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

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**Abstract**

Understanding how ecosystems respond to changing environments remains a fundamental question in ecology. Marine ecosystems in the North Pacific support some of the most productive fisheries in the world and a diverse suite of ecosystem services. Here we present a spatiotemporal analysis using data from three decades of ichthyoplankton surveys in the Gulf of Alaska to investigate temporal patterns in species richness, Shannon diversity, and community synchrony. Then we use Dynamic Factor Analysis (DFA) to synthesize the ichthyoplankton community 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 in the community, and generally synchronous dynamics among ichthyoplankton species. Shannon diversity was largely driven by the dominance of larval walleye pollock (*Gadus chalcogrammus*). Correlations between climate drivers and DFA trends suggest that the North Pacific Gyre Oscillation and Pacific Decadal Oscillation were stronger than local-scale drivers like regional sea surface temperature. Our work demonstrates the potential value of ichthyoplankton surveys to provide leading indicators of climate-driven ecosystem variability and long-term change.

**Keywords**

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

**Introduction**:

Understanding how species, communities, and ecosystems respond to changing environments remains a fundamental challenge in ecology. Most observed responses have multiple potential explanations. In marine ecosystems, for example, changes in fishing, climate, and oceanographic conditions can have direct biological consequences and indirect consequences that propagate through a food web (Hunt et al., 2011). One way to reduce the dimensionality of this problem is to focus on ecological indicators that can track shifts in community structure or the physical environment (Coll et al., 2016). Biodiversity indicators are one type 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).

The idea that biodiversity confers stability to communities has long been debated (McCann, 2000). MacArthur (1955) first posited that communities with greater numbers of trophic linkages would be more stable in the face of environmental variability. While early studies found support for this idea (Elton, 1958; Odum, 1953), others suggested that more speciose communities should be less stable due to increasing numbers of interactions (May, 1973; Pimm, 1979; Yodzis, 1981). One mechanism through which diversity can stabilize a community is by introducing species that respond independently to environmental conditions (Doak et al., 1998; Ives et al., 2000; Loreau and de Mazancourt, 2013). Indeed, empirical evidence suggests that interspecific interactions confer stability to community biomass (Gross et al., 2014).

Temporal variability in species interactions and responses to perturbations can be measured with metrics of synchrony, which describe how species or 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 the intensity, strength, and coherence of trophic interactions (Leibhold 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 PDO is the first mode of variability in sea surface temperature in the North Pacific Ocean. The NPGO describes the second mode of variability of SST, and is related to chemical and biological properties in the GOA (Di Lorenzo et al., 2008). 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, 1993, 1998). The North Pacific Index describes sea level pressure over the area 30N-65N, 160E-140W (Trenberth and Hurrell, 1994). The GOA is typically a downwelling system; however, the upwelling index captures offshore Ekman transport driven by wind stress, which could drive transport of early stage ichthyoplankton larvae. The most well-known shift occurred in 1976/1977 characterized by a phase shift of the Pacific Decadal Oscillation (PDO) 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. Another significant 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, rather, it was described by shifts in the North Pacific Gyre Oscillation (NPGO, 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 atmospheric forcing variables, beyond the PDO-driven regime. 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, lowering ocean temperatures and impacting circulation.

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 (Anderson and Piatt, 1999; Litzow, 2006; Mueter and Norcross, 2000, 2002; 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.

Dominant species may have particularly strong impacts on assemblage structure and trophic interconnectivity. In the western GOA, walleye pollock (*Gadus chalcogrammus;* hereafter, pollock) are among the most abundant species in the groundfish community, serving as an important ecological link between upper and lower trophic communities (Aydin and Mueter, 2007; Duffy-Anderson et al., 2016; Sturdevant et al., 2012). As larvae, pollock dominate the ichthyoplankton community. ,Typical abundances in local patches ranging from 1000 - 6000 larvae 10 m–2 in spring in the western GOA, and ranging to orders of magnitude larger (Duffy-Anderson et al., 2002). Due to their sheer numbers in the system, pollock could strongly influence the dynamics of the ichthyoplankton community by altering the access of other larval fish species to zooplankton prey resources, competing with those that are co-occurring for habitat, and grazing down the zooplankton prey field.

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 community structure, biodiversity, synchrony, and pollock dominance; 2) describe temporal trends shared among multiple species in the community; and 3) explore potential physical and biological drivers of patterns in shared trends and diversity indices.

**Methods**

*Ichthyoplankton sampling*

Ichthyoplankton data were collected in May and June from the western Gulf of Alaska 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 between the two mesh sizes (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). Therefore, we used an upwelling index from the Pacific Fisheries Environmental Laboratory at the closest station to the study area (60°N 149°W). We also calculated a local temperature index from satellite monthly mean temperatures within the study area. In all cases, we used climate data from the first half 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, 1993, 1998) |
| 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 June, 1981-2013 | http://www.pfeg.noaa.gov/products/PFELData/upwell/monthly/upanoms.mon |  |
| 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 community

**../map.pdfFigure 1.** Map of historical ichthyoplankton sampling for EcoFOCI using plantkon nets in the Gulf of Alaska (1972 – present). Points represent 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). In some cases, species were aggregated to the genus level due to differences in levels of taxonomic resolution over the years or as an effort 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 |
| 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 |
| Bathylagidae | *Bathylagus pacificus* | Slender blacksmelt | 0.353 |
| 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 cell 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 (*pi*) of presence of each species *i* in each year *y* across *s* species: . 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:

*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: where *Yi* 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). Small loading values indicate poor fit, and we used the typical cut-off of 0.2 as a lower bound to consider species as loading on a trend (Jorgensen et al., 2016; 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:

where is the prediction for each species in each year from the DFA model and is the mean of the posterior of the standardized index for species *i* in year *j*.

*Exploring potential physical and biological drivers of biodiversity and shared trends*

We explored the potential influence of environmental and biological drivers on the ichthyoplankton community using 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 limits 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 generally 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 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 and remained relatively low during the 1990s (except for 1994). Higher diversity occurred between 1998-2005 (except 2000), but has declined since then, with a minimum observed in 2013.

The time series of synchrony also shows evidence of abrupt shifts, and reflects the dominant role of pollock in the community (difference between blue and gray lines, Fig. 2, lower panel). The largest divergence in non-pollock and full community synchrony occurred from 1995-2001 (moving window from 1985-2001), a period of strong pollock dominance. The non-pollock species were independent to weakly asynchronous during this time (synchrony values of 0 to -0.2). From 2001-2011 (moving window period from 1991-2011) synchrony has been positive in the full community and in the non-pollock species, indicating that pollock and rest of the community have been fluctuating in similar ways in recent years. Synchrony in the most recent year (2013) dropped as numbers of pollock larvae in the community increased dramatically.

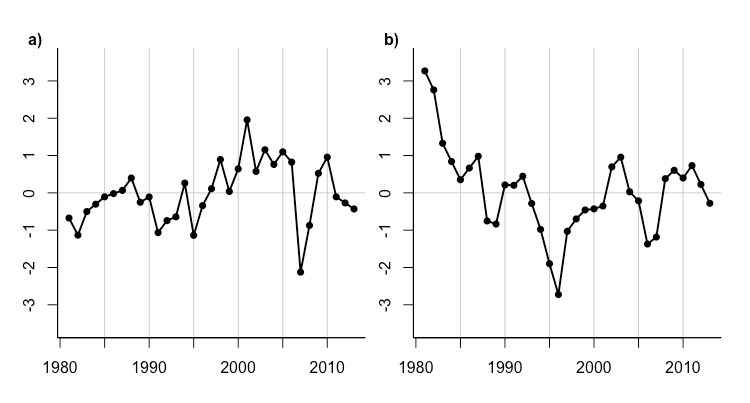


**Figure 2**. Ichthyoplankton community dynamics between 1981-2013. Top panel shows species richness. Middle panel shows Shannon diversity (lines) and the proportion of total sampled larvae that were pollock (bars). Bottom panel shows community synchrony within an 11-year moving window (where x-value is the last year in the window), where each line represents synchrony with one species left out of the community. Heavy gray line shows community synchrony with all species and heavy blue line shows synchrony without pollock.

*Shared temporal trends among ichthyoplankton species*

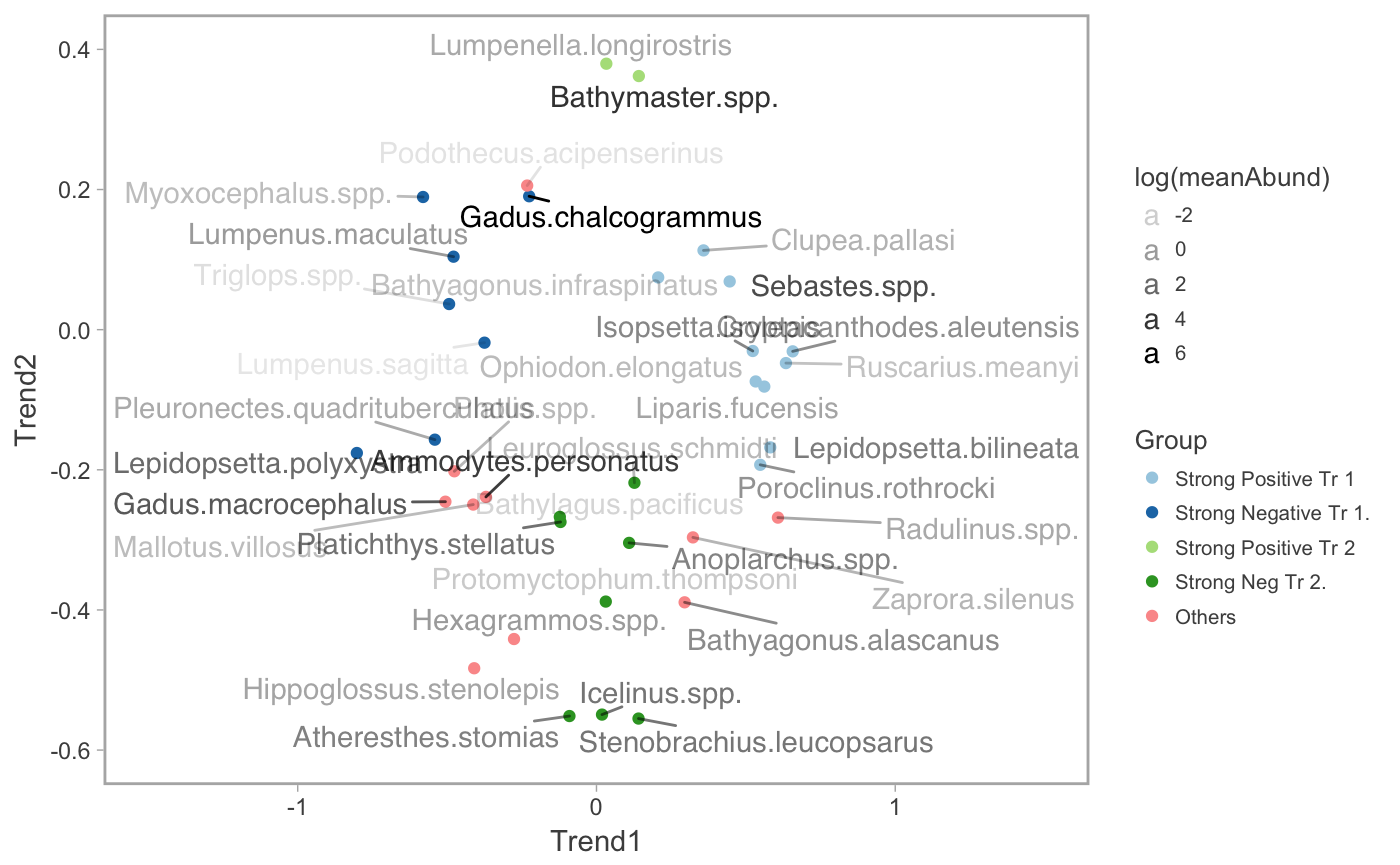
We fit 8 potential models to describe shared trends among ichthyoplankton, and model selection with AICC revealed the best model was a two-trend model with an equal variance-covariance matrix (Appendix C). The model with the next lowest AICC value was nearly 20 units higher, thus we did not consider 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 community over 1981-2013 (Fig. 3). Trend 1 showed moderate-to- low abundances 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 low frequency 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.

Species loadings on the trends revealed several groups that defined ichthyoplankton community structure (Fig. 4). Species loading positively on Trend 1 and weakly on Trend 2 (|loading| <0.2) were generally those that increased in abundance after 1996 (Appendices B-C). Of the nine species that showed this pattern (Fig. 4), several of these species were either warm-water associated (e.g., *Lepidopsetta bilineata, Sebastes spp.* (Pacific ocean perch), *Ophiodon elongatus*) and/or showed increasing trends in adult biomass over this same period (Pacific ocean perch). Conversely, another group of nine species loaded strongly negative on Trend 1 and weakly on Trend 2, indicating a decrease in abundance after the early 1990s. These decreasing species included some species that are cold-water associated (e.g. *Lepidopsetta polyxystra*) and/or species where adult abundance has also declined in recent years (e.g. pollock). Species loading heavily positive on trend 2 and weakly on trend 1 included species that experienced strong declines in the 1980s and 1990s (*Lumpenella* *longirostris* and *Bathymaster spp.*) and species that showed the opposite pattern, increasing over this period (8 species, Fig. 4).



**Figure 4**. Loadings of ichthyoplankton species on DFA Trend 1 (x-axis) and Trend 2 (y-axis). Species with |loadings| <0.2 omitted from plot. Label shading is proportional to the log-scaled mean abundance of each species across all years. Groupings were based on the strength of loadings on each of the two trends.

*Potential physical and biological drivers of biodiversity and shared trends*

Our analysis of diversity revealed that ichthyoplankton species richness was negatively correlated with 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. Because Pacific cod also declined over this time period, species richness was negatively correlated with that species.

Shannon diversity was positively correlated with the NPGO during most of the 1980s and 1990s, and negatively correlated with the NPI index during 1998-2013. 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 survey and the Shannon diversity index. 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 (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. 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 ENSO during 1987 to 1997. Similar to Trend 1, Trend 2 was negatively correlated with the upwelling anomaly from 1982-1994. For adult fish indices, Trend 2 represents a slightly different signal – both Trend 1 and 2 were correlated with pollock, in the 1980s and early 1990s Trend 2 was also negatively correlated with 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., value for 1991 represents years 1981 to 1991). Red and blue points represent correlations in which the confidence intervals are greater or less than zero, respectively.

**Discussion**

Ecological indicators developed from ichthyoplankton surveys are potentially useful tools to monitor and assess 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 Gulf of Alaska 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 the dominant larval species, pollock, on the co-occurring ichthyoplankton community, and the community response to the environmental forcing events relative to the abundance of walleye 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 Gulf of Alaska pursuant to overall ocean warming. We noted that abundances of larval southern rock sole, Pacific ocean perch, lingcod (*Ophiodon elongates*), and starry flounder (*Platichthys 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 (*Lepidopsetta polyxystra*) with the warm water species (*L. bilineata*) 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 variability are important environmental drivers of the spring ichthyoplankton community. Specifically, the NPGO appeared to have a stronger influence than other drivers we explored. While the PDO has received significant attention for contributing to ecosystem regime shifts in the Gulf of Alaska, we noted a dominance of the influence of the NPGO over the PDO in terms of responsiveness of the ichthyoplankton community from the late 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 (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 marine ecosystem.

Despite the dominance of the NPGO, the PDO was also correlated with Trend 1, but not significantly. The absence of a significant PDO trend may be due to the ichthyoplankton time series beginning several years after the most influential PDO regime shift of 1976-1977. Both DFA trends had peaks in 2007/2008, the same year as the PDO regime shift. 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 community 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.

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, which examined such different datasets yet found similar trends in biological responses indicates that the various components of the GOA ecosystem may respond similarly to broad-scale climate forcing.

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 suggests that the abundance of pollock could modulate the strength of competition among the other larval fish species. When pollock were abundant, the other species were asynchronous or independent, but when pollock were less abundant, all species fluctuated synchronously. 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. Reductions of the number of pollock larvae in the system could alleviate competition for prey resources and homogenize responses to environmental fluctuations. How pollock could intensify trophic interactions is unclear, though previously-demonstrated impacts of larval pollock grazing (Duffy-Anderson et al., 2002) suggest that competition for microzooplankton prey could play a role. Of course, all samples analyzed here were collected from a relatively small geographic region (Kodiak vicinity of the WGOA), so synchrony may reflect similar responses to stochastic, 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 Gulf of Alaska integrates signals from the physical environment and adult spawning stock biomass. Our analyses revealed the composition of the community 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, and as such they can provide useful indicators of food availability as well as 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 indicies, and time series of GAK1 temperature