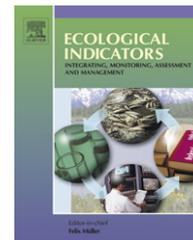


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/ecolind

Ichthyoplankton dynamics and biodiversity in the Gulf of Alaska: Responses to environmental change

Wiebke J. Boeing^{a,b,*}, Janet T. Duffy-Anderson^c

^a Joint Institute for the Study of Atmosphere and Oceans, University of Washington, PO Box 354235, Seattle, WA 98195, USA

^b Department of Fishery and Wildlife Sciences, New Mexico State University, 2980 S Espina, Las Cruces, NM 88003, USA

^c National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA

ARTICLE INFO

Article history:

Received 4 November 2006

Received in revised form

27 February 2007

Accepted 1 March 2007

Keywords:

Fish larvae

Regime shifts

Climate change

Ecosystem shifts

Metrics

ABSTRACT

Climate variation can cause major changes in the marine food web. We analyzed over 24 years of ichthyoplankton data from the Gulf of Alaska to evaluate lower trophic level responses to environmental change and judge their usefulness as ecological indicators. We standardized abundance data for each of 77 ichthyoplankton taxa, and used the Bray-Curtis distance measure and Flexible Beta linkage method, which grouped them into 22 discrete clusters. Variance Partitioning Analysis stressed the importance of geographical and seasonal processes for ichthyoplankton dynamics, and helped us identify the specific region(s) and month(s) for each response variable (cluster abundance, diversity) in which annual variation was maximized. Response variables were linked to environmental explanatory variables (atmospheric pressure, temperature, salinity and circulation indices) by Canonical Correspondence Analysis. The North Pacific Index (atmospheric pressure) and meso-scale climate variables like the El Niño Index (temperature), wind, and freshwater input (circulation) had the strongest impacts on ichthyoplankton species clusters. Specifically, the El Niño Index was negatively correlated with several ichthyoplankton clusters that were dominated by cold water species. Circulation was predominantly positively related to diversity and ichthyoplankton clusters, with the exception of clusters that mainly consisted of offshore taxa. The immediate response of ichthyoplankton to environmental forcing might make them suitable ecological indicators of environmental change although additional work is needed to assess effects on survival and recruitment.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Environmental factors have received increasing attention as important agents responsible for the restructuring of marine ecosystems (Southward, 1980; Aebischer et al., 1990; Anderson and Piatt, 1999; Beaugrand et al., 2002; Duffy-Anderson et al., 2005). A major climate transition occurred in the North Pacific Ocean and Bering Sea in 1976/77, which was subsequently linked, in part, to a phase reversal of the Pacific Decadal Oscillation (PDO) (Ebbesmeyer et al., 1991; Hare and Mantua,

2000). It has been suggested this variation in atmospheric forcing has led to fundamental differences in the pelagic ecosystem in terms of production (Piatt and Anderson, 1996; Anderson and Piatt, 1999) and community control (Bailey, 2000). However, nearly a decade passed before the magnitude of the impact on the biological community was recognized, and nearly two decades for those repercussions to be fully realized in ecology and functioning of the region. For fisheries management it would be an invaluable asset if the effects of phase transitions on the biological community could be

* Corresponding author. Tel.: +1 505 646 1707; fax: +1 505 646 1281.

E-mail address: wboeing@nmsu.edu (W.J. Boeing).

1470-160X/\$ – see front matter © 2007 Elsevier Ltd. All rights reserved.

doi:10.1016/j.ecolind.2007.03.002

predicted, or at least recognized, more quickly, potentially while the shift is taking place or soon thereafter. In theory, lower trophic level organisms should be more sensitive to changes in climate through the process of bottom-up forcing, and might reflect responses to environmental perturbations more quickly than higher trophic levels. Alternatively, early life stages may be environmentally sensitive prior to buffering through density-dependent mechanisms and community effects. [Beaugrand and Reid \(2003\)](#) have linked long-term changes in phytoplankton biomass to meteorological forcing in the North Atlantic Ocean, and [Beaugrand et al. \(2002\)](#) found that strong biogeographical shifts in copepod populations were related to temperature changes and the North Atlantic Oscillation. Likewise, [Brodeur et al. \(2002\)](#) determined that recent increases in jellyfish biomass in the Bering Sea are related to a climate-driven release from competition with zooplanktivorous forage fishes. Finally, [Hollowed et al. \(2001\)](#) have shown that climate forcing can directly affect fish recruitment potentially through the survival and recruitment of early life history stages. Thus, it may be possible to detect ecosystem changes sooner by focusing on planktonic stages.

Ichthyoplankton data provide a base for research into population dynamics of major fishery species ([Brodeur et al., 1995](#); [Rutherford et al., 1997](#); [Butler et al., 2003](#)), and information on ichthyoplankton ecology comprise an important component of stock assessment and fishery management plans ([Rutherford, 2002](#)). The Ecosystems and Fisheries-Oceanography Coordinated Investigations (Eco FOCI) program at the NOAA/Alaska Fisheries Science Center (AFSC), Seattle, WA, has collected ichthyoplankton data from the Gulf of Alaska (GOA) shelf for over 20 years (for example see [Matarese et al., 2003](#)), and we used data generated from this time series of collections (1972–2000) to examine the utility of ichthyoplankton data (assemblage abundance, species diversity) as quantitative indicators (metrics) of biological change in response to large-scale meteorological forcing. The GOA is characterized by two major circulation features: offshore, the Alaska Stream (AS) is a westward current that flows near the shelf break, and nearshore, the buoyancy driven Alaska Coastal Current (ACC) is a vigorous feature with a distinct freshwater core and annual mean transport of approximately $1.0 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ ([Stabeno et al., 1995, 2004](#)). Winds and freshwater input to the ACC can cause eddy formation, especially in spring, and can considerably increase retention time of plankton within an area ([Napp et al., 1996](#)). The rugged bottom topography of the GOA shelf (punctuated by fjords, deep troughs, and shallow banks) and strong tidal currents likely also contribute to eddy formation. During May, a seasonal peak in phytoplankton occurs in the ACC ([Napp et al., 1996](#)), followed by a peak in copepod production in May and other zooplankton in mid-summer ([Coyle and Pinchuk, 2003](#)). Seasonally availability of plankton, as well as the presence of eddies and meanders, likely influence the abundance, diversity, and distribution of ichthyoplankton in the GOA.

The objectives of the present study were to: (1) identify functional ichthyoplankton groups in the GOA based on similarities in seasonal and interannual abundance and distribution, (2) relate ichthyoplankton assemblage indices to oceanographic variables, and (3) evaluate whether ichthyo-

plankton data are useful as indicators of greater ecosystem change in the North Pacific.

2. Materials and methods

2.1. Sampling methodology

Ichthyoplankton data used in the present study were collected in 1972, between 1977–1979, and 1981–2000 in the GOA. The data were collected on 77 ichthyoplankton cruises and from a total of 7152 tows (range: 59–526 tows per year). Ichthyoplankton were collected from quantitative, oblique tows from bottom (or 200 m depth maximum) to surface with a 60 cm diameter bongo net (333 or 505 μm mesh) in a standardized manner. Calibrated flowmeters in each net mouth estimated the volume filtered. A paired t-test analysis, when one side of the bongo nets contained a 333 μm mesh and the other a 505 μm mesh (76 samples), demonstrated that there was no significant difference in ichthyoplankton catch rates between the two mesh sizes ([Boeing, unpublished data](#)). Thus, the data from both meshes were used. Samples were preserved in 5% formalin. Ichthyoplankton were sorted, and species were identified to the lowest taxonomic level possible, and enumerated at the Plankton Sorting and Identification Center in Szczecin, Poland. All fish larvae from sorted samples were returned to the AFSC, the taxonomic identifications were verified, and all the data were archived in a relational database (ICHBASE).

2.2. Response variables

The geographic area covered in the GOA ranged from 53.6 to 60.2°N and 139.4 to 165.6°W. The seasonal coverage extends from January to July and from September to November, depending on year, with most samples taken in April and May ([Matarese et al., 2003](#)). We divided the GOA region into seven regions ([Fig. 1](#)) according to [Bailey and Picquelle](#)

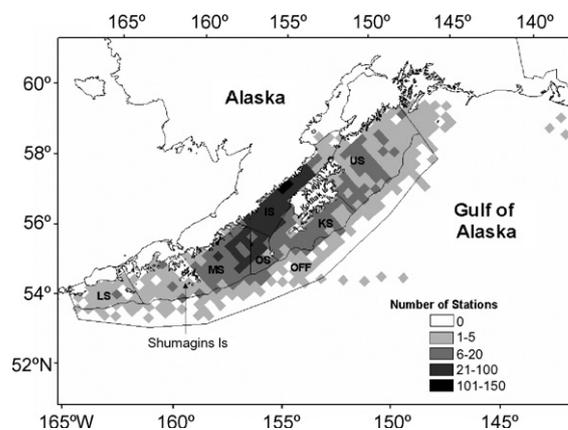


Fig. 1 – Geographic regions and ichthyoplankton sampling density in the Gulf of Alaska (GOA). LS: Lower Shelf; MS: Middle Shelf; OS: Outer Shelf; IS: Inner Shelikof Strait; KS: Kodiak Shelf; US: Upper Shelf; OFF: Offshore. Regions adapted from [Bailey and Picquelle \(2002\)](#). Darker colors within the GOA indicate higher sampling density.

Table 1 – Ichthyoplankton taxa that occurred in >5% of collected samples

Taxa	Common Name	Family	Cluster	Years of Max. Abundance	Months of Max. Abundance	Main Region of Occurrence	Adult Temperature Preference, Trophic characterization, Habitat ¹
<i>Artedius harringtoni</i>	Scalyhead sculpin	Cottidae	1	1990, 1998, 2000	Jun/Sep	KS, US	temperate, 3.41, demersal
<i>Baihyagonus infraspinus</i>	Spinycheek starsnout	Agonidae	1	1993, 1997, 1999	May-Jun	KS, LS, IS	temperate, ?, demersal
<i>Lepidopsetta bilineata</i>	Southern rock sole	Pleuronectidae	1	2000, 1997	May-Jun	KS, US, IS	temperate, 3.34, demersal
<i>Radulimus asprellus</i>	Slim sculpin	Cottidae	1	1997, 1996, 1998	May-Jun/Sep	LS, KS, IS	temperate, ?, demersal
<i>Anoploarctus</i> spp.	Cockscombs	Stichaeidae	1	1997, 1994, 1983	May-Jun	KS, IS, OS	temperate, 3.15, demersal
<i>Liparis</i> spp.	Snailfishes	Liparidae	1	2000, 1993, 1999	May-Jun	KS, LS, IS	flexible, 3.40, demersal
<i>Ruscarius meanyi</i>	Pudget Sound sculpin	Cottidae	2	2000, 1990, 1999	May-Jun/Sep	US, KS	temperate, ?, demersal
<i>Stichaeus punctatus</i>	Arctic shanny	Stichaeidae	2	1999, 2000, 1992	May-Jun	US, IS, KS	cold, 3.08, demersal
<i>Anoplogomus inermis</i>	Smooth alligatorfish	Agonidae	3	1994, 1999, 1996	Apr-Jun	LS, KS, OS	?, ?, demersal
<i>Pholis</i> spp.	Gunnels	Pholidae	3	1997, 1996, 1992	Apr-Jun	KS, LS	temperate, 3.41, demersal
<i>Podothecus acipenserinus</i>	Sturgeon poacher	Agonidae	3	1997, 1983, 1999	Apr-Jun	LS, KS, OS	flexible, 3.45, demersal
<i>Baihyagonus alascamus</i>	Gray starsnout	Agonidae	4	1996, 1997, 1992	Apr-Jun	OS, MS, IS	flexible, ?, demersal
<i>Lumpenus</i> spp.		Stichaeidae	4	1996, 1986, 1989	Apr-Jun	IS, MS, KS	cold, 3.25, demersal
<i>Theragra chalcogramma</i>	Walleye pollock	Gadidae	4	1996, 1981, 1995	Apr-Jun	IS, LS, OS	flexible, 3.79, benthopelagic
<i>Gadus macrocephalus</i>	Pacific cod	Gadidae	4	1995, 1989, 1996	Apr-Jun	LS, MS	flexible, 3.92, demersal
<i>Lepidopsetta polyxstra</i>	Northern rock sole	Pleuronectidae	4	1989, 1996, 1986	Apr-Jun	LS, KS, US	cold, ?, demersal
<i>Pleuronectes quadrituberculatus</i>	Alaska plaice	Pleuronectidae	4	1999, 1997, 1996	May-Jun	LS, IS, OS	cold, 3.14, demersal
<i>Bathymaster</i> spp.		Bathymasteridae	5	1997, 1983, 1981	May-Jul	MS, KS, IS	cold, 3.49, demersal
<i>Hippoglossoides elassodon</i>	Flathead sole	Pleuronectidae	5	1997, 1987, 2000	May-Jul	IS, OS, MS	flexible, 3.56, demersal
<i>Poroclinus rothrocki</i>	Whitebarred prickleback	Stichaeidae	5	1996, 2000, 1995	May-Jun	LS, MS, IS	flexible, ?, demersal
<i>Zaprora silenus</i>	Prowfish	Zaproridae	5	1996, 1984, 2000	May-Jul	MS, OFF, US	cold, ?, demersal
<i>Clupea pallasii</i>	Pacific herring	Clupeidae	6	1996, 1999, 1993	Jun	IS, KS	temperate, 3.40, pelagic
<i>Isosetta isolepis</i>	Butter sole	Pleuronectidae	7	2000, 1998, 1978	May-Jul	IS, OFF, US	temperate, 3.61, demersal
<i>Platichthys stellatus</i>	Starry flounder	Pleuronectidae	7	1993, 1996, 1999	May-Jun	IS, US, LS	flexible, 3.40, demersal
<i>Glyptocephalus zachirus</i>	Rex sole	Pleuronectidae	8	1998, 1990, 1985	May-Jul	OFF, KS, MS	flexible, 3.32, demersal
<i>Microstomus pacificus</i>	Dover sole	Pleuronectidae	8	1998, 1990, 1999	May-Jul	OFF, KS, US	flexible, 3.31, demersal
<i>Sebastes</i> spp.	Rockfishes	Scorpaenidae	8	1998, 1978, 1997	May-Jul	OFF, US, KS	flexible, 3.67, demersal
<i>Ronquihus jordani</i>	Northern ronquil	Bathymasteridae	9	1998, 1978, 1999	May-Jul	KS, US, IS	temperate, 3.13, demersal
<i>Icelinus</i> spp.		Cottidae	10	1997, 2000, 1998	May-Jul	MS, US, OS	flexible, 3.55, demersal
<i>Psychrolutes paradoxus</i>	Tadpole sculpin	Psychrolutidae	10	1997, 2000, 1999	May-Jun	OS, LS, KS	cold, 3.13, demersal
<i>Ammodytes hexapterus</i>	Pacific sand lance	Ammodytidae	11	1996, 1989, 1985	Mar-Jun	KS, OS, IS	flexible, 2.96, benthopelagic
<i>Lumpenus sagitta</i>	Snake prickleback	Stichaeidae	11	1992, 1999, 1989	Mar-May	KS, LS, IS	cold, 3.21, demersal
<i>Chirolophus</i> spp.	Warbonnets	Stichaeidae	11	2000, 1991, 1998	Mar-Jun	KS, LS, US	flexible, 3.60, demersal
<i>Hexagrammos decagrammus</i>	Kelp greenling	Hexagrammidae	12	1989, 1992, 1993	Feb-Jun	LS, IS, KS	flexible, 3.51, demersal
<i>Hemilepidotus hemilepidotus</i>	Red Irish lord	Cottidae	12	1986, 1993, 1991	Mar-May	LS, OS, IS	flexible, 3.53, demersal
<i>Nectoliparis pelagicus</i>	Tadpole snailfish	Liparidae	13	1982, 1993, 1992	Apr-May	OFF, OS, IS	cold, ?, pelagic
<i>Dasycottus setiger</i>	Spinyhead sculpin	Psychrolutidae	14	1992, 1979, 1997	Apr-Jun	KS, IS, MS	cold, 3.51, demersal
<i>Lumpenella longirostris</i>	Longsnout prickleback	Stichaeidae	15	1997, 1982, 1981	Apr-Jun	IS, OS, MS	cold, 3.00, demersal
<i>Ptilichthys goodei</i>	Quillfish	Ptilichthyidae	16	1994, 1979, 2000	Apr-May	LS, KS, MS	temperate, ?, demersal
<i>Gymnocranius</i> spp.		Cottidae	17	1972, 1982, 1984	Apr-May	KS, US, LS	cold, 3.17, demersal
<i>Myoxocephalus</i> spp.		Cottidae	17	1997, 1972, 1989	Apr-Jun	KS, LS, US	cold, 3.83, demersal
<i>Leptogomus frenatus</i>	Sawback poacher	Agonidae	18	1983, 1972, 1996	Apr-May	LS, IS, MS	cold, ?, demersal
<i>Mallotus villosus</i>	Capelin	Osmeridae	19	1990, 1978, 1979	Sep-Oct	US, KS	cold, 3.05, pelagic
<i>Pleurogrammus monopterygius</i>	Atka mackerel	Hexagrammidae	20	1977, 1978, 1979	Nov	KS, OFF, US	cold, 3.45, demersal
<i>Atheresthes stomias</i>	Arrowtooth flounder	Pleuronectidae	21	1996, 1992, 1993	Mar-Jun	OFF, US, OS	temperate, 4.11, demersal
<i>Hippoglossus stenolepis</i>	Pacific halibut	Pleuronectidae	21	1996, 1985, 1994	Mar-May	OFF, LS, US	cold, 3.97, demersal
<i>Protomyctophum thompsoni</i>	Northern flashlightfish	Myctophidae	21	1998, 1996, 1984	all year	OFF, US, OS	temperate, ?, pelagic
<i>Stenobrachius leucosparus</i>	Northern lampfish	Myctophidae	21	1996, 1998, 1993	Apr-Jun	OFF, US, OS	flexible, 3.41, pelagic
<i>Bathylagus pacificus</i>	Pacific blacksmelt	Bathylagidae	22	1985, 1996, 1992	Feb-Jul	OFF, OS	flexible, 3.28, bathypelagic
<i>Leuroglossus schmidti</i>	Northern smoothtongue	Bathylagidae	22	1985, 1977, 1983	Feb-Jul/Nov	OFF, US, LS	cold, 3.24, bathypelagic
Macrouridae	Grenadiers	Macrouridae	22	1979, 1985, 1982	Mar-Jul	LS, OFF	flexible, 3.88, benthopelagic

The table was ordered according to Fig. 2. Of each taxa year, months and regions of larval maxima as well as temperature preference, trophic level and habitat of adults are also presented. The regions are labeled identically to Fig. 1. (a) Information obtained from Matarese et al. (2003) and Froese and Pauly (2006).

(2002), and calculated the mean abundance (individuals per 10 m²) for 77 taxa for each available region, month and year when sample size ≥ 3 (Table 1). These taxa were chosen according to Matarese et al. (2003) based on frequency of occurrence >1% and average abundance >5 per 10 m² in positive tows.

We ran a cluster analysis for the 51 most abundant taxa (occurrence >5% of stations) to divide them into functional groups. We chose to eliminate rare species (<5% occurrence) as their inclusion led to chaining (single linkage clusters) in the analyses. Abundance data were standardized within each taxon by dividing each data point by the mean of the abundance over months, region and years. Standardized data were then clustered with the Bray-Curtis distance measure and Flexible Beta ($\beta = -0.25$) linkage method

using PC-ORD software (Fig. 2; McCune and Mefford, 1999). Hierarchical cluster analyses such as Bray-Curtis, are often preferred for ecological community data (McCune and Mefford, 1999). Furthermore, the analysis on standardized data clusters samples into naturally co-occurring groups based on their overall similarity of occurrence to one another (McCune and Mefford, 1999), independent of total abundance. With 63% information remaining, we divided the taxa into 22 discrete groups or clusters that seemed ecologically similar (Table 1, Fig. 2). Dendrograms are often trimmed at the level of 50% information remaining and may even go below 30% (Ellyson and Sillet, 2003; Brodeur et al., 2004). The clusters were named according to the most abundant ichthyoplankton taxon within the cluster.

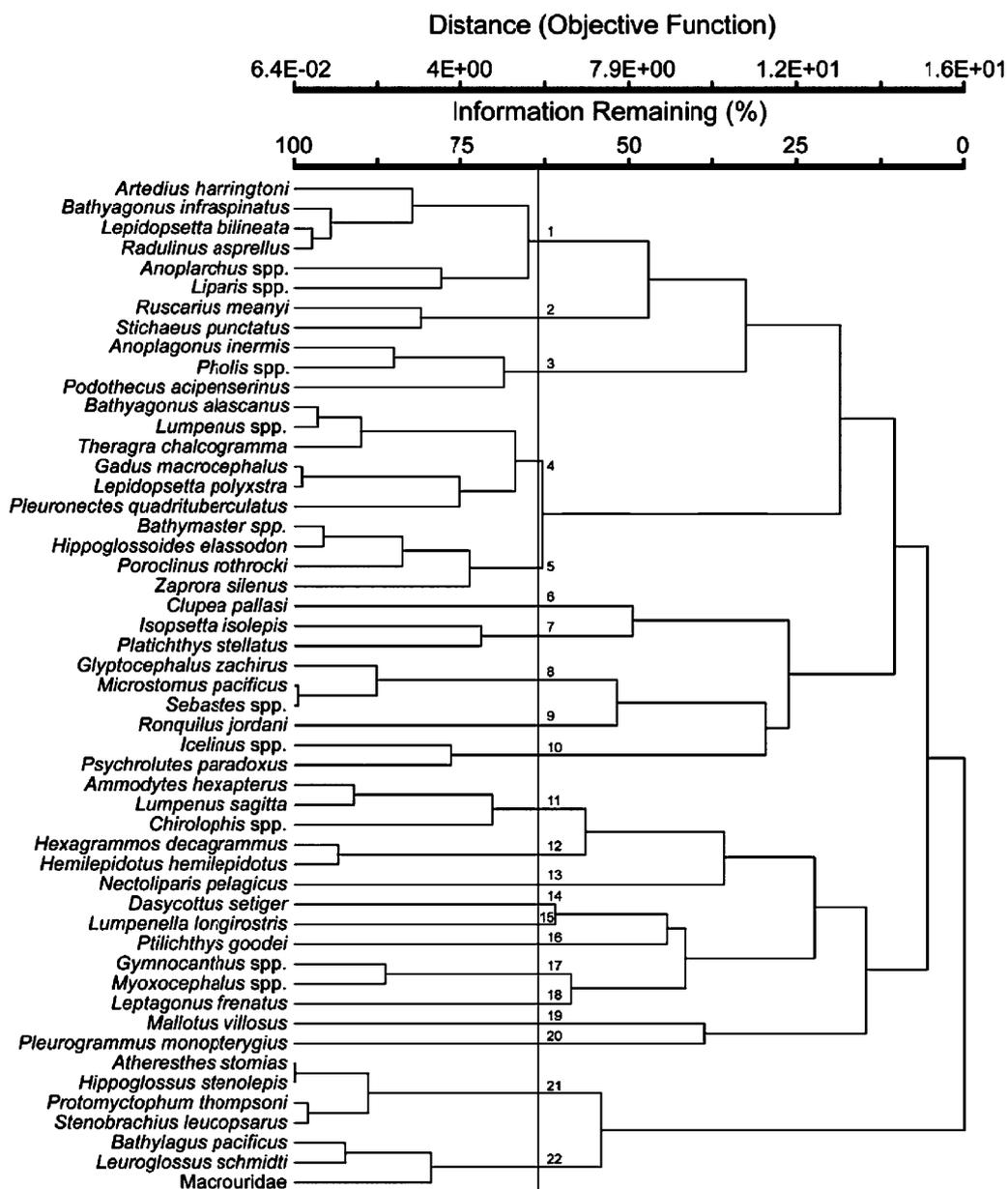


Fig. 2 – Cluster analysis of abundant (>5%) ichthyoplankton species using Bray-Curtis distance measure and Flexible Beta ($\beta = -0.25$) linkage method. Species named represent the most abundant species within each cluster.

Species diversity (H') was estimated with the Shannon-Wiener index for each region and month according to the formula:

$$H' = - \sum p_i \ln p_i \quad (1)$$

where p is the proportion of each species, i .

There was no correlation between sample size and Shannon-Wiener index ($Y = -0.0025X + 1.2865$, $n = 232$, $r^2 = 0.0232$, $p > 0.1$).

Similarly, species richness (total number of species) was calculated for every region and month. However, there was a logarithmic relationship between sample size and richness, when all data were considered ($Y = 6.0628 \ln(X) + 0.1109$, $n = 232$, $r^2 = 0.3807$, $p < 0.01$). Species richness increased as

more regions or months were sampled in any particular year. We eliminated this bias by narrowing the spatial and temporal scales to consider only the Inner Shelikof region in May, when sample size ≥ 21 ($Y = 0.0417X + 30.451$, $n = 16$, $r^2 = 0.0869$, $p > 0.1$). The Inner Shelikof region and May were chosen as the geographic area and month of interest because they provided the largest coverage over years.

2.3. Explanatory variables

Ichthyoplankton response variables were related to predominant environmental variables (atmospheric pressure, temperature, freshwater runoff and water circulation) (Table 2). We examined the relationships with pressure using: the North

Table 2 – Selected environmental data series available for the Gulf of Alaska used in the present study as explanatory variables

Variable	Description	Temporal domain	Source
Pressure			
North Pacific Index (NPI)	Intensity of Aleutian low	1899–2003 (monthly)	http://www.cgd.ucar.edu/cas/jhurrell/indices.html
Water temperature			
El Nino index (multivariate) (ENIX)	Measure of strength of El Nino (SST anomaly)	1856–2000 (monthly)	ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/nino34.long.latest
Pacific decadal oscillation index (PDO)	SST anomaly	1900–2003 (monthly)	ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/PDO.latest
Temperature at depth (GAK1)	Temperatures 50–75 m depth	1971–2001 (monthly)	S. Salo (personal communication); http://www.ims.uaf.edu/gak1/
Salinity			
Salinity at depth (GAK 1) (GAK Sal)	Salinities 50–75 m depth	1971–2001 (monthly)	S. Salo (personal communication); http://www.ims.uaf.edu/gak1/
Total river discharge into GOA (River)		1970–2002 (monthly)	Royer et al. (2001)
Circulation			
Costal upwelling at 60°N 149°W (Upwell)		1946–2003 (monthly)	ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon
Transport through shelikof Strait (at 40 m) (Transp)		1978–2002 (monthly)	M. Spillane (personal communication); http://www.pmel.noaa.gov/foci/spem-ibm.html
Alongshore wind (Wind)	Average along-shore component of wind (m/s) (positive = from southwest) at 57.5°N, 155°W	1946–2003 (monthly)	N. Bond (personal communication); http://www.cdc.noaa.gov/ncep_reanalysis , http://www.pfeg.noaa.gov:16080/products/las/docs/
Wind mixing (Wind mix)	Average wind mixing (m ³ /s ³) at 57.5°N, 155°W	1946–2003 (monthly)	N. Bond (personal communication); http://www.cdc.noaa.gov/ncep_reanalysis , http://www.pfeg.noaa.gov:16080/products/las/docs/

Pacific Index (NPI), which is a measure of the strength of the winter Aleutian Low (Trenberth and Hurrell, 1994). Water temperature indices included: (1) an El Niño Index (ENIX) which was derived from SST anomalies (5N–5S, 170–120W; Climate Diagnostics Center OISST archives at URL: <http://nic.fb4.noaa.gov:80/data/cddb/>), (2) the Pacific Decadal Oscillation (PDO) Index (Mantua et al., 1997), and (3) temperature at depth (50–75 m) (Seward hydrographic line, GAK1). Freshwater input indices used were: (1) salinity at depth (50–75 m) (Seward hydrographic line, GAK) and (2) estimated monthly fresh water discharge (River) into the Gulf of Alaska (Royer, 1982). Finally, the effects of variations in water circulation were investigated using: (1) monthly Bakun coastal upwelling index (Upwell) at 60°N 149°W which is an indirect measure of coastal upwelling, (2) total transport through Shelikof Strait (Transp), and (3) wind mixing (Wind mix) and alongshore winds (Wind) (N. Bond, personal communication). Transp was derived from a Sigma-coordinate Primitive Equation Model (SPEM) animation of circulation and salinity (at 40 m depth) model for the Shelikof Strait region of the GOA (Hermann and Stabeno, 1996; Stabeno and Hermann, 1996). SPEM estimates the extent of eddy formation and the degree of variability of overall flow in each year. Total transport is determined as the summed flow along grid points across a line in lower Shelikof Strait (M. Spillane, NOAA, PMEL, personal communication). Monthly estimates of wind mixing and alongshore winds were derived from a 50+ year record of atmospheric variables from the National Centers for Environmental Prediction/National Center for Atmospheric Research Reanalysis data set (Kalnay et al., 1996). The estimates were generated using a numerical weather prediction model and data assimilation system incorporating available surface, upper-air and satellite-based observations (N. Bond, University of Washington, JISAO, personal communication). The consistency in the procedure used for the reanalysis makes it well suited for studying climate variability from short-term to decadal time scales (Ladd and Bond, 2002). Effects of coastal terrain on the winds are accounted for following published procedures (Stabeno et al., 2004). Collectively, these environmental variables were chosen for examination as they reflect decadal scale variations in pattern, and because they either have been shown or are suspected to exert significant effects on fish abundance, diversity, and/or recruitment. It should be noted that meteorological data collected from one sampling location may not accurately represent effects at other locations since weather patterns are spatially heterogeneous in the GOA.

Environmental variables were available in monthly intervals, but we used spring averages (March–May) of the explanatory variables as that was the time period during which most ichthyoplankton taxa occurred at peak abundances (Table 1; Matarese et al., 2003, Doyle, unpublished data). Wind indices were available as averages between April 15 and June 15.

2.4. Statistical analyses

To calculate how much of the variance of the response variables (cluster abundance, Shannon–Wiener index and richness) was explained by geographical, seasonal, and annual factors, we estimated partitioned variance components

Table 3 – Region(s) and month(s) for each cluster and the Shannon–Wiener Index (H') that maximized annual variance and minimized geographical and seasonal variance

Cluster number	Region(s)	Month(s)
1	IS, OS, MS	May–June
2	US, IS, OS	Mar–June
3	IS, OS, KS	May–June
4	IS, OS	May–June
5	All regions	May–July
6	IS	June
7	IS, OS, MS	May–June
8	OFF, LS	May–July
9	US, KS	May–July
10	IS, OS, KS, MS, LS	May–June
11	IS, OS, KS	March–June
12	IS, OS, KS	March–May
13	US, IS, OS, OFF	February–June
14	IS, OS, KS	April–June
15	IS, OS	May–June
16	IS	May
17	US, IS, OS, KS, MS, LS	April–May
18	IS, MS	April–May
19	US, IS, OS, KS, MS, LS	March–May
20	US, KS, OS, OFF	February–April
21	OFF	May
22	US, OFF	April–July
H'	US, IS, OS, KS, MS	May–June

In case only one region was used, variance was calculated among stations within that region. In case only 1 month was used, variance was calculated among weeks within that month. See Fig. 1 for regions.

(Borcard et al., 1992) using the restricted (or residual) maximum likelihood methods (REML) (all factors random) with STATISTICA software (version 6, StatSoft, 2001). REML is the recommended method to estimate variance components because of the unbalanced design of our data (Robinson, 1987). For this analysis the original data were fourth-root transformed to buffer extreme values. We calculated relative variance as the percentage of total variation for each cluster. Since we were particularly interested in long-term climate effects, we identified a geographical region and a time frame for each cluster and the Shannon–Wiener index that maximized annual variance and minimized the other factors (Table 3), and used those data for further analyses.

Ichthyoplankton diversity and richness were related to abiotic parameters (Table 2) by canonical correspondence analysis (CCA). CCA relates patterns in community composition to variations in the environment, and is a robust, non-linear, constrained ordination method (ter Braak and Šmilauer, 1998). The order in which environmental explanatory variables were included was determined by stepwise forward selection (999 Monte Carlo permutations).

3. Results

The cluster analysis divided 51 ichthyoplankton taxa in 22 discrete clusters (Fig. 2). Nine clusters contained single taxa, while two clusters were comprised of six taxa each. The

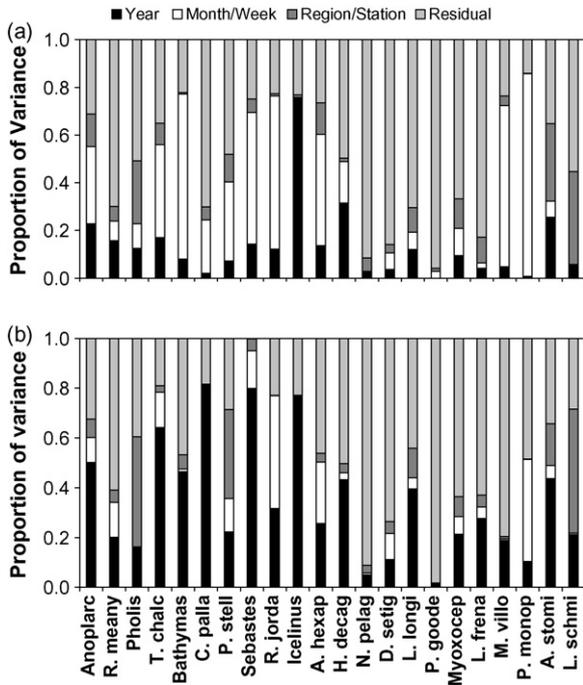


Fig. 3 – (a) Partitioning of annual (year), seasonal (month), geographical (region) and residual variance for the 22 clusters. Clusters are named after the dominant species with that cluster. (b) Partitioning of annual (year), seasonal (week), geographical (station) and residual variance for the 22 clusters. For each cluster, the region and time interval that maximized the annual variance and minimized the seasonal, geographical and residual variance was chosen.

clusters formed according to geographical regions in which taxa were found, and months and years during which taxa peaked in abundance. The dynamics of the clusters were typically explained by seasonal (month), geographical (region) and random factors (Fig. 3a). Since we were interested in how climate factors might be related to temporal variation in ichthyoplankton dynamics, we narrowed the region(s) and month(s) that allowed for the largest portion of the variance to be explained by annual variance (Fig. 3b, Table 3). Thus, the average proportion explained by annual variance could be enhanced from 13.7 to 34.5%.

A correlation matrix linking environmental variables to ichthyoplankton clusters in a linear fashion resulted in only very few significant relationships, and correlation coefficients were usually <0.5. We deemed non-linear approaches more appropriate, a conclusion similar to that of Doyle et al. (unpublished data). We ran the CCA to examine non-linear relationships between ichthyoplankton clusters, species richness and Shannon–Wiener diversity and environmental variables. Alongshore wind (*Wind*) entered the model first, then the El Niño Index (*ENIX*), followed by wind mixing (*Wind mix*), the North Pacific Index (*NPI*) and total river discharge (*River*) (Table 2, Fig. 4). Other variables are not presented on the graph since they did not result in significant relationships with ichthyoplankton clusters. Strength of the relationship is indicated by distance away from the center axis; clusters

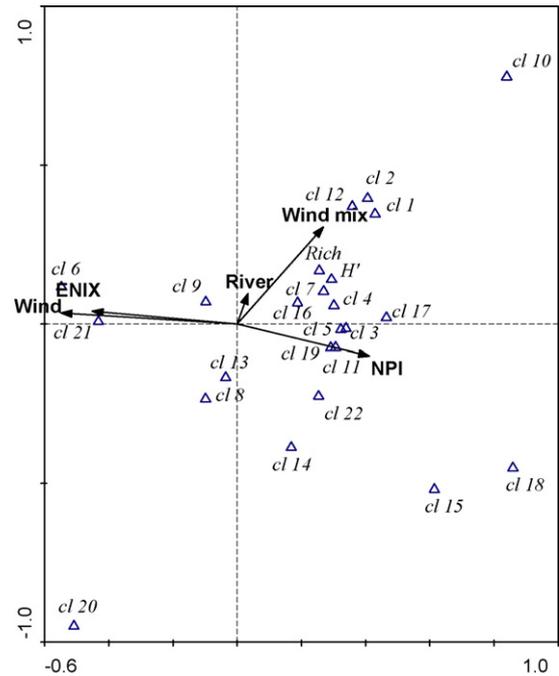


Fig. 4 – Canonical correspondence analysis relating biological response variables to environmental explanatory factors. Axes represent standard deviations. Biological parameters that are located in the same quadrant as an environmental parameter (arrows) correspond positively, biological parameters located in the opposite quadrant correspond negatively. The further the biological variable is away from the center point, the stronger the correspondence. Location at a right angle means no relationship between biological and environmental variable. Only environmental variables depicted as arrows significantly drive biological responses.

further from the center had stronger relationships with the environmental variable than those close to the origin. Clusters that are in the same quadrant as *Wind* and *ENIX* (clusters 6, 9, 21) were positively influenced by those environmental variables, with clusters 21 and 6 being strongly influenced and cluster 9 weakly influenced. These clusters tended to include temperate water species. Clusters dominated by cold water species were in the opposite quadrant from *ENIX* and *Wind*. *NPI* had an opposite effect on clusters than *Wind* and *ENIX*. *Wind mix* and *River* had a negative effect on clusters that tended to occur further away from shore (e.g., offshore) like clusters 13, 8 and 20 (Tables 1 and 3). Species richness and Shannon–Wiener diversity indices appeared to be positively influenced by wind mixing and river runoff.

4. Discussion

Several ichthyoplankton clusters were strongly related to environmental forcing factors. Cluster 21 corresponded positively to alongshore wind (*Wind*) and the El Niño Index

(ENIX), and negatively to the North Pacific Index (NPI). Cluster 21 was comprised of larvae from species that spawn offshore in deep waters along the continental shelf. Arrowtooth flounder are known to spawn in deep water along the continental shelf (>400 m) in the GOA (Blood et al., in press), and highest numbers of halibut, Northern lampfish, and Northern flashlight fish larvae are collected over the shelf break (Matarese et al., 2003). In the GOA, positive alongshore winds (from the NE, along the Peninsula) are downwelling favorable, and related to cross shelf transport. The positive relationship between cluster 21 and along-shore wind activity may be explained, in part, by Ekman forcing. As wind activity increases in the GOA, larvae that are spawned offshore may be drawn upslope, and onto the shelf by wind-driven Ekman transport. Further, wind-induced accelerations in the Alaska Coastal Current flow entrain slope waters in the trough and canyons that punctuate the GOA shelf. These two mechanisms, coupled with bathymetric steering, may facilitate up-canyon transport of slope-spawned larvae onto the shelf. Bailey and Picquelle (2002) postulated similar mechanisms after examining ingress of Pacific halibut and arrowtooth flounder larvae in the GOA. They also noted higher abundances of larger-sized larvae further inshore during El Nino years compared with non-El Nino years, and have suggested that enhanced onshelf transport during warm-year anomaly years is responsible for the observed differences. We report a positive correlation between ENIX and species abundance for cluster 21, which concurs with the hypotheses put forward by Bailey and Picquelle (2002). Taken together, results indicate that larvae of slope-spawning fish species may benefit from environmental conditions that contribute to increased basin-shelf exchange. Ladd et al. (2005b) postulated an additional mechanism of basin-slope connectivity, the presence of offshore eddies that periodically impinge on the shelf margin and deposit offshore water onto the shelf. Future work to examine the relationship between abundances of species in cluster 21 to the presence and timing of offshore eddies in the GOA may strengthen arguments that larvae of slope-spawned fishes are benefited by factors contributing to on-shelf transport.

Several clusters demonstrated positive relationships with degree of wind mixing (*Wind mix*) and river runoff (*River*). These clusters tended to be comprised of shelf-spawned species, which is reasonable given that shelf-spawned larvae are affected by on-shelf processes for the greatest portion of their larval life. In general, higher freshwater input and wind mixing on the shelf can lead to increased eddy formation, potentially entraining larvae together with high food concentrations in certain areas (Duffy-Anderson et al., 2002; Doyle et al., 2002; Hinrichsen et al., 2002). We were particularly interested in the response of cluster 4 to these two environmental variables, because cluster 4 contained walleye pollock, a well-studied shelf-spawned gadid in the North Pacific. Larval entrainment in mesoscale eddies in the GOA (Shelikof Strait) has been shown to be important to transport and feeding success in this species (Canino et al., 1991; Bailey et al., 1996a; Hermann et al., 1996; Kendall et al., 1996), and has implications for walleye pollock recruitment in the GOA (Bailey et al., 1996b). Our data support previously published information on the links between walleye pollock larval abundance and river

runoff. Effects may be particularly pronounced for walleye pollock, since the constriction of Shelikof Strait, which is a significant pollock spawning site, acts to amplify and accelerate water flow. Enhanced flow can contribute to eddies, increased nutrient flux, and production (Ladd et al., 2005a). Interestingly, larvae of several other species that co-occurred with walleye pollock in this cluster, Alaska plaice, Pacific cod, and gray starsnout, also demonstrate high abundances of larvae in Shelikof Strait and the Shelikof exit region (Matarese et al., 2003). This suggests that larvae in this cluster are particularly affected by entrainment variables, which may have greater effects in narrow Shelikof Strait than elsewhere in the GOA.

Eight clusters responded negatively to ENIX and *Wind* and positively to NPI, and these clusters tended to contain primarily offshore species. For example cluster 22, which was comprised of Macrourids and Bathylagids, had a negative relationship with these variables. Grenadiers (macrourids) are slope-dwelling species whose larvae are rarely collected on the continental shelf. Likewise, *Bathylagus pacificus* is also rarely collected over the continental shelf, though *Leuroglossus schmidti* occurs in low numbers there relative to the continental slope. It may be that factors that act to transport basin water onto the shelf (*ENIX* and *Wind*) bring larvae of these deep-dwelling species into unfavorable habitats (shelf habitat), contributing to their overall mortality. Further, the variable that we used as a measure of El Nino activity, ENIX, is a measure of temperature and thus it is not surprising that it is associated with decreased abundance of cold water species larvae. The relationship of cluster 22 to NPI is also intuitive. NPI is a measure of the intensity of the winter Aleutian Low, a low pressure zone which relaxes during spring and summer, and intensifies during autumn and winter. One hypothesis for the positive relationship between cluster 22 and NPI may be that increased storm activity in winter, the time of maximal spawning for species in this cluster, acts to mix down nutrients and biological materials, providing an increased available energy source for newly-hatched larvae over the continental slope.

Though we were able to demonstrate some relationships between ichthyoplankton clusters and environmental variables, we were not able to determine whether these were due to direct effects on larval survival, or due to indirect effects such as advection out of the study area or diffusion. However, transport away from suitable nursery habitat should also result in low survival rates (Brodeur and Wilson, 1996; Bailey et al., 1997; Wilson et al., 2005). Future work should include efforts to examine larval survival and recruitment in relation to forcing factors.

4.1. Diversity

The ichthyoplankton species diversity in the Gulf of Alaska (GOA) is high when compared to other ecosystems (Witting et al., 1999; Perez-Rezafa et al., 2004, however see Moser and Smith, 1993), but it is similar to what was found by Shackell and Frank (2000) for the Scotian shelf ecosystem. The GOA has approximately 100 distinguishable ichthyoplankton taxa in a multi year study (Matarese et al., 2003). Interestingly, it has been hypothesized that the GOA might be a geographic

breakpoint (Bailey et al., 2003), harboring both more northerly coldwater species at the southern extent of their range and more southerly temperate water species living at the northern extent of their range. For example, on one hand, larvae of species like bigscales (Melamphaidae), scalyhead sculpin (*A. harringtoni*), Puget Sound sculpin (*Ruscarius meanyi*), Northern ronquil (*Ronquilus jordani*) and southern rock sole (*Lepidopsetta bilineata*), occur off the Oregon coast and in the GOA, but are not typically found in the Bering Sea. On the other hand, adults and larvae of Atka mackerel (*Pleuragrammus monompterygius*), Northern smoothtongue (*Leuroglossus schmidti*), *Gymnocanthus* spp., *Myoxocephalus* spp., sawback poacher (*Leptagonus frenatus*), spinyhead sculpin (*Dasycottus setiger*), tadpole sculpin (*Psychrolutes paradoxus*), Northern rock sole (*Lepidopsetta polyxystra*) and Alaska plaice (*Pleuronectes quadrituberculatus*) are caught in the Bering Sea and GOA, but not off the Oregon coast (Matarese et al., 2003). Further, some species only occur in the GOA, and cannot be found in either the Bering Sea or off the Oregon coast like smooth alligatorfish (*Anoplagonus inermis*) or soft sculpin (*Psychrolutes sigalutes*). Often, only the larvae, but not the adults, are found in the GOA (Matarese et al., 2003), which stresses the importance of ichthyoplankton surveys as an indicator for presence and absence of certain fish species.

Despite fairly relaxed requirements for species to be within the same cluster (63% information remaining), we noted 22 cluster groups forming from 51 total species. Nine species formed clusters by themselves. Clusters with several taxa gave no indication of those taxa being closely related or within the same functional group (Table 1). This indicates that mainly seasonal, geographical and annual (climate) as well as random processes (as indicated by the high residual variance in the variance partitioning analysis) determine which species co-occur. It is also possible, that only few species within the same functional group will dominate within any particular year as they compete with each other.

Both, richness and Shannon–Wiener diversity indices were positively influenced by *Wind mix* and *River*. This is probably due to the fact that more and larger clusters positively responded to those environmental parameters. There were 8 clusters with a total of 23 species that also corresponded positively to *Wind mix* and *River*, while the other quadrants only had 8 clusters containing 17 species, 4 clusters containing 5 species and 3 clusters containing 6 species.

4.2. Environmental variables

Of all environmental variables tested, wind variables and freshwater discharge indices seem to be most influential and may have the greatest potential as indicator of ichthyoplankton response. River runoff has a greater contribution to the GOA freshwater input than precipitation (Stabeno et al., 2004), so precipitation indices (rainfall at Kodiak Island, for example) may not be as robust as direct estimates of river runoff which is also influenced by snowpack melt. Overall however, increased freshwater discharge into the GOA has two indirect effects: (1) it increases the number of eddies formed, thereby potentially enhancing retention of fish larvae and co-entraining them with zooplankton prey, and (2) it decreases salinity in the surface layers. Although we included retention and salinity indices, none of them successfully entered the CCA

model. The transport index (*Transp*) is a model led result based on circulation and salinity at 40 m in the Shelikof Strait, and the salinity index was obtained from the GAK-line, which is located north-east of Shelikof Strait. Both indices might be too localized to significantly impact a substantial portion of the ichthyoplankton community of the entire GOA. Most indices that proved relevant for the ichthyoplankton community seemed to be on a meso-scale, both spatially (wind indices and river discharge vs. temperature and salinity at depth, or most basin wide parameters—with the exception of NPI) and temporally (ENIX was relevant which operates on a multi-year scale as opposed to variables that change on a decadal scale like PDO that oscillate at low frequency). Alongshore wind (*Wind*) and wind mixing (*Wind mix*) had opposing effects on fish larvae, and these two variables might differentially influence eddy formation. While alongshore winds seem to favor eddy formation and retention of some larvae, wind mixing seems to be disruptive of eddies and could act to decouple larvae from their plankton prey.

5. Conclusions

Results from this study suggest that indices derived from ichthyoplankton data could be useful in evaluating biological change in response to meso-scale meteorological forcing. Responses are typically non-linear and complex. We found several clusters responding to meso-scale environmental forcings, might indicate their suitability as ecological indicators, however, the stability of those relationships need to be surveyed in the future, as more data become available.

Although we did find significant environmental (climate) forcing factors on the ichthyoplankton community, the relationship may be obscured by other forcings such as competition, predation, disease and fishery. However, a major driving force for fish larvae are climatic factors, while adult fishes are mainly influenced by competition and fishing pressure (Boeing et al., 2007). Since many adult female fishes can spawn thousands of eggs, the response to climate should be most obvious in early life-history stages, while adult stage should be most sensitive to effects of fisheries.

The next step would be to investigate the delay in response from fish larvae to adult stages to incorporate ichthyoplankton as a meaningful indicator for regime shifts. Ichthyoplankton predictors should be included into forecasting models such as the Alaska Fishery Science Center Resource Ecology and Ecosystem Modeling (<http://access.afsc.noaa.gov/reem/ecoweb>).

Acknowledgements

We would like to thank K. Bailey, M. Wilson, M. Doyle, J. Napp and A. Matarese for discussing various aspects of the paper with us. We are indebted to K. Mier and S. Picquelle for statistical advice. This contribution was partly funded by the Joint Institute for the Study of the Atmosphere and Ocean under NOAA Cooperative Agreement No. NA178RG1232, contribution number 1387. This research is contribution Eco FOCI-N617 to NOAA's Fisheries-Oceanography Coordinated Investigations.

REFERENCES

- Aebischer, N.J., Coulson, J.C., Colebrook, J.M., 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347, 753–755.
- Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* 189, 117–123.
- Bailey, K.M., 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Mar. Ecol. Prog. Ser.* 198, 215–224.
- Bailey, K.M., Picquelle, S.J., 2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: potential transport pathways and enhanced onshore transport during ENSO events. *Mar. Ecol. Prog. Ser.* 236, 205–217.
- Bailey, K.M., Brodeur, R.D., Hollowed, A.B., 1996b. Cohort survival patterns of walleye pollock in Shelikof Strait, Alaska: a critical factor analysis. *Fish. Oceanogr.* 5 (Suppl. 1), 179–188.
- Bailey, K.M., Brown, E., Duffy-Anderson, J.T., 2003. Aspects of distribution, transport and recruitment of Alaska plaice (*Pleuronectes quadrituberculatus*) in the Gulf of Alaska and Bering Sea: comparison of marginal and central populations. *J. Sea Res.* 50 (2–3), 87–95.
- Bailey, K.M., Picquelle, S.J., Spring, S.M., 1996a. Mortality of larval walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska, 1988–1991. *Fish. Oceanogr.* 5 (Suppl. 1), 124–136.
- Bailey, K.M., Stabeno, P.J., Powers, D.A., 1997. The role of larval retention and transport features in mortality and potential gene flow of walleye pollock. *J. Fish Biol.* 51 (Suppl. A), 135–154.
- Beaugrand, G., Reid, P.C., 2003. Long-term changes in phytoplankton, zooplankton, and salmon related to climate. *Global Change Biol.* 9, 801–817.
- Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692–1694.
- Blood, D.M., Matarese, A.C., Busby, M.S., in press. Spawning, egg development, and early life history dynamics of arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska. NOAA Prof. Paper NMFS.
- Boeing, W.J., Martin, M.H., Duffy-Anderson, J.T., 2007. Groundfish. In: Spies, R.B. (Ed.), Long-term Ecological Change in the Northern Gulf of Alaska. Elsevier, pp. 300–311.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055.
- Brodeur, R.D., Wilson, M.T., 1996. A review of the distribution, ecology, and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fish. Oceanogr.* 5 (Suppl. 1), 148–166.
- Brodeur, R.D., Busby, M.S., Wilson, M.T., 1995. Summer distribution of early-life stages of Walleye Pollock, *Theragra chalcogramma*, and associated species in the Western Gulf of Alaska. *Fish B: NOAA* 93, 603–618.
- Brodeur, R.D., Fisher, J.P., Teel, D.J., Emmett, R.L., Casillas, E., Miller, T.W., 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current. *Fish B: NOAA* 120, 25–46.
- Brodeur, R.D., Sugisaki, H., Hunt Jr., G.L., 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Mar. Ecol. Prog. Ser.* 233, 89–103.
- Butler, J.L., Jacobson, L.D., Barnes, J.T., Moser, H.G., 2003. Biology and population dynamics of cowcod (*Sebastes levis*) in the southern California Bight. *Fish B: NOAA* 101, 260–280.
- Canino, M.F., Bailey, K.M., Incze, L.S., 1991. Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. *Mar. Ecol. Prog. Ser.* 79, 27–35.
- Coyle, K.O., Pinchuk, A.I., 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. *Fish. Oceanogr.* 12, 327–338.
- Doyle, M.J., Busby, M.S., Duffy-Anderson, J.T., Picquelle, S.J., Materese, A.C., 2002. Early life history of capelin (*Mallotus villosus*) in the northwest Gulf of Alaska: a historical perspective based on larval collections October 1977–March 1979. *ICES J. Mar. Sci.* 59, 997–1005.
- Duffy-Anderson, J.T., Bailey, K.M., Ciannelli, L., 2002. Consequences of a superabundance of larval walleye pollock *Theragra chalcogramma* in the Gulf of Alaska in 1981. *Mar. Ecol. Prog. Ser.* 243, 179–190.
- Duffy-Anderson, J.T., Bailey, K.M., Ciannelli, L., Cury, P., Belgrano, A., Stenseth, N.C., 2005. Phase transitions in marine fish recruitment processes. *Ecol. Complex.* 2, 205–218.
- Ebbesmeyer, C.C., Cayan, D.R., McLain, D.R., Nichols, F.H., Peterson, D.H., Redmond, K.T., 1991. 1976 step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1985. In: Proceedings of the 7th Annual Pacific Climate Workshop, California Department of Water Resources, Interagency Ecological Studies Progress Report 26.
- Ellyson, W.J.T., Sillet, S.C., 2003. Epiphyte communities on Sitka spruce in an old-growth redwood forest. *Bryologist* 106, 197–211.
- Froese, R., Pauly, D. (Eds.), 2006. FishBase, World Wide Web Electronic Publication: <http://www.fishbase.org>, Version (12/2006).
- Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* 47, 103–145.
- Hermann, A.J., Stabeno, P.J., 1996. An eddy-resolving model of circulation on the western Gulf of Alaska Shelf. 1. Model development and sensitivity analyses. *J. Geophys. Res.* 101 (C1), 1129–1149.
- Hermann, A.J., Hinckley, S., Megrey, B.M., Stabeno, P.J., 1996. Interannual variability of the early life history of walleye pollock near Shelikof Strait as inferred from a spatially explicit, individual based model. *Fish. Oceanogr.* 5 (suppl. 1), 39–57.
- Hinrichsen, H.-H., Mollmann, C., Voss, R., Koster, F.W., Kornilovs, G., 2002. Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Can. J. Fish. Aquat. Sci.* 59, 1858–1873.
- Hollowed, A.B., Hare, S.R., Wooster, W.S., 2001. Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. *Prog. Oceanogr.* 49, 257–282.
- Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Leetmaa, A., Reynolds, B., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Jenne, R., Joseph, D., 1996. The NCEP/NCAR 40-year reanalysis project. *Bull. Am. Meteorol. Soc.* 77, 437–471.
- Kendall Jr., A.W., Schumacher, J.D., Kim, S., 1996. Walleye pollock recruitment in Shelikof Strait: applied fisheries oceanography. In: Kendall Jr., A.W., Schumacher, J.D., Kim, S. (Eds.), Fisheries Oceanography of Walleye Pollock in Shelikof Strait, Alaska. *Fish. Oceanogr.* 5 (Suppl. 1), 4–18.
- Ladd, C., Bond, N.A., 2002. Evaluation of the NCEP-NCAR reanalysis in the northeast Pacific and the Bering Sea. *J. Geophys. Res.* 107, 3158–3166.

- Ladd, C., Kachel, N.B., Mordy, C.W., Stabeno, P.J., 2005a. Observations from a Yakutat eddy in the northern Gulf of Alaska. *J. Geophys. Res.* 110, C03003.
- Ladd, C., Stabeno, P., Cokelet, E.D., 2005b. A note on cross-shelf exchange in the northern Gulf of Alaska. *Deep-Sea Res. II* 52, 667–679.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78, 1069–1079.
- Matarese, A.C., Blood, D.M., Picquelle, S.J., Benson, J.L., 2003. Atlas of abundance and distribution patterns of ichthyoplankton from the northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center (1972–1996). NOAA Professional Paper 1, 281 pp.
- McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon, USA.
- Moser, H.G., Smith, P.E., 1993. Larval fish assemblages of the California Current region and their horizontal and vertical distribution across a front. *Bull. Mar. Sci.* 53 (2), 645–691.
- Napp, J.M., Incze, L.S., Ortner, P.B., Siefert, D.L.W., Britt, L., 1996. The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. *Fish. Oceanogr.* 5, 19–38.
- Perez-Rezafa, A., Quispe-Becerra, J.I., Garcia-Charton, J.A., Marcos, C., 2004. Composition, structure and distribution of ichthyoplankton in a Mediterranean coastal lagoon. *J. Fish. Biol.* 64, 202–218.
- Piatt, J.F., Anderson, P., 1996. Response of common murrelets to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. *Am. Fish. Soc. Symp.* 18, 720–737.
- Robindson, D.L., 1987. Estimation and use of variance components. *Statistician* 36, 3–14.
- Royer, T.C., 1982. Coastal fresh-water discharge in the northeast Pacific. *J. Geophys. Res.* 87 (NC3), 2017–2021.
- Royer, T.C., Grosch, C.E., Mysak, L.A., 2001. Interdecadal variability of northeast Pacific coastal freshwater and its implications on biological productivity. *Prog. Oceanogr.* 49, 95–111.
- Rutherford, E.S., 2002. Fishery management. In: Fuiman, L.A., Werner, R.G. (Eds.), *Fishery Science. The Unique Contributions of Early Life Stages*. Fishery Blackwell Publishing, pp. 206–221.
- Rutherford, E.S., Houde, E.D., Nyman, R.M., 1997. Relationship of larval-stage growth and mortality to recruitment of striped bass, *Morone saxatilis*, in Chesapeake Bay. *Estuaries* 20, 174–1983.
- Shackell, N.L., Frank, K.T., 2000. Larval fish diversity in the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* 57, 1747–1760.
- Southward, A.J., 1980. The western English Channel—an inconstant ecosystem. *Nature* 285, 361–366.
- Stabeno, P.J., Hermann, A.J., 1996. An eddy-resolving model of circulation on the western Gulf of Alaska Shelf. 2. Comparison of results to oceanographic observations. *J. Geophys. Res.* 101 (C1), 1151–1161.
- Stabeno, P.J., Reed, R.K., Schumacher, J.D., 1995. The Alaska Coastal Current: continuity of transport and forcing. *J. Geophys. Res.* 100, 2477–2485.
- Stabeno, P.J., Bond, N.A., Hermann, A.J., Kachel, N.B., Mordy, C.W., Overland, J.E., 2004. Meteorology and oceanography of the Northern Gulf of Alaska. *Cont. Shelf Res.* 24, 859–897.
- StatSoft, 2001. STATISTICA Visual Basic Primer. StatSoft Inc., Tulsa, OK, USA.
- ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (Version 4). Centre for Biometry Wageningen/Microcomputer Power, Wageningen, NL/Ithaca NY, USA, 352 pp.
- Trenberth, K.E., Hurrell, J.W., 1994. Decadal atmosphere-ocean variations in the Pacific. *Climate Dyn.* 9, 303–319.
- Wilson, M.T., Brown, A.L., Mier, K.L., 2005. Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): evidence of mesoscale variation in nursery quality? *US Fish Bull.* 103, 207–218.
- Witting, D.A., Able, K.W., Fahay, M.P., 1999. Larval fishes of a Middle Atlantic Bight estuary: assemblage structure and temporal stability. *Can. J. Fish. Aquat. Sci.* 56, 222–230.