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Zooplankton and pelagic fish samples collected on the eastern Bering Sea shelf in late summer 2003–2010 were used to evaluate spatial and temporal changes in the plankton and nekton community structure. The zooplankton were sampled by vertical towing of a Juday net (168 µm mesh) and oblique towing of a Bongo net (505 µm mesh), and pelagic fish were caught by midwater rope trawl. The communities were compared across climate regimes (in relatively warm and cold years), by latitude (in the northern and southern parts of the shelf), and by water depth (in the inner, middle, and outer domains of the shelf). Zooplankton were dominated by the small copepod *Oithona* spp. in warm years but relatively larger copepods *Pseudocalanus* spp. and *Acartia* spp. in cold years. Notably, the large copepod *Calanus* spp., an important energy-rich prey for fish, were more abundant in cold years than warm years. Age-0 walleye pollock *Gadus chalcogrammus* were more abundant in warm years, while capelin *Mallotus villosus* were abundant within cold-year communities over the northern shelf. Latitudinal variations in communities were more prominent in the cold years, particularly in 2007 and 2010. Cross-shelf variations were evident, particularly for large zooplankton and fish, with communities corresponding to specific oceanographic domains. Outer shelf communities varied less than inner and middle shelf communities between warm and cold periods, suggesting that this region may be less impacted by climate variability. An understanding of the overlap of zooplankton (prey) and fish communities within specific shelf regions or climate regimes may provide information for ecosystem-based approaches to fisheries management.

Key words: eastern Bering Sea, zooplankton, pelagic fish, climate change, community structure, water temperature.

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Состояние планктонных и нектонных сообществ, пространственные и межгодовые изменения их структуры рассмотрены по материалам, собранным летом 2003–2010 гг. на шельфе восточной части Берингова моря. Облов мелкоразмерного планктона проводился сетью Джели (с размером ячеи 0,168 мм), крупноразмерного — сетью Бонго (с размером ячеи 0,505 мм), пелагические рыбы облавливались разноглубинным канатным тралом. Выявлены различия между сообществами планктона и нектона в пределах шельфа (между внутренней, средней и внешней областями и между северной и южной частями шельфа), а также между разными по климатическому режиму годами (холодными и теплыми). Показано, что мелкие копеподы рода *Oithona* доминировали в теплые годы, а относительно крупные копеподы родов *Pseudocalanus* и *Acartia* — в холодные годы. Крупные копеподы рода *Calanus*, отличающиеся высокой калорийностью и поэтому имеющие большое значение в питании рыб, также были обильны в холодные годы. В нектонных сообществах в теплые годы преобладали сеголетки минтая *Gadus chalcogrammus*, в то время как в холодные годы в северной части шельфа была обильна мойва *Mallotus villosus*. Отмечено, что наибольшие различия в пространственном распределении видов (особенно для крупного зоопланктона и рыб) между южной и северной частями наблюдались в холодные 2007 и 2010 гг. При этом в сообществах в пределах внутреннего и среднего шельфа межгодовые изменения были более выражены, чем в сообществах внешнего шельфа. Проанализированы случаи наложения распределения зоопланктона (пищи для рыб) и его нектонных потребителей, при этом отмечено совпадение в распределении мойвы с границами распределения ее кормовых объектов — копепод рода *Calanus* и эвфаузиид. Кроме того, показано, что в холодные годы при обилии пищи, богатой липидами (крупные копеподы и эвфаузииды), выживаемость молоди минтая после зимнего периода выше, чем в теплые годы, когда в зоопланктоне доминируют мелкие копеподы. Полученная информация о распределении видов-жертв и видов-потребителей в зависимости от климатических условий может быть использована для управления рыболовством на основе экосистемного подхода.

Ключевые слова: восточная часть Берингова моря, зоопланктон, пелагические рыбы, изменение климата, структура сообщества, температура воды.

Introduction

The eastern Bering Sea (EBS) is characterized by a broad continental shelf (> 500 km wide and > 1000 km long) and supports a highly productive ecosystem owing to on-shelf flow of nutrient-rich waters. Due to persistent ecological differences, the shelf has been delineated into northern and southern regions at ~ 59–60° N (Stabeno et al., 2012a); north of 63° N the ecosystem processes may be more similar to the Chukchi Sea than the Bering Sea (Stabeno et al., 2010). From spring to early fall, persistent oceanographic fronts (Hunt and Stabeno, 2002) separate the shelf into three domains: the inner shelf (inside of the 50 m depth contour), the middle shelf (between 50 and 100 m), and the outer shelf (between 100 and 200 m) (Iverson et al., 1979; Coachman, 1986). During summer, the inner shelf is well mixed by tides and wind, the middle shelf is highly stratified with a wind-mixed surface layer and a tidal-mixed bottom layer, and the outer shelf has a multi-layer system with the surface and bottom layers separated by a transition zone (Stabeno et al., 2010). Circulation on the Bering Sea shelf is generally northwestward, with water from the Alaska Stream and Alaska Coastal Current (ACC) in the Gulf of Alaska entering through the Aleutian passes and exiting through Bering Strait into the Chukchi Sea. The Bering Slope Current flows north along the shelf break at speeds of 5–20 cm/s (Danielson et al., 2012), while currents over the shelf are more sluggish with speeds of 1–5 cm/s (Danielson et al., 2011). The shelf is seasonally ice covered every year in the north and during cold climatic periods in the south. Seasonal ice over the southern shelf leaves a footprint of cold bottom waters < 2 °C (i.e., the cold pool), which extends southward almost to the Alaska Peninsula during cold years. The most extensive ice cover and coldest water column temperatures since the early 1970s were observed beginning in 2007 and continued through at least the winter of 2010/11 (Stabeno et al., 2012b).

Climate conditions driven by decadal-scale oscillations (i.e., Aleutian Low Pressure System, Arctic Oscillation) can cause extended periods of warm (or cold) conditions overlaid on the natural variability of the system. The Oscillating Control Hypothesis (Hunt et al., 2002, 2011) provides a framework within which to predict ecosystem responses to warm and cold conditions in the EBS. In warm years with early sea ice retreat, stratified waters maintain

production within the pelagic system (Walsh and McRoy, 1986; Mueter et al., 2006), which was predicted to result in enhanced survival of species such as walleye pollock *Gadus chalcogrammus* (Hunt and Stabeno, 2002; Mueter et al., 2006; Moss et al., 2009). However, recent studies have shown that changes in prey composition and quality during a warm regime may be detrimental to walleye pollock survival (Heintz et al., 2013; Siddon et al., 2013).

Northward shifts in species' distributions and altered community compositions in response to temperature increases have been observed in the North Atlantic (Brander et al., 2003), the North Sea (Perry et al., 2005), and on the Bering Sea shelf (Mueter et al., 2007; Mueter and Litzow, 2008; Spencer, 2008). Shifts in species' ranges may lead to atypical species interactions or impacts to commercial and subsistence harvests as northern species are displaced by more southern species (Overland and Stabeno, 2004). However, available habitat and prey resources may not be able to support extensive northward shifts.

Analyzing assemblage patterns across trophic levels can inform ecosystem-based approaches to fisheries management (EBFM). Integrated Ecosystem Assessments (www.noaa.gov/iea; Levin et al., 2009) are in development for many large marine ecosystems in the US; understanding community-level responses to climate variability will inform such approaches. A framework for EBFM for the northwest Atlantic identified the need for developing ecosystem indicators and conducting multi-species assessments and modeling to understand the effects of multiple processes acting simultaneously on the ecosystem (Link et al., 2011). Predator-prey dynamics are also a structuring force in ecosystems (Hunsicker et al., 2011), so further understanding of these interactions will enhance EBFM.

The goals of this study are to (1) describe changes in the community composition of small and large zooplankton and pelagic fish across warm and cold conditions in the eastern Bering Sea and (2) relate the assemblages to environmental gradients to look at factors affecting the spatial and temporal patterns of assemblages. Patterns will be compared qualitatively among recent warm (2003–2005), average (2006), and cold (2007–2010) periods, which are based on water temperature anomalies and southerly sea ice extent (Stabeno et al., 2012b).

Materials and methods

This work is part of the Bering Aleutian Salmon International Survey (BASIS) program to study salmon and forage fish ecology in the Bering Sea. US BASIS surveys were conducted in the eastern Bering Sea, at stations spaced approximately 60 km apart from 54.5–63.0 °N and 159.0–174.0 °W, from mid-August to early October 2003–2010 (Table 1). Almost 900 stations were sampled across eight years of the study, ranging from 31 stations in 2008 to 121 stations in 2007. Large zooplankton and fish were collected at each station and small zooplankton at a subset of stations for a total of 528 small zooplankton, 803 large zooplankton, and 875 fish samples for all years combined. Rare taxa (found at less than 5 % of stations) were excluded from analysis. We analyzed 17 small zooplankton, 20 large zooplankton, and 27 fish taxa or taxa groups (Table 1).

Temperature data. Vertical profiles of temperature were collected at each station with a Sea-Bird* Model 25 or Model 9plus Conductivity-Temperature-Depth profiler (CTD) from near surface (~1–2 m depth) to near bottom (5–10 m off bottom). Data were processed into 1-m vertical bins using Sea-Bird software. Temperature was averaged above and below the mixed layer depth (MLD). The MLD was estimated as the depth where σ_t is 0.10 kg/m³ higher than the value at 5m (Danielson et al., 2011).

Zooplankton sample collection and lab analysis. Zooplankton samples were collected and analyzed using methods described in Coyle et al. (2011) and Eisner et al. (2014). Briefly, small zooplankton assemblages were sampled with a 0.1-m² Juday net with 168 μ m mesh, towed vertically from near bottom to the surface (Volkov, 1984, 2012; Volkov et al., 2007). Small zooplankton samples were counted on-board the ship by Pacific Research Fisheries Center (TINRO-Center) scientists. Large zooplankton assemblages were collected with a 60-cm bongo frame with 505 μ m mesh, towed obliquely from near bottom to the surface. These samples

* Use of trade names does not signify an endorsement by the U.S. National Oceanic and Atmospheric Administration.

Table 1

Climate regime, cruise start and end dates, north-south (N-S) regions covered, and average taxa abundance (using all available samples) by year. See Figs. 3–5 for station locations. Predominantly juveniles unless indicated

Таблица 1

Характеристика данных по годам: тип климатического режима, даты начала и окончания проведения съемки, обследованные участки шельфа, среднее обилие таксонов. См. расположение станций на рис. 3–5. Возраст рыб преимущественно 0+, кроме особо обозначенного

Year	2003	2004	2005	2006	2007	2008	2009	2010
Climate regime	Warm	Warm	Warm	Average	Cold	Cold	Cold	Cold
Start date	31-Aug	14-Aug	14-Aug	18-Aug	16-Aug	11-Sep	30-Aug	18-Aug
End date	9-Oct	1-Oct	7-Oct	20-Sep	8-Oct	27-Sep	28-Sep	8-Oct
Regions	N-S	N-S	N-S	N-S	N-S	S	N-S	N-S
Small Zooplankton Taxa (no./m²)								
<i>Acartia</i> spp.	26349	1080	28424	3210	37618	34748	49378	26130
Polychaeta	14304	12859	19380	4674	4670	325	37859	12312
Bivalvia	46807	48828	50141	4244	15429	5465	0	8959
<i>Centropages abdominalis</i>	8215	9050	9811	1012	3599	2109	461	805
Cirripedia	7417	6436	3824	795	576	40	197	294
Echinodermata larvae	31159	33957	17425	5263	2548	8215	13362	1865
<i>Eurytemora herdmani</i>	4540	1747	1807	37	248	0	0	42
<i>Evadne</i> sp.	0	3270	1012	31	49	0	0	52
<i>Fritilaria</i> sp.	0	0	477	0	2447	0	1712	2479
<i>Metridia</i> spp. copepodites	2739	2654	3136	16250	3383	1468	4701	1823
<i>Microcalanus pygmaeus</i>	789	240	354	9082	390	0	694	312
<i>Oithona</i> spp.	248643	213663	279203	238665	183526	115259	125262	111117
<i>Podon</i> sp.	2664	2706	526	21	125	0	0	0
<i>Pseudocalanus</i> spp.	55559	83340	41868	71514	84338	199080	67972	76508
<i>Tortanus discaudatus</i>	115	351	1111	124	511	0	0	9
<i>Scolecithricella</i> sp.	0	27	0	82	104	0	98	56
Harpacticoida	303	433	248	1302	1157	52	194	602
Large Zooplankton Taxa (no./m²)								
Anomura	4	8	6	14	8	5	7	3
Appendicularia	187	415	239	169	548	708	161	112
Brachyura	5	20	16	25	27	5	15	6
<i>Calanus pacificus</i>	7	2	6	5	4	0	4	0
<i>Calanus</i> spp.	105	817	373	703	3656	8030	3769	2229
Caridea	43	67	40	16	16	6	9	4
<i>Clione limacina</i>	1	4	21	5	7	6	8	2
Cnidaria	147	408	869	185	547	30	111	50
Ctenophora	0	1	0	1	3	0	1	0
Cumacea	1	19	6	12	88	3	45	7
<i>Epilabidocera amphitrites</i>	69	39	39	15	47	85	15	3
<i>Eucalanus bungii</i>	82	117	165	703	388	226	1117	150
<i>Eukrohnia hamata</i>	1	0	3	16	45	1	18	0
Gammaridae	7	17	32	28	86	43	36	12
Hyperiididae	19	23	28	64	272	267	91	118
<i>Limacina helicina</i>	130	552	59	1759	527	2843	2385	1228
<i>Metridia pacifica</i>	137	122	205	389	649	15	708	144
Mysida	3	12	3	3	9	17	4	5
<i>Neocalanus</i> spp.	8	16	36	210	248	81	119	76
<i>Parasagitta elegans</i>	179	405	418	567	1394	987	755	239
Fish Taxa (no./km²)								
<i>Ammodytes hexapterus</i>	10	102	5	48	84	133	17	103
<i>Anarhichas orientalis</i>	0	0	1	1	3	0	1	5
<i>Anoplopoma fimbria</i>	15	9	21	42	1	0	0	0
<i>Blepsias bilobus</i>	1	1	3	1	1	0	0	0
<i>Clupea pallasii</i>	1262	2968	2112	1106	877	66	220	117

Table 1 finished
Окончание табл. 1

Year	2003	2004	2005	2006	2007	2008	2009	2010
Climate regime	Warm	Warm	Warm	Average	Cold	Cold	Cold	Cold
Start date	31-Aug	14-Aug	14-Aug	18-Aug	16-Aug	11-Sep	30-Aug	18-Aug
End date	9-Oct	1-Oct	7-Oct	20-Sep	8-Oct	27-Sep	28-Sep	8-Oct
Regions	N-S	N-S	N-S	N-S	N-S	S	N-S	N-S
<i>Gadus chalcogrammus</i>	45430	91126	73271	11003	4794	9416	204	713
<i>Gadus macrocephalus</i>	10	40	479	573	84	165	3	472
<i>Gasterosteus aculeatus</i>	3	36	49	120	1	97	0	0
<i>Lethenteron camtschaticum</i>	2	2	1	1	1	0	1	1
<i>Limanda aspera</i>	1	13	15	26	11	23	11	21
<i>Mallotus villosus</i>	11	22	188	79	668	32	2497	7043
<i>Oncorhynchus gorbuscha</i> *	0	1	0	1	0	0	0	0
<i>Oncorhynchus gorbuscha</i>	66	56	49	23	104	11	114	24
<i>Oncorhynchus keta</i> *	10	18	9	33	17	0	50	12
<i>Oncorhynchus keta</i>	94	51	85	32	118	12	86	117
<i>Oncorhynchus kisutch</i> *	0	1	2	1	0	0	0	0
<i>Oncorhynchus kisutch</i>	31	13	4	5	5	14	2	3
<i>Oncorhynchus nerka</i> *	4	1	1	21	9	0	4	1
<i>Oncorhynchus nerka</i>	200	126	374	53	253	66	107	114
<i>Oncorhynchus tshawytscha</i> *	1	1	1	1	1	1	1	24
<i>Oncorhynchus tshawytscha</i>	13	15	12	3	9	1	7	5
<i>Osmerus mordax dentex</i>	1	139	8	14	65	14	1	0
<i>Pleurogrammus monopterygius</i>	63	13	1	3	26	1	19	0
<i>Podotheucus acipenserinus</i>	0	1	1	0	1	0	0	0
<i>Sebastes</i> spp.	0	0	0	14	26	118	123	126
<i>Trichodon trichodon</i>	110	47	29	47	94	71	124	12

* Indicates a mix of immature and maturing salmon.

were preserved in 5 % formalin buffered with seawater. Zooplankton samples from 2003–2004 were sorted at the Polish Plankton Sorting and Identification Center (Szczecin, Poland) and samples from 2005–2010 were processed at the University of Alaska (Coyle et al., 2008). The lowest taxonomic level of sorting varied between labs, so we used the lowest taxonomic stage available for all years. We excluded euphausiids from our analysis since zooplankton tows were collected primarily during the daytime when euphausiids may be concentrated within 1–2 m of the bottom (Coyle and Pinchuk, 2002), below the reach of our nets. Unidentified copepod nauplii were also excluded from analysis.

Fish sample collection. Pelagic fish taxa were captured at each station with a midwater rope trawl with a mean horizontal spread of 55 m, configured to sample the top 15–20 m of the water column (Farley et al., 2007). The net had hexagonal mesh wings and a 1.2-cm mesh cod liner. Trawls were towed at 3.5–5.0 knots (6.5–9.3 km/h) for 30 min. The whole catch was immediately sorted to species and counted to estimate abundance of each taxon (no./km²). For large catches, a random sub-sample was sorted and counted, and results were extrapolated to estimate the total catch by taxa. Sampled fish were predominantly juvenile life stages, as well as immature and maturing stages for salmonids. While small numbers of adult fish were collected, they did not have a large influence on analyses based on overall fish abundance.

Statistical analyses. The taxonomic composition (relative abundances of taxa) and distribution of zooplankton and fish were evaluated qualitatively using data from all stations and years. Separate analyses were conducted for abundances of small zooplankton, large zooplankton, and fish taxa. Statistical analyses included cluster analysis and similarity percentage contribution of individual taxa (SIMPER) in the software package, PRIMER-E, version 6.1.15 (Clarke and Warwick, 2001; Clarke and Gorley, 2006).

For grouping stations, abundance data (no./m² and no./km² for zooplankton and fish, respectively) were 4th root transformed to down-weight the contribution of dominant taxa to

similarity/dissimilarity patterns (Clarke and Warwick, 2001). We then applied a hierarchical cluster analysis using group average linkage of Bray-Curtis dissimilarities among stations. Clusters were identified by drawing a line across branches on each dendrogram. We used the degree of similarity, the length of branches (indicating stability of groups), and SIMPROF (an *a priori* permutation based procedure that tests for grouping (Clarke and Warwick, 2001; Clarke and Gorley, 2006)) to determine where to place this line. Cluster groups were also subjectively evaluated to determine if they were biologically relevant. We designated clusters as outliers if they contained less than 1 % of the sampled stations. We then used SIMPER analysis to determine the average percent contribution of each taxon to each cluster.

For grouping taxa, we used (untransformed) data standardized to the total abundance of each taxa group to give equal weight to all species, regardless of their average numerical abundance (i.e., so that rare and common taxa were of equal importance). We applied separate cluster analyses to determine which taxa grouped together across all stations combined for small zooplankton, large zooplankton, and fish.

Results and discussion

Temperature data

Surface (above the MLD) water temperature was higher in 2003–2005 than in 2006–2010 in the south, but appeared to cool a year earlier (starting in 2005) in the north (Fig. 1). The coldest surface temperatures were seen in 2008–2010. Temperature below the MLD on the middle shelf reflects the location of the cold pool. The cold pool began to expand southward over the shelf starting in 2006, followed by a greater southward extent in 2007–2010 (Fig. 2). Surface temperatures remained relatively colder in the northern Bering Sea in all years of the study while temperatures over the southern shelf cooled during the study period.

Spatial and temporal patterns of zooplankton assemblages

Small zooplankton. Multivariate analyses of small zooplankton abundance identified 13 main clusters over the EBS shelf (Fig. 3). Taxa contributing to at least 80 % of within-cluster similarities based on total small zooplankton abundances are shown in Table 2. Similarities within clusters ranged from 69–74 %.

On the middle and inner shelves, Cluster ZS2 had broad spatial coverage in warm years and was strongly dominated by *Oithona* spp. (Copepoda), followed by *Pseudocalanus* spp. (Copepoda), molluscan Bivalvia larvae, Echinodermata larvae, and Polychaeta (annelid worms). In cold years, this was replaced by Clusters ZS5 and ZS13, dominated by *Pseudocalanus* spp., *Acartia* spp., and *Oithona* spp. (ZS5 only). One cluster was common for all years in the southern outer shelf, Cluster ZS4, dominated by large numbers of *Oithona* spp., followed by *Pseudocalanus* spp. and *Acartia* spp. Clusters with the largest numbers of *Oithona* spp. (> 200,000/m²) included Cluster ZS2 (present in warm years), Clusters ZS3 and ZS8 (both with patchy distributions), and Cluster ZS4 (located on the outer shelf). Overall, *Oithona* spp. was in higher concentrations in warm years and *Pseudocalanus* spp. and *Acartia* spp. higher in average and cold years (Volkov, 2012; see also Eisner et al., 2014).

Community variations between the northern and southern Bering Sea shelf were observed during the latest years (2009 and 2010). In 2009, a cluster (ZS10) characterized by high polychaete abundances was seen in the north, but not in the south. Similar taxa were found within many cluster groups, but in different ratios. In 2010, Cluster ZS1 observed in the north had high and similar levels of *Pseudocalanus* spp. and *Oithona* spp., followed by lower levels of *Acartia* spp. In the south, Cluster ZS5 was dominated by *Pseudocalanus* spp., followed by *Oithona* spp. and *Acartia* spp. Mean abundances of all taxa were higher in Cluster ZS1 than in ZS5.

Additional analysis of taxa across all stations combined indicates that the small copepods, *Oithona* spp., *Pseudocalanus* spp., and *Acartia* spp. often co-occur (> 40 % similarity) (data not shown). Neritic near-shore taxa, *Podon* sp. and *Evadne* sp. (Cladocera) also co-occurred, as did *Centropages abdominalis* and *Eurytemora herdmanni* (Copepoda) (~ 38 % similarity).

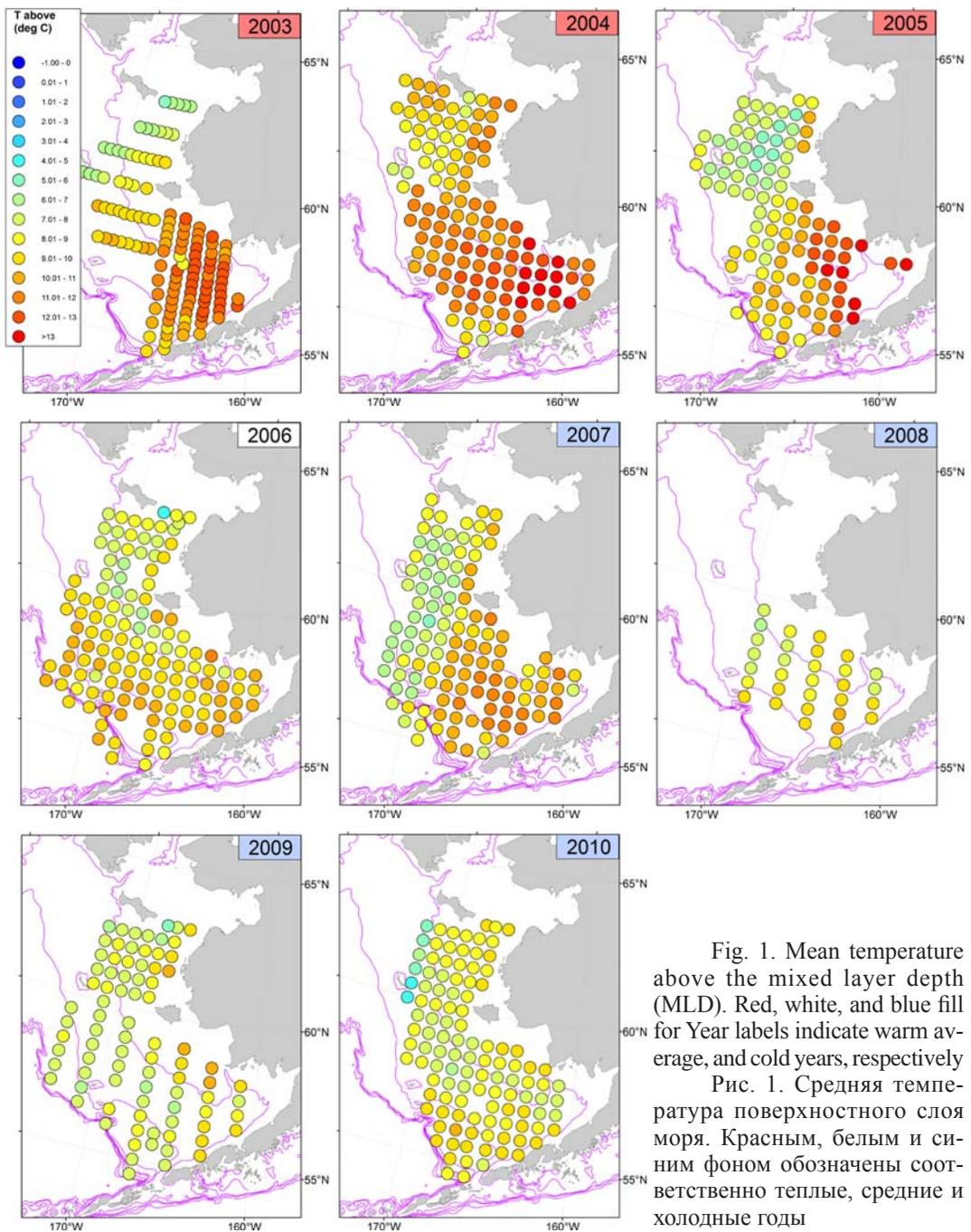


Fig. 1. Mean temperature above the mixed layer depth (MLD). Red, white, and blue fill for Year labels indicate warm average, and cold years, respectively

Рис. 1. Средняя температура поверхностного слоя моря. Красным, белым и синим фоном обозначены соответственно теплые, средние и холодные годы

Large zooplankton. Multivariate analyses of large zooplankton abundance identified 11 main clusters over the EBS shelf (Fig. 4). Taxa contributing to at least 80 % of within-cluster similarities are shown in Table 3. Similarities within clusters ranged from 61–70 %.

On the middle shelf, Clusters ZL2 and ZL4, dominated by *Parasagitta elegans* (Chaetognatha), Cnidaria (gelatinous zooplankton, primarily *Aglantha digitale* in our study), *Calanus* spp. (Copepoda, a combination of *Calanus marshallae* and *C. glacialis*), and Appendicularia (larvaceans) were common in warm years shifting to Clusters ZL9, ZL10, and ZL11, dominated by *Calanus* spp. and *P. elegans* in cold years. Note that *P. elegans* was often dominant in clusters, but abundances were higher in cold than warm years. On the inner shelf, Cluster ZL1, dominated by *P. elegans*, *Epilabidocera amphitrites* (Copepoda), Cnidaria, and Caridea (shrimp) was more common in warm than average and cold years. The main cluster on the southern outer shelf for

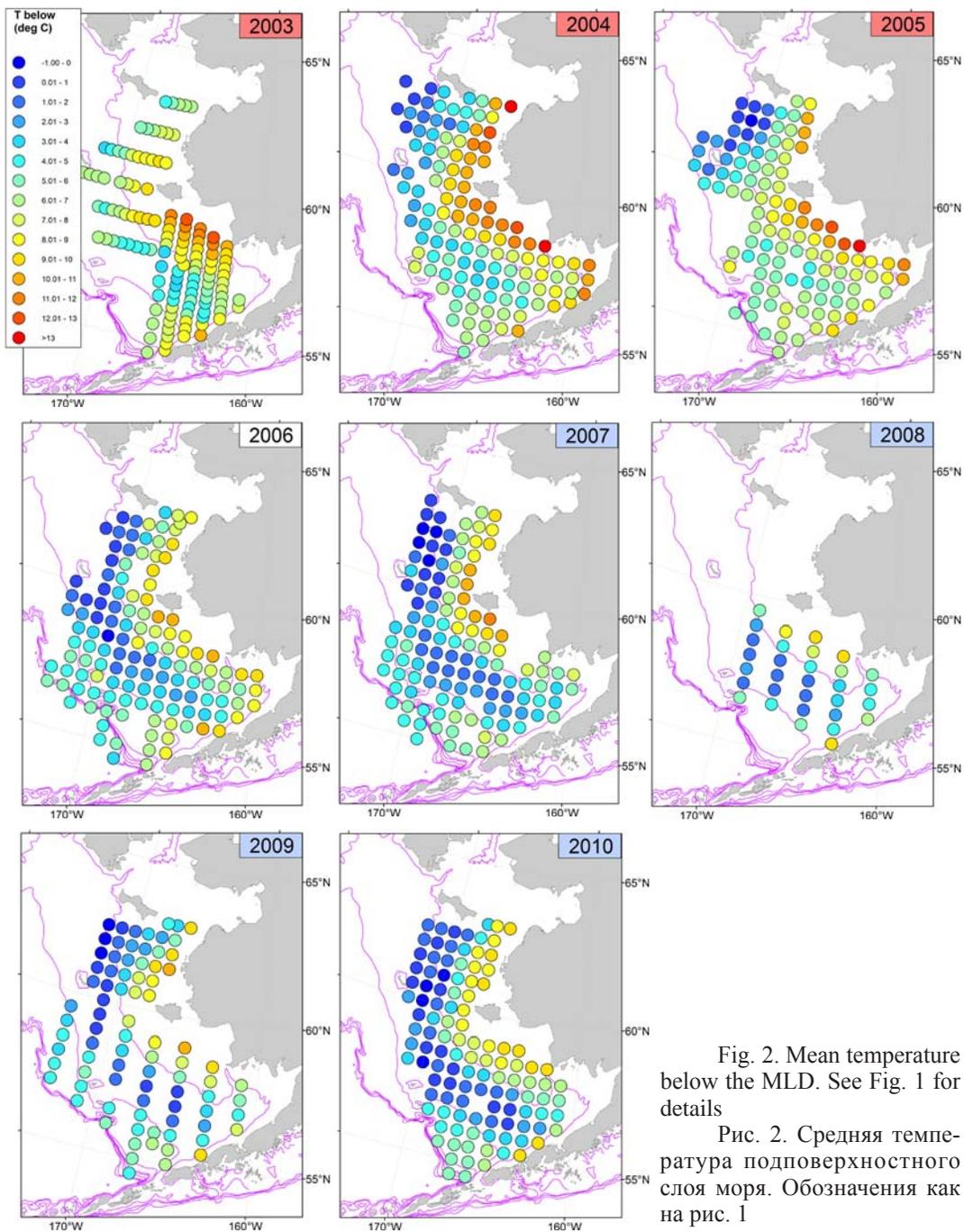


Fig. 2. Mean temperature below the MLD. See Fig. 1 for details

Рис. 2. Средняя температура подповерхностного слоя моря. Обозначения как на рис. 1

all years was Cluster ZL3, dominated by *Eucalanus bungii* (Copepoda), *Calanus* spp., *P. elegans*, *Metridia pacifica* (Copepoda), *Limacina helicina* (Pteropoda), *Neocalanus* spp. (Copepoda), and Hyperiididae (Amphipoda), many of which are considered resident to the outer shelf or advected from off-shelf (Coyle and Pinchuk, 2002; Gibson et al., 2013). Near the southern middle front (~ 100 m bathymetry) and Pribilof Islands, Cluster ZL2 in warm years was replaced by ZL10 in cold years. Of note, *Calanus* spp. were dominant in more clusters in cold years with overall abundances higher in cold than warm years. The highest *Calanus* spp. numbers were seen in the cold year Cluster ZL11.

Clusters often varied between north and south in the Bering Sea. For example, Cluster ZL8, which was dominated by *Calanus* spp., Appendicularia, *P. elegans*, and Cnidaria, was only common in the north (2007 and 2010, in particular). Overall, there was a higher abundance of

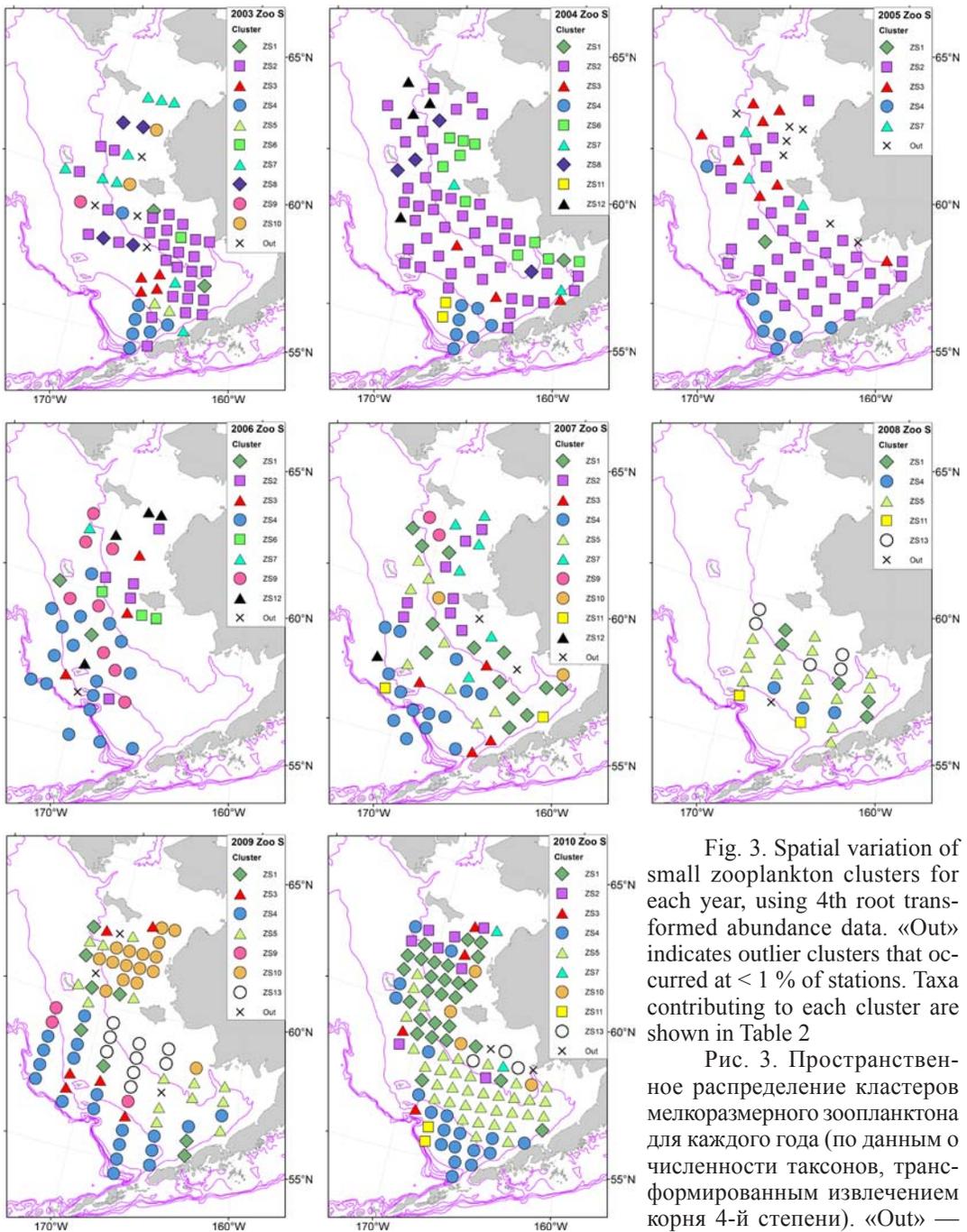


Fig. 3. Spatial variation of small zooplankton clusters for each year, using 4th root transformed abundance data. «Out» indicates outlier clusters that occurred at < 1 % of stations. Taxa contributing to each cluster are shown in Table 2

Рис. 3. Пространственное распределение кластеров мелкоразмерного зоопланктона для каждого года (по данным о численности таксонов, трансформированным извлечением корня 4-й степени). «Out» —

станции с уникальным видовым составом, отмеченным для < 1 % станций. Характерные для каждого кластера таксоны представлены в табл. 2

gelatinous zooplankton (e.g., Cnidaria, Appendicularia) in the north, as observed by Eisner et al. (2014). Cluster ZL9 was common in the northern Bering Sea in the warm years of 2004 and 2005, then expanded southward in 2006 and 2007, indicating that increases in *P. elegans* and *Calanus* spp. in the north preceded increases in these taxa in the south.

Additional analysis of large zooplankton taxa across all stations combined indicated that outer shelf taxa, *Neocalanus* spp., *E. bungii*, and *M. pacifica* often co-occur (> 40 % similarity, data not shown). *P. elegans* and *Calanus* spp. also co-occurred; both had higher abundances in cold compared to warm years. Other taxa that co-occurred included Cumacea and Gammaridae, as did *E. amphitrites* and Caridea.

Table 2

Small zooplankton taxa that make up at least 80 % of similarity (80 % cumulative contribution) within a cluster, determined from SIMPER analysis conducted on 4th root transformed abundance data (Abund 4th rt; no./m²). SIMPER results show the overall similarity between stations within each cluster (Sim %), the individual percent contributions from each taxa (Contrib %), and the cumulative percent contribution after inclusion of a taxa (Cum %). Untransformed abundances (Abund untrans) also shown

Таблица 2

Кластеры, выделенные SIMPER-анализом данных по мелкоразмерному планктону, трансформированных извлечением корня 4-й степени (Cluster); таксоны, обеспечивающие 80 % сходства (80 % совокупного вклада) в кластерах (Species) и их численность после трансформации (Abund 4th rt); уровни сходства между станциями внутри кластеров (Sim, %), вклад в сходство каждого таксона (Contrib, %) и совокупный вклад после включения таксона, от доминантных к субдоминантным (Cum, %). Также приведены данные о численности таксонов, не подвергнутые трансформации (Abund untrans, экз./м²)

Cluster	Sim, %	Species	Abund untrans	Abund 4th rt	Contrib, %	Cum, %
ZS1	72	<i>Pseudocalanus</i> spp.	155334	18.65	29.6	30
		<i>Oithona</i> spp.	145032	17.96	27.5	57
		<i>Acartia</i> spp.	77857	15.31	23.1	80
ZS2	70	<i>Oithona</i> spp.	272518	21.64	27.1	27
		<i>Pseudocalanus</i> spp.	65249	14.67	17.8	45
		Bivalvia	69943	13.51	14.4	59
		Echinodermata larvae	23011	10.32	11.4	71
		Polychaeta	19825	10.04	11.1	82
ZS3	69	<i>Oithona</i> spp.	288470	22.24	35.4	35
		<i>Pseudocalanus</i> spp.	50495	14.07	21.6	57
		Echinodermata larvae	122192	13.26	14.5	72
		<i>Acartia</i> spp.	27304	10.45	13.9	85
ZS4	69	<i>Oithona</i> spp.	266628	21.87	42.4	42
		<i>Pseudocalanus</i> spp.	66167	14.65	27.3	70
		<i>Acartia</i> spp.	13490	8.30	12.0	82
ZS5	71	<i>Pseudocalanus</i> spp.	97424	16.23	40.1	40
		<i>Oithona</i> spp.	52955	12.98	29.5	70
		<i>Acartia</i> spp.	27236	11.43	26.2	96
ZS6	69	<i>Oithona</i> spp.	117107	17.96	26.9	27
		<i>Pseudocalanus</i> spp.	159284	18.42	26.1	53
		<i>Centropages abdominalis</i>	20234	10.30	12.9	66
		Bivalvia	35231	9.80	9.2	75
		<i>Podon</i> sp.	5511	6.78	7.1	82
ZS7	71	<i>Oithona</i> spp.	68148	14.78	26.5	26
		<i>Pseudocalanus</i> spp.	28420	11.78	20.6	47
		<i>Acartia</i> spp.	7694	8.16	13.1	60
		Polychaeta	6077	7.71	12.4	73
		Bivalvia	26783	9.09	10.7	83
ZS8	72	<i>Oithona</i> spp.	319316	23.36	44.9	45
		<i>Pseudocalanus</i> spp.	40784	13.60	24.8	70
		<i>Centropages abdominalis</i>	9823	8.41	12.6	82
ZS9	72	<i>Oithona</i> spp.	287057	22.34	58.6	59
		<i>Pseudocalanus</i> spp.	61166	14.54	36.1	95
ZS10	71	<i>Oithona</i> spp.	19097	11.02	25.4	25
		<i>Acartia</i> spp.	32704	11.57	24.7	50
		<i>Pseudocalanus</i> spp.	22317	11.10	24.2	74
		Polychaeta	124800	12.84	22.8	97
ZS11	74	<i>Oithona</i> spp.	72806	16.01	40.3	40
		<i>Pseudocalanus</i> spp.	6024	8.53	21.1	61
		<i>Metridia</i> sp. copepodites	6697	7.15	12.1	74
		Bivalvia	913	4.82	10.4	84
ZS12	73	<i>Oithona</i> spp.	112538	17.34	33.3	33
		<i>Pseudocalanus</i> spp.	26222	11.91	22.2	55
		Polychaeta	4314	7.53	13.5	69
		Cirripedia	3183	6.42	10.3	79
		Harpacticoida	3534	6.04	8.9	88
ZS13	71	<i>Pseudocalanus</i> spp.	139487	17.85	48.3	48
		<i>Acartia</i> spp.	76191	15.17	41.5	90

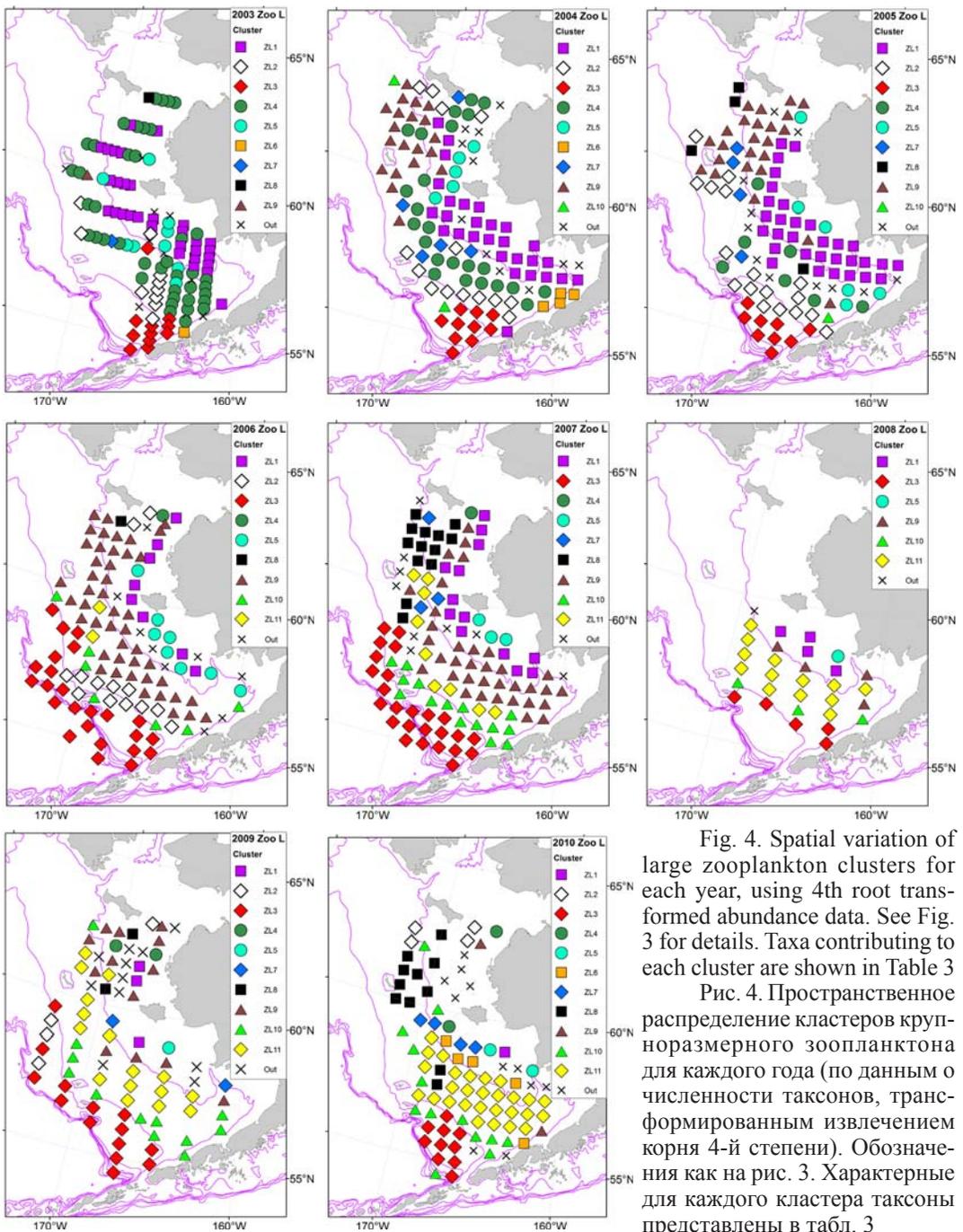


Fig. 4. Spatial variation of large zooplankton clusters for each year, using 4th root transformed abundance data. See Fig. 3 for details. Taxa contributing to each cluster are shown in Table 3
 Рис. 4. Пространственное распределение кластеров крупноразмерного зоопланктона для каждого года (по данным о численности таксонов, трансформированным извлечением корня 4-й степени). Обозначения как на рис. 3. Характерные для каждого кластера таксоны представлены в табл. 3

Spatial and temporal patterns of fish assemblages

Multivariate analyses of fish abundance identified 12 main clusters over the EBS shelf (Fig. 5). Taxa contributing to at least 80 % of within-cluster similarities are shown in Table 4. Similarities for stations within clusters ranged from 42–54 %, substantially lower than observed for zooplankton.

Fewer species clusters occurred over the shelf in the warm years of 2003–2005 as compared to the average and cold years of 2006–2010. Two main clusters, F1 and F2, dominated the species assemblages during the warm years with Pacific herring *Clupea pallasii* and walleye pollock contributing to 40 % and 69 % of the total abundance in those clusters, respectively. More species clusters, and therefore greater species diversity, characterized the average and

Table 3
Large zooplankton taxa that make up at least 80 % of similarity within a cluster, determined from SIMPER analysis conducted on 4th root transformed abundance data (no./m²). See Table 2 heading for details

Таблица 3

Кластеры, выделенные SIMPER-анализом данных по крупноразмерному планктону, трансформированных извлечением корня 4-й степени (Cluster); таксоны, обеспечивающие 80 % сходства в кластерах (Species) и их численность после трансформации (Abund 4th rt); уровни сходства между станциями внутри кластеров (Sim, %), вклад в сходство каждого таксона (Contrib, %) и совокупный вклад после включения таксона, от доминантных к субдоминантным (Cum, %). Также приведены данные о численности таксонов, не подвергнутые трансформации (Abund untrans, экз./м²)

Cluster	Sim, %	Species	Abund untrans	Abund 4th rt	Contrib, %	Cum, %
ZL1	65	<i>Parasagitta elegans</i>	360	3.90	21.3	21
		<i>Epilabidocera amphitrites</i>	181	3.27	18.2	39
		Cnidaria	409	3.44	17.1	57
		Caridea	148	2.96	15.1	72
		Gammaridae	42	1.97	8.8	80
ZL2	62	<i>Parasagitta elegans</i>	359	3.94	21.7	22
		Cnidaria	167	3.12	16.8	39
		<i>Calanus</i> spp.	181	3.13	16.3	55
		Appendicularia	807	2.93	10.8	66
		<i>Eucalanus bungii</i>	273	2.70	10.7	76
ZL3	69	<i>Limacina helicina</i>	211	2.42	9.8	86
		<i>Eucalanus bungii</i>	2395	6.42	16.7	17
		<i>Calanus</i> spp.	3250	6.49	15.8	33
		<i>Parasagitta elegans</i>	566	4.51	11.7	44
		<i>Metridia pacifica</i>	2281	5.40	11.4	56
ZL4	61	<i>Limacina helicina</i>	6109	5.92	10.6	66
		<i>Neocalanus</i> spp.	714	4.36	10.4	77
		Hyperiididae	449	3.98	10.0	87
		Cnidaria	225	3.12	28.6	29
		<i>Parasagitta elegans</i>	149	2.94	27.1	56
ZL5	64	Appendicularia	140	2.57	22.3	78
		<i>Epilabidocera amphitrites</i>	9	1.13	7.0	85
		Cnidaria	45	2.36	23.6	24
		<i>Epilabidocera amphitrites</i>	32	2.08	19.9	43
		<i>Parasagitta elegans</i>	30	2.00	18.5	62
ZL6	64	Caridea	37	2.09	18.0	80
		<i>Calanus</i> spp.	70	2.68	17.9	18
		<i>Parasagitta elegans</i>	72	2.49	15.9	34
		Brachyura	26	1.99	12.2	46
		Anomura	9	1.57	10.5	56
ZL7	65	Gammaridae	9	1.47	9.0	65
		Cnidaria	15	1.61	8.8	74
		Appendicularia	228	2.31	7.3	82
		<i>Parasagitta elegans</i>	433	4.18	27.8	28
		<i>Calanus</i> spp.	150	3.09	18.7	46
ZL8	69	Gammaridae	82	2.67	16.3	63
		Cnidaria	95	2.40	12.3	75
		Cumacea	18	1.54	7.6	83
		<i>Calanus</i> spp.	1413	5.56	26.5	27
		Appendicularia	856	4.81	22.7	49
ZL9	63	<i>Parasagitta elegans</i>	584	4.55	22.5	72
		Cnidaria	208	2.93	11.2	83
		<i>Parasagitta elegans</i>	739	4.84	33.0	33
		<i>Calanus</i> spp.	690	4.15	24.8	58
		Cnidaria	1040	4.22	22.9	81
ZL10	63	<i>Calanus</i> spp.	3400	6.54	29.5	29
		<i>Parasagitta elegans</i>	602	4.41	20.4	50
		<i>Eucalanus bungii</i>	187	2.87	11.0	61
		<i>Limacina helicina</i>	1184	3.37	9.7	71
		Hyperiididae	88	2.11	7.9	78
ZL11	70	Cnidaria	36	1.85	7.1	86
		<i>Calanus</i> spp.	6528	7.91	48.4	48
		<i>Parasagitta elegans</i>	870	5.11	32.4	81

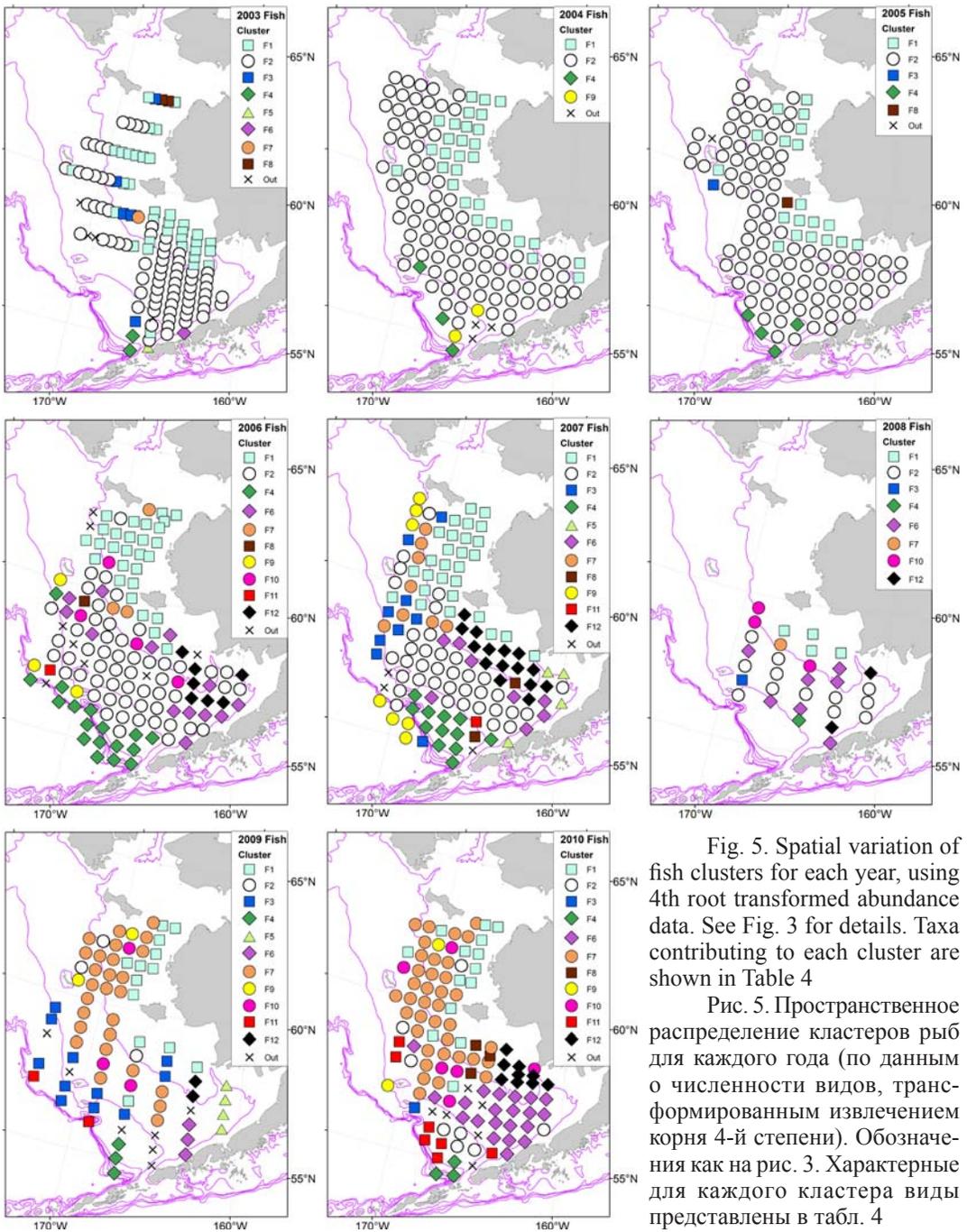


Fig. 5. Spatial variation of fish clusters for each year, using 4th root transformed abundance data. See Fig. 3 for details. Taxa contributing to each cluster are shown in Table 4

Рис. 5. Пространственное распределение кластеров рыб для каждого года (по данным о численности видов, трансформированным извлечением корня 4-й степени). Обозначения как на рис. 3. Характерные для каждого кластера виды представлены в табл. 4

cold years over the shelf. In 2010, 11 clusters occupied from 1 to 37 stations. Clusters F1-9 occurred in all temperatures stanzas, while Clusters F10-12 only occurred during average and cold years. All individual species (except Bering wolffish *Anarhichas orientalis*) comprising these cold year clusters were observed in all years, but occurred in unique species assemblages in the average and cold years.

Spatial distributions of species clusters were driven in part by physical oceanographic conditions. Water temperature directly affects distribution patterns, while the formation of strong fronts indirectly affects species' distributions. For example, the spatial extent of Cluster F1, dominated by Pacific herring, extended into the southern shelf but remained inshore of the 50 m isobath. Cluster F6, walleye pollock and Pacific cod *Gadus macrocephalus*, was patchily distributed along frontal boundaries in most years, then covered the middle domain of the south-

Table 4

Fish taxa that make up at least 80 % of similarity within a cluster, determined from SIMPER analysis conducted on 4th root transformed abundance data (no./km²). See Table 2 heading for details

Таблица 4

Кластеры, выделенные SIMPER-анализом данных по рыбам, трансформированных извлечением корня 4-й степени (Cluster); таксоны, обеспечивающие 80 % сходства в кластерах (Species) и их численность после трансформации (Abund 4th rt); уровни сходства между станциями внутри кластеров (Sim, %), вклад в сходство каждого таксона (Contrib, %) и совокупный вклад после включения таксона, от доминантных к субдоминантным (Cum, %). Также приведены данные о численности таксонов, не подвергнутые трансформации (Abund untrans, экз./км²)

Cluster	Sim, %	Species	Common name	Abund untrans	Abund 4th rt	Contrib, %	Cum, %
F1	48	<i>Clupea pallasii</i>	Pacific herring	5387	6.00	39.8	40
		<i>Oncorhynchus keta</i>	Chum salmon	177	2.68	18.0	58
		<i>Oncorhynchus tshawytscha</i>	Chinook salmon	32	1.70	11.1	69
		<i>Oncorhynchus gorbuscha</i>	Pink salmon	132	2.00	10.8	80
F2	52	<i>Gadus chalcogrammus</i>	Walleye pollock	77336	13.58	68.7	69
		<i>Clupea pallasii</i>	Pacific herring	385	2.18	6.3	75
		<i>Oncorhynchus nerka</i>	Sockeye salmon	228	2.15	6.0	81
F3	43	<i>Oncorhynchus gorbuscha</i>	Pink salmon	223	3.23	45.0	45
		<i>Oncorhynchus keta</i>	Chum salmon	63	2.35	33.2	78
		<i>Sebastes</i> spp.	Rockfish	219	1.52	5.7	84
F4	45	<i>Oncorhynchus keta</i> *	Chum salmon*	142	3.09	40.6	41
		<i>Oncorhynchus nerka</i> *	Sockeye salmon*	78	2.20	24.4	65
		<i>Zaprora silenus</i>	Prowfish	9	1.02	7.0	72
		<i>Pleurogrammus monopterygius</i>	Atka mackerel	116	1.30	6.9	79
F5	48	<i>Gadus chalcogrammus</i>	Walleye pollock	137	1.32	4.3	83
		<i>Trichodon trichodon</i>	Pacific sandfish	1527	5.82	60.2	60
		<i>Limanda aspera</i>	Yellowfin sole	102	2.46	18.4	79
F6	44	<i>Oncorhynchus nerka</i>	Sockeye salmon	68	1.63	8.2	87
		<i>Gadus chalcogrammus</i>	Walleye pollock	914	4.46	43.9	44
		<i>Gadus macrocephalus</i>	Pacific cod	751	3.85	32.7	77
F7	51	<i>Limanda aspera</i>	Yellowfin sole	16	1.07	4.4	81
		<i>Mallotus villosus</i>	Capelin	13615	7.58	65.0	65
		<i>Gadus chalcogrammus</i>	Walleye pollock	82	1.84	11.4	76
F8	43	<i>Clupea pallasii</i>	Pacific herring	121	1.81	9.1	86
		<i>Ammodytes hexapterus</i>	Pacific sandlance	904	4.05	84.3	84
F9	45	<i>Oncorhynchus keta</i> *	Chum salmon*	262	2.76	66.4	66
		<i>Gadus chalcogrammus</i>	Walleye pollock	51	1.53	17.3	84
F10	43	<i>Clupea pallasii</i>	Pacific herring	134	2.69	75.8	76
		<i>Limanda aspera</i>	Yellowfin sole	7	1.11	18.6	94
F11	54	<i>Sebastes</i> spp.	Rockfish	2170	6.09	51.4	51
		<i>Gadus chalcogrammus</i>	Walleye pollock	680	3.37	18.8	70
		<i>Zaprora silenus</i>	Prowfish	23	1.70	11.3	81
F12	42	<i>Limanda aspera</i>	Yellowfin sole	108	2.58	37.0	37
		<i>Anarhichas orientalis</i>	Bering wolffish	8	1.30	16.7	54
		<i>Oncorhynchus nerka</i>	Sockeye salmon	473	2.42	16.0	70
		<i>Ammodytes hexapterus</i>	Pacific sandlance	89	1.73	12.1	82

* Indicates immature and maturing salmon.

ern shelf in 2010. The influence of ACC waters over the EBS shelf is evident by the diversity of species clusters near Unimak Pass.

Walleye pollock were the dominant species collected over the time series, and occur in half of the species clusters, representing 4.3–69.0 % contribution based on total abundance. Species associations changed over time, with walleye pollock predominantly co-occurring with Pacific herring and sockeye salmon *Oncorhynchus nerka* (F2) in 2003–2008, but with capelin *Mallotus villosus* and Pacific herring (F7) in 2009–2010 as well as Pacific cod and yellowfin

sole *Limanda aspera* (F6) in 2010. Additional analysis of fish taxa across all stations combined indicate that similarities among taxa were generally low, however, close to 40 % similarity was seen between juvenile pink *O. gorbuscha* and chum *O. keta* salmon and close to 30 % for juvenile chinook *O. tshawytscha* and coho *O. kisutch* salmon and likewise for immature chum and sockeye salmon (data not shown).

Pacific herring co-occur with juvenile salmonids (F1) in nearshore waters during warm years. As water temperatures decrease, this assemblage retreats northward and is replaced by an assemblage comprised of capelin, walleye pollock, and Pacific herring (F7). This assemblage, which capelin comprise 65 % of, becomes the dominant forage fish group in 2010 spanning the 50 m isobath and middle shelf in the northern Bering Sea. Additionally, in the cold years, Pacific herring and yellowfin sole form a unique assemblage that occurs patchily along the 50 m isobath and into the middle shelf in 2009 and 2010.

Juvenile salmonids (less than ~ 300 mm fork length (FL)) predominantly occur in shallow nearshore waters with Pacific herring (F1), while juvenile pink and chum salmon also co-occur with rockfish (*Sebastes* spp.) (F3) further offshore. This assemblage is rare during the warm years, but more prevalent in the northwest region of the study area in 2007 and 2009. Immature and maturing salmon (> ~ 300 mm FL; F4 and F9) occur in the southern Bering Sea along the shelf break and near Unimak Pass. Occurrences were low in the warm years and later cold years, but more abundant in the intermediate years of 2006 and 2007 along the shelf break.

Overlap of zooplankton and fish communities

Warm year inner shelf communities of large zooplankton (Cluster ZL1) and fish (Cluster F1) were dominated by *P. elegans*, *E. amphitrites*, Cnidaria, Caridea, Gammaridea, Pacific herring, chum, chinook, and pink salmon. Warm year middle shelf communities (Clusters ZL4, ZL2, and F2) were dominated by *P. elegans*, Cnidaria, *Calanus* spp., Appendicularia, *E. bungii*, *L. helicina*, walleye pollock, Pacific herring, and sockeye salmon. For small zooplankton there was a single community (Cluster SL2) over the inner and middle shelves dominated by *Oithona* spp., *Pseudocalanus* spp., bivalvia larvae, echinoderm larvae, and polychaetes.

Inner shelf communities of small and large zooplankton were not consistent across average and cold years. Average and cold year inner shelf fish communities were also somewhat variable with Cluster F1 persisting in the north, and Cluster F12 dominated by yellowfin sole, Bering wolffish, sockeye salmon, and sandlance *Ammodytes hexapterus* present in two years (2007 and 2010) in the south. Middle shelf small zooplankton communities (Cluster ZS5) were dominated by *Pseudocalanus* spp., *Oithona* spp., and *Acartia* spp. and large zooplankton communities (Clusters ZL9 and ZL11) by *P. elegans*, *Calanus* spp., and Cnidaria. Middle shelf fish communities were dominated by Cluster F1 in 2006–2008, and by Cluster F7 dominated by capelin, walleye pollock, and Pacific herring in the north and Cluster F6 dominated by walleye pollock, Pacific cod, and yellowfin sole in the south in the coldest years (2009 and 2010).

On the southern outer shelf, communities (Clusters ZS4, ZL3, F4) remained fairly constant across years, although this was true for zooplankton more so than fish. Dominant taxa included *Oithona* spp., *Pseudocalanus* spp., *Acartia* spp., *E. bungii*, *Calanus* spp., *P. elegans*, *M. pacifica*, *L. helicina*, *Neocalanus* spp., Hyperiidea, immature chum, and sockeye salmon.

This paper represents a comprehensive portrayal of zooplankton and fish communities in the eastern Bering Sea across contrasting climate regimes. Late-summer surveys conducted from 2003–2010 demonstrate that zooplankton and fish assemblages are delineated by physical habitat properties (bathymetry) and influenced by water mass characteristics (temperature). The development of such information on faunal distributions and qualitative descriptions of paired environmental parameters will inform fisheries scientists and managers when tracking ecosystem responses to climate variability and changes in habitat availability. The type of community-level analyses presented here can elucidate ecosystem responses to environmental variability.

Spatial variations

The disparity between the influence of water temperature on zooplankton and fish assemblages between the northern and southern Bering Sea supports the hypothesis of a north/south

gradient in species composition. Even during late summer, water masses on the middle shelf were colder in the northern compared to the southern Bering Sea (Eisner et al., 2014). Assemblages in the northern Bering Sea may be more influenced by Arctic water masses and winter sea ice coverage. Species composition may be more limited due to harsher environmental conditions. The southern Bering Sea experiences wider temperature fluctuations and greater potential influx of species via ACC and Bering Slope currents (i.e., larval transport), contributing to greater species diversity. Total biomass of large zooplankton was fairly constant across climate regimes in the north, whereas in the south, biomass increased in cold years due to the large increase in *Calanus* spp. (Eisner et al., 2014). For fish communities, north-south variations appeared stronger in average and cold than in warm years due to a southern contraction of walleye pollock, southern expansion of capelin, and a northern contraction of juvenile Pacific salmon, with the exception of sockeye. Additionally, capelin may be centered further north than the northern boundary in this study (Andrews et al., in press), or further offshore and deeper in the water column (Parker-Stetter et al., 2013), potentially dampening the perceived effect of climate change on an abundant forage fish species.

Zooplankton (small and large) and fish communities in the current study varied considerably inshore to offshore. Water masses also varied across the shelf with warmer less saline water on the inner shelf and colder more saline water located further offshore (Danielson et al., 2011), although the coldest water was found in the middle shelf below the pycnocline (cold pool). Small zooplankton communities were more diverse nearshore than offshore with small invertebrate larvae (bivalves and echinoderms) and polychaetes as well as small copepods (*Oithona* spp., *Pseudocalanus* spp., and *Acartia* spp.) common in the inner and middle shelf, while communities on the outer shelf were mainly comprised of copepods. In general, large zooplankton were least diverse on the middle shelf compared to the inner and outer shelves, particularly in cold years, when the middle shelf was dominated by *Calanus* spp. and *P. elegans*. Fish communities appeared to have similar diversity inshore to offshore, but community composition varied considerably.

Juvenile Pacific salmon appear to have distinct distribution patterns. Individual species distributions are likely defined by outmigration timing, thermal conditions, and stock origin. There are two pulses of juvenile chum salmon originating from the Yukon River. Fall chum juveniles emerge from the river at an earlier date, are larger at the time of the survey, and are farther offshore than summer Yukon River chum juveniles (Farley et al., 2005). Juvenile sockeye salmon switch seaward migration routes via thermal gateways. In warmer years, they expand directly westward into the southern middle domain, placing them in direct proximity with age-0 walleye pollock. During colder years, they tend to avoid the cold pool by staying closer to the Alaska Peninsula in warmer, shallower waters (Farley et al., 2005). Juvenile Yukon River Chinook and coho salmon both tend to stay inshore of the 50 m isobath, their seaward migration route has been hypothesized to be southwesterly, along the western Alaska coastline (Farley et al., 2005). This may also be a reflection of their prey field distribution, with higher abundances of immature forage fishes in the nearshore environment. Juvenile pink salmon inside the 50 m isobath are most likely of western Alaska origin; however, those juveniles in the offshore domain in the northern Bering Sea are potentially of Russian origin.

Immature and maturing chum and sockeye salmon occur almost exclusively over the shelf break and up to the transition between the outer and middle domains. The fish are coming onto the shelf out of the basin. These fish are a conglomeration of Asian, Russian and Alaskan stocks, with the potential for an influx of Asian and Russian chums (Urawa et al., 2009) as well as Gulf of Alaska, Bristol Bay, and Asian sockeye salmon on the slope (Habicht et al., 2010). These are the areas where offshore prey resources are advected onto the shelf in high numbers (pteropods, larvaceans, and some species of large copepods ZL3, 8, and 10). This is an area of community structure that needs more information. Better genetic and age stock structure and diet information will better allow for the interpretation of these patterns.

Climate variations

Communities also varied between warm, and average and cold years. On the inner and middle shelves, zooplankton communities had greater numbers of large copepods (*Calanus*

spp.) and chaetognaths in cold years and greater numbers of small copepods (*Oithona* spp.) in warm years (Coyle et al., 2011; Eisner et al., 2014). Variations in small and large zooplankton taxa between warm and cold years were related to water temperature. Temperature below the pycnocline, an indication of spring sea ice, had the strongest relationship with large zooplankton community structure (Eisner et al., 2014). The increase in *Calanus* spp. in cold years may be related to the increased southerly extent of sea ice and availability of ice algae as an early spring food source promoting reproduction and growth (Baier and Napp, 2003; Sigler et al., 2013). On the outer shelf, large zooplankton communities varied less between climate regimes (Eisner et al., 2014). This is similar to observations for fish assemblages, with larger differences in species composition observed for the inner and middle shelf, compared to the outer shelf, which may be more insulated from interannual climate variability (Siddon et al., 2011). For small zooplankton, few species made up the bulk of abundance in average and cold years (Eisner et al., 2014), which is opposite of fish results where more species clusters were present in average and cold years. Variations in climate may also affect pelagic fish communities, either directly due to taxon-specific temperature tolerances, or indirectly by altering availability of prey resources or competitor and predator abundances.

The across shelf distribution of walleye pollock between warm and cold years is influenced by water temperature (e.g., the cold pool; Hollowed et al., 2012), zooplankton prey distributions (Siddon et al., 2013), currents (Danielson et al., 2012), and frontal boundaries (Duffy-Anderson et al., 2006). In warm years, the mean abundance of walleye pollock in surface waters was an order of magnitude greater than in cold years, which led to the dominance of this taxa in our surface community analysis for warm years (see Table 1). However, acoustic research suggests that walleye pollock were distributed deeper in the water column and further offshore in cold years (Parker-Stetter et al., 2013). Species co-occurring with walleye pollock varied with climate state, altering predator-prey dynamics and competition for resources. In warm years, walleye pollock dominated the species assemblages contributing nearly 70% by abundance. Conversely, in cold years, capelin abundance and spatial distribution increased, and co-occurred with walleye pollock on the inner and middle domains over the northern Bering Sea shelf. This spatial overlap increases predation risk and competition for prey (Hollowed et al., 2012), potentially affecting survival of age-0 walleye pollock in cold years. Thus, shifts in individual species distributions in response to environmental variability cause community-level changes in the ecosystem.

Other cross shelf distributional patterns may be less apparent. Pacific herring occurred in a number of community clusters in this analysis, appearing to blanket the entire middle and inner domain of the eastern Bering Sea. However, there may be differences between those Pacific herring occurring nearshore, and those that are farther offshore. Average Pacific herring length increases with distance from shore in the eastern Bering Sea (Andrews et al., in press). Fish cluster F1 persisted inside of the 50 m isobaths across thermal conditions, and had the highest abundance of Pacific herring. This is likely a reflection of spawn timing and the abundance of age-0 fish. Age structure within these assemblages may illuminate previously overlooked life history strategies, and would be a valuable future research priority.

Predator-prey dynamics

An evaluation of the overlap of zooplankton (prey) and fish within specific regions or climate regimes may help explain variations in fish physiology, growth, and survival. Pelagic fish may be able to alter their distribution to locate preferred zooplankton prey, provided they can remain within habitat tolerances (for example optimal temperature ranges; Mueter et al., 2011). Climate change prompted a greater response from capelin than in Pacific herring. This may be due to a shorter, more efficient food chain, which produced a shorter linkage between capelin, their prey field and thermal conditions. Capelin stocks in both the Pacific and Atlantic sub-arctic have experienced displacement following changes in thermal conditions, in either spawning location, forage location, or both (Rose, 2005). While capelin have a range of thermal tolerances (most often -1.5 to 6.0 °C, but are found in waters up to 14 °C (Rose, 2005)) that would allow them to occupy much of the Bering Sea, they tended to more closely mirror the distribution of their prey field. Capelin first appeared in our community clusters in 2006, concurrent with the

southern expansion of *Calanus* spp. (ZL9 in 2006–2007 and ZL11 in 2007–2010) and euphausiids (Ressler et al., 2012), both of which comprise large proportions of the diet in eastern Bering Sea capelin (Andrews et al., in press). Alternatively, forage fish diets may reflect the available prey within specific preferred habitats or locations. In the southeastern Bering Sea, diets of age-0 walleye pollock and juvenile salmon reflect changes in zooplankton prey availability, with more small copepods consumed in warm years and more large copepods and chaetognaths in average and cold years (Coyle et al., 2011). Consumption of euphausiids also increased in cold years (Coyle et al., 2011), which may relate to the higher availability of this prey as shown by acoustic studies (Ressler et al., 2012). Additionally, during warm conditions, large lipid rich prey items have been reduced and age-0 walleye pollock become a large portion of the diet in many fishes, such as juvenile salmon (Moss et al., 2009; Coyle et al., 2011), Pacific herring (Andrews et al., in press), and age-0 Pacific cod (Farley et al., 2014). These lipid-rich (higher energy) prey items contributed to greater overwinter survival of walleye pollock and recruitment to age-1 during cold years (bottom-up control; Heintz et al., 2013). In warm years, the lack of these prey items in the water and in fish diets, resulted in lower fish energy densities and reduced age-1 recruitment, even though high abundances were seen in surface waters during the preceding summer.

Conclusions

Community analysis of zooplankton and fish in the eastern Bering Sea provides insights into environmental factors regulating abundances and distributions of multiple species and multiple trophic levels (i.e., ecosystems). Our analysis demonstrated that communities vary by oceanographic shelf domain, characterized by specific bathymetry and temperature ranges. Climatic effects on single fish species have been well documented (i.e., Farley et al., 2007; Farley and Moss, 2009; Ianelli et al., 2011), but multi-species evaluations are more limited (Mueter and Litzow, 2008). Upcoming research includes advanced statistical analysis on the effects of environmental variation (climate and oceanographic factors) on community structure within specific shelf domains. The current study provides groundwork for future evaluations of juvenile fishes with respect to habitat, environmental conditions, and prey resources during the critical late summer period (prior to overwintering) in the eastern Bering Sea.

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References

- Andrews A.G. III, Strasburger W.W., Farley E.V. Jr. et al.** Effects of warm and cold climate conditions on capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*) in the eastern Bering Sea // Deep-Sea Res. II (in press).
- Baier C.T. and Napp J.M.** Climate-induced variability in *Calanus marshallae* populations // J. Plankton Res. — 2003. — Vol. 25. — P. 771–782.
- Brander K.M., Blom G., Borges M.F. et al.** Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? // ICES Mar. Sci. Symp. — 2003. — Vol. 219. — P. 260–273.
- Clarke K.R. and Gorley R.N.** PRIMER v6: user manual/tutorial. — Plymouth : PRIMER-E, 2006.

- Clarke K.R. and Warwick R.M.** Change in marine communities: an approach to statistical analysis and interpretation. 2nd ed. — Plymouth : PRIMER-E, 2001.
- Coachman L.K.** Circulation, water masses, and fluxes on the southeastern Bering Sea shelf // Cont. Shelf Res. — 1986. — Vol. 5(1–2). — P. 23–108.
- Coyle K., Eisner L., Mueter F. et al.** Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the Oscillating Control Hypothesis // Fish. Oceanogr. — 2011. — Vol. 20(2). — P. 139–156.
- Coyle K.O. and Pinchuk A.I.** Climate-related differences in zooplankton density and growth on the inner shelf of the southeastern Bering Sea // Prog. Oceanogr. — 2002. — Vol. 55. — P. 177–194.
- Coyle K.O., Pinchuk A.I., Eisner L.B. and Napp J.M.** Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: the potential role of water column stability and nutrients in structuring the zooplankton community // Deep-Sea Res. II. — 2008. — Vol. 55. — P. 1775–1791.
- Danielson S., Eisner L., Weingartner T. and Aagaard K.** Thermal and haline variability over the central Bering Sea shelf: Seasonal and interannual perspectives // Cont. Shelf Res. — 2011. — doi:10.1016/j.csr.2010.12.010.
- Danielson S., Weingartner T., Aagaard K. et al.** Circulation on the central Bering Sea shelf, July 2008 to July 2010 // J. Geophys. Res. — 2012. — Vol. 117. — C10003, doi:10.1029/2012JC008303.
- Duffy-Anderson J.T., Busby M.S., Mier K.L. et al.** Spatial and temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea shelf 1996–2000 // Fish. Oceanogr. — 2006. — Vol. 15. — P. 80–94.
- Eisner L., Napp J., Mier K. et al.** Climate-mediated changes in zooplankton community structure for the eastern Bering Sea // Deep-Sea Res. II. — 2014. — doi: 10.1016/j.dsr2.2014.03.004.
- Farley E., Murphy J., Adkison M. and Eisner L.** Juvenile sockeye salmon distribution, size, condition and diet during years with warm and cool spring sea temperatures along the eastern Bering Sea shelf // J. Fish Biol. — 2007. — Vol. 71(4). — P. 1145–1158.
- Farley E.V. and Moss J.H.** Growth rate potential of juvenile chum salmon on the eastern Bering Sea shelf: an assessment of salmon carrying capacity // North Pacific Anadr. Fish Comm. Bull. — 2009. — Vol. 5. — P. 265–277.
- Farley E.V., Heintz R.A., Andrews A.G. and Hurst T.P.** Size, diet, and condition of age-0 Pacific Cod (*Gadus macrocephalus*) during warm and cool climate states in the eastern Bering Sea // Deep-Sea Res. II. — 2014. — doi:10.1016/j.dsr2.2014.12.011.
- Farley E.V. Jr., Murphy J.M., Wing B.W. et al.** Distribution, migration pathways, and size of western Alaska juvenile salmon along the eastern Bering Sea shelf // Alsk. Fish. Res. Bull. — 2005. — Vol. 11(1). — P. 15–26.
- Gibson G.A., Coyle K.O., Hedstrom K. and Curchitser E.N.** A modeling study to explore on-shelf transport of oceanic zooplankton in the Eastern Bering Sea // J. Mar. Sys. — 2013. — Vol. 121. — P. 47–64.
- Habicht C., Seeb L.W., Myers K.W. et al.** Summer-fall distributions of stocks of immature sockeye salmon in the Bering Sea as revealed by single-nucleotide polymorphisms // Trans. Am. Fish. Soc. — 2010. — Vol. 139(4). — P. 1171–1191.
- Heintz R.A., Siddon E.C., Farley E.V. Jr. and Napp J.M.** Correlation between recruitment and fall condition of age-0 walleye pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions // Deep-Sea Res. II. — 2013. — Vol. 94. — P. 150–156.
- Hollowed A.B., Barbeaux S.J., Cokelet E.D. et al.** Effects of climate variations on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea // Deep-Sea Res. II. — 2012. — Vol. 65–70. — P. 230–250.
- Hunsicker M., Ciannelli L., Bailey K.M. et al.** Functional responses and scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts // Ecol. Lett. — 2011. — doi: 10.1111/j.1461-0248.2011.01696.x.
- Hunt G.L. Jr. and Stabeno P.J.** Climate change and the control of energy flow in the southeastern Bering Sea // Prog. Oceanogr. — 2002. — Vol. 55. — P. 5–22.
- Hunt G.L. Jr., Coyle K.O., Eisner L. et al.** Climate impacts on eastern Bering Sea foodwebs: A synthesis of new data and an assessment of the Oscillating Control Hypothesis // ICES J. Mar. Sci. — 2011. — doi:10.1093/icesjms/fsr036.
- Hunt G.L. Jr., Stabeno P.J., Walters G. et al.** Climate change and control of the southeastern Bering Sea pelagic ecosystem // Deep-Sea Res. II. — 2002. — Vol. 49. — P. 5821–5853.
- Ianelli J.N., Hollowed A.B., Haynie A.C. et al.** Evaluating management strategies for eastern Bering Sea walleye pollock (*Theragra chalcogramma*) in a changing environment // ICES J. Mar. Sci. — 2011. — Vol. 68(6). — P. 1297–1304.
- Iverson R.L., Coachman L.K., Cooney R.T. et al.** Ecological significance of fronts in the southeastern Bering Sea // Ecological Processes in Coastal and Marine Systems. — N.Y. : Plenum Press, 1979. — P. 437–466.

Levin P.S., Fogarty M.J., Murawski S.A. and Fluharty D. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean // PLoS Biol. — 2009. — Vol. 7(1), e1000014. doi:10.1371/journal.pbio.1000014.

Link J., Bundy A., Overholtz W.J. et al. Ecosystem-based fisheries management in the Northwest Atlantic // Fish and Fish. — 2011. — Vol. 12. — P. 152–170.

Miss J.H., Farley E.V., Feldman A.M. and Ianelli J.N. Spatial distribution, energetic status, and food habits of eastern Bering Sea age-0 walleye pollock // Trans. Am. Fish. Soc. — 2009. — Vol. 138. — P. 497–505.

Mueter F.J. and Litzow M.A. Sea ice retreat alters the biogeography of the Bering Sea continental shelf // Ecol. Appl. — 2008. — Vol. 18(2). — P. 309–320.

Mueter F.J., Hunt G.L. Jr. and Litzow M.A. The Eastern Bering Sea shelf: a highly productive seasonally ice-covered sea // ICES CM2007/D:04. — 2007. — P. 1–10.

Mueter F.J., Ladd C., Palmer M.C. and Norcross B.L. Bottom-up and top-down controls of walleye pollock (*Theragra chalcogramma*) on the Eastern Bering Sea shelf // Prog. Oceanogr. — 2006. — Vol. 68. — P. 152–183.

Mueter F.J., Siddon E.C. and Hunt G.L. Jr. Climate change brings uncertain future for subarctic marine ecosystems and fisheries // North by 2020: Perspectives on Alaska's Changing Social-Ecological Systems. — Fairbanks : Univ. of Alaska Press, AK, 2011. — P. 329–357.

Overland J.E. and Stabeno P.J. Is the climate of the Bering Sea warming and affecting the ecosystem? // EOS Trans. Am. Geophys. Union. — 2004. — Vol. 85(33). — P. 309–312.

Parker-Stetter S.L., Horne J.K., Farley E.V. et al. Summer distributions of forage fish in the eastern Bering Sea // Deep-Sea Res. II. — 2013. — Vol. 94. — P. 211–230.

Perry A.L., Low P.J., Ellis J.R. and Reynolds J.D. Climate change and distribution shifts in marine fishes // Science. — 2005. — Vol. 308. — P. 1912–1915.

Ressler P.H., De Robertis A., Warren J.D. et al. Developing an acoustic survey of euphausiids to understand trophic interactions in the Bering Sea ecosystem // Deep-Sea Res. II. — 2012. — Vol. 65–70. — P. 184–195.

Rose G.A. Capelin (*Mallotus villosus*) distribution and climate: a sea «canary» for marine ecosystem change // Ices J. Mar. Sci. — 2005. — Vol. 62. — P. 1524–1530.

Siddon E.C., Duffy-Anderson J.T. and Mueter F.J. Community-level response of larval fish to environmental variability in the southeastern Bering Sea // Mar. Ecol. Prog. Ser. — 2011. — Vol. 426. — P. 225–239.

Siddon E.C., Kristiansen T., Mueter F.J. et al. Spatial match-mismatch between juvenile fish and prey explains recruitment variability across contrasting climate conditions in the eastern Bering Sea // PLoS ONE. — 2013. — Vol. 8(12), e84526. doi:10.1371/journal.pone.0084526.

Sigler M.F., Stabeno P.J., Eisner L.B. et al. Spring and fall phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea, during 1995–2011 // Deep-Sea Res. II. — 2013. — doi: 10.1016/j.dsr2.2013.12.007.

Spencer P.D. Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfish // Fish. Oceanogr. — 2008. — Vol. 17. — P. 396–410.

Stabeno P., Napp J., Mordy C. and Whitley T. Factors influencing physical structure and lower trophic levels of the eastern Bering Sea shelf in 2005: Sea ice, tides and winds // Prog. Oceanogr. — 2010. — Vol. 85. — P. 180–196.

Stabeno P.J., Farley E.V., Kachel N.B. et al. A comparison of the physics of the northern and southern shelves of the eastern Bering Sea and some implications for the ecosystem // Deep-Sea Res. II. — 2012a. — Vol. 65–70. — P. 14–30.

Stabeno P.J., Kachel N.B., Moore S.E. et al. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem // Deep-Sea Res. II. — 2012b. — Vol. 65–70. — P. 31–45.

Urawa S., Sato S., Crane P.A. et al. Stock-specific ocean distribution and migration of chum salmon in the Bering Sea and north Pacific Ocean // North Pacific Anadr. Fish Comm. Bull. — 2009. — Vol. 5. — P. 131–146.

Volkov A.F. Recommendations for Expedited Zooplankton Sample Processing at Sea. — Vladivostok : TINRO, 1984. — 31 p (in Rus.).

Volkov A.F. The Results of Zooplankton Studies in the Bering Sea under the NPAFC Program (BASIS Expedition). Part 1. Eastern Areas // Russian J. Mar. Biol. — 2012. — Vol. 38(7). — P. 474–494.

Volkov A.F., Efimkin A.Y. and Kuznetsova N.A. Characteristics of the plankton community of the Bering Sea and several regions of the North Pacific in 2002–2006 // Izv. TINRO. — 2007. — Vol. 151. — P. 338–364 (in Rus.).

Walsh J.J. and McRoy C.P. Ecosystem analysis in the southeastern Bering Sea // Cont. Shelf Res. — 1986. — Vol. 5. — P. 259–288.

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