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

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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) was 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.

Keywords

Gulf of Alaska, ichthyoplankton, biodiversity, synchrony, walleye pollock, climate, ecosystem indicators

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 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 (Beaugrand 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.

Methods

Ichthyoplankton sampling

Ichthyoplankton data were collected in May and June from the western GOA by the EcoFOCI from 1972 – 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 um and 505 um; 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).

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 (Tab. 1). We calculated a local temperature index from satellite monthly mean temperatures within the study area. We also calculated a local sea level 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.

Index	**Description**	**Source**	**Reference**
PDO	Pacific Decadal Oscillation: Average of monthly anomalies from Jan thru June, 1981-2013	http://jisao.washington.edu/pdo/PDO.latest	(Mantua et al., 1997)
NPGO	North Pacific Gyre Oscillation: Average of monthly anomalies from Jan thru June, 1981-2013	http://www.o3d.org/npgo/npgo.php	(Di Lorenzo et al., 2008)
MEI	Multivariate ENSO Index: Average of bimonthly values from Jan thru June, 1981-2013	http://www.esrl.noaa.gov/psd/enso/mei/table.html	(Wolter and Timlin, 1998, 1993)
NPI	North Pacific Index: Average of bimonthly values from Jan thru June, 1981-2013	https://climatedataguide.ucar.edu/sites/default/files/climate_index_files/npindex_monthly.ascii	(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	http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html	(Reynolds et al., 2002)
Upwelling	Upwelling index: average of monthly anomalies from Jan thru	http://www.pfeg.noaa.gov/products/PFELData/upwell/month	

	June, 1981-2013, from station at 60°N 149°W	ly/upanoms.mon	
MSL	Mean Sea Level: average of monthly mean water level from Jan thru June, 1981-2013, from Seldovia, AK (9455500)	https://tidesandcurrents.noaa.gov/inventory.html?id=9455500	
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)

Table 1. Environmental and biological variables investigated to explain temporal variation in ichthyoplankton assemblage

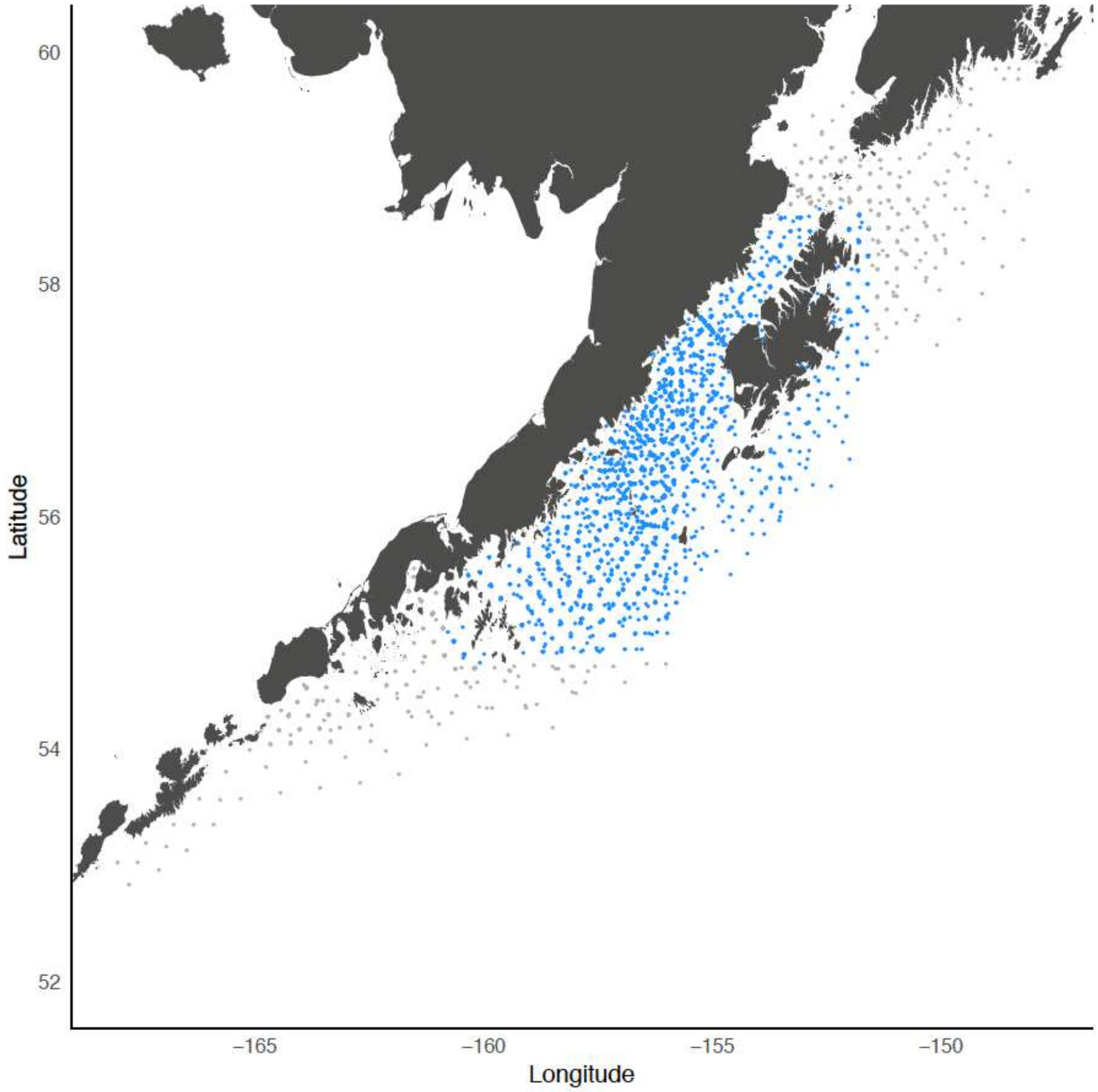

Figure 1. Map of historical ichthyoplankton sampling for EcoFOCI using plankton nets in the Gulf of Alaska (1972 – 2013). Points show all sampled locations over all years. Blue points were those locations included in the present analyses, representing the 90 percent quantiles of the tow locations.

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 (Tab. 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 x 20 km grids contained within the 90% quantiles of all grids sampled.

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	*Clupea pallasi*	Pacific herring	0.468
Bathylagidae	*Leuroglossus schmidti*	Northern smoothtongue	0.844
	Bathylagus pacificus	Slender blacksmelt	0.353
Osmeridae	*Mallotus villosus*	capelin	0.293
Myctophidae	*Protomyctophum thompsoni*	Northern flashlight fish	0.412
	Stenobrachius leucopsarus	Northern lampfish	4.656
Gadidae	*Gadus macrocephalus*	Pacific cod	6.477
	Gadus chalcogrammus	Walleye pollock	11.216
Scorpaenidae	*Sebastes* spp.	Rockfishes	4.881
Hexagrammidae	*Ophiodon elongatus*	Ling cod	0.35
	Hexagrammos spp.	Greenlings	1.266
Cottidae	*Icelinus* spp.	Sculpins	4.36
	Myoxocephalus spp.	Sculpins	0.584
	Radulinus spp.	Sculpins	1.187
	Ruscarius meanyi	Puget Sound sculpin	0.656
	Triglops spp.	Scuplins	0.178
Agonidae	*Bathyagonus alascanus*	Gray starsnout	2.833
	Bathyagonus infraspinatus	Spinycheek starsnout	0.534
	Podothecus acipenserinus	Sturgeon poacher	0.185
Liparidae	*Liparis fucensis*	Slipskin snailfish	1.049
Bathymasteridae	*Bathymaster* spp.	Ronquils	8.577
Stichaeidae	*Lumpenella longirostris*	Longsnout prickleback	0.554
	Lumpenus maculatus	Daubed shanny	1.273
	Lumpenus sagitta	Snake prickleback	0.162
	Poroclinus rothrocki	Whitebarred prickleback	1.721

	Anoplarchus spp.	Cockscombs	2.404
Cryptacanthodidae	*Cryptacanthodes aleutensis*	Dwarf wrymouth	2.058
Pholididae	*Pholis* spp.	Gunnels	3.034
Zaproridae	*Zaprora silenus*	Prowfish	0.765
Ammodytidae	*Ammodytes personatus*	Pacific sandlance	9.468
Pleuronectidae	*Atheresthes stomias*	Arrowtooth flounder	2.572
	Glyptocephalus zachirus	Rex sole	1.19
	Hippoglossoides elassodon	Flathead sole	10.094
	Hippoglossus stenolepis	Pacific halibut	1.342
	Isopsetta isolepis	Butter sole	0.861
	Lepidopsetta bilineata	Southern rock sole	3.453
	Lepidopsetta polyxystra	Northern rock sole	4.762
	Microstomus pacificus	Dover sole	0.854
	Platichthys stellatus	Starry flounder	2.49
	Pleuronectes quadrituberculatus	Alaska plaice	0.772

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.

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: $H_y = -\sum_{i=1}^{s} a_{iy} \log a_{iy}$

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 represents the correlation between the biomass of each species and the total biomass of all the other species, averaged across species: $\eta = \left(\frac{1}{s}\right) \sum_i cor(Y_i, \sum_{j \neq i} Y_j)$ 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.

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:

$$R^2 = 1 - \frac{\sum(Y_{ij}^{pred} - Y_{ij}^{obs})^2}{\sum(\bar{Y}_j^{obs} - Y_{ij}^{obs})^2}$$

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

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).

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.

Results

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 elongatu*s, *Platichthys stellatus*, and *Sebaste*s 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 1998-2005 (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.

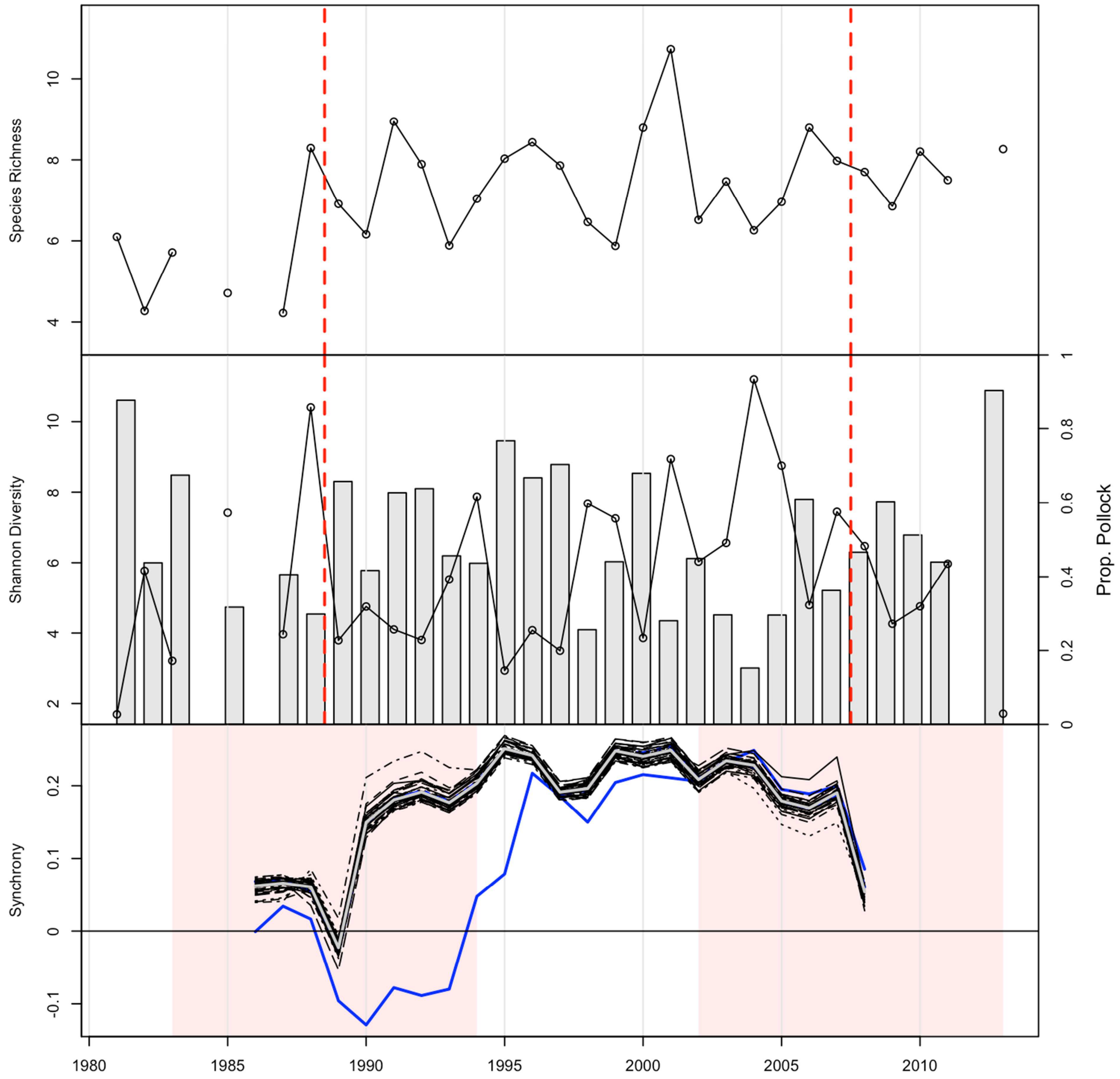

Figure 2. Ichthyoplankton assemblage dynamics between 1981-2013. Top panel shows species richness. Middle panel shows Shannon diversity (lines) and the proportion of total sampled larvae that were pollock (bars). Bottom panel shows synchrony within an 11-year moving window (x-value is midpoint of the window), where each black line represents synchrony with one species left out of the assemblage. Heavy gray line shows synchrony with all species and the

blue line shows synchrony without pollock. Vertical red lines indicate years of regime shifts in the GOA, and shaded red areas in bottom panel indicate the moving windows that include the years of the regime shifts.

Constructing shared temporal trends among ichthyoplankton species

We fit 8 potential DFA models to describe shared trends among ichthyoplankton, and model selection with AIC_C revealed the best 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 - 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.

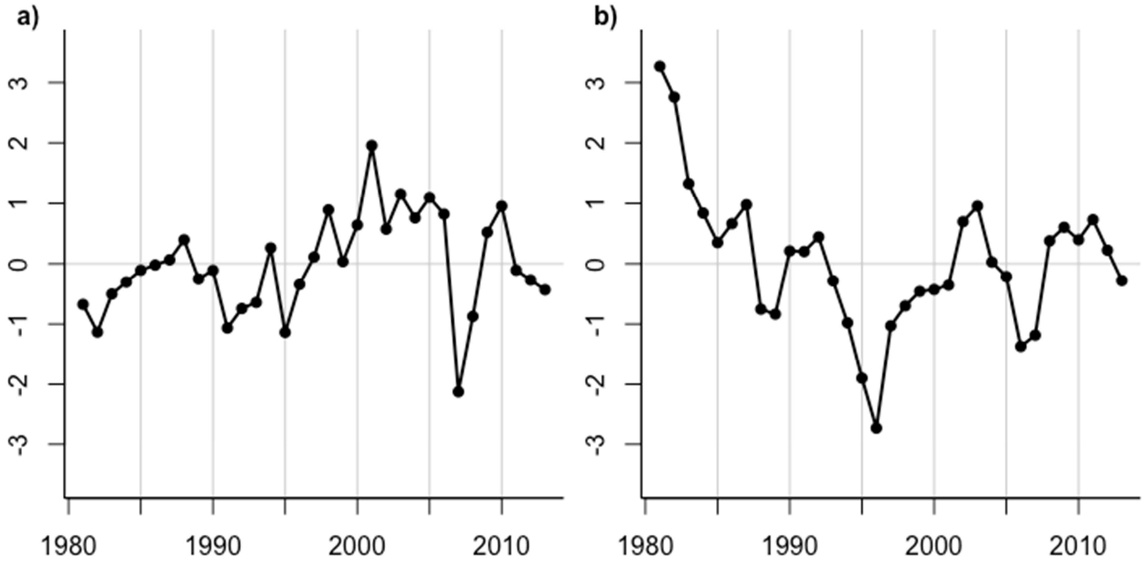

Figure 3. Common Trends 1 (a) and 2 (b) estimated from Dynamic Factor Analysis on 40 species of ichthyoplankton from 1981 to 2013.

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, Tab. 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 (Tab. 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 (Tab. 3). The third cluster included species loading positively on Trend 1 and weakly on 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,* Tab. 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 (Tab. 3).

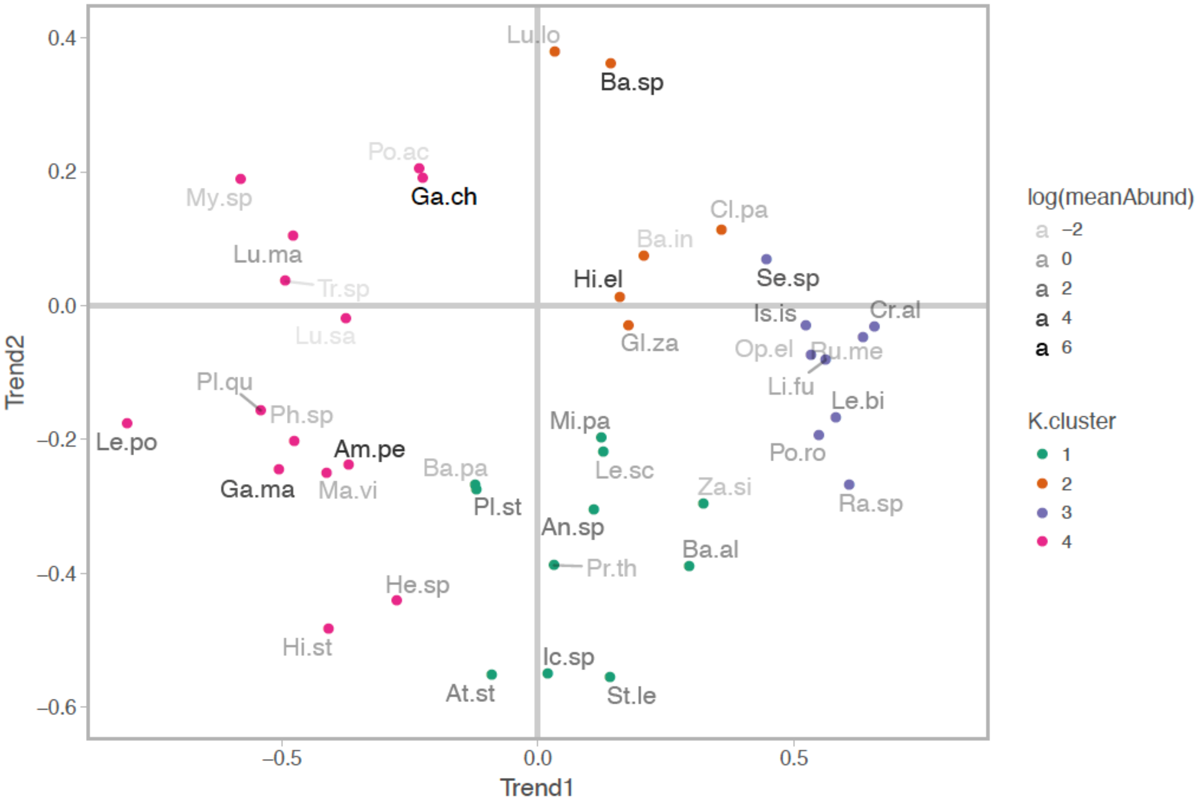

Figure 4. Loadings of ichthyoplankton species on DFA Trend 1 (x-axis) and Trend 2 (y-axis). Label shading is proportional to the log-scaled mean abundance of each species across all years. Point colors indicate clusters identified by hierarchical cluster analysis. Species abbreviations described in Table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

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**
Anoplarchus.spp.	An.sp	benthic	nearshore	spring	demersal	3	northern	1
Icelinus.spp.	Ic.sp	benthic	nearshore	spring	demersal	NA	northern	1
Platichthys.stellatus	Pl.st	benthic	slope	late spring	pelagic	2	southern	1
Stenobrachius.leucopsarus	St.le	pelagic	slope	spring	pelagic	8	both	1
Atheresthes.stomias	At.st	benthic	slope	winter	pelagic	5	both	1
Microstomus.pacificus	Mi.pa	benthic	slope	spring	pelagic	8	southern	1
Bathyagonus.alascanus	Ba.al	benthic	shelf	spring	demersal	3	both	1
Leuroglossus.schmidti	Le.sc	pelagic	slope	winter	pelagic	3	northern	1
Protomyctophum.thompsoni	Pr.th	pelagic	slope	winter	pelagic	8	both	1
Bathylagus.pacificus	Ba.pa	pelagic	slope	winter	pelagic	3	both	1
Zaprora.silenus	Za.si	benthic	slope	spring	demersal	4	northern	1
Bathymaster.spp.	Ba.sp	benthic	shelf	late spring	demersal	5	both	2
Hippoglossoides.elassodon	Hi.el	benthic	slope	early spring	pelagic	4	northern	2
Glyptocephalus.zachirus	Gl.za	benthic	slope	spring	pelagic	8	southern	2
Clupea.pallasi	Cl.pa	pelagic	nearshore, shelf	late spring	demersal	3	southern	2
Lumpenella.longirostris	Lu.lo	benthic	shelf	spring	demersal	3	northern	2
Bathyagonus.infraspinatus	Ba.in	benthic	shelf	spring	demersal	3	both	2
Sebastes.spp.	Se.sp	benthic	slope	spring	live bearing	5	both	3
Isopsetta.isolepis	Is.is	benthic	nearshore, shelf	early spring	pelagic	2	southern	3
Lepidopsetta.bilineata	Le.bi	benthic	shelf	late spring	demersal	4	southern	3
Cryptacanthodes.aleutensis	Cr.al	benthic	shelf	spring	demersal	3	both	3
Poroclinus.rothrocki	Po.ro	benthic	shelf	spring	demersal	4	both	3
Radulinus.spp.	Ra.sp	benthic	shelf	spring	demersal	NA	southern	3
Liparis.fucensis	Li.fu	benthic	shelf	late spring	demersal	2	both	3

Ruscarius.meanyi	Ru.me	benthic	shelf	spring	demersal	3	southern	3
Ophiodon.elongatus	Op.el	benthic	shelf	late winter	demersal	3	southern	3
Gadus.chalcogrammus	Ga.ch	benthic	shelf	early spring	pelagic	4	both	4
Ammodytes.personatus	Am.pe	pelagic	nearshore, shelf	late winter	demersal	8	both	4
Gadus.macrocephalus	Ga.ma	benthic	shelf	early spring	demersal	3	northern	4
Lepidopsetta.polyxystra	Le.po	benthic	shelf	early spring	demersal	5	northern	4
Lumpenus.maculatus	Lu.ma	benthic	nearshore	spring	demersal	5	northern	4
Hexagrammos.spp.	He.sp	benthic	nearshore	winter	demersal	8	both	4
Hippoglossus.stenolepis	Hi.st	benthic	slope	winter	pelagic	5	northern	4
Pleuronectes.quadrituberculatus	Pl.qu	benthic	shelf	late spring	pelagic	2	northern	4
Mallotus.villosus	Ma.vi	pelagic	nearshore	summer	demersal	8	northern	4
Pholis.spp.	Ph.sp	benthic	nearshore	late winter	demersal	3	both	4
Myoxocephalus.spp.	My.sp	benthic	shelf	spring	demersal	5	northern	4
Podothecus.acipenserinus	Po.ac	benthic	shelf	spring	demersal	3	both	4
Triglops.spp.	Tr.sp	benthic	shelf	spring	demersal	3	both	4
Lumpenus.sagitta	Lu.sa	benthic	shelf	late winter	demersal	3	northern	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. Due to declines during this same time period, species richness was negatively correlated with Pacific cod.

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 (Figs. 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 1982-1994. 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.

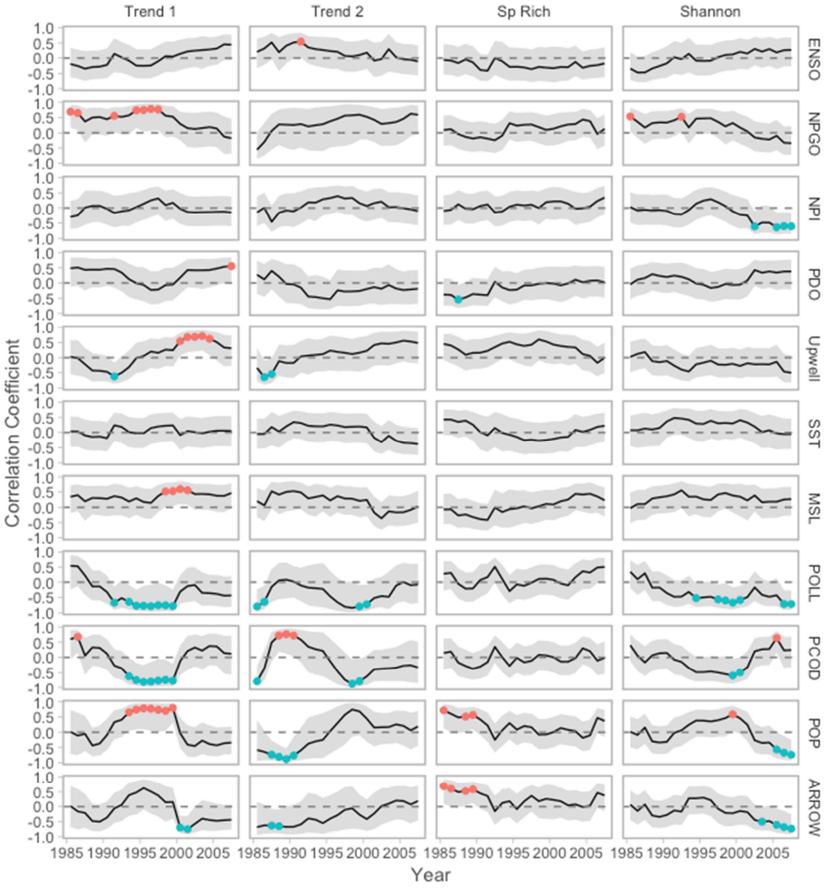

Figure 5. Moving window cross correlations between environmental and spawning stock biomass variables and DFA trends and diversity indices. Each panel shows a time series of Pearson correlations (black line) with 90 percent confidence intervals that account for autocorrelation (CI, grey-shaded region)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

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 1981-2013. 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 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 (Oncorhyncus 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 (Stabeno 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 1980-1995, and switched to negative between 1996-2008. 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 (Figs. 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.

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Supplementary Material

Appendix A: Time series of standardized probabilities of occurrence by species

Appendix B: Time series of standardized abundance by species

Appendix C: Model predictions from Dynamic Factor Analysis, by species

Appendix D: Model selection table, time series of environmental and SSB indices, and time series of GAK1 temperature