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Defining Essential Fish Habitat for Atka Mackerel with Respect to Feeding within and Adjacent to Aleutian Islands Trawl Exclusion Zones

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Abstract
The distribution patterns of Atka mackerel Pleurogrammus monopterygius were examined, both seasonally and spatially, to identify essential feeding habitat and to add to existing knowledge of diet composition. The study focused on two local aggregations in the Aleutian Islands, Alaska: one at Seguam Pass and one near Amchitka Island. At each locale, we examined the mean stomach fullness (i.e., feeding intensity) and diet composition of randomly selected fish within and outside of trawl exclusion zones (TEZs). The trawl exclusion zones extend out 10–20 nm from Steller sea lion Eumetopias jubatus rookeries and haulouts; no trawling is allowed inside these zones. During four of the six periods examined, mean stomach fullness was higher inside the TEZ than outside it. At Seguam Pass, fish were distributed into northern and southern aggregations and diet composition varied by age, season, and location relative to the TEZs. Feeding intensity appeared to be greatest inside the TEZ in the northern portion of Seguam Pass near a productive frontal region characterized by a transition zone of well-mixed (upwelling) and stratified water. At Seguam Pass, piscivory occurred almost entirely inside the TEZ in June. Near Amchitka Island, feeding intensity was significantly higher inside the TEZ, which coincided with an increase in egg cannibalism in October. Based on these observations, we suggest that the areas of increased feeding activity in conjunction with diet composition at Seguam Pass and Amchitka Island represent essential feeding habitat for Atka mackerel.
Areas of high fish concentrations can be an indication of favorable habitat for reproduction, feeding, or both (Valavanis et al. 2004; Bergmann et al. 2004). Several factors can determine what makes a particular habitat favorable for feeding. Areas of high relief may support a complex community of benthos and offer protection while foraging (Rooper and Boldt 2005). Water column structure can also play an important role in determining areas that may be optimal for foraging. For example, nutrient rich upwellings, meso-scale eddies, and transition zones between well-mixed and stratified waters are often associated with increased fish abundances (Thomson et al. 1992; Maravelias 1997).

Under this umbrella, we examined the spatial and temporal feeding habits of adult Atka mackerel Pleurogrammus monopterygius to identify areas that may be important for feeding. Atka mackerel make up the largest fraction of groundfish biomass in the Aleutian Islands, Alaska (Rooper 2008), generally aggregating in dense patches and inhabiting sites of strong current and rocky relief, such as in the Aleutian Island passes. Their center of abundance lies within the Aleutian Island archipelago, where a large-scale commercial fishery is conducted (Lowe et al. 2009). Atka mackerel are considered semipelagic; they have been described to engage in diel movements in the water column, the majority of vertical migrations taking place during daylight hours and little to no movement off the bottom during night (Nichol and Somerton 2002). These migrations are presumably to feed on migrating euphausiids and other prey in the water column. Despite their semipelagic movements during feeding, Atka mackerel are demersal spawners. Females deposit egg masses on the bottom, and males guard nests for several months (Zolotov 1993; Lauth et al. 2007). Atka mackerel are a crucial component to the Aleutian Island ecosystem. They are a major prey for Steller sea lions Eumetopias jubatus, particularly in the western Aleutians, where they can be present in sea lion diets up to 92% of the time during summer months (Sinclair and Zeppelin 2002). Atka mackerel also play a significant role in the diet of other fish species (Yang 1999), such as Pacific cod Gadus macrocephalus, arrowtooth flounder Atheresthes stomias, and Pacific halibut Hippoglossus stenolepis.

To identify possible EFH for Atka mackerel feeding, we examined the patterns of feeding intensity and diet composition of two local populations in the Aleutian Islands, Alaska: one at Seguam Pass and one near Amchitka Island. We examined food habits in terms of location relative to trawl exclusion zones (TEZs), which were put into effect in 1992 in response to rapidly declining sea lion populations. The TEZs extend out 10 nautical miles (nm; 18.52 km; Amchitka Island) or 20 nm (Seguam Pass) from sea lion rookeries and haulouts, and no trawling is allowed inside these zones. However, the Atka mackerel commercial fishery is allowed to harvest outside the TEZ, which is regulated by annual quotas based on stock assessment forecasts (Lowe et al. 2009).

METHODS

A two-sample t-test was used to test for differences in the mean stomach fullness of fish inside and outside the TEZs at Seguam Island and near Amchitka Island during the summer and fall months. At each area we qualitatively described the diet composition of Atka mackerel by age-class within a 1-year period (intra-annual) and over a 2–3-year period during the month of October (interannual). We then grouped the age-classes and examined diet composition inside and outside the TEZs.

Data collection.—Study sites were located at Seguam Pass and Amchitka Island in the Aleutian Island chain, Alaska (Figure 1). The study platform was a commercial fishing vessel chartered for an Atka mackerel mark–recapture study (McDermott and Haist 2011, this issue). All demersal trawl hauls targeted locations that had both suitable habitat for trawling, and historically large fishable aggregations of Atka mackerel. However, no formal sampling via grids or transects was conducted. Instead, subareas were defined within each study area. Trawls were limited by the number that could occur per subarea, and the amount of time between each trawl was limited (S. McDermott and V. Haist, National Marine Fisheries Service, unpublished data). For this study, hauls were conducted both inside and outside the 20-nm TEZ at Seguam Pass. At Amchitka Island, hauls were conducted at the north and south end of Amchitka Island, both inside and outside the 10-nm TEZ. Commercial trawl gear (nonstandardized) was used for all fish collections as part of the mark–recapture platform; therefore, the gear selected for commercial sizes of Atka mackerel, generally fish age 3 or greater (approximately 28 cm). Hauls generally remained under 2 metric tons during June and July sampling (to obtain live fish for tagging), and were less than 25 metric tons, on average, during October.

At Seguam Pass, samples were collected in June, August, and October of 2002 and in October of 2003 and 2004. At Amchitka Island samples were collected in July and October 2003 and October 2004. Samples collected in June or July were during daylight hours over a 12-h period. In August and October, collections were over a 24 h diel period. At Seguam Pass, large Atka mackerel aggregations are often observed in the northern portion of the study area. To verify this observation as an index of abundance, catch per unit effort (CPUE; metric tons/h) for October in 2002, 2003, and 2004 was estimated for the northern portion of the study area, both inside and outside the TEZ, by dividing the total Atka mackerel catch by the time spent towing.

A total of 213 hauls were conducted at Seguam Pass and Amchitka Island between 2002 and 2004. Approximately 10 fish (5 males and 5 females) were collected from each haul. Fish were randomly chosen from each haul, and their fork lengths (mm) and weight (g) were recorded and their gonads, stomachs, and otoliths (age structures) collected. A total of 2,018 fish were collected and analyzed between 2002 and 2004. Results of the diet composition were summarized by total number of fish examined. For the two-sample t-test, stomach fullness was...
averaged for the 10 fish per haul, and the haul was defined as the observation. Diet was examined by age rather than size because spatial stratification based on maturity stage is hypothesized for this species (Cooper and McDermott 2011, this issue), and age is a better predictor of maturity than length in this species (Cooper et al. 2011, this issue).

Fish were aged in conjunction with the Alaska Fisheries Science Center’s age and growth program following the protocol outlined in Anderl et al. (1996). Stomach samples were fixed in a solution of 10% buffered formalin in the field and neutralized in the laboratory with Neutralex (Tissue-Tek-Neutralex). After neutralizing the specimens for several hours, the samples were stored in a solution of 70% ethyl alcohol (EtOH) until laboratory analysis. In the laboratory, stomach contents were excised, excess moisture was blotted, and all nonprey items were removed (e.g., rocks). If a stomach contained no prey items, it was recorded as “empty.” The wet weight of stomach contents was recorded to the nearest 1.0 mg. All prey items in each stomach sample were sorted to the lowest possible taxonomic level, weighed to the nearest milligram, and aggregated by prey groups (related taxa). When Atka mackerel eggs were present in the stomach, the total number and weight of eggs was recorded.

Data analysis.—The diet composition of age-3–12 fish from both Seguam Pass and Amchitka Island were examined by year and month. Fish less than age 3 were seldom captured due to gear selectivity and, therefore, were not included in the analysis. Diets of age-7–12 fish were combined because diet composition varied little in this age range. To examine diets both intra-annually and interannually at each study site, predominant prey species by weight were placed into broad taxonomic categories, and the percent by weight (g) of the diet was calculated. The taxon categories included Copepoda, Amphipoda (Gammaridea, Hyperiidea, Caprellidea), Euphausiidae, Chaetognatha (arrow worms), nongadoid fish remains (unidentified fish, Myctophidae, and northern smoothtongue Leuroglossus schmidti), Atka mackerel eggs (cannibalized), and “other.” The latter includes species of the order Copelata (class: Larvacea), Mysidae, Gastropoda, Polychaeta, Cephalopoda, and Decapoda. To examine diets relative to TEZs, the percent weight (g) was calculated for all taxa identified for June, August, and October 2002 at Seguam Pass and for July and October 2003 at Amchitka Island.

Stomach fullness was expressed as a percentage of the fish’s body weight and was used as a proxy for feeding intensity. Stomach fullness was averaged by haul (sexes combined), that is,

\[
SF_h = \frac{1}{n} \sum_{i=1}^{n} \frac{C_i}{W_i},
\]
where $\overline{SF}_h$ is the mean stomach fullness per haul ($h$), $i$ is the specimen, $n$ is the number of specimens in the haul (~10), $C_i$ is the total prey weight for specimen $i$, and $W_i$ is the total body weight (including the stomach and its contents). The sex ratio of males to females was assumed to be close to 50:50 over a given sampling period, based on approximately 150 sexed-lengths that were randomly collected from each haul.

Mean stomach fullness as a percentage of fish body weight is highly variable. Because mean stomach fullness is a proportion and values are close to zero, the data were arcsine transformed to meet the assumption of parametric statistics (Zar 1999). We tested for differences in mean stomach fullness between inside and outside the TEZ for six periods and both study sites (two sample $t$-test). The significance level was set at 0.05.

RESULTS

Seguam Pass Diet Composition

Euphausiids dominated the Atka mackerel diet by percent weight for all 3 years in October (Figure 2). Overall, diets remained similar among years, the only shifts being in the percent composition of prey species (Figure 2). For 2002, intra-annual diet composition by age-class varied between months and age-classes (Figure 3). Consumed prey species shifted between June and August from primarily copepods (ages 3 and 4) and fish (ages 5 and 7–12; Figure 3A) to euphausiids for all age-classes combined (Figure 3B, C). In October, the diets of age-3–4 fish were dominated by euphausiids, those of age-5–6 fish by Atka mackerel eggs (cannibalism), and those of age-7–12 fish by fish (Figure 3C).

The age distribution of the June sample shows that approximately 56% of the total sample consisted of Atka mackerel age 5 and older (Figure 3A), which are the main consumers of fish, although fish first appear in their diet at age 4. A large shift in the age composition takes place between June and August because the percentage of age-3 mackerel increased substantially during that period (Figure 3A, B), representing just over 50% of the sample in August and October (Figure 3B, C). This influx of young fish diluted the age-5 and older age-classes to less than 20% of the total sample size by the August sampling period.

The calculated CPUE for Atka mackerel inside the TEZ at Seguam Pass during the October sampling was 266 metric tons/h in 2002, 130 metric tons/h in 2003, and 250 metric tons/h in 2004. The respective CPUEs in the area outside the TEZ were 45, 81, and 73 metric tons/h.

Differences in diet composition between inside and outside of the TEZ were observed in 2002 (Table 1). Fish consumption (all categories) almost exclusively occurred inside the TEZ (95%), very little to no fish consumption occurring outside the TEZ (Table 1). The consumption of copepods outside the TEZ was almost double that inside the TEZ, and the consumption of squid occurred almost entirely outside the TEZ in June (Table 1). Egg cannibalism only occurred inside the TEZ in August and October, and there was no egg cannibalism in June (Table 1).

Amchitka Island Diet Composition

Atka mackerel eggs dominated the diet by percent weight (g) in October 2003, whereas no particular prey items dominated in October 2004 (Figure 4). Similar to Seguam Pass, the diet composition remained similar between the 2 years, the only shift being in the percent diet composition (Figure 4). Intra-annual diet composition by age-class for 2003 is shown in Figure 5. In July the diets were dominated by copepods across all age-classes (Figure 5A); by October, euphausiids dominated the diet for ages 3 and 4, whereas egg cannibalism predominated in ages 5 and older (Figure 5B). Approximately 92% of the total sample size in July consisted of age 5 and older (Figure 5A). By October these age-classes made up approximately 57% of the total sample (Figure 5B).

There were some observed differences in diet composition between inside and outside the TEZ in 2003 (Table 2). Squid consumption occurred almost entirely outside the TEZ in July; however, there is no difference in October (Table 2). Fish consumption, in general, occurred in October outside the TEZ, few fish being consumed inside the TEZ (Table 2). In October, egg cannibalism inside was almost double that outside the TEZ, and there was no egg cannibalism in July (Table 2).

Stomach Fullness

Mean stomach fullness was significantly greater inside the TEZ than outside it in four of the six periods examined (Table 3). There was no significant difference in mean stomach fullness in inside versus outside the TEZ at Seguam Pass or near Amchitka Island in October, 2004 (Table 3). Spatial patterns of mean stomach fullness between months (i.e., June–July and August–October) and inside–outside the TEZ were apparent at both Seguam Pass (Figure 6) and Amchitka Island (Figure 7). The harvest of Atka mackerel by the commercial fishery in 2003 and 2004 ranged from 2,741 to 10,964 metric tons at Seguam Pass (outside of the TEZ; Figure 6) and from 9,900–19,736 metric tons at Amchitka Island (outside the TEZ; Figure 7).
DISCUSSION

Areas inside the trawl exclusion zones may directly or indirectly enhance or preserve some essential fish habitat characteristics for feeding (and perhaps spawning) of Atka mackerel. Both feeding intensity and diet composition varied intra-annually, inside versus outside the TEZs, and between study areas. Our results of diet composition align with those published by Yang (1999) for the summer months; however, this study highlights food habit differences that occurred on a small spatial scale (i.e., 10–20 nm), both temporally (i.e., intra-annual) and spatially (i.e., between study areas and inside–outside TEZs within each study area). Based on the results of Cooper and McDermott (2011), we speculate that during the fall months, when Atka mackerel are actively spawning (age 4 and older; McDermott and Lowe 1997), their spawning habitat may overlap with their foraging habitat; fish not actively spawning (less than age 4;
McDermott and Lowe (1997) may forage in the spawning habitat as well as other locations. This may explain our observations that age-4 fish at both study locations begin to cannibalize eggs from spawning habitat in October, whereas age-3 fish at both locations do not cannibalize eggs in October. The size of an Atka mackerel egg is similar to that of a small copepod, well within the size range of prey for age-3 fish at both locations, indicating that prey size is not a limiting factor for these observed prey preferences.

An important element of the Atka mackerel diet is fish consumption. Piscivory was a substantial part of Atka mackerel diets inside the Seguam Pass TEZ in June. Fish consumption only occurs in fish age 4 and older, probably because of small mouth gap size in fish younger than age 4. Yang (1999) found fish consumption was less than 5% by weight of total stomach contents during the 1991 Alaska Fisheries Science Center’s (AFSC) summer survey season. Also, Logerwell et al. (2005), who summarized diets over several years, report fish

|                | June 2002 | August 2002 | October 2002 |
|----------------|-----------|-------------|--------------|
|                | Inside    | Outside     | Inside       | Outside     | Inside       | Outside     |
|                | n = 207 (20) | n = 77 (8)  | n = 141 (15) | n = 39 (4)  | n = 106 (11) | n = 40 (4)  |
| Hydrozoa       | 0.00      | 0.32        | 0.00         | 0.00        | 0.00         | 0.00        |
| Jellyfish      | 0.00      | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Polychaeta (worm) | 0.01      | 0.00        | 0.00         | 0.04        | 0.00         | 0.00        |
| Gastropoda     | 0.14      | 0.72        | 0.09         | 0.27        | 1.03         | 0.24        |
| Nudibranchia   | 0.00      | 0.00        | 0.00         | 0.00        | 0.00         | 0.02        |
| Cephalopoda    | 0.56      | 0.25        | 0.00         | 0.00        | 0.00         | 0.00        |
| Teuthoidea (squid) | 2.30      | 21.28       | 2.21         | 3.41        | 1.15         | 2.39        |
| Octopoda (octopus) | 0.00      | 0.24        | 0.00         | 0.00        | 0.00         | 0.00        |
| Octopodidae (octopus) | 0.26      | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Crustacea      | 0.14      | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Copepoda       | 0.00      | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Calanoida      | 23.41     | 54.93       | 8.86         | 16.50       | 8.19         | 14.95       |
| Candacia sp.   | 0.01      | 0.12        | 0.01         | 0.04        | 0.07         | 0.12        |
| Mysisacea Mysida | 0.00     | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Mysisaeae      | 0.01      | 0.08        | 0.00         | 0.00        | 0.00         | 0.00        |
| Isopoda        | 0.04      | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Amphipoda      | 0.01      | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Gammaridea     | 0.12      | 0.28        | 0.06         | 0.01        | 0.01         | 0.07        |
| Hyperidea      | 0.13      | 0.90        | 2.95         | 5.79        | 1.08         | 1.80        |
| Caprellidea    | 0.01      | 0.07        | 0.00         | 0.10        | 0.00         | 0.00        |
| Euphausiaaeae  | 0.00      | 0.00        | 0.00         | 0.00        | 0.00         | 0.44        |
| Euphausiiidae  | 2.11      | 7.91        | 63.22        | 63.65       | 34.60        | 57.33       |
| Natantia (shrimp) | 0.06     | 0.30        | 0.06         | 0.04        | 0.92         | 0.05        |
| Caridea (shrimp) | 0.28      | 0.22        | 0.12         | 0.25        | 0.00         | 0.00        |
| Echinooza      | 0.00      | 0.00        | 0.00         | 0.00        | 0.01         | 0.00        |
| Chaetognatha (arrow worm) | 7.10     | 9.17        | 5.01         | 9.78        | 13.20        | 22.46       |
| Copelata (larvaecean) | 0.06     | 0.08        | 0.36         | 0.06        | 0.02         | 0.11        |
| Teleostei (unidentified) | 27.73    | 2.79        | 3.84         | 0.00        | 8.89         | 0.00        |
| Osmeridae (smelts) | 19.04    | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Northern smoothtongue | 11.51    | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Myctophidae (lanternfish) | 4.49     | 0.00        | 7.91         | 0.00        | 18.26        | 0.00        |
| Coryphaenoides (rattail) | 0.00    | 0.14        | 0.00         | 0.00        | 0.00         | 0.00        |
| Atka mackerel eggs | 0.00     | 0.00        | 4.80         | 0.00        | 12.34        | 0.01        |
| Cottidae (sculpin) | 0.02     | 0.00        | 0.00         | 0.00        | 0.00         | 0.00        |
| Unidentified organic material | 0.49   | 0.21        | 0.48         | 0.06        | 0.23         | 0.00        |
FIGURE 5. Percent diet composition by weight of age 3–12 Atka mackerel from Amchitka Island in (A) July and (B) October of 2003. Sample sizes (n) are shown above the age-class bars. The “other” category is defined in Figure 2.

FIGURE 6. Average Atka mackerel stomach fullness expressed as a percentage of body weight for individual trawl hauls at Seguam Pass in June, August, and October of 2002 superposed over the 2003–2004 Atka mackerel fishery harvest (metric tons [mt]). The occurrence of catch areas (shaded) in the trawl exclusion zone (where no bottom trawling occurs) are an artifact of fishery haul summations.
TABLE 2. Diet composition at Amchitka Island by percent weight (g) inside and outside the trawl exclusion zone. See Table 1 for additional details.

| Prey               | July 2003 | October 2003 |
|--------------------|-----------|--------------|
|                    | Inside n = 118 (12) | Outside n = 83 (9) | Inside n = 274 (28) | Outside n = 143 (15) |
|                    | [31–45 cm] | [32–44 cm]   | [27–44 cm]   | [29–46 cm]   |
| Hydrozoa           | 0.03      | 0.09         | 0.36         | 1.52         |
| Jellyfish          | 0.00      | 1.79         | 0.00         | 0.00         |
| Polychaeta (worm)  | 0.04      | 0.00         | 0.04         | 1.82         |
| Gastropoda         | 0.07      | 0.25         | 0.16         | 0.48         |
| Nudibranchia       | 0.00      | 0.00         | 0.00         | 0.00         |
| Cephalopoda        | 0.00      | 3.01         | 0.06         | 0.00         |
| Teuthoidea (squid) | 0.83      | 9.30         | 12.47        | 11.49        |
| Octopoda (octopus) | 0.00      | 0.00         | 0.00         | 0.00         |
| Octopodidae (octopus) | 0.00    | 0.00         | 0.00         | 0.00         |
| Crustacea          | 7.13      | 9.37         | 1.61         | 2.31         |
| Copepoda           | 45.55     | 33.34        | 0.85         | 1.90         |
| Calanoida          | 0.00      | 0.00         | 0.07         | 0.01         |
| *Candacia* sp.     | 0.19      | 0.11         | 1.50         | 3.11         |
| Mysida             | 0.00      | 0.00         | 0.01         | 0.00         |
| Mysidae            | 0.00      | 0.00         | 0.00         | 0.00         |
| Isopoda            | 0.00      | 0.00         | 0.00         | 0.00         |
| Amphipoda          | 0.00      | 0.00         | 0.01         | 0.00         |
| Gammaridea (amphipod) | 0.04   | 0.33         | 2.25         | 0.06         |
| Hyperidae (amphipod) | 6.74     | 2.77         | 3.55         | 10.67        |
| Caprellidea (amphipod) | 0.49   | 0.01         | 0.01         | 0.00         |
| Euphausiacea       | 1.05      | 0.49         | 0.00         | 0.04         |
| Euphausiidae       | 15.43     | 14.40        | 19.21        | 20.40        |
| Natantia (shrimp)  | 0.00      | 0.00         | 0.00         | 0.00         |
| Caridea (shrimp)   | 0.59      | 0.38         | 0.03         | 0.79         |
| Echinodermata      | 0.00      | 0.00         | 0.00         | 0.00         |
| Chaetognatha (arrow worm) | 20.67 | 19.52        | 6.45         | 6.09         |
| Copepoda (larvacean) | 0.00     | 0.00         | 0.00         | 0.00         |
| Teleostei (unidentified) | 0.10 | 0.05         | 1.41         | 10.23        |
| Osmeridae (smelts) | 0.00      | 0.00         | 0.00         | 0.00         |
| Northern smoothtongue | 0.00    | 0.00         | 0.00         | 0.00         |
| Myctophidae (lanternfish) | 0.00 | 0.00         | 0.00         | 0.00         |
| Coryphaenoides (rattail) | 0.00 | 0.00         | 0.00         | 0.00         |
| Atka mackerel eggs | 0.23      | 0.00         | 47.56        | 24.54        |
| Cottidae (sculpin) | 0.00      | 0.00         | 0.00         | 0.00         |
| Unidentified organic material | 0.83 | 4.77         | 2.41         | 4.54         |

Consumption as being a small percentage of the Atka mackerel diet in the Aleutian Islands. The disparity in these studies compared with our study is probably due to spatial locations of demersal trawls, the timing of data collections, the scale at which diets were examined, and the fact that age-class was not taken into account in either study. Few AFSC survey trawls have occurred inside the TEZ at Seguam Pass because the habitat is not conducive to trawling. Also, the commercial fishery is only allowed access to areas outside the TEZs at any point during the Atka mackerel commercial fishery, which primarily occurs in the fall and winter months. Piscivory can be a major component of the diet of other greenlings. Fish consumption by the masked greenling *Hexagrammos octogrammus* was over 33% by weight for fish age 3 and older in the summer months (Pushchina and Antonenko 1999), and for the whitespotted greenling *H. stelleri*, it varied from 30% to 100% by weight, depending on greenling size and year (Napazakov 2008). This intensive period of piscivory inside the Seguam Pass TEZ in June may provide essential caloric needs for fish going into a reproductive season.

Atka mackerel eggs are cannibalized from demersal nests and composed a significant portion of Atka mackerel diets during October, especially at the Amchitka Island study site,
where almost 50% of the diet consisted of such eggs (mostly inside the TEZ). This result also coincides with results from Cooper and McDermott (2011), who examined the reproductive organs of the same Atka mackerel specimens we collected and found that male nest-guarding mostly occurred inside the TEZ. In addition, egg masses collected from the demersal trawls were primarily found inside the TEZ (Cooper and McDermott, 2011). Similar results of egg cannibalism were reported for the masked greenling (Pushchina and Antonenko 1999), where 15–20% by weight of their fall (September–October) diet was composed of conspecific eggs. Similar to the intensive period of piscivory observed at Seguam Pass, egg cannibalism at Amchitka Island is an important part of their fall diet.

At Seguam Pass, results showed that feeding inside the TEZ was significantly greater than feeding outside the TEZ, particularly in the northern portion. It is likely that this pattern, as it relates to feeding, could be attributed to the unique habitat and oceanographic features of this local area. Water movement and water column mixing within Aleutian Island passes are primarily dominated by tidal currents (Hunt and Stabeno 2005; Stabeno et al. 2005) and are highly variable and dynamic; Seguam Pass is known to be a deep and highly mixed pass (Coyle 2005). Very large aggregations of Atka mackerel have been captured within this vicinity of strong mixing and upwelling (Fritz and Lowe 1998). The observed spatial patterns of mean stomach fullness

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### TABLE 3. Results of the two-sample *T*-tests for average Atka mackerel stomach fullness inside trawl exclusion zones and outside the trawl exclusion zones for Amchitka Island and Seguam Pass in 2002, 2003, and 2004 (α = 0.05). There were too few data at Seguam Pass in October 2002 to test for differences.

| Area and date          | df  | *P*-value |
|------------------------|-----|-----------|
| Amchitka Island        |     |           |
| July 2003              | 19  | 0.02      |
| October 2003           | 41  | 0.02      |
| October 2004           | 21  | 0.57      |
| Seguam Pass            |     |           |
| June, July, August 2002| 45  | 0.04      |
| October 2002           | –   | –         |
| October 2003           | 34  | 0.06      |
| October 2004           | 27  | 0.44      |
evident at Seguam Pass may be a reflection of Atka mackerel aggregating to feed near a well-documented frontal zone (Coyle 2005; Mordy et al. 2005). In June 2001, Coyle (2005) collected temperature, salinity, fluorescence and zooplankton data within Seguam Pass on a transect that ran through the pass in a north–south direction. Coyle (2005) reported well-mixed water within Seguam Pass and observed a high abundance of zooplankton in a frontal region at the north end of the transect, where there is a transition zone between the well-stratified and well-mixed water column. This frontal zone may be an important feature, making this optimal foraging habitat for Atka mackerel.

Atka mackerel in the Amchitka Island and Seguam Pass study sites differed in diet composition but had similar spatial patterns of mean stomach fullness. As at Seguam Pass, it appears that at Amchitka Island feeding intensity is higher inside the TEZ than outside; however, we speculate that this is for different reasons. The TEZ at the Amchitka study site (10 nm around sea lion rookeries) bisects the 90–150-m bathymetric range. As a result, we would expect feeding intensity to be the same inside and outside the TEZ boundary, but in fact, it is greater inside the TEZ. At Seguam Pass, the 20-nm TEZ, by chance, happens to encompass a well documented frontal zone. One possible explanation for the observed differences in mean stomach fullness at Amchitka Island is that the habitat inside the TEZ is relatively undisturbed (i.e., no bottom trawling) compared with sites outside the TEZ, where there is a commercial fishery that operates in January and September. Also, inside the TEZ, Atka mackerel nests are relatively undisturbed, and egg cannibalism is double of that outside the TEZ in October.

In summary, we found that diet composition differed temporally, spatially, and by age-class at both the Seguam Pass and Amchitka Island study areas. The existing TEZs may provide protected habitat for Atka mackerel foraging, which coincides with management objectives requiring identification of essential fish habitat.

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