Broecker WS and Peng TH (1982) *Tracers in the Sea*. Palisades: Eldigio Press.

Butcher SS, Charlson RJ, Orians GH and Wolfe GV (eds) (1992) *Global Biogeochemical Cycles*. London: Academic Press.

Chameides WL and Perdue EM (1997) *Biogeochemical Cycles: A Computer-Interactive Study of Earth System Science and Global Change*. Oxford: Oxford University Press.

Föllmi KB (1995) 160 My record of marine sedimentary phosphorus burial: coupling of climate and continental weathering under greenhouse and icehouse conditions. *Geology* 23: 859–862.

France-Lanord C and Derry LA (1997) Organic carbon burial forcing of the carbon cycle from Himalayan erosion. *Nature* 390: 65–67.

François LM and Walker JCG (1992) Modelling the Phanerozoic carbon cycle and climate: constraints from the ^{87}Sr/^{86}Sr isotopic ratio of sea water. *American Journal of Science* 292: 81–135.

Freeman KH and Hayes JM (1992) Fractionation of carbon isotopes by phytoplankton and estimates of ancient CO_2 levels. *Global Biogeochemical Cycles* 6: 185–198.

Goddéris Y and François LM (1996) Balancing the Cenozoic carbon and alkalinity cycles: constraints from isotopic records. *Geophysical Research Letters* 23: 3743–3746.

Harland WB, Armstrong RL, Cox AV, *et al.* (1990) *A Geologic Time Scale 1989*. Cambridge: Cambridge University Press.

Hayes JM, Strauss H and Kaufman AJ (1999) The abundance of ^{13}C in marine organic matter and isotopic fractionation in the global biogeochemical cycle of carbon during the past 800 Ma. *Chemical Geology* 161: 103–125.

Kump LR and Arthur MA (1997) Global chemical erosion during the Cenozoic: weatherability balances the budgets. In: Ruddiman WF (ed.) *Tectonic Uplift and Climate Change*. New York: Plenum Press.

Kump LR, Kasting JF and Crane RG (1999) *The Earth System*. New Jersey: Prentice Hall.

Lasaga AC, Berner RA and Garrels RM (1985) An improved geochemical model of atmospheric CO_2 fluctuations over the past 100 million years. In: Sundquist E and Broecker WS (eds) *The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present* Geophysical Monograph 32, pp. 397–411. Washington, DC: American Geophysical Union.

Opdyke BN and Wilkinson BH (1988) Sea surface area control of shallow cratonic to deep marine carbonate accumulation. *Paleoceanography* 3: 685–703.

Pearson PN and Palmer MR (2000) Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406: 695–699.

Raymo ME (1991) Geochemical evidence supporting T.C. Chamberlin's theory of glaciation. *Geology* 19: 344–347.

Ruddiman WF (ed.) (1997) *Tectonic Uplift and Climate Change*. New York: Plenum Press.

Van Andel TH (1975) Mesozoic-Cenozoic calcite compensation depth and the global distribution of calcareous sediments. *Earth and Planetary Science Letters* 26: 187–194.

Van Andel TH (1994) *New Views on an Old Planet: a History of Global Change*, 2nd edn. Cambridge: Cambridge University Press.

Walker JCG, Hays PB and Kasting JF (1981) A negative feedback mechanism for the long-term stabilization of Earth's surface temperature. *Journal of Geophysical Research* 86: 9776–9782.

CEPHALOPODS

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Introduction

The Cephalopoda is the class of the Mollusca comprising the octopuses, cuttlefish, squid, and their allies. Exclusively marine and present in all of the world's oceans and seas, their lineage can be traced from the Ordovician to the present due to fossilization of their large, heavy, chambered shells. The Pearly Nautilus (*Nautilus* spp.) of the Indo-Pacific region is the only surviving relative of this ancient ancestry (10–12 000 extinct species) Modern living cephalopods (subclass Coleoidea), having reduced or lost the ancestral shell, are represented by only about 650–700 species. These are characteristically large, active, soft-bodied predators, with complex behavioral and physiological capabilities. Occupying a wide range of benthic and pelagic habitats they are abundant in productive shelf regions, where genera such as *Octopus* and the common cuttlefish *Sepia* are each credited with over 100 species. The greatest diversity of form and biomass of cephalopods is oceanic and mesopelagic in distribution, but the biology of these offshore species is little understood and generalizations are based mostly on coastal forms. Now, and throughout their evolutionary history, representatives of the cephalopods reach the largest of all invertebrate body sizes.

With the exception of *Nautilus* (and some of the deep-sea forms), cephalopods generally share common life cycle features. The large eggs hatch directly to free-swimming juvenile forms resembling the adult (paralarvae). Growth is very rapid (exponential and logarithmic phases) and adult size is reached in about a year (6–24 months). The sexes are separate and there are complex arrangements for mating and fertilization. After spawning of the fertilized egg masses, either attached to the bottom or freely into the water column, most individuals of both sexes die within a short period of time afterwards. Although there are some variations between species in the timing of breeding and the duration of spawning, uniseasonal breeding appears to be more or less universal. The consequences of this life cycle at the population level are that there is little overlap of generations, the species biomass present at any time tends to build and crash seasonally. Distribution and abundance of the shelf species at least is thus highly dependent on inter-annual conditions for recruitment and growth.

Cephalopods have a very significant role in the trophic relations of marine ecosystems. Universally predatory, they consume a wide variety of fish, crustacea and other invertebrates. Cephalopods themselves are also preyed upon by many other large marine organisms such as fish, marine mammals of all sorts, and many oceanic birds. Conservative estimates of consumption of cephalopods by these predators considerably exceed 100 million tonnes annually. Human fisheries for cephalopods have increased steadily and are reaching about 3 million tonnes annually. Critical assessment of the role of cephalopods in the world's oceans is compromised by the relative lack of information on the oceanic and deep-water forms and the consequent extrapolation of knowledge from the better-known coastal species.

Diagnosis of the Cephalopoda
(Table 1)

As a class of the Mollusca cephalopods share fundamental features of their body layout and development with the other classes (gastropods, bivalves, chitons, etc.) including absolutely characteristic molluskan features such as the radula (feeding organ). Other typically molluskan features such as the calcareous shell are reduced or absent (it remains as the 'cuttlebone' in Sepia and the gladius or 'pen' in squid) and there are no specialized larval forms (no molluscan trochophore or veliger). Cephalopods have also developed quite unique systems of locomotion and mobility (jet propulsion, suckers), brain development, color change (chromatophores), and light production (photophores).

Although the molluskan relationships of cephalopods are without doubt, the scale and dynamics of their extant populations are better understood in terms of comparison with the teleost fishes – co-evolution and competition for the most productive marine environments.

Biology

Buoyancy and Jet Propulsion

The reduction and loss of a calcareous shell in the modern cephalopods (Coleoidea) has allowed the evolution of their highly mobile, active lifestyles, quite distinct from the other molluscan classes. Cuttlefish (*Sepia*) and *Spirula* retain an internal remnant of the shell which functions as a buoyancy organ. The distribution of gas and fluid space within the chambers is controlled osmotically and allows neutral buoyancy to be achieved. The physiological mechanism in these Sepiodea appears to be similar to that used by *Nautilus* for controlled vertical movements through 1000 m of the water column and is thought to be the ancestral buoyancy mechanism common to the extinct nautiloids and ammonoids. The squids and octopuses have lost this mechanism entirely, most of them are negatively buoyant, but mesopelagic forms commonly reduce their density by chemical means such as retention of ammonium ions and loss of protein.

Active locomotion of the pelagic species is by jet propulsion – regular spasmodic forcing of water from the muscular mantle through the ventral funnel which can be directed forwards, backwards or side-to-side to allow great maneuverability. Paired fins contribute to directional control of swimming and their undulations are used for 'hovering' and slow swimming. The common coastal octopuses (Incirrata) are mainly benthic, using the suckered arms for relaxed scrambling over the bottom, and jet propulsion only for rapid attacking or escape movements.

Brain and Senses

The nervous system of cephalopods is still arranged in the basic molluscan layout as ganglionic masses grouped around the esophagus. It is centralized and developed to a much greater degree than that of other Mollusca. Coupled with large and complex sense organs, especially the eyes and statocysts (gravity and movement senses), the central nervous system supports an extensive and flexible repertoire of behavior unequalled by other invertebrate taxa. Especially in *Octopus*, the capability of the animal to discriminate between environmental cues and to make appropriate behavioral responses has been

Table 1 Diagnosis of the Cephalopoda: Classification is not entirely consistent between different authors and only the principal categories are given here, some common genera are listed and the common names of classification categories are shown in bold. (Abbreviated with permission from Boyle, 1983 (*Cephalopod Life Cycles*, Vol 1, 1–8, Academic Press, London) with additional information on the numbers of living species from Nesis, 1987.)

Class **CEPHALOPODA**

All marine; bilaterally symmetrical; primitively with a chambered external shell. Radula enclosed within chitinous mandibles ('beaks'); ring of prehensile appendages around mouth; one or two pairs of gills; water circulation in mantle cavity expelled through ventral 'funnel' tube for jet propulsion. Centralized nervous system; highly organized sense organs; complex behavior. Sexes separate; sperm transferred in complex spermatophores; eggs large and yolky; direct development (no veliger).

Subclass **Nautiloidea**

Cephalopods with straight or coiled external shells; appearing in Cambrian period; numerous species populous throughout warm seas; all extinct except for one family (Nautilidae) now limited to Indo-Pacific Oceans. Body occupies terminal chamber of shell and by retraction displaces water from mantle cavity for jet propulsion; inner chambers form buoyancy organ by adjusting contained fluid/gas spaces; numerous unsuckered appendages. **Nautiluses**. 1 family, 1 genus, 3–6 species.

Subclass **Ammonoidea**

Chambered external shells; usually coiled and with complex septa and sutures separating chambers. Very numerous from the Devonian to the Cretaceous periods but now all extinct. **Ammonites**.

Subclass **Coleoidea**

Modern forms. Devonian period to present. Shell internal and reduced. Muscular fins (absent in incirrate octopods) and muscular mantle forming a sac enclosing the viscera; large mantle cavity; ink sac typically present; skin containing pigment organs (*chromatophores*) variably expanded by neuromuscular control.

Order **BELEMNOIDEA**

Internal shell, straight and with a solid posterior portion; commonly fossilized; all extinct. **Belemnites**.

Order **SEPIODEA**

Calcareous chambered shell present internally and functioning as a buoyancy organ in some genera (*Spirula*, *Sepia*); shell greatly reduced to a purely organic pen in others (*Sepiola*, *Euprymna*, *Sepietta*, *Idiosepius*). Eight suckered arms plus two long tentacles with suckered club; suckers pedunculate with horny rims. **Spirula**, **Cuttlefish** and **Sepiolids**. 5 families, 20 genera, 150–180 species.

Order **TEUTHOIDEA**

Shell reduced to chitinous 'pen' (gladius) lying dorsally. Elongate body usually finned. Eight suckered arms plus two long tentacles with suckered club, suckers pedunculate with horny rims, some with hooks. **Squid**.

Suborder **Myopsida**

Eyes with transparent corneal covering. Eggs spawned in masses attached to seabed. Typical of the continental shelf and including many abundant and valuable fished genera of the family Loliginidae (e.g., *Loligo*, *Sepioteuthis*, *Loliolus*, *Alloteuthis*). 2 families, 8 genera, 42–51 species.

Suborder **Oegopsida**

Eyes without corneal covering, a large assemblage of many families. Oceanic and midwater, seldom over the shelf or near coasts. Eggs apparently spawned in midwater gelatinous masses. Includes many genera significant in the diets of top predators (e.g., *Gonatus*, *Histioteuthis*) and the giant squids *Architeuthis* spp.; includes the family Ommastrephidae with most of the genera significant to shelf-break and oceanic fisheries (e.g., *Illex*, *Todarodes*, *Todaropsis*, *Martialia*, *Dosidicus*, *Ommastrephes*, *Nototodarus*, *Sthenoteuthis*). 23 families, 77–81 genera, 200–230 species.

Order **OCTOPODA**

Internal shell drastically reduced and split into two lateral rods or absent. Eight arms only with nonpedunculate suckers. Globular body with or without fins. **Octopuses**.

Suborder **Cirrata**

Deep-water benthic or benthopelagic animals, gelatinous, jelly-like tissues. Locomotion by a pair of paddle-shaped fins, arms with reduced suckers and bearing lateral cirri (e.g., *Opisthoteuthis*, *Cirroteuthis*, *Stauroteuthis*, *Grimpoteuthis*). 2–3 families, 7–8 genera, 28–33 species.

Suborder **Incirrata**

A large group with several pelagic families (e.g., *Argonauta*, *Tremoctopus*). The common octopods of coastal waters all belong to one benthic family (Octopodidae, e.g., *Octopus*, *Benthoctopus*, *Eledone*, *Pareledone*). 9 families, 33–35 genera, 165–180 species.

Order **VAMPYROMORPHA**

The **vampire squid**, a subtropical, bathypelagic species. Eight long arms united by a swimming web, two small tendril-like arms in dorso-lateral position. 1 family, 1 genus, 1 species.

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intensively studied and the detailed neuroanatomy has shown how the motor, sensory, and integrative functions of the brain are spatially located in its many subdivisions. Learning the significance of environmental cues and adapting its behavior accordingly is highly developed in *Octopus*.

Color and Pattern

The most remarkable, and immediately visible manifestation of the behavior and responses of cephalopods, is their ability to control and change the colors, pattern, and texture of body surface. The skin of cephalopods is a delicate epithelial surface beneath which are layers of connective tissue, active colored cells (chromatophores), passive reflecting bodies (iridophores, leucophores), and a complex system of muscle fibers for moving the skin over the underlying somatic muscle surface. This capability for altering the appearance of the animal is present throughout the Cephalopoda but is expressed to the greatest degree among the coastal octopuses, cuttlefish, and loliginid squid.

The unique functional components of color change in the cephalopod skin are the chromatophores. Each one consists of a single cell within which is an elastic sac of pigment (yellow-red-brown-black). Inserted onto the pigment sac is a series of muscle fibers (25–30) radiating out into the surrounding connective tissue. In the relaxed state, the pigment sac is passively retracted to a microscopic dark point, the muscle fibers are extended, and the skin surface appears white due to reflection from the underlying somatic muscle. In the active state, the chromatophore muscle fibers contract, extending the pigment sac and spreading the area covered by its contained pigment. The pigment now screens the underlying muscle, the incident light is selectively absorbed by the pigment and the reflected wavelengths give color to the surface.

The chromatophore muscles responsible for these pigment movements are innervated by fine nerve fibers ramifying throughout the skin. Contraction of the individual muscles may take only 200–300 ms, and the animal may change its complete appearance in a few seconds. In addition to these active chromatophores there may be several classes of passively 'reflecting cells' responsible for colors in the blue-green range (iridophores) or white by scattering of all wavelengths (leucophores). The arrangement of these layers, overlaying each other throughout the depth of the skin, allows almost infinite combinations of effects. Since the chromatophores are innervated directly from the brain, their activity can be controlled to express a great variety of pattern and contrast.

The use of color, contrast, and textural change in the intra- and inter-specific behavior patterns of cephalopods has been described for many species. These capabilities are mostly involved in crypsis (camouflage), mating activities, prey and predator responses, and are generally assumed to be of great survival significance and selective value. Surprisingly, there is no evidence that cephalopods themselves can discriminate colors, they respond mostly to contrast and pattern information. The scientific literature on cephalopod behavior is dominated by their visual capabilities. It is certain that they have also developed senses for tactile, vibration, and chemical stimuli, but little is known about the significance of these senses to behavior.

Escape and Luminescence

Squid have evolved a rapid 'escape response' behavior which is mediated by three sets of nerve cells with exceptionally large fibers < 1 mm in diameter ('giant fibers') and specialized connections (synapses). This 'giant fiber system' distributes the motor commands from the brain simultaneously to all parts of the mantle musculature, and synchronously to each side, ensuring the maximum power of mantle contraction and speed of escape.

In common with fish and other invertebrate life of the deep sea, most of the mesopelagic squid show various forms of luminescent display. Most commonly present as a pattern of light-emitting organs distributed on the surface, symbiotic luminescent bacteria are also present in some of the internal organs or may be released into water as a luminescent cloud (*see* **Bioluminescence**). The functions of these systems are not fully understood, but presumably they are involved in counter-shading of the animal against surface illumination, sexual signalling, or predator–prey encounters.

The Life Cycle

Feeding and Growth

The life cycles of coastal cephalopods share many features. All are predators, feeding on a wide range of species especially crustacea and fish, many are also cannibalistic on smaller members of their own species. They ingest food at high rates, ranging between 1.5 and 15% body weight per day in different species and at a range of temperatures. Individual growth rates have been estimated to range from 1% to over 10% body weight per day, with estimates for gross growth efficiency (growth increment as a percentage of food ingested) between 10 and 70% per day for animals in captivity. Feeding and growth rates decline at large body sizes and at lower temperatures, and gross growth efficiency is generally lower in active squid species than the more sedentary octopuses and cuttlefish.

Feeding generally entails visual orientation and forward strike at the prey, gripping and pulling it in towards the mouth with the tentacles and arms. Squid and cuttlefish bite immediately into the tissues with the powerful chitinous mandibles (beaks), ingesting the most accessible parts and often releasing the dead remains partially eaten. Octopuses, in contrast, have evolved elaborate methods of prey handling – particularly effective on crustacea – involving external toxins and enzymes, before cleanly extricating the flesh from the carapace. After capture, a minute penetration of the carapace is made (< 1 mm long) and a cocktail of compounds, including protease and chitinase enzymes together with paralyzing toxins, is injected. As well as subduing the prey, the enzymes have the effect of releasing the attachments of the crustacean tissues, allowing them to be selectively eaten.

Reproduction

All cephalopods are diecious, the sexes are separate and no hermaphroditism or sex change is described. Among the better-studied coastal species, sexual maturation occurs rapidly, often at wide range of body sizes, and is usually associated with slowing or cessation of growth. In females, maturation is primarily a process of egg growth due to the accumulation of large amounts of lipoprotein yolk. Males mature spermatozoa, package them into complex spermatophores, and store them in the spermatophoric (Needham's) sac. Individual matings occur in which the male transfers the spermatophores directly to a receptive female. In many species there may be complex reproductive behavior, allowing the possibility of mate selection by either sex, In addition, females may mate with several males and usually have the capacity for storage of the transferred sperm and the possibility of multiple paternity of offspring.

Spawning and Death

Coastal squid (family Loliginidae), octopuses (family Octopodidae), and all of the cuttlefish (order Sepiidae) encapsulate their eggs, often in tough secreted coatings, and attach them to the bottom or other hard surfaces in clusters or strings. Some octopuses (e.g., *Octopus vulgaris*), subsequently stay with the egg mass, protecting it from epigrowths and defending it against predators. Most of the oceanic squid families (suborder Oegopsida) apparently spawn their eggs in fragile mid-water masses, but very little is known about the details of their mating and spawning habits.

Compared with other molluscs, cephalopod eggs are large (1–25 mm long) and yolky. Fecundity is estimated to be as low as 10–25 eggs/female for some sepiolids and octopus; 10 000–100 000 for most coastal squid and octopus; and 100 000 to over 1 million for oceanic squid (e.g., family Ommastrephidae). The eggs hatch directly, without any specialized larval forms, to an active swimming miniature of the adult form. Because the hatchling may have different habits and occupy a different ecological zone from the adult, they are usually referred to as 'paralarvae'.

Reproduction in many cephalopods occurs with a seasonal peak which is often rather inconsistent in duration and timing. In most populations some breeding individuals may be found throughout the year. Evidence from captive individuals and field populations consistently shows that modern cephalopods (with the exception of *Nautilus*) have only one breeding season. Taking account of some variations, such as 'batch spawning' (the release of the reproductive output in several episodes over a short period of time), and the apparently 'continuous' release of single eggs by deep-water octopods (suborder Cirrata); there is no indication that, after spawning, there is regeneration of the 'spent' gonads for a subsequent breeding season. Instead, there is every indication that spawning in both sexes marks the end of their lives and that death soon follows (called semelparous reproduction).

Ecology

Population Biology

The cephalopod life cycle paradigm of fast growth, single breeding, and short life has profound consequences for the population biology of any species. In its most extreme expression, if breeding is more or less synchronous and strongly seasonal throughout the population, it means that there will be only one adult size mode; biomass will strongly build and crash; and there will be little overlap of generations to buffer the influence on recruitment of environmental variables. In fact, tendencies to asynchronous breeding and lack of seasonality coupled with plasticity of feeding and growth characters, operate to spread the risks to the population of this life cycle and are shown schematically in **Figure 1**.

Trophic Relations

Numerous studies have shown that cephalopods are of great significance in the diets of many marine top predators. This evidence arises from the presence of the indigestible mandibles or 'beaks' in the gut contents of predators such as large fish, many seals, whales, and oceanic birds. As many as 30 000 have been found in the stomach of a sperm whale. The shape, size, and features of the upper beaks can be used to identify the cephalopod family or species, and estimate the size of the individual from which it came. Despite inherent errors in the procedure due to the unknown residence time of beaks in the gut, these beaks can be used to estimate the species composition and relative biomass of different cephalopods in the predator diet.

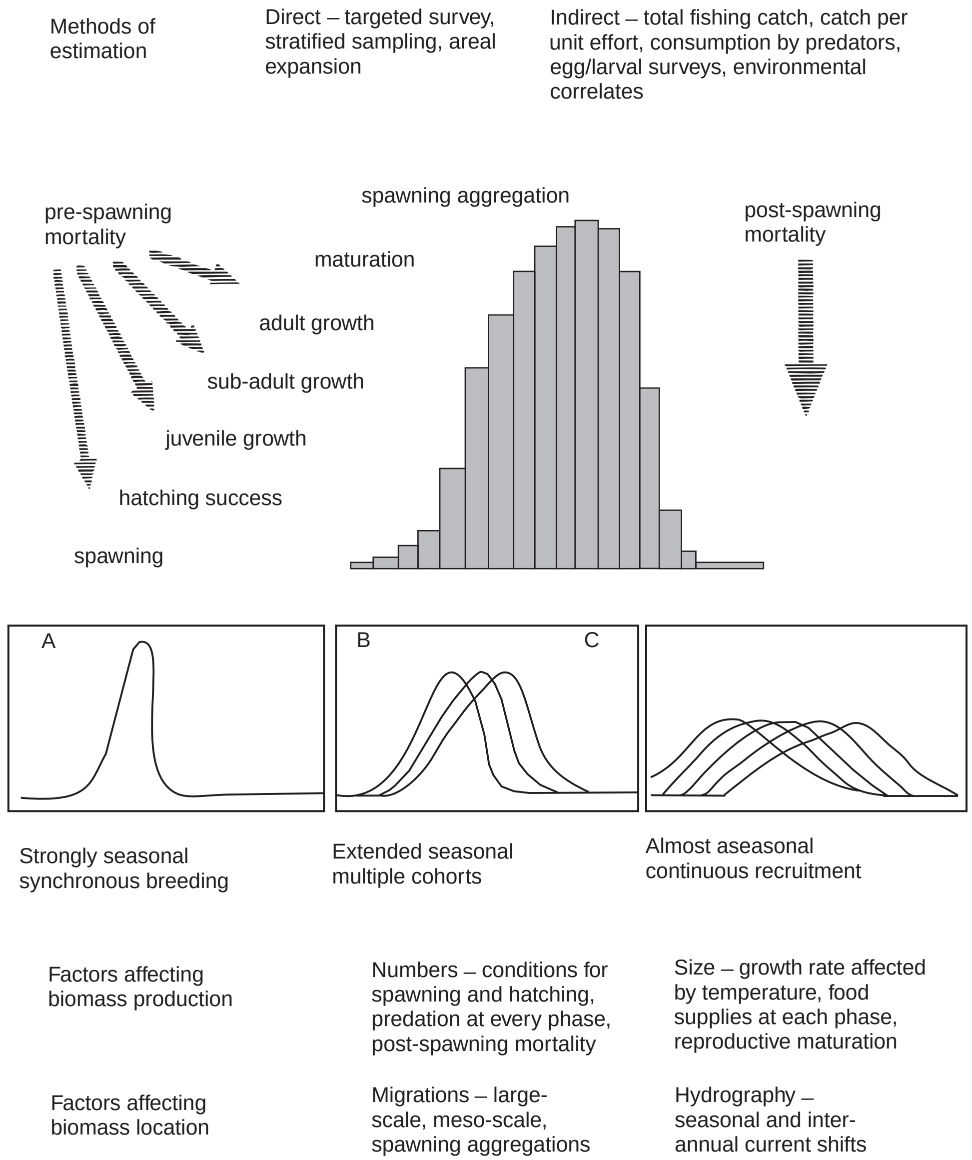

Figure 1 Diagrammatic representation of the periodic fluctuations of biomass of an annual semelparous species. Variations in the pattern of breeding and recruitment are suggested in (A), (B) and (C). Methods of estimation and the factors affecting biomass production are summarized. (Reproduced with permission from Boyle PR and Boletzky SV (1996) Cephalopod populations: definition and dynamics. *Philosophical Transactions of the Royal Society of London: Series B* 351: 985–1002.)

No cumulative estimate of consumption by these large vertebrate predators is available, but taking into account the estimated predator population size and consumption rates it has been variously estimated that sperm whales alone could consume $213–320 \times 10^6$ t of cephalopods from open ocean areas.

Fisheries

Human fisheries for cephalopods have been recorded at least since classical times. Coast dwellers throughout the world still catch octopuses with traditional traps of pots or baskets, while cuttlefish and squid are taken on simple hand lures. The quantities taken by these hand capture fisheries are usually unrecorded.

Cephalopods are also valuable fishery products traded on a global market. Using large bottom trawls specially tuned for cephalopods, oceanic drift nets (now banned in many areas), and highly efficient mechanized jigging vessels, the annual commercial harvest has risen steadily from about 1 million tonnes in 1970 to around 3 million tonnes by the mid-1990s. This was achieved largely by the extension of fishing to previously unexploited areas (North Pacific, South Atlantic) and also from increased catches in areas where the teleost fishes have been heavily exploited (Saharan Bank).

Role in the Oceans

Combining data from commercial harvest fisheries with crude estimates of total consumption by predators, the global biomass (standing stock of adults and sub-adults) of cephalopods in the oceans has been variously estimated to lie between 193 and 375×10^6 t. These figures have been derived by tentatively accumulating the estimate ranges for mesopelagic squid (150–300×10^6 t); oceanic epipelagic squid (30–50×10^6 t); slope/shelf-edge squid (8–15×10^6 t); and shelf sepioids and octopuses (5–10×10^6 t).

Whether or not these apparently massive estimates of biomass are realistic, their compatibility with other global estimates of marine productivity and consistency with the productive potential of cephalopods is uncertain. Overestimation of cephalopod frequency in predator diets could arise because cephalopod remains persist longer than those of other prey. Another source of uncertainty is the scaling up of limited predator and fishery data to ocean basin scales and the low carbon content (watery tissues) of many mesopelagic cephalopods. Some studies suggest the cephalopod biomass in the open sea (nektonic) to be about half that of fish and the mismatch between direct sampling with nets and indirect sampling from higher predators in this environment is well known.

Conclusions

Cephalopods are undoubtedly one of the most charismatic groups of marine animals. Sharing a basic body with the other molluscs they have evolved very distinctive biological characters, advanced behavior, and life cycle patterns. Cephalopods comprise a major sector of marine biomass, having central significance to higher tropic levels and global fisheries. Little is understood about the biology of the oceanic and mesopelagic species and, consequently major uncertainties remain surrounding the quantitative role of cephalopods in the world's oceans.

See also

Bioluminescence. Molluskan Fisheries.

Further Reading

Boucaud-Camou E (ed.) (1991) *La Seiche*. Caen: Université de Caen.

Boyle PR (ed.) (1983) *Cephalopod Life Cycles*, vol. 1. *Species Accounts*. London: Academic Press.

Boyle PR (1986) Neural control of cephalopod behaviour. In: Willows AOD (ed.) *The Mollusca*, vol. 9(2), pp. 1–99. New York: Academic Press.

Boyle PR (ed.) (1987) *Cephalopod Life Cycles*, vol. 2. *Comparative Reviews*. London: Academic Press.

Clarke MR (ed.) (1996) The role of cephalopods in the world's oceans. *Philosophical Transactions of the Royal Society of London, Series B* 351: 977–1112.

Hanlon R and Messenger J (1996) *Cephalopod Behaviour*. Cambridge: Cambridge University Press.

Nesis KN (1987) *Cephalopods of the World: Squids, Cuttlefishes, Octopuses and Allies*. TFH Publications (English translation of the original Russian edition, 1982 VAAP Copyright Agency of the USSR for Light and Food Industry Publishing House, Moscow).

Nixon M and Messenger JB (eds) *The Biology of Cephalopods*. Symposium of the Zoological Society, London, no. 38. London: Academic Press.

Rodhouse PG, Dawe EG and O'Dor RK (eds) (1998) *Squid Recruitment Dynamics. The Genus* Illex *as a Model, the Commercial* Illex *species and Influences on Variability*. FAO Fisheries Technical Paper, no. 376.

Roper CFE, Sweeney MJ and Nauen CE (1984) *FAO Species Catalogue*, vol. 3. *Cephalopods of the World. An Annotated and Illustrated Catalogue of Species of Interest to Fisheries*. FAO Fisheries Synopsis.

Saunders WB and Landman NH (eds) (1987) *NAUTILUS: The Biology and Paleobiology of a Living Fossil*. New York: Plenum Publishing.

Wells MJ (1978) *Octopus: Physiology and Behaviour of an Advanced Invertebrate*. London: Chapman and Hall.

CFCs IN THE OCEAN

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Introduction

The oceans, atmosphere, continents, and cryosphere are part of the tightly connected climate system. The ocean's role in the climate system involves the transport, sequestration, and exchange of heat, fresh water, and carbon dioxide (CO_2) between the other components of the climate system. When waters descend below the ocean surface they carry with them atmospheric constituents. Some of these are gases such as carbon dioxide and chlorofluorocarbons (CFCs). The CFCs can serve as a physical