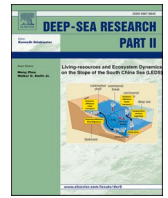




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Synthesizing integrated ecosystem research to create informed stock-specific indicators for next generation stock assessments

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ABSTRACT

Over the past two decades, numerous ecosystem surveys and process studies have emerged to monitor and assess the large marine ecosystems of Alaska. Several regional collaborative integrated ecosystem research projects (IERPs) were conducted to gain understanding of fish population fluctuations in relation to the surrounding environment. The Gulf of Alaska (GOA) IERP is one example of such an effort. Products of this program include a suite of *in situ* observations from fully integrated ecosystem surveys, laboratory experiments of physical thresholds for fish condition, and high-resolution oceanographic, planktonic, and habitat distribution models. When coupled, the synthesis products of this program can be utilized to understand system connectivity and highlight the primary ecosystem drivers of the GOA. Much of this information was included in annual GOA ecosystem status reports through individual indicator contributions. However, assimilation of these data into single-species stock assessments has remained limited. We provide a clear and direct avenue for including the products of these IERPs through the new ecosystem and socioeconomic profile (ESP) framework that identifies mechanistic relationships and tests ecosystem linkages within the stock assessment process. We present a case study using a data synthesis of the five commercially and ecologically valuable focal species of the GOA IERP (sablefish, pollock, Pacific cod, arrowtooth flounder, and Pacific ocean perch). Information was organized along the categories of distribution, phenology, and condition by life history stage to develop life history narratives for each species. These narratives identified critical ecosystem processes that could impact survival of each species. We then used habitat distribution models, seasonal phenology, and energy allocation strategies to sequentially reduce two gridded temperature datasets to reflect the life experience of the stock. This method essentially aligns ecosystem information at a spatial and temporal scale relevant to a stock and creates informed indicators that could then be related to a stock assessment parameter of interest, such as recruitment. Informed temperature

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indicators differed in magnitude and variability when compared to non-informed indicators and demonstrating species and stage-specific thermal preferences. The difference between the informed indicators and the non-informed indicators can also highlight thresholds and trends in habitat preference that could be further investigated with targeted process studies or laboratory experiments. The coordinated nature of the IERP allowed for the creation of these informed indicators that would not be possible with the results of any one process study. Both the stock-specific narratives and the informed indicators can be included into the ESPs for further monitoring and development. This integration ensures that the identified ecosystem linkages are evaluated concurrently with the stock assessment and ultimately transferred to fishery managers in an efficient and effective format for informing management decisions.

1. Introduction

Over the past two decades, numerous ecosystem surveys and process studies have been conducted to monitor and assess the status of Alaska's large marine ecosystems. This is in response to the growing need for ecosystem-based science for effective marine conservation and resource management (Levin et al., 2009) as mandated by the United States (U.S.) national standard guidelines (16 U.S.C. 1851 (1,2)). Generally, the output of these surveys or studies contribute to a comprehensive ecosystem assessment such as an ecosystem status report (ESR) and provide contextual advice for the fisheries management process (Zador et al., 2016). However, assimilation into single-species stock assessment has remained limited (Skern-Mauritzen et al., 2016). This may largely be due to the lack of a standardized framework to rationally adjust stock assessments based on ecosystem research (Shotwell et al., *In Review*). However, an additional limitation is the nature of the ecosystem surveys and process studies that are usually designed to address tightly focused hypotheses regarding environmental processes over limited spatiotemporal scales. This local-level focus can be a hindrance to integration into stock assessments that are generally conducted at the population (or regional) level.

In addition to the smaller-scale studies, several large, integrated ecosystem research programs have been established to understand the dynamics of Alaska's large marine ecosystems and their influence on fish populations. The Gulf of Alaska (GOA) has been particularly well studied by multiple programs. The international Global Oceans Ecosystem Dynamics (GLOBEC) program (Fogarty and Powell, 2002) identified the coastal GOA as one of three regions of interest in the U.S. and created the GOA GLOBEC program which ran from 1997 to 2004 (Batchelder et al., 2005). In 2012, Gulf Watch Alaska (GWA) began as a long-term program to monitor recovery of GOA areas affected by the *Exxon Valdez* oil spill. The program was developed to sustain long-term monitoring of near-shore and offshore ecosystems in the northeastern GOA, from Prince William Sound to lower Cook Inlet (Neher et al., 2015). Finally, one of the Integrated Ecosystem Research Projects (IERP) funded by the North Pacific Research Board (NPRB) was conducted in the GOA to understand variability in recruitment of five commercially and ecologically valuable fish stocks (Dickson and Baker, 2016; Ormseth et al., 2019). The first phase of IERP research was conducted from 2010 to 2014 and products of this phase included a suite of *in situ* observations from fully integrated ecosystem surveys, laboratory experiments of physical thresholds for fish condition, and high-resolution regional oceanographic, planktonic, and habitat distribution models. The second phase of the GOAIERP (termed GOAIERP Synthesis) was a combining and summarizing phase occurring from 2014 to 2018 and designed around connectivity themes to meld the various large-scale fully integrated and local-scale process study programs in the GOA (Ormseth et al., 2019). When combined, the products of these programs can be utilized to understand system connectivity and to highlight the primary ecosystem drivers of a large marine ecosystem like the GOA. These collaborative regional efforts can be more readily integrated into the stock assessment process because the research is organized at the same spatial scale as the fisheries.

Collectively, these broad-scale studies have contributed to annual GOA ecosystem status reports (ESR) (e.g., Zador and Yasumiishi, 2017;

Ferriss and Zador, 2020). However, assimilation of the relevant information from the ESRs into single-species stock assessments has remained limited due to the lack of a clear process for evaluating ecosystem information for use in stock assessments. Conveniently, a new standardized framework termed the ecosystem and socioeconomic profile (ESP) has recently been developed to test ecosystem linkages within the stock assessment process (Shotwell et al., *In Review*; Shotwell et al., 2019a). The ESP uses data collected from a variety of sources in a four-step process to generate a set of standardized products that culminate in a focused, succinct, and meaningful communication of potential drivers on a given stock. The four steps include 1) focusing on priority stocks for conducting ESPs, 2) grading a set of metrics and evaluating processes to identify vulnerabilities throughout the life history of the stock, 3) testing a suite of indicators for potential inclusion in the stock assessment model, and 4) reporting a set of standardized products that are integrated within the stock assessment process. This process effectively and efficiently communicates the results of the ESP to fisheries managers, stakeholders, and the public (Shotwell et al., *In Review*).

1.1. Challenges

When first initiating an ESP, a baseline set of stock measures are evaluated to determine vulnerabilities in the life history for a particular species or stock. Generally, this initial information is available from a set of national initiatives, such as climate vulnerability assessment (Morrison et al., 2015), stock or habitat assessment prioritization (Methot, 2015; NMFS, 2011), and productivity susceptibility analysis (Patrick et al., 2010). The majority of these national metrics are limited to one or two life history stages rather than a complete synopsis of the life cycle model. For some metrics (e.g., depth range, habitat specificity), this lack of detail can be misleading when identifying the potential vulnerability for the stock survival. For this reason, the ESP contains a supplemental ecosystem processes section that provides more information throughout the life cycle of the stock to highlight bottlenecks and to pinpoint mechanisms potentially causing the vulnerability identified in the baseline measures. This supplemental section ultimately leads to more informed indicators for subsequent evaluation in the ESP. However, collating full life cycle information can be challenging given the local scale and specific deliverables of many research projects. Furthermore, even though many ecosystem, habitat, and climate data sets are available to create potential indicators for ESPs, they lack the necessary stock-specific elements for inclusion in the stock assessment models. Indicators often suffer from being either too narrowly defined by specific research project goals to characterize a stock at the population level, or indicators representing a large marine ecosystem are too broadly defined to relate to characteristics of stock-specific life stages and habitats. In the former case, the indicator may correctly capture the important aspects of a species life history under study, but it would be limited by the spatial extent of the project. In the latter case, the indicator may adequately capture the dynamics of the ecosystem, but it may include regions that the stock does not inhabit, and therefore include processes that the stock did not experience. Some attempts have been made to restrict environmental indices to fisheries management areas to

capture the spatial extent of management, but this too, may over- or under-represent the experience of a given stock within that management area.

1.2. Purpose and goals

Here we use the synoptic nature of the GOA IERP Synthesis (Ormseth et al., 2019) to overcome some of these challenges and demonstrate the added value of the full life history information for use within the ESP framework. We first create a set of life history tables to capture what is known from the literature and stock assessments and provide the baseline metrics that are currently generated for an ESP (e.g., Shotwell et al., 2019a). Based on the combined products in the GOA IERP Synthesis (Ormseth et al., 2019), we aim to complete two primary goals, 1) generate stock-specific life history narratives that can be directly used within the supplemental ecosystem processes section of an ESP, and 2) utilize the information in the narratives to create a methodology for informing indicators to further evaluate within the ESP. We organized the life history narratives by three distinct categories: distribution, phenology, and condition. The distribution of the stock by life stage can be paired with habitat predictor variables to inform on thresholds that influence stock tolerance and vulnerability in any given life stage. The timing or phenology of the successive life stages can be compared to the seasonal climatology of environmental data to determine match/mismatch with resources that may influence survival. Finally, the condition of the stock by life stage can provide insight as to the mechanisms underlying energy allocation strategies. We will then use information from these three categories to refine a potential indicator to create ontogenetically informed indicators that reflect the life experience of the stock. We will compare the informed indicators to an uninformed version of that indicator that is typically available at the large marine ecosystem level.

We demonstrate the benefits of these methods with a case study using the five focal species of the GOA IERP: sablefish (*Anoplopoma fimbria*), walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*), and Pacific ocean perch (*Sebastes alutus*). Taken together, this functional grouping of species account for the vast majority of the groundfish biomass in the GOA (Aydin et al., 2007; Gaichas and Francis, 2008; Gaichas et al., 2011) and include species of high biomass (arrowtooth flounder and walleye pollock; A'mar et al., 2008; Spies et al., 2019; Dorn et al., 2020), high commercial value (e.g., sablefish; Sumaila et al., 2007; Goethel et al., 2020; Fissel et al., 2020) and high trophic connectivity (e.g., arrowtooth flounder; Aydin et al., 2007; Marsh et al., 2012, Marsh et al., 2015; Doyle et al., 2018), as well as species with widespread distribution across habitats on the continental shelf (Pacific cod; Baker and Hollowed, 2014), and across the outer shelf and slope (Pacific ocean perch; Hanselman et al., 2001; Conrath and Knoth, 2013). The life history strategies of these species span a wide range of opportunistic to selective foragers, mesopelagic to benthic adult habitat along the continental shelf to slope, nearshore to offshore juvenile habitat along the continental shelf, slow to fast growth rates, and a short to long lifespan. A variety of life history strategies have evolved to tolerate various environmental conditions, and specific population response to the same climate event may be different depending on the strategy (Yatsu et al., 2008). Understanding the fluctuations of these five species in concert allows identification of successful strategies given a particular set of ecological conditions. Ultimately, the refinement and evolution of this multi-species and multi-life-stage approach should result in better informed short- and long-term fisheries management by facilitating tactical responses to emerging environmental change (Shotwell et al., 2014; Cunningham et al., 2018).

2. Methods

Throughout the GOA IERP, background life history information was

collected on the five focal species regarding various ecological classification categories to generate a synthesis of what was known prior to the integrated program (see Pirtle et al., 2019 for more details). This initial collection effort was then supplemented here through a variety of process studies, standardized surveys, laboratory experiments, and regional reports (Table 1). Further details for these data sources are provided below.

Table 1

Data sources for ecological classification tables, baseline initiative metric data, distribution, phenology, and condition for the five focal species.

Title	Description	Years	Extent
EcoFOCI Spring Survey	Shelf larval survey in May-early June in Kodiak to Unimak Pass using oblique 60 cm bongo tows, fixed-station grid, catch per unit effort in numbers per 10 m ²	1978 - present	Western GOA
AFSC Ecosystem Survey	Shelf and slope age-0 summer ecosystem survey during June and July using Nordic and CanTrawl surface trawls	2010–2017	Eastern GOA
ADF&G Large Mesh Survey	Bottom trawl survey of crab and groundfish on fixed-grid station design using eastern otter trawl	1988–2018	Western GOA to Aleutians
AFSC Bottom Trawl Survey	Bottom trawl survey of groundfish in June–August, using Poly Nor [®] Eastern trawl on stratified random sample grid, catch per unit of effort in metric tons	1984 - present	Gulf of Alaska
NOAA Coral Reef Watch Program	5 km Satellite Coral Bleaching Heat Stress Monitoring Product Suite Version 3.1, derived from CoralTemp v1.0. product	1985 - present	Global
ROMS/NPZ Model Output	Coupled hydrographic Regional Ocean Modeling System and lower tropic Nutrient-Phytoplankton-Zooplankton dynamics model	1996–2018	Gulf of Alaska
Essential Fish Habitat Models	Habitat suitability MaxEnt models for describing essential fish habitat of groundfish and crab in Alaska, EFH 2016 Update	1991–2013	Alaska
RECA Energetics Database	Compositional data and associated analyses by the Recruitment Energetics and Coastal Assessment (RECA) Program, AFSC on multiple platforms	1997 - present	Alaska
Fish Life History Database	Life history information for species in eastern Bering Sea, Aleutian Islands, and Gulf of Alaska federal management areas (https://access.afsc.noaa.gov/reem/LHWeb/Index.php)	various	Alaska
Ichthyoplankton Information System	Information on fish eggs and larvae collected in the northeast Pacific Ocean, Bering Sea, Chukchi Sea, and Beaufort Sea (https://access.afsc.noaa.gov/ichthyo/index.php)	various	Alaska
FishBase	Access to summary information on fish life history, distribution, and various ecosystem and socioeconomic factors (http://www.fishbase.org/search.php)	various	Global

2.1. Data

Supplemental information for the first year of life was derived from ecosystem surveys run by the Alaska Fisheries Science Center's (AFSC) Recruitment Processes Alliance (RPA) and data from the GOAIERP (Table 1). Data pertaining to the larval life history stage were primarily collected from the Western Gulf of Alaska Survey (Kodiak west to Unimak Pass) during late spring (May to early June) from 1978 to 2017. Larvae of a variety of species were collected in a bongo net towed obliquely and a neuston net towed at the surface. Catch-per-unit-effort (CPUE) was measured in numbers per 10 m² for the bongo tows and 1000 m³ for the neuston tows (Matarese et al., 2003). Young-of-the-year or age-0 samples of fish and invertebrates were sampled during the summer in the eastern GOA by the AFSC Ecosystem Assessment Survey from 2010 to 2017 (Table 1; Strasburger et al., 2017, 2018). However, standardization for samples of fish from this survey has not yet been applied to the catch estimates due to the differences in selectivity between the nets used throughout the sampling period. Data for early stage juveniles through adult stages were consistently available from standardized bottom trawl surveys and inshore fish surveys using a variety of demersal gear types (Pirtle et al., 2019) (Table 1). The AFSC has conducted both bottom trawl and longline surveys since the 1980s and the information is used for the majority of groundfish stock assessments in Alaska (e.g., Hanselman et al., 2019). Length composition data are available for the majority of species in the groundfish fishery management plan (FMP; <https://www.npfmc.org/wp-content/PDFdocuments/fmp/GOA/GOAfmfp.pdf>). Age and weight are also available for otoliths taken during the bottom trawl and longline surveys. Environmental data used in this study were obtained from both remote sensing and ocean model output (Table 1). Daily sea surface temperatures (SST) from the NOAA Coral Reef Watch Program (Skirving et al., 2020) are served through the ERDDAP maintained by NOAA CoastWatch West Coast Regional Node and Southwest Fisheries Science Center's Environment Research Division (Simons, 2019). High-resolution regional ocean modeling system (ROMS) and nutrient-phytoplankton-zooplankton (NPZ) output were generated from the model described in Coyle et al. (2019) and summarized from various publications (e.g., Laman et al., 2017; Gibson et al., 2019) derived from this model data. Other supplementary data sources were provided through personal communication, ESR contributions, published reports, and peer-reviewed papers.

2.2. Comprehensive life history table

We expanded the original early juvenile life history and ecological classification table from Pirtle et al. (2019) to include all major developmental life history stages for each of the five focal species. Information for this comprehensive table was primarily derived from published literature, stock assessments, and online databases (Table 1). Life history stages started with the recruit stage which we defined as the age or size when a stock is first encountered in the survey or fishery and all ages thereafter. The remaining life history stages describe major developmental breaks from spawning through the pre-recruit stage. Following the life history stage column, we streamlined the rest of the table column organization to reflect the major characteristics of each stock along six primary categories that were selected to capture the potential biophysical processes that could potentially modulate survival at each life stage. The habitat and distribution category provides information on general spatial location and depth as well as primary substrate associations. Phenology includes information on seasonality (which months) and length (number of weeks) for each life stage within the first year of life as well as first age of capture by surveys or fisheries, and movement of the juvenile and adult stages. The age, length, and growth category includes parameter values and general statistics derived from the stock assessment and ecosystem surveys where available and size ranges for each life stage. Energetics consists of information on fecundity, temperature and salinity thresholds, and energy density regulation. Diet provides

general categories of primary prey fields for each life stage. Predators, competitors, and associations list the main species influencing each life stage where available (P = predators, C/A = competitors and/or associations). Reference numbers are specific to each table and listed as stock-specific subsections within the literature cited.

2.3. ESP metric panel

Baseline data for the ESPs consist of information gathered through a variety of national initiatives that were conducted by AFSC personnel in 2015 through 2016 (Shotwell et al., In Review). These include (but are not limited to) stock assessment prioritization (Methot, 2015), habitat assessment prioritization (McConnaughey et al., 2017), climate vulnerability analysis (Spencer et al., 2019), productivity susceptibility analysis (Ormseth and Spencer, 2011) and stock assessment categorization (Lynch et al., 2018). The resulting synthesis included information from the main stock assessment and published research papers or reports for each managed species. This information serves as the starting point for developing the ESP metric panel (e.g., Shotwell et al., 2019b; Fedewa et al., 2020) for GOA groundfish and crab FMPs as well as stocks in the Bering Sea and Aleutian Islands. We provided information on the baseline metrics from the national initiative exercises. A panel of the metrics was produced following the ESP framework (e.g., Shotwell et al., 2019a) and was used to identify initial vulnerability and resilience traits for each stock over a wide variety of categories. We followed the definitions for these categories within each of the national initiatives conducted for the Alaska groundfish and crab stocks (Methot, 2015; McConnaughey et al., 2017; Spencer et al., 2019; Ormseth and Spencer, 2011; Lynch et al., 2018). The categories range from specific parameter values from a stock assessment (e.g., recruitment variability, natural mortality, growth rate) to categorical scores from a vulnerability assessment (e.g., reproductive strategy, habitat specificity, ecosystem value).

2.4. Supplemental ecosystem processes evaluation

The baseline metric panel only provides limited detail by life history stage. We can enhance the interpretation of these metrics by providing detailed life history information along the categories of distribution, phenology, and condition. Supplemental information allows for additional insight on the potential vulnerabilities and resilience at specific life stages and assists in better identification of bottlenecks throughout the life history of the stock.

2.4.1. Distribution

A suite of habitat variables can be used to predict the distribution of the stock by life history stage. An update to the Essential Fish Habitat (EFH) for Alaska groundfish included models and maps of these species habitat-related distributions and density (Rooney et al., 2018) for several life history stages from AFSC bottom trawl surveys of older juveniles and adults and Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) midwater net surveys of pelagic early life history stages (Table 1). During the second phase of the GOAIERP, a set of habitat distribution models were generated for the settled juvenile and adult life history stages, including an early juvenile life history stage not included in the EFH models. GOAIERP habitat distribution models of the five focal species used maximum entropy methods (Phillips et al., 2006) to combine inshore and offshore fish survey data and a more comprehensive suite of benthic terrain, substrate, and biophysical habitat metrics, extending the first set of GOAIERP habitat distribution models developed by Pirtle et al. (2019). Additional data were also included from the middle and upper trophic level component survey sampling of the GOAIERP (Moss et al., 2018; Ormseth et al., 2018). Here we combine the pelagic larvae life stage of the EFH update with the early juvenile, late juvenile, and adult stages of the second phase GOAIERP models to include all life history stages with sufficient data of the five

focal species and the enhanced habitat metric suite. Length-based life stage breaks were determined for the larval, early juvenile, late juvenile, and adult stages using information from the EFH update and the Pirtle et al. (2019) study. The larval stage break was designated in the sampling protocol (larval stages were collected using neuston and bongo nets), while the juvenile to adult stage break was based on the maximum length of immature individuals recorded in the bottom trawl survey. The juvenile category was further split into two stages to differentiate between juveniles in the nursery areas versus juveniles transitioning to the adult habitat (Pirtle et al., 2019). This early juvenile to late juvenile stage break was based on the approximate first size observed in the beach seine or bottom trawl survey samples. We provide model output on the depth ranges, percent contribution of predictor variables, sign of directional deviation from the mean predictor value, and associated maps for each stage of the five focal species.

2.4.2. Phenology

The timing of different life stages can also be examined seasonally to understand match or mismatch with both physical and biological properties of the ecosystem (Doyle et al., 2019). We collected summary information by month for each life stage that could potentially manifest a seasonal dependence. Information on these life stages was gathered from the EcoFOCI data (Table 1) and restricted to the core sampling area for consistency across years. Data from the juvenile and adult stages were only consistently available from summer bottom trawl and long-line surveys and thus did not contain observations from other seasons. Physical and biological habitat indices were derived from a coupled 3 km resolution ROMS and NPZ model originally developed during the GOA IERP and used in the EFH Update (Laman et al., 2017; Rooney et al., 2018). These environmental and ecosystem indices were averaged over all years by month of the model hindcast (1997–2012) to create a seasonal climatology of the different indices. We provide graphic representations of the seasonally dependent observational data overlaid on the physical and biological indices for the five focal species.

2.4.3. Condition

Information on body composition (wet mass) for percent lipid, percent protein, and energy density by size can be used to understand shifts in energy allocation through the life history stages. In some species, lipid content and energy density can decrease dramatically during transition phases indicating a clear cost during the transition. Generally, protein synthesis remains constant as fish are growing rapidly. High variability in percent lipid or protein content among individuals can indicate susceptibility to variable environmental conditions. Identifying sections of the life history when this variability may occur should highlight a potential bottleneck when environmental conditions could influence survival. Body composition data for juvenile life stages of several of the focal species have been used to understand energy allocation strategies under controlled laboratory temperatures (e.g., Sreenivasan and Heintz, 2016). Here we expand on these studies by compiling body composition for percent lipid and protein data from wild-caught fish for the five focal species and summarizing by size with associated size-based life stage transitions developed from the comprehensive life history tables.

2.5. Informed indicators

The three categories of supplemental information can be used to refine potential indicators to more appropriately reflect the life experience of the stock. We first used the habitat distribution model information to mask the spatial extent for each life history stage for the five focal species. The stages created from available data were larval, early juvenile, late juvenile, and adult. Egg data were limited or non-existent for four of the five focal species and habitat distribution models were not created; therefore, we do not include the egg stage in this part of the analysis. Life stage masks were generated from the core habitat area of

the species habitat distribution models, which is defined as the upper 50th percentile of the probability of predicted habitat area (Simpson et al., 2017). EFH in Alaska is defined as the upper 95th percentile of the predicted habitat area from habitat distribution models and the core area has a reduced spatial extent (Laman et al., 2017; Simpson et al., 2017). Extraction tools were applied in ArcGIS (version 10.2.1, ESRI) to first create a raster of the core habitat area by life stage from the habitat distribution model rasters and then each life stage raster was converted to a polygon shapefile of the core habitat for the five focal species.

The most important explanatory variables from models describing the habitat distribution of the five focal species were often related to temperature for the majority of life history stages evaluated (Rooney et al., 2018; Pirtle et al., 2019). We, therefore, used the life stage masks to extract data from two temperature datasets, SST and bottom temperature (BT; generated from the model described in Coyle et al., 2019). Complete years of data were available from 1986 to 2020 for the SST data and from 2000 to 2018 for the BT data. The SST dataset was applied to the pelagic larval stage, while the BT dataset was applied to the benthic stages of each species (species-dependent but typically early juvenile, sub-adult, and adult). We first used a point-in-polygon operation conducted in R to extract the temperatures for only those gridded locations that fell within the stage-specific core habitat polygons for each species from the habitat distribution models. We then used information from the phenology synthesis to refine the extracted daily temperature values to only the months that related to a given life stage (e.g., larval time period for a stock extends from April through May). The daily temperature values were then averaged over a given species- and life stage-specific seasonal range. Finally, we used information on energy allocation strategies combined with information from the comprehensive life history tables on temperature thresholds to identify the most critical life stages that could potentially limit survival. For example, a narrow preferred temperature range in the nearshore environment combined with an energetic cost to settlement between the early and late juvenile stages would suggest a bottleneck during that life history stage transition. Indicators from these two life stages may be potentially more important to monitor than other life stages. This process using distribution, phenology, and condition produced the potential temperature indicators for each focal species and we compared these indicators to non-informed annual (no seasonal range) time series of SST and BT over the GOA. The non-informed time series covered the full extent of the GOA where depths were shallower than 1000 m.

3. Results

Ecological information was summarized in the comprehensive life history tables according to the primary life history stages for the five focal species along the six major categories with associated references where possible (Table 2a–e). The baseline ESP metric panel was generated using the national initiative data for the five focal species and rescaled by using a percentile rank for the stock relative to all other stocks in the Alaska groundfish fishery management plan (FMP) (Fig. 1). We organized the metric panel with ecosystem variables followed by socioeconomic variables (three bottom variables). Within the ecosystem category we first listed variables with estimated values followed by variables with categorical scores (starts with Dispersal ELH or early life history). These baseline panels demonstrate the differences between the productivity parameters of these stocks, which emulate the reasoning behind the initial selection of these five species as the focal point for the GOA IERP. Additionally, each stock contained some metrics that fell into the very high vulnerability category. Most notably, the highest values were recruitment variability (coefficient of variation for recruitment from stock assessment estimates) and other external stressors (e.g., predators) for sablefish, recruitment variability for pollock, narrow depth range and top-down ecosystem value (change in this major predator would impact many other managed stocks) for Pacific cod, spawning duration for arrowtooth flounder, and temperature sensitivity,

Table 2a

Ecological information by life history stage for Alaska sablefish, please refer to Comprehensive Life History Table section (2.2) and Life History Narrative (3.1.1) for more details. Subscripts are references, please see Note below table.

Stage	Habitat & Distribution	Phenology	Age, Length, Growth	Energetics	Diet	Predators, Competitors & Associations
Recruit	Shelf edge, slope, gullies (>200 m), GOA to Bering, benthic ₍₁₈₎	First recruit to survey and fishery age 2, high movement (10–88%) ₍₁₈₎	Max: 73yrs _(18,19,28) , 134♀/138♂ cm Average: 12 yrs L _{inf} = 80♀/68♂ cm, K = 0.22♀/0.29♂	Low conversion efficiency, low metabolic rate ₍₂₁₎	Opportunistic, euphausiids, pol/cod, capelin, herring, squid, jelly _(12,18)	P: Sperm whales, orca, fisheries, C/A: slope groundfish ₍₁₈₎
Spawning	Shelf break ₍₁₎ , deep water pelagic	Winter-spring, batch spawner, peak March, 25 wks, high production _(1,26,17)	1st mature: 5.5 yr, 50%: 6.6 yr/65 cm ♀, 5 yr/57 cm ♂ _(17,18) , females > males	Oviparous, high fecundity (120–1000·10 ³) eggs, Skip-spawning _(1,17,18)	Opportunistic, euphausiids, pol/cod, capelin, herring, squid, jelly _(12,18)	P: Sperm whales, orca, fisheries, C/A: slope groundfish ₍₁₈₎
Egg	Slope (>200–400 m), sink to deeper depths, negatively buoyant ₍₁₎	Late winter to early spring, 10 wks peak egg to peak larvae ₍₁₇₎	Egg size: 1.8–2.2 mm, large egg size ₍₁₇₎	Max survival to hatch, 34–35 ppt, 4–6.6 °C (lab) ₍₂₂₎	Yolk	
Larvae	Slope (>200–600 m) (hatch to yolk-sac), epipelagic over shelf and slope, 160 km offshore _(1,2,7,17)	Late spring and summer, peak end May, 12 wks, epipelagic _(7,16,17,19)	10–80 mm SL _(17,16) , 1.2 mm/day, develop as obligate neuston _(7,10,16)	Growth threshold 22 °C, optimum 12–16 °C (lab) ₍₉₎	copepod nauplii, nauplii, small copepods, small and large copepods _(1,29)	C/A: larval cottids, hexagrammids, wrymouths, non-obligate neustonic taxa ₍₇₎
YOY	Shelf, slope neuston and near surface (upper 10–20 cm of water column) _(1,10,17, 32,33)	No marked transition time to stage, move to nearshore _(1,19)	60–230 mm FL (120 mm avg, neustonic), rapid growth, 1.2 mm/day _(10,32,33)	Upper thermal limit near upper limit survival ₍₉₎ , absence lipid regulation ₍₂₃₎	Euphausiids, pelagic tunicates, other crustaceans, larval fish _(1,10)	P: Pomfret, Coho and chinook salmon ₍₃₁₋₃₃₎ , seabirds, C/A: active inshore migration ₍₁₎
Juvenile	Nearshore (6–214 m), inlet, bay, fjord, strait, mixed mud, soft, proximity to rock _(3,4,6)	Late summer-fall, diel pelagic feeding excursions _(4,30)	300–400 mm after second summer, age 2+ yrs ₍₂₅₎		Herring, smelts, salmon remains, jellies ₍₃₀₎	P: Salmon, halibut _(12,31) , seabirds, C/A: macroalgae, sponge, anemone, whip, basket star, eelgrass, shelf groundfish _(3, 12,15)
Pre-Recruit	Nearshore, shelf (10–207 m), inlet, bay, fjord, strait, mixed mud, soft, proximity to rock _(3,4,6,8)	Offshore movement begins after 2nd summer ₍₂₅₎	<600 mm FL ₍₅₎ , age 2+ yrs ₍₁₀₎		Euphausiids, shrimp, pollock, crustaceans, fish, cephalopods, jellies, salmon _(12,13,14)	P: Salmon, halibut _(12,31) , seabirds, C/A: sponge, whip, sea pen, coral, basket star, anemone, shelf groundfish _(3,12)

Note: Subscripts in table correspond to the following citations in sequential order 1. Kendall and Matarese (1987), 2. Wing and Kamikawa (1995), 3. Carlson et al. (1982), 4. Blackburn and Jackson (1982), 5. Low and Marasco (1979), 6. Haight et al. (2006), 7. Doyle et al. (1995), 8. Wespestad et al. (1978), 9. Sogard and Olla (2001), 10. Sigler et al. (2001), 11. McFarlane and Beamish (1992), 12. Yang and Nelson (2000), 13. Yang et al. (2006), 14. Sturdevant et al. (2009), 15. Murphy et al. (2000), 16. Rugen (1990), 17. Doyle and Mier (2012), 18. Hanselman et al. (2014), 19. Doyle and Mier (2016), 20. Shotwell et al. (2014), 21. Sullivan and Smith (1982), 22. Alderdice et al. (1982), 23. Sogard and Spencer (2004), 24. Sogard and Olla (2003), 25. Rutecki and Varosi (1997), 26. Mason et al. (1983), 27. Wing (1997), 28. Echave et al. (2012), 29. Grover and Olla (1990), 30. Coutre (2014), 31. Wing (1985), 32. Strasburger et al. (2017), 33. Strasburger et al. (2018).

spawning cycle and spawning duration for POP. However, there are relatively few stage-specific metrics and the quality of the data declines as the metrics become categorical (near the middle of the panel) where there is less information regarding spawning, early life distribution, settlement timing, habitat preferences, predator/prey requirements, and ecosystem value. This dearth of information highlights the need for a supplemental ecosystem processes section to elucidate where the potential vulnerabilities may be for these stocks and may highlight areas to concentrate further research.

3.1. Life history narratives

We provide stage-specific information along the categories of distribution (Fig. 2a–e), phenology (Fig. 3a and b), and condition (Fig. 4a–e) for the five focal species. We developed a life history narrative combining the information in the comprehensive life history table and the three stage-specific categories to identify mechanistic linkages with key ecosystem indicators for each species. Habitat variables used to predict the distribution of the stock by life history stage in the habitat suitability models provide insight on the preferred properties of suitable habitat (Table 3, Fig. 2). The timing or phenology of the pre-settlement life stages along with feeding versus spawning of the post-settlement stages can be examined to understand match or mismatch with both physical and biological properties of the ecosystem (Table 4, Fig. 3). Finally, information on body composition, percent lipid and percent protein by size, can be used to understand shifts in energy allocation through the different life history stages (Fig. 4) and identify

potential condition bottlenecks.

3.2. Sablefish

Alaska sablefish or the northern population of sablefish, are assessed as a single population in the federal waters off Alaska from British Columbia to the Bering Sea (McDevitt, 1990; Saunders et al., 1996; Kimura et al., 1998). They have a propensity for large-scale movements (Heifetz and Fujioka, 1991; Hanselman et al., 2015) and adult sablefish are typically encountered between 200 and 1000 m along the continental slope, shelf gullies, and deep-sea canyons (Wolotira et al., 1993). Size range breaks for the habitat distribution models were developed from the literature and stock assessment reports and were determined for larval (<150 mm), early juvenile (<400 mm), late juvenile (<550 mm), and adult stages (≥550 mm) sablefish (Table 3). Highly suitable larval habitat was characterized by bottom depth (250–850 m, 38% contribution), colder surface temperature (33%), and low ocean color (a measure of primary productivity, 12%). However, the sampling for the larval stage was not synoptic for the GOA and large gaps exist between survey grids. Recent surveys in the eastern GOA show higher abundance and larger larval size relative to those captured in western GOA surveys during the same season suggesting different population pressures in the eastern survey areas (Siddon et al., 2019). Early juvenile habitat was characterized by low tidal current speed (30%), colder bottom temperature (21%), and low probability of sponge presence (11%), and less so by depth (10–260 m, 10% contribution). Depth was more important for late juvenile stage fish that were distributed deeper (135–590 m, 37%

Table 2b

Ecological information by life history stage for GOA walleye pollock, please refer to Comprehensive Life History Table section (2.2) and Life History Narrative (3.1.2) for more details. Subscripts are references, please see Note below table.

Stage	Habitat & Distribution	Phenology	Age, Length, Growth	Energetics	Diet	Predators, Competitors & Associations
Recruit	Shelf (0–300 m)	Recruit to survey and fishery ~ age 1, length 5–16 cm ₍₁₉₎	Max: 31yrs, 105♀/92♂ cm Average: 10 yrs ₍₁₉₎ L _{inf} = 65.2 cm, K = 0.3 ₍₁₉₎		Euphausiids, shrimp, copepods, juvenile pollock (<1%) ₍₁₉₎	P: Arrowtooth flounder, halibut, Pacific cod, steller sea lions, sablefish, fisheries ₍₁₇₎ C/A: shelf pelagic/benthic groundfish ₍₁₉₎
Spawning	Shelf (150–300 m, x ⁻ 200 m), Shelikof Strait/Valley _(5,9,11)	February–May, peak mid-March, 13 wks _(1,20,25)	1st mature: 3–4 yr ₍₁₁₎ , 50%: 4.9 yr/44 cm ₍₁₉₎ , ↑ size 50% to 48 since 2008 ₍₁₉₎	Oviparous, high fecundity (385–662·10 ³) eggs ₍₁₁₎ , 1.1–7.2 °C at depth ₍₁₁₎	Euphausiids, shrimp, copepods, juvenile pollock (<1%) ₍₁₉₎	P: Arrowtooth flounder, halibut, Pacific cod, steller sea lions, sablefish, fisheries ₍₁₇₎ C/A: shelf pelagic/benthic groundfish ₍₁₉₎
Egg	Pelagic; shelf (0–200 m, x ⁻ 150–200 m), Shelikof St/Valley, canyons _(2,5,6,8-11)	mid-March-April, ~2 wks _(10,11,20,25-26)	Egg size: 1.2–1.77 mm ₍₂₀₎	5.0–5.5 °C at 150–250 m depth _(10,11)	Yolk	P: Invertebrates, detritivores, pelagic fishes _(23,24)
Yolk-sac Larvae	Pelagic; shelf and coastal areas (0–200 m, primarily upper 50 m), Shelikof St _(2,3,5,6-8,10,11)	April ₍₅₎ , peak end April, 1 wk _(20,25-26)	3–5 mm SL _(2,3,5,6,8,10,11) , growth rate 0.12–0.25 mm·day ⁻¹ ₍₁₁₎	Preferred, 31.5–32.2 ppt, 3.6–7.0 °C _(8,10)	Yolk	P: Planktonic predators (zooplankton, birds, fishes) C/A: larval groundfishes _(5,6,8)
Feeding Larvae	Pelagic; shelf and coastal areas (0–200 m, primarily upper 50 m), Shelikof St _(2,3,5,6-8,10,11)	May–July ₍₅₎ , peak May, 4–5 wks _(22,25-26)	25–40 mm SL at transformation _(RACE) , growth rate 0.12–0.25 mm·day ⁻¹ ₍₁₁₎	Preferred salinity = 31.5–32.2, temperature = 3.6–7.0 °C _(8,10)	Copepod eggs & nauplii, copepodites ₍₈₎	P: Planktonic predators (zooplankton, birds, fishes), Pollock ₍₁₇₎ C/A: larval groundfishes _(5,6,8)
Juvenile	Semi-demersal; shelf, coastal areas, bays, fjords, inlets (20–30 m and >30 m with age), mixed substrate _(1,3,4,18)	Aug–Mar (1+ yr); 8–24 wks _(25,26)	25–40 mm FL (offshore) ₍₅₎ ; >40 mm SL (nearshore) ₍₅₎ ; growth sensitive to diet, competition	Energy density ↑ with length, > over slope, spatial shifts due to ± <i>C. marshallae</i>	Copepods, euphausiids ₍₁₆₎	P: Arrowtooth flounder, sablefish, cod, pollock ₍₁₇₎ C/A: juvenile groundfish, macroalgae _(12,18) , macroinvertebrates ₍₁₈₎
Pre-Recruit	Semi-demersal; shelf, coastal areas, bays, fjords, inlets, mixed substrate, mud ₍₁₈₎		>250 mm FL ₍₁₁₎ , age 2+ yrs ₍₁₀₎		Euphausiids, copepods, pollock ₍₁₆₎	P: Arrowtooth flounder (~50% < 20 cm) ₍₁₉₎ , sablefish, Pacific cod, Pollock ₍₁₇₎ C/A: juvenile groundfish, macroalgae, macroinvertebrates _(12,18)

Note: Subscripts in table correspond to the following citations in sequential order 1. Carlson (1995), 2. Favorite et al. (1975), 3. Brodeur et al. (1995), 4. Blackburn and Jackson (1982), 5. Doyle et al. (2009), 6. Doyle et al. (1995), 7. Olla and Davis (1990), 8. Kendall et al. (1987), 9. Dunn et al. (1984), 10. Kendall et al. (1994), 11. Dunn and Matarese (1987), 12. Johnson et al. (2003), 13. Abookire et al. (2001), 14. Bailey (2000), 15. Bailey et al. (1995), 16. Smith et al. (1978), 17. Yang and Nelson (2000), 18. Carlson et al. (1982), 19. Dorn et al. (2014), 20. Doyle and Mier (2012), 21. Doyle and Mier (2016), 22. Porter and Theilacker (1991), 23. Bunn et al. (2000), 24. Nielsen et al. (In Review), 25. Kendall et al. (1996), 26. Schumacher and Kendall (1995).

contribution), in areas with colder bottom temperature (23%), low tidal current (12%), and low bathymetric position index (BPI, 8%), which characterize low-lying areas (e.g., channels, gullies, and flats). Finally, depth is the primary predictor for adults (180–770 m, 89% contribution) with minor contribution (<5%) from other predictor variables. A clear ontogenetic habitat shift occurs between the early juvenile and later juvenile to adult stages with progression from nearshore bays and inlets to the colder continental shelf and slope (Fig. 2a).

Sablefish are highly fecund, early spring, deep-water spawners. They have an extended spring through summer neustonic (extreme surface) pelagic phase that culminates in nearshore settlement in the early fall of their first year when sablefish are around 300–400 mm in size (Doyle and Mier 2016; Doyle et al., 2019). The early life strategy for sablefish has been termed “extreme epipelagic” because of their association with the surface for many months (Doyle and Mier, 2016). At some point following the first winter, sablefish juveniles begin movement to their adult habitat arriving between 4 and 5 years later and starting to mature within 3–6 years (Hanselman et al., 2019). Sablefish eggs caught in bongos are in the water column from February to April when there is lower bottom temperature, lower mesoscale variability (e.g., eddies), and higher potential transport to the nearshore (Fig. 3a). Pelagic eggs in deep water over the slope and basin may provide a relatively stable environment for embryonic development as cold temperatures during winter favor slow development. Relatively large size at hatching (~6 mm) and rapid growth of larvae with good swimming ability likely confers an advantage in terms of larval feeding at the sea surface (Doyle

et al., 2019). Larvae are most abundant in neuston samples collected over the shelf and slope; as such, larval abundance information was restricted to neuston samples only. Peak abundance of larvae (May–June) coincides with advanced development of the spring peak in zooplankton production following the onset of stratification (measured by a shallowing of the mixed layer), which likely means a plentiful supply of prey (Fig. 3b). The temporal match with the onset of the zooplankton bloom suggests a need to be at the highest peak of productivity due to their non-discriminating prey selection (Deary et al., 2019). Sablefish larvae are characterized by early development of large pectoral fins to assist with swimming ability but have delayed bone-development in their jaws, potentially resulting in non-discriminating prey selection (Matarese et al., 2003; Deary et al., 2019). With the lack of overall ossification of the skeleton, pre-flexion sablefish larvae lack the rigidity in their jaw elements to quickly open and expand their mouths to suck in prey. Sablefish in this preflexion larval stage are only able to pick prey from the water and are thus restricted to prey that is small and prevalent.

Throughout the first year, larvae and age-0 fish grow very rapidly until settlement in the nearshore environment (Sigler et al., 2001). Fish from 0 to 400 mm (Fig. 4a, pre-settlement to settlement phases), have a fairly stable lipid and protein content. These fish are putting energy toward growth and not toward lipid energy storage. A potential bottleneck may occur pre-settlement as overwintering during the first year of life may incur an energetic cost that results in a change in body condition with reduced lipid content at about 200 mm that appears to be

Table 2c

Ecological information by life history stage for GOA Pacific cod, please refer to Comprehensive Life History Table section (2.2) and Life History Narrative (3.1.3) for more details. Subscripts are references, please see Note below table.

Stage	Habitat & Distribution	Phenology	Age, Length, Growth	Energetics	Diet	Predators, Competitors & Associations
Recruit	Shore to Shelf (0–500 m), depth varies by age then size ₍₂₄₎ , sublittoral-bathyal zone, move w/in, between LMEs ₍₂₄₎	Recruit to survey and fishery age-1, length 20–27 cm ₍₂₄₎	Max: 12 yrs, 147♀/134♂ cm L _{inf} = 99 cm, K = 0.17 ₍₂₇₎		Opportunistic, small on inverts, large on fish _(20, 21, 24)	P: Halibut, Steller sea lions, whales, tufted puffins, fisheries ₍₂₄₎ C/A: shelf groundfish ₍₂₄₎
Spawning	Shelf (40–290 m) _(13, 16, 24) , semi-demersal in shelf areas _(13, 15, 16) , seasonal migrations variable duration ₍₂₆₎	Winter-spring, peak mid-March, 13 wks _(1, 20, 25)	1st mature: 2 yr, 26♀/36♂cm, 50%: 4–5yr, 45–65 cm ₍₂₄₎	Oviparous, high fecundity (250–2220·10 ³) eggs _(13, 15) , range 4–6 °C _(14, 16)	Opportunistic _(20, 21)	P: Halibut, Steller sea lions, whales, tufted puffins, fisheries ₍₂₄₎ C/A: shelf groundfish ₍₂₄₎
Egg	Shelf (20–200 m), demersal, adhesive eggs _(13, 15, 17, 24)	Incubation is ~20 days, 6 wks _(14, 22)	Egg size: 0.98–1.08 mm ₍₂₈₎	Optimal incubation 3–6 °C, 13–23 ppt, 2–3 ppm dO ₂ ₍₂₇₎	Yolk is dense and homogenous	
Yolk-sac Larvae	Epipelagic, nearshore shelf, coastal, upper 45 m, semi-demersal at hatching _(13, 15, 18, 24)	Spring, peak mid May, 14 wks _(22, 29)	3–4.5 mm NL at hatch _(13, 15, 24, 28)	Hatch temperature 4.5–5.8 °C ₍₂₎	Endogenous	C/A: Share larval period with pollock ₍₁₃₎
Feeding Larvae	Epipelagic, nearshore shelf _(13, 15, 24) , 0–45 m ₍₂₄₎	Late spring, April–June ₍₂₂₎	25–35 mm SL at transformation _(3, 13, 15, 24)	1–2 weeks before onset of feeding _(28, 29)	Copepod eggs, nauplii, and early copepodite stages (Strasburger et al. 2014)	C/A: Share larval period with pollock ₍₁₃₎
Juvenile	Nearshore (2–110 m), 15–30 m peak density, inside bays, coastal, mixed, structural complexity _(1, 6, 11, 21)	Nearshore settlement in June, deeper water migrations in October _(3, 13, 15)	YOY: 35–110 mm FL ₍₂₎ , age 1+: 130–480 mm FL _(1, 3, 4, 6, 10) ; growth sensitive to temp	Energy density ↑ with length, lower in pelagic stage	Copepods, mysids, amphipods ₍₂₎ , small fish ₍₁₀₎ , crabs _(19, 21)	P: Pollock, halibut, arrowtooth flounder _(19, 20) C/A: macroalgae, eelgrass, structural inverts, king crab, skate egg case, juvenile pollock _(1, 5, 7, 9)
Pre-Recruit	Nearshore, shelf (10–216 m) ₍₄₎ , inside bays, coastal, mixed, mud, sand, gravel, rock pebble _(1, 2, 4, 6)	Age-2 may congregate more than age-1 ₍₂₅₎	Begin to mature age 2–3, 480–490 mm FL ₍₁₅₎	Energy density and condition lower than in pelagic stage	Opportunistic, benthic invert, pollock, small fish, crabs _(19, 21)	P: Pacific cod, halibut, salmon, fur seal, sea lion, porpoise, whales, puffin ₍₂₄₎ C/A: macroalgae, macroinvertebrate, king crab _(4, 5, 7, 9)

Note: Subscripts in table correspond to the following citations in sequential order 1. Abookire et al. (2001), 2. Abookire et al. (2007), 3. Blackburn and Jackson (1982), 4. Carlson et al. (1982), 5. Murphy et al. (2000), 6. Haight et al. (2006), 7. Dean et al. (2000), 8. Johnson et al. (2003), 9. Harris et al. (2005), 10. Laurel et al. (2009), 11. Laurel et al. (2007), 12. Laurel et al. (2003), 13. Doyle et al. (2009), 14. Rugen and Matarese (1988), 15. Dunn and Matarese (1987), 16. Hirschberger and Smith (1983), 17. Yamamoto (1939), 18. Hurst et al. (2009), 19. Yang and Nelson (2000), 20. Yang et al. (2006), 21. Livingston (1989), 22. Doyle and Mier (2012), 23. Doyle and Mier (2016), 24. A' mar and Palsson (2014), 25. Ueda et al. (2006), 26. Savin (2008), 27. Barbeaux et al. (2020), 28. Laurel et al. (2008), 29. Laurel et al. (2021).

maintained until the late juvenile stage at about 400 mm (R. Heintz, AFSC, pers. comm.). At lengths greater than 400 mm, where fish are maturing (i.e., a portion of fish are mature) and at lengths where fish are presumably adult (>650 mm), the percent lipid is much higher than at lengths less than 400 mm. This is likely because mature fish have a higher lipid content than immature fish. These data show that there is an ontogenetic shift that is related to how sablefish store energy and may be related to the size at which fish migrate from nearshore to offshore waters. The variability in lipid content at lengths greater than 400 mm could be attributed to some fish being mature and some being immature or skip spawning. For example, relative condition (body weight relative to length) and relative liver size (liver weight related to total weight), are higher in fish that will spawn than in skip spawning and immature female sablefish (Rodgveller, 2019). Variability could also be an effect of sex, sampling date, sampling area, and year. However, these data show a strong shift in lipid accumulation as fish grow and enter the late juvenile to adult stage. These lipid accumulation shifts suggest that the fish in the nearshore are still growing quickly with an associated high energetic cost, but as they move offshore the fish have relatively low energetic demands and can begin to allocate surplus lipid to storage with age as they grow. The juvenile nearshore stage appears to continue to be an energetically-demanding period as all surplus energy is allocated toward growth (protein). A potential alternative explanation for this pattern is that food is a limiting factor and surplus energy is not available. Later during the early offshore residence for juveniles, the energetic constraints are relieved and fish obtain surplus energy that is stored as lipid. In addition to reducing the pressure for rapid growth, the extreme increase in lipid storage may represent considerably better feeding

grounds, and/or life history constraints to increase lipid content as the fish move into the deeper depths of the adult habitat as they age.

Transport to the nearshore environment during the first year of life is thought to relieve potential vulnerability if conditions are poor (Doyle and Mier, 2016). Above average recruitment for sablefish has been associated with a more northerly winter current direction, warmer sea surface temperatures, summer upwelling favorable winds, and less freshwater discharge in the eastern GOA (Sigler et al., 2001; Coffin and Mueter, 2016). Colder than average wintertime sea surface temperatures in the central North Pacific along the North Pacific Polar Front were hypothesized to set up downstream oceanic conditions that create positive recruitment events for sablefish during their early life history (Shotwell et al., 2014). At first this may seem conflicting with the sablefish warm temperature requirements; however, the colder wintertime temperature index may represent a shifting of the polar front spatially rather than any true temperature signal. This sort of mechanism can be seen in a sea surface temperature heat map (Shotwell et al., 2014, Fig. 2), during the 1976/77 regime shift and again in the 2000s. This would imply that large ocean-scale events that translate temperature signals across domains, such as recently seen with the Warm Blob event being translated from the west coast U.S. to Alaska in 2013–2014 (Bond et al., 2015), may create these conditions that sablefish are finely tuned to exploit. The potential vulnerability in their extended pelagic phase may be limiting under average conditions, but may also be a strength under anomalous conditions where their astounding growth capacity and early swimming ability allows widespread exploitation of available resources. Also, under average conditions, enhanced transport to the nearshore environment may be critical for maintaining a base to

Table 2d

Ecological information by life history stage for GOA arrowtooth flounder, please refer to Comprehensive Life History Table section (2.2) and Life History Narrative (3.1.4) for more details. Subscripts are references, please see Note below table.

Stage	Habitat & Distribution	Phenology	Age, Length, Growth	Energetics	Diet	Predators, Competitors & Associations
Recruit	Abundant, 20–800m, most 100–300m, mesopelagic, troughs, canyons, shelf/slope ₍₂₂₎	First recruit to survey and fishery age 3, length 40 cm ₍₂₂₎	Max: 23yr, 79♀/40–63♂cm Average: 10 yrs, L _{inf} : 81.9♀/49.7♂ cm, K: 0.102♀, 0.236♂ ₍₂₂₎		Fish 15–30 cm: shrimp, capelin, euphausiids, misc fish, herring _(18,22)	P: Pacific cod, halibut, Steller sea lions, sharks, fisheries ₍₂₂₎ , C/A: shelf groundfish ₍₂₂₎
Spawning	Deep, shelf edge, mesopelagic, troughs, canyons, slope (≥300 m, most ≥400 m) _(5,13)	Jan–Apr, peak mid-January, 17 wks _(13,20,21)	1st mature: 6 yr 50%: 10–11 yr, 47♀/42♂ cm ₍₂₂₎	Oviparous, high fecundity (0.25–2.22·10 ⁶ eggs) ₍₁₃₎ , 4.2–5.4 °C ₍₅₎	Fish >40 cm: pollock, herring, capelin, shrimp, euphausiids _(18,22)	P: Pacific cod, halibut, Steller sea lions, sharks, fisheries ₍₂₂₎ , C/A: shelf groundfish ₍₂₂₎
Egg	Shelf edge, slope (most ≥400 m) ₍₅₎ , mesopelagic, troughs, canyons ₍₁₃₎	Incubation 15–20 days ₍₅₎ , peak egg - peak larval 4 wks ₍₂₀₎	Egg size: 1.58–1.98 mm, larger egg size ₍₂₀₎ , RACE)	Incubation temp is 4.3–5.4 °C	Extended lipid reserves ₍₂₁₎ , yolk is homogenous	
Larvae	Shelf edge, slope (early stage ≥400m, late stage 50 ₍₁₆₎ -200 m), mesopelagic, troughs, canyons _(5,13)	Jan–Aug _(6,16,21) , peak mid-Feb, extended, 26 wks ₍₂₀₎	3.9–26 mm SL, ascend as yolk-sac larvae _(5,13) , slow growth Jan–Apr		Possibly lipid-rich, deep water, oceanic copepod eggs and nauplii ₍₂₁₎	P: Pacific ocean perch (infrequent), other fishes ₍₁₈₎ , C/A: share larval period with Pacific halibut ₍₁₃₎
YOY	Shelf, nearshore, coastal areas _(6,13)		26–40 mm FL _(6,13)	No relation size and energy density	Large/small copepods	P: Adult arrowtooth flounder, pollock, cod ₍₁₇₎
Juvenile	Shelf, nearshore (6–200+ m), near bays, straits, coastal areas, mixed mud, sand, not gravel, near rocky _(1,2,3,4,8,12,14)	Settlement timing September ₍₆₎	ages 0–2 yrs (40–211 mm) _(4,6,7) , 0–1yr roughly 20 cm ₍₂₂₎	5–9.5 °C and 32–33 ppt (temp preference < with age) _(1,2,3)	mysids, cumaceans, euphausiids, other crustaceans _(1,19)	Adult arrowtooth flounder, pollock, cod, halibut, sablefish _(17,22)
Pre-Recruit	Nearshore, shelf (100–200+ m) ₍₁₄₎ , near bays, straits, coastal areas, mixed mud and sand, near rocky _(1,2,12)		age-2+ (200–390 mm) ₍₉₎ , females mature as young as age-3 (>400 mm) ₍₁₀₎ deeper depth with age	Energy density > with length prior to maturity	euphausiids, pollock, capelin, shrimp, (9,17,19,22)	P: Adult arrowtooth flounder, cod, sablefish, halibut _(17,22)

Note: Subscripts in table correspond to the following citations in sequential order 1. Norcross et al. (1993), 2. Norcross et al. (1994), 3. Norcross et al. (1999), 4. Abookire et al. (2001), 5. Blood et al. (2007), 6. Bouwens et al. (1999a), 7. Bouwens et al. (1999b), 8. Blackburn and Jackson (1982), 9. Knoth and Foy (2008), 10. Stark (2008), 11. Kendall and Ferraro (1988), 12. Haight et al. (2006), 13. Doyle et al. (2009), 14. Carlson et al. (1982), 15. Boeing and Duffy-Anderson (2008), 16. Bailey and Picquelle (2002), 17. Yang and Nelson (2000), 18. Yang (1993), 19. Smith et al. (1978), 20. Doyle and Mier (2012), 21. Doyle and Mier (2016), 22. Spies and Turnock (2013), 23. Bailey et al. (2008).

average level of recruitment. An individual based model (IBM) recently developed for sablefish (Gibson et al., 2019) suggested that overall connectivity from the offshore spawning sites to the nearshore nursery areas was positively correlated to sablefish recruitment over the 1996–2011 time period when there were very few high recruitment events. The strength of southerly wind over the eastern GOA from January to March appears to be an important factor in controlling the strength of this onshore transport.

3.3. Pollock

Walleye pollock (or pollock) are assessed in the central and western GOA and are managed independently of pollock in the eastern Bering Sea and Aleutian Islands. They are typically encountered between 0 and 300 m along the continental shelf (Dorn et al., 2020). Size range breaks for habitat distribution models were developed from the literature and stock assessment reports and were determined for larval (<40 mm), early juvenile (<140 mm), late juvenile (<370 mm), and adult stage (≥370 mm) pollock (Table 3). Once hatched, larvae will move to the upper 50 m (Kendall et al., 1994) and are widely distributed along the GOA shelf but are most abundant in Shelikof Strait with other hot spots on the northeast side of the Kodiak Archipelago and proximal to the Shumagin Islands (Doyle and Mier, 2016). Highly suitable larval habitat was characterized by low surface temperature (36% contribution), bottom depth (75–300 m, 29%), and low surface current speed (10%). Early stages of pollock are generally much less abundant in the eastern GOA relative to the western GOA, and there is a considerable degree of interannual variability in the eastern GOA (Siddon et al., 2019). Early juveniles are semi-demersal in nearshore areas as well as occurring in the upper 40 m in offshore areas of the continental shelf (Bailey et al.,

1989). Early juvenile habitat was more related to depth (25–295 m, 39% contribution) with average bottom temperatures (22%), low bathymetric position index (BPI, 12%), and low probability of sponge presence (9%), characterizing the early juvenile habitat as moderate temperature with low-lying areas (e.g., channels, gullies, and flats), little biogenic structure and less current. The use of the nearshore zone by juvenile pollock seems especially transitory and this habitat may serve as a stable refuge from adverse offshore conditions (Ormseth and Rand, This Issue). Late juvenile and adult preferred habitats were similar to early juvenile habitat with slight shifts in the percent contribution and the addition of the non-rocky areas in the late juvenile habitat. However, spatially, a clear ontogenetic habitat shift occurs between the larval to early juvenile stage and late juvenile to adult stages with progression from the hotspot areas in the western GOA to a fairly wide distribution along the continental shelf (Fig. 2b). The preferred habitat seems to switch from a reliance on a particular thermal environment during larval and early juvenile stages to a greater tolerance of thermal variability and instead a preference for specific physical structure, including low-gradient, low lying areas such as channels, gullies, and flats that are not rocky and within 20–300 m depth during late juvenile and adult stages.

During the early spring, GOA pollock aggregate to spawn in high densities in the GOA, with females releasing 10–20 batches of eggs over a period of weeks (Hinckley, 1990). This species is a batch spawner, with spawning duration varying from 17 to 57 days (Doyle and Mier, 2016; Rogers and Dougherty, 2019). This batch spawning is considered a “bet hedging” strategy that may mitigate vulnerability in terms of synchrony with optimal levels of larval prey (Doyle and Mier, 2016; Doyle et al., 2019). In the Shelikof region, most spawning occurs from late March to early May, although spawn timing and duration are impacted by both

Table 2e

Ecological information by life history stage for GOA Pacific ocean perch, please refer to Comprehensive Life History Table section (2.2) and Life History Narrative (3.1.5) for more details. Subscripts are references, please see Note below table.

Stage	Habitat & Distribution	Phenology	Age, Length, Growth	Energetics	Diet	Predators, Competitors & Associations
Recruit	Semi-demersal, shelf, upper slope (150–420m), 150–300m feeding, patchy local aggregations _(17,19) , stock structure, break Yakutat ₍₁₅₎	Recruit to survey and fishery age-2, shelf feeding in summer ₍₁₉₎	Max: 84yrs, 70 cm Average: 11 yr L, inf: 41.4 cm, K: 0.19, T ₀ : 0.47 _(17,18)		Euphausiids, copepod, squids, amphipods, gel filter, pteropod ₍₁₄₎	P: sablefish, Pacific halibut, sperm whales, fisheries ₍₁₇₎ , C/A: slope groundfish ₍₁₇₎
Spawning	Pelagic, shelf break (200–250 m), slope _(1,9) , 300–420m, move deeper and offshore ₍₁₉₎	Insemination in fall, fertilization 2 mo later _(17,19) , 30 wks, late production ₍₂₀₎	1st mature: 7 yr ₍₂₀₎ 50%: 9 yr, time-varying (<) ₍₁₈₎ , 26–29 cm ₍₁₇₎	Viviparous, high fecundity (10–300·10 ³) eggs ₍₂₂₎		P: sablefish, Pacific halibut, sperm whales, fisheries ₍₁₇₎ , C/A: slope groundfish ₍₁₇₎
Egg	Internal to adult ₍₁₇₎	Hatch internally ₍₁₇₎				
Larvae	Pelagic, shelf break, gully, slope, structure similar to adults, limited dispersal ₍₁₆₎	Parturition Apr–May, peak July, 24 wks _(3,9,20)	3.8–20 mm SL _(9,16)			
YOY	nearshore, inlet, bay, fjord, structure, limited dispersal, rocky outcrop, pinnacle, high relief _(3,4,5,16)		<160 mm FL _(3,4,5) , < protein synthesis at 30 mm, > energy stores	Energy density > rapidly with length	Planktivorous, euphausiids, copepods _(2,6,17)	P: salmon, pomfret
Juvenile	nearshore, shelf (37–230 m), rock, boulder, cobble, mixed sand, complexity _(3,8,11)		Settle by age-1, (<250 mm FL _(1,2,3) , higher growth warm temp than age-1, lipid > protein < with temp	Energy density lower than YOY, strategy shift for settlement	Planktivorous, euphausiids, copepods _(2,6,17)	P: halibut, arrowtooth ₍₁₄₎ , C/A: pollock, macroalgae, sponge, anemone, coral, whip, star, brachiopod, bryozoan _(3,4,5,7,11)
Pre-Recruit	shelf (6–225 m) ₍₁₎ , nearshore, rock, boulder, mixed hard and soft, complexity _(2,5,7,8,11, 12)		ages 3–5, mature by age-6, >250 mm FL _(1,2,3,12) , higher growth cool temp than age-0, lipid < protein > with temp	Energy density starts to increase at maturity	euphausiids, copepods, chaetognaths, larvaceans, amphipods _(2,6,13)	P: halibut ₍₁₄₎ , seabirds, other rockfish, salmon, lingcod ₍₁₇₎ , C/A: sponge, coral, anemone, whip, brachiopod, basket star _(5,7,11)

Note: Subscripts in table correspond to the following citations in sequential order 1. Rooper and Boldt (2004), 2. Boldt and Rooper (2009), 3. Carlson and Haight (1976), 4. Carlson and Straty (1981), 5. Carlson et al. (1982), 6. Rooper et al. (2012a,b), 7. Rooper et al. (2007), 8. Krieger (1993), 9. Doyle et al. (2009), 10. Rooper et al. (2012a,b), 11. Williams et al. (2010), 12. Haight et al. (2006), 13. Yang (1993), 14. Yang and Nelson (2000), 15. Palof et al. (2011), 16. Kamin et al. (2014), 17. Hanselman et al. (2013), 18. Hulson et al. (2014), 19. Love et al. (2002), 20. Doyle and Mier (2012), 21. Doyle and Mier (2016), 22. Leaman (1991).

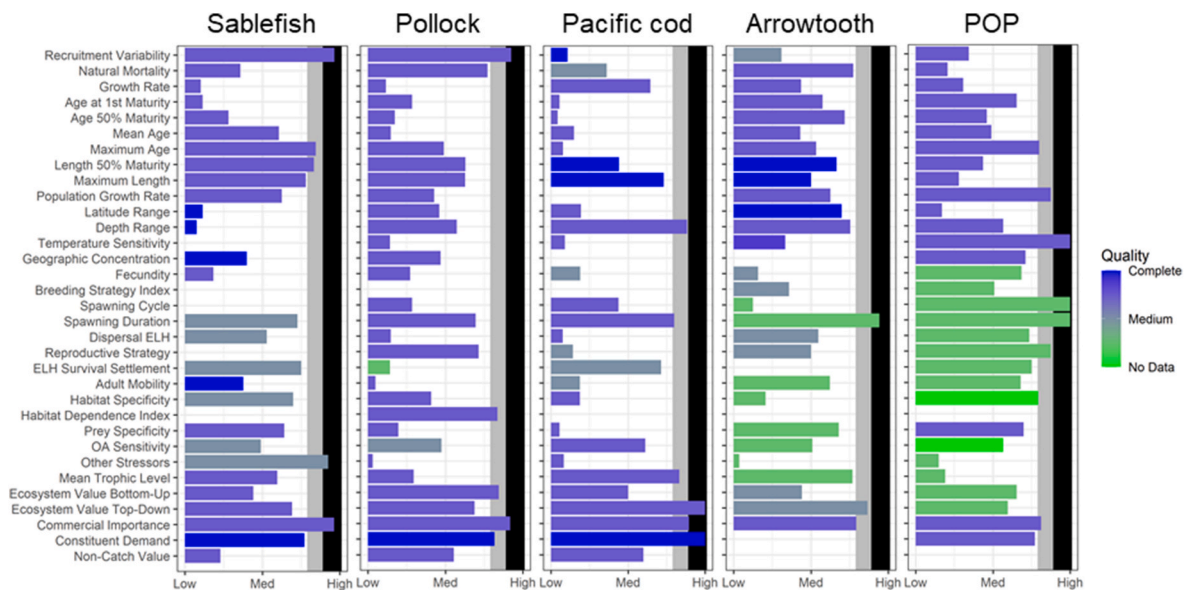


Fig. 1. Baseline metrics for five focal species graded as percentile rank over all groundfish in the fisheries management plan. Black bar indicates 90th percentile, gray bar indicates 80th percentile of all groundfish measures. Higher rank values indicate a vulnerability and color of the horizontal bar describes data quality of the metric from no data (green) to complete data (blue).

spawner age structure and water temperature (Rogers and Dougherty, 2019). Pollock eggs are pelagic and vulnerable to physical processes that influence transport and buoyancy, which may result in the eggs sinking to the seafloor (M. Wilson, pers. comm.) as well as being vulnerable to predators in the plankton (Brodeur et al., 1996). Peak egg abundance estimates over the season occur prior to the shallowing of the mixed

layer and onset of stratification (Fig. 3a). Larvae hatch from the eggs after incubating for approximately 14 days at about 3 mm in length (Blood et al., 1994). Peak abundance of newly hatched larvae (less than 5 mm) corresponds to an increase in water temperature but prior to the peak temperatures and the onset of the zooplankton bloom (Doyle and Mier, 2016). Once feeding is initiated after yolk-sac absorption, larval

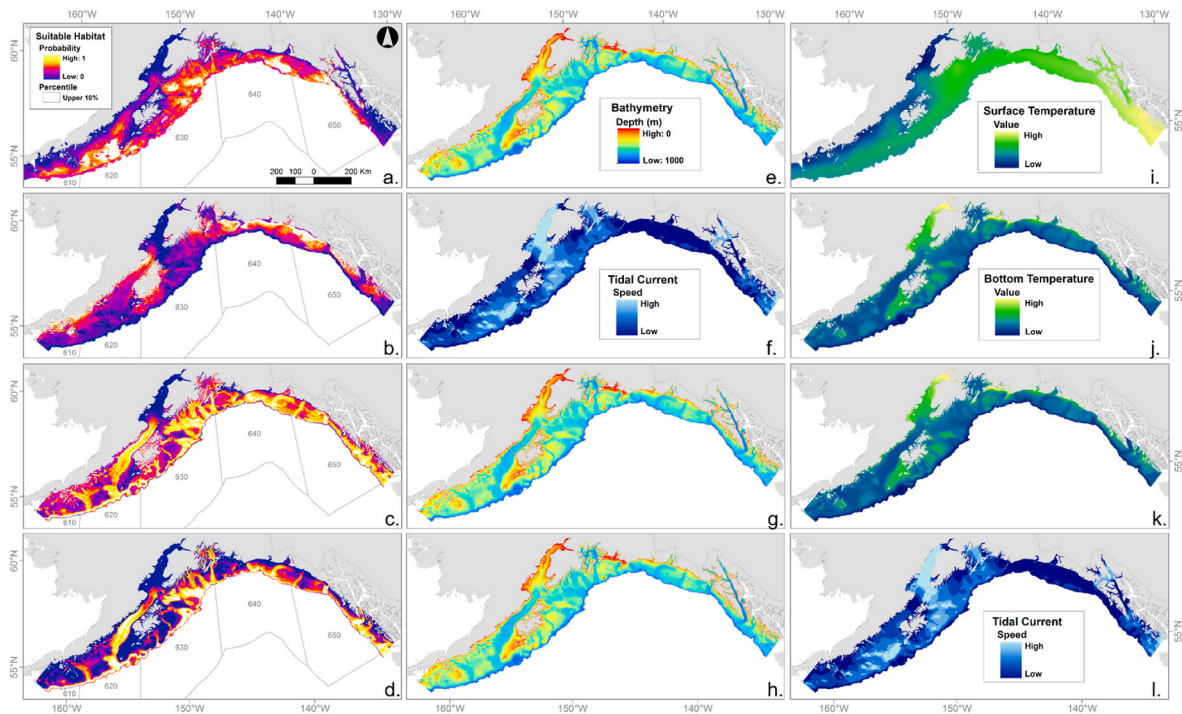


Fig. 2a. Sablefish probability of suitable habitat by life stage (a = larval, b = early juvenile, c = late juvenile, and d = adult) with corresponding predictor habitat variables representing the highest (e,g,h = depth, and f = tidal current speed) and second highest contribution (i = surface temperature, j,k = bottom temperature, and l = tidal current speed). Upper 10 percentile of suitable habitat is shown in white within the probability of suitable habitat range (yellow to purple).

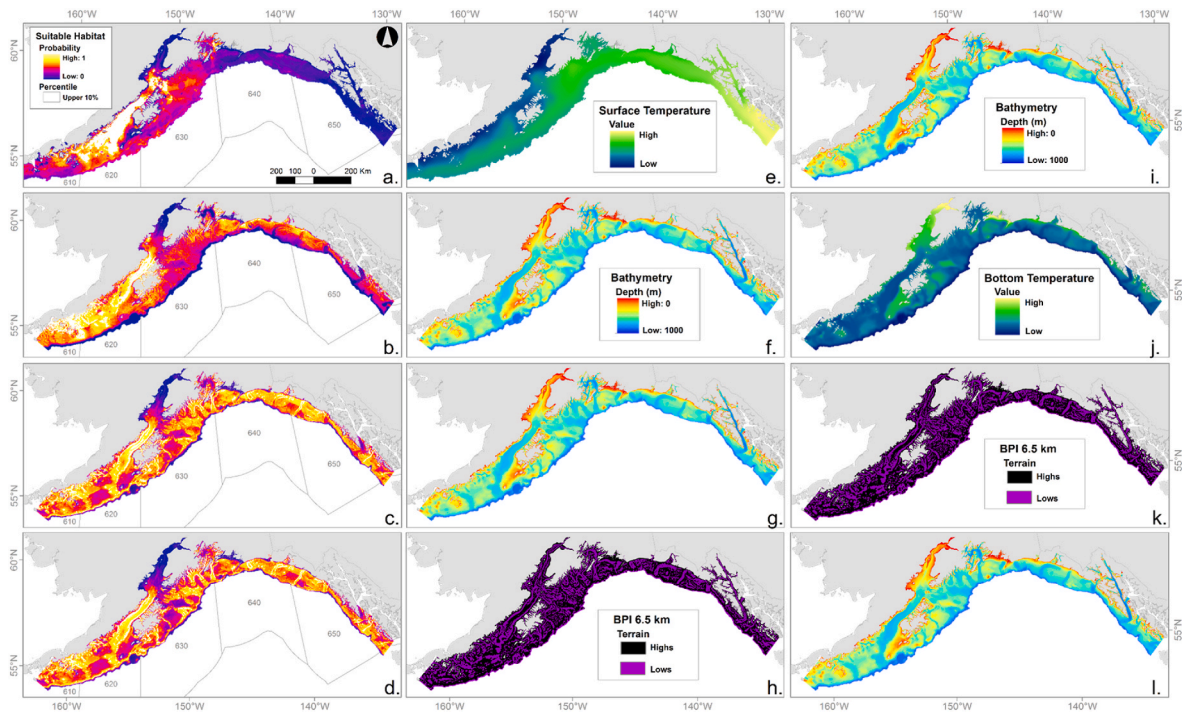


Fig. 2b. Pollock probability of suitable habitat by life stage (a = larval, b = early juvenile, c = late juvenile, and d = adult) with corresponding predictor habitat variables representing the highest (e = surface temperature, f,g = depth, and h = bathymetric position index) and second highest contribution (i,l = depth, j = bottom temperature, and k = bathymetric position index). Upper 10 percentile of suitable habitat is shown in white within the probability of suitable habitat range (yellow to purple).

pollock predominantly feed on copepod nauplii (Kendall et al., 1987; Strasburger et al., 2014), and they may be susceptible to food-limited growth and subsequent increased predation mortality (Canino et al., 1991). The degree of match or mismatch of first-feeding larval pollock

with optimal zooplankton prey production may thus be critical for larval survival and dependent on fluctuations in the thermal environment and onset of the spring plankton blooms (Fig. 3b). At 25 mm standard length, which corresponds to an age greater than 60 days, GOA pollock begin

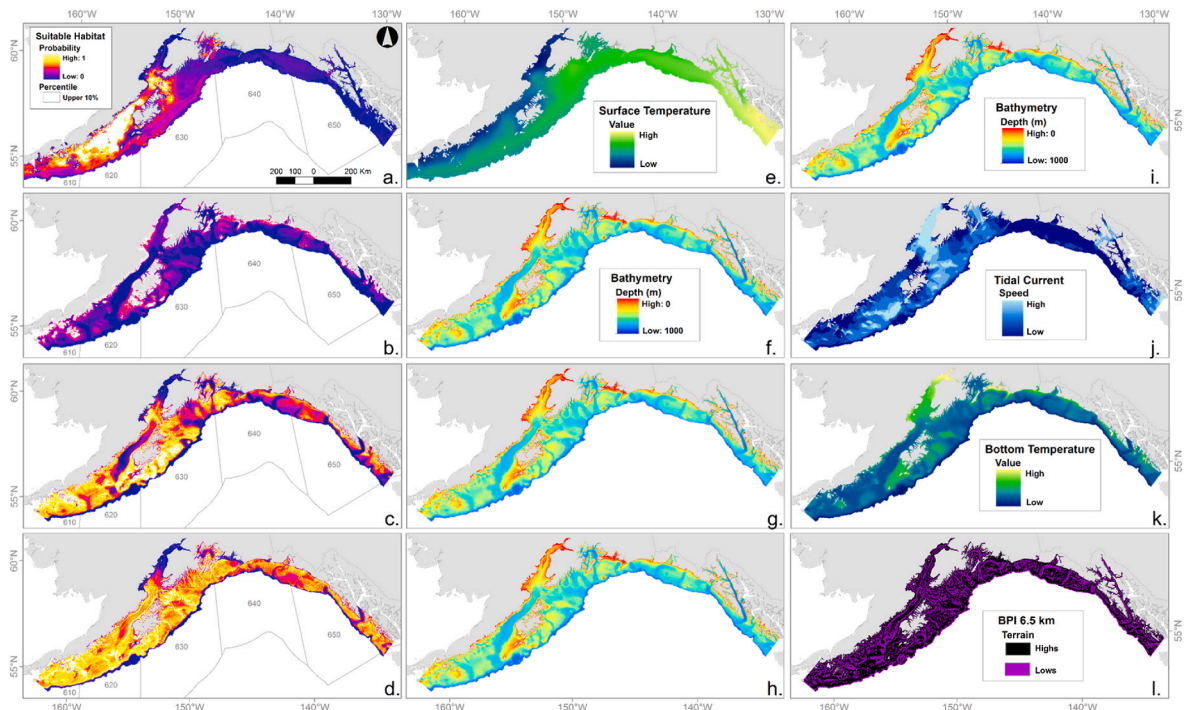


Fig. 2c. Pacific cod probability of suitable habitat by life stage (a = larval, b = early juvenile, c = late juvenile, and d = adult) with corresponding predictor habitat variables representing the highest (e = surface temperature, and f,g,h = depth) and second highest contribution (i = depth, j = tidal current speed, k = bottom temperature, and l = bathymetric position index). Upper 10 percentile of suitable habitat is shown in white within the probability of suitable habitat range (yellow to purple).

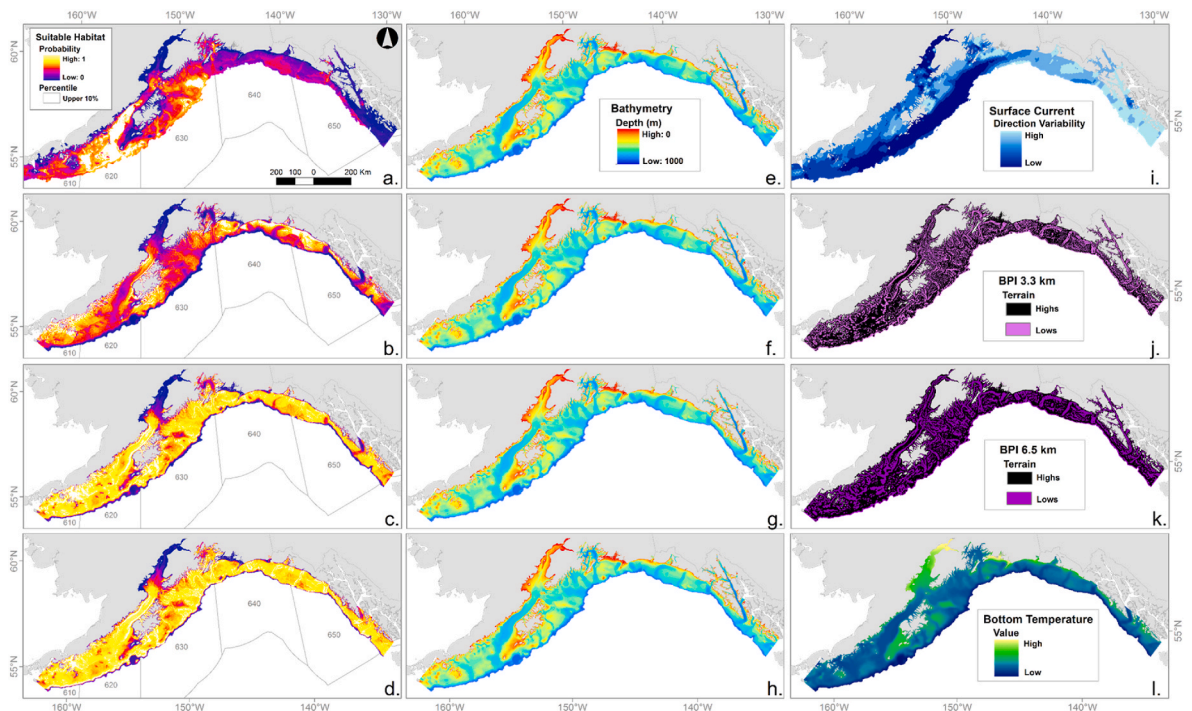


Fig. 2d. Arrowtooth flounder probability of suitable habitat by life stage (a = larval, b = early juvenile, c = late juvenile, and d = adult) with corresponding predictor habitat variables representing the highest (e,f,g,h = depth) and second highest contribution (i = surface current direction variability, j,k = bathymetric position index, and l = bottom temperature). Upper 10 percentile of suitable habitat is shown in white within the probability of suitable habitat range (yellow to purple).

juvenile transformation that is complete by ~40 mm (Kendall et al., 1994; Brown et al., 2001).

There was no trend in the energy allocation data suggesting that GOA

pollock have a fairly stable lipid and protein content throughout their life history (Fig. 4b). This stability implies an energy allocation strategy toward increasing growth rather than toward energy storage. However,

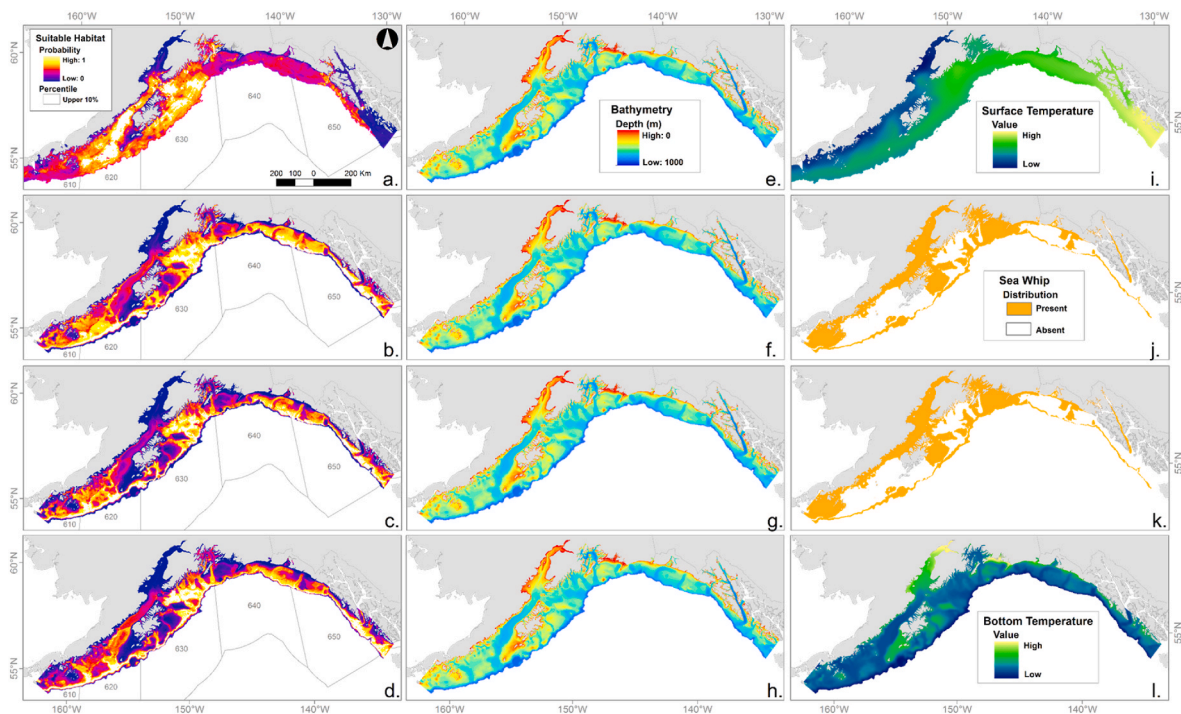


Fig. 2e. Pacific ocean perch probability of suitable habitat by life stage (a = larval, b = early juvenile, c = late juvenile, and d = adult) with corresponding predictor habitat variables representing the highest (e,f,g,h = depth) and second highest contribution (i = surface temperature, j,k = sea whip distribution, and l = bottom temperature). Upper 10 percentile of suitable habitat is shown in white within the probability of suitable habitat range (yellow to purple).

there may be a potential bottleneck just prior to overwintering (termed the “settlement stage”, but pollock do not really settle) as there was an observed increase in the variability of the percent lipid. Overwintering during the first year of life may incur an energetic cost that results in a change in body condition with reduced lipid content. In the Bering Sea, high lipid storage prior to the first winter has been associated with stronger year classes for pollock (Heintz et al., 2013; Siddon et al., 2013). Young fish with greater energy stores may be less susceptible to predation during their first winter. There may be an additional gain to the higher energy stores to mitigate high variability in maturation schedule, spawn timing, and spawning duration.

The spring time period is particularly important for pollock because eggs and larvae are in the water column and subject to wind-driven transport. Northeasterly wind has been associated with retention of pollock larvae (Stabeno et al., 1996) and juveniles (Wilson and Laman, 2021) in favorable areas in the Kodiak Island/Shelikof sea valley vicinity. This is consistent with the low surface current speed during the larval stages of the habitat distribution model and may be a habitat preference of this stage because there is less potential for advection out of preferred nursery areas (Wilson and Laman, 2021). The IBM for pollock suggests that spawners in this region are most likely to successfully settle in a suitable nursery area (Parada et al., This Issue). Additionally, the recent study by Wilson and Laman (2021) found that northeasterly winds (i.e., trajectories down Shelikof Strait) for April through May had a positive relationship with recruitment estimates (age-1) of GOA pollock, presumably due to downwelling-related retention of larvae and juveniles in areas that favor survival.

3.4. Pacific cod

Pacific cod is currently managed as a single stock in the GOA, occurring at depths from shoreline to 500 m. There does appear to be some genetic differentiation within the GOA and potential for cross migration between the western GOA and the Pacific cod stock in the Bering Sea (Barbeaux et al., 2020; Spies et al., 2019a,b). Size range

breaks for the habitat suitability models were developed from the literature and stock assessment reports and were determined for larval (<40 mm), early juvenile (<150 mm), late juvenile (<420 mm), and adult stage (≥ 420 mm) Pacific cod (Table 3). The spatial-temporal distribution of Pacific cod larvae shifts with ontogeny and is dependent on a number of behavioral and oceanographic processes. In early April, Pacific cod larvae are most abundant around Kodiak Island before concentrations shift downstream to the southwest in the Shumagin Islands in May and June (Doyle and Mier 2016). Newly hatched larvae are surface oriented and make extended diel vertical migrations with increased size and development (Hurst et al., 2009). Highly suitable larval habitat was characterized by low surface temperature (42%), bottom depth (50–300 m, 27%), and low surface current (12%). Shallow, coastal nursery areas provide age-0 juvenile Pacific cod ideal conditions for rapid growth and refuge from predators (Laurel et al., 2007). Depth was by far the top contributing habitat predictor for the early and late juvenile life stages (1–80 m at 79% and 20–140 m at 72%, respectively). A fairly narrow and shallow depth range for the early juveniles suggests the importance of these nearshore habitats for GOA Pacific cod. Pacific cod were the most abundant species in the nearshore zone and likely rely heavily on nearshore habitats for survival (Ormseth and Rand, This Issue). Tidal current and bottom temperature also contribute to the spatial distribution in the early and late juvenile stages suggesting some influence of transport mechanisms and temperature specificity during this stage as well (Fig. 2c). A preference for mixed mud, sand, and pebble sediments with some structural complexity was also noted (Pirtle et al., 2019). Interestingly, depth becomes less important during the adult stage (38–230 m, 31%) with more preference to higher relief areas (26%) and low bottom temperature (17%).

Pacific cod release all their eggs near the bottom in a single event during the late winter/early spring period in the Gulf of Alaska (Stark, 2007). Unlike most gadid species, Pacific cod eggs are negatively buoyant and are semi-adhesive to the ocean bottom substrate during development (Alderice and Forrester, 1971, Ormseth and Norcross, 2007) (Fig. 3a). Eggs hatch as 4 mm larvae after ~2 weeks at 5 °C

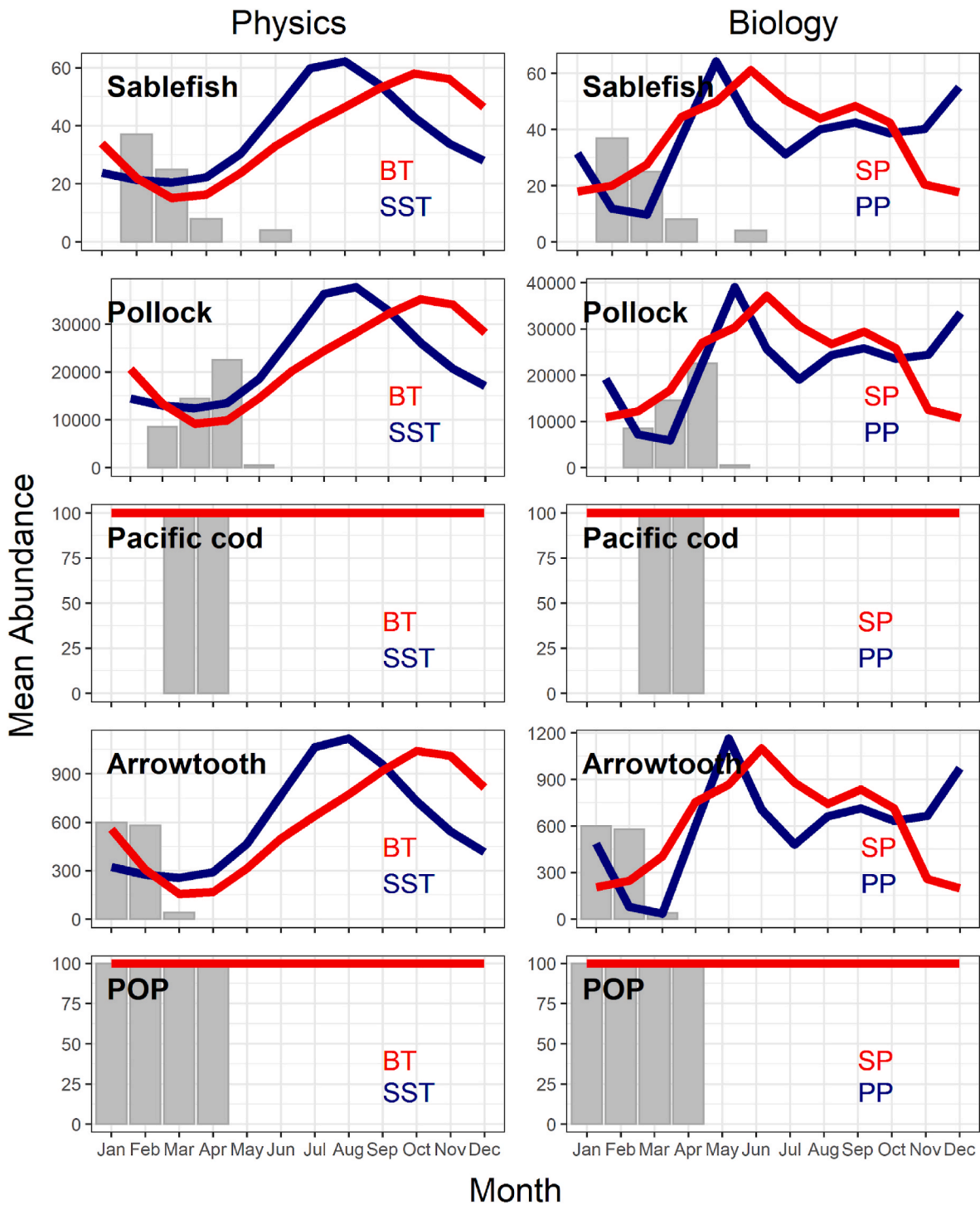


Fig. 3a. Average abundance (catch per 10 m² from bongo tows) by month over all years available for the egg stage of the five focal species. The approximate month at an arbitrary value of 100 was used for Pacific cod and POP as no eggs were available to survey gear for these two species. Pacific cod have demersal, adhesive eggs and POP are viviparous with eggs that hatch internally. Relevant climatologies from the ROMS and NPZ models provide physical and biological indices (SST/BT = surface and bottom temperature, PP/SP are primary and secondary productivity).

(Laurel et al., 2008) and become surface oriented and available to pelagic ichthyoplankton nets during the spring (Doyle and Mier 2016). Hatch timing/success is highly temperature-dependent (Laurel et al., 2008), with optimal hatch occurring in waters ranging between 4 and 6 °C (Bian et al., 2016; Laurel and Rogers 2020) over a broad range of salinities (Alderdice and Forrester, 1971). The single-batch spawning and associated narrow temporal peak in larval production (“eggs in one basket” strategy; Doyle and Mier, 2016) confers a significant degree of

vulnerability in terms of synchrony with optimal levels of larval prey, especially if warmer temperatures speed up larval metabolism and growth through the endogenous feeding stage (Doyle et al., 2019; Laurel et al., 2021). Pacific cod larvae feed principally on eggs, nauplii, and early copepodite stages of copepod prey <300 μm (Strasburger et al., 2014) and the degree of match or mismatch with the zooplankton prey field may be critical for survival (Fig. 3b). Warm surface waters can accelerate larval growth when prey are abundant (Hurst et al., 2010),

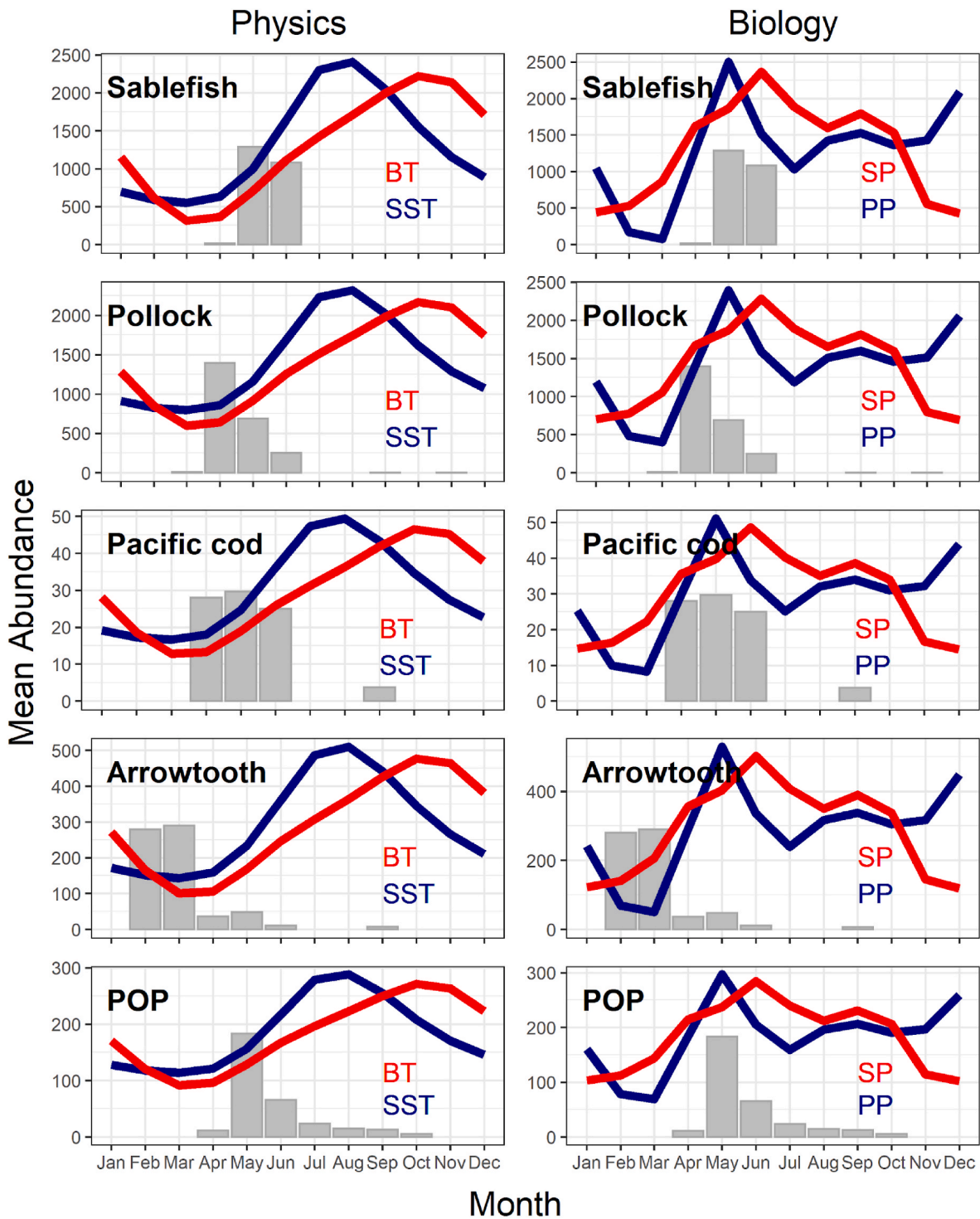


Fig. 3b. Average abundance (catch per 1000 m³ from neuston tows for sablefish and catch per 10 m² from bongo tows for all other species) by month over all years available for the larval stage of the five focal species. Relevant climatologies from the ROMS and NPZ models provide physical and biological indices (SST/BT = surface and bottom temperature, PP/SP are primary and secondary productivity).

but field observations indicate a negative correlation between temperature and abundance of Pacific cod larvae in the Central and Western Gulf of Alaska (Doyle et al., 2009; Doyle and Mier, 2016). Laboratory studies suggest warm temperatures can also indirectly impact Pacific cod larvae by way of two mechanisms: 1) increased susceptibility to starvation when the timing and biomass of prey is ‘mis-matched’ under warm spring conditions (Laurel et al., 2011), and 2) reduced growth by way of changes in the lipid/fatty acid composition of the zooplankton

assemblage (Copeman and Laurel, 2010). Very late-stage larvae (‘pelagic juveniles’) eventually settle to the bottom in early summer around 30–40 mm and use nearshore nurseries through the summer and early fall in the Gulf of Alaska (Laurel et al., 2017). Settled juvenile cod associate with bottom habitats and feed on small calanoid copepods, mysids, and gammarid amphipods during this period (Abookire et al., 2007). At the end of August, age-0 cod become less associated with structural habitats and transition into deeper water in the fall (Laurel

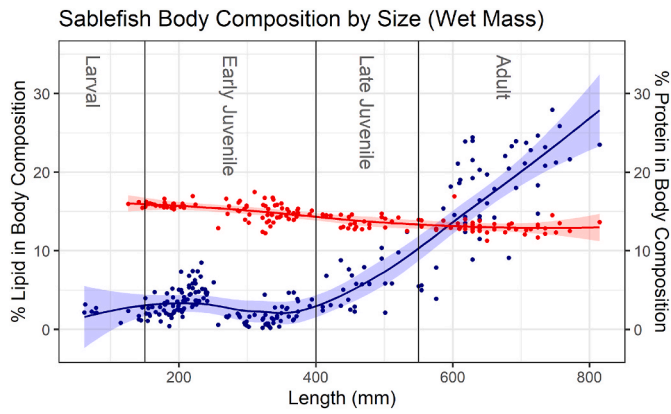


Fig. 4a. Sablefish percent body composition by length (mm), blue dots are % lipid by size, red dots are % protein by size and lines represent smoother (loess) for trend visualization. Vertical lines depict the size at different life stage transitions.

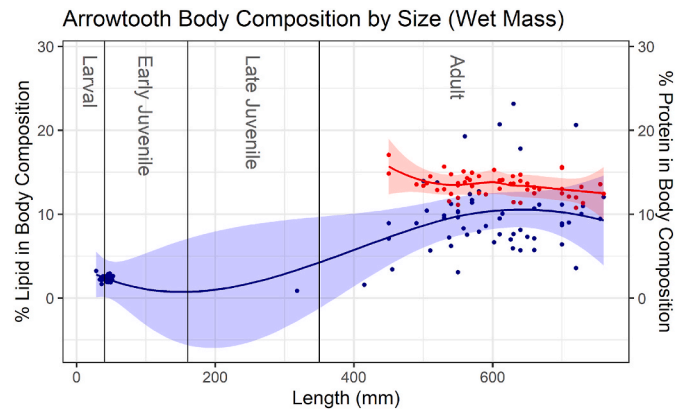


Fig. 4d. Arrowtooth flounder percent body composition by length (mm), blue dots are % lipid by size, red dots are % protein by size and lines represent smoother (loess) for trend visualization. Vertical lines depict the size at different life stage transitions.

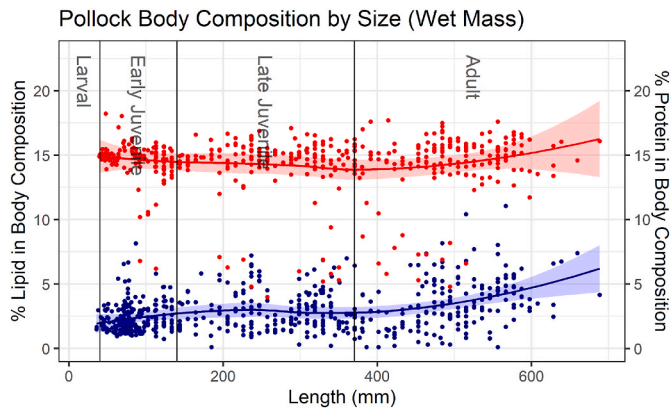


Fig. 4b. Pollock percent body composition by length (mm), blue dots are % lipid by size, red dots are % protein by size and lines represent smoother (loess) for trend visualization. Vertical lines depict the size at different life stage transitions.

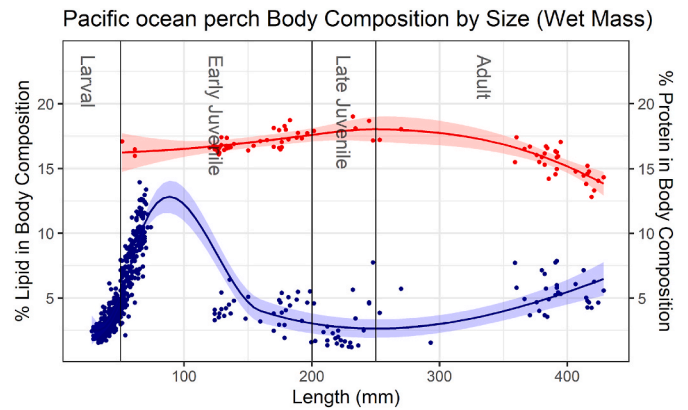


Fig. 4e. Pacific ocean perch percent body composition by length (mm), blue dots are % lipid by size, red dots are % protein by size and lines represent smoother (loess) for trend visualization. Vertical lines depict the size at different life stage transitions.

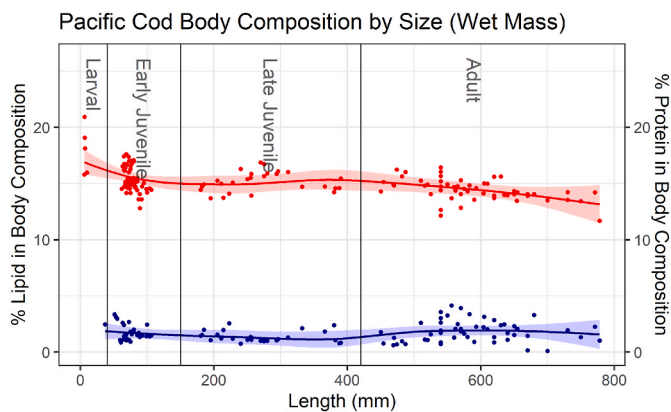


Fig. 4c. Pacific cod percent body composition by length (mm), blue dots are % lipid by size, red dots are % protein by size and lines represent smoother (loess) for trend visualization. Vertical lines depict the size at different life stage transitions.

et al., 2009). Overwintering dynamics are currently unknown for Pacific cod, although laboratory-held age-0 juveniles are capable of growth and survival at very low temperature (0 °C) for extended periods (Laurel et al., 2016).

Similar to pollock, Pacific cod in the samples for this study did not manifest a trend in their percent lipid or protein content throughout their life history (Fig. 4c). However, other studies have found a large increase in lipid prior to settlement and then a decline through the summer. Impacts of temperature on life history processes in Pacific cod are stage- and size-dependent and these relationships generally are ‘dome shaped’ like other cod species (e.g., Hurst et al., 2010; Laurel et al., 2016a). In the earliest stages (eggs and yolk-sac larvae), individuals have less flexibility to behaviorally adapt and have finite energetic reserves (non-feeding). In later juvenile stages, individuals can move to more favorable thermal or food habitats that better suit their metabolic demands. Changes in seasonal temperatures also influence how energy is allocated. In recent laboratory studies, heightened lipid synthesis was observed for age-0 and age-1+ juveniles at colder temperatures (Sreenivasan and Heintz, 2016; Copeman et al., 2017). This may be a strategy to offset limited food access during the winter (Copeman et al., 2017), but it also suggests that there is an inhibiting effect of warmer temperatures on energy allocation (Sreenivasan and Heintz, 2016). The summer thermal conditions in the Central/Western GOA have historically been well-suited for supporting high growth and survival potential for juvenile Pacific cod (Laurel et al., 2017), but it may have been sub-optimal during the 2014-16 marine heatwave (Barbeaux et al., 2020). However, the absence of age-0 fish arriving to nurseries in years with warm springs strongly suggests pre-settlement processes (egg/larval) are limiting reproductive output in the GOA (Laurel et al.,

Table 3

Habitat distribution model results for each species life stage, including percent individual contribution for up to four top contributing habitat predictor variables, with sign (<, >, <> or equal) of the directional deviation from the mean value of the predictor variable in relationship with the species response variable if applicable, and percent contribution. Since depth was frequently a top habitat predictor, we report the predicted depth range. Depth is from shoreline seaward (0–1000 m), BPI is Bathymetric Position Index, Temp is temperature (°C), Current is current speed (tidal $\text{cm}\cdot\text{s}^{-1}$; surface, bottom $\text{m}\cdot\text{s}^{-1}$), Current Var is surface current directional variability, Surface Color is chlorophyll-a concentration ($\text{Carbon}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$), and Sponge and Whips are presence-absence.

Species life stage	Variable-1 (sign, %)	Variable-2 (sign, %)	Variable-3 (sign, %)	Variable-4 (sign, %)
Sablefish				
Larvae	Depth (250–850, 38)	Surface Temp (<, 33)	Surface Color (<, 12)	–
Early Juvenile	Tidal Current (<, 30)	Bottom Temp (<, 21)	Sponge (<, 11)	Depth (10–260, 10)
Late Juvenile	Depth (135–590, 37)	Bottom Temp (<, 23)	Tidal Current (<, 12)	BPI 6.5 km (<, 8)
Adult	Depth (180–770, 89)	Tidal Current (<, 3)	Bottom Temp (<, 2)	Sponge (>, 1)
Walleye Pollock				
Larvae	Surface Temp (<, 36)	Depth (75–300, 29)	Surface Current (<, 10)	–
Early Juvenile	Depth (25–295, 39)	Bottom Temp (<>, 22)	BPI 6.5 km (<, 12)	Sponge (<, 9)
Late Juvenile	Depth (46–280, 42)	BPI 6.5 km (<, 26)	Tidal Current (<, 12)	Rockiness (<, 10)
Adult	BPI 6.5 km (<, 31)	Depth (105–380, 16)	Bottom Temp (<, 14)	Tidal Current (<, 11)
Pacific cod				
Larvae	Surface Temp (<, 42)	Depth (50–300, 27)	Surface Current (<, 12)	–
Early Juvenile	Depth (1–80, 79)	Tidal Current (<, 9)	Rockiness (>, 8)	Bottom Temp (>, 4)
Late Juvenile	Depth (30–140, 72)	Bottom Temp (<, 13)	Tidal Current (<, 8)	BPI 6.5 km (<, 7)
Adult	Depth (38–230, 31)	BPI 6.5 km (>, 26)	Bottom Temp (<, 17)	Bottom Current (<, 4)
Arrowtooth flounder				
Larvae	Depth (200–900, 44)	Current Var (<, 18)	–	–
Early Juvenile	Depth (30–200, 40)	BPI 3.3 km (<, 19)	Bottom Temp (<, 14)	Tidal Current (<, 12)
Late Juvenile	Depth (75–235, 55)	BPI 6.5 km (<, 16)	Tidal Current (<, 15)	Bottom Temp (<, 12)
Adult	Depth (100–470, 54)	Bottom Temp (<, 20)	BPI 6.5 km (<, 9)	Tidal Current (<, 7)
Pacific ocean perch				
Larvae	Depth (200–800, 30)	Surface Temp (<, 30)	–	–
Early Juvenile	Depth (110–255, 65)	Whips (<, 15)	Bottom Temp (<, 12)	Sponge (>, 9)
Late Juvenile	Depth (120–270, 54)	Whips (<, 22)	Sponge (>, 10)	Bottom Temp (<, 8)
Adult	Depth (145–495, 49)	Bottom Temp (<, 27)	Whips (<, 10)	Sponge (>, 7)

2016b). Changes in connectivity may be one such mechanism (see below). Two other recently identified processes include reduced egg survival (Laurel and Rogers, 2020) and increased larval mortality through prey mismatch (Laurel et al., 2021). Unidentified sources of post-settlement mortality may also be identified by way of future seasonal sampling through the winter.

Connectivity analysis from an IBM for Pacific cod supports the idea that limited larval drift and retention of larvae over preferred habitat (vicinity of the Shumagin Islands) is of primary importance for recruitment success. Cross-shelf transport from deeper spawning areas to nearby shallow nursery areas may also be an important process for assisting larvae and early juveniles to the nearshore nurseries for settlement (Hinckley et al., 2019). Results suggest that sustained

Table 4

Seasonal ranges by life stage for five focal species based on literature and sampling.

Stock	Stage	Timing
Sablefish	Egg	February–April
	Larval	May–June
	Early Juvenile	July–October
	Late Juvenile (feeding)	April–November
	Adult (spawning)	December–March
Walleye pollock	Egg	February–April
	Larval	April–May
	Early Juvenile	June–October
	Late Juvenile (feeding)	May–January
	Adult (spawning)	February–April
Pacific cod	Egg	March–April
	Larval	April–June
	Early Juvenile	July–October
	Late Juvenile (feeding)	May–January
	Adult (spawning)	February–April
Arrowtooth flounder	Egg	January–February
	Larval	February–April
	Early Juvenile	May–October
	Late Juvenile (feeding)	April–December
	Adult (spawning)	January–March
Pacific ocean perch	Egg	Hatch Internally
	Larval	May–August
	Early Juvenile	September–April (year +1)
	Late Juvenile (feeding)	January–September
	Adult (spawning)	October–December

along-shore currents may sweep eggs and larvae from the system before they can settle to the bottom as juveniles (Hinckley et al., 2019). Mesoscale oceanographic features such as eddies or gap winds (defined in Ladd et al., 2016 as an offshore directed flow channeled through mountain gaps) may assist in entraining eggs and larvae in the system to allow time for growth to a large enough size to settle in preferred nearshore habitat (Sinclair and Crawford, 2005; Ladd et al., 2016). Eddies have also been shown to influence distribution of nutrients, phytoplankton, and ichthyoplankton in the GOA and areas near Kodiak are known to have high, persistent mesoscale energy (Ladd, 2020). Additionally frequent gap wind events can affect the regional oceanography resulting in disruption of the Alaska Coastal Current and decreased flow down Shelikof Strait. Correlative studies reveal that recruitment of Pacific cod in Hecate Strait, BC, Canada, was negatively related to sea level pressure which is influenced by the Haida Eddy (Sinclair and Crawford, 2005) and GOA Pacific cod was positively related to gap wind events in the Kodiak region (Ladd et al., 2016).

3.5. Arrowtooth flounder

One of the most abundant groundfish species in the GOA, arrowtooth flounder (or arrowtooth) is currently managed as a single stock in the GOA and occurs in depths from 20 to 800 m, with highest catch-per-unit-effort between 100 and 300 m (Spies et al., 2019a,b). There is some evidence that arrowtooth migrate to deeper water as they grow (Zador et al., 2011) and that larger fish may move to deeper water in winter and shallower water in summer (Spies et al., 2019a,b). Size range breaks for the habitat distribution models were developed from the literature and stock assessment reports and were determined for larval (<40 mm), early juvenile (<160 mm), late juvenile (<350 mm), and adult stages (≥ 350 mm) arrowtooth (Table 3). Highly suitable larval habitat was characterized by bottom depth (200–900 m, 44%) and low current fluctuations (i.e., variability in surface ocean current direction, Laman et al., 2017) (18%). During the 2011 and 2013 GOA IERP field years, arrowtooth larvae were comparable in abundance in the eastern and western GOA but larval size distributions suggest that spawning may have occurred earlier and/or larval growth rates may have been slightly higher in the eastern survey area relative to the west (Siddon et al., 2019). Seasonal progression in distribution of larvae indicates transport

onto the shelf from deep water with apparent enhanced shoreward transport in the major canyons intersecting the slope (e.g., Amatuli Trough and Outer Shelikof Strait) where “hot-spots” in larval abundance are observed (Doyle et al., 2018; Goldstein et al., 2020). On-shelf transport of larvae seems critical, and variability in such transport may have a significant influence on larval survival to the early juvenile settlement stage (Goldstein et al., 2020). Early and late juvenile habitat were very similar and indicative of habitat generalists with more restricted depths than the larval stage (30–200 m at 40% and 75–235 m at 55%, respectively), but including fine- and large-scale low-lying areas (e.g., flats, embayments, channels, and gullies, 19% and 16%, respectively), low bottom temperature (14% and 12%, respectively), and low tidal current (12% and 15%, respectively). Settled early juveniles (age-0) are more ubiquitous across depths in the GOA than previously understood and are encountered throughout coastal and shelf waters, and older juveniles also occur in deep water along the slope (Doyle et al., 2018). Additionally, arrowtooth juveniles were largely absent from the nearshore sampling during the GOA IERP indicating that inshore areas and bays are not used extensively as nursery habitat for this species (Doyle et al., 2018). Adult habitat included more depth range (100–470 m, 54%) than juvenile habitat but still indicative of habitat generalists utilizing benthic habitat extensively throughout the GOA from east to west, with low bottom temperature (20%), low-lying areas (9%), and low tidal current (7%). Recent trends in recruitment and biomass may indicate that arrowtooth has reached some maximum threshold in terms of habitat utilization in the GOA, and that density-dependent effects at the juvenile stage may dominate population trends going forward (Spies et al., 2019a,b; Doyle et al., 2018).

Historical ichthyoplankton data indicate peak release of arrowtooth eggs in deep water over the slope in January to early February (Fig. 3a) followed by a more extended peak in recently hatched larvae January to mid-March and continued presence of larvae in the plankton through summer months (Doyle and Mier, 2016). Arrowtooth exhibit an early life strategy termed a “holding pattern” because of slow larval growth in cold, food poor environments during winter to early spring while remaining almost exclusively over deep water (Doyle and Mier, 2016). The extended pelagic larval phase is characterized by very slow growth of larvae through April with an increased growth rate from May–June in association with warming water and spring peak in plankton production (Fig. 3b). This slow growth during winter is considered advantageous in terms of extending utilization of lipid reserves prior to first-feeding. However, this strategy can cause an extreme mismatch with prey availability for first-feeding arrowtooth larvae during winter due to both a spatial and temporal separation from spring zooplankton production on shelf. Two hypotheses suggest potential mitigation of this mismatch by 1) “holding pattern” physiology which confers endurance during early ontogeny because of extended lipid reserves at very low physiological rates and 2) spatial/temporal synchrony with winter production of eggs/nauplii of the *Necoalanus* copepods that may be an important food source for first-feeding larvae (Doyle and Mier, 2016; Doyle et al., 2018, 2019). These proposed mismatch mitigating factors may provide population resilience under “normal” conditions in the GOA, but arrowtooth early ontogeny may be particularly vulnerable to anomalous conditions such as significant warming events that could potentially speed up larval growth rates and/or disrupt timing of production of larval zooplankton prey. There was a positive (but weak) correlation between larval length and water temperature across the late spring GOA time series which may be indicative of enhanced growth during “warm” years (Doyle and Mier, 2016).

Similar to sablefish, early life stages of arrowtooth (Fig. 4d, pre-settlement to settlement phases), have a fairly stable lipid and protein content. These fish are putting energy toward growth and not toward lipid energy storage. Average energy density of age-0 pelagic arrowtooth showed no change with size, although there were some interannual differences, which were attributed to changes in temperature and diet composition. Large copepods were most important in the diets of these

fish, with small copepods and decapods less abundant but persistent (Debenham et al., 2019). Newly settled demersal arrowtooth from ancillary sampling showed a distinct shift from a copepod-dominated diet to one dominated by shrimp, euphausiids, and capelin even though pelagic feeding was still occurring. Energy density of the “settled” fish continued to remain stable as size increased, and held true until fish reached ~320 mm, a size fairly close to the size associated with 50% maturity. This implies resilience during age-0 to a range of biophysical conditions such as temperature and food availability (Debenham et al., 2019). Percent lipid content increased rapidly as arrowtooth matured to the adult stage and then appeared to level off at around 600 mm (Fig. 4d), suggesting changes in diet following sexual maturity as may be expected in a generalist apex predator such as arrowtooth (Yang et al., 2006).

On-shelf transport may be an important process for larvae and early juveniles that were spawned in deep water along the continental slope to reach nurseries on the continental shelf for settlement. An IBM for arrowtooth provided new insight into potential larval drift patterns during the extended planktonic phase from winter spawning to summer settlement. High dispersion distances and complex drift trajectories included on-shelf and off-shelf transport and entrainment in features such as eddies and meanders (especially in the eastern GOA where the shelf is narrow) (Stockhausen et al., 2019a). Evaluation of settlement success for larvae originating in deep water to the southwest of Kodiak Island suggests a high probability for these larvae to be “lost” to the GOA system (Stockhausen et al., 2019a), and the role of eddies in retaining those larvae near nursery habitats in the GOA to enhance settlement magnitude and juvenile recruitment (Goldstein et al., 2020). The extended IBM for pollock (Parada et al., 2016) suggests that larvae that are advected outside of the GOA ecosystem may also have a “second chance” at settlement if they are transported through the Aleutian Island passes to suitable habitat in the southeast Bering Sea shelf (Doyle et al., 2018).

3.6. Pacific ocean perch

Pacific ocean perch (or POP) has a wide distribution in the North Pacific but are most abundant in British Columbia and Alaska and are managed as a single stock in the GOA. Adults are generally found on the continental shelf and upper slope in depths between 150 and 420 m (Hulson et al., 2020). There is some evidence of seasonal shifts in depth distribution with adults inhabiting shallower depths in the summer and deeper depths in the winter that may be related to summer feeding and winter spawning (Hulson et al., 2020). Although distributed throughout their depth range in the GOA, much of the POP population occurs in patchy, localized aggregations (Hanselman et al., 2001). Size range breaks for the habitat distribution models were developed from the literature and stock assessment reports and were determined for larval (<50 mm), early juvenile (<200 mm), late juvenile (<250 mm), and adult stages (≥250 mm) POP (Table 3). Highly suitable larval habitat was characterized by bottom depth (200–800 m, 30%) and low surface temperature (30%). During spring of the GOA IERP surveys, rockfish larvae considered to be predominantly POP, were equally abundant in the eastern and western GOA survey areas and there was no significant difference detected in larval lengths implying relatively uniform timing of parturition and suitability of early life history habitat across the GOA basin (Siddon et al., 2019). Early and late juvenile habitat were very similar and indicative of habitat specificity with more restricted depths than the larval stage (110–255 m at 65% and 120–270 m at 54%, respectively), and including biogenic habitat of sea whip absence (15% and 22%, respectively) and sponge presence (9% and 10%, respectively), and low bottom temperature (12% and 8%, respectively). Juveniles (species unidentified, but may include POP) were ubiquitous in the nearshore zone of the eastern and western GOA and encountered during spring, summer and autumn sampling of the GOA IERP surveys (Ormseth et al., 2018). Also, the habitat distribution model predicted

that the eastern GOA has a higher proportional area of habitat available for POP early juvenile stages than the western GOA. Adult habitat included more depth range (145–495 m, 49%) and higher preference for low bottom temperatures (27%), but still included some habitat specificity with sea whip absence (10%) and sponge presence (7%). IBM results for POP indicated that the highest fraction of individuals that successfully settled in inshore nursery areas originated from parturition areas in the eastern GOA, while the nursery areas to which those individuals dispersed were in the central and western GOA (Stockhausen et al., 2019b). This contradicts with recent studies that have identified pronounced stock structure in adult and juvenile POP with patchy aggregations and suggested a lifetime movement of ~100 km or less (Hanselman et al., 2001; Palof et al., 2011; Kamin et al., 2014). Based on the genetic results, it is possible there is a high degree of retention. Indeed, though the general trend of the IBM was for larvae to move north and west following prevailing circulation patterns, individual larval trajectories were complex indicating the influence of mesoscale eddies (Stockhausen et al., 2019b).

POP are viviparous (i.e., eggs develop internally) with insemination in the fall, internal fertilization approximately 2 months later in winter, and parturition (release of larvae) in April to May (Hulson et al., 2020). Larval studies are hindered by difficulty in species identification, but analysis of historical ichthyoplankton data from the western GOA revealed two major seasonal cohorts of rockfish larvae representing a spring and a separate summer release of smaller larvae as indicated by larval length frequency distributions (Doyle and Mier, 2016). Because of the dominance of POP among rockfish populations in the GOA and known deep water parturition during spring, the spring cohort of larvae from historical ichthyoplankton samples is considered to be a valid representation of annual POP larval populations. This is also supported by genetic studies of the GOA IERP rockfish samples (J. Heifetz, AFSC, pers. comm.). During spring to early summer, larvae are most abundant over the outer shelf and slope but a seasonal progression in distribution patterns indicates shoreward transport of larvae that fills in the shelf region; hot spots in larval abundance suggest that troughs like Amatuli and outer Shelikof Sea Valley are important areas for enhancing on-shelf transport (Doyle and Mier, 2016). Peak abundance of larvae is synchronized with the spring bloom in zooplankton production and likely results in plentiful availability of larval prey such as copepod nauplii for the newly released larvae that have minimal lipid reserves (Fig. 3b). This timing is considered to be a strategy of resilience (Doyle and Mier, 2016; Doyle et al., 2019). The late spring GOA larval abundance time series indicated positive anomalies in larval production of POP (*Sebastes* spp. with POP signal) from 2011 onwards with very high anomalies in 2013 and 2015 (Zador et al., 2016) in association with the recent warming event. The positive association with higher temperature in recent years reflects a previously established positive relationship with temperature from earlier in the time series (Doyle et al., 2009), but it is contradictory to the habitat distribution models showing preference for low surface temperature. This may be due to the lack of species identification during the larval stage of the habitat distribution models.

Distinct from the other four focal species, POP exhibit a sharp increase in lipid storage during larval transformation with a subsequent drop once settlement occurs, indicating a large cost to settlement for this species (Fig. 4e). A laboratory feeding study on age-0 and age-1 rockfish from the GOA IERP surveys (thought to be primarily POP through a genetics analysis) found that there was a linear growth response to temperature and that the energy allocation strategy was age-dependent (A. Sreenivasan, Sitka Sound Science Center, pers. comm.). There was higher lipid content at warmer temperatures for age-0 fish, while colder temperatures were optimum for age-1 fish. These data indicate that the growth response and energy allocation strategies of rockfish are temperature and age-dependent, and could reflect a strategy evolved to maximize growth and condition in the differing habitats occupied by each age class (A. Sreenivasan, Sitka Sound Science Center, pers. comm.). Diet may also play a role in this energy allocation shift as

stomach samples of pre-versus post-settlement POP indicate a switch from small *Pseudocalanus* spp. to larger *Calanus* spp. (R. Heintz, AFSC, pers. comm.). Fatty acid analysis of rockfish juvenile diets from near-shore summer and autumn sampling during the GOA IERP revealed a clear preference for calanoid copepods as prey for the youngest cohort indicating the importance of pelagic foraging in the plankton. The fatty acid biomarkers also indicated that smaller fish in the summer ate more pteropods, copepods and flagellate-sourced prey while later in autumn they ate more molluscs and diatom-based prey (Ormseth et al., 2018). Following settlement, both percent lipid and percent protein remained relatively stable throughout the life history even through maturity (Fig. 4e).

3.7. Informed indicators

The previous narratives provide a method for developing an organized evaluation of stage-specific mechanistic relationships along the lines of distribution, phenology, and condition to identify indicators that may be useful to monitor within the ESP framework. Temperature was identified throughout the majority of life stages as a primary explanatory variable for each species' distribution, phenology, and condition. SST was identified with high contribution to the larval stage habitat distribution model in four out of five species (sablefish, pollock, Pacific cod, and POP). Bottom temperature was identified with some contribution in all the remaining stages except the late juvenile stage for pollock. Match or mismatch dynamics in the larval stage was identified as critical for sablefish, Pacific cod, and pollock, and to a lesser extent arrowtooth and POP. There appears to be a critical energetic cost that occurs during the pre-settlement stage for POP and to a lesser extent sablefish, while increased lipid storage occurs in the maturing to adult stages for sablefish and arrowtooth. Literature review also suggests that overwintering condition may be particularly important for pollock and Pacific cod. The strict thermal limitations in hatch timing and success for Pacific cod suggest that spawning habitat availability is an important mechanism limiting reproductive output. These relationships suggest that SST indicators should be monitored for larval stages of sablefish, pollock, and Pacific cod, while BT indicators should be monitored for early juvenile stages of sablefish, pollock, Pacific cod, and POP, late juvenile stages of sablefish and arrowtooth, and adult stages of sablefish, Pacific cod, and arrowtooth (Table 5, bold).

The distribution masks and phenology ranges provide a method for creating informed stock-specific indicators that may be more representative of the stock life experience than a simple non-informed indicator. These informed indicators are essentially spatially and temporally reduced versions of a non-informed (annual average of all depths shallower than 1000 m with no seasonal component) time series of GOA SST or BT (Table 5, Figs. 5 and 6). Larval stages were all pelagic and so informed versions were based on the SST dataset, while the remaining stages were all benthic and so informed versions were based on the BT dataset. Overall, the correlation coefficient between the different stages and the non-informed annual time series were quite high, suggesting that the overall trends were similar (Table 5). Some clear differences exist, however, between the average magnitude of the different stages compared to the non-informed annual time series (Table 5). For the larval stages, pollock, Pacific cod, and arrowtooth time series were all generally colder than the annual time series at -2.6 , -1.5 , and -3.3 °C, respectively, while POP was warmer at 2.0 °C and sablefish was similar at 0.3 °C to the annual time series. For the early juvenile stages, all species were warmer than the annual time series, with Pacific cod much warmer at 2.7 °C. Late juvenile and adult stages were mixed and below 1 °C difference, except for Pacific cod where the late juvenile was 1.1 °C warmer and the adult was 1.1 °C colder than the annual time series. The coefficient of variation between the informed versus the uninformed time series seemed to vary more for the shelf species than the slope species. The sablefish and POP CVs were generally similar to the uninformed time series, with larval sablefish being slightly higher. Larval and late

Table 5

Comparison metrics by life stage for five focal species between the annual uninformed sea surface temperature (for larval stage) or bottom temperature (early juvenile, late juvenile, and adult stage). Correlation is the correlation coefficient between the uninformed and informed temperature over the time series. Difference is the average difference between the informed and uninformed temperature over the time series. CV is the coefficient of variation of the time series in percent. The uninformed CV for SST and BT was 6.8% and 7.2%, respectively.

Stock	Stage	Correlation	Difference	CV (%)
Sablefish	Larval	0.865	0.315	9.2
	Early Juvenile	0.883	1.099	6.2
	Late Juvenile (feeding)	0.902	-0.274	8.6
	Adult (spawning)	0.956	-0.601	7.5
Walleye pollock	Larval	0.919	-2.558	12.9
	Early Juvenile	0.945	1.016	6.4
	Late Juvenile (feeding)	0.933	0.374	10.5
	Adult (spawning)	0.972	-0.861	6.6
Pacific cod	Larval	0.932	-1.543	11.5
	Early Juvenile	0.926	2.656	4.7
	Late Juvenile (feeding)	0.988	1.121	12.8
	Adult (spawning)	0.937	-1.118	6.0
Arrowtooth flounder	Larval	0.834	-3.334	15.5
	Early Juvenile	0.948	0.786	6.7
	Late Juvenile (feeding)	0.973	0.340	10.1
	Adult (spawning)	0.956	-0.600	6.9
Pacific ocean perch	Larval	0.912	2.036	7.8
	Early Juvenile	0.807	0.788	6.4
	Late Juvenile (feeding)	0.974	-0.365	7.0
	Adult (spawning)	0.779	0.380	8.4

juvenile pollock, Pacific cod, and arrowtooth were higher, while early juvenile and adult were slightly lower than the uninformed time series, with the exception of arrowtooth early juvenile which was much lower than the uninformed time series (Table 5).

The trajectories of the difference between the informed and uninformed time series may also be helpful to identify where the informed indicators captured local scale trends that were not represented in the uninformed indicators. These potential trends all differed by stage and somewhat by species (Fig. 7). Larval trends (dotted lines) were generally interannual, with some evidence of an increasing trend in the first part of the time series for POP and the last part of the time series for Pacific cod. Early juvenile trends (solid lines) were decadal for POP and slightly decadal for sablefish, while steadily decreasing for Pacific cod and stable for pollock and arrowtooth. Late juvenile trends (dashed open lines) were decadal for sablefish, pollock, and POP and slightly for arrowtooth, while stable for Pacific cod. Adult trends (dashed lines) were decadal for Pacific cod, and stable for the other species with a slight increase in the last decade for sablefish, pollock, and arrowtooth.

4. Discussion

Integrated ecosystem research programs allow for larger-scale coordinated data collection to address a broad array of research questions (Baker and Smith, 2018). Smaller-scale process studies address tightly-focused hypotheses regarding specific ecosystem processes. When combined in a synthesis effort, the recent large-scale collaborative efforts along with the historical collection of process studies allowed us to complete our two primary goals. We generated stock-specific life history narratives for our five focal species and we used information in those narratives to create spatially and temporally informed indicators that more accurately reflect the stage-specific experience of the stocks. The life history narratives can be directly incorporated within the ecosystem processes section of an ESP to identify mechanistic linkages between ecosystem processes and stock productivity. The informed

stage-specific indicators can be further evaluated within the ESP monitoring analysis section which tests potential indicators for inclusion within the operational stock assessment (Shotwell et al., In Review). Since the ESP is directly integrated into the stock assessment and fishery evaluation reports, this represents significant progress toward implementing the ecosystem approach to fisheries management and creating next generation stock assessment models.

We organized the life history narratives into the categories of distribution, phenology, and condition. This information was used to sequentially refine potential indicators such as temperature to more accurately represent the stock life experience at different life stages. This method highlighted important attributes of the stocks that could be further developed or explored in the future. For instance, the life stage breaks could be refined to more accurately reflect specific transitions throughout the life history. The early juvenile life stage break was based on the approximate first size observed in beach seine or bottom trawl samples, while the late juvenile life stage break was based on the maximum length of immature individuals recorded in the bottom trawl survey (Rooney et al., 2018; Pirtle et al., 2019). This means that the early juvenile and the adult stage categories contain fish that are potentially transitioning between life stages and habitats. Young-of-the-year fish transition from the offshore pelagic environment to nearshore settlement areas after transformation from the larval stage. Therefore, pre-settlement juveniles experience a pelagic habitat while post-settlement juveniles are in benthic environments. Adults may contain fish at multiple maturity stages (maturing, skip spawning, or spawning) that may utilize different habitats (McBride et al., 2015). It may be useful to further split juvenile and adult stages to capture the different potential habitats where these fish may occur (e.g., pelagic early juvenile, spawning adult). In addition, some stock assessments are sex-specific because of sexually dimorphic growth or other characteristics that could be related to environmental habitat preferences or spawning behaviors. Specific developmental thresholds could also be incorporated into the life stage breaks if growth was impacted (either positively or negatively) due to surpassing some known value. For example, the delayed ossification of the jaw for sablefish may influence the ability to feed on larger prey and cause an additional bottleneck within the larval stage (Deary et al., 2019). It may, therefore, be informative to additionally split the larval stage into yolk-sac and feeding larvae.

There are several important caveats to consider along the lines of the three organizational categories. Regarding distribution, the amount of habitat may vary from year to year and impact the availability of certain life stages to surveys and survey sampling gear (McBride et al., 2015). The EcoFOCI ichthyoplankton surveys for the pelagic life stages (egg and larvae) have limited spatial and seasonal extent (e.g., western GOA) that has fluctuated throughout the time series (Matarese et al., 2003; Doyle et al., 2019). Care must be taken when interpreting habitat distribution models generated from these data as the results may reflect changes in sampling effort or survey design rather than the distribution of the stock (Laman et al., 2018). Much of the data for the juvenile through adult stages were from bottom trawl surveys that do not adequately sample untrawlable habitat (Williams et al., 2010; Rooper et al., 2012). Habitat distribution models based on these observations may be biased for some species such as rockfish that utilize untrawlable grounds (Jones et al., 2021). However, catchability for POP has been estimated to be above 1 (e.g., 1.15 from Jones et al., 2021, 1.8 from Hulson et al., 2020) suggesting that there is herding from the net or POP are less abundant in the untrawlable grounds. The underrepresented samples in untrawlable habitat may not be as concerning for POP, but the bias is still an important consideration, particularly if applying this method to more cryptic species such as northern or dusky rockfish (Jones et al., 2021). The habitat distribution models could be expanded by inclusion of multibeam sonar data (Stienessen et al., 2021) and benthic terrain layers derived from National Ocean Service smooth sheets that are available over a large geographic range (Baker et al., 2019). Many of these benthic

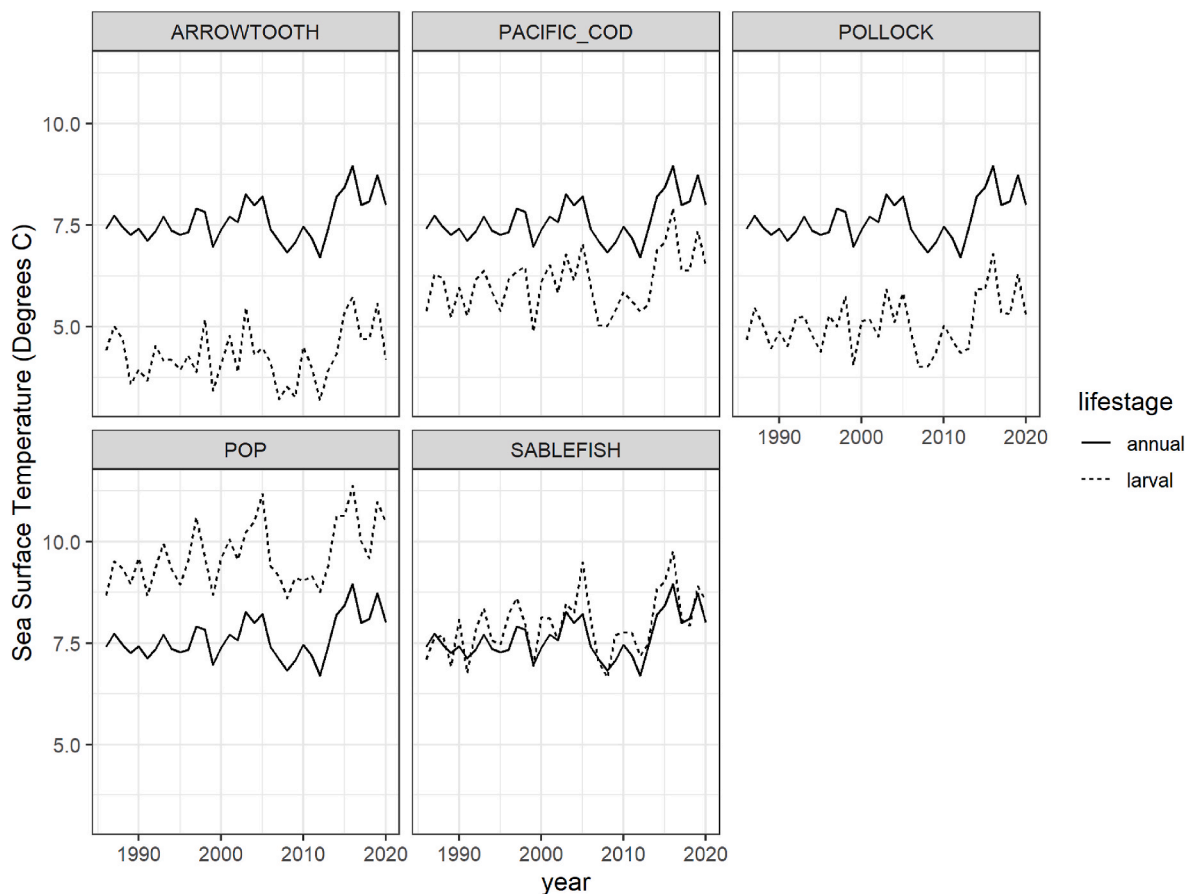


Fig. 5. Informed pelagic (larval) life stage sea surface temperature indicators (dotted line) measured in degrees Celsius (C) from 1986 to 2020 for five focal species compared to annual sea surface temperatures (solid line in degrees C) in the Gulf of Alaska. ARROWTOOTH = arrowtooth flounder, POP = Pacific ocean perch.

terrain metrics have high precision for estimating untrawlable habitat (Stienessen et al., 2021; Baker et al., 2019) and could be used to update the habitat distribution models. For some species such as sablefish, the observed early life stage samples have been historically very low and samples from more recent surveys following the GOAIERP in the eastern GOA were not included in the habitat distribution models (Strasburger et al., 2018; 2017). These GOAIERP surveys revealed new habitat where sablefish reside that was not previously considered in the standard survey extent. Ensemble methods (e.g., combining generalized linear models with presence only models) could also be used to update the habitat distribution model reflecting different assumptions on gear and selectivity. Dynamic habitat models may also be useful to capture the shifting spatio-temporal components of the stock distribution (C. Barnes, AFSC, pers. comm.) and ultimately link to time-varying selectivity within the stock assessment model.

Phenology of the life stages was defined fairly broadly as a range of months and was not well known for some stages (e.g., late juvenile feeding) and species (e.g., POP). No surveys sample throughout the entire year, so estimates of phenology may be impacted by this lack of observations, particularly in the winter when spawning occurs. Even though the EcoFOCI surveys target the larval life stage for some species (e.g., gadids), the larval timing for species such as flatfish and rockfish are relatively unknown as they start before or continue after the standard survey sampling period. Rockfish larvae are also not identified to species during the ecosystem surveys and even though the GOAIERP genetic sampling suggested that the initial summer pulse of YOY was almost entirely POP, it is not clear if this applies to the entire larval sampling period. Focused laboratory or process studies could be used to more accurately define the length of these stages and resolve identification concerns. Also, individual-based model (IBM) output could be

used to further inform on the relevance of different life stages through trajectory analysis (Gibson et al., This Issue). IBMs may reveal potential behavioral traits or mechanisms that are currently unknown. For example, the sablefish IBM demonstrated that the transport predicted by the 3 km ROMS model was not sufficient to get juvenile sablefish into locations where they are consistently observed (Gibson et al., 2019). This suggests that the existence of those observed juveniles was either due to localized spawning, fine-scale physical processes, or active movement to that area. One could use the IBMs for sensitivity experiments to determine the impact of timing and length of each life stage on overall settlement success and determine which life stages were more critical to define accurately (i.e., the yolk-sac larvae may be more critical than other stages).

Limited spatial and temporal sampling from the surveys also causes data gaps in the condition profile which made it difficult to determine the energetic strategy or if any potential costs were incurred during transition from one stage to the next (e.g., larval stage, overwinter stage). Targeted sampling during these life stages with large data gaps would be very useful to better define the energy allocation and identify more critical life stages. Once fully developed, the energy allocation curves could be used to qualify condition samples taken from the field in a given year. An energetic composition falling below the curve would indicate poor health and vice versa. Fish that can put on weight faster may have a higher chance for survival or reproductive output than fish experiencing suboptimal conditions. Future investigations could consider comparing these energy allocation curves to composition data in a given year from a regional distribution of samples representing different life stages of the focal species. This information could be made into several indicators to monitor within the ESP along with other condition indicators such as from length/weight residuals collected

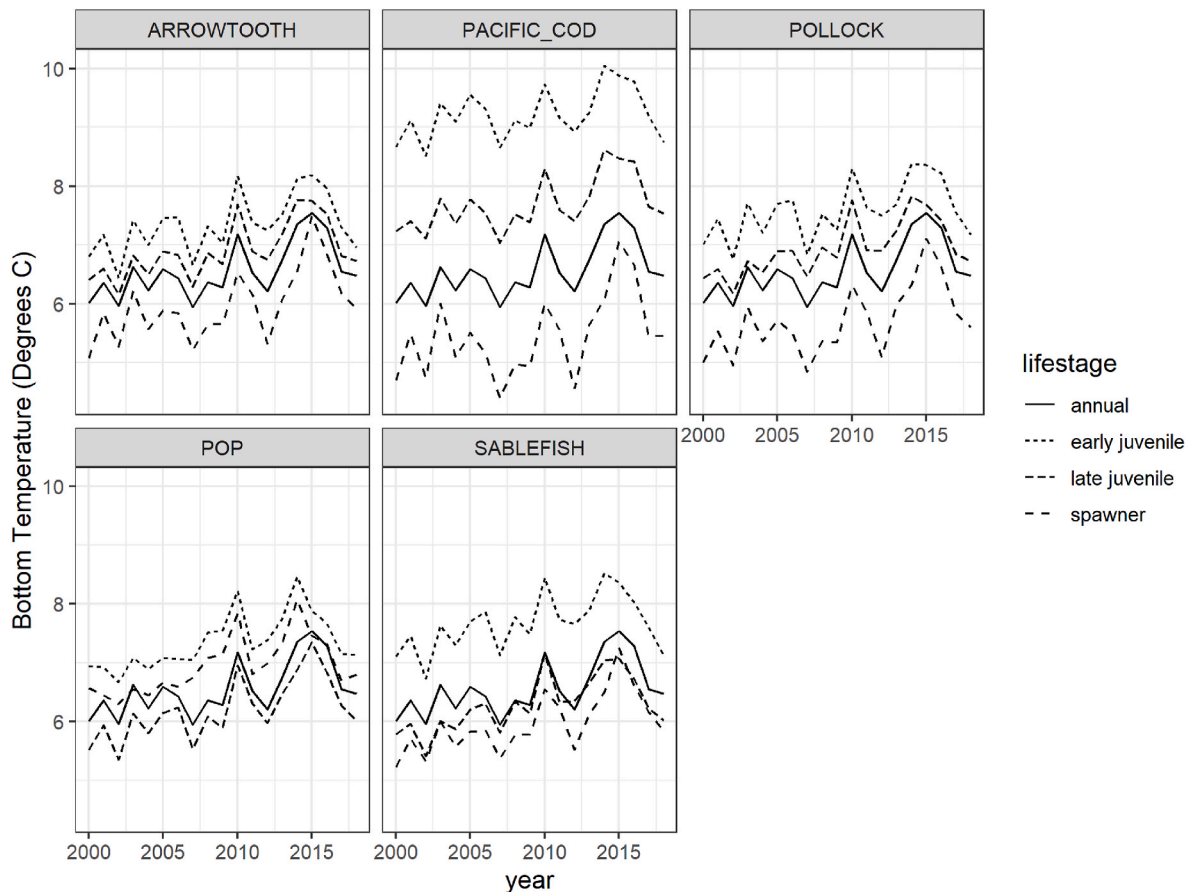


Fig. 6. Informed benthic (early juvenile, late juvenile, and spawner) life stage bottom temperature indicators (dotted and dashed lines) measured in degrees Celsius (C) from 2000 to 2018 for the five focal species compared to annual bottom temperatures (solid line in degrees C) in the Gulf of Alaska. ARROWTOOTH = arrowtooth flounder, POP = Pacific ocean perch.

during surveys (Laman and Rohan, 2020) or derived from bioenergetics models (K. Holsman, AFSC, pers. comm.). The impact of interactions with competitors or predators (e.g., salmon) on available food resources (e.g., Daly et al., 2019) could also be evaluated with respect to condition. A variety of metrics may be developed from spatio-temporal models to quantify spatial predator-prey overlap (Carroll et al., 2019). Finally, responses to warm and cold climate regimes and dramatic events such as the marine heat wave are life stage and species-specific (Barbeaux and Hollowed, 2018; Yang et al., 2019; Li et al., 2019) and may alter the distribution, timing, and relevant bottlenecks identified in this study.

The informed temperature indicators that we developed presented advantages over the non-informed temperature indicators for the whole GOA. The larval and early juvenile stage indicators generally differed in magnitude than the non-informed indicators, suggesting specific thermal preferences during the first year of life. The direction of that difference during the larval stage was also dependent on the species, with pollock, Pacific cod, and arrowtooth preferring colder temperatures, and POP preferring warmer temperatures than the annual mean for the GOA. This preference for specific temperatures may highlight potential vulnerabilities or resilience in each species' early life phenology (Doyle et al., 2019) and allow for mechanistic understanding. For example, hatch success for Pacific cod is highly temperature-dependent with an optimal temperature range between 4 and 6 °C (Bian et al., 2016; Laurel and Rogers 2020). Although we do not have synoptic sampling of Pacific cod eggs, we can infer the potential thermal experience of the egg stage from the bottom temperature time series evaluated for adult locations during spawning (Fig. 6). For the majority of the time series the temperature ranges between 4 and 6 °C, but in 2014–2016 that bottom

temperature was higher than that optimal range due to the heatwave and this had dramatic implications for survival (Barbeaux et al., 2020). Similarly, young-of-the-year (YOY) sablefish exhibit thermal intolerance to very cold water (Sogard and Spencer, 2004) and laboratory studies have shown very high growth potential occurring at a narrow thermal range between 12 and 16 °C with sufficient food (Sogard and Olla 2001; Krieger et al., 2020). Recent ecosystem surveys in the eastern GOA that captured YOY sablefish in very high numbers recorded station temperatures ranging from 11 °C to 16 °C (Strasburger et al., 2018) suggesting that temperatures were in the optimal range for high growth in this region. Even though the adult spawner, larval, and early juvenile time series do not reach these high temperatures, it is clear that during the recent years of extremely high recruitment, these three stages reached the highest temperatures in the time series (particularly for adult spawners), implying that some threshold may have been reached.

A variety of other indicators may be developed using the life history narratives and the informed indicator method along the three organizational categories. The results from the habitat distribution models suggest that habitat for these focal species is often more influenced by variables other than depth. This is supported by clear fluctuations in observed population estimates at different life stages and throughout the SST and BT time series. There were several other habitat variables with high contribution in the various habitat distribution models such as tidal current, surface current variability, and surface ocean color that could be further explored as indicators. The difference between the SST and BT can be thought of as a measure of mixing and could serve as a proxy for the tidal current variable rather than using ordinary kriging (Rooney et al., 2018). Many of these other habitat variables were derived from the ROMS-NPZ model that was first developed during the GOA IERP. As

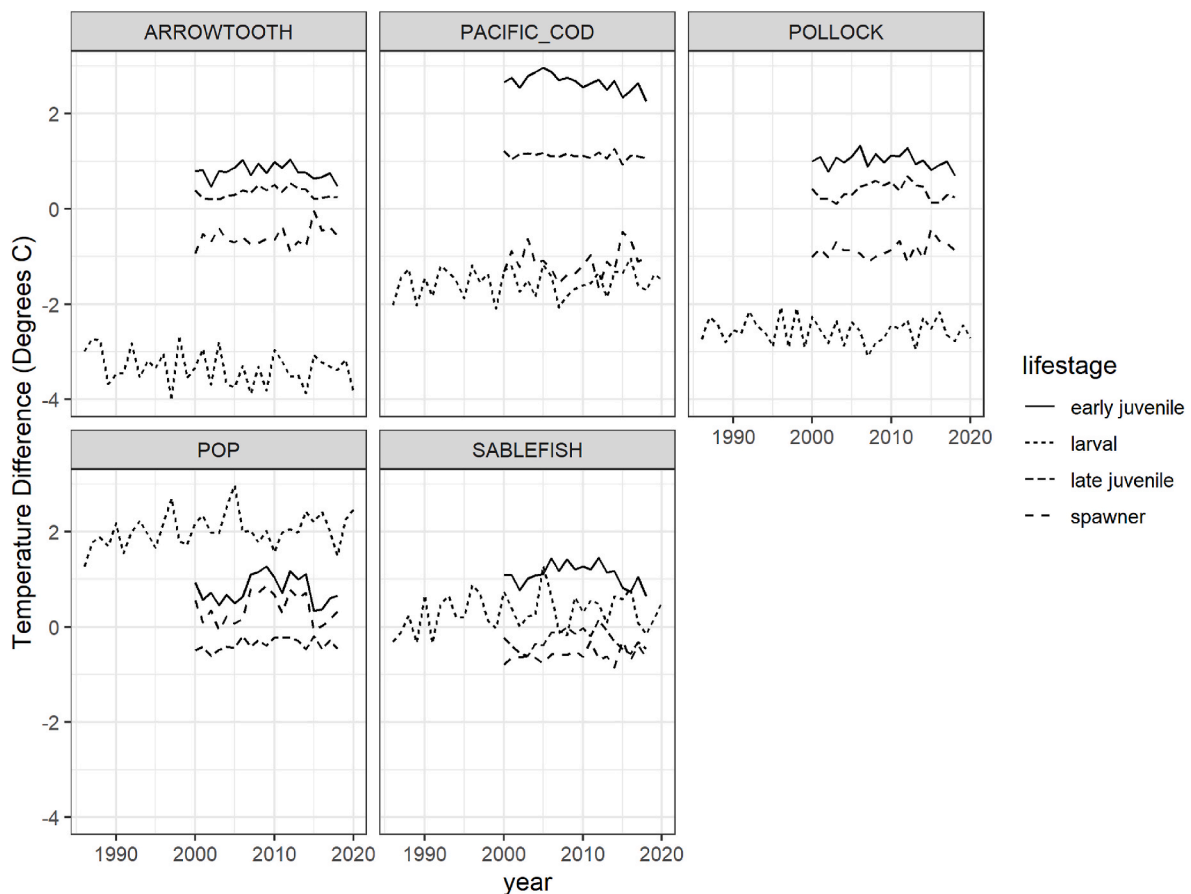


Fig. 7. Difference in temperature measured in degrees Celsius (C) between informed and non-informed indicators for the five focal species in the Gulf of Alaska. Sea surface temperatures were used for the pelagic larval life stage (dotted line, 1986–2020), while bottom temperatures were used for the benthic life stages (early juvenile = solid line, late juvenile = dashed line, and spawner = wide dashed line, 2000–2018). For each species and life stage, the annual non-informed temperature value was subtracted from the informed life stage-specific values. Positive temperature differences suggest warmer than the non-informed temperature value, while negative temperature differences suggest cooler than the non-informed temperature value. ARROWTOOTH = arrowtooth flounder, POP = Pacific ocean perch.

this model becomes more refined and increases in predictive skill, additional habitat variables can be derived and tested within future habitat distribution modeling applications to the GOA ecosystem. Variables with high contribution in the updated models could be used to develop new indicators. IBMs that use the updated ROMS-NPZ model could also be used to develop connectivity indicators from offshore spawning to nearshore settlement areas (Gibson et al., 2019) or use trajectory analysis to track spatiotemporal shifts in life history stage transitions. Regional downscaled ROMS-NPZ models also exist in many other areas (e.g., eastern Bering Sea) and the informed indicator method defined in this paper can be used to create informed species-specific indicators for a large variety of habitat variables from those models (Kearney et al., 2020). Additional satellite-derived variables (e.g., surface wind, sea surface height, sea ice, bloom timing) also exist on the global scale and can be refined to a specific region and species using the same technique.

There are several important considerations to be taken into account when applying this method of informing indicators. First, it is critical that indicators are up-to-date and readily accessible to be useful for stock assessment. The satellite time series are generally updated to the present; however, the ROMS-NPZ model was only available until 2018. This delay in current data can cause the time series to be rendered obsolete for use in the stock assessment as the information from the adult abundance surveys is sufficient to estimate population trends. The advantage of the ecosystem information in next generation stock assessments is to reduce uncertainty in the more recent population estimates where there is no information from the surveys or fishery to

explain trends. Additionally, in some cases, current year ecosystem data can provide up to several years advanced notice on trends due to an older age of recruitment used in some stock assessment models (e.g., both sablefish and POP recruitment is estimated at age 2). Data processing should also be taken into consideration when developing these informed indicators. The extraction grids may take a considerable amount of time so parallel processing may be useful. If the resolution of the data grids increase substantially (e.g., through higher resolution ROMS models) computational demands may create bottlenecks and should be considered when developing the overall process. Finally, data accessibility needs to be maintained beyond the scope of the integrated projects to allow for continued use and potential application to stock assessment. The reliable and consistent production of an indicator is as important as the mechanism it may explain and is critical to the integration within a stock assessment model.

The results of this study have immediate application to fisheries management. An expanded version of the species narratives have been included in recent ESPs for three of the five focal species (Shotwell et al., 2019a, 2019b, 2020) and the informed indicator method may help improve current indicators in the ESPs that rely on gridded data. An automated system has been developed for ingesting satellite or ocean model data and for extracting the gridded data that fall within relevant habitat suitability polygons. Such processes streamline the effort for integrating ecosystem data into the ESPs, thus enabling managers to be proactive in their understanding of potential changes as cohorts move through the life stages. The refined indicators are more realistic and specific to the stock experience allowing for more informed assessment

of unaccounted for uncertainty (Dorn and Zador, 2020) and increases the potential for inclusion within an ecosystem linked stock assessment model (Barbeaux et al., 2020; Dorn et al., 2020; Goethel et al., 2020). These improvements further our mechanistic understanding of how ecosystem processes influence a particular stock and allow us to create relevant indicators that have the potential to advance our current stock assessment enterprise into the next generation of ecosystem linked assessments.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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