Shellfish Committee

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REPORT OF THE
WORKING GROUP ON CEPHALOPOD FISHERIES AND LIFE HISTORY

Lisbon, Portugal

17–19 April 1996

International Council for the Exploration of the Sea

Conseil International pour l'Exploration de la Mer

Palægade 2–4 DK–1261 Copenhagen K Denmark

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1 INTRODUCTION

1.1 Terms of Reference

ICES C.Res. 1995/2:44 stated that the Working Group on Cephalopod Fisheries and Life History (Chairman: Dr U. Piatkowski, Germany) would meet in Lisbon, Portugal, from 17–19 April 1996 to:

a) update currently available landing statistics;

b) collect and evaluate data on the life history and exploitation of relevant cephalopod stocks in the ICES Area;

c) describe trophic interactions between cephalopods and other marine resources.

1.2 Participants

The following twenty-three persons participated in the meeting. Seventeen participants are formal members of the Working Group. Their names are marked with an *.

Pedro Andrade	Faro, Portugal
Herman Bjørke*	Bergen, Norway
Teresa Borges*	Faro, Portugal
Peter Boyle*	Aberdeen, UK
Manuela Morais da Cunha*	Lisbon, Portugal
Earl Dawe*	St. John's, Canada
Maria del Mar Fernandez*	Santa Cruz de Tenerife, Spain
Graham Gillespie	Nanaimo, Canada
Angel González*	Vigo, Spain
Vicente Hernández-García *	Las Palmas de Gran Canaria, Spain
Colm Lordan	Cork, Ireland
William Macy	Narragansett, USA
Helen Martins	Horta, Azores, Portugal
Ana Moreno*	Lisbon, Portugal
João Pereira *	Lisbon, Portugal
Uwe Piatkowski (Chairman)*	Kiel, Germany
Graham Pierce*	Aberdeen, UK
Julio Portela*	Vigo, Spain
João Quintela	Faro, Portugal
Jean-Paul Robin*	Caen, France
Francisco Rocha	Vigo, Spain
Paul Rodhouse*	Cambridge, UK
Carlos Sousa Reis*	Lisbon, Portugal

A list of the participants' names and addresses is attached as Annex 1. A list of names and addresses of the Working Group members (as of April 1996) is given in Annex 2.

The following Working Group members excused their absence: Nick Bailey, UK; Angel Guerra, Spain; Lisa Hendrickson, USA; and Mike Vecchione, USA.

1.3 Opening of the Meeting

The meeting took place in the conference room of the Instituto Português de Investigação Marítima (IPIMAR) in Lisbon. The Chairman welcomed the participants, and Dr Carlos Sousa Reis, Director of IPIMAR and active member of the Working Group, gave some introductory remarks and wished the Working Group a stimulating and successful meeting. Local arrangements were extremely well-organized by the hosts, in particular by Manuela Morais da Cunha, Ana Moreno, and João Pereira, and the Working Group appreciated the superb atmosphere of the meeting. The Chairman further expressed his conviction that the meeting would not only contribute to the scientific work on cephalopods, but would also increase transnational contacts and exchanges of information between ICES cephalopod scientists and cephalopod scientists of adjacent areas.

1.4 General Considerations

During the 78th ICES Statutory Meeting in Copenhagen in 1990 the re-establishment of the former ICES Study Group on Squid Biology was decided. Since that time the Study Group had met four times and reports have been regularly presented at annual ICES Statutory Meetings (now the ICES Annual Science Conference). The Study Group developed into a Working Group on Cephalopod Fisheries and Life History mostly due to the growing economic importance of cephalopod fisheries in Europe. The Working Group collected available cephalopod catch statistics relevant to the ICES region and compiled comprehensive information on the life history and exploitation of cephalopod species which are of economic importance in the ICES area (ICES, 1993; 1994; 1995). Because cephalopod fisheries research is currently a very active science the permanent study of new publications is required and regular detailed updating of cephalopod life history data is necessary.

In the 1990s the Working Group largely benefited from two comprehensive projects of the European Community's Research Programmes in the Fisheries Sector (FAR: 1990–1992; AIR: 1993–1995) which concentrated on research on Northeast Atlantic cephalopods. On the other hand, ICES conferences have been the most important fora to introduce and discuss the results of these projects. In fact, nearly all European members of the present Working Group participated actively in the projects. They contributed substantially to the scientific sessions of the ICES Shellfish Committee.

This is documented in numerous ICES papers and posters on all subjects of cephalopod fisheries biology which dominated the ICES Shellfish Committee in recent years and which significantly improved our knowledge of the biology and fishery of Northeast Atlantic cephalopods. Most of the data compiled for the Working Group reports are also essential for the work undertaken within the projects.

The two projects of the European Community's Research Programmes in the Fisheries Sector related to cephalopod fisheries biology were *Fishery Potential of Northeast Atlantic Squid Stocks* (1990–1992) and *Stock Dynamics, Interactions and Recruitment in Northeast Atlantic Squid Fisheries* (1993–1995). They involved several ICES Member Countries such as the UK, France, Germany, Portugal, and Spain. The aims of the projects were to improve understanding of the basis life-cycle biology, stock structure, trophic interactions and fisheries exploitation of Northeast Atlantic squid, in particular the loliginids *Loligo forbesi* and *Loligo vulgaris*. Results of the first project have been published in a special issue of *Fisheries Research* (Boyle and Pierce, 1994a) comprising seventeen papers covering all aspects of the fishery biology of Northeast Atlantic squid; e.g., life history, population structure, fecundity, diet, stock assessment methods and economy of the squid catching industry. Detailed reports and publications on the work of the second project will appear in the near future.

At present no transnational European research projects on cephalopod fisheries biology exist. However, a third big European project on *Cephalopod Resources Dynamics: Patterns in Environmental and Genetic Variation* was proposed to the Third Call of the European Communitys Research Programmes in the Fisheries Sector. In addition, some smaller proposals related to cephalopod science have been or will be submitted to the European Community's Research Programmes. These proposed projects will form the basis of future transnational cephalopod fisheries research within the EEC and maintain active contributions to all cephalopod fisheries biology-related subjects relevant to ICES, such as advice on assessment and management of cephalopod fisheries.

2 CEPHALOPOD LANDING STATISTICS

2.1 Compilation of Landing Statistics

The present report updates the landing statistics available for cephalopod groups within the ICES area (see Tables 1 to 5). The data are largely based on last year's report (ICES, 1995). Tables 1 to 4 give information on annual catch statistics (1989–1995) per cephalopod group in each ICES division or sub-area separated for each nation. The cephalopod groups of the tables comprise the following species:

- Table 1. Cuttlefish (Sepiidae) and bobtail squid (Sepiolidae). The big majority of landings summarised in these tables are catches of *Sepia officinalis*, the common cuttlefish.
- Table 2. Common squid (includes the long-finned squids *Loligo forbesi*, *Loligo vulgaris* and *Alloteuthis subulata*).
- Table 3. Short-finned squid (*Illex coindetii* and *Todaropsis eblanae*) and European flying squid (*Todarodes sagittatus*).
- Table 4. Octopus (*Eledone cirrhosa* and *Octopus vulgaris*).

A compilation divided by species is not possible because fishing nations report landings for groups, mostly in the format presented in the tables. The data in the tables are based on official ICES statistics and information on national catch statistics supplied by Working Group members. When values differed between official ICES data and available national statistics, the higher value was included in the tables. Table 5 summarises cephalopod landings for the whole ICES area (FAO region 27). In contrast to last year's report, ICES data and national data available to the Working Group members have been used for this table instead of data published by the FAO. Data are compiled for each year (1989–1995), categorised according to cephalopod species groups and fishing nations. Table 6 comprises annual landings (1989–1995) for the entire ICES region separated into species groups. Information on the most important fishing techniques is given in various ICES papers prepared by Working Group members during recent years.

The quality of available landing statistics has been discussed in detail in earlier reports of the Working Group (ICES, 1993; 1994; 1995; see also "Recommendations for Improvement in Cephalopod Fishery Data" (ICES, 1994)). There have been some improvements since the last meeting of the Working Group. As already outlined in the 1995 report, difficulties remain in several aspects of data collection. Where cephalopod data are recorded there is frequently uncertainty on the species composition. The extent of this problem varies from country to country with some making no distinctions, some distiguishing between major groups (cuttlefish, squid, octopus), and some providing details on individual species.

Belgium reports data for cuttlefish, common squid (loliginid squid), and octopus. Cephalopods are only caught as bycatch and yields are relatively low. Major fishing areas are the southern North Sea and the English Channel. Loliginids are the most important cephalopods with a maximum annual catch of 546 tonnes in 1990.

Denmark reports landings of cuttlefish. However, these numbers most likely refer to common squid (*Loligo* spp.) as inspection of catches in Danish fishing ports (Hwide Sande, Hirtshals) demonstrate. Squid is caught as bycatch in the trawl fishery and numbers are low with a maximum of 54 tonnes in 1992.

England and Wales regularly provide data to ICES per species group. Landings increased significantly during the last years peaking in 1995 with more than 3,000 tonnes of cuttlefish and nearly 3,000 tonnes of common squid. Major fishing areas are the English Channel and the Celtic Sea.

France is the most important nation concerning landings of common cuttlefish (*Sepia officinalis*) and common squid (*Loligo* spp.) in the ICES region. Major fishing grounds are the English Channel and the Bay of Biscay. During recent years catches have been on a constant level with ca. 9,000 to 10,000 tonnes for common cuttlefish (peaks in 1990 with 17,776 tonnes and in 1995 with 14,741 tonnes) and 4,500 to 6,000 tonnes for common squid (peaks in 1989 with 6,404 tonnes and in 1995 with 6,011 tonnes). Landings for 1995 were only available as totals for each cephalopod group. Therefore, provisional data for ICES region/sub-areas were estimated according to the 1994 percent distribution of each species group in each area. Detailed information on French loliginid catches is provided by Robin and Boucaud-Camou (1995).

In Germany cephalopods are of no commercial importance and they are only landed occasionally as bycatch in the North Sea shrimp or flatfish fishery. A maximum bycatch of ca. 11 tonnes was yielded in 1995 in the North Sea and was composed of loliginid squid. As in Denmark the catches are erroneously reported as cuttlefish landings to ICES.

Surprisingly, Iceland again has reported catches of *Todarodes sagittatus*, the European flying squid. According to information provided by Einar Jonsson (Marine Research Institute in Reykjavik), the species appeared in the bycatch of redfish trawlers south of Iceland in autumn 1995. Although catch statistics of 11 tonnes for 1995 are low, this is the first record of *T. sagittatus* in Icelandic waters since 1985.

As in many other nations cephalopods are not "quota species" in Ireland. Therefore, available catch data have to be treated with caution. Common squid (mainly *Loligo forbesi*) contribute the major share of cephalopods landed in Ireland. They are caught in ICES divisions VI and VII. Yields ranged from ca. 150 to 450 tonnes during recent years. It should be mentioned, however, that a considerable amount of common squid caught in Irish waters is landed in Spanish ports. Detailed information on Irish cephalopod catches is provided by Collins *et al.* (1995a; 1995b) and Lordan *et al.* (1995).

In Norway the only important cephalopod fishery has been that of *Todarodes sagittatus* which was caught by a directed jigging fishery in the early 1980s. The fishery peaked in 1983 with ca. 18,000 tonnes. Since 1985 the fishery decreased dramatically due to the absence of the squid in coastal Norwegian waters, and since 1990 the squid was virtually absent according to available catch statistics. As in Iceland the squid appeared again in the fishery statistics in 1995 with ca. 352 tonnes which were caught in autumn. The possible "return" of *T. sagittatus* in North European waters should be observed with great interest as this species provided an important cephalopod fishery in the early 1980s. Recently Bjørke (1995) noted that the gonate squid *Gonatus fabricii* could become an economically interesting species in Norwegian waters as an estimated biomass of 1.5 million tonnes in July 1994 indicates.

Portugal regularly provides catch statistics for all major groups to ICES. Together with France and Spain it is the most important cephalopod fishery nation. During recent years Portugal yielded the highest octopus catches (*Octopus vulgaris* and *Eledone cirrhosa*) in the ICES region, particularly in ICES sub-area IX. The yields ranged from ca. 7,000 to 10,000 tonnes between 1989 and 1995. The other cephalopod groups are also exploited and show constant high catch rates with some slight declines in the loliginid fishery (see Tables 1 to 5). Detailed information on the fishery and population structure of cephalopods is given by Coelho *et al.* (1994), Cunha and Moreno (1994), Cunha *et al.* (1995), Moreno *et al.* (1994), and Porteiro and Martins (1994).

Scotland has also reported regular catch statistics during recent years. The most important catches are those of common squid (only *Loligo forbesi* in Scottish waters) with a peak of 1,937 tonnes in 1989. Since then, catches are somewhat lower varying between 300 and 1,500 tonnes per year. Catches of octopus (only *Eledone cirrhosa* in Scottish waters) were in the range of 5 to 122 tonnes between 1989 and 1995. For further information see Boyle and Pierce (1994a; 1994b; 1994c) and Pierce *et al.* (1994a; 1994b) among others.

For the first time, official catch statistics of Spain were made available to the Working Group. A document summarising available Spanish cephalopod landings for the period 1990–1995 separated by species and into ICES sub-areas VI, VII, VIII and IX is attached as Annex 3. Spain is the most important cephalopod fishery nation within the ICES region besides France and Portugal. Major fisheries exist on octopus and short-finned squid with annual landings of ca. 2,000 to 4,000 tonnes and 1,000 to 2,500 tonnes, respectively. Further information regarding the Galician coast was compiled by González *et al.* (1994a), Guerra and Rocha (1994), Guerra *et al.* (1994), and Simón *et al.* (1995).

USA. Landings statistics and stock assessments of the long-finned squid *Loligo pealei* and the short-finned squid *Illex illecebrosus* within the US EEZ (NAFO sub-areas 5 and 6) were submitted by Lisa Hendrickson. The draft documents were circulated among the participants. Data are not included in the present report. Data on recruitment of long-finned squid *L. pealei* in New England (USA) waters were published by Macy (1995).

Canada. Catch statistics of *Illex illecebrosus* in NAFO sub-areas 3 to 6 were discussed according to information published in the recent Scientific Council Report of the Northwest Atlantic Fisheries Organization (NAFO, 1996). After the decline of the *Illex* fishery in the early 1980s, recent catches began increasing in NAFO sub-areas 3 and 4 in 1989 and peaked at 11,000 tonnes in 1990. They declined again to ca. 2,000 tonnes in 1992. Since then, catches increased to ca. 6,000 tonnes in 1994 which were mostly taken as bycatch in the silver hake fishery.

Current fishery statistics of the opal squid *Loligo opalescens* (175 tonnes in 1994) and *Octopus* spp. (142 tonnes in 1993) off British Columbia were circulated by Graham Gillespie from Nanaimo, Canada.

During the meeting the Working Group also discussed the present cephalopod fisheries in seas adjacent to the ICES region such as the CECAF area (Hernández-García, 1995). Of particular interest is the Saharan Bank fishery where a directed trawl fishery yields nearly 110,000 tonnes of octopus per year. Vicente Hernández-Garcia reported on the squid fishery in the Canary Island region. An artisanal fishery on the short-finned squid *Sthenoteuthis pteropus* exists which yields ca. 800 to 1,000 kg per day during the summer season in very warm years. This fishery takes only immature females which attain 28 to 40 cm dorsal mantle length and which are sold for ca. 1,200 Ptas per kg.

In conclusion, it should be emphasized that with a total of at least 44,792 tonnes the cephalopod landings in the ICES region rose remarkably in 1995 (see Table 6). This was mostly due to the increase of landings of cuttlefish and common squid in the English Channel and adjacent waters. England and Wales, and France were the major fishery nations in these regions (Tables 1, 2, 5). Landings of short-finned squid and octopus remained comparatively constant during the past seven years. The major fishery of these groups took place in ICES sub-area IX (Portuguese waters) with Portugal and Spain being the dominating fishery nations (Tables 3, 4, 5).

2.2 Assessment of Squid

Cephalopods remain an extremely important component of marine ecosystems in many parts of the world and in some places offer a significant resource supporting large fisheries. In ICES waters, particularly the Northeast Atlantic, the position is presently less clear. However, fisheries for various species exist with increasing catch rates.

In the Northwest Atlantic the situation is different. There, two cephalopod species are exploited. Management advice is provided for their stocks and they have been of commercial importance for a long time: the long-finned squid *Loligo pealei* and the short-finned squid *Illex illecebrosus*. Total US landings of *L. pealei* averaged 17,500 tonnes during 1990–1992. Since then, they increased to an average of ca. 22,000 tonnes during 1993–1994. Almost all commercial landings were taken with otter trawl gear. Detailed landing statistics are available for recent decades as well as LPUE (tonnes/days fished) and standardized fishing efforts (days fished). *L. pealei* was last assessed by the 17th Stock Assessment Review Committee (SARC) during December 1993 (NEFSC, 1994) which found that the stock was probably fully-exploited and at a medium level of biomass.

A commercial fishery for *Illex illecebrosus* exists from Newfoundland to Cape Hatteras. The fishery is managed, in the US EEZ (NAFO sub-areas 5 and 6), by the Mid-Atlantic Fishery Management Council (MAFMC) and, in NAFO sub-areas 2, 3, and 4, by the NAFO. Since 1980, the NAFO total allowable catch (TAC), for sub-areas 2–4, has been 150,000 tonnes (NAFO, 1996). An assessment of the *I. illecebrosus* stock in the US EEZ was last conducted for review by the 17th Stock Assessment Review Committee in December 1993 (NEFSC, 1994). It was concluded that the stock was under-exploited and at a medium biomass level. An updated and revised analytical assessment of the US EEZ portion of the stock, for the period 1967–1993, based on analyses of statolith ageing, commercial fishery data, and research survey data will be available soon (Hendrickson *et al.*, in prep.).

At present, assessments on cephalopod species exploited in the Northeast Atlantic are not available and TACs for the most important species cannot be recommended. This is mostly due to the inadequacy of basic fisheries data. In its 1995 report (ICES, 1995) the ICES Working Group on Cephalopod Fisheries and Life History pointed out that ICES should be more proactive in encouraging Member Countries to collect and collate basic fisheries data—disaggregated to the statistical square level. This will provide a better picture of the actual removals by fishing, a clearer picture of cephalopod distributions, and the basic data for use in fisheries or population models.

However, first attempts to assess the loliginid stock around the British Isles, including the English Channel and the Celtic Sea, are now underway and will become available as a result of the second European transnational cephalopod research project *Stock Dynamics, Interactions and Recruitment in North East Atlantic Squid Fisheries* (1993–1995). Overall loliginid squid catches per ICES division landed in France are available for 1989–1994 (Figure 1). In addition, as an example, monthly fishing effort data per ICES rectangle (CPUE in kg per fishing hour of a 100 kW fishing boat) are shown for 1994 (Figures 2–4). The data demonstrate the development of the fishery in the course of one year. Based on these statistics, DeLury methods were used to assess the stock and its level of exploitation (Pierce *et al.*, 1996).

Further, Scottish landings of *Loligo forbesi* have been correlated with sea surface temperature offering the potential for forecasting of the fishery (Pierce, 1995). Stock assessment methods used for cephalopod fisheries have recently been reviewed (see ICES, 1993, Table 1; Pierce and Guerra, 1994).

2.3 Management Advice

The Working Group cannot at present provide reliable assessments of cephalopod stocks under exploitation in ICES waters, and consequently advice on TACs for the major species is not possible.

However, in the following table some regulations for exploited cephalopod species are compiled which are currently valid legislations in Spanish and Portuguese fisheries. They should be considered as regulation advice for developing fisheries in other ICES regions.

Portugal		**Spain**	
Minimum sizes		**Minimum sizes**	
Loligo vulgaris	10 cm DML*	*Loligo vulgaris*	10 cm DML
Sepia spp. (for inland waters)	10 cm DML	*Sepia officinalis*	8 cm DML
Sepia spp. (in Sado river)	15 cm DML	*Sepia elegans*	4 cm DML
Sepia spp. (Ria Formosa)	15 cm DML	*Octopus vulgaris*	750 g
Loligo vulgaris (Ria Formosa)	10 cm DML		
Octopus vulgaris (Ria Formosa)	500 g		
		Maximum number of *Octopus* traps per boat (Galicia)	
		Boat size	**No. of traps**
		< 2.50 TRB**	90
		2.50–5.00 TRB	135
		5.01–7.00 TRB	180
		7.01–10.00 TRB	225
		> 10.00 TRB	270

*DML = Dorsal mantle length.
**TRB = Registered brutto tonnes.

In Galician waters traps should be carried to port daily, and it is not allowed to fish with traps between 10.00 hrs on Saturday and 10.00 hrs on Monday. Traps for *Octopus*: there are limitations according to the type of trap and to fish in the Rias. Fishing is only allowed during the day. Portuguese traps (wire basket for *Octopus*) are not permitted in the Rias. Traps for *Sepia*: bait is not permitted.

The Working Group recommends that legislations on exploitation should be established. In addition, restrictions on the length and weight of exploited stocks should be introduced.

3 COLLECTION OF DATA ON CEPHALOPOD LIFE HISTORY

3.1 Compilation of Data

Cephalopod life history data are extensively compiled in Tables 7 to 11. All major species are covered. The data were first presented in the 1994 report of the Working Group (ICES, 1994). Since then, a large amount of new data was collected and the present report represents an updated and comprehensive data collection. For the first time, life history data on the European flying squid *Todarodes sagittatus* and the gonate squid *Gonatus fabricii* are also included in the tables (see Table 10).

The life history data will be reviewed on a regular basis with new interesting species added to existing data sets.

In the future, ICES should initiate links between activities on cephalopods and those in environmental disciplines such as hydrography in order to investigate more fully possible factors controlling recruitment in squid and distribution/migration patterns of juveniles and adults. Fisheries for these species are frequently characterised by their sporadic nature and environmental factors have been implicated—evidence has not, however, been fully considered and whether processes operate at the egg, paralarval, or later life stages is not known.

3.2 Reproductive Strategies in Cephalopods

Among cephalopod biologists there is a discussion about whether female cephalopods lay their eggs in one single spawning or in several consecutive spawnings. This is of great importance in estimating fecundity and recruitment. There are a number of definitions which explain the possible ways that cephalopods spawn. These definitions and possible examples within the animal group have been studied in detail by Rocha *et al.* (Working Group paper) who presented a review paper on this subject during the meeting which is attached as Annex 4.

The reproductive strategies of *Loligo forbesi* have recently been descibed in detail by Boyle *et al.* (1995a; 1995b)

4 TROPHIC INTERACTIONS INVOLVING CEPHALOPODS

4.1 Cephalopods as Predators

Cephalopods are entirely predatory. Early studies of diet composition suggest that approximately half of their food consists of crustaceans or fish, respectively. Among the fish prey identified many are of commercial importance. Neritic squid such as loliginids prey heavily on early life stages of gadoid fish and flatfish, thus potentially having a significant impact on the recruitment of economically important finfish. Recent studies show that *Loligo forbesi* feeds primarily on Gadidae, Ammodytidae, and Clupeidae. Fishes occurred in more than 80% of non-empty stomachs (Pierce *et al.*, 1994c). Importance of cephalopods increases in the diet of *L. forbesi* with growth showing considerable cannibalism in loliginid squid (Rocha *et al.*, 1994). The ommastrephid squid *Illex coindetii* also feeds primarily on fish such as Clupeidae and Sparidae (Castro and Hernández-García, 1995).

Detailed information on the role of cephalopods as predators will be soon available in a review paper compiled for the second EU project on cephalopod fisheries biology (see above; Pierce *et al.*, in prep) and in a review by Rodhouse and Nigmatullin (in press).

4.2 Cephalopods as Prey

The importance of cephalopods in the diet of marine mammals was reviewed by Pierce (1992) and González *et al.* (1994b). Furness (1994) has estimated the quantity of squid consumed by seabirds in the Northeast Atlantic. According to his assessment, annual squid consumption by seabirds reaches ca. 100,000 tonnes in the Northeast Atlantic. Further, it was recently shown that in the central eastern Atlantic, the swordfish *Xiphias gladius* is an important predator of oceanic squid such as ommastrephids (Clarke *et al.*, 1995; Hernández-García, 1995).

There is little evidence available as to what determines the proportion of cephalopods in the diet of different predators. Many predators are thought to be opportunistic. Also, the relative importance of trophic links involving cephalopods is largely unknown.

However, it is certain that some larger-toothed cetaceans, particularly sperm whales, are largely dependent on oceanic squids for their food. There are insufficient data on cephalopods as prey to make realistic estimates of natural mortality, although estimates of 50 million *Loligo* removed annually by porpoises, if reliable, may set a lower limit to the natural mortality parameter (Pierce and Santos, 1996).

Preliminary calculations have been done to estimate the numbers of cephalopods removed by seals in Scotland (Pierce and Santos, 1996). The calcutions are based on recent estimates of seal population sizes, literature values for daily energy requirements, and data on diet composition. Although cephalopods are generally a small proportion of the diet, amounts are large, exceeding significantly the amounts taken by commercial fisheries as demonstated in the table below.

ICES should encourage that the Working Group make use of existing ICES stomach sampling data to establish likely quantities of cephalopods removed by predators. At present, publications on investigations of fish stomach contents are of little use, because cephalopods are not identified at the species level. ICES should require that future stomach sampling programmes make greater attempts to identify cephalopod material in fish stomachs or to make such material available to cephalopod experts. This information would help to establish the relative importance of natural processes compared to fishery-induced mortality.

4.3 Review on Trophic Interactions of Squid in Scottish Waters

Trophic interactions of squid in Scottish waters was examined by Pierce and Santos (1996). This publication authored by two members of the Working Group is the first document that reviews the importance of the long-finned squid *Loligo forbesi* in the trophic food chain of the Northeast Atlantic. It provides a wealth of information on this subject and is attached as Annex 5 to the present report.

5 CEPHALOPOD SYMPOSIUM

During the 83rd ICES Statutory Meeting, the Shellfish Committee proposed a Mini-Symposium on "Cephalopods: Their role in the trophic chain". This could include particularly their abundance, the importance of fish predation by cephalopods, and their predation by marine mammals. The symposium should take place in 1997 or 1998. The Working Group discussed this suggestion in detail and concluded that a symposium on trophic interactions might be too late in 1997. There will appear a considerable amount of new publications on this subject during the next months (e.g.; "Role of cephalopods in the world's oceans"; theme issue of the *Phil Trans R Soc Lond B*). Therefore, the Working Group concluded that a symposium on this subject would not attract many participants.

Instead, the Working Group proposes a symposium on "Environmental changes and the reactions of cephalopod populations". This topic would cover all factors determining biomass and abundance of cephalopods. It would also address many subjects outlined in the GLOBEC programme. It should take place in Portugal in 1998 either just before or shortly after the ICES Annual Science Conference in Lisbon.

6 RECOMMENDATIONS/FUTURE WORK

Traditional finfish resources in the ICES convention area are heavily exploited and the importance of cephalopod resources may increase in the future. First indications are already apparent as the review on catch statistics over recent years indicates (see Section 2.1; Tables 1 to 6). Most cephalopod species are very short-lived and their biomass levels cannot currently be reliably assessed (see Section 2.2). Therefore, any increase in their exploitation should be approached with great caution and management advice (see Section 2.3) should be considered.

Species	**Area, year**	**cephalopod in diet %**	***Loligo* in diet %**	**Annual population cephalopod consumption (tonnes)**	**Annual population *Loligo* consumption (tonnes)**
Common seal	UK, 1991 Scotland, 1991	1.7%	0.06%	874 819	32 30
Grey seal	UK, 1991 Scotland, 1991	9.4%	0.25%	21,211 19,373	552 504
Harbour porpoise	North Sea, 1994	3.8%	1.98%	23,680	12,229

As previously outlined in the 1995 report of the Working Group it should, again, be stressed that recent projects funded by the EU (see above) have furnished considerable data on basic biology, reproduction, distribution, and genetic variability of a number of commercially important squid species. These projects have also begun to address quantitative aspects of cephalopod populations with the application of fishery models. It is still the case, however, that information on abundance and population dynamics are lacking for many Northeast Atlantic species. Amongst the various areas of work which could be addressed by ICES, those related to a better understanding of cephalopod populations, their role in North Atlantic ecosystems, and the likely effects of continued exploitation are probably the most pressing.

The Working Group recommends that it should continue work on its current terms of reference plus two additional ones:

a) update currently available landing statistics;

b) collect and evaluate data on the life history and exploitation of relevant cephalopod stocks in the ICES area;

c) describe trophic interactions between cephalopods and other marine resources;

d) review trade statistics of cephalopods relevant to the ICES area;

e) review current assessments of loliginid squid in France and UK.

The next meeting of the Working Group is proposed for 3–4 days in March 1997 at the Centro Oceanografico de Canarias (IEO) in Santa Cruz de Tenerife, Spain.

The Chairman closed the meeting at 17.00 hrs on 19 April 1996.

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Table 1. Landings (in tonnes) of Cuttlefish (Sepiidae) and Bobtail Squid (Sepiolidae).

Country	1989	1990	1991	1992	1993	1994P	1995P
ICES Division IVa (Northern North Sea)							
Scotland	+	+	+	+	+	+	+
Total	+	+	+	+	+	+	+
ICES Division IVb (Central North Sea)							
Belgium	0	0	2	12	6	+	1
England & Wales	1	0	+	+	2	+	2
France	+	2	+	+	+	+	+
Total	1	2	2	12	8	+	3
ICES Division IVc (Southern North Sea)							
Belgium	0	0	9	13	25	13	8
England & Wales	10	2	15	26	22	47	163
France	82	117	42	109	172	182	348
Total	92	119	66	148	219	242	519
ICES Division VIa (NW coast of Scotland and North Ireland)							
England & Wales	1	0	+	1	+	1	3
France	1	2	4	+	1	+	+
Total	2	2	4	1	1	1	3
ICES Division VIIa (Irish Sea)							
Belgium	0	0	1	4	1	2	1
England & Wales	3	6	5	46	11	13	16
France	2	6	2	+	1	+	+
Total	5	12	8	50	13	15	17
ICES Divisions VIIb,c (West of Ireland and Porcupine Bank)							
England & Wales	0	0	0	0	0	5	+
France	+	1	+	+	+	+	+
Total	+	1	+	+	+	5	+
ICES Divisions VIId,e (English Channel)							
Belgium	0	0	15	20	24	19	17
Channel Islands	7	20	1	4	2	2	?
England & Wales	1,292	3,000	642	898	1,882	1,797	3,113
France	5,517	9,144	2,820	3,281	6,561	4,151	7,966
Scotland	1	12	1	0	0	0	0
Total	6,817	12,176	3,479	4,203	8,469	5,969	11,096

Table 1. continued.

Country	1989	1990	1991	1992	1993	1994	1995P
ICES Division VIIf (Bristol Channel)							
Belgium	0	0	4	4	11	14	4
England & Wales	10	83	28	35	95	38	42
France	5	99	11	15	13	17	32
Scotland	0	5	0	0	0	0	0
Total	15	187	43	54	119	69	78
ICES Divisions VIIg-k (Celtic Sea and SW of Ireland)							
Belgium	0	0	3	9	12	4	5
England & Wales	68	443	39	101	114	134	197
France	386	2,295	1,215	347	373	295	566
Spain	?	16	20	2	0	0	0
Total	454	2,754	1,277	459	499	433	768
ICES Sub-area VIII (Bay of Biscay)							
Belgium	0	0	0	3	5	4	0
England & Wales	9	7	42	58	41	56	39
France	3,068	6,110	4,411	5,463	3,707	3,043	5,829
Portugal	12	12	11	4	4	5	5
Spain	?	445	581	542	0	1	0
Total	3,089	6,574	5,045	6,070	3,757	3,109	5,873
ICES Sub-area IX (Portuguese Waters)							
Portugal	1,562	1,608	1,197	1,230	1,205	1,120	1,000
Spain	?	49	37	17	14	94	102
Total	1,562	1,657	1,234	1,247	1,219	1,214	1,102
Grand Total	12,037	23,484	11,158	12,244	14,304	11,057	19,459

Table 2. Landings (in tonnes) of Common Squid (includes *Loligo forbesi*, *Loligo vulgaris* and *Alloteuthis subulata*).

Country	1989	1990	1991	1992	1993	1994	1995P
ICES Division IIIa (Skagerrak and Kattegat)							
Denmark	14	19	13	37	2	0	1
Sweden	0	1	1	3	0	+	2
Total	14	20	14	40	2	+	3
ICES Division IVa (Northern North Sea)							
Denmark	1	5	7	7	1	1	1
England & Wales	1	4	1	9	1	1	276
France	19	27	11	7	2	0	+
Germany	+	+	1	3	1	+	+
Scotland	609	952	549	561	242	93	255
Total	630	988	569	587	247	95	532
ICES Division IVb (Central North Sea)							
Belgium	24	38	4	6	22	13	14
Denmark	3	9	2	10	2	+	+
England & Wales	87	83	22	50	22	4	47
France	1	4	2	1	1	1	1
Germany	+	+	1	2	1	1	3
Scotland	70	151	62	106	36	5	25
Total	185	287	93	175	84	24	90
ICES Division IVc (Southern North Sea)							
Belgium	68	142	19	35	84	113	153
Denmark	0	0	0	0	0	+	+
England & Wales	6	3	2	4	3	10	13
France	118	102	111	119	299	193	254
Germany	+	+	1	2	1	2	6
Total	192	247	133	160	387	318	426
ICES Division Vb (Faroe Grounds)							
England & Wales	0	+	0	0	0	1	+
Faroe Islands	+	+	+	+	+	1	+
Scotland	+	2	+	5	+	+	+
Total	+	2	+	5	+	2	+

Table 2. continued.

Country	1989	1990	1991	1992	1993	1994	1995P
ICES Division VIa (NW coast of Scotland and North Ireland)							
England & Wales	14	2	1	50	24	129	444
France	338	330	246	227	148	86	113
Ireland	206	30	15	30	78	36	?
Northern Ireland	+	1	3	21	4	15	?
Scotland	565	267	248	339	182	91	257
Total	1,123	630	513	667	436	357	810
ICES Division VIb (Rockall)							
England & Wales	21	6	1	8	1	6	11
France	+	+	1	+	+	0	+
Ireland	0	10	26	50	5	6	?
Northern Ireland	4	0	+	0	0	0	?
Scotland	681	70	21	65	9	28	4
Total	706	86	49	123	15	40	15
ICES Division VIIa (Irish Sea)							
Belgium	32	36	1	6	0	3	2
England & Wales	92	37	25	74	112	133	161
France	111	32	42	65	47	15	20
Ireland	175	5	4	5	112	66	?
Isle of Man	21	12	7	15	15	6	?
Northern Ireland	105	73	33	89	62	101	?
Scotland	10	9	6	19	10	4	2
Total	546	204	118	273	358	328	185
ICES Divisions VIIb,c (West of Ireland and Porcupine Bank)							
England & Wales	0	0	1	13	47	79	107
France	120	62	60	21	56	11	14
Ireland	11	10	24	40	35	11	?
Northern Ireland	0	0	0	0	1	0	?
Scotland	2	2	2	5	1	18	1
Total	133	74	87	79	140	119	122
ICES Divisions VIId,e (English Channel)							
Belgium	142	213	45	86	70	132	220
Channel Islands	3	2	0	1	0	0	0
England & Wales	720	566	416	698	869	727	667
France	2,777	1,360	1,736	2,218	3,083	1,962	2,584
Total	3,642	2,141	2,197	3,003	4,022	2,821	3,469

Table 2. continued.

Country	1989	1990	1991	1992	1993	1994	1995P
ICES Division VIIf (Bristol Channel)							
Belgium	56	23	10	2	+	4	13
England & Wales	65	56	35	57	134	161	132
France	286	254	191	370	351	298	392
Total	407	333	236	429	485	463	537
ICES Divisions VIIg-k (Celtic Sea and SW of Ireland)							
Belgium	46	54	4	3	2	9	26
England & Wales	43	74	24	122	282	600	970
France	967	519	354	569	624	310	408
Germany	0	0	0	0	0	0	2
Ireland	39	112	80	135	133	164	?
Scotland	0	2	1	8	14	34	1
Spain	?	28	31	62	85	34	27
Total	1,095	789	494	899	1,140	1,151	1,434
ICES Sub-area VIII (Bay of Biscay)							
Belgium	23	40	6	34	36	17	40
England & Wales	22	17	84	65	94	96	56
France	1,667	1,850	1,135	1,222	1,313	1,691	2,225
Portugal	2	7	1	1	0	1	1
Spain	?	260	162	198	2	22	0
Total	1,714	2,174	1,388	1,520	1,445	1,827	2,321
ICES Sub-area IX (Portuguese Waters)							
Portugal	1,001	1,283	1,869	1,569	508	309	831
Spain	?	124	200	246	137	153	167
Total	1,001	1,407	2,069	1,815	645	462	998
ICES Sub-area X (Azores Grounds)							
Portugal+	473	333	258	72	108	114	250
Total	473	333	258	72	108	114	250
Grand Total	11,861	9,715	8,218	9,847	9,514	8,121	11,199

+Landings consist exclusively of *Loligo forbesi*.

Table 3. Landings (in tonnes) of Short-finned Squid (*Illex coindetii* and *Todaropsis eblanae*) and European Flying Squid (*Todarodes sagittatus*).

Country	1989	1990	1991	1992	1993	1994	1995P
ICES Sub-areas I + II (Barents Sea and Norwegian Sea)							
Norway	5	0	0	0	0	0	352
Total	5	0	0	0	0	0	352
ICES Division Va (Iceland Grounds)							
Iceland	0	0	0	0	0	0	11
Total	0	0	0	0	0	0	11
ICES Division VIa, b (NW coast of Scotland and North Ireland, Rockall)							
France	1	1	1	1	+	+	+
Spain	?	0	68	2	0	0	0
Total	1	1	69	3	+	+	+
ICES Divisions VIIb,c (West of Ireland and Porcupine Bank)							
France	1	+	3	4	+	+	+
Total	1	+	3	4	+	+	+
ICES Divisions VIId,e (English Channel)							
England & Wales	1	7	0	0	0	0	+
France	2	1	2	2	1	+	+
Total	3	8	2	2	1	+	+
ICES Division VIIf (Bristol Channel)							
France	+	+	+	1	+	+	+
Total	+	+	+	1	+	+	+
ICES Divisions VIIg-k (Celtic Sea and SW of Ireland)							
England & Wales	0	0	0	0	0	0	29
France	38	37	63	70	44	28	66
Spain	?	741	909	469	374	611	299
Total	38	778	972	539	418	639	394
ICES Sub-area VIII (Bay of Biscay)							
England & Wales	5	0	0	0	0	0	6
France	189	188	173	426	377	222	523
Portugal	2	3	3	11	1	4	3
Spain	?	244	25	364	21	6	0
Total	196	435	201	801	399	232	532

++Landings consist exclusively of *Todarodes sagittatus*.

Table 3. continued.

Country	1989	1990	1991	1992	1993	1994	1995P
ICES Sub-area IX (Portuguese Waters)							
Portugal	267	310	509	766	259	190	96
Spain	?	694	1,410	1,616	632	743	928
Total	267	1,004	1,919	2,382	891	933	1,024
Grand Total	>511	2,226	3,166	3,732	1,709	1,804	2,313

Table 4. Landings (in tonnes) of Octopus (*Eledone cirrhosa* and *Octopus vulgaris*).

Country	1989	1990	1991	1992	1993	1994	1995P
ICES Division IVa (Northern North Sea)							
England & Wales	1	1	0	0	0	0	1
Scotland	59	110	86	31	10	2	12
Total	60	111	86	31	10	2	13
ICES Division IVb (Central North Sea)							
Belgium	0	0	43	24	10	3	0
England & Wales	1	7	2	8	1	4	+
Scotland	0	1	1	1	2	1	0
Total	1	8	46	33	13	8	+
ICES Division IVc (Southern North Sea)							
Belgium	0	0	1	0	1	1	2
England & Wales	0	0	+	1	+	4	8
Total	0	0	1	1	1	5	10
ICES Division VIa, b (NW coast of Scotland and North Ireland, Rockall)							
England & Wales	0	1	5	4	+	1	13
Scotland	8	11	1	3	1	2	39
Spain	?	0	90	4	0	0	0
Total	8	12	96	11	1	3	52
ICES Division VIIa (Irish Sea)							
Belgium	0	0	1	14	8	14	14
England & Wales	3	2	1	2	4	24	1
France	0	0	+	0	0	+	+
Ireland	1	0	0	0	0	+	0
Total	4	2	2	16	12	38	15

Table 4. continued.

Country	1989	1990	1991	1992	1993P	1994	1995P
ICES Divisions VIIb,c (West of Ireland and Porcupine Bank)							
England & Wales	0	0	0	0	+	+	3
Ireland	0	0	0	0	3	2	+
Total	0	0	0	0	3	2	3
ICES Divisions VIId,e (English Channel)							
Belgium	0	0	0	1	2	+	6
England & Wales	47	9	9	20	21	60	77
France	0	638	38	1	2	32	97
Total	47	647	47	22	25	92	180
ICES Division VIIf (Bristol Channel)							
Belgium	0	0	1	2	4	6	9
England & Wales	4	1	1	8	13	26	7
France	0	5	+	1	+	3	9
Total	4	6	2	11	17	35	25
ICES Divisions VIIg-k (Celtic Sea and SW of Ireland)							
Belgium	0	0	1	2	6	10	27
England & Wales	14	3	3	22	57	77	215
France	0	+	+	+	+	6	18
Ireland	0	0	0	1	1	4	?
Spain	?	187	163	179	139	108	134
Total	14	190	167	204	203	205	394
ICES Sub-area VIII (Bay of Biscay)							
Belgium	0	0	0	0	7	6	3
England & Wales	18	0	22	0	0	0	8
France	12	3	4	3	2	56	170
Portugal	57	17	82	144	111	154	200
Spain	?	240	90	214	+	1	0
Total	87	260	198	361	120	217	381
ICES Sub-area IX (Portuguese Waters)							
Portugal	9,831	6,913	7,440	9,476	7,099	7,319	8,842
Spain	?	2,914	2,694	3,499	2,994	2,547	1,898
Total	9,831	9,827	10,134	12,975	10,093	9,866	10,740
ICES Sub-area X (Azores Grounds)							
Portugal^{+}	5	33	7	11	7	7	8
Total	5	33	7	11	7	7	8
Grand Total	10,061	11,096	10,786	13,676	10,505	10,480	11,821

Tab. 5. Total annual cephalopod landings (in tonnes) in ICES area by country and separated into major cephalopod species groups.

Country	1989	1990	1991	1992	1993	1994	1995P
(a) Cuttlefish (Sepiidae) and Bobtail Squid (Sepiolidae).							
Belgium	0	0	34	65	84	56	36
Channel Islands	7	20	1	4	2	2	?
England & Wales	1,394	3,541	771	1,165	2,167	2,091	3,575
France	9,061	17,776	8,505	9,215	10,828	7,688	14,741
Portugal	1,574	1,620	1,208	1,234	1,209	1,125	1,005
Scotland	1	17	1	0	0	0	0
Spain	?	510	638	561	14	95	102
Total	12,037	23,484	11,158	12,244	14,304	11,057	19,459
(b) Common Squid: *Loligo forbesi, Loligo vulgaris, Alloteuthis subulata.*							
Belgium	391	546	89	172	214	291	468
Channel Islands	3	2	0	1	0	0	?
Denmark	18	33	22	54	5	1	2
England & Wales	1,071	848	612	1,150	1,589	1,947	2,884
Faroe Islands	+	+	+	+	+	1	+
France	6,404	4,540	3,889	4,819	5,924	4,567	6,011
Germany	+	2	3	7	3	3	11
Ireland	431	167	149	260	363	283	?
Isle of Man	21	12	7	15	15	6	?
Northern Ireland	109	74	36	110	67	116	?
Portugal	1,476	1,623	2,128	1,642	616	424	1,082
Scotland	1,937	1,455	889	1,108	494	273	545
Spain	?	412	393	506	224	209	194
Sweden	0	1	1	3	0	+	2
Total	11,861	9,715	8,218	9,847	9,514	8,121	11,199
(c) Short-finned Squid: *Illex coindetii, Todaropsis eblanae, Todarodes sagittatus*							
England & Wales	6	7	0	0	0	0	35
France	231	227	242	504	422	250	589
Iceland*	0	0	0	0	0	0	11
Norway*	5	0	0	0	0	0	352
Portugal	269	313	512	777	260	194	99
Spain	?	1,679	2,412	2,451	1,027	1,360	1,227
Total	>511	2,226	3,166	3,732	1,709	1,804	2,313

* Landings consist exclusively of *Todarodes sagittatus*.

Table 5. continued.

Country	1989	1990	1991	1992	1993	1994	1995P
(d) Octopus: *Eledone cirrhosa, Octopus vulgaris.*							
Belgium	0	0	47	43	38	40	61
England & Wales	88	24	43	64	96	196	333
France	12	646	42	5	4	97	294
Ireland	1	0	0	1	4	6	?
Portugal	9,893	6,963	7,529	9,631	7,217	7,480	9,050
Scotland	67	122	88	35	13	5	51
Spain	?	3,341	3,037	3,896	3,133	2,656	2,032
Total	10,061	11,096	10,786	13,676	10,505	10,480	11,821

Tab. 6. Total annual cephalopod landings (in tonnes) in ICES area separated into major cephalopod species groups.

Cephalopod Group	1989	1990	1991	1992	1993	1994	1995P
Cuttlefish	12,037	23,484	11,158	12,244	14,304	11,057	19,459
Common squid	11,861	9,715	8,218	9,847	9,514	8,121	11,199
Short-finned squid	>511	2,226	3,166	3,732	1,709	1,804	2,313
Octopus	10,061	11,096	10,786	13,676	10,505	10,480	11,821
Total	34,470	46,521	33,328	39,499	36,032	31,462	44,792

Table 7. *Sepia officinalis* and *Alloteuthis subulata*. Data on life history, environmental factors and fisheries.

	Sepia officinalis	*Alloteuthis subulata*
LIFE HISTORY		
Eggs:		
Egg principal axis (mm)	20 - 30	1.2 - 1.8
Potential fecundity	5,000	unknown
No. of eggs spawned per female	500 - 5,000	400 - 1,500
No. of spawning episodes	several (1 - 5)	several
Benthic or pelagic	benthic	benthic, attached to substrate
Duration of embryological development	80 - 90 days (15°C); 40 - 45 days (20°C)	not investigated
Paralarvae:		
Size at hatching (mantle lenghth in mm)	6 - 9	1.4 - 1.8
Temperature dependence	weak - medium	medium
Location in water column	benthic	rarely found; pelagic?
Duration in plankton	no planktonic phase	15 - 30 days
Reproductive cycle:		
Spawning season	early spring to summer	all year; mainly spring to autumn
Spawning location	shallow waters	shallow waters
Spawning depth	2 - 50 m	8 - 200 m
Preferred substrate	sandy and muddy bottoms	sandy and hard bottoms
No. of cohorts per year	at least 2	2 (or 3)
Growth:		
Mantle length at full maturity; male (mm)	70 - 210	40 - 200
Mantle length at full maturity; female (mm)	42 - 250	50 - 120
Weight range at full maturity; male (g)	33 - 957	4 - 10
Weight range at full maturity; female (g)	72 - 1,560	5 - 16
Lifespan	16 - 24 months	10 - 12 months
Minimum age at maturity	16 months	variable; at ca. 10 months
Form of growth (mantle length)	sigmoid	exponential
Population recruitment: how variable	unknown	unknown
Natural mortality rates	unknown	high during early stages
Distibution:		
Geographic	North East Atlantic (25-57°N) and Mediterranean shelf waters	North East Atlantic (20-60°N) and Mediterranean shelf waters
Bathymetric	surface - 300 m	surface - 200 m; max. 2,000 m
Migration pattern (e.g. inshore-offshore)	offshore - inshore	inshore - offshore
Migration scale (e.g. m; km; etc.)	30 - 50 km	unknown

Table 7. Continued.

	Sepia officinalis	*Alloteuthis subulata*
ENVIRONMENTAL FACTORS		
Habitat:		
Depth range of paralarvae (m)	epibenthic in shallow waters	45 - 100
Depth range of juveniles/adults (m)	10 - 300	15 - 300
Temperature range of paralarvae (°C)	10 - 30	2 - 25
Temperature range of juveniles/adults (°C)	10 - 30	2 - 25
Salinity range of paralarvae (S ‰)	18 - 36	unknown
Salinity range of juveniles/adults (S ‰)	18 - 36	unknown
Effects on survival, development, growth	not as important as in squid	probably very strong
FISHERIES		
Directed or by-catch	both	by-catch
Seasonality of fishery	all year; mostly NOV - JUL	no season
Geographic location of fishery, main fishery nations	English Channel to Portugal; France, Portugal, Spain, UK	throughout range of distribution
Inshore or offshore	inshore	inshore
Fishing methods	traps and gillnets, artisanal fishery (91% in Portugal)	trawling
Estimated catch data:		
Quality	poor	not available and mixed with other loliginid squids
Landings in ICES region (= FAO 27)	ca. 25,000 t (1995)	353 t (Portugal, 1990)
Range of landings over past 10 years in ICES region	5,000 - 27,000 t	unknown
Availability of CPUE data	not available	not available
Mantle length range of exploited population	40 - 350 mm	100 - 200 mm
Weight range of exploited population	15 - 2,800 g	5 - 35 g
Exploitation level	high	unknown
Stock recruitment relationship	unknown	unknown
Timing of recruitment to fishery	JAN - JUL	early summer
Variability of recruitment into fishery	unknown	unknown
Environmental influences on catch	new moon, storms	currents, hydrography
Assessment:		
Stock biomass or abundance	unknown	Max.= 132 ind./h; 0.7 hg/h Min.= 14 ind./h; <0.1 kg/h (Portugal 1990; 1992)
No. of stocks identified	local stocks identified	unknown
Method applied	no assessment	swept area method; abundance indices from survey cruises (Portugal)
Research activities in ICES area:		
Country	France, Portugal, Spain	Portugal
Region	ICES divisions VII - IX	ICES division IX

Table 8. *Loligo forbesi* and *Loligo vulgaris*. Data on life history, environmental factors and fisheries.

	Loligo forbesi	*Loligo vulgaris*
LIFE HISTORY		
Eggs:		
Egg principal axis (mm)	3 - 5	2 - 4.1
Potential fecundity	5,000 - 32,000	3,000 - 25,000 (average 17,000)
No. of eggs spawned per female	ca. 2,000	ca. 3,000 - 5,000
No. of spawning episodes	several (2 - 3?)	several (1 - 2?)
Benthic or pelagic	benthic, attached to substrate	
Duration of embryological development	1 - 3 months	40 - 45 days (13°C); 26 days (22°C)
Paralarvae:		
Size at hatching (mantle lenghth in mm)	2.7 - 4.9	1.2 - 3
Temperature dependence	strong	
Location in water column	planktonic; rarely found, low numbers close to bottom	
Duration in plankton	1 - 3 months	ca. 2 months
Reproductive cycle:		
Spawning season	OCT - MAY; extended; peak in DEC - JAN	all year, extended; peak mainly in winter
Spawning location	coastal shallow waters	
Spawning depth	10 - 300 m	5 - 195 m
Preferred substrate	hard substrate	hard substrate; coarse sand
No. of cohorts per year	multiple "microcohorts"; ≤ 2	multiple cohorts
Growth:		
Mantle length at full maturity; male (mm)	100 - 650; (240 - 937)*	75 - 500
Mantle length at full maturity; female (mm)	175 - 350; (200 - 462)*	75 - 350
Weight range at full maturity; male (g)	155 - 3,700 (average 2,000) (370 - 8,300)*	22 - 1,690
Weight range at full maturity; female (g)	200 - 1,150 (average 1,500) (260 - 2,200)*	23 - 1,272
Lifespan	6 - 18 months (average 15 - 18)	7 - 22 months (average 12 - 14)
Minimum age at maturity	6 months; variable	7 months; variable
Form of growth (mantle length)	exponential	initially exponential
Population recruitment: how variable	variable; higher during summer	variable; high in spring/summer
Natural mortality rates	high, if compared to fish	
Distibution:		
Geographic	North East Atlantic (25-62°N) and Mediterranean shelf waters; Azores; central East Atlantic	North East Atlantic (15-60°N) and Mediterranean shelf waters; central East Atlantic
Bathymetric	shelf & shelf edge; 10 - 550 m; mainly in 50 - 250 m	shelf & shelf edge; 10 - 300; mainly in 10 - 100 m
Migration pattern (e.g. inshore-offshore)	inshore - offshore	
Migration scale (e.g. m; km; etc.)	<500 km	<200 km

* in Azores region

Table 8. Continued.

	Loligo forbesi	*Loligo vulgaris*
ENVIRONMENTAL FACTORS		
Habitat:		
Depth range of paralarvae (m)	10 - 100 m	10 - 120 m
Depth range of juveniles/adults (m)	10 - 500 m; mainly 100-200m	10 - 300 m; mainly 15-100m
Temperature range of paralarvae (°C)	10 - 20	10 - 20
Temperature range of juveniles/adults (°C)	6 - 24	10 - 25
Salinity range of paralarvae (S ‰)	30 - 36	30 - 36
Salinity range of juveniles/adults (S ‰)	30 - 36	30 - 36
Effects on survival, development, growth	high	
FISHERIES		
Directed or by-catch	both	both
Seasonality of fishery	all year; with variable peaks, mostly in early autumn	
Geographic location of fishery	throughout range of distribution	
Inshore or offshore	coastal continental shelf; mainly inshore	
Fishing methods	trawling; hand-jigging	mostly trawling, manual jigging
Estimated catch data:		
Quality	poor; data not fully reported and not separated by species	
Landings in ICES region (= FAO 27)	11,000 t (1995)	
Range of landings over past 10 years in ICES region	8,000 - 12,000 t	
Availability of CPUE data	available only for some countries	
Mantle length range of exploited population	70-640 mm (average 110 mm) <940 mm (Azores) 340-680 mm (Canaries)	60-500 mm (average 110 mm)
Weight range of exploited population	20 - 3,700 g (average 60 g) <8,300 g (Azores) 1,050 - 4,100 (Canaries)	10 - 1,000 g (average 40 g)
Exploitation level	variable/unknown	
Stock recruitment relationship	weak	
Timing of recruitment to fishery	all year; seasonal peaks	
Variability of recruitment into fishery	high	
Environmental influences on catch	moon light; rough weather	
Assessment:		
Stock biomass or abundance	preliminary estimates for northern range; abundance indices from research cruises (Portugal)	
No. of stocks identified	offshore and coastal European stock differences; separated stock around Azorers	1 (European shelf)
Method applied	DeLury depletion methods	
Research activities in ICES area:		
Country	France, Portugal, Spain, UK	France, Portugal, Spain, UK
Region	throughout ICES regions	throughout ICES regions

Table 9. *Illex coindetii* and *Todaropsis eblanae*. Data on life history, environmental factors and fisheries.

	Illex coindetii	*Todaropsis eblanae*
LIFE HISTORY		
Eggs:		
Egg principal axis (mm)	<1.0	1.4 - 1.7
Potential fecundity	6,500 - 285,000 (max.: 729,000)	124,000 ± 18,000
No. of eggs spawned per female	4,000 - 120,000	122,000 ± 18,000
No. of spawning episodes	several	several; probably 4 - 10
Benthic or pelagic	pelagic	probably pelagic
Duration of embryological development	unknown	
Paralarvae:		
Size at hatching (mantle lenghth in mm)	0.8 - 1.0	unknown
Temperature dependence	strong	probably strong
Location in water column	planktonic	
Duration in plankton	unknown	
Reproductive cycle:		
Spawning season	all year, peaks in spring, autumn	all year, peaks in spring
Spawning location	probably slope water	probably shel edge
Spawning depth	unknown	probably above 150 m
Preferred substrate	unknown	associated with sandy or muddy bottom
No. of cohorts per year	unknown	
Growth:		
Mantle length at full maturity; male (mm)	95 - 360	98 - 168
Mantle length at full maturity; female (mm)	79 - 380	107 - 222
Weight range at full maturity; male (g)	30 - 1,549 (average 400)	94 - 300
Weight range at full maturity; female (g)	32 - 1,180 (average 750)	180 - 720
Lifespan	12 - 14 months	ca. 12 months
Minimum age at maturity	unknown	220 - 280 days
Form of growth (mantle length)	linear?	linear
Population recruitment: how variable	linear in post-recruits	highly variable
Natural mortality rates	very high in early stages	
Distibution:		
Geographic	Eastern Atlantic Ocean: 15°S to 60°N; Mediterranean and Black Seas; Caribbean Sea	Eastern Atlantic Ocean: 36°S to 60°N; Mediterranean Sea; Australia; Indian Ocean
Bathymetric	30 - 1,000 m	20 - 800 m
Migration pattern (e.g. inshore-offshore)	unknown	seasonal bathymetric migrations
Migration scale (e.g. m; km; etc.)	unknown	km

Table 9. Continued.

	Illex coindetii	*Todaropsis eblanae*
ENVIRONMENTAL FACTORS		
Habitat:		
Depth range of paralarvae (m)	60 - 100	60 - 100
Depth range of juveniles/adults (m)	30 - 1,000	20 - 800
Temperature range of paralarvae (°C)	13 - 20	13 - 20
Temperature range of juveniles/adults (°C)	7.5 - 18	6 - 18
Salinity range of paralarvae (S ‰)	unknown	
Salinity range of juveniles/adults (S ‰)	unknown	
Effects on survival, development, growth	very strong	
FISHERIES		
Directed or by-catch	by-catch	
Seasonality of fishery	all year; higher in spring and autumn	
Geographic location of fishery, main fishery nations	continental shelf and slope regions off Ireland, Portugal, Spain	
Inshore or offshore	offshore	
Fishing methods	trawling	
Estimated catch data:		
Quality	poor; data not fully reported, species not separated and mixed with other short-fin squids	
Landings in ICES region (= FAO 27)	ca. 2,300 t (1995)	
Range of landings over past 10 years in ICES region	1,500 - 6,000 t	
Availability of CPUE data	not available	
Mantle length range of exploited population	55 - 380	42 - 220
Weight range of exploited population	4 - 1,500	6 - 720
Exploitation level	low	probably low
Stock recruitment relationship	unknown	
Timing of recruitment to fishery	all year; peaks in autumn	
Variability of recruitment into fishery	high	moderate
Environmental influences on catch	hydrography; currents	
Assessment:		
Stock biomass or abundance	unknown	
No. of stocks identified	1 in Galician waters by morphometrics and enzymes	1 in Galician waters by morphometrics and enzymes
Method applied	no assessment	no assessment
Research activities in ICES area:		
Country	Ireland, Portugal, Russia (ageing studies), Spain	Ireland, Portugal, Spain
Region	ICES divisions VIII - IX	ICES divisions VIII - IX

Table 10. *Todarodes sagittatus* and *Gonatus fabricii*. Data on life history, environmental factors and fisheries.

	Todarodes sagittatus	*Gonatus fabricii*
LIFE HISTORY		
Eggs:		
Egg principal axis (mm)	unknown	5
Potential fecundity	unknown	unknown
No. of eggs spawned per female	12,000 - 18,000	ca. 10,000
No. of spawning episodes	1?	unknown
Benthic or pelagic	Benthic?	Benthic
Duration of embryological development	unknown	unknown
Paralarvae:		
Size at hatching (mantle lenghth in mm)	unknown	3
Temperature dependence	unknown	3.9 - 4.4
Location in water column	unknown	0 - 1,000 m
Duration in plankton	unknown	ca. 6 months
Reproductive cycle:		
Spawning season	winter, early spring (northern range)	DEC - APR
Spawning location	slope waters; west off Ireland?	continental slope of North East Atlantic; grounds of bottlenose whales
Spawning depth	unknown	>400 m
Preferred substrate	unknown	unknown
No. of cohorts per year	unknown	unknown
Growth:		
Mantle length at full maturity; male (mm)	>260	175 - 250
Mantle length at full maturity; female (mm)	>370	250 - 340
Weight range at full maturity; male (g)	unknown	88 - 226
Weight range at full maturity; female (g)	493 - 1,156 (Canaries)	400 - 615
Lifespan	<24 months	>12 months
Minimum age at maturity	ca. 12 months	unknown
Form of growth (mantle length)	linear	linear
Population recruitment: how variable	probably highly variable	unknown
Natural mortality rates	very high in early stages	unknown
Distibution:		
Geographic	whole North East Atlantic	Labrador Sea, Barents Sea and Norwegian Sea and adjacent waters
Bathymetric	0 - 1,000 m	0 - 2,700 m
Migration pattern (e.g. inshore-offshore)	pronounced feeding migrations	unknown
Migration scale (e.g. m; km; etc.)	unknown	unknown

Table 10. Continued.

	Todarodes sagittatus	*Gonatus fabricii*
ENVIRONMENTAL FACTORS		
Habitat:		
Depth range of paralarvae (m)	surface waters?	0 - 2,000
Depth range of juveniles/adults (m)	0 - 1,000	<2,700
Temperature range of paralarvae (°C)	unknown	0.5 - 14
Temperature range of juveniles/adults (°C)	5 - 7 (northern range) 16 - 24 (Canaries)	0.5 - 14
Salinity range of paralarvae (S ‰)	unknown	31.2 - 35.3
Salinity range of juveniles/adults (S ‰)	unknown	31.2 - 35.3
Effects on survival, development, growth	strong	unknown
FISHERIES		
Directed or by-catch	directed and by-catch	by-catch
Seasonality of fishery	AUG - DEC (ICES sub-area IIa)	all year
Geographic location of fishery, main fishery nations	North East Atlantic slope regions; Norwegian fjords	North East Atlantic slope regions; Norwegian fjords
Inshore or offshore	mainly inshore	offshore
Fishing methods	jigging; purse seines (Canaries)	trawling
Estimated catch data:		
Quality	poor; data not fully reported, species not separated and mixed with other squids	
Landings in ICES region (= FAO 27)	ca. 400 t (1995)	unknown
Range of landings over past 10 years in ICES region	0 - 15,000 t	unknown
Availability of CPUE data	not available	not available
Mantle length range of exploited population	ca. 200 - 400 mm (Norway) 147 - 340 mm (Canaries)	>200 mm in by-catch
Weight range of exploited population	150 - 4,000	unknown
Exploitation level	variable	no exploitation
Stock recruitment relationship	unknown	unknown
Timing of recruitment to fishery	3 - 4 months	unknown
Variability of recruitment into fishery	high (one year class)	unknown
Environmental influences on catch	hydrography, currents	unknown
Assessment:		
Stock biomass or abundance	unknown	unknown
No. of stocks identified	probably 2 (northern range, and southwestern range)	unknown
Method applied	no assessment	no assessment
Research activities in ICES area:		
Country	Ireland, Norway; Spain	Germany, Iceland, Norway
Region	whole ICES region	ICES divisions I, II, Va; IX

Table 11. *Octopus vulgaris* and *Eledone cirrhosa*. Data on life history, environmental factors and fisheries.

	Octopus vulgaris	*Eledone cirrhosa*
LIFE HISTORY		
Eggs:		
Egg principal axis (mm)	2.0 - 3.0	6.7 - 7.5
Potential fecundity	500,000	2,000 - 7,500
No. of eggs spawned per female	100,000 - 500,000	unknown
No. of spawning episodes	1 (within 1 - 2 months)	1 (extended over 3 - 4 weeks)
Benthic or pelagic	Benthic, protected by female	
Duration of embryological development	125 days (13°C); 30 - 60 days (15-20°C); 25 days (25°C)	3 - 4 months
Paralarvae:		
Size at hatching (mantle lenghth in mm)	1.4 - 2.0; 1.4 mg	ca. 3
Temperature dependence	strong	strong
Location in water column	planktonic	planktonic
Duration in plankton	5 - 12 weeks	few days
Reproductive cycle:		
Spawning season	FEB - OCT; peaks in June and September	all year; peaks between April to October
Spawning location	shallow waters, inshore	
Spawning depth	< 100 m	< 200 m
Preferred substrate	rocky and sandy bottom, caves	flat muddy and rocky bottom
No. of cohorts per year	2 or more	probably 1 annual recruitment
Growth:		
Mantle length at full maturity; male (mm)	95 - 250	50 - 180
Mantle length at full maturity; female (mm)	185 - 260	120 - 400
Weight range at full maturity; male (g)	200 - 6,100	400 - 700
Weight range at full maturity; female (g)	390 - 4,300	1,200 - 2,000
Lifespan	12 - 24 months	12 - 24 months
Minimum age at maturity	10 - 18 months, variable	ca. 12 months, variable
Form of growth	exponential	exponential ?
Population recruitment: how variable	highly variable	highly variable (MAR-JUL)
Natural mortality rates	very high	
Distibution:		
Geographic	cosmopolitan; in all North East Atlantic coastal waters, from southern North Sea to west of Africa	North East Atlantic coastal and shelf waters from Norway to Portugal, Iceland; eastern Mediterranean Sea
Bathymetric	benthic; 2-100 m; max. 400 m	benthic; 0-200 m (shore line); max. 770m
Migration pattern (e.g. inshore-offshore)	inshore for spawning	inshore for spawning
Migration scale (e.g. m; km; etc.)	< 50 km	unknown (few km?)

Table 11. Continued.

	Octopus vulgaris	*Eledone cirrhosa*
ENVIRONMENTAL FACTORS		
Habitat:		
Depth range of paralarvae (m)	surface - 500	0 - 500
Depth range of juveniles/adults (m)	surface - 200	0 - 770
Temperature range of paralarvae (°C)	10 - 25	unknown
Temperature range of juveniles/adults (°C)	10 - 30	unknown
Salinity range of paralarvae (S ‰)	not documented	unknown
Salinity range of juveniles/adults (S ‰)	32 - 40%	unknown
Effects on survival, development, growth	strong	strong
FISHERIES		
Directed or by-catch	both	by-catch
Seasonality of fishery	all year	MAR - JUL
Geographic location of fishery, main fishery nations	whole range of distribution; Portugal, Spain	whole range of distribution in 10 - 12 m; Portugal, Spain
Inshore or offshore	inshore	mostly inshore
Fishing methods	traps and pots; trawling	bottom trawls; seines; pots
Estimated catch data:		
Quality	poor; data not fully reported and not separated by species	
Landings in ICES region (= FAO 27)	ca. 12,000 t (1995)	
Range of landings over past 10 years in ICES region	7,000 - 18,000 t	
Availability of CPUE data	not available	not available
Mantle length range of exploited population	34 - 260 mm	unknown
Weight range of exploited population	100 - 14,000 g (average 500 g)	<ca. 2,000 g
Exploitation level	high	variable/unknown
Stock recruitment relationship	unknown	unknown
Timing of recruitment to fishery	all year	unknown
Variability of recruitment into fishery	variable; mostly high	unknown
Environmental influences on catch	wind; hydrography	unknown
Assessment:		
Stock biomass or abundance	unknown	unknown
No. of stocks identified	unknown	unknown
Method applied	no assessment	no assessment
Research activities in ICES area:		
Country	Portugal, Spain	Scotland
Region	ICES divisions VIII - X	Scottish waters

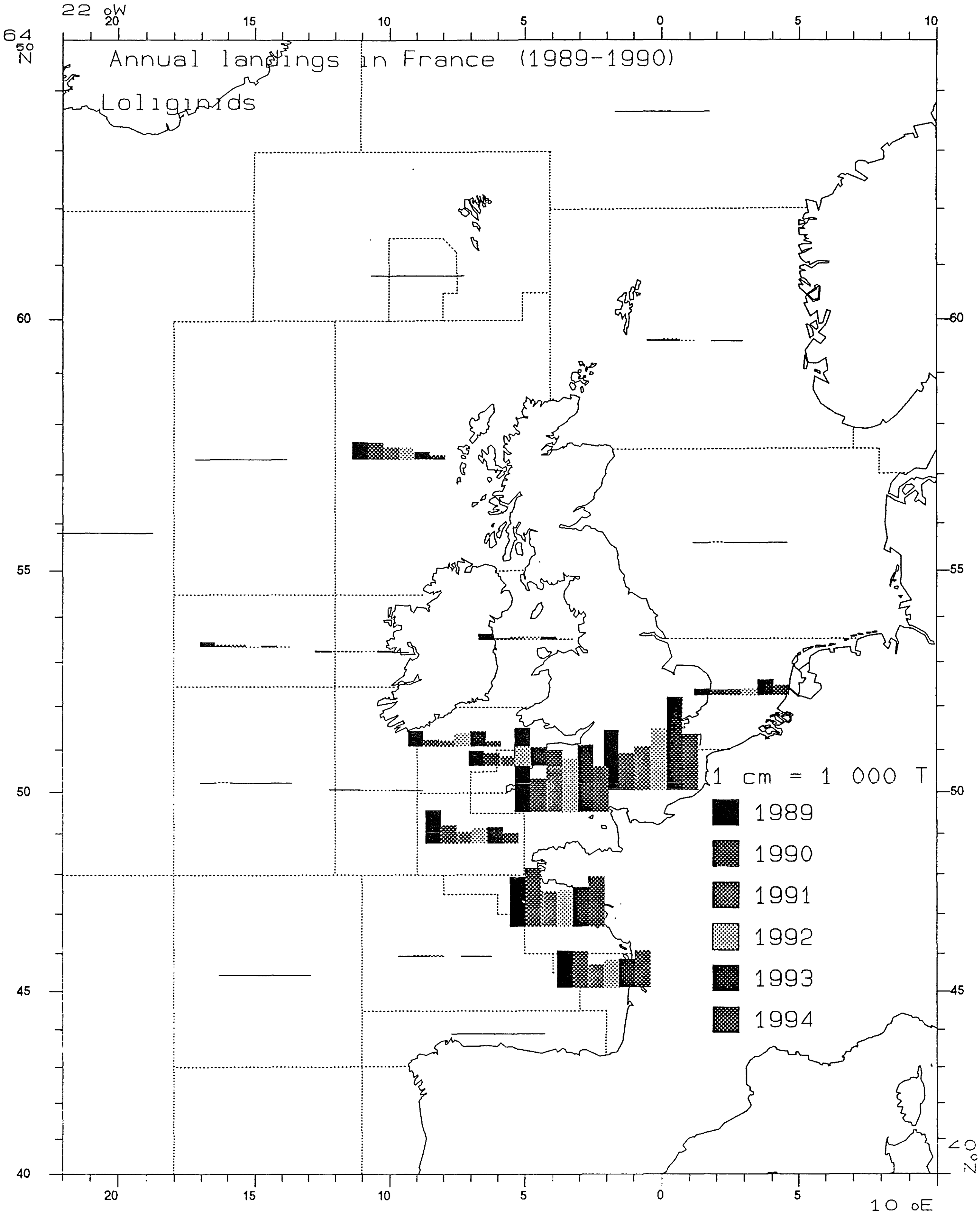
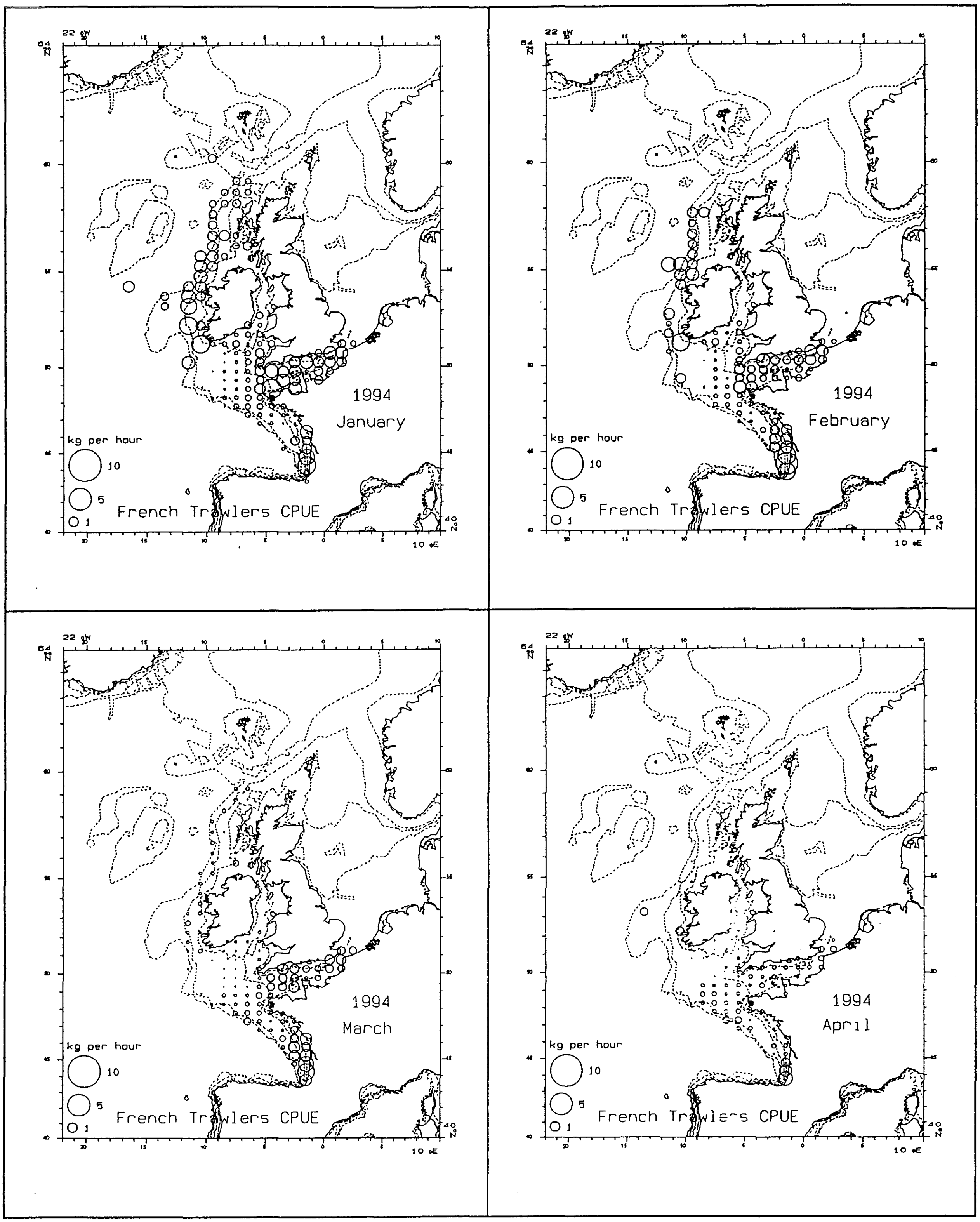


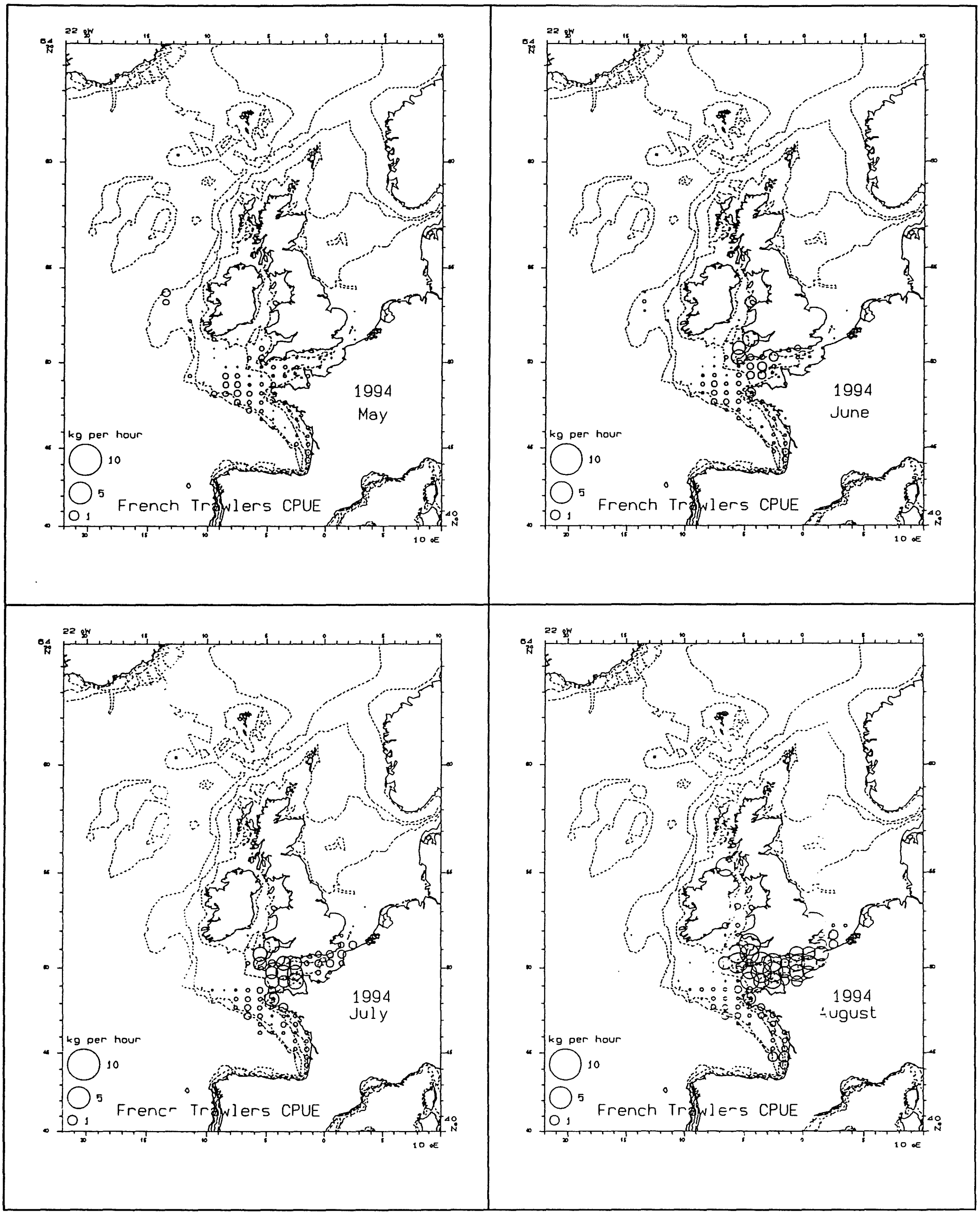
Fig. 1

Loliginid Annual Landings per ICES division in the French Fishery (1989 - 1994)



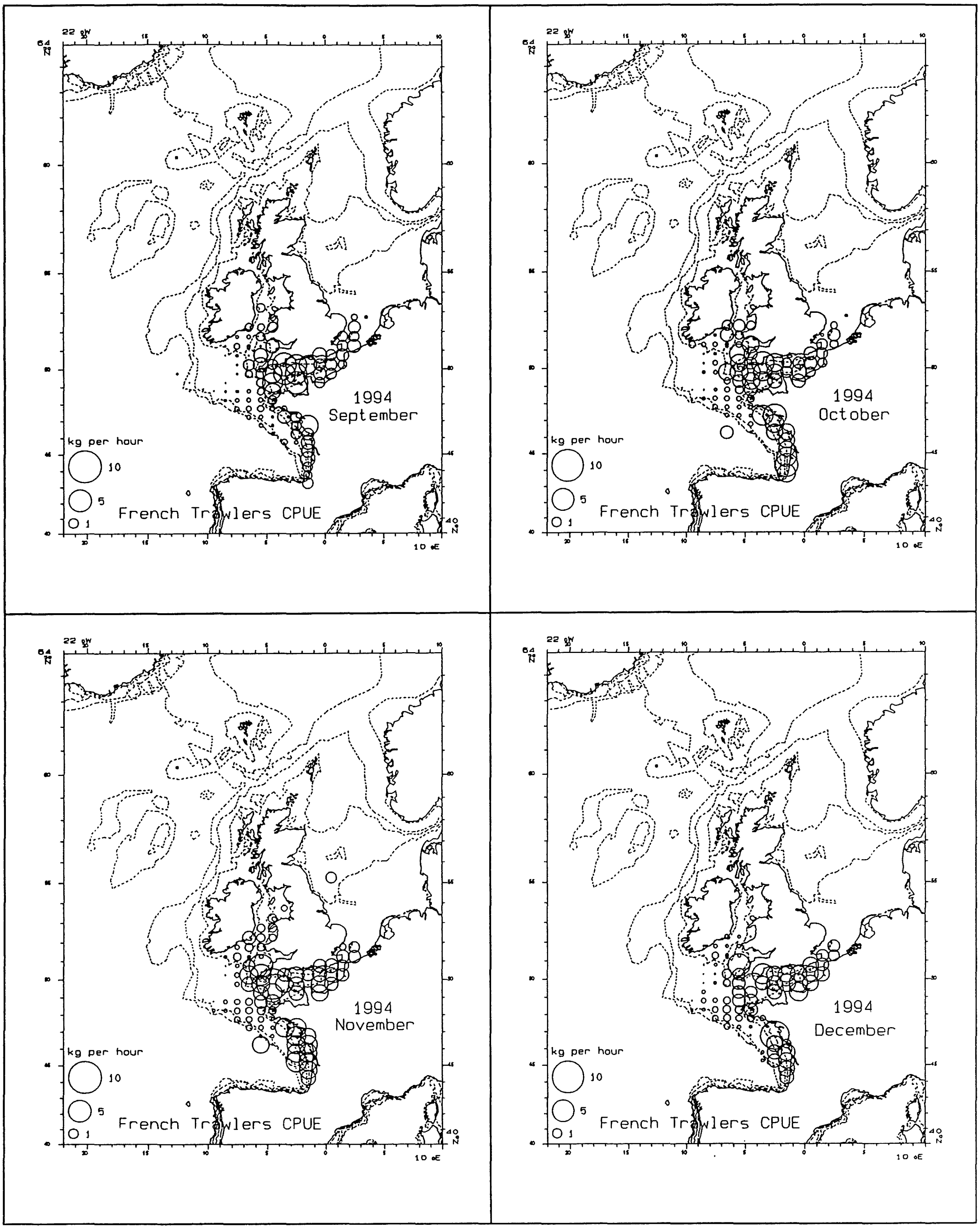
Loliginid CPUE in the French Trawlers Fishery: period 1994 January - April
(CPUE in kg per fishing hour of a 100kW fishing boat)

Fig. 2



Loliginid CPUE in the French Trawlers Fishery: period 1994 May - August
(CPUE in kg per fishing hour of a 100kW fishing boat)

Fig. 3



Loliginid CPUE in the French Trawlers Fishery: period 1994 September- December
(CPUE in kg per fishing hour of a 100kW fishing boat)

Fig. 4

ANNEX 1

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ANNEX 3

Working document to the ICES Working Group on Cephalopods Fisheries
and Life History
Lisbon, 17-19 April 1996.

SPANISH CEPHALOPOD LANDINGS IN ICES WATERS, 1990-1995
(Sub-areas VI, VII, VIII and IX)

by

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ABSTRACT

In this paper, available data on Spanish cephalopod landings for the period 1990-1995 in the ICES waters are presented. Catches were obtained in ICES Sub-areas VI, VII, VIII and IX by artisanal and industrial vessels.

The results indicate that Spanish cephalopod landings from ICES waters during the period ranged from 3600 to 7400 metric tonnes, with an average of 5400 tonnes/year. The main contribution to these landings was that of the octopods (*Octopus vulgaris* and *Eledone cirrosa*) accounting for 56 % of the total. Landings of ommastrephid squid (*Illex coindetii* and *Todaropsis eblanae*) and cuttlefish (particularly *Sepia officinalis*), show a marked seasonal distribution, with higher landings in autumn to spring, and lower in summer. Landings of *Alloteuthis* spp. occur only in the first half of the year, probably indicating the existence of an important spring recruitment. *Loligo* spp. is caught throughout the year, occurring higher landings in the second half, mainly in summer.

The total catch of *Octopus vulgaris* and *Alloteuthis* spp. was obtained in Divisions VIIIc and IXa, while most of the cuttlefish and a third of *Loligo* spp. were caught in Divisions VIIIa,b.

The seasonality observed in catches may be related to seasonality in fishing behaviour, abundance and/or in recruitments.

MATERIAL AND METHODS

Data on landings of cephalopods was collected in the main fishing harbours of north and north-west Spain, using the statistical database compiled in the fish markets of those ports (Figure 1). Due to the difficulty for achieving an exhaustive monitoring of landings in the fish markets, occasionally, an unknown portion of landings is not registered in the statistics, mainly in some artisanal harbours (Table 1 shows data available by harbour and year). For this reason, the information presented in this document should be considered with caution.

Cephalopods are caught by artisanal vessels targeting *Loligo* spp., *Sepia* spp. and *Octopus vulgaris* in ICES divisions VIIIc and IXa, or as a by-catch by industrial vessels operating in ICES areas VI, VII, VIII and IX, being *Illex coindetii, Todaropsis eblanae* and *Eledone cirrhosa* the main species for this vessels.

Sometimes the statistics do not indicate the origin of landings, but we have estimated that in these cases, more than 80% of the catch originates in Divisions VIIIc and IXa, even though we cannot assess the proportion coming from each one of them.

Although statistics have some lacks and deficiencies, the figures can be taken as an approach to real landings, and as an index of the evolution of the fisheries.

Since most of the landings were not separated by species in the statistics, data is classified as follows:

"Loligo spp" includes *Loligo vulgaris* and *L.forbesi*.

"Cuttlefish" consists of *Sepia officinalis, S. elegans* and *S. orbignyana*, although most of the catch is made up of the first species.

"Ommastrephids" comprise *Illex coindetii* and *Todaropsis eblanae*, and some irrelevant quantities of *Todarodes sagitattus*.

"Unspecified octopods" includes *Eledone cirrhosa* and *Octopus vulgaris*, for those harbours in which landings of both species are not distinguished in the statistics.

"Alloteuthis spp." includes *Alloteuthis media* and *A. subulata*.

RESULTS AND DISCUSSION

Table 2 shows total cephalopod landings in Spanish harbours (caught in ICES waters), by species or group of species for the study period. Landings are given by year, but also the period average for each species or group of species and the standard deviation (STD) is shown in the table.

The results indicate a general decrease in landings since 1993, particularly in *Loligo* spp. and *Sepia* spp. The explanation for this change is the absence of statistics for Pasajes and Ondarroa harbours (Basque Country) since 1993, when control of these ports was transferred to the Basque Government. Ondarroa and Pasajes have an important trawling fleet, and the lack of information since 1993 is well reflected in the data, particularly for Divisions VIIIab (see Table 5), where Basque trawlers have historically exerted an important activity. Data in Table 2 are represented in Figure 2 (except *Alloteuthis* spp., whose catches are irrelevant).

In Tables 3 and 4, landings of cephalopods coming from Sub-areas VI and VII are presented respectively, while these landings from Divisions VIIIab are shown in table 5.

Table 6 shows landings from divisions VIIIc and IXa. All landings of *Octopus vulgaris* and Alloteuthis spp. are caught in these divisions.

Figure 3 shows the relative importance (average percentage) of each cephalopod group in landings for the whole period. Octopods are by far the most important cephalopod resource to the Spanish fishing fleet in ICES waters, with 56 % of the total landings, while ommastrephids in second place represents 31.6 %. Results shown in Figure 3 are highly coincident with the results obtained in Galician waters (between Guarda and Ribadeo, Figure 1) by González et al. (in press) for the period 1980-1991. The similarity of the results suggests that no significant changes took place in the fishery pattern between both periods.

Figure 4 shows the origin of the landings for each cephalopod group, and indicates that most of the landings originate in Spanish waters (divisions VIIIc and IXa). *Octopus vulgaris* and *Alloteuthis* spp. are not included in the figure because, as stated above, the total catch comes from the divisions mentioned. Most of the cuttlefish, and a little more than a third of *Loligo* spp., are caught off the French coast (Divisions VIII a,b). Landings from Sub-areas VI and VII are not significant, except for ommastrephids (one third of the short-finned squid landings have been caught in Sub-area VII).

Figure 5 shows average monthly landings for the period 1994-1995, using statistics from Riveira and Grove harbours exclusively. These statistics have an acceptable level of confidence, and, very probably, the temporary pattern of coastal catches in these ports represents the general pattern in Divisions VIIIc and IXa. A certain degree of seasonality in the landings of all the groups can be observed. Such seasonality is probably related to some biological features that will be briefly discussed in the following paragraphs.

Landings of ommastrephid squid have a marked seasonal distribution, with peak landings occurring from October-November to March-May, and lower landings in summer. This pattern has also been observed by González et al. (1994 and 'in press'). Besides a possible change in the fishing behaviour of the fleet during summer, the biological explanation could be the existence of an intense recruitment during autumn and winter, and a high post-spawning mortality at the end of spring, both causing the comparatively low catches of summer (González et al, 1994 and 'in press').

Landings of Cuttlefish (and less clearly, of *Octopus vulgaris*) have a temporal pattern similar to that of the ommastrephids, the causes of which may be similar to those discussed for short-finned squid. *Alloteuthis* spp. catches occur only in the first half of the year (especially in spring), probably indicating the existence of an important spring recruitment. *Loligo* spp. is caught throughout the year, the higher landings occurring in the second half, especially in summer. This is coincident with the observations by Guerra et al (1994) and Simon et al. (in press) in Galician waters, Pierce et al (1994) in Scotland, and Cunha and Moreno (1994) in Portugal. The seasonality observed in catches can be related to seasonality in fishing behaviour (especially in the hand-jig fishery; Simon et al, 1994), abundance and recruitment (Pierce et al., 1994; Guerra et al., 1994).

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TABLE 1. Fishing harbours in north and northwestern Spain where landing statistics were obtained. Columns indicate the years and species for which statistics were available.

PORT	*Loligo* spp.						Cuttlefish						Ommastrephids						*Octopus vulgaris*						*Eledone cirrhosa*						Unespecified Octopods						*Alloteuthis* spp.					
	90	91	92	93	94	95	90	91	92	93	94	95	90	91	92	93	94	95	90	91	92	93	94	95	90	91	92	93	94	95	90	91	92	93	94	95	90	91	92	93	94	95
AVILES	X	X	X	X	X		X	X	X	X	X		X	X	X	X	X								X	X	X	X	X													
BAIONA					X						X												X																			
BURELA	X	X	X	X	X								X	X	X	X	X		X	X	X	X	X		X	X	X	X	X													
CAMARIÑAS	X	X	X	X															X	X	X	X	X																			
CAMELLE																							X																			
CARIÑO	X	X	X	X	X								X	X	X	X	X		X	X	X	X	X																			
CAYON																			X	X	X	X	X																			
CEDEIRA	X	X	X	X	X														X	X	X	X	X																			
CILLERO	X	X	X	X	X		X	X	X	X	X		X	X	X	X	X														X	X	X	X	X							
CORUÑA	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X						
FERROL	X	X	X	X															X	X	X	X																				
FINISTERRE	X	X	X											X	X	X	X		X	X	X	X	X																			
FOZ	X	X	X	X	X														X	X	X	X	X																			
GROVE					X	X					X	X					X						X	X																		
GUARDA																							X																			
LAXE	X	X	X	X	X		X	X	X	X	X		X	X	X	X	X		X	X	X	X	X																			
MALPICA	X	X	X	X	X														X	X	X	X	X																			
MARIN		X	X	X	X	X								X	X	X	X	X														X	X	X	X	X						
MUXIA	X	X	X	X	X		X	X	X	X	X								X	X	X	X	X																			
ONDARROA	X	X	X				X	X	X				X	X	X										X	X	X															
PASAJES	X	X	X				X	X	X				X	X	X										X	X	X															
PORTO DO SON					X	X					X	X											X	X																		
RIBADEO	X	X	X	X	X		X	X					X	X	X	X	X		X	X	X	X	X																			
RIVEIRA					X	X					X	X					X	X																	X	X					X	X
SADA	X	X	X	X	X																																					
SANTANDER	X	X	X	X	X		X	X	X	X	X		X	X	X	X	X								X	X	X	X	X													

TABLE 2. Total Spanish cephalopod landings (tonnes) in ICES waters for the period 1990-1995.

YEAR	*Loligo* spp.	Cuttlefish	Ommastrephids	*Octopus vulgaris*	*Eledone cirrhosa*	Uns. Octopods	*Alloteuthis* spp.	YEARLY TOTAL
1990	412.0	510.6	1680.0	1708.3	1105.6	527.3		5943.8
1991	393.5	637.0	2412.0	1173.3	718.2	1145.3		6479.4
1992	505.9	560.8	2450.9	1255.5	1341.4	1298.9		7413.4
1993	223.8	13.7	1026.6	1170.2	1066.1	897.2		4397.6
1994	197.1	93.9	1360.7	1110.8	471.5	1072.9	12.3	4319.3
1995	185.8	101.7	1261.3	230.4	588.1	1259.2	7.9	3634.5
GROUP AVERAGE	319.7	319.6	1698.6	1108.1	881.8	1033.5	10.1	**YEARLY AVERAGE**
STD	134.7	278.4	605.3	481.7	339.6	286.5	3.1	5364.7 ± 1469.5

TABLE 3. Spanish cephalopod landings (tonnes) in ICES Sub-area VI for the period 1990-1995.

YEAR	*Loligo* spp.	Cuttlefish	Ommastrephids	*Octopus vulgaris*	*Eledone cirrhosa*	Uns. Octopods	*Alloteuthis* spp.
1990							
1991			67.8		89.7		
1992			1.7		3.5		
1993							
1994							
1995							

TABLE 4. Spanish cephalopod landings (tonnes) in ICES Sub-area VII for the period 1990-1995.

YEAR	*Loligo* spp.	Cuttlefish	Ommastrephids	*Octopus vulgaris*	*Eledone cirrhosa*	Uns. Octopods	*Alloteuthis* spp.
1990	27.7	16.0	741.3		186.7		
1991	30.9	19.5	908.9		162.8		
1992	61.9	2.0	469.1		178.6		
1993	84.5		374.3		139.1		
1994	34.3		611.3		107.7		
1995	26.8		298.7		133.6		

TABLE 5. Spanish cephalopod landings (tonnes) in ICES Divisions VIIIa,b for the period 1990-1995.

YEAR	*Loligo* spp.	Cuttlefish	Ommastrephids	*Octopus vulgaris*	*Eledone cirrhosa*	Uns. Octopods	*Alloteuthis* spp.
1990	260.4	445.4	244.4		240.1		
1991	162.4	581.0	25.1		90.1		
1992	198.2	541.6	364.4		214.4		
1993	2.1		20.7		0.1		
1994	22.2	0.1	6.1		0.8		
1995							

TABLE 6. Spanish cephalopod landings (tonnes) in ICES Divisions VIIIc and IXa for the period 1990-1995.

YEAR	*Loligo* spp.	Cuttlefish	Ommastrephids	*Octopus vulgaris*	*Eledone cirrhosa*	Uns. Octopods	*Alloteuthis* spp.
1990	123.9	49.2	694.3	1708.3	678.8	527.3	
1991	200.1	36.5	1410.2	1173.3	375.7	1145.3	
1992	245.8	17.2	1615.6	1255.5	944.9	1298.9	
1993	137.2	13.7	631.5	1170.2	926.9	897.2	
1994	140.6	93.8	743.3	1110.8	363.1	1072.9	12.3
1995	159.0	101.7	927.9	230.4	407.9	1259.2	7.9

FIGURE 1. Chart showing the northern coast of Spain, and the ports where fishing statistics were obtained for the present study.

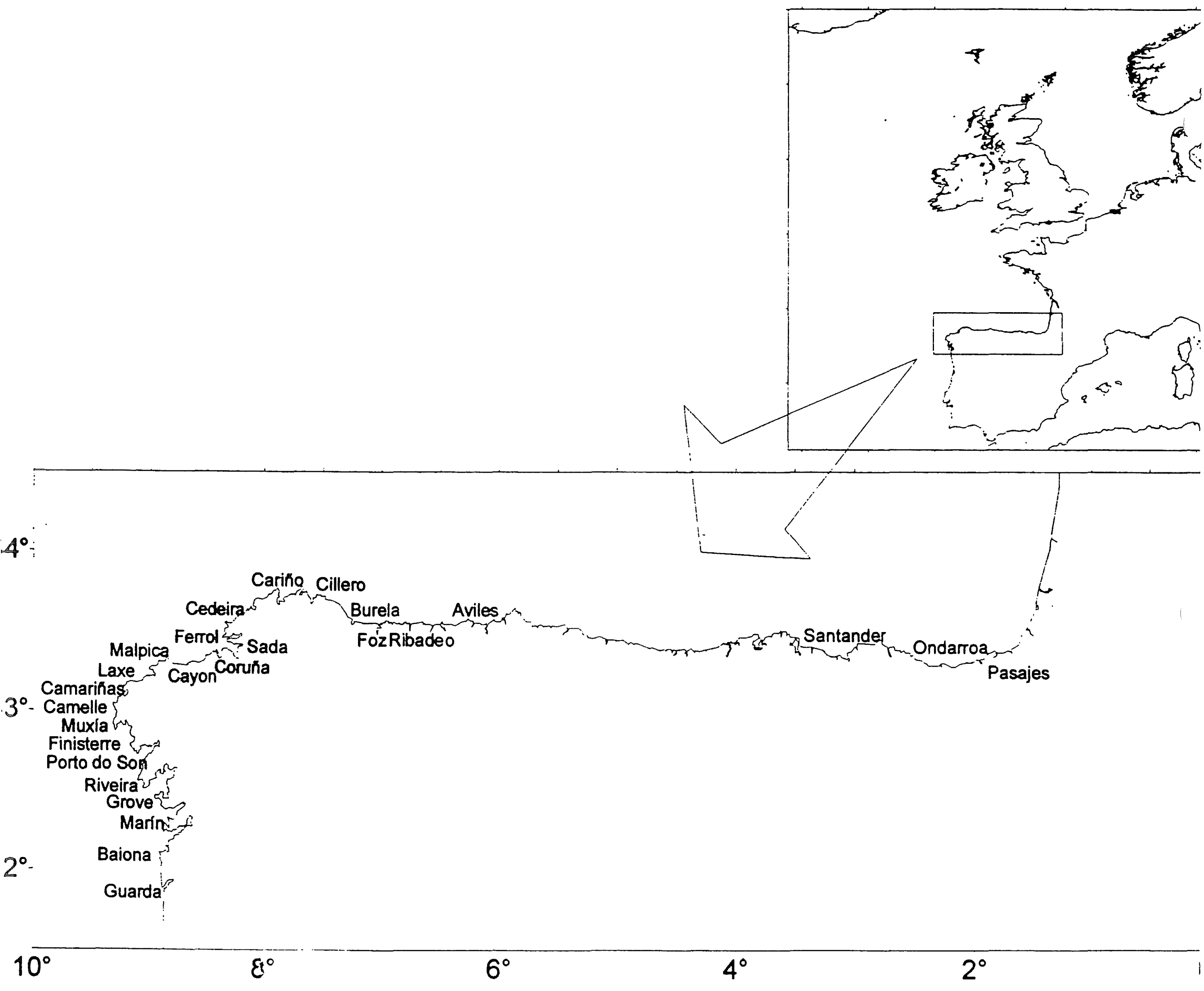


FIGURE 2.Total Spanish landings of squid, cuttlefish and octopus in ICES waters, for the period 1990-1995. *Alloteuthis* spp. is not included.

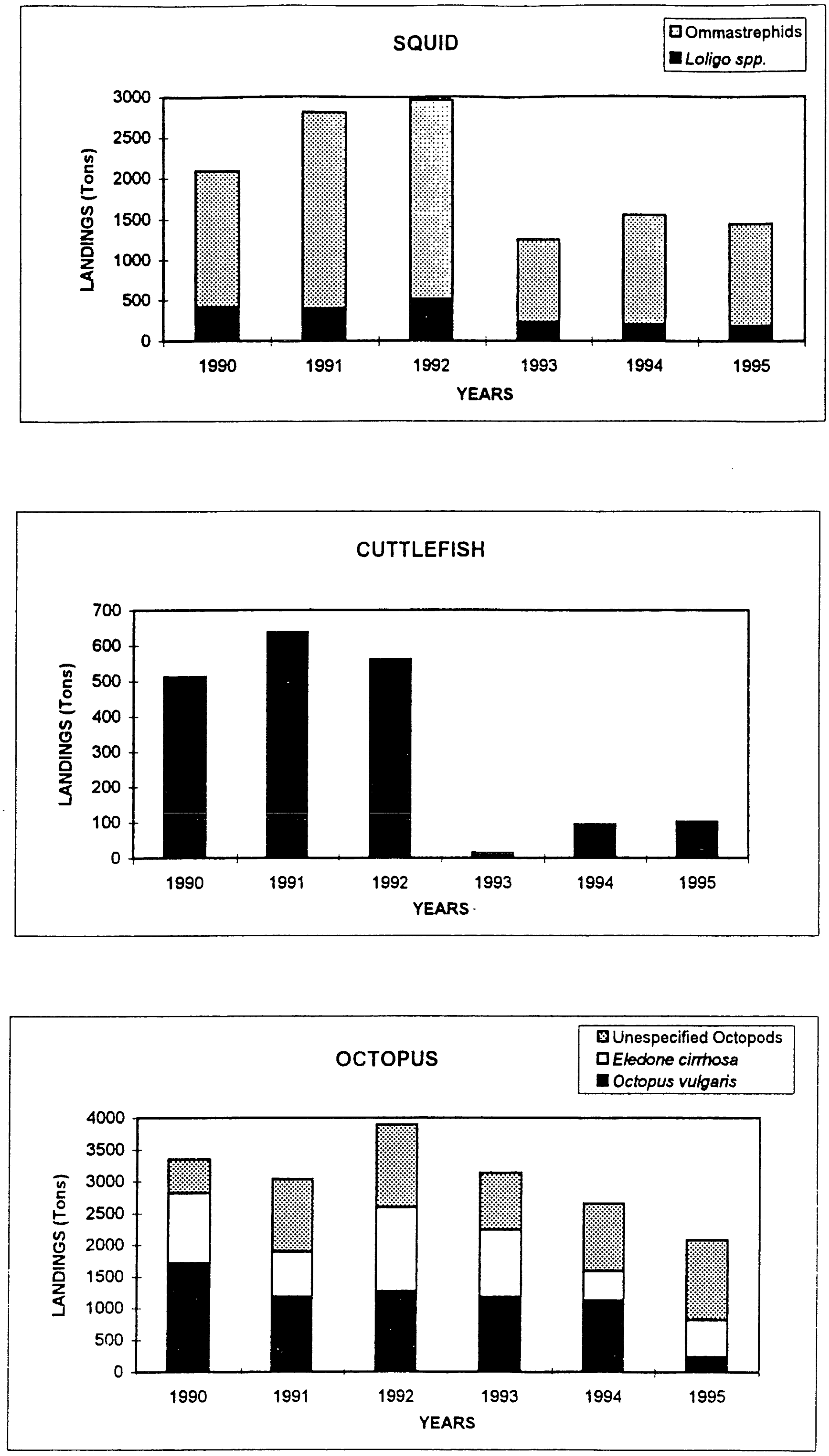


FIGURE 3. Average percentage for each cephalopod group, for the period 1990-1995.

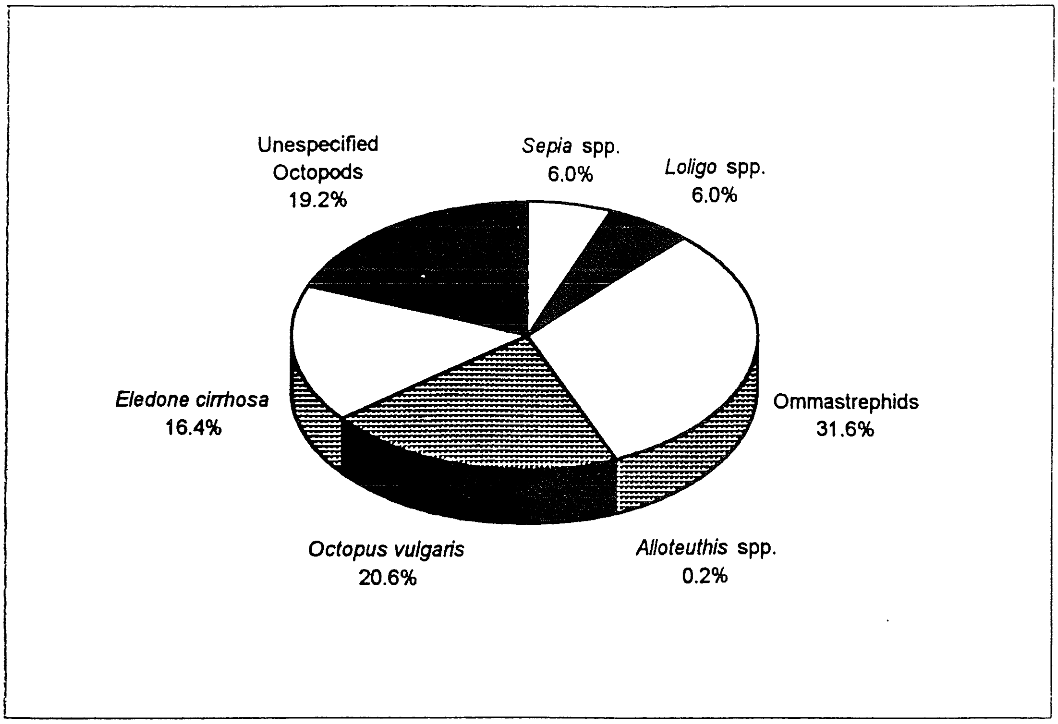


FIGURE 4. Area of origin of the landings for *Loligo* spp., Cuttlefish, Ommastrephids and *Eledone cirrhosa*. Average percentage for the period 1990-1995. Unespecified octopods are not shown. *Octopus vulgaris* and *Alloteuthis subulata* have been caught exclusively in Subarea VIIIc and IXa.

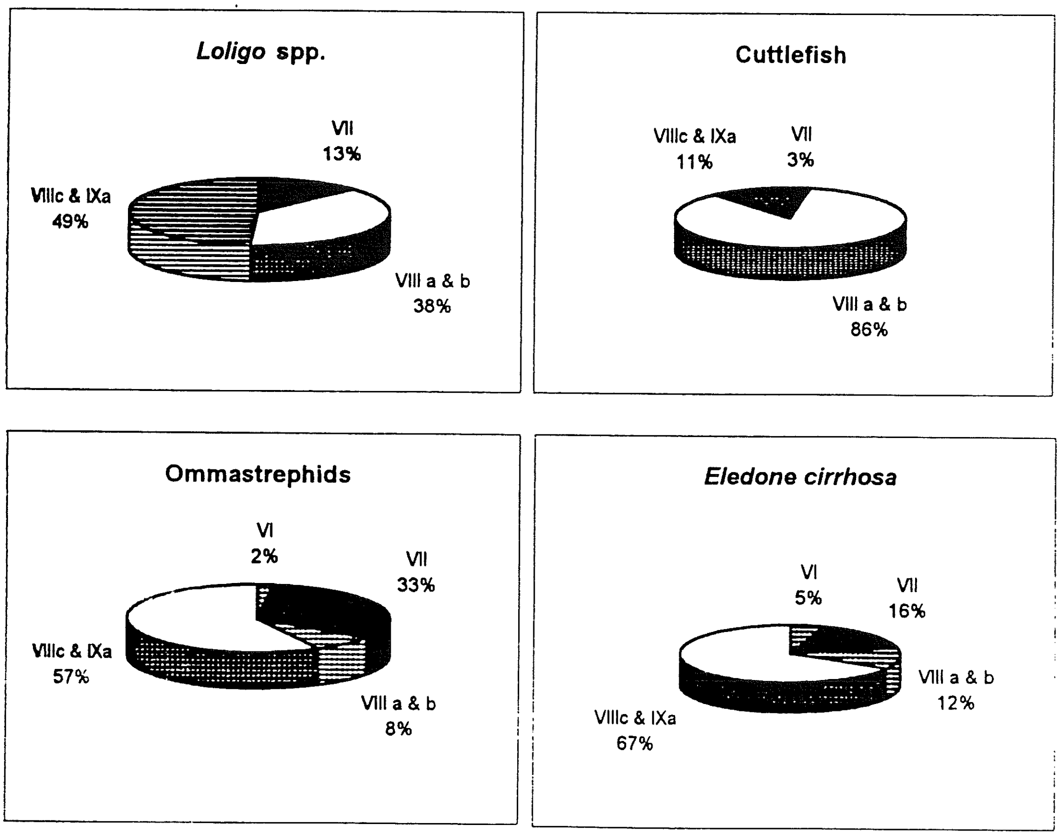
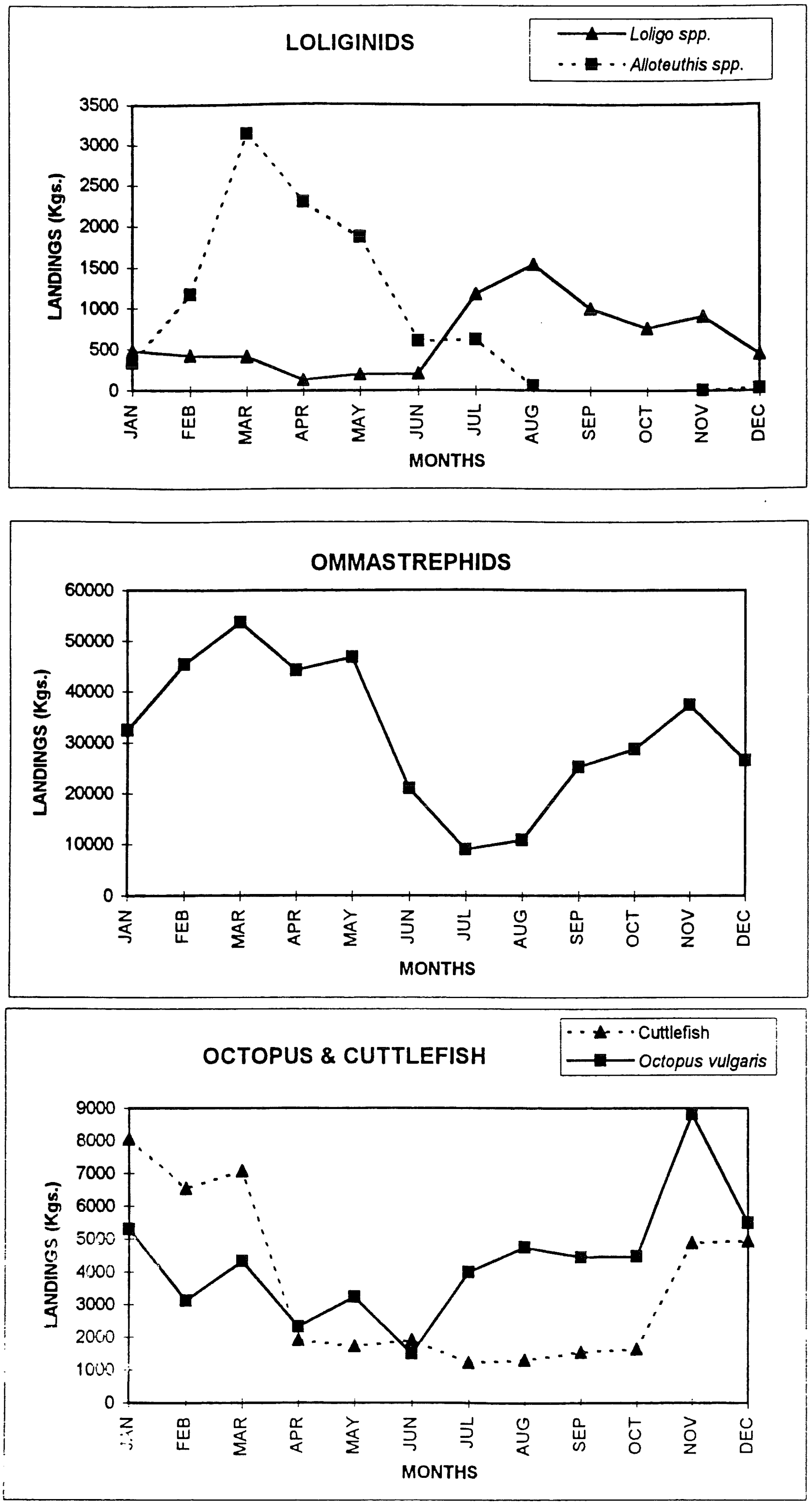


FIGURE 5. Evolution of the monthly catches of loliginids, ommastrephids, octopus and cuttlefish in the NW of Spain. Data from two Galician ports (Grove and Riveira) averaged for 1994-1995.



ANNEX 4

Rocha et al., 1996: *Reproductive strategies in cephalopods*

ICES Working Group on Cephalopod Fisheries and Life History
17-19 April 1996, Lisbon, Portugal

An overview on the reproductive strategies in Cephalopoda

by

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Introduction

Until recently, it was generally accepted that female cephalopods lay their eggs in one single spawning or in several consecutive ones, after which they would die of exhaustion (McGowan, 1954; Mangold, 1987; Harman *et al.*, 1989; Mangold *et al.*, 1993). The animals with this reproductive pattern where gonad regeneration is absent are known as semelparous. Conversely, iteroparous species are those in which gonadal regeneration following spawning occurs, making new reproductive cycles possible.

As knowledge has grown regarding the biology of this group, it has become increasingly difficult to support the notion of a single reproductive pattern (Boletzky, 1981, 1986; Rodaniche, 1984; Harman *et al.*, 1989; Mangold *et al.*, 1993). A case in point is *Nautilus* spp., with a life span of 20 years, which must be considered as an iteroparous species since the females spawn once a year, surviving, feeding, growing and regenerating their gonads for a further reproductive event the following year (Ward, 1987). With the exception of this particular case, the other cephalopods may be considered as semelparous, although there are significant differences between the maturation processes and spawning from one species to another (Boletzky, 1975; Mangold, 1987; Mangold *et al.*, 1993). Based on these differences, several reproductive strategies may be defined in cephalopods with regard to the oocyte maturation process and the type of spawning process in each species (Boletzky, 1981, 1986; Harman *et al.*, 1989; Villanueva, 1992; Mangold *et al.*, 1993; González, 1994; Rocha, 1994; Boyle *et al.*, 1995; Rasero, 1996; Rocha & Guerra, *in press*). In general, the current definitions for the different cephalopod reproductive strategies are confusing. For clarity and accuracy in this paper several reproductive strategies are defined, particularly regarding the duration of breeding period and types of ovulation and spawning.

Definitions

The diferent reproductive strategies presented in this paper (Table 1) are:

Iteroparous Reproductive Pattern

"**Iteroparous spawning**". This is a type of spawning where the gonads regenerate after each breeding season, making new reproductive cycles possible. There appears to be a single breeding season each year, and with the animal surviving, feeding and growing between spawning events (Kirkendall & Stenseth, 1985). Egg-laying may occur in separate batches during each spawning period. The species of the genus *Nautilus* have been found which exhibit iteroparous spawning (Ward, 1983, 1987).

Semelparous Reproductive Pattern

"**Simultaneous terminal spawning**". This is a type of spawning where ovulation is synchroneous, egg-laying occurs in a very short period at the end of the animal's life before death, and there is not oocyte maturation during spawning period. Several species have been found which exhibit simultaneous terminal spawning, e.g. *Loligo opalescens*, *Illex illecebrosus* and *Todarodes pacificus* (Hixon, 1983; O'Dor, 1983; Ikeda *et al.*, 1993). This type of spawning is also called "terminal spawning" and "single spawning" (Hixon, 1983; Mangold *et al.*, 1993).

"**Intermittent terminal spawning**". In this type of spawning "partial ovulation" occurs. Partial ovulation implies the presence of oocytes at various stages of development in the ovaries, thus enabling the continued production of ova once spawning has commenced. Partial ovulation has been described in several species: *Sthenoteuthis oualaniensis, Loligo bleekeri* and *Idiosepius pygmaeus* (Harman *et al.*, 1989; Hun Baeg *et al.*, 1993; Lewis & Choat, 1993). In intermittent terminal spawning egg-laying occurs in separate batches during the spawning period, which is usually relatively long, although in no case does it represent the greatest fraction of the animal's life. The species *Loligo vulgaris reynaudii, L. bleekeri, L. vulgaris vulgaris, L. forbesi, Illex coindetii* and *Todaropsis eblanae* (Sauer & Lipinski, 1990; Hung Baeg *et al.*, 1993; Rocha & Guerra, *in press*; Collins *et al.*, 1995; González & Guerra, *in press*; Rasero *et al.*, 1995) seem to be intermittent terminal spawners in which somatic growth does not take place between spawning events. This type of spawning corresponds to "intermittent spawning" defined by Boletzky (1975).

"**Multiple spawning**" (Harman *et al.*, 1989). This is a form of the intermittent terminal spawning. "Multiple spawning" is when somatic growth occurs between separate spawning events. Several species have been found which exhibit multiple spawning, e.g. *Octopus chierchiae, Sepia officinalis* and *Sthenoteuthis oualaniensis* (Rodaniche, 1984; Boletzky, 1975, 1987, 1988; Forsythe *et al.*, 1991; Harman *et al.*, 1989).

"**Continuous spawning**" (Villanueva, 1992). This is a type of reproductive strategy in which partial ovulation occurs with a continued production of ova once spawning has commenced and adults spawn many times during their extended life spans. Two species of cirrated octopods have been found which exhibit continuous spawning. e.g. *Opisthoteuthis agassizii* and *O. vossi* (Villanueva, 1992).

Table 1: Characteristics of the principal reproductive strategies in cephalopods and some examples.

Reproductive pattern	Breeding season pattern	Ovulation pattern	Spawning pattern	Growth between egg batches or breeding seasons	Reproductive strategy name	Possible species example
Iteroparous	Single annual during several years	Partial ovulation	Egg-laying occurs in separate batches	Yes	Iteroparous spawning	*Nautilus* spp.
Semelparous	Single and short at the end at the animal's life	Simultaneous ovulation	Egg-laying occurs in a very short period	No	Simultaneous terminal spawning	*Loligo opalescens* *Illex illecebrosus*
		Partial ovulation	Egg-laying occurs in separate batches	Yes	Multiple spawning	*Sepia officinalis* *Sthenoteuthis oualaniensis* *Octopus chierchiae*

Rocha et al., 1996: *Reproductive strategies in cephalopods*

Table 1: Characteristics of the principal reproductive strategies in cephalopods and some examples (Cont.)

Reproductive pattern	**Breeding season pattern**	**Ovulation pattern**	**Spawning pattern**	**Growth between egg batches or breeding seasons**	**Reproductive strategy name**	**Possible species example**
Semelparous	Single and short at the end at the animal's life	Partial ovulation	Egg-laying occurs in separate batches	No	Intermittent terminal spawning	*Loligo vulgaris* *Loligo forbesi* *Todaropsis eblanae* *Illex coindetii*
	Single and extended during the animal's life	Continuous ovulation	Egg-laying occurs in a extended and continuous period of spawning	Yes	Continuous spawning	*Opisthoteuthis agassizii* *Opisthoteuthis vossi*

Discussion

The main problem in the use of these reproductive strategies is the knowledge of the main aspects involved in the definitions: ovulation pattern, spawning pattern and existence of growth between egg batches or breeding seasons. Data about these three caracteristics have been reported just in a few species. Information about some of these aspects have been reported for several species, but it is not enough to locate each one in the corresponding reproductive strategies. Therefore, it is necessary to improve the knowledge of these reproductive aspects for each species in order to classify them according to each reproductive strategies.

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ANNEX 5

CHAPTER 9

Trophic interactions of squid *Loligo forbesi* in Scottish waters

G.J. Pierce and M.B. Santos

SUMMARY

(1) Squid are an increasingly important fishery resource in the north-east Atlantic but their role as predators and prey of other marine organisms is poorly known. The main squid species of commercial importance in the northern north-east Atlantic is the veined squid *Loligo forbesi*. The present paper reviews trophic interactions involving this species in Scottish waters.

(2) Fishery and population data are used to develop a simple model of the squid population. Stock size estimates, combined with available data on diet and energetic requirements are used to estimate consumption of the main prey species for two annual cohorts (1990/91, 1991/92).

(3) *Loligo forbesi* is primarily piscivorous, although the diet also includes crustaceans and there is some cannibalism. In 1990/91, depending on assumptions about natural mortality, the Scottish population of *Loligo forbesi* may have eaten between 9000 and 16 000 tonnes of food, including 1700–3000 tonnes of sandeels (Ammodytidae), a similar amount of *Trisopterus* spp. and 1000–1700 tonnes of whiting *Merlangius merlangus*.

(4) *Loligo forbesi* is eaten by various predatory fish, seabirds and marine mammals in the north-east Atlantic. Harbour seals *Phoca vitulina* and grey seals *Halichoerus grypus* eat *Loligo forbesi* in small amounts. *Loligo forbesi* is more important in the diets of harbour porpoise *Phocoena phocoena* and these three mammal species alone may remove more squid from Scottish waters every year than the commercial fishery.

(5) The importance of *Loligo forbesi* in fish and seabird diets is not well documented, although many studies indicate that other squid species are eaten. Many toothed cetaceans are specialist feeders on cephalopods and good quantitative data on the diets of more of these potential predators is needed to obtain realistic estimates of natural mortality in *Loligo forbesi*.

Key-words: food consumption, *Loligo forbesi*, marine mammals, north-east Atlantic, population size

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INTRODUCTION

The veined squid *Loligo forbesi* is widely distributed in the north-east Atlantic, primarily in shelf and shelf edge waters and is the subject of increasingly important fisheries, both directed and by-catch. Recent studies in Scottish waters have examined distribution and abundance, population ecology, diet and the nature of the commercial fishery (Pierce *et al.* 1994a,b,c) but no previous attempts have been made to quantify the trophic interactions. The diet of *Loligo forbesi* has been documented in Scottish, Irish and Spanish waters (Ngoile 1987, Collins *et al.* 1993, Rocha *et al.* 1993, Pierce *et al.* 1994b) and the species is primarily piscivorous. However, there are no estimates of population size and the potential impact on fish stocks remains unknown. Data on the importance of squid as prey are patchy. There are many relevant studies on diets of fish, seabirds and marine mammals in the north-east Atlantic, but few attempts to quantify the amounts of cephalopods eaten, although Furness (1994) estimates consumption of squids by seabird populations.

The present paper uses existing data to quantify some of the trophic interactions involving *Loligo forbesi* in the north-east Atlantic, focusing on the fished population in Scottish waters.

SOURCES OF DATA

Consumption by squid

Squid energy requirements

Based on data for *Illex illecebrosus* and *Loligo* spp. compiled by O'Dor & Wells (1987), daily food intake (I, $g \cdot day^{-1}$) may be expressed in relation to body weight (W, g) as:

$$I = 0.0683 + 0.0474 \times W \qquad (1)$$

Using this regression, daily food intake was estimated for all individuals in monthly population samples (July 1990–July 1992) (Pierce *et al.* 1994a), and the mean daily food requirement per individual calculated for each month.

Squid population size

A simple difference equation model is used here, including terms for recruitment, fishing mortality and natural mortality. Immigration and emigration are assumed to be negligible. Data on the monthly landings in Scotland (SOAFD, unpublished data) and monthly size composition (Pierce *et al.* 1994a) were used to estimate the number of *Loligo* landed monthly between July 1990 and July 1992. This assumes that all squid caught in Scottish waters are *Loligo forbesi* and are landed in Scotland, and the size composition in monthly samples was representative of the population. Recruitment in *Loligo forbesi* occurs during much of the year, although with varying seasonal peaks (Lum-Kong *et al.* 1992, Boyle & Ngoile 1993; Pierce *et al.* 1994a). The proportion of recruits (animals of <150 mm mantle length) in monthly samples is assumed to be representative of the rate of recruitment to the population:

$$N_t = (N_{t+1} + C_t)/(1 + r_t - m) \qquad (2)$$

where N_t is the population size at the start of month t, r_t is the recruitment in month t expressed as a proportion of N_t, C_t is the commercial catch in month t and m is the monthly natural mortality, expressed as a (fixed) proportion of N_t.

Pauly (1985) gives values in the range 0.53–2.13 for instantaneous (annual) natural mortality (M) in squids. This corresponds to values for m as defined above between 0.043 and 0.163. Most adults disappear from the fished population in July, while in 1991 recruitment reached a peak in August (Pierce *et al.* 1994a). Setting the population level at the end of July in each year to zero, population sizes for the preceding months were estimated using Equation (2) for different levels of monthly natural mortality (m = 0, 0.04, 0.16). Input catch parameters and population results for m = 0.16 are illustrated in Figure 9.1.

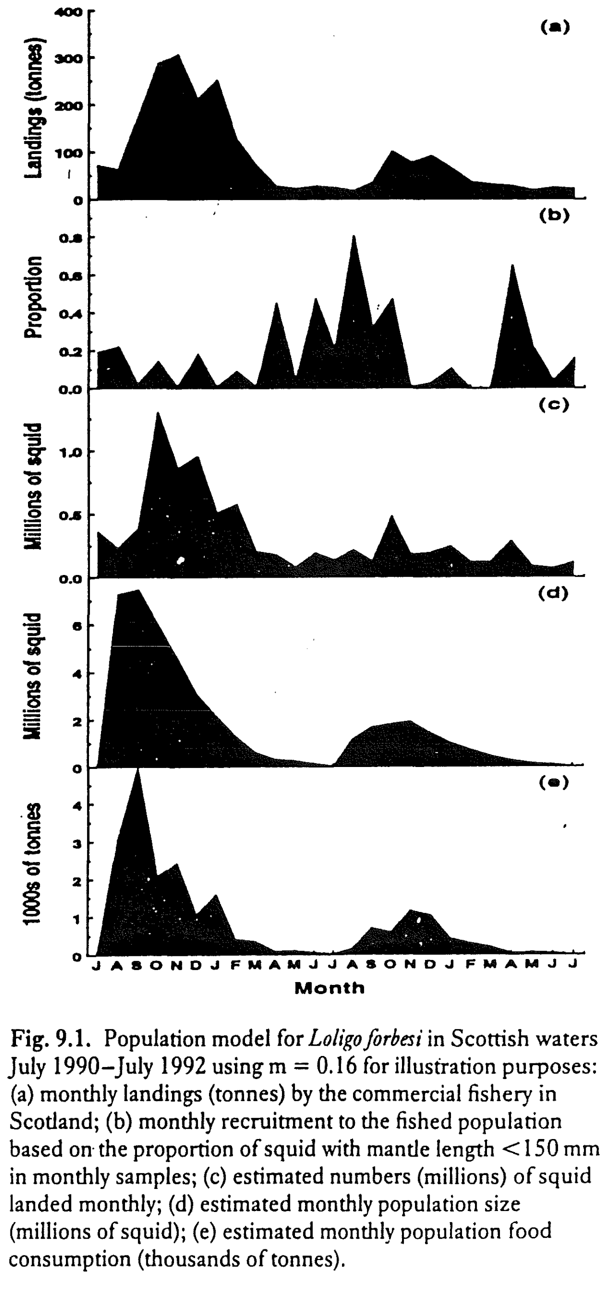

Fig. 9.1. Population model for *Loligo forbesi* in Scottish waters July 1990–July 1992 using m = 0.16 for illustration purposes: (a) monthly landings (tonnes) by the commercial fishery in Scotland; (b) monthly recruitment to the fished population based on the proportion of squid with mantle length <150 mm in monthly samples; (c) estimated numbers (millions) of squid landed monthly; (d) estimated monthly population size (millions of squid); (e) estimated monthly population food consumption (thousands of tonnes).

Squid diet

Data on the diet of *Loligo forbesi* in Scottish waters were taken from Pierce *et al.* (1994b). Variation in diet with body size and season is ignored. Assuming that meals of different prey taxa are normally of equivalent weight, the proportion by weight in the diet is equivalent to the modified frequency of occurrence: fish (75.7%), crustacean (17.4%), cephalopod (6.9%). Within taxa, relative weights eaten are assumed to be proportional to the number of individuals identified from bones, otoliths (fish) and beaks (cephalopods). Fish identified only as *Gadidae* were assigned *pro rata* to those gadid species which were identified, while beaks of decapod cephalopods were similarly assigned.

Population food intake

Monthly food intake by the squid population (I, tonnes) for prey type i is given by:

$$I = N_t \times P_i \times F_t \times T_t \qquad (3)$$

where N_t is the squid population size at the start of month t, T_t is the number of days in month t, P_i is the proportion by weight of prey-type i in the diet, F_t is the average weight of food eaten daily per individual. Monthly food intake was summed to give annual food consumption (Table 9.1).

Consumption of squid by marine mammals and other predators

Population consumption is calculated for marine mammals on which we have some dietary data: harbour seals *Phoca vitulina*, grey seals *Halichoerus grypus* and harbour porpoise *Phocoena phocoena* (Table 9.2). For other potential predators on squid, data in the literature are summarized (Table 9.3). Ignoring within-year variation and effects of population structure, annual consumption of squid by a population of marine mammals (I, tonnes) is given by:

$$I = \frac{365 \times N \times E}{10^6 \times D_s} \times \frac{P_s \times D_s}{P_o \times D_o} \qquad (4)$$

where N is the estimated population size, E is the average individual daily energy intake (kcal), D_s is the calorific density of squid ($kcal \cdot g^{-1}$), D_o is the average calorific density of other prey in the diet ($kcal \cdot g^{-1}$), P_s is the proportion (by weight) of squid in the diet and P_o is the proportion (by weight) of other prey.

Not all data are precisely known. Estimated energetic intake for the harbour porpoise (Table 9.2) assumes a normal daily energy expenditure of approximately three times the basal metabolic rate predicted, using the Kleiber relationship, from body weight (after Worthy *et al.* 1987, Murie 1987). Taking average body weight to be 45 kg (at the lower end of the range for mean adult body size) (Leatherwood *et al.* 1983), this is equivalent to approximately 3600 $kcal \cdot day^{-1}$. At 90% assimilation efficiency (a realistic figure for seals) (Prime & Hammond 1987) this would require a daily intake of 4000 $kcal \cdot day^{-1}$.

Croxall & Prince (1982) give a figure of 3.5 $kJ \cdot g^{-1}$ for average calorific density of cephalopods, i.e. 836 $kcal \cdot kg^{-1}$, noting that values for fish are usually higher. However, although calorific densities often quoted for fish such as sandeels (1367), sprat (≤1587) and *Tri-*

Table 9.1. Amounts of food eaten by *Loligo forbesi* 1990/91 and 1991/92, based on estimated importance of main prey species in the diet and estimates of squid population size using various values for natural mortality (m).

Prey species	Proportion of diet	Weights (tonnes) eaten 1990/91 for m =			Weights (tonnes) eaten 1991/92 for m =		
		0	0.04	0.16	0	0.04	0.16
Trisopterus	0.166	1559	1754	2678	467	524	800
Haddock	0.060	563	634	968	169	190	289
Whiting	0.104	976	1099	1678	292	329	501
Cod	0.009	85	95	145	25	28	43
Sandeel	0.183	1718	1933	2952	515	579	881
Clupeidae	0.088	826	930	1419	247	278	423
Mackerel/scad	0.022	207	232	355	62	70	106
Other fish	0.126	1183	1331	2032	354	398	606
Crustacea	0.174	1634	1838	2806	489	550	838
Loligo forbesi	0.049	460	518	790	138	155	236
Other ceph.	0.020	188	211	323	56	63	96
Total	1.000	9389	10563	16130	2812	3161	4817

Table 9.2. Estimated annual cephalopod consumption for seals and porpoises.

	Harbour seal		Grey seal		Harbour porpoise
	UK 1991	Scotland 1991	UK 1991	Scotland 1991	North Sea 1994
Population size	24640 (1)	23089 (1)	93500 (1)	85400 (1)	352500 (5)
Daily energy intake (kcal)	4680 (2)		5530 (4)		4000 (6), (7)
Daily food intake (kg)	5.6 (2)		6.6 (4)		4.8 (6), (7)
%Diet = Cephalopod	1.7 (3)		9.4 (3)		3.8 (3), (8)
%Diet = *Loligo*	0.06 (3)		0.25 (3)		1.98 (3), (8)
Annual population Cephalopod consumption (tonnes)	874	819	21211	19373	23680
Annual population *Loligo* consumption (tonnes)	32	30	552	504	12229

Sources: (1) Hiby *et al.* (1993); (2) Härkönen & Heide-Jørgensen (1991); (3) G.J. Pierce *et al.* unpublished data; (4) Fedak & Hiby (1985); (5) Hammond *et al.* (1995); (6) Worthy *et al.* (1987); (7) Leatherwood *et al.* (1983); (8) Santos *et al.* (1994).

sopterus spp. (1058–1146) are higher than values for most Gadidae and flatfish (700–800) (Murray & Burt 1969, Prime & Hammond 1987), Hislop *et al.* (1991a) show that there are very large seasonal and size-related changes in calorific density. Thus small sprat may on average be no more energy rich than cod or whiting. We make the simplifying assumption that fish and cephalopods are on average of equal calorific value.

Diet was quantified by analysis of harbour seal faeces (N = 658), grey seal faeces (N = 495) and porpoise stomachs (N = 108). Weights of fish and cephalopods eaten were calculated from measurements on otoliths and beaks (Pierce *et al.* 1991a,b, unpublished data, Santos *et al.* 1994).

RESULTS AND DISCUSSION

Predation by *Loligo forbesi*

Maximum population size for *Loligo forbesi* in Scottish waters during the study period is estimated to have ranged between 4 million (for m = 0) and 7.5 million (for m = 0.16). Depending on m, the population would have eaten between 9000 and 16000 tonnes of food in 1990/91 and 3000 to 5000 tonnes in 1991/92 (Table 9.1). In 1990/91, the food eaten included 1700–3000 tonnes of sandeels (Ammodytidae), 1600–2700 tonnes of *Trisopterus* spp. and 1000–1700 tonnes of whiting *Merlangius merlangus*. This excludes any estimate of consumption by pre-recruit and paralarval squid. Empirical estimates of natural mortality, on a seasonal or monthly basis, are needed to provide meaningful confidence limits for the size of the squid population. Scottish squid landings vary widely from year to year, possibly reflecting cyclic variations in population size (Pierce *et al.* 1994c). From a low of 88 tonnes in 1979, annual landings rose to approximately 1900 tonnes in 1989. Landings in 1990, 1991 and 1992 were relatively large (approximately 1400, 900 and 1100 tonnes, respectively) and estimated consumption by squid in these years would therefore be towards the upper end of the natural range of values. To put the amount of food eaten by squid in Scottish waters in perspective, predators in the North Sea are estimated to have eaten approximately 2.2 million tonnes of fish and 6.1 million tonnes of other food during 1991 (Anon. 1994), and these figures may even be underestimates (Greenstreet, in press).

Predation by seals and propoises on *Loligo forbesi*

Seals ate very little *Loligo forbesi* (Table 9.2); in fact only single specimens were found in faeces of both species. Most of the cephalopods eaten by grey seals were octopus *Eledone cirrhosa*. Porpoises probably have a more significant impact on *Loligo forbesi*, although population estimates are for the North Sea rather than for Scotland (Table 9.2). Mortality of *Loligo forbesi* due to marine mammals appears to be of at least a similar order of magnitude to fishing mortality (see Pierce *et al.* 1994c) and probably rather higher, implying that the higher values for natural mortality in the preceding squid model are more realistic.

Predation by other predators on cephalopods

As the selective list of predators in Table 9.3 makes clear, there is a long way to go before natural mortality of *Loligo forbesi* can be fully quantified. Large-scale

Table 9.3. Marine predators of cephalopods in the north-east Atlantic.

Area	Predator	% of diet = cephalopods[a]	Species eaten[b]; other comments	Sources
North Sea	Cod *Gadus morhua*	0–11	Not stated but includes A	Daan (1981), Anon. (1994), J.R.G. Hislop, personal communication
	Haddock *Melanogrammus aeglefinus*	0–11		
	Whiting *Merlangius merlangus*	0–14	Cephalopods mainly eaten in 1st quarter of year	
	Saithe *Pollachius virens*	0–30		
	Mackerel *Scomber scombrus*	0–80		
	Grey gurnard *Eutrigla gurnardus*	0–11		
	Ray *Raja radiata*	0–1		
NE Atlantic	Swordfish *Xiphias gladius*	(4)	H, T, ocs	Guerra *et al.* (1993)
Scotland	Puffin *Fratercula artica*	(1)	A	Harris & Hislop (1978)
Skomer (Wales)	Guillemot *Uria aalge*	(1)	Squid	Hatchwell (1990)
Rum	Manx shearwater *Puffinus puffinus*	40	Omm, ocs	Furness (1994)
Foula, St Kilda	Northern fulmar *Fulmarus galcialis*	1	Omm	Furness (1994)
	Leach's stormpetrel *Oceanodroma leucorhoa*	(1)	Omm	
	British stormpetrel *Hydrobates pelagicus*	(1)	Omm	
Foula	Great skua *Catharcta skua*	0.1	L	Furness (1994)
	Various other seabirds	Absent		
UK waters	Harbour seal *Phoca vitulina*	(1)–(2)	E, L, S	Steven (1934), Sergeant (1951), Rae (1968), Pierce *et al.* (1991b), Thompson *et al.* (1993)
	Grey seal *Halichoerus grypus*	(1)	E, L, R, T	Rae (1968), SMRU (1984), Pierce *et al.* (1991a)
UK and other NE Atlantic waters, Mediterranean	Fin whale *Balaenoptera physalus*	(1)		Rae (1965), Rae (1973), Clarke & MacLeod (1974), Clarke & Kristensen (1980), Leatherwood *et al.* (1983), Clarke & Pascoe (1985), Clarke (1986), Martin & Clarke (1986), Corbet & Harris (1991), Bello (1992), Würtz *et al.* (1992), Clarke *et al.* (1993), Haug *et al.* (1993), González *et al.* (1994a), Santos *et al.* (1994)
	Sei whale *Balaenoptera borealis*	(2)		
	Minke whale *Balaenoptera acutorostrata*	(1)–(2)		
	Sperm whale *Physeter macrocephalus*	(4)	B, G, H, T, ocs	
	Pygmy sperm whale *Kogia breviceps*	(4)	E, H, L, Sl, ocs	
	White whale *Delpinapterus leucas*	(4)		
	Narwhal *Monodon monocerus*	(2)		
	Northern bottlenose whale *Hyperoodon ampullatus*	(4)	G, H, L, S, T, ocs	
	Cuvier's beaked whale *Ziphius cavirostris*	(3)	B, H, ocs	
	Sowerby's beaked whale *Mesoplodon bidens*	(3)	Omm?	
	True's beaked whale *Mesoplodon mirus*	(4)		
	Harbour porpoise *Phocoena phocoena*	(1)	L	
	Common dolphin *Delphinus delphis*	(2)	A, L, Sa	
	Striped dolphin *Stenella coeruleoalba*	(2)	A, G, H, I, L, Sl, T	
	Bottle-nosed dolphin *Tursiops truncatus*	(1)	L, S	
	Atlantic white-sided dolphin *Lagenorhynchus acutus*	(2)	L	
	White-beaked dolphin *Lagenorhynchus albirostris*	(2)	L	
	Melon-headed whale *Peponocephala electra*	(2)–(3)		
	False killer whale *Pseudorca crassidens*	(1)		
	Killer whale *Orcinus orca*	(1)	I, L, S, T	
	Long-finned pilot whale *Globicephala melaena*	(3)	B, E, G, H, L, O, Sl, S, T	
	Risso's dolphin *Grampus griseus*	(4)	E, G, H, L, R, S, St, T, Te	

[a] Where no data on %weight were available, importance of cephalopods in the diet is expressed as: (1) some, (2) considerable, (3) large proportion, (4) main food (after Clarke, 1986).

[b] Key to cephalopods: A, *Alloteuthis*; B, *Brachioteuthis*; E, *Eledone*; G, *Gonatus*; H, *Histioteuthis*; L, *Loligo* (*L. forbesi* + *L. vulgaris*); I, *Illex*; O, *Ommastrephes*; Omm, Ommastrephidae; ocs, oceanic squids; R, *Rossia*; S, *Sepia*; Sl, *Sepiola*; St, *Sepietta*; T, *Todarodes*; Te, *Todaropsis*.

studies on fish diets in the North Sea (Daan 1981, Anon. 1994) showed that cephalopods are seasonally important prey of some commercial fish. The squid *Alloteuthis subulata* was the principal cephalopod prey at least in the case of whiting (Hislop *et al.* 1991b). For younger fish, any *Loligo forbesi* eaten would probably be pre-recruits. Although squid are among the main prey of the swordfish *Xiphias gladius*, it takes oceanic species rather than the (neritic) loliginids (Guerra *et al.* 1993). Furness (1994) estimated that seabirds may remove 100 000 tonnes of squid annually from the north-east Atlantic, but most squid eaten are probably ommastrephids rather than *Loligo*. Also, the smaller loliginid *Alloteuthis subulata* is a more likely prey for most seabirds than adult *Loligo forbesi*, which may reach weights of more than 1 kg (Pierce *et al.* 1994a).

Many cetaceans of north-east Atlantic waters eat *Loligo* spp. (Clarke, 1986, Corbet & Harris 1991) and some, e.g. Risso's dolphin and sperm whales, are specialist feeders on cephalopods. Some of the other cephalopods eaten are also fished commercially in Europe, e.g. the cuttlefish *Sepia officinalis* and the ommastrephid squids *Todaropsis eblanae* and *Illex coindetii* (Pierce *et al.* 1994c, González *et al.* 1994a,b).

Quantitative information on consumption by a wider array of predators is needed to provide realistic estimates of natural mortality in *Loligo forbesi*.

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