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Comparison of Life Cycles of Five Ommastrephid Squids Fished by Japan: *Todarodes pacificus*, *Illex illecebrosus*, *Illex argentinus*, *Nototodarus sloani sloani* and *Nototodarus sloani gouldi**

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Abstract

The life cycles of five ommastrephid squids (*Todarodes pacificus*, *Illex illecebrosus*, *I. argentinus*, *Nototodarus sloani sloani* and *N. sloani gouldi*) are described comparatively on the basis of some original data and the available literature. Unknown parts of the life cycles of some species are analogized from those of other species. Working hypotheses, which are generally applicable to the life cycles of these species, lead to the following conclusions: each of these squids has a life cycle of 1 year, and this cycle is closely related to a warm current; eggs, larvae and, in some cases, juveniles are transported by the current from the spawning areas to the feeding grounds; the route and distance of migration are regulated strongly by the course and speed of the current; and there is the tendency for the squid populations with a long-range type of migration to be larger in size and to have greater fluctuations in annual abundance than the populations which exhibit short-range migrations.

Introduction

Short-finned squids of the family Ommastrephidae are widely distributed in the seas of the world. In the waters around Japan, the squid stocks have been utilized on a large scale since the 17th century. The annual catch of the Japanese common squid, the major component of the fishery, attained a peak of 680,000 tons in 1968. Since then, however, the annual catch declined rapidly to about 300,000 tons, and consequently the market price for short-finned squids increased substantially in the late 1970's. With the increase in price, Japanese trawlers began to exploit the squid resources in other parts of the world, such as the Northwest Atlantic, Southwest Atlantic and New Zealand waters, and their squid catches in these areas totalled about 60,000 tons in 1982. In addition, about 100 squid-jigging vessels fished in New Zealand waters and caught about 30,000 tons annually in recent years. During the 1970's, several countries (e.g. Argentina, Canada, Korea and Poland) developed fisheries for squid which were aimed at the Japanese market.

Japanese exploitation of squid resources in various oceans of the world led to initiation of studies on the biology and population dynamics of several species. However, because of the short life spans and complicated life cycles of these squids, it is difficult to plan and conduct effective researches. Although the levels of knowledge are different for the various species, descriptions of the life cycles of five short-finned squids are given in this paper. An attempt is made to analogize the lacking parts in the life cycles of some species from known aspects of the life cycles of others. Three species and two subspecies are considered: Japanese common squid (*Todarodes pacificus*) in the Northwest Pacific; short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic; short-finned squid (*I. argentinus*) in the Southwest Atlantic; New Zealand arrow squid (*Nototodarus sloani sloani*) and Australian arrow squid (*N. sloani gouldi*) in the Southwest Pacific. *N. sloani gouldi* occurs also in New Zealand waters, but, for convenience in this paper, the New Zealand populations are referred to as *N. sloani sloani*.

Reference to squid length in this paper implies dorsal mantle length.

Growth and Life Span

Todarodes pacificus

Araya (1967) estimated the growth of this species in the Northwest Pacific from seasonal changes in length distributions (Fig. 1) and assumed that the life

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span (the period from birth to mass mortality upon spawning) is 1 year on the basis of the growth and the mean length at maturity (i.e. the length at which 50% of the squid have spermatophores in the spermatophoric sac for males and matured eggs in the oviduct for females). Many tagged squid have been released in Japanese water, but there has not been a single recapture of a squid which spent more than 1 year in the sea after release. This supports the hypothesized 1-year life span of this species. Furthermore, females grow faster than males after their transition from juveniles to maturing adults (Fig. 1).

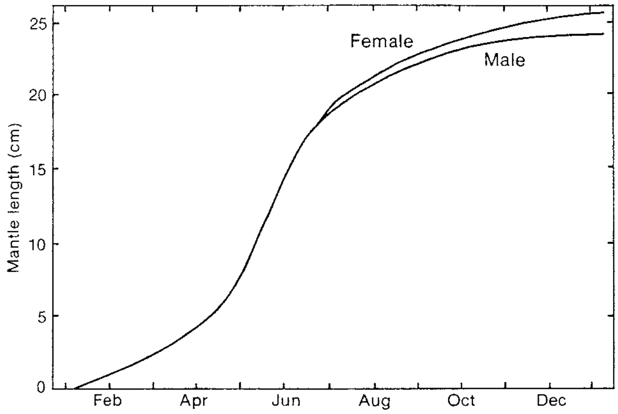

Fig. 1. Growth of the winter-spawning population of *T. pacificus* in Japanese waters (from Araya, 1967).

Illex illecebrosus

For this species in the Northwest Atlantic, length-frequency data of Amaratunga (MS 1980) are used to illustrate the seasonal pattern of growth (Fig. 2). The life span was assumed by Squires (1967) to be about 1 year. Like *T. pacificus*, females of *I. illecebrosus* evidently grow faster and attain a larger maximum size than males. Mesnil (1977) hypothesized that this species may have a life cycle of 1.5 years, with alternation of the spawning season between summer and winter for different generations of squid. However, it is difficult to fit this hypothesis into the situation as it is presently known.

Illex argentinus

For this species in the Southwest Atlantic, the pattern of growth was also determined from length-frequency data (Fig. 3), and the life span was estimated

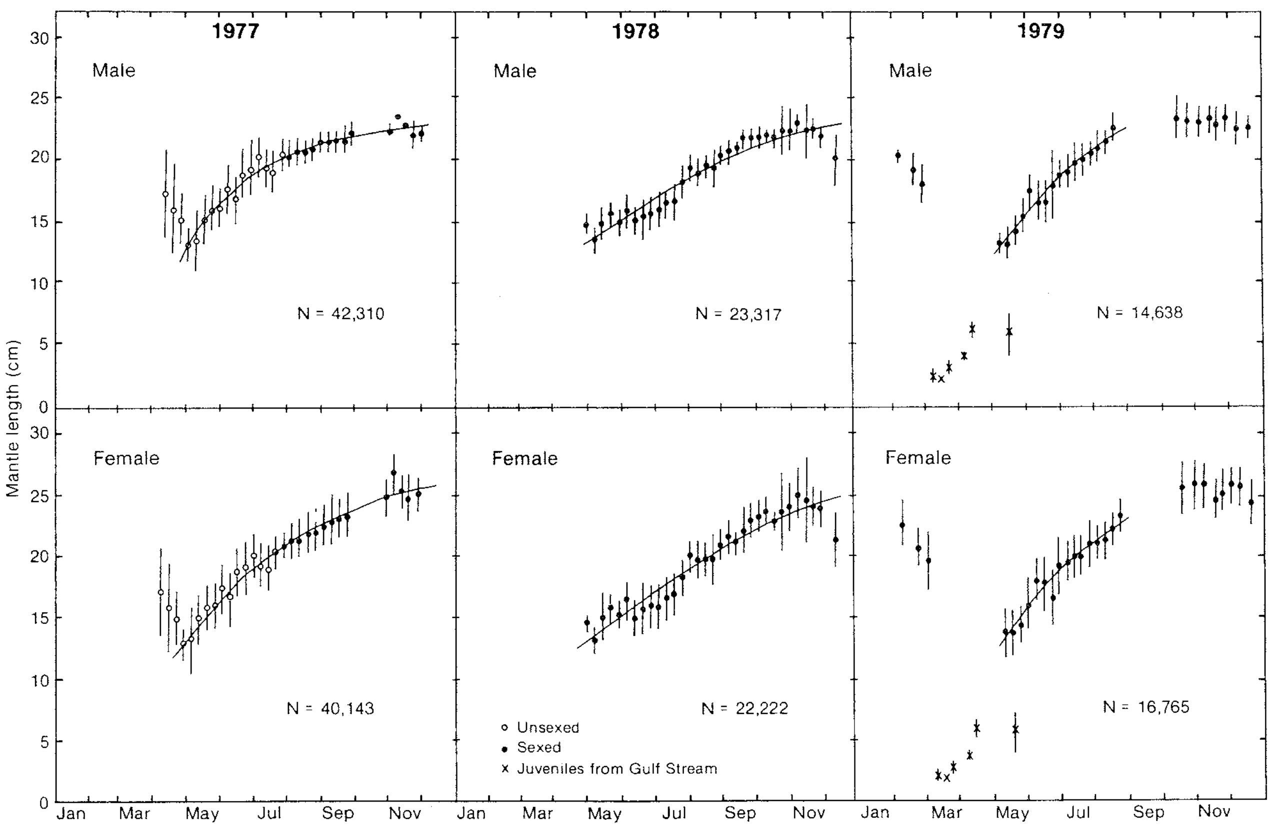

Fig. 2. Growth of *I. illecebrosus* from weekly sampling on the Scotian Shelf during 1977–79 and samples of juveniles from the Gulf Stream in 1979 (from Amaratunga, MS 1980). (Curves are based on fitting the equation $L_t = L_\infty(1-e^{Kt})$; vertical lines represent one standard deviation from the means.)

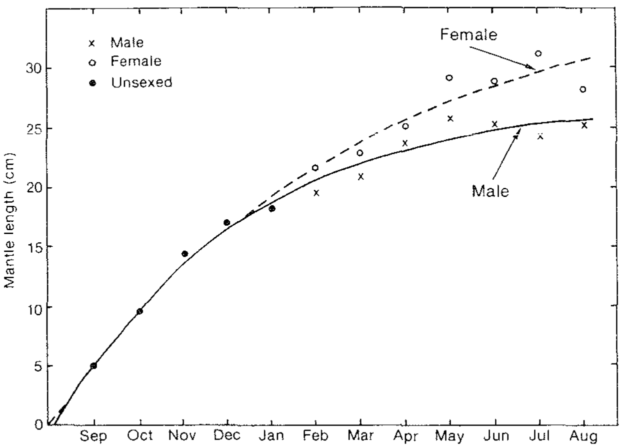

Fig. 3. Growth of *I. argentinus* in Argentina waters (from Hatanaka, MS 1983).

to be about 1 year (Hatanaka, MS 1983). Like the two aforementioned species, females grow faster than males.

Nototodarus sloani sloani

In New Zealand waters, there are two subspecies of this squid. The length distributions of each subspecies are often polymodal, and this makes it difficult to estimate the growth pattern and life span from length data. However, Roberts (1983) reported a growth rate of 2.5-4.0 cm per month for small squid (18-24 cm) and 1.5-3.0 cm per month for larger squid (24-33 cm), based on length-frequency data for 6 months from December to May. With mean lengths at maturity of 28 cm for males and 30-35 cm for females, the life spans of both subspecies, if the squid die after spawning, are estimated to be about 1 year by extrapolating the monthly growth data from Roberts (1983) to a full year.

Nototodarus sloani gouldi

Although no growth information is available on this subspecies in Australian waters, the most prominent mode in length frequency data moved from 17 cm in December to 25-27 cm in March (Machida, 1983). Consequently, the growth rate is estimated to be 2.0-2.5 cm per month. As the mean length at maturity is about 23 cm for males and 30 cm for females (Machida, 1983), the life span seems to be approximately 1 year, in the light of the assumptions that were made for *N. sloani sloani*.

Summary

Available information on the life cycles of the five "species" indicates that the life span of each is more or less 1 year and that females generally grow faster than males. This latter phenomenon is probably the result of maturation beginning earlier or at smaller sizes in males than in females.

Spawning and Feeding Migrations

Todarodes pacificus

It is generally accepted that there are three populations of this species around Japan, with different spawning seasons (winter, summer and autumn) but with considerable overlap of the spawning areas and migration patterns (Fig. 4) (Kasahara, 1982). These hypotheses have been partially supported by the results of larval surveys and tagging experiments in recent years. Winter spawners, which constitute the largest population (at least up to the late 1960's), have a spawning area that extends over the north and central-east parts of the East China Sea, but the feeding grounds are far to the northwest off Hokkaido. Consequently, this population can be characterized as having a long-range type of migration. In the feeding area, the squid are generally immature, even at the end of the feeding season (Nakata, 1984). The autumn-spawning population, which spawns in the northeastern part of the East China Sea off southern Japan, feeds mainly in the offshore part of the Japan Sea. The distance from the feeding grounds to the spawning area is shorter than that for the winter-spawners, and gonads of autumn spawners have developed noticeably by the time when they leave the feeding grounds (Kasahara and Ito, 1972). Summer spawners appear in coastal waters of Kyushu and Honshu in summer. They are almost mature at that time, and the mean length at maturity is considerably less than those of the other two populations. The migration is thought to be rather small-scale by comparison.

Illex illecebrosus

In Canadian waters, juvenile squid migrate to the continental shelves off Nova Scotia and Newfoundland in late spring (Amaratunga, MS 1980). They feed and grow during the summer and autumn and leave the shelves in late autumn. The gonads, especially those of females, are seldom fully mature when they leave the feeding grounds. Although the off-shelf distribution of adults in these northern waters is unknown, larvae were found to be abundant along the northern edge of the Gulf Stream in winter (Fig. 5) (Hatanaka *et al.*, 1985). It has been postulated that this species spawns during the winter in the Gulf Stream or associated water masses between Cape Hatteras and Florida. Therefore, the migration of the population from feeding grounds in Canadian waters to the southern spawning area seems to be a long-range migration, similar to that of the winter-spawning population of the

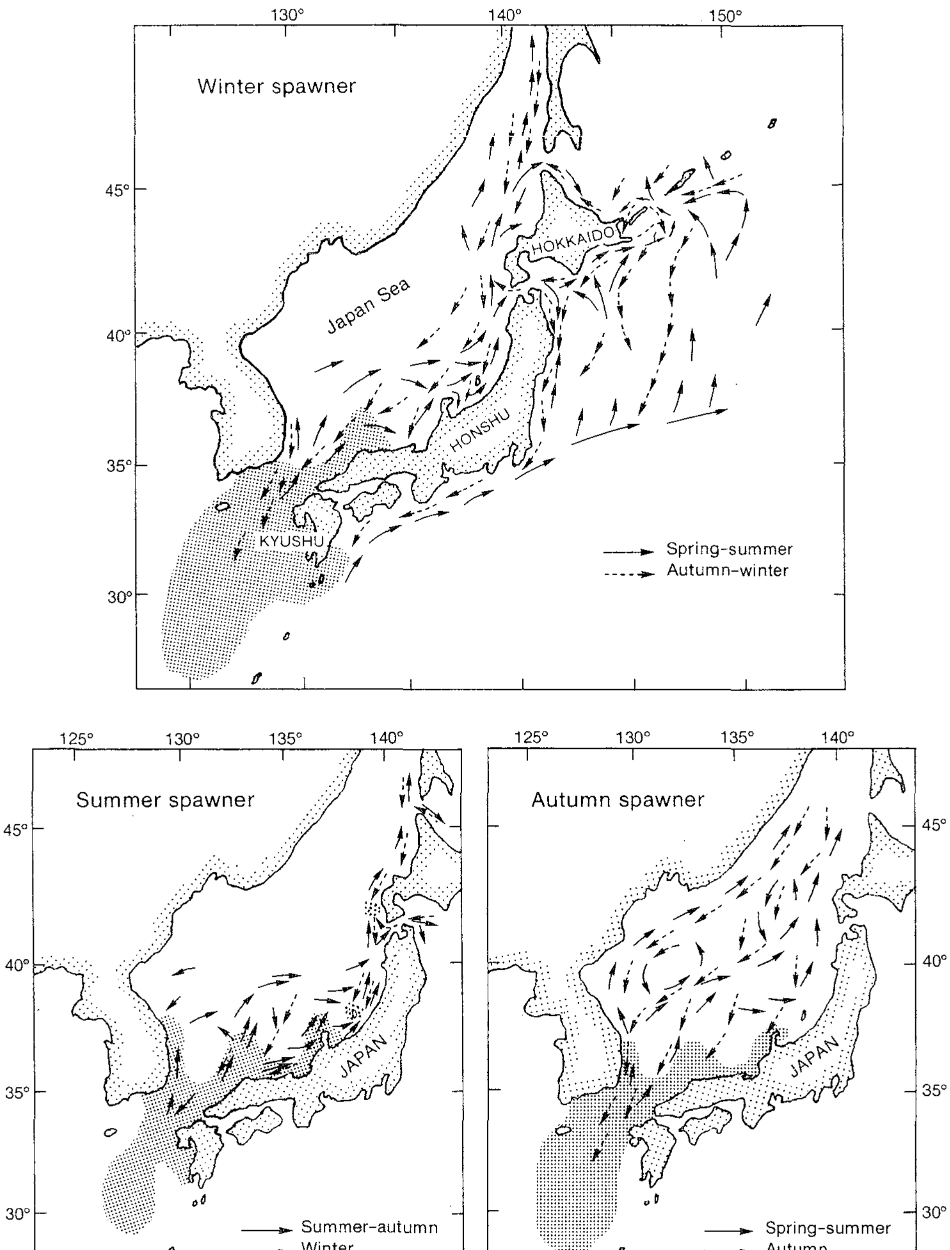

Fig. 4. Spawning areas (shaded) and migration routes of the three populations of *T. pacificus* in the waters around Japan (from Kasahara, 1982).

Japanese common squid. Lange and Sissenwine (MS 1981) noted the occurrence of summer spawners off the United States coast, but the spawning area is not yet known.

Illex argentinus

The jigging and trawl fisheries for this squid off Argentina start in summer (February) and autumn (April) respectively. Maturing females appear in April and about half of the females have mature eggs in the oviducts in July and August. Both fisheries end in August (winter) when the squid leave the feeding grounds on the continental shelf for spawning. By analogy with the two aforementioned species, the higher proportion of mature individuals on the feeding (fishing) grounds implies that the distance to the spawning area is shorter. Therefore, the migration of this species between the feeding and the spawning areas is probably the "short-range" type. In addition to the major winter-spawning population, there is a small population of squid which matures at a smaller size (about 5 cm less than that of the winter spawners) in coastal waters during the summer, but information on this group is very limited.

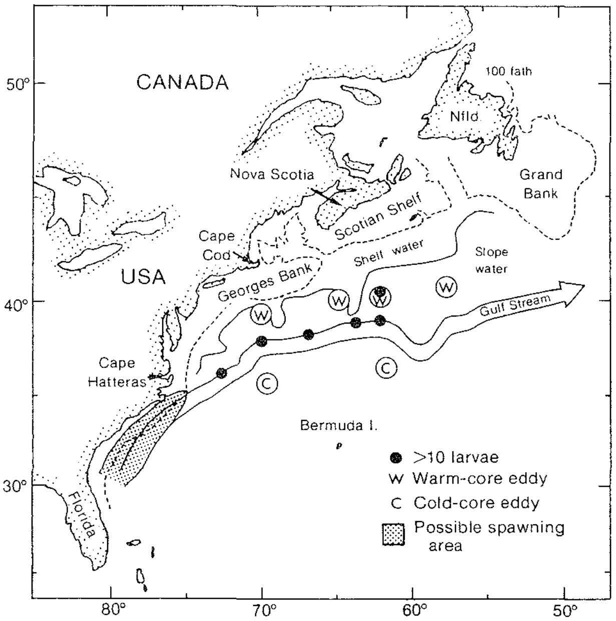

Fig. 5. Larval distribution and possible spawning area of *I. illecebrosus* in relation to the Gulf Stream System of the Northwest Atlantic (from Hatanaka *et al.*, 1985).

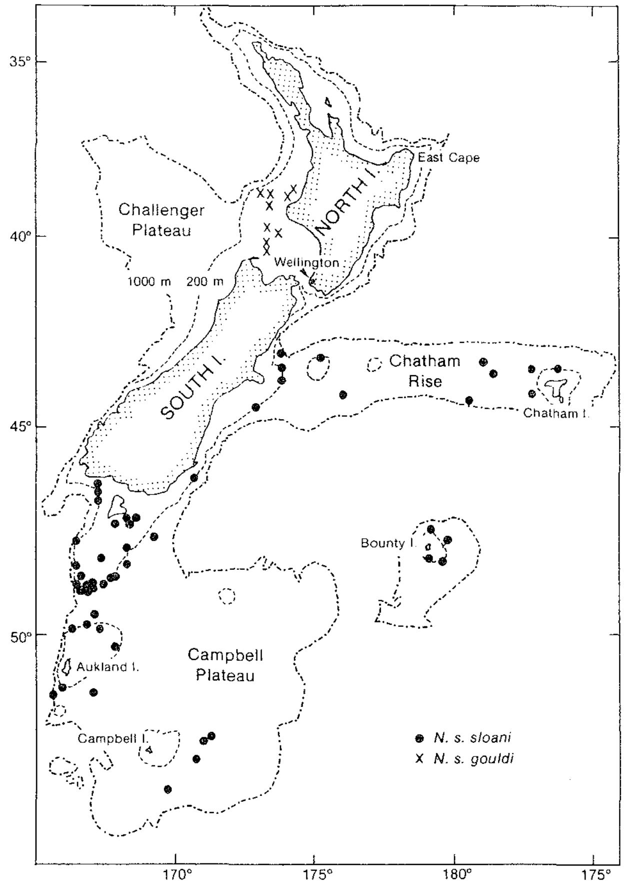

Fig. 6. Distribution of mature *N. sloani sloani* and *N. sloani gouldi* in New Zealand waters.

Nototodarus sloani sloani

The spawning season and area for this subspecies in New Zealand waters are not yet known. Mature individuals appear throughout the year on almost all fishing grounds (Fig. 6). Two subspecies have been reported to occur in New Zealand waters, and the length compositions of catches are commonly bimodal or trimodal. Furthermore, the maturity stage of the gonads differs by size-groups of squid. The available information indicates the presence on the fishing grounds of several cohorts which may be derived from spawning in different seasons and areas. The occurrence of fully mature squid on the fishing (feeding) grounds indicates that the spawning migration may be the "short-range" type.

Nototodarus sloani gouldi

The spawning season and area of this subspecies in Australian waters are also not known. Length compositions of catches are usually polymodal, and mature squid are present on the fishing grounds (Machida, 1983). Like *N. sloani sloani* in New Zealand waters, it is likely that several cohorts are produced in different seasons and areas and that the spawning migration is the "short-range" type.

Summary

The distances from the feeding grounds to the spawning areas vary considerably among the different species. In the case of species with short-range migrations, the distance may be a few hundred kilometers and both areas may even overlap to some extent for some species. In the case of species with long-range migrations, the distance from the feeding ground to the spawning area is usually more than 1,500–2,000 km. For example, a short-finned squid (*I. illecebrosus*) which was tagged off northeastern Newfoundland in September 1979 was caught off Maryland in December 1979, having travelled a minimum straight-line distance of 2,300 km (Dawe *et al.*, 1981). Squid which undertake long-range migrations to the spawning areas have less well-developed gonads when they leave the feeding grounds than those which undertake short-range migrations. In the case of species with well-known spawning areas, these areas are located in or near the warm currents which pass through the habitats.

Current System and Type of Migration

Todarodes pacificus

The Kuroshio Current in the Northwest Pacific, which is one of the strongest warm currents in the world, flows northward along the Pacific coast of Japan. The warm Tsushima Current, which is derived from the Kuroshio south of Japan, flows into the Japan Sea and consists of three branches. One branch which passes through the channel east of Tsushima Island

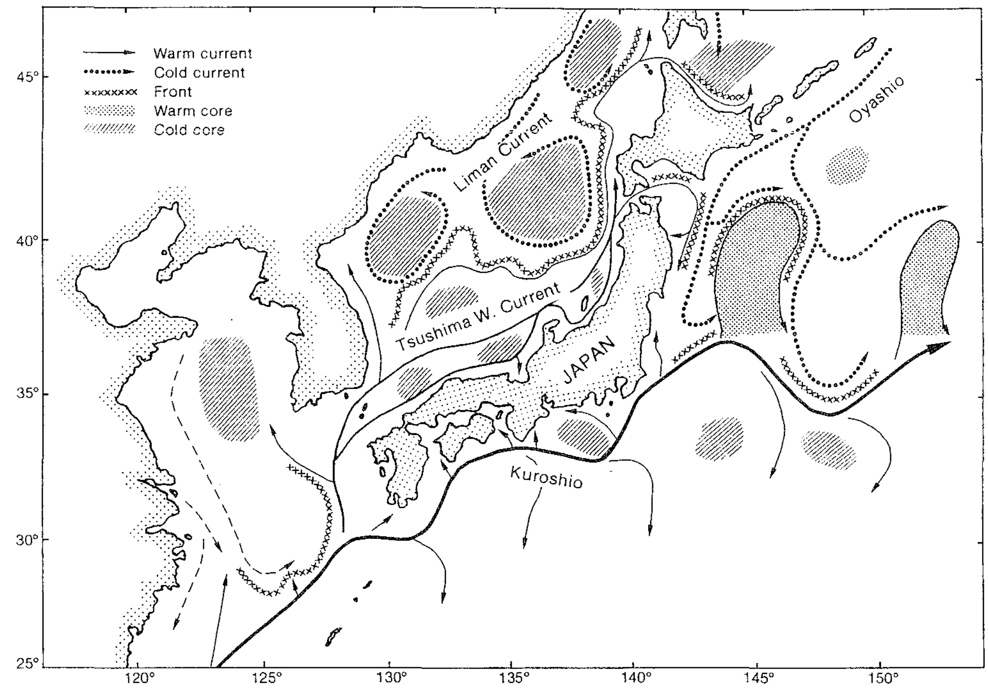

Fig. 7. Schematic representation of the currents around Japan (from Anon, 1972).

flows northeastward along the coast of Japan. The second and third branches, which are derived from the current passing through the western channel, flow northward into the central part of the Japan Sea and along the coast of Korea respectively (Fig. 7).

The winter-spawning population of *T. pacificus*, which is characterized as having a "long-range" type of migration, is closely associated with the Kuroshio Current and the first branch of the Tsushima Current. The autumn-spawning population, which undertakes a somewhat smaller-scale migration, depends mainly on the second and third branches of the Tsushima Current (Araya, 1967) for transport of larvae. The summer spawners which inhabit mainly the coastal waters are affected by coastal currents in addition to the Tsushima Current.

Illex illecebrosus

In the Northwest Atlantic, the Gulf Stream, comparable to the Kuroshio Current, flows northeastward off the east coasts of the United States and Canada, and the life cycle of *I. illecebrosus* seems to be closely connected with this major current system. From information on the distribution of larvae and juveniles (Fig. 5), it has been hypothesized that larvae are transported northeastward by the Gulf Stream from the spawning areas south of Cape Hatteras to warm Slope Water off the northeastern United States and Canada, where the juveniles remain for a few months (February to April or May) before moving onto the continental shelves (Hatanaka *et al.*, 1985).

Illex argentinus

The cold Falkland Current, which originates from the Antarctic Westerly Wind Drift, flows northward off eastern Argentina and meets the warm Brazilian Current off Uruguay and northern Argentina (Fig. 8). The waters along the coast of Argentina are warmer than the offshore waters throughout the year.

There is no information on spawning and larval distribution of *I. argentinus*. However, the catch rates of squid decline rapidly as individuals approach maturity, and no partly-spawned or spent squid have been caught in any of the feeding areas on the continental shelf. Because the juveniles appear on the northern part of the feeding grounds (north of 45° S) in spring and early summer, the spawning area is probably located somewhere farther north. If the adults spawn in the upper water of the warm current, as seems to be the case for some other species, the major winter-spawning population may be associated with the Brazilian Current and the minor summer-spawning population with the warm coastal waters.

Nototodarus sloani sloani

The major current in New Zealand waters is the warm Tasman Current which divides into two branches southwest of South Island. One branch (Westland Current) flows north along the west coast of South Island and the other (Southland Current) flows north along the east coast of South Island and then turns eastward in the vicinity of Banks Peninsula (Fig. 9). This complex

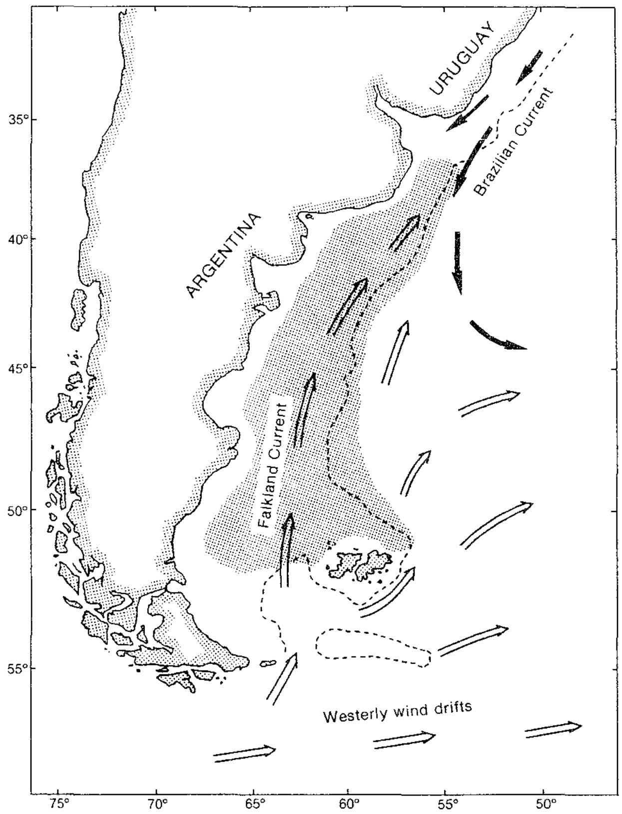

Fig. 8. Schematic representation of the currents in Argentina waters and the main feeding grounds (from Anon, 1971).

current system may play an important role in the life cycle of *N. sloani sloani* with its several seasonal populations. The currents in this region are fairly weak, in contrast with the Kuroshio Current and Gulf Stream, and this kind of oceanographic regime favors the hypothesis that squid migration to the spawning areas is the "short-range" type. The extent of migration may to some degree be influenced by the strength of the available warm current system.

Nototodarus sloani gouldi

The fishing grounds for this subspecies are located around Tasmania and are affected by the warm East Australian Current (Fig. 9). The life cycle of the squid may be closely associated with this current. Little is known about the relationships between the New Zealand and Australian populations of this subspecies.

Summary

Each of the squids seems to have a life cycle that is associated with warm water, and some of the populations occur in areas where several warm currents (or branches of currents) exist. The direction and distance of migration to the spawning area may be determined, to a large extent, by the direction and speed of the corresponding current which transports the larvae and juveniles to the vicinity of the feeding area. However, summer spawners may be more closely related to the oceanographic regimes of coastal waters.

Migration Type and Abundance

Todarodes pacificus

The annual catch of winter spawners attained a peak of 680,000 tons in 1968 and subsequently declined to about 100,000 tons in 1981 (Fig. 10). On the Pacific coast of Japan where the distribution of the winter-spawning population is related to the Kuroshio Current, the annual catch declined from 480,000 tons in 1968 to 6,500 tons in 1982. The autumn-spawning population inhabits the offshore waters in the Japan Sea, where squid-jigging vessels expanded their operations in the late 1960's to compensate for the rapidly-declining catch of winter spawners. The catch of autumn spawners increased to 200,000 tons in 1972 but declined to about 70,000 tons in recent years (Fig. 10). It is assumed that these fluctuations reflect changes in abundance of the fishable populations and thus may be related to the type of migration. The winter-spawning population, which is characterized by a migration of the long-range type in association with the strong current along the Pacific coast of Japan, may be quite large and fluctuate on a large scale, whereas the population of autumn spawners in the Japan Sea (short-range migration type) is smaller and tends to fluctuate on a smaller scale.

Illex illecebrosus

The relative abundance of this species (winter spawners) on the continental shelf in Canadian waters ranged from 12.7 in 1976 to 0.08 in 1982, whereas the abundance (including summer spawners) in United States waters also fluctuated during this period but on a smaller scale (Fig. 11). The annual catch in Canadian waters increased to a peak of 162,000 tons in 1979 and declined rapidly thereafter to 13,000 tons in 1982. The catch in United States waters was stable at a level of 20,000 tons during the same period, but this was due mainly to catch limitations which were imposed after 1977. The values of relative abundance (Fig. 11) were estimated from trawl survey data and, consequently, are subject to sampling error. Nevertheless, they indicate extremely large fluctuations in abundance. Furthermore, nearly 60% of the 1979 catch in Canadian waters was taken by Canadian fishermen in coastal areas, whereas the catches by distant-water fleets of several countries on the offshore fishing grounds were restricted by catch quotas. If there had been no catch restrictions in that year, the total catch would have been much higher. Therefore, the winter-spawning populaton of *I. illecebrosus* (with long-range type of

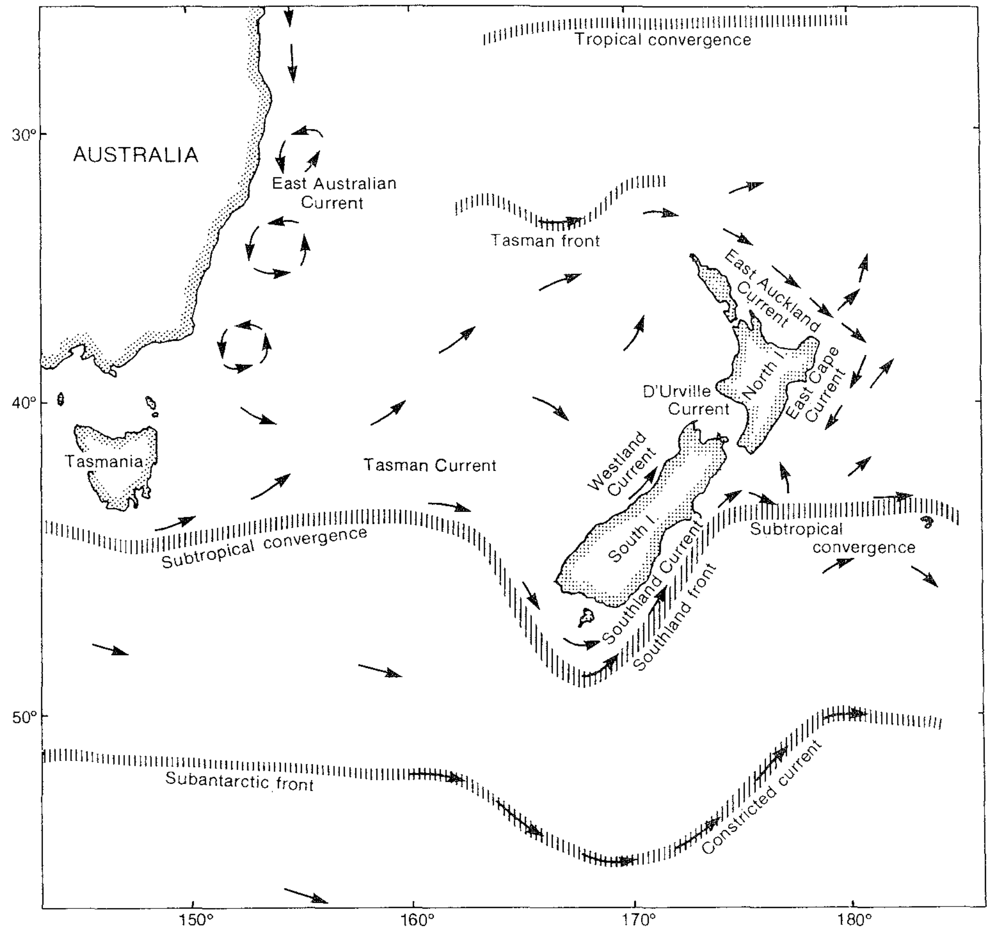

Fig. 9. Schematic representation of the currents in New Zealand and East Australian waters (from Fenaughty and Bagley, 1982).

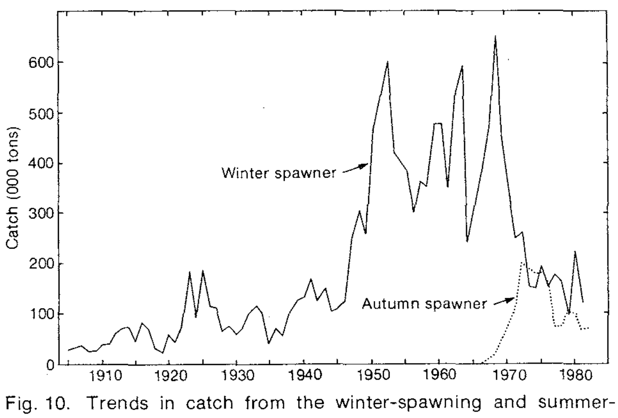

Fig. 10. Trends in catch from the winter-spawning and summer-spawning populations of *T. pacificus* in Japanese waters, 1905-81.

migration) may be comparable in size to the winter-spawning population of *T. pacificus* in Japanese waters.

Illex argentinus

A substantial fishery for this species in Argentina waters began in 1978, and the total catch peaked at 122,000 tons in 1979 (Fig. 12), with the aim of supplying the Japanese market. The catch was much lower in 1980 because of depressed market price and a decline in catch rate. Nevertheless, the variation in catch rate during the 6-year period for this species was much less than the variation in relative abundance index for *I. illecebrosus*.

Nototodarus sloani sloani

The Japanese squid fisheries in New Zealand waters began with squid-jigging in the early 1970's and trawling in the late 1970's. In addition, Korean and USSR vessels took part in the squid fisheries in recent years. The annual squid catch by all countries increased to 50,000 tons in the 1976/77 fishing season (December-June) and has ranged from 60,000 to 80,000 tons since then. The catch rates of Japanese squid-jigging vessels varied between 1.5 and 4.0 tons per day during 11 years of fishing operations (Fig. 13). Little is known about fluctuations in abundance of different spawning populations of this subspecies, but it is likely that they have a compensating effect on the population as a whole, leading to apparent stability in yearly catches and catch rates.

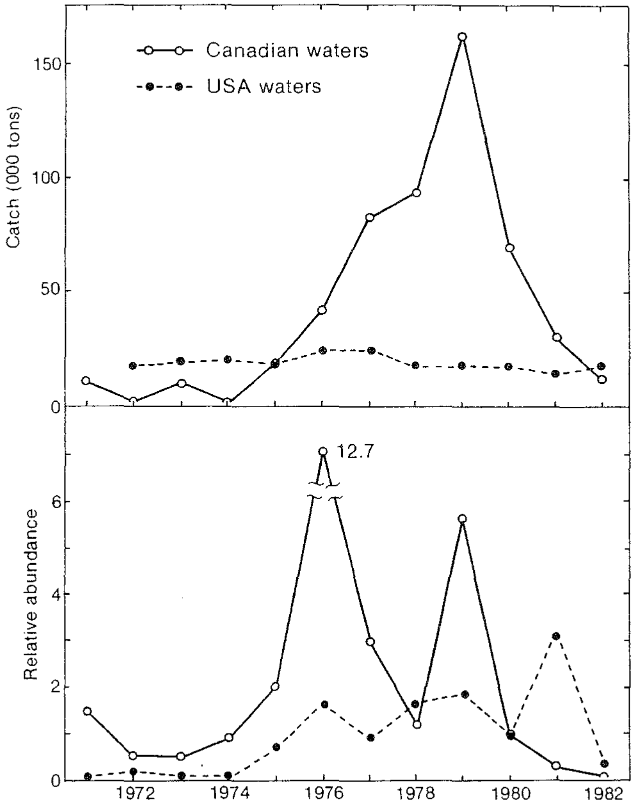

Fig. 11. Trends in catch and relative abundance of *I. illecebrosus* in Canadian and United States waters of the Northwest Atlantic, 1971-82 (NAFO, 1982, 1983).

Nototodarus sloani gouldi

Fishing activity in Australian waters was on a much smaller scale than in New Zealand waters and little is known about population size and annual fluctuations in abundance. However, the evidence from Japanese exploratory surveys (Machida, 1983) indicates that the population is much smaller than the winter-spawning population of *T. pacificus* in Japanese waters.

Summary

Each of the squid populations, which exhibit a long-range type of migration, such as the winter-spawning *T. pacificus* and *I. illecebrosus*, is characterized by large population size and large-scale fluctuations in abundance. On the other hand, squid populations which exhibit migrations of the short-range type are characterized by smaller population sizes with more stable abundance than the populations with long-range migrations. In areas where several populations intermingle, the fluctuations in abundance may be compensatory, with consequent stability in total catch.

Discussion

The lengths at maturity and monthly growth rates of the three species and two subspecies under consid-

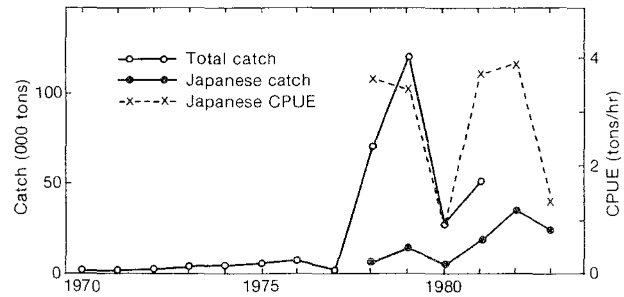

Fig. 12. Trends in catch and catch-per-unit-effort (CPUE) of *I. argentinus* by Japanese trawls (>2,500 GRT) in Argentina waters, 1970–83.

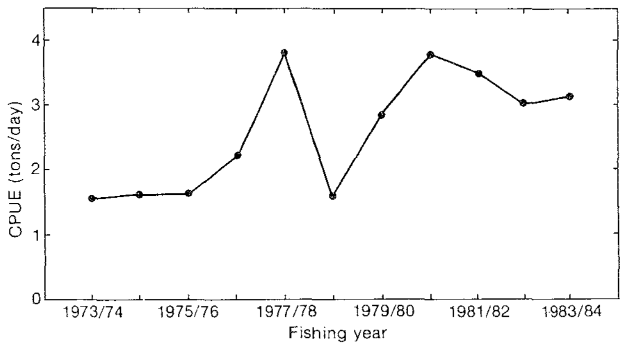

Fig. 13. Trends in catch-per-unit-effort (CPUE) of *N. sloani* by Japanese squid-jigging vessels in New Zealand waters, 1973-74.

eration are rather similar, and it appears that each has a life span of about 1 year.

The spawning areas of some populations are in the upper layers of warm currents or in warm water masses such as coastal water in summer. Laboratory studies have shown that *I. illecebrosus* eggs developed normally in water with temperatures higher than 13° C (O'Dor *et al.*, 1982) and that a temperature range of 14° to 21° C was suitable for *T. pacificus* eggs (Hamabe, 1962). A working hypothesis that squid spawn in the upper layers of warm currents or in warm coastal waters may be useful in detecting the spawning areas of the squid species about which little is known.

Winter spawners tend to predominate in quantity in waters which are inhabited by more than one population of the same species. Evidently, winter spawners utilize the period of low productivity of the ocean as the spawning season and the summer period of high productivity as the growing season. However, further investigations of the various populations are necessary to verify this hypothesis.

In this paper, only the routes and strengths of the current systems are discussed with reference to the interrelationship between the life cycle of squid and the oceanographic regime. However, the current systems (especially warm currents) must play an important role in the migratory habits of squid and fluctuations in abundance. Squid, especially the winter spawners whose feeding grounds are located far from the spawning areas, are transported by currents not only as planktonic eggs and larvae but also as juveniles. Therefore, the scale of a particular migration should be correlated with the strength of the associated current. In the case of the major currents, squid with a long range migration can utilize a broad feeding ground and the population may become quite large, but such a population may experience large variation in conditions which affect survival during the early life history stages and result in large-scale fluctuations in abundance and consequent recruitment of squid to the fishing grounds.

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