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## Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003

Miriam J. Doyle<sup>a,\*</sup>, Susan J. Picquelle<sup>b</sup>, Kathryn L. Mier<sup>b</sup>, Michael C. Spillane<sup>a</sup>, Nicholas A. Bond<sup>a</sup><sup>a</sup>Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, P.O. Box 355672, Seattle, WA 98195, USA<sup>b</sup>NOAA National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA

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## ABSTRACT

The present study investigates ecological patterns and relationships to environmental variables among a time-series of larval fish species abundance from late spring surveys (1981–2003) in the northwest Gulf of Alaska (GOA). Links between interannual variation in species abundance and the physical environment were explored using generalized additive modeling (GAM). Trends in larval abundance and connections with physical variables displayed patterns that indicate unique and complex responses among species to environmental forcing during the larval period. In particular, the observed patterns suggest that ontogenetic-specific responses, representing sub-intervals of early life, are important. In addition, a notable degree of synchrony in larval abundance trends, and similarity in links with physical variables, were observed among species with common early life history patterns. The deepwater spawners, northern lampfish, arrowtooth flounder, and Pacific halibut, were most abundant in the study area during the 1990s, in association with enhanced wind-driven onshore and alongshore transport. Years of high abundance for Pacific cod, walleye pollock, and northern rock sole were associated with cooler winters and enhanced alongshore winds during spring. High larval abundance for spring–summer spawning rockfish species and southern rock sole seemed to be favored by warmer spring temperatures later in the time-series. This apparent exposure–response coupling seems to be connected to both local-scale and basin-scale environmental signals, to varying degrees depending on specific early life history characteristics. Understanding such ecological connections contributes to the evaluation of vulnerability and resilience among GOA species' early life history patterns to fluctuating climate and oceanographic conditions. This investigation also provides crucial information for the identification of “environmental indicators” that may have a broad-spectrum effect on multiple species early life history stages, as well as those that may be more species-specific in exerting control on early life history survival. Of particular interest was the emergence of the EP–NP (East Pacific–North Pacific) teleconnection index as the top-ranked variable in the GAM models exploring the connections between late spring larval abundance and the physical environment. The EP–NP index represents an important and often primary mode of spring–summer atmospheric variability in the northeast Pacific, with a strong expression in the GOA, and its connection with species in this study implies that it may be a climate mode of significant ecological importance.

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## 1. Introduction

The prevailing conceptual view of marine fish recruitment is that of a complex system of interacting biological and physical processes operating at a broad range of spatial and temporal scales (Rothschild, 2000; Hollowed et al., 2001; Bailey et al., 2003, 2005; Ciannelli et al., 2005; Hsieh et al., 2005a). Recruitment is the result of processes operating over several life stages, with a myriad of deterministic and stochastic factors interacting at each stage and across scales to ultimately influence population abundance and variability. Fundamental to understanding complex patterns of recruitment is a detailed knowledge of individual species'

biology and life history patterns, and information on prevailing climate and ocean conditions to which each life phase is connected. This is particularly important in the context of the potential impacts of global climate change on fish populations, especially in high latitudes that are experiencing some of the most rapid and severe changes (IPCC, 2007). Knowledge of fish early life history patterns (from the egg stage, through the larval and juvenile phase) and their specific linkages to the marine ecosystem is critical to the development of valid mechanistic models of recruitment prediction. For many marine ecosystems there is a dearth of information on early life history characteristics of their constituent fish populations and their specific connections to prevailing climate and ocean conditions. This inhibits the development of meaningful ecological frameworks for predicting population responses to environmental change. Such predictive models need to incorporate

\* Corresponding author. Tel.: +1 206 526 4318; fax: +1 206 526 6723.

E-mail address: [miriam.doyle@noaa.gov](mailto:miriam.doyle@noaa.gov) (M.J. Doyle).

species-specific patterns of exposure to the environment prior to recruitment.

Several decades of fisheries science and oceanographic studies in the Gulf of Alaska (GOA), especially by the Ecosystems and Fisheries Oceanography Coordinated Investigations (EcoFOCI) Program at the National Oceanic and Atmospheric Administration's (NOAA) Alaska Fisheries Science Center in Seattle, WA, USA, has produced an extensive body of knowledge of this ecosystem, including physical and biological (lower trophic level) processes as well as life history patterns of the diverse range of resident fish populations (Napp et al., 1996; Coyle and Pinchuk, 2003; Matarese et al., 2003; Doyle et al., 1995, 2002; Stabeno et al., 2004; Bailey et al., 2005; and others). Fluctuations in biomass of major commercial and ecologically important groundfish species, including walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), and a variety of flatfish species (Pleuronectidae), as well as certain small forage species such as capelin (*Mallotus villosus*), herring (*Clupea harengus*) and greenlings (Hexagrammidae), have been documented over the past four decades in the GOA. Many studies have suggested associations between production of these species and certain patterns of climate change, particularly the major shift in the late 1970s (termed a climate regime shift) from relatively cool to relatively warm ocean conditions (Anderson and Piatt, 1999; Hare and Mantua, 2000; Hollowed et al., 2001; Ciannelli et al., 2005; Litzow, 2006; Mueter et al., 2007). Despite the observed patterns in fish production and the ocean environment in the GOA, reliable predictions of recruitment strength remain elusive for most species. For certain species, such as walleye pollock, we have some understanding of mechanisms of environmental forcing during the earliest life history phase and their impact on the general patterns of recruitment (Bailey et al., 2005). However, much can still be gained from ongoing studies in this region. In particular, investigating relationships between the early life history dynamics of fish species and their ocean and climate environment is likely to contribute significantly to our understanding of the impact of changing ocean conditions on recruitment processes in the GOA.

The present study investigates a 21-year time-series of abundance of numerically dominant larval fish species from 1981 to 2003 (there was no sampling in 1984 and 1986) in the northwest GOA. The main objective of the ichthyoplankton surveys during this period was the investigation of factors affecting the recruitment of the population of walleye pollock that spawns in Shelikof Strait, GOA, during late winter to early spring. The late spring collections were timed and located primarily to coincide with the occurrence of late-stage walleye pollock larvae in the plankton of shelf and adjacent deep waters in and downstream from Shelikof Strait (Kendall et al., 1996). This mid-May to early June time-series of ichthyoplankton data also yields significant information on the early life history stages of other winter and spring spawning fish species in the GOA. During spring, larval abundance is at a peak for most GOA fish populations (Matarese et al., 2003), and larval fish species diversity is highest in the vicinity of Shelikof Strait, indicating the importance of these coastal and shelf waters as spawning and hatching areas for local fish populations (Doyle et al., 2002). In combination with basin- and local-scale measures of the state of the atmosphere and ocean during these years, these ichthyoplankton data offer an important opportunity to explore multispecies links between fish early life history and the physical environment in the GOA.

Our principal objectives in this study were to document inter-annual patterns of variation in the abundance of the numerically dominant larval fish species in the GOA during late spring, and to investigate relationships between the larval abundance patterns and physical oceanographic and climate variables. In addition, we identify among-species synchronicity in the larval abundance

time-series, and similarities in the species to physical variable connections. Links between the species abundance and the physical variables are interpreted from the perspective of fish life history strategies and potential mechanisms of physical forcing on early life history aspects of recruitment processes in the GOA ecosystem.

## 2. Methods

### 2.1. Study area

The bottom topography of the western GOA is complex. It is characterized by a relatively narrow continental shelf (65–175 km wide) punctuated by many deep canyons, shallow banks, and numerous bays and inlets intersecting the coast. Along the shelf edge the continental slope drops abruptly to depths of 5000–6000 m (Fig. 1). The regional meteorology is dominated by strong cyclonic winds that blow from fall through spring, and by strong storms that vary on monthly to decadal scales (Stabeno et al., 2004). Substantial freshwater runoff occurs from late spring through fall, and with the winds drives the coastal circulation along the Alaska Peninsula. Two current systems dominate the circulation in the western GOA, the Alaskan Stream (the western boundary current of the eastern sub-arctic gyre) along the margin of the ocean basin and the Alaska Coastal Current (ACC), a vigorous coastal current with a seasonally variable freshwater core, on the continental shelf (Stabeno et al., 2004) (Fig. 1). The Alaskan Stream flows southwesterly and roughly parallel to the shelf break at  $>50 \text{ cm s}^{-1}$  near the surface. Nearshore, the upper layer of the ACC flows southwesterly, and in the vicinity of Shelikof Strait the ACC is one of the most vigorous and dynamic coastal currents in the world (Stabeno et al., 1995). In response to variations in wind forcing and freshwater input, maxima in alongshore transport can exceed  $3.0 \times 10^6 \text{ m}^3 \text{ s}^{-1}$  and daily averaged speeds can exceed  $100 \text{ cm s}^{-1}$  (Stabeno et al., 2004). At the northeast entrance to Shelikof Strait, the ACC bifurcates around Kodiak Island with the majority of the annual transport continuing down the Strait. The ACC is a primary path of dispersal for many planktonic organisms including fish eggs and larvae. Circulation features such as eddies, and deep advection in canyons, also influence the influx and retention of plankton organisms on the shelf as well as the supply of nutrients from deeper water (Napp et al., 1996; Stabeno et al., 2004).

Water temperatures follow a clear seasonal pattern, with the coldest values occurring in March and the warmest values in August (Reed and Schumacher, 1986; Stabeno et al., 2004). A seasonal peak in phytoplankton production occurs first in the ACC, and then in the adjacent shelf area, during early May, and production of copepod nauplii and other zooplankton usually accelerates significantly at this time (Cooney, 1986; Napp et al., 1996; Coyle and Pinchuk, 2003). The zooplankton production season on the GOA shelf extends from March to October with copepod dominated biomass and abundance peaks occurring in May and July, respectively (Ince et al., 1997; Coyle and Pinchuk, 2003). Seasons are defined in this study by solstice and equinox intervals: winter extends from December 22nd to March 21st, spring from March 22nd to June 21st, summer from June 22nd to September 21st, and autumn from September 22nd to December 21st.

### 2.2. Ichthyoplankton data

Ichthyoplankton data were collected during spring surveys conducted by the Recruitment Processes Program at the Alaska Fisheries Science Center (AFSC), from 1981 to 2003 (Matarese et al., 2003). For these years ichthyoplankton sampling was most intense

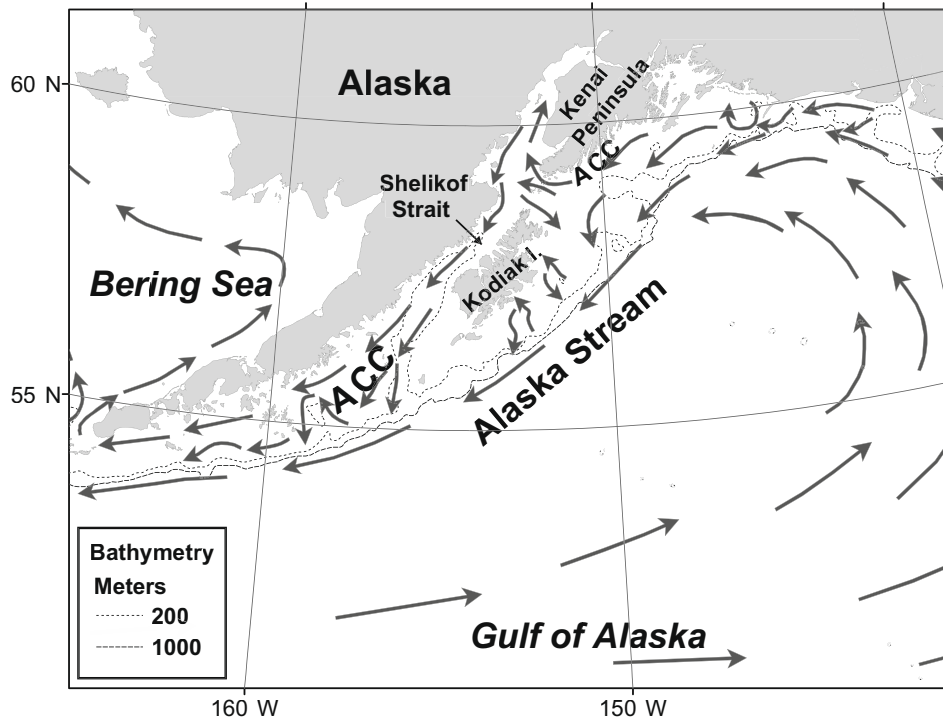


Fig. 1. Map of the Northwest Gulf of Alaska showing bathymetry and prevailing circulation features (after Stabeno et al., 2004).

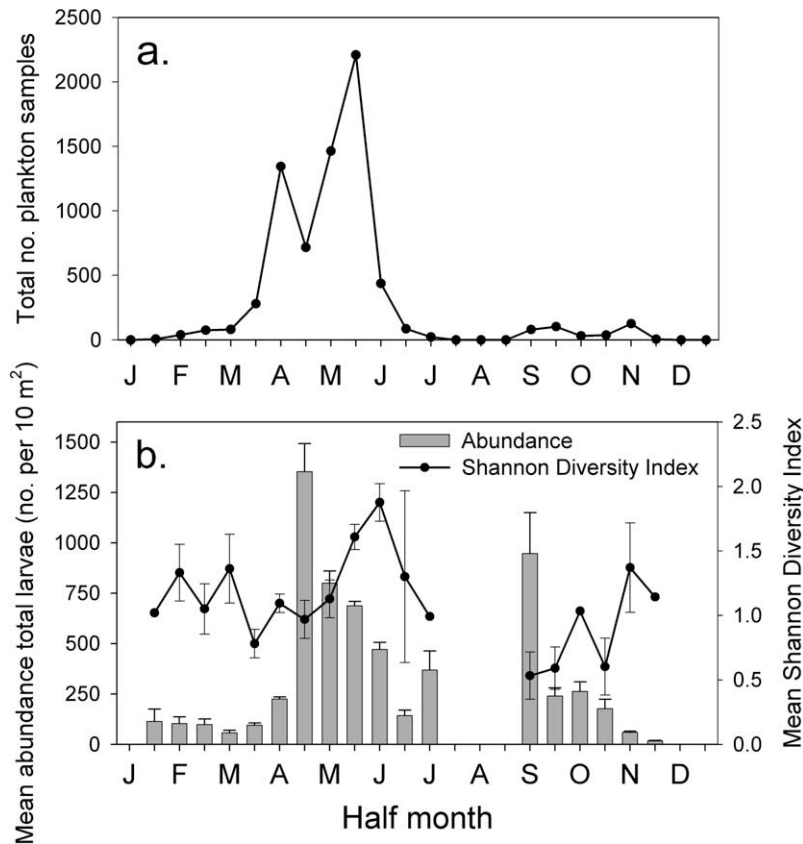


Fig. 2. (a) Annual pattern of ichthyoplankton sampling in the northwest Gulf of Alaska for the years 1972 and 1977–2003, and (b) associated means (and standard errors) of total larval fish abundance and species diversity for these samples.

during May (Fig. 2a). In the GOA, the annual spring peak in larval fish abundance extends from April to May (the April peak consist-

ing mostly of walleye pollock) and species diversity as indicated by the Shannon Diversity Index (Shannon, 1948) is highest from

mid-May to early June (Fig. 2b). For the majority of surveys, samples were collected using 60 cm paired bongo samplers, fitted with 333 or 505  $\mu\text{m}$  mesh nets, towed obliquely from 100 m depth to the surface or from 10 m off bottom in shallower water. A paired *t*-test analysis, when one side of the bongo sampler contained a 333  $\mu\text{m}$  mesh net and the other a 505  $\mu\text{m}$  mesh net (76 samples), has shown that there are no significant differences in ichthyoplankton catch rates between the two mesh sizes (Boeing and Duffy-Anderson, 2008). During 1988 and 1989, a 1-m<sup>2</sup> Tucker trawl was used to sample ichthyoplankton instead of a 60 cm bongo sampler during the late May surveys. The resulting data were added to our time-series because others found no significant difference in total catch or size distribution of larvae caught by these two gears in our study region (Shima and Bailey, 1994). Calibrated flowmeters suspended in the mouths of the samplers were used to determine the volume of water filtered by each net. Plankton samples were preserved in the field using a 5% formalin–seawater solution buffered with sodium tetraborate. Plankton samples were sorted at the Plankton Sorting and Identification Center in Szczecin, Poland. Fish larvae were removed and identified to the lowest possible taxon, and enumerated. Up to 50 larvae per taxon and sample were measured to the nearest 0.1 mm standard length (SL). Counts were converted to catch per 10 m<sup>2</sup> sea surface. Identifications of fish larvae were accomplished using taxonomic information provided by Matarese et al. (1989) and Orr and Matarese (2000). Fish larvae from sorted samples were returned to the AFSC where taxonomic identifications were verified and all data were archived in a relational database (IchBase). The majority of the time-series is available through the Ichthyoplankton Information System of the Alaska Fisheries Science Center <http://access.afsc.noaa.gov/ichthyo/index.cfm>.

To minimize variance from interannual differences in sampling coverage among cruises, data were selected from an area (47,000 km<sup>2</sup>) and time (May 18–June 6) that had the highest sampling density and the most consistent sampling over the years (Figs. 2 and 3). This selection yielded a total of 1706 samples from 23 research cruises, 1981–2003 (Table 1). No sampling was conducted during late spring of 1984 and 1986 (Table 1 and Fig. 4). Taxa that occurred in 10% or more of all samples combined, and

**Table 1**

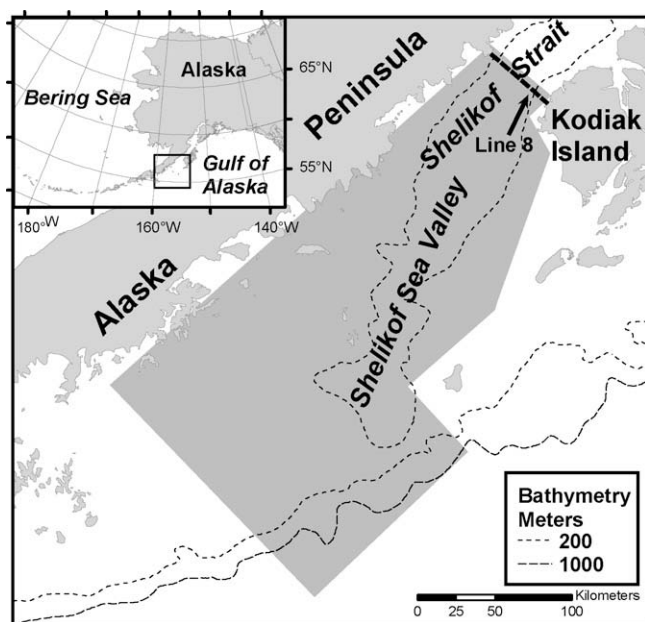
Survey schedule and number of stations sampled for ichthyoplankton using a 60 cm bongo sampler, except for 4MF88 and 4MF89 when a 1 m<sup>2</sup> Tucker trawl was used.

Year	Cruise	Dates	No. of stations
1981	3SH81	May 23–28	34
	4MF81	May 21–24	56
1982	2DA82	May 23–28	29
1983	1CH83	May 21–28	52
1985	2PO85	May 23–June 1	55
1987	3MF87	May 19–23	47
1988	4MF88	May 21–June 6	149
1989	4MF89	May 29–June 5	95
1990	4MF90	May 30–June 5	102
1991	4MF91	May 19–24	70
1992	4MF92	May 18–26	102
1993	5MF93	May 27–June 1	72
1994	6MF94	May 24–June 1	105
1995	8MF95	May 22–28	77
1996	8MF96	May 25–31	100
1997	8MF97	May 24–30	91
1998	5MF98	May 22–28	91
1999	2WE99	May 25–June 1	65
	5MF99	May 26–31	25
2000	6MF00	May 28–June 2	85
2001	3MF01	May 27–31	78
2002	4MF02	May 27–30	59
2003	5MF03	May 28–June 1	67
Total	Total	Range	Total
21	23	May 18–June 6	1706

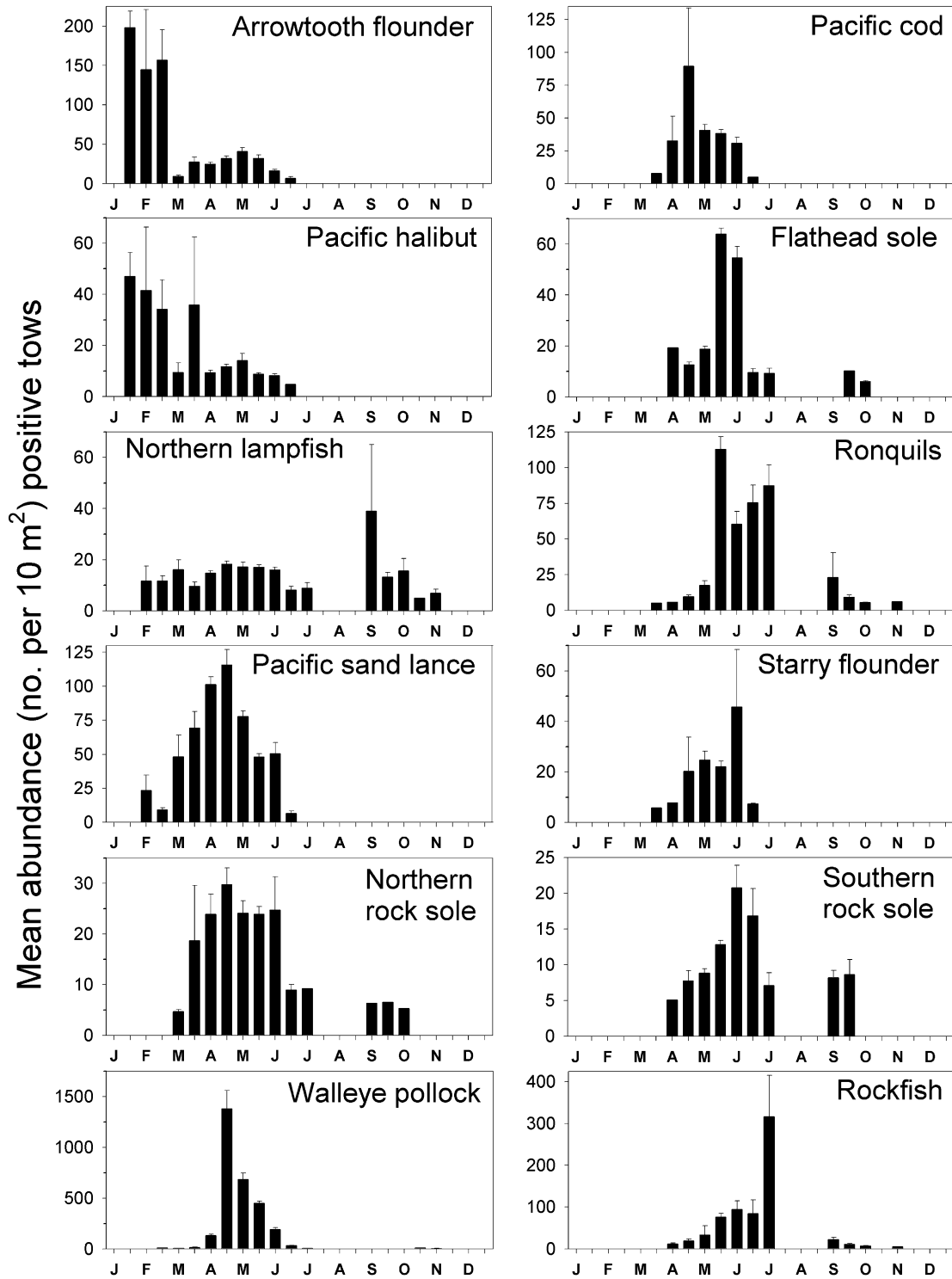
with a mean abundance >1 per 10 m<sup>2</sup>, were chosen for inclusion in the analysis (Table 2). The resulting 12 taxa included the mesopelagic species *Stenobrachius leucopsarus* (northern lampfish), the gadids *Gadus microcephalus* (Pacific cod) and *Theragra chalcogramma* (walleye pollock), unidentified rockfish larvae of the genus *Sebastes*, unidentified ronquil larvae of the genus *Bathymaster*, *Ammodytes hexapterus* (Pacific sand lance), and five flatfish species; *Hippoglossoides elassodon* (flathead sole), *Platichthys stellatus* (starry flounder), *Hippoglossus stenolepis* (Pacific halibut), *Lepidopsetta bilineata* (southern rock sole), and *Lepidopsetta polyxystra* (northern rock sole). Mean abundance of each taxon in the study area for each year was calculated (zero catches included) by multiplying the catch per 10 m<sup>2</sup> for each station by the polygonal area represented by that station, and then averaging over all polygonal areas (Kendall and Picquelle, 1990). Mean lengths of each taxon for each year were similarly calculated as a weighted mean, where the mean lengths of taxa sampled at each station were weighted by the station's polygonal area multiplied by the station's catch per 10 m<sup>2</sup>. Grand mean lengths, representing the average length for each taxa during late spring in the GOA, were also calculated in this way using data from the study area combined over all years (1981–2003).

### 2.3. Environmental data

The environmental time-series includes climate indices, and atmospheric and oceanographic variables representative of both the broader basin of the Gulf of Alaska and northeast Pacific Ocean, and the local study area (Table 3). The five basin-scale variables include the North Pacific Index (NP), the Arctic Oscillation Index (AO), and the East Pacific–North Pacific Index (EP–NP), (representing broad-scale northeast Pacific atmospheric conditions), the multivariate ENSO – El Niño Southern Oscillation Index (MEI) (describing variability in tropical Pacific atmosphere–ocean climate system), and the Pacific Decadal Oscillation Index (PDO) (which represents the leading pattern of North Pacific sea surface temperatures (SST)). These indices, with probably one exception, are well known by the climate community and have been related to various elements of the marine ecosystem of the North Pacific



**Fig. 3.** Study area in the vicinity of Kodiak Island for which mean abundance of larval fish species were calculated. Line 8 is a station transect where time-series of oceanographic measurements by the EcoFOCI program have been located.



**Fig. 4.** Annual patterns of half-monthly mean abundance (and standard errors) for numerically dominant larval fish species in the northwest Gulf of Alaska, based on all ichthyoplankton sampling carried out during 1972 and 1977–2003 (Fig. 2a). Species arranged in order of appearance and seasonal peak abundance of their larvae in the plankton.

(especially the PDO; e.g., Mantua et al., 1997). The exception is the EP–NP index. Climate variability in winter has received most of the attention, and at that time of year the EP–NP is of lesser prominence. In spring and summer, however, the EP–NP represents an important and often the primary mode of atmospheric variability in the northeast Pacific, with a strong expression in the GOA. The positive phase of the EP–NP index is associated with anomalously high sea level pressure (SLP) over the GOA with a pole centered on

the Kenai Peninsula (Fig. A1). The positive phase of the EP–NP tends to be accompanied by anomalously warm air temperatures over southern Alaska, reduced precipitation in southeast Alaska, and anomalous winds from the northeast over Shelikof Strait. The essential difference between the EP–NP pattern in SLP and the SLP pattern associated with the NP and PDO modes is that the former consists of a north–south dipole and the latter is a monopole related to the strength of the Aleutian Low. Because

**Table 2**

Species of fish larvae included in the study, ranked according to percent occurrence during late spring for all years combined.

Species	Family	Common name	% Occurrence	Mean abundance (No. per 10 m <sup>2</sup> )
<i>Theragra chalcogramma</i>	Gadidae	Walleye pollock	90.2	362.1
<i>Hippoglossoides elassodon</i>	Pleuronectidae	Flathead sole	76.6	50.0
<i>Ammodytes hexapterus</i>	Ammodytidae	Pacific sand lance	75.1	33.4
<i>Bathymaster</i> spp.	Bathymasteridae	Ronquils (genus <i>Bathymaster</i> )	66.4	99.4
<i>Gadus macrocephalus</i>	Gadidae	Pacific cod	49.8	14.6
<i>Lepidopsetta polyxystra</i>	Pleuronectidae	Northern rock sole	35.1	5.3
<i>Stenobrachius leucopsarus</i>	Myctophidae	Northern lampfish	33.0	5.9
<i>Sebastes</i> spp.	Scorpaenidae	Rockfishes	31.0	29.0
<i>Lepidopsetta bilineata</i>	Pleuronectidae	Southern rock sole	20.6	2.8
<i>Atheresthes stomias</i>	Pleuronectidae	Arrowtooth flounder	18.8	7.3
<i>Platichthys stellatus</i>	Pleuronectidae	Starry flounder	18.6	3.2
<i>Hippoglossus stenolepis</i>	Pleuronectidae	Pacific halibut	10.0	1.1

**Table 3**

Environmental variables included in GAM analysis (abbreviation on left), source of data and associated reference. Monthly mean values for January through May were used in all instances except for FLOWKLS and RI. SPEM model output is unavailable prior to March so the latter variables are represented by March, April, and May means. Data for 1981 through 2003 were available for all variables except the SST reanalysis data which commences in 1982.

Abbreviation	Variable name	Source	Reference
<i>1. Basin-scale variables</i>			
PDO	Pacific Decadal Oscillation (leading pattern of North Pacific sea surface temperature)	Joint Institute for the Study of the Atmosphere and Ocean, University of Washington	Mantua et al. (1997)
NP	North Pacific Index (intensity of the mean winter Aleutian Low pressure cell – sea level pressure)	NOAA – National Center for Atmospheric Research	Trenberth and Hurrell (1994)
AO	Arctic Oscillation Index (see-saw pattern of polar-middle latitude atmospheric pressure at sea level)	NOAA – Climate Prediction Center	Thompson and Wallace (1998)
EP-NP	East Pacific–North Pacific Index (teleconnection pattern of anomalous atmospheric pressure and circulation featuring changes in the Pacific jet stream and downstream winds – considered the leading mode of North Pacific atmospheric variability in spring)	NOAA – Climate Prediction Center	Barnston and Livezey (1987)
MEI	Multivariate El Niño–Southern Oscillation Index (see-saw pattern of tropical sea level pressure, East–West Pacific)	NOAA – Climate Diagnostics Center	Wolter and Timlin (1998)
<i>2. Local-scale variables</i>			
FRESH	GOA Freshwater Runoff from river discharge	Tom Royer, Old Dominion University, Norfolk, Virginia	Royer et al. (2001)
ALONG	Alongshore Wind Index (speed/direction)	} Calculated from coastal wind data at 59°N, 150°W	} Stabeno et al. (2004)
MIXING	Wind Mixing Index (wind speed cubed)		
SST	Sea surface temperature (SST) 57.5°N, 155.5°W	NOAA – Climate Prediction Center: Optimal Interpolation Reanalysis	Reynolds et al. (2002)
FLOWKLS	Flow through Line 8, Kodiak side	} Computed from the SPEM circulation model	} Hermann and Stabeno (1996)
RI	Retention Index (percent particles released in study area not lost to advection after 15 days)		

the EP–NP index signifies both an important mode of large-scale atmospheric variability at a crucial time of year, and relates to local and regional aspects of the atmospheric forcing, it represents a prime candidate for exploration in the present study along with the more familiar large-scale indices.

On the local scale, six variables representing freshwater input, wind patterns, sea surface temperature, and circulation were included: GOA Freshwater Runoff (FRESH), Alongshore Wind (ALONG) and Wind Mixing (MIXING) Indices, sea surface temperature (SST) in Shelikof Strait, total flow of water along the southern half of Line 8 (FLOWKLS) (Fig. 3) (where direction of flow is frequently opposite to the ACC representing an onshore transport mechanism for deep water larvae), and a Retention Index (RI) (representing potential retention of larvae in the study area) (Table 3). FLOWKLS and RI were generated from an eddy-resolving, semi-spectral primitive equation model (SPEM) of circulation on the western GOA shelf (Hermann and Stabeno, 1996). The influence of environmental conditions on the abundance and survival of various species of fish larvae is likely to be significant from the initial

production of the eggs (predominantly winter–spring in the GOA) through the period of late larval development, weeks to months later. Consequently, both time-lagged and survey time values of the environmental time-series were used in the analysis with monthly mean values included for January through May of each year (Table 3).

#### 2.4. Data analyses

In order to identify among-species synchronicity in the larval abundance time-series, a two-dimensional, non-metric, multidimensional scaling ordination (NMDS) was performed using Bray–Curtis dissimilarity measures on yearly mean abundance, standardized by species totals. NMDS is a technique that projects multidimensional data onto a two- (or more) dimensional plot by preserving the rank distance of the dissimilarity measure (McCune and Grace, 2002). Because of the extreme outlier for walleye pollock abundance in 1981, data from this year was removed for the NMDS analysis. Synchronicity in late spring mean larval size

among species was also investigated using NMDS. The ordination was performed using species correlations expressed as distance measures  $((1 - r)/2$  where  $r$  is the Pearson correlation coefficient) of standardized annual mean length anomalies (species annual mean length minus its grand mean length averaged over all years, expressed as a fraction of the grand mean). For those few species where there were no larvae caught in a particular year, we assumed a zero anomaly for those years.

Relationships between larval fish abundance in late spring (response variable) and environmental conditions during winter and spring months (predictor variables), January–May, were examined using generalized additive modeling (GAM) (R Statistical Computing Software, <http://www.rproject.org/>). GAM is a form of nonparametric multiple regression that models a response (dependent) variable as a function of one or more predictor (independent) variables (Hastie and Tibshirani, 1990). The main advantages of GAM over traditional regression methods are its capability to model non-linearity using nonparametric smoothers and that there is no need for *a priori* specification of the functional form between the response variable and the predictor variables. It is preferable when using GAMs that there is no interaction between the predictor variables (i.e., the effect of one predictor variable is independent of the effect of another). Clearly, this might not be the case with every climate and oceanographic variable considered here. Nevertheless, it is a useful tool for exploratory analysis that is able to identify functional relationships suggested by the data, and it has been favored in the recent fisheries science literature as an appropriate method for investigating relationships between various aspects of recruitment and the environment (e.g., Cury et al., 1995; Daskalov, 1999; Ciannelli et al., 2004; Megrey et al., 2005; Porter et al., 2005).

For each group of environmental variables (basin- and local-scale), GAMs were run for individual species. The dependent (or response) variables in the GAMs were the late spring abundance estimates for each species, and the independent (or predictor) variables were the monthly mean values for the environmental variables. No direct transformation to the dependent variable was needed as GAMs generally use an appropriate link function to assure validity of the model. In our case, we used a gaussian family (normal distribution with an identity link function) using the mgcv library in R, version 2.5.1 (Wood, 2004). For each species and month, a GAM was run for every possible combination of environmental variables, rather than the standard stepwise procedure. Many of the environmental variables were correlated with each other (concurvity, which is analogous to collinearity in linear models); hence stepwise procedures were not appropriate because inclusion of a variable in the final model would depend on what other correlated variables were already in the model. Therefore, the order of adding or removing a variable impacts its contribution to the model. By considering every possible combination of environmental variables, we considered all possible orderings for inclusion of the variables in the model.

For each species, and month, a subset of environmental variables that yielded the best-fit models was selected using generalized cross validation (GCV) methods (Green and Silverman, 1994). The GCV is a measure of the predictive error of the model and takes into account the fit and also the model complexity. We used the GCV measure to compare models, choosing 1–3 models with the smallest GCV values to examine further. We assessed the significance of the independent variables using the Chi-square statistics calculated by R for the independent variables. In addition, for each model run, partial regression plots showing the partial additive effect of each environmental variable on larval species abundance were examined for linearity, significance, and positive or negative effect. We examined plots of the residuals from the best model to check the assumption of independence (i.e., no auto-

correlation) and identical distributions (i.e., no heteroscedasticity). The most important assumption was met in that no autocorrelation errors were detected. Heteroscedasticity was observed in only a few species-month GAM results, but we did not correct for this heteroscedasticity by transforming data so that all species were treated the same. Some species-month GAMs contained outliers. However, any departures from the assumption of heteroscedasticity were not strong enough to invalidate the ecological interpretations of the models. The resulting best-fit models were used to suggest which predictor variables may have an important effect on the abundance of each species.

### 3. Results

#### 3.1. Seasonal and spatial patterns of larval production

Based on the AFSC's ichthyoplankton collections from the northwest GOA, 1972 and 1977–2003 (Fig. 2a), annual patterns in mean larval abundance indicate the sequence of occurrence, peak abundance, and duration of species in the plankton (Fig. 4 and Table 4). Arrowtooth flounder and Pacific halibut spawn primarily during winter months over the continental slope and their larvae are most abundant during January and February. Although less abundant during spring months, they persist in the plankton over the outer shelf and slope (Doyle et al., 2002; Matarese et al., 2003), and by late May they are well developed (Table 4). Northern lampfish are unusual in that there is no definitive annual peak in their larval abundance in the GOA, and they have been collected during all months of sampling (Fig. 4). The early September peak with a high standard error is an anomaly based on high densities from one sample. Size distribution data indicate that spawning occurs primarily from March to summer in this region (Matarese et al., 2003). Pacific sand lance spawn intertidally on gravel and sand beaches during fall months in certain coastal areas of the northern GOA (Robards et al., 1999a,b), although extension of spawning into winter months is thought to occur. Their larvae, however, do not appear in GOA plankton samples until February (Fig. 4) and hatching peaks during March (Doyle, unpublished data), indicating extended periods of egg incubation in coastal sediments. They are most abundant during April and by late May have reached a mean size of 16.7 mm SL (Table 4). Pacific cod, walleye pollock, and northern rock sole have similar early life history patterns with late winter to spring spawning on or close to the bottom in shelf waters (primarily Shelikof Strait for walleye pollock and Pacific cod), and a peak abundance of relatively small larvae in April–May. The late May–early June sampling coincided with the annual peak in larval abundance for the spring to summer spawners (i.e., flathead sole, ronquil species, starry flounder, and southern rock sole), whereas it occurred prior to the summer peak in abundance of rockfish larvae (Table 4 and Fig. 4). Mean size for the rockfish species at this time is within the known range of larval sizes at extrusion (Table 4).

#### 3.2. Interannual trends in larval abundance

Five distinct patterns were identified visually from the species abundance time-series (Fig. 5), and among-species synchronicity was validated statistically by the grouping of species on the NMDS plot (Fig. 6). The deepwater spawning northern lampfish, arrowtooth flounder, and Pacific halibut displayed a quasi-decadal pattern of enhanced abundance during the 1990s relative to the 1980s and 2000–2003 (Pattern 1), and were positioned close to each other on the NMDS plot. Pacific cod, walleye pollock and northern rock sole were also most abundant from 1989 to the 1990s, but the highest levels of abundance were occasional rather

**Table 4**

Life history information for GOA taxa in this study. Information from populations in the eastern Bering Sea is used where none is available for the GOA. Fecundity information is from the Alaska Fisheries Science Center's Life History Database: <http://access.afsc.noaa.gov/reem/LHWeb/Index.cfm> Seasonal and spatial patterns of larval production, larval standard length (SL) at hatching and transformation, and mean standard length (SL) from samples collected during late spring (mid- to end of May). Species are arranged in order of their annual pattern of occurrence in the plankton. Early life history information from Matarese et al. (1989, 2003), Porter (2005), Doyle et al. (2002), and Blood et al. (2007). A question mark indicates no data or incomplete information.

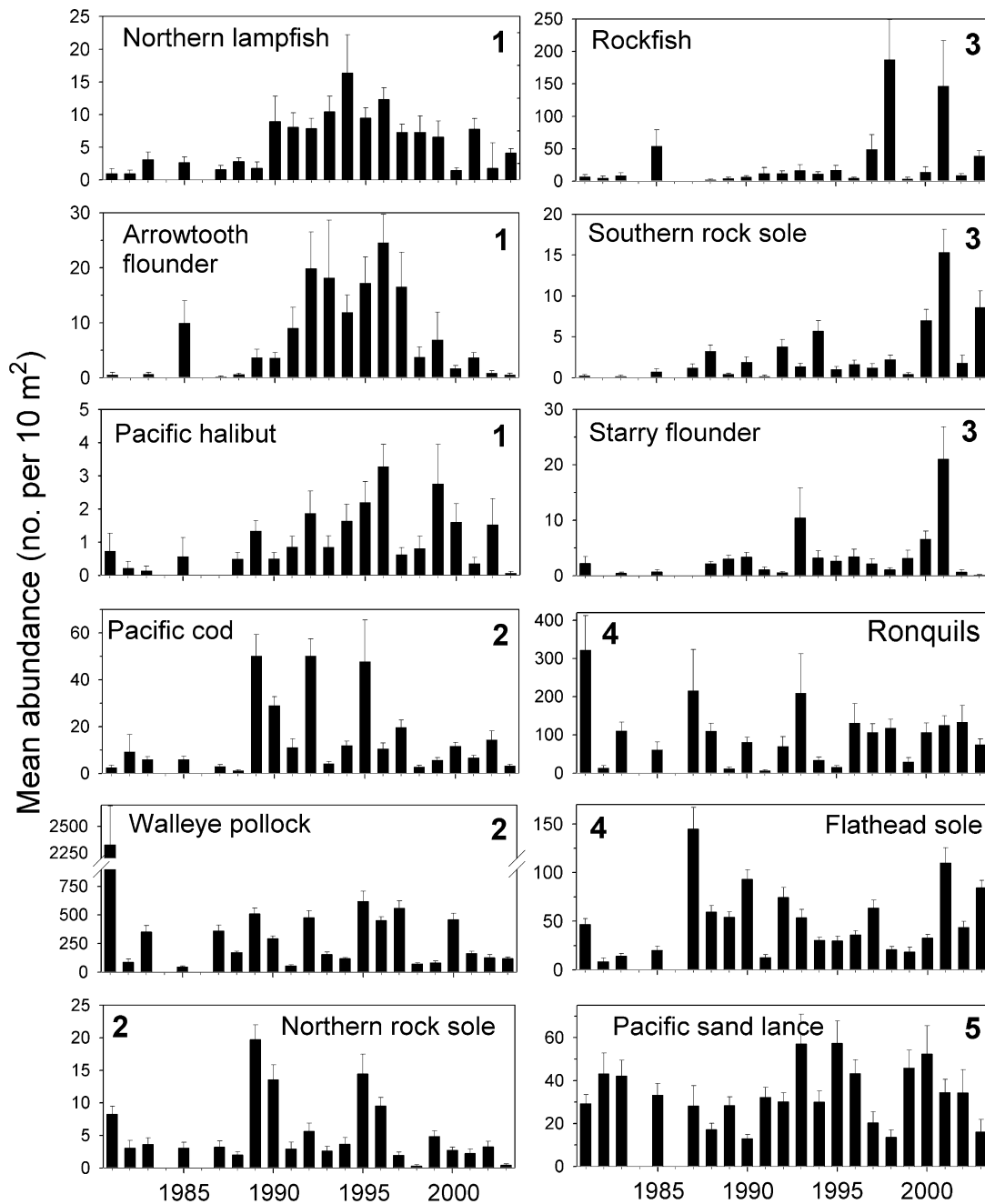
Species	Maximum age (years)	Maximum length (cm)	Absolute fecundity Millions eggs/ female	Spawning			Annual peak Larval abundance	Larval habitat	Larval standard length (mm)		
				Mode	Time	Habitat			Hatching	Transformation	Late spring
Arrowtooth flounder	23	91	0.25–2.22	Deep pelagic	December(?)–April	Upper slope	January–February	Slope/Shelf edge	3.9–4.8	25.6–44	13.3
Pacific halibut	55	290	0.57–2.34	Deep pelagic	November–March	Upper slope	January–February	Slope/Shelf edge	~8	~24	19.7
Northern lampfish	8	13	?	Mesopelagic	March(?)–August(?)	Ocean basin-Shelf edge	No definitive peak	Slope/Shelf edge	~2	16–19	6.6
Pacific sand lance	5	19	0.001–0.016	Demersal	October–February(?)	Intertidal	March–May	Coastal/Shelf	6–7	50–80	16.7
Northern rock sole	24	64	0.404(?) <sup>a</sup>	Demersal	March–June(?)	Coastal/Shelf	April–May	Coastal/Shelf	>3	~30	8.1
Walleye pollock	31	105	0.10–1.08	Deep pelagic	February–May	Shelikof Strait	April–May	Coastal/Shelf	3–4	25–40	8.0
Pacific cod	25	147	1.40–6.40	Semi-demersal	February(?)–May(?)	Shelf	April–May	Coastal/Shelf	3–4	~35	7.3
Flathead sole	27	74	0.05–0.16	Pelagic	March–July	Shelf	May–June	Coastal/Shelf	5.3–6.9	18–35	6.7
Ronquil species	9 <sup>c</sup>	43 <sup>c</sup>	?	Demersal(?)	March(?)–October(?)	Slope/Shelf (?)	May–July	Coastal/Shelf	?	?	6.1
Starry flounder	21	77	0.91–2.29	Pelagic	March(?)–June(?)	Coastal/Estuaries	May–June	Coastal/Inner shelf	1.9–2.1	8.3–8.5	4.4
Southern rock sole	28	65	0.404(?) <sup>a</sup>	Demersal	April(?)–September(?)	Coastal/Shelf	June	Coastal/Shelf	<3	~30	5.2
Rockfish species	>100	>70	?	Viviparous	April(?)–November(?)	Upper slope (?)	July	Slope/Shelf edge	3.8–7.5 <sup>b</sup>	15–20	5.8

<sup>a</sup> Reported fecundity for *Lepidopsetta* spp. in the eastern Bering Sea.

<sup>b</sup> Length at which rockfish larvae are extruded.

<sup>c</sup> Data for *Bathymaster signatus*.



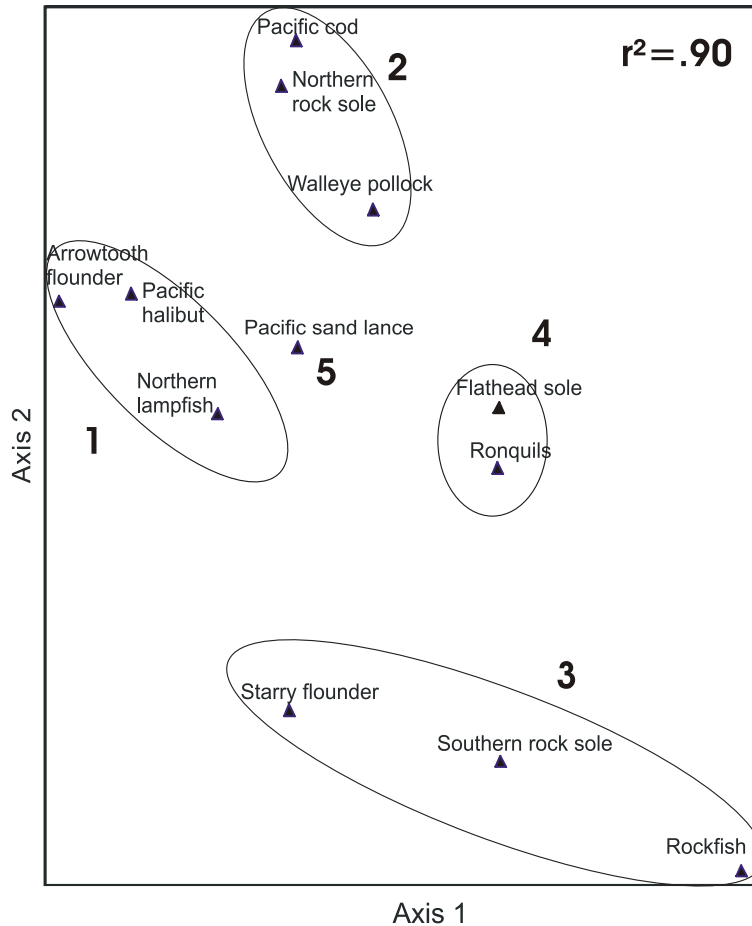


**Fig. 5.** Interannual trends in species mean larval abundance (and standard errors) from the late spring time-series of samples. Species are grouped based on common patterns of interannual trends and the pattern numbers are indicated in each species plot.

than continuous (Pattern 2). They grouped together on the NMDS plot and were spatially distinct from the Pattern 1 species. One exceptional year in this pattern was the anomalous super-abundance of walleye pollock larvae recorded in late spring of 1981, associated with the highest ever recorded annual level of egg production in this area (Picquelle and Megrey, 1993). The general signal in the abundance time-series for walleye pollock is masked by the influence of this single year; hence we excluded 1981 data for investigating links between abundance and environmental variables in the GAM analysis. The larval abundance trends for rockfish, southern rock sole, and starry flounder were characterized by a pattern of increasing abundance towards the end of the time series culminating in shared high abundance in 2001, followed by lower levels in 2002 and 2003 (Pattern 3). They formed a loose

group on the NMDS plot, but at a significant distance from the other species. Ronquils and flathead sole displayed a pattern that was distinguished by high amplitude of variation in abundance during the 1980s to early 1990s, and moderate variation in abundance for the rest of the time-series (Pattern 4). They plotted close together on the NMDS ordination (Fig. 6). A distinct pattern of low amplitude of variation and moderate abundance throughout the time-series was unique to Pacific sand lance (Pattern 5), and reflected in its central position in the NMDS plot relative to the other species groups.

The observed synchronicity in the interannual trends in late spring larval abundance reflects similarities in aspects of species spawning and early life history strategies (Figs. 4, 5 and Table 4). For instance, Pattern 1 species, characterized by highest levels of



**Fig. 6.** Non-metric, multidimensional scaling (NMDS) plot from ordination of species by abundance, using Bray–Curtis dissimilarity measures on yearly mean abundance, standardized by species totals.

abundance during the 1990s, spawn pelagic eggs in deep water and their early larval habitat is primarily over the slope and shelf edge in the GOA. Pattern 2 species are similar in terms of temporal and spatial patterns of larval production, with spawning occurring on or close to the bottom in shelf waters during late winter through spring and an April–May peak in larval abundance. In addition, Pattern 2 species have overlapping size ranges at hatching and transformation (Table 4) implying similarity in larval duration in the plankton. Although spawning habitat and mode, and larval habitat and duration are different among Pattern 3 species, timing of spawning and larval hatching is similar with the annual peak in larval abundance occurring during late spring to early summer. Similarly, the common feature of the two Pattern 4 species is temporal synchrony in larval abundance with an extended seasonal larval duration and a late spring to early summer peak in larval abundance.

### 3.3. Interannual trends in mean larval size

Time-series plots of mean standard length of larvae indicate that the amplitude of interannual variation in larval size among species is primarily related to the timing of spawning and larval hatching (Fig. 7 and Table 4). Variability in mean standard length of late spring larvae was highest by far for Pacific sand lance. Eggs of this species are deposited in coastal sediments during fall, and hatching takes place during late winter (March peak) to early spring, so that by late May the combined exposure of their eggs and larvae to the coastal and shelf environment is the most extensive of all the species. Arrowtooth flounder and Pacific halibut also displayed relatively high levels of variability in mean larval length over the

time-series. By late May, their larvae have been in the pelagic environment for up to 5 months. The amplitude of variation in mean larval length was similar and moderate for Northern rock sole, walleye pollock, and Pacific cod, reflecting a shared larval duration in late May of 2–3 months (Table 4 and Fig. 4). It is noteworthy that the extraordinarily high mean abundance value recorded for walleye pollock larvae in 1981 (Fig. 5) is not matched by an anomalous value in mean larval size that year (Fig. 7). For flathead sole, ronquils, starry flounder, southern rock sole, and rockfish, the amplitude of variation in mean larval length over the time-series was very low (Fig. 7). During late May these species' larvae range from newly hatched to a few weeks old. This low amplitude of variation in larval size suggests stability in the timing of spawning and larval production over the time-series.

Whereas amplitude of variation in mean larval length seems primarily a reflection of timing of larval production, among-species synchronicity in the interannual trends in mean larval length also seems to be connected to spawning and larval habitat as defined by water depth (Figs. 7, 8 and Table 4). Pacific sand lance and starry flounder plotted closest together in a central location on the NMDS plot (Fig. 8), and although timing of spawning is months apart for these species, they share a shallow water origin (Table 4). The synchronicity in their larval length over the time-series is notable in that the trend for Pacific sand lance appears to be a more exaggerated version (higher amplitude of variation) than the pattern for starry flounder (Fig. 7). Gradation in mean larval length synchronicity relative to early life history habitat is further reflected in the position of the remaining species on the NMDS plot (Fig. 8). Species whose spawning and larvae are primarily associated with

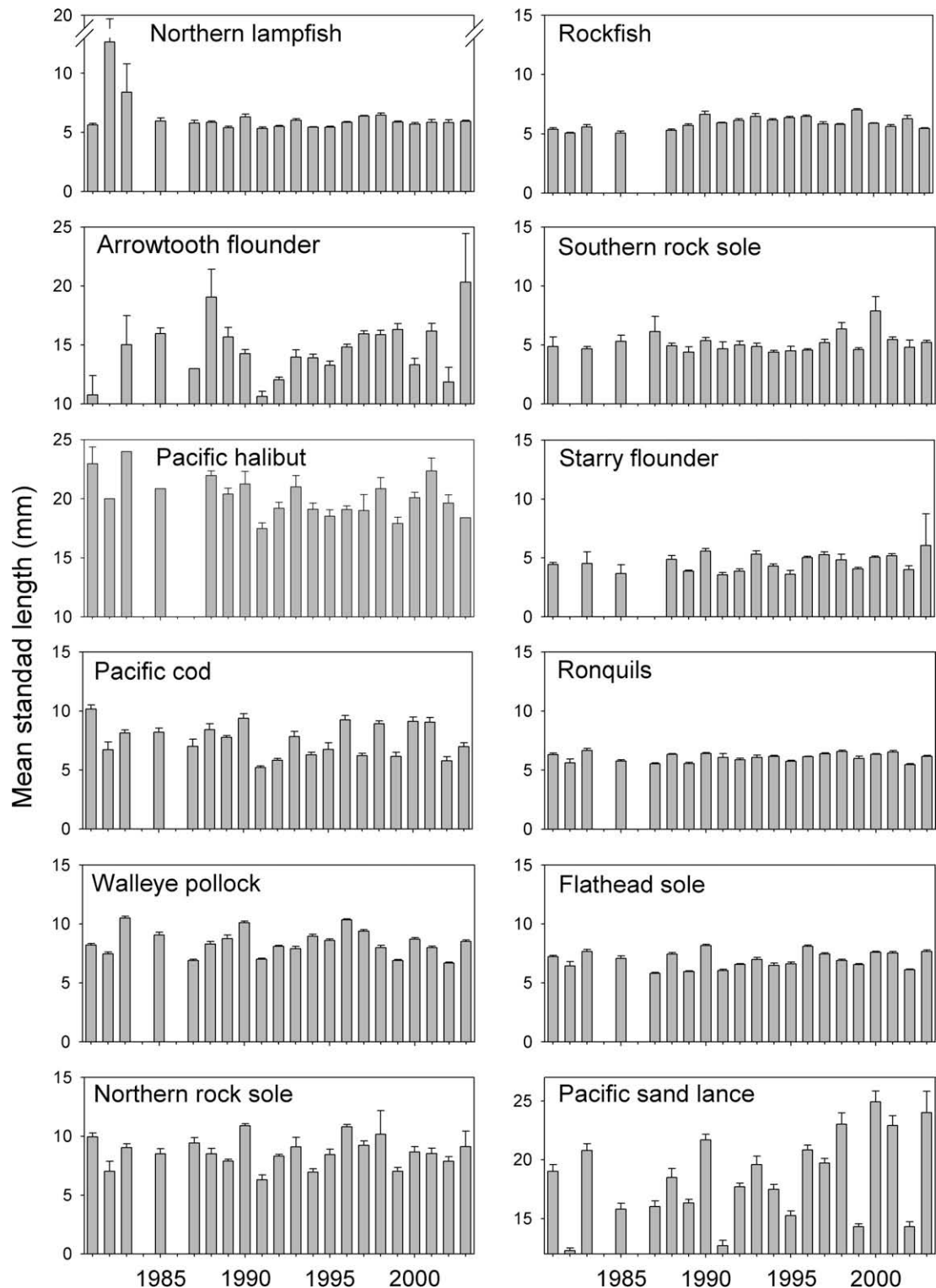
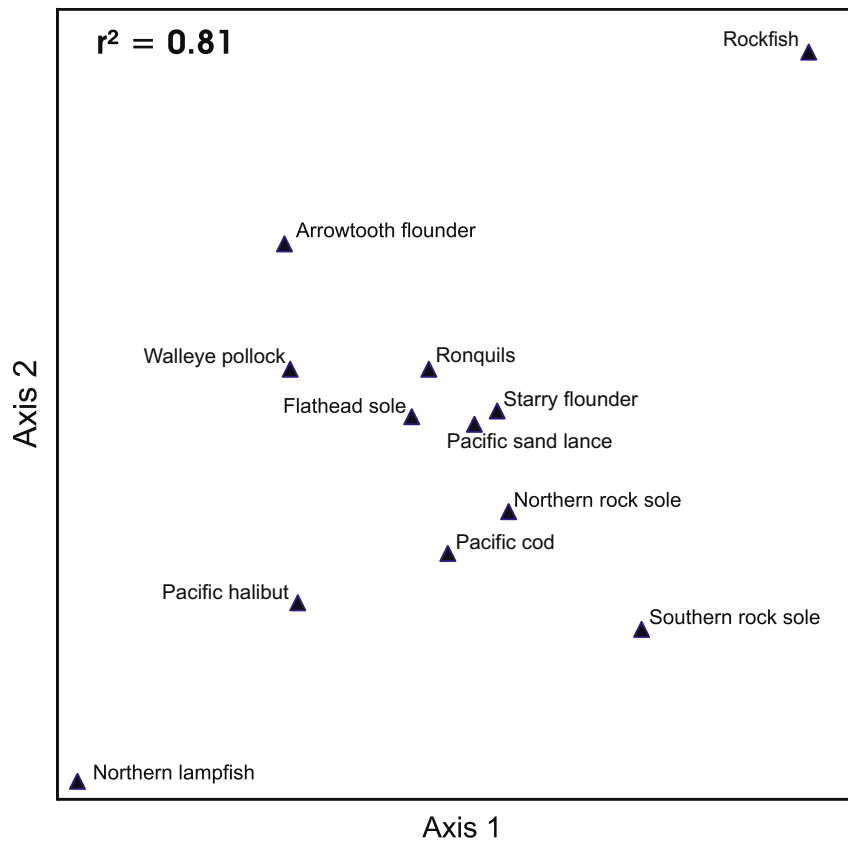


Fig. 7. Interannual trends in species mean larval lengths (and standard errors) from the late spring time-series of samples.

coastal and shelf waters (ronquils, flathead sole, walleye pollock, northern rock sole, and Pacific cod) plotted closest to each other and to the centrally positioned starry flounder and Pacific sand lance. Southern rock sole was somewhat of an outlier in this sense. In contrast, the deepwater spawners whose larvae are most abundant over the continental slope and outer shelf (arrowtooth flounder, Pacific halibut, northern lampfish and rockfish) were peripheral on the NMDS plot.

### 3.4. Linkages between species abundance and the environment

Results of the GAM analysis for each species indicate certain unique patterns of linkages with the monthly mean values for the basin- and local-scale variables (Table 5). There is also, however, a notable degree of similarity in the model-generated linkages among species with similar interannual trends in late spring larval abundance.



**Fig. 8.** Non-metric, multidimensional scaling (NMDS) plot from ordination of species by lengths, using species correlations expressed as distance measures  $((1 - r)/2$  where  $r$  is the Pearson correlation coefficient) of standardized annual mean length anomalies.

For Pattern 1 species, GAM results for spring months yielded stronger best-fit models than for winter months (Table 5). The May models for arrowtooth flounder and Pacific halibut included a positive association with the EP–NP index, and the latter species and northern lampfish were linked to the March value of this index, implying some influence from basin-scale atmospheric conditions from late winter to spring. Common to these three species was a significant positive association with the alongshore wind index for April implying the importance of alongshore winds to the transport of their larvae from slope waters onto the shelf and into Shelikof Strait. Fewer winter values of the variables contributed significantly to the models, with the exception of a strong model for arrowtooth flounder with the January values of the local-scale circulation variables, again suggesting their importance to the on-shore transport of eggs and larvae.

The strongest best-fit GAMs for the Pattern 2 species were the February–May models for basin-scale variables, and March–April models for local-scale variables (Table 5). Common to the three species at the basin scale were a positive link with the February AO index and a mostly positive association with April and May values of the EP–NP index. This suggests a persistent influence of broad-scale atmospheric conditions from the spawning and early larval phase through the planktonic phase. Further evidence of likely atmospheric influence on larval transport was the link between these species and April alongshore winds. Pacific cod and walleye pollock were also linked significantly with March alongshore winds and with the April Retention Index (RI). A negative association between Pattern 2 species and winter temperatures emerged as a link to January or February SST values, perhaps reflecting a negative impact of unusually warm winter conditions on their larval abundance. The negative link with SST persisted through May for northern rock sole.

The GAM models for Pattern 3 species (rockfish, southern rock sole, and starry flounder) yielded very weak links overall with the basin-scale variables (Table 5). An exception was the May model for rockfish in which the NP and EP–NP indices contributed significantly. Southern rock sole and starry flounder also shared a significant link with the EP–NP index through their March best-fit models, even though these models were weak. A shared association with winter freshwater runoff (FRESH), positive for southern rock sole and starry flounder, and a link to the May alongshore wind index characterized the best-fit models for the local-scale variables. The connection with winter FRESH is unlikely to reflect any influence on larvae as these species are primarily spring–summer spawners, whereas the strong association with spring alongshore winds implies influence from wind-driven transport variability on larval abundance trends. The positive associations of rockfish and southern rock sole with March–April SST values suggest that larval abundance for these spring–summer spawning species may be favored by relatively warm conditions. A striking feature of the GAM results for starry flounder is the overall weakness of the best-fit models compared to other species. These weak links with ocean–climate conditions are likely related to the very short larval phase that characterizes this species; transformation to juveniles and settlement out of the plankton occurs at 8–9 mm in length (Table 4).

Strong connections with the January values of the basin-scale variables, including a positive association with the PDO, were unique to the Pattern 4 species (ronquils and flathead sole) (Table 5). Spawning for these species in the GOA commences at very low levels during March (Table 4). The model-implied influence of basin-scale conditions during January therefore seems curious but perhaps reflects some degree of environmental forcing on spawning adults and habitat. Variable connections in common

**Table 5**

Results of GAM analysis for late spring larval species abundance versus monthly mean basin-scale variables (top half of list), and local-scale variables (bottom half of list).  $r^2$  values and level of variable significance are for best-fit GAM models for each species and month combination. Blank columns indicate weak best-fit models with insignificant level of contribution (at  $p > 0.05$ ) from constituent variables. Species are numbered and arranged in columns according to the groups described in Figs. 5 and 6.

Northern lampfish (1)						Pacific cod (2)						Rockfish (3)						Ronquils (4)					
Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May
PDO						PDO						PDO						PDO	Pos	Pos		Pos	
NP						NP				Pos		NP					Pos	NP			Neg		
AO						AO		Pos	Pos	Neg		AO	Neg					AO				Pos	
EP-NP						EP-NP				Pos	Pos	EP-NP						EP-NP					
MEI						MEI		Pos				MEI						MEI					
$r^2$ (adj)	0.05	0.15	0.41	0.22	0.26	$r^2$ (adj)	0.16	0.66	0.19	0.70	0.33	$r^2$ (adj)	0.22	0.05	0.03	0.00	0.55	$r^2$ (adj)	0.49	0.17	0.26	0.45	0.17
SST						SST		Neg				SST		Pos	Pos	Pos		SST				Pos	Pos
ALONG				Pos		ALONG						ALONG						ALONG					
MIXING					Pos	MIXING						MIXING						MIXING					
FRESH	Neg					FRESH			Neg			FRESH	Pos					FRESH			Pos		
FLOWKL8				Pos		FLOWKL8						FLOWKL8						FLOWKL8				Neg	
RI						RI						RI						RI					
$r^2$ (adj)	0.38	0.05	0.09	0.34	0.70	$r^2$ (adj)	0.04	0.17	0.50	0.48	0.05	$r^2$ (adj)	0.44	0.38	0.62	0.37	0.50	$r^2$ (adj)	0.13	0.19	0.81	0.52	0.53
Arrowtooth flounder (1)						Walleye pollock (2)						Southern rock sole (3)						Flathead sole (4)					
Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May
PDO				Neg		PDO						PDO						PDO	Pos				
NP				Neg		NP						NP						NP					
AO				Neg		AO		Pos		Neg		AO						AO					
EP-NP					Pos	EP-NP				Pos	Pos	EP-NP			Neg			EP-NP	Neg				
MEI						MEI						MEI						MEI					
$r^2$ (adj)	0.01	0.31	0.23	0.69	0.34	$r^2$ (adj)	0.07	0.50	0.02	0.50	0.40	$r^2$ (adj)	0.02	-0.03	0.26	0.02	0.09	$r^2$ (adj)	0.79	0.01	0.22	0.19	0.13
SST						SST	Neg					SST			Pos	Pos		SST					
ALONG		Pos		Pos		ALONG			Pos			ALONG						ALONG		Neg			
MIXING		Neg				MIXING						MIXING						MIXING		Pos			
FRESH		Neg				FRESH						FRESH	Pos	Pos				FRESH	Pos	Pos	Pos		
FLOWKL8						FLOWKL8						FLOWKL8				Pos		FLOWKL8					
RI						RI						RI						RI					
$r^2$ (adj)	0.58	0.06	0.15	0.66	0.03	$r^2$ (adj)	0.31	0.23	0.23	0.42	0.04	$r^2$ (adj)	0.20	0.60	0.16	0.47	0.45	$r^2$ (adj)	0.22	0.58	0.26	0.45	0.31
Pacific halibut (1)						Northern rock sole (2)						Starry flounder (3)						Pacific sand lance (5)					
Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May	Variables	Jan	Feb	Mar	Apr	May
PDO						PDO						PDO						PDO			Neg		Neg
NP						NP						NP						NP			Neg		
AO						AO		Pos				AO						AO					Neg
EP-NP			Pos		Pos	EP-NP				Pos		EP-NP			Neg			EP-NP					
MEI				Neg		MEI						MEI						MEI					
$r^2$ (adj)	0.11	0.21	0.37	0.40	0.17	$r^2$ (adj)	0.11	0.46	0.15	0.32	0.41	$r^2$ (adj)	0.07	0.04	0.27	-0.01	0.04	$r^2$ (adj)	0.16	0.28	0.35	0.21	0.42
SST				Neg		SST		Neg	Neg	Neg	Neg	SST						SST					
ALONG				Pos		ALONG				Pos		ALONG						ALONG			Pos		
MIXING						MIXING						MIXING						MIXING					
FRESH			Neg	Neg		FRESH						FRESH		Pos				FRESH	Neg		Neg		
FLOWKL8				Pos		FLOWKL8						FLOWKL8						FLOWKL8					
RI						RI						RI						RI			Neg		
$r^2$ (adj)	0.15	0.16	0.33	0.82	0.03	$r^2$ (adj)	0.00	0.26	0.66	0.56	0.20	$r^2$ (adj)	0.18	0.45	0.03	0.05	0.33	$r^2$ (adj)	0.37	0.21	0.65	0.03	0.27

variable contribution to model significant at  $P < 0.05$ 
 variable contribution to model insignificant at  $P \geq 0.05$ 
 variable absent from model

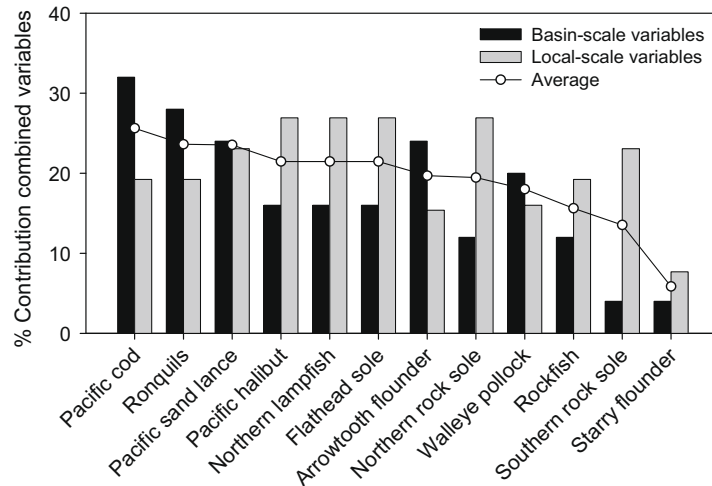
Pos variable effect significant and positive
 Neg variable effect significant and negative
  data unavailable

for the local-scale models were the links with winter alongshore winds and freshwater discharge suggesting that local conditions may also be important during the commencement of spawning. Influence of spring transport variability on larval abundance is implied by the connection between both species and April FLOWKL8, and by flathead sole's link with the May RI. A persistent influence on ronquil larval abundance from ocean temperature is implied by the positive association with the January and April values of the PDO and April–May SST values.

For Pacific sand lance, the strongest best-fit model was for the March local-scale variables (Table 5) suggesting that physical forcing, especially locally, is strongest during the period of peak hatching from coastal sediments. The positive association with alongshore winds implies enhanced larval dispersal from shallow water when wind-driven circulation is vigorous. Conversely, the negative link with the March RI suggests that dispersal of newly hatched larvae may be inhibited by sluggish circulation in Shelikof Strait and Sea Valley. Although dispersal of these larvae from coastal sediments is essential for their distribution throughout

shelf waters, the negative association with winter freshwater discharge may reflect some destructive effect at high levels of freshwater runoff on eggs in the sediment and newly emerging larvae. The May model was strongest for basin-scale variables (PDO, AO, and EP–NP indices) perhaps reflecting the importance of basin-scale climate forcing during late larval development. The link with the February, March, and May PDO, and the presence of SST in the January and March models imply a persistent influence from ocean temperatures.

Species are ranked according to their total combined links with the basin and local-scale variables; i.e., the total number of times basin- or local-scale variables were significant in monthly best-fit GAM models, expressed as a percentage of the maximum number possible of significant contributions for each species and each variable group (Table 5 and Fig. 9). This ranking of species is proposed here as a gradient of early life history vulnerability to the GOA physical environment. Pacific cod is the species displaying the highest number of links, and is therefore considered the most vulnerable to variability in the pelagic environment. Starry flounder



**Fig. 9.** Ranking of species according to their total combined links with the basin and local-scale variables; i.e., the total number of times basin- or local-scale variables were significant in monthly best-fit GAM models, expressed as a percentage of the maximum number possible of significant contributions for each species and each variable group (Table 5).

has the lowest number of connections to its environment implying the greatest resiliency to a changing environment.

### 3.5. Comparative influence of the physical environment on larval abundance

The relative influence of different aspects of the physical environment on larval fish abundance in late spring was evaluated by summarizing the GAM results for each monthly set of variable values across species (Table 5), and ranking the variables according to their total number of significant contributions to the 12 species best-fit models (Table 6). In addition, Appendix Tables A1 and A2 summarize the GAM results by the top-ranked variables, and Appendix Figs. A2–A10 show partial regression plots of variable effects for best-fit models that represent the most consistent variable effects among species. For both the basin-scale and the local-scale variables, the combined occurrences of the variables in the models were strongest for the April values relative to the other months. Seasonal variation in links with the variables was most pronounced for the EP–NP index and the Alongshore Wind Index, both with strong connections between spring values and species abundance, and for Freshwater Runoff that was primarily connected by the winter values (Table 6).

Ranking the variables according to their overall level of contributions to the models, and the number of species to which they were linked (Table 6) is a useful indicator of their relative influence on larval fish species abundance. It seems that basin-scale atmospheric circulation during spring (EP–NP index as proxy) and the related local-scale spring wind conditions (Alongshore Wind Index) impart the strongest influence on the prevalence of larval fish in the productive shelf waters of Shelikof Strait and Sea Valley in late May. Influence of larval transport by atmospheric forcing of Alaska Coastal Current (ACC) dynamics during April and May seems the most likely mechanism of environmental control in this respect. Freshwater runoff (FRESH) during winter months and sea surface temperature (SST) for winter and spring months also ranked highly. The former is most likely to affect larval abundance and survival by flushing eggs and larvae from coastal waters during winter, and also by influencing ACC dynamics and subsequent larval transport. Among species that displayed a persistent seasonal link with SST, the likely operative mechanisms are the potential influence of temperature on the dynamics of egg and larval production and the physiology of egg and larval development.

The three inter-related basin-scale climate indices, the AO, NP, and the PDO, were linked significantly to May larval abundance for several species, but with lower contributions to the models

**Table 6**  
Total number of significant contributions ( $p < 0.05$ ) of variables by month to 12 best-fit species models and total number of species to which each variable was linked. Variable contributions are based on data presented in Table 5. See Table 3 for definitions of variable acronyms.

Variables	Months					Months combined	
	Jan	Feb	Mar	Apr	May	% Contribution	No. of species
<i>Basin-scale</i>							
EP–NP	2	0	4	4	7	28.3	12
AO	2	3	1	5	1	20.0	9
NP	1	2	3	3	2	18.3	7
PDO	2	4	1	2	1	15.0	4
MEI	1	1	0	1	0	5.0	3
% Contribution Total variables	13.3	15.0	15.0	25.0	18.3	18.7	
<i>Local-scale</i>							
ALONG	1	1	4	6	4	26.7	12
FRESH	5	4	5	1	1	26.7	10
SST	1	3	3	5	3	25.0	8
FLOWKLS	No data	No data	1	5	0	16.7	6
MIXING	2	1	2	2	1	13.3	6
RI	No data	No data	1	2	1	11.1	4
% Contribution Total variables	18.8	18.8	22.2	29.2	13.9	20.8	

than the EP–NP index and the local variables ALONG, SST, and fresh (Table 6). The most persistent pattern for these variables was the positive association with February AO values for Pattern 2 species and a negative association with April values for most of the Pattern 1 and 2 species. The strength of the AO signal in the models for Pattern 2 species seems to reflect a connection with cooler winter conditions, as indicated by concurrent negative associations with winter SST values for these species (Table 5). Likewise, the links with spring values of the NP index for most species connected with this variable were mirrored in the associations between these species and local spring alongshore winds (Table 5). The weaker connection with the PDO among species relative to SST suggests that the basin-scale temperature signal is less important to ichthyoplankton abundance than local temperature conditions. This is further implied by the very weak connection that emerged between species abundance and the MEI index (Table 6).

Larval transport and retention in Shelikof Strait, as described by FLOWKL8 and the RI, contributed significantly to the spring models for six and four species, respectively (Table 6). Their ranking relative to the basin-scale atmospheric circulation (EP–NP) and northern GOA alongshore winds, however, implies dominance of the upstream transport dynamics for prevalence of larvae in the Shelikof area during late May, relative to transport within the study area itself. Wind mixing had a limited contribution to the models, but was most connected to Pattern 1 species that are transported in to the study area from the slope (Tables 5 and 6). Northern lampfish and arrowtooth flounder had a negative association with January values of MIXING implying an inhibiting effect from winter storm events.

### 3.6. Among-species affinity and synchrony in larval abundance trends, links with physical variables, and early life history strategies

The overall pattern that emerges from the GAM analysis is that larval fish abundance in late spring is linked to combinations of

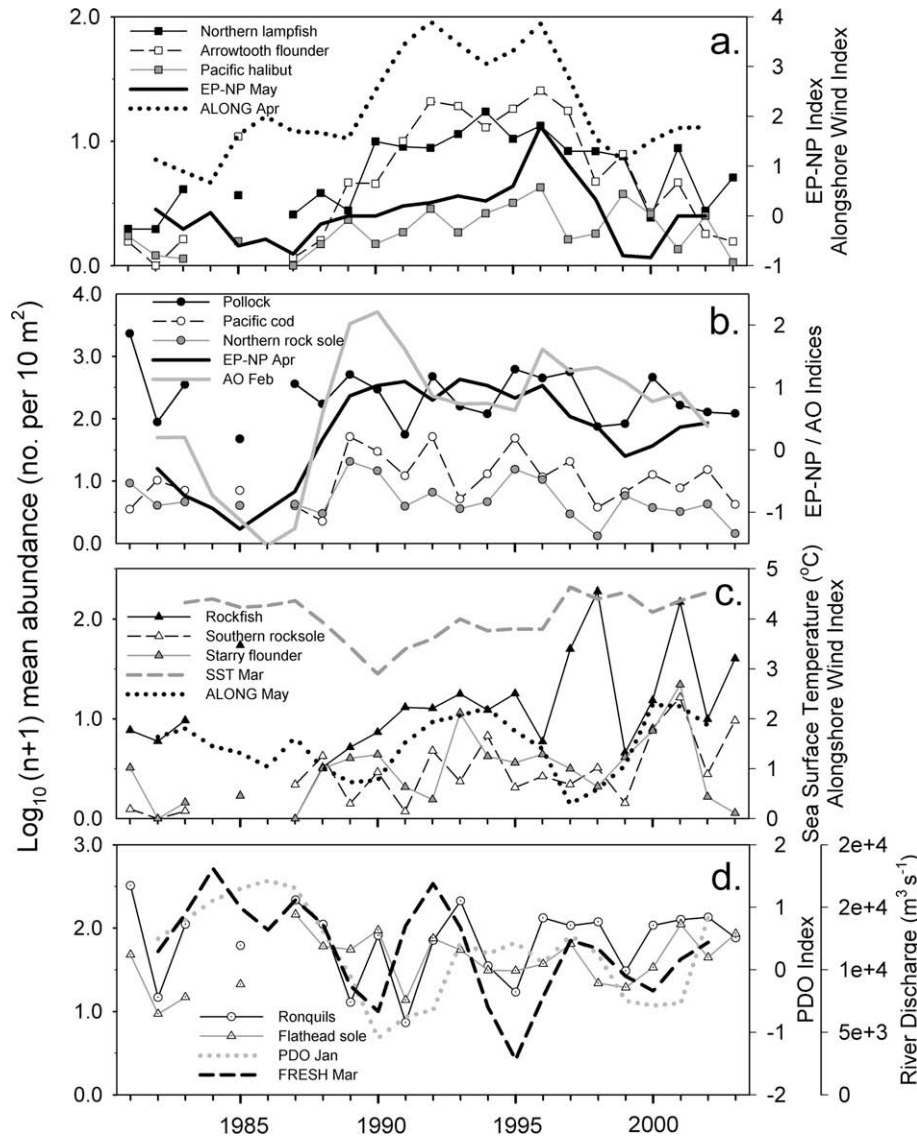
environmental variables with seasonal variation in linkages. In addition, the nature of the links between the larval abundance and the physical variables reflects details of individual species early life history strategies. Observed similarities in interannual trends in larval abundance, variable connections, and early life history traits among species suggest common mechanisms of environmental control on prevalence of larvae in late May (Table 7). Furthermore, they imply synchrony among species in early life history driven responses to environmental forcing in the study area.

Such synchrony seems evident visually in time-series plots of species larval abundance ( $\log_{10}(n+1)$  values) and 3-year running means of the highest ranking physical variables to which they were linked in the GAM models (Fig. 10). Three-year running means were plotted to emphasize the smoothed trends in the physical variables time-series. Species are grouped according to common interannual trend patterns (Figs. 5 and 6) and shared connections with the physical environment (Tables 5 and 7). For instance, the period of elevated abundance for northern lampfish, arrowtooth flounder, and Pacific halibut larvae during the 1990s coincides with a persistent positive phase of the spring EP–NP index and enhanced April alongshore winds (Fig. 10a). Given that occurrence in the study area for these species is largely dependent on transport from deep water over the slope, it seems that the primary mode of physical forcing on their larval abundance is the prevailing pattern of atmospheric circulation and associated local winds that drive onshore and alongshore larval transport (Table 7). Similarly, years of high levels of abundance of Pattern 2 species (walleye pollock, Pacific cod, and northern rock sole) coincided with the 1990s positive phase of both the spring EP–NP index and the February AO index (Fig. 10b), implying that elevated late spring abundance is favored primarily by cooler winters and enhanced basin-scale atmospheric circulation in spring with associated optimal local wind conditions (Table 7). The trend of increasing larval abundance towards the end of the time-series for rockfish, southern rock sole,

**Table 7**

Common linkages with physical variables relative to interannual patterns in larval abundance and species life history strategies, and implied nature of physical environmental forcing on late spring larval abundance in the vicinity of Shelikof Strait, Gulf of Alaska. See Table 3 for interpretation of variable abbreviations.

Species	Interannual trend pattern	Early life history traits for GOA populations	Emergent variable connections from GAM analysis	Implied influence of physical forcing on late spring larval abundance
<i>Pattern 1</i> Northern lampfish Arrowtooth flounder Pacific halibut	Decadal pattern of highest levels of abundance during 1990s.	Winter–spring spawning deep water. Mesopelagic eggs. Shoreward from slope and along-shelf larval drift.	Primarily positive with spring EP–NP and ALONG. Negative with winter FRESH (A. flounder, P. halibut). Link with spring SST or PDO, negative for A. flounder and P. halibut.	Favored by enhanced wind-driven onshore and alongshore transport in spring. Negative effect from high winter freshwater runoff and high spring temperatures (A. flounder and P. halibut).
<i>Pattern 2</i> Pacific cod Walleye pollock Northern rock sole	Occasional years of high levels of abundance, late 1980s to mid 1990s.	Late winter–early spring spawning in shelf waters on or close to bottom. April peak in larval abundance. Larval size range and duration similar. Along-shelf larval drift.	Positive with Feb AO and spring EP–NP. March–April ALONG. Negative with winter SST. April RI (P. cod and walleye pollock).	Favored by positive phase of AO index with associated cooler winters, and by a positive spring EP–NP index with associated optimal local alongshore winds. Larval retention important in April.
<i>Pattern 3</i> Rockfish Southern rock sole Starry flounder	Trend of increasing abundance towards the end of the time-series.	Late spring–summer spawning (Rockfish, S. rock sole). Dispersal from shallow water (S. rocksole, S. flounder), shoreward from slope (rockfish). Along-shelf larval drift.	May ALONG. March or May EP–NP. Positive with winter FRESH (S. rock sole, Starry flounder). Positive with winter–early spring SST (rockfish, S. rock sole).	Favored by optimal levels of local alongshore winds in late spring. Warmer early spring temperatures favorable to rockfish and southern rock sole.
<i>Pattern 4</i> Ronquils Flathead sole	Greatest amplitude of variation in abundance 1980 through early 1990s. Moderately abundant mid-1990s through 2003.	Late winter–summer spawning with peak larval abundance May–June and larvae present in plankton through October. Along-shelf larval drift.	Strongest connections with Jan basin-scale variables including positive with PDO. Positive with late winter FRESH. Positive with spring SST (ronquils), April FLOWKL8.	Favored by positive phase of winter PDO, optimal winter alongshore winds and enhanced late winter freshwater runoff. Spring local temperatures and Shelikof transport important to larvae.
<i>Pattern 5</i> Pacific sand lance	Low level amplitude of variation in abundance throughout time-series.	Primarily fall spawning, eggs overwinter in coastal sediments, peak hatching in March. Dispersal from beaches, seaward, and along-shelf larval drift.	Strongest connections with March local-scale conditions, especially transport variables. Negative with Jan and March FRESH. Negative with March and May PDO.	Larval dispersal favored by vigorous alongshore winds and inhibited by sluggish circulation. Negative effect from enhanced winter freshwater runoff. Negative phase of late-winter/spring PDO favorable.



**Fig. 10.** Time-series plots of species larval abundance ( $\log_{10}(n+1)$ ), and 3-year running means of the highest ranking physical variables to which they were linked in the GAM models. (a) is for Pattern 1 species, (b) for Pattern 2 species, (c) for Pattern 3 species, and (d) for Pattern 4 species.

and starry flounder appears synchronous with the combined trends for early spring SST and late spring alongshore winds (Fig. 10c). In particular, the warmer early spring temperatures from the late 1990s to the end of the time-series appears favorable to late spring larval abundance of the spring–summer spawning rockfish and southern rock sole (Tables 5, 7 and Fig. 10c). This apparent influence from water temperatures may be moderated by the effect of late spring alongshore winds on larval dispersal (Fig. 10c). Given that ronquils and flathead sole are late winter to summer spawners, a mechanism of physical forcing that acts primarily prior to and during early spawning activity is implied by the largely synchronous and positive relationship of these species larval abundance with the early winter PDO index and the late winter freshwater runoff (Fig. 10d). Most noteworthy in the time-series is the steep decline in abundance of these species during the late 1980s in synchrony with the precipitous decline in the January PDO and March freshwater runoff (Fig. 10d). In addition, both these species seemed to respond similarly to spring local temperature conditions (SST) and transport in Shelikof Strait (ALONG, FRESH, and FLOWK18) during their early larval phase (Tables 5 and 7).

The idea that emerges from these results is that detailed knowledge of individual species' early life history strategies is a key

factor to understanding links between larval fish abundance trends and the physical environment, and potential response of individual fish species to physical forcing during their early life history phase.

#### 4. Discussion

The vicinity of Shelikof Strait and Sea Valley in the northwest GOA is an important spawning area and nursery habitat for many northeast Pacific fish species (Kendall and Dunn, 1985; Brodeur et al., 1995; Kendall et al., 1996; Bailey and Picquelle, 2002; Doyle et al., 2002; Stark and Somerton, 2002; Bailey et al., 2003; Matarese et al., 2003; Porter, 2005; Abookire and Bailey, 2007). Given the physical and biological complexity of this ecosystem (Bailey et al., 2005), and the diversity of life history strategies among the fish species, it is expected that the time-series of larval fish abundance presented here may be limited in terms of yielding a realistic representation of fluctuations in larval fish populations. Nevertheless, the co-variation that emerged in patterns of larval abundance, and the nature of the links between species and the physical environment, indicate that the temporal trends observed reflect actual fluctuations.



Larval abundance is considered to primarily reflect the reproductive effort of the adult stock in an area, although any correlation between a measure of annual larval abundance and spawning biomass is likely to become weaker with increasing age of the larvae (Pepin, 2002; Hsieh et al., 2005a). Our study area represents variable spatial coverage of the geographical spawning and early larval habitat range of the fish species under investigation (Matarese et al., 2003). Furthermore, timing of spawning and annual peak in larval abundance is variable among species. Therefore, variation in species larval abundance over the time-series is likely to represent varying proportions of both the interannual variation (temporal and spatial) in initial production of eggs and larvae, and the subsequent influence from the cumulative effect of the environment on larval abundance and survival.

Starry flounder, southern rock sole, and rockfish species have peak spawning in late spring to summer and larvae that are small in late May. Therefore, it is reasonable to assume that the observed interannual trends in their larval abundance reflect aspects of initial larval production (spawning, hatching, and early larval survival) more than an extended period of larval drift and development. Population assessment trends in GOA female spawning biomass for starry flounder, southern rock sole, and two of the commercially caught rockfish species (Pacific Ocean perch and dusky rockfish) provide some evidence for this assumption. Larval trends of highest levels of abundance at the end of the 1990s and early 2000s reflect an increase in spawning biomass for these stocks over this period (<http://www.afsc.noaa.gov/refm/stocks/assessments.htm>). Actual years of highest larval abundance anomalies, however, do not necessarily match up with years of highest actual spawning biomass (assessed from groundfish surveys every 2–3 years). In contrast, larval abundance trends for winter spawners such as arrowtooth flounder and Pacific halibut also incorporate the cumulative effect of the environment from spawning of eggs through an extended period of larval drift, development, and survival to the late-larval stage encountered in May. An intermediate balance of influences from both the initial production of eggs and larvae, and the cumulative exposure of larvae to the pelagic environment is presumed for the remaining species that display seasonal patterns in spawning and larval abundance intermediate to the latter two extremes. Trends in larval abundance and spawning biomass for these winter–spring spawners tend to be poorly matched over the time-series (<http://www.afsc.noaa.gov/refm/stocks/assessments.htm>), suggesting a diminished influence of initial spawning levels on larval trends relative to the cumulative effect of the environment.

Any shift in timing of spawning and larval hatching among fish species over the time-series would confound the interpretation of the larval abundance trends in terms of the influence of initial level of egg and larval production versus cumulative environmental influence. Phenological shifts in marine fish reproductive timing have been difficult to document due to the paucity of adequate time-series of data (Edwards and Richardson, 2004; Sims et al., 2004; Greve et al., 2005). However, even in the absence of high-frequency sampling over the full temporal extent of a species spawning and early life history phase, some indication of a phenological shift in larval production may be gained from an examination of mean larval length over the time-series. The very low amplitude of interannual variation in mean larval length observed for the spring–summer spawning species suggests consistency in the timing of larval production over the time-series, implying stability for the peak period of spawning and larval hatching. This phenological stability is also implied by the close relationship between the amplitude of variation in mean length among species and the duration that their larvae have been in the plankton at the time of sampling. The extent of larval exposure to environmental forcing, therefore, is likely to be the primary determinant of the observed

amplitude of interannual variation in species mean larval length. The absence of a significant phenological signal in the larval abundance time-series is also supported by the fact that the superabundance of walleye pollock larvae recorded in 1981 was not matched by an anomalous mean length value that year. The extraordinary 1981 record seems more a reflection of enhanced spawning biomass and egg production in the study area (Picquelle and Megrey, 1993) rather than a shift in timing of larval production, or an unusual level of larval survival.

The larval size data suggests that the degree of variation in the physical environment encountered by these fish species over the course of the study may perhaps have remained within the range of optimal conditions suitable for normal temporal patterns in reproduction to prevail. Whereas temporal consistency in egg and larval production in the study area may have been the norm over these years, the physiological, drift, and survival response of individual eggs and larvae is likely to have been much more sensitive to variability in the physical environment, especially at the local scale. The connection between synchronicity in mean larval lengths over the time-series and shared early life history habitats suggests that there may be a similar growth response to physical forcing among species with similar patterns of exposure to the pelagic environment.

In their review of recruitment processes of walleye pollock in the physically and biologically complex ecosystem of the GOA, Bailey et al. (2005) consider that variability in the dynamics of the population begins during the egg and larval stage with the impact of generally small-scale, environmental processes (termed “activating factors” in the recruitment process) on egg and larval survival. The collective early life history response of GOA fish species to such “activating factors” is presumably represented in the time-series of larval abundance trends, and in their relationships with the physical variables generated by the GAM models. Support for this idea is evident in the affinities that emerged between species larval abundance trends, their relationships with the physical variables, and their individual early life history strategies. This commonality of life history traits among species that displayed similar interannual trends and shared variable connections is indicative of a common pattern of exposure and response to physical aspects of the pelagic environment, at the scale of spawning location and egg and larval habitats.

Unique aspects of certain species’ early life history traits were reflected in a pattern of links to the physical variables unique to that species, providing further evidence for a strong connection between the nature of a species environmental exposure and their associated response during early life history. In the case of Pacific sand lance, the extended incubation of primarily fall spawned eggs in intertidal sediments over winter months (Robards et al., 1999a,b) is followed in March by what appears to be an intense period of hatching (Matarese et al., 2003; Doyle, unpublished data), and peak vulnerability of newly hatched larvae to the local physical environment, as indicated by the strong GAM-generated connections with all March local-scale variables. Conversely, starry flounder had the weakest connections overall with the physical variables, implying the strongest larval resilience to the physical environment, and reflecting the short larval duration and therefore limited exposure to the pelagic environment for this species. The implications for recruitment dynamics are that Pacific sand lance are likely to suffer elevated levels of mortality during hatching and emergence of yolk-sac larvae into the plankton, whereas starry flounder may endure lower levels of mortality during the larval phase relative to other species because of its reduced larval duration and exposure.

Bailey et al.’s (2005) concept of “activating” environmental factors (influencing recruitment outcome) operating at a high-frequency temporal scale during the egg and larval phase is

supported here by the monthly and seasonal variation in the apparent influence of the physical variables on larval abundance levels in late May. The GAM-generated species links with various physical variables were not persistent over the five monthly mean values used in the models, and in many instances only one monthly mean value of a particular variable contributed significantly to any of the five monthly best-fit models. Seasonal progression in relative influence of variables was also apparent. This emphasizes the importance of using short temporal scale measurements of physical variables (weekly and monthly means being preferable to seasonal means) when investigating their potential influence on larval abundance and survival. Individual fish species responses to environmental change will vary from the spawning stage through early ontogeny, because of varying physiological and behavioral responses of different life stages and varying degrees of environmental exposure encountered within the spawning, egg, and larval habitats.

Among various marine organisms, timing and duration of ontogenetic intervals are recognized as important variables determining how populations respond to external forcing. Although non-linear responses to physical forcing is considered the norm (Dixon et al., 1999; Hsieh et al., 2005b), it has also been hypothesized that populations are most likely to track stochastic environmental forcing when their generation time matches the characteristic time scale of the environmental signal (Hsieh and Ohman, 2006). The GAM analysis presented here supports the idea of a linear response (or curvilinear response with a strong positive or negative trend) among species to certain physical variables, at a temporal scale of one to four months. For instance, the positive and predominantly linear association of late spring larval abundance for Pacific cod, walleye pollock, northern rock sole, arrowtooth flounder, and Pacific halibut with spring values of the EP–NP index, and the absence of any link with winter values of this variable, implies a linear response by these species, during part of their larval phase, to climate fluctuations represented by this mode of atmospheric variability. Similarly, the positive and linear association with winter freshwater discharge for ronquils and flathead sole suggests a linear response to this variable during the commencement of spawning for these species. Pacific sand lance also tracked winter values of freshwater discharge (negatively) during the incubation of eggs in coastal sediments (January) and the peak period of larval hatching (March) for this species. A linear response to water temperature during the early larval phase seems probable for northern rock sole (negative) and southern rock sole (positive), whereas the positive association of rockfish with February through April values of SST implies a response during the commencement of larval extrusion of these viviparous species. In the context of understanding the influence of physical forcing on larval fish populations, the “Linear Tracking Window” hypothesis of Hsieh and Ohman (2006) therefore seems an appropriate framework for investigating underlying mechanisms of early life history response to environmental change. It can be refined further by considering the potential ecological response at shorter time scales than the complete generation time of a particular cohort of larvae. Rather, among individual species the intervals of spawning, egg incubation, hatching, early larval development, and late larval phase, are important and their associated unique patterns of exposure and response to the marine environment need to be considered.

Evaluating and ranking the physical variables according to their number of significant contributions to the GAM best-fit models has good potential for aiding in the identification of ecological indicators for larval fish abundance among GOA fish species. The position of alongshore winds, GOA freshwater runoff, and Shelikof SST as the highest ranked local-scale variables implies that ACC dynamics, especially upstream of Kodiak, and associated temperature condi-

tions are the most important components of local physical forcing on the prevalence of various larval fish species in the favorable habitat of Shelikof Strait and vicinity. This is not surprising given that the Alaska Coastal Current is the main path of dispersal for most larval fish in this region, and given the present understanding of wind, freshwater runoff and temperature influence on the dynamics of Shelikof larval walleye pollock populations (Bailey and Macklin, 1994; Bailey et al., 1996, 2005; Kendall et al., 1996; Stabeno et al., 2004). More interesting is the emergence of the EP–NP index as the overall top ranking variable. Its connection with all the species, primarily through the spring values, suggests that the variability in atmospheric circulation in the North Pacific that it represents has a significant and detectable influence on fish early life history dynamics at the local scale. The PDO, NP, and MEI indices, but especially the PDO, have recently been the more traditional choice for representing basin-scale climate change and its potential biological consequences (Hare and Mantua, 2000; Mackas et al., 2001; Hollowed et al., 2001; Petersen and Schwing, 2003; Hsieh et al., 2005b; Lees et al., 2006). These indices were developed to characterize winter conditions over the North Pacific as a whole, which may explain their lower rankings in this study, particularly relative to the EP–NP index, but also in relation to the AO index representing polar vortex variability and associated sub-arctic atmospheric anomalies. The EP–NP mode has its strongest expression in the northern GOA, and at a crucial time of year (spring) for larval development among GOA fish species. The EP–NP index may therefore be a good choice as an ecological indicator that could connect aspects of fisheries variability with basin-scale climatic processes, and merits further investigation in this respect.

The phenomenon of synchrony in recruitment patterns and biomass trends among northeast Pacific fish populations, and potential mechanistic links with physical environmental forcing, has received much interest in recent years, especially as it relates to the development of ecosystem-based fisheries management (Boldt, 2005; Mueter et al., 2007). Patterns of variation in recruitment and survival of marine and anadromous fishes show synchronicity among stocks ranging from regional to broad geographical scales, and a common hypothesis emerging from such studies is that strong co-variation in recruitment trends is likely to reflect common responses to environmental forcing (MacCall, 1996; McGowan et al., 1998; McFarlane et al., 2000; Hollowed et al., 2001; Botsford and Lawrence, 2002; Mueter et al., 2002, 2007; Field and Ralston, 2005). Furthermore, it is recognized that life history traits are fundamental to the mechanistic links between environmental change and recruitment (Winemiller and Rose, 1992; Spencer and Collie, 1997; King and McFarlane, 2003, 2006; Conover et al., 2005; Field and Ralston, 2005; Shuter and Abrams, 2005; Winemiller, 2005). The synchrony in GOA species larval abundance, similarities in links with physical variables, and commonality of early life history strategies that emerged in this study imply that a common response to physical forcing takes place during early life history, particularly the planktonic phase, among species with common patterns of exposure to the physical environment. This exposure–response coupling seems connected to both local-scale and basin-scale environmental signals, to varying degrees depending on specific early life history characteristics.

Further evidence of the link between synchronous responses at the early life history phase and broad-scale climate ocean conditions is the apparent responses of the GOA larval fish abundance trends to the proposed “regime shifts” in oceanic and climatic conditions of 1989 and 1998 in the North Pacific. The highest amplitude of variation in larval species abundance and associated physical variables took place at the end of the 1980s, corresponding to the regime shift identified in 1989 (Hare and Mantua, 2000; Benson and Trites, 2002; Rodionov and Overland, 2005; Lees et al., 2006), and at the end of the 1990s, corresponding to the suggested

1998 regime shift (Petersen and Schwing, 2003; Bond et al., 2003; Rodionov and Overland, 2005; Lees et al., 2006). Relatively abrupt changes in zooplankton biomass and species composition in the northeast Pacific have been documented in response to these particular regime shifts (Mackas et al., 2001, 2004; Batten and Welch, 2004), implying a broad planktonic connection with basin-scale change that may have affected these populations in the northern Gulf of Alaska. In addition, Smith and Moser (2003) noted shifts in larval abundance trends among a variety of fish species in the California Current region in association with the 1989 and 1999 ocean–climate changes, although mechanistic links with particular oceanographic variables remain unclear. For each of the latter studies, the proposed regime shifts of 1989 and 1999 have been associated with ENSO events, specifically the El Niño event of 1987 and the El Niño–La Niña transition of 1998–1999. This implies a connection between GOA larval abundance trends and ENSO signal variability that was not reflected in the model-generated links between larval species abundance and the MEI index in this study. Rather than indicating a lack of response to ENSO events, it is likely that the episodic nature of the MEI index makes it less suitable as a predictive climate metric for larval abundance trends than other associated physical variables.

This type of study is valuable in the following respects. It has good potential for assessing the degree of vulnerability or resilience of individual species early life history patterns to fluctuating climate and oceanographic conditions. It also provides crucial information to help identify “environmental indicators” that may have a broad-spectrum effect on multiple species early life history stages as well as those that may be more species-specific in exerting control on early life history survival. In both instances it can contribute to our understanding of early life history aspects of recruitment processes and potential mechanistic links between climate change and recruitment among northeast Pacific fish species. Bailey’s (2000) “shifting control hypothesis” states that the dominant mechanisms of walleye pollock survival changed over contrasting climate regimes, with larval and juvenile survival varying in importance to ultimate recruitment outcome. It is likely that this shifting stage-specific control of recruitment may also apply to other fish species in this region, and this underlines the importance of considering different ontogenetic stages and their associated exposure and response connections with their physical and biological environments.

Ultimately, investigations of ichthyoplankton dynamics and stage-specific life history connections with the ocean environment can contribute to the development of predictive models for marine ecosystems. This process begins with a conceptual model of the operative mechanisms that regulate or control recruitment. Early life history studies such as this provide important information on what processes to incorporate into these models. Recent advances in ocean ecosystem modeling include recognition of the need for coupling individual-based modeling of marine organisms, such as commercially important fish species, and life history theory (de Young et al., 2004). In this respect, an ecosystem model should incorporate developmental stage-structured representations of target species in which key life history stages and their links to the environment are explicitly formulated (de Young et al., 2004; Rose, 2005). Clearly, there is a need for improving our knowledge of comprehensive life history characteristics of marine fish species, including stage-specific environmental links, to affect an ecosystem approach to fisheries management.

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### Appendix A

**Table A1**

GAM results summarized by the top-ranked basin-scale physical variables. Significance level, positive (Pos) or negative (Neg) trends for the variable effect, and linearity are indicated for partial regression plots of species with individual variables.

Variable	Month	Species	Species group	p Value	Variable effect	Linear
EP-NP	January	Ronquils	4	0.020	Neg	
		Flathead sole	4	<0.0001	Neg	
	March	Northern lampfish	1	0.022		
		Pacific halibut	1	0.019	Pos	
		Southern rock sole	3	0.047	Neg	
	April	Starry flounder	3	0.031		
		Arrowtooth flounder	1	0.018		
		Pacific cod	2	<0.0001	Pos	
		Walleye pollock	2	0.006	Pos	
	May	Northern rock sole	2	0.009	Pos	Yes
		Arrowtooth flounder	1	0.034	Pos	Yes
		Pacific halibut	1	0.030	Pos	Yes
		Pacific cod	2	0.030	Pos	Yes
		Walleye pollock	2	0.002	Pos	Yes
		Northern rock sole	2	0.008		
		Rockfish	3	0.014		
Pacific sand lance	5	0.024				

(continued on next page)

**Table A1** (continued)

Variable	Month	Species	Species group	p Value	Variable effect	Linear
AO	January	Rockfish	3	0.039	Neg	
		Flathead sole	4	0.037		
	February	Pacific cod	2	0.002	Pos	
		Walleye pollock	2	0.001	Pos	
		Northern rock sole	2	0.002	Pos	
	March	Pacific cod	2	0.029	Pos	Yes
		April	Pacific cod	2	0.008	Neg
	Walleye pollock		2	0.017	Neg	
	Ronquils		4	0.042	Pos	Yes
	Arrowtooth flounder		1	0.011	Neg	Yes
	Pacific halibut		1	0.004	Neg	Yes
	May	Pacific sand lance	5	0.009	Neg	Yes
		February	Pacific cod	2	0.020	
	March		Walleye pollock	2	0.016	Neg
		Northern lampfish	1	0.038		
Ronquils		4	0.011	Neg	Yes	
April	Pacific sand lance	5	0.038	Neg	Yes	
	Northern lampfish	1	0.019	Neg	Yes	
	Arrowtooth flounder	1	0.002	Neg		
	Pacific cod	2	0.012	Pos	Yes	
May	Northern lampfish	1	0.011	Pos	Yes	
	Rockfish	3	0.004	Pos	Yes	
PDO	January	Ronquils	4	0.003	Pos	Yes
		Flathead sole	4	0.0007	Pos	Yes
	February	Arrowtooth flounder	1	0.017		
		Ronquils	4	0.035	Pos	Yes
		Pacific sand lance	5	0.028		
	March	Pacific sand lance	5	0.018	Neg	
		April	Arrowtooth flounder	1	0.035	Neg
	Ronquils		4	0.001	Pos	Yes
	May	Pacific sand lance	5	0.032	Neg	

**Table A2**

GAM results summarized by the top-ranked local-scale physical variables. Significance level, positive (Pos) or negative (Neg) trends for the variable effect, and linearity are indicated for partial regression plots of species with individual variables.

Variable	Month	Species	Species group	p Value	Variable effect	Linear	
ALONG	January	Arrowtooth flounder	1	0.013	Pos	Yes	
		February	Flathead sole	4	0.008	Neg	
	March	Pacific cod	2	0.006			
		Walleye pollock	2	0.045	Pos		
		Ronquils	4	<0.0001			
	April	Pacific sand lance	5	0.003	Pos		
		Northern lampfish	1	0.005	Pos	Yes	
		Arrowtooth flounder	1	<0.0001	Pos		
		Pacific halibut	1	0.001	Pos		
		Pacific cod	2	0.024			
	May	Walleye pollock	2	0.012			
		Northern rock sole	2	0.037	Pos	Yes	
		Northern lampfish	1	0.007	Neg		
		Rockfish	3	0.004			
		Southern rock sole	3	0.003			
	FRESH	January	Starry flounder	3	0.014		
			Arrowtooth flounder	1	<0.0001	Neg	Yes
Rockfish			3	0.027	Pos		
February		Southern rock sole	3	0.030	Pos	Yes	
		Flathead sole	4	0.220	Pos	Yes	
		Pacific sand lance	5	0.019	Neg	Yes	
		Pacific halibut	1	0.048	Neg		
		Southern rock sole	3	0.001	Pos		
March		Starry flounder	3	0.002	Pos		
		Flathead sole	4	<0.0001	Pos	Yes	
		Pacific halibut	1	0.005	Neg	Yes	
		Pacific cod	2	0.034	Neg		
		Ronquils	4	<0.0001	Pos	Yes	
		Flathead sole	4	0.010	Pos	Yes	
		Pacific sand lance	5	0.015	Neg	Yes	
April		Pacific halibut	1	0.006			
		May	Northern lampfish	1	0.047		

Table A2 (continued)

Variable	Month	Species	Species group	p Value	Variable effect	Linear	
SST	January	Walleye pollock	2	0.007	Neg	Yes	
		February	Pacific cod	2	0.040	Neg	Yes
		Northern rock sole	2	0.013	Neg	Yes	
	March	Rockfish	3	0.006	Pos		
		Northern rock sole	2	0.011	Neg	Yes	
		Rockfish	3	0.0001	Pos		
	April	Southern rock sole	3	0.047	Pos	Yes	
		Pacific halibut	1	0.022	Neg	Yes	
		Northern rock sole	2	0.018	Neg		
		Rockfish	3	0.008	Pos		
		Southern rock sole	3	0.008	Pos		
	May	Ronquils	4	0.008	Pos		
		Northern lampfish	1	0.010			
		Northern rock sole	2	0.028	Neg	Yes	
		Ronquils	4	0.001	Pos		

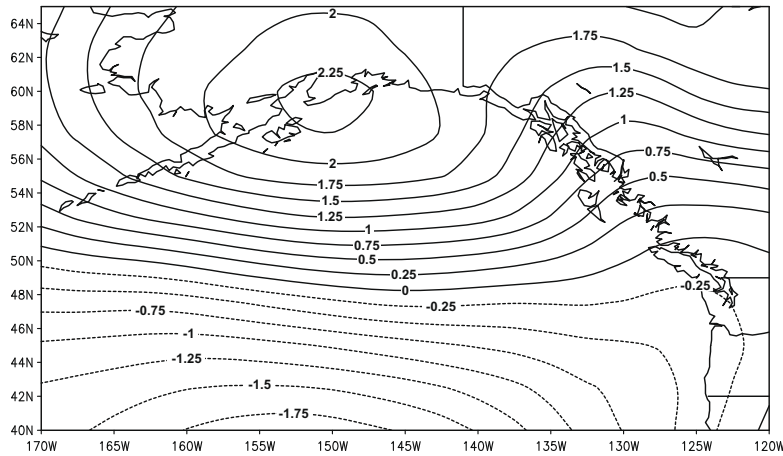


Fig. A1. Sea level pressure (hPa) over the Northeast Pacific regressed against the EP-NP Index for the months of April and May, 1948–2005. Sources: Sea level pressure from NCEP/NCAR Reanalysis Project (Kalnay et al., 1996); EP-NP Index from NOAA/Climate Prediction Center.

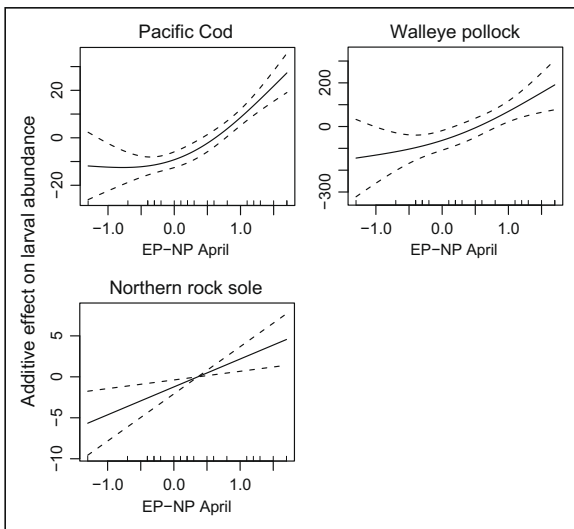


Fig. A2. Partial regression plots of the April East Pacific–North Pacific (EP–NP) Index on late spring larval abundance for selected species best-fit GAM models.

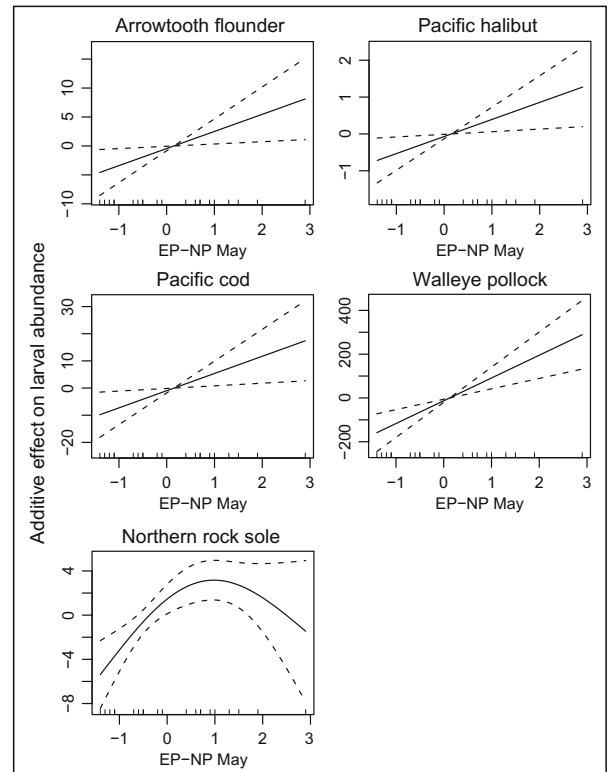


Fig. A3. Partial regression plots of the May East Pacific–North Pacific (EP–NP) Index on late spring larval abundance for selected species best-fit GAM models.

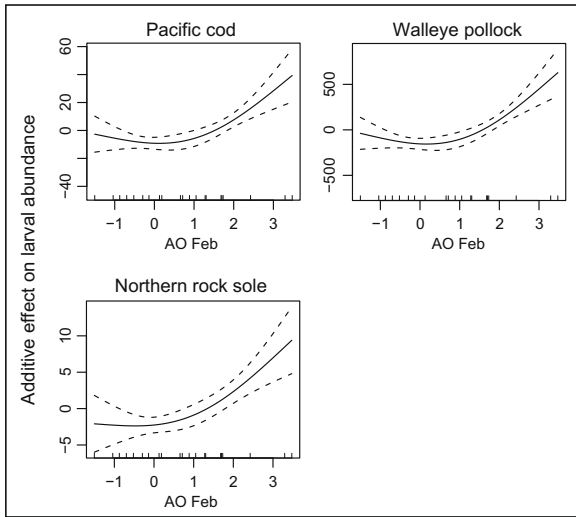


Fig. A4. Partial regression plots of the February Arctic Oscillation (AO) Index on late spring larval abundance for selected species best-fit GAM models.

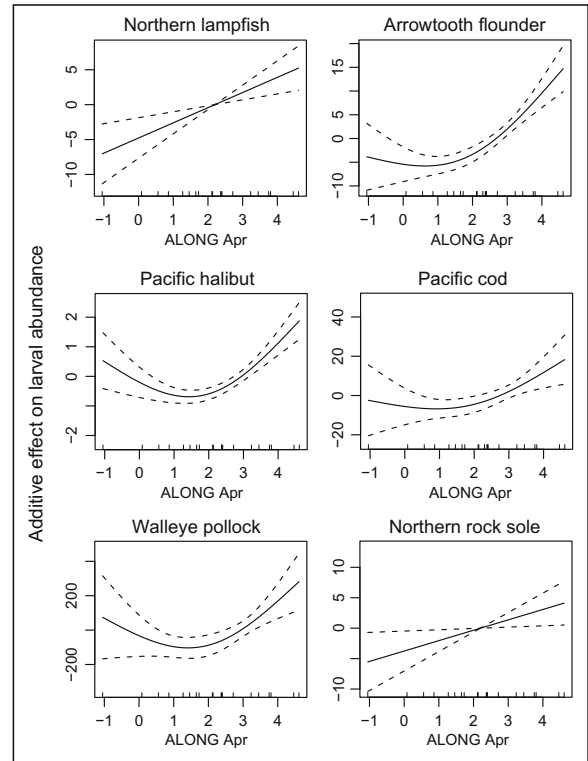


Fig. A7. Partial regression plots of the April Alongshore Wind Index (ALONG) on late spring larval abundance for selected species best-fit GAM models.

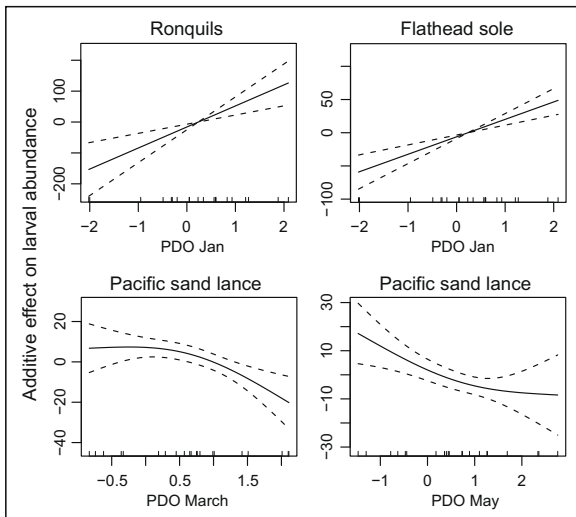


Fig. A5. Partial regression plots of the January, March and May Pacific Decadal Oscillation (PDO) Index on late spring larval abundance for selected species best-fit GAM models.

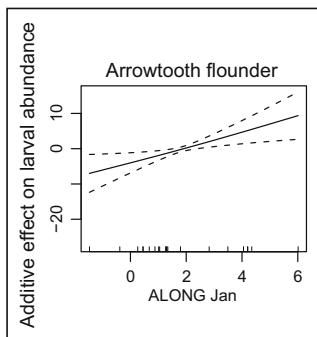


Fig. A6. Partial regression plot of the January Alongshore Wind Index (ALONG) on late spring larval abundance for the arrowtooth flounder best-fit GAM model.

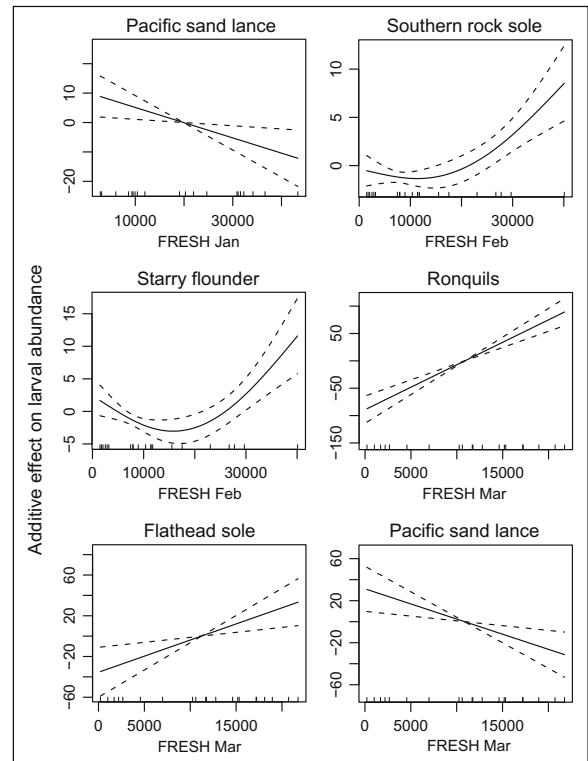
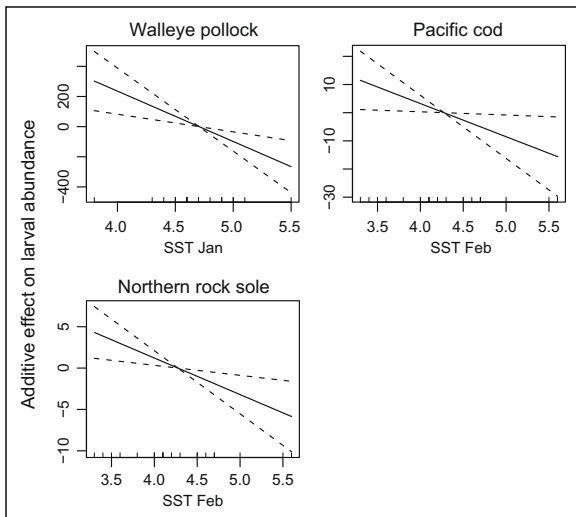
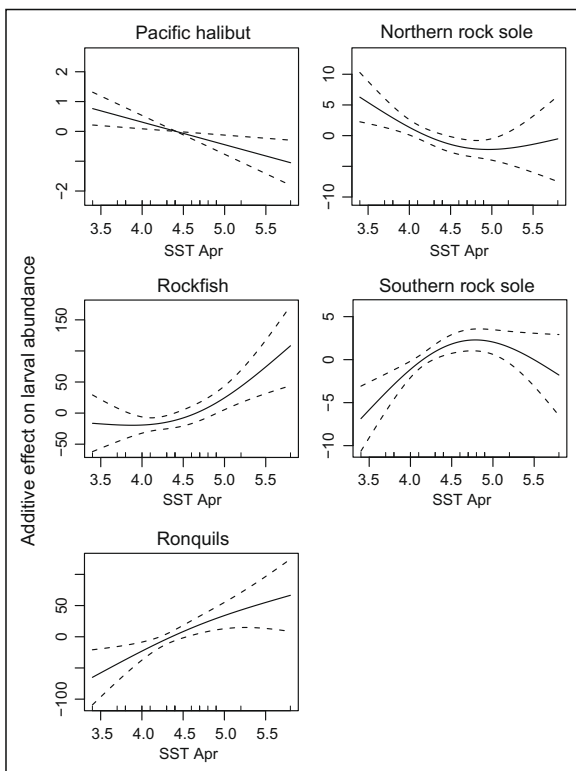


Fig. A8. Partial regression plots of January, February and March GOA Freshwater Runoff (FRESH) on late spring larval abundance for selected species best-fit GAM models.



**Fig. A9.** Partial regression plots of January and February Sea Surface Temperature (SST) on late spring larval abundance for selected species best-fit GAM models.



**Fig. A10.** Partial regression plots of April Sea Surface Temperature (SST) on late spring larval abundance for selected species best-fit GAM models.

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