Ecology of age-0 arrowtooth flounder (*Atheresthes stomias)* inhabiting the Gulf of Alaska.

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ABSTRACT

Age-0 arrowtooth flounder (*Atheresthes stomias*) were collected from surface waters, throughout the summer months in the Gulf of Alaska. As the most abundant groundfish species in the Gulf of Alaska, arrowtooth flounder are an important ecological component of this ecosystem. While information is available for juvenile and adult arrowtooth flounder, and to some extent the ichthyoplankton life stage and spawning processes, the late-pelagic, post-larval stage of arrowtooth flounder has been the subject of fewer inquiries. This study examined the effects of environmental parameters on age-0 arrowtooth flounder in the pelagic environment. Based on data collected from 2010-2013, this study provided information on the abundance, distribution, pelagic duration, size, growth, diet and energy content of age-0 arrowtooth flounder in the Gulf of Alaska. Mean settlement to the benthos occurred at approximately 41 mm standard length, which corresponded to early August. Average energy density was 20.42 ± 0.07 kJ g^{-1} dry mass and showed no change with size, although there were some interannual differences that were attributed to changes in temperature and diet composition. This study helps fill critical gaps in the knowledge of the early life history of arrowtooth flounder and how they respond to the biophysical parameters in the Gulf of Alaska.

Key words: Arrowtooth flounder; Gulf of Alaska, Energy storage, Early life history strategy, Basic early life history biology, Diet

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1. Introduction

Environmental conditions experienced by groundfish in their post-metamorphic pelagic phase are important because they are vulnerable to predation during this stage, actively growing, and acquiring energy stores needed for settlement (Hoey and McCormick, 2004) and overwinter survival (Farley et al., 2014; Heintz et al., 2013; Mazur et al., 2007; Moss et al., 2009). Marine fish that spawn offshore and require nearshore nursery habitats must be passively or actively transported onto the shelf in order to eventually settle on suitable habitat (Vestfals et al., 2014). Environmental conditions such as temperature, predator density and food availability can influence their survival during transport. Identifying basic life history patterns and requirements during this period is therefore an important step toward understanding how biophysical factors may influence early life stage survival and ultimately recruitment. This understanding is particularly important for flatfish because their transition from the pelagic larvae to benthic juveniles includes a number of energetically demanding processes such as larval development, growth, and eye migration (Geffen et al., 2007; Fedewa et al., 2016; Fraboulet et al., 2010). For flatfish, factors such as temperature and food supply have been shown to influence growth, timing of metamorphosis, and settlement (Benoît et al., 2000; Fedewa et al., 2016).

Understanding these processes for arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska (GOA) is of particular value because of their ecological importance. Adult arrowtooth flounder are widely distributed, extending from Northern California to the Bering Sea (Turnock et al., 2003; Zimmermann and Goddard, 1996), and as of 2017 represented the greatest biomass of a single groundfish species in the GOA (Mundy and Hollowed, 2005; Spies et al., 2015). Although arrowtooth flounder are of limited commercial value, they are an important component of the North Pacific marine ecosystem as both predators and competitors (Blood et al., 2007; Hollowed et al., 2000; Yang and Nelson, 2000). Their life history, which includes offshore spawning and a prolonged pelagic life stage (Doyle and Mier, 2015), exposes them to variability in the pelagic environment. Arrowtooth flounder reproduce along the shelf break at depths greater than 400 m during the winter months in the GOA (Blood et al., 2007; Stark, 1997; Zimmermann, 1997); as a result, arrowtooth flounder eggs and larvae are found in relatively deep waters and further offshore compared to most other flatfish in the GOA (Bailey et al., 2008; Blood et al., 2007). Early and prolonged spawning as a life history strategy for arrowtooth flounder could be advantageous by increasing the amount of time larvae remain in the water column and grow before the spring bloom occurs (Doyle and Mier, 2015), optimizing the temporal and spatial overlap with zooplankton prey (Cushing, 1995; Durant et al., 2007). This phenology may also be beneficial to arrowtooth flounder because it enhances the active transport of larger age-0 fish to nearshore nursery habitats through submarine canyons (Bailey and Picquelle, 2002).

Arrowtooth flounder were one of five focal species investigated by the Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP; hereafter GOA project). This large-scale fisheries oceanographic survey aimed to quantify the major ecosystem processes that affect the early life history, and ultimately regulate the recruitment strength, of key groundfish species in the GOA. A limited amount of information on early life history patterns and recruitment exists for arrowtooth flounder during the larval stage (Bailey et al., 2008; Bailey and Picquelle, 2002; Blood et al., 2007; Doyle and Mier, 2015), and even less information is available for the late pelagic phase (De Forest et al., 2014). The GOA project provided the opportunity to collect arrowtooth flounder from the surface waters in the GOA during a poorly sampled and under-examined life stage. This report provides basic data describing the early life history and ecology of the age-0 arrowtooth flounder in the GOA including information on their abundance, distribution, pelagic duration, size, growth, diet and energy content. These observations occurred over multiple years, allowing us to relate them to environmental conditions. Finally, in order to place the energetic data in context we examined the energy content of older post-settlement arrowtooth flounder from other surveys.

2. Methods and Materials

2.1. Survey information

Arrowtooth flounder were collected over the four-year span of the GOA project (2010-2013). The project involved large-scale fisheries oceanographic surveys conducted each year aboard the 49 m F/V *Northwest Explorer* between July and September in the eastern (EGOA) and central (CGOA) GOA at pre-determined stations (Fig. 1). Surface trawling was conducted at each station to determine the spatial distribution and abundance of pelagic species, including arrowtooth flounder. Specimens were collected using a Cantrawl model 400 midwater rope trawl. The 400 model is comprised of hexagonal mesh wings in the body, and has a 1.2 cm mesh codend liner at the foot. The trawl was modified to fish at the water surface by stringing buoys along the headrope. Surface tows were 30 minutes in duration and were made at speeds that ranged from between 1.6 to 4.8 knots with an average tow speed of 3.1 knots. Mouth openings averaged approximately 40 m wide x 35 m deep. Catch per unit effort (CPUE, fish/km^2) was obtained by dividing the number of fish caught by the area swept, which was a product of the distance towed (km) and the horizontal net spread (km). Physical and biological oceanographic sampling were also conducted at each sample station location. This study used surface temperatures for all analyses and comparisons, which was defined as the temperature at one meter of depth, obtained using a Conductivity-Temperature-Depth recorder (CTD; model SBE-25, Seabird Electronics, Bellevue, WA, USA).

2.2. Biological sampling, distribution, and abundance

All arrowtooth flounder present in the trawl catches were enumerated and standard lengths (SL; mm) were recorded in the field. Up to 20 random fish were retained from each trawl for diet processing and bomb calorimetry. These fish were individually labeled and immediately frozen at sea (-40 °C). Individual wet weights (g) were obtained in the laboratory for preserved fish. At the end of each survey leg samples were transferred to and stored in a -80 °C freezer at the National Oceanic and Atmospheric Administration (NOAA) Auke Bay Laboratory in Juneau, Alaska.

Mean settlement times and body size (in SL) at time of settlement were estimated by examining catch frequency histograms. The upper 95th percentile of the lengths and Julian day that arrowtooth flounder were found in the pelagic environment during the surveys were used to infer the size and date of settlement to the benthos. This is similar to a previous method used for determining the size of settlement (Bouwens et al., 1999b), with the exception that we used the 95th percentile to account for variance rather than the maximum size.

Stomach contents were dissected from arrowtooth flounder prior to biochemical analysis, pooled by haul, and weighed. Average stomach fullness for each haul was calculated by dividing the average stomach content weight by the average fish mass. Prey items were identified to the lowest possible taxa, weighed, and the percentage of contribution to the diet for each prey taxa was recorded by haul. As species identification was not always possible, copepods were broken down into large and small size bins. The large copepods grouping contained species such as *Neocalanus* spp., *Calanus marshallae* and *Calanus pacificus*, while species such as *Pseudocalanus* spp. were considered small copepods. Once stomachs were removed, arrowtooth flounder were re-weighed and dried in a drying oven at 60 °C until a constant weight (± 0.003 g) was achieved. Dry mass was recorded and percent moisture values were calculated. The dried samples were then homogenized using a mortar and pestle to a uniform consistency. Energy density (kJ g^{-1} dry mass) was measured by bomb calorimetry. Dry homogenized samples were pressed into pellets weighing at least 25 mg. Samples were combusted using a Parr 6725 semimicro bomb calorimeter. Homogenates were analyzed for lipid content and expressed as a percentage of wet tissue mass (% lipid). Lipid extraction was performed following a modified Folch's method using a Dionex 200 Accelerated Solvent Extractor, followed by gravimetric determination of lipid mass as described in Vollenweider et al. (2011).

2.3. Supplementary sampling

For this study arrowtooth flounder less than 20 mm were considered to be larvae. The term age-0 refers to fish greater than 20 mm that were found in the pelagic environment prior to their metamorphosis and settlement to the benthos. Benthic fish less than 100 mm were considered to be young of the year (YOY) and all fish greater than 100 mm were considered to be age 1+. Benthic (YOY and age 1+) arrowtooth flounder samples were provided by Alaska Department of Fish and Game small mesh bottom trawl surveys and the NOAA Resource Assessment and Conservation Engineering Groundfish Assessment Program. Samples were collected by means of bottom trawls from the CGOA in 2011 and 2012, and sent to the Auke Bay laboratory where they were processed for diet and energy density by the same methods as described earlier. Calorimetric data for archived samples were calculated from proximate compositions. Energy content was calculated using the energy equivalents of 36.43 and 201.10 kJ g^{-1} for lipid and protein, respectively (Vollenweider et al., 2011). Ichthyoplankton data from GOAIERP spring cruises were provided by scientists conducting physical and biological oceanographic sampling as part of the GOA Program. See Siddon et al. (2016) for sampling methods and details.

2.4. Data analysis

Initial analyses were designed to understand how temperature, year and region affected measured biological responses. Differences in surface temperatures, fish lengths, energy density, settlement date and size at settlement were compared across regions and years using one-way Analysis of variance (ANOVA) tests with either year or region as fixed factor. Fish lengths were compared across years using Analysis of covariance (ANCOVA) with temperature as a covariate. Data were analyzed using the statistical software R version 3.2.0 (R Core Team, 2015). Linear regression models were used to examine the relationship between energy density with percent lipid, standard length and surface temperature. A Loess smoothing curve was created to fit energy density versus standard length for all age classes, and a one-way ANOVA was used to examine the difference between size age classes.

Variation in growth across years was examined by fitting the length of the fish on each sampling day to a von Bertalanffy growth curve and comparing the residuals for each year. Size on a given day was estimated for each year as the catch-weighted average length. This included larval fish data provided by M. Doyle (personal communication). All of the years were combined and fit to the curve using the Fisheries Stock Analysis (FSA) package in R (Ogle, 2016). The resulting parameters were used to predict the average size of the fish for each day of the year between May and August. The residual value for each year's observation was estimated and compared by a one-way ANOVA with year as the factor. The extreme predicted values used to estimate the average growth rate of arrowtooth flounder were obtained from the following equation.

$$G_x = [(\log Y_2 - \log Y_1)/(t_2-t_1)] \times 100 \qquad (1)$$

Where G_x is the specific growth rate, t_1 is the initial time and t_2 is the assumed settlement date and Y_2, Y_1 are the predicted values at their respective time. Specific growth rates are provided as percent gain in wet mass per day. Wet masses were obtained by fitting the extreme lengths to a regression model relating weight and length. Absolute growth rates were calculated by taking the change in size divided by the change time (Busacker et al., 1990).

3. Results

3.1. Survey results

Age-0 arrowtooth flounder were most abundant in the EGOA in cool years. More than 80% of the 841 age-0 arrowtooth flounder collected in surface trawls throughout the project were caught in the EGOA during the 2010 and 2012 field seasons (Table 1). Water temperatures in the EGOA averaged less than 11.5 °C in 2010 and 2012 compared with more than 12 °C in 2011 and 2013 (Fig. 2A, Table 2). Catches were lower in the CGOA, but the same pattern of high abundance in cool years was maintained. Most fish were caught in the CGOA in 2012 when temperatures averaged 11.05 °C, temperatures were similar between regions for during 2012 (F=2.58, p=0.116; Table 2). Fewer fish were caught in 2011 and 2013 when temperatures averaged more than 13.3 °C. The low catches in the CGOA in 2011 and 2013 prevent any regional comparisons for those years. Only catch and distribution information for the EGOA was available for 2010. This was due to 2010 being a pilot study year and the CGOA was not sampled.

3.2. Size and settlement

The size of the arrowtooth flounder collected in surface trawls in the EGOA depended on both the surface temperature and the year of collection. The average lengths of the fish were significantly influenced by an interaction between temperature and year (F= 3.918, p<0.001). The largest fish were caught in 2010, averaging 35.05 ± 0.22 mm while 2013 had the smallest average size (31.11 mm ± 0.57 mm, Fig. 2B). The effect of year was also significant (F=9.88, p<0.001), but not that of temperature (F=0.116, p=0.733). A separate test conducted to compare the size of fish in the EGOA with those from the CGOA in 2012 indicated that the fish were larger in the CGOA (F= 122.44, p<0.001). The length of the fish from the EGOA ranged from 19 mm to 45 mm with a mean size for all years equal to 34.48 ± 0.14 mm.

Age-0 arrowtooth flounder were detected in the surface waters until mid-August. The earliest date arrowtooth flounder were caught in the surface trawl was July 3rd (the first day of the survey), and the latest date any were caught in the EGOA was August 4th, and August 19th in the CGOA. By August 12th (Julian day 225) of any year at least 95% of arrowtooth flounder had been caught in the GOA and 95% of these fish were smaller than 41 mm. An ANOVA failed to detect an effect of year on the date of the last observed catch and the average size on that date ($F=0.294$, $p=0.642$ and $F=1.744$, $p=.0317$ respectively). Similarly, the mean temperature of the survey year had no effect on date ($F=1.1$, $p=0.404$), but did have an effect on settlement size ($F=21.53$, $p=0.043$).

3.3. Growth

Growth from larvae to settlement of arrowtooth flounder in the GOA was determined using a von Bertalanffy growth model. The model outputs of L_∞, k and T_0 were 96.10, 0.0036 and 82.92 (March 24th) respectively (Fig. 3), these parameters led to an estimated length of 4.4 mm on day 96 (April 4th) and 38.6 mm on day 225 (August 12th), indicating an overall increase equal to 0.26 mm/d between the larval and settlement stages. The ANOVA on the residuals from the model indicated that growth differed among years ($F=3.639$, $p=0.0153$). Subsequent pairwise contrasts indicated growth was greatest in 2010, a cool year, and least in 2011, a warm year. The residuals from the four years averaged 1.66, -1.54, 0.46, and -.052 in 2010, 2011, 2012 and 2013, respectively. The length-weight relationship (Fig. 4) was used to estimate the weights on day 184 (July 3rd) and 225 (August 12th) for the average lengths on those days. The resulting weights led to an estimated growth of 2.01% of wet mass per day during the post-larval pelagic stage.

Weights increased isometrically with length during the age-0 life stage as indicated by the length exponent of 3.072.

3.4. Diet

Large copepods composed the largest proportion of diet by percent mass (72.8%), followed by small copepods (13.7%), and decapod larvae (7.7%). After examining the differences in diet between survey years, large copepods still dominated the diet for all years (Fig. 5). Notably decapod larvae were absent from the diet in 2013, which also corresponds to the sampling year with the lowest stomach fullness and mean energy density (Fig. 2C, Fig. 5). When demersal arrowtooth flounder were included in diet analyses a distinct shift in prey could be seen, with a switch from a copepod dominated diet to that of a diet dominated by shrimp and fish (Fig. 6A). A post hoc Tukey's HSD test showed there were no significant differences ($p < 0.05$) in energy density between size classes or between sampling years (Fig. 6B).

3.5 Energy density

The amount of energetic reserves stored by age-0 arrowtooth flounder depended on the year and ambient water temperature that they were sampled in. The mean energy density was 20.42 ± 0.07 kJ g^{-1} dry mass and wet-mass percent lipid was 2.33 ± 0.05%, with an average moisture content of 77.48%. Energy density was weakly correlated with percent lipid ($p=0.002$, $r^2=0.238$). The values for energy density varied significantly between years ($F= 6.35$, $p=0.003$,

Fig. 2B), while there was no significant difference in energy density observed between regions during the 2012 sampling year (F =0.019, p=0.89, Table 2). Energy density was inversely related to temperature (p= 0.019, r^2=0.117), with 2011 having the highest average energy densities, while 2013 had the lowest values (Table 2). There was no relationship between energy density and length (p=0.4991, r^2 <0.001, Fig. 7A). There was no detectable difference between the energy density of the pelagic age-0 and the benthic YOY fish (F=1.18, p=0.218, Fig. 7B). Furthermore, smaller arrowtooth flounder appear to maintain constant energy density levels, however after reaching 314 mm in length they rapidly increased their energy density with size (Fig. 7C).

4. Discussion

This study provides early life history information on the age-0 arrowtooth flounder in the GOA to provide a better understand the ecology of this species. During this research, we were able to sample arrowtooth flounder just prior to their descent from the surface waters and collect data that complement and further strengthen the available larval and age-0 information (Blood et al., 2007). Regional comparisons were not possible due to insufficient catches in the CGOA, which was most likely an artifact of survey timing. Measurements of energy density, combined with the associated oceanographic, biological, and dietary information, provided new insight into the early life history of the most abundant groundfish in the GOA (Spies et al., 2015). Despite a weak correlation between energy density and temperature, arrowtooth flounder found in warmer waters tended to have lower energy densities than those found in cooler temperatures. Age-0 arrowtooth flounder primarily consumed large copepods, which accounted for more than 50% of the diet by weight each year (Fig. 5). A shift in diet composition was observed between pelagic age-0 and demersal YOY fish, however diet shifts were not related to changes in energy density. Energy density had little relationship with length. Weight scaled isometrically with length, suggesting that the strategy for allocating energy between structure and storage remains constant during the pelagic life phase of arrowtooth flounder. This strategy differs from that employed by many other species in pelagic habitats (Anthony et al., 2000; Heintz and Vollenweider, 2010; Siddon et al., 2013a). There does not appear to be an increase in energy density prior to settlement and metamorphosis, despite what is mostly likely a costly ontogenetic change (Geffen et al., 2007; Hossain et al., 2003). For settled demersal fish, energy density remained stable as size increased and this pattern seemed to hold true until arrowtooth flounder reached ~320 mm, a size which has been associated with the onset of sexual maturation (Spies et al., 2015; Stark, 2012). Overall the data on arrowtooth flounder support a strategy of resilience to a diverse range of biophysical conditions, such as water temperature and food availability. (Doyle and Mier, 2012; Doyle and Mier, 2015).

Arrowtooth flounder have been classified as members of an “Early Phenology” group, spawning during winter months in deep water with a prolonged larval phase (Doyle and Mier, 2012). This long larval duration, combined with a prolonged spawning season, suggests a variable size-appropriate settlement time which has been estimated to occur during July and

August (Bailey et al., 2008) or as late as October (Bouwens et al., 1999a). The size at settlement estimated during this study closely fits previously reported values for arrowtooth flounder in the GOA (Bouwens et al., 1999b), suggesting an average settlement date of mid-August. The majority of arrowtooth flounder were caught during July in the EGOA. This suggests that survey timing most likely accounts for the low numbers of arrowtooth flounder caught during the survey in the CGOA, as the earliest sampling date in the CGOA was August 5th. Earlier, or concurrent, sampling in the CGOA would help to clarify if the low catches were an artifact of sample timing or if there are regional differences in abundances of age-0 arrowtooth flounder. It should be noted that the catches of arrowtooth flounder were sporadic during the entire research project and that the observed CPUE for such an abundant species was relatively low. This could be due to a combination of factors such as gear selectivity, sampling location and survey timing. However, as the gear, survey stations and timing remained constant from 2011 onwards the CPUE can be used as a relative index of abundance of age-0 arrowtooth flounder found in the upper water column.

The highest catches of arrowtooth flounder occurred in 2010 and 2012, which were also the years with the largest average fish sizes (35.03 mm and 34.59 mm) and coolest temperatures (11.52 °C and 11.33 °C). This suggests that either arrowtooth flounder had prolonged planktonic life stage stages or had favorable environmental conditions during these years. However, growth was highest in 2010 and residuals were positive in 2011, indicating that increased size in cool years resulted from increased growth rates. Although there is no empirical data on the effect of temperature on the settlement of age-0 arrowtooth flounder, it was found that the growth, timing and size of other North Pacific flatfish such as northern rock sole (*Lepidopsetta polyxystra*) are temperature dependent (Laurel et al., 2014). Temperature has been shown to be positively correlated with larval growth rates, suggesting a shorter planktonic duration in warmer years (Benoît et al., 2000; O'Connor et al., 2007). The mean sizes of age-0 arrowtooth flounder varied from 2010-2013 but the range of sizes of the fish were similar between years. As the fish were caught just prior to their maximum size in the pelagic environment they would be expected to have similar sizes between years. One possible explanation for the differences in length is that large catch numbers in 2010 and 2012 provided a more robust and representative catch of arrowtooth flounder. The low catch numbers in other years may have resulted in a non-representative length sample. Alternatively, environmental conditions such as temperature may not have been as favorable and the fish caught during 2011 and 2013 were only the remnants of the pelagic population, with most fish having already descended to the demersal habitat. An examination of historical catch data regarding the abundance of age-0 and YOY arrowtooth flounder in relationship to temperature would help answer these questions.

As weight data were unavailable for the ichthyoplankton, the growth of arrowtooth flounder in the pelagic zone was examined by changes in length over time. The growth rate of 0.26 mm d^{-1} calculated during this study was slightly higher than the previously reported values of 0.22 mm d-1 (Bouwens et al., 1999b). This calculation assumes of a linear relationship; however, growth rates are usually exponential over intervals of a year or less, growth rates should therefore be expressed as the specific growth (percent change per day) which is a reported as percentage of the instantaneous rate (Busacker et al., 1990). Our specific growth rate closely matches previously-reported values for arrowtooth flounder (Bouwens et al., 1999b). Based on an analysis of the residuals, 2010 and 2012 had positive values, which suggests that during these years arrowtooth flounder had faster growth rates. This may account for the larger size of the fish caught during these years and supports the idea that environmental conditions were not as favorable during 2011 and 2013. These results should be viewed with caution because we combined larval and age-0 data from different sources and there was at least a month-long gap between the ichthyoplankton and age-0 sampling. There were also no ichthyoplankton data available in 2012 and both 2011 and 2013 had low catch numbers.

Variability in the energetic condition of arrowtooth flounder was likely due to differences in water temperatures across years. The energy density of fish caught in warmest year, 2013, was significantly less than the energy density of those from 2011 and 2012. This suggests that warmer conditions in the GOA during that year were negatively affecting the condition of age-0 arrowtooth flounder. The average temperature where arrowtooth flounder were caught in 2013 was 13.35 °C, more than a degree warmer than any of the other years during the study. Fish caught in 2013 also had the smallest size (31 mm) and lowest mean energy density (19.99 kJ g^{-1} dry mass; Fig. 2). This may indicate that the fish were caught above their optimal temperature during their pelagic stage, although optimal values are unknown for arrowtooth flounder. In previous studies, it was found that daily length increments of post-metamorphosed rock sole (*Lepidopsetta spp.*), Pacific halibut (*Hippoglossus stenolepis*) and English sole (*Parophrys vetulus*), decreased as temperature increased from 13 to 16 °C (Ryer et al., 2012).

Another important factor to consider when examining the energy density of arrowtooth flounder is the composition of their diet, as prey abundance and quality has been shown to directly affect the energetic condition of larval fish (Heintz et al., 2013; Moss et al., 2015). Large copepods dominated the diet of age-0 arrowtooth flounder. Diet appeared to shift from 2011 to 2013 with increasing abundance of small copepods and the absence of decapod larvae in 2013. This may explain the slightly higher energy density values in 2011 as decapod larvae are relatively richer in lipids than copepods and other zooplankton (E. Fergusson, NOAA, personal communication). The highest mean energy density of sampled arrowtooth flounder and highest percent stomach fullness occurred in 2011, while 2013 had the lowest percent stomach fullness and diet diversity. It has been suggested that warm water can increase starvation risks when prey availability is limited, and this may be the case for arrowtooth flounder in the GOA (Laurel and Blood, 2011). It has been shown that environmental conditions in the Bering Sea can have a direct impact on the zooplankton quality, and ultimately the fish that prey on them (Siddon et al., 2013b). We found that the pelagic age-0 arrowtooth flounder diet was primarily composed of small pelagic zooplankton while the demersal fish switched prey and relied on shrimps, euphausiids, and capelin. This is similar to what has been reported for juvenile diets elsewhere in the GOA (Aydin et al., 2007). Despite this change in diet the energy density between pelagic and demersal fish remained constant. This suggests that diet composition may not be as important a factor in the energetic condition of juvenile arrowtooth flounder relative to other marine fish. For example, pollock that consumed energy-rich foods during cold years in the Bering Sea had higher lipid values then those consuming less energy rich food during the warm years (Heintz et al., 2013).

Energy density values reported here were similar to those observed in the Bering Sea, where it was found that there was little change in energy allocation between larval and juvenile stages (De Forest et al., 2014). Many flatfish species display reduced growth rates just prior to and during metamorphosis (Geffen et al., 2007), while some flatfish increase energy storage prior to metamorphosis followed by a post-metameric decline (Yúfera et al., 1999). This study shows no indication of changes in energy allocation prior to or after metamorphosis. This suggests they can sustain their lipid reserves during settlement in contrast to species such as Atlantic cod (*Gadus morhua*) that lose significant reserves during settlement (Copeman et al., 2008). Data were not available for arrowtooth immediately after settlement, therefore if there was any associated energetic cost it may not have been observed.

Energy density of the demersal fish processed during this study were similar to previously reported values for arrowtooth flounder (Perez, 1994). Data suggest that energy allocation changes little during arrowtooth flounder early life history and subsequent ontogenetic changes. This is supported by the energy density values of larger fish that seem to remain relatively stable until they reach a size of approximately 314 mm and increase rapidly at larger sizes. This size corresponds to when there is a noticeable change in diet (Yang et al., 2006) and when sexual maturity starts to occur (Zimmermann, 1997).

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Table 1. Survey dates, mean catch per unit effort (CPUE, fish/km^2), frequency of occurrence and total number (N) of arrowtooth flounder caught during the Gulf of Alaska project for both the Eastern (EGOA) and Central (CGOA) Gulf of Alaska. *Indicates the 2nd survey leg for each year.

Region	Year	Survey dates	CPUE (fish/km^2)	Frequency of occurrence	N
EGOA	2010	7/4 - 7/22	89.87	57.35	308
	2011	7/3 - 7/21 8/2 - 8/4*	2.27	15.25	17
	2012	7/3 - 7/21, 8/3 - 8/4*	46.47	54.05	389
	2013	7/3 - 7/21, 8/3 - 8/5*	4.98	27.85	34
CGOA	2011	8/5 - 8/20*	0.16	2.13	1
	2012	8/5 - 8/21*	14.45	33.33	90
	2013	8/6 - 8/21*	1.15	4.255	2

Table 2. Mean surface temperature and arrowtooth flounder energy densities for hauls conducted during the Gulf of Alaska project, by year and region. Temperatures are °C ± 1 standard error. Energy density values are kJ g^{-1} dry mass ± 1 standard error. N represents the number of hauls included in each average.

Year	Temperature (°C)	N	Energy density (kJ g^{-1}, dry mass)	N
2010 - EGOA	11.52 ± 0.10	39	-	-
2011 - EGOA	12.18 ± 0.25	6	20.94± 0.24	15
2012 - Gulf Wide	11.33 ± 0.11	40	20.49± 0.08	68
2012 - EGOA	11.38± 0.11	22	20.51± 0.11	43
2012 - CGOA	11.05± 0.18	18	20.46± 0.12	25
2013 - EGOA	13.35± 0.15	13	19.99± 0.09	28
All Years	-	-	20.42± 0.07	111

Figure captions

Fig. 1. Surface-trawl catch per unit effort (CPUE, fish/km^2) of age-0 arrowtooth flounder in the Gulf of Alaska during summer 2010-2013. Size of shaded circles indicates CPUE, and crosses indicate survey stations where no arrowtooth flounder were caught. Inset in panel B shows relative location of larger maps.

Fig. 2. Mean water temperatures and arrowtooth flounder mean length and mean energy density in the Gulf of Alaska project surface-trawl survey by year. (A) Mean ambient water temperature (°C) where arrowtooth flounder were caught. (B) Mean standard length (mm) of arrowtooth flounder. (C) Energy density (kJ g^{-1} dry mass) of arrowtooth flounder. Letters at bottom of plots indicate significant differences ($p < 0.05$) between years.

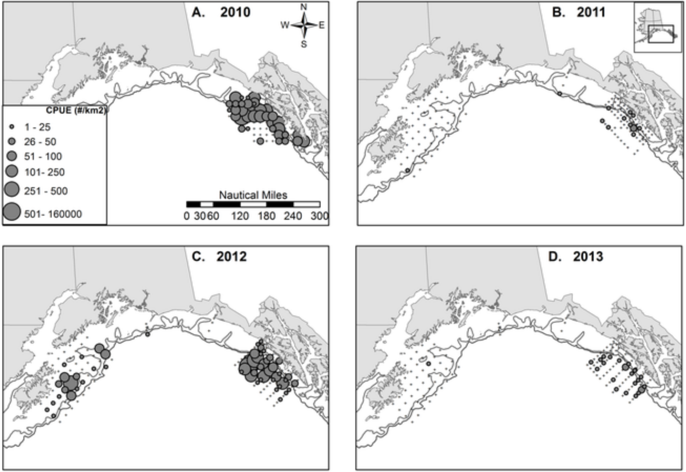
Fig. 3. Day of year versus catch-weighted daily mean length for larval and age-0 arrowtooth flounder captured during 2010-2013. Solid line represents length predicted by a von Bertalanffy growth model; the model parameters are included in the upper left of the plot.

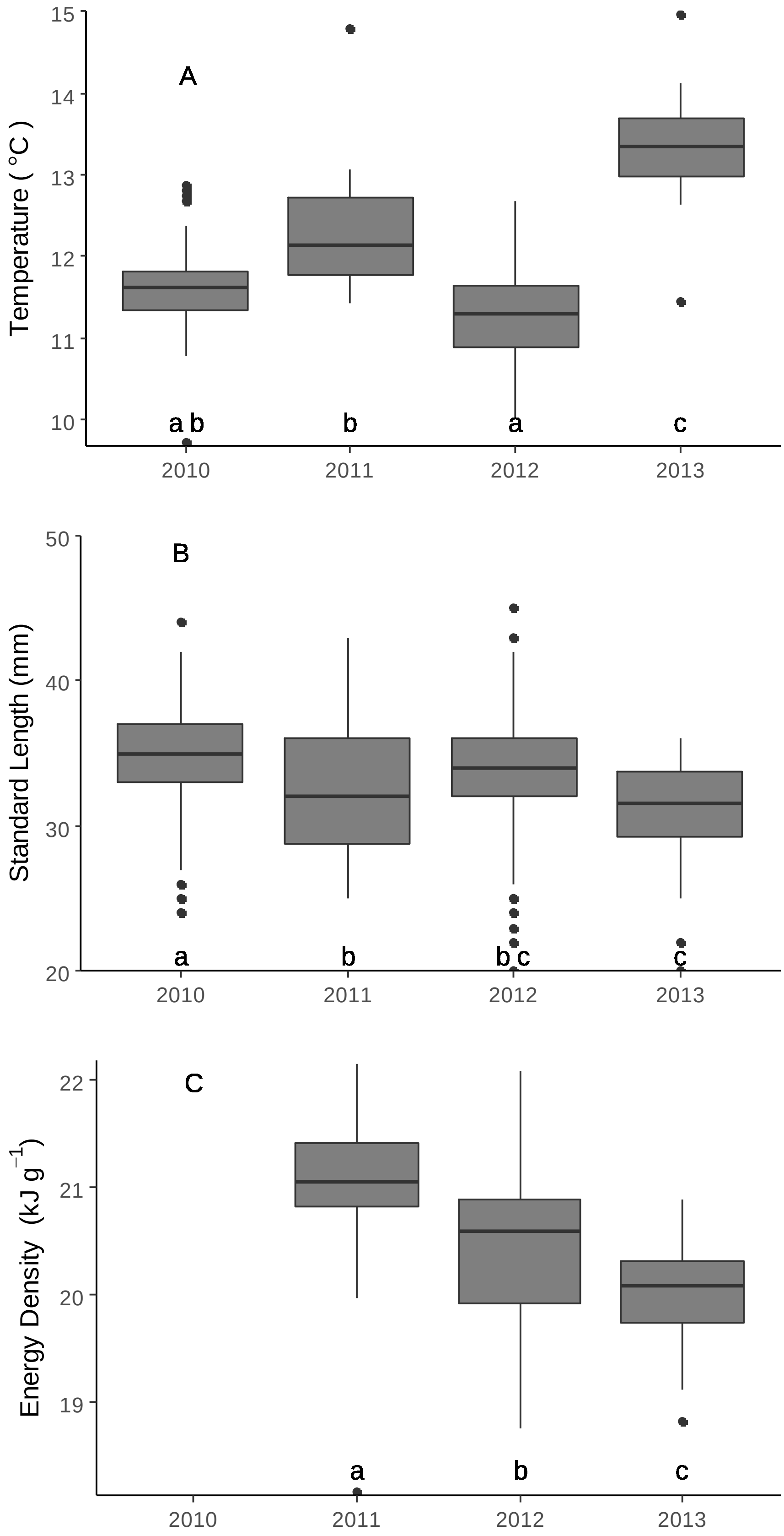
Fig. 4. Length-weight relationship for age-0 arrowtooth flounder captured during the Gulf of Alaska project surface-trawl survey, 2010-2013. Data are aggregated from all years; the solid line and equation represent the linear model.

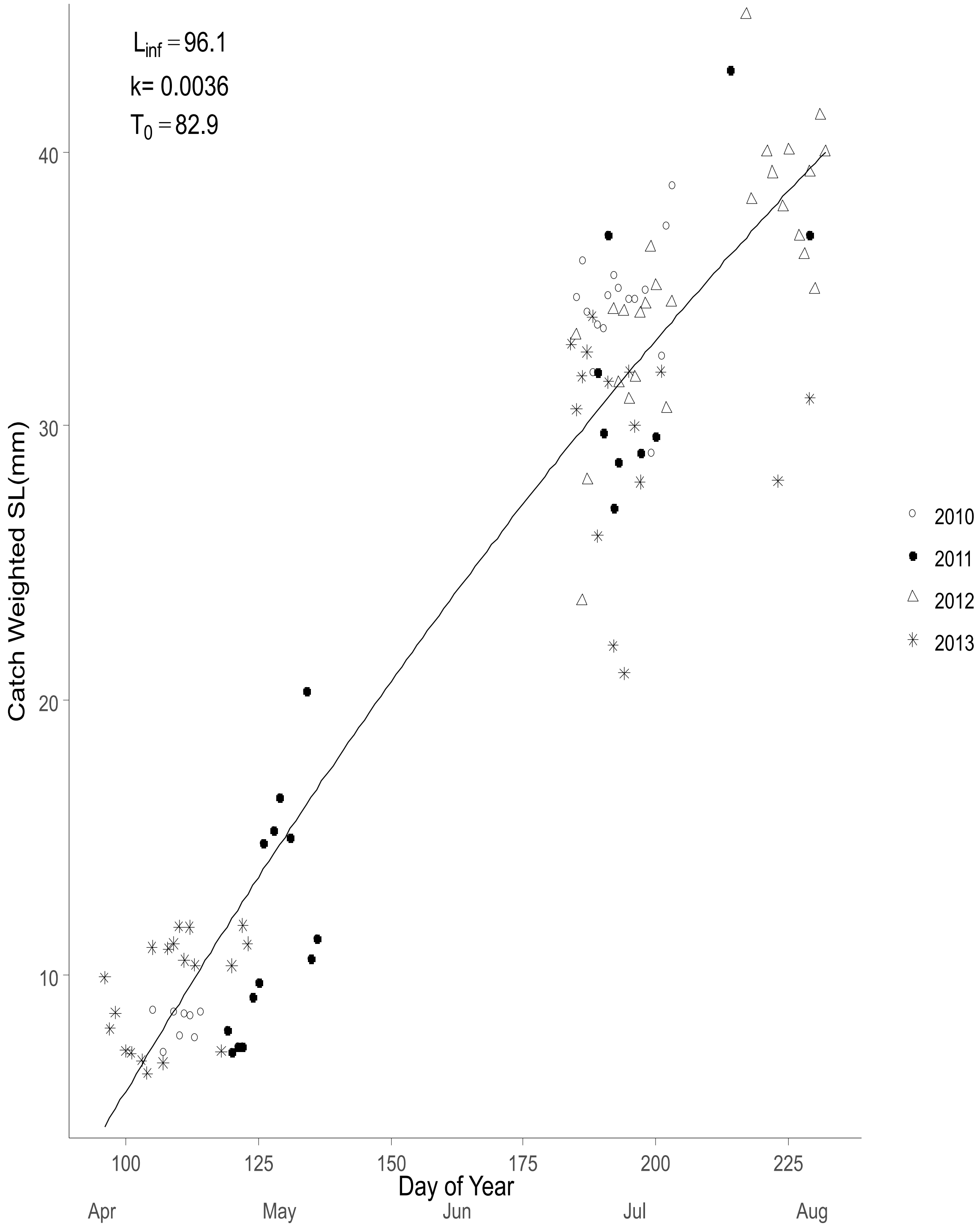
Fig. 5. Diet composition for age-0 arrowtooth flounder in the Gulf of Alaska, 2011-2013. Data are the percentage of each taxonomic group in the stomach contents by weight.

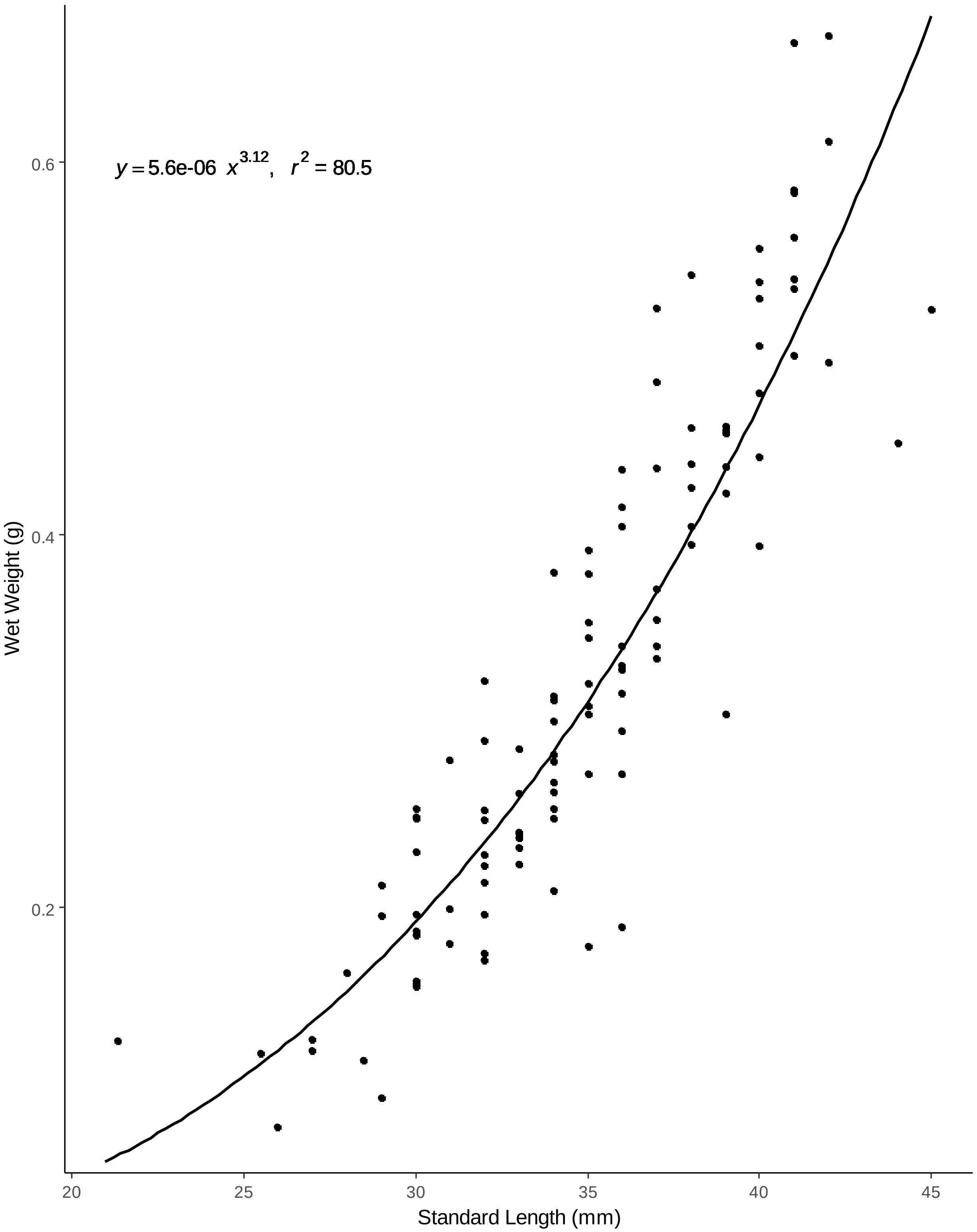
Fig. 6. Diet composition and energy density of arrowtooth flounder by size bin. (A) Percent by weight of dominant taxa in stomach contents. (B) Mean energy density (kJ g^{-1} dry mass) for arrowtooth flounder in the Gulf of Alaska. Data are aggregated across years and regions. All fish smaller than 50 mm are considered pelagic while those greater than 50 mm are benthic fish. Energy densities were not significantly different between any size classes.

Fig. 7. Energy density (kJ g^{-1} dry mass) vs. standard length for arrowtooth flounder at different size ranges and collected during separate surveys. The solid line represents a LOESS fit with 95% confidence intervals. (A) Only age-0 arrowtooth flounder (0-45 mm) caught during the Gulf of Alaska (GOA) project; (B) GOA project age-0 fish and older individuals captured in CGOA bottom-trawl surveys; (C) All fish processed in this study as well as archived data and data from other surveys.

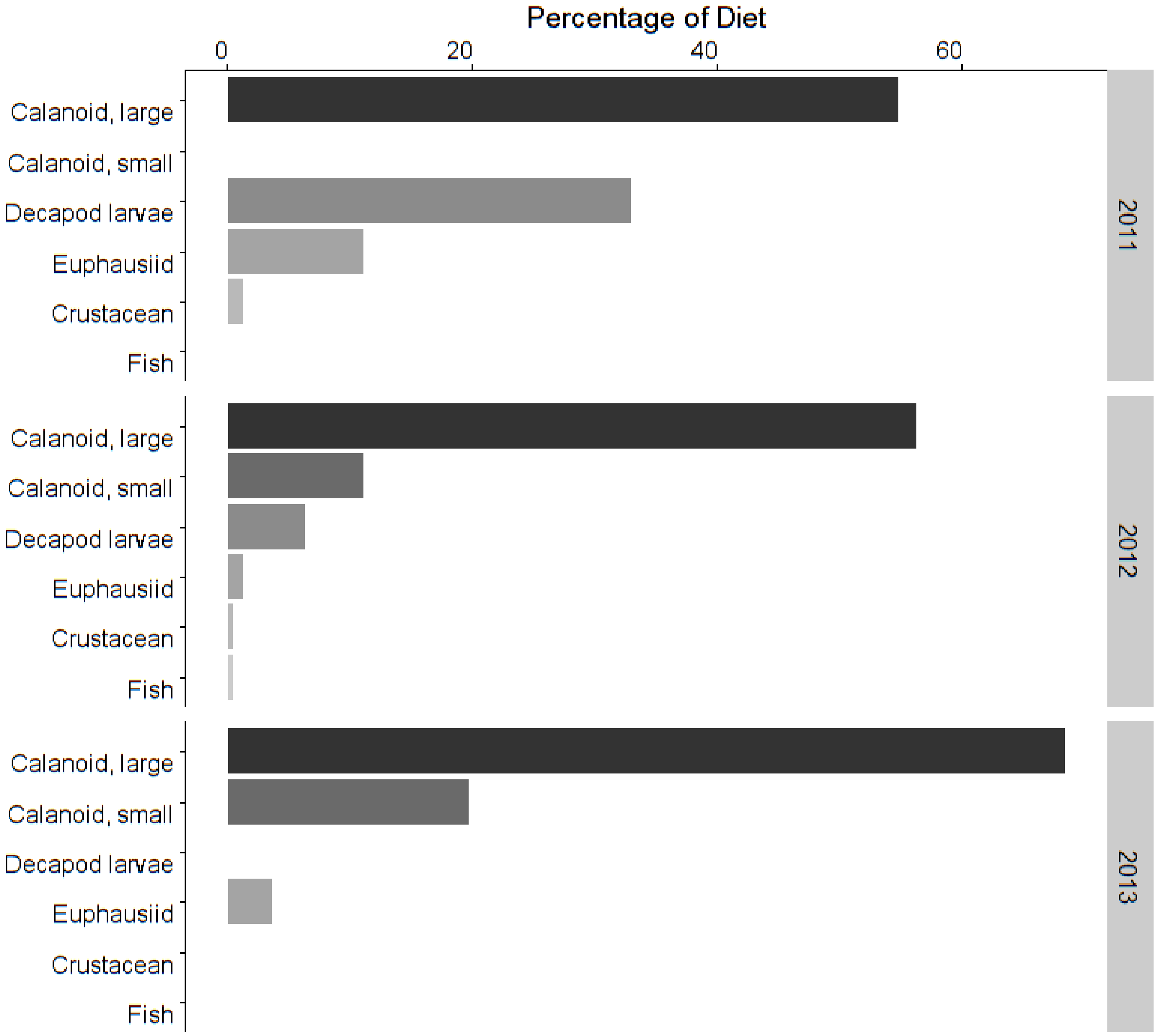

A. 2010
N
W
E
S
CPUE (#/km2)
1 - 25
26 - 50
51 - 100
101- 250
251 - 500
501- 160000
Nautical Miles
0 30 60 120 180 240 300
B. 2011
C. 2012
D. 2013

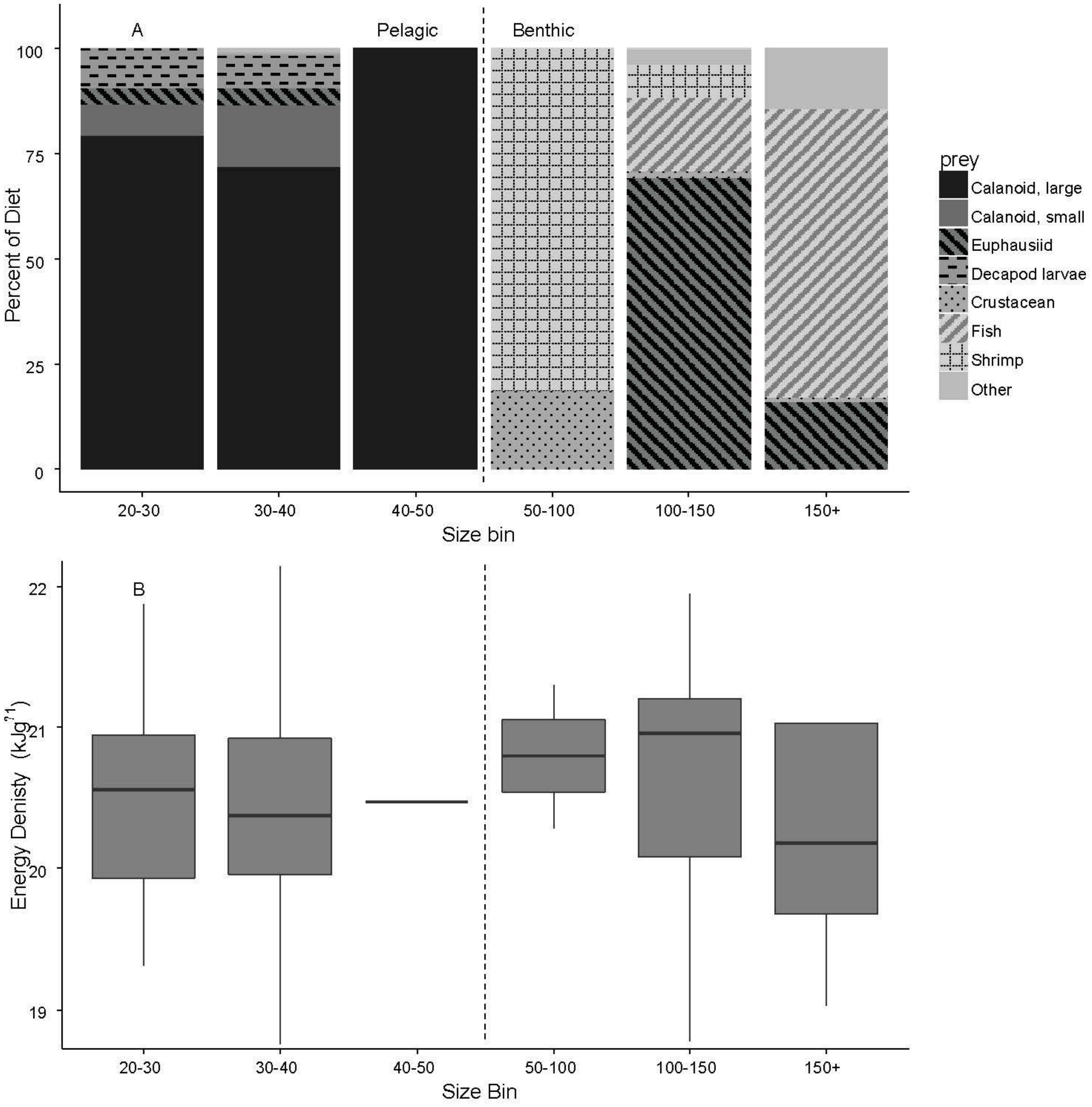

A
Temperature (°C)
15
14
13
12
11
10
a b
b
a
c
2010
2011
2012
2013
B
Standard Length (mm)
50
40
30
20
a
b
b c
c
2010
2011
2012
2013
C
Energy Density (kJ g^{-1})
22
21
20
19
a
b
c
2010
2011
2012
2013

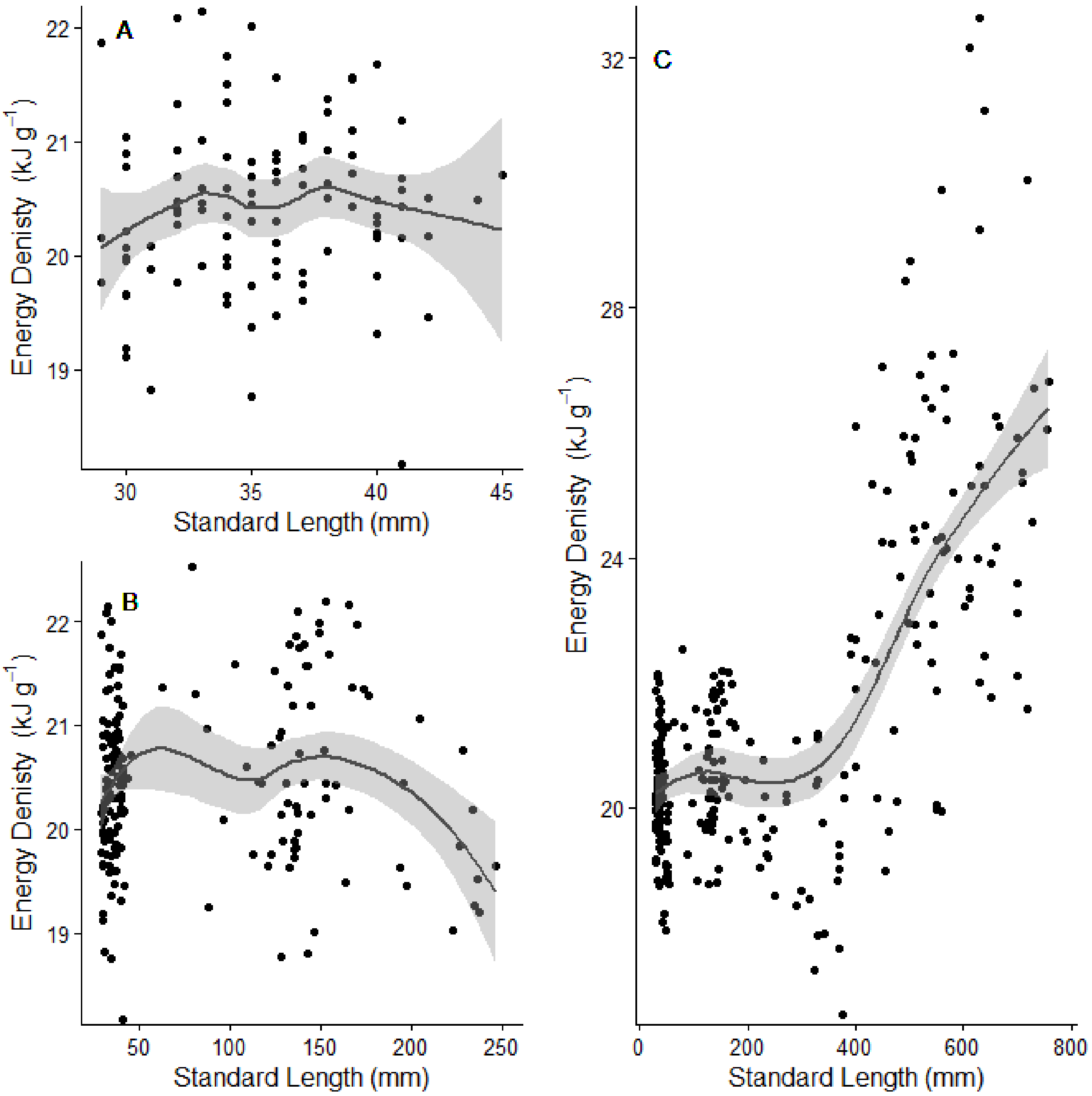

$L_{inf} = 96.1$
k= 0.0036
$T_0 = 82.9$
Catch Weighted SL(mm)
10
20
30
40
100
125
150
175
200
225
Day of Year
Apr
May
Jun
Jul
Aug
2010
2011
2012
2013



$y = 5.6e\text{-}06\ x^{3.12},\ \ r^2 = 80.5$
0.6
0.4
0.2
Wet Weight (g)
20
25
30
35
40
45
Standard Length (mm)


Percentage of Diet
0
20
40
60
Calanoid, large
Calanoid, small
Decapod larvae
Euphausiid
Crustacean
Fish
2011
2012
2013


A
Pelagic
Benthic
Percent of Diet
0
25
50
75
100
20-30
30-40
40-50
50-100
100-150
150+
Size bin
prey
Calanoid, large
Calanoid, small
Euphausiid
Decapod larvae
Crustacean
Fish
Shrimp
Other
B
Energy Denisty (kJg⁻¹)
19
20
21
22
20-30
30-40
40-50
50-100
100-150
150+
Size Bin


A
Energy Denisty (kJ g^{-1})
22
21
20
19
30
35
40
45
Standard Length (mm)
B
Energy Denisty (kJ g^{-1})
22
21
20
19
50
100
150
200
250
Standard Length (mm)
C
Energy Denisty (kJ g^{-1})
32
28
24
20
0
200
400
600
800
Standard Length (mm)