Temperature effects on spatiotemporal patterns of forage fish and crustaceans in Gulf of Alaska groundfish diets

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Abstract

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Recently, the North Pacific Ocean has experienced unprecedented and extreme marine heat waves (MHWs), which have caused cascading ecological effects within marine food webs. Examining past responses of groundfish feeding ecology to temperature shifts will help illuminate how they may respond in the future. In this study, we investigated the role of temperature in explaining spatiotemporal patterns in the diets of four groundfish predators in the Gulf of Alaska (GOA). The objectives of this research were to 1) characterize spatiotemporal patterns of groundfish predation on forage fish and crustacean prey species; and 2) evaluate effects of temperature on patterns of prey occurrence in predator diets. Prey species were identified for analysis based on hypothesized relationships with temperature, relevance to management, and empirical measures of relative importance in groundfish diets. We used 15 years (1990 - 2022) of groundfish stomach contents data to model prey occurrence as a function of temperature, year, location, depth, predator species, and predator length. Our model results showed seven relationships between temperature and prey occurrence in diets, including a negative effect for euphausiids and pandalids, and a positive effect for pagurids and tanner crab. Euphausiids in particular showed consistent negative trends in response to temperature in the diets of Pacific cod, walleye pollock, and arrowtooth flounder. Euphausiids are a high lipid, energy-rich food source for GOA predators including groundfish, whales, and seabirds. The complex and unprecedented effects of the GOA MHW demonstrate the need to better understand the predator-prey interactions in this system across multiple species and trophic levels. This work can help to inform development of prey abundance and biomass surveys and to supplement data-limited species or years.

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ABSTRACT

Recently, the North Pacific Ocean has experienced unprecedented and extreme marine heat waves (MHWs), which have caused cascading ecological effects within marine food webs. Examining past responses of groundfish feeding ecology to temperature shifts will help illuminate how they may respond in the future. In this study, we investigated the role of temperature in explaining spatiotemporal patterns in the diets of four groundfish predators in the Gulf of Alaska (GOA). The objectives of this research were to 1) characterize spatiotemporal patterns of groundfish predation on forage fish and crustacean prey species; and 2) evaluate effects of temperature on patterns of prey occurrence in predator diets. Prey species were identified for analysis based on hypothesized relationships with temperature, relevance to management, and empirical measures of relative importance in groundfish diets. We used 15 years (1990 - 2022) of groundfish stomach contents data to model prey occurrence as a function of temperature, year, location, depth, predator species, and predator length. Our model results showed seven relationships between temperature and prey occurrence in diets, including a negative effect for euphausiids and pandalids, and a positive effect for pagurids and tanner crab. Euphausiids in particular showed consistent negative trends in response to temperature in the diets of Pacific cod, walleye pollock, and arrowtooth flounder. Euphausiids are a high lipid, energy-rich food source for GOA predators including groundfish, whales, and seabirds. The complex and unprecedented effects of the GOA MHW demonstrate the need to better understand the predator-prey interactions in this system across multiple species and trophic levels. This work

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INTRODUCTION

Since the late 1970s, temperature variability and regime shifts have been documented in the Gulf of Alaska (GOA), which have impacted food web dynamics. In 1976, changes in oceanographic conditions led to a well-documented regime shift, characterized by a period of rapid warming and community reorganization that persisted over time (Anderson and Piatt 1999; Hare and Mantua 2000). In addition, anthropogenic climate change has caused an increase in the frequency and intensity of extreme temperature events (Oliver et al. 2019), including marine heatwaves (MHWs), which are discrete, prolonged, anomalously warm water events in a particular region (Hobday et al. 2016). MHWs cause cascading ecological effects within marine food webs, disrupting energy transfer at multiple trophic levels (Suryan et al. 2021). In 2014 through 2016, the GOA experienced an unprecedented MHW, which produced sea surface temperature (SST) anomalies exceeding three standard deviations (Bond et al. 2015). The MHW began to weaken in March of 2015; however, subsurface temperatures remained anomalously warm to depths of 250 m and the MHW later re-intensified in the winter of 2018 and through fall 2019 (Suryan et al. 2021). The ecological responses to the GOA MHWs were broad and included species range shifts (Li et al. 2019; Thorson 2019), predator mortality events (Barbeaux et al. 2020; Di Lorenzo and Mantua 2016; Piatt et al. 2020), harmful algal blooms (Gentemann et al. 2017), and novel biological community patterns (Batten et al. 2018; Suryan et al. 2021).

While shifts in oceanographic conditions and ecological communities have been recorded in the past, it is predicted that climate change will cause an increase in frequency of events and changes will be less predictable due to the non-stationarity of previously established species-environment relationships (Litzow et al. 2014; Suryan et al. 2021). During the 1976 regime shift groundfish were able to colonize new regions, which increased predation on crustaceans and transformed epibenthic communities from crustacean- to groundfish-dominated (Anderson and Piatt 1999). This change in biomass significantly altered GOA commercial fisheries, and led to the development of a highly productive and economically valuable groundfish fishery (Fissel et al. 2019). Following the regime shift, a basin-wide analysis investigated non-stationary trends and the effects of temperature on biomass and recruitment for groundfish predators and prey in the GOA (Puerta et al. 2019). This study found a positive relationship between temperature and tanner crab (*Chionoecetes bairdi*) biomass before 1995 and then a reversal of this trend, with a negative relationship after 1995 (Puerta et al. 2019). Similarly, walleye pollock (*Gadus chalcogrammus*) recruitment showed a positive relationship with temperature, switching to a negative relationship after 1989 (Puerta et al. 2019). In addition to prey biomass shifts, there is evidence that groundfish show a non-uniform geographic distributional response to anomalous temperatures (Li et al. 2019), which may result in predator-prey mismatches and prey switching (Puerta et al. 2019).

There is substantial evidence that the 2014 to 2016 GOA MHW caused changes in phenology, abundance, and energetic content of key groundfish prey species, potentially leading to bottom up forcing. Years characterized by warm SST in the GOA are associated with low primary productivity in winter (Whitney 2015) and changes in zooplankton community structure (Kimmel and Duffy-Anderson 2020), with increased abundance of smaller, lipid-poor zooplankton species (Batten et al. 2022). The MHW also drove changes in abundances of forage fish species, including capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), and walleye pollock (Arimitsu et al. 2021; Suryan et al. 2021). Forage fish in the GOA are essential prey items for numerous marine predators and mediate the transfer of energy from plankton to upper trophic level consumers, but they also tend to show large fluctuations in abundance (McClatchie et al. 2017). Capelin and herring abundance declined during the MHW, and capelin also declined in the diets of Pacific cod (*Gadus macrocephalus*) and seabirds (Arimitsu et al. 2021; Barbeaux et al. 2020; Suryan et al. 2021). Sudden declines were observed in piscivorous seabirds due to reduced breeding success arising from nutritional stress caused by declines in forage fish (Piatt et al. 2020; Suryan et al. 2021). Juvenile (age-0) walleye pollock, a crucial prey source for groundfishes (Buckley et al. 2016, Thompson et al. 2014), declined during the MHW (Rogers et al. 2020), but increased directly after the marine heatwave (Suryan et al. 2021). The impacts of the MHW on the production and composition of plankton, forage fish, and seabird communities are relatively well-studied, but less is known about effects on commercially important groundfish and the implications for their nutritional condition, growth, and survival.

These temperature related shifts in recruitment, movement patterns, and prey biomass can lead to altered nutritional demands and diet compositions of groundfish predators. Recent warm winters in the GOA increased bioenergetic stress for groundfishes because of their reliance on cool temperatures to maintain lipid reserves through periods of reduced prey availability (Holsman and Aydin 2015). Warming can cause changes in the energetic demand of consumers, leading to higher metabolic demands and lower size-at-age in some groundfish predators (Barbeaux et al. 2020). Negative effects of dietary changes on growth and condition can result in poor recruitment, and a weakening of age class structure (Sewall et al. 2019). The 2014 - 2016 GOA MHW triggered an unexpected collapse of the Pacific cod stock, which fell by 71 percent (Barbeaux et al. 2020). This decline was attributed to increased metabolic demand of Pacific cod, coupled with decreased prey availability, changes in movement patterns, and decreased survival of eggs (Barbeaux et al. 2020).

The GOA region has been the focus of several multi-species ecosystem models, which incorporate groundfish dietary data (Adams et al. 2022; Barnes et al. 2018; Gaichas and Francis 2008). However, there has been limited work focused on patterns of forage fish prey in diets and the environmental factors that explain variation in groundfish predator diet composition. Thompson et al. (2014) examined the influence of environmental factors and predator interactions on walleye pollock prey occurrence, and found that temperature was negatively related to the consumption of pollock by halibut. The effect of temperature on other groundfish prey are not as well studied. Improved understanding of how temperature changes are altering the feeding ecology of commercially-important groundfish predators will strengthen information supporting ecosystem-based management in the GOA (Ferriss et al. 2022). In this study, we investigated the role of temperature in explaining spatiotemporal patterns in the diets of focal groundfish predators in the GOA. The objectives of this research were to 1) characterize spatiotemporal patterns of groundfish predation on forage fish and crustacean prey species; and 2) evaluate effects of temperature on patterns of prey occurrence in predator diets.

Groundfish stomach contents provide a snapshot of the diet that reflects an integrated physiological and behavioral response to the environment by both predators and prey, as well as ontogenetic factors influencing diets (e.g., size-selective predation; Chipps and Garvey 2006). Temperature directly affects predator metabolism (therefore, feeding rates and hunger levels), and can drive shifts in distribution and spatiotemporal overlap of predators and prey (Gerking 1994). Therefore, predicting the effects of temperature on patterns of prey occurrence in stomachs is not straightforward. Diets of generalist predators, which can track fluctuations of forage fish prey in the environment, have been used as an indicator of prey abundance and distribution in the environment (Buckley et al. 2016; Suryan et al 2021). Although data are lacking on abundance of many prey species in the GOA, known relationships between temperature and forage fish and crustacean abundance can inform hypotheses about how temperature may affect occurrence of those prey in groundfish predator stomachs. Specifically, we hypothesized that euphausiids (Euphausiacea) in groundfish diets would show a nonlinear effect of temperature, because mild warming (< 7º C) is linked to an increase in abundance (Kimmel and Anderson 2020), but extreme temperatures (> 7º C) cause a decrease in biomass (Arimitsu et al. 2021). We hypothesized that occurrence of walleye pollock prey in diets would show a negative relationship with temperature, as observed in Pacific halibut (*Hippoglossus stenolepis*) and Pacific cod diets (Thompson et al. 2014), and age-0 walleye pollock abundance declined during the MHW (Dougherty and Rogers 2017). We predicted that occurrence of smelts (Osmeridae) in groundfish diets would show a negative response to temperature, because they declined in abundance during the warming regime shift and MHW (Suryan et al. 2021). Herring (Clupeidae) increased in abundance following the regime shift but declined during the MHW, so we hypothesized that occurrence of this prey group in diets would show a nonlinear trend with temperature (Suryan et al. 2021). Pandalid shrimp (Pandalidae) declined in biomass and abundance following the 1976 warming regime shift (Anderson and Piatt 1999; Litzow and Ciannelli 2007; Puerta et al. 2019), so we hypothesized a negative relationship between temperature and pandalid shrimp occurrence in groundfish diets. Tanner crab have undergone large fluctuations in occurrence but have slowly increased in abundance since the early 2000s through the MHW, so we predicted that occurrence of tanner crab in diets would show a nonlinear trend with temperature (Ferriss et al. 2022; Puerta et al. 2019). There is limited research on hermit crabs (Paguridae), but some research shows that warming temperatures may increase metabolic rates (Rangel and Sorte 2022). These prey are mobile and can move to deeper waters during warm periods, which may make them more susceptible to predation, so we hypothesize a positive association between temperature and occurrence in predator diets.

METHODS

Data description and preparation

Stomach content data for GOA predators were collected as part of a fishery-independent bottom trawl survey program conducted by the National Marine Fisheries Service (NMFS). The Alaska Fisheries Science Center (AFSC) has collected 17 years of bottom trawl survey data in the GOA, triennially from 1987 to 1999, and then biennially to the present (Figure 1). Groundfish survey and diet sampling methods are described by Livingston et al. (2017) and briefly summarized here. The survey region is sub-divided into strata defined by depth and oceanographic features, and stations for performing bottom trawls are selected using a stratified random sampling design. Stations in the survey region are sampled from west to east during summer months, typically beginning in the last week of May and ending the first week of August. For a given predator, at each station, up to five individuals from each size category were sampled for stomach contents analysis (Supplementary Table 1). Individuals showing signs of net feeding or regurgitation were excluded from sampling and substituted with new, randomly selected individuals.

Stomach contents were processed by the Trophic Interactions Laboratory (https://www.fisheries.noaa.gov/resource/document/resource-ecology-and-ecosystem-modeling-stomach-content-analysis-procedures) at the AFSC in Seattle. The taxonomic resolution obtained for some prey groups has varied over time, but fish and crabs have been identified to the species level consistently when possible. Diet data used in this analysis are publicly available (https://apps-afsc.fisheries.noaa.gov/refm/reem/webdietdata/dietdataintro.php).

Food habits data for the GOA from the REEM database were accessed October 2022. We identified four groundfish species that were sampled consistently every year in the groundfish survey to prioritize for analysis: arrowtooth flounder (*Atheresthes stomias*), Pacific halibut (hereafter, halibut), walleye pollock, and Pacific cod (hereafter, cod). Diet data prior to 1990 were excluded due to changes in sampling methodology (Livingston et al. 2017). We chose to exclude empty stomachs (10,354 out of 50,089 total stomachs) to model the probability occurrence of focal prey taxa in stomachs of only those predators that had consumed prey of any type (i.e., probability of prey occurrence, given that a predator had eaten). This allowed clearer interpretation of results, because the frequency of occurrence of empty versus non-empty stomachs can signify broader patterns in nutritional condition within a sampled predator population (Beaudreau and Essington 2007). We excluded samples collected from stations greater than 300 m depth (55 hauls out of 4903 total hauls), because deeper regions beyond the shelf were surveyed inconsistently. We also excluded hauls with missing environmental data for depth and temperature (210 hauls out of 4903 total hauls). Predators with low occurrences of prey in their diets (number or stomachs sampled with prey present <100 instances) were not selected for modeling (Table 1). Gear temperature, gear depth, latitude, and longitude are collected for each bottom trawl haul (hereafter, haul). Gear temperature and gear depth are averages collected by a sensor at the head of the net.

Visualization and identification of key prey

We summarized diet compositions using percent weight (%W) and percent frequency of occurrence (%O; Table 1) and visualized size-based patterns in diets of the four groundfish predators to identify key prey taxa and inform construction of statistical models. Diet metrics (%W and %O) were calculated for each predator species and across size classes. Size classes were set to 10 cm length bins, ranging from 20 to 70+ cm for arrowtooth flounder and walleye pollock, 20 to 80+ cm for cod, and 20 to 120+ cm for halibut. We chose the narrowest length bins possible, given sample sizes, in order to best visualize shifts in diet over a range of predator lengths. For data visualization purposes, prey taxa were aggregated into coarser groupings (Supplementary Table 2). We chose seven focal prey groups for statistical analysis based on one or more of the following criteria: (1) prey contributing a relatively high proportion by weight or occurrence to the diet of a predator (Table 1); (2) prey that have shown sensitivity to temperature fluctuations in the environment according to previous research, as described in the Introduction (Table 2); (3) and prey that are shared by multiple focal predators. Although both metrics were used to inform model selection, for statistical analysis, we chose to model prey occurrence as the response variable rather than prey weight due to potential biases associated with the digestion level of prey.

Model fitting and model selection

We evaluated spatiotemporal variation in the occurrence of the key prey groups and their association with temperature using generalized additive models (GAMs). Specifically, we developed models for each prey taxon where prey occurrence (presence or absence) was treated as a Bernoulli response. Within our model, gear temperature serves as a proxy for the thermal experience of the predator. Depth and location (latitude and longitude) were included in the model to account for varying spatial distributions of prey (Barnes et al. 2018). Predator length accounts for ontogenetic changes in metabolic rate and gape limitation that change throughout a species' life history. Year is a nuisance parameter which captures additional environmental variability not explicitly included in the model, such as varying distributions of prey over time.

We modeled the probability of occurrence (O) of prey species (i) at time (t) as a function of survey year (Y), average haul gear temperature (T), average haul gear depth (D), haul location (longitude λ, latitude φ), and predator length (L), using a GAM, assuming a Bernoulli distribution and a logit link function (f). The full model took the form:

$$f(O_{i,t}) = B + Y + s_1(T_{i,t}) + s_2(D_{i,t}) + s_3(\varphi_{i,t}, \lambda_{i,t}) + s_4(L_{i,t}) + \epsilon_{i,t} \quad (1)$$

where s indicates univariate (s_1, s_2, s_4) and bivariate (s_3) smoothing spline functions. B indicates the intercept term, and ϵ the error.

Survey year was treated as a categorical variable, and gear temperature, depth, location, and predator length were treated as continuous variables. We constrained the temperature, depth, and length smoothing spline functions to four knots to reduce overfitting, after Barnes et al. (2018). The knots for the depth and location (latitude, longitude) smoothing spline functions were not constrained in order to allow for higher order patterns in space (Thompson et al. 2014). We screened predictor variables for multicollinearity but correlations were relatively modest (<0.60); we therefore retained all variables for the analysis (Zuur et al. 2009).

After constructing the full models for predator and prey we used the function "dredge" from the 'MuMIn' package in R to compare their performance using Akaike's Information Criterion (AIC), which balances goodness of fit and model complexity (Bartoń 2022). We used fixed parameters in the dredge function for the latitude/longitude bivariate predictor, and the predator length univariate predictor. The dredge function tests all alternative models by sequentially excluding non-fixed parameters. The model with the lowest AIC value was chosen as the best fit model (*b*) and used to calculate ΔAIC for each model (*i*) using the equation: $\Delta AIC_i = AIC_i - AIC_b$, where the best fit model $\Delta AIC_b = 0$. Models with a $\Delta AIC \leq 2$ were considered equally good fits, and could not be discounted (Burnham and Anderson 2002). We calculated parameter weights by summing the Akaike weights across models that included the given parameter. The function "gam.check" in the package 'mgcv' was used to inspect residuals, effective degrees of freedom, and convergence for all global models (Wood 2004).

Data analysis was performed using the statistical programming environment R (v4.2.2; R Core Team 2022). A detailed description of data used in this study, including metadata, and code can be found at: https://github.com/cadlaburch/BurchThesis_GOADietModels

RESULTS

Identification of prey species for analysis

The diet compositions of the four focal predators varied by length (Figure 2). Invertebrates comprised a larger proportion of the diets for gadid predators compared to halibut and arrowtooth flounder predators, which are more piscivorous throughout their life history (Figure 2). Halibut and cod undergo stronger ontogenetic shifts in diet relative to arrowtooth flounder and walleye pollock (Figure 2). Walleye pollock diets include only a small proportion of fish (< 25% of the diet by weight) even at larger size classes, whereas arrowtooth flounder are piscivorous (> 50% of the diet) across all length classes (Figure 2). Halibut and cod shift to diets composed of a majority of fish prey (>50% of the diet) at lengths of around 70-80 cm (Figure 2). Euphausiids contributed to diets of walleye pollock across all length classes and diets of smaller arrowtooth flounder and cod, but were not a major component of halibut diets (Figure 2). Walleye pollock were a large dietary component (>25% of the diet) for arrowtooth flounder, halibut, and cod, particularly at larger size classes, but walleye pollock cannibalism was less common (Figure 2). Forage fish, which included Ammodytidae*,* Bathylagidae*,* Clupeidae*,* and Osmeridae*,* composed a substantial proportion of the diet across all four predator species, particularly for individuals smaller than 70 cm. Commercial crab species, which included *Chionoecetes bairdi, Chionoecetes opilio,* and *Paralithodes camtschaticus*, were a moderate component (5 – 15 % of the diet) for cod and halibut diets across most predator lengths (Figure 2). Arthropods, which include but are not limited to Pandalidae and Paguridae*,* were a substantial component (> 25 % of the diet) for cod and halibut, and a moderate component (10 – 20 % of the diet) for pollock and arrowtooth flounder diets (Figure 2).

Based on our selection criteria (Table 1 and Table 2) we identified seven prey groups to evaluate using GAMs:

1. Euphausiids (*Euphausiacea*) were selected because this prey item contributed a relatively high percent occurrence (>20%) in the diets of arrowtooth flounder, cod, and walleye pollock (Table 1). This prey group is well-studied but there is not a clear positive or negative impact of temperature on the group overall, so we expect to see a nonlinear trend (Table 2).
2. Walleye pollock were selected due to a high percent weight (>20%) in the diets of arrowtooth flounder, halibut, and cod (Table 1). The percent occurrence is much lower, but overall sample sizes are very high (N > 500), which makes it a suitable prey group for modeling. This prey group has been well-studied because it is a commercial species and an important forage species, with previous findings showing a negative response to

temperature (Table 2).

3. Osmeridae and Clupeidae had the lowest %O and %W of the prey groups selected for modeling (<12%; Table 1). These groups were selected because forage fish have a high ecological importance, and previous research shows a sensitivity to temperature (Table 2). Arrowtooth flounder and halibut were selected for modeling this prey item due to relatively higher sample sizes (N > 150) (Table 1), and high diet compositions of forage fish at small size classes (Figure 2).
4. Pandalidae was selected for modeling because of relatively high percent occurrence (>10%), and large sample sizes (N > 1000) for arrowtooth flounder, cod, and walleye pollock (Table 1). Previous research showed a clear decline in abundance in response to temperature (Table 2).
5. Tanner crab had relatively high percent occurrence (>10%) and large sample size (N > 900) for halibut and cod (Table 1). Tanner crab response to temperature was unclear in the literature, due to large oscillations in abundance, so we expect to see a non-linear trend (Table 2).
6. Paguridae was selected for modeling because it is a large component (38 %O) in halibut diets, and a modest component (16 %O) in cod diets (Table 1). There is limited research on this prey species, but based on limited knowledge of its response to temperature we predicted a positive trend (Table 2).

Model selection and relative importance of predictors

The clupeid model for halibut predators was the only model that did not include the global model as one of the best performing models (ΔAIC ≤ 2; Table 3). For all other prey models, the best performing models included the global model, with the predictors location, gear depth, gear temperature, predator length, and year (Table 3). The set of best models for walleye pollock prey and cod predators, and for pandalid prey and arrowtooth flounder predators, included the global model and a reduced model that excluded gear temperature (Table 3). The set of best models for clupeid prey and arrowtooth flounder predators included the global model, and models excluding gear temperature, gear depth, and both gear temperature and gear depth (Table 3).

Gear depth and gear temperature showed relatively low Akaike weights for 10 out of 17 models run (Table 4). Location (latitude/longitude) and predator length were fixed in the dredge function, so these parameters always had Akaike weights of 1. Year was not fixed in the dredge, but it also showed high importance in model selection with a Akaike weight of 1 across all models. Five models had lower parameter weights for temperature (< 0.8), including the walleye pollock model for arrowtooth flounder, the pandalid model for arrowtooth flounder, the clupeid model for arrowtooth flounder, the clupeid model for halibut, and the tanner crab model for halibut (Table 4).

The adjusted R^2 for models ranged from 0.11 to 0.45, which are reasonable values in ecology (Møller 2002; Table 3). The two lowest R^2 models were the pagurid model for cod ($R^2 = 0.11$) and the euphausiid model for cod ($R^2 = 0.15$). The models for walleye pollock prey and clupeid prey had the highest R^2 values across all predators modeled.

Spatiotemporal patterns of predation on key prey species

The partial effects plots for all models and parameters are included in Appendix 1. These plots were visually inspected from the best fit global GAMs to assess changes in the predicted probability of prey occurrence in diets as a function of year and location, when all other parameters are held constant. Spatiotemporal patterns are described for each of the 7 prey groups:

1. Euphausiids showed high occurrence in walleye pollock, cod, and arrowtooth flounder diets along the outer shelf. Walleye pollock showed higher occurrence of euphausiids nearshore, and cod showed higher occurrence of euphausiids in the western GOA, compared to the other predators. Euphausiid occurrence in walleye pollock stomachs was relatively high compared to other predators, with a slight declining trend, across the time series. Cod diets showed large oscillations in euphausiid prey occurrence over the time series. Both walleye pollock and cod diets showed lowest euphausiid occurrence in 2017, compared to other years. Euphausiid occurrence in arrowtooth flounder stomachs showed no trend over the time series.
2. Walleye pollock showed high occurrence in diets nearshore, within the western GOA. Both halibut and cod diets showed increasing occurrence of walleye pollock from 2011 through 2019, followed by a decline. Walleye pollock occurrence in arrowtooth flounder stomachs showed no trend across the time series.
3. Pandalids showed high occurrence nearshore in the central GOA, and no temporal trend in occurrence for all predators modeled.
4. Clupeids showed high occurrence in the east GOA for halibut, and very low occurrence across the GOA for arrowtooth flounder. Clupeids occurrence in diets of both predators was low and varied without trend across the time series.

5. Osmerids showed high occurrence in the central GOA, both nearshore and offshore. Osmerid occurrence showed no temporal trend in halibut stomachs, and a decline from 2015 to 2021 in arrowtooth flounder stomachs.
6. Tanner crab showed higher occurrence nearshore in the western GOA, relative to other areas, for halibut and cod. Tanner crab occurrence in halibut and cod diets was higher from 2007 to 2021 compared to 1990 to 2007, with the exception of a low occurrence in 2015.
7. Pagurids showed high occurrence in the western GOA in halibut and cod diets. Pagurid occurrence in stomachs was lowest for both predators in 2001, but otherwise showed no trend across the time series.

Effects of temperature on patterns of prey occurrence

The effects of temperature on prey occurrence varied among combinations of predators and prey. Based on parameter weights, temperature was a relatively important predictor of the probability of prey occurrence for walleye pollock consuming euphausiids and pandalids (weight ≥ 0.9), for cod consuming euphausiids, pandalids, tanner crab, walleye pollock, and cod (weight > 0.6), for halibut consuming walleye pollock, osmerids, tanner crab, and pagurid crab (weight $>$ 0.7), and for arrowtooth flounder consuming euphausiids, walleye pollock, and osmerids (weight > 0.9; Table 4). Temperature was a relatively unimportant predictor (weight ≤ 0.5) of prey occurrence for arrowtooth flounder consuming pandalids, halibut consuming clupeids, and arrowtooth flounder consuming clupeids (Table 4). We describe the relationship between temperature and probability of prey occurrence for select models, in which temperature was a relatively important predictor and partial effects plots were interpretable (i.e., did not have large confidence intervals or no trend; Figure 3):

1. Euphausiid occurrence showed a negative effect of temperature across predators. The shape of these negative trends varied. Cod showed a steep decline in prey occurrence across the entire temperature range (Figure 3A). Walleye pollock showed no effect of temperature below ~ 8 °C; above that temperature, occurrence of euphausiid prey showed a steep decline (Figure 3B). Euphausiids showed a more gradual decline in occurrence within arrowtooth flounder stomachs across the temperature range (Figure 3C).
2. Pandalid occurrence in cod diets showed a negative relationship with temperature (Figure 3D).
3. Tanner crab occurrence in cod and halibut diets showed a positive relationship with temperature. Tanner crab occurrence showed a linear increasing trend for cod (Figure 3F), and varied without trend for halibut except at temperatures exceeding 8 °C (Figure 3G).
4. Pagurid occurrence in cod diets showed a positive effect of temperature (Figure 3E).

DISCUSSION

Our results suggest that spatiotemporal, environmental, and biological covariates affect the occurrence of prey in the stomachs of groundfish predators. Although stomach contents data are generated from complex and noisy trophic processes (Gerking 1994), large sample sizes allowed us to gain insight from models for four major predators in the GOA. Partial effects plots for year, geographic location, and temperature revealed patterns of prey occurrence that were consistent across multiple predator species. Our model results showed seven relationships between temperature and prey occurrence in diets. The three euphausiid models supported our hypothesis, showing a nonlinear effect of temperature on euphausiids, with a negative relationship above 7º C across predators. The pandalid model of cod diets supported our hypothesis of a negative effect of temperature. The pagurid model of cod diets supported our hypothesis of a positive effect of temperature. The tanner crab models of cod and halibut showed an unexpected positive effect of temperature, which opposes our hypothesis based on the literature of reduced cod predation during the MHW (Barbeaux et al. 2020). Model selection revealed that all parameters were important for explaining variance in probability of prey occurrence, and although gear depth and gear temperature had lower Akaike weights across models compared to year, the overall parameter weights were high (> 0.8) in 12 out of 17 models. These findings support previous work that incorporates environmental factors within ecological models to better understand predator-prey interactions (Buchheister and Latour 2015; Thompson et al. 2014).

Stomach contents are a result of prey availability (Buchheister and Latour 2015), predator physiology (Christensen 1996), and predator preference. Our model uses latitude, longitude, and depth parameters to account for the spatial variability of prey in the environment, and predator length to account for physiological constraints such as gape limitation (Christensen 1996). There are multiple potential interpretations of the model-predicted temperature trends. A positive relationship may indicate a predation response to an increase in prey availability driven by temperature. Alternatively, the increase in occurrence in diets could signify increased predation arising from temperature-driven increases in metabolic demand by predators (Holsman et al.

2015). Conversely, a negative relationship may indicate that there is a reduction in prey availability, or that predator preferences change at high temperatures. This study looks at single species interactions, but unaccounted for systems level complexity may also influence our results. For example, temperature related declines in unmodeled prey groups may be linked to increased or decreased predation on these modeled prey groups, due to changes in predator demand and preference. Future work could incorporate available prey abundance data into the model in order to better understand the implications of these temperature trends.

This study identified a negative relationship between euphausiid occurrence in diets and temperature, which supports our hypothesis and builds on previous research in the GOA. Euphausiids are a high lipid (Dalpadado et al. 2012), energy-rich food source for multiple predators in the GOA including groundfish (Buckley et al 2016), whales (Witteveen et al 2012), and seabirds (Piatt et al. 2020). Previous findings in the GOA showed mixed effects of temperature on euphausiid abundance, with a positive response at moderate temperatures (< 7º C; Kimmel and Anderson 2020) but a negative response at extreme temperatures (>7º C; Arimitsu et al. 2021). Temperature-related declines in euphausiids could disrupt energy transfer within the food web or translate into nutritional stress for some groundfish predators with strong reliance on euphausiids. For example, walleye pollock consume a high proportion of euphausiids in their diets, and are also a substantial forage prey species for other groundfish predators. Notably, our forage fish models (walleye pollock, clupeids, osmerids), did not reveal relationships between prey occurrence in predator diets and temperature, which is counter to our hypotheses based on the literature. The power to detect effects of temperature was weaker for these prey groups compared to others due to low sample sizes of observed prey items, complicating the interpretation of this result. The positive relationships between tanner crab occurrence and temperature were unexpected and may indicate greater availability of tanner crab prey, lower availability of more preferred prey (i.e., prey-switching), or greater consumption demand overall due to increased feeding rates.

In this study, gear temperature served as a proxy for the thermal experience of predators. This relies on several simplifying assumptions. First, we assume that gear temperature, which is the average temperature at the head of the net throughout the duration of the bottom trawl, is representative of the temperature at which the sampled predator captured and consumed the prey observed in its stomach. Flatfishes and cod are demersal species, which are more likely to feed on or near the bottom, where the bottom trawl samples are collected (Lopez-Lopez et al. 2015). In contrast, walleye pollock are semi-pelagic species, which makes them more likely to move through the water column and feed outside the depth range of the bottom trawl survey (Kotwicki et al. 2015). Departures from this assumption may have influenced our results, considering the multi-scale effects that temperature has on fish diets.

Assuming that groundfish are semi-opportunistic samplers, predator diets can be used to represent a sample of their prey field, and at large spatial and temporal scales this data can provide insight into variation in prey availability (Buckley et al. 2016; Suryan et al 2021). There is some evidence that diets can provide better insight into prey populations than other sampling methods due to net avoidance and limitations on the availability of long term prey abundance data (Wiebe et al. 1982). However, the taxonomic resolution of diet data is coarse, and many organisms are only identified to the family level, such as Clupeidae, Osmeridae, and Pandalidae which were used in these models. By modeling these higher level taxonomic prey groupings it is possible that our models were unable to detect a response to temperature due to differing responses across individual species (Kimmel and Duffy-Anderson 2020). However, this is a common constraint in trophic ecology due to the challenges of identifying partially digested prey items in stomachs (Livingston et al. 2017). The GOA bottom trawl surveys are conducted bi-annually during summer months, but MHW events are known to persist through the winter (Bond et al. 2015). Sampling winter groundfish diet data could improve the ability to model and detect changes in prey occurrence within diets; however, the logistics and costs of collecting these data may make winter sampling infeasible. Lastly, one limitation inherent to fish diet data is the potential for regurgitation or net feeding, although fish displaying signs of this behavior were excluded from sampling (Livingston et al. 2017). We chose to use prey occurrence data instead of prey weight to minimize the error of sampling bias due to these behaviors.

Our results demonstrate that diets data can be a useful method for detecting changes in commercial groundfish predator diets, which can inform ecosystem-based fishery management. Ecosystem-based fishery management builds upon the single stock approach by incorporating trophic interactions and environmental factors (Barbeaux et al. 2020). Alaskan commercial groundfish fisheries are highly productive and economically valuable, and climate related uncertainty threatens the perpetuity of this industry (Fissel et al. 2019). In the last decade, the North Pacific Fishery Management Council has increasingly incorporated ecosystem research into management documents (Barbeaux et al. 2020). The complex and unprecedented effects of the GOA MHW demonstrate the need to better understand the predator-prey interactions in this system across multiple species and trophic levels. Our study demonstrates that diets can be used to measure concurrent changes in prey across multiple predators, which strengthens the ecological inferences that can be gained by examining patterns in diets. This work can help to inform development of prey abundance and biomass surveys and to supplement data-limited species or years. A better understanding of trophic dynamics will support initiatives to transition fisheries management to a more holistic and ecosystem-based approach.

Data Accessibility Statement

All data used in this study are publicly accessible in databases administered by the Alaska Fisheries Science Center (NOAA Fisheries, National Oceanic and Atmospheric Administration). Bottom trawl food habits data are maintained by the Resource Ecology and Ecosystem Modeling (REEM) Division, and can be found online at: https://apps-afsc.fisheries.noaa.gov/refm/reem/webdietdata/dietdataintro.php.

Code and relevant metadata from this project can be found online (https://github.com/cadlaburch/BurchThesis_GOADietModels), and are managed by Catalina Burch as part of her Master's thesis project.

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TABLES

Table 1. Focal prey sample sizes for generalized additive model analysis including the number of predator stomachs sampled (N Pred), the number of stomachs where prey items were present (N Prey), the percent occurrence of prey (%O), and the percent weight of prey (%W). Values in grey indicate predator/prey combinations that were not modeled due to low values in the diet (%W, %O).

Predator	Metric	Euphausiacea	Paguridae	Pandalidae	Tanner crab	Walleye pollock	Clupeidei	Osmeridae
Walleye pollock	N Pred	10880	10880	10880	10880	10880	10880	10880
	N Prey	6977	270	1184	8	139	5	310
	%O	64	2	11	0	1	0	3
	%W	45	0	12	0	4	0	7
Pacific halibut	N Pred	6859	6859	6859	6859	6859	6859	6859
	N Prey	201	2588	185	936	1011	174	383
	%O	3	38	3	14	15	3	6
	%W	0	4	0	6	43	2	3
Pacific cod	N Pred	9840	9840	9840	9840	9840	9840	9840
	N Prey	2147	1618	2572	1656	572	39	192
	%O	22	16	26	17	6	0	2
	%W	3	4	8	9	27	1	2
Arrowtooth flounder	N Pred	9751	9751	9751	9751	9751	9751	9751
	N Prey	3558	6	1093	4	1337	215	1148
	%O	36	0	11	0	14	2	12
	%W	4	0	2	0	58	7	8

Table 2. Justifications of model hypotheses based on previous research on the response of prey groups to temperature. Columns show the prey group modeled as a response, the predator species modeled, a summary of previous research on the general response and the MHW response to temperature, and the hypothesis selected.

Response	**Predators Modeled**	**Previous Research in GOA**	**Temperature Hypothesis**
Euphausiacea	A. flounder Pacific cod Walleye pollock	General response: Euphausiid larva abundance shows a positive response to temperature, however this study did not model temperatures above 7 °C (Kimmel and Duffy-Anderson 2020). Euphausiid adult abundance shows a varied response to temperature with some species showing a positive or negative relationship (Pinchuk et al. 2008; Sousa et al. 2016). MHW response: There was an increase in the contribution of Euphausiids in salmon diets (Fergusson et al. 2020). Overall biomass of euphausiids declined due to loss of cool water species (Arimitsu et al. 2021).	nonlinear
Walleye pollock	A. flounder Pacific halibut Pacific cod	General response: Negative relationship between temperature and the occurrence of pollock in halibut and cod diets (Thompson et al. 2014). Decline in the proportion of pollock in the diet of puffin diet during warm years (Thorson et al. 2021). MHW response: Age-0 pollock abundance declined during the MHW, but were abundant in 2013 and 2017 in proximal years (Rogers et al. 2020; Suryan et al. 2021). Walleye pollock are a significant component of cod diet's, and cod populations dramatically declined following the MHW (Barbeaux et al. 2020). This is partially attributed to an increase in metabolic demand and decrease in prey availability.	negative
Clupeidae	A. flounder Pacific halibut	General response: The *Clupeidae* family includes herring, which are considered warm water favoring species (Thorson et al. 2022). MHW response: Herring declined in abundance during the MHW, as did kittiwake (herring predator) nests (Suryan et al. 2021).	nonlinear

Osmeridae	A. flounder Pacific halibut	General response: The *Osmeridae* family includes capelin, which declined after the 1976 warming regime shift (Anderson and Piaat 1999). This species is a late spawner so they are likely to be negatively impacted by temperature driven shifts to earlier plankton blooms. MHW response: Capelin abundance and presence in the diets of seabirds declined during the MHW (Suryan et al. 2021).	negative
Pandalidae	A. flounder Pacific cod Walleye pollock	General response: Declined in biomass and abundance following regime shift but has been stable since 1981 (Anderson and Piatt 1999; Puerta et al. 2019). Pacific cod are thought to have contributed to decline through top down control (Litzow and Ciannelli 2007).	negative
Tanner crab	Pacific halibut Pacific cod	General response: Shows large interannual variability in biomass (Puerta et al. 2019). Tanner crab abundance has slowly increased in the GOA since the early 2000s (Ferriss et al. 2022). MHW response: The %W of tanner crab in cod stomachs declined during the MHW (Barbeaux et al. 2020).	nonlinear
Paguridae	Pacific halibut Pacific cod	General response: There is limited research on this prey species, but some research suggests that warming temperatures may cause increases in metabolic rates of Paguridae (Rangel and Sorte 2022). These are more mobile species that are able to move to deeper waters during periods of temperature stress, which may increase their susceptibility to predation.	positive

Table 3. Summary of full and threshold GAM selection with ΔAIC <= 2. Columns show the response variable tested, predator modeled, explanatory parameters included in model indicated by (+), adjusted R^2, percent deviance, degrees of freedom, log likelihood, AIC, ΔAIC, and Akaike weight.

Response	**Predator Modeled**	**Long/ Lat**	**Gear Depth**	**Gear Temp**	**Predator Length**	**Year**	**Adj R^2**	**Deviance**	**df**	**Log Lik**	**AIC**	**ΔAIC**	**weight**
1) Euphausiid	Walleye pollock	+	+	+	+	+	0.20	0.12	51	-6249	12602	0	1
	Cod	+	+	+	+	+	0.15	0.10	47	-4668	9432	0	1
	A. Flounder	+	+	+	+	+	0.35	0.23	49	-4956	10012	0	0.92
2) Walleye pollock	Halibut	+	+	+	+	+	0.36	0.27	48	-2098	4293	0	1
	Cod	+	+	+	+	+	0.37	0.32	48	-1490	3076	0	0.66
	Cod	+	+	NA	+	+	0.37	0.32	46	-1493	3078	1.35	0.33
	A. flounder	+	+	+	+	+	0.38	0.30	49	-2740	5579	0	0.96
3) Pandalidae	Walleye pollock	+	+	+	+	+	0.32	0.25	49	-2812	5724	0	0.90
	Cod	+	+	+	+	+	0.28	0.18	49	-4611	9322	0	1
	A. flounder	+	+	+	+	+	0.22	0.17	49	-2842	5783	0	0.50
	A. flounder	+	+	NA	+	+	0.22	0.17	47	-2844	5783	0.03	0.50
4) Clupeidei	Halibut	+	+	NA	+	+	0.45	0.42	36	-468	1009	0	0.68
	A. flounder	+	NA	NA	+	+	0.38	0.35	42	-670	1425	0	0.41
	A. flounder	+	+	+	+	+	0.38	0.35	45	-667	1426	1.05	0.24
	A. flounder	+	NA	+	+	+	0.38	0.35	43	-670	1427	1.57	0.19
	A. flounder	+	+	NA	+	+	0.38	0.35	43	-670	1427	1.96	0.15
5) Osmerid	Halibut	+	+	+	+	+	0.29	0.25	47	-1105	2305	0	0.84
	A. flounder	+	+	+	+	+	0.24	0.18	48	-2889	5874	0	0.99
6) Tanner crab	Halibut	+	+	+	+	+	0.25	0.19	49	-2222	4544	0	0.79
	Cod	+	+	+	+	+	0.27	0.19	50	-3591	7283	0	1
7) Paguridae	Halibut	+	+	+	+	+	0.34	0.22	50	-3567	7235	0	1
	Cod	+	+	+	+	+	0.11	0.08	48	-4064	8225	0	1

Table 4. Parameter weights for each model. Columns show the response variable, predator modeled, and explanatory variable parameter weights.

		Sum of Akaike weights (w_i)				
Response	**Predator**	**Lat/Long**	**Gear Depth**	**Gear Temp**	**Predator Length**	**Year**
1) Euphausiacea	Walleye pollock	1	1	1	1	1
	Cod	1	1	1	1	1
	A. Flounder	1	1	0.92	1	1
2) Walleye pollock	Halibut	1	1	1	1	1
	Cod	1	0.99	0.67	1	1
	A. Flounder	1	1	0.96	1	1
3) Pandalidae	Walleye pollock	1	1	0.90	1	1
	Cod	1	1	1	1	1
	A. Flounder	1	1	0.50	1	1
4) Clupeidei	Halibut	1	0.92	0.30	1	1
	A. Flounder	1	0.40	0.43	1	1
5) Osmerid	Halibut	1	1	0.84	1	1
	A. Flounder	1	1	0.99	1	1
6) Tanner crab	Halibut	1	1	0.79	1	1
	Cod	1	1	1	1	1
7) Paguridae	Halibut	1	1	1	1	1
	Cod	1	1	1	1	1

FIGURES

Figure 1. Map of bottom trawl survey area in the Gulf of Alaska, with data from 1990 to 2021. Red points show locations of individual survey stations that were included in the analysis. The blue dashed line shows the Ecosystem Status Report boundary between eastern GOA and western GOA. The black solid lines show the International North Pacific Fisheries Commission statistical areas: Shumagin, Chirikof, Kodiak, Yakutat, and Southeast (SE).

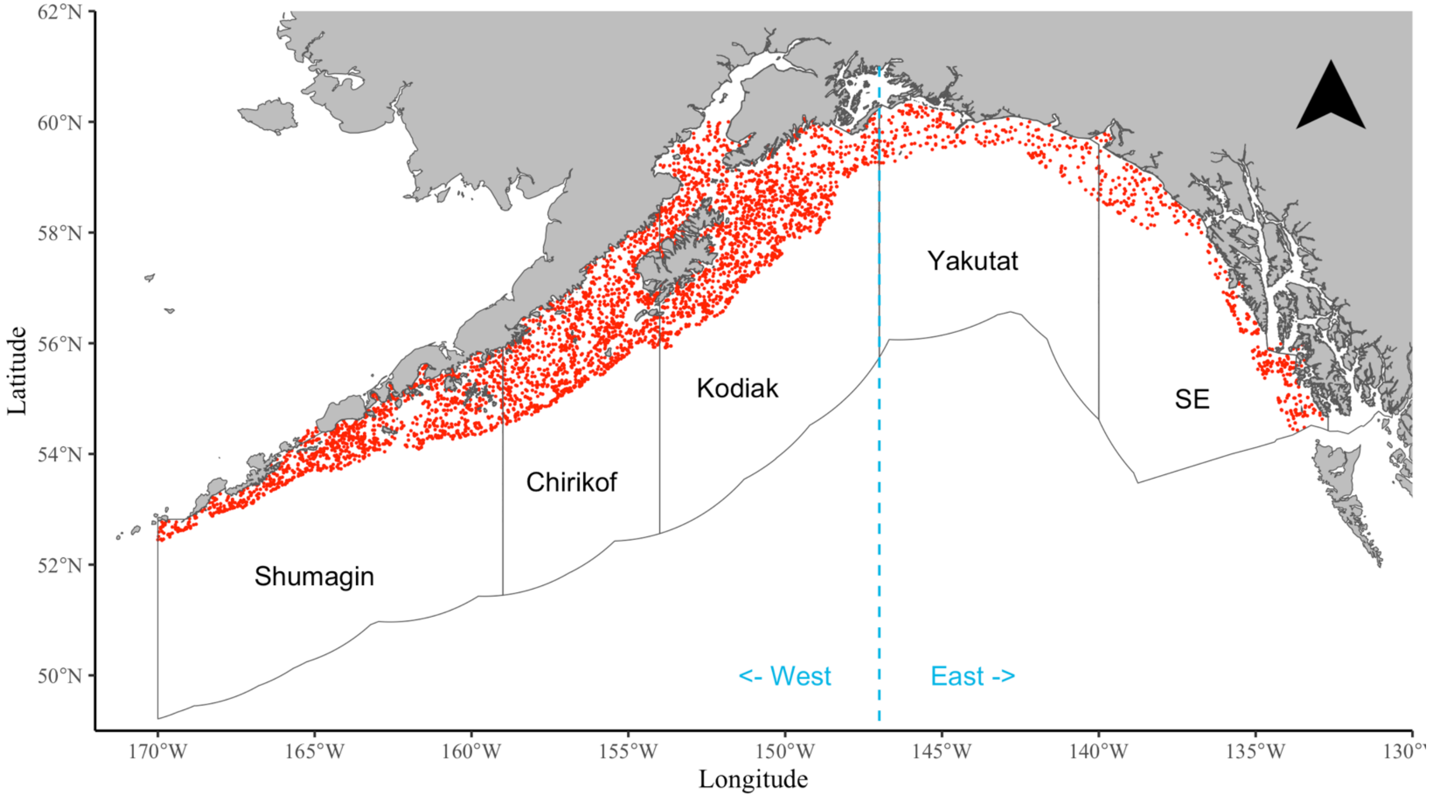


Figure 2. The percent weight of prey items in the diets of four groundfish predators, grouped by 10 cm length bins; the bin size is wider than 10 cm for the smallest and largest predator size classes due to low sample size. Prey groups are depicted in shades of blue for fishes and shades of red for invertebrates. Species were aggregated into taxonomic or functional groups based on sample size and ecological relevance, which is described in supplementary tables.

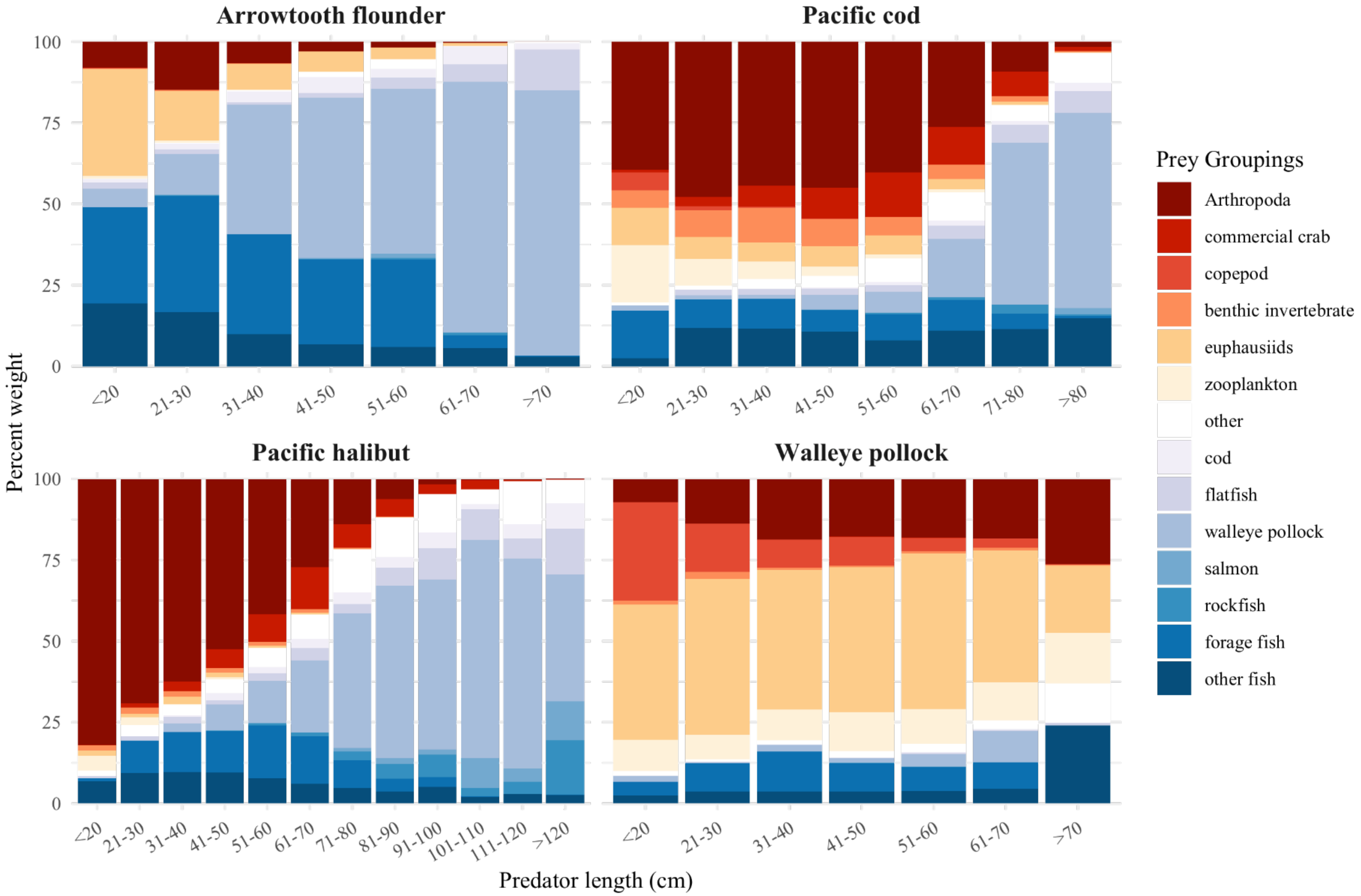
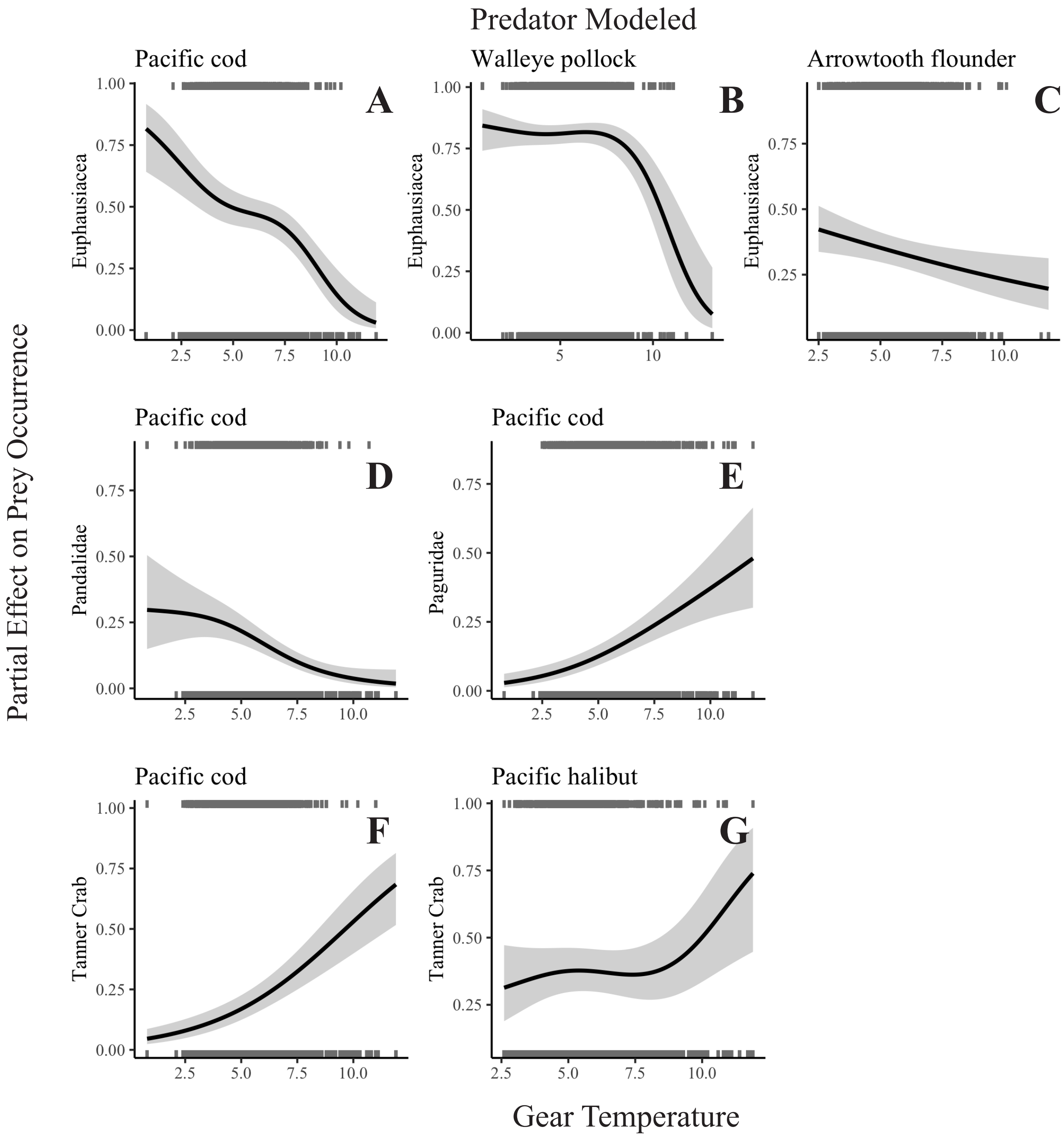


Figure 3. Partial effects of gear temperature on occurrence of prey in the stomachs of predators. (A, B, C) Partial effect of gear temperature on Euphausiacea occurrence in cod, walleye pollock, and arrowtooth flounder stomachs. (D) Partial effect of gear temperature on Pandalidae occurrence in cod stomachs. (E) Partial effect of gear temperature on Paguridae occurrence in cod stomachs. (F, G) Partial effect of gear temperature on tanner crab occurrence in the stomach of cod and halibut.



Supplementary Tables

Supplementary 1. Predator length bins for bottom trawl sampling. For a given predator, at each station, up to 5 individuals from each size category were sampled for stomach contents analysis.

	Fork Length (cm)			
Predator Name	**Bin 1**	**Bin 2**	**Bin 3**	**Bin 4**
Walleye Pollock	1-24	25-39	40-54	55+
Pacific Cod	1-29	30-44	45-59	60+
Arrowtooth Flounder	1-29	30-49	50+	
Pacific Halibut	1-39	40-69	70+	

Supplementary 2. Prey grouping based on taxonomic and functional groups. Unid = unidentified

Category	Prey Names	
Arthropoda	Anomura	Brachyura
	Caprellidae	Caridea
	Crangonidae	Crustacea
	Decapoda	*Hippolytidae*
	Lithodidae	*Majidae*
	Paguridae	*Pandalidae*
Commercial Crab	*Chionoecetes bairdi*	*Chionoecetes opilio*
	Chionoecetes sp.	*Paralithodes camtschaticus*
Copepod	Copepoda	
Benthic Invertebrate	Annelida	Chaetognatha
	Isopoda	Polychaeta
Euphausiids	Euphausiacea	
Zooplankton	Amphipoda	Appendicularia
	Cumacea	Fish Eggs
	Gammaridea	*Hyperiidea*
	Mysidacea	Eggs unid.
Other	Aves	Bivalvia
	Cephalopoda	Clypeasteroida
	Cnidaria	*Ctenophora sp.*
	Echiondea	Echinodermata
	Gastropoda	Holothuroidea
	Invertebrate	Mollusca
	Octopoda	Offal
	Ophiurida	Teuthida
	Thecosomata	Tunicata
	Unid.	
Cod	*Gadidae*	*Gadus macrocephalus*
Flatfish	*Atheresthes evermanni*	*Atheresthes stomias*
	Hippoglossoides ellassodon	*Hippoglossus stenolepis*
	Lepidopsetta bilineata	*Lepidopsetta polyxystra*
	Lepidopsetta sp.	*Liminda aspera*
	Pleuronectes quadrituberculatus	*Pleuronectiformes*
	Reinhardtius hippoglossoides	
Walleye pollock	*Gadus chalcogrammus*	

Salmon	*Salmonidae*	
Rockfish	*Sebastes sp.*	
Forage Fish	*Ammodytidae*	*Bathylagidae*
	Clupeidei	*Osmeridae*
Other Fish	*Agonidae*	*Anoplopoma fimbria*
	Cottidae	*Cyclopteridae*
	Hexagrammidae	*Macrouridae*
	Myctophidae	Non-teleost fish
	Pholidae	*Pleurogrammus monopterygius*
	Ragidae	*Sebastolobus sp.*
	Stichaeidae	Teleostei unid.
	Trichodon trichodon	*Zoarcidae*

Supplementary 3. Summary of GAM dredge selection. Columns show the response variable tested, predator modeled, explanatory parameters included in model indicated by (+), adjusted R^2, percent deviance, degrees of freedom, log likelihood, AIC, ΔAIC, and Akaike weight.

Response	Predator	Long/ Lat	Gear Depth	Gear Temp	Predator Length	Year	Adj R^2	% Deviance	df	logLik	AIC	delta	weight
Euphausiacea	Walleye pollock	+	+	+	+	+	0.20	0.12	51.00	-6249	12602	0.00	1.00
		+	+	NA	+	+	0.19	0.12	48.00	-6269	12636	34.14	0.00
		+	+	+	+	NA	0.17	0.10	37.00	-6375	12825	222.64	0.00
		+	NA	+	+	+	0.17	0.10	48.00	-6377	12851	248.89	0.00
		+	+	NA	+	NA	0.17	0.10	34.00	-6393	12856	253.88	0.00
		+	NA	NA	+	+	0.16	0.10	45.00	-6414	12920	317.71	0.00
		+	NA	+	+	NA	0.14	0.08	34.00	-6502	13074	472.40	0.00
		+	NA	NA	+	NA	0.14	0.08	31.00	-6535	13133	531.04	0.00
	Pacific Cod	+	+	+	+	+	0.15	0.10	47.00	-4668	9432	0.00	1.00
		+	+	NA	+	+	0.14	0.09	46.00	-4683	9459	27.50	0.00
		+	NA	+	+	+	0.14	0.09	46.00	-4689	9470	38.68	0.00
		+	NA	NA	+	+	0.14	0.09	44.00	-4702	9491	59.82	0.00
		+	+	+	+	NA	0.11	0.07	34.00	-4795	9659	227.89	0.00
		+	+	NA	+	NA	0.11	0.07	32.00	-4802	9668	236.51	0.00
		+	NA	+	+	NA	0.10	0.07	32.00	-4818	9702	270.68	0.00
		+	NA	NA	+	NA	0.10	0.07	30.00	-4825	9710	278.35	0.00
	Arrowtooth Flounder	+	+	+	+	+	0.35	0.23	49.00	-4956	10012	0.00	0.92
		+	+	NA	+	+	0.35	0.22	48.00	-4959	10017	4.76	0.08
		+	+	+	+	NA	0.32	0.20	35.00	-5113	10298	285.92	0.00
		+	+	NA	+	NA	0.32	0.20	34.00	-5118	10305	293.43	0.00
		+	NA	+	+	+	0.28	0.17	48.00	-5303	10704	691.60	0.00
		+	NA	NA	+	+	0.27	0.17	45.00	-5322	10735	722.79	0.00
		+	NA	+	+	NA	0.24	0.14	35.00	-5472	11014	1002.38	0.00
		+	NA	NA	+	NA	0.23	0.14	32.00	-5490	11045	1033.04	0.00
Walleye pollock	Pacific halibut	+	+	+	+	+	0.36	0.27	48.00	-2098	4293	0.00	1.00
		+	+	NA	+	+	0.35	0.26	46.00	-2108	4309	15.56	0.00
		+	NA	+	+	+	0.35	0.26	46.00	-2112	4317	23.32	0.00
		+	+	+	+	NA	0.34	0.25	35.00	-2145	4362	69.06	0.00
		+	+	NA	+	NA	0.33	0.25	32.00	-2158	4381	87.87	0.00

		+	NA	NA	+	+	0.33	0.25	43.00	-2151	4389	95.31	0.00
		+	NA	+	+	NA	0.32	0.24	32.00	-2182	4430	136.58	0.00
		+	NA	NA	+	NA	0.31	0.23	29.00	-2212	4484	190.61	0.00
	Pacific cod	+	+	+	+	+	0.37	0.32	48.00	-1490	3076	0.00	0.66
		+	+	NA	+	+	0.37	0.32	46.00	-1493	3078	1.35	0.33
		+	NA	+	+	+	0.36	0.31	45.00	-1497	3085	8.32	0.01
		+	NA	NA	+	+	0.36	0.31	43.00	-1507	3101	24.75	0.00
		+	+	+	+	NA	0.33	0.28	34.00	-1565	3199	122.38	0.00
		+	+	NA	+	NA	0.32	0.28	31.00	-1576	3216	139.21	0.00
		+	NA	+	+	NA	0.32	0.27	31.00	-1583	3230	153.32	0.00
		+	NA	NA	+	NA	0.31	0.27	29.00	-1594	3247	170.92	0.00
	Arrowtooth flounder	+	+	+	+	+	0.38	0.30	49.00	-2740	5579	0.00	0.96
		+	+	NA	+	+	0.38	0.30	47.00	-2745	5586	6.21	0.04
		+	NA	+	+	+	0.38	0.29	47.00	-2768	5633	53.20	0.00
		+	NA	NA	+	+	0.37	0.29	45.00	-2783	5656	76.74	0.00
		+	+	+	+	NA	0.29	0.22	35.00	-3045	6162	582.24	0.00
		+	+	NA	+	NA	0.29	0.21	32.00	-3061	6187	607.89	0.00
		+	NA	+	+	NA	0.28	0.21	34.00	-3086	6240	660.98	0.00
		+	NA	NA	+	NA	0.26	0.20	31.00	-3134	6332	752.78	0.00
Pandalidae	Walleye pollock	+	+	+	+	+	0.32	0.25	49.00	-2812	5724	0.00	0.90
		+	+	NA	+	+	0.31	0.25	46.00	-2818	5729	4.44	0.10
		+	+	+	+	NA	0.30	0.24	35.00	-2862	5795	71.03	0.00
		+	+	NA	+	NA	0.30	0.23	32.00	-2867	5800	75.37	0.00
		+	NA	+	+	+	0.30	0.23	46.00	-2875	5842	117.26	0.00
		+	NA	NA	+	+	0.29	0.22	45.00	-2905	5901	176.96	0.00
		+	NA	+	+	NA	0.27	0.21	32.00	-2947	5960	235.14	0.00
		+	NA	NA	+	NA	0.27	0.21	31.00	-2969	6001	276.65	0.00
	Pacific cod	+	+	+	+	+	0.28	0.18	49.00	-4611	9322	0.00	1.00
		+	+	+	+	NA	0.27	0.18	35.00	-4640	9352	30.20	0.00
		+	+	NA	+	+	0.27	0.18	47.00	-4634	9363	41.37	0.00
		+	+	NA	+	NA	0.26	0.17	33.00	-4678	9423	100.55	0.00
		+	NA	+	+	+	0.26	0.17	48.00	-4708	9512	189.92	0.00
		+	NA	+	+	NA	0.24	0.16	33.00	-4765	9599	276.92	0.00
		+	NA	NA	+	+	0.21	0.14	45.00	-4875	9841	519.34	0.00
		+	NA	NA	+	NA	0.20	0.13	31.00	-4919	9901	579.17	0.00

Pandalidae	Arrowtooth flounder	+	+	+	+	+	0.22	0.17	49.00	-2842	5783	0.00	0.50
		+	+	NA	+	+	0.22	0.17	47.00	-2844	5783	0.03	0.50
		+	+	NA	+	NA	0.21	0.16	33.00	-2877	5821	38.48	0.00
		+	+	+	+	NA	0.21	0.16	35.00	-2876	5822	39.75	0.00
		+	NA	+	+	+	0.17	0.13	49.00	-2973	6045	262.51	0.00
		+	NA	+	+	NA	0.15	0.11	34.00	-3029	6128	345.59	0.00
		+	NA	NA	+	+	0.15	0.11	46.00	-3033	6158	375.84	0.00
		+	NA	NA	+	NA	0.14	0.10	32.00	-3066	6198	415.20	0.00
Clupeidei	Pacific halibut	+	+	NA	+	+	0.45	0.42	36.00	-468	1009	0.00	0.68
		+	+	+	+	+	0.45	0.42	37.00	-468	1011	2.01	0.25
		+	NA	+	+	+	0.46	0.43	47.00	-460	1014	5.01	0.06
		+	NA	NA	+	+	0.46	0.43	45.00	-462	1015	6.87	0.02
		+	+	NA	+	NA	0.44	0.41	34.00	-477	1022	13.86	0.00
		+	+	+	+	NA	0.42	0.39	23.00	-491	1029	20.54	0.00
		+	NA	+	+	NA	0.42	0.39	21.00	-496	1036	27.09	0.00
		+	NA	NA	+	NA	0.41	0.38	18.00	-502	1042	33.56	0.00
	Arrowtooth flounder	+	NA	NA	+	+	0.38	0.35	42.00	-670	1425	0.00	0.41
		+	+	+	+	+	0.38	0.35	45.00	-667	1426	1.05	0.24
		+	NA	+	+	+	0.38	0.35	43.00	-670	1427	1.57	0.19
		+	+	NA	+	+	0.38	0.35	43.00	-670	1427	1.96	0.15
		+	+	+	+	NA	0.31	0.29	30.00	-732	1526	101.16	0.00
		+	NA	+	+	NA	0.31	0.29	29.00	-734	1527	101.97	0.00
		+	NA	NA	+	NA	0.30	0.28	26.00	-742	1538	112.96	0.00
		+	+	NA	+	NA	0.30	0.28	27.00	-742	1540	114.90	0.00
Osmerid	Pacific halibut	+	+	+	+	+	0.29	0.25	47.00	-1105	2305	0.00	0.84
		+	+	NA	+	+	0.29	0.25	44.00	-1110	2308	3.26	0.16
		+	NA	+	+	+	0.27	0.23	46.00	-1134	2361	56.95	0.00
		+	NA	NA	+	+	0.26	0.22	43.00	-1154	2395	90.37	0.00
		+	+	+	+	NA	0.24	0.21	33.00	-1173	2413	108.23	0.00
		+	+	NA	+	NA	0.23	0.20	30.00	-1184	2427	122.68	0.00
		+	NA	+	+	NA	0.19	0.16	30.00	-1238	2536	231.60	0.00
		+	NA	NA	+	NA	0.19	0.16	29.00	-1241	2540	235.63	0.00
	Arrowtooth flounder	+	+	+	+	+	0.24	0.18	48.00	-2889	5874	0.00	0.99
		+	+	NA	+	+	0.24	0.18	45.00	-2896	5884	9.84	0.01
		+	NA	+	+	+	0.24	0.18	46.00	-2902	5898	24.19	0.00

		+	NA	NA	+	+	0.23	0.17	44.00	-2919	5926	52.30	0.00
		+	+	+	+	NA	0.17	0.13	34.00	-3087	6244	370.01	0.00
		+	+	NA	+	NA	0.17	0.12	32.00	-3097	6258	384.58	0.00
		+	NA	+	+	NA	0.16	0.12	33.00	-3109	6285	410.88	0.00
		+	NA	NA	+	NA	0.16	0.12	30.00	-3115	6291	416.85	0.00
Tanner crab	Pacific halibut	+	+	+	+	+	0.25	0.19	49.00	-2222	4544	0.00	0.79
		+	+	NA	+	+	0.25	0.19	47.00	-2226	4547	2.66	0.21
		+	+	+	+	NA	0.22	0.16	35.00	-2285	4641	97.41	0.00
		+	NA	+	+	+	0.22	0.16	47.00	-2295	4685	141.27	0.00
		+	+	NA	+	NA	0.21	0.15	32.00	-2311	4687	142.96	0.00
		+	NA	NA	+	+	0.20	0.15	44.00	-2330	4749	205.44	0.00
		+	NA	+	+	NA	0.19	0.14	33.00	-2345	4756	212.11	0.00
		+	NA	NA	+	NA	0.16	0.12	29.00	-2419	4897	353.42	0.00
	Pacific cod	+	+	+	+	+	0.27	0.19	50.00	-3591	7283	0.00	1.00
		+	+	NA	+	+	0.27	0.19	49.00	-3611	7320	37.24	0.00
		+	+	NA	+	NA	0.24	0.17	35.00	-3692	7455	172.51	0.00
		+	+	+	+	NA	0.24	0.17	37.00	-3690	7456	173.38	0.00
		+	NA	+	+	+	0.22	0.16	48.00	-3757	7610	327.36	0.00
		+	NA	NA	+	+	0.22	0.15	46.00	-3779	7650	367.55	0.00
		+	NA	+	+	NA	0.21	0.14	34.00	-3816	7701	418.08	0.00
		+	NA	NA	+	NA	0.19	0.14	32.00	-3855	7775	491.83	0.00
Paguridae	Pacific halibut	+	+	+	+	+	0.34	0.22	50	-3567	7235	0.00	1.00
		+	NA	+	+	+	0.34	0.21	46	-3577	7248	13.23	0.00
		+	+	NA	+	+	0.33	0.21	47	-3578	7251	16.11	0.00
		+	NA	NA	+	+	0.33	0.21	43	-3589	7267	31.75	0.00
		+	+	+	+	NA	0.33	0.21	36	-3603	7278	42.64	0.00
		+	+	NA	+	NA	0.33	0.21	33	-3610	7287	52.57	0.00
		+	NA	+	+	NA	0.32	0.20	32	-3614	7294	58.99	0.00
		+	NA	NA	+	NA	0.32	0.20	30	-3625	7310	75.34	0.00
	Pacific cod	+	+	+	+	+	0.11	0.08	48	-4064	8225	0.00	1.00
		+	NA	+	+	+	0.10	0.07	45	-4085	8261	35.76	0.00
		+	+	NA	+	+	0.10	0.07	48	-4084	8264	38.79	0.00
		+	NA	NA	+	+	0.10	0.07	44	-4098	8286	60.92	0.00
		+	+	+	+	NA	0.10	0.07	35	-4112	8295	69.60	0.00
		+	+	NA	+	NA	0.09	0.06	34	-4126	8321	96.08	0.00

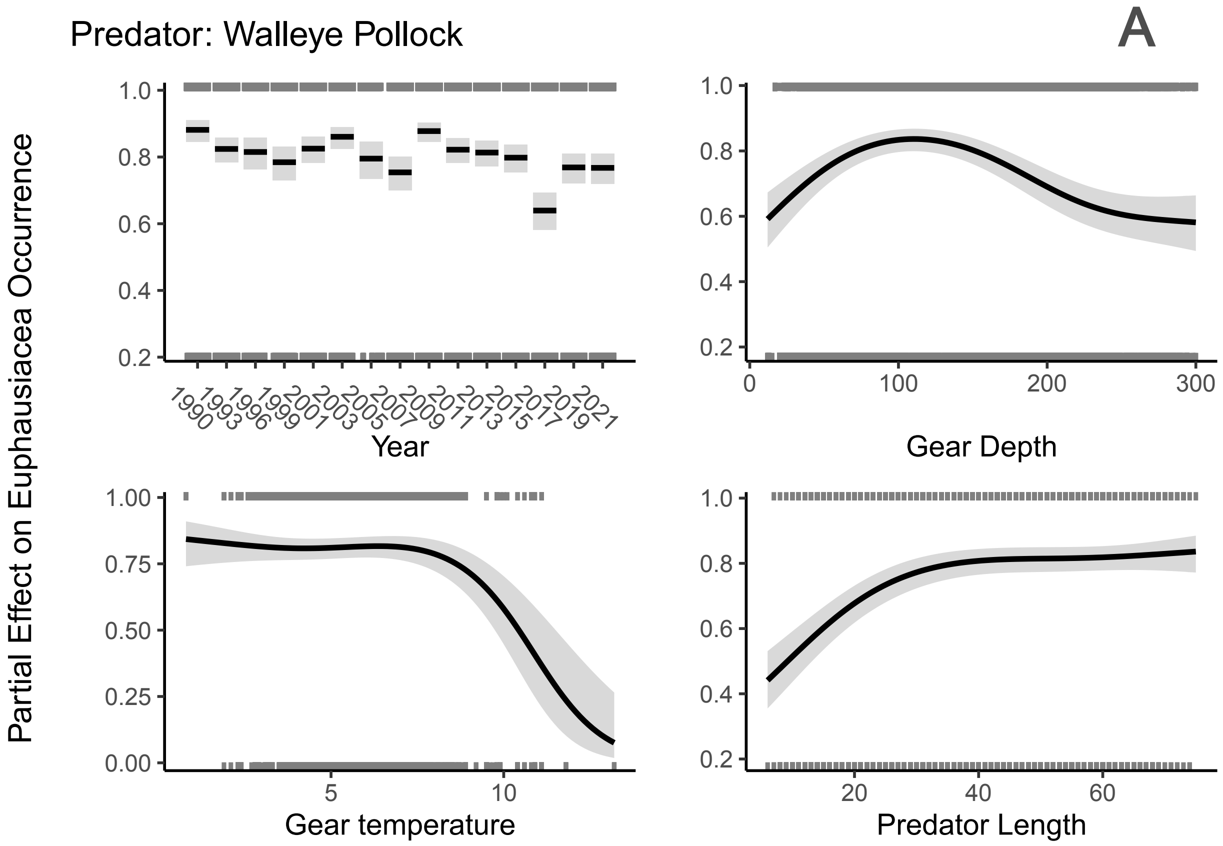
		+	NA	+	+	NA	0.09	0.06	32	-4128	8321	96.31	0.00
		+	NA	NA	+	NA	0.09	0.06	30	-4142	8346	121.25	0.00

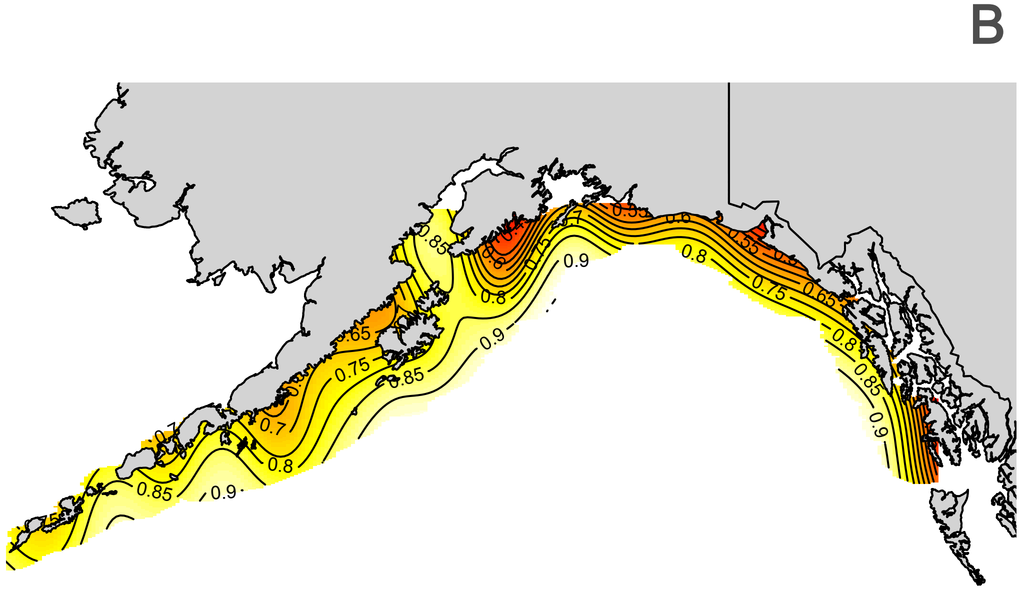
Appendix 1

GAM Models:
Partial Effects Plots

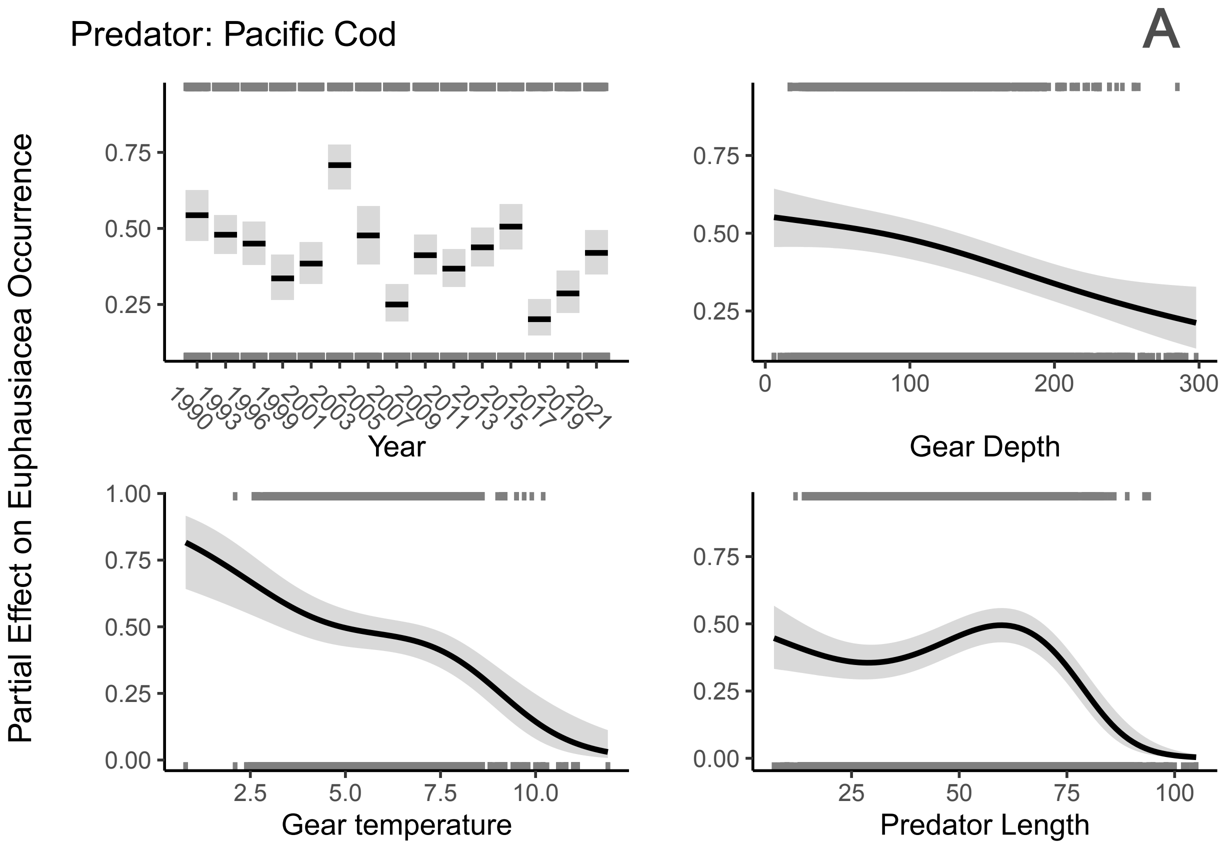
Appendix 1 contains partial effects plots for all covariates in each GAM model. Plots were produced with the 'mgcv' package functions 'visreg' and 'vis.gam.' A) Partial effects of year, gear depth, gear temperature, and predator length on probability of prey occurrence. The black line indicates model predictions, the grey band indicates 95% confidence intervals, and the black ticks at the top and bottom of the figure show observations. B) Spatial partial effect on probability of prey occurrence. Black bands indicate the model predictions in intervals of 0.05 probability of occurrence. Model predictions are plotted with 2.5% extrapolation from the data.

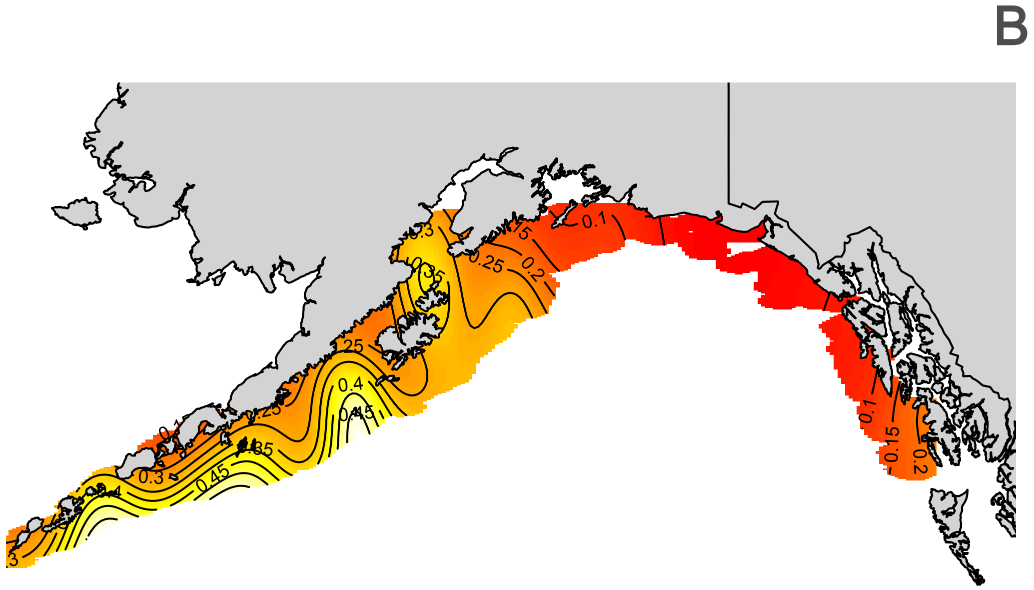
Model 1: Euphausiacea Prey



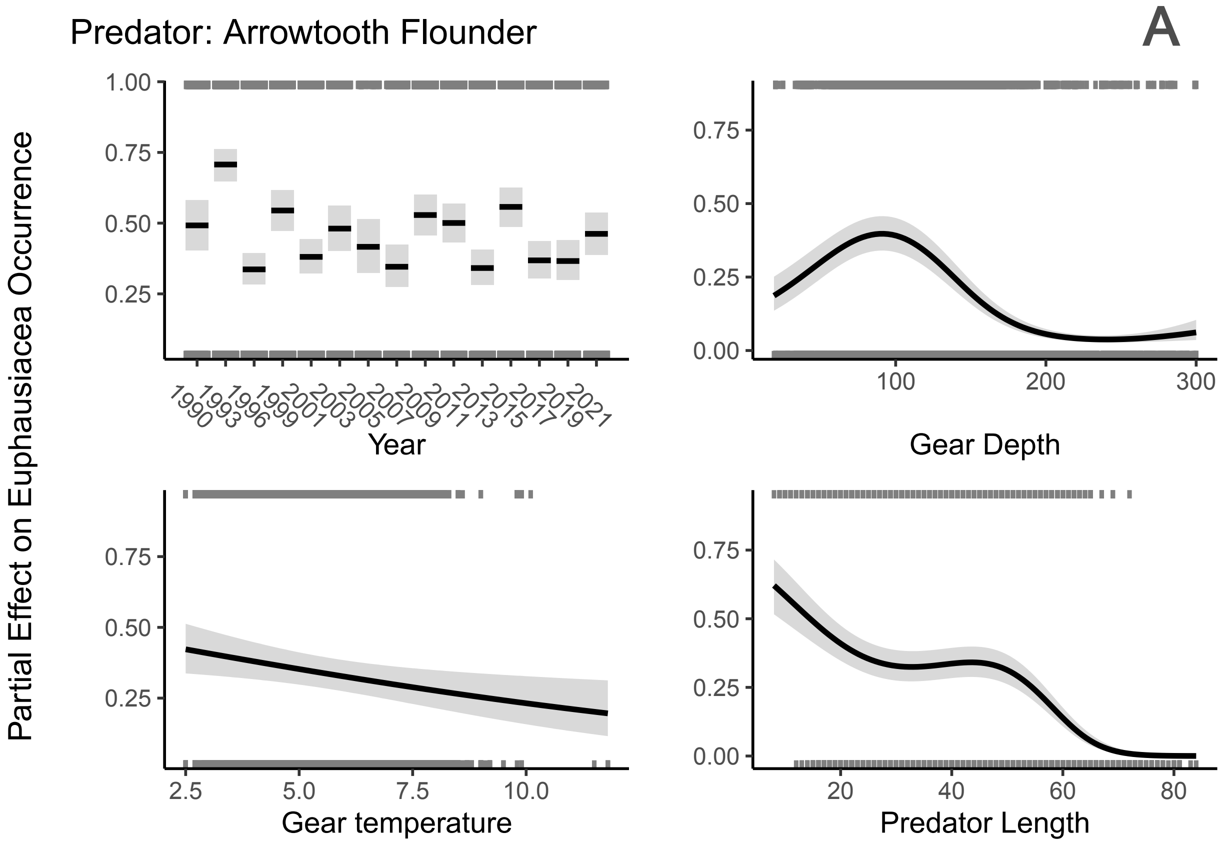


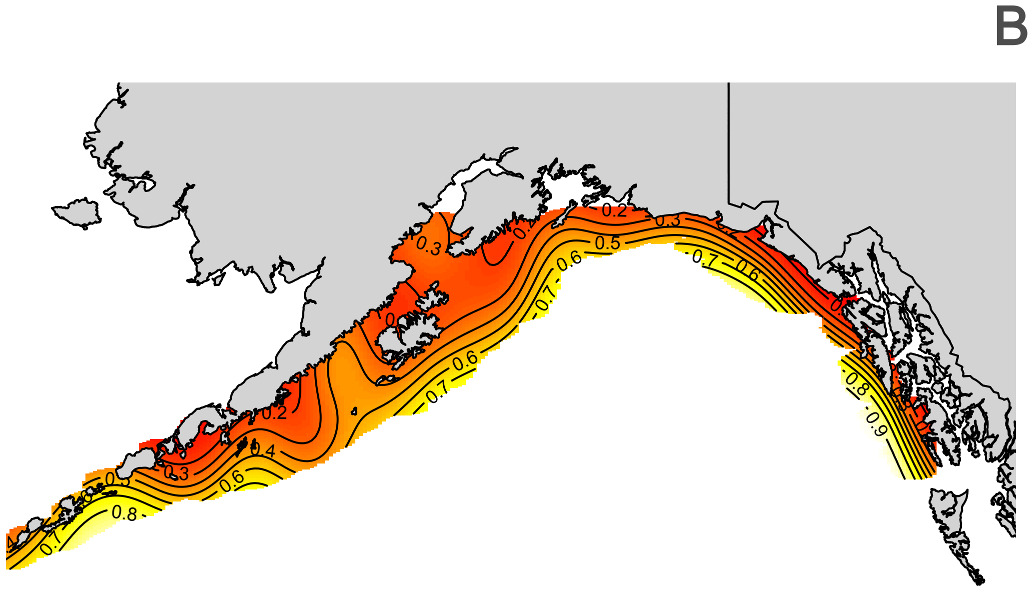
Model 1: Euphausiacea Prey



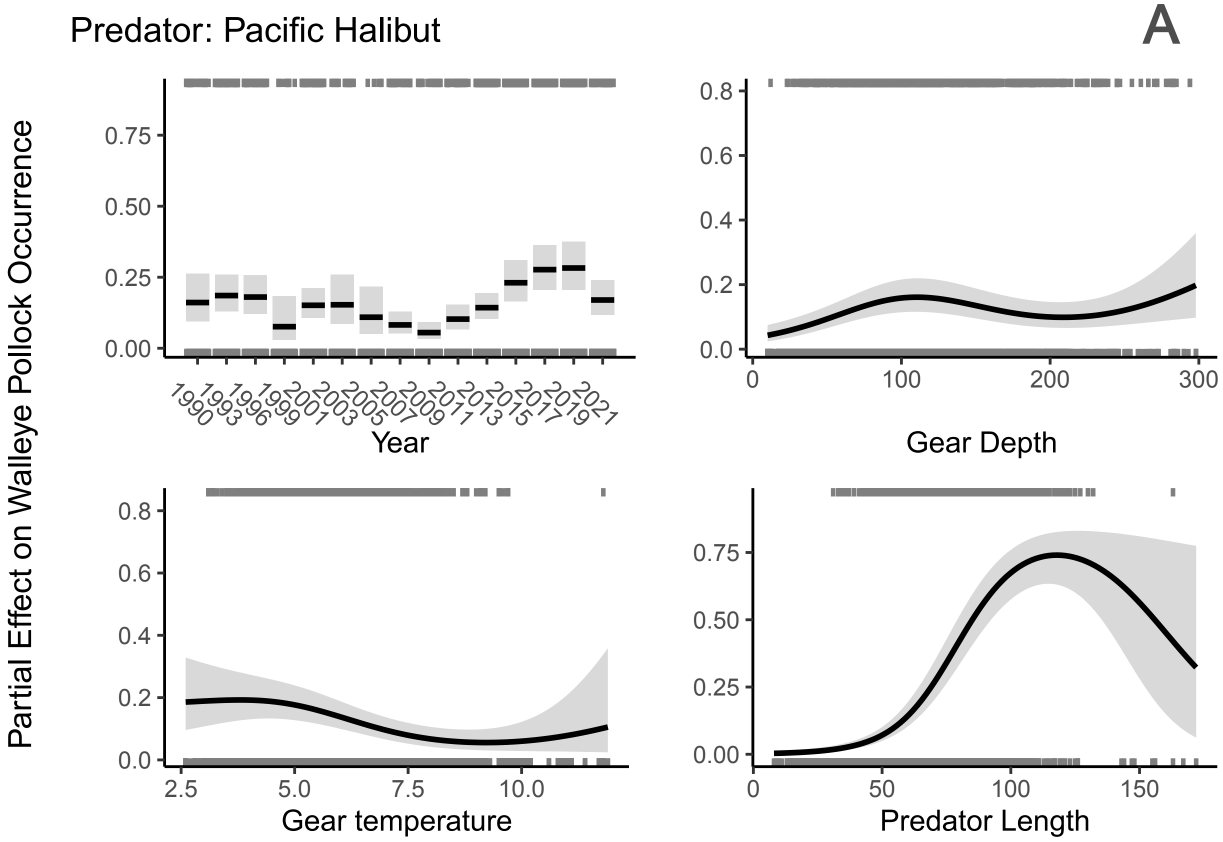


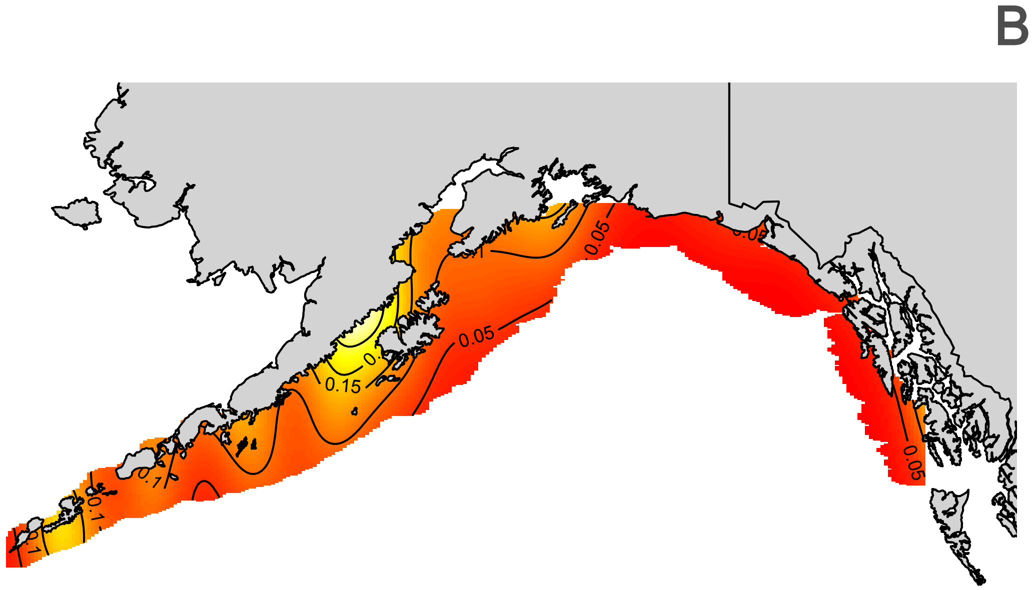
Model 1: Euphausiacea Prey



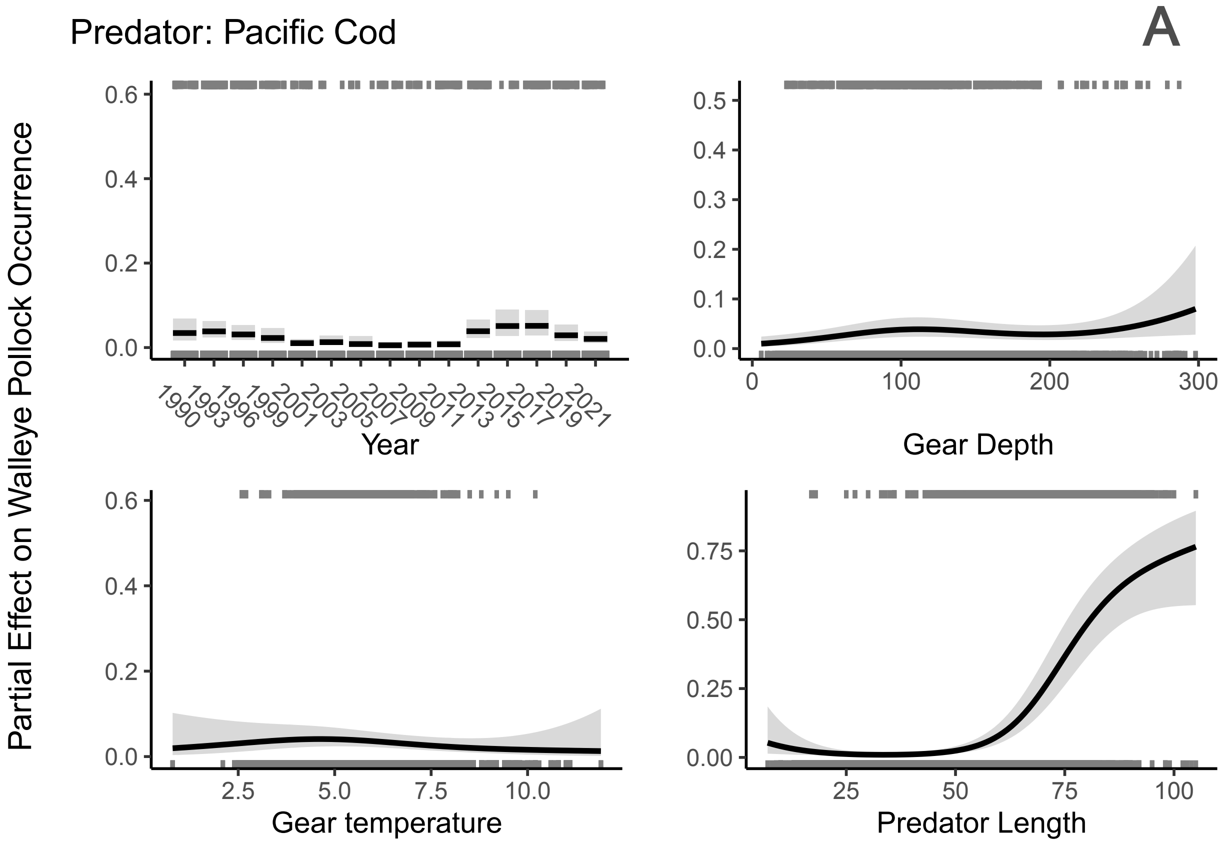


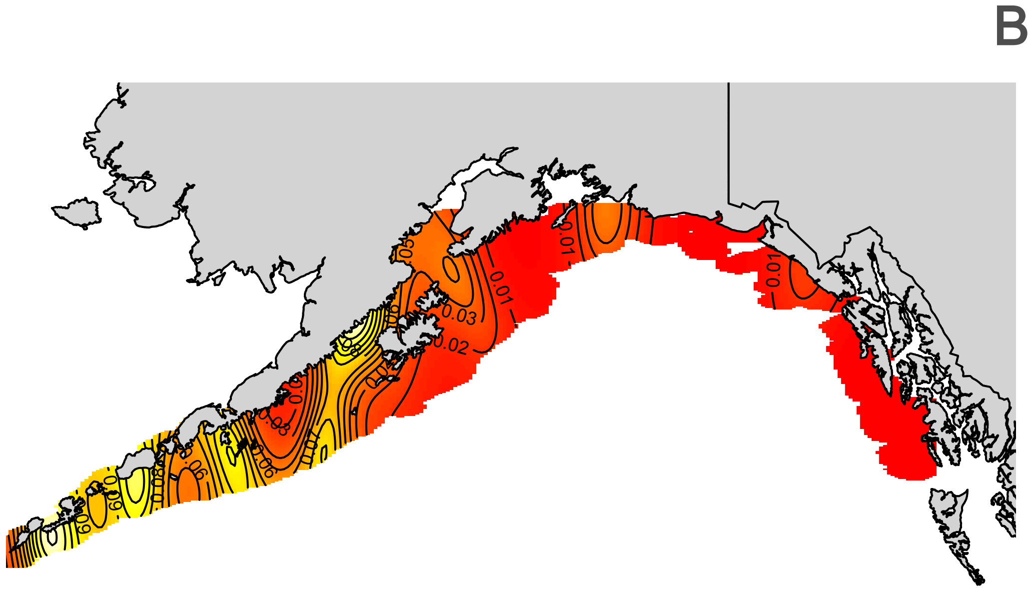
Model 2: Walleye Pollock Prey



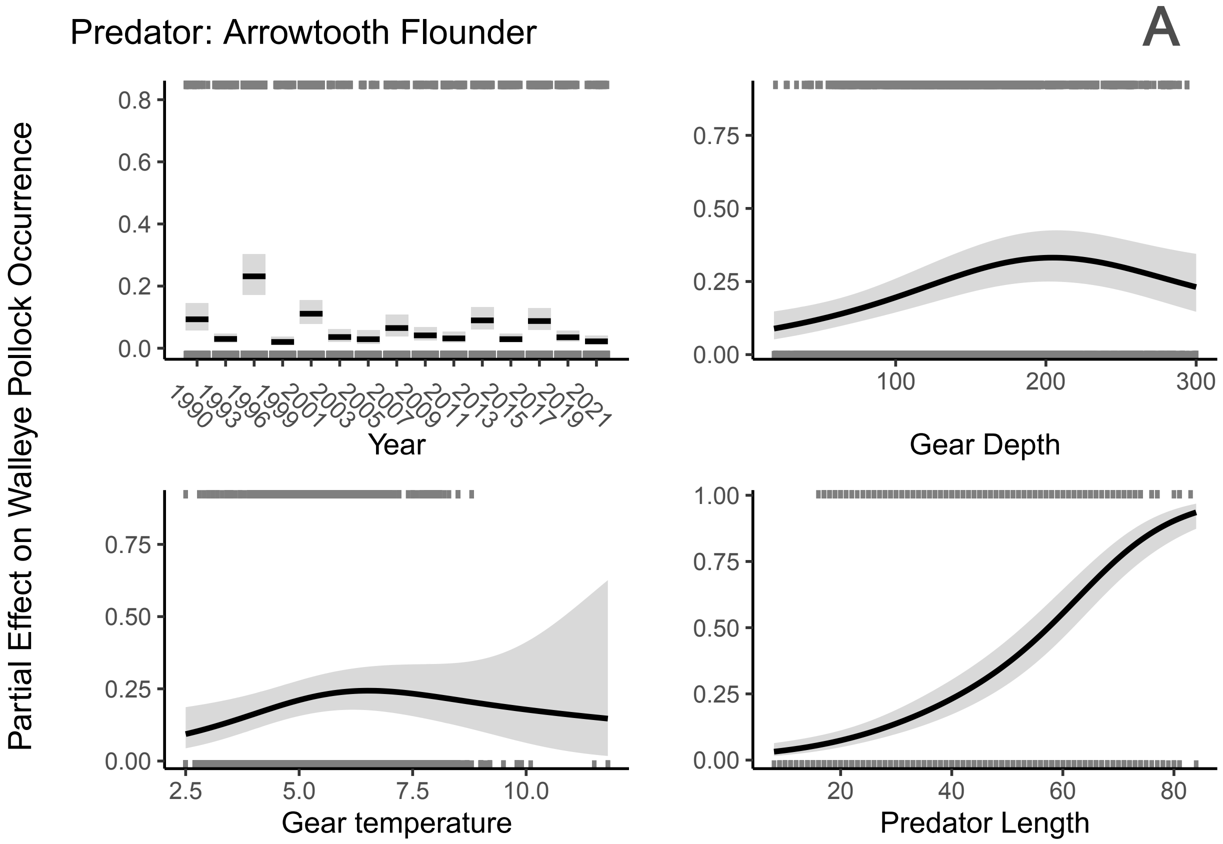


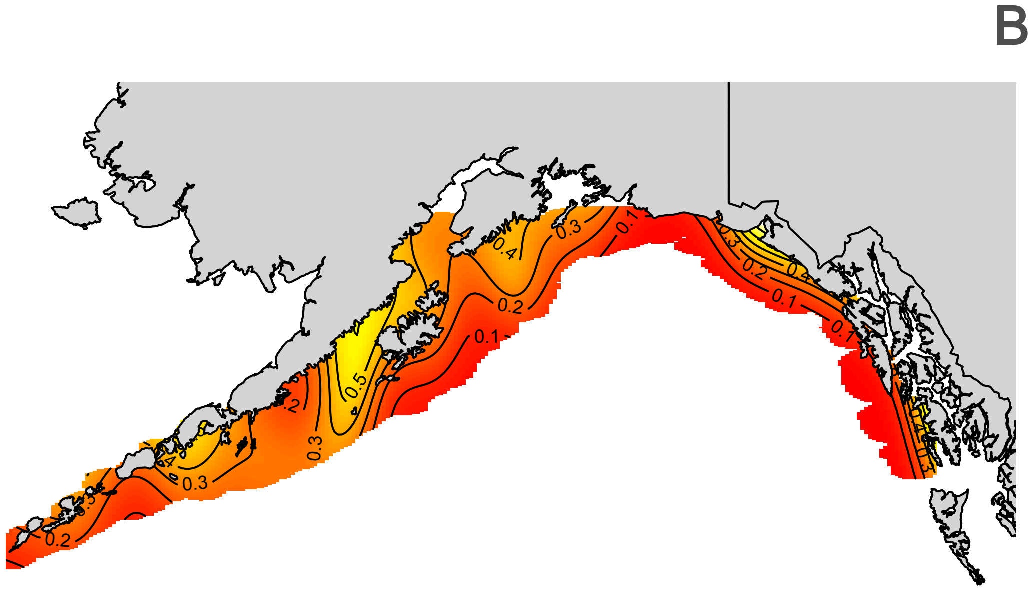
Model 2: Walleye Pollock Prey



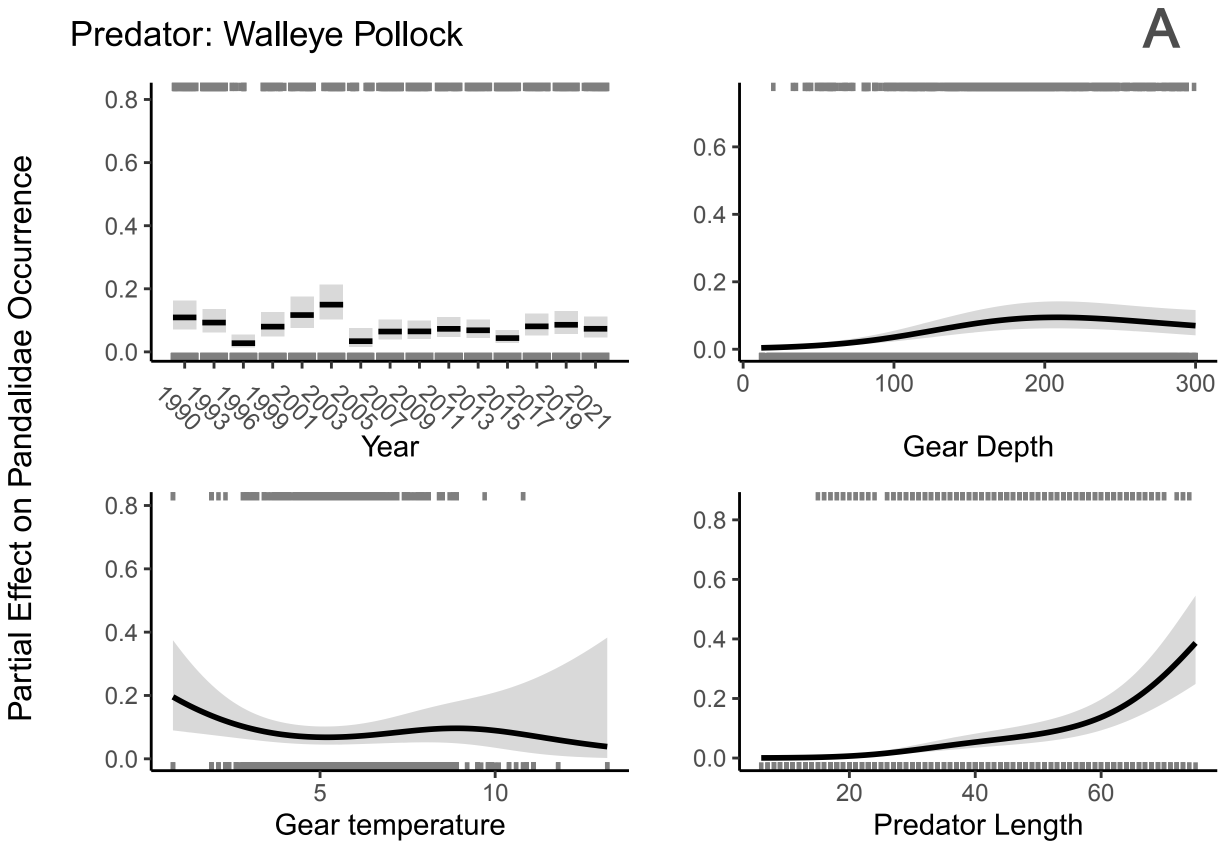


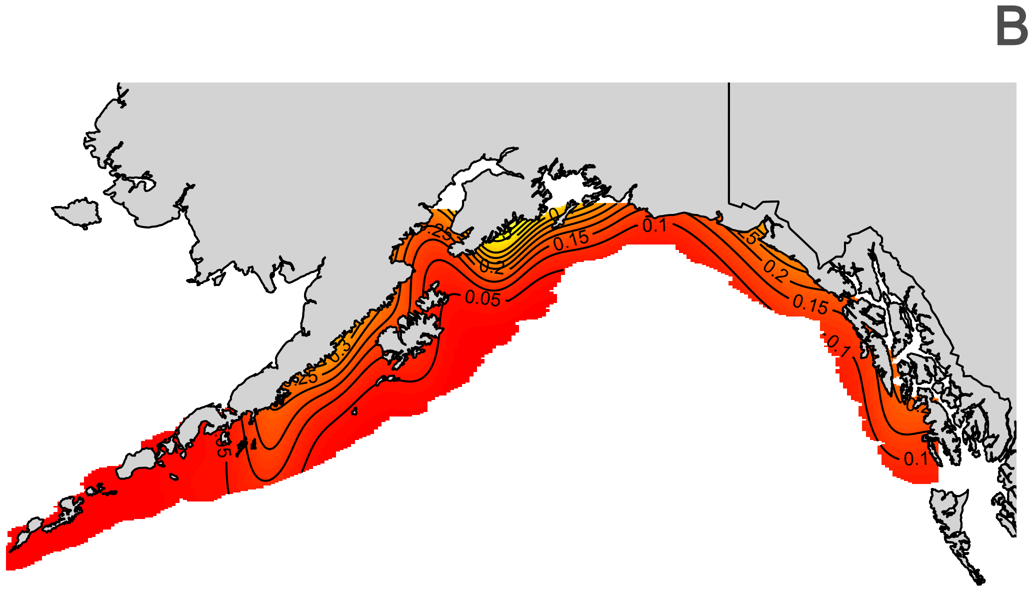
Model 2: Walleye Pollock Prey





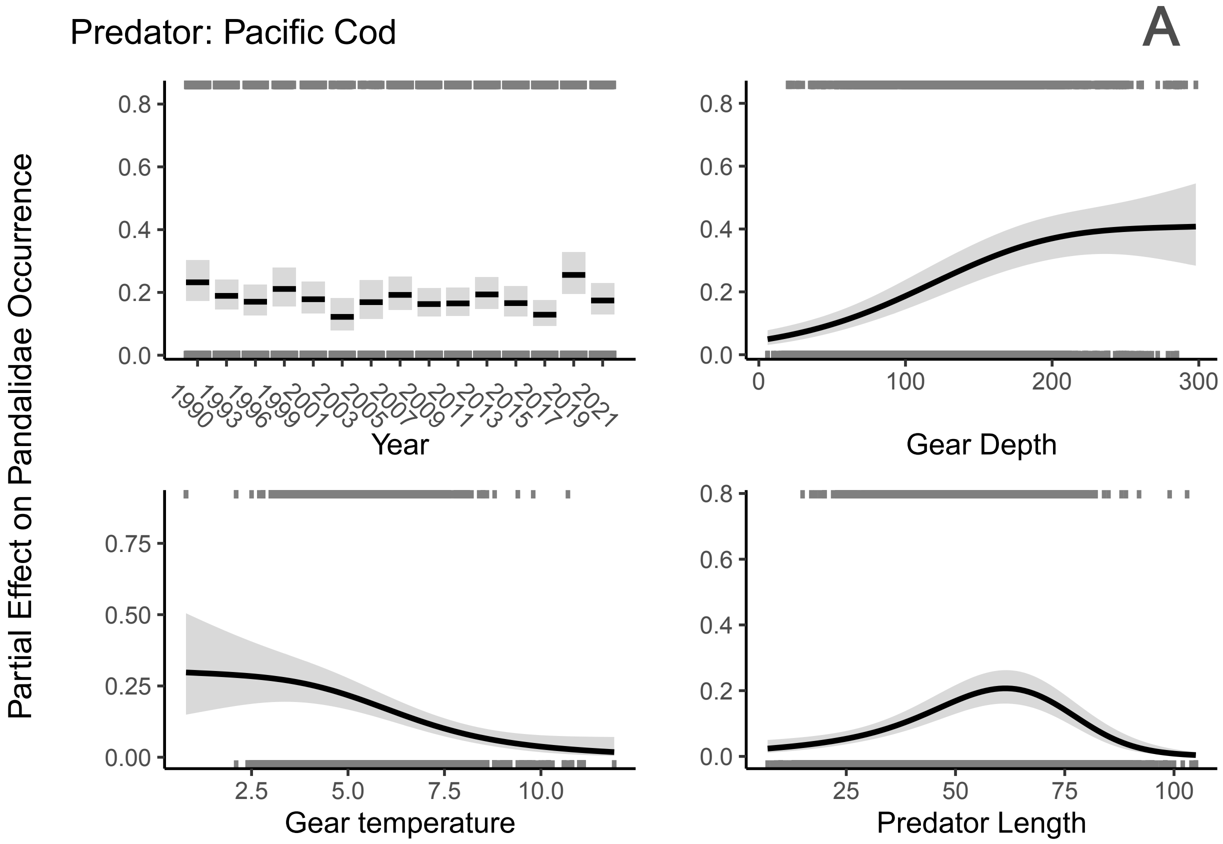
Model 3: Pandalidae Prey

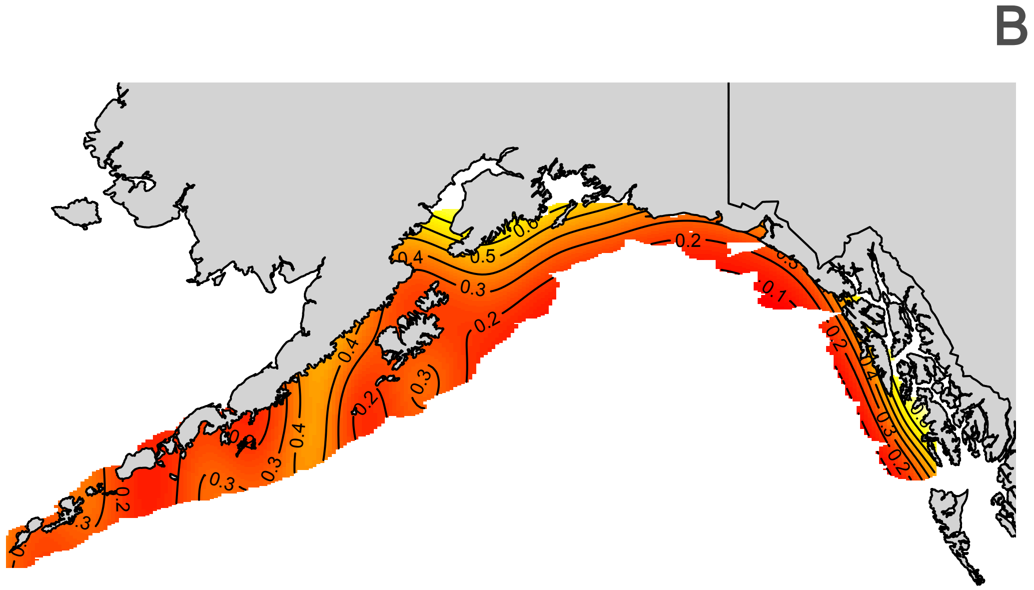




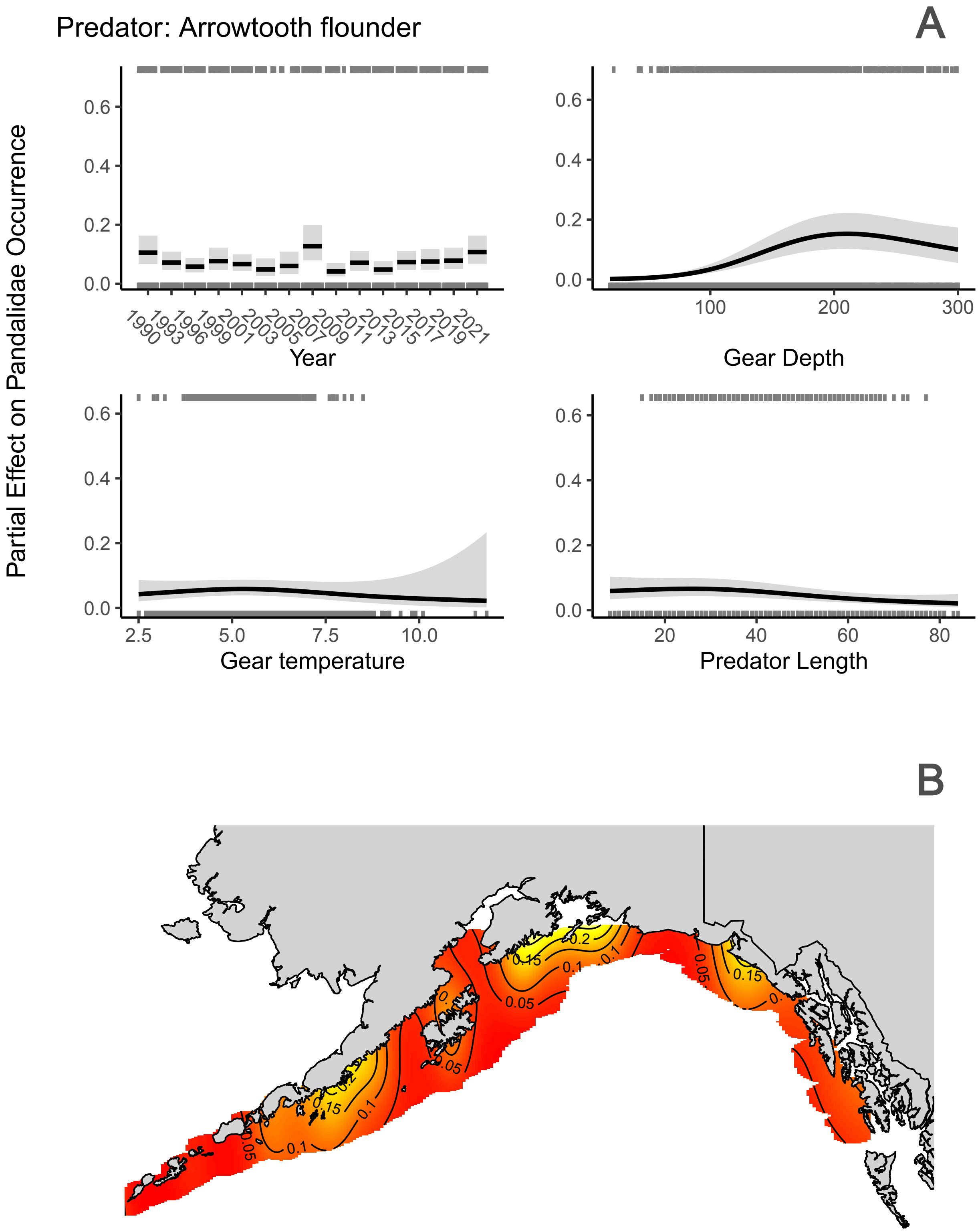
Model 3: Pandalidae Prey

Predator: Pacific Cod

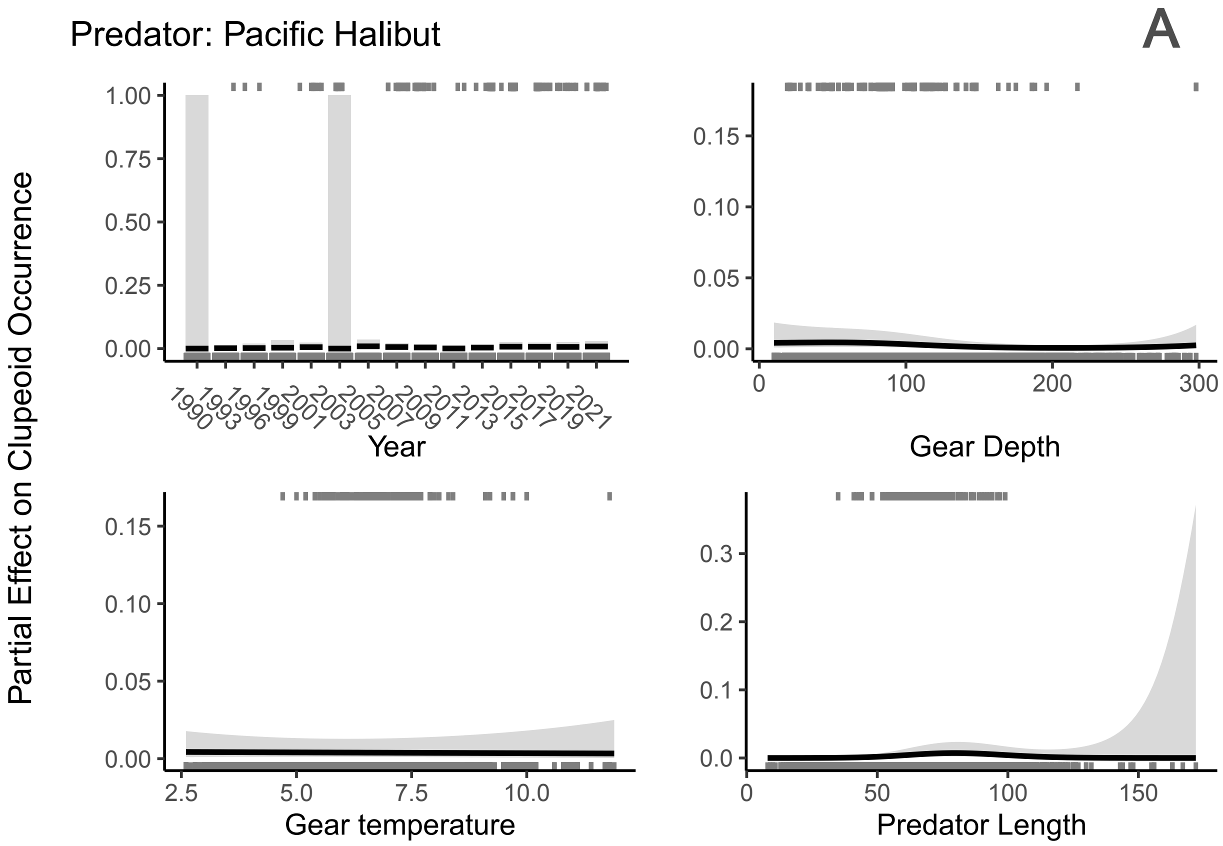


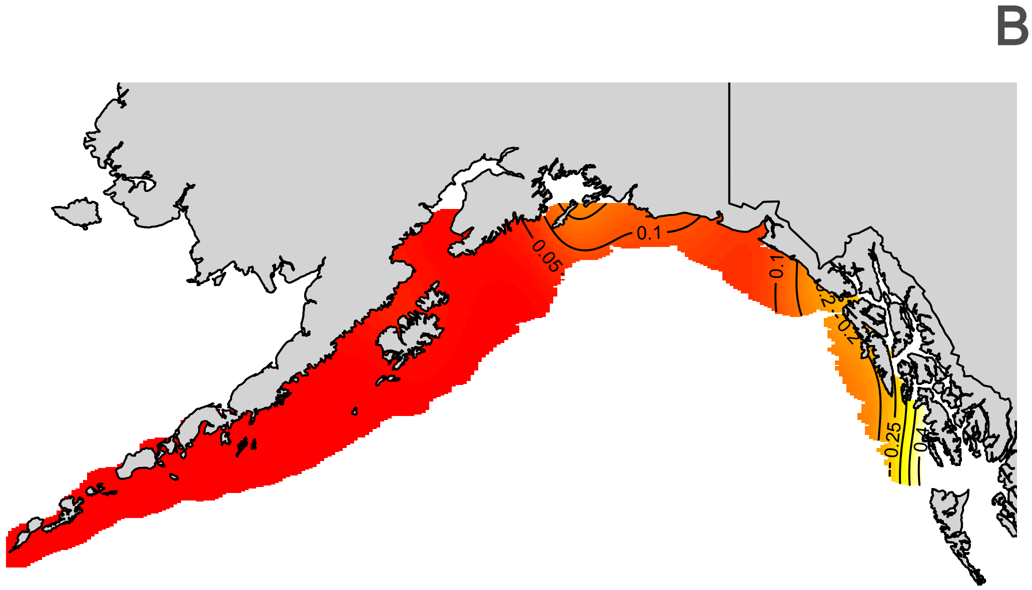


Model 3: Pandalidae Prey

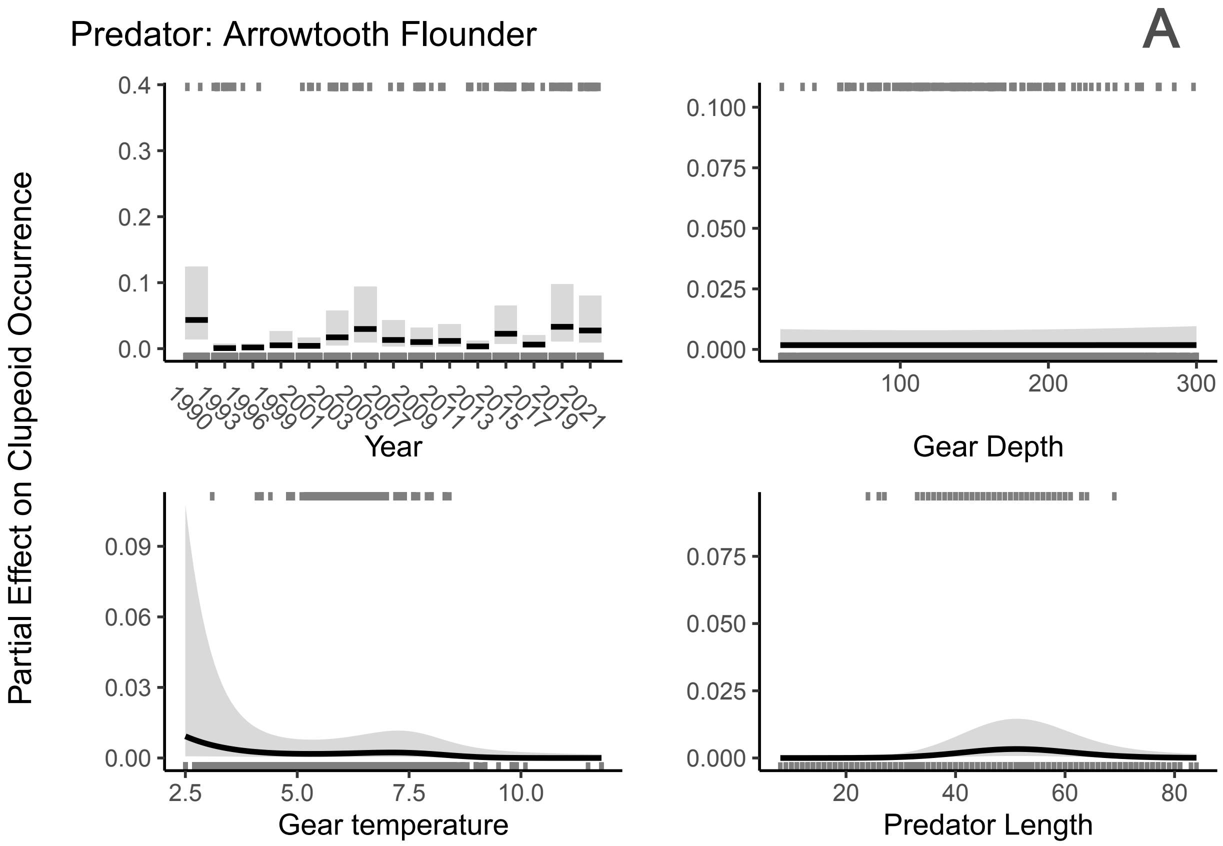


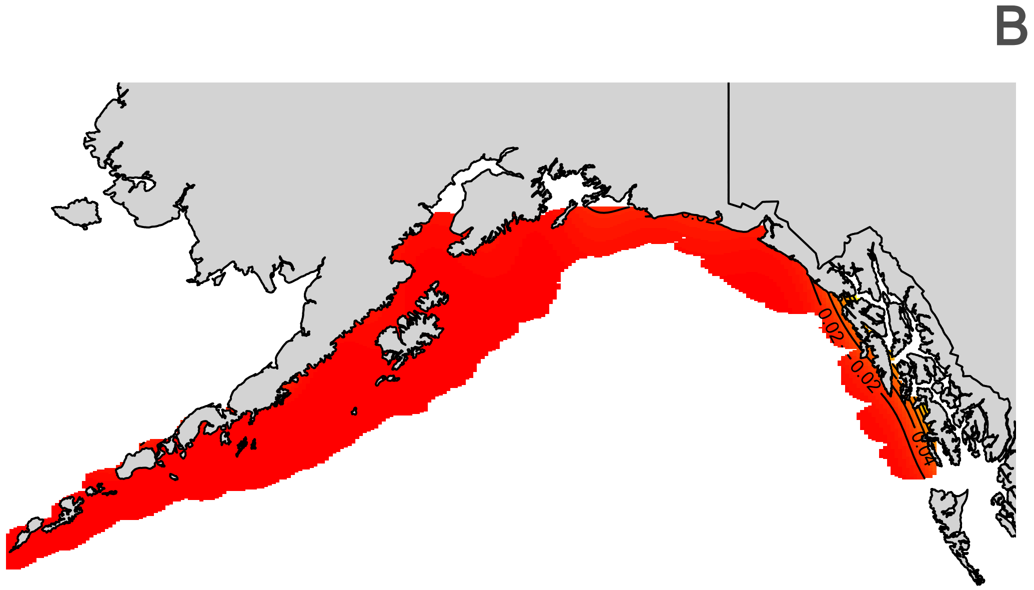
Model 4: Clupeoid Prey



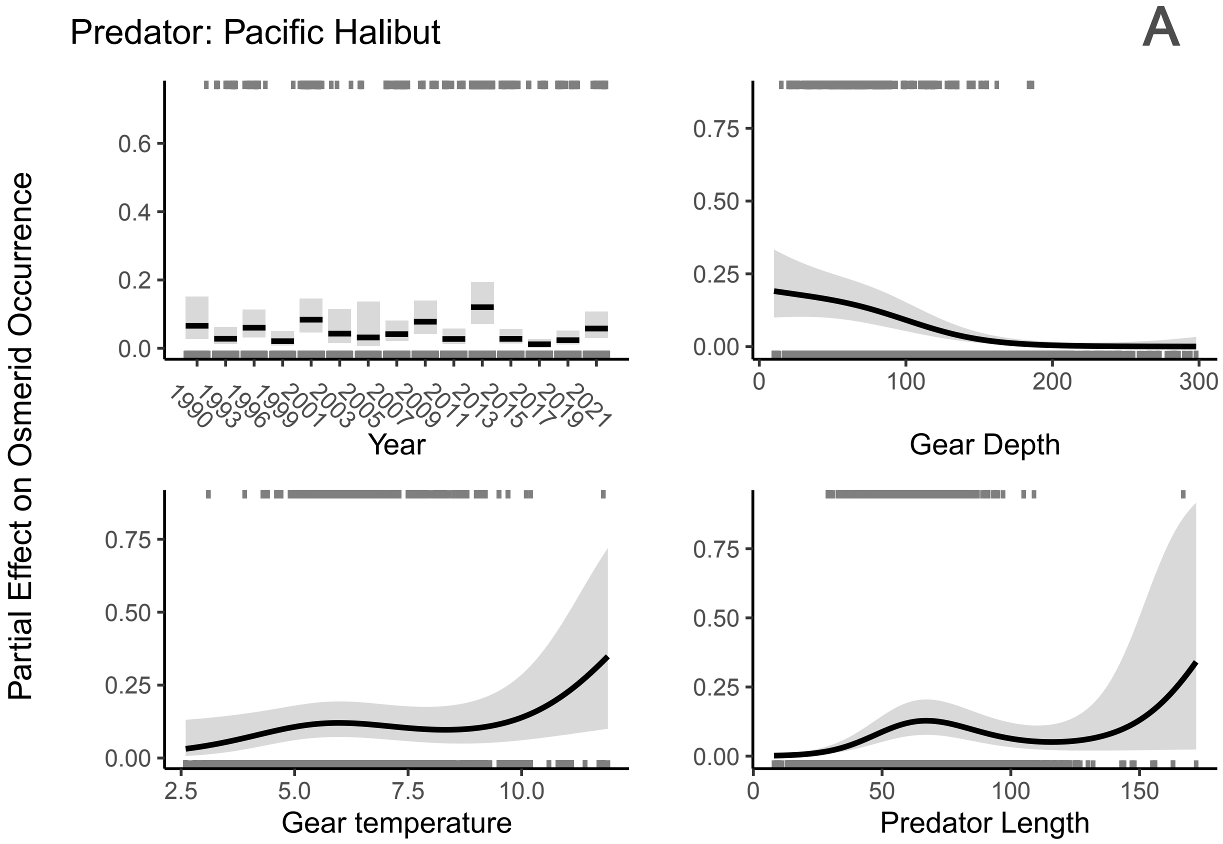


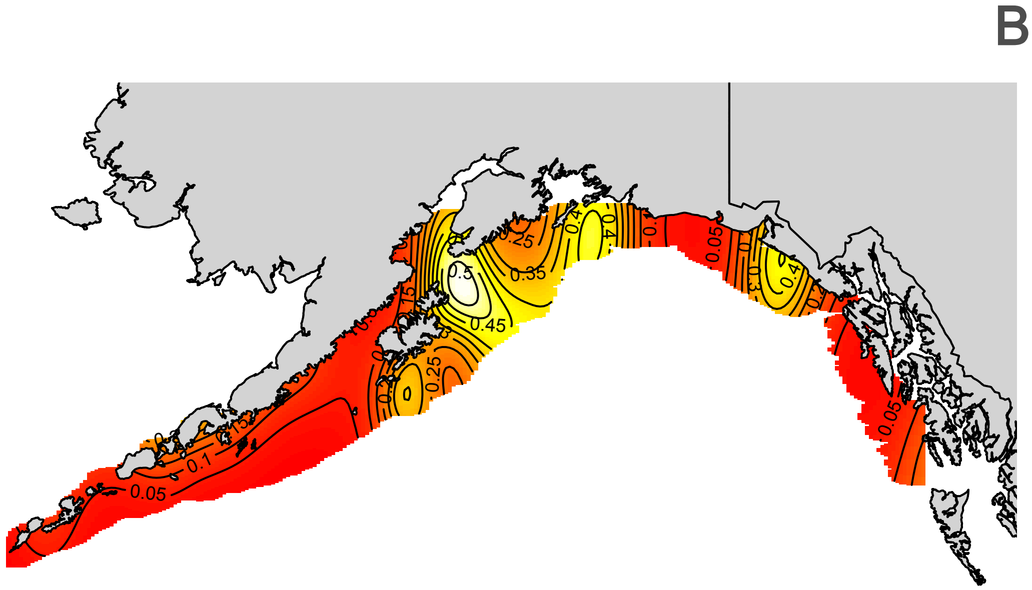
Model 4: Clupeoid Prey



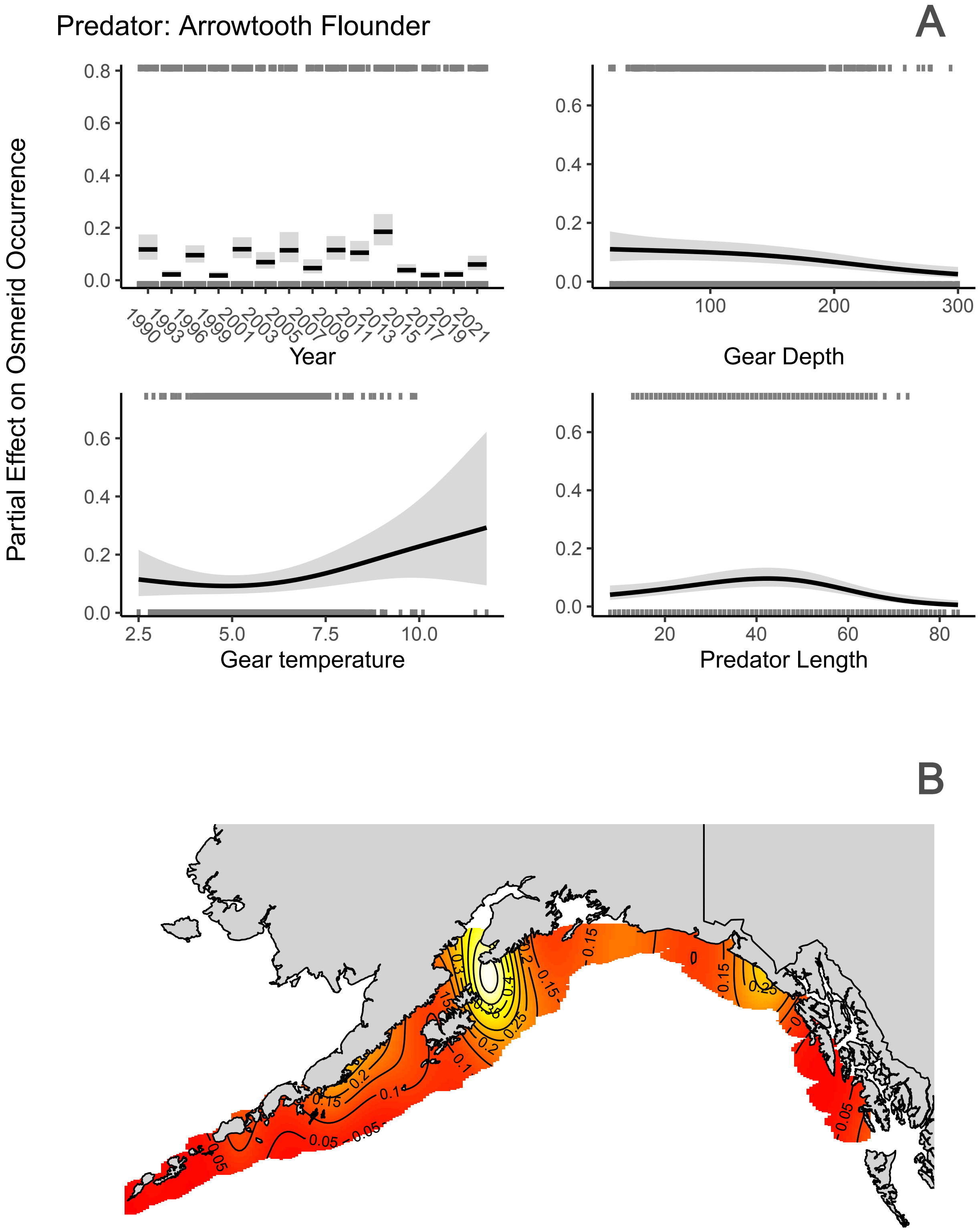


Model 5: Osmerid Prey

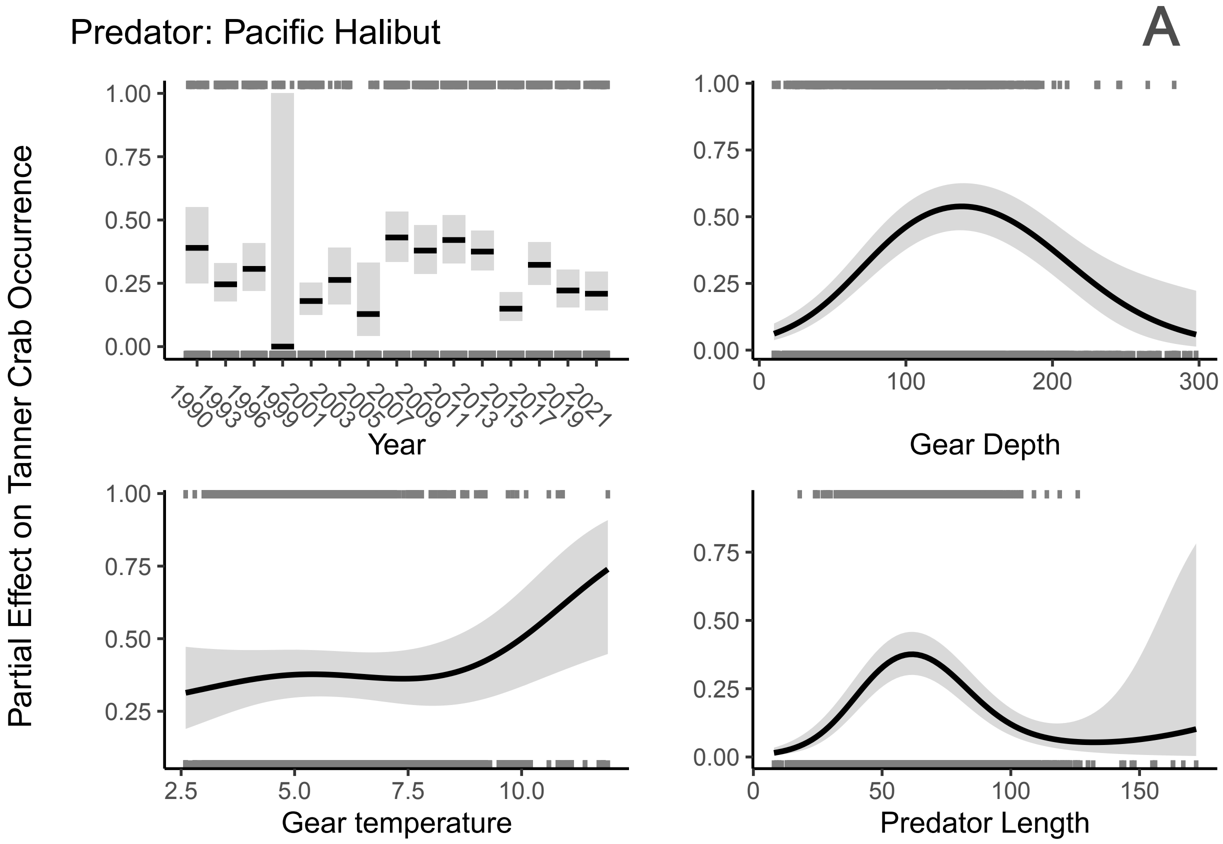


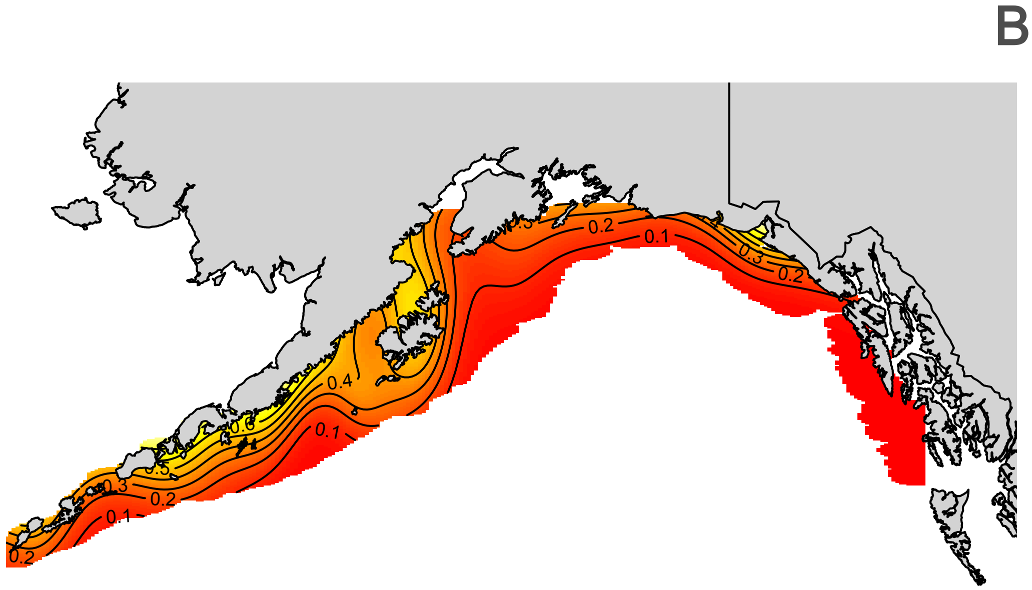


Model 5: Osmerid Prey

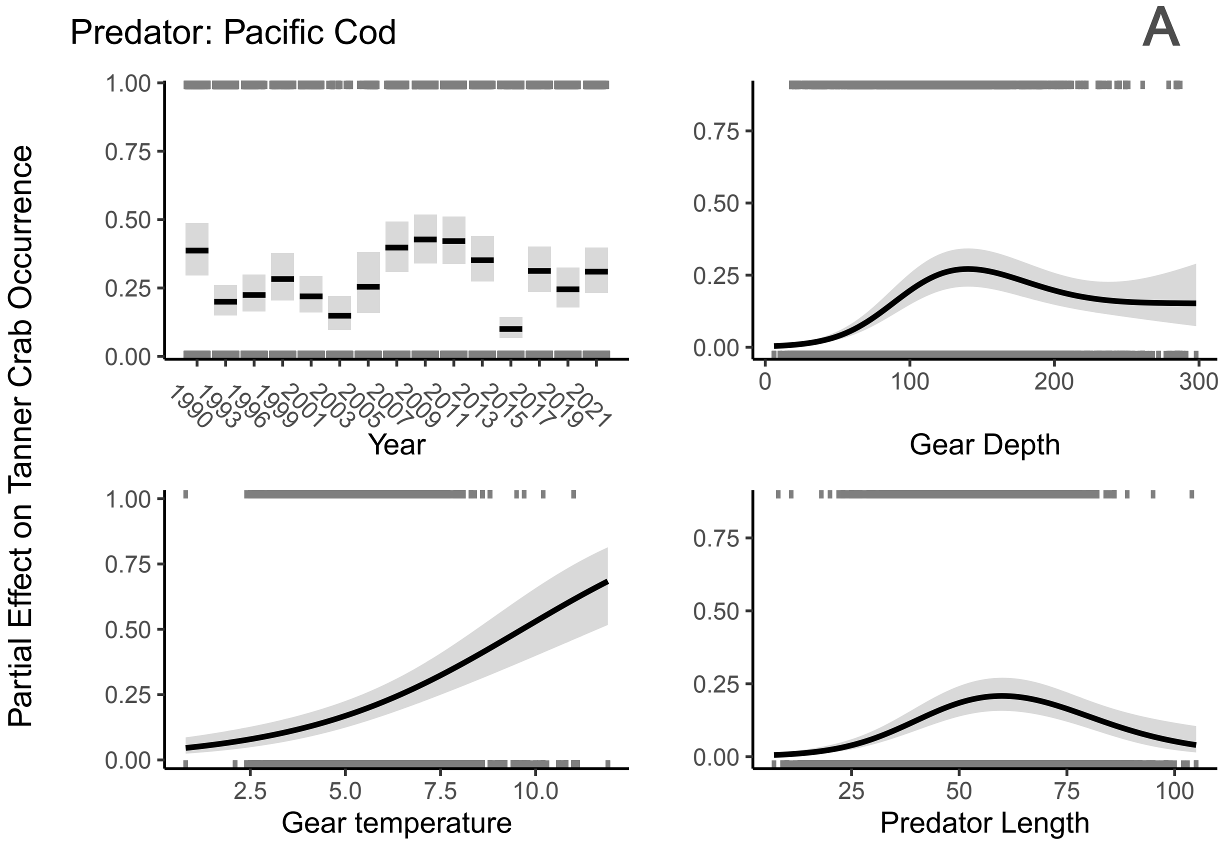


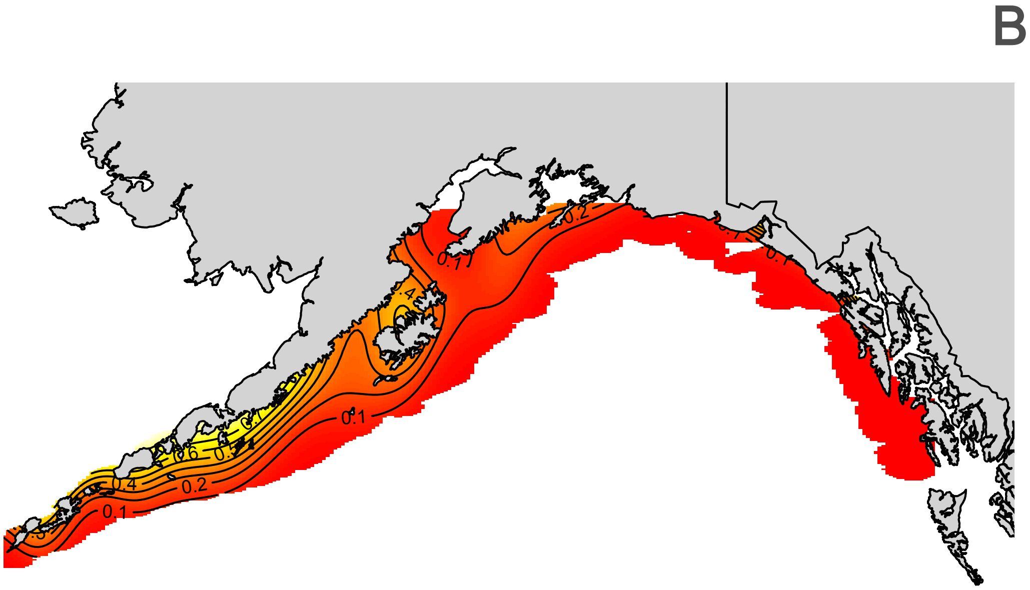
Model 6: Tanner Crab Prey Occurrence



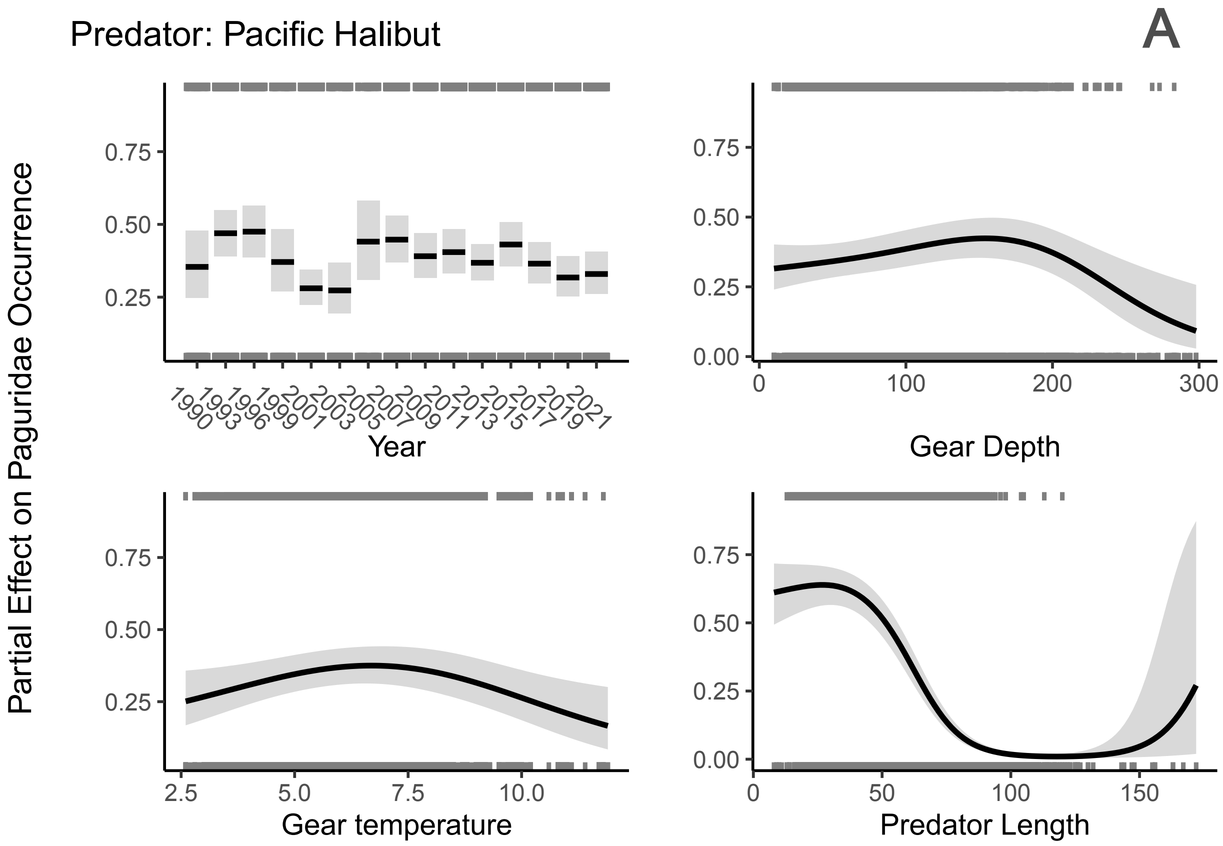


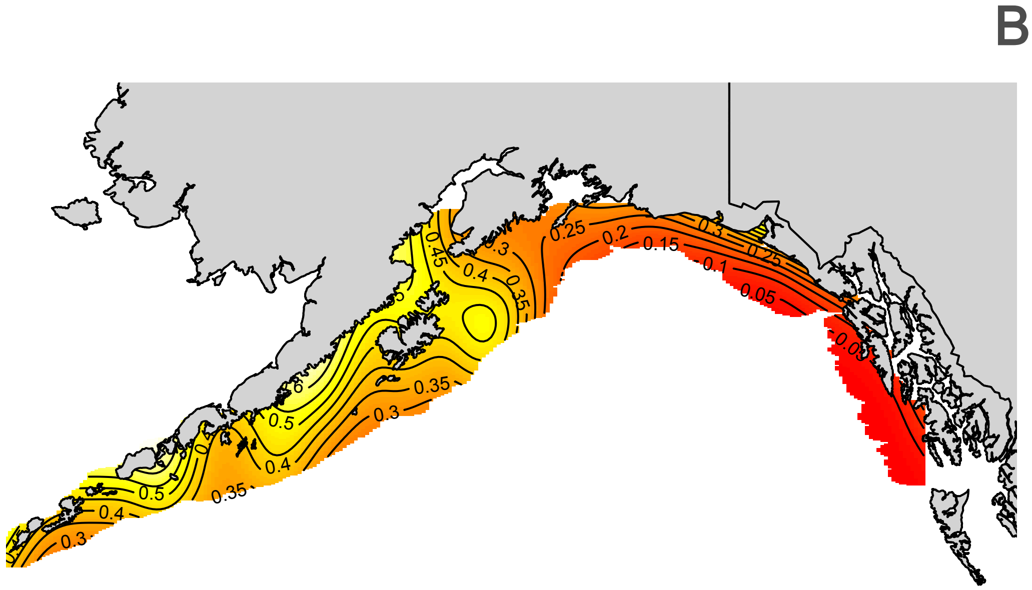
Model 6: Tanner Crab Prey Occurrence



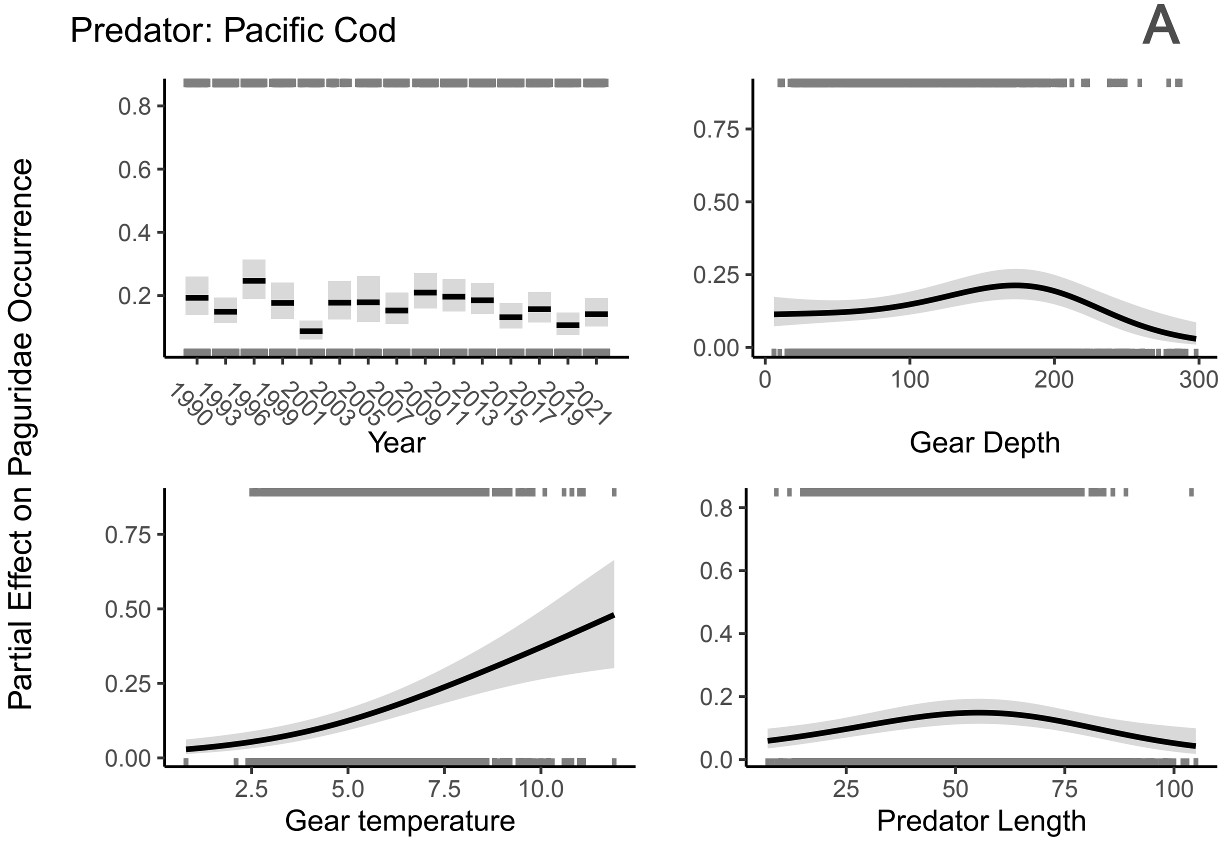


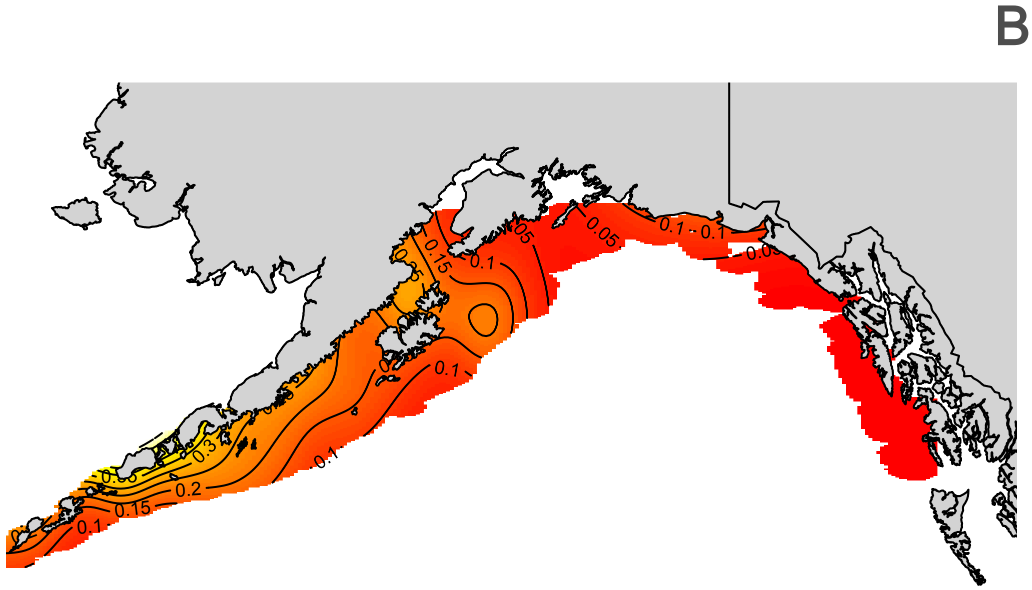
Model 7: Paguridae Prey Occurrence





Model 7: Paguridae Prey Occurrence





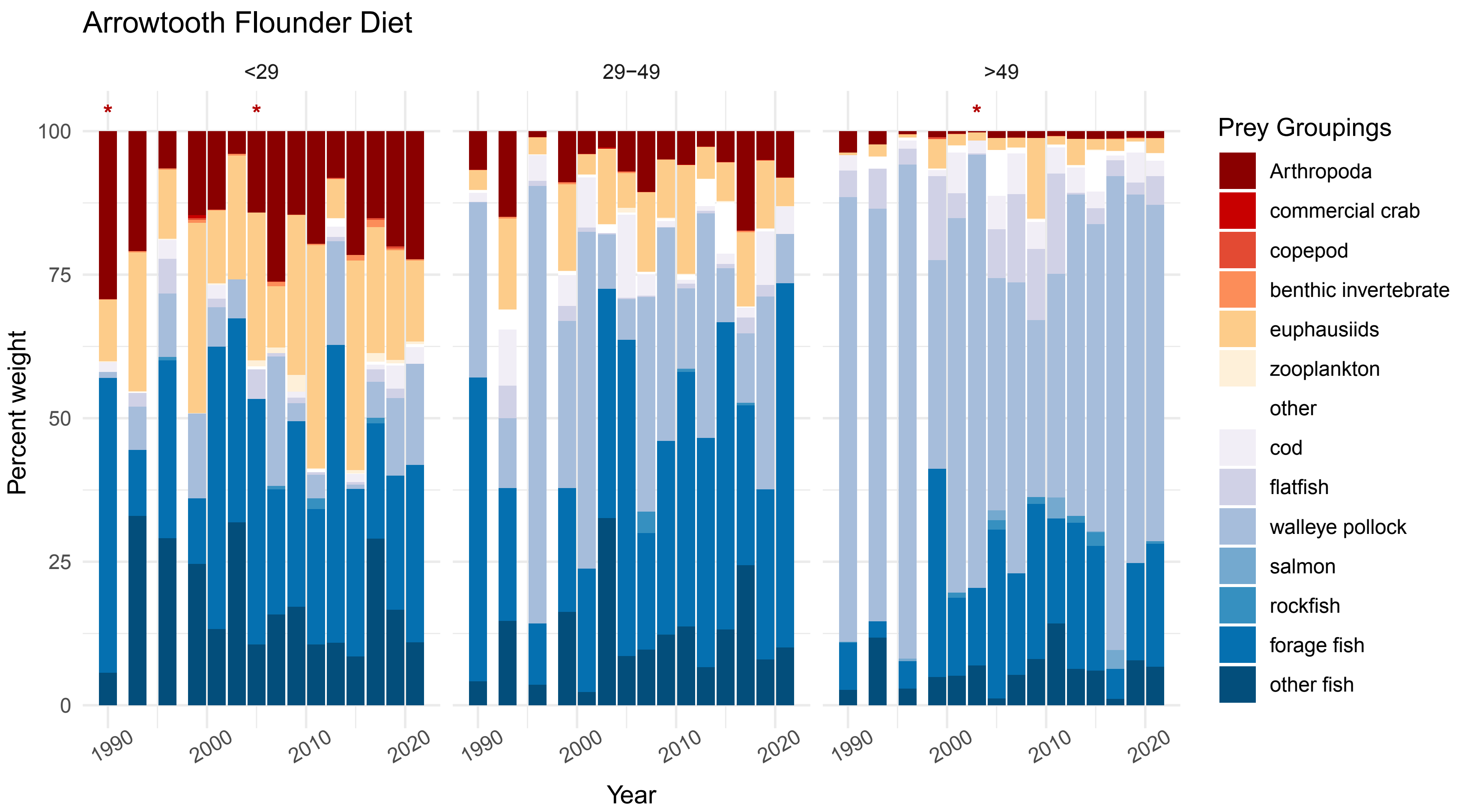
Appendix 2 Diet Summaries

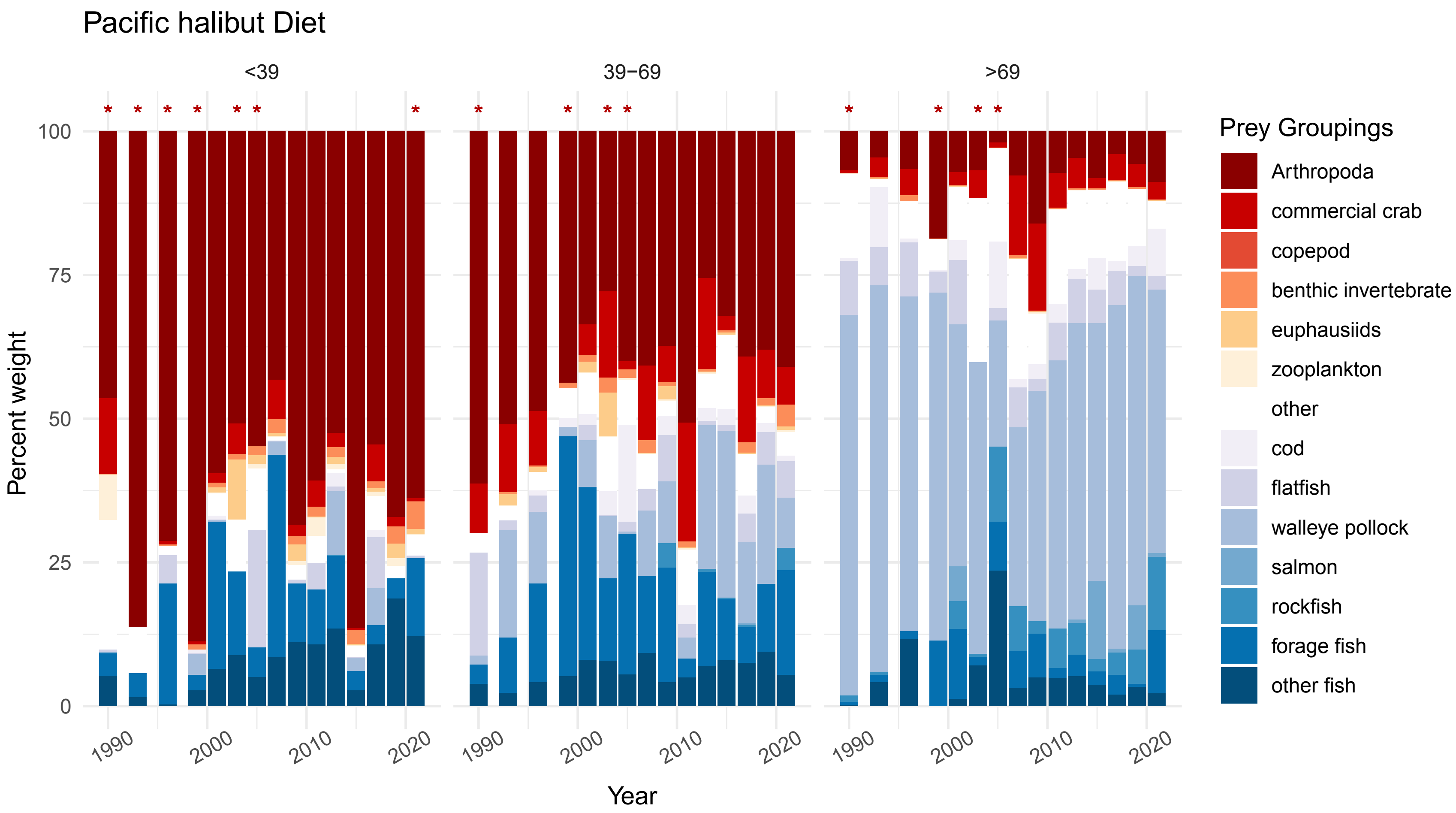
Catalina Burch

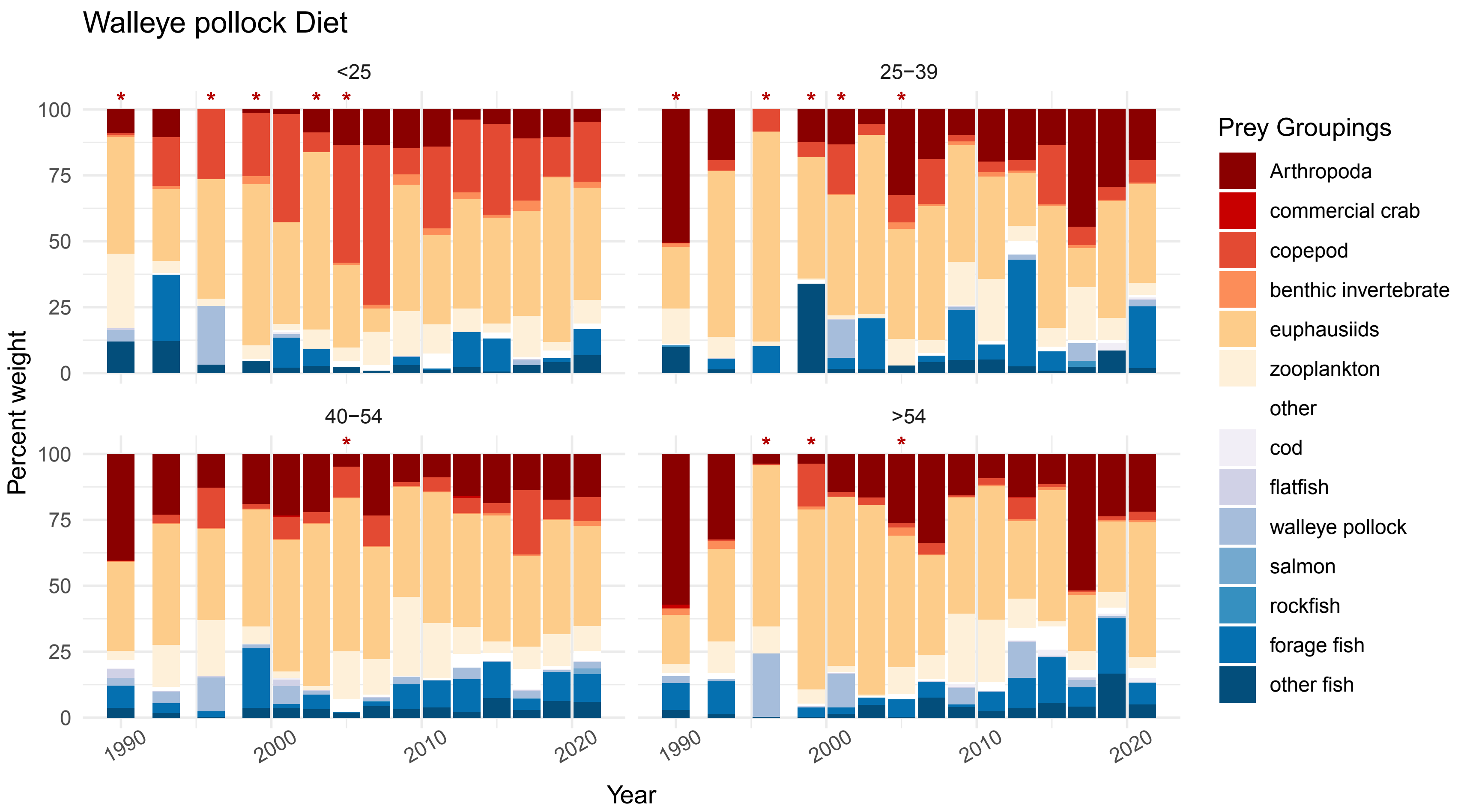
2023-05-22

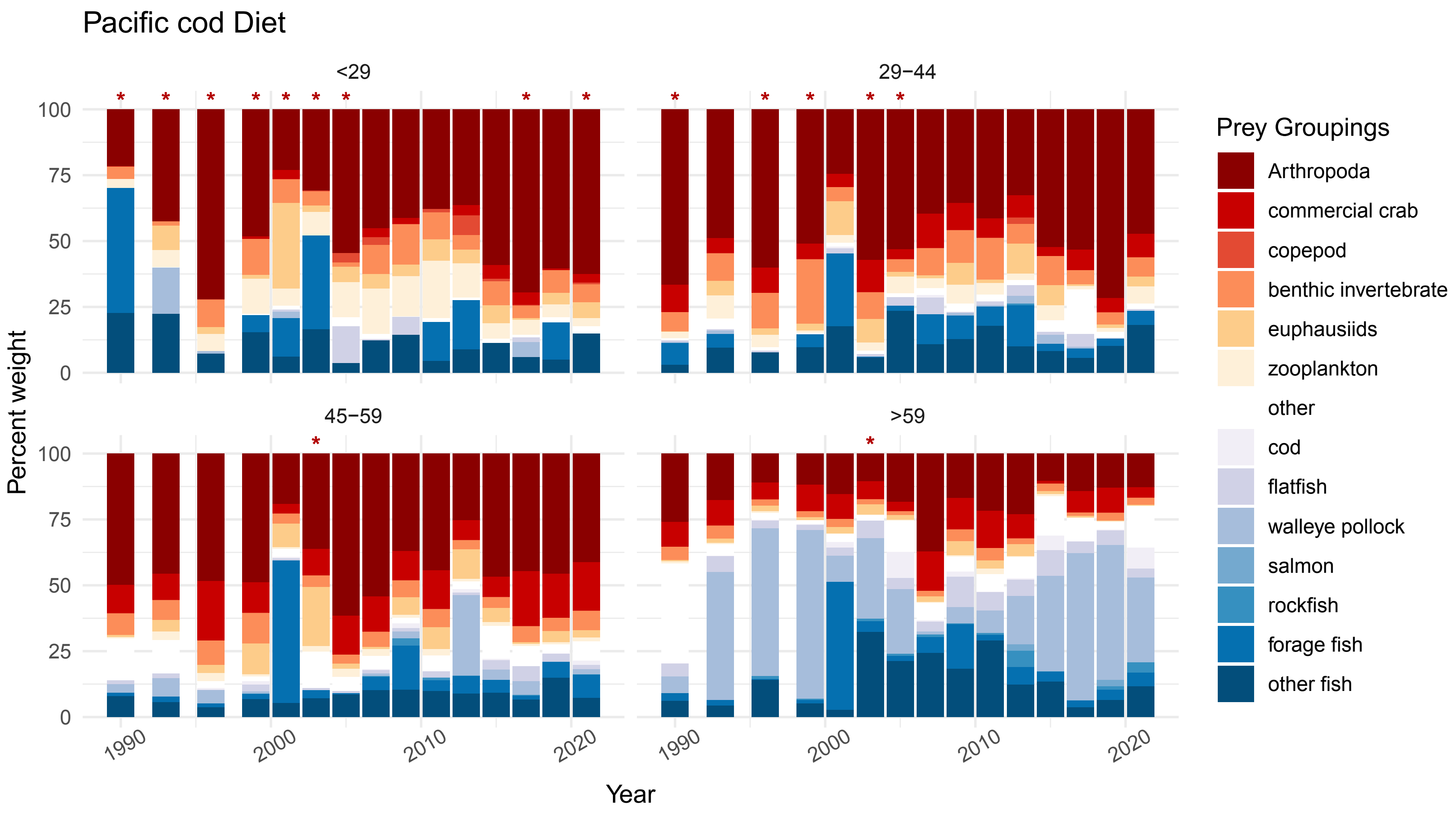
Appendix 2A: Focal Predator Diet Compositions over Time

An additional component of this research project was to create data visualizations of diet summaries. These plots are intended to fill knowledge gaps in management documents, including the GOA Ecosystem Status Report and the ecosystem components of commercial predators Stock Status Reports. Appendix 2A visualizes the change in the percent weight of prey contributions to diet over time for the four focal predator species at each size class. The size class is indicated at the top of each panel in black text. Red asterisks above bars indicates that there were fewer than 30 samples collected for that species/year/size class.

Arrowtooth Flounder Diet
<29
29−49
>49
*
*
*
Percent weight
100
75
50
25
0
1990
2000
2010
2020
Year
Prey Groupings
Arthropoda
commercial crab
copepod
benthic invertebrate
euphausiids
zooplankton
other
cod
flatfish
walleye pollock
salmon
rockfish
forage fish
other fish


Pacific halibut Diet
<39
39−69
>69
Percent weight
0
25
50
75
100
1990
2000
2010
2020
Year
Prey Groupings
Arthropoda
commercial crab
copepod
benthic invertebrate
euphausiids
zooplankton
other
cod
flatfish
walleye pollock
salmon
rockfish
forage fish
other fish

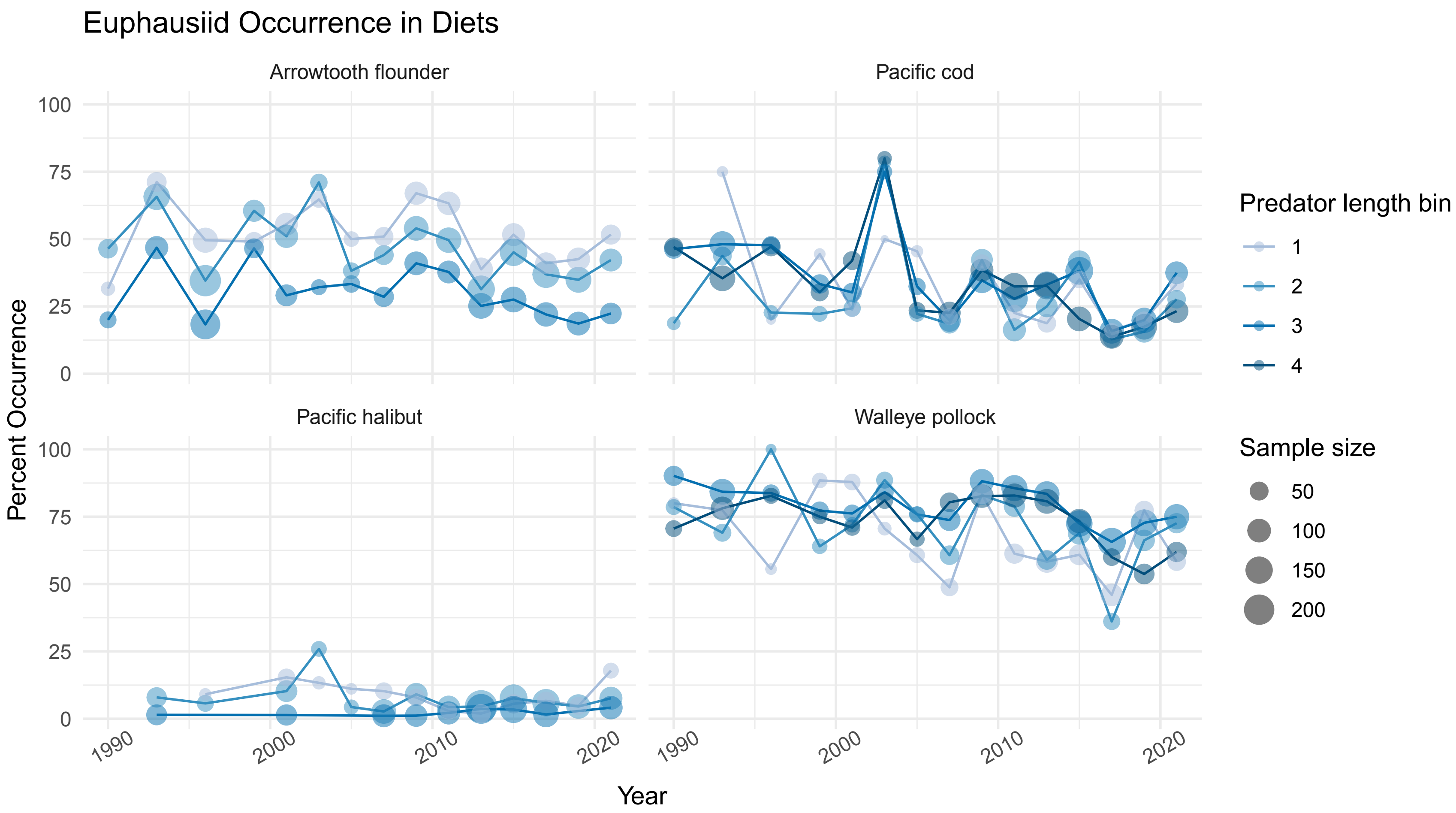

Walleye pollock Diet
<25
25−39
40−54
>54
Percent weight
100
75
50
25
0
Year
1990
2000
2010
2020
Prey Groupings
Arthropoda
commercial crab
copepod
benthic invertebrate
euphausiids
zooplankton
other
cod
flatfish
walleye pollock
salmon
rockfish
forage fish
other fish

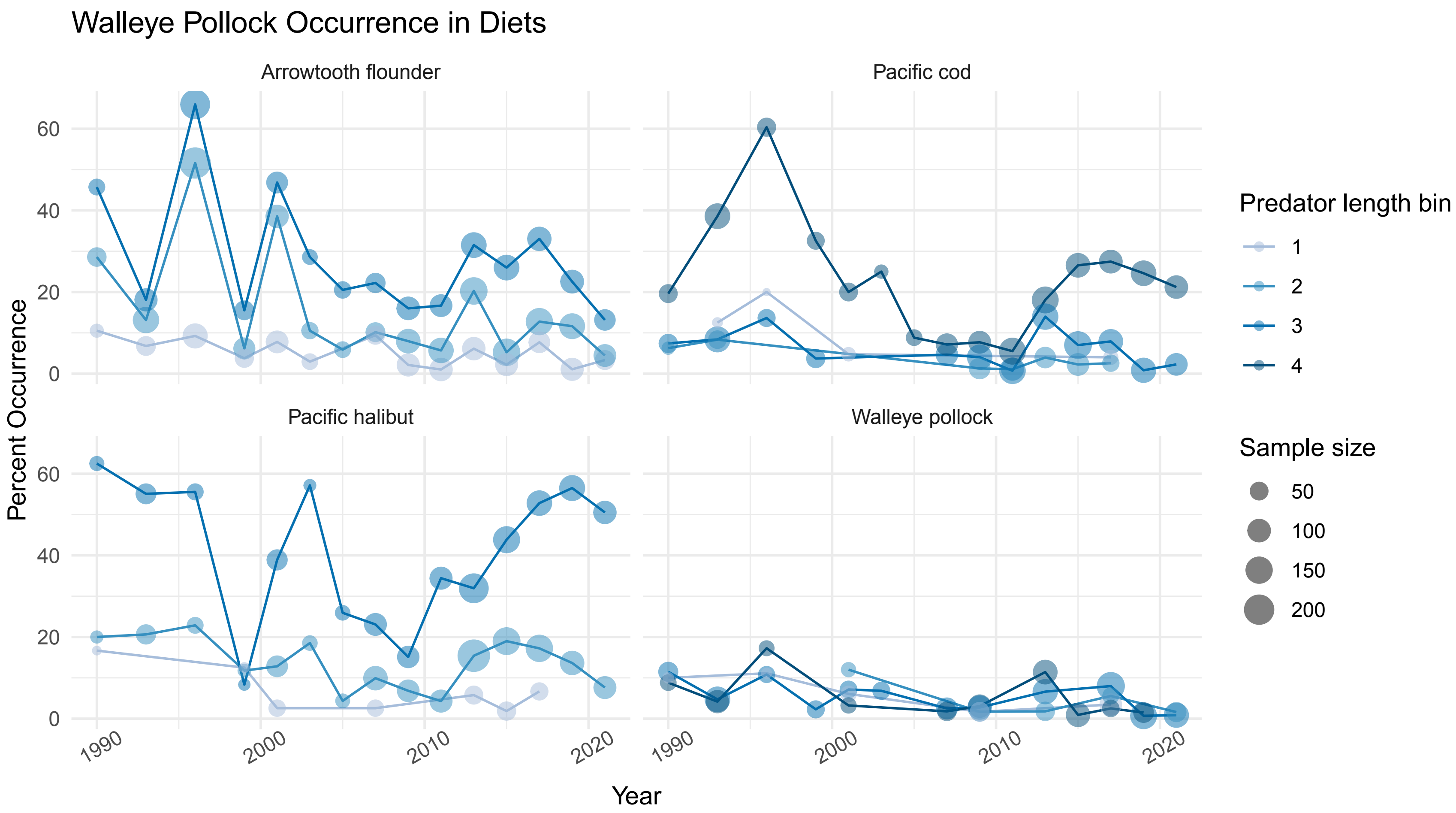


Pacific cod Diet
<29
29−44
45−59
>59
*
Percent weight
100
75
50
25
0
1990
2000
2010
2020
Year
Prey Groupings
Arthropoda
commercial crab
copepod
benthic invertebrate
euphausiids
zooplankton
other
cod
flatfish
walleye pollock
salmon
rockfish
forage fish
other fish

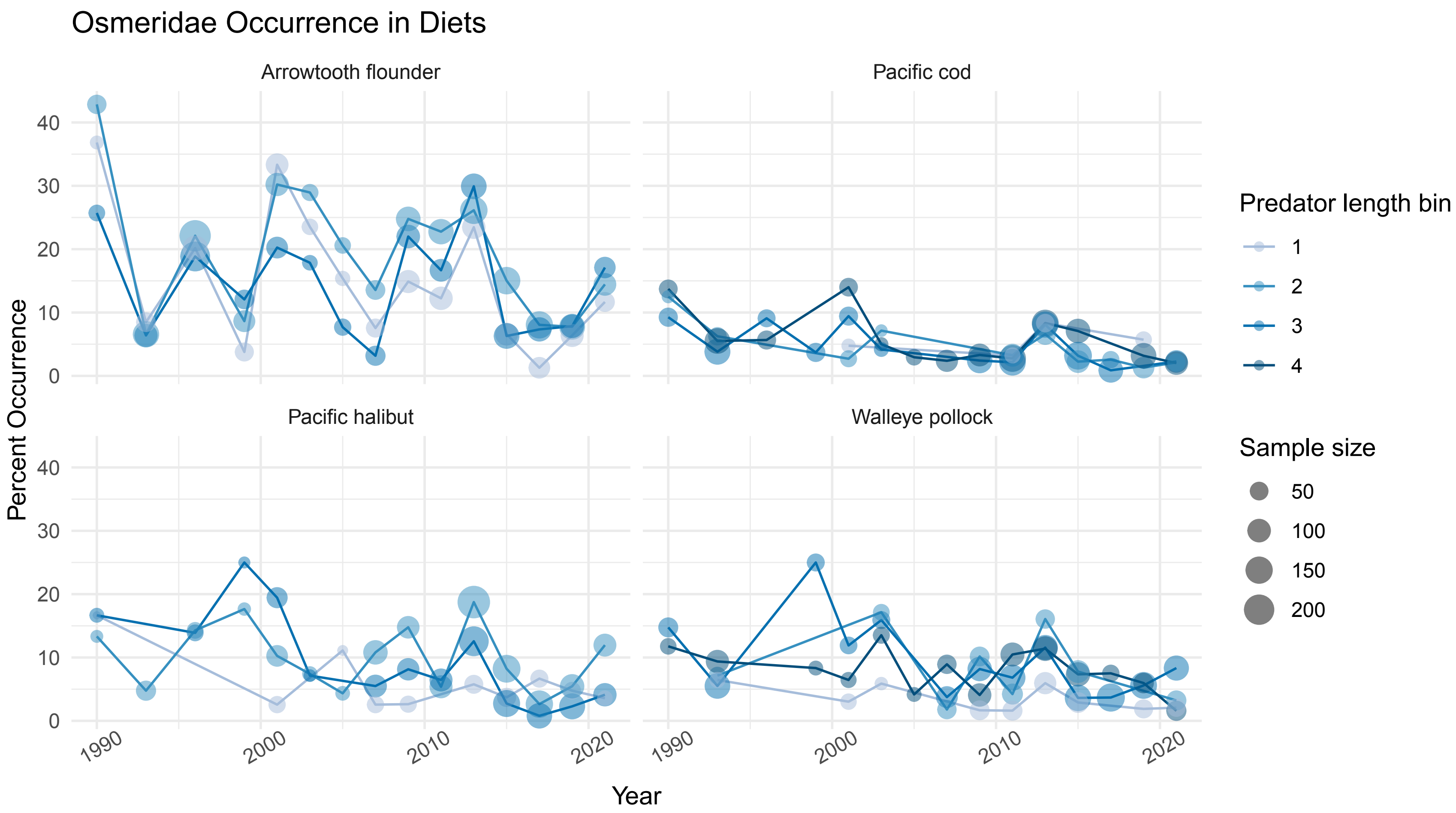
Appendix 2B: Focal Prey Occurrence Over Time

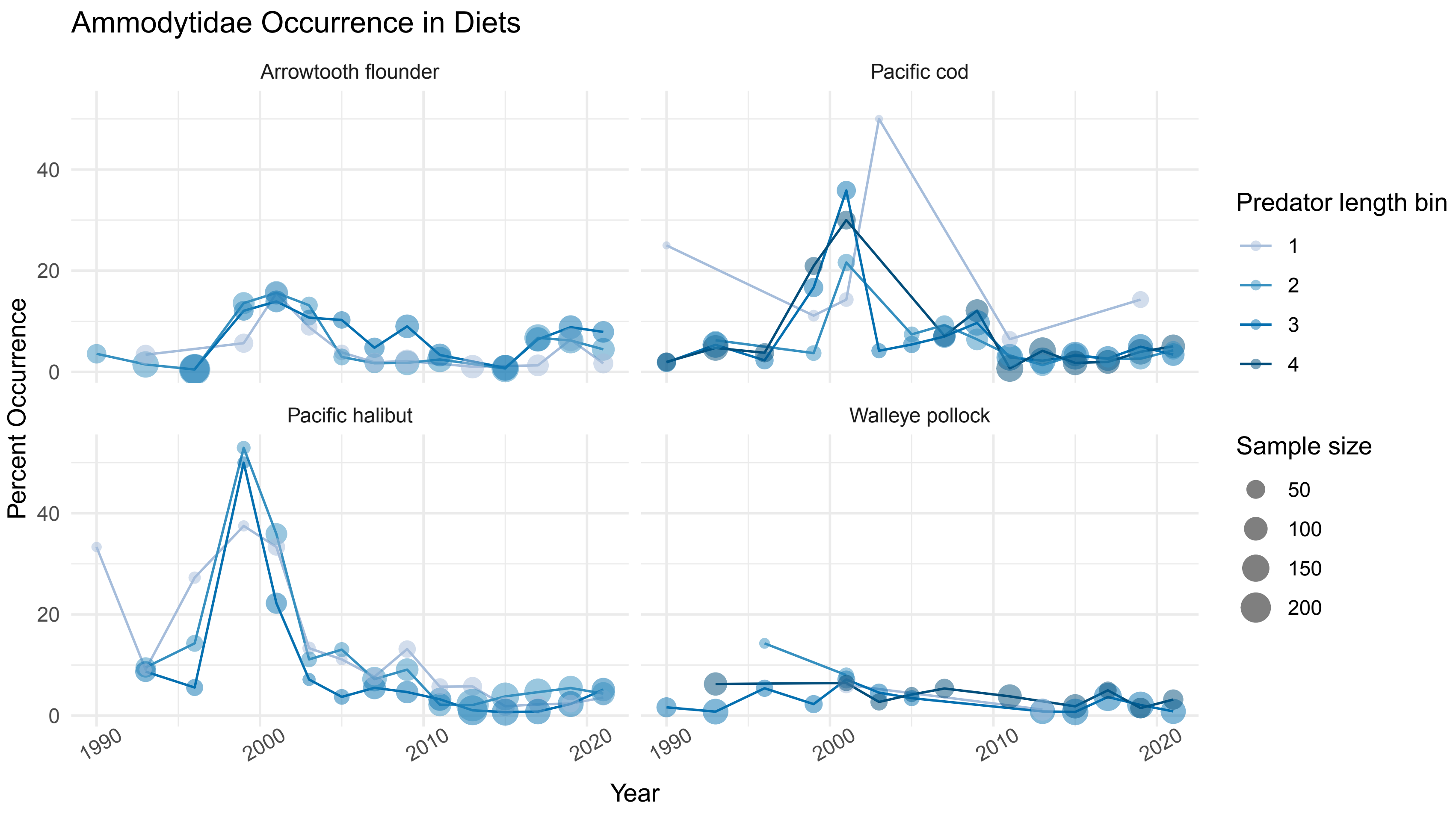
Appendix 2B visualizes the change in the percent occurrence of prey in diets over time for the four focal predator species at each size class. The predator length bins are described in supplementary tables, with 1 as the smallest length bin and 4 as the largest. Sample sizes, which are the number of predator stomachs sampled in a given year and size class, are indicated by point size.

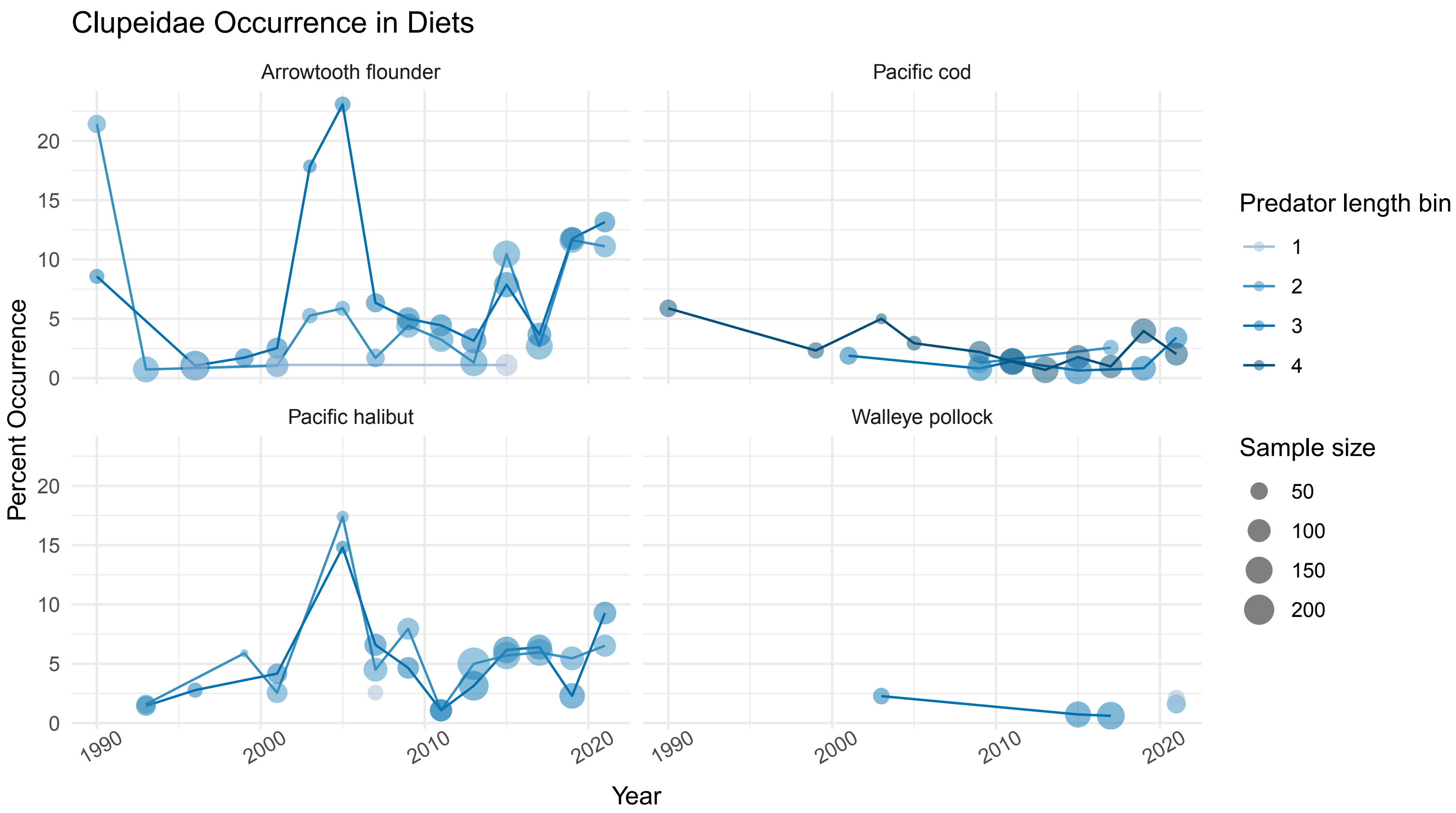

Euphausiid Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
100
75
50
25
0
1990
2000
2010
2020
Year
Predator length bin
1
2
3
4
Sample size
50
100
150
200

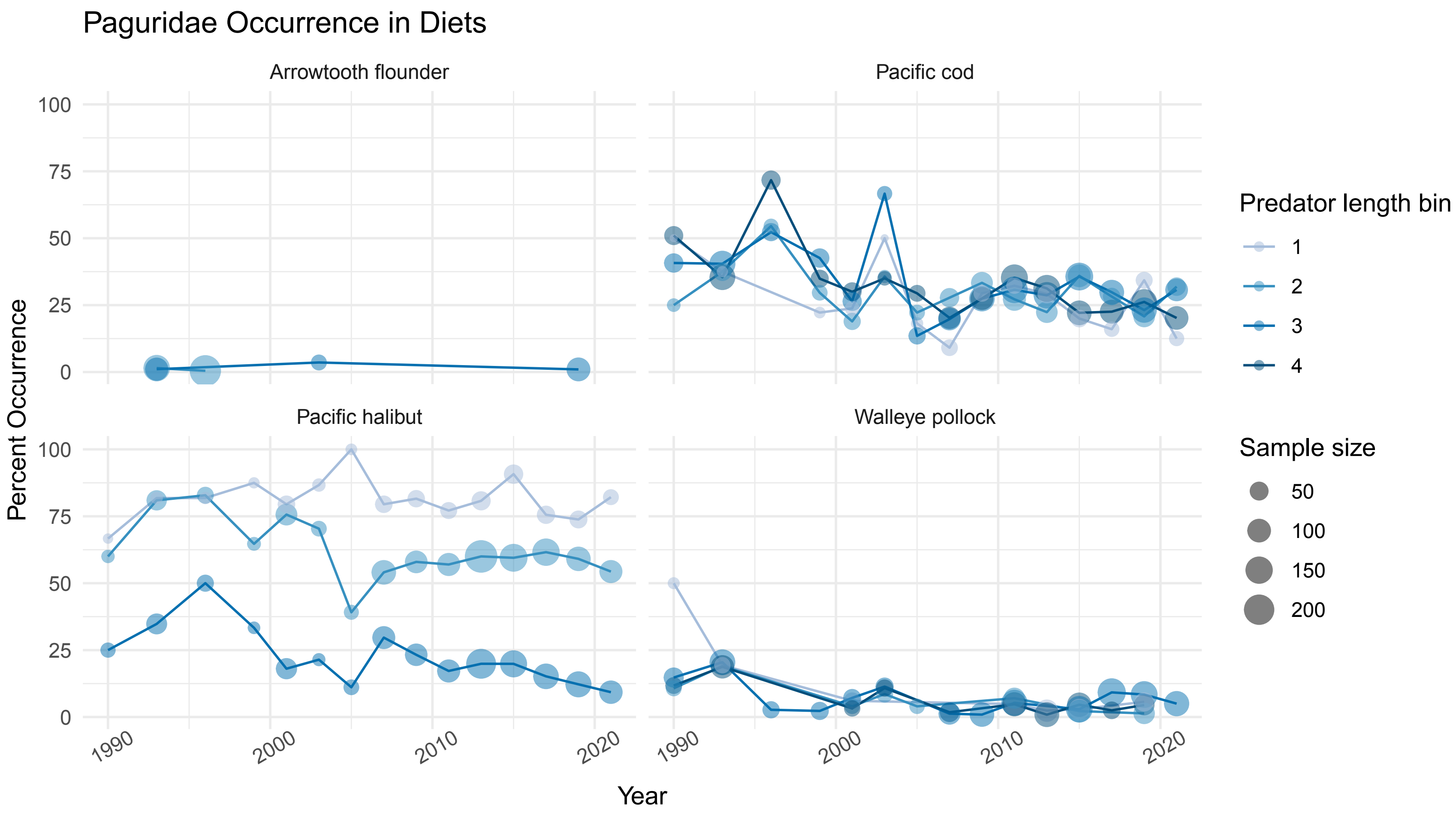


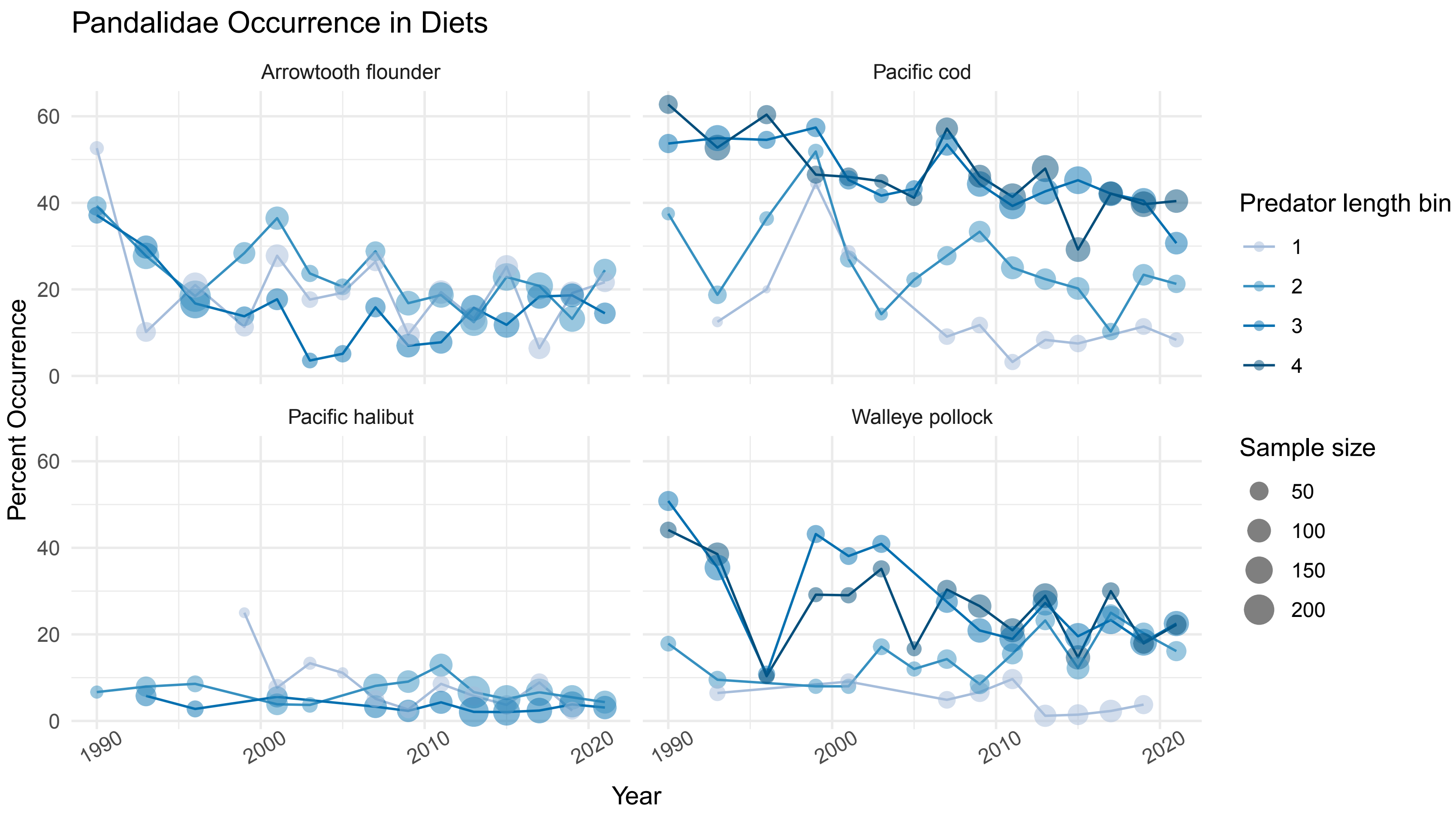
Walleye Pollock Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
0
20
40
60
1990
2000
2010
2020
Year
Predator length bin
1
2
3
4
Sample size
50
100
150
200

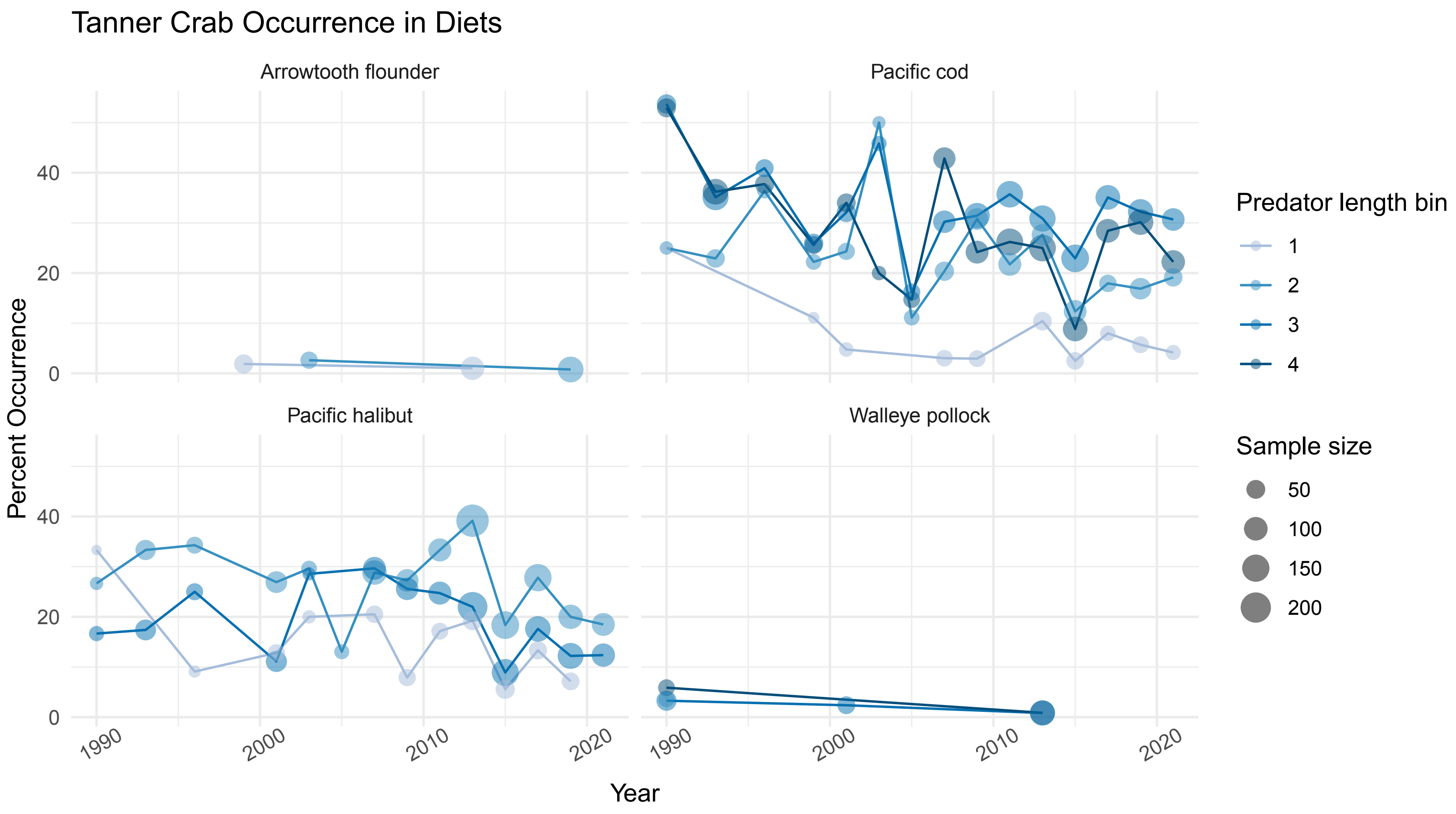

Osmeridae Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
0
10
20
30
40
1990
2000
2010
2020
Year
Predator length bin
1
2
3
4
Sample size
50
100
150
200


Ammodytidae Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
0
20
40
1990
2000
2010
2020
Year
Predator length bin
1
2
3
4
Sample size
50
100
150
200


Clupeidae Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
0
5
10
15
20
Year
1990
2000
2010
2020
Predator length bin
1
2
3
4
Sample size
50
100
150
200

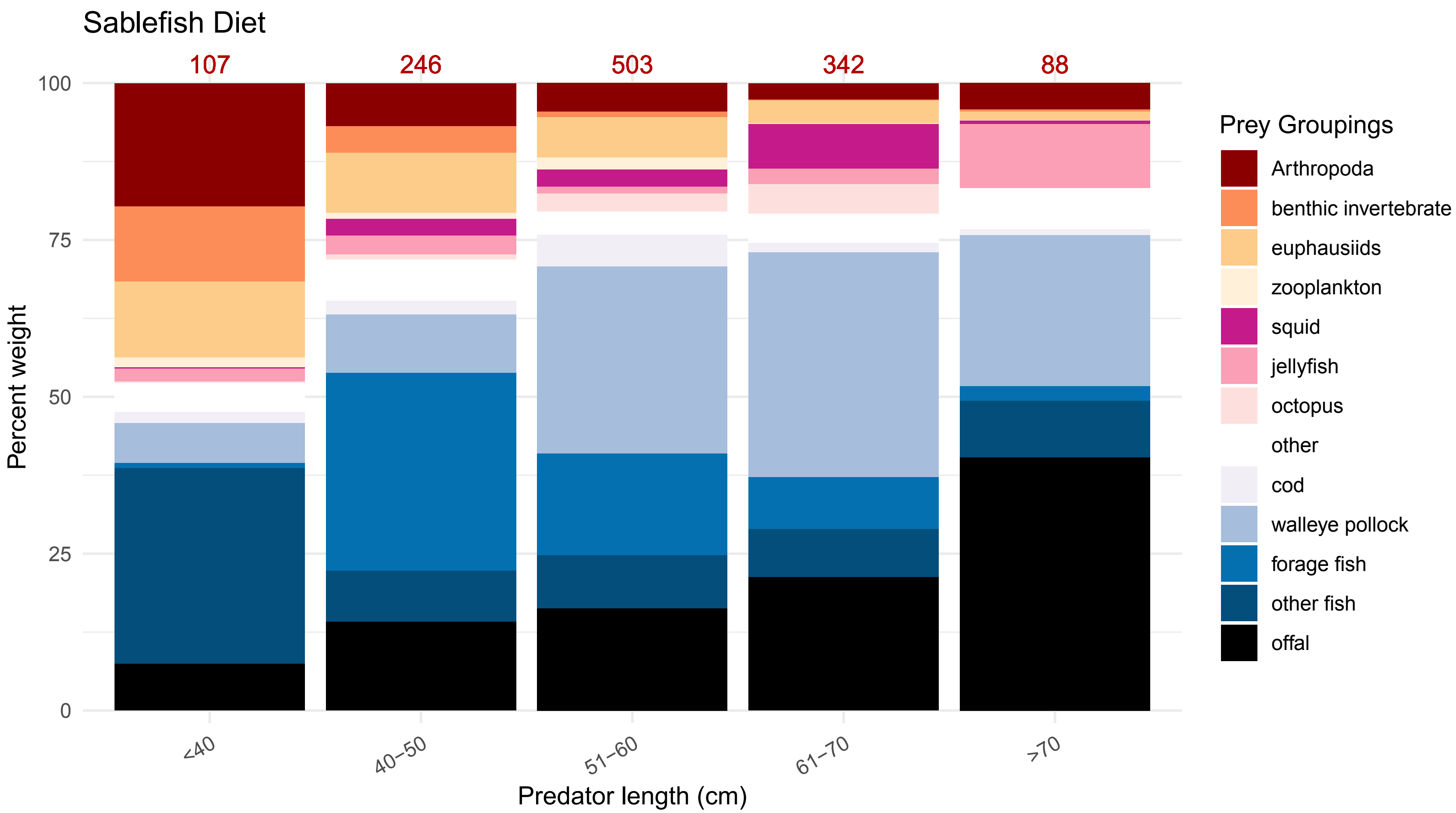

Paguridae Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
Year
0
25
50
75
100
1990
2000
2010
2020
Predator length bin
1
2
3
4
Sample size
50
100
150
200


Pandalidae Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
0
20
40
60
Year
1990
2000
2010
2020
Predator length bin
1
2
3
4
Sample size
50
100
150
200

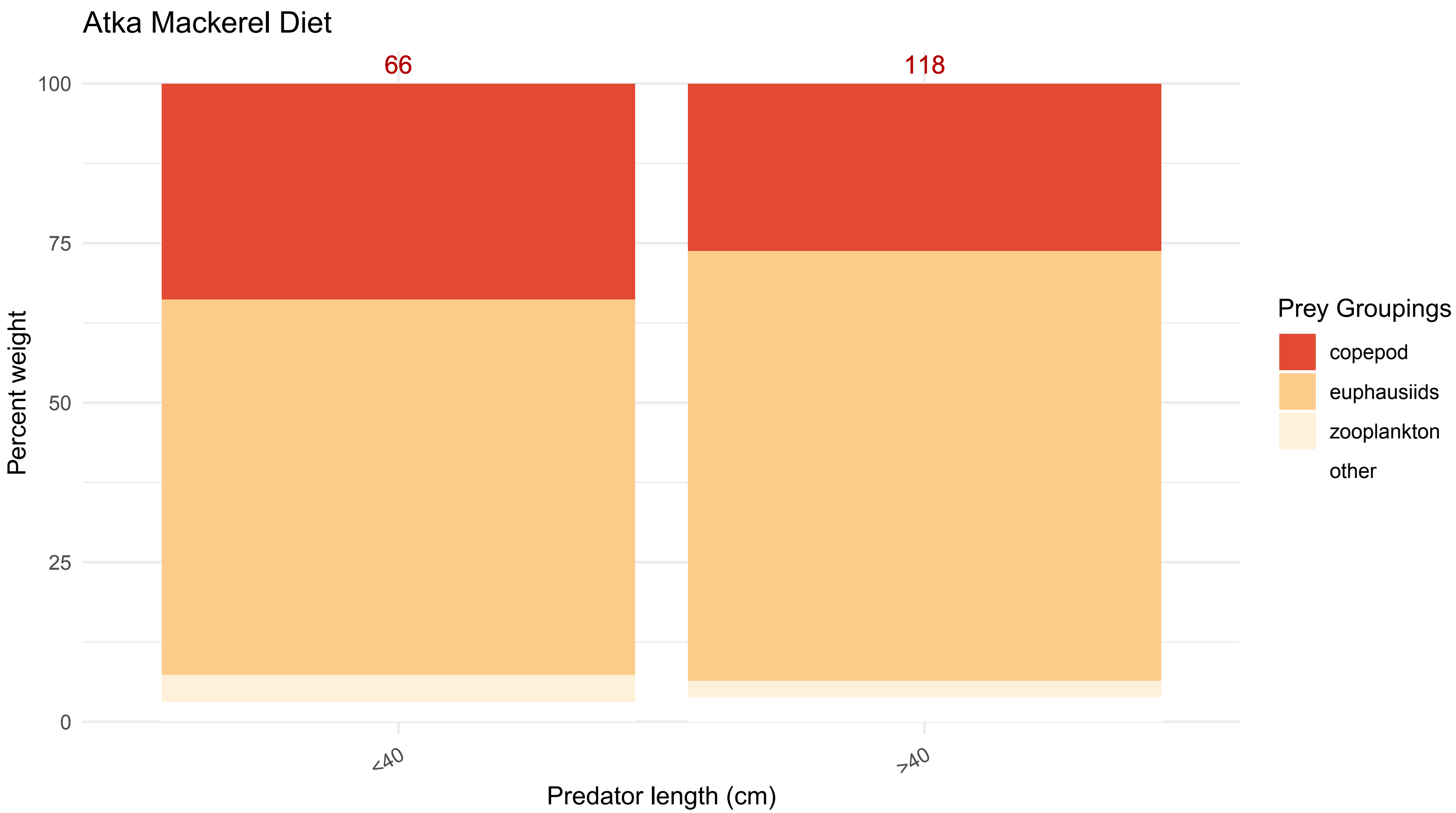

Tanner Crab Occurrence in Diets
Arrowtooth flounder
Pacific cod
Pacific halibut
Walleye pollock
Percent Occurrence
0
20
40
1990
2000
2010
2020
Year
Predator length bin
1
2
3
4
Sample size
50
100
150
200

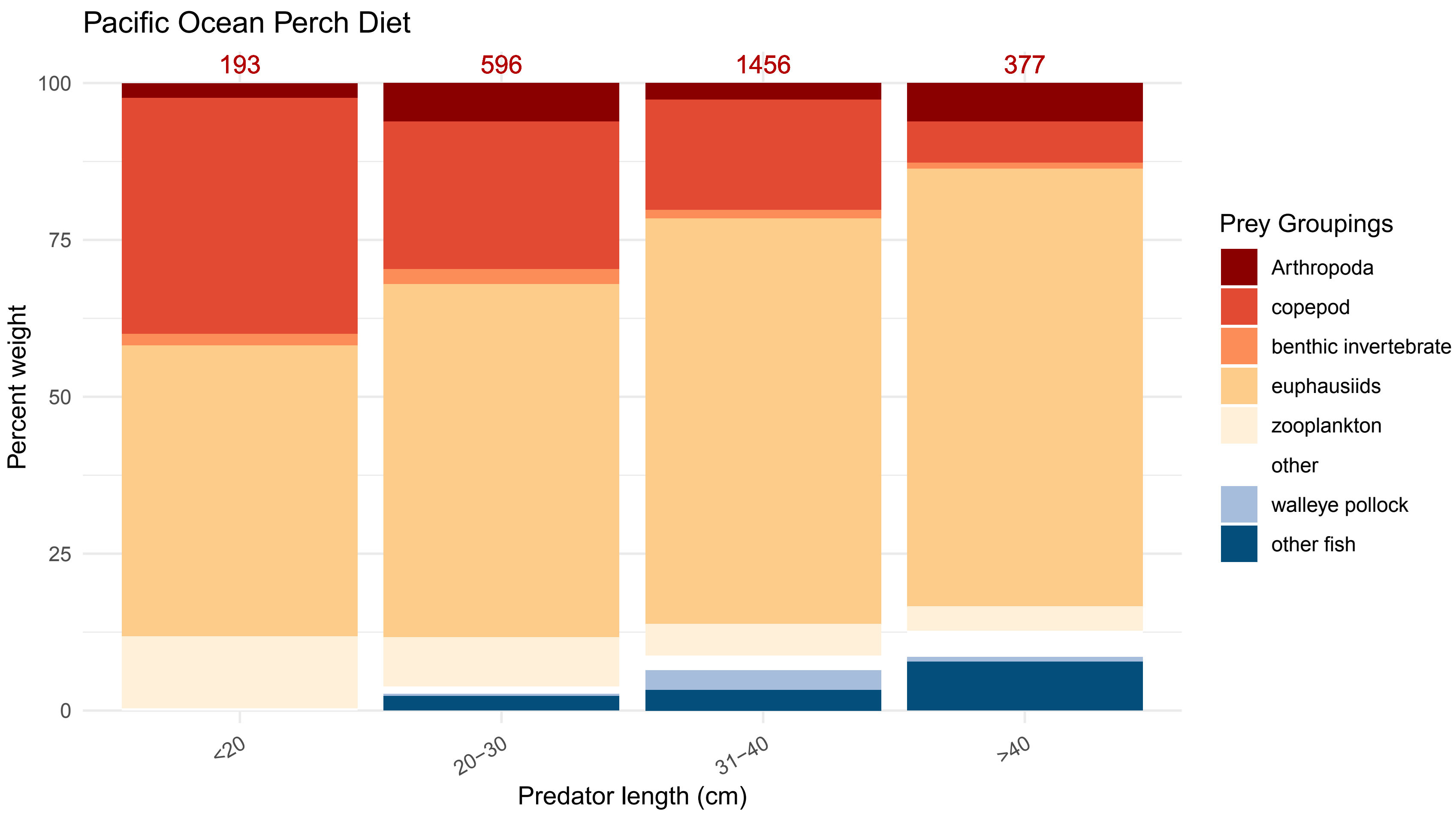
Appendix 2C: Non-focal Predators General Diet Summaries

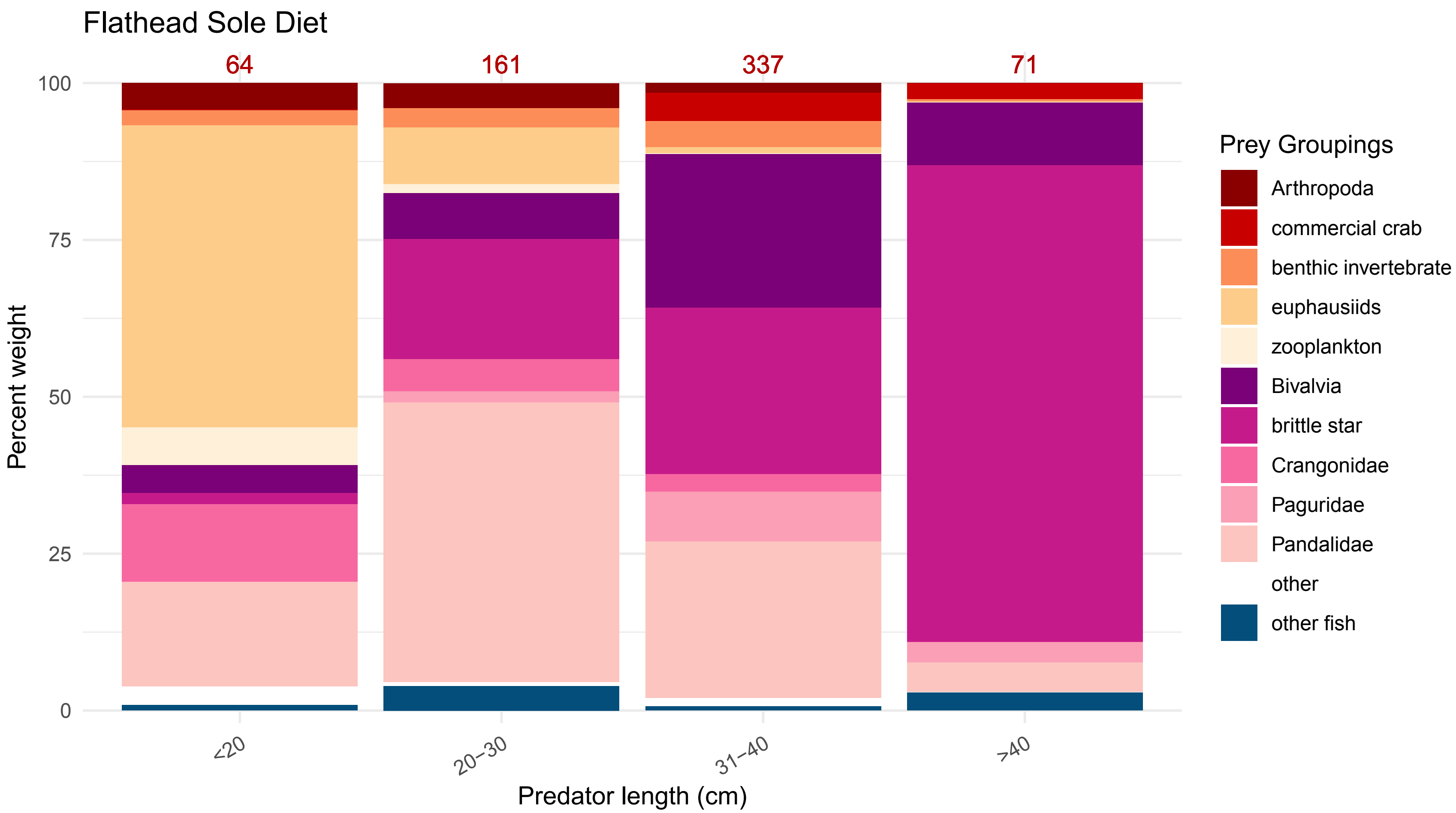
Appendix 2C provides diet summaries for the non focal predators including, sablefish, atka mackeral, Pacific Ocean perch, and flathead sole. These figures show the percent weight of prey items in the diets of predators, grouped by the smallest size bins possible while maintaining >50 sample sizes for each bar. Prey groups are depicted in shades of blue for fishes and shades of red for invertebrates. Sample sizes are displayed in red text above each bar. Species were aggregated into taxonomic or functional groups based on sample size and ecological relevance, which is described in supplementary tables.



Sablefish Diet
107
246
503
342
88
100
75
50
25
0
Percent weight
<40
40–50
51–60
61–70
>70
Predator length (cm)
Prey Groupings
Arthropoda
benthic invertebrate
euphausiids
zooplankton
squid
jellyfish
octopus
other
cod
walleye pollock
forage fish
other fish
offal


Atka Mackerel Diet
66
118
100
75
50
25
0
Percent weight
<40
>40
Predator length (cm)
Prey Groupings
copepod
euphausiids
zooplankton
other


Pacific Ocean Perch Diet
193
596
1456
377
100
75
50
25
0
Percent weight
<20
20–30
31–40
>40
Predator length (cm)
Prey Groupings
Arthropoda
copepod
benthic invertebrate
euphausiids
zooplankton
other
walleye pollock
other fish


Flathead Sole Diet
64
161
337
71
100
75
50
25
0
Percent weight
<20
20–30
31–40
>40
Predator length (cm)
Prey Groupings
Arthropoda
commercial crab
benthic invertebrate
euphausiids
zooplankton
Bivalvia
brittle star
Crangonidae
Paguridae
Pandalidae
other
other fish