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Interannual fluctuations in recruitment of walleye pollock in the Oyashio region related to environmental changes

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Abstract

The Japanese Pacific walleye pollock (*Theragra chalcogramma*) stock is the largest stock of this species in Japanese waters. It is a key component of the Oyashio ecosystem. In southern Hokkaido waters, these fish spawn mainly during January and February near the mouth of Funka Bay (FB), and most eggs and larvae are transported into FB. During midsummer juvenile pollock migrate along the southern coast of Hokkaido to a nursery ground on the continental shelf off eastern Hokkaido (Doto area). However, some eggs and larvae are transported southward to the Tohoku region (TR). Transport depends largely on the Oyashio, which generally flows southward along the eastern coasts of Hokkaido and Tohoku. Thus, this stock has two different recruitment routes: FB–Doto and FB–TR. In the 1980s, when the southward flow of the Oyashio was strong, the number of age-2 pollock estimated from a virtual population analysis

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(VPA) indicated that recruitment to the entire stock remained at a medium level. In the 1990s, when the Oyashio weakened, strong year-classes occurred in 1991, 1994, and 1995, but not in the latter half of the 1990s. Juvenile catches in the TR by commercial fisheries, which can be taken as indices of recruitment level via FB-TR, were high during the 1980s and decreased in the 1990s. Although there was no significant difference in the average number of recruits between the 1980s and the 1990s as estimated from a VPA, the recruitment patterns differed between the two decades. Here, we propose that recruitment routes of this stock shifted in response to environmental changes.

Keyword: climate changes; environmental conditions; Oyashio; recruitment; water temperature; Walleye pollock,
Regional Index Terms: Japan; Funka Bay; Tohoku region; Pacific coast of eastern Hokkaido (Doto area)

1 Introduction

The Japanese Pacific walleye pollock (*Theragra chalcogramma*) stock is the most abundant stock of this species in the waters around northern Japan (Hamatsu et al., 2004). It is distributed off the Pacific coast of the Tohoku region and Hokkaido (Fig. 1; Tsuji, 1989) and is a key component of the Oyashio ecosystem, as well as an important target species for local fisheries (Sakurai and Miyake, 1994). Four walleye pollock stocks (the Japanese Pacific stock, the northern Japan Sea stock, the southern Okhotsk Sea stock and the Nemuro Strait stock) occur in Japanese waters, and annual landings of these stocks, except for the Japanese Pacific stock, decreased dramatically from the late 1980s to the early 1990s (Honda et al., 2003). Recently, changes in pollock abundance correlated with fluctuations in the physical environment have been reported, and Oh et al. (2002) noted that changes in water temperature influenced reproduction in the northern Japan Sea walleye pollock stock and led to fluctuations in stock abundance. With respect to the Japanese Pacific stock, many scientists have discussed the relationship between interannual variation in environmental conditions and pollock recruitment (e.g., Isoda et al., 1998; Suzaki, 2003). Hamatsu et al. (2004) also reported decadal-scale changes in environment conditions around the main spawning ground of the Japanese Pacific stock between the 1980s and 1990s. However, these studies did not explain why the abundance of the Japanese Pacific stock remained relatively stable over the last two decades. This paper reviews information on the Japanese Pacific walleye pollock stock and environmental conditions during the 1980s and 1990s. We focus on the early life stages because larval survival is important for determining the year-class strength of this stock (Kendall and Nakatani, 1992; Nishimura et al., 2002; Hamatsu et al., 2004). We discuss the relationship between interdecadal fluctuations in recruitment location and environmental changes, and we propose a possible mechanism.

2 Life history

There are several spawning areas (Fig. 1) in the distribution area of the Japanese Pacific pollock stock (Wakabayashi et al., 1990). The main spawning area is near the mouth of Funka Bay (FB; Kobayashi, 1985; Wakabayashi et al., 1990). Adult walleye pollock spawn there from November to March with a peak in January and February (Yoon, 1981; Maeda, 1986). The majority of eggs and larvae are transported into FB, where they remain until early summer (Nakatani and Maeda, 1981, 1987; Shimizu and

Isoda, 1997). In July and August, juvenile fish migrate from FB to the continental shelf of eastern Hokkaido (Doto area; Honda et al., 2004), where pollock, from age-0 juveniles to adults, are distributed across the continental shelf to the slope (Watanabe et al., 1993; Miyake et al., 1996; Shida, 2002). The continental shelf region is considered the most important nursery area for pre-recruit fish (Nishimura et al., 2002; Shida and Nishimura, 2002; Honda et al., 2004), but currents transport some eggs and larvae spawned around FB southward to Pacific waters off the Tohoku region (TR; Hashimoto and Ishido, 1991), which is also considered a nursery area for pre-recruit fish. Therefore, the Japanese Pacific stock has one main spawning ground (FB) and two different recruitment routes (FB–Doto and FB–TR).

3 Walleye pollock recruitment

The estimated biomass of the Japanese Pacific stock based on a virtual population analysis (VPA) showed that year-class strength appeared to be the major factor driving changes in the biomass of this stock (Fig. 2; Yabuki and Honda, 2005). We used the number of age-2 fish estimated from a VPA as an index of recruitment to the entire stock. The relationship between spawning stock biomass (SSB) and age-2 recruitment is shown in Fig. 3 (Yabuki and Honda, 2005). The estimated SSB was lowest in 1989 (for the 1990 year-class) and highest in 1998 (for the 1999 year-class), indicating twofold variability. However, the SSB did not show any obvious relationship with the age-2 abundance, strongly suggesting that, during the 1980s and 1990s, environmental factors affected the level of recruitment to this stock, rather than the SSB, (Yabuki and Honda, 2005). Age-2 recruitment varied fivefold (Fig. 2). The 1995 year class was highest (2.5×10^9 individuals) and the 1997 year class was lowest (0.5×10^9 individuals). The 1980, 1981, 1991, 1994, and 1995 year-classes were considered strong (Isoda et al., 1998; Yabuki and Honda, 2005). The overall recruitment levels were medium and relatively stable during the 1980s. Conversely, recruitment was high in the early 1990s when strong year-classes occurred and decreased in the late 1990s, resulting in relatively large variations in the recruitment levels during the 1990s overall. Although there were differences in the recruitment patterns between the 1980s and 1990s, there was no significant difference in the average age-2 recruitment between the two decades (Fig. 4).

4 Environmental conditions

4.1 Interannual changes in water temperature around Funka Bay (FB) in winter

It is believed that the water temperature around FB during the early life stages strongly affects recruitment levels (Isoda et al., 1998; Nakatani et al., 2003b). Hokkaido University records the sea surface temperatures (SSTs) daily at Muroran (the mouth of FB), and Hokkaido Fisheries Experimental Station has recorded the water temperatures daily at a depth of 10 m at Toyoura (inside FB) since 1986. The monthly mean temperatures in January and February are shown in Fig. 5. The mean SSTs at Muroran ranged from 2.6 to 7.0°C in January and from 1.0 to 4.4°C in February. The mean values for January and February during the 1980s were 4.2 and 2.2°C, respectively, and both were lower than the values in the 1990s (4.8 and 3.3°C, respectively). The mean temperatures at Toyoura showed the same tendency. Age-2 pollock recruitment showed a positive correlation with mean temperatures from January to February around FB (Fig. 6). Strong year-classes (1980, 1991, 1994 and 1995) occurred in warm years, except for the 1981 class.

4.2 Environmental conditions and recruitment success in the Tohoku Region (TR)

The Pacific coast of the Hokkaido and Tohoku regions is under the influence of three water masses: the Oyashio (cold) water, extremely cold Coastal Oyashio water (COW) and Tsugaru Warm Current water (Fig.1). The transport of eggs and larvae from Funka Bay (FB) to the TR and their survival during early life stage in the TR depend on the distribution of these water masses along the coast (Hashimoto and Ishido, 1991; Suzaki, 2003). Suzaki (2003) identified three types of oceanographic conditions during winter to early spring (Fig. 7). Type A is the pattern in an extremely cold year when the COW flows through the Doto area to the TR along the Pacific coast of Hokkaido. The COW reaches the southern part of the TR, and the nearshore area of the TR is covered with extremely cold low-salinity water. Type B is the pattern in a cold year when the Oyashio water flows through the Doto area to the TR. The nearshore area of the TR is covered with the Oyashio water, and the influence of the extremely cold COW is absent. In type C, during warm years, the Tsugaru warm current is strong and covers a wide section of the nearshore area of the TR. The interannual variation in the hydrographic conditions in February – April as categorized by Suzaki (2003) is shown in Fig. 8. Type B dominated in the 1980s, whereas type C dominated in the 1990s. Another index of the environmental conditions in the TR is the latitude of the Oyashio's southern limit, which generally shows a negative correlation with the Pacific Decadal Oscillation Index (Yatsu et al., 2005). Inada and Murakami (1993) found that the southward extension of the distribution and density of juvenile and older walleye pollock in the TR were closely related to this index. The latitude of the Oyashio's southern limit was low in many years during the 1980s, reflecting the current's strong southward flow (Fig. 9; Nihira et al., 2003; Nihira, 2006). In contrast, the latitudinal index was high in many years during the 1990s, reflecting its weak southward flow of the Oyashio.

The annual catch of age-0 walleye pollock in the TR by commercial fisheries, which serves as an index of the age-0 abundance in the TR (Tohoku National Fisheries Research Institute, unpublished data), is shown in Fig. 10. The catch levels were above average during the 1980s and the maximum catch was observed in 1981. The 1990s was a period of low catches. Taken together, these events indicated a pattern consistent with the changes in oceanographic conditions; i.e., Type B conditions during early life stage and strong southward extension of the Oyashio, observed in the 1980s, appeared to promote high walleye pollock abundance in the TR, while their abundance was reduced during type C conditions with less of a southward extension of Oyashio waters in the 1990s.

5 Discussion

Hamatsu et al. (2004) reported that changes occurred in the winter ocean environment around Funka Bay (FB) at the end of 1980s and postulated that they were related to "minor regime shifts" in the North Pacific Ocean (Minobe, 2000). The change was from a cold regime in the 1980s to a warm regime in the 1990s (Suzaki, 2003; Hamatsu et al., 2004). Here, we sought to determine how the Japanese Pacific walleye pollock stock responded to the environmental changes related to the regime shift in the last two decades.

The recruitment levels of the Japanese Pacific walleye pollock stock and environmental conditions during the 1980s and 1990s are summarized in Table 1. The recruitment levels of this stock were defined by the number of age-2 fish estimated from a VPA. Year-class strength appeared to be the major factor driving changes in the biomass of this stock, and strong year-classes (1980, 1981, 1991, 1994, 1995) had great effects on stock abundance (Yabuki and Honda, 2005). Our previous studies showed that the Doto area was an important nursery area in the 1990s (Nishimura et al., 2002;

Shida and Nishimura, 2002). Shida et al. (1999) reported that the age-0 abundance index in the Doto area was high in 1995 when a strong year-class took place, and Honda (2004) also observed that the 1995 year-class was distributed in the Doto area during the early summer of 1996. The numerical catch of age-0 pollock by commercial fisheries in the Tohoku Region (TR), an index of abundance there, was low in the 1990s. These findings suggest that a main recruitment route is via the FB-Doto and the strong year-classes in the 1990s originate via this route.

Events during the early life stages have been considered important for the recruitment of this stock (Nishimura et al., 2002), and high larval survival is necessary for recruitment success (Kendall and Nakatani, 1992; Nishimura et al., 2002; Hamatsu et al., 2004), similar to pollock in the Gulf of Alaska (GOA; Bailey and Spring, 1992). Nakatani et al. (2003b) postulated that warm water temperatures in FB during the early life stages promotes strong recruitment. Also in this study, strong year-classes occurred in warm years when the water temperature around FB was relatively high during the early life stages. These findings strongly indicate that environmental conditions around FB are important. Hunt et al. (2002) proposed the Oscillating Control Hypothesis (OCH) in the southeastern Bering Sea based on fisheries results and oceanographic data. The OCH predicts that during cold regimes, strong year classes for walleye pollock and other fish should be infrequent because of low zooplankton abundance and higher fish egg-mortality. In contrast, during warm regimes, the OCH predicts that zooplankton prey abundance for larval and juvenile fish will be strong, mortality of larval and juvenile fish will be lower, strong year classes for pollock and other fish should be frequent. The decreased frequency of strong year classes of the Japanese Pacific stock in the 1980s and their increase in the early 1990s are consistent with the OCH predictions, indicating that recruitment of this stock may be partly controlled by an OCH-like mechanism.

Recruitment from the TR is the second recruitment route of the Japanese Pacific stock. Most of the pollock in the TR are spawned in FB and then transported as larvae and juveniles to the region (Hashimoto and Ishido, 1991). The TR is located south of the main spawning ground and is the southern limit of pollock distribution. Age-0 abundance in the FB-TR route was high in the 1980s and clearly decreased in the 1990s. Hamatsu et al. (2004) showed that the relationship between stock fecundity and age-0 abundance in the TR changed noticeably after 1991, such that the decrease in the age-0 abundance in the TR did not depend on stock fecundity. This strongly suggests that environmental conditions may have been largely responsible for the age-0 abundance in the TR. Type B years (Suzaki, 2003) were frequent in the 1980s, and the age-0 abundance indices were high during those years. Additionally, the latitude of the Oyashio's southern limit tended to be low in the 1980s, which contributed to better survival of juvenile pollock in the TR and an expanding juvenile and older pollock distribution southward (Inada and Murakami, 1993). In contrast, the age-0 abundance in the TR decreased dramatically during Type C years, when warm years dominated in the 1990s, and the latitude of the Oyashio's southern limit tended to be high. Suzaki (2003) showed that age-0 abundance in the TR was negatively correlated with the SST in that region during winter. These results show that recruitment from the FB-TR route increases in the cold years and decreases in the warm years contrary to the FB-Doto route, and played an important role in the recruitment process in the 1980s.

Recent studies have shown that the juvenile stage is also important for determining year-class strength and for regulating stock abundance (Bailey and Spring, 1992; Bailey, 2000; Nishimura et al., 2002). It appears that only the Doto area was used as a nursery area for juvenile fish in the 1990s. Age-0 to adult pollock are distributed in this area (Watanabe et al., 1993; Shida, 2002). The diet of smaller pollock is mainly mesozooplankton (Yamamura et al., 2002). An age-structured trophodynamic model indicated that pollock growth in weight was density-dependent in this area, being slower at high densities (Yamamura, 2004). Therefore, the strong 1994 and 1995 year-classes possibly affected the survival of the 1996 and later year-classes via competition for food. Both the decreased recruitment from the TR and food competition in the Doto area appeared to cause poor year classes in the late 1990s. The OCH also predicts that as the warm regime continues over time, the biomass of adult predatory fish will increase, and control will switch to being primarily top-down (Hunt et al., 2002). Yamamura et al. (2001) described how walleye pollock cannibalism in the Doto area might affect year class strength. However, we do not have sufficient data to analyze regulation of abundance during juvenile stages. Future study will focus on defining the mechanisms.

We conclude that, in response to environmental changes, the location of the development of early life stages of the Japanese Pacific stock of walleye pollock shifted in the location (FB–Doto and FB–TR) where year-class strength was established, but that, possibly because of biological impacts on larval and juvenile pollock, this shift resulted in no difference in the average recruitment levels between the 1980s and 1990s.

6 Further investigations

The key questions of how and when the year-class strength of the Japanese Pacific stock is established remain unanswered. Nakatani et al. (2003b) stated that the water temperature around Funka Bay (FB) alone did not determine the survival of eggs and larvae directly. As described above, further studies of other environmental factors, such as food availability and predation, are necessary to improve our understanding of this process. Furthermore, Hamatsu et al. (2004) noted that decadal-scale changes in the ocean environment might have altered the contribution rate of spawning areas, FB and others. Here, we focused on the early life stages, but a comprehensive survey of all pollock life stages, including the late juvenile stage, is necessary.

In the 1990s, the HUBEC (Hokkaido University suBarctic Ecosystem dynamics and Climate) and WPEC (Walleye Pollock ECosystem dynamics and Walleye Pollock, Euphausiid, and Climate or Copepods) projects generated some hypotheses and research programs (Watanabe, 1993; Sakurai and Miyake, 1994). These have been discussed in the Study Meeting of the Pacific Walleye Pollock Resources in recent years (Nishimura et al., 2002). We reevaluated these hypotheses and have proposed a new hypothesis summarized in Fig. 11 (Shida et al., 2005). Successive controls are thought to be important in determining the year-class strength of this stock. These controls or “switches” are factors related to survival in each stage. We identified 11 controls from biological and environmental conditions related to recruitment success. We consider that the “transport and aggregation of eggs and larvae” switch is important for the regulation of recruitment routes. Under our proposed scenario, that switch, which is affected by the Oyashio, is turned on in cold years, so that enough eggs and larvae are transported to the TR where they are aggregated in a suitable nursery area. “Diet” switches, indicating that enough food is supplied to larvae and juveniles, are considered most important in producing strong year classes (Kendall and Nakatani, 1992; Nakatani, 1995; Nakatani et al., 2003b). The temperature around FB is determined by various environmental conditions, such as current flows, and is related to this diet switch (Nakatani, 1995; Nakatani et al., 2003a, b). This switch in FB could be turned off by bottom-up processes in cold years and be turned on by them in warm years. On the other hand, this switch in the TR, which is affected by distribution of water masses and southward intrusion of the

Oyashio, was turned on in cold years during the 1980s. Additionally, switches in juvenile and age-1 fish may be important for density-dependent mortality in the Doto area. These switches may have been controlled by top-down processes in the late 1990s. Recently, a comprehensive research project has been initiated to elucidate the interrelationship between environmental changes and recruitment variability in this stock. A full understanding of the mechanisms regulating recruitment dynamics awaits the further empirical investigation of this the new project.

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Table and figure captions

Table 1. Summary of recruitment levels of the Japanese Pacific walleye pollock stock and environmental conditions during the 1980s and 1990s.

Fig. 1. The distribution and spawning grounds of the Japanese Pacific walleye pollock stock, and the main circulation features. The Dashed lines show the borders of the Doto area, Funka Bay (FB) area and the Tohoku region (TR).

Fig. 2. Estimated biomass at age for the Japanese Pacific walleye pollock stock from 1981 to 1999. Values were estimated using a VPA (Yabuki and Honda, 2005).

Fig. 3. Relationship between spawning stock biomass (SSB) and age-2 recruits of the Japanese Pacific walleye pollock stock. Values were estimated using a VPA (Yabuki and Honda, 2005).

Fig. 4. Average numbers of age-2 recruits during the 1980s and 1990s. The error bars indicate the standard deviation.

Fig. 5. Time series of the monthly mean sea surface temperatures in January and February at the mouth of Funka Bay (Muroran) and inside Funka Bay (Toyoura; ca. 1986). The data were collected by Hokkaido University and Hokkaido Fisheries Experimental Station. Arrows indicate years when strong year-classes occurred.

Fig. 6. The relationship between the average temperature for January - February at the mouth of Funka Bay (Muroran) and inside Funka Bay (Toyoura; ca. 1986), and the number of age-2 recruits. * Significant at the 5% level.

Fig. 7. The three types of oceanographic conditions in the Tohoku region categorized by Suzaki (2003). Arrows indicate direction of current flows.

Fig. 8. Interannual variation in the types of oceanographic conditions in the Tohoku region from February to April (Suzaki, 2003).

Fig. 9. Interannual variation in the latitude of the southern limit of the Oyashio (Nihira et al., 2003).

Fig. 10. Interannual fluctuation in the relative catch of age-0 walleye pollock in the Tohoku region by commercial fisheries as an index of age-0 abundance in this region (Tohoku National Fisheries Research Institute, unpublished data). The unit is the relative value, which is scaled to the average value from 1980 to 1999 as 1.

Fig. 11. Conceptual model of the mechanisms to determine the year-class strength of the Japanese Pacific walleye pollock stock (modified from Shida et al., 2005). The switches are factors related to pollock survival. This has been discussed as part of the Study Meeting of the Pacific Walleye Pollock Resources.

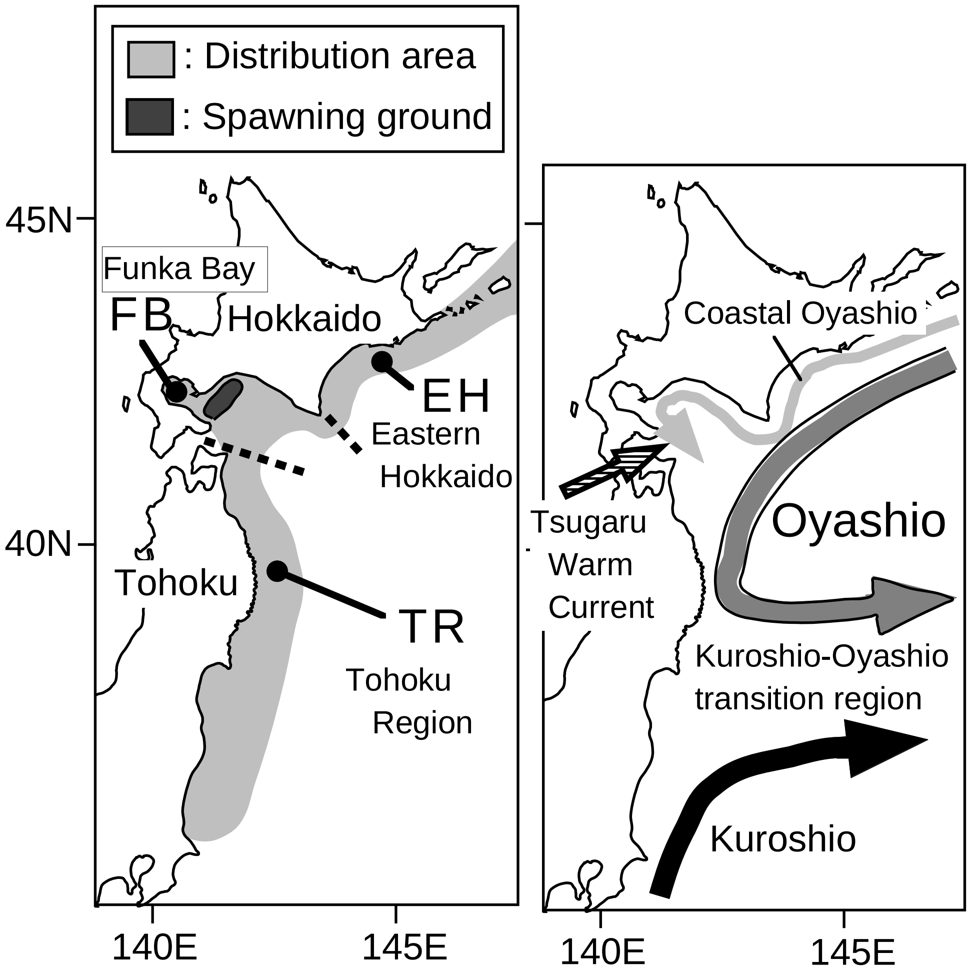

: Distribution area
: Spawning ground
45N
40N
Funka Bay
FB
Hokkaido
EH
Eastern
Hokkaido
Tohoku
TR
Tohoku
Region
140E
145E
Coastal Oyashio
Tsugaru
Warm
Current
Oyashio
Kuroshio-Oyashio
transition region
Kuroshio
140E
145E

Figure 1

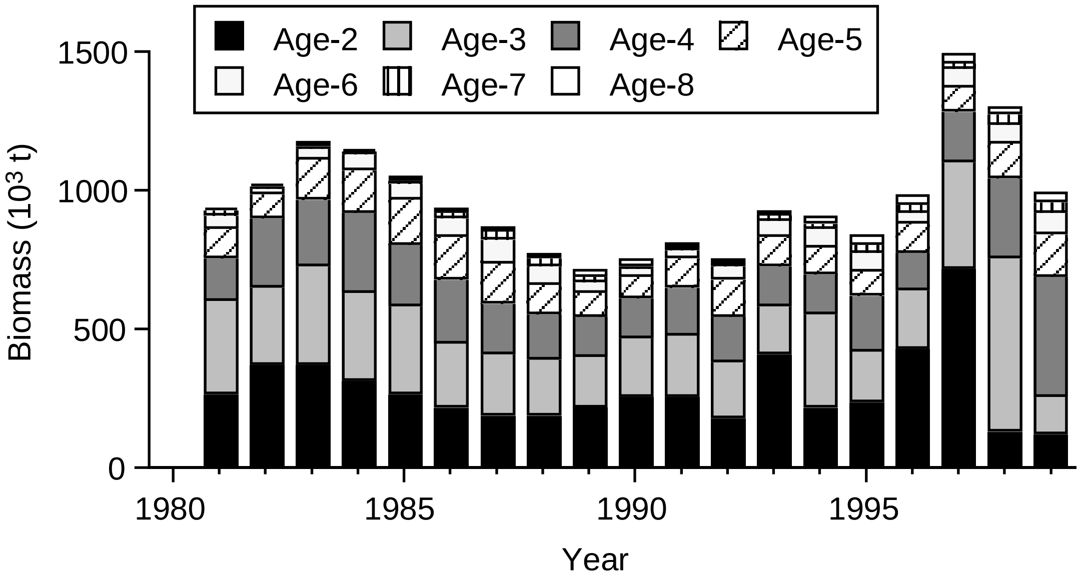

Age-2
Age-3
Age-4
Age-5
Age-6
Age-7
Age-8
Biomass (10³ t)
0
500
1000
1500
1980
1985
1990
1995
Year

Figure 2

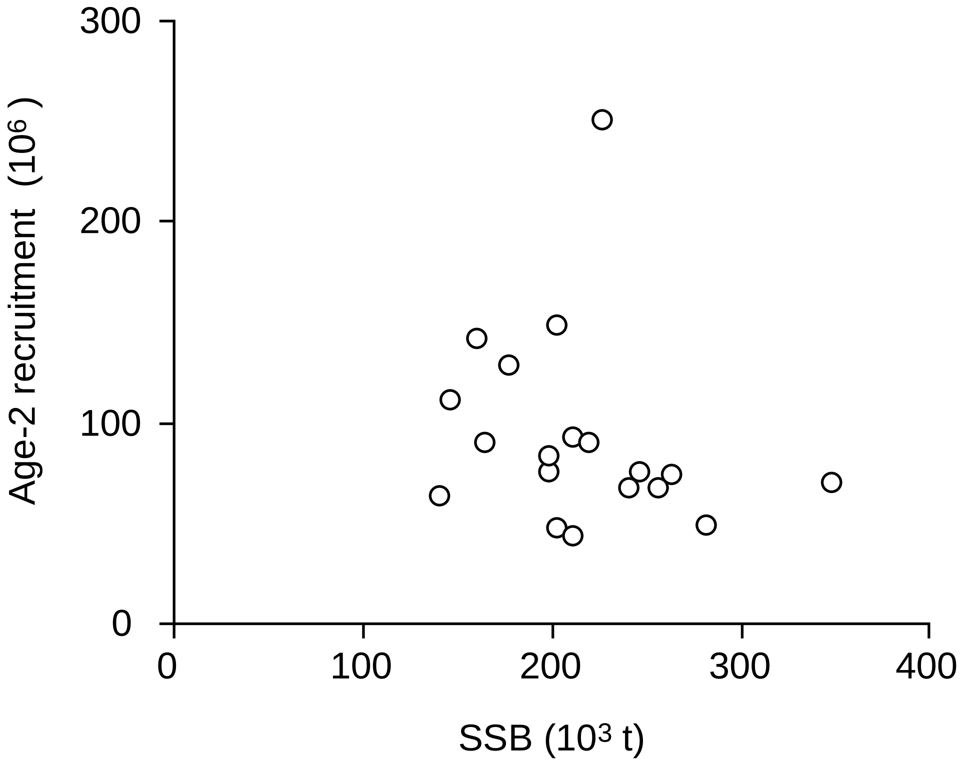


Figure 3

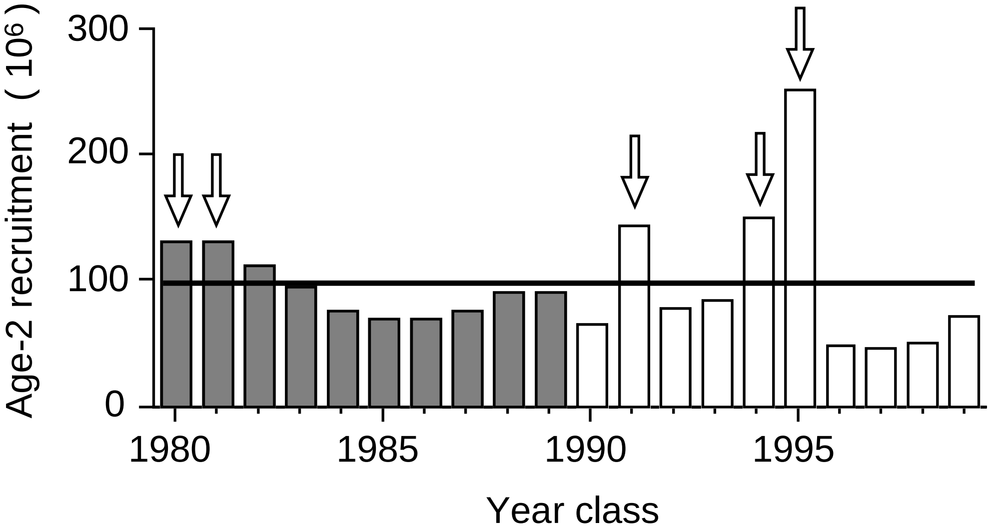

Age-2 recruitment (10^6)
300
200
100
0
1980
1985
1990
1995
Year class

Figure 4


200
150
100
50
0
Age-2 recruitment (10^6)
1980-89
1990-99
Year classes

Figure 5

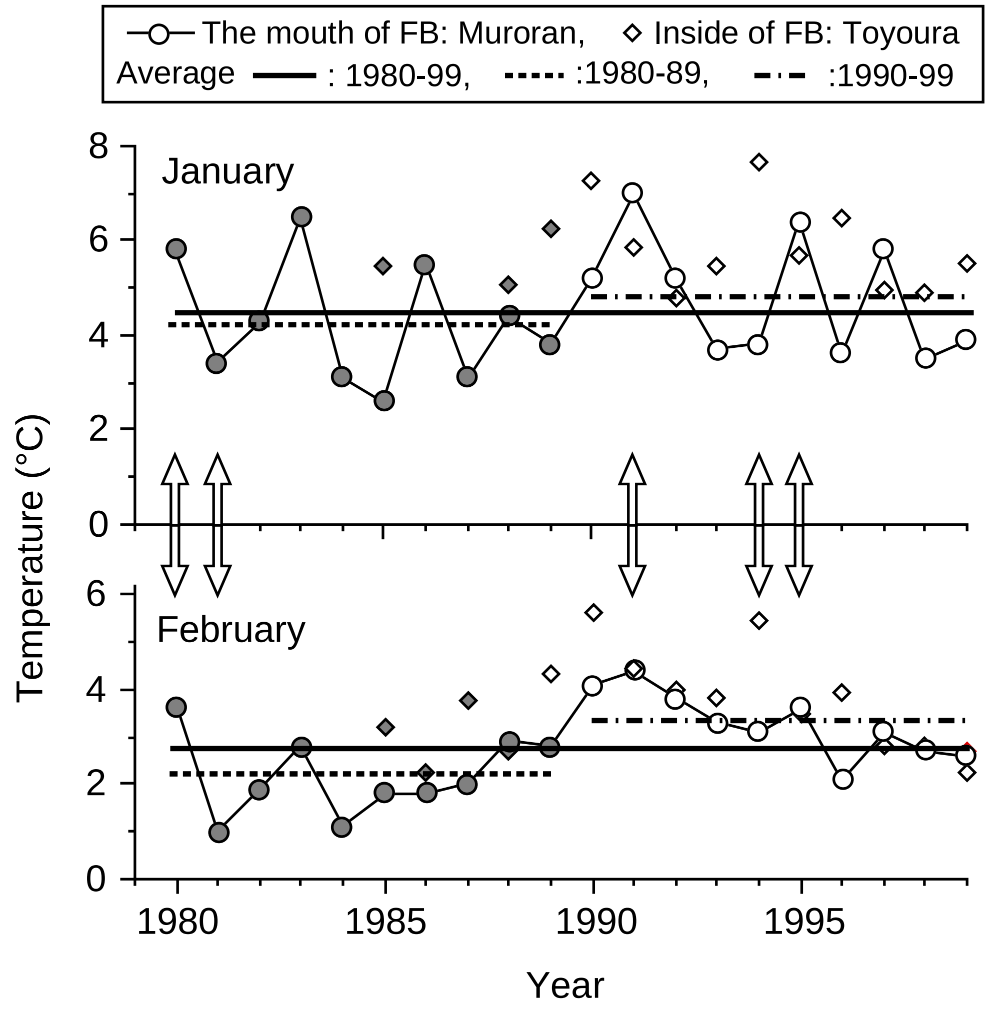

The mouth of FB: Muroran,
Inside of FB: Toyoura
Average
: 1980-99,
:1980-89,
:1990-99
January
February
Temperature (°C)
Year
8
6
4
2
0
6
4
2
0
1980
1985
1990
1995

Figure 6

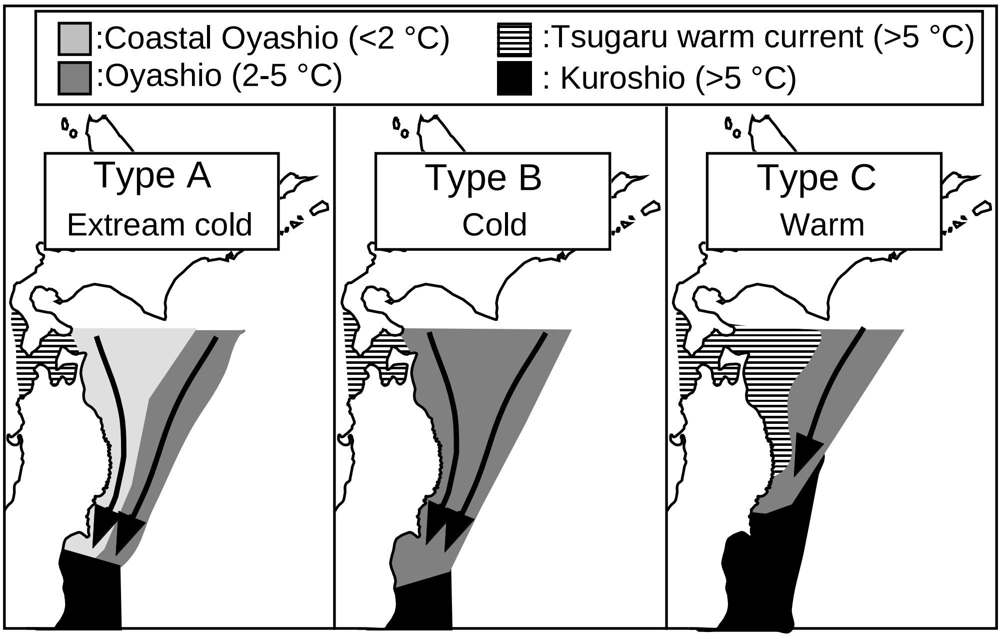
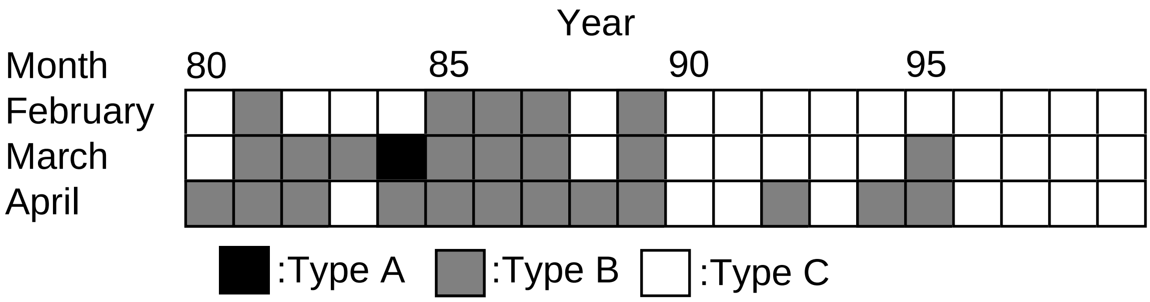

:Coastal Oyashio (<2 °C)
:Oyashio (2-5 °C)
:Tsugaru warm current (>5 °C)
: Kuroshio (>5 °C)
Type A
Extream cold
Type B
Cold
Type C
Warm

Figure 7



Year

Month	80					85					90					95				
February	□	▨	□	□	□	▨	▨	▨	□	▨	□	□	□	□	□	□	□	□	□	□
March	□	▨	▨	▨	■	▨	▨	▨	□	▨	□	□	□	□	□	▨	□	□	□	□
April	▨	▨	▨	□	▨	▨	▨	▨	▨	▨	□	□	▨	□	▨	▨	□	□	□	□

■ :Type A ▨ :Type B □ :Type C

Figure 8

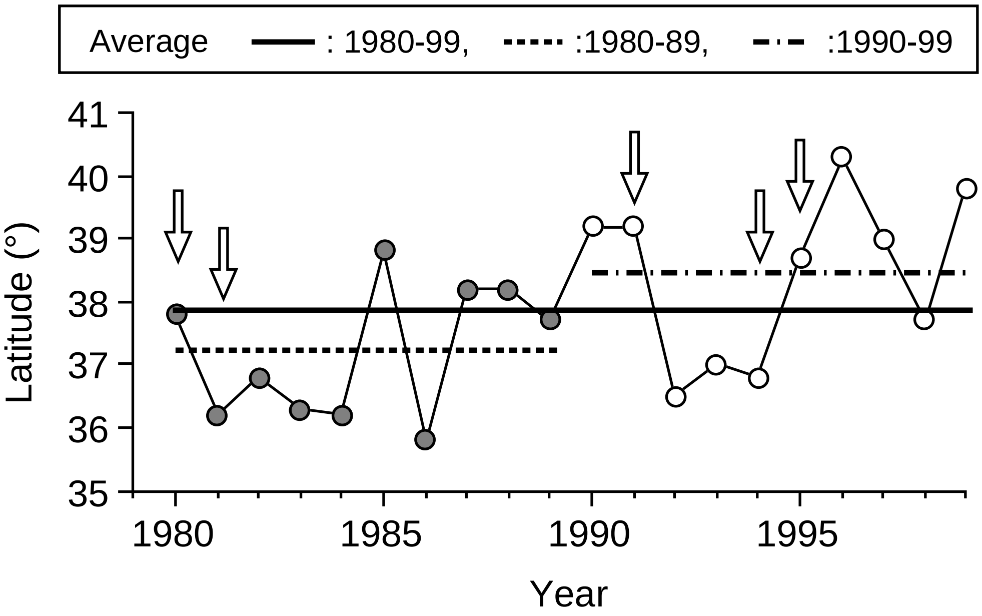

Average
: 1980-99,
:1980-89,
:1990-99
41
40
39
38
37
36
35
Latitude (°)
1980
1985
1990
1995
Year

Figure 9

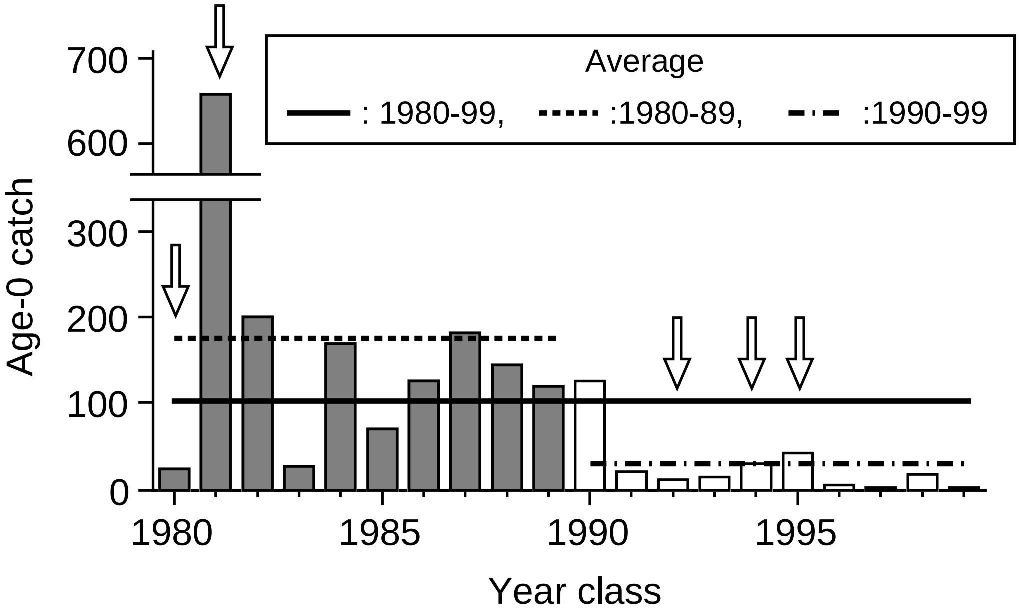

Average
: 1980-99,
:1980-89,
:1990-99
700
600
300
200
100
0
Age-0 catch
1980
1985
1990
1995
Year class

Figure 10

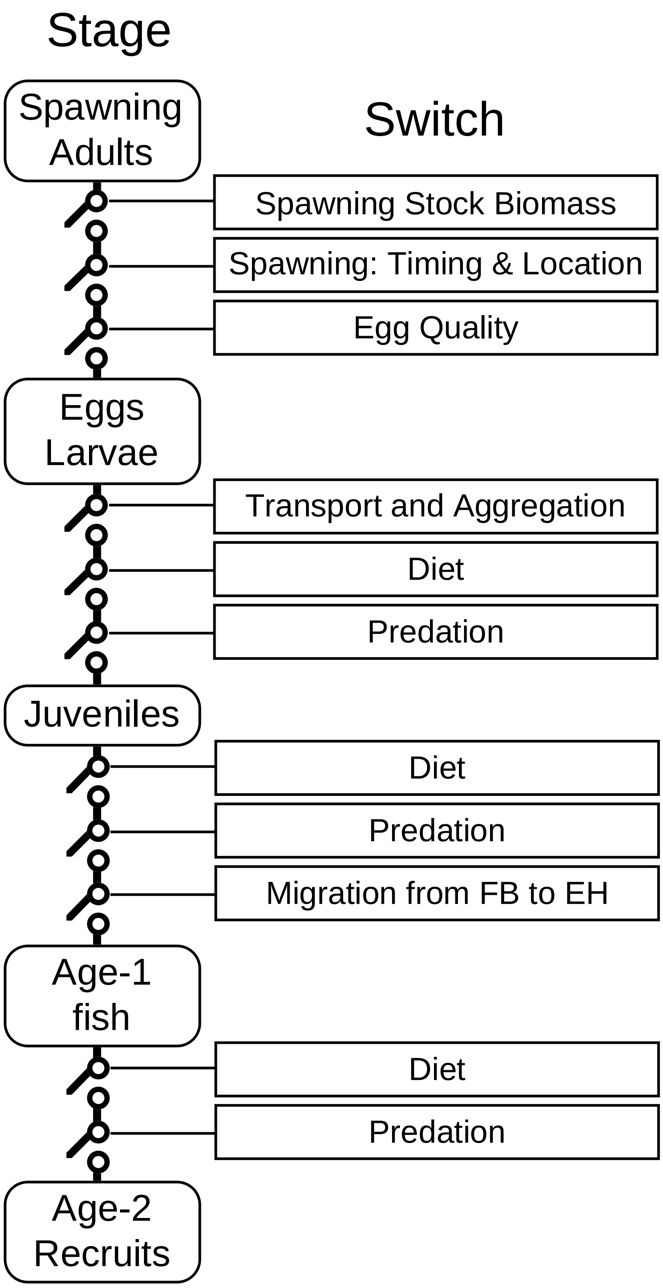

Stage
Switch
Spawning Adults
Spawning Stock Biomass
Spawning: Timing & Location
Egg Quality
Eggs Larvae
Transport and Aggregation
Diet
Predation
Juveniles
Diet
Predation
Migration from FB to EH
Age-1 fish
Diet
Predation
Age-2 Recruits

Figure 11

Location	Month	
	January	February
Muroran	0.40(20)	0.28(20)
Toyoura	0.63(12)*	0.66(13)**

Table 1