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Chapter IX

***Todarodes pacificus*, Japanese Common Squid**

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Abstract

The Japanese common squid, *Todarodes pacificus* (Cephalopoda; Ommastrephidae) is a commercially important squid in Japan and Korea. *T. pacificus* is found to the west of Japan in the Sea of Japan and the East China Sea as well as in the Oyashio and Kuroshio Current Systems off eastern Japan.

There are 3 subpopulations with different peak spawning seasons; summer, autumn and winter, with the later two the largest and most important. The autumn spawning occurs mainly in the southern Sea of Japan, including Tsushima Strait between Japan and South Korea, while winter spawning is in the East China Sea off Kyushu Island south of Japan.

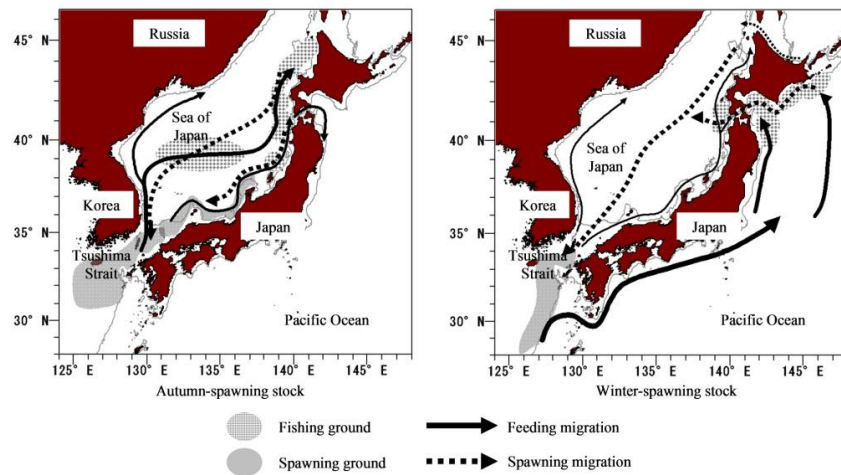
Annual catches have fluctuated widely since the 1990s, with a marked increase occurring after the late 1980s; this increase appears to have been related to a climatic

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regime shift from a cool to a warm regime that occurred in 1988/89. We review *T. pacificus* life history biology, ecology and fisheries.

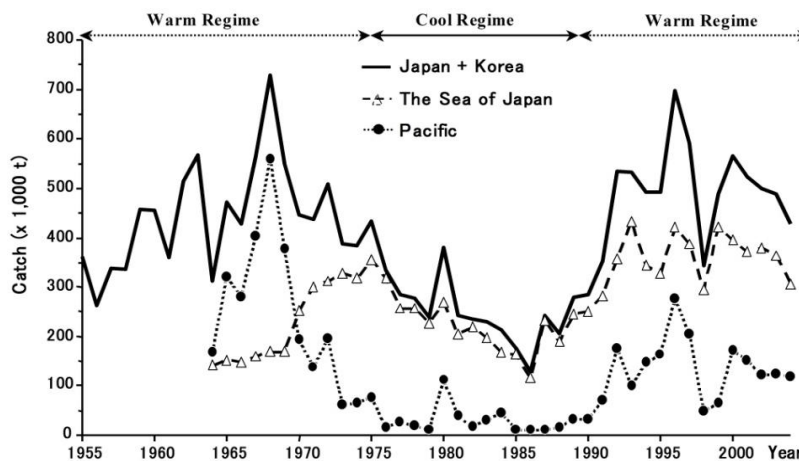
1. Introduction

The Japanese common squid, *Todarodes pacificus* (Cephalopoda; Ommastrephidae) is a commercially important squid in Japan and Korea. Its Japanese and Korean name is “surume-ika” and “ojingo”, respectively; other local name in Japan includes “ma-ika”. *T. pacificus* is a nerito-oceanic squid, which is found to the west of Japan in the Sea of Japan and the East China Sea as well as in the Oyashio and Kuroshio current systems off eastern Japan.



(From Kidokoro *et al.*, 2010).

Figure 1. The distribution range and migration pattern of *Todarodes pacificus*.



(Data derived from the Japan Sea Research Institute, Japan and the National Fisheries Research and Development Institute, Korea).

Figure 2. Annual fluctuation in Japanese common squid, *T. pacificus* catches of Korea and Japan during 1955 - 2004.

There are 3 subpopulations with different peak spawning seasons; summer, autumn and winter, with the later two the largest and most important (Figure 1, Murata, 1990; Sakurai *et al.*, 2000). The autumn spawning occurs mainly in the southern Sea of Japan, including Tsushima Strait between Japan and South Korea, while winter spawning is in the East China Sea off Kyushu Island south of Japan. This species has a 1 year life cycle with the autumn spawned squid migrating to the northern Sea of Japan and then back again to spawn before dying. Some of the winter spawned squid migrate to feed in the northern Sea of Japan while others migrate in the waters off eastern Japan to the Oyashio region where they feed during the summer and autumn. Annual catches have fluctuated widely since the 1990s, with a marked increase occurring after the late 1980s; this increase appears to have been related to a climatic regime shift from a cool to a warm regime that occurred in 1988/89 (Figure 2, Sakurai *et al.*, 2000, 2002).

2. Life History Biology

2.1. Early Stages

T. pacificus paralarvae occurred widely in the southwest Sea of Japan, the East China Sea and pacific coast of Japan (Shojima 1972, Okutani and Watanabe 1983, Goto 2002, Goto *et al.*, 2002). The distributions of the paralarvae are associated with the Tsushima Warm Current in the Sea of Japan and the Kuroshio along the Pacific coast of Japan (Okutani and Watanabe 1983, Hatanaka *et al.*, 1985, Bower *et al.*, 1999). Paralarvae shows no large diel vertical migration, and hatching sized paralarvae occurred near surface and as size increases, paralarvae gradually descend in the water column and the variability in depth increases with ontogeny (Yamamoto *et al.*, 2002, 2007).

The development of a technique of artificial fertilization for ommastrephid squids (Sakurai *et al.*, 1995) has made it possible to examine the development and early life stages of *T. pacificus* (Figure 3, Watanabe *et al.*, 1996, Sakurai *et al.*, 1996). After hatching, paralarvae were maintained for up to seven days without being fed while the internal yolk was completely absorbed (Watanabe *et al.*, 1996). Paralarval mantle lengths measured 0.95 mm at hatching and 1.25 mm after seven days. To date, there have been no successful long-term rearing experiments, as all attempts to feed the hatchling paralarvae have failed. Normal embryonic development occurs at temperatures between 14.0 and 26.0°C with highest survival rates occurring between 14.7-22.2°C (Sakurai *et al.*, 1996).

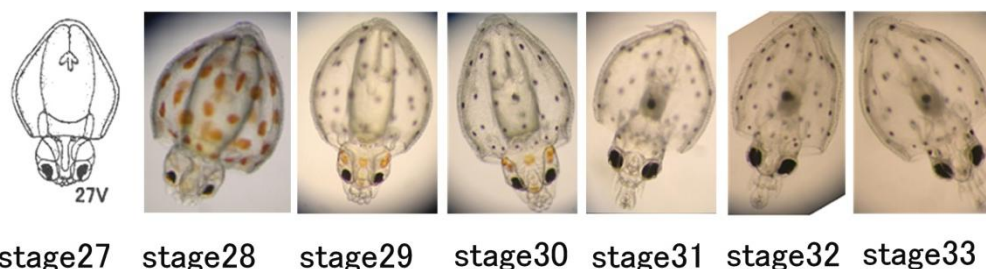


Figure 3. Development stage of hatchling (Watanabe *et al.*, 1996).

While the swimming ability of hatchling increased between 18 and 24°C, especially in 19.5-23°C (Yamamoto *et al.*, 2012) at development Stage 31-32, which was classified by Watanabe *et al.* (1996).

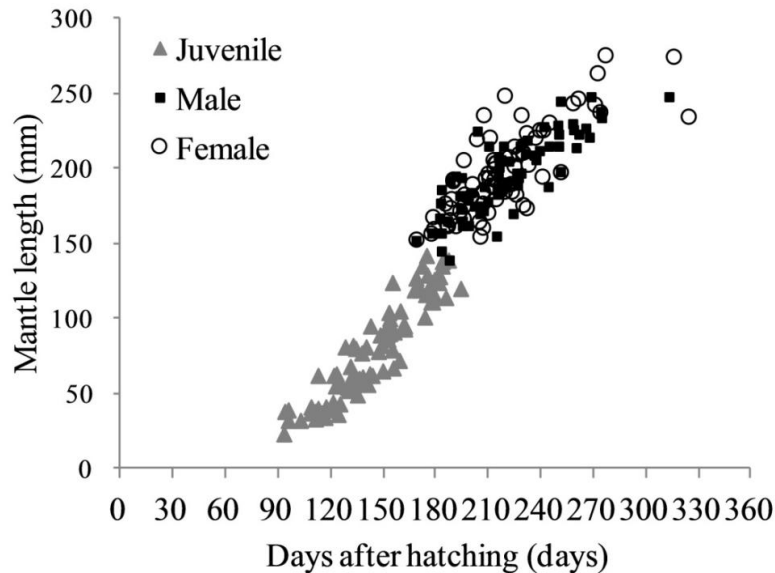
2.2. Age and Growth

The growth of *T. pacificus* had been examined based on the monthly shifts in the mantle length composition of the commercial catches until 1980s (Araya, 1967), and on the growth increments in a statolith microstructure since 1990s (Nakamura and Sakurai, 1993). The growth in the juvenile stage take 4 months to reach 5cm mantle length size after hatching (Figure 4). Then, the growth rate began to increase rapidly after 4 month age, and it is estimated that the age at 20cm mantle length (ML) is about 7 month. There is a difference by sex in the growth rate of individuals of ML above 20cm in which gonads begin to grow in males. Basically, females grow about 1 - 2cm larger than males in the end of their life (Araya, 1967; Kidokoro *et al.*, 1999). The growth pattern of *T. pacificus* was reported to be different in hatching season (Araya, 1967; Okutani, 1983). The ML of the cohort hatched during spring and summer reach up to 20 - 23cm while those of the cohort hatched autumn and winter reached up to 25-30cm. The growth pattern of *T. pacificus* varied not only by hatching season but also by migration routes and feeding areas. In the Sea of Japan, *T. pacificus* which migrate up to subarctic waters are bigger than that migrate within Tsushima warm current region (Kidokoro and Hiyama, 1996). The variation in the growth pattern by migration areas is considered to be caused by differences in environmental conditions e.g. thermal condition, food availability (Kidokoro and Hiyama, 1996).

2.3. Reproductive Characteristics

2.3.1. Gonad Development

The maturation process in *T. pacificus* has been studied by histological observations (Takahashi and Yahata, 1973; Ikeda *et al.*, 1991a,b). Ikeda *et al.* (1991a) divided female maturation into six stages based on histological observation of ovaries. The stage composition in oocytes in ovaries of maturing females shows asynchron development. The female maturation process consists of two phases, and ovary and oviduct development are correlated with nidamental gland development. In the first phase, ripe ova are produced in the ovary with rapid development of the nidamental gland, and in the next phase, ripe ova are transferred into the oviduct and stored there until spawning. Male maturation was in five stages (Ikeda *et al.*, 1991b). Spermatozoa are produced in the testis even when the testis is relatively small, and the male maturation process consists of two phases. In the first phase, spermatozoa are produced in the testis, and in the next phase, spermatozoa are transferred into the accessory gland, where they are packed in spermatophores and stored until mating.



(From Kidokoro *et al.*, 1999).

Figure 4. The growth pattern of *Todarodes pacificus* examined based on statolith microstructure.

A clear definition of the different maturity stages is of great importance for fisheries biologists, particularly for recognizing spawning populations. Ikeda *et al.* (1991a) also showed that female maturity of *T. pacificus* is well correlated with both the gonad somatic index (*GSI*: ovary and oviduct weight as a percentage of body weight) and nidamental gland index (*m*: a ratio of nidamental-gland length to mantle length). In immature female (i.e., those in maturity stages I-III), the *GSI* is <1.0% and *m* is <0.21. In maturing female, the *GSI* is between 1.0 and 2.6% and *m* is between 0.21 and 0.29. In mature female, the *GSI* is >2.6% and *m* is >0.29. In male *T. pacificus*, Ikeda *et al.* (1991b) showed that maturity could be expressed numerically using the testis somatic index (*TSI*: testis weight as a percentage of body weight) and accessory gland somatic index (*AGSI*: accessory gland weight as a percentage of body weight). These numerical values are *TSI*>0.5% and *AGSI*>0.1% in the maturing stage, when there are no spermatophores and the vas deferens is white, and *TSI*>2.0% and *AGSI*>1.0% in the mature stage, when spermatophores are present in the spermatophore sac and penis.

2.3.2. Maturation, Mating and Spawning

Since 1988, Hokkaido University scientists have conducted captive experiments to clarify the reproductive characteristics of *T. pacificus* in a filtered, recirculating raceway tank (15,000 L in capacity) at the Marine Biological Station of Hokkaido University (Sakurai *et al.*, 1993). Immature squid have been collected from inshore waters of southern Hokkaido, Japan, and maintained in the tank, where they mature, mate and spawn (Sakurai *et al.*, 2003).

In cephalopods, high temperature promotes the development of the gonad of *Octopus* species and *Sepiidae* (Mangold, 1987), but little is known the physiological effect of water temperature on development of the gonads of *T. pacificus*. Song *et al.* (accepted) found the

effect of the water temperature on the maturity mechanism of *T. Pacificus* differed between the sexes in captivity.

The squid were maintained at five constant temperatures, considered to be representative of their feeding and spawning areas: 12, 13, 15, 17 and 19 °C (Song *et al.*, accepted). The results show that the effect of the water temperature on the maturity mechanism differed between the sexes (Figure 5).

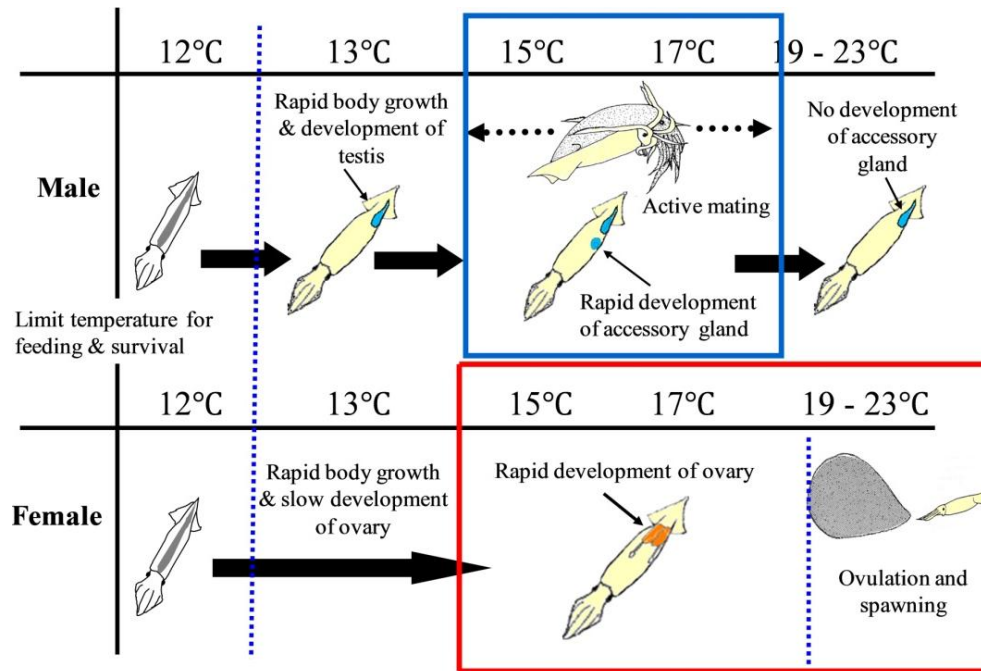


Figure 5. Effect of the water temperature on the maturity mechanism of *T. Pacificus* differed between the sexes in captivity. The squid were maintained at five constant temperatures, considered to be representative of their feeding and spawning areas: 12, 13, 15, 17 and 19 °C.

Males started maturing at 13 °C and copulated frequently at 15-17 °C, but less frequently at 19 °C. Females started maturing at 15 °C, and the sexual maturation increased as water temperature rose. In conclusion, the optimum water temperature for males was 15-17 °C, but higher temperatures are suitable for the maturation mechanism of females.

During mating, the male quickly approaches the female from below and grasps her around the head and mantle. The hectocotylus (the male's fourth right arm) then picks up spermatophores and drives them into the buccal membrane of the female within a few seconds (Sakurai *et al.*, 2003). Generally a few days before spawning, females stop feeding and often rest on the tank bottom (Bower and Sakurai, 1996). While resting, their chromatophores flash rapidly over the entire body surface; this characteristic is now known to be a sign that spawning is imminent. Spawning has been observed only once (Sakurai *et al.*, 2003). The female's arms just prior to spawning were slightly flattened and lowered. After one minute in this posture, the arms opened gradually, allowing the small egg mass to be formed and held within the arms. The egg mass expanded and was not clearly visible during the spawning. Egg-mass formation resembled the swelling of a balloon and lasted about seven minutes. The spawning behavior and property of egg mass were similar to those of *Illex*

illecebrosus ((Durward *et al.*, 1980, O'Dor *et al.*, 1982, O'Dor and Balch 1985, see Chapter 13). The results of our captive experiments suggest that mature females usually spawn once and then die, but some females spawned twice in a week when their spawning was disturbed (Ikeda *et al.*, 1993).

2.3.3. Egg Mass and Fecundity

No naturally spawned egg masses of *T. pacificus* had ever been found in the spawning ground, but a laboratory study revealed the complete property of the egg masses (Bower and Sakurai, 1996). The egg masses spawned from reared females were gelatinous, spherical, nearly neutrally buoyant. Externally, the masses were covered with a jelly-like secretion, presumably from the nidamental glands, and the interior of the masses consisted of a jelly presumably secreted by the oviducal glands. Eggs were positioned 0.4-2.0 cm apart throughout the inner mass and the chorion surrounding each egg expanded to diameters of 1.9-2.3 mm. The egg-mass surface layer effectively prevented crustaceans, protozoans, and bacteria from infesting the masses. An egg mass with diameter 80 cm contained *ca.* 200,000 eggs and more than 90% of the eggs were fertilized. Paralarvae hatched 4-6days (18-23°C) and the egg masses disintegrated soon after hatching. Paralarvae swim vertically out of the egg masses and no paralarvae remain within the masses.

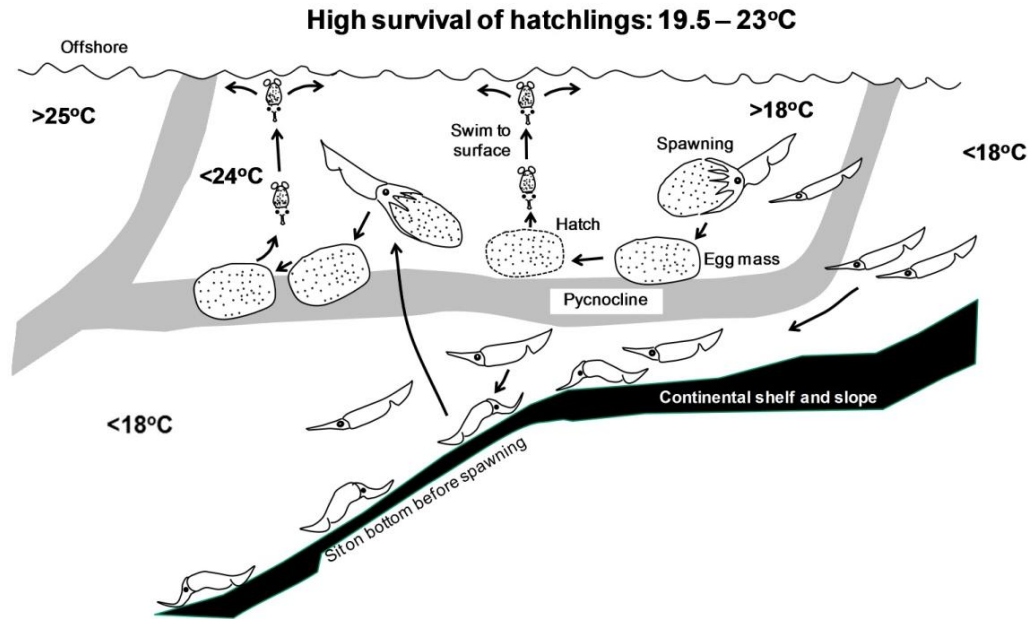
The fecundity of *T. pacificus* based on counts of ripe ova in oviducts of pre-spawning females is estimated to be between 320,000 and 470,000 (Soeda, 1956). However, in the ovaries of spawning females, oocytes occurred in all stages of development, from yolkless to mature stages and in exhausted females with thin mantles, the ovary and oviducts composed 28 % of the total body weight (Ikeda *et al.*, 1993a). The oviducts of dead post-spawning females still contained many ova (Bower and Sakurai, 1996) suggesting that females do not necessarily spawn all ova before dying.

2.3.4. Hypothesis of Reproduction Process

Based on the laboratory studies, a hypothetical process in the early stage was proposed by Sakurai (2006; Figure 6) which revised the similar hypothesis by Sakurai *et al.* (2000).

Spawning is assumed to occur above the continental shelf and slope around Japan, because captive females regularly sit on the tank bottom just before spawning (Bower and Sakurai, 1996). Also bottom trawls often collect exhausted spent females on the continental shelf and slope at 100-500 m depth (Hamabe and Shimizu, 1966).

By combining results from field surveys and captive experiments, Sakurai *et al.* (2000) proposed the following reproduction process. After sitting on the bottom the adult squid swim to an upper layer and spawns in surface water above thermocline. The spawned egg masses, due to differences in density, sink until reaching a buoyancy depth above thermocline. Once hatched the hatchlings will swim to the surface and are transported to the respective feeding grounds by the currents. Laboratory experiments have shown that higher hatchling survival rates and swimming activities are obtained when the water temperature range between 19.5°C and 23°C (Yamamoto *et al.*, 2012), while most hatchlings collected off southern Japan occur at sea surface temperatures of 17-23 °C (Bower *et al.*, 1999).



(Modified from Sakurai *et al.*, 2000, Sakurai, 2006).

Figure 6. New schematic view of reproductive processes of Japanese common squid, *T. pacificus*.

3. Ecology

3.1. Distribution and Abundance

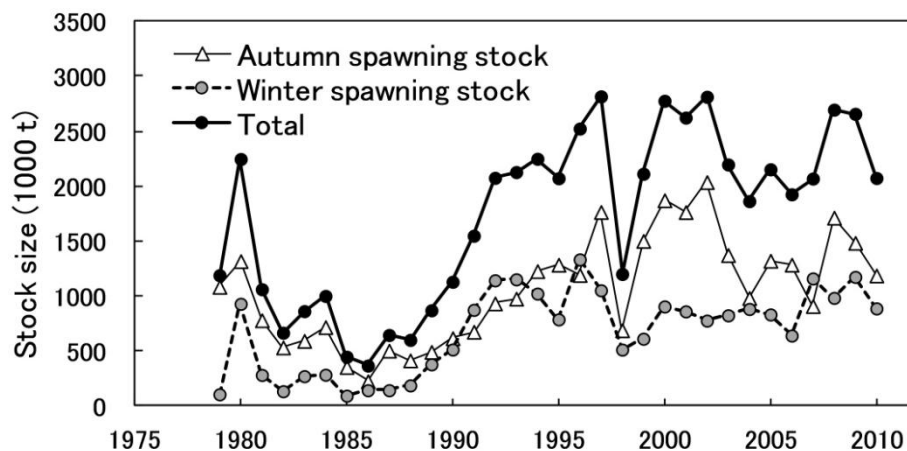
T. pacificus is distributed mainly in the northwest Pacific along the Japanese Island including the East China Sea, the Sea of Japan and the southern Okhotsk Sea (Figure 1). The distribution range shifts seasonally with changes in temperature. The distribution range usually expanded up to 50N° in September, but it is about 40N° in April. The abundance of the *T. pacificus* is assumed to be varied on a decadal scale. It was estimated at about 2 – 3 million tons around Japanese Island during 1990s and 2000s, but it was estimated below 1 million ton in the 1980s (Figure 7).

3.2. Temporal Variations

The distribution range, migration patterns and spawning grounds of *T. pacificus* were varied with changing stock size based on the observations over 50 years, which are assumed to be caused by changing oceanographic conditions.

The distribution range on the Pacific side of Japanese waters shrunk with the decline of the stock size of winter spawning stock during the 1970s and 1980s, and fishing ground east of Hokkaido Island disappeared (Nakata, 1993). Basically, the winter spawning stock migrates around the Japanese Islands counterclockwise, but such migration pattern was not observed in this period (Nakata, 1993). The distribution range had expanded to the same range which was observed during the 1950s and 1960s on the Pacific side of Japanese waters,

with the rebound of the stock size of winter spawning since 1990s. It was indicated that the main spawning grounds of the autumn spawning stock expanded coincided with 1989 regime shift based on the paralarval survey in the Sea of Japan (Goto, 2002; Kidokoro *et al.*, 2010). In the Sea of Japan, not only spawning grounds but also spawning migration patterns have changed coincided with 1989 regime shift (Kidokoro *et al.*, 2010). The migration patterns of the autumn-spawning stock can be summarized into two patterns based on oceanographic conditions or stock size. During warm oceanographic conditions (in the 1960s and 1990s), the autumn-spawning stock moved towards the Korean Peninsula and the Tsushima Strait, but during cold oceanographic conditions (in the 1980s), the autumn-spawning stock moved towards the central part of Honshu Island (Kidokoro *et al.*, 2010).



(From Kidokoro *et al.*, 2011; Yamashita and Fukuwaka, 2011).

Figure 7. Estimated stock size of *Todarodes pacificus*.

3.3. Feeding Ecology

T. pacificus is a generalist rather than specialist predator, feeding opportunistically and take whatever is available. The squid feed on zooplankton and small fish, including juvenile walleye pollock *Theragra chalcogramma* with the consumption of pollock by squid on the Oyashio Shelf during autumn being sufficient to affect pollock recruitment (Sakurai, 2007). Prey items of *T. pacificus* vary by region, but crustaceans, fish and squids are generally dominating the diet (Hamabe and Shimizu, 1966; Okiyama, 1965; Okutani, 1962). Crustaceans are mainly composed of copepods, amphipods and euphausiids. Okutani (1962) has been reported that brachyuran decapod larvae (megalopa) were predominant prey in the Pacific coast of central Japan. It has also been reported that *T. pacificus* ingested other zooplankton taxa such as ostracods and chaetognaths, but they were of limited importance (Okutani, 1962; Uchikawa and Kidokoro, 2011). Various fish such as Japanese ancovy *Engraulis japonicus*, Pacific saury *Cololabis saria*, mytophids, *Mauloricus japonicus* and juvenile walleye pollock are recorded from the stomach contents (Hamabe and Shimizu, 1966; Hashimoto and Ishito, 1991 Okiyama, 1965; Okutani, 1962). The broad breadth of the feeding spectrum of fish prey may reflect regional prey availability. *T. pacificus* feeds other

squids such as firefly squids *Watasenia scintillans* and its own species (cannibalism) (Araya, 1967; Hamabe and Shimizu, 1966; Kidokoro and Uji, 1999; Okiyama, 1965). In cannibalism of *T. pacificus*, it has been reported that larger (>120 mm ML) individuals fed on smaller (<50mm ML) ones (Kidokoro and Uji, 1999). Cannibalism in *T. pacificus* appears to occur frequently when squid of a wide size range distribute sympatrically. *T. pacificus* also feed on benthic organisms (Hamabe and Shimizu, 1966; Tanaka, 1993). In the Sea of Okhotsk, *T. pacificus* caught by bottom trawls during daytime over the continental shelf has been reported that polychaetes were the most frequent prey (Tanaka, 1993). This suggest that *T. pacificus* will be associated with the sea bottom in shallow sea topographies such as continental shelf, islands and seamounts, and benthic prey may be more important in their diet during daytime near the bottom.

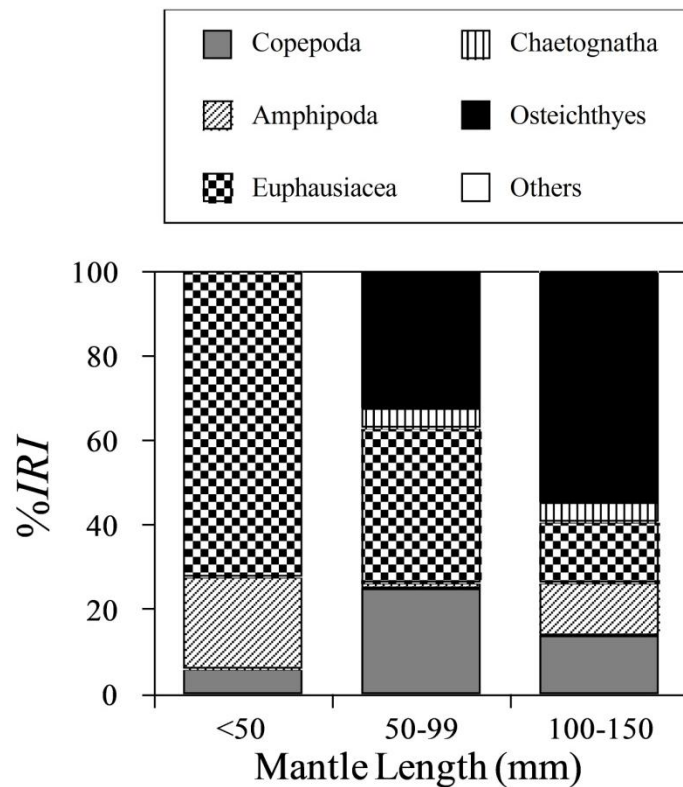


Figure 8. Diet of juvenile (<150mm ML) *Todarodes pacificus* in the Sea of Japan during spring. Based on data from Uchikawa and Kidokoro (2011), an index of relative importance (*IRI*) (Pinkas *et al.*, 1971) was calculated for each prey taxon as $IRI_i = F_i \times (N_i + W_i)$, where *i* represents *i*th prey taxon, *F* is the percentage frequency of occurrence, *N* is the percentage number and *W* is the percentage wet mass. The *IRI* for each major group of prey taxa was then standardized to %*IRI* (Cortés, 1997) as $\%IRI_i = 100 \times IRI_i / \sum IRI_i$.

Changes in diet during ontogeny have been described in *T. pacificus*. Uchikawa and Kidokoro (2011) have reported that details of prey composition of juvenile (<150mm ML) *T. pacificus* based on gut content analysis in the Sea of Japan during spring (Figure 8): squids smaller than 50mm ML feed exclusively on crustaceans such as copepods, amphipods and euphausiids, and then shift to crustaceans and fish at ML of 50-99mm; after reaching a ML of

100mm, fish was the most important prey and crustaceans were less important. Squids larger than 150mm ML mainly feed on fish and squids (Hamabe and Shimizu, 1966), although amphipods (*Themisto japonica*) and euphausiids (*Euphausia pacifica* and *Thysanoessa longipes*) dominated in the diet of squids larger than 150mm ML in offshore waters of the Sea of Japan (Uchikawa, personal observation).

The first prey of *T. pacificus* paralarvae is not known. It has been postulated that paralarvae of ommastrephids might suspension feeder (O'Dor *et al.*, 1985) and prey capture begins after the proboscis divides (Shigeno *et al.*, 2001; Uchikawa *et al.*, 2009). It was also suggested that beak protrusion might signal the beginning of raptorial feeding in ommastrephids (Uchikawa *et al.*, 2009). Like neon flying squid *Ommastrephes bartramii* (Uchikawa *et al.*, 2009), the first prey of *T. pacificus* paralarvae is presumably small zooplankton such as copepods. However, no information is available on its feeding habits. To understand the early life stages of *T. pacificus*, information about early feeding ecology such as first prey, feeding behavior and development of feeding apparatus are still wanting.

3.4. Predators

T. pacificus was preyed upon in great numbers by large fish such as mackerels, *Scomber japonicus*, *S. australasicus*, yellowtail, *Seriola quinqueradiata*, bluefin tuna, *Thunnus thynnus*, sharks, and by marine mammals such as dolphins through its life cycle. In the Sea of Japan, about 40 individuals freshly consumed *T. pacificus* were found in stomachs of Dall's porpoise collected throughout the day in summer and autumn (Ohizumi *et al.*, 2000). The minke whale, *Balaenoptera acutorostrata* is widely distributed throughout the world. 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 and Fujise, 2002). On the Pacific side of Japan, this species feeds mainly on Japanese sardine, *Sardinops melanostictus*, Japanese anchovy, *Engraulis japonicus*, Pacific saury, *Cololabis saira* and *T. pacificus* (Tamura and Fujise, 2002).

3.5. Parasites

Larval anisakid nematodes are the most famous parasites of *T. pacificus*. They are infected by two species of third-stage larvae of anisakid nematodes. The larvae of *Anisakis simplex* s.l. (henceforth referred to as *A. simplex*) were commonly found in the outside walls of stomach and caecum of *T. pacificus*, whereas the larvae of *Lappetascaris* sp. were found in the anterior end of mantle (Nagasawa and Moravec, 1995; Takahara and Sakurai, 2010).

A. simplex is one of the common nematodes in marine fishes and squids. The life cycle involves several hosts (Figure 9, Sakanari and McKerrow, 1989; Nagasawa, 1990, 1993; Audicana and Kennedy 2008). One paratenic host is *T. pacificus*, a commercially important species comprising two main cohorts (autumn and winter) that have different migration routes and feeding areas.

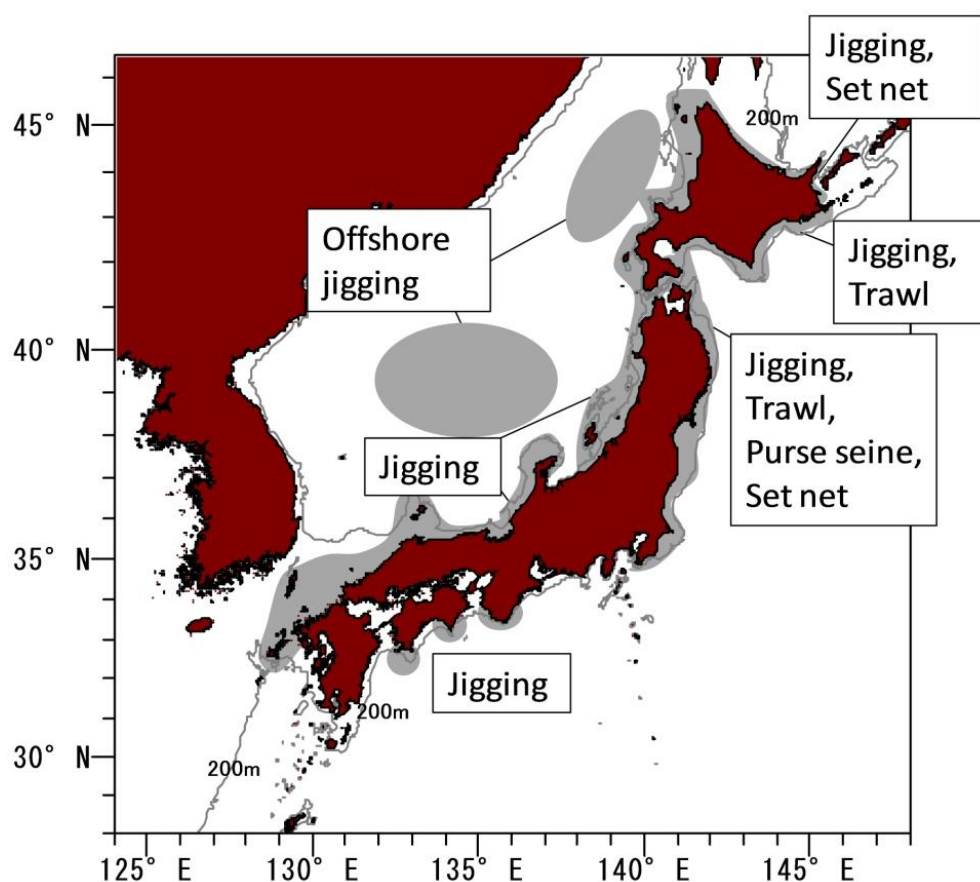
The prevalence of *A. simplex* is higher in the winter cohort than in the autumn one (Takahara and Sakurai, 2010), presumably because the winter cohort forages in the Sea of

4. Fisheries

4.1. Stock Definition

Basically, *T. pacificus* is divided into two or three stocks by spawning season (Araya, 1967; Okutani, 1977; Osako and Murata, 1983; Kidokoro *et al.*, 2003). In general, units for stock assessment are divided into geographical regions, and catch statistics for each stock are totaled in each region. But for *T. pacificus*, the catch statistics of each stock are divided based on the differences found in the fishing grounds throughout the seasons by using the monthly catch statistics (Kidokoro *et al.*, 2003), which also include landings from South Korean fisheries.

It must be noted that the methods (including the definition of the stock units) are being currently used for stock assessment in Japan, but there are no agreements or discussions with South Korean researchers or their government.



(Modified from Yamashita and Mori 2009).

Figure 10. Major fishing grounds and fishing methods for *Todarodes pacificus* around the Japanese waters.

4.2. Fishing Methods and Fishing Grounds

4.2.1. Japanese Fisheries

T. pacificus is fished by using several fishing methods. *T. pacificus* is mostly fished by jiggers. However, the characteristics of fishing methods have variations among the regions in Japan (Figure 10). *T. pacificus* is mostly fished by coastal jiggers and offshore jiggers in the Sea of Japan. The catches in coastal areas are landed as fresh catch, and offshore catches are frozen on board then landed (Kidokoro *et al.*, 2011). Along the Pacific side of Japanese waters, *T. pacificus* is mainly taken by coastal jiggers, but more than a half of the total catch along the Pacific side is taken by other fisheries, *i.e.* offshore trawlers, large-and medium scale purse seiners and set nets (Yamashita and Fukuwaka, 2011). In the Sea of Okhotsk and the Nemuro Strait, most of the catches are taken by set nets and coastal jiggers (Sakaguchi and Sawamura, 2009). Annual catches have been changing drastically in these regions.

4.2.2. Korean Fisheries

In the Korean waters, *T. pacificus* is fished in the Sea of Japan, the Yellow Sea and the East China Sea by several fishing methods. Most of the catch is made by offshore jigging, large trawl and eastern sea trawl in those areas, recently. In the case of Japanese fisheries, the ratio of offshore and coastal jigger catches have decreased, and the ratio of trawlers catches have increased since 1990.

The fishing grounds of coastal jiggers, whose vessels are classed less than 8 tons, are along the coast of Korea (Choi *et al.*, 2002). In the fishing grounds of offshore, jiggers vessels classed the range from 8 tons to 90 tons, are mostly in the central part of the Sea of Japan and around Yamato Bank (Choi *et al.*, 2002).

4.3. Landings and CPUE

4.3.1. Landings

Total annual landing of *T. pacificus* by the Japanese and South Korean fisheries was about 500,000 t during the 1950s and 1960s, but it decreased significantly during the 1970s and dropped to 200,000 t in the mid 1980s. In the 1990s the landings increased and have rebounded to about 500,000 t in recent years. Annual catch in the Sea of Japan was approximately 100,000 – 150,000 tons during the 1950s and 1960s. It rose to 300,000 tons in the beginning of 1970s however it declined to 200,000 tons during the middle of 1970s and the 1980s (Kasahara, 1978; Osako and Murata, 1983). Annual catch in the Sea of Japan increased again in the 1990s, and has remained at approximately 300,000-400,000 tons. Annual catch in the Pacific region was approximately 300,000 – 500,000 tons during the 1950s and 1960s. It declined drastically around the beginning of 1970s, and was approximately 10,000-30,000 tons during the 1970s and 1980s. Annual catch in the Pacific region increased again in the 1990s, and has remained at approximately 100,000-200,000 tons.

4.3.2. CPUE

In the Sea of Japan, CPUE (ton/vessel/day) of offshore jiggers was mainly under 1.0 ton / vessel / day in 1980s. The CPUE increased since 1989, and were at high levels during 2000 – 2003. The CPUE are around 2.5 tons/vessel/day, recently. The operations of offshore jiggers are limited to offshore regions, thus the CPUE implies the abundance index in the offshore regions. Along the Pacific side of Japanese waters, the level of CPUE of coastal jiggers was in the range of 500 – 1,000 individuals / vessel / day, until the latter half of 1980s. The CPUE of coastal jiggers increased to a high level over approximately 2,000 ind. / vessel / day since 1990s in this region, and are around 3,000 ind. / vessel / day in recent years. The detailed catch statistics of *T. pacificus* by Japanese fisheries were described in the stock assessment reports around the Japanese waters (Kidokoro *et al.*, 2011; Yamashita and Fukuwaka 2011).

4.4. Recruitment and Environmental Variability

Low-pass filtered SST data off southwestern Japan show alternate warm and cold periods at decadal scales that correspond with the variability in the Pacific Decadal Oscillation (PDO). For example, there was a sudden decrease in SSTs in the late 1970s (shift to positive PDO) and an increase in SSTs (negative PDO) during the mid to late 1980s (Senjyu and Watanabe 2004). Note that the positive phase of the PDO corresponds to cool conditions on the western side of the Pacific and warm on the eastern side and vice versa in its negative phase. *T. pacificus* decreased during the cool regime period from the late-1970s to late-1980s (Figure 2; Sakurai *et al.* 2000, Rosa *et al.*, 2011), while Japanese sardine, *Sardinops japonicus* increased exponentially. Squid catch has increased after the late-1980s warm regime period (Sakurai *et al.*, 2000). These catch fluctuations are similar with those of Jack mackerel, *Trachurus japonicus* and the Japanese anchovy. After 1989, the feeding area of the winter spawning stock expanded to the Oyashio region during summer-autumn. During the warm regime period after 1989, the inferred spawning areas of the winter spawning group have occurred along the continental edge off the Kyushu Island and the Nansei Islands, and the inner flow of the Kuroshio has transported the hatchlings in the surface layer northeastward along the continental edge from the spawning areas to the nursery areas (Figure 1). However, during the cool regime of the 1980s, when winter wind stress was stronger, air temperature at the sea surface was lower, and mixed layer depth at the spawning grounds was deeper than after 1989, so the spawning areas were not connected along the continental edge.

The catch is considered a good proxy for abundance and hence reproductive success (Choi *et al.* 2008). One reason for the increased larval survival during warm periods might be related to an increase in the size of the spawning areas. In the warm periods, the autumn and winter spawning area extends northward into Tsushima Strait and farther eastward to the continental slope. For the latter, the inner flow of the Kuroshio helps transport the hatchlings into the Oyashio region to feed. Thus during warm periods more squid may be transported to the feeding grounds via this circulation. During cool periods there is less spawning along the continental slope and the squid are deeper due to an increased mixed layer depth caused by stronger winds. This may result in less squid being transported into the Oyashio region. Fluctuations in the strength of the northward flowing Tsushima Warm Current influences the area of the warm water region in the Sea of Japan, which also matches the variability in squid catches from this region (Choi *et al.* 2008). The current's effect on squid is believed to be

through its prey as the changes of annual zooplankton biomass are also closely connected to the fluctuations in the Tsushima Warm Current. This too may contribute to the increased survival of *T. pacificus* in the Sea of Japan during warm years.

4.5. Management and Stock Assessment

4.5.1. Management in Japanese Fisheries

The Japanese Fisheries Agency has adopted TAC as a method of stock management for the seven major fisheries since 1997. *T. pacificus* was added to the TAC management plan in 1998. The annual TAC is set by the government through a process that weighs a combination of socioeconomic factors and the allowable biological catch (ABC), recommended by researchers of the national fisheries research institute.

The calculations of the Japanese ABCs are modeled after those used in the U.S. (Restrepo *et al.*, 1998). ABC (ABC_{limit}) is calculated from the fishing mortality (F_{limit}) and forecasted stock abundance in the target year. The F_{limit} usually uses biological reference points (e.g. F_{msy} , F_{med} , $F_{0.1}$; see Caddy and Mahon, 1995) or current fishing mortality in the case where the current stock size is above a threshold stock size (B_{limit}). If the current stock size is below the B_{limit} , then the F_{limit} should be set below the biological reference point accordingly for rebuilding stock status to an acceptable level within an appropriate time frame (Restrepo *et al.*, 1998). The biological reference point used as the F_{limit} is revised slightly every year using data from the latest surveys.

It has become clear that not only fishing effort but also changing environmental conditions affect the size of *T. pacificus* stocks. For ommastrephid squids, annual variability in oceanographic conditions causes annual variation in recruitment strength (Dawe *et al.*, 2000; Waluda *et al.*, 2001). Moreover, decadal or inter-decadal variations or regime shifts also influence the stock status (Sakurai *et al.*, 2000). Because both human and environmental pressures cause stock size fluctuations, effective management of ommastrephid squid stocks must balance an understanding of fishing effort and environmental conditions.

4.5.2. Current Stock Assessment Methods Being Used in Japan

Change in the annual stock size of *T. pacificus* has been monitored by surveys conducted by scientific research vessels with squid-jigging machines at the beginning of the fishing season since the 1970s (Kidokoro *et al.*, 2011; Yamashita and Fukuwaka 2011). The density of *T. pacificus* at each station is estimated based on the CPUE (the number of individuals caught/squid-jigging machine/hour (ind./h)) of the research vessels, and the average CPUE of all the stations is used to calculate the annual stock index. Stock abundance is quantified based on the stock index, which is supposed to be in proportion to the stock abundance. Biological reference points are estimated based on the estimated spawner–recruit relationship which is shown in the relationship between number of recruits and spawning stock.

The change in the stock size of *T. pacificus* coincided with changing environmental conditions, and the spawner–recruit relationship is assumed to change with changing environmental conditions. In particular, decadal or inter-decadal changes are assumed to influence stock status and spawner–recruit relationship of *T. pacificus*, therefore we used the data collected since 1990 to estimate the spawner–recruit relationship (Kidokoro *et al.*, 2011;

Yamashita and Fukuwaka 2011). The parameters used in our spawner-recruit relationship are estimated from data collected since 1990 following this apparent regime shift, but when the current regime changes, these parameters should be revised accordingly. However, it is difficult to predict when regime shifts might occur.

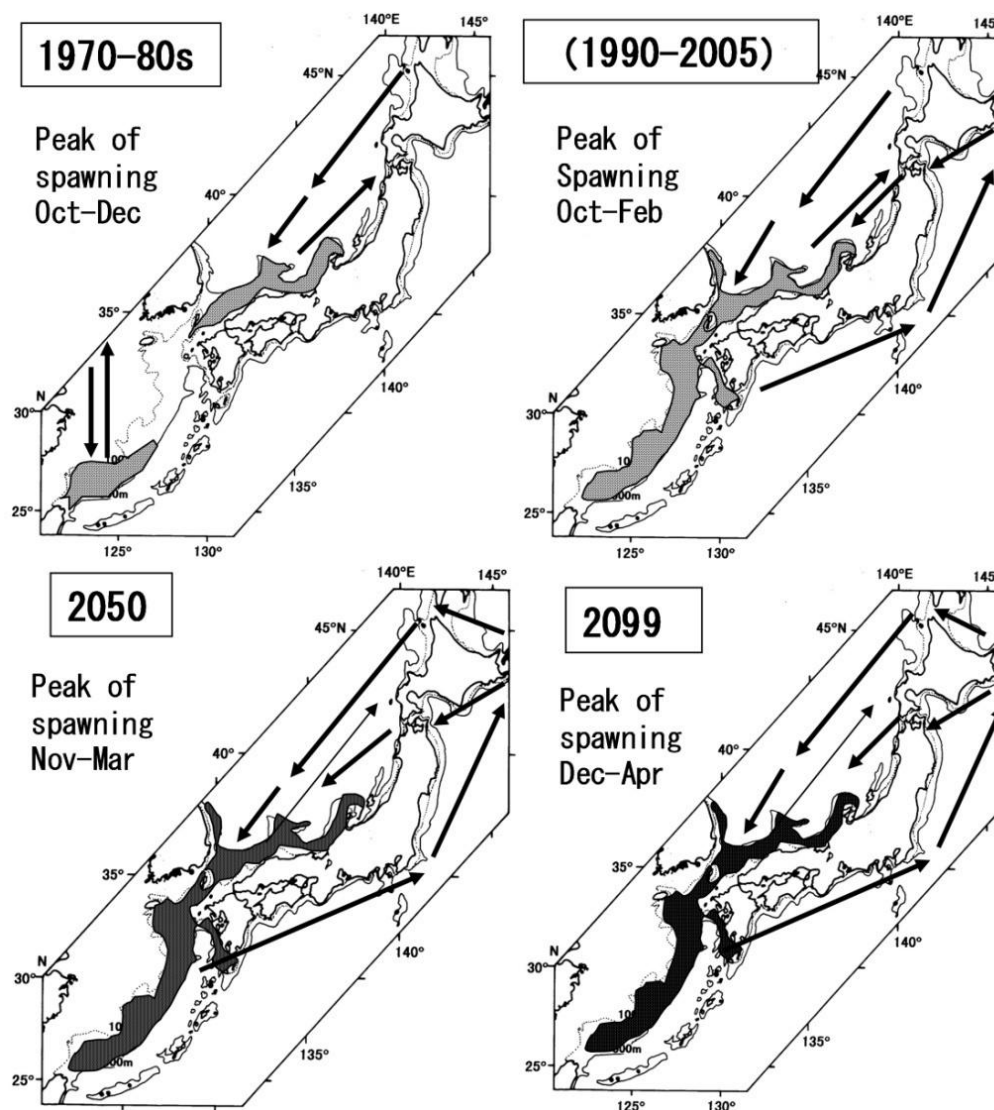


Figure 11. Predicted spawning periods, areas, and migration routes of *T. pacificus* during 1970-80s (cool regime), 1990-2005 (warm regime), 2050 (SST: 2° increase), and 2099 (SST: 4° increase). Estimated environmental changes in waters around Japan based on the IPCC global warming scenario.

4.6. How to Predict Life History Based on the Global Warming Scenario

Short and long-term change of *T. pacificus* stock can be explained and predicted by physical parameters such as wind stress, air temperature, SST, and mixed layer depth during

the spawning period based on the reproductive hypothesis. Although we cannot forecast climate change even in the next month or season, we can map the inferred spawning grounds using the SST areas between 18–24°C, especially between 19.5–23°C and within a specific range of bottom topography (100–500m depth) (Rosa *et al.*, 2011).

Based on this method, we can monitor the trend of stock fluctuation and structural change such as the recent seasonal changes of inferred spawning areas and predict the stock condition of the next year's cohort. Further, we can try to predict whether the squid will be extinct or will occupy a marine ecosystem during the 21st Century based on the Global Warming Scenario (IPCC, International Panel of Climate Change) using the Earth Simulation System (FRCGC, Frontier Research Center of Global Change, Japan).

If we examine the monthly changes of squid distribution (temperature range of distribution: 12–23°C at 50m depth) and inferred spawning areas in 2005, 2050, and 2099, the northern limit of the squid distribution shifts to the north by 1°N/50 yrs and covers the water around Hokkaido Island by 2099. The inferred main spawning grounds also move from the southern Sea of Japan and the East China Sea around Tsushima Strait to the East China Sea by 2099. The peak of the inferred spawning period will shift from October–February in 1990–2005 to November–March in 2050, and December–April in 2099 (Figure 11).

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