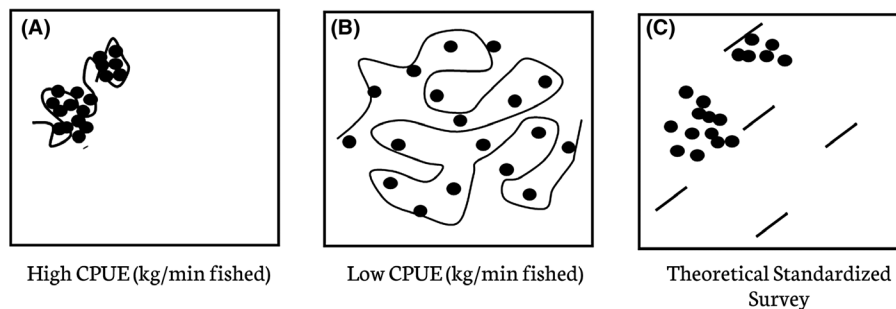


FIGURE 2. Examples of (A) a high CPUE, (B) a low CPUE, and (C) a theoretical standardized survey sampling scheme; all three boxes have the same number of "fish."

ANOVA was used to compare average bottom depth measured with a net-mounted temperature–depth recorder inside and outside of the TEZ at each study site to determine whether depth ranges inside of TEZs were shallower (i.e., closer to landmasses). During most research cruises, trawling occurred both inside and outside of the TEZ at each study site within a 2-week period. Three study sites (Petrel, Tahoma, and Ingenstrem) did not have TEZs and were not included in the TEZ analysis (Table 2; Figure 1). Furthermore, because of management strategies that were implemented during research time periods, the following data were not included in the TEZ analyses: (1) two cruises at Seguam in 2011 and 2012 because sampling was restricted to areas outside of the TEZs; and (2) hauls collected at Kiska, Buldir, and Agattu during 2014 because the entire NMFS Area 543 was closed to commercial fishing (Table 2; Figure 1).

All CPUE estimates were assessed for normality (Shapiro–Wilk tests) and equality of variances (F -tests) by site prior to statistical testing for differences inside and outside of the TEZs. The CPUE data that met assumptions of normality and equality of variances were subjected to a two-way ANOVA to determine whether there was a difference in average CPUE inside versus outside of TEZs, with study site used as an interaction term. The CPUE data that did not meet these assumptions were subjected to the nonparametric Mann–Whitney test.

Evaluating environmental effects on CPUE.—Data from all study sites and years were used to evaluate the environmental effects on CPUE. A suite of explanatory variables was used in a multivariate statistical analysis to assess effects on CPUE. Some of these data were collected aboard the vessel during haul operations, and others were derived from Turner et al. (2017). Bottom temperature ($^{\circ}\text{C}$) and depth (m) measurements were collected at 3-s intervals by using a net-mounted temperature–depth

recorder (SBE 39; Seabird Electronics, Bellevue, Washington) and averaged over the duration the net was actively fishing on bottom. Average CPUE estimates of invertebrates in the catch were used as a proxy for bottom habitat structure; higher catches of invertebrates may be associated with more rugose substrate and undisturbed habitat—the habitat type expected within TEZs. The remaining variables used in the analysis were from various sources (Table 3). Model estimates of bathymetric slope, maximum tidal current, average bottom current, and surface color were extracted for haul locations for all sites and years from sources compiled by Turner et al. (2017) specifically for the Aleutian Islands ecosystem. The modeled estimates were not time specific but instead were averaged over several time periods (Turner et al. 2017). Slope was predicted from a National Ocean Service smooth sheet based on a $100\text{-}\times\text{100-m}$ gridded bathymetry raster averaged to a $1\text{-}\times\text{1-km}$ grid and expressed as a percentage (Zimmerman et al. 2013, cited by Turner et al. 2017). Maximum tidal current (cm/s) was estimated for 369 consecutive days starting on January 1, 2009, by utilizing a tidal inversion program parameterized for the Aleutian Islands on a 1-km^2 grid (Egbert and Erofeeva 2002, cited by Turner et al. 2017). Mean bottom current (m/s) was predicted from the Regional Ocean Modeling System averaged on a $10\text{-}\times\text{10-km}$ grid from 1970 to 2004 (Danielson et al. 2011, cited by Turner et al. 2017). Surface color ($\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), which was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) and averaged over 8 years (2003–2011) during the spring and summer months (Turner et al. 2017), was used as a proxy for primary production. Although there was a temporal mismatch between the MODIS data (spring and summer months) and our study hauls, which occurred primarily during fall and spring months, we included this metric as a measure of relative productivity among sites, as greater

TABLE 2. Total number of trawl hauls by year and study site (listed longitudinally from east to west) across the Aleutian Islands. Empty cells indicate that no sampling was conducted. Note that two cruises occurred in 2002 (August and October). Petrel, Tahoma, and Ingenstrem had no trawl exclusion zones (TEZs). Asterisks indicate data that were not included in the TEZ analysis because there were no TEZs or because management strategy changes precluded sampling inside the TEZs. All years and sites were included in the redundancy analysis.

Year	Seguam	Tanaga	Petrel	Amchitka	Kiska	Buldir	Tahoma	Ingenstrem	Agattu
2002	19								
2002	15	33							
2003	41			54					
2004	30	14		27					
2006	42				31				
2007	5				41				
2011	41*	17	15*						
2012	23*	12	17*						
2014	19				1*	25*	29*	11*	9*
2015	32				2	33	41*	5*	19

TABLE 3. Variables considered (initial model) and used in the final redundancy analysis model (TEZs = trawl exclusion zones). The variables bottom temperature and management area (asterisks) were removed from the model, as both were correlated with longitude. The remaining variables with a “No” in the final model column were eliminated from the final model because they did not contribute to the total amount of variation explained.

Variable (units)	Final model	Source
Depth (m)	Yes	Vessel sampling
Bottom temperature (°C)	No*	Vessel sampling
Management area	No*	Vessel sampling
Longitude (continuous)	Yes	Vessel sampling
Season (binary)	No	Vessel sampling
Inside versus outside of TEZs (binary)	No	Vessel sampling
Atka Mackerel percent female	No	Vessel sampling
Average CPUE, invertebrates (kg)	Yes	Vessel sampling
Slope (%)	No	Turner et al. 2017
Maximum tidal current (cm/s)	Yes	Turner et al. 2017
Surface color ($\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	Yes	Turner et al. 2017
Average bottom current (m/s)	Yes	Turner et al. 2017

productivity has the potential to influence fish distributions. In addition, three non-environmental variables were included in the analysis: season (fall and spring research periods), whether the haul occurred inside or outside of a TEZ, and the percentage of female Atka Mackerel, which served as a proxy for potential Atka Mackerel spawning grounds that often occur inside TEZs (Lauth et al. 2007a, 2007b).

Using the package *vegan* (Oksanen et al. 2015) in the statistical modeling software R (R Core Team 2013), we ran a multivariate redundancy analysis (RDA) to examine CPUE estimates of Atka Mackerel and Northern Rockfish constrained by a set of explanatory variables. This ordination technique is appropriate when linear relationships between response and explanatory variables are observed (Rao 1964; Palmer et al. 2008; Legendre et al. 2011). Redundancy analysis is an extension of multiple linear regression, but it allows for multiple response variables (Atka Mackerel CPUE and Northern Rockfish CPUE) and multiple explanatory variables (e.g., bottom depth), similar to a constrained version of a principal components analysis. The results of RDA illustrate correlations between species and constraining variables and are represented in a correlation biplot wherein the first two axes generally account for most of the observed variance. The biplot illustrates the response variables (species CPUE),

explanatory variables (longitude, depth, etc.), and data points (hauls) simultaneously.

To select the explanatory variables used in the final model, several iterations of the model were ordinated and highly correlated variables (i.e., arrows directly on top of or adjacent to each other in the biplot) were eliminated so that only one variable of the highly correlated pair was used in further analyses (Table 3). The R package *psych* (Revelle 2018), which calculates correlation coefficients, was used to ensure that the remaining variables were in fact not correlated. The final model consisted of variables that maximized the amount of explained variation while eliminating those variables that did not increase the total amount of variation explained (Table 3). The final model was permuted 1,000 times by each term to test whether the result was significantly better than a random model; the null hypothesis was that the final model did not significantly explain the variation between the response and explanatory variables.

A generalized linear model (gamma family based on a nonnegative, right-skewed distribution) was used to test for significance in the observed linear trends between Atka Mackerel CPUE and longitude and between Northern Rockfish CPUE and longitude. Linear models were used to test for significant relationships between longitude and several explanatory environmental variables used in the RDA model.

Atka Mackerel diel migration.—During exploratory data analyses, we observed that Atka Mackerel CPUE might be related to time of day. Since our study efforts occurred around the clock, we graphically examined trends in CPUE over a 24-h period at each of the study sites. We compared these trends (Pearson's correlation coefficient r) between NMFS Areas 541 and 543 to evaluate whether relationships between Atka Mackerel CPUE and time of day were uniform between these two subareas.

RESULTS

From 2002 to 2015, 703 trawl hauls were completed across the Aleutian Islands (Figure 1; Tables 1, 2). The Atka Mackerel was the dominant species in the catch and present in over 99% of all trawl hauls, and the Northern Rockfish was present in 96% of trawl hauls. The catch composition by weight of Atka Mackerel and Northern Rockfish shifted from east to west. Total catch weight at the eastern Aleutian Islands study site, Seguam (Figure 1), averaged over 91% Atka Mackerel and 2% Northern Rockfish, with the remaining 7% comprising other species. At the westernmost study site, Agattu (Figure 1), the total catch weight consisted of 46% Atka Mackerel and 39% Northern Rockfish, whereas the remaining 15% of the catch consisted of other species.

Effects of Trawl Exclusion Zones on CPUE

Of the 703 trawl hauls, 457 hauls were included in the CPUE and TEZ analyses. There was no significant difference in the average bottom depth inside versus outside of the TEZ at any study site (Tables 4, 5).

We tested for differences in CPUE estimates among years at the Seguam study site because it was the only site visited during all years of the study. There was no effect of year on Atka Mackerel population distributions (TEZ and non-TEZ stations combined); therefore, data were pooled across years within each study site (Table 5).

There was no difference in Atka Mackerel median CPUE inside versus outside of the TEZ at the Seguam study site (NMFS Area 541). The remaining five study sites (Tanaga, Amchitka, Kiska, Buldir, and Agattu) were combined for analysis, and there was no difference in average CPUE inside and outside of the TEZs (Table 5; Figure 3A). The interaction for the five combined study sites was significant (Table 5; Figure 3A), indicating that CPUEs were variable among sites with respect to TEZs.

There was a significant difference in Northern Rockfish median CPUE inside versus outside of the TEZ at the Seguam study site (Table 5; Figure 3B). The remaining study sites (Tanaga, Amchitka, Kiska, Buldir, and Agattu) were combined for analysis, and there was no difference in average CPUE inside and outside of the TEZs (Table 5; Figure 3B). Similar to the results for Atka Mackerel, the interaction for study site was significant (Table 5; Figure 3B).

There was a significant difference in the invertebrate distribution inside versus outside of the TEZs at all study sites combined, with higher densities observed inside of the TEZs (Table 5; Figure 3C).

Environmental Effects on CPUE

Four non-environmental variables (management area, season, inside versus outside of TEZs, and Atka Mackerel percent female) and two environmental variables (bottom temperature and slope) did not account for any observed variability in species distributions based on the full RDA

model with all variables included, and these variables were therefore eliminated (Table 3). The final RDA model and its explanatory variables (Table 3) accounted for a significant amount of the variance compared to a random model using an ANOVA-like permutation test (1,000 permutations, $P < 0.001$; Oksanen et al. 2015). The results of the RDA accounted for 22% of the constrained variation, whereas the remaining 78% of the variation was not accounted for by using the explanatory variables (Table 6; Figure 4). The haul points (Figure 4, open circles) were dispersed in a “cloud” configuration, which is a good indication that there are linear relationships associated with the variables, as opposed to unimodal distributions.

Atka Mackerel and Northern Rockfish (Figure 4, in red) were distributed in different quadrants, indicating that the variables used in the model contributed differently to the observed variance in CPUE of these two species (McGarigal et al. 2000). Atka Mackerel CPUE, maximum tide, and average bottom current decreased significantly with longitude (east to west, $\sim 180^\circ$ angle, $P < 0.001$; Table 7; Figure 4). In contrast, Northern Rockfish CPUE increased significantly from east to west (longitude), in the opposite direction from Atka Mackerel ($P < 0.001$; Table 7; Figure 4). The cosine angle between average bottom depth and maximum tide or between average bottom depth and longitude indicated little correlation between these variables in each case (Figure 4). However, maximum tide and average bottom current decreased longitudinally from east to west (180° angle; Table 7; Figure 4). Invertebrate CPUE and surface color increased with decreasing tide (Figure 4).

Atka Mackerel Diel Migration

Average Atka Mackerel CPUE during each hour was not correlated between NMFS Areas 541 and 543 ($r = 0.11$, $P = 0.60$), suggesting differences in diel vertical behavior between the two subareas. At Seguam (NMFS Area 541), the Atka Mackerel CPUE was lowest during daylight hours (starting at 1200 hours), which meant that Atka Mackerel were not on the bottom during this time period ($n = 267$ hauls; Figure 5A). At the same site, the Atka Mackerel CPUE was highest during nighttime hours, when Atka Mackerel were on or near the bottom (Figure 5A). However, at Buldir, Tahoma, Ingenstrem, and Agattu combined (NMFS Area 543), the Atka Mackerel CPUE was highest during the daylight hours (starting at 1300 hours; $n = 179$ hauls; Figure 5B), indicating that fish were on or near the bottom during afternoon hours—opposite of what was observed at the Seguam study site.

DISCUSSION

Based on the present study, we can draw three important conclusions with respect to SSL foraging resources.

TABLE 4. Total number of trawl hauls (n) and average depths of areas sampled inside and outside of the trawl exclusion zones (TEZs).

Study site	Inside of TEZ		Outside of TEZ	
	n	Depth (m)	n	Depth (m)
Seguam	125	137.03	78	131.39
Tanaga	22	107.12	25	112.94
Amchitka	57	118.13	24	121.52
Kiska	43	103.51	31	109.47
Buldir	15	119.76	18	122.42
Agattu	6	91.81	13	101.19

TABLE 5. Results of the CPUE (cube-root transformed; kg/min fished) and trawl exclusion zone (TEZ) analysis; statistics were used to test for differences in average CPUE estimates inside (closed to the commercial fishery) versus outside (open to the commercial fishery) of the TEZs for Atka Mackerel, Northern Rockfish, and all invertebrates combined. The term “combined” in the area column includes the combined sites of Tanaga, Amchitka, Kiska, Buldir, and Agattu.

Area(s)	Test	Model	<i>P</i> -value	Response	Inside versus outside of TEZ
Combined	Two-way ANOVA	CPUE ~ TEZ × Site	0.363	Atka Mackerel	Not different
		Site interaction	<0.001	Atka Mackerel	Significant
Sequam	Mann–Whitney	CPUE ~ TEZ	0.437	Atka Mackerel	Not different
Combined	Two-way ANOVA	CPUE ~ TEZ × Site	0.111	Northern Rockfish	Not different
		Site interaction	<0.001	Northern Rockfish	Significant
Sequam	Mann–Whitney	CPUE ~ TEZ	0.001	Northern Rockfish	Different
All sites	Mann–Whitney	CPUE ~ TEZ	<0.001	Invertebrates	Different
All sites	Two-way ANOVA	Depth ~ TEZ	0.38	Bottom depth	Not different; no interaction

First, Atka Mackerel formed dense, consistent aggregations in the eastern Aleutian Islands (Figure 1; NMFS Area 541), where SSL pup and non-pup counts have stabilized and are slowly increasing. In contrast, Atka Mackerel distributions were more diffuse over a larger area in the western Aleutian Islands (Figure 1; NMFS Area 543), where the SSL pup and non-pup counts continue to decline. Second, Atka Mackerel in the eastern Aleutian Islands were on the seafloor bottom during hours that overlap with adult female SSLs diving to those depths (Loughlin et al. 1998), whereas this pattern was not observed in the western Aleutian Islands. Third, there was no significant difference between open and closed (i.e., TEZ) areas in terms of CPUE estimates for Atka Mackerel and Northern Rockfish; however, TEZs remain an important tool in fish habitat protection, which we discuss further below.

In both the eastern and western Aleutian Islands, Atka Mackerel dominate the SSL diet throughout the year in terms of frequency of occurrence, percent weight, and percent bioenergetic prey contribution (Sinclair et al. 2005, 2013; Tollit et al. 2017). Northern Rockfish also comprise a portion of SSL diets, although at much lower frequencies compared to Atka Mackerel (Sinclair et al. 2013; Tollit et al. 2017). Interestingly, the presence of rockfish species in SSL diets decreases in the far western Aleutian Islands when incorporating genetic techniques (Tollit et al. 2017), even though NMFS survey biomass estimates of Northern Rockfish are an order of magnitude higher than biomass estimated anywhere else in the Aleutian Islands (Spencer and Ianelli 2018). Despite the higher availability of rockfishes in the western Aleutian Islands, the consistent dominance of Atka Mackerel in SSL diets may indicate a general preference for Atka Mackerel (Merrick et al. 1997; Sinclair et al. 2013; Tollit et al. 2017).

For SSLs, foraging success requires not only an adequate amount of prey but also reasonable traveling times from haulouts and rookeries such that foraging trips are

on the whole energetically favorable. Adult female SSLs generally forage within about 10 km (~5.4 nautical miles) of their rookeries, diving at depths ranging from 4 m to more than 250 m, with a mean diving depth of 53 m (Loughlin et al. 1998). Young foraging SSLs remain in relatively shallow waters and close to shore (<18.52 km [<10 nautical miles]) while developing their foraging skills during their first year (Fadely et al. 2005). Adult female SSLs can also remain relatively shallow (<100 m) and nearshore depending on their reproductive status and prey availability (Merrick and Loughlin 1997). Both NMFS surveys and stock assessments yield similar estimates of Atka Mackerel biomass in the eastern and western Aleutian Islands (Lowe et al. 2016, 2018). However, the significantly lower Atka Mackerel CPUE estimates observed in the western Aleutian Islands during this study (Figure 2B) and the consequent decreases in prey encounter rates may translate into longer SSL foraging times compared to the eastern Aleutian Islands, where there remain consistently large, dense aggregations of Atka Mackerel. In support of this, Lander et al. (2010) found that the maximum trip duration of juvenile SSLs was significantly longer in the western Aleutian Islands than in the eastern Aleutian Islands. This difference in foraging times suggests that there are tradeoffs while an animal is foraging for patchily distributed prey. At some point in time while the animal is foraging in a patch, the prey will decrease below a threshold that requires the animal to travel to another patch of prey. If these patches of prey are sparse and the amount of traveling time is increased (due to exhausting the prey patches more frequently; Figure 2B), the animal may expend more energy than it would expend in an environment where less travel is required because the prey patch is relatively large (Figure 2A). Simply stated, it likely takes more energy for an SSL to forage for Atka Mackerel in the western Aleutian Islands than in the eastern Aleutian Islands.

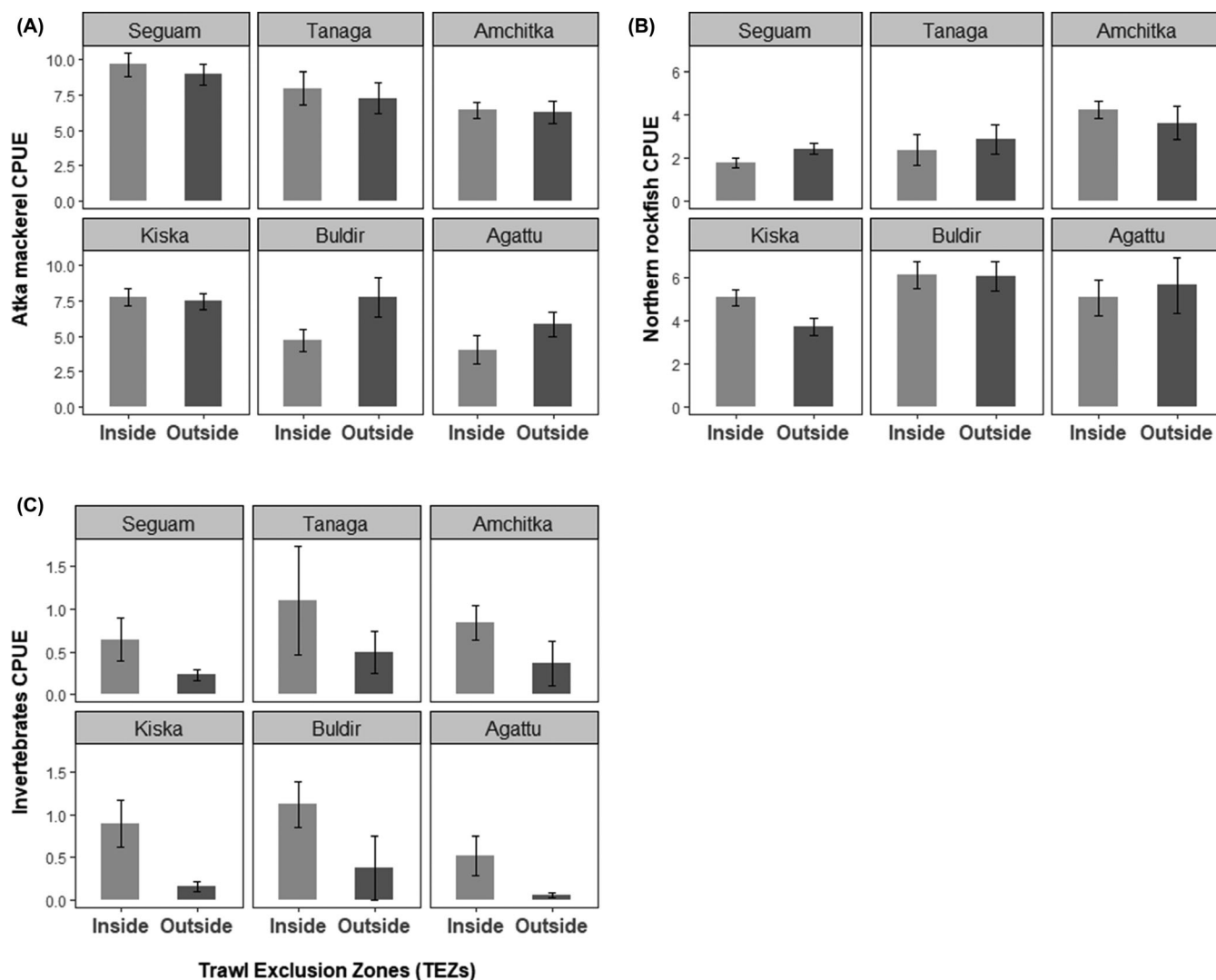


FIGURE 3. Bar graph of average CPUEs (cube-root transformed; kg/min fished) inside and outside of trawl exclusion zones (TEZs) for (A) Atka Mackerel, (B) Northern Rockfish, and (C) invertebrates (note the difference in y-axis scale among panels). The light gray bar in each panel is the average CPUE inside of the TEZ (closed to Atka Mackerel commercial fishing), and the dark gray bar is the average CPUE outside of the TEZ (open to commercial fishing). Error bars represent 95% confidence intervals. The bar graph does not include data from 2011 and 2012 at Seguam (the area inside of the TEZ was closed to research) or data from 2014 in the western Aleutian Islands study sites (Buldir and Agattu; those sites were closed to all commercial trawling).

In addition to the longitudinal gradient in Atka Mackerel distribution, we also observed differences in diel migration behavior between Atka Mackerel in the eastern and western Aleutian Islands. During daylight hours, Atka Mackerel form dense schools and vertically migrate in the water column, presumably to feed on benthic and pelagic zooplankton (Yang 1999); during nocturnal hours, they reside on or near the bottom (Nichol and Somerton 2002). At the eastern Aleutian Islands study site, Atka Mackerel CPUE estimates were consistently high between 0300 and 0400 hours (Figure 5A), suggesting that Atka Mackerel are on the seafloor coincident with the period when adult

female SSLs forage at depths over 100 m (Loughlin et al. 1998). The diving depths and durations for adult female SSLs vary by individual and rookery location, but diving generally occurs in the late afternoon through early morning, with almost all dives more than 100 m occurring between 2100 and 0300 hours (Loughlin et al. 1998). An archival tag study of Atka Mackerel in Seguam Pass (Nichol and Somerton 2002) independently confirmed the same diel migration pattern observed in this study using CPUEs from that site. In contrast, Atka Mackerel CPUE estimates in the western Aleutian Islands were consistently lower during the evening and morning hours (0000–1200

TABLE 6. Results of the redundancy analysis (RDA) evaluating extrinsic effects on the CPUEs of Atka Mackerel and Northern Rockfish. The variables used in the model are shown in Table 3. The analysis accounted for 21.6% of the constrained variation (unconstrained variation, or 78.4% of the variance, was not accounted for by the explanatory variables). The first two axes of the model (RDA1 and RDA2) accounted for 97.3% of the explained variation out of all 10 axes.

RDA result	Value	Variation explained (%)
Total inertia	14.71	
Constrained (all axes)	3.24	22
Unconstrained	11.48	78
R^2	0.22	
R^2 , adjusted	0.21	
Eigenvalue, RDA1	2.75	18.7
Eigenvalue, RDA2	0.48	3.3

hours; Figure 5B), suggesting that Atka Mackerel are not on the seafloor bottom and therefore not available to adult female SSLs during their typical foraging period. It should be noted that these spatial differences in Atka Mackerel diel migrations across the Aleutian Islands have not been observed prior to the present study. One possible explanation for these observations includes potential differences in Atka Mackerel prey, prey availability, and

prey consumption rates between the eastern and western Aleutian Islands. Indeed, Rand et al. (2010) found large differences in the diets of Atka Mackerel in the eastern Aleutian Islands (NMFS Area 541) relative to those in the western Aleutian Islands (Figure 1; NMFS Area 542), with the former consuming more energetically rich prey. The diel patterns described in the present study should be explored further with respect to Atka Mackerel prey fields across the Aleutian Islands archipelago.

Overall, there was no consistent effect of TEZs on Atka Mackerel or Northern Rockfish spatial distributions. However, invertebrate CPUE estimates were much higher inside TEZs at all sites, suggesting that these boundaries protect bottom habitats from the impacts of trawling. The known effects of bottom trawling on the ocean floor are dependent on several factors, including the invertebrate community composition (e.g., sedentary versus mobile), bottom type (e.g., soft versus rocky), and fishing gear type (McConnaughey et al. 2000). Although no consistent effects of TEZs on fish densities were observed, these closures may indirectly benefit fish species by offering greater protection to structure-forming invertebrates. Invertebrate communities can provide vertical structure for protection from predators and habitat for feeding, especially for juvenile fish (Rooper and Boldt 2005; Laman et al. 2015). For example, numbers of adult and juvenile Pacific Ocean

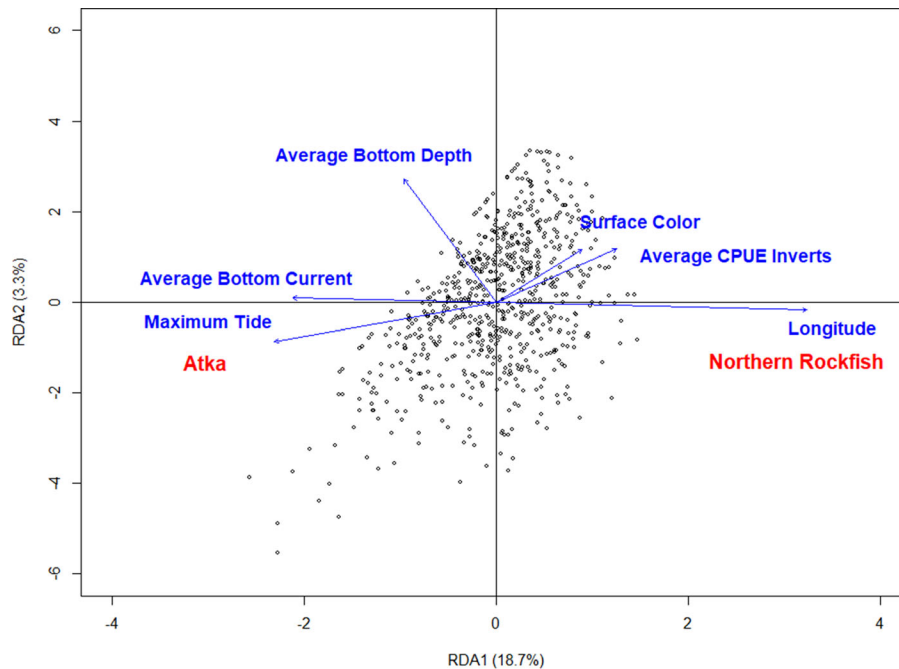


FIGURE 4. Correlation biplot (weighted average scores, scale = 2; Oksanen et al. 2015) illustrating the results of the redundancy analysis (RDA). The final model included those variables that accounted for a significant portion of species CPUE (cube-root transformed; kg/min fished) distribution and are shown in blue text (inverts = invertebrates). Arrow length indicates the strength of the relationship. Arrows at 180° to each other show strong negative trends between the variables; arrows at 90° angles show no correlative relationship. Species names are listed at the centroid of their distribution in red text, and the open circles are individual hauls (which include both Atka Mackerel [Atka] and Northern Rockfish) for all years and study sites.

TABLE 7. Results of the linear models testing for significance of variables from the redundancy analysis results in Figure 4 (GLM = generalized linear model; NA = not applicable; units: maximum tide, cm/s; average bottom current, m/s; surface color, $g\ C\cdot m^{-2}\cdot d^{-1}$).

Model	Test	P	Adjusted R	Result
Atka Mackerel CPUE ~ Longitude	GLM	<0.001	NA	Decreased from east to west
Northern Rockfish CPUE ~ Longitude	GLM	<0.001	NA	Increased from east to west
Maximum tide ~ Longitude	Linear model	<0.001	0.19	Decreased from east to west
Average bottom current ~ Longitude	Linear model	<0.001	0.67	Decreased from east to west
Surface color ~ Longitude	Linear model	<0.001	0.17	Increased from east to west
Average CPUE, invertebrates ~ Longitude	Linear model	0.620	NA	No relationship

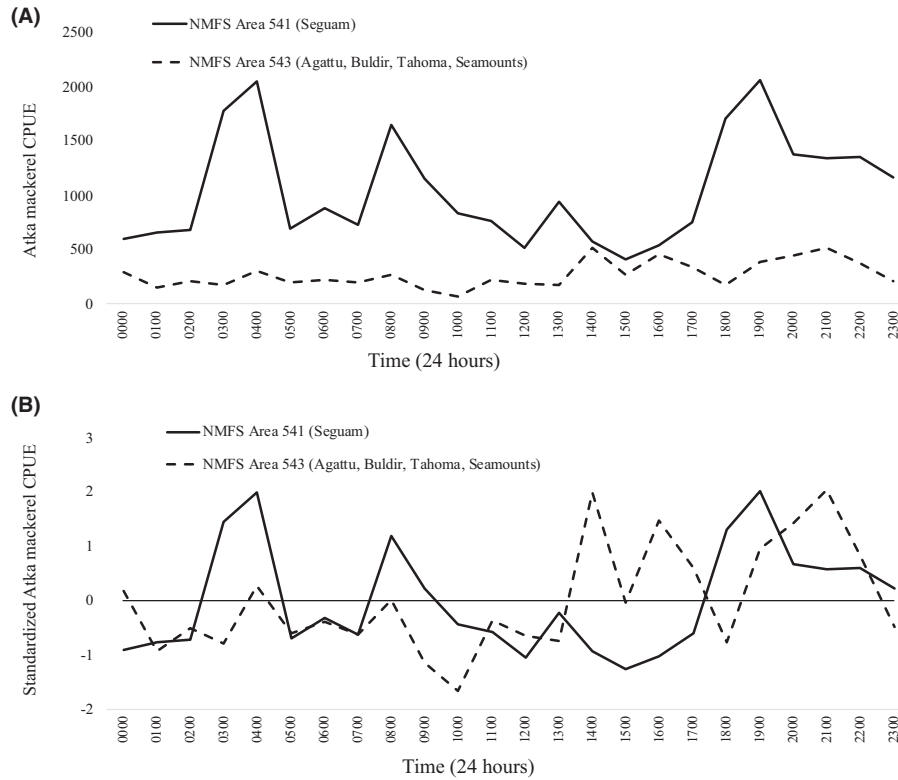


FIGURE 5. Atka Mackerel CPUE (kg/min fished) and time of day (24 h) at (A) Seguam (National Marine Fisheries Service [NMFS] Area 541; solid line) and at Buldir, Tahoma, Ingenstrem, and Agattu combined (NMFS Area 543; dashed line). (B) Average CPUE standardized (i.e., subtracting the mean and dividing by the SD) for NMFS Areas 541 and 543 is shown. Lower CPUEs indicate that fish were not on the seafloor bottom; higher CPUEs indicate that fish were on the seafloor bottom. There was no significant correlation between CPUEs in NMFS Areas 541 and 543 ($r=0.11$, $P=0.60$).

Perch *S. alutus*—another common species in the Aleutian Islands—increased in the presence of certain sponge shapes, which may act as refugia for both life stages (Laman et al. 2015). In addition to providing protective structures to juvenile- or adult-stage fish, several studies have documented Atka Mackerel nesting grounds inside TEZs, where eggs are deposited in association with sessile invertebrates on rocky, high-relief habitats (Lauth et al. 2007a, 2007b, 2010; Cooper et al. 2010; Cooper and McDermott 2011; Rand and Lowe 2011). Although we

saw a strong difference in CPUEs of invertebrates between the open and closed areas, there was no significant longitudinal trend in invertebrate CPUE across the Aleutian Islands even though Northern Rockfish CPUE increased in the western Aleutian Islands. Our multivariate analyses demonstrated that Northern Rockfish have a slightly stronger association with invertebrate densities, likely because rockfish generally prefer habitats with greater substrate relief and complexity (Love et al. 2002; Rooper et al. 2010; Laman et al. 2015).

The TEZs protect not only seafloor bottom habitat but also persistent oceanographic features. This leads us to one possible explanation for the observed patterns in Atka Mackerel distribution: oceanographic conditions in the western Aleutian Islands study sites may not be favorable for Atka Mackerel populations. The two most important variables that influenced Atka Mackerel spatial aggregations were higher tidal and bottom currents, both of which decreased in the western Aleutian Islands. High current areas create environments with swiftly moving water and potentially a high exchange of oxygen and nutrients—two conditions that are important for Atka Mackerel feeding and reproduction. Atka Mackerel are demersal spawners that lay their eggs in nests over a period of 7 months, with males guarding the nests for up to 3 months (Lauth et al. 2007a, 2007b). Results from this study suggest that adult Atka Mackerel prefer these highly dynamic environments, which balance high water exchange and movement with narrow temperature ranges that are optimal for long periods of egg incubation (Lauth et al. 2007a, 2007b). This is demonstrated at our easternmost study site, Seguam, where a well-known large, dense Atka Mackerel aggregation consistently occurs inside the TEZ (Figure 1). This dense aggregation of Atka Mackerel is located near a precipice, where deep upwelling occurs and where Atka Mackerel feed heavily on myctophids (Rand and Lowe 2011). This area is characterized by a well-mixed water column that overlies a topographic depression wherein tidal and bottom currents are swift (Ladd et al. 2005a), a habitat type that our multivariate analysis suggests is preferred by Atka Mackerel. These same waters are considered a biological “hot spot” (Piatt et al. 2006), hosting large aggregations of northern fulmars *Fulmarus glacialis* (Jahncke et al. 2005), shearwaters (Procellariidae; Ladd et al. 2005b), and other seabirds.

The present study highlights patterns in the spatial and temporal distributions of Atka Mackerel, the dominant prey item in SSL diets, and is unique in that it occurred during seasons and times that had not been previously sampled (e.g., fall and spring; nighttime) and within highly rugose habitats. This unique sampling design allowed us to capture a longitudinal gradient in Atka Mackerel CPUE that was not observed by the NMFS survey. Given that the Atka Mackerel remains the dominant prey item in the SSL diet—including the western portion of the Western DPS, where SSL numbers continue to decline—continued monitoring of fall and winter prey distributions in the western Aleutian Islands is necessary. Shifts in prey distributions, changes in prey abundance, and fish movement in and adjacent to TEZs are still largely unknown. Additionally, simultaneous sampling of prey and SSLs, as was recommended by Logerwell et al. (2009), would provide a greater understanding of the prey requirements of SSLs in this area. It is likely that researchers will not

pinpoint the exact reason(s) for the sharp decline in SSL populations that occurred during the 1990s and early 2000s, but their continuing decline in the far western portion of the Aleutian Islands warrants further study.

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