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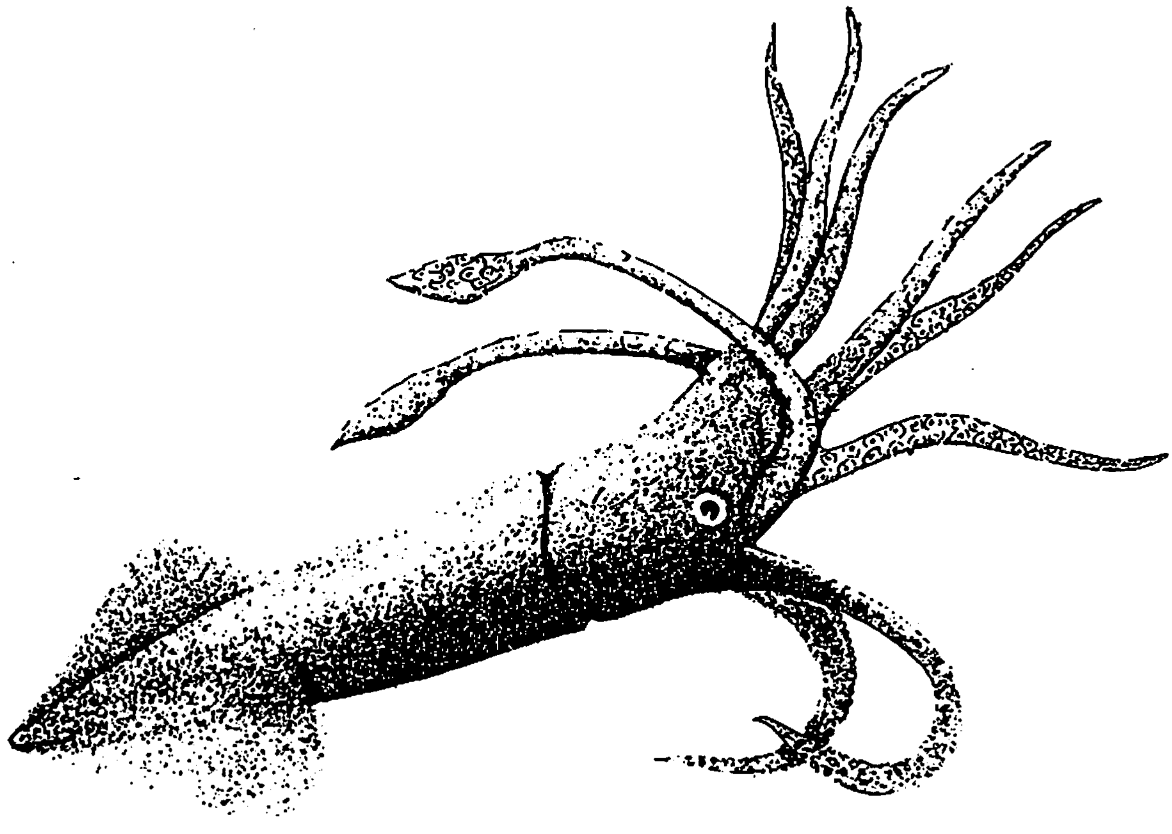
SQUID
A review of their biology & fisheries



G.P. ARNOLD

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SQUID - A REVIEW OF THEIR BIOLOGY AND FISHERIES

by G. P. Arnold

1. INTRODUCTION

Worldwide interest in squid fisheries remained at a low level until shortly after the second world war when the Japanese developed their fishery for Todarodes pacificus into a major industry. In 1960 this produced a peak catch in excess of 690 000 tonnes. Subsequently the Japanese have exploited squid in several other parts of the world and over the last two decades a major fishery has developed in the North-west Atlantic involving distant-water fleets from most of the major fishing nations.

Squid is not a traditional species for consumption in the United Kingdom but there is an assured export market for it in Europe. Its value is rising steeply and the volume of the UK catch is increasing. This leaflet reviews our knowledge of squid biology, surveys the major world fisheries and discusses potential resources. An FAO manual "Squid fishing from small boats" should shortly be available (Hamuro et al., in press).

2. GLOBAL IMPORTANCE AND SYSTEMATICS

Cephalopod molluscs, of which there are about 500 species, occur in all oceans of the world and are generally believed to form a major unexploited resource. The recent annual world catch is about 1.2 million tonnes and the potential catch is thought to be between 10 and 100 million tonnes (Gulland, 1971) or even greater (FAO 1975a, b) Present exploitation is limited to a few of the coastal and offshore stocks, in particular off the coast of Japan. The annual world catch of cephalopods consists of some 900 000 tonnes of squid, 190 000 tonnes of octopus and 60 000 tonnes of cuttlefish (Suda, 1973).

The cephalopods are all marine and closely resemble fish in much of their way of life. They occupy all the main zones of the sea from intertidal pools to the deepest and coldest waters of the open ocean. Many fossil forms had an external shell but, with the exception of Nautilus (Sub-class Ectocochlia), this has been lost during evolution. Modern cephalopods (Sub-class Coleoidea) retain only a small internal pen and are characterized by a large, fleshy body or mantle. Movement is by jet propulsion, most species are highly mobile and the faster forms obtain dynamic lift from large, horizontal fins. Water is taken into the mantle cavity and forcibly expelled through a siphon, which can be rotated so that the animal can move forwards or backwards with great rapidity. Cephalopods have well developed eyes and many are rapacious predators. All have an ink sac or reservoir containing a brown or black viscous fluid, which is ejected through the siphon when the animal is alarmed. The resulting cloud of ink forms an effective screen behind which the animal can escape. In addition it is believed that the alkaloids present in the ink can further confuse a potential predator by paralysing its olfactory sense.

Squid, cuttlefish and octopus form three of the four orders of modern cephalopods and, although they are classified separately, the squid and cuttlefish together are commonly known as decapods; the members of both orders have ten suckered appendages to the head. These consist of four pairs of arms and one pair of tentacles, which are often more than twice the length of the arms. Each order is divided into a number of families and those discussed in this leaflet are listed in Table 1. The squid are additionally divided into two suborders or superfamilies, the Oegopsida and the Myopsida.

Table 1 A classification of the cephalopods to show the families and genera discussed in the text, based on Clarke (1966), Packard (1972) and Herring (1977).

CLASS, CEPHALOPODA: SUB-CLASS, COLEOIDEA

(Order and suborder)	(Family)	(Genera)
TEUTHOIDEA	Squid	
OEGOPSIDA	Ommastrephidae	Ommastrephes, Illex, Todarodes, Nototodarus, Todaropsis, Dosidicus, Symplectoteuthis
	Onychoteuthidae	Onychoteuthis
	Gonatidae	Gonatus
	Architeuthidae	Architeuthis
	Enoploteuthidae	Abraliopsis
MYOPSIDA	Loliginidae	Loligo, Doryteuthis, Alloteuthis, Sepioteuthis
SEPIOIDEA	Cuttlefish	
	Sepiidae	Sepia
	Sepiolidae	Sepiola
OCTOPODA	Octopus	
	Octopodidae	Octopus

Octopus and cuttlefish are bottom living (benthic) organisms and, although there are some deep-sea octopods, most live in shallow coastal waters (Figure 1). Squid on the other hand are present at all depths in the sea (Voss, 1967). Myopsid squid are confined to shallow coastal waters (neritic) while nearly all the oegopsid families occur in the deep oceans. There they comprise a mesopelagic fauna in the "twilight zone" from 100 m down to 1 000 m and a bathypelagic fauna in the "sunless depths" below. The surface living oegopsids are very similar in habit to epipelagic (see Figure 1) teleost fish such as herring and mackerel. They are larger than most of the neritic squid and are fast swimming, voracious carnivores engaging in extensive migrations.

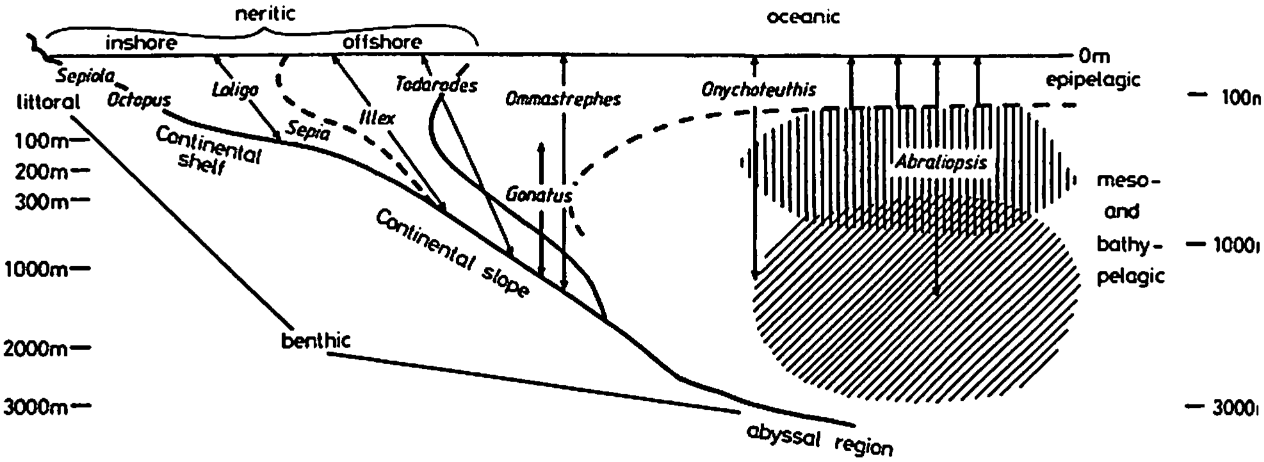

Figure 1 The depth distribution of cephalopods in the major regions of the sea (after Packard, 1972, modified according to Clark and Lu, 1975, and Roper and Young, 1975). |||||||||| = mesopelagic decapods; ////// = bathypelagic decapods.

Two families of squid, the Ommastrephidae and the Loliginidae, are extensively exploited. The loliginids are distinguished by a membrane covering the eye, which in ommastrephids is slit exposing the lens to the sea. Three quarters of the world catch of squid consists of ommastrephids. When fully grown these squid are found from the surface down to a depth of several hundred metres. Their mantle lengths generally range from 15-30 cm, although in some they may reach 60 cm*. Loliginid squid are coastal and their biomass (total weight of the stock in the sea) may not be particularly large. They occur sporadically and can probably only support local fisheries, but, on the other hand, they yield a higher quality meat than the ommastrephids (Suda, 1973). There are also local fisheries for a few species of the family Gonatidae.

Much less is known about cephalopods than fish and less about oceanic than neritic squid. Clarke's (1966) review of the systematics and biology of oceanic squid shows how little quantitative or even approximately quantitative information is available. Rather more is known about the growth and life histories of the four commercially exploited species of Loligo. A key to the identification of North Sea squid has been compiled by Grimpe (1925); Holme (1974) discusses the identification of the European species of Loligo. Figure 2 illustrates four species.

3. GEOGRAPHICAL DISTRIBUTION

Loliginid squid are distributed worldwide in tropical and temperate seas. Of the commercially important genera, Sepioteuthis is strictly tropical and two of its species are associated with coral reef regions. Doryteuthis is also primarily tropical and its most widely distributed species extends from East Africa to Japan. By far the most important genus is Loligo with fisheries for five main species: L. forbesi in Europe south to Madeira; L. vulgaris from Europe and the Mediterranean south to the Gulf of of Guinea; L. edulis in the Indo-West Pacific; L. pealii from New England to the Caribbean; and L. opalescens in California. Numerous other species, of local commercial importance, have more limited ranges (Voss, 1973).

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* Giant squid belong to the family Architeuthidae. The largest recorded specimen of Architeuthis had a mantle length of 3.3 m and a total length of 18 m (Clarke, 1966).

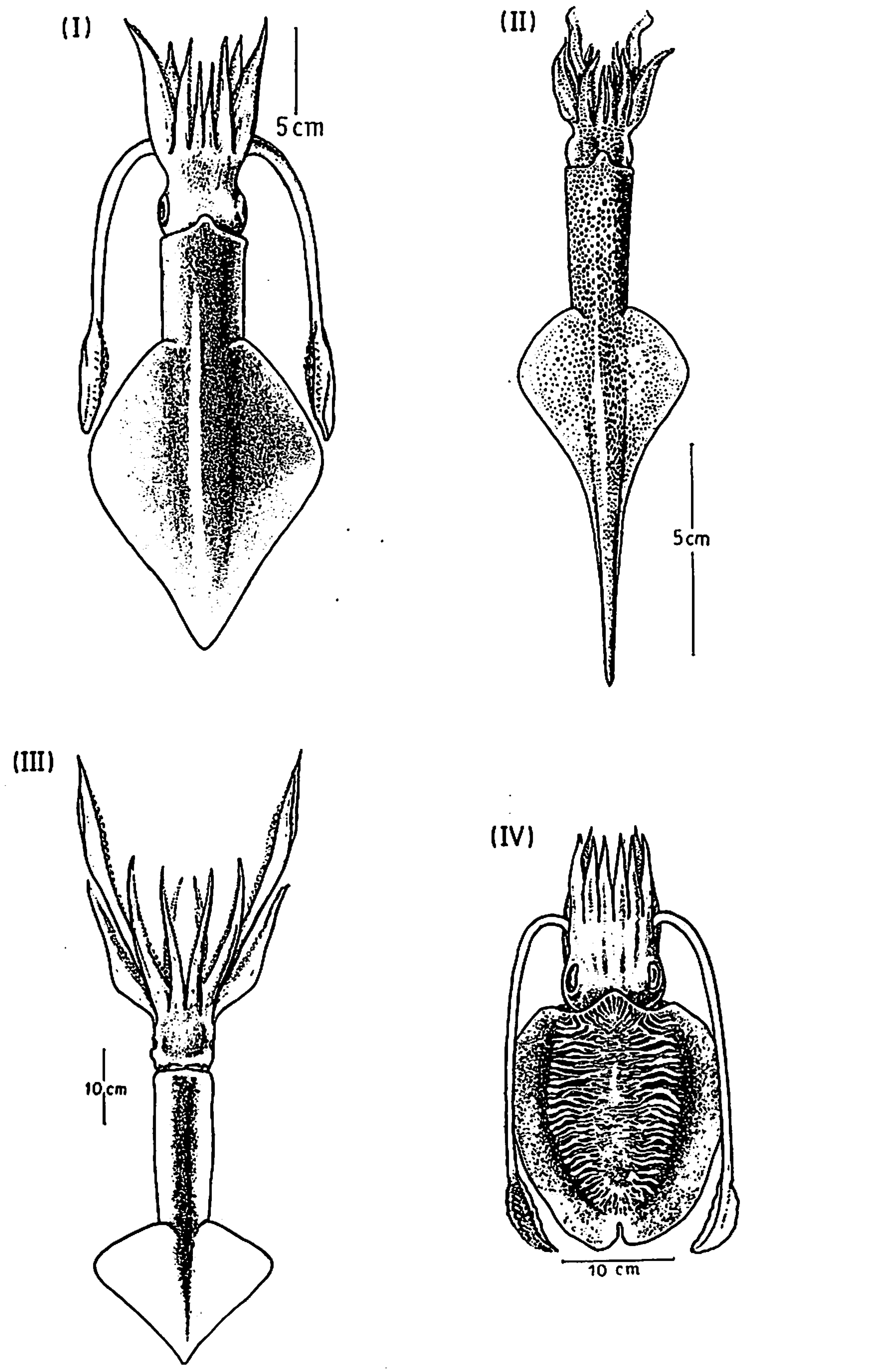

Figure 2 Some species of cephalopods from the North-east Atlantic: (I)-(III) the squids Loligo forbesi, Alloteuthis subulata, Todarodes sagittatus and (IV) the cuttlefish Sepia officinalis, (from Muus, 1963; reproduced by kind permission of the International Council for the Exploration of the Sea).

Ommastrephid squid occur in all seas and while some are totally oceanic others migrate inshore during certain seasons. The distribution of six species is shown in Figure 3.

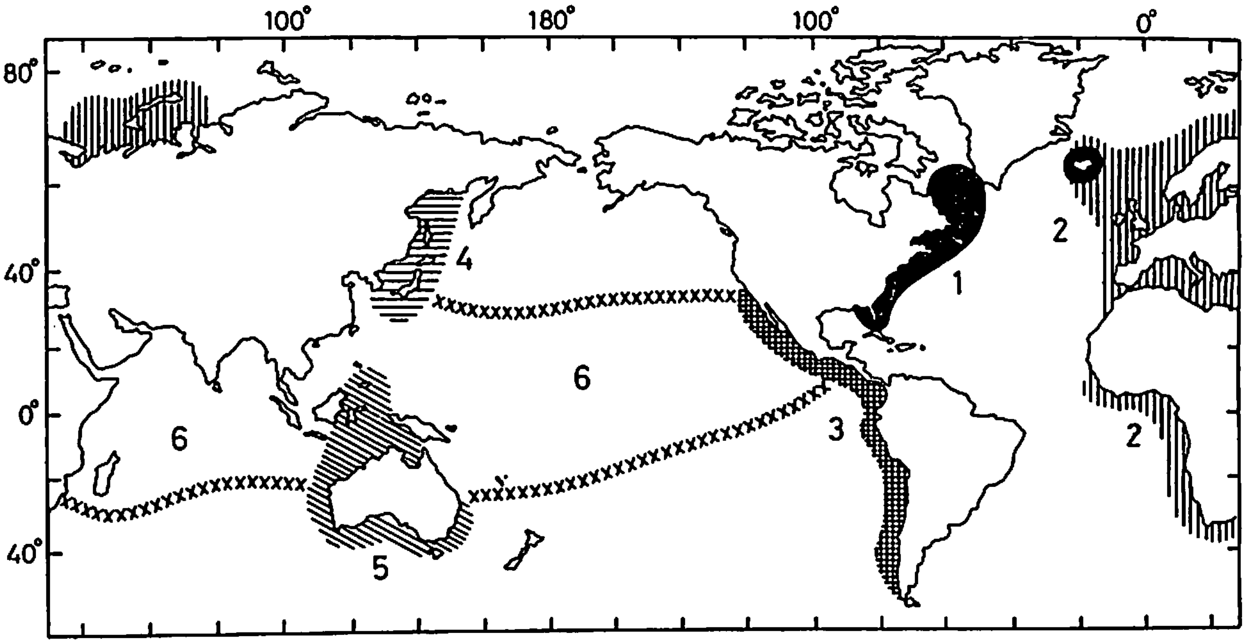

Figure 3 The world distribution of six species of ommastrephid squids (Suda, 1973):

(1) Illex illecebrosus; (2) Todarodes sagittatus; (3) Dosidicus gigas; (4) T. pacificus; (5) Nototodarus sloani gouldi; (6) Symplectoteuthis oualaniensis.

4. FISHERIES

The major fisheries for ommastrephid squid are shown in Table 2. By far the largest is the Japanese fishery for Todarodes pacificus, which takes some 500 000 tonnes annually and represents approximately 33% of the Japanese catch of pelagic organisms (Suda, 1973). There is a much smaller fishery in the North-west Atlantic for Illex illecebrosus and also one for Loligo pealii. There are small localized fisheries for other loliginids in various parts of the world.

Table 2 World distribution of fisheries for ommastrephid squids. Species marked with an asterisk are known to be abundant (modified from Suda, 1973)

Species	Maximum mantle length in cm	Area of occurrence	Fisheries
Illex illecebrosus*	25-28	Northern part of the Atlantic (continental shelf and slope)	ICNAF area 100 000 tonnes
Illex coindeti*	25	Atlantic Ocean	Gulf of Guinea by Japanese fleets
Todarodes sagittatus	47 (female)	Atlantic and Indian Oceans	Norway < 10 000 tonnes human consumption, and bait
Todarodes pacificus*	36	Waters adjacent to Japan	Japan, 500 000 tonnes by jig, trawl and trapnet
Nototodarus sloani sloani*	36	Waters adjacent to New Zealand	Japanese fleets 20 000 tonnes
Dosidicus gigas*	350 cm total length	Pacific coast of North and South America and Australia	Central America by Japanese fleets
Ommastrephes calori	61	North-eastern coast of the Atlantic and Mediterranean	Local fisheries; human consumption and bait
Ommastrephes pteropus	38	South Atlantic and Caribbean Sea	

4.1 Japan

There are three populations of the Japanese common squid, Todarodes pacificus, breeding independently in winter, autumn and summer and each with a life span of only one year (Murata et al., 1973). The main spawning ground of all three is in the East China Sea but, while the winter population is distributed all round Japan extending as far north as the Kurile Islands and Sakhalin, the autumn population is restricted to the western side of Japan and the summer population to the Pacific coast of south Honshu. The winter population is the most abundant and provides the exploitable schools in the coastal waters around Japan (Figure 4). The autumn population is the basis for the offshore fishery in the Sea of Japan (Araya, 1976a, b), which in recent years has involved approximately 3 000 vessels catching some 200 000 tonnes of squid annually (Kasahara, 1978). Together these two populations account for 90-95% of the total Japanese catch of T. pacificus. The timing and duration of each fishery within the overall area depends on the extensive feeding migrations of both populations (see Section 7.3). Good fishing grounds are found at frontal zones (where warm and cold water meet) and in areas of upwelling, where production is high and there are aggregations of zooplankton (Suzuki, 1963; Araya, 1976a, b; Kasahara, 1978).

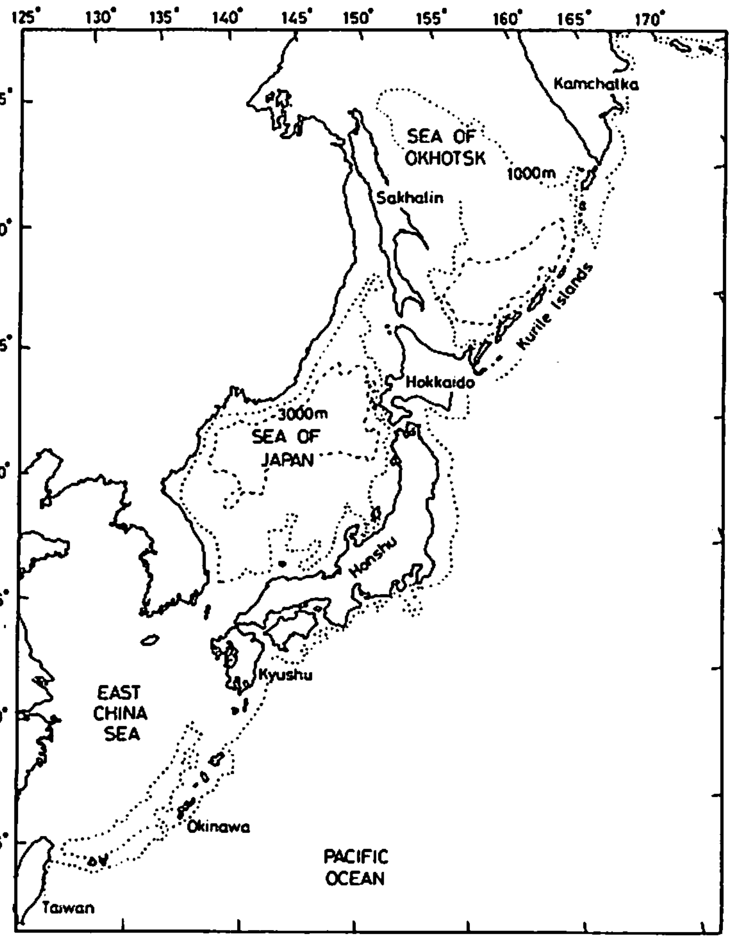

Figure 4 The fishing grounds for the winter population of Todarodes pacificus around Japan (after Araya, 1976a, b).

Catches of Todarodes pacificus have declined on the Pacific coasts of Honshu and Hokkaido in recent years. But since 1971 comparatively large quantities have been taken of two other oceanic squid (Ommastrephes bartrami and Onychoteuthis borealijaponicus) which were rarely landed previsously. Catches were 17 000 and 5 000 tonnes, respectively, in 1974. The relative abundance of these three species has fluctuated markedly from year to year, apparently governed in part by differing hydrographic regimes and temperature tolerances (Murata et al., 1976; Naito et al., 1977 (see Section 7.3).

There is a spring and summer fishery for the loliginid squid Doryteuthis bleekeri on the western and south-western coasts of Hokkaido. Annual catches have fluctuated widely between 250 and 2 600 tonnes over the last 20 years. The fishery is based on an annual migration and the squid are mainly caught by set nets as they congregate inshore to spawn in warm water (Araya and Ishii, 1974; Ishii and Murata, 1976).

In recent years the Japanese have begun fishing for various other squid in distant waters, beginning in 1969 with Loligo pealii in the North-west Atlantic (Rathjen, 1973) and Nototodarus sloani sloani off New Zealand in 1972 (Hamabe et al., 1976). Other species of interest have been Dosidicus gigas off the west coast of South and Central America as far north as Baja California since 1971, Illex illecebrosus in the North-west Atlantic since 1972 and I. coindeti off the west coast of Africa since 1974 (FAO, 1975a).

4.2 North America

Illex illecebrosus, the short-finned squid, and Loligo pealii, the long-finned squid, are both common on the continental shelf off the eastern seaboard of North America and both are reported to range as far south as the Gulf of Mexico and the Caribbean (Squires, 1957; Voss, 1971; Rathjen, 1973). There is an overlap of their distribution in the North-west Atlantic but Loligo is most abundant from Cape Hatteras to Cape Cod and Georges Bank, while during the inshore phase Illex is particularly abundant from Cape Cod to Newfoundland. Both species spend the winter offshore on the edge of the continental shelf migrating inshore in spring, Loligo to spawn and Illex to feed (Rathjen, 1973). Illex spawns at some time during the offshore phase probably beyond the edge of the continental shelf (Lux et al., 1978).

Loligo was caught in the late 19th and early 20th centuries in the coastal pound net fishery in southern New England; in Newfoundland there is a traditional inshore fishery for Illex for use as bait in the longline cod fishery. Since 1964, however, with the advent of the distant-water fleets (Tibbetts, 1977), there has been a rapid expansion of the squid fisheries in the North-west Atlantic. Known catches of Illex have increased progressively from less than 5 000 tonnes in 1970 to over 100 000 tonnes in 1977 (ICNAF, 1978). Illex is caught primarily on inshore grounds in the summer (Figure 5) and in 1977, 78% of the total catch came from ICNAF (International Commission for the North-west Atlantic Fisheries) subareas 2, 3 and 4. In 1976 and 1977 over 60% of the catch was taken by Canada and the USSR, with the rest accounted for by fleets from Cuba, Japan and various European countries (Table 3). Loligo is caught by the international fleet offshore in winter, when it is concentrated on the outer edge of the continental shelf in the mid-Atlantic Bight. The 1976 catch of Loligo at 22 912 tonnes (ICNAF, 1977) was approximately one third of the size of the Illex catch for the same year. Spawning Loligo are also taken inshore as a by-catch of small trawlers from the USA (Lux et al., 1974).

Although few of the many regular spawning concentrations along the Pacific coast are exploited (Longhurst, 1969), the Californian squid fishery for Loligo

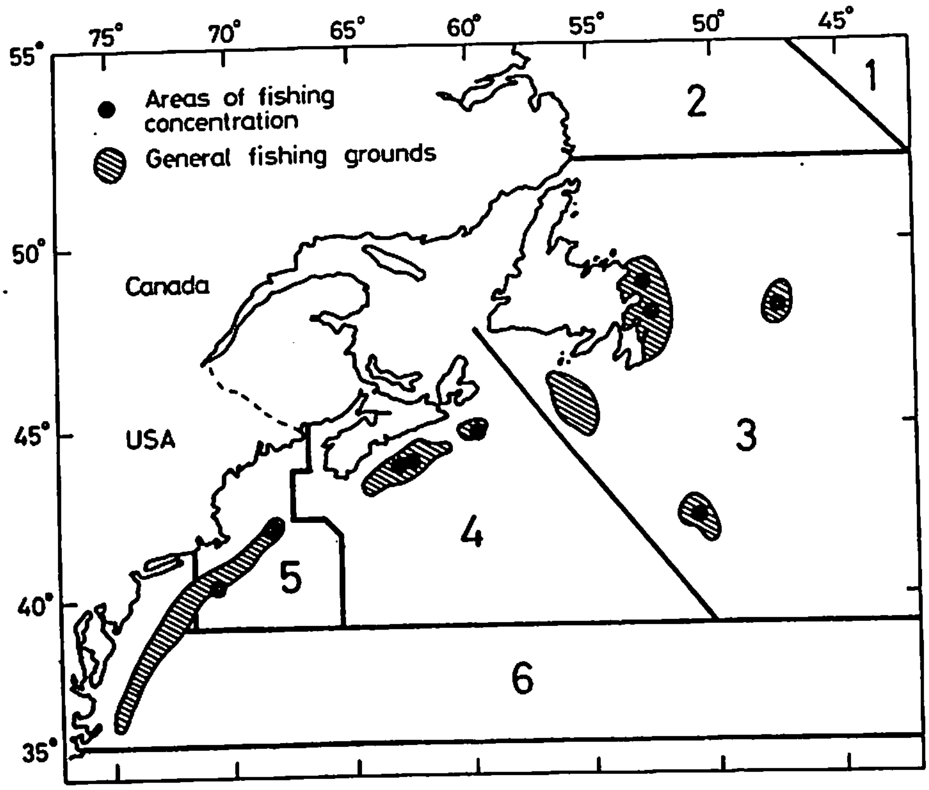

Figure 5 The fishing grounds for Illex illecebrosus in the North-west Atlantic (ICNAF, 1978). The boundaries of sub-areas 1-5 and statistical area 6 are shown.

Table 3 Nominal catches (tonnes) of short-finned squid (Illex illecebrosus) in ICNAF Subareas 2-5 and Statistical Area 6 by country, 1970-77 (ICNAF, 1978, Tables 1 and 2)

Country	1970	1971	1972	1973	1974	1975	1976	1977(1)
Bulgaria	-	80	479	364	420	196	1 034	2 962
Canada	80	1 623	26	633	82	3 293	10 926	37 712
Cuba	-	-	14	-	-	121	3 256	4 669
France	-	-	8	27	-	-	442	1 039
F R Germany	-	-	-	-	-	-	1 128	2 774
German D R	20	-	-	313	-	899	996	-
Italy	-	-	1 200	805	980	884	2 472	4 422
Japan	452	234	2 409	1 091	3 332	3 744	6 311	7 876
Poland	-	-	5 464	8 516	5 003	3 051	8 640	3 592
Portugal	-	-	-	-	-	-	264	-
Romania	-	-	-	-	6	48	9	1 054
Spain	1 636	3 324	4 878	3 784	7 034	2 472	4 997	10 893
USSR(2)	1 242+	7 226+	1 831+	8 992+	85+	13 634+	23 712	25 985
USA	408	455	472	530	148	107	229	1 016
Ireland	-	-	-	-	-	3 098	5 068	-
Totals	3 838+	12 942+	16 781+	25 055+	17 090+	31 547+	69 484	103 994

(1) Preliminary data

(2) USSR catches of squid in areas 5 and 6 for the years 1970-5 were 1 065, 6 138, 6 976, 8 977, 8 495 and 8 928 tonnes respectively; Loligo pealii and Illex illecebrosus were not distinguished.

opalescens accounted for about 90% of the US catch of squid up until 1971 (Ampola, 1974). This is a year-round fishery but maximum catches are taken each summer when the squid aggregate inshore in vast numbers to spawn (Fields, 1965). The fishery began about 1863 with the establishment of a Chinese fishing village at Monterey. Squid were taken in small purse seines, sun-dried and exported to China. In 1905 lampara nets (see Section 5. 2) were introduced by Italian fishermen, who took complete control of the fishing, although the Chinese and Japanese continued to dry and market the catch.

4.3 North-west Africa

One of the richest cephalopod fisheries in the world lies along the continental shelf of North-west Africa. The main fishing area is the Saharan Bank and the coast of Mauritania off Cape Blanc Bay. With the advent of Japanese trawlers the fishery has extended south and east into the Gulf of Guinea (Voss, 1973).

The Saharan Bank lies to the south-east of the Canary Islands and is heavily fished by medium-to-large stern trawlers from most European countries and the USSR. Three species account for most of the catch: Octopus vulgaris, the squid Loligo vulgaris and the cuttlefish Sepia officinalis. Octopus can account for up to 70% of the catch. Several other species of Sepia are caught and also three species of ommastrephid squid: Illex coindeti, Todarodes sagittatus and Todaropsis eblanae (Voss, 1973). L. vulgaris and Sepia are found at depths of 20-80 m, while the ommastrephids occur at depths in excess of 90 m (Porebski, 1970).

4.4 Europe

Squid, cuttlefish and octopus are widely caught in the Mediterranean and large catches of the ommastrephid squid Ommastrephes caroli, O. pteropus and Todarodes sagittatus are taken around Madeira both for human consumption and for bait (Rees and Maul, 1956; Clarke, 1966). In Norway (Table 2) there is a fishery for T. sagittatus which is used traditionally for bait in the longline fisheries. It has also been used for meal and oil (Wiborg, 1972) and more recently for human consumption (Wiborg, 1978). From 1948 to 1953 there was a Danish and Swedish fishery for Loligo forbesi in the North Sea and Skagerrak. It was conducted along the 200 m contour in the Norwegian Deep and in 1949, the best year, 1 300 tonnes were landed. The average annual catch of cephalopods for the North-east Atlantic is 12 000 tonnes, shared principally between Spain, Scotland, Norway and France (Kristensen and Broberg, 1978).

There has never been a significant British market for squid for human consumption but, with the advent of deep-freeze facilities and an export market in Europe, a Scottish fishery has developed progressively since 1954. Scottish landings reached a record 1 367 tonnes in 1971. The principal species is Loligo forbesi, the "common squid", which can grow up to 60 cm in length. A very few of the "small squid", Alloteuthis subulata, are marketed with Loligo. Other species such as Todaropsis eblanae and Todarodes sagittatus are sold cheaply as line bait (Thomas, 1973). Loligo forbesi is also of some economic importance in the English Channel and off the west coast of England and Wales. In recent years there has been a marked increase in the quantity of squid landed in the south-west of England and some small boats now fish specifically for squid. At Brixham and Newlyn, in 1977, squid accounted for some 3.7% of the value of all fish landed. The value of the total UK squid catch in 1977 was recorded as £770 000 (MAFF, 1978). In the statistical tables "squid" includes both squid and cuttlefish.

5. FISHING TECHNIQUES

5.1 Trawling

The directed offshore fisheries for Illex in the North-west Atlantic are conducted with bottom otter trawls and midwater trawls with cod-end mesh sizes of 40-48 mm. By-catches are lower in the midwater trawls and experiments with off-bottom trawls using hanging chains or bobbins indicate that it would be possible to fish selectively for squid with this type of gear (ICNAF, 1978). A trial trip in 1973 by a 92 m West German stern trawler fishing for Loligo on the edge of the western Atlantic continental shelf (36°N-40°30'N) in depths of 80-100 m, yielded catches of 2-3 tonnes per 3 h tow during the day but only 100-200 kg per 4-5 h tow at night (see Section 7.4). This vessel towed a 76 m footline Engel 3-bridle high-headline bottom trawl with a 50 mm cod-end mesh at a speed of 4½-5 knots (WFA, 1974). Most bottom trawl fishing for Illex in the ICNAF area takes place in depths of 100-200 m and maximum catch-rates are of the order of 30 tonnes per day (Tibbetts, 1977). Full details of the various trawls used in this fishery are given by Engel (1976) and Koyama (1976).

In Scotland the squid Loligo forbesi is taken principally as a by-catch in the white fish and Nephrops fisheries by inshore vessels - seine-netters and light trawlers - fishing in depths of less than 150 m. The grounds are off the east coast, in the Clyde and also at Faroe. In the Moray Firth some boats fished specifically for squid during the haddock scarcity of 1961-62. In the 1970's, however, there was a directed fishery for squid at Rockall by Granton trawlers using a modified "French" bottom trawl with a groundrope of 38 m and a headrope of 21 m. The mesh size in the belly of the trawl has been reduced from 135 to 100 mm and the cod-end has a 70 mm mesh, which retains 50% of Loligo of 11.4 cm body length. Haddock is the principal by-catch in this fishery.

These fisheries for squid are seasonal with peak landings in autumn and winter. At Rockall the fishery is a summer one with a peak in June; at Faroe squid are caught throughout the year but most abundantly in December. In 1970-71, when squid were particularly abundant, the average catch-rates for the appropriate peak season in these areas ranged from 150 to 470 kg/100 h fishing with a maximum of 31 000 kg/100 h fishing at Rockall (Thomas, 1973).

5.2 Roundhaul nets

The Californian squid fishery at Monterey employs a pelagic roundhaul net - the lampara – to catch schooling Loligo opalescens. The lampara, which is of Mediterranean origin, differs radically from the purse seine and its essential features are a large central bunt, graduated mesh sizes and no purse lines or rings. Both wings are hauled together (Scofield, 1951). A modern lampara net may have a central sack of small 30 mm mesh some 55-73 m wide by 46-55 m deep. Each wing is 73-119 m long tapering to a point with the meshes graded from 10 cm nearest the main net to 40 cm at the extremity. The weighted lead line along the bottom of the net is shorter than the buoyant cork line at the top and as the wings are hauled simultaneously the lower margine of the sack is drawn beneath the school. When the wings are inboard and the lead line has been raised the squid are entirely enclosed by the fine meshes. The large meshes of the wings ease the hauling of the net yet retain the squid, which avoid the luminescence induced by its strands (Fields, 1965). Purse seining was prohibited in this fishery in 1953 because the lead lines of the nets dragging across the sea bed uprooted the sessile egg masses laid by the squid. For various reasons attracting lights were banned in 1959 (Kato and Hardwick, 1976).

5.3 Jigging

Squid jigging is at present by far the most important method of squid fishing, accounting as it does for 95% of the Japanese catch. The squid jig is a type of grapnel usually about 10-15 cm long. One or two rings of barbless hooks project from the end of the shaft, which may pass through a lead weight (Figure 6) or a bait fish. Various designs of jig are described by Von Brandt (1972) and Ben-Yami (1976). The jig is jerked up and down and the squid takes it as it moves. The hooks may be baited or coloured for attraction but it is probably the contrast of the jig against the surrounding water rather than the colour that is important (Flores et al., 1978). Traditionally jigging is done by hand, but the Japanese have developed mechanized jiggers which can operate several lines simultaneously. Light attraction (see Section 5.4) is necessary.

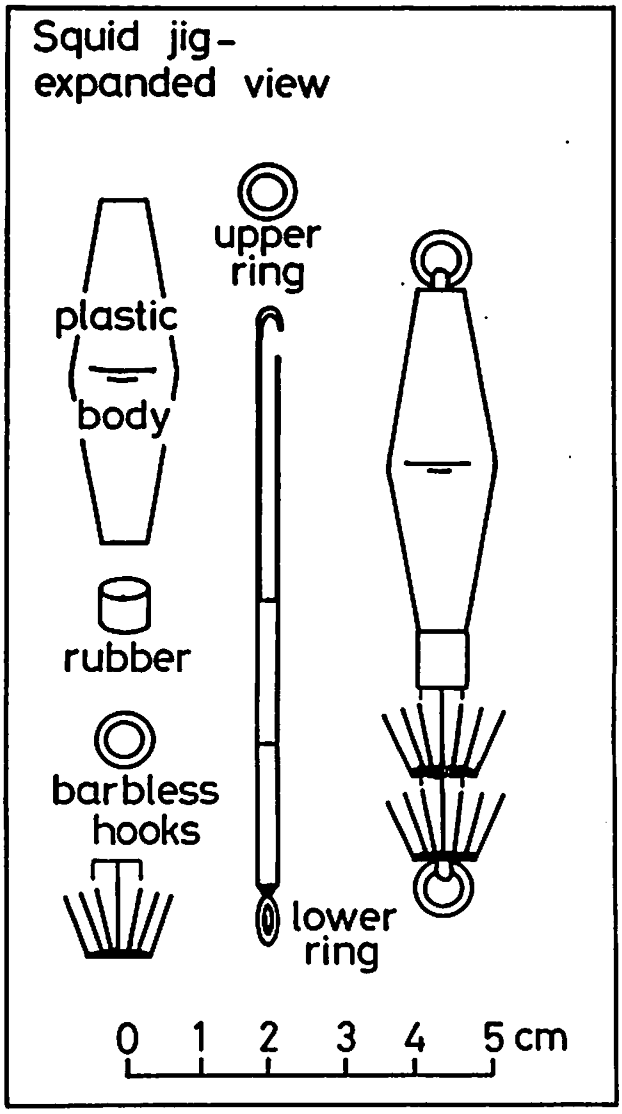

Figure 6 A typical squid jig. (WFA, 1976).

The essential components of a mechanical jigger are a metal frame supporting a sheet of wire netting fitted outboard from the gunwale of the boat, one or more rollers, and a hauling drum (Figure 7). Double-line jigging machines are usual, with the two hauling drums driven through a common gear box by a 1/4 or 1/3 h.p. electric motor or by hydraulics. Each monofilament line has up to 75 hooks on it and is run out to a depth of as much as 100 m by a sinker weighing 0.7-1.0 kg.

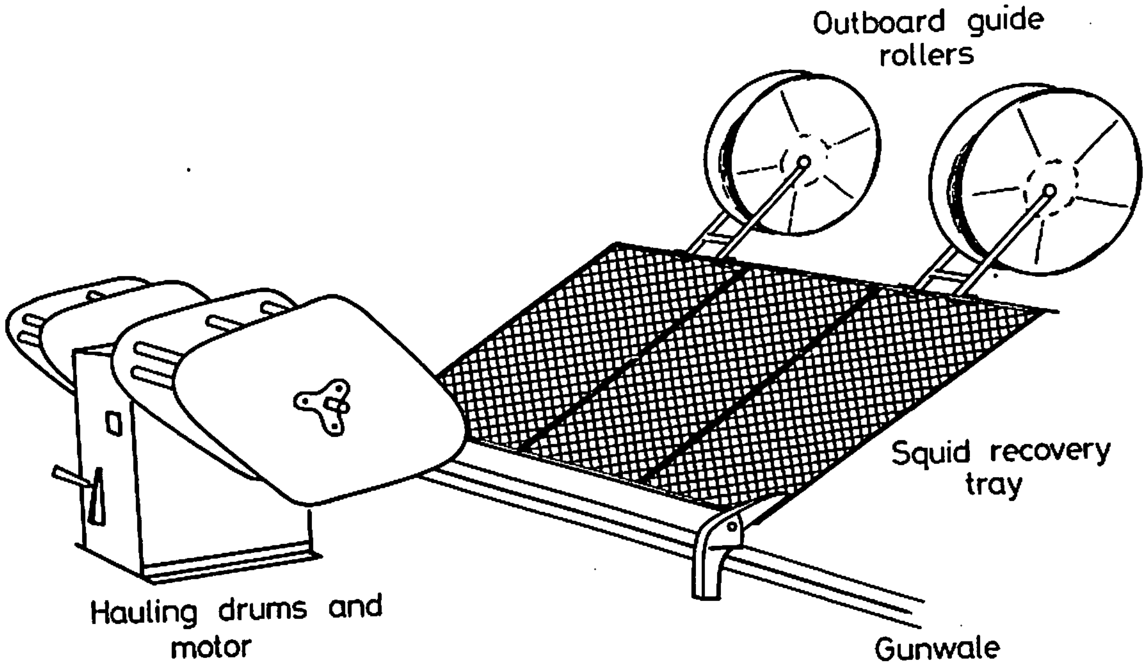

Figure 7 A typical double-line squid jigging machine. (WFA, 1975).

The hauling drum is usually oval or octagonal in section so that although the line is hauled at an average speed of 70-75 m per minute the jig moves in a series of more rapid jerks as it is hauled in (Suzuki, 1963; Igarashi et al., 1968). After passing over the outboard roller the squid unhook, drop onto the wire mesh and slide inboard into collecting baskets (Ben-Yami, 1976).

While handline fishing is still practised in some areas, the modern Japanese squid fishery is highly mechanized with some 30 000 jigging vessels of which 300 are over 100 tonnes (Kawahara, 1978). Distant-water vessels of up to 500 tonnes displacement carry up to 30 automatic jigging machines and are fitted with deep freezing and refrigerated storage facilities. Most vessels are, however, in the 50-100 tonnes range. A 100 tonnes vessel carrying 21 double-line jigging machines (7 on each side, 4 on the bow and 3 at the stern) can be operated by nine men (Hamuro and Mizushima, 1976) and remain at sea for 20-30 days (Kasahara, 1978). On the fishing grounds echo searching for squid schools starts in the late afternoon. Once the characteristic echo traces (Shibata and Flores, 1972; see Section 5.6) have been found, a marker buoy is dropped and the vessel allowed to drift with the current and remain with the school until fishing begins after dark. The catch rate usually increases around midnight with a peak between 0400 and 0500 h. Catches also fluctuate with the phase of the moon, the best conditions occurring during dark nights. Minimum catches are taken during the full moon period (Flores, 1972), presumably because light attraction (see Section 5.4) is then not so effective.

5.4 Light attraction

Squid are readily attracted at night to lights at the surface and the technique adopted by the Chinese, who originated the Californian fishery for *Loligo opalescens* at Monterey, was to row a skiff round the bay, with a blazing torch at the bow, until enough squid collected to be caught by a purse seine. Successful jigging depends completely on light attraction and modern Japanese vessels carry generators with capacities of up to 250 kW to operate their fishing lamps. The arrangement of the lights is simple but specific, consisting of a row of lamps attached to a pole or line stretched horizontally between the foremast and mizzen mast. The lights range in power from 1 to 5 kW and are commonly incandescent lamps, although mercury vapour lamps may be more efficient. Catches increase with light intensity up to a certain limit and a 100 tonnes vessel may have a generator with a capacity of 160-250 kW and as many as 40, 5 kW lamps arranged in two parallel rows (Ogura and Nasumi, 1976). The position of the lamps above the vessel, rather than over the water as in other light fisheries, is due to the behaviour of the squid, which aggregate in the boundary between the shadow of the ship's hull and the lighted zone. The position of this boundary in relation to the jigs is therefore of great importance and depends on the height of the lamps and their position in relation to the centre-line of the vessel (Figure 8a). In practice the height of the lamps ranges from 2.2 to 6.5 m. Underwater lamps attract more squid than surface lamps but fishing efficiency is not improved, probably because of lack of the appropriate shadow. They may therefore only be useful as an ancillary means of concentrating the squid (Ben-Yami, 1976).

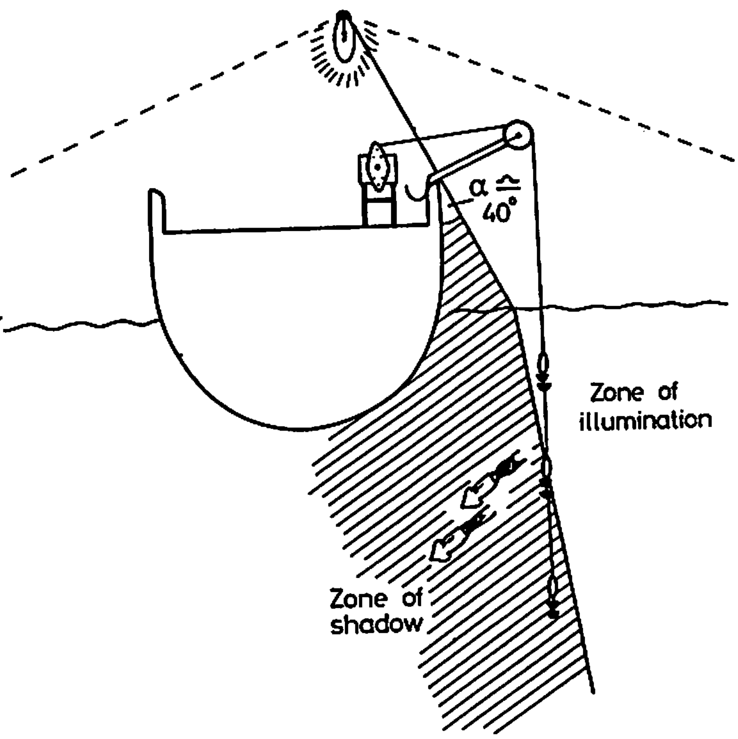

Figure 8a   Light attraction for jigging (WFA, 1976).

The mechanized Japanese jigging system with attracting lights has been tried successfully with small boats off the coast of Newfoundland each boat having only a few 100 W lamps (Quigley, 1964), but catching very many more squid than with the traditional hand jigs (Rathjen, 1973). Similar trials in Australia were not a success (Anon 1974); neither were attempts to combine light attraction and purse seining in New England (Taber, 1977).

5.5 Pumping

Squid have also been caught in the Californian fishery for Loligo opalescens at San Pedro by pumping from an anchored boat. Traditionally in this fishery the boat is anchored over a squid school located during the daytime by echo sounder or by the presence of sea lions or flocks of birds. Attracting lights (1.5 kW) are switched on at dusk and brailing begins when sufficient numbers of squid have gathered alongside. Trials have shown that brailing can be avoided by the use of a submersible pump (capacity 6 245 l/min at 6 m head) and a 20 cm diameter pipe connected to a rectangular funnel containing a 500 W underwater tungsten halogen lamp (Kato, 1970). Some of the disadvantages encountered in rough seas may be overcome by constructing the wings of the funnel with 50 mm mesh netting (Kato and Hardwick, 1976). Under good conditions as much as 80 tonnes of squid have been caught in a single night using a funnel opening of 1.8 x 1.2 m (Anon, 1970a, b). The attracting lights are hung outboard and additional concentrating lights may be used at gunwale level (Ben-Yami, 1976; Kato and Hardwick, 1976) (Figure 8b).

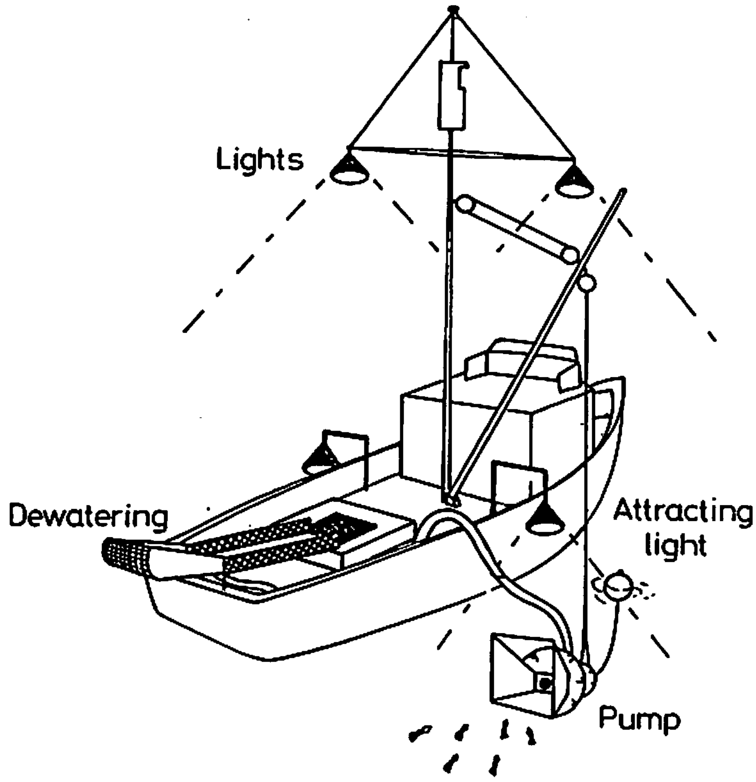

Figure 8b Light attraction for pumping (Rathjen, 1973).

5.6 Detection

The Japanese can detect areas of good squid fishing by the aerial location of current rips (Suzuki, 1963) and luminescent schools of squid are sometimes detectable at night from aircraft flying over the clear waters off California (Squire, 1972). It might, therefore, ultimately prove possible in some areas to employ low-light level devices (Roithmayr, 1970) and remote sensing to detect squid schools and assess potential resources (Rathjen, 1973). In most areas, however, echo sounders are likely to prove the only practical tool for finding squid. Compared with those fish which have a gas-filled swimbladder, squid reflect very little sound. There are very few data on the target strengths of marine organisms other than fish but tank measurements by

Smith (1954) and Matsui et al., (1972) show that squid of the genus Loligo of approximately 12 cm mantle length have a target strength of between -42 and -48 dB at frequencies of 15-200 kHz. The effective acoustic area of a squid of this size is some 4-8 cm^2, approximately 4% of its actual surface area (McCartney, 1976). Despite these poor acoustic properties the Japanese have found that in practice echo sounding is a very good technique for locating squid and they have used frequencies of 28, 50, 75 and 200 kHz. At all four frequencies squid produce distinct echo traces, which can be detected from a stationary or a moving vessel. The optimum sounder characteristics for squid detection are frequencies of 75-200 kHz with a narrow beam (half-power beam angles of 8^o and 3^o at 75 and 200 kHz respectively) and minimum pulse length (Kawaguchi and Nazumi, 1972; Suzuki et al., 1974).

6. HANDLING, PROCESSING AND MARKETING

The edible portion of squid, which consists of the mantle, tail, arms and tentacles, comprises some 60-80% of the body weight and is greater than that of most fish (20-50%) and shellfish (20-40%). Squid meat is equal to fish meat in protein content (16-20%) and amino acid composition and has a food energy equivalent to 2-3 J/g* of raw flesh (Voss, 1973; Ampola, 1974; Stroud, 1978). The inedible part need not be wasted. The sepia or ink of cephalopods has been refined and used by artists for many years. The viscera and pen can be processed to make a high grade nitrogenous fertilizer or animal feed supplement and whole squid not suitable for human consumption can be used similarly (Ampola, 1974). The viscera are especially rich in vitamins B_2 and B_{12} (Takahashi, 1965).

Squid undergo rapid spoilage and are particularly susceptible to mechanical damage. Bulk icing, shovelling of the catch and dense packing lead to crushing, torn skin and broken ink sacs all of which detract from the quality of the final product. Squid therefore need to be carefully handled and preserved on board ship. For periods of 6-8 days, icing or chilling with subsequent storage in ice, is sufficient. Longer range operations require deep freezing and cold storage on board. Illex and Loligo both have excellent freezing characteristics and can be stored whole or cleaned for periods of at least 1 year. Whole squid frozen for 1 year can be thawed, cleaned and processed into breaded strips and refrozen with an expected shelf life of another 6-12 months (Learson and Ampola, 1977). For good quality the catch should be chilled or iced immediately after capture and shelved or boxed to reduce physical damage. A squid-to-ice ratio of 2:1 is recommended with the squid and ice well mixed. Alternatively, a chilled seawater system can be used with a 3:1:1 ratio of squid-to-ice-to-water. Only good quality squid should be frozen, the containers and cartons should be relatively thin to permit rapid cooling and plate or blast freezing is recommended. Storage temperatures of -18°C to -30°C are necessary (Learson and Ampola, 1977; Stroud, 1978). Both flat-cleaned mantles and eviscerated squid can be skinned and diced mechanically but full process automation requires the development of machinery to behead the squid and remove its beak, pen and viscera, jobs that at present are done by hand (Ampola, 1974; Stroud, 1978). The development of a UK domestic market for squid probably requires extensive sales promotion but there is a considerable export potential to be explored in southern Europe and Asia. Such an approach has already been adopted in the USA, where the New

* 1 J = 1 joule = 0.24 calories.

England Fisheries Development Program (NEFDP) has been set up jointly by the National Marine Fisheries Service and the fishing industry, to exploit the resources that have come under direct US control as a result of extended coastal state jurisdiction. A survey by the NEFDP in 1975 found that there were large potential export markets for New England squid in western Europe, particularly in Italy and other Mediterranean countries. The NEFDP also exhibited at the 52nd International Fair in Milan in 1976, where Italian buyers expressed a strong preference for Loligo pealii, while Spanish and English buyers were prepared to purchase large quantities of both L. pealii and Illex illecebrosus (McAvoy and Earl, 1977). In Japan and the USA most squid products are canned but in the USA frozen breaded squid and marinated squid both show commercial promise (Ampola, 1974). As part of its promotional drive the NEFDP has published a squid recipe booklet to encourage domestic interest (Rathjen, 1977). There is little incentive towards the development of new squid products in the UK but possibilities include frozen strips or rings of squid cased in batter, and paella or other seafood dishes containing pieces of squid meat (Stroud, 1978). Japanese experience of canning and processing squid has been reviewed by Takahashi (1965, 1974).

7. BIOLOGY

7.1 Life cycle and growth

Most squid grow extremely rapidly, are short lived and do not survive spawning which occurs when they are 1-3 years old. For a number of the more important commercial species, for example Illex illecebrosus (Squires, 1967), most of the population spawns at 1 year old so that the bulk of the catch consists of only one age group. The Japanese squid Todarodes pacificus spawns at 1 year old only (Hamabe and Shimizu, 1966; Ishii, 1977).

Although spawning may occur all the year round where temperatures are sufficiently high (Summers, 1971; Mesnil, 1977), squid of the genus Loligo generally have a peak spawning period in the winter or spring with a subsidiary spawning in the summer or autumn (Summers, 1971; Holme, 1974). This apparently gives rise to two reproductive cycles of alternating length (Mesnil, 1977). Squid hatching in the spring from winter spawned eggs mostly mature during their first winter and spawn the following summer, thus having a short cycle. Squid hatching from this summer spawning are, however, not sufficiently developed to mature during their first winter and remain immature during the following summer and autumn, when environmental factors such as temperature and photoperiod inhibit maturation (Mesnil, 1977; Mangold and Froesch, 1977). They mature as large squid during their second winter and thus have a long cycle. The ommastrephid Illex illecebrosus apparently adopts the same strategy (Mesnil, 1977). In this species, which spawns offshore in deep water when food is scarce, starvation stimulates the growth of the ovaries (Rowe and Mangold, 1975).

Unlike most marine fish, which spawn vast numbers of eggs to be fertilized and develop freely in the water, cephalopods lay fertilized eggs surrounded by a tough outer coating and this requires copulation preceded by elaborate courtship behaviour (Packard, 1972). Loliginid squid lay their eggs in large strings or clumps either directly on a sandy bottom (Kristensen, 1959; Fields, 1965) or attached to submerged objects (Stevenson, 1934; Packard, 1972; Holme, 1974). In the various species of Loligo the clumps are constructed by the successive addition of egg capsules by different females (Stevenson, 1934; McGowan, 1954; Tardent, 1962) and during the mass spawning of L. opalescens (see Section 4.2) the clumps may reach 12 m in diameter (McGowan, 1954). Males of L. pealii have been observed to stand guard over the clumps of eggs (Stevenson, 1934). Little is known of the spawning of ommastrephids, which apparently occurs in deep water on the continental slopes (Squires, 1957; Araya, 1976a, b), perhaps at depths in excess of 1 000 m (Clarke, 1966). Todarodes pacificus lays large adhesive egg masses on the sea bottom (Hamabe, 1963), although these masses may disintegrate towards the end of development and float upwards which would account for some eggs being taken in plankton hauls (Okiyama, 1965b). Large masses of eggs of other, unidentified, oceanic squid have been seen on the surface of the sea on several occasions (Clarke, 1966). In captivity Illex illecebrosus lays spherical egg masses of 40-120 cm in diameter containing up to 10^5 ova. These masses are neutrally buoyant and not attached to the bottom; in the sea they probably drift with the current (Durward et al., 1979).

Young squid are pelagic and subject to drift by tidal (McGowan, 1954; Fields, 1965) or ocean (Okiyama, 1965b; Araya, 1976a, b) currents and are rarely caught in plankton nets or young fish trawls (McGowan, 1954; Holme, 1974). The growth rate of larval loliginids probably does not exceed 4-5 mm mantle length per month (Fields, 1965; Hurley, 1976) increasing later to 10-20 mm/month, and in some species 30-40 mm/month (Araya and Ishii, 1974; Holme, 1974). The higher rates apply to the summer months, when growth is at a maximum, and are typical of ommastrephids also. In Ommastrephes bartrami the growth rate is 30-40 mm/month in the summer decreasing to 10-20 mm/month in the autumn and 5-10 mm/month in the winter (Murata and Ishii, 1977). Comparable values for Todarodes sagittatus in Icelandic waters for 30 day periods are 76 mm in July, 52 mm in August, 28 mm in October and 22 mm during winter (Fridriksson, 1943).

In the English Channel young Loligo forbesi first appear in trawl catches in late May. The mantle length is then about 10 cm. Subsequent growth is rapid, the males reaching 30 cm and the females 25 cm by November with respective mean growth rates of 37 and 27 mm/month between June and November. Peak spawning occurs in December and January and incubation takes 30-40 days. There is also a summer population which grows to a rather smaller size at maturity. In the Channel L. forbesi appears to be an annual with neither sex surviving beyond spawning (Holme, 1974). In Scotland two year-classes are found in the commercial catches with 2 year old males up to 50 cm in length (Thomas, 1973). The relationship between weight in g and dorsal mantle length in cm for L. forbesi is given by Holme (1974).

7.2 Food and predators

Squid are important members of marine food chains and the loliginids and ommastrephids both occupy approximately the same trophic level as mackerel (Suda, 1973). They are voracious predators feeding when young on macroplankton and subsequently on small fish (Okiyama, 1965a; Naito, Murakami and Kobayashi, 1977). Larval squid are probably important predators of larval fish (Hurley, 1976).

On the Newfoundland Grand Banks euphausids are the predominant food of small Illex illecebrosus (10-12 cm mantle length) but as these squid grow and migrate inshore crustaceans decrease in significance in their diet and fish such as capelin, redfish, cod and haddock become the main constituent (Squires, 1957). A comparable change occurs in the diet of Loligo opalescens. The ratio of crustacea to fish is 3:1 in young squid, 1:1 in young-mature animals and 1:3 in spawning individuals (Fields, 1965). This change in food is accompanied by a concomitant change in feeding behaviour. Young Illex move in well-defined evenly-spaced schools, each squid holding its arms and tentacles compactly together in a streamlined cone and travelling backwards at a steady speed. When moving through swarms of small crustaceans, however, the arms are expanded, greatly enhancing the turbulence in the animal's wake and sweeping the prey onto the suckers of the arms and tentacles (Squires, 1966). This mode of feeding is accomplished without breaking up the school but is no longer adequate when the squid begin to feed on small active fish. Then the old Illex continue to swim backwards in schools but, on passing a potential prey or a jig, individual squid stop, reverse their direction of movement and make rapid forward attack; this behaviour breaks up the school (Williamson, 1965; Squires, 1966). The speed of attack is high, approximately 2.5 m/s in Todarodes pacificus (Shibata and Flores, 1972), and the prey is seized in the centre of the arms (Baker, 1957); it is killed immediately by a bite which severs the spinal cord (Bradbury and Aldrich, 1969). In daylight in clear water Illex commonly reconnoitre fishing jigs, manoeuvering slowly to touch them with their arms and tentacles. Many then retire again without making an attack, having apparently recognized the jig as an inanimate object (Williamson, 1965). Those that do attack blanch to a translucent white just before attacking. The attack is begun from a distance of about 1 m and the colour change renders the squid inconspicuous when viewed head-on. From the side, however, conspicuousness is increased and attacks on jigs involve progressively more and more squid in bursts of frenzied activity. The vertical movements of the jig are essential in releasing the attacking behaviour (Bennett, 1978).

Squid take a considerable toll of their own kind through cannibalism* but their main predators are fish and they are eaten by many species (Fields, 1965; Clarke, 1966; Tibbetts, 1977). On the Grand Banks cod and mackerel are important predators of Illex illecebrosus (Squires, 1957) and off California salmon, mackerel and tuna all prey on Loligo opalescens (Fields, 1965). Toothed whales, porpoises and seals are also major predators (Clarke, 1966) and flocks of seabirds have been observed feeding on squid when they are debilitated and accessible at the surface after spawning (Fields, 1965). On the Grand Banks the pilot whale Globicephala melaena feeds almost entirely on squid and subsists on Illex illecebrosus for at least six months of each year. A conservative estimate suggests that at least 100 million tonnes of squid are eaten by sperm whales each year (Clarke, 1977).

7.3 Seasonal migrations

The commercially exploited species of squid all make extensive migrations and the resulting distributions are governed largely by water temperature. Loliginid and ommastrephid squid alike appear in warm, shallow, coastal seas during summer and autumn. With the exception of the Japanese work with Todarodes pacificus, however, few such migrations have yet been properly described by tagging experiments.

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* In Illex illecebrosus cannibalism becomes progressively more important during the year (Ennis and Collins, 1979). It appears likely that a significant portion of the late season (September-November) growth of the larger individuals is based on the consumption of smaller squid, when other prey is significantly depleted. From studies on captive squid it is suggested that much of the biomass of the population results from early season feeding (March-July) when crustaceans are the principal prey (O'Dor et al., 1979b).

Skin lesions caused by handling and by the tags themselves are a major cause of mortality and few squid survive for more than a few days after tagging. With Illex illecebrosus spaghetti-tubing anchor tags offer most promise for longer-term survival. Attached to the lip of the mantle they cause minimal effects on balance, swimming and behaviour (O'Dor et al., 1979a). Despite such difficulties with tagging the Japanese have managed to trace the long and complex migrations of T. pacificus by careful selection of time and site of release, achieving an average recapture of 3% (Hamabe and Shimizu, 1966).

The common American squid Loligo pealii must migrate considerable distances each year as the northern limit of its range is 600 km further south in winter than it is in summer. In winter the bulk of the population is concentrated in the centre of the mid-Atlantic Bight on the outer edge of the continental shelf and must cover distances of up to 200 km when it comes inshore in spring to spawn (Summers, 1969). Between Georges Bank and Cape Hatteras the distribution and relative abundance changes markedly between spring and autumn (Figure 9). In early spring the squid are located in modest numbers offshore in depths of 111-183 m, while in autumn individuals of the greatly increased population are most abundant in depths of less than 110 m (Serchuk and Rathjen, 1974). These changes are correlated with temperature, Loligo pealii being most abundant where the bottom temperature exceeds 8°C.

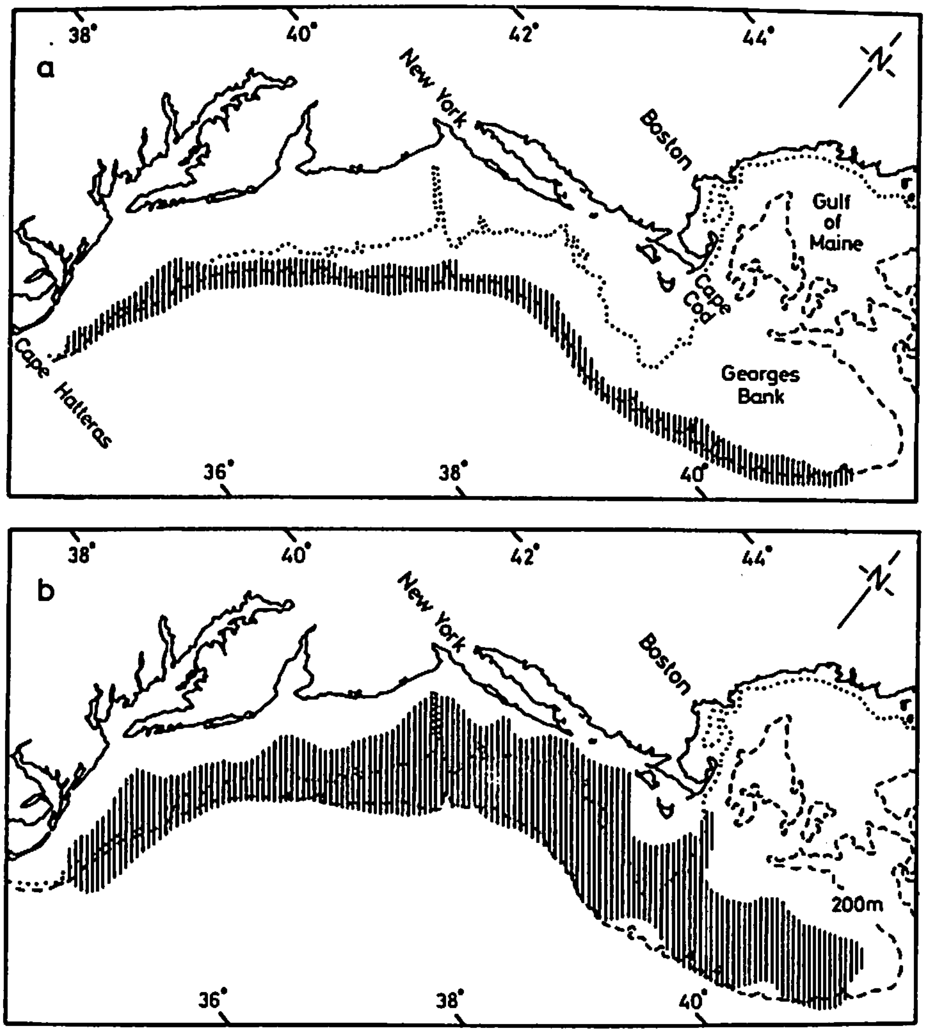

Figure 9 Seasonal distributions of Loligo pealii in the Northwest Atlantic (a) March-May, (b) September-November (Rathjen, 1973).

Trawl catches diminish abruptly when the temperature falls below this value (Summers, 1969; Serchuk and Rathjen, 1974). Further to the north (see Section 4.2) the short-finned squid Illex illecebrosus makes a similar migration apparently with both northern and inshore distribution limited seasonally by temperature. Illex is tolerant of somewhat lower temperatures than Loligo (Squires, 1957). The exceptionally high abundance of Illex on the Scotian shelf in 1976 appears to have been correlated with a mean bottom temperature of 6.9°C contrasting with values of 5.3°C to 5.8°C in the previous six years (Scott, 1978). Within these seasonal distributions the larger squid are found in deeper water (Summers, 1969; Serchuk and Rathjen, 1974; Mesnil, 1977).

There are similar migrations in European waters. Loligo forbesi, which is common along the whole Atlantic coast of Europe, is thought to winter offshore in midwater, moving in spring round the north of Scotland and through the English Channel into the North Sea, where it is found in summer (Kristensen, 1959). In some years (see Section 7.5) large schools occur inside the Skagerrak and northern Kattegat (Kristensen and Broberg, 1978). During early spring the southern part of this population is mainly concentrated towards the western end of the English Channel and young squid do not appear off Plymouth until late May. As the summer advances the squid spread into the eastern Channel and the southern North Sea and may become scarce or absent in the western Channel. This indicates not only an easterly movement but also an incursion into shallower water. L. forbesi becomes common again off Plymouth in late September, apparently as the result of a westward migration away from the shallower waters of the eastern Channel and southern North Sea where winter temperatures are too low. The lower limit of its temperature tolerance is not precisely known but L. forbesi occurs where temperatures are at least 8.5°C* (Holme, 1974). Loligo vulgaris is more tolerant of cold, occurring regularly in the English Channel during the winter. It moves into the southern North Sea in spring and spawns along the Dutch coast in summer (Tinbergen and Verwey, 1945; Kristensen, 1959; Holme, 1974) but here it is at the northern extremity of its range and is represented only by larger individuals. Further south in the Bay of Biscay it migrates only short distances between coastal waters and the slopes of the continental shelf. Large spring spawners move inshore early and the offshore migration is late; two reproductive cycles are observed and summer breeders are quite common. Further south again off North-west Africa, near the southern limits of its range, L. vulgaris remains inshore all year long and the breeding period is extended (Mesnil, 1977; see Section 7.1).

Ommastrephid squid also show temperature-related seasonal movements in the North-east Atlantic. Illex coindeti migrates onto the continental shelf once or twice

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* In the North-west Atlantic in winter the isotherms tend to run parallel to the continental slope. There is a very sharp temperature gradient across the slope and the inshore shelf waters become extremely cold (< 1°C). On the European shelf, because of the influence of the North Atlantic Current, conditions are never so extreme. From May to November bottom temperatures are generally above 8°C. In February in the North Sea bottom temperatures drop to 5°-6°C but to the north and west of the British Isles they rarely fall below 7°C (Lee and Ramster, 1979). Peak landings of Loligo forbesi are made around the Scottish mainland in October and November and at Shetland from December to February (Thomas, 1973).

during its life. Mature individuals and mated females are found inshore in the Bay of Biscay in November and June prior to the offshore migration and large winter spawners are caught by trawlers off the Spanish coast in January and February (Mesnil, 1977). Annual migrations are made by Ommastrephes caroli and O. pteropus into Madeiran waters. Small individuals of O. caroli of both sexes appear first in July and August and are caught in large numbers. They are followed by schools of maturing female O. pteropus apparently on their spawning migration. Males are absent from Madeira and the eastern North Atlantic generally and the females may come either from the West African coast or the Caribbean, where both sexes are common. O. pteropus reaches Madeira at about the same time as the northward moving, 22°C mean surface isotherm, which appears to be the northern limit of its distribution. The southern limit appears to be 13°25'S coincident with the southern limit of the 25°C isotherm (Clarke, 1966). Almost every year large numbers of Todarodes sagittatus appear off the south and south-west coasts of Iceland in June and early July and by August enormous schools are often found in the fjords of the north-west, where they remain until November. Similar concentrations occur in the Faroes, in Norway and in some years on Scottish coasts. During this inshore period large numbers are often stranded on the beaches (Clarke, 1966). Spawning is thought to occur in the Atlantic to the west of Ireland and south to the Azores and Canary Islands from December to February (Wiborg, 1972). The gonatid squid Gonatus fabricii, a pelagic form widely distributed in boreal and subarctic waters, is abundant in the surface layers of the central and eastern Norwegian Sea in summer and autumn. Peak spawning occurs between April and June and the life cycle is closely connected with the current system of the Norwegian Sea and adjacent waters (Wiborg, 1979).

In the waters around Japan the winter population of Todarodes pacificus, which makes up the bulk of the commercial catches (see Section 4.1), makes extensive migrations between latitudes 30° and 51°N, with an annual migration circuit of about 4 000 km. Spawning occurs in winter to the south-west of Japan, centering on the edge of the continental shelf of the East China Sea. The larvae (< 2 cm mantle length) are transported north by the Kuroshio current in the Pacific and the warm Tsushima current in the Sea of Japan, growing to a length of 12-20 cm by early summer, when they reach the fishing grounds of northern Honshu and southern Hokkaido. The northward movement in the warm water continues during the summer with schools moving up the western side of Hokkaido from May to August reaching Sakhalin and the Sea of Okhotsk by July and August. On the eastern coast of Hokkaido jigging begins in July, when the surface temperature reaches 13°C, the squid arriving there by two warm branches of the Kuroshio current extending northwards between longitudes 144°-146°E and 148°-150°E (Figure 10). Some squid in addition pass outside the Kurile islands and reach the southern tip of the Kamchatka peninsula (Araya, 1976a, b). In October and November the squid migrate south again and fishing ceases when the sea temperature drops to 10°C; in November in northern Hokkaido, in December in southern Hokkaido and December-January in northern Honshu. The major migration routes appear to occur along the boundaries between warm and cold water masses, in the Sea of Japan between the Tsushima current and the colder offshore water and in the Pacific between the Kuroshio and Oyashio currents. The distribution of the autumn spawned population is similarly closely related to the oceanographic conditions in the Sea of Japan (Kasahara, 1978).

Todarodes pacificus is found where the surface temperature is between 5° and 15°C (Flores, 1972; Murata et al., 1976) but because of its extensive vertical migrations (Suzuki, 1963; Kasahara, 1978; see Section 7.4) it must be tolerant of rather lower temperatures. North-east of Hokkaido it appears to congregate in and above the thermocline formed in September between 10 and 40 m (Murata and Araya, 1970). At the same time of year echo traces of squid have been found in the Sea of Japan associated with the scattering layer in the thermocline between 20 and 40 m (Suzuki et al., 1974). T. pacificus avoids avoids higher temperatures by moving offshore to the west of Sakhalin in summer when the surface of the Tsushima current rises above 15°C (Araya, 1976a, b).

The movements of the other commercially-utilized, oceanic Japanese squids are also related to the movements of warm and cold water masses. Ommastrephes bartrami occurs in the Kuroshio current, and in the summertime extensions of it, northwards to Hokkaido. Onychoteuthis borealijaponicus and Gonatopsis borealis are subarctic species approaching Japan from the north-east in the autumn and winter with the development of the cold Oyashio current (Murata et al., 1976).

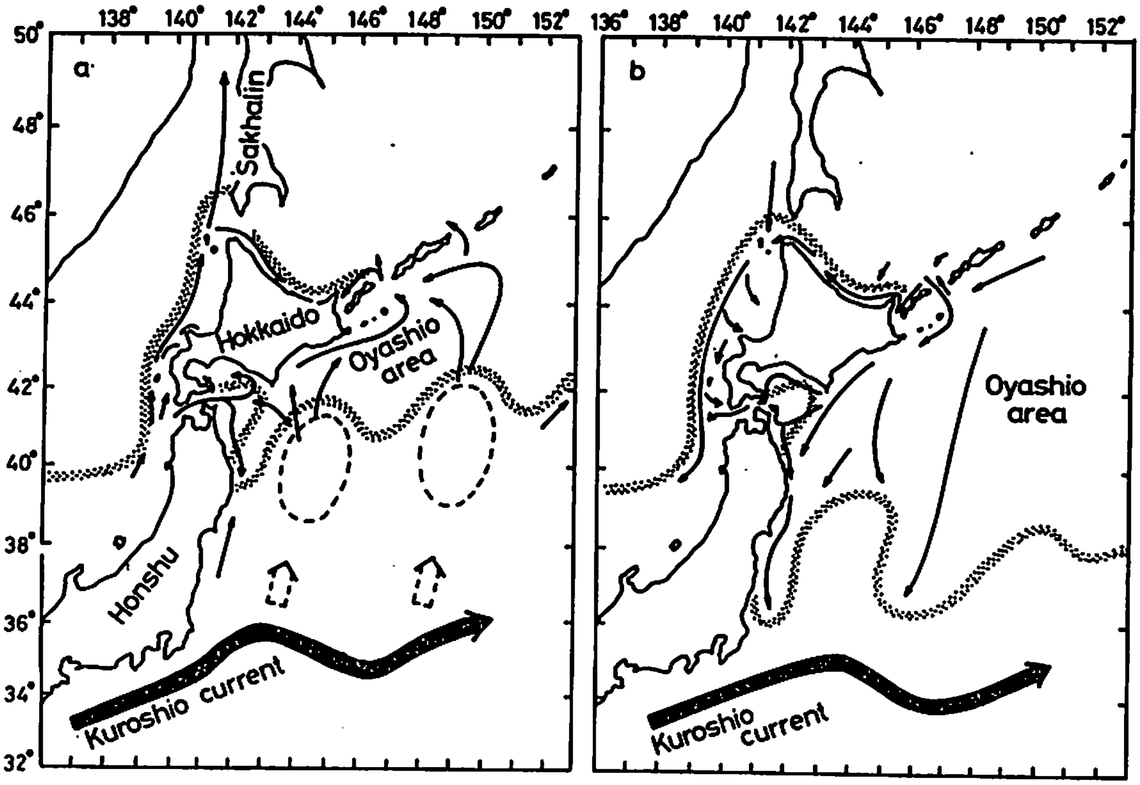

Figure 10 The migrations of the winter population of Todarodes pacificus off northern Japan (a) in spring and summer, (b) in autumn. ⟶ = major migration routes; ∴∴∴ = frontal zone between warm and cold water masses; --- = warm water extensions of the Kuroshio current (Araya, 1976a, b).

7.4 Vertical migration, schooling and luminescence

Loliginid and ommastrephid squid both show a diurnal cycle of vertical migration moving up in the water column by night. Ommastrephids are commonly seen at the surface at night (Baker,1960) and their vertical movements must frequently be several hundred metres in extent. Small scale, vertical movements of Illex illecebrosus have been observed in aquaria (O'Dor et al., 1977). Catches of Loligo pealii (Summers, 1969; Serchuk and Rathjen, 1974; Lux et al., 1974) and L. forbesi (Holme, 1974) taken by bottom trawl show a corresponding decline at night.

Squid are schooling animals and, like fish, the schools are maintained visually with each individual keeping station no more than two or three body lengths from its neighbours. The members of individual schools are also frequently of a very limited size range (Fields, 1965; Hurley, 1976). Schools of Ommastrephes caroli vary widely in size but generally become smaller as the squid increase in length (Clarke, 1966). During mating and spawning, however, Loligo opalescens forms large schools estimated to contain as much as 35-45 tonnes each (Anon, 1978), and there are frequently large concentrations in the vicinity of the deep scattering layer (Hurley, 1978). From a submersible diving off Cape Hatteras, on the east coast of North America, Milliman and Manheim (1968) saw large numbers of oceanic squid, which may have been Illex illecebrosus, concentrated in two layers at 220-250 m and 490-510 m. The estimated density in the upper layer was 0.5 squid per cubic metre and the depth coincided with that of the strongest scattering layer. Myctophid fish were also present in the middle and at the lower edge of the squid layer.

It is thought that the vertical migrations of L. pealii may be associated with the pursuit of food organisms such as euphausids (Serchuk and Rathjen, 1974) and Suzuki (1963) suggests that the vertical movements of Todarodes pacificus are correlated with the vertical movements of the deep scattering layer. Off Hokkaido the layer forms in the cold water on the outer margin of the warm Tsushima current and consists principally of Euphausia pacificus and Parathemisto japonica. During the day it is situated at a depth of 100-150 m but at dusk, with descreasing light intensity, it rises to the surface at a rate of 0.5-1.5 m/min remaining in the depth zone bounded by the 0.1 and 1.0 lux isolumes (lines of equal light intensity). In the offshore region of the Sea of Japan the rate of feeding of T. pacificus reaches a peak at sunset as the deep scattering layer reaches the surface (Okiyama, 1965a). Schools of T. pacificus swimming in the middle and lower part of the scattering layer at a depth of 30-50 m and attracted by lights move up towards the surface at an estimated rate of 1.5 m/min (Shibata and Flores, 1972).

Luminescence is a common phenomenon among deep-sea animals and is one example of the remarkable degree of convergent evolution between cephalopods and fishes (Packard, 1972). Light organs are well developed in ommastrephid squid and myctophid fish, both of which inhabit the upper mesopelagic and epipelagic zones (see Figure 1) and migrate to the surface at night. The light organs vary greatly in number and complexity between species, but probably serve in both groups to camouflage the animal, which would otherwise be silhouetted against the sea surface, (Herring, 1977). The squid Abraliopsis responds to overhead illumination by turning on downward-directed photophores. It is invisible from below when the intensity of the photophores matches that of the illumination (Young and Roper, 1976).

7.5 Abundance

Squid fisheries are characterized by large fluctuations in catches and this is best exemplified by the Newfoundland inshore fishery for Illex illecebrosus. Records dating from 1879 (Squires, 1957) and landing statistics from 1955 (ICNAF, 1978) show that during the last two decades the catch has fluctuated over four orders of magnitude and that years of great abundance are commonly followed by years of extreme scarcity, for example, 6 917 tonnes were caught in 1967 but only 13 tonnes in 1968. Such dramatic differences can be explained by a combination of varying hydrographic conditions, which determine the availability in inshore waters, and fluctuations in year-class strength affecting overall abundance. Young Illex move onto the Grand Banks in early summer probably in the deeper layers with the influx of warm, saline Atlantic water, apparently at the same time making vertical feeding excursions into midwater, where the mixture of Atlantic and Arctic water produces a rich food supply of small crustaceans (Frost and Thompson, 1932, 1933). The final inshore movement into the coves and bays of the Newfoundland coast appears to be governed by water temperature (see Section 7.3), the availability of suitable food (Frost and Thompson, 1932, 1933) and also local weather conditions, since squid disappear rapidly from the jigging grounds with the onset of onshore winds (Squires, 1957). Research vessel surveys in the North-west Atlantic since 1968 have shown that squid abundance may fluctuate by a factor of several times from one year to the next (ICNAF, 1978; Scott, 1978) and, clearly, the coincidence of a poor year-class and unsuitable hydrographic conditions will, as postulated by Frost and Thompson (1934), lead to a scarcity of squid. Conversely, a good year-class and high temperatures will, as in 1976, lead to an abundance of squid in inshore waters. In the summer and autumn of that year Illex was unusually abundant in the inshore waters of northern New England and eastern Canada from Newfoundland to Cape Cod. In the Gulf of Maine and Massachussetts Bay the average catch per 2 h tow increased from the normal 25-35 kg to 400-500 kg (Testaverde, 1977). Illex is commonly stranded on the beaches but during 1976 stranding occurred to an unprecedented extent and it is estimated that at least 10 million squid died on the shore of Cape Cod Bay. Reasons for the strandings remain speculative but it seems possible that these squid were trapped in the warm water of the Bay with Cape Cod forming a natural barrier to their normal offshore autumn migration (Lux et al., 1978).

While recent surveys suggest that there has been a pronounced increase in the relative abundance of both Illex illecebrosus and Loligo pealii in the ICNAF area, coincident with a decline in the abundance of various species of fish occupying similar ecological niches (Clark and Brown, 1977), fluctuations in the biomass of Illex have nonetheless continued with periods of high abundance in 1955-67 and 1975-77 and low abundance in 1968-74. There is no evidence in the catch records, however, of any regular cycles of abundance (Squires, 1957) and in this respect Illex contrasts with Loligo forbesi in Scotland, where catches have shown fairly regular fluctuations with peaks during the periods 1904-10, 1922-40, 1953-63 and 1970-74 (Figure 11). While some of these peaks, like that of the early 1960s, coincide with periods of influx of warm saline Atlantic water (Dickson, 1971) there is clearly no consistent correlation - catches of Loligo were, for example, very low during the major salinification of 1949-51 - and it may be assumed that, as with Illex, the fluctuating catches of Loligo forbesi reflect changes both in abundance and in availability on the fishing grounds. In 1961 there was an invasion of Scottish waters by large numbers of the cuttlefish Sepia officinalis* and of the squid Todaropsis eblanae both of which are southern forms; on some grounds Todaropsis, which is not commercially acceptable, significantly outnumbered Loligo (Rae, 1961). Large invasions of Todarodes sagittatus in Norwegian waters are similarly correlated with major influxes of Atlantic water but probably also depend on stock size (Wiborg, 1972). In the autumn of 1977 T. sagittatus reappeared in Norwegian coastal waters after an absence of 5 years. As in earlier years its appearance coincided with that of large quantities of salps. These are indicative of Atlantic water but the influx does not seem to have been very large and the squid catch was only 200 tonnes (Wiborg, 1978).

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* The most extensive incursion of Sepia officinalis into northern waters occurred during the salinification of 1933, when it invaded the North Sea and penetrated the Kattegat (Thomsen, 1934; Stephen, 1938).

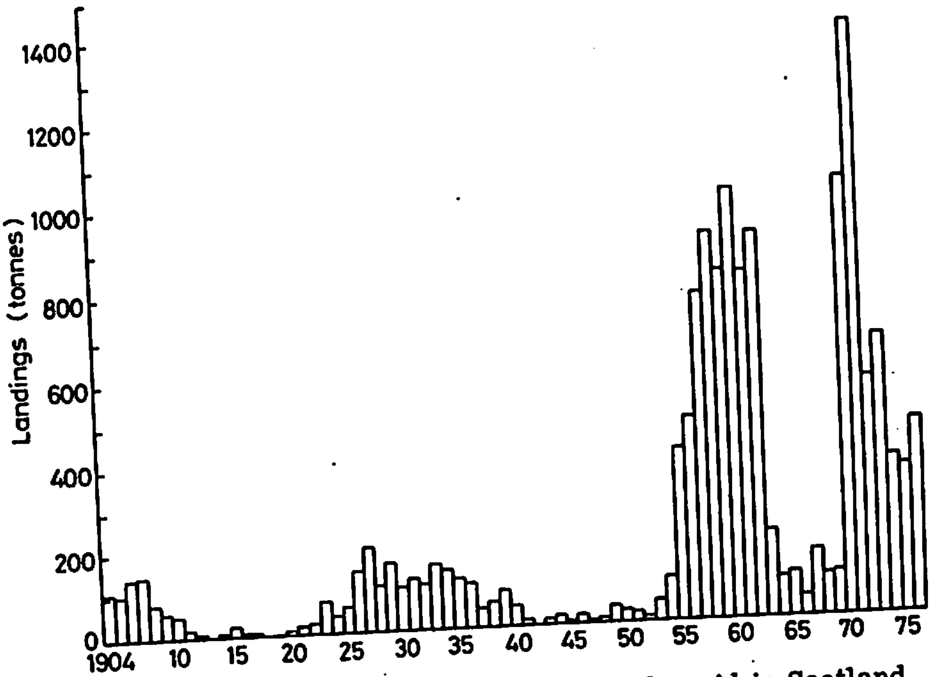

Figure 11 Annual landings in tonnes of squid in Scotland, 1904-1976 (Thomas, 1973; DAFS, 1977).

8. FISHERY MANAGEMENT

Illex illecebrosus and Todarodes pacificus are now fully exploited in the ICNAF area and in the seas around Japan respectively and require routine fisheries management. Difficulties of management arise because of the extremely short-life cycles; the fisheries are conducted each year on new recruits. At present squid fisheries in the ICNAF area are regulated by mesh size, type of fishing gear, open seasons and areas, and catch quotas, but the feasibility of adopting effort regulation is under consideration (ICNAF, 1978). Attempts have recently been made to simulate the effect of exploitation on the populations of Loligo and Illex (Sissenwine and Tibbetts, 1977) and to age Illex by counting what appear to be daily growth rings in the statoliths which are structures comparable to fish otoliths (Hurley et al., 1979). The Japanese carry out regular synoptic surveys with several research vessels in the Sea of Japan, in the spring when recruitment is assumed to be complete and again in the autumn when migration has reached its fullest extent. They attempt to forecast both the abundance of squid and areas of good fishing from experimental jigging and oceanographic surveys. Egg and larval surveys have now been adopted to obtain an earlier estimate of year-class strength. The Japanese limit by licence the number of boats in each size class that are allowed to fish for squid (Kasahara, 1978). They also regulate the effort of their larger vessels (30-100 tonnes) by limiting the number of lamps to approximately 50 or the power supply to 150 kW (FAO, 1975a). This is a rare example of effort regulation and one that should be closely watched.

9. POTENTIAL WORLD RESOURCES

Conservative estimates suggest that the potential annual world catch for cephalopods on the continental shelves and the upper regions of the continental slopes is of the order of 8-10 million tonnes. But a very large effort would be required to realize this potential; some 3 000 jigging vessels are required to catch 200 000 tonnes of squid per annum in the sea of Japan (see Section 4.1). In addition there are large oceanic resources which, on the basis of the estimated consumption of squid by whales, are assessed at between 8 and 60 times greater than the shelf resource (Voss, 1973; FAO,1975a, b). Fishing for oceanic squid, however, presents a major technological problem, which has not yet been solved.

For squid stocks on the continental shelves there is a reasonable estimate of around 0.5 million tonnes as the potential catch of Todarodes pacificus in the North-west Pacific. Estimates for other areas such as Newfoundland are much rougher and within an order of magnitude only. The estimate for the potential catch of squid in the whole of both the ICNAF and the ICES (International Council for the Exploration of the Sea) areas is of the order of 100 000 to 1 million tonnes each.

In the open ocean squid are probably less abundant per unit area than on the continental shelves, except perhaps along the equatorial upwelling zone, but occur over a much wider area (Gulland, 1971). Many species of oceanic squid are very gelatinous and full of ammonia and have only half the calorific value of a muscular squid of the same weight. Others occur in large numbers in deep water but are known only indirectly from the stomach contents of whales and are rarely, if ever, caught in nets. The possibility of exploiting these oceanic squid has been discussed by Clarke (1963, 1966), Gulland (1971) and Voss (1973) but the problem of how best to fish them is unresolved. Of the 24 species of oceanic squid listed by Voss (1973) as of potential economic importance, the ommastrephid genera Ommastrephes, Symplectoteuthis, Todarodes, Nototodarus and Dosidicus are dominant forms which approach the surface at night. For these, at least, it should be possible to develop fisheries using jigging and light attraction, especially as in the areas where they occur individuals appear rapidly at night when lights are turned on (Baker, 1960; Voss, 1973; Yesaki, 1977). During a trial cruise in the south-western Atlantic oceanic ommastrephids were attracted to a research vessel within minutes of switching on a 6 kW lighting system over water exceeding 1 000 m in depth. These ommastrephids were lured to the jigs and many attacked them but, because of their heavy weight and the small size of the jigs, only a fraction of the squid attracted to the lights were actually landed. Larger jigs would have certainly increased the catch but it is possible that trolling with night-lights might be a much more effective method. A vessel underway trolling at even a slow speed would cover a much greater area than a vessel adrift jigging and theoretically it should attract a correspondingly higher number of squid. Either static or continuously-revolving lines carrying jiggers at regular intervals could be used in such a method (Yesaki, 1977). Before the deep-water squid can be caught in quantity commercially-suitable fishing gear must be developed and this is likely to be a large midwater trawl (Clarke, 1963; Voss, 1973). Comparative fishing experiments have shown that an Engel midwater trawl (1 400 x 200 mm mesh) with a much larger area of mouth opening catches a significantly greater number of species, more specimens of each species and very much larger specimens than either the 3 m Isaacs-Kidd or the 8 m^2 rectangular midwater research trawls (Roper, 1977).

10. POTENTIAL UK FISHERIES

In the North Atlantic there are four species of ommastrephid squid which are thought to occur in sufficient abundance to be exploited. These are Ommastrephes pteropus, O. caroli, Todarodes sagittatus and Illex coindeti. The first three are already exploited locally on a small scale (Clarke, 1963, 1966).

Ommastrephes caroli extends from Iceland to at least south of the Canary Islands and into the Mediterranean. O. pteropus extends from Madeira southwards to West Africa and westwards to the Gulf of Mexico. It is very numerous south of Madeira, while O. caroli occurs in large numbers between Madeira and a line running from the Bay of Biscay to the Azores. Both species make annual migrations into Madeiran waters, where they are exploited for food and bait (Clarke, 1963, 1966). O. pteropus and O. caroli are the dominant near-surface species where they occur and, although they have been caught at depths of 1 500 and 3 000 m respectively, they appear regularly at the surface at night and form schools of up to 50 individuals (Baker, 1957, 1960). Illex coindeti, the predominant species of squid on the broad continental shelf off Morocco, is replaced completely by O. pteropus at a depth of about 180 m (Clarke, 1963).

Ommastrephes pteropus is known as the "orange-back" squid in the Caribbean on account of the large orange-coloured light organ on its back, which glows plainly even from a distance (Voss, 1971). It reaches a large size (26-38 cm mantle length in the adult female (Clarke, 1966)), is heavy and meaty and is present in very large numbers on both sides of the Atlantic (Voss, 1971, 1973). With O. caroli it is an obvious candidate for a United Kingdom fishery and the two species are probably present in sufficient numbers to justify extensive exploitation (Clarke, 1963).

Todarodes sagittatus is a Mediterranean and Atlantic species extending to Iceland and northern Norway (see Figure 1). In late winter and early spring it appears in large numbers in the surface waters around Iceland, Bear Island and the Lofoten Islands, where it used to be caught by UK trawlers fishing for cod. It enters the fishing grounds round Madeira in large numbers during March, April and May. This species also comes to the surface at night but in daylight apparently prefers to stay on the bottom, where it is caught with trawls at depths of 70-800 m. Evidence from underwater photographs suggests that its vertical range extends at least down to 1 000 m. T. sagittatus is a fleshy squid growing to about 2. 3 kg in weight (Clarke, 1966). It is not at present acceptable to Scottish processors for human consumption (Thomas, 1973) but it is exploited for both food and bait in Madeira (Rees and Maul, 1956) and Norway (Wiborg, 1978). Jigging, bottom trawling and midwater trawling would appear to be appropriate methods for exploratory fishing for these ommastrephid squid (Clarke, 1963, 1966; Gulland, 1971). Any investigations into the distribution of T. sagittatus should probably be concentrated along the Atlantic slope from the west of Scotland south to the Azores (Wiborg, 1978).

In the Norwegian Sea there is the possibility of a summer fishery for the gonatid squid Gonatus fabricii. Jigging would be suitable for the larger squid, midwater trawls, lights and dipnets or pumps for the juveniles (Wiborg, 1979).

Quite apart from the ommastrephids, there are several species of loliginids, sepiids, sepiolids and octopods that are principal food species round the Mediterranean. These occur in large numbers on nearly all the continental shelves bordering the North Atlantic and could perhaps be further exploited. The cuttlefish Sepia officinalis is probably fairly abundant around the UK and is very good eating. Loligo forbesi is already caught in the UK and makes a significant addition to mixed catches. There has been a directed fishery at Rockall by Granton trawlers and, on a more limited scale, there are local coastal fisheries by smaller vessels. The Danes have recently suggested that a fishery for L. forbesi could be developed to the west of the UK in May and June, after the closure of the blue whiting fishery but on the same grounds. Japanese trials yielded catches of 36 tonnes/100 hours trawling at Porcupine Bank in July 1969. The Danes have also undertaken a trial cruise in the northern North Sea to assess the practicability of high-speed midwater trawling for squid (Kristensen and Broberg, 1978). Jigging, which was also tried on this cruise, might be suitable for catching L. forbesi where the water is of sufficient clarity and there are schools of an adequate size. Recent trials by the White Fish Authority (WFA, 1975, 1976), however, suggest that even in summer the Atlantic swell may preclude the use of jigging on the exposed offshore grounds of the Rockall and Faroe Banks. Jigging might be undertaken inshore on an opportunistic basis if mackerel gurdies were modified to take simple squid drums (WFA, 1978).

11. SUMMARY

(1) Cephalopod molluscs occur in all oceans of the world and are thought to form a major underexploited resource. The current annual world catch of cephalopods is about 1.2 million tonnes, of which some 900 000 tonnes are of squid. The potential catch is thought to be between 10 million and 100 million tonnes or even greater.

(2) Squid are found worldwide at all depths in the sea. The myopsids are confined to shallow coastal waters, but nearly all of the oegopsid families occur in the deep ocean. The surface living oegopsids are fast-swimming, voracious carnivores engaging in extensive migrations. Much less is known about the biology of cephalopods than about fish, and less about oceanic than coastal squid.

(3) Present exploitation is limited to a few of the coastal and offshore stocks, and only two families, the Ommastrephidae (oegopsids) and Loliginidae (myopsids), are caught commercially. By far the largest squid fishery is the Japanese one for Todarodes pacificus, which accounts for some 500 000 tonnes annually. There are smaller fisheries for other ommastrephids in the North-west Atlantic, off North-west Africa and in Europe, and over the last decade the Japanese have been fishing for squid worldwide. There are localized fisheries for various loliginid squid in both tropical and temperate latitudes.

(4) The principal method of capture is jigging, but the fisheries also employ bottom and midwater trawls, roundhaul nets, and in one instance pumping. The jig is a type of grapnel, which is jerked up and down in the water; the Japanese use automatic double-line, multihook jigs. Successful jigging is completely dependent on light attraction when the squid approach the surface at night. Despite their poor acoustic properties squid can be satisfactorily located by echo-sounders from both stationary and moving vessels; the best frequencies are 75-200 kHz.

(5) Most species of squid are short-lived, grow very rapidly and do not survive spawning. Age at spawning is commonly only 1 year. Most species make extensive vertical migrations to the surface at night and those which are found on the continental shelves make seasonal movements onto, or over, the shelf, which appear to be governed largely by temperature. The major migration routes of the Japanese squid Todarodes pacificus appear to occur along the boundaries between the warm and cold water masses of the Kuroshio, Oyashio and Tsushima currents. In the North Atlantic many oceanic squid move onto the continental shelf when the bottom water temperature exceeds a lower limit of approximately 8°C.

(6) Squid are important members of marine food chains and the loliginids and ommastrephids both occupy approximately the same trophic level as mackerel, feeding when young on macroplankton and subsequently on small fish. Their main predators are fish and marine mammals and a conservative estimate suggests that 100 million tonnes of squid are eaten by sperm whales each year.

(7) Squid fisheries are characterized by large fluctuations in catches apparently determined by the interaction of fluctuating year-class strength and varying hydrographic conditions. Routine fisheries management is difficult because of the extremely short life cycle; new recruits are exploited each year. The Japanese regulate the effort in their squid fisheries and attempt to forecast abundance by annual egg and larval surveys.

(8) Conservative estimates suggest that the potential annual world catch for cephalopods on the continental shelf and the upper region of the continental slope is of the order of 8-10 million tonnes. In addition there are large oceanic resources which may be as much as 8-60 times larger than the shelf resources. Among squid stocks on the continental shelves there is a reasonable estimate of 0.5 million tonnes for the potential catch of Todarodes pacificus in the North-west Pacific but estimates for other areas are much rougher. The potential catches for the ICES and ICNAF areas are probably of the order of 100 000-1 million tonnes each.

(9) In the North Atlantic there are four species of ommastrephid squid which are thought to occur in sufficient abundance to be extensively exploited. Three are already exploited locally on a small scale. The problem of how to catch them remains unresolved but probably depends on the development of a very large midwater trawl. Jigging poses serious problems in the large swells at Rockall, even in the summer, and might not be feasible in the North-east Atlantic generally. There may be scope to extend the UK inshore fishery for loliginid squid on a localized and opportunistic basis.

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