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Spatial Differences in the Distributions of Arctic and Pacific Lampreys in the Eastern Bering Sea

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Abstract

The Arctic Lamprey *Lethenteron camtschaticum* and Pacific Lamprey *Entosphenus tridentatus* are ecologically and culturally valuable native species that co-occur in the eastern Bering Sea. Lamprey wounds are often observed on fishes in this region, yet there is a paucity of information on the distribution of anadromous lampreys, lamprey–host interactions, and foraging behavior in the ocean. Our hypothesis was that each lamprey species would be positively associated (distribution and abundance) with their presumed hosts: Arctic Lampreys with smaller fish that could easily be killed, and Pacific Lampreys with larger hosts that could sustain blood feeding. To examine lamprey distribution, abundance, and associations, we utilized data from two fishery-independent surveys—one epipelagic trawl survey and one benthic trawl survey—conducted between 2002 and 2012 in the eastern Bering Sea. Distinct distributions of lamprey species were evident in models of their presence and absence by latitude and longitude. Arctic Lampreys inhabited the northern regions on the inner/middle continental shelf in depths less than 100 m, while Pacific Lampreys inhabited waters deeper than 150 m along the continental slope. Pacific Herring *Clupea pallasii* and juvenile salmonids were found in regions with relatively high Arctic Lamprey catches in the epipelagic trawl survey, and catches of lampreys and these potential hosts were positively correlated. Demersal groundfishes were found in regions with relatively high Pacific Lamprey abundance in the benthic trawl survey, but catches of Pacific Lampreys and these hosts were not consistent. We conclude that Arctic Lampreys and Pacific Lampreys are segregated in the eastern Bering Sea, and although differences in their distributions may be explained by species-specific host preferences, alternate explanations include differences in seasonal movements, source river locations, and marine residence times. This study provides an initial baseline of the oceanic ecology of lampreys, which increases our understanding of species-specific differences beyond traditional freshwater studies.

[INTRODUCTION]

Anadromous lampreys (Petromyzontiformes) are jawless fishes that play important ecological roles in freshwater and marine environments and are valuable to the cultures that harvest them (Renaud 2011). During their life cycle, lampreys are prey for a variety of fishes, birds, terrestrial and marine mammals, and invertebrates (Cochran 2009). Adult lampreys feed on aquatic vertebrates via consumption of blood, flesh, or both during their trophic phase (Potter and Hilliard 1987). Species of lamprey that feed as adults are referred to as parasites (though some are in fact more predatory than parasitic), whereas those that forgo feeding as adults are nonparasitic and generically referred to as brook lampreys (Hardisty and Potter 1971). Although lamprey fisheries occur in freshwater rivers, the parasitic species that feed in the ocean are the type targeted because of their large size, high caloric content, and predictable spawning runs. Anadromous lampreys were historically a regal food enjoyed by Roman and English nobility, and fisheries for European River Lampreys *Lampetra fluviatilis* and Sea Lampreys *Petromyzon marinus* continue across Europe today (Renaud 2011). In the USA, Alaska Natives living on the lower Yukon and Kuskokwim rivers target Arctic Lampreys *Lethenteron camtschaticum* in late November to early December by using dip nets swept through holes cut in the frozen surface of the river (Brown et al. 2005). In the U.S. Pacific Northwest, Native Americans fish for Pacific Lampreys *Entosphenus tridentatus* in the summer by using nets, poles with hooks, and bare hands (Close et al. 2002).

The trophic ecology of adult lampreys can be evaluated using evidence of lamprey–host interactions, including lampreys still attached to hosts and the wounds left as a result of these encounters. Although lampreys are occasionally observed attached to large-bodied vertebrates, such as whales (Pike 1951; Nichols and Tscherter 2011; Samarra et al. 2012) and sharks (Gallant et al. 2006), teleosts more frequently exhibit evidence of parasitic lamprey interactions—specifically wounds in their skin and muscle. These wounds have been observed on the following groups of teleosts in the North Pacific Ocean: Gadidae, Clupeidae, Salmonidae, Sebastidae, and Pleuronectidae (Sviridov et al. 2007; Orlov et al. 2009; Shevlyakov and Parensky 2010). Conversely, lamprey wounds are apparently absent on teleosts that possess protective body structures, slender body forms, slimy skin, or watery flesh, such as members of Cottidae, Psychrolutidae, Hemitripteridae, Agonidae, Zoarcidae, Stichaeidae, Liparidae, and Macrouridae (Orlov et al. 2009).

Additional information about the trophic ecology of adult anadromous lampreys can be inferred from the ocean habitats in which specimens are opportunistically captured. Lamprey captures in the Atlantic Ocean provide evidence that first-year Sea Lampreys feed on small fishes in benthic waters of the continental shelf, whereas older Sea Lampreys feed on large pelagic species near the continental slope (Halliday 1991). Long-term data on Arctic Lamprey captures in the North Pacific Ocean (TL range = 15–79 cm) suggest that the greatest abundance occurs in the western Bering Sea within the upper 100 m of the water column (Orlov et al. 2014), which coincides with pelagic fishes found in nearshore areas. Similarly, Pacific Lamprey captures in the North Pacific Ocean (TL range = 12–85 cm) are most abundant in the Bering Sea but are located in deeper waters and throughout the water column (Orlov et al. 2008), which coincides with benthic and pelagic fishes found offshore.

Understanding the trophic ecology of adult lampreys in the ocean is important because hosts may experience adverse impacts from parasitic interactions with lampreys. For example, in the Fraser River plume, British Columbia, the flesh-feeding Western River Lamprey *Lampetra ayresii* was estimated to consume hundreds of millions of juvenile salmonids *Oncorhynchus* spp. and Pacific Herring *Clupea pallasii* (Beamish and Neville 1995). In the Amur River estuary, Russia, the greatest source of early stage mortality for Chum Salmon *Oncorhynchus keta* and Pink Salmon *O. gorbuscha* smolts was attributed to feeding by Arctic Lampreys (Novomodnyy and Belyaev 2002). In the Laurentian Great Lakes, parasitism by invasive Sea Lampreys reduced populations of native species, such as the Burbot *Lota lota* and Lake Trout *Salvelinus namaycush,* and negatively impacted the rehabilitation of the imperiled Lake Sturgeon *Acipenser fulvescens* (Sutton et al. 2004; Stapanian et al. 2006). The potential severe consequences of lamprey–host interactions for host populations cannot be overstated.

An increased understanding of lamprey–host interactions has been identified as a research need for native lamprey species in the North Pacific Ocean (Mesa and Copeland 2009; Clemens et al. 2017). However, the vast geographic area over which anadromous lampreys feed and the difficulty in capturing them at sea make this an arduous task. Although general distributions have been established for Arctic Lampreys and Pacific Lampreys by combining multiple years and multiple sources of data for the North Pacific Ocean (Orlov et al. 2008, 2014), details pertaining to interannual variation or ecosystem correlates are precluded in this approach. As a result, it is unknown whether specific habitats are consistently utilized by lampreys or why certain areas may be more important for one species or another. Furthermore, single-species distributions of Arctic Lampreys and Pacific Lampreys in the North Pacific Ocean show an apparent segregation of habitat use in the eastern Bering Sea, but to date this phenomenon has not been explored, obviating underlying differences in how these species are distributed. Because it is known that the adult phase of anadromous lampreys is characterized by feeding, one potential driver of the distributions of Arctic Lampreys and Pacific Lampreys in the eastern Bering Sea is the availability of suitable hosts.

Feeding behavior can differ among parasitic lamprey species (Potter and Hilliard 1987), and this may play a role in host selection and lamprey distribution. Lampreys that feed on blood are expected to select larger hosts that can sustain longer feeding events, whereas lampreys that feed on flesh target smaller hosts that are easily killed and more abundant (Beamish 1980; Renaud et al. 2009). Pacific Lampreys are known to consume both the flesh and blood of their hosts (Renaud et al. 2009); thus, they are expected to select larger-bodied hosts. Along the continental slope in the eastern Bering Sea, large-bodied fishes have been observed with lamprey wounds (Figure 1), which are suspected to have been inflicted by Pacific Lampreys. When Pacific Cod *Gadus macrocephalus* in the eastern Bering Sea were examined for lamprey wounds, differences in oral disk morphology between the Arctic Lamprey and the Pacific Lamprey were used to determine that the larger Pacific Lamprey was most likely to have inflicted the observed wounds (Siwicke and Seitz 2015). In contrast, Arctic Lampreys are inferred to be flesh feeders (Renaud et al. 2009), making them more of a predator or scavenger than a parasite, despite the latter term being used to refer to any lamprey species that feeds as an adult. Therefore, Arctic Lampreys are expected to target smaller prey, to which they would attach and consume tissue. In the northern nearshore region of the eastern Bering Sea, Pacific Herring and juvenile salmon have been observed with lamprey wounds (Figure 2).

For parasitic lampreys, the primary function of migrating to the ocean is to feed, and fishes that are found to co-occur with lampreys are the most probable hosts for those lampreys. To test this premise, we hypothesized that distributions and catches of lampreys would be positively associated with those of their presumed hosts: Arctic Lampreys with small-bodied fish that they can easily capture and kill, and Pacific Lampreys with large-bodied fish to which they can attach and upon which they can feed for a prolonged period. To assess this, we first compiled information on the presence and absence of Arctic Lampreys and Pacific Lampreys to establish each species' distribution in the eastern Bering Sea. Next, we examined whether fish assemblages differed between regions with relatively high and low abundances of each lamprey species, and we contrasted this with a similar comparison of temperature. We then explored correlations between the catches of potential host fishes and lampreys in fishery-independent surveys. Utilizing the best available data on lampreys in the eastern Bering Sea, this study takes an initial step toward understanding the ecology of trophic-phase anadromous lampreys in this region.

[A]METHODS

We analyzed lamprey and fish catch data from two fishery-independent surveys occurring in the eastern Bering Sea. One survey was conducted in epipelagic waters, and the other took place in benthic waters; when combined, these surveys provided comprehensive coverage of the region. To analyze the distributions of Arctic Lampreys and Pacific Lampreys in the eastern Bering Sea, we first modeled the probability of overall lamprey presence and absence by using station data. We then analyzed differences in fish assemblages and temperatures in regions of relatively high and low lamprey abundances. Finally, we explored correlations between the catches of lampreys and potential hosts suggested by our fish assemblage analyses.

[C]*Epipelagic and benthic survey data*.—Catches of lampreys and surface-oriented teleosts were acquired from an epipelagic rope trawl survey conducted by the National Marine Fisheries Service (NMFS) as part of the Bering Aleutian Salmon International Survey (BASIS). This survey in the eastern Bering Sea occurred annually from mid-August to early October of 2002–2012; however, effort in 2008 was reduced because of a transition in survey programs, so that year was excluded from the analysis (Farley et al. 2009). Prior to 2008, the entire survey was conducted with one vessel. After 2008, the survey was carried out concurrently in the northern and southern (south of 60°N) portions of the eastern Bering Sea by using two vessels. Epipelagic survey gear consisted of a 198-m midwater rope trawl that was modified for use in the epipelagic zone; mesh sizes ranged from 162 cm to a 1.2-cm cod-end mesh liner, and tows were 30 min in duration (Farley et al. 2009). Surface temperatures were recorded for each station by using a bathythermograph. At 26 stations sampled during one leg of the BASIS epipelagic survey in 2002, the species of captured lampreys was not identified, but this was an artifact of the data recorder, and all were believed to be Arctic Lampreys (J. Murphy, National

Oceanic and Atmospheric Administration [NOAA]-NMFS, personal communication). The CPUE for each species was standardized to mass per unit of area swept by the trawl (kg/ha) by dividing the mass (kg) by 25 ha, the average area swept during a 30-min tow (Murphy et al. 2009). We further confirmed species identification by retaining most of the lampreys captured during the 2012 survey (*N* = 28), all of which were positively identified as Arctic Lampreys based on dentition (Mecklenburg et al. 2002). Because Pacific Lampreys were infrequently captured in the epipelagic survey (<0.1% of stations), we limited our analysis of epipelagic data to Arctic Lampreys.

Catches of lampreys and bottom-oriented teleosts were obtained from a benthic rope trawl survey conducted by the NMFS Resource Assessment and Conservation Engineering Division's Groundfish Assessment Program. This survey occurred annually between June and August on the Bering Shelf from 1982 to 2013 and biennially along the Bering Slope from 2002 to 2012; however, the Bering Slope survey was not conducted in 2006 due to a lack of funding (Hoff 2013; Lauth and Nichol 2013). Survey gear consisted of an 83-112 eastern otter trawl with a 25.3-m headrope, 34.1-m footrope, 8.9–10.2-cm-mesh net, and 3.2-cm cod-end mesh liner (Hoff 2013; Lauth and Nichol 2013). Bottom temperatures were recorded at each station by using a bathythermograph. During one leg of the 2010 Bering Slope survey, the species of captured lampreys was not identified; however, based on the fact that all other lampreys captured by this survey in all years were identified as Pacific Lampreys, those unidentified lampreys were assumed to be the same species (G. Hoff, NOAA–NMFS, personal communication) and are included herein to avoid creating a geographical "hole" by exclusion of this survey leg. The CPUE data (kg/ha) were downloaded from the Groundfish Survey Data website (AFSC 2013). We further confirmed species identification by retaining most of the lampreys captured during the 2012 survey (*N* = 46), all of which were positively identified as Pacific Lampreys based on dentition (Mecklenburg et al. 2002). Arctic Lampreys were never identified at a benthic survey station, so we limited our analysis of benthic data to Pacific Lampreys.

Prior to analysis, rare species were removed, and salmon were divided into two life history stages. Rare species were defined as those occurring at less than 5% of stations within the study area for all years of a survey. They were unlikely to influence lamprey distribution and would tend to distort clustering patterns that might exist in their absence. For the epipelagic trawl survey, the five species of Pacific salmon were further divided into (1) a juvenile group, consisting of individuals in their first summer in the ocean (generally <300 mm in length); and (2) an immature/maturing group, comprising individuals that had already spent at least one winter in the ocean.

Lamprey and teleost catch data were pooled by year and region within each survey type (epipelagic or benthic). There were 16 Bering Sea Integrated Ecosystem Research Program (BSIERP) regions (Figure 3), which divided the eastern Bering Sea along known oceanographic, bathymetric, and ecological boundaries (Ortiz et al. 2012). For example, the eastern Bering Sea was separated into three depth domains of 0–50, 51–100, and 101–150 m (Coachman 1986), and the boundaries of BSIERP regions often coincided with these domains. Any stations located outside of the BSIERP region boundaries were not examined further in this analysis. The mean CPUE was calculated for each species from all stations within these predetermined regions for each year and each survey type (hereafter, survey–year–region combination). A minimum of three stations sampled per survey–year–region combination was required for inclusion in subsequent analyses to avoid inadequate characterization of fish assemblages in undersampled regions.

To explore the relationship between the abundances of lampreys and their potential hosts, each survey–year–region combination was categorized as “high” or “low” lamprey catch (defined below), and this factor was used for statistically testing differences between areas with relatively high and low lamprey abundances. The selected criterion for establishing the high and low lamprey catch categories varied slightly between surveys because the larger mesh size of the benthic trawl was believed to be less efficient at sampling lampreys compared to the smaller mesh of the epipelagic trawl. The high lamprey catch category was defined as two or more Arctic Lampreys and one or more Pacific Lampreys per survey–year–region combination.

[C]*Modeling the distributions of Arctic Lampreys and Pacific Lampreys*.—General distributions of lampreys in the eastern Bering Sea were determined by the presence or absence of lampreys at all examined stations. The probability of catching a lamprey at a station based on geography was modeled for Arctic Lampreys in the epipelagic trawl survey and for Pacific Lampreys in the benthic trawl survey. We utilized a generalized linear model framework assuming a binomial distribution, where the response was 1 if a lamprey was captured at a station and 0 otherwise. For both species, a pre-analysis using a generalized additive model suggested starting with a full model that included a quadratic term for both latitude and longitude. Therefore, our full model included interactions as follows: <AQ: in Methods, please check the revised equation for *P*(lamp > 0) to ensure that it is accurate.>

$$P(\text{lamp} > 0) = \text{Lat} + \text{Long} + (\text{Lat} \times \text{Long}) + \text{Lat}^2 + \text{Long}^2 + (\text{Lat} \times \text{Long}^2) + (\text{Long} \times \text{Lat}^2),$$

where *P*(lamp > 0) is the probability of a lamprey being present, Lat is the latitude of a sampling station, and Long is the longitude of a sampling station. The best model was selected by utilizing a backwards stepwise approach based on Akaike's information criterion, which penalizes models with more parameters and poorer fits. This analysis was conducted using the R platform (R Core Team 2016) and the package "mgcv" (Wood 2006, 2011).

[C]*Ordination analysis*.—To investigate whether fish assemblages in regions with high and low lamprey catches differed from one another, we employed nonparametric multivariate analyses in PRIMER version 6.1.15 (Clarke and Gorley 2006). Because lamprey species were segregated by survey, data from the epipelagic survey and the benthic survey were treated separately in the analysis. Because Pacific Lamprey captures were predominantly obtained along the continental slope, analysis of benthic survey data was limited to years in which both a Bering Shelf survey and a Bering Slope survey were conducted (2002, 2004, 2008, 2010, and 2012). The resulting matrices were 121 survey–year–region combinations × 25 teleost groups from the epipelagic survey and 68 survey–year–region combinations × 64 teleost groups from the benthic survey.

A two-part analysis was conducted for each survey type to visualize and test for differences in fish assemblages among year–region combinations with high and low lamprey catches. First, we visualized patterns in fish assemblages among year–region combinations by using nonmetric multidimensional scaling (NMDS), a nonparametric method that reduces similarities to rank order. To do this, we applied a square-root transformation to the mean CPUE data, de-emphasizing high CPUE values but not overemphasizing low CPUE values. A similarity matrix was then constructed from the square-root-transformed data for each survey by using a Bray–Curtis dissimilarity measure (Clarke and Gorley 2006). An NMDS plot was then created for each survey based on rank orders from the similarity matrix, and multidimensional data were reduced to two or three dimensions. Kruskal's stress value was used to estimate how well the NMDS scaling represented the multivariate data; stress values closer to zero provide a better representation of the data (Kruskal 1964). For this study, we only examined the three-dimensional solution if Kruskal's stress value for the resulting NMDS in two dimensions was greater than 0.2, indicating a poor fit (Kruskal 1964).

Second, we used an analysis of similarity (ANOSIM) routine to test for significant differences in fish assemblages by lamprey catch group (high versus low). The ANOSIM test is a rank-based analog of an ANOVA, establishing a permutation-based null distribution from the similarity matrix by which a test statistic *R* is compared (Clarke and Gorley 2006). We ran 9,999 permutations of the data for each survey type to create a null distribution, and we used *R*-values to aid in interpreting group similarities. An *R*-value close to zero indicated that fish assemblages were similar in the high and low lamprey catch groups, while an *R*-value closer to 1 indicated greater dissimilarity in fish assemblages between catch groups (Clarke and Gorley 2006). Additionally, an index of multivariate dispersion (MVDISP) was used to assess differences in variability between groups (Clarke and Gorley 2006). Significant differences between high and low lamprey catch groups from an ANOSIM test ($\alpha = 0.05$) were interpreted by using a similarity percentage (SIMPER) routine, which partitioned the contributions of individual teleost groups to the dissimilarity between year–region combinations with high and low lamprey catch.

[C]*Temperature analysis*.—In addition to fish assemblages, temperatures from high and low catch groups of Arctic Lampreys and Pacific Lampreys were compared. Welch's *t*-test was used to identify significant differences between groups, and means and SEs are reported. Statistical comparisons were conducted in R (R Core Team 2016).

[C]*Lamprey and host correlation analysis*.—To identify potentially important teleost hosts for Arctic Lampreys and Pacific Lampreys, we tested for positive correlations between means of lamprey CPUE and potential host CPUEs by utilizing a nonparametric Spearman's rank-order correlation (Hollander and Wolfe 1973). For this portion of the analysis, we only included regions with three or more stations sampled during each included year within a survey type. Additionally, regions in which lampreys were rarely captured (i.e., <5% of stations) were excluded to avoid including excessive zeros in the data. The potential hosts investigated were selected by using the results of the previously described SIMPER routine. Included teleost groups had a greater mean CPUE for the high lamprey catch group compared to the low lamprey catch group in the SIMPER analysis; contributed more than 2% to the dissimilarity between these groups; and consistently contributed to the dissimilarity (defined here as [dissimilarity/SD] > 1). Because sampling took place during 10 years for the epipelagic survey compared to 5 years for the benthic survey, an additional analysis of correlations between annual mean lamprey CPUE and mean suspected host CPUEs for each included region was conducted separately. Significance was determined at an adjusted α of 0.05, reducing the chance of making a type I error associated with multiple comparisons.

[A]RESULTS

[B]*Modeling the Distributions of Arctic Lampreys and Pacific Lampreys*

Distributions of Arctic Lampreys and Pacific Lampreys in the eastern Bering Sea differed geographically and in the survey depth in which they were found. In the study area, Arctic Lampreys were captured at 19.0% of epipelagic stations and 0.0% of benthic stations, whereas Pacific Lampreys were captured at less than 0.1% of epipelagic stations and 8.3% of benthic stations. Arctic Lampreys were predominantly captured in regions on the inner and middle continental shelf and in northern regions of the study area, whereas Pacific Lampreys were predominantly captured in regions along the continental slope (Figure 4). Arctic Lampreys and Pacific Lampreys were never captured at the same station, but both species were captured in the north middle shelf region during the 2002 epipelagic survey. Among sampled years in the study region, 2002 exhibited the highest annual catch for both Arctic Lampreys and Pacific Lampreys, and lamprey catches were relatively depressed in subsequent years (Tables 1, 2).

Logistic models were able to capture general geographical trends in Arctic Lamprey and Pacific Lamprey presence. Utilizing 1,345 epipelagic stations, the best-fit model for Arctic Lamprey distribution based on latitude and longitude was

$$P\left(\text{A.Lamp} > 0\right) = \text{Lat} + \text{Long} + \left(\text{Lat} \times \text{Long}\right) + \text{Lat}^2 + \text{Long}^2 + \left(\text{Lat} \times \text{Long}^2\right),$$

where P(A.Lamp > 0) is the probability of an Arctic Lamprey being present. Utilizing 2,837 benthic stations, the best-fit model for Pacific Lamprey distribution based on latitude and longitude was the full model,

$$P\left(\text{P.Lamp} > 0\right) = \text{Lat} + \text{Long} + \left(\text{Lat} \times \text{Long}\right) + \text{Lat}^2 + \text{Long}^2 + \left(\text{Lat} \times \text{Long}^2\right) + \left(\text{Long} \times \text{Lat}^2\right),$$

where P(P.Lamp > 0) is the probability of a Pacific Lamprey being present. Both models did well at predicting the observed probabilities (Figure 4), with multiple terms found to be significant (Table 3). <AQ: in Results, please check the revised equations for P(A.lamp > 0) and P(P.lamp > 0) to ensure that they are accurate.>

[B]*Ordination Analysis*

Ordination of teleost CPUE data from survey–year–region combinations allowed for the detection of differences in fish assemblages in regions with relatively high and low lamprey abundances. Teleost CPUE data from the epipelagic survey clustered by high and low Arctic Lamprey catch groups. These clusters were evident in a two-dimensional NMDS plot (Kruskal's stress value = 0.22), but due to the high stress value, we further examined a three-dimensional NMDS plot (Kruskal's stress value = 0.14). Latitudinal and longitudinal gradients were evident in epipelagic fish assemblages occurring in the eastern Bering Sea, suggesting regional consistency in fish assemblages over time (Figure 5). Fish assemblages were significantly different between high and low Arctic Lamprey catch groups (ANOSIM: $R = 0.158$, $P < 0.05$), although the low group did exhibit more within-group variability of fish assemblages compared to the high group (MVDISP = 1.15 and 0.64, respectively). A SIMPER routine identified that the Pacific Herring was the most distinguishing teleost group between high and low Arctic Lamprey catch groups, contributing more than 19% to the dissimilarity. The NMDS plot further illustrated that the low Arctic Lamprey catch group included a few year–region combinations that were similar to the high catch group in having relatively great Pacific Herring CPUEs; however, the majority of the low catch group that was distinct from the high catch group had low or no Pacific Herring

CPUEs. The high Arctic Lamprey catch group had greater average abundances of Pacific Herring, juvenile Chum Salmon, juvenile Chinook Salmon *O. tshawytscha*, juvenile Coho Salmon *O. kisutch*, and juvenile Pink Salmon, whereas the low Arctic Lamprey catch group had greater abundances of Walleye Pollock *Gadus chalcogrammus*, immature/maturing Chum Salmon, and immature/maturing Chinook Salmon (Table 4).

Teleost CPUE data from the benthic survey clustered by high and low Pacific Lamprey catch groups. Overall, benthic fish assemblages in the eastern Bering Sea exhibited both latitudinal and depth gradients, evident from a two-dimensional NMDS plot (Kruskal's stress value = 0.08) and reflecting regional consistency of fish assemblages (Figure 6). Fish assemblages were significantly different between high and low Pacific Lamprey catch groups (ANOSIM: $R = 0.48$, $P < 0.05$), although the low catch group exhibited more within-group variability of fish assemblages than did the high catch group (MVDISP = 1.01 and 0.90, respectively). A SIMPER routine identified the high Pacific Lamprey catch group as having greater abundances of Pacific Ocean Perch *Sebastes alutus*, Arrowtooth Flounder *Atheresthes stomias*, Flathead Sole *Hippoglossoides elassodon*, Greenland Halibut *Reinhardtius hippoglossoides*, Kamchatka Flounder *Atheresthes evermanni*, and Rex Sole *Glyptocephalus zachirus* compared to the low Pacific Lamprey catch group. Additionally, the Giant Grenadier *Coryphaenoides pectoralis*, Popeye Grenadier *Coryphaenoides cinereus*, and Shortspine Thornyhead *Sebastolobus alascanus* were abundant in the high Pacific Lamprey catch group and completely absent from the low catch group. The low Pacific Lamprey catch group had higher abundances of Walleye Pollock, Yellowfin Sole *Limanda aspera*, Northern Rock Sole *Lepidopsetta polyxystra*, Alaska Plaice *Pleuronectes quadrituberculatus*, and Pacific Cod compared to the high catch group (Table 5).

[B]*Temperature Analysis*

Surface temperatures from epipelagic stations ranged from 0.0°C to 16.6°C, while bottom temperatures from benthic stations were between −1.7°C and 12.3°C. Surface temperatures were similar for both the high (9.0 ± 0.2°C) and low (9.1 ± 0.3°C) Arctic Lamprey catch groups (*t*-test: $P = 0.77$). Bottom temperatures were significantly greater for the high Pacific Lamprey catch group (3.0 ± 0.2°C) than for the low Pacific Lamprey catch group (2.0 ± 0.3°C; *t*-test: $P < 0.05$).

[B]*Lamprey and Host Correlation Analysis*

There were six regions (south Bering Strait, north inner shelf, mid-north inner shelf, south inner shelf, St. Matthews, and south middle shelf) in which three or more epipelagic stations were sampled for each year included in this study and in which Arctic Lampreys were present at a minimum of 5% of the stations. Of the five potential hosts suggested by the epipelagic SIMPER analysis results, mean Arctic Lamprey CPUE was positively and significantly correlated with the mean CPUEs of Pacific Herring and juvenile Chinook Salmon ($P < 0.05$); although not significant, mean Arctic Lamprey CPUE was positively correlated with the mean CPUEs of juvenile Chum Salmon, Coho Salmon, and Pink Salmon (Table 4). Region-specific analysis indicated that no suspected hosts had a significantly positive relationship with mean Arctic Lamprey CPUE for the south Bering Strait, north inner shelf, St. Matthews, or south middle shelf region. However, mean Arctic Lamprey CPUE was significantly and positively correlated with the mean CPUEs of juvenile Chinook Salmon (Spearman's rank correlation coefficient [ρ] = 0.93, adjusted $P < 0.05$) and juvenile Pink Salmon ($\rho = 0.92$, adjusted $P < 0.05$) for the south inner shelf region (Figure 7).

There were two regions (off-shelf north and off-shelf southeast) in which three or more benthic stations were sampled for each year included in the study and in which Pacific Lampreys were present at a minimum of 5% of the stations. Mean CPUEs for six of the nine identified potential hosts were negatively correlated with mean Pacific Lamprey CPUE, but the mean CPUEs of Greenland Halibut, Kamchatka Flounder, and Shortspine Thornyheads were positively correlated with the mean CPUE of Pacific Lampreys. No positive relationships were identified as significant, but the relationship was greatest for Greenland Halibut (Table 5).

[A]DISCUSSION

Nonoverlapping distributions of the Arctic Lamprey and Pacific Lamprey in the eastern Bering Sea emphasize the unique life history patterns of these two species. Arctic Lampreys were consistently found in epipelagic trawl catches from waters of northerly regions on the inner and middle continental shelf, while Pacific Lampreys were only captured in a few epipelagic trawl stations further west. Pacific Lampreys were consistently captured in benthic trawl catches from waters along the continental slope, whereas Arctic Lampreys were never captured in the benthic trawl survey. During this study, Arctic Lampreys and Pacific Lampreys were never captured at the same station, suggesting habitat separation of these species in the eastern Bering Sea. Additionally, the only instance in which both species were captured within the same region (the north middle shelf region's epipelagic survey in 2002 that included stations with 1-h tows not used in this analysis), the single station where Pacific Lampreys were present was located westward of the 11 stations where Arctic Lampreys were present. Although less comprehensive and less systematic, previous compilations of single-species distributions of anadromous lampreys in this region similarly placed the Arctic Lamprey's distribution near shore and the Pacific Lamprey's distribution near the continental slope (Orlov et al. 2008, 2014).

[B]*Arctic Lamprey*

Juvenile salmonids and Pacific Herring were distributed in surface waters of the same regions of the eastern Bering Sea as Arctic Lampreys. In general, Arctic Lampreys were not present in regions that lacked Pacific Herring, and the average Pacific Herring CPUE was more than double for year–region combinations in which Arctic Lampreys were present, suggesting an association between Arctic Lamprey distribution and Pacific Herring presence. In addition, for juveniles of four salmon species (Chinook Salmon, Chum Salmon, Coho Salmon, and Pink Salmon), the average CPUEs in survey–year–region combinations with Arctic Lampreys present were more than double those in survey–year–region combinations without Arctic Lampreys, suggesting a similar association between Arctic Lamprey distributions and juvenile salmonid presence. These results support our hypothesis that Arctic Lampreys would be positively correlated with their presumed prey, small-bodied fishes. Arctic Lampreys may be distributing where Pacific Herring and juvenile salmon are more abundant; or Arctic Lampreys, Pacific Herring, and juvenile salmon may all simply co-occur in shallow nearshore areas, resulting in the observed coincidental overlap of their distributions. Nevertheless, Pacific Herring and juvenile salmon are the most likely hosts for Arctic Lampreys in the eastern Bering Sea simply because overlapping distributions make them the most available hosts. This is supported by the positive rank-order correlation between the CPUE of Arctic Lampreys and the CPUEs of all five potential teleost hosts. Temperature did not appear to differ between high and low Arctic Lamprey catch groups and does not seem to be a driver of lamprey distribution. Walleye Pollock, immature Chinook Salmon, and immature Chum salmon were all more abundant in the low catch group, possibly the result of Arctic Lampreys being preyed upon more in regions with greater abundances of these potential predators. We believe that the Arctic Lamprey's distribution in the eastern Bering Sea may be a function of the presence of one or more of the five potential hosts we identified, while the density of Arctic Lampreys may be related to the abundances of those hosts.

In the south inner shelf region, the mean Arctic Lamprey CPUE was significantly and positively correlated with mean CPUEs of juvenile Chinook Salmon and juvenile Pink Salmon, suggesting that (1) Arctic Lampreys are only found in the south inner shelf region when potential hosts are there and (2) Arctic Lampreys are more abundant when their hosts are more abundant (Figure 7). This overall trend was evident in the south inner shelf region for the CPUEs of Arctic Lampreys and the remaining three potential hosts identified (Pacific Herring, juvenile Chum Salmon, and juvenile Coho Salmon); although these relationships were not significantly correlated, they further indicate the positive relationship between Arctic Lampreys and juvenile salmonids. Few or no potential hosts were present in the south inner shelf region during 2010–2012, likely reflecting the shift to later sampling dates starting in 2009 rather than declines in the abundances of potential hosts. However, the small catch of potential hosts and Arctic Lampreys in 2009 (i.e., after the change in survey timing) and the lack of hosts and Arctic Lampreys in 2006 (i.e., prior to the change in survey timing) suggest that Arctic Lampreys vary in concordance with Pacific Herring and juvenile salmonids. The overall lack of region-specific correlation found for the northerly regions analyzed could be attributable to the fact that Arctic Lampreys and the potential hosts identified are ubiquitous in these regions during the sampled periods.

[B]*Pacific Lamprey*

The results of this study indicate that the continental slope is an important habitat for Pacific Lampreys. There were no significant positive correlations between the CPUEs of any of the 10 potential hosts and the CPUE of Pacific Lampreys, but the diversity of fish present on the continental slope (68 teleost groups were present at >5% of stations) may reflect a great diversity of hosts available to Pacific Lampreys such that no specific species drive their density. Teleosts that utilize the continental slope but are not likely to drive Pacific Lamprey density, as suggested by negative or near-zero correlation coefficients, include the Arrowtooth Flounder, Flathead Sole, Rex Sole, Giant Grenadier, Popeye Grenadier, Pacific Ocean Perch, Kamchatka Flounder, and Shortspine Thornyhead. Greenland Halibut did have the greatest positive correlation coefficient ($\rho = 0.54$); though the correlation was not significant, this species is a likely host associated with Pacific Lampreys in the eastern Bering Sea. In the western Bering Sea, Pacific Cod and Greenland Halibut were suspected of being important hosts for Pacific Lampreys (Orlov et al. 2009), and our evidence suggests that this may also be the case in the eastern Bering Sea. Our hypothesis that Pacific Lampreys should be associated with large-bodied fish is not refuted, although it is clear that for predicting the Pacific Lamprey's distribution, the unique physical location along the continental slope is more important than the distribution of any individual or group of teleost species. The significantly warmer bottom temperatures found for high Pacific Lamprey catch groups compared to low catch groups may also indicate a thermal limitation in Pacific Lamprey dispersal; alternatively, this could be a characteristic of preferred Pacific Lamprey habitat in the eastern Bering Sea (i.e., the continental slope) relative to the continental shelf.

Interestingly, Pacific Cod typically had a higher CPUE in continental shelf regions that lacked Pacific Lampreys in this study, despite evidence that Pacific Lampreys parasitize this species along the continental slope in the eastern Bering Sea (Siwicke and Seitz 2015). However, Pacific Cod are known to spawn on the outer continental shelf in waters between 100 and 200 m from March to April (Neidetcher et al. 2014), and lamprey parasitism may be occurring during these episodic spawning events, but the survey months did not coincide with this period. The biomass of gadids in the eastern Bering Sea may be so great compared to Pacific Lamprey biomass that even in regions with low abundances of Pacific Cod or Walleye Pollock, there are sufficient opportunities for a feeding interaction. Additionally, it is possible that gadids are predatory on Pacific Lampreys, and when these species are very abundant, Pacific Lampreys may be less likely to survive.

[B]*Contrasting Arctic Lampreys and Pacific Lampreys*

In general, our results did not lead to rejection of the hypothesis that Arctic Lampreys and Pacific Lampreys are associated with different fish assemblages according to their different feeding strategies. We found significant positive relationships between the CPUE of Arctic Lampreys and the CPUEs of the small hosts that we expected a flesh-feeding lamprey to target. Although co-occurrence by no means equals a feeding relationship, observations of juvenile salmon and Pacific Herring with recently inflicted lamprey wounds present during the BASIS epipelagic trawl survey (Figure 2) and Arctic Lampreys attached to them (J. Murphy, NOAA–NMFS, personal communication) do indicate that Arctic Lampreys in fact feed on these same small fishes. Pacific Lampreys were more abundant in regions characterized by large-bodied fishes, and we found a positive correlation between the CPUEs of the Pacific Lamprey and the Greenland Halibut, a large-bodied species that is a known host in the Bering Sea and is a suitable host for a large, blood-feeding lamprey. There is evidence that physical features, such as the relief of the slope and warmer bottom temperatures, are attracting a multitude of fish, and these features might distinguish the Pacific Lamprey's distribution and abundance more so than any potential hosts.

In addition to lamprey species targeting different fish, another possible mechanism contributing to the longitudinal separation of Arctic Lamprey and Pacific Lamprey distributions is the eastern Bering Sea cold pool, which annually forms on the middle continental shelf. In this study, both Arctic Lampreys and Pacific Lampreys had relatively broad distributions during the warm year of 2002, which was associated with a small cold pool extent. In contrast, lamprey distributions were relatively restricted during the cold year of 2010, which was associated with a vast cold pool extent (Stabeno et al. 2012). The observed separation of Arctic Lamprey and Pacific Lamprey distributions occurs in the same region as the cold pool, and this could be explained by thermal limitations on the lampreys or the fishes they are targeting. Pacific Lampreys were consistently found in warmer waters and were potentially avoiding entry into the cooler waters associated with the cold pool, whereas Arctic Lampreys did not appear to have a temperature preference in surface waters. The cold pool restricts the dispersion of a variety of fishes that lampreys may parasitize, such as the Pacific Herring, Walleye Pollock, Pacific Cod, and Capelin *Mallotus villosus* (Hollowed et al. 2012; Stabeno et al. 2012); thus, cold water could directly impede lamprey movements or could indirectly influence their distribution through a limitation on their preferred hosts.

A glimpse of a finer-scale understanding of Arctic Lamprey and Pacific Lamprey distributions and associations with potential host fishes can be provided through examination of the north middle shelf region's data from the 2002 epipelagic survey, in which both lamprey species were captured (note that some of the tows were 1 h in duration, and those tows were not included in the main analysis). Of the 13 stations sampled, Arctic Lampreys were captured at 11 sites, and Pacific Lampreys were captured at one site. The single station with Pacific Lampreys also produced the maximum Walleye Pollock CPUE in the region. However, a quantitative understanding of the relationship between Pacific Lampreys and Walleye Pollock in pelagic habitats is not possible here because Pacific Lampreys were excluded from the epipelagic analysis.

Of the 11 stations at which Arctic Lampreys were captured, the site with the maximum Arctic Lamprey CPUE was also observed to exhibit the maximum Capelin CPUE. This suggests that Capelin abundance may be associated with Arctic Lamprey distribution at finer scales, whereas the broader-scale regional analysis did not indicate this possibility. One potential reason for this discrepancy is the high annual variability in Capelin abundance observed in epipelagic surveys, making this species an available host when abundant but not when rare. Because Arctic Lampreys and Pacific Lampreys likely feed on a variety of hosts, localized or annual abundances of some fishes may actually be related to lamprey distributions at finer scales while going unnoticed at broader scales, thus precluding those potential lamprey–host interactions from being inferred by the approach utilized in this study.

Our interpretation of these results was limited because the epipelagic and benthic surveys utilized in this study employed different sampling gear with differing levels of sampling efficacy. The smaller mesh used in the epipelagic survey (1.2 cm) is certainly more effective at capturing both Arctic Lampreys and Pacific Lampreys than the larger mesh used in the benthic survey (3.2 cm). The absence of Pacific Lampreys in inner and middle continental shelf epipelagic and benthic trawls indicates that this species is not actively using these geographic regions. Pacific Lampreys were captured in five epipelagic trawls conducted over the outer continental shelf and continental slope despite the low sampling effort, suggesting that Pacific Lampreys are utilizing epipelagic waters in these regions in addition to the benthic environment. Despite a complete lack of Arctic Lamprey captures in the benthic trawl survey, it is probable that they would have slipped through the large mesh if encountered. Because the epipelagic trawl survey consistently captured Arctic Lampreys and their distribution was clearly limited to the inner and middle domains of the continental shelf, there is a possibility that Arctic Lampreys were near the benthos on the inner and middle domains but could not be captured by the larger mesh. As such, we believe that the observed geographic separation between Arctic Lampreys and Pacific Lampreys is accurate (Figure 4), but the difference between trawl mesh sizes leaves us to assume that within these regions, both species could inhabit the entire water column.

Timing of surveys, freshwater origins, and marine residence times may all contribute to the observed difference in distributions between Arctic Lampreys and Pacific Lampreys. No sampling occurred in any year from November through May, and though not known, distributions of lampreys during these colder months may shift with or without hosts. Arctic Lamprey distribution appeared centered on the Yukon River, their likely source, with some probably originating from the nearby Kuskokwim River; both rivers are known to have populations of this species (Brown et al. 2005). The ocean residence time of Arctic Lampreys is unknown, but if it is only one summer, this could explain their limited dispersal from these presumed freshwater origins. Pacific Lampreys in the Bering Sea likely travel great distances from their freshwater origin, as documented occurrences of this species in Alaskan rivers are rare (Luzier et al. 2011). Pacific Lampreys are known to spend up to 3.5 years in the ocean (Beamish 1980), allowing them to disperse much further from their sources. It is even possible that Pacific Lampreys from the Columbia River, Washington–Oregon, could travel to the Bering Sea.

Finally, surveys were spatially limited, potentially missing important episodic shifts in distribution as the lampreys moved from freshwater to the ocean. Survey data used in this analysis did not include nearshore estuarine habitats and would not have captured lampreys utilizing these habitats, but lampreys are often found feeding in estuaries in other regions. For example, Arctic Lampreys in the western Bering Sea were estimated to consume 75% of Pink Salmon and Chum Salmon smolts in the Amur River estuary (Novomodnyy and Belyaev 2002), and Western River Lampreys fed on Pacific Herring and Pacific salmon smolts in the nearshore Fraser River plume (Beamish and Neville 1995). Similarly, Pacific Lampreys and Western River Lampreys were observed feeding on a variety of hosts in the Columbia River estuary (Weitkamp et al. 2015). Similar predation events on juvenile salmon can be expected to occur in the western Alaska river deltas due to the close proximity of Arctic Lampreys to the estuaries of the Yukon and Kuskokwim rivers, and sampling of these habitats could find concentrations of lampreys not identified by this study.

[B]*Conclusions*

In the future, several improvements can be incorporated into research on adult trophic-phase lampreys. Analysis into the relative importance of different hosts should be pursued in more detail, with stable isotopes as one possible method for investigating contributions of different species to lamprey diets (Harvey et al. 2008). The present study found correlation between lampreys and potential hosts, but a diet analysis would be able to test the proposed hypothesis that feeding is the cause for this correlation, bolstering the argument that the association is related to feeding. Furthermore, lamprey sampling components should be included in estuarine and nearshore research occurring in Alaska, as these habitats are believed to be important for lampreys. To determine the rivers of origin for adult lampreys captured in the Bering Sea, which may aid in explaining the nearshore distributions of Arctic Lampreys and the magnitude of Pacific Lamprey movements, genetic and tagging studies should be pursued. Finally, the NMFS Observer Program provides a platform that already captures and records lampreys in the eastern Bering Sea (AFSC 2013), and efforts should be made to confirm species identification using dentition, an easily distinguishable characteristic for separating Arctic Lampreys and Pacific Lampreys, as demonstrated by Mecklenburg et al. (2002) and Siwicke and Seitz (2015).

With the continuation of lamprey harvests (commercial and subsistence) and evident declines in many lamprey populations (Murauskas et al. 2016), it is important to understand all life history stages of parasitic, anadromous lampreys and not just those stages occurring in freshwater. The role of the adult trophic phase in shaping lamprey populations has not been well studied, but host availability has been suggested as potentially limiting the number of spawning adults returning to rivers (Luzier et al. 2011; Murauskas et al. 2013). Further inference of lamprey–host interactions through the study of distributions can aid in understanding which regions and host species are likely important for anadromous lampreys while in the ocean. If the adult trophic phase is important in maintaining lamprey survival and health, conservation and restoration programs will need to consider factors occurring during the adult trophic phase in their plans. For example, restoration efforts are underway for the Pacific Lamprey in the U.S. Pacific Northwest (Luzier et al. 2011), but we do not currently know where or on which hosts these animals are feeding while in the ocean. This study is an initial step toward understanding the adult trophic phase of Arctic Lampreys and Pacific Lampreys in the eastern Bering Sea, illustrating that the two species inhabit different regions, occur with different fish assemblages, and thus are likely to parasitize different fishes. As such, these two species will be impacted differently by stressors such as commercial fisheries, climatic shifts, or a warming ocean. Going forward, resource managers will need to consider and reconcile these differences to establish effective measures that support the conservation of Arctic Lampreys and Pacific Lampreys when needed, thereby sustaining harvests of these species for generations to come.

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[A]References

AFSC (Alaska Fisheries Science Center). 2013. AFSC/FMA: web map observer groundfish data, Alaska, 1993–2012. Available: www.afsc.noaa.gov/maps/FMA/datamap/obsmap.html. (December 2013).

Beamish, R. J. 1980. Adult biology of the River Lamprey (*Lampetra ayresi*) and the Pacific Lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Canadian Journal of Fisheries and Aquatic Sciences 37:1906–1923.

Beamish, R. J., and C. E. M. Neville. 1995. Pacific salmon and Pacific Herring mortalities in the Fraser River plume caused by River Lamprey (*Lampetra ayresi*). Canadian Journal of Fisheries and Aquatic Sciences 52:644–650.

Brown, C. L., J. Burr, K. Elkin, and R. J. Walker. 2005. Contemporary subsistence uses and population distribution of non-salmon fish in Grayling, Anvik, Shageluk, and Holy Cross. U.S. Fish and Wildlife Service, Final Report 02-037-2, Anchorage, Alaska.

Clarke, K. R., and R. N. Gorley. 2006. User manual/tutorial. PRIMER-E, Plymouth, UK.

Clemens, B. J., R. J. Beamish, K. C. Coates, M. F. Docker, J. B. Dunham, A. E. Gray, J. E. Hess, J. C. Jolley, R. T. Lampman, B. J. McIlraith, M. L. Moser, J. G. Murauskas, D. L. Noakes, H. A. Schaller, C. B. Schreck, S. J. Starcevich, B. Streif, S. J. Van Der Wetering, J. Wade, L. A. Weitkamp, and L. A. Wyss. 2017. Conservation challenges and research needs for Pacific Lamprey in the Columbia River basin. Fisheries 42:268–280.

Close, D. A., M. S. Fitzpatrick, and H. W. Li. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific Lamprey. Fisheries 27:19–25. <AQ: Close et al., please provide the issue number for Fisheries magazine.>

Coachman, L. K. 1986. Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. Continental Shelf Research 5:23–108.

Cochran, P. A. 2009. Predation on lampreys. Pages 139–151 *in* L. R. Brown, S. D. Chase, P. B. Moyle, R. J. Beamish, and M. G. Mesa, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

Farley, E. V. Jr., J. Murphy, J. Moss, A. Feldmann, and L. Eisner. 2009. Marine ecology of western Alaska juvenile salmon. Pages 307–330 *in* C. C. Krueger and C. E. Zimmerman, editors. Pacific salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Gallant, J., C. Harvey-Clark, R. A. Myers, and M. J. Stokesbury. 2006. Sea Lamprey attached to a Greenland Shark in the St. Lawrence Estuary, Canada. Northeastern Naturalist 13:35–38.

Halliday, R. C. 1991. Marine distribution of the Sea Lamprey (*Petromyzon marinus*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 48:832–842.

Hardisty, M. W., and I. C. Potter. 1971. The general biology of adult lampreys. Pages 127–206 *in* M. W. Hardisty and I. C. Potter, editors. The biology of lampreys, volume 1. Academic Press, London.

Harvey, C. J., M. P. Ebener, and C. K. White. 2008. Spatial and ontogenetic variability of Sea Lamprey diets in Lake Superior. Journal of Great Lakes Research 34:434–449.

Hoff, G. R. 2013. Results of the 2012 eastern Bering Sea upper continental slope survey of groundfish and invertebrate resources. NOAA Technical Memorandum NMFS-AFSC-258.

Hollander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. Wiley, New York.

Hollowed, A. B., S. J. Barbeaux, E. D. Cokelet, E. Farley, S. Kotwicki, P. H. Ressler, C. Spital, and C. D. Wilson. 2012. Effects of climate variations on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography 65:230–250.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29:1–27.

Lauth, R. R., and D. G. Nichol. 2013. Results of the 2012 eastern and northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. NOAA Technical Memorandum NMFS-AFSC-256.

Luzier, C. W., H. A. Schaller, J. K. Brostrom, C. Cook-Tabor, D. H. Goodman, R. D. Nelle, K. Ostrand, and B. Streif. 2011. Pacific Lamprey (*Entosphenus tridentatus*) assessment and template for conservation measures. U.S. Fish and Wildlife Service, Portland, Oregon.

Mecklenburg, C. W., T. A. Mecklenburg, and L. K. Thorsteinson. 2002. Fishes of Alaska. American Fisheries Society, Bethesda, Maryland.

Mesa, M. G., and E. S. Copeland. 2009. Critical uncertainties and research needs for restoration and conservation of native lampreys in North America. Pages 311–321 *in* L. R. Brown, S. D. Chase, P. B. Moyle, R. J. Beamish, and M. G. Mesa, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

Murauskas, J. G., A. M. Orlov, and K. A. Siwicke. 2013. Relationships between the abundance of Pacific Lamprey in the Columbia River and their common hosts in the marine environment. Transactions of the American Fisheries Society 142:143–155.

Murauskas, J. G., L. Schultz, and A. M. Orlov. 2016. Trends of Pacific Lamprey populations across a broad geographic range in the North Pacific Ocean, 1939–2014. Pages 73–96 *in* A. Orlov and R. Beamish, editors. Jawless fishes of the world, volume 2. Cambridge Scholars Publishing, Newcastle, UK.

Murphy, J. M., W. D. Templin, E. V. Farley Jr., and J. E. Seeb. 2009. Stock-structured distribution of western Alaska and Yukon juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) from United States BASIS surveys, 2002–2007. North Pacific Anadromous Fish Commission Bulletin 5:51–59.

Neidetcher, S. K., T. P. Hurst, L. Ciannelli, and E. A. Logerwell. 2014. Spawning phenology and geography of Aleutian Islands and eastern Bering Sea Pacific Cod (*Gadus macrocephalus*). Deep Sea Research Part II: Topical Studies in Oceanography 109:204–214.

Nichols, O. C., and U. T. Tscherter. 2011. Feeding of Sea Lampreys *Petromyzon marinus* on minke whales *Balaenoptera acutorostrata* in the St. Lawrence Estuary, Canada. Journal of Fish Biology 78:338–343.

Novomodnyy, G. V., and V. A. Belyaev. 2002. Predation by lamprey smolts *Lampetra japonica* as a main cause of Amur Chum Salmon and Pink Salmon mortality in the early sea period of life. North Pacific Anadromous Fish Commission, Technical Report 4, Vancouver.

Orlov, A. M., A. A. Baytalyuk, and D. V. Pelenev. 2014. Distribution and size composition of Arctic Lamprey *Lethenteron camtschaticum* in the North Pacific. Oceanology 54:180–194.

Orlov, A. M., R. J. Beamish, A. V. Vinnikov, and D. Pelenev. 2009. Feeding and prey of Pacific Lamprey in coastal waters of the western North Pacific. Pages 875–877 *in* A. Haro, K. L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, M. J. Dadswell, R. A. Cunjak, J. E. Cooper, K. L. Beal, and T. S. Avery, editors. Challenges for diadromous fishes in a dynamic global environment. American Fisheries Society, Symposium 69, Bethesda, Maryland.

Orlov, A. M., V. F. Savinyh, and D. V. Pelenev. 2008. Features of the spatial distribution and size structure of the Pacific Lamprey *Lampetra tridentata* in the North Pacific. Russian Journal of Marine Biology 34:276–287.

Ortiz, I., F. K. Wiese, and A. Grieg. 2012. Marine regions boundary data for the Bering Sea shelf and slope. University Corporation for Atmospheric Research/National Center for Atmospheric Research, Earth Observing Laboratory, Computing, Data, and Software Facility, Boulder, Colorado. Available: http://dx.doi.org/10.5065/D6DF6P6C. (November 2013).

Pike, G. C. 1951. Lamprey marks on whales. Journal of the Fisheries Board of Canada 8:275–280.

Potter, I. C., and R. W. Hilliard. 1987. A proposal for the functional and phylogenetic significance of differences in the dentition of lampreys (Agnatha: Petromyzontiformes). Journal of Zoology 212:713–737.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Renaud, C. B. 2011. Lampreys of the world: an annotated and illustrated catalogue of lamprey species known to date. Food and Agriculture Organization of the United Nations, Rome.

Renaud, C. B., H. S. Gill, and I. C. Potter. 2009. Relationships between the diets and characteristics of the dentition, buccal glands and velar tentacles of the adults of the parasitic species of lamprey. Journal of Zoology 278:231–242.

Samarra, F. I., A. Fennell, K. Aoki, V. B. Deecke, and P. J. Miller. 2012. Persistence of skin marks on killer whales (*Orcinus orca*) caused by the parasitic Sea Lamprey (*Petromyzon marinus*) in Iceland. Marine Mammal Science 28:395–401.

Shevlyakov, V. A., and V. A. Parensky. 2010. Traumatization of Kamchatka River Pacific salmon by lampreys. Russian Journal of Marine Biology 36:396–400.

Siwicke, K. A., and A. C. Seitz. 2015. Interpreting lamprey attacks on Pacific Cod in the eastern Bering Sea. Transactions of the American Fisheries Society 144:1249–1262.

Stabeno, P. J., N. B. Kachel, S. E. Moore, J. M. Napp, M. Sigler, A. Yamaguchi, and A. N. Zerbini. 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Research Part II: Topical Studies in Oceanography 65:31–45.

Stapanian, M. A., C. P. Madenjian, and L. D. Witzel. 2006. Evidence that Sea Lamprey control led to recovery of the Burbot population in Lake Erie. Transactions of the American Fisheries Society 135:1033–1043.

Sutton, T. M., B. L. Johnson, T. D. Bills, and C. S. Kolar. 2004. Effects of mortality sources on population viability of Lake Sturgeon: a stage-structured model approach. Great Lakes Fishery Commission, Technical Report, Ann Arbor, Michigan. <AQ: Sutton et al., please provide the Technical Report number.>

Sviridov, V. V., I. I. Glebov, A. N. Starovoytov, A. V. Sviridova, M. A. Zuev, V. V. Kulik, and M. A. Ocheretyanny. 2007. Wounding of Pacific salmon in relation to the spatio-temporal variation in distribution patterns of important predatory fishes in the Russian economic zone. North Pacific Anadromous Fish Commission Bulletin 4:133–144.

Weitkamp, L. A., S. A. Hinton, and P. J. Bentley. 2015. Seasonal abundance, size, and host selection of Western River (*Lampetra ayresii*) and Pacific (*Entosphenus tridentatus*) lampreys in the Columbia River estuary. U.S. National Marine Fisheries Service Fishery Bulletin 113:213–226.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC Press, Boca Raton, Florida.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society B 73:3–36.

FIGURE 1.—Lamprey wounds observed on Pacific Cod (top) and Pacific Halibut (bottom) captured near the continental slope of the eastern Bering Sea.

FIGURE 2.—Lamprey wounds observed on a Pacific Herring (top), a juvenile Pink Salmon (middle), and a juvenile Chinook Salmon (bottom) captured during the epipelagic trawl survey (as part of the Bering Aleutian Salmon International Survey) in 2015. All lampreys captured during the epipelagic survey in 2015 were confirmed to be Arctic Lampreys.

FIGURE 3.—Map of Bering Sea Integrated Ecosystem Research Program regions used for summarizing lamprey and teleost CPUE data, with map extent shown as a rectangle in the lower right inset (source: Ortiz et al. 2012). Isobaths are shown for 50-, 100-, and 200-m depths. Regions of the inner continental shelf are south Bering Strait (S.B.St), Norton Sound (Nrt.S), north (N.In), mid-north (M.In), and south (S.In); regions of the middle continental shelf are St. Lawrence (St.Law), north (N.Mid), St. Matthews (St.Mat), mid-north (M.Mid), south (S.Mid), and Alaska Peninsula (AK.Pen); regions of the outer continental shelf are north (N.Out), Pribilof Islands (Prib), and south (S.Out); and off-shelf regions are north (OS.N) and southeast (OS.SE).

FIGURE 4.—Arctic Lamprey CPUEs and occurrence probabilities determined from the epipelagic trawl survey (top panels); and Pacific Lamprey CPUEs and occurrence probabilities determined from the benthic trawl survey (bottom panels). Maps on the left show stations with lamprey CPUEs reflected in the size of the circle (X indicates no lamprey captured). Maps in the center show the predicted probability of lamprey occurrence from the selected models. Stations were binned by predicted probability of lamprey occurrence (0.05 increments), and plots on the right show the predicted probability (midpoint) versus the observed proportion of lamprey occurrence (the line with a slope of 1 and a *y*-intercept of 0 indicates a perfect model fit).

FIGURE 5.—Nonmetric multidimensional scaling ordination of epipelagic fishes, reduced to three dimensions (Kruskal's stress value = 0.14) and based on a Bray–Curtis similarity matrix of square-root-transformed teleost CPUE data. Year–region combinations with two or more Arctic Lampreys present (high catch) are shown in black; those with fewer than two Arctic Lampreys present (low catch) are shown in gray. Letters refer to the location of each region on the continental shelf, as described in Figure 1: inner (I), middle (M), outer (O), and off-shelf (S). <AQ: in Figures 5 and 6, should there be *x*- and *y*-axis labels?>

FIGURE 6.—Nonmetric multidimensional scaling ordination of benthic fishes, reduced to two dimensions (Kruskal's stress value = 0.08) and based on a Bray–Curtis similarity matrix of square-root-transformed teleost CPUE data. Year–region combinations with at least one Pacific Lamprey present (high catch) are shown in black; those with no Pacific Lamprey present (low catch) are shown in gray. Letters refer to the location of each region on the continental shelf, as described in Figure 1: inner (I), middle (M), outer (O), and off-shelf (S).

FIGURE 7.—Catches of Arctic Lampreys and host fishes in epipelagic trawls from the south inner continental shelf region of the eastern Bering Sea. Black bars indicate Arctic Lamprey mean CPUE + SE (× 10^{-4}), gray bars indicate juvenile Chinook Salmon mean CPUE + SE (× 10^{-3}), and white bars indicate juvenile Pink Salmon mean CPUE + SE (× 10^{-3}).

TABLE 1.—Number of Arctic Lampreys captured in epipelagic surveys by year–region combination, number of stations (in parentheses), and annual mean weight (kg). An "X" indicates years in which no sampling occurred. Region codes are defined in Figure 3.

Region code or statistic	2002	2003	2004	2005	2006	2007	2009	2010	2011	2012
S.B.St	8 (15)	12 (13)	5 (7)	3 (4)	4 (7)	13 (12)	1 (8)	16 (12)	0 (11)	11 (12)
Nrt.S	1 (5)	6 (3)	0 (5)	1 (2)	7 (6)	0 (4)	6 (7)	7 (12)	17 (11)	10 (8)

Region code or statistic	2002	2003	2004	2005	2006	2007	2009	2010	2011	2012
N.In	7 (15)	17 (15)	8 (16)	7 (16)	16 (17)	4 (13)	4 (15)	6 (15)	11 (17)	11 (14)
M.In	10 (14)	3 (7)	4 (10)	3 (10)	1 (9)	9 (10)	2 (3)	0 (8)	0 (4)	0 (9)
S.In	8 (30)	20 (29)	12 (19)	10 (18)	0 (14)	3 (16)	3 (7)	0 (15)	0 (10)	0 (11)
St.Law	8 (12)	2 (4)	6 (9)	X	0 (4)	4 (8)	0 (2)	0 (2)	0 (3)	0 (2)
N.Mid	12 (7)	4 (1)	19 (15)	4 (9)	8 (9)	0 (8)	2 (8)	10 (10)	1 (7)	1 (1)
St.Mat	1 (5)	4 (9)	7 (10)	1 (15)	2 (9)	1 (10)	3 (7)	2 (8)	0 (5)	0 (4)
M.Mid	1 (2)	0 (10)	3 (10)	0 (6)	0 (15)	1 (15)	0 (8)	0 (12)	0 (12)	0 (16)
S.Mid	1 (30)	0 (27)	0 (25)	1 (24)	1 (30)	0 (27)	0 (14)	0 (22)	0 (21)	0 (25)
AK.Pen	0 (12)	0 (11)	0 (5)	0 (7)	0 (5)	0 (5)	0 (3)	0 (8)	0 (5)	0 (7)
N.Out	X	X	X	X	0 (5)	0 (2)	0 (6)	X	X	0 (3)
Prib	X	X	0 (2)	0 (2)	0 (4)	0 (4)	0 (1)	0 (1)	0 (4)	0 (4)
S.Out	0 (1)	1 (4)	0 (8)	0 (10)	0 (12)	0 (10)	0 (4)	0 (17)	0 (10)	0 (10)
OS.N	X	X	X	X	0 (3)	0 (1)	X	X	X	0 (1)
OS.SE	0 (1)	0 (1)	0 (1)	0 (1)	0 (7)	0 (6)	0 (2)	0 (2)	0 (1)	0 (2)
Total *N*	100	69	64	30	39	35	21	41	29	33
Mean weight	0.09	0.09	0.10	0.12	0.07	0.10	0.07	0.10	0.05	0.08

TABLE 2.—Number of Pacific Lampreys captured in benthic trawl surveys by year–region combination, number of stations (in parentheses), and annual mean weight (kg). An “X” indicates years in which no sampling occurred. Region codes are defined in Figure 3.

Region code or statistic	2002	2004	2008	2010	2012
S.B.St	X	X	X	0 (23)	X
Nrt.S	X	X	X	0 (22)	X
N.In	0 (7)	0 (7)	0 (7)	0 (40)	0 (7)
M.In	0 (24)	0 (24)	0 (24)	0 (24)	0 (24)
S.In	0 (55)	0 (55)	0 (54)	0 (55)	0 (55)

Region code or statistic	2002	2004	2008	2010	2012
St.Law	X	X	X	0 (25)	X
N.Mid	0 (13)	0 (13)	0 (13)	0 (46)	0 (13)
St.Mat	0 (43)	0 (43)	0 (43)	0 (45)	0 (42)
M.Mid	0 (41)	0 (41)	0 (41)	0 (41)	0 (41)
S.Mid	3 (64)	0 (64)	0 (62)	0 (64)	0 (63)
AK.Pen	0 (19)	0 (19)	0 (8)	1 (19)	4 (20)
N.Out	1 (76)	1 (75)	0 (75)	2 (75)	1 (79)
Prib	0 (14)	0 (15)	0 (14)	0 (14)	0 (14)
S.Out	0 (22)	0 (23)	0 (11)	0 (24)	0 (25)
OS.N	44 (72)	30 (101)	24 (101)	28 (97)	30 (95)
OS.SE	64 (66)	55 (126)	34 (97)	45 (100)	24 (82)
Total *N*	112	86	58	76	59
Mean weight	0.32	0.36	0.33	0.31	0.30

TABLE 3.—Logistic model results, including estimates, SEs, and *P*-values for variables from the best-fit models describing the probability of Arctic Lamprey presence in the epipelagic trawl survey and Pacific Lamprey presence in the benthic trawl survey.

Variable	Arctic Lamprey			Pacific Lamprey		
	Estimate	SE	*P*-value	Estimate	SE	*P*-value
Intercept	−15,310	6,854	<0.05	10,560	7,994	0.187
Latitude	248.9	113.5	<0.05	436.7	232.1	0.060
Longitude	−180.7	82.2	<0.05	436.7	167.4	0.051
Latitude × Longitude	2.82	1.36	<0.05	−3.41	1.71	<0.05
Latitude^2	−0.16	0.02	<0.05	−13.2	5.15	<0.05
Longitude^2	−0.55	0.25	<0.05	1.36	0.74	0.065
Latitude × Longitude^2	0.009	0.004	<0.05	−0.028	0.013	<0.05

Variable	Arctic Lamprey Estimate	Arctic Lamprey SE	Arctic Lamprey *P*-value	Pacific Lamprey Estimate	Pacific Lamprey SE	Pacific Lamprey *P*-value
Longitude × Latitude^2	–	–	–	−0.067	0.029	<0.05

TABLE 4.—Epipelagic similarity percentage (SIMPER) and correlation results, quantifying relative dissimilarity in epipelagic fish assemblages between year–region combinations of relatively high and low Arctic Lamprey abundances. Square-root-transformed mean CPUE in the low Arctic Lamprey catch group (CPUE_{Low}), square-root-transformed mean CPUE in the high Arctic Lamprey catch group (CPUE_{High}), and average dissimilarity between these groups are listed for each species with a dissimilarity divided by SD (Dissimilarity/SD) greater than 1.0 and a percent contribution to overall dissimilarity greater than 2%. Bold italics denote species that were suspected hosts of Arctic Lampreys from the SIMPER routine; values of Spearman's rank correlation coefficient (ρ) are listed for comparisons between mean Arctic Lamprey CPUE and the mean CPUEs of the listed species (asterisks denote significant positive correlations with CPUEs of suspected host fishes; adjusted $P < 0.05$).

Species	CPUE_{Low}	CPUE_{High}	Average dissimilarity	Dissimilarity/SD	Contribution (%)	ρ
Pacific Herring	0.36	0.83	12.61	1.29	19.24	0.49*
Chum Salmon	0.54	0.25	7.68	1.02	11.72	
Walleye Pollock	0.40	0.29	7.48	1.01	11.41	
Juvenile Chum Salmon	0.10	0.24	4.03	1.24	6.16	0.32
Juvenile Pink Salmon	0.08	0.16	2.63	1.17	4.01	0.32
Chinook Salmon	0.14	0.12	2.62	1.07	4.00	
Juvenile Coho Salmon	0.05	0.11	2.10	1.03	3.21	0.31
Juvenile Chinook Salmon	0.03	0.12	2.08	1.44	3.17	0.48*

TABLE 5.—Benthic similarity percentage (SIMPER) and correlation results, quantifying the relative dissimilarity in benthic fish assemblages between year–region combinations with relatively high and low Pacific Lamprey abundances. Square-root-transformed mean CPUE in the low Pacific Lamprey catch group (CPUE_{Low}), square-root-transformed mean CPUE in the high Pacific Lamprey catch group (CPUE_{High}), and average dissimilarity are listed for each species with a dissimilarity divided by SD (Dissimilarity/SD) greater than 1.0 and a percent contribution to the overall dissimilarity greater than 2%. Bold italics denote species that were suspected hosts of Pacific Lampreys from the SIMPER routine; values of Spearman's rank correlation coefficient (ρ) are listed for comparisons between mean Pacific Lamprey CPUE and the mean CPUE of the listed species (no significant relationships were detected; adjusted $P > 0.05$).

Species	CPUE_{Low}	CPUE_{High}	Average dissimilarity	Dissimilarity/SD	Contribution (%)	ρ
Giant Grenadier	0.00	7.37	7.73	1.10	11.66	−0.53
Walleye Pollock	6.62	6.21	5.49	1.30	8.28	
Yellowfin Sole	5.12	1.49	5.43	1.35	8.20	
Northern Rock Sole	5.56	1.61	5.13	1.27	7.75	
Pacific Ocean Perch	0.33	4.30	4.53	1.36	6.84	−0.64
Arrowtooth Flounder	1.64	4.34	3.56	1.74	5.37	−0.14
Alaska Plaice	2.97	0.65	2.86	1.58	4.32	
Popeye Grenadier	0.00	2.31	2.44	1.16	3.68	−0.36
Flathead Sole	2.23	3.09	2.27	1.48	3.43	−0.30
Greenland Halibut	0.20	1.94	1.97	1.68	2.98	0.54
Pacific Cod	3.26	2.25	1.88	1.39	2.84	
Kamchatka Flounder	0.46	2.09	1.88	1.60	2.83	0.18
Shortspine Thornyhead	0.00	1.67	1.79	1.12	2.71	0.21
Rex Sole	0.30	1.51	1.43	2.04	2.16	−0.08

Table 1. Number of Arctic Lampreys captured in epipelagic surveys by year-region combination, number of stations in parentheses, and annual mean weight (kg). An X indicates when no sampling occurred.

Region	2002	2003	2004	2005	2006	2007	2009	2010	2011	2012
S.B.St	8 (15)	12 (13)	5 (7)	3 (4)	4 (7)	13 (12)	1 (8)	16 (12)	0 (11)	11 (12)
Nrt.S	1 (5)	6 (3)	0 (5)	1 (2)	7 (6)	0 (4)	6 (7)	7 (12)	17 (11)	10 (8)
N.In	7 (15)	17 (15)	8 (16)	7 (16)	16 (17)	4 (13)	4 (15)	6 (15)	11 (17)	11 (14)
M.In	10 (14)	3 (7)	4 (10)	3 (10)	1 (9)	9 (10)	2 (3)	0 (8)	0 (4)	0 (9)
S.In	8 (30)	20 (29)	12 (19)	10 (18)	0 (14)	3 (16)	3 (7)	0 (15)	0 (10)	0 (11)
St.Law	8 (12)	2 (4)	6 (9)	X	0 (4)	4 (8)	0 (2)	0 (2)	0 (3)	0 (2)
N.Mid	12 (7)	4 (1)	19 (15)	4 (9)	8 (9)	0 (8)	2 (8)	10 (10)	1 (7)	1 (1)
St.Mat	1 (5)	4 (9)	7 (10)	1 (15)	2 (9)	1 (10)	3 (7)	2 (8)	0 (5)	0 (4)
M.Mid	1 (2)	0 (10)	3 (10)	0 (6)	0 (15)	1 (15)	0 (8)	0 (12)	0 (12)	0 (16)
S.Mid	1 (30)	0 (27)	0 (25)	1 (24)	1 (30)	0 (27)	0 (14)	0 (22)	0 (21)	0 (25)
AK.Pen	0 (12)	0 (11)	0 (5)	0 (7)	0 (5)	0 (5)	0 (3)	0 (8)	0 (5)	0 (7)
N.Out	X	X	X	X	0 (5)	0 (2)	0 (6)	X	X	0 (3)
Prib	X	X	0 (2)	0 (2)	0 (4)	0 (4)	0 (1)	0 (1)	0 (4)	0 (4)
S.Out	0 (1)	1 (4)	0 (8)	0 (10)	0 (12)	0 (10)	0 (4)	0 (17)	0 (10)	0 (10)
OS.N	X	X	X	X	0 (3)	0 (1)	X	X	X	0 (1)
OS.SE	0 (1)	0 (1)	0 (1)	0 (1)	0 (7)	0 (6)	0 (2)	0 (2)	0 (1)	0 (2)
Total N	100	69	64	30	39	35	21	41	29	33
Mean Weight	0.09	0.09	0.10	0.12	0.07	0.10	0.07	0.10	0.05	0.08

Table 2. Number of Pacific Lamprey captured in benthic trawl surveys by year-region combination, number of stations in parentheses, and annual mean weight (kg). An X indicates when no sampling occurred.

Region	2002	2004	2008	2010	2012
S.B.St	X	X	X	0 (23)	X
Nrt.S	X	X	X	0 (22)	X
N.In	0 (7)	0 (7)	0 (7)	0 (40)	0 (7)
M.In	0 (24)	0 (24)	0 (24)	0 (24)	0 (24)
S.In	0 (55)	0 (55)	0 (54)	0 (55)	0 (55)
St.Law	X	X	X	0 (25)	X
N.Mid	0 (13)	0 (13)	0 (13)	0 (46)	0 (13)
St.Mat	0 (43)	0 (43)	0 (43)	0 (45)	0 (42)
M.Mid	0 (41)	0 (41)	0 (41)	0 (41)	0 (41)
S.Mid	3 (64)	0 (64)	0 (62)	0 (64)	0 (63)
AK.Pen	0 (19)	0 (19)	0 (8)	1 (19)	4 (20)
N.Out	1 (76)	1 (75)	0 (75)	2 (75)	1 (79)
Prib	0 (14)	0 (15)	0 (14)	0 (14)	0 (14)
S.Out	0 (22)	0 (23)	0 (11)	0 (24)	0 (25)
OS.N	44 (72)	30 (101)	24 (101)	28 (97)	30 (95)
OS.SE	64 (66)	55 (126)	34 (97)	45 (100)	24 (82)
Total N	112	86	58	76	59
Mean Weight	0.32	0.36	0.33	0.31	0.30

Table 3. Logistic model results from the best fit model by species where (AL) represents Arctic Lamprey in the epipelagic trawl and (PL) represents Pacific Lamprey in the benthic trawl survey. Includes estimates, standard error (SE), and p-values for included variables.

Variable	Estimate (AL)	SE (AL)	P-value (AL)	Estimate (PL)	SE (PL)	P-value (PL)
Intercept	-15310	6854	< 0.05	10560	7994	0.187
Lat	248.9	113.5	< 0.05	436.7	232.1	0.060
Long	-180.7	82.2	< 0.05	436.7	167.4	0.051
Lat*Long	2.82	1.36	< 0.05	-3.41	1.71	< 0.05
Lat^2	-0.16	0.02	< 0.05	-13.2	5.15	< 0.05
$Long^2$	-0.55	0.25	< 0.05	1.36	0.74	0.065
$Lat*Long^2$	0.009	0.004	< 0.05	-0.028	0.013	< 0.05
$Long*Lat^2$	-	-	-	-0.067	0.029	< 0.05

Table 4. Epipelagic similarity percentage (SIMPER) and correlation results, quantifying relative dissimilarity in epipelagic fish assemblages between year-region combinations of relatively high and low Arctic Lamprey abundance. Square-root-transformed mean CPUE in the Low Arctic Lamprey catch group (Low), square-root-transformed mean CPUE in the High Arctic Lamprey catch group (High), and average dissimilarity between these groups (Av. Diss) are listed for each species with a dissimilarity divided by standard deviation (Diss/SD) greater than 1.0 and contribution to the overall dissimilarity (%) greater than 2%. Bolded species were suspected hosts of Arctic Lamprey from the SIMPER routine, and values of Spearman's correlation coefficient rho (ρ) are listed for comparisons between mean Arctic Lamprey CPUE and the mean CPUE of the listed species. Asterisks denote significant positive correlation between CPUE of Arctic Lamprey and the CPUE of suspected host fishes ($P_{adj} < 0.05$).

Species	Low	High	Av. Diss	Diss/SD	%	ρ
Pacific Herring	0.36	0.83	12.61	1.29	19.24	0.49^{*}
Chum Salmon	0.54	0.25	7.68	1.02	11.72	
Walleye Pollock	0.40	0.29	7.48	1.01	11.41	
Juvenile Chum Salmon	0.10	0.24	4.03	1.24	6.16	0.32
Juvenile Pink Salmon	0.08	0.16	2.63	1.17	4.01	0.32
Chinook Salmon	0.14	0.12	2.62	1.07	4.00	
Juvenile Coho Salmon	0.05	0.11	2.10	1.03	3.21	0.31
Juvenile Chinook Salmon	0.03	0.12	2.08	1.44	3.17	0.48^{*}

Table 5. Benthic similarity percentage (SIMPER) and correlation results, quantifying the relative dissimilarity in benthic fish assemblages between year-region combinations with relatively high and low Pacific Lamprey abundance. Square-root-transformed mean CPUE in the Low Pacific Lamprey catch group (Low), square-root-transformed mean CPUE in the High Pacific Lamprey catch group (High), and average dissimilarity (Av. Diss) are listed for each species with a dissimilarity divided by standard deviation (Diss/SD) greater than 1.0 and contribution to the overall dissimilarity (%) greater than 2%. Bolded species were suspected hosts of Pacific Lamprey from the SIMPER routine, and values of Spearman's correlation coefficient rho (ρ) are listed for comparisons between mean Pacific Lamprey CPUE and the mean CPUE of the listed species; no significant relationships were detected ($P_{adj} < 0.05$ level).

Species	Low	High	Av. Diss	Diss/SD	%	ρ
Giant Grenadier	0.00	7.37	7.73	1.10	11.66	-0.53
Walleye Pollock	6.62	6.21	5.49	1.30	8.28	
Yellowfin Sole	5.12	1.49	5.43	1.35	8.20	
Northern Rock Sole	5.56	1.61	5.13	1.27	7.75	
Pacific Ocean Perch	0.33	4.30	4.53	1.36	6.84	-0.64
Arrowtooth Flounder	1.64	4.34	3.56	1.74	5.37	-0.14
Alaska Plaice	2.97	0.65	2.86	1.58	4.32	
Popeye Grenadier	0.00	2.31	2.44	1.16	3.68	-0.36
Flathead Sole	2.23	3.09	2.27	1.48	3.43	-0.30
Greenland Halibut	0.20	1.94	1.97	1.68	2.98	0.54
Pacific Cod	3.26	2.25	1.88	1.39	2.84	
Kamchatka Flounder	0.46	2.09	1.88	1.60	2.83	0.18
Shortspine Thornyhead	0.00	1.67	1.79	1.12	2.71	0.21
Rex Sole	0.30	1.51	1.43	2.04	2.16	-0.08

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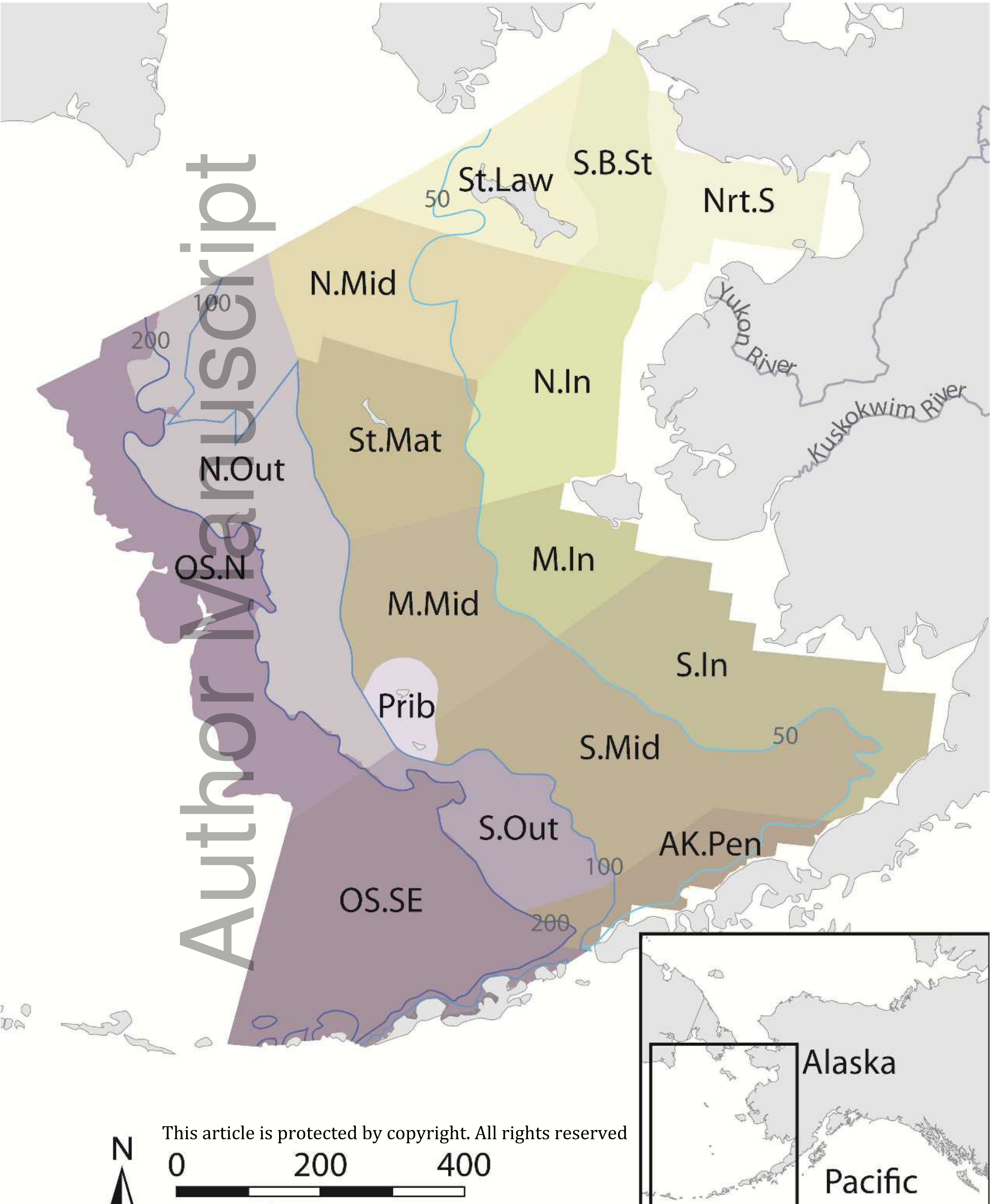
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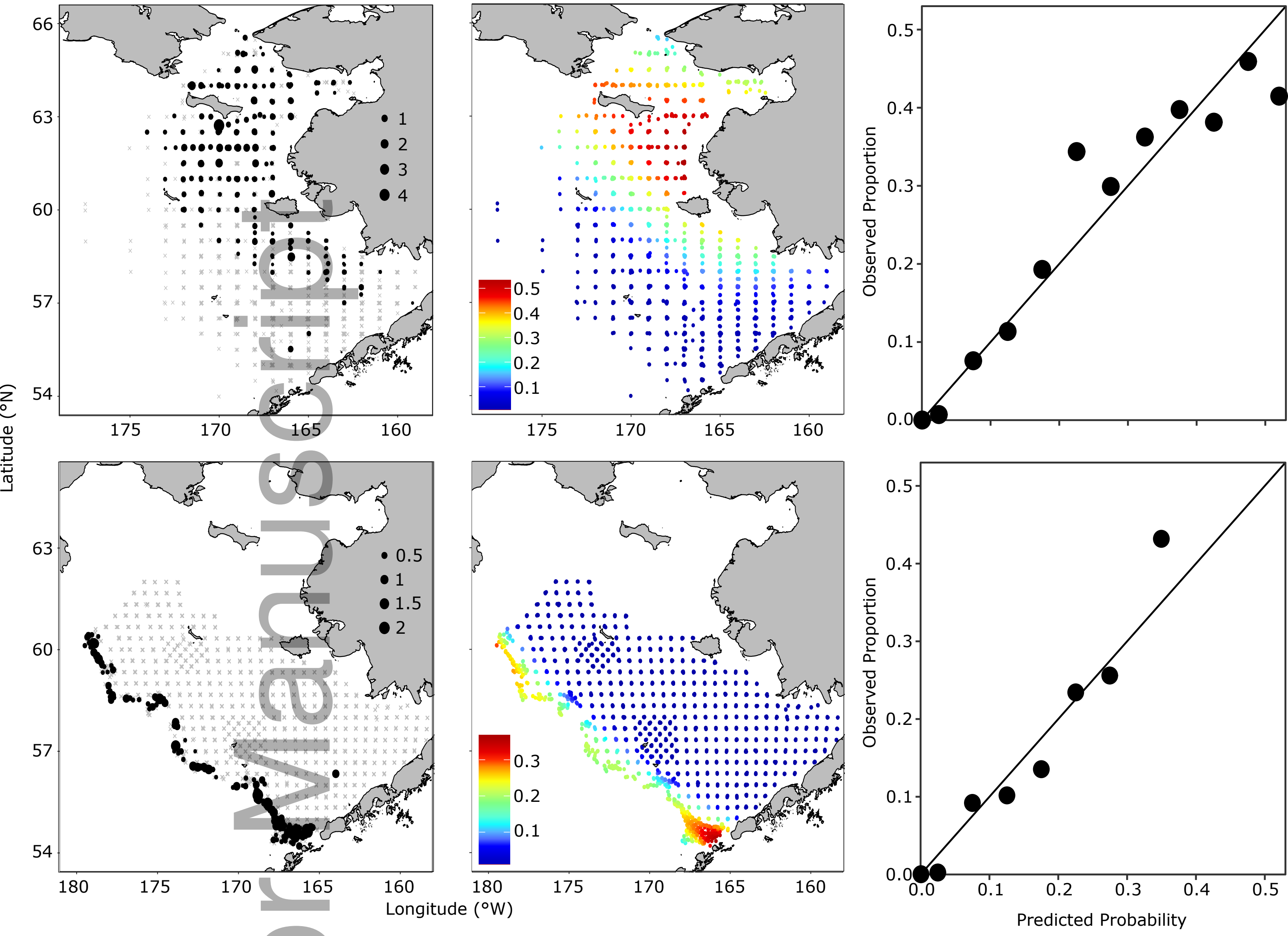

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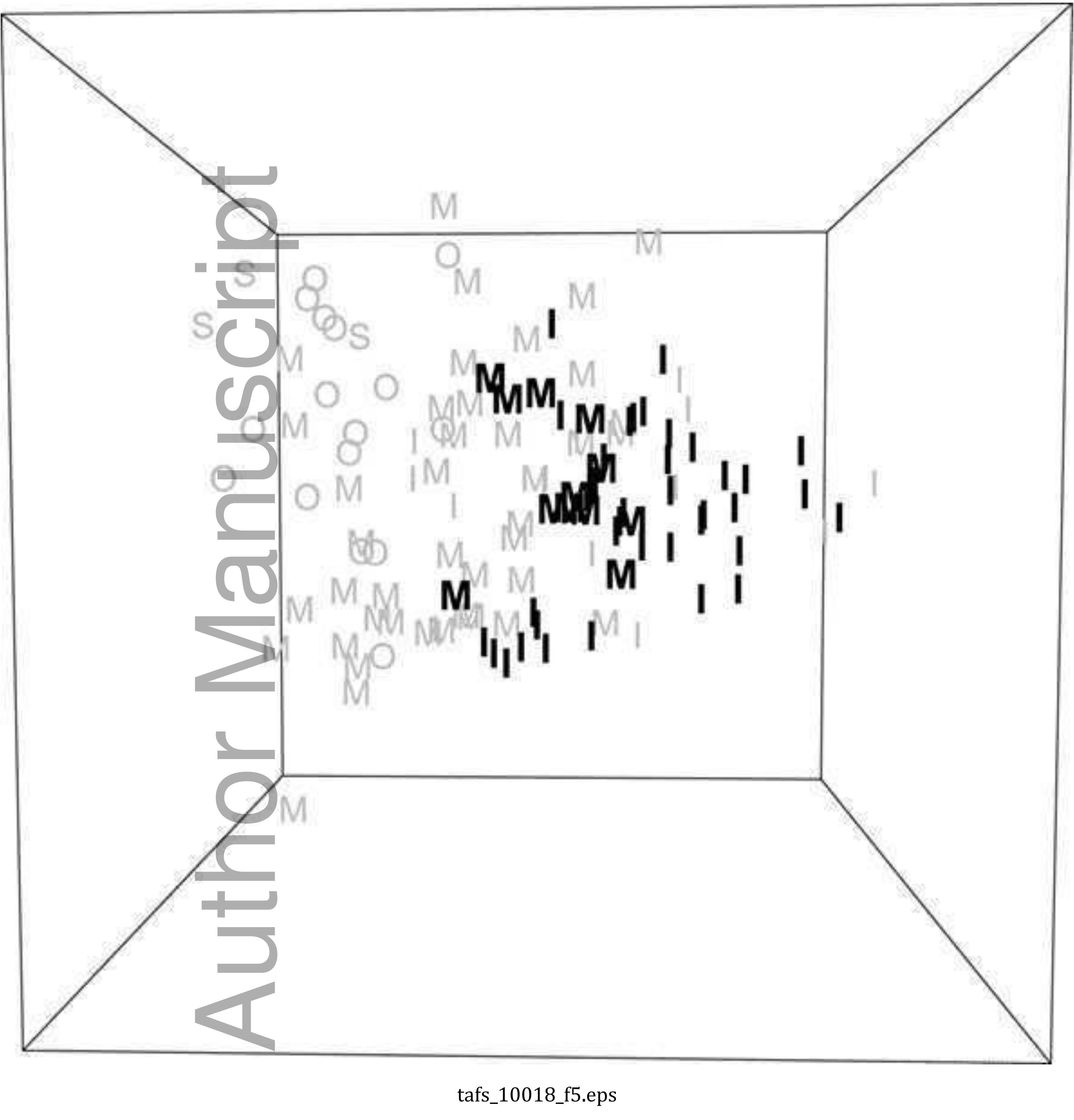

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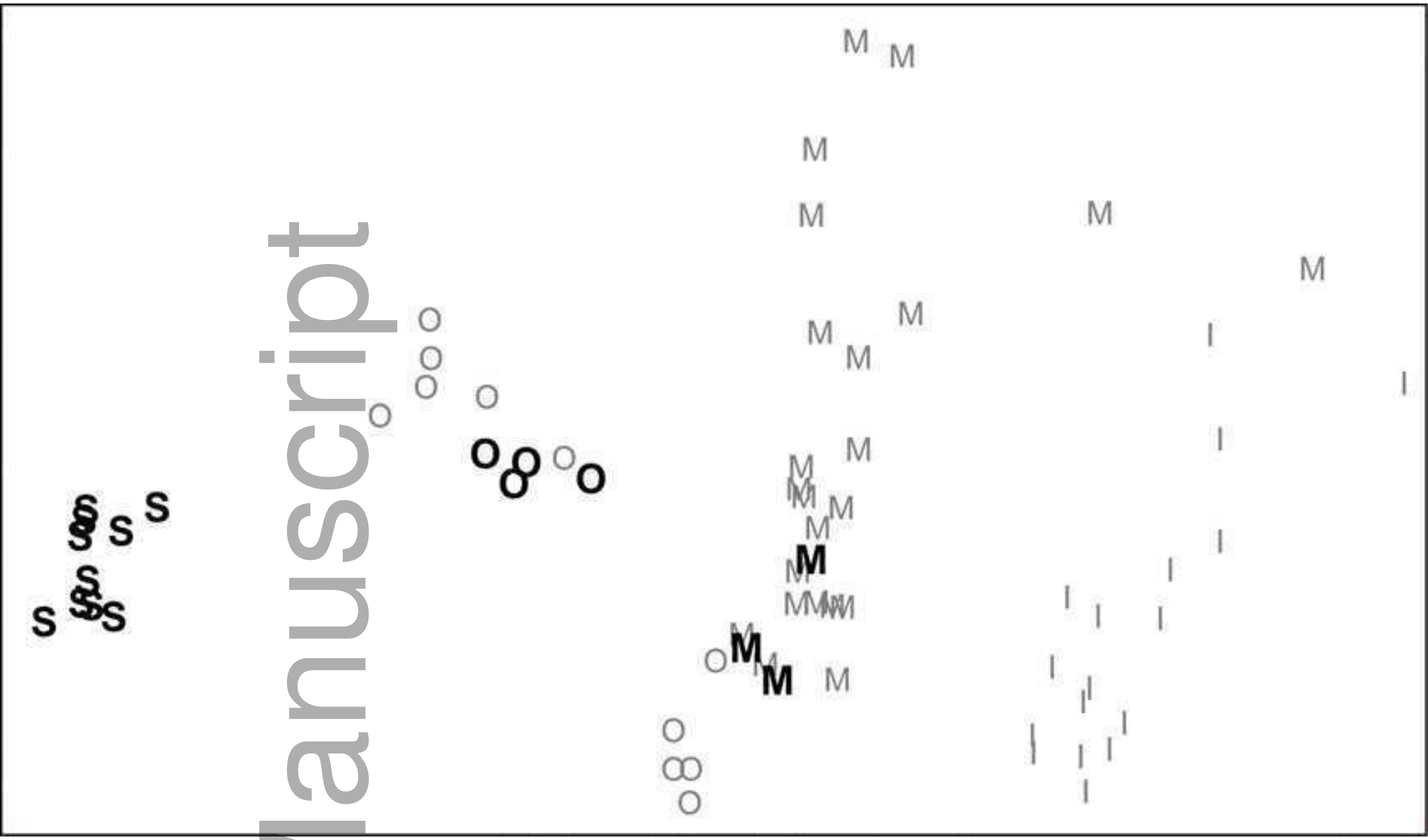

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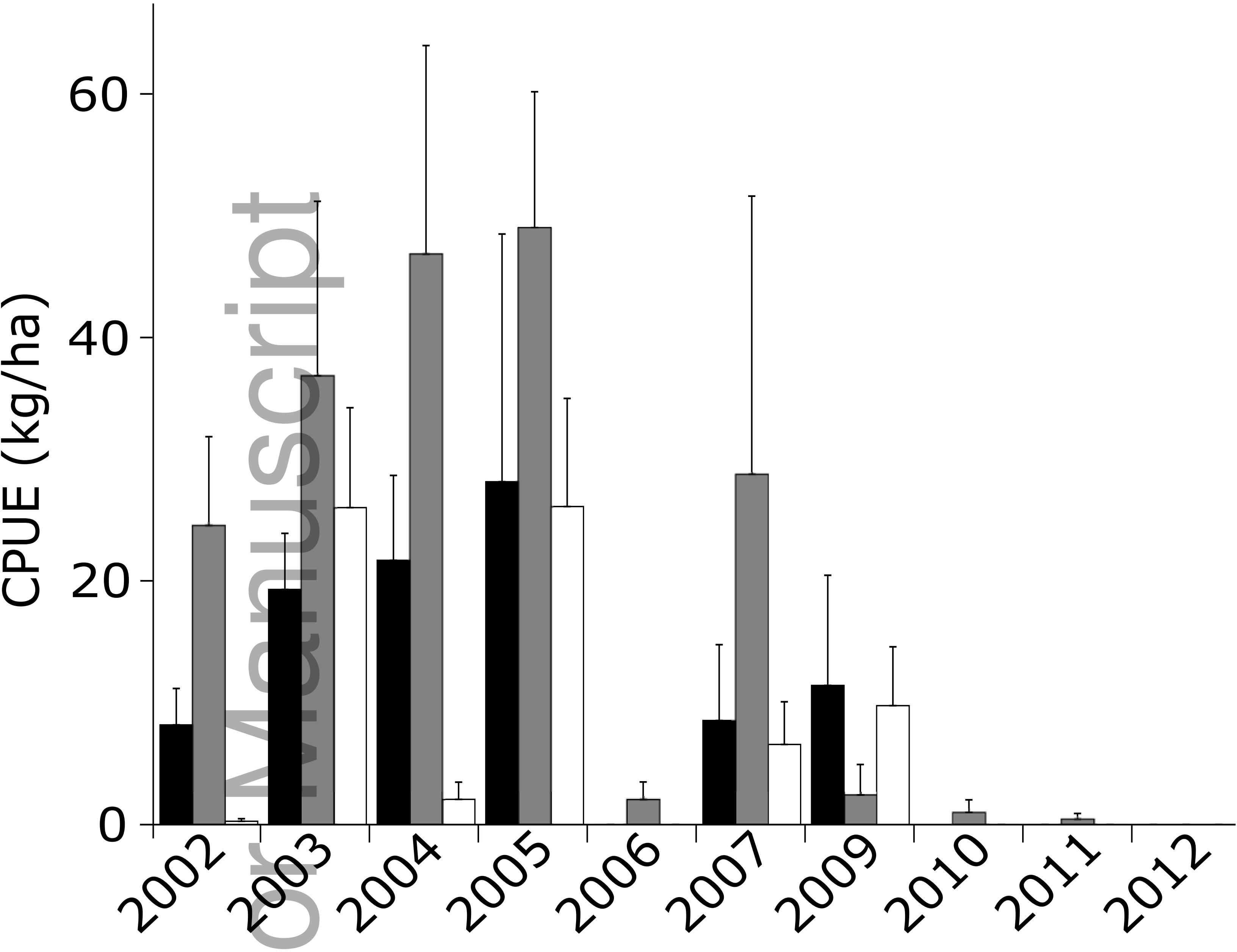

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