PREVIOUS PAGE

# 1. INTRODUCTION

by Patrizia Jereb, Clyde F.E. Roper and Michael Vecchione

With the increasing exploitation of finfish resources, and the depletion of a number of major fish stocks that formerly supported industrial-scale fisheries, increasing attention continues to be paid to the so-called ‘unconventional marine resources’, which include numerous species of cephalopods. Cephalopod catches have increased steadily in the last 30 years, from about 1 million metric tonnes in 1970 to more than 3 million tonnes in 2001. This increase confirms a potential development of the fishery predicted by G.L. Voss in 1973, in his first general review of the world’s cephalopod resources prepared for FAO. The rapid expansion of cephalopod fisheries in the decade or so following the publication of Voss’s review, meant that a more comprehensive and updated compilation was required, particularly for cephalopod fishery biologists, zoologists and students. The FAO Species Catalogue, ‘Cephalopods of the World’ by C.F.E. Roper, M.J. Sweeney and C.E. Nauen was published in 1984 to meet this need.

The number of cephalopod species that enter commercial fisheries has continued to grow significantly since 1984, as a result of a still-growing market demand and the expansion of fisheries operations to new fishing areas and to deeper waters. It has been suggested that the cephalopod ‘life-strategy’ may guarantee survival against environmentally stressful conditions, including those caused by heavy fishing. However, as cephalopod fisheries experienced further extensive development, parallel concern developed regarding potential overexploitation. Thus, a broad consensus developed among fishery biologists to apply the experience gained from errors made in finfish management to avoid possible failures in cephalopod exploitation. To help prevent potential failures, refined species identification capabilities are required, as well as a more detailed and accurate compilation of information on cephalopod species, distribution, biology, fisheries and catch statistics. Consequently, FAO recognized that a new edition of the ‘Cephalopods of the World’ catalogue was needed. To achieve this expanded goal, several authors with particular areas of specialization were assembled to enhance the accuracy, coverage and utility of this revised catalogue.

In our attempt to make this document as comprehensive and as useful as possible, the taxonomic coverage of this edition of the catalogue is organized into 3 levels of interest:

**Level 1 :** species of cephalopods currently exploited commercially and species utilized at the subsistence and artisanal levels;

**Level 2 :** species of occasional and fortuitous interest to fisheries; this includes species considered to have a potential value to fisheries, based on criteria such as edibility, suspected abundance, accessibility, marketability, etc.;

**Level 3 :** species with no current interest to fisheries, which are listed only with the basic information available.

The inclusion of such a wide range of species is necessary to provide the most comprehensive inventory of species possibly useful to mankind, regardless of their current commercial status. For example, this work should be useful for the ever-expanding search for development and utilization of ‘natural products’, pharmaceuticals, etc.

The catalogue is based primarily on information available in published literature. However, yet-to-be-published reports and working documents also have been used when appropriate, especially from geographical areas where a large body of published information and data are lacking, and we are particularly grateful to colleagues worldwide who have supplied us with fisheries information, as well as bibliographies of local cephalopod literature.

The fishery statistics presented herein are taken from the FAO official database, FISHSTAT, now available on the Worldwide web (FISHSTAT Plus 2000). This information is supplemented by field observations made by the authors in many parts of the world, both in preparation of the 1984 volume, as well as for the current edition. These field visits provided opportunities to examine fresh material at landing sites, markets and laboratories, as well as to obtain first-hand information about local cephalopod fisheries from regional fisheries workers.

During the 20-plus years separating the two editions, the rapid development of cephalopod fisheries worldwide and the simultaneous increase in the population of fisheries scientists, their research and publications, made available an enormous amount of new data and research results. Sometimes it is difficult to evaluate the reliability of published data, especially with regard to the identification of species in areas where the cephalopod fauna has not been sufficiently studied. It is entirely understandable that field workers isolated from good library and museum/collection facilities have difficulties in correctly identifying the species they encounter in the field. Moreover, the discovery of new species, the more accurate delimitation of known species, or even the introduction of nomenclatural changes, may cause confusion and lead to the use of scientific names that are incorrect by modern standards. Although great care was exercised to evaluate and correct such published information used in the catalogue, some incorrect interpretations may have occurred. Another difficulty, in the taxonomic literature especially, is that information on the economic importance of species is rather scarce or of a very general nature. Also, we may have overlooked important information published only in relevant local fisheries literature that is unavailable on a broader scale. All of these potential difficulties, however, have been significantly mitigated during the preparation of the new edition because of the availability on-line of fisheries databases and bibliographic search capabilities.

With regard to the limitations mentioned above, we heartily request that readers who detect any errors in the information presented, or who have any additional information and data that will enhance the accuracy and utility of this book, please contact and inform one of the authors or the Species Identification and Data Programme (SIDP) of the Marine Resources Service, Fisheries Resources Division, Fisheries Department, FAO Rome.

For further reading and information on cephalopod biology, fishery and resources, additional references and websites are listed at the end of references.

## 1.1 Plan of the Catalogue

This catalogue is organized by families and their appropriate genera within major cephalopod groups, then alphabetically by species.

**Level 1**, the most important species for fisheries, consists of detailed information in all 12 categories listed below. **Level 2**, which comprises those species of occasional, fortuitous or potential interest to fisheries, consists of whatever information is available and appropriate in the 12 categories. **Level 3**, those species for which there is no current interest to fisheries, consists of basic information (i.e. scientific name, size, geographical distribution, literature). The format within the species sections includes the first two levels of treatment (Level 1 and Level 2) presented together. Species included in Level 3 are presented at the end of each family.

Consequently, each major group and family is introduced with general descriptive remarks, illustrations of diagnostic features, highlights of the biology and relevance to fisheries. The information that pertains to each species in Levels 1 and 2 is arranged by categories as follows: (1) scientific name; (2) synonymy; (3) misidentifications; (4) FAO names; (5) diagnostic features with illustrations; (6) maximum known size; (7) geographical distribution with map; (8) habitat and biology; (9) interest to fisheries; (10) local names; (11) remarks and (12) literature.

**(1) Scientific Name:** Reference to author, date and publication is given for the original description of each species.

**(2) Frequent Synonyms:** Principal synonyms and name combinations are listed.

(**3) Misidentifications:** Misidentifications as other species are reported here and discussed in detail under section 11, Remarks, along with other nomenclatural points.

**(4) FAO Names:** English, French and Spanish names for each species, used primarily within FAO, are selected on the basis of the following criteria: (i) each name must apply to one species only, in a worldwide context; (ii) the name must conform to FAO nomenclatural spelling; (iii) the name should apply only to a cephalopod species, and should not lead to confusion with species names in other major animal groups. Wherever possible, these names are selected based on vernacular names (or parts of names) already in existence within the areas where the species is fished. FAO species names, of course, are not intended to replace local species names, but they are considered necessary to overcome the considerable confusion caused by the use of a single common name for many different species, or several names for the same species.

**(5) Diagnostic Features:** Principal distinctive characters of the species are given as an aid for identification, accompanied by pertinent illustrations. Species identifications should be attempted only after verification of the family through use of the illustrated key to families. Reference to FAO Species Identification Guides is given wherever relevant.

**(6) Size:** The known mantle length (or total length in some cases) of both males and females is provided where possible. Sizes or measurements might not be completely comparable because they were taken mostly from preserved or fixed specimens, but measurements of commercially important species often come from fresh material. Because of the elasticity of tentacles and arms total length is not a very accurate measurement. Where both total length and mantle length are given, the respective figures do not necessarily pertain to the same specimen but may have been obtained from different sources. The available information on the size attained by some species often is very meagre, so the maximum reported size cited here might be considerably smaller than the actual maximum size. Maximum weight is given when available.

**(7) Geographical Distribution:** The entire known geographic range of the species, including areas of seasonal occurrence, is given in the text and shown on a map. In cases where only scattered records of occurrence are available, question marks have been used to indicate areas of suspected or unconfirmed distribution.

**(8) Habitat and Biology:** The known depth range of the species and information on salinity and temperature of its habitat are given where available. For the sake of exactness actual depth data are reported, as given in the literature referenced. Information on biological aspects, such as migrations, spawning seasons and areas, longevity, food, and predators, is also included.

**(9) Interest to Fisheries:** This paragraph gives an account of the areas where the species is fished and of the nature of the fishery; its importance is either qualitatively estimated (minor, moderate, major or potential) or actual figures of annual landings are provided. Data on utilization (fresh, dried, cooked, frozen, canned, etc.) are also given where available. Here, too, the quality and quantity of the available information varies considerably among the species.

**(10) Local Names:** These are the names used locally for the various species. The present compilation is necessarily incomplete, since only a fraction of the local names applied to specific entities is actually published. In many cases, local names are available only for species that support traditional fisheries. Apart from possible omissions due to limitations of literature available, some of the names included may be somewhat artificial, i.e. through transliteration of indigenous words into English. The local species name is preceded by the name of the country concerned in capital letters and, where necessary, by geographical specifications in lower case letters.

**(11) Remarks:** Important information concerning the species, but not specifically linked to any of the previous categories, is given here. For example, in some cases the taxonomic status of certain scientific names requires further discussion. Other nomenclatural problems are discussed in this section, such as the use of subspecies names.

**(12) Literature:** This includes references to the most important publications relevant to the species, the emphasis being on biology and fisheries. Additional references are included in the bibliography. In the case of a few uncommon species, only systematic papers are available.

## 1.2 General Remarks on Cephalopods

The group known as cephalopods (class **Cephalopoda**) is the most complex in the phylum Mollusca, and indeed, in all of the invertebrate phyla. It includes exclusively marine animals that live in all oceans of the world with the exception of the Black Sea, from the Arctic Sea to the Antarctic Ocean and from the surface waters down into the deep sea.

Cephalopods first appeared as a separate molluscan taxonomic entity, the nautiloids, in the Upper Cambrian period (over 500 million years ago), but more than half of these ancestors were already extinct by the end of the Silurian, 400 million years ago, when only the nautiluses survived. Meanwhile, other forms arose in the late Palaeozoic (between 400 and 350 million years ago), including those of the Subclass Coleoidea, but most of them became extinct by the end of the Mesozoic, about 150 million years ago. The only members of the subclass Coleoidea that exist today are the forms that developed in the Upper Triassic and Lower Jurassic (between 200 and 150 million years ago).

Although there is a long fossil record of many different groups, all living cephalopods belong to two 'subclasses': the **Coleoidea**, which includes the major groups known as squids, cuttlefishes *sensu lato*, octopods and vampires, and the **Nautiloidea**, containing two genera, ***Nautilus*** and ***Allonautilus***, the only surviving cephalopods with an external shell.

At the present time the status and understanding of the **Systematics and Classification** of the Recent Cephalopoda is under considerable discussion. The families of living cephalopods are, for the most part, well resolved and relatively well accepted. Species-level taxa usually can be placed in well-defined families. The higher classification, however, still is not resolved. The classification above the family level is controversial and a broad consensus still needs to be achieved. This situation is not unexpected for a group of organisms that has undergone explosive research attention in recent decades.

Consequently, rather than accept and promote any particular scheme of classification, before consensus and stability are achieved, we will use an 'operational breakdown' that is satisfactory for the objectives of this Catalogue. For practical purposes we separate the cephalopods into several groups, without assigning or implying taxonomic relationships. Figure 1 diagrams several of the classification schemes currently under discussion.

In this work the following groups are used, as illustrated in Figure 2[1/]:

Nautiluses
Cuttlefishes
Bobtail squids
Bottletail squids
Pygmy squids
Ram's horn squid
Myopsid squids
Oegopsid squids
Vampires
Cirrate octopods
Incirrate octopods

**Unresolved taxa:**
*Spirula*
*Idiosepius*
*Bathyteuthis*
*Chtenopteryx*
Sepiadariidae

Plural versus singular usage of cephalopod common group names is standardized as follows:

**squid, cuttlefish, octopod, octopus, vampire, nautilus** refer to one individual or one species;

**squids, cuttlefishes, octopods, octopuses, vampires, nautiluses** refer to two or more individuals and/or species. These terms are also used to indicate the major groups.

The term **'cuttlefishes'** is also used '*sensu lato*' to indicate the following groups: Cuttlefishes, Bobtail squids, Bottletail squids, Pygmy squids and the Ram's horn squid.

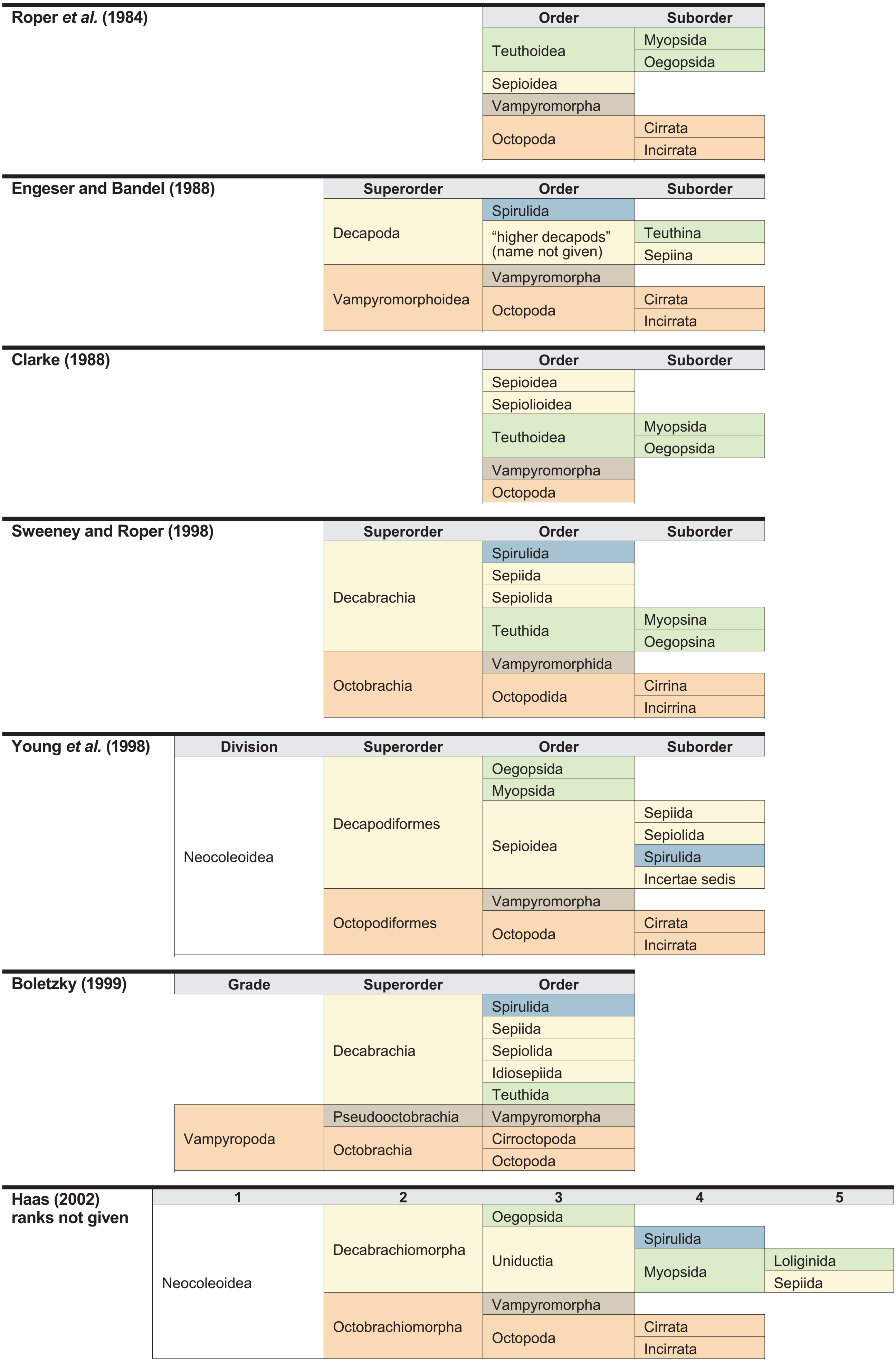
We differentiate between the members of the family Octopodidae, which are called **octopus/octopuses** and the members of the whole group (Incirrate and Cirrate or any combination of non-Octopodidae taxa), which are called **octopod/octopods**.

Cephalopods **occur in all marine habitats** of the world: benthic forms are found on coral reefs, grass flats, sand, mud and rocks; epibenthic, pelagic and epipelagic species occur in bays, seas; and epipelagic, mesopelagic, bathypelagic and benthopelagic species are all present in the open ocean. Salinity is considered to be a limiting factor in cephalopod distribution; they are generally restricted to salinity concentrations between 27 and 37‰. However, ***Lolliguncula brevis***, which lives and reproduces in waters of 17‰, demonstrates a capacity for a higher degree of salinity tolerance (Hendrix *et al*., 1981). Some species inhabit the Red Sea and the southern coasts of the Iberian Peninsula (Guerra, 1992), where the salinity is higher than 37‰ and other species have been found in waters where salinity ranges between 25 and 18‰ (Sea of Marmara; Unsal *et al*., 1999). The habitat depth range extends from the intertidal to over 5 000 m. Many species of oceanic cephalopods undergo diel vertical migrations: they occur at depths of about 200 to 700 m during the day, then at the onset of twilight and increasing darkness, they ascend into the uppermost 200 m for the night. A deeper-living layer of diel migrators occurs from about 1 000 m to 600 m during the daytime. The abundance of cephalopods varies, depending on group, habitat and season, from isolated, territorial individuals (primarily benthic octopods and sepioids), through small schools of squids with a few dozen individuals, to huge schools of neritic and oceanic species with millions of specimens.

The **size of adult** cephalopods ranges from less than 1 cm (Jackson, 1989) to the giant squid at approximately 20 m in total length, including the tentacles. The largest specimens may weigh well over 500 kg, but the average size of commercial species is 20 to 40 cm mantle length and about 0.1 to 2.0 kg total weight.

Cephalopods are **soft-bodied, bilaterally symmetrical** animals with a well-developed head and a body that consists of the muscular mantle, the mantle cavity that houses the internal organs, and, when present, the external fins. The head bears an anterior circumoral (surrounding

[1/] The endings used in the group names do not imply any level of classification.



**Roper *et al.* (1984)**

| Order | Suborder |
|---|---|
| Teuthoidea | Myopsida |
| | Oegopsida |
| Sepioidea | |
| Vampyromorpha | |
| Octopoda | Cirrata |
| | Incirrata |

**Engeser and Bandel (1988)**

| Superorder | Order | Suborder |
|---|---|---|
| Decapoda | Spirulida | |
| | “higher decapods” (name not given) | Teuthina |
| | | Sepiina |
| Vampyromorphoidea | Vampyromorpha | |
| | Octopoda | Cirrata |
| | | Incirrata |

**Clarke (1988)**

| Order | Suborder |
|---|---|
| Sepioidea | |
| Sepiolioidea | |
| Teuthoidea | Myopsida |
| | Oegopsida |
| Vampyromorpha | |
| Octopoda | |

**Sweeney and Roper (1998)**

| Superorder | Order | Suborder |
|---|---|---|
| Decabrachia | Spirulida | |
| | Sepiida | |
| | Sepiolida | |
| | Teuthida | Myopsina |
| | | Oegopsina |
| Octobrachia | Vampyromorphida | |
| | Octopodida | Cirrina |
| | | Incirrina |

**Young *et al.* (1998)**

| Division | Superorder | Order | Suborder |
|---|---|---|---|
| Neocoleoidea | Decapodiformes | Oegopsida | |
| | | Myopsida | |
| | | Sepioidea | Sepiida |
| | | | Sepiolida |
| | | | Spirulida |
| | | | Incertae sedis |
| | Octopodiformes | Vampyromorpha | |
| | | Octopoda | Cirrata |
| | | | Incirrata |

**Boletzky (1999)**

| Grade | Superorder | Order |
|---|---|---|
| | Decabrachia | Spirulida |
| | | Sepiida |
| | | Sepiolida |
| | | Idiosepiida |
| | | Teuthida |
| Vampyropoda | Pseudooctobrachia | Vampyromorpha |
| | Octobrachia | Cirroctopoda |
| | | Octopoda |

**Haas (2002)**
**ranks not given**

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| Neocoleoidea | Decabrachiomorpha | Oegopsida | | |
| | | Uniductia | Spirulida | |
| | | | Myopsida | Loliginida |
| | | | | Sepiida |
| | Octobrachiomorpha | Vampyromorpha | | |
| | | Octopoda | Cirrata | |
| | | | Incirrata | |

**Fig. 1 Some conflicting suprafamilial classifications of living coleoid cephalopods**

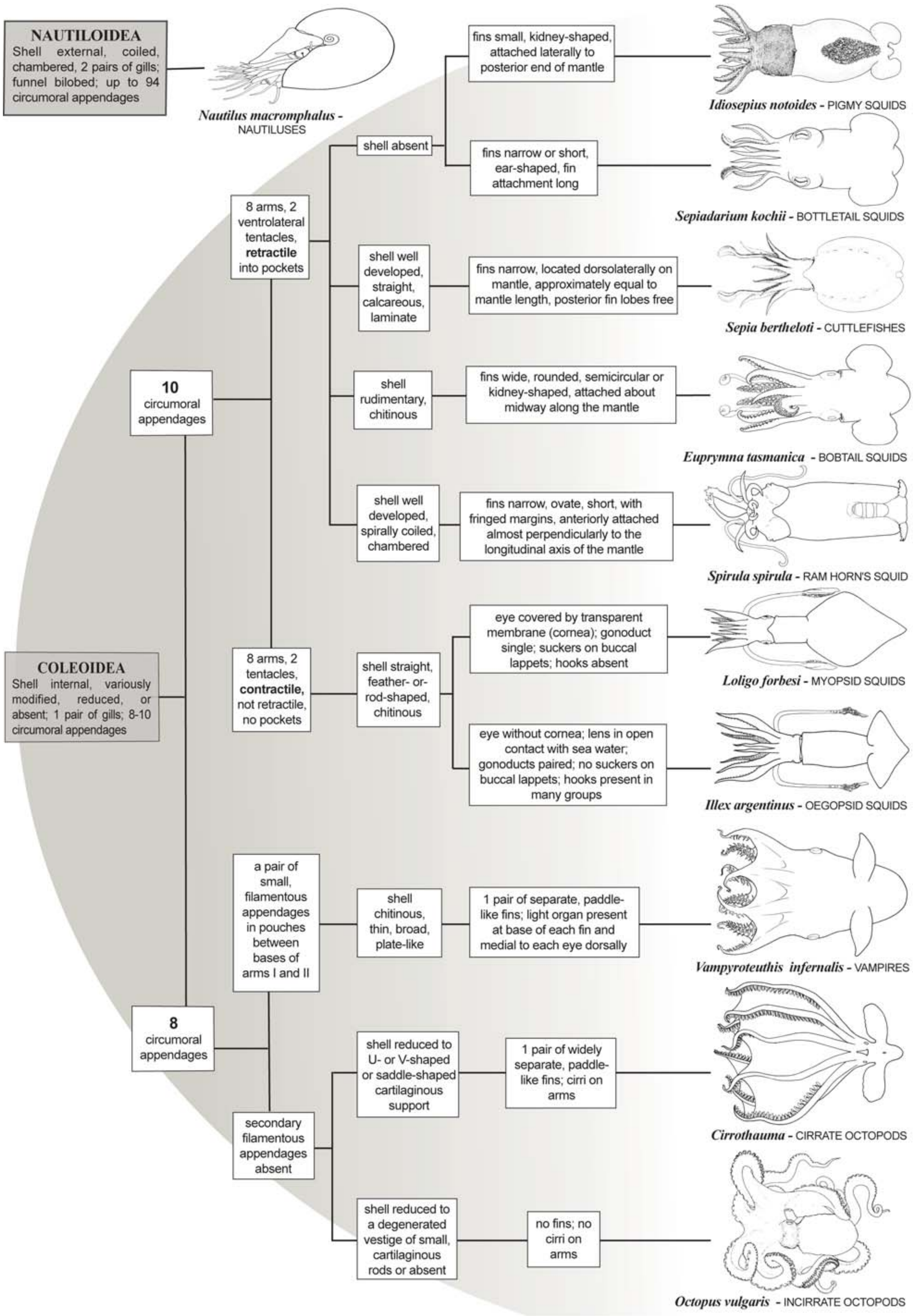


**Fig. 2 Living cephalopods**

the mouth) crown of mobile appendages (arms, tentacles). This characteristic feature reflects the origin of the name Cephalopoda, which derives from the union of the two Greek words: ‘kefale’, head, and ‘pous’, feet. The name was erected by Schneider in 1784, and it became permanently in use within the scientific context with the publication of Cuvier’s work (1798). Arms and tentacles bear suckers and/or hooks (except in ***Nautilus***), which are powerful tools to seize prey. The mouth has a pair of chitinous jaws (the beaks) and, as in other molluscs, a chitinous tongue-like radula (band of teeth) occurs in most cephalopod species. The ancestral mollusc shell is variously modified, reduced, or absent in living coleoids. It is a calcium carbonate structure in cuttlefishes (the cuttlebone of sepiids and the ram’s horn shell of ***Spirula***), reduced to a rigid structure composed of chitin in squids (the gladius or pen, sometimes quite flexible) and to a cartilaginous structure in finned octopods. In some sepiolids no vestige of shell is found. A true external shell occurs only in the primitive nautiluses (restricted to the Indo-Pacific), although a shell-like egg case is produced and carried by female argonauts (pelagic octopods often misnamed ‘paper nautilus’).

The loss of the external shell allowed the development of a **powerful muscular mantle** that became the main locomotory organ for fast swimming, via water jetting from the funnel. The funnel (siphon) is a unique, multifunctional, muscular structure that aids in respiration and expulsion of materials in addition to locomotion. Oxygenated water is drawn through the mantle opening around the head (neck) into the mantle cavity, where it bathes the gills for respiration. Mantle muscular contraction expels the deoxygenated water from the mantle cavity through the ventrally located funnel. The discharge jet serves to eliminate nephridial and digestive wastes, as well as to complete the respiratory cycle and for locomotion. Female reproductive products (eggs, egg masses) also are discharged through the funnel. Most coleoids produce ink, a dark, viscous fluid also expelled through the funnel. The ink may take the form of a mucoidal ‘pseudomorph’ (false body) to decoy potential predators, or of a cloud to obscure the escaping cephalopod.

One pair of gills (ctenidia) is present, except in ***Nautilus*** and ***Allonautilus***, which have two pairs for **respiration**, i.e. to extract the oxygen from the water. However, in contrast with coleoids, ***Nautilus*** makes use of anaerobic respiration during periods of high activity and can survive in water with very low oxygen content. Coleoids also use anerobic muscle layers. Cutaneous respiration also occurs in some cephalopods.

The cephalopod **circulatory system** is distinctive within the Mollusca. It is a closed system (blood contained within vessels), similar in many respects to that of vertebrates and fulfilling the demand for the more efficient circulation required by an active locomotory system. There is a principal, or systemic, heart, two branchial hearts and developed arterial, venous and capillary systems supplying blood to the muscles and organs. From the gills, the oxygenated blood goes through the efferent branchial vessels to the systemic heart, where it is expelled from the ventricle through three aortas: the cephalic or dorsal aorta, which supplies the head and the anterior part of the gut; the posterior, minor or abdominal aorta that supplies the mantle and fins along with the posterior part of the gut and the funnel; and the gonadal aorta that develops gradually with sexual maturation of the animal. The blood is collected through sinuses and capillaries into the veins, through which it goes to the branchial hearts that pump it through the filaments of the gills. The circulating respiratory pigment used for oxygen transport is copper-containing haemocyanin, a system of rather lower efficiency than the iron-containing haemoglobin of vertebrates. In living cephalopods blood sinuses are much reduced and replaced functionally by muscles. The circulatory system therefore has to work against the peripheral muscle-induced pressure, which increases with increasing activity (maximum during jet-swimming). It also has to cope with the resistance of the small diameter of the final capillary blood vessels, and the low oxygen carrying capacity of the blood (less than 4.5% by volume). In spite of these limitations, the system has other functional modifications (see for example Wells and Smith, 1987; Martin and Voight, 1987) that achieve the capacity to deliver oxygen at a rate comparable to that of active fishes, enabling cephalopods to accomplish extraordinary performances.

The **excretory system** also differs markedly from that of other molluscs and, along with the closed circulatory system and the branchial circulation, enables unique relationships between blood and the final secretion, the urine. The excretory system differs between living nautiloids and coleoids and also among coleoids, but the general organization is similar, consisting basically of the renal sac with the renal appendages (organs comparable to vertebrate kidneys), the pericardial glands, the branchial hearts and the gills. Cephalopods are ammoniotelic, and ammonium ions are continuously released by the gill epithelium and by renal appendages into the surrounding water. Ammonium ions are used by buoyant squids to replace denser chloride ions in fluids in the coelom and in the body tissues. Because this solution is less dense (and hence more buoyant) than seawater, it provides lift.

The **nervous system** is highly developed in recent cephalopods, with a large brain and peripheral connections, contrasting with the original molluscan circumesophageal nerve ring. Among its most remarkable features is the giant fibre system of squids and cuttlefishes that connects the central nervous system with the mantle muscles. This system consists of three orders of cells and fibres and ensures the immediate and simultaneous contraction of mantle, fins and retractor muscles of both sides, rather than an anterior to posterior sequential contraction that would be counter-productive for water movement (expulsion). Also remarkable is the eye development of most coleoids, for which vision plays a major role in life. Their eyes are large, have a design generally similar to that of fishes and other vertebrates (e.g. a lens focuses images on the retina), and all the available evidence suggests the ocular/visual performance to be comparable to that of vertebrates. The cephalopods also developed a system to keep the focused image stationary on the retina while the animal turns, by moving the eyes in coordination with the head/body movement. This is extremely important for hunters that rely on sight, and it is accomplished by connections of the eye muscles with the statocysts, a mechanism similar to the vestibulo-optic system of fishes. The statocyst system provides cephalopods with information on their orientation, as well as changes in position and direction of movement. The statocyst system is highly developed in coleoids, where it consists of separate cavities located in the cartilaginous skull, posteroventral to the brain. The statocysts contain nervous cells and receptors differentiated to detect both linear acceleration, with the aid of calcareous stones called statoliths, and angular acceleration. Many coleoids also have extra-ocular photoreceptors (photosensitive vesicles) about which little is known; in mesopelagic squids they appear to monitor light intensity in order to enable the animals to match the counter-illumination with the ambient light by their own photophores (light-producing organs). Cephalopods are provided with numerous mechano- and chemoreceptors and recent evidence indicates that in some species, like ***Loligo vulgaris***, ***Sepia officinalis*** and ***Octopus*** sp., ciliate cells form lines in several parts of the body, a system analogous to the lateral-line system in fishes.

Most Coleoidea are able to change colour by using a complex system of **chromatophores** under nervous control. The chromatophores are pigment-filled sacs present in the skin, and capable of remarkable expansion and contraction. This system responds to current situations in the environment, e.g. background coloration and threatening predators, and it is critical for survival, especially for shallow-water benthic forms. Coloration capabilities are variable depending on taxonomic group and habitat. Most species also have **iridocytes** (shiny, reflective platelets) in the skin. Most cephalopod behaviour includes rapid changes in overall colour and colour patterns, as well as changes in the texture of the skin, from smooth to heavily papillate, tubercular, or with erected flaps. While shallow-living cephalopods are able to conceal themselves by chromatophore-produced colour patterns, chameleon-like colour changes and textural presentations, many deep-sea forms camouflage themselves by producing bioluminescent light from photophores which eliminate their silhouettes against the downwelling sunlight in the dimly-lit mid-depths.

**Locomotion** is achieved by any of, or a combination of, the following methods, depending on the taxonomic group: 1) jet propulsion; 2) flapping or undulating the fins on the mantle; 3) crawling along the bottom on the arms; 4) medusoid swimming with arms and interbrachial webs. The fins on the mantle also provide balance and steering during jet propulsion. Many families of midwater squids have evolved to ‘low energy life styles’ and achieve neutral buoyancy by producing and storing in tissues or in different organs substances/elements with specific properties, such as oils or solutions of ammonium ions. This capability enabled coleoid cephalopods to inhabit open water, even in the great depths in the ocean, the greatest volume of living space on earth.

Cephalopods are voracious, active **predators** that feed upon crustaceans, fishes, other cephalopods and, in the case of some benthic octopods, on bivalved molluscs. The speed of cephalopods, their high mobility and powerful visual systems, along with strongly-muscled arms and tentacles, both equipped with suckers and/or hooks, make them extremely efficient hunters. A common hunting technique in sepioids and loliginids involves extremely rapid shooting forward of the tentacles to capture the prey, while in some oegopsid squids the tentacles may be used like long, sucker-covered fishing lures. Some octopods use their web to envelop crabs and occasionally may wait until prey touches them before attacking. The captured prey of cephalopods is brought to the mouth and killed by bites of the strong, chitinous beaks, equipped with powerful muscles. Sometimes the prey are first paralysed with a fast-acting toxin, immobilization being a strong advantage in case of large and/or very active prey such as large crabs. The Incirrate octopods and ***Sepia*** species usually poison their prey before eating them, while squids do not seem able to produce such strongly toxic secretions. Digestion in cephalopods is rapid and efficient and cephalopod metabolism is essentially proteinic: there is little or no digestion/assimilation of carbohydrates and lipids. Food conversion is highly efficient, especially in octopuses, where up to 50% of the food eaten can be converted into body mass. More active cephalopods like squids, however, need several times the amount of food required by octopuses and can eat from 3 to 15% of their body weight each day.

All cephalopods are **dioecious** (separate sexes) and many, though not all, exhibit external sexual dimorphism, either in morphological or in size differences. Females frequently are larger than males, a phenomenon which reaches its extreme in some pelagic octopods (such as ***Argonauta***) where males are truly dwarf forms. Males of many species possess one, occasionally two, modified arm(s) (the hectocotylus) for transferring spermatophores to females during mating. The males of some species also exhibit modifications to other arms, in addition to the hectocotylus. The hectocotylus may be simple or complex and can consist of modified suckers, papillae, membranes, ridges and grooves, flaps. The one or two limbs function to transfer the spermatophores (tubular sperm packets) from the male’s reproductive tract to an implantation site on the female. The spermatophores may be implanted inside the mantle cavity (where they may penetrate the ovary), into the oviducts themselves, around the mantle opening on the neck, on the head, in a pocket under the eye, around the mouth or in other locations. Females of a few species also develop gender-specific structures (e.g. arm-tip photophores) when mature. Mating is often preceded or accompanied by courtship behaviour that involves striking chromatophore patterns and display. Copulatory behaviour varies significantly among species, in colour and textural display, proximity of male and female, duration of display and spermatophore transfer, and the location of implantation of the spermatophores on the female.

The **gonads** form a single mass at the posterior end of the mantle cavity, and female gonoducts may be paired (in oegopsids and incirrate octopods) or single, as in other coleoids and in the nautiluses. Cephalopod reproductive systems are highly complex structures with ducts, glands and storage organs. Female octopods have oviducal glands, while decapods, in addition, have nidamental glands and, in some families, accessory nidamental glands. Spermatophores are produced in the multi-unit spermatophoric gland and stored in the Needham’s sac, from which they are released through the terminal part of the duct, the penis. This term is not strictly accurate in many groups, because the spermatophores are passed to, or taken by, the hectocotylized arm(s), which in turn transfer(s) the spermatophore(s) to the female. Some families do not possess a hectocotylus. Instead, the terminal portion of the male reproductive tract forms a functional penis that can be greatly enlarged and elongated, often extending out of the mantle cavity and past the head. It is likely that these structures directly transfer the spermatophores to the female. The number and size of spermatophores vary greatly, depending on the species and group (for reviews on spermatophore structures and function see Mann *et al*., 1966, 1970; Mann, 1984). Once in contact with seawater, the so called ‘spermatophoric reaction’ begins. The spermatophores evert, with the resultant extrusion of the sperm packet caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher. The resulting extruded sperm packet is named spermatangium (or sperm bulb or body). Sperm are able to survive several months once stored in the female, at least in some species, and fertilization of mature ova may take place either in the ovary, the oviducal glands, the mantle cavity or the cone formed by the outstretched arms while the eggs are laid. Males of the pelagic octopod ***Argonauta*** (and its relatives) insert sperm into a detachable hectocotylized arm. Mating occurs by the arm severing and crawling into the female's mantle cavity.

Fertilized **eggs** are embedded in one or more layers of protective coatings produced by the oviducal and nidamental glands and generally are laid as egg masses. Egg masses may be benthic or pelagic, varying among the major taxonomic groups. Some oceanic mesopelagic and deep-sea species, however, lay individual eggs.

Eggs of neritic, inshore squids, except in ***Sepioteuthis***, generally are very small (only a few millimetres in diameter) and frequently are laid in finger-like pods each containing from a few to several hundred eggs. Deposited in multifinger masses (sometimes called 'sea mops'), these eggs are attached to rocks, shells or other hard substrates on the bottom in shallow waters. Many oceanic squids lay their eggs into large sausage-shaped or spherical gelatinous masses containing tens or even hundreds of thousands of eggs that drift submerged in the open sea. Other pelagic species lay individual eggs, not enmeshed in gelatinous masses.

Cuttlefishes *sensu lato* lay few, relatively large (around 10 to 40 mm in diameter), grape-like eggs that are attached to hard substrates. Some species camouflage the eggs from predators by making them dark using a coating of ink deposited by the female at egg laying.

Cirrate octopods lay rather large (from 10 to 25 mm length) single eggs, enclosed in a tough protective coating (see Boletzky, 1982, 1986), and they are laid individually or in small clusters of a very few eggs.

Benthic incirrate octopods lay their eggs singly or in grape-like clusters and strands. Most species attach the eggs to hard surfaces such as rock or shells while some carry the eggs within their arms and webs. The eggs vary in size from a few millimetres to 40 mm long. They are attached to each other and/or to the substratum by cement produced by the oviducal gland. They lack the gelatinous outer matrix found in squid and cuttlefish eggs and the outer shell found in the Cirrate octopod eggs: the protective function has been 'replaced' by the brooding behaviour of the female parent. The female of the pelagic octopod ***Argonauta*** constructs a thin, decorative shell-like egg case, which encases her mantle and into which she periodically lays and attaches festoons of minute eggs.

The mode of reproduction and egg-laying still is unknown for many species, especially those of oceanic and deep-sea environments.

**Development** of cephalopod embryos is direct, without true metamorphic stages. Hatchlings of species with large eggs look like miniatures of the adult, while hatchlings of species with small eggs undergo gradual changes in proportions during development. The young of some species, however, differ conspicuously from the adults. Thus, the term 'paralarva' has been introduced for these early stages of cephalopods that differ morphologically and ecologically from older stages. Hatchlings from large-egged benthic octopods are either benthic crawl-away young or temporarily planktonic, quickly settling back to the adult benthic habitat. Small-egged benthic octopuses produce planktonic hatchlings with very simple skin patterns of large chromatophores. The paralarvae of many deep-sea species of squids and octopods occur in the upper 100 m of the open ocean; then they exhibit an ontogenetic descent, gradually descending to deeper depths with increasing size until the adult depth is attained. Time of embryonic development varies widely, from a few days to many months, depending on the species and the temperature conditions. Hatching may occur synchronously from a single clutch or be extended over a period of 2 or 3 weeks.

In spite of the large number of studies and research carried out on cephalopods, especially in recent decades, the **life history** of the majority of species is still unknown, and our knowledge of the life cycles of the members of this interesting class remains fragmentary. Information comes from studies in the field as well as from observations in the laboratory. However, little is known of life history for species that are not targets of regular fisheries, and only a handful of cephalopod species have been reared successfully in the laboratory.

Studies and monitoring of **growth** in cephalopods are complicated by the high variability in individual growth rates. This makes it difficult to apply conventional methods, e.g. length frequency analysis, used for more traditional resources such as fishes and crustaceans. Determination of age in Recent coleoids is also difficult, because they have few hard structures that show daily marks (rings) that would enable direct estimates of age. In the last 15 years, progress has been made on the study and analysis of statoliths that has resulted in an increased knowledge of age, in squids at least. This has led to changes in our perspectives about the physiology and ecology of many teuthoids, but more research is required before a full understanding is achieved (see Jereb *et al*., 1991; Okutani *et al*., 1993; Jackson, 1994 and Lipinski and Durholtz, 1994 for reviews and discussions). Principle results obtained from the research generally confirm a very high growth rate in cephalopods, comparable to that of the fastest-growing fishes.

***Nautilus*** species have a **life span** of about 20 years, during which they spawn intermittently when first mature, then annually when fully mature, laying a few large eggs at a time. The life expectancy of most coleoids appears to range from a few months to one or two years. Many small oceanic squids, such as pyroteuthids may complete their life cycles in less than six months, while some minute forms of sepioids have a life span of only 2 to 3 months. Recent evidence, however, suggests that larger species of squids and octopods, for example the giant squid (***Architeuthis*** spp.) and the giant octopus (***Enteroctopus dofleini***), as well as those that live in coldest habitats, may live for several years.

A general consensus exists that **spawning** is a terminal event, in spite of the high variability in the duration of individual spawning periods (5 to 50% of ontogenesis; Nigmatullin, 2002) as well as the type of spawning, e.g. from one-time, total spawning, to prolonged, intermittent, multiple batches. A recent review of coleoid reproductive strategies (Rocha *et al*., 2001) defined five comprehensive, flexible strategies:

A) **Single event spawning**, formerly termed semelparity, consists of synchronous ovulation, and monocyclic, simultaneous terminal spawning; ***Octopus vulgaris*** is the typical example of this life strategy.

B) **Multiple event spawning**, formerly termed iteroparity, with the following possibilities:

1 - polycyclic spawning: egg-laying occurs in separate batches during the spawning season and growth occurs between production of egg batches and subsequent spawning events (e.g. ***Nautilus*** species);

2 - multiple spawning, with group-synchronous ovulation, monocyclic spawning and growth between egg batches (e.g. ***Sthenoteuthis oualaniensis***);

3 - intermittent terminal spawning with group-synchronous ovulation, monocyclic spawning and no growth between egg batches (e.g. ***Sepia officinalis***, ***Loligo vulgaris***, ***Illex coindetii***);

4 - continuous spawning, with asynchronous ovulation, monocyclic spawning and growth between egg batches (e.g. ***Idiosepius pygmaeus***, ***Opisthoteuthis*** spp., ***Argonauta*** spp.).

All coleoids die after their spawning period.

The **total number** of living species of cephalopods that have been described is fewer than 1 000; over 720 are listed in the present catalogues. However, many species still wait to be described and this is particularly true for the octopuses, where at present at least another 100 undescribed species are estimated to exist.

The status of the **systematics** of cephalopods has changed in the last 30 years, as research and associated scientific discussions have increased substantially. However, phylogenetic relationships among most families within the major groups remain uncertain, and new species are described fairly frequently as new habitats are explored and as families are gradually better-understood.

The major groups of living cephalopods, i.e. squids, cuttlefishes, bobtail and bottletail squids, octopods, vampires and chambered nautiluses, are easily distinguished by external characteristics.

The **squids** have an elongate, cylindrical body with posterolateral fins on the mantle (rarely, the fins extend for the length of the mantle); 10 circumoral appendages anteriorly on the head, not connected at bases with a web (except Histioteuthidae); 8 arms with 2 (occasionally 4 or more) series of stalked suckers with chitinous rings (and/or chitinous hooks in some groups) that extend along the entire arm length; 2 longer tentacles with an organized cluster of 2 or more series of stalked suckers (and/or hooks) at the distal section (tentacular club); the proximal tentacular stalks usually are devoid of suckers or hooks.

The **cuttlefishes** have broad sac-like bodies with lateral fins that are narrow and extend along the length of the mantle; posterior lobes of the fins free (subterminal) and separated by the posterior end of the mantle; 10 circumoral appendages, the longest 2 (tentacles) are retractile into pockets on the ventrolateral sides of the head; the 8 remaining arms frequently with 4 series of stalked suckers with chitinous rings, never hooks (otherwise 2 series); eyes covered with a transparent membrane and eyelids present; dorsal, internal, finely chambered shell, thick, chalky, calcareous (cuttlebone).

The **bobtail** and **bottletail squids** have sac-like bodies with short, round and flap-like fins, attached laterally about midway along the mantle, with pronounced anterior lobes and free posterior lobes; 10 circumoral appendages as above, 8 short arms, 2 retractable tentacles, each with a well defined club; large eyes covered with a transparent membrane; shell thin, chitinous or lost.

The **octopods** have a short, sac-like body, either with no lateral fins or with separate, paddle-like fins in the deep-sea cirrate octopods; 8 circumoral arms only (no tentacles) with bases connected by a membranous web, and unstalked suckers in one or two series, without chitinous rings or hooks, along the length of the arms.

The **vampires** have 8 circumoral arms, plus an additional pair of long, thin, suckerless filaments, retractile into pockets, located between arms I and II; one pair of posterior, elongate-oval fins (2 pairs in juveniles); numerous small photophores over body, posteriorly a pair of large, external photophores; single series of suckers bordered with cirri on each arm.

The chambered **nautiluses** are characterized by an external, smooth, coiled, chambered shell, numerous circumoral appendages without suckers (up to 100 appendages), a ‘funnel’ of rolled muscular flaps or lobes not fused in the ventral midline and simple eyes without lenses.

More detailed descriptions of these groups are presented in the appropriate systematic section.

Cephalopods are important experimental animals in **biomedical research** with direct applications to humans. Because of their highly developed brains and sensory organs, they are valuable in behavioural and comparative neuroanatomical studies. In addition, the extremely large single nerve axons of some cephalopods, the largest in the animal kingdom, are used extensively in neurophysiological research.

The bite of cephalopods, especially octopuses, can be painful at the least to humans, poisonous or secondarily infected, or, rarely, lethal. Several human deaths have been recorded in the western Pacific Ocean and Australia as a result of poisonous bites from the small blue-ringed octopus, ***Hapalochlaena*** spp.; the lethal toxin is a neural blocker considered a form of tetrodotoxin. Another documented threat by squids to humans is from the large ommastrephid squid, ***Dosidicus gigas***, which forms large aggressive schools that are known to have attacked fishermen that have fallen in the water, causing several confirmed deaths. Scuba divers also have been attacked. Therefore, cephalopods must be handled carefully.

## 1.3 Interest to Fishery and Role in the Ecosystem

Cephalopods are very important for human consumption. They have been fished on an artisanal basis for several thousand years and were already well known and highly valued as food by ancient Greeks, Romans and Chinese. In more recent times, increasingly heavy demand for cephalopods by the Japanese led to the development of a commercial fishery that started in the 1960s and rapidly expanded to become global in scope. Fishing pressure on cephalopods has increased as stocks of finfishes have been depleted worldwide, and cephalopod resources now are exploited throughout the world oceans.

A catch of around 3.3 million tonnes was reported for 2001 by FAO statistics (FAO, 2000); this figure represents about 3.6% of the world total marine catch for the same year. Estimated value for this catch was around US$5 billion, a value that positions cephalopods in fifth place in the monetary value scale, following miscellaneous coastal fishes, shrimps, tunas, cods and hakes.

**Table 1** reports the world catch of cephalopods since 1950, by major fisheries 'categories'. The discrepancies in the last digit of the totals in the tables are caused by rounding off the individual figures. Squids, both inshore and oceanic, are by far the main component in the world cephalopod fishery production, accounting for about 70% of the total catch, followed by cuttlefishes (species of ***Sepia***, ***Sepiella*** and allied genera), then by octopuses (mainly ***Octopus*** spp. and ***Eledone*** spp.). The impressive increase in production during the last 20 years is due mainly to the increase of squid catches, from a little more than 1 million tonnes in 1980 to over 2.2 million tonnes for 2001; this value represents an increase of 250%. Such a significant increase in production was mostly related to the 'discovery' and increasing exploitation of squid resources in the southwest Atlantic (Fig. 3b), principally for ***Illex argentinus***, (Fig. 4b), as well as an increase in the production of other major squid target species, mainly ***Todarodes pacificus*** in the northwest Pacific and ***Dosidicus gigas*** in the eastern Pacific (Figs 3d–e and 4b). ***Illex argentinus*** catches exceeded 1 million tonnes in 1999 (Table 2), a record peak which placed this species at the eleventh position in value of the total world marine-species production of that year. Fluctuations in squid catches are responsible for the major fluctuations in total cephalopod landings, changes usually related to a combination of environmental, marketing and/or political reasons. For example, the low cephalopod catch in 1998 in the eastern Pacific, reflected the poor catch of ***Dosidicus gigas*** as a result of the El Niño weather system in the southern and central areas that year. By contrast, the low catch in the southwest Atlantic and in the northwest Pacific in the same year was mainly a result of low fishing activities by the main squid-producing countries (i.e. Korea, Japan and Taiwan Province of China). This was caused by a lower market demand due to very high catches of the previous year, together with higher fishing fees set by Argentina on foreign trawlers fishing in its waters that year.

Cuttlefishes *sensu lato* production also increased strikingly over the last two decades, doubling between 1980 and 2001 (Table 1; Fig. 4d). The main producer is China (over 50% of the total), followed by Thailand (western Pacific and central Indo-Pacific areas) and by Morocco (eastern central Atlantic), where production increased steadily in recent years.

Octopus catches have increased as well, but not as conspicuously (Table 1; Fig. 4e). The main producer is Morocco, which accounted for slightly more than 35% of the total reported octopus production in 2001, followed by Japan (about 14% of total world production). Mexico ranks first in the '***Octopus vulgaris***' landings, with over 20 000 tonnes reported for 2001, followed by Spain (nearly 15 000 tonnes); Mexican production accounts for more than one-third (38.7%) of total '***Octopus vulgaris***' species-complex reported production.

Cephalopod fisheries and landings are unevenly distributed in the world's oceans, as shown in Table 3 (Antarctic zone captures are not reported in the figure because they are minimal; these catches are discussed in the individual species sections). More than half of the total cephalopod catch (about 58% in 2001) is taken in the northwest Pacific and the southwest Atlantic combined. Other important areas are the western central Pacific, eastern Atlantic and eastern Pacific, but smaller-scale fishing activities in other areas also developed consistently in the last decades (see, for example, the Indian Ocean fisheries). Cephalopod fisheries are especially intense in Japan, southeastern Asia and China and in the Mediterranean Sea, where, however, cephalopod catches show a decreasing trend for all three main groups in the last decade (Fig. 3g).

Japan remains the leading cephalopod-producing country; over 560 000 tonnes were caught by Japanese fleets in 2001, which represents about 17% of the total world cephalopod catch (Table 4). However, China, Korea and Argentina follow closely. In fact, Korea was the main producer in 1999, principally as a consequence of the peak in ***Illex argentinus*** production.

International commerce of cephalopod products also increased strikingly during the last 20 years. Imported and exported cephalopod products were estimated at around 325 000 and 240 000 tonnes, respectively, in 1980, compared with more than 1.3 million tonnes estimated for 2001 (Table 5).

Estimated cephalopod import value reached US$ 2 700 billion in 2001. This represents about 4.6% of the value of the total world fisheries commodities imports for the same year, while the value of cephalopod exports was a little higher than US$ 2 500 billion, i.e. about 4.5% of the total world fisheries commodities export value.

Argentina was the lead exporter in the 2001 statistics in terms of quantity, followed by Spain, then by Morocco and the United States (Table 5). However, the highest monetary values of exports are those attained by Morocco (frozen ***Octopus*** spp. and squids, both ***Loligo*** spp. and ***Todarodes sagittatus***), followed by Thailand (frozen cuttlefishes and squids, as well as cephalopod 'preparations') and Viet Nam (dried squids, followed by various frozen cephalopods, including ***Octopus*** spp.).

European countries are the main market at present for imported cephalopod products, with Spain, Italy, Greece, Portugal and France accounting for 49.6% of the world total (Table 5). Spain has been the leading European importer (by tonnage) in the world since 1997. The highest import values, however, remain those spent by Japan, mainly for frozen ***Octopus*** spp., followed by various other cephalopod commodities.

## Table 1

Total world cephalopod catch in thousand metric tonnes since 1950, by major fisheries categories

| | Squids Total[1/] | | *Loligo* spp. | Ommastrephidae | Non-identified Squids | Octopuses | | Cuttlefishes | | Non-identified Cephalopods | | World Cephalopod Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | mt | % | mt | mt | mt | mt | % | mt | % | mt | % | mt |
| **1950** | 494.5 | 85 | 12.4 | 431.4 | 50.7 | 35.8 | 6.20 | 47.2 | 8.10 | 3.0 | 0.50 | 580.5 |
| **1951** | 548.5 | 85 | 9.9 | 483.1 | 55.5 | 39.9 | 6.20 | 55.6 | 8.60 | 3.0 | 0.50 | 647.0 |
| **1952** | 686.4 | 85 | 15.7 | 605.3 | 65.4 | 49.7 | 6.20 | 67.9 | 8.40 | 3.0 | 0.40 | 807.0 |
| **1953** | 505.9 | 81 | 14.8 | 429.4 | 61.7 | 53.6 | 8.60 | 62.6 | 10.00 | 3.0 | 0.50 | 625.1 |
| **1954** | 470.4 | 78 | 13.4 | 400.2 | 56.8 | 56.6 | 9.40 | 69.6 | 11.60 | 3.0 | 0.50 | 599.7 |
| **1955** | 477.2 | 78 | 16.9 | 393.8 | 66.5 | 60.0 | 9.80 | 72.7 | 11.80 | 4.0 | 0.70 | 613.9 |
| **1956** | 402.4 | 75 | 16.7 | 313.7 | 72.0 | 60.9 | 11.30 | 70.4 | 13.10 | 4.0 | 0.70 | 537.7 |
| **1957** | 479.6 | 76 | 17.8 | 393.5 | 68.3 | 67.4 | 10.70 | 77.3 | 12.30 | 4.6 | 0.70 | 628.9 |
| **1958** | 468.2 | 75 | 18.4 | 391.4 | 58.4 | 68.4 | 10.90 | 86.7 | 13.80 | 4.8 | 0.80 | 628.0 |
| **1959** | 611.9 | 78 | 17.8 | 512.1 | 82.0 | 70.7 | 9.00 | 95.0 | 12.10 | 4.3 | 0.50 | 781.9 |
| **1960** | 612.2 | 78 | 23.1 | 510.7 | 78.4 | 76.0 | 9.70 | 94.6 | 12.00 | 4.5 | 0.60 | 787.3 |
| **1961** | 575.1 | 76 | 24.1 | 481.2 | 69.8 | 79.9 | 10.60 | 94.3 | 12.50 | 4.1 | 0.50 | 753.4 |
| **1962** | 708.1 | 78 | 24.6 | 592.4 | 91.1 | 93.0 | 10.30 | 100.6 | 11.10 | 4.1 | 0.50 | 905.8 |
| **1963** | 830.2 | 81 | 24.8 | 705.4 | 100.0 | 95.1 | 9.30 | 96.2 | 9.40 | 4.8 | 0.50 | 1 026.3 |
| **1964** | 448.8 | 66 | 27.2 | 348.4 | 73.2 | 97.9 | 14.50 | 125.5 | 18.50 | 5.0 | 0.70 | 677.2 |
| **1965** | 616.3 | 70 | 33.9 | 498.9 | 83.5 | 116.4 | 13.20 | 144.4 | 16.40 | 4.8 | 0.50 | 881.9 |
| **1966** | 602.8 | 71 | 33.5 | 481.5 | 87.7 | 111.1 | 13.00 | 133.6 | 15.70 | 5.7 | 0.70 | 853.1 |
| **1967** | 684.6 | 70 | 31.8 | 539.6 | 113.2 | 146.1 | 14.90 | 146.8 | 14.90 | 5.0 | 0.50 | 982.5 |
| **1968** | 902.1 | 72 | 37.1 | 764.2 | 100.7 | 188.9 | 15.10 | 154.4 | 12.40 | 4.8 | 0.40 | 1 250.2 |
| **1969** | 697.5 | 69 | 34.9 | 548.6 | 114.1 | 163.8 | 16.10 | 151.2 | 14.90 | 4.6 | 0.50 | 1 017.1 |
| **1970** | 680.3 | 69 | 76.4 | 501.7 | 102.1 | 153.1 | 15.50 | 151.4 | 15.30 | 6.3 | 0.60 | 991.1 |
| **1971** | 640.1 | 66 | 79.3 | 427.0 | 133.8 | 150.6 | 15.40 | 178.8 | 18.30 | 7.6 | 0.80 | 977.1 |
| **1972** | 805.4 | 66 | 112.3 | 550.9 | 142.2 | 212.1 | 17.50 | 181.3 | 15.00 | 13.5 | 1.10 | 1 212.4 |
| **1973** | 717.5 | 68 | 111.3 | 434.4 | 171.9 | 178.9 | 16.80 | 150.0 | 14.10 | 15.6 | 1.50 | 1 062.0 |
| **1974** | 718.0 | 66 | 117.9 | 388.1 | 211.9 | 228.0 | 20.80 | 139.5 | 12.70 | 10.3 | 0.90 | 1 095.8 |
| **1975** | 797.8 | 67 | 120.6 | 458.5 | 218.7 | 249.1 | 20.80 | 137.3 | 11.50 | 13.7 | 1.10 | 1 197.9 |
| **1976** | 782.5 | 64 | 104.6 | 429.9 | 248.0 | 232.0 | 19.10 | 186.5 | 15.40 | 12.9 | 1.10 | 1 213.9 |
| **1977** | 800.6 | 64 | 117.6 | 357.5 | 325.5 | 206.2 | 16.50 | 223.0 | 17.90 | 17.5 | 1.40 | 1 247.3 |
| **1978** | 873.4 | 64 | 114.5 | 418.3 | 340.6 | 203.7 | 15.00 | 263.3 | 19.30 | 21.4 | 1.60 | 1 361.7 |
| **1979** | 1 059.8 | 70 | 114.5 | 571.6 | 373.7 | 157.9 | 10.40 | 285.8 | 18.80 | 19.6 | 1.30 | 1 523.1 |
| **1980** | 1 091.0 | 71 | 118.5 | 536.3 | 436.1 | 181.7 | 11.70 | 252.9 | 16.40 | 20.9 | 1.40 | 1 546.5 |
| **1981** | 944.7 | 68 | 124.2 | 448.0 | 372.5 | 222.2 | 16.10 | 198.6 | 14.40 | 17.5 | 1.30 | 1 383.1 |
| **1982** | 1 114.2 | 69 | 136.5 | 457.1 | 520.6 | 202.3 | 12.50 | 281.0 | 17.40 | 18.6 | 1.10 | 1 616.1 |
| **1983** | 1 085.5 | 65 | 175.0 | 392.8 | 517.6 | 250.3 | 14.90 | 316.5 | 18.90 | 22.4 | 1.30 | 1 674.6 |
| **1984** | 1 125.8 | 68 | 150.5 | 511.9 | 463.3 | 213.3 | 12.80 | 294.8 | 17.70 | 32.3 | 1.90 | 1 666.2 |
| **1985** | 1 260.2 | 70 | 178.9 | 530.9 | 550.4 | 211.1 | 11.80 | 280.8 | 15.70 | 36.2 | 2.00 | 1 788.3 |
| **1986** | 1 205.7 | 69 | 250.5 | 467.2 | 488.0 | 250.5 | 14.20 | 275.3 | 15.70 | 26.5 | 1.50 | 1 758.1 |
| **1987** | 1 756.5 | 76 | 328.4 | 871.1 | 557.0 | 245.5 | 10.70 | 247.5 | 10.80 | 47.6 | 2.10 | 2 297.1 |
| **1988** | 1 644.0 | 74 | 293.3 | 846.9 | 503.8 | 253.7 | 11.30 | 268.6 | 12.00 | 69.1 | 3.10 | 2 235.4 |
| **1989** | 1 973.8 | 75 | 357.7 | 968.9 | 647.2 | 275.1 | 10.40 | 279.3 | 10.60 | 115.9 | 4.40 | 2 644.0 |
| **1990** | 1 720.0 | 73 | 296.6 | 822.2 | 601.2 | 294.4 | 12.40 | 299.1 | 12.60 | 57.5 | 2.40 | 2 371.1 |
| **1991** | 1 856.1 | 72 | 293.7 | 1 072.4 | 489.9 | 319.3 | 12.50 | 301.0 | 11.80 | 84.7 | 3.30 | 2 561.1 |
| **1992** | 2 095.3 | 76 | 310.2 | 1 362.4 | 422.7 | 297.4 | 10.70 | 267.4 | 9.70 | 106.9 | 3.90 | 2 767.0 |
| **1993** | 1 973.6 | 73 | 317.1 | 1 390.4 | 266.1 | 296.6 | 11.00 | 310.5 | 11.60 | 107.1 | 4.00 | 2 687.8 |
| **1994** | 1 959.5 | 70 | 318.4 | 1 322.3 | 318.8 | 275.4 | 9.80 | 383.6 | 13.70 | 184.9 | 6.60 | 2 803.4 |
| **1995** | 2 001.8 | 68 | 328.0 | 1 313.0 | 360.8 | 304.3 | 10.40 | 421.7 | 14.40 | 210.6 | 7.20 | 2 938.4 |
| **1996** | 2 276.2 | 72 | 305.2 | 1 607.4 | 363.7 | 305.6 | 9.70 | 381.4 | 12.10 | 186.5 | 5.90 | 3 149.7 |
| **1997** | 2 487.9 | 72 | 269.2 | 1 909.8 | 308.9 | 273.4 | 7.90 | 469.4 | 13.60 | 225.9 | 6.50 | 3 456.6 |
| **1998** | 1 883.5 | 66 | 295.4 | 1 243.6 | 344.5 | 319.6 | 11.20 | 441.5 | 15.50 | 213.0 | 7.50 | 2 857.6 |
| **1999** | 2 582.1 | 72 | 268.3 | 1 860.2 | 453.6 | 352.5 | 9.80 | 453.1 | 12.60 | 210.0 | 5.80 | 3 597.7 |
| **2000** | 2 560.7 | 70 | 304.9 | 1 773.8 | 482.0 | 312.2 | 8.50 | 497.4 | 13.60 | 284.8 | 7.80 | 3 655.2 |
| **2001** | 2 242.6 | 67 | 288.9 | 1 574.5 | 379.2 | 317.2 | 9.50 | 533.3 | 15.90 | 253.7 | 7.60 | 3 346.8 |

(Source: FAO, 2000)

[1/] Squids are broken down into Loliginids, Ommastrephids and unidentified squids to show each group’s relative importance.

## Table 2

Total world cephalopod catch in thousand metric tonnes since 1980, by major species (Source: FAO, 2000)

| Cephalopod species | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Illex argentinus* | 16.0 | 33.3 | 79.7 | 56.2 | 106.1 | 204.9 | 271.3 | 546.3 | 564.3 | 558.5 | 410.1 | 559.5 | 609.8 | 638.5 | 505.7 | 520.9 | 656.5 | 980.3 | 693.5 | 1145.0 | 930.8 | 743.0 |
| *Todarodes pacificus* | 405.4 | 290.4 | 274.2 | 245.9 | 286.5 | 214.3 | 141.5 | 262.0 | 227.8 | 319.8 | 321.5 | 403.0 | 545.2 | 548.4 | 504.4 | 513.4 | 715.9 | 603.4 | 378.6 | 497.9 | 570.4 | 528.5 |
| *Dosidicus gigas* | 19.1 | 9.8 | 1.2 | 0.1 | 0.4 | 15.9 | 1.2 | 0.3 | 1.7 | 10.4 | 14.9 | 45.8 | 109.4 | 124.4 | 195.2 | 136.3 | 142.2 | 162.5 | 27.5 | 134.8 | 182.4 | 223.8 |
| *Nototodarus sloani* | 0.8 | 48.8 | 48.9 | 55.7 | 90.1 | 67.1 | 28.1 | 32.7 | 38.5 | 53.0 | 29.8 | 35.1 | 64.4 | 45.1 | 79.4 | 94.1 | 53.7 | 64.6 | 55.6 | 31.4 | 25.6 | 45.1 |
| *Ommastrephes bartrami* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 49.9 | 55.0 | 36.1 | 47.4 | 23.9 |
| *Illex illecebrosus* | 88.7 | 50.2 | 31.3 | 12.0 | 10.6 | 6.9 | 6.7 | 18.1 | 5.9 | 17.7 | 25.6 | 19.7 | 23.9 | 25.6 | 30.7 | 18.6 | 29.0 | 34.8 | 26.6 | 9.9 | 11.2 | 5.7 |
| *Todarodes sagittatus* | 6.4 | 15.5 | 21.8 | 22.5 | 18.1 | 21.8 | 9.8 | 11.4 | 8.4 | 8.3 | 8.3 | 7.5 | 7.8 | 6.5 | 5.8 | 5.2 | 5.9 | 5.6 | 6.6 | 4.9 | 4.9 | 4.3 |
| *Illex coindetii* | 0.0 | 0.0 | 0.1 | 0.4 | 0.1 | 0.1 | 0.2 | 0.3 | 0.2 | 1.2 | 0.5 | 0.6 | 0.8 | 0.8 | 0.7 | 0.6 | 0.4 | 0.4 | 0.2 | 0.3 | 0.4 | 0.3 |
| *Martialia hyadesi* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 8.4 | 0.0 | 0.0 | 0.2 | 11.6 | 1.4 | 1.0 | 1.3 | 0.4 | 24.0 | 3.8 | 8.4 | 0.1 | 0.0 | 0.7 | 0.0 |
| **Ommastrephids** | **536.3** | **448.0** | **457.1** | **392.8** | **511.9** | **530.9** | **467.2** | **871.1** | **846.9** | **968.9** | **822.2** | **1 072.4** | **1 362.4** | **1 390.4** | **1 322.3** | **1 313.0** | **1 607.4** | **1 909.8** | **1 243.6** | **1 860.2** | **1 773.8** | **1 574.5** |
| *Loligo* spp. | 93.1 | 99.6 | 114.0 | 131.6 | 113.9 | 148.4 | 189.5 | 245.4 | 224.8 | 234.7 | 218.3 | 221.4 | 215.9 | 244.3 | 234.6 | 216.8 | 216.7 | 227.6 | 218.1 | 199.8 | 215.0 | 213.6 |
| *Loligo gahi* | 0.0 | 0.0 | 0.0 | 16.0 | 13.0 | 9.2 | 39.7 | 68.6 | 44.0 | 89.2 | 57.1 | 45.8 | 71.8 | 44.3 | 55.5 | 85.2 | 68.5 | 21.7 | 51.7 | 42.5 | 67.0 | 57.7 |
| *Loligo pealei* | 23.6 | 22.5 | 20.8 | 25.7 | 22.4 | 17.0 | 17.1 | 11.7 | 19.1 | 23.0 | 16.3 | 19.6 | 19.7 | 22.2 | 22.5 | 18.9 | 12.5 | 16.2 | 18.9 | 18.7 | 16.9 | 14.2 |
| *Loligo reynaudi* | 1.9 | 2.1 | 1.7 | 1.7 | 1.2 | 4.3 | 4.2 | 2.7 | 5.4 | 10.7 | 5.0 | 7.0 | 2.8 | 6.3 | 5.8 | 7.0 | 7.5 | 3.7 | 6.7 | 7.2 | 6.0 | 3.4 |
| ***Loligo* species** | **118.5** | **124.2** | **136.5** | **175.0** | **150.5** | **178.9** | **250.5** | **328.4** | **293.3** | **357.7** | **296.6** | **293.7** | **310.2** | **317.1** | **318.4** | **328.0** | **305.2** | **269.2** | **295.4** | **268.3** | **304.9** | **288.9** |
| Non-identified squids | **436.1** | **372.5** | **520.6** | **517.6** | **463.3** | **550.4** | **488.0** | **557.0** | **503.8** | **647.2** | **601.2** | **489.9** | **422.7** | **266.1** | **318.8** | **360.8** | **363.7** | **308.9** | **344.5** | **453.6** | **482.0** | **379.2** |
| **SQUIDS** | **1 091.0** | **944.7** | **1 114.2** | **1 085.5** | **1 125.8** | **1 260.2** | **1 205.7** | **1 756.5** | **1 644.0** | **1 973.8** | **1 720.0** | **1 856.1** | **2 095.3** | **1 973.6** | **1 959.5** | **2 001.8** | **2 276.2** | **2 487.9** | **1 883.5** | **2 582.1** | **2 560.7** | **2 242.6** |
| Octopodidae | 113.2 | 131.5 | 137.8 | 146.1 | 145.4 | 144.5 | 183.3 | 180.1 | 192.4 | 210.8 | 229.2 | 235.7 | 218.0 | 223.6 | 205.2 | 235.0 | 230.8 | 210.8 | 245.4 | 295.0 | 259.7 | 261.8 |
| *Octopus vulgaris* | 66.4 | 88.7 | 61.9 | 99.8 | 65.1 | 62.9 | 64.4 | 62.5 | 57.8 | 61.8 | 62.2 | 80.2 | 75.8 | 69.4 | 66.3 | 66.8 | 72.9 | 60.3 | 72.5 | 56.1 | 50.5 | 53.1 |
| *Eledone spp.* | 2.1 | 2.0 | 2.6 | 4.3 | 2.7 | 3.7 | 2.7 | 2.9 | 3.6 | 2.5 | 3.0 | 3.4 | 3.6 | 3.5 | 3.9 | 2.5 | 1.9 | 2.3 | 1.8 | 1.4 | 2.0 | 2.4 |
| **OCTOPUSES** | **181.7** | **222.2** | **202.3** | **250.3** | **213.3** | **211.1** | **250.5** | **245.5** | **253.7** | **275.1** | **294.4** | **319.3** | **297.4** | **296.6** | **275.4** | **304.3** | **305.6** | **273.4** | **319.6** | **352.5** | **312.2** | **317.2** |
| Sepiidae, Sepiolidae | 248.1 | 194.7 | **275.8** | 311.3 | 288.2 | 273.2 | 266.7 | 236.4 | 253.3 | 262.1 | 283.1 | 289.2 | 254.1 | 297.9 | 371.0 | 411.4 | 370.0 | 455.7 | 429.1 | 438.3 | 484.7 | 519.3 |
| *Sepia officinalis* | 4.8 | 4.0 | 5.2 | 5.2 | 6.6 | 7.6 | 8.6 | 11.1 | 15.3 | 17.2 | 16.0 | 11.8 | 13.2 | 12.6 | 12.5 | 10.4 | 11.4 | 13.8 | 12.4 | 14.9 | 12.7 | 14.0 |
| **CUTTLEFISHES** | **252.9** | **198.6** | **281.0** | **316.5** | **294.8** | **280.8** | **275.3** | **247.5** | **268.6** | **279.3** | **299.1** | **301.0** | **267.4** | **310.5** | **383.6** | **421.7** | **381.4** | **469.4** | **441.5** | **453.1** | **497.4** | **533.3** |
| Non-identified cephalopods | **20.9** | **17.5** | **18.6** | **22.4** | **32.3** | **36.2** | **26.5** | **47.6** | **69.1** | **115.9** | **57.5** | **84.7** | **106.9** | **107.1** | **184.9** | **210.6** | **186.5** | **225.9** | **213.0** | **210.0** | **284.8** | **253.7** |
| **WORLD TOTAL** | **1 546.5** | **1 383.1** | **1 616.1** | **1 674.6** | **1 666.2** | **1 788.3** | **1 758.1** | **2 297.1** | **2 235.4** | **2 644.0** | **2 371.1** | **2 561.1** | **2 767.0** | **2 687.8** | **2 803.4** | **2 938.4** | **3 149.8** | **3 456.7** | **2 857.6** | **3 597.7** | **3 655.2** | **3 346.8** |

**Table 3**
World cephalopod capture production in thousand metric tonnes, by FAO areas during the years 1980–2001

| Area | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **NW Pacific** | 882.3 | 691.9 | 761.6 | 738.8 | 717.3 | 709.3 | 596.0 | 706.6 | 691.4 | 877.9 | 861.7 | 815.6 | 913.8 | 873.7 | 937.9 | 1 006.5 | 1 165.5 | 1 154.1 | 1 033.6 | 1 117.8 | 1 222.0 | 1 137.5 | 34.0 |
| **SW Atlantic** | 31.0 | 54.1 | 208.4 | 205.2 | 252.1 | 352.9 | 410.5 | 763.9 | 681.4 | 764.3 | 550.9 | 696.9 | 734.3 | 719.5 | 586.2 | 645.2 | 747.9 | 1016.6 | 750.0 | 1 192.7 | 1 001.0 | 802.9 | 24.0 |
| **WC Pacific** | 119.6 | 130.0 | 153.6 | 183.1 | 170.2 | 182.6 | 195.5 | 204.9 | 215.7 | 239.1 | 259.8 | 270.0 | 279.8 | 314.2 | 359.3 | 355.8 | 343.9 | 360.0 | 366.1 | 364.6 | 435.3 | 390.5 | 11.7 |
| **EC Atlantic** | 138.0 | 190.5 | 175.9 | 211.6 | 156.6 | 154.0 | 194.3 | 167.7 | 165.0 | 184.5 | 202.4 | 238.8 | 188.4 | 195.0 | 179.1 | 191.2 | 190.6 | 150.4 | 183.7 | 250.3 | 216.4 | 212.9 | 6.4 |
| **SE Pacific** | 0.3 | 1.2 | 3.0 | 2.8 | 3.4 | 19.5 | 5.9 | 4.8 | 7.2 | 9.8 | 20.6 | 72.5 | 117.5 | 135.5 | 199.6 | 109.2 | 36.0 | 32.1 | 11.4 | 82.8 | 127.6 | 175.0 | 5.2 |
| **EC Pacific** | 30.7 | 32.3 | 19.8 | 16.0 | 17.7 | 24.7 | 35.5 | 67.9 | 76.6 | 80.8 | 80.2 | 64.6 | 40.8 | 38.2 | 58.8 | 111.3 | 201.5 | 213.1 | 30.4 | 150.6 | 202.5 | 167.1 | 5.0 |
| **W Indian Ocean** | 23.7 | 11.9 | 11.8 | 10.1 | 20.0 | 27.3 | 24.0 | 32.0 | 42.0 | 45.1 | 37.5 | 70.5 | 77.2 | 81.7 | 102.0 | 110.6 | 94.9 | 148.6 | 112.4 | 121.3 | 119.0 | 140.1 | 4.2 |
| **E Indian Ocean** | 27.4 | 22.6 | 23.4 | 25.4 | 34.3 | 32.9 | 39.1 | 53.6 | 60.5 | 92.5 | 51.8 | 62.3 | 84.1 | 73.3 | 71.3 | 88.4 | 104.6 | 109.4 | 115.7 | 111.8 | 124.1 | 116.0 | 3.5 |
| **SW Pacific** | 80.2 | 63.3 | 71.1 | 81.0 | 116.8 | 88.8 | 72.1 | 73.6 | 75.0 | 107.1 | 67.9 | 63.7 | 113.0 | 69.7 | 116.7 | 139.6 | 73.3 | 84.8 | 71.0 | 43.6 | 35.5 | 57.3 | 1.7 |
| **Mediterranean & Black Sea** | 51.7 | 47.1 | 49.4 | 55.3 | 56.7 | 65.7 | 68.4 | 67.7 | 83.3 | 76.9 | 72.5 | 67.8 | 71.7 | 65.4 | 68.7 | 62.5 | 59.3 | 60.1 | 54.3 | 50.7 | 53.8 | 53.8 | 1.6 |
| **NE Atlantic** | 29.2 | 37.4 | 41.9 | 48.5 | 37.2 | 38.2 | 25.4 | 43.4 | 42.4 | 49.7 | 55.5 | 41.2 | 49.9 | 49.0 | 44.0 | 54.0 | 53.4 | 51.0 | 49.9 | 53.1 | 58.8 | 44.5 | 1.3 |
| **WC Atlantic** | 8.4 | 8.9 | 9.3 | 12.3 | 10.2 | 10.4 | 13.3 | 11.5 | 12.0 | 18.2 | 19.3 | 20.3 | 21.5 | 18.8 | 20.0 | 20.7 | 31.1 | 20.8 | 24.1 | 20.1 | 24.4 | 23.2 | 0.7 |
| **NW Atlantic** | 111.3 | 72.0 | 52.1 | 39.9 | 33.1 | 23.9 | 23.7 | 23.5 | 22.0 | 37.6 | 39.0 | 36.3 | 40.7 | 46.4 | 52.0 | 35.6 | 38.9 | 48.7 | 44.7 | 26.8 | 26.4 | 18.4 | 0.6 |
| **SE Atlantic** | 8.5 | 11.1 | 10.1 | 10.0 | 8.3 | 12.1 | 12.6 | 20.2 | 11.4 | 14.7 | 7.8 | 9.9 | 8.2 | 7.1 | 6.5 | 7.4 | 8.2 | 4.1 | 7.8 | 8.3 | 7.5 | 4.7 | 0.1 |
| **NE Pacific** | 4.3 | 8.9 | 24.7 | 34.7 | 32.4 | 46.0 | 41.7 | 55.8 | 49.7 | 45.7 | 43.9 | 30.9 | 26.0 | 0.3 | 1.4 | 0.3 | 0.7 | 2.8 | 2.3 | 3.1 | 0.7 | 3.0 | 0.1 |
| TOTAL | **1 546.5** | **1 383.1** | **1 616.1** | **1 674.6** | **1 666.2** | **1 788.3** | **1 758.1** | **2 297.1** | **2 235.4** | **2 644.0** | **2 371.1** | **2 561.1** | **2 767.0** | **2 687.8** | **2 803.4** | **2 938.4** | **3 149.7** | **3 456.6** | **2 857.6** | **3 597.7** | **3 655.2** | **3 346.8** | |

(Source: FAO, 2000)

**Table 4**
World cephalopod capture (in metric tonnes) ranked by the 10 main producing countries from 1990 to 2001

| Country | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Japan** | 622 235 | 595 516 | 772 777 | 639 683 | 647 090 | 599 685 | 728 759 | 700 036 | 446 927 | 558 527 | 668 147 | 566 371 |
| **China** | 69 918 | 70 167 | 70 836 | 122 159 | 193 561 | 225 421 | 175 835 | 246 690 | 379 056 | 417 031 | 482 802 | 504 287 |
| **Korea, Republic of** | 333 709 | 411 673 | 475 625 | 432 160 | 381 040 | 421 492 | 449 352 | 481 960 | 310 631 | 591 087 | 426 679 | 412 513 |
| **Argentina** | 27 778 | 46 375 | 77 746 | 194 653 | 197 971 | 200 400 | 292 851 | 414 041 | 291 993 | 342 934 | 279 914 | 229 874 |
| **Thailand** | 135 072 | 154 402 | 150 315 | 153 237 | 144 436 | 156 397 | 173 183 | 173 648 | 188 156 | 174 382 | 171 990 | 170 945 |
| **Taiwan Province of China** | 223 868 | 280 878 | 207 948 | 219 926 | 191 257 | 187 820 | 171 847 | 250 811 | 237 060 | 297 528 | 258 907 | 165 521 |
| **Morocco** | 74 143 | 92 162 | 82 368 | 91 685 | 83 047 | 90 134 | 91 324 | 63 963 | 68 553 | 112 829 | 147 727 | 140 829 |
| **Viet Nam** | 23 000 | 28 000 | 32 000 | 33 000 | 87 000 | 103 000 | 92 000 | 92 500 | 103 000 | 110 000 | 180 000 | 130 000 |
| **India** | 30 907 | 55 273 | 72 682 | 70 423 | 95 109 | 103 739 | 85 120 | 117 624 | 95 834 | 93 709 | 96 408 | 114 681 |
| **USA** | 43 497 | 63 307 | 50 975 | 73 646 | 97 879 | 104 119 | 108 878 | 101 506 | 45 240 | 117 124 | 143 808 | 105 125 |
| **World Total** | **2 371 064** | **2 561 100** | **2 766 970** | **2 687 779** | **2 803 421** | **2 938 392** | **3 149 764** | **3 456 670** | **2 857 620** | **3 597 670** | **3 655 150** | **3 346 828** |

(Source: FAO, 2000)

**Table 5**
World cephalopod export and import quantities and values in 2001 for the 10 leading countries

| 2001 Exports | | | | 2001 Imports | | | |
|---|---|---|---|---|---|---|---|
| **Quantity (Thousand tonnes)** | | **Value (Millions US$)** | | **Quantity (Thousand tonnes)** | | **Value (Millions US$)** | |
| **Argentina** | 158.5 | **Morocco** | 399.7 | **Spain** | 286.2 | **Japan** | 812.8 |
| **Spain** | 126.1 | **Thailand** | 319.0 | **Japan** | 198.7 | **Spain** | 567.3 |
| **Morocco** | 111.9 | **Viet Nam** | 269.7 | **China** | 195.9 | **Italy** | 421.9 |
| **USA** | 108.1 | **Spain** | 254.7 | **Italy** | 186.2 | **USA** | 143.6 |
| **China** | 101.4 | **China** | 213.1 | **Korea, Republic of** | 66.2 | **China** | 131.0 |
| **Thailand** | 92.4 | **Argentina** | 149.4 | **USA** | 62.1 | **Korea, Republic of** | 124.2 |
| **Korea, Republic of** | 76.6 | **India** | 106.1 | **Thailand** | 49.8 | **Thailand** | 65.9 |
| **Taiwan Province of China** | 62.5 | **USA** | 85.9 | **Greece** | 33.5 | **Portugal** | 61.0 |
| **India** | 60.1 | **Korea, Republic of** | 71.7 | **Portugal** | 31.2 | **Greece** | 56.2 |
| **Viet Nam** | 59.8 | **Mauritania** | 65.5 | **France** | 25.8 | **France** | 55.4 |
| **World Total** | **1 310.8** | **World Total** | **2 506.0** | **World Total** | **1 329.4** | **World Total** | **2 750.9** |

(Source: FAO, 2000)

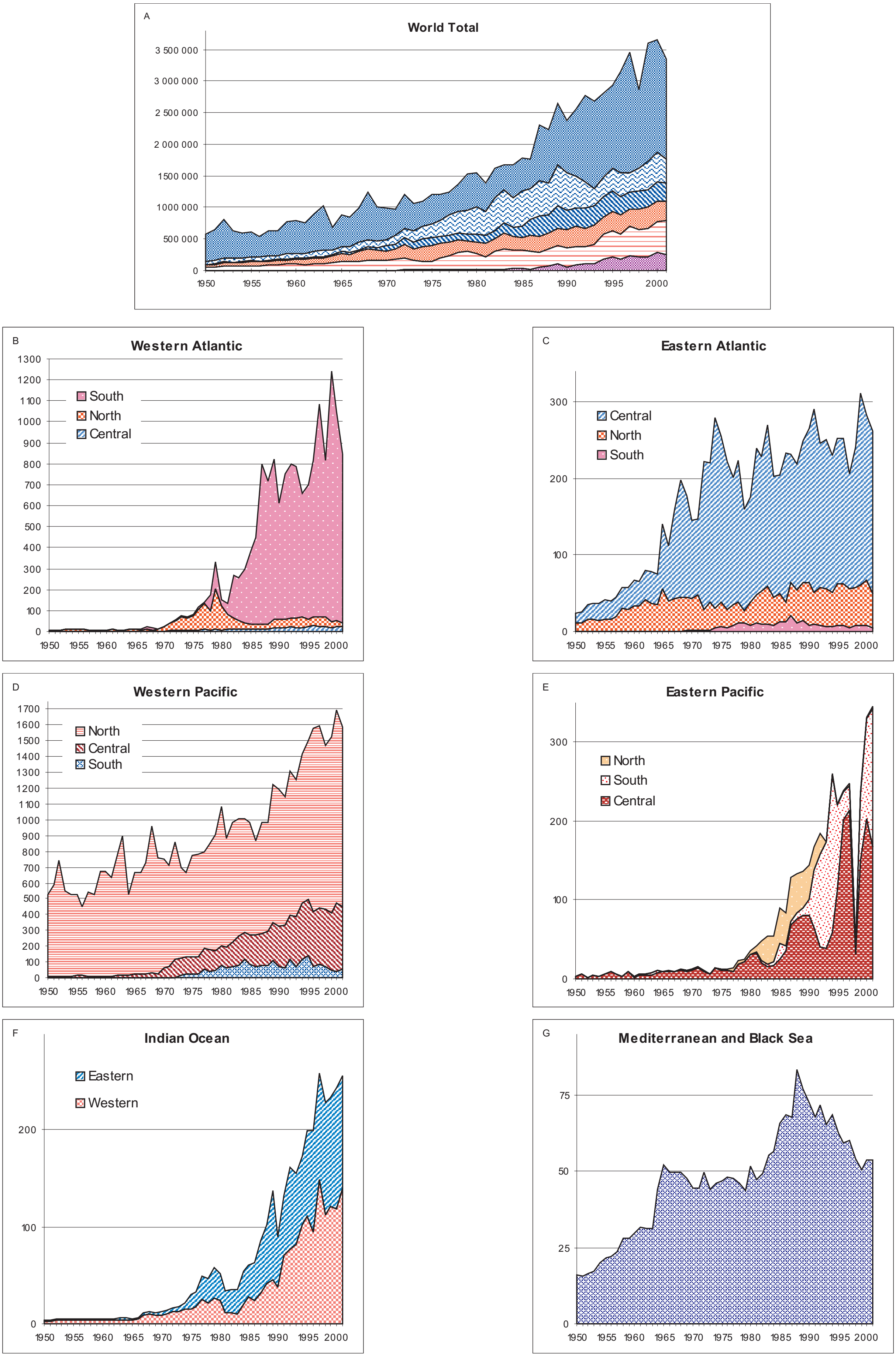


**Fig. 3 Cephalopod capture (tonnes) by main FAO fisheries areas**

(Source: FAO, 2000)

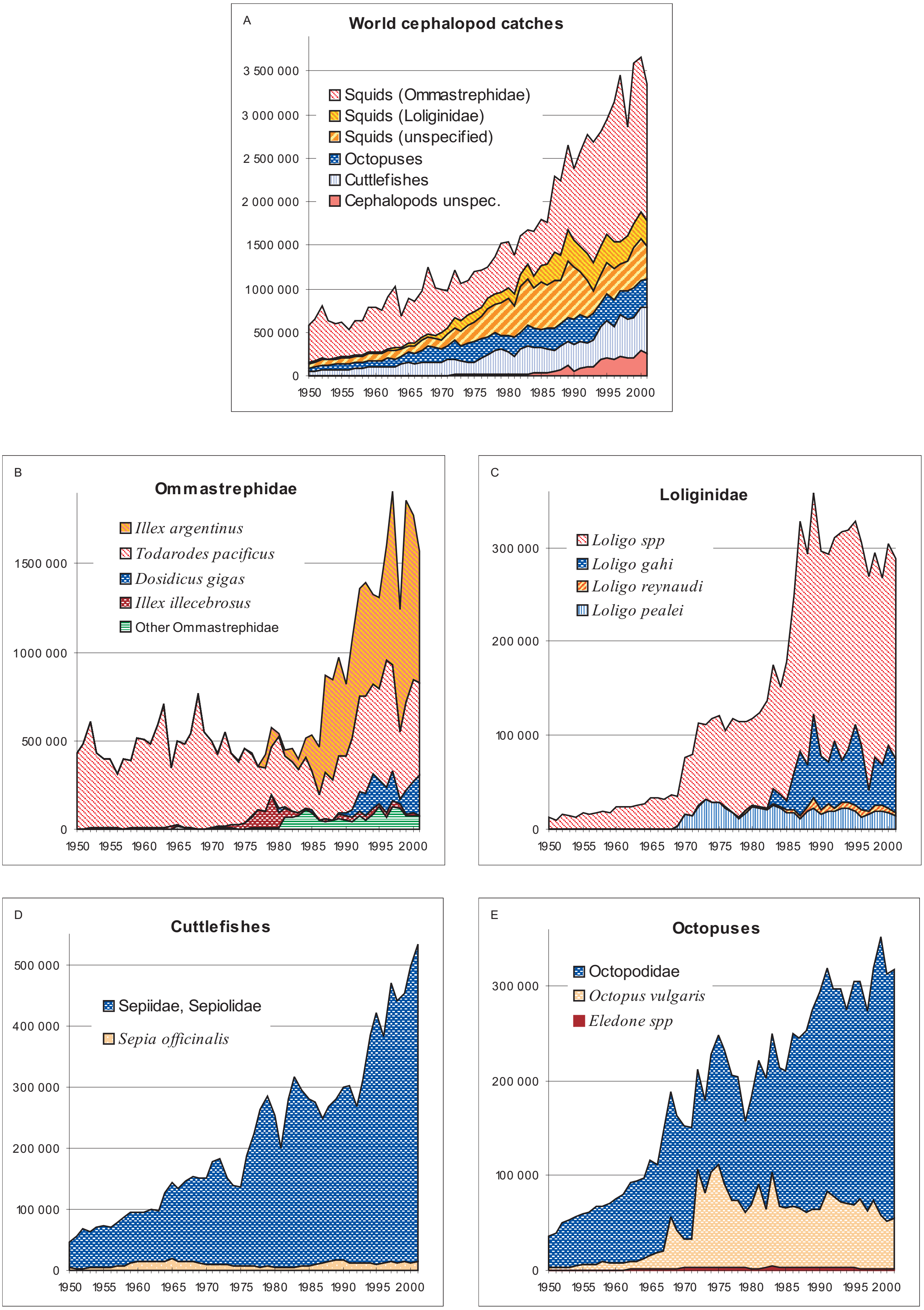


**Fig. 4 Total world cephalopod capture (tonnes) by main species groups or species**
(Source: FAO, 2000)

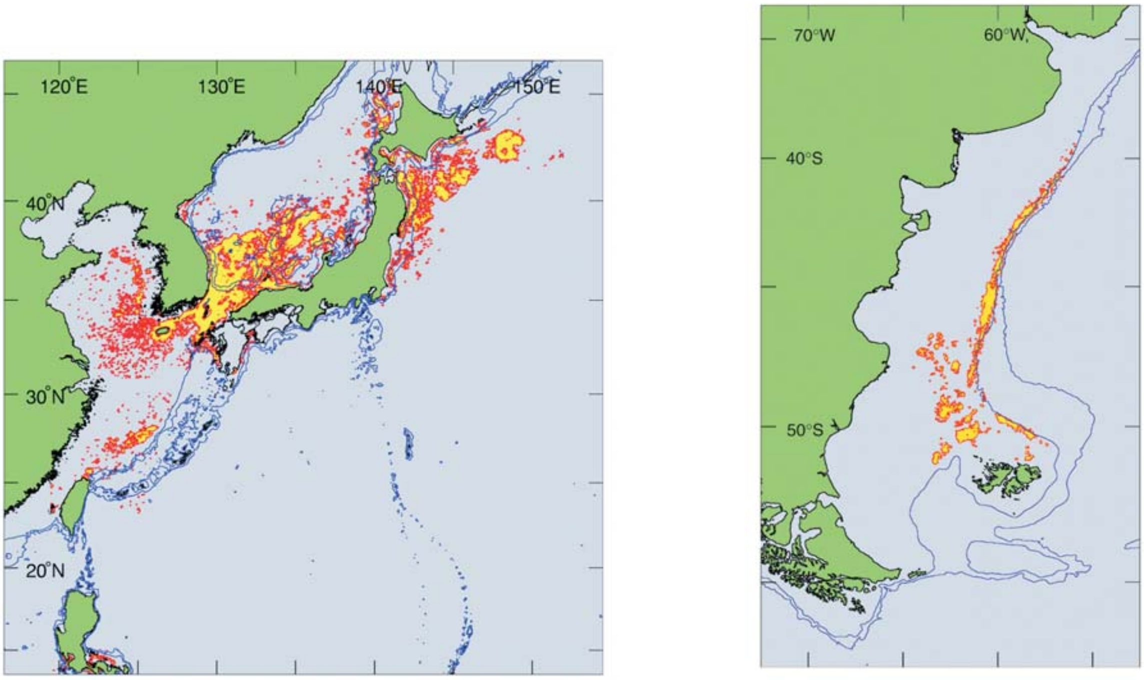
Numerous fishing techniques and methods to capture cephalopods have been developed over time. These were extensively reviewed, for example, by Rathjen (1984, 1991) and Roper and Rathjen (1991). They include hand collection, small traps, spears, lures, jigs, lampara nets, chemical flushing, midwater trawls and otter trawls.

**Jigging** is the most widely used method, which accounts for almost half of the world cephalopod catch: all squids, primarily ommastrephids, but also a few loliginids. This technique is employed primarily at night, when many species of squids are attracted to the fishing vessel by lights. Figure 5 shows the distribution of the world’s light fishery for some of the most important squid species. Jigs, which feature numerous, variously-arranged, barbless hooks (Plate IX, 60), are lowered and retrieved by jigging machines that simulate the constant swimming behaviour of natural prey, inducing the squids to attack them. While simple hand-jigging machines are still used in small-scale, artisanal fisheries, large modern vessels for industrial fishing activities are equipped with scores of automated, computer-controlled jigging machines, each capable of catching several tonnes per night (Plate VIII, 50; Plate IX, 56). Occasionally, cuttlefishes also are captured by hand jig.

**Trawling** is the secondmost productive fishery method to catch cephalopods (Plate VIII, 51). Formerly, many species of squids, octopods and cuttlefishes *sensu lato* were caught as bycatch in trawl fisheries for finfishes and shrimps, but some specialized small-scale fisheries trawling for cephalopods also existed (e.g. for cuttlefishes in the Mediterranean Sea). The amount of cephalopods taken as bycatch in bottom trawls for finfish fisheries drove increasing attention to the resource by the 1980s; this led to the development of the (principally) midwater trawl fisheries specifically targeting squids, particularly the South Atlantic/Subantarctic fishery for ***Illex argentinus***. Trawling is a very efficient technique to catch benthic and epibenthic species, but soft-bodied animals like cephalopods are often damaged by the other species in the catch, particularly in benthic and epibenthic otter trawls. Even in fisheries in which squid-specific trawling occurs, the huge catches of squids per tow often result in crushed and damaged product. Consequently, trawled squid product generally is less valuable than jig-caught squids. However, modern oceanic trawlers can process on board many metric tonnes of cephalopods per day, which helps insure a high-quality product. Bottom trawling can be very dangerous for benthic habitats because of the physical damage it causes to the seabed and associated fauna and because of its lack of selectivity. Consequently, less intense exploitation by this traditional fishing technique and an approach toward diversification of methods and redistribution of the fisheries through different areas were encouraged and still are highly recommended, especially in situations where small-scale fisheries still exist and new, more efficient methods can be implemented.

The remaining cephalopod catches come from **several different methods** (Plate VIII, 47, 49, 52-54; Plate IX, 55, 59). Cuttlefishes are captured by dredges, seines, jigs and pots specifically developed for these species and very popular in some regions, e.g. the Mediterranean Sea. Nearshore, neritic squids are caught by purse seines, octopuses are taken by pots, dragnets, hooks and spears, while ***Nautilus*** spp. are caught in deep-set wicker or wire traps.

The **utilization of cephalopods** for human consumption is extensive and diverse. Products range from fresh food, eaten raw as ‘sashimi’ in Japan and, in recent years, worldwide, and fresh-cooked, as well as various types of processed product (dried, canned, frozen, reduced to meal, etc.). The high protein and low fat content of cephalopods make them an important and healthy element in the human



**a) Kuroshio Current Province**
**(*Todarodes pacificus* and *Ommastrephes bartrami*)**

**b) Southwest Atlantic Province**
**(*Illex argentinus*)**

**Fig. 5 Distribution of the world’s light fisheries for ommastrephids** (illustrations based on night-time satellite imagery) (from Rodhouse *et al*., 2001) diet. With the increasing demand for food for human consumption, cephalopod resources probably will receive even more attention in the future.

Considering the present level of exploitation of the commercially-fished cephalopod populations, a further increase in such fishery production is likely to occur first by expansion of the fisheries into the less-fished regions of the oceans, e.g. the Southern Ocean, probably the ‘last frontier’ in the field of marine fisheries. There, a standing stock of squid biomass as high as 100 million tonnes was estimated by scientists, based on an estimate of 30 million tonnes consumed by vertebrate predators (see Rodhouse *et al.*, 1994 for details), even though squid captures are rarely successful. Therefore, a priority for the future research in the field of Antarctic cephalopod biology will be to assess the squid biomass there, quantitatively and qualitatively, with the objective of determining a sustainable fishery production. However, polar cephalopods probably are longer living and slower growing than species currently harvested. Therefore, caution must be exercised in assumptions and decisions for management of polar cephalopod fisheries.

In the future, it is likely that attention will be focused on finding other species and families to replace fish stocks that become severely reduced by overfishing. Even though clear evidence reveals the existence of large cephalopod resources available for exploitation in the open oceans, based on the estimated consumption by predators (see Clarke, 1996; Piatkowski *et al.*, 2001 for reviews), many oceanic squids are distasteful for human consumption as their tissues have a high ammonium content. Research is being carried out on how to remove this factor on a commercial scale, but results will take time and catches will need to be processed before utilization. A number of ommastrephid squids that lack ammonium are considered to be underexploited. These include: ***Sthenoteuthis pteropus***, ***Ommastrephes bartrami***, ***Martialia hyadesi***, ***Todarodes sagittatus***, ***Sthenoteuthis oualaniensis***, ***Nototodarus philippinensis*** and ***Dosidicus gigas***, and the circumpolar, subantarctic ***Todarodes filippovae***. Exploitation of these species would provide large tonnages of high quality cephalopods and would require only minor development in catching techniques. However it will be necessary to determine where these species congregate for feeding and spawning activities. An analysis of biomass, production and potential catch for the 21 species of Ommastrephidae is presented in Nigmatullin (2004).

Although a number of other oceanic squid families have large populations and high quality flesh, they are not currently exploited on a commercial scale except for a few seasonal fisheries. These include members of the families Thysanoteuthidae, Gonatidae and Pholidoteuthidae, for example. Increased exploitation of these groups, however, would also require some research and development of catching techniques. Commercial exploitation of the cosmopolitan family Histioteuthidae also could be considered, since at least one large commercial-level catch has been made in the North Atlantic (see Okutani, personal communication, *in* Clarke, 1996). However, the increased exploitation of these oceanic squid species might have unpredictable, far-reaching negative effects on the mesopelagic ecosystem. Therefore, great caution must be exercised in developing this kind of fishery.

Almost all of our knowledge of the general biology of cephalopods, in fact, is limited to the shelf-living species as well as to those ommastrephids that move onto the shelf at certain seasons. These represent only about 15% of all cephalopod species (Clarke, 1996). Even so, many gaps still exist in our knowledge about their life cycles, especially as far as the relationships among species are concerned (e.g. prey-predator balances). Some populations of harvested species have shown sudden, occasionally catastrophic, declines before adequate biological data could be gathered and analysed. Squid stocks, for example, experienced true collapses at least in two well-known and documented cases. These were the northwest Pacific ***Todarodes pacificus*** fishery failure in the 1970s and the northwest Atlantic ***Illex illecebrosus*** fishery collapse in the 1980s. While the ***T. pacificus*** fishery has recovered, the ***I. illecebrosus*** fishery has remained insignificant. These collapses are thought to have occurred mainly as a consequence of temporarily unfavourable environmental conditions or actual long-term environmental changes, probably aggravated by heavy fishing pressure (Dawe and Warren, 1993).

A significant challenge thus exists to deepen our knowledge and learn the details of distribution, life history and biology of exploited species in order to allow rational utilization of the stocks. The necessity for research as a key factor towards attaining this goal has been stressed by many authors (e.g. Lipinski *et al.*, 1998) and it is especially important in the fields of life-cycle clarification, stock structure and genetics, role in the food web and interactions with the environment. The last topic seems of particular interest within the more general context of climate/environmental global changes, since the unusual biological characteristics and short life cycles of cephalopods are strongly linked to immediate, temporal environmental circumstances. Therefore, cephalopods are potentially very good ‘indicator species’ to predict or reflect changes in environmental conditions, both locally and on a broader scale (O’Dor and Dawe, 1998; Arkhipkin *et al.*, 2001; Bendik, 2001; Dawe *et al.*, 2000, 2001; Jereb *et al.*, 2001; Laptikhowsky and Remelso, 2001; Roberts, 2001).

Perhaps even more significant is the challenge that exists for future exploitation of new species or populations. The **role** of cephalopods **in the ecosystem**, in fact, is more complex than it was thought to be only a few decades ago. Cephalopods can be considered subdominant predators that tend to increase in biomass when other species, particularly their predators and competitors for food, become depleted, as a result of a combination of heavy or excessive fishing, other human impacts, oceanographic fluctuations and competition for food (see Caddy, 1983, and Caddy and Rodhouse, 1998 for a detailed analysis of the transition from finfish-targeted fisheries to cephalopod-targeted fisheries). A thoroughly studied case is that of the snapper fishery on the Endeavour Bank (Balguerias *et al.*, 2000), which was replaced by a cephalopod fishery between 1960 and 1970. In turn, cephalopods are major food items in the diets of innumerable species of fishes, toothed whales (e.g. sperm whales, beaked whales, dolphins, porpoises), pinnipeds (seals, sea lions) and seabirds (penguins, petrels, albatrosses).

Muscular cephalopods derive their energy from crustaceans, fishes and other cephalopods. At the same time, they are a very efficient food store for the large, oceanic predators, by rapidly converting oceanic resources into high energy food. On the other hand, neutrally buoyant ammoniacal squids, which probably greatly outnumber the muscular squids in biomass, also provide food to many of the same predators, but not over the continental shelf and with consistently lower energy per unit body mass. We know virtually nothing about the details of feeding, growth, life cycles, periodicities, distribution and spawning in ammoniacal species.

In spite of our relatively poor knowledge, it is now clear that cephalopods are a dominant component within marine ecosystems and that their abundance ultimately may influence the abundance of their predators and prey populations. Recent studies of the effects of consumption of important pelagic squids and fishes by predatory fishes on the northeastern shelf of the United States (Overholtz *et al.*, 2000), concluded that changes in predator abundance may have important implications for the long-term fishery yields of pelagic species.

What seems consistent with our present knowledge is that removal of cephalopods through fisheries would have a consistent impact on the environment: populations of small midwater fishes would increase, while top predators like cetaceans, seabirds, seals and even some fish populations would decrease.

Taking into consideration these factors, increasing effort should be focused on improving our scientific knowledge of this group. Cephalopod catches need increased monitoring, especially in those areas of major environmental fluctuations and where fisheries management is complicated by multiple countries fishing the same resource. Cooperation, collaboration and commitment are required to better understand these important and fascinating animals.

NEXT PAGE