



Responses of a pelagic fish community to reduced fishing pressure in the central Bering Sea

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ABSTRACT: Ecosystem-based fishery management (EBFM) requires minimizing the risk of irreversible change to a natural assemblage of species. Because pelagic fisheries modify the biotic community rather than the physical environment and often target migratory species, the pelagic community can be expected to respond quickly after fishing pressure is reduced. We monitored the pelagic zooplanktivore community over 4 decades in the central Bering Sea before and after the closures of large-scale pelagic fisheries. We found a quick and steep change in the pelagic fish community structure after fishing pressure was reduced, which reflected increased abundance of salmon species; however, walleye pollock stocks, one of the most valuable fisheries resources in this area, have not recovered. A lower population growth rate might contribute to the slow recovery of pollock stocks. Long-term ecosystem monitoring of fishing grounds and surrounding ecosystems will be required for successful implementation of EBFM of pelagic fish stocks.

KEY WORDS: Fishing closure · Community structure · Planktivores · Pelagic fisheries · Long-term monitoring · High seas · Ecosystem-based fishery management · Bering Sea

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1. INTRODUCTION

Ecosystem-based fishery management (EBFM) requires minimizing the risk of irreversible change to the natural assemblage of species and ecosystem processes (Pikitch et al. 2004). In a vulnerable ocean ecosystem, fisheries should be sustained by careful management with consideration for ecosystem structure and dynamics. Because bottom fishing gear such as bottom trawls or dredges can substantially modify substrate properties and benthic community structure, recovery of the demersal fish community and its habitat can take a long time (Kaiser et al. 2002, Pusceddu et al. 2014). On the other hand, pelagic fisheries affect only the fish stocks caught in the gear and not the habitat itself. Therefore, one might expect a short recovery time for a fish community after a reduction in pelagic fishery pressure. However, long-term observations of fish communities

before and after pelagic fishery closures are not widely available.

The Bering Sea is one such place where there have been long-term observations of fish communities before and after fisheries closures. The Bering Sea is a semi-enclosed, high-latitude sea located between Asia and North America and is divided in area almost equally between the central deep basin (maximum depth 3500 m) and the continental shelf (<200 m) (Stabeno et al. 1999, see Fig. 1). The highly productive eastern shelf supports one of the richest fisheries in the world and its ecosystem has been well studied (e.g. Van Pelt et al. 2016). In contrast, the basin area in the central Bering Sea (CBS) is an iron-limited, high-nutrient, low-chlorophyll region and has much lower primary production than shelf waters (Aguilar-Islas et al. 2007). Nevertheless, a large biomass of micronekton-/zooplankton-feeding Pacific salmon *Oncorhynchus* spp. and walleye pollock *Gadus chalcoides*

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cogrammus migrate seasonally or opportunistically into the basin area (Wespestad 1993, Myers et al. 1996, Mito et al. 1999, Davis et al. 2009).

The high-seas area (international waters) in the CBS is surrounded by the Russian and US exclusive economic zones (EEZs; see Fig. 1). The high-seas area historically supported a Japanese mothership driftnet salmon fishery and an international pollock mid-water trawl fishery. The mothership driftnet salmon fishery developed after 1952. At its maximum, the salmon fishery caught 12.1 million (count) salmon in 1959 in the Bering Sea (INPFC 1979). In the 1980s, a trawl fishery began targeting pollock in the high-seas area, catching 1.45 million t of pollock in 1989 at its maximum (Wespestad 1993). Since 1993 in the CBS, directed high-seas fishing for salmon has been prohibited and a moratorium on the pollock fishery has been in place because of low stock biomass (Wespestad 1993, NPAFC 2016). Ianelli et al. (2018a) recently reported that the biomass of walleye pollock in the Bogoslof region, which is estimated to be 60% of the basin stock, has not yet fully recovered.

Salmon and pollock fisheries in the eastern and western Bering Sea have continued under management by coastal nations in their respective EEZs. The coastal and in-river total catch of Pacific salmon increased from the 1980s to the 1990s and attained and remained at historically high levels in the 2000s and 2010s (Irvine & Fukuwaka 2011, NPAFC 2019). Ocean climate changes, indexed by the Aleutian Low Pressure Index (ALPI) or Pacific Decadal Oscillation (PDO), were linked to an increase in salmon stocks (Beamish & Bouillon 1993, Mantua et al. 1997). Improved hatchery techniques increased the number of salmon juveniles released from hatcheries, particularly chum salmon releases from hatcheries in Japan and Russia and pink salmon releases from hatcheries in central Alaska (Irvine & Fukuwaka 2011, Ruggerone & Irvine 2018). In summer, Asian chum salmon migrate into the Bering Sea, while pink salmon from central Alaska migrate in the Gulf of Alaska (Takagi et al. 1981, Urawa et al. 2018). In the eastern Bering Sea, the estimated total allowable catch of walleye pollock in 2020 was 1792 thousand t (Ianelli et al. 2018b), which remains one of the largest fisheries in the world.

After the 1950s, observers and scientists aboard Japanese research vessels monitored the status of salmon stocks in the North Pacific and Bering Sea. After 1971, a standardized research gillnet design was utilized aboard these vessels to catch a wide range of salmon body sizes (Takagi 1975). Secondly, the nets also caught a variety of pelagic species

including walleye pollock. Observations of these catches provide us with a unique opportunity to analyze temporal changes in the pelagic fish community during and after the fishery closures. The purpose of our study was to (1) describe the temporal pattern of species composition, (2) evaluate effects of fishing, hatchery releases of Asian chum salmon, and ocean climate on the pelagic fish community, and (3) discuss the effect of fishing closures on the CBS pelagic fish community, including target species of fisheries.

2. MATERIALS AND METHODS

2.1. Data sources

Japanese salmon research vessels surveyed the abundance of Pacific salmon and other species from 1972–2010 using a standardized research gillnet in the North Pacific Ocean and Bering Sea. The research gillnet consisted of panels (tans; each tan about 50 m long) of 10 different mesh sizes (48, 55, 63, 72, 82, 93, 106, 121, 138, and 157 mm) to catch all sizes of salmon (Takagi 1975). The research gillnet was usually set at the surface to ca. 7 m depth at 16:00 h in the afternoon and was retrieved at 04:00 h the next morning. Sea surface temperature (SST) was measured when the net was set. After removal from the gear, the number of salmon and other species was counted. The survey data were collected annually in June and July in the CBS (53–60° N, 170° E–175° W) from 1972–2010 (Fig. 1). After removal of incomplete data, 815 gillnet operations

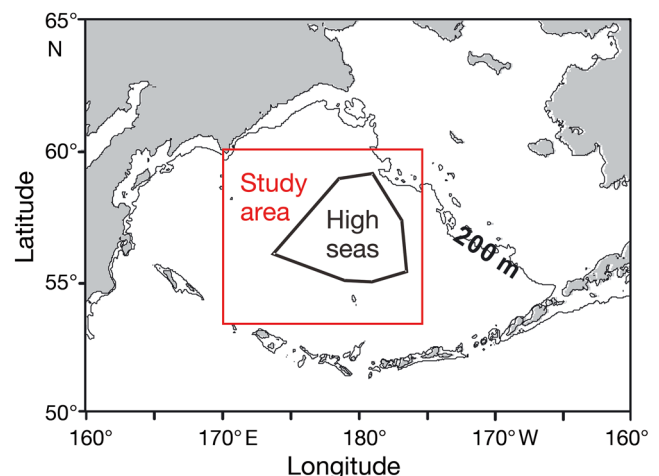


Fig. 1. Bering Sea, showing the study area (red rectangle) in the central basin, including the area of international waters of the high seas (inside the thick black line). Thin line: 200 m isobath

were analyzed. The number of individuals by fish or squid species and the total count of seabirds (aggregated species) caught per 1.5 km of research gillnet (catch per unit effort; CPUE) was estimated. We limited the species for our analyses to those where the total number caught was >1000 during the study period. The species included sockeye *Oncorynchus nerka*, chum *O. keta*, pink *O. gorbusha*, and Chinook salmon *O. tshawytscha*, Dolly Varden *Salvelinus malma*, walleye pollock, Atka mackerel *Pleurogrammus monopterygius*, eight-armed squid *Gonatopsis borealis*, and aggregated seabird species (short-tailed *Puffinus tenuirostris* and sooty shearwaters *P. griseus*, thick-billed murre *Uria lomvia*, horned puffin *Fratercula corniculata*, and others). All these species are micronekton/zooplankton predators.

Commercial salmon fishery effort data were obtained for high-seas mothership operations conducted east of 170° E in the North Pacific and Bering Sea from 1972–1992. Fishing effort was estimated as the total number of tans (panels) of commercial driftnet (1 tan: ca. 50 m in length, 121–130 mm in mesh size) fished each year by the fleet. These data were compiled by the International North Pacific Fisheries Commission (INPFC 1975–1996; www.npafc.org/inpfc).

Asian chum salmon hatchery releases were the total number released from Japanese, Russian, and Korean hatcheries. These data were compiled by the North Pacific Anadromous Fish Commission (NPAFC; www.npafc.org). For the correlation analysis, we lagged the number of hatchery releases by –1 yr because most hatchery-released Asian chum salmon migrate into the CBS in the summer of their second (and subsequent) years at sea (Urawa et al. 2018).

We selected large-scale climate forcing indices related to ecosystem regime shifts in the North Pacific and Bering Sea following Litzow et al. (2014). Data

were averages for the winter season or average of the year with a –1 year lag time (Table 1). The El-Niño–Southern Oscillation Index (MEI) annual mean value was lagged by –1 yr to account for delay of the signal to the study region.

2.2. Statistical analyses

To analyze annual differences in species composition of pelagic fish, we used distance-based redundancy analysis (dbRDA; Legendre & Legendre 2012) on the salmon research vessel data. We transformed the CPUE data using $\log(\text{CPUE} + 1)$ to remove the effect of large differences in abundance between dominant and rare species. The Bray-Curtis dissimilarity index was used as the distance measure in the dbRDA. Factor constraints were year and 10 d periods (i.e. early, middle, or late June or July), and a continuous constraint was SST at each fishing operation. We analyzed only the main effects of these variables. The significance of each term in the dbRDA was assessed using a permutation test. We used the ‘vegan’ package in R v.4.0.2 for these analyses (Oksanen et al. 2019, R Core Team 2020).

To extract annual changes in species composition, we used the partial dbRDA (pdbRDA), where effects of constraint variables other than survey year can be removed (Legendre & Legendre 2012). To quantify annual changes in species composition from the pdbRDA, we used the centroid of scores of fishing operations each year on the first and second canonical axes (pdbRDA1 and pdbRDA2, respectively). The significance of autocorrelation coefficients for pdbRDAs was estimated under the assumption of a moving average model (Hamilton 1994). To examine lagged relationships between pdbRDAs and environ-

Table 1. Large-scale climate forcing indices related to regime shifts in the North Pacific and Bering Sea that were used to characterize the physical environment in the study area

Climate index	Season (months)	Variable used	Source
Pacific Decadal Oscillation (PDO)	Winter (November–March)	Mean value for winter months	http://research.jisao.washington.edu/pdo
North Pacific Gyre Oscillation (NPGO)	Winter (November–March)	Mean value for winter months	http://www.o3d.org/npgo
Arctic Oscillation (AO)	Winter (January–March)	Mean value for winter months	https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml
Pacific–North American Pattern (PNA)	Winter (January–March)	Mean value for winter months	https://www.cpc.ncep.noaa.gov/products/precip/CWlink/ENSO/veri/new.pna.shtml
North Pacific Index (NPI)	Winter (December–February)	Mean value for winter months	https://climatedataguide.ucar.edu/climate-data/north-pacific-np-index-trenberth-and-hurrell-monthly-and-winter
El-Niño–Southern Oscillation Index (MEI)	Annual (12 mo)	Annual mean value lagged by –1 yr	https://www.psl.noaa.gov/enso/mei.old/

mental factors, we used cross-correlation analysis. To avoid cross-correlation bias caused by multiplicity, we limited the number of lags to less than 10 % of the time series, i.e. to 3 yr (Olden & Neff 2001). Significance of the cross-correlation coefficient of pdbRDAs with driftnet fishing effort, hatchery releases, or climate indices was estimated after adjusting autocorrelations of variables using the modified Chelton method (Pyper & Peterman 1998).

3. RESULTS

3.1. Temporal pattern of species composition

Research survey data from 1972–2010 showed there were large CPUEs of salmon and diminishing CPUEs of pollock in the pelagic ecosystem of the CBS during June and July (Fig. 2a,b). CPUEs of chum and sockeye salmon were high in the first half of the 1980s and in the 1990s–2000s (Fig. 2a). Walleye pollock CPUEs peaked in the first half of the 1980s, decreased in the late 1980s, and were very small in the 1990s and 2000s (Fig. 2b). CPUE of pink salmon fluctuated in a biennial cycle, i.e. higher in odd-numbered years than in even-numbered years. Pink salmon CPUEs in odd-numbered years were large in the 1990s to 2000s, which was similar to other salmon species (Fig. 2a,b). CPUEs of Chinook salmon and aggregated seabird species were larger in the 1990s and 2000s than in previous decades (Fig. 2a,c).

Species composition of the pelagic fish community in the CBS depended on survey year and 10 d periods, and species composition was also correlated with SST (Fig. 3; $p < 0.001$). These variables jointly explained 47.5% of the total variation of dissimilarity among fishing operations. Considered independently, survey year explained 39.4%, 10 d period explained 14.8%, and SST explained 9.7% of the total variation. The first (dbRDA1) and second (dbRDA2) axes explained 18.4 and 13.1 %, respectively (i.e. 31.4 % jointly).

A negative score on dbRDA1 meant large abundances of walleye pollock, while a positive score meant large abundances of salmon species. A negative score on dbRDA2 meant large abundances of pink salmon, while a positive score meant large abundances of walleye pollock and chum and sockeye salmon. SST corre-

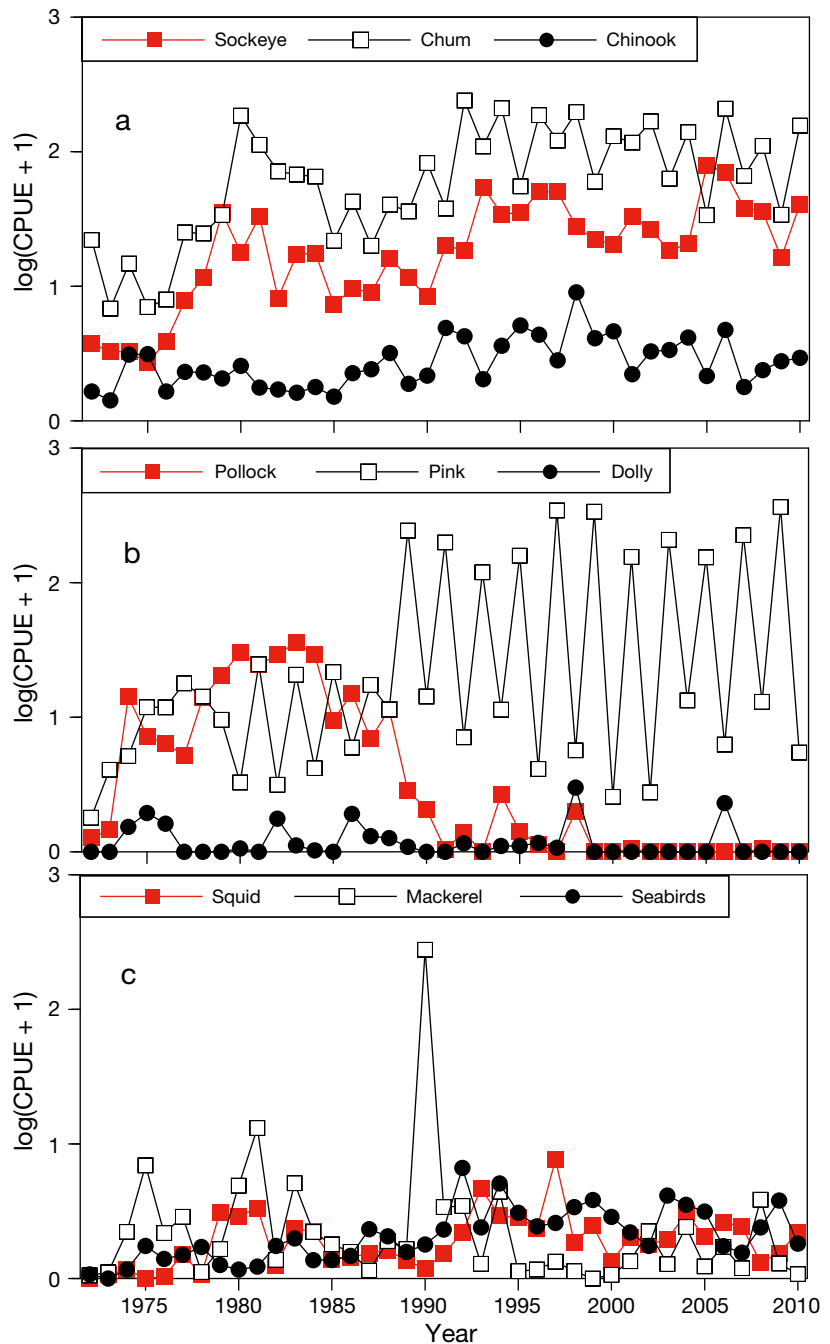


Fig. 2. Annual log-transformed mean number of organisms caught per 1.5 km of research gillnet (catch per unit effort; CPUE) in the central Bering Sea basin during June and July, 1972–2010. Time series are displayed for (a) sockeye, chum, and Chinook salmon; (b) walleye pollock, pink salmon, and Dolly Varden; and (c) eight-armed squid, Atka mackerel, and aggregated seabird species

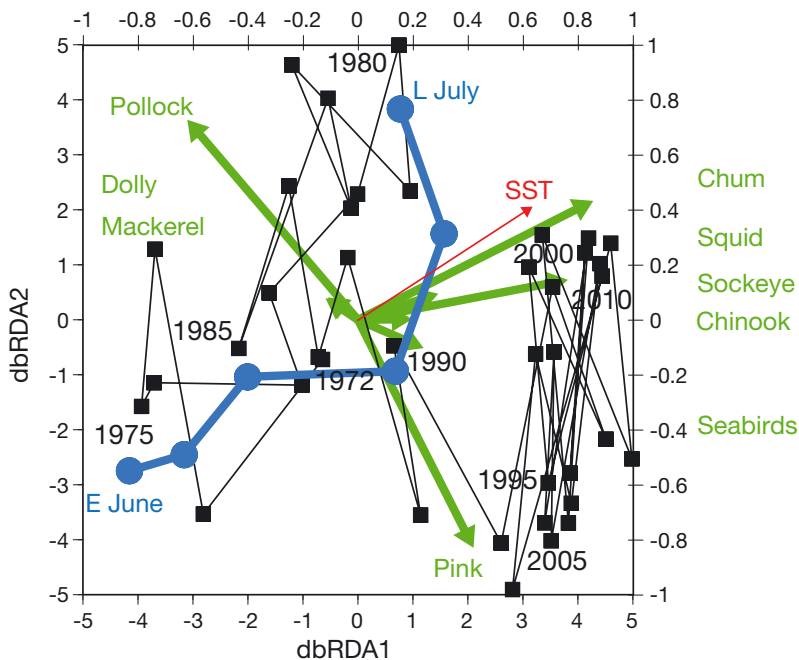


Fig. 3. Triplot summarizing results of distance-based redundancy analysis (dbRDA) for the pelagic fish community in the central Bering Sea during June and July, 1972–2010. Green: species scores on the bottom and left-handed axes; blue: centroids of site scores for 10 d period of the survey; black: centroids of site scores for years of the survey; red: constraint for sea surface temperature in the top and right-handed axes

lated positively both with dbRDA1 and dbRDA2. Generally, the 10 d period shifted from negative scores to positive scores through the season on both axes. Survey years prior to 1991 had lower scores on dbRDA1 than more recent years, which reflected large abundances of walleye pollock in the 1970s and 1980s and salmon species in the 1990s and 2000s. Odd-numbered years had generally lower scores on dbRDA2 than even-numbered years, which reflected large abundances of pink salmon in odd-numbered years.

We extracted 2 series of annual changes in species composition using the pdbRDA by controlling for the effect of 10 d period and SST within a season (Fig. 4a). Survey year explained 30.1% of the total variation after controlling for the other explanatory variables. Centroid scores for pdbRDA1 (representing species composition by year) were negative in 1972 and 1973, positive in 1974–1990 except for 1989, and negative in 1991–2010. This indicated a regime shift

Fig. 4. (a) Annual changes of centroids of site scores from results of the partial distance-based redundancy analysis (pdbRDA) for the pelagic fish community in the central Bering Sea during June and July, 1972–2010; (b) annual changes of the number of tans (panels) of commercial drift gillnets (1 tan: ca. 50 m in length) used in the high seas area east of 170° E in the North Pacific and Bering Sea, and the number of hatchery releases of Asian chum salmon with -1 yr lag

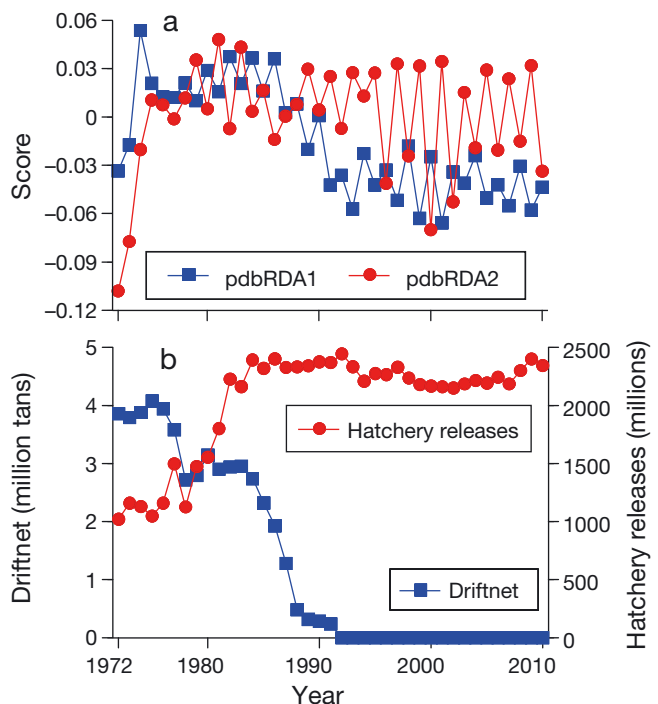
between 1990 and 1991. Scores for pdbRDA2 showed a biennial cycle, and the difference between odd- and even-years was larger after 1996 than before.

3.2. Effects of fishing, hatchery releases, and ocean climate on the pelagic fish community

During the study period, fishing effort decreased from the 1970s to the 1990s, while hatchery releases of Asian chum salmon increased from the late 1970s to the early 1980s (Fig. 4b). In the middle of the 1970s, the commercial driftnet fishing effort was ca. 4 million tans yr⁻¹. Effort was reduced to less than 3 million tans by the late 1970s, decreased steeply in the latter half of the 1980s, and was zero by 1992 when the fishery closed. Asian chum salmon hatchery releases were stable in the early 1970s, increased from the late 1970s to the early 1980s, and

were stable afterward at levels between 2000 and 2500 million.

Extracted annual changes in species composition of the pelagic fish community were correlated with



themselves and with fishing effort at a time lag, but not with hatchery releases or climate indices (Table 2). Autocorrelation coefficients of pdbRDA1 were positive in -1 to -3 yr lags, which indicates slow, low-frequency changes in species composition (Fig. 4a). After adjusting the degrees of freedom considering these autocorrelations, pdbRDA1 positively correlated with driftnet effort with -1 and -2 yr lags. The pdbRDA2 positively autocorrelated with a -2 yr lag, indicating the biennial cycle of this series (Fig. 4a). No significant correlations were observed between pdbRDA2 and driftnet effort or between pdbRDA2 and hatchery releases or climate indices.

4. DISCUSSION

4.1. Effect of fishing closures on the CBS pelagic fish community

The pelagic fish community structure in the CBS quickly and steeply changed after fishing pressure

Table 2. Auto- and cross-correlation coefficients of annual changes in centroids of site scores from the partial distance-based redundancy analysis (pdbRDA). These data reflect the correlations between the pelagic fish community during the summer (June and July) and the number of panels of commercial driftnet used (driftnet) in the central Bering Sea, hatchery releases of Asian chum salmon (hatchery), and climate indices: the Pacific Decadal Oscillation index (PDO); North Pacific Gyre Oscillation (NPGO); Arctic Oscillation (AO); multivariate El Niño–Southern Oscillation Index (MEI); Pacific–North American Pattern (PNA); North Pacific Index (NPI), 1972–2010. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns: $p \geq 0.05$

	Lags (years)			
	0	-1	-2	-3
pdbRDA1 (acf)	1	0.678***	0.758***	0.554*
vs. Driftnet	0.762 ^{ns}	0.830*	0.867*	0.808 ^{ns}
vs. Hatchery	-0.406 ^{ns}	-0.518 ^{ns}	-0.615 ^{ns}	-0.590 ^{ns}
vs. PDO	0.214 ^{ns}	0.167 ^{ns}	0.041 ^{ns}	-0.069 ^{ns}
vs. NPGO	-0.046 ^{ns}	-0.040 ^{ns}	0.011 ^{ns}	0.004 ^{ns}
vs. AO	-0.191 ^{ns}	-0.210 ^{ns}	-0.292 ^{ns}	-0.291 ^{ns}
vs. MEI	-0.042 ^{ns}	-0.018 ^{ns}	-0.124 ^{ns}	-0.198 ^{ns}
vs. PNA	-0.003 ^{ns}	0.047 ^{ns}	-0.062 ^{ns}	0.034 ^{ns}
vs. NPI	-0.172 ^{ns}	-0.078 ^{ns}	0.014 ^{ns}	-0.020 ^{ns}
pdbRDA2 (acf)	1	-0.097 ^{ns}	0.463**	-0.324 ^{ns}
vs. Driftnet	-0.140 ^{ns}	0.006 ^{ns}	0.123 ^{ns}	0.176 ^{ns}
vs. Hatchery	0.272 ^{ns}	0.087 ^{ns}	-0.060 ^{ns}	-0.162 ^{ns}
vs. PDO	0.240 ^{ns}	0.257 ^{ns}	0.040 ^{ns}	-0.020 ^{ns}
vs. NPGO	-0.128 ^{ns}	-0.077 ^{ns}	-0.085 ^{ns}	0.038 ^{ns}
vs. AO	-0.003 ^{ns}	-0.000 ^{ns}	-0.016 ^{ns}	-0.116 ^{ns}
vs. MEI	0.241 ^{ns}	0.203 ^{ns}	0.026 ^{ns}	-0.043 ^{ns}
vs. PNA	0.193 ^{ns}	0.059 ^{ns}	0.086 ^{ns}	-0.053 ^{ns}
vs. NPI	-0.143 ^{ns}	-0.168 ^{ns}	0.082 ^{ns}	-0.060 ^{ns}

was reduced. This change did not correlate with either climate indices or hatchery releases of chum salmon. All species of pelagic fish and seabirds in the community can be reduced by target or incidental catches of the driftnet fishery. However, responses to climate indices or hatchery releases of chum salmon may differ among species. For example, responses in fish production were different among species after the 1989 regime shift, as indexed by the North Pacific Index (NPI) or ALPI in the Bering Sea and northeast Pacific (Benson & Trites 2002). Chum salmon abundance can increase from hatchery releases, but responses of other species to chum hatchery releases may differ among species through species interactions with chum salmon. Therefore, closure of the driftnet fishery, to which most species of the CBS pelagic fish community similarly respond, may have a strong effect on temporal changes in the community. We think steep changes in the pelagic fish community would not be expected if the gillnet fishery continued.

The population growth rate of species likely affects the response time after reducing fishing pressure. Since the early 1990s, the stock status of walleye pollock in the CBS has been at a low level, while populations of pink, chum, and sockeye salmon have increased. Salmon species have relatively short life spans of about 2–6 yr (Farley et al. 2018, Radchenko et al. 2018, Urawa et al. 2018). Walleye pollock live on average about 9 yr, and 21 yr is the record for oldest age (Wespestad 1993). Walleye pollock migrate into the CBS after age 5, after years of living on the shelf and in coastal areas where they are subject to being caught in fisheries. Walleye pollock in the major spawning ground near the Bogoslof Islands are much older than pollock in the eastern Bering Sea (Ianelli et al. 2018a). The size and fecundity of walleye pollock in the Aleutian Basin are lower than pollock caught on the continental shelf (Hinckley 1987). A lower reproductive rate and a longer life span might be the cause for the slower recovery of walleye pollock than salmon species in the CBS.

Interspecific competition for food can depress populations of plankton feeders. In the CBS, recent large abundances of pink salmon reduced zooplankton abundance and induced a trophic cascade in the ocean pelagic ecosystem (Shiomoto et al. 1997, Batten et al. 2018). Interspecific competition can reduce the somatic growth rate or nutritional condition of salmon and seabirds (Ruggerone & Nielsen 2004, Toge et al. 2011, Springer et al. 2018, Morita & Fukuwaka 2020). Pollock consume copepods, euphausiids, and fish, which is similar to what salmon eat (Mito et al. 1999, Davis et al. 2009, Coyle et al.

2011). In the central Baltic Sea, after the collapse of piscivorous Atlantic cod *Gadus morhua* stocks, increased zooplanktivorous sprat *Sprattus sprattus* stocks depressed zooplankton biomass and competed with zooplanktivorous cod larvae, which may have hindered cod recovery (Casini et al. 2009). Therefore, interspecific competition among plankton feeders cannot be ruled out as a cause of the long recovery time of walleye pollock after the closure of the pollock fisheries in the CBS.

Walleye pollock not only compete with salmon for prey; pollock are preyed upon by salmon and other pollock. Age-0 walleye pollock were the most widely distributed forage fish and an important nekton prey for salmon species in the Bering Sea (Brodeur et al. 1999, Davis et al. 2009). During warm years, age-0 pollock dominated in the diet of larger predatory fish, including salmon species and older pollock, which may have led to poor recruitment of pollock stock on the Bering Sea shelf (Coyle et al. 2011). Quick increases of salmon stocks after the fishing closure might have depressed pollock stock abundances through competition for prey and by salmon consumption of pollock. However, even if salmon stocks had not increased after the fishery closure, the recovery of pollock stock abundances would still need a long time because of the low population growth rate of pollock.

4.2. Other factors affecting the pelagic fish community

Temporal autocorrelations in fish community structures are plausible because past species abundances can affect current abundances. Except for ca. 1 yr for pink salmon and eight-armed squid (Roper et al. 2010, Radchenko et al. 2018), some fish species have multi-year life spans, and their individuals can occur in the CBS over several years. For species with a multi-year life span, the strength of year-classes and fishing pressure may determine abundances during several years of ocean life. Past abundance may affect present abundance through reproduction. The biennial cycle of the pelagic fish community may reflect the spawner–recruit relationship of pink salmon, whose abundance of odd-numbered year classes is larger than even-numbered year classes (Radchenko et al. 2018).

Our results showed hatchery releases of Asian chum salmon were not correlated with the annual change in the pelagic fish community in the CBS. Increases in hatchery releases from the late 1970s to

the early 1980s did not coincide with increases in salmon abundance in research gillnet catches in the CBS during the early 1990s. However, increased hatchery releases could potentially contribute to increased salmon abundance through increases of young salmon entering into the CBS. The catch efficiency of the research gillnet was higher for larger salmon than smaller ones (Fukuwaka et al. 2008). Because the commercial fishery targeted larger salmon using gillnets with 121–130 mm mesh size, it cannot be ruled out that we might overestimate the effect of fishing effort and underestimate the effect of Asian chum salmon hatchery releases on temporal changes of pelagic fish community in the CBS.

Ocean climate likely affects the pelagic fish community, although we failed to detect a statistically significant effect of large-scale atmospheric climate indices on annual changes in the pelagic community composition in the CBS. In the demersal ecosystems of the Northwest Atlantic, temporal changes in fishing pressure related more strongly with changes in fish species composition than climate indices (Shackell et al. 2012). However, ocean climate affects the regional atmospheric and oceanographic environment (Hurrell 1995, Mantua et al. 1997). Temporal changes in environmental factors were found to control the fish community more than fishing in demersal ecosystems of the Northeast Atlantic (ter Hofstede et al. 2010, Mérillet et al. 2020). Global warming affected species richness of demersal fish through elevated bottom temperature (ter Hofstede et al. 2010). Ocean climate indirectly affects productivity of pink and chum salmon stocks around the North Pacific through regional ocean environmental factors, such as coastal precipitation or water temperature (Fukuwaka et al. 2011). Ocean climate may produce indirect effects through regional ocean conditions that affect the pelagic fish community structure in the CBS. In the CBS pelagic community, perhaps climate factors were mitigated, which produced statistically insignificant relationships between climate indices and species composition in our results.

We found significant effects of water temperature and 10 d period on the pelagic fish community structure. While the effect of 10 d period could be caused by phenological changes in fish community when water temperature is elevated during early to mid-summer, the effect of water temperature may be explained by the selection of thermal habitat or changes in phenological migration timing. Salmon and seabirds are long-distance migrants in the Pacific Ocean. Immature chum and sockeye salmon migrate seasonally between

the Bering Sea in summer and the North Pacific in winter (Urawa et al. 2018, Farley et al. 2018). Distribution of salmon is strongly affected by thermal habitat in the open ocean (Morita et al. 2010). Annual changes in migration timing to natal rivers for maturing salmon are affected by ocean climate as indexed by the PDO (Kovach et al. 2015). Seasonal abundance of pelagic seabirds is related to the marine climate in the Gulf of Alaska (Thompson et al. 2012). While our data, which was collected over only 2 mo of the year, may have been too short-term to have detected phenological changes in the pelagic community structure, changes in water temperature can affect the pelagic community structure through changing ocean distribution and migration timing of fish and seabird species.

4.3. Implications of EBFM for pelagic fish stocks in high-seas fisheries

Pelagic fisheries may have less of an impact on ocean ecosystems than bottom fisheries because pelagic fisheries modify the pelagic fish community but not their environment, such as seawater properties or the zooplankton community. In this study, the CBS pelagic fish community responded quickly after reducing fishing pressure. However, pelagic fisheries target highly mobile and often migratory species. Migratory species utilize the particular pelagic ecosystem for a limited period of time. For example, salmon species spawn in freshwater habitats around the North Pacific and utilize the open ocean during the immature and maturing stages. Immature chum and sockeye salmon migrate seasonally and utilize the CBS in summer and fall (Farley et al. 2018, Urawa et al. 2018). Walleye pollock spawn on the shelf or slope areas and some migrate into the CBS basin area (Wespestad 1993). Shearwaters breed on ocean islands in the South Pacific and utilize the CBS as a feeding ground (Springer et al. 2018). An inclusive evaluation of the impacts of pelagic fisheries may need to assess surrounding ecosystems outside of the fishing grounds. A global or international policy for EBFM should be developed to manage and conserve such migratory species because these species move beyond single management jurisdictions (Malick et al. 2017, Dunn et al. 2019).

We could not evaluate the impact of pelagic fisheries on higher trophic levels due to the small number caught in research vessel catches in the CBS (e.g. Dall's porpoise *Phocoenoides dalli*, N = 15; salmon shark *Lamna ditropis*, N = 14). However, large-bodied top predators have a strong effect on ocean eco-

system function and structure (Estes et al. 2016). Top-down control tends to be stronger in colder-water ocean ecosystems (Boyce et al. 2015). To evaluate the impact of pelagic fisheries on the whole ocean ecosystem, other survey methods, such as visual observations of marine mammals, would be needed. Reduction in the abundance of top predators could potentially have a large impact on ecosystem function in the CBS by decreasing predation on zooplanktivores.

Even though pelagic fisheries do not modify the ocean habitat in the same way that bottom fisheries do, long-term monitoring of ocean ecosystems is required for EBFM of pelagic fish stocks. This information is necessary if we are to evaluate the effects of stock removals on the ecosystem and have realistic expectations for recovery of stocks after fishing effort has been substantially reduced or fisheries closed.

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