Early life history ecology for five commercially and ecologically important fish species in the eastern and western Gulf of Alaska

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Abstract

The Gulf of Alaska Integrated Ecosystem Research Program is a multi-disciplinary study examining interactions between physical and biological oceanography to understand how the environment influences the survival and recruitment of early life stages of select commercially and ecologically important groundfish species. Biological and oceanographic surveys in the eastern and western Gulf of Alaska were conducted during spring and summer of 2011 and 2013; we present a synthesis of ichthyoplankton data. The results describe seasonal (spring vs. summer), regional (eastern vs. western Gulf of Alaska), and interannual (2011 vs. 2013) variation in distribution, abundance, and larval sizes of the focal species. In spring, Pacific Cod (*Gadus macrocephalus*) larvae were more abundant in 2013 than 2011 and occurred primarily in the western Gulf of Alaska near Kodiak Island, over the shelf, and over the continental slope. Walleye Pollock (*Gadus chalcogrammus*) larvae were also more abundant in the western Gulf of Alaska, with substantially higher abundance in 2013. Larval rockfish (predominantly Pacific Ocean Perch; *Sebastes alutus*) were collected in deep water or were associated with the slope, troughs and canyons intersecting the slope, and the outer shelf. Rockfish larvae were collected throughout the study region in spring, with no significant differences in abundance between regions or years. In summer, rockfish (predominantly species other than Pacific Ocean Perch) were more widely distributed over the shelf and were more abundant in the eastern Gulf of Alaska both within and across years, indicating species-specific spawning events. Sablefish

(*Anoplopoma fimbria*) larvae, however, were more abundant in the eastern Gulf of Alaska and in 2011 and were predominantly collected near areas of deep water such as Yakutat Canyon. In 2011, Arrowtooth Flounder (*Atheresthes stomias*) abundances of larvae were higher in the western Gulf of Alaska, whereas in 2013 abundances were higher in the eastern Gulf of Alaska. Arrowtooth Flounder larvae were collected primarily along the slope and near canyons and troughs. The results from individual years presented here can be used in individual-based model validation of connectivity matrices, delineating transport patterns to suitable nursery habitat, and evaluating recruitment bottlenecks for these focal species in the Gulf of Alaska. Future research will examine patterns of community structure and assemblage diversity using the comprehensive ichthyoplankton dataset. The observed ecological patterns provide insight into how environmental forcing may influence early life history aspects of recruitment.

1. Introduction

The Gulf of Alaska (GOA) is a dynamic and highly productive body of water in the northern Pacific Ocean. Both commercial and recreational fisheries are important to the economy of coastal communities around the GOA and research on all the life stages of the species impacted by these fisheries is of great interest. The Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP) is a multi-disciplinary program whose aim is to understand the physical and biological factors that influence the survival of larval and juvenile fishes to the adult stage and recruitment into the fisheries. Five commercially or ecologically important groundfish species were selected as the focus of the Program: Pacific Cod (*Gadus macrocephalus*), Walleye Pollock (*Gadus chalcogrammus*), Pacific Ocean Perch (POP; *Sebastes alutus*), Sablefish (*Anoplopoma fimbria*), and Arrowtooth Flounder (*Atheresthes stomias*). Understanding how interannual, climate-driven variability in early life history affects survival is critical in order to predict future year-class strength for these GOA fish populations.

The GOAIERP was motivated by foundational hypotheses of recruitment control (e.g., “critical period hypothesis” [Hjort 1914], “match-mismatch hypothesis” [Cushing 1990]). Survival to recruitment of the focal groundfish species is controlled by the complex and variable biophysical environment that they encounter from the egg through the larval drift stage, and subsequently in nearshore demersal juvenile habitats. To investigate these drivers, integrated physical, chemical, and biological oceanographic sampling was conducted along a comprehensive predetermined sampling grid extending from off Baranof Island in the east to Kodiak Island in the west (Fig. 1) during spring, summer, and fall of 2011 and 2013. Environmental conditions and processes influencing the different ontogenetic stages of these fish species in the GOA were examined, and results applied to the development of Individual Based Models (IBMs) that will predict recruitment outcome for each of the focal species under different environmental scenarios during early life (see this volume). The present study synthesizes and interprets the ichthyoplankton data for the focal species collected from the eastern GOA (EGOA) and western GOA (WGOA) during spring and summer 2011 and 2013 and documents along- and cross-shelf distributions of eggs and larvae.

The physical oceanography of the GOA is influenced by complex bottom topography, significant freshwater runoff, strong cyclonic winds, and cyclonic current systems (Stabeno et al. 2004). In the WGOA, the Alaskan Stream flows along the slope and shelf edge while the Alaska Coastal Current flows along the coast. In the EGOA, the Alaska Current flows over the basin and the Alaska Coastal Current is a discontinuous feature (Stabeno et al. 2004, 2016). Although it is predominantly a down-welling system, nutrient delivery from onshore transport from the basin ensures that the continental shelf region is highly productive. The bottom topography in the EGOA is characterized by a narrow shelf south of Cross Sound (as opposed to a broader shelf in the western region) and is in close proximity to the divergence of the Alaska Current and the California Current.

The GOA is composed of the Aleutian and Oregonian zoogeographic provinces. The Aleutian province extends from west of Kodiak Island to the U.S.-Canada border, although recent studies suggest that the southern boundary of the Aleutian region is the tip of Vancouver Island (Briggs and Bowen 2012). The Oregonian province overlaps the Aleutian province from Baranof Island to the U.S.-Canada border and extends to the California-Mexico border. The coast of southeastern Alaska is a transitional zoogeographic region with characteristics similar to both the Aleutian and Oregonian regions, whereas Kodiak Island is within the Aleutian zoogeographic region (Allen and Smith 1988). Therefore, species assemblages in the eastern region may reflect these topographic and biogeographical differences.

The GOAIERP has revealed further complexities in the system that reflect a high degree of regional, seasonal, and interannual variability in the physical oceanography and productivity in the GOA pelagic ecosystem (Waite and Mueter 2013; Stabeno et al. 2004, 2016). Historical data, primarily from the western region of the GOA, indicate that spawning patterns and the early life history ecology of the GOAIERP focal species is strongly linked to seasonal and spatial variability in the physical and biological environment (Doyle et al. 1995, 2002, 2009; Boeing and Duffy-Anderson 2008; Doyle and Mier 2012, 2016). In addition, interannual variability in these environmental conditions can elicit a detectable response in the ichthyoplankton of the GOA (Bailey et al. 1995; Bailey and Picquelle 2002; Doyle et al. 2009) that may reflect variability in production, transport, and survival of larvae. Similar responses of ichthyoplankton community structure have been observed in the eastern Bering Sea (Siddon et al. 2011), suggesting broad-scale continuity in environmental drivers on survival and recruitment success of focal fish species.

Although fish early life history ecology is well described for the WGOA (Matarese et al. 2003; Doyle and Mier 2012, 2016; see AFSC's online Ichthyoplankton Information System [http://access.afsc.noaa.gov/ichthyo/] for all species occurring in the GOA), ichthyoplankton patterns and fish early life history dynamics are poorly described or understood in the EGOA. The GOAIERP provides an opportunity to investigate and compare patterns in the eastern region (east of Prince William Sound) with those in the west (near Kodiak Island) during spring and summer in two years with distinct oceanographic conditions (Stabeno et al. 2016).

The objectives of this study are to 1) synthesize the ichthyoplankton data for focal species collected during 2011 and 2013 to describe regional (EGOA vs. WGOA) and interannual (2011 vs. 2013) variation in distribution, abundance, and larval sizes; 2) identify new information on larval pelagic durations and drift pathways to settlement areas; and 3) identify potential early life history bottlenecks for survival and recruitment success to better understand mechanistic links between early life history stages of commercially and ecologically important fish species and the physical and biological environment in the GOA.

2. Materials and Methods

2.1. Sampling Surveys

A total of eight surveys collected samples in the Gulf of Alaska in the spring and summer of 2011 and 2013 (Table 1). Metadata and individual survey data are given in AFSC's Ichthyoplankton Cruise Database (http://access.afsc.noaa.gov/icc/index.php). Each survey followed a predetermined sampling grid extending from the eastern to the western GOA (Fig. 1), used by the Lower, Middle, and Upper Trophic Level components of the GOAIERP project, unless time or weather impacted sampling efforts. Due to weather and equipment failures, sampling in the WGOA during spring of 2013 was reduced. For purposes of this study, the EGOA is separated from the WGOA by Prince William Sound (PWS); all stations to the east of PWS are designated EGOA and all stations west are WGOA. The spring surveys occurred concurrently in 2011; the 2013 EGOA survey occurred one month earlier than the WGOA survey. Sampling on the summer EGOA surveys occurred one month earlier than the WGOA surveys in both years.

On all surveys, samples were collected using a paired 60-cm bongo (505-µm mesh nets) and a Sameoto neuston sampler (Sameoto and Jaroszynski 1969; 505-µm mesh net). The bongo nets were deployed obliquely from the surface to 200 m depth or 10 m off-bottom, whichever was shallower; one net sample was designated for zooplankton, while the second net sample was designated and subsequently processed for ichthyoplankton. The neuston net was used to sample the surface layer (upper 10–15 cm depth depending on sea conditions; Jump et al. 2008). The duration of neuston tows was approximately 10 minutes and the entire net collection was processed for ichthyoplankton. The nets were equipped with a calibrated flow meter; therefore, catch rates were standardized to catch per unit effort (CPUE; number•10 m^{-2} for bongo samples and number•1000 m^{-3} for neuston samples). Protocols for sampling during the surveys, sample handling, sorting, and identification are outlined in Matarese et al. (2003).

2.2. Ichthyoplankton sampling preservation and processing

Ichthyoplankton samples were initially preserved in 5% formalin-seawater solution buffered with sodium borate. All samples were sent to the Plankton Sorting and Identification Center in Szczecin, Poland. All fish eggs and larvae were sorted to the lowest taxonomic level possible and larval specimens were measured to the nearest 0.1 mm (standard length; SL). Verification and further identification of specimens was conducted at NOAA's Alaska Fisheries Science Center (AFSC) in Seattle, WA. As time permitted at sea, a subsample of fish larvae was removed from the bongo net sample being processed for zooplankton prior to preservation. Larvae were placed directly in 95% ethanol and subsequently identified at the AFSC; *Sebastes* spp. larvae were retained for subsequent genetic studies. POP larvae are presently morphologically indistinguishable from other species of rockfish and are therefore reported as *Sebastes* spp. Genetic identification of select larval rockfish from spring and summer surveys was completed.

This analysis separates POP from other rockfishes (see Garvin et al. 2011); individual species other than POP were not identified. Early life history information for species occurring in the GOA can be found in Matarese et al. (2003), Doyle and Mier (2012, 2016), and AFSC's online Ichthyoplankton Information System (http://access.afsc.noaa.gov/ichthyo/index.cfm).

2.3. Data analysis

Distribution maps for each species were created using ArcInfo mapping software (ESRI 2008) and were generated using egg or larval abundance (CPUE) data from each survey. Data were converted into ArcInfo data layers, which show the sampling locations referenced geographically with point locations overlaid onto a regular grid (20 km x 20 km). More than one station might occur within one grid cell, in which case a mean abundance value was calculated and assigned to each cell. To show the quantity and distribution of samples, fish density is plotted as continuous in space even though the density may be zero at some locations. The resulting data layer shows all grid cells where samples were taken and their associated abundance based on catch at one or more stations.

To test for significant differences in larval abundance of the focal species, and egg abundance for Walleye Pollock, between regions (EGOA and WGOA) and years (2011 and 2013), a two-factor ANOVA was performed. Abundance data were fourth-root transformed to help meet the assumptions of ANOVAs (Underwood 1997). To test for significant differences in larval lengths between years and regions, a linear mixed-effects model was performed. Stations were nested within regions and treated as a random effect in the models. In cases where the interaction term was significant in the 2-factor ANOVA, main effects were not further investigated (Underwood 1997). Following the full-factorial models (for abundance or length), separate one-factor ANOVAs were performed to test for differences within years or regions. All analyses were performed using R Statistical Software (R version 3.0.2; R Core Team 2013).

3. Results

The ichthyoplankton surveys collected eggs and larval fish (Appendices 1–3) using both bongo and neuston nets to describe changes in distribution, abundance, and larval size. Seasonal comparisons show differences in assemblage-wide composition that reflect species-specific life history traits (i.e., spawning times), while regional comparisons highlight the influence of water currents, eddies, and topography on larval transport to juvenile settlement habitat. Interannual differences may reflect species-specific responses to different oceanographic conditions or timing of the spring bloom, but results must be interpreted with caution with respect to the timing of the surveys.

3.1. Spring Surveys

Egg taxa collected exclusively on spring surveys included both focal gadid species, Flathead sole (*Hippoglossoides elassodon*), Alaska Plaice (*Pleuronectes quadrituberculatus*), and others (Appendix 1). Many larval taxa were collected exclusively on the spring surveys, including focal species Arrowtooth Flounder and Pacific Cod, all agonid and stichaeid species, as well as Pacific Herring (*Clupea pallasi*), Pacific Sand Lance (*Ammodytes hexapterus*), Pacific Halibut (*Hippoglossus stenolepis*), Northern Rock Sole (*Lepidopsetta polyxystra*), and others (Appendix 2).

Larvae of the five focal species occurred in the EGOA and WGOA in both years, except Pacific Cod were not collected from the EGOA in 2011. *Sebastes* spp. was the most abundant and frequently collected target taxon from bongo samples in the EGOA, while Walleye Pollock was the most frequently collected, though not always the most abundant, target taxon in the WGOA. Both Walleye Pollock and Pacific Cod were more prevalent in the WGOA; in 2013, Walleye Pollock were collected at approximately 80% of stations in the WGOA. Northern Lampfish (*Stenobrachius leucopsarus*), an oceanic mesopelagic species, was the most frequently collected taxon from bongo samples from the EGOA and WGOA surveys in 2011 and also the EGOA survey in 2013. Sablefish was the most abundant and most frequently collected taxon from neuston net samples in the EGOA in 2011 and Kelp Greenling (*Hexagrammos decagrammus*) was the most abundant and most frequently collected taxon in the WGOA in 2011, and both EGOA and WGOA surveys in 2013.

3.2. Summer Surveys

Egg taxa collected only on summer surveys included Pacific Sanddab (*Citharichthys sordidus*), and C-O Sole (*Pleuronichthys coenosus*) (Appendix 1). Larval taxa collected exclusively on summer surveys included thornyheads (*Sebastolobus* spp.), Rex Sole (*Glyptocephalus zachirus*), Sand Sole (*Psettichthys melanostictus*), and others (Appendix 2).

The focal species were not consistently collected on summer surveys except rockfish, which were collected in both bongo and neuston nets, and rare collections of Walleye Pollock and Sablefish larvae. *Sebastes* spp. was the most frequently collected taxon in bongo samples, collected at approximately 90% of the stations in the EGOA in 2011. *Sebastes* spp. was also the most abundant taxon in the EGOA and WGOA in 2011 and EGOA in 2013, while Capelin (*Mallotus villosus*) was the most abundant taxon in the WGOA in 2013.

3.3. Focal Species

3.3.1. Pacific Cod

Pacific Cod have benthonic eggs and are not routinely collected in plankton surveys; larvae were not collected during summer surveys so larval analyses were restricted to spring collections only. Pacific Cod larvae occurred primarily in the WGOA at stations located near Kodiak Island and over the shelf (Fig. 2). In 2011, no larvae were collected in the EGOA and larvae were exclusively collected near Kodiak Island in the WGOA. In 2013, abundance levels were low in the EGOA on the shelf, at the slope, and near areas of deep water while significantly more larvae were collected in the WGOA, spanning the shelf and at the slope ($p<0.001$; Table 2). In 2013, the area with the highest abundance was located at the slope. In the WGOA, larvae were significantly more abundant in 2013 than 2011 ($p<0.001$; Table 2).

The mean standard length (± standard deviation; SD) of larvae collected in WGOA in 2011 was 5.1 ± 1.1 mm, compared to 4.6 ± 0.9 mm in WGOA in 2013 and 4.9 ± 0.9 in EGOA in 2013 (Table 3; Fig. 3). Although the timing of surveys varied between regions and years, no significant differences in larval lengths were detected (Table 4). In 2013, the WGOA survey (April 26–May10) occurred one month later than the EGOA survey (April 6–24), but the mean size was smaller in WGOA. In the WGOA, the timing of surveys was similar, but larvae were smaller in 2013 than in 2011.

3.3.2. Walleye Pollock

Walleye Pollock eggs were collected on all spring surveys with significantly higher abundances in 2013 ($p<0.001$) and in the WGOA ($p<0.001$) (Table 2). In 2011 in the EGOA, eggs were associated with Yakutat Canyon, Cross Sound, and Chatham Strait; in the WGOA, eggs were located close to shore over the shelf as well as at the shelf break. In 2013, Walleye Pollock eggs were more abundant and collected from stations over the shelf and at the shelf break in both the EGOA and WGOA with the EGOA having several stations with very high abundances (Fig. 4).

Walleye Pollock larvae were not collected during summer surveys, therefore larval analyses were restricted to spring collections only. A significant interaction of Year and Region occurred in the two-factor ANOVA, therefore main effects were not examined further (Table 2;

Underwood 1997). Walleye Pollock larvae were more abundant in the WGOA within each year of the study, but WGOA in 2013 had much higher abundances than WGOA in 2011. Larval abundances were higher in 2013 across regions (Table 2). Larvae were collected from stations over the shelf and at the slope in both regions and years; in 2013, when abundances were higher, concentrations of larvae were associated with troughs that intersect the shelf (e.g., Amatuli Trough and Yakutat Canyon; Fig. 5). The distribution of larvae is similar to that of Walleye Pollock eggs, with higher abundances in the WGOA and in 2013.

The mean standard length (±SD) of larvae collected in 2011 was larger in the WGOA (5.3 ± 1.4 mm) compared to the EGOA (4.9 ± 0.6 mm); a similar but more pronounced difference was seen in 2013 (WGOA: 5.2 ± 1.4 mm, EGOA: 4.5 ± 0.6 mm) (Table 3). Larval lengths were similar across regions in 2011 and across years within the WGOA. In 2013, larvae in WGOA were significantly larger than EGOA ($p<0.01$; Table 4), but the EGOA survey occurred one month earlier. Within the EGOA, larvae were larger in 2011 ($p=0.04$; Table 4), but the 2011 survey occurred one month later (Fig. 6).

3.3.3. Rockfish (includes POP)

Based on genetic identifications as well as larval size ranges observed between spring and summer cruises (see Table 3), spring analyses best describe patterns for the focal rockfish species (i.e., POP), while summer analyses describe other rockfish species. Larvae processed for genetic identification verified that spring collections were predominantly POP and that the vast majority of summer rockfish collections were not POP (A. Gharrett, University of Alaska Fairbanks, unpubl. data). Additionally, the primary months of parturition for POP are April–May, overlapping with the timing of the spring surveys (Westrheim 1975).

In spring, larval rockfish (predominantly POP) were collected in deep water or associated with the slope, troughs intersecting the slope, and the outer shelf (Fig. 7). Rockfish were collected throughout the study region with no significant differences in abundance between regions or years (Table 2), although rockfish distribution was more widespread in 2011.

In spring, rockfish larvae were approximately 5.5 ± 0.8 mm SL across regions and years (Table 3). The majority of rockfish were 3–7 mm SL and length frequency histograms indicate the fish were likely from the same cohort (Fig. 8). While a linear model showed no significant differences in larval length between years or regions (results not shown), the mixed effects model (accounting for station variability) showed a significant interaction of Year and Region

(Table 4). In addition, in 2013, rockfish were larger in the WGOA (Table 4) although the EGOA survey occurred one month earlier.

During summer, rockfish (largely species other than POP) were more widely distributed over the shelf, slope, and nearshore (Fig. 9). Rockfish were more abundant in the EGOA both within and across years (Table 2). Although a greater size range of larvae was collected in summer, the majority of rockfish were small (approximately 4 mm SL; Table 3; Fig. 10). A small number of larger (>13.0 mm SL) rockfish were genetically identified as POP, but collections were not adequate for qualitative or quantitative analysis. This indicates that separate (i.e., species-specific) spawning events occurred.

Spring rockfish larvae were distributed over deeper waters (e.g., slope, troughs) in spring while summer rockfish (predominantly not POP) collections reflect a more shallow distribution over the shelf (Figs. 7 and 9). The spring and summer rockfish collections represent different species and/or spawning cohorts based on length frequency histograms. The distribution of summer rockfish denotes species that may extrude their larvae on the shelf, as opposed to POP that release larvae in deeper waters.

3.3.4. Sablefish

Sablefish spawn in late winter or early spring at depth (~300 m), therefore eggs were not collected during the study. Since larvae were rare in summer collections, analysis of larval data was restricted to spring collections only. Sablefish larvae move to the surface layer early in ontogeny and are poorly sampled by bongo gear, so results are predominantly based on neuston samples.

Sablefish larvae were more abundant in 2011 than 2013 and in the EGOA than WGOA, although a formal two-way ANOVA was not conducted because only one larva was collected in the WGOA in 2013. During 2011, Sablefish were more abundant in the EGOA than the WGOA ($p<0.01$). Within the EGOA, larvae were more abundant in 2011 than 2013 ($p<0.001$) (Table 2). Larvae were predominantly collected near areas of deep water (slope, canyons, and troughs), though some stations with large catches were located on the shelf (Fig. 11). Sablefish larvae were collected sporadically in the bongo net and abundance patterns showed higher abundance in 2013 and in the EGOA (results not shown).

The mean standard length (±SD) of larvae collected in the EGOA was 12.2 ± 2.1 mm in 2011 and 12.3 ± 1.3 mm in 2013. In the WGOA, larvae averaged 10.6 ± 1.5 mm in 2011 (Table

3). Larvae were significantly larger in the EGOA compared to the WGOA in 2011 (p<0.01; Table 4); within the EGOA there was no difference in larval size between years (Fig. 12).

3.3.5. Arrowtooth Flounder

Arrowtooth Flounder spawn from January through early March over the continental shelf edge and slope (400–500 m), therefore eggs were not collected during the study, larvae were not collected during summer surveys, and therefore larval analyses were restricted to spring collections only.

Larval Arrowtooth Flounder were collected primarily along the slope and near canyons and troughs (Fig. 13). A significant interaction of Year and Region occurred in the two-way ANOVA, therefore main effects were not examined further (Table 2; Underwood 1997). In 2011, larval abundances were higher in the WGOA than EGOA (p<0.001), whereas in 2013, abundances were higher in the EGOA (p=0.03) (Table 2). Within the EGOA, abundances were higher in 2013 than 2011 (p<0.001), but similar across years in the WGOA (Table 2).

The mean standard length (±SD) of larvae collected in EGOA in 2011 (14.7 ± 3.8 mm SL) was larger than WGOA in 2011 (8.5 ± 2.1 mm SL) and either region in 2013 (EGOA: 9.4 ± 2.6 mm SL; WGOA: 9.7 ± 3.4 mm SL) (Table 3). A significant interaction of Year and Region occurred in the mixed-effects model for larval length. Larvae were significantly larger in the EGOA than WGOA in 2011 (p<0.001) with no difference between regions in 2013. The regions were sampled at approximately the same time in 2011, but in 2013 the EGOA was sampled one month earlier. Within the EGOA, larvae were larger in 2011 (p<0.001); there was no difference between years in the WGOA (Table 4; Fig. 14).

4. Discussion

4.1. Regional Differences

In the EGOA, the narrow shelf south of Cross Sound and eddies in the Alaska Current lead to high levels of on-shelf flow of slope water and off-shelf flow of coastal water, which greatly influences larval transport and assemblages over the shelf (Atwood et al. 2010). Mixing near Cross Sound provides nutrients over the shelf to the north of Cross Sound and supports prolonged production through summer (Stabeno et al. 2016). The bloom starts and peaks earlier in the EGOA relative to the WGOA, which may help explain larger larval lengths across species observed in 2011 and 2013 (Strom et al. in press). Species-specific regional differences in larval size may reflect earlier spawning events in response to an earlier bloom or warmer water temperatures, faster larval growth due to greater prey availability or differences in water temperature, or a combination of these factors.

The EGOA-WGOA break occurs in the vicinity of PWS, and reflects both topographic and oceanographic differences as well as distinctions in fish species assemblages (Mueter and Norcross 2002; Waite and Mueter 2013). In the WGOA, the Alaska Coastal Current is a continuous, well-defined system along the coast from the western side of PWS to Samalga Pass in the Aleutian Islands. The interaction of the Alaska Coastal Current with topography results in mixing and prolonged production around the Kodiak Archipelago (Stabeno et al. in press). Historical sampling identified important spawning areas in Shelikof Strait (Walleye Pollock), southwest of Kodiak Island (Pacific Cod), and near Amatuli Trough (rockfish, Sablefish) (Doyle and Mier 2016). Spawning activity coupled with retention to suitable juvenile habitat explain greater abundances of these gadid species in the WGOA.

Regional patterns observed in this study indicate that habitat variation, including topography and associated transport processes, is important in structuring fish distributions. Deep-water features, such as troughs and canyons bisecting the shelf, appear to be ‘hot spots’ for larvae originating from spawning habitat over the slope or basin (e.g., rockfish, Sablefish, and Arrowtooth Flounder) (Mordy et al. in press). Such features are also important transport pathways for these deep-water-origin larvae onto the shelf (Bailey and Picquelle 2002; Duffy-Anderson et al. 2015). Spawning activity (based on egg distribution) and larval habitat availability are greater in the WGOA for gadids, while Sablefish are more abundant over the narrower shelf in the EGOA. Available larval and juvenile habitat, including features such as troughs and canyons available in both regions, supports comparable abundances of rockfish species, including POP, across the GOA. Arrowtooth Flounder showed an interaction of region and year effects, indicating that larval distribution and survival may be driven by multiple factors, both biotic and abiotic. For example, variability in the spatial overlap with food resources and/or slow larval development in deep, cold waters can exacerbate or mitigate larval mortality rates.

Many of the non-focal species collected during the spring and summer surveys were members of the Aleutian zoogeographic fauna and were found in both the eastern and western GOA. However, some species were more abundant in the WGOA as eggs (e.g., Rex Sole, Flathead Sole, and Dover Sole [*Microstomus pacificus*]) or larvae (e.g., Capelin, greenlings [*Hexagrammos* spp.], Ronquils, and Rock Soles [*Lepidopsetta* spp.]). Species occurring exclusively in the WGOA included the poacher (*Aspidophoroides monopterygius*), the pricklebacks (*Bryozoichthys lysimus* and *Stichaeus punctatus*), and the Longhead Dab (*Limanda proboscidea*). In contrast, some species found only in the eastern GOA are more closely aligned with the Oregonian fauna including eggs of Sand Flounders (*Citharichthys* spp.), Medusafish (*Icichthys lockingtoni*), and Ragfish (*Icosteus aenigmaticus*) and larvae of Thornback Sculpin (*Paricelinus hopliticus*), Darter Sculpin (*Radulinus boleoides),* Cabezon (*Scorpaenichthys marmoratus)*, and Blackeye Goby (*Rhinogobiops nicholsii*) (see Appendices 1–3).

A time series of larval abundances has been calculated based on historical sampling near Kodiak Island and Shelikof Straight (Fig. 15) in the WGOA through 2010 (Doyle and Mier 2016); comparable samples collected in the region from 2011 and 2013 were added to the time series to investigate long-term patterns in species abundances (Fig. 16). Samples were predominantly collected using 60-cm bongo samplers, except during 1988 and 1989 when a 1-m^2 Tucker trawl was used (see Shima and Bailey 1994; Doyle et al. 2009). The abundance of Pacific Cod in 2011 was among the lowest levels, while 2013 had the highest abundance over the time series. An anomalously high abundance of Walleye Pollock larvae occurred in 1981, followed by periodic highs and lows through 2011, with levels in 2013 reaching the second highest in the time series. Rockfish have been increasing in the WGOA since the early 2000's with 2011 and 2013 having among the highest abundances in the time series. The abundance of Sablefish larvae collected using a bongo net from the WGOA has fluctuated over the time series with periodic high pulses followed by periods of low abundance. In 2011, the abundance of Sablefish was among the highest on historical record, while 2013 was among the lowest, although relative abundances from bongo samples should be interpreted with caution because sablefish are neustonic. Arrowtooth Flounder larvae had sustained high abundances through most of the 1990s with levels varying from low to moderate through 2013 (Fig. 16).

4.2. Interannual Differences

Basin-scale oceanographic differences may have contributed to bottom-up effects on larval growth and survival between 2011 and 2013. In 2011, chlorophyll-*a* concentrations were low in the EGOA during spring and summer, while levels were more typical of the coastal subarctic bloom in 2013 (Stabeno et al. 2016). Whereas the spring bloom usually peaks in May (Waite and

Mueter 2013), 2013 saw an early appearance (April) of bloom concentrations and by summer near surface water temperatures were 1–2 °C warmer than 2011 (Stabeno et al. 2016).

In spring of 2011, phytoplankton and micro-zooplankton cell size was small (especially in the EGOA) and biomass was low. The small size structure of the phytoplankton community and lower production levels likely resulted in reduced energy and mass transfer to higher trophic levels, including larval fish, which could impact growth and survival (Strom et al. in press). The abundance of small copepods was much lower during spring of 2011 compared to 2013, but large copepod abundances were relatively similar between years (R. Hopcroft, University of Alaska Fairbanks, unpubl. data). These observed differences in spring phytoplankton and micro-zooplankton communities were generally weaker or absent by summer and fall.

The spring plankton community is typically characterized by high biomass of larger (i.e., >20 µm) organisms (phytoplankton, micro-zooplankton, and copepods). A significant shift in the species composition occurs seasonally, with summer and fall communities more dominated by smaller-sized species (i.e., phytoplankton < 20 µm; Strom et al. 2010), which may be due to the persistent lack of an extensive fall bloom in the GOA (Strom et al. in press). Large zooplankton (e.g., *Neocalanus* spp., euphausiids) was more abundant from spring through fall in 2013 than 2011 across the GOA, although abundance in the EGOA in 2011 was relatively high given anomalously low phytoplankton production (R. Hopcroft, unpubl. data). Such large zooplankton taxa (across developmental stages) are an important prey resource for larval (Strasburger et al. 2014) and juvenile (Siddon et al. 2013; Strasburger et al. 2014) Walleye Pollock and Pacific Cod in the eastern Bering Sea. Similar environmental processes may have resulted in increased abundances of both large copepods and larval production, or increased zooplankton may have contributed to bottom-up positive effects for larval Walleye Pollock and Pacific Cod in the GOA during spring of 2013.

Among the deep-water spawners, Arrowtooth Flounder was more abundant in the EGOA in 2013. In contrast, Sablefish were more abundant in 2011 in both regions. Sablefish may encounter different habitat and feeding conditions in the neuston relative to deeper in the water column. The timing of peak larval abundance in relation to prey availability (i.e., copepod eggs, nauplii, and copepodites [Grover and Olla 1990]) in the neuston affects growth rates and survival (Doyle and Mier 2016). However, Kelp Greenling and Lingcod were more abundant in neuston collections across the GOA in 2013 than in 2011, whereas Red and Brown Irish Lord

(*Hemilepidotus hemilepidotus* and *H. spinosus*) were higher in the EGOA, but lower in the WGOA in 2013 relative to 2011.

The EGOA spring survey in 2013 occurred earlier in the year than other surveys, which may have shifted the temporal overlap with certain ichthyoplankton species, affecting the interpretation of abundance and length patterns. For example, species that spawn earlier in the season (e.g., Arrowtooth Flounder) were observed in greater abundances during the EGOA 2013 survey (Table 2), but this likely reflects differences in ontogeny (i.e., younger larvae are more abundant than older larvae) rather than interannual differences in abundance. Within the EGOA, Arrowtooth Flounder larvae were larger in 2011 than 2013 (Table 4), which likely resulted from earlier survey timing rather than oceanographic conditions and prey availability.

4.3. Key Ecological Findings

4.3.1. Pacific Cod

The scarcity of Pacific Cod larvae in the EGOA (this study; Wing et al. 1997; Atwood et al. 2010), and distribution patterns based on historical WGOA sampling, indicate that spawning activity and associated occurrence of larvae in the epipelagic zone is concentrated in shelf waters from Kodiak Island to the Aleutians. The area from the Shumagin Islands to Unimak Pass has been identified as primary larval habitat. In historical ichthyoplankton samples, larvae are rare in the water column by the end of June and juveniles are common in nearshore areas by July (Laurel et al. 2007); therefore coastal habitat may also be critically important for juveniles. Vertical behavior of larvae is affected by water temperature and light and influences drift trajectories (Hurst et al. 2009). The bays around Kodiak Island have been identified as important nursery areas for age-0 Pacific Cod (Mueter and Norcross 1999; Abookire et al. 2007; Laurel et al. 2007) and concurrent nearshore surveys during the GOAIERP program collected juvenile Pacific Cod from bays in the eastern and western GOA (O. Ormseth, NOAA/AFSC, unpubl. data). Given the relatively limited larval drift period for this species (approximately 3 months; Doyle and Mier 2016), these benthic age-0 juveniles likely resulted from local spawning activity.

The movement of Pacific Cod larvae from spawning areas on the continental shelf to inshore nursery habitat is a critical transition affecting recruitment success and this transition from pelagic to benthic habitat is poorly understood. Large-scale atmospheric conditions affect basin-scale circulation speeds, and therefore larval drift trajectories, in the Gulf of Alaska. Periods governed by La Niña conditions, low MEI (multivariate ENSO index), and high NPI

(North Pacific Index) result in slower circulation speeds. Slower basin-scale circulation may enhance the retention of larvae in the Gulf (as opposed to being transported through Unimak Pass to the Bering Sea shelf). The retention of larvae to suitable settlement areas such as the central GOA and Shumagin Islands may positively affect survival and subsequent recruitment success (Hinckley et al. in press). The MEI index was negative in 2011 and fluctuated between negative and positive values in 2013. Therefore, 2011 likely had reduced northwestward wind stress, while 2013 had more average conditions (Hermann et al. in press). Although 2011 had lower wind stress, likely resulting in slower circulation speeds and enhanced retention of larvae, the abundance of Pacific Cod larvae in the WGOA in 2011 was among the lowest level since 1981 (Fig. 16).

4.3.2. Walleye Pollock

Walleye Pollock larvae have a similar distribution pattern to Pacific Cod in the Gulf of Alaska and likely experience similar early life history challenges, although Walleye Pollock have a broader temporal and spatial production of eggs and larvae, which potentially increases the likelihood of survival. In 2011, no Pacific Cod were collected in the EGOA while small numbers of Walleye Pollock larvae were observed. In the WGOA, however, Pacific Cod were concentrated near Kodiak Island while Walleye Pollock were more abundant to the northeast of Kodiak Island near Amatuli Trough.

Based on egg abundance and distribution, spawning activity is concentrated in the WGOA, although eggs were present in high abundances in both regions. Historical sampling in the WGOA identified peak egg abundance in early April, which coincides with the earlier timing of the EGOA survey in 2013. This earlier survey timing could explain differences in larval size (i.e., smaller) and increased egg and larval abundances relative to 2011. Larvae have an average larval phase duration (approximately 4–5 months), longer than Pacific Cod, before transitioning to pelagic habitat along the slope, over the shelf, and in nearshore waters.

Survival and recruitment success depends on several life history stages, including the transition to first feeding and overlap with preferred prey sources, as well as the transition to suitable nearshore juvenile habitat (see Bailey et al. 2005 and references therein). Drift trajectories and transport influence cannibalism, survival, and eventual recruitment success (Wespestad et al. 2000). Bioenergetic modeling of age-0 Walleye Pollock from the eastern and western GOA in 2012 and 2013 shows prey quality is more important than water temperature in determining growth and survival (R. Heintz, NOAA/AFSC, unpubl. data). In the EGOA, individual-based modeling from simple (i.e., no biology included) tracking results indicates strong retention of larvae associated with PWS, explaining approximately 70% of the variability. Connectivity of suitable habitats occurred between Sitka and Yakutat with PWS and coastal regions, and PWS was connected to the WGOA regions of Kodiak, Shelikof Strait, and the Shumagin Islands (Parada et al. in press).

4.3.3. Rockfish (includes POP)

Parturition is associated with troughs and canyons along the shelf and newly extruded pelagic larvae move rapidly into the upper water column. Juveniles are located offshore over deeper water and are transported to preferred nursery habitats in nearshore rocky and high relief areas. Juveniles are epipelagic (mixed layer) until settlement in rocky benthic habitat. Adults transition into deeper, less complex habitat (Hanselman et al. 2013).

The limited historical ichthyoplankton surveys in the EGOA provide evidence for high levels of production and release of rockfish larvae during spring both over the shelf and in adjacent deep water (this study; Wing et al. 1997; Atwood et al. 2010). Levels of abundance encountered in the EGOA during spring and summer are comparable to those recorded in the WGOA, indicating that the entire GOA provides important early life history habitat for the rockfish species assemblages encountered here, especially deep-water troughs and canyons intersecting the shelf.

IBM results indicate minimal retention along the EGOA due to offshore eddy recirculation; modeled larval stages originating in the EGOA are transported into the central GOA. However, little information on early life stages of rockfishes was available to parameterize the IBM (Stockhausen et al. in press A). Seascape genetic work shows significant differences across regions, suggesting high levels of larval retention and affinity to local habitat of origin (Palof et al. 2011; Kamin et al. 2014). Larval rockfish have been observed in association with large mesoscale eddies (100–200 km) that propagate along the shelf break in the GOA, and especially in the EGOA (Atwood et al. 2010). Larvae entrained in currents surrounding the eddy while the eddy is close to the shelf could be delivered back to the shelf; larvae found in the eddy interior would likely be transported away from the shelf (C. Ladd, NOAA/AFSC, pers. comm.). Further research is needed bridging available datasets and working with modelers to better understand key drivers of early life history survival and recruitment success for rockfish in the Gulf of Alaska.

A total of 26 rockfish species occur throughout the Gulf of Alaska; five species are found exclusively in the eastern GOA, while no species are unique to the western GOA (Mecklenburg et al. 2002). Based on genetic identifications and size compositions, this project documented that rockfish larvae present in the water column during spring are mainly POP. In addition, our results corroborate that POP spawn in the spring over deep water while other rockfish species spawn closer to summer and over the continental shelf, although further genetic research is needed to describe species-specific patterns for the summer assemblage of rockfish spawners.

4.3.4. Sablefish

Understanding factors affecting the early life stages of Sablefish could help explain the highly variable recruitment patterns observed in the GOA. Strong year classes from the early 1960s and late 1970s have sustained the population, with episodic high-recruitment events observed more recently in 1997, 2000, 2008, and possibly 2014. The large fluctuations in recruitment are not related to spawning stock biomass, however, which has recently shown a declining trend. Environmental processes, including an intensifying Aleutian Low, influence sea surface temperatures along the Polar Front and affect Sablefish survival through the pelagic early life history stage (McFarlane and Beamish 1992; King et al. 2000; Shotwell et al. 2014). Both 2011 and 2013 had weak Aleutian Low conditions (http://www.beringclimate.noaa.gov/data/index.php), which would predict decreased survival of Sablefish (Trenberth and Hurrell 1994; Shotwell et al. 2014).

Hatching occurs in late spring and larvae swim to the neustonic layer, with the peak abundance at the end of May in the WGOA. The distinct ontogenetic shifts in vertical distribution of Sablefish may have influenced the observed larval abundances between regions and years. The EGOA survey in 2013 occurred one month earlier than other surveys; therefore, larvae may have been deeper in the water column. The bongo net collected more Sablefish larvae than the neuston net, indicating that perhaps most larvae were not neustonic yet.

Historical data indicate that spawning intensity and subsequent larval densities during spring tend to be very high in the EGOA relative to the WGOA, especially over deep water (this study; Wing and Kamikawa 1995; Wing et al. 1997). In the EGOA south of Cross Sound, areas of deep water are adjacent to a very narrow shelf with close proximity to eventual coastal nursery habitat; therefore the EGOA may provide more favorable larval habitat. The narrow shelf and eddies in the Alaska Current mean large on-shelf flow of slope water and off-shelf flow of coastal water (Stabeno et al. 2016).

The association of ichthyoplankton with prevailing mesoscale eddies (100–200 km in diameter) in the EGOA has been hypothesized to facilitate transport of larvae onto the shelf from the basin. However, observations of Sablefish larvae indicate they had a greater affinity to basin waters than within eddies or over the adjacent shelf (Atwood et al. 2010). The spatial distribution of sablefish larvae collected in neuston samples was more variable in the WGOA in 2011 with only a single larva collected in 2013. IBM results indicate that young Sablefish settling to nursery habitats in the GOA were likely spawned in the EGOA, with spawning activity in the WGOA unlikely to contribute to the Alaska Sablefish population (Gibson et al. in press).

Other factors, such as wind, may influence drift trajectories of neustonic larvae and subsequent transport to suitable juvenile habitat. Previous research in the Gulf of Alaska found that years of higher recruitment were correlated with stronger northerly drift as well as increased water temperatures (Sigler et al. 2001). Both northward and eastward Ekman transport explained significant amounts of variability in Sablefish recruitment within the California Current System (Schirripa and Colman 2006).

Sablefish larvae were significantly larger in the EGOA than WGOA in 2011 (Table 4) and a similar trend occurred in 2013, indicating that Sablefish may spawn earlier in the season or achieve faster larval growth in the EGOA. Latitudinal effects on the timing of spawning have been observed (Kendall and Matarese 1987). Differences in water temperature between the EGOA and WGOA may influence the timing of the spring bloom (Strom et al. in press), which may ultimately affect larval growth rates. Water temperatures were warmer in the EGOA than WGOA in both years, with 2013 being warmer than 2011 (see http://www.esrl.noaa.gov/psd/). Length frequency distributions based on historical sampling in the WGOA indicate comparable sizes collected in April to the current study collected in April/May. Historical collections in May and June from the WGOA have a similar size distribution to current samples collected in the EGOA in April/May indicating EGOA larvae may be persistently larger than WGOA larvae.

4.3.5. Arrowtooth Flounder

The limited survey data from the EGOA indicates comparable timing of larval occurrence and patterns of abundance relative to the WGOA. Arrowtooth Flounder eggs are spawned very deep in the water column, peak spawning occurs in January/February, and larval abundances are highest from January through early March. Therefore, Arrowtooth Flounder larvae have an extended planktonic phase relative to the other focal species during which they are exposed to predation, starvation, and other sources of mortality. This extended planktonic phase allows for transport and connectivity between spatially distinct adult spawning areas and juvenile nursery areas (Duffy-Anderson et al. 2015). IBM results indicate that passive transport by oceanographic currents provides a small possibility of retention in adult habitats along the EGOA via offshore eddy recirculation, but most eggs and larvae originating in the EGOA are transported northward along the shelf into the central GOA (Stockhausen et al. in press B).

In 2011, the EGOA and WGOA surveys occurred at approximately the same time, however the EGOA had larger larvae with a larger mean size than those in the WGOA. No differences in larval size were observed in 2013 when surveys occurred one month apart. Thus, spawning may occur earlier, larvae may take advantage of earlier spring bloom timing, or larvae may have faster growth rates in the EGOA than the WGOA.

The early ontogeny of Arrowtooth Flounder may help explain their success in the GOA, including spawning in deep and cold water to help avoid predation and lower metabolic demands. Ontogenetic patterns in energy density show steady values throughout the larval and juvenile stages indicating there is no apparent energetic cost associated with settlement or metamorphosis (R. Heintz, NOAA/AFSC, unpubl. data). This energy allocation strategy may enable Arrowtooth Flounder to withstand variable environmental and/or prey conditions. Arrowtooth Flounder may employ a “holding pattern” strategy during their prolonged pelagic larval phase, enabling them to withstand environmental variability.

5. Conclusions

The results of this study further enhance our understanding of the early life history strategies of the focal species in the GOA and provide new information on early ontogeny patterns in the EGOA. The focal species display distinct ecological niches and, as such, show different responses to regional and interannual variability. The five focal species have disparate strategies in response to early life history sources of mortality. Pacific Cod and Walleye Pollock were more abundant in the WGOA, reflecting preferred habitat for spawning adults and settling juvenile fish. Conversely, Sablefish were more abundant in the EGOA, which may be driven by greater spawning activity in the east relative to the west. Rockfish larvae (predominantly POP in spring) were ubiquitous across the region in both years of the study. Arrowtooth Flounder abundance varied by region and year; increasing abundance in the GOA since the 1970s may reflect environmental conditions that favor ATFs early ontogeny and energy allocation strategies. The results from 2011 and 2013, in concert with historical knowledge from the WGOA, provide key ecological findings for the early life stages of the focal species; these results may be used to better understand recruitment processes for survival and recruitment success in the GOA.

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Figure legends

Figure 1. Map of the general GOAIERP study area highlighting features of interest. Inset shows location of study area expanded in the main map. The light blue area depicts the Aleutian zoogeographic region and the darker blue area is the transition zone between the Aleutian and Oregonian zoogeographic regions.

Figure 2. Distribution maps of Pacific Cod (*Gadus macrocephalus*) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013.

Figure 3. Length frequency histograms for Pacific Cod (*Gadus macrocephalus*) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013. Length is binned by 1-mm increments.

Figure 4. Distribution maps of Walleye Pollock (*Gadus chalcogrammus*) eggs collected using 60-cm bongo nets in the spring in 2011 and 2013.

Figure 5. Distribution maps of Walleye Pollock (*Gadus chalcogrammus*) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013.

Figure 6. Length frequency histograms for Walleye Pollock (*Gadus chalcogrammus*) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013. Length is binned by 1-mm increments.

Figure 7. Distribution maps of Rockfish (*Sebastes* spp.) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013.

Figure 8. Length frequency histograms of Rockfish (*Sebastes* spp.) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013. Length is binned by 1-mm increments.

Figure 9. Distribution maps of Rockfish (*Sebastes* spp.) larvae collected using 60-cm bongo nets in the summer in 2011 and 2013.

Figure 10. Length frequency histograms of Rockfish (*Sebastes* spp.) larvae collected using 60-cm bongo nets in the summer in 2011 and 2013. Length is binned by 1-mm increments.

Figure 11. Distribution maps of Sablefish (*Anoplopoma fimbria*) larvae collected using neuston net in the spring in 2011 and 2013.

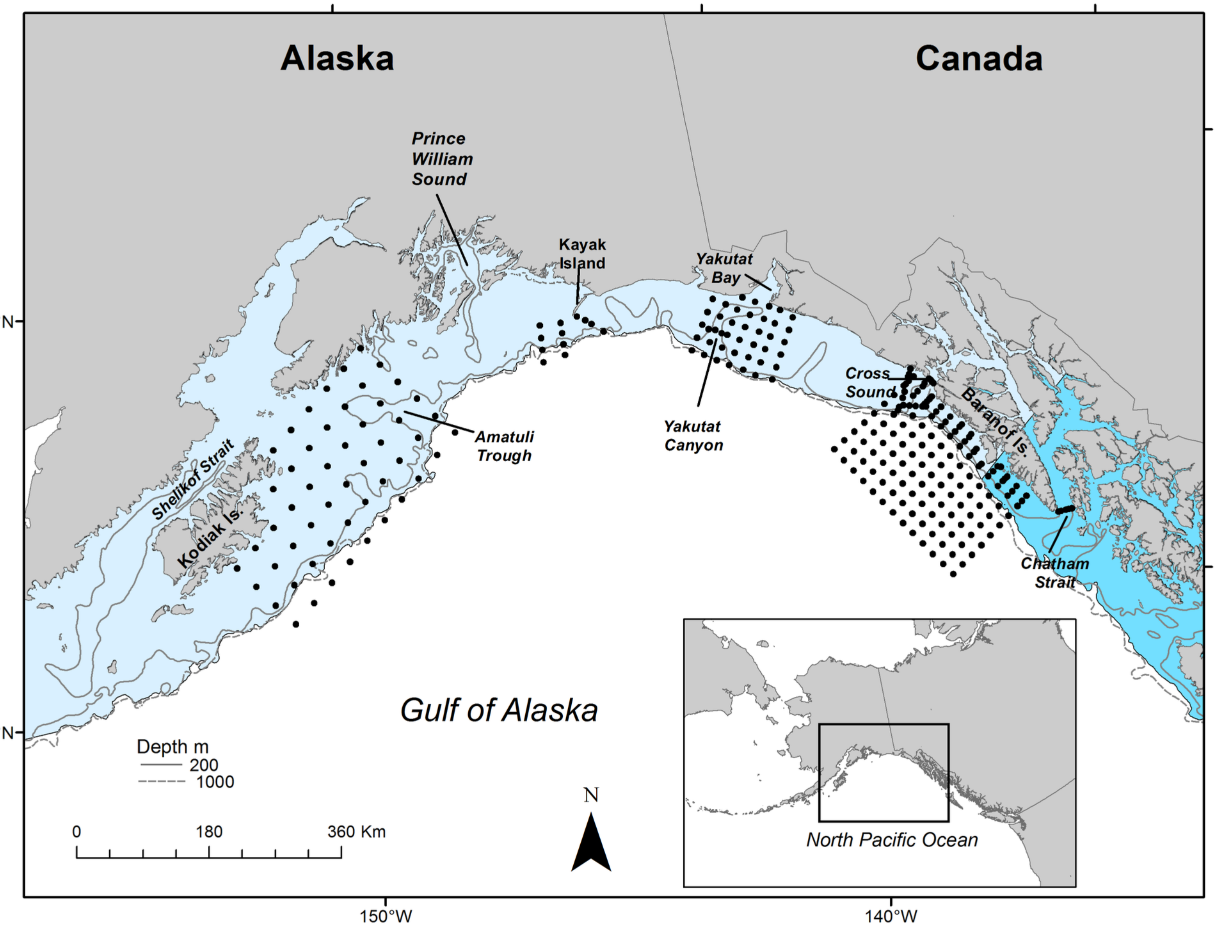
Figure 12 Length frequency histograms of Sablefish (*Anoplopoma fimbria*) larvae collected using neuston net in the spring in 2011 and 2013. Length is binned by 1-mm increments.

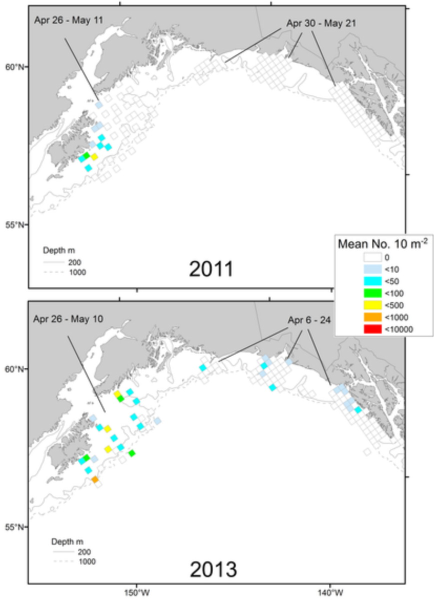
Figure 13. Distribution maps of Arrowtooth Flounder (*Atheresthes stomias*) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013.

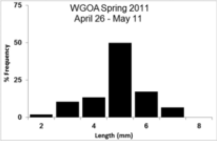
Figure 14. Length frequency histograms of Arrowtooth Flounder (*Atheresthes stomias*) larvae collected using 60-cm bongo nets in the spring in 2011 and 2013. Length is binned by 1-mm increments.

Figure 15. Map of the historical (1981–2010) larval sampling grid in the western Gulf of Alaska. See AFSC's online Ichthyoplankton Cruise Database (http://access.afsc.noaa.gov/icc/) for individual cruise reports.

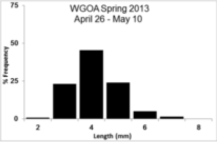
Figure 16. Time series of larval abundance for focal species collected from the western Gulf of Alaska using 60-cm bongo nets. Historical sampling (1981–2010) and current study (2011, 2013). Updated from Doyle and Mier (2016).

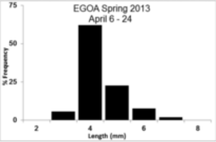

Alaska
Canada
Prince William Sound
Kayak Island
Yakutat Bay
Yakutat Canyon
Cross Sound
Baranof Is.
Chatham Strait
Amatuli Trough
Shelikof Strait
Kodiak Is.
Gulf of Alaska
Depth m
200
1000
0
180
360 Km
N
North Pacific Ocean
60°N
55°N
150°W
140°W

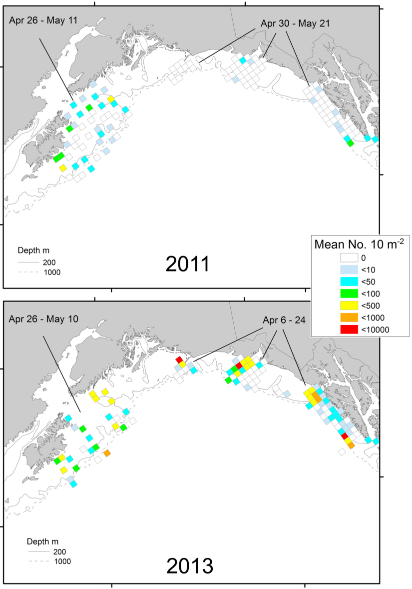

Apr 26 - May 11
Apr 30 - May 21
60°N
55°N
Depth m
200
1000
2011
Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<10000
Apr 26 - May 10
Apr 6 - 24
60°N
55°N
Depth m
200
1000
2013
150°W
140°W

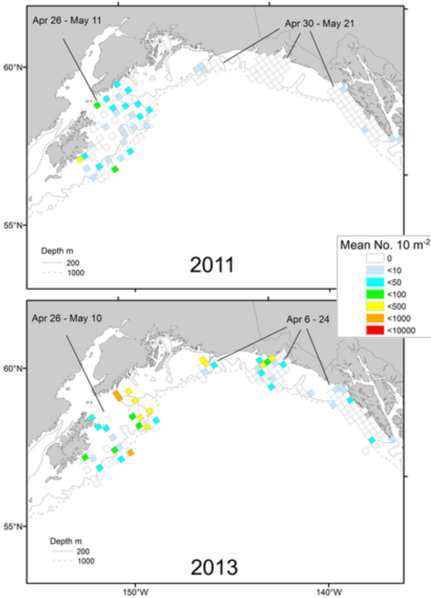

WGOA Spring 2011
April 26 - May 11
% Frequency
75
50
25
0
2
4
6
8
Length (mm)

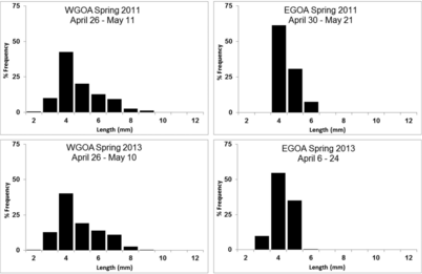

EGOA Spring 2011
April 30 - May 21
N = 0
% Frequency
75
50
25
0
2
4
6
8
Length (mm)

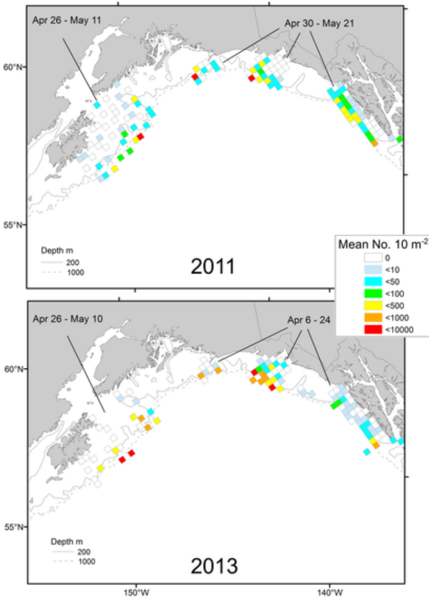

WGOA Spring 2013
April 26 - May 10
% Frequency
75
50
25
0
2
4
6
8
Length (mm)

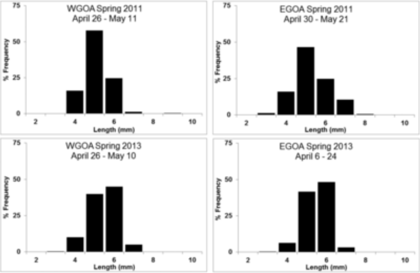

EGOA Spring 2013
April 6 - 24
% Frequency
75
50
25
0
2
4
6
8
Length (mm)

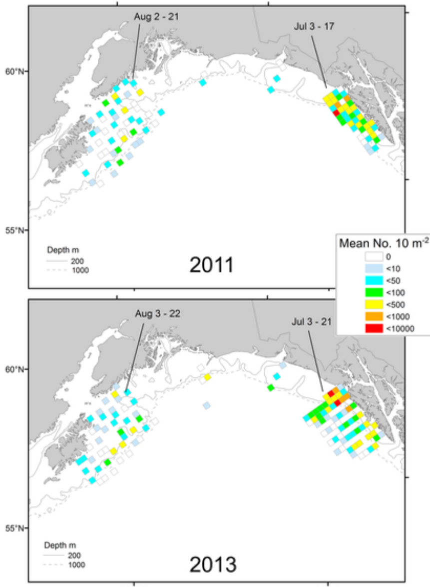

Apr 26 - May 11
Apr 30 - May 21
60°N
55°N
Depth m
200
1000
2011
Mean No. 10 m^{-2}
0
<10
<50
<100
<500
<1000
<10000
Apr 26 - May 10
Apr 6 - 24
60°N
55°N
Depth m
200
1000
2013
150°W
140°W

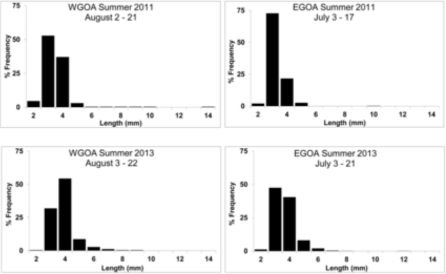

Apr 26 - May 11
Apr 30 - May 21
60°N
55°N
Depth m
200
1000
2011
Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<10000
Apr 26 - May 10
Apr 6 - 24
60°N
55°N
Depth m
200
1000
2013
150°W
140°W

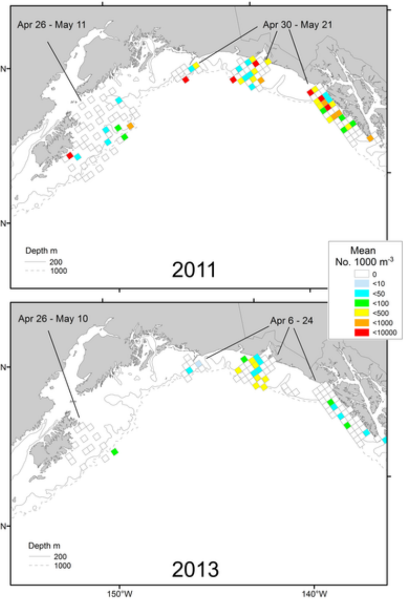

WGOA Spring 2011
April 26 - May 11
EGOA Spring 2011
April 30 - May 21
WGOA Spring 2013
April 26 - May 10
EGOA Spring 2013
April 6 - 24
% Frequency
75
50
25
0
2
4
6
8
10
12
Length (mm)

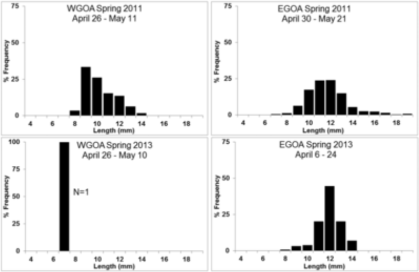

Apr 26 - May 11
Apr 30 - May 21
60°N
55°N
Depth m
200
1000
2011
Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<10000
Apr 26 - May 10
Apr 6 - 24
60°N
55°N
Depth m
200
1000
2013
150°W
140°W

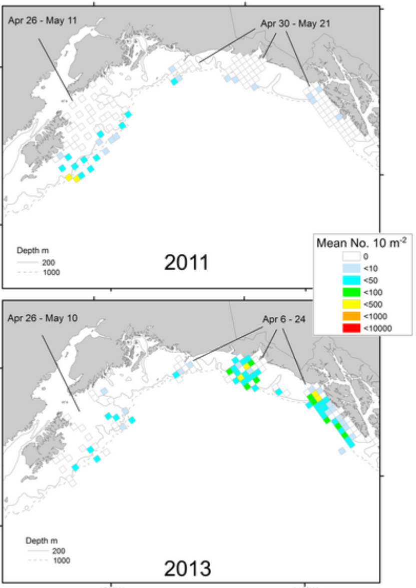

WGOA Spring 2011
April 26 - May 11
EGOA Spring 2011
April 30 - May 21
WGOA Spring 2013
April 26 - May 10
EGOA Spring 2013
April 6 - 24
% Frequency
0
25
50
75
Length (mm)
2
4
6
8
10

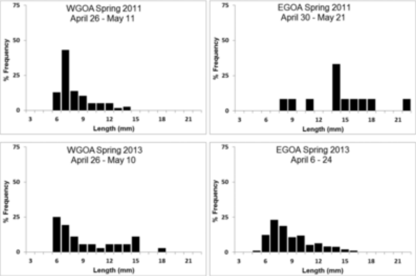

Aug 2 - 21
Jul 3 - 17
60°N
55°N
Depth m
200
1000
2011
Mean No. 10 m⁻²
0
<10
<50
<100
<500
<1000
<10000
Aug 3 - 22
Jul 3 - 21
60°N
55°N
Depth m
200
1000
2013
150°W
140°W

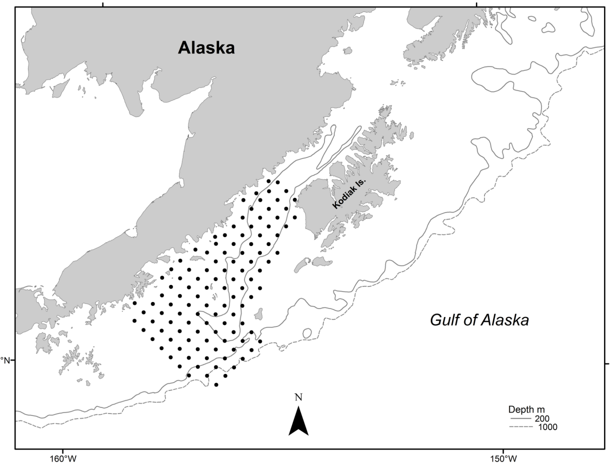

WGOA Summer 2011
August 2 - 21
% Frequency
75
50
25
0
2
4
6
8
10
12
14
Length (mm)
EGOA Summer 2011
July 3 - 17
% Frequency
75
50
25
0
2
4
6
8
10
12
14
Length (mm)
WGOA Summer 2013
August 3 - 22
% Frequency
75
50
25
0
2
4
6
8
10
12
14
Length (mm)
EGOA Summer 2013
July 3 - 21
% Frequency
75
50
25
0
2
4
6
8
10
12
14
Length (mm)


Apr 26 - May 11
Apr 30 - May 21
60°N
55°N
Depth m
200
1000
2011
Mean
No. 1000 m-3
0
<10
<50
<100
<500
<1000
<10000
Apr 26 - May 10
Apr 6 - 24
60°N
55°N
Depth m
200
1000
2013
150°W
140°W


WGOA Spring 2011
April 26 - May 11
EGOA Spring 2011
April 30 - May 21
WGOA Spring 2013
April 26 - May 10
N=1
EGOA Spring 2013
April 6 - 24
% Frequency
Length (mm)
0
25
50
75
100
4
6
8
10
12
14
16
18


Apr 26 - May 11
Apr 30 - May 21
60°N
55°N
Depth m
200
1000
2011
Mean No. 10 m-2
0
<10
<50
<100
<500
<1000
<10000
Apr 26 - May 10
Apr 6 - 24
60°N
55°N
Depth m
200
1000
2013
150°W
140°W


WGOA Spring 2011
April 26 - May 11
EGOA Spring 2011
April 30 - May 21
WGOA Spring 2013
April 26 - May 10
EGOA Spring 2013
April 6 - 24
% Frequency
0
25
50
75
Length (mm)
3
6
9
12
15
18
21


Alaska
Kodiak Is.
Gulf of Alaska
55°N
160°W
150°W
N
Depth m
200
1000

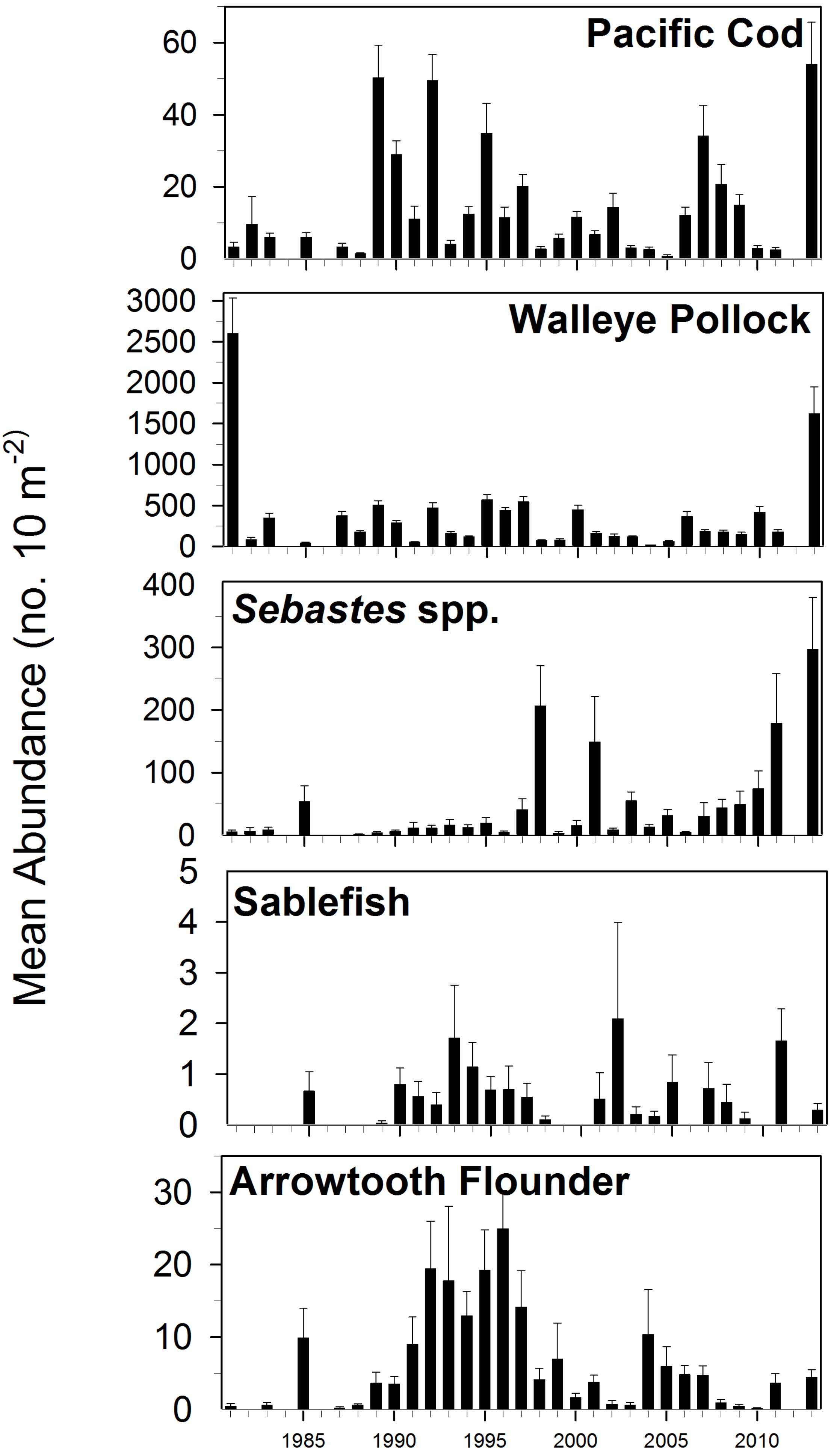

Mean Abundance (no. 10 m^{-2})
Pacific Cod
0
20
40
60
Walleye Pollock
0
500
1000
1500
2000
2500
3000
Sebastes spp.
0
100
200
300
400
Sablefish
0
1
2
3
4
5
Arrowtooth Flounder
0
10
20
30
1985
1990
1995
2000
2005
2010

Table 1. Sampling survey details for spring and summer research cruises in the eastern and western Gulf of Alaska (GOA) during 2011 and 2013. The total number of ichthyoplankton samples collected and processed for fish eggs and larvae are given for 60-cm bongo and neuston net collections.

Cruise	Ship	Year	Season	Sampling Dates	No. Sampling Stations 60-cm Bongo	Neuston
Eastern GOA:						
1TT11	R/V *Thomas Thompson*	2011	Spring	30 April – 21 May	114	116
1NW11	F/V *Northwest Explorer*	2011	Summer	3–17 July	49	52
DY1304	NOAA ship *Oscar Dyson*	2013	Spring	6–24 April	113	112
1NW13	F/V *Northwest Explorer*	2013	Summer	3–21 July	68	68
Western GOA:						
1TX11	R/V *Tiglax*	2011	Spring	26 April – 11 May	46	47
2NW11	F/V *Northwest Explorer*	2011	Summer	2–21 August	53	55
1TX13	R/V *Tiglax*	2013	Spring	26 April – 10 May	26	14
2NW13	F/V *Northwest Explorer*	2013	Summer	3–22 August	52	54

Table 2. Results of Analysis of Variance on fourth-root transformed larval abundance between years (2011 and 2013) and regions (East [E] and West [W]). All data are from the 60-cm bongo net samples (number per 10 m^2) except for Sablefish which are from the neuston net (number per 1000 m^3). n/a = not applicable because no Pacific Cod were collected in 2011 in the East and only one Sablefish was collected in 2013 in the West; SS = Sum of Squares; F = F-statistic; * = main effects not provided where a significant interaction occurred; – = not significant results. See Table 1 for sample sizes. All analyses conducted in R statistical software (version 3.0.2; R Core Team 2013).

Species	**Main Effects**			**Within Years**		**Within Regions**	
	Year	**Region**	**Year X Region**	**2011 East vs West**	**2013 East vs West**	**East 2011 vs 2013**	**West 2011 vs 2013**
Pacific Cod	n/a	n/a	n/a	n/a	p<0.001 (W>E) SS=53.7, F=71.8	n/a	p<0.001 (13>11) SS=30.1, F=22.4
Walleye Pollock Eggs	p<0.001 (13>11) SS=116.9, F=59.7	p<0.001 (W>E) SS=49.2, F=25.1	—	p<0.001 (W>E) SS=30.7, F=41.5	p=0.02 (W>E) SS=18.5, F=5.7	p<0.001 (13>11) SS=107.0, F=51.2	p<0.001 (13>11) SS=30.5, F=19.8
Walleye Pollock	*	*	p<0.001 SS=9.9, F=12.1	p<0.001 (W>E) SS=34.4, F=80.2	p<0.001 (W>E) SS=76.7, F=60.3	p<0.001 (13>11) SS=8.2, F=13.8	p<0.001 (13>11) SS=26.4, F=17.1
Rockfish (Spring)	—	—	—	—	—	—	—
Rockfish (Summer)	—	p<0.001 (E>W) SS=70.3, F=37.9	—	p<0.001 (E>W) SS=44.7, F=26.8	p<0.001 (E>W) SS=27.3, F=13.6	—	—
Sablefish (neuston)	n/a	n/a	n/a	p<0.01 (E>W) SS=42.9, F=7.5	n/a	p<0.001 (11>13) SS=70.4, F=15.7	n/a
Arrowtooth Flounder	*	*	p<0.001 SS=19.4, F=20.5	p<0.001 (W>E) SS=14.1, F=27.5	p=0.03 (E>W) SS=6.9, F=4.8	p<0.001 (13>11) SS=73.2, F=83.3	—

Table 3. Mean (± standard deviation) standard length of larvae sampled between years (2011 and 2013) and regions (East and West). All data are from the 60-cm bongo net samples except for Sablefish which are from the neuston net. n/a = not applicable because no Pacific Cod were collected in 2011 in the East. *n* = sample size. All analyses conducted in R statistical software (version 3.0.2; R Core Team 2013).

Species	**2011**		**2013**	
	East	**West**	**East**	**West**
Pacific Cod	n/a	5.1 ± 1.1 (*n* =60)	4.9 ± 0.9 (*n* =34)	4.6 ± 0.9 (*n* =123)
Walleye Pollock	4.9 ± 0.6 (*n* =12)	5.3 ± 1.4 (*n* =107)	4.5 ± 0.6 (*n* =102)	5.2 ± 1.4 (*n* =185)
Rockfish (Spring)	5.5 ± 0.9 (*n* =438)	5.5 ± 0.8 (*n* =117)	5.6 ± 0.8 (*n* =336)	5.6 ± 0.8 (*n* =126)
Rockfish (Summer)	3.9 ± 1.6 (*n* =284)	4.0 ± 1.4 (*n* =139)	4.2 ± 1.0 (*n* =408)	4.3 ± 1.0 (*n* =140)
Sablefish (neuston)	12.2 ± 2.1 (*n* =336)	10.6 ± 1.5 (*n* =44)	12.3 ± 1.3 (*n* =71)	7.8 (*n* =1)
Arrowtooth Flounder	14.7 ± 3.8 (*n* =12)	8.5 ± 2.1 (*n* =91)	9.4 ± 2.6 (*n* =368)	9.7 ± 3.4 (*n* =36)

Table 4. Results of Linear Mixed Effects models for larval standard lengths (mm) between years (2011 and 2013) and regions (East [E] and West [W]). All data are from the 60-cm bongo net samples except for Sablefish which are from the neuston net. n/a = not applicable because no Pacific Cod were collected in 2011 in the East and only one Sablefish was collected in 2013 in the West; * = main effects not provided where a significant interaction occurred; – = not significant results. See Table 3 for total sample sizes per survey. All analyses conducted in R statistical software (version 3.0.2; R Core Team 2013).

Species	**Main Effects**			**Within Years**		**Within Regions**	
	Year	**Region**	**Year X Region**	**2011 East vs West**	**2013 East vs West**	**East 2011 vs 2013**	**West 2011 vs 2013**
Pacific Cod	n/a	n/a	n/a	n/a	—	n/a	—
Walleye Pollock	—	—	—	—	p<0.01 (W>E)	p=0.04 (11>13)	—
Rockfish (Spring)	*	*	p=0.05	—	p<0.001 (W>E)	—	—
Rockfish (Summer)	p=0.04 (13>11)	—	—	—	—	—	—
Sablefish (neuston)	n/a	n/a	n/a	p<0.01 (E>W)	n/a	—	n/a
Arrowtooth Flounder	*	*	p<0.001	p<0.001 (E>W)	—	p<0.001 (11>13)	—