

Abstract—Cannibalism is thought to be an influential top-down process affecting walleye pollock (*Theragra chalcogramma*) recruitment in the eastern Bering Sea (EBS). In summer, many age-1 pollock occupy the same depths as those of adult walleye pollock, making them vulnerable to cannibalism. We examine factors that influence the occurrence and amount of cannibalism, as well as the abundance and co-occurrence of predator and prey walleye pollock. Large walleye pollock were generally found in deeper waters and avoided cold temperatures; whereas, age-1 walleye pollock were found in broader bottom depth and temperature ranges. The occurrence of cannibalism was highest in the area where predator and prey walleye pollock co-occurred and the amount of cannibalism was highest on the middle and outer EBS shelf. Both the occurrence and amount of cannibalism were influenced by location, bottom temperature and bottom depth, and the abundance of prey walleye pollock. The abundance of both large and small walleye pollock decreased during the 1982–2006 survey period in the EBS and, hence, the occurrence and amount of cannibalism also decreased. The occurrence and amount of cannibalism observed in the diet samples from the summer survey were good indicators of year-class strength, as estimated by the stock assessment model. There was more cannibalism of age-1 walleye pollock when predicted recruit abundance was highest, indicating that summer cannibalism on age-1 walleye pollock, a top-down process, does not control walleye pollock recruitment in the EBS.

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Factors influencing cannibalism and abundance of walleye pollock (*Theragra chalcogramma*) on the eastern Bering Sea shelf, 1982–2006

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Recruitment of fish to fisheries depends on survival during the early life history (Hjort, 1914; Parker, 1966; Bailey and Spring, 1992; Bradford, 1992). Factors that can affect survival during early life stages and subsequent recruitment to fisheries may be related to environmental or bottom-up factors (Hollowed and Wooster, 1992; Hunt et al., 2002) and predatory or top-down factors (Wespestad et al., 2000; Hunt et al., 2002; Mueter et al., 2006). Both top-down and bottom-up forces have been hypothesized as contributing to recruitment of one of the largest fishery resources in the eastern Bering Sea, walleye pollock (*Theragra chalcogramma*; hereafter referred to as pollock; Mueter et al., 2006)

Pollock in the eastern Bering Sea (EBS) comprise the highest-volume commercial fishery in the United States (NMFS, 2010). Their recruitment is widely believed to be influenced by a combination of environmental and density-dependent effects (Hollowed and Wooster, 1992; Mueter et al., 2006). In the EBS, for example, bottom-up forces that may affect pollock recruitment include the effect of the extent, timing, and duration of ice, ocean currents, and temperature on primary and secondary productivity (Wespestad et al., 2000; Mueter et

al. 2006; Coyle et al., 2011; Hunt et al., 2011). Top-down processes, such as predation, including cannibalism, are also important influences on EBS pollock survival (Dwyer et al., 1987; Mueter et al., 2006, 2011).

Cannibalism is recognized as an important factor occurring year-round and affecting the survival and recruitment of pollock in the EBS (Bailey and Houde, 1989; Mueter et al., 2006, 2011). In the fall, age-0 pollock are heavily cannibalized by older pollock (Dwyer et al., 1987), a density-dependent process that is hypothesized to affect the year-class strength and recruitment to the adult population (Wespestad et al., 2000). Additionally, in the summer, cannibalism on age-1 pollock occurs (Bailey and Dunn, 1979; Francis and Bailey, 1983; Dwyer et al., 1986, 1987) and may also affect subsequent year-class strength. Factors hypothesized to affect pollock cannibalism include: water column stratification and temperature and their effects on food availability; and the horizontal and vertical overlap of prey and predator pollock (Francis and Bailey, 1983; Bailey, 1989; Wespestad et al., 2000; Duffy-Anderson et al., 2003; Mueter et al., 2006; Hunt et al., 2011).

Summer temperatures and water column stratification on the EBS shelf

are largely determined by sea-ice conditions during the preceding winter and mixing forces during the summer (Kachel et al., 2002; Stabeno et al., 2010). As a result, the EBS shelf comprises 3 depth domains (generally, coastal <50 m, middle 50–100 m, and outer 100–180 m), each with its own hydrographic features: a mixed water column in the coastal domain, a 2-layered water column in the middle domain, and a 3-layered water column in the outer domain (Stabeno et al., 2001). Water temperature and stratification can affect the amount of primary and secondary production, the growth and timing of zooplankton, and zooplankton species composition (Stabeno et al., 2001; Napp et al., 2002; Rho et al., 2005), thereby affecting food availability for EBS fish and their subsequent survival. Mueter et al.¹ found evidence for environmental effects on age-1 pollock survival and recruitment. During November to March, ice forms and extends from the Bering Strait in the north to the Alaska Peninsula in the south (Napp et al., 2000). The southerly extent and timing of ice (arrival and persistence) in winter and early spring have a strong effect on the size and southerly extent of the cold pool (bottom water <2°C) (Stabeno et al., 1998, 2001; Kachel et al., 2002). The cold pool can directly affect the distribution of some upper trophic level species, including adult pollock (Napp et al., 2000).

The vertical and horizontal distribution of pollock varies ontogenetically, seasonally, and temporally (Hinckley, 1987; Kotwicki et al., 2005; Bacheler et al., 2010). Adults generally spawn at depths between 100 and 250 m from January to August, depending on the spawning area (Hinckley, 1987; Bacheler et al., 2010). As part of a feeding migration in summer, most pollock on the shelf migrate towards the northwest and pollock on the southeast shelf migrate towards the northeast (Kotwicki et al., 2005). Adult pollock are demersal and distributed on the outer and middle depth domains in summer. Adults prefer cooler and stable temperatures (Duffy-Anderson et al., 2003) but avoid the cold pool (Chen, 1983; Bakkala and Alton, 1986). Upon hatching, young pollock larvae are distributed in the upper water column and are subject to currents and wind-driven advection (Nishiyama et al., 1986). Larvae undertake small diel vertical migrations within the upper 30 m of the water column (Pritchett and Haldorson, 1988). Bailey (1989) observed that, in the fall months, small-size age-0 pollock (<60 mm fork length) remained in surface EBS waters above the thermocline, but larger age-0 pollock (70–89 mm fork length) moved to deeper depths, below the thermocline in the daytime, thereby making them vulnerable to cannibalistic adults at that time of year. In the summer months, older pollock (age-1 and age-2) have been found within and inshore of the cold

pool (Francis and Bailey, 1983), as well as throughout the water column (Bakkala and Alton, 1986) because they are able to tolerate more variable temperatures than adults (Chen, 1983; Duffy-Anderson et al., 2003). There is a tendency for age-1 and age-2 pollock to be vertically separated, with the age-1 pollock near the bottom and age-2 pollock distributed higher in the water column (Duffy-Anderson et al., 2003). In the summer months, therefore, age-1 pollock are vulnerable to cannibalistic adults. In fact, in the EBS during summer, age-1 pollock comprised the majority of cannibalized prey pollock (Dwyer et al., 1987). The factors that determine the occurrence and amount of cannibalism on age-1 pollock are not well understood.

Our goal was to determine the factors that affect the occurrence and amount of cannibalism on vulnerable pollock in the summer. Age-1 pollock often occupy the same depths as adult pollock in the summer, thereby making them vulnerable to cannibalism (Dwyer et al., 1987; Duffy-Anderson et al., 2003). Our specific objectives were to determine which environmental factors influence the occurrence and amount of pollock cannibalism, as well as the factors that influence the abundance of predator and prey pollock and their co-occurrence. One working hypothesis was that the abundance of large predatory pollock and small prey pollock and their co-occurrence are determined by temperature, depth, location, the presence of the cold pool, and year. These covariates were also examined for their influence on the occurrence of cannibalism, along with other covariates: the size of predators, and the co-occurrence of both large predatory pollock (>200 mm standard length [SL]) and small prey pollock. Owing to their vertical distribution in the water column, small prey pollock that may be vulnerable to cannibalism measure 60 to 200 mm SL, a size that corresponds to the size of age-1 pollock in the summer. A final hypothesis tested was that, where cannibalism occurs, the amount of cannibalism is determined by the size of predators, bottom temperature, bottom depth, location, the presence of the cold pool, year, and the abundance of vulnerable prey pollock (60–200 mm SL).

Materials and methods

Pollock abundance

Abundance, co-occurrence, and diet data on predator and prey pollock were collected during the annual National Marine Fisheries Service (NMFS) bottom trawl surveys of the EBS shelf (≤200 m depth) from 1982 to 2006 (excluding 1983 and 1984, when pollock diet data were not collected). Groundfish species were captured at stations on a regular grid of the EBS shelf (Fig. 1). The details of the survey design and sampling methods are described in Lauth (2010) and Stauffer (2004). Pollock captured in the bottom trawl were weighed and measured for length. A subset of pollock was selected for stomach content analyses. Pollock catch per unit of effort (CPUE,

¹ Mueter, F. J., M. C. Palmer, and B. L. Norcross. 2004. Environmental predictors of walleye pollock recruitment on the Eastern Bering Sea shelf. Pollock Conservation Cooperative Research Center, Univ. Alaska, Fairbanks. [Available from [http://www.sfos.uaf.edu/pcc/projects/03/norcross/MueterNorcross Final Report 2003.pdf](http://www.sfos.uaf.edu/pcc/projects/03/norcross/MueterNorcross%20Final%20Report%202003.pdf), accessed April 2012.]

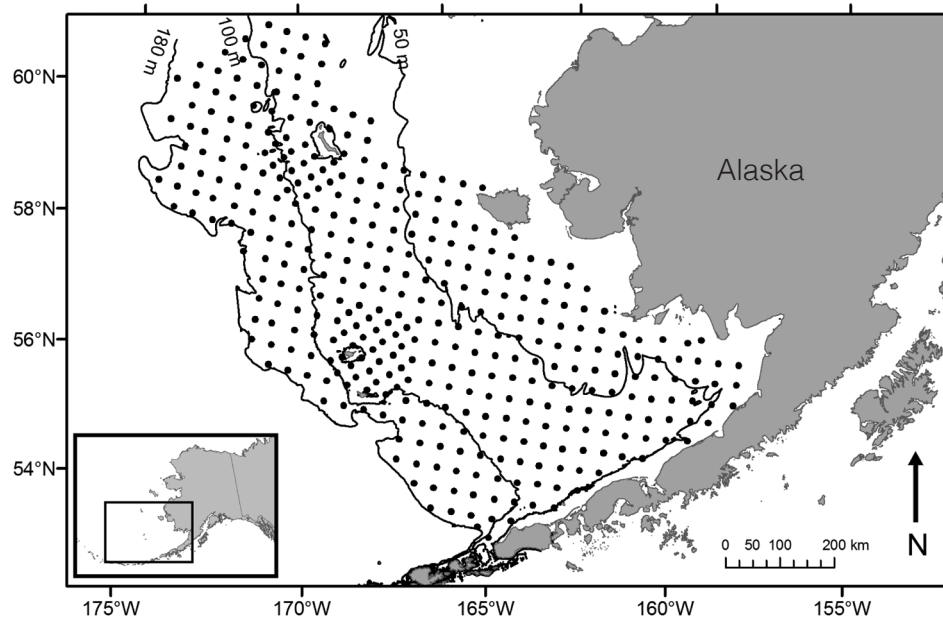


Figure 1

Study area on the eastern Bering Sea shelf (≤ 200 m depth) showing the stations sampled annually in the National Marine Fisheries Service bottom trawl survey for groundfish species, including walleye pollock (*Theragra chalcogramma*), during 1982–2006 (excluding 1983 and 1984). Three depth domains of the shelf are delineated by depth contours (coastal < 50 m, inner 50–100 m, and outer 100–180 m).

number of fish per hectare) was estimated by size class by using the area swept by the net (average net width measured during the bottom trawl haul multiplied by the distance the net was towed over the seafloor). Based on diet information, the assumption was made that small pollock caught in the survey were potential prey (sum of small [60–200 mm SL] pollock CPUE; *SmallPollock*), and large pollock were assumed to be potential predators (sum of large [> 200 mm SL] pollock CPUE; *LgPollock*). Predator-prey co-occurrence (*Overlap*) between *SmallPollock* and *LgPollock* was determined for each station and designated a value of 1 (co-occurrence) if the CPUE values of both were greater than zero, otherwise a value of 0 was assigned (no co-occurrence).

Bottom temperature, cold pool, and depth

Water temperature and depth profiles were collected at each station by using bathythermographs attached to the headrope of the bottom trawl net (expendable models before 1993 and microbathythermographs in later years). Bottom depths and temperatures were recorded for each station. It was also noted whether the cold pool (temperatures $< 2^\circ\text{C}$) was present or absent at each station (binomial variable, *ColdPool*; see Buckley et al. [2009] for a description).

Pollock abundance models

General additive models (GAMs) were used to explore the relationship between pollock abundance and pre-

dictor variables (covariates). The 3 response variables examined were large predatory pollock CPUE (> 200 mm SL, *LgPollock*), small prey pollock CPUE (60–200 mm SL, *SmallPollock*), and the co-occurrence of *LgPollock* and *SmallPollock* (*Overlap*). Pollock CPUE values (*SmallPollock* and *LgPollock*) were $\ln+1$ transformed to achieve normality. Because the timing of the survey and overall abundance of pollock changed from year to year, “Year” was included as a categorical predictor. Pollock catch or the occurrence of cannibalism (e.g., inshore vs. offshore stations) may have been influenced by station location; therefore, station location (latitude and longitude) was included as a single, smoothed bivariate term, $s(\text{latitude}, \text{longitude})$, and referred to as “Location” in the GAMs. Latitude may limit the northerly distribution of pollock and longitude may be important in terms of distribution with depth. Because bottom temperature and bottom depth are related, a smoothed bottom temperature and bottom depth interaction term was included (*TempDepth*). The presence or absence of the cold pool was included as a binomial term (*ColdPool*) in the model as well. Survey duration typically extended over the entire summer period from June to August (i.e., fish likely grew or moved during the time it took to complete the survey and collect the data in one year), therefore Julian day was considered for inclusion in models. The groundfish survey, however, began in the southeast and proceeded to the northwest Bering Sea, and the day of year was significantly correlated with latitude and longitude (coefficient of determination [r^2]=0.390 and 0.817, $P < 0.001$ and < 0.001 , respectively).

Separation of the effect of Julian day from the effect of location on abundance and cannibalism was, therefore, not possible and Julian day was not directly included in further analyses.

A step-wise model-selection approach was used for GAMs, where all covariates were included in initial models and covariates with the least significant P -values ($P > 0.05$) were removed one at a time in subsequent models until all covariates in the model were significant. The “mgcv” (Wood, 2000) library in R (R Development Core Team, 2010) was used to run the GAM models.

Pollock diet

For pollock that were subsampled from each trawl haul for diet information, lengths and weights were measured and stomach contents were removed. Stomach contents of pollock were identified to the lowest possible taxonomic category (10 prey categories), enumerated, and weighed, and in the case of prey fish, measured. The 10 prey categories were chaetognaths, euphausiids, amphipods, copepods, crab, miscellaneous, and pollock (<60 mm standard length [SL], 60–200 mm SL, ≥200 mm SL, and unmeasured). If unmeasured (i.e., too digested to measure), and prey pollock were accompanied by measured prey pollock in the same predator stomach, the unmeasured prey items were assigned the same average length as the measured pollock, otherwise, they were not included in the analyses. The percent frequency of occurrence, partial fullness, and percent body weight of each prey item were calculated for each predator pollock and then averaged over predator size categories (*PredatorLength*) at each station in each year. Predator length categories were 1–19 cm, 20–29 cm, 30–39 cm, 40–49 cm, 50–59 cm, and >60 cm fork length (FL). The presence or absence (*PA*) of cannibalism (1=cannibalism present; 0=cannibalism absent) was recorded. Percent frequency of occurrence (%*FO*) was calculated as

$$\%FO = \frac{n_p}{n_f},$$

where n_p = the number of predators that consumed prey type p ; and

n_f = the number of predators with food (f) in their stomachs at that station.

Percent body weight (%*BW*) was calculated as

$$\%BW = \left(\frac{100}{n_p} \right) \times \sum \left(\frac{W_{pj}}{BW_j} \right),$$

where W_{pj} = the weight of prey type p in predator j ; and BW_j = the body weight of predator j .

Partial fullness (*PF*) was calculated as

$$PF = \%FO \times \%BW.$$

If %*FO* was zero, a value of zero was assigned to *PF*.

Pollock diet models

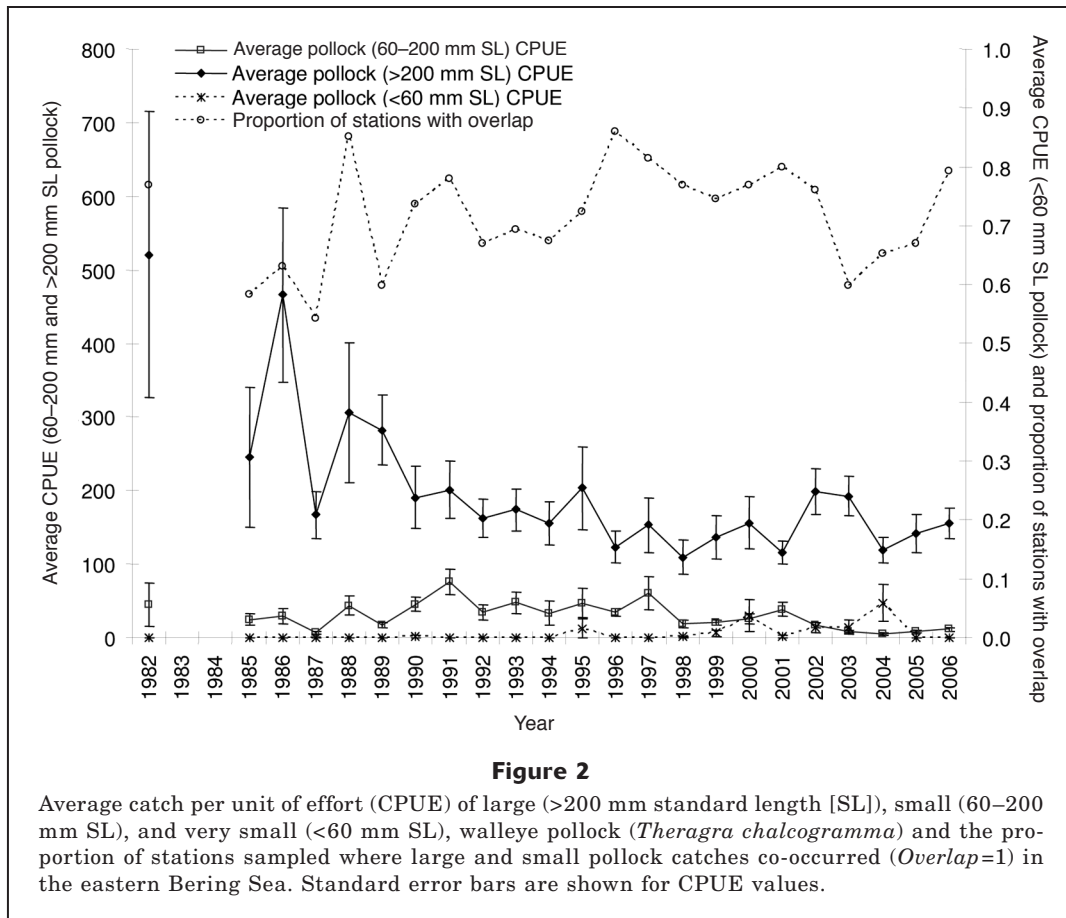
GAMs were also used to explore the relationship between pollock cannibalism on age-1 pollock (60–200 mm SL) and important covariates. There were many zeros in the pollock diet database—a feature typical of this type of data. To address this issue, the first step was to examine whether the presence or absence (*PA*) of cannibalism (binary response variable) was related to the covariates, therefore, data from all stations were used (stations where cannibalism was and was not found to occur). GAMs were used to explore the relationship between the occurrence of pollock cannibalism on age-1 pollock (*PA*) and covariates, which were the following: *Year*, *ColdPool*, *PredatorLength*, *Overlap*, *TempDepth* (s[bottom temperature, bottom depth]), and *Location* (s[latitude, longitude]). The time of day that pollock were sampled was not included in GAMs because it likely would not affect evidence of cannibalism as digestion of pollock prey takes longer than 24 hours (Dwyer et al., 1987).

The subsequent step was to determine those factors affecting the relative amount of cannibalism (hereafter referred to as simply the amount of cannibalism) at stations where cannibalism occurred. The amount of cannibalism on age-1 pollock was estimated by weighting %*FO*, %*BW*, and *PF* of prey pollock (60–200 mm SL) by the abundance of large predatory pollock (e.g., %*FO* × *LgPollock*). These weighted estimates were then ln+1 transformed and, hereafter, are referred to as %*FO*_{LgPollock}, %*BW*_{LgPollock}, and *PF*_{LgPollock} and were the response variables assessed. The covariates in these GAMs included *ColdPool*, *PredatorLength*, *TempDepth*, *Location*, and a smoothed *SmallPollock* term (s[*SmallPollock*]). The covariate *Overlap* was not tested as a predictor of the amount of cannibalism because it was assumed that where cannibalism occurred, predator and prey pollock co-occurred. Instead, *SmallPollock* was included as a covariate because the amount of prey pollock available may influence the amount of cannibalism that occurred. The same step-wise model-selection approach that was used for the abundance GAMs was used for the diet GAMs.

Results

Pollock abundance

During 1982–2006, 2754 bottom trawls were conducted on the EBS shelf (Fig. 1). The number of stations sampled ranged from a low of 13 in 1982 to a high of 170 in 1993, with an average of 120 stations sampled per year. Average CPUE of large pollock (>200 mm SL; *LgPollock*) declined until the late 1990s; whereas, average CPUE of small (60–200 mm SL; *SmallPollock*) pollock was high and variable before 1998 and lowest during 2003–2006 (Fig. 2). CPUE of very small pollock (<60 mm SL) was rare (<0.06 ha⁻¹) in all years. The proportion of sta-



tions where the *SmallPollock* and *LgPollock* co-occurred (*Overlap*=1) ranged from 0.54 to 0.86, and there was no temporal trend; minimum values occurred in 1985, 1987, 1989, and 2003 and peak values occurred in 1988 and 1996 (Fig. 2).

Pollock abundance models

Of the four covariates examined (*TempDepth*, *Location*, *Year*, and *ColdPool*), *TempDepth* and *Location* were both significant predictors of large pollock CPUE (*LgPollock*), small pollock CPUE (*SmallPollock*), and *Overlap*. In addition, *Year* and *ColdPool* were significant predictors of *LgPollock*, *Year* was a significant predictor of *SmallPollock*, but neither *Year* nor *ColdPool* were significant predictors of *Overlap*. Significant covariates explained 51.0%, 22.2%, and 17.1% of the deviance in models for *LgPollock*, *SmallPollock*, and *Overlap*, respectively (Table 1). Over the years examined, *LgPollock* and *SmallPollock* decreased significantly (Table 1, Fig. 2). *LgPollock* was highest in the northwest, outer, and middle domains of the EBS and was lowest in the east EBS and in the coastal domain (Fig. 3). Large pollock tended to avoid the cold pool and *LgPollock* was highest in bottom temperatures greater than 1°C with bottom depths of 75–150 m (Fig. 3). Small pollock were found primarily

in the middle and outer domains of the northwest EBS, but had a broader distribution than large pollock (Fig. 3). Small pollock (*SmallPollock*) were found at slightly shallower bottom depths (50–125 m) than large pollock, but there was considerable overlap in *SmallPollock* and *LgPollock* bottom depth ranges (Fig. 3). Small pollock were found in a wider range of bottom temperatures than the range found for large pollock. *SmallPollock* was high at temperatures between –1°C to 5°C (Fig. 3). *Overlap* was, as expected from *LgPollock* and *SmallPollock* trends, highest in the middle and outer domains of the northwest EBS, at bottom depths less than 100 m, with bottom temperatures between 0°C and 5°C (Fig. 3).

Pollock diet

Pollock sampled in the EBS during 1982–2006 consumed primarily euphausiids and copepods (Fig. 4). Other important prey included amphipods, chaetognaths, crabs, and pollock (Fig. 4). Miscellaneous prey items included other fish, larvaceans, mysids, shrimp, and other prey (Fig. 4). The %*BW* of prey pollock (60–200 mm SL) consumed decreased during the time period examined (Fig. 4). Prey pollock 60–200 mm SL were the dominant-size pollock consumed by predator pollock measuring >19 cm FL (Fig. 5). Prey pollock >200 mm

Table 1

Final general additive models from a backward selection process and the associated adjusted r^2 values, deviance explained (%), and sample size (n). b =intercept, s =nonparametric smoothing function, E =error term. Response variables are: $LgPollock$ = $\ln+1$ transformed predator walleye pollock (*Theragra chalcogramma*) (>200 mm standard length [SL]) catch per unit of effort (CPUE) in the NMFS bottom trawl survey; $SmallPollock$ = $\ln+1$ transformed prey pollock (60–200 mm SL) CPUE in the bottom trawl survey; PA =binomial presence or absence of cannibalism; $\%FO_{LgPollock}$, $\%BW_{LgPollock}$, and $PF_{LgPollock}$ = $\ln+1$ transformed percent frequency of occurrence, percent body weight, and partial fullness of prey pollock in predator pollock stomachs, weighted by $LgPollock$, respectively. Covariates were the following: *Location*, a smoothed station location covariate, s (latitude, longitude); *TempDepth*, a smoothed bottom temperature and depth covariate, s (bottemp, botdepth); *ColdPool*, a binomial covariate indicating presence or absence of the cold pool; *PredatorLength*, a predator length categorical covariate; *Overlap*=binomial covariate indicating the spatial overlap between predator and prey pollock; s (*SmallPollock*), a smoothed *SmallPollock* covariate.

Model type	Final model formulation	r^2 (adjusted)	Deviance explained (%)	n
CPUE	$LgPollock = b + s(Location) + s(TempDepth) + Year + ColdPool + E$	0.50	51.0	2754
CPUE	$SmallPollock = b + s(Location) + s(TempDepth) + Year + E$	0.21	22.2	2754
CPUE	$Overlap = b + s(Location) + s(TempDepth) + E$	0.19	17.1	2754
Diet	$PA = b + s(Location) + s(TempDepth) + Year + PredatorLength + Overlap + E$	0.13	21.1	7479
Diet	$\%FO_{LgPollock} = b + s(Location) + s(TempDepth) + s(SmallPollock) + E$	0.52	55.1	610
Diet	$\%BW_{LgPollock} = b + s(Location) + s(TempDepth) + s(SmallPollock) + PredatorLength + E$	0.63	65.5	610
Diet	$PF_{LgPollock} = b + s(Location) + s(TempDepth) + s(SmallPollock) + PredatorLength + E$	0.55	58.3	610

SL were generally consumed by predators measuring >60 cm FL and prey pollock <60 mm SL were consumed in small proportions by all sizes of predator pollock (Fig. 5). Additional pollock were consumed but could not be included in the analyses because they were too digested to obtain length measurements (Fig. 5). The occurrence of cannibalism in the EBS varied spatially and temporally (Figs. 4 and 6). The proportion of stations where cannibalism occurred ranged from 0.02 (in 2003 and 2004) to 0.18 (in 1990) and decreased during the years examined (Figs. 4 and 6). Fewer samples were collected in 1982, 1985, and 1986 (Fig. 6).

Pollock diet models

The presence or absence of pollock cannibalism on age-1 pollock (60–200 mm SL) was significantly affected by most covariates examined, *TempDepth*, *Location*, *Year*, *PredatorLength*, and *Overlap* (excluding *ColdPool*), and the model explained 21.1% of the deviance (Table 1). The occurrence of cannibalism was highest in the northwest EBS and covered portions of all depth domains, but primarily in the middle and outer domains (Fig. 7). The presence of cannibalism generally occurred most often at bottom temperatures between 0°C and 5°C (Fig. 7).

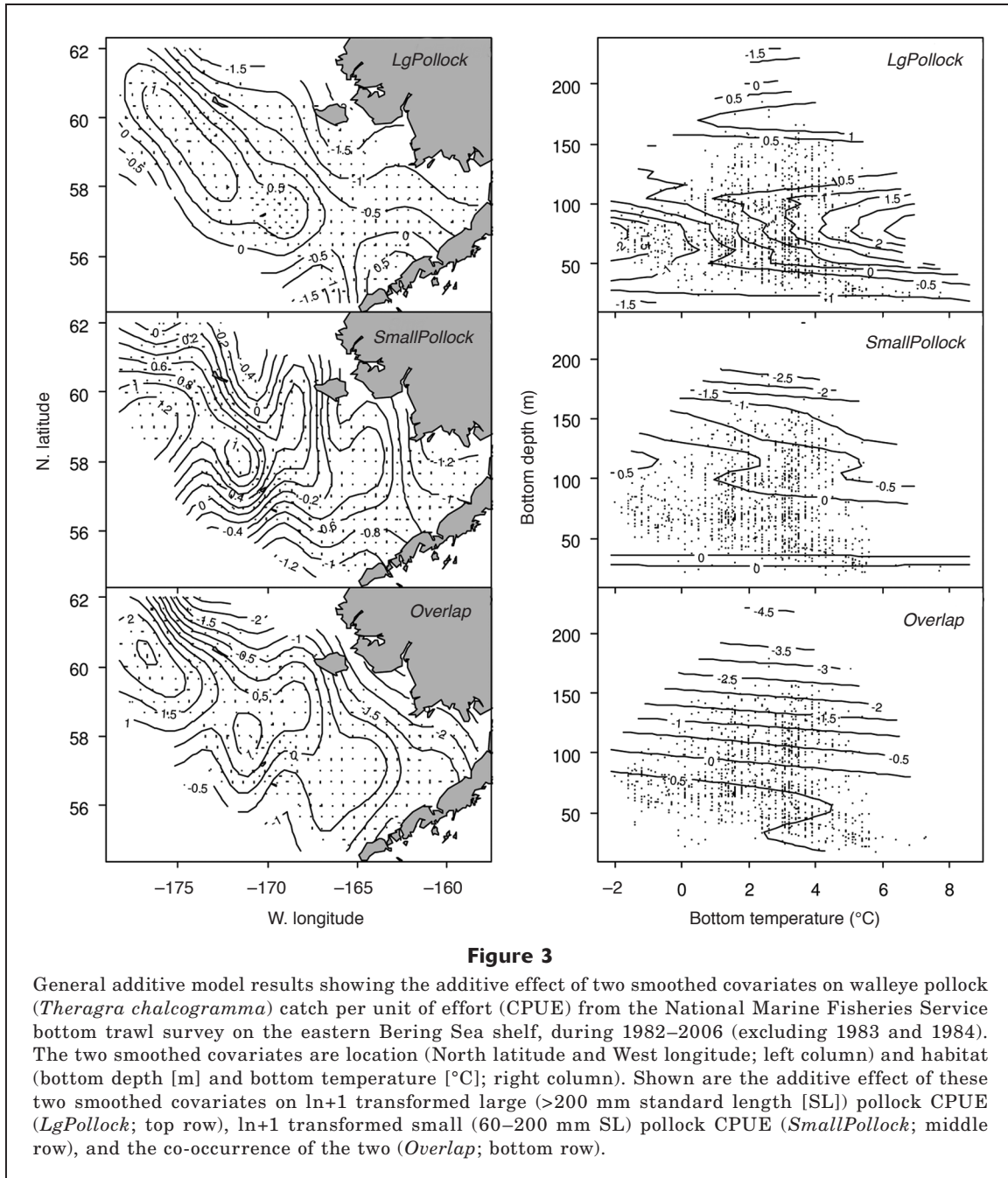
Where cannibalism occurred, the amount of cannibalism ($\%FO_{LgPollock}$, $\%BW_{LgPollock}$, and $PF_{LgPollock}$) on age-1 pollock (60–200 mm SL) was significantly affected by *TempDepth*, *Location*, *SmallPollock*, and *PredatorLength* (except *PredatorLength* in the $\%FO_{LgPollock}$ GAM). Covariates that were not significant in the diet GAMs were *ColdPool* (except in the $\%FO_{LgPollock}$ GAM) and *Year*. Significant covariates explained 55.1%, 65.5%, and 58.3% of the deviance in models for $\%FO_{LgPollock}$, $\%BW_{LgPollock}$, and $PF_{LgPollock}$, respectively

(Table 1). Generally, the amount of cannibalism was highest in the northwest EBS, in the outer half of the middle depth domain and in the outer domain (Fig. 7). The amount of cannibalism increased with increasing temperatures between 1°C and 5°C and with increasing bottom depths (Fig. 7). In addition, the amount of cannibalism increased with increasing abundance of small pollock (*SmallPollock*) and increasing predator size (*PredatorLength*; Fig. 7).

Discussion

The GAM approach, used in this study, enabled us to test hypotheses regarding pollock distribution and cannibalism. Results from this study showed that the distributions of large cannibalistic pollock and vulnerable age-1 prey pollock were affected by environmental factors and varied among years. Large pollock were generally found in deeper waters of the outer and middle domains and they avoided the cold pool; whereas, age-1 pollock were more broadly distributed and were generally found in slightly shallower (but overlapping) depths in the northwest middle and outer domains and in cooler temperatures. These results are consistent with what has been found in previous studies regarding pollock distribution in the EBS (Swartzman et al., 1994; Kotwicki et al., 2005; Mueter et al., 2011). The area where cannibalism on age-1 pollock could potentially have occurred (area of overlap between predator and prey pollock) was in the middle and outer domains of the northwest EBS at depths less than 100 m and at bottom temperatures between 0°C and 5°C.

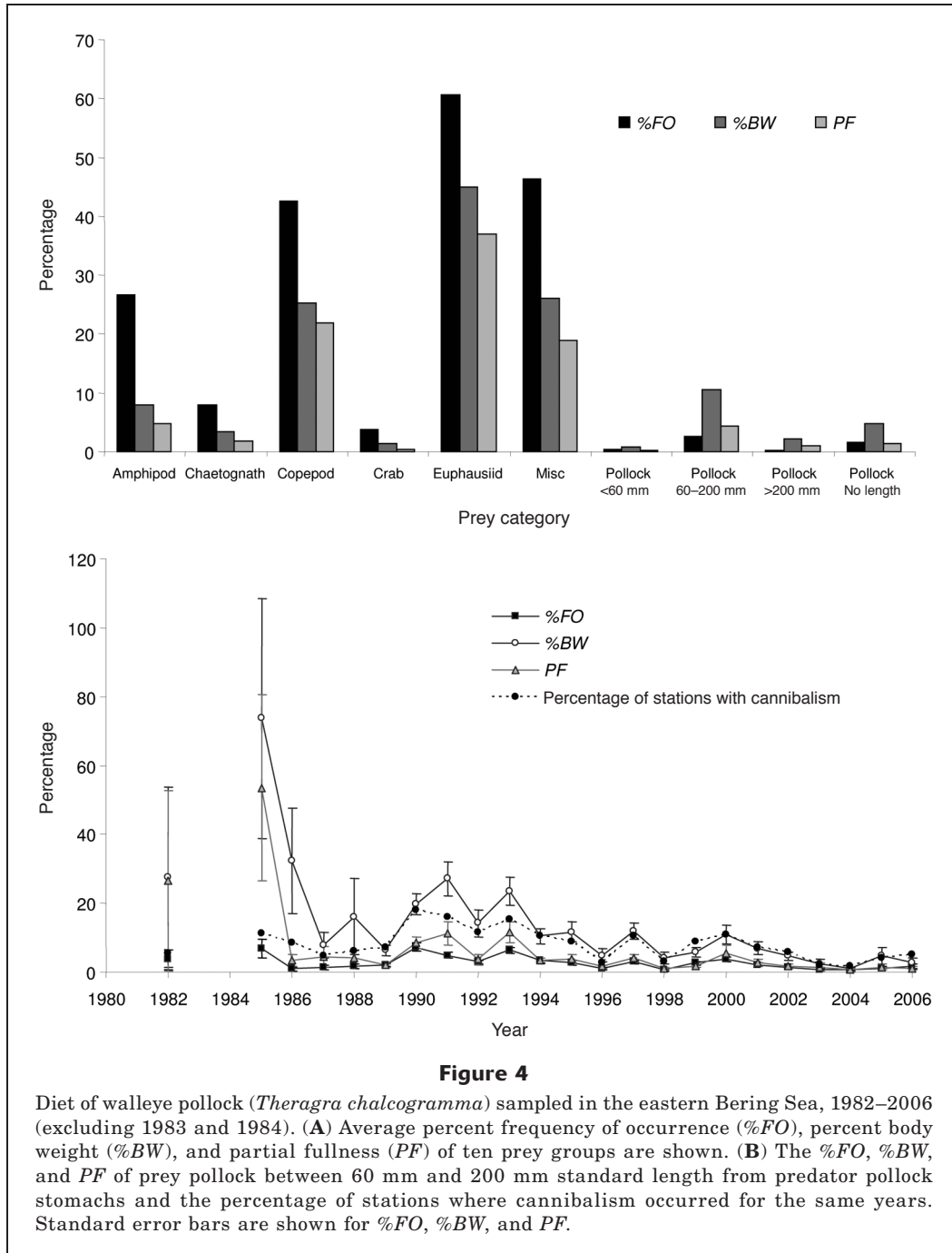
Although diet samples represent snapshots in time, the spatial coverage over the 23 years examined pro-



vided an opportunity to improve our understanding of factors affecting cannibalism. As found in previous studies (Dwyer et al., 1987; Lang and Livingston, 1996), the diet of pollock comprised mainly euphausiids and copepods, and cannibalism was prevalent in many samples. The occurrence and amount of cannibalism in the EBS decreased during 1982–2006 and were affected by environmental factors. As expected, the area of overlap between predator and prey pollock was the area where the occurrence of cannibalism was most frequently observed, on the northwest middle and outer domains. The greatest amount of cannibalism occurred in the

offshore portion of the middle domain and the outer domain and increased with temperatures (between 1°C and 5°C) and bottom depths. Moreover, the amount of cannibalism increased with higher prey pollock abundances and increasing predator sizes.

We found that, in the summer, the occurrence of cannibalism was related to location with its associated bottom depth and temperature, the presence of the cold pool, and the overlap between adult and age-1 pollock. The less frequent occurrence of cannibalism in the cold pool reflected the tendency of large pollock to avoid these areas. Where cannibalism did occur, the



amount that occurred was also related to location and its associated bottom depth and temperature, and the abundance of age-1 prey pollock, but was not related to the presence of the cold pool. Mueter et al. (2006) also found no evidence that the presence of the cold pool was related to total predation mortality (by multiple species of predators) on age-1 pollock, as estimated by a multispecies virtual population analysis; instead total predation mortality of age-1 pollock was related to the abundance of adult pollock and the spatial association between juveniles and adults.

The spatial overlap variable between predator and prey pollock in this study was a measure of horizontal overlap and did not account for potential differences in vertical distribution. Age-0 pollock are found above the thermocline in the summer, and several studies have examined the hypothesis that water column stratification separates them from cannibalistic adults during the summer (Bailey, 1989; Swartzman et al., 1994). In the summer, the majority of prey pollock available to large fish are age-1 pollock, which are often found near the bottom (Duffy-Anderson et al., 2003). The spatial

overlap variable in this study indicated stations where age-1 pollock and adult pollock were caught in the same bottom trawl haul, and hence, both age groups of pollock would have occupied similar depths at these stations. Spatial overlap between age 0 and other pollock age classes could not be estimated in this study because the bottom trawl net does not catch small individuals efficiently and age-0 pollock are distributed higher in the water column. It is worth noting, that we also tested the effect of an indicator of water column stratification (and its interaction with depth) on the occurrence and amount of cannibalism. The water column stratification indicator was calculated as residuals from a linear regression between the day of year and the temperature difference between surface and bottom waters (an indicator of the level of water column stratification). The results were similar to those of the GAM models presented here that included bottom temperature instead of water column stratification, and in fact the stratification variable was significantly correlated with bottom temperature. The most parsimonious model, therefore, was based on bottom temperature and is the only result presented in this study.

A confounding factor in our models was the day of year that samples were collected. The dates of the NMFS EBS shelf bottom trawl surveys varied annually and the sampling started in the southeast EBS and generally proceeded northwestward. Start dates for the surveys usually occurred in the first week of June of each year, but ranged from 24 May in 1999 to 19 June in 1986. End dates for the survey were typically in the last week of July in each year, but ranged from 11 July in 1982 to 14 August in 1985. Day of year is, therefore, confounded with the factors year and location to some degree in our models, and as such, the effect of sample day cannot be completely separated from these factors.

Water temperatures and water column stratification can affect multiple biological processes on the EBS shelf and have implications for the zooplankton community and predation on pollock. In warm years, stratification of the water column tends to occur earlier and result in stronger summer stratification (Coyle et al., 2008; McKinnell and Dagg, 2010). During warm years, both the zooplankton community and diet of age-0 pollock tend to be dominated by smaller copepods, whereas, in cold years, diets are dominated by larger copepods and euphausiids (Baier and Napp, 2003; Coyle et al., 2008, 2011; Hunt et al., 2011). Accompanying the reduction in prey availability in warm years, more cannibalism on age-0 pollock was observed in warm than in cold years (Moss et al., 2009; Coyle et al., 2011). Warm years also bring more potential pollock predators, such as arrowtooth flounder (*Atheresthes stomias*), northward and onto the EBS

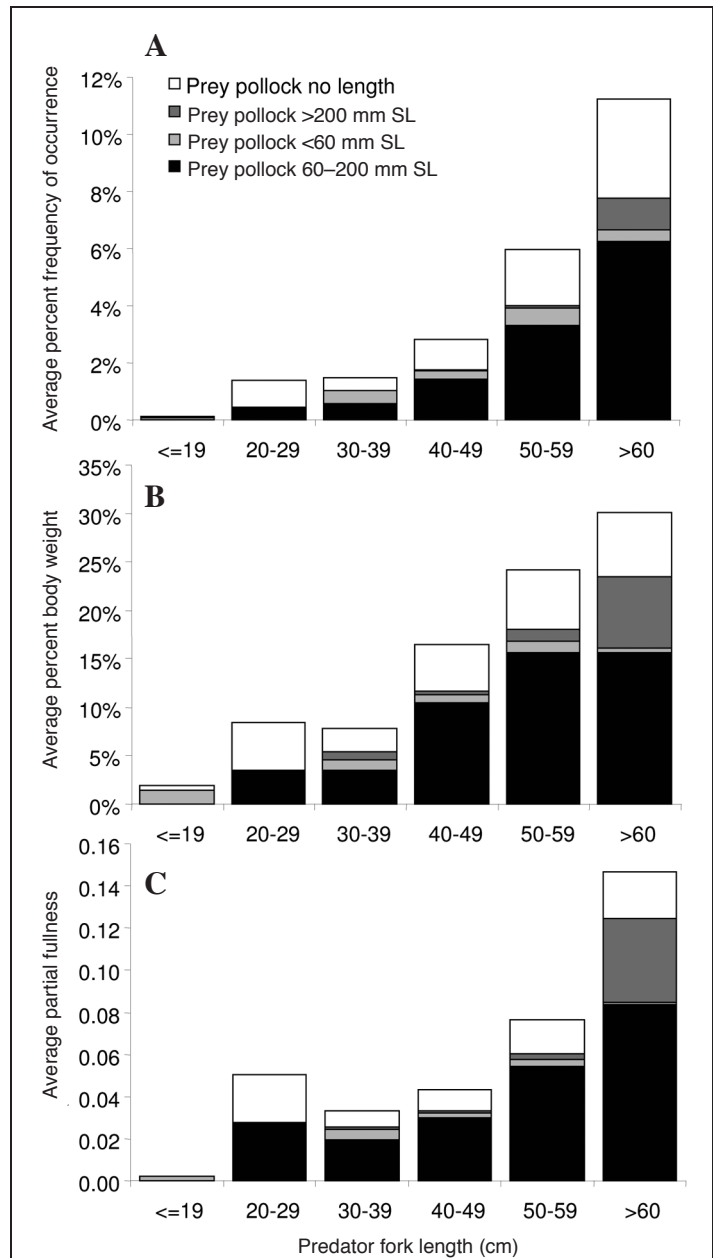


Figure 5 Walleye pollock (*Theragra chalcogramma*) cannibalism by predator pollock fork length (cm) in the eastern Bering Sea during 1982–2006 (excluding 1983 and 1984). (A) Average percent frequency of occurrence (%FO), (B) average percent body weight (%BW), and (C) average partial fullness (PF) of prey pollock measuring less than 60 mm, 60–200 mm, and greater than 200 mm standard length, and those prey pollock that were too digested to measure (no length).

shelf (Mueter and Litzow, 2008; Ianelli, et al., 2011). We found that the cold pool affected the distribution of large pollock and, therefore, in years with a large cold pool, a reduced overlap in distribution of large and small pollock may reduce the occurrence of can-

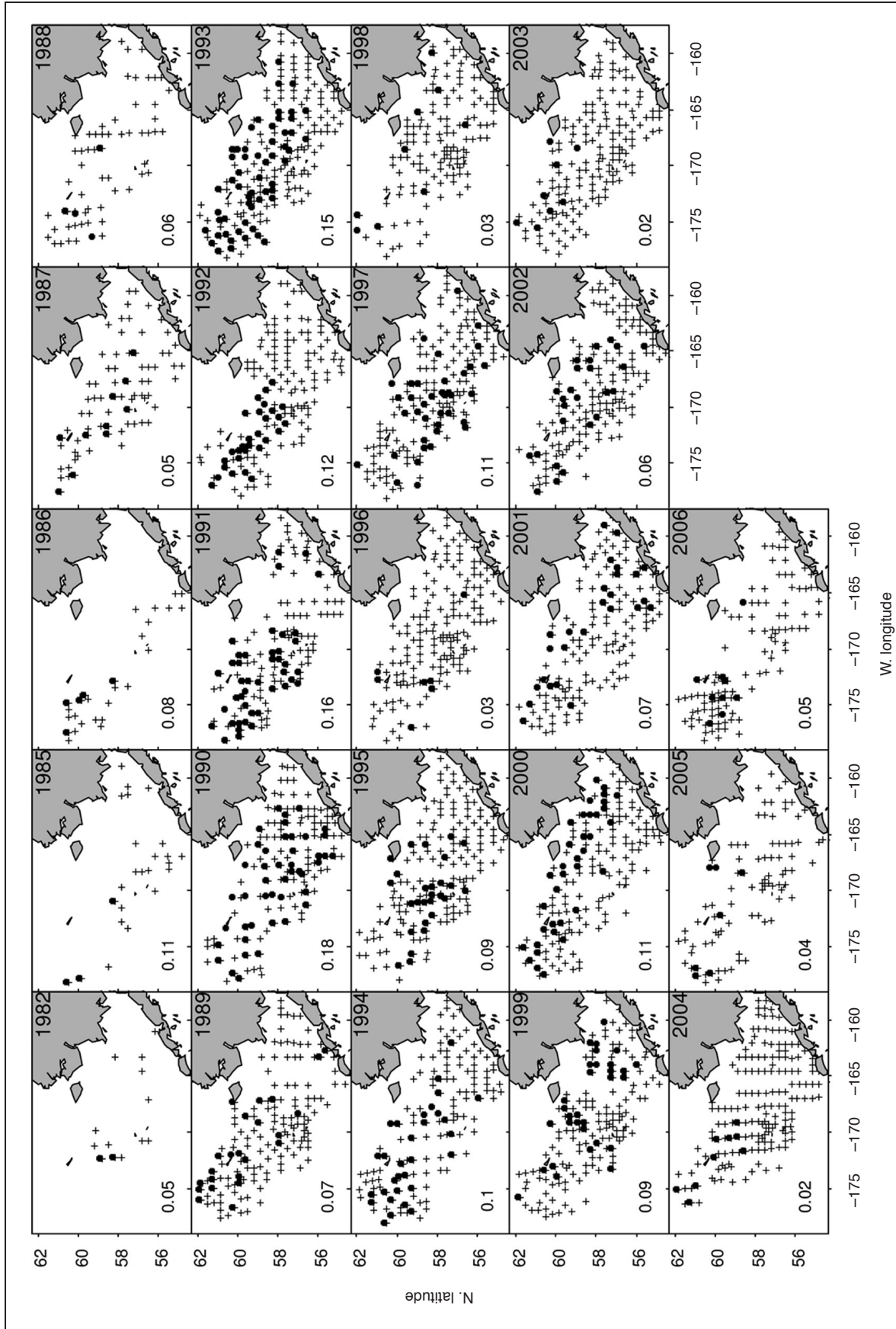
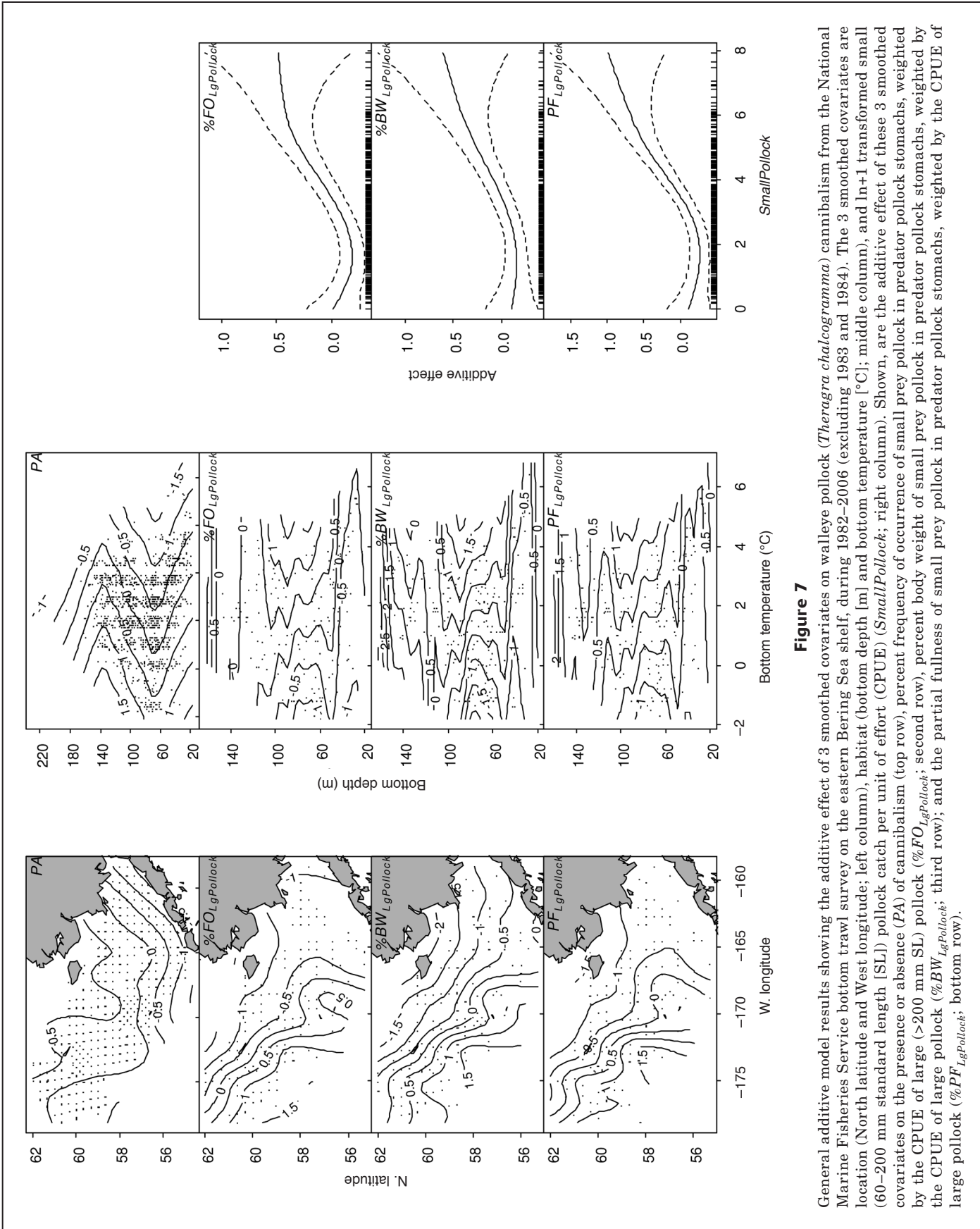


Figure 6

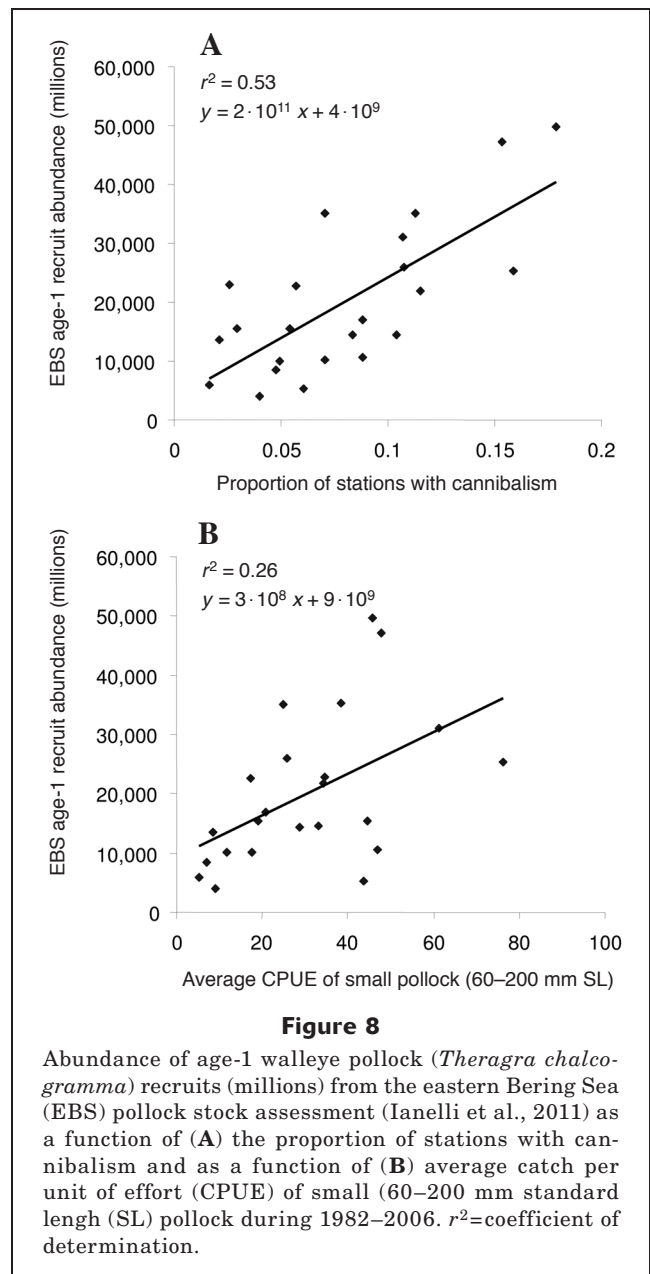
Locations where walleye pollock (*Theragra chalcogramma*) cannibalism was observed (circles) in the eastern Bering Sea during 1982–2006 (excluding 1983 and 1984). A “+” indicates stations where samples were collected and examined, but no cannibalism was observed. Numbers in lower left corners of maps indicate the proportion of stations with cannibalism each year.



nibalism. Also, the amount of cannibalism generally increased with increasing temperatures; however, the amount of cannibalism on age-1 pollock was low during the warm years of 2000–2005, possibly because of the reduced abundance of both large and small pollock. The revised oscillating control hypothesis (Hunt et al., 2002, 2011) and studies of age-0 pollock diet (Moss et al., 2009; Coyle et al., 2011) predict that during warm years there is increased top-down control of age-0 pollock (<150 mm) in the upper water column, but these studies do not address cannibalism of demersal, age-1 pollock.

In the fall, cannibalism on age-0 pollock is high and influences year-class strength (Dwyer et al., 1987) and age-1 pollock cannibalism occurs, but is less prevalent (Dwyer et al., 1987; Bailey, 1989). During summer months, age-1 pollock comprise the majority of cannibalized prey pollock (Dwyer et al., 1987). Mueter et al. (2006) found that predation (including cannibalism) of age-1 pollock by multiple predator species explained up to 76% of the variability in survival estimates (log-transformed recruit per spawner biomass) and concluded that cannibalism was a significant factor affecting the survival of pollock. To explore the possibility that cannibalism on age-1 pollock in summer months affects year-class strength, we examined the relationship between summer cannibalism and the abundance of age-1 recruits from the stock assessment model (Ianelli et al., 2011). In our study, there were significant, positive relationships between the number of age-1 recruits and 1) the amount of pollock cannibalized ($r^2=0.40$, 0.49, and 0.39; and $P=0.001$, <0.001 , and 0.001, for $\%BW_{LgPollock}$, $\%FO_{LgPollock}$, and $PF_{LgPollock}$, respectively) and 2) the proportion of stations where cannibalism was present ($r^2=0.53$, $P<0.001$; Fig. 8). The occurrence and amount of cannibalism increased significantly with increasing age-1 recruit abundances, suggesting that cannibalism on age-1 pollock is not controlling recruitment, and strong year classes may overwhelm the capacity for cannibalism. These results imply that summer cannibalism of age-1 pollock, a top-down process, is not the sole determinant of age-1 pollock abundance.

In this study, we found that the occurrence and amount of cannibalism observed in the survey diet samples were good indicators of year-class strength, because when there were more age-1 pollock consumed, the predicted abundance of age-1 recruits in the stock assessment model was higher. The relationship between the small pollock CPUE (*SmallPollock*) in the bottom trawl survey and the abundance of age-1 recruits from the stock assessment model is also significant and positive ($r^2=0.26$, $P=0.013$; Fig. 8); however, *SmallPollock* does not explain as much variability in age-1 recruit abundance from the stock assessment model as the occurrence of cannibalism does. This result is likely due to the selectivity of the survey bottom trawl net, from which smaller fish may escape. Adult pollock are thus better samplers of age-1 pollock because the occurrence and amount of cannibalism is indicative of age-1 abundance.



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