



# Long-term trends in ichthyoplankton assemblage structure, biodiversity, and synchrony in the Gulf of Alaska and their relationships to climate

Kristin N. Marshall<sup>a,\*</sup>, Janet T. Duffy-Anderson<sup>b</sup>, Eric J. Ward<sup>c</sup>, Sean C. Anderson<sup>d,1</sup>, Mary E. Hunsicker<sup>e</sup>, Benjamin C. Williams<sup>f,g</sup>

<sup>a</sup> Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd E, Seattle, WA 98112, USA

<sup>b</sup> Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA

<sup>c</sup> Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd E, Seattle, WA 98112, USA

<sup>d</sup> School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105, USA

<sup>e</sup> Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2032 SE OSU Drive, Newport, OR 97365, USA

<sup>f</sup> College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, AK, USA

<sup>g</sup> Alaska Department of Fish and Game, Juneau, AK, USA

## ARTICLE INFO

### Keywords:

Gulf of Alaska  
Ichthyoplankton  
Biodiversity  
Synchrony  
Walleye pollock  
Climate  
Ecosystem indicators

## ABSTRACT

Understanding and tracking how ecosystems respond to changing environments is an ongoing challenge. Marine ecosystems in the North Pacific support productive fisheries and diverse ecosystem services, and they are subject to large-scale environmental, human, and ecological perturbations. Ichthyoplankton time-series from these ecosystems may provide an important indicator of lower trophic level dynamics and ecosystem functioning. Here we present a spatiotemporal analysis using data from three decades of ichthyoplankton surveys in the Gulf of Alaska to investigate temporal patterns in indicators of species richness, Shannon diversity, and synchrony. Then we use Dynamic Factor Analysis (DFA) to synthesize the ichthyoplankton assemblage with two dominant trends. We relate the biodiversity indices and DFA trends to local and regional climate indices in the North Pacific. We find evidence for increased temperatures driving increased species richness, and changes in synchrony coincident with shifting assemblage composition and the 1988/1989 regime shift. Shannon diversity was largely driven by the dominance of larval walleye pollock (*Gadus chalcogrammus*). Correlations between climate drivers and DFA trends suggest that the influence of basin scale drivers (North Pacific Gyre Oscillation and the Pacific Decadal Oscillation) were stronger than the influence of local-scale drivers like regional sea surface temperature. Our work demonstrates the potential value of ichthyoplankton surveys to provide indicators of climate-driven ecosystem variability and long-term ecological change.

## 1. Introduction

Understanding how species, communities, and ecosystems respond to changing environments and how to track those responses remains a fundamental challenge. In marine ecosystems, for example, changes in fishing, climate, and oceanographic conditions can have a range of biological consequences from no effect to strong cascading effects that propagate through a food web (Hunt et al., 2011). A key part of this challenge is the complexity of biophysical systems, and one way to

reduce the dimensionality is to focus on ecological indicators that can track shifts in community structure or the physical environment (Coll et al., 2016). For example, indicators of biodiversity are commonly proposed because they integrate across biotic scales, rely on data derived from multiple species, and can represent shifts in the status of groups of species, community vulnerabilities, species loss, the adaptive capacities of species and ecosystems, and ecosystem complexity and stability (Coll et al., 2016; Kershner et al., 2011; Longo et al., 2015).

While biodiversity metrics provide insight on the status of an

\* Corresponding author.

E-mail address: [kristin.marshall@noaa.gov](mailto:kristin.marshall@noaa.gov) (K.N. Marshall).

<sup>1</sup> Present address: Pacific Biological Station, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, BC V6T 6N7, Canada.

assemblage or community at a point in time, synchrony metrics describe how population abundances or biomasses fluctuate through time with respect to each other (Micheli et al., 1999). Synchrony can reflect the extent to which the response to a stochastic, exogenous forcing factor is coincident among species, or it can represent the intensity, strength, and coherence of trophic interactions (Liebhold et al., 2004). Large-scale forcing events have been shown to increase synchrony with coincident changes observed across species (Cottingham et al., 2001; Keitt, 2008; Tilman, 1996; Vasseur and Gaedke, 2007), potentially destabilizing systems by unifying community response. The consequences of a perturbation can be ephemeral, temporarily driving the community out of a stable configuration, or enduring, forcing the system into a new stable state. Previous research has shown that effects of small-scale forcing events may be temporary (Duffy-Anderson et al., 2006; Frost et al., 2006; Mittelbach et al., 2006), while large-scale events can have effects that persist over several decades (Beauprand et al., 2002; Scheffer et al., 2001; Walsh et al., 2015; Walther et al., 2002).

One of the largest marine ecosystems in the world where the interactions between climate forcing, species interactions, and ecosystem resilience have been studied extensively is the Gulf of Alaska (GOA). As a high-latitude system, the GOA is susceptible to climate-mediated environmental variation and rapid changes in population and community structure. Extensive sampling of the marine environment has occurred since the early 1980s, providing important time series that can be used to evaluate effects of decadal-scale regime shifts. The most well-known shift occurred in 1976/1977 characterized by a phase shift of the Pacific Decadal Oscillation (PDO), the first mode of variability in sea surface temperature in the North Pacific Ocean, from a negative to positive value (Mantua and Hare, 2002). This shift was accompanied by an intensified Aleutian Low (AL) pressure system, ocean warming, increased circulation, and increased stratification that persisted for over two decades. A second regime shift occurred in 1988/1989, driven by a strong polar vortex and weak AL (Overland et al., 1999; Yasunaka and Hanawa, 2002) that lowered ocean temperatures and weakened overall circulation. Unlike the well-characterized PDO-driven regime shift of 1976/1977, the 1988/1989 shift was not described by PDO variability. Instead, a shift in the North Pacific Gyre Oscillation (NPGO), which describes the second mode of variability of SST and relates to the gyre circulation and chemical and biological properties in GOA, characterized this regime (Bond et al., 2003; Di Lorenzo et al., 2008; Kilduff et al., 2015). This second shift raised awareness of the complex and dynamic relationships between the major (physical) atmospheric and oceanographic forcing variables, beyond the PDO. A third regime shift in 2007/2008 was less well described but is potentially important. A recent comprehensive examination by Litzow and Mueter (2014) described the 2007/2008 shift as a transition to a PDO-negative, NPGO-positive state, featuring lower ocean temperatures and changing circulation.

Other large-scale climate drivers may also correlate with variability in the GOA. The Multivariate El Niño/Southern Oscillation Index (MEI) combines sea level pressure, winds, sea surface temperature, air temperatures, and cloudiness across the tropical Pacific (Wolter and Timlin, 1998, 1993). The North Pacific Index (NPI) describes sea level pressure over the area 30N–65N, 160E–140W (Trenberth and Hurrell, 1994). The GOA is typically a downwelling system and the relaxation of that downwelling relates to Ekman transport driven by wind stress, which could affect cross-shelf transport.

In addition to being a system that has experienced several large-scale climate shifts, the GOA has also been the focus of long-term monitoring programs across multiple trophic levels in the marine environment. A number of these datasets have been used to examine fish community response to the climate-mediated perturbations described above, including regime shifts (Anderson and Piatt, 1999; Litzow, 2006; Mueter and Norcross, 2002, 2000; Shelton et al., 2017). Though less studied (but see Boeing and Duffy-Anderson, 2008; Doyle et al., 2009),

high resolution datasets of fish early life-history stages may be useful for understanding climate-mediated impacts on fisheries. In particular, early life-history stages of fishes have informed studies on the effects of non-native species (Manchester and Bullock, 2000), stock reductions (Hoff, 2006; Hutchings and Baum, 2005), spatial shifts (Perry, 2005), and restructured trophic interactions (Worm et al., 2006). One of the most data rich surveys that has spanned multiple climate shifts in the GOA is run by the Ecosystems and Fisheries Oceanography Coordinated Investigations (EcoFOCI) program, which has been collecting marine fish larvae from the western GOA since the 1970s, and systematically over a gridded survey since the early 1980s (McClatchie et al., 2014). These surveys are fishery independent, may provide early indicators of future changes in the adult fish community, and may describe changes in adult species composition, species interactions, spawning distribution, and phenology. As such, they are useful indicators of bottom-up forcing on overall fish communities.

In this paper, we use three decades of ichthyoplankton data collected from the western GOA to examine temporal variability in the structure of the spring ichthyoplankton assemblage with respect to large-scale climate regimes. Our objectives were threefold: (1) explore temporal trends in larval fish assemblage structure, biodiversity, synchrony, and pollock dominance; (2) describe temporal trends shared among multiple species in the assemblage; and (3) explore potential physical and biological drivers of patterns in shared trends and diversity indices. We use the term “larval assemblage” to refer to co-occurring species, and the term “larval community” to refer to groups of larvae that may interact directly or indirectly through shared prey resources.

## 2. Methods

### 2.1. Ichthyoplankton sampling

Ichthyoplankton data were collected in May and June from the western GOA by the EcoFOCI from 1972 to 2013 (Table 1; McClatchie et al., 2014). These surveys were conducted annually, with the exception of years 1984, 1986, and 2012. The historical distribution of ichthyoplankton sampling extends along the Alaskan mainland and Peninsula on the continental shelf from Prince William Sound southwest to Unimak Island (Fig. 1). The most intense sampling has been in the vicinity of Shelikof Strait and Shelikof Sea Valley from mid-May through early June. Ichthyoplankton were collected from oblique tows from the bottom (or 100 m depth maximum) to the surface with a 60 cm diameter bongo net (333 or 505 mm mesh) in a standardized manner (Matarese et al., 2003). Data from both bongo net mesh sizes were combined as prior analyses indicated no significant differences in ichthyoplankton catch rates (selected species) between the two mesh sizes (333  $\mu$ m and 505  $\mu$ m; Boeing and Duffy-Anderson, 2008). Calibrated flowmeters in the net mouth were used to estimate the volume of water filtered. Samples were preserved in 5% formalin at sea and returned to the laboratory for sorting. All ichthyoplankton were sorted at the Plankton Sorting and Identification Center in Szczecin, Poland. Species were enumerated, identified to the lowest taxonomic level possible, and measured. Fish larvae from sorted samples were returned to the National Oceanic and Atmospheric Administration's Alaska Fisheries Science Center (AFSC), taxonomic identifications were verified, and all data were archived in a relational database housed at the AFSC (also available online from the Ichthyoplankton Information System <http://access.afsc.noaa.gov/ichthyo/index.cfm>).

### 2.2. Environmental and biological indices

We used large-scale climate indices and spatially targeted descriptors of the physical environment in our study region to investigate the influence of environmental indices on ichthyoplankton (Table 1). We calculated a local temperature index from satellite monthly mean temperatures within the study area. We also calculated a local sea level



**Table 1**

Environmental and biological variables investigated to explain temporal variation in ichthyoplankton assemblage.

Index	Description	Source	Reference
PDO	Pacific Decadal Oscillation: Average of monthly anomalies from Jan thru June 1981–2013	<a href="http://jisao.washington.edu/pdo/PDO.latest">http://jisao.washington.edu/pdo/PDO.latest</a>	Mantua et al. (1997)
NPGO	North Pacific Gyre Oscillation: Average of monthly anomalies from Jan thru June 1981–2013	<a href="http://www.o3d.org/npgo/npgo.php">http://www.o3d.org/npgo/npgo.php</a>	Di Lorenzo et al. (2008)
MEI	Multivariate ENSO Index: Average of bimonthly values from Jan thru June 1981–2013	<a href="http://www.esrl.noaa.gov/psd/enso/mei/table.html">http://www.esrl.noaa.gov/psd/enso/mei/table.html</a>	Wolter and Timlin (1998, 1993)
NPI	North Pacific Index: Average of bimonthly values from Jan thru June 1981–2013	<a href="https://climatedataguide.ucar.edu/sites/default/files/climate_index_files/npindex_monthly.ascii">https://climatedataguide.ucar.edu/sites/default/files/climate_index_files/npindex_monthly.ascii</a>	Trenberth and Hurrell (1994)
SST	Sea Surface Temperature: average of monthly means from Jan thru June 1982–2013, subsetted to 90% quantiles of lat-long of ichthyoplankton data	<a href="http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html">http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html</a>	Reynolds et al. (2002)
Upwelling	Upwelling index: average of monthly anomalies from Jan thru June 1981–2013, from station at 60°N 149°W	<a href="http://www.pfeg.noaa.gov/products/PFELData/upwell/monthly/upanoms.mon">http://www.pfeg.noaa.gov/products/PFELData/upwell/monthly/upanoms.mon</a>	
MSL	Mean Sea Level: average of monthly mean water level from Jan thru June 1981–2013, from Seldovia, AK (9455500)	<a href="https://tidesandcurrents.noaa.gov/inventory.html?id=9455500">https://tidesandcurrents.noaa.gov/inventory.html?id=9455500</a>	
POLL	Pollock spawning stock biomass, 1981–2013		Dorn et al. (2015)
PCOD	Pacific cod spawning stock biomass, 1981–2013		A'Mar and Palsson (2015)
ARR	Arrowtooth flounder spawning stock biomass, 1981–2013		Spies and Turnock (2015)

index from tide gauge data from the closest station to the study area that had complete data over the study years (Seldovia). In all cases, we used data from the first half of the year (Jan–June) to represent the period during which most species spawned and ichthyoplankton were collected.

The presence and abundance of early life stages may reflect the status or abundance of adult life stages during spawning (Koslow and Wright, 2016). To account for this, we used spawning stock biomasses (SSB) of three of the most abundant species, pollock, Pacific cod (*Gadus macrocephalus*), and arrowtooth flounder (*Atheresthes stomias*), from the 2015 GOA stock assessments to represent these potential biological drivers (A'Mar and Palsson, 2015; Dorn et al., 2015; Spies and Turnock, 2015). We lagged SSB by one year such that SSB was a predictor for the following spring's ichthyoplankton data.

### 2.3. Ichthyoplankton index standardization

We applied spatiotemporal index standardization methods to account for spatiotemporal variability in sampling effort and autocorrelation. Though these methods are increasingly used in fisheries (Shelton et al., 2014; Thorson et al., 2015), to our knowledge this is the first time they have been applied to larval fish data or sampling of smaller organisms. These methods extend generalized linear mixed models to include spatial random effects, and have been shown to substantially reduce bias and uncertainty compared to traditional strata-based estimators (Thorson et al., 2015). Because ichthyoplankton densities are commonly zero-inflated, we applied models in a delta-generalized linear model (GLM) framework, fitting one statistical model to presence-absence data to describe variability in occurrence, and a second model to density data to describe variability in positive catch rates (Maunder and Punt, 2004; Pennington, 1983). Estimation was conducted separately for each species as latent Gaussian Markov random fields in the R package INLA (Rue et al., 2009; Ruiz-Cárdenas et al., 2012). Following previous work with Gaussian processes models and marine organisms, we modeled the spatial correlation between locations with a Matérn covariance function (Ono, 2014; Ward et al., 2015).

We focused our modeling efforts on the most abundant 40 species in the ichthyoplankton surveys (1981–2013), representing 90% of occurrences in the dataset (Table 2). Preliminary analyses showed that including additional species beyond the top 40 resulted in poor convergence of the standardization method, and therefore we chose 40

species as a cut-off. In some cases, species were aggregated to the genus level due to interannual variation in taxonomic resolution or to include taxa that would have otherwise been dropped due to lower species-specific occurrences. Spatially, surveys are most often concentrated in Shelikof Strait and Shelikof Sea Valley, though more recent efforts have expanded the sampling to the north or east sides of Kodiak Island (Fig. 1). To reduce the influence of infrequently sampled locations, we restricted samples to the core sampling area, defined as those 20 × 20 km grids contained within the 90% quantiles of all grids sampled.

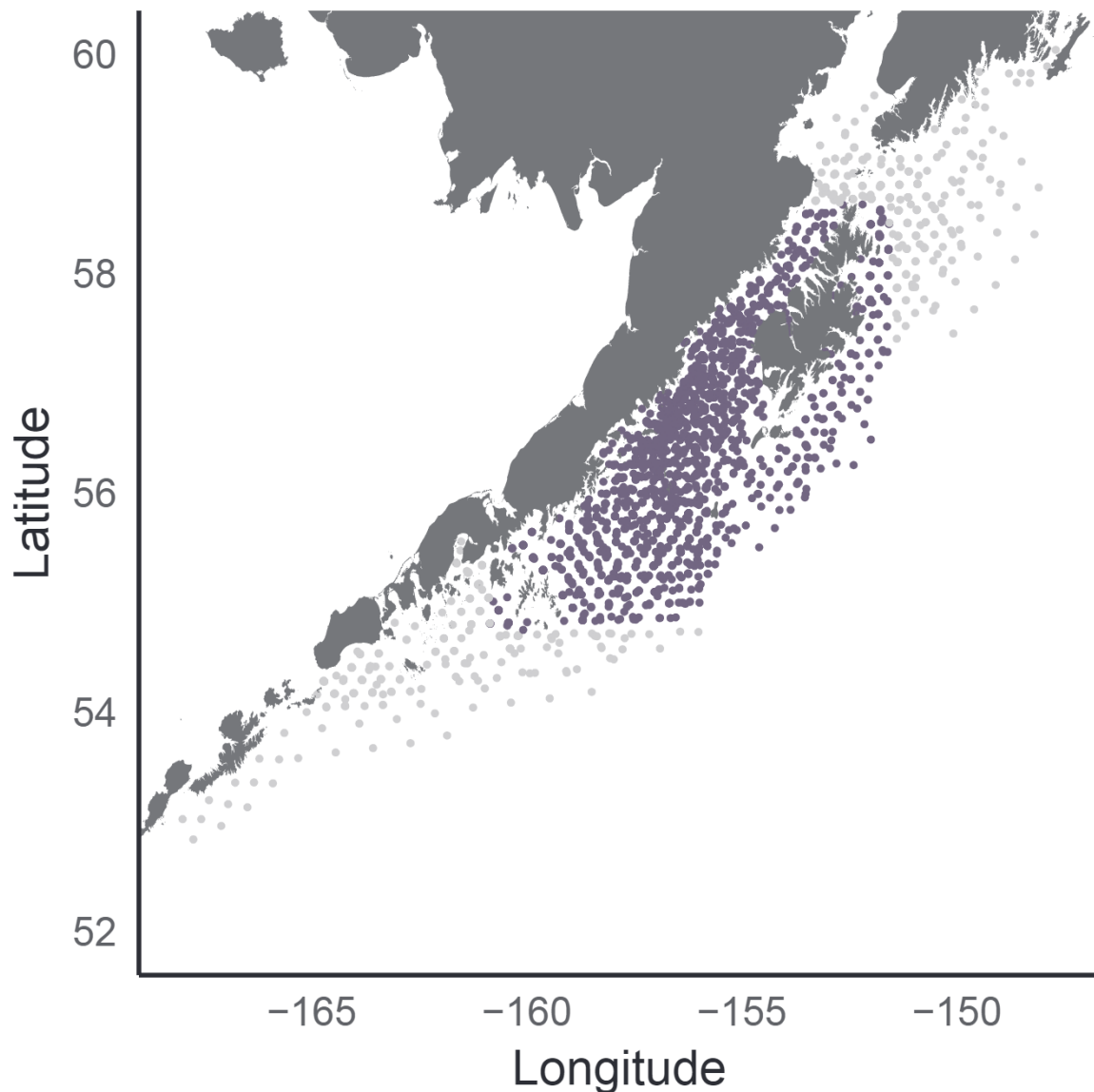
We conducted Markov chain Monte Carlo sampling from the approximate posterior distribution of each delta-GLM model, and used the resulting estimates of occurrence and positive catch rates to generate estimates of density. We projected these estimates to the centroid of an equally spaced 2-km grid within the core survey area, and summed the estimates across grid cells to generate an annual index of abundance. Repeating this process across posterior samples allowed us to compute posterior credible intervals for the density of each species in each year. For subsequent analyses, we used the means of the posterior densities of abundance for each species in each year. Code and data to replicate the analysis is available at <https://github.com/NCEAS/pfx-ichthyo>.

### 2.4. Describing temporal trends in species diversity

We estimated annual species richness and Shannon diversity indices from the standardized time series of ichthyoplankton abundances. Species richness was calculated from the presence-absence model output as the sum of probabilities ( $p_i$ ) of presence of each species  $i$  in each year  $y$  across  $s$  species:  $R_y = \sum_{i=1}^s p_{iy}$ . Shannon diversity represents the evenness of species present. We chose the Shannon index over other diversity metrics because it is least sensitive to dominant species (Jost, 2006) and pollock is dominant in our data (Fig. 2). We calculated the Shannon index from the standardized indices of abundance:  $H_y = -\sum_{i=1}^s a_{iy} \log a_{iy}$ .

### 2.5. Describing temporal trends in synchrony among species

Synchrony describes the similarity or dissimilarity of a group of species fluctuations through time. Like diversity, many metrics of synchrony exist, each with strengths and weaknesses. Gross et al. (2014) recently proposed a synchrony metric based on correlations, which they showed to be less sensitive to dominant species than other metrics based on variances or coefficient of variations (CVs). Gross's metric



**Fig. 1.** Map of historical ichthyoplankton sampling for EcoFOCI using plankton nets in the Gulf of Alaska (1972–2013). Points show all sampled locations over all years. Purple (dark gray in print version) points were those locations included in the present analyses, representing the 90 percent quantiles of the tow locations.

represents the correlation between the biomass of each species and the total biomass of all the other species, averaged across species:  $\eta = \left(\frac{1}{s}\right) \sum_i \text{cor}(Y_i, \sum_{j \neq i} Y_j)$  where  $Y_i$  is the biomass of species  $i$  in  $s$  species. This metric varies between  $-1$  (maximum asynchrony) and  $1$  (perfect synchrony), and is centered on  $0$  when species fluctuate independently.

We calculated a time series of synchrony using a moving window approach over 11-year intervals such that the value of synchrony in 1991 represents the period over the previous 11 years (1981–1991). We investigated the sensitivity of synchrony to each contributing species in the assemblage by jackknifing each species out of the analysis one at a time and re-calculating the synchrony metric.

## 2.6. Describing shared temporal trends among ichthyoplankton species

We used Dynamic Factor Analysis (DFA) to describe the dominant patterns or trends in the standardized ichthyoplankton data. DFA is a multivariate approach for time series data (Zuur et al., 2003). Similar to a principal components analysis, DFA decomposes multivariate data into a smaller number of components that describe the dominant patterns in the data. In DFA, the shared trends and loadings of each species

on each trend are estimated. We performed the DFA using the MARSS package in R (Holmes et al., 2014, p. 201) on the standardized ichthyoplankton time-series after rescaling each species by subtracting its mean and dividing by its standard deviation across all years. AICc was used to determine the most parsimonious model. We considered DFA models with 1–4 trends, and diagonal covariance matrices with either equal or unequal elements. Missing values from years without surveys were treated as NAs. Rotated trends and loadings were calculated using a varimax rotation (Zuur et al., 2003). We describe the proportion of variation explained by the best-fit DFA model using the residuals from the model prediction and means of the standardized indices such that:

$$R^2 = 1 - \frac{\sum (Y_{ij}^{\text{pred}} - Y_{ij}^{\text{obs}})^2}{\sum (\hat{Y}_{ij}^{\text{obs}} - Y_{ij}^{\text{obs}})^2}$$

where  $Y_{ij}^{\text{pred}}$  is the prediction for each species in each year from the DFA model and  $\hat{Y}_{ij}^{\text{obs}}$  is the mean of the posterior of the standardized index for species  $i$  in year  $j$ .

**Table 2**

Top 40 most commonly occurring species collected from ichthyoplankton sampling 1981–2013. Percent occurrence calculated as number of tows in which each species was observed over all records and all years.

Family	Species Name	Common Name	Percent Positive Tows
Clupeidae	<i>Clupea pallasii</i>	Pacific herring	0.468
Bathylagidae	<i>Leuroglossus schmidtii</i>	Northern smoothtongue	0.844
	<i>Bathylagus pacificus</i>	Slender blacksmelt	0.353
Osmeridae	<i>Mallotus villosus</i>	capelin	0.293
Myctophidae	<i>Protomyctophum thompsoni</i>	Northern flashlight fish	0.412
	<i>Stenobrachius leucopsarus</i>	Northern lampfish	4.656
	<i>Gadus macrocephalus</i>	Pacific cod	6.477
Gadidae	<i>Gadus chalcogrammus</i>	Walleye pollock	11.216
	<i>Sebastes</i> spp.	Rockfishes	4.881
Scorpaenidae	<i>Ophiodon elongatus</i>	Ling cod	0.35
Hexagrammidae	<i>Hexagrammos</i> spp.	Greenlings	1.266
	<i>Icelinus</i> spp.	Sculpins	4.36
Cottidae	<i>Myoxocephalus</i> spp.	Sculpins	0.584
	<i>Radulinus</i> spp.	Sculpins	1.187
	<i>Ruscarius meanyi</i>	Puget Sound sculpin	0.656
	<i>Triglops</i> spp.	Sculpins	0.178
Agonidae	<i>Bathyaegonus alascanus</i>	Gray starsnout	2.833
	<i>Bathyaegonus infraspinitus</i>	Spinycheek starsnout	0.534
	<i>Podothecus acipenserinus</i>	Sturgeon poacher	0.185
	<i>Liparis fuscus</i>	Slipskin snailfish	1.049
Liparidae	<i>Bathymaster</i> spp.	Ronquils	8.577
Bathymasteridae	<i>Lumpenella longirostris</i>	Longsnout prickleback	0.554
	<i>Lumpenus maculatus</i>	Daubed shanny	1.273
Stichaeidae	<i>Lumpenus sagitta</i>	Snake prickleback	0.162
	<i>Poroclinus rothrocki</i>	Whitebarred prickleback	1.721
Cryptacanthodidae	<i>Anoplarchus</i> spp.	Cockscombs	2.404
	<i>Cryptacanthodes aleutensis</i>	Dwarf wrymouth	2.058
Pholididae	<i>Pholis</i> spp.	Gunnels	3.034
Zaproridae	<i>Zaprora silenus</i>	Prowfish	0.765
Ammodytidae	<i>Ammodytes personatus</i>	Pacific sandlance	9.468
Pleuronectidae	<i>Atheresthes stomias</i>	Arrowtooth flounder	2.572
	<i>Glyptocephalus zachirus</i>	Rex sole	1.19
	<i>Hippoglossoides elassodon</i>	Flathead sole	10.094
	<i>Hippoglossus stenolepis</i>	Pacific halibut	1.342
	<i>Isopsetta isolepis</i>	Butter sole	0.861
	<i>Lepidopsetta bilineata</i>	Southern rock sole	3.453
	<i>Lepidopsetta polyxystra</i>	Northern rock sole	4.762
	<i>Microstomus pacificus</i>	Dover sole	0.854
	<i>Platichthys stellatus</i>	Starry flounder	2.49
	<i>Pleuronectes quadrituberculatus</i>	Alaska plaice	0.772

## 2.7. Describing structure in the ichthyoplankton assemblage

We used hierarchical cluster analysis to group species based on their loading values on Trend 1 and Trend 2. We determined an optimal number of clusters to represent the 40 species using the elbow method and gap statistic (Tibshirani et al., 2001). We then explored how clusters and trends associated with a suite of documented life history traits. We focused on traits that previous studies identified as potentially important in characterizing the GOA spring ichthyoplankton assemblage (Doyle et al., 2002). In particular, we characterized adult habitat, spawn timing, larval duration, and species distribution (Table 3).

## 2.8. Exploring potential physical and biological drivers of biodiversity and shared trends

Given the documented climate regime shifts in the GOA, we used moving window cross correlation analysis to explore if and how correlations between ichthyoplankton diversity metrics and trends and environmental indices varied over time. There are many examples of nonstationary interactions between environmental/biological indices and fish populations in Alaska ecosystems (Ciannelli et al., 2012; Duffy-Anderson et al., 2005; Litzow and Ciannelli, 2007) and other ecosystems as well (Deyle et al., 2013; Myers, 1998; Ottersen et al., 2013; Stige et al., 2013). Often, fish populations seemingly respond to certain dominant variables for a period of time, and then the dominant variables shift. This can be caused by changes in the magnitude of environmental variables, indirect or interacting effects, and shifts in ecosystem state (e.g., Stige et al., 2013; Sugihara et al., 2012). Here, we used a moving window cross-correlation analysis, combining output of the DFA model with potential environmental drivers. We calculated Pearson correlation coefficients between each environmental driver and the two DFA trends and two diversity indices over an 11-year moving window. Ninety percent confidence intervals were calculated using the Pyper-Peterman correction for autocorrelated data (Pyper and Peterman, 1998). We investigated different lengths of moving windows and found the results to be generally robust to window length.

## 3. Results

### 3.1. Temporal trends in diversity and synchrony

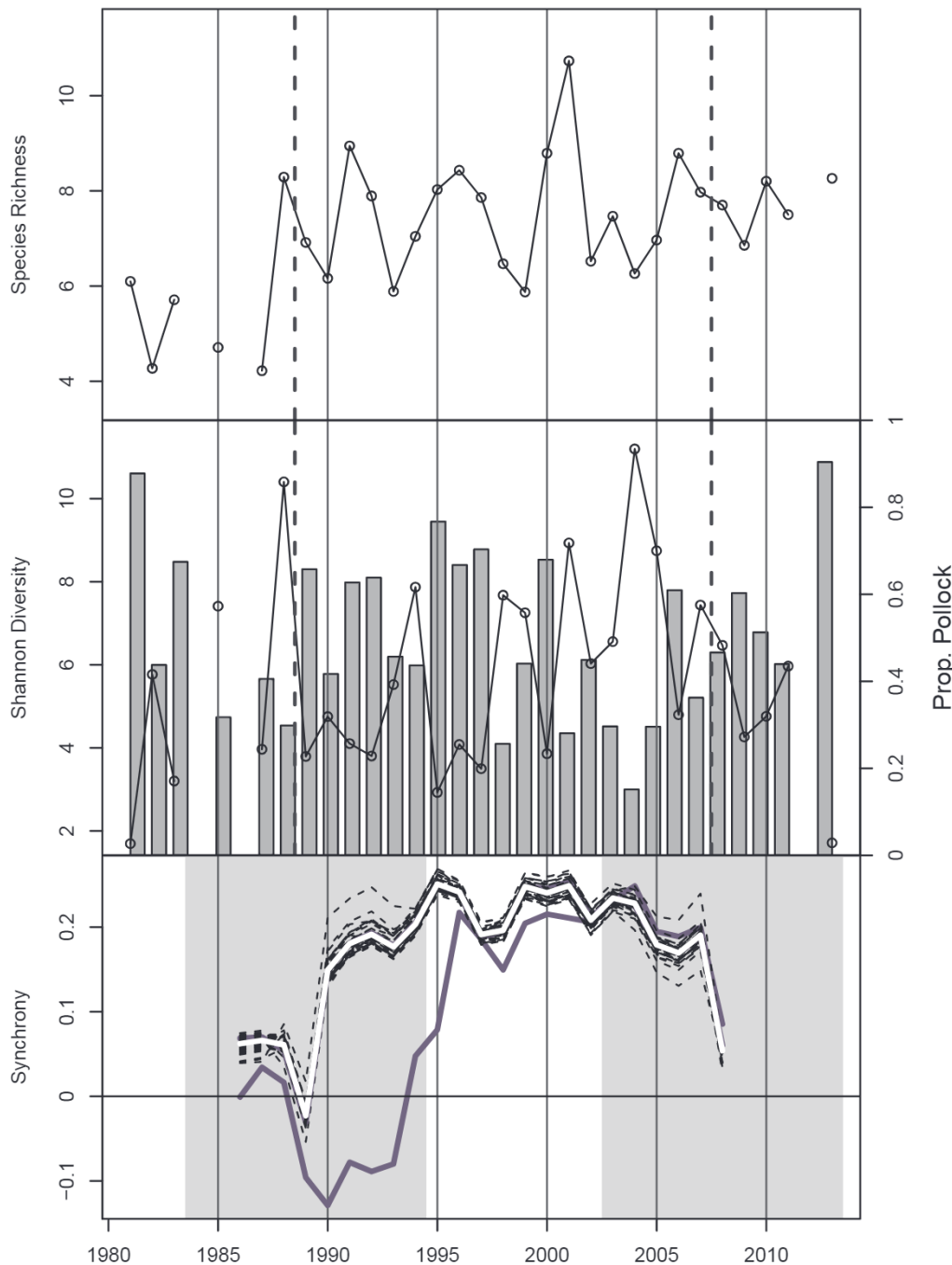
The diversity and synchrony indices from 1981 to 2013 illustrated shifts in the probability of occurrence and abundance of species (Fig. 2). They also highlight the variable role of pollock in structuring the ichthyoplankton community. Species richness gradually increased over three decades (Fig. 2, upper panel), driven by increased probabilities of occurrence of warm water associated species in the GOA in later years (*Lepidopsetta polyxystra*, *Ophiodon elongatus*, *Platichthys stellatus*, and *Sebastes* spp., a complex which is primarily comprised of Pacific ocean perch, *Sebastes alutus*, in spring collections, Appendix A). The Shannon diversity index exhibited strong negative correlation with the proportion of larval pollock observed in the survey (Fig. 2, middle panel). Shannon diversity increased during the 1980s, but dropped between 1988 and 1989, coincident with the 1988/1989 regime shift in the GOA. Shannon diversity was relatively low during the 1990s (except for 1994 when pollock abundance was low). Higher diversity occurred between 1998 and 2005 (except 2000 when pollock abundance was high), but then declined, with a minimum observed in 2013 (when pollock abundance was very high).

The time series of synchrony also shows evidence of abrupt shifts, and reflects the dominant role of pollock in the ichthyoplankton assemblage, particularly in the early years of these data. Pollock clearly drives the overall synchrony index through the early 1990s (difference between blue and gray lines, Fig. 2, lower panel). Removing the effect of pollock, the other ichthyoplankton species were independent to weakly asynchronous during this period (blue line, synchrony values of 0 to −0.2). Synchrony shifted to positive values in the mid-1990s, in metrics with and without pollock, indicating that pollock and rest of the assemblage fluctuated in similar ways from the 1990s to 2013. This positive shift in synchrony coincided with the 1988/1989 regime shift in the GOA, reduced dominance of pollock in the samples, and higher Shannon diversity. Synchrony over 2003–2013 dropped as numbers of pollock larvae in the assemblage increased dramatically in 2013.

### 3.2. Constructing shared temporal trends among ichthyoplankton species

We fit 8 potential DFA models to describe shared trends among ichthyoplankton, and model selection with AIC<sub>c</sub> revealed the best





**Fig. 2.** Ichthyoplankton assemblage dynamics between 1981 and 2013. Top panel shows species richness. Middle panel shows Shannon diversity (lines) and the proportion of total sampled larvae that were pollock (bars). Bottom panel shows synchrony within an 11-year moving window (x-value is mid-point of the window), where each dashed line represents synchrony with one species left out of the assemblage. Heavy white line shows synchrony with all species and the purple (dark gray in print version) line shows synchrony without pollock. Vertical dashed lines indicate years of regime shifts in the GOA, and shaded areas in bottom panel indicate the moving windows that include the years of the regime shifts.

model was a two-trend model with an equal variance-covariance matrix (Appendix C). The model with the next lowest  $AIC_c$  value was nearly 20 units higher, thus we did not consider any other candidate models. The best fit model explained 28 percent of the total variation.

The best-fit model had two shared trends that described the dynamics of the ichthyoplankton assemblage over 1981–2013 (Fig. 3). Trend 1 showed moderate-to-low amplitude until the mid-1990s (most values between 0 and  $-1$  SD of the mean). From 1996 to 2010 Trend 1 was generally positive, with a peak in 2001. But, two years in the 2000s (2007–2008) were very low ( $-2$  SD below the mean). The most recent years of Trend 1 were close to the mean. Trend 2 declined from a peak ( $+3$  SD) in 1981 to its lowest value in 1996 ( $-3$  SD). By 2000, Trend 2 increased to the mean and has exhibited multi-year fluctuations through 2013, with low values in 2006 and 2007.

### 3.3. Describing structure in the ichthyoplankton assemblage

The cluster analysis of species loadings on the trends revealed four groups that characterized ichthyoplankton assemblage structure (Fig. 4, Table 3). Cluster 1 contained species loading negatively on Trend 2 that increased over the 1980s and 1990s (11 species, Fig. 4). Many of these species, but not all, occupy waters over the slope as adults and spawn in winter (Table 3). Species loading strongly positive on Trend 2 and weak to positive on Trend 1 formed another cluster (Cluster 2), which also included species that did not load strongly on either trend. Some of these species experienced substantial declines in biomass in the 1980s and 1990s (*Bathymaster* spp. and *Lumpenella longirostris*). The species in Cluster 2 did not appear to share life history traits (Table 3). The third cluster included species loading positively on Trend 1 and weakly on

**Table 3**

Life history traits of ichthyoplankton assemblage and clusters identified from cluster analysis.

Species	Abbv	Adult Habitat	Adult bathymetric	Spawn timing	Egg Ecology	Larval duration (months)	Range	Cluster
<i>Anoplarchus</i> spp.	An.sp	Benthic	Nearshore	Spring	Demersal	3	Northern	1
<i>Icelinus</i> spp.	Ic.sp	Benthic	Nearshore	Spring	Demersal	NA	Northern	1
<i>Platichthys stellatus</i>	Pl.st	Benthic	Slope	Late spring	Pelagic	2	Southern	1
<i>Stenobrachius leucopsarus</i>	St.le	Pelagic	Slope	Spring	Pelagic	8	Both	1
<i>Atheresthes stomias</i>	At.st	Benthic	Slope	Winter	Pelagic	5	Both	1
<i>Microstomus pacificus</i>	Mi.pa	Benthic	Slope	Spring	Pelagic	8	Southern	1
<i>Bathylagonus alascanus</i>	Ba.al	Benthic	Shelf	Spring	Demersal	3	Both	1
<i>Leuroglossus schmidti</i>	Le.sc	Pelagic	Slope	Winter	Pelagic	3	Northern	1
<i>Protomyctophum thompsoni</i>	Pr.th	Pelagic	Slope	Winter	Pelagic	8	Both	1
<i>Bathylagus pacificus</i>	Ba.pa	Pelagic	Slope	Winter	Pelagic	3	Both	1
<i>Zaprora silenus</i>	Za.si	Benthic	Slope	Spring	Demersal	4	Northern	1
<i>Bathymaster</i> spp.	Ba.sp	Benthic	Shelf	Late spring	Demersal	5	Both	2
<i>Hippoglossoides elassodon</i>	Hi.el	Benthic	Slope	Early spring	Pelagic	4	Northern	2
<i>Glyptocephalus zachirus</i>	Gl.za	Benthic	Slope	Spring	Pelagic	8	Southern	2
<i>Clupea pallasii</i>	Cl.pa	Pelagic	Nearshore, shelf	Late spring	Demersal	3	Southern	2
<i>Lumpenella longirostris</i>	Lu.lo	Benthic	Shelf	Spring	Demersal	3	Northern	2
<i>Bathylagonus infrapinnatus</i>	Ba.in	Benthic	Shelf	Spring	Demersal	3	Both	2
<i>Sebastes</i> spp.	Se.sp	Benthic	Slope	Spring	Live bearing	5	Both	3
<i>Isopsetta isolepis</i>	Is.is	Benthic	Nearshore, shelf	Early spring	Pelagic	2	Southern	3
<i>Lepidopsetta bilineata</i>	Le.bi	Benthic	Shelf	Late spring	Demersal	4	Southern	3
<i>Cryptacanthodes aleutensis</i>	Cr.al	Benthic	Shelf	Spring	Demersal	3	Both	3
<i>Poroclinus rothrocki</i>	Po.ro	Benthic	Shelf	Spring	Demersal	4	Both	3
<i>Radulinus</i> spp.	Ra.sp	Benthic	Shelf	Spring	Demersal	NA	Southern	3
<i>Liparis fucensis</i>	Li.fu	Benthic	Shelf	Late spring	Demersal	2	Both	3
<i>Ruscarius meanyi</i>	Ru.me	Benthic	Shelf	Spring	Demersal	3	Southern	3
<i>Ophiodon elongatus</i>	Op.el	Benthic	Shelf	Late winter	Demersal	3	Southern	3
<i>Gadus chalcogrammus</i>	Ga.ch	Benthic	Shelf	Early spring	Pelagic	4	Both	4
<i>Ammodytes personatus</i>	Am.pe	Pelagic	Nearshore, shelf	Late winter	Demersal	8	Both	4
<i>Gadus macrocephalus</i>	Ga.ma	Benthic	Shelf	Early spring	Demersal	3	Northern	4
<i>Lepidopsetta polyxystra</i>	Le.po	Benthic	Shelf	Early spring	Demersal	5	Northern	4
<i>Lumpenus maculatus</i>	Lu.ma	Benthic	Nearshore	Spring	Demersal	5	Northern	4
<i>Hexagrammos</i> spp.	He.sp	Benthic	Nearshore	Winter	Demersal	8	Both	4
<i>Hippoglossus stenolepis</i>	Hi.st	Benthic	Slope	Winter	Pelagic	5	Northern	4
<i>Pleuronectes quadrituberculatus</i>	Pl.qu	Benthic	Shelf	Late spring	Pelagic	2	Northern	4
<i>Mallotus villosus</i>	Ma.vi	Pelagic	Nearshore	Summer	Demersal	8	Northern	4
<i>Pholis</i> spp.	Ph.sp	Benthic	Nearshore	Late winter	Demersal	3	Both	4
<i>Myoxocephalus</i> spp.	My.sp	Benthic	Shelf	Spring	Demersal	5	Northern	4
<i>Podothecus acipenserinus</i>	Po.ac	Benthic	Shelf	Spring	Demersal	3	Both	4
<i>Triglops</i> spp.	Tr.sp	Benthic	Shelf	Spring	Demersal	3	Both	4
<i>Lumpenus sagitta</i>	Lu.sa	Benthic	Shelf	Late winter	Demersal	3	Northern	4

Trend 2 ( $|loading| < 0.2$ ) that generally increased in abundance after 1996 (Appendices B–C). Of the eight species in that cluster (Fig. 4), several were either warm-water associated or had more southern ranges (e.g., *Lepidopsetta bilineata*, *Sebastes* spp. (Pacific ocean perch), *Ophiodon elongatus*, Table 3) and/or showed increasing trends in adult biomass over this same period (Pacific ocean perch). Species in cluster 3 were generally spring spawning with demersal eggs and occupying benthic shelf habitat as adults. Cluster 4 contained 14 species that loaded

strongly negative on Trend 1, indicating a decrease in abundance after the early 1990s. These decreasing species included some species that are cold-water associated or have more northern ranges (e.g. *Lepidopsetta polyxystra*) and/or species where adult abundance has also declined in recent years (e.g. pollock). Most species in Cluster 4 occupied shelf or nearshore benthic habitat as adults (Table 3).

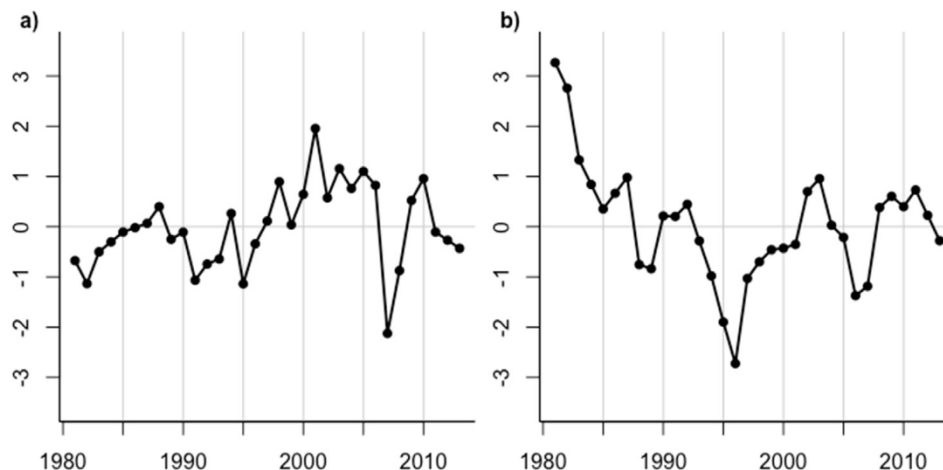
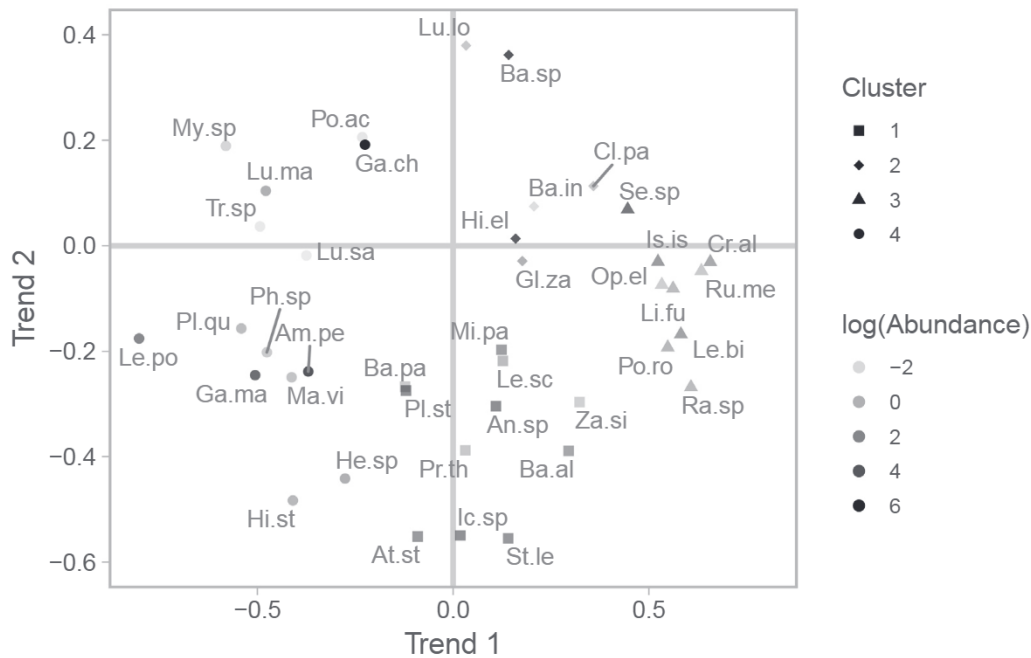


Fig. 3. Common Trends 1 (a) and 2 (b) estimated from Dynamic Factor Analysis on 40 species of ichthyoplankton from 1981 to 2013.



**Fig. 4.** Loadings of ichthyoplankton species on DFA Trend 1 (x-axis) and Trend 2 (y-axis). Point shapes indicate clusters identified by hierarchical cluster analysis and point shading is proportional to the log-scaled mean abundance of each species across all years. Species abbreviations described in Table 3.

### 3.4. Potential physical and biological drivers of biodiversity and shared trends

Our analysis of diversity revealed that ichthyoplankton species richness was negatively correlated with the PDO during one 11-year window (from 1983 to 1993), but was not correlated with any other environmental drivers over this same period (Fig. 5). Species richness was generally positively correlated with increasing spawning stock biomass of Pacific ocean perch and arrowtooth flounder during 1981–1995.

Shannon diversity was positively correlated with the NPGO during most of the 1980s and 1990s, but this correlation diminished after the 1988/1989 regime shift (characterized by the NPGO shifting negative). During the late 1990s to 2013, Shannon diversity was negatively correlated with the NPI. Shannon diversity was also negatively correlated with lagged pollock SSB in most years after 1990, echoing the negative correlation between the proportion of larval pollock observed in the spring survey and the Shannon diversity index (Fig. 2). SSB of the other species either increased or declined during most of the three decades, which caused inconsistent correlations with the more variable Shannon diversity time series.

To guide our interpretation of the common trends from DFA, we examined correlations with environmental indices and SSB indices. Trend 1 was positively correlated with NPGO from 1981 until 2003 (years indicate edges of moving windows, Fig. 5) with both exhibiting similar high values in 2001 and low values in the same years in the 1980s and 1990s (Fig. 3 and D2). The correlation between upwelling and Trend 1 was negative from 1987 to 1997, but switched to positive in 1996 to 2010. Mean sea level was correlated with Trend 1 from 1994 to 2002. For fish time series, Trend 1 was negatively correlated with pollock and Pacific cod SSB during 1987 to 2005 and positively correlated with Pacific ocean perch during those same years. Trend 2 was positively correlated with the MEI during 1987 to 1997. Similar to Trend 1, Trend 2 was negatively correlated with the upwelling anomaly from 1982 to 1994. For adult fish indices, both Trend 1 and 2 were correlated with adult pollock, but Trend 2 was negatively correlated in the first few years of the time-series, picking up an extreme value in 1981. In the 1980s and early 1990s Trend 2 was also negatively

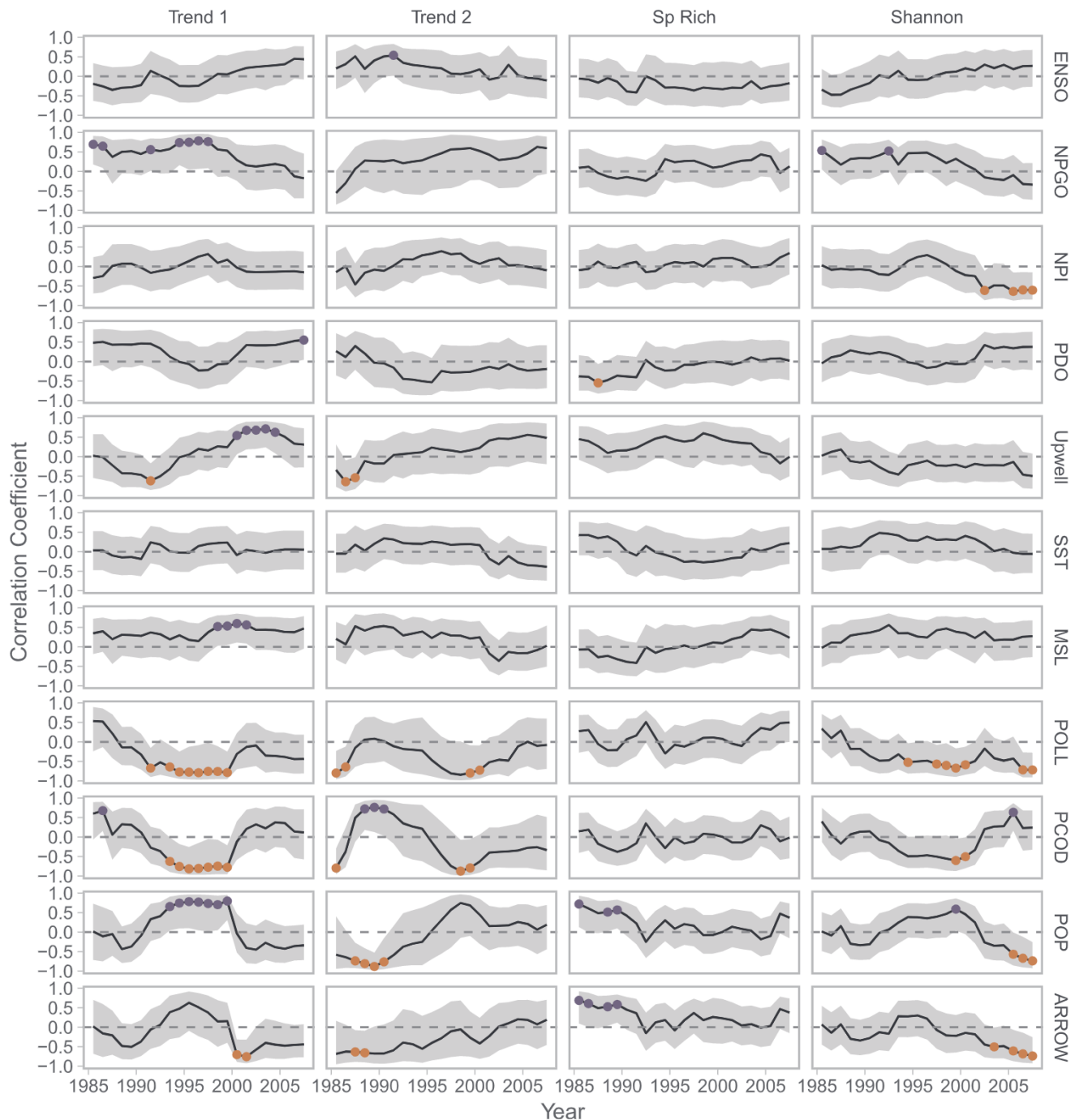
correlated with adult Pacific ocean perch and arrowtooth flounder but positively correlated with Pacific cod. We saw no correlations between Trend 2 and any of the environmental or SSB covariates after 2006.

## 4. Discussion

Our analysis shows that ecological indicators developed from ichthyoplankton surveys are potentially useful for monitoring and assessing the effects of gradual change and abrupt shifts in Large Marine Ecosystems. The standardized indices of probability of occurrence and abundance we estimated for the 40 ichthyoplankton species shown here represent the most precise and least biased estimates of abundance for spring ichthyoplankton in the GOA over three decades. The biodiversity indices, synchrony, and DFA trends we developed show evidence of long-term gradual change in this ecosystem, as well as supporting evidence for abrupt shifts. These patterns were correlated with several factors: climate shifts that occurred in the North Pacific ecosystem in 1988/1989 and 2007/2008, the influence of pollock - the dominant larval species - on the co-occurring ichthyoplankton assemblage, and the assemblage response to environmental forcing events relative to the abundance of pollock.

Species richness and DFA Trend 1 both showed gradual changes from 1981 to 2013. These trends may reflect a range shift of southern latitude species into the western GOA pursuant to overall ocean warming. Abundances of larval southern rock sole (*L. bilineata*), Pacific ocean perch (*S. alutus*), lingcod (*O. elongatus*), and starry flounder (*P. stellatus*, Appendix B) have increased, consistent with an increase in bottom temperatures in the GOA (Fig. D2). DFA Trend 1 separated some warm and cold-water associated species, which could be a leading indicator of replacement of cold water species like northern rock sole (*L. polyxystra*) with a warm water congeneric, southern rock sole, over time. Climate-mediated changes in ichthyoplankton phenology, distribution, and community structure have been documented in other Large Marine Ecosystems (e.g., Asch, 2015; Brodeur et al., 2008; Greve et al., 2005; Walsh et al., 2015) and erratic occurrences of adults of warm water affinity species have been documented recently in the GOA (skipjack tuna (*Katsuwonus pelamis*), ocean sunfish (*Mola mola*), thresher shark (*Alopias vulpinus*; J. Orsi, NOAA AFSC, personal





**Fig. 5.** Moving window cross correlations between environmental and spawning stock biomass variables and DFA trends and diversity indices. Each panel shows a time series of Pearson correlations (black line) with 90 percent confidence intervals that account for autocorrelation (CI, grey-shaded region) with a window length of 11 years (e.g., x-value for 1986 represents years 1981 to 1991). Purple (dark gray in print version) and orange (medium gray in print version) points represent correlations in which the confidence intervals are greater or less than zero, respectively.

communication).

Our results support the idea that large-scale modes of North Pacific atmospheric and oceanographic variability are important environmental drivers of the spring ichthyoplankton assemblage. Specifically, the NPGO appeared to have greater influence than other drivers we explored. While the PDO has received significant attention for contributing to ecosystem regime shifts in the GOA, we found stronger evidence of correlations between the spring ichthyoplankton assemblage and the NPGO over the PDO from the 1980s to the mid 2000s. [Litzow and Mueter \(2014\)](#) noted a similar phenomenon during the same

period, which they attributed to the white noise-dominated signal of the PDO during those years. Variations in the NPGO have been correlated to production indices, including shifts in nutrient availability and phytoplankton, zooplankton, and salmon (*Oncorhynchus* spp., [Di Lorenzo et al., 2008](#); [Ohlberger et al., 2016](#); [Sydeman et al., 2013](#)). Our results provide further support for the influence of the NPGO on the North Pacific marine ecosystem from the 1980s to mid-2000s.

Despite the dominance of the NPGO, our results cannot rule out the PDO as a potential driver of spring ichthyoplankton. Trend 1 was positively correlated with the PDO in the most recent years of data

(2003–2013). Further, both DFA trends had strong anomalies in 2007/2008, the same year as the most recent PDO shift. The absence of significant correlations with the PDO in other years may be due to the ichthyoplankton time series beginning several years after the most influential PDO regime shift of 1976/1977. It is also possible that more local indices better reflect ocean conditions most relevant to the spring ichthyoplankton assemblage, suggested by similar correlation patterns between Trend 1 and sea level, upwelling, and the PDO beginning in the mid-1990s. While the dominance of the PDO and NPGO in the North Pacific has been described elsewhere (Bond et al., 2003; Di Lorenzo et al., 2008; Litzow and Mueter, 2014), our results demonstrate that the spring larval fish assemblage may be sensitive to the fluctuations and relative strengths of both and therefore may be useful indicators of the impacts of climate variability on lower trophic dynamics in the GOA.

Observed positive correlations between Trend 1, upwelling, and some warm water-affinity species may seem counterintuitive. However, “upwelling” in the GOA (a downwelling system) is more accurately a relaxation of the intense downwelling that occurs throughout winter. The climatological upwelling index in summer is near zero (Ladd et al., 2005). Weakened summer winds prompt relaxation events and influxes of cold, deep, slope-origin water during those times are assumed due to observed increases in salinity at depth (Stabenho et al., 2004). Strong vertical stratification in late spring/summer can preclude mixing of on-shelf slope waters to the depths of larval occurrence (typically < 50 m in late spring), and shoaling of the mixed layer depth is observed during relaxation events. Moreover, relaxation of downwelling winds reduces the on-shelf flux of cold, basin water in the Ekman surface layer (Ladd et al., 2005), which may lead to warmer water near surface during upwelling periods. As such, it may not be so unusual to observe positive relationships between warm-affinity species and downwelling relaxation events in late spring.

Both DFA trends bear resemblance to trends from a separate examination of climate-biological interactions using entirely different biological datasets (Litzow and Mueter, 2014). In that paper, the authors also examined the relationships between biological time-series data collected from the GOA (large invertebrates, groundfish recruitment, recruitment of small neritic species, salmon, and zooplankton) and leading climate indices. Their first axis of biological variability was described by a pattern very similar to our DFA Trend 2, with a strong decline noted from the 1970s through the 1990s, and a shift to variability afterward. Inflection points were similar in years 2000–2011, inclusive of very low values in years 2007–2008. Their second axis of biological variability was positive from 1980 to 1995, and switched to negative between 1996 and 2008. This pattern was similar to our DFA Trend 1. The fact that these two studies, focusing on different species and life stages, found similar trends in biological responses suggests that many components of GOA ecosystem may respond similarly to broad-scale climate forcing, or are in other ways linked.

Despite the contrasting patterns of fluctuations indicated by the two DFA trends, the synchrony metric we calculated was generally positive and relatively constant across the three decades. However, we saw asynchrony and independence during the 1980s and early 1990s when pollock were removed from the dataset. This coincided with the highest years of pollock SSB, and many years of high proportional abundance of larval pollock (Fig. 2, D2). This pattern could be explained by several possible mechanisms. An abundance of pollock larvae could indicate ecosystem conditions that are favorable for larval feeding and survival across species. In this case, numerous pollock indicate a hospitable environment (less limiting) that supports an array of prey types, habitat, and refuges. Such an environment could facilitate the expression of species diversity, leading to greater asynchrony across species. In less productive years pollock abundances are low, as are abundances of other species, due to greater ecosystem constraints on resources. Synchrony under constrained conditions might be realized when ecosystem conditions are insufficient to support diversity. Another possible

explanation is that the abundance of pollock could modulate the strength of competition among the other larval fish species. Pollock are versatile zooplanktivores and numerically dominant in the system. These qualities may allow them to compete for resources at a level well above that of other co-occurring species. Pollock ascendancy could increase trophic interactions among other species for remaining resources, leading to dissimilar responses, variable competitive outcomes, and differential survivorship. Reduced numbers of pollock larvae in the system could alleviate competition for prey resources and homogenize responses to environmental fluctuations. How pollock abundance could intensify trophic interactions is unclear, though it has been previously demonstrated that larval pollock grazing can have a measurable effect on zooplankton standing stock due to the sheer numbers of pollock larvae present in the system (Duffy-Anderson et al., 2002). A third possibility is that years of high pollock abundance could trigger predator-mediated apparent competition, where predators of larval pollock increase predation on abundant pollock and less abundant other species simultaneously. Of course, all samples analyzed here were collected from a relatively small geographic region (Kodiak vicinity of the western GOA), so a fourth explanation is that synchrony is reflected as similar responses to local events. Nevertheless, we demonstrated that a pronounced change in synchrony during the 1990s persisted for over a decade, suggesting long-term impacts to the plankton community as a whole.

Overall, our work shows that spring ichthyoplankton in the GOA integrates signals from the physical environment and adult spawning stock biomass. Our analyses revealed the composition of the assemblage is indicative of both gradual change and abrupt regime shifts. The biodiversity, synchrony, and DFA trends we presented are a first step towards developing ecosystem indicators from ichthyoplankton time series for the GOA. Ichthyoplankton are an important component of the lower trophic levels of the marine food web, as such, they can provide useful indicators of food availability, and they may also be potential leading indicators of change in marine ecosystems.

## Acknowledgements

This work evolved from a working group hosted by the National Center for Ecological Synthesis and Analysis (NCEAS) and funded by the Exxon Valdez Oil Spill Trustee Council. We thank the working group members for discussions and feedback on this work. Thanks to M. Busby for assistance with ichthyoplankton life history traits. We thank three anonymous reviewers, the editor, N. Manuta, and O. Shelton for comments that improved this manuscript. JDA was funded in part by NOAA's North Pacific Climate Regimes and Ecosystems Productivity (NPCREP) and Fisheries and the Environment Program (FATE) Programs. SCA was funded by a David H. Smith Conservation Research Fellowship. This is research is contribution EcoFOCI-0882 to NOAA's Fisheries-Oceanography Coordinated Investigations.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pcean.2018.11.002>.

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