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A full life history synthesis of Arrowtooth Flounder ecology in the Gulf of Alaska:
Exposure and sensitivity to potential ecosystem change.

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Abstract

Arrowtooth Flounder (*Atheresthes stomias*) is at present the most abundant groundfish in the Gulf of Alaska and an apex predator with trophic links to many pelagic and benthic species. Its abundance and trophic status implies that a small change in survival may result in substantial uncertainty in the ecosystem, with potentially large effects across multiple species. A synthesis of Arrowtooth Flounder ecology in the Gulf of Alaska was undertaken to determine exposure to the environment during different life history stages, and to develop hypotheses regarding population response to environmental forcing. Historical data sets were used to identify mechanisms of interaction with the pelagic environment during the egg and larval phase, assess habitat utilization and trophic interactions from early settlement through adult life, and evaluate sensitivity and potential response of the population to climate-induced variability in the Gulf of Alaska ecosystem. Modeling approaches include Individual-Based Modeling of the planktonic drift phase from spawning to settlement, Generalized Additive Modeling to examine the effects of location, bottom temperature, and depth on the distribution and density of different size categories of fish, and Habitat Suitability Modeling which integrates presence-absence and environmental data to develop predictive maps of suitable habitat for early juveniles, late juveniles, and adults. A strategy of high endurance characterizes the early ontogeny phase. Spawning and hatching occur during winter in deep water where predation risk is relatively low, and cold temperatures along with intrinsically low metabolic rates ensure extended availability of yolk reserves, lowering the risk of larval starvation in a food-poor environment. Larval duration and drift is protracted, contributing to widespread delivery of larvae to coastal, continental shelf and slope waters throughout the Gulf of Alaska, as well as expected transportation into the Bering Sea through the Aleutian Island Passes. Connectivity between spawning and settlement areas is less directed and juveniles are more ubiquitous across depths than previously understood. Juvenile and adult Arrowtooth Flounder are habitat and prey generalists, with some ontogenetic shifts apparent. Based on this comprehensive ecological synthesis, a preliminary climate-related vulnerability assessment indicates low risk, high resilience overall for this species in the Gulf of Alaska. However, some stage-specific sensitivity is hypothesized primarily relating to the potential for exacerbated temporal mis-match between early larvae and suitable zooplankton prey with increased temperatures. Density-dependent effects during the juvenile to adult stage may constrain further increases in Arrowtooth Flounder biomass in the Gulf of Alaska. This comprehensive ecological approach to assessing environmental sensitivities across life history stages for a commercially and ecologically important fish species has substantial merit for furthering the ecosystem approach to fisheries management, especially in marine ecosystems where there are robust sampling programs across trophic levels.

Keywords

Arrowtooth Flounder; Gulf of Alaska; ecological synthesis; vulnerability assessment; resilience

1. Introduction

A critical aspect of marine fisheries ecosystem research is assessing the ecology of species that play a major role in the structure and function of the ecosystem. Arrowtooth Flounder (*Atheresthes stomias*) is at present the most abundant groundfish in the Gulf of Alaska (GOA), both numerically and by biomass, and significantly higher densities are encountered there than in either the Eastern Bering Sea or the Aleutian Islands Large Marine Ecosystems (Spies et al., 2017). It is considered a key component of the GOA ecosystem with direct trophic links to a majority of species groups. The predation pressure exerted by Arrowtooth Flounder (ATF) in the GOA is broad as it consumes a wide variety of prey including zooplankton, shrimp, forage fish, other groundfish, and benthic invertebrates (Aydin et al., 2007). Further, ATF competes with other top level predators including fish, birds and marine mammals for prey resources. The present abundance, and trophic status and connections of ATF in the GOA indicate that a small change in ATF survival may result in substantial uncertainty in the ecosystem, with potentially large effects on multiple species (Aydin et al. 2007; Gaichas and Francis, 2008; Spies et al., 2017).

ATF have not always been as abundant in the GOA as documented in recent decades. Biomass increased dramatically from the 1970s onwards with peak estimates documented in 2008-2010 (Fig. 1 a SM; Spies et al., 2017). Estimates of Age-1 recruits to the population also increased dramatically from the 1970s and have remained mostly above the long-term mean over the last three decades, but interannual variation and an apparent decline after 2006 (Fig. 1 b SM)." The increases in ATF were concurrent with increasing trends in recruitment and biomass of other groundfish species (Gadids and Pleuronectids), and declining trends in Pandalid Shrimp and Capelin (*Mallotus villosus*), in association with a shift from a cold to a warm oceanographic regime identified in the late 1970s (Hollowed and Wooster, 1992; Anderson and Piatt, 1999). Ecological mechanisms leading to this community reorganization in the GOA remain poorly understood. Such fluctuations, however, suggest multi-decadal instability for a variety of species, especially in relation to climate forcing and changing ocean conditions. An important consideration regarding continued dominance versus potential decline is that predation mortality on both adult and juvenile ATF in the GOA is very low relative to other species, and fishing mortality is limited because of the poor flesh quality. Consequently, ATF production in the GOA remains largely unconsumed and unharvested, and predation impact on a variety of species remains very high (Gaichas et al., 2011; Spies et al., 2017).

Recent trends in recruitment and biomass may indicate that ATF has reached some maximum abundance threshold and that density-dependent effects may dominate population trends going forward (Fig. 1 SM). Trophic modeling studies suggest that ATF biomass may be strongly influenced by changes in bottom-up production in the plankton (Aydin et al., 2007). ATF adults and juveniles consume mostly pelagic prey including zooplankton (e.g. Euphausiids) and planktivorous fish (e.g. Capelin and juvenile Walleye Pollock [*Gadus chalcogrammus*]). Pelagic habitat resources are therefore likely important as a density-dependent factor limiting population growth. Variability in plankton production can also act as a density-independent factor contributing to fluctuations in survival of ATF as well as other species during the larval and early juvenile phase, although we have no information to date on prey preference or limitation during the planktonic phase for ATF. Climate and oceanographic processes affecting distribution, abundance, and development of early life history stages are also important as are intrinsic physiological rates of ATF at different ontogenetic stages (Doyle et al. 2009; Stachura et al., 2014; Doyle and Mier, 2016; Mordy et al., accepted).

Given the expansion of the ATF population in the GOA, it seems that its juvenile and adult ecology as well as reproductive and early life history strategies have conferred a high degree of resilience to environmental forcing in this region. Many questions remain, however, regarding ecological mechanisms that brought about population expansion and dominance in the GOA, and the potential instabilities in mechanisms that could lead to a decline in the future. Here we evaluate the ecology of ATF across all life history stages with respect to exposure, sensitivity, and potential response to physical and biological environmental forcing in the GOA. Discerning stage-specific ecological links and sensitivities to the environment is considered critical for determining the relative vulnerability of fish stocks to a changing climate (Hare et al., 2016).

Ichthyoplankton, juvenile stage, and stock assessment survey data from NOAA's Alaska Fisheries Science Center (AFSC) provide the foundation for this synthetic study, along with published literature pertaining to ATF in Alaska marine ecosystems. Aspects of ATF biology, ecology, distribution, abundance and size across ontogenetic stages, from spawning through juvenile settlement to recruitment are reviewed. Subsequently, data from the stock assessment surveys are synthesized and presented to illustrate habitat utilization from older juveniles through different size categories of adult fish. Food-habits data are included to examine ontogenetic trends in prey consumption by, and predation on ATF. Additional data are incorporated from the North Pacific Research Board-sponsored GOA Integrated Ecosystem Research Program (GOA-IERP), including data from ichthyoplankton and juvenile collections. GOA-IERP results and further synthesis from the biophysical Individual-Based Model developed for ATF early life history (Stockhausen et al., accepted), and from the demersal life stage habitat modeling (Pirtle et al., 2017) are also included.

The objectives of this synthesis study are to 1) decipher mechanisms of early life history interaction with the pelagic environment, 2) assess habitat utilization and ecological patterns from settlement through adult life, and 3) evaluate the synthesized patterns in terms of sensitivity and potential response of the ATF population in the GOA to climate-induced variability in the ecosystem.

2. Materials and Methods

2.1. Gulf of Alaska Data Sets and Survey Region

NOAA AFSC survey data sets used in this study are identified in Table 1 with associated metadata and links to relevant databases, research programs, reports and publications. The survey region is illustrated to show bathymetry, topographic features, place names used in the text, and prevailing circulation patterns (Fig. 1). We divide the eastern and western GOA at the 145°W meridian which reflects an observed distinction in oceanographic and biological processes; the narrower shelf area in the east results in more dynamic mesoscale circulation with greater exchange between shelf and deep water (Stabeno et al., 2004, 2016), and apparent lower average seasonal amplitude in primary production relative to shelf waters in the western GOA (Waite and Mueter, 2013). This lower average productivity in the east may be related to higher levels of interannual variability in nutrient availability and associated phytoplankton production in this region (Strom et al., 2016).

2.1.1. Ichthyoplankton Data

Ichthyoplankton surveys in the western GOA began in 1972 (no sampling 1973-1976), with annual sampling from 1977-2011 and bi-annual surveys in following years (McClatchie et al., 2014). They were carried out by the Recruitment Processes program and the Ecosystem and Fisheries-Oceanography Coordinated Investigations program (EcoFOCI) at the AFSC. The full extent of sampling coverage in the western GOA is from east of Prince William Sound to Umnak Island in the west, and the most intensively sampled area extends along the continental shelf and slope from Kodiak Island to the Shumagin Islands (Fig. 1). Full details of temporal and spatial coverage of ichthyoplankton sampling (60-cm bongo nets) as well as sampling protocol, and processing of samples for ichthyoplankton data are given in AFSC's online Ichthyoplankton Information System (IIS) http://access.afsc.noaa.gov/ichthyo/, and associated ichthyoplankton cruise data base http://access.afsc.noaa.gov/icc/index.php. Sampling methods specific to special studies of ATF early life history in the GOA are also included in Blood et al. (2007) and Doyle and Mier (2016).

2.1.2. Transitioning Larvae and Juvenile Data

As part of the GOA-IERP program, sampling of the upper water column was carried out during summer months 2010-2014 using a Cantrawl 400 model midwater rope trawl at a grid of stations in the western and eastern GOA (Table 2; Moss et al., 2016). The trawl (198-m midwater rope trawl) was modified to fish at the surface, and tows were 30 minutes in duration with an average tow speed of 3.1 knots. Mouth openings averaged approximately 40 m wide x 35 m deep. ATF were counted and measured (standard length mm), and catch per unit effort (CPUE) was calculated as number of fish km^{-2} at each station. Average weights at each station were recorded by dividing the total mass of ATF by the number caught.

During October 3-14 2011, a special study was undertaken of flatfish habitat in the western GOA (vicinity of Kodiak Island west to the Shumagin Islands) during a survey of neritic forage fishes and zooplankton (Wilson et al., 2016). Juvenile flatfishes on or near the bottom were collected with a plumb-staff beam trawl (3 m x 0.78 m opening) with a codend liner of 2 x 3 mm, and those in midwater were sampled with a Stauffer trawl fitted with a 2 x 3 mm codend liner (Wilson et al., 2016). The beam trawl was towed on bottom for approximately 15 minutes at 1 m sec^{-1}. The midwater trawl was fished over a double-oblique tow path of 0-200 m over deep water or 7 m off bottom in shallower water. Both bottom and midwater sampling were carried out at each station when bottom sampling was possible. Flatfishes including ATF were sorted from these samples and size was measured as total length (mm). Abundance at each site was estimated from beam-trawl sampling and expressed as number of fish 1000 m^{-2}. Midwater sampling was used only to indicate presence or absence of ATF in the water column.

2.1.3. Groundfish Survey Data

Data for this study were collected during the triennial (1984-1999) and biennial (2001-2015) GOA bottom trawl surveys (Table 3) conducted by the AFSC Groundfish Assessment Program. The GOA bottom trawl survey provides data on distribution, abundance, and biological characteristics of GOA groundfish resources on the GOA shelf in waters between 20 m and depending on year from 500 m to 1,000 m. Stations in the survey are selected in a stratified random survey design and data are collected using standardized bottom trawl gear (Stark and Clausen, 1995; Raring et al. 2011). Age data presented here are from all NOAA AFSC GOA surveys (1984-2015) as well as previous surveys in the GOA from which ATF length and age data were collected (Table 1 SM; Fig. 2 SM). In addition to biological information on groundfish resources, oceanographic data such as temperature and salinity at depth are also recorded concurrent with trawl hauls. All catch and oceanographic data are stored in the AFSC Oracle database.

2.1.4. Food Habits Data

During summer GOA bottom trawl surveys, as well as special studies and fisheries operations in the GOA, groundfish species were sampled for stomach content analyses (Livingston et al., 2017; http://www.afsc.noaa.gov/REFM/REEM/data/default.htm). At opportunistically selected survey hauls within a multispecies sampling scheme, stomachs were collected from a subsample of species in the catch since 1990 (Table 1). The length and sex of each sampled individual, and the time and location of the catch, were recorded. Stomachs were removed, and either analyzed at sea or fixed in a 10% buffered formalin and seawater solution for return to the AFSC for laboratory analysis. Stomach contents were removed, separated into lowest practical taxonomic prey categories, and the weight (g) of each prey category was determined and recorded. The standard lengths (SL) of all intact prey fish were measured and recorded.

2.2. Data Synthesis and Analyses

2.2.1. Ichthyoplankton Data

ATF egg and larval data from the historical GOA collections have been synthesized previously in an investigation of spawning and development of eggs and larvae (Blood et al., 2007), and in the determination of early life history strategies and ecology among Gulf of Alaska fish species (Doyle et al., 2009; Doyle and Mier, 2012 and 2016). Temporal and spatial patterns in occurrence and abundance of eggs and larvae throughout the western GOA, links with environmental variables, larval drift patterns, and larval length frequency distributions have been evaluated in these studies, and are further integrated here in an ecological profile of ATF early ontogeny.

2.2.2. Transitioning Larvae and Juvenile Data

A summary of metadata associated with the GOA-IERP program surface trawls targeting transitioning larvae and juveniles carried out during 2010-2014 in the GOA is given in Table 2 and includes frequency of occurrence of ATF in the samples as well as mean CPUE per survey. Given that only one and two ATF, respectively, were caught during the 2011 and 2013 surveys in the western GOA these data were excluded from further analysis. For the remaining six surveys, ATF abundance was plotted on the sampling grids using ArcMap 10.3 mapping software (ESRI 2011), and length-frequency distributions generated for each of these data sets. For the purpose of estimating growth rates, the GOA ATF length data from the surface trawls (all years) were combined with the ATF larval length data from ichthyoplankton samples collected during the GOA-IERP 2011 and 2013 spring ichthyoplankton surveys (Siddon et al., in press). Catch weighted lengths were plotted against Julian Day and a LOESS smooth curve was fitted to simulate growth.

For the October 2011 EcoFOCI survey in the western GOA, ATF patterns of distribution among sampling stations were also plotted on maps generated with GIS software ArcMap (ESRI, 2011) for both the bottom trawling and midwater sampling. Length-frequency distributions were generated for each of the sampling gears. Plots of variation in CPUE of fish by time of sampling were also constructed to examine patterns of diel variation in occurrence and abundance of fish in the water column versus on the bottom.

2.2.3. Early Life History Individual-Based Model (IBM)

As part of the GOA-IERP program, a spatially-explicit, coupled biophysical Individual-Based Model (IBM) for ATF early life history and dispersal was developed (Stockhausen et al., accepted). The purpose was to explore ways in which environmental forcing in the GOA may affect survival of ATF early life stages to recruitment, with an emphasis on transport variability and connectivity between deep water spawning areas and presumed nearshore nursery areas (to 50 m depth), and integrating oceanographic processes affecting individuals along these pathways. Egg stage duration was influenced by water temperature (Blood et al., 2007), but it was not possible to incorporate variable growth rates of larvae relative to suitable food availability because larval prey and consumption characteristics for ATF during early ontogeny are unknown. In this study, we reevaluate the model parameterization and output in light of the present ecological synthesis of historical and recent data. The IBM was re-run here with a newly defined nursery settlement area of 0-150 m.

2.2.4. Groundfish Survey Data

The ATF stock assessment estimates population biomass, recruitment (age 1 fish), and several other parameters, including selectivity for fishery and survey, fishing mortality, and recruitment deviations. Instantaneous natural mortality, survey catchability, Von Bertalanffy growth parameters were fixed in the model and are assessed based on an age-structured population dynamics model that includes separate sexes and different natural mortality for males and females (male M=0.35, female M=0.21; Spies et al., 2017).

For the investigation of spatial and temporal trends in ATF distribution and abundance all retrieval and processing of data were done in R (R Core Team 2015). The ATF catch per unit effort by number weighted means were calculated by length size category (set at 100 mm increments from 0 to 600 mm and then > 600 mm) for longitude, latitude, bottom depth, and bottom temperature following the methods described in Barbeaux (2017). Methods described in Spencer (2008) were used to calculate the annual weighted mean GOA bottom trawl survey-wide bottom temperature (Table 3). For our analysis, each year was identified as warm or cold as to whether it was above or below the overall weighted mean bottom temperature for all years. Survey timing varied very little over the course of the years sampled, and the annual bottom temperature was based on an area weighted mean with little influence from the very limited extent of the deep water stations over the slope. The analysis was re-run without the “deep stations” and it made no difference to the designation of so-called warm or cold years based on the annual mean temperatures calculated.

Delta-log gamma (Punt et al., 2000) Generalized Additive Models (GAMs, Hastie and Tibshirani 1991) were employed to examine the effects of location, bottom temperature, and depth on the distribution and density or catch per unit effort (CPUE) of ATF by size category using the R package **mgcv** (Wood, 2006) and fit through generalized cross validation. For this two-step process, a binomial model with a logit link function was first used to examine presence and absence data, and subsequently a gamma error structure model with a log link function was used to examine CPUE (no. km^{-2}) where ATF were present. Thin plate regression splines were used for non-additive smoothers (Wood 2006) on location (latitude and longitude), bottom depth (m), and bottom temperature (°C) for each length bin. The default basis dimension (k) was employed for all splines. Year and bin size were both treated as independent factors in both GAMs. Three sets of GAMs were employed; one with all data, one with data from cold years, and one with data from warm years; warm and cold years are defined as above or below the mean, respectively based on mean survey-wide bottom temperature for groundfish survey years 1984-2015 (Table 3). The binomial model dataset had entries for each station and length bin; therefore there were seven entries for each survey station for each year. Cells (size bin and station combinations) which contained ATF were marked present. For the log gamma distribution models only cells (bin and station combinations) with ATF present were included in the analysis. This effort resulted in the probability of encountering an ATF of a certain size range given the location and conditions across the survey area, and if encountered the expected density (no. km^{-2}) for each length range bin. Multiplying these two components together provided a predictive surface for each ATF length bin. The Delta-log gamma and Delta-log normal approaches were compared and although results from both were similar, the Delta-log gamma had a lower root mean square error (RMSE; 5,230 vs. 5,470 over 35,988 data points). For visualizations of the bottom temperature and bottom depth affects we chose 2009 and 56° N latitude 155° W longitude to predict ATF density for the general model and cold year models, while 2001 and the same location for warm year models. These were chosen for demonstration purposes as the year effect in the general model was approximately the same between years and the location effect was near 0 in both models.

2.2.5. Habitat Suitability Modeling

As part of the GOA-IERP research, several groundfish survey data sources (Table 2 SM) were integrated with environmental data in presence-only habitat suitability models to develop predictive maps of suitable habitat for settlement stage juveniles of focal species in the GOA, including ATF (Pirtle *et al.*, 2017). These models were updated here with additional habitat predictor variables and new models were developed for older juvenile and adult life stages as only early juvenile stages were assessed in Pirtle et al. (2017). Maximum entropy modeling (MaxEnt) was used to develop the demersal stage habitat suitability models using presence-only data (Phillips *et al.*, 2006). Focal life stages for the models were: 1) an early juvenile stage from settlement through residency in nursery areas (40-160 mm FL); 2) a late juvenile stage that may be considered immature fishery pre-recruits (161-350 mm FL); and 3) adults (> 350 mm FL). Length-based life stage breaks were based on information from the literature and available species catch data from demersal gear (Blackburn and Jackson, 1982; Zimmermann, 1997; Norcross *et al.*, 1999). The occurrence data were assembled from groundfish stock-assessment surveys and research programs that sampled marine habitats at inshore and offshore locations on the continental shelf and slope, using a variety of gear types (Table 2 SM; Pirtle et al., 2017).

Habitat predictor variables were applied to the models. A compiled bathymetry surface and associated benthic terrain metrics described attributes of seafloor morphology, including slope, curvature, aspect eastness and northness, and bathymetric position index (BPI) (Wilson et al., 2016; Pirtle *et al.*, 2017). Other habitat predictors included a substrate rockiness surface representing a continuous gradient from areas with high to low occurrence of rocky substrate, modeled presence-absence for upright sponges, corals, and sea whips, tidal current speed derived from a regional tidal model, and bottom current speed, bottom temperature (May-September), and spring surface primary productivity derived from the GOA ROMS 3 km model (1996-2011) (Rooper *et al.*, 2014; Pirtle *et al.*, 2017). Habitat predictor variables were produced as 100 m^2 resolution rasters from shore to the 1000 m depth contour, and from the Shumagin Islands at the westernmost portion to Dixon Entrance in the east. MaxEnt models were implemented in R (R Core Team) using the dismo and raster packages (Hijmans *et al.*, 2014a, 2014b). Two sets of models were produced because the spatial extent of the substrate data was less than the other habitat variables. These included models produced using all habitat variables with the bathymetry data extent (habitat suitability models; HSM) and models produced with a reduced spatial extent using all habitat variables and substrate rockiness (HSM with substrate). Models were developed separately for each ATF demersal life stage (Pirtle *et al.*, 2017). We developed an averaged mosaic of the mean predicted probability of suitable habitat for overlapping areas from the final model replicates for the two sets of model evaluation (HSM and HSM with substrate).

2.2.6. Food Habits Data

For this synthesis, we used groundfish food habits data from the GOA to describe the ATF diet and the patterns in predation on ATF. Detailed, annual prey lists for ATF and many ATF predators in the GOA are available (Yang, 1993; Yang and Nelson, 2000; Yang et al., 2006; http://access.afsc.noaa.gov/REEM/WebDietData/DietTableIntro.php). To provide a general description of the ATF diet, prey were consolidated into the following major prey categories: Zooplankton (including larval phases of benthic invertebrates), Decapods (Shrimp and Crabs), Ammodytids (Sand Lance), Osmerids (Smelts), Clupeids (Herring and Sardine), Walleye Pollock, Other Gadids (Cods; including Pacific Cod [*Gadus macrocephalus*] and some unidentifiable gadids that may be Walleye Pollock), Pleuronectids (Flatfishes), Other fish (including some unidentifiable fish that may be from the fish groups listed), and Other prey (including some unidentifiable stomach contents that may be from the identified prey groups listed).

Ontogenetic shifts in the diet of ATF in the GOA are well documented (Yang, 1993; 1995; Yang and Nelson, 2000; Yang et al., 2006; Knoth and Foy, 2008), and provide a means to consider stage-specific ecological links to the environment. Over the years, stomach samples were collected from a wide length-range of ATF, 8-85 cm fork length (FL) by the AFSC, and we illustrate changes in the weight composition of the diet across this size range. Weight composition, where the stomach contents of each fish are weighted proportionally to their mass, is appropriate for estimating the energetic reliance on prey populations (Chipps and Garvey, 2007; Ahlbeck et al., 2012). However, this can overemphasize the prey consumed by larger fish within a group due to their larger stomach capacity (Buckley et al., 2015). To show size-related shifts in diet we chose narrower size categories than were used in previous studies: 8-19, 20-29, 30-39, 40-49, 50-59, 60-69, and 70-85 cm FL. The weight composition (%W) of the diet was calculated for each size category in each survey year. Then the average diet composition for each size category was calculated as the average of each annual diet composition.

Information about groundfish predators of ATF has not previously been compiled. We examine patterns in the species that prey on ATF at various sizes to illustrate stage-specific ecological links to the environment. Most ATF less than 100 mm are less than a year old, and ATF of this size were divided into three size categories based on physiological or behavioral changes occurring at 30 mm (beginning transformation) and 60 mm (strong association with the bottom). Prey ATF larger than 99 mm were divided into 100 mm (or 10 cm) increments except for the largest category. All occurrences of prey ATF in the Groundfish Food Habits Database (Livingston et al., in revision; http://www.afsc.noaa.gov/REFM/REEM/data/default.htm) from each size category were located and the predator species was recorded. The percentage of predation events attributed to each predator species was calculated for each size category. To minimize misinterpretation of the results due to the unevenness of the sampling effort among groundfish species and the unevenness of the frequency of predation on ATF by each groundfish species, the total number of specimens examined and the percent frequency of occurrence of prey ATF was presented for each predator. In addition, the diets of many groundfish species in the GOA have been examined without detecting predation of ATF (http://www.afsc.noaa.gov/REFM/REEM/data/default.htm). We also investigated monthly trends in the size of small ATF (< 100 mm) found in the stomach contents of groundfish species. The distribution of prey ATF among the three larval and juvenile phases of age-0 ATF described above (<30, 30-59, and 60-99 mm) was presented for the months of June through September and the remaining months were aggregated into two 4-month periods (October-January, February-May) due to much lower sampling intensity during the non-summer (non-survey) months.

2.2.7. Climate-related Vulnerability Assessment

Based on the ecological synthesis results presented here, a vulnerability assessment of ATF in the GOA is developed according to 12 “sensitivity attributes” recommended by NOAA for assessing the sensitivity of fish stocks to potential climate change and associated ecosystem shifts (Morrison et al., 2015; Hare et al., 2016). The sensitivity attributes represent a comprehensive overview of Arrowtooth Flounder’s population status, life history attributes, and ecological characteristics in the GOA in the context of environmental exposure and adaptive capacity of the species in this ecosystem. The individual attributes are identified (Results section 3.7.) along with the goal of each attribute, and a score is assigned representing low to high levels of vulnerability to potential climate-driven shifts in the environment of the GOA. As recommended in Morrison et al. (2015) and Hare et al. (2016), the attribute scores are assigned based on the "expert opinion" of this manuscript's authors, and their evaluation of published information and historical data pertaining to ATF in the Gulf of Alaska.

3. Results

3.1. Population Trends

Gulf of Alaska ATF age data from 1977-2013 indicate a decrease in length-at-age over time in several of the younger year classes (Table 4). Decreases in length-at-age were observed at similar ages in males and females, and only prior to age five. During these life stages males and females grow at similar rates (Fig. 2 SM b). There is an increasing age of older fish in the population, which reflects a signature of increasing population size and decreasing mortality (Fig. 2 SM c). Females generally represent the oldest individuals. However, more females than males are sampled due to a skewed sex ratio with higher numbers of females than males (Spies et al. 2017). Coincidentally, the oldest fish observed was a male, age 34, in 2010.

3.2. Spawning and egg stage

Based on historical AFSC data, ATF are batch spawners and in the GOA release their eggs deep in the water column over the continental slope ($\geq$ 400 m) from December through March, but primarily during January to February (Zimmerman, 1997; Matarese et al., 2003; Turnock et al., 2005). Eggs are mesopelagic and range in size from 1.58 to 1.98 mm. Incubation time varies with water temperature and for an observed range of temperatures (4.3 – 5.4 ^{o}C) where spawning ATF have been found, laboratory studies indicate that time to hatching takes approximately 15-20 days, but can be as fast as 13 days at 6.2 ^{o}C (Blood et al., 2007). Eggs seem to remain neutrally buoyant deep in the water column until hatching, and occurrence of eggs in ichthyoplankton samples is restricted to slope waters (Blood et al., 2007; Doyle and Mier, 2016).

3.3. Larval stage from hatching to metamorphosis and settlement

Yolk-sac larvae hatch from eggs at a standard length (SL) of 3.7 to 4.8 mm and newly hatched larvae possess a relatively large yolk mass measuring approximately 30% (length) x 24 % (depth) of larval length (Blood et al., 2007). Absorption of yolk is completed by 6.5–7 mm SL and the mouth appears functional by that size. Flexion of the notochord begins at approximately 10-12 mm, and growth of fin rays is initiated with a fin development sequence of caudal, dorsal and anal, pelvics and pectorals (Matarese et al., 2003; IIS). The relationship between ATF sub-ontogenetic intervals and size is illustrated in Figure 2, and is also aligned with length frequency distributions of ATF larvae by month based on all GOA historical ichthyoplankton samples through 2010 (Doyle and Mier, 2016). The length-frequency distributions indicate that larval growth is slow from January through April with the vast majority of larvae remaining less than 10 mm SL. Through March, it seems that most larvae remain less than 7 mm and are therefore likely to retain yolk reserves. Even during April, many larvae are less than 7 mm SL. In May, growth rates increase significantly as illustrated by a significant jump in median and maximum larval size (Fig. 2). Doyle and Mier (2016) document a change in mode for these length data from 7 mm in April to 14 mm in May. By July, all larvae caught in the 60-cm bongo nets are > 25 mm SL. Although transformation may begin when larvae are < 30 mm long, transitioning larvae up to 45 mm SL are caught in plankton nets and small-mesh pelagic trawls through summer months (IIS; Debenham pers. comm.). The 60-cm bongo sampler is not, however, efficient at catching these large, late-stage transitioning ATF larvae and they are rare in historical GOA ichthyoplankton collections.

During peak abundance (January to mid-March), larvae are distributed almost exclusively in slope waters with limited occurrence on the outer shelf (Blood et al., 2007; Doyle and Mier, 2016). From April through June, ingress of larvae on to the shelf is apparent especially in association with troughs and gullies intersecting the continental slope such as Amatuli Trough and Outer Shelikof Sea Valley (Bailey and Picquelle, 2002; Bailey et al., 2008; Doyle and Mier, 2016). Abundance of larvae over the slope and outer shelf still remain high through mid-June. By late June and early July, ATF larvae are scarce in bongo net samples from both shelf and slope waters. Vertical distributions illustrate an ontogenetic migration of larvae from depths ($\geq$ 400 m) where they hatched from mesopelagic eggs, with most large larvae (> 10 mm SL) occurring in the upper 50 m of the water column (Doyle and Mier, 2016). It is also apparent that larvae < 10 mm may take weeks to migrate through the water column as small larvae were frequently captured in nets deployed below 100 m during spring months.

The trend in abundance of late-stage ATF larvae from a 1981-2013 late spring time series is characterized by a period of anomalous high levels of abundance from 1992 through 1997 (Doyle and Mier., 2016; Siddon et al., in press), previously attributed to enhanced wind-driven cross-shelf and alongshore transport (Doyle et al., 2009). The amplitude of variation in mean abundance for all other years is more limited, and during the GOA-IERP field years of 2011 and 2013 values were similar and slightly negative relative to the long term mean (Rogers and Mier, 2016). At this time of year, ATF larvae can range in size from 4 to 35 mm SL but most are 8–17 mm (Fig. 2). There is no significant relationship between mean larval size and mean larval abundance for the time series, but a positive although weak correlation has been established between size and water temperature (Doyle and Mier, 2016). Length-frequency distributions for ATF larvae across the time series reflect this correlation; distributions tended to be more contracted towards the smaller size range in colder years and extended to the upper size ranges in warmer years (Doyle and Mier, 2016).

The summer surface trawl sampling in 2010-2014 (Table 2) provided new information on distribution patterns of late stage ATF larvae in the GOA (Fig. 3). Levels of abundance were variable with highest concentrations encountered during July 2010 and 2012 on the eastern sampling grid over the shelf and in adjacent slope and deep water (Fig. 3 a and d). Frequency of occurrence at stations and concentrations of larvae were lowest during 2011, 2013 and 2014 (Fig. 3 b, e and f), and although sampling was more limited in the west in 2011 and 2013, only 1 and 2 ATF larvae were caught respectively in those years for that region (Table 2). Although levels of abundance during 2012 were similar in the vicinity of Kodiak Island at stations where larvae occurred, fewer stations had catches of larvae (Fig. 3 c). However, sampling occurred a month later here relative to the east. Most larvae in the surface trawls were in the size range associated with transformation to the juvenile stage; i.e. 30-45 mm (Fig. 2, Fig. 4). For 2010 and 2012 in the east when abundance was greatest, length frequency distributions for the larvae were similar. The larger larvae in the west during 2012 (Fig. 4 c) likely reflect the later sampling in that region. Although larvae encountered were in the transitioning size range, no metamorphosing larvae were observed; i.e. there was no indication of eye migration among the specimens encountered (Debenham, unpublished data). The LOESS smooth curve fitted to the combined spring (2010, 2011 and 2013) and summer (2010-2014) larval data describes the relationship between larval sizes and Julian day, and simulates the growth of larvae over these months (Fig. 5). Throughout April (Julian Day < 120) the slow growth of larvae is apparent, and in May growth rates seem to increase significantly as also observed in the historical larval lengths between April and May (Fig. 2). The accelerated growth rate seems to continue through the summer months with perhaps some leveling off by late August. It was expected that the GOA-IERP summer and autumn sampling in selected nearshore area and bays of the GOA during 2011 and 2013 would have provided plentiful data on newly-settled and Age 1+ juveniles of ATF. However, only three ATF specimens were recorded during these surveys implying limited utilization of these nearshore habitats, or sampling methodology that did not favor the collection of newly settled or older juveniles.

The biophysical IBM model of ATF early life history and dispersal was run for the years 1996-2011, with simulated individuals released as eggs through early winter in presumed spawning and hatching areas along the shelf break (Fig. 3 SM) and tracked through time until they reached a larval size of 42 mm SL and were regarded as competent to settle in benthic nursery areas on the shelf (Stockhausen et al., accepted). For the initial model run, preferred nursery habitat was defined as areas < 50 m deep (Fig. 3 SM), based on previous assumptions that nearshore settlement areas are favored (Norcross et al., 1995; Bailey et al., 2008). Settlement-stage individuals that arrived above a preferred nursery area before the end of an 8-day “window of opportunity” were considered to have successfully recruited to juvenile nursery habitat. Dispersal patterns of “successful” (settling in areas < 50 m depth) and “unsuccessful” individuals onto the continental shelf and into the deep basin are illustrated at the completion of subsequent early life stages (Fig. 4 SM) for a typical simulated year (2011). Based on the twelve alongshore zones for spawning and settlement (Fig. 3 SM; Stockhausen et al., accepted), the model simulations indicate that most (> 80%) individuals were unsuccessful in dispersing from presumed spawning areas along the continental slope to inshore “preferred” nursery grounds (Fig. 5 a SM). For those that were successful, most originated in the eastern GOA and settled in the central and western GOA such that connectivity was primarily directed from southeast to northwest following prevailing current patterns. Typical dispersion distances for successful individuals were on the order of 100s of km alongshore. Individual trajectories were complex (illustrated in Stockhausen et al., accepted), and although most “successful” individuals stayed on or near the shelf, some were also transported off the shelf and then returned from deep water via eddies and gyres. According to this dispersive model the most effective spawning areas were in the southeast off Sitka and Cross Sound, while the most effective nursery areas were in the central and western GOA including Prince William Sound and North Kodiak areas (Fig. 5 b SM). Interannual variability in the model-generated connectivity patterns was fairly large but did not correlate well with estimated recruitment to the population three years later (Stockhausen et al., accepted).

It is likely that ATF utilize a much wider range of shelf habitat as nursery areas than was originally considered in Stockhausen et al. (accepted) as young of the year and older juveniles can occur in a wide range of depths (Spies et al., 2017). Rerunning the IBM with an expanded definition of suitable nursery habitat to include on-shelf areas < 150 m deep (Fig. 3 SM, Fig. 6) increased the overall chance of an individual successfully reaching suitable nursery habitat (by a factor of 2, approximately; Fig. 7 a), but did not substantially alter the qualitative picture of counterclockwise connectivity along the shelf or the patterns of temporal variability in the connectivity patterns (Fig. 6, Fig. 7 b).

3.4. Settled juveniles and adult fish

3.4.1. Juveniles caught during October 2011 small-mesh trawl survey

Catches of ATF were low in these collections, with juveniles at about a third of the stations sampled and distributed from near shore to outer shelf, seaward of Kodiak as well as to the southwest of Shelikof Sea Valley (Fig. 8 a and b). They occurred in both the bottom and mid-water samples. Length-frequency distributions indicate Age-0 fish (Age 1 fish tend to be > 100 mm SL) with size ranges between 50 and 95 mm. Most of the bottom trawl fish were between 60 and 80 mm (Fig. 8 c) whereas the majority of those caught in the midwater trawl were < 70mm (Fig. 8 d). Diel variation in catches did not suggest a day-night difference for the bottom occurring fish (Fig. 9 a) whereas occurrence and abundance of fish in the water column were highest during hours of darkness; 20 hrs to 04 hrs Alaska local time (Fig. 9 b). Although avoidance of pelagic sampling gear may be enhanced during daylight hours, the diel pattern in catches suggests that excursions from the benthos into the water column may be confined primarily to night time.

3.4.2. Juvenile and adult data from AFSC groundfish surveys

Analysis of AFSC groundfish catch data for the summer assessment surveys (1984-2015) shows a very high (> 80%) proportion of trawl stations with ATF present (Table 3) indicating widespread distribution throughout the shelf. The proportions were lowest for 1984 and 1987, the earliest years in the time series, and may reflect the lower biomass levels for ATF that were documented prior to 1990 (Fig. 1 SM, Table 3). For the GAM models that included all data for the full time series the binomial GAM explained 40.3% of the deviance in the presence and absence data, and the log gamma GAM explained 38.8% of the deviance in density where ATF were encountered. Location (Lat., Long.), year and fish size (seven size bins) effects show ATF concentrated in the middle of the shelf (Fig. 10), with annually variable ubiquity and density (Fig. 11 a). The size effect shows a dome shape indicating differences in survey selectivity for different sizes of fish, availability in the surveyed area, and abundance at size (Fig. 11 b). The smallest fish (< 100 mm in particular) of course are not sampled well by the large mesh nets, and the largest and oldest fish are less abundant.

Combined, the models show that although ATF are ubiquitous in the survey area occupying between 82% and 92% of the survey stations (Table 3, Fig. 10), they are more often encountered at higher densities in waters between 100 m and 200 m bottom depth on the continental shelf (Fig. 12). The GAMs also show an ontogenetic expansion in distribution of fish to include deep water over the continental slope. At larger sizes (> 300 mm) fish occurred in deeper waters extending down to below 800 m albeit at low densities (predicted at < 30 km^{-2}) at depths > 400 m (Fig. 12). Bottom temperature was also a factor in ATF distribution and density. Fish in the 100-400 mm size range occurred in highest concentrations in colder waters (< 4°C), while larger fish were observed more often and in higher densities in warmer waters (4-8°C). Even though juvenile ATF in the < 100 mm size category are not sampled efficiently by the bottom trawl surveys, their signal in these data indicate widespread distribution at all bottom depths and temperatures sampled on the shelf (Fig. 12, Panel 1). At temperatures < 5°C, their distribution also extends down to depths of approximately 400 m indicating that newly settled juveniles can occur beyond the shelf edge. Distributions for the 100-200 mm size category (likely age 1-2 fish, Fig. 12, Panel 2) extend almost to the full depth range at which older fish are encountered which suggests a high level of ubiquity for pre-recruit, immature fish.

When the data are split between warm and cold years (as defined in Table 3) the effect of temperature on distributions is apparent among all size categories of ATF (Fig. 13). The models suggest that fish < 300 mm tend to occur at depths primarily < 400 m in warm years (Fig. 13 a), but expand their distribution to deeper water in the cold years (Fig. 13 b). For the youngest fish encountered (< 100 mm) occurrence beyond the shelf edge (> 200 m) seems to be confined to cooler years. In the warm years, the full extent of occurrence of ATF in the 300-600 mm size bins is broadest and includes the deepest survey stations at 800 m and slightly deeper (Fig. 13 a). In contrast, however, high densities of fish (> 3800 km^{-2}) are more extensive in the 200-400 m depth range in cold (Fig. 13 b) relative to warm years (Fig. 13 a). For the largest and oldest fish (> 600 mm), the highest densities are encountered exclusively over the slope in cold years.

It should be noted that changes in sampling methodology accounts for some of the interannual variability in distribution patterns presented here. Over the survey time series there have been changes that may have affected availability and catchability of ATF in the bottom trawl survey. In 1993 the survey switched from 30 minute to 15 minute duration tows. This may have reduced the catchability of larger fish. Incremental improvements to trawl technology allowed the bottom trawl survey net to better tend to the bottom, improving net performance and leading to more precise on bottom and off bottom time estimates. Improvements in fish identification in the early 1990s likely lead to some changes in survey estimates (Stevenson and Hoff, 2009). This interannual variability was captured in the annual effects (Fig. 11 a) in the GAMs making the interpretation of the annual effect problematic except as an overall repository for all annual variability, not just trends in population abundance.

3.4.3. Habitat suitability models

Results of the habitat modeling provided new synthetic information on ATF habitat utilization, and geographic and physical habitat characteristics associated with each of the three demersal life stages. Further, the model output yielded a ranking of such physical features enabling their evaluation as habitat predictors.

Early juvenile stages of ATF (40-160 mm) were captured in nearshore areas and bays around Kodiak Island and the Alaska Peninsula primarily by the ADFG small-mesh bottom-trawl survey. Several early juvenile stage ATF were captured by hauls made with larger mesh trawl gear by the AFSC surveys on the continental shelf and slope within 22-558 m depth (mean ± SD; 116 ± 50 m) (Table 2 SM, Fig. 6 a SM). Final habitat models produced from k-fold cross-validation of model replicates demonstrated the top contributing habitat predictors were depth, broad-scale terrain features (BPI 3.3 and 6.5 km), bottom temperature, and tidal current speed (Table 5). Contribution of other habitat metrics was minimal (< 5%) except for coral (5.6%) and rocky substrate (5.1%) presence. The models characterized early juvenile stage habitat as bathymetrically low-lying areas, such as bays and channels, and flats offshore of the main rivers and glaciated bays around the GOA. Highly suitable habitat includes areas with relatively low tidal current speed and reduced presence of corals and rocky substrate in nearshore and continental shelf areas. The top 25th percentile of predicted suitable habitat was within 35-200 m depth and the top 10th percentile within 70-140 m depth. Model averaging performed with the final surface from each set of replicated models produced a mosaic of the mean probability of suitable habitat on a continuous scale (0-1), where habitat of high suitability is represented by values close to 1 and habitat of low suitability by values close to 0 (Fig. 14 a). Habitat of high predicted suitability occurred on the continental shelf west of Cross Sound and offshore of Yakutat Bay, Icy Bay, the Copper River, Kodiak Island, and the Shumagin Islands west of Shelikof Strait. Suitable habitat in the vicinity of northeast Kodiak Island is highlighted by the map inset, demonstrating a preference by these young stages for entrances and deeper channels of bays and not along the shoreline.

Late juvenile stage ATF (161-350 mm) were the most abundant of the three demersal life stages examined and nearly ubiquitous in the bottom-trawl survey area on the continental shelf and upper slope (Table 2 SM, Fig. 6 b SM). Sample locations were also available from inside waters in southeast Alaska and Prince William Sound, and by the ADFG small-mesh bottom-trawl survey nearshore around Kodiak Island and the Alaska Peninsula. The final models demonstrated the top contributing habitat predictors were depth, broad-scale terrain features (BPI 3.3 and 6.5 km), tidal current speed, and bottom temperature (Table 5). The contribution of other habitat predictors was minimal (< 3%) with the exception of substrate rockiness (4.4%). The models described ATF late juvenile stage habitat as bathymetrically low-lying areas such as channels and gullies, and flats offshore of the main rivers and glaciated bays. Highly suitable habitat includes areas with relatively low tidal current speed and reduced presence of rocky substrate. Although late juvenile ATF were widely distributed, the top 25th percentile of predicted suitable habitat was within 80-230 m depth and the top 10th percentile within 120-180 m depth. ATF older juvenile habitat shifts to deeper depths and occurs extensively from nearshore across the continental shelf and over the slope with less terrain specificity than the younger juvenile stage (Fig. 14 b).

Adult ATF (> 350 mm) catch locations were ubiquitous in the NOAA AFSC RACE bottom-trawl survey sampling extent on the continental shelf and slope, similar to older juveniles (Table 2 SM, Fig. 6 c SM). Adults were also captured in nearshore areas by the ADFG small-mesh bottom-trawl survey. NOAA AFSC underwater visual surveys of groundfish and fish habitat provided additional sample locations for adults. The final models demonstrated the top contributing habitat predictors; depth, bottom temperature, broad-scale terrain features (BPI 3.3 and 6.5 km), and tidal current speed (Table 5). The contribution of other habitat metrics was minimal (< 3%). As for the juvenile stages, the models described adult ATF habitat as bathymetrically low-lying areas such as channels and gullies with relatively low tidal current speed, and flats offshore of the main rivers and glaciated bays. Adult habitat extends to deeper depths than immature fish. The top 25th percentile of predicted suitable habitat was within 100-470 m and the top 10th percentile 150-470 m depth. Adult ATF habitat is distributed broadly over the continental shelf and slope, occurring deeper than immature fish captured by the ADFG and AFSC summer bottom-trawl surveys (Fig. 14 c).

3.5. *Feeding and predation*

The diet of late-stage larval ATF is dominated by large Calanoid copepods by percent weight of stomach contents (73%) followed by small Calanoid copepods (14%) and Decapod larvae (7.7%) (Debenham et al., unpublished data). Some settled ATF juveniles from the benthic environment have also been analyzed for gut contents and a distinct shift in prey from copepods to the dominance of shrimp and fish is apparent (Debenham et al., unpublished data). No larval diet data are available for ATF winter first-feeding stages through spring months.

An ontogenetic shift in diet of ATF is also apparent from food habit data based on AFSC summer groundfish assessment surveys (Fig. 15). Fish smaller than 200 mm consume mostly zooplankton (primarily Euphausiids) and Osmeriid fish (primarily Capelin), with approximately 30% of remaining diet by weight consisting of “other fish”, Sand Lance (*Ammodytes hexapterus*), Shrimp and Crabs. Subsequently, as the fish grow through 10 cm increments, zooplankton and Capelin diminish in importance, and Walleye Pollock becomes dominant. The largest ATF (> 600 mm) also have increasing amounts of Pleuronectid fish in their diet, probably because their larger mouth size facilitates the capacity to swallow whole flatfish.

Predation on different size categories of ATF by fish predators also reveals a progression with age from pelagic to benthic habitat utilization by ATF (Fig. 16). With increasing ATF size, relative amounts of predation by pelagic, zooplanktivorous predators such as Walleye Pollock, Northern Rockfish (*Sebastes polyspinis*) and Pacific Ocean Perch (*Sebastes alutus*) decreased rapidly, whereas relative amounts of predation by primarily benthic predators increased. The heavily sampled Pacific Cod and Pacific Halibut (*Hippoglossus stenolepis*) represent the highest proportion of predation on 30-399 mm ATF. Cannibalism by ATF on the 30-299 mm prey size also occurs. Only very large fish can consume ATF > 400 mm, such as Pacific Sleeper Sharks (*Somniosus pacificus*) and a few Pacific Halibut and Skates. Consumption of different size groups of the young of the year (< 100 mm) ATF by total predators indicates heaviest predation during summer months on the 30-59 mm size group (Fig. 17). At this size ATF are undergoing metamorphosis (including eye migration and lateral compression of the body) and transition from a pelagic drift phase to benthic settlement.

3.6. New conceptual model of habitat utilization from spawning to settlement

Occupation and utilization of pelagic and benthic habitat by ATF from spawning through settlement appears to be more extensive than previously thought based on the synthesis of historical and recent

GOA ichthyoplankton data, IBM results, and habitat modeling (Fig. 18). This represents a change from previous paradigms of ATF early life history ecology which described a continuous larval transport trajectory from deep water spawning areas along the slope to nearshore nursery areas (Bailey et al., 2008; Fig. 2 in Stockhausen et al., accepted). In this new schematic, we illustrate the observed distributions of larvae from winter through summer with seasonal expansion across the shelf to nearshore as well as retention over the outer shelf and slope. In addition, summer to autumn distribution of recently settled juveniles is shown to be broader than previously reported with occupation of nearshore to slope habitat. Concurrent seasonal progression in ATF larval sizes (upper panel, Fig. 18) shows that feeding larvae start to grow rapidly from May onwards as they become more abundant on the continental shelf, subsequent to very slow winter growth through the yolk-sac stage (< 7 mm).

3.7. Climate-related vulnerability assessment for Arrowtooth Flounder in the GOA

Utilizing the ecological synthesis across life stages, a climate-related vulnerability assessment for evaluating the sensitivity of individual fish stocks or populations to potential climate change (Morrison et al., 2015) is applied to ATF here. Assessment scores are assigned, and associated resilience or vulnerability factors are identified for the 12 sensitivity attributes recommended (Table 6). Large ATF stock size and high productivity in combination with very low levels of predation and fishing mortality render low scores in terms of vulnerability of the existing ATF adult population in the GOA to climate change impacts. Further, the lack of specificity in both habitat utilization and prey organisms consumed by ATF throughout the juvenile and adult stages yields low vulnerability scores for these attributes. There is no present indication that ATF would be highly sensitive to even moderate increases in ocean acidity. Calcifying organisms known to be sensitive to acidification such as bivalve shellfish do not seem critical in ATF diets across juvenile to adult stages, although decapod crustaceans can represent up to approximately 14% by weight of prey consumed by ATF < 40 cm in length (Fig. 15). The direct impact of water pH changes on zooplankton crustaceans such as copepods and euphausiids, important especially as prey for larval and juvenile stages respectively, has not been studied in the GOA. Their response to acidification remains largely unknown in this region, but based on negative responses evaluated for temperate mesozooplankton species generally (Busch and McElhany, 2016), a low to moderate sensitivity score for ATF seems appropriate in this regard (Table 6). Aspects of reproductive and early life history strategies that yield low vulnerability scores include spawning of mesopelagic eggs in cold, deep water during winter over the slope, and an extended larval drift period that results in high dispersal with potential for colonization of new habitat. The utilization of cold, deep water for deposition of eggs ensures a stable environment with low predation risk, and low metabolic demand during early ontogeny when yolk-sac reserves are being utilized. The so-called larval “endurance” strategy, or physiological “holding pattern” observed with ATF larvae (Doyle and Mier, 2016) is considered a factor of resilience in a winter, food-poor environment. Doyle and Mier (2016) also propose that the observed synchrony in peak abundance of ATF larvae with the winter release of eggs and nauplii of *Neocalanus* copepod species in deep water may be a potential food source for first-feeding larvae in the GOA and would add to this endurance strategy.

Although climate-related resilience seems to be the dominant feature of ATF life history and ecology in the GOA, three low-moderate (1.5) and one moderate to high (2.5) vulnerability scores are assigned (Table 6). Wind plays a significant role in both alongshore and cross-shelf transport of larvae in the GOA, and delivery of ATF larvae from deep water spawning areas on to the shelf (Doyle et al., 2009). Climate-induced variability in such larval transport could be a point of vulnerability in the early life ecology of ATF. This could potentially compromise the larval “endurance” strategy described above and so a low-moderate score overall is assigned for the “Early Life History Survival and Settlement Requirements” sensitivity attribute. The moderate-high vulnerability score is also associated with early ontogeny and is attributed on the basis of potential temperature-induced variability in larval developmental rates that could influence the relationship between timing of larval feeding and prey availability. Finally, a negative affect from warming bottom temperatures is also suggested by the GAM modeling of ATF abundance in relation to temperature and depth presented earlier (Fig. 13). The contraction in depth distribution apparent in warm relative to cold years, especially for fish < 40 cm, is considered a moderate level of vulnerability. Because ATF are encountered in the full range of bottom temperatures measured during groundfish surveys in the GOA from shallow to deep water, this level of risk is on balance considered low to moderate with population distribution being affected primarily at the edges. With a minimum possible score of 12 and a maximum of 36 (Table 6 rubric), a total vulnerability score of 15 is calculated for ATF in the GOA.

4. Discussion

It is important to consider the detailed ecological patterns and environmental links across life history stages for an apex predator species such as ATF in the GOA. Its continued population growth since the 1970s, and status of persistent numerical dominance associated with limited fishing and predation pressure (Spies et al., 2015) seems to confer a higher level of resilience for this species, relative to most, in terms of its sensitivity to environmental fluctuations. The trajectory of the ATF population in the GOA in the next decade and beyond is unclear. However, some decline in biomass has been observed (Spies et al., 2017), and a decline in the size of younger ATF indicate that the species may be approaching or at carrying capacity in this ecosystem. The comprehensive ecological synthesis presented here certainly supports a general outlook of environmental resilience. However, some sensitivities and potential vulnerabilities have been identified, especially during early life, and their consideration with respect to possible fluctuations in the ecosystem contributes to the development of hypotheses regarding future variability in the status of this species in the GOA. Interaction with the ocean environment is variable at different life history stages, even at sub-intervals of early ontogeny for marine fish species, which likely drives stage-specific responses and survival outcomes (Doyle and Mier, 2012, 2016). Understanding stage-specific ecological patterns and environmental affects is critical to gauging the influence of ecosystem dynamics and shifts for a given fish species, and for successful ecosystem-based management of fish stocks (Bailey, 2000; Hollowed et al., 2009; Rijnsdorp et al., 2009).

4.1. Mechanisms of early ontogeny interaction with the pelagic environment and associated sensitivities

ATF is at the earliest end-point of a phenology gradient for GOA fish species that represents a broad range in timing of spawning and occurrence of eggs and larvae in the pelagic environment (Doyle and Mier, 2012). This winter phenology is associated with deep water, continental slope habitat in which eggs and newly hatched larvae develop (Blood et al., 2007). This environment may confer stability to the timing of spawning of ATF from year-to-year as the amplitude of variability in physical conditions is more limited at depth than near the surface. Cold water temperatures are advantageous for slow development of the mesopelagic eggs, and minimizing predation from planktonic predators that would be more abundant in the upper water column, and on the continental shelf especially later in the year. Cold conditions also favor slow larval development. Slow growth is crucial if first-feeding larvae occur in association with low availability of potential prey organisms during early winter, but still need to encounter and feed on high levels of prey on the shelf in spring (e.g. copepod nauplii) to develop and settle out of the plankton. Prolonged ontogeny is also an advantage for extended larval duration and drift. ATF larvae are transported from deep water onto the shelf very gradually during winter and spring. Doyle and Mier (2016) attribute the term “holding pattern” to this slow development and gradual transport of larvae, and consider it an early ontogeny strategy of endurance. Further, intrinsic physiological rates seem to result in very low metabolic demand by larvae such that from January through March most remain < 7 mm, the size at which yolk absorption is usually complete (Blood et al., 2007). The high proportion of 6-8 mm larvae encountered through April suggests some availability of lipid reserves even in spring. This extended utilization of intrinsic nourishment, and slow growth, contrasts with that observed for Pacific Halibut whose early ontogeny occurs in the same deep water habitat and at the same time as ATF in the GOA (Doyle et al., 2012). Halibut larvae hatch out at a much larger size than ATF and grow much more quickly, even in the same cold and food-poor environment, emphasizing the importance of intrinsic rates as well as extrinsic factors in terms of progression through sub-intervals of early ontogeny.

Another potential environmental buffering effect that could mitigate the risk factor of minimal larval food availability is the reproduction of oceanic species of copepods in deep water during early winter, following a period of diapause. Doyle and Mier (2016) note spatial and temporal synchrony between ATF early ontogeny and the reproduction of *Neocalanus* species of copepods (considered primarily to be *N. plumchrus* and *N.* flemingeri; Miller and Clemons, 1988; Coyle et al., 2013), and argue that their lipid-rich eggs and nauplii are a potential key food source for first-feeding larvae. During late winter and early spring months the ATF larvae and *Neocalanus* spp. early life stages utilize the same cross-shelf transport processes to gain access to continental shelf habitat (Coyle et al., 2013; Mordy et al., accepted). It is also probable that populations of small-sized copepods such as *Pseudocalanus* spp. and *Oithona similis* that numerically dominate the shelf assemblage may provide some prey for ATF larvae in late winter as well as during spring. They have multiple generations per year, and even though levels of abundance are relatively low in winter months (Coyle and Pinchuk, 2003), copepodite and naupliar abundance levels on the outer shelf are several orders of magnitude higher (Coyle and Pinchuk, 2005) than those documented for ATF larvae (Doyle and Mier, 2016) implying availability as larval prey.

Despite such adaptive features and potential environmental buffering effects, the early ontogeny planktonic phase of ATF is still assigned a medium to high vulnerability score with respect to potential for climate-induced disruption (Table 6). The early life history characteristic of “endurance” is a robust strategy that likely results in a broader range of optimal conditions for early survival relative to most fish species in the GOA. Nevertheless, the increased exposure to the pelagic environment from winter to summer months, along with the early spatial and temporal mis-match with peak availability of zooplankton prey resources confers a level of complexity to this early life strategy that implies enhanced sensitivity to environmental variability. Doyle and Mier (2016) document a positive shift in sizes relative to temperature for a variety of larval species, including ATF, in the GOA late spring ichthyoplankton time series, suggesting increased metabolic rates and enhanced growth with warming. Increased development rates for eggs and larvae have also been observed with small increases in water temperature in laboratory rearing studies of ATF (Blood et al., 2007). Under warming conditions, it is likely that ATF eggs and larvae will develop more quickly, and larvae may use up their yolk-sac lipid reserves earlier than normal. There is potential, therefore, for an exacerbation of the mis-match between peak larval abundance and spring plankton production on the GOA shelf that could result in fewer ATF larvae surviving long enough to encounter a plentiful supply of copepod nauplii. Further, if as hypothesized there is a critical trophic link with *Neocalanus* spp. eggs and nauplii for survival of first feeding larvae in late winter, such prey specificity implies extra sensitivity and perhaps vulnerability.

Effects of warming on different groups of zooplankton organisms can be variable and complex, and different sensitivities and responses are observed (Mackas et al., 2012). Synchronicity in response to environmental disruption is therefore unlikely between larval fish and their zooplankton prey. The dynamics are not simple, and a great deal of uncertainty prevails in terms of potential for shifting, and the temporal direction and amplitude of such shifts from favorable to unfavorable trophic conditions for larval fish growth and survival (Batten and Mackas, 2009). However, if *Neocalanus* spp. is a critical food source for ATF larvae, during late winter as eggs and nauplii over deep water and in spring to early summer as later copepodite stages on the shelf, perhaps this copepod taxon could be an important biological indicator of survival. For settled ATF juveniles that continue to feed on large Calanoid copepods, the lipid-rich *Neocalanus* adults are also likely to be an important food source on the shelf during spring to early summer prior to their migration into deep water diapause. Significant temporal shifts in annual biomass peaks have been documented for *Neocalanus* spp. in the Gulf of Alaska basin (Mackas et al., 1998; Batten et al., 2003). Anderson and Piatt (1999) hypothesize that an earlier biomass peak for *Neocalanus* copepods associated with a switch to a warmer oceanographic regime at the end of the 1970s (Mackas et al., 1998) favored early spawning fish species whose larvae could take advantage of that peak, and contributed to the rise of ATF, along with other groundfish species in the GOA. An earlier peak abundance of adult stage *Neocalanus* copepods could be an advantage to well-developed late stage larvae, such as ATF in May-June that are mostly greater than 10 mm at that time. It would be difficult for smaller larvae to eat the later copepodite stages that are 3-4 mm in body length for *N. flemingeri* and *N. plumchrus* (Kobari et al., 2003). Further, Anderson and Piatt (1999) propose that the concurrent decline of shrimp populations in the GOA (larval stages negatively affected by an earlier zoopolankton biomass peak) resulted in a significant reduction in predation on *Neocalanus* copepods freeing up that food source for fish populations that feed on plankton such as young Walleye Pollock and ATF. Further research is necessary to verify the existence of such an important trophic link by conducting gut content analysis on larval and juvenile ATF in the GOA, during winter and spring months, and over years with variable conditions so as to evaluate possible climate-induced changes in production and consumption of such prey.

Variability in larval transport may also influence survival of ATF to juvenile settlement. The association of hot spots in abundance of eggs and larvae with deep-sea valleys and troughs intersecting the slope has been well established and seasonal progression in distribution of larvae onto the shelf has been described (Blood et al., 2007; Bailey et al., 2008; Doyle and Mier, 2016). Cross-shelf transport is enhanced at Amatuli, Chiniak, and Barnabus Troughs, as well as Shelikof Sea Valley with an estuarine type flow observed (Stabeno et al., 2004; Mordy et al., accepted) offering clear evidence for a previously proposed mechanism of onshore transport of larvae in association with these features (Bailey and Picquelle, 2002). Elevated levels of abundance of ATF larvae on the western GOA shelf have been linked previously with enhanced onshore advection during ENSO (El Niño Southern Oscillation) conditions (Bailey and Picquelle, 2002), and with increased alongshore and cross-shelf winds (Doyle et al., 2009). Recruitment of ATF along with other deep water spawning flatfish in the GOA has been positively although weakly associated with basin-wide sea surface height which is presumed to be connected to enhanced onshore transport of larvae (Stachura et al., 2014). Investigating the relationship between transport processes in the canyons intersecting the GOA continental slope, at spatial and temporal scales relevant to the early ontogenetic stages of ATF, would likely provide a better predictor of early life survival and recruitment than basin-scale climate-ocean variables which integrate across spatial scales that are too coarse.

Further insight into larval transport dynamics is provided by the IBM (Stockhausen et al., accepted). Whereas the IBM-generated connectivity indices did not correlate well with age-3 recruitment to the population, Stockhausen et al. propose a variety of explanations for this disconnect. Predominant alongshore transport to the west although real was probably overemphasized by the regional scale of the ROMS oceanographic circulation model, especially given the dominance of the Alaskan Stream that flows in a counterclockwise direction parallel to the continental slope. The IBM is based on ATF-specific Lagrangian integration with this model so even small differences between the model and reality can lead to large effects on individual larval drift trajectories. The IBM weighted the spawning areas equally and considered egg and larval production to be uniform across the GOA in the 300-600 m bathymetric depth range. Ichthyoplankton data do not support such uniformity as hot spots of abundance are associated with the mouths of the troughs and canyons intersecting the slope (Doyle and Mier, 2016). Variability in the relative importance of the different spawning areas, especially on an interannual scale, would degrade any relationship between the model-generated connectivity indices and recruitment. Biological processes captured in the IBM include extremely simple characterizations of behavior (e.g., undirected swimming) and larval growth (constant growth rates). Directed swimming behavior could substantially reduce alongshore dispersion or facilitate onshore transport, especially via the canyons and troughs. Environmentally-sensitive growth rates could reduce or prolong life stage durations, altering the timing when pelagic larvae become competent to settle to the benthos and thus altering connectivity. Clearly the predictive capacity of the IBM could be improved significantly by fine-tuning spatial and temporal variability in egg and larval distribution and abundance, accounting for availability and consumption of zooplankton prey, and an improved understanding of intrinsic physiological rates and their response to extrinsic factors.

A successful feature of the IBM results is the comprehensive insight gained into potential larval drift patterns across the entire GOA. High dispersion distances and complexity of such trajectories, including on-shelf and off-shelf transport and entrainment in features such as eddies and meanders are expected characteristics of the extended larval duration (Stockhausen et al., accepted). In fact the model-generated dynamic interplay of on-shelf and off-shelf larval transport, particularly in the eastern GOA where the shelf is narrower, is reflected in the observed distribution patterns of late stage larvae from the summer surface-trawl collections; larvae were either equally or more abundant over the slope and deep water as on the shelf in the eastern GOA. The total planktonic drift period for ATF encompasses weeks to months of very small and likely behaviorally incompetent yolk-sac and preflexion larvae that occur primarily in association with slope waters and the westerly flowing Alaskan Stream. This phase is followed by weeks to months of larger post-flexion to transforming stage larvae that may be able to have some influence on directed transport. The prevailing pattern of transport in a counterclockwise direction over the slope and outer shelf, particularly of preflexion larvae, likely contributes to poor settlement success overall in coastal habitats. The IBM indicates that this is especially true for larvae that originate in deep water spawning areas to the west of Kodiak Island. Although these larvae may be "lost" to the GOA system, they could have a second chance at settlement on the southeast Bering Sea shelf. Using an IBM modelling approach, Parada et al. (2016) evaluated connectivity of Walleye Pollock nursery habitat with spawning areas in the GOA and identified a prominent connection between the western GOA shelf in the vicinity of the Shumagin Islands and the outer domain of the southeast Bering Sea shelf. The proposed process for connection is larval transport through the Aleutian Island passes, and this is very likely applicable to ATF as a mechanism for colonization of new habitat in the eastern Bering Sea. The longevity of the larval stage and the low metabolic demand during early ontogeny is a strategy that would favor ultimate settlement success on the Bering Sea shelf for this species. Colder temperatures in the Bering Sea may also diminish already slow growth rates, further enhancing survival of pre-feeding larvae along their extensive drift path.

4.2. Habitat utilization and associated environmental sensitivities from metamorphosis and settlement through adult life

The period of transition from pelagic larva to settled juvenile, which occurs during summer and early autumn months in the GOA, is still the least documented phase of ATF early life. Metamorphosing larvae with eye migration at an intermediate stage or completed are rarely caught in plankton nets. The surface small-mesh trawl used to sample the upper 30 m of the water column during the GOA-IERP program was effective at capturing late stage pelagic and symmetrical larvae. Average energy density for these fish have been measured and show no change with size (even with the inclusion of settled juveniles for comparison), although some low amplitude interannual variation has been attributed to changes in temperature and diet composition with a slightly negative effect documented in warmer years (Debenham et al., unpublished data). De Forest et al. (2014) also report little change in energy allocation between the late larval and juvenile stages of ATF in the southeast Bering Sea. It was surprising that no metamorphosing larvae were caught in the summer pelagic trawl samples, especially given that larvae were in the size range for transformation to juvenile settlement. Once eye migration begins, larvae may start to migrate downwards through the water column so as to take up residence on the bottom once transformation is complete. This would explain their absence from the upper 30 m of the water column and their susceptibility to predation by benthic predators such as Pacific Cod, Skates, Rougheye Rockfish (*Sebastes aleutianus*), and larger ATF. Eye migration, 90° rotation in body posture, and asymmetrical development of pigmentation on the “new” dorsal side is a complex ontogenetic transformation needed for settlement in flatfishes. It is considered an interval of immense physiological demand and structural change that likely compromises the behavioral abilities of metamorphosing larvae to detect and avoid predators (Fuiman, 1997; Osse and Van den Boogaart, 1997). Occurring deeper in the water column, intermediate between the upper high visibility euphotic zone and the lower portion close to the benthos, would likely reduce the predation risk associated with this developmental phase. Once ATF larvae settle out of the plankton as fully metamorphosed early juvenile flatfish, results presented here and in Wilson et al. (2016) suggest that they still partly occupy pelagic habitat especially for feeding on plankton, and that this pelagic foraging may occur primarily at night. It is also appropriate to acknowledge that an alternate reason for the absence of juveniles in the pelagic trawl during hours of darkness could be that the fish were unable to sense the trawl in the dark, and were perhaps not herded towards the fine mesh of the codend (Reyer, 2008).

Historically, nursery habitat for ATF was presumed to encompass nearshore and inner shelf regions. This can be primarily attributed to limited sampling and assessment of age-0 and juvenile stages, and the nearshore bias of previous survey work for juvenile flatfish in the GOA (Norcross et al., 1995; Bouwens et al., 1999; Anderson et al., 1999; Mueter and Norcross, 2000; Abookire et al., 2001). Although ATF settled juvenile stages are frequent in such collections, they tend to be less abundant than other flatfish species and these and more recent studies have found them to be less abundant at the shallowest stations (Hurst, 2016). When sampling is extensive across the shelf, depth does not factor as a predictive variable (Wilson et al., 2016). ATF were notably absent from the GOA-IERP summer and autumn nearshore surveys, and they are not listed in a recent field guide to the nearshore marine fishes of Alaska although juvenile stages of other flatfish species like Pacific Halibut feature prominently (Johnson et al., 2015). It is now apparent that ATF nursery habitat extends from coastal areas throughout shelf waters. Even the smallest specimens (< 100 mm) are picked up in groundfish trawl survey stations over the full extent of depths sampled, including deep water locations beyond the shelf edge. Clearly, ATF juveniles are habitat generalists and utilize benthic habitat extensively throughout the GOA, from east to west. It is noteworthy that the assessment of connectivity patterns by the IBM between spawning and settlement areas was improved significantly by expanding the definition of nursery habitat to include bottom depths down to 150 m. This is relevant for future application of the IBM in understanding ATF recruitment processes.

The GAM models also support the characterization of newly settled juveniles as habitat generalists. Distribution of small ATF (≤ 100 mm) throughout the shelf is indicated, and some extension even into deep water over the slope. Older juveniles and all size categories of adults are also shown to be ubiquitous, but the models indicate an association between highest densities and the middle and outer shelf domain (approximately 100 – 200 m), with expansion into slope water for fish larger than 300 mm. The significant effect of bottom temperature on densities implies some sensitivity to warming in terms of habitat utilization. Both the edges of the full distribution extent, as well as the core highest density areas, seem to contract into slightly shallower water overall during relatively warmer years, but mostly for the youngest (< 300 mm) and oldest (> 600 mm) fish. Given the overall ubiquity of multiple size groups of ATF across depth and temperature ranges, it is unlikely that most age groups in the GOA are highly sensitive to temperature. Some sensitivity is apparent but it is likely that bottom temperatures within the GOA would have to increase substantially in order to cause a significant latitudinal shift overall. Less clear, however, is the indirect effect of temperature on the population via potential changes in ecosystem productivity and food availability. Beyond the potential effects on distribution and survival of juveniles and adults, direct and indirect temperature effects on the larval phase are likely to be more immediate and drastic especially on early ontogeny survival as outlined above.

The habitat modelling work further refines our understanding of habitat utilization (this study, and Pirtle et al., 2017). The early juvenile stage models had the best fit, likely due to increased ubiquity across the shelf and over the slope for older fish. The effectiveness of the adult stage model in determining the most suitable habitat is reduced because older ATF are essentially everywhere. Despite such ubiquity, the top habitat predictor variable for all ATF demersal life stage models was depth. This was in contrast to the absence of depth from the Wilson et al. (2016) predictive models for juvenile ATF habitat, but the latter study was dealing with a much more geographically limited sampling area which did not include the nearshore zone. Habitat occurrence for all stages including newly settled fish is limited in the shallow areas, especially in the interior of bays or along the shore within the intertidal zone, although fish can be abundant in the deepest channels and at bay entrances. Further, as indicated by the habitat suitability maps, early juvenile stage habitat is also less likely to occur in the deepest areas of the shelf, such as Shelikof Strait, or over the continental slope. A clear ontogenetic shift in depth distribution occurs for ATF between younger and older juvenile fish, presumably due to an expansion in distribution from areas of initial settlement. There is also a decrease in the relative importance of fine-scale habitat features (e.g., substrate type, rocks or not, presence of invertebrate structure or not) with age. The presence or location of large-scale seafloor terrain features as described by bathymetric position index, like the gullies, flats, and to some extent the banks were important habitat predictors in all of the demersal life stage models. It also seems that fine-scale characteristics may have some moderating effect on habitat suitability. For instance, results suggest that nursery habitat suitability may be enhanced by substrate characteristics offshore of the glacial bays (Icy, Yakutat) and large rivers (Copper), including presence of unconsolidated, fine-grainsize sediments. Nutrient enrichment in association with freshwater runoff may contribute to increased prey resources in these areas, at least in the benthos.

The flexible, opportunistic trophic ecology of ATF is consistent with its characterization as a habitat generalist. Even though they occupy benthic habitat from the juvenile stage through maturity and senescence, most of their diet by weight is from the pelagic component of the ecosystem. Newly settled and early juveniles feed primarily on zooplankton, with Euphausiids and copepods being a major component. Throughout its range, the food habits of juvenile and adult ATF indicate that it is an opportunistic predator of locally abundant schooling fishes, Pandalid shrimp, and Euphausiids. Although species may differ among regions, studies in the California Current system (Gotshall, 1969; Buckley et al., 1999), British Columbia (Kabata and Forrester, 1974), the Aleutian Islands (Yang, 1996) and eastern Bering Sea (Yang and Livingston, 1986; Yang 1991; Livingston et al., 1993; Lang et al., 2005) indicate the importance of these general prey groups. The ontogenetic diet pattern shown here, aggregating over two decades of stomach contents data from the GOA, indicates a shift from Euphausiids (zooplankton), small fishes (Capelin and other Osmerids) and Pandalid shrimp (Decapods) to subsequently larger fishes like Pacific Herring (Clupeids), Walleye Pollock, and flatfishes (Pleuronectids). Similar patterns are evident in other areas where ATF diets have been studied (Buckley et al., 1999; Yang 1991; Livingston et al., 1993; Lang et al., 2005), and the sizes of each prey species may increase with ATF size as it does for Pacific Herring and Walleye Pollock (Yang et al., 2006). The pattern of increasing prey size and piscivory with increasing predator size is common among fishes due to the increase in swimming speed and/or in gape size of the predator (Mittelbach and Persson, 1998). ATF exhibit flexibility in their feeding behavior in the GOA and consume species that are characterized by relatively high temporal and spatial variability in abundance (Yang and Nelson, 2000; Knoth and Foy, 2008). Many of the schooling fish that comprise the majority of the ATF diet are pelagic zooplanktivores, conferring the dominance of pelagic energy sources to ATF of all sizes. Although the proportion of benthic Decapods in the diet decreases with increasing ATF size, Pleuronectids and other fish species are important benthic energy sources of larger ATF. Thus, both pelagic and benthic energy inputs have been factored into the trophic modelling of ATF (Aydin et al., 2007), and stable isotope analysis confirms the reliance of ATF on energy from both pelagic and benthic sources (Marsh et al., 2012). The omnivorous and opportunistic feeding ecology of ATF likely confers a significant advantage in terms of achieving and maintaining a dominant status in the GOA ecosystem, as well as resilience to ecosystem shifts.

Ontogenetic variability in habitat utilization by ATF is also reflected in predation patterns on this species in the GOA. Walleye Pollock is the dominant predator on ATF < 30 mm with diminishing predation on subsequent size groups, and Pacific Ocean Perch also features as a predator on juveniles. When benthic settlement is more fully established, juveniles larger than 30 mm through adults less than 400 mm seem to be consumed predominantly by Pacific Cod with Pacific Halibut also increasing in importance. As predation mortality is low overall for ATF in the GOA, it’s interesting to speculate regarding the potential for such mortality to increase significantly if populations of Pacific Cod or Pacific Halibut should increase to a point where they would have a negative influence on ATF production. However, the frequency at which ATF are found in their stomachs is low; 0.8% and 1.1%, respectively. A consistent pattern of consumption by ATF itself across all size groups except fish > 400 mm implies that cannibalism may be a density-dependent control mechanism, but again the overall frequency is low (0.5%). Nevertheless, the prevalence of ATF juveniles and immature fish throughout a wide variety of benthic habitat in this region makes them a more abundant potential food source than the young of many other groundfish species.

4.3. Gauging sensitivities and potential response of Arrowtooth Flounder populations in the Gulf of Alaska to ecosystem change

The climate vulnerability assessment applied here yields a very low score for ATF, implying a high level of population resilience overall to climate-induced ecosystem perturbations in the GOA. Some vulnerability is hypothesized, however, primarily relating to the potential for exacerbated temporal mis-match between first-feeding larvae and availability of prey. The larval phase although ecologically robust relative to many other species ("endurance" strategy), could theoretically represent a recruitment "bottleneck" under certain environmental scenarios. For instance, variability in production and availability of suitable larval prey resources in the zooplankton, as influenced by water temperature or other environmental factors could significantly disrupt ATF larval survival, especially during the winter first-feeding stage. Expected variability in larval growth rates in response to water temperature is also relevant to such match/mis-match trophic dynamics. A moderate to high vulnerability score seems appropriate in representing this complexity in the early life history strategy of ATF. As mentioned above, the *Neocalanus* species of copepods may play some critical trophic role in this regard, and it is worth investigating further (Doyle and Mier, 2016). Susceptibility to variable larval transport onto the shelf (Stachura et al., 2014), and presumed sensitivity to ocean acidification via crustacean zooplankton prey (Busch and McElhany, 2016) are considered low to moderate vulnerability factors for ATF larvae. The apparent sensitivity to temperature observed among early juvenile (<49 cm) fish suggests the possibility for some limited distribution contraction with warming in the GOA. ATF juveniles and adults are observed to be prey generalists with highly adaptable feeding behavior which also presumably confers ecological resilience.

Expansive availability of nursery habitat to ATF in the GOA has likely contributed to its numerical dominance, but there are likely upper limits to this availability. Unlike other deep water spawning flatfish such as Pacific Halibut, whose larvae must reach nearshore nursery grounds to settle out of the plankton, ATF it seems may settle to the benthos across broad areas of the GOA from the coastal zone and across the entire shelf to deep water. The nursery size hypothesis for flatfish proposes that mean recruitment is related to, and can be constrained by, the areal extent of suitable seafloor habitat for growth and survival of juveniles with density-dependent population control at play (Rijnsdorp et al., 1992; Van der Veer et al., 2000). The extensive utilization of seafloor across depths by ATF seems to be somewhat of an anomaly among pleuronectid flatfish in general. Most flatfish species are characterized by a more narrow spatial and bathymetric extent of suitable nursery habitat, and the concentration of juveniles in benthic habitat post settlement is thought to constrain (density-dependent effect) the amplitude of variation in recruitment relative to other non-flatfish species (Gibson et al., 2015). Wilson et al. (2016) found a positive relationship between mean recruitment at age 3 for four flatfish species and percent occurrence of their age-0 juveniles on the western GOA shelf during autumn 2011, with ATF recruitment and station occupation higher by several orders of magnitude than for the other species. They imply support for the nursery-size hypothesis in the GOA. As biomass increased constantly in the GOA over recent decades, it seems that nursery habitat for ATF was not likely to be a constraining factor. Broad geographic availability of suitable areas for settlement and growth, and a combination of plentiful pelagic and benthic prey resources and low predation mortality likely contributed to the continued expansion of the population. However, there must be some upper limit to this expansion, and especially if levels of juvenile survival push utilization of benthic habitat to some maximum threshold. Perhaps recent years of more limited recruitment and diminishing biomass could signal proximity to such a threshold? Further, as indicated by diet data, cannibalism of juvenile ATF by older ATF could provide some density-dependent constraints on survival rates of pre-recruit fish. Parasite infestation is another biological stressor that could potentially contribute to density-dependent control of the population. A common parasite of ATF, particularly at the southern end of its range is the eye parasite *Phrixocephalus cinncinnatus* (Copepoda Pennilidae). It seems to have grown in prevalence in the GOA in recent years in association with increased abundance of ATF (Buckley, pers. comm.). Such infestations could also be exacerbated if, as expected, the geographic range and transmission rates of such parasites increase with warming trends (Marcogliese, 2008).

The ecological mechanisms and stage-specific environmental sensitivities proposed here for the ATF population in the GOA can be evaluated in future modeling efforts that relate recruitment trends to ecosystem variability. They can also contribute to fisheries and ecosystem assessments and management efforts. This type of ecological evaluation is critical for the development of climate-based projections of fish stocks under different environmental scenarios, and has been recommended for accomplishing an ecosystem approach to fisheries management in U.S. fisheries ecosystems (Hare et al., 2016; Shotwell et al., 2017). The climate vulnerability assessment along with several other U.S. national programs are designed to set the stage for establishing research priorities for integrating ecosystem and habitat information within stock assessment. The initial evaluations for Alaska groundfish from these programs are an integral part of what is being termed a baseline Ecosystem and Socioeconomic Profile or EPS for assessed species (Shotwell et al., 2017). An ATF baseline EPS is currently in development for future use within the GOA ATF stock assessment and results from this synthesis are being used to enhance that baseline. Although ATF may be considered an endurance stock, the proposed vulnerable period in the early larval phase highlights potential prey and transport indicators that could be related to fluctuations in recruitment. These indicators are collected in a report card which is part of the EPS process and evaluated for future integration within the ATF stock assessment model. Given the ecological importance of ATF in the GOA, the broad synthesis presented here can also contribute to the development of an effective Integrated Ecosystem Assessment (Levin et al., 2014) for this marine ecosystem. Finally, this comprehensive ecological approach to assessing environmental sensitivities across life history stages for commercially and ecologically important fish species has substantial merit for furthering the ecosystem approach to fisheries management globally, especially where there are robust sampling programs across trophic levels in marine ecosystems.

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Figure Captions

Figure 1. Gulf of Alaska showing coastal geography, bathymetry, features of interest, and prevailing surface currents as described in Stabeno et al. (2004).

Figure 2. Arrowtooth Flounder sub-ontogenetic intervals by size and month during the early life history planktonic phase, based on Gulf of Alaska historical ichthyoplankton data, and Blood et al. (2007).

Figure 3. Age-0 pelagic Arrowtooth Flounder distributions from small-mesh surface trawls by the Alaska Fisheries Science Center (GOA-IERP surveys 2010, 2011, and 2013).

Figure 4. Length-frequency distributions for Age-0 Arrowtooth Flounder from GOA caught during summer surface trawls; panels a. to f. correspond to panels in Figure 4.

Figure 5. Simulated growth curve fitted to larval length (SL) by Julian Day; data from GOA-IERP spring ichthyoplankton and summer small-mesh surface trawl surveys.

Figure 6. Selected outcome from the ATF early life history IBM (Stockhausen et al., accepted) run for the year 2011 showing locations of “successful” (yellow circles) and “unsuccessful” (red circles) simulated individuals at the end of four early life stages when “successful” is defined by ultimate settlement in nursery habitat defined by 0-150 m depth

Figure 7. Selected outcome from the ATF early life history IBM (Stockhausen et al., accepted) run for the year 2011 showing a. the fraction of individuals for each spawning area of origin (Fig. 2 SM) successfully settling in 0-150 m nursery areas anywhere in the model domain, and b. the average alongshore zone, by spawning area, to which successful individuals settled.

Figure 8. Distribution and size composition of juvenile (<100 mm TL) Arrowtooth Flounder during October 2011 in the vicinity of Kodiak Island, sampled on the bottom with beam trawl (a and c), and in the water column with the anchovy trawl (b and d).

Figure 9. Diel variation in catches of Arrowtooth Flounder juveniles during the October 2011 survey in the western GOA in a. the bottom trawl, and b. the pelagic trawl.

Figure 10. Isolines of deviations from the mean a. probability of occurrence (ln [p/(1-p)]) from the binomial model and b. log density (tons nm^{-2}) from the log gamma model, due to location [s(LAT,LON)] for Arrowtooth Flounder, based on groundfish surveys 1984-2015.

Figure 11. Generalized Additive Modeling results showing: a. Year effect, and b. Size Bin (mm) effect on Arrowtooth Flounder distribution from the binomial models (i) and the log gamma models (ii). Changes in the Year effect values indicate both changes in distribution and changes in sampling methodology from year to year and can’t be interpreted directly as annual ecological effects. Changes in the Size Bin

effect values indicate changes in survey selectivity, Arrowtooth Flounder availability, and population abundance at length. Size Bins are: 0 = 0<100 mm, 100 = 100<200 mm etc., and 600 = >600 mm.

Figure 12. Prediction of 2009 Arrowtooth Flounder density (no. km^{-2}) at 56° N latitude and 155° W longitude from the Delta-log gamma model for all GOA bottom trawl survey data 1983-2015 for seven length bins by bottom depth (m) and bottom temperature (°C).

Figure 13. Prediction of Arrowtooth Flounder density (no. km^{-2}) at 56° N latitude and 155° W longitude from the Delta-log gamma model for GOA bottom trawl survey data; a. 2001 density using warm years (1984, 1987, 1990, 1993, 2001, 2003, 2005, and 2015), and b. 2009 density using cold years (1996, 1999, 2007, 2009, 2011, and 2013) for seven length bins by bottom depth (m) and bottom temperature (°C).

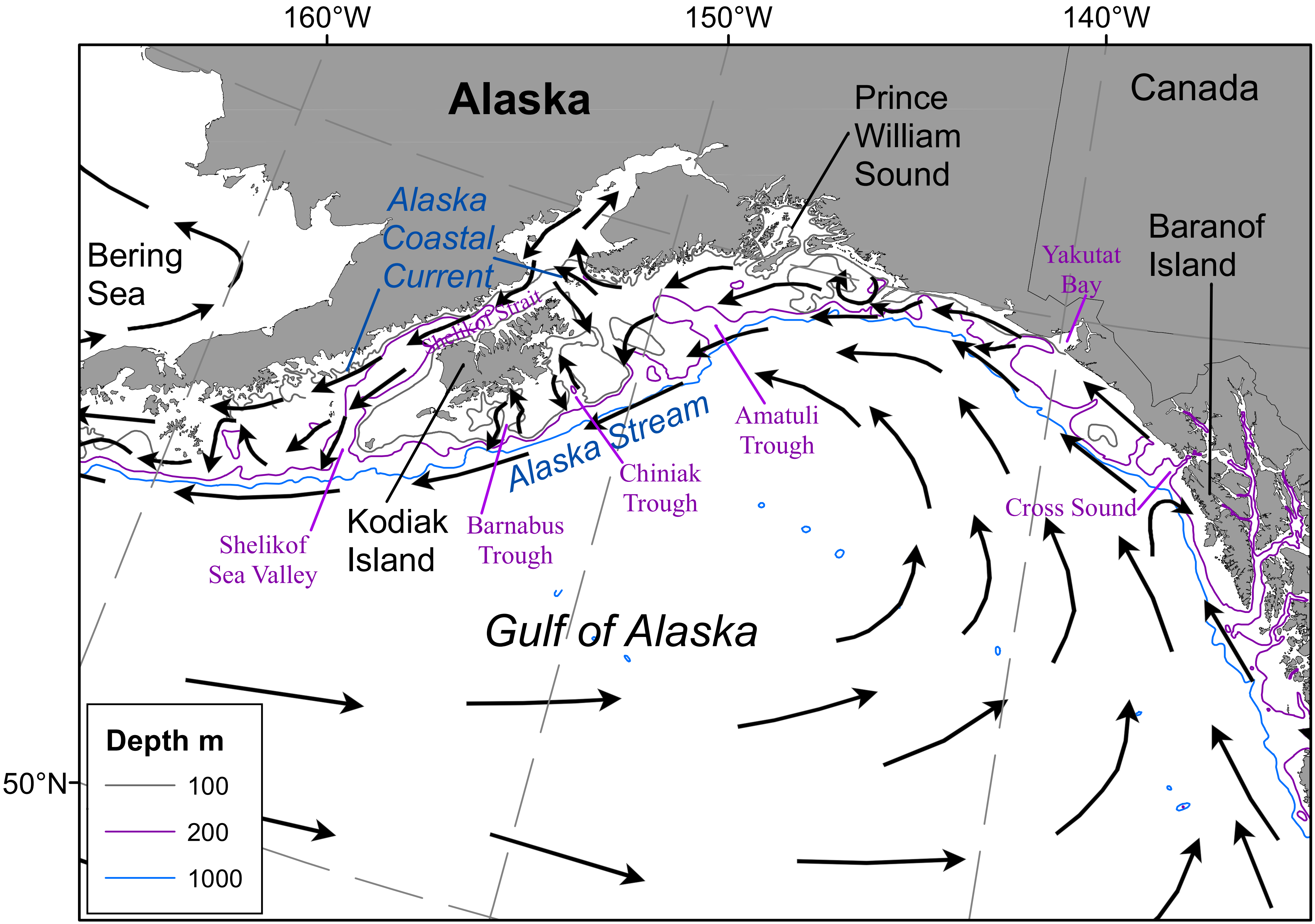
Figure 14. Arrowtooth Flounder mean habitat suitability from the mosaic models (MaxEnt HSM; Pirtle et al., in press), based on presence locations for different size groups of fish: a. Demersal settlement through early stage juveniles (40-160 mm) resident in presumed nursery areas; b. Late juvenile stage (161-350 mm), and c. Adults (>350 mm). Predicted probability of suitable habitat is shown on a continuous scale where highest suitability is yellow and lowest suitability is blue. Insets show detail for the continental shelf and bays on the northeast of Kodiak Island.

Figure 15. Composition of Arrowtooth Flounder diet weight for different size categories of fish, based on stomach content analysis of specimens from groundfish surveys in the Gulf of Alaska. *See Materials and Methods section 2.2.6. for explanation of these prey categories.

Figure 16. Predation on different size categories of Arrowtooth Flounder by fish predators in the Gulf of Alaska, based on stomach content analysis of fish from groundfish surveys. The number of Arrowtooth Flounder identified from stomach contents is shown at the top of each column. Sample sizes for each predator, and percent frequency of occurrence of Arrowtooth Flounder prey is shown in parentheses for each predator.

Figure 17. Total predation by groundfish predators on small Arrowtooth Flounder (< 100 mm) by month. Sample size (in parentheses) for September through May are low because groundfish surveys are conducted primarily during summer months.

Figure 18. Conceptual model of Arrowtooth Flounder ontogeny and habitat utilization in the Gulf of Alaska from the egg stage through metamorphosis and juvenile settlement.

160°W
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Alaska
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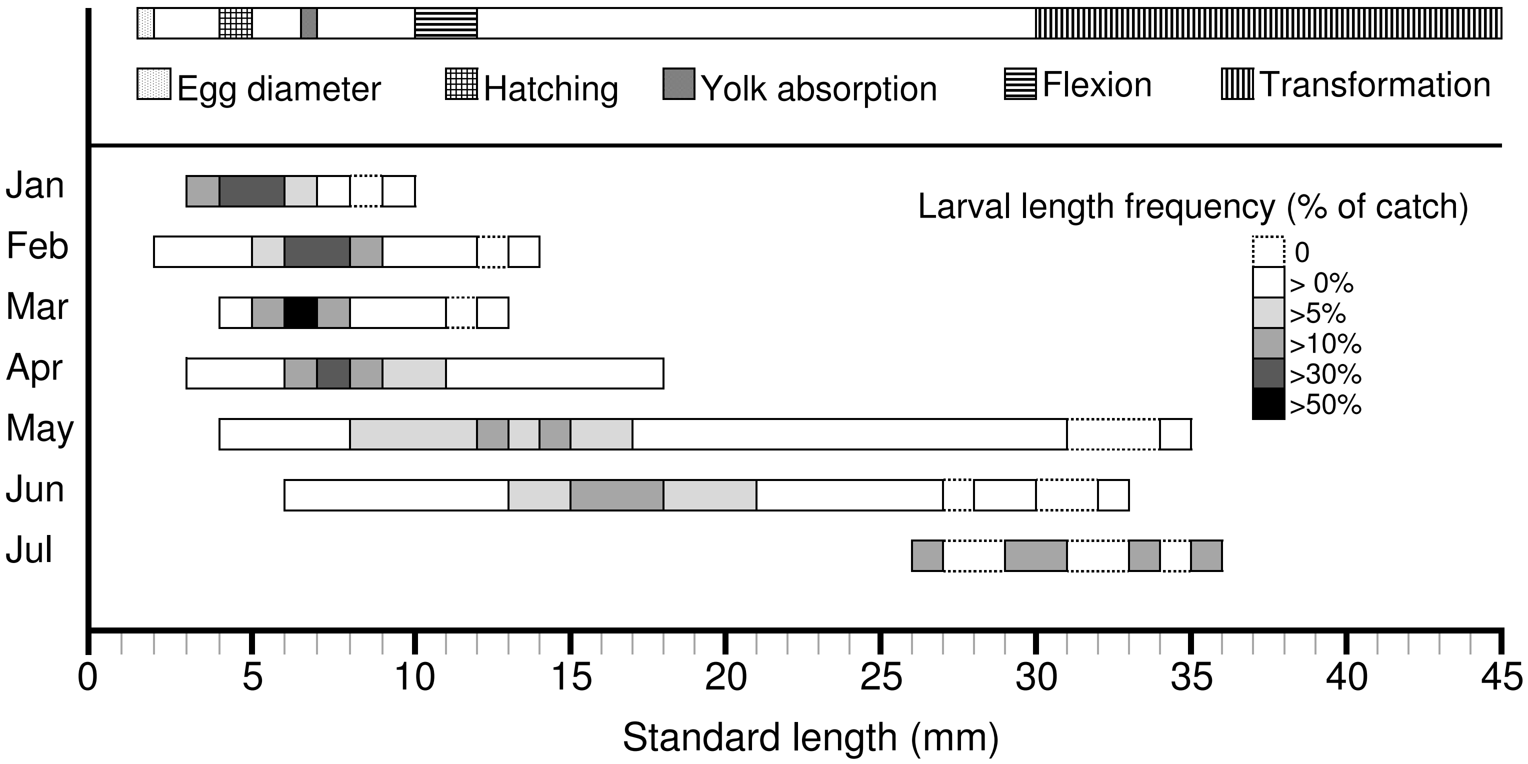
Egg diameter
Hatching
Yolk absorption
Flexion
Transformation
Jan
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Larval length frequency (% of catch)
0
> 0%
>5%
>10%
>30%
>50%
0
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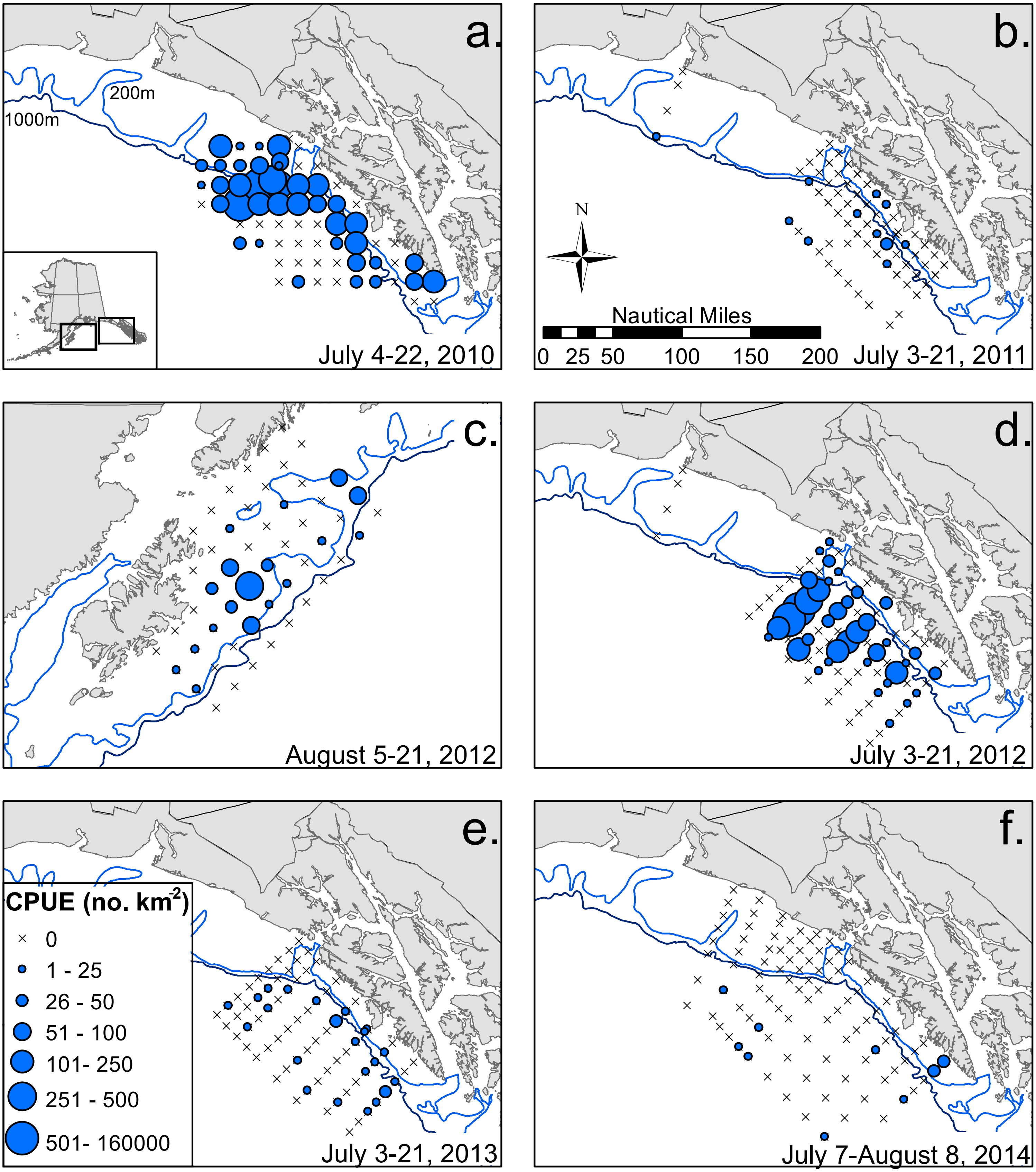
Standard length (mm)


a.
200m
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July 4-22, 2010
b.
N
Nautical Miles
0 25 50 100 150 200
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c.
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CPUE (no. km2)
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● 51 - 100
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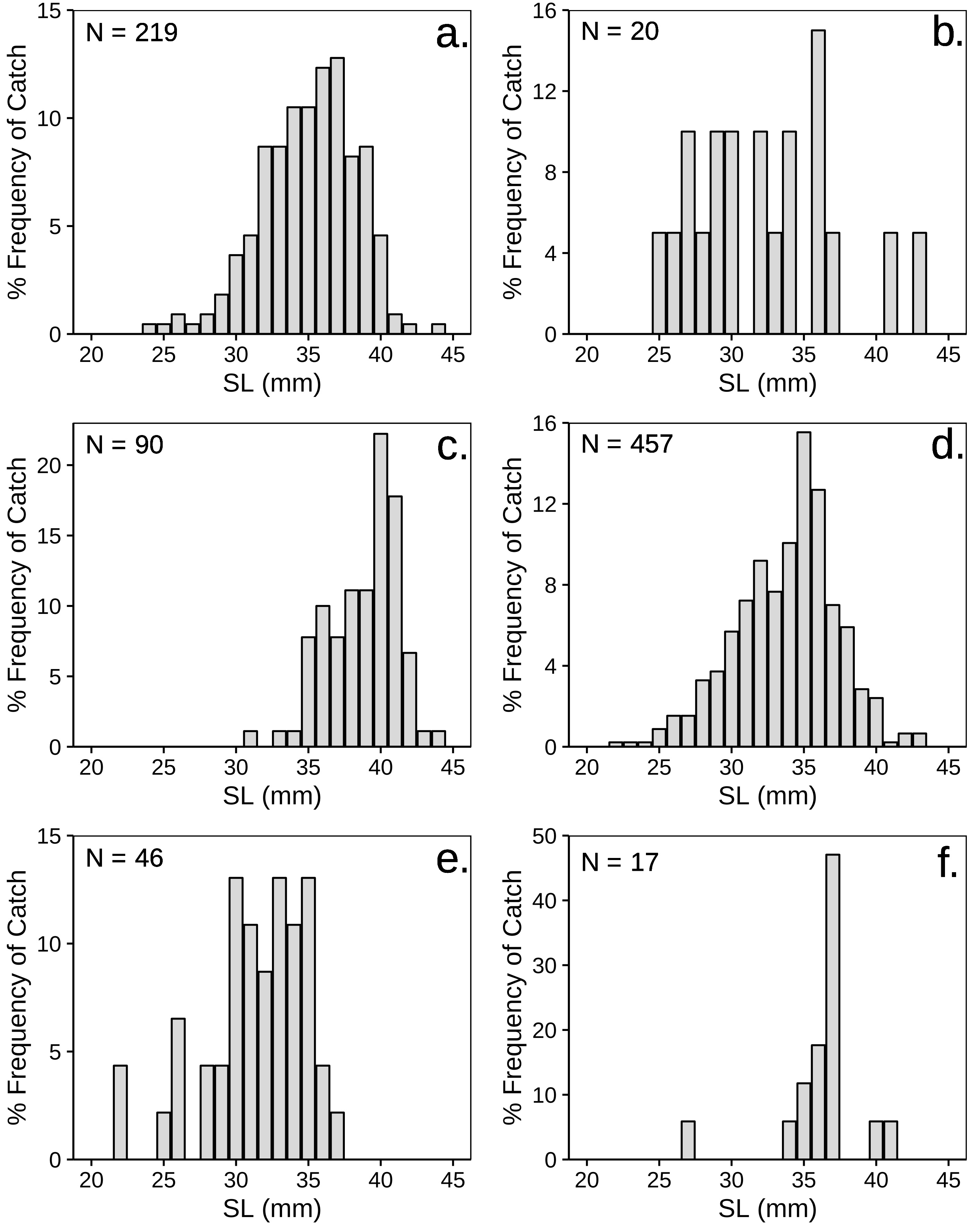
July 7-August 8, 2014


N = 219
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% Frequency of Catch
SL (mm)
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15
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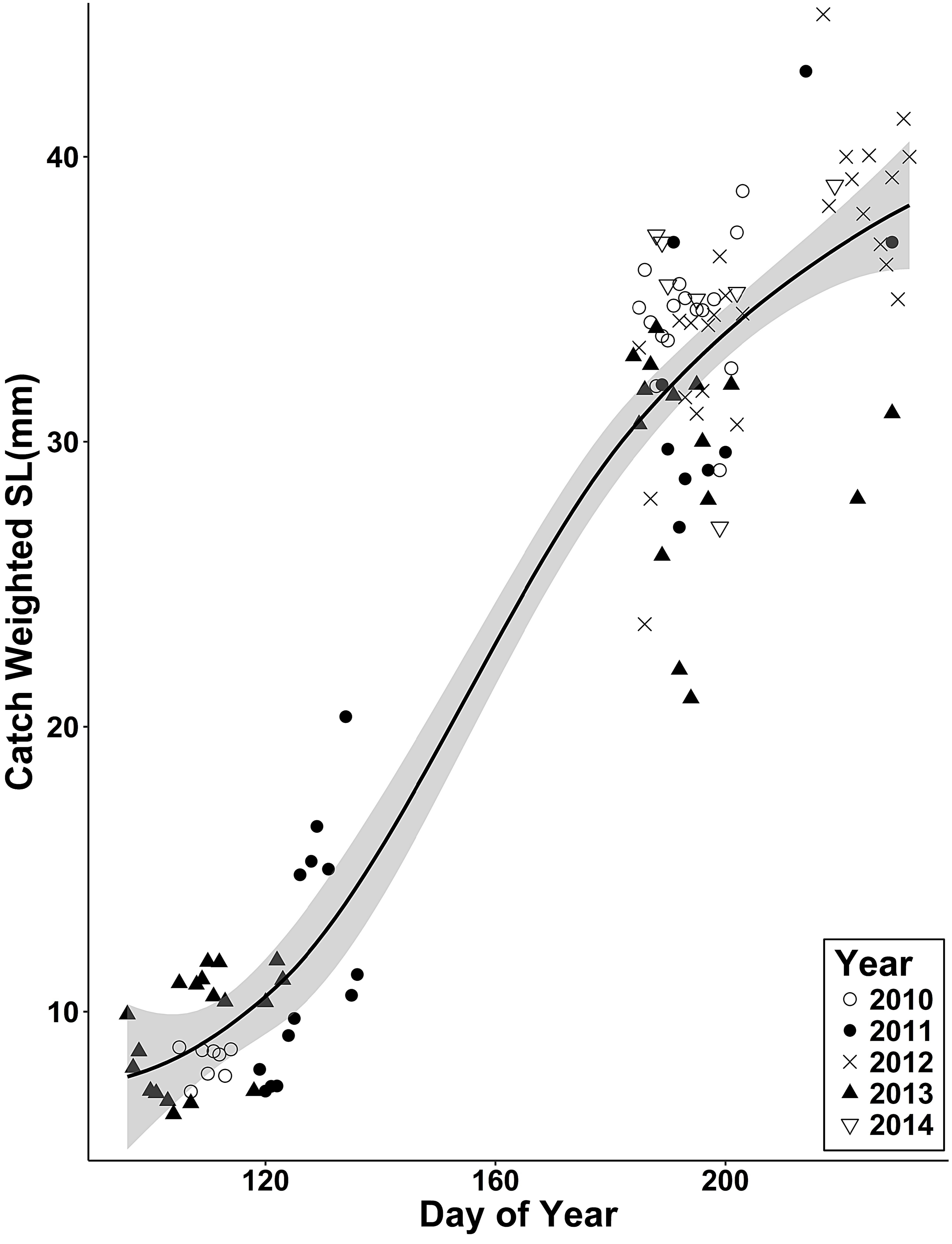
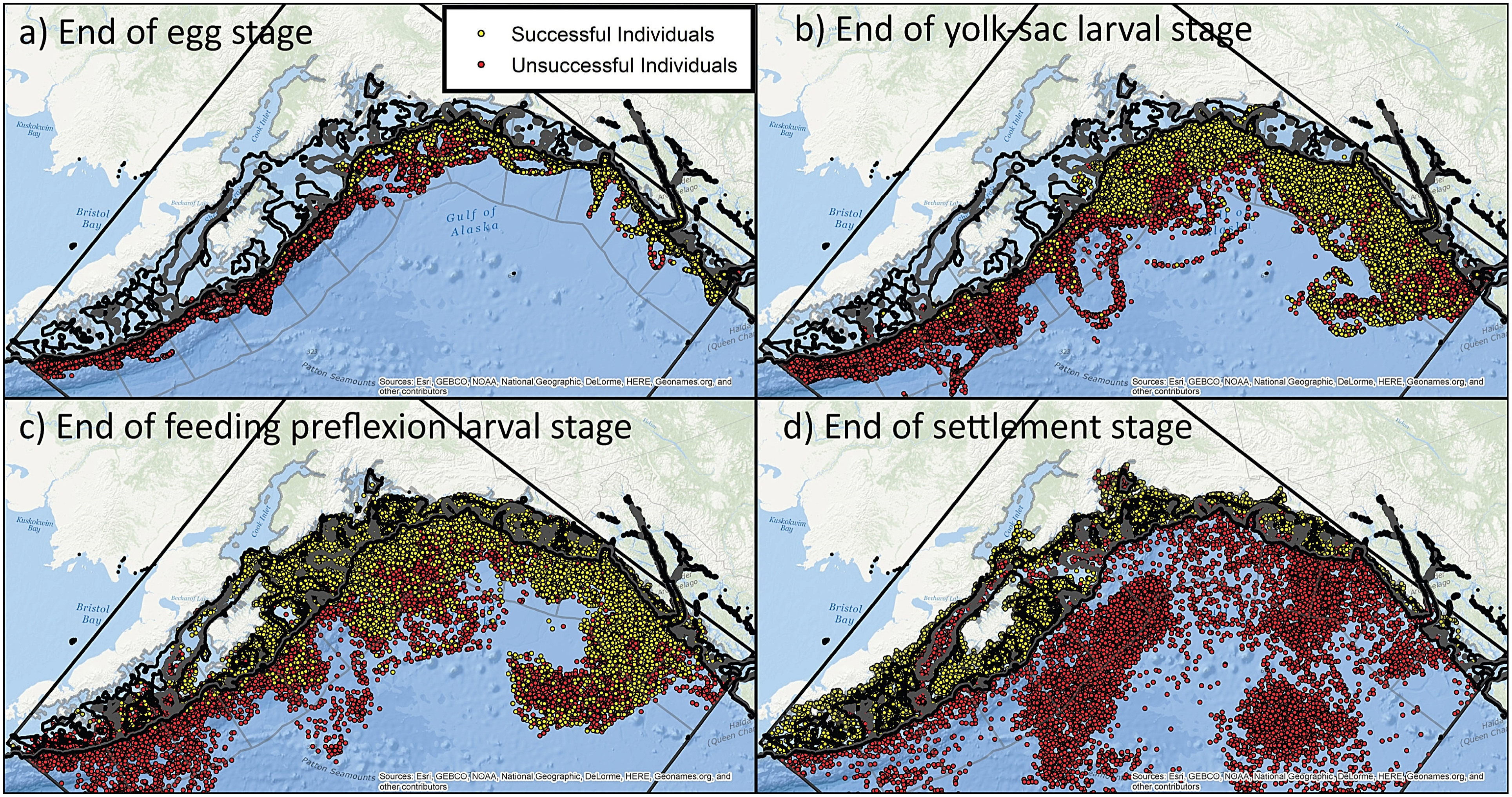
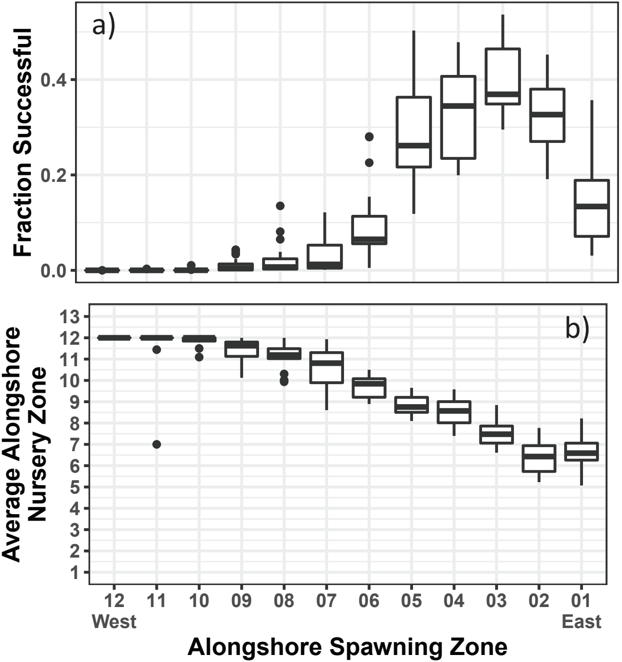
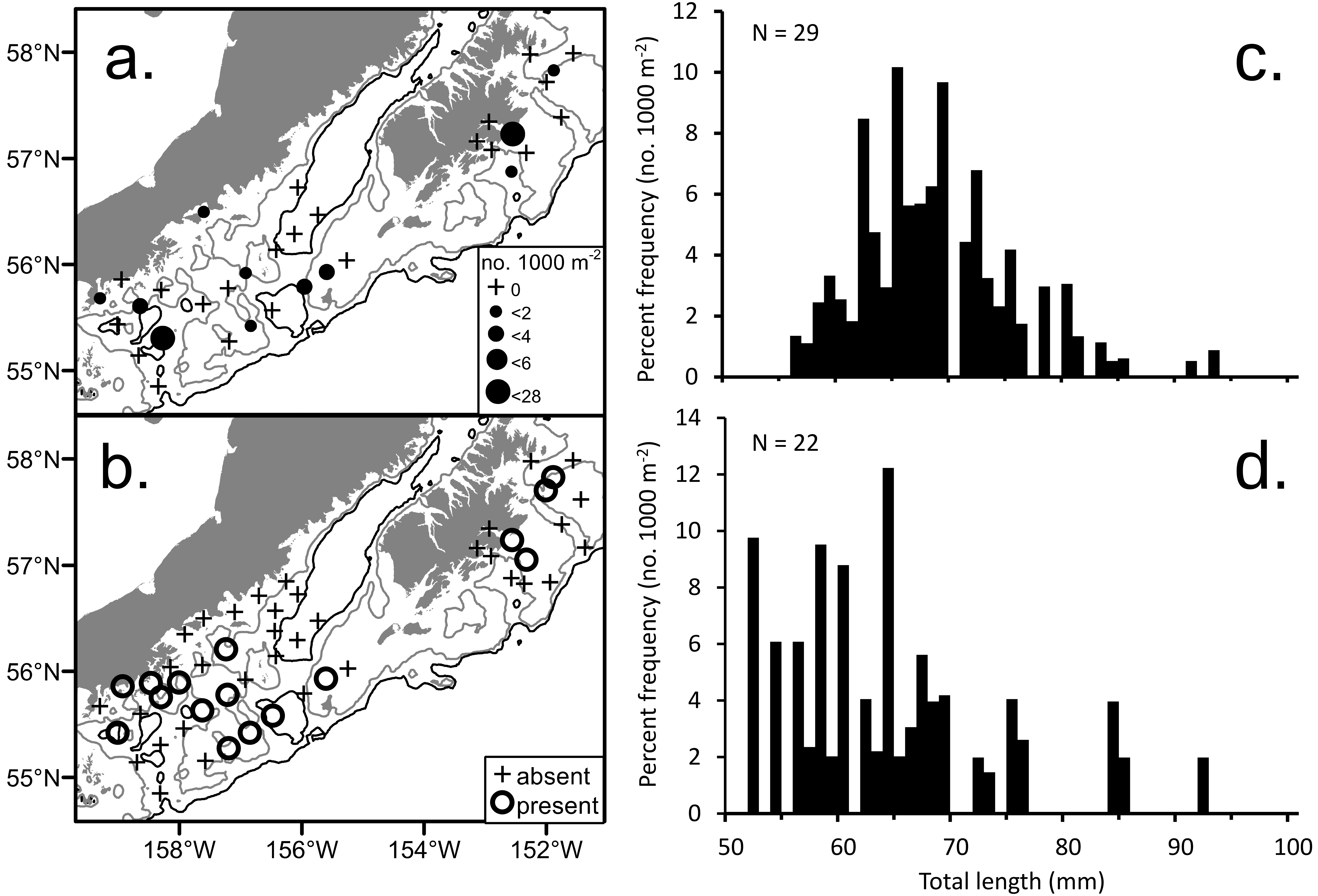
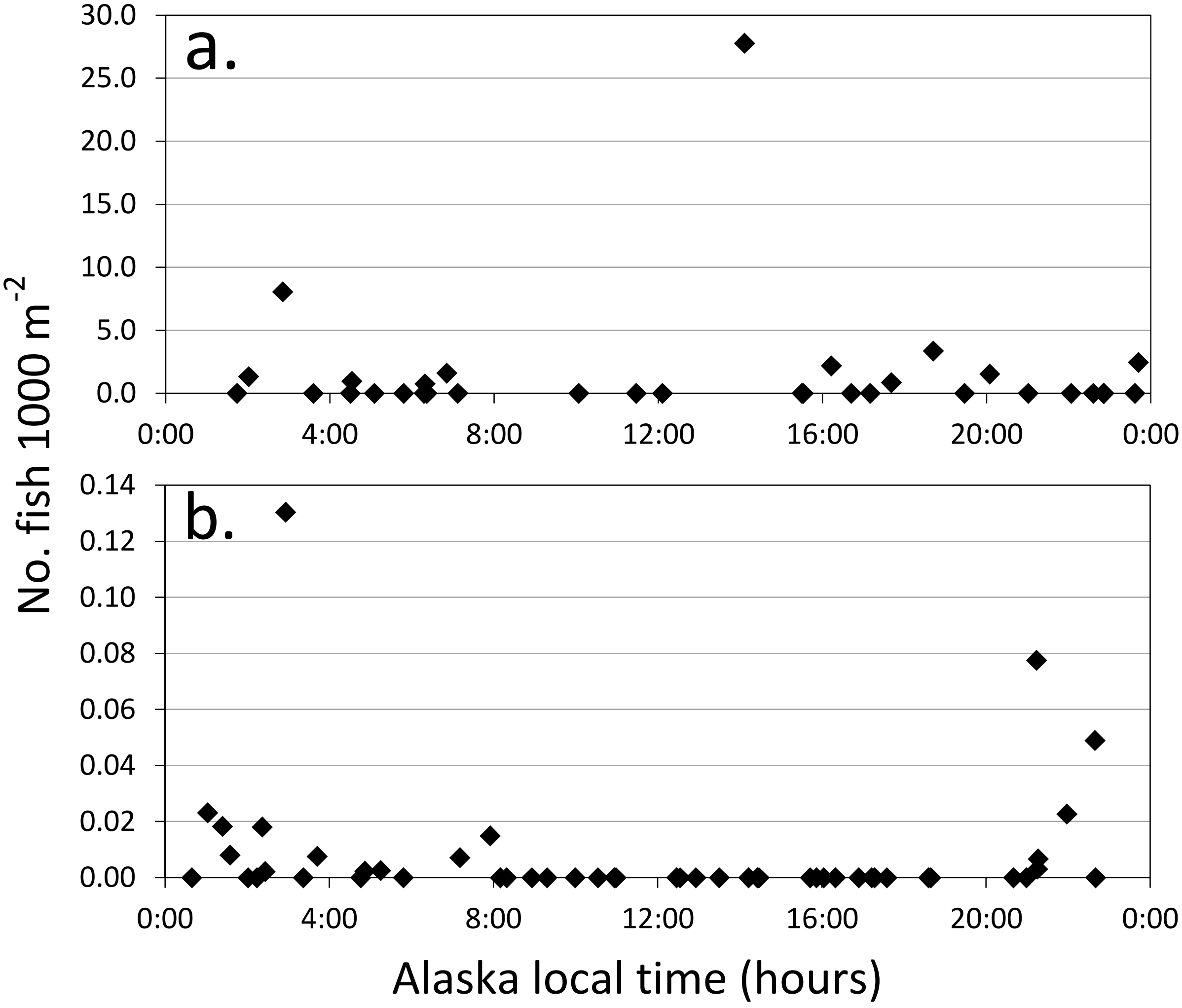
40
45

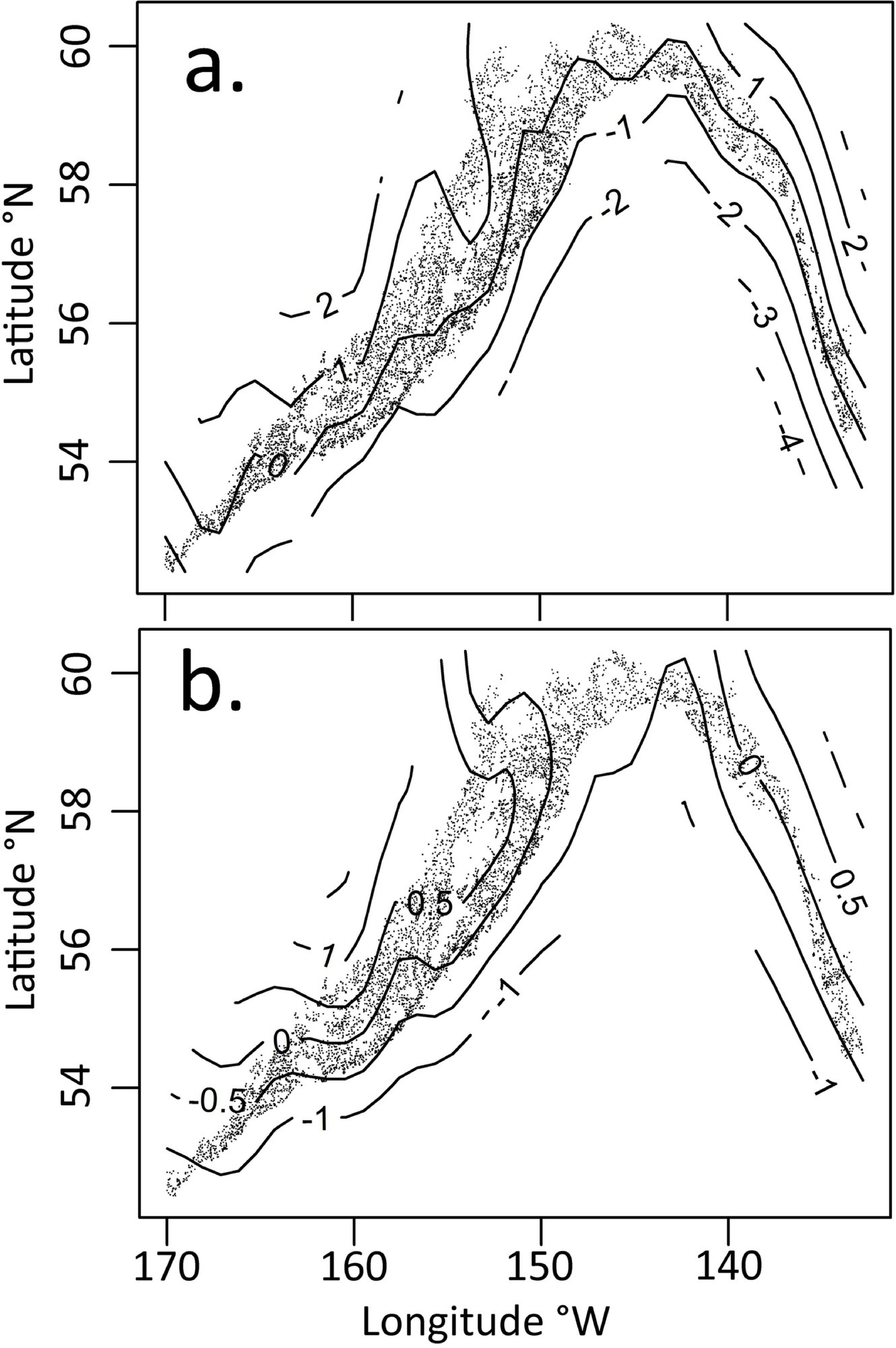

Catch Weighted SL(mm)
10
20
30
40
Day of Year
120
160
200
Year
○ 2010
● 2011
× 2012
▲ 2013
▽ 2014

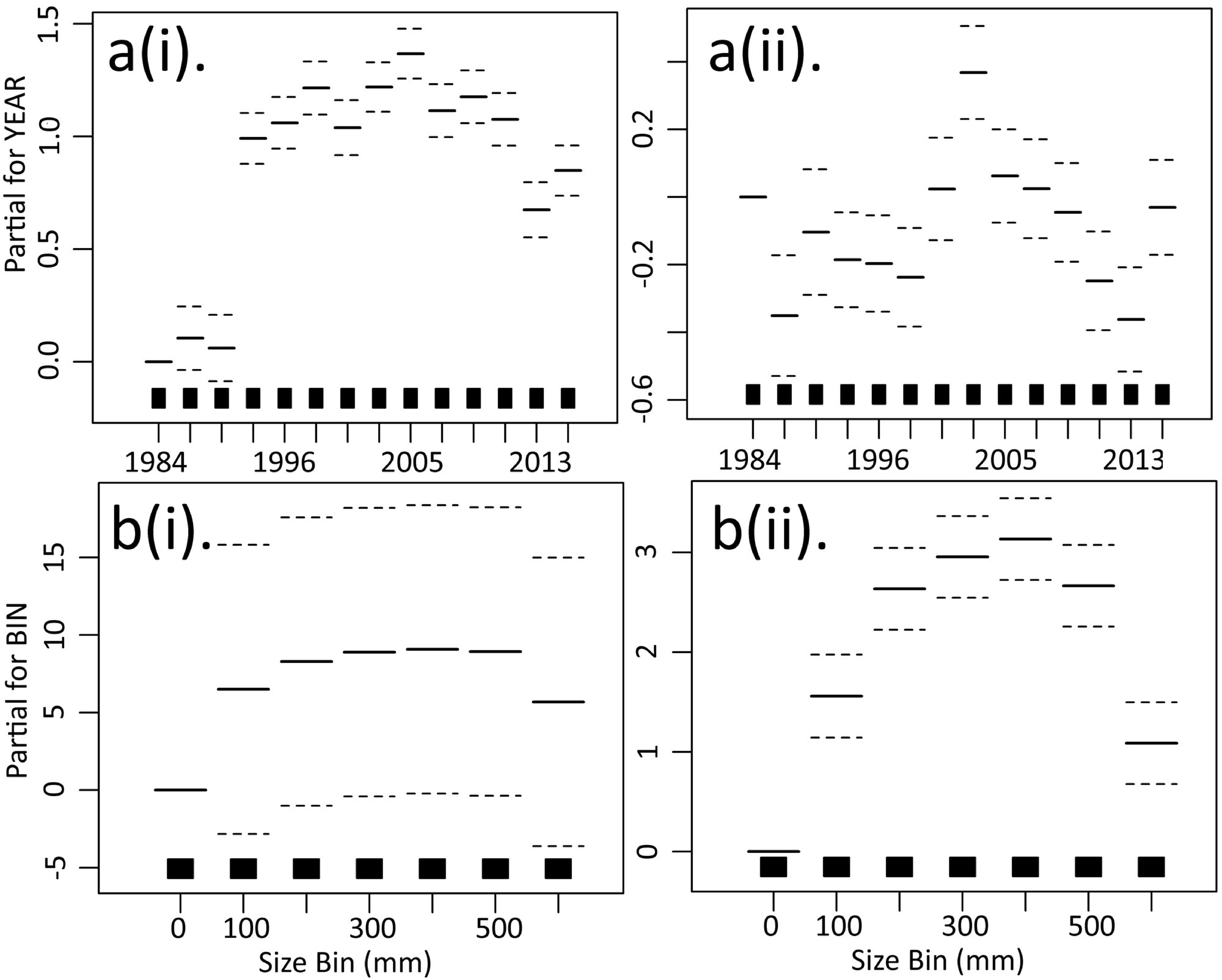

a) End of egg stage
Successful Individuals
Unsuccessful Individuals
b) End of yolk-sac larval stage
c) End of feeding preflexion larval stage
d) End of settlement stage
Kuskokwim Bay
Bristol Bay
Cook Inlet
Becharof Lake
Gulf of Alaska
Patton Seamounts
Haida (Queen Cha
Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors

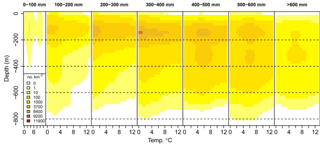

a)
Fraction Successful
0.0
0.2
0.4
b)
Average Alongshore Nursery Zone
1
2
3
4
5
6
7
8
9
10
11
12
13
12
11
10
09
08
07
06
05
04
03
02
01
West
East
Alongshore Spawning Zone

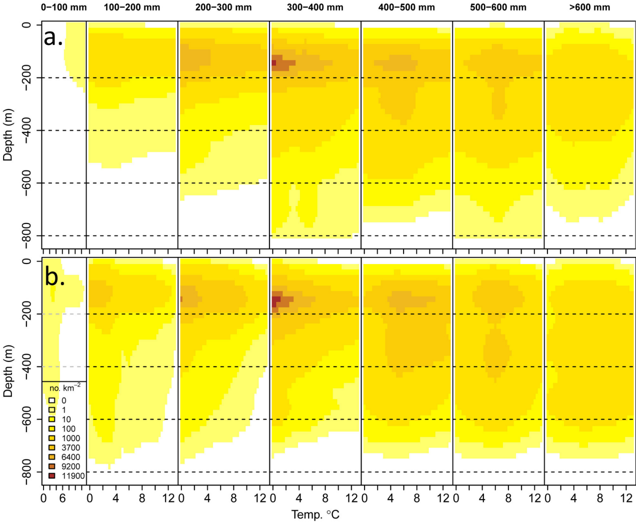

a.
b.
c.
d.
58°N
57°N
56°N
55°N
158°W
156°W
154°W
152°W
no. 1000 m^{-2}
+ 0
<2
<4
<6
<28
+ absent
○ present
N = 29
N = 22
Percent frequency (no. 1000 m^{-2})
Total length (mm)
0
2
4
6
8
10
12
14
50
60
70
80
90
100

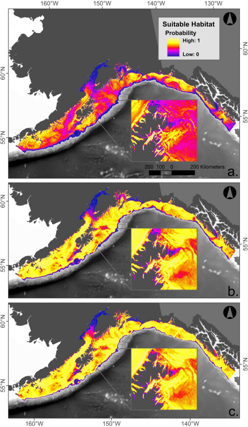

a.
b.
30.0
25.0
20.0
15.0
10.0
5.0
0.0
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0:00
4:00
8:00
12:00
16:00
20:00
0:00
No. fish 1000 m^{-2}
Alaska local time (hours)

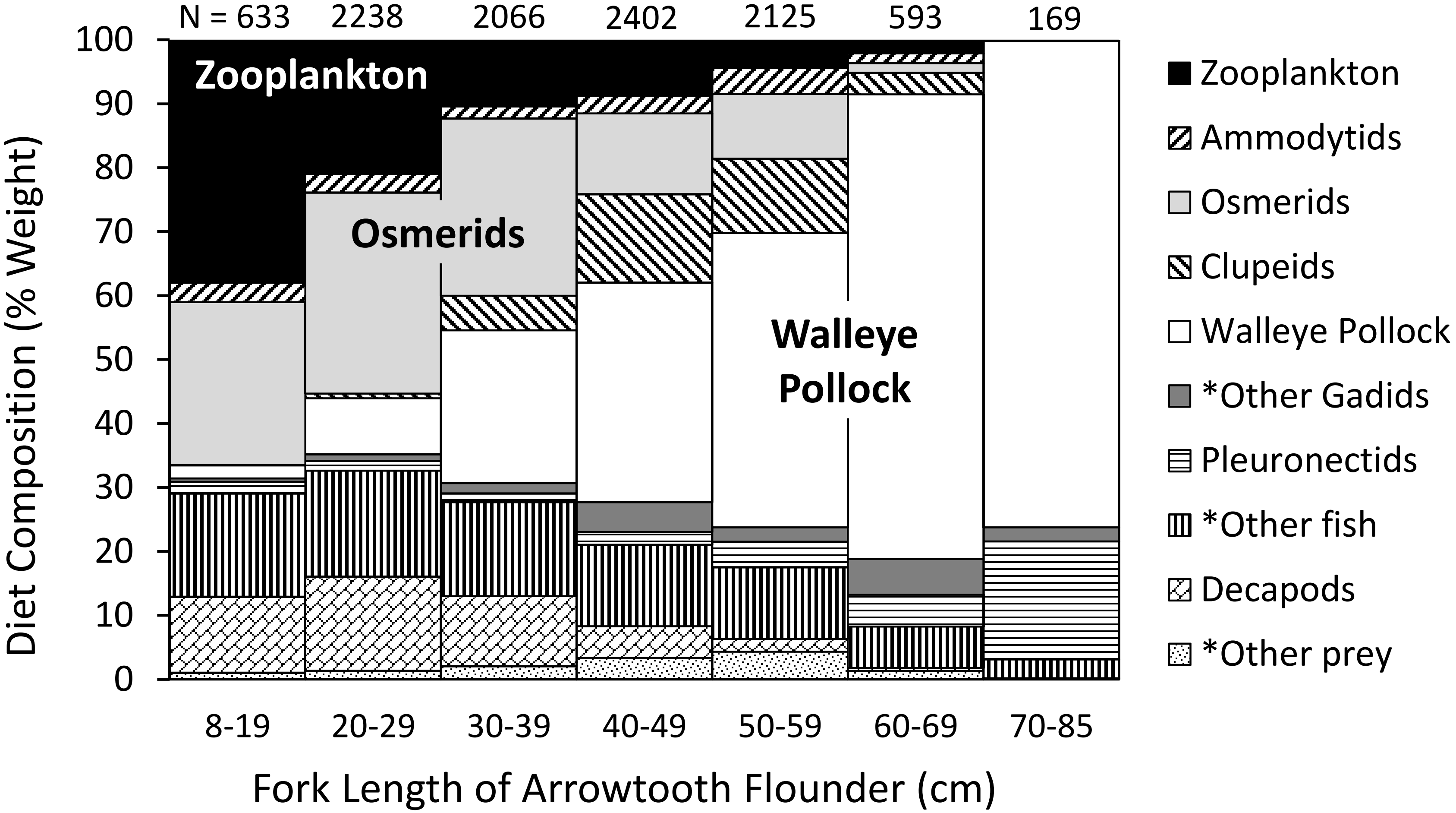

a.
1
-1
-2
-2
2
1
0
-3
-4
2
60
58
56
54
Latitude °N
b.
0.5
1
0
-0.5
-1
-1
0
0.5
-1
60
58
56
54
Latitude °N
170
160
150
140
Longitude °W

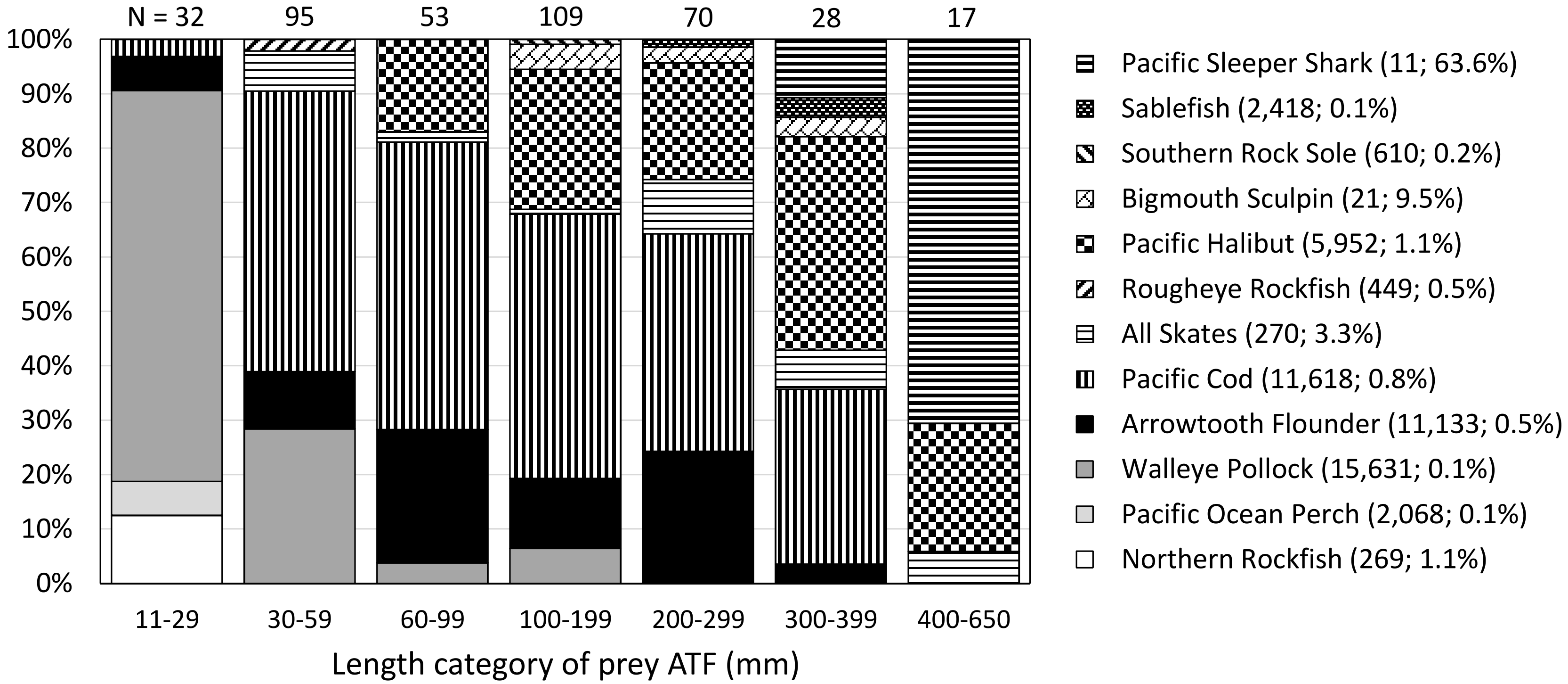

a(i).
a(ii).
b(i).
b(ii).
Partial for YEAR
Partial for BIN
1.5
1.0
0.5
0.0
0.2
-0.2
-0.6
1984
1996
2005
2013
15
10
5
0
-5
3
2
1
0
100
300
500
Size Bin (mm)
Size Bin (mm)

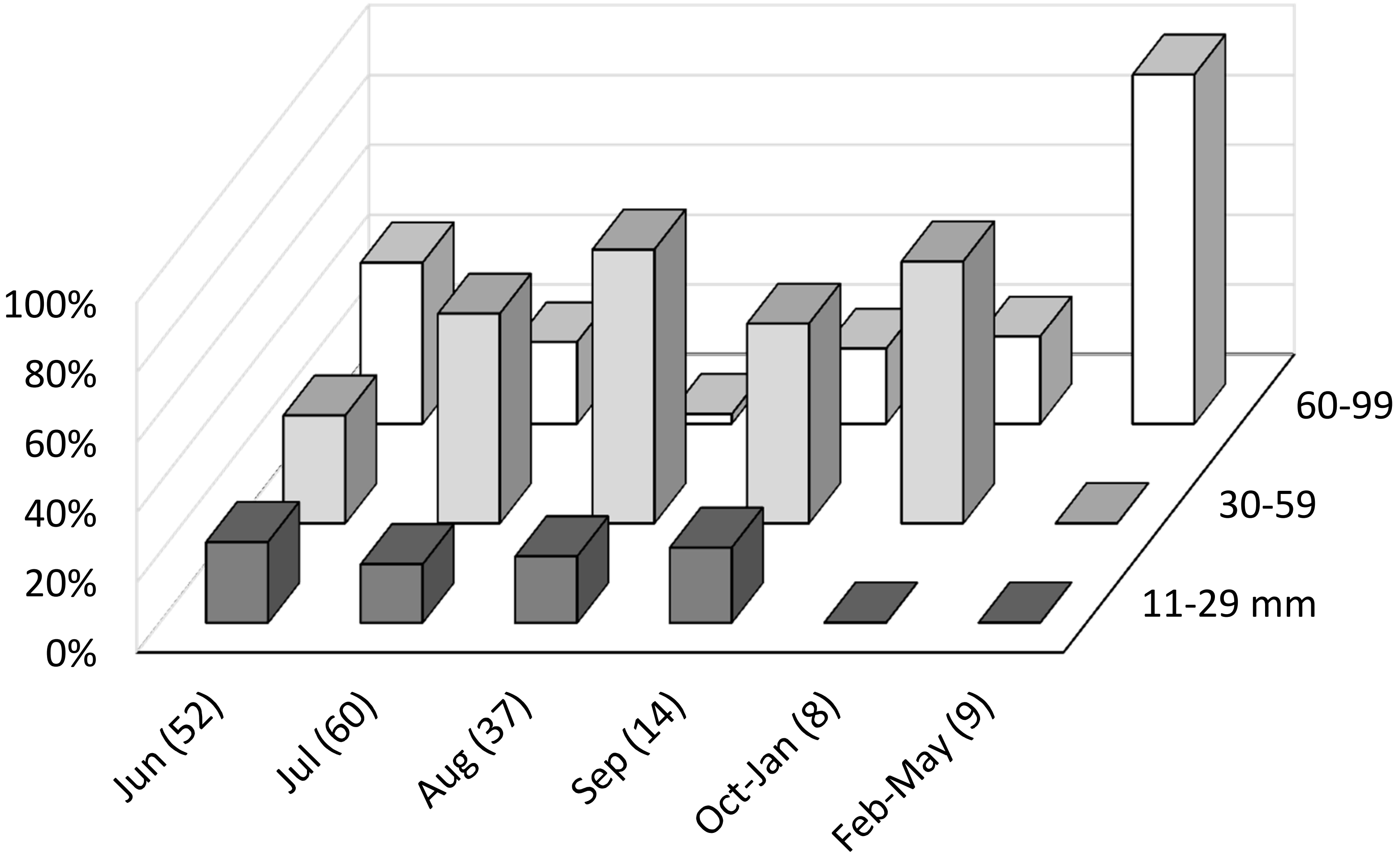

0–100 mm
100–200 mm
200–300 mm
300–400 mm
400–500 mm
500–600 mm
>600 mm
Depth (m)
0
-200
-400
-600
-800
no. km^{-2}
0
1
10
100
1000
3700
6400
9200
11900
0
6
0
4
8
12
Temp. °C


0–100 mm
100–200 mm
200–300 mm
300–400 mm
400–500 mm
500–600 mm
>600 mm
a.
b.
Depth (m)
0
-200
-400
-600
-800
Depth (m)
0
-200
-400
-600
-800
no. km^{-2}
0
1
10
100
1000
3700
6400
9200
11900
0
6
0
4
8
12
0
4
8
12
0
4
8
12
0
4
8
12
0
4
8
12
0
4
8
12
Temp. °C


160°W
150°W
140°W
130°W
Suitable Habitat
Probability
High: 1
Low: 0
60°N
55°N
200 100 0 200 Kilometers
a.
b.
c.


N = 633
2238
2066
2402
2125
593
169
100
90
80
70
60
50
40
30
20
10
0
Diet Composition (% Weight)
Zooplankton
Osmerids
Walleye Pollock
8-19
20-29
30-39
40-49
50-59
60-69
70-85
Fork Length of Arrowtooth Flounder (cm)
Zooplankton
Ammodytids
Osmerids
Clupeids
Walleye Pollock
*Other Gadids
Pleuronectids
*Other fish
Decapods
*Other prey

N = 32
95
53
109
70
28
17
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
11-29
30-59
60-99
100-199
200-299
300-399
400-650
Length category of prey ATF (mm)
Pacific Sleeper Shark (11; 63.6%)
Sablefish (2,418; 0.1%)
Southern Rock Sole (610; 0.2%)
Bigmouth Sculpin (21; 9.5%)
Pacific Halibut (5,952; 1.1%)
Rougheye Rockfish (449; 0.5%)
All Skates (270; 3.3%)
Pacific Cod (11,618; 0.8%)
Arrowtooth Flounder (11,133; 0.5%)
Walleye Pollock (15,631; 0.1%)
Pacific Ocean Perch (2,068; 0.1%)
Northern Rockfish (269; 1.1%)


100%
80%
60%
40%
20%
0%
Jun (52)
Jul (60)
Aug (37)
Sep (14)
Oct-Jan (8)
Feb-May (9)
60-99
30-59
11-29 mm

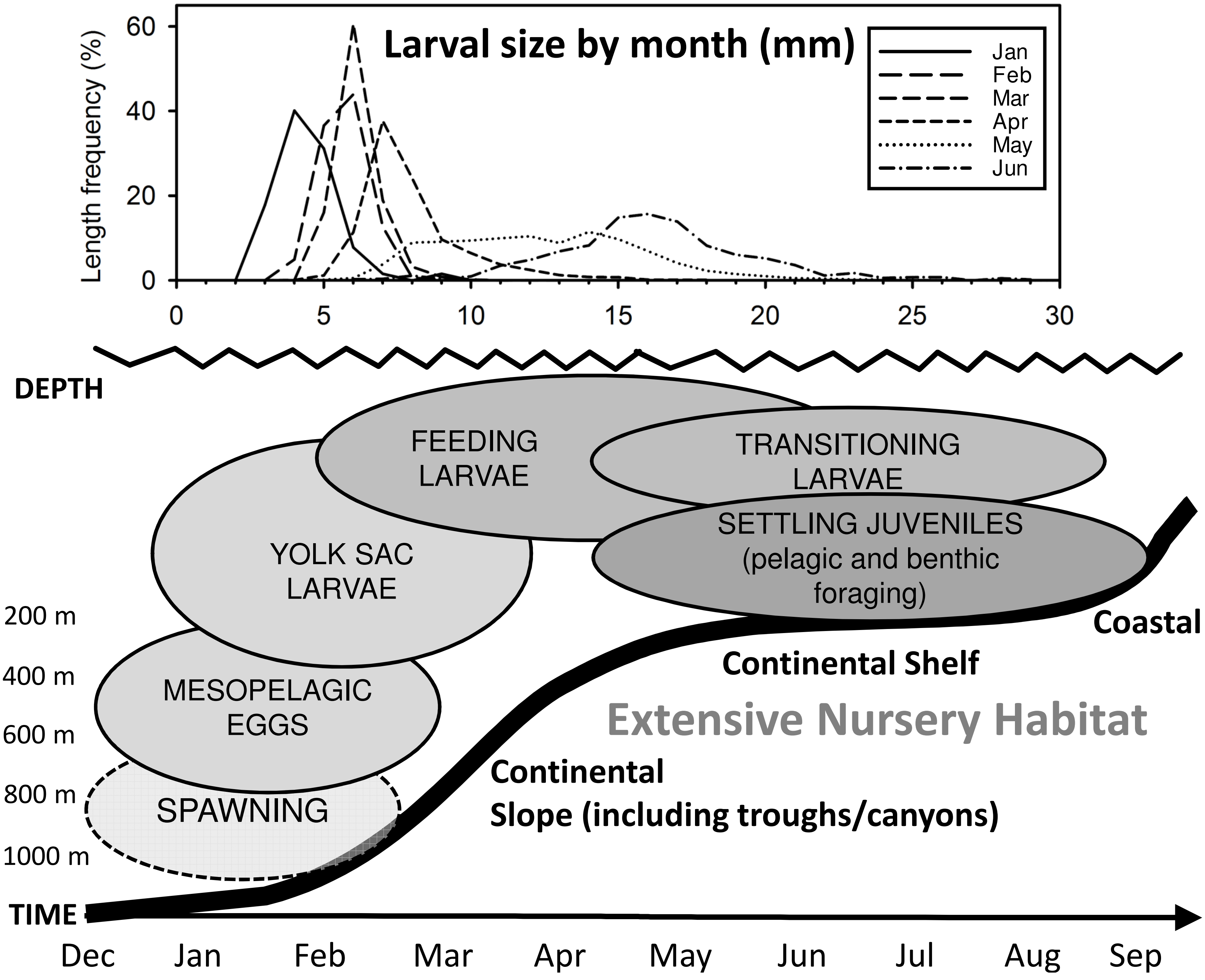

Larval size by month (mm)
Length frequency (%)
0
20
40
60
0
5
10
15
20
25
30
Jan
Feb
Mar
Apr
May
Jun
DEPTH
FEEDING LARVAE
TRANSITIONING LARVAE
YOLK SAC LARVAE
SETTLING JUVENILES (pelagic and benthic foraging)
MESOPELAGIC EGGS
SPAWNING
200 m
400 m
600 m
800 m
1000 m
Coastal
Continental Shelf
Extensive Nursery Habitat
Continental Slope (including troughs/canyons)
TIME
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep

Table 1. NOAA, Alaska Fisheries Science Center (AFSC) data sets used in this study for assessment of ecological patterns across life history stages of Arrowtooth Flounder in the Gulf of Alaska. For the purposes of this study, the division between eastern and western Gulf of Alaska is given as 145°W longitude.

Data Type	AFSC Surveys and areas	Seasonal Coverage	Years Sampled	AFSC Databases and Links to Program Research, Reports and Publications
Ichthyoplankton	EcoFOCI Ichthyoplankton surveys; 60 cm Bongo nets, shelf and slope waters; western GOA	Winter, Summer and Autumn, occasional years. Spring, all years.	1972, 1977-2011, 2013	Ichthyoplankton Information System (IIS): https://access.afsc.noaa.gov/ichthyo/index.php EcoFOCI website: http://www.ecofoci.noaa.gov/
Juvenile Fish	EcoFOCI Juvenile surveys; Small-mesh Midwater and Bottom trawls, shelf and slope waters; eastern and western GOA	Summer or Autumn	2010-2014	EcoDAAT data base, EcoFOCI website as above Ecosystem Monitoring and Assessment (EMA) website: http://www.afsc.noaa.gov/ABL/EMA/EMA_default.php NPRB-sponsored GOA-IERP website: http://www.nprb.org/gulf-of-alaska-project
Adult Fish	Groundfish Assessment Surveys; Bottom trawls, shelf and slope waters; eastern and western GOA	Summer	1984, 1987, 1990, 1993, 1996, 1999, 2001, 2003, 2005, 2007, 2009, 2011, 2013, 2015	Groundfish survey data base: http://www.afsc.noaa.gov/RACE/groundfish/survey_data/ Stock assessments: http://www.afsc.noaa.gov/REFM/Stocks/
Predator/Prey	As above	As above	As above	Fish Food Habits Database: http://www.afsc.noaa.gov/REFM/REEM/Data/

Table 2. GOA-IERP surface trawl summary data for each summer survey 2010-2014 in the eastern and western GOA including sampling date, number of grid stations sampled (No. stations), total number of Arrowtooth Flounder caught (N), frequency of occurrence (% frequency) at all stations sampled, and mean catch per unit effort (CPUE) of ATF for each survey.

Year and Region	Sampling Dates	No. Stations	N	% Frequency	Mean CPUE (no. km^{-2})
2010 East	July 4-22	68	308	57.35	89.87
2011 East	July 3-21	59	17	15.25	2.27
2012 East	July 3-21	74	389	54.05	46.47
2013 East	July 3-21	79	34	27.85	4.98
2014 East	July 7- August 8	91	18	9.89	1.52
2011 West	August 5-20	56	1	2.13	0.16
2012 West	August 5-21	54	90	33.33	14.45
2013 West	August 3-21	47	2	4.26	1.15

Table 3. GOA bottom trawl summary data. No. stations is the number of survey stations sampled. Mean temp. (°C) is the mean survey-wide bottom temperature; bolded values are warmer and regular font values colder than the 1984-2015 average of 5.72°C. Biomass in tons (t × 10^3) is the estimated biomass from each survey from Spies et al. (2017). Frequency is the percentage of survey stations at which ATF were caught. Mean CPUE is the mean number of ATF km^{-2} at stations where ATF were encountered.

Year	No. stations	Mean temp. (°C)	Biomass (t × 10^3)	Frequency (% stations)	Mean CPUE (No. km^{-2})
1984	797	**6.46**	1,112	82.3	5,872
1987	782	**6.30**	932	87.0	5,152
1990	708	**6.02**	1,907	92.4	9,359
1993	774	**6.02**	1,552	92.2	7,616
1996	807	5.65	1,640	92.2	6,966
1999	788	5.07	1,262	88.5	5,636
2001	489	**5.98**	1,622	87.1	9,060
2003	809	**6.17**	2,819	90.2	13,339
2005	837	**5.83**	1,900	90.9	10,145
2007	816	5.06	1,939	87.6	9,605
2009	823	5.00	1,772	91.7	8,166
2011	670	5.54	1,747	92.1	7,428
2013	548	5.42	1,291	89.2	6,171
2015	772	**6.24**	1,659	89.4	9,511

Table 4. Statistical test for significance in decreasing length-at-age observed over time (1977-2013) for different age-groups of Arrowtooth Flounder in the Gulf of Alaska. The number of age observations is shown for each sex, followed by the p-value of the test and the slope. Test results in bold are significant after a sequential goodness of fit test alpha correction for multiple tests (Carvajal-Rodriguez 2009).

Age	Males			Females		
(Years)	No.	p-value	slope	No.	p-value	slope
1	17	0.5757	-0.038	16	**0.0056**	-0.295
2	62	**0.0014**	-0.142	67	**0.0006**	-0.132
3	79	**0.0007**	-0.148	77	**0.0023**	-0.116
4	82	**0.0154**	-0.090	83	0.0916	-0.072
5	62	0.0524	-0.080	74	0.3483	-0.048
6	51	0.0659	-0.053	66	0.0979	-0.060
7	35	0.9584	0.002	58	0.5600	0.024
8	25	0.3502	0.030	46	0.6885	-0.014
9	13	0.8216	-0.008	39	0.7133	0.019
10	8	0.0697	-0.128	34	0.4016	-0.041

Table 5. Maximum Entropy model results for Arrowtooth Flounder demersal life stages, including early juveniles (40-160 mm), late juveniles (161-350 mm), and adults (> 350 mm) for habitat suitability models using habitat metrics (HSM) and models using habitat metrics and substrate rockiness (HSM with Substrate), including sample size of presence locations, value of the regularization multiplier β with all possible feature types (Pirtle et al., in press), AUC (Area Under the receiver operating characteristic Curve) value for test locations, mean ± SD of k-fold replicates (k = 5), and percent individual contribution (in parentheses) of the top four habitat predictor variables from jackknife analysis (V1-4). BPI = bathymetric position index (Pirtle et al., in press).

Life Stage and Model Type	Sample Size	β	AUC Test Mean ± SD	V1 (%)	V2 (%)	V3 (%)	V4 (%)
Early Juveniles:							
HSM	1,536	2.5	0.7 ± < 0.1	Depth (39.8)	BPI-3.3 km (18.8)	Temperature (13.6)	Tidal Current (11.6)
HSM with Substrate	1,001	2.5	0.8 ± < 0.1	Depth (35.0)	BPI-6.5 km (18.1)	Temperature (14.5)	Tidal Current (9.2)
Late Juveniles:							
HSM	5,781	1.5	0.6 ± < 0.1	Depth (55.5)	Temperature (12.6)	BPI-3.3 km (12.3)	Tidal Current (12.0)
HSM with Substrate	3,615	1.5	0.7 ± < 0.1	Depth (43.6)	BPI-6.5 km (15.6)	Tidal Current (15.1)	Temperature (11.7)
Adults:							
HSM	4,121	1.5	0.6 ± < 0.1	Depth (54.3)	Temperature (20.2)	BPI-3.3 km (9.5)	Tidal Current (7.5)
HSM with Substrate	2,983	1.0	0.7 ± < 0.1	Depth (43.9)	BPI-6.5 km (16.1)	Temperature (15.0)	Tidal Current (7.6)

Table 6. A climate-related vulnerability assessment proposed for Arrowtooth Flounder in the Gulf of Alaska (GOA) that uses the ecological synthesis from this study to evaluate scores according to 12 "sensitivity attributes" identified in Morrison et al. (2015). A low/medium/high score indicates a low/medium/high level of vulnerability for this aspect of ATF population status, life history, or ecology to climate-induced change in the GOA. When two scores are indicated, an intermediate score is suggested overall, e.g. low to medium (1.5) or medium to high (2.5). Overall ATF score here is 15 out of a possible range of 12-36.

Sensitivity Attribute	**Goal**	**Assigned Assessment Scores and Associated Resilience/Vulnerability Factors** **Low (1)**	**Medium (2)**	**High (3)**
Stock Size/Status	To determine if the stock's resilience is compromised due to low abundance	High biomass and numerical dominance in the GOA		
Other Stressors	To account for other factors that could limit population responses to climate change	Predation mortality and fishing mortality very low		
Population Growth Rate	Estimate the productivity of a stock	Consistently high productivity and growth since the 1970s		
Complexity in Reproductive Strategy	Identify reproductive strategy that may be disrupted by climate change		The high spatial and temporal mis-match between larvae and nauplii is, however, mitigated by seemingly extended yolk-sac phase with slow utilization of lipid reserves (see "endurance" strategy below)	High spatial and temporal mis-match between winter peak in larval abundance and spring peak in shelf production of copepod nauplii; may be exacerbated by warmer temperatures (increased egg/larval development rates) or shift in larval prey production
Spawning Cycle	Identify spawning strategies that are more sensitive to changes	Spawn in deep water over the slope during winter months in stable, cold conditions; high fecundity; mesopelagic eggs in predator poor environment		

Early Life History Survival and Settlement Requirements	Determine the relative importance of early life history requirements for a stock	Larval “endurance” strategy; low metabolic demand, slow growth, extended yolk-sac phase, first-feeding synchrony with winter production of *Neocalanus* spp. (copepod) nauplii. Extensive availability of juvenile settlement habitat and food resources	Diminished transport of larvae on to shelf can have a negative impact on early survival	
Sensitivity to Ocean Acidification	Determine the stock's relationship to "sensitive taxa"	Sensitive taxa (e.g. Pteropods, Decapods) not a major source of food	Sensitivity of important zooplankton prey (copepods, euphausiids) unknown but potential for negative response with impact on ATF feeding	
Habitat Specificity	Determine the relative dependence a stock has on habitat and the abundance of the habitat	Habitat generalist from coastal to deep water and nursery habitat extends throughout shelf to slope		
Prey Specificity	Determine if the stock is a prey generalist or a prey specialist	Prey generalist, and feeding behavior considered highly adaptable		
Sensitivity to Temperature	Known temperature of occurrence or distribution as a proxy for sensitivity to temperature	Juveniles and adults found in broad temperature range and distributed across wide latitudinal range and depths	Fish <40 cm most abundant in colder water (<4°C); some distribution contraction with warmer bottom temperatures	*[Larval phase may be most sensitive to temperature – see above]*
Adult Mobility	Determine the ability of the stock to move if their current location becomes unsuitable	Adult mobility moderate but extensive larval drift and available settlement habitat		
Dispersal of Early Life Stages	Estimate ability of the stock to colonize new habitats	Extended larval planktonic phase with high dispersal		
Total Score by Sensitivity Attribute		**8**	**4.5 (1.5 x 3)**	**2.5**