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Influence of Oceanographic Factors on Cephalopod

Distribution and Life Cycles: a Review

by

M. Lucilia Coelho

Department of Biology, Dalhousie University
Halifax, Nova Scotia, Canada B3H 4J1

Introduction

Consideration of the distribution and life history of cephalopod species is difficult due to the lack of reliable information on depth distribution. In general, life history data for the group are rare or imprecise and their complex behaviours also contribute to the difficulty of finding realistic relationships between these organisms and their environment.

The role of temperature as an important requirement for growth and spawning (Boletzky et al 1973; O'Dor 1982, 1983) has been useful in constructing hypotheses about the life cycles of some species, and may be critical to understanding their migratory patterns. The relatively large salinity tolerance of cephalopods and the dependence on photoperiod changes for maturation and spawning are other relevant abiotic parameters in the ecology of these species (Richard 1966; Mangold 1963; Wells 1977). However, general trends in the ecology of widely distributed species are probably better identified by looking at large-scale physical factors, such as climate, topography and major currents. This seems to be particularly important for pelagic squid which include the most commercially important species and, consequently, the best studied genera (*Illex*, *Todarodes*, *Loligo*).

Pelagic squid probably take advantage of ocean currents to achieve fast growth and extensive distributions in a relatively short life span. Ocean currents have been suggested to play a role in the transport of fish larvae and juveniles (Parrish et al 1981) and in some squid (Fields 1965; Okutani 1977; Trites 1982). Migration of adult marine organisms is also often clearly related to currents which provide conditions for energetically lower cost transport and, in some cases, for rest (Laevastu and Helda 1970). The existence of larval dispersion or larval retention (Parrish et al 1981) favoured by different hydrographic regimes (strong currents, eddies) seems to be critical for understanding the migratory patterns of other species.

In fact, the biology, distribution and population structure of some cephalopods have been clarified by considering the local hydrographic regimes (Okutani 1977; Smith et al 1981). Examples include the species *Todarodes pacificus* and *Nototodarus sloani* in the Northwest Pacific and South Pacific, respectively. Although the life cycle of another related species (*Illex illecebrosus*) is less well understood, it has also been suggested to be associated with the Gulf Stream (Fedulov and Froermam 1980; Trites 1982). The differences in the population structure of *Nototodarus sloani* which were found between populations from the east and west coasts of New Zealand were related both to morphological and genetic characteristics and were shown to be closely linked to hydrography. This is probably a unique system, not really comparable to larger systems such as the Kuroshio and the Gulf Stream in the Northwest Pacific and Northwest Atlantic, respectively. Another example which is also not comparable to these systems, is the species *Loligo opalescens* from the coast of California. However, it has been suggested that its life cycle was also influenced by the current pattern characteristic of the area (Fields 1965).

The main focus of the present review is to analyse two comparable large-scale systems, the Kuroshio with Todarodes pacificus and the Gulf Stream with Illex illecebrosus comparing them to a smaller-scale system such as Loligo opalescens in the California Current. A brief review of the available information on fisheries and the physical environment for other important cephalopods will also be added in order to discuss the general relationship between the ecology of cephalopods and their physical environment. It is not intended to explain the mechanisms by which life cycle patterns are linked to physical events such as currents or other abiotic features. Rather, the objective is to document some of the recurring patterns, to consider how and why they develop and to describe common characteristics of the species on a world-wide scale.

Brief review of world cephalopod fisheries, abundance and geographical distribution

Most of the existing knowledge about cephalopod biology has resulted from relatively recent studies on species involved in rapidly developing fisheries. The commercial value of cephalopod fisheries is close to 49% of the total for all of the fisheries in the world (Lipinski 1972). Squid constitute about 75% of the cephalopod catch with the two squid families, Ommastrephidae and Loliginidae, being the most important. Loliginid squid are neritic, generally restricted to coastal areas, while ommastrephids are mainly oceanic. The surface-living species of these families are very similar in habitat to epipelagic teleost fish such as herring and mackerel (Arnold 1979).

Changes in world fishery catches observed during the last decades stimulated a wide interest in this group of species. Large stocks of squid were identified and have begun to be fully exploited. First, following World War II, the squid Todarodes pacificus in the Sea of Japan became an important fishery with catches reaching a maximum of 650×10^3 t in 1968. Later, a Illex illecebrosus fishery developed in the Northwest Atlantic, with the highest catch of 150×10^3 t recorded in 1979. Along with these two species, fisheries for other squid such as Todarodes sagittatus in Norway, Illex argentinus in Argentina and Nototodarus sloani in New Zealand developed. These are local, less important fisheries, with maximum catches of 10^3 t in 1965, 90×10^3 t in 1979 and 20×10^3 t in 1975, respectively. The catches for all of the above fisheries have shown marked fluctuations, which have been particularly dramatic in the Sea of Japan and the Northwest Atlantic Ocean.

Several squid species which can be caught using jigging and lights are also important as by-catch from demersal fisheries. They include long-finned squid such as Loligo opalescens in the Northeast Pacific, Loligo pealei in the Northwest Atlantic, Loligo vulgaris and Loligo forbesi in the Northeast and Central Atlantic. The ommastrephids, Illex coindetii and Todaropsis eblanae in the Atlantic and Dosidicus gigas in the Southeast Pacific, also occur frequently as by-catch in the trawling fishery.

Other groups of cephalopods may have considerable fisheries potential. Some are commercially exploited. For example, Octopus vulgaris and Sepia officinalis in the Northwest African coast have maximum catches of about 100×10^3 and 40×10^3 t respectively for the entire areas (Guerra and Gandaras 1983). These species which inhabit very shallow waters, are also common in the Sea of Japan and Indian Ocean. As benthic species, they are to a considerable degree independent from the oceanic regimes. The Mediterranean Sea constitutes a major area for the fishery of these species.

Table 1 attempts to summarize the more important species and their respective fishery areas, catches and estimated potential yields based on data from Guerra and Gandaras (1983). Long and short-finned squid, octopus and cuttlefish are represented nearly everywhere. The discrepancy between estimated potentials and actual catches strongly suggests that most of the stocks are still underexploited (a unique situation in today's fisheries). In the largest oceans the most productive cephalopod fisheries are associated with the western and eastern boundaries. The Continental Shelves which represent 10% of the total oceanic area, produce about 99% of the total cephalopod catches (Table 1). These evaluations are mainly based on general statistics which are frequently incomplete, and should be considered only as indications of the real potential. The oceanographic areas beyond the continental shelves are at the

present essentially unexploited and their potential has been calculated from stomach-content data from whales, tunnids and other predators (Clark 1966; 1976; Mercer 1969; Okutani 1977; Voss 1973). These estimates give values ranging from 50×10^5 t (Clark 1976) to $100-300 \times 10^5$ t (Voss 1973). The potential for the species related to more coastal fisheries was suggested to be about 10×10^5 t (Guerra and Gandaras 1983). However, the variability in abundance of some of these species, the squids in particular, make these estimates very speculative.

The distribution of cephalopods is dependent on topographic, climatic, and hydrographic features as well as on the productivity as reflected by the most productive fisheries which are found on the shelf areas in coastal seas and upwelling zones. However, the distributional limits of the respective species are diffuse and not well described. Table 2 and 3 summarizes the information available for vertical and horizontal distributions of the major species along with data on their latitudinal ranges.

Climate and topography

The general distribution ranges shown in Table 2 indicate limits from approximately 70°N to 50°S for the listed species. They are concentrated in the Northern Hemisphere, reflecting the fact that this hemisphere contains the most extensive continental shelves. However, this conclusion is biased since 90% of the exploitable area, the oceanic waters, remains almost unknown.

The species groups, including (1) the loliginids, (2) the ommastrephids and other short-finned squid and (3) the octopuses and sepioids, while partially overlapping, generally occupy distinct marine habitats (Table 2). The first group, being fundamentally temperate-water-adapted species occupies the epipelagic zone on the continental shelves (neritic). The epi- and mesopelagic ommastrephids, which include neritic and oceanic species, have a much broader climatic range from sub-boreal to temperate and tropical waters. Other short-finned squid, exemplified by *Gonatus fabricii*, are mesopelagic to bathypelagic, occurring from boreal to temperate zones, including the deeper oceanic areas. However, some ommastrephid squid also show a much narrower distribution. Examples are *Ommastrephes bartrami*, *Nototodarus sloani* and *Symplectoteuthis oualaniensis* with ranges from about 20°S to 20°N in the North and South Pacific and the Indo-Pacific Ocean, respectively. The octopuses are benthic animals in tropical and temperate areas. They are also most common in the Northern Hemisphere associated with its continental climatic conditions and more extensive continental shelves. Among sepioids, the species vary more in their latitudinal ranges but they are also tropical to temperate.

Table 2

Large-scale Oceanographic Features and Fisheries in the Atlantic and Pacific

Fisheries can be characterized topographically in relation to continental shelf or slope regions or hydrographically, in relation to upwelling or open-sea areas. In both the North Atlantic and North Pacific Oceans the strongest major currents occur along the western boundaries: the Gulf Stream in the Northern Atlantic and the Kuroshio in the Northern Pacific. They are mainly associated with slope and open-sea fishery areas. These currents are narrow and high-speed, flowing polewards. In contrast, along the eastern boundaries, broad slow-flowing currents flow equatorwards. In spite of these general shared features, the two oceans are markedly different in topography and distribution of climatic areas. The Atlantic Ocean is smaller, about one-half of the area of the Pacific but the corresponding continental shelf is 1.5 times greater in area. The fact that the warm Gulf Stream in the Atlantic moves more northwards towards the coast of Norway compared with the Kuroshio which flows in a more easterly direction, also produces climatic differences. During the Winter no ice covers the Norwegian Sea and the Southwestern Barents Sea. In contrast, in the Pacific, the corresponding areas north of 50°N are completely ice-covered during Winter. The mean temperatures at corresponding latitudes are also different. In the Atlantic Ocean at the 0 and 30° meridians the temperature of the upper layer at 60°N latitude varies annually by only 4.5 - 5°C (from 5 - 7°C to 10 - 12°C) whereas, in the Pacific Ocean within the Bering Sea at 180°W it varies by 10°C (from -1.7°C to 8°C) (Rass 1959).

The eastern boundary currents are associated with shelf regions and major coastal upwelling systems such as California and Peru in the eastern Pacific and the Canary and Benguela currents in the eastern Atlantic. The mixing between surface and deep water in the upwelling coastal regions results in high biological productivity. The upwelling ecosystems show particular features in their faunas, including a high ratio of pelagic to demersal species in the commercially exploited biomass. In these areas pelagic species seem to have developed life-history strategies which take advantage of upwelling events which are relatively unpredictable in space and time.

The western-boundary currents although geographically variable, can be considered to be relatively persistent in both space and time. At the western boundaries, the life history of cephalopod species may be defined by the linkage in time and space between the rich feeding areas which develop during a short period in cold northern waters and spawning in the warmer southern areas. The larger populations of commercially important ommastrephid squid (Illex and Todarodes) appear to be associated with these areas where they are also the dominant cephalopod species. In contrast, at the eastern boundaries, the cephalopod fisheries constitute an association of several species typically dominated by the loliginids or, in some cases, by octopods and sepioids.

General aspects of cephalopod biology

In spite of their biological and commercial interest, cephalopod populations are far from being completely understood and many aspects of their biology remain obscure. One difficulty is the fact that being in general short-lived animals, the classical methods employed for population studies are insufficient for cephalopod population analysis. Ageing techniques were not validated until recently. The distributional ranges are diffuse and complicated by complex movements including daily vertical displacements. Confusion still persists about cephalopod taxonomy. Morphological aspects such as texture and shape make them difficult to standardize in terms of comparable morphometrics. These produce errors, both in systematics and in population studies. As a consequence, no proper standardization for sampling methods exists and the resulting data, in particular field data, are in most cases difficult to interpret. Table 3

The relatively well-studied species, Todarodes pacificus and Illex illecebrosus, have provided important biological information. Other cephalopods have been studied persistently over the years in the Mediterranean Sea (Mangold 1963). Table 3 summarizes some of the available biological data. In general, cephalopods live for one or two years; longer-lived species or individuals are rare. They are reproductively monocyclic and they die after spawning. Differences arise mainly in relation to the migratory and distributional ranges, spawning seasons and areas and habitats, from pelagic to bottom spawners and from inshore shallow-water to offshore deep-water spawners. The fecundity also varies from species to species and probably within species. The estimates for some species are based on few field observations or on experimental work (Coelho et al 1982; Durward et al 1979; Lipinski 1973).

The growth rates appear to be high but they are very difficult to summarize since growth is also dependent on food availability. Experimental work has shown that cephalopods achieve high growth rates if they are continuously fed (O'Dor et al. 1979). The growth rates also vary from juvenile to adults and are dependent on temperature. Typically, mature adults do not appear to feed, but this is not universal (Macy 1982).

Major currents of the Northwest Atlantic and Northwest Pacific and squid ecology

The Gulf Stream and the Kuroshio

These currents are narrow and swift, extending to great depths and flowing generally poleward. They differ markedly from the broad, diffuse and slow

equatorward flow along the eastern boundaries such as the California Current. The western current speeds are higher (200 cm/sec) compared with those of the eastern currents (20 cm/sec). The principal flow of both the Gulf Stream and the Kuroshio is confined to a band 10 km wide or less with a higher slope than in eastern currents. The two currents are considered to be analogues (Walsh 1977) in producing large-scale effects such as temperature anomalies in the North Atlantic and North Pacific oceans.

The Gulf Stream is characterized by high horizontal temperature and salinity gradients. A decrease in salinity (from 36.5‰-36.1‰) and in temperature (18-14°C at 200m to 17-10°C at 400-500m) is observable in the Gulf Stream between the Sargasso Sea and slope waters. Decreases in salinity and temperature also occur in the zone directly adjacent to the northern edge of the Gulf Stream (transitional zone) with values of 35.8-36.4‰ and 13-17°C to 35.1-35.2‰ and 10-15°C corresponding to the transitional zone and the slope water, respectively.

The Kuroshio is characterized by high surface temperatures during Summer (25-27°C) and an average salinity of 35‰. Because of the excess of precipitation over evaporation which is generally found north of 45°N in the North Pacific, the salinities in the upper layer are around 33.0‰. In the Sea of Japan the range in salinity is lower compared with the Northwest Pacific. Another aspect which might be of interest to the bathymetric distribution of squid is the fact that the Kuroshio flows at a distance of only 140 km from the coast of southern Japan. Also, as a result of topographical conditions, the Kuroshio branches to form the Tsushima current, flowing northward along the west coast of Japan (Fig. 2).

Both currents are very complex systems. In addition to the features already referred to, the occurrence of warm eddies and counter-currents of deeper cold waters have been described in more recent studies. The intrusions of deep cold water - the Labrador Current and the Oyashio in relation to the Gulf Stream and the Kuroshio, respectively - generate areas of plankton richness. The high productivity of these areas is related to the more intense vertical mixing.

Data on primary and secondary production are scarce in the Northwest Atlantic area and almost restricted to local inshore areas. On the contrary, for the Kuroshio, the Oyashio, and the Japan Sea, the existing information clearly distinguishes seasonal and spatial differences. The Oyashio region differs from the Kuroshio primarily because the latter mixes vertically at greater depths. In the Oyashio, mixing extends beyond the euphotic layer, but is then halted by the permanent halocline at depths of about 200m (Gulland 1971). The zooplankton biomass in the Oyashio is also higher during the Summer. In the Kuroshio current this seasonal pattern in zooplankton biomass is not evident. The low seasonal variability in plankton biomass is probably similar to the situation in the Gulf Stream. Compared with the Sea of Japan, the offshore areas have a much earlier phytoplankton bloom. In the Sea of Japan, zooplankton biomass in Summer is higher in the north than in the south, but less than in the Oyashio. In the central part of the Sea of Japan greater vertical mixing is identified with the transitional zone. The interaction of the warm Tsushima current and the cold Liman current, added to the continental shelf effect, produces zones of local upwelling.

Comparative ecology of *I. illecebrosus* and *T. pacificus*

These species constitute, in the context of this review, the well studied species related to the western-currents. The life cycles of both species are schematically shown in Figs. 1 and 2. These figures illustrate the similar latitudinal ranges, and the locations of the spawning grounds (known and possible) and fishery areas in relation to the current directions.

For *I. illecebrosus* in the Northwest Atlantic, a single population has been recognized, but the proposed life cycle (Squires 1967; Amarutunga 1982) remains supported only by data from juveniles through maturing adults. The spawning area has not been identified but the occurrence of larvae and juvenile has been associated with the Gulf Stream. A one-year life cycle probably includes offshore spawning (Fig. 1). Early in the season, during February, March and May, juveniles ranging from 1.1mm in mantle length are caught in the Gulf

Stream slope waters with a total distribution ranging from Cape Hatteras (North Carolina) to off the Grand Banks. Larvae of 8mm were collected in the upper layer near the Gulf Stream (Hatanaka et al 1982). Some juveniles (130-150mm) can be found in May in warmer waters around the Grand Banks, close to the continental shelf. The juveniles migrate to inshore Canadian waters during June or July. Growth is fast during this period (1.5mm/day), slowing before November when they leave the feeding areas for more offshore areas. Many of the males are mature in November although females are still far from sexual maturity.

In contrast to I. illecebrosus, T. pacificus in the Northwest Pacific is reported to include three sub-populations with different breeding seasons: winter, autumn and summer populations. These are separated on the basis of size composition, maturation and migratory patterns. The winter-spawning population is the major group which supports the fishery on the Pacific coast of Japan and in offshore areas. The autumn-spawning population supports the major part of the offshore fishery in the Japan Sea. The summer-spawning group is caught in restricted areas around Honshu in the Japan Sea.

The present discussion mainly focuses on the winter-spawning sub-population, which is the principal catch component and presents biological and abiotic features similar to those of I. illecebrosus. The winter-spawning group occupies the largest distributional range and also produces 80% of the total catches. It spawns between January and April in the East China Sea. Larvae and juveniles are presumed to migrate northwards along the Pacific coast in association with the Kuroshio current and with the Tsushima in the Sea of Japan (Okutani 1977) (Fig 2). The summer fishery, based on the winter spawners around Honshu and Hokkaido at about 40°N, is directed to animals averaging 250mm in mantle length. Uda (1959c), cited by Laevastu and Helda (1970), lists several hydrographic indicators associated to favourable fishing grounds for this squid, such as slack tidal currents and eddies with upwelling.

A comparison between the dominant populations of both I. illecebrosus and T. pacificus suggests similarities with respect to spawning season, migratory pattern and the strong current system hypothesized to be associated with the transport of larvae and juveniles. Also, for both, the major fishery grounds are in areas where cold water masses from the north meet with warm water from the south. However, the particulars of each system produce specific biological features. The main difference between these two areas is the existence of the semi-enclosed Sea of Japan in the Northwest Pacific. The influence of the surrounding land masses and the isolation from the open ocean by shallow sills cause larger fluctuations in temperature and salinity. Additional distinctions relate to the bottom topography. The South Honshu Ridge influences the flow pattern of the Kuroshio by the development of a large-scale eddy accompanied by some upwelling (Gulland 1971).

The complex population structure of T. pacificus seems to parallel the complexity of the major physical events in its area of distribution. The fact that the most intense flow of the Tsushima current occurs in September might be of some advantage for the transport of young squid arising from summer-spawning. The existence of small counter-clockwise currents flowing between the warm boundary of the Tsushima and the Liman current may result in the narrower spatial pattern of the summer subpopulation. The lower abundance of this group is probably due to the smaller size of the corresponding distributional area. The autumn and winter subpopulations make use of the more productive Oyashio, which is an area of intense vertical mixing and consequent zooplankton richness. The countercurrents along the Pacific coast probably aid the migration of maturing adults towards the south.

Similar associations between the life history features and physical oceanographic regimes can be identified for I. illecebrosus. The convergence between the Labrador and Gulf Stream currents occurs in the vicinity of submarine banks off Nova Scotia and Newfoundland. These represent areas of local upwelling due to the convergence of slope water, water from shallow areas and intrusions of deep, cold water from the north. These areas form the main feeding grounds of Illex. Furthermore, within the range of the species there is an environmental gradient defined by varying conditions of temperature, salinity, photoperiod and food availability. This might explain the existence of groups which do not conform to the one-year winter-spawning cycle. Such environmental influences could be reflected in variable growth rates resulting in the presence of several cohorts within a year class (Mesnil 1977; Lange 1981).

These subgroups have been mostly identified in terms of length-frequency data. A better knowledge of the population reproductive structure over time is fundamental for determining the importance of each cohort in the Illex stock/s.

The California Current and the ecology of *L. opalescens*

In view of the preceding systems, this is a contrasting situation whose analysis may aid in understanding the different trends in squid biology which represent adaptation to different physical environments. In this area there are no large populations of ommastrephids, a situation which is similar to that of the counterpart North/Central East Atlantic. Here, as a consequence of competition with a larger number of pelagic fish species, there does not exist a marked dominance of a single cephalopod species. Due to the fact that the shelves at the eastern boundaries are much narrower (about 20 km), the exploited squid are mainly coastal loliginids. The well studied species in this area is *L. opalescens* which is distributed from middle Baja California northward to Southern British Columbia. The California *L. opalescens* fishery, in the north, is directed towards spawning schools located in a very small area in the southern bight of Monterey Bay. In the south, the fishery uses their strong positive phototaxis to catch squid with lampara nets and lights.

The California Current

This current originates in cold waters carried from the Northwest Pacific and turns south in the West Wind Drift which is blocked by the North American Continent. The southward flowing current, aided by the predominantly north and northwest winds, produces strong upwelling along the coast, with a peak in summer (April-May off Baja California, and progressively later further north/-August off Oregon). When the winds weaken during winter a coastal countercurrent is present at the surface. The high latitudes, from which the California Current flows, are regions where precipitation exceeds evaporation (Wooster 1980). This results in relatively low surface salinity (33.0 to 34.0‰) which is later modified during upwelling events bringing higher salinity water to the surface. Near shore salinity generally increases with depth. The inshore countercurrent, the Davidson Current, flowing poleward during winter from near the top of Baja California to 45° N, also carries warmer and more saline water. There is a significant seasonal variation in the along-shore component of the current referred to as 'dominant oceanic periods' (Fields 1965). In fall and winter, the mean component is northward, but the direction of the current is highly variable. During spring and summer, the mean is strongly southward, and the flow is hardly ever northward. Close inshore there are complex eddy systems which arise from local topographical irregularities and wind-pattern fluctuations.

With regard to the productivity of the area, the average values for the rate of carbon fixation are high (Gulland 1971). The area is also characterized by high standing crops of zooplankton. However, zooplankton was shown to have a cyclic pattern in biomass fluctuations from north to south (Bernal 1979; 1981). This variability was suggested to be more related to the transport from the north (California Current-transport) than to regeneration of nutrients resulting from local upwelling. The offshore extent of zooplankton enrichment is about 200-300 km which is wider than the zone expected to be influenced by coastal upwelling processes.

The ecology of *L. opalescens*

In the south spawning takes place mainly at night on the bottom of shallow inshore grounds during the winter (December to March). In the North (Monterey Bay) it occurs between April and November with a peak in May and June. In some years, this northern population has shown less pronounced peaks during November. The sex ratio of schools is close to 1:1 (Fields 1965). The size (mantle length) at maturity is variable, from 81 mm (April) to 140 mm (November). Fecundity is close to 10^3 to 10^4 eggs per individual. The rate of embryonic development is three to four weeks at 16°C. A mean growth rate of 4mm per month was suggested (Fields 1965) but this figure is probably

underestimated according to statolith readings (Spratt 1978). Squid feed mainly during the day on Crustacea, including Euphausia and fish, the most common species being Engraulis mordax.

Fields (1965) and Karpov and Calliet (1978) suggested that cannibalism in the spawning population is a behavioural response to the high density that occurs during schooling of the mature adults. Larvae are probably dispersed by currents because juveniles have been found in the more offshore neritic habitat. The migration is probably restricted to movement from inshore (spawning) to offshore (feeding) grounds (Fig.3). Large scale migrations seem to be in consistence with the metabolic rates estimated from laboratory work (O'Dor, 1983). Population size, as indicated by catch statistics records (Fields 1965), has been shown to fluctuate in time. The highest annual catch was obtained in 1946 (19,012 t); between 1970-1980 they ranged from about 6,000-19,000 t.

The Monterey area is described by Fields (1965) as having noticeable seasonal events related to the current system: an upwelling period from March to August, followed by an oceanic period during September to October and the Davidson Current period, from November to February. In Southern California the upwelling has a peak in April-May. This area is also characterized by marked fluctuations of different sorts (wind, stratification, tides) as well as the existence of a counter-clockwise eddy in the shelter of Point Conception and the channel Islands of Southern California (Fields 1965).

The major group of squid in the Monterey area consists of mature animals which spawn inshore during the March to August upwelling period. A second group, spawning in November does not consistently appear in the samples. Fields (1965) suggested that it might originate from the Baja California population in the south. The southern population spawns during the winter, a similar time to the inshore Davidson Current. It would be possible for northern transport of larvae and juveniles to occur in conditions where short periods dominated by this current coincide with the squid post-spawning period. Failure of this mechanism of transport and mixing between northern and southern groups is explained by the interference of the counter-clockwise eddy which would favour retention or offshore transport, thus reducing possible northward movement. A scheme of L. opalescens movements in the California Current area is hypothesized in Fig.3. This scheme clearly emphasizes the possible mixing between southern and northern population groups, as well as the existence of more than one cohort in each one-year cycle due to different routes. These routes could represent alternative strategies depending on the physiological condition of squid and the physical conditions prevailing in the area.

Discussion and conclusions

All cephalopods seem to have relatively short life spans, wide prey spectra, high growth rates, no 'true' larval stage and monocyclic reproduction. They vary in population size, areas occupied, mobility and reproductive effort. Despite the limitations in the amount and quality of biological information (Table 3), a comparison between benthic and pelagic cephalopods is possible, considering a possible balance between the high growth rates (based on adult size) and locomotory costs. However, the size of large benthic animals (Octopus for example) can also be attained by some pelagic species such as Todarodes sagittatus and Dosidicus gigas which have high locomotory costs. This suggests the existence of alternative strategies selected by conditions for rapid growth (food availability, temperature and mechanisms of passive transport such as strong currents) or extended life span. The alternative strategies would be balanced by the size at maturity and breeding costs which also vary widely.

Considering the existence of these possible trade-offs and the lack of ageing data in cephalopods, it is impossible to state that size is directly related with sedentary behaviour or to life span. However, it is reasonable to suggest that part of the observed phenotypic variation simply reflects the plasticity of these species in response to different conditions of food supply, temperature and other abiotic conditions such as currents which can provide low cost transport (for example the Kuroshio and the Gulf Stream) or conditions for dispersal or increased productivity (California Current). Benthic species or at least those species which lack a planktonic phase during early development are relatively independent of the current regimes. They could still take advantage

of areas of high productivity (upwelling zones) and optimum temperatures (temperate to tropical climates). Their limited mobility also requires them to select areas which balance the optimal conditions for spawning (protected sites) and growth.

The neritic species exemplified by Loligo, are much more mobile and characterized by relatively extensive horizontal and vertical movements. The available fecundity data for neritic species suggests higher numbers of eggs and smaller egg size compared with benthic species. No specialized brooding exists, but the encapsulated eggs attached to a substratum represent a good alternative for squid. Pelagic species, on the contrary, probably spawn within the water column. In this case, the egg mass structure could be associated with the dynamics of the water masses and water density. This may result in a higher mortality for the pelagic species which seems to be balanced by higher fecundity.

Pelagic species also present higher concentrations of animals than do neritic and benthic species and seem to suffer greater fluctuations in abundance. In part, this could be related to the fact that they are associated with larger and stronger physical systems which are more stable compared with the relatively unpredictable coastal environments. This stability provides conditions for dominance by one species and the fluctuations in abundance are the reflection of environmental changes, such as temperature anomalies. On the contrary, an unstable environment where competition is high permits the existence of several species with less pronounced variations in abundance due to the fact that the species became less sensitive to the environmental changes.

The systems analyzed in this study appear to present biological and physical features which conform to a general trend. L. opalescens in the California Current exhibits differences in spawning seasons between the extremes of the distributional area. The inshore/offshore components of each population (northern and southern) suggest an accommodation to the 'dominant oceanic periods' previously described. The northern population spawns during upwelling (Summer) followed by possible dispersion of juvenile stages during the period dominated by California Current. The southern population spawns during winter when the Davidson Current brings warmer and more saline water and provides a mechanism of transport of juveniles to more northern areas where mixing with the northern squid population would be possible.

The upwelling eastern boundary ecosystems show remarkable parallels in their faunas. The narrower longitudinal distribution of the dominant pelagic species in these areas may be an evolved consequence of intense competition with a small number of temperate pelagic fishes, including sardines, mackerel and hake, which are characterized by large populations. Apparently the Northeast Pacific shows less diversity in cephalopod species than the comparable Northeast Atlantic. However, the hydrographic pattern in the Northeast Atlantic is more complicated and the resulting diversity allows a more pronounced differentiation. However, cephalopod research in this area is still in the exploratory phase and further generalizations are not justified.

The other systems discussed refer to population structures (I. illecebrosus and T. pacificus) associated with larger distributional ranges. These ranges cover, for both the Gulf Stream and Kuroshio areas, temperate to sub-tropical latitudes without zones of important coastal upwelling. In contrast there are large submarine banks where productivity is very high during spring. These banks constitute very important feeding areas. However, in both cases the requirements for successful pelagic spawning oblige squid to perform long migrations to more suitable southern areas. The existence of strong countercurrents also accounts for the large distances covered by the maturing adults. The strong flows which characterize both ecosystems favour the effective transport of juveniles to the feeding grounds.

Thus, there are similar general trends within the two systems (Kuroshio and Gulf Stream) which reflect biological similarities. However, particularities of each physical environment also appear to be reflected in the biology of each species. In T. pacificus the existence of three subpopulations probably reflects the different degrees of association with the open-sea regime. As a geographic feature the Sea of Japan favours such population differentiation. Both the Sea of Japan and the NW Pacific have plausible mechanisms of larval transport, but they differ in the area occupied by squid, salinity, water mixing conditions and seasonal production cycles.

In spite of the topographic and hydrographic parallels in both areas, the bathymetric distributions of I. illecebrosus and T. pacificus differ significantly (Table 3). The proximity of the Kuroshio from the coast compared with the Gulf Stream, and the physical conditions of the Japan Sea account for such differences. Furthermore the existence of the Honshu Ridge in the Northwest Pacific and the semi-enclosed Japan Sea system favour the establishment of barriers among the three sub-populations of T. pacificus. If heterogeneity also exists in I. illecebrosus population structure, it may be accounted for by the distance between the offshore and inshore areas. Stock heterogeneity for short-lived species may be caused by protracted spawning arising from successive departures from the feeding areas. In addition, the summer-spawning in I. illecebrosus suggested to occur in the southern part of its distributional area could also be related to features of the production cycles.

Summer spawning could be followed by the autumn plankton maximum bloom, which is much weaker than the spring maximum one. Consequently, growth and investment for migration would be limited, and differences in size and maturity pattern would be expected.

More detailed information on the Gulf Stream regime would help to design more realistic hypothesis for the I. illecebrosus population structure. Very recent work (McWilliams 1983) has described the time mean circulation of the Gulf Stream, including the Bermuda Rise and Hatteras abyssal plain to the northeast Grand Banks. Heterogeneity in the whole area is shown by variations in velocity both vertically and horizontally (Fig. 1 of McWilliams 1983). This information strongly suggests possible differentiation between the southwestern and northeastern Grand Banks in terms of Gulf Stream dynamics and possible biological consequences.

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Table I. World Cephalopod Fisheries (based on data from Guerra and Gandaras, 1983)

Oceans	Atlantic						Pacific						Indian		Medit. Sea
	NW	NE	CW	CE	SW	SE	NW	NE	CW	CE	SW	SE	W	E	
Sectors	5703	16877	14681	13979	17756	18594	20476	7503	33530	57467	33312	16471	30198	29485	2980
Area fished km ² x 10 ³															
Continental shelf km ² x 10 ³	1260	1736	1370	480	1950	210	1950	965	3200	450	470	177	1640	1580	500
Prim. Prod. gC/m ² /yr	100-150	50-150	50-100	106-365	50-200	50-500	100-200	150	50-200	2.5-137	50-100	50-500	50-200	50-200	90
Fisheries yield T/km ² /yr	2.3	6.7	1.3	5.9	0.8	13.7	9.4	2.4	1.8	4.5	0.8	38.9	1.3	0.8	2.6
<i>Loligo vulgaris</i>															
<i>Loligo forbesi</i>															
<i>Loligo pealii</i>															
<i>Loligo opalescens</i>															
<i>Loligo brasiliensis</i>															
<i>Loligo duvaucelli</i>															
<i>Loligo edulis</i>															
<i>Doriteuthis bleekeri</i>															
<i>Loliguncula brevis</i>															
<i>Illex coindetii</i>															
<i>Illex illecebrosus</i>															
<i>Illex argentinus</i>															
<i>Todaropsis albaniae</i>															
<i>Todarodes sagittatus</i>															
<i>Todarodes pacificus</i>															
<i>Onnastrephes pteropus</i>															
<i>Onnastrephes bartramii</i>															
<i>Symplectoteuthis oualaniensis</i>															
<i>Natalodarus sloani</i>															
<i>Dasidicus gigas</i>															
<i>Gonatus fabricii</i>															
<i>Gonolopsis borealis</i>															
<i>Onychoteuthis banksi</i>															
<i>Thysanoteuthis rhombus</i>															
<i>Octopus maya</i>															
<i>Octopus vulgaris</i>															
<i>Octopus dofleini</i>															
<i>Eledone cirrosa</i>															
<i>Eledone macchata</i>															
<i>Octopus sp.</i>															
<i>Sepia officinalis</i>															
<i>Sepia esculenta</i>															
<i>Sepia pharaonis</i>															
<i>Sepia lycidas</i>															
<i>Sepietta japonica</i>															
<i>Rossia macrassoma</i>															
Catches 1979 MT x 10 ³	104	16	8	96	124	12	641	29	137	27	55	276	18	9	44
Estim. Potential MT x 10 ³	500	100	100	1000	500	1000	1000	100	500	100	200	1000	100	100	100

□ - loliginids
 ◊ - ammonastrephids
 ◊ - octopuses
 ◊ - sepioids

Table 2. Cephalopod Distribution and Marine Zoogeography

Species	Vertical/ Horizontal		Stratification		Topography			Latitude 60° N 0 S 60°	Currents	
	Pelagic	Horizontal	Demersal	Benthic	Neritic	Oceanic	Western		Eastern	
Cephalopods										
<i>Loligo vulgaris</i>										
<i>Loligo forbesi</i>										
<i>Loligo pealei</i>										
<i>Loligo opalescens</i>										
<i>Loligo brasiliensis</i>										
<i>Loligo duvaucelli</i>										
<i>Loligo edulis</i>										
<i>Doriteuthis bleekeri</i>										
<i>Lalliguncula brevis</i>										
<i>Ilex colideti</i>										
<i>Ilex illecebrosus</i>										
<i>Ilex argentinus</i>										
<i>Todaropsis eblananae</i>										
<i>Todarodes sagittatus</i>										
<i>Todarodes pacificus</i>										
<i>Ommastrephes pteropus</i>										
<i>Ommastrephes bartramii</i>										
<i>Symplectoteuthis ovalansalis</i>										
<i>Notarodarus sibani</i>										
<i>Dosidicus gigas</i>										
<i>Gonatus fabrici</i>										
<i>Gonatopsis borealis</i>										
<i>Onychoteuthis banksi</i>										
<i>Thysanoteuthis rhombus</i>										
<i>Octopus maya</i>										
<i>Octopus vulgaris</i>										
<i>Octopus doffleini</i>										
<i>Eledone cirrosa</i>										
<i>Eledone mochata</i>										
<i>Octopus sp.</i>										
<i>Sepia officinalis</i>										
<i>Sepia esculenta</i>										
<i>Sepia pharaonis</i>										
<i>Sepia lycidas</i>										
<i>Sepietta japonica</i>										
<i>Rossia macrostoma</i>										

Table 3. Biological Data on Some Important Cephalopod Species

Species	Life Span mo.	Horizontal Migration m.	Vertical Migration m.	Bathymetric Distribution m.	Temperature Range °C	Growth Rate mm./mo.	Length at Maturity cm.	Maximum Length cm.	Average Length cm.	Spawning Season	Fecundity egg number 10 ³	Egg size mm.	Incubation Days / °C
<i>Loligo vulgaris</i>	24-30	small	X	10-100	12-14			45-50	20-30	W-Sp-S	3-6	2 x 1.5	30
<i>Loligo pedelei</i>	24?	small	X	25-360	8-15	20		30-40	15-20	W-S	6	1.5 x 1.0	
<i>Loligo opalescens</i>	12-30	small	X	10-200		12	7-14	20-25	12-15	W-Sp-S	1-3?	2 x 1.3	20-30/13-18°
<i>Loligo forbesi</i>	12-30	small	X	50-200	10-20	27-37		90-100	30-40	Winter			30-40
<i>Loligo brasiliensis</i>	12	small	X					25-30	15-20	Nov.-Mar.			
<i>Illex illecebrosus</i>	12-18	very large	X	10-1000	1-25	45		30-35	12-25	Winter	20-30	0.6-1.0	
<i>Illex coindetii</i>	24	large	X	200-600	7-20			40-45	25-30	Feb.-Oct.		0.25-1.0	9-16
<i>Illex argentinus</i>	12-30	very large	X	100-300	-			35-40	12-25				
<i>Todarodes pacificus</i>	12	very large	X	30-200	5-20	45		50-55	30-45	S.-A.-W.	3-5		
<i>Todarodes sagittatus</i>	24?	very large	X	70-1000	1-25	22-76	10	70-80	30-40				
<i>Todaropsis eblanae</i>	12-24	large	X	20-600	7-20				15-20?	Feb.-Nov. Apr.-Dec.	5-10		
<i>Dosidicus gigas</i>	-	very large?		-									
<i>Gonatus fabricii</i>	24-30	large		100-4000									
<i>Ommastrephes pteropus</i>	-	large	X					40	20-25				
<i>Nototodarus sloani</i>	-	very large		80-800	3-28			40	17-40	Sp.-A.	2-20		20-65
<i>Octopus vulgaris</i>	12-24	very small		0-150	6-30			130-180	50-70	Feb.-Oct.	150	0.8-2.4	28/2.5°
<i>Octopus maya</i>	12-24	very small		1-50				130	50-60	Nov.-Dec.	1.5-2		40-90/20°
<i>Sepia officinalis</i>	-	small		5-150	10-25			40-45	20-25	Feb.-Oct.	0.2-0.5	8-9	80-90/15°

* Mangold, 1963, Guerra et Gandarás, 1983, Boyle, 1983

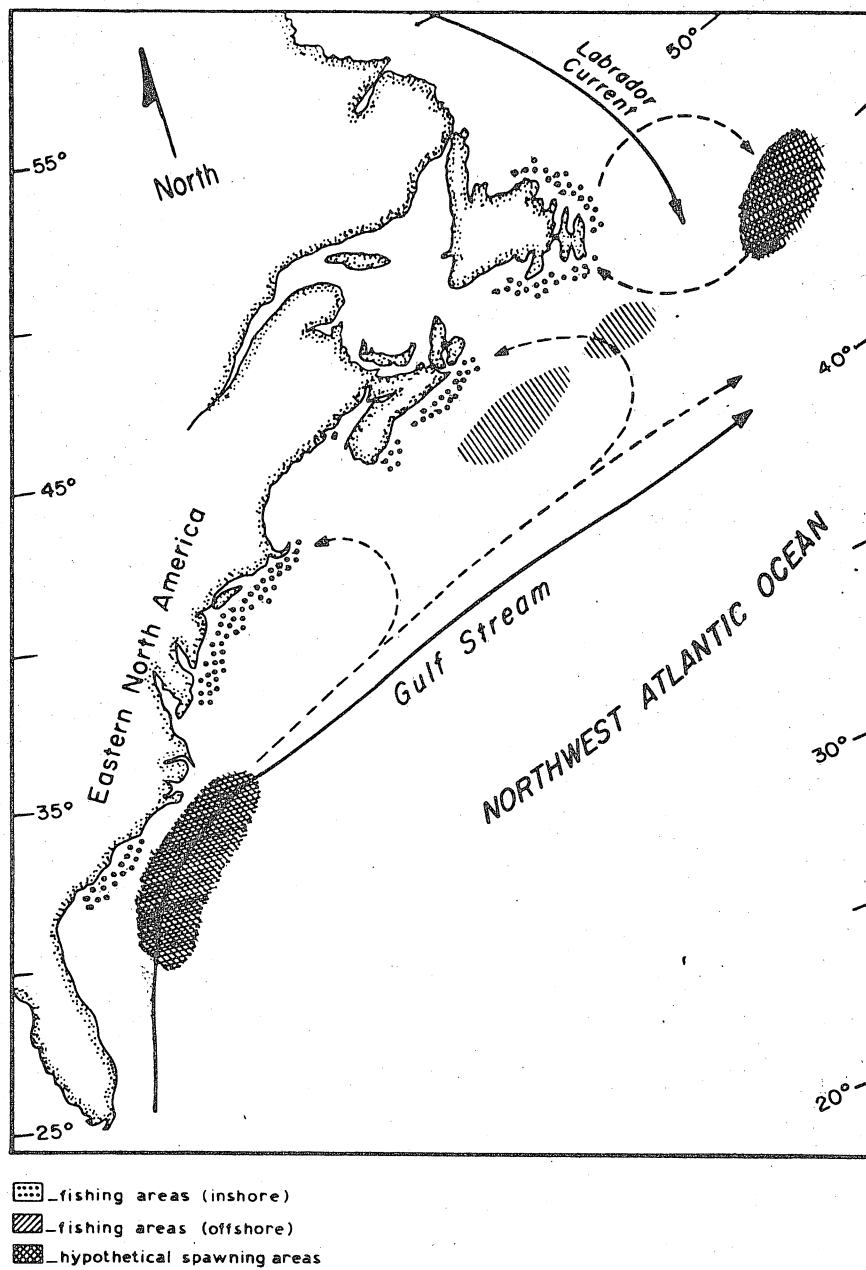


Fig. 1 - Hypothetical migratory routes, and spawning areas of I. illecebrosus. Fishery grounds.

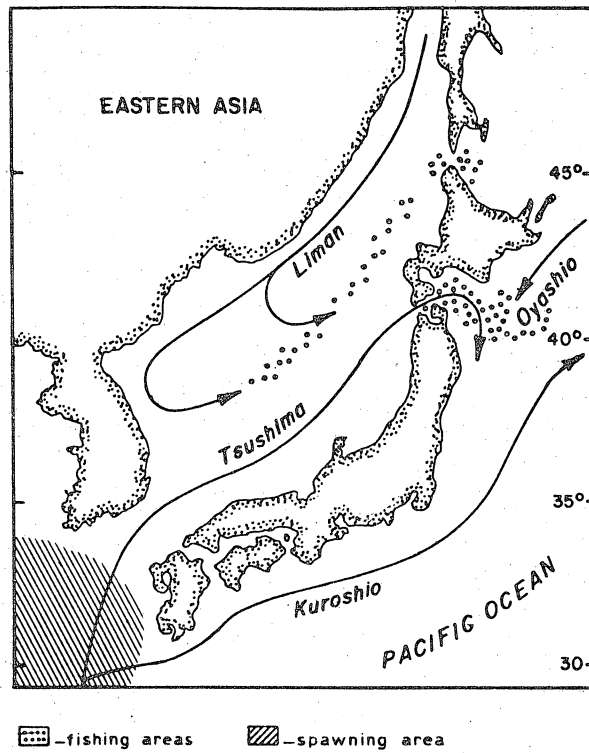


Fig. 2 - *Todarodes pacificus* migration routes, fishery and spawning areas.

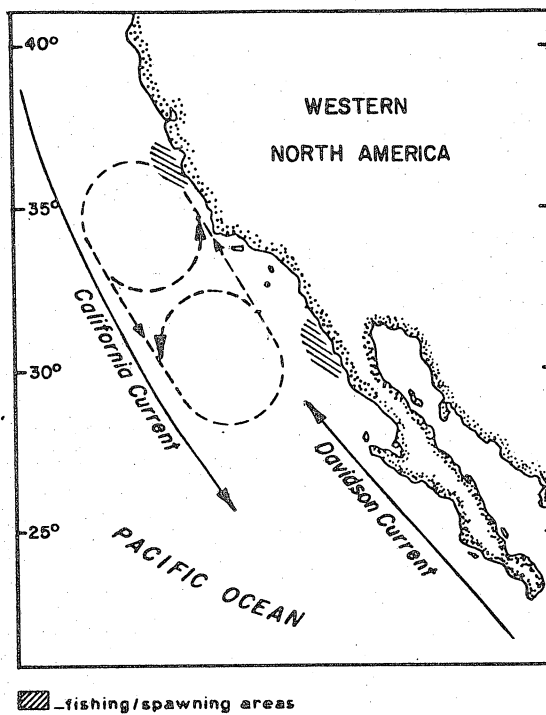


Fig. 3 - Hypothetical movements of *Loligo opalescens*.
Fishing and Spawning areas.