

Fluctuations of Pelagic Fish Populations in Relation to the Climate Shifts in the Far-East Regions

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ABSTRACT: Based on a time series of ocean climate indices and catch records for seven pelagic fish species in the Tsushima Warm Current (TWC) and Kuroshio-Oyashio Current (KOC) regions from 1910 to 2004, we detected regional synchrony in the long-term fluctuations of the fish populations and identified alternation patterns of dominant species related to climate shifts. The annual catches of Pacific herring, Japanese sardines, Japanese anchovies, jack mackerel, chub mackerel, Pacific saury and common squid in the TWC region fluctuated in phase with those in the KOC region, which suggests that they were controlled by the same basin-wide climate forcing. After the collapse of the herring fishery, the alternation sequence was: sardines (1930s), Pacific saury, jack mackerel, common squid and anchovies (1950s~1960s), herring (late 1960s~early 1970s), chub mackerel (1970s) and then sardines (1980s). As sardine biomass decreased in the late stages of the cool regime, catch of the other four species increased immediately during the warm period of the 1990s. Regional differences in the amplitude of long-term catch fluctuations for the seven pelagic fishes could be explained by regional differences in availability, fishing techniques and activity.

Key words: Abundance, Alternation, Climate shifts, Kuroshio-Oyashio Current, Migration circuit, Pelagic fish, Synchrony, Tsushima Warm Current

INTRODUCTION

Climate fluctuations influence marine ecosystems (Trenburth and Hurrell 1994, Polovina et al. 1995, Yatsu et al. 2005). In the 20th century, climate regimes in the North Pacific have lasted about 25 to 35 years. Regime shifts occurred around 1890, 1925, 1947 and 1976 (Minobe 1997). These regime shifts, indicated by the sea surface temperature (SST), are almost synchronized with changes in Pacific Decadal Oscillation (PDO) and Arctic Oscillation (AO) (Thompson and Wallace 2000a, 2000b, Yasunaka and Hanawa 2002). The abundance of sardines was related to climate changes in separate regions in the Pacific (Kawasaki 1983, 1991). Research on catch trends for fish populations around the world suggest some degree of local rather than remote synchrony (Freon et al. 2003).

Some pelagic fish species such as sardines, anchovies and chub mackerel show large variance in their spatial ranges due to alternating expansions and contractions. For example, the abundance of sardine increases in the Northwest Pacific when local waters are cool and more productive, whereas it increases in the eastern boundary current systems off California and Peru when those regions are

warm and less productive (Chavez et al. 2003, Bakun and Broad 2003). Alternation of dominant fish species were observed in the western and eastern boundary current systems (Ogawa and Nakahara 1979, Fukushima and Ogawa 1988, Matsuda et al. 1991, 1992, Watabe 1992a, 1992b, Kawasaki 1993, McCall 1996, Schwartzlose et al. 1999, Klyashtorin 2001). It was suggested that chub mackerel and sardine were abundant in the waters off Japan during cold periods, while jack mackerel and anchovies were abundant during warm periods (Ogawa and Nakahara 1979, Yatsu et al. 2005). However, the related mechanisms are not well known. Many pelagic fishes have large distribution ranges and migrate northward to feed in spring-summer and southward to spawn in autumn-winter in the north-western Pacific (KOC) and its adjacent regions. However, it is not clear whether these fish species are controlled by the same climate changes in the two regions or not.

The objectives of this study were 1) to investigate relationships between changes in oceanic conditions in the Tsushima Warm Current (TWC) and the Kuroshio-Oyashio Current (KOC) regions, which are influenced by climate shifts, and the alternation of dominant pelagic fish species inhabiting the regions, and 2) to demonstrate synchrony between the two regions in catch trends of

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fishes and homogeneity in fish population structures in the two regions. The TWC region covers the Yellow Sea, the East China Sea and the East/Japan Sea, and the KOC region covers the Northwest Pacific including Seto-Inland and the Okhotsk Sea.

MATERIALS AND METHODS

Time series of climate indices such as the Southern Oscillation Index (SOI), the Monsoon Index (MOI), the North Pacific Index (NPI), the Arctic Oscillation Index (AOI) and the Pacific Decadal Oscillation (PDO) index (Tian et al. 2006), and time series for oceanic conditions such as anomalies of temperature, location of oceanic fronts and zooplankton biomass (Odate 1994, Uehara and Mitani 2004, Sugisaki 2006) were obtained to examine changes in ocean climate in the distribution ranges of seven pelagic fish species. Time series of catch by region (TWC, KOC) for seven pelagic fishes in the Far-East during the 20th century were compiled based on the annual Reports of Fishery Statistics of Korea, Japan, China, Russia and Taiwan, the national fish catch reports for FAO area 61, Northwest Pacific and previous reports on catch records (Table 1).

Year-to-year catch per unit fishing effort (CPUEs) were compared with the catch for each species from the Korean fishing fleet in the last 25 years to see if the catch series can be regarded as indices of fluctuation of population abundance. Responses of the fish species to the ocean climatic changes were explained in relation to life history, spatial distribution and habitat of the species (Table 2). The migration circuits of each species were examined with respect to ocean current systems. Alternation of dominant species

and basin-scale synchrony in the long-term fluctuations of the seven species were detected from time series of the estimated abundances (catches) from 1910~2004. Possible factors explaining the regional differences in the long-term abundance trend were summarized based on the life history, climate factors and fishing methods for the seven species.

RESULTS

Ocean Climate Changes

Abrupt climatic changes in 1976/77 were common among the SOI, NPI, PDO and AOI and changes in the late 1980s were found in the MOI, PDO and AOI. Changes in the late 1990s were found in all five indices. Thermal conditions shifted from warm to cool regimes in the Northwest Pacific in the mid 1920s and mid 1970s in association with the climate shifts as seen in the North Pacific Index (PDO), the First Oyashio Intrusion (FOI) and sea temperature anomalies with a time lag of several years in the TWC region (Figs. 1 and 2). The anomalies of upper layer temperatures and estimated zooplankton biomass in the TWC and KOC regions were lower in the 1980s and higher than average in the 1990s (Fig. 3).

Current Mediated Migration Circuits

Based on comparisons of migration circuits and spatial distributions of the seven fish species with the ocean current systems in the Northwest Pacific (KOC region) and its adjacent regions (TWC regions), we postulate that the larvae and juveniles can be transported to the nursery and feeding grounds by the northward warm

Table 1. Summary of catch data sources for 7 pelagic fish species in the Far-East

NO.	Common name	Scientific name	Fishing country	Time	Catch data sources
1	Pacific herring	<i>Clupea pallasii</i>	K, J, C, R	1870~2004	①, ②, ③, ⑨, ⑩
2	Japanese sardine	<i>Sardinops melanostictus</i>	K, J, C	1910~2004	①, ②, ③, ⑦
3	Japanese anchovy	<i>Engraulis japonicus</i>	K, J, C, T	1910~2004	①, ②, ③, ⑧
4	Jack mackerel	<i>Trachurus japonicus</i>	K, J, T, R	1953~2004	①, ②, ③
5	Chub mackerel	<i>Scomber japonicus</i>	K, J, C, T, R	1926~2004	①, ②, ③
6	Pacific saury	<i>Cololabis saira</i>	K, J, R, T	1921~2004	①, ②, ③, ④, ⑤
7	Common squid	<i>Todarodes pacificus</i>	K, J, T	1895~2004	①, ②, ③, ⑥

Note; 1. K (Korea, Rep. of), J (Japan), C (China), T (Taiwan), R (Russia).

2. Catches for the period of 1952~2004 are divided into two regions (TWC, KOC). TWC region covers the East China Sea, Yellow Sea and East/Japan Sea and KOC region covers the Northwest Pacific including the Okhotsk Sea and Seto Inland.

① Year books of Fisheries Statistics of Korea (Rep. of) and Japan, ② FAO Yearbooks of Fisheries Statistics, ③ Chikumi (1985) The fish resources of the northwest Pacific, ④ Gong (1984), ⑤ Gong and Suh (2004), ⑥ Gong et al. (2006), ⑦ Zhigalin and Belayev (1999), ⑧ Wada and Jacobson (1998), ⑨ Park (1976), ⑩ Hanamura (1963).

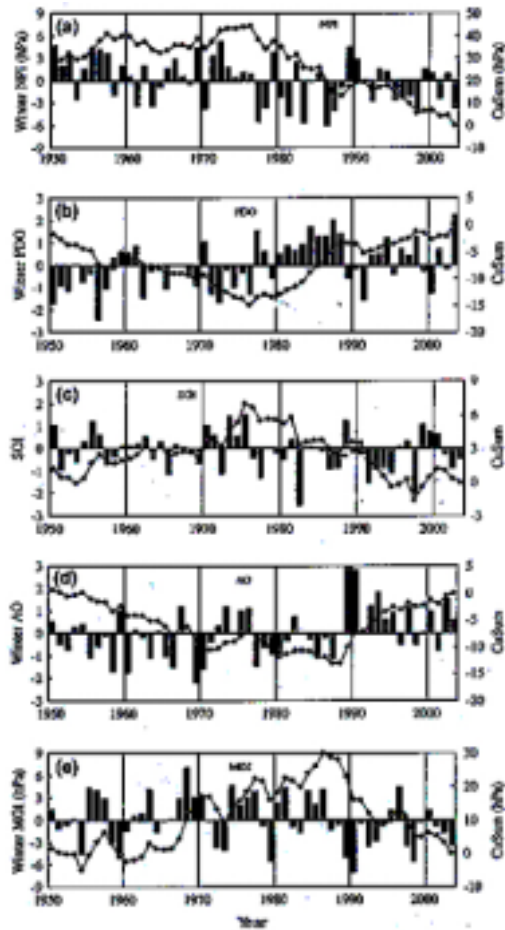


Fig. 1. Anomaly values (vertical bars) and their cumulative sums (CuSum, solid circles) for five climate indices from 1950 to 2003: (a) Winter North Pacific Indices (NPI); (b) Winter Pacific Decadal Oscillation (PDO); (c) Annual Southern Oscillation Index (SOI); (d) Winter Arctic Oscillation Index (AOI); (e) Winter Asian Monsoon Index (MOI) (After Tian et al. 2006).

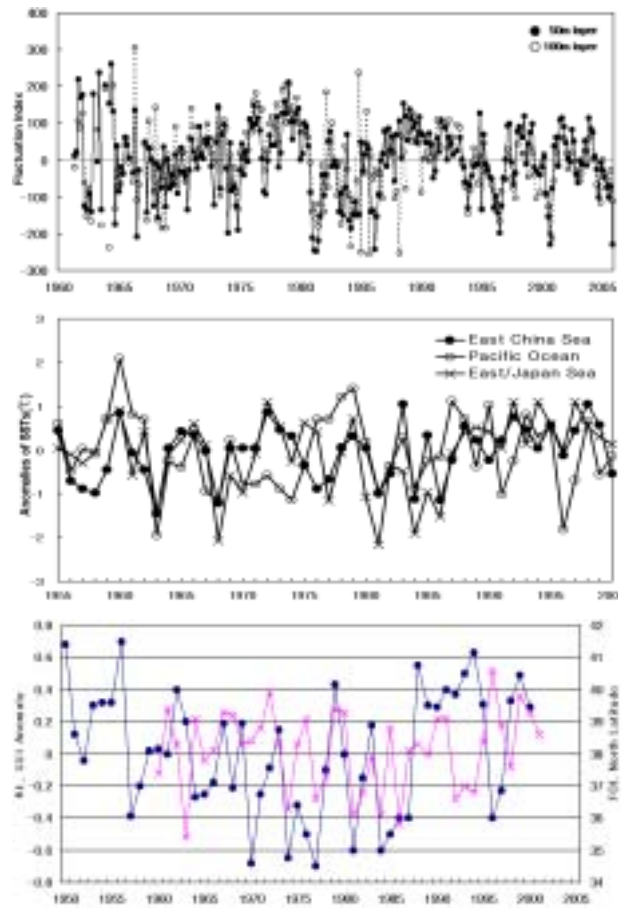


Fig. 2. Fluctuation indices of subsurface (50, 100 m) temperature in the southwestern East/Japan Sea (34°30'N~38°30'N, 128°30'~133°30'E) (top): Anomalies of winter SSTs in the East China Sea (30°N, 126°E), western Pacific (34°N, 138°E) and southeastern East/Japan Sea (35°N, 131°E) (Uehara and Mitani 2004) (middle); Anomalies of winter SST in the Kuroshio Extension (KE) (dot) and position of southern limit of First Oyashio Intrusion (FOI) (cross) (bottom).

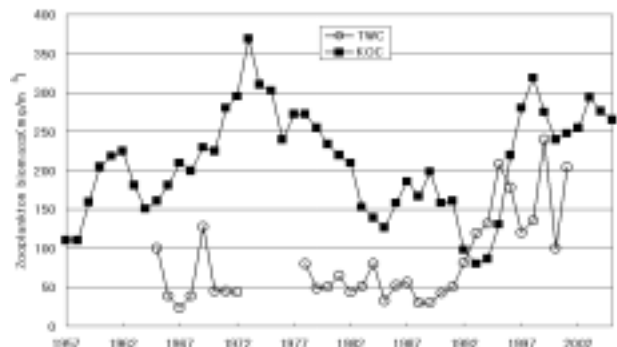
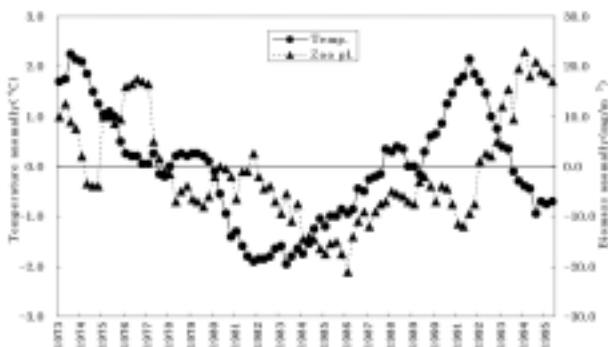


Fig. 3. Anomalies of integrated mean (0~150 m) temperatures (dot) and zooplankton biomass along PM line (36°N, 136°E~41°N, 132°E) (triangle) (Minami et al. 1999) (top); Year-to-year zooplankton biomass in the southwestern East/Japan Sea (34°30'N~38°30'N, 128°30'E~133°30'E) (NFRDI 1964~2005) (circle) and in the Oyashio region (rectangle) (revised from Odate 1994 by Sugisaki 2006) (bottom).

currents, while the adults may migrate denatantly with the cold current systems in the north and then contranatanly against the warm warmcurrent to the spawning grounds (Figs. 4 and 5, Table 2).

Abundance Indices

The time series of catch per unit fishing effort (CPUE) for the 7 pelagic fishes were shorter than those of catch by each fishing country. The time series of CPUEs and catch for the 7 fishes from Korean fishing records for the period of 1980~2004 had the same patterns, and were significantly positively correlated ($r=0.70\sim 0.80$, $p<0.01$, $n=25\sim 26$) (except Japanese anchovies, $r=-0.29$, $n=26$). Therefore, the time series of catch for each species were employed as indices of long-term fluctuations in the population abundance (Fig. 6).

Alternation of Dominant Species

During the period 1910~2004, an orderly alternation (replacement) of dominant pelagic fish was observed in the Northwest Pacific (TWC and KOC regions combined) (Figs. 7 and 8). After the collapse of the herring fishery in the late 1920s, the sardine dominated in the 1930s, four other species (Pacific saury, jack mackerel, common squid, anchovy) in the 1950s~1960s, herring again in the late 1960-early 1970s, chub mackerel in the 1970s and then the sardine again in the 1980s. As sardine biomass decreased in association with the climate shifts, catch of the four other species increased immediately in the warm regime from the late 1980s to the 1990s. The dominant period of each species or set of species lasted for 10~20 years (Figs. 7 and 8).

Regional Differences in the Long-term Fluctuations of Catches

In some cases, the amplitude (catch) of the long-term fluctuations of the species showed regional differences (Figs. 7 and 8, Table 3). Significant differences in catches for the Pacific herring and Pacific saury ($KOC>TWC$) and for the jack mackerel ($KOC<TWC$) were observed during the entire periods of catch records. The catch of Pacific sardine and chub mackerel during the first abundant periods showed the same patterns but different regional amplitude in the second abundant periods. The catch of common squid in the KOC region decreased earlier than that of TWC region in the early 1970s (Figs. 7 and 8, Table 3).

DISCUSSION

Climate Shifts

The climate variability in the late 1970s attracted much attention among fisheries scientists, when a deep Aleutian Low, warmer sea surface temperatures (SSTs) in the eastern North Pacific and cooler SSTs in the central and western middle latitude were replaced with

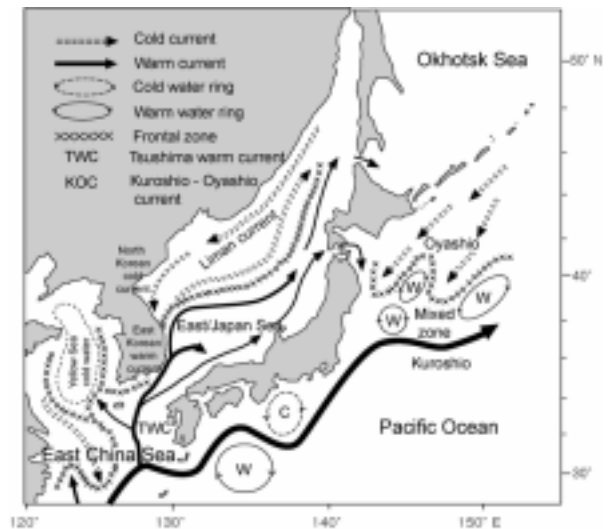


Fig. 4a. Schematic current systems in the Far Eastern waters. The TWC (Tsushima Warm Current) region covers the East/Japan Sea, East China Sea and Yellow Sea, and the KOC (Kuroshio-Oyashio Current) region covers the northwestern Pacific including the Okhotsk Sea and Seto Inland.

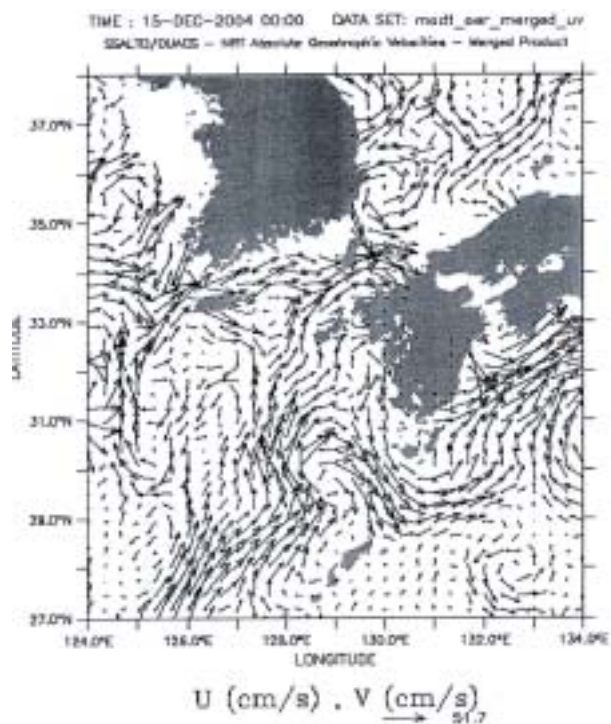


Fig. 4b. Map of geostrophic current in the Korea Strait and its adjacent regions in mid December 2004. The anticyclonic circulation with strong northward flow in the bifurcation of the Tsushima Warm Current from the Kuroshio and the flows the southwest in the Korea Strait are noticeable (Arvelyna and Oshima 2006).

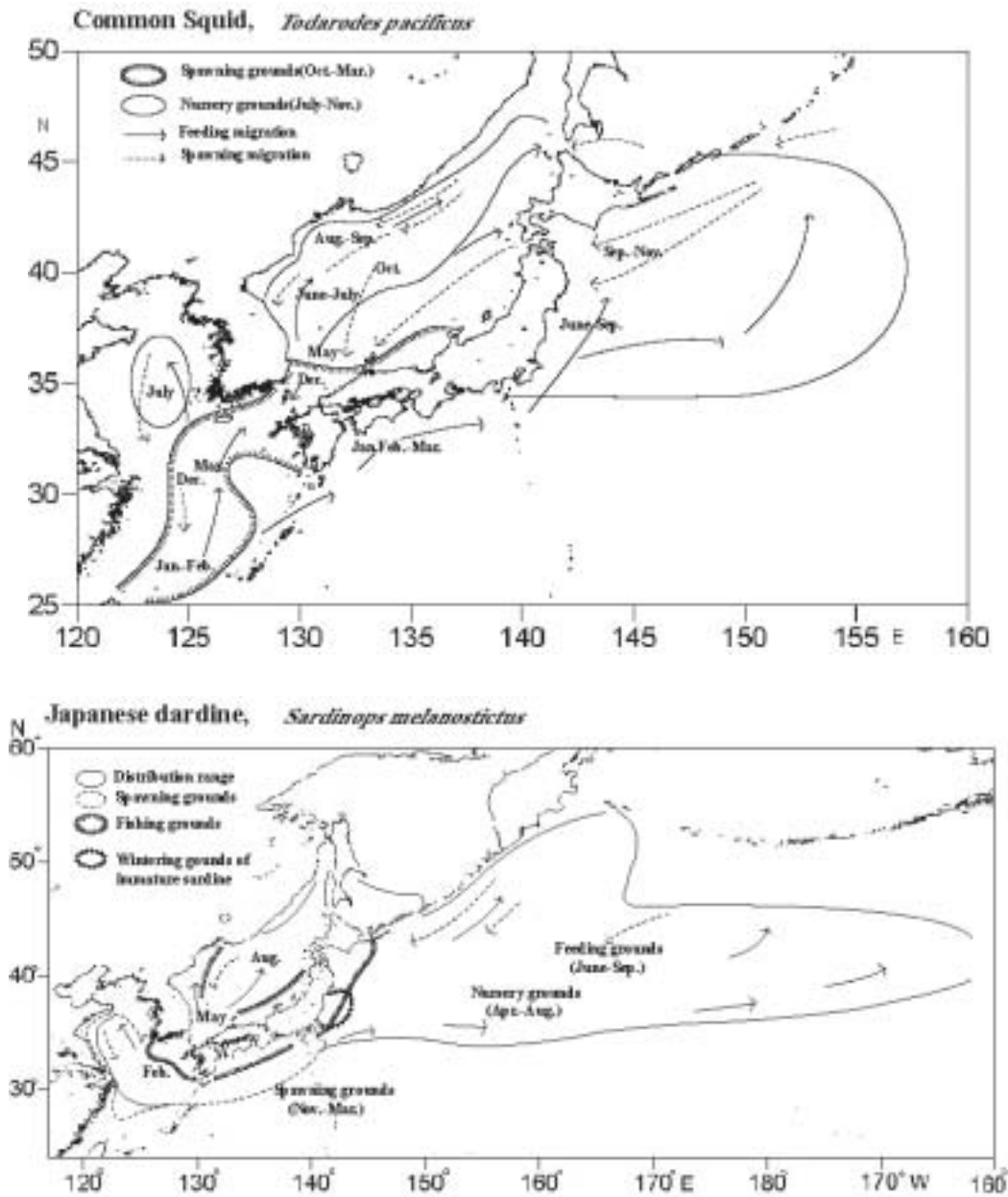


Fig. 5. Hypothetical migration circuits of Japanese sardine (top) and common squid (bottom) in the Far-Eastern regions.

the opposite conditions. The Aleutian Low co-varies not only with the Pacific North American pattern, but also with the Arctic Oscillation and Asian Monsoon (Thompson and Wallace 2000a, 2000b, Tian et al. 2004, 2006).

The cool regime in the Kuroshio-Oyashio transition zone might be due to the intensified westerly wind caused by the deep Aleutian Low with the Arctic Oscillation. In the period of 1900~1997, the ocean climate regime possibly shifted around 1925, 1947 and 1976 (Minobe 1997). In the time series of SSTs, six regime shifts were detected from 1910s to 1990s: i.e., 1925/26, 1945/46, 1957/58,

1970/71, 1976/77 and 1988/89 (Yasunaka and Hanawa 2002) and another regime shift was detected in 1998/99 (Figs 1 and 2). The First Oyashio Intrusion (FOI) was shifted to the south in association with the deep Aleutian Low during the late 1970s~1980s (Ogawa et al. 1987, Hanawa 1995, Nihira 2005) (Figs. 1 and 2).

Zooplankton biomass in the feeding grounds of the migratory species in the East/Japan Sea (main TWC region) and the Oyashio Current systems (the main feeding grounds in the KOC region) were lower than the long-term average during the cool period between the climate shifts of 1976/77 and 1988/89, and increased during the

Table 2. Life history, distribution and habitat of pelagic fish species in the Far-East (FAO 61 area)

NO.	Common name	Age at maturity length	Life span L ∞	Main food	Population structure (this study)	Distribution range	Spawning area	Spawning season	Habitat, responses to climate change
1	Pacific herring	2 (Y.S) 2~4 (HK) 4~6 (OK) 21 cm	7~8 (5~15) 30 cm (52 cm)	Zoo-plankton	6 marine stocks (2)	Bering Sea, Okhotsk Sea Hokkaido East/Japan Sea Yellow sea (North of 34°N	Inlet, coast north of 35°N From W. Bering Sea to Yellow Sea	Feb.~May (Mar.~Apr.)	Boreal, coast-offshore, pelagic-mesopelagic, 0~250 m Taraba-community I, 0~7 (4~7)°C abundant during cool regime
2	Japanese sardine	2 17~20 cm	5~6 (7~8) 24 cm	Phyto.pl (main) Zoopl. (sub.)	4 (1)	28°~55°N 120°E~160°W	28°~35°N 120°~140°E	Dec.~June (Feb.~May)	Cool temperate, coast-offshore pelagic 0~200 m Okaba-III, 12~20 (13~15)°C abundant during cool regime
3	Japanese anchovy	1 9 cm metamo. 2.0~4.0 cm	2.5 15 cm	Zoopl. (main) Phyto. (sub)	4 (1)	25°~46°N 120°~ 170°E	27°~38°N 122°~142°E	Spring~ summer	Warm temperate, inshore-offshore pelagic 0~100 m, Okaba- I, 10~28 (17~24)°C Euryhaline, abundant during warm regime.
4	Jack mackerel	1.5~2 25~27 cm 3.5~4 (1960s)	8 42 cm	Zoopl. Phyto.	2 (1)	25°~41°N 122°~150°E	25°~36°N 122°~145°E	Jan.~July (Feb.~Mar. Mar.~May)	Warm temperate, coast-offshore pelagic 0~150 m Okaba- II, 10~25 (15~20)°C Abundant during warmer water prevails
5	Chub mackerel	2~3 27~33 cm	6 40 cm	Zoopl.	3 (1)	25°~48°N 120°~170°E	26°~40°N 122°~150°E	Mar.~May	Mild temperate, coast-offshore pelagic-mesopelagic in winter (0~150 m) Okaba-II (young, 14~21°C) Okaba-III (adult 12~16°C)
6	Pacific saury	1 20 cm	1.5~2 28 cm	Zoopl.	2 (1)	25°~55°N 125~170°E	30°~45°N 125°~160°E	Sep.~June (autumn~ winter~ spring)	Mild temperate, offshore pelagic-0~100 m, Okaba-II Inhabit, haline waters (33.6~34.8psu), 10~22(13~19°C) Sensitive responses to thermal conditions
7	Common squid	0.8(9mo.) 20 cm	1 30 cm DML	Zoopl.	2~3(1)	25°~46°N 121°~160°E	25°~40°N 122~140°E	Autumn~ winter 6(summer)	Coast-offshore, pelagic, 0~250 m Okaba-II, Euryhaline 7~23 (12~18)°C Annual semelparous, cannibalism Abundant during warmer water prevails

warm period in the 1990s (NFRDI 1962-2005, Odate 1994, Minami et al. 1999, Gong et al. 2006). Zooplankton biomass in the Oya-shio Current system was reported to vary by the thermal regime (Tomosada and Odate 1995) (Fig. 3). The zooplankton biomass in the two (TWC and KOC) regions showed decadal-scale fluctuations in association with the thermal regime (Figs. 2 and 3). The year-to-year zooplankton biomass was negatively correlated ($r=-0.70$, $p<0.01$, $n=92$) with the upper layer (0~150 m) mean temperature along the PM line in the East/Japan Sea (a part of TWC region). However, inter-decadal variability of the two variables was positively correlated, with 3- year time lag. Both variables were low during the 1980s but increased after the climate regime shift (1988/

89) and remained higher than average in the 1990s (Fig. 3).

Variations in the Fish Migration Circuits Mediated by Ocean Currents

The ocean current systems in the Northwest Pacific (KOC region) and its adjacent regions (TWC region) were schematically established based on the studies of the current patterns (Gong et al. 2006) (Fig. 4). Migration circuits of the seven species were established based on previous studies on their migration routes and considering the properties of the waters they inhabit. Migration circuits for Japanese sardine and common squid are presented here (Fig. 5). The fishes migrate northward following the northward shifting of

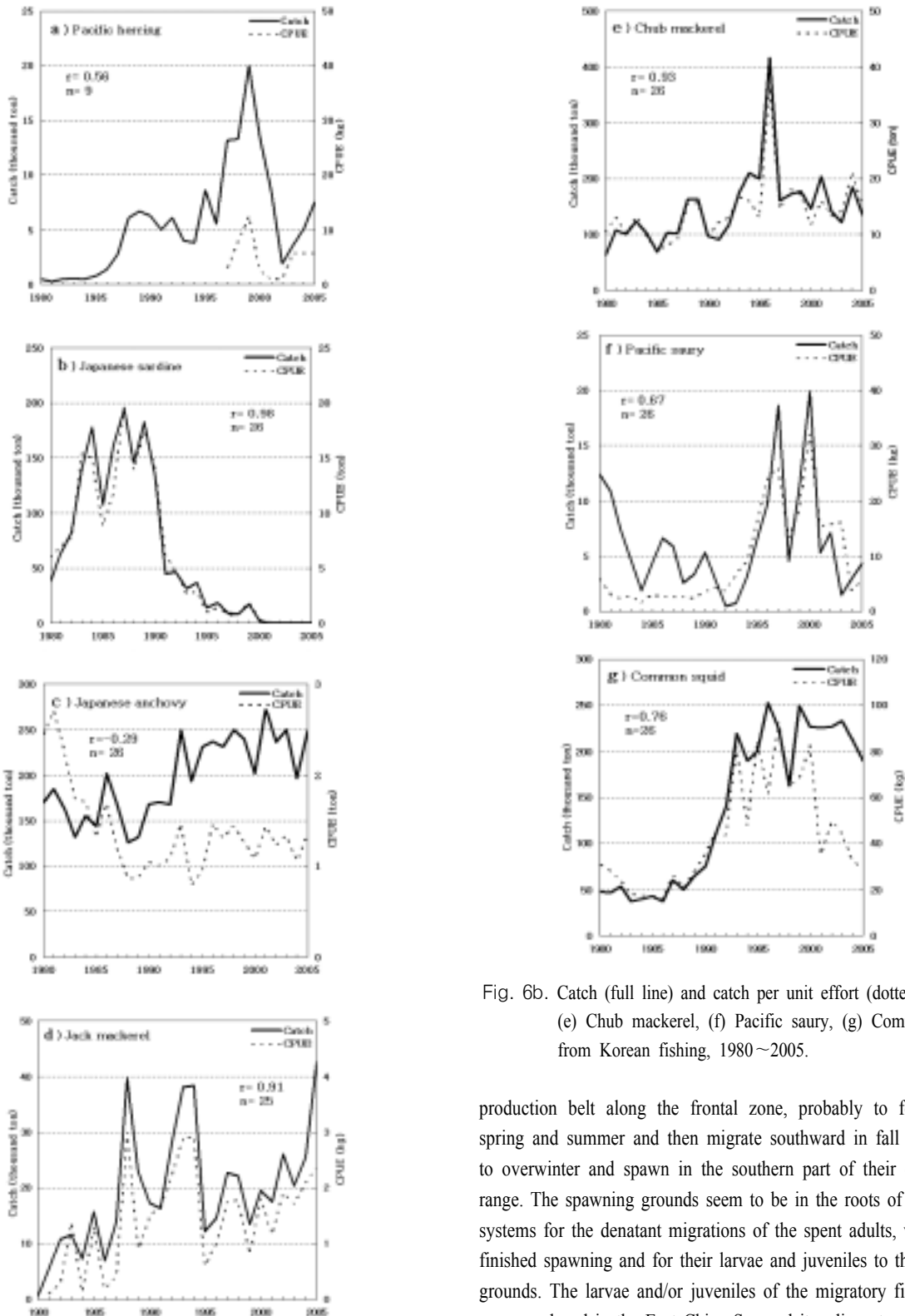


Fig. 6a. Catch (full line) and catch per unit effort (dotted line) for (a) Pacific herring, (b) Japanese sardine, (c) Japanese anchovy and (d) Jack mackerel from Korean fishing, 1980~2005.

Fig. 6b. Catch (full line) and catch per unit effort (dotted line) for (e) Chub mackerel, (f) Pacific saury, (g) Common squid from Korean fishing, 1980~2005.

production belt along the frontal zone, probably to feed during spring and summer and then migrate southward in fall and winter to overwinter and spawn in the southern part of their distribution range. The spawning grounds seem to be in the roots of the current systems for the denatant migrations of the spent adults, which have finished spawning and for their larvae and juveniles to their feeding grounds. The larvae and/or juveniles of the migratory fishes which were produced in the East China Sea and its adjacent regions seem to migrate northward following the Kuroshio and the Tsushima Warm Current between the winter and spring. They then appear to migrate for feeding to the transition zone and Oyashio Current

system, and to the central East/Japan Sea and Yellow Sea during the summer and fall.

Two distinct migration patterns, 1) by juveniles from spawning to feeding ground, and 2) by adults from feeding to spawning ground

comprising the circuit of migration, were proposed as a mechanism that a marine stock maintains its population from generation to generation, insofar as wind and currents permit (Cushing 1975). However, annual and long-term changes in wind and current in associa

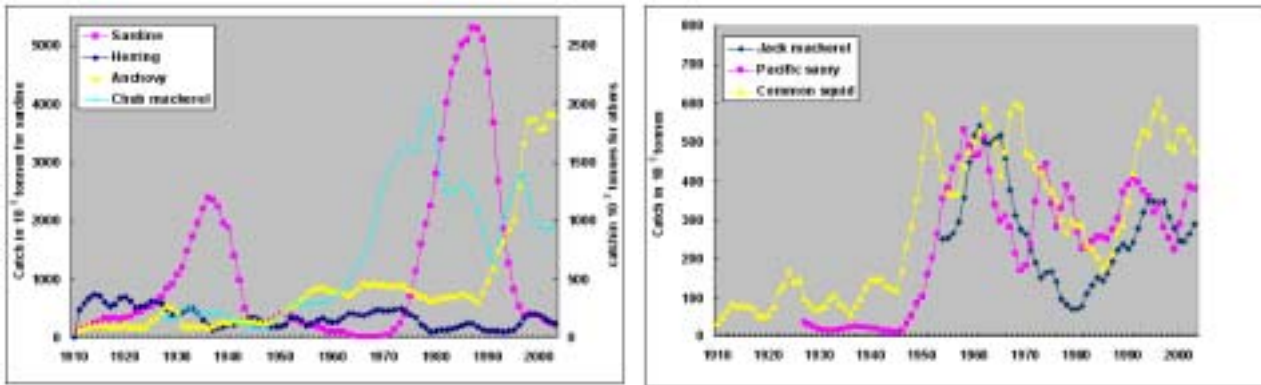


Fig. 7a. Time series of catches in 3-year running average for sardine, herring, anchovy and chub mackerel (left), jack mackerel, Pacific saury and common squid (right) in the Far-East (KOC+TWC) regions.

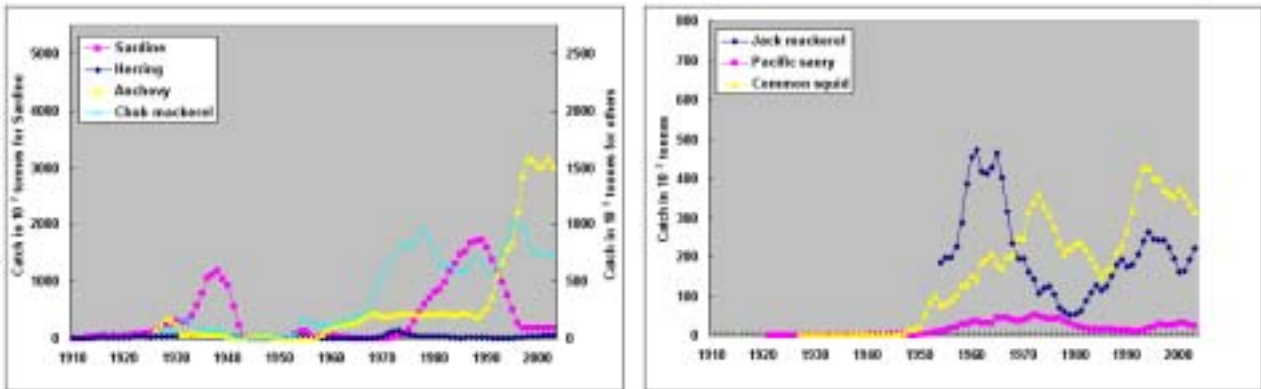


Fig. 7b. Time series of catches in 3-year running average for sardine, herring, anchovy and chub mackerel (left), jack mackerel, Pacific saury and common squid (right) in the Tsushima Warm (TWC) region.

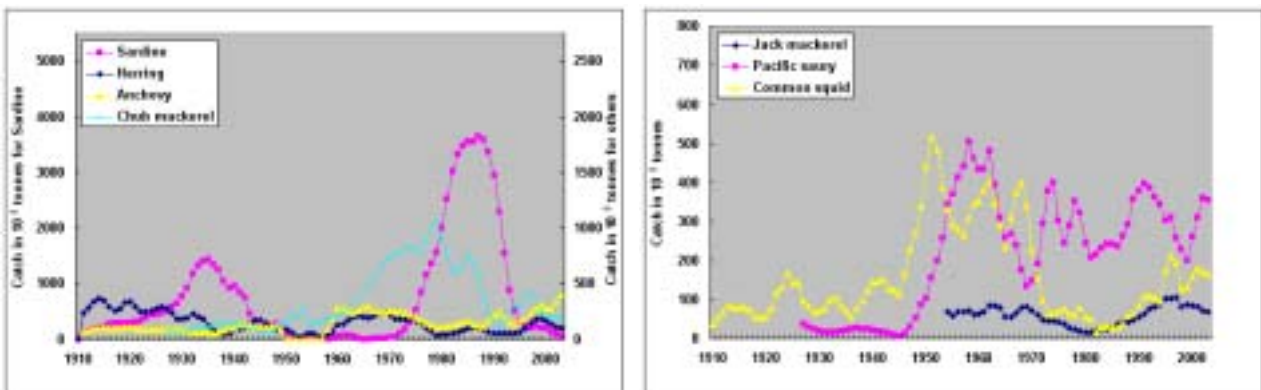


Fig. 7c. Time series of catches in 3-year running average for sardine, herring, anchovy and chub mackerel (left), jack mackerel, Pacific saury and common squid (right) in the Kuroshio-Oyashio (KOC) region.

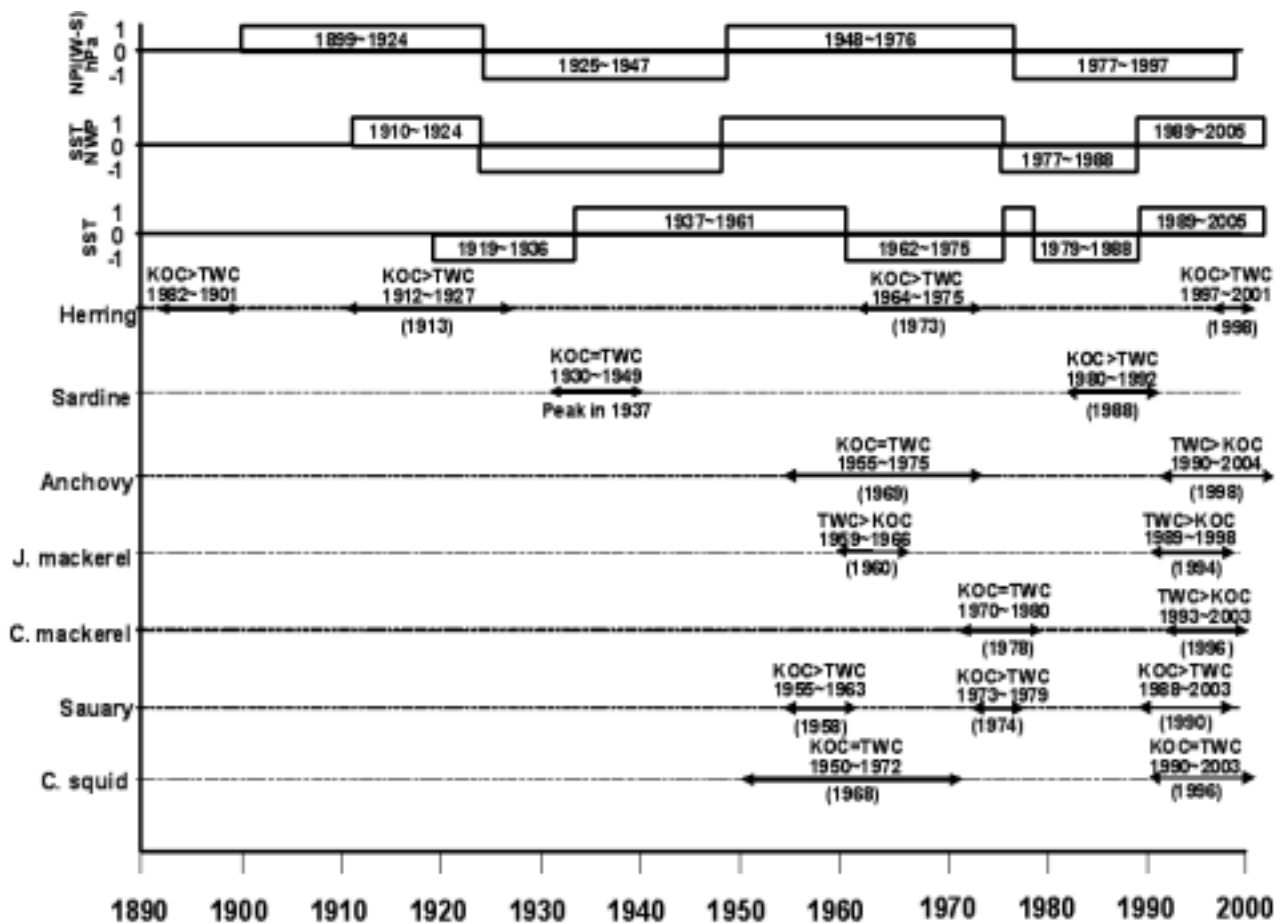


Fig. 8. Changes in climate (NPI in winter-spring) and ocean (SST in the KOC and TWC regions), and abundant periods of pelagic fishes in the TWC and KOC regions during 1890~2005.

tion with climate shifts can disturb the migration circuits of pelagic fishes as seen in the case of the common squid (Gong et al. 2006). The Kuroshio and Tsushima Warm Currents and their branches can transport larvae and juveniles produced in the East China Sea northward to the nursery and feeding grounds (Sassa et al. 2006). The transport rates of the early life stage to the TWC region will be high when the bifurcation of the Kuroshio-Tsushima Current system is abnormally shifted to the north (Fig. 4).

Eggs and larvae of the pelagic fishes produced in the East China Sea in winter (Jan. ~Feb.) can be transported to the Pacific Ocean (KOC region) with the Kuroshio Current by the monsoon and those produced in early spring (Mar. ~Apr.) can be transported to the East/Japan Sea (TWC region) by the Tsushima Warm Current (Morinaga 2004). Therefore, regional difference in long-term fluctuations of the abundance of pelagic fishes produced in the spawning grounds of the East China Sea are closely dependent on the fluctuations of the winter monsoon/Arctic Oscillation and the Kuroshio/ Tsushima Current systems.

Long-term Changes in Fish Catch

Off Japan, higher landings of sardine, chub mackerel and Pacific saury lasted for 10~15 year intervals from 1912 to 1986 (Fukushima and Ogawa 1988), but higher landings of the common squid and anchovy lasted for about 20 years (Figs. 7 and 8). The length of abundant periods with peak years for each species in the two regions (TWC and KOC region combined) and regional difference in catch records are shown in Fig. 8 and Table 3.

Dominant Species during Periods from Which No Catch Records are Available

Chub mackerel was dominant in catches of TWC and KOC regions during the interim period between the late 1960s and early 1970s when herring dominated and the 1980s when the sardine dominated. Based on the alternation pattern, despite the absence of catch data, we speculated that chub mackerel might have been dominant during the late 1920s because the sardine subsequently dominated in the 1930s. After the first sardine-dominant period (1930s)

Table 3. Abundant periods and fishing nature for pelagic fishes in KOC (Northwest Pacific and Okhotsk Sea) and TWC (Yellow Sea, East China Sea and East/Japan Sea), 1870~2004

NO.	Common name	Time	Abundant periods (peak year) and regional difference in catch			Main fishing gear	Factors leading to different amplitude
1	Pacific herring	1870~2003	1880~1910 (1897) 1912~1927 (1913) KOC>TWC	1964~1975 (1973) KOC>TWC	1997~2000 (1998) KOC>TWC	Gillnet, Purse seine	KOC>TWC (cont.) Inhabit subarctic coastal waters and Yellow Sea
2	Japanese sardine	1910~2003	1930~1941 (1937) KOC=TWC	1980~1992 (1988) KOC>TWC		Purse seine, Set net	KOC>TWC (1980s) Incidental fishing in limited area of TWC
3	Japanese anchovy	1910~2003	1955~1975 (1969) KOC=TWC		1990~2003 (1998) KOC<TWC	Purse seine, Boat seine (KOC) Dagnet, Gillnet, Set-net (TWC)	KOC<TWC (1990s) due to changes in community of TWC
4	Jack mackerel	1953~2003	1959~1966 (1960) KOC<TWC		1989~1998 (1994) KOC<TWC	Purse seine	KOC<TWC (cont.) Inhabit warm waters
5	Chub mackerel	1926~2003	(possible 1920s)	1970~1980 (1978) KOC=TWC	1993~2003 (1996) KOC<TWC	Purse seine	KOC<TWC (1990s) Heavy fishing in KOC
6	Pacific saury	1921~2003	1955~1963 (1958) KOC>TWC	1973~1979 (1974) KOC>TWC	1988~2003 (1990) KOC>TWC	Stick held-dipnet (KOC), Gillnet (TWC)	KOC>TWC (cont.) Inhabit haline waters Abundant in KOC
7	Common squid	1895~2003	1950~1972 (1968) KOC>TWC		1990~2003 (1996) KOC<TWC	Jigging (~1980), Jigging and Trawl (1990~)	KOC<TWC (1990s) Availability, shifted fishing to TWC

fisheries for four species (Pacific saury, jack mackerel, common squid and anchovies) were not active until the 1950's because of the Second World War and underdeveloped fishing techniques. A quantity of Pacific saury was incidentally caught in fishing nets targeting sardines in the TWC region in the late 1930s (Gong 1984). Therefore, we speculate that actual dominant periods of the four species occurred earlier than those indicated in the time series of catch records (Figs. 7 and 8).

Revised Alternation of Dominant Species and Number of Alternations

If we accept the above-described sequence of dominant periods for the different species and the nature of fishing for the entire period from which catch records are available, then the revised sequence is as follows; Pacific herring (1920s), chub mackerel (possibly in the late 1920s), Japanese sardines (1930s), followed by a group of four species (Pacific saury, jack mackerel, common squid, anchovies) possibly in the early 1950s~1960s, Pacific herring (late 1960s~early 1970s) and chub mackerel (1970s) and then sardines (1980s). As sardine biomass decreased in association with the cli-

mate shift (1988/89), catches of four species rose immediately and remained high at the warm regime in the 1990s. The replacement of the dominant species among 7 pelagic fishes occurred 5 times in the KOC and TWC regions combined in 1910~2004.

Pacific herring (*Clupea pallasii*)

Pacific herring is a typical pelagic-mesopelagic fish inhabiting oligohaline cold waters (0~7°C) including brackish to marine waters along the northern coasts of the Asian continent. Herring is one of the Taraba community-1, occurring below the permanent thermocline (50~250 m) in the southern East/Japan Sea (Nishimura 1969) and in the cold waters of the Yellow Sea (Gong 1972, Tang 1991). The Pacific herring were abundant during cool periods associated with the deep Aleutian Low (Tables 2 and 3). Pacific herring in the northwest Pacific west of 180° (FAO area 61) have been separated geographically into 6 marine groups but it appears that genetic mixing among groups might be common (Chikuni 1985, Naumenko 2002). The Sakhalin-Hokkaido group once predominated from the mid-1870s to the mid 1920s. The reason for the drastic change in catch and habitat use in the late 1930s was not clear. However, a

key factor might be the warming of the sea water from 1932~38 and after 1955 (Chikuni 1985, Tanaka 2002).

Pacific herring has been a major target of Korean fisheries, together with yellow crocker and pollock, since the 15th century. The Pacific herring in the Yellow Sea have been intensively exploited by Chinese fishermen since 1968 and the catch by Korean fishermen has been negligibly small. The Chinese catch statistics showed an abrupt increase in the early 1970s (180,000 tons in 1972). The age at maturity of the herring in the Yellow Sea (2 yr) was younger than that in the northern groups (2~4 or 4~6 years) (Table 2). Catches of Pacific herring in the northeastern Pacific also appeared to respond to climate (Brown 2002). The patterns of fluctuation in the Pacific herring populations were out of phase with those of Japanese sardine (Kawasaki 1991, Mori and Kawasaki 1995). Since the herring inhabit oligohaline coastal waters in the subarctic regions and in the cold water of the Yellow Sea, the distribution range is broader in the north and hence the catch is higher in the KOC region than in the TWC region.

Japanese sardines (*Sardinops melanostictus*)

Japanese sardines are distributed along the coast and offshore in the northwestern Pacific (Fig. 5). The fish is part of the Okaba community-111 in the TWC region, inhabiting the upper layer (0~200 m) of waters with a temperature range of 12~20°C (optimum range, 13~15°C). It feeds mainly on phytoplankton while the other species almost exclusively feed on zooplankton (Table 2). Spawning of Japanese sardines occurs year-round but peaks during November-March in the southern regions of the population's range. Spawning is followed by a feeding migration to the north and offshore on the Pacific side and the East/Japan Sea during summer. During winter mature sardines return to the spawning grounds, while immature fish tend to remain in the southern part of the feeding grounds to overwinter. Nearly all catch were by purse seine in the KOC region. When abundance was high, fishing grounds were expanded to Hokkaido in the KOC and to the northwestern East/Japan Sea in the TWC region (Nakai 1959, Watabe 1992a, 1992b, Kawasaki 1993, Wada and Jacobson 1998).

During the cold period in the 1980s when sardines were dominant, primary production increased, but zooplankton biomass decreased (Fig. 3), providing favorable conditions for sardines but not for the other four species, probably because warm spawning grounds and cold feeding grounds developed after strong winter monsoons (Tomosada 1988, Hanawa 1995, Wada and Jacobson 1998). In the time series of ocean climate indices and dominant periods for seven pelagic fishes, two cold, sardine-dominant periods in the 1930s and 1980s were notable in both KOC and TWC regions. These two periods were immediately followed by warm periods when Pacific saury,

jack mackerel, common squid and anchovies became dominant.

Schwartzlose et al. (1999) suggested that the sardine population in the East/Japan Sea (main TWC region) is genetically different from the population on the Pacific side (KOC region) on the basis of reduced distribution, low catch and different lipid contents during the second sardine period (1980s). Noto and Yatsuda (1999) noted that large-scale fluctuations of sardine populations in the two regions were related to population changes of sardines in the Pacific KOC region). Watanabe et al. (2003) observed that the Tsushima-Current subpopulation of Japanese sardines (*Sardinops melanostictus*) in the East China Sea and East/Japan Sea peaked in the late 1980s, like the Pacific subpopulation. However, no genetic differences were found among the sardines in the East China Sea, the East/Japan Sea (TWC) and the northwest Pacific (KOC) regions (Okazaki et al. 1996).

We suggest that the regional differences in the catch (KOC>TWC) in the 1980s was due to limited fishing activity in the TWC region, particularly by Korean fishermen. During the 1980s, sardines were caught incidentally by Korean purse seine nets targeting chub mackerel, jack mackerel and file fish in the waters south of 38° 30' N, whereas about two-thirds of catch was taken by gillnets and purse seine nets in the waters off of the northern Korean Peninsular during the first sardine period (1930s) (Nakai 1959, Park 1978). Therefore, the abundance of sardines in the TWC region probably was not as low during the cold period of the 1980s as it appears in the CPUE time series (Fig. 6) (Kim et al. 2006). We speculate that the sardine population fluctuated with a synchronous pattern in the two (KOC and TWC) regions due to the same climate forcing, but with that the catch fluctuated with different amplitudes because of differences in fishing techniques and varying availability, and hence that sardines should be managed as a single large population, particularly during periods of high abundance.

Japanese anchovies (*Engraulis japonicus*)

Japanese anchovies prefer inshore warm waters more than do other pelagic fishes (Nishimura 1969, Nakahara and Ogawa 1978, Ogawa and Nakahara 1979, Chikuni 1985) (Table 2). The anchovy is a member of the Okaba Community-1 and is distributed in the upper layers (0~100 m) of waters of temperature 10~28°C (17~24°C). However, they are transported to the open ocean by the Kuroshio current in the northwest Pacific and by the Tsushima Warm Current in the East/Japan Sea. Takahashi and Watanabe (2004, 2005) suggested that fast growing anchovies in the metamorphosis stage (20~35 mm in standard length) could survive better in the Kuroshio-Oyashio transition region. The distribution ranges of Japanese sardines and anchovies expanded from the coastal to offshore waters during the high population period (Takahashi and Watanabe 2005), suggesting the high possibility of intermixing between adja-

cent sub-populations.

The time-series for anchovy catch displays very low variation with weak low-frequency components in the KOC region, while they had the highest variation with strong low-frequency components without clear periodicities in the TWC region (Figs. 7, 8). The big regional difference in anchovy catch (KOC << TWC) in the 1990s was attributed to changes in community structure in the northern East China Sea. The depletion of most demersal and large piscivorous pelagic fishes resulted in the increased abundances of small planktivorous pelagic fish in the Yellow Sea (Jin and Tang 1996). The trend in the anchovy catch outside of the Yellow Sea in the 1990s showed a synchronous pattern between the two regions and the patterns of fluctuation for the anchovy in these regions were out of phase with those of Pacific sardine (Klyashtorin 2001) (Fig. 7).

Jack mackerel (*Trachurus japonicus*)

Jack mackerel are distributed from the coast to offshore in the warm temperate zone (Nishimura 1969, Nakahara and Ogawa 1978, Ogawa and Nakahara 1979). The fish is one of Okaba Community-11 inhabiting warmer water of 10~25°C (15~20°C). The center of distribution of this fish is to the south of that of chub mackerel (Table 2). The time-series for jack mackerel catch had low variation in the KOC region, while they had high variation and higher catch in the TWC region (Fig. 7). An estimated biomass series for jack mackerel in Korean waters (the southwestern part of TWC) fluctuated in phase with the catch trends (Zhang and Lee 2001). The CPUEs (tonnes/set net) for jack mackerel along the Tsushima Warm Current in the south eastern East/Japan Sea fluctuated in association with the catch, suggesting high abundance in the early 1960s and 1990s. Annual variability for the jack mackerel catch in the TWC region was negatively correlated with that in the KOC region, suggesting oscillation in the recruitment from the same source area, the East China Sea, in association with changes in transportation by Kuroshio and its branches (Uehara and Mitani 2004). We speculate that the regional difference in jack mackerel catch (KOC << TWC) throughout the period 1952~2004 was due to its limited range of distribution in the KOC region. It is suggested that jack mackerel and anchovies evolved in the southern waters during a warm period (Ogawa and Nakahara 1979). Therefore, fluctuations of jack mackerel and anchovy populations are relatively stable, while the abundance of the anti-tropical species such as Pacific herring and Japanese sardine fluctuated with high amplitude (Watanabe 2003).

Chub mackerel (*Scomber japonicus*)

Chub mackerel are distributed in coastal and offshore mild temperate areas, and inhabit the pelagic zone in summer and the meso-pelagic zone in winter. Juveniles belong to the Okaba Commu-

nity-11 and inhabit waters of temperature 14~21°C whereas adults belong to the Okaba Community-111, inhabiting waters of temperature 12~16°C, which suggests a vertical stratification between juveniles and adults like that displayed by bigeye tuna in the tropical zone (Gong et al. 1993). The chub mackerel is found widely in the Far-Eastern regions, namely from the East China Sea to the Yellow Sea, the East/Japan Sea and the northwestern Pacific off of Japan. The age at first maturity is estimated to be 2 to 3 years, varying slightly by region and with abundance. Spawning takes place from the southern-central East China Sea (Feb.~Mar.), to the northern East China Sea (Apr.~June), the southern East/Japan Sea and the waters off of central Japan in the Pacific (May~July). After spawning, adults and their offspring migrate northeast and are distributed throughout the feeding grounds in the Kuroshio-Oyashio transition zone and the Oyashio Currents well as in the Yellow Sea and the East/Japan Sea, and mature fish migrate further south to the spawning grounds around southern Japan and the East China Sea (Nishimura 1965, Novikov 1977, Wang 1991, Watanabe and Yatsu 2006). The chub mackerel was dominant in the 1970s, followed by the sardine in the 1980s. Heavy fishing activity in the Kuroshio-Oyashio Current (KOC) region seemed to be responsible for the low catch (KOC < TWC) in the 1990s. The environment and surplus production are important but the effects of fishing are also important. The chub mackerel population probably could have shifted to a new favorable region in the early 1990s if fishing mortality had been lower (Yatsu et al. 2005).

Pacific saury (*Cololabis saira*)

Pacific saury inhabiting waters of salinity 33.6~34.8 psu and temperature 10~22°C (13~19°C) seemed to respond sensitively to disturbances in the ecosystem (e.g. changes in thermal regime and plankton biomass) and its annual catches show high frequency components (Fig. 7). Pacific saury spawning starts in the mixed water region in the northwest Pacific and the southern East/Japan Sea in autumn, and moves to the Kuroshio area and East China Sea in winter, and then moves back to the mixed water region and the East/Japan Sea in spring (Fukutaki 1966, Odate 1977, Watanabe and Lo 1989, Watanabe et al. 1997, Ito et al. 2002, Gong and Suh 2003, 2004). Juveniles are transported to the Kuroshio extension with the Kurushio and to the East/Japan Sea with Thushima Warm Current, where they grow and migrate to the Oyashio region and the central and northern East/Japan Sea for feeding. After sufficient feeding they migrate back to the Kuroshio region and East China Sea for spawning.

Pacific saury are fished in the East/Japan Sea while on the northward migration in spring and summer and the southward migration in autumn, while they are fished only on the southward migration

in autumn in the Pacific Ocean off of Russia and Japan (Gong 1984, Ito et al. 2002). No adult saury were found in the oligohaline (salinity <30.0 psu) Yellow Sea and western East China Sea. The main fishing gear used for saury have been gillnets and set nets in the TWC region and stick held-dip nets in the KOC region since 1949. Catches per unit fishing effort by gillnets were higher in the KOC region than those in the TWC region in the 1930s and early 1940s (Fukataki 1966; Gong and Suh 2004). Significant regional difference in catch of Pacific saury (KOC>>TWC) throughout the period of 1912~2003 was probably due to their limited distribution, differences in abundance and inaccurate catch records. No catch records have been available since 1945 for the northwestern part of the East/Japan Sea where about a half of the annual catch in the TWC region was landed in the 1930s and 1940s (Gong 1984). Despite regional differences in abundance and fishing techniques, the similarity of the patterns of long-term and inter-annual catch trends between the two regions suggest that Pacific saury populations might be controlled by the same environmental factors in both the TWC and KOC regions (Gong 1984, Gong and Suh 2004). (Fig. 7)

Corrected catch trends for Pacific saury for the period of 1907~2000 in the KOC region reveal that their abundance was high in the early 1910s, 1920s, 1950s and 1990s. The year-to-year CPUEs (tonnes per haul of stick held-dip net) for the fish (Kitagawa, Tomosada 2000) fluctuated with the same trends as the catch for the period of 1970s~1990s (Fig. 7). Decadal variations in Pacific saury abundance in the Kuroshio region corresponded well with the regime shifts of 1976/1977, 1988/1989 and possibly 1997/1998. It is suggested that a density-dependent effect on growth is not evident, and that the recruitment success and growth of saury are strongly affected by oceanographic conditions in the Kuroshio region (Tian et al. 2004). The investigations for the main small pelagic species suggest that the climate/ocean regime shift in the late 1980s occurred basin-wide in the pelagic ecosystem of the northwestern Pacific, and that Pacific saury could be used as a bio-indicator of oceanographic regime shifts in Kuroshio waters (Tian et al. 2004).

The population structure and abundance of the Pacific saury seems to have returned to normal conditions after the climate regime shift (1988/89). However, we speculate that its catches did not increase because of the limited fishing activity caused by price controls in the KOC region (Oozaki et al. 1998) and technical interactions with the other fisheries in the TWC region (Gong and Suh 2004).

Common squid (*Todarodes pacificus*)

The life cycle of the common squid is annual and semelparous. The squid belong to the Okaba Community-11 of euryhaline and eurythermal water (7~23°C, 12~18°C). The squid are distributed

from the East China Sea to the Yellow Sea, the East/Japan Sea and the northwest Pacific (Table 2, Fig. 5). Spawning of the squid takes place from the East China Sea to the southern East/Japan Sea mainly in autumn and winter. A portion of the squid caught by jigging fishing in the TWC region in the late 1960s and 1970s were landed at the fishing ports along the Pacific coast (KOC region) which were included to the TWC region (Kawai 1995, Gong et al 2006) (Fig. 7). Significant regional difference in the squid catch (KOC<TWC) in the 1990s was probably due to shifts of fishing grounds caused by changes in current-mediated migration circuits (Gong et al. 2006). The phase difference in the collapse of common squid fishing between the TWC and KOC regions in the 1970s could be explained by heavy fishing efforts in the waters off of northeastern Japan before the response of squid to the climate shifts in the mid 1970s (Figs. 1, 2, 7).

Population Structure

The pelagic fish and squid appeared to change their spawning and feeding grounds over time. The spawning grounds of jack mackerel and anchovies, which apparently evolved in southern (sub-tropical) waters, shifted to the south while those of herring and sardine shifted to the north during low abundance periods. Pelagic species showed greater variance in their spatial ranges in response to population level changes (Lluch-Belda et al. 1989, Kikuchi et al. 1992, Nakata 1993, Gong et al 2006). The pelagic species listed in Table 1 expand their feeding grounds when their population levels increased, and their sub-populations are not necessarily completely segregated. Therefore, we suggest that each of the pelagic fishes except herring can be regarded as a single population as indicated (1) in the Table 2 in this study.

CONCLUSION

We propose that there has been an alternating pattern of dominant pelagic fish species based on catch records from Far Eastern countries during the 20th century. The alternation sequence was as follows; Pacific herring in the 1910s~1920s, possibly chub mackerel in the 1920s, Japanese sardines in the 1930s, four species (Pacific saury, jack mackerel, common squid and Japanese anchovies) in the 1950s~1960s, Pacific herring in the late 1960s~early 1970s, and again chub mackerel in the 1970s, and then Japanese sardines in the 1980s. As climate shifts reduced sardine biomass, catches of the four species increased in the warm periods of the late 1980s~1990s. The dominant periods for the seven species lasted for 10~20 years. Annual catches of the seven species showed synchronous patterns with variability in the Tsushima Warm Current (TWC) region and the Kuroshio-Oyashio Current (KOC) region during the

period of 1900~2004, suggesting that their population levels were controlled by the same climate forcing, but they showed different amplitudes of population changes due to the regional difference in fishing techniques and varying availability. We conclude that, despite their wider distribution areas, a single large population has been maintained for each species during the past 100 years. There is a need for large-scale research on the recruitment of the pelagic fishes in relation to ocean climate changes, current-mediated migration circuits and oscillations of larval transportation, and on the availability of adult fishes in the two (KOC and TWC) current systems.

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