

Contributions of the VENFISH program: meso-zooplankton, Pacific saury (*Cololabis saira*) and walleye pollock (*Theragra chalcogramma*) in the northwestern Pacific

SHIN-ICHI ITO,^{1,*} HIROYA SUGISAKI,¹
ATSUSHI TSUDA,² ORIO YAMAMURA³ AND
KUNIYUKI OKUDA⁴

¹Tohoku National Fisheries Research Institute, Fisheries Research Agency (FRA), Shiogama, Miyagi 985-0001, Japan

²Ocean Research Institute, The University of Tokyo, Nakano-ku, Tokyo 164-8639, Japan

³Hokkaido National Fisheries Research Institute, Fisheries Research Agency (FRA), Kushiro-shi, Hokkaido 085-0802, Japan

⁴National Research Institute of Fisheries Science, Fisheries Research Agency (FRA), Kanazawa, Yokohama 236-8648, Japan

ABSTRACT

The comprehensive study of the variation of the oceanic environment and fish populations in the northwestern Pacific (VENFISH) was an interdisciplinary scientific program to enhance our understanding of relationships between the ocean environment and the pelagic fishes, Pacific saury and walleye pollock. As prey of saury and walleye pollock, key species of zooplankton were selected and their life history and production were elucidated. Retrospective analyses were also conducted to investigate the mechanisms of production variation in some zooplankton species. Life history and ecology of Pacific saury and walleye pollock were also investigated and substantial improvements to our understanding of them were achieved. In addition, improved information from VENFISH were used to develop several models to investigate saury growth, and population dynamics, and predatory pressure on zooplankton from walleye pollock. Observational and model results indicate the importance of the Kuroshio and the Kuroshio–Oyashio transition region to saury recruitment and of Oyashio transport to walleye pollock recruitment. Moreover, models developed under VENFISH will become the basis of fisheries management models for saury, walleye pollock, and other fishes in the future.

Key words: fisheries oceanography, meso-zooplankton, Pacific saury, walleye pollock

INTRODUCTION

The comprehensive study of the variation of the oceanic environment and fish populations in the northwestern Pacific (VENFISH) was an interdisciplinary pelagic fisheries ecosystem project conducted as a global ocean ecosystem dynamics and coupling (GLOBEC) related program from FY1997 to FY2001, funded by the Japan Ministry of Agriculture, Forestry and Fishery. VENFISH focused upon oceanic ecosystems around Pacific saury (*Cololabis saira*) in the northwestern Pacific and walleye pollock (*Theragra chalcogramma*) (the Japan Pacific population: JPP). The goal of VENFISH was to improve substantially our understanding of the relationship between environmental factors and the stock variation of these species to facilitate improvement in predicting accuracy of population abundance for future fisheries management strategies.

The VENFISH covered the area from the Kuroshio (subtropical) region (KRR) south of Japan, the major spawning ground of Pacific saury, to the (subarctic) Oyashio region (OYR) east of northern Japan, the feeding region of Pacific saury and spawning (Fig. 1) and nursery grounds of walleye pollock (Fig. 2). In this sea area, small and meso-scale physical variability dominates and is associated with frontal eddies in the frontal region of the Kuroshio, meandering of the Kuroshio and the Kuroshio Extension, warm core rings separated from the Kuroshio Extension and the southward intrusions of the Oyashio waters (Kawai, 1972). These physical features are considered to affect local biological dynamics, for example, primary production, survival of fish larvae and migration routes of pelagic fishes. In this study area, signals of atmosphere/ocean climate change of interannual, decadal and interdecadal time scales have been well observed, which are related to long-term variations in plankton biomass (Odate, 1994; Sugimoto and Tadokoro, 1998), change of population size of Japanese sardine (Noto and

*Correspondence. e-mail: goito@affrc.go.jp

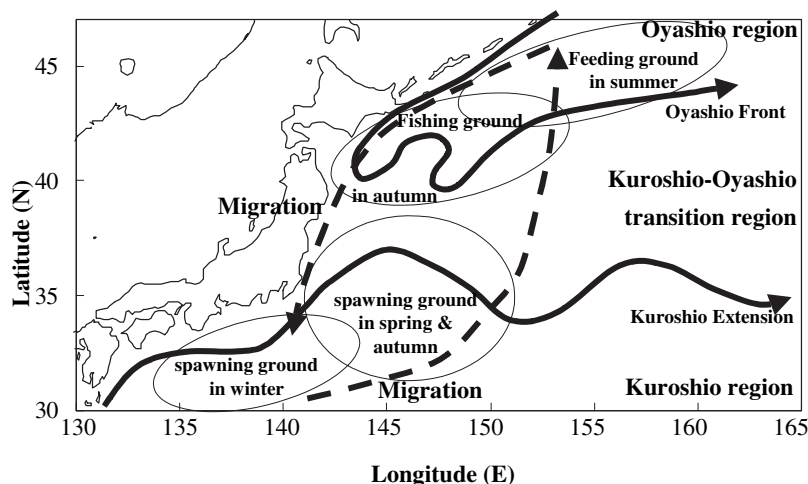
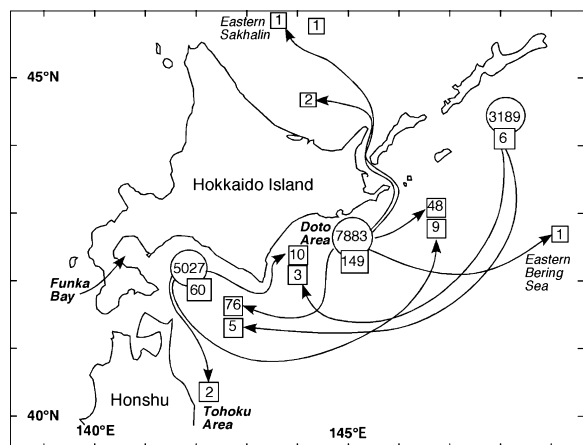


Figure 1. Schematic diagram of life history of Pacific saury (*Cololabis saira*) and ocean circulations in the northwestern Pacific (modified from Sugisaki and Kurita, 2004). Solid lines indicate dominant current systems and dashed lines the migration routes.

Figure 2. Results of tag-release experiments on walleye pollock (*Theragra chalcogramma*) made during the 1970s by Japanese scientists. Pollock were captured by hook and line fishing, tagged by ribbon tags and then released. Figures in circles and squares represent the number of pollock released and recaptured, respectively (redrawn from Yoshida, 1979).



Yasuda, 1999), and Japanese common squid (Sakurai, 2002), and catches of various species of pelagic fishes in the coastal waters of northern Japan (Kodama *et al.*, 1995). These coupled changes of climate, ecosystem and fish populations are considered signals of global-scale regime shifts in the northwestern Pacific (Kawasaki, 1992; Hare and Mantua, 2000). These interannual-decadal variations are also associated with EL Niño/Southern Oscillation (ENSO) events.

As our understanding of the physical processes of atmosphere/ocean interannual-decadal variations in the northwestern Pacific has been considerably improved in recent years (Fukasawa, 2003; Yasuda, 2003) under the sub-Arctic gyre experiment (SAGE),

which was a physical oceanography project simultaneously running with VENFISH, we have a good opportunity to incorporate this information into our interdisciplinary understanding of ecosystems including Pacific saury and walleye pollock. Therefore, in VENFISH, our major effort has been devoted to collecting accurate information on distribution, predator-prey relationships, life history and productivity from amassed field and experimental research, rather than to seek new evidences for linkages between physical environmental variations and biological variations using long-term data sets. Essential studies of this project were the ecology and production of prey of larval saury in their spawning ground (KRR), life history of prey zooplankton of Pacific saury and walleye pollock in their feeding ground (OYR and the Kuroshio-Oyashio transition region: KROYTR), ecology (feeding, spawning and growth) of saury, migration process of larval pollock and the role of pollock in the food web. The ecological and vital parameters obtained by this research were incorporated into a population model (Tian *et al.*, 2004) and a growth model (Ito *et al.*, 2004) of Pacific saury and a nutrition dynamics model of walleye pollock (Yamamura, 2004), and investigations on the relationships between environmental factors variations and fisheries resource variations.

In the following sections, we describe the framework of the research for meso-zooplankton, Pacific saury and the JPP of walleye pollock, and review for representative results of VENFISH including other related studies.

MESO-ZOOPLANKTON

The northwestern Pacific is one of the most productive areas for small pelagic fish fisheries such as Japanese

sardine, anchovy and saury. Generally, high production of small pelagic fish is supported by upwelling system such as the California Current area (e.g. Lasker, 1979) and such systems form major fishing grounds in the world (Kawasaki, 1992), in contrasts to the Kuroshio–Oyashio system. One of the characteristic features of the small pelagic fish in Kuroshio–Oyashio area is their large-scale horizontal migrations (e.g. Sugisaki and Kurita, 2004). They mainly spawn in the southern area from winter to early spring, and the juveniles migrate to the north, then return to the south for overwintering or spawning. The dominant prey of their larvae in the southern area is small copepods such as the nauplius stage of calanoid copepods, *Oncaea* and *Oithona*, and prey size increases with fish growth (Fig. 3). The dominant zooplankton size increases with latitude, and the start of active production of phytoplankton and zooplankton being early in the south and later in the north. These facts suggest that ontogenetic horizontal migrations of these pelagic fish are consistent with the 'surf riding theory' in temporal and spatial scales (Pope *et al.*, 1994).

On the contrary, stocks of pelagic fish as well as walleye pollock in the subarctic area show decadal to centennial oscillations, and the oscillations are well correlated with climatic variations. For example, the anomaly of SST in the Kuroshio Extension during winter to spring highly correlates with the survival rate of Japanese sardine juveniles (Noto and Yasuda, 1999). However, the mechanisms existing between climatic changes and fish production are poorly understood. Meso-zooplankton production has been assumed to be one of the most probable links between climate and fish stocks. Zooplankton biomass also shows decadal oscillations in the North Pacific (e.g. Brodeur and Ware, 1992; Odate, 1994); however, the intensity of the variations were much lower than those

of fish stocks, and the periods of high zooplankton biomass were not always coincident with those of high fish productions in basin-scale analyses. These facts suggest that match/mismatch processes probably exist between zooplankton and fish production at smaller temporal and spatial scales. Moreover, fish themselves have specific preferences of prey items by size and taxon. Consequently, we need detailed information on the distribution, production and life histories of the dominant species of zooplankton in each area of the Kuroshio–Oyashio system.

In this decade, understandings of the lower trophic levels, including zooplankton, of the North Pacific have intensively progressed because of joint global ocean flux study (JGOFS) and GLOBEC related studies. In VENFISH which is a GLOBEC related study, we focused on the important prey organisms of Pacific saury and walleye pollock in three regions of their habitats. In KRR, which is the spawning and nursery ground of Pacific saury, life histories and production of *Oncaea* were studied. *Oncaea* copepods are widely distributed and abundant in the world oceans, but their life histories and production are poorly understood because of their small body size (<0.6 mm) and of the difficulties of identification of species. We have recognized three dominant *Oncaea* copepods from the surface water of this region, and their production were primarily determined by temperature and primary production (Nakata *et al.*, 2004). Moreover, retrospective analysis has shown that small copepod biomass was negatively correlated with solar radiation and positively correlated with diatoms and nano-sized particles, while large copepod abundance mainly *Calanus sinicus* was positively correlated with winter wind stress and diatom abundance (Nakata *et al.*, 2001).

In KROYTR, we focused on *Euphausia pacifica*, which is an important food item for migrating Pacific

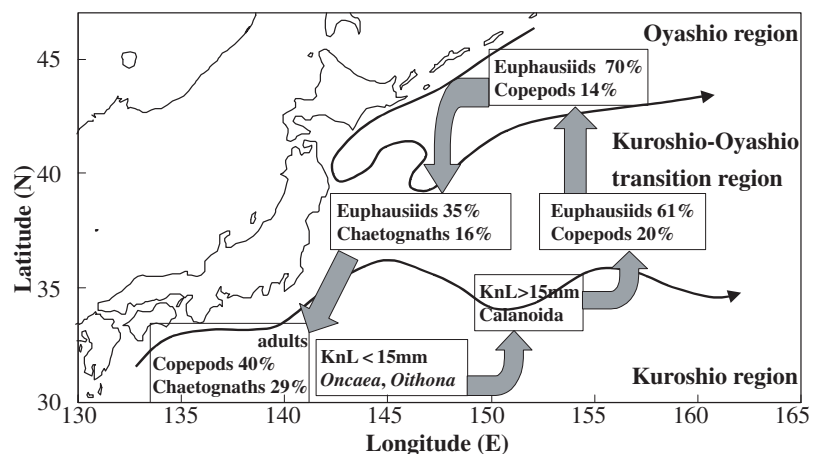


Figure 3. Schematic diagram of feeding habits of Pacific saury (*Cololabis saira*). The percentage numbers show the percentage wet weight of gut contents of Pacific saury during the dusk period (data source is Table 4 in Sugisaki and Kurita, 2004).

saury and all stages of walleye pollock (Yamamura *et al.*, 1998; Sugisaki and Kurita, 2004). Because the physical environment is highly heterogeneous in this area, several thousands net samples were analyzed to make clear the life history and the distribution of this euphausiid. The spawning area is organized in the southern edge of KROYTR, and moves north with the progress of the season and finally reaches OYR in fall (Taki, 2004). In OYR, *E. pacifica* showed a biennial life history.

In OYR, we focused on the large suspension-feeding copepods (*Neocalanus* spp. and *Eucalanus bungii*). These copepods occupy a large proportion of the epipelagic layer in summer and the mesopelagic layer in winter (Kobari and Ikeda, 1999; Mackas and Tsuda, 1999), and are important food items for walleye pollock and Pacific saury as well as other pelagic and mesopelagic organisms (Odate, 1994; Moku *et al.*, 2000; Yamamura *et al.*, 2002). *Neocalanus flemingeri* was established as a new species in 1988 (Miller, 1988), then the life histories of the three species of *Neocalanus* were re-examined (Miller and Clemons, 1988). These studies revealed that these species of *Neocalanus* (*N. cristatus*, *N. flemingeri* and *N. plumchrus*) have an annual life cycle with dormancy as adults or preadult stages in the deep layer from summer to winter, and their offspring rise to the surface or subsurface layers for growth. Segregation of the growing season between *N. flemingeri* and *N. plumchrus*, and vertical segregation between surface grazers (*N. plumchrus* and *N. flemingeri*) and subsurface grazers (*N. cristatus* and *Eucalanus bungii*) are also characteristics of life cycles of these copepods (Mackas *et al.*, 1993). In the western subarctic Pacific, the life cycles of these copepods are basically identical to those in the eastern Pacific (Kobari and Ikeda, 1999, 2001a,b; Tsuda *et al.*, 1999;). However, we found some differences. First, *N. flemingeri* with a biennial life cycle was found in the Sea of Okhotsk, the Japan Sea and OYR (Miller and Terazaki, 1989; Tsuda *et al.*, 1999). In OYR, both annual and biennial life cycles were found with a difference in the body sizes (Tsuda *et al.*, 1999). Kobari and Ikeda (2001a) suggested that the bimodal size distribution of *N. flemingeri* in OYR occurs due to sexual dimorphism; however, Tsuda *et al.* (2001) showed bimodal size distribution even in the adult stage and strongly suggested that large *N. flemingeri* with a biennial life cycle in OYR are advected from the Sea of Okhotsk. Secondly, body sizes vary significantly among the basins in all species of *Neocalanus* and *Eucalanus bungii*. Thirdly, although timing of life cycles are nearly identical for *Neocalanus* species among the basins, that of *E. bungii* varied locally

depending on the timing of the primary production maximum (Tsuda *et al.*, 2004). More importantly, spawning characteristics and early developments were described for the three species of *Neocalanus* (Saito and Tsuda, 2000), which make it possible for us to estimate their mortalities throughout their life cycles by demographic analysis (Mackas and Tsuda, 1999). In addition to the studies on large suspension-feeding copepods, life cycles of other zooplankton species have been intensively studied in the western subarctic Pacific. These studies include chaetognaths, *Sagitta elegans*, amphipods, *Cyphocaris challengerii* and *Primno abyssalis* (Yamada and Ikeda, 2000; Yamada *et al.*, 2002), ostracods, *Discoconchoecia pseudodiscophora*, *Orthoconchoecia haddoni*, and *Metaconchoecia skogsbergi* (Kaeriyama and Ikeda, 2002) and copepods, *Gaidius variabilis*, *Pleuromamma scutellata*, *Heterorhabdus tanneri*, *Paraeuchaeta elongata* (Ozaki and Ikeda, 1998, 1999; Yamaguchi and Ikeda, 2000a,b). These studies clearly show that most zooplankton species have annual life cycles. However, some species (some populations of *N. flemingeri*, *E. bungii*, *S. elegans* and *G. variabilis*) show a longer life cycle and a small number of small copepods show multiple generations per year (*Metridia pacifica*, *Scolecithricella minor*, *Pseudocalanus newmani*). Some of the results from life cycle analysis were put into an ecological–physical coupled model, and the effects of ontogenetic migration by the dominant mesozooplankton on the phytoplankton community were quantified (Kishi *et al.*, 2001; Ito *et al.*, 2004).

PACIFIC SAURY IN THE NORTHWESTERN PACIFIC

Pacific saury (*Cololabis saira*) is one of the important pelagic commercial fish in the northwestern Pacific. The average total catch of saury is about 250 000 tonnes (t). The knob length (KnL: distance from the tip of the lower jaw to the posterior end of the muscular knob on the caudal peduncle) of saury reaches 30 cm in adults and landed saury are categorized into large (29.0–31.9 cm), medium (24.0–28.9 cm), and small (20.0–23.9) sizes. The total catch has fluctuated between 575 000 and 52 000 t during the last half century and the size composition of the landed saury has also fluctuated (Watanabe *et al.*, 1997). It has been considered that the saury population is composed of autumn-, winter-, and spring-spawned cohorts corresponding to the large, medium, and small size categories of landed saury in the fishing season (Fukushima *et al.*, 1990). Stable commercial catch of medium size saury, compared with large

interannual variations of large and small size saury, is consistent with stable winter-cohort production of preschooling juveniles (Watanabe *et al.*, 1997); however, the data source of juvenile production was limited to 1990–94. Moreover, adult saury have a hyaline zone in the otolith and the unclearness of otolith growth increments in the hyaline zone obscures accurate estimates of saury age. Therefore, there is no conclusive evidence that the medium size category corresponds to the winter-cohort. For example, Watanabe *et al.* (1988) estimated that Pacific saury grows to 30 cm within 1 yr in the western Pacific whereas Suyama *et al.* (1996) estimated that it took about 560–690 days to grow to 31.5 cm. This unclearness of growth rate and life span of saury makes it difficult to elucidate the mechanisms of fluctuation in saury population and size distribution. Therefore, we focused on following three items in VENFISH:

1. Life history of Pacific saury especially related to growth rate (life span), feeding habits, and reproduction;
2. Modeling growth (and then life history) of Pacific saury; and
3. Modeling the population of Pacific saury linked with environmental factors.

Saury migrates widely from KRR to OYR (Fig. 1) and feeding habits of saury change according to their life stages and locations (Odate, 1994); however, there is little quantitative data on saury feeding habits. Kurita and Sugisaki (2004) estimated that the feeding ration of saury is higher in summer (in OYR), and lower in fall (in KROYTR). They also showed that the feeding activity is high in winter (in KRR) spawning season, even though abundance of zooplankton is low. Kurita (2004) showed that about 35% of this relatively high ration in winter is apportioned to egg production. Sugisaki and Kurita (2004) elucidated the feeding habits of saury quantitatively (Fig. 3): saury mainly feed on the euphausiid, *Euphausia pacifica*, in spring (in KROYTR); feed on *E. pacifica*, chaetognaths, and copepods in summer (in OYR); feed on *E. pacifica* and chaetognaths in autumn (in KROYTR); and feed on copepods in winter (in KRR). Their data imply the importance of *E. pacifica*.

Concerning saury spawning, Y. Kurita (unpublished) surveyed the seasonal changes in saury distribution and the ratio of the mature stage. His results showed that almost all saury are mature in KRR in winter. Kurita (2004) estimated the spawning interval and batch fecundity. He also showed that the most important season for spawning is winter. These results are consistent with larval production (Watanabe and Lo, 1989).

Watanabe *et al.* (2003) estimated the growth rate of larvae and juveniles of saury using widely sampled field data in the northwestern Pacific during 1990–98. They also estimated the survival rate and the production of juveniles in each season and suggested that the survival process after hatching controlled recruitment of the autumn- and the spring-cohorts in KROYTR, while a stable high survival sustained stable high growth rate and low mortality of the winter-cohort. This result suggests the importance of KROYTR for the recruitment of saury. To clarify the mechanism of the environmental effect on hatching of eggs, Oozeki and Watanabe (2000) conducted a laboratory incubation experiment on eggs of saury. Their results showed that growth rate increased linearly with temperature and also increased with larval age. They also analyzed the relationship between otolith increments and KnL of the larvae in the laboratory. Their results showed the possibility of estimating the growth rate of saury juveniles from otolith field data. Then, they estimated the instantaneous growth rate from field otolith data and analyzed the relationship between recent growth rate and the oceanic environment (Oozeki *et al.*, 2003, 2004). Their results showed that sea surface temperature (SST) and food density affected larval growth during the early stages and SST and chlorophyll becomes more important in the later larval stage.

However, as mentioned above, it is difficult to estimate the growth rate of adult saury because of the hyaline zone in otoliths (Suyama, 2002). The biggest breakthrough for this problem has been the development of a new method to estimate the hatch date from the age at which the otolith increment width reached a maximum for the second time (Kurita *et al.*, 2004). It has become possible to estimate the age of saury using this method even if there is a hyaline zone. They estimated the hatch date of large-size saury and built a new scenario of the life history of Pacific saury incorporating information on the growth of saury with no hyaline zone. According to this scenario, saury which are hatched earlier in the season spawn in their first winter and also in their second winter. But those that hatch later in the season do not spawn in their first year but spawn in their second year (Okuda, 2002). They also estimated the life span of saury as 2 yr or more.

Using this new information acquired under VENFISH, a saury growth model coupled with a lower-trophic model (North Pacific Ecosystem Model for Understanding Regional Oceanography. For including Saury and Herring: NEMURO.FISH) was developed (Ito *et al.*, 2004). Although several parameters have

been incorporated from other pelagic fish studies, a lot of information was integrated from VENFISH contributions and the model succeeded in reproducing a realistic estimate of saury growth. Moreover, in the process of building the model, several data gaps were identified and the priority of parameters to be investigated was clarified by sensitivity analysis.

A population dynamics model of saury was also developed (Tian *et al.*, 2004). Tian *et al.* (2002, 2003) showed that SST variation in the Kuroshio Extension region was closely related to long-term abundance variations in Pacific saury of the large size category and SST variation in the north KROYTR was closely related to the abundance variation of the medium size category. They also showed the ENSO effects on survival processes during the early life stage of the winter-cohort (large size category). Tian *et al.* (2004) incorporated the effects of SST in KRR and ENSO into the model according to results of previous studies. Model results also suggest that SST in KRR affects decadal change and ENSO events influence interannual variations in saury abundance.

Several of the model parameters in Tian *et al.* (2004) and Ito *et al.* (2004) are not complete and need to be improved; however, the most distinctive progress in saury studies in VENFISH is development of these models. As for the next steps beyond VENFISH, observational and experimental plans to improve model parameters are ready to be designed from the points of model developments. We also recommend coupling the saury growth model (NEMURO.FISH) with a fish population model like that of Tian *et al.* (2004) in the future. Moreover, a three dimensional extension of the coupled fish growth-population model with fish migration is possible. This kind fish migration model is inevitable to develop quantitative fishery management of Pacific saury which is widely distributed and migrates from KRR to OYR.

JAPAN PACIFIC POPULATION OF WALLEYE POLLOCK

Walleye pollock *Theragra chalcogramma* is widely distributed along the continental shelves and upper slopes of the entire subarctic North Pacific. It is an important link between lower and higher trophic levels and represents the largest economic impact of a single-species fishery (e.g. Springer, 1992). Of the four populations of walleye pollock occurring in the Japanese waters, JPP, which extends from 36°N off northeastern Honshu Island (Tohoku area) through the southern Kuril Islands, represents the largest population and economic impact (Bakkala *et al.*,

1986). A classic tag and release study conducted during the 1970s revealed the regular exchanges among pollock residing in Funka Bay, Doto (off southeastern coast of Hokkaido Island), Tohoku (off northeastern coast of Honshu) and Southern Kuril Island areas (Yoshida, 1979 cited in Maeda, 1986; Fig. 2). The number of recaptures of JPP pollock in the Japan Sea, Okhotsk and eastern Bering Sea was very limited, but it suggests their potential to colonize or exchange between other major populations (Bailey *et al.*, 1999).

The recruitment of JPP has varied by an order of magnitude, whereas its catch has been rather stable ranging from 1800 to 3000 t in the last two decades, being supported by strong year classes occurring every 5–6 yr (Nishimura *et al.*, 2002). This characteristic is common with those populations found in the Gulf of Alaska (Kendall *et al.*, 1996) and in the Bering Sea (Bakkala *et al.*, 1987). As with other r-selected species, survival processes during egg, larval and early juvenile periods have been believed to be more important in determining year-class strength of pollock compared with later life stages (Cushing, 1990). Early life stages, thus, have been studied in the area of Funka Bay, the major spawning ground of JPP; egg and larval distribution, larval diet, prey distribution and numerical modeling of egg transport. These studies clarified that spawning occurs mainly during January and February at the outer shelf of Funka Bay, and the spawned eggs are then transported into the Bay where they hatch after 10–30 days; the strength of coastal Oyashio branch at the time of hatching, and the density of copepod nauplii have been indicated to affect pollock recruitment (Nakatani and Maeda, 1992).

Although these studies have successfully extracted the factors affecting larval survival of pollock, a series of comprehensive studies made in the Gulf of Alaska (Kendall *et al.*, 1996) have shown that high larval abundance was merely a necessary condition to generate a strong year class of walleye pollock in the Gulf of Alaska, but not a sufficient condition (Bailey and Spring, 1992). More recently, Bailey (2000) postulated that the 'critical period' of pollock in the Gulf of Alaska changed from the larval to juvenile period after a major regime shift occurring in the late 1970s. These studies indicate that survival processes during juvenile periods are also important in determining pollock recruitment. We, therefore, focused on the post-larval juvenile periods of JPP rather than covering the entire life history.

In addition to Funka Bay, spawning of pollock has been reported also from the Doto and Tohoku areas. T. Hattori, A. Nishimura, D. Kitagawa and

Y. Narimatsu (in preparation) examined daily increments of pollock otolith collected in the Tohoku area. They found two distinct groups of age-0 pollock with different growth rates, and then considered these groups to represent pollock from different spawning grounds: one from Funka Bay, and another from the Tohoku area. However, it was then concluded that the importance of these additional spawning grounds is rather insignificant compared to Funka Bay (Shida and Nishimura, 2002).

The Doto and Tohoku areas have been considered to be a nursery area for JPP. Whereas, the former is strongly affected by the cold Oyashio current, the latter is situated in KROYTR and cold water from the Oyashio coastal branch (OCB) and warm water from the Kuroshio form a confluence there. The allocation of settling pollock to these nursery grounds varied interannually, with larger allocations to the Tohoku area in the years of stronger OCB (T. Hattori, A. Nishimura, D. Kitagawa and Y. Narimatsu, in preparation). This relationship implies a southward passive transport of larval/juvenile pollock settling in the Tohoku area via OCB.

However, settling in the Doto area should be related to migration against the southwesterly Oyashio current, rather than being transported passively; Honda *et al.* (2004) illustrated the movement of age-0 pollock occurring in Funka Bay to the Doto area during summer. Although we have no direct evidence determining the factors promoting the migration, one possible reason for the migration would be predator avoidance. Virtually all ages of pollock are cannibalistic. Juveniles, especially age-0 pollock, thus need to segregate from adults to avoid predation; the wide continental shelves along the Doto coast offer refuges protected by thermal barriers (Yamamura *et al.*, 2001).

Another virtue of the Doto area would be prey availability. Pollock are typical pelagic feeders depending mainly on copepods, euphausiids, micronekton and pollock (i.e. cannibalism). During spring, when pollock recover their condition rapidly from wintering and spawning, juveniles depend mainly on *Neocalanus cristatus*, which show an immediate increase in response to the spring diatom bloom (Yamamura *et al.*, 2002). To analyze the effect of prey availability and predation on post-settlement growth and mortality of pollock, a correlative dynamic model has been constructed (Yamamura, 2004). By this analysis, the Doto ecosystem has been characterized as the 'top-heavy structure', in which the pollock biomass outstrips the production of prey, and pollock population will collapse unless the zooplankton prey is supplemented by an advective supply. The velocity of the

southwesterly flow of the Oyashio Current in the Doto area averages at about 30 cm s^{-1} , (Uehara *et al.*, 1997) suggesting a substantial supply of zooplankton prey via alongshore stream and cross-shore compensation flow.

ACKNOWLEDGEMENTS

We thank the Agriculture, Forestry and Fisheries Research Council and Fisheries Agency for supporting the VENFISH program. We also owe thanks to our Scientific Advisory Members: Prof. Makoto Terazaki, Ocean Research Institute of University of Tokyo, and Prof. Yasunori Sakurai, Hokkaido University, for keeping us on track as VENFISH evolved. A. W. Kendall and H. Nakata read the drafts of the manuscripts. Their constructive and instructive comments improved this supplement. We also thank the officers and crew of the R/V Hokko-Mar, Hokuho-Mar, Hokushin-Mar, Kaiyo-Mar, Kaiyo-Mar 3, Seitoku-Mar 2, Soyo-Mar, Tankai-Mar, Tanshu-Mar, Torishima, Wakataka-Mar and Yokoh-Mar for their shipboard cooperation.

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