Spatial and temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea shelf 1996–2007

M. S. BUSBY,* J. T. DUFFY-ANDERSON, K. L. MIER AND L. G. DE FOREST

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA, 98115-6349, USA

ABSTRACT

Larval and early juvenile fishes were sampled from the eastern Bering Sea (EBS) shelf from 2001 to 2005, and in 2007. Data from these collections were used to examine spatial and temporal patterns in species assemblage structure and abundance. The years 2001–2005 were unusual because the EBS water temperature was ‘warm’ compared with the long-term mean temperature. In contrast, 2007 was a ‘cold’ year. The abundance of the five most numerous taxa at 12 stations common to all years sampled (1996–2005, 2007) were significantly different among years. Larval and early juvenile stage *Theragra chalcogramma* (walleye pollock), a commercially important gadid, were by far the most abundant fish in all years. Bottom depth alone best explained assemblage structure in most years, but in others, bottom depth and water column temperature combined and percent sea-ice coverage were most important. Abundance of *T. chalcogramma* larvae increases with water column temperature until 5°C and then becomes level. Higher abundances of *Gadus macrocephalus* (Pacific cod) larvae occur in years with the greatest percent sea-ice cover as indicated by GAM analysis. Larvae of *Lepidopsetta polyxystra* (northern rock sole) increase in abundance with increasing maximum wind speed, but decrease at a later date during the last winter storm. The data are consistent with the hypothesis that oceanographic conditions, specifically water temperature and sea-ice coverage, affect the spatial and temporal pattern of larval abundances. In general, ichthyoplankton species assemblages can be important early indicators of environmental change in the Bering Sea and potentially other subarctic seas as well.

Key words: assemblages, Bering Sea, environmental variables, fish larvae, juveniles, spatial distribution

INTRODUCTION

The distribution of planktonic organisms in marine environments has been central to numerous studies throughout oceanic and coastal areas of the world or ‘large marine ecosystems’ (Sherman, 2000; Sherman *et al.*, 2007). Planktonic fish eggs and larvae, commonly referred to as ichthyoplankton, have been collected in regional surveys for many purposes including studies of ecosystem functions, stock assessment, and investigations of recruitment processes (Kendall and Duker, 1998; Kendall, 2000).

It is well known that the complexity of species assemblages and biodiversity is related to ecosystem health and functioning (Magurran, 2004), and that links between ecosystem variations and shifts in species richness have been shown in marine systems across the globe (Meyers and Worm, 2003; Micheli and Halpern, 2005; Wilson *et al.*, 2006; Cheung *et al.*, 2009). Many of these studies have focused on the interactions among adult members of the community, but the study of species associations among earlier life stages, such as larvae and juveniles, may also be important harbingers of phase shifts in ecosystem dynamics. In particular, ichthyoplankton are greatly influenced by dynamic physical processes, including oceanographic features such as bathymetry (Doyle *et al.*, 2002), eddies (Atwood *et al.*, 2010), currents and fronts (Norcross *et al.*, 2010; Siddon *et al.*, 2011), as well as meteorological features such as precipitation and freshwater discharge (Boeing and Duffy-Anderson, 2008), wind variation (Rodriguez *et al.*, 2011), and temperature (Genner *et al.*, 2010), which can lead to shifts in community structure, changes in biotic control, and variable species interactions. The sensitivity of early life stages to these and other forcing phenomena potentially make marine fish larvae important sentinels of regional climate variation and ecosystem change.

The Bering Sea is one of the most productive ecosystems in the world and accounts for approximately 5% of the world fish and shellfish catch and over 40%

*Correspondence. e-mail: morgan.busby@noaa.gov

Received 13 February 2013

Revised version accepted 13 January 2014

of all US finfish and shellfish landings (Stabeno *et al.*, 2012a). The eastern Bering Sea (EBS) has been shown to respond rapidly to climate (Napp and Hunt, 2001). Increasingly, and in light of recent climate variability, there is concern over the present status of the Bering Sea and the future of its ecosystem health (Grebmeier *et al.*, 2006). Studies that examine processes that might be driving ecosystem regime shifts (Niebauer and Day, 1989; Stabeno *et al.*, 2001, 2007), what the environmental effects are on the biota (Brodeur *et al.*, 1999; Hunt *et al.*, 2002; Kotwicki *et al.*, 2005), what the consequences are for biodiversity and species interactions, and how long effects may be expected to last (Benson and Trites, 2002; Duffy-Anderson *et al.*, 2006) are critical to the evaluation of potential impacts of climate change.

The extent and concentration of sea-ice coverage and timing of retreat directly influence the dynamics of primary and secondary production, which in turn have substantial effects on energy flow and ecosystem function in the EBS (Hunt and Stabeno, 2002). Winter sea-ice concentration in the EBS has declined since the mid-1970s, but some marked fluctuations in yearly mean water column and sea surface temperatures (SST), manifested as alternating periods of variable duration, have been noted and classified as either 'warm' or 'cold' years (Stabeno *et al.*, 2012a). Depth-averaged spring and summer temperatures are closely related to the previous winter's temperatures and ice cover. Variations in depth-averaged temperatures and timing of sea-ice retreat directly influence the timing and location of the spring phytoplankton bloom and the availability, abundance, and species composition of zooplankton, particularly copepods, which are the primary components in the diets of fish larvae and juveniles (Hunt *et al.*, 2011). During the previous decade, an unusual event occurred, characterized by five consecutive 'warm' years (2001–2005) followed by a 'normal' or transition year (2006) and four consecutive 'cold' years (2007–2010) (Stabeno *et al.*, 2012a). This provides a unique opportunity to study the biological and physical processes of the EBS ecosystem in two different climatic 'regimes.' The temperatures recorded during this recent warm period are thought to be characteristic of those predicted by 2050 under a climate warming scenario (Stabeno *et al.*, 2012b).

The influence of ice retreat timing and related consequences to ecosystem dynamics and function persist into the summer. Species composition, relative abundance, and length of larval and juvenile fishes in Bering Sea ichthyoplankton assemblages during summer are of particular interest as this is a period of ontogenetic transition for many species. For example, larvae

of winter and spring spawning flatfish species are undergoing transformation and eye migration is nearly complete. Age-0 *Theragra chalcogramma* (walleye pollock), a commercially important gadid fish, form scales and begin to resemble adults in morphology and behavior (Brown *et al.*, 2001), which includes forming schools and feeding at night (Merati and Brodeur, 1996; Sogard and Olla, 1996; Ryer and Olla, 1997, 1998). It is during this critical stage of development that many demersal fish species make the transition from pelagic to benthic habitats and are particularly vulnerable to mortality from predation and other causes (Toole *et al.*, 1993). Survival of age-0 *T. chalcogramma* is linked to biochemical condition prior to onset of their first winter (Siddon *et al.*, 2013; Heintz *et al.*, 2013). Changes in the timing of transitions between early life history stages due to substantial shifts in prevailing environmental conditions may have significant consequences for survival and recruitment of certain species and the structure of species assemblages.

Our objectives in this study were to (i) describe midwater assemblages of larval and juvenile fishes in the EBS in summer for 2001–2005, and 2007; (ii) relate observations of fish abundances and lengths to oceanographic conditions; (iii) examine the interannual stability of species assemblages using data from the present study (2001–2005, 2007) and data from a prior investigation (1996–2000; Duffy-Anderson *et al.*, 2006), which together span a series of warm and cold regimes over the EBS shelf, and (iv) compare results of our analyses of the 2001–2005 and 2007 ichthyoplankton data with those from 1996–2000. To accomplish these objectives we adopted a two-step approach. First, we undertook a within-year examination of species assemblages during the most recent years of collection (2001–2005, 2007) and made quantitative and qualitative comparisons to assemblage structure from 1996–2000. Next, we conducted a time-series analysis over the entire data set (1996–2005, 2007) to examine interannual variations in species lengths and abundances.

MATERIALS AND METHODS

Field collections

Ichthyoplankton samples used in this study were collected from the EBS shelf during a series of cooperative research cruises between scientists at the Alaska Fisheries Science Center (AFSC), Seattle, WA, USA, and the Graduate School of Fisheries, Hokkaido University, Japan, on the T/S *Oshoro Maru* during the years 2001–2005 and in 2007. In July (and sometimes

August) of each year (Table 1), a grid of stations on the EBS shelf was occupied, extending mostly eastward and south from the Pribilof Islands (Fig. 1). Conductivity-temperature-depth (CTD) casts were made immediately prior to fish sampling at nearly every station in each year. A modified beam trawl (MBT), with a 5-m² mouth opening fitted with a 3 × 2 mm oval mesh net and a 1-mm mesh cod end, was towed obliquely from 200 m (or 10 m off bottom if shallower) to the surface. Net depth was measured using an acoustic netsonde. The MBT was designed to collect late larval and early juvenile stage fishes in the midwater and is similar to the Methot trawl (Methot, 1986). The MBT differs from the Methot trawl in not having a depressor and weight is contained within the tubular frame. A flowmeter was fitted into the mouth of the net frame to determine volume filtered. Samples were preserved in 5% formaldehyde-seawater solution buffered with sodium borate. Because of the large mesh size of the MBT, preflexion and early flexion stage larvae of all species were likely not quantitatively sampled. Supplemental surface and bottom temperature data were obtained from AFSC annual bottom trawl surveys of

the EBS shelf in summer (June–August). Only temperature data collected from within the same geographic extent as the present study were used. Field collection methods generally follow those of Duffy-Anderson *et al.* (2006).

Sample processing

Preserved samples were sorted and fishes identified to the lowest taxonomic level possible at the Plankton Sorting and Identification Center in Szczecin, Poland. Taxonomic identifications were verified at the AFSC. Some fish were categorized as taxonomic groups (e.g., *Atheresthes* spp., *Sebastes* spp.) due to limitations associated with identifying larval stages to the species level. Fish were measured for standard length (SL) to the nearest 1.0 mm. The separation point between the larval and juvenile stages for *Theragra chalcogramma* and *Gadus macrocephalus* is 25.0 mm SL based on the size at the transformation of *T. chalcogramma* determined by Brown *et al.* (2001). Catch in each tow was converted to catch per 10 m² of sea surface area.

Ichthyoplankton data

Two data sets were used. The first from field sampling conducted in 2001–2005 and in 2007 was analyzed to describe species associations and to relate patterns to predominant oceanographic conditions. The second data set combined previously published data from 1996–2000 (Duffy-Anderson *et al.*, 2006) with the 2001–2005 and 2007 data to derive a time series (1996–2005, 2007) that could be used to examine interannual variability in assemblage structure, species abundance and length, and environmental associations.

Table 1. Cruise information for data used in this study.

Year	Dates	No. of stations
2001	14 July–29 July	23
2002	28 July–11 August	27
2003	19 July–26 July	22
2004	28 July–4 August	25
2005	15 July–21 July	26
2007	24 July–3 August	20

Figure 1. Map of the eastern Bering Sea with grid stations for surveys 1996–2005, 2007 denoted by dots. Boxed area encloses ‘core’ stations used to examine interannual variations in fish abundance. Star indicates a station within the ‘core’ station box that was not sampled every year.

Environmental data

Bottom depth, temperature, and salinity were recorded at each sampling station using a CTD data recorder. Sea ice data were collected using the special sensor microwave interferometer (SSM/I) and obtained from the National Snow and Ice Data Center (NSIDC, <http://nsidc.org/>). Data were extracted into nominally diagonal 25 × 25 km regions and reported as percent ice coverage for each. Definitions of 'warm' and 'cold' years are based on depth averaged temperature criteria reported by Stabenho *et al.* (2012a).

The wind velocity data were derived using algorithms from the NCEP/NCAR Reanalysis data set (Kalnay *et al.*, 1996). This data set was produced using a numerical weather prediction model with the assimilation of available observations. Ladd and Bond (2002) have shown that it provides an accurate characterization of the winds in the Bering Sea. The present project incorporates daily averaged surface wind speeds for the years 1996–2007 at the gridpoint locations 56.2°N, 165.0°W and 56.2°N, 168.8°W. The data were used to determine the timing (date) of the first storm event after ice retreat (last winter storm) similar to that shown by Hunt *et al.* (2002). Criteria for defining a 'storm' includes a minimum 3-day period of winds exceeding 5 ms⁻¹ with at least one day being >10 ms⁻¹. The date assigned to each storm was the day of the year (DOY) at the midpoint of the event. The maximum wind velocity reported from each storm event was used as a variable to represent the force of mixing in the upper water column.

Spatial analyses (2001–2005, 2007)

Methods used to evaluate species composition for 1996–2000 data (Duffy-Anderson *et al.*, 2006) were applied to the 2001–2005 and 2007 data. Only species occurring in at least 4% of the samples for a particular year were included. Removal of rare species was deemed appropriate because these were not likely to contribute significantly to the broader spatial and temporal patterns. Separate hierarchical clustering analyses for species and stations (using abundance as catch per 10 m²) were performed for each year using the Bray–Curtis dissimilarity coefficient as the distance measure. A hierarchical agglomerative cluster analysis was used, specifically the flexible beta clustering method with beta = -0.25. A fourth-root transformation was applied to the abundance data before calculating the Bray–Curtis dissimilarity coefficient for clustering stations (samples) to more equally weight the contribution of rare and abundant species.

Interannual analyses (1996–2005, 2007)

Differences in species composition across all years (1996–2005, 2007) were examined using a two-way analysis of similarity (ANOSIM), using year and station as factors. As with the cluster analysis, the matrix of Bray–Curtis dissimilarity coefficients calculated on fourth-root transformed catch (10 m⁻²) was used as input. ANOSIM is a nonparametric, multivariate analysis that uses permutation techniques to test for differences in species composition among years, analogous to a univariate analysis of variance (ANOVA). When the overall test was found to be significant, permutational pairwise multiple comparison tests were conducted. Wherever there were significant differences ($P \leq 0.05$), a similarity percentages (SIMPER) analysis (Clarke and Warwick, 2001) was used to calculate each species contribution to the Bray–Curtis dissimilarity, therefore defining the discriminating species that best explain each significant difference.

Variations in abundances and lengths among all years were investigated for the five most abundant taxa. Since there were slight variations in the geographic area sampled in each year a subset of 12 stations spanning the middle and outer shelf were identified as having been sampled in all study years, and variations in abundance and length among the years were evaluated from this 'core' group of 12 stations (Fig. 1). These analyses were conducted for each of the five most common taxa within this core group of stations; *T. chalcogramma*, *Hippoglossoides elassodon*, *G. macrocephalus*, *Lepidopsetta polyxystra*, and *Atheresthes* spp. A mixed model analysis of length data, weighted by the haul catch per unit effort (CPUE) was used to test for length differences among years, and ANOVAs were used to test for differences in abundance, using station location as a block. These were followed by Tukey multiple comparison tests to see which years were significantly different.

Environmental analyses (1996–2005, 2007)

A quantitative biotic-environmental (BIO-ENV) analysis was applied (Clarke and Warwick, 2001) to each year (1996–2005, 2007) to determine which physical variables were most related to the species composition based on abundance. The physical variables were bottom depth, integrated water column temperature, bottom temperature, salinity, and percentage of area covered by ice in winter. To investigate the relationships of environmental variables with interannual differences in abundance of the five most abundant taxa, a generalized additive model (GAM) was employed based on the 'core' stations (Fig. 1).

The variables used were water column temperature, salinity, percent sea-ice coverage, date (DOY) of last winter storm, and maximum wind speed during last winter storm. The GAM was used instead of multiple linear regression to allow for possible nonlinear relationships as well as to relax the normality assumption. The best fit GAM was determined by checking all possible combinations of the environmental variables and selecting the one with the lowest GCV (general cross-validation) as well as the one containing variables with P -values < 0.05 .

RESULTS

Species composition (2001–2005, 2007)

A total of 18 290 larval and juvenile fishes comprising at least 43 taxa representing 17 families was collected during the study period. These fish were predominantly in the postflexion and transformation stage of development. Taxonomic richness was lowest in 2002 and 2003 with only 17 and 18 taxa collected, respectively, compared with 21–28 in other years (Table 2). The family Pleuronectidae (flatfishes) was represented by the greatest number of taxa (10), followed by Cottidae and Agonidae (7). Taxonomic richness within certain families was variable throughout the study period. Particularly noteworthy is the family Cottidae where only one of the seven taxa reported for the 6 yr studied were caught in 2002 (*Hemilepidotus hemilepidotus*) and in 2004 (*Icelus* spp.). Richness of pleuronectids was lowest in 2003, when only three taxa (*Atheresthes* spp., *H. elassodon*, and *L. polyxystra*) were collected.

The gadids *T. chalcogramma* and *G. macrocephalus* were caught every year, as were *Liparis* spp., *Lumpenus maculatus*, *Ammodytes hexapterus*, *Atheresthes* spp., *H. elassodon*, and *L. polyxystra*. Seven taxa were collected for 5 of the 6 yr; *Sebastes* spp., *H. hemilepidotus*, *Bathyagonus alascanus*, *Podothecus veternus*, *Zaprora silenus*, *L. bilineata*, and *Reinhardtius hippoglossoides*. Eleven taxa were only collected in a single year: *Stenobranchius leucopsaurus* (2005), *Rhamphocottus richardsoni* (2004), *Psychrolutes paradoxus* (2003), *Leptagonus leptorhynchus* and *Ulcina olrikii* (2007), *Aptocyclus ventricosus* (2004), *Ronquilus jordani* (2007), *Cryptacanthodes aleutensis* (2001), *Embassichthys bathybius* (2002), *Glyptocephalus zachirus* (2001), and *Limanda proboscidea* (2007). Gadids dominated the catch numerically in all years, and *T. chalcogramma* was by far the most common species, making up 91.5% of the total number of fish caught (Table 3). *Hippoglossoides elassodon*, *G. macrocephalus*, *L. polyxystra*, and *Atheresthes* spp. made up the remainder of the five most common taxa in the order listed,

but when combined only accounted for 5.6% of the total catch.

Spatial patterns (2001–2005, 2007)

Results from the cluster and NMDS analyses of 2001–2005 and 2007 indicated that species and station groups from 2001 and 2007 were unique (Table 4, Figs 2–5). ANOSIM results supported this; 2001 and 2007 were different from each other ($P = 0.001$, $R = 0.67$) and from all other years ($P \leq 0.02$, $R \geq 0.19$). The taxa contributing most to these differences as calculated by the SIMPER analysis were *T. chalcogramma*, *H. elassodon*, *G. macrocephalus*, *L. polyxystra*, *Atheresthes* spp., *A. hexapterus*, *L. bilineata*, *B. alascanus*, and *Liparis* spp.

With the exception of 2007, species and station groups from cluster analyses of the 2001–2005 and 2007 abundance data in the present study appear somewhat less related to bathymetry than was seen in the previous study of 1996–2000 (Figs 2–5). Results of the cluster analyses are presented graphically only for 2001, 2005, and 2007 to show 1 yr with clearly defined cluster groups (2007) and 1 yr with less clearly defined cluster groups (2005), a ‘cold’ year (2007), and two ‘warm’ years with very different assemblage structure (2001 and 2005).

In 2001, the first of five consecutive ‘warm’ years, the assemblage structure consisted of five species groups and three station groups (Fig. 2). A relatively cohesive outer domain (100–200 m) (station group 1; Fig. 3) assemblage consisted of moderate abundances of *T. chalcogramma* (species group D) with lower abundances of *C. aleutensis*, *G. macrocephalus*, *H. elassodon*, and *Z. silenus* (species group E). The middle domain (50–100 m) assemblage (station group 3) was dominated by *T. chalcogramma* with *L. polyxystra*. For 2001–2004 station, group 2 straddled the middle and outer domain and although *T. chalcogramma* was also in high abundance as in station group 3, there were no unique species (not present in the other years) present or distinct patterns (Table 4, Fig. 3).

In 2005, the last of five consecutive ‘warm’ years, the highest number of taxa ($n = 28$, Table 2) were present. Cluster analysis revealed eight species groups, but only two were well defined by having one of the two dominant taxa – species groups C and E (Table 4, Fig. 4). Species group C consisted of *G. macrocephalus* in moderate abundance with *Z. silenus*, *Icelinus borealis*, and *Liparis* spp. also present. This group was mostly associated with station group 3 in the outer domain and near the Pribilof Islands (Fig. 3). Station group 4 (Figs 3 and 4) over the middle domain had the highest abundances of *T. chalcogramma*. The other

Table 2. Fish taxa present in at least 4% of the samples for each year. 'X' indicates whether that taxon was collected in a particular year. The total number of taxa collected in each year is given at the bottom (total includes rare taxa that were removed before the analysis).

Species name	Common name	2001	2002	2003	2004	2005	2007
Bathylagidae							
<i>Leuroglossus schmidti</i>	Northern Smoothtongue	X	X		X	X	
<i>Bathylagus pacificus</i>	Pacific Blacksmelt			X	X		
Myctophidae							
<i>Stenobrachius leucopsaurus</i>	Northern Lampfish					X	
Gadidae							
<i>Gadus macrocephalus</i>	Pacific Cod	X	X	X	X	X	X
<i>Theragra chalcogramma</i>	Walleye Pollock	X	X	X	X	X	X
Macrouridae							
<i>Coryphaenoides</i> spp.	Unidentified grenadiers				X	X	
Scorpaenidae							
<i>Sebastes</i> spp.	Unidentified rockfishes	X	X	X	X	X	
Rhamphocottidae							
<i>Rhamphocottus richardsoni</i>	Grunt Sculpin				X		
Cottidae							
<i>Artediellus pacificus</i>	Hookhorn Sculpin			X			
<i>Hemilepidotus hemilepidotus</i>	Red Irish Lord	X	X	X		X	X
<i>Hemilepidotus jordani</i>	Yellow Irish Lord	X					
<i>Icelinus borealis</i>	Northern Sculpin	X				X	
<i>Icelus</i> spp.	Unidentified sculpin				X	X	X
<i>Myoxocephalus</i> spp.	Unidentified sculpin	X		X		X	X
<i>Ruscarius meanyi</i>	Puget Sound Sculpin	X				X	
Psychrolutidae							
<i>Dasycottus setiger</i>	Spinyhead Sculpin				X	X	X
<i>Malacocottus zonurus</i>	Darkfin Sculpin			X		X	
<i>Psychrolutes paradoxus</i>	Tadpole Sculpin				X		
Agonidae ¹							
<i>Aspidophoroides monoptygius</i>	Alligatorfish	X			X	X	X
<i>Bathyagonus alascanus</i>	Gray Starsnout	X	X	X	X	X	
<i>Bathyagonus infraspinnatus</i>	Spinycheek Starsnout		X	X		X	
<i>Bathyagonus nigripinnis</i>	Blackfin Poacher	X				X	
<i>Leptagonus leptorhynchus</i>	Longnose Poacher						X
<i>Podothecus veterinus</i>	Veteran Poacher	X		X	X	X	X
Liparidae							
<i>Liparis</i> spp.	Unidentified Snailfishes	X	X	X	X	X	X
Cyclopteridae							
<i>Aptocyclus ventricosus</i>	Smooth Lump sucker				X		
Bathymasteridae							
<i>Ronquilus jordani</i>	Northern Ronquil						X
Stichaeidae							
<i>Lumpenus maculatus</i>	Daubed Shanny	X	X	X	X	X	X
Cryptacanthodidae							
<i>Cryptacanthodes aleutensis</i>	Dwarf Wrymouth	X					
Zaproridae							
<i>Zaprora silenus</i>	Prowfish	X	X	X	X	X	
Ammodytidae							
<i>Ammodytes hexapterus</i>	Pacific Sand Lance	X	X	X	X	X	X
Pleuronectidae ¹							
<i>Atheresthes</i> spp.	Arrowtooth/Kamchatka Flounder	X	X	X	X	X	X
<i>Embassichthys bathybicus</i>	Deepsea Sole		X				
<i>Hippoglossoides elassodon</i>	Flathead Sole	X	X	X	X	X	X

Table 2. (Continued)

Species name	Common name	2001	2002	2003	2004	2005	2007
<i>Glyptocephalus zachirus</i>	Rex Sole	X					
<i>Hippoglossus stenolepis</i>	Pacific Halibut					X	
<i>Lepidopsetta bilineata</i>	Southern Rock Sole	X	X		X	X	X
<i>Lepidopsetta polyxystra</i>	Northern Rock Sole	X	X	X	X	X	X
<i>Pleuronectes quadrituberculatus</i>	Alaska Plaice	X					X
<i>Reinhardtius hippoglossoides</i>	Greenland Halibut	X	X		X	X	X
Total		25	17	18	23	28	21 ¹

¹Two additional species, *Ulcina olrikii* (Agonidae) and *Limanda proboscidea* (Pleuronectidae), were collected in 2007 but were present in <4% of samples and not included in analysis.

Table 3. Number of individuals caught and percent of total for the five most abundant and all other taxa combined at all stations 2001–2005, and 2007.

Taxon	n	%
<i>Theragra chalcogramma</i>	16,735	91.5
<i>Hippoglossoides elassodon</i>	644	3.5
<i>Gadus macrocephalus</i>	225	1.2
<i>Lepidopsetta polyxystra</i>	85	0.5
<i>Atheresthes</i> spp.	76	0.4
All other taxa	525	2.9
Total	18,290	100.0

taxa present were in low abundance and species in groups A, B, D, and F were absent. Station group 3, mostly in the outer domain and Pribilof Island region, had greater richness and all taxa in species group E were present at all stations with the exceptions of *H. elassodon* and *T. chalcogramma*, which were each absent at one station. Station group 1 and an outlier station located off the edge of the continental shelf were represented by the deepwater taxa *Coryphaenoides* spp., *L. schmidtii*, *S. leucopsaurus*, and *Sebastes* spp., and *G. macrocephalus*, *M. zonurus*, and *B. nigripinnis*, which are not typically considered deep water species, were also present.

In 2007 there were four species and three station groups (Table 4, Fig. 5) with the clearest distinction of species and station groups reflecting both bathymetry and temperature patterns (Figs 3 and 5). It was also the first truly 'cold' year since 1999 and had the lowest abundance of *T. chalcogramma* over the entire 1996–2007 time series (Fig. 6). There were no stations off the continental shelf break as in previous years and thus no deepwater species were collected. Station group 1 located in the outer domain comprised only taxa from group D that included *Atheresthes* spp., *Dasycottus setiger*, *G. macrocephalus*, and *H. hemilipidotus*, in addition to *T. chalcogramma*, which was caught at every station. Station group 2 in the middle domain

comprised all seven taxa in species group C, of which all but *L. bilineata* were unique to station group 2. Species group B, composed of *H. elassodon* and *R. hippoglossoides*, was also unique to station group 2. The three taxa in species group A and *A. hexapterus* were only present at the two stations in station group 3 straddling the boundary of the inner and middle domains. Three species, *U. olrikii*, *R. jordani*, and *L. proboscidea*, were only collected in 2007 (Table 2).

In general, with the exception of 2003 and 2007, there was a deepwater assemblage present, usually consisting of the bathylagids *B. pacificus* or *L. schmidtii*, macrourids *Coryphaenoides* spp., scorpaenids *Sebastes* spp., or pleuronectids *Atheresthes* spp. Another noteworthy result from the cluster analyses was the very different taxa each year in the species groups that included *T. chalcogramma* (Table 4). In 2001, for example, *L. polyxystra* was the second most frequently occurring and abundant species (and thus most closely associated with *T. chalcogramma*: Fig. 2), whereas *H. elassodon* took this position in 2002 and 2005 (closely followed by *Atheresthes* spp.). In 2003, *T. chalcogramma* dominated species group B, occurring at all but two stations; the other species in this group, *A. hexapterus* and *L. maculatus*, occurred at only two and one stations respectively. In 2004, *T. chalcogramma* was closely affiliated with *G. macrocephalus*, which although in low abundance, co-occurred at several stations. *Dasycottus setiger* was the species most closely associated with *T. chalcogramma* in 2007.

Interannual comparisons (1996–2005, 2007)

The ANOVA and multiple comparison test results showing differences in abundance among all 11 yr of sampling at the 'core' stations indicated that *T. chalcogramma* was most abundant in 2001 but with no significantly higher abundance than in 2000 and 2004, and lowest in abundance in 1998, 2002 and 2007 (Table 5, Fig. 6). *Hippoglossoides elassodon* was present in high abundance in 1998, 2001, 2002, 2003, 2004, and 2005

Table 4. Species groupings as identified by cluster analyses. Proximity of letter groups signifies distance between species clusters in dendrograms for each year (refer to Fig. 2, 2001 for comparison). Order of taxa present within letter groups in each year indicates proximity of adjacent taxa within a cluster. Dash indicates cluster group not present. Refer to Table 2 for generic names.

Year	A	B	C	D	E
2001	<i>B. alascanus</i> <i>B. nigripinnis</i> <i>G. zachirus</i> <i>Sebastes</i> spp. <i>L. schmidt</i>	<i>A. hexapterus</i> <i>H. jordani</i>	<i>A. monopterygius</i> <i>L. maculatus</i> <i>Liparis</i> spp. <i>Atheresthes</i> spp. <i>I. borealis</i>	<i>L. bilineata</i> <i>Myoxocephalus</i> spp. <i>L. polyxystra</i> <i>T. chalcogramma</i> <i>P. veternus</i> <i>R. hippoglossoides</i>	<i>C. aleutensis</i> <i>G. macrocephalus</i> <i>H. elassodon</i> <i>Z. silenus</i> <i>R. meany</i> <i>H. hemilepidotus</i>
2002	<i>A. hexapterus</i> <i>Liparis</i> spp. <i>R. hippoglossoides</i>	<i>L. schmidt</i> <i>Sebastes</i> spp.	<i>G. macrocephalus</i> <i>H. elassodon</i> <i>T. chalcogramma</i> <i>L. polyxystra</i> <i>L. maculatus</i> <i>Z. silenus</i>	<i>Atheresthes</i> spp. <i>B. alascanus</i> <i>E. bathybius</i>	<i>B. infraspinus</i> <i>H. hemilepidotus</i> <i>L. bilineata</i>
2003	<i>A. pacificus</i> <i>P. veternus</i>	<i>A. hexapterus</i> <i>L. maculatus</i> <i>T. chalcogramma</i>	<i>B. alascanus</i> <i>B. infraspinus</i> <i>Sebastes</i> spp. <i>G. macrocephalus</i> <i>H. elassodon</i> <i>Atheresthes</i> spp. <i>B. alascanus</i> <i>H. elassodon</i> <i>Sebastes</i> spp. <i>L. maculatus</i>	<i>Atheresthes</i> spp. <i>Z. silenus</i> <i>B. pacificus</i> <i>M. zonurus</i>	<i>H. hemilepidotus</i> <i>L. polyxystra</i> <i>Liparis</i> spp. <i>Myoxocephalus</i> spp.
2004	<i>A. ventricosus</i> <i>R. richardsoni</i>	<i>B. pacificus</i> <i>Coryphaenoides</i> spp. <i>L. schmidt</i>	<i>Atheresthes</i> spp. <i>B. alascanus</i> <i>H. elassodon</i> <i>Sebastes</i> spp. <i>L. maculatus</i>	<i>A. hexapterus</i> <i>L. polyxystra</i> <i>R. hippoglossoides</i> <i>A. monopterygius</i> <i>Liparis</i> spp. <i>P. veternus</i> <i>G. macrocephalus</i> <i>T. chalcogramma</i>	<i>D. setiger</i> <i>Icelus</i> spp. <i>L. bilineata</i> <i>Z. silenus</i> <i>P. paradoxus</i>
2005 ¹	<i>B. nigripinnis</i> <i>M. zonurus</i> <i>S. leucopsaurus</i>	<i>Coryphaenoides</i> spp. <i>L. schmidt</i>	<i>G. macrocephalus</i> <i>Z. silenus</i> <i>I. borealis</i> <i>Liparis</i> spp.	<i>D. setiger</i> <i>Icelus</i> spp.	<i>Atheresthes</i> spp. <i>B. alascanus</i> <i>H. elassodon</i> <i>T. chalcogramma</i>
2007	<i>Icelus</i> spp. <i>R. jordani</i> <i>P. quadrituberculatus</i>	<i>H. elassodon</i> <i>R. hippoglossoides</i>	<i>A. monopterygius</i> <i>L. Leptorhynchus</i> <i>Podothecus veternus</i> <i>L. bilineata</i> <i>L. polyxystra</i> <i>Liparis</i> spp. <i>Myoxocephalus</i> spp.	<i>Atheresthes</i> spp. <i>L. maculatus</i> <i>D. setiger</i> <i>T. chalcogramma</i> <i>G. macrocephalus</i> <i>H. hemilepidotus</i>	

¹2005 has three additional species cluster groups F: *Bathygonus infraspinus*, *Sebastes* spp., *L. maculatus*, *Ruscarius meany* G: *H. hemilepidotus*, *L. bilineata*, *R. hippoglossoides*, *P. veternus* H: *A. hexapterus*, *A. monopterygius*, *L. polyxystra*.

and in low abundance in 1996, 1997, 1999, 2004, and 2007. *Gadus macrocephalus* abundance was highest in 1996, 2000, 2001, 2003, 2004 and 2005. *Lepidopsetta polyxystra* was most abundant in 2001 and 2007. *Atheresthes* spp. abundance was significantly lower in 1998 and 2002 and higher in 2001 than in several other years in the series; however, there were no other significant differences in abundance among years.

The ANOVA and multiple comparisons results for differences in lengths ('core' stations only) indicated that *T. chalcogramma* in 1996 and 2005 was significantly longer than in all other years (1996:

$P < 0.003$, 2005: $P < 0.001$; Fig. 7). Although the length of *T. chalcogramma* in 2004 was significantly less than in 1996 and 2005, the length was significantly larger than all other years except 1998 ($P < 0.003$). Significant differences in length were also detected among years for *G. macrocephalus*, *Atheresthes* spp., *H. elassodon*, and *L. polyxystra*, but lacked any consistency.

Environmental patterns (1996–2005, 2007)

The BIO-ENV procedure conducted within each year (1996–2005, 2007) determined which environmental

Figure 2. Results of cluster analyses showing species/station clusters with relative abundances of fishes collected in 2001. White lines indicate groups, dashed lines indicate subgroups. Individual species clusters identified by letters, station clusters identified by numbers.

factors were most consistent with the ichthyoplankton assemblage structure. Bottom depth was usually, but not always, the environmental factor most correlated with taxonomic composition (Table 6). In 1996, 1997, 2001–2003, and 2005, bottom depth alone was most correlated with assemblage structure, but in 1998, 1999, and 2007 bottom depth and water column temperature were equally correlated. In 2004, bottom depth and salinity were the environmental variables most highly correlated with assemblage structure, and in 2000, percent sea-ice coverage was correlated with ichthyoplankton assemblage structure. Date (DOY)

and strength of last winter storm were not correlated with assemblage structure.

A correlation analysis of environmental variables indicated that average water column temperature and bottom temperature were correlated with one another; therefore, bottom temperature was not included in the GAM analyses. GAM analyses conducted to evaluate potential influences of environmental factors on abundances of the five most common taxa at the 12 'core' stations over all years sampled, indicated that abundance of *T. chalcogramma* larvae increased with increased mean water column temperature until about

Figure 3. Map showing geographic positions of station cluster groups identified by non-zero numbers revealed by cluster analysis showing temperature interpolations 2001–2005 and 2007. Outlier station groups are indicated by zeros.

5°C, at which point it leveled off ($P = 0.003$; Fig. 8a). Percent sea-ice cover was significant for *G. macrocephalus* ($P = 0.02$), with the abundance of larvae increasing with increased percent sea-ice cover (Fig. 8b). Maximum wind speed had a significant positive linear effect for *L. polyxystra* ($P = 0.005$) when combined with the date (DOY) of the last winter storm (abundance of larvae increasing with wind speed, Fig. 9a),

whereas abundance decreased with later date of the last winter storm (Fig. 9b).

DISCUSSION

We hypothesized that ichthyoplankton species associations would be sensitive to environmental perturbations, and anticipated that we would observe

Figure 4. Results of cluster analyses showing species/station clusters with relative abundances of fishes collected in 2005. White lines indicate groups, dashed lines indicate subgroups. Individual species clusters identified by letters, station clusters identified by numbers.

differences in assemblage structure related to anomalously warm or cold thermal conditions over the shelf. Indeed, we observed changes in ichthyoplankton assemblage structure in cold years (1997, 1999, 2007) relative to warm (1998, 2001–2005) and ‘average’ years (1996, 2000) (Duffy-Anderson *et al.*, 2006; present study). A contributing factor to these changes were shifts in species composition consistent with ingress of warm and cold water species in warm and cold years.

In comparing the 10 most abundant taxa from the 1996–2000 sampling (alternating warm and cold years) with 2001–2005 and 2007 (five consecutive

warm years and one cold year), we observed replacement of three taxa (Table 7). Two of these, *Sebastes* spp. and *R. hippoglossoides*, are deepwater or slope taxa, the latter being a pleuronectid with a circumpolar distribution that might be considered an indicator species affiliated with colder Arctic water masses (Mecklenberg *et al.*, 2011). The abundance of *R. hippoglossoides* larvae declined somewhat during the warm period, suggesting a shift in prevailing oceanographic conditions (Fig. 10a). More frequent occurrences during the warm years (2001–2005) of larval *L. bilineata*, a pleuronectid with a more southerly range, may be indicative

Figure 5. Results of cluster analyses showing species/station clusters with relative abundances of fishes collected in 2007. White lines indicate groups, dashed lines indicate subgroups. Individual species clusters identified by letters, station clusters identified by numbers.

of a northern range expansion under conditions of rising temperatures (Fig. 10b). It should also be noted, however, that occurrences of adult *L. bilineata* in AFSC groundfish surveys are limited to only five stations immediately north and east of Unimak Island (Fig. 1) and the individuals collected were relatively small and probably not of spawning age (D. Stevenson, AFSC pers. com.). However, it is possible that larvae originating from adult *L. bilineata* spawning in the Gulf of Alaska are transported northward through Unimak Pass and onto the southeast Bering Sea shelf, as the

prevailing currents are often very strong here with considerable seasonal and interannual variability (Stabeno *et al.*, 2002; Duffy-Anderson *et al.*, 2006). It is not surprising that our 10 most abundant taxa apparently respond differently in terms of larval/juvenile abundance (see Table 7) to environmental influences, as this is most likely related to the evolutionary history of each taxon.

Moreover, we observed that oceanographic conditions, notably temperature and sea-ice, have a significant effect on the larval abundances of two

Figure 6. Interannual variations in abundance $\pm$ standard error (SE) of the five most abundant taxa collected from the 'core' stations. Note differences in abundance scales between species (number 10 m²).

Table 5. Results from ANOVAs and multiple comparisons tests showing significant differences in interannual abundance of the five most commonly collected species/taxa overall within the 'core' stations. Years sharing the same letters indicate no significant difference ($P < 0.05$). 'A' indicates lowest means and 'F' indicates highest means within that species.

Species	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2007
<i>Theragra chalcogramma</i>	BCD	BCD	AB	CD	EF	F	ABC	CD	F	E	A
<i>Hippoglossoides elassodon</i>	ABC	AB	CD	AB	BC	D	BC	CD	ABC	D	A
<i>Gadus macrocephalus</i>	BCDE	AB	A	ABC	BCDE	BCD	ABC	DE	CDE	E	AB
<i>Lepidopsetta polyxystra</i>	AB	C	A	AB	AB	BC	A	A	A	AB	C
<i>Atheresthes</i> spp.	ABC	AB	A	BC	ABC	C	A	AB	BC	BC	AB

commercially important gadid species. Accordingly, we hypothesize that, given their sensitivity to environmental forcing, ichthyoplankton can be important early indicators of environmental change in the Bering Sea and potentially other subarctic seas as well. An interesting result derived from the previously published study (Duffy-Anderson *et al.*, 2006) was that assemblages in 1998 were significantly different from other years examined, and that a short-term fluctuation in oceanographic conditions, the unusually strong 1997–1998 El Niño, appeared to disrupt predominant species assemblage patterns over the continental shelf, although effects were transitory. Lower larval abundances were also observed during the El Niño, with a return to previous levels the following year. Indeed, unique patterns were observed that appeared to be related to thermal conditions.

Revisiting the 1996–2000 data examined in the initial study provided the opportunity to update some

Figure 7. Interannual variations in mean length ($\pm$ SE) of *Theragra chalcogramma* collected from the 'core group' of stations.

Figure 8. Results of GAM analyses showing relationships of abundances of (a) *Theragra chalcogramma* larvae and juveniles with water column temperature and (b) *Gadus macrocephalus* larvae and juveniles with percent sea-ice cover. Solid lines indicate fitted GAM model and dashed lines indicate ± 2 SE, and points indicate residuals of fit. Y-axis is in the scale of the transformed abundance, CPUE^{0.25}.

Table 6. Environmental factors most correlated with taxonomic composition for each year of the study as determined by BIO-ENV analysis. Date and strength of last winter storm was not correlated with assemblage structure in any year.

Year	Environmental factors				Correlation	
	Bottom depth	Percent ice cover	Salinity	Water column temperature	Spearman rank	P-value
1996	X				0.52	0.02*
1997	X				0.71	0.18
1998	X			X	0.46	0.14
1999	X			X	0.54	0.03*
2000		X			0.67	0.05
2001	X				0.64	0.01*
2002	X		X		0.46	0.01*
2003	X				0.64	0.01*
2004	X		X		0.65	0.01*
2005	X				0.59	0.01*
2007	X			X	0.57	0.01*

*Significant at 5%.

Figure 9. Results of GAM analyses showing relationships of abundances of (a) *Lepidopsetta polyxystra* larvae with maximum wind speed and (b) *L. polyxystra* larvae with date of last winter storm. Solid lines indicate fitted GAM model and dashed lines indicate ± 2 SE, and points indicate residuals of fit. Y-axis is in the scale of the transformed abundance, $\text{CPUE}^{0.25}$.

Table 7. The 10 most commonly collected taxa listed by abundance ranking for each study period. Shaded taxa were only present at that abundance level during that sampling period. Lists are based on average abundance (catch per 10 m^2) at the 12 common stations sampled in all 11 yr.

Rank	1996–2000	2001–2005, 2007
1	<i>Theragra chalcogramma</i>	<i>Theragra chalcogramma</i>
2	<i>Hippoglossoides elassodon</i>	<i>Hippoglossoides elassodon</i>
3	<i>Gadus macrocephalus</i>	<i>Gadus macrocephalus</i>
4	<i>Atheresthes</i> spp.	<i>Lepidopsetta polyxystra</i>
5	<i>Lepidopsetta polyxystra</i>	<i>Ammodytes hexapterus</i>
6	<i>Ammodytes hexapterus</i>	<i>Atheresthes</i> spp.
7	<i>Lumpenus maculatus</i>	<i>Liparis</i> spp.
8	<i>Reinhardtius hippoglossoides</i>	<i>Podothecus veternus</i>
9	<i>Sebastes</i> spp.	<i>Lepidopsetta bilineata</i>
10	<i>Zaprora silenus</i>	<i>Lumpenus maculatus</i>

data used in the interannual comparisons presented here. Some examples of this pertain to taxonomic identifications. Many larvae previously identified as *Icelus* spp. were later identified as *Icelinus borealis* (Cartwright, 2009). This reduced the number of occurrences of *Icelus* spp. below the 4% threshold required for inclusion in the analysis. *Psychrolutes* spp. was included in the 5% group in the initial study, but only occurs in 2.6% of the 1996–2000 hauls in our taxonomically updated data set. In addition, *Podothecus veternus* was one of the agonid species collected in the recent sampling, not *P. acipenserinus* as previously reported. Although these specimens previously identified in the initial study were not re-examined, it is likely that they are mostly, if not all, *P. veternus*.

Sampling in additional ‘cold’ years after 2007 would have allowed us to gain a more in-depth understanding of assemblage structure and variability under these conditions. It appears from our observations in 2007 that assemblage structure is more cohesive and boundaries between species and station clusters (groups) and oceanographic (thermal) fronts are more distinct than in ‘warm’ years. During the five consecutive ‘warm’ years (2001–2005), the early ice retreat likely led to low standing stocks of large zooplankton species, which may have limited overwinter survival of age-0 *T. chalcogramma* by depriving them of important energy-rich prey resources in summer and autumn (Hunt et al., 2011). This hypothesis is based on more recent observations determining that cold conditions lead to greater production and availability of large higher-energy-content zooplankton such as the euphausiids *Thysanoessa raschii* and *T. inermis* and the copepod *Calanus marshallae* (Coyle et al., 2011). Although 2007 was the first ‘cold’ year after a transition (2006, an average year, unsampled) it had the lowest age-0 *T. chalcogramma* abundance over the entire time series. In addition, overall zooplankton availability in 2007 was high, but survival of the age-0 *T. chalcogramma* was low compared with subsequent cold years 2008–2010 (Heintz et al., 2013). One possible explanation for this is that the standing stock of larger zooplankton species with high lipid content had not yet fully recovered after several years of poor production to replace the smaller lipid poor species that were very abundant. Overwinter survival is also important for recruitment of these zooplankton species in the following year.

Unfortunately, this study could not determine the actual source of interannual variations in larval

Figure 10. Interannual variations in abundance ($\pm$ SE) of (a) *Reinhardtius hippoglossoides* and (b) *Lepidopsetta bilineata* collected from the 'core' stations. Note differences in abundance scales between species (number per 10 m²).

abundances of the taxa studied. Differences could be due to variations in larval supply, mortality, advection, and/or availability of nursery habitat, among other things. Moreover, observed trends in larval and juvenile abundance do not necessarily correlate with trends in age-1 recruitment estimates (Ianelli *et al.*, 2010), suggesting that other factors also play a role in recruitment. Nevertheless, our results show that the early life history stages of marine fishes do respond to environmental perturbations relatively quickly, in terms of both changes in their abundances and/or changes in their species associations. The data we presented here encompass late larval, transformation, and early juvenile stages, but the influences of gradual environmental change or irregular 'disruptions' on spawning behavior (timing), hatching, and survival of earlier stages must also be considered as there are remnant or linked effects to later stages. Perhaps the most important conclusion from this study is that an 11-yr time series is not long enough to fully understand the underlying mechanisms that influence change in ichthyoplankton assemblages and adult fish populations. As such, ichthyoplankton metrics remain useful

harbingers of environmental variability and ecosystem change.

ACKNOWLEDGEMENTS

The authors thank the officers, crew, and students (cadets) of the T/S *Oshoro Maru*. Sigrid Salo and Nick Bond assisted by obtaining sea-ice coverage and wind data. Miriam Doyle, Ann Matarese, Jeff Napp, and Phyllis Stabeno provided guidance and helpful suggestions throughout the study and on earlier drafts of the manuscript. Deborah Blood provided editorial assistance. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

REFERENCES

- Atwood, E., Duffy-Anderson, J.T., Horne, J. and Ladd, C. (2010) Influence of mesoscale eddies on ichthyoplankton

- assemblages in the Gulf of Alaska. *Fish. Oceanogr.* **19**:493–507.
- Benson, A.J. and Trites, A.W. (2002) Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish. Fish.* **3**:95–113.
- Boeing, W. and Duffy-Anderson, J.T. (2008) Ichthyoplankton dynamics and biodiversity in the Gulf of Alaska: responses to environmental change. *Ecol. Indic.* **8**:292–302.
- Brodeur, R.D., Mills, C.E., Overland, J.E., Walters, G.E. and Schumacher, J.D. (1999) Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fish. Oceanogr.* **8**:296–306.
- Brown, A.L., Busby, M.S. and Mier, K.L. (2001) Transformation from the larval to juvenile stage in walleye pollock (*Theragra chalcogramma*) – the relationship between otolith and osteological development. *Mar. Biol.* **139**:845–851.
- Cartwright, R.L. (2009) Description of early life history stages of the northern sculpin (*Icelinus borealis* Gilbert) (Teleostei: Cottidae). *Fish. Bull.* **107**:175–185.
- Cheung, W.L., Lam, V.Y., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish. Fish.* **10**:235–251.
- Clarke, K.R. and Warwick, R.M. (2001) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edn. Plymouth: PRIMER-E.
- Coyle, K.O., Eisner, L.B., Mueter, F.J. et al. (2011) Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. *Fish. Oceanogr.* **20**:139–156.
- Doyle, M.J., Mier, K.L., Busby, M.S. and Brodeur, R.D. (2002) Regional variation in springtime ichthyoplankton assemblages in the northeast Pacific Ocean. *Prog. Oceanogr.* **53**:247–281.
- Duffy-Anderson, J.T., Busby, M.S., Mier, K.L., Deliyandis, C.M. and Staben, P.J. (2006) Spatial and temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea shelf 1996–2000. *Fish. Oceanogr.* **15**:80–94.
- Genner, M.J., Halliday, N.C., Simpson, S.D., Southward, A.J., Hawkins, S.J. and Sims, D.W. (2010) Temperature-driven phenological changes within a marine larval fish assemblage. *J. Plank. Res.* **32**:699–708.
- Grebmeier, J.M., Overland, J.E., Moore, S.E. et al. (2006) A major ecosystem shift in the northern Bering Sea. *Science* **311**:1461–1464.
- Heintz, R.A., Siddon, E.C., Farley, E.A. Jr and Napp, J.M. (2013) Climate related changes in the nutritional condition of young-of-the year walleye pollock (*Theragra chalcogramma*) from the eastern Bering Sea. *Deep-Sea Res. II* **94**:150–156.
- Hunt, G.L. and Staben, P.J. (2002) Climate change and the control of energy flow in the southeastern Bering Sea Ecosystem. *Prog. Oceanogr.* **55**:5–22.
- Hunt, G.L., Staben, P.J., Walters, G. et al. (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. II* **49**:5821–5853.
- Hunt, G.L., Coyle, K.O., Eisner, L.B. et al. (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. *ICES J. Mar. Sci.* **68**:1230–1243.
- Ianelli, J.N., Barbeaux, S., Honkalehto, T., Kotwicki, S., Aydin, K. and Williamson, N. (2010) Eastern Bering Sea Walleye Pollock. pp 53–156 In: 2010 North Pacific Groundfish Stock Assessment and Fishery Evaluation Reports for 2011 North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage 99501.
- Kalnay, E., Kanamitsu, M., Kistler, R. et al. (1996) The NCEP/NCAR 40-year reanalysis project. *Bull. Am. Meteor. Soc.* **77**:437–471.
- Kendall, A.W. Jr (2000) Status of recruitment studies of northeast Pacific fishes. *Bull. Sea Fish. Inst.* **3**:21–42.
- Kendall, A.W. Jr and Duker, G.J. (1998) The development of fisheries oceanography in the United States. *Fish. Oceanogr.* **7**:69–88.
- Kotwicki, S., Buckley, T.W., Honkalehto, T. and Walters, G. (2005) Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration. *Fish. Bull.* **103**:574–587.
- Ladd, C. and Bond, N.A. (2002) Evaluation of the NCEP-NCAR reanalysis in the northeast Pacific and the Bering Sea. *J. Geophys. Res.* **107**:3158.
- Magurran, A.E. (2004) Measuring Biological Diversity. Blackwell Publishing Company: Oxford, UK, 215 pp.
- Mecklenberg, C.W., Rask, P. and Steinke, D. (2011) Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Mar. Biodiv.* **41**:109–140.
- Merati, N. and Brodeur, R.D. (1996) Feeding habits and daily ration of juvenile walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. In: Ecology of Juvenile Walleye Pollock, *Theragra Chalcogramma* (eds) NOAA Tech. Rep. NMFS 126:65–80. R.D. Brodeur, P.A. Livingston, T.R. Loughlin & A.B. Hollowed (eds), pp. 65–80.
- Methot, R.D. (1986) Frame trawl for sampling juvenile fish. *CalCOFI Rep.* **27**:267–278.
- Meyers, R.A. and Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* **423**:280–283.
- Micheli, F. and Halpern, B.S. (2005) Low functional redundancy in coastal marine assemblages. *Ecol. Lett.* **8**:391–400.
- Napp, J.M. and Hunt, G.L. (2001) Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean, and biology. *Fish. Oceanogr.* **10**:61–68.
- Niebauer, H.J. and Day, R.H. (1989) Causes of interannual variability in the sea ice cover of the eastern Bering Sea. *GeoJournal* **18**:45–59.
- Norcross, B.L., Holladay, B.A., Busby, M.S. and Mier, K.L. (2010) Demersal and larval fish assemblages in the Chukchi Sea. *Deep-Sea Res. II* **57**:57–70.
- Rodriguez, J.M., Gonzalez-Pola, C., Lopez-Urrutia, A. and Nogueira, E. (2011) Composition and daytime vertical distribution of the ichthyoplankton assemblages in the Central Cantabrian Sea shelf, during summer: an Eulerian study. *Cont. Shelf Res.* **31**:1462–1473.
- Ryer, C.H. and Olla, B.L. (1997) Altered search speed and growth: social versus independent foraging in two pelagic juvenile fishes. *Mar. Ecol. Prog. Ser.* **153**:273–281.
- Ryer, C.H. and Olla, B.L. (1998) Effect of light on juvenile walleye pollock shoaling and their interaction with predators. *Mar. Ecol. Prog. Ser.* **167**:215–226.
- Sherman, K. (2000) Marine ecosystem management of the Baltic and other regions. *Bull. Sea Fish. Inst.* **3**:89–100.
- Sherman, K., Aquarone, M. and Adams, S. (2007) Global Applications of the Large Marine Ecosystem Concept 2007–2010. US Dept. Comm. NOAA/NMFS Technical Memorandum NMFS-NE-208 71 pp.
- Siddon, E.C., Duffy-Anderson, J.T. and Mueter, F. (2011) Community-level response of fish larvae to environmental

- variability in the southeastern Bering Sea. *Mar. Ecol. Prog. Ser.* **426**:225–239.
- Siddon, E.C., Heintz, R.A. and Mueter, F.J. (2013) Conceptual model of energy allocation in walleye pollock (*Theragra chalcogramma*) from age-0 to age-1 in the southeastern Bering Sea. *Deep-Sea Res. II* **94**:140–149.
- Sogard, S.M. and Olla, B.L. (1996) Diel patterns of behavior in juvenile walleye pollock *Theragra chalcogramma*. *Environ. Biol. Fishes* **47**:379–386.
- Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A. and Schumacher, J.D. (2001) On the temporal variability of the physical environment over the south-eastern Bering Sea. *Fish. Oceanogr.* **10**:81–98.
- Stabeno, P.J., Reed, R.K. and Napp, J.M. (2002) Transport through Unimak Pass, Alaska. *Deep-Sea Res. II* **49**:5919–5930.
- Stabeno, P.J., Bond, N.A., Kachel, N.B. and Salo, S.A. (2007) On the recent warming of the southeastern Bering Sea shelf. *Deep-Sea Res. II* **54**:2599–2618.
- Stabeno, P.J., Kachel, N.B., Moore, S.E., Napp, J.M., Sigler, M. and Zerbini, A.N. (2012a) Comparison of warm and cold years on the southeastern Bering Sea shelf. *Deep-Sea Res. II* **65–70**:31–45.
- Stabeno, P.J., Farley, E.V., Kachel, N.B. *et al.* (2012b) A comparison of the northern and southern shelves of the eastern Bering Sea and some implications for the ecosystem. *Deep-Sea Res. II* **65–70**:14–30.
- Toole, C.L., Markle, D.F. and Harris, P.M. (1993) Relationships between otolith microstructure, microchemistry, and early life history events in Dover Sole, *Microstomus pacificus*. *Fish. Bull.* **91**:732–753.
- Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P. and Polunin, N.V.C. (2006) Multiple disturbances and the global degradation of coral reefs: are reef fisheries at risk or resilient? *Global Change Biol.* **12**:2220–2234.