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ABSTRACT

Within- and among-year variations in the diet and feeding activity of arrowtooth flounder (*Atheresthes stomias*) were examined in order to expand the existing knowledge of their food habits to include temporal variability in the western Gulf of Alaska. Stomach samples were collected during bottom trawl surveys conducted near Kodiak Island, Alaska, in May and August 2002-2004. In 2002 and 2003, walleye pollock (*Theragra chalcogramma*) were the dominant prey for arrowtooth flounder (≥ 40 cm total length (TL)), whereas in 2004 the importance of walleye pollock declined significantly. In 2004, the importance of euphausiids and Pacific sand lance (*Ammodytes hexapterus*) in the arrowtooth flounder diet increased significantly. Several within-year dietary trends were noted during 2004. Most notably, the importance of euphausiids in the arrowtooth flounder diet decreased significantly from May to August, whereas the importance of capelin (*Mallotus villosus*) increased significantly. Ontogenetic dietary trends were found to vary both temporally and spatially and temporal changes in feeding activity were more pronounced in the smaller arrowtooth flounder (20-39 cm TL). The dietary trends generally reflected differences in prey availability or abundance and highlighted the adaptable feeding behavior of this key predator.

CONTENTS

INTRODUCTION

Arrowtooth flounder (*Atheresthes stomias*), a relatively large, predatory flatfish species in the family Pleuronectidae, are becoming increasingly important in the Gulf of Alaska food web because of their dramatic increase in abundance over the past 25 years. Since the early 1970s, the biomass of arrowtooth flounder in the Gulf of Alaska has increased nearly sevenfold and they are currently the most abundant groundfish species in the system with an estimated biomass of over 2 million metric tons (t) (Turnock et al. 2005). Juvenile arrowtooth flounder are important prey for many groundfish species including Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), and Pacific halibut (*Hippoglossus stenolepis*) (Yang and Nelson 2000), as well as marine mammals such as Steller sea lions (*Eumetopias jubatus*) (Sinclair and Zeppelin 2002). Conversely, adult arrowtooth flounder are top-level predators that feed on forage fish species such as juvenile walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*), and eulachon (*Thaleichthys pacificus*) and their diet overlaps with other top-level fish and marine mammal predators in the Gulf of Alaska (Yang 1995, Yang and Nelson 2000, Sinclair and Zeppelin 2002). To date, temporal and spatial variations in these species interactions are not known in detail. In order to quantify the significance of such a dramatic population increase for this top-level predator a thorough understanding of these variations is needed.

The analysis of the food habits of abundant top-level fish predators is critical in assessing ecosystem dynamics. Knowledge of diet composition and feeding patterns may afford insight into the interactions among key species, such as predator-prey relationships, and help clarify the roles of various species in marine ecosystems (Wootton 1990). A better understanding of the underlying dynamics of marine ecosystems, including species interactions, is essential to facilitate ecosystem-based fishery management practices (Larkin 1996).

The food preferences of arrowtooth flounder in Alaska waters have been previously described in some detail (Rose 1980, Yang and Livingston 1986, Yang 1995, Yang and Nelson 2000). Large arrowtooth flounder (> 40 cm) are mostly piscivorous and typically consume commercially and ecologically important species such as walleye pollock, Pacific herring (*Clupea pallasii*), and capelin. In addition, invertebrate prey including shrimp and cephalopods are also relatively important diet components. Small arrowtooth flounder consume higher proportions of euphausiids, shrimp, and forage fish than larger cohorts. At this time, it is not clear if the ontogenetic trends are consistent on different spatial and temporal scales throughout their range.

Despite the considerable number of studies describing the diet of arrowtooth flounder in the Gulf of Alaska, relatively little is known about temporal variability in their diet. Reports describing temporal trends in the diet of arrowtooth flounder are mostly anecdotal and limited in scope (Rose 1980, Livingston et al. 1986). High-latitude fish species commonly exhibit temporal variability in food habits that are a reflection of seasonal changes in the marine environment and the resulting prey availability (MacKinnon 1972, Livingston et al. 1986, Yamamura et al. 2002). Arrowtooth flounder are opportunistic predators and as such, temporal changes in their prey consumption would likely reflect changes in prey abundance or availability. More detailed studies are required on appropriate scales to quantify the breadth of trophic interactions between arrowtooth flounder and their prey in the Gulf of Alaska.

We studied trends in the food habits of arrowtooth flounder during the summer feeding period of 2002-2004 near Kodiak Island, Alaska. These waters provided an excellent area to study the food habits of arrowtooth flounder because they are highly productive and support some of the largest concentrations of arrowtooth flounder in the western Gulf of Alaska (Turnock et al. 2005). Our objectives were 1) to quantify the interannual variations in the diet composition and feeding activity of arrowtooth flounder from 2002 to 2004, 2) to quantify the within-year variations (between May and August) in the diet composition and feeding activity of separate arrowtooth flounder size classes in each year and 3) to quantify the ontogenetic variations in diet composition and feeding activity of arrowtooth flounder during each sampling period (May and August) in 2004. These objectives allow for a more detailed assessment of the trophic relationships of this key predator in the nearshore ecosystem of the western Gulf of Alaska.

MATERIALS AND METHODS

Study Area and Sampling Procedure

This study was based on the analysis of stomach contents from arrowtooth flounder collected in the nearshore waters of Kodiak Island in the western Gulf of Alaska (Fig. 1). The study area encompassed waters of Chiniak and Marmot Bays and sampling stations were located within a 20 nautical mile (nmi) radius around Long Island. Fixed sampling stations were distributed among a variety of locations and depths in the study area and they were sampled twice annually, in May and August, from 2002 to 2004.

Bottom trawls were conducted onboard a commercial stern trawler using a DanTrawl Fiska Trawl II 380/55 model net with a 2.22 cm codend liner with 4.0 m^2 NETS (Nor' Eastern Trawl Systems) Fishbuster doors at each station. The vessel maintained a speed of 3 knots (5.5 km/hr) for the duration of each 10 minute tow and covered an average distance of 0.90 km. All tows were conducted during daylight between 0600 and 2300 hours. The catches were sorted by species and counted upon retrieval.

Up to 20 arrowtooth flounder specimens from each tow were set aside for analysis. Only arrowtooth flounder $\geq$ 40 cm total length (TL) were collected in 2002 and 2003; however, all size classes were collected in 2004 in order to investigate ontogenetic dietary shifts. Specimens that displayed evidence of regurgitation or net feeding activities were excluded from the samples. Each specimen's total length (to the nearest 1.0 cm), wet weight (to the nearest 0.01 kg), sex, and macroscopic maturity status were recorded. Stomach samples were preserved in 10% formalin–seawater solution and brought back to the laboratory for analysis.

Laboratory Analysis

Stomachs were removed from cloth bags, blotted dry, and weighed (to the nearest 0.001 g) in the laboratory. The stomach wall was rinsed, blotted dry, and re-weighed after the contents were removed. Total stomach content weight (to the nearest 0.001 g) was calculated by subtracting the stomach wall weight from the initial stomach weight. Stomach contents were placed on a 300 μm mesh sieve and gently rinsed with distilled water before analysis. Prey organisms were separated and identified to the most practical taxonomic level with an emphasis on the identification of fish, crab, and shrimp prey. Identification keys and reference collections of fish otoliths and diagnostic bones were used to identify digested fish prey.

Intact prey organisms were counted, weighed (to the nearest 0.001 g), and measured (to the nearest 1.0 mm TL). The total count of paired structures such as invertebrate eyes and fish otoliths were divided by 2 in order to estimate the number of completely digested prey. The total length of digested (and partially digested) walleye pollock, capelin, and Pacific sand lance (*Ammodytes hexapterus*) was estimated using regressed relationships between fish total length (cm) and diagnostic bone length (mm) (including the cleithra, opercle, and dentary bones). Fresh samples of prey species collected during this study were used to derive the relationships between fish total length and bone length.

Data Analysis

A qualitative analysis of stomach contents did not detect substantial dietary differences related to sex therefore the diet composition data for the two sexes were pooled. Arrowtooth flounder dietary differences related to depth of capture have been previously reported (Yang 1995); therefore, the stomach content samples were qualitatively examined for depth-related differences. As expected, depth-related differences were observed and thus the samples were categorized into < 100 m, 100–200 m, and > 200 m depth intervals for all further analyses. Samples from waters deeper than 200 m were excluded from all subsequent analyses because of small sample sizes (Table 1). Additionally, the stomach content samples were categorized into two size categories (20-39 and ≥ 40 cm TL) for all analyses because previous studies have indicated arrowtooth flounder change their feeding behavior and become more piscivorous around 40 cm (Yang 1995, Yang and Nelson 2000).

Individual prey items were grouped into categories to analyze temporal and ontogenetic variations. Fish species that did not occur in at least 5% of the specimens were pooled into an “other fish” category. Walleye pollock, capelin, and Pacific sand lance each exceeded these requirements and they were not pooled into the other fish category. Individual shrimp and euphausiid species were pooled into “shrimp” and “euphausiid” categories, respectively, because no individual species occurred in at least 5% of the specimens. Similarly, all other invertebrate prey items were pooled into an “other prey” category because no individual species occurred in at least 5% of the specimens. Lastly, unidentified digested prey material was excluded from all dietary analyses because it may have contained more than one prey taxon and, therefore, could have biased the results (Schafer et al. 2002).

Diet Analysis

The general diet composition of the arrowtooth flounder samples was described by the percent frequency of occurrence (%FO) and percent weight (%W) for each prey category. These indices provide independent information into the feeding habits of the predator (Hyslop 1980). Frequency of occurrence data gives insight into population-wide feeding habits (Cailliet 1977) and weight data reveals the prey item’s nutritional value (Macdonald and Green 1983). Temporal variations in the diet and feeding activity of arrowtooth flounder were assessed among the study years (2002-2004) and within each year (between the May and August). Specifically, the analyses of interannual variations in the diet and feeding activity included only adult arrowtooth flounder (> 40 cm TL) and were restricted to specimens collected in the 100-200 m depth interval due to small sample sizes at other depths. Within-year variations were assessed using only stomach samples of adult arrowtooth flounder (≥ 40 cm TL) captured in the 100-200 m depth interval in 2002 and 2003. The within-year dietary variations in 2004 were analyzed separately for each size class (20-39 and ≥ 40 cm TL) and depth interval (< 100 and 100-200 m). Finally, ontogenetic variations in arrowtooth flounder diet and feeding activity were quantified for each sampling period and depth interval in 2004.

The diet composition and feeding activity data failed normality tests, therefore non-parametric methods were chosen for all statistical comparisons. Kruskal-Wallis and Mann-Whitney U-tests (Zar 1984) were employed to test for significant variations in the percent weight contribution of the main prey categories. A prey item's percent weight contribution was used as the principal index in the statistical comparisons because it is an appropriate measure of the energetic value of the prey. Feeding activity was assessed by analyzing both stomach fullness (stomach content mass as a percentage of body mass) and the percentage of empty stomachs. These two indices combined provide a more accurate description of feeding activity than using a stomach fullness index alone (Cortés 1997). Temporal and ontogenetic variations in these indices were also analyzed using non-parametric tests (Kruskal-Wallis test, Mann-Whitney U-test or X^2 -test of independence).

RESULTS

General Diet Description

A total of 742 arrowtooth flounder stomachs were examined and 465 (63.0%) contained some food. Over 2,800 prey items consisting of 41 different taxa were identified (Table 2). The predominance of pelagic prey in the stomachs, including forage fish, pelagic shrimp, and euphausiids, reveals arrowtooth flounder feed mainly in the water column. Fish were clearly the most important prey category and included at least 11 species. Walleye pollock, Pacific sand lance, and capelin were the most important fish prey on both a weight and occurrence basis. Other fish prey included unidentified eelpouts, flathead sole (*Hippoglossoides elassodon*), and juvenile arrowtooth flounder. Euphausiids, mainly *Thysanoessa* spp., occurred in 30% of the stomachs and comprised 17.7% by weight of the total stomach contents. Shrimp were also relatively important and occurred in 12.0% of the arrowtooth flounder stomachs. Pandalid shrimp, including *Pandalus borealis*, were the most important shrimp in the diets. Other prey items including miscellaneous mysids, copepods, and bivalves were largely incidental and contributed relatively little (by weight) to the total stomach contents.

Interannual Food Habit Variations

Arrowtooth flounder (≥ 40 cm TL) displayed substantial differences in diet composition among the years in each of the sampling periods (Table 3, Fig. 2). In the May sampling period, walleye pollock were the main prey item in arrowtooth flounder diets in 2002 and 2003 but were significantly less important ($H_s = 6.68$, 2 df, $P = 0.036$) in 2004. Other fish prey also decreased in importance in the arrowtooth flounder diet during 2004. Conversely, euphausiids were significantly more important ($H_s = 12.11$, 2 df, $P = 0.002$) in the diets of these fish during 2004. A similar trend was observed during the August sampling period in that walleye pollock were significantly less important ($H_s = 6.25$, 2 df, $P = 0.044$) in the arrowtooth flounder diet in 2004 compared to previous years. However, a similar trend in the importance of euphuasiids among the years was not observed during this sampling period. It is also worth noting that Pacific sand lance were not found in arrowtooth flounder stomachs in either sampling period during 2002 or 2003 but they occurred frequently in each sampling period in 2004.

Interannual trends in stomach fullness and percentage of empty stomachs suggest that arrowtooth flounder feeding activity decreased in 2004 (Table 4). Arrowtooth flounder stomach fullness differed significantly among the years in each sampling period (May- $H_s = 6.58$, 2 df, $P = 0.040$) (August- $H_s = 12.29$, 2 df, $P = 0.002$) and the stomachs were the least full ($P < 0.05$) in 2004. Additionally, the proportion of empty stomachs varied significantly among the years (May- $X^2 = 13.87$, $P < 0.05$) (August- $X^2 = 18.80$, $P < 0.05$) and the highest percentages of empty stomachs were found in 2004 (May 48.9%, August 46.4%). The size of walleye pollock consumed by arrowtooth flounder varied considerably among the years. The mean size (range) of walleye pollock in 2002 and 2003 was 325 (229-519) and 378 (290-489) mm (TL), respectively, while in 2004 it was 118 (50-455) mm (TL). The smaller mean walleye pollock size in 2004 resulted from the high abundance of age-0 fish (< 100 mm TL) in the diets. Age-0 walleye pollock were not found in arrowtooth flounder stomachs in 2002 or 2003. It appears that arrowtooth flounder consumed only adult capelin (> 85 mm TL), whereas they consumed both juvenile and adult Pacific sand lance (55-115 mm TL) during the study years.

Within-year Food Habit Variations

2002

In 2002, the diet of arrowtooth flounder (≥ 40cm TL) was noticeably similar between the May and August sampling periods (Table 3, Fig. 3). Walleye pollock and other fish were the dominant prey and together they comprised ≥ 70% (by weight) of the total stomach contents in each of the sampling periods. Shrimp were also relatively important in each of the sampling periods. There was no noticeable difference in the feeding activity of these fish between May and August as indicated by a lack of significant difference in either stomach fullness ($U_s = 118$, $P = 0.940$) or percentage of empty stomachs ($X^2 = 0.25$, $P > 0.05$) (Table 4).

2003

There were no discernible trends in the diet composition of the arrowtooth flounder (≥ 40 cm TL) collected in 2003 (Table 3, Fig. 3). Similar to 2002, walleye pollock and other fish were the dominant prey in each of the sampling periods. At this time, these prey comprised nearly 80% (by weight) of the total stomach contents in each of the sampling periods. We did not detect any noticeable change in arrowtooth flounder feeding activity between May and August in 2003 (Table 4).

2004

Each size class of arrowtooth flounder displayed substantial within-year diet differences during 2004 in depths 100-200 m (Table 3, Fig. 4). For the smaller arrowtooth flounder (20-39 cm TL), euphausiids, shrimp, and other prey were the dominant prey during May. The importance of euphausiids in the diets of these fish decreased significantly ($U_s = 252.50$, $P = 0.007$) from May to August, whereas the importance of capelin significantly increased ($U_s = 241.50$, $P = 0.001$). Other fish were also an important prey for these during August. The smaller arrowtooth flounder appeared to increase their feeding activity between May and August as evidenced by a significant increase ($U_s = 227$, $P = 0.008$) in stomach fullness and the slight decrease (38.0% to 32.0%) in the percent of empty stomachs (Table 4). For the larger arrowtooth flounder (≥ 40 cm TL), euphausiids were clearly the dominant prey during May (Table 3, Fig. 4). Pacific sand lance, shrimp, and walleye pollock were relatively important at this time as well. The importance of euphausiids in the diets of these fish significantly decreased ($U_s = 304$, $P < 0.001$) from May to August, whereas the importance of capelin significantly increased ($U_s = 462.50$, $P = 0.037$). This trend is similar to the one observed for the smaller arrowtooth flounder. Other fish and walleye pollock replaced euphausiids as the dominant prey in August. There was no noticeable change in the feeding activity of these large arrowtooth flounder, as indicated by a lack of significant difference in both the stomach fullness ($U_s = 493$, $P = 0.477$) and percentage of empty stomachs ($X^2 = 0.21$, $P > 0.05$) between May and August (Table 4).

We also observed substantial within year diet differences for each arrowtooth size class in the shallow depths (< 100 m) in 2004 (Table 3, Fig. 5). The smaller arrowtooth flounder (20-39 cm TL) fed almost exclusively on euphausiids in May and the importance of euphausiids in the diets of these fish significantly decreased ($U_s = 66$, $P < 0.001$) in August. Conversely, the importance of capelin in the diets significantly increased ($U_s = 182$, $P < 0.001$) in August for these fish. In addition, Pacific sand lance and other prey were significantly more important in the diet of these smaller fish (Pacific sand lance- $U_s = 263$, $P = 0.046$ and other prey- $U_s = 262$, $P = 0.042$) during August. Further, the smaller arrowtooth flounder had significantly fuller ($U_s = 139$, $P < 0.001$) stomachs during August, although the proportion of empty stomachs did not differ significantly ($X^2 = 0.47$, $P > 0.05$) (Table 4). Pacific sand lance and euphausiids were the dominant prey items, in terms of occurrence and weight, in the diet of larger arrowtooth flounder (≥ 40 cm TL) in both sampling periods at these depths (Table 3, Fig. 5). The importance of both walleye pollock ($U_s = 553.50$, $P = 0.040$) and capelin ($U_s = 533$, $P = 0.017$) increased significantly during August even though each item contributed little to the overall diet at this time. The feeding activity of the larger arrowtooth flounder did not differ between May and August, as indicated by a lack of significant difference in both the stomach fullness ($U_s = 561$, $P = 0.530$) and percent of empty stomachs ($X^2 = 0.76$, $P > 0.05$), at these depths (Table 4).

Ontogenetic Food Habit Variations in 2004

May

We found substantial ontogenetic diet differences for arrowtooth flounder collected from shallow depths (< 100 m) during May 2004 (Table 3, Fig. 6). Euphausiids were clearly the dominant prey, in terms of weight and occurrence, in the diets of the smaller arrowtooth flounder

(20-39 cm TL). The smaller arrowtooth flounder also frequently consumed other fish, shrimp, and other prey, although these prey contributed very little (< 10% of total stomach content weight) to the overall diet at this time. Euphausiids were significantly more important ($U_s = 159$, $P < 0.001$) in the diets of smaller arrowtooth flounder, whereas Pacific sand lance were significantly more important ($U_s = 683.5$, $P < 0.001$) in the diets of larger arrowtooth flounder (≥ 40 cm TL) in May. We detected no substantial changes in either stomach fullness or percentage of empty stomachs among the two size classes of arrowtooth flounder in the shallower depths during May 2004 (Table 4). The ontogenetic dietary differences were less noticeable in the deeper depths (100-200 m) during this sampling period (Table 3, Fig. 6). Euphausiids were the dominant prey, in terms of weight and occurrence, for both size classes at these depths. Other prey and shrimp were somewhat more important in the diets of smaller arrowtooth flounder (20-39 cm TL), whereas walleye pollock and other fish were relatively more important to the larger arrowtooth flounder (≥ 40 cm TL). The two size classes of arrowtooth flounder displayed similar levels of feeding activity in these waters (Table 4).

August

The diet composition of the two size classes of arrowtooth flounder differed considerably in the shallower depths (< 100 m) during August 2004 (Table 3, Fig. 7). Capelin and other prey were significantly more important in the diets of the smaller arrowtooth flounder (capelin- $U_s = 228$, $P = 0.036$ and other prey- $U_s = 279$, $P = 0.031$) at these depths. Conversely, Pacific sand lance were noticeably more important in the diets of large arrowtooth flounder. Interestingly, euphausiids were relatively important, in terms of both weight and occurrence, for both of the size classes in these waters. The smaller arrowtooth flounder had significantly fuller ($U_s = 145$, $P < 0.001$) stomachs compared to the large arrowtooth flounder, although the proportion of empty stomachs did not differ significantly ($X^2 = 0.09$, $P < 0.001$) in the shallow waters at this time (Table 4). We also found substantial ontogenetic diet differences in the deeper waters (100-200 m) during this sampling period (Table 3, Fig. 7). Capelin comprised a significantly larger portion ($U_s = 634$, $P = 0.026$) of the diets of small arrowtooth flounder and walleye pollock comprised a greater portion ($U_s = 647.50$, $P = 0.013$) of the diets of large arrowtooth flounder in these depths. The remaining prey groups were relatively similar for each size class of arrowtooth flounder at these depths. Similar to the trend observed in specimens collected in the shallow waters, the smaller arrowtooth flounder had significantly fuller ($U_s = 419$, $P < 0.001$) stomachs and a smaller percentage of empty stomachs, compared to the large arrowtooth flounder, at this time (Table 4).

DISCUSSION

General Diet Composition

The diet composition results indicate the arrowtooth flounder near Kodiak Island consumed mainly fish, euphausiids, and shrimp, which are consistent with previous findings. For example, Rose (1980) found that fish, decapods, and euphausiids were the main prey, respectively, in arrowtooth flounder diets in the northeast Gulf of Alaska. Similarly, fish were the top prey (by weight) in arrowtooth flounder stomachs sampled during Gulf-wide trawl surveys in 1993, 1996, and 1999 (Yang and Nelson 2000). Benthic invertebrate prey such as mollusks, annelids, and echinoderms were incidental items in the arrowtooth flounder diets, which is also consistent with previous findings.

Despite these similarities, we found several key differences in arrowtooth flounder prey composition between this study and previous reports that appear to reflect changes in the Gulf of Alaska community during the past 30 years. Rose (1980) reported that osmerids were the most common fish prey in arrowtooth flounder diets and that walleye pollock occurred in less than 2% of the samples during his 1975-76 study. Conversely, walleye pollock were the most common fish encountered in the arrowtooth flounder diets in this study (Table 2). Furthermore, shrimp were seen twice as frequently in arrowtooth flounder diets in the 1975-76 study compared with the present study. The Gulf of Alaska was dominated by forage fish and shrimp species in 1975-76 and in the late 1970s the ecosystem underwent a large-scale shift to a community dominated by piscivorous flatfish and gadid species (Anderson et al. 1997, Anderson and Piatt 1999). Hence, changes in the diet reflect the differences in prey availability during these two periods.

Additionally, Pacific sand lance was a far more important prey item in this study compared to earlier studies (Rose 1980, Yang 1995, Yang and Nelson 2000). Pacific sand lance tend to be patchily distributed in nearshore waters because they prefer shallow depths and sandy substrates (Ostrand et al. 2005). Therefore, the importance of such a site-specific species may have been obscured in previous studies, which sampled a far wider range of habitats, compared with this project. Consequently, Pacific sand lance appear to be a locally important prey of arrowtooth flounder in the shallow waters of Marmot and Chiniak Bays.

Temporal Variations

Interannual diet comparisons revealed several key shifts in the diets of adult arrowtooth flounder among the study years that appear to reflect temporal changes in prey availability. For example, the consumption of Pacific sand lance varied significantly among years and was highest in 2004. In fact, only 2 of 121 arrowtooth flounder stomachs examined in 2002 and 2003 contained this prey species. Little is known about the population dynamics of Pacific sand lance within the study area, however, changes in their abundance or availability may be reflected in the diets of other top level predators. For instance, there was an increase in the importance of Pacific sand lance in the diets of tufted puffins *Fratercula cirrhata* in Chiniak Bay from 2002 to 2004 (Cory Williams, University of Alaska Fairbanks, Fairbanks, Alaska, pers. commun.). Taken together, these findings suggest that Pacific sand lance were more available as a prey source in 2004. Furthermore, it would benefit arrowtooth flounder energetically to consume Pacific sand lance when available because they are one of the most energy-rich fish in the area (Payne et al. 1999, Anthony et al. 2000).

There were also noticeable changes in the importance of euphausiids in arrowtooth flounder diets among years, especially during the May sampling period. Zooplankton abundance and species composition are mainly influenced by changes in the salinity and temperature of the water column in Gulf of Alaska shelf waters (Coyle and Pinchuk 2003). The temperature and salinity of the surface waters of Chiniak and Marmot Bays fluctuated among the study years and within these waters the production of the local zooplankton community varied accordingly (Xian Wang, University of Alaska Fairbanks, Fairbanks, Alaska, pers. commun.). It is possible that fluctuating oceanographic conditions affected euphausiid abundance, which in turn influenced their relative rates of consumption by arrowtooth flounder, during the study years.

It appears that arrowtooth flounder shifted from consuming mostly age-1 and -2 walleye pollock in 2002 and 2003 to age-0 walleye pollock in 2004. In 2004, age-0 walleye pollock were highly abundant in the bottom trawls conducted in the study area unlike previous years when they were not as prevalent (Robert Foy, University of Alaska Fairbanks, Kodiak, Alaska, unpubl. data). The increase in the consumption of juvenile walleye pollock as their availability increased in 2004 reflects the trophic adaptability of arrowtooth flounder.

The increase in the number of samples collected and analyzed in 2004, compared to the previous years, may have resulted in an increase in prey diversity in the diets. However, the principal prey items were consistent throughout the study years, with the exception of Pacific sand lance. The importance of Pacific sand lance may have been overstated in 2004 (or understated in previous years) due to discrepancy of sample sizes among the years. Although the frequent occurrence of Pacific sand lance in the diets during 2004 regardless of size class, depth interval, or sampling period, indicates they were more highly available at this time.

Seasonal variations in temperature and day length in high latitude regions impose strong seasonal effects on the composition and production of nearshore fish communities (Nash 1988, Robards et al. 1999). As a result, top-level predators experience considerable variability in the abundance and quality of prey throughout the year. Seasonal dietary differences have been observed for many predatory flatfish species (Libey and Cole 1979, Livingston et al. 1986, Tokranov 1990). Arrowtooth flounder are believed to feed opportunistically on the most abundant prey in the environment (Rose 1980, Yang and Livingston 1986) and consequently within-year dietary shifts most likely reflect seasonal changes in prey abundance and/or availability.

The importance of euphausiids and capelin in the arrowtooth flounder diets varied most strongly between May and August in this study. Euphausiids tended to be more important in the diets during May, which is consistent with previous findings for arrowtooth flounder in the northeast Gulf of Alaska (Rose 1980). In the northern Gulf of Alaska shelf waters, the annual biomass peak for zooplankton occurs during May (Coyle and Pinchuk 2003). Furthermore, in high latitude regions many fish species begin moving onshore in May as water temperatures increase and do not peak in relative abundance until mid-summer (Robards et al. 1999). Therefore, the importance of euphausiids in arrowtooth flounder diets during May possibly reflects a combination of the high zooplankton production and relatively low availability of fish prey at this time.

Unlike euphausiids, capelin were mostly non-existent in the arrowtooth flounder diets in May but rose in importance in August. Capelin spawn on intertidal beaches in the North Pacific during a protracted spawning period from late spring through early summer (Pahlke 1985) and spawning activity near Kodiak Island, Alaska, generally peaks around June or July (Doyle et al. 2002). Only adult capelin (90 to 120 mm TL) were consumed by arrowtooth flounder in this study and ripe females were noted frequently in stomach samples. This finding indicates that arrowtooth flounder were possibly targeting adult capelin congregating nearshore to spawn during August. This behavior would benefit arrowtooth flounder because capelin may be more vulnerable to predation during spawning and they are a particularly energy-rich food source, especially the ripe females (Payne et al. 1999, Anthony et al. 2000). The ability to take advantage of this energetically valuable late summer food source demonstrates their adaptable feeding behavior.

Temperate fish species commonly exhibit seasonal cycles of feeding activity that are driven by changes in abiotic and biotic factors such as water temperature, food supply, and reproduction (MacKinnon 1972, Dawson and Grimm 1980, Dygert 1990). In this study, we found that the smaller arrowtooth flounder displayed higher feeding activity levels during August when bottom temperatures were on average 1.48°C higher than in May (Knoth 2006). The higher feeding levels in August may be a mechanism to cope with greater energetic costs, associated with the higher temperatures, during this time. These differences may also reflect a more diverse and abundant food supply available to these fish during August. Larger arrowtooth flounder may utilize different strategies to counter changes in their thermal environment, such as migrating to deeper, cooler waters and benefiting from the associated lower metabolic costs.

Ontogenetic Variations

We found that the ontogenetic diet variations varied spatially. For instance, Pacific sand lance were noticeably more important in the diets of the larger arrowtooth flounder, compared to smaller cohorts, in the shallow depths only. This is likely a combination of factors including prey availability and physical limitations. Pacific sand lance have a preference for sand and gravel substrates in shallow waters, which limits their availability to predators (O'Connell and Fives 1995). It has been noted previously that arrowtooth flounder display an increasing trend towards piscivory as they grow (Rose 1980, Yang and Livingston 1986, Yang and Nelson 2000), thus prey consumption for each size group may be dictated by a physical limitation such as gape size.

The ontogenetic diet differences also varied temporally and appeared more pronounced during the August sampling period. At this time, capelin were more important in the diets of smaller arrowtooth flounder compared to larger cohorts in each depth interval. The larger arrowtooth flounder favored larger fish prey such as walleye pollock or Pacific sand lance during the August sampling period. The larger arrowtooth flounder would be able to consume a wider size range and diversity of fish prey compared to smaller cohorts because of their larger gaping mouths (Yang and Livingston 1986). This type of ontogenetic diet shift may reduce the competition for food between large and small individuals of the same species (Grossman 1980) and is consistent with the optimum foraging theory (Gerking 1994). It is important to note that there may be ontogenetic differences based on sexual maturity that were overlooked. Sexual maturity was not examined and changes in feeding habits may be driven by changes in energetic needs due to reproduction. Arrowtooth flounder exhibit sexual dimorphism with respect to size at maturity, with females maturing at a larger size (females 50% maturity at 47 cm, males at 42 cm (Zimmermann 1997)). These lengths correspond roughly with the size cutoff (40 cm) that we used to designate the two size classes in our study. Arrowtooth flounder are group synchronous batch spawners with a fall to winter spawning period (Rickey 1995). In the Gulf of Alaska, the spawning season for arrowtooth flounder is unclear, but it is believed to begin after September (Zimmermann 1997). Taken as a whole, the August sampling period would represent a critical feeding period for large, sexually mature arrowtooth flounder seeking to acquire the necessary energy levels for reproduction. Thus, these factors may have contributed to the temporal variability associated with the ontogenetic diet differences.

Ecosystem Considerations

The ability to adapt to changing feeding conditions is a necessary trait for a species to be successful, particularly in a fluctuating environment like the Gulf of Alaska. The Gulf of Alaska ecosystem alternates between anomalous warm and cool states or “regimes” characterized by distinct atmospheric, oceanic, and biological conditions (Mantua et al. 1997, Hare and Mantua 2000). Following the shift to a warm regime in the late 1970s, there was a marked improvement in the recruitment of groundfish species, including arrowtooth flounder, and a concurrent decrease in shrimp and forage fish species in the Gulf of Alaska (Hollowed and Wooster 1992). The ability of arrowtooth flounder to adapt to large-scale changes in prey resources likely contributed to their success during this period of transition. Furthermore, there have been at least two other documented climate shifts in the North Pacific since the late 1970s, but the biological response to these shifts have yet to be fully realized (Hare and Mantua 2000, Benson and Trites 2002, Peterson and Schwing 2003). It is unlikely that a major decline in any single prey source would negatively affect the arrowtooth flounder population in the Gulf of Alaska because of their adaptable feeding behavior.

Results of this study support previous findings that arrowtooth flounder mainly feed on pelagic and semi-pelagic forage fish and invertebrates (Rose 1980, Yang and Livingston 1986, Yang 1995, Yang and Nelson 2000). These prey species are critical links between primary producers (phytoplankton) and higher trophic level predators in the nearshore Kodiak Island ecosystem and throughout the western Gulf of Alaska. Additionally, other top-level fish, marine mammal, and seabird predators rely on these forage prey to varying degrees (Perez 1990, Hayes and Kuletz 1997, Witteveen et al. 2006, Yang and Nelson 2000, Yang et al. 2005). Consequently, the large arrowtooth flounder population in the Gulf of Alaska may affect multiple trophic levels in the system through predation and competition.

Our findings may have important management implications because ecosystem-based management models rely extensively on detailed diet information in order to describe complex species interactions. We found significant temporal variations in the diet of arrowtooth flounder even though the time span of our study was limited in its scope. Many other marine fish display temporal, spatial, and ontogenetic variations in their diets as well (Libey and Cole 1979, Grossman 1980, Tokranov 1990, Gerking 1994) and these types of dietary variations are difficult to incorporate into ecosystem-based models (Pauly et al. 2000). Nevertheless, a lack of understanding of such diet variability may misrepresent the importance of key prey species across temporal and spatial scales. Therefore, the diet information included in ecosystem-based models needs to cover significant temporal variations in predator diets (Hanson and Chouinard 2002, Pauly et al. 1998).

Arrowtooth flounder display a highly adaptable feeding behavior that is evident in the degree of temporal variability in their food habits in an area of high abundance in the western Gulf of Alaska. We found that arrowtooth flounder diet and feeding activity, based on size class and depth distribution, vary both within and among years near Kodiak Island, Alaska. Arrowtooth flounder diets may reflect changes in prey availability and abundance or differences in feeding behavior associated with prey selection. To address this, future studies that assess the breadth of interactions between arrowtooth flounder and its prey need to concurrently measure prey abundance and distribution. Documenting arrowtooth flounder feeding behavior, in response to changing levels of prey abundance and composition, will allow for a better understanding of the trophic interactions of this key predator in the nearshore ecosystem of Kodiak Island and throughout the western Gulf of Alaska.

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Table 1. -- Arrowtooth flounder (*Atheresthes stomias*) stomach samples* collected for each size, depth interval, sampling period and year near Kodiak Island, Alaska.

			Depth interval (m)		
Year	Size (cm TL)	Sampling period	< 100	100-200	> 200
2002	≥ 40	May	5	20	3
		August	13	44	0
2003	≥ 40	May	0	18	0
		August	26	37	10
2004	≥ 40	May	71	87	37
		August	45	105	0
	20-39	May	40	70	8
		August	38	65	0

* All stomachs collected including empty stomachs

Table 2. -- Percent weight (%Wt) and percent frequency of occurrence (%FO) of arrowtooth flounder (*Atheresthes stomias*) diets sampled near Kodiak Island, Alaska, from 2002 to 2004. Categories including fish, shrimp, euphausiid, and other prey show the sum of the components within that category. Asterisks indicate value was less than 0.1%.

Prey categories	% Wt	% FO
Fish	43.5	51.0
Ammodytes hexapterus (Pacific sand lance)	9.6	12.9
Atheresthes stomias (arrowtooth flounder)	1.1	1.3
Cottidae (sculpin)	*	0.2
Fishery offal	0.2	0.2
Gadidae (gadid fish)	1.4	2.2
Hippoglossoides elassodon (flathead sole)	1.4	1.5
Lumpenus sagitta (snake prickleback)	0.2	0.2
Mallotus villosus (capelin)	8.5	9.7
Pleuronectidae (unidentified flatfish)	0.5	0.6
Sebastes sp. (rockfish)	*	0.2
Teleostei (unidentified fish)	5.0	8.0
Thaleichthys pacificus (eulachon)	0.2	0.4
Theragra chalcogramma (walleye pollock)	13.3	14.0
Trichodon trichodon (Pacific sandfish)	0.2	0.2
Zoarcidae (unidentified eelpout)	1.7	1.9
Euphausiid	17.7	29.7
Euphausia pacifica	0.2	0.2
Euphausiacea (unidentified)	8.1	17.0
Thysanoessa inermis	2.6	3.0
Thysanoessa raschii	0.7	0.9
Thysanoessa sp.	4.3	5.6
Thysanoessa spinifera	1.9	2.8
Shrimp	8.2	12.0
Crangon communis	*	0.2
Crangon dalli	*	0.2
Crangonidae (unidentified)	0.0	0.2
Eualus gaimardii	0.3	0.4
Eualus sp.	*	0.2
Pandalopsis dispar	0.2	0.2
Pandalopsis sp.	0.5	0.6
Pandalus borealis	2.4	3.7
Pandalus sp.	1.4	1.9
unidentified shrimp	3.2	4.7
Other prey	3.2	9.2
Bivalvia (clam)	0.2	0.9
Calanoida (copepod)	*	0.6
Chionoecetes bairdi (Tanner crab)	0.2	0.2
Crustacea (unidentified)	1.0	3.7
Decapoda (unidentified crab)	*	0.4
Echiuridae (marine worm)	0.2	0.4
Gammaridea (unidentified amphipod)	*	0.2
Mysidae (unidentified mysid)	0.9	1.3
Psolus sp. (sea cucumber)	0.3	0.4
Snail eggs (unidentified)	*	0.2
Unidentified digested material	27.3	32.7

Table 3. -- Interannual, within-year and ontogenetic variations in the percent frequency of occurrence (% FO) of the major prey categories in the arrowtooth flounder (*Atheresthes stomias*) diets collected in two depth intervals (< 100 m and 100-200 m) near Kodiak Island, Alaska.

	Year											
	2002		2003		2004							
	100-200 m		100-200 m		< 100 m				100-200 m			
	≥ 40 cm		≥ 40 cm		20-39 cm		≥ 40 cm		20-39 cm		≥ 40 cm	
Prey categories	May	August	May	August	May	August	May	August	May	August	May	August
Capelin	0	8	5.9	0	0	41.7	0	12.5	0	36.8	0	15.6
W. pollock	40	44	47.1	44.4	0	8.3	0	9.4	0	5.3	10.3	24.4
P.sand lance	0	0	0	0	3.2	20.8	47.8	40.6	8.7	13.2	20.7	6.7
Other fish	40	32	35.3	29.6	41.9	8.3	13	15.6	4.4	23.7	13.8	33.3
Shrimp	20	24	11.8	7.4	38.7	12.5	8.7	6.3	21.7	23.7	13.8	15.6
Euphausiids	10	16	11.8	14.8	83.9	45.8	43.5	43.8	43.5	21.1	51.7	22.2
Other prey	0	8	17.7	14.8	48.4	37.5	39.1	18.8	39.1	10.5	20.7	22.2
Sample size (n)	10	24	17	23	28	23	41	30	21	37	25	44

Table 4. – Kruskal-Wallis (H_s), Mann-Whitney (U_s), and Chi-square (X^2) test results investigating variations in arrowtooth flounder (*Atheresthes stomias*) stomach fullness and percentage of empty stomachs in specimens collected near Kodiak Island, Alaska. Interannual (2002 vs. 2003 vs. 2004), within-year (May vs. August), and ontogenetic (20-39 cm TL vs. ≥ 40 cm TL) comparisons were made. Significant P-values of the respective test statistic are denoted by: * P < 0.05, ** P < 0.01, and *** P < 0.001.

Comparisons	Stomach fullness		Empty stomachs	
Interannual	H_s	P-value	X^2	P-value
May	6.58	0.040*	13.87	< 0.05*
August	12.29	0.002**	18.80	< 0.05*
Within-year	U_s	P-value	X^2	P-value
2002 (100-200 m)	118	0.940	0.25	> 0.05
2003 (100-200 m)	171	0.503	0.12	> 0.05
2004 (100-200 m; 20-29 cm TL)	227	0.008**	3.11	> 0.05
2004 (100-200 m; ≥ 40 cm TL)	493	0.477	0.21	> 0.05
2004 (< 100 m; 20-29 cm TL)	139	< 0.001***	0.47	> 0.05
2004 (< 100 m; ≥ 40 cm TL)	561	0.530	0.76	> 0.05
Ontogenetic	U_s	P-value	X^2	P-value
May 2004 (< 100 m)	522	0.525	1.61	> 0.05
May 2004 (100-200 m)	187	0.096	1.37	> 0.05
August 2004 (< 100 m)	145	< 0.001***	0.09	> 0.05
August 2004 (100-200 m)	419	< 0.001***	3.69	> 0.05

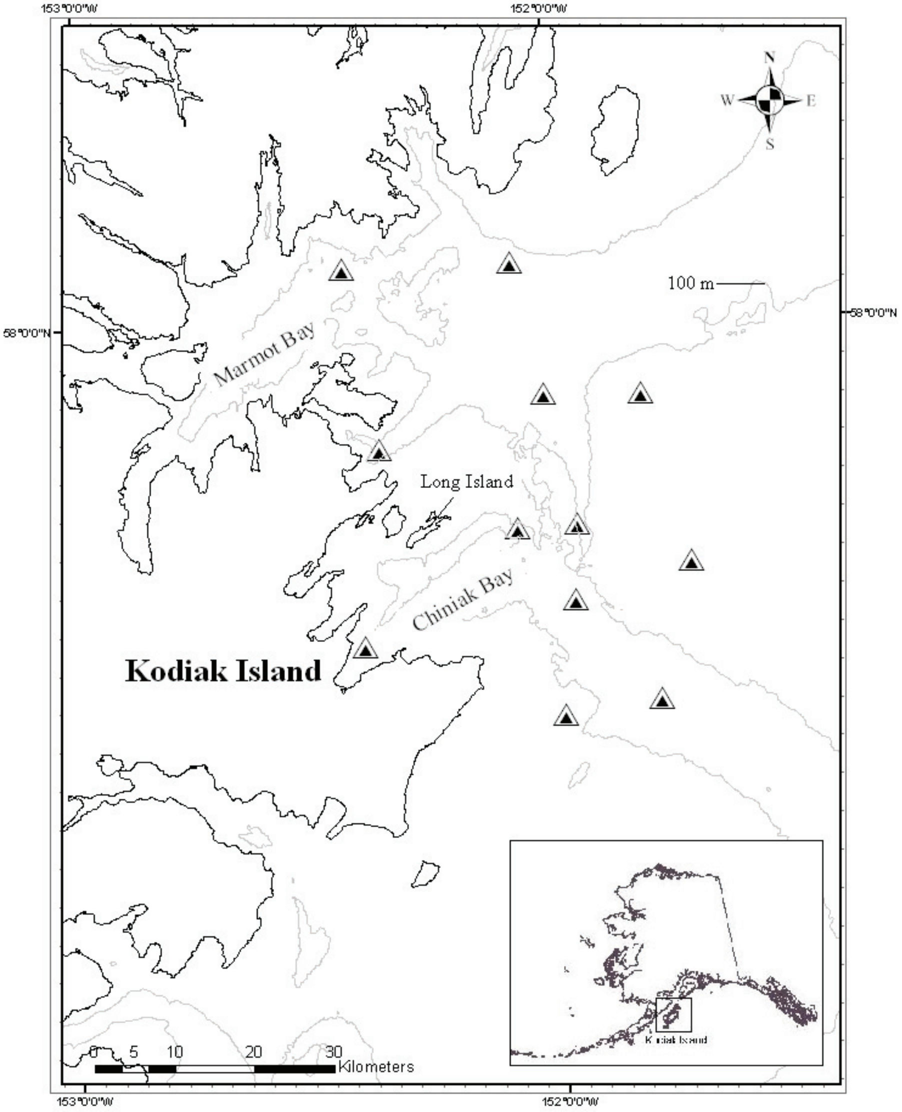

Figure 1-- Locations of bottom trawl stations (filled triangles) in the nearshore waters of Kodiak Island, Alaska. Fixed sampling stations were sampled during May and August annually in 2002, 2003, and 2004.

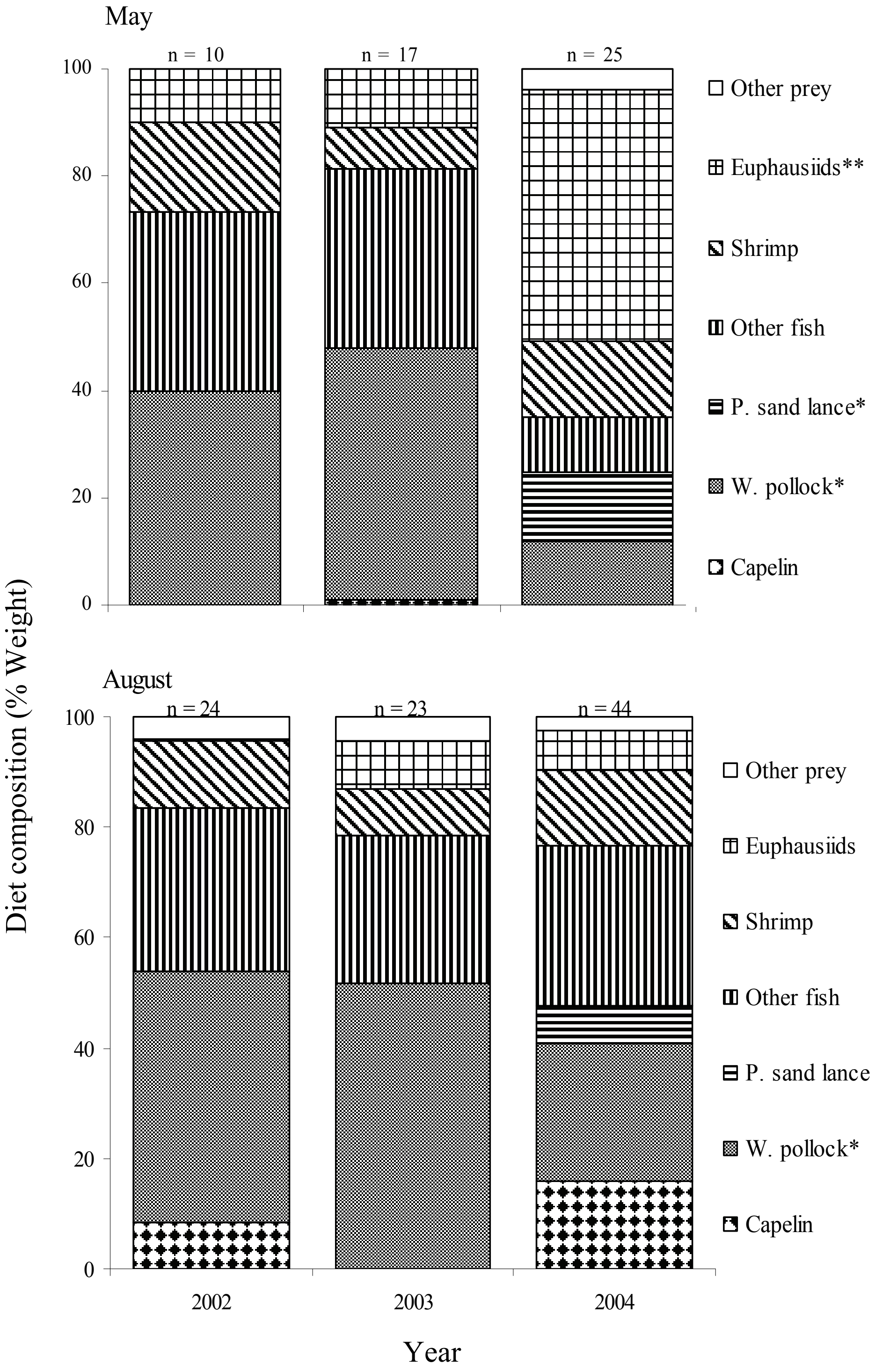

Figure 2-- Interannual variations in diet composition (by % weight) of arrowtooth flounder (*Atheresthes stomias*) (≥ 40 cm) sampled near Kodiak Island, Alaska, during May (top) and August (bottom) of 2002, 2003, and 2004. Significant Kruskal-Wallis tests are denoted by * $P < 0.05$ and ** $P < 0.01$.

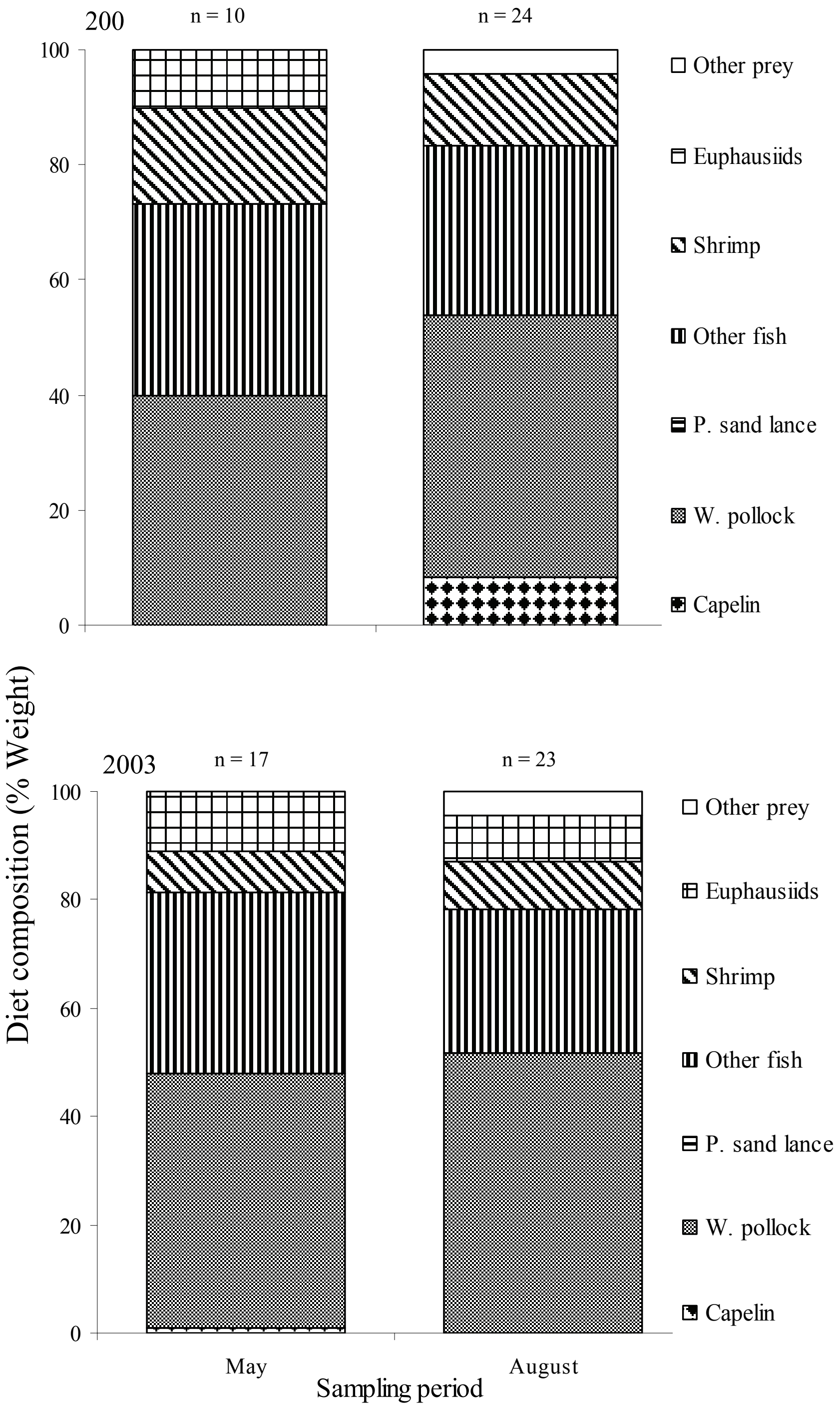

Figure 3-- Within-year variations in the diet composition (by % weight) of arrowtooth flounder (*Atheresthes stomias*) (≥ 40 cm) sampled near Kodiak Island, Alaska, during 2002 (top) and 2003 (bottom).

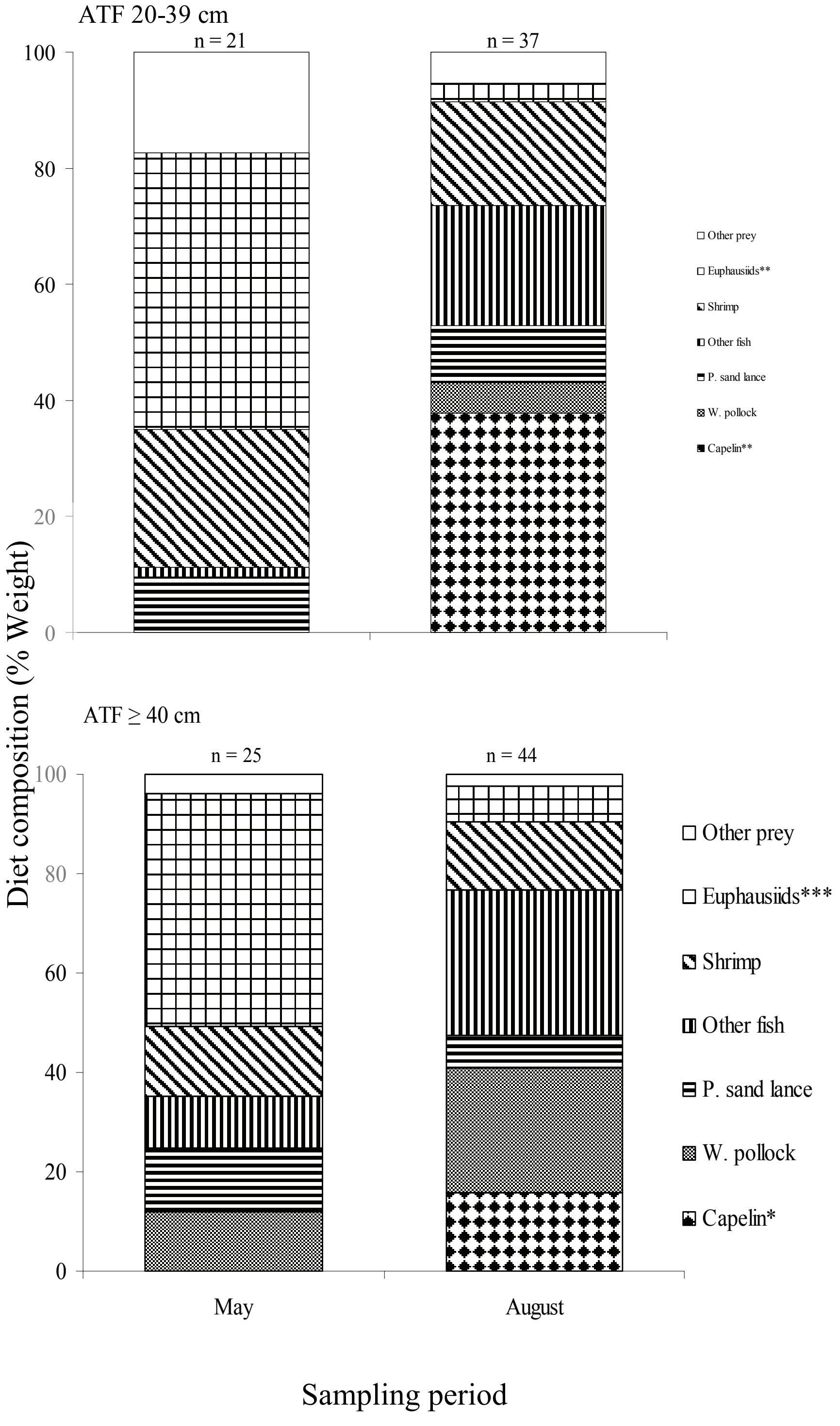

Figure 4-- Within-year variations in the diet composition (by % weight) of arrowtooth flounder (*Atheresthes stomias*) 20-39 cm (top) and ≥ 40 cm (bottom) sampled in depths 100-200 m near Kodiak Island, AK in 2004. Significant Mann-Whitney U-tests are denoted by * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

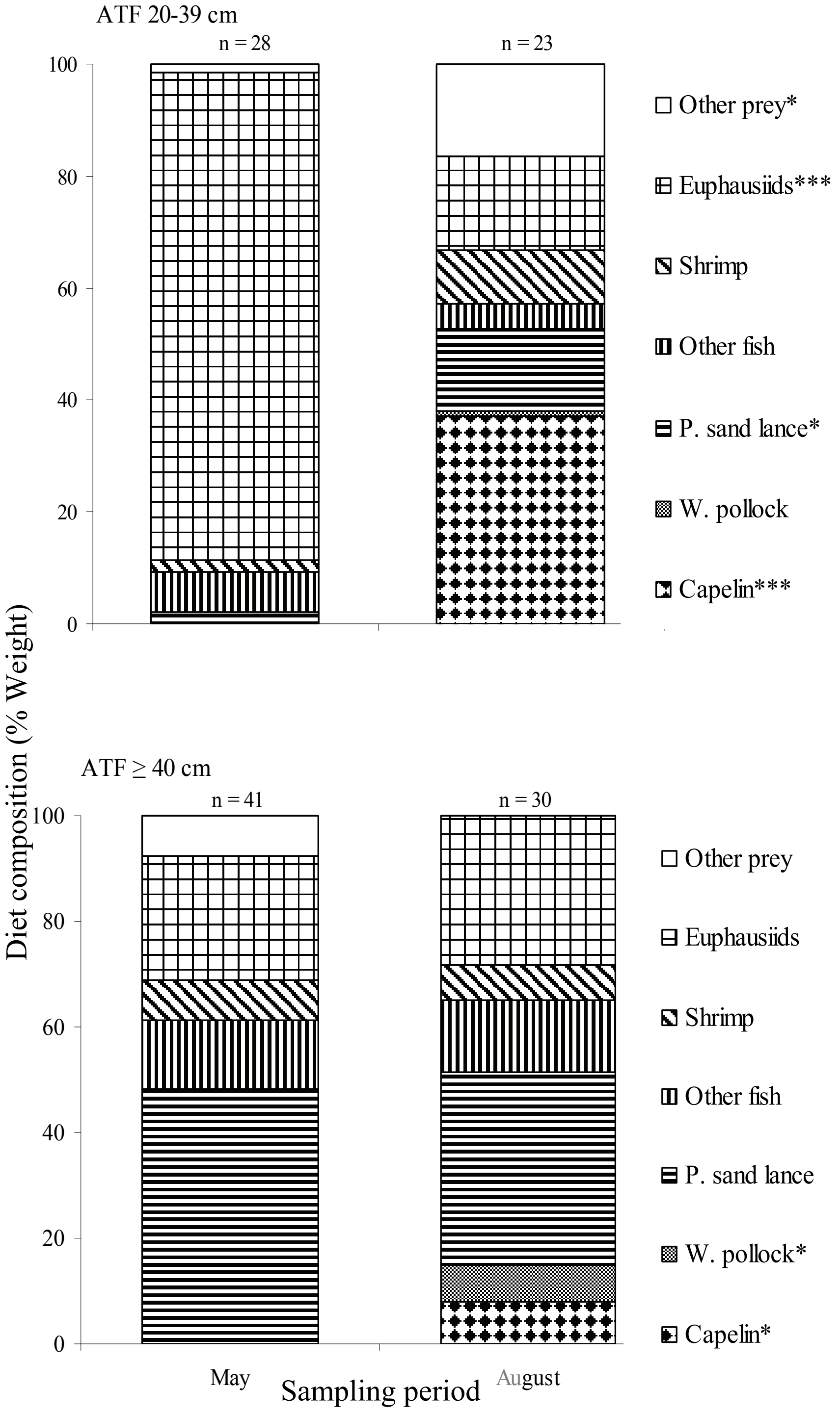

Figure 5-- Within-year variations in the diet composition (by % weight) of arrowtooth flounder (*Atheresthes stomias*) 20-39 cm (top) and ≥ 40cm (bottom) sampled in depths < 100 m near Kodiak Island, Alaska, in 2004. Significant Mann-Whitney U-tests are denoted by * P < 0.05 and *** P < 0.001.

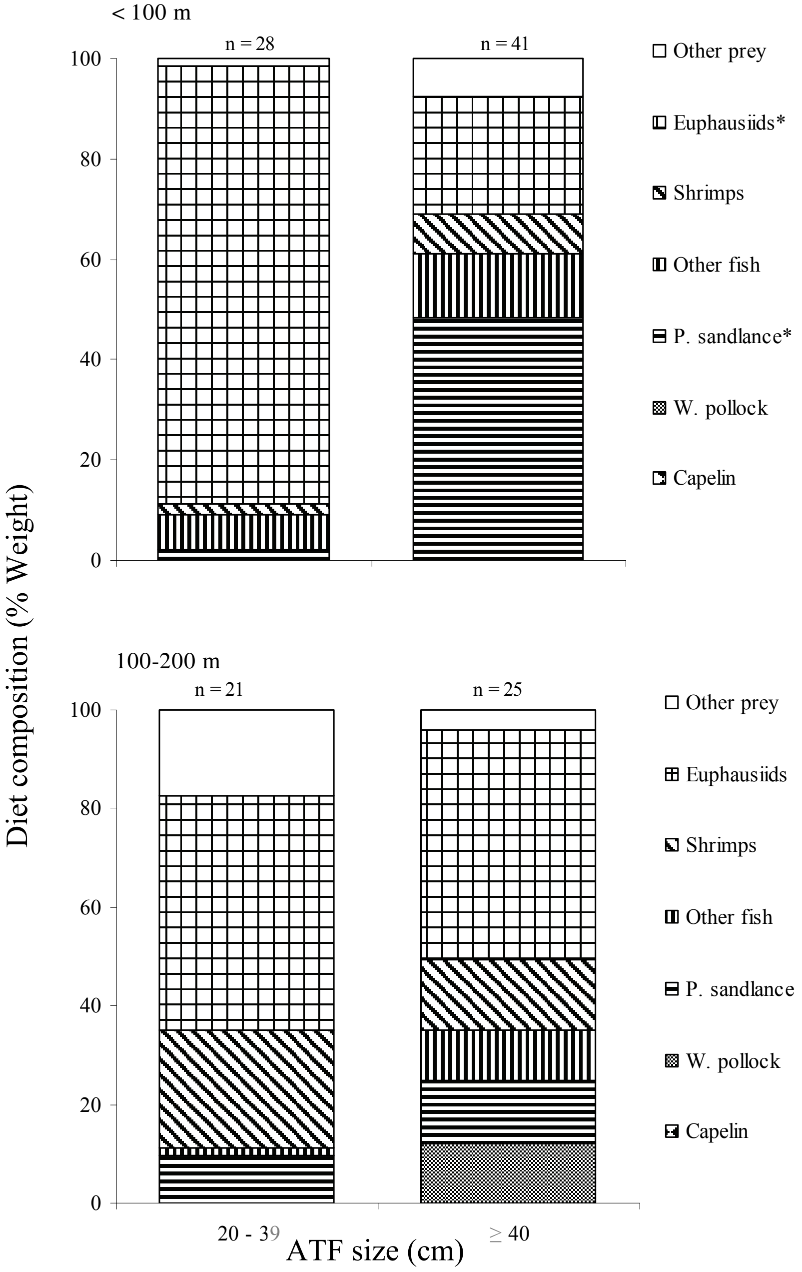

Figure 6-- Ontogenetic variations in the diet composition (by % weight) of arrowtooth flounder (*Atheresthes stomias*) sampled during May 2004 near Kodiak Island, Alaska, in depths < 100 m (top) and 100-200 m (bottom). Significant Mann-Whitney U-tests are denoted by * P < 0.001.

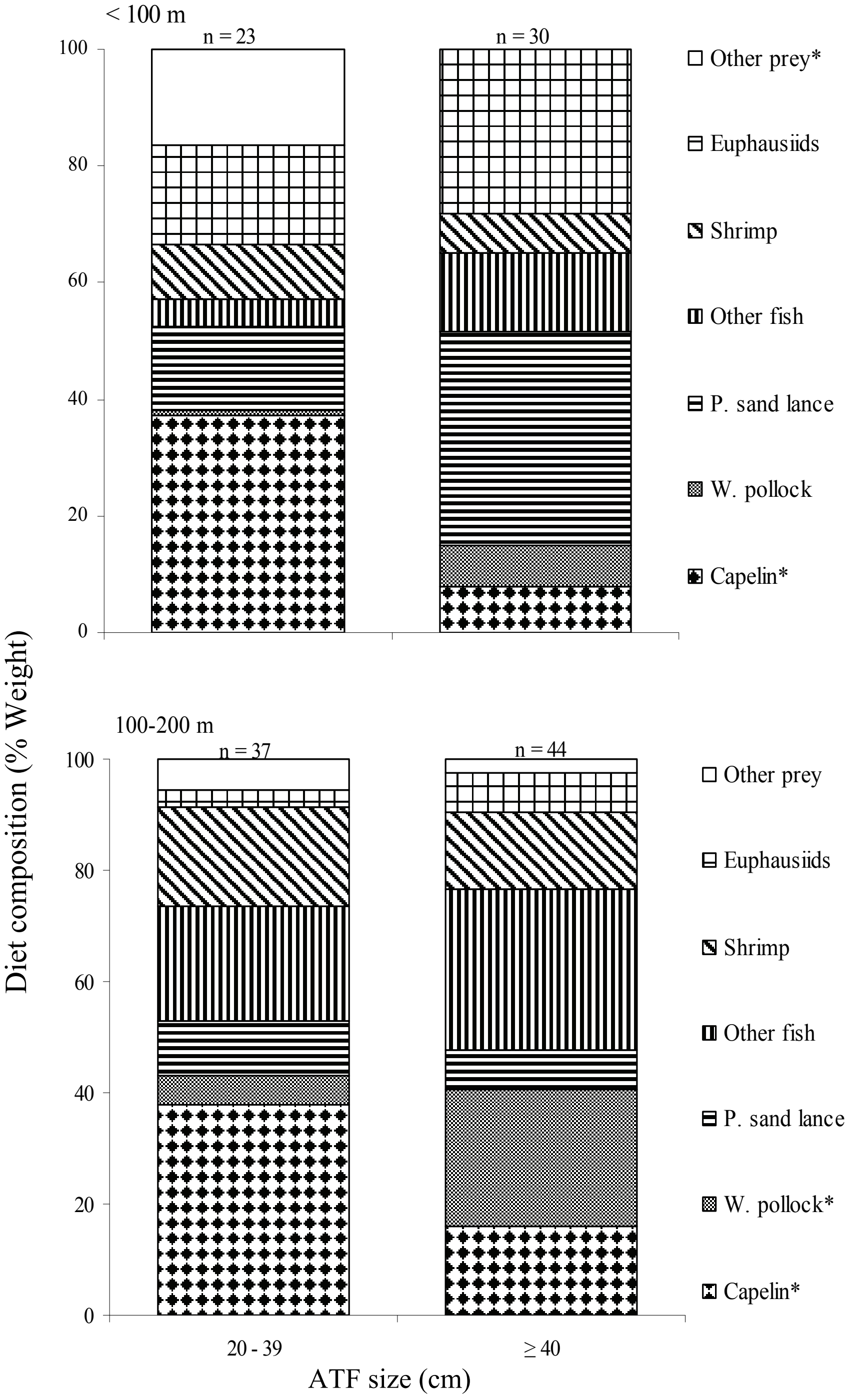

Figure 7-- Ontogenetic variations in the diet composition (by % weight) of arrowtooth flounder (*Atheresthes stomias*) sampled during August 2004 near Kodiak Island, Alaska, in depths < 100 m (top) and 100-200 m (bottom). Significant Mann-Whitney U-tests are denoted by * $P < 0.05$.

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