ORIGINAL ARTICLE

The contribution of diet to the dramatic reduction of the 2013 year class of Gulf of Alaska walleye pollock (*Gadus chalcogrammus*)

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Abstract

A survey-based time series (2001–2019) showed that age-0 walleye pollock (*Gadus chalcogrammus*) occurred in very high abundances in 2013 compared with other years; however, recruitment of the 2013 year class to age-1 was lower than average. Diet composition of age-0 fish was examined from the 2013 year class to assess the potential impact of the consumed prey on walleye pollock. High abundances of smaller age-0 fish were found at stations southwest of the Shumagin Islands compared with low abundances of larger fish found surrounding Kodiak Island. Fish in the southwest region showed a higher intake of low-quality food items such as pteropods and larvaceans compared with fish in the northwest region that had consumed mostly higher quality prey such as large copepods and euphausiids. Even though no significant differences were found in fish condition between regions overall, spatial differences in fish weight were found after accounting for sample day of year. Prey-specific Index of Relative Importance analysis showed southwest region fish had consumed a larger diversity of taxa, whereas fish from the rest of study area primarily consumed large copepods and euphausiids. These results suggest that high abundances of smaller pollock found in the southwestern part of the study region consumed a higher percentage of low-quality, lipid-poor prey taxa, which likely contributed to reduced overwinter survival and increased mortality.

KEYWORDS
assemblage, diet, fish, growth, Gulf of Alaska, juvenile, pollock, recruitment, seasonal, shelf, zooplankton

1 | INTRODUCTION

Gadus chalcogrammus (walleye pollock, hereafter: pollock) is a fish of high commercial value in North Pacific Ocean. In 2017, Gulf of Alaska pollock ex-vessel value was $35.6 million (Dorn et al., 2019). Because of their value, determining the relative year-class strength, overwinter survival, and recruitment to age-1 are vital steps in the sustainable management of pollock in this region. The Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) Program has been

studying the early life stages of pollock and other fishes in the Gulf of Alaska since 1979 (Kendall et al., 1996; McClatchie et al., 2014; Rogers & Dougherty, 2019). Surveys conducted in spring focus on eggs and larvae, with fall surveys focusing on juvenile (age-0) fishes. EcoFOCI has conducted many studies of juvenile pollock in the Western Gulf of Alaska (WGOA), including age-0 abundance estimations (Bailey & Spring, 1992), distribution, ecology, and population dynamics (Brodeur & Wilson, 1996), regional differences in size and geographic distribution (Wilson, 2000; Wilson et al., 2005), studies of habitat

selection relating to the prey field (Logerwell et al., 2010; Wilson, 2009; Wilson et al., 2013), and the effects of climate on population dynamics (Ciannelli et al., 2004, 2005). The 2013 year class was characterized by high abundance of both larval and age-0 pollock, yet very low recruitment (here defined as the age-1 abundance in the following year) (Figure 1). This paper explores possible mechanisms to explain the high juvenile abundance to low recruitment disconnect by focusing on the interaction between age-0 pollock and their forage base.

Previous studies have examined aspects of spatial distribution and feeding ecology of pollock in the western GOA. Wilson (2009) found that interannual distributions of age-0 are much broader and variable compared with age-1 pollock. During fall, there is a general pattern of few, larger age-0 pollock surrounding Kodiak Island (Figure 2), with large abundances of smaller age-0 pollock southwest, extending to Unimak Pass (Wilson, 2009; Wilson et al., 2013). In comparison with other age-0 forage fish in the region (e.g., capelin, *Mallotus villosus*), age-0 pollock utilize a broader suite of zooplankton prey (Wilson et al., 2006), with smaller fish preferring the larger, lipid-rich calanoid copepod *Calanus marshallae* followed by a ontogenetic switch to euphausiids (Siddon et al., 2013; Wilson, 2009; Wilson et al., 2006). Wilson (2009) also recorded instances of age-0 pollock depleting the euphausiid standing stock in some site-specific study locations, based on five meso-scale regions within the WGOA. In a multiyear study of age-0 pollock during differing climate conditions (warm vs. cold) in the eastern Bering Sea, Siddon et al. (2013) found that spatial heterogeneity in pollock growth conditions resulted from a combination of prey quality and quantity, water temperature, and metabolic costs, which could possibly contribute to size-dependent fish survival and subsequent variability in recruitment to age-1. Increased growth potential

was found when higher age-0 pollock abundance and lipid-rich prey abundance spatially overlapped (i.e., "hot spots").

In 2013, EcoFOCI conducted a survey of oceanography, zooplankton, juvenile pollock, and forage fish in the western Gulf of Alaska from northeast of Kodiak Island to Unimak Pass. The survey showed an anomalously high abundance of age-0 juvenile pollock compared with years with similar spatial sampling effort, yet subsequent year-to-year observations show 2013 had low recruitment (Dorn et al., 2019). We propose to explore the possible mechanisms underlying poor recruitment of this year class of pollock by addressing two hypotheses: (1) pollock size and condition was related to prey choice; and (2) spatial differences in age-0 pollock abundances were related to prey distribution. We predicted that age-0 pollock in good condition would select particular prey; that is, larger and/or with a higher energetic content, more frequently. Furthermore, areas with high age-0 abundance would show a depletion of more highly selected prey, reflected both in low relative prey abundances spatially and the lack of these prey within diets, negatively affecting age-0 body condition. The overall goal was to elucidate potential mechanisms for low recruitment of the 2013 year class despite very high age-0 pollock abundance in the autumn prior to first winter.

2 | METHODS

2.1 | Study area

Our study area was the western Gulf of Alaska (WGOA), a large, coastal ocean system dominated by the Alaska Coastal Current (ACC), which is forced by alongshore winds and freshwater runoff

(a) **(b)**
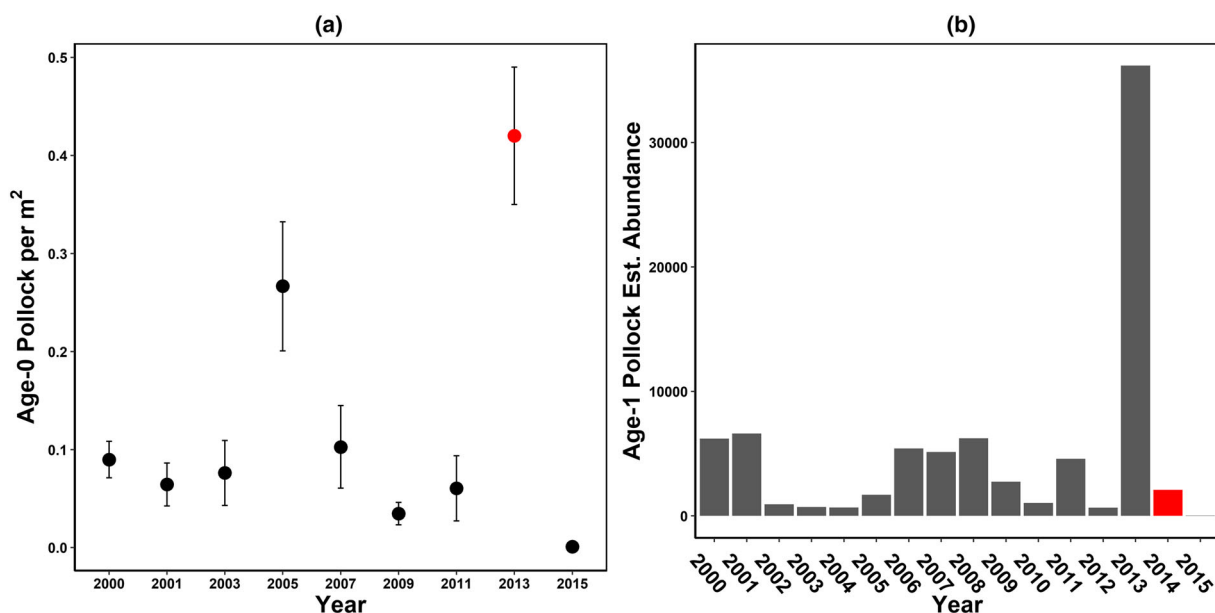
FIGURE 1 (a, b) Left: Western Gulf of Alaska age-0 pollock catch (m^2) from EcoFOCI surveys from 2000 to 2015 with 2013 values in red, noting high abundance. Also note that surveys became biennial after 2001. Right: Total estimated abundance at age (millions) of GOA pollock from the age-structured assessment model, from table 1.20 in Dorn et al. (2019), with the 2013 (age-1 in 2014) recruitment year again labeled in red

FIGURE 2 Survey stations divided into domains based on previous studies of age-0 pollock, with 200 m isobath. Domain A: stations west of Shumagin Islands; Domain B: stations between Shumagin Islands and Kodiak Island, and Domain C: stations surrounding and northeast of Kodiak Island
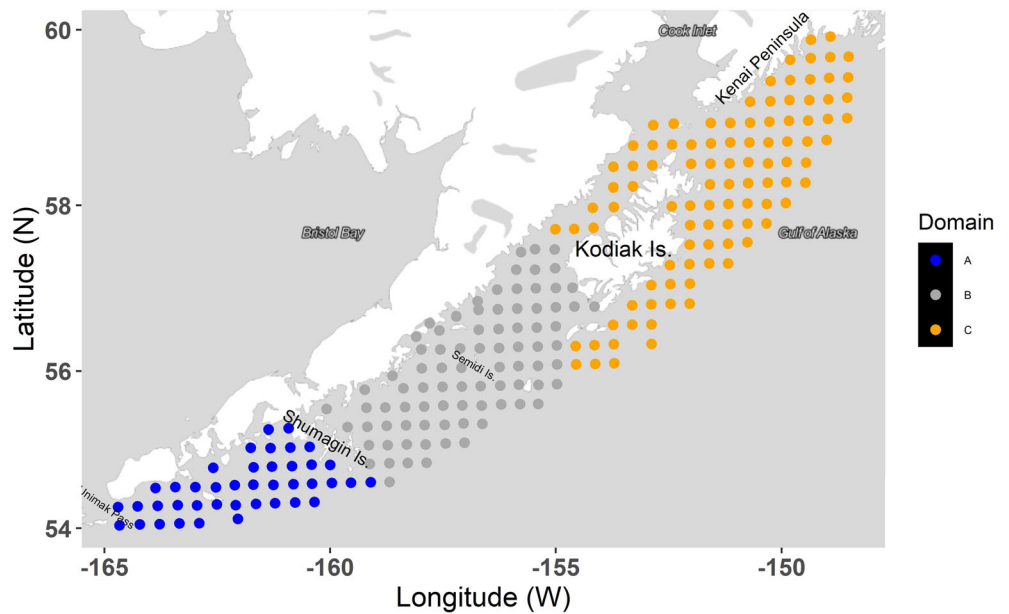
(Royer, 1981; Stabeno et al., 2004; Weingartner et al., 2005). The WGOA is predominantly a downwelling system, yet is productive in part because the regional oceanography also produces eddies, upwelling, and flux in the surface Ekman layer (Mordy et al., 2019; Stabeno et al., 2004). Specifically, our study was located between the southeast end of the Kenai Peninsula to the southern end of Unimak Pass (Figure 2). A total of 223 stations were sampled on two legs from August 17 to September 17, 2013, with a break of 5 days mid-survey between legs 1 and 2. Leg 1 sampling started inshore of the Shumagin Islands, moving southwest through nearshore stations along the Alaska Peninsula to Unimak Pass, then sampling transects inshore to offshore moving northeast, ending on the southwest tip of Kodiak Island. Leg 2 began on the northeast opening of Shelikof Strait, encircling Kodiak Island, and finishing just southeast of the Kenai Peninsula. For this study, age-0 pollock abundance, size, condition, and diet composition as well as zooplankton community composition (representing the prey field) were analyzed.

2.2 | Walleye pollock

2.2.1 | Field sampling protocol

Fish were collected using an anchovy trawl (also known as a Stauffer Trawl; Wyllie-Echeverria et al., 1990), a midwater trawl composed of a square mouth with 26-m-long sides equipped with a 3-mm mesh codend liner. The trawl was fished over an oblique path deployed to a depth of 200 m, or 10 m off the bottom, whichever was shallowest (Coyle & Pinchuk, 2005). The net depth was monitored using the ship's Simrad[1] ITI (trawl eye) or Furuno system. Catch estimates were calculated to individuals per m^2 following Wilson (2009).

Pollock were sorted from the catch and enumerated, with age-0 fish delineated by a standard length (SL) < 140 mm (Brodeur & Wilson, 1996). When hauls were determined to be too large to process due to time constraints, a subsampling protocol was implemented prior to enumerating and measuring individuals from some tows. All age-0 fish (if fewer than 100) or a randomly drawn subsample of approximately 100 age-0 fish were measured for body length. Age-0 pollock catch per m^2 was calculated by dividing total age-0 pollock counts by volume filtered by the trawl (per Wilson, 2009) and multiplying by the maximum depth fished by the net. A length-stratified sample of 25 individuals of differing size of age-0 pollock were flash frozen in the −80°C freezer and then moved to the −20°C freezer for later diet analysis in the laboratory.

2.2.2 | Fish diet processing protocol

We used prey-accumulation curves to determine the appropriate number of age-0 walleye pollock stomachs to analyze per station (Ferry et al., 1997; MacKinlay & Shearer, 1996). Prey-accumulation curves are used to determine the number of stomachs needed to capture the highest percentage of prey taxa found in predator stomachs within a defined region. The prey curves were developed using historical pollock diet data from the study region and indicated **N** number of fish stomachs were required to adequately describe diets within this habitat. In our laboratory, the frozen fish selected from each station for stomach contents analysis were thawed, blotted dry, measured to the nearest 1-mm SL, and weighed to the nearest 1 mg. All stomachs were then excised from the fish and placed into vials with a sodium borate-buffered 5% formalin solution. The total number of stomachs examined for this analysis was 791.

Once adequately preserved in formalin (a minimum of 2 weeks based on experience), the excised gut was blotted dry, weighed to the

nearest 0.01 mg, and then dissected to determine prey contents. We recorded the gut content weight, followed by recording the gut lining weight, all to the nearest 0.01 mg. All gut contents were then identified to the lowest taxonomic level possible (e.g., genus or species) and then organized by taxa levels, life-history stage (if possible), and level of digestion. Each prey taxa group was enumerated, dried, and weighed separately to the nearest 0.01 mg.

2.3 | Zooplankton

Zooplankton sampling was conducted using oblique tows of a 60-cm frame bongo (505-μm mesh) paired with a 20-cm frame bongo (153 μm mesh). A FastCat SBE 49 (Seabird Electronics) was mounted above the bongo to provide CTD data. All nets were equipped with calibrated General Oceanics flowmeter mounted inside each net mouth to calculate volume filtered (m^3). Oblique tows were conducted to 200 m depth or 10 m off the bottom if depth was less than 200 m. For each zooplankton tow, samples were preserved in 5% buffered formalin. After the survey, all zooplankton samples were sent and enumerated at the Polish Plankton Sorting and Identification Center (Szczecin, Poland) and then subsequently verified at the Alaska Fisheries Science Center for accuracy.

2.4 | Statistical analysis

We divided our sampling region into three distinct domains: one surrounding Kodiak Island (Domain C), one southwest of Kodiak Island (Domain B), and a third spanning southwest of the Shumagin Islands to Unimak Pass (Domain A) due to differences in age-0 pollock size and diet composition found in multiple previous studies (Bailey & Spring, 1992; Wilson, 2009; Wilson et al., 2005, 2013) (Figure 2). After pooling all age-0 pollock caught per domain, we used Welch's ANOVA (Welch, 1947) to test for differences between mean lengths and mean wet weights across the three domains. As wet weight values were not normally distributed, they were Log10 transformed prior to statistical analysis. We further explored pairwise differences in these measures between all domains by performing Tukey honest significant differences tests (Tukey, 1977) due to unequal sample sizes and variances. We reduced the possibility of pseudoreplication by conducting unit means ANOVA (Picquelle & Mier, 2011). Therefore, instead of pooling all age-0 pollock by domain, we compared mean lengths and weights standardized to haul to avoid artificial inflation of sample size.

Furthermore, as our survey moved from the southwest edge to the northeast portion of the sampling grid over the period of a month, we found it necessary to account for the effect of pollock growth over the survey within our proposed domains. For this, we used two different models for comparison:

$$A_i = \beta_0 + \beta_1 \; Day_i + \varepsilon_i. \tag{1}$$

$$A_i = \beta_0 + \beta_1 \; Day_i + \beta_2 \; DomB_i + \beta_3 \; DomC_i + \varepsilon_i, \tag{2}$$

where A_i is either length (mm) or Log10 weight (g) of individual i and Day_i is the day of year fish i was sampled. In Equation (2), domain was added as a factor to test for differences in length among domains, while accounting for differences in sampling day. Also in Equation (2), $\beta0$ is the intercept for Domain A, with $DomB$ and $DomC$ as dummy variables (coded 0 or 1) such that $\beta2$ and $\beta3$ represent the differences in length or weight between Domains A and B and A and C, respectively. We then used AIC (Burnham & Anderson, 2004) to compare both models. We also tested for differences among domains in fish condition by using the log wet weight residuals derived from the relationship of weight as a function of length of individual age-0 pollock, as wet weight residuals are representative of traditional condition indices (Brodeur et al., 2004; Buchheister et al., 2006). We also tested each model to determine if either factor, Day or Domain, was having an outsized influence when combined in the model. We did this using the *vif* (variance inflation factor, VIF) function in R, found in the *car* package (Fox & Weisberg, 2019). The results indicated that neither Day (1.11) nor Domain (3.78) had VIF > 5, suggesting neither factor was exerting a stronger influence on the linear model. These results confirm that Domain and Day do not represent collinear factors in the combined model.

For diet analysis, pollock were binned in 10-mm-size bins. For example, all pollock with a length between 30 and 39 mm were placed into the 30-mm-length bin. As stated above, we identified all prey items to species level, if possible. However, for simplicity, prey taxa were grouped as follows: anomuran crabs, brachyuran crabs, large calanoid copepods (copepods > 2.5 mm prosome length), small calanoid copepods (copepods < 2.5 mm prosome length), chaetognaths, cumaceans, cyclopoid copepods, adult and juvenile euphausiids, fishes, hyperiid amphipods, larvaceans, pteropods, and "others." The "other" category represents the sum total of taxa found in less than 3% of stomachs per pollock 10-mm-length bin.

To determine prey importance in the age-0 pollock diets, we used the percentage of the prey-specific index of relative importance (% PSIRI) (Brown et al., 2012). Fish diet characterization from stomach content analysis traditionally involved relative measures of prey quantity: percent number (%N), percent weight (%W), and percent frequency of occurrence (%FO), which were used to calculate a percent Index of Relative Importance (%IRI; Cortès, 1997). However, because discrete absences were averaged into all measures (i.e., it was not possible to have %N or %W > 0 with %FO = 0), %IRI was flawed in combining mathematically dependent measures: FO was included into the %N or %W equation and then redundantly combined with %FO in the end. This caused %IRI to overemphasize frequently occurring prey and underemphasize rarely occurring prey. In order to alleviate these issues, Amundsen et al. (1996) introduced prey-specific abundance and/or weight. Unlike %N and %W, prey-specific abundances (%PN) or prey-specific weights (%PW) are calculated only using values from stomachs for which that prey occurs. %PSIRI is therefore calculated using %PN and %PW with %FO. %PSIRI was calculated across the entire size range of pollock and in two ways for comparison: one for

generalized taxa groups and another to the highest taxonomic resolution possible. Frequency of occurrence (FO), prey-specific count (% PN_i), and prey-specific weight (%PW_i) were calculated using the following equations:

Frequency of occurrence (FO):

$$FO_i = \frac{n_i}{n}.$$

Prey-specific count (%PN):

$$\%PN_i = \sum_{j=1}^{n} \%N_{ij}/n_i.$$

Prey-specific weight (%PW_i):

$$\%PW_i = \sum_{j=1}^{n} \%W_{ij}/n_i,$$

where %N_{ij} is the count (PN_i) and %W_{ij} is the weight (PW_i)) of prey category i in stomach sample j; n_i is the number of stomachs containing prey i, and n is the total number of stomachs.

The %PSIRI is then calculated

$$\%PSIRI_i = \frac{\%FO_i * (\%PN_i + \%PW_i)}{2}.$$

All data analysis was conducted using R statistical analysis software (R Core Team, 2020).

3 | RESULTS

3.1 | Walleye pollock spatial distribution

The highest concentrations (greater than 5 per m^2) of age-0 pollock were found in Domain A with lower concentrations found predominately inshore of Domain B (Figure 3a). Mean pollock abundance (number m^{-2}) in Domain A (0.92, SE ± 1.21) was exponentially greater than both Domain B (0.0086, SE ± 1.66) and Domain C (0.000067, SE ± 1.89). Very low or zero abundances of age-0 pollock were found on a large swath of offshore stations from the middle of Domain B spanning to the northeast portion of the survey grid. Conversely, the mean weight (g) of individual age-0 pollock caught per station
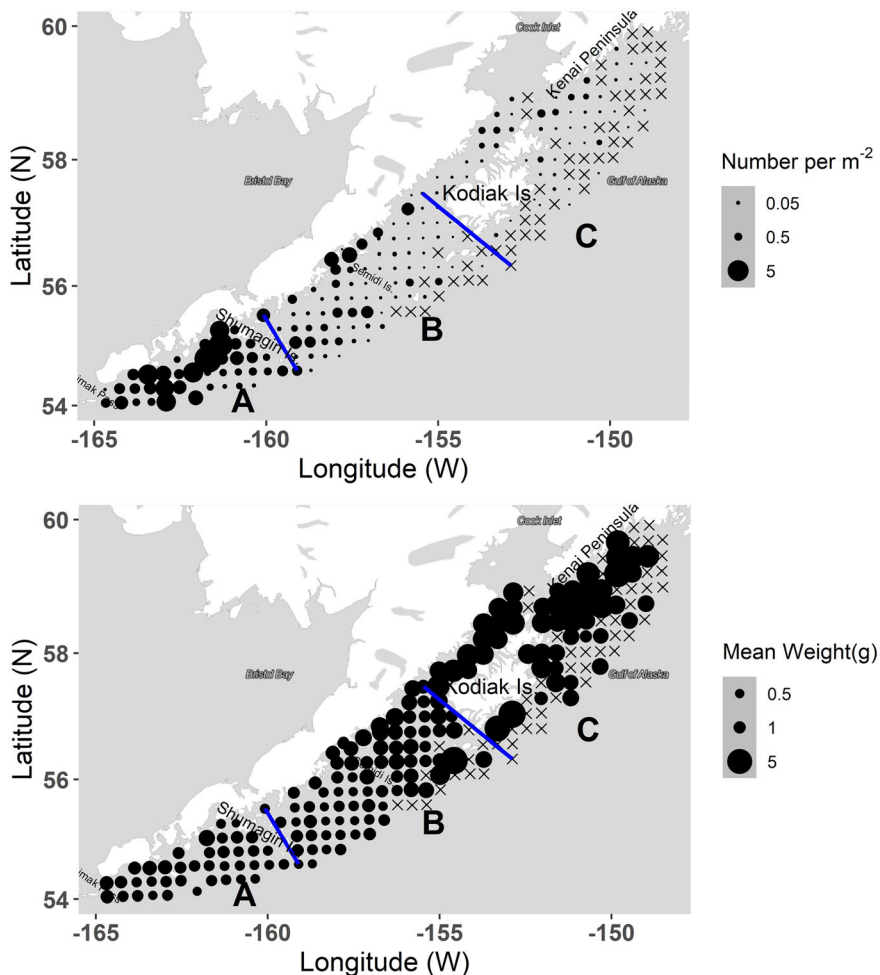
FIGURE 3 . (a, b) Top: Abundance (number m^{-2}) of age-0 pollock. Bottom: Mean weight (g) of age-0 pollock by station. Stations with "**x**" indicate an abundance of zero

followed a gradient of small to large from southwest to the northeast along the survey grid (Figure 3b).

3.2 | Effect of sample date

Results of linear models on fish length and weight being either a function of only sample timing (day of year) or of both sample timing and spatial area (domain) yielded a lower AIC value for the latter model (length: Equation 1 AIC = 10904.49 vs. Equation 2 AIC = 10854.58; weight: Equation 1 AIC = 319.47 vs. Equation 2 AIC = 287.01). Even though we found statistical differences in log wet weight residuals by domain, we believe that this is an artifact of high sample size ($n = 1462$). Boxplots of log wet weight residuals revealed median values very close to zero for all three domains (Figure 4).

3.3 | Walleye pollock domain length and weight comparisons

Standard length (mm) histogram showed a median fish length of 47 mm for pollock found in Domain A, 51 mm for pollock in Domain B, and 72 mm for pollock found in Domain C (Figure 5). A length versus weight scatterplot (Figure 6) and boxplots of fish lengths, weights, and abundance (Figure 7a–c) showed differences between the domains. Welch's ANOVA found significant differences in mean fish abundance (p value $= 2.2 \times 10^{-8}$), mean length (p value $< 2.2 \times 10^{-16}$), and mean wet weight (p value $< 2.2 \times 10^{-16}$) between the domains. The post hoc test (Tukey honest significant differences) found significant differences (adjusted p < 0.001, all cases) in both mean standard length and wet weight between all domains. The differences in mean standard length

(mm) between domains were as follows: A vs. B = 4.43, A vs. C = 24.18, B vs. C = 19.74; and differences in mean wet weight (g) between all domains were as follows: A vs. B = 1.28, A vs. C = 3.67, B vs. C = 2.86. The results of the unit means ANOVA analysis, where we accounted for the possible effect of station haul, also found significant differences between domains: mean standard length (mm): A vs. B = 5.14 (adjusted p value = 0.002), A vs. C (adjusted $p < 0.001$) = 22.68, B vs. C = 17.54 (adjusted $p < 0.001$); and differences in mean Log10 wet weight (g) between all domains: A vs. B = 0.12 (adjusted p value = 0.002), A vs. C = 0.53 (adjusted $p < 0.001$), B vs. C = 0.41 (adjusted $p < 0.001$).

3.4 | Diet overview by pollock size

Age-0 pollock diet composition differed primarily in Domain A versus the other two domains (Figure 8). A high percentage of pteropods and small copepods (around 45%) were consumed by 30-mm ($n = 17$) pollock in Domain A, whereas 30-mm pollock in Domain B consumed a similar percentage of large calanoid copepods and hyperiid amphipods. Domain A and B fish in the same size class consumed similar amounts of adult and juvenile euphausiids (between 40% and 50%). There were differences in diet composition in 40-mm pollock between all three domains. Even though 40-mm pollock in Domain A ($n = 62$) consumed pteropods (around 15%), both Domains A and B ($n = 73$) consumed similar amounts of euphausiids and large calanoid copepods, while 40-mm pollock from Domain C ($n = 4$) consumed around 90% large calanoid copepods, understanding that this is merely observational with such a small sample size. Size 50-, 60-, and 70-mm pollock found in domains B and C had almost identical diet compositions of decreasing amounts of large calanoid copepods (20% to 10%) and increasing amounts of adult and juvenile euphausiids
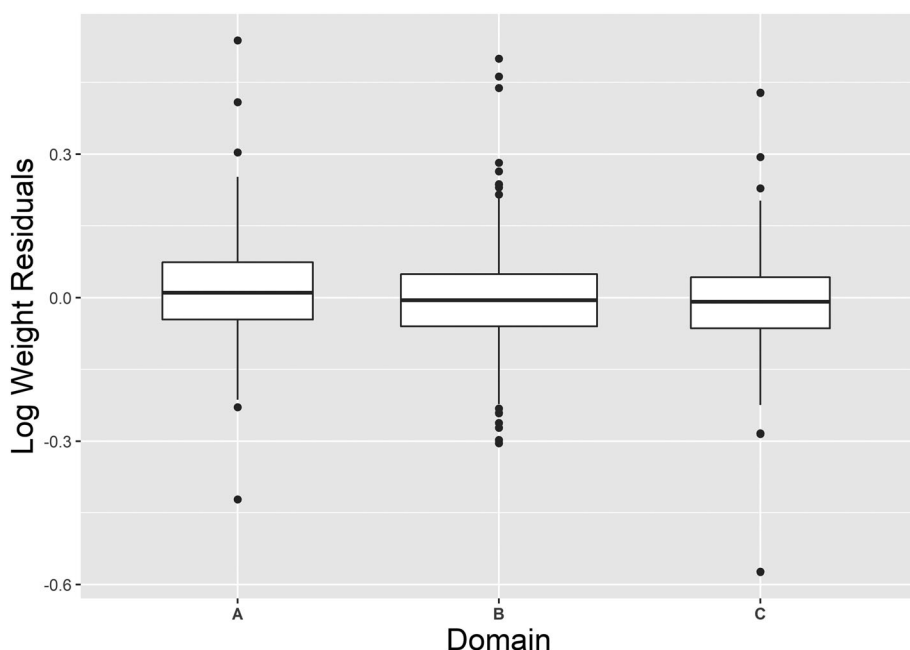

FIGURE 4 Log wet weight residuals for age-0 pollock by domain. Weight residuals are derived from the linear relationship between standard length and wet weight (log-transformed data). The boxes represent the 25% quantile (lower hinge) to 75% quantile (upper hinge). The lower whisker represents the smallest observation ≥ the lower hinge ($-1.5 \times$ inter-quartile range [IQR]); the upper whisker represents the largest observation ≥ the upper hinge ($+1.5 \times$ IQR). All dots below or above the whiskers represent outliers

FIGURE 5 Standard length (mm) histogram of age-0 pollock collected for diet analysis by domain. Dotted lines indicate median fish length in each domain. Number of fish by domain: A ($n = 1158$); B ($n = 1648$); C ($n = 681$)
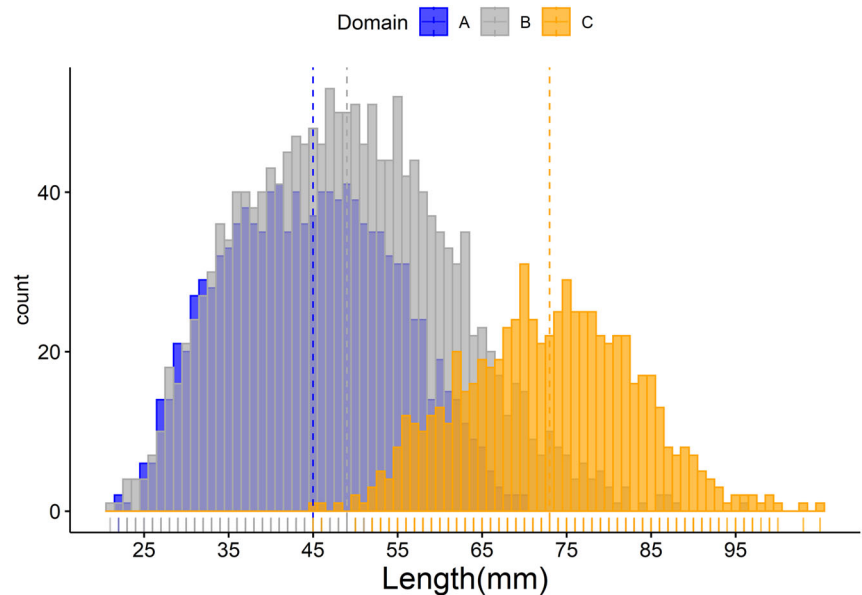
FIGURE 6 Length versus weight scatter plot of age-0 pollock by domain
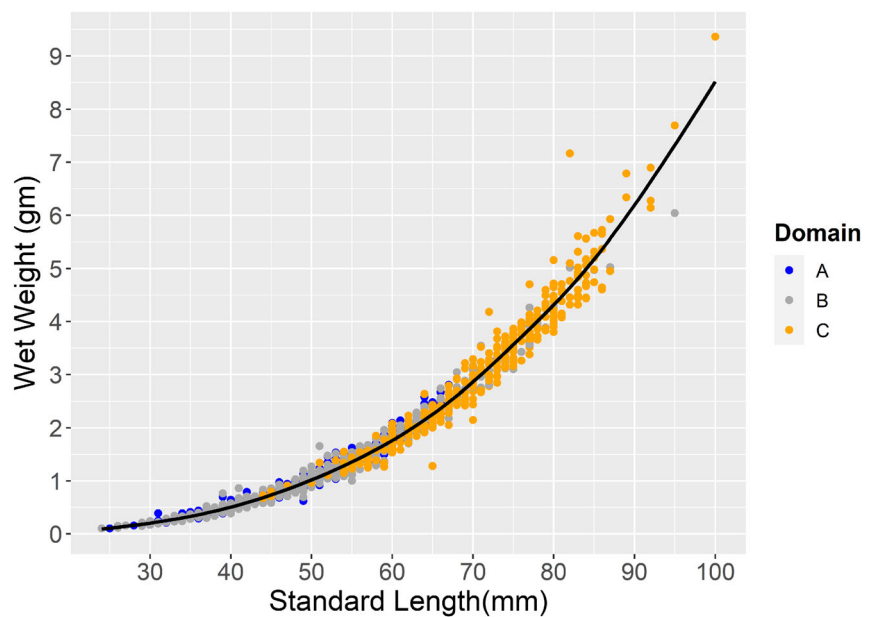
(60% to 80%) as pollock size increased. Within the same size bins, Domain A also displayed increased consumption of adult and juvenile euphausiids with increasing fish size as domains B and C (65% to 75%) and showed decreasing consumption of large calanoid copepods and increasing consumption of larvaceans (10% to 25%). Pollock in the 80-mm bin (domains B, $n = 1$, and C, $n = 53$, only) primarily consumed adult and juvenile euphausiids (Domain B = 50%, Domain C = 75%), with the rest of the prey consisting of large calanoid copepods (35%) and hyperiid amphipods (10%) for Domain B and an even mix of large calanoid copepods, larvaceans, and fish (as prey) (around 5% each) for Domain C. Pollock of 90 mm were only found in Domain C ($n = 6$), consumed 75% adult and juvenile euphausiids, with an increased percentage of fish (as prey) of around 20%.

3.5 | PSIRI results

Adult and juvenile euphausiids were the most important prey items in PSIRI in all three domains (Domain A = 32.8%, B = 43.0%, C = 47.8%) (Figure 9). This was followed by large calanoid copepods for domains B (34.8%) and C (24.5%), but not Domain A, where pteropods were ranked second (19.5%) followed by large calanoids (18.31%). Except for small calanoid copepods (found in all domains), certain taxa were found in two domains only (i.e., Hyperiid amphipods in Domain B and C; pteropods in A and B), and larvaceans in Domains A and C.

Multiple species of euphausiids and _Calanus marshallae_ (a lipid-rich, large calanoid copepod) were found to be important prey in all three domains (Table 1). While Domain A includes these taxa, the
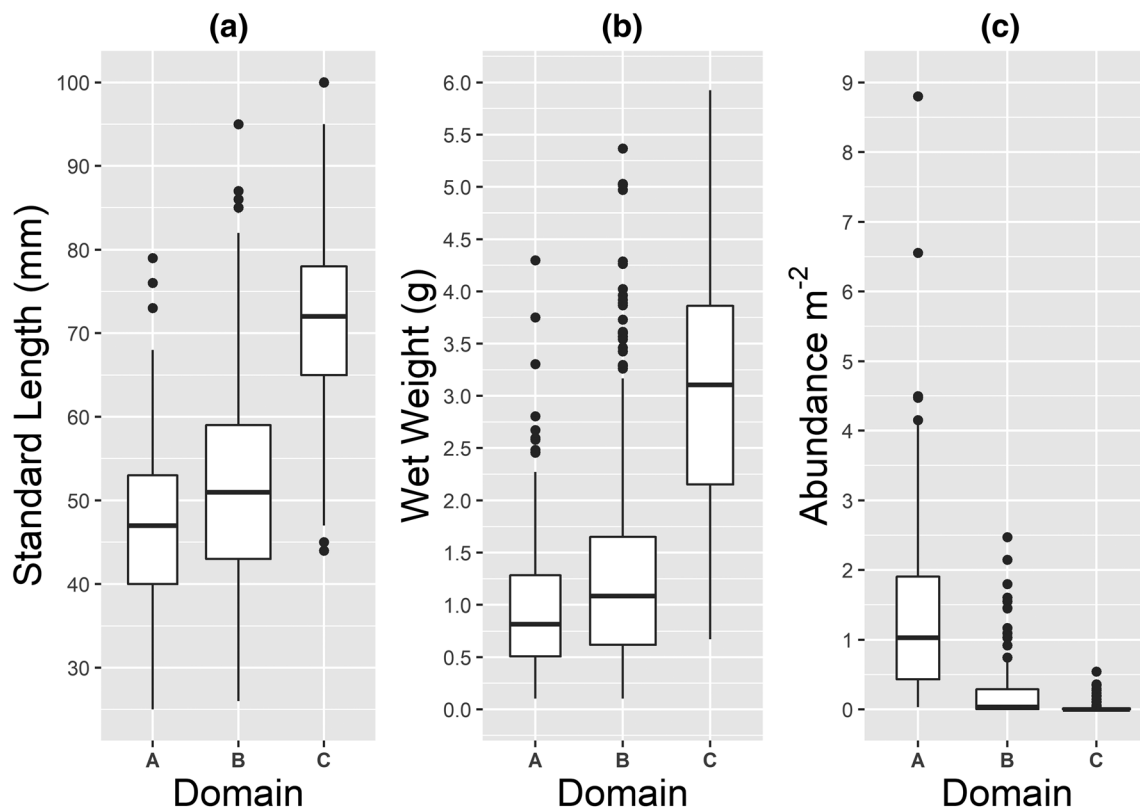
FIGURE 7 (a, b, c) Boxplots showing standard length (mm) (a), wet weight (g) (b), and abundance (m^{-2}) of age-0 pollock (c). The boxes represent the 25% quantile (lower hinge) to 75% quantile (upper hinge). The lower whisker represents the smallest observation ≥ the lower hinge ($-1.5 \times$ inter-quartile range [IQR]); the upper whisker represents the largest observation ≥ the upper hinge ($+1.5 \times$ IQR). All dots below or above the whiskers represent outliers

pteropod *Limacina helicina* was the most important. Domain A pollock also had a high preference for two small copepod species: *Oithona similis* (a cyclopoid copepod) and *Pseudocalanus* spp. (a calanoid copepod). When %PSIRI values are summed by putting euphausiids and *C. marshallae* into one category and all other taxa into another (Figure 9), other taxa have a higher combined %PSIRI value than euphausiids/*C. marshallae* only in Domain A (31% vs. 41% [A], 64% vs. 0% [B], 58% vs. 19% [C]).

3.6 | Top PSIRI zooplankton abundances by domain

Median zooplankton abundances were similar across domains for most taxa, except for pteropods (*L. helicina*), which were almost an order of magnitude higher in median abundance in Domain A compared to B and C (Figure 10). There were also an order of magnitude lower median abundances of larvaceans in Domain B compared with Domains A and C and virtually no hyperiid amphipods in Domain C compared with few in Domains A and B. These findings are supported by the station-specific data, which highlights the high pteropod abundance in Domain A (Figure 11). We also saw a gradient of increasing abundance from southwest to northeast of both small and large calanoid copepods. Adult and juvenile euphausiids, although patchy,

were found in moderate abundances throughout the entire sampling grid. Larvaceans and hyperiid amphipods were found predominately in domains A and C.

4 | DISCUSSION

4.1 | Overview

The 2013 year class of pollock had roughly six times higher abundance as age-0 fish than any year in the data record (2000–2015) and the highest mean abundance per m^2 since 2000 (Figure 1a). This abundance was spatially concentrated between the Shumagin Islands and Unimak Pass (Domain A). Important prey taxa were similar within fish length bins over the entire survey area; that is, the PSIRI found the relative importance of prey in the diet was the same, regardless of location. We found that pollock diet composition was related to lower age-0 size in Domain A, where lower abundance of lipid-rich prey (large copepods and euphausiids) and higher abundance of lipid-poor prey (pteropods and larvaceans) were consumed (Heintz et al., 2013; Lee et al., 2006; Mazur et al., 2007). However, fish condition was similar across all domains, which did not support our hypothesis that condition would be related to pollock diet. Differences in pollock abundance did appear to relate to prey distribution in that the higher
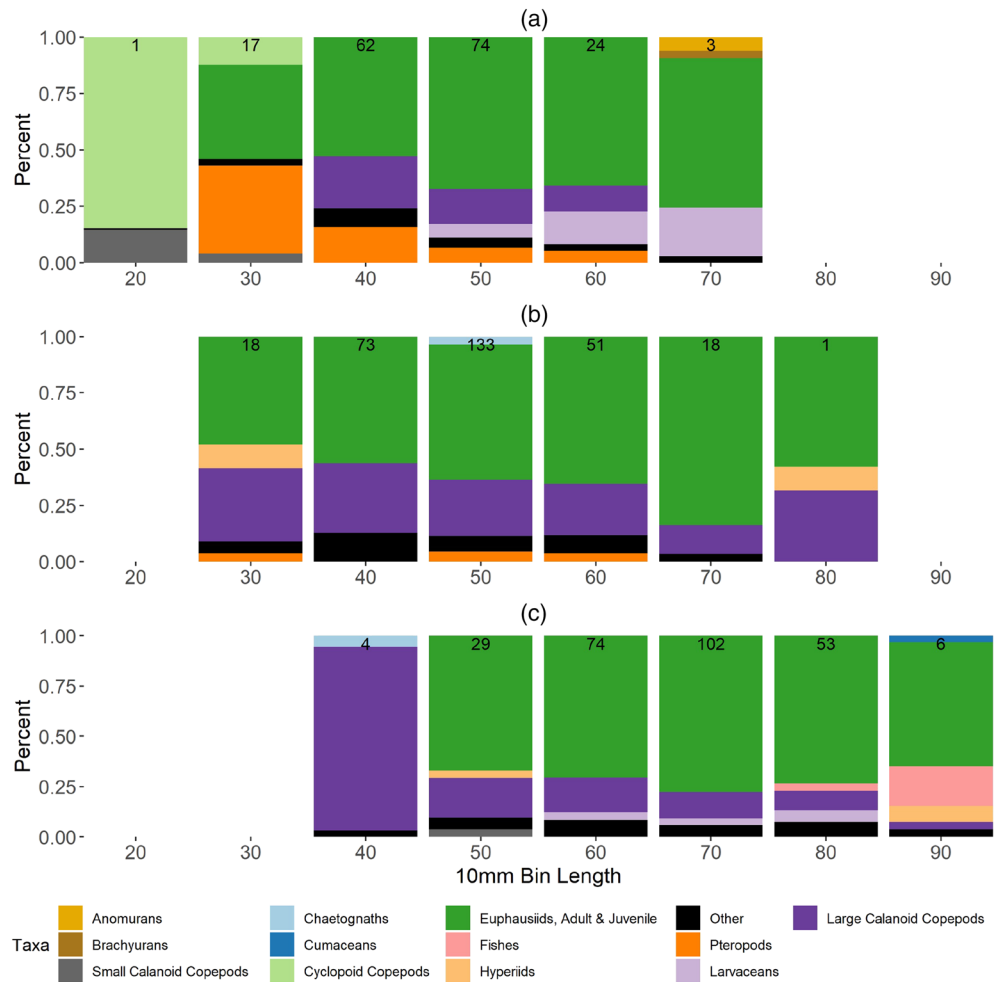
abundance of pollock in the southwest had diets that had a higher proportion of larvaceans and pteropods. These results provide evidence that regional differences in prey taxa affected the survival and eventual low recruitment of the 2013 year class to the pollock fishery. However, we cannot rule out a number of other important factors not explored in this study and in the following we examine the role of diet in relation to these other potential factors affecting recruitment.

The 2013 year class of pollock exhibited the highest age-0 abundances, mean abundance = 0.42 per nautical mile (nmi)^2, in surveys of this spatial scale, with the highest concentrations of pollock found within Domain A. For comparison, previous EcoFOCI surveys with the same sampling methodology as ours show the mean abundance 1.6 times greater than 2005 (0.27 per nmi^2), four times greater than 2007 (0.10 per nmi^2), and many times greater than all other surveys since 2000. Even though age-0 pollock abundance was estimated to be lower in other years, observations of "patchy" aggregations have been noted (Bailey & Spring, 1992; Stabeno et al., 1996; Wilson, 2000). In a previous study (1975–1988) of larval, age-0, and age-2 pollock abundance using the same defined domains as our study, Bailey and Spring (1992) found that relative levels of abundance per domain changed from year to year with no one domain having consistently

more fish. The mean percent abundance of age-0 pollock during that period was 33% in Domain A, 45% in Domain B, and 22% in Domain C. From 2000 to 2015, the average percent abundance per domain (including 2013 data) was 24% Domain A, 76% Domain B, and 12% Domain C. Not including 2013 data, the average was 7% Domain A, 85% Domain B, and 14% Domain C; 2013 was unique, with age-0 percent abundance of 71% Domain A, 25% Domain B, and 4% Domain C. In the Bailey and Spring (1992) study, only 1977 showed a similarly large aggregation in Domain A (64% Domain A, 25% Domain B, and 11% in Domain C).

4.2 | Effect of diet on recruitment

Studies of juvenile pollock have shown that overwinter survival and recruitment success increases when fish attain larger body size and increased lipid content as a result of preying upon lipid-rich, high energetic taxa (Heintz et al., 2013; Siddon et al., 2013; Sogard & Olla, 2000). High body condition and energy reserves from lipid storage have been shown to be important for overwinter survival. It has been well documented that many marine zooplankton accumulate storage lipids that have a high-energy content (Heintz et al., 2013;
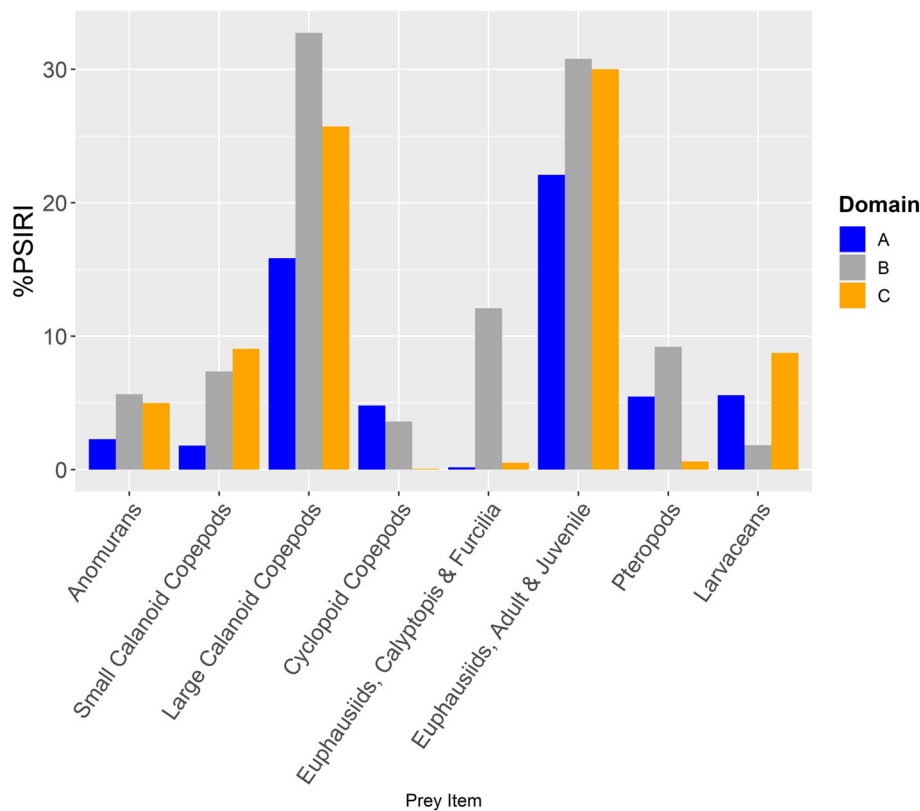
FIGURE 9 Top percent PSIRI group taxa for all domains

TABLE 1 All specific taxa with a %PSIRI value greater than 5%, by domain

| Prey	%PSIRI > 5%
Domain A: SW of Shumagin Is.	
Limacina helicina	19.5
Euphausiidae	14.7
Thysanoessa spp.	11.0
Oithona similis	8.7
Oikopleura spp	7.6
Pseudocalanus spp.	5.4
Calanus marshallae	5.2
Domain B: Between Shumagin Is. and Kodiak Is.	
Euphausiidae	26.1
Calanus marshallae	23.9
Thysanoessa inermis	7.5
Thysanoessa spp.	6.7
Domain C: Kodiak Is. and NE	
Euphausiidae	20.3
Thysanoessa spp.	15.9
Calanus marshallae	12.9
Oikopleura spp.	12.4
Thysanoessa inermis	8.8
Metridia lucens/pacifica	6.4

Note: Digestion level of prey items was a determining factor on the level of specificity of identification, which is why "Euphausiidae" were grouped above because they could not be identified to genus.

Lee et al., 2006). A large portion of the "large calanoid copepod" prey category in this study consists of the lipid-rich calanoid copepod *Calanus marshallae*. In a study of temperature and prey quality effects on the growth of juvenile pollock within our study region, Mazur et al. (2007) found the mean energetic content of calanoid copepod species (including *C. marshallae*) was 24.6 kJ dry g^{-1} and 20.9 kJ dry g^{-1} for all species of juvenile and adult euphausiids. Conversely, lower energetic values were found for pteropods (11.9 kJ dry g^{-1}) and larvaceans (15.0 kJ dry g^{-1}) (Mazur et al., 2007). *Oithona similis* (female size range: 0.43–0.82 mm) is a very small copepod compared with *C. marshallae* (female size range: 2.9–4.5 mm) and has lower energy content (mean total lipid mass of 0.6 µg per individual^{-1}, Lischka & Hagen, 2007). Therefore, the scenarios presented above could have cascading effects on Domain A pollock overwinter survival and recruitment.

4.3 | Advection

A potential explanation for the higher pollock abundances in Domain A could be advection. It has been documented that the majority of pollock in the WGOA spawn in Shelikof Strait, where the Alaska Costal Current (ACC) carries larvae to the southwest along the Alaska Peninsula or into offshore waters of the Gulf of Alaska (Hinckley et al., 1991; Hinckley et al., 2001; Parada et al., 2016). Multiple studies have found high abundances of age-0 pollock along the continental shelf of the Alaska Peninsula, anywhere from the Semidi Islands to past the Shumagin Islands (Wilson et al., 1996). A spring
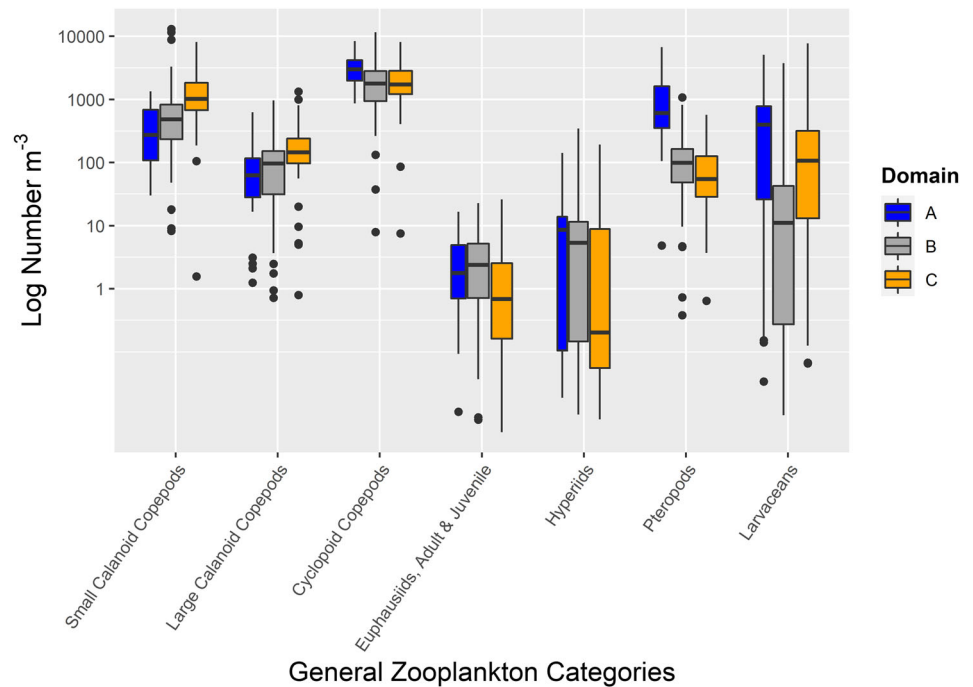
ichthyoplankton survey conducted earlier in 2013 and in the same region as Domain A found very dense aggregations of larval pollock (>5000 10 m^{-2}) centered just southwest of Kodiak Island (data not shown). Using both drifters and 1 year of mooring data, it is believed that 75% of the Alaska Coastal Current flows southwest in the sea valley between the Chirikof and Semidi islands, with the remaining 25% flowing along the Alaska Peninsula, bifurcating at the Shumagin Islands (Stabeno, Danielson, et al., 2016). Even though it is possible that this larval aggregation was advected along the Alaska Peninsula and into Domain A, we have no applicable data from 2013 to test this hypothesis. However, a recent study by Wilson and Laman (2020) found that hypothetical displacement (based on cumulatively summed wind vectors and measured in km) of age-0 pollock was strongest in 2013 compared with all other years of their study. They also found that age-0 pollock population density and recruitment to age-2 was dependent upon region. The percent variance in age-2 recruitment explained by age-0 abundance was highest in the Kodiak (96%) and Shelikof (88%) regions, our domains C and B, respectively. Lastly, Wilson and Laman (2020) found no significant relationships between age-0 abundance and age-2 recruitment for the southwest region, our Domain A.

With its proximity to Domain A, there is also the possibility that the large aggregation of age-0 pollock could have been advected through Unimak Pass after our sampling, affecting Gulf of Alaska stock assessment estimations of recruitment. Water from the WGOA enters the Bering Sea through the Aleutian Passes, with the greatest net transport through Unimak Pass. During the winter months, Unimak Pass and Bering Canyon replace half the water on the southeastern Bering Sea shelf (Stabeno et al., 2017; Stabeno, Bell, et al., 2016). Mooring data have shown a strong seasonal flow through the pass, with weak mean flow between May and September

(6.2 cm s^{-1}) and the strongest mean flow between October and April (21.3 cm s^{-1}). Our survey for age-0 pollock occurred in August and September 2013. From July to December 2013, flow through Unimak Pass to the Bering Sea increased from ~6 to 16 cm s^{-1} (Figure 9; Stabeno et al., 2017). Routine swimming speeds of juvenile pollock with a standard length between 70 and 90 mm range from 5 to 8.5 cm s^{-1} at 5°C water temperature (Hurst, 2007a.). Assuming that fish smaller than 70 mm routinely swim slower, the current speeds through Unimak Pass were greater than the swimming speeds of juvenile pollock found in our study, making advection into the Bering Sea possible. Also, given the relatively poor feeding conditions in Domain A suggests these fish advected into the southeastern Bering Sea may have been in search of higher quality prey. However, in the time period after our survey, the ACC became stratified and many of the pollock in question would be over 70 mm and able to migrate vertically, so this advection seems unlikely.

4.4 | Density dependence

The high abundances of relatively small age-0 pollock found in Domain A could increase the likelihood of overwinter mortality due to density-dependent competition for food (Cowan et al., 2000; Houde, 1997; Sogard, 1997; Sogard & Olla, 2000). The full size range of pollock in the study consumed very similar prey taxa and prey abundances did not differ greatly between regions. In other words, there was little evidence of food limitation overall. The most important prey taxa consumed by pollock in domains B and C consisted of both euphausiids and large calanoid copepods, which has been observed in other studies (Wilson, 2009; Wilson et al., 2006, 2013). However, in Domain A, a higher percentage of other taxa were
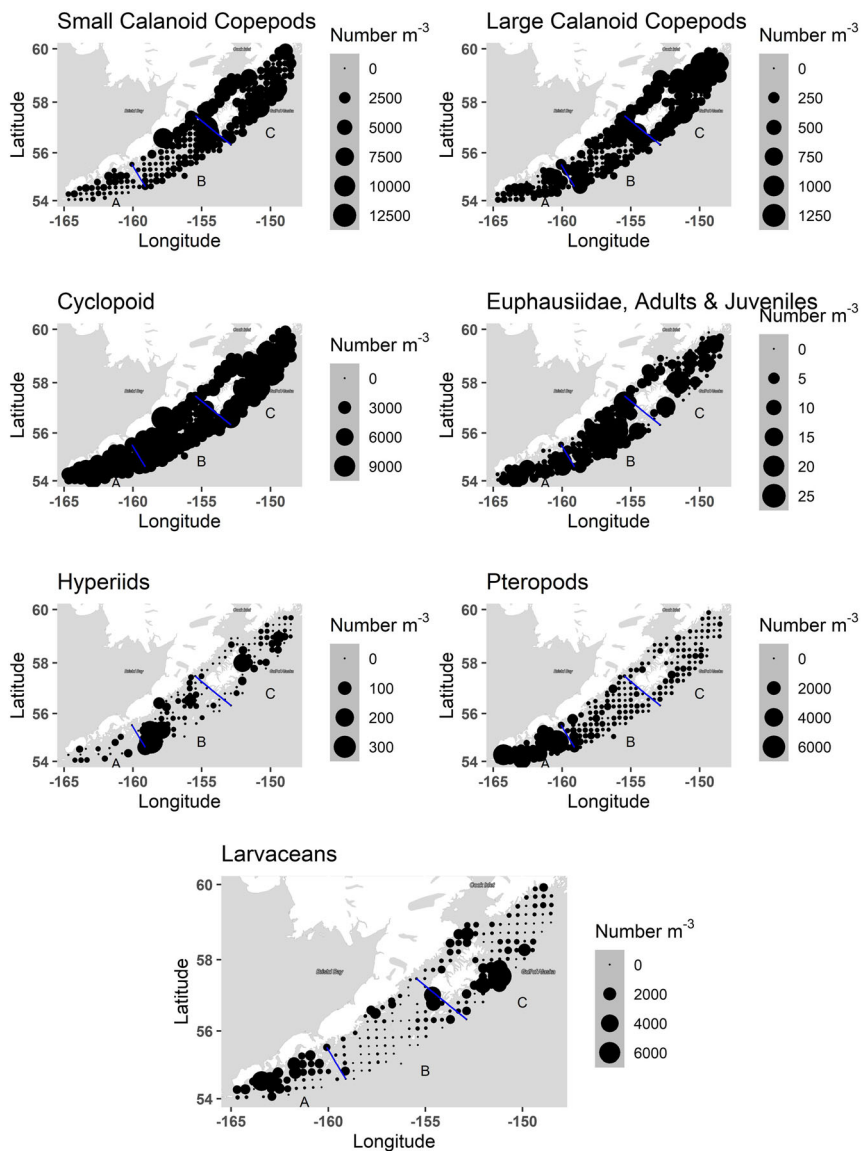
FIGURE 11 Spatial zooplankton abundance (number m^{-3}) of top %PSIRI taxa, by domain

consumed: the pteropod *Limacina helicina*, the pelagic tunicate larvacean *Oikopleura* spp., and the small cyclopoid copepod *Oithona similis*. One hypothesis for this observation would be that the exponentially higher abundance of both *L. helicina* and *Oikopleura* spp. observed in Domain A caused these prey items to appear in higher numbers in the diet. This would not indicate density-dependent competition. However, as abundances of large calanoid copepods were lower and euphausiids were similar compared with the other domains, it could be hypothesized that competition for large copepods and euphausiids occurred. Our data cannot test either hypothesis directly, therefore we can only suggest competition as another factor that may have affected the recruitment of the 2013 year class.

4.5 | Cannibalism

Smaller fish may also be more susceptible to predation and cannibalism, increasing the likelihood of overwintering mortality (Hurst, 2007b;

Hurst & Conover, 1998; Sogard, 1997). Walleye pollock cannibalism can impact population sizes of specific year classes, as has been shown in the Bering Sea (Wespestad et al., 2000). The likelihood of cannibalism acting as a density-dependent regulator of population size increases in conditions of low food availability, high fish abundance, greater size disparity among fishes, and an absence of refuge areas (Smith & Reay, 1991). The estimated age-1 returns of the 2012 year class of pollock were extremely high (figure 1b from Dorn et al., 2019; table 1.20). Given the conditions of very high age-1 pollock abundance combined with dense spatial aggregations of age-0 pollock, we believe it was possible that the high abundances of small age-0 s in Domain A were cannibalized by the much larger 2012 age-1 pollock.

4.6 | Summary

In summary, we believe that poor recruitment of the 2013 age-0 pollock year class in the WGOA was mostly likely due to the

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combined effects of sub-optimal diet in a large portion of the population (this study), wind-driven advection of a large proportion of the population to the southwest (Wilson & Laman, 2020), and perhaps cannibalism from the 2012 year class. A large portion of age-0 pollock consumed less energy-rich prey could decrease the chances of reaching an adequate weight necessary for overwinter survival. Information gathered from this study should inform fisheries managers to consider the spatial distribution of age-0 pollock throughout a survey region and the potential impact consuming low-quality prey will have on subsequent recruitment.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare with this research.

AUTHOR CONTRIBUTIONS

JFL conceived of the project, acquired the EcoFOCI fish data, analyzed the data, and drafted the manuscript. DGK helped with project design, analysis, and writing. Both authors give final approval of the version to be published, take public responsibility for its content, and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

DATA AVAILABILITY STATEMENT

Data available on request of the authors.

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