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# Review of the Influence of Oceanographic Factors on Cephalopod Distribution and Life Cycles

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## Abstract

The general relationship between the ecology of cephalopods and their environments is briefly reviewed from available information on the fisheries, biology and physical environments of various species which constitute the major cephalopods resources of the world's oceans. The relationship is further examined by reviewing the features of two large-scale oceanographic systems and a relatively small-scale system. The large-scale systems are the Kuroshio Current in the Northwest Pacific relative to the ecology of *Todarodes pacificus* and the Gulf Stream in the Northwest Atlantic relative to the ecology of *Illex illecebrosus*. Similar biological characteristics of both ommastrephid squids are found in relation to the dynamics of both ocean currents. However, differences in the oceanographic regimes of both regions seem to account for the differences that are known to exist in the structure of the squid populations in the regions. The small-scale system is the California Current in the Northeast Pacific relative to the ecology of *Loligo opalescens*, for which association between life-history features and the physical oceanographic regime can also be identified. Comparison of the Kuroshio Current and the Gulf Stream systems are considered to be important in clarifying incomplete aspects of the life cycle of *I. illecebrosus* in the Northwest Atlantic.

## Introduction

In general, the difficulty of finding realistic relationships between cephalopods and their environment is complicated by their complex behavior and incomplete information on the distributions and life histories of the different species. The role of temperature, as an important factor in growth and spawning (Boletzky *et al.*, 1973; O'Dor, 1982, 1983; O'Dor *et al.*, 1982), has been useful in constructing hypotheses about life cycles of some squids and may be critical to understanding their migratory patterns. The rather large salinity tolerance of cephalopods and their dependence on photoperiod changes for maturation and spawning are other relevant abiotic parameters in the ecology of most species (Mangold, 1963; Richard, 1966; Wells and Wells, 1977). However, general patterns in the ecology of widely-distributed species are probably better identified by examining large-scale physical factors such as ocean climate and major currents. This may be possible for the pelagic squids which include the commercially-important and best-studied genera (*Illex*, *Todarodes* and *Loligo*).

Pelagic squids probably take advantage of ocean currents to achieve fast growth and extensive distribution during a very short life-span. Ocean currents play an important role in the transport of fish larvae and juveniles (Parrish *et al.*, 1981) and some squids (Fields, 1965; Okutani, 1977; Trites, 1983). Migrations of adult fishes and squids are often related to currents which provide conditions for energetically low-cost transport and, in some cases, rest (Laevastu and Hela, 1970). The phenomena of larva dispersion and larval retention, which are facilitated by different hydrographic regimes (strong currents and eddies), seem to be important in understanding the migratory patterns of many species.

The biology, distribution and population structure of some squids have been clarified by considering local hydrographic regimes. Examples include the Japanese common squid (*Todarodes pacificus*) in the Northwest Pacific (Okutani, 1977) and the New Zealand arrow squid (*Nototodarus sloani*) in the South Pacific (Smith *et al.*, 1981). Although the life cycle of a related species (*Illex illecebrosus*) in the Northwest Atlantic is less well understood, the Gulf Stream is considered to play an important role in its ecology (Fedulov and Froerman, MS 1980; Trites, 1983). The populaton of *N. sloani* on the west and east coasts of New Zealand exhibit different morphological and genetic characteristics which have been attributed to different hydrographic regimes (Smith *et al.*, 1981). However, this system is probably unique and not really comparable to larger systems such as the Kuroshio Current in the Northwest Pacific and the Gulf Stream in the Northwest Atlantic. Another example, which may be comparable to the larger systems, is the influence of the California current on the life cycle of the longfin squid (*Loligo opalescens*) (Fields, 1965).

The main focus of this paper is to review the features of two large-scale systems (the Kuroshio Current and the Gulf Stream relative to the ecology of *T. pacificus* and *I. illecebrosus* respectively) and a relatively small-scale system (California Current relative to the ecology of *L. opalescens*). Available information on the fisheries and physical environments of other important

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cephalopods is reviewed briefly in order to discuss the general relationship between the ecology of cephalopods and their environments. The primary objective is not to explain the mechanisms by which life-cycle patterns are linked to physical events but rather to document some of the recurring patterns, to consider how and why they develop, and to describe common characteristics of the various species on a world-wide scale.

## Review of World Cephalopod Resources

Most of the existing knowledge about cephalopod biology has resulted from relatively recent studies on species that have been involved in rapidly developing fisheries. Lipinski (1973) noted that the economic value of the cephalopod fisheries is about 49% of the total for all fisheries of the world. Squids constitute about 75% of the total cephalopod catch, with two families (Ommastrephidae and Loliginidae) being the most important ones. Loliginid squids are generally restricted to coastal areas, whereas ommastrephids are mainly oceanic. The habitats of the squid species which live near the ocean surface are very similar to epipelagic fishes such as herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) (Arnold, 1979).

Changes in world catches of marine organisms during recent decades reflect the development of fisheries on various species of squids. After World War II, a major fishery developed on *T. pacificus* in the Sea of Japan, and catches peaked at 650,000 tons in 1968. Later, a fishery for *I. illecebrosus* developed in the Northwest Atlantic, with the highest catch of 180,000 tons in 1979. Other squid fisheries include *Illex argentinus* off Argentina with a peak catch of 90,000 tons in 1979, and *N. sloani* off New Zealand with a catch of 64,000 tons in 1983. The catches of all of these species have varied markedly, with the greatest fluctuations in the *T. pacificus* and *I. illecebrosus* fisheries. Several other squid species, which are taken primarily by jigging after attraction to the surface with lights, also occur as by-catches in the demersal trawl fisheries on the continental shelves. These include the loliginids *L. opalescens* in the Northeast Pacific, *L. pealei* in the Northwest Atlantic, *L. vulgaris* in the Northeast Atlantic and *L. forbesi* in the Central Atlantic. The ommastrephids, *Illex coindetii* and *Todaropsis eblanae* in the Atlantic and *Dosidicus gigas* in the Southeast Pacific, also occur as by-catches in the trawl fisheries of these regions.

Other groups of cephalopods have considerable fishery potential and some are commercially exploited. For example, catches of *Octupus vulgaris* and *Sepia officinalis* in the Eastern Central Atlantic have been as high as 100,000 tons and 40,000 tons respectively. Major fisheries for these species occur in the Mediterranean Sea (Guerra and Gandaras, 1983). These species, which inhabit very shallow waters, also occur in the Sea of Japan and the Indian Ocean. As benthic species, they are less influenced by the major currents than loliginids and ommastrephids.

The catches and estimated potential yields of various cephalopods in the major fishing areas of the world, based on data from Guerra and Gandaras (1983), are summarized in Table 1. Long-finned squids (Loliginidae), short-finned squids (Ommastrephidae), octopuses (Octopodidae) and cuttlefishes (Sepiidae) occur in most regions. The discrepancies between estimated potential yields and actual catches indicate that the stocks are generally underexploited. In the major oceans, the most productive cephalopod fisheries are associated with the continental shelves. These shelves, which represent about 10% of the surface area of the oceans, yield about 99% of the total catch of cephalopods, whereas the oceanic areas beyond the continental shelves are at present essentially unexploited because the oceanic species are widely dispersed by area and depth. Various researchers, in attempts to calculate the potential yield of these oceanic areas from the stomach contents of whales, tunas and other predators of squids (Clarke, 1966; Mercer, 1969; Voss, 1973; Clarke *et al*, 1976; Okutani, 1977), have produced crude estimates in the range of 5-30 million tons. The potential for cephalopod species that are related to fisheries on the continental shelves was suggested by Guerra and Gandaras (1983) to be about 1 million tons. However, these estimates must be considered very imprecise because of the great variability in abundance of cephalopods, especially the squids.

## General Aspects of Distribution and Biology

The general distributions of the cephalopod species listed by Guerra and Gandaras (1983) indicate limits from approximately 70° N to 50° N (Fig. 1). They tend to be concentrated in the northern hemisphere, reflecting the fact that the most extensive shelves are located there. However, this conclusion is biased, because 90% of the surface area of the oceans consists of oceanic waters, where exploitation of cephalopods is practically non-existent and information on their distribution is sparse.

The species groups in Fig. 1, which include loliginids, ommastrephids, octopodids and sepiids, generally occupy distinct marine habitats, although there is some overlapping. The first group, which includes species mainly adapted to temperate waters, occupies the epipelagic zone on the continental shelves (neritic). The epipelagic and mesopelagic ommastrephids, which include both neritic and oceanic species, have a

TABLE 1. Cephalopod fisheries of the World (based on data reported by Guerra and Gandaras, 1983).

| | | Atlantic Ocean | | | | | | Pacific Ocean | | | | | | Indian Ocean | | Medit. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NW | CW | SW | NE | CE | SE | NW | CW | SW | NE | CE | SE | W | E | Sea |
| | Area fished (000 km²) | 5,703 | 14,681 | 17,756 | 16,877 | 13,979 | 18,594 | 20,476 | 33,530 | 33,312 | 7,503 | 57,467 | 16,471 | 30,198 | 29,485 | 2,980 |
| | Continental shelf (000 km²) | 1,260 | 1,370 | 1,950 | 1,736 | 480 | 210 | 1,950 | 3,200 | 470 | 965 | 450 | 177 | 1,640 | 1,580 | 500 |
| | Primary production (gC/m²/yr) | 100-150 | 50-100 | 50-200 | 50-150 | 106-365 | 50-500 | 100-200 | 50-200+ | 50-100 | 150 | 3-137 | 50-500 | 50-200 | 50-200+ | 50 |
| | Fisheries yield (tons/km²/yr) | 2.3 | 1.3 | 0.8 | 6.7 | 5.9 | 13.7 | 9.4 | 1.8 | 0.8 | 2.4 | 4.5 | 38.9 | 1.3 | 0.8 | 2.6 |
| LOLIGINIDS | *Doryteuthis bleekeri* | — | — | — | — | — | — | X | — | — | — | — | — | — | — | — |
| | *Loligo brasiliensis* | — | — | X | — | — | — | — | — | — | — | — | — | X | — | — |
| | *Loligo duvaucelli* | — | — | — | — | — | — | — | X | — | — | — | — | X | — | — |
| | *Loligo edulis* | — | — | — | — | — | — | — | X | — | — | — | — | — | — | — |
| | *Loligo forbesi* | — | — | — | X | X | — | — | — | — | — | — | — | — | — | — |
| | *Loligo opalescens* | — | — | — | — | — | — | — | — | — | X | X | — | — | — | — |
| | *Loligo pealei* | X | X | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | *Loligo vulgaris* | — | — | — | X | X | — | — | — | — | — | — | — | — | — | X |
| | *Loliguncula brevis* | — | X | X | — | — | — | — | — | — | — | — | — | — | — | — |
| OMMASTREPHIDS | *Dosidicus gigas* | — | — | — | — | — | — | — | — | — | — | — | X | — | — | — |
| | *Gonatopsis borealis* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | *Gonatus fabricii* | — | — | — | X | — | — | — | — | — | X | — | — | — | — | — |
| | *Illex argentinus* | — | — | X | — | — | — | — | — | — | — | — | — | — | — | — |
| | *Illex coindetii* | — | X | — | — | X | X | — | — | — | — | — | — | — | — | X |
| | *Illex illecebrosus* | X | X | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | *Nototodarus sloani* | — | — | — | — | — | — | — | — | X | — | — | — | X | X | — |
| | *Ommastrephes bartrami* | — | — | — | — | — | X | X | X | X | X | — | — | X | X | — |
| | *Ommastrephes pteropus* | — | X | — | — | — | X | — | — | — | — | — | — | — | — | — |
| | *Onychoteuthis banksii* | — | — | — | — | — | — | — | — | — | X | — | — | — | — | — |
| | *Symplectoteuthis oualaniensis* | — | — | — | — | — | — | — | X | — | — | — | — | — | — | — |
| | *Thysanoteuthis rhombus* | — | — | — | — | — | — | X | — | — | — | — | — | — | — | — |
| | *Todarodes eblanae* | — | — | — | X | X | X | — | — | — | — | — | — | — | — | X |
| | *Todarodes pacificus* | — | — | — | — | — | — | X | X | — | X | — | — | — | — | — |
| | *Todarodes sagittatus* | — | — | — | X | X | X | — | — | — | — | — | — | X | — | X |
| OCTOPODIDS | *Eledone cirrhosa* | — | — | — | X | X | — | — | — | — | — | — | — | — | — | X |
| | *Eledone moschata* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | X |
| | *Octopus doflieni* | — | — | — | — | — | — | X | — | — | — | — | — | — | — | — |
| | *Octopus maya* | — | X | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | *Octopus vulgaris* | — | — | — | X | X | X | X | — | — | — | — | X | — | X | X |
| SEPIOIDS | *Rossia macrosoma* | — | — | — | — | X | — | — | — | — | — | — | — | — | — | X |
| | *Sepia esculenta* | — | — | — | — | — | — | — | X | — | — | — | — | — | — | — |
| | *Sepia lycidas* | — | — | — | — | — | — | X | — | — | — | — | — | — | — | — |
| | *Sepia officinalis* | — | — | — | X | X | X | X | X | — | — | — | — | — | — | X |
| | *Sepia pharaonis* | — | — | — | — | — | — | X | — | — | — | — | — | X | X | — |
| | *Sepiella japonica* | — | — | — | — | — | — | X | X | — | — | — | — | — | — | — |
| | Catches in 1979 (000 tons) | 104 | 8 | 124 | 16 | 96 | 12 | 641 | 137 | 55 | 29 | 27 | 276 | 18 | 9 | 44 |
| | Estimated potential (000 tons) | 500 | 100 | 500 | 100 | 1,000 | 1,000 | 1,000 | 500 | 200 | 100 | 100 | 1,000 | 100 | 100 | 100 |

much broader climatic range from subboreal to temperate and tropical waters. Other short-finned squids, exemplified by *Gonatus fabricii*, are mesopelagic and bathypelagic, occurring in boreal and temperate waters. However, some ommastrephid squids, e.g. *Ommastrephes bartrami*, *Nototodarus sloani* and *Symplectoteuthis oualaniensis*, have restricted distributions, with relatively narrow ranges in the North and South Pacific and Indo-Pacific Oceans. The octopodids and sepiids are benthic animals which inhabit temperate and tropical waters of the continental shelves, mainly in the northern hemisphere.

Despite the extensive exploitation of cephalopod populations, many aspects of their biology and ecology remain obscure. One difficulty is that the classical methods of studying the population dynamics of fishes are not suitable for cephalopods, because the latter are short-lived animals and ageing techniques are only now being developed. Another problem is that the taxonomy of many groups is still unsettled. Also, the shape and texture of different cephalopods make standardization of morphometric measurements difficult to achieve, and, consequently, the lack of standardization of sampling methods results in data for different areas and species being, in many cases, difficult to interpret. Furthermore, the distributional ranges of many species are diffuse and complex, and migration patterns are poorly understood.

Among the cephalopods which have been relatively well-studied are *T. pacificus* of the Northwest Pacific and *I. illecebrosus* of the Northwest Atlantic, although some species in the Mediterranean Sea have been studied persistently for many years (Mangold, 1963). Some of the available data are summarized in Table 2. In general, cephalopods live for 1-2 years, longer-living species or individuals being rare. They are reproductively monocyclic and they die after spawning. Differences among species are evident in relation to migratory and distributional ranges, spawning seasons, and spawning habitats, which may range from pelagic to demersal and from inshore shallow-water to offshore deep-water areas. Fecundity varies

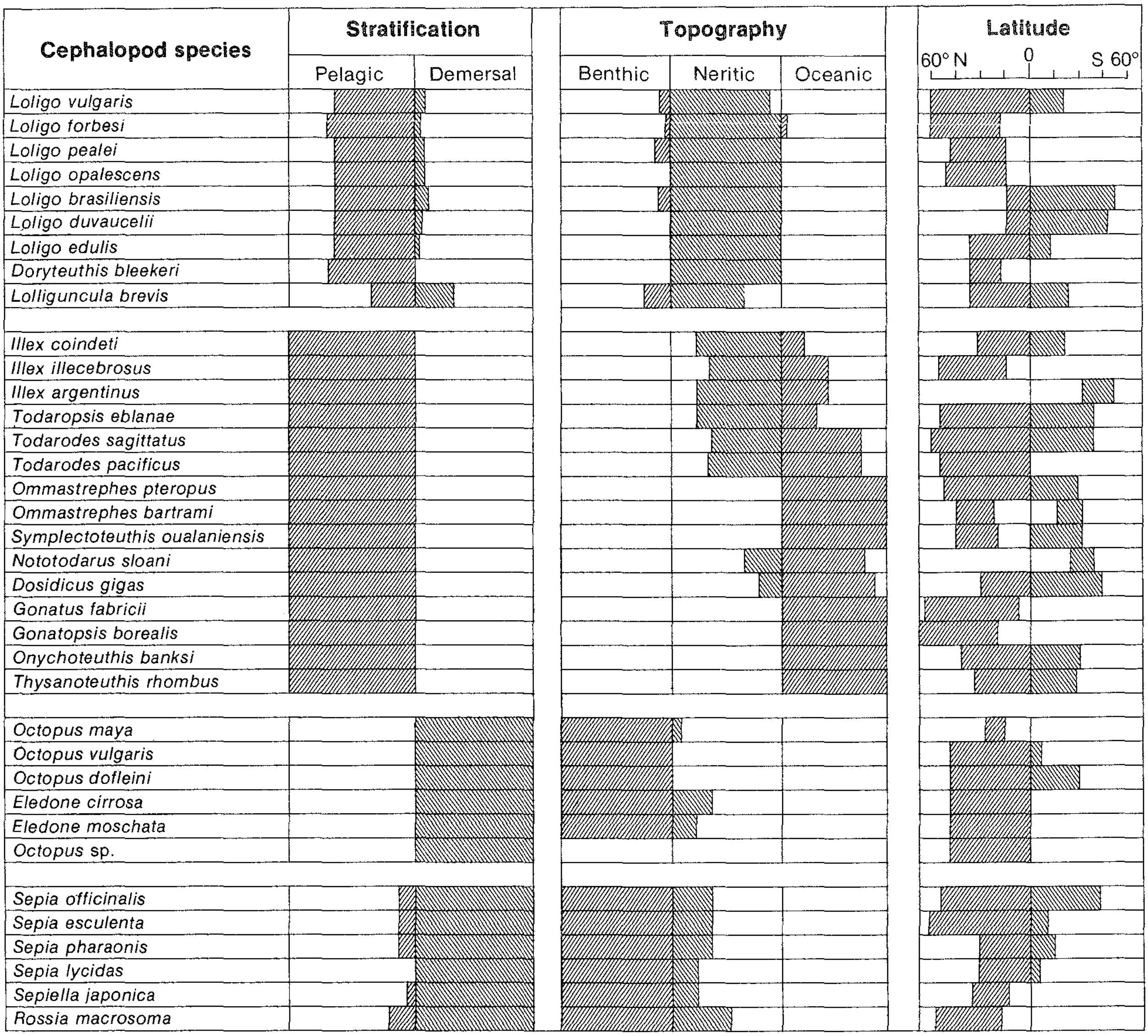

Fig. 1. World distribution and zoogeography of the major cephalopods in terms of stratification (vertical/horizontal), topography and latitude.

from species to species and probably within the same species, the available estimates being based on few field observations or on laboratory experiments (Lipinski, 1973; Durward *et al*., 1979; Coelho *et al*., MS 1982). Cephalopods may achieve high growth rates, as has been shown for *I. illecebrosus* in the laboratory (O'Dor *et al*., 1980). However, in nature, growth rates are dependent on food availability and hydrographic conditions. Typically, mature adults do not appear to feed, but this is not universal (Macy, 1982).

## Fisheries and Large-scale Oceanographic Features

Fisheries can be characterized topographically in relation to continental shelf and slope regions or hydrographically in relation to upwelling areas. In the North Atlantic and North Pacific Oceans, the major currents (Gulf Stream and Kuroshio Current) occur along their western margins. Both currents are narrow and flow generally northward at relatively high speed. In contrast, the currents along the eastern margins of these oceans are broad and flow southward toward the equator. Despite the similarity of these features, the two oceans are markedly different in topography and climatic regimes. The Atlantic is only about half the area of the Pacific Ocean, but its continental shelf area is 50% greater. In the Atlantic, the warm Gulf Stream-Atlantic Current system flows northeastward to the Norwegian Sea, whereas the Kuroshio Current flows in a more easterly direction. Thus, during the winter, there is no ice in the Norwegian Sea and southwestern Barents Sea, whereas the corresponding area north of

TABLE 2. Biological data for some important cephalopods. (Source: Mangold, 1963; Guerra and Gandaras, 1983; Boyle, 1983.)

| Species | Horizontal migration | Bathymetric distribution (m) | Temp. range (°C) | Growth rate (mm/mo) | Size at maturity (cm) | Maximum length (cm) | Average length (cm) | Spawning season | Fecundity ($10^3$ eggs) | Egg size (mm) | Incubation | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | Days | (°C) |
| *Loligo brasiliensis* | small | ... | ... | ... | ... | 25-30 | 15-20 | Nov-Mar | ... | ... | ... | |
| *Loligo forbesi* | small | 50-200 | 10-20 | 27-37 | ... | 90-100 | 30-40 | Jan-Mar | ... | ... | 30-40 | |
| *Loligo opalescens* | small | 10-200 | ... | 12 | 7-14 | 20-25 | 12-15 | Jan-Aug | 1-3? | 2.0x1.3 | 20-30 | (13-18°) |
| *Loligo pealei* | small | 25-360 | 8-15 | 20 | ... | 30-40 | 15-20 | Jan-Aug | 6 | 1.5x1.0 | ... | |
| *Loligo vulgaris* | small | 10-100 | 12-14 | ... | ... | 45-50 | 20-30 | Jan-Aug | 3-6 | 2.0x1.5 | 30 | |
| *Dosidicus gigas* | very large | ... | ... | ... | ... | ... | ... | Apr-Dec | ... | ... | ... | |
| *Gonatus fabricii* | large | 100-4000 | ... | ... | ... | ... | ... | ... | ... | ... | ... | |
| *Illex argentinus* | very large | 100-300 | ... | ... | ... | 35-40 | 12-25 | ... | ... | ... | ... | |
| *Illex coindetti* | large | 200-600 | 7-20 | ... | ... | 40-45 | 25-30 | Feb-Oct | ... | 0.3-1.0 | 9-16 | |
| *Illex illecebrosus* | very large | 10-1000 | 1-25 | 45 | ... | 30-35 | 12-25 | Jan-Mar | 20-30 | 0.6-1.0 | ... | |
| *Nototodarus sloani* | large | 80-800 | 3-28 | ... | ... | 40 | 17-40 | Oct-Mar | 2-20 | ... | 20-65 | |
| *Ommastrephes pteropus* | large | ... | ... | ... | ... | 40 | 20-25 | ... | ... | ... | ... | |
| *Todarodes pacificus* | very large | 30-200 | 5-20 | 45 | ... | 50-55 | 30-45 | Jul-Mar | 3-5 | ... | ... | |
| *Todarodes sagittatus* | very large | 70-1000 | 1-25 | 22-76 | ... | 70-80 | 30-40 | ... | ... | ... | ... | |
| *Todaropsis eblanae* | large | 20-600 | 7-20 | ... | 10 | ... | 15-20? | Feb-Nov | 5-10 | ... | ... | |
| *Octopus maya* | very small | 1-50 | ... | ... | ... | 130 | 50-60 | Nov-Dec | 1-2 | ... | 40-90 | (20°) |
| *Octopus vulgaris* | very small | 0-150 | 6-30 | ... | ... | 130-160 | 50-70 | Feb-Oct | 150 | 0.6-2.4 | 28 | (2.5°) |
| *Sepia officinalis* | small | 5-150 | 10-25 | ... | ... | 40-45 | 20-25 | Feb-Oct | <1 | 8-9 | 80-90 | (15°) |

50° N in the Pacific is completely ice-covered. The mean water temperatures at corresponding latitudes in the two oceans are also different: at the 0° and 30° meridians in the Atlantic, the mean temperature of the surface layer at 60° N varies only by about 5° C annually (from 6° to 11° C), whereas at the same latitude in the Bering Sea (180° meridian) the mean temperature varies by about 10° C annually (from -1.7° to 8° C) (Rass, 1959).

The eastern-boundary currents are associated with shelf regions and major coastal upwelling systems, such as the California and Peru Currents in the eastern Pacific and the Canary and Benguela Currents in the eastern Atlantic. These upwellings in coastal regions result in high biological productivity, and the ecosystems show particular features in their faunas, including a high ratio of pelagic to demersal species in the commercial catches. In these areas, pelagic species seem to have developed life-history strategies which take advantage of upwelling events that are somewhat unpredictable in space and time.

The western-boundary currents of the Atlantic and Pacific Oceans are considered to be relatively persistent in both space and time. In these regions, the life histories of some cephalopod species appear to be associated with the linkage in time and space between spawning in the southern warm waters of the systems and the rich feeding areas which develop during a short period in the northern cold waters. The populations of commercially-important ommastrephids (*I. illecebrosus* and *T. pacificus*) are associated with these regions where they are the dominant cephalopod species. In contrast, the cephalopod fisheries of the eastern-boundary regions constitute an association of several species which are typically dominated by loliginids or, in some cases, by octopodids and sepiids.

## Major Currents and Squid Ecology

### Gulf Stream and Kuroshio Current

These currents, which generally flow northward along the western boundaries of their respective oceans in the Northwest Atlantic and the Northwest Pacific, are narrow and swift and extend to great depth. They differ markedly from the diffuse and slow currents (such as the California Current) which flow southward along the eastern boundaries of these oceans in the northern hemisphere. The speed of the western currents (about 200 cm/sec) is much higher than that of the eastern currents. The principal flow of both major currents is confined to a narrow band (about 10 km or less wide) which meanders greatly and has a complex pattern of countercurrents and eddies along its margins. The two currents are considered to be analogous (Walsh, 1977) in producing large-scale effects on marine life in their respective oceans.

Both systems have high horizontal temperature and salinity gradients. Significant changes in temperature and salinity are observable in the Gulf Stream system between the Sargasso Sea and Slope Water, particularly in the frontal zone along the northern edge of the Gulf Stream. Comparatively, the Kuroshio Current system exhibits more pronounced gradients, particularly in summer. The low salinity of the near-surface layer north of 45° N in the Pacific Ocean is due to the excess of precipitation over evaporation. This also promotes low salinity levels in the Sea of Japan relative to those in the Northwest Pacific.

In respect to the location of both currents, the Kuroshio flows at a distance of only 140 km from the coast of southern Japan, whereas the Gulf Stream is located much farther offshore in the region north of

Cape Hatteras. This may be reflected in the different distributions of squid in the two areas. Another important difference is that the Kuroshio Current branches to form the Tsushima Current which flows northward along the west coast of Japan (see Fig. 3).

Both currents are very complex systems. In addition to the features that have been noted, warm-core eddies form in slope water along the northwestern boundaries of the currents and these have a significant effect on the ecosystems of the adjacent continental shelves. Also, the mixing of the cold Labrador Current with the Gulf Stream off Newfoundland and the cold Oyashio Current with the Kuroshio Current off northern Japan generates areas of high productivity and plankton richness.

Data on primary and secondary production are scarce for the Northwest Atlantic, being restricted mainly to local inshore areas. On the other hand, for the Kuroshio and Oyashio Currents and the Sea of Japan in the Northwest Pacific, the existing information clearly distinguishes seasonal and spatial differences. The Oyashio Current differs from the Kuroshio Current primarily because the latter mixes vertically at greater depth. In the Oyashio Current, mixing extends beyond the euphotic zone but is halted by the permanent isohaline at about 200 m (Gulland, 1971). Zooplankton biomass in the Oyashio Current is high during the summer, but this seasonal pattern is not so evident in the Kuroshio Current. The low seasonal variability in plankton biomass in the latter current is probably similar to the situation in the Gulf Stream. The offshore areas of the Northwest Pacific have a much earlier phytoplankton bloom than the Sea of Japan. In the latter area, zooplankton biomass in summer is higher in the north than in the south but less than in the Oyashio region. In the Sea of Japan, the warm Tsushima Current and the cold Liman Current, in conjunction with the continental shelf effect, produce zones of local upwelling.

## Ecology of *I. illecebrosus* and *T. pacificus*

These species, in the context of this review, constitute the well-studied species which are associated with the western boundary currents of the North Atlantic and North Pacific Oceans. Figures 2 and 3 illustrate the similar latitudinal ranges of *I. illecebrosus* and *T. pacificus* respectively and the locations of spawning areas (known and hypothetical) and fishing areas relative to the directions of the major currents.

A single population of *I. illecebrosus* has been recognized in the Northwest Atlantic, but the hypothesized life cycle (Squires, 1967; Amaratunga, MS 1982) remains supported only by data for that part of the life span from juveniles to maturing adults. The spawning areas have not been identified, but larvae and juveniles have been found to be associated with the Gulf Stream system (Roper and Lu, 1979; Amaratunga *et al.*, MS 1980; Fedulov and Froerman, MS 1980). More recently during the period from late January to early March, larvae were found in slope water along the northern edge of the Gulf Stream, with distribution ranging from Cape Hatteras northeastward to an area south of the Grand Bank (Hatanaka *et al.*, 1985; Dawe and Beck, 1985). In May, juveniles (130–150 mm ML) are frequently found in warm waters along the southern slope of the Grand Bank from which they migrate to Canadian inshore waters in late June and July (Squires, 1957). Growth is fast during the summer (1.5 mm/day) but slows down considerably by November when the squid disappear from the inshore and continental shelf feeding areas. Many of the males are sexually mature in November, but the maturity condition of females is less advanced.

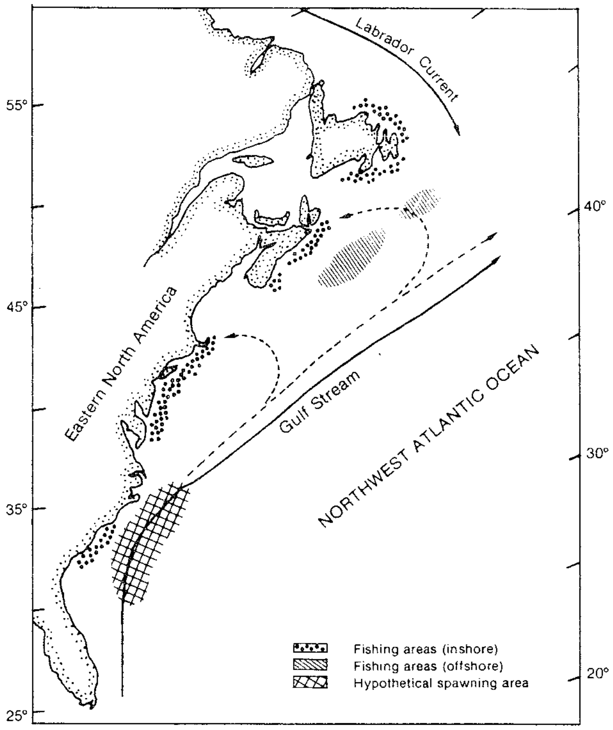

Fig. 2. Fishing areas of *I. illecebrosus* in relation to the hypothetical spawning area and the Gulf Stream system in the Northwest Atlantic.

In contrast to *I. illecebrosus*, *T. pacificus* in the Northwest Pacific is reported to consist of three subpopulations with different breeding seasons: winter, summer and autumn (Okutani, 1977). These groups have been separated on the basis of size composition, maturation and migratory patterns. The winter-spawning subpopulation is the major group which supports the fishery along the Pacific coast of Japan and in offshore waters. The summer-spawning group contributes to catches around Honshu Island and in the Sea of Japan. The autumn-spawning group supports the offshore fishery in the Sea of Japan.

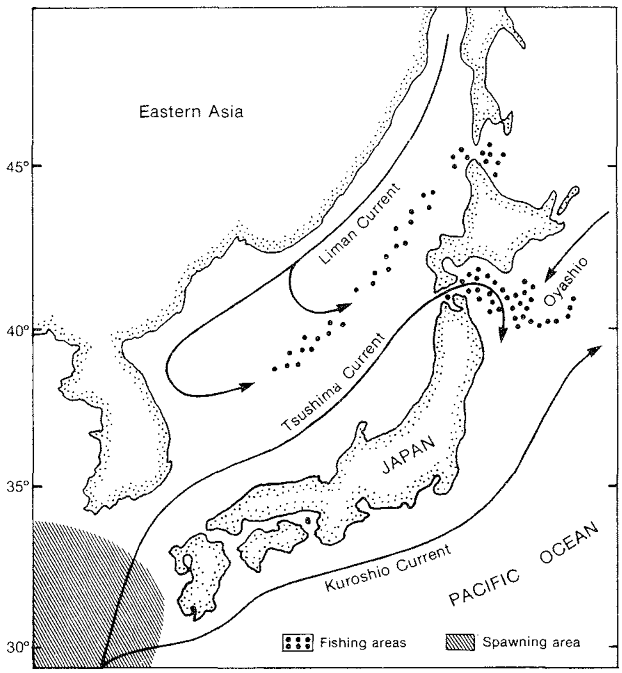

Fig. 3. Fishing areas of the winter-spawning population of *T. pacificus* in relation to the spawning area and the major currents of the Northwest Pacific.

The present review focuses on the winter-spawning group of *T. pacificus*, which forms the principal component of the total squid catch in the region and reflects characteristics similar to those of *I. illecebrosus*. The winter-spawning group has the largest distributional range and produces 80% of the total catch. Spawning occurs during January-April in the East China Sea. Larvae and juveniles move northward along the east and west coasts of Japan in association with the Kuroshio and Tsushima Currents respectively (Okutani, 1977) (Fig. 3). The major summer fishery, based on recruits from the winter spawning, occurs between Honshu and Hokkaido Islands at about 40° N and is directed toward catching squid about 250 mm ML. Uda (MS 1959) listed several hydrographic indicators of favorable fishing grounds for this squid, such as slack tidal currents and eddies with upwelling.

Comparison of the dominant populations of *I. illecebrosus* and *T. pacificus* indicates similarity with respect to spawning season, migratory pattern and current system for the transport of larvae and juveniles. Also, the major fishing grounds of both species are in areas where cold water from the north meets warm water from the south. The main difference between the two regions is the open-water continental shelf areas in the Northwest Atlantic in contrast to the semi-enclosed Sea of Japan in the Northwest Pacific. In the latter region, the influence of surrounding land masses and isolation from the open ocean by shallow sills cause large seasonal fluctuations in temperature and salinity (Gulland, 1971; Fukuoka *et al.*, 1983). Also, the South Honshu Ridge influences the flow pattern of the Kuroshio Current by the formation of a large-scale eddy which is accompanied by some upwelling (Gulland, 1971).

The complex population structure of *T. pacificus* seems to parallel the complexity of major hydrographic events in the area of its distribution. The flow of the Tsushima Current is most intense in September, and this may be advantageous for the transport of young squid which arise from summer spawning. The existence of small counterclockwise currents between the boundaries of the warm Tsushima Current and the cold Liman Current may cause the rather narrow spatial pattern of the fishery on the summer-spawning group. The much lower abundance of this group is probably due to the smaller size of its distributional area. The autumn and winter subpopulations make use of the more productive Oyashio-Kuroshio convergence, which is an area of intense vertical mixing and consequent zooplankton richness. The countercurrents along the east coast of Japan probably aid the migration of maturing adults southward toward the spawning area.

Similar associations between life history features and physical oceanographic regimes can be identified for *I. illecebrosus* in the Northwest Atlantic. The convergence of the cold Labrador Current and the warm Gulf Stream occurs in the vicinity of the continental shelf off Nova Scotia and Newfoundland. These are areas of local upwelling due to the convergence of Slope Water, Shelf Water and cold water from the north. These continental shelf areas are the main feeding grounds of *I. illecebrosus* during summer and autumn. However, within the distributional range of this species, there is an environmental gradient due to varying conditions of temperature, salinity, photoperiod and food availability. This may explain the existence of cohorts which are not consistent with the one-year-winter-spawning life cycle. Such environmental influences may be reflected in variable growth rates which result in the presence of several cohorts (modal length groups) within a year-class (Mesnil, 1977; Lange and Sissenwine, MS 1981). Although the progeny of winter spawners constitute the bulk of the population which migrates to the Nova Scotia and Newfoundland areas in summer, the presence of more than one modal group in length distributions off the northeastern United States indicates that protracted spawning probably occurs during the summer (Lange and Sissenwine, MS 1981). Better knowledge of the reproductive features of the *I. illecebrosus* population is fundamental to determining the relative importance of these cohorts.

### California Current and ecology of *L. opalescens*

Relative to the systems described above, this is a contrasting situation whose analysis may aid in understanding the different aspects of squid biology which represent adaptation to different physical environments. There are no large-scale ommastrephid populations in the eastern North Pacific, a situation which is similar to that of the eastern North Atlantic. In these regions, there are no dominant populations of cephalopods because of competition with numerous pelagic fish species (Fields, 1965). Also, becuase the coastal shelves are much narrower than those along the western boundaries of the oceans, the exploited squids are mainly coastal loliginids. In the Northwest Pacific, *L. opalescens* ranges from middle Baja California northward to southern British Columbia. The fishery takes place on spawning concentrations in a small area of Monterey Bay and also off Baja California, using lampara nets.

The California Current, which originates as cold, low-salinity water in the North Pacific, flows southward along western North America, being aided by the prevailing winds from the north and northwest. It produces strong upwelling along the coast, with a peak in the spring (April–May) off Baja California and progressively later (August) northward off Oregon. When the winds weaken in winter, a coastal counter-current is present at the surface. As the California Current flows southward, the low salinity of surface water (Wooster and Reid, 1965) is modified by upwelling of high salinity water, but near-shore salinity generally increases with depth. The inshore countercurrent (Davidson Current), which flows northward during winter, carries warm saline water. There is considerable seasonal variation in the along-shore component of this current, referred to as "dominant oceanic periods" (Fields, 1965). The direction of flow is highly variable, the mean component being northward during autumn and winter and strongly southward during spring and summer. Close to the shore, there are complex eddy systems which arise from local topographical irregularities and wind-pattern fluctuations.

With regard to productivity of this region, average values of the rate of carbon fixation are high (Gulland, 1971). The area is also characterized by high standing crops of zooplankton. However, zooplankton has been shown to have a cyclic pattern in biomass fluctuations from north to south (Bernal, 1979, 1981). This variability was considered to be related more to transport from the north by the California Current than to regeneration of nutrients from local upwelling. The offshore extent of zooplankton enrichment (200–300 km) is much wider than the zone that would be influenced by local upwelling processes.

In the southern part of the region, spawning of *L. opalescens* occurs on the bottom in shallow inshore waters mainly at night during the winter (December–March). In the north (Monterey Bay), spawning occurs during April to November with the major peak in May or June.

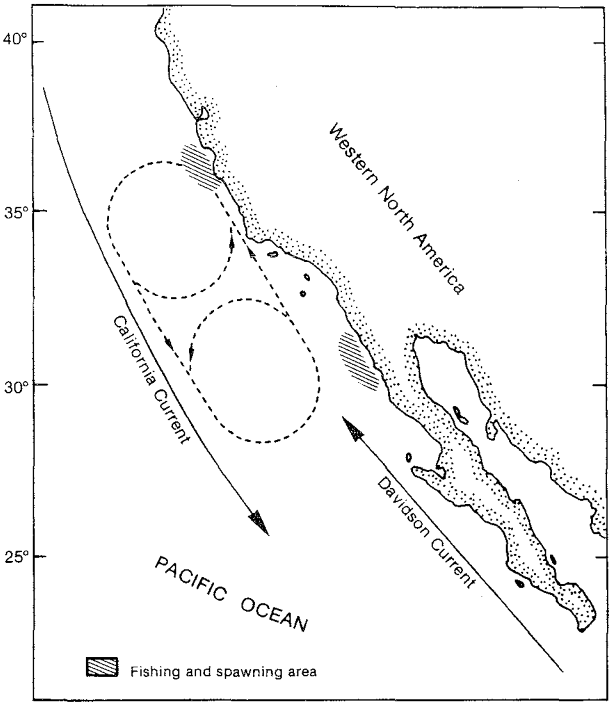

Fig. 4. Fishing and spawning areas and hypothetical movements of *L. opalescens* in relation to currents off California in the eastern Pacific.

Fields (1965) and Karpov and Calliet (1978) suggested that cannibalism in the spawning population is a behavioral response to the high density of schooling mature adults. Larvae are presumably dispersed by currents, because juveniles have been found in the offshore neritic zone. Migration is probably restricted to movement from inshore spawning areas to offshore feeding areas (Fig. 4). Large-scale migrations seem to be inconsistent with metabolic rates that have been estimated in the laboratory (O'Dor, 1982). Catches have fluctuated greatly (Fields, 1965), with peak catch of 19,000 tons in 1946. Catches were in the range of 6,000–19,000 tons during 1970–80.

The Monterey area is described by Fields (1965) as having noticeable seasonal events that are related to the current system, with an upwelling period during March–August followed by an "oceanic" period during September–October and the "Davidson Current" period during November–February. Off southern California, the peak upwelling occurs during April–May, and the area is also characterized by marked fluctuations of various kinds (winds, stratification, tides) as well as the existence of a counterclockwise eddy in the vicinity of 33° N.

In the Monterey area, major spawning occurs inshore during the March–August upwelling period, but a second group occasionally spawns in November. Fields (1965) suggested that this latter group may originate from the Baja California population in the south.

The southern population spawns during the winter when the northward flow of the Davidson Current is strongest. The northward movement of larvae and juveniles in the postspawning period may be interrupted by the counterclockwise eddy, thus reducing the possible mixing of the northern and southern groups. On the basis of the information provided by Fields (1965), a schematic representation of *L. opalescens* movements within the California Current system is proposed (Fig. 4) to illustrate different routes of transport which favor the mixing of the northern and southern groups and contribute to the development of more than one cohort of squid during the one-year cycle. These routes may represent alternative strategies for survival, depending on the physiological condition of the squid and the prevailing oceanographic conditions.

## Discussion and Conclusions

All cephalopods seem to have short lifespans, wide food spectra, high growth rates, monocyclic reproduction and no "true" larval stage. They vary in population size, areas inhabited, mobility and reproductive capacity. Despite the great variability in the quantity and quality of biological information available for cephalopods (Table 2), a comparison between benthic and pelagic cephalopods is possible by considering a balance between high growth rates (based on size of adults) and the energy required for movement. However, the size of large benthic animals (e.g. some octopuses) can also be attained by some pelagic squids, such as *Todarodes sagittatus* and *Dosidicus gigas*, which require a high level of energy for locomotion. This seems to indicate the existence of different life-cycle strategies among cephalopods. Rapid growth and shortened life-span might be enhanced by such factors as adequate food supply, favorable temperature conditions and mechanisms for the passive transport of larvae (strong currents). Opposite environmental conditions might result in an extended life-span with consequent variation in size-at-maturity and maximum size.

In view of the great variation in size of cephalopods and the lack of ageing data, size cannot be related to sedentary behavior or to life span. However, it is reasonable to suggest that part of the observed phenotypic variation reflects the plasticity of these species to respond to different conditions of food supply, temperature and other abiotic factors, such as currents which provide low-cost transport (e.g. Kuroshio Current and Gulf Stream) or conditions for dispersal (e.g. California Current). Benthic species, or at least those species which lack the pelagic phase during early development, are rather independent of current regimes. Nevertheless, they take advantage of areas of high productivity (upwelling zones) and favorable temperatures (temperate to tropical climates). Their limited mobility also requires them to select areas where conditions are optimal for spawning (sheltered sites) and growth.

The neritic species, exemplified by *Loligo* sp., are characterized by much greater mobility and more extensive horizontal and vertical movements than the benthic types. The available fecundity data for neritic species indicate higher numbers of eggs and smaller egg sizes than those of benthic forms whose encapsulated eggs are usually attached to the substrate. Pelagic species, on the other hand, probably spawn within the water column where the egg masses are neutrally buoyant (O'Dor and Balch, 1985). This likely results in higher mortality which may be balanced by higher fecundity.

Pelagic cephalopods tend to occur in greater abundance than neritic and benthic species but they are also subject to greater fluctuations in abundance. The greater abundance of pelagic species may be related to their association with the larger oceanic systems which tend to be more stable than the coastal environments. This stability provides conditions for the dominance of one species, and the fluctuations in abundance are a reflection of environmental variability, such as temperature changes. In contrast, an unstable environment where competition is intense permits the existence of several species with less pronounced variations in abundance because these species have become less sensitive to environmental changes.

The systems which are analyzed in this paper appear to represent a range of biological and physical features. *L. opalescens* off California exhibits different spawning seasons at the extremes of the distributional area. The inshore (northern) and offshore (southern) components of the species seem to have adapted themselves to the "dominant oceanic periods" described by Fields (1965). The northern population spawns during upwelling in summer and the dispersion of larvae and juveniles occurs during the period when the California Current is strongest. The southern population spawns during the winter when the coastal Davidson Current, with its warm saline water, is the mechanism of transport of larvae and juveniles to northern areas where mixing with the northern population is possible.

The upwelling ecosystems of the eastern boundary regions of the major oceans show remarkable parallels in their fauna. The rather small latitudinal distributions of the dominant pelagic squids in these areas may be an evolved consequence of intense competition with temperate pelagic fishes, such as mackerel, sardine and hake, which are characterized by large populations. Apparently, the Northeast Pacific shows less diversity of cephalopod species than the Northeast Atlantic. The hydrographic features of the Northeast Atlantic are more complicated and the resulting diversity allows more pronounced differentiation. However, cephalopod research in this region is less well advanced than in the Northeast Pacific and further generalizations are not justified.

The other two systems relate to the population structures (*I. illecebrosus* and *T. pacificus*) with larger distributional ranges. The Gulf Stream and Kuroshio Current systems extend from subtropical to temperate latitudes without major zones of coastal upwelling. In contrast, there are large submarine banks where productivity is high during the spring. These banks are very important feeding areas. For both species, the requirements for successful pelagic spawning compel the squid to undertake long migrations to more suitable areas in the south. The long distances that are covered by the maturing adults are assisted by strong countercurrents. The strong northward flow which characterizes both ecosystems favors the effective transport of larvae and juveniles to the northern feeding grounds.

Although the Gulf Stream and Kuroshio Current systems have similar features which are reflected in biological similarities of the species, peculiarities of each physical environment also appear to be reflected in the biology of each species. For example, the existence of three subpopulations of *T. pacificus* probably reflects the different degrees of association with the open-sea regime. Geographically, the Sea of Japan favors such population differentiation. Both the Sea of Japan and the offshore waters of the Northwest Pacific have plausible mechanisms of larval transport, but they differ in salinity, water-mixing conditions, seasonal production cycles, and the size of the area occupied by squid.

Despite the topographic and hydrographic parallels in the Northwest Atlantic and the Northwest Pacific, the bathymetric distributions of *I. illecebrosus* and *T. pacificus* differ significantly (Table 2). The proximity of the Kuroshio Current to the coast, in contrast to the more offshore position of the Gulf Stream, and the physical conditions of the Sea of Japan probably account for such differences. Furthermore, the existence of the Honshu Ridge in the Northwest Pacific and the semi-enclosed Sea of Japan represent barriers which favor the differentiation of the *T. pacificus* population into three groups. If heterogeneity exists in the *I. illecebrosus* populaton of the Northwest Atlantic, it may be due to spawning in different parts of the region under different environmental conditions, or to protracted spawning in the same general area which may result from successive departures of maturing groups from the feeding grounds on the continental shelves.

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