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An overview of the Oyashio ecosystem

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Abstract

The Oyashio shelf region and the seasonally ice-covered areas north of Hokkaido are highly productive, supporting a wide range of species including marine mammals, seabirds and commercially important species in the western subarctic Pacific. The fishes include gadids, such as walleye pollock and Pacific cod, and subarctic migratory pelagic fishes such as chum salmon and pink salmon. It is also an important summer feeding ground for subtropical migrants such as the Japanese sardine, Japanese anchovy, Pacific saury, mackerels, Japanese common squid, whales and seabirds. In recent decades, some components of the Oyashio ecosystem (i.e., phytoplankton, mesozooplankton, gadid fish, and subtropical migrants) have shown changes in species abundance or distribution that are correlated with environmental changes such as the 1976/77 and 1988/89 regime shifts. The First Oyashio Intrusion moved northward from the mid 1960s until the late 1970s when it moved southward until the 1980s, after which it returned to the north again after the mid 1990s. The sea surface temperature in spring decreased after the late 1970s, increased after the late 1980s, and remained high during the 1990s. The extent of ice cover in the Sea of Okhotsk also decreased during the latest warming in the 1980-90s but has increased again since the late 1990s. These and other kinds of variability are described in this overview of the status of the Oyashio ecosystem and the surrounding region.

Keywords: Oyashio; Physical and chemical oceanography; Ecosystem properties; Fish and invertebrates; Marine mammals

1. Introduction

The Oyashio region is located in the northwestern North Pacific Ocean from northern Honshu Island, Japan to the Kamchatka Peninsula of Russia. It has a narrow continental shelf that features a steep slope along its southeast margin. The oceanography of the region is dominated by the Oyashio, a western boundary current that flows southward from the subarctic North Pacific Ocean (Fig. 1). Its name, “*oya*” (parent) and “*shio*” (stream), reflects its great productivity (Qiu, 2001). The Oyashio is fed by cold, nutrient-rich, upwelled waters from the western subarctic gyre. East of the Kuril Islands it flows southward as the western boundary current of the western subarctic gyre, and continues southward along the east coast of Japan with two dominant intrusions toward the south. The characteristics of these intrusions vary annually in response to changes in the wind field over the North Pacific. Northeastern Hokkaido (the Doto area including the Shiretoko Peninsula), is one of the southernmost areas in the northern hemisphere with seasonal sea ice floes.

The western subarctic Pacific, including the shelf region, supports a wide range of commercially important marine fishes, including gadids such as the walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*), and subarctic migratory pelagic species such as chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*). The region is also an important summer feeding ground for subtropical migrants such as the Japanese sardine (*Sardinops melanostictus*), Japanese anchovy (*Engraulis japonicus*), Pacific saury (*Cololabis saira*), chub mackerels (*Scomber japonicus*, *S. australasicus*), Japanese common squid (*Todarodes pacificus*), whales and seabirds. In recent decades, various components of the Oyashio ecosystem, notably the Japanese sardine and walleye Pollock, have shown significant changes in abundance and distribution related with changes in the physical oceanography of the region.

Important questions concerning the biological oceanography of the Oyashio region and the seasonal sea-ice areas off northern Hokkaido include the following:

- How does variability in the Oyashio and seasonal sea ice affect the ecology of walleye pollock, a key species in the region, during its early developmental stages when variation in these factors may affect recruitment?
- How can we clarify the effect of the oceanic environment, phytoplankton and zooplankton on pelagic and demersal fish species through process studies and ecosystem modeling?

- How will changes in ocean climate alter the productivity of key species, including walleye pollock, salmon and pelagic migratory fishes and squids?
- How will changes in physical and anthropogenic forcing mechanisms influence the relative importance of top-down vs. bottom-up control of energy flow in the Oyashio ecosystem?
- What are the mechanisms that link physical forcing to biological processes and their spatial and temporal scales of interaction?
- To what extent do biological processes regulate the structure, energy flow, and dynamics of the food webs in the Oyashio ecosystem?
- What are the societal and economic impacts of climate variability on the Oyashio ecosystem and the feedbacks from changes in ecosystem use on these impacts?

This contribution reviews the present status of the Oyashio ecosystem, including parts of the Kuroshio region and seasonal sea ice areas in the Sea of Okhotsk northeast of Hokkaido.

2. Physical and chemical oceanography

The 530,000 km² Oyashio Large Marine Ecosystem (Fig. 2) is one of the most productive ecosystems in the North Pacific. North of 38°N, the continental shelf is narrow but the shelf slope is comparatively gentle, especially at depths over 1,000 m. South of 38°N, the shelf is wider but the slope is steep with a complicated and rugged topography at depths below 1,000 m. Beyond the shelf, the western subarctic gyre is formed by the westward flowing Alaska Stream, part of which enters the western Bering Sea between 168° and 172° E. Here it has a counterclockwise circulation, with its western limb forming the East Kamchatka Current (Fig. 1) (Ohtani, 1991). This southward flowing current is joined by the portion of the Alaska Stream that did not enter the Bering Sea, then passes south toward the Kurile Islands. The East Kamchatka Current splits, with some of its water passing through the Kurile Island archipelago into the deep Kurile Basin of the Sea of Okhotsk. There it forms a counterclockwise gyre, and subsequently leaves the Sea of Okhotsk through Bussol' Strait, where it rejoins the East Kamchatka Current. South of this strait, the East Kamchatka Current is renamed the Oyashio. It differs from the East Kamchatka Current in that the Oyashio is a mixture of East Kamchatka Current water and Sea of Okhotsk water (Qiu, 2001).

The characteristics of water in the Oyashio are a result of processes related to winter ventilation and sea ice formation in the waters east of Kamchatka and in the northern part of

the Sea of Okhotsk. The Oyashio has low temperature, low salinity, and is rich in nutrients-characteristics that differ from those found upstream in the East Kamchatka Current. A subsurface temperature maximum that appears in the halocline at 150-200 m depth in the East Kamchatka does not appear in the Oyashio (Qiu, 2001). As the Oyashio flows southward along the Kuril Islands and the coasts of Hokkaido and Honshu, it has a large potential thickness, which is characteristic of Okhotsk Sea Mode Water (Yasuda, 2004). Part of the Oyashio is entrained by the subtropical gyre along the western boundary current region and flows southward to the Kuroshio Extension (Yasuda, 2004). In the Mixed Water Region, the Oyashio is defined several ways (PICES, 2004). One definition is that it is the water found off the Etorofu Islands and Hokkaido, where salinity increases monotonically to the bottom. Its southern boundary is called the Oyashio Front, which is also the western part of the Subarctic Front. Next to the Hokkaido coast, the Oyashio is defined as a boundary current which may be reduced as the Oyashio separates from the coast and turns eastwards as the Oyashio Front (PICES, 2004). The influence of the Oyashio in the Mixed Water Region is often defined by the location of the 5° C isotherm at 100 m.

The Shiretoko region is located in the northeastern part of Hokkaido and is considered to be the southernmost limit of seasonal ice floes in the northern hemisphere. The physical oceanographic structure in this area is very similar to that of the southern Sea of Okhotsk (Ohsima et al., 2001; Fayman, 2004). Due to the nutrients provided by melting sea ice, by vertical mixing in winter and from seasonal upwelling, the Shiretoko region supports a rich and diverse marine ecosystem, which is closely connected with the Sea of Okhotsk and Oyashio ecosystems.

Seasonal and interannual dynamics of the Oyashio, which are closely linked to climate change, are known to influence the migration and abundance of pelagic and demersal fishes and higher trophic animals in the northwestern Pacific Ocean. The Oyashio forms two tongue-shaped intrusions into more southerly latitudes off the coast of northern Honshu. These are known as the First Oyashio Intrusion (SLO1: coastal intrusion) and the Second Oyashio Intrusion (SLO2: offshore intrusion) (PICES, 2004). A decadal-scale trend in SLO1 was observed as well as a multi-year variability (Fig.3). The SLO1 moved northward from the mid 1960s and shifted southward from the late 1970s to 1980s, and north again from the 1990s (Yasunaka and Hanawa, 2002).

In the Sea of Okhotsk, the large interannual variation in sea ice volume depends on the strength and duration of northerly winter winds (Glebova and Khen, 2002). In the 20th century,

the extent of sea ice cover followed a cycle with a period of about 50 years (Khen, 1997). The extent of ice cover in the Sea of Okhotsk decreased during the 1980s and 1990s, and has increased again since the late 1990s (see the section on the Sea of Okhotsk). In the southwestern part of the Okhotsk Sea, the East Sakhalin Current transports thick “first-year” ice to the coastal areas of northern Hokkaido. These floes pass through the straits along the Kurile Islands and Nemuro Strait to the Oyashio region via Cape Erimo, Hokkaido (Fig. 4). However, the relationship between the extent of sea ice and the strength of the Oyashio intrusion is not well known.

Ono et al. (2001) found bidecadal oscillations of water properties from subsurface to intermediate layer (from 26.4 to 27.5 σ_{θ}) in the four areas around the northwestern Pacific including the Oyashio area and the Sea of Okhotsk. These oscillations are synchronized with the 18.6-year period nodal tidal cycle (Osafune and Yasuda, 2006). Coincident bidecadal oscillations of apparent oxygen utilization (AOU) and phosphate are also found in the Oyashio area (Ono et al. 2001). Osafune and Yasuda (2006) presented a hypothesis for these oscillations that focuses on the strong diurnal period tides (Fig. 5); higher surface salinity water around the Kuril straits is caused by strong tidal mixing there (Fig. 5, item 1). This high salinity water may be transported northward in the cyclonic Okhotsk Sea Gyre (Fig. 5, item 2) and possibly enhances the formation of dense shelf water (DSW) (Fig. 5, item 3). They suggested that DSW lowers the apparent oxygen utilization, phosphate, and potential vorticity in Okhotsk Sea Mode Water and in the Oyashio (Fig. 5, items 4-6). The bidecadal variability in these intermediate waters may cause cyclic changes of productivity in the Oyashio area.

3. Ecosystem Properties

3. 1. Productivity

The western subarctic Pacific, including the Oyashio shelf region, is one of the high-productivity zones of the world. Based on SeaWiFS global primary production estimates ($> 300 \text{ g C m}^{-2} \text{ y}^{-1}$), it is a Class I, highly productive ecosystem (Fig. 6) (Tadokoro et al., 2005). The Oyashio region has classical spring bloom dynamics, with a strong burst of diatom production in spring (Kasai et al., 1997). This, in turn, supports a high biomass of meso- and macro-zooplankton, on the order of $1.1 - 3.7 \times 10^6 \text{ t}$ (about $13 - 44 \text{ g m}^{-2}$) in the whole region (Odate, 1994). However, both primary production and mesozooplankton biomass in the

Oyashio water have fluctuated with environmental changes, such as the 1976/77 and 1988/89 regime shifts (Tadokoro et al., 2005).

In the region bounded by 40-45°N, 141-150°E (Fig. 7), the sea surface temperature (SST) in spring decreased after the late 1970s, increased after the late 1980s, and remained high during the 1990s (Fig. 7) (Tadokoro et al., 2005). Although the sea surface salinity (SSS) had a similar pattern to the SST, it decreased after the mid-1990s. Comparing mean values before and after the regime shifts, the SST decreased significantly after the 1976/77 regime shift, and SST and SSS increased after the 1988/89 regime shift (Tadokoro et al., 2005). In the summer, there is no clear pattern of interannual variation in SST and SSS (Fig. 7).

Interannual variation of primary production and mesozooplankton biomass in Oyashio waters are evident from data collected along transect PH (see Fig. 6) from 1972 to 1999 (Tadokoro et al. 2005). The chlorophyll *a* concentration at the surface in spring decreased after the 1976/77 climate regime shift and remained low thereafter (Fig. 8) (Tadokoro et al., 2005). Although diatom abundance at the surface showed a pattern similar to that of chlorophyll *a*, no significant decrease is evident after the regime shift (Tadokoro et al., 2005). Annual mean summer values of chlorophyll *a* concentration and diatom abundance fluctuated greatly, and both were relatively low during the 1980s (Fig. 8). The mean chlorophyll *a* concentration decreased significantly after the 1976/77 regime shift, whereas diatom abundance did not show a significant decrease at this time.

In the mid-1970s, total mesozooplankton biomass in spring was high but decreased significantly in the late 1970s (Fig. 9) (Tadokoro et al., 2005). The timing of the decrease corresponded with the 1976/77 climatic regime shift. The biomass of *Neocalanus flemingeri*, the most abundant species of this genus, was roughly constant from 1980 to 1999 (Fig. 10) (Tadokoro et al., 2005). Although species-level estimates of *Neocalanus* biomass are not available for the 1970s, Hirakawa (1981) reported that *Neocalanus* copepods were the predominant genus in the mesozooplankton in the Oyashio waters in spring during the 1970s. Net springtime production of the mesozooplankton was low then, leading Tadokoro et al. (2005) to suggest that the cause was reduced food availability. New biological production may have been limited by a combination of reduced subsurface iron, increased water column stability, and reduced vertical water mixing in winter, which diminished iron entrainment in winter (Ono et al., 2002).

In summer, the mesozooplankton biomass decreased significantly after the 1976/77 climatic regime shift and began to increase after the 1988/89 shift (Fig. 9). *N. plumchrus* is

the dominant component of the *Neocalanus* community in summer. Biomass was low in the 1980s and increased in the early 1990s (Fig 10). The biomass of the sub-dominant copepod, *N. cristatus*, also increased in the early 1990s. Tadokoro et al. (2005) suggested that the abundance of the Japanese sardine, an important predator of *Neocalanus* copepods, was inversely related to mesozooplankton biomass. When sardine biomass peaked in 1984, they consumed 32–138% of the daily *Neocalanus* production during summer. Therefore, predation pressure on *Neocalanus* by Japanese sardine is likely to affect interannual variation in mesozooplankton biomass during the summer as a top-down influence.

3. 2. Key species

3. 2. 1. Fish and invertebrates

Walleye pollock (hereafter pollock) is a demersal and semi-pelagic fish occurring in waters from 30 m to > 500 m deep. It is found mostly on the continental shelves of the North Pacific from the southern Sea of Japan to central California. Pollock exhibit diurnal vertical migrations, sometimes reaching the surface (Cohen et al., 1990). They reach sexual maturity at 3–4 years of age at about 30–38 cm total length. In Japanese waters, spawning takes place from December to March in the waters off southern Hokkaido. They produce pelagic, separable eggs that are spawned at intervals of a few days over a one-month period (Fig. 11) (Sakurai, 1989). In Oyashio waters, young pollock feed mainly on copepods and copepod eggs. In this region, adult pollock eat mysids, euphausiids, silver smelt and capelin (Yamamura, 2005). The pollock catch in the Oyashio region has decreased gradually from about 300,000 t in the early 1970s to 200,000 t in the mid-1990s (Fig. 12). After that, the strong 1995 year-class led to increasing catches in the late 1990s, but the catch declined to 100,000 t by 2002.

The pollock stock around northern Japan is abundant (Hamatsu et al., 2004) and is distributed on the shelf from the southern Kuril Islands to the Tohoku region (northeastern Honshu Island) (see Fig. 2). It is a key component of the Oyashio ecosystem, as well as an important target species for local fisheries (Sakurai & Miyake, 1994). The main spawning ground is around Funka Bay in southeastern Hokkaido. Spawning occurs mainly at depths of 100–150 m near the entrance of the bay in January and February (see Shida et al., this volume). As they develop, the pollock eggs drift into the bay with intrusions of the coastal Oyashio

(Kendall & Nakatani, 1992). Some of the eggs and larvae are transported by the Oyashio, which generally flows southward along the eastern coasts of Hokkaido and Tohoku. The favorable temperature range for survival of eggs and larvae is 2-7 °C (Kendall & Nakatani, 1992). It is believed that strong year-classes occur as a result of transport and aggregation of pollock eggs and larvae in the Funka Bay nursery ground where there is a high density of food organisms such as copepod nauplii. There is currently no information about the contribution to year-class strength of offshore pollock or those transported southward to the Tohoku area by the intrusion of the coastal Oyashio.

Pollock catches off the Tohoku region have decreased drastically since 1993. Suzaki et al. (2003) examined how annual variations in the abundance of age-0 pollock were related to variation in the Oyashio Current off the Tohoku region between 1981-1995 (Fig. 13). During the 1980s, when the Oyashio flow was located near shore, pollock abundance was relatively high. However during the early 1990s, when the flow moved further offshore (and not as far south due to interactions with the Tsugaru Warm Current and the Kuroshio Extension), age-0 pollock abundance decreased. The near-shore flow caused a decrease in the sea bottom temperature over the continental shelf during the 1980s. When the coastal Oyashio flowed near the shore along southeastern Hokkaido and northeastern Honshu (*e.g.*, in 1989 and 1995), larval survival and year-classes were strong. However, when this flow occurred farther offshore (*e.g.*, in 1991 and 1992), survival decreased and year-classes were weak. These results indicate that the Oyashio plays an important role in determining the success of early life stages of pollock from Funka Bay. After 1989, the usually distinct distributions of juvenile and adult pollock overlapped over the continental shelf and slope off Hokkaido. This may have resulted in a decrease of the pollock stock from cannibalism or increased predation by Pacific cod, banded Irish lord (*Hemilepidotus gilberti*) and Kamchatka flounder (*Atheresthes evermanni*) (Fig. 14) (Yamamura, 2005).

In Nemuro Strait (see Figs. 2, 4), which is covered by ice-floes during February and March, pollock spawn near the coast from January to March on the continental slope. They are caught on the bottom by longlines and submerged gill nets. A peak catch of 110,000 t occurred in 1990, but it has decreased drastically to 5000 t by 2004 (Fig. 11). This decline may reflect the effects of intensive fisheries and/or the general decline in pollock stocks in the Sea of Okhotsk caused by environmental change (Radchenko, 2001). Comparative studies among pollock stocks in the North Pacific are needed in the context of response to climate

change such as the effects of long-term variation of the sea ice conditions in the Sea of Okhotsk, and vulnerability to intensive fisheries.

Pacific cod is widely distributed in the northern part of the North Pacific Ocean and adjacent waters in water temperatures from near freezing to 15°C. It occurs mainly along the continental shelf and upper slope of the North Pacific from Korea to the western Chukchi Peninsula in the west and from Norton Sound (Bering Sea) to Oregon in the east. Its depth range extends from near the surface (10 m) to about 550 m, but it mainly occurs at 100-400 m (Cohen et al., 1990). Age and size at first maturity vary geographically, with the southern stocks maturing at an earlier age (Hattori et al., 1992a); they are 2–3 years and 40–44 cm standard length (SL) off Washington, USA, 3 years and 41–48 cm SL off Kinka-san in northern Japan, and 7–8 years and 60–63cm SL off west Kamchatka (Hattori et al., 1992a). Fecundity is high, with 2 million eggs for a 4 kg female, and up to 4 million eggs for a 7 kg female in Mutsu Bay (Hattori et al., 1995) (see Fig. 2, northernmost Honshu, Japan). The body size difference among stocks may be due to differences in temperature (Hattori et al., 1992a).

Spawning varies among populations, occurring mostly from winter to early spring; from January to May in the western Pacific, and from December to February in Mutsu Bay (Hattori et al., 1992b, 1993). Variation in their spawning migration has been linked to annual changes in ocean temperature in various parts of the geographical range (Cohen et al., 1990). Pacific cod inhabiting waters near northern Japan migrate to shallow bays (about 50 m in bottom depth) with silty or sandy bottoms and water temperatures of 4 - 8° C to spawn. The distribution of this stock extends from Kushiro in northeastern Hokkaido to Mutsu Bay off northern Honshu. The seasonal migratory route was learned by tagging and recovering juvenile and adult cod (Fukuda et al., 1985).

Females spawn only once each season. The spawning behavior of Pacific cod differs from the single-pair, ventral mounting, and multiple spawning over a several day period that is seen in pollock and Atlantic gadid species (Sakurai & Hattori, 1996) (Fig. 11). Pacific cod spawn demersally and have slightly adhesive eggs, which disperse and settle on the bottom. Ripe males and females do not display the ventral mounting behavior. The female releases all ripe eggs in a single spawning within 20 seconds. Just after the eggs are released, one or a few males follow the female and spread the sperm around the eggs using tail beats. Egg diameter is from 0.9 to 1.0 mm and hatching takes place after 21 days at 5°C and after 15 days at 8°C. The size of larvae at hatching ranges from 3.8 to 4.5 mm total length. The larvae are pelagic

for 4 to 5 months, then descend to the bottom (Takatsu et al., 1995). The food of the pelagic larvae is composed mainly of copepod nauplii (Takatsu et al., 1995). The growth rate is rather high, reaching 20 cm SL at the end of first year (Hattori et al., 1992a). The young cod eat euphausiids and benthic invertebrates, whereas the diet of adults includes fish, octopus, and large benthic and benthopelagic crustacea such as crabs and shrimps. Growth is similar in male and female Pacific cod reaching 40 cm SL at 2 years, and 77 cm SL at 6 years off the southern coast of Hokkaido. The life span of a Pacific cod is up to 12 years.

In the Oyasho region off Tohoku, Pacific cod catches fluctuated and were estimated to be at low abundance levels in the late 1970s, but gradually increased during the 1980s, decreased during the early 1990s, and increased again after the late 1990s, particularly the 1996-1998 year classes (Fig. 15). However the local spawning stock in Mutsu Bay drastically decreased after the early 1990s. In the western North Pacific, environmental conditions shifted from a cool regime in the late 1970s to a warm regime in the late 1980s. Variation in Pacific cod catches, especially in the Mutsu Bay, where it is warmer during the spawning season than in the Oyashio region, appears to coincide with the timing of the climatic regime shifts. (Fig. 13; right panel).

Chum salmon is the second most abundant salmonid in the North Pacific Ocean (PICES 2004). Its distribution ranges from southern Japan and Korea in the west to Oregon in the east (Groot and Margolis, 1991). In Japan, chum salmon are produced by hatcheries, where the number of returning adults peaked at about 87 million fish in 1996. The Bering Sea and the Gulf of Alaska are important habitats for feeding Japanese chum salmon during the ocean phase of their life history (Fig. 16) (Urawa, 2004). After the mid 1960s, the number of fry released and the number of adults returning increased until the mid 1990s. Accompanying the increased abundance was a decrease in mean adult body size and increases in age-at-maturity (Ishida et al., 1993). After the 1990s, the number of returning adults decreased drastically, and the size of the adults again increased (Kawasaki, 2002). The total biomass of Pacific salmon (*Oncorhynchus* spp.) has a 40- or 50-year periodicity in the North Pacific Ocean in connection with long-term climate conditions (Klyashtorin, 1998). The carrying capacity of Pacific salmon in the North Pacific Ocean may be closely related to long-term climate change and density-dependent effects (Kaeriyama et al., 2004).

Japanese sardine (hereafter, sardine) abundance has fluctuated greatly over the last two decades. The total catch of sardine was 20,000 t in 1970, increased to 2,210,000 t in 1980, and reached a maximum of 4,490,000 t in 1988. The catch has been declining since 1989,

falling to about 130,000 t by 2000 (Fig. 17, 18). During its most abundant phase in the 1980s, the sardines that spawn between the coast of southern Honshu and the Kuroshio Current in late winter-early spring, migrated northward across the Kuroshio-Oyashio transitional region and, in summer, fed on the abundant zooplankton and phytoplankton in the Oyashio water. In autumn, they migrated south to the waters off the Boso Peninsula (see Fig. 2) in central Honshu, Japan. It has been suggested that the drastic changes of the sardine stock during the last two decades changed both the structure and the function of the Oyashio ecosystem (Yatsu et al., 2005).

Both the biomass and Japanese commercial catches of small pelagic fishes including sardine reflect decadal changes or alternations of dominant species called “species replacements” (Kawasaki, 1983; Matsuda et al., 1992). Although the mechanisms for species replacements have not yet been fully resolved, ocean-climate regime shifts appear to have profound impacts on species dynamics and interactions (PICES, 2004). The role of sardines in the Oyashio region is particularly important as it is the most abundant species to invade the Oyashio from sub-tropical regions (Fig. 17). There is little information on how they interact with the more subarctic cold-water species, particularly the gadids.

Japanese anchovy (hereafter, anchovy) is a major commercial pelagic species in Japan. Of the four stocks around Japan (northern Pacific, southern Pacific, East China Sea and Japan Sea), the northern Pacific stock is the most abundant. Total annual landings in Japan were 350,000-450,000 t in 1950-1960s, but they decreased rapidly after 1975 during a period when sardine abundance was increasing (Figs. 17, 18). Anchovy abundance remained relatively low during the 1980s (150,000-200,000 t) but since 1989, landings have increased while the sardine biomass has declined.

As the stock size increases, anchovies become widely distributed off the Pacific coast of Japan (Funakoshi, 1992; Zenitani and Kimura, 1997). Larval anchovy are transported offshore and migrate northward (Aoki & Miyashita, 2000; Takasuka & Aoki, 2002, 2006) under the influence of a complex physical environment associated with the warm and cold waters of the Kuroshio and Oyashio currents, respectively. Currently, the annual anchovy migration extends to the Oyashio region during summer and autumn, but both their distribution and abundance in the Oyashio region can fluctuate annually (Fig. 17). The anchovy is the most abundant species to invade the Oyashio from subtropical regions after the late-1980s. Its role in relation to “species replacements” must be considered within the more general issues of

factors that affect recruitment success such as climate change, regime shifts and global warming.

Mackerel, including chub (*S. japonicus*) and spotted mackerels (*S. australasicus*), catches were high during the 1970s and decreased in the early 1990s, thereafter increasing slightly (Fig. 17, 18). Despite the occurrence of strong year-classes of chub mackerel in 1992 and 1996, intensive fishing of immature fishes prevented stock recovery (FAJ, 2002). Yatsu et al. (2005) suggested that chub mackerel might have shifted into a favorable fishery regime in 1992 had fishing mortality been lower. They also suggested that managers might consider varying fishing effort in response to changing stock productivity and to protect strong year-classes during favorable regimes such as the 1970s. If carnivorous mackerels invade the Oyashio region, it will be important to consider how they might affect the structure and function of the ecosystem. Learning how to adaptively control catch will be important (Yatsu et al., 2005).

Pacific saury (hereafter referred to as saury) is distributed throughout most of the northern North Pacific. In the west, it is one of the major species taken by Japanese, Russian and Korean fisheries. There is no estimate of population size because the distribution of larvae, juveniles and adults is continuous from the western to the eastern Pacific. After World War II, a new fishing gear (the stitch-held dipnet or bouke-ami), was introduced in Japan. Thereafter, the total catch increased remarkably, reaching a maximum of 575,000 t in 1958 during the peak period from 1955-1963 (Fig. 18). By 1969, the catch of saury had declined to 52,000 t. The annual catch fluctuated widely in the 1970s ranging between 87,000-427,000 t. In the late 1980s, the Japanese catch stabilized because of landing regulations adopted by the Japanese saury fishermen's association.

Saury spawn off northern Honshu in autumn and spring and in the Kuroshio area in winter. Juveniles produced in different spawning seasons start migrating northward to the Oyashio area in early summer where they feed on abundant zooplankton, especially *N. plumchrus* and euphausiids (Ito et al., 2004). In the western Pacific, saury reach a length of 30 cm in 1 year (Watanabe et al., 1988). Their life span has been estimated to be 1.5-2.0 years (Suyama et al., 1996). The fishing grounds in the Oyashio region in autumn vary depending on the location of the Oyashio and warm core rings that originate in the Kuroshio and Tsugaru Warm Current.

A fish bioenergetics model (NEMURO.FISH, the saury version) coupled with a lower trophic level ecosystem model (NEMURO) was able to reproduce saury growth trajectories (Ito et al., 2004). Tian et al. (2004) examined the influence of oceanic and climatic changes on

the dynamics of saury in the northwestern Pacific using a life-cycle model. These results suggested that SST in the Kuroshio region is responsible for decadal-scale changes in saury abundance. They also found that ENSO events influence the survival of the winter spawning cohort and are responsible for the large interannual variations in their abundance.

Japanese common squid (hereafter common squid) is a commercially important squid in Japan and Korea. Annual catches in Japanese and Korean waters have increased markedly since the late 1980s, and catches of the late 1990s are equal to those of the 1960s (c.a. 400,000-700,000 t) (Fig.17, 18). Compared to the late 1970s and mid-1980s, paralarval abundances have also been higher since the late 1980s (Murata, 1989). In the western North Pacific, atmospheric temperatures and SSTs shifted from a warm regime, which began in the late 1940s, to a cool regime in the late 1970s, and back to a warm regime in the late 1980s (Minobe, 1997). These regimes coincided with variation in common squid catches, particularly the declines in the early 1980s catch, and the increases in the late 1980s. Sakurai et al. (2000, 2002) suggested that the winter spawning areas for common squid in the East China Sea shrank when the adult stocks decreased during the cool regime. Fall and winter spawning areas expanded and overlapped in the Sea of Japan and East China Sea when adult stocks increased during the warm regime that occurred after 1989. After 1989, the feeding area of the winter spawning stock expanded to the Oyashio region during summer-autumn. Common squid feed on small fishes and large zooplankton. It has also been suggested that it feeds on juvenile walleye pollock on the Oyashio shelf region during autumn (Sakurai and Yasui, unpublished data).

3. 2. 2. Marine mammals and seabirds

The Oyashio region supports a diverse assemblage of temperate and sub-arctic marine mammals and seabirds. Thirty-three species of Pinnipedia (sea lions, fur seal and seals) and Cetacea (whales, dolphins and porpoises) are present in the region for varying amounts of time during the year (Hunt et al., 2000). Some species are resident throughout the year (*e.g.*, harbor seal and Dall's porpoise), while others migrate into the Oyashio region during summer months to feed (*e.g.*, minke, sei, and killer whales). About 60 species of seabirds are present in the Oyashio/Kuroshio regions, however, information on their ecology and distribution is generally lacking. Therefore, only the Steller sea lion, *Eumetopias jubatus*, and the common minke whale, *Balaenoptera acutorostrata*, are discussed here.

Steller sea lion, is listed as an endangered species by IUCN and is listed as a threatened species in Japan, where it causes about US\$10 million annually in damage to fishing gear. After the late 1980s, winter haulout sites of Steller sea lion shifted from the Oyashio region to the Sea of Japan (Hosino et al., 2006). Counts of Steller sea lion wintering along the Hokkaido coast of the Sea of Japan have varied from about 390 in 2000-2001, to 135 in 2001-2002, and 200 in 2002-2003 (Sakurai et al., 2004). These relatively high numbers may be due to ecosystem changes that have occurred in the neighboring Sea of Okhotsk where, for example, the abundance of walleye pollock is lower (Radchenko, 2001). Since the late 1980s, some pelagic species such as anchovy, common squid, and arabesque greenling (*Pleurogrammus azonus*) have migrated to the Sea of Okhotsk during summer and fall, and to the Sea of Japan in winter. Steller sea lions are thought to follow this prey into the Sea of Japan. Aerial surveys have shown that movement occurred between the Rishiri-Rebun Islands and Tsugaru Strait from February to April centering on two haul-out sites: Cape Ofuyu during mid-November to early May, and Cape Kamui during mid-December to early March (Hoshino et al., 2006). Both sites appear to serve as winter haulouts for Steller sea lions feeding on spawning schools of arabesque greenling and walleye pollock.

The common minke whale (hereafter, minke whale) is widely distributed throughout the world. In the western North Pacific, two stocks have been recognized: one in the Sea of Japan-Yellow Sea-East China Sea (J stock) and the other in the Sea of Okhotsk-West Pacific (O stock) (Tamura & Kato, 2003). In the western North Pacific, the minke whale is an opportunistic feeder with a broad diet and flexible feeding habits. The daily consumption of a mature minke whale is 200 kg (Tamura & Fujise, 2002). On the Pacific side of Japan, this species feeds mainly on sardine, anchovy and saury (Tamura & Fujise, 2002). The occurrence reflects a change of abundant species from chub mackerel to sardine in 1977, and from sardine to saury in 1996 (Fig. 19) (Tamura & Fujise, 2002).

4. Conclusion

This review described recent decadal changes of the Oyashio ecosystem including oceanography, productivity and some key species, such as fish, invertebrates, and marine mammals. The Oyashio ecosystem has shown drastic changes in pelagic species abundance or distribution called “species replacements (Kawasaki, 1983; Matsuda et al., 1992)” that have been correlated with environmental changes that occurred during 1976/77 and 1988/89 regime shifts (i.e., SST, Oyashio Intrusion, and productivity). Sardines were abundant in the Oyashio

region during the 1980s, but there is little information on how they interacted with the more subarctic cold-water species, particularly the gadids. During the 1990s, the most abundant subtropical species in the region have been Japanese anchovy and Japanese common squid. If carnivorous mackerels invade the Oyashio region in the future, as they did in the 1970s, we must consider how they might affect the structure and function of the ecosystem. Ecosystem change in the Oyashio region must be considered within the more general issues of factors that affect the productivity, “species replacements ” and their recruitment success, such as changing environment conditions. Comparative and cooperative studies among marginal marine ecosystems in the North Pacific are needed to understand their response to climate change such as the effects of their variation in sea ice conditions in the Sea of Okhotsk and vulnerability to intensive fisheries.

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Captions of Figures

Figure 1. Diagram of the relationship of the Oyashio Current to other currents in the Northwest Pacific Ocean. Modified from Qiu, 2001.

Figure 2. Topography of Oyashio region and the adjacent areas.

(JODC, <http://www1.kaiho.mlit.go.jp/KAN9/sodan/kaiteitikei/japan006.jpg>)

Figure 3. Changes in annual mean latitude of South Limit of First Oyashio Intrusion (SL01: coastal intrusion) from 1960 to 2005. Thick line indicates 5-year running mean.

Figure 4. Maximum ice cover area in each year.

Left: March 10, 2006, 903 thousand km². Red line denotes the edge of sea ice in normal year. Right (upper): Year of maximum sea ice cover, Feb. 28, 1978, 1,525 thousand km². Right (lower): Year of minimum sea ice cover, Feb. 25, 1984, 858.1 thousand km².

(JMA,

http://www.data.kishou.go.jp/kaiyou/shindan/rinji/2006_no1/nh_snow_time_series.html)

Figure 5. Schematic diagram of a bidecadal variation related with the 18.6-year nodal tidal cycle. This figure corresponds to the strong diurnal tide period. Enhanced EPS (Osafune and Yasuda, 2006)

Figure 6. Chlorophyll (mg m⁻³) averaged in May, 1999 from the Sea WiFS satellite. Blue line indicates PH-line stations at which biological data were collected (Tadokoro et al., 2005)

Figure 7. Interannual variation in annual mean SST (°C) and SSS of the Oyashio waters in spring and summer from 1970 to 1999. Solid and broken lines show the 5-yr running means. (Tadokoro et al., 2005)

Figure 8. Interannual variation in annual mean diatom abundance (cells m³) and chlorophyll *a* concentration (mg m³) at the surface in spring and summer from 1972 to 1999. Solid and broken lines show the 5-yr running means. (Tadokoro et al., 2005)

Figure 9. Interannual variation in annual mean zooplankton biomass in spring and summer determined from surveys along the PH-line from 1972 to 1999 and from surveys conducted by the Tohoku National Fisheries Research Institute (TNFRI) during 1970 – 99 in the area bounded by 36 and 45°N, 155°E. Units are mg WW m⁻³ for the PH-line and mg WW m⁻² for TNFRI data. Bars denote ± SD. Solid and broken lines show the 5-yr running

means. (Tadokoro et al., 2005)Figure 10. Interannual variation in annual mean abundance (individuals m³) and biomass (mg WW m³) of *N. flemingeri*, *N. plumchrus*, and *N. cristatus* during spring and summer from 1980 to 1999. Bars denote ±SD. Solid and broken lines show the 5-yr running means.

Figure 11. Schematic illustration of spawning strategy and reproductive characteristics of Pacific cod and walleye Pollock. (Sakurai, 1989; Sakurai and Hattori, 1996) Figure 12.

Walleye pollock catches in the Oyashio region and the Nemuro Strait, northern Hokkaido.

Figure 13. Schematic illustration of reproductive success of the Pacific pollock stock in the Tohoku region related to variation in the Oyashio, coastal Oyashio, Tsugaru Warm Current and Kuroshio. (Suzaki et al., 2003)Figure 14. Diagram showing components and major processes included in the trophodynamic modelling of walleye pollock.

(Yamamura, 2004)

Figure 15. Pacific cod catches in the Oyashio region off Tohoku and off Hokkaido.

Figure 16. A seasonal migration model of Japanese chum salmon estimated by genetic stock identification. (Urawa, 2004)Figure 17. Japanese catches of sardine, anchovy, chub mackerel and common squid along the Pacific coast of Japan. (PICES, 2005)Figure 18.

Catches for Japanese small pelagic fisheries. Selected environmental information includes time periods when the Kuroshio Current followed 'type A' paths (large meandering), and pentadecadal (50 yr) and bidecadal (20 yr) shifts in the Pacific Decadal Oscillation (PDO, Minobe, 2000) Mackerels include chub and spotted mackerels. (Yatsu et al., 2005)Figure 19.

Annual changes of relative frequency of occurrence of each dominant prey species consumed by minke whale (A) and the commercial catch of pelagic fishes in the Pacific coast of Hokkaido (B). (Tamura and Kato, 2003)

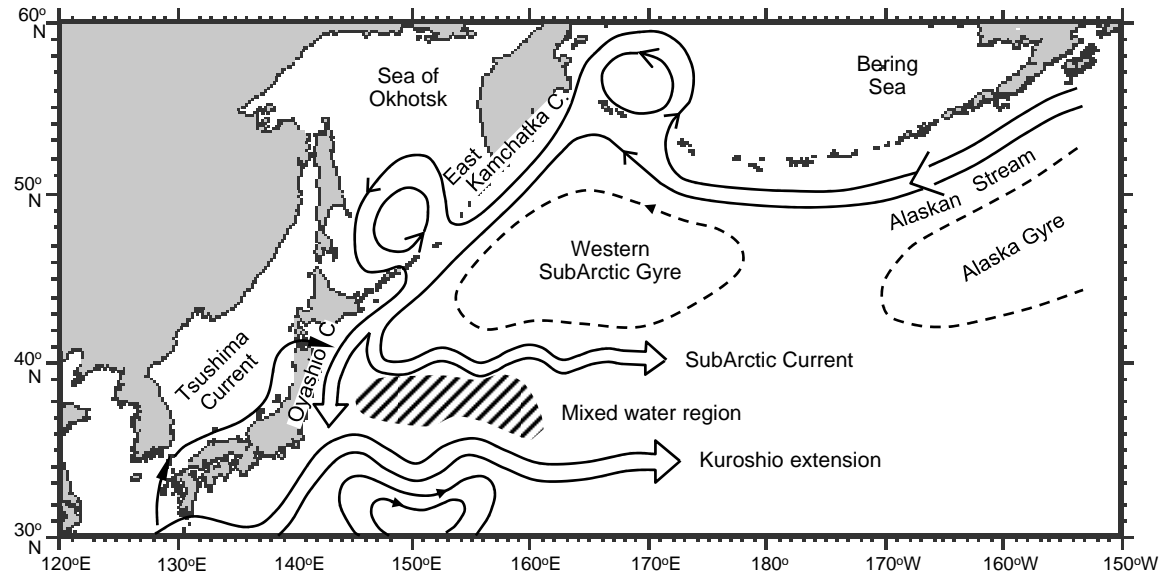


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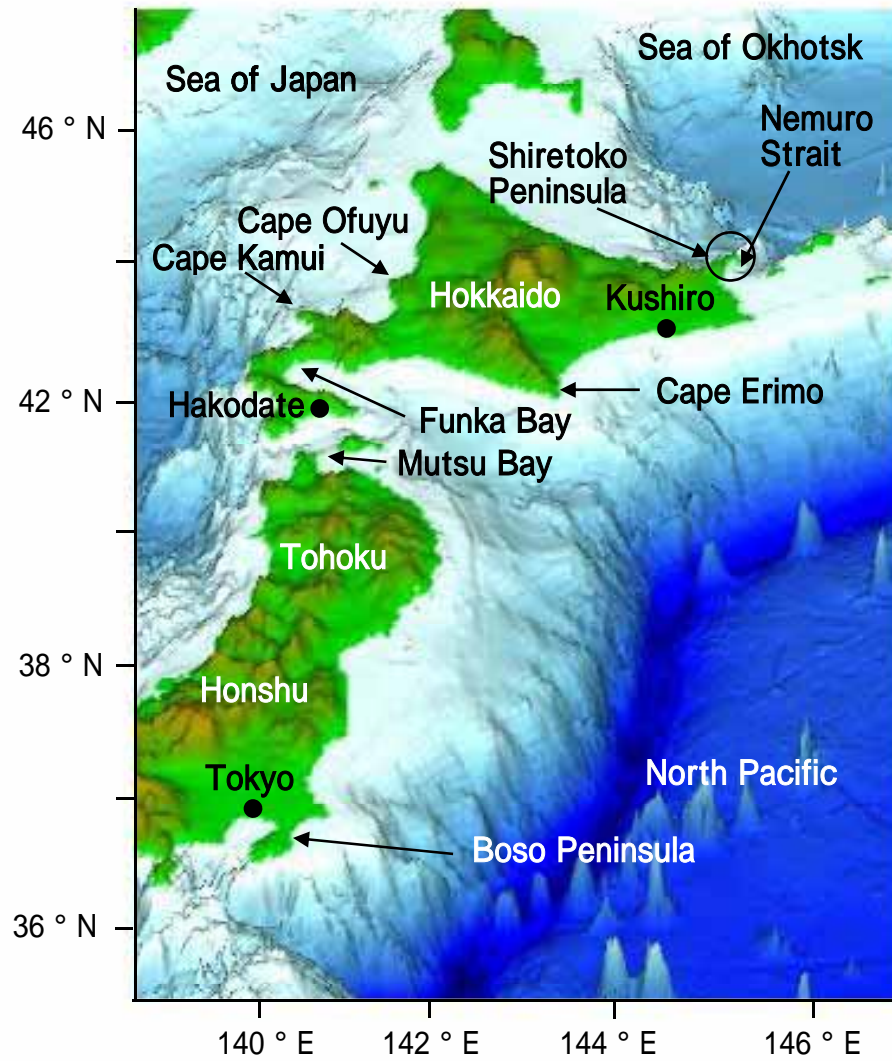


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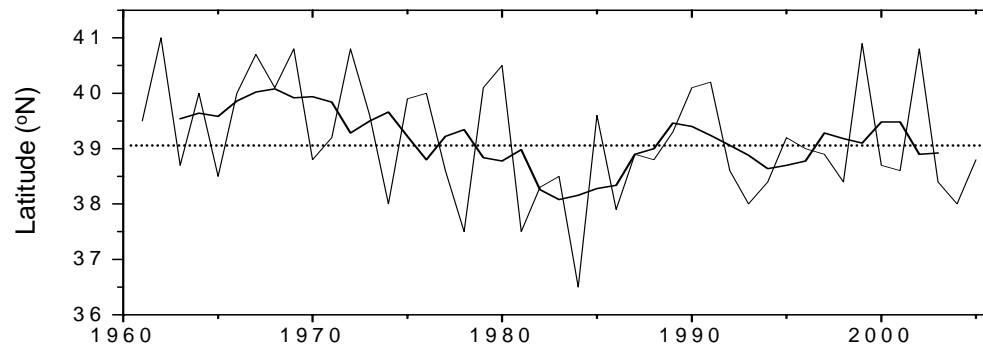


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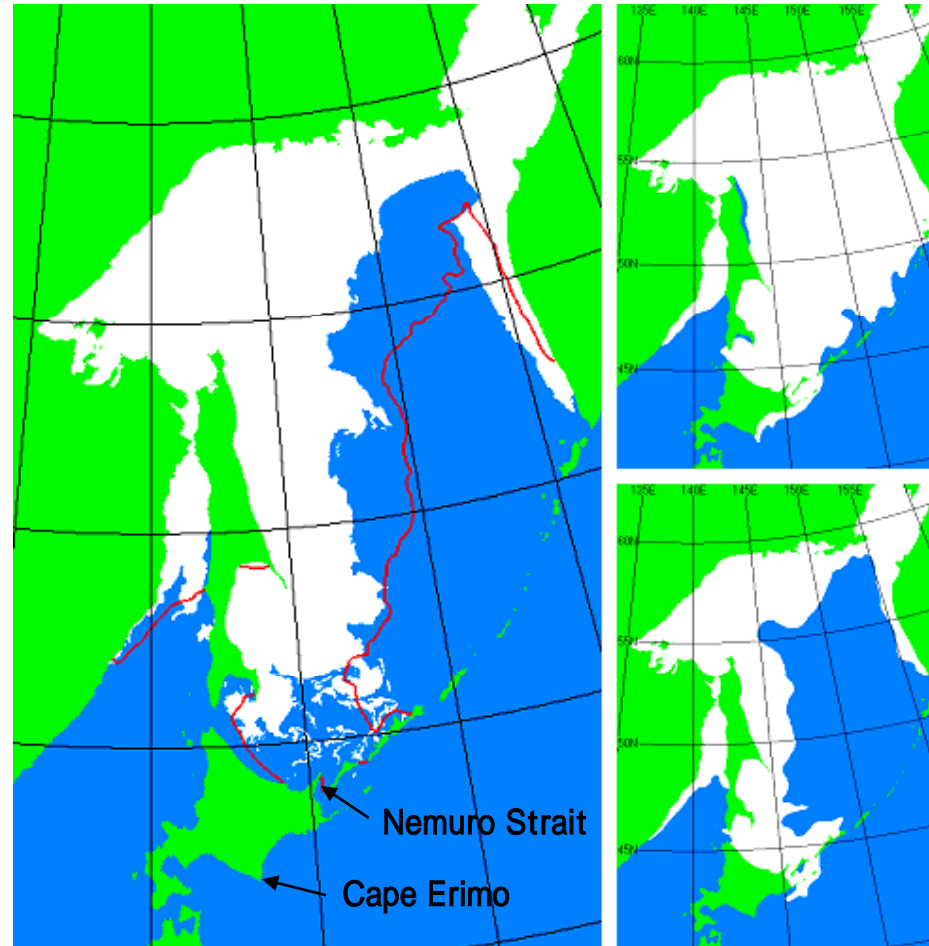


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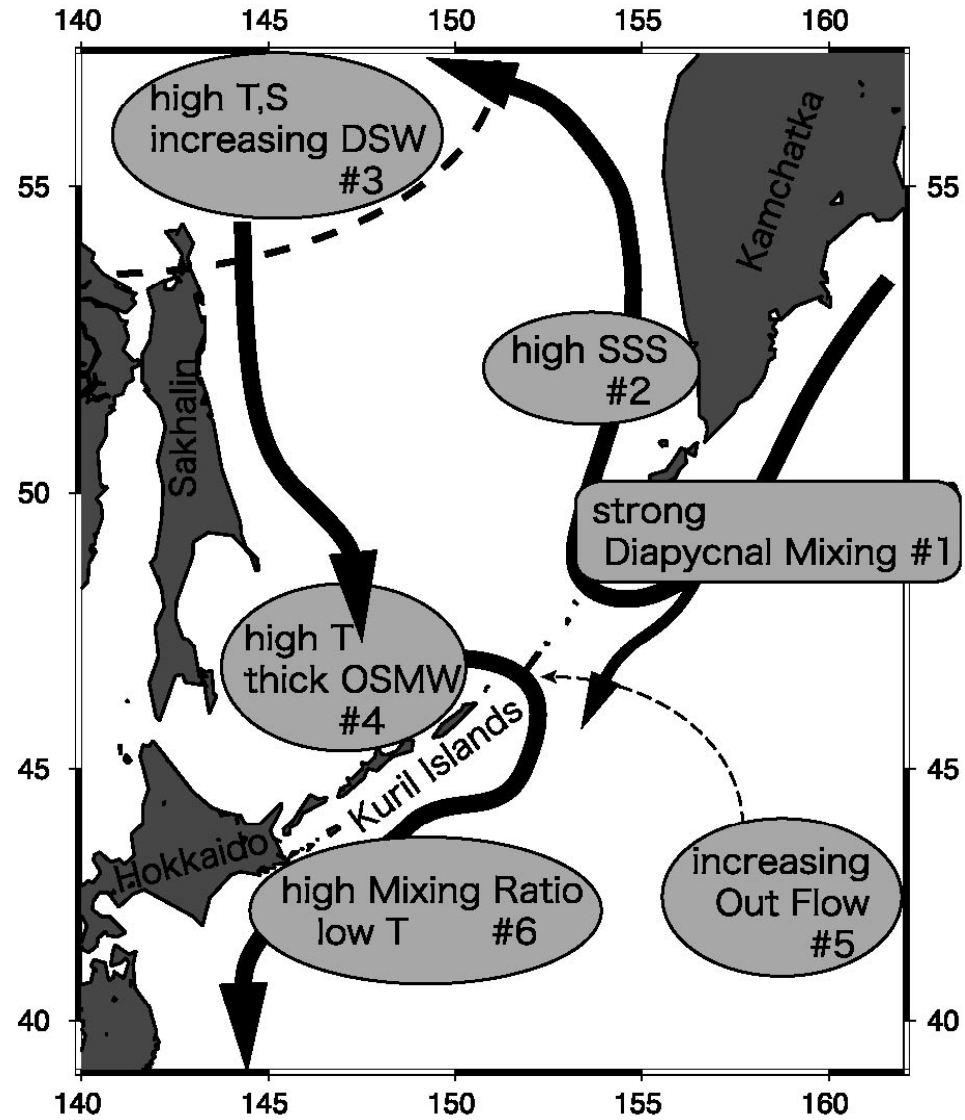


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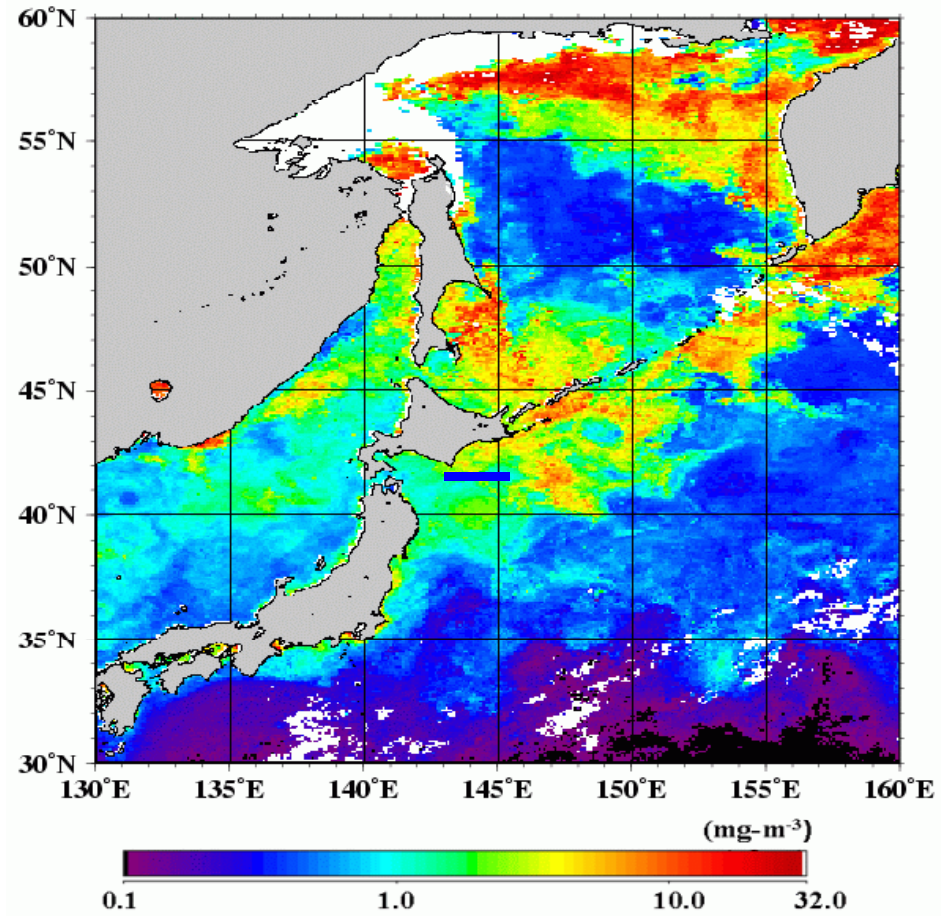


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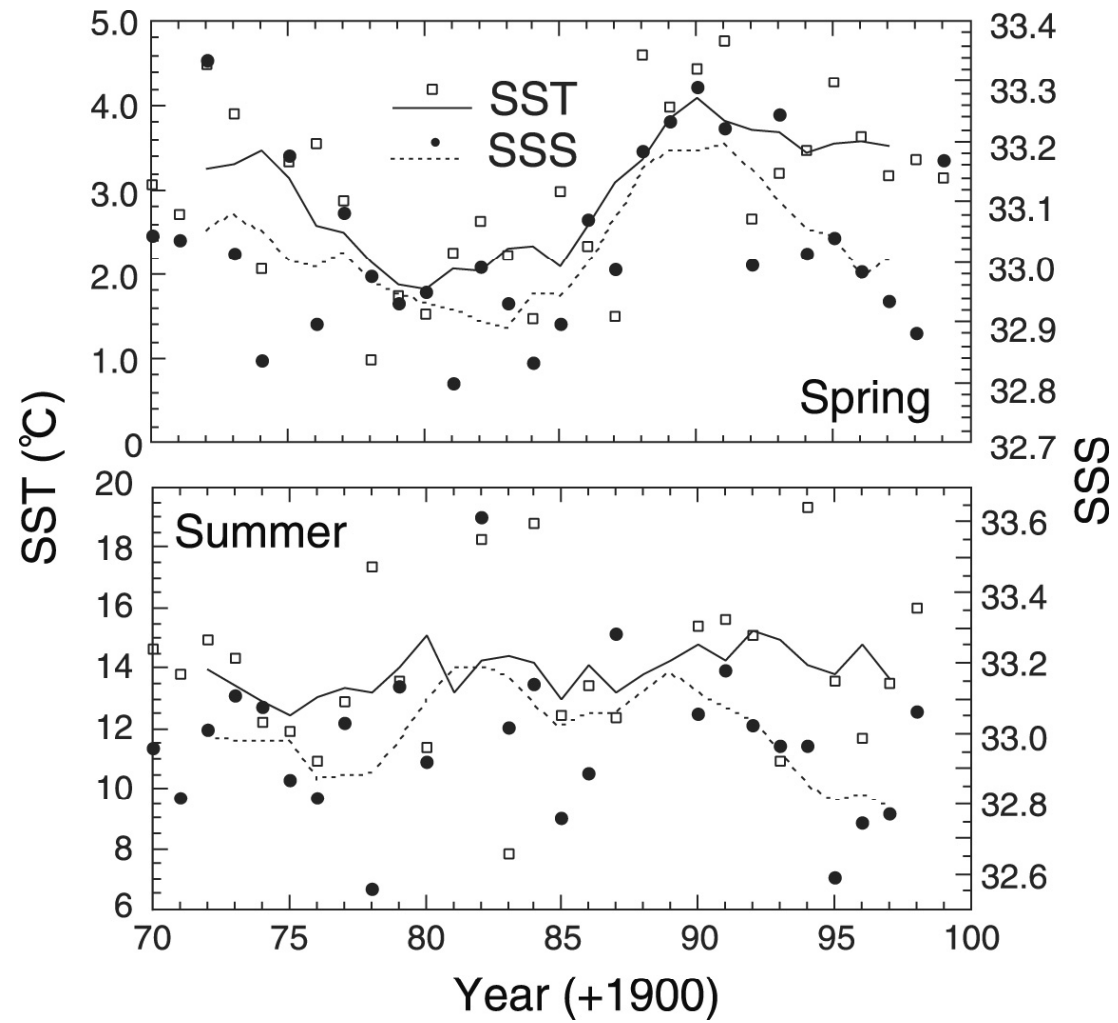


Fig. 7. Interannual variation in annual mean SST ($^{\circ}$ C) and SSS of the Oyashio waters in spring and summer from 1970 to 1999. Solid and broken lines show the 5-yr running means. (Tadokoro et al., 2005)

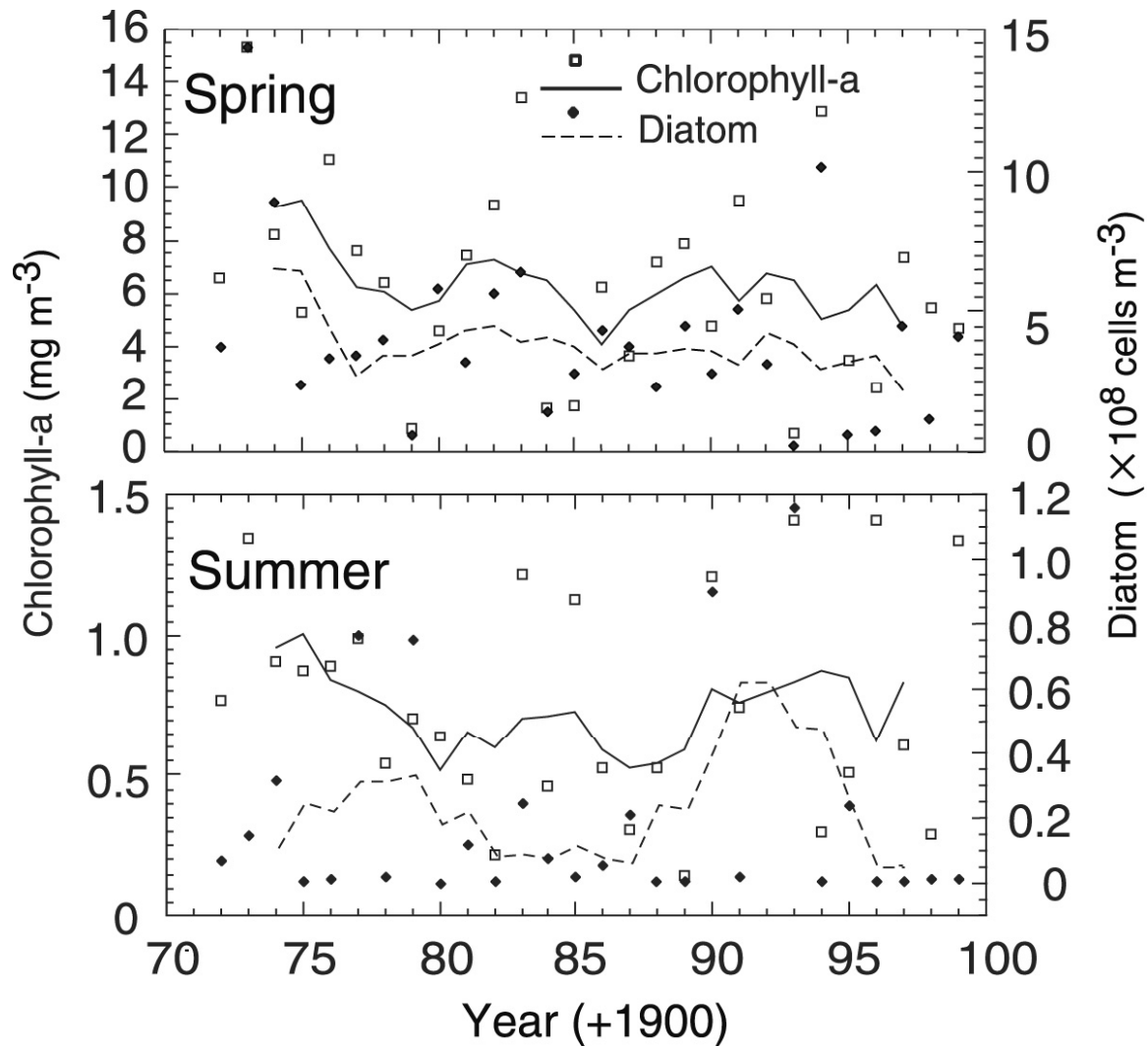


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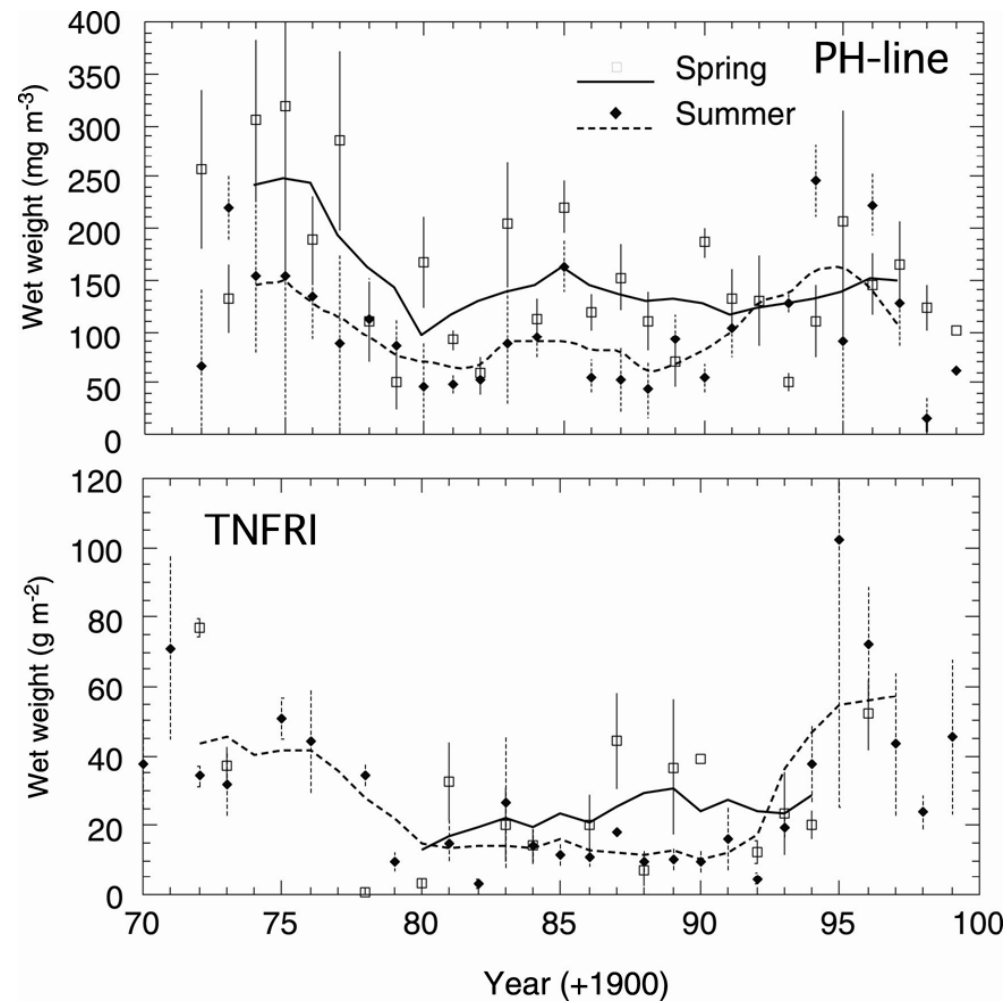


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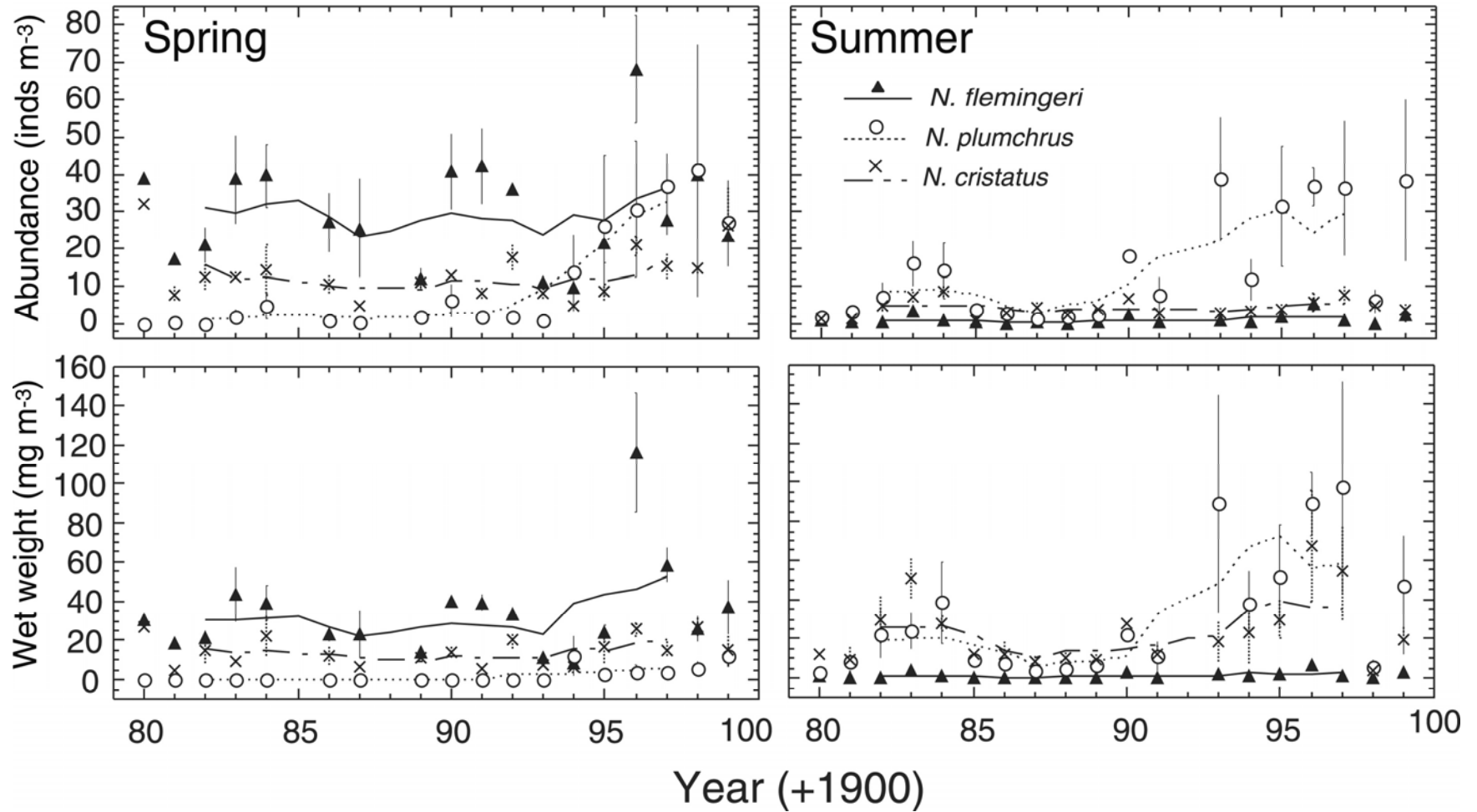


Fig. 10. Interannual variation in annual mean abundance (individuals m³) and biomass (mg WW m³) of *N. flemingeri*, *N. plumchrus*, and *N. cristatus* during spring and summer from 1980 to 1999. Bars denote \pm SD. Solid and broken lines show the 5-yr running means.

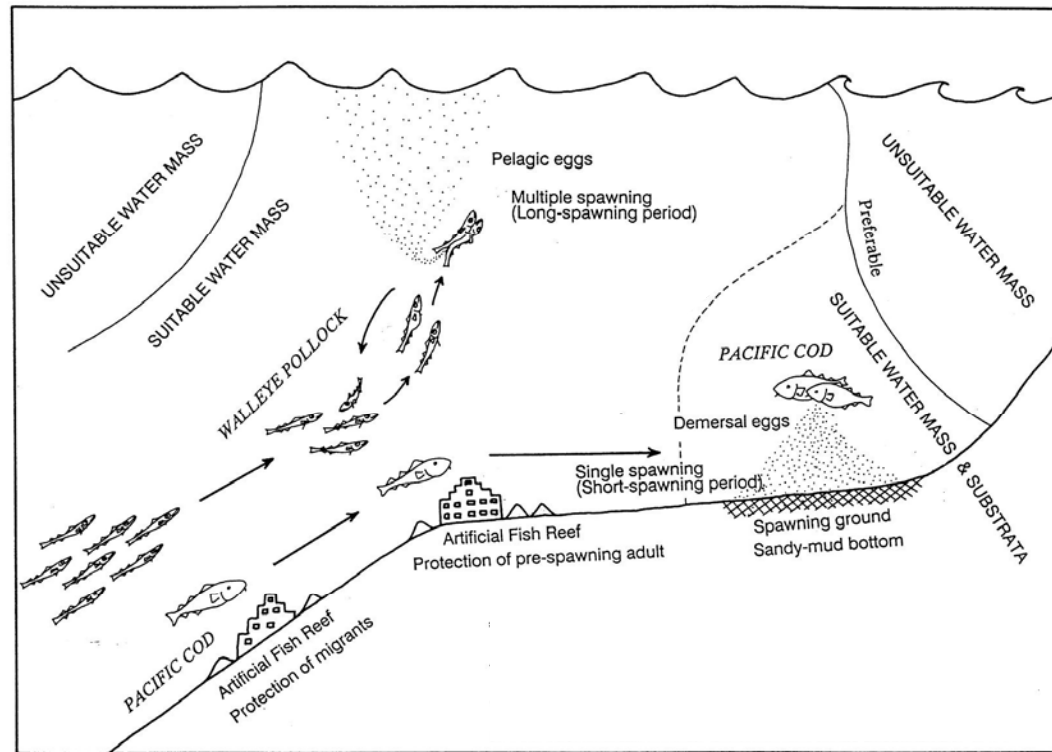


Fig. 11. Schematic illustration of spawning strategy and reproductive characteristics of Pacific cod and walleye Pollock. (Sakurai, 1989; Sakurai & Hattori, 1996)

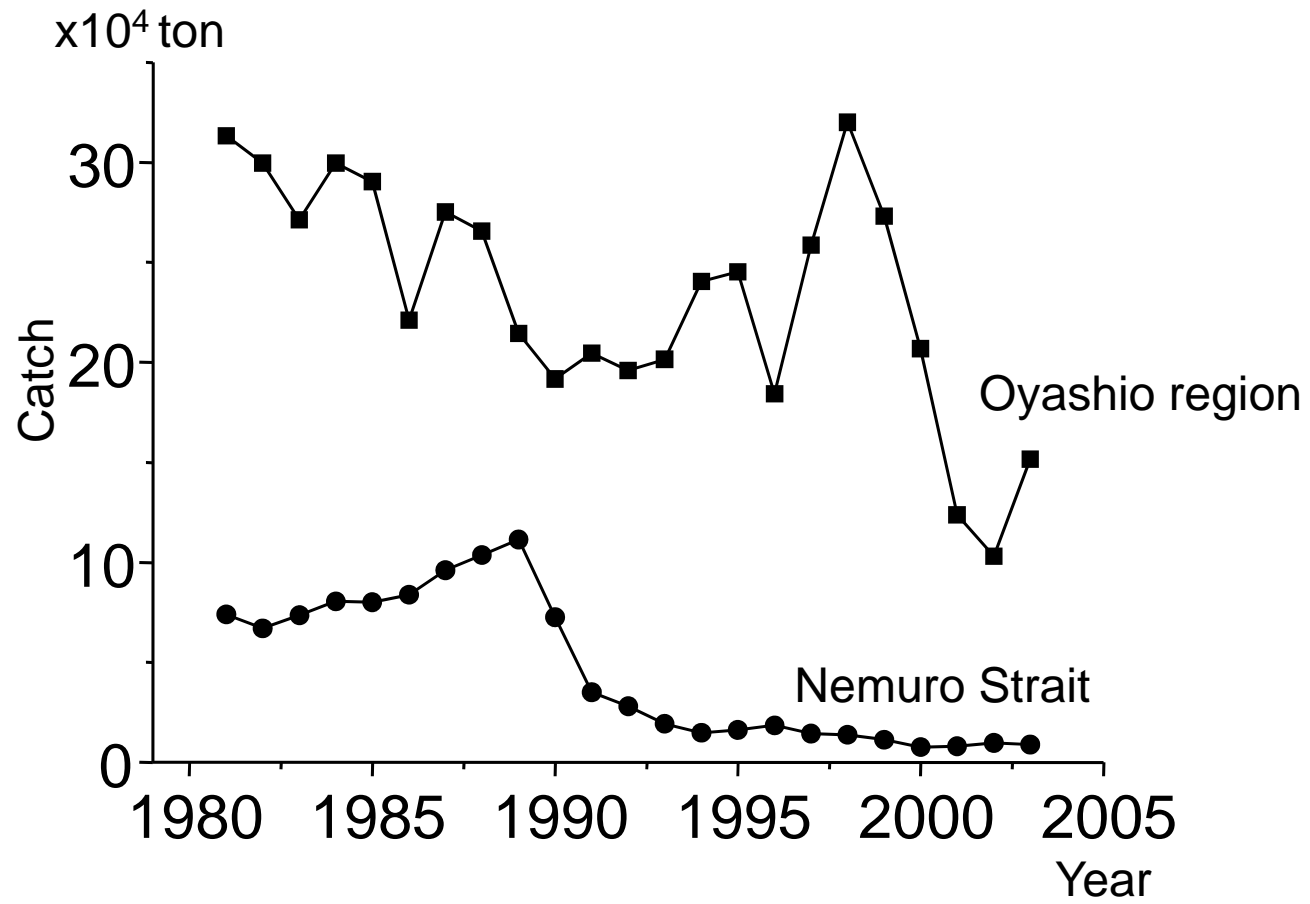


Fig. 12. Walleye pollock catches in the Oyashio region and the Nemuro Strait, northern Hokkaido.

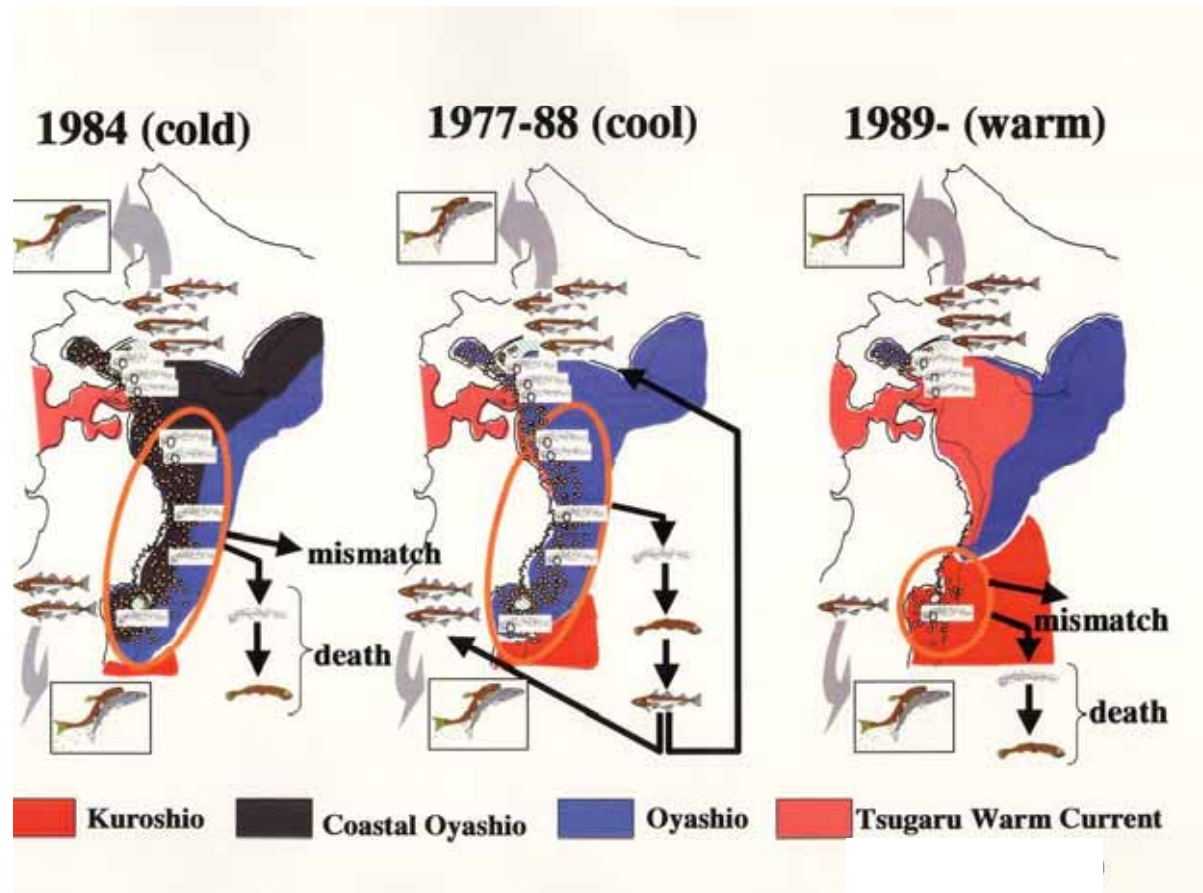


Fig. 13. Schematic illustration of reproductive success of the Pacific pollock stock in the Tohoku region related to variation in the Oyashio, coastal Oyashio, Tsugaru Warm Current and Kuroshio. (Suzaki et al., 2003)

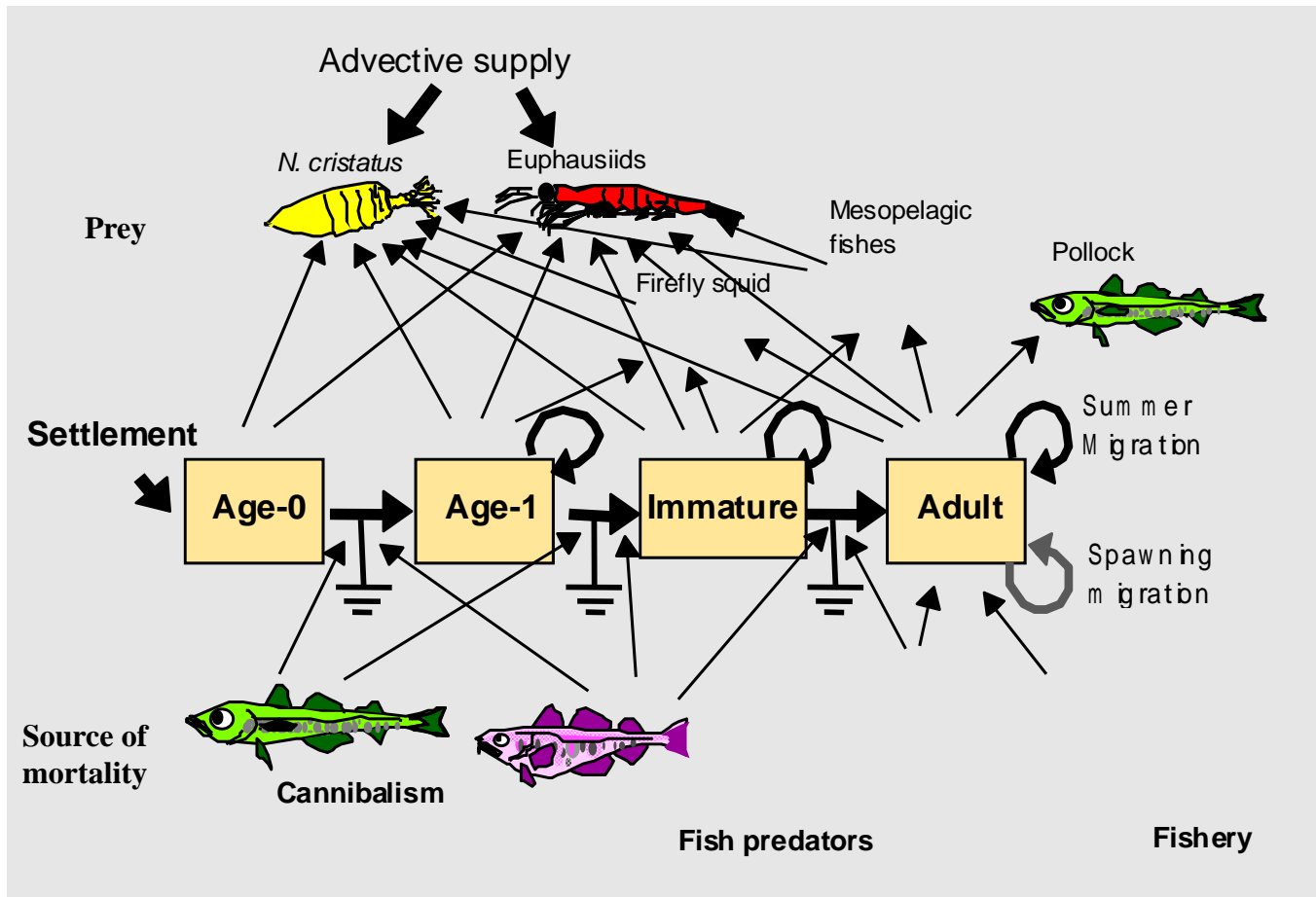


Fig. 14. Diagram showing components and major processes included in the trophodynamic modelling of walleye pollock. (Yamamura, 2004)

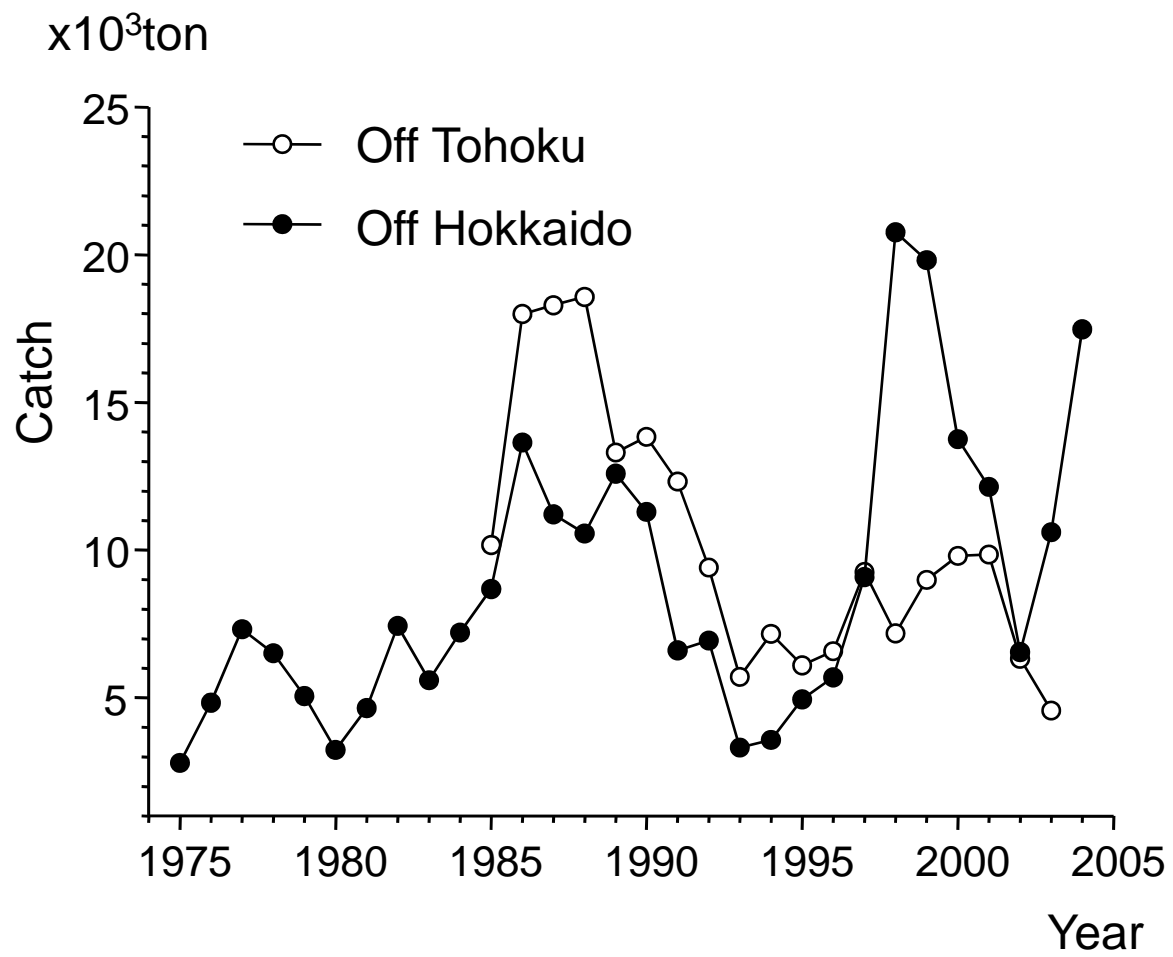


Fig. 15. Pacific cod catches in the Oyashio region off Tohoku and off Hokkaido.

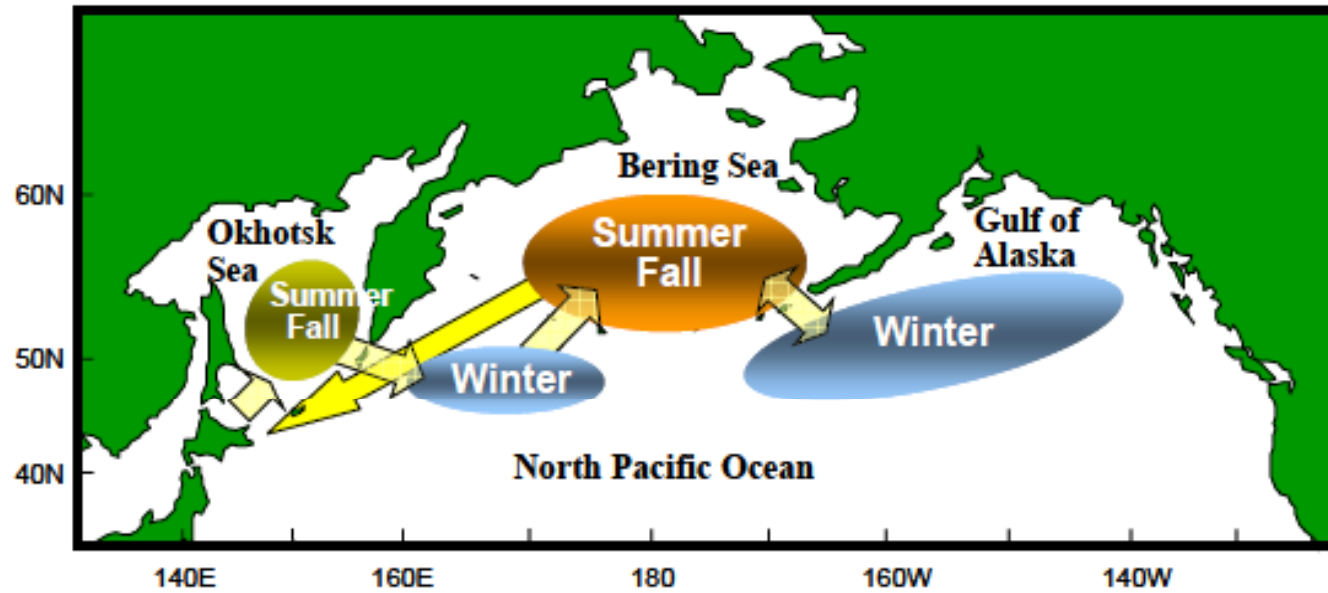


Fig. 16. A seasonal migration model of Japanese chum salmon estimated by genetic stock identification. (Urawa, 2004)

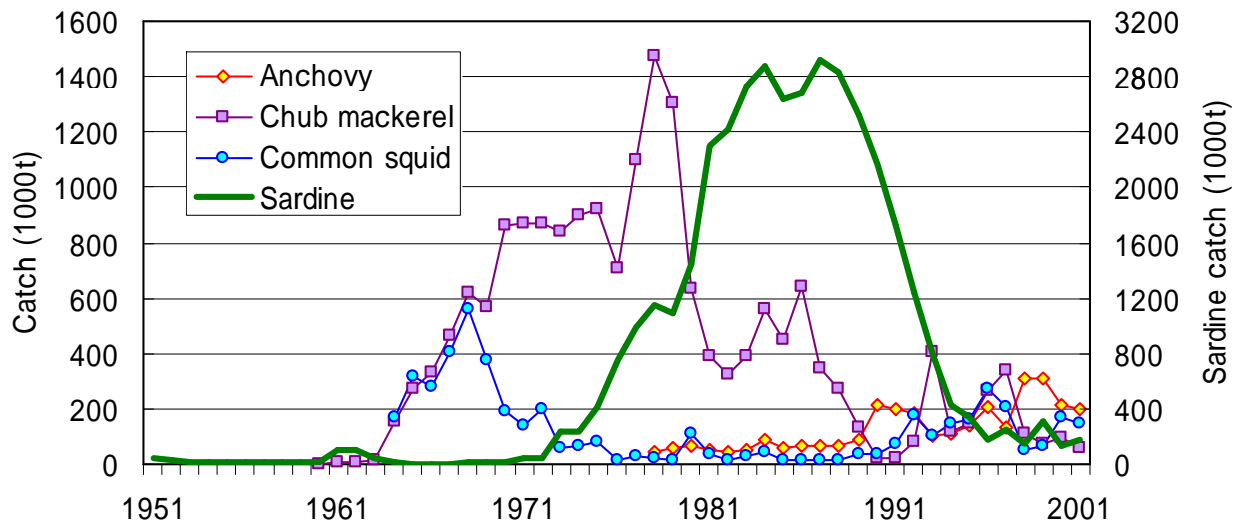


Fig. 17. Japanese catches of sardine, anchovy, chub mackerel and common squid along the Pacific coast of Japan. (PICES, 2005)

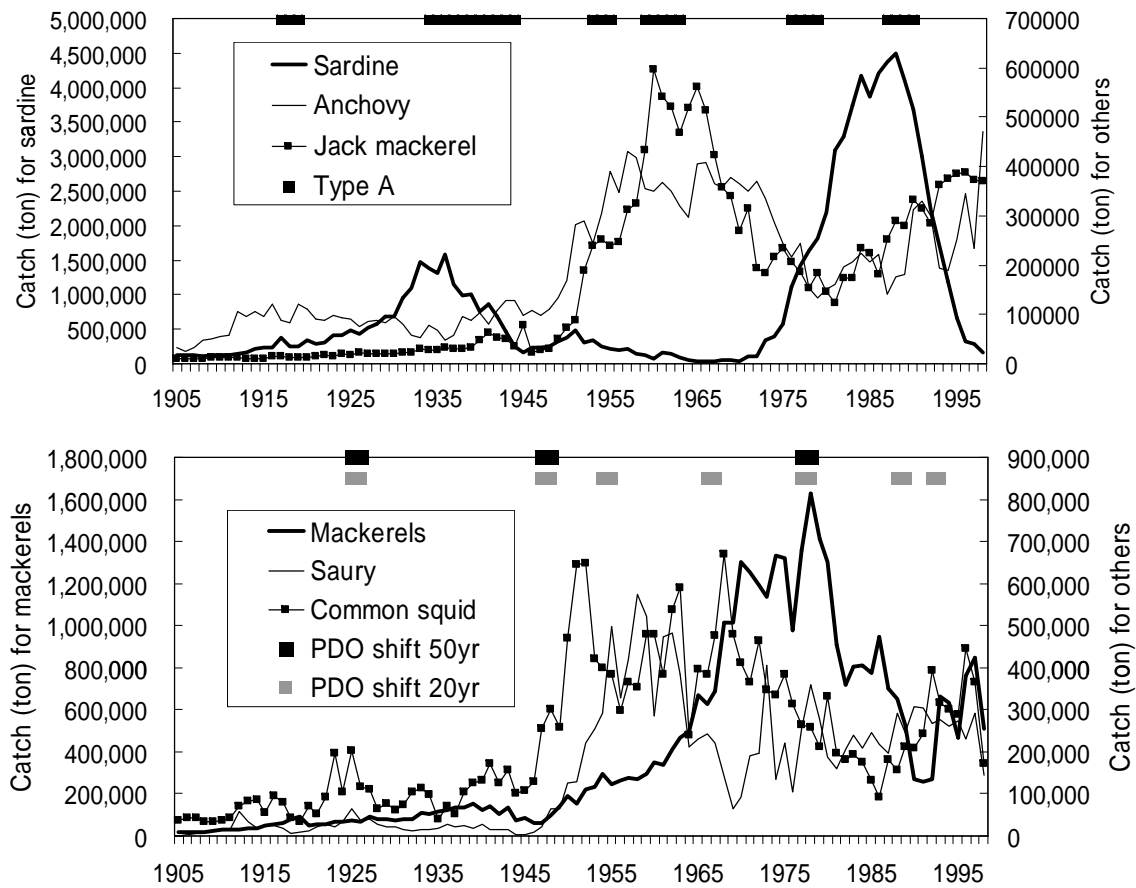


Fig. 18. Catches for Japanese small pelagic fisheries. Selected environmental information includes time periods when the Kuroshio Current followed 'type A' paths (large meandering), and pentadecadal (50 yr) and bidecadal (20 yr) shifts in the Pacific Decadal Oscillation (PDO, Minobe, 2000) Mackerels include chub and spotted mackerels. (Yatsu et al., 2005)

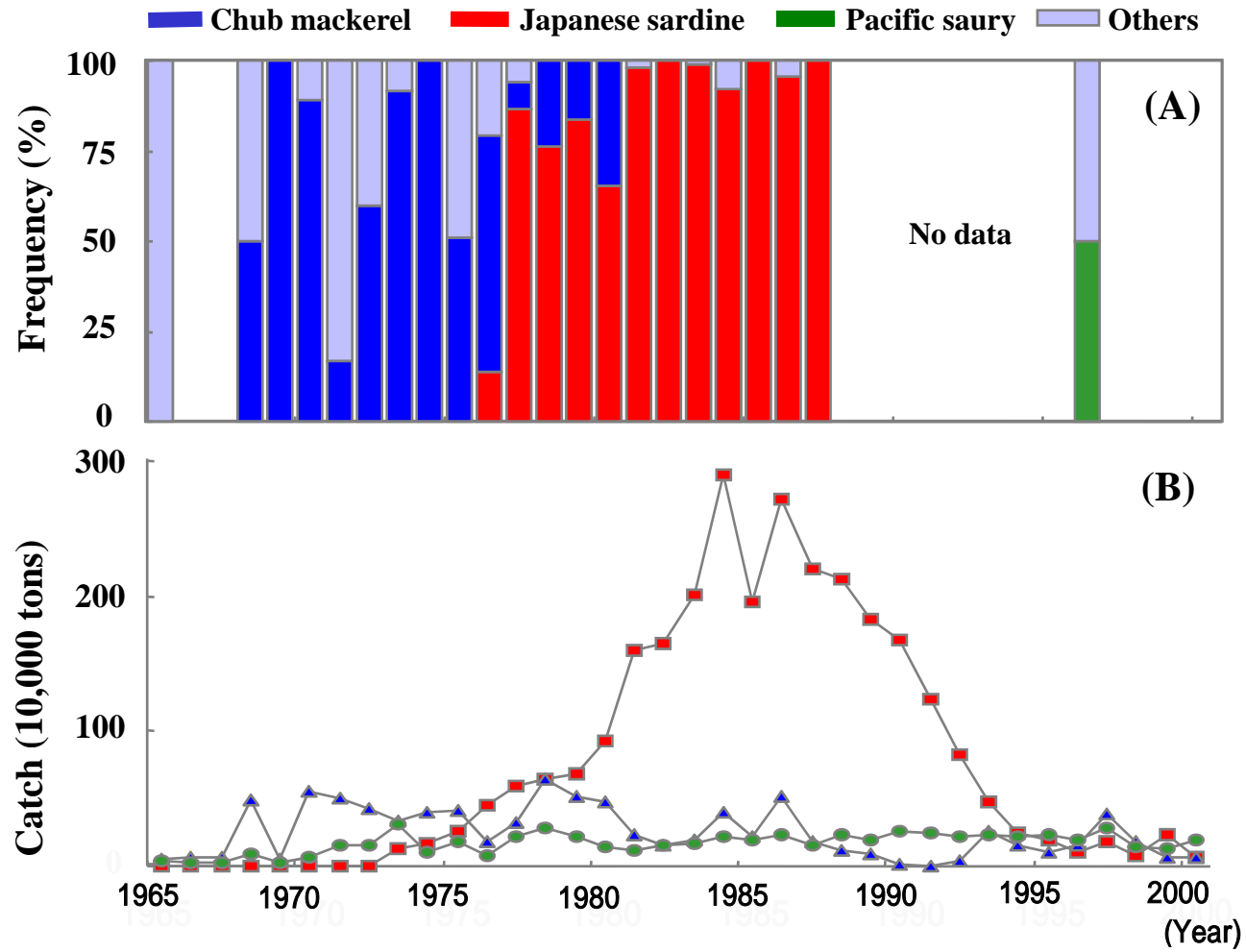


Fig. 19. Annual changes of relative frequency of occurrence of each dominant prey species consumed by minke whale (A) and the commercial catch of pelagic fishes in the Pacific coast of Hokkaido (B). (Tamura and Kato, 2003)