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Early life history pelagic exposure profiles of selected commercially important fish species in the Gulf of Alaska

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Abstract

A synthesis of nearly four decades of ichthyoplankton survey data from the Gulf of Alaska was undertaken to provide the most comprehensive information available on the early life history ecology of five focal species; Pacific Cod (*Gadus macrocephalus*), Walleye Pollock (*Gadus chalcogrammus*), Pacific Ocean Perch (*Sebastes alutus*), Sablefish (*Anoplopoma fimbria*), and Arrowtooth Flounder (*Atheresthes stomias*). This analysis of historical data, along with information from published studies, is presented here in the form of ecological reviews of the species during their planktonic phase. The reviews include descriptions of temporal and spatial patterns of exposure to the environment, and interpretation regarding associated sensitivities to environmental forcing. On a temporal scale, patterns in abundance of eggs and larvae are synthesized that characterize seasonal exposure to the pelagic environment, and interannual variation that is presumed to incorporate responses to long-term environmental forcing. Spatial patterns are synthesized to identify horizontal and vertical extent of egg and larval distributions, delineate areas of primary larval habitat, and illuminate egg and larval drift pathways. The observed patterns are discussed with respect to characterizing species early life history strategies, identifying long-term adaptations to the Gulf of Alaska environment, and associated resilience and vulnerability factors that may modulate early life history responses to environmental forcing in this region. For each species, gaps in knowledge are identified and are concerned primarily with the period of transition between the larval and juvenile stage, and feeding habits and ecology across seasons, habitats and sub-intervals of early ontogeny. These early life history reviews advance our ecological understanding of the pelagic phase, and fine-tune our focus for the investigation of potential response mechanisms to environmental forcing at appropriate, species-specific temporal and spatial scales.

1. Introduction

The overall goal of the Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP) is to identify and quantify the major ecosystem processes that regulate recruitment strength of five key groundfish species in the Gulf of Alaska (GOA); Pacific Cod (*Gadus macrocephalus*), Walleye Pollock (*Gadus chalcogrammus*[1]), Pacific Ocean Perch (*Sebastes alutus*), Sablefish (*Anoplopoma fimbria*), and Arrowtooth Flounder (*Atheresthes stomias*). These five focal species are commercially important (although Arrowtooth Flounder is only lightly exploited) and account for most of the predatory fish biomass in the GOA (Gaichas et al., 2011). Taken together they encompass a range of life history strategies and geographic distributions. Mechanisms underlying recruitment fluctuations among these species remain poorly understood, although substantially more is known about Walleye Pollock than the other species. Processes and mechanisms regulating the quantity, condition, and distribution of these species during optimal environmental windows for survival of their early life history stages need further investigation. In the context of fisheries management, this research is critical to developing abilities to project recruitment strength.

The hypothesis providing the framework for this integrated research program is that survival during early life is influenced by climate-driven variability in nearshore and offshore productivity, larval transport, and location of settlement to demersal habitats. Fieldwork for GOAIERP is designed to illuminate the individual critical environmental windows for these five focal species by examining the gauntlet they endure while crossing from offshore (deep water and shelf) spawning grounds to nearshore settlement areas. Retrospective data analysis combined with environmental covariates and multispecies stock assessment models will determine the relative influence of environmental parameters and identify processes influencing recruitment. The focus is on two regions: the central to western GOA with a broad shelf dominated by high oceanographic variability and large demersal fish biomass; and the eastern GOA with a narrower shelf, lower demersal biomass, and higher species diversity (Mundy, 2005). Most of our knowledge about ichthyoplankton distributions comes from extensive historical sampling in the central to western GOA (Matarese et al., 2003; Doyle and Mier, 2012), with a limited amount of information from occasional surveys in the eastern GOA (Wing, 1997; Atwood et al., 2010).

The lower trophic level component of the GOAIERP seeks to determine how the physical oceanographic environment, particularly transport mechanisms, influence plankton production and distribution dynamics, and subsequently early life stage abundance, distribution and survival to recruitment of the focal fish species. As part of this endeavor, a retrospective analysis has

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[1] Scientific name for Walleye Pollock prior to Page et al. (2013) was *Theragra chalcogramma*

been undertaken of four decades of historical ichthyoplankton data collected in the central and western GOA by the Recruitment Processes Program of NOAA's Alaska Fisheries Science Center (AFSC). Since the 1970s, the latter program along with the related Ecosystem and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) Program has supported a multitude of studies and publications on the early life history of commercially and ecologically important fish species in northeast Pacific and Alaskan marine ecosystems (http://www.ecofoci.noaa.gov/efoci). Critical gaps in our knowledge of the GOAIERP focal species can be filled by a comprehensive synthesis of these existing data sets.

Current information on GOA early life history patterns and recruitment processes among the GOAIERP species is comprehensive for Walleye Pollock (Bailey, 2000; Bailey et al., 1995, 1999, 2003, 2005; Brodeur et al. 1995; Kendall et al. 1996; Porter et al., 2005; Wilson et al. 2005, 2006; and others), and limited for Pacific Cod (Dunn and Matarese, 1987; Abookire et al., 2007; Hurst et al., 2009), Sablefish (Mason et al., 1983; Kendall and Matarese, 1987; Wing, 1997), and Arrowtooth Flounder (Bailey and Picquelle, 2002; Blood et al., 2007; Bailey et al., 2008). These publications are based on single species studies where data are presented and synthesized for the named species only. Although rockfish larvae (*Sebastes* spp.) are abundant in GOA ichthyoplankton samples, and many publications include data on this multispecies assemblage of larvae (Matarese et al., 2003; Doyle et al., 2002), the identification to species using morphological characteristics is not yet possible because larval features tend to be identical among species (Matarese et al., 1989; Kendall, 1991). Data exclusive to Pacific Ocean Perch (*Sebastes alutus*) is therefore not presented in this publication; rather the data for *Sebastes* spp. are summarized and synthesized with respect to possible patterns that may pertain to *S. alutus*.

Multispecies studies and synthesis of ichthyoplankton historical data from the GOA has provided insight into the occurrence and structure of species assemblages in the neuston and water column, along with the distribution of species relative to temporal and spatial features of the GOA ecosystem (Brodeur and Rugen, 1994; Doyle et al., 1995 and 2002; Boeing and Duffy-Anderson, 2008; Atwood et al., 2010). In addition, a three decade time-series of species abundance during late spring is available for the Shelikof Strait region of GOA. From this time-series, larval abundance among species has been related to regional and local oceanographic forcing with synchrony in species responses reflecting patterns of early life temporal and spatial exposure to the pelagic environment (Doyle et al., 2009; Doyle and Mier, 2012). These multispecies studies of GOA early life history patterns provide a framework for the present GOAIERP investigation of factors that influence recruitment response to the oceanic environment among the focal species. Building on these and the previously mentioned single species studies, the approach taken here is to construct pelagic exposure profiles for these species in the GOA by synthesizing available historical data and information. The “Early life history pelagic exposure profiles” are defined here as a synthetic construct of ecological characteristics that define the interaction with and sensitivities to the pelagic environment during early ontogeny, and that elucidate potential response mechanisms for hypothesis development and testing.

The objectives of this retrospective analysis are to 1) Describe temporal patterns in abundance of eggs and larvae that characterize seasonal exposure to the pelagic environment, and interannual variation that may reflect responses to long-term environmental forcing; 2) Examine spatial patterns to identify horizontal and vertical extent of egg and larval distributions, delineate areas of primary larval habitat, and illuminate egg and larval drift pathways; 3) Synthesize the descriptive information into species’ early life history pelagic exposure profiles that contribute to the identification of potential vulnerabilities and resilience to environmental forcing; and 4) Identify remaining gaps in information needed for determining early life history aspects of recruitment processes.

2. Materials and Methods

2.1. Ichthyoplankton sampling protocol

The NOAA AFSC Ichthyoplankton database includes data from collections in the GOA since 1972, and with annual sampling since 1981. For the present study, data have been synthesized from the years 1972 to 2010. Metadata, individual survey data, and information on early life history for all species occurring in GOA ichthyoplankton samples are given in the AFSC’s online Ichthyoplankton Information System (http://access.afsc.noaa.gov/ichthyo/index.cfm) and associated Ichthyoplankton Cruise Database (http://access.afsc.noaa.gov/icc/index.php). The primary sampling gear used for these collections was a 60-cm bongo sampler fitted with 333 or 505-µm mesh nets (catch differences between mesh sizes have been determined as insignificant; Boeing and Duffy-Anderson, 2008), and oblique tows were generally from 100 m depth to the surface or from 10 m off bottom in shallower water. Oblique tows were sometimes extended below 100 m when the focus was fish species that spawn in very deep water over the continental slope, such as Arrowtooth Flounder (Blood et al., 2007). For a few surveys, a 1-m^2 Tucker trawl (333 or 505-µm mesh nets) was deployed instead of the bongo sampler. The Tucker data are comparable to 60-cm bongo sampler in terms of larval fish catches (Shima and Bailey, 1994) and therefore are included here. Neuston samples were collected using a Sameoto sampler (Sameoto and Jaroszynski, 1969; Jump et al., 2008) with a frame mouth opening of 30 cm high by 50 cm wide and 505-µm mesh net. Neuston data are relevant for species whose larvae are associated with the surface layer of the ocean, e.g. Sablefish. Occasionally during the late 1980s through 2004, a 1-m^2 Multiple Opening Closing Net and Environmental Sampling System (MOCNESS; Wiebe et al., 1976) plankton sampler (fitted with 505-µm mesh nets) was deployed to investigate the distribution of fish eggs and larvae in different depth strata of the water column. Data from the MOCNESS samples are included here to examine vertical distribution patterns of the GOAIERP species at various ontogenetic stages. Further details of sampling protocols, preservation of samples, and calculations of standardized catches for each of these gears are given in Matarese et al. (2003), and in Broduer and Rugen (1994) for the MOCNESS.

2.2. Sampling coverage

For the historical survey data included in this study, ichthyoplankton sampling was carried out during 102 research cruises over 35 years with data synthesized from a total of 9798 bongo samples, 1197 neuston samples, 275 1-m^2 Tucker Trawl samples, and 663 MOCNESS samples (Table 1). Distribution of sampling effort extended from the coastal area to the east of Prince William Sound southwestwards along the Alaska Peninsula to Umnak Island, part of the Aleutian Island chain, covering coastal, shelf and adjacent deep water (Fig. 1). Sampling was most intense in the vicinity of Kodiak Island for both bongo (Fig. 1a) and neuston (Fig. 1b) collections, with the greatest concentration of historical samples in Shelikof Strait and to the immediate southwest over Shelikof Sea Valley and out to adjacent slope waters. Although sampling has been carried out during all seasons, highest sampling effort was from April through June (Table 1, Fig. 2). Spatial coverage also varied seasonally with more extensive coverage during spring than for winter, summer and fall months.

2.3. Data Synthesis

To examine seasonal variation in abundance of eggs and larvae of the focal species, data were combined from 1972-2009 and mean abundance (stratified by year) was calculated for half month periods from all bongo net samples in which the specific eggs or larvae occurred. Data were synthesized in the same way from the more limited neuston collections for Sablefish eggs and larvae. Similarly, larval length data (standard length in mm) were combined over these years and length-frequency distributions were constructed for each month during which larvae are common in the plankton.

A subset of three decades of GOA ichthyoplankton data has been developed into a time-series of larval species abundance, based on annual 60-cm bongo collections in the vicinity of Kodiak Island during mid-May through early June 1981-2010 (Table 1, Fig. 1a) (Doyle et al., 2009; Doyle and Mier, 2012). Data are absent for the years 1984 and 1986 when ichthyoplankton sampling was not accomplished during late spring. The 60-cm bongo net was the sampling gear used during all late spring cruises except for 4MF88 and 4MF89 when the 1-m^2 Tucker trawl was used (Table 1). Details of the method of calculation of the weighted mean abundance values, and associated weighted mean larval lengths, are given in Doyle et al. (2009). Patterns of interannual variation in larval abundance and lengths of the GOAIERP species from this data set are presented here. Larval mean lengths and length frequencies were developed from samples collected during the full spatial and temporal extent of the late spring cruise in each year. Incorporating all available length data was deemed important in order to assess length frequency distributions for species whose larvae do not occur in high densities at this time of year (Doyle et al., 2009). Spearman’s Rank Correlation Coefficients were calculated to assess correlative relationships between the interanual trends in weighted mean abundance and lengths of larvae, and interannual trends in water temperature (Sea Surface Temperature time-series from NOAA Optimal Interpolation Reanalysis SST V2; Reynolds et al., 2002) based on monthly mean SST values during the seasonal extent of larval occurrence for each species. The rank correlation method was chosen rather than a regular parametric test because of lack of normality in the abundance and length data. Timing of sampling as represented by the mid-survey date (Julian Day) in each year was also included in these correlations in order to evaluate the influence of temporal shift in sampling on abundance and length of larvae collected.

To investigate the general patterns of seasonal progression in horizontal distribution and likely drift pathways for eggs and larvae, mean abundance data were plotted on a grid of 20 x 20 km grid cells (400 km^2) for each half month period during which eggs or larvae of each species were common in the plankton. Data for each half month period were combined over all years of sampling in the GOA, and calculation of mean abundance from stations within each grid cell was stratified by year, as in Matarese et al. (2003). The extent of the grid coverage on maps representing each half month varies because of seasonal variation in sampling distribution.

Vertical patterns of distribution of eggs and larvae in the water column were synthesized from MOCNESS collections at various locations in the central and western GOA survey area over the years (Table 1). The number of nets deployed and the depth range sampled by each net varied across stations, months, and years depending on water depth at the sampling location and purpose of the MOCNESS tows. Given inconsistencies in depth strata sampled, plots of abundance and larval size by depth were constructed using mid-net depth (i.e. if a net sampled from 20 to 40 m depth, the mid-net depth would be 30 m). It is acknowledged here that using mid-net depth to represent depth strata where larvae occur underestimates the full vertical extent of occurrence of the larvae in the water column, especially when nets were deployed below 100 m and the strata sampled could include 50 m or more. Also using mid-net depth data, weighted mean depth of larvae was calculated for individual length bins (<3, 3<5, 5<7, 7<10, 10<15 mm) in order to illustrate variation in vertical distribution of larvae with ontogenetic development.

Weighted mean depth of larvae for individual length bins was calculated as:

$$\overline{D}_l = \frac{\sum_{i=1}^{n_l} \sum_{j=1}^{m} N_{ijl} D_{ijl}}{\sum_{i=1}^{n} \sum_{j=1}^{m} N_{ijl}}$$

where $\overline{D}_l$ = weighted mean depth of occurrence of larvae for larval length bin *l* (e.g. 3<5 mm)

n_l = total number of hauls for length bin *l*

N_{ijl} = density of larvae in net *j* in haul *i* for length bin *l*

D_{ijl} = mid-point of depth range sampled for net *j* in haul *i* for length bin *l*

m = number of nets or depth stratified samples per haul

Standard deviation of the weighted mean depth was calculated as the square root of the variance of the weighted mean depth ($Var\ \overline{D}_l$):

$$Var\ \overline{D}_l = \frac{n_l}{(\sum_{i=1}^{n} N_{il})^2(n_l - 1)} \sum_{i=1}^{n_l} {N_{il}}^2 (\overline{D}_{il} - \overline{D}_l)^2$$

where n_l = total number of hauls for length bin *l*

N_{il} = total density (no. 10 m^{-2}) of larvae in haul *i* for larval length bin *l*

$\overline{D}_{il}$ = weighted mean depth of occurrence of larvae in haul *i* for larval length bin *l*

$\overline{D}_l$ = weighted mean depth of occurrence of larvae for larval length bin *l*

3. Results

3.1. Pacific Cod (*Gadus macrocephalus*)

3.1.1. Temporal patterns

Pacific Cod larvae are documented in historical GOA plankton samples during spring months. They are rare in March samples, common in June, and most abundant during April and May with the annual peak associated with the second half of April (Fig. 3a). Larval length frequency distributions indicate a peak in abundance of newly hatched larvae (<5 mm) during April, a slight increase in the length mode to 5 mm in May, and a more pronounced increase to 8 mm by June in association with increasing catches of larger larvae (Fig. 4a). Larvae >15 mm in length are scarce in the bongo samples, although during May and June, larvae >20 mm do occur. The maximum size recorded for a Pacific Cod larva from these samples was 28.7 mm.

The late spring time-series of larval abundance for Pacific Cod (Fig. 5a) indicates years of high and low abundance with most of the high abundance years occurring during the period 1989-1997, as well as 2006-2009. These time-series data include larvae that are newly hatched as well as larvae that may be up to two months old (Fig. 4a). Interannual variation in larval length frequencies indicate variability among years in proportions of larvae belonging to different size categories ranging from 3 to 23 mm in length (Fig. 6). A correlation of -0.47 between abundance and length of larvae over the time-series indicates that smaller larvae tend to be more abundant than larger larvae (Table 2). A positive correlation (0.46) between mean larval length and mid-survey date was recorded. Mean larval length was positively correlated with sea surface temperature (SST) from January through May, and the strongest correlation was with April-May SST. Correlations between larval abundance and temperature were also strong but negative. Interannual patterns in length frequency distributions for Pacific Cod larvae also illustrate a correspondence between larval size and water temperatures (Fig. 6). Lengths tended to be contracted during relatively cold years (e.g. 1991, 1999, and 2007-09) whereas highest proportions of larvae >8 mm were recorded during relatively warm years (e.g. 2000-2006).

3.1.2. Spatial patterns

Within the relatively narrow time period in spring when Pacific Cod larvae are caught in bongo samples, plots of mean abundance on 20 x 20 km grid squares over half month periods indicate primary larval habitat and some northeast to southwest progression in occurrence of larvae (Fig. 7). During the first half of April, larvae appear in shelf waters mostly in the vicinity of Kodiak Island and to the northeast with limited occurrences to the southwest of Kodiak (Fig. 7a). Larvae are still common and abundant around Kodiak Island during the second half of April but with an increased incidence of larvae in shelf waters to the southwest, extending as far as Unimak Pass and with “hot spots” in abundance associated with the area around the Shumagin Islands (Fig. 7b). During May and early June, incidence and abundance of larvae to the northeast of Kodiak has diminished, and larvae occur continuously from Shelikof Strait to Unimak Pass with highest concentrations persisting to the southwest of the Shumagins (Fig. 7c, d, and e). Although larvae are abundant throughout shelf waters, including the outer shelf, larvae are scarce in samples collected over the continental slope.

Limited data from historical MOCNESS samples indicate that Pacific Cod larvae of all sizes are most abundant in the upper 50 m of the water column (Fig. 8a), but that larvae <7 mm in length can be found deeper in the water column, including depths between 100-200 m (Fig. 9a). The estimated weighted mean depths of different size categories of larvae clearly show the ontogenetic vertical migration of larvae towards the surface, and indicate that newly hatched larvae move rapidly to the upper 50 m of the water column (Fig. 10a).

3.2. Walleye Pollock (*Gadus chalcogrammus*)

3.2.1. Temporal Patterns

Although rarely caught in plankton samples prior to March, Walleye Pollock eggs have been recorded to a limited extent during February (Fig. 3b(i)). Peak levels of abundance of eggs at very high concentrations are observed during late March through mid-April after which they diminish substantially. They are common in samples during May and June, but absent during summer months. Larvae first appear in the plankton in February or March and peak in abundance during the second half of April (Fig. 3b(ii)). Concentrations remain high through May and June and larvae are largely absent after June. A few records of larvae have been documented during October and November. Seasonal variation in larval length frequency distributions indicates that most larvae caught during March and April are newly hatched and less than 5 mm standard length (Fig. 4b). Newly hatched larvae are still present during May and June but by June most larvae are between 5 and 15 mm in length. Larvae >20 mm are present during May and June but are not abundant in the samples, and the maximum size recorded was 27 mm.

The late spring time-series of larval abundance is characterized by an extraordinarily high anomaly in 1981, followed by a pattern of periodic highs and lows (Fig. 5b). The periodicity in highs to lows is on a scale of 2-5 years, similar to that observed for Pacific Cod larvae. Length frequency distributions of the larvae over the time-series indicate variability in mean larval size and proportions of newly hatched to well-developed larvae (Fig. 11). Highest proportions of smallest larvae tended to be associated with relatively cold years (e.g. 1991, 1999, and 2007-2009), and most extended length frequencies with some of the warmest years (e.g. 2000-2006) as reflected in the positive correlations with winter to spring water temperatures (Table 2). A weak, positive correlation between larval length and survey timing over the time-series suggests that shifts in the latter were of limited influence as a confounding factor. Larval abundance was weakly correlated with larval length but there was no correlation between larval abundance and either the survey dates or water temperature.

3.2.2. Spatial Patterns

The earliest appearance of Walleye Pollock eggs in the plankton of the western GOA is associated primarily with Shelikof Strait and Sea Valley, but also shelf waters to the northeast of Kodiak Island and in the vicinity of the Shumagin Islands to the southwest (Fig. 12a-c). This pattern is maintained by the time egg abundance is at a peak during the first half of April, with highest concentrations in the vicinity of Shelikof, and scattered “hot spots” in abundance along the outer shelf and slope northeast of Kodiak and offshore of Shelikof Sea Valley to Unimak Pass (Fig. 12d). This pattern is similar during the second half of April (Fig. 12e). During May to June, occurrence and abundance of eggs has diminished to the northeast of Kodiak Island but highest concentrations are still observed in Shelikof Strait and along the shelf to the southwest as far as Unimak Pass (Fig. 12f-h). From April to June, there appears to be an onshore trend in abundance of eggs. High concentrations are observed during April in shelf waters but also along the continental slope, particularly offshore of Shelikof Sea Valley and to the southwest (Fig. 12d and e), whereas during May and early June the highest concentrations are now observed on the inner shelf (Fig. 11f-h). Seasonal progression in distribution and abundance of the larvae follows a very similar pattern to that of the eggs (but with a lag of about a month) with highest concentrations associated with Shelikof Strait and the shelf to the northeast of Kodiak Island during April, and additionally from Shelikof and waters around Kodiak Island southwest to Unimak Pass during May (Fig. 13a-f). An onshore shift in occurrence and abundance of larvae is not as apparent, however, and larvae remain abundant throughout the shelf and over adjacent slope water during May in particular. By late June, occurrence and levels of abundance in the bongo samples have diminished considerably (Fig. 13g).

Walleye Pollock eggs are recorded throughout the water column down to depths of approximately 250 m with highest concentrations observed below 100 m (Fig. 8b(i)). Larvae are also abundant throughout the water column, but with highest concentrations occurring in the upper 50 m (Fig. 8b(ii)). Depth distribution of larvae changes with ontogeny; larvae less than 5 mm length occur relatively evenly throughout the full extent of the water column whereas larvae >5 mm are most abundant in the upper 50 m (Fig. 9b). This ontogenetic movement of larvae towards the surface is also clearly evident in the estimated weighted mean depths by larval size category (Fig. 10b). The smallest larvae up to 3 mm in length are associated with the layer below 150 m, larvae from 3-5 mm have a weighted mean depth from 50-75 m, and larvae >5 mm are associated with the upper 50 m with a slight decreasing trend in weighted mean depth with larval size over the length categories 5<7 mm, 7<10 mm, and 10<15 mm.

3.3. Rockfish (*Sebastes* spp.)

3.3.1. Temporal Patterns

Rockfish larvae of the genus *Sebastes* occur first in the plankton of the western GOA in April and are recorded continuously through spring, summer and fall months (Fig. 3c). The annual peak in abundance appears to be the first half of July, but levels are also high from late May through July. The apparent absence of larvae in early August is because no samples were collected during that period. Records in October and November were limited to a small number of stations. Larval sizes ranged from 2-27 mm standard length and the vast majority of larvae were less than 10 mm with a very high proportion less than 5 mm indicating that they were recently extruded (Fig. 4c). A bimodal pattern in length frequencies is apparent for spring and summer months; the modes for April, May and June are between 5 to 6.5 mm, whereas July, August and September modes are smaller at 3-4 mm indicating a newly released cohort of larvae (Fig. 4c).

The late spring time-series of larval abundance for rockfish is characterized by consistently low levels of abundance from 1981 through 1996 (except for moderate levels in 1985), and a high amplitude of variation subsequently including five years of very low abundance, seven years of moderate abundance and exceptionally high concentrations in 1998 and 2001 (Fig. 5c). The year 1987 was unusual in that no rockfish larvae occurred in the samples. Interannual variability in length frequency distributions of the larvae was much less pronounced than for abundance of the larvae with all years except a few having a mean larval length falling in the range 5-6.5 mm (Fig. 14). Notable exceptions were 1990, 1999, 2005 and 2006 which were characterized by more extended length frequency distributions, and 1982 for which length frequencies were more contracted. The largest larvae collected during these late spring surveys were 15 mm in length. There was no relationship between mean larval abundance and mean lengths over the time-series or between abundance or lengths and the temporal shift in sampling (Table 2). Mean larval abundance was, however, positively but weakly related to sea surface temperatures, particularly for April through May. Conversely, mean larval lengths were negatively and weakly correlated with sea surface temperatures during late winter and spring months.

3.3.2. Spatial Patterns

Distribution patterns for the spring cohort of rockfish larvae indicate a seasonal progression in onshore distribution of larvae, and larval habitat associated primarily with outer shelf and adjacent slope water in the vicinity of Amatuli Trough to the northeast of Kodiak and offshore of Shelikof Sea Valley to the southwest (Fig. 15a-f). Although larvae remain most abundant over the outer shelf and slope, ingress of larvae to middle and inner shelf waters is apparent as spring progresses. This is especially pronounced for Shelikof Strait where larvae were almost entirely absent in April (Fig. 15a and b), but from mid-May through early June larvae appear to be filling in this area from the two deep water "hot spots" in abundance; Amatuli Trough and outer Shelikof Sea Valley with adjacent slope (Fig. 15d and e). The limited sampling during July through early October, primarily offshore of Kodiak Island and over the shelf to the northeast, also indicates a deep water origin for the summer cohort of larvae (Fig. 15g-l). Highest concentrations are associated with stations over the continental slope during July, and larvae were also recorded over deep water a considerable distance offshore of the slope (Fig. 15g and h). From mid-August through early October, low to moderate levels of larval abundance have been recorded in shelf waters to the northeast and offshore of Kodiak Island (Fig. 15i-l).

Rockfish larvae have been recorded deep in the water column below 200 m, but concentrations are low at these depths (Fig. 8c) and the larvae are small; <6 mm (Fig. 9c). Larvae are most common in the upper 100 m of the water column and highest concentrations occur in the upper 50 m. The estimated weighted mean depths of occurrence of different size categories of larvae from the MOCNESS net samples indicates very little variability in vertical distribution patterns across ontogenetic stages, with all estimated mean depths associated with the upper 30 m of the water column. (Fig. 10c).

3.4. Sablefish (*Anoplopoma fimbria*)

3.4.1. Temporal Patterns

Sablefish eggs have been recorded in 60 cm bongo net samples from late February through early April with a peak in abundance in late February (Fig. 3d(i)). Eggs were absent from bongo samples during late April through May and a single record was documented in early June with absence of eggs in all later months. Larvae appear first in the bongo net samples in April and levels of abundance are low throughout spring months with a slight peak observed in late May (Fig. 3d(ii)). Larvae in the bongo samples range in size from 4 to 21 mm in length with increasing modes and length ranges from April through June (Fig. 4d(i)). The biggest difference in larval length modes was between April (7-8 mm) and May (14 mm). Sablefish larvae are most abundant in historical neuston collections and a late spring annual peak in abundance is apparent from mid-May through early June with earliest records of larvae in late April and latest records in July (Fig. 3d(iii)). Length measurements from the neuston samples were limited primarily to May and June collections, and size ranges for these larvae were comparable to those caught in the 60 cm bongo samples during May and June (Fig. 4d(ii)).

Levels of mean abundance of Sablefish larvae in the GOA late spring time-series are low and larvae were not present in collections during all years of sampling (Fig. 5d). They were absent mostly during the 1980s (1981-83, 1987, and 1988), and during 1999, 2000, 2006 and 2010. Presence and levels of abundance were most consistent from 1990 through 1997. Subsequently, the fluctuations in abundance were more dramatic although the highest anomaly recorded in 2002 was associated with a high standard error value. Given the very low numbers of Sablefish larvae collected in the GOA late spring time-series, the data were inadequate for developing a time-series of larval length frequencies and mean lengths as was done for the other species.

3.4.2. Spatial Patterns

The limited records of Sablefish eggs in the historical bongo samples are associated almost exclusively with deep water stations over the slope (Fig. 16a-d). During April, larvae from the bongo samples are also associated with the slope and adjacent deep water, especially near Amatuli Trough and the outer Shelikof Sea Valley, but with some appearances of larvae on the shelf inshore of these locations (Fig. 17a and b). By May, larvae are more common on the shelf, but again with a strong association with the areas around Amatuli Trough and Shelikof Sea Valley (Fig. 17c and d). Neuston collections during spring months also indicate the deep water and slope habitat for these larvae as well as a primary association with the Amatuli and Shelikof locations (Fig. 18a-f). The most extensive sampling coverage was in late May, which also had the annual peak in abundance of Sablefish larvae. Highest concentrations of larvae in the neuston were again associated with the slope and adjacent shelf waters in both these locations (Fig. 18d). The limited sampling during July was carried out along the slope offshore of Kodiak Island and yielded low to moderate levels of abundance of neustonic Sablefish larvae (Fig. 18g). For vertical distribution patterns, a total of only three Sablefish larvae were recorded from the historical MOCNESS sampling in the western GOA, and these occurred in April of 2003 in nets that fished the upper 40 m of the water column.

3.5. Arrowtooth Flounder (*Atheresthes stomias*)

3.5.1. Temporal patterns

Arrowtooth Flounder eggs have been recorded in 60 cm bongo samples in the western GOA from mid-January through early March with a peak in abundance evident for January through early February (Fig. 3e(i)). Larvae are most abundant from January through early March, occur in low to moderate concentrations in April through July, and are scarce in samples from late August through September (Fig. 3e(ii)). Larval length frequencies indicate slow development of larvae from January through April with overlapping modes for the coldest months, February and March, and the vast majority of larvae are less than 10 mm in length through April (Fig. 4e). A dramatic increase in larval size is evident from April to May with the mode changing from 7 mm in April to 14 mm in May. The range of larval lengths is much broader for May than for April. By June the majority of larvae are greater than 15 mm and a few larvae >30 mm have been recorded. The few larvae caught and measured from July samples ranged from 26 to 35 mm in length, and those from August and September were 37 to 44 mm.

The late spring time-series of larval abundance for Arrowtooth Flounder suggests a decadal trend of low abundance during the 1980s (except for 1985; no sampling in 1984 and 1986), a gradual increase from 1989 to 1992, sustained peak abundance 1992-1997, and diminishing levels through 2003 (Fig. 5e). Moderate levels of abundance from 2004-2007 were followed by very low levels 2008-2010. The pattern of interannual variation in mean larval length, and length frequency distributions, is quite different from that presented for the two gadid species and rockfish as Arrowtooth Flounder larvae are quite well developed by late May through early June, mean levels of abundance tend to be relatively low, and the range of sizes recorded is broad (Fig. 19). Larval length was not correlated with larval abundance over the time series (Table 2). Larval abundance was not correlated with either the timing of sampling or water temperatures, but larval lengths were positively correlated with these variables although weakly. The positive relationship with temperature is reflected in the extent of the length distributions in some years (Fig. 19). For instance, even though few larvae were sampled and measured during the coldest years of the time-series (2007-2009), larval length frequencies were contracted in those years relative to some of the warmest years (e.g. 1998 and most years 2001-2006) when they were more extended. Again, the positive relationship between larval length and the temporal shift in sampling confounds the length to temperature relationships.

3.5.2. Spatial patterns

Except for one record off the southern tip of Kodiak Island in early February, the occurrence of Arrowtooth Flounder eggs in historical samples from January through early March is restricted to deep water stations along the continental slope (Fig. 20). A similar pattern is apparent for recently hatched and small larvae sampled during the same half month periods but with some evidence of movement of larvae onto the shelf during mid-February through mid- March (Fig. 21a-d). By late March, records of larvae on the shelf have increased, especially in the vicinity of Amatuli Trough, and larvae appear in Shelikof Strait (Fig. 21e). Highest concentrations of larvae during April and May are still associated with the outer shelf and slope, but a gradual "filling in" of larvae is apparent as these months progress, culminating in extensive distribution of larvae at low levels of abundance on the shelf northeast of Kodiak, throughout Shelikof Strait and southwest along the shelf to the Shumagin Islands (Fig. 21f-j). The association of highest concentrations of larvae with slope and shelf waters offshore of Amatuli Trough and Shelikof Sea Valley suggests that these are primary regions of ingress of larvae onto the shelf during spring. Larvae were also evident and relatively abundant at many deep water stations beyond the continental slope from April though early June, particularly offshore of Amatuli Trough (Fig 21f-j). By late June, occurrence of larvae was restricted to shelf waters in the vicinity of the Shumagin Islands (Fig. 21k) although in early July low concentrations of larvae were also recorded over the shelf to the northeast of Kodiak Island (Fig. 21l).

Arrowtooth Flounder eggs were not recorded in any of the historical MOCNESS sampling during spring in the western GOA. Larval records from this sampling gear indicate that larvae are common throughout the water column down to depths of approximately 200 m, but that most occur in the upper 100 m (Fig. 8d). Highest concentrations of larvae are associated with the upper 50 m of the water column, especially larvae >15 mm in length (Fig. 9d). This ontogenetic migration towards the upper 50 m of the water column is also evident in the weighted mean depth distributions for different size categories of larvae (Fig. 10d). In general, larvae <10 mm in length occur deeper in the water column than those >10 mm and weighted mean depths for larvae in the 10<15 mm, 15<20 mm, and 20<25 mm ranges are very similar.

3.6. Species' early life history strategies and Gulf of Alaska climatology

Using phenology of early ontogeny stages as the primary gradient, a conceptual schematic of the focal species' early life history strategies in relation to seasonal variation in the GOA pelagic environment is developed in Figure 22. This conceptual representation of species' temporal exposure to the pelagic oceanographic environment indicates similarities and differences in the interaction with the environment during different sub-intervals of early life. All species occur as pelagic juveniles during summer months when water temperatures are on the increase to a maximum in September, and when zooplankton abundance as represented by copepod species is at an annual peak. The occurrence of pelagic juveniles for each species in the autumn is not well documented, mainly due to sampling limitations beyond September. It is reported, however, that Pacific Ocean Perch (*Sebastes alutus*) remains pelagic for most of its first year of life (Hulson et al., 2014), and this has been incorporated into Figure 22.

The greatest differentiation in pelagic early life history schedules among the focal species is during the egg and larval stage, as outlined in the individual species sections. Demersal eggs for Pacific Cod, and viviparity for rockfish species reduces and removes, respectively, exposure to the pelagic environment during embryonic development. In contrast, egg development for Arrowtooth Flounder, Sablefish, and Walleye Pollock takes place at depth in the water column during the coldest months of the year, January through April. Larvae of Arrowtooth Flounder are at peak abundance during January through early March in association with lowest levels of phytoplankton production, and shelf-based zooplankton abundance as represented by copepod nauplii. Peak densities of these larvae in deep water over the slope during winter are synchronized, however, with reproduction of certain species of oceanic copepods such as *Neocalanus* species that are later transported onto the shelf as nauplii and early copepodite stages (Coyle et al., 2013). In contrast, peak densities of rockfish larvae are associated with rapidly warming water, the annual peak in phytoplankton production, and the early spring rise in abundance of shelf-based copepod nauplii. For Sablefish, Walleye Pollock and Pacific Cod larvae, the peak abundance period coincides with coldest water temperatures, minimum to maximum levels of phytoplankton production, and low to moderately high levels of copepod nauplii abundance on the shelf. Further to the timing of peak abundance of larvae, the duration of occurrence of larvae in GOA plankton samples ranges from a minimum of approximately three months for Pacific Cod to a maximum extent of nine months for Arrowtooth Flounder. These different larval durations result in a variable extent of temporal exposure to the pelagic environment, and in the associated range of conditions encountered such as water temperature and larval food availability (Fig. 22).

Discussion

Incorporating environmental forcing into marine fisheries stock assessment models is one of the principal challenges in contemporary fisheries science. There is limited success in this endeavor to date, primarily because of the difficulty in establishing robust and consistent relationships between annual recruitment of young to the adult populations and climate-ocean indices that best represent environmental forcing throughout the pre-recruit period for any particular species (Myers, 1998; Haltuch and Punt, 2011; Stachura et al., 2014). The highly complex nature of interacting biological and physical factors integrated across life stages, for any particular species in a given ecosystem, is a major challenge in this regard (Bailey et al., 2003, 2005; Yatsu et al., 2008). Nevertheless, it is recognized that rigorous attention to early life history aspects of complex recruitment processes can significantly advance our understanding of fish-environment mechanistic relationships beyond what may be discerned by the more limited approach of relating recruitment metrics to environmental indices (Houde, 2008; Bailey et al., 2012; Doyle and Mier, 2012). Among marine fish species, ecological interactions are profoundly different during embryonic and early life than later during the juvenile and adult stage (Fuiman, 2002; Miller and Kendall, 2009). Subintervals of early life are important and even within species, the nature of the response to environmental forcing can vary across different ontogenetic stages (Doyle et al., 2009; Laurel et al., 2011). Therefore, the challenge of modeling recruitment processes calls for a multifaceted approach in which target species are represented by key life history stages whose links to the environment are explicitly formulated (deYoung et al., 2004; Rose, 2005). A synthesis of early life history patterns for a given fish species is the primary information needed to develop such explicit formulations within a given ecosystem. Construction of comprehensive pelagic exposure profiles for the focal species in this study is a vital step towards illuminating mechanistic linkages between species abundance and conditions in the GOA ecosystem during critical subintervals of early ontogeny.

3.7. Pacific Cod

Pelagic exposure begins for Pacific Cod during the larval stage. Total fecundity is extremely high for this species (maximum values 3-6.4 million eggs per female; NOAA Alaska Fisheries Science Center, Life History database, http://access.afsc.noaa.gov/reem/LHWeb/Index.cfm), and eggs are deposited on or close to the bottom in one batch. They remain negatively buoyant, but on hatching larvae migrate rapidly towards the surface (Matarese et al., 1989; Mecklenburg et al., 2002; Hurst et al., 2009), and as evidenced in this study by the occurrence of the smallest larvae at depths below 100 m and the predominant association of all sizes of larvae with the upper 50 m of the water column. Seasonal variation in the abundance and size of larvae documented here also agrees with observed patterns of late winter to spring spawning activity for Pacific Cod in Alaska waters (Stark, 2007). This pattern of spawning places a peak abundance of small (<5 mm) larvae in the pelagic ecosystem when water temperatures begin to rise just after the annual water temperature minimum in March-April (Stabeno et al., 2004; and see Fig. 22), and before the full development of the spring zooplankton bloom of copepod nauplii that follows the annual April to May peak in phytoplankton production (Napp et al., 1996; Coyle and Pinchuk, 2005). The growth and development of Pacific Cod larvae through the pre-feeding yolk-sac stage seems to coincide therefore with the initiation and early development of this spring peak in zooplankton production. This early life history strategy likely confers a significant degree of vulnerability to Pacific Cod first feeding larvae with respect to co-occurrence with optimal levels of suitable zooplankton prey. However, it is also possible that early spring production of both phytoplankton and microzooplankton (e.g. ciliate protozoans, heterotrophic dinoflagellates, and tintinnids) may provide suitable nourishment for the smallest larvae (Montagnes et al., 2010), thus facilitating their survival through periods of inadequate availability of copepod eggs and nauplii. In the Southeast Bering Sea, Strasburger et al. (2014) identified diatoms as a consistent component in diets of pre-flexion Pacific Cod larvae during spring, even when eggs, nauplii and early copepodite stages of a variety of copepod species were also present in larval guts.

The temporal match between peak abundance of Pacific Cod larvae and sufficient quantities of their suitable prey, such as dominant GOA shelf species of copepod nauplii, is likely to vary annually as such naupliar production is strongly influenced by water temperature, standing stock of female copepods and timing of the spring phytoplankton bloom (Napp et al., 1996). Interannual variability in timing of larval hatching, and larval growth rates, are also strongly influenced by water temperatures (Hurst et al., 2010). Laurel et al. (2008, 2011) conclude from laboratory experiments that the length of the larval hatch period for Pacific Cod is generally temperature-specific, and that larval growth is slower or faster under cooler or warmer conditions, respectively. Asynchronous hatching among batches of eggs that experience common environmental conditions has also been observed, however, and is thought to facilitate avoidance of a complete mismatch with larval food resources (Laurel et al., 2008). In addition, slow growth of early hatching larvae in water temperatures of 0-4°C seems to favor retention of sufficient endogenous reserves of lipids by yolk-sac larvae such that cold environments allow larvae to bridge gaps in prey availability (Laurel et al., 2011). The advantage of cold temperatures and slower growth may not persist, however, as later larval stages seem unable to survive past 4 weeks in the absence of food (Laurel et al., 2008).

Correlations between abundance and size of Pacific Cod larvae in the GOA late spring time-series and winter-spring water temperatures seem to reflect the relationships with temperatures discerned from laboratory experiments. The negative association between larval abundance and water temperature suggests that enhanced survival of Pacific Cod larvae may occur during cold years. Doyle et al. (2009) also identified a negative association between Pacific Cod larval abundance and winter temperatures from an earlier portion (1981-2003) of the time-series. The strong positive correlation between larval length and water temperature, especially during April-May, supports laboratory observations of enhanced growth under warm conditions. The negative relationship between larval abundance and size is acknowledged here as a confounding factor, however. For a particular cohort of larvae, abundance will be higher for newly hatched than for later stage larvae that have had to endure the vagaries of the pelagic environment for a longer period of time. Nevertheless, the relatively strong positive relationship between larval length and the temporal shift in sampling over the time-series is also indicative of stability in timing of spawning and peak larval hatching during these decades. Such stability has also been noted by Stark (2007) based on ovarian maturities and spawning activity for Pacific

Cod in the GOA and Bering Sea. Interannual variability in the availability and consumption of suitable zooplankton prey has not been explored in this study, but is also likely to be a significant influence on the abundance and size of Pacific Cod larvae documented in the GOA time-series.

The patterns of distribution that emerged from the historical data indicate that spawning activity and associated occurrence of larvae in the epipelagic zone is most intense in shelf waters from Kodiak Island to the Aleutians, and that the area from the Shumagin Islands to Unimak Pass may be prime larval habitat. Given that Pacific Cod larvae are rare in historical ichthyoplankton samples by the end of June and that juveniles are common in nearshore areas of the GOA by July (Laurel et al., 2007), this region may also be critically important coastal habitat for juveniles. The bays around Kodiak Island have also been identified as important nursery areas for age-0 Pacific Cod (Mueter and Norcross, 1999; Abookire et al., 2007; Laurel et al., 2007), and it would seem given the relatively short larval drift period for this species that these benthic juveniles resulted from spawning activity close by.

In a comparative analysis of early life history patterns of GOA fish species, Pacific Cod have been assigned to the “Abundant” strategy group in which high fecundity is associated with limited temporal and spatial spread of larvae in the pelagic environment (Doyle and Mier, 2012). The advantage of this strategy is that production of eggs and larvae tends to be sufficient to withstand very high levels of mortality during early ontogeny. For Pacific Cod, this resilience is tempered by production and release of only a single batch of eggs per female per year (Stark, 2007) and relatively short larval duration (compared to other species; see Fig. 22) for the population as a whole; a type of “All-Eggs-In-One-Basket” strategy that may result in a mismatch with larval food availability or the exposure of the bulk of a larval cohort to other unfavorable conditions (e.g. sub-optimal temperatures or transport conditions). The apparent stability in timing of spawning from year-to-year, despite varying temperature regimes and associated timing in plankton production, would also contribute to this vulnerability.

The paucity of larvae greater than 15 mm in length in GOA ichthyoplankton samples indicates that early postflexion larvae seem competent at avoiding plankton nets. This also suggests that they may be sufficiently competent swimmers to facilitate their transport and early settlement to nearshore nursery grounds. The occurrence of very low numbers of late larvae and newly transformed juveniles (25-45 mm in length) in fine-mesh pelagic trawls in shelf waters in the vicinity of the Shumagin Islands during July (Brodeur et al., 1995), and the association of highest catches with coastal waters, seems to support this idea of early settlement. Further evidence for the relatively rapid movement of newly transformed juveniles inshore to coastal nursery grounds is provided by their absence from pelagic midwater trawls in GOA shelf waters during September (Wilson, 2009). The transition from pelagic to benthic habitat and the ecology of this phase in the Pacific Cod life cycle remains very poorly understood. In addition, the biggest knowledge gap overall for Pacific Cod early life history in the GOA is the lack of information on trophic ecology throughout the different ontogenetic stages, but especially the larval stage. Recent work from the GOAIERP program, however, contributes new information on juvenile (age-0) Pacific Cod feeding on copepod species during summer months, prior to settlement (Moss et al., this volume). Strasburger et al. (2014) has identified the importance of copepod eggs, nauplii and copepodite stages, and of non-copepod prey, in the diet of Pacific Cod larvae and age-0s during spring, summer and fall of 2008 in the Bering Sea, and documented ontogenetic and habitat variation in diet composition. Similar studies could be undertaken for early life history stages of Pacific Cod in the Gulf of Alaska from archived historical samples.

3.8. Walleye Pollock

Female Walleye Pollock are determinate batch spawners, producing up to a maximum of 1.2 million pelagic eggs each season (more common range of 100-500,000 per female, depending on age; Hinckley, 1990) and eggs are pelagic in deep water in the GOA. This early pelagic exposure increases the vulnerability to predation during the egg incubation period, and consumption of eggs by invertebrate planktonic predators, particularly euphausiids, is common (Brodeur et al., 1996). However, the release and retention of eggs deep in the water column (predominantly below 150 m) for most of the embryonic development period is a mitigating factor that reduces predation mortality on the egg through newly hatched larval stage. The vertical distribution data presented here corroborates prior observations that Walleye Pollock larvae quickly rise to the upper 50 m of the water column upon hatching (Kendall et al., 1994).

Spawning patterns, and subsequent egg and larval distributions have been well documented for Walleye Pollock in the western GOA (Kendall et al. 1996; Matarese et al., 2003; Bailey et al., 2005). The species migrates in large schools to spawn primarily in the Shelikof Strait sea valley, with most spawning occurring in late March through early April. The occurrence of peak densities of eggs in the plankton during late March and early April, and of larvae during late April through early May reflect this long-term, spawning phenology. The annual late April peak in abundance of Walleye Pollock larvae occurs in association with the commencement of the early spring increase in water temperatures, and prior to the full development of the spring zooplankton bloom of copepod nauplii in May–June (Fig. 22). Field observations of larval nutritional condition in the Shelikof Strait region have indicated that prey availability (copepod nauplii and eggs) and associated larval feeding and growth are more limited in early spring (late April – early May) relative to mid-spring (mid-May), and that larvae are most susceptible to starvation in the first two weeks after hatching (Canino et al., 1991; Theilacker and Porter, 1995). Vulnerability to starvation for first feeding larvae might be mitigated by nourishment from early spring production of phytoplankton and non-crustacean microzooplankton that may bridge the gap with availability of optimal quantities of copepod eggs and nauplii. In addition, it seems that meso-scale circulation features that can concentrate larval pollock and their prey in patches may also enhance successful feeding by larvae during early spring when average prey concentrations tend to be sub-optimal (Canino et al., 1991).

Interannual variability in both hatch date distributions and larval growth have been related previously to water temperatures, with colder temperatures associated with later hatch dates and slower growth (Dougherty et al., 2007). However, relationships between larval abundance and growth and temperatures are not always clear (Bailey et al., 1996). The positive correlation between mean larval length and winter through spring water temperatures across the late spring time-series suggests enhanced larval growth during warmer conditions. Further evidence for this temperature-mediated variable growth is the association of extended larval length frequencies with warm years (described by April-May temperatures) and the most contracted length frequencies with the coldest years. The lack of a correlation between larval abundance and either winter to spring temperatures or the temporal shift in sampling over the GOA time series may reflect the complex mix of environmental controlling factors that are in operation during early ontogeny and influencing larval survival. It is also possible that a clear relationship between larval abundance and temperature is less likely to emerge when multiple batches of eggs are produced over an extended period of time, with consequent variability in hatch dates, and environmental conditions encountered.

Spatial patterns presented here corroborate the prevalence of the Shelikof Strait region as the primary location in the western GOA for both spawning and hatching of larvae. The seasonal progression in distribution of eggs and larvae also indicate the predominant drift pattern of larvae to the southwest with prevailing currents along the shelf. With the synthesis of historical data, it is also interesting to see the full seasonal (February-June/July, and October-November) and spatial (from off Prince William Sound to the vicinity of Unimak Pass) extent of occurrence of eggs and larvae of Walleye Pollock in this region. As indicated by the occurrence of patches of very high concentrations of eggs and newly hatched larvae from March through April, the most important outlying areas of spawning activity seem to be northeast of Kodiak Island especially in the vicinity of Amatuli Trough, along the slope from the outer Shelikof Sea Valley to the Shumagin Islands, and also in shelf waters from the Shumagin Islands to Unimak Pass. A previous modeled synthesis of 20 years of GOA egg data from AFSC ichthyoplankton collections also confirms the existence of secondary, and possibly transitory, centers of spawning and egg distribution that can occur at various locations along the shelf and slope regions of the western GOA (Cianneli et al. 2007). Clearly, the prevalent pattern of late winter production followed by a major peak in abundance of larvae in Shelikof Strait is not entirely an "All-Eggs-InOne-Basket" strategy. The marginal times and areas are likely important bet-hedging opportunities that extend the ability of the species to take advantage of favorable conditions beyond the primary reproductive and early life history phenology and environment. Evidence for occasional enhanced, as well as diminished, survivorship among progeny originating from marginal spawning aggregations has been provided from age and growth studies of age-0 Walleye Pollock in the western Gulf of Alaska (Dougherty et al., 2007; 2012).

The "Abundant" early life history strategy group identified for GOA species includes Walleye Pollock as well as Pacific Cod because of their shared features of high fecundity, a relatively narrow period of peak abundance of larvae during early spring, and associated vulnerability of the bulk of the larval cohort to unfavorable conditions such as sub-optimal zooplankton prey availability (Doyle and Mier, 2012). As a population in the GOA, Walleye Pollock displays an enhanced resilience to encountering unfavorable environmental conditions during early ontogeny because of the increased temporal and spatial ubiquity in egg and larval production beyond the core period and location; a "Bet-Hedging" strategy. Cury (1994) and LePage and Cury (1997) explore this issue of bet-hedging or innovation (temporal and spatial strays) versus inertia (temporal and spatial fidelity) in fish reproductive strategies and survival outcomes. Under drastic environmental changes, they conclude that populations combining both strategies of inertia and innovation remain viable and avoid extinction. It would seem that Walleye Pollock in the GOA has successfully combined both “inertia” and “innovation” in reproductive and early life history patterns to ensure both viability and dominance in the GOA ecosystem.

We have a good understanding of the habitat (pelagic) and ecology of the juvenile stage for GOA Walleye Pollock in the region of GOA west of Prince William Sound (Brodeur et al., 1995; Brodeur and Wilson, 1996; Dougherty et al., 2007, 2012) because age-0 fish remain pelagic for at least six months prior to settlement in nearshore nursery areas. In addition, Moss et al. (this volume) provide new information on feeding and energetics of age-0 Walleye Pollock in the eastern GOA, from GOAIERP sampling. There are still gaps in our knowledge, however, because of the ability of post-flexion larvae to avoid plankton nets, and limited sampling during summer months when larvae are transitioning out of the plankton. For instance a comprehensive understanding of ontogenetic variation in diets during the full pelagic phase is lacking, but would contribute significantly to discerning the influence of diet variability during early life on growth and survival outcomes.

3.9. Rockfish (Sebastes spp.*)*

Among GOA fish species, rockfish of the genus *Sebastes* are unique in that they release live young into the pelagic environment. This viviparity renders an early life history advantage of negating environmental exposure during the egg stage and embryonic development. Larvae are extruded with functional eyes, jaws and pectoral fins (Matarese et al., 1989), and are therefore more developed, with presumably better swimming and visual abilities, than most newly-hatched first feeding fish larvae. Disadvantages to this strategy are diminished fecundity (although this is mitigated by extraordinary longevity in rockfishes), and limited lipid reserves for larvae at the commencement of the pelagic phase.

The annual pattern of larval abundance in the GOA as synthesized from the historical data suggests that a continuous supply of rockfish larvae to the pelagic environment extends from April through October/November, with peak densities occurring during June and July. It is not possible to attribute the abundance data over these months accurately among the numerous species of rockfish that occur in the GOA, because of the inability to distinguish the larvae to species. The interesting dichotomy of two modes of larval length frequencies, however, indicates a distinct spring and summer cohort of larvae. Pacific Ocean Perch (POP; *Sebastes alutus*) are known to extrude larvae during April and May (Hulson et al., 2014), and given that they are the dominant rockfish species in the GOA in terms of abundance (Rooper, 2008), it is likely that larvae collected during April to June in the GOA are comprised substantially of POP. Northern Rockfish (*S. polyspinus*) and Dusky Rockfish (*S. variabilis*) are also known to release larvae during spring months, primarily April-May (Chilton, 2007, 2010; Tenbrink and Spencer, 2013). They are both common and commercially important species in the GOA and therefore should also be considered as significant components of the spring cohort of Rockfish larvae. The smaller cohort of larvae (< 5 mm) collected in July through September most likely represents new larvae that belong to other rockfish species for which parturition occurs during summer to autumn months. Genetic analysis of specimens from new GOA field collections of larvae in spring, summer and autumn of the GOAIERP surveys will contribute significantly to further distinguishing some of these taxonomic specific patterns.

The spring cohort of larvae is at peak abundance from late May through June. This peak is synchronized well with the prevailing spring peak in suitable zooplankton prey such as copepod eggs and nauplii (Fig. 22). Given that rockfish larvae do not have significant yolk reserves when released into the water column, the latter synchrony seems like a key strategy for successful first feeding. Larvae released in April may therefore be more susceptible to starvation, given sub-optimal levels of zooplankton prey that have been assessed in the western GOA at that time (Canino et al., 1991). In comparison with Pacific Cod and Walleye Pollock, however, Rockfish larvae encountered during April tend to be larger by about 2 mm (Doyle and Mier, 2012), with a presumed competitive advantage in terms of behavioral competence for capturing prey. The smaller-sized summer cohort of GOA rockfish larvae may not need this extra size advantage as a more diverse and abundant range of zooplankton prey organisms may be encountered during summer months than in spring. Another advantage for the summer cohort of larvae is that water temperatures at this time facilitate a physiology of rapid growth when food is available.

For the 1981-2010 larval abundance time series, the pattern of interannual variation represents the spring cohort of larvae that have been released into the pelagic environment from April through early June, which likely include POP, and both Northern and Dusky Rockfish. The substantial variation in level of abundance across the time series, especially for the latter half, may represent variation in production and release of larvae in the vicinity of the study area, but also transport of larvae into the Shelikof Strait region from deep water over the slope and beyond. Variation in mean length and length frequencies of larvae across the time series were minimal and did not correlate with variation in timing of sampling. This pattern seems to indicate a very stable timing of production and release of these larvae into the western GOA, despite the variation in levels of larval abundance. A positive (although weak) correlation between larval abundance and spring water temperatures does corroborate the positive relationship between abundance and water temperatures that emerged in the Doyle et al. (2009) analysis of the time-series through 2003. The latter study assumes that the larval trends over the time series are primarily a result of variation in larval release and early survival in the study area, rather than an extended period of larval drift and exposure to the pelagic environment. This is because the spring cohort of larvae has been sampled simultaneously with the peak period of parturition for these species. Warmer temperatures may enhance early larval survival through improving physiological competence with respect to food capture and consumption, and subsequent growth. The absence of rockfish larvae from the late spring samples in one year (1987) is unusual among the dominant taxa of ichthyoplankton encountered in the study area. This could be related to the phenomenon of occasional skipped spawning which has been attributed to some rockfish as well as other species, or to delayed and extended parturition of larvae that can also occur (Tenbrink and Spencer, 2013).

The seasonal progression in distribution and abundance of rockfish larvae identifies the outer shelf, slope and adjacent deep water as important early life history habitat. In particular, Amatuli Trough and the outer Shelikof Sea Valley seem to be primary conduits for transport of larvae onto the shelf and subsequently into inner shelf and coastal waters. The importance of troughs and gulleys along the continental slope as areas of release for larvae is also indicated by patterns of vertical distribution of larvae; occurrence of larvae in the water column is deepest (100-250 m) for the smallest larvae. As is the case with other species, newly pelagic larvae seem to rapidly migrate to the upper 50 m of the water column and remain most abundant above 30 m. This may facilitate their transport onto the shelf in association with onshore Ekman transport that is characteristic of downwelling processes in this region (Stabeno et al. 2004).

Genetic studies on populations in the GOA indicate that dispersal of POP is limited in all life stages and that adults appear to belong to “neighborhoods” at geographic scales of 70-400 km (Palof et al., 2011; Kamin et al., 2013). Features such as Amatuli Trough and outer Shelikof Sea Valley fall within the lower end of this geographic scale and may represent important habitat to which adult POP, and other rockfish species, maintain fidelity. The high densities of newly released larvae associated with these features in the western GOA certainly indicate their importance as centers of larval production and initiation of dispersal. Further evidence for fidelity to natal sites and specific geographic habitats among rockfish in the GOA is an observed east-west division or break in species assemblages (Rooper, 2008), and associated distinctions in POP populations that have been genetically identified (Palof et al., 2011).

The comparative analysis of early life history patterns of GOA fish species by Doyle and Mier (2012) assigns rockfish to the "Synchronous" early life history strategy group. This strategy is characterized by reproductive timing that matches larvae to spring-summer peaks in production of zooplankton food resources. Although this phenology suggests that in the GOA pelagic ecosystem as a whole, vulnerability of rockfish larvae to starvation may be minimized relative to other species, currently we have no information on specific trophic requirements or prey selectivity of rockfish larvae at different stages of ontogeny. Studies that examine feeding habits of rockfish larvae at different stages of development and in different locations during larval drift could contribute to a better mechanistic understanding of larval trophic ecology among these so-called "Synchronous" species.

3.10. Sablefish (Anoplopoma fimbria)

A unique feature of the early life history ecology of Sablefish is the association of its larvae with the neuston (Kendall and Matarese, 1987; Doyle, 1992; Doyle et al., 1995; Matarese et al., 2003). Initially, pelagic exposure begins for this species deep in the water column in winter usually over the slope or in the GOA basin. There appears to be a relatively extended phase of embryonic and early larval development, likely due to coldest water temperatures encountered at this time of year. Kendall and Matarese (1987) note that Sablefish yolk-sac larvae tend to be rare in field collections because eggs and newly hatched larvae occur almost exclusively below 200 m, beyond most standard oblique plankton tows (upper 100 m). The historical data suggests that in the western GOA spawning peaks in February, and the peak in larval abundance occurs in May. Newly hatched larvae are encountered in bongo net samples taken in deep water but they are not very abundant, which corroborates previous observations that upon hatching the larvae swim to the surface remaining primarily in the neuston (Kendall and Matarese, 1987). The strategy of egg deposition in very deep, cold water in winter is likely advantageous in terms of minimizing predation during embryonic development. Fecundity is relatively high for this species which could also mitigate losses overall among annual cohorts.

In addition to the apparent extended period of egg incubation and embryonic development in deep water, Sablefish have an extended epipelagic phase from spring through summer and unlike most other marine fish species there is no marked morphological transition from larval to juvenile stage (Kendall and Matarese, 1987). This observed long epipelagic phase (previous reference, and also see Fig. 22) is also characterized by extensive spatial utilization of the surface layer of the ocean from shelf waters to deep water over the slope and Northeast Pacific basin (Doyle, 1992; Matarese et al., 2003). Once the swimming ability of larvae is well developed during summer months, they are no longer sampled efficiently by neuston nets and so the ecology of late larvae and early juveniles is not well understood. Limited surveys with surface gillnets, however, have provided valuable information on young-of-the year in the GOA and diets for this stage seem to be dominated by euphausiids (Sigler et al., 2001). Larval and age-0 Sablefish seem to be well adapted to the epipelagic life style, particularly in terms of utilization of food resources, as growth rates for young of the year can exceed 2 mm/day which establishes them as one of the fastest growing marine juvenile fish known (Shenker and Olla, 1986). Warmer temperature conditions at the surface of the ocean during summer through autumn are likely to enhance physiological rates and favor faster growth. Conversely, it could be speculated that higher fluctuations in water temperature at the surface, including anomalous cool conditions, may moderate age-0 growth rates. Because of limited information on the neustonic biotope as a whole in the GOA and other marine ecosystems, issues of relevance to Sablefish early life history feeding success such as seasonal and spatial (e.g. patchiness) patterns in zooplankton prey availability are not well understood.

The trophic ecology of Sablefish larvae is likely to be unique because of its neustonic habitat. The May peak in larval abundance, along with a fairly large larval size at hatching, renders an advantage to first feeding larvae in terms of encountering and capturing food resources. In addition, optimal zooplankton prey levels are considered to be available during May to June (Fig. 22). Larvae that occur during April, however, may be more susceptible to starvation. There have been some limited studies of the diets of Sablefish larvae off the US west coast and in the Bering Sea that indicate consumption of a diverse range of zooplankton prey which includes copepod eggs, nauplii and copepodites of certain species (Grover and Olla, 1986; 1990). Diets were most diverse for the largest larvae (>12 mm), and smaller larvae were considered to be more food-limited with incidence of starvation observed. These studies also identified regional differences in diets. Diet studies on larval Sablefish from archived samples in the western GOA could provide important information regarding variation in feeding across seasons, habitat, and sub-intervals of early ontogeny. This information is necessary to identify mechanistic links between the neustonic larvae and lower trophic level components of the epipelagic zone in the GOA ecosystem.

Patterns of seasonal progression in distribution of Sablefish eggs and larvae from the historical sub-surface collections indicate that spawning occurs primarily over the slope, and that Amatuli Trough and the outer Shelikof Sea Valley are important locations for transport of larvae on to the shelf, and particularly into Shelikof Strait. This is also corroborated by the more limited distribution data from the neuston samples as highest concentrations of larvae are associated with these troughs and shoreward of them especially during late May. Epipelagic juveniles are still abundant over deep water in the GOA (basin and slope) during summer months (Sigler et al., 2001), but young-of-the year are also found over the shelf and in coastal waters during summer (Kendall and Matarese, 1987).

Interannual variation in abundance of Sablefish larvae in the GOA late spring time-series is of limited value being based on the bongo sub-surface samples that inefficiently catch the larvae as they swim rapidly to the surface. The trend in abundance nevertheless implies a pattern of periodic highs and lows in the vicinity of Shelikof Strait. Larval length data were insufficient to yield interannual trends in larval length frequencies in association with the long-term trend in abundance.

Because of the “Extreme Epipelagic” strategy that characterizes Sablefish early life history, understanding the ecological dynamics of this period is thought to be critical to determining the environmental processes that drive recruitment trends. Sablefish recruitment is characterized by wide fluctuations in year-class strength and it is hypothesized that the extensive epipelagic phase renders this species particularly sensitive to the influence of large, basin-scale oceanographic features (Shotwell et al., 2012). Results of an investigation of oceanic properties along the “North Pacific Polar Front” (Belkin et al., 2002) relative to recruitment outcomes suggest that colder than average winter sea surface temperatures in the central North Pacific represent favorable oceanic conditions for enhanced early life survival and recruitment strength (Shotwell et al., 2012). This effort and emergent conceptual hypotheses developed regarding links between early life survival and recruitment is foundational for incorporating environmental processes into recruitment modeling for Sablefish. Much remains to be discerned, however, regarding environmental exposure and response during various sub-intervals of early life to pinpoint critical environmental variables that can be successfully incorporated into stock assessment models.

3.11. Arrowtooth Flounder (Atheresthes stomias)

Because of its rise to dominance in terms of biomass and abundance in the GOA ecosystem since the 1970s (Spies and Turnock, 2013) and its ecological importance as a voracious predator, especially of juvenile Walleye Pollock, there is considerable interest in early life history aspects of the recruitment process for Arrowtooth Flounder. The GOA historical ichthyoplankton data have provided detailed information on timing and location of spawning for this species, egg and larval development, and patterns of distribution and abundance of different sizes of larvae in shelf and adjacent deep water (Bailey and Picquelle, 2002; Doyle et al., 2002; Blood et al., 2007; Bailey et al., 2008). Additional synthesis of the western GOA data by Doyle et al. (2009) and Doyle and Mier (2012) has advanced current knowledge to include identification of early life history and environmental factors that may influence the ecological success of this species. Results presented here further this insight into environmental links with recruitment processes.

Arrowtooth Flounder spawn in deep water (≥400 m) along the continental slope during winter, and the historical data indicate peak release of eggs from January through early February, followed by a more extended peak in abundance of newly hatched larvae from January through early March. The subsequent diminished levels of abundance encountered from late March through June, with occasional collections of larvae from July through September, illustrates an extended pelagic larval phase for this species. The apparent extreme mismatch between the winter peak in larval abundance and the peak period of larval food resources in the GOA during spring (Fig. 22) seems like an early life strategy that confers a substantial disadvantage to this species. However, early life history traits such as slow development of larvae in association with cold winter temperatures and relatively large larval size at hatching (>4 mm) are hypothesized to reduce the risk of starvation of Arrowtooth Flounder larvae in food poor environments (Doyle and Mier, 2012). The larval length frequency data certainly supports the idea of very slow growth of larvae during winter months with length modes increasing only very gradually from January through April. Larval lengths increase much more substantially from April to May suggesting that the onset of increasing water temperatures and the spring zooplankton bloom facilitates a rapid increase in larval growth rates. The strategy during early ontogeny seems to be one of holding out for better conditions in spring. Certainly the cold temperatures in deep water during winter months are likely to facilitate this “holding pattern”, especially if lipid reserves are maintained by very low metabolic rates, as has been observed for Pacific Cod larvae (Laurel et al., 2011).

Given that Arrowtooth Flounder is such a successful species in the GOA, its early life history phenology of apparent extreme mismatch with spring copepod production does not seem to be disadvantageous. The low abundance of zooplankton predators in the environment during the early larval phase may confer a survival advantage (Doyle and Mier, 2012). However, the question of food availability for first-feeding larvae in slope and oceanic waters during winter (January-March) remains a mystery. It is interesting to hypothesize about potential larval prey based on what is known about seasonal patterns in zooplankton production at the shelf break and in adjacent deep water over the basin. For instance, it is known that large, lipid-rich oceanic copepods, primarily *Neocalanus plumchrus* and *N. flemingeri*, reproduce off the shelf at depths mostly greater than 500 m in the northern GOA during winter, and early copepodid stages are transported on to the shelf in March (Miller and Clemons, 1988; Coyle et al., 2013). It is hypothesized, therefore, that eggs, nauplii and earliest copepodite stages of these *Neoclanus* species are an important source of nutrition for Arrowtooth flounder during early ontogeny, and may be critical to bridging the gap between peak abundance of larvae and peak availability of shelf based spring zooplankton production. Also unkown is the potential availability and utilization of protozoan plankton in the diets of first-feeding Arrowtooth Flounder and other larvae that are abundant during winter months off the shelf (Montagnes et al., 2010).

The early life history “Holding Pattern” is also apparent on a spatial scale in the seasonal progression in distribution of eggs and larvae in the western GOA. From January through early March, eggs and larvae remain almost exclusively over the continental slope region, and are most abundant in association with troughs and canyons that intersect the slope. During this period, larvae are almost entirely smaller than 8 mm in length. The apparent ingress of larvae onto the shelf, especially in association with Amatuli Trough and outer Shelikof Sea Valley, occurs primarily from April onwards. By May and June larvae are distributed throughout the shelf although high densities remain over the outer shelf and slope. These older, larger, and likely more behaviorally competent larvae may be better able to enhance their onshore transport than younger larvae and perhaps this is also related to the ontogenetic movement of larvae towards the surface apparent in the vertical distribution data. Arrowtooth Flounder nursery grounds are nearshore and so successful cross shelf transport of larvae from the slope regions is an essential life cycle feature (Bailey and Picquelle, 2002). Several different cross-shelf transport mechanisms for deep water spawned flatfish larvae have been identified for the GOA. They include episodes of downwelling relaxation that result in transport of offshore water onto the shelf at depth, bathymetric steering in canyons, eddies along the slope that can occasionally mix water onto the shelf, and seasonal or episodic periods of downwelling favorable conditions (e.g. wind induced) that may transport larvae occurring in surface waters inshore (Stabeno et al., 2004; Bailey et al., 2008; Atwood et al., 2010). Arrowtooth Flounder larvae presumably take advantage of all of these mechanisms dependent on ontogenetic stage of development, location in the water column, and swimming ability.

For Arrowtooth Flounder, the GOA late spring time-series of larval abundance is representative of survival to the late larval stage with the extended early ontogeny environmental exposure and response presumably incorporated into this trend. The high mean length values, and degree of variability in the larval length frequencies across years, seem to reflect this extended interaction with the pelagic environment and consequent complex outcome. Nevertheless, the positive correlation between larval length and water temperature does seem to represent enhanced growth during warm conditions, which may favor higher levels of survival. Even though abundance levels for larvae are relatively low at this time of year, and the time series location is not likely to be representative of the entire population, Doyle et al. (2009) did identify a significant positive relationship between larval abundance and enhanced wind-driven alongshore and onshore transport. Similarly, Bailey and Picquelle (2002) found that Arrowtooth Flounder larvae were more abundant in coastal areas of the western GOA during El-Nino events which they attribute to enhanced onshore transport during those years.

Arrowtooth Flounder is identified as a member of the “Early Phenology” group among species early life history strategies in the GOA, with the primary characteristic being occurrence of spawning during winter, and usually in deep water (Doyle and Mier, 2012). Although vulnerabilities of this strategy in relation to mismatch with larval food resources may be important for early larvae, it seems to be a successful strategy in which the species displays a considerable degree of resilience to environmental forcing during early life. For Arrowtooth Flounder, the resilience may in large part be due to the observed temporal and spatial “Holding Pattern” that is manifest in slow growth, extended lipid reserves, and retention of eggs and early larvae in cold water off the shelf during winter. The established connection with onshore transport processes due to deposition of pelagic eggs in deep water also highlights the critical nature of the extensive larval drift phase for this species, which ultimately has to traverse the shelf to nearshore nursery areas. Focusing efforts on determining environmental exposure and response patterns during this extensive pelagic phase, and onshore drift and migration, is essential to understanding the mechanisms driving early life history survival.

3.12. Conclusions

Characterization of fish species’ interaction with the pelagic environment during early ontogeny facilitates the identification of factors that may influence early life history aspects of the recruitment response to the oceanic environment. The early life history exposure profiles presented here for the GOAIERP focal species are valuable in this regard. They advance our ecological understanding of the pelagic exposure phase, and fine-tune our focus for the discernment of potential response patterns to environmental forcing at appropriate, species-specific temporal and spatial scales representing sub-intervals of early life. The comprehensive early life history details have also been incorporated into the GOAIERP Individual-Based Models (IBMs) that have been developed to represent the complex ontogenetic pathway from spawning to recruitment for these species. Specifically, the early ontogeny data and synthesis presented here have been utilized for setting initial conditions for the IBMs of the focal species. Further examination of these data to synthesize patterns in individual (or subsets of) years from the historical range can be utilized for validation of the IBM results.

Unique characteristics of each species’ exposure profile are identified, and evaluated as adaptive features that may confer resilience or vulnerability to the planktonic phase of life, depending on variability in the environment relative to long-term prevailing conditions. Pacific Cod's "All-Eggs-In-One-Basket" strategy of single-batch spawning during late winter with an associated narrow, early spring peak in larval abundance seems disadvantageous in terms of temporal match with optimal conditions, especially in relation to food availability. However, this is moderated by extremely high fecundity, and a limited pelagic drift phase for this species seems to favor retention of larvae in shelf waters close to potential nursery areas. Although the phenology of peak spawning and abundance of larvae for Walleye Pollock is the same as for Pacific Cod, with similar vulnerabilities, Walleye Pollock displays a strategy of "Bet-Hedging" in that the temporal and spatial range of spawning is extended, and multiple batches of eggs are produced by individual females. In addition, its pelagic life is longer and juveniles remain pelagic, extending the utilization of planktonic food resources. The "Synchronized" characteristic of rockfish reproduction in spring (representative of Pacific Ocean Perch), that matches extrusion and peak abundance of larvae with the peak period of zooplankton prey abundance, is an adaptive feature that offsets the disadvantage of limited lipid reserves for these larvae. The "Extreme Epipelagic" early life history strategy of Sablefish has the advantage of allowing extensive temporal and spatial utilization of food resources throughout the surface layer of the ocean from shelf waters to deep water over the slope and Northeast Pacific basin. An inherent disadvantage of this strategy, however, may be the greater degree of variability in conditions at the ocean surface relative to deeper in the water column. Suspended progress in both growth and transport of larvae during winter months characterizes the "Holding Pattern" early life history strategy of Arrowtooth Flounder. Extended utilization of lipid reserves in cold water over the slope, and observed synchrony between peak abundance of first-feeding larvae and winter production of oceanic species of copepods (*Neocalanus* spp.), seems to offset the extreme mismatch between early larvae and the spring copepod production on the shelf.

Along with output from the IBMs, these pelagic exposure profiles contribute to the development of hypotheses regarding physical and biological environmental variables that could be tested as plausible predictors of early life history aspects of recruitment variation. Furthermore, they can be incorporated into risk analysis and management strategy evaluations for species in the context of a changing climate.

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References

Abookire, A.A., and K.M. Bailey, 2007. The distribution of life cycle stages of two deep-water pleuronectids, Dover sole (*Microstomus pacificus*) and rex sole (*Glyptocephalus zachirus*), at the northern extent of their range in the Gulf of Alaska. J. Sea Res. 57: 198–208.

Atwood, E., J.T. Duffy-Anderson, J. Horne and C.A. Ladd. 2010. Influence of mesoscale eddies on ichthyoplankton assemblages in the Gulf of Alaska. Fish. Oceanogr. 19(6): 493-507.

Bailey, K.M. 2000. Shifting control of recruitment of walleye pollock, *Theragra chalcogramma*, after a major climatic and ecosystem change, Mar. Ecol. Prog. Ser. 198: 215–224.

Bailey, K.M., and S.J. Picquelle. 2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: potential transport pathways and enhanced onshore transport during ENSO events. Mar. Ecol. Prog. Ser. 236: 205-217.

Bailey, K.M., M.F. Canino, J.M. Napp, S.M. Spring and A.L. Brown. 1995. Contrasting years of prey levels, feeding conditions and mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska . Mar. Ecol. Prog. Ser. 119:11-23.

Bailey, K.M., N. Bond, and P. Stabeno. 1999. Anomalous transport of walleye pollock larvae linked to ocean and atmospheric patterns in May 1996. Fish. Oceanogr. 8: 264-273.

Bailey, K.M., L. Ciannelli and V.N. Agostini. 2003. Complexity and constraints combined in simple models of recruitment, pp. 293-302. *In* H.I. Browman and A.B. Skiftesvik (Eds.), The Big Fish Bang: Proceedings of the 26th annual larval fish conference Bergen, Institute of Marine Research, Bergen, Norway.

Bailey, K.M., L. Ciannelli, N.A. Bond, A. Belgrano, and N.C. Stenseth. 2005. Recruitment of walleye pollock in a physically and biologically complex ecosystem: A new perspective. Prog. Oceanogr. 67: 24-42.

Bailey, K.M., Brown, A.L., Yoklavich, M.M., and Mier, K.L. 1996. Interannual variability in growth of larval and juvenile walleye pollock *Theragra chaclcogramma* in the western Gulf of Alaska. Fish. Oceanogr. 5(Suppl. 1): 137-147.

Bailey, K.M., A.A. Abookire, and J.T. Duffy-Anderson. 2008. Ocean transport paths: a comparison of spawning areas, larval distributions and juvenile nurseries of offshore spawning flatfishes in the Gulf of Alaska. Fish and Fisheries 9: 44-66.

Bailey, K.M., Zhang, T., Chan, K-s, Porter, S.M., and Dougherty, A.B. 2012. Near real-time forecasting of recruitment from larval surveys: application to Alaska Pollock. Mar. Ecol. Prog. Ser. 452: 205-217.

Belkin, I., Krishfield, R., and Honjo, S. 2002. Decadal variability of the North Pacific Polar Front: Subsurface warming versus surface cooling. Geophys. Res Lett. 29(9): 1351-1354.

Blood, D.B., A.C. Matarese, and M.S. Busby. 2007. Spawning, egg development, and early life history dynamics of arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska. U.S. Dep. Commer., NOAA Prof. Paper NMFS 7, 28 pp.

Boeing, W.J., and J.T. Duffy-Anderson. 2008. Ichthyoplankton dynamics and biodiversity in the Gulf of Alaska: Responses to environmental change. Ecol. Indicat. 8: 292–302.

Brodeur, R.D., and W.C. Rugen. 1994. Diel vertical distribution of ichthyoplankton in the northern Gulf of Alaska. Fish. Bull., U.S. 92: 223-235.

Brodeur, R.D., M.S. Busby, and M.T. Wilson. 1995. Summer distribution of early life stages of walleye pollock, *Theragra chalcogramma*, and associated species in the western Gulf of Alaska, Fish. Bull., U.S. 93: 603–618.

Brodeur, R.D., and M.T. Wilson. 1996. A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. Fish. Oceanogr. 5(Suppl. 1): 148-166.

Brodeur, R.D., S.J. Picquelle, D.M. Blood, and N. Merati. 1996. Walleye pollock egg distribution and mortality in the western Gulf of Alaska. Fish. Oceanogr. 5(Suppl. 1): 92-111.

Canino, M.F., K.M. Bailey, and L.S. Incze. 1991. Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 79: 27-35.

Chilton, E. 2007. Maturity of female Northern Rockfish *Sebastses polyspinus* in the central Gulf of Alaska. Alaska Fish. Res. Bull. 12: 264-269.

Chilton, E. 2010. Maturity and growth of female Dusky Rockfish *Sebastses variabilis* in the central Gulf of Alaska. Fish. Bull., U.S. 108: 70-78.

Ciannelli, L., K.M. Bailey, K.-S. Chan, and N.C. Stenseth. 2007. Phenological and geographical patterns of walleye pollock (*Theragra chalcogramma*) spawning in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. 64: 713–722.

Coyle, K.O., and A.I. Pinchuk. 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fish. Oceanogr. 12(4/5): 327-338.

Coyle, K.O., and A.I. Pinchuk. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep Sea Res. II 52: 217-245.

Coyle, K.O., G.A. Gibson, K. Hedstrom, A.J. Hermann, and R.R. Hopcroft. 2013. Zooplankton biomass, advection and production on the northern Gulf of Alaska shelf from simulations and field observations. J. Mar. Syst. 128: 185-207.

Cury, P. 1994. Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. Can J. Fish. Aquat Sci. 51:1664-1673.

deYoung, B., M. Heath, F.E.Werner, F. Chai, B.A. Megrey, and P. Monfray. 2004. Challenges of modeling ocean basin ecosystems. Science 304(5676): 1463–1466.

Dougherty, A.B, K.M. Bailey, and K.L. Mier. 2007. Interannual differences in growth and hatch date distributions of age-0 walleye Pollock *Theragra chalcogramma* (Pallas) sampled from the Shumagin Islands region of the Gulf of Alaska, 1985-2001. J. Fish. Biol. 71:763-780.

Dougherty, A., K. Bailey, T. Vance, and W. Cheng. 2012. Underlying causes of habitat-associated differences in size of age-0 walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. Mar. Biol. 159:1733-1744.

Doyle, M.J. 1992. Neustonic ichthyoplankton in the northern region of the California Current ecosystem. Calif. Coop. Oceanic Fish. Invest. Rep. 33: 141-161.

Doyle, M.J., W.C. Rugen, and R.D. Brodeur. 1995. Neustonic ichthyoplankton in the western Gulf of Alaska during spring. Fish. Bull., U.S. 93: 231-253.

Doyle, M.J., K.L. Mier, R.D. Brodeur, and M.S. Busby. 2002. Regional variations in springtime ichthyoplankton assemblages in the northeast Pacific Ocean. Prog. Oceanogr. 53: 247-282.

Doyle, M.J., S.J. Picquelle, K.L Mier, M. Spillane, and N. Bond. 2009. Larval fish abundance and environmental forcing in the Gulf of Alaska, 1981-2003. Prog. Oceanogr. 80:163-187.

Doyle, M.J., and K.L. Mier, 2012. A new conceptual framework for evaluating the early ontogeny phase of recruitment processes among marine fish species. Can. J. Fish.Aquat. Sci. 69: 2112-2129.

Dunn, J.R., and A.C. Matarese. 1987. A review of the early life history of Northeast Pacific gadoid fishes. Fish. Res. 5: 163-184.

Fuiman, L.A. 2002. Special considerations of fish eggs and larvae. In Fishery Science: The unique contributions of early life stages. Edited by L.A. Fuiman and R.G. Werner. Blackwell Science, Oxford, UK. pp. 1-32.

Gaichas, S.K., K.Y. Aydin, and R.C. Francis. 2011. What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling. Can. J. Fish.Aquat. Sci. 68: 1553-1578.

Grover, J.J., and B.L. Olla. 1986. Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria*. Fish. Bull., U.S. 84: 484-489.

Grover, J.J., and B.L. Olla. 1990. Food habits of larval sablefish *Anoplopoma fimbria* from the Bering Sea. Fish. Bull., U.S. 88(4): 811-814.

Haltuch, M.A., and A.E. Punt, 2011. The promises and pitfalls of including decadal-scale climate forcing of recruitment in groundfish stock assessment. Can. J. Fish. Aquat. Sci. 68: 912-926.

Hinckley, S. 1990. Variation in egg size of walleye pollock *Theragra chalcogramma* with a preliminary examination of the effect of egg size on larval size. Fish. Bull., U.S. 88: 471-483.

Houde, E.D. 2008. Emerging from Hjort's Shadow. J. Northw. Atl. Fish. Sci. 41: 53-70.

Hulson, P.J.F, D.H. Hanselman, S.K. Shotwell, C.R. Lunsford, and J. Ianelli. 2014. Assessment of the Pacific ocean perch stock in the Gulf of Alaska. In Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, 605 W 4th Ave, Suite 306 Anchorage, AK 99501. pp. 547-638.

Hurst, T.P., D.W. Cooper, J.S. Scheingross, E.M. Seale, B.J. Laurel, and M.L. Spencer. 2009. Effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod (*Gadus macrocephalus*). Fish. Oceanogr. 18: 301-311.

Hurst, T.P., B.J. Laurel, and L. Ciannelli. 2010. Ontogenetic patterns and temperature-dependent growth rates in early life stages of Pacific cod (*Gadus macrocephalus*). Fish. Bull., U.S. 108: 382-392.

Jump, C.M., J.T. Duffy-Anderson, and K.L. Mier. 2008. Comparison of the Sameoto, Manta, and MARMAP neustonic ichthyoplankton samplers in the Gulf of Alaska. Fish. Res. 89: 222–229.

Kamin, L.M., K.J. Palof, J. Heifetz, and A.J. Gharrett. 2013. Interannual and spatial variation in population genetic composition of young-of-the-year Pacific ocean perch (*Sebastes alutus*) in the Gulf of Alaska. Fish. Oceanogr. 23 (1): 1-17.

Kendall, A.W., Jr. 1991. Systematics and identification of larvae and juveniles of the genus *Sebastes*. Environ. Biol. Fishes 30: 173-190.

Kendall, A.W., Jr., and A.C. Materese. 1987. Biology of eggs, larvae, and epipelagic juveniles of sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. Mar. Fish. Rev. 49: 1-13.

Kendall, A.W., Jr., L.S. Incze, P.B. Ortner, S.R. Cummings, and P.K. Brown. 1994. The vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S. 92: 540-554.

Kendall, A.W., Jr., R.I. Perry, and S. Kim (eds.) 1996. Fisheries oceanography of walleye pollock in Shelikof Strait, Alaska. Fish. Oceanogr. 5 (Suppl. 1), 203p.

Laurel, B.J., A.W. Stoner, C.H. Ryer, T.P. Hurst, and A.A. Abookire. 2007. Comparative habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras and laboratory techniques. J. Exp. Mar. Biol. Ecol. 351: 42-55.

Laurel, B.J., T.P. Hurst, L.A. Copeman, and M.W. Davis. 2008. The role of temperature on the growth and survival of early and late hatching Pacific cod larvae (*Gadus macrocephalus*). J. Plankton Res. 30(9): 1051-1060.

Laurel, B.J., T.P Hurst, and L. Ciannelli. 2011. An experimental examination of temperature interactions in the match-mismatch hypothesis for Pacific cod larvae. Can. J. Fish. Aquat. Sci. 68: 51-61.

Le Page, C., and P. Cury. 1997. Population viability and spatial fish reproductive strategies in constant and changing environments: an individual-based modeling approach. Can. J. Fish. Aquat. Sci. 54: 2235-2246.

Mason, J.C., R.J. Beamish, and G.A. McFarlane. 1983. Sexual maturity, fecundity, spawning and early life history of sablefish (*Anoplopoma fimbria*) off the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 40: 2126-2134.

Matarese, A.C., A.W. Kendall Jr., D.M. Blood, and B.M. Vinter. 1989. Laboratory guide to the early life history stages of Northeast Pacific fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80, 652 pp.

Matarese, A.C., D.M. Blood, S.J. Picquelle, and J.L. Benson. 2003. Atlas of the abundance and distribution patterns of ichthyoplankton from the northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center (1972-1996). U.S. Dep. Commer., NOAA Prof. Paper NMFS 1, 281 pp.

Mecklenburg, C.W., T.A. Mecklenburg, and L.K. Thorsteinson. 2002. Fishes of Alaska. American Fisheries Society, Bethesda, Md., 1037 pp.

Miller, C.B., and M.J. Clemons. 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Progr. Oceanogr. 20: 293-313.

Miller, B.S., and A.W. Kendall Jr. 2009. Early life history of marine fishes. University of California Press, Berkeley and Los Angeles, CA. 364 pp.

Montagnes, D.J.S., J.F. Dower, and G.M. Figueiredo. 2010. The protozoan-ichthyoplankton trophic link: an overlooked aspect of aquatic food webs. J. Eukaryotic Microbiol. 57: 223-228.

Moss, J.H., M.A. Zaleski, and R.A. Heintz (in press). Distribution, diet and energetic conditions of age-0 Walleye Pollock (*Gadus chalcogrammus*) and Pacific Cod (*Gadus macrocephalus*) inhabiting the Gulf of Alaska. Deep Sea Res. II, this volume.

Mueter, F.J., and B.L. Norcross. 1999. Linking community structure of small demersal fishes around Kodiak Island, Alaska, to environmental variables. Mar. Ecol. Prog. Ser. 190: 37-51.

Mundy, P.R. (Editor). 2005. The Gulf of Alaska: Biology and Oceanography. Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, AK. 220 pp.

Myers, R.A. 1998. When do environment-recruitment correlations work? Rev. Fish. Biol. Ecol. 8: 285-305.

Napp, J.M., L.S. Incze, P.B. Ortner, D.L. Siefert, and L. Britt. 1996. The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. Fish. Oceanogr. 5 (Suppl.1): 19-38.

Page, L.M., H. Espinosa-Pérez, L.T. Findley, C.R. Gilbert, R.N. Lea,N.E. Mandrak, R.L. Mayden, and J.S. Nelson. 2013. Common and Scientific Names of Fishes from the United States, Canada, and Mexico, 7th edition. American Fisheries Society Special Publication 34. 243 p.

Palof, K.J., J. Heifetz, and A.J. Gharrett. 2011. Geographic structure in Alaskan Pacific ocean perch (*Sebastes alutus*) indicates limited lifetime dispersal. Mar. Biol. 158: 779-792.

Porter, S.M., L. Ciannelli, N. Hillgruber, K.M. Bailey, K.-S. Chan, M.F. Canino and L.J. Haldorson. 2005. Environmental factors influencing larval walleye pollock *Theragra chalcogramma* feeding in Alaskan waters. Mar. Ecol. Prog. Ser. 302: 207–217.

Reynolds, R.W., N.A. Rayner, T.M. Smith, D.C. Stokes, and W. Wang. 2002. An improved in situ and satellite SST analysis for climate. Journal of Climate, 15, 1609-1625.

Rooper, C.N. 2008. An ecological analysis of rockfish (*Sebastes* spp.) assemblages in the North Pacific Ocean along broad-scale environmental gradients. Fish. Bull., U.S. 106: 1-11.

Rose, K.A. 2005. Lack of relationship between simulated fish population responses and their life history traits: inadequate models, incorrect analysis, or site-specific factors. Can. J. Fish. Aquat. Sci. 62(4): 886-902.

Sameoto, D.D., and L.O. Jaroszyinski. 1969. Otter surface trawl: a neuston net. J. Fish. Res. Board. Can. 26: 2240-2244.

Shenker, J.M., and B.L. Olla. 1986. Laboratory feeding and growth of juvenile sablefish *Anoplopoma fimbria*. Can. J. Fish. Aquat. Sci. 43: 930-937.

Shotwell, S.K., D.H. Hanselman, I.M. Belkin. 2012. Toward biophysical synergy: Investigating advection along the Polar Front to identify factors influencing Alaska sablefish recruitment. Deep-Sea Res. II (2012) http://dx.doi.org/10.1016/j.dsr2.2012.08.024.

Sigler, M.F., T.L. Rutecki, D.L. Courtney, J.F. Karinen, and M.-S. Yang. 2001. Young of the year sablefish abundance, growth, and diet in the Gulf of Alaska. Alaska Fish. Res. Bull. 8(1): 57-70.

Shima, M., and K.M. Bailey. 1994. Comparative analysis of ichthyoplankton sampling gear for early life stages of walleye pollock (*Theragra chalcogramma*). Fish. Oceanogr. 3: 50-59.

Spies, I., and B.J. Turnock. 2013. 7. Assessment of the arrowtooth flounder stock in the Gulf of Alaska. North Pacific Fishery Management Council, 605 W. 4th Ave., Anchorage, AK 99501. Gulf of Alaska, Stock Assessment and Fishery Evaluation Report. Pp. 541-610.

Stabeno, P.J., N.A. Bond, A.J. Hermann, N.B. Kachel, C.W. Mordy, and J.E. Overland. 2004. Meteorology and oceanography of the northern Gulf of Alaska. Cont. Shelf Res. 24(7-8): 859–897.

Stachura, M.M., T.E. Essington, N.J. Mantua, A.B. Hollowed, M.A. Haltuch, P.D. Spencer, T.A. Branch, and M.J. Doyle. 2014. Linking Northeast Pacific recruitment synchrony to environmental variability. Fish. Oceanogr. 23(5): 389-408. DOI: 10.1111/fog.12066

Stark, J.W. 2007. Geographical and seasonal variations in maturation and growth of female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and Bering Sea. Fish. Bull., U.S. 105: 396-407.

Strasburger, W.W., N. Hillgruber, A.I. Pinchuk, and F.J. Mueter. 2014. Feeding ecology of age-0 walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) in the Southeastern Bering Sea. Deep Sea Res. II 109: 172-180.

Tenbrink, T.T., and P.D. Spencer. 2013. Reproductive biology of Pacific Ocean Perch and Northern Rockfish in the Aleutian Islands. N. Amer. J. Fish. Manag. 33: 373-383.

Theilacker, G.H. and S.M. Porter. 1995. Condition of larval walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska assessed with histological and shrinkage indices. Fish. Bull., U.S. 93: 33-44.

Waite, J.N., and F.J. Mueter. 2013. Spatial and temporal variability of chlorophyll-*a* concentrations in the coastal Gulf of Alaska, 1998-2011, using cloud-free reconstructions of SeaWIFS and MODIS-Aqua data. Progr. Oceanogr. 116: 179-192.

Wiebe, P.D., K.H. Burt, S.H. Boyd, and A.W. Morton. 1976. A multiple opening/closing net and environmental sensing system for zooplankton. J. Mar. Res. 34: 313-326.

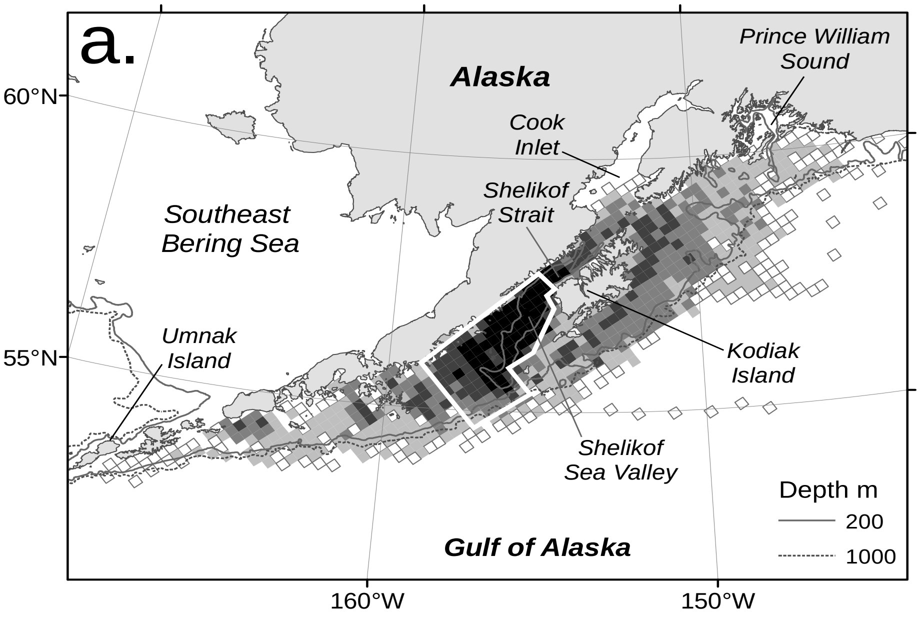
Wilson, M.T., A.L. Brown, and K.L. Mier. 2005. Geographic variation among age-0 walleye pollock (Theragra chalcogramma): evidence of mesoscale variation in nursery quality? Fish. Bull., U.S. 103(1): 207–218.

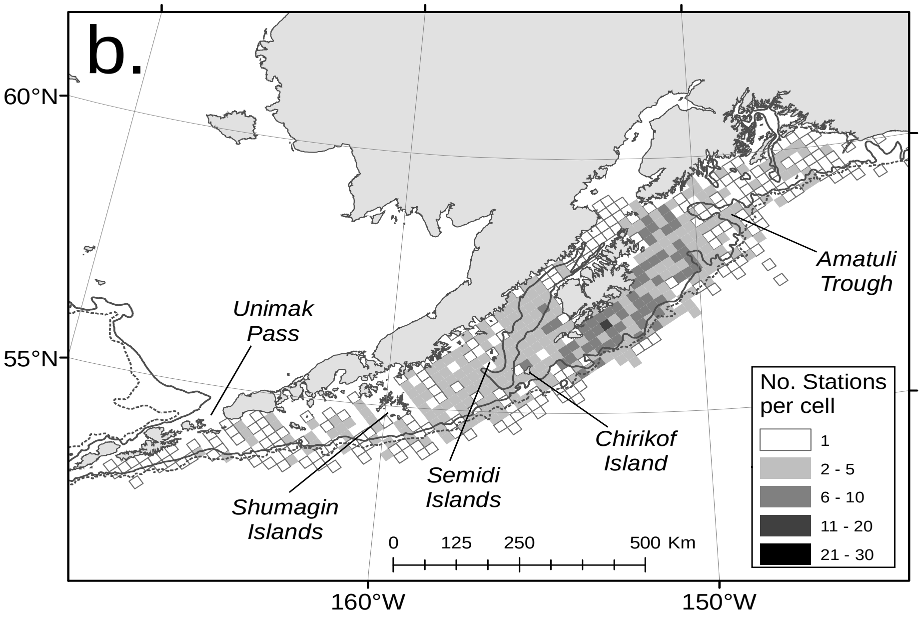
Wilson, M.T., C.M. Jump, and J.T. Duffy-Anderson. 2006. Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin (*Mallotus villosus*) and walleye pollock (*Theragra chalcogramma*). Mar. Ecol. Prog. Ser. 317: 245–258.

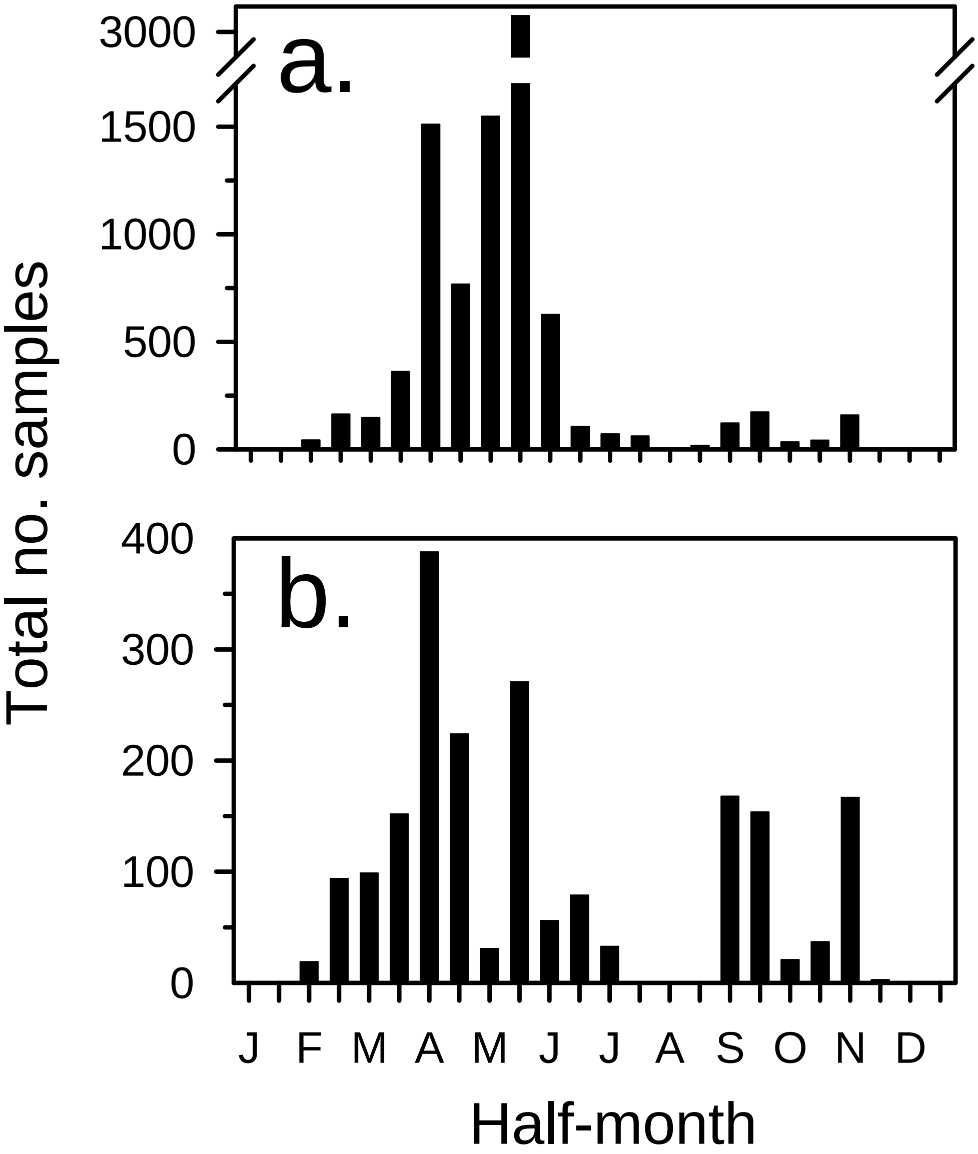
Wilson, M.T. 2009. Ecology of small neritic fishes in the western Gulf of Alaska. I. Geographic distribution in relation to prey density and the physical environment. Mar. Ecol. Prog. Ser. 392: 223-237.

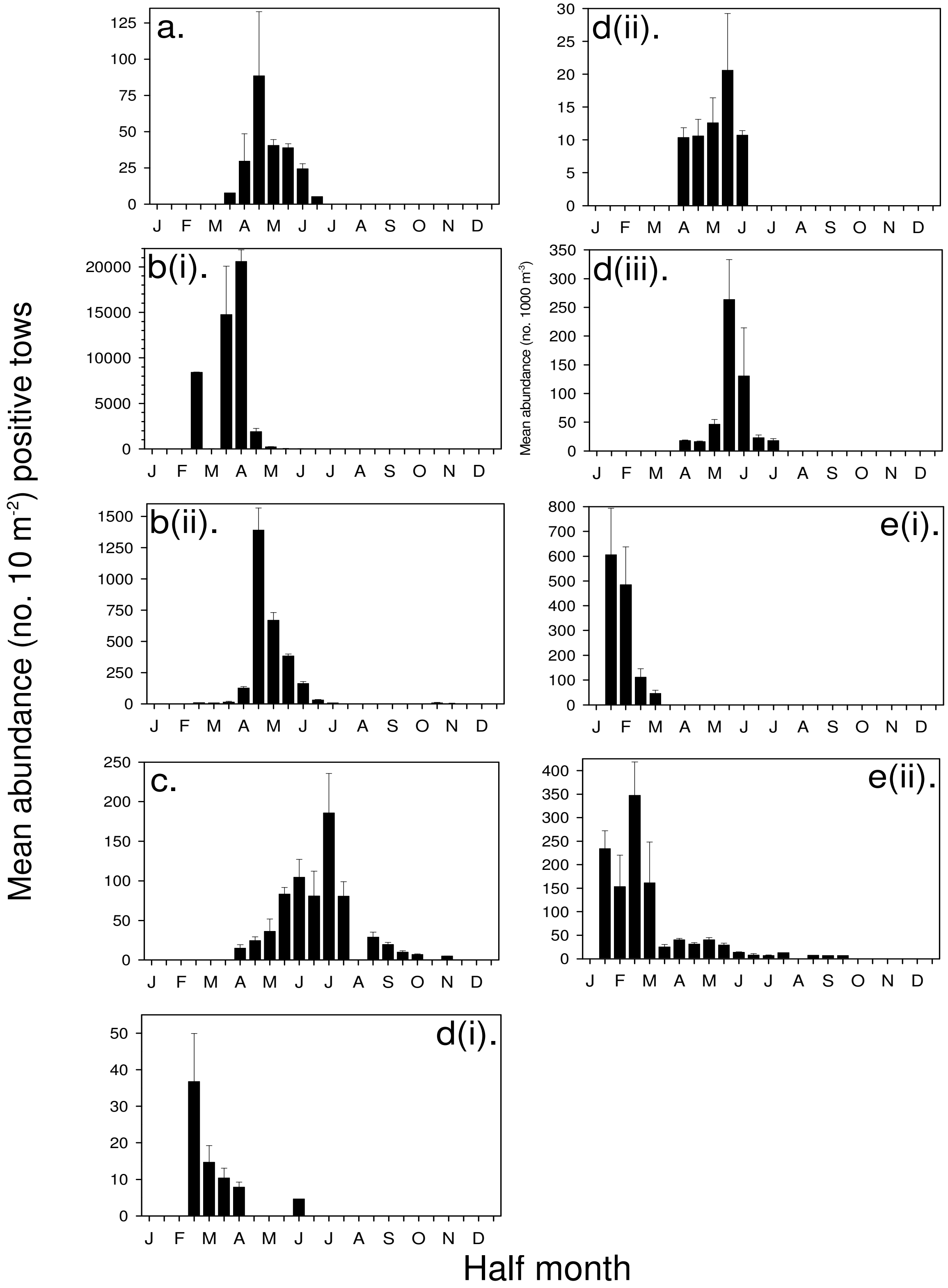
Wing, B.L. 1997. Distribution of sablefish, *Anoplopoma fimbria*, larvae in the eastern Gulf of Alaska: neuston-net tows versus oblique tows. *In* M.E. Wilkins and M.W. Saunders (Eds.), Biology and Management of Sablefish, *Anoplopoma fimbria*, p. 13-25. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 130.

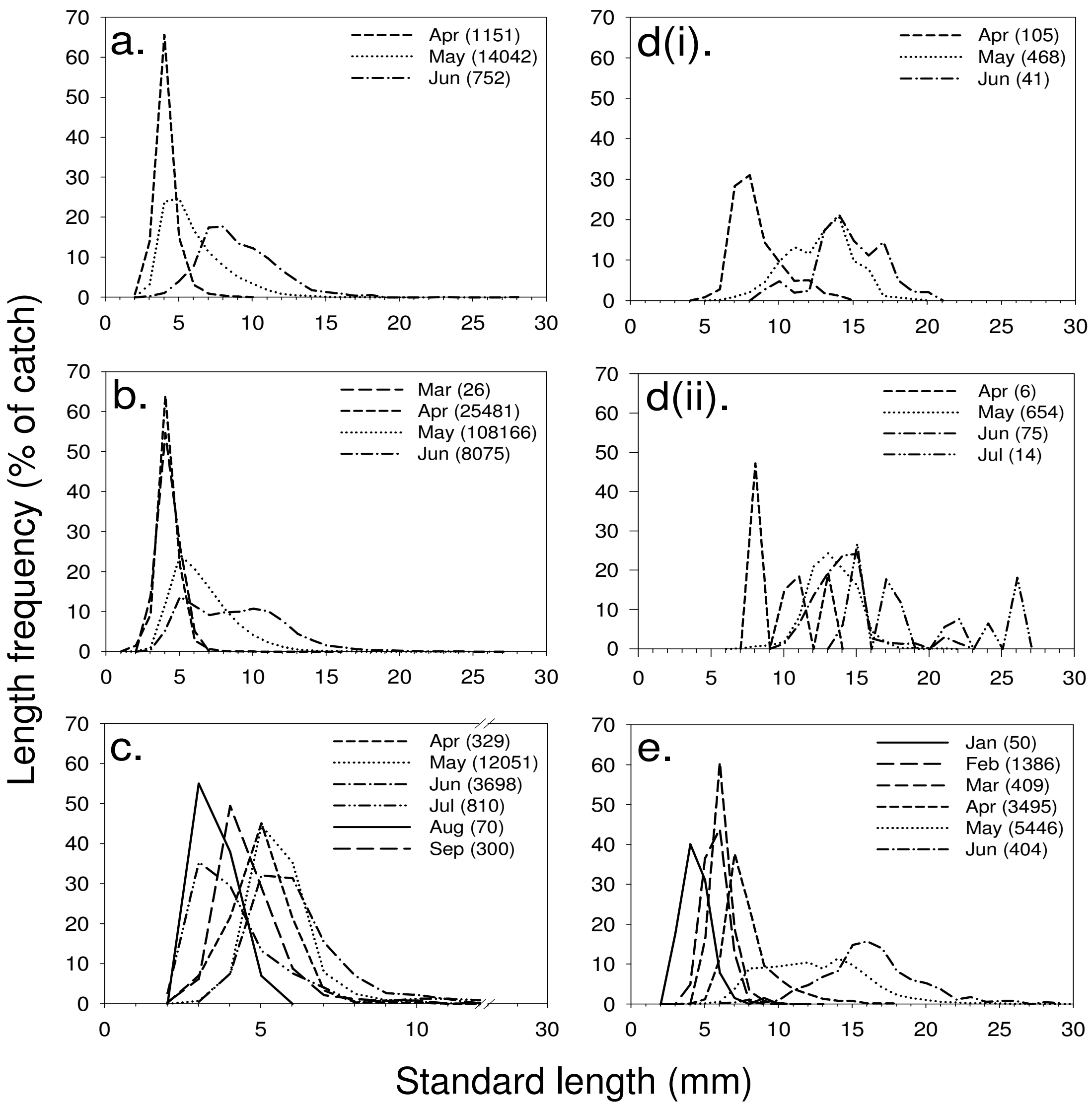
Yatsu, A., K.Y. Aydin, J.R. King, G.A. McFarlane, S. Chiba, K. Tadokoro, M. Kaeriyama, and Y. Watanabe. 2008. Elucidating dynamic responses of North Pacific fish populations to climatic forcing: Influence of life-history strategy. Prog. Oceanogr. 77: 252-268.

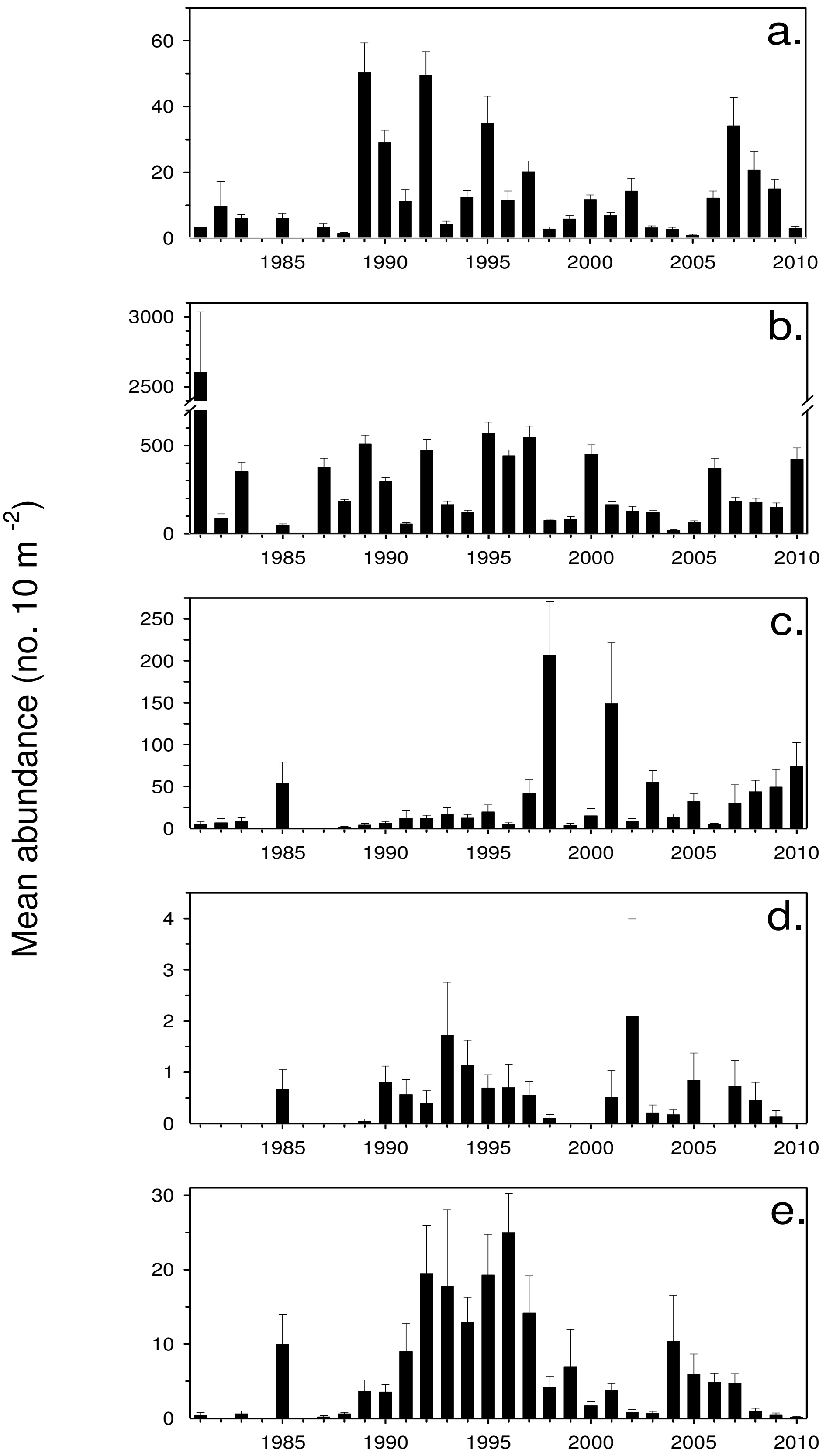

a.
60°N
55°N
160°W
150°W
Alaska
Prince William Sound
Cook Inlet
Shelikof Strait
Southeast Bering Sea
Umnak Island
Kodiak Island
Shelikof Sea Valley
Gulf of Alaska
Depth m
200
1000

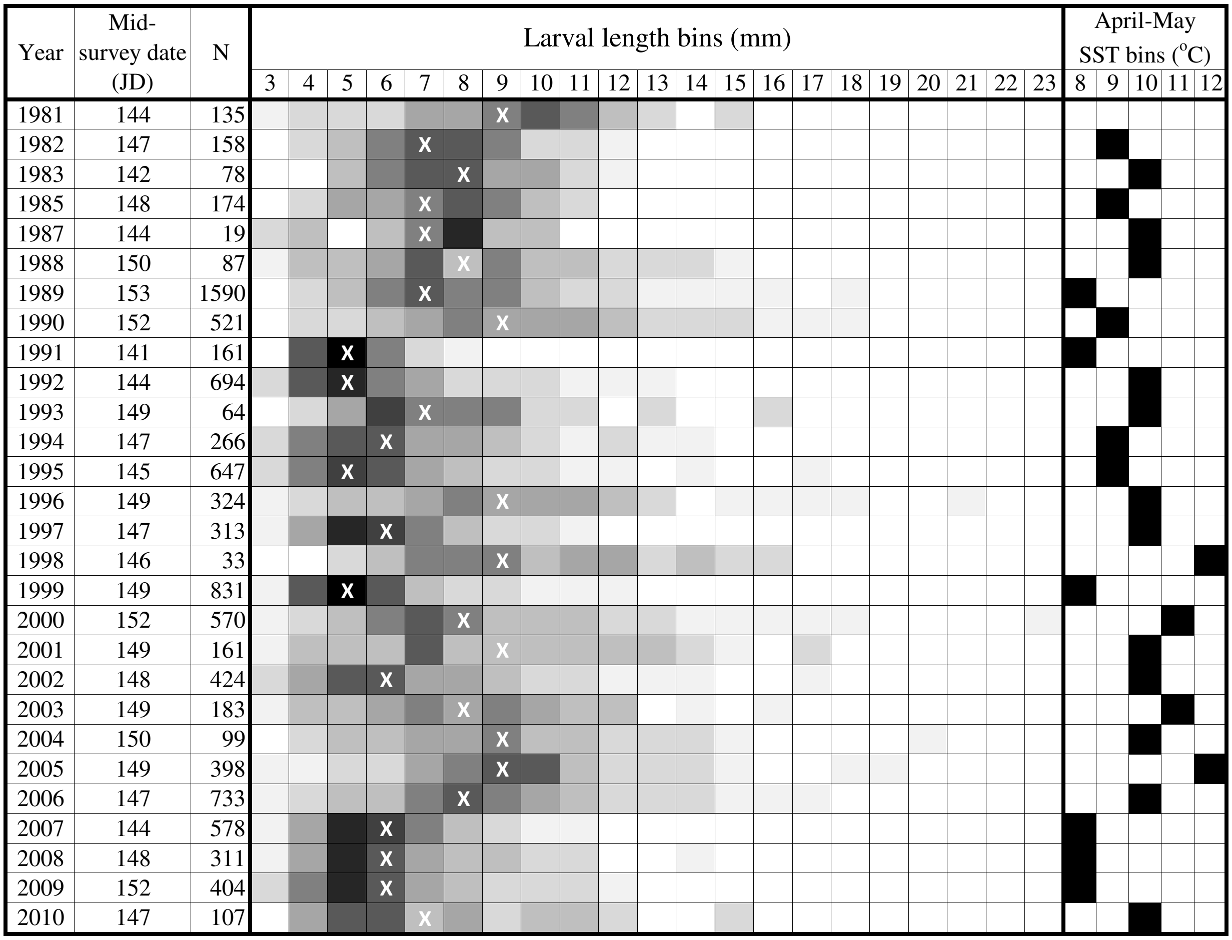

b.
60°N
55°N
160°W
150°W
Amatuli Trough
Unimak Pass
Chirikof Island
Semidi Islands
Shumagin Islands
0
125
250
500 Km
No. Stations per cell
1
2 - 5
6 - 10
11 - 20
21 - 30


a.
b.
Total no. samples
3000
1500
1000
500
0
400
300
200
100
0
J
F
M
A
M
J
J
A
S
O
N
D
Half-month


a.
0
25
50
75
100
125
b(i).
0
5000
10000
15000
20000
b(ii).
0
250
500
750
1000
1250
1500
c.
0
50
100
150
200
250
d(i).
0
10
20
30
40
50
d(ii).
0
5
10
15
20
25
30
d(iii).
0
50
100
150
200
250
300
350
Mean abundance (no. 1000 m^3)
e(i).
0
100
200
300
400
500
600
700
800
e(ii).
0
50
100
150
200
250
300
350
400
J F M A M J J A S O N D
Mean abundance (no. 10 m^{-2}) positive tows
Half month


a.
Apr (1151)
May (14042)
Jun (752)
d(i).
Apr (105)
May (468)
Jun (41)
b.
Mar (26)
Apr (25481)
May (108166)
Jun (8075)
d(ii).
Apr (6)
May (654)
Jun (75)
Jul (14)
c.
Apr (329)
May (12051)
Jun (3698)
Jul (810)
Aug (70)
Sep (300)
e.
Jan (50)
Feb (1386)
Mar (409)
Apr (3495)
May (5446)
Jun (404)
0
10
20
30
40
50
60
70
0
5
10
15
20
25
30
Length frequency (% of catch)
Standard length (mm)


Mean abundance (no. 10 m $^{-2}$)
a.
0
20
40
60
1985
1990
1995
2000
2005
2010
b.
0
500
2500
3000
1985
1990
1995
2000
2005
2010
c.
0
50
100
150
200
250
1985
1990
1995
2000
2005
2010
d.
0
1
2
3
4
1985
1990
1995
2000
2005
2010
e.
0
10
20
30
1985
1990
1995
2000
2005
2010

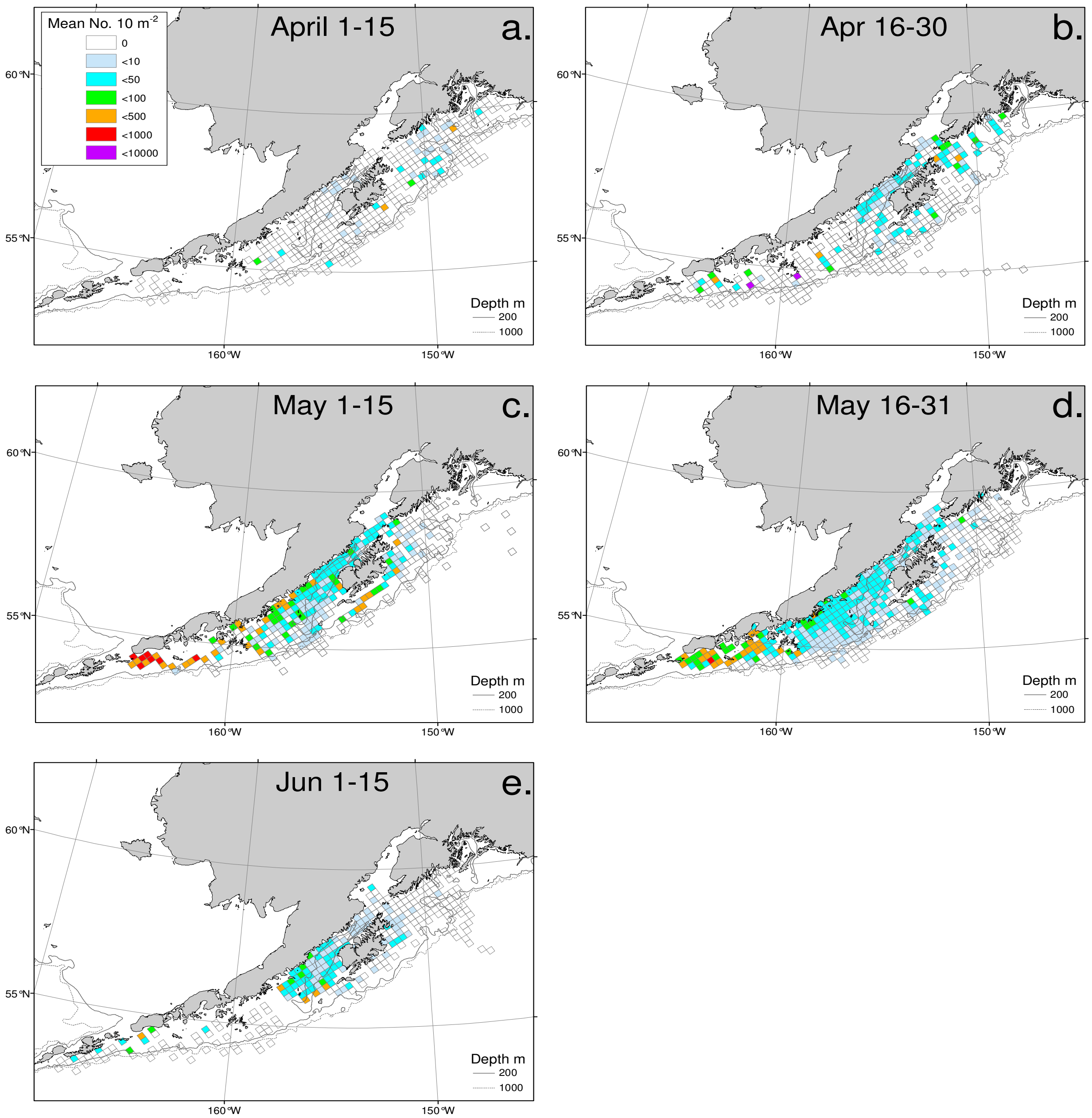


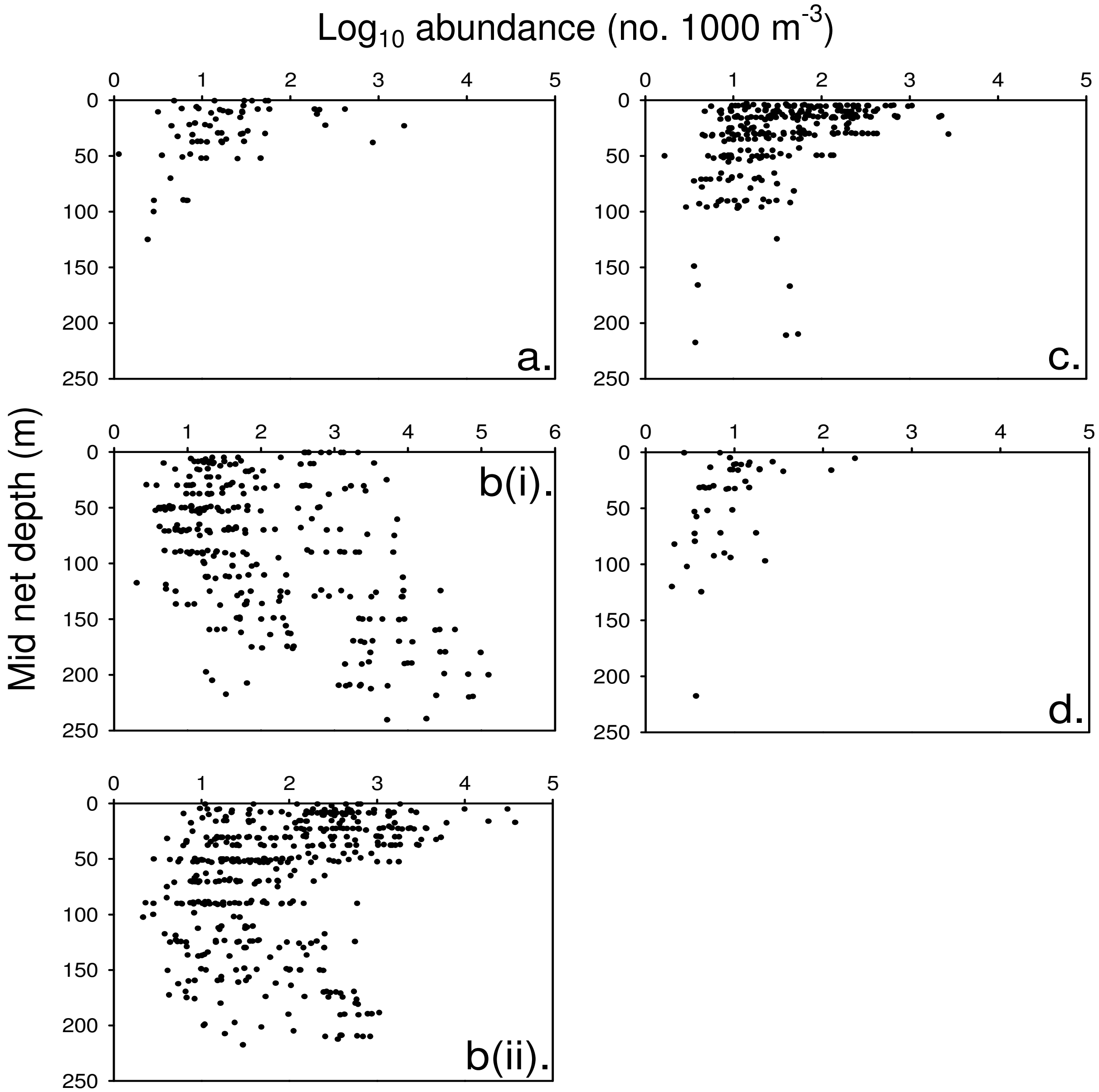
Year	Mid-survey date (JD)	N	Larval length bins (mm)																					April-May SST bins (°C)				
			3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	8	9	10	11	12
1981	144	135							X																			
1982	147	158					X																		■			
1983	142	78						X																		■		
1985	148	174					X																		■			
1987	144	19					X																			■		
1988	150	87						X																		■		
1989	153	1590					X																	■				
1990	152	521							X																■			
1991	141	161			X																			■				
1992	144	694			X																					■		
1993	149	64					X																			■		
1994	147	266				X																			■			
1995	145	647			X																				■			
1996	149	324							X																	■		
1997	147	313				X																				■		
1998	146	33							X																			■
1999	149	831			X																			■				
2000	152	570						X																			■	
2001	149	161							X																	■		
2002	148	424				X																				■		
2003	149	183						X																			■	
2004	150	99							X																	■		
2005	149	398							X																			■
2006	147	733						X																		■		
2007	144	578				X																		■				
2008	148	311				X																		■				
2009	152	404				X																		■				
2010	147	107					X																			■		

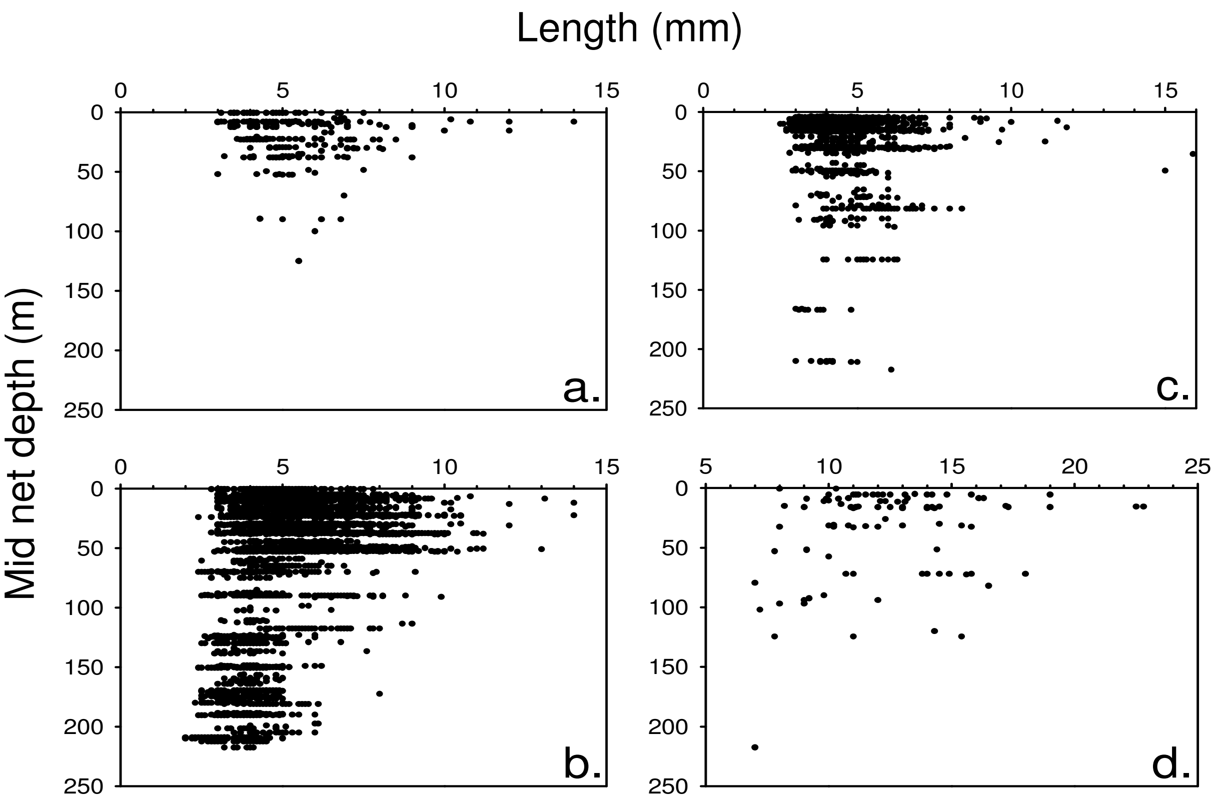
% Frequency of catch by length: 0 <1 1<5 5<10 10<15 15<20 20<25 25<30 30<35 35<55

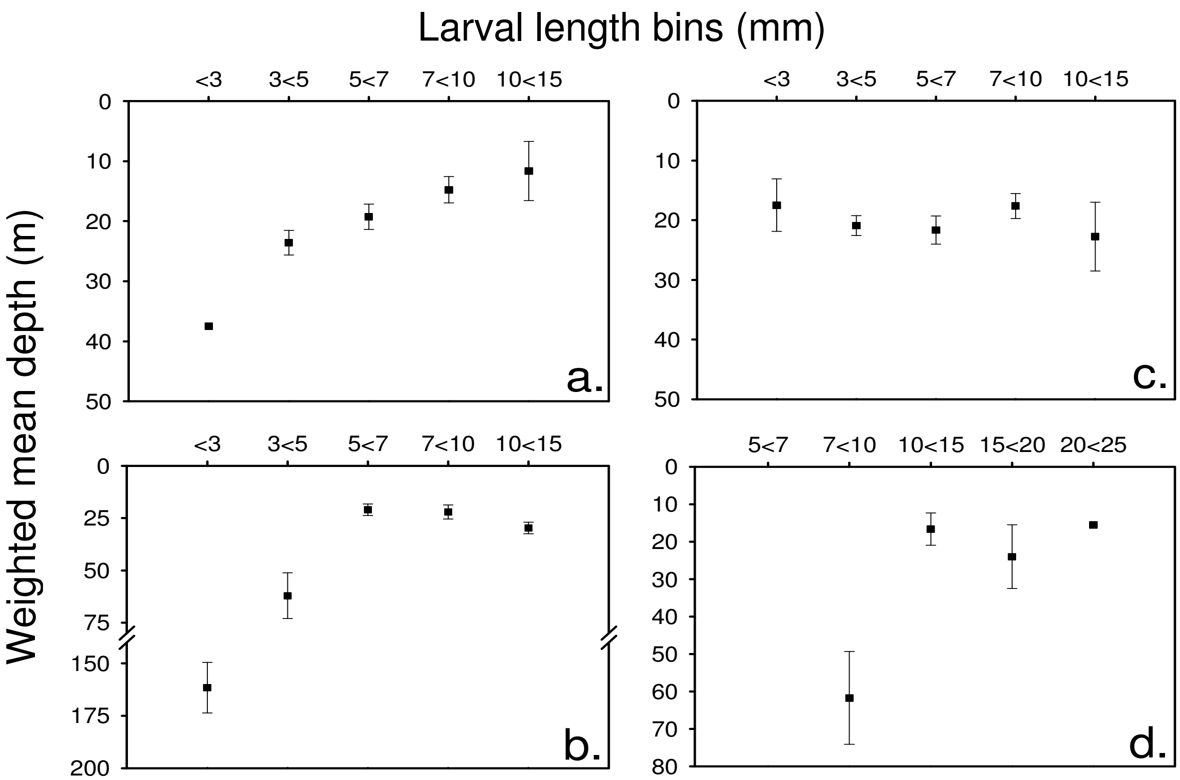
Length bin for weighted mean larval length: X

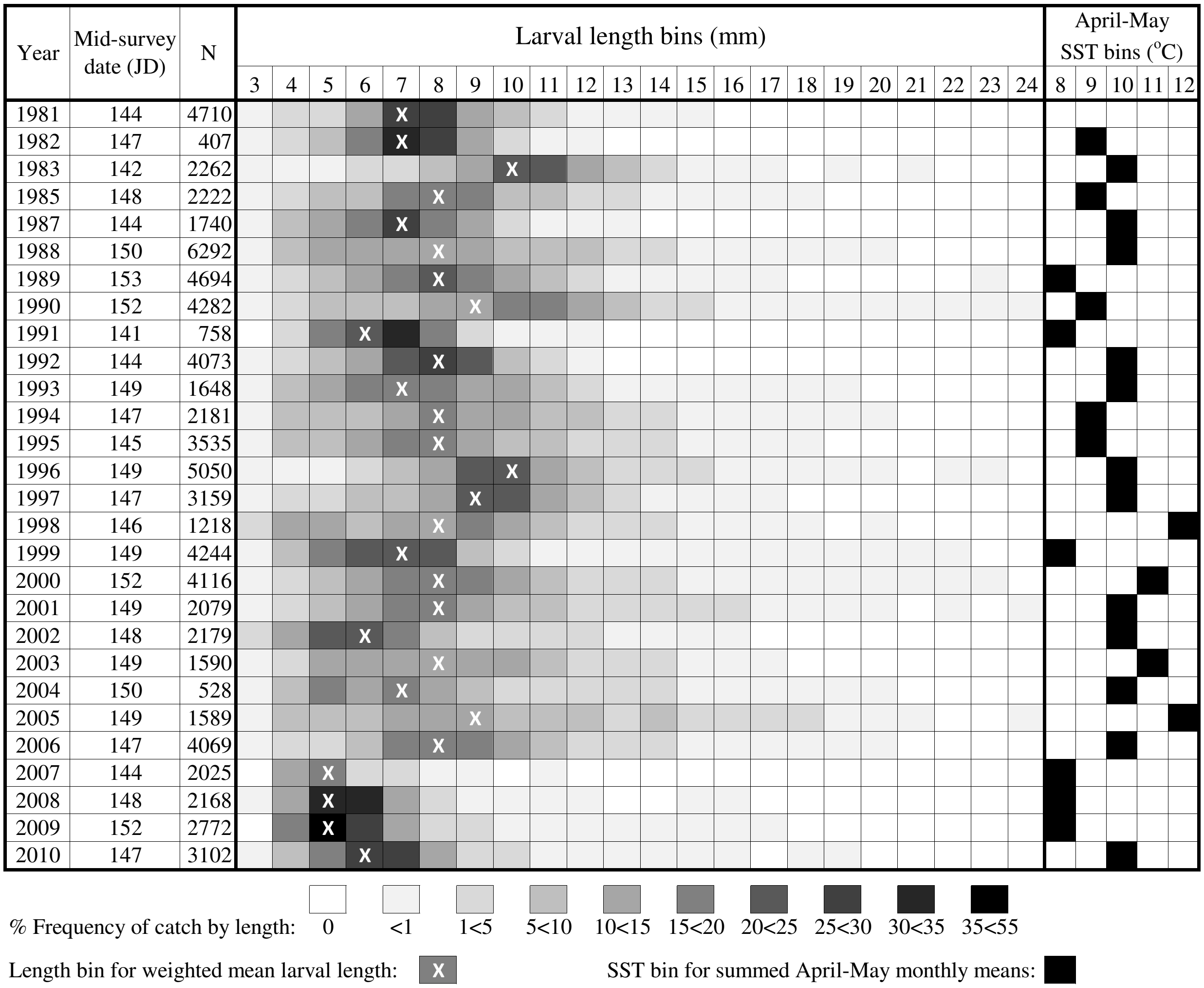
SST bin for summed April-May monthly means: ■


Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<10000
April 1-15
a.
Apr 16-30
b.
May 1-15
c.
May 16-31
d.
Jun 1-15
e.
60°N
55°N
160°W
150°W
Depth m
200
1000


Log10 abundance (no. 1000 m-3)
Mid net depth (m)
0
1
2
3
4
5
6
50
100
150
200
250
a.
b(i).
b(ii).
c.
d.


Length (mm)
Mid net depth (m)
0
5
10
15
0
50
100
150
200
250
a.
b.
c.
d.
20
25


Larval length bins (mm)
Weighted mean depth (m)
<3
3<5
5<7
7<10
10<15
0
10
20
30
40
50
a.
<3
3<5
5<7
7<10
10<15
0
10
20
30
40
50
c.
<3
3<5
5<7
7<10
10<15
0
25
50
75
150
175
200
b.
5<7
7<10
10<15
15<20
20<25
0
10
20
30
40
50
60
70
80
d.

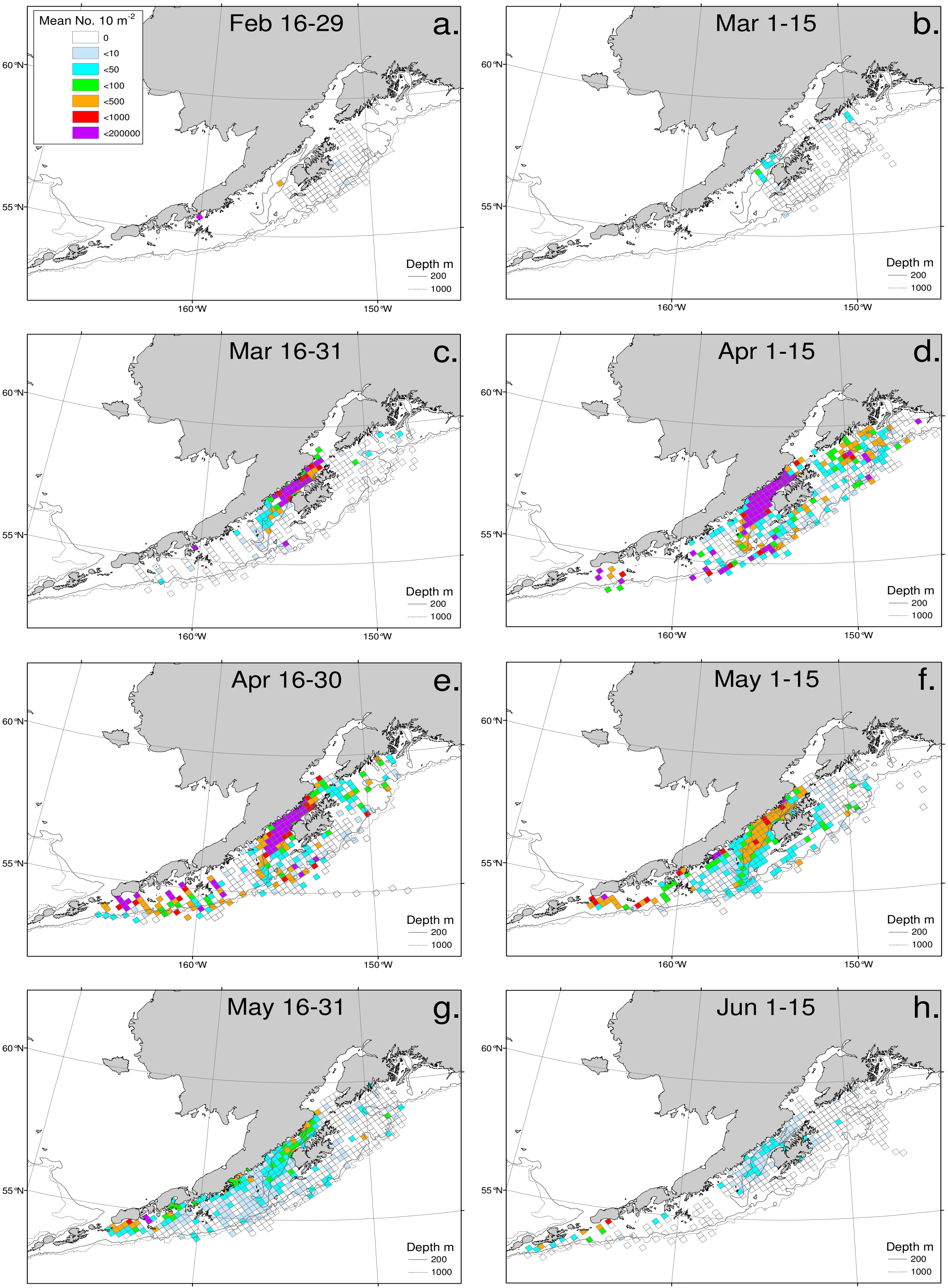


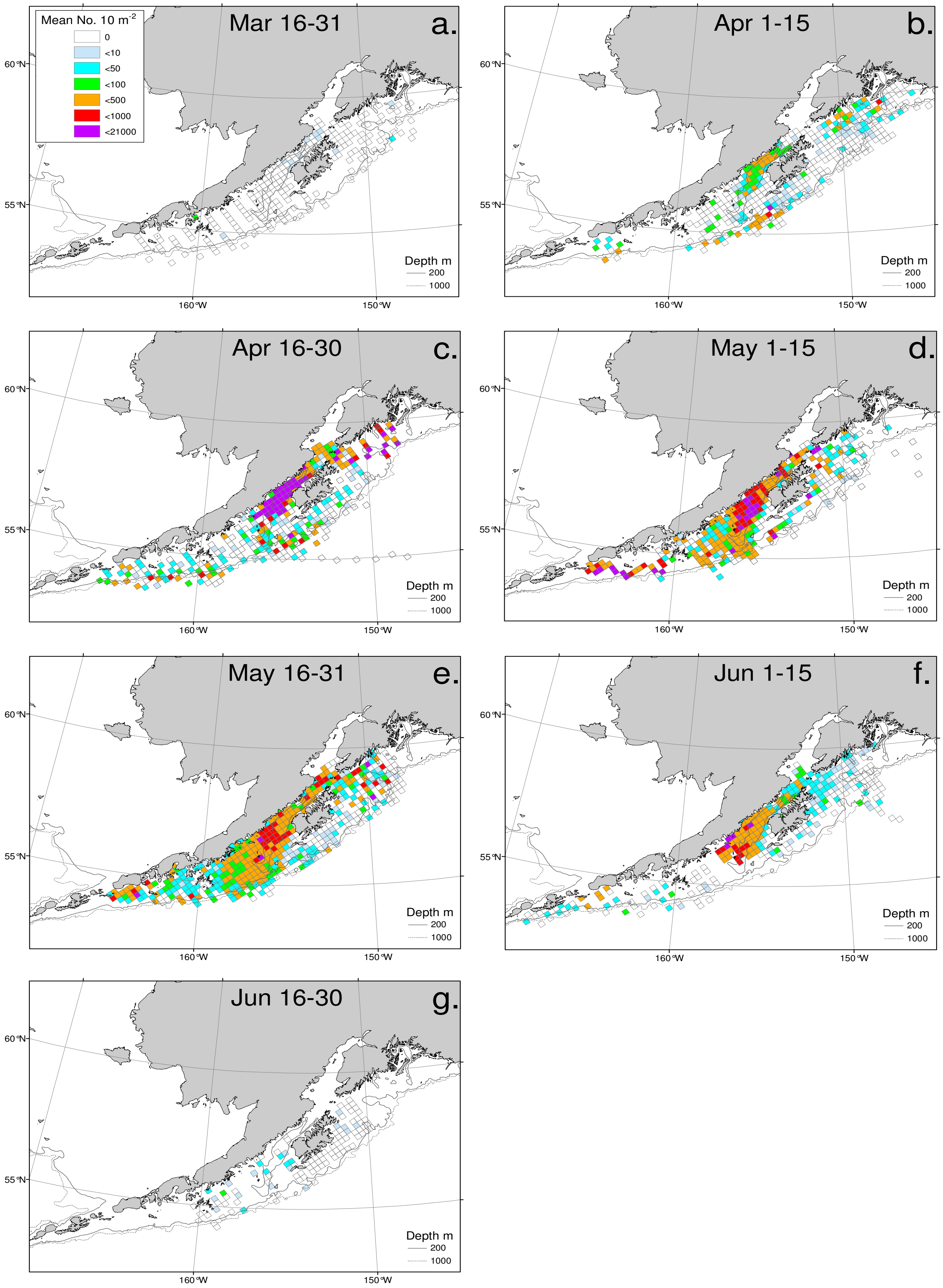
Year	Mid-survey date (JD)	N	Larval length bins (mm)																						April-May SST bins (°C)				
			3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	8	9	10	11	12
1981	144	4710					X																						
1982	147	407					X																			■			
1983	142	2262								X																	■		
1985	148	2222						X																		■			
1987	144	1740					X																				■		
1988	150	6292						X																			■		
1989	153	4694						X																	■				
1990	152	4282							X																	■			
1991	141	758				X																			■				
1992	144	4073						X																			■		
1993	149	1648					X																				■		
1994	147	2181						X																		■			
1995	145	3535						X																		■			
1996	149	5050								X																	■		
1997	147	3159							X																		■		
1998	146	1218						X																					■
1999	149	4244					X																		■				
2000	152	4116						X																				■	
2001	149	2079						X																			■		
2002	148	2179				X																					■		
2003	149	1590						X																				■	
2004	150	528					X																				■		
2005	149	1589							X																				■
2006	147	4069						X																			■		
2007	144	2025			X																				■				
2008	148	2168			X																				■				
2009	152	2772			X																				■				
2010	147	3102				X																					■		

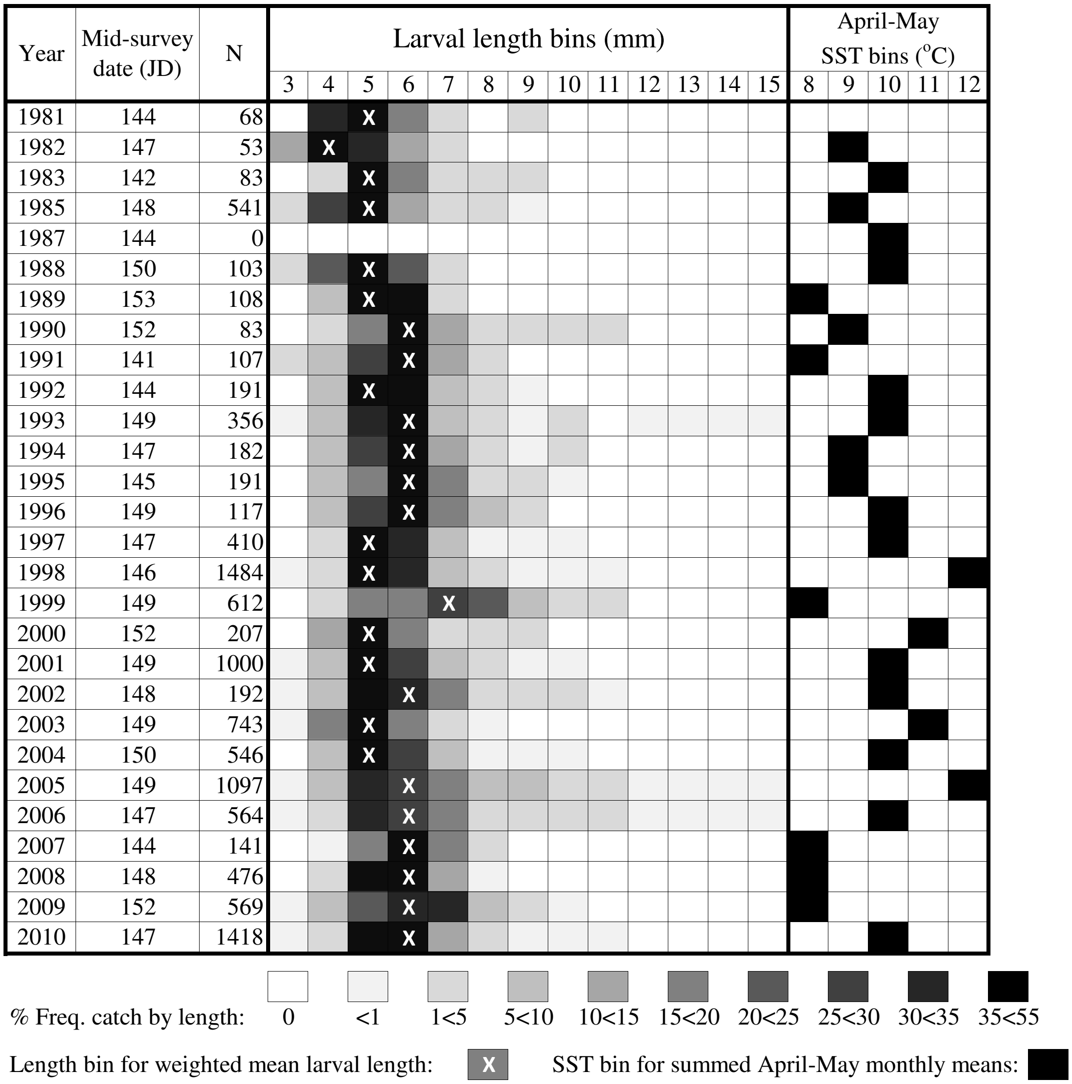
% Frequency of catch by length: 0, <1, 1<5, 5<10, 10<15, 15<20, 20<25, 25<30, 30<35, 35<55

Length bin for weighted mean larval length: X

SST bin for summed April-May monthly means: ■


Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<200000
Feb 16-29
a.
Mar 1-15
b.
Mar 16-31
c.
Apr 1-15
d.
Apr 16-30
e.
May 1-15
f.
May 16-31
g.
Jun 1-15
h.
60°N
55°N
160°W
150°W
Depth m
200
1000

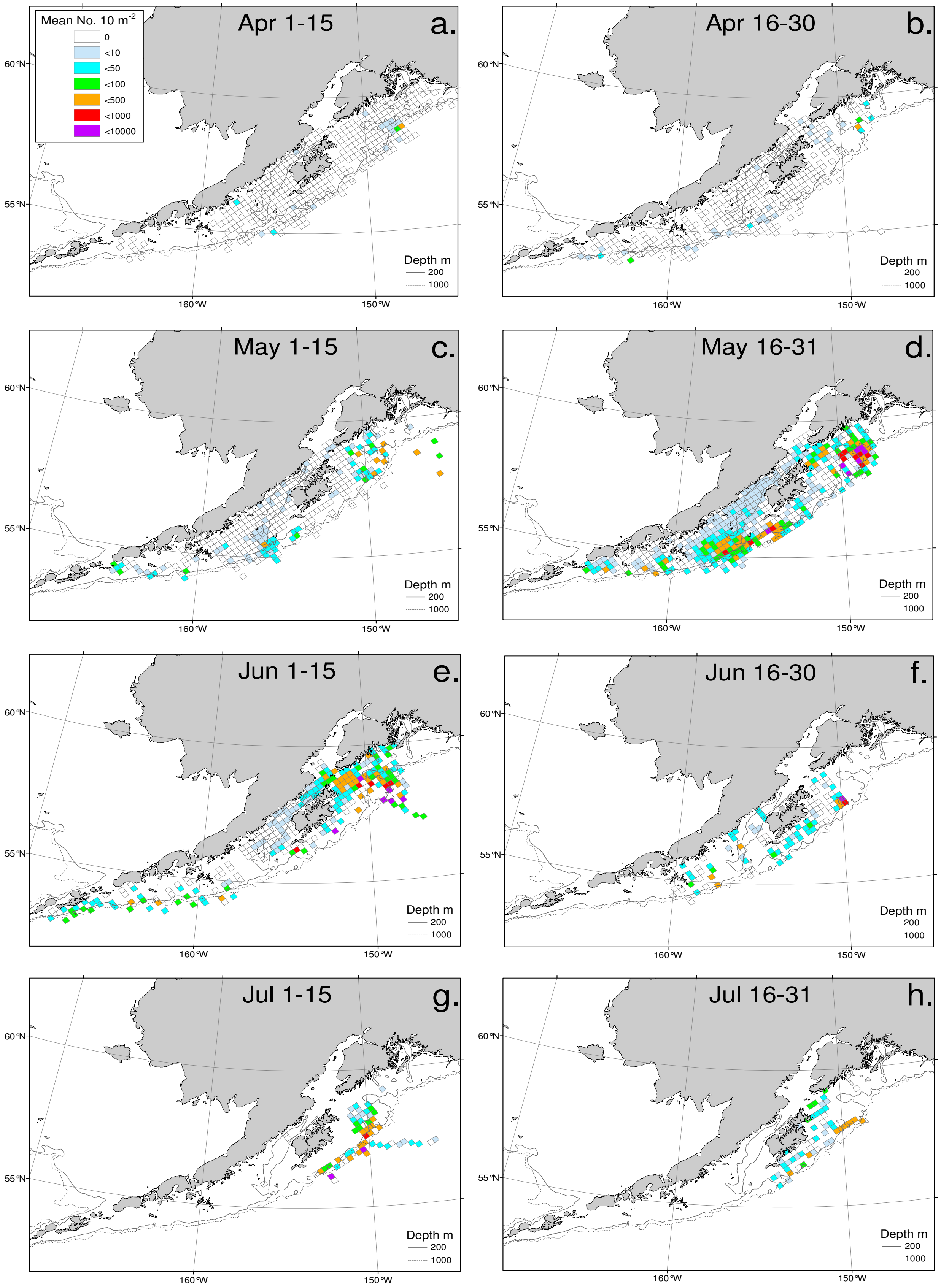

Mean No. 10 m^{-2}
0
<10
<50
<100
<500
<1000
<21000
Mar 16-31
a.
Apr 1-15
b.
Apr 16-30
c.
May 1-15
d.
May 16-31
e.
Jun 1-15
f.
Jun 16-30
g.
60°N
55°N
160°W
150°W
Depth m
200
1000

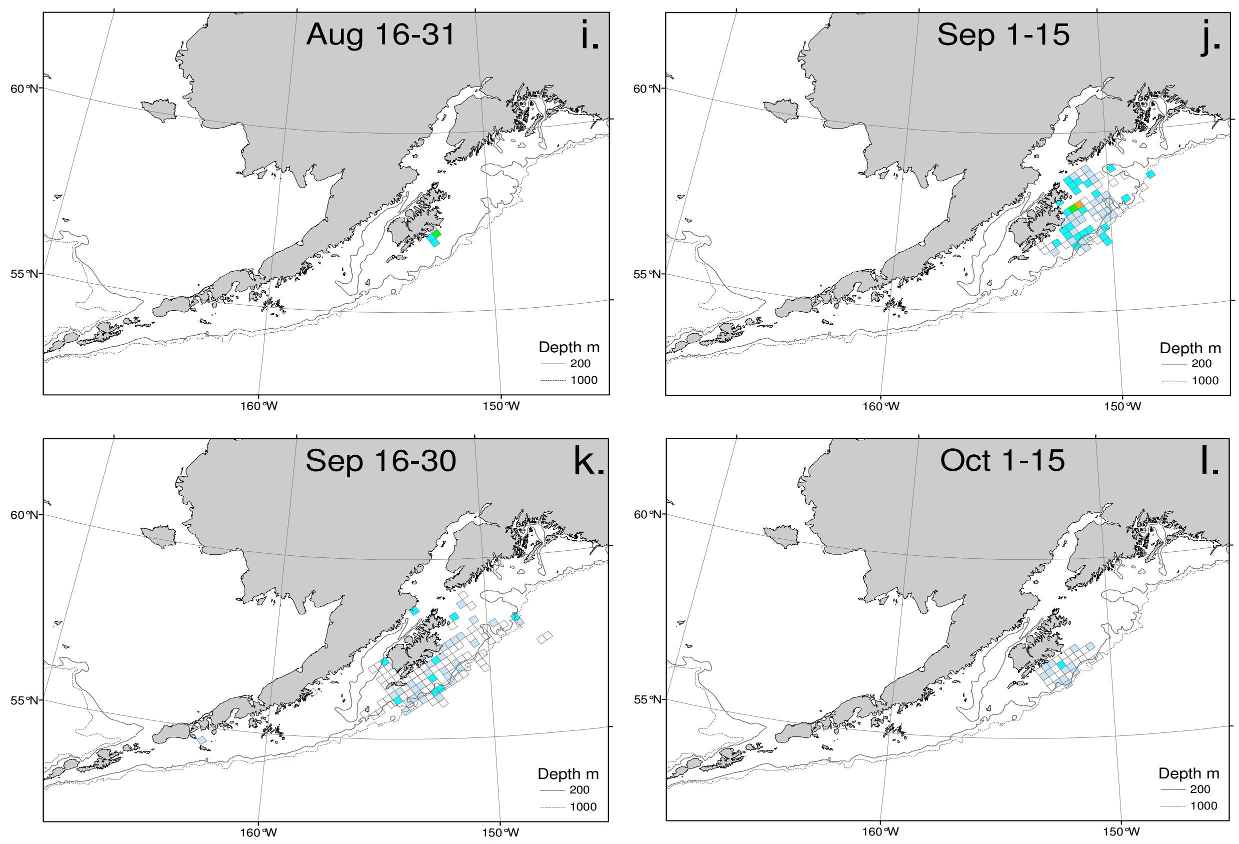


Year	Mid-survey date (JD)	N	Larval length bins (mm) 3	4	5	6	7	8	9	10	11	12	13	14	15	April-May SST bins (^{o}C) 8	9	10	11	12
1981	144	68			X															
1982	147	53		X													■			
1983	142	83			X													■		
1985	148	541			X												■			
1987	144	0																■		
1988	150	103			X													■		
1989	153	108			X											■				
1990	152	83				X											■			
1991	141	107				X										■				
1992	144	191			X													■		
1993	149	356				X												■		
1994	147	182				X											■			
1995	145	191				X											■			
1996	149	117				X												■		
1997	147	410			X													■		
1998	146	1484			X															■
1999	149	612					X									■				
2000	152	207			X														■	
2001	149	1000			X													■		
2002	148	192				X												■		
2003	149	743			X														■	
2004	150	546			X													■		
2005	149	1097				X														■
2006	147	564				X												■		
2007	144	141				X										■				
2008	148	476				X										■				
2009	152	569				X										■				
2010	147	1418				X												■		

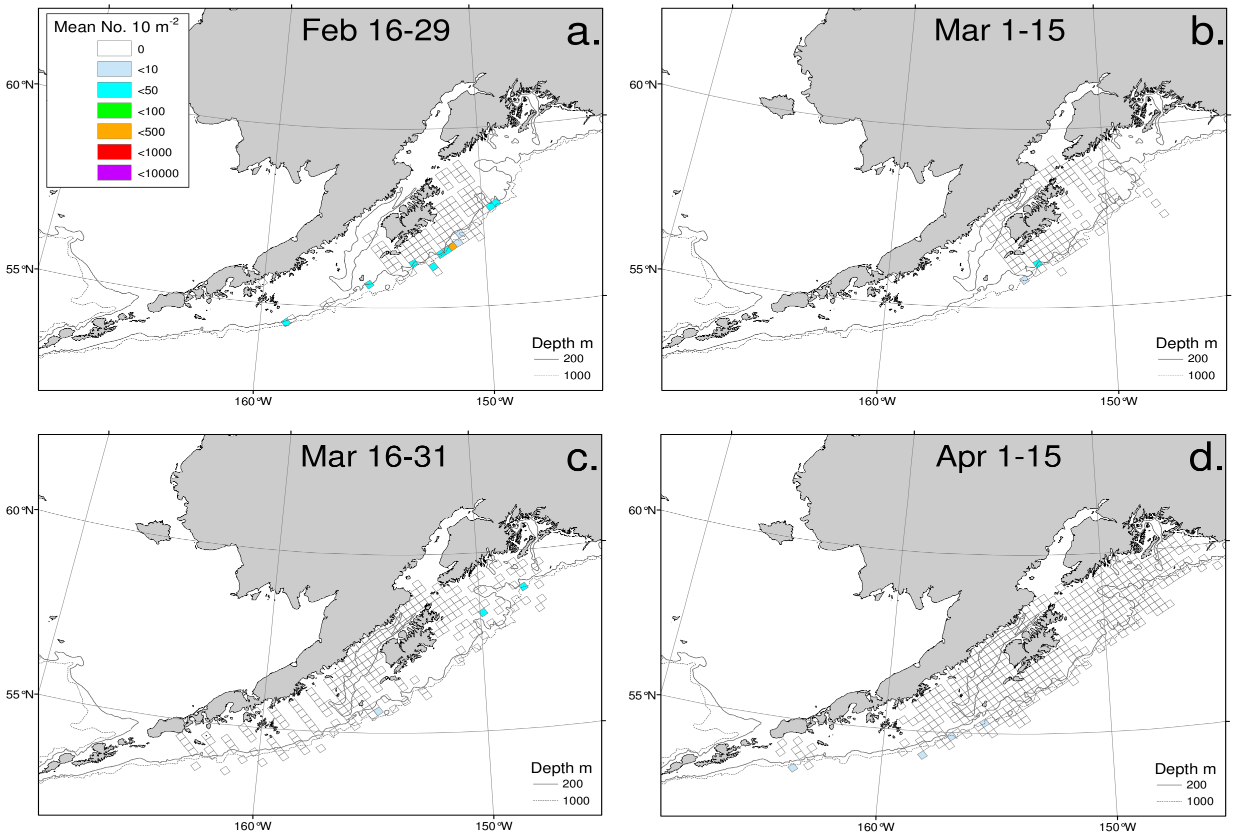
% Freq. catch by length: 0 <1 1<5 5<10 10<15 15<20 20<25 25<30 30<35 35<55

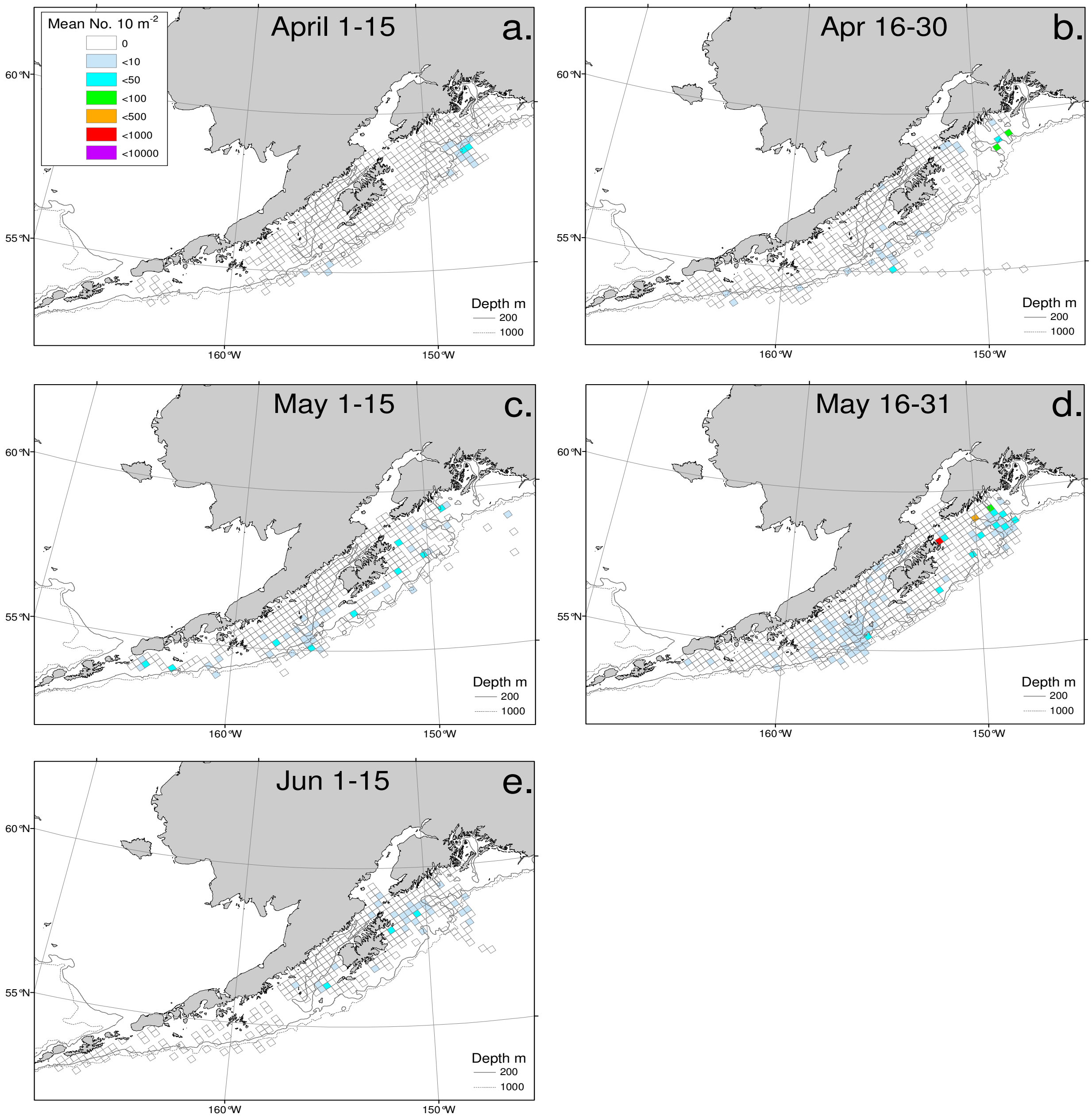
Length bin for weighted mean larval length: X SST bin for summed April-May monthly means: ■

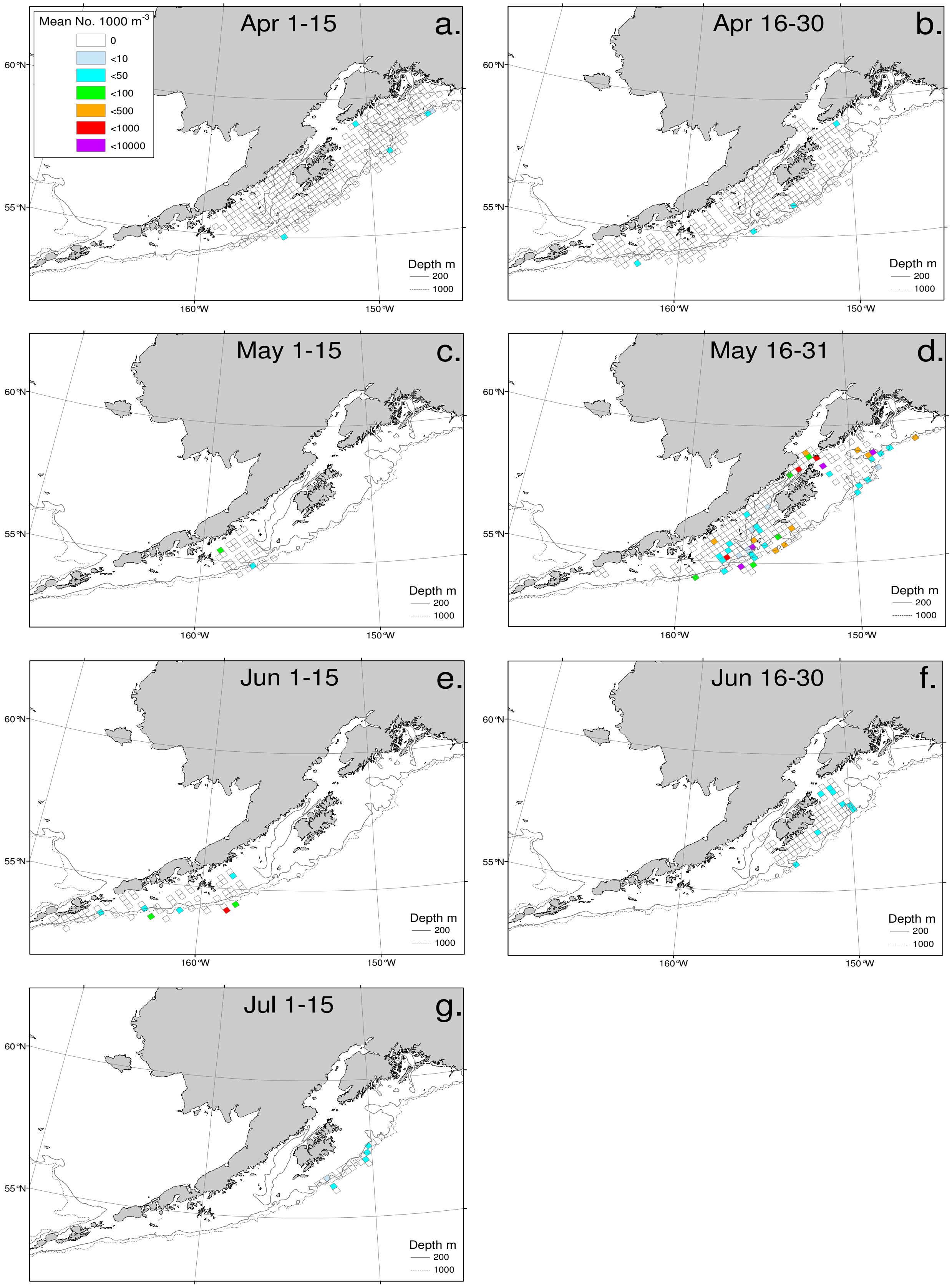

Mean No. 10 m^{-2}
0
<10
<50
<100
<500
<1000
<10000
Apr 1-15
a.
Apr 16-30
b.
May 1-15
c.
May 16-31
d.
Jun 1-15
e.
Jun 16-30
f.
Jul 1-15
g.
Jul 16-31
h.
60°N
55°N
160°W
150°W
Depth m
200
1000

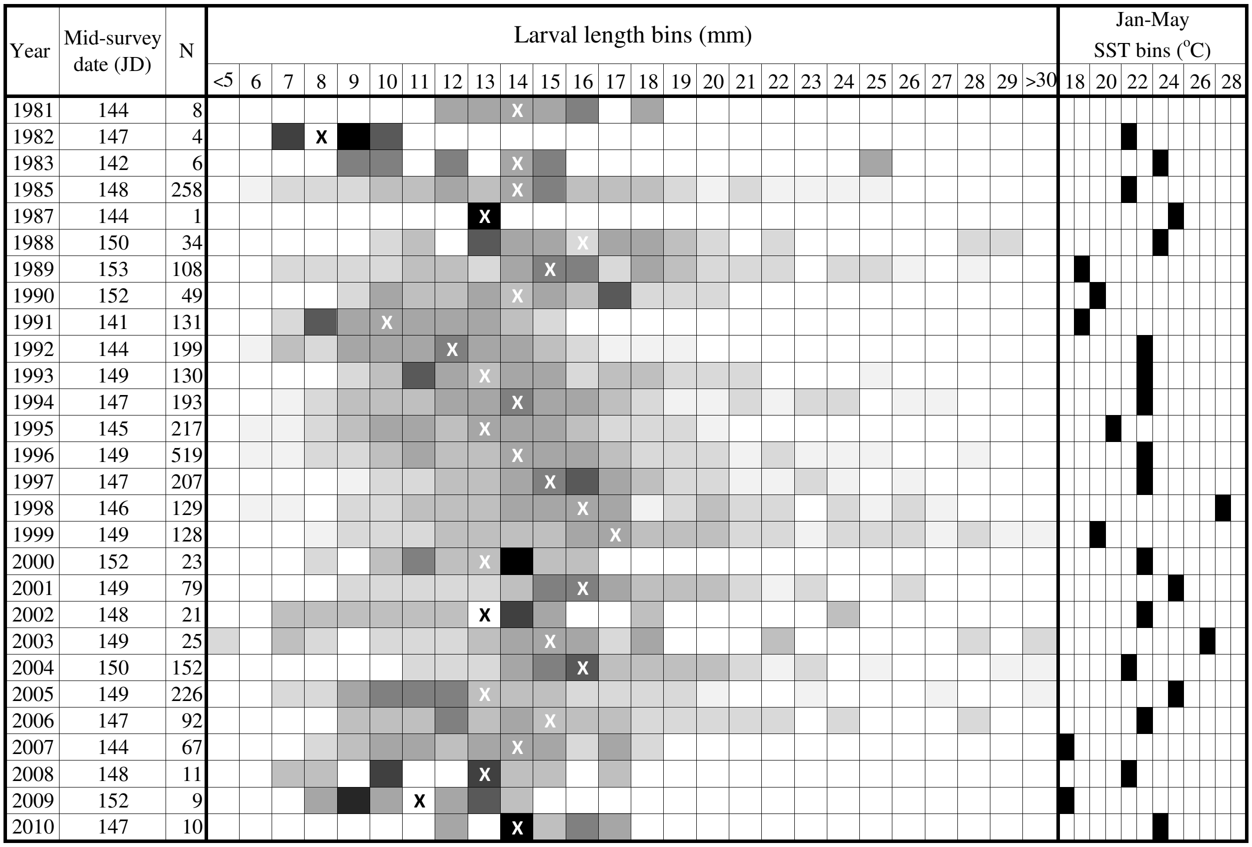


Aug 16-31
i.
Sep 1-15
j.
Sep 16-30
k.
Oct 1-15
l.
60°N
55°N
160°W
150°W
Depth m
200
1000


Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<10000
Feb 16-29
a.
Mar 1-15
b.
Mar 16-31
c.
Apr 1-15
d.
60°N
55°N
160°W
150°W
Depth m
200
1000


Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<10000
April 1-15
a.
Apr 16-30
b.
May 1-15
c.
May 16-31
d.
Jun 1-15
e.
60°N
55°N
160°W
150°W
Depth m
200
1000

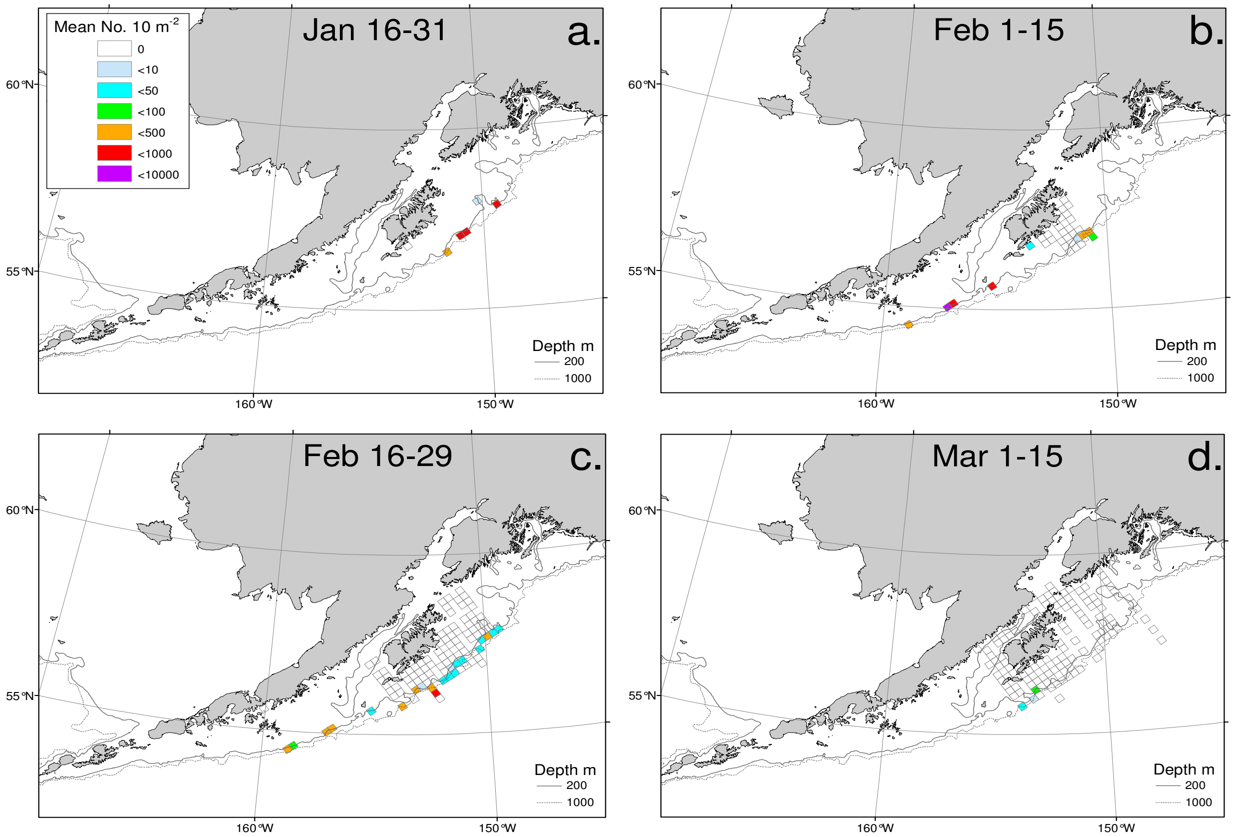

Mean No. 1000 m^{-3}
0
<10
<50
<100
<500
<1000
<10000
Apr 1-15
a.
Apr 16-30
b.
May 1-15
c.
May 16-31
d.
Jun 1-15
e.
Jun 16-30
f.
Jul 1-15
g.
60°N
55°N
160°W
150°W
Depth m
200
1000

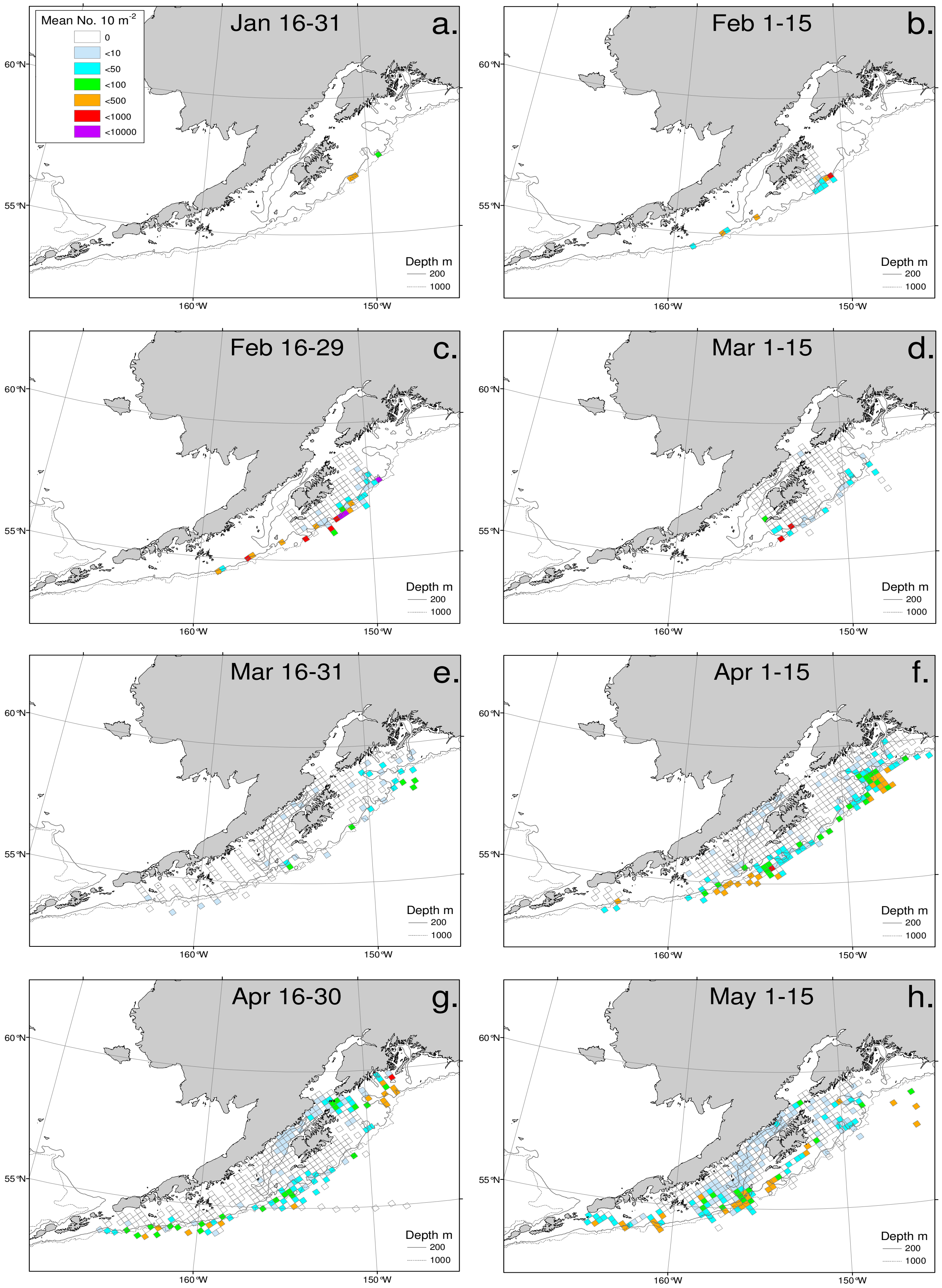


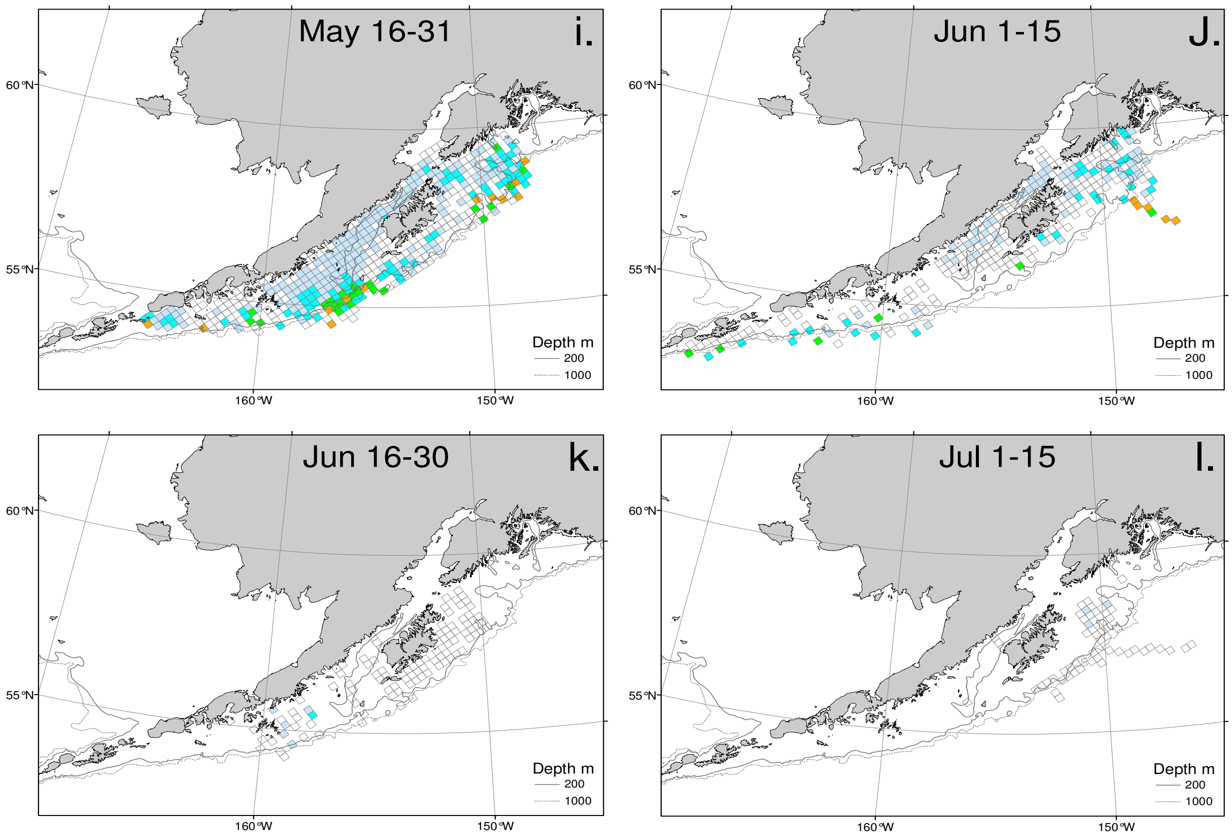
Year	Mid-survey date (JD)	N
1981	144	8
1982	147	4
1983	142	6
1985	148	258
1987	144	1
1988	150	34
1989	153	108
1990	152	49
1991	141	131
1992	144	199
1993	149	130
1994	147	193
1995	145	217
1996	149	519
1997	147	207
1998	146	129
1999	149	128
2000	152	23
2001	149	79
2002	148	21
2003	149	25
2004	150	152
2005	149	226
2006	147	92
2007	144	67
2008	148	11
2009	152	9
2010	147	10

% Frequency of catch by length: ☐ 0 ▨ <1 ▨ 1<5 ▨ 5<10 ▨ 10<15 ▨ 15<20 ▨ 20<25 ▨ 25<30 ▨ 30<35 ■ 35<55

Length bin for weighted mean larval length: X or X SST bin for summed January-May monthly means: ■


Mean No. 10 m^{-2}
0
<10
<50
<100
<500
<1000
<10000
Jan 16-31
a.
Feb 1-15
b.
Feb 16-29
c.
Mar 1-15
d.
60°N
55°N
160°W
150°W
Depth m
200
1000


Mean No. 10 m^{-2}
0
<10
<50
<100
<500
<1000
<10000
Jan 16-31
a.
Feb 1-15
b.
Feb 16-29
c.
Mar 1-15
d.
Mar 16-31
e.
Apr 1-15
f.
Apr 16-30
g.
May 1-15
h.
60°N
55°N
160°W
150°W
Depth m
200
1000


May 16-31
i.
60°N
55°N
160°W
150°W
Depth m
200
1000
Jun 1-15
J.
60°N
55°N
160°W
150°W
Depth m
200
1000
Jun 16-30
k.
60°N
55°N
160°W
150°W
Depth m
200
1000
Jul 1-15
l.
60°N
55°N
160°W
150°W
Depth m
200
1000

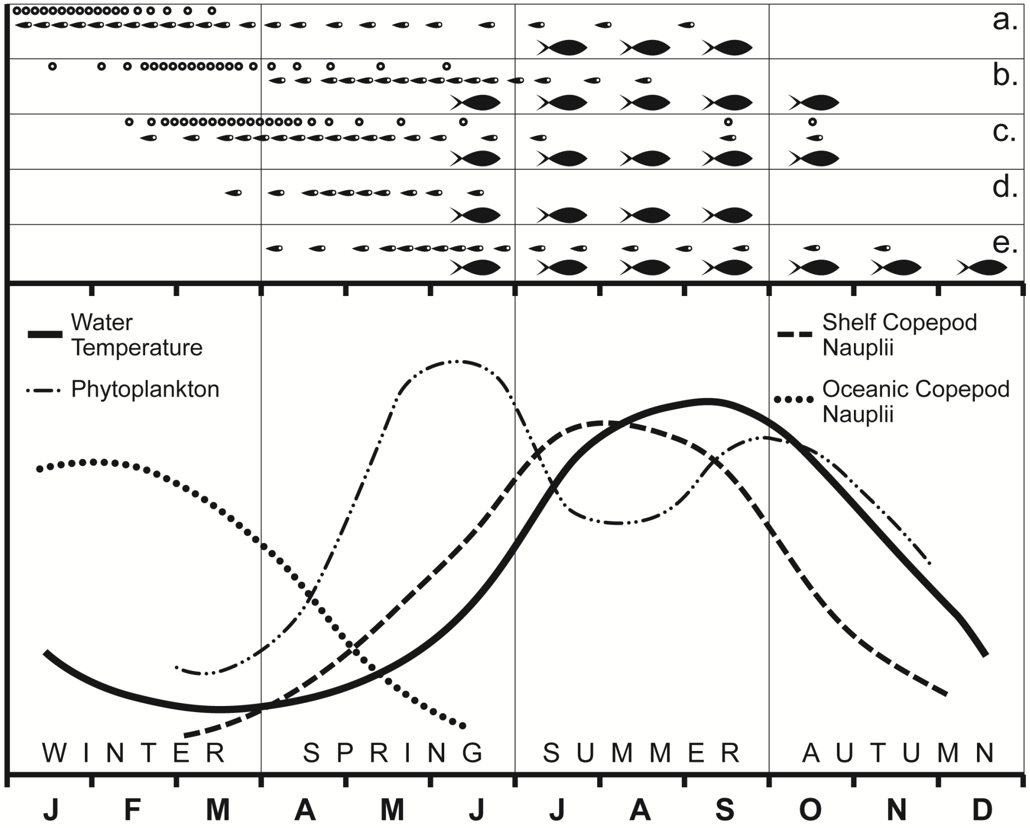

a.
b.
c.
d.
e.
Water Temperature
Phytoplankton
Shelf Copepod Nauplii
Oceanic Copepod Nauplii
WINTER
SPRING
SUMMER
AUTUMN
J
F
M
A
M
J
J
A
S
O
N
D

Table 1. Summary information for research surveys in the Gulf of Alaska (GOA), 1972-2010, from which ichthyoplankton data were used in this study. Further information can be found in [AFSC's Ichthyoplankton Cruise Database: http://access.afsc.noaa.gov/icc/index.php](http://access.afsc.noaa.gov/icc/index.php)

Year	Cruise	Dates	No. ichthyoplankton samples by sampling gear			
			60-cm Bongo*	Neuston$^+$	Tucker Trawl$^\#$	MOCNESS^
1972	2KE72	19 Apr - 11 May	67			
1977	4MF77	31 Oct - 14 Nov	59			
1978	4DI78	28 Mar - 20 Apr	85	113		
	2MF78	19 Jun - 9 Jul	89	112		
	3MF78	8 - 21 Sep	7			
	4MF78	24 Sep - 7 Oct	66			
	5MF78	15 Oct - 1 Nov	19			
	1WE78	25 Oct - 17 Nov	99			
	6MF78	5 - 16 Nov	43			
1979	1MF79	13 Feb - 11 Mar	88			
	5TK79	16 - 24 May	58			
	1PO79	1 - 11 Sep	48			
1980	1MF80	2 - 11 Apr	46	6		
1981	1SH81	5 - 18 Mar	131			
	1MF81	12 - 20 Mar	31			
	2MF81	30 Mar - 8 Apr	89			
	2SH81	16 - 24 Apr	60	60		
	3 MF81	26 Apr - 2 May	28			
	4 MF81	20 -24 May	80 (59)			
	3SH81	20 - 28 May	57 (34)			
1982	1DA82	4 - 23 Apr	83	82		
	2DA82	21 - 31 May	62 (32)	61		
1983	1CH83	16 - 28 May	70 (52)	73		
1984	1SH84	17 Apr - 9 May	157	157		
1985	1DI85	11 Mar - 2 Apr	69			
	1PO85	29 Mar - 21 Apr	154	151		
	1MF85	1 - 12 Apr	36			
	2MF85	1 - 12 May	62			
	2PO85	16 May - 8 Jun	189 (55)	189		
1986	1GI86	30 Mar - 20 Apr	149	149		
	1MF86	2 - 13 Apr	81			
	2MF86	1 - 19 May	108			15
1987	2MF87	2 - 17 Apr	154			8
	1BB87	9 - 27 Apr	117			
	3MF87	18 - 29 May	60 (40)			12
1988	1DN88	18 Mar - 11 Apr	203			
	1MF88	31 Mar - 13 Apr	173			
	2MF88	16 Apr - 2 May	64			10

Table 1 continued.

Year	Cruise	Dates	No. ichthyoplankton samples by sampling gear			
			60-cm Bongo*	Neuston^{+}	Tucker Trawl$^{\#}$	MOCNESS^
	3MF88	5 - 14 May	13			
	4MF88	20 May - 6 Jun	10 ($^{\#}$149)		176	
1989	1MF89	5 - 16 Apr	135			
	2MF89	19 Apr - 5 May	92			
	3MF89	9 - 25 May	226			
	4MF89	28 May - 6 Jun	8 ($^{\#}$95)		99	
1990	1MF90	5 - 14 Apr	107			
	2MF90	6 - 15 May	94			5
	3MF90	17 - 25 May	17			
	4MF90	27 May - 5 Jun	136 (102)			4
1991	1MF91	31 Mar - 13 Apr	90			
	2MF91	15 - 28 Apr	152			
	3MF91	30 Apr - 15 May	119			12
	4MF91	17 - 25 May	97 (70)			
1992	1MF92	3 - 11 Apr	94			
	3MF92	30 Apr - 15 May	295			4
	4MF92	17 - 29 May	139 (105)			
1993	2MF93	1 - 11 Apr	122			
	4MF93	1 - 16 May	142			5
	5MF93	25 May - 2 Jun	115 (74)			
1994	3MF94	11 Mar - 9 Apr	19			
	5MF94	1 - 15 May	89			
	6MF94	22 May - 2 Jun	139 (98)			
1995	4MF95	17 - 29 Mar	5			
	8MF95	20 - 29 May	199 (77)			
1996	1DI96	25 Apr - 6 May	155			
	6MF96	1 - 15 May	249			4
	8MF96	23 May - 1 Jun	130 (96)			
1997	8MF97	23 - 31 May	100 (94)			
1998	4MF98	1 - 10 May	72			5
	5MF98	21 - 30 May	130 (95)			11
	3WE98	17 - 30 Jun	26			
1999	1WE99	7 - 9 May	6			
	5MF99	21 May - 2 Jun	114 (25)			2
1999	2WE99	21 May - 5 Jun	202 (67)			
2000	6MF00	25 May - 4 Jun	142 (81)			
2001	1MF01	28 Jan - 5 Feb	18			
	2MF01	28 Apr - 8 May	148			
	1RB01	13 - 23 May	81			
	3MF01	24 May - 2 Jun	148 (78)			
	4MF01	2 - 19 Sep		40		

Table 1 continued.

Year	Cruise	Dates	No. ichthyoplankton samples by sampling gear			
			60-cm Bongo*	Neuston^{+}	Tucker Trawl$^{\#}$	MOCNESS^
2002	1EW02	22 May - 10 Jun	124			23
	4MF02	23 May 1 Jun	137 (59)			
	5MF02	8 - 23 Sep	122			29
	6MF02	25 Sep - 4 Oct				28
2003	1MF03	13 - 22 Feb	66			26
	1HX03	24 Apr - 15 May				155
	2 KM03	29 Apr - 11 May	67			
	5MF03	25 May - 2 Jun	115 (72)	4		
	2HX03	20 Jul - 12 Aug				201
	3KM03	20 - 26 Sep	6			
2004	5MF04	23 May - 3 Jun	194 (84)			
	2HX04	8 - 19 Jul	60			
	7MF04	9 - 22 Sep	91			104
2005	2MF05	22 Feb - 4 Mar	132			
	6MF05	22 May - 3 Jun	189 (85)			
	1FA05	19 - 27 Jul	47			
	1TT05	28 Apr - 7 May	23			
2006	4MF06	21 May - 1 Jun	175 (81)			
	5MF06	16 - 31 Aug	19			
2007	2MF07	6 - 12 Apr	75			
	5MF07	19 - 28 May	130 (79)			
2008	4DY08	24 - 30 May	95 (82)			
2009	4DY09	26 May - 6 Jun	152 (83)			
2010	3DY10	22 May - 1 Jun	163 (83)			
Total: 35	103		9798 (2286)	1197	275	663

*No. in parentheses = no. of samples used to calculate the late-spring abundance time-series.

Neuston^{+}: This is a subset of the total neuston collections illustrated in Figure 2b. Sablefish larvae were recorded in neuston samples exclusively during spring surveys.

$^{\#}$ 1-m^2 Tucker Trawl data used in late spring time-series when bongo data were limited.

^ multiple net samples per tow for MOCNESS gear - varied with water depth at sampling station.

Table 2. Spearman rank correlations for late spring mean larval abundance and lengths with timing of sampling (mid-survey date, Julian Day) and Sea Surface Temperature (SST) across the 1982-2010 time-series (no SST data available for 1981). The SST time-series is from the NOAA Optimal Interpolation SST V2 at 155.5 longitude and 57.5 latitude in Shelikof Strait, and the values used are the cumulative monthly means for the months indicated. Insufficient time-series data available for Sablefish. Significant correlations are as follows: *P<0.05; **P<0.01; ***P<0.005.

	Correlation coefficients			
Correlations	Pacific Cod	Walleye Pollock	Rockfish	Arrowtooth Flounder
Larval abundance vs. larval length:	**-0.47	0.22	-0.11	0.11
Larval abundance vs. variables:				
Mid-survey date	-0.08	-0.08	-0.01	-0.10
SST January through May	***-0.60	-0.01	0.22	-0.14
SST April through May	***-0.57	0.03	0.27	-0.13
Larval length vs. variables:				
Mid-survey date	*0.38	0.18	-0.02	*0.35
SST January through May	***0.52	*0.41	-0.32	0.30
SST April through May	***0.57	*0.44	*-0.35	0.26