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Early life history phenology among Gulf of Alaska fish species: Strategies, synchronies, and sensitivities

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ABSTRACT

Synthesis of four decades of Gulf of Alaska ichthyoplankton data indicates that species diversity and total abundance peaks during spring, a common pattern in temperate and sub-arctic ocean regions due to synchrony with the spring peak in plankton production. Nevertheless, fish larvae occur in the plankton at all times of year and peak abundance periods vary significantly by species and habitat. Larval size at hatching and at transformation to the juvenile stage is also highly variable and associated with a variety of larval durations and temporal supply of larval cohorts to pelagic habitats. This phenological diversity represents variability in exposure and adaptation to seasonal cycles in the ocean. Water temperature, winds and currents, and availability of suitable zooplankton prey vary significantly on a seasonal scale affecting degrees of synchrony among larval species with optimal environmental conditions for growth, transport and survival. This synchrony is also affected by interannual shifts in the oceanographic environment, and different early life phenologies among species generate different sensitivities to such interannual variability. Early life history strategies and synchronies are evaluated here and environmental sensitivities are proposed for the numerically dominant species of fish larvae occurring in Gulf of Alaska plankton, including commercially and ecologically important species. For winter to early spring spawners, cold temperatures are an advantage in terms of slowing development so that larvae do not use up all their lipid reserves prior to optimal availability of suitable larval zooplankton prey. Interannual variability in winter temperature may therefore be a good indicator of survival outcomes, especially as influenced by the timing of the switch to exogenous feeding. Variability in temperature-influenced larval growth during late spring and summer months may be less consequential in maintaining synchrony with larval food availability for spring-summer spawners. Rapid growth in association with warm summer conditions facilitates access to a wide size range of prey organisms and minimizes critical periods of vulnerability to trophic mismatch. The Gulf of Alaska is a highly advective environment; storms and alongshore winds promote onshore advection of surface waters. This onshore Ekman transport is strongest during winter and spring when deep water spawned larvae are most abundant over the slope and require access to the shelf. Enhanced shoreward transport of larvae in the canyons intersecting the slope is also an important mechanism. Interannual variability in such transport mechanisms may be critical in determining early ontogeny survival for these species. During all seasons, but especially spring and summer, there are species of larvae for which retention nearshore is vital for survival and mesoscale oceanographic features as well as larval behavioral abilities may be crucial. Annual patterns in phytoplankton and zooplankton production and abundance indicate high-amplitude variation in the composition of prey fields available to larvae, including variability in abundance and the size spectrum of organisms that larvae might encounter and consume. Food limitation seems less likely for larval species that are most abundant in spring-summer than for species with peak abundance in winter-spring. It is probable that the more selective a species is in terms of zooplankton prey, the more susceptible that species is to a trophic mismatch. Species-specific intrinsic rates and morphological development during early ontogeny also influence the interaction of larvae with their environment, and larval growth trajectories can be quite different even among species with identical early life

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phenology. This insight clearly indicates that although phenology is critical, timing is not everything and all fish larvae are not equal. For the 23 species and two genera of fish in this study, a synoptic overview is provided of their early ontogeny environmental synchronies and proposed sensitivities. This ecological synthesis of phenologies helps us characterize vulnerability and resilience factors for intervals of the planktonic phase in the pelagic environment. It also identifies environmental signals that could be tested as species-specific ecosystem indicators of population trends for fish stocks in the Gulf of Alaska. Further, understanding seasonal dynamics in the ichthyoplankton is considered important for gauging food availability and energy flow more broadly in this and other pelagic ecosystems, as well as to understanding environmental forcing on the fish populations themselves.

1. Introduction

Contemporary fisheries science has advanced the concept of an ecosystem-based approach to fisheries management, and new efforts are underway to improve our understanding of broad ecological connections that are relevant to fish stocks and populations in large marine ecosystems (Marshak et al., 2016). There is tension between two realities in the application of ecological data to fisheries management: 1) the objective of fisheries scientists to develop metrics capturing the dominant environmental forcing on an individual fish species prior to recruitment that can be factored into assessment models, and 2) the recognition by ecologists of the need to investigate multiple species-specific and life-stage-specific connections between species and their physical and biological environment to fine-tune selection and testing of ecosystem metrics that will be valid indicators of fish population trends. Ecological complexity limits possibilities for finding singular metrics that determine the annual survival of young to the adult reproducing population for marine fish species (i.e. recruitment). Nevertheless, investigating early life history strategies and the interaction between larval fish and the oceanographic environment elucidates sensitivity and potential mechanisms of response to environmental forcing during early ontogeny (Bailey et al., 2005; Houde, 2008; Doyle and Mier, 2016). Early life history studies incorporated into integrated marine ecosystem research programs go a long way towards illuminating species-environment mechanisms of interaction that are relevant to fish population fluctuations. Understanding such mechanisms is essential for identifying species-specific ecosystem indicators of importance that ultimately may be incorporated into not only individual stock assessment models but also marine ecosystem models that advance the implementation of Ecosystem-Based Fisheries Management (Hare et al., 2016; Shotwell et al., 2018; Zador et al., 2017).

Fisheries-related integrated ecosystem research has been carried out in the Gulf of Alaska (GOA) since the 1980s, and has included the U.S. National Oceanic and Atmospheric Administration (NOAA) Alaska Fisheries Science Center's (AFSC) Ecosystem and Fisheries Oceanography Investigations program (EcoFOCI; https://www.ecofoci.noaa.gov/), the Global Ocean Ecosystem Dynamics program (U.S. GLOBEC; http://www.usglobec.org/), and more recently the North Pacific Research Board-sponsored Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP; http://www.nprb.org/gulf-of-alaska-project/). These programs have contributed substantially to our present understanding of oceanographic and ecological processes in this region, and the plankton and oceanographic data continue to be valuable for the investigation of early life history ecology and recruitment processes among fish species in the GOA ecosystem. As part of the synthesis phase of the GOAIERP program, this study was undertaken to provide a comprehensive review of the phenology of early life history patterns and processes among commercially and ecologically important fish species in the GOA, and to develop hypotheses regarding associated sensitivities to environmental forcing.

Climate change and multi-decadal variability in ocean conditions have been implicated in shifting distributions, abundance, and phenology of fish and shellfish production in U.S. marine ecosystems (Asch, 2015; Auth et al., 2018), and vulnerability assessments are being undertaken to evaluate individual species' exposure and sensitivity to ecosystem change (Morrison et al., 2015; Hare et al., 2016). Quantitative approaches that determine climate impacts on the abundance and distribution of individual fish species are difficult to apply to fisheries assessments in most instances due to limitations in understanding relevant ecological mechanisms. In contrast, qualitative ecological information advances the development of predictive capacity by providing regional, species, and life stage-specific guidance in identifying ecosystem indicators of importance that may be tested in assessment modelling efforts (Zador et al., 2017). Reproductive and early life history strategies and traits are particularly important because they can be used to build “exposure profiles” for species during early ontogeny that represent species' interaction with, and sensitivity to, the pelagic environment in a particular ecosystem (Doyle and Mier, 2016; Hare et al., 2016; Shotwell et al., 2018). The early ontogeny phase is particularly important in the annual trajectory towards recruitment for marine fish species, and especially the planktonic phase when interaction with, and sensitivities to, the environment are very different from both the juvenile and adult phases (Fuiman and Werner, 2002; Miller and Kendall, 2009). Timing of this early ontogeny phase dictates many of the ecological characteristics of a species during early life and in conjunction with knowledge of spatial patterns in the ichthyoplankton advances the development of species’ ecological profiles and associated assessment of climate vulnerability.

Northern latitude fish populations are hypothesized to be particularly sensitive to climate-induced phenological shifts in plankton communities as recruitment success is highly dependent on synchronization of the larval stage with pulsed plankton production (Cushing, 1990; Edwards and Richardson, 2004). Timing of reproduction and early ontogeny among fishes is also adapted to long-term physical oceanographic processes such as annual temperature cycles and seasonal variability in transport. Interannual shifts in the physical and biological environment can therefore disrupt temporal synchrony with species-specific optimal conditions for embryonic development, larval feeding and growth, and favorable transport to nursery habitat. Studying early life history phenologies and how they are connected to prevailing annual patterns in the pelagic environment is an essential first step in evaluating the potential for such disruptions among marine fish species.

The timing and duration of fish spawning and larval occurrence in GOA pelagic habitats is variable among taxonomic groups, although a peak in larval fish abundance and species diversity occurs during spring (Matarese et al., 2003; Doyle et al., 2009). A principal component analysis of early life history traits and ecological characteristics among GOA fish species identified phenology of spawning and early ontogeny as a primary gradient accounting for a high level of the variability among species (Doyle and Mier, 2012). Timing of production may range from single-batch spawning over a short period of time to the production of multiple batches of eggs that may result in an extended temporal supply of larval cohorts in the plankton. Variability in spawning times and locations as well as the development rates, durations and drift patterns of larvae also contributes to differences in pelagic habitat utilization from coastal to deep water (Doyle and Mier, 2016). This diversity of early life history phenologies represents trade-offs in adaptation to prevailing environmental conditions in the GOA,

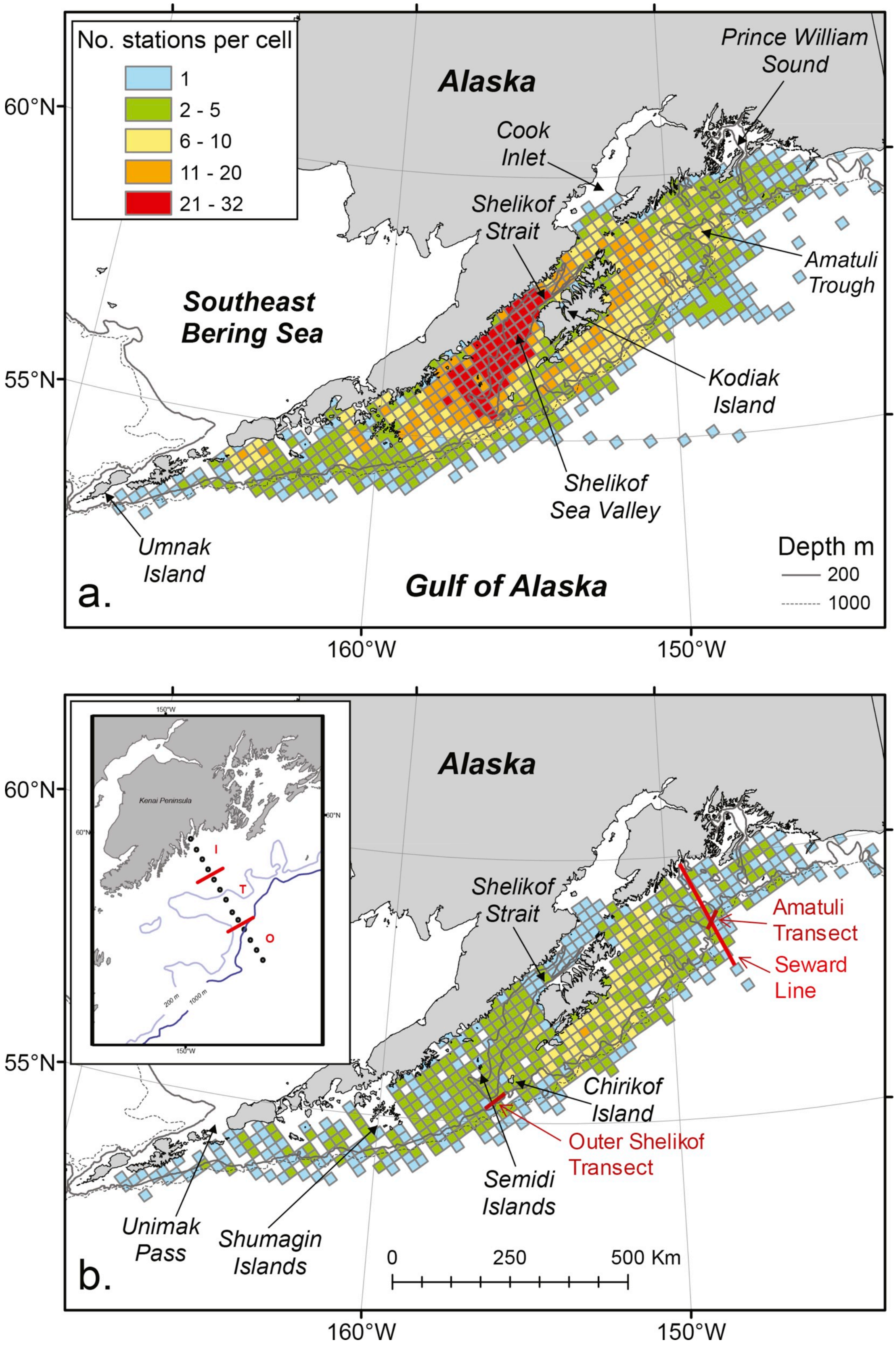


Fig. 1. Geographic and bathymetric features of the western Gulf of Alaska, and distribution of historical ichthyoplankton sampling (1972–2011) by sampling gear: a) 60 cm bongo net, b) Sameoto neuston net. Variability in sampling among years and months is illustrated in Fig. 2. Fig. 1b also shows the location of the Seward Line and the locations of cross-canyon transects. Inset map in 1b shows detail of the Seward Line and relevant distribution of stations among the different depth zones: I = inner, T = transitional, O = outer.

especially with respect to synchrony of early ontogeny with optimal conditions for successful growth and survival (e.g. temperature, transport processes, and prey availability). Vulnerability and resilience factors associated with these different phenologies may modulate species' sensitivities and responses to environmental variability.

Using phenology of early life history as a framework, the objectives of this paper are to 1) describe long-term seasonal patterns in occurrence, abundance, and ontogenetic development of larval fish species in the Gulf of Alaska; 2) evaluate these early ontogeny phenologies in relation to synchrony with, and adaptation to seasonal patterns in the physical and biological oceanographic environment; and 3) propose sensitivities of species during early ontogeny to variability in the pelagic environment of the GOA and recommend stock-specific susceptibilities for use in fishery management applications.

2. Materials and methods

2.1. Ichthyoplankton data

Ichthyoplankton surveys conducted by the EcoFOCI program began in the western GOA in 1972 (no sampling 1973–1976), with annual sampling from 1977 to 2011 and biennial surveys thereafter. The full extent of sampling coverage in the western GOA is from east of Prince William Sound to Umnak Island in the west, and the most intensively sampled area extends along the continental shelf and slope from Kodiak Island to the Shumagin Islands (Fig. 1). Full details of temporal and spatial coverage of ichthyoplankton sampling as well as sampling protocol and processing of samples for ichthyoplankton data are given in Matarese et al. (2003) and in the AFSC's online Ichthyoplankton Information System (IIS; http://access.afsc.noaa.gov/ichthyo/), and associated ichthyoplankton cruise catalog (http://access.afsc.noaa.gov/icc/index.php). The primary sampling gear used for these collections was a 60 cm bongo net fitted with 333 or 505 μm mesh nets, and oblique tows were carried out mostly from 100 m depth to the surface or from 10 m off bottom in shallower water throughout the western GOA (Fig. 1a). Prior to 1990, variability in sampling depth included sampling to 200 m in locations such as Shelikof Strait (Fig. 1a) to capture Walleye Pollock larvae newly hatched from pelagic eggs spawned deep in the water column (Matarese et al., 2003). A Sameoto neuston net was used less frequently (Fig. 1b) to sample the upper 15 cm (approximately) of the water column, but with sufficient samples to allow evaluation of temporal and spatial patterns for species such as Sablefish whose larvae occur primarily in the surface layer of the ocean. Data for this study incorporate all ichthyoplankton data through 2011, which was the end of the annual sampling. Sampling east of the 140° meridian was rare for most of the time series, but in 2011 included sampling in the eastern GOA as part of the GOAIERP program (Siddon et al., 2019). Distribution of sampling by year and month for each of the sampling gears is given in Fig. 2.

The focus for this study was the larval stage because many species have demersal eggs that are not represented in the ichthyoplankton samples (Table 1). Species included in the analysis were those that occurred in greater than 5% overall of historical ichthyoplankton samples during periods of peak abundance. To describe long-term

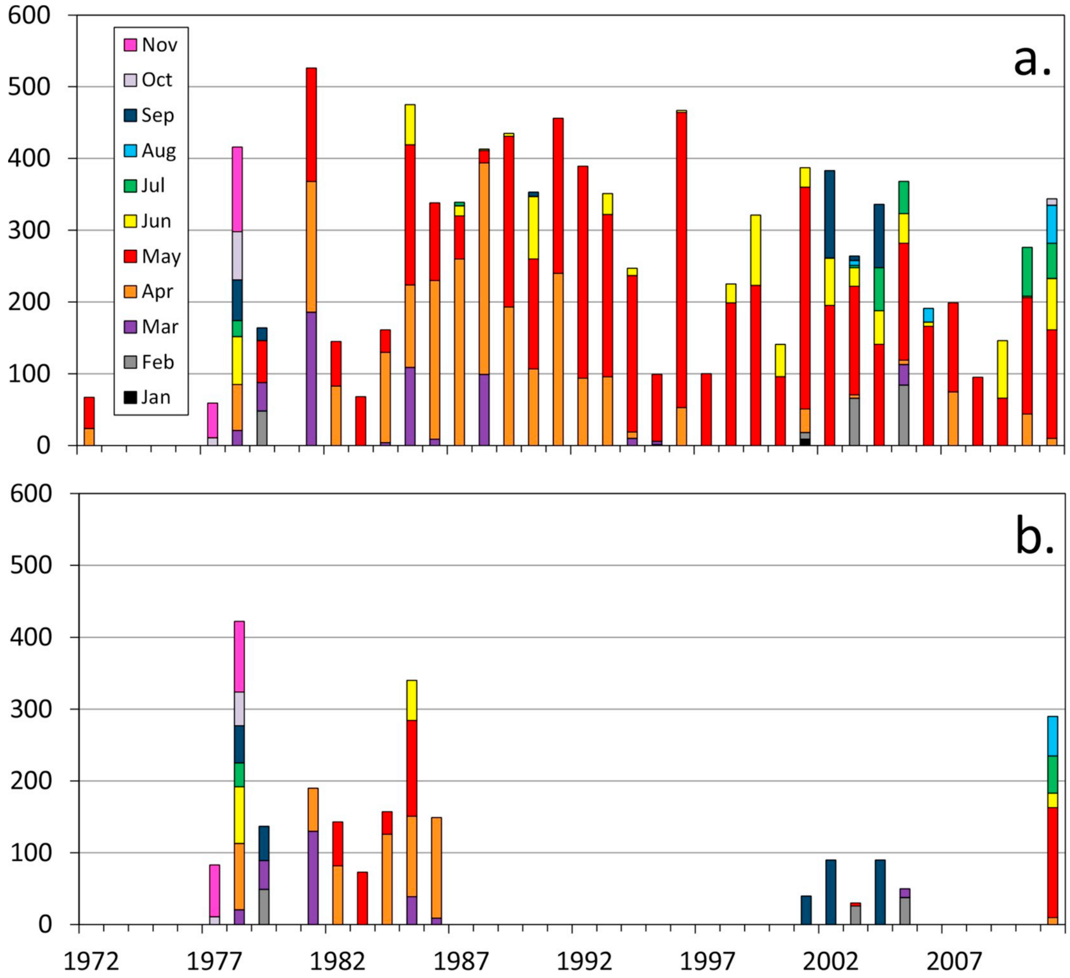


Fig. 2. Distribution of ichthyoplankton sampling in the Gulf of Alaska among years and months with number of samples collected by gear shown on the y-axis: a) 60 cm bongo net samples, b) Sameoto neuston net samples.

Table 1

Gulf of Alaska fish species included in the study, listed in taxonomic order and with life history traits relevant to early life ecology. Species in bold are commercially exploited. Seasons are winter (Win; January–March), spring (Spr; April–June), summer (Sum; July–September), and autumn (October–December). Sources for life history and ecological information are from the NOAA AFSC'S Life History Data Base (https://access.afsc.noaa.gov/reem/lhweb/Index.php), Ichthyoplankton Information System (https://access.afsc.noaa.gov/ichthyo/), and EcoFOCI publications (https://www.pmel.noaa.gov/foci/focipubn.shtml), except where otherwise indicated. *Multiple species but values given for Pacific Ocean Perch, a GOAIERP focal species that releases larvae during spring in deep water. **From King and McFarlane (2003).

Family	Species	Common Name	Longevity (years)	Age at First Maturity(years)	Fecundity (1000 eggs/female)	Spawning Season	Spawning Habitat	Egg Type
Clupeidae	***Clupea pallasi***	**Pacific herring**	15	2–3	12–80	Spr	Nearshore	Demersal, adhesive
Bathylagidae	*Leuroglossus schmidti*	Northern Smoothtongue	6	2	5–8	Win-Spr	Deepwater	Epipelagic
Osmeridae	*Mallotus villosus*	Capelin	6	2–3	9–25	Sum-Aut	Nearshore	Demersal
Myctophidae	*Stenobrachius leucopsarus*	Northern Lampfish	8	3–4	12.6**	Spr-Sum	Deepwater	Deep Pelagic
Gadidae	***Gadus macrocephalus***	**Pacific Cod**	25	2–3	1000–5000	Late Win	Shelf	Demersal
	Gadus chalcogrammus	**Walleye Pollock**	31	3	95–1080	Late Win	Shelf	Deep Pelagic
Scorpaenidae	***Sebastes* spp.***	**Rockfish (unidentified)**	80	7	10–210	Spr-Sum	Deepwater	Viviparous
Anoplopomatidae	***Anoplopoma fimbria***	**Sablefish**	73	5–6	100–1280	Late Win	Deepwater	Deep Pelagic
Hexagrammidae	*Hexagrammos decagrammus*	Kelp Greenling	18	3	5–900	Aut-Win	Nearshore-Shelf	Demersal
	Ophiodon elongatus	**Lingcod**	33	3	60–500	Win-Spr	Nearshore-Shelf	Demersal, adhesive
	Pleurogrammus monopterygius	**Atka Mackerel**	14	2–3	5–43	Sum-Win	Shelf	Demersal, adhesive
Cottidae	*Hemilepidotus*	Red Irish Lord	6	4	59–126	Aut-Win	Nearshore	Demersal, adhesive
Bathymasteridae	*Bathymaster* spp.	Genus of Ronquils	unknown	unknown	unknown	Spr-Sum?	Nearshore-Shelf?	Demersal
Ammodytidae	*Ammodytes hexapterus*	Pacific Sand Lance	7	1	1–16	Aut-Win	Nearshore	Demersal, adhesive
Pleuronectidae	***Atheresthes stomias***	**Arrowtooth Flounder**	23	6	130–2240	Winter	Deepwater	Deep Pelagic
	Glyptocephalus zachirus	**Rex Sole**	29	3	4–238	Spr-Sum	Deepwater	Epipelagic
	Hippoglossoides elassodon	**Flathead Sole**	27	2	50–160	Spr	Shelf	Epipelagic
	Hippoglossus stenolepis	**Pacific Halibut**	55	4	500–4000	Win	Deepwater	Deep Pelagic
	Isopsetta isolepis	**Butter Sole**	11	3	350–650	Spr-Sum	Nearshore	Epipelagic
	Lepidopsetta bilineata	**Southern Rock Sole**	28	3	130–400	Spr-Sum	Nearshore-Shelf	Demersal, adhesive
	Lepidopsetta polyxystra	**Northern Rock Sole**	24	3	152–404	Win-Spr	Nearshore-Shelf	Demersal, adhesive
	Microstomus pacificus	**Dover Sole**	53	5	40–167	Spr-Sum	Deepwater	Epipelagic
	Platichthys stellatus	**Starry Flounder**	21	5	900–3671	Win-Sum	Nearshore	Epipelagic
	Limanda aspera	**Yellowfin Sole**	34	6	100–3635	Sum	Nearshore	Epipelagic
	Pleuronectes quadrituberculatus	**Alaska Plaice**	35	4	56–520	Spr	Nearshore-Shelf	Epipelagic

prevailing seasonal patterns in larval abundance, mean abundance values were calculated by combining data across years for each month. Mean abundance values by half-month, stratified by year, have also been given for most of these species previously (Doyle et al., 2009; Doyle and Mier, 2016). Most sampling was carried out during spring (April–June). Sampling coverage was much more limited during summer (July–September), autumn (October–November), and winter (February and March, with very few samples in January), so abundance values from those seasons may be less reliable. However the data were considered appropriate for providing insight into general seasonal patterns in occurrence, abundance, and size of larval fish species in the GOA ecosystem. Length frequency distributions of larvae for each month were calculated by weighting the lengths by the standardized catches (specimens per volume of water sampled), and combining data across years. These length frequency distributions illustrate a general pattern of seasonal progression in larval sizes among species, and are considered a coarse representation of larval growth rates across months. Mean sizes of life stages at ontogenetic intervals (e.g. size at hatching) for each species were obtained from Matarese et al. (1989), and the IIS. To provide examples of variability among species in morphological development of larvae, illustrations of larvae by size categories were included in the manuscript.

2.2. Climate and oceanographic data

Sea surface temperature (SST) is from NOAA's 1/4° daily Optimum Interpolation Sea Surface Temperature (OISST) constructed by combining observations from different platforms (satellites, ships, buoys) on a regular global grid (Banzon et al., 2016; Reynolds et al., 2007). Wind data are from the North American Regional Reanalysis (NARR) data set (Mesinger et al., 2006). The NARR model uses the very high resolution NCEP Eta Model (32-km/45 layer) together with the Regional Data Assimilation System which assimilates available surface, upper-air, and satellite-based observations. The high spatial resolution of the NARR dataset makes it more suitable than coarser reanalyses for coastal regions near complex topography.

Circulation and transport processes were derived from the Regional Oceanographic Modelling System (ROMS) ocean circulation model. ROMS is a free-surface, hydrostatic primitive equation ocean circulation model (Haidvogel et al., 2008; Moore et al., 2004; Shchepetkin and McWilliams, 2004) which has been adapted to the Gulf of Alaska (Hermann et al., 2009; Dobbins et al., 2009; Coyle et al., 2012). Years 1997–2011 were simulated using a model grid with ~3-km horizontal resolution and 42 vertical layers; this continuous multiyear simulation includes coastal runoff and tidal dynamics. Model-generated flows were interpolated to cross-canyon sections at two locations (Fig. 1b): the entrance to the Shelikof Sea Valley (55.3°N, 156.5°W to 55.7°N, 155.7°W) and Amatuli Trough (58.5°N, 148.5°W to 59.0°N, 148.2°W). Weekly averages from the curvilinear ROMS output were re-gridded to regular lat-long-depth coordinates (spacing of 0.03° latitude, 0.06° longitude, and z-levels at 0, 5, 10, 15, 20, 30, 40, 50, 60, 75, 100, 125, 150, 200, 250, 300 m), and subsequently interpolated to a uniform spatial grid (cross-canyon distance and depth) for each of the sections. Finally, we calculated the velocities in the direction perpendicular to each section (i.e. directly into/out of the canyon, here defined as positive/negative flow, respectively). The spatial integral of the flux into each canyon was calculated as weekly averages of total along-canyon flux; these were subsequently used to calculate a monthly climatology of flows during 1997–2011 and the monthly anomalies from climatology over that time period. The weekly spatial patterns were summarized into a long-term multiyear average for each canyon. The weekly average, re-gridded ROMS output was also used to generate a time series of temperature averaged over the full water column at a mid-channel location in Shelikof Strait (57.6 N, 155 W) in order to represent interannual variation in water temperature over the years of the model run, 1997–2011.

2.3. Primary production and microzooplankton data

Chlorophyll-a (Chl*a*) and microzooplankton samples were collected during CTD casts in the northern GOA, either along the Seward Line (Fig. 1b) transect extending from the mouth of Resurrection Bay off the Kenai Peninsula to beyond the shelf break ('Seward region'), or on a station grid encompassing the continental shelf and slope to the south and east of Kodiak Island ('Kodiak region'). Most sampling was carried out during the two GOAIERP field years of 2011 and 2013, with data presented here representing three seasons: spring, summer (Kodiak region only) and autumn (Table 2). Historical primary production and microzooplankton data are more limited than the ichthyoplankton data in this region, but some additional chlorophyll data were included from sampling along the Seward Line in 2001, 2003, 2012, and 2014–2016. Station locations are shown in Strom et al. (2019; their Fig. 1). Water samples for Chl*a* analysis were collected at 10-m intervals from 0 to 50 m at each station, and filtered and processed as described in Strom et al. (2016). Microzooplankton samples were preserved and processed as described in Strom et al. (2019).

2.4. Mesozooplankton data

Mesozooplankton data presented here are from an ongoing time-series of collections from the Seward Line (http://research.cfos.uaf.edu/sewardline/) and include abundance, life stage, and size data for

Table 2
Distribution of sampling among years and total number of field observations for phytoplankton (chlorophyll-a) and microzooplankton from Kodiak and Seward regions. N = number of vertical profiles (e.g. estimates of integrated 0–50 m water column content) for chlorophyll-a; and number of biomass estimates at 10 m for microzooplankton.

Region	Season	2001	2003	2011	2012	2013	2014	2015	2016	N
Chlorophyll-a										
Kodiak	Spring			x		x				88
	Summer			x	x	x				144
	Autumn			x		x				47
Seward	Spring	x	x	x		x	x	x	x	108
	Summer	x	x							35
	Autumn			x		x	x	x	x	69
Microzooplankton										
Kodiak	Spring			x		x				13
	Summer			x		x				19
	Autumn			x		x				11
Seward	Spring			x		x				14
	Summer									0
	Autumn			x		x				11

the dominant copepod species in this region. Small zooplankton (target size < 2 mm) were collected with a 25 cm diameter CalVET array with 150 µm mesh nets, and large zooplankton (target size > 2 mm) were sampled from the upper 100 m of the water column with a 1 m^2 MOCNESS system or a 0.25 m^2 Hydrobios Multinet system (2005 onwards) using 500 µm mesh nets (Coyle and Pinchuk, 2003, 2005; Coyle et al., 2013). The MOCNESS and Multinet samplers were fished at night so that species that undergo diel vertical migrations are represented in the catches. Samples were processed and numerically dominant taxa enumerated as outlined in Coyle and Pinchuk (2003, 2005), with the addition that in later years lengths in Calvet samples were also measured for all zooplankters enumerated (Roff and Hopcroft, 1986). Thus for abundant species/stages more length measurements are available. Additional data on copepod egg size come from egg production experiments (Napp et al., 2005; Hopcroft et al., 2005). *Neocalanus flemingeri* naupliar lengths were measured during laboratory rearing (Hopcroft, unpublished). For other species, naupliar sizes were inferred from data on the size of eggs and copepodite stage-1 (CI), allowing for 10% expansion upon hatch and 50% increase associated with metamorphosis from nauplius stage-6 to CI.

Abundance calculations used data from 1998 to 2004 collected five or six times annually, typically during March, April, May, July, August and October, and from 2005 to 2015 during each May and September (Table 3). Mean zooplankton abundance in the upper 100 m by taxon and month was computed for three different zones along the Seward Line: the inner shelf, transitional zone, and outer zone (Fig. 1b, inset). These zones were identified previously based on cross-shelf distribution patterns of zooplankton representing the inner shelf area influenced primarily by the Alaska Coastal Current and characterized by neritic species, the outer continental slope to ocean basin influenced by the Alaskan Stream and characterized by an oceanic community of zooplankton, and a transitional mid-shelf to shelf break area characterized by a mixture of neritic and oceanic zooplankton taxa (Coyle and Pinchuk, 2005; Sousa et al., 2016).

2.5. Nutrient-Phytoplankton-Zooplankton (NPZ) model-generated data

As part of the GOAIERP, the ROMS was refined to address biological dynamics of relevance to fish early life history survival by adding an ecosystem component. A Nutrient-Phytoplankton-Zooplankton (NPZ) model was embedded within ROMS to provide output to drive Individual-Based Models for five focal fish species. This ROMS-NPZ model is of intermediate complexity, simulating the carbon biomass of phytoplankton, microzooplankton and zooplankton in response to photosynthetically active radiation (PAR); biological and circulation-driven changes in nitrate, ammonium and iron concentrations; and zooplankton biomass (Coyle et al., 2012, 2013, 2019). The NPZ model is based on the equations in the models of Frost (1987, 1993) as modified for the GOA (Hinckley et al., 2009; Coyle et al., 2012). From the 1998–2011 runs of the ROMS-NPZ model, average monthly patterns were generated to illustrate spatial variability in biomass in the GOA of different lower trophic level components in the upper 25 m of the water column. A selection of these maps is included here to provide insight into spatial patterns of zooplankton production that influence availability of prey organisms for larval fish species in different pelagic habitats at different times of the year.

3. Results

3.1. Early life history phenology – patterns and strategies

Twenty-three individual fish species and two species complexes from 12 families were included in this study and represent commercially and ecologically important species in the GOA that are most frequently caught in ichthyoplankton samples (Table 1 and Table 4). Walleye Pollock and Pacific Cod (Gadidae), several species of Rockfish (Scorpaenidae), Lingcod and Atka Mackerel (Hexagrammidae), Sablefish (Anoplopomatidae), and 11 species of flatfish (Pleuronectidae) are abundant groundfish of commercial importance. Rockfish of the genus *Sebastes* spp. are not identified to species as larvae are impossible to distinguish morphologically (Matarese et al., 1989, 2003). Pacific Ocean Perch (*Sebastes alutus*) releases its larvae into the plankton in spring and genetic studies indicate that it is numerically dominant in the spring cohort of Rockfish larvae, whereas the summer cohort of smaller Rockfish larvae includes multiple species (Doyle and Mier, 2016; Siddon et al., 2019). Forage species included the coastal pelagics Pacific Herring (Clupeidae) and Capelin (Osmeridae), Pacific Sand Lance (Ammodytidae), and the oceanic mesopelagic species Northern Lampfish (Myctophidae) and Northern Smoothtongue (Bathylagidae). Among the forage species, only Pacific Herring is exploited commercially. The remaining non-commercial species are demersal and include the coastal-dwelling (as adults) Kelp Greenling (Hexagrammidae) and Red Irish Lord (Cottidae) and Ronquils of the genus *Bathymaster* that occur from the intertidal zone to the outer shelf and slope. Three species of *Bathymaster* occur in the GOA but are also indistinguishable as larvae morphologically (Matarese et al., 2003; Canino et al., 2017). They are included here as they rank highly in terms of abundance in GOA ichthyoplankton samples. Sablefish, Kelp Greenling, Lingcod, Atka Mackerel and Red Irish Lord larvae are known to be primarily neustonic, and are most abundant in the upper 10–20 cm of the water column (Doyle et al., 1995; Matarese et al., 2003). Capelin, *Bathymaster* spp., and Pacific Sand Lance also occur in the neuston but generally as older larvae that undertake diel migrations to the surface at night (Doyle et al., 1995).

Life history traits of relevance to population productivity and the abundance and timing of occurrence of larvae in the plankton are included in Table 1, along with sources of the data. The smaller forage species tend to have low maximum age (longevity) generally ranging from 5 to 8 years, but Pacific Herring and Kelp Greenling are exceptions at 15 and 18 respectively. Of the larger commercial groundfish species, Butter Sole and Atka Mackerel have relatively low maximum age (11 and 14 respectively). Longevity for the remaining species ranges from 21 to 35 except for the extreme outliers of Dover Sole (53), Pacific Halibut (55), Sablefish (73), and Rockfish as represented by Pacific Ocean Perch (88). Age at first maturity generally follows the same pattern, with the longest living species maturing later than the short-

Table 3
Distribution of sampling among years and months for zooplankton along the Seward Line, using the CalVET (C), MOCNESS (MO), and Multinet (MU) plankton samplers. Beginning in 2005, the Multinet replaced the MOCNESS. N = total number of samples collected across years for each month, listed respectively by gear type.

	Mar	Apr	May	Jul	Aug	Sep	Oct
1998	C,MO	C,MO	C,MO	C,MO			C,MO
1999	C,MO	C,MO	C,MO		C,MO		C,MO
2000	C,MO	C,MO	C,MO		C,MO		C,MO
2001	C,MO	C,MO	C,MO	C,MO	C,MO		C,MO
2002	C,MO	C,MO	C,MO	C,MO	C,MO		C,MO
2003	C,MO	C,MO	C,MO	C,MO	C,MO		C,MO
2004	C,MO		C,MO	C,MO			C,MO
2005			C, MU			C, MU	
2006			C, MU			C, MU	
2007			C, MU			C, MU	
2008			C, MU			C, MU	
2009			C, MU			C, MU	
2010			C, MU			C, MU	
2011			C			C, MU	
2012			C, MU			C, MU	
2013			C, MU			C, MU	
2014			C, MU			C, MU	
2015			C, MU			C, MU	
N	91, 91	78, 78	234, 221	65, 65	65, 65	143, 143	91, 91

Table 4a

Percent occurrence of larval fish species in all 60 cm Bongo net samples by month, all years combined (1972, 1977–2011). * = species that are primarily neustonic. No sampling was carried out in December. N = total number of samples for each month.

Common Name	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Pacific Halibut	22.22	7.78	3.02	8.86	10.51	5.71		1.64			
Arrowtooth Flounder	22.22	28.14	11.60	18.73	19.88	16.55	1.45	1.64	0.43		
Northern Smoothtongue		19.76	12.30	8.30	7.22	8.84	8.70		6.38	1.20	7.79
Red Irish Lord*		39.52	6.26	6.23	2.19	0.29				2.41	
Kelp Greenling*		27.54	11.37	19.29	12.22	4.85	0.48			1.20	6.49
Atka Mackerel*		4.20	0.93	0.10							9.74
Pacific Sand Lance		7.78	58.00	77.42	77.05	54.92					
Pacific Cod			0.23	9.92	46.41	30.39					
Walleye Pollock		0.60	3.94	60.30	83.60	66.19	0.48			1.20	0.65
Northern Rock Sole			4.87	20.51	34.82	28.39	0.48		0.85	1.20	
Northern Lampfish		20.36	11.37	25.97	37.14	39.23	54.59	18.03	14.47	9.64	1.95
Alaska Plaice				0.66	4.52	3.28			1.28		
Sablefish*				2.78	4.01	4.99					
Lingcod*				0.56	2.06	3.57					
Pacific Herring					1.28	12.27					
Flathead Sole				3.29	58.30	68.90	7.73		0.85	2.41	
Starry Flounder			0.23	0.71	12.46	21.68					
Rex Sole				0.15	4.60	16.12	14.01	1.64	0.43	1.20	
Dover Sole				0.05	2.86	16.69	7.73		0.43		
Ronquils			0.23	1.32	43.38	71.47	19.32	24.59	11.49	6.02	0.65
Southern Rock Sole				0.56	15.52	27.82	8.70	18.03	10.64	1.20	
Butter Sole				0.05	3.45	11.41	2.42	1.64	0.43		
Rockfish				5.22	27.62	51.64	85.51	75.41	34.89	18.07	1.95
Capelin		30.54	10.21	5.22	3.45	2.00	18.36	34.43	51.49	56.63	33.77
Yellowfin Sole							1.45		5.53		
N	9	208	512	2335	4991	808	252	79	297	87	166

lived ones. Spawning season and fecundity influence the timing, abundance, and temporal spread of larvae in the plankton. Pacific Cod is an example of a short spawning season (starts in February but mostly March to April) combined with high fecundity, resulting in a temporally narrow but very high peak in abundance of these larvae in the plankton during April (Table 1; Doyle and Mier, 2016). In contrast, spawning of the two mesopelagic species (Northern Smoothtongue and Northern Lampfish) with low fecundity is spread over two to three seasons ensuring an extended occurrence of their larvae in the plankton during most of the year. Egg type also influences the temporal and spatial ubiquity of larvae in the plankton and is indicated here along with spawning habitat (Table 1). Spawning of species with demersal, adhesive eggs is associated with nearshore and shelf habitat but not deep water, and can occur in any season. Epipelagic spawning occurs throughout all habitats and seasons, whereas species with deep pelagic eggs spawn in continental slope and basin waters primarily during winter. The 11 species of pleuronectid flatfish included here display a wide variety of strategies for a single taxonomic group with spawning occurring among all seasons and habitats, and a wide range in fecundity with each egg type represented although most are pelagic.

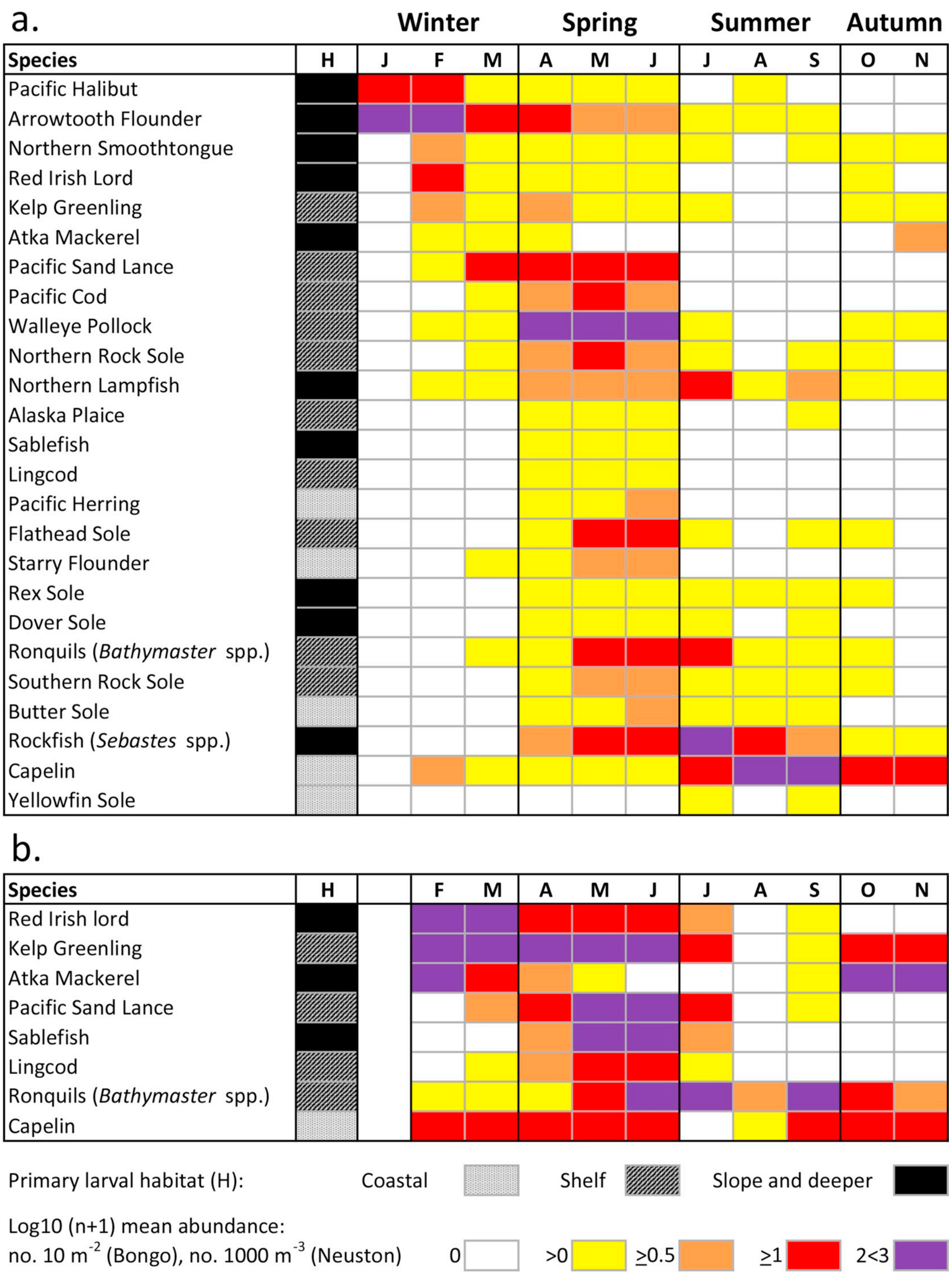
3.1.1. Phenology and larval habitat

For each of the sampling gears, the frequency of occurrence of species in ichthyoplankton samples by month is indicated in Table 4. Species are listed in order of timing of occurrence and peak abundance in the plankton. Seasonal variation in mean abundance (log scale) of species is presented in Fig. 3, and the primary observed larval habitat is also indicated as coastal (nearshore and inner shelf), shelf (throughout shelf), or slope (continental slope and adjacent basin). Habitat preferences as indicated are based on distribution data from previous studies, including neuston as well as water column assemblages (Doyle et al., 1995, 2002 a, 2002 b; Matarese et al., 2003; Doyle and Mier, 2016). Larvae spawned in deep water occur in fewer samples overall than species whose larval habitat is primarily the shelf where most of the samples have been taken (e.g. Arrowtooth Flounder and Pacific Halibut vs. Pacific Cod and Pollock). Northern Lampfish is a deep-water species with relatively high ubiquity occurring in a high proportion of samples especially during spring and summer months when it is abundant on the shelf as well as over the slope. Among coastal species, Pacific Herring, Butter Sole, Starry Flounder and Yellowfin Sole occur in a limited number of samples whereas Pacific Sand Lance and Capelin are highly ubiquitous.

Table 4b

Percent occurrence of larval fish species in all neuston net samples by month, all years combined (1977–79, 1981–86, 2001–2005, and 2011). No neuston sampling was carried out in January or December. * = species that are primarily neustonic, ** = species that can be abundant in the neuston as well-developed larvae, especially at night.

Common Name	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Red Irish lord*	27.43	11.55	18.81	14.51	23.23	9.41		0.31		
Kelp Greenling*	93.81	70.92	68.97	66.59	61.94	28.24		0.31	37.93	48.24
Atka Mackerel*	27.43	23.51	5.47	0.44				0.62	37.93	40.59
Pacific Sand Lance**		3.59	7.23	21.98	26.45	7.06		0.31		
Sablefish *			1.61	22.20	17.42	15.29				
Lingcod*		0.40	0.48	8.79	5.16	2.35				
Ronquils**	5.31	1.99	1.61	10.55	30.97	21.18	7.27	41.93	36.21	12.35
Capelin**	27.43	5.98	9.81	4.18	3.87		3.64	18.63	29.31	14.71
N	113	251	622	455	155	85	55	320	58	170



a.

		Winter			Spring			Summer			Autumn	
Species	**H**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**
Pacific Halibut	■	🟥	🟥	🟨	🟨	🟨	🟨	⬜	🟨	⬜	⬜	⬜
Arrowtooth Flounder	■	🟪	🟪	🟥	🟥	🟧	🟧	🟨	🟨	🟨	⬜	⬜
Northern Smoothtongue	■	⬜	🟧	🟨	🟨	🟨	🟨	🟨	⬜	🟨	🟨	🟨
Red Irish Lord	■	⬜	🟥	🟨	🟨	🟨	🟨	⬜	⬜	⬜	🟨	⬜
Kelp Greenling	▨	⬜	🟧	🟨	🟧	🟨	🟨	🟨	⬜	⬜	🟨	🟨
Atka Mackerel	■	⬜	🟨	🟨	🟨	⬜	⬜	⬜	⬜	⬜	⬜	🟧
Pacific Sand Lance	▨	⬜	🟨	🟥	🟥	🟥	🟥	⬜	⬜	⬜	⬜	⬜
Pacific Cod	▨	⬜	⬜	🟨	🟧	🟥	🟧	⬜	⬜	⬜	⬜	⬜
Walleye Pollock	▨	⬜	🟨	🟨	🟪	🟪	🟪	🟨	⬜	⬜	🟨	🟨
Northern Rock Sole	▨	⬜	⬜	🟨	🟧	🟥	🟧	🟨	⬜	🟨	🟨	⬜
Northern Lampfish	■	⬜	🟨	🟨	🟧	🟧	🟧	🟥	🟨	🟧	🟨	🟨
Alaska Plaice	▨	⬜	⬜	⬜	🟨	🟨	🟨	⬜	⬜	🟨	⬜	⬜
Sablefish	■	⬜	⬜	⬜	🟨	🟨	🟨	⬜	⬜	⬜	⬜	⬜
Lingcod	▨	⬜	⬜	⬜	🟨	🟨	🟨	⬜	⬜	⬜	⬜	⬜
Pacific Herring	░	⬜	⬜	⬜	🟨	🟨	🟧	⬜	⬜	⬜	⬜	⬜
Flathead Sole	▨	⬜	⬜	⬜	🟨	🟥	🟥	🟨	⬜	🟨	🟨	⬜
Starry Flounder	░	⬜	⬜	🟨	🟨	🟧	🟧	⬜	⬜	⬜	⬜	⬜
Rex Sole	■	⬜	⬜	⬜	🟨	🟨	🟨	🟨	🟨	🟨	🟨	⬜
Dover Sole	■	⬜	⬜	⬜	🟨	🟨	🟨	🟨	⬜	🟨	⬜	⬜
Ronquils (*Bathymaster* spp.)	▨	⬜	⬜	🟨	🟨	🟥	🟥	🟥	🟨	🟨	🟨	⬜
Southern Rock Sole	▨	⬜	⬜	⬜	🟨	🟧	🟧	🟨	🟨	🟨	🟨	⬜
Butter Sole	░	⬜	⬜	⬜	🟨	🟨	🟧	🟨	🟨	🟨	⬜	⬜
Rockfish (*Sebastes* spp.)	■	⬜	⬜	⬜	🟧	🟥	🟥	🟪	🟥	🟧	🟨	🟨
Capelin	░	⬜	🟧	🟨	🟨	🟨	🟨	🟥	🟪	🟪	🟥	🟥
Yellowfin Sole	░	⬜	⬜	⬜	⬜	⬜	⬜	🟨	⬜	🟨	⬜	⬜

b.

Species	**H**		**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**
Red Irish lord	■		🟪	🟪	🟥	🟥	🟥	🟧	⬜	🟨	⬜	⬜
Kelp Greenling	▨		🟪	🟪	🟪	🟪	🟪	🟥	⬜	🟨	🟥	🟥
Atka Mackerel	■		🟪	🟥	🟧	🟨	⬜	⬜	⬜	🟨	🟪	🟪
Pacific Sand Lance	▨		⬜	🟧	🟥	🟪	🟪	🟥	⬜	🟨	⬜	⬜
Sablefish	■		⬜	⬜	🟧	🟪	🟪	🟧	⬜	⬜	⬜	⬜
Lingcod	▨		⬜	🟨	🟧	🟥	🟥	🟨	⬜	⬜	⬜	⬜
Ronquils (*Bathymaster* spp.)	▨		🟨	🟨	🟨	🟥	🟪	🟪	🟧	🟪	🟥	🟧
Capelin	░		🟥	🟥	🟥	🟥	🟥	⬜	🟨	🟥	🟥	🟥

Primary larval habitat (H): Coastal ░ Shelf ▨ Slope and deeper ■

Log10 (n+1) mean abundance:
no. 10 m^{-2} (Bongo), no. 1000 m^{-3} (Neuston) 0 ⬜ >0 🟨 ≥0.5 🟧 ≥1 🟥 2<3 🟪

Fig. 3. Larval occurrence and mean abundance by month in the Gulf of Alaska (GOA) in (a) 60 cm Bongo net and (b) Sameoto neuston net. Species included are numerically dominant, and commercially or ecologically important in the GOA. They are arranged in order of appearance and peak abundance in the plankton of the western GOA. Data include all samples collected, as described in Fig. 2. Primary larval habitat (H) is indicated as observed in this region (Doyle et al., 1995, 2002a).

Habitat appears related to the timing and spatial extent of larval species in the plankton, with early-phenology species associated with deep water and slope habitats and late-phenology species occupying primarily coastal and shelf habitats (Fig. 3a). Exceptions are the deep water larvae of Rex Sole and Dover Sole that are most abundant in spring through summer, as well as the release of Rockfish larvae into deep water habitat during spring and summer. Of the species that are most abundant in winter, all are spawned in deep water and the primary larval habitat is over the slope. This group includes Arrowtooth Flounder, Pacific Halibut, Northern Smoothtongue, and Red Irish Lord. Their occurrence extends through spring and to a lesser extent summer, and in the case of the latter two species there have been limited records in autumn. Red Irish Lord larvae are also abundant in the neuston during winter and spring and with low to moderate abundance in summer (Fig. 3b). Spring is the period of peak occurrence and abundance for fish larvae in the GOA plankton with peak diversity of species in April through May (Table 4 and Fig. 3). Yellowfin Sole is the only species whose larvae do not occur during spring and they have been recorded during July and September only; occurrence in August and possibly October samples would be expected but sampling has been very limited in those months. All other species occur during April to June except for Atka Mackerel, which has been collected in the water column in April only and in the neuston samples in April and May. Rockfish and Capelin are most abundant during summer and also occur during autumn.

3.1.2. Phenology and larval duration

Larval duration varies significantly among GOA species. Occurrence and abundance data across months presented here (Table 4 and Fig. 3) represent population-level larval duration rather than individual development time for larval life stages, which is undetermined for many species. Two major patterns exist for larval duration. Discounting the neustonic species whose larvae tend to remain pelagic for a relatively long period of time, early-phenology and deep water-spawning species (e.g. Arrowtooth Flounder, Pacific Halibut, Northern Smoothtongue) tend to have longer larval durations than late-phenology and coastal-spawning species (e.g. Pacific Herring, Starry Flounder, Yellowfin Sole). There are also some deep water-spawning species that release pelagic eggs in spring to summer and have extended larval durations, especially the flatfish Rex Sole and Dover Sole. Shelf spawners such as Walleye Pollock and Flathead Sole are more intermediate in terms of larval duration and timing of spawning (late winter to early spring). Pacific Cod larvae have a more limited period of occurrence and peak abundance in the plankton than Walleye Pollock although spawning phenology is similar (Table 1). Species with the longest larval duration include the mesopelagic Northern lampfish that has very extended production of larvae, Pacific Sand Lance whose larvae remain pelagic from late winter through summer (mostly caught in neuston as older larvae in summer-autumn), and Capelin whose larvae overwinter in the plankton after summer hatching and remain planktonic into spring with occurrence in the neuston as well as water column samples throughout the year. Pacific Sand Lance is unique in terms of an extended period of time between spawning in nearshore environments during autumn and peak abundance of larvae in the plankton during spring (Table 1, Fig. 3). No other species listed here has such an extended period of egg incubation.

Larval duration at the individual and population level is dictated initially by species-specific intrinsic physiological rates of ontogenetic development. Here we consider the following ontogenetic intervals that represent different morphological and ecological characteristics: the egg stage including embryonic development, hatching of larva from the egg, yolk-sac absorption or first-feeding when extrinsic feeding becomes necessary, flexion at which the notochord tip is fully flexed (considered synonymous with onset of skeletal ossification that significantly enhances swimming ability), and transformation at which there is a loss of larval characters and attainment of juvenile/adult characters. Standard length (SL) at these ontogenetic intervals is variable among species which influences their interactions with the pelagic environment at different times of year. Sizes at the different stages are mostly well known for the GOA species (Matarese et al., 1989) and are illustrated with the species listed in phenological order of occurrence, and with the primary larval habitat indicated (Fig. 4). A common

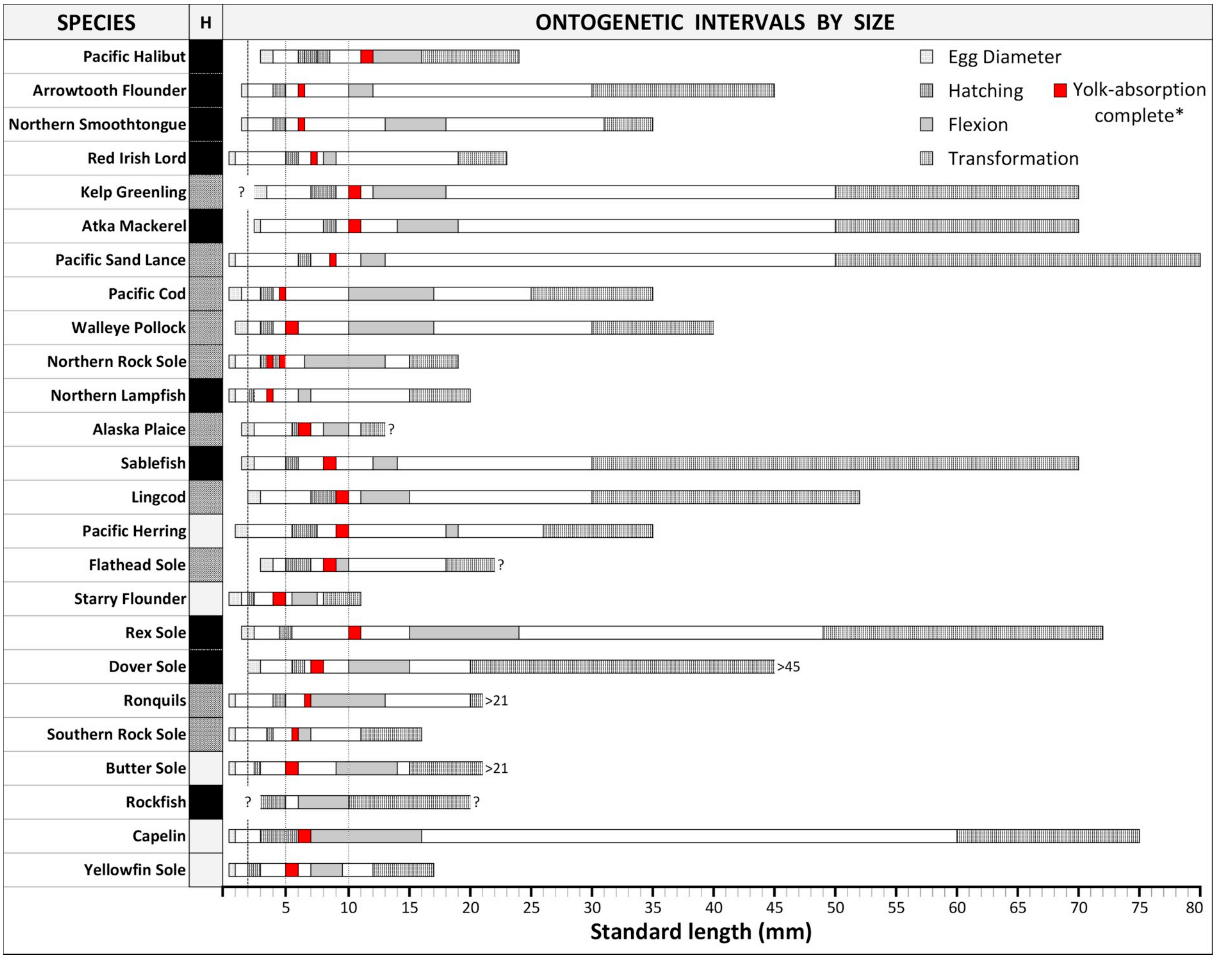


Fig. 4. Size range of Gulf of Alaska fish species at different ontogenetic intervals from the egg stage through the larval planktonic stage ending in transformation to juvenile morphology. *Size at which yolk-absorption is complete is not documented for all species in which case it is estimated from illustrations of larval development at different sizes (Matarese et al., 1989; IIS). Species are listed in phenological order of appearance in the plankton and primary larval habitat is indicated, as in Fig. 3.

pattern is that larvae with extended planktonic duration (Fig. 3) are relatively large with a large size range at transformation, and those with more limited seasonal occurrence in the plankton tend to be smaller at transformation. For example, Pacific Sand Lance and Capelin whose larvae remain in the plankton through multiple seasons have the largest maximum SL at transformation, 80 and 75 mm respectively, and the largest size range for the postflexion stage prior to the beginning of transformation. The extended epipelagic phase of the primarily neustonic larvae including Kelp Greenling, Atka Mackerel, Sablefish and Lingcod (Fig. 3b), is also reflected in their extensive size ranges for the preflexion and transformation stages (Fig. 4). Red Irish Lord seems to be somewhat of an outlier in this regard as its larvae transform at less than 25 mm SL, relative to >50 mm for the other neustonic species. A common trait for species with the smallest size at transformation and limited stage duration is peak abundance of larvae during spring and summer in nearshore to shelf larval habitat (Fig. 3a). Starry Flounder is the smallest at transformation (8–11 mm SL) followed in order by Alaska Plaice (<15 mm SL), Southern Rock Sole, Yellowfin Sole, Northern Rock Sole, Northern Lampfish, and Butter Sole (all 15–20 mm SL). Although the upper size at transformation is not known for most Rockfish species, they seem to transition from flexion to transformation rapidly and can begin transformation at 10 mm SL. Most deep-water spawners with extended stage durations by size have a period of peak larval abundance in winter (Figs. 3 and 4). Exceptions include Rex Sole and Dover Sole that spawn in slope waters during spring and summer. Rex Sole is extraordinary among GOA pleuronectids in that it does not begin transformation until larvae are ~50 mm SL.

Species that have identical or comparable early life history phenologies may also diverge with respect to stage duration and size at stage. Arrowtooth Flounder and Pacific Halibut are identical in terms of timing and location of spawning and period of peak larval abundance in the plankton during winter in slope waters (Table 5 and Fig. 3a; Blood et al., 2007). However the post-flexion larval phase of Pacific Halibut is relatively short and the larvae can be as small as 15 mm SL at the beginning of transformation, whereas Arrowtooth Flounder do not transform until they have reached a minimum SL of 30 and can be > 45 mm SL when they are fully transformed and leave the plankton (Fig. 4). Other differences are that Pacific Halibut eggs and larvae at yolk-absorption are significantly larger than for Arrowtooth Flounder. Pacific Herring and Pacific Sand Lance have similar nearshore spawning habitat and larval hatching and peak abundance phenologies, but widely divergent larval stage durations and sizes at transformation (Fig. 4). Egg size and larval size at yolk-absorption are variable across early life history phenologies but tend to be larger for the winter and deep-water spawners than for the nearshore spring-summer spawners.

3.1.3. Phenology and larval development rates

Larval length data for species at different times of year also reflect larval duration but provide additional insight into development rates. Based on data integrated across years, length-frequency distributions of larvae at 1 mm SL increments by month were created for each species where larval measurements were available from water column (Fig. 5) and neuston (Fig. 6) collections. These length-frequency distributions reflect general patterns of growth by month for each species as well as the size spectrum of larvae that are present in planktonic assemblages across seasons in the GOA. It should be noted, however, that the upper size range of larvae occurring in plankton net samples varies considerably by species and can reflect variability in larval development, behavior and net-avoidance capability at different sizes. For example, Pacific Cod and Walleye Pollock larvae larger than 15 mm SL are rare in the 60-cm bongo net samples (Fig. 5) even though transformation does not begin until ≥25 and 30 mm SL, respectively (Fig. 4). In contrast, the much larger postflexion and early transformation stages of Capelin and Pacific Sand Lance larvae (Fig. 4) are common in GOA water column and neuston samples (Figs. 5 and 6).

During winter most fish larvae caught in plankton nets are at the preflexion stage with sizes reflecting species-specific size ranges from hatching to flexion (Figs. 4 and 5). Most are <10 mm SL and many <5 mm SL. Notable differences from February to March are the slight increase in larval sizes overall, the disappearance of Atka Mackerel from the bongo samples with occurrence as mostly flexion stage larvae in the neuston, and the appearance of newly-hatched Walleye Pollock and Northern Rock Sole in the water column (Figs. 5a and 6). In contrast, Capelin larvae in the bongo and neuston samples are all >20 mm SL and postflexion with some >50 mm SL indicating longevity in the plankton. The divergence in size at age and developmental rates between Pacific Halibut and Arrowtooth Flounder is marked: the former are mostly ≥9 mm SL, and the latter ≤6 mm SL (Fig. 5a).

By April the winter-spawned larval populations are advancing in growth through the first-feeding (yolk-absorption complete) and flexion stages, and newly-hatched larvae are absent (Figs. 5a and 6). The abundant larvae at newly-hatched sizes (most ≤5 mm SL) in the bongo samples include Pacific Cod, Walleye Pollock, Northern Rock Sole, Northern Lampfish, Alaska Plaice, Flathead Sole, Ronquils, Southern

Table 5

Sizes of numerically dominant GOA copepod taxa by life stage. Eggs were measured as diameter, nauplii as total length and copepodites as prosome length, all in μm. For nauplii the range encompassing first to sixth stage are presented, whereas for copepodites, sizes of each stage are presented as means with their standard deviation. Italicized values denote low sample size (<10). Unknown size ranges are represented by a dash.

Prosome Length (μm)	Egg	Nauplius	C1		C2		C3		C4		C5		Adult Female	
	Mean	Range	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Large Copepods														
Calanus pacificus	145	160–420	629	44	826	61	1130	91	1459	78	1859	142	2108	131
C. marshallae	170	190–520	779	43	1093	90	1502	121	2047	157	2657	210	2879	232
Eucalanus bungii	170	190–840	1264	86	1893	237	2608	266	3482	246	4365	306	5825	322
Metridia pacifica	145	160–290	428	38	582	50	763	61	1021	162	1307	141	2051	150
Neocalanus cristatus	375	410–670	*985*	*61*	1623	81	2631	193	4294	270	6354	269	–	–
N. plumchrus	155	190–420	782	75	1168	75	1864	133	2796	197	3818	236	–	–
N. flemingeri	155	190–420	782	75	1168	75	1864		2566	305	3396	271	–	–
Small Copepods														
Acartia spp.	80	90–240	352	31	437	44	516	48	634	55	701	45	904	118
Centropages abdominalis	75	80–250	*365*	*24*	*477*	*36*	588	34	792	121	1066	156	1332	119
Mesocalanus tenuicornis	115	125–350	*513*	*17*	*679*	*21*	*870*	*66*	1098	82	1369	102	1567	121
Microcalanus spp.	–	–	–	–	292	292	347	347	401	401	456	456	475	475
Oithona similis	60	65–160	235	23	283	23	328	28	377	28	409	28	446	68
Oithona setigera	65	70–160	–	–	*298*	*66*	*394*	*36*	*516*	*156*	493	80	708	60
Paracalanus parva	65	70–190	*283*	*34*	339	26	409	34	501	51	626	85	678	54
Pseudocalanus spp.	110	120–260	386	75	483	89	579	122	689	141	855	191	988	184

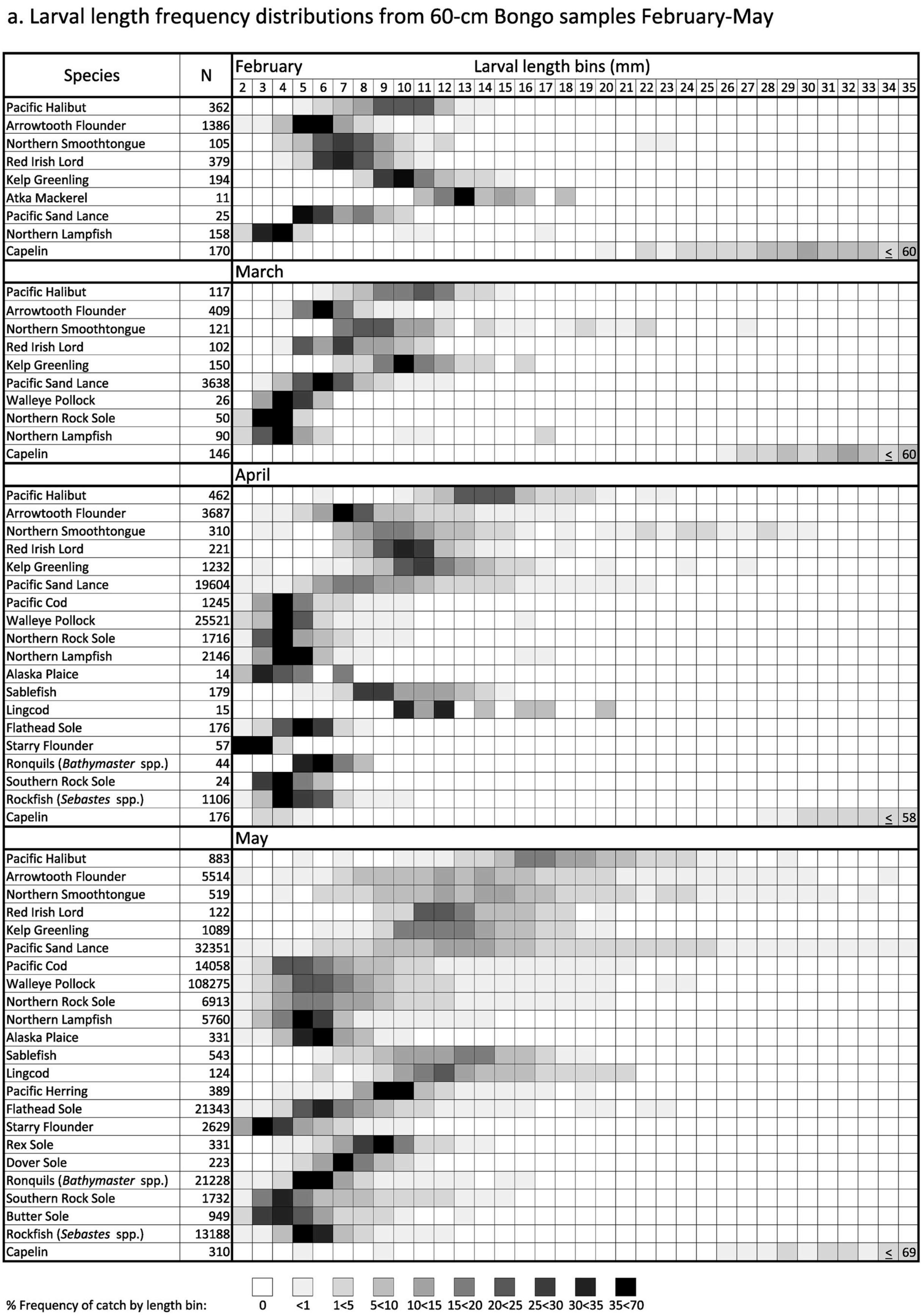
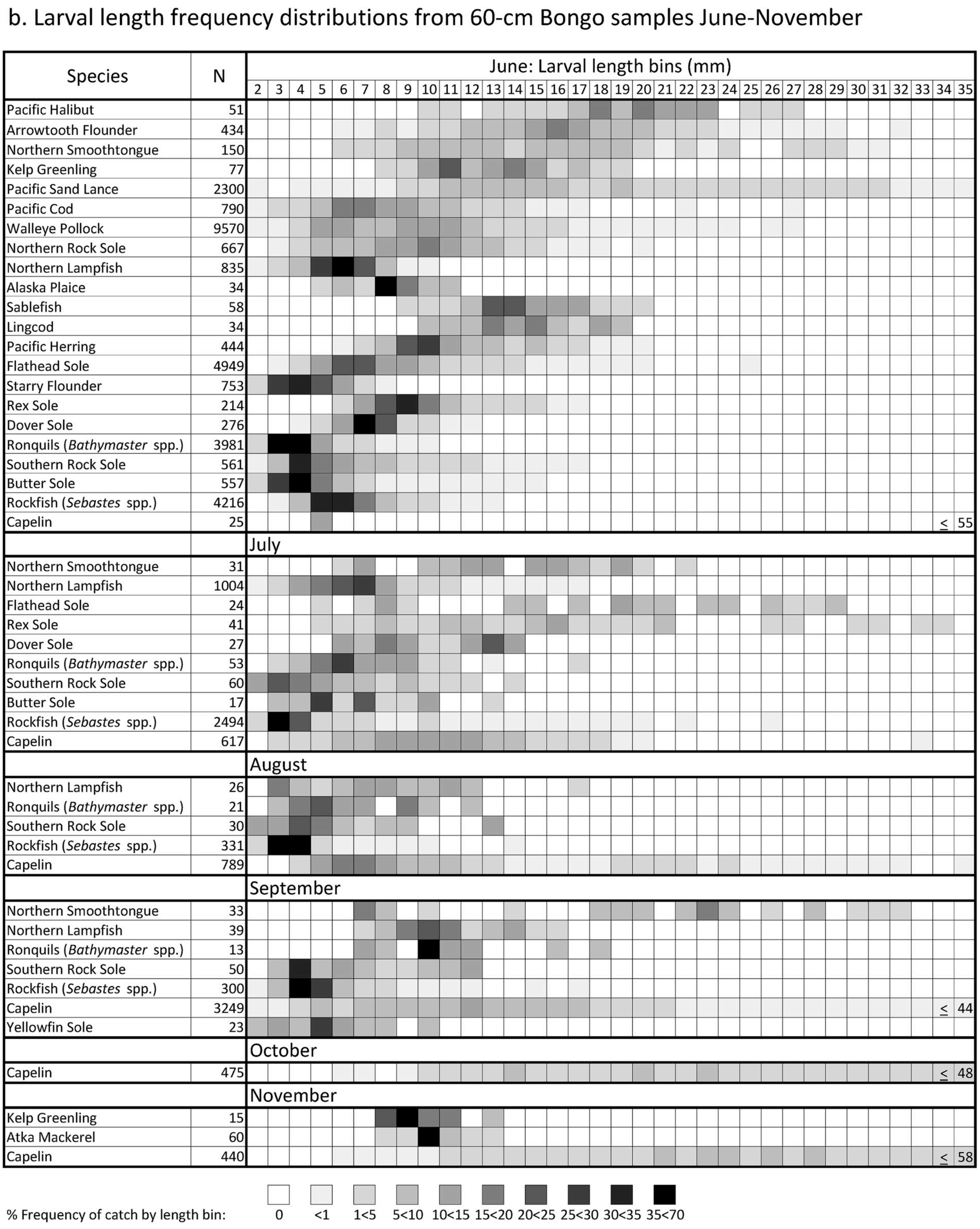


Fig. 5. Length frequency distributions for larval fish species that are abundant or common in GOA ichthyoplankton samples (60-cm bongo sampler) during a) February through May, and b) June through November. N = total number of specimens measured and for which length data are available in the historical ichthyoplankton data set. Species are listed in phenological order of appearance in the plankton as in Fig. 3. Upper length range is indicated for capelin larvae that remain planktonic longer than most species.



b. Larval length frequency distributions from 60-cm Bongo samples June-November

Fig. 5. (*continued*)

Rock Sole, and Rockfish (Fig. 5a). Many Pacific Sand Lance larvae are still small enough to be recently hatched (5–8 mm SL), and at this time larvae up to 16 mm SL are also common in neuston samples along with the larger neustonic species and preflexion Sablefish (Fig. 6). The pattern of larval sizes during the rest of spring, from May through June, are similar to April but with upper sizes stretching into the 20–30 mm SL range for many of the winter-spring spawners, and even >35 mm SL specimens documented for Ronquils, Pacific Sand Lance and Kelp Greenling in the neuston (Figs. 5 and 6). Capelin are still present as very large larvae (30–60 mm SL) in both bongo and neuston samples, whereas the majority of spring-spawned species are <10 mm SL and some such as Starry Flounder, Southern Rock Sole, and Butter Sole are mostly ≤ 5 mm SL. Pacific Herring, Rex Sole and Dover Sole larvae although recently hatched are notably larger than the latter flatfish species.

During July a diminished diversity of larvae is characterized by larger spring spawners such as Northern Smoothtongue, Northern Lampfish, and Flathead Sole as well as rapid growth of Rex Sole and

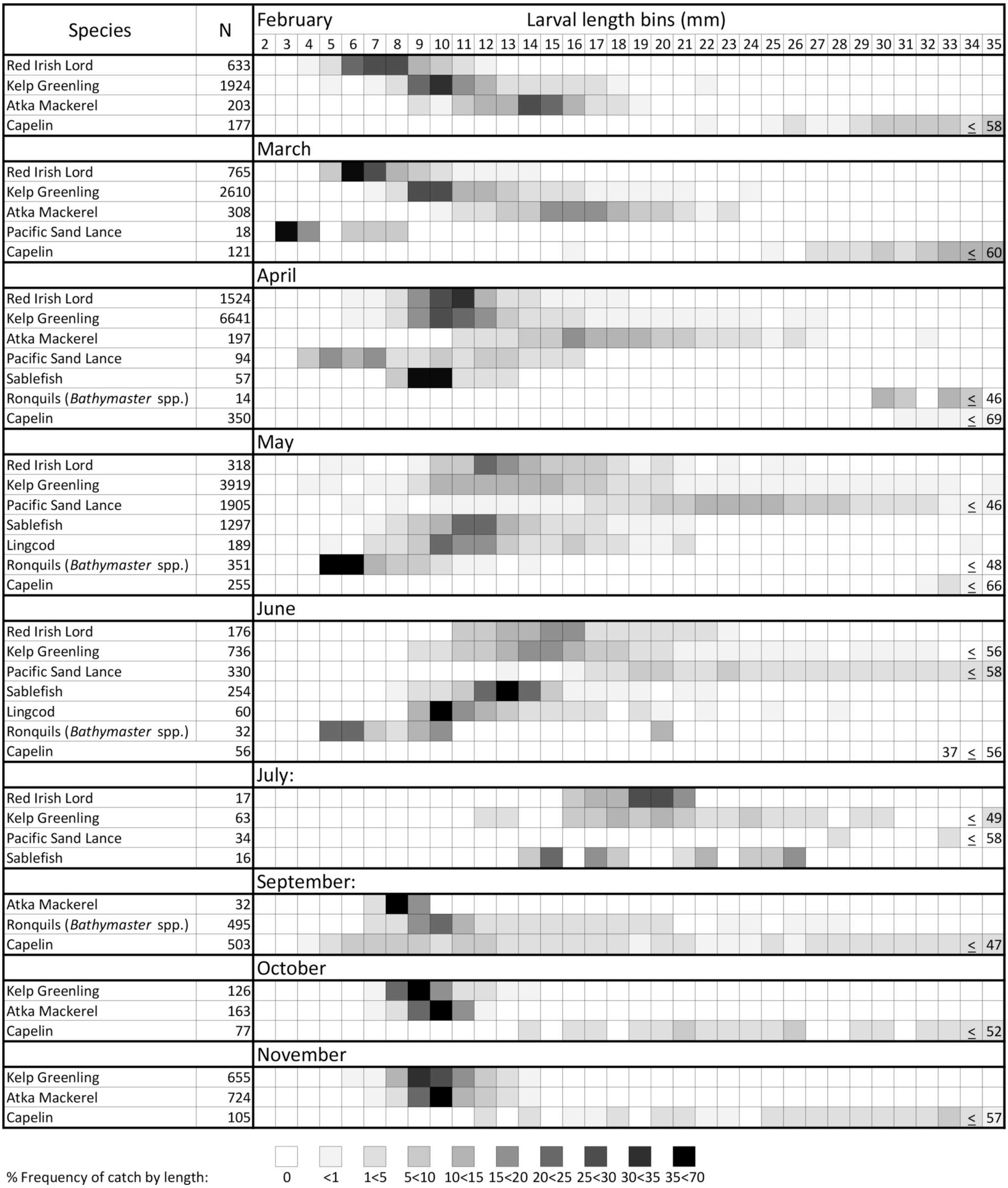


Fig. 6. Length frequency distributions for larval fish species that are abundant or common in GOA neuston samples during February through November. N = total number of specimens measured and for which length data are available in the historical ichthyoplankton data set. Species are listed in phenological order of appearance in the plankton as in Fig. 3. Upper length range is indicated for certain species that have extended larval durations in the neuston.

Dover Sole to 34 and 14 mm SL, respectively (Fig. 5 b). Although the upper size range has increased for Southern Rock Sole, a high proportion of larvae are still <5 mm SL throughout summer months implying recent hatching. A new cohort of Rockfish larvae (<5 mm SL) is apparent in summer bongo net samples (Fig. 5b) indicating a different assemblage of species than those present during spring months (Fig. 5a). Newly hatched Capelin larvae (≤6 mm SL) are present during July–September, although the upper size range extends to approximately 20 mm SL indicating rapid growth. Larvae of Yellowfin Sole in September are 2–10 mm SL. In the neuston, most of the few larvae caught in July are 15–30 mm SL (Fig. 6). Pacific Sand Lance is exceptional with most specimens in the 40–60 mm SL range. Recently-hatched Kelp Greenling and Atka Mackerel larvae (<10 mm SL) occur during autumn months in both bongo and neuston samples (Figs. 5b

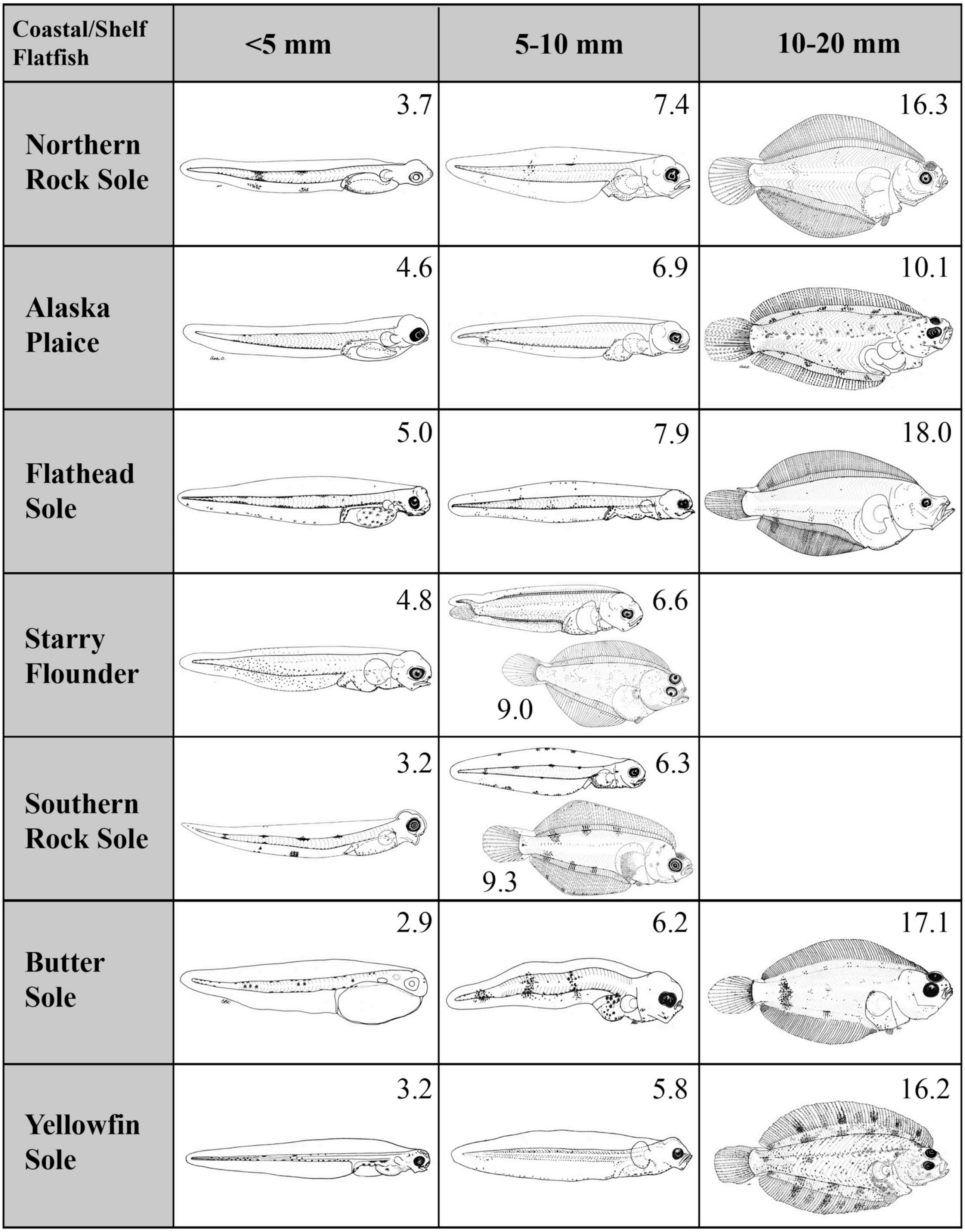


Fig. 7. Morphological development by size category for coastal and shelf flatfish larvae.

and 6). Capelin larvae during these months are again characterized by a very broad range of sizes (10–55 mm SL) in both bongo and neuston samples.

3.1.4. Phenology and larval morphology

In addition to larval sizes and stage durations, larval fish morphology is important as an indicator of larval behavioral competence and interaction with the pelagic environment at different times of year. For GOA species there are commonalities in morphology among taxonomic groups and among species that have similar ecological characteristics during early ontogeny, including timing of occurrence in the plankton (see Matarese et al., 1989 and the IIS for a full range of illustrations across ontogenetic intervals for GOA larval fish species). Pacific Cod and Walleye Pollock (Gadidae) have similar developmental trajectories (Fig. 4) and morphology at size, and develop distinct sets of dorsal, ventral and caudal fins and look like juvenile gadid fish by the time they are 25 mm SL. Small mesopelagic species (e.g. Northern Smoothtongue and Northern Lampfish) have similar body shapes including gut lengths and fin development. Although they are members of three different families, the coastal pelagic species Pacific Sand Lance, Pacific Herring, and Capelin have very similar morphology from hatching through the preflexion larval phase, characterized by elongated bodies and small heads. Larvae that are primarily neustonic, e.g. hexagrammids and Sablefish, tend to be well developed morphologically by 15 mm SL and are characterized by very heavy pigmentation especially on the dorsal surface. All pleuronectid flatfish larvae undergo the same morphological transformation that includes eye migration and 90° rotation in body posture prior to settling out of the plankton. Nevertheless, the highest diversity of developmental variability at size is observed among these flatfish species and is related to both timing of early ontogeny and primary larval habitat (Figs. 7 and 8). Coastal and shelf spawning flatfish species that tend to be spring-summer spawners have shorter larval durations (Fig. 3a) and all metamorphose by a length of 20 mm SL (Fig. 7). In the case of Starry Flounder and Southern Rock Sole, larvae can be fully metamorphosed with eye migration and fin development complete by as small as 8 and 11 mm SL, respectively. Among the deep water spawned flatfish that remain planktonic as larvae for much longer, size at transformation tends to be much larger (Figs. 4 and 8). However, there is still a considerable contrast among the four members of this group with divergence also apparent between the species that share the same phenology of spawning and hatching. Pacific Halibut can be fully transformed by 24 mm SL whereas Arrowtooth Flounder that are also spawned and hatch in winter take longer to accomplish metamorphosis and are mostly > 40 mm SL when fully transformed. Similarly, the spring-spawned Rex Sole and Dover Sole have contrasting developmental trajectories from flexion to transformation with the former transforming at a much larger size range (49–72 mm SL) than the latter (20–45 + mm SL).

3.2. Synchronies with the physical environment

Seasonal patterns in water temperature and circulation in the GOA are critical aspects of the physical environment that influence distribution, abundance, growth, and survival of fish larvae in the plankton at different times of year. The annual pattern of sea surface temperature in the western GOA (Fig. 9a) is typical for temperate to sub-arctic regions with coldest temperatures in late winter to early spring (February–April) and warmest temperatures in summer months (July–September). The winter to summer temperature range at the surface is ~4–12 °C, although fish larvae in the upper water column can experience lower or higher temperatures in any given year. The climatological pattern is similar throughout the water column although the amplitude of variation diminishes with depth (Seward Line mooring temperature time series; http://www.ims.uaf.edu/gak1/). For the majority of fish species in the GOA, the late winter to spring peak abundance of larvae in the plankton (Fig. 3) means that early ontogeny coincides with coldest temperatures (mostly 2–6 °C) initially followed by an average increase of 1–4 °C across April–June depending on the year and their depth in the water column. Larvae of spring-summer spawned species encounter rising temperatures during late spring

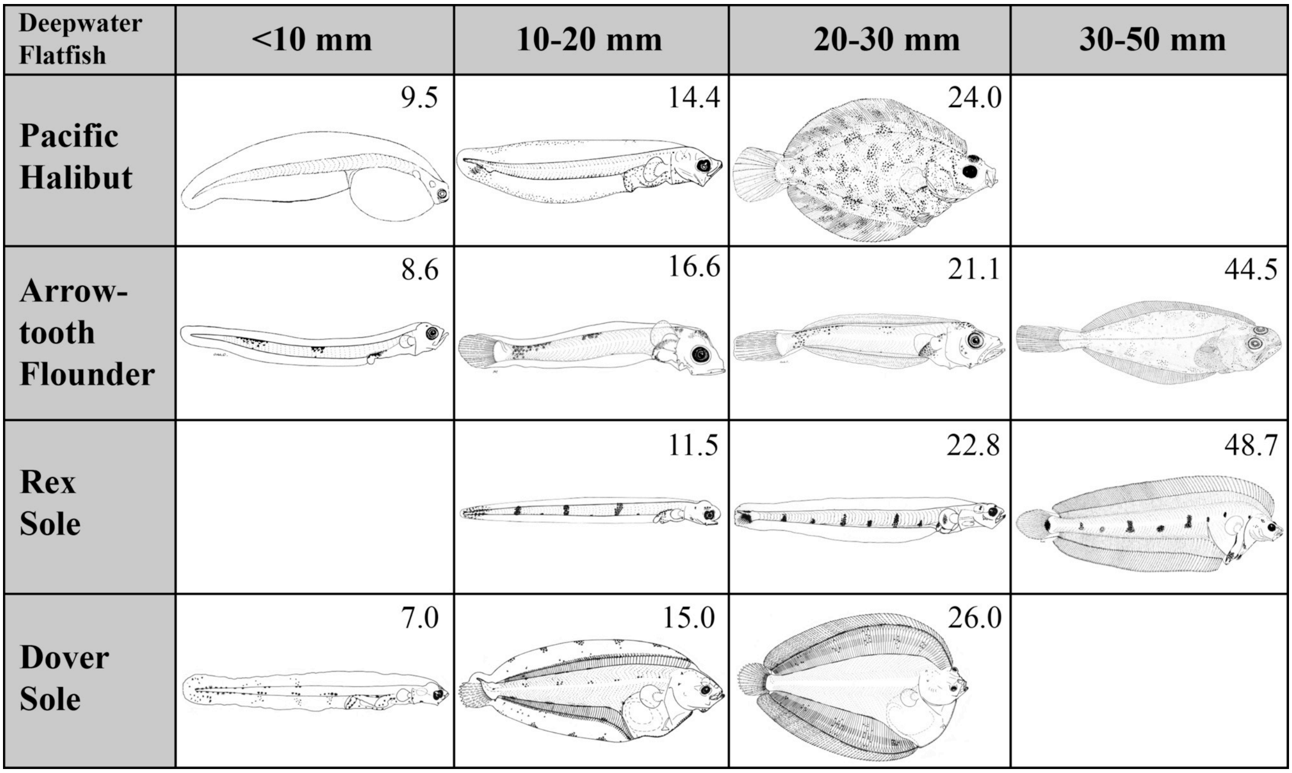


Fig. 8. Morphological development by size category for deep water flatfish larvae.

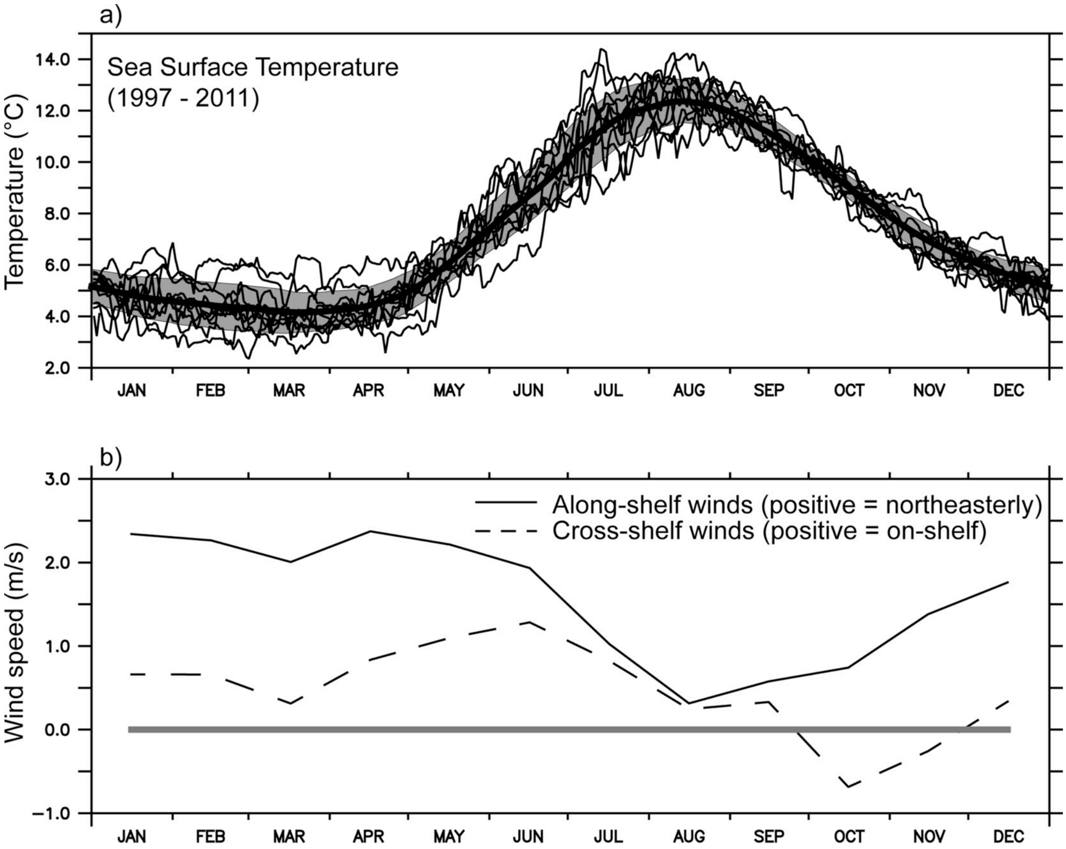


Fig. 9. Seasonal variation in surface water temperature and coastal winds in the western GOA: a) NOAA OI SST V2 daily sea surface temperature (°C) at 56.9 °N, 155.6 °W in Shelikof Sea Valley for each year (1997–2011). Monthly climatology (bold line) ±1 standard deviation (gray shading) is overlaid; b) NARR monthly climatology (1979–2000) of along-shelf (solid) and cross-shelf (dash) components of 10-m wind (m s^{-1}) at 59 °N, 150 °W, on the shelf near the head of Amatuli Trough (see Fig. 1). The zonal and meridional components were rotated into along-shelf and cross-shelf components assuming an angle of 45°.

followed by warmest summer conditions (~10–14 °C near surface) July–September. Species whose larvae are most abundant from summer to autumn months experience the warmest conditions for growth and development followed by slowly decreasing temperatures from October to December. Interannual variability in temperatures is higher in winter-spring than in late summer-autumn (Fig. 9a), a pattern also observed in mooring data on the GOA shelf (Janout et al., 2010; see their Fig. 7). Given seasonal patterns in peak abundance of fish larvae (Fig. 3), variability in winter-spring temperatures would affect a greater number of species than interannual variability in summer-autumn temperatures, which tends to be less dramatic.

Winds are the primary forcing factor for circulation in the GOA (Stabeno et al., 2004, 2016) and can have a measureable influence on the transport of larval fish in the upper water column (Doyle et al., 2009). Fish larvae occurring on the inner shelf during January through June experience the strongest along-shelf winds and associated southwestward transport along the shelf in the Alaska Coastal Current (ACC), whereas from July through October the strength of these winds is at a minimum (Fig. 9b). The cross-shelf component of winds is directed onshelf during most of the year (maxima in May–June) with off-shelf direction only in October and November. Planktonic stages of fish in the upper water column from January through June have the highest chance of encountering wind-driven cross-shelf transport. This is particularly important for species spawned in deep water whose larvae need to move from slope to shelf habitat in order to survive, and for some species to connect with inner-shelf or nearshore nursery grounds (Table 1 and Fig. 3). The southwestward along-shelf winds also contribute to an onshelf Ekman transport at the surface (downwelling) and offshore at depth, with strongest downwelling during winter (Ladd et al., 2005).

The Alaskan Stream is a strong western boundary current that flows along the continental slope of the western GOA, driving southwestward transport along the shelf edge (Stabeno et al., 2004). Despite this strong directional forcing, canyons and troughs that intersect the slope can influence cross-isobath flow, facilitating transport of organisms such as fish larvae up the canyons and onto the shelf (Mordy et al., 2019; Ladd et al., 2005; Stabeno et al., 2004). It is instructive, therefore to examine transport variability in these features with the 3-km ROMS model-generated flow as an indicator of temporal patterns in on-shelf transport potential for larvae spawned in deep water. Mean flow across the Outer Shelikof Strait and Amatuli Trough transects in the western GOA indicate positive onshore flow throughout the water column on the northeast side of each of these features, and offshore flow along the opposite side (Fig. 10a and b). The onshore flow is relatively evenly balanced with offshore transport in Outer Shelikof Strait but stronger overall onshore in Amatuli Trough. Monthly climatologies of the inflow/outflow patterns (data not shown) are very similar in appearance to the annual averages, but vary by month in amplitude. In particular, onshore flow occurs throughout the water column primarily on the northeast side of the canyons throughout the year. The spatially integrated monthly climatology of flows into each canyon is shown in Fig. 10c. One striking feature of this comparison is that the inflows into Amatuli vs. Shelikof canyons are approximately 180° out of phase. For the Outer Shelikof Strait transect, onshore flow is strongest during June–August and weakest from December through March, with intermediate levels during remaining spring and autumn months. For the Amatuli transect, onshore transport is at its most extensive and strongest during autumn and winter months and weakest although still extensive during May–August. Offshore flow appears to be strongest in the upper 50 m of the water column along the southwest half of the Shelikof

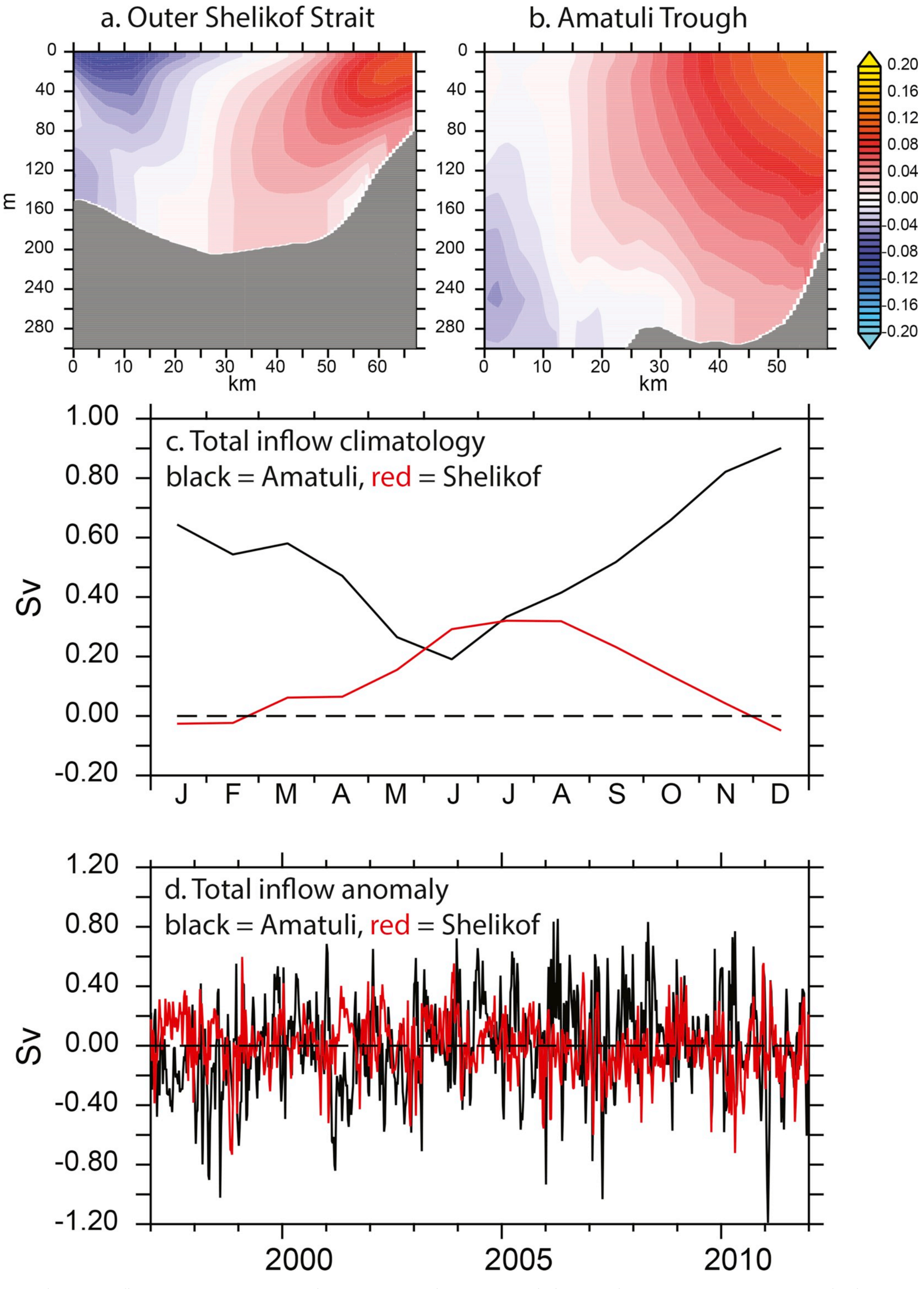


Fig. 10. Model-generated (ROMS) flow into two major troughs intersecting the continental slope in the western GOA (see Fig. 1 for locations): a-b) mean cross-transect flow for 1997–2011 (m/s) as a function of cross-transect distance and depth for Outer Shelikof Sea Valley and Amatuli Trough, with positive values representing onshore flow into the troughs from the slope, and negative values representing outflow; c) monthly climatology of flow in Sverdrups (Sv), spatially integrated across transects (black = Amatuli, red = Shelikof); d) anomalies from monthly climatology of the spatially integrated flows during 1997–2011. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

transect and varies seasonally (Fig. 10a, c), implying that the location and timing of occurrence of larvae along this transect is important with respect to on-shelf transport. Along the Amatuli Trough transect, there seems to be a higher chance of larvae being transported onto the shelf at any time of year with relatively weak offshore transport restricted mostly to below 50 m on a limited portion of the southern end (Fig. 10b). A notable degree of interannual variability in the strength of onshore flow across these transects (Fig. 10d) has implications for year-to-year variation in successful transport of fish larvae onto the shelf in these locations. This is especially true for the Amatuli transect, where deviations from climatology can exceed one Sv.

3.3. Synchronies with the biological environment

Concentration and size of small planktonic organisms are critical determinants of prey availability for larval fish, and phyto- and microzooplankton each show seasonal and spatial variation in these properties that is relevant with respect to timing of the larval phase among the different GOA fish species (Fig. 3). Even though some of the smallest phytoplankton and microzooplankton may not be a primary food source for larval fish, data are presented here because they are consumed by other larger protists (e.g. microzooplankton grazers) and mesozooplankton that are important nutritional sources for fish larvae. The seasonal cycles of the former influence the seasonal cycles of the latter. Data for phytoplankton, microzooplankton, and mesozooplankton in the GOA are mainly limited to spring, summer and early autumn months with no available data for November through February (Tables 2 and 3). Historical micro- and mesozooplankton data from the Seward Line collections in March do, however, provide some indication of food availability during late winter when larvae of winter spawning fish species can be abundant in the plankton (Fig. 3).

For phytoplankton, both measured (Table 2) and remotely sensed Chl*a* show seasonal cycles on the shelf (Fig. 11a and c), with highest median and maximum values in spring (on average, peak in mid-May according to satellite data; Waite and Mueter, 2013). The spring bloom is evident as a 2-3x elevation of median Chl*a* and a 3-6x elevation of maxima relative to summer and autumn values on the shelf. The spring bloom appears modified spatially on the Seward Line, where the median on the slope is relatively low (Fig. 11c). The phytoplankton carbon-biomass enhancement associated with these elevated Chl*a* times and regions is likely less than suggested here, as both spring and inshore C:Chl*a* ratios tend to be lower than those in summer and in offshore waters (Coyle et al., 2012; S. Strom, unpublished data). In general, the Kodiak region exhibits higher median and maximum Chl*a* concentrations on both shelf and slope, particularly in spring and, to some extent, in autumn (Fig. 11a). The higher Kodiak Chl*a* biomass is consistent with mechanisms known to enhance productivity in that region, including a high frequency of mesoscale eddies on the slope (Henson and Thomas, 2008) and enhanced nutrient pumping and water mass retention on the Kodiak shelf (Mordy et al., in press; Cheng et al., 2012).

Phytoplankton in coastal and shelf waters of the GOA range in size from ~1 µm (e.g. picocyanobacteria) to 100s of µm (e.g. chain diatoms such as *Thalassiosira* and *Chaetoceros* spp.; Strom et al., 2016). As for Chl*a* concentration, phytoplankton size, as indicated by the fraction of Chl*a* in >20 µm particles, is also elevated on the shelf in spring, (Fig. 11b and d). Increased phytoplankton size is a crucial property for direct availability to larval fish and efficient transfer of primary production to higher trophic levels of larger-bodied potential prey (e.g. zooplankton). Again the Kodiak region appears to be a somewhat richer potential feeding environment for larval fish, with a spring median of 81% (versus 43% at the Seward Line) of Chl*a* in >20 µm particles. During spring, these large Chl*a*-containing particles are mainly diatoms and, in lower Chl*a* locations, chloroplast-retaining ciliates (Strom et al., 2016 and 2019). The limited data available for the Kodiak region indicate that large phytoplankton cells may sometimes characterize the slope as well as the shelf collections during spring, and are also abundant on the shelf during autumn, generally reflecting the higher Chl*a* biomass of these times and sub-regions (Fig. 11b). In the Seward region, large cells account for a lower portion (<20%) of the phytoplankton biomass over the slope during each sampling period (Fig. 11 d). Extreme values suggest patches of higher chlorophyll in larger particles even during periods of low productivity. For the shelf, the coast-hugging Alaska Coastal Current constitutes such a patch; for the slope, transient mesoscale eddies promote higher Chl*a* and larger cells episodically (Batten and Crawford, 2005; Ladd et al., 2007).

Microzooplankton, as defined here, include phagotrophic protists >15 µm (primarily ciliates and dinoflagellates) as well as larger grazers up to approximately 200 µm in size. Many of these protists are functional mixotrophs, in that they are both photosynthetic and they prey on other microbes. Microzooplankton biomass shows a seasonal cycle

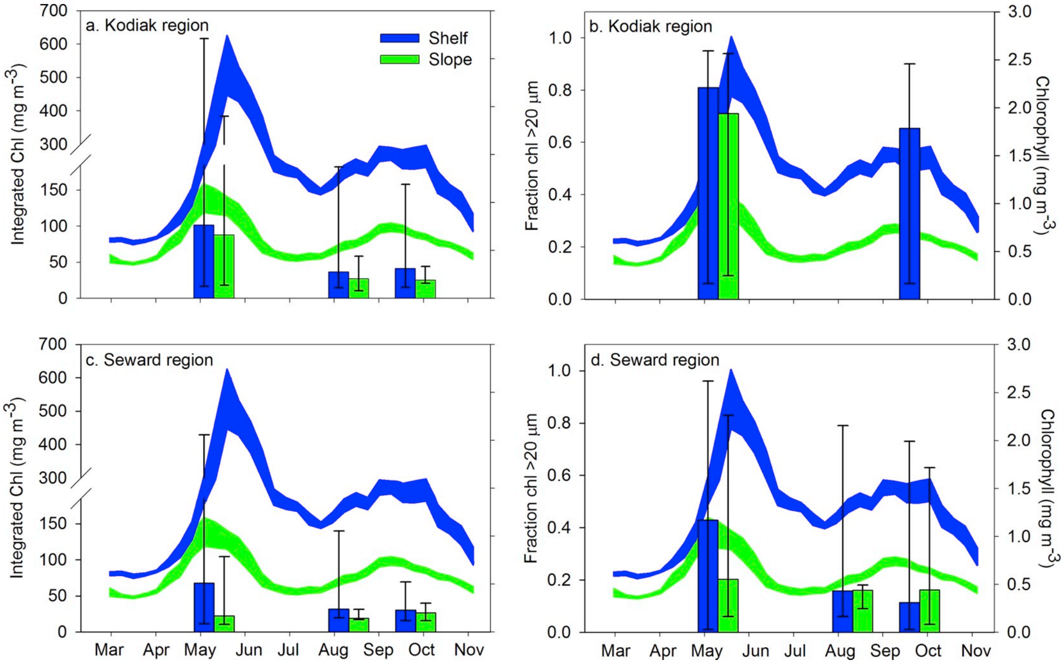


Fig. 11. Seasonal cycles in phytoplankton biomass and size composition in the GOA shelf and slope, as indicated by Chlorophyll-*a* in two sub-regions; Kodiak (a and b) and Seward Line (c and d). Seasonal line trends are near surface Chl*a* concentrations (mean ± 1 SE mg m^{-3}) as estimated from satellite ocean color observations 1998–2011 (Waite and Mueter, 2013; their Fig. 8; data for 'western shelf' and 'western offshelf' shown in all panels). Bars in panels a and c show median integrated (0–50 m) water column Chl*a* from field measurements, with error bars showing range of observations, for Spring, Summer, and Autumn months. Bars in panels c and d show median size composition (i.e. fraction of total Chl*a* in particles >20 µm). In general, Chl*a* field data are from 2011 to 2013, with more extensive coverage during some seasons on the Seward Line (see Table 2). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

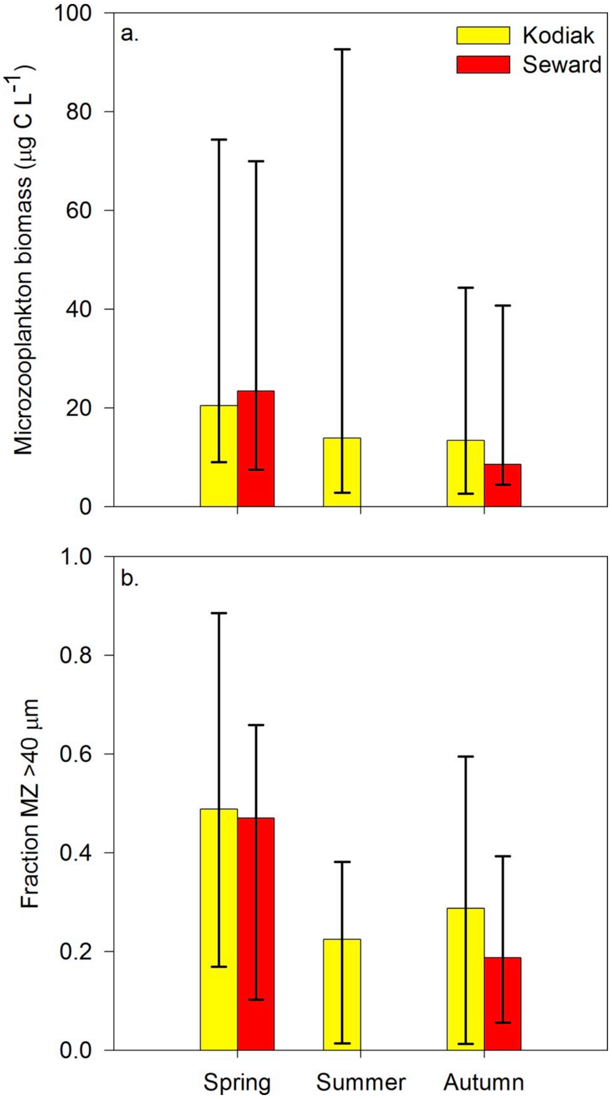


Fig. 12. Seasonal cycles in a) biomass and b) size composition of microzooplankton in the Kodiak and Seward Line sub-regions of the Gulf of Alaska, based on sampling at 10 m depth in the water column. Values are medians with error bars showing range of observations for Spring, Summer, and Autumn with shelf and slope samples combined. Data are from 2011 to 2013, and sampling frequencies are given in Table 2.

similar to that of Chl*a*, with 1.5-2.7x enhancements in spring relative to summer and autumn (Fig. 12a). Data are insufficient to evaluate shelf and slope habitats separately, but earlier work from a single year showed a gradient of decreasing biomass with distance offshore (Strom et al., 2007), which would not be surprising given cross-shelf primary productivity gradients. In a further parallel with the phytoplankton community, the highest proportion of large (> 40 μm) individuals is seen in spring (~50% of the community in both regions; Fig. 12b). In general, a higher biomass is associated with a greater proportion of larger cells for both phytoplankton and microzooplankton in coastal and inner shelf water of the GOA (Strom et al., 2016 and 2019). Patchiness (maxima that are 4-5x higher than medians in all seasons) is prevalent in microzooplankton as it is for Chl*a*. These microzooplankton maxima are often associated with the ACC or with shallow banks offshore of Kodiak Island, both locations that also support high chlorophyll concentrations in summer (Stabeno et al., 2004; their Fig. 24). In contrast to the phytoplankton, no substantial difference between Kodiak and Seward region microzooplankton is evident, at least in these bulk measures of biomass and size composition.

Copepods from a variety of families are the most abundant mesozooplankton organisms (0.2–20 mm) in the GOA, and as in many other marine ecosystems are known to be critical in the diets of fish larvae, and especially the naupliar stages. Abundance data are presented here for two size groups of copepods: < 2 mm and > 2 mm prosome lengths that numerically dominate the CalVET (150 μm mesh net) and MOCNESS/Multinet (500 μm mesh net) catches respectively (Fig. 13). The smallest group (< 2 mm) also includes the unidentified naupliar stages of all copepod taxa represented in these samples (Fig. 13a). The youngest and smallest life stages of copepods, eggs and nauplii, are highly suitable prey for first-feeding larvae in particular given that they are < 1 mm in size, nutritious with high lipid content, and abundant (relative to fish larvae) in the pelagic environment especially during spring to summer. Given size ranges of GOA larval fish species at yolk-absorption, mostly 5–10 mm but with some smaller (Fig. 4), copepod nauplii (< 1 mm) are an ideal prey size for first-feeding larvae (Table 5). As copepod nauplii grow to adulthood, many of the smallest GOA species would still be small enough (≤ 1 mm) through copepodite stages CI-CV for consumption by first-feeding fish larvae (e.g. *Oithona similis*, *Microcalanus* spp., *Mesocalanus tenuicornis*, *Acartia* spp., *Paracalanus parva* and *Pseudocalanus* spp.; Table 5). The maxima of the size ranges for adult stages of the smallest copepod taxa dominant in the GOA samples is 0.9–1.6 mm, which implies availability as prey for fish larvae ≥ 10 mm (presuming a mouth gape size of 1-2 + mm). Further, adult stages of the species *O. similis, Microcalanus* spp. and many *Pseudocalanus* spp. remain < 1 mm (Table 5) which likely makes them available as prey to even first-feeding stages of many fish larvae (Fig. 4). Among the large and abundant copepod species in the GOA, the earliest copepodite stages (CI-CII) range in size from 0.4 to 2 mm but many are > 2 mm from CIII stage onwards. The largest species belong to the genus *Neocalanus*; *N. cristatus* is largest by far with CIV sizes of 6–7 mm, and *N. plumchrus* and *N. flemingeri* are 3–4 mm (Table 5). Fish larvae would need to be well developed and likely larger than 20 mm to successfully feed on late copepodite or adult stages of these species.

For winter and spring months in the GOA, most fish larvae caught in Bongo net samples are < 10 mm SL in length and a high proportion are < 5 mm SL (Fig. 5) indicating their need for small prey (< 1 mm) such as microzooplankton as well as the smallest mesozooplankton organisms (e.g. copepod eggs and nauplii). A notable exception to this pattern is the occurrence of very large (> 30 mm SL) capelin larvae during these months that likely can consume a broad size range of zooplankton organisms. Copepod eggs and nauplii are present March through May and most copepodite to adult stages for many of the small taxa of copepods are present during these months in the upper 100 m of the water column (Table 6). Eggs and nauplii of the large *N. plumchrus* and *N. flemingeri* are produced in deep water below 100 m during winter (January–March) over the slope and in the GOA basin at the end of the adult diapause period for these species (Miller and Clemons, 1988; Coyle et al., 2013). Their availability coincides with the occurrence of newly-hatched and first-feeding Arrowtooth Flounder and Pacific Halibut larvae that are spawned in the same deep pelagic habitat (Figs. 3 and 5 a). Progressively larger fish larvae that characterize the summer through autumn ichthyoplankton assemblage in the GOA (Fig. 5b) may be able to consume more of the late copepodite through adult stages of many of the copepod species that they encounter during these months (Table 6). The absence of data on zooplankton taxa in the neuston makes it difficult to connect neustonic fish larvae with seasonable availability of prey organisms in that habitat. However, fish larvae in the neuston tend to be larger overall (Fig. 6) than those occurring in the water column implying an advantage in terms of prey fields available to them, and behavioral capacity for capturing them.

The most abundant components by far of the copepod assemblage in the GOA are the calanoid nauplii, and the small copepods *O. similis* and *Pseudocalanus* spp. (Fig. 13). Even during winter (March) and autumn (October) sampling along the Seward Line, average levels of abundance

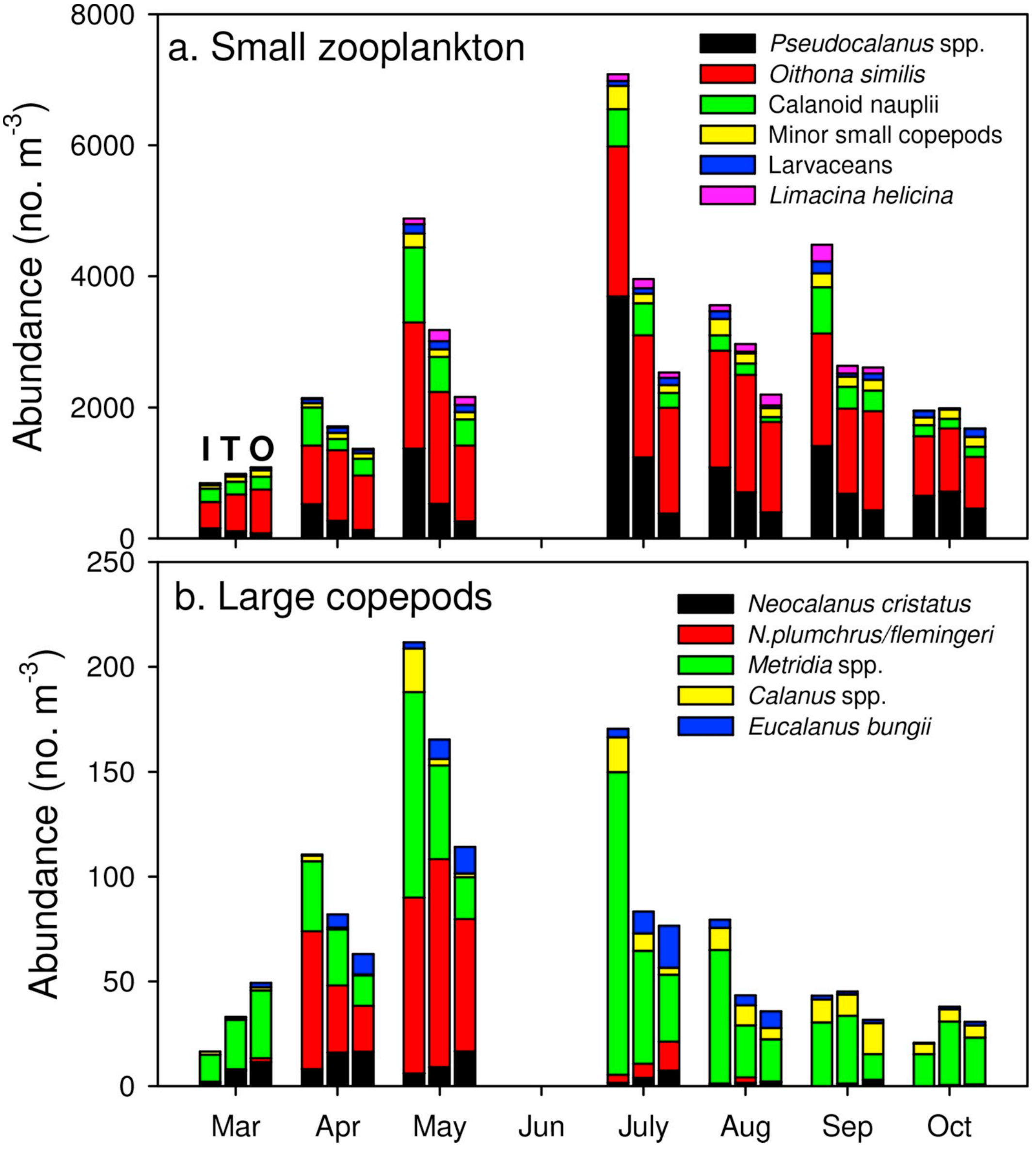


Fig. 13. Seasonal variation in mean abundance of a) the most abundant small zooplankton, mainly copepods (< 2 mm prosome length) collected by the CalVET plankton sampler (150 µm mesh net); and b) the most abundant large copepods (> 2 mm prosome length), collected by the MOCNESS or Multinet plankton sampler (500 µm mesh net), in the upper 100 m of the water column along the Seward Line, and representing the Inner (I), Transitional (T), and Outer (O) zones (Fig. 1) during 1998–2015. See Table 3 for distribution of sampling by months.

Table 6

Seasonal occurrence of numerically dominant large bodied (i.e. > 2 mm adult) copepod taxa by copepodite-adult life stages (see Table 5 for life stage codes) in upper 100 m of the water column along the Seward Line from 1998 to 2015. *Neocalanus* species descend as C5 to enter diapause in deep water, becoming absent from surface waters during summer. All small copepods follow similar cycles, with only late stages observed during winter, earlier stages beginning to appear during spring and then all stage present into autumn.

Large copepods:	Winter	Spring		Summer			Autumn
	Mar	Apr	May	Jul	Aug	Sep	Oct
Calanus pacificus	–	–	–	C4-C5,A	C1-C5,A	C1-C5,A	C1-C5,A
Calanus marshallae	C5,A	C3-C5,A	C1-C5,A	C1-C5,A	C1-C5,A	C1-C5,A	C5,A
Eucalanus bungi	C5,A	C5, A	C1-C5,A	C1-C5,A	C1-C5,A	C1-C5,A	C5,A
Metridia spp.	C1-2,C5,A	C1-C5A	C1-C5,A	C1-C5,A	C1-C5,A	C1-C5,A	C1-C5,A
Neocalanus cristatus	C1	C1-C3	C3-C5	C4-C5	C5	–	–
N. plumchrus & N. flemingeri	C1-C2	C1-C4	C4-C5	C5	–	–	–

for these taxa collectively in the upper 100 m of the water column are many orders of magnitude higher (~700–1000 individuals m^{-3}) than average levels of abundance recorded for species of fish larvae at peak periods of their abundance in the plankton (Fig. 3; Matarese et al., 2003; Doyle et al., 2009). The amplitude of seasonal variation in abundance of these copepods is highest at the inner stations along the Seward Line (Figs. 1b and 13a) with peak abundance of calanoid nauplii in May and of *O. similis* and *Pseudocalanus* spp. in July. Late summer (August–September) abundance of *O. similis* and *Pseudocalanus* spp. is comparable to those recorded in May, whereas naupliar abundance at this time is similar to levels recorded in March and April. Seasonal variability in abundance of these taxa is similar for the transitional (outer shelf to slope) and outer stations over the slope and basin (Fig. 13), although the amplitude of variation is diminished with seasonal maxima lower and at a minimum for these station groups, respectively. Seasonal variation in total abundance of the less abundant small copepod taxa (minor small copepods; Fig. 13a) has the least amount of seasonal variation as well as cross-transect variation, although a minor elevation is apparent during summer months. Data for three of the most abundant non-copepod taxa in the CalVET catches also indicate the persistent occurrence of non-crustacean zooplankton across months and from coastal to deep water (Fig. 13a). Larvaceans are most abundant during late spring and summer months and least abundant in March. A similar pattern is apparent for the pteropod *Limacina helicina*, and across the three Seward Line zones the annual peak in abundance seems to extend from May through September. More information on the composition and distribution and interannual variability of these three taxa is reported elsewhere (Doubleday and Hopcroft, 2015).

The most numerous large-bodied copepods (>2 mm) caught in the MOCNESS and Multinet samplers (500 µm mesh nets) are in aggregate most abundant from April to July with an annual peak in May, persistence across the shelf, and with diminishing amplitude of seasonal variation in abundance from coastal to deep water (Fig. 13 b). *Metridia* spp. is present during all months and most abundant during May and July, especially at the inner shelf stations. The *Neocalanus* species are most abundant during April and May across zones and absent from late summer on as they go into diapause deep in offshore waters. *N. plumchrus* and *N. flemingeri* are together more abundant than *N. cristatus.* The *Calanus* species (primarily *C. marshallae* and *C. pacificus*) are most abundant from late spring through summer months. Although considerably less abundant than the small copepods, levels of abundance for the large copepods are still orders of magnitude higher than average levels of larval fish species in the GOA in shelf and deep water habitats (Fig. 3; IIS https://access.afsc.noaa.gov/ichthyo/). Nevertheless, many of these large-bodied copepods are too big during the late copepodite to adult life stages (Table 5) to be consumed by first-feeding and preflexion larvae of many GOA fish species (Fig. 4). Again, there are notable exceptions such as the large (>30 mm SL) overwintering Capelin larvae that occur during winter and spring, and some of the winter-spawned species (e.g. Pacific Halibut, Northern Smoothtongue, Atka Mackerel, and Pacific Sand Lance) whose larvae may reach ≥20 mm SL during spring months (Figs. 5 and 6).

Spatial climatologies of likely zooplankton prey sources for larval fish were generated by the GOA-NPZ model for the entire GOA basin and selected months are illustrated in maps to best represent the full

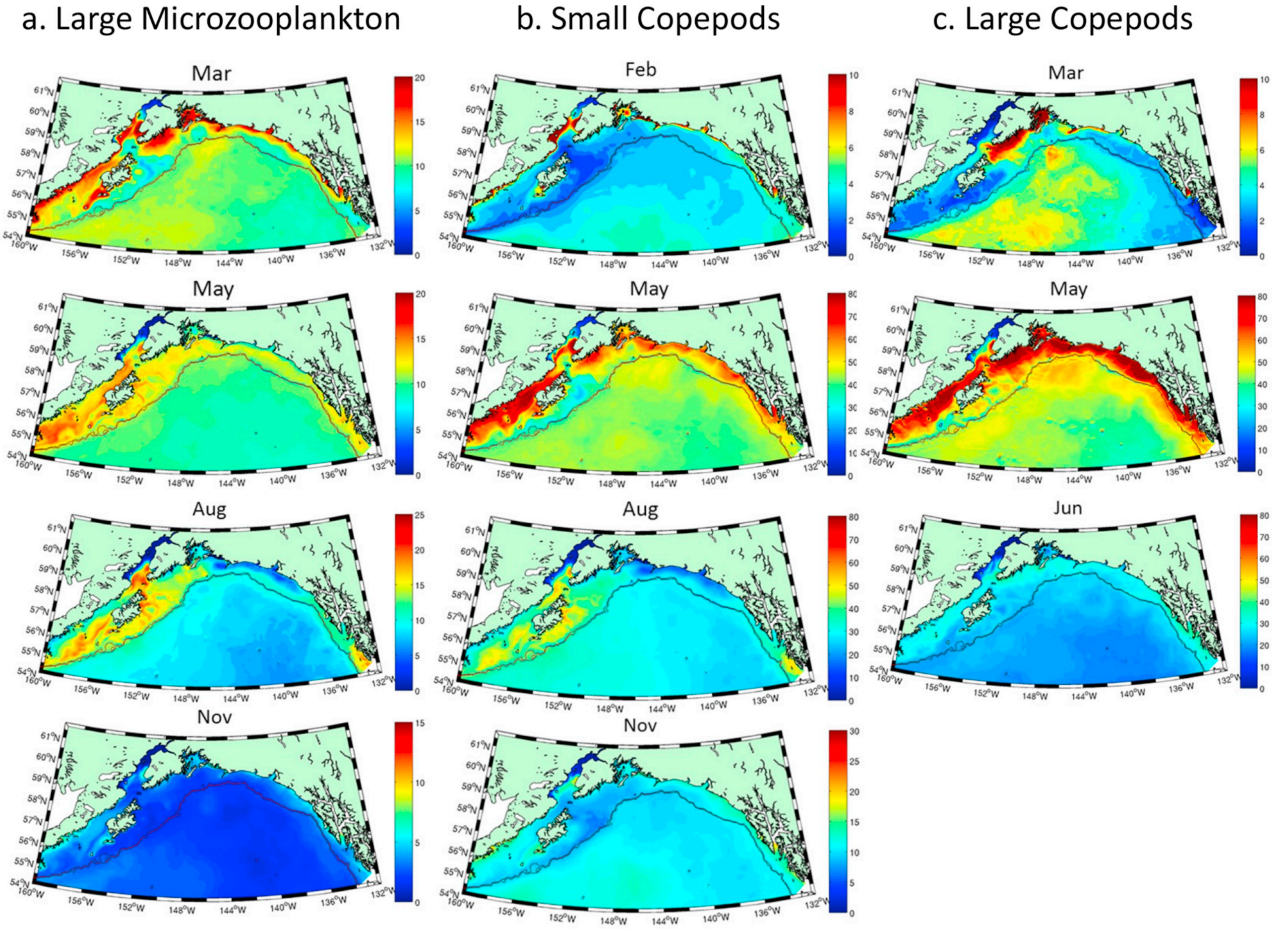


Fig. 14. Selected panels from the Gulf of Alaska ROMS/NPZ model output (1996–2011 model runs) indicating climatological spatial patterns in simulated production for four trophic groups, and four months that best represent seasonal variability for each group. Color scale indicates biomass in g C m^{-2} and the scale varies among months. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

extent of seasonality (Fig. 14). For the large microzooplankton (likely representing ciliates primarily) and the small copepods (< 2 mm, including nauplii), the outer shelf and slope remain areas of very low biomass during late winter (Fig. 14a and b). Higher levels of production particularly of the large microzooplankton are apparent in March, however, especially off the Kenai peninsula and to the southwest of Kodiak Island, as also noted by Coyle et al. (2019). By May, biomass values of 10–20 mg C m^{-3} of microzooplankton are apparent throughout the shelf, especially from Kodiak Island to the southwest. Peak levels of biomass for small copepods (up to 80 mg C m^{-3}) are also indicated in May, especially along the inner shelf throughout the GOA and with highest intensity apparent in the Shelikof Strait region and to the southwest. By August, biomass levels for both of these components have diminished significantly in coastal and inner shelf waters, particularly in the eastern GOA, but levels remain relatively high on the outer shelf particularly offshore and to the southwest of Kodiak Island. By November, large microzooplankton biomass is at a minimum throughout much of the GOA basin with some very low levels (~5 mg C m^{-3}) detected in coastal and inner shelf waters. Biomass levels for the small copepods remain higher (mostly within the range 5–10 mg C m^{-3}) in November throughout the shelf and basin. The highest degree of seasonal variability in biomass is observed for the large copepods (*Neocalanus* spp.) that enter diapause in deep water in late spring-summer (Fig. 14c). In late winter, low levels of biomass (5–10 mg C m^{-3}) are apparent in association with deep water in the basin and also in inner shelf and coastal waters of Prince William Sound and the Kenai Peninsula. This pattern reflects the earliest appearance of copepodite stages of these large copepods in near surface waters, subsequent to January–February egg production and naupliar development in deep water over the slope and basin, and in the deepest areas of Prince William Sound (Miller and Clemons, 1988; Coyle and Pinchuk, 2005). Large copepod biomass is at a peak in May with high levels (> 60 mg C m^{-3}) apparent throughout the GOA shelf, and most intense in the inner to mid-shelf zones. By June, biomass levels of large copepods have diminished significantly throughout GOA surface waters as the adults start to migrate into deep water to go into diapause.

3.4. Summary of species-specific synchronies and sensitivities

We provide a final synthesis of the ecological characteristics described in the previous subsections relating to the early life history phenology of fish species that are dominant in GOA ichthyoplankton samples in Table 7. The Table also includes recommendations on species' environmental sensitivities based on their vulnerability and resilience to relevant physical and biological factors that are potential indicators for consideration in current fisheries management applications. A new framework for including ecosystem considerations within the stock assessment process is currently being developed for federally-managed groundfish species (Shotwell et al., 2018; in review). This ecosystem and socioeconomic profile (ESP) uses a four step process to generate a set of standardized products that culminate in a focused communication of potential drivers on a given stock. In the framework, a set of metrics are evaluated that identify sensitivities of the stock with respect to biological or socioeconomic processes that then lead to developing a suite of indicators for monitoring. Where possible, the standardized metrics should be broken down by life history stage to further refine the influential processes and highlight life history bottlenecks that lead to more informed indicators. Life history traits provided in several of the tables and figures presented in previous sections (e.g. Table 1 and Fig. 3) can be incorporated into the ESP metric assessment to more fully evaluate intervals of ontogeny and identify the ecological diversity amongst groundfish species. The synoptic information (Table 7) includes potential vulnerabilities and resilience of species that can be utilized to gain mechanistic understanding of ecosystem pressures on the federally managed stocks in the GOA. The sensitivities listed here are hypothesized based on the strategies of early ontogeny outlined in the previous sections, and their synchrony with observed seasonal patterns in the physical and biological environment. The proposed indicators are suggested within the context of these sensitivities to be developed for potential use in the ESPs.

4. Discussion

The annual pattern of reproduction of many fishes in high-latitude marine ecosystems such as the GOA is linked to the timing of the spring phytoplankton bloom that generates the spring to summer peak in production of copepods and other zooplankton, which are primary food for larval fishes (Miller and Kendall, 2009). This adaptation to the high-amplitude seasonal variation in abundance of larval food organisms has been the foundation for the critical-period hypothesis for marine fish species during early ontogeny (originally Hjort, 1914), and the associated match-mismatch hypothesis (Cushing, 1990). These hypotheses propose that food limitation during the larval phase increases larval mortality through starvation and diminished growth, and that variable synchrony between larval fish and zooplankton production can result in a match or mismatch between larvae and their food with subsequent levels of survival significantly influencing year-class strength. The so-called "critical period" is associated with the planktonic larval phase and especially the absorption of the yolk sac when a switch to exogenous feeding must occur. A large body of research on larval fish ecology has been generated by these hypotheses. As a result, our understanding of complexity and survival outcomes in the early life ecology of marine fish species has expanded greatly in recent decades (Houde, 2008). Contemporary research efforts have evolved to recognize the importance of understanding the influence of climate forcing (e.g. warming trends) and associated shifts in oceanographic conditions on marine pelagic phenology, zooplankton community interactions, and trophic mismatch during fish early life across different ontogenetic stages (Edwards and Richardson, 2004; Kristiansen et al., 2011; Francis et al., 2012). More recently, evaluating the phenology of marine fish reproduction and early life is considered an essential component of efforts to assess commercial fish species vulnerabilities to climate change (Gaichas et al., 2014; Hare et al., 2016).

The data presented here reflect the previously documented pattern of a peak in taxonomic diversity and abundance during late spring in the ichthyoplankton of the GOA (Doyle et al., 2009). Nevertheless, for ecologically and commercially important fish species in this ecosystem phenological diversity prevails. Timing and duration of the planktonic phase is variable and widely divergent sizes at ontogenetic intervals and inferred growth rates are also observed. Many different fish early life history strategies have evolved in adaptation to the long-term prevailing conditions in the GOA, and phenology of the early ontogeny phase is a primary gradient of this variability (Doyle and Mier, 2012). A comprehensive examination of this phenology gradient among GOA species reveals a high level of species-specific diversity and complexity in terms of the planktonic phase scheduling, and associated patterns of exposure to physical and biological conditions that likely generate the response to environmental forcing.

4.1. Phenology and temperature

Development rates of fish eggs and yolk-sac larvae are influenced primarily by water temperature (Miller and Kendall, 2009). For the winter to early spring spawners in the GOA, cold temperatures are an advantage in terms of slowing development so that larvae do not exhaust all of their lipid reserves prior to optimal availability of suitable larval prey, especially at first-feeding. This has been established with laboratory studies for Pacific Cod larvae (Laurel et al., 2008, 2011), and implied from the historical GOA data by a negative association between larval abundance of the late winter spawners Pacific Cod, Walleye Pollock, and Northern Rock Sole and winter water temperatures (Doyle et al., 2009). A positive and significant correlation between larval size

Table 7

Synoptic review of observed environmental synchronies (temperature, transport, food availability, and larval development), proposed sensitivities (vulnerability and resilience), and proposed environmental indicators for early life stages of Gulf of Alaska species/taxa (phenological order as in Fig. 3).

	Observed Early Ontogeny Environmental Synchronies				Proposed Sensitivities		Proposed Critical Indicators
	Temperature	Transport	Food availability	Larval Development	Vulnerability	Resilience	
Pacific Halibut	Deep water egg incubation winter, peak larval abundance prior to and during winter temperature minimum.	On-shelf during winter, cross-shelf/along-shelf to nearshore settlement winter-spring. Enhanced on-shelf transport in canyons/troughs.	Limited in winter; *Neocalanus* nauplii may be critical, late stage larvae encounter increasing spring zooplankton abundance on shelf.	Larval feeding phase relatively short. Metamorphosis and settlement in late winter to spring, larvae <25 mm.	Diminished on-shelf and cross-shelf transport to nearshore nursery habitat winter-spring. Limited prey resources especially at 1st feeding.	Large eggs and size at hatching and 1st feeding; relatively fast development to metamorphosis and settlement. Synchrony with *Neocalanus* early life stages.	On-shelf and cross-shelf transport, winter-spring especially in canyons/troughs. Timing and level of peak abundance of *Neocalanus* nauplii.
Arrowtooth Flounder	Deep water egg incubation winter, peak larval abundance prior to and during winter temperature minimum. Extended larval pelagic phase through summer.	On-shelf during winter, cross-shelf/along-shelf to extensive shelf nursery habitat spring to summer. Enhanced on-shelf transport in canyons/troughs.	Limited in winter; *Neocalanus* nauplii may be critical, late stage larvae encounter increasing spring and peak summer zooplankton abundance on shelf.	Growth very slow until late spring. Metamorphosis and settlement primarily spring to summer, mostly >40 mm.	Warmer winters/faster growth; lipid reserves used up too quickly, prey mismatch. Diminished onshelf transport.	Slow metabolism extends lipid reserves through winter; "endurance" strategy. Synchrony with *Neocalanus* early life stages. Habitat generalist at settlement.	On-shelf transport, winter-spring especially in canyons/troughs. Winter water temperatures. Timing and level of peak abundance of *Neocalanus* nauplii.
Northern Smoothtongue	Egg incubation/peak larval abundance winter, larvae in full range of temperatures late winter-autumn.	Directed transport unnecessary; extensive epipelagic larval habitat throughout GOA basin.	Limited in winter; basin assemblages of protists may be important. Likely utilize basin and shelf assemblages of zooplankton spring-autumn.	Gradual winter through summer.	Low fecundity. Winter 1st feeding prey limited.	Spatial ubiquity; extended batch-spawning GOA basin, larval and pelagic juvenile habitat extensive.	Winter zooplankton prey availability basin and shelf.
Red Irish Lord	Egg deposition and incubation autumn-winter nearshore. Peak larval abundance, winter-early spring temperature minimum.	From nearshore hatching to off-shore shelf and slope pelagic habitat winter-summer, surface.	Neustonic prey assemblages unknown. Likely limited winter-early spring.	Rapid growth apparent hatching-flexion (winter-spring). Early migration to neuston, early transformation ≤23 mm.	Low fecundity. Transport off-shelf and away from nearshore settlement areas. Food limitation winter-early spring in neuston.	Large eggs, larval size at hatching and yolk absorption. Robust neustonic larvae winter to summer; good feeding ability.	Off-shelf transport. Winter-spring prey availability in neuston.
Kelp Greenling	Egg deposition and incubation autumn-winter nearshore and shelf. Peak larval abundance, temperature minimum through spring increase.	From nearshore/shelf hatching to off-shore shelf and slope pelagic habitat all seasons, surface.	Neustonic prey assemblages unknown. Likely limited winter-early spring.	Rapid growth apparent hatching-flexion (winter-spring). Early migration to neuston, extended larval phase until >50 mm.	Low fecundity. Food limitation winter-early spring in neuston.	Large eggs, larval size at hatching and yolk absorption. Robust neustonic larvae winter to summer; good feeding ability.	Winter-spring prey availability in neuston.

	Early Ontogeny Environmental Synchronies				Proposed Sensitivities		Proposed Critical Indicators
	Temperature	Transport	Food availability	Larval Development	Vulnerability	Resilience	
Atka Mackerel	Egg deposition and incubation autumn-winter nearshore and shelf. Peak larval abundance during autumn-winter decreasing temperature.	From nearshore/shelf hatching to off-shore shelf and slope pelagic habitat autumn through spring, surface.	Neustonic prey assemblages unknown. Likely limited winter-early spring.	Rapid growth apparent winter-spring. Early migration to neuston, extended larval phase until >50 mm.	Low fecundity. Transport off-shelf and away from settlement areas. Food limitation winter-early spring in neuston.	Large size at hatching and yolk-absorption. Large neustonic larvae winter-spring/early summer; good feeding ability.	Off-shelf transport. Winter-spring prey availability in neuston.
Pacific Sand Lance	Overwinter egg incubation in coastal sediments, peak hatch at temperature minimum. Larval development with rising spring-summer temperatures.	Flushed from sub-tidal sediments late winter, off-shore transport throughout shelf and slope winter-summer.	Limited late winter-early spring, plentiful late spring-summer. Diel migration to neuston observed, likely for feeding at night.	Newly hatched larvae weak, ribbon-like (late winter-early spring), likely poor swimming ability. Rapid growth spring-summer.	Low fecundity, overwintering of small eggs in coastal sediments, high predation risk on hatching, limited lipid reserves prior to first feeding.	Spatial ubiquity, extended planktonic phase including utilization of neuston. Relatively rapid growth spring-summer.	Timing and value of winter temperature minimum nearshore (hatching trigger?) and subsequent increase. Abundance of suitable prey, inner-shelf March-April.
Pacific Cod	Egg deposition and hatching near bottom on shelf late winter-early spring during temperature minimum. Larval development with rising spring temperature.	Along- and cross-shelf during spring; retention in meso-scale features may be important.	Limited at 1st feeding, early spring. More plentiful for late stage larvae. Some preference for copepod nauplii observed.	Small size at hatching and at yolk-absorption (<5 mm) early spring, most larvae transformed and settled out of plankton nearshore by summer.	"All eggs in one basket" spawning strategy. Warm early spring, faster growth; prey mismatch. Small size at 1st feeding. Transport away from settlement habitat in spring.	Super high fecundity can offset high mortality from narrow temporal range in production. Early settlement to nearshore nurseries in summer.	Winter-early spring temperatures. Timing of availability of copepod nauplii on shelf, early spring. Occurrence of meso-scale transport features.
Walleye pollock	Late winter deposition/hatching of deep pelagic eggs during temperature minimum. Larval development with rising spring-early summer temperatures.	Along- and cross-shelf, spring-early summer; retention in meso-scale features may be important.	Limited at 1st feeding, late winter-early spring. More plentiful for late stage larvae. Preference for copepod nauplii observed.	Small size at hatching early spring. Slightly larger than P. Cod at yolk absorption, more extended larval planktonic phase through early summer, pelagic early juveniles.	Warm early spring, faster growth; prey mismatch. Small size at 1st feeding. Diminished retention on shelf and within optimal prey concentrations.	Batch spawning, peripheral spawning areas, extends temporal and spatial utilization of pelagic habitat. Spreads risk.	Winter-early spring temperatures. Abundance of copepod nauplii on shelf, late winter-spring. Occurrence of meso-scale transport features.
Northern Rock Sole	Egg deposition (nearshore, shelf), larval hatching and growth during winter-spring, temperature minimum and spring increase.	Along- and cross-shelf, spring-early summer; retention in meso-scale features may be important.	Limited at 1st feeding, late winter-early spring. More plentiful for late stage larvae.	Small size at hatching/yolk-absorption (<5 mm) winter-spring, metamorphosis at small size, settlement spring-summer.	Small demersal eggs, larval size at hatching and 1st feeding, food limitation winter-early spring. Faster early growth may result in prey mismatch.	Batch spawning, multiple larval cohorts late winter-spring, early transformation and settlement at small size (spring-summer).	Winter-early spring temperatures. Timing of availability of copepod nauplii on shelf, early spring. Occurrence of meso-scale transport features.

(continued on next page)

Table 7 (*continued*)

	Early Ontogeny Environmental Synchronies				Proposed Sensitivities		Proposed Critical Indicators
	Temperature	Transport	Food availability	Larval Development	Vulnerability	Resilience	
Northern Lampfish	Mesopelagic eggs, cold deep water winter-summer. Peak abundance epipelagic larvae during spring temperature rise, late larvae during summer temperature maximum-autumn early decline.	Directed transport unnecessary; extensive epipelagic larval habitat throughout GOA basin.	Limited late winter-early spring, presumably plentiful late spring-summer and early autumn. Basin zooplankton assemblages largely unknown.	Small size at hatching and 1st feeding, winter-spring. Juvenile characteristics and transformation observed during summer.	Very small size at hatching and 1st feeding, presumed food limitation winter-early spring.	Spatial ubiquity, very abundant population; extended batch-spawning GOA basin, larval and pelagic juvenile habitat extensive.	Winter-spring zooplankton prey availability basin and shelf.
Alaska Plaice	Pelagic egg incubation and larval development during spring temperature rise.	Along- and cross-shelf during spring; retention in meso-scale features may be important to achieve settlement on shelf and nearshore.	Somewhat limited early spring, likely plentiful late spring.	Short larval phase during spring with transformation beginning in larvae as small as 10 mm.	Transport away from suitable settlement areas.	Relatively large pelagic eggs, limited larval duration in spring, early metamorphosis and settlement at small size (<15 mm).	Timing and level of peak spring abundance of zooplankton prey. Occurrence of meso-scale transport features.
Sablefish	Egg incubation/hatching in cold deep water, slow migration to surface during winter temperature minimum. Late larvae experience spring-summer surface temperatures.	On-shelf, cross-shelf and along-shore spring-summer at surface. Enhanced on-shelf transport in canyons/troughs.	Neustonic prey assemblages unknown. May be limited in early spring.	Large size at 1st feeding, rapid growth of larvae late spring-summer. Early development of large pectoral fins, extended transition phase.	Extensive spatial and temporal exposure to variable surface conditions in neuston, 1st feeding to epipelagic juvenile stage.	Larvae relatively large at 1st feeding, robust neustonic larvae, good swimmers for feeding at surface and directing transport.	Surface temperature and circulation spring-summer, including on-shelf canyon transport. Spring-summer abundance of neustonic zooplankton prey.
Lingcod	Egg incubation/hatching late winter-early spring, nearshore/shelf during temperature minimum. Larval phase coincides with rising spring temperature at surface.	Cross-shelf and along-shore at/near surface, primarily during spring.	Neustonic prey assemblages unknown. May be limited in early spring. Sub-surface foraging also likely.	Large size at hatching/1st feeding, flexion size reached relatively quickly. Larvae transformed and mostly out of plankton in summer.	Exposure to variable surface conditions on shelf in spring.	Large demersal eggs, larval size at 1st feeding. Robust neustonic larvae most abundant late spring, also occur sub-surface.	Spring abundance of suitable neustonic zooplankton prey.
Pacific Herring	Demersal eggs nearshore during spring rising temperatures. Larvae most abundant late spring nearshore, inner shelf.	Retention close to nearshore nursery habitat during spring. Offshore transport seems minimal.	Nearshore spring zooplankton assemblages. Peak abundance of larvae synchronized with late spring peak in copepod production.	Large size at hatching/1st feeding, although mouth small. Growth to transformation during spring seems relatively rapid.	Transport away from nearshore nursery habitat.	Larval swimming ability/behavior effects successful retention in coastal habitat. Larval phase synchronized well with spring production.	Nearshore meso-scale circulation during spring. Availability of nearshore zooplankton prey.
Flathead Sole	Pelagic eggs on shelf during spring rising temperature. Larvae super abundant in late spring.	Along- and cross-shelf in spring; retention in meso-scale features may be important to maintain larvae on shelf.	Shelf spring zooplankton assemblages. Peak abundance synchronized with late spring peak in copepod production.	Period from hatching to 1st feeding and flexion seems rapid, most larvae pre-flexion in spring, post-flexion -to transformation early summer.	Food limitation for larvae in early spring. Transport off shelf.	Batch spawning, large eggs, larvae ubiquitous throughout shelf. Larval phase synchronized well with spring production on shelf.	Early spring zooplankton prey availability. Meso-scale circulation on shelf.

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Table 7 (*continued*)

	Early Ontogeny Environmental Synchronies				Proposed Sensitivities		Proposed Critical Indicators
	Temperature	Transport	Food availability	Larval Development	Vulnerability	Resilience	
Starry Founder	Pelagic eggs and larvae abundant during spring temperature rise.	Retention on inner shelf and nearshore seems important.	Nearshore/inner shelf spring zooplankton assemblages. Peak abundance synchronized with late spring peak in copepod production.	Very small size range from hatching to early transformation, mostly late spring.	Small size at hatching. Transport away from coastal and inner shelf settlement areas.	Very limited larval pelagic exposure, metamorphosis and settlement mostly at <10 mm.	Nearshore meso-scale circulation during spring.
Rex Sole	Pelagic eggs over deep water during spring-summer temperature rise. Extended larval phase may span late spring-autumn (temperature maximum), and overwinter (declining temperature).	On-shelf, cross-shelf and along-shore spring-summer. Enhanced on-shelf transport in canyons/troughs.	Larval phase synchronized well with peak spring-summer production of zooplankton. Larvae occurring in early spring, or over winter, may be food limited.	Large size at 1st feeding (late spring), rapid growth evident June-July. Extraordinarily extended larval phase for flatfish, and large size at metamorphosis >50 mm.	High predation pressure in plankton during summer-autumn. Extremely extended larval phase; greater transport loss prior to settlement, and overwintering of late larvae may occur.	Larval phase synchronized well with high temperatures, and peak period of spring-summer zooplankton production from deep water to nearshore.	On-shelf transport, summer-autumn especially in canyons/troughs. Winter availability of suitable zooplankton prey.
Dover Sole	Pelagic eggs over deep water during spring-summer temperature rise. Extended larval phase may span late spring-autumn (temperature maximum).	On-shelf, cross-shelf and along-shore spring-summer. Enhanced on-shelf transport in canyons/troughs.	Larval phase synchronized well with peak spring-summer production of zooplankton. Larvae occurring in early spring may be food limited.	Slightly larger eggs and hatch size than Rex Sole, but smaller at 1st feeding (late spring). Summer-autumn settlement, large size range at metamorphosis.	High predation pressure in plankton during summer-autumn. Extended larval phase; greater transport loss prior to settlement.	Larval phase synchronized well with high temperatures, and peak period of spring-summer zooplankton production from deep water to nearshore.	On-shelf transport, summer-autumn especially in canyons/troughs.
Ronquils (*Bathymaster* spp.)	Demersal eggs nearshore/shelf, spring-summer; larvae most abundant May-June during rising temperatures, some neustonic occurrence.	Cross-shelf and along-shore spring-summer.	Larval phase synchronized well with peak spring-summer production of zooplankton. Larvae occurring in early spring may be food limited.	Multiple species (three in GOA), earliest ontogeny mostly unknown.	Widespread distribution of small larvae during spring, perhaps some transport loss.	Larval phase synchronized well with peak period of spring-summer zooplankton production nearshore and shelf.	Temperature and suitable zooplankton prey availability late spring, including in neuston.
Southern Rock Sole	Pelagic eggs and smallest larvae most abundant during late spring rising temperatures. Larval phase extends through summer-early autumn peak temperatures.	Cross-shelf and along-shore spring-summer.	Larval phase synchronized well with peak spring-summer production of zooplankton. Larvae occurring in early spring may be food limited.	Small eggs, larvae metamorphose and settle at small size mostly <15 mm.	Small size at 1st feeding.	Larval phase synchronized well with peak period of spring-summer zooplankton production nearshore and shelf.	Temperature and suitable zooplankton prey availability late spring.

	Early Ontogeny Environmental Synchronies				Proposed Sensitivities		Proposed Critical Indicators
	Temperature	Transport	Food availability	Larval Development	Vulnerability	Resilience	
Butter Sole	Pelagic eggs and smallest larvae most abundant during late spring temperature rise. Larval phase extends through summer peak temperature.	Retention nearshore/inner shelf seems important.	Larval phase synchronized well with peak spring-summer production of zooplankton. Larvae occurring in early spring may be food limited.	Small eggs, larval size at hatching and 1st feeding during late spring. Mostly transformed and settled by 20 mm, and rare by late summer.	Small size at hatching and 1st feeding. Transport away from shallow water.	Larval phase synchronized well with peak period of spring-summer zooplankton production nearshore and shelf.	Meso-scale circulation features nearshore.
Rockfish (*Sebastes* spp.)*	Late spring peak in larval abundance over deep water coincides with rising temperature and increasing metabolic demand.	Cross-shelf and along-shore during summer. Enhanced on-shelf transport in canyons/troughs.	Larval phase synchronized well with peak spring-summer production of zooplankton. Larvae occurring in early spring may be food limited.	Viviparity with release of live larvae late spring (Pacific Ocean Perch). Size at transformation thought to be 15-20 mm; early settlement?	Newly released small larvae have little or no lipid reserves, first feeding needs to occur rapidly.	Internal embryonic development. Rapid larval growth during spring-summer in association with high levels of zooplankton prey.	On-shelf transport during summer-autumn especially in canyons/troughs. Zooplankton prey availability over slope late spring-summer.
Capelin	Demersal eggs in sub-tidal sediments summer-autumn; peak abundance newly hatched and smallest larvae during summer temperature peak; largest larvae autumn-winter (and some in spring) experience declining and minimum temperatures.	On-shelf, cross-shelf and along-shore summer autumn. Larger more behaviorally competent larvae during winter-spring likely mitigates passive drift.	Larval phase synchronized well with peak summer production of zooplankton prey, and likely plentiful supply through early autumn. Winter-spring more food limited but larvae large; greater swimming and feeding ability.	Small eggs, larval size at hatching and 1st feeding during summer. Extended larval phase with diel utilization of neuston autumn-winter. Gradual transformation to pelagic juveniles; very large size (>60 mm) at transformation.	Very small newly hatched larvae flushed from coastal sediments during summer; probably very high predation risk.	Early larval phase synchronized well with peak period of summer zooplankton production nearshore and shelf. Larvae utilize neuston as well as sub-surface as they grow. Fast growth and very extensive range of larval sizes autumn-spring.	Nearshore temperature and meso-scale circulation summer. Nearshore zooplankton prey availability for first feeding larvae. Abundance of neustonic zooplankton prey summer-winter.
Yellowfin Sole	Pelagic eggs and small larvae nearshore during summer peak in temperature.	Retention close to nearshore nursery habitat during summer. Offshore transport seems minimal.	Larval phase synchronized well with peak abundance of zooplankton in summer.	Very small eggs and larval hatch size, summer. Rapid development and transformation to settlement apparent.	Very small size at hatching; presumed early feeding necessary due to high temperature-induced metabolic rates.	Rapid growth during summer in nearshore environment, likely favors retention close to suitable settlement habitat.	Nearshore temperature and meso-scale circulation during summer. Nearshore zooplankton prey availability for first feeding larvae.

and temperature in winter and spring months is documented for Pacific Cod and Walleye Pollock in the GOA late spring time series (Doyle and Mier, 2016) implying a positive growth response to warmer temperatures and the potential for a timing shift in larval food requirements. The deep water early winter spawners, Pacific Halibut and Arrowtooth Flounder, encounter the coldest temperatures for the longest period of time as larvae with extended durations over winter to spring months, and peak abundance in January and February. This type of early phenology in association with cold conditions that maintains slow growth is considered advantageous for bridging the extensive spatial and temporal gap between peak abundance of larvae of these species and peak availability of zooplankton prey on the GOA shelf during spring (Doyle and Mier, 2016). Many GOA species would seem susceptible in this way to the negative effect of warmer winter temperatures as early ontogeny pre-feeding stages are abundant for the highest number of species during late winter and early spring. Observation of high interannual variability in winter temperature minima suggests that winter temperature may be a good indicator of annual variability in early larval development rates and survival, especially as influenced by the timing of the switch to exogenous feeding. The early ontogeny of Pacific Sand Lance may also be affected by winter temperatures during the unusually long egg incubation phase for this species, with eggs dormant in nearshore sediments for weeks to months subsequent to spawning in autumn (Robards et al., 1999). Based on the dramatic peak in abundance of newly-hatched larvae in the plankton of the GOA during March, it has been previously hypothesized that peak emergence from the sediments may be triggered by the initial rise in water temperature immediately following the annual water temperature minimum in March (Doyle et al., 2009). If this synchronous relationship exists, it is feasible that timing of hatching for Pacific Sand Lance and associated peak in abundance of larvae in the plankton could shift significantly with variation in the scale, timing and duration of winter temperature minima in coastal waters.

Variability in temperature-influenced larval growth rates during late spring and summer months may be less consequential with regard to maintaining synchrony with larval food availability than during winter and early spring. Warmer temperatures (conducive to rapid growth) and a plentiful supply of larval prey characterizes this period of peak zooplankton production in the GOA (Stabeno et al., 2004; Coyle and Pinchuk, 2003). Newly-hatched through first-feeding and preflexion larval stages of Capelin, Rockfish, Southern Rock Sole, Butter Sole, Rex Sole, Dover Sole, and Yellowfin Sole coincide with this period. Larval length data indicate that growth rates for these species tend to be more rapid from spring to summer months than those for the winter-spawned larvae from winter to spring months. Rapid growth is an advantage for gaining earlier access to a wider range of prey organisms and minimizing critical periods of vulnerability to trophic mismatch. Capelin is extraordinary among this group of species with continuous production and rapid growth of larvae during the warmest summer months, and post-flexion larvae remaining planktonic through autumn, winter and into the following spring. This unusual strategy of a very extended larval phase (including utilization of the neuston) means that Capelin is poised to take advantage of favorable conditions at any time of the year in the plankton, likely buffering negative effects of less than optimal conditions that may also be encountered. It provides an interesting contrast to the winter-spawning Pacific Cod that produces a huge quantity of eggs per female (~3 million), and releases them in a single batch that results in a very narrow temporal peak in abundance of larvae in the plankton during early spring, a strategy termed "all eggs in one basket" with respect to vulnerability to unfavorable conditions (Doyle and Mier, 2016).

The GOA late-spring time series of larval abundance (Doyle et al., 2009) provides some evidence for the ability of species with spring-summer larval production to withstand warmer conditions better than species with winter-spring larval production. A synthesis of data from this time series collected from 2013 on indicates that the lowest-ever levels of mean larval abundance for Pacific Cod, Walleye Pollock, Pacific Sand Lance, Northern Rock Sole, and Pacific Halibut were recorded in 2015 (Rogers and Mier, 2016) in association with record positive temperature anomalies in the GOA following the North Pacific marine heatwave of 2014–2015 (Bond et al., 2015; Di Lorenzo and Mantua, 2016). In contrast, for the spring-summer spawning Rockfish and Southern Rock Sole (species well represented in the GOA late spring time series) larval abundance was at an all-time high and average in 2015, respectively (Rogers and Mier, 2016). A direct effect of warmer temperatures on the winter-spawned larvae could be faster growth that facilitates a mismatch with optimal prey availability. An indirect effect is also possible in that the anomalous warm conditions of 2014-15 seem to have affected the spring planktonic food web by promoting a community of small-celled ($<20\,\mu m$) phytoplankton and microzooplankton and associated diminished biomass levels (Strom, unpublished data). If large protists are important in the diets of first-feeding larvae during these months, winter-spawned larvae could experience higher levels of starvation under such conditions.

4.2. Phenology and transport

The GOA is a highly advective environment and larval fish in the different habitats are subject to a variety of transport mechanisms from the prevailing currents and wind-forcing of circulation near the surface. The Alaska Coastal Current associated with the inner shelf and Alaskan Stream over the continental slope and adjacent basin drive the persistent south-westerly direction of transport influencing distribution of zooplankton, including larval fish, throughout the central to western GOA (Stabeno et al., 2004; Doyle et al., 2009). Further, the GOA is predominantly a downwelling system and storms promote onshore advection of surface waters, which transport nutrients and plankton shoreward near the surface (Coyle et al., 2013). Transport of deep water spawned flatfish larvae on to the shelf has been hypothesized previously to be associated with enhanced onshore transport associated with El-Niňo Southern Oscillation events, wind-forcing, and on-shelf flow in canyons intersecting the slope (Bailey and Picquelle, 2002, bailey et al., 2008; Doyle et al., 2009). Atmospheric forcing of such onshore transport has also been linked positively to recruitment trends of deep water spawned flatfish in the GOA (Stachura et al., 2014). These onshore transport mechanisms are also likely to apply for Sablefish and Rockfish larvae that originate over the slope. Evidence for such larval drift pathways have been provided by the synthesis of historical ichthyoplankton data from the western GOA, and seasonal patterns in larval distribution for these species illustrate how larvae that hatch in deep water during winter become progressively more abundant on the shelf as they develop over a period of weeks to months (Doyle and Mier, 2016). In addition, hotspots in larval abundance are associated with the mouths of canyons and troughs intersecting the slope, where intensified onshore flow is observed generally on the northern side of the canyon walls providing a mechanism for larvae to be delivered on to the shelf (Mordy et al., 2019).

Seasonal variability in the cross-shelf component of winds indicates that from December through September, wind-driven transport of larval fish near the surface is on average in a shoreward direction. Ekman circulation (onshore at surface, offshore at depth) generated by the alongshore winds, and strongest during winter and spring, is also an important mechanism enabling transport onto the shelf of fish larvae and other zooplankton organisms spawned in deep water (Stabeno et al., 2004; Coyle et al., 2013). Ekman downwelling is likely more important for cross-shelf transport than the much weaker cross-shelf component of the winds for larval fish in the surface Ekman layer. Wind-driven transport can of course vary significantly on a temporal, regional and local scale, and meso-scale features like eddies and meanders can contribute to both onshore and offshore transport of larvae along the shelf edge (Stabeno et al., 2004; Ladd et al., 2007; Atwood et al., 2010). Further, Ladd et al. (2016) found that episodic (timescale of days) regional-scale "gap winds" (blow in offshore direction through gaps in the coastal mountains) can have important implications for transport on the GOA shelf, particularly in the vicinity of Kodiak Island. These wind events are most frequent during October to April, and their strength and offshore direction can potentially disrupt favorable onshore transport processes for larval fish as well as retention of larvae on the shelf.

For the two major canyons intersecting the continental slope in the western GOA the ROMS-generated monthly mean flow across the water column indicates that for deep-spawning fish species it is likely that their larvae are transported successfully on to the shelf from the slope in association with these topographic features, especially on the northeastern side. In particular, evidence of onshore transport throughout the water column across most of Amatuli Trough implies that larvae of species such as Pacific Halibut, Arrowtooth Flounder, and Sablefish that occur below 200 m when newly hatched, can experience larval drift in a shoreward direction. If such mechanisms are critical to successful delivery of deep water-spawned larvae onto the shelf, it seems that interannual variability in flow associated with these features would provide a better indication of variable larval survival than measures of flow integrated across the entire GOA slope which tends to be dominated by the strong signal of the Alaska Stream flowing parallel to the shelf edge. Spatial scale is particularly important in this respect, and fine scale horizontal resolution (e.g. the 3-km scale ROMS model) provides needed resolution of this canyon associated cross-shelf transport (Mordy et al., 2019). Finally, the differing phenologies of the flow into different canyons may itself have implications for the timing and location of spawning, and merits further study.

4.3. Phenology and food

Larval feeding across different sub-ontogenetic intervals is not well studied among GOA fish species, and information is primarily available for Walleye Pollock, which has been the focus of historical investigations in the GOA (Grover, 1990; Canino et al., 1991; Theilacker et al., 1996). Copepod nauplii are likely the most critical component of larval diets in the GOA although large phytoplankton, various heterotrophic protists, small microzooplankton, and copepod eggs may also be important for first feeding larvae and varieties of mesozooplankton for later stage larvae (Kendall et al., 1987; Munk, 1997; Miller and Kendall, 2009). The spring bloom in the GOA is usually composed of large phytoplankton (diatoms), which could be directly available as prey to some larval fish (they are observed in larval guts). Diatoms also support other large protists (microzooplankton grazers) and mesozooplankton that are likely important prey for larval fish (Strom et al., 2006; Strom et al., 2019). In contrast, the autumn bloom is dominated by small flagellates that may be less suitable as a bulk source of larval prey. Annual patterns in phytoplankton and zooplankton production and abundance in the GOA indicate high amplitude variation in the composition of prey fields available to larvae, including variability in abundance, biomass and size spectra of organisms that larvae might encounter and consume. The 2014-15 North Pacific marine heat wave and resulting anomalies in plankton assemblages (noted above) is a case in point regarding interannual variability in the physical environment that can cause significant disruption to the "normal" seasonal patterns in plankton assemblages. Spatial variability is also significant in the different larval habitats from coastal to deep water, as indicated by the Seward Line data, the GOA-NPZ model output and previous GOA studies (Incze and Siefert, 1990; Napp et al., 1996; Coyle and Pinchuk, 2005), and should be considered when evaluating larval food availability seasonally.

Food limitation may be less common for species that are abundant in spring-summer than for species with peak abundance in winter-spring. The late-phenology species have been identified previously as having a "synchronous" early life history strategy because of the good temporal overlap of their larval phase (and particularly first-feeding) with the annual peak in plankton production in the GOA (Doyle and Mier, 2012). Spring-summer spawners at the first-feeding stage (e.g. Rockfish, Southern Rock Sole, Capelin) and later larval stages of autumn and/or winter spawners (e.g. Pacific Halibut, Arrowtooth Flounder, Atka Mackerel, Pacific Sand Lance, Pacific Cod, Walleye Pollock, Northern Rock Sole, and Sablefish among others) can take advantage of a plentiful supply of zooplankton prey, particularly copepod nauplii, during these months. Average biomass levels, levels of abundance many orders of magnitude greater than the most abundant fish larvae (i.e. Walleye Pollock), and broad size spectra of planktonic organisms encountered during the peak production spring-summer months suggest adequate feeding opportunity for larval fish in the upper 50–100 m of the water column across shelf and slope habitats. Even with diminishing levels of abundance beyond the shelf, abundance of the smallest copepods (copepodite and adult stages <2 mm) and copepod nauplii are plentiful relative to larval fish species. However, ratios of mean abundance of larval prey organisms relative to fish larvae themselves are inadequate for gauging food availability and larval feeding success.

Small-scale patchiness of zooplankton prey and fish larvae is important, and spatial overlap of prey and larvae is critical for successful feeding and development of Walleye Pollock larvae in the western GOA (Incze et al., 1989; Grover, 1990; Theilacker et al., 1996). Fine-scale processes, including prey concentrations and behavioral interactions, also complicate the accurate assessment of larval fish and other zooplankton trophic ecology, as indicated by recent studies using in situ plankton imaging systems (Cowan and Guigand, 2008; Greer and Woodson, 2016; Greer et al., 2016). Such patchiness along with associated feeding patterns of larvae need to be investigated to have a realistic understanding of feeding conditions for larval species during these high productivity months and across pelagic habitats. Gut-content analysis of larval fish species across ontogenetic intervals, and assessment of the zooplankton assemblage from the same samples in different habitats, would provide some clear indication of feeding selectivity or omnivory among different species. Prey selectivity has been documented for larval fish species that occur in the same habitat (Llopiz et al., 2010), including Pacific Cod and Walleye Pollock in the Bering Sea (Strasburger et al., 2014). It is likely that the more selective a species is in terms of zooplankton prey, the more susceptible that larval species is to a trophic mismatch under certain conditions. This type of selectivity and associated vulnerability could also be heightened during intervals of early development, such as first-feeding when starvation is more likely (Miller and Kendall, 2009) or during metamorphosis when metabolic demand and physiological stress are heightened (Osse and Van den Boogaart, 1997).

In contrast to the "synchronous" strategy of the spring-summer spawners, it seems that the first-feeding larvae of the winter spawners are likely most vulnerable to food limitation in winter to early spring months. These larvae also tend to be at the small end of the spectrum in terms of size at hatching and at yolk-absorption which is relevant to feeding behavior and food availability (Doyle and Mier, 2012). First-feeding larvae of many of the late winter spawners occur from March onwards, and are most abundant during April which is prior to the later peak in near-surface production of copepod nauplii in the western GOA. On average, abundance levels for copepod nauplii and the copepodite to adult stages of the smallest (<2 mm) copepod species are several orders of magnitude higher than larval fish at this time of year, implying but not confirming availability as suitable prey. However, prey availability and associated larval feeding and growth for Walleye Pollock larvae in Shelikof Strait are more limited in April relative to the period of full development of the spring zooplankton bloom of copepod nauplii in May–June (Canino et al., 1991). In addition, the two-week period after first-feeding has been identified as a critical period when Walleye Pollock larvae are most vulnerable to starvation (Theilacker et al., 1996). High mortality rates during the 1990s in Shelikof Strait have also been correlated with poor nutritional condition of larvae, and low levels of copepod nauplii prey availability (Bailey et al., 1995). Larval abundance trends during late spring across three decades in the western GOA tend to be correlated among species with similar early life history strategies, including timing of spawning and peak abundance of larvae (Doyle et al., 2009). Environmental forcing from copepod nauplii prey availability could have similar effects on larval abundance, and perhaps survival, among species in the GOA with similar early life phenology to Walleye Pollock, e.g. Pacific Sand Lance, Pacific Cod, Northern Rock Sole, Flathead Sole, and Starry Flounder. Despite similarities in phenology, detailed information is needed on the diets of these larval species during early ontogeny and whether or not species-specific prey selectivity or larval distribution patterns modify the sensitivity to variable zooplankton prey concentrations. In terms of distribution patterns, newly-hatched and first-feeding larvae tend to be more concentrated in patches than later stages which have experienced longer periods of larval drift. In addition, meso-scale circulation features that can concentrate larval Walleye Pollock and their prey in patches are proposed as favorable to successful feeding by larvae during early spring when average prey concentrations tend to be sub-optimal (Canino et al., 1991). Net samples of ichthyoplankton and zooplankton integrated across depths, while indicative of average prey availability, do not provide sufficient resolution to determine optimal conditions for successful larval feeding, such as fine-scale overlap of larval fish patches with optimal prey concentrations. First-feeding larvae are also not as behaviorally competent as post-flexion larvae further compromising the ability to capture mobile prey.

If levels of abundance of zooplankton prey during early spring can be suboptimal (Canino et al., 1991; Theilacker et al., 1996), it would seem logical that biological conditions during January through March could be deleterious to fish larvae searching for food. For the earliest phenology species in the GOA (Pacific Halibut, Arrowtooth Flounder, Northern Smoothtongue, Red Irish Lord, Kelp Greenling and Atka Mackerel), the smallest first-feeding larvae are most abundant over deep water during January to February when production in the plankton is at a minimum. There is a tendency for these species to have larger eggs, larger size at hatching, and larger size at yolk-absorption than later phenology species (Doyle and Mier, 2012). An advantage is that larger lipid reserves in the eggs and yolk-sac stage last longer, especially at cold winter temperatures, delaying the need for exogenous feeding. Larger larvae at first-feeding may have a better chance of feeding success than smaller larvae, especially in food-poor environments, due to greater behavioral ability and access to a larger size range of prey organisms. Doyle and Mier (2016) and Doyle et al. (2018) hypothesized a potential trophic link between the larval phase of these deep-water, winter spawners and the reproduction of the large *Neocalanus* copepods (especially *N. plumchrus* and *N. flemingerii*) that reproduce in deep water of the GOA basin and slope in January to February after the adults have been in diapause from summer through autumn (Miller and Clemons, 1988). There is notable temporal and spatial synchrony between the occurrence of eggs, nauplii and early copepodite stages of these *Neocalanus* species, and newly hatched and first-feeding larvae of the above mentioned fish species, as they migrate upwards in the water column at the same time and are subject to the same transport processes on to the shelf (Coyle and Pinchuk, 2003, 2005; Doyle and Mier, 2016). It would be interesting to investigate this potential trophic connection by examining larval fish diets and zooplankton food availability in plankton collections over deep water during winter months, and especially in association with the troughs and canyons that facilitate cross-shelf transport for these organisms.

Theoretically, levels of abundance of copepod nauplii and copepodites of the smallest copepod species observed during March along the Seward Line, even at the outer stations, would seem sufficient for feeding success of winter-spawned larvae over the slope and outer shelf, especially as many of those larvae are now >8 mm SL. *Oithona similis* and *Microcalanus* spp. copepods are relatively abundant, and the larvaceans *Oikopleura* spp. and *Fritillaria* spp. are also plentiful it seems and potentially available to larvae as food over deep water. Again, establishing such links needs further investigation both in terms of prey selectivity and predator-prey patchiness and spatial overlap. The potential availability and utilization of protozoan plankton in the diets of first-feeding larvae that are abundant during winter months over the slope and outer shelf also remains unknown, and in general protozoan-ichthyoplankton trophic links are not well studied (Montagnes et al., 2010). However, De Figueiredo et al. (2007) found that protist prey occurred in the diets of 11 taxonomic groups of larval fish in the Irish Sea, and proposed that ciliates and other protozoans prevent food limitation when metazoan prey are rare or inaccessible. An investigation of biological standing stocks in the central GOA basin during two winter surveys (March 1993 and February 1994) indicated that the abundance and composition of the autotrophic and heterotrophic assemblages at these times were similar to those observed during late spring and summer by others in this region (Boyd et al., 1995). The implication is that these winter subsistence communities may be available to first-feeding larval fish over deep water during winter, and may be important in bridging the temporal and spatial gap with peak copepod nauplii availability on the shelf in spring.

4.4. *Species-specific development trajectories*

Is timing everything? Certainly, the phenology of reproduction and the planktonic phase (timing and duration) among marine fish species provides a detailed understanding of the temporal patterns of exposure to physical and biological forcing in pelagic ecosystems. These exposure details are essential for gauging sensitivities and potential responses of fish species during early ontogeny to environmental forcing (Doyle and Mier, 2012, 2016), and are critical to the development of climate vulnerability assessments that incorporate early life history aspects of the recruitment process (Hare et al., 2016). There is another level of ecological complexity that also needs to be considered, based on species-specific intrinsic rates and morphological development during early ontogeny. Unique physiological rates and development patterns (Matarese et al., 1989) can modify sensitivities and response to the environment among species with similar patterns of temporal and spatial exposure as larvae, and even among closely related species within taxonomic groups. Pacific Cod and Walleye Pollock have identical periods of peak larval abundance on the GOA shelf during early spring and are morphologically similar during the planktonic phase. However the former larvae develop more rapidly than the latter and transform and migrate to inshore nursery grounds earlier in summer, whereas Walleye Pollock remain pelagic as age-0 juveniles and are ubiquitous on the shelf during summer months (Wilson, 2009; Doyle and Mier, 2016). Larvae of Pacific Herring and Pacific Sand Lance begin their life in nearshore sediments of the GOA during spring. Higher development rates and size at hatching for Pacific Herring results in larval retention in coastal nursery areas, whereas the thin and behaviorally incompetent Sand Lance larvae are flushed out of nearshore sediments and distributed broadly across the entire shelf (Doyle and Mier, 2012). Pleuronectid flatfish in the GOA also provide a good example of such developmental diversity as indicated by the variable sizes at ontogenetic intervals and range of larval durations. Starry Flounder and Flathead Sole larvae are most abundant in shelf waters during spring but diverge significantly in terms of larval durations with the former transforming and settling out of the plankton at 8–11 mm SL, whereas the latter remains planktonic into summer months transforming at around 20 mm SL. Arrowtooth Flounder and Pacific Halibut display very different larval growth trajectories from winter through spring months. Pacific Halibut hatch at a larger size, and develop relatively quickly so that by 24 mm SL they can be fully transformed and settled out of the plankton in nearshore nursery grounds during summer. In contrast, suspended progress in both growth and transport of larvae during winter to early spring months characterizes the “holding pattern” early life history strategy of Arrowtooth Flounder, with transformation and settlement delayed until larvae are mostly > 40 mm (Doyle and Mier, 2016), and juvenile settlement habitat is associated with broad areas of the GOA shelf (Doyle et al., accepted). Similarly, the deep water spring-spawning Dover Sole and Rex Sole diverge significantly during the late larval phase (Pearcy et al., 1977; Abookire and Bailey, 2007). Both display a wide range of sizes at transformation but the former can be completely metamorphosed by 20–30 mm SL whereas Rex Sole has one of the longest larval durations of any flatfish species and can remain planktonic until a size of 50-70 + mm with later metamorphosis and settlement. These different larval growth trajectories call for a more nuanced interpretation of the early life history phenology framework with respect to vulnerability or resilience to shifting physical and biological conditions in the pelagic ecosystem of the GOA. Clearly, timing is not everything and all fish larvae are not equal.

4.5. Implications

Scale is a critical factor when considering environmental forcing on various fish species during early life, especially during the planktonic phase (Mullin, 1993; Doyle and Mier, 2016). It is also important more broadly when incorporating predator-prey interactions of marine fish species into ecosystem models (Hunsicker et al., 2011). Multiple environmental drivers, operating at different spatial and temporal scales likely influence larval survival, a conclusion also reached with individual-based model experiments in the GOA (Gibson et al., 2019; Hinckley et al., 2019; Stockhausen et al., 2019a and b).

Local-scale environmental conditions with species- and ontogenetic stage-specific temporal and spatial resolution are critical for the identification of relevant environmental indicators of species early life survival. Basin-scale climate and oceanographic conditions and signals (especially model-generated) tend to be blunt instruments for the prediction of early life history survival and fish stock recruitment success. Such indices are certainly useful as broad indicators of system conditions and shifts, but investigating local conditions at the scale of the planktonic habitat for larval fish assemblages is essential for discerning relevant environmental forcing during the early phase of the recruitment process.

Dickey-Collas et al. (2014) propose that technique-driven approaches that neglect the incorporation of biological knowledge into stock assessments in favor of statistically-based correlations between recruitment trends and environmental variables are hazardous in terms of modelling outcome, and the resulting advice given to fisheries managers. Higher resolution of species-environment linkages and response mechanisms can only be gained through ecological monitoring and empirical biological data, so this aspect of model-development should not be neglected. In this paper, we are highlighting the importance of species-specific biological and ecological details in assessing environmental influence on fish population trends. It is also possible to match the "generation time" of species' planktonic phases (i.e. larval exposure at different ontogenetic intervals) with seasonal patterns in the physical and biological environment to identify environmental signals of relevance that could be tested for influence on population trends. For example, variability in winter temperature affecting growth rates and prey match-mismatch is likely critical for survival of winter-spawned larvae, on-shelf transport in canyons during the early larval phase is crucial for deep water spawned species, and zooplankton prey resources during relevant time periods at the sea surface is likely most important for species with neustonic larvae (Table 7). Such proposed environmental factors and sensitivities can be used to develop indicators for the ESPs of the different stocks listed (Shotwell et al., 2018, in review). These indicators can be monitored and provide early warning of impending ecosystem change which can be translated through the stock assessment process to consider adjustments to harvest recommendations. In some cases, the proposed critical indicators (Table 7) have not yet been developed for the GOA (e.g. abundance or timing of availability of certain species of copepod nauplii) and this would constitute a potential data gap for the stock indicators. Recommendations for future research priorities are a fundamental part of the ESP framework and the synthesis provides the context for critical data needs of several commercially and ecologically important species in the GOA. Early life history strategies and sensitivities as evaluated here for species in the GOA could also be applied to the same species in the adjacent Bering Sea ecosystem, but with some further evaluation regarding vulnerability and resilience factors in relation to the differences in pelagic phenology and seasonal physics within that more northerly, ice-influenced ecosystem.

Within marine pelagic communities, different responses to climate forcing are observed among different functional groups and trophic levels and although phenological shifts are noted among all organisms, the intensity and direction of the shift is variable (Edwards and Richardson, 2004; Greve et al., 2005). Although some plasticity is observed, timing of spawning and larval development among fish species in the GOA is less variable from year-to-year (Bailey et al., 2005; Ciannelli et al., 2007; Doyle et al., 2009) than interannual variability in phytoplankton and zooplankton production which is much more dynamic given shorter generation times and high levels of spatial heterogeneity (Brickley and Thomas, 2004; Stabeno et al., 2016; Strom et al., 2016, 2019). Effects of warming on different groups of zooplankton organisms in the northeast Pacific can be variable and complex, and different sensitivities and responses are observed (Mackas et al., 2012). Doyle et al. (2018) propose that synchronicity in response to environmental disruption is therefore unlikely between larval fish and their zooplankton prey. The mechanism of occurrence and the temporal direction and amplitude of such phenological shifts among different taxonomic groups in the plankton is uncertain, and especially with respect to influencing favorable to unfavorable trophic conditions for larval fish growth and survival (Batten and Mackas, 2009). This review of early life history phenologies among fish species in the GOA helps us identify intervals of early ontogeny that may be more or less resilient to certain shifts in the pelagic environment. Incorporating this information within the new ESPs for each species will highlight data gaps and assist with developing research priorities attuned to the needs of each stock (Shotwell et al., 2018). Going forward, investigations of larval trophic ecology among species to address prey selectivity at different ontogenetic stages, and in different seasons, will be especially important as this represents a significant knowledge gap at present for modelling trophic linkages in fisheries ecosystems. Identification of key prey organisms at different larval stages among species is crucial for evaluation of vulnerabilities during early ontogeny, and for the identification of key species of zooplankton that may be critical to multiple or individual fish species during their planktonic phase.

There are broad pelagic food -web implications for understanding phenological patterns, synchronies and sensitivities in the reproduction and early ontogeny of fish species in this ecosystem. We did not address predation on fish larvae with this early life phenology framework because knowledge is limited. Demersal fish eggs are subject to predation by a host of invertebrate and fish predators, and planktonic eggs and larvae are preyed upon by a wide variety of planktonic predators including ctenophores, scyphomedusae, chaetognaths, crustaceans (adult euphausiids are particularly important), juvenile and adult fish, and planktivorous birds (Bailey and Houde, 1989; Cowan and Houde, 1992; Miller and Kendall, 2009). There is seasonality to this predation pressure and peak periods of zooplankton prey availability in the plankton for fish larvae (spring to summer) also tend to be periods of highest abundance of plankton predators. Cannibalism on fish eggs and larvae is also common (Brodeur et al., 1991; Fortier and Villeneuve, 1996) and can enhance the nourishment and survival of the population as a whole, especially if fecundity is very high (Nellen, 1986). Just as climate forcing can shift synchronicity between the occurrence of larval fish and their prey, temporal and spatial overlap between fish eggs or larvae and their predators can also shift to be more or less favorable to the survival of either. Enormous quantities of fish eggs and larvae enter the pelagic ecosystem of the GOA annually, peaking in abundance and diversity during spring but also available throughout all seasons. This is particularly true for many commercially important groundfish species that are characterized by very high fecundity. The vast majority (≫99%) of larvae do not survive to adulthood but presumably are a significant source of nourishment for other species. Fish larvae can provide important trophic links between phytoplankton and microzooplankton on which they feed, and larger mesozooplankton and nekton that eat them. For instance, they have been identified as particularly important in the diets of juvenile salmon species feeding in the ocean environments of the northern California Current (Brodeur et al., 2007) and the Gulf of Alaska (Sturdevant et al., 2012). Further, winter ichthyoplankton abundance and biomass continues to be an important indicator of salmon survival and returns from the ocean off the US west coast (Daly et al., 2013, 2017). Reproductive success of planktivorous sea birds has also been associated with temporal and spatial availability of larval and age-0 juvenile small pelagic fish species (Kitaysky and Golubova, 2000; Cury et al., 2011). Seasonal pulses in larval fish species and phenological synchronies and sensitivities to the ocean environment as described here are broadly relevant therefore to gauging food availability and energy flow in marine pelagic ecosystems, as well as to understanding environmental forcing on the fish populations themselves.

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