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

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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%
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). Conduct-
vitity-temperature-depth (CTD) casts were made
immediately prior to fish sampling at nearly every sta-
tion 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 obli-
quely 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
diffs 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. Supple-
mental surface and bottom temperature data were
obtained from AFSC annual bottom trawl surveys of
the EBS shelf in summer (June–August). Only temper-
ature 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 deter-
dined 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, spe-
cies abundance and length, and environmental
associations.

| 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.

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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 (SSMI) 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 Stabeno 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 unit effort (CPUE) weighted by the haul catch per unit effort (CPUE)) 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 ≤ 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, Ammododexes hexapterus, Atheresthes spp., H. elassodon, and L. polyxystra. Seven taxa were collected for 5 of the 6 yr; Sebastes spp., H. hemilepidotus, Bathyagonus alascanus, Podotrichus veternus, Zaprora silenus, L. bilineata, and Reinhardtius hippoglossoides. Eleven taxa were only collected in a single year: Stenobrachius leucopsarus (2005), Rhamphocottus richardsoni (2004), Psychrolutes paradoxus (2003), Leptagonus leptorhynchus and Ulcina obrila (2007), Aptocyclus ventricosus (2004), Romaulus 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 ≤ 0.02, R ≥ 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                  |                           |      |      |      |      |      |      |
| Leuroglossus schmidti         | Northern Smoothtongue     | X    | X    |      | X    | X    |      |
| Bathylagus pacificus          | Pacific Blacksmelt        |      |      | X    | X    |      |      |
| Myctophidae                   |                           |      |      |      |      |      |      |
| Stenobrachius leucopsaterus   | Northern Lampfish         |      |      |      |      |      | X    |
| Gadidae                       |                           |      |      |      |      |      |      |
| Gadus macrocephalus           | Pacific Cod               |      | X    | X    | X    | X    | X    |
| Theragra chalcogramma         | Walleye Pollock           | X    | X    | X    | X    | X    | X    |
| Macrouridae                   |                           |      |      |      |      |      |      |
| Coryphaenoides spp.           | Unidentified grenadiers   |      |      |      |      |      |      |
| Scorpaeniidae                 |                           |      |      |      |      |      |      |
| Sebastes spp.                 | Unidentified rockfishes   | X    | X    | X    | X    |      |      |
| Rhamphocottidae               |                           |      |      |      |      |      |      |
| Rhamphocottus richardsoni     | Grunt Sculpin             |      |      |      |      |      | X    |
| Cottidae                      |                           |      |      |      |      |      |      |
| Arctedius pacificus           | Hookhorn Sculpin          | X    |      |      |      |      |      |
| Hemilepidotus hemilepidotus   | Red Irish Lord            | X    | X    | X    | X    |      |      |
| Hemilepidotus jordani         | Yellow Irish Lord         |      |      |      |      |      | X    |
| Icelus borealis               | Northern Sculpin          | X    |      |      |      |      |      |
| Icelus spp.                   | Unidentified sculpin      |      |      |      |      |      |      |
| Myxocephalus spp.             | Unidentified sculpin      | X    | X    | x    | X    |      |      |
| Ruscinus meanyi               | Puget Sound Sculpin       | X    |      |      |      |      |      |
| Psychrolutidae                |                           |      |      |      |      |      |      |
| Dasycottus setiger            | Spinyhead Sculpin         | X    | X    | X    | X    |      |      |
| Malacocottus zonurus          | Darkfin Sculpin           | X    |      |      |      |      |      |
| Psychrolutes paradoxis        | Tadpole Sculpin           |      |      |      |      |      | X    |
| Agonidae                      |                           |      |      |      |      |      |      |
| Aspidophoroides monopterygius | Alligatorfish             | X    |      |      |      |      |      |
| Bathyagonus alascanus          | Gray Starsnout            | X    | X    | X    | X    |      |      |
| Bathyagonus infraspinatus      | Spinycheek Starsnout      | X    |      |      |      |      |      |
| Bathyagonus nigripinnis       | Blackfin Poacher          | X    |      |      |      |      |      |
| Leptagonus leptorhynchus      | Longnose Poacher          | X    |      |      |      |      |      |
| Podothercus vederus           | Veteran Poacher           | X    | X    | X    |      |      |      |
| Liparidae                     |                           |      |      |      |      |      |      |
| Liparis spp.                  | Unidentified Snailfishes  | X    | X    | X    | X    | X    | X    |
| Cyclopteridae                 |                           |      |      |      |      |      |      |
| Aptyctus ventricosus          | Smooth Lumpsucker         |      |      |      |      |      | X    |
| Bathymasteridae               |                           |      |      |      |      |      |      |
| Ronquilus jordani             | Northern Ronquil          |      |      |      |      |      | X    |
| Stichiaeidae                  |                           |      |      |      |      |      |      |
| Lumpenus maculatus            | Daubed Shanny             | X    | X    | X    | X    | X    |      |
| Cryptacanthoididae            | Dwarf Wrymouth            | X    |      |      |      |      |      |
| Cryptacanthodes aleutensis    |                           |      |      |      |      |      |      |
| Zaproridae                    |                           |      |      |      |      |      |      |
| Zaprora silenus               | Prowfish                  | X    | X    | X    | X    | X    | X    |
| Ammodontidae                  |                           |      |      |      |      |      |      |
| Ammodys tetrapus              | Pacific Sand Lance        | X    | X    | X    | X    | X    | X    |
| Pleuroneidae                  |                           |      |      |      |      |      |      |
| Patheresthes spp.             | Arrowtooth/Kamchatka Flounder | X    | X    | X    | X    | X    | X    |
| Embassichthys bathybius       | Deepsea Sole              | X    |      |      |      |      |      |
| Hippoglossoideles elassodon   | Flathead Sole             | X    | X    | X    | X    |      |      |

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Table 2. (Continued)

| Species name                          | Common name          | 2001 | 2002 | 2003 | 2004 | 2005 | 2007 |
|---------------------------------------|----------------------|------|------|------|------|------|------|
| Glyptocephalus zachirus               | Rex Sole             | X    |      |      |      |      |      |
| Hippoglossus stenolepis              | Pacific Halibut      |      |      |      |      |      |      |
| Lepidopsetta bilineata                | Southern Rock Sole   | X    | X    |      |      |      |      |
| Lepidopsetta polyxystra              | Northern Rock Sole   | X    | X    | X    |      |      |      |
| Pleuronectes quadrituberculatus       | Alaska Plaice        | X    |      |      |      |      |      |
| Reinhardtus hippoglossoides           | Greenland Halibut    | X    | X    | X    | X    |      |      |
| Total                                 |                      | 18,290 | 100.0 |      |      |      |      |
| All other taxa                        |                      | 525 | 2.9 |      |      |      |      |
| Atheresthes spp.                     |                      | 76 | 0.4 |      |      |      |      |
| Atheresthes schmidti                 |                      | 225 | 1.2 |      |      |      |      |
| Greenland Halibut                    | X                    | 16,735 | 91.5 | X    | X    | X    | X |
| Total                                 |                      | 18,290 | 100.0 |      |      |      |      |

1Two additional species, Ulcina olriki (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     | %     |
|-------------------------------|-------|-------|
| Theragra chalcogramma         | 16,735 | 91.5  |
| Hippoglossoides elassodon     | 644   | 3.5   |
| Gadus macrocephalus           | 225   | 1.2   |
| Lepidopsetta polyxystra      | 85    | 0.5   |
| Atheresthes 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. schmidti, S. leucopsaenus, 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., Dasyctinus 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 groups 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. olriki, 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. schmidti, 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. Dasyctinus 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 dendograms 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 | B. alascanus | A. hexapterus    | A. monopterygius          | L. bilineata          | C. aleutensis              |
|      | B. nigripinnis | H. jordani       | L. maculatus             | Myoxocephalus spp.    | G. macrocephalus           |
|      | G. zachirus | Sebastes spp.    | Liparis spp.             | L. polyxystra         | H. elassodon               |
|      | L. schmidt |                   | Atheresthes spp.         | T. chalogramma        | Z. silenus                 |
|      |            |                   | I. borealis             | P. verternus          | R. meanyi                 |
|      |            |                   |                            | R. hippoglossoides    | H. hemilepidotus           |
|      |            |                   |                            | Atheresthes spp.      | B. infraspinatus           |
|      |            |                   |                            | B. alascanus          | H. hemilepidotus           |
|      |            |                   |                            | Liparis spp.          | L. bilineata               |
|      |            |                   |                            | M. zonurus            |                           |
|      |            |                   |                            | Myoxocephalus spp.    |                           |
| 2002 | A. hexapterus | L. schmidt       | G. macrocephalus          | Atheresthes spp.      | H. hemilepidotus           |
|      | Liparis spp. | Sebastes spp.    | H. elassodon             | B. pacificus          | L. polyxystra              |
|      | R. hippoclossoides |            | T. chalogramma          | B. infraspinatus      | Liparis spp.               |
|      |            |                   | L. polyxystra           | M. zonurus            | Myoxocephalus spp.         |
|      |            |                   | L. maculatus            |                           |                           |
| 2003 | A. pacificus | L. maculatus    | B. alascanus             | Atheresthes spp.      |                           |
|      | P. verternus | T. chalogramma  | B. infraspinatus         | Z. silenus            |                           |
|      |            |                   | Sebastes spp.           | B. pacificus          |                           |
|      |            |                   | G. macrocephalus        | M. zonurus            |                           |
|      |            |                   | H. elassodon            | Myoxocephalus spp.    |                           |
| 2004 | A. ventricosus | B. pacificus    | Atheresthes spp.         | D. setiger            |                           |
|      | R. richardsoni | Coryphaenoides spp. | Liparis spp.             | Icelus spp.          | B. alascanus               |
|      |             | L. schmidt      | H. elassodon             |                           | H. elassodon               |
|      |             |                   | Sebastes spp.           |                           | T. chalogramma             |
|      |             |                   | L. maculatus            |                           |                           |
| 2005 |                     | Coryphaenoides spp. | L. schmidt             | G. macrocephalus      |                           |
|      |                     | L. schmidt      | Z. silenus              | Z. silenus            |                           |
|      | B. nigripinnis |                      | I. borealis             |                           |                           |
|      | M. zonurus       |                        | Liparis spp.            |                           |                           |
|      | S. leucopsaurns |                        |                            |                           |                           |
| 2007 | Icelus spp. | H. elassodon | Atheresthes spp.         |                           | Atheresthes spp.          |
|      | R. jordani      | R. hippoclossoides | L. maculatus            | Liparis spp.          | Liparis spp.               |
|      | P. quadrituberculatus |              | D. setiger              | L. polyxystra         | Myoxocephalus spp.         |
|      |                   | H. elassodon     |                           | T. chalogramma        | H. hemilepidotus           |
|      |                   | L. polyxystra   |                           |                           |                           |

12005 has three additional species cluster groups F: Bathyagonus infraspinatus, Sebastes spp., L. maculatus, Ruscarius meanyi G: H. hemilepidotus, L. bilineata, R. hippoclossoides, P. verternus 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. chalogramma 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. chalogramma 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

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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
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...
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.
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 ± standard error (SE) of the five most abundant taxa collected from the ‘core’ stations. Note differences in abundance scales between species (number 10 m⁻²).

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 |
|---------------------------|------|------|------|------|------|------|------|------|------|------|------|
| Theragra chalcogramma     | BCD  | BCD  | AB   | CD   | EF   | F    | ABC  | CD   | F    | E    | A    |
| Hippoglossoides elassodon | ABC  | AB   | CD   | AB   | BC   | D    | BC   | CD   | ABC  | D    | A    |
| Gadus macrocephalus       | BCDE | AB   | A    | ABC  | BCDE | BCD  | ABC  | DE   | CDE  | E    | AB   |
| Lepidopsetta polyxystra   | AB   | C    | A    | AB   | AB   | BC   | A    | A    | A    | AB   | C    |
| Atheresthes spp.          | ABC  | AB   | A    | BC   | ABC  | C    | A    | AB   | BC   | BC   | AB   |

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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 (±SE) of *Theragra chalcogramma* collected from the ‘core group’ of stations.

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

| Year | 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            |                   |          | X                        | 0.64          | 0.01*   |
| 2002 | X            |                   | X        |                          | 0.46          | 0.01*   |
| 2003 | X            |                   |          |                          | 0.64          | 0.01*   |
| 2004 | X            |                   |          |                          | 0.65          | 0.01*   |
| 2005 | X            |                   |          | X                        | 0.59          | 0.01*   |
| 2007 | X            |                   |          | X                        | 0.57          | 0.01*   |

*Significant at 5%.

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**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$^{0.25}$. 
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

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 m²) at the 12 common stations sampled in all 11 yr.

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

Figure 9. Results of GAM analyses showing relationships of abundances of (a) *Lepidopsetta polyxstra* larvae with maximum wind speed and (b) *L. polyxstra* 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, CPUE^{0.25}.

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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.

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