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Fluctuations in the Abundance of Common Squid, *Todarodes pacificus* and Environmental Conditions in the Far East Regions during 52 Years

Gong, Yeong*, Hee Dong Jeong**[1], Kwang Ho Choi[1], Ki-Tack Seong[1] and Sang-Woo Kim[1]
Korea Fisheries Associations, Seoul 120-012, Korea
[1]*National Fisheries Research and Development Institute, Busan 619-902, Korea*

ABSTRACT: Environmental variables, fishing and biological data of the common squid, *Todarodes pacificus* were used to describe changes in structure, migration and abundance of the squid population in relation to ocean climate shifts. It was possible to consider the main groups of the squid (autumn and winter-spawned groups) as a single population to aid conservation in the waters around Korea and Japan (TWC and KOC regions). The patterns of yearly fluctuations in abundance of the squid population in the two regions were the same during 52 years of 1952～2003. The abundance of the squid began to decrease in both regions in the early 1970s, remained low in the 1980s and the main squid groups synchronously increased in the 1990s coincident with favorable changes of thermal conditions and plankton production in those ecosystems. The mechanisms of changes in the structure, distribution and abundance of common squid population in relation to current-mediated migration circuits are explained on the basis of phenological variables responding to climate shifts.

Key words: Abundance, Climate shift, Common squid, Current system, Migration circuit, Population structure

INTRODUCTION

The common squid, *Todarodes pacificus* is a nerito-oceanic species with wide distribution range from the Philippine Sea to the central Okhotsk Sea. The life cycle of the squid is annual and nearly semelparous, with a peak spawning period in the East China Sea from autumn to winter, being most abundant in the East/Japan Sea and North Pacific off northern Japan (O'Dor 1992, Sakurai et al. 2003). Three spawning groups are known in the common squid population; the winter group has the widest distribution around Japan and is harvested mainly by Japanese jigging fleets, the autumn group has its highest density in the East/Japan Sea and is harvested by Korean and Japanese fleets, and the other is (Murata 1983). There is extensive overlap in the migration routes of the spawning groups (Mori and Nakamura 2001). It is suggested that the population structure varied during different periods of abundance (Nakata 1993, Takayanagi 1993, Kubota and Kawabata 1996).

The Tsushima Warm Current transports paralarvae and juvenile squid bred in the East China Sea to the nursery and feeding grounds in the East/Japan Sea and the Kuroshio Current transports them to the feeding ground in the Oyashio area. In autumn when they reach the coupling stage, they start southward migration to the spawning ground until late autumn and winter (Araya 1976, Hatanaka et al. 1985, Kasahara 1991, Murata 1991). Paralarvaes and immature squids can be transported to unfavorable area by wind or current, which seems to change the feeding and spawning migrations (Hamabe and Kawakami 1972). The long annual migration to spawn upstream in the Kuroshio and Tsushima Warm Current systems require young common squids to maximize their growth rate. Only large individuals can swim the distance required to spawn upstream in the current systems, allowing juveniles to drift into the productive regions (O'Dor 1992).

Annual catches of the squid in the Tsushima Warm Current (TWC) region by Korean and Japanese fisheries and in the Kuroshio-Oyashio Current (KOC) region by Japanese fisheries have fluctuated widely since 1920s and peaked at 753,000 tones in the late 1960s. Thereafter the catch decreased drastically and remained low during the period 1970s and 1980s and again increased markedly in the 1990s. These fluctuations in the population abundance seem to be related to the long-term or short-term changes in oceanic conditions (Murata and Araya 1977, Okutani and Watanabe 1983, Sakurai et al. 2000). It was suggested that the increased catch in the early 1990s was related to the expanded optimum thermal regime in the spawning ground after the climate shifts in the North Pacific (e.g. Aleutian Low) occurred in 1988/89 (Sakurai et al. 2000) and the northward shift of squid fishing ground and increased

* Corresponding author; Phone: +82-51-743-3283, e-mail: gongyeong@yahoo.co.kr
** Alternate corresponding author; Phone: +82-51-720-2210, e-mail: hdjeong@nfrdi.re.kr

catch were related to the increased temperature and zooplankton biomass (Kang et al. 2002). Possible causes of the decline in the squid abundance in the Pacific off northern Japan are explained by the predator-prey relationships (Ogawa and Sasaki 1988). However, the mechanisms that control the population structure and abundance of the squid in the whole distribution range are still far from clear.

In this study we examined the long-term fluctuations in the abundance of common squids by each spawning group and by region in relation to environmental variables to investigate whether any changes occurred due to fishing or by climate changes in the whole distribution range. A possible mechanism explaining the changes was presented on the basis of phenological variables for the squid occurring in the changing ecosystems.

MATERIALS AND METHODS

Long-term changes in thermal regimes were examined from the fluctuation indices of temperatures at the subsurface (50 and 100m layer) based on monthly mean temperatures at the 67 stations in the southern East/Japan Sea (35˚N～38˚30'N, 128˚30'N～132˚E) for the 43 years period 1961~2003 (National Fisheries and Development Institute (NFRDI) 1964~2004). Year-to-year zooplankton biomasses in the region for the period 1965~2000 (Kang and Lee 2002) and in the central region (PM line, 36˚N, 136˚E～41˚N, 132˚E) for the period 1973~1995 (Minami et al. 1999) were adopted to explore the changes in food environments in the squid fishing grounds.

Year-to-year and seasonal positions of the subpolar front in the East/Japan Sea were determined based on the maximum temperature gradients from monthly horizontal distribution of temperatures at the subsurface (50 and 100 m layers) to compare with the shifts in fishing grounds of dense squids.

Year-to-year catches of common squids taken in the TWC region (Yellow Sea-East China Sea-East/Japan Sea) and in the KOC region (Pacific off northern Japan and Okhotsk Sea) (Fig. 1) were based on the Yearbooks of Fishery Statistics of Korea and Japan for the period 1952~2003, and on the catches from various reports (Gong and Oh 1977, Kasahara 1978, 1983, 1991, Murata et al. 1981, Osako and Murata 1983, Nakamura et al. 1993, Hasegawa 1993, e.g. Suzuki 1963).

Year-to-year catch per unit fishing effort (CPUE) for squid fishing by Korea (Choi 2005) and by Japan (Kidokoro et al. 2004) were used to examine the changes in abundance. Year-to-year catch rates of two spawning groups were based on the previous reports (Kidokoro et al. 2005, Mori et al. 2005).

Year-to-year changes in seasonal mean mantle length of *Todarodes pacificus* were based on the body size measurements by NFRDI from the samples taken by Korean jigging and purse seine

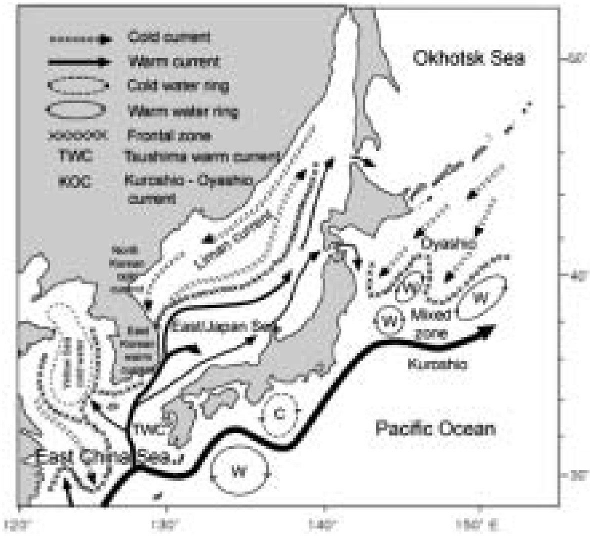

Fig. 1. Schematic current systems in the East/Japan Sea and its adjacent waters. TWC indicates the East/Japan Sea, East China Sea and Yellow Sea, and KOC indicates the Kuroshio-Oyashio Current regions and the Okhotsk Sea.

fleets in the East/Japan Sea for the period 1971~2002 (Choi 2005).

RESULTS

Changes in Thermal Regimes and Zooplankton Biomass

The thermal regime at the subsurface (50 and 100 m layers) showed oscillation with high amplitude in the late 1970s and thereafter decadal scale quasi-steady state of low temperatures in the central and southern East/Japan Sea. The temperatures in the subsurface layer were far above the 45 years average in the early 1990s (Fig. 2).

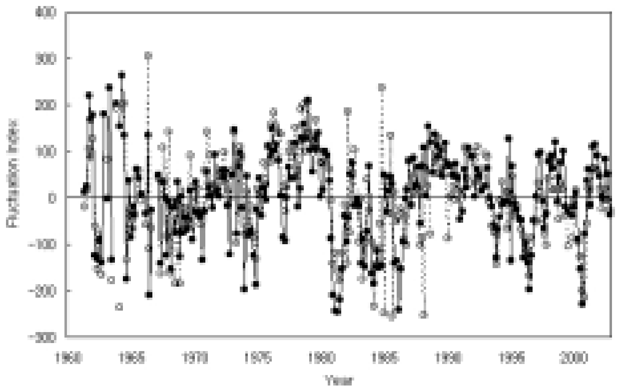

Fig. 2. Subsurface (50m and 100m) temperature anomalies in the East Korea Warm Current region from 67 offshore stations, 1961～2002. Fluctuation Index =100(x−xbar)/σ (x: temperature, σ: standard deviation).

The zooplankton biomass in the southern East/Japan Sea (35˚N～38˚30'N, 128˚30'E～132˚E) decreased in the 1980s but increased in the 1990s. Interdecadal variability of zooplankton biomass (wet weight) along the PM line (35˚N, 136˚E～41˚N, 132˚E) was positively correlated with that of 0 to 150 m mean temperature (Fig. 3).

Shifts in Frontal Zone and Area with Dense Squid

The high year-to-year variations in the positions of the subpolar front in the western region of the East/Japan Sea indicate the instability of the warm currents (EKWC/TWC) and cold currents (NKCC/LCC). Positions of the subpolar front are shifted further north around 40˚～41˚N in the western East/Japan Sea (west of 134˚E) with the strong East Korean Warm Current (EKWC) in June 1972, 1976 and 1988 (warm type), while they were shifted further south with the weak EKWC in May 1963, June 1974, 1981 and 1996 (cold type) (Fig. 4).

In spring and early summer the high density zones of squids move northward with the shifting of the front. In normal oceanic conditions (e.g. June 1973 and 1983), the areas with dense squids were found along the frontal zone between 38°N and 39°N (Kasahara 1984).

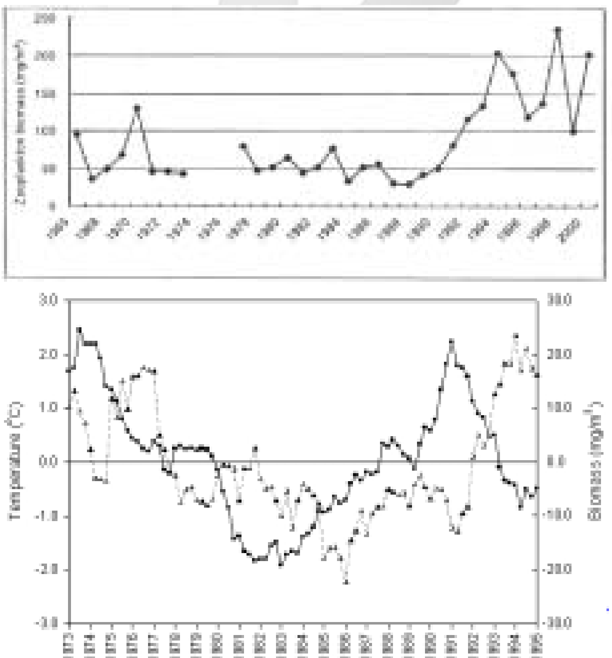

Fig. 3. Zooplankton biomass in the southwestern East/ Japan Sea off Korea (35°N～38°30'N, 128°30'～133 °E) (Kang and Lee 2002) (A), Anomalies of zooplankton biomass (wet weight, circle) and integrated mean temperatures (0～150m, triangle) along PM line (36°N, 136°E～41°N, 132°E) (B) (Minami et al. 1999).

In abnormal warm conditions (e.g. spring and summer 1972 and 1976) high CPUE belts of the squid along the frontal zone were found further northwestern East/Japan Sea, while they were shifted further south with the weak current (e.g. June 1981 and 1996).

Fluctuations in Squid Abundance in the Far East Regions

Year-to-year catches of common squid by Korea and Japan in the TWC region and those by Japan in the KOC region showed the same pattern of fluctuations with positive relationship during the 52 years period 1952～2003 (Fig. 5).

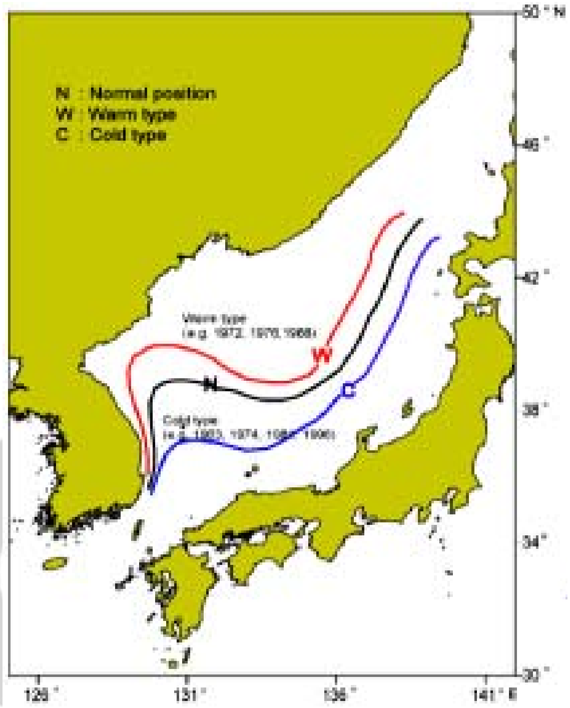

Fig. 4. Positions of the subpolar front at the 50 and 100 m depth layers in the East/ Japan Sea during warm (W), normal (N) and cold (C) periods.

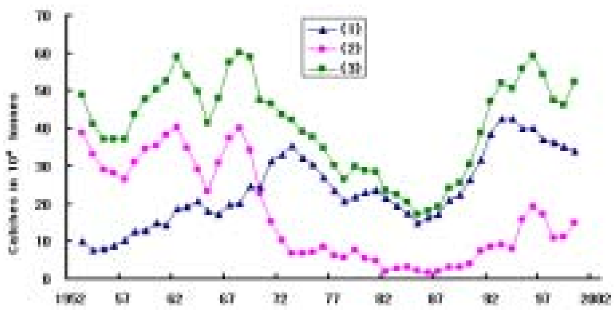

Fig. 5. Trends in the annual catches of *Todrodes pacificus* by Korea and Japan in the Tsushima Warm Current region (1) and by Japan in the Kuroshio-Oyashio Current region (2), and the total (3), 1952～2001 (3-year running average, based on revised data).

Between two high periods of 1950s∼1960s and 1990s∼2000s, there was long-lasted low catch period (1970s∼1980s) in the KOC region due to shifts of heavy fishing from KOC to TWC region. Year-to-year catch per unit effort (CPUE) and density indices from jigging fishing in the TWC region were low in the 1980s but increased in the 1990s, coincident with the year-to-year catch fluctuations (Fig. 6).

If the catch and CPUE for the squid are regarded as indices of fluctuations of the population abundance, the year-to-year and inter-decadal changes in the abundance of the population in the TWC and KOC regions might have the same pattern. Catches for the autumn-spawned group were about two times higher than those for the winter-spawned group during the low catch period 1980s, while the catches for both groups synchronously increased in the whole regions during the high catch period 1990s (Fig. 7).

Body Size of Common Squid

Seasonal mean mantle length of the squids taken by Korean jigging and purse seine fleets in the East/Japan Sea from June through August and from September through November in the 1980s were smaller than those in the 1990s (Fig. 8).

Monthly mantle length of the squid taken by experimental jigging by Japan in the East/Japan Sea from May through December 1981, 1984∼1986 were smaller than those in 1962, 1966∼1969 and 1973 (Fig. 9).

In brief, squids in the feeding grounds of the East/Japan Sea during the low abundance period from the mid-1970s to mid-1980s were smaller than those during the high abundance period 1960s and 1990s (Figs. 5, 6, 8 and 9).

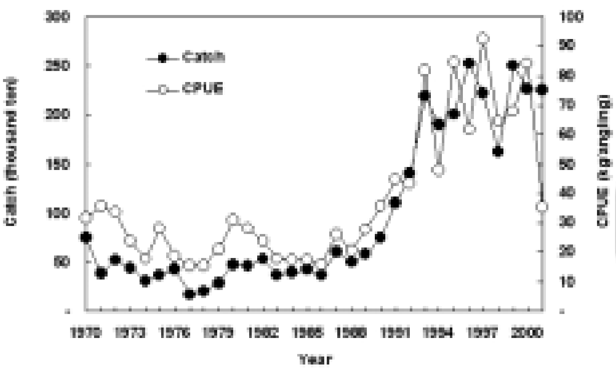

Fig. 6. Catch and catch per unit effort for Korean squid fishing during 1970∼2001 (Data from Choi 2005).

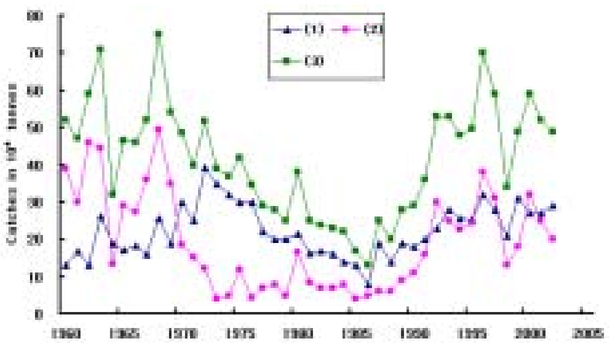

Fig. 7. Catches of autumn-breed group (1), winter-breed group (2) and total (3) of *Todarodes pacificus* taken by Korea and Japan in the Tsushima Warm Current region and by Japan in the Kuroshio-Oyashio Current region, 1960∼2001.

DISCUSSION

Current Systems and Disturbed Marine Ecosystems

1) Large Scale Current Systems in the Far East Regions

Ocean current systems and boundary zones in the waters around Korea and Japan are schematically presented based on the previous reports; Uda (1934), Yoon (1997) and Yoshikawa et al. (1999) for the East/ Japan Sea, Gong (1970), Inoue (1981), Huh (1982), Kondo (1985) and Lie and Cho (2002) for the Yellow Sea and East China Sea, and Kawai (1955), Hirano (1985) and Nakamura and Hinata (1999) for the Pacific (Fig. 1).

The warm Kuroshio and cold Oyashio Currents converge in the waters off Hokkaido and Tohoku district to form a transition (mixed) zone which yields the high production and aggregation of food organisms. There are wide variations in the positions of the subtropical front between the Kuroshio and the transition zone and subarctic front between the Oyashio Current and the transition zone (Ogawa 1989, Hanawa 1995). The locations of southern limit of the first Oyashio Intrusion were shifted further south during the cool regime in the late 1970s and 1980s in relation to the climate

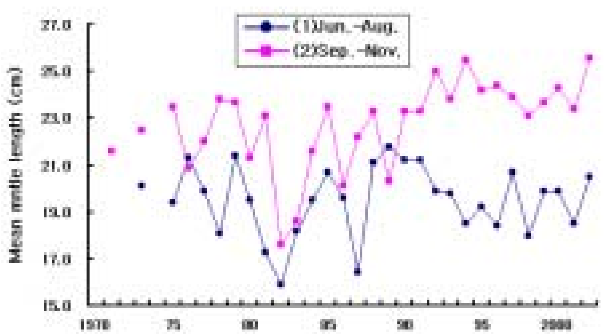

Fig. 8. Year-to-year changes in seasonal mean mantle length of *Todarodes pacificus* taken by Korean jigging and purse seine fleets in Korean waters during northward migration from June through August (1) and southward migration from September through November (2), from 1971 to 2002.

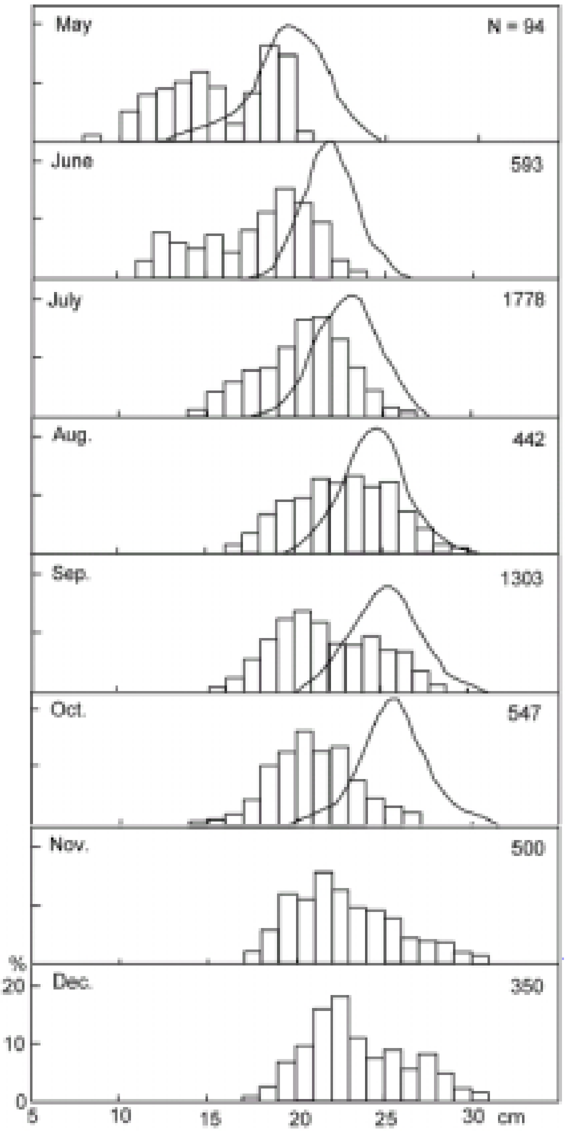

Fig. 9. Monthly dorsal mantle length compositions of common squid taken in East/Japan Sea, May-Dec. 1986. Line graphs indicate the monthly average for 1962 and 1966 to 69 (data from Kasahara 1987).

shifts in the North Pacific (Hanawa 1995, Minobe 1997, Ogawa 1989, Ogawa et al. 1987).

In the East/Japan Sea, there are wide variations in the positions and contours of the front not only from season to season but also for same month in different year (Uda 1958, Gong and Lie 1984, Gong and Son 1982, Katoh 1994). The year-to-year variations in the positions of the frontal zones in the west are higher than those in the eastern East/Japan Sea (Uda 1958, Gong and Lie 1984), which indicates the instability of the warm and cold current systems.

The existence of the EKWC is very variable and hence the positions of the subpolar front also vary. The EKWC was weak or not recognized in the southwestern East/Japan Sea in the spring and early summer 1981, when the main flow of the TWC shifted to the southeast in the sea (Katoh 1994, Isoda and Tanaka 1999). Deepen mixed layer depth (MLD) and colder than normal mixed layer temperatures (MLT) were recognized in the PM line in 1977, 1981 and 1985/86, while the deepen MLD and warmer than normal temperature was noticed in 1988 (Kim and Isoda 1998).

2) Disturbed Marine Ecosystem

The climate regime shift in the 1970s was marked by significant changes in physical environment that resulted in dramatic changes of marine ecosystem in the North Pacific and western North America (Trenberth and Hurrell 1994, Mantua et al. 1997, Hare and Mantua 2000). In the time series of SST and intensity of Aleutian Low, six regime shifts are detected from the 1910s to the 1990s: 1925/26, 1945/46, 1957/58, 1970/71, 1976/ 77 and 1988/89 (Yasunaka and Hanawa 2002). The climate regime shifts around 1890s, 1920s, 1940s and 1970s are associated with 50～70 years climate variability over the North Pacific (Minobe 1997, 1999).

Intensification of Aleutian low-pressure system strengthened the wintertime East Asian monsoon over the Siberia and the northern East/Japan Sea. The strong westerlies cooled surface water of the northern East/Japan Sea and facilitated subduction of cold water below the TWC (Chiba and Saino 2002). Springtime solar radiation increased in the 1980s. These conditions led to enhancement of stratification between subsurface and surface waters in spring, resulting in limiting the nutrient supply to the surface to the level that only a summer-adapted plankton community was favored (Chiba and Saino 2002).

Therefore, zooplankton biomass decreased in the south of sub-polar front in spring and in the north of the front in the East/Japan Sea in summer in the late 1970s and 1980s, which must have been detrimental to the growth of pelagic communities such as anchovy, Pacific saury and common squid during their feeding migrations (Chiba et al. 2003, Gong and Suh 2004).

Population Structure of Common Squid

Annual squid stocks can only achieve diversity and stabilization by having micro-cohorts spawned throughout the year and being dispersed widely in space to find microhabitats with equivalent variability (O'Dor 1998).

Three spawning groups in common squid, *Todarodes pacificus* are known. The winter-spawned group has the widest distribution from the Pacific to the East/Japan Sea and Yellow Sea and the autumn-spawned group has its highest density in the central and northern East/Japan Sea (Adachi 1979, Araya 1967, Hamabe and

Shimizu 1966, Matsui and Kawasaki 1971, Ito 1972, Shimizu and Hamabe 1975, Kasahara 1982, 1991, Murata 1983, 1991, Kang et al. 1996). Recently the seasonal spawned groups are divided into two cohorts; autumn-spawned and nonautumn-spawned cohorts in the East/Japan Sea, of which the young squid of the former distribute offshore with short/small range of migration, while those of the later inshore along the coast off Japan with long/large range (Mokrin and Katugin 2000).

To generate differences between stocks over a long period, a difference in spawning season on the same grounds or a difference in grounds at the same season is needed (Cushing 1969). However, the spawning seasons and grounds of the main components of spawning groups (autumn and winter-spawned) of the common squid are close each other in the East China Sea, Korea Strait and southern East/Japan Sea (Araya 1981, Sakurai et al. 2000).

In the East/Japan Sea largest number of the squid mature in autumn, the next largest in winter, and the smallest in summer (Kasahara 1991), suggesting the main spawning season for the squid in the sea is autumn. However, mantle length distribution of the squid in the East/Japan Sea (35°N～45°N, 130°E～140°E) from May through October 1974 showed one mode except September (Murayama et al. 1993).

It is suggested that the population structure of common squid must be reexamined because of the extensive overlap in the migration routes of the subpopulations or seasonal spawning groups (Nagasawa et al. 1993, Nakata 1990, Mori and Nakamura 2001). Many of the common squid (mainly winter-spawned group) migrate southward from the Pacific off northern Japan to the spawning grounds in the East China Sea via the East/Japan Sea after passing through the Tsugaru Strait and/or Soya Strait (Mori and Nakamura 2001), which suggests the possible intermingling with the squid (mainly autumn-spawned group) migrating from the northern East/Japan Sea to the spawning ground.

They seem to have a considerable ability to shift or transfer to other subpopulations (spawning groups or micro-cohorts) in the course of reproduction, because the spawning periods are continuous and breeding grounds and feeding grounds are geographically close, and the life cycle of the squid is annual and semelparous (Osako and Murata 1983).

It is suggested that the fisheries for these spawning groups appear to collapse and recover independently (Ogawa and Sasaki 1988, O'Dor 1992, Nakata 1993). However, the year-to-year and long-term fluctuation in abundance in the TWC and KOC regions revealed the same pattern and the catch rates of the two main spawning groups increased synchronously in the high abundance period (Figs. 5～7).

Recently the changes in the stock size (abundance) have been analyzed on the assumption that squid around Korea and Japan can be regarded as two main components; autumn-spawned cohort and winter spawned cohort (Kidokoro et al. 2005, Moti 2005). It is suggested that a single group of the squid around Japan makes a long migration (Soeda 1950). An attempt has been made to analyze changes in the stock size on the assumption that the common squid around Japan can be regarded as one population on the large scale (Doi and Kawakami 1979).

So far, it fails to distinguish between distribution and temporal isolation. Therefore, they may be mutually related and not separate into independent population. It then becomes possible to consider them (autumn-spawned and winter-spawned groups) as a single population of *Todarodes pacificus* in the waters around Korea and Japan (TWC and KOC regions).

Fluctuation in Abundance of Common Squid

Common squid were caught in the coastal and offshore zones of the TWC and KOC regions mostly by jigging boats before 1980s. However, about half of the annual catches were taken by mid-water trawling with attracting light system, danish seine and the other gears from the mid-1990s (East Sea Fish. Res. Inst. 1993～2003, Gong and Oh 1977, Park et al. 1998, 2000, Choi 2005) The catch in the KOC region began to decline from the early 1970s after the big catch in 1968 (495,000 tones) and remained low during the 20 years period from 1970 to 1989 (Fig. 5, Ogawa and Sasaki 1988, Osako and Murata 1983, Shingu et al. 1983, Nakata 1993). However, the catch in the Tsugaru Strait began to decline from the mid-1970s and remained low during the period 1976～1989 (Takayanagi 1993) as that in the East/Japan Sea, and the catch increased in both areas in the early 1990s (Fig. 5, Akamine et al. 1992, Kubota and Kawabata 1996, Sakurai et al. 2003).

As soon as the fishery in the Pacific off northern Japan (KOC region), based on the so called winter-spawned group, has collapsed in the early 1970s (Osako and Murata 1983, O'Dor 1992), Japanese jigging fleets moved to the offshore and northern East/Japan Sea (main fishing ground of the TWC region) where the squid population composed of so called autumn-spawned group were peaking in the 1960s and the early 1970s (Fig. 5, Kasahara and Ito 1977). Common squid catches by Korean jigging fleets in the East/Japan Sea amounted to 117,000 tones in 1963 and thereafter decreased to 38,000 tones in 1971 and then remained below the 20 years (1960～1979) average in the later period 1971～1979 (Kim and Lee 1981, Choi et al. 1997, Korea Fisheries Association 2004). The increased catches in the TWC region (mainly in the East/Japan Sea) in the late 1960s and early 1970s were attributed to the increased fishing intensities shifted from the KOC region.

A large amount (half or one third) of the squid taken in the later fishing ground (TWC region) were landed at the fishing ports along the Pacific coast (main KOC region) during the period of the late 1960s and 1970s (Kasahara 1978, 1983, Kawai 1995) which are recorded as high as those in the TWC region on the Yearbooks of Fishery Statistics of Japan. Therefore, the actual catches from the KOC region were extremely low during the period from 1970 to 1989 (Fig. 5). Common squid were by-caught in the Japanese trawl-net targeting demersal fishes in the Yellow Sea in the early 1970s. Thereafter the squid were taken by jigging since 1974 and much of them were landed at the fishing ports along the western Japan (e.g. Kyushu) (Gong and Oh 1977, Kasahara 1977, 1978). The squid in the Yellow Sea were harvested by the Korean fleets in the period 1970s, 1980s and 1990s and the highest catch amounted to about 20,000 tones in 1987 (Kim et al. 1984, Choi et al. 1997).

Even though the catches in the TWC region were smaller than those in the KOC region in the 1950s and 1960s (Fig. 5), the abundance of the population seems not to be so different because the squid were not fully harvested due to poor fishing techniques and low availability of the population, in particular, in the early stage of Korean fishing (Gong and Oh 1977). The negative correlation between the year-to-year catches in the two regions during the period of the late 1960s and early 1970s attributed to the shifts of Japanese fleets from the KOC region to the TWC region as soon as the collapse of the fishery in the former region occurred.

Therefore, it is postulated that the level of abundance of the common squid in the whole distribution range was higher in the period 1950s～1960s than in the period 1990s～2000s. The squid abundance in the two regions began to decline synchronously from the early 1970s (Kim and Lee 1981, Murata 1983), even though the year-to-year catch trend showed negative correlation between the two regions in the particular period of shifts of heavy fishing.

The year-to-year catch and catch per unit effort (CPUE) revealed the same trend of fluctuations in the period 1980s and 1990s (Figs. 5 and 6). The squid catch per boat per day in the waters around Japan (KOC and TWC region excluded Korean data) revealed that the abundance decreased sharply from the early 1970s and remained low in the early 1980s (Murata 1991). Year-to-year population size indices ($P=\sum Ai \cdot fi$; A=area index, f= density index) in June, July and September decreased from the mid-1970s coincident with catches in the East/Japan Sea (36˚N～45˚30'N, east of 130˚30'E) (Kasahara 1987). Abundance in terms of CPUE in the Pacific off the northern Japan (38˚N～43˚N, 141˚E～146˚E) from late August to early September increased from the late 1980s, coincident with the catches (Nakamura et al. 1993). Catch rates of the autumn-spawned group in the East/Japan Sea (TWC region) increased from 1988 (Kasahara 1991).

Abundance of the winter-spawned group in the waters around Japan represented extremely low level in the 1970s (Doi and Kawakami 1979, Murata 1983). Most of the catches since 1971 in the East/Japan Sea were thought to be from the autumn-spawned group. Since catch per unit fishing boat per day had decreased since 1971～72, the autumn-spawned group had declined in abundance in the early 1970s (Okutani 1977, Murata 1983).

If the catch and CPUE for the squid are regarded as indices of fluctuations of the population abundance, it follows that the year-to-year and interdecadal changes in abundance of the population in the TWC and KOC regions have the same pattern. In between the two high catch periods of 1950s～1960s and 1990s～2000s, there has been long-lasted low catch level (1970s～1980s) in the KOC region (Pacific off northern Japan) due to the shifts of heavy fishing from KOC to TWC region.

From above discussion on the population abundance, several points are summarized as following; between the high catch periods (1950s～1960s and 1990s～2000s), there have been low level in the KOC region(mainly Pacific off northern Japan) for 20 years period 1970s～1980s and in the TWC region (mainly East/Japan Sea) for 10 years period 1980s. The negative correlation in the year-to-year catches between the two regions in the period of the late 1960s and 1970s are due to the shifts of heavy fishing from KOC region to the TWC region. The abundance in the first high level period 1950s ～1960s seems to be higher than those in the second high period 1990s and 2000s if the changes in fishing efficiency and availability are taken into consideration. The year-to-year and long- term fluctuations in the abundance showed the same pattern in the two regions for the 52 years period 1952～2003.

In the year-to-year fluctuations in catches by spawning groups of the squid population, the level of the winter group was lower than those of the autumn group during the period of low abundance in the 1980s because of the earlier collapse of the fishery targeted the former group. In contrast, those of both groups increased during the high abundance period in the 1990s, which suggests the possible homogeneity of the population structure in the whole distribution range. As a whole, the year-to-year catch trend revealed the earlier decrease in the marginal zone (KOC region; Pacific off northern Japan) than in the central zone (TWC region; mainly East/Japan Sea), but the year-to-year and long-term fluctuations in the abundance have the same pattern in the two regions. Year-to-year catch trend of the two spawning groups (autumn-spawned and winter-spawned) (Fig. 7) suggests that the population structure is homogeneous during the high abundance period.

Body Size in Relation to Abundance

The squid taken during the cool regime in the East/Japan Sea by

Korean fleets from June to August during the low abundance periods 1980s were smaller than those during the high abundance periods 1990s (Figs. 5 and 8). The body size of the squid in the East/Japan Sea during northward and southward migration seasons in the periods of the late 1970s and 1980s were smaller than those from the late 1960s and the early 1970s, suggesting poor growth rate during the cool regime and low abundance (Figs. 5 and 9).

However, it is not clear whether the diminution of the body size is due to the difference in sampling season and limited sampling area or not. It is noteworthy that the growth rates of the squid are higher in the cold-water region of the East/Japan Sea where the research activities were prohibited by the EEZ since 1977. The squids taken in the cold-water area were larger than those in the Tsushima Warm Current area (Kidokoro and Hiyama 1996). However, it is not clear whether the large-sized group migrated earlier to the cold area than the small-sized group or the squid in the cold-water area took advantage of abundant food and low metabolic rate.

Individual squid continue to grow even when food is extremely limited but numbers decline. The average size of squid in a school may increase even faster during food shortages because smaller squids are being removed by the social canibalism (Okiyama 1965, Kidokoro and Uji 1999, O'Dor and Perez 2000). These problems seemed to rule out the possibility of using squid as indicators of environmental conditions until we recognized that skewness from a normal distribution in squid size was a potential index in populations (O'Dor and Perez 2000).

High temperatures accelerate sexual maturation (Richard 1966) and can reduce growth due to a shift in the balance between metabolic rate and feeding rate (O'Dor and Wells 1987). Regardless of cause, the consequence is that squid even of the same species, grow larger, reproduce later and are individually more fecund in cooler waters (O'Dor 1992). It is suggested that population structure varied during different periods of abundance (Nakata 1993, Takayanagi 1993, Kubota and Kawabata 1996). Therefore, the diminution in the mean body size of *Todarodes pacificus* seems to be a probable consequence of major changes in population structure during the changes in abundance in accordance with the changes in current mediated migration circuits.

Changes in Thermal Regimes, Zooplankton Biomass and Squid Abundance

Temperatures and zooplankton biomass at the upper layer (0～150 m) in the East/Japan Sea were low during the 1980s but increased after the North Pacific climate shift (1988/89) and remained higher than average in the 1990s (Minami et al. 1999, Kang and Lee 2005, Figs. 2 and 3). The abundance of common squid in the East/Japan Sea and in the Pacific off northern Japan began to decrease from the early 1970s (Kasahara 1978, Kim and Lee 1981, Murata 1983) and remained low in the 1980s and increased in the 1990s, even though the catches in the TWC region remained high until the mid-1970s due to the shifts of high fishing intensity from the KOC region to the TWC region (Figs. 5 and 6). It was suggested that the decreased prey (anchovy) and increased predator (bluefin tuna) were the possible causes of the decreased squid abundance in the northwestern Pacific in the early 1970s and 1980s (Ogawa and Sasaki 1988).

Zooplankton biomass in the Oyashio area was estimated to vary, chiefly regulated by the water temperature (Tomosada and Odate 1995). Increased temperature with the northward shift of the First Oyashio Intrusion (FOI) in the 1990s might have had a positive impact on the plankton ecosystem in the area, resulting in favorable feeding ground for common squid. Abundance of common squid decreased in the FOI transition period 1973～1979 and remained low in the FOI southward regression period 1980～1987, while the abundance increased in the northward regression period 1990～1999. The decrease in abundance of the squid in the KOC and TWC region was attributed to the heavy fishing as well as to the climate shifts in the 1970/71 and 1976/77. The squid abundance in the two regions increased from the late 1980s coincident with favorable changes in thermal regimes and plankton ecosystems with the 1988/89 climate shift.

Distribution and Migration of Common Squid

Maximum horizontal temperature gradients were used as the criterion for determining the position of the front (subpolar front between the Tsushima Warm Current water and the cold water) in the East/Japan Sea. Kasahara and Ito (1977) illustrated detailed schemes of migration routes of common squid in the East/Japan Sea. The areas with dense squid could be found along the frontal zone which were shifted further to the northwest or southeast in the East/Japan Sea in association with the pattern and strength of current systems (Naganuma 1967, Tameishi 1991). In summer the squid can move to the further north of the subpolar front with the dispersed superficial warm water, when the areas with dense squid can be found in the cold water systems north of the front, where the squid inhabit surface layer over the cold water below (Kasahara 1984).

The migration routes of the main group of the squid will be determined by current pattern and strength which are manifested by the pattern and positions of the fronts. The northwestward shifts of main group during the feeding migration from May through August will associate with the strong EKWC and the eastward shifts will associate with the near shore branch of the TWC along the coastal zone off Japan (Fig. 4). In particular, the instability of the western boundary current systems manifested by the year-to-year variations in the positions of subpolar front is responsible for the zonal shifts of the areas with dense squid in the TWC region.

When the TWC is strong, the high density areas of the squid are expected to be shifted to the continental side in the East/Japan Sea. When the TWC flows mainly along the southeastern region of the sea, the migration routes of the main components (autumn and winter-spawned group) are expected to be shifted to the southeastern region, and hence they can easily move to the Pacific through the Soya and Tsugaru Straits. In the later case the abundance of the squid in the KOC region is expected to increase as far as the other group along the Pacific coast keeps moderate level similar to the high population level in the 1960s.

Previous reports on the migrations and spawning grounds of the common squid suggested that the winter-spawned group migrate in the waters around Japan, while the autumn-spawned group migrate northward from the spawning ground in the Korea Strait to the western half of the East/Japan Sea. However, both groups take the same way during their spawning migrations from the northeast to the spawning grounds in the Korea Strait and northeastern East China Sea (Araya 1976, 1981, Kiyofuji et al. 2001).

Murata et al. (1971) suggested that the autumn-spawned group migrates to the northwest, while the winter-spawned group migrates in the Tsushima Warm Current region along the coast of Japan, and that both groups move to the Tartary Strait in late summer. Majority of the autumn group inhabit the waters south of 44°N, while the winter group south of 45°N in the East/Japan Sea.

The juvenile and immature squid appearing off the northeastern East/Japan Sea in spring (May and June) migrate to the waters off Sakhalin and Okhotsk Sea in summer (July and August). However, most of the squid in the Okhotsk Sea are those from the Pacific. In their southward migration, there are some squid that move southward into the East/Japan Sea via the Soya Strait more abundantly than those return along the Pacific coast of Hokkaido (Araya 1976, Mori and Nakamura 2001). The mature autumn group migrates earlier than the immature in late summer-autumn (August～September) from the cold waters of the northern East/Japan Sea to the Korea Strait via the Yamato Bank, Ulneung Island and the southeastern coast of Korea (Murata et al. 1971, 1973).

It is suggested that *Todarodes pacificus* migrated southward from the north of the subpolar front to the spawning ground near the Korea Strait via the east coast of Korea along the frontal zone during high abundance period 1967～1971 and 1996～1999, while the squid migrated southward directly from the south of frontal zone to the spawning area in the southern East/Japan Sea during low abundance period 1984～1987 (Kasahara and Ito 1968,

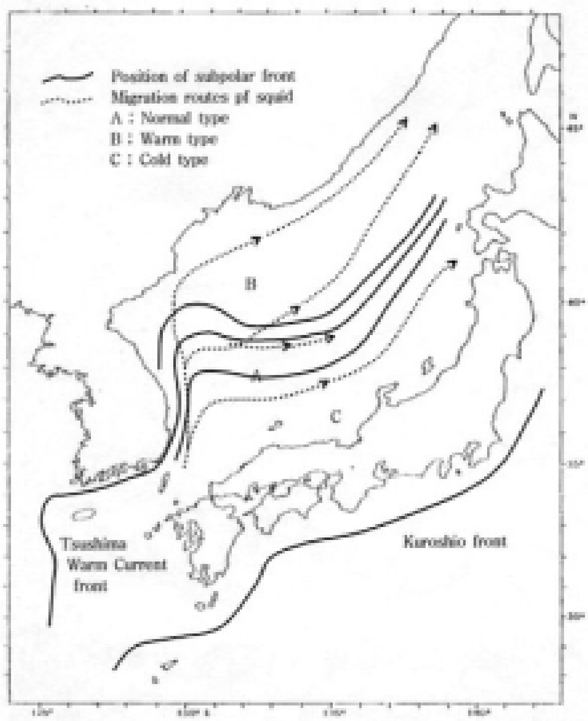

Fig. 10. Hypothesized feeding migration routes of *Todarodes pacificus* in relation to the positions of the Subpolar Front in the East/Japan Sea in spring-summer.

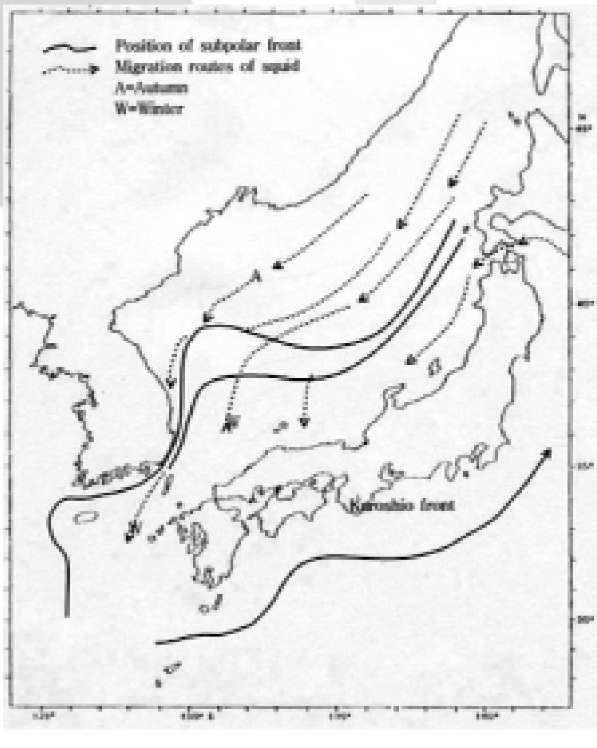

Fig. 11. Hypothesized spawning migration routes of *Todarodes pacificus* in relation to the positions of the Subpolar Front in the East/Japan Sea in autumn-winter.

Kidokoro et al. 2000). Recently the squid fishing grounds in autumn, as seen in the nighttime visible DMSP/OLS image derived on 25 December 1998, were formed in the southwestern East/Japan Sea and Korea Strait, suggesting the main groups of the squid take the way to the spawning grounds along the coast off Korea rather than the southeastern region of the Sea (Kiyofuji et al. 2001). It is suggested that the autumn-bred group of the squid migrates to the northwest taking advantage of food and return to the spawning ground, while the non-autumn-bred groups migrate further north to the northeastern East/Japan Sea along the Japanese Islands taking risks by the long distance of migration (Mokrin and Katugin 2000).

Referring the dislocation of subpolar front with the changes in current patterns, the distribution of high density zones of the squid, and the previous reports on the northward and southward migration of the population (autumn-winter-spawned group) hypothesized current-mediated migration routes for the feeding and spawning migration seasons are presented in the waters between Korea and Japan (Figs. 10 and 11).

Offspring of the squid reachs the nursery grounds and feeding grounds continuously in spring and summer (Fig. 10) and the adults quid progressively moves toward the spawning grounds as their sexual maturity advances (Fig. 11). Important fishing grounds may in fact locate in the transient zones(subpolar frontal zones in the East/Japan Sea and Oyashio front, in particular FOI, in the Pacific) where migrating schools of maturing squid are intercepted (Arkhipkin 1993).

In autumn the squid from the north of the subpolar front migrates southward along the frontal zone and rarely across the front, escaping from the physical impacts of the convergence zone, while the squid from the south of the front can move directly to the spawning grounds in the Korea Strait (Fig. 11). In the former case, the southward migrating squid takes longer time to reach the spawning sites in the Korea Strait and northern East China Sea.

The squid fishing conditions in the waters off Korea depend very much on the adult squid migrating southward along the subpolar front from the northern East/Japan Sea in autumn. It is postulated

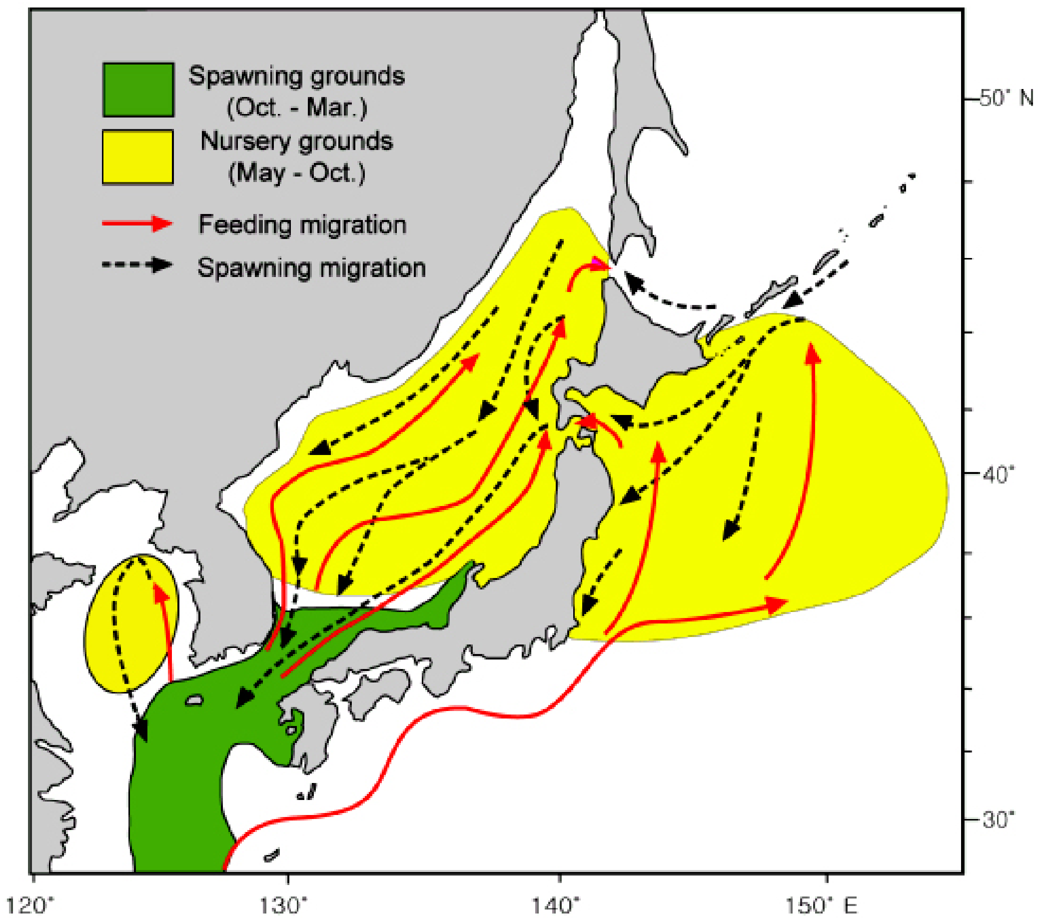

Fig. 12. Hypothetical migration circuits of *Todarodes pacificus* in the East/Japan Sea and its adjacent waters. Fishing ground ranges from the northern spawning ground to the entire nursery grounds.

that the decreased catches by Korean jigging fleets in the early 1970s seem to be partly attributed to the heavy fishing shifted to the central East/Japan Sea from the Pacific in the late 1960s.

1) Large Scale Migration Circuits of Common Squid in the Tsushima Warm Current (TWC) and Kuroshio-Oyashio Current (KOC) regions

A hypothesized large scale current-mediated migration circuits of a large-single population of common squid, *Todarodes pacificus* fished in the waters around Korea and Japan and thought to be depended on spawning in autumn-winter in the East China Sea is presented on the basis of the current systems (Fig. 1), seasonal migration routes (Figs. 10 and 11) and previous reports(e.g. Araya 1967, 1976, 1981, Lim 1967, Kasahara 1972, 1991, Kasahara and Ito 1977, Hatanaka et al. 1985, Murata 1991, Suzuki and Hamabe 1976).

Paralarvae of *Todarodes pacificus* hatch quickly in the warm Kuroshio and Tsushima Current waters and move to their landward edges and north of the frontal zone in the East/Japan Sea and transition zone between the Kuroshio and Oyashio Currents in the Pacific to feed on the wave of secondary production in the frontal zone and transition zone, respectively. The larvae of the squid (mainly winter-spawned group) which bone in the East China Sea are transported to the north by the Kuroshio and the Tsushima Warm Current from winter to spring. The squid occur in the transition zone and Oyashio area at the period of feeding migration in summer and autumn.

The spring phytoplankton bloom in the waters inshore of the western boundary currents (Kuroshio and EKWC) begin in March and move northward in wave, peaking at the north of the subpolar front in the East/Japan Sea (Nishimura 1969, Sorokin 1974, Kim et al. 2000, Yamata et al. 2004, Zhang and Gong 2005), and north of the Kuroshio front in the Pacific in June (Odate 1994, Tomosada and Odate 1995).

The immature squids migrate northward with the Kuroshio in the Pacific and with the Tsushima Warm Current in the East/Japan Sea to the vicinity of the frontal zones, then further north into the cold Oyashio Current region and North Korean/Liman cold Current regions, respectively. In summer the squid migrate to further northern East/Japan Sea and to the Kuril Islands. When they reach the coupling stage, they start migration to the spawning ground in late autumn and winter (Osako and Murata 1983, Nakata 1984).

It is noted that autumn-spawned group of the squid is just at the period of high production in the frontal zone of the East/Japan Sea for the growth in the life cycle (Murayama et al. 1993), while the winter-spawned squid is just at the period of high production in the mixed zone of the western North Pacific (Araya 1976).

The two distinct migrations, that of the immature squid from spawning ground to feeding ground, and that of the adult to the spawning ground comprise the circuit of migration by which the population maintains its identity from generation to generation in so far as wind or current permit (Cushing 1975, Harden Jones 1980).

The highly productive inshore upwelling areas and frontal zones associated with large currents sustain large population of migratory fish and squid and such current systems provide powerful selection regime for large individuals (O'Dor 1992). Only large individuals can swim the distances required to spawn upstream in the current systems, allowing juveniles to drift into the productive regimes (O'Dor 1988, 1992).

Long annual migration to spawn upstream in the Kuroshio and Tsushima Warm Current systems in the East China Sea requires the short-lived squid to maximize rates of growth. Therefore such systems provide the opportunity and a powerful selective advantage for large and rapid growth. Increased fecundity and canibalism provide additional selection for large individuals. Because squid are semelparous, disruption of delicately balanced lifecycles by physical events can virtually annihirate stocks (O'Dor 1992).

It is suggested that common squid in the waters of northern Japan are dominated by the group immigrated from the East/Japan Sea in a certain period and by the other group immigrated from the Pacific in the other period, forming periodic alternation of dominance (Kawasaki 1973). The year-to-year and decadal scale zonal shifts of current systems must have been related to the changes in migration circuits of the main component (autumn-winter-spawned group) of the common squid, resulting in zonal shift of the distribution.

It is postulated that main components of the squid population (autumn-winter-breed group) originated from the spawning grounds in the East china Sea can be drifted to the continental side by the EKWC when the abundance of the population will be high in the TWC region (mainly East/Japan Sea) as in the period of late 1960s to the early 1970s and the early 1990s (Fig. 5). To the contrary, when they are transported to the Pacific side (KOC region) either by the TWC through the Korea Strait and Tsugaru Strait or by the Kuroshio, the abundance in the KOC region will be high as in the period 1960s and 1990s.

The squid can save energy by taking advantage of southward wind drift or subsurface cold current systems during their spawning migration in the East/Japan Sea. Therefore, most of the squid migrate from the Oyashio Current region to the spawning grounds (upstream of Kuroshio and TWC systems) via the East/Japan Sea rather than via Pacific coast of Japan.

The squid transported to the Pacific side by the strong Kuroshio need long time and much energy to overcome the hard physical impacts on the way to the spawning grounds which form the long/large/cold loop of the currents (contranatant against to the current direction). Therefore, many of the squid take the way through the Tsugaru and Korea Straits that form a normal migration routes (denatant with the wind drift southward currents in the East/Japan Sea in late autumn and early winter).

The farther polwards the young squid travel, the greater the productivity, the larger they grow, the longer they take to return and the greater their fecundity, when the squid form a long/large/cold loop of migration circuits. Squids that do not grow large enough to complete the migration loop (Harden Jones 1980) to suitable spawning areas will not contribute to the gene pool. Squid that stay at home will not grow as large and may well fall prey to returning canibal hordes (larger group) when the former group forms a short/small/warm loop of migration circuit (O'Dor and Coelho 1993). However, as the migratory loop gets longer, the risks increase. A current meander, a year of low productivity or overfishing cause a year-class failure, which for an annual semelparous species essentially means annihilation (O'Dor 1992, Mokrin and Katugin 2000). For example, generations of progressively larger squid may regularly over extend their migratory loop and suffer partial collapses (O'Dor 1998).

Most major commercial squid species have suffered such collapses, but have also eventually recovered. There may even be an inherent collapse cycle of 7～10 years, as seen in *Todarodes pacificus* (Dawe 1981), resulting from loop expansion to the point that return time forces spawning at a time when paralarvae survival is poor (O'Dor and Coelho 1993). It is important to remember that the strategy that such population use has large rewards in terms of production, but also takes large risks.

The year-to-year and long-term changes in the western boundary current systems, as seen in the abnormal shifts of the frontal zones, are responsible for the changes in the routes of squid larval drifts and adult migrations and the changes in migration circuits to a long/large/cold loop or a short/small/warm loop. It is postulated that the zonal differences of high density areas are associated with the zonal shifts of the frontal zones, and that the changes in population structure and abundance are associated with the changes in the migratory loops.

Changes in the Structure, Distribution and Abundance in Relation to the Climate Changes

Low zooplankton biomass during the cool regime in the late 1970s and 1980s and the limited migration range of the squid due to the weak warm current systems are responsible for the earlier maturation with limited growth rates, resulting in transfer of spawning groups and in recruitment failure due to the low fecundity in the TWC and KOC regions.

The mechanisms of changes in structure, distribution and abundance of common squid population in relation to current-mediated migration circuits are explained on the basis of phenological variables (e.g. timing and migration ranges, growth rate and fecundity) responding climate changes as following modes.

Mode Ⅰ. Weak warm current systems

① Ocean climate shift
② Weak Tsushima Warm Current (frontal layer shift to the south)
③ Short/small/warm loop of migration (stay in the warm region near the spawning ground)
④ Low growth rate (e.g. winter-breeding group)
⑤ Early matured small sized group with low fecundity-low recruitment-low abundance
⑥ Early arrival to spawning grounds
⑦ Winter-breed group transferred to autumn breed group-population structure shift
⑧ Migratory loop reduction and short return time and/or escape from heavy fishing forces at the period when paralarvae survival can be good
⑨ Recruitment success in their parent feeding grounds in the TWC region. Few of them migrate to the KOC region along the Kuroshio because of the small loop of migration

Note; From stage ⑧, the effects act positively

Mode Ⅱ. Strong warm current systems

① Ocean climate shift
② Strong Tsushima Warm Current (frontal layer shift to the north)
③ Long/large/cold loop of migration (extending to the cold region)
④ High growth rate (e.g. autumn-breeding group)
⑤ Late matured large sized group with high fecundity-high recruitment-high abundance
⑥ Late arrival to spawning grounds
⑦ Autumn-breeding group transferred to winter breeding group-population structure shift
⑧ Migratory loop expansion and longer return time and/or heavy fishing forces at the period when paralarvae survival can be poor
⑨ Recruitment failure in their parent feeding grounds in the TWC region. Some of them migrate to the KOC region along the Kuroshio

Note; From stage ⑧, the effects act negatively

CONCLUSION

The year-to-year and long-term fluctuations in the abundance of common squid population in the waters around Korea and the west of Japan (TWC region) and those in the Pacific off northern Japan (KOC region) revealed the same pattern with positive correlations for the 52 years period 1952～2003. The abundance of the main components (autumn and winter-spawned groups) of the squid population began to decrease with different catch rates in the 1970s and 1980s but increased synchronously in the 1990s coincident with favorable changes in thermal regime and the plankton ecosystems in both regions, indicating the homogeneity of the population during the periods of high abundance. The diminution in the mean size of common squid is a probable consequence of major changes in foods and population structure in relation to the current induced migration loop.

A hypothesized large scale current-mediated migration circuits of a single population composed of the autumn-winter-spawned group of common squid in the TWC and KOC regions is presented on the basis of previous reports on the current systems and migration routes. Mechanisms of changes in population structure and abundance of the squid are explained on the basis of phenological variables responding to climate shifts. Probably the best that can be achieved is management strategy that minimizes recovery times by emphasizing population linkages rather than population separation.

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