PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1996 **351**, 985-1002
doi: 10.1098/rstb.1996.0089

Cephalopod populations: definition and dynamics

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SUMMARY

The study of cephalopod populations currently lacks the means to define populations adequately and to resolve basic systematic confusions. Quantitative data are usually only available from indirect sources such as commercial fisheries and from estimates of consumption by higher predators. Despite these methodological difficulties it is clear that cephalopods comprise a major component of biomass globally, throughout all fully marine habitats.

Life-cycle characteristics common to the coleoids – early and/or semelparous breeding, rapid growth, short lifespan, little overlap of generations, vulnerability to predation and environmental variables – result in wide inter-annual fluctuations in abundance. Most of the pelagic forms also undertake large- or meso-scale migrations which, coupled to shifting patterns of oceanographic variables, contribute to the unpredictability of distribution and density associated with many cephalopod species.

Temporal and spatial patterns of breeding, seasonality, growth, recruitment and mortality are clearly evident in most of the better-studied species. But exceptions to pattern (e.g. variable growth rates, extended breeding, complex recruitment) also seem to be important intrinsic characteristics. Levels of genetic variation in cephalopods are relatively low, and their population dynamics appear to be influenced principally by phenotypic plasticity in response to environmental variability. In such universally short-lived species the maintenance of this diversity balances the risks of mortality factors combining at any one time to cause periodic local extinction.

The extent and scale of the interactions between cephalopod populations and other trophic levels suggests that major ecological perturbations such as environmental shifts, or imposed effects such as commercial fishing, whether directed at cephalopods or other species, are likely to have an impact on their populations. As short-lived species with high turnover of generations, plastic growth and reproductive characteristics, high mobility and catholic predatory habits, they are always poised to respond to changed balances in their environment.

Studies on cephalopod populations have expanded considerably in numbers and scope in the last 25 years, driven by increased interest in and recognition of their roles in the marine ecology, as well as their increasing value as globally exploited resources. Despite these recent advances, the information and concepts arising from their study is only slowly entering mainstream biological thought and becoming accommodated in broad-scale models of the marine ecosystem.

1. INTRODUCTION

In common with most marine organisms, the major populations of cephalopods are hidden from view and subject only to coarse methods of study and estimation. Study of the structure and dynamics of cephalopod populations has little framework of predictive theory. Life cycle characteristics inherent in cephalopods, their short lifespan coupled with high growth and early reproduction, exaggerate the difficulties of establishing useful generalizations about populations: populations of individuals which are also highly mobile, able to avoid many types of sampling gear and which may move actively on geographical-scale migrations. The biological features contributing to population instability and the limitations of scientific sampling for cephalopods are more or less common to all of the better-known coastal and oceanic species.

Necessarily our approach to this review is largely descriptive – attempting to refine the definitions of cephalopod populations; describe where they can be observed and how they can be measured; record the nature of their variability and the factors contributing to it, with special reference to the role of migrations; touching briefly on their interactions with other biological and physical modalities, before finally returning to the overall aim of drawing general conclusions about the study of cephalopod populations relevant to their role in the world's oceans.

The quantity and quality of the information on cephalopod populations is completely conditioned by the methods of study available and applicable in practice. Systematic and taxonomic methods in use for the definition of species and taxa are largely traditional. Quantitative morphometric and electrophoretic methods are making contributions to some questions, and molecular methods are at a development stage. Distributional information comes largely from cumu-

Phil. Trans. R. Soc. Lond. B (1996) **351**, 985–1002
Printed in Great Britain

lative historical sources, but increasingly comprehensive data on the biology of cephalopod populations are available from direct scientific studies on commercial fisheries. Much information on cephalopod populations is also arising indirectly from the identification and quantification of their links to other trophic levels in the sea, both predators and prey.

2. DEFINITIONS

The term 'population' is loosely understood to mean a large group of individuals of the same species maintaining itself by reproduction in a describable geographic area or habitat, ignoring the precise number of individuals and the encompassed smaller groups of individuals. A study focused on one population does not necessarily address the question of how many distinct populations exist within the species under consideration.

May and his colleagues (1984, pp. 345–346) define: 'POPULATION – Strictly speaking, a distinct group of members of a species inhabiting a certain region, which are reproductively isolated from other populations. In loose usage, the term is often synonymous with STOCK.' In practice, it is virtually impossible to discover the number of individual members of a species inhabiting a given region (except for certain relic populations of large land animals). In the marine environment the term 'stock' is taken to refer to a fishable subset of a population which is available to fishing in a given season or area.

Some ambiguity arises depending on whether the term population is used in a strictly non-explanatory manner, as proposed by Schwerdtfeger (1978), or whether causation is integrated, as in the names designating other collectives (e.g. societies, aggregations). In the definition proposed by May and his colleagues (1984), sexual reproduction is implicit as a causative element of population existence. Sinclair (1988) uses '(local) population' based on the concept of 'a self-sustaining component of a particular species' and insists on its reality: 'to the degree that the population is accurately delineated, it is clearly a real phenomenon of nature rather than an ecologist's abstraction'.

Sinclair (1988) draws attention to the difference between species having a single or only very few, broadly distributed populations and species containing large numbers of populations. This difference provides the criterion of population richness of a species. The number of observed local populations is not necessarily identical with the number of truly distinct populations. Occasionally, dispersing individuals may connect local populations in an ensemble called the metapopulation; so population continuity through time depends on the existence of an isolate, which has the potential to become the founder of a new species (Allmon 1992). As long as the genetic make-up of local populations and their position in a metapopulation, if that obtains, is unknown, systematic categories below the species level are indeed abstractions rather than 'real phenomena of nature *sensu*' Sinclair (1988).

The biological species concept of Mayr (1970) defines only the enclosure of something that can be variably structured, because the species as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups, may contain anything between one and many populations of variable distinctness.

Some of the well-known cephalopod species provide ample illustration of the species identity problem. The 'cosmopolitan' *Octopus vulgaris* is likely to represent a species group, with the historically designated species restricted to a more limited area of distribution (Mangold & Hochberg 1991). As presently recognized, the cuttlefish species, *Sepia officinalis*, extends southwards only to about 15° N on the northwestern coast of Africa; the earlier so-called subspecies *Sepia officinalis hierredda* of tropical West Africa and *S. o. vermiculata* of South Africa and the Western Indian Ocean clearly are distinct species (Khromov *et al.* 1996). Incidentally, at the next higher level, new evidence (Perez-Losada *et al.* 1995) confirms earlier suggestions (Rochebrune 1884) that subdivision of the genus *Sepia* will be necessary.

The neritic squid *Sepioteuthis lessoniana* might represent more than one species, as suggested by differences in the spawning mode within local populations in Okinawa (Segawa *et al.* 1993). Three main forms of *Sthenoteuthis oualaniensis* in the Indian Ocean are recognized and discussed by Nesis (1993*b*). For sepiolid squids of the Mediterranean, Gabel-Deickert (1995) considers the possibility of hybrid species of *Sepiola affinis*. Orsi Relini & Bertuletti (1989) and Okutani & Takayama (1991) emphasize the morphological variability of some hectocotylus structures used as species characters as a potential source of errors in identification. These are only a few recent examples. They all reflect the present awareness of the effect that excessive 'lumping' of regionally known species (for the sake of taxonomic inclusiveness) can have on biogeographic analysis. The opposite trend of 'splitting' into more species is restrained by the proper use of cladistic methods (Ax 1987), which aim at the identification of monophyletic groupings.

Application of biochemical and molecular methods for the identification of isolates will no doubt improve our knowledge of cephalopod species and their respective population richness, but it seems doubtful that one will be able to capture the time dimension of fluctuations in populations and metapopulations, which may split and merge repeatedly. According to Allmon (1992), allopatric speciation involves at least three stages: formation, persistence and differentiation of an isolated population. At each of these stages the process can be reversed. In conclusion, any definition of population as a 'real phenomenon of nature' has to cope with technical limitations imposed on the sampling of natural populations.

Definitional problems exist also with regard to reproductive cycles and features of juvenile development. Cephalopods are conventionally viewed as semelparous reproducers, the females producing massive 'terminal' spawning. When earlier evidence for repeated spawning (e.g. pelagic octopods like *Argonauta* *argo*; Naef 1923) was combined with recent data on prolonged or multiple spawning (e.g. benthic octopods like *Octopus chierchiae*), it was necessary to address the question of definitions (Boletzky 1986*a*). The terms proposed by Kirkendall & Steneth (1985) were then used to characterize examples of extremely long spawning as multiseasonal or continuous-iteroparous (e.g. *Nautilus* spp., cirroctopods), whereas species like *Octopus chierchiae* would be uniseasonal-iteroparous (Rodaniche 1984). In no case does this mean, however, that cephalopod males or females interrupt reproductive activities and undergo one or several phases of sexual rest; at least nothing suggesting this has ever been observed. Thus 'iteroparous' as used with cephalopods is not necessarily identical with the meaning applied to other animals. The effects of variation in the duration of cephalopodan 'terminal' reproduction at the population level are reviewed in section 5.

The definitional problem related to semelparity versus iteroparity has a conceptual sideline in life history theory. The typical 'big bang' terminal spawners producing many small eggs within a few days are sometimes considered as examples of *r*-selected species, whereas cephalopods producing larger eggs over a longer time are considered as *K*-selected (MacArthur & Wilson 1967). Only few cephalopod groups, for example benthic sepiolid squids, show really clustered features of either *r* or *K* strategies (Boletzky 1981). As the theory of *r* and *K* strategies is no longer considered a satisfactory framework for life history theory (Stearns 1992), there is no need for further discussion.

The difference between the markedly terminal 'big bang' spawners and the quasi-iteroparous long-term spawners is generally reflected also in egg size. This difference in egg size persists as a difference in offspring size when hatchlings of different species are compared. Since the yolk reserves of the individual eggs are the only energy source for the development of the embryo, small eggs produce small hatchlings while larger eggs produce larger hatchlings. The smaller the hatchling, the greater the physical constraints imposed on functional morphology of organs responsible for swimming and food capture; the bigger the corresponding adults, the greater the overall difference between hatchling and adult.

The criterion of 'overall difference' between hatchling and adult has led to the usage of calling very small hatchlings 'larvae', especially when they live in the plankton. It has been shown that there is no satisfactory definition of larval features in young cephalopods (Boletzky 1974), and the designation 'paralarva' has therefore been proposed for those planktonic cephalopod hatchlings occupying a depth level distinct and/or having a lifestyle different from that/those of the adult (Young & Harman 1988). This term draws attention to the ecological analogy with true larvae, whose 'niche' the 'paralarvae' share. For population biology, the most important consequence is that planktonic and micronektonic young cephalopods may undergo long distance displacements without much active locomotion. On the other hand, even the smallest young cephalopods are able to cover short distances by active swimming, and to move up and down in the water column (see section 6). Thus in terms of locomotor activity, cephalopod hatchlings living in (and on) the plankton are essentially micronektonic.

Demographic data from commercially fished populations of cephalopods are the most frequently used sources of evidence to define population characteristics, and will be repeatedly used throughout this review. Processes such as 'recruitment', 'growth' and 'mortality' are usually inferred from study of the size frequency and age structure of the sampled population. Caddy (1991) contributes a valuable cautionary review of the pitfalls associated with the uses of such data to describe and define population processes. The effects of sampling selection, of immigration and emigration and of differential mortality, all may have profound effects on population size/age structures.

3. LOCATIONS

The gross geographical area over which the total population(s) of a cephalopod species is distributed may vary widely and often in a way not obviously related to habitat or mode of life. This variability seems to apply across systematic and environmental categories; to those species which are demersal or pelagic in habitat and neritic or oceanic in distribution. The limits of distribution of most species are not clearly defined, and they may be additionally complicated by uncertainties of species identification. The review of Nesis (1987) and the simplified distribution maps available for species of fisheries interest by Roper *et al.* (1984), compiled from historical sources, provide little evidence of general patterns of distributional extent. It must be emphasized, however, that many of the nominal species' distributions outlined in these reviews may be considerably altered when new approaches to the definition of species become incorporated into the conventional taxonomy.

The squid family Loliginidae is a rather homogeneous grouping of 30–40 species, typically limited worldwide to coastal regions of the shelf (< 200 m deep). Egg masses are laid close to, or on the bottom, attached to hard or soft substrata. A species such as *Loligo kobiensis* apparently occupies only a small region (about 5° of latitude and longitude) around the southwestern tip of Japan. *Loligo* (*Photololigo*) *edulis*, however, overlaps this distribution in the north to about 35° N but extends south across the equator to the east and west coasts of Australia at least to 20° S. In the western Atlantic Ocean, *Loligo surinamensis* is known only from the mouth of the Suriname River (Surinam), while on the eastern side, *Loligo vulgaris* is continuously distributed from about 55° N to 20° S and throughout the Mediterranean. Presumably such close congeners exist sympatrically by subtle subdivision of the habitat for food or breeding.

Squid of the suborder Oegopsida are typically oceanic in distribution and at least some of them apparently lay large numbers of eggs enclosed in weak gelatinous masses. These fragile deposits are neutrally

Table 1. *Heterogeneity in cephalopod populations*

(Examples of approaches to the subdivision of cephalopod populations using criteria of: (1) geographic separation, discontinuous or arbitrarily defined; (2) spawning characteristics, seasonality/length at maturity; (3) recruitment pattern, sequential timing and simultaneous size modes; (4) morphometric and meristic variation; (5) allozymes; (6) behaviour/colour pattern; (7) parasite fauna. Positive results for evidence of population variation are graded informally on a scale of 1* to 3*** (0 for inconclusive). Methods for study of the variability of DNA are currently under development in several research groups and are beginning to be applied to cephalopod systematics (Bonnaud *et al.* 1994; Nishiguchi *et al.* 1995) but have not yet reached the point of application to ecological or systematic questions.)

species	method	result	reference
Berryteuthis magister	5	**	Katugin 1993
Eledone cirrhosa	4	*	Boyle *et al.* 1988
Illex argentinus	5	**	Carvalho *et al.* 1992
Illex illecebrosus	1,2,3	**	Coelho & O'Dor 1993
Loligo spp.	6	*	Hanlon 1988
Loligo bleekeri	5	*	Suzuki *et al.* 1993
Loligo chinensis	4,5	***	Yeatman & Benzie 1993
Loligo forbesi	5	***	Brierley *et al.* 1993*b*
	3	**	Boyle & Ngoile 1993
	4	**	Pierce *et al.* 1994*d*
Loligo gahi	5	**	Carvalho & Loney 1989
	2,4,5	**	Carvalho & Pitcher 1989
Loligo opalescens	4	0	Kashiwada & Recksiek 1978
	5	0	
	5	**	Ally & Keck 1978
			Augustyn & Grant 1988
Loligo pealei	5	*	Garthwaite *et al.* 1989
Loligo plei	5	0	Garthwaite *et al.* 1989
Loligo vulgaris	4,5	***	Augustyn & Grant 1988
Loligo vulgaris reynaudii	2	**	Augustyn *et al.* 1993
Loliguncula brevis	5	0	Garthwaite *et al.* 1989
Martialia hyadesi	5	***	Brierley *et al.* 1993*a*
Nototodarus sloani sloani	1,2,3	*	Kawakami 1976 (In Okutani 1977)
Nototodarus gouldi	5	*	Richardson 1983
Octopus spp.	6	***	Roper & Hochberg 1988
	6	*	Hanlon 1988
	4,6	***	Norman 1992*b*, *c*
Octopus vulgaris	1	*	Bravo de Laguna 1989
	4	***	Mangold & Hochberg 1991
Ommastrephes bartrami	3	*	Dunning 1993
	7	**	Bower & Margolis 1990
Photololigo edulis	2	**	Natsukari *et al.* 1988
Sepia officinalis	5	***	Perez-Losada *et al.* 1995
	5	**	Tranvouez & Boucher-Rodoni 1990
Sepia orbignyana	5	***	Perez-Losada *et al.* 1995
Sepioteuthis lessoniana	2	*	Segawa *et al.* 1993
Sthenoteuthis oualaniensis	1,2,3,4	***	Nesis 1993
Sthenoteuthis pteropus	1,2	**	Zuev & Nikolsky 1993
Todarodes pacificus	1,2,3	***	Araya 1976

buoyant and probably drift for large distances at intermediate depths, perhaps at some density cline of temperature or salinity in the water column (O'Dor *et al.* 1977; O'Dor & Balch 1985). Not surprisingly squid of this type may have very extensive distributional areas. The summary maps in Roper *et al.* (1984) are particularly useful for species of the family Ommastrephidae as they are relatively well known as major global fisheries. Distributed from the surface to 1000 m or more, large populations of ommastrephids frequently congregate in shelf-break and slope areas and may undergo extensive migrations between breeding and feeding areas (see sections 5 and 6). Some, like *Ommastrephes bartrami*, have an almost global distribution in subtropical and temperate oceanic waters, or in one hemisphere only, as in the case of *Todarodes filippovae* which is circum-polar south of 35° S. The long-distance migratory patterns of many ommastrephids (and to a lesser extent the loliginids of the continental shelf) have profound effects on the locations and movement of cephalopod biomass and are treated in more detail in subsequent sections.

In the Atlantic, *Illex coindetii* is considered to range in the east from 15° S to 60° N, including the Mediterranean, and from 10° S to 30° N on the western side (where there are difficulties in distinguishing between *I. coindetii*, *I. illecebrosus* and *I. oxygonius*). Another pan-Atlantic species, *Ommastrephes pteropus*, occurs in tropical and warm temperate waters at least between 35° S and 30° N. *Todarodes sagittatus* also occurs in both hemispheres, but in the eastern Atlantic only (13° S to the Arctic Ocean and including the

Mediterranean). Wide and continuous distributions in the Pacific and Indian Ocean are known for species such as *Sthenoteuthis oualaniensis*, which occurs throughout this enormous region between approximately 40° S to 40° N (Okutani 1995).

Contrasting with these global-scale distribution patterns for some ommastrephids are the disjunct or highly restricted ranges of other, closely related and biologically similar species. *Todaropsis eblanae*, for example, is distributed in two totally disconnected areas, the eastern Atlantic (36° S to 60° N), and the southwest Pacific and southeast Indian Oceans off the coast of Australia. *Nototodarus gouldi* occurs only in the temperate and subtropical waters off Australia, while *Nototodarus sloani* is limited to the shelf-break zones of New Zealand. Reviews by Nesis (1993*a*, *b*) and Zuev & Nikolsky (1993) provide comprehensive summaries of some of the ecological factors involved in the distribution of selected oceanic ommastrephids.

Distinctly benthic and apparently similar octopus species (family Octopodidae) also have drastically different distributional ranges (Roper *et al.* 1984). *Octopus variabilis*, common only around the coasts of Japan, can be compared with the apparently worldwide distribution of *Octopus vulgaris* in temperate and tropical waters (but see above, section 2 and the impending revision of this species; Mangold & Hochberg 1991). Other octopuses have narrowly defined habitat requirements which clearly limit both geographical distribution and scale of the population (Norman 1992*a*, *b*, *c*). *Octopus micropyrsus*, for example, is restricted to the holdfasts of the giant kelp *Macrocystis* of the California coast (Hochberg 1980).

Cuttlefish species, although belonging to a morphologically and biologically very homogeneous group (family Sepiidae), also have widely different geographical ranges. *Sepia murrayi*, for example, is limited to the area of Indian Ocean between the Gulf of Aden and western Gulf of Oman, while the common cuttlefish, *Sepia officinalis*, extends throughout the eastern Atlantic from the Skagerrak and North Seas to the Mediterranean and northwest Africa. The family is unaccountably absent from both the east and west continental coastlines of the North and South American continent (Voss 1974).

Heterogeneity within populations is often described on the basis of patterns of breeding or recruitment of young. Attempts to subdivide cephalopod populations more formally or to define stocks on the basis of differentiation within the overall distribution of a species have had mixed results (table 1). Detailed morphometric measurements, coupled with multivariate statistics, have been used to subdivide the Azores population of *Loligo forbesi* from the population of the European mainland (Pierce *et al.* 1994*d*), but morphometrics are not generally sufficiently sensitive, due to difficulties in taking consistent measurements from soft-bodied animals, and compensating for the effects of size variation, sample treatment or interworker bias (Pierce *et al.* 1994*b*).

Differentiation of allozymes by electrophoresis has been used successfully in some cases to recognize distinct populations (Brierley *et al.* 1993*a*, *b*, 1995; Carvalho *et al.* 1992; Carvalho & Loney 1989; Katugin 1993) but is more likely to be useful at the species level and above (Yeatman & Benzie 1993; Boucher-Rodoni *et al.* 1995; Perez-Losada *et al.* 1995). Mostly these cephalopod studies are at relatively such an early stage that questions of stock identity grade into issues of species description or even challenge the integrity of genera.

Some of the contrasts and inconsistencies apparent in the distribution patterns of related cephalopod types may become resolved by clearer definition of species (see section 2). The need for a comprehensive rationalization of cephalopod systematics identified by Voss (1977) is still awaited, and more urgently now to take account of the advances in methodology.

4. POPULATION DATA AND THEIR USES

The most obvious quantitative data on the scale of cephalopod populations are the catches taken by commercial fisheries. Figures for fisheries landings worldwide (Globefish 1994) show that the gross total annual landings recorded for all cephalopods increased from 1 million tonnes (mt) in 1970 to 1.5 mt in 1980 to peak catches of 2.7 mt in 1989 and 1992. Estimates for 1993 and 1994 are slightly lower. Over this period of time the cuttlefish landings remained more or less stable at about 250000 t annually; octopus landings increased steadily, approximately doubling to 320000 t. Squid compose the greatest proportion of the catch and the spectacular increase in cephalopod catches has been almost entirely due to the discovery and exploitation of new squid fishery resources in the southeast Pacific and southwest Atlantic Oceans. Individual squid species may contribute annual catches of > 500000 t (*Todarodes pacificus*); *Illex argentinus* has exceeded 200000 t annually and a number of other species have reached or exceeded annual catches of > 100000 t (*Illex illecebrosus*, *Nototodarus sloani*, *Octopus vulgaris*). Considered either as a category or by representative species, few other uncultivated exploited invertebrate resources yield commercial catches on this scale. Possible exceptions to this generalization might be krill, *Euphausia superba* (Sahrhage 1989), and the penaeid shrimps (Klima 1989; Garcia 1989) at the peaks of their catches.

The scientific use of fishery landings statistics for quantitative population biology is hedged with uncertainties. Fished resources are often not identified to the species level and, when species are recognized, their identification may be incorrect or lost if the records are subsequently accumulated into broad statistical categories. For example, for many years an unknown quantity of *Illex argentinus* from the Atlantic coast of South America was recorded within the *I. illecebrosus* figures from the north. Indeed, over 50% of the global cephalopod catch recorded by FAO for 1992 is not segregated into single species categories.

For various reasons even the total catch quantity landed may be incorrect. Most often the recorded landing will be an underestimate of the amount actually caught, principally because small catches and

Table 2. *Quantities of selected cephalopod species removed annually by fishing*

(Data for landings (tonnes) taken from FAO *Yearbooks*: *catches and landings* 1990, 1992. More detailed information for selected species may be available from national sources and for earlier periods of time, but for the purposes of inter-species and inter-annual comparisons the FAO provide the most consistent and comparable international statistics.)

year	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Octopus vulgaris	96 559	62 206	99 802	65 139	62 934	64 455	62 575	57 769	61 791	62 534	78 091	85 049
Sepia officinalis	14 820	17 610	18 669	19 293	22 508	23 500	22 681	29 268	27 421	27 869	22 211	22 952
Loligo pealei	21 699	21 380	20 017	16 401	16 389	17 189	11 658	19 392	23 042	16 251	19 571	19 711
Loligo reynaudii	2 062	1667	1689	1218	4572	4232	2726	5418	10730	4986	7036	2805
Illex illecebrosus	48 188	27 642	12 148	10 475	7070	5982	18 069	5926	16 212	27 479	18 933	23 435
Illex argentinus	13 707	42 947	32 388	43 343	126 981	149 238	265 390	235 335	224 635	156 985	201 215	194 526
Todarodes sagittatus	15 542	21 762	22 339	16 974	21 798	9800	11 371	8420	8617	8576	7775	8209
Todarodes pacificus	259 233	247 922	230 876	219 529	192 466	127 570	243 447	205 558	277 538	284 683	351 843	534 157
Nototodarus sloani	32 400	41 000	48 569	55 620	52 451	55 506	58 189	71 944	129 638	38 115	41 777	62 941
Dosidicus gigas	9726	264	89	364	177	269	225	885	7380	5630	5846	8549

those from small landing areas are likely to miss any official recording system. It is likely that the so-called 'artisanal' catches in many countries are completely omitted. On a world scale, the use of catch statistics is limited to catch trends in the three main cephalopod groups, their more detailed use being restricted to selected species where identification and recording methods are likely to be reasonably reliable.

Nevertheless, commercial fisheries represent a scale of sampling of cephalopod populations which is enormous when compared with scientific data sources and which is representative of the most abundant accessible species. In Japanese waters especially, where cephalopod resources have been highly exploited and monitored for many decades, the scientific uses of fishery data are generally well advanced (Murata 1990; Okutani 1990; Suzuki 1990; Takeda 1990). A major consideration in the use of fishery statistics is that the scale of the catch is responsive to factors of market supply and demand, the price obtained and the consequent fishing effort, and fluctutions in catches of other species. The size range of cephalopod fisheries catches together with the scale of inter-annual fluctuation is shown for a selection of species in table 2. Trends in landings are clearly not usually interpretable as changes in population size, although in cases where fishing effort can be estimated the catch per unit effort (CPUE) represents the availability of the target species to fishing and provides a widely acceptable index of abundance.

Exploited populations of marine resource species are usually subdivided into 'stocks' for fishery purposes. These units are defined conveniently for the assessment or management of resources rather than clear evidence of separation, although characteristics such as the geographical location of major concentrations (Araya 1976); the timing and strength of breeding (Coelho & O'Dor 1993); recruitment (Boyle & Ngoile 1993); or variable features suggesting a degree of genetic separation within the overall distribution of a species (Pierce *et al.* 1994*d*), may support a biological basis for the designation. Numerical methods evolved for the quantitative assessment of such stocks in biomass or numbers of individuals comprising the population, often based on purely heuristic models (Hilborn & Walters 1992; Fogarty 1989), are the basis of applied fishery biology. Pierce & Guerra (1994) give a review of the application of stock assessment models to cephalopod fisheries.

Total or partial biomass estimations have not often been attempted for cephalopods because of the many difficulties in relating catch size to total population. It is also true that stock estimates based on rather comprehensive data from the fisheries are not released for scientific uses (*Illex argentinus* within the Falklands Islands Conservation Zone). A range of published values, some limited to selected stocks or areas, and made by various assessment methods is given in table 3. The very wide range of values estimated for any one species reflects the uncertainty of the estimate more than the likely inter-annual fluctuations.

In the absence of large-scale scientific population surveys for cephalopods there are few methods available for independent evaluation of the quantitative estimates derived from commercial fishing. The realization, however, that cephalopod beaks retained in the digestive tracts of vertebrate predators such as fish and mammals, or regurgitated meal remains of marine birds, could be used to evaluate the cephalopod diet of these higher trophic levels (Clarke 1962*a*, *b*, 1986) has provided an important tool for indirect population assessments. Estimates of the consumption of cephalopods (Clarke 1977, 1983) established the very large scale of the biomass taken by a wide range of marine top predators and suggested the 'real' population size of many species to be much greater than previously suspected. However, as Caddy (personal communication) points out, with estimated values for instantaneous mortality rates in cephalopods as high as 2.0, a high yield of production may be taken from a relatively small biomass estimated at any fixed time. The estimate of consumption by predators then should not be taken to represent a specific fraction of a total population biomass. It is also notable that the bulk of the biomass taken by marine predators, particularly in the Antarctic region, is from species not currently accessible or sought by commercial fishing.

Table 3. *Published population biomass (stock size) estimates (tonnes) computed for selected fished cephalopod species*

(Estimates for other species may be made for management purposes but not published.)

species	'stock'	biomass tonnes × 10^3	estimation method	reference
Loligo forbesi	UK – Scottish fishing area only	1.75–35 converted from numbers	landings and samples, simple difference model	Pierce & Santos (1996)
Loligo reynaudii	South Africa – west coast	0.2–16	bottom trawl survey	Augustyn *et al.* 1996
	South Africa – south coast	9–20		
Illex argentinus	South Patagonian shelf, winter-spawned	3–125	energetics model	Rodhouse & Nigmatullin (1996)
Martialia hyadesi	Total – antarctic circum-polar	> 330	consumption by predators	Rodhouse *et al.* 1993
Sthenoteuthis pteropus	Total – pan-Atlantic tropical and warm temperate	3000–5000	visual and jig fishing	Zuev *et al.* 1985 (In Zuev *et al.* 1993)
Todarodes pacificus	Japan – Sanriku and Hokkaido Pacific grounds	50–1100	stock depletion by fishing	Murata 1989

5. VARIABILITY IN POPULATION DENSITY/BIOMASS/LOCATION

The biomass of many cephalopod populations appears to be highly variable. Fluctuations are generated firstly by the basic life-cycle characteristics of rapid growth, seasonal breeding, and more or less universal mortality of the adult population after breeding. The lifespans of most of the neritic octopuses, cuttlefish and squid, as well as many of the fished oceanic ommastrephid squid, are estimated to be no more than 1–2 years in total. These assumptions are based on such evidence as the sudden disappearance of large animals from the population; the absence of individuals aged by current methods at not much over 450 days; and, in some cases (*Loligo opalescens*) observed mass mortality at the spawning grounds, or death of individual females after hatching of their brood of eggs (*Octopus vulgaris*). Consequently, the main period of juvenile and adult growth, the attainment of breeding condition and spawning in temperate conditions, occurs on an annual basis. Since massive post-spawning mortality is normal it follows that biomass production in many of the better-known populations of cephalopods is a strongly cyclical, usually annual, phenomenon (except in some small and/or tropical species), and that there may be virtually no overlap of adult generations.

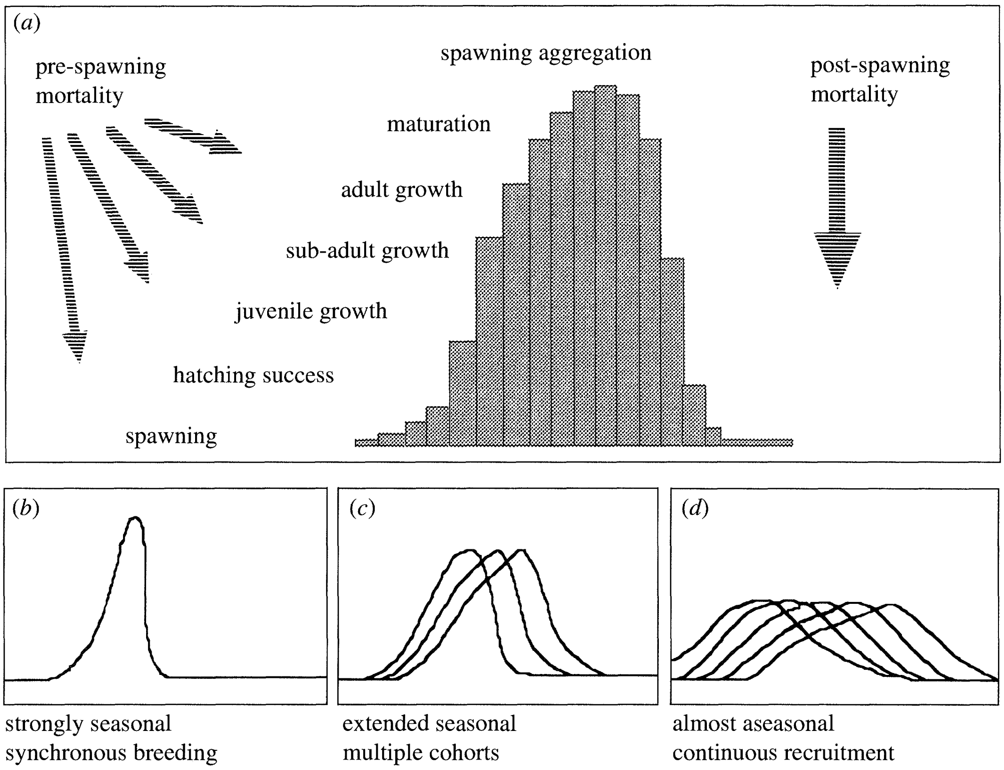
Variations in the degree of seasonality and synchronicity of the breeding population in different species serve to emphasize or to smooth out these cycles. The factors involved in the cyclical changes of cephalopod biomass are summarized diagrammatically in figure 1*a*. In this figure the horizontal axis (time) implicitly represents 1 year, although the same model would apply on shorter or longer scales.

The extreme form of the life/biomass cycle is seen (figure 1*b*) in loliginid squid such as *Loligo opalescens* (Fields 1965; Hixon 1983). Breeding occurs in dense aggregations over a short timescale on clearly defined spawning grounds. This species is clearly semelparous, each animal expressing its lifetime fecundity in a spawning episode lasting hours or days, followed by universal mortality while still over the spawning grounds. Populations of other loliginids such as *L.vulgaris reynaudii* (Sauer & Smale 1993), *Loligo pealei* (Summers 1983) and *L.forbesi* (Pierce *et al.* 1994*a*) may extend the breeding season up to several months and indulge in several spawning episodes resulting in successive waves of recruitment and a more complicated population structure (figure 1*c*).

Methods of size mode analysis applied to several of the major fished populations of ommastrephids, such as *Illex illecebrosus* (O'Dor 1983; Coelho *et al.* 1994) or *Todarodes pacificus* (Okutani 1983) have revealed subcomponents of the annual recruitment. The introduction of techniques for ageing individual animals (Jereb *et al.* 1991), while essentially confirming the annual pattern of life cycle and recruitment (e.g. Arkhipkin & Laptikovsky 1994) has suggested that such substructuring may result from recruitment of successive 'micro-cohorts' (Caddy 1991). New evidence for episodic or 'batch' spawning in some species (Harman *et al.* 1989; Boyle *et al.* 1995) provides a mechanism by which successive 'micro-cohorts' could arise from the spawning behaviour of individuals. However, it is possible that at the population level, the 'micro-cohorts' separated by age or size may be more apparent than real, being imposed arbitrarily by the sampling intervals. It has also been shown that later spawned broods may 'catch up' with the earlier broods in size due to coinciding with higher temperatures and better feeding conditions (Rodhouse & Hatfield 1990).

The result of uncoupling the population still further from seasonal and synchronous breeding cues is seen in some of the smaller sepiolids (Gabel-Deickert 1995) and tropical species such as *Idiosepius pygmaeus* (Jackson 1992; Lewis & Choat 1993), where fluctuations in biomass production are almost evened out (figure 1*d*), although arguably the basic model of cyclic biomass production still applies to each subcomponent of the population.

methods of estimation	**direct** – targeted survey; stratified sampling; areal expansion	**indirect** – total fishing catch; catch per unit effort; consumption by predators; egg/larval surveys; environmental correlates



strongly seasonal synchronous breeding

extended seasonal multiple cohorts

almost aseasonal continuous recruitment

factors affecting biomass production	**numbers** – conditions for spawning and hatching; predation at every phase; post-spawning mortality	**size** – growth rate affected by temperature; food supplies at each phase; reproductive maturation
factors affecting biomass location	**migrations** – large-scale, meso-scale; spawning aggregations	**hydrography** – seasonal and inter-annual current shifts

Figure 1. (*a*) Diagrammatic representation of the periodic fluctuations of biomass of an annual semelparous species. (*b*), (*c*) and (*d*) show variations in the pattern of breeding and recruitment. Methods of estimation and the factors affecting biomass production are summarized.

The population structure of most fished cephalopod populations is inherently simple – consisting of a single annual size mode which may show 'growth' when sampled at successive time intervals – although this apparent simplicity may incorporate a complex underlying pattern of periodic or successive recruitment. It is argued by Pauly (1985) that despite the biological differences between cephalopods and the longer-lived fish species their population dynamics can be modelled in essentially similar ways. Caddy (1991), though, emphasizes the caution needed in interpreting size/age structures of cephalopod populations due to: their extreme lability of growth and survival in response to environmental conditions; the population substructures ('micro-cohorts') of recruitment of successive broods; and the effects of immigration and/or emigration from the population on simple modal analysis.

The inter-dependence of cephalopod biomass production and life-cycle characteristics is further complicated by the possibility that in some species, for example in *Sepia* and *Loligo*, there may be alternating long and short generation times (Mesnil 1977; Le Goff & Daguzan 1991) influenced year to year by changing conditions favouring growth and reproduction. This model has been used to provide an explanation for fluctuating patterns of reproduction and recruitment, although in *Loligo forbesi* it was not supported by data from ageing of various cohorts (Boyle *et al.* 1995). Controversy also surrounds the generalization that cephalopods are semelparous, and the degree to which some become iteroparous (*Octopus chierchiae*; Rodaniche

1984). A discussion of this point is provided by Mangold *et al.* 1993, but these arguments do not seem to undermine the thesis advanced above for the basically cyclic nature of cephalopod biomass.

An important factor contributing to the growth of biomass of cephalopod populations is the apparently high gross conversion efficiencies of cephalopods of all types. Many studies of captive octopuses, cuttlefish and squid (for a review of growth studies see Forsythe & Van Heukelem 1987) have established the high increment of somatic growth achieved for a given food intake. In part, this performance is due to their exclusively predatory habit and ability to selectively ingest a high quality protein diet. Values of 40–60% growth efficiency (weight of growth increment as a percentage of weight of food ingested) are typical for sedentary species of octopus and cuttlefish, falling to 20–30% for the more active squid (O'Dor & Wells 1987). This topic is revisited in detail by Clark & Wells (1996).

The life-cycle characteristics of cephalopods contribute the main reasons for the large inter-annual fluctuations in fished catches and the apparent instability of population densities (Boyle 1990). They differ from most comparable stocks of exploited teleost fish, in temperate waters at least, in having almost no overlap of generations. Hence, the biomass present in any year depends almost entirely on the success of recruitment in that year. In these circumstances any stock/recruitment relationship is likely to be even weaker than for most fish. It is the dynamic interactions of physical and biological variables, effective on very short timescales, which are the most influential factors bearing on individual survival and growth and the consequent build of population biomass.

Causal links between physical and biological variables and the population biomass in any year are difficult to establish because, although acting directly on individuals, such variables are also characteristics of water masses such as warm core rings or oceanic intrusions into coastal water. Inter-annual shifts in oceanographic patterns of water movement as well as the geographic scale of migratory movements bring a complex and contradictory set of variables to bear. It is notable, however, that there are a number of examples where physical and oceanographic variables have proved to be better predictors of fishing catches than biological indices. McInnis & Broenkow (1978) found correlations between catches of *Loligo opalescens* and oceanographic variables in Monterey Bay, California, and Rowell (in Caddy 1983) plotted the relationship between annual biomass estimate for *Illex illecebrosus* and the mean seawater temperature. Rasero (1994) pointed out the relationship between abundance of *Todaropsis eblanae* and upwelling features, and Pierce (1995) has established a highly significant relationship between annual fluctuations in sea-surface temperatures in the North Sea and landings of *Loligo forbesi* in Scotland. Landings in the peak months of the autumn fishery could be forecast with a high degree of accuracy from mean February sea-surface temperatures in the same year for a 15-year dataset.

The abundance and location of cephalopod populations is highly influenced by the prevalence and scale of their migrations. Cephalopod populations are known to undertake migratory movements on all geographic scales. Large-scale migrations of several thousands of kilometres, linked to the continental boundary currents, are known for many of the large populations of ommastrephid squid. The movements of *Todarodes pacificus* in the Kuroshio and related currents off Japan; *Illex illecebrosus* in the northeast-flowing Gulf Stream; *Illex argentinus* in Brazilian and Falkland currents; *Nototodarus sloani* (Tasman Current); *Nototodarus gouldi* (East Australian Current) (Hatanaka *et al.* 1984; O'Dor & Coelho 1993); and *Dosidicus gigas* in the Humbolt Current (Nesis 1983), all provide examples of major population movements on oceanographic scales. The review volume edited by Rodhouse *et al.* (1996) provides many clear illustrations of the interdependence between squid population dynamics and oceanography for the genus *Illex*.

Often associated with the availability and movements of food supplies (Rodhouse & Nigmatullin 1996), these migrations involve transfer of hundreds of millions of individuals during phases of high growth. Population movements on this scale must be associated with considerable demands on the productivity of the system and represent major transfers of biomass across geographical areas. Relevant to the implications of large-scale migration is the possible role of cannibalism. The diets of most cephalopods include a proportion of other cephalopods including conspecifics, and energetic considerations (O'Dor 1988) suggest that feeding during the migration is essential. The mixed sizes of individuals in migrating populations mean that a wide range of food organisms can be utilized; coupled with the increasing incidence of cannibalism, it is suggested that biomass growth is optimized by maximizing individual growth of the largest animals (O'Dor *et al.* 1980).

Meso-scale migrations, in the order of a few hundred kilometres at most are known for many cephalopod species resident on the continental shelf. Squid such as *Loligo edulis* (Ogawa *et al.* 1983), *L. gahi* (Hatfield & Rodhouse 1991, 1994) and *L. vulgaris reynaudii* (Augustyn 1990; Roberts & Sauer 1994) move on a seasonal basis between aggregating on inshore spawning grounds and dispersing offshore to feed. Similar meso-scale movements are known for *Sepia officinalis* (Boucaud-Camou & Boismery 1991) and are suggested for *Octopus vulgaris* (Mangold 1983). Without necessarily implying active migration, Arkhipkin *et al* (1988) have reported the presence of dense meso-scale aggregations of the oceanic squid *Sthenoteuthis pteropus* associated with cyclonic meanders and eddies of the Southern Trade Wind Current.

Local or fine-scale movements, of one to several kilometres, often on a diurnal pattern, can be found in loliginid squid associating on spawning grounds by day and dispersing at night (Sauer personal communication). Octopuses too show diurnal patterns of foraging activity away from their 'home' site (Altman 1966–67; Yarnall 1969), although these are not comparable to population movements as there is no net direction. In the vertical dimension, many of the oceanic midwater squid undergo diurnal changes in vertical distribution. In Hawaiian waters, peaks of species richness occurred at 500–800 m depth during the day, rising to 250 m depth at night (see Young 1978 for a review). The functions of these vertical movements are poorly understood but probably are related to changes in the distribution of food supplies; nevertheless, they would represent substantial changes in distribution of biomass available to potential predators.

6. FACTORS AFFECTING VARIABILITY

The generally short lifespan of cephalopods means that their populations are extremely reponsive to inter-annual fluctuations in biological and physical variables. As there is little overlap between adult generations, the potential numbers and biomass of any cephalopod population, outside the tropical belt, is totally dependent on the success of recruitment, conditions for growth and exposure to predation in that year. Variation in annual recruitment strength is notoriously high in most marine species, and in cephalopods this variability is carried through to affect the whole annual production of biomass. Mechanisms such as extension of the breeding season, batch-spawning, sequential broods and variable growth rates will all tend to reduce the probability of large inter-annual changes in population size.

The main phases at which population biomass (numbers and individual size) is affected by these variables is summarized in figure 1*a*. Cephalopod hatchlings are relatively large and well endowed with maternal yolk supplies from the egg. Within a few days, however, they are critically dependent for survival on the supply of zooplanktonic food of appropriate kinds (Boletzky & Hanlon 1983; Villanueva 1994), as well as being exposed to predation by hosts of planktonic predators. The direct relationships between feeding rate, ration size and growth in cephalopods are analysed later in this volume (see Clark & Wells 1996).

Growth rate at any stage is typically influenced strongly by temperature in all poikilotherms. The recent analysis by Forsythe (1993) of the effect of temperature on growth of hatchlings and juveniles illustrates the importance of the interaction between the timing of hatching and environmental temperature in achieving maximal growth rate. Broods hatching later in the year but coinciding with higher environmental temperatures would be capable of higher growth rate, overtaking earlier broods in size, and, theoretically, of reaching greater eventual adult sizes. Clearly this effect offers an explanation of the poor size-at-age relationships of several cephalopod populations (Caddy 1991), and provides a mechanism for the selective advantage of extending the breeding season to operate (figure 1*c*). The recognition of 'micro-cohorts' of sequential ages in fished populations of *Illex argentinus* may be due to this cause (Arkhipkin & Laptikhovsky 1994). Data from Rodhouse (personal communication) for this species suggests that the higher growth rate of later hatchers allows them to catch up with, but not overtake, their predecessors. Counter-intuitively, in certain species, such as *Sepia officinalis*, it appears that final adult size is inversely proportional to growth rate (Richard 1971). Although, because in most cephalopod species growth is slowed or stopped at sexual maturation, the interaction between growth rate and the onset of maturity needs further investigation.

Given the large scale of global commercial fisheries on many cephalopod species (table 2) it is reasonable to look for evidence of direct effects of fishing on population abundance. Catch statistics (FAO) are the main source of quantitative data on abundance but, as noted above, due to uncertainties of collection and treatment of statistics, they often cannot be used in a rigorous way. Procedural changes such as the splitting or grouping of species catches or changes in their allocation to different statistical areas causes large but spurious changes in the total catch recorded.

The fishing methods employed for cephalopods have been reviewed on a number of occasions (Voss 1983; Rathjen & Voss 1987). Those such as pots and traps for octopuses or jigs for squid are very highly selective in their effect, subtract a precisely measurable component of the population and have virtually no other impact on the environment or other biota. In contrast, the large-scale nets such as bottom and pelagic trawls, drift nets and seines, which are also used for finfish species and mixed fisheries, have much more widespread and less measurable effects on the fished populations. Such methods are also likely to have other deleterious effects on the environment such as disturbance to benthos (trawls; Jones 1992) or serious incidental by-catches of mammals and birds (driftnets; Ito *et al.* 1993). Several of the major resource species of ommastrephid squid (e.g. *Todarodes pacificus*, *Dosidicus gigas*, *Illex illecebrosus*, *I. argentinus*) have shown wide fluctuations of recorded catch over the past three decades. Despite heavy targeted fishing pressure on these species no clear opinion has been formed that any downward catch trends have resulted from fishing pressure (but see Osaka & Murata 1983, for possible changes in Japanese waters due to fishing).

Within any single fishing season the effects of intense fishing may be quantifiable and used as the basis for assessment and management. Within the managed fishing zone around the Falkland Islands catch rates in the fishery for *Illex argentinus* are monitored on a daily basis. Assuming that CPUE is at its peak at the beginning of the season, when the annual stock is unexploited, its decline as the fishing season progresses is an index of falling abundance. Given the rather complete knowledge available on the fishing effort and catch within the prescribed area, the decline in CPUE is used to back-calculate the estimated population at the start of the season (Beddington *et al.* 1990; Rosenberg *et al.* 1990). As a species assessment, however, the dataset suffers from the unknown effects of migration, and because the Falklands Islands Conservation Zone to which the assessment is applied encompasses only part of the species distribution.

Although this methodology does require very close monitoring of the fishery, these methods have been attempted for other squid fisheries in circumscribed areas (Erhardt *et al.* 1983; Murata 1989; Brodziak & Rosenberg 1993). In some circumstances, targeted fishing by trawling for species that concentrate their breeding activity on defined shallow grounds may damage the breeding population. Examples may be the cuttlefish *Sepia pharaonis* in the Arabian Sea, where indiscriminate trawling occurred through breeding areas (Sanders 1979) and *Loligo vulgaris reynaudii* off South Africa where special measures are in force to protect breeding areas (Sauer *et al.* 1992; Augustyn *et al.* 1993).

Many cephalopod fisheries arise as by-catches from fishing operations directed towards other stocks. Most of the coastal loliginid squid catch arises in this way, for example the catches of *Loligo forbesi* and *L. vulgaris* in European north east Atlantic waters (Boyle & Pierce 1994). In such cases fishing effort is more or less independent of the squid catch (as it is directed at other target species), CPUE and total catch are consequently reasonable indices of squid abundance (Pierce *et al.* 1994*c*). Effects on the population due to by-catch fisheries are currently unmeasurable. Their exploitation, by any method, also differs greatly from the pattern typical of longer-lived molluscs and crustacea, where high initial catches are based on a large and available 'accumulated stock' when fishing begins in a new area, to be followed by steeply declining catches in subsequent years. Initial and subsequent cephalopod catches are far more volatile and dependent on environmental variables.

Among the factors affecting variability of populations, migration generates particularly complex patterns. If the existence of migration is recognized in a population, the temporal and spatial characteristics of the movements achieved by the animals may at least be scrutinized to some extent. There are classic examples of seasonal migration in squids that support large fisheries, entraining whole fishing fleets in corresponding displacements (e.g. Hatanaka 1988). If the occurrence of migration in a species has gone unnoticed, however, the hidden effects of immigration or emigration can greatly upset the interpretation of demographic records, mortality and growth estimations (Caddy 1991; Hatfield & Rodhouse 1994). Horizontal migratory movements that are generally seasonal can overlap with daily vertical migrations, which will be modulated by a more or less important locomotory exploitation of currents at different depths. Currents can provide effective means for either remaining in a given area (by shuttling between depths with currents of opposite direction) or, on the contrary, for covering great distances, especially for small juvenile stages that have a relatively limited swimming capacity. Moreover, pelagic cephalopods often show a directed 'ontogenetic vertical migration' between the depths where the animals hatch from the eggs (that may be neutrally or negatively buoyant) and the depths where advanced juveniles and/or adults live. Vecchione (1987) noted that ontogenetic vertical migration is especially pronounced in species with bathypelagic adults, although it can be found in most groups that have pelagic hatchlings.

Depending on where the eggs are laid, the embryos will have different survival chances despite their generally high protection by egg cases (or by 'brooding' provided by the mother individual in the incirrate octopods). High pollution levels and other man-made changes along many coastlines are a major threat to spawning grounds, especially where eggs are deposited in dense masses that turn easily anoxic when development of fouling organisms combines with reduced water movement (e.g. *Sepia officinalis* in the Mediterranean). A further consequence of the egg laying conditions is that the newly hatched animals undergo different predation pressures, have different opportunities to feed themselves (Villanueva 1994) and run greater or smaller risks from chemical or physical disturbance (e.g. salinity shock, wave action, stranding).

Migratory cycles appear to be more or less closely tuned to the reproductive cycle of the species, often (but not always) in correspondence with seasonal cycles. Many neritic cephalopods migrate shorewards in spring before spawning. However, laboratory cultures have shown that such migratory species as *Sepia officinalis* (Boucaud-Camou & Boismery 1991) become sexually mature and reproduce in captivity, under extremely limited space conditions and under entirely artificial temperature and light conditions (see Boletzky & Hanlon 1983, for a review). Thus, laboratory studies so far provide little or no information about the determining factors of migration. Field studies in turn suggest, for example, that *Sepia officinalis*, whether mature or immature, begin to move inshore after the winter solstice, at the latest around spring equinox. As the low water temperatures at the depths where the animals overwinter are very stable, it is likely that increasing day length provides the necessary trigger. In autumn, however, the offshore migration of maturing and immature individuals is more likely triggered by the first drastic temperature decrease, rather than by decreasing day length (Boucaud-Camou & Boismery 1991). In contrast, the inshore-dwelling phase of *Sepia hierredda* on the north western African coast seems to be limited by the very high summer temperatures, which apparently induce offshore migration in summer (Bakhayokho 1983).

Although it is very widespread across systematic groups, inshore spawning is not general in cephalopods. This is shown by trawling samples taken at various depths that contain cephalopod eggs, including eggs of some species known to *generally* spawn close to shore in spring and summer (Boletzky 1986*b*). In the western Mediterranean, for example, female *Octopus vulgaris* with eggs are occasionally taken at depths down to 85 m, generally in autumn. These individuals have apparently not migrated inshore, perhaps because they have become fully mature during an offshore migration. Hatchlings from such autumn spawns start their planktonic phase in winter, several months earlier than the animals hatched from eggs laid in spring. It is unknown as yet whether this, probably rather small, fraction of the reproductive output of the population forms a cohort sufficiently strong to influence the overall population structure. Conceivably it could have some major compensation effect after thorough disturbance of inshore life conditions has decimated the population.

7. INTERACTIONS OF CEPHALOPOD POPULATIONS

The cephalopod component of the marine biomass depends directly on its food sources. Exclusively predatory, cephalopods of all types seem to be remarkably catholic in their dietary habits, using a wide variety of food sources and opportunistically exploiting the most abundant and available prey, a topic which is fully explored by Rodhouse & Nigmatullin (1996). The high protein quality of cephalopod diet, their exceptionally efficient food conversion rates and their short lifespan suggests that the overall food requirement of the population may not be as great as might be supposed. O'Dor & Wells (1987) estimate that the lifetime food requirement of an octopus may only be 2.5–3 times its final body weight. The more active squid were similarly estimated to need 4–8 times body weight. In common with most aquatic invertebrates, octopuses and cuttlefish survive well in aquarium conditions, although they steadily lose weight in the absence of food (squids do not adapt readily to captivity whether fed or starved). Taken together, these features of cephalopods suggest that for most species absolute numbers in the population are unlikely to be limited by food supplies although growth in biomass may be. If cannibalism has a major role in feeding the larger squid (see previous section), then its effect would be contradictory – tending to increase biomass at the expense of numbers.

Most cephalopods are susceptible to predation at all stages of development from hatching to spawning (figure 1*a*). The quantitative importance of cephalopods in the diets of marine fish, birds, seals and cetaceans (Smale 1996; Croxall & Prince 1996; Klages 1996; Clarke 1996) suggests that they are essential links in the food webs supporting these top predator populations. Just how the cephalopods are so available to predation is not fully understood as in many cases the prey species most prevalent in the diet is hardly caught by research methodology. Clarke (1977), drawing together information on the cephalopod diet of the sperm whale (*Physeter catodon*) with data from research trawls in the same sea area, points out the great differences in species composition and size frequencies of squid in the two sets of data.

The very large quantities of cephalopods estimated to be taken by marine predators, up to two orders of magnitude greater than current commercial catches worldwide, has provided the main line of argument for suggestions that cephalopod populations are capable of providing still greater resources to the human population (Voss 1973); indeed, that they may represent the last major living marine resource capable of significant expansion. The flaw in this argument is that, because of the short lifespan and the lack of evidence for any exploited cephalopods living for more than about 2 years, possibly nearly all of the population falls to predation at some stage of development, continuity of the species being almost totally through the success of the annual reproductive event (however concentrated or spread throughout the year). Any increase in the quantity taken by human fishing activity would, therefore, potentially be at the expense of availability to one of the other predatory populations. Although, as previously pointed out, the major cephalopod groups taken by the large marine vertebrate predators are unlikely to be available to current fishing practice (too deep) and unlikely to be desirable as fished resources (too ammoniacal).

Indirectly, heavy exploitation of certain finfish species may be having a positive effect on the abundance of cephalopods. Caddy (1983) traces the fishing history of the Mauritanian trawl fishery off the Western Sahara. Early exploratory trawl fishing (1940*s*) was dominated by catches of sparid fish with negligible amounts of cephalopods. After several decades of heavy fishing, research trawling showed the proportion of cephalopods in the catch to rise rapidly and progessively to 3% (1962), 36% (1968) and to 90% in 1975 (Pereiro & Bravo de Laguna 1979). Currently almost all of the catch from this still rich fishing area is in the form of *Octopus vulgaris*. Similar changes – an increase in the abundance of cephalopods following years of intensive fishing for demersal fish – have been noted for the Gulf of Thailand (Pauly 1979; but see Chotiyaputta 1993). Caddy (1983) suggests that these changes result from perturbations caused by intensive fishing on the interactions between fish and cephalopods. Mainly, the reduction in the fish biomass has increased food availability to cephalopods and has reduced predation on them. The larger population of cephalopods now exerts increased predation pressure on juvenile fish, tending to maintain a new equilibrium favouring dominance of the cephalopod component over the previously dominant fish, and replacement by shorter-lived species. It is also notable that the cephalopods all have shorter lifespans and generation times than the finfish they appear to replace.

It is suggested that the heavy fishing pressure on the sparids in this ecosystem has caused sufficient perturbation to rebalance its components to a new (alternative and stable?) state now favouring the cephalopods. The concept of multiple stable states in marine ecosystems has been current for some time (Beddington 1984) and there are several examples for which evidence is available to support this interpretation (Paine 1974; Barkai & Branch 1988; Barkai & McQuaid 1988). These ideas are presently untested in a situation involving ecological interactions between cephalopods and fish. If these population responses are really the result of competition and/or predation effects, then they add a new dimension to the views advanced by Packard (1972) in his seminal review of convergent evolution between cephalopods and fish and also to the considerations of O'Dor & Webber (1986).

Based on the FAO fishing catch statistics for cephalopods and demersal fish from all of the major world fishing areas, Caddy (1995) examines the trends in catch rates of both resource categories over a 23-year period, and estimates a groundfish:cephalopod catch ratio for each sector. With some notable exceptions (north east and south east Pacific, where groundfish catches increased faster than cephalopods; Mediterranean, where there were equal catch rates; and the north east Atlantic where the groundfish:cephalopod ratio was anomalously high), in most of the statistical areas cephalopod catch rates were increasing faster than those for groundfish, and the groundfish:cephalopod ratio tended to be lower for areas with a longer history of industrial fishing. Although there is no direct evidence for compensatory changes in the cephalopod population due to fishing pressure on finfish the implication is there in these statistical trends. There are significant weaknesses in this extended and generalized application of a cephalopod/fish interactive model: the growth of the cephalopod catch since the early 1970*s* has been mainly due to the extension of fishing to new areas (south west & north Pacific, south west Atlantic) rather than increased catches from traditional grounds; and the increase has been mostly of oceanic squid species (*Ommastrephes*), shelf edge species (*Nototodarus*) or species migrating over the shelf (*Illex*) and not the typically neritic species (Loliginidae, Sepioidea, Octopoda) which are closely associated with the bottom for feeding and breeding and which might be expected to be interacting most directly with demersal fish.

8. CONCLUDING REMARKS

The study of cephalopod populations currently lacks the means to define populations adequately and to resolve basic systematic confusions. Quantitative data are usually only available from indirect sources such as commercial fisheries and from estimates of consumption by higher predators. Despite these methodological difficulties it is clear that cephalopods comprise a major component of biomass globally, throughout all fully marine habitats.

Life-cycle characteristics common to the coleoids – early and/or semelparous breeding, rapid growth, short lifespan, little overlap of generations, vulnerability to predation and environmental variables – result in wide inter-annual fluctuations in abundance. Most of the pelagic forms also undertake large- or meso-scale migrations which, coupled to shifting patterns of oceanographic variables, contribute to the unpredictability of distribution and density associated with many cephalopod species.

Temporal and spatial patterns of breeding, seasonality, growth, recruitment and mortality are clearly evident in most of the better-studied species. But exceptions to pattern (e.g. variable growth rates, extended breeding, complex recruitment) also seem to be important intrinsic characteristics. Levels of genetic variation in cephalopods are relatively low, and their population dynamics appear to be influenced principally by phenotypic plasticity in response to environmental variability. In such universally short-lived species the maintenance of this diversity balances the risks of mortality factors combining at any one time to cause periodic local extinction.

The extent and scale of the interactions between cephalopod populations and other trophic levels suggests that major ecological perturbations such as environmental shifts or imposed effects such as commercial fishing, whether directed at cephalopods or other species, are likely to have an impact on their populations. As short-lived species with high turnover of generations, plastic growth and reproductive characteristics, high mobility and catholic predatory habits, they are always poised to respond to changed balances in their environment.

Studies on cephalopod populations have expanded considerably in numbers and scope in the last 25 years, driven by increased interest in and recognition of their roles in the marine ecology as well as their increasing value as globally exploited resources. Despite these recent advances, the information and concepts arising from their study is only slowly entering mainstream biological thought and becoming accommodated in broad-scale models of the marine ecosystem.

We wish to thank the many colleagues with whom these ideas have been discussed but especially Dr John Caddy (FAO, Rome), Dr Graham Pierce (University of Aberdeen, Scotland), Dr Paul Rodhouse (BAS, Cambridge) and Dr Malcolm Smale (Port Elizabeth Museum, South Africa) for their critical and constructive comments on our draft manuscript. Professor Malcolm Clarke has provided much encouragement and many suggestions for the content.

REFERENCES

Allmon, W. D. 1992 A causal analysis of stages in allopatric speciation. In *Oxford Surveys in Evolutionary Biology* vol. 8 (ed. D. Futuyma & J. Antonovics), pp. 219–257. Oxford University Press.

Ally, J. R. R. & Keck, S. A. 1978 A biochemical – genetic population structure study of market squid, *Loligo opalescens*, along the California coast. *Cal. Dept. Fish & Game, Fish Bull.* **169**, 113–121.

Altman, J. S. 1966–67 The behaviour of *Octopus vulgaris* Lam. in its natural habitat: a pilot study. *Underwat. Ass. Rep.* **1966–67**, 77–83.

Araya, H. 1976 Migration and fishing ground of winter subpopulation of the squid, *Todarodes pacificus* Steenstrup, in the northern waters of Japan. *Bull. Hokkaido Reg. fish. res. Lab.* **41**, 119–129.

Arkhipkin, A. I., Loktidnov, Y. A. & Shchetinnikov, A. S. 1988 Environmental conditions for the formation of local mesoscale concentrations of the squid *Sthenoteuthis pteropus* in the Western Gulf of Guinea. *Oceanology* **28**, 106–110.

Arkhipkin, A & Laptikhovsky, V. 1994 Seasonal and interannual variability in growth and maturation of winter spawning *Illex argentinus* (Cephalopoda, Ommastrephidae) in the Southwest Atlantic. *Aquat. Living Resour.* **7**, 221–232.

Augustyn, C. J. 1990 Biological studies on the chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. *S. Afr. J. mar. Sci.* **9**, 11–26.

Augustyn, C. J. & Grant, W. S. 1988 Biochemical and morphological systematics of *Loligo vulgaris vulgaris* Lamarck and *Loligo vulgaris reynaudii* d'Orbigny *Nov. Comb.* (Cephalopoda: Myopsida). *Malacologia*, **29** 215–233.

Augustyn, C. J., Roel, B. A. & Cochrane, K. L. 1993 Stock assessment in the chokka squid *Loligo vulgaris reynaudii* fishery off the coast of South Africa. In *Recent Advances in Cephalopod Fisheries Biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 3–14. Tokyo: Tokai University Press.

Ax, P. 1987 *The phylogenetic system: the systemization of organisms on the basis of their phylogenesis*. Chichester: John Wiley & Sons.

Bakhayokho, M. 1983 Biology of the cuttlefish *Sepia officinalis hierredda* off the Senegalese coast. In *Advances in Assessment of World Cephalopod Resources* (ed. J. F. Caddy). FAO Fisheries Technical Paper **231**, 204–263.

Barkai, A. & Branch, G. M. 1988 The influence of predation and substratal complexity on recruitment to settlement plates: a test of the theory of alternative states. *J. exp. mar. Biol. Ecol.* **124**, 215–237.

Barkai, A. & McQuaid, C. D. 1988 Reversals of predator-prey roles in a marine benthic ecosystem. *Science* **242**, 62–64.

Beddington, J. R. 1984 The response of multispecies systems to perturbations. In *Exploitaton of Marine Communities* (ed. R. M. May), pp. 209–225. *Dahlem workshop reports: Life Sciences research report*, **32**. Berlin: Springer Verlag.

Beddington, J. R., Rosenberg, A. A., Crombie, J. A. & Kirkwood, G. P. 1990 Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. *Fish. Res.* **8**, 351–365.

Boletzky, S. v. 1974 The 'larvae' of Cephalopoda: a review. *Thal. Jugosl.* **10**, 45–76.

Boletzky, S. v. 1981 Réflexions sur les stratégies de reproduction chez les céphalopodes. *Bull. Soc. zool. Fr.*, **106**, 293–304.

Boletzky, S. v. 1986*a* Reproductive strategies in cephalopods: variation and flexibility of life-history patterns. In *Advances in invertebrate reproduction* (ed. M. Porchet, J. C. Andries & A. Dhainaut), pp. 379–389. Amsterdam: Elsevier Science Publishers.

Boletzky, S. v. 1986*b* Encapsulation of cephalopod embryos: a search for functional correlations. *Amer. Malacol. Bull.* **4**, 217–227.

Boletzky, S. v., & Hanlon, R. T. 1983 A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *Mem. Nat. Mus. Victoria* **44**, 147–187.

Bonnaud, L., Boucher-Rodoni, R. & Monnert, M. 1994 Phylogeny of decapod cephalopods based on partial 16S rDNA nucleotide sequences. *C.r. Acad. Sci., Paris, Sciences de la vie/Life Sciences* **317**, 581–588.

Boucaud-Camou, E. & Boismery, J. 1991 The migrations of the cuttlefish (*Sepia officinalis*) in the English Channel. In *The Cuttlefish* (ed. E. Boucaud), pp. 179–189. Caen: Univ. Caen Documentation Center.

Boucher-Rodoni, R., Martin, M. & Peduzzi, R. 1995 Preliminary results of a comparative study of cephalopod eye-lens proteins: the sepiolids. *Bull. Inst. oceanogr. Monaco* **16** (Special), 93–98.

Bower, S. M. & Margolis, L. 1990 Potential use of helminth parasites in stock identification of flying squid, *Ommastrephes bartrami*, in North Pacific waters. *Can. J. Zool.* **69**, 1124–1126.

Boyle, P. R. 1990 Cephalopod biology in the fisheries context. *Fish. Res.* **8** 303–321.

Boyle, P. R., Mangold, K. & Ngoile, M. 1988 Biological variation in *Eledone cirrhosa* (Cephalopoda: Octopoda): simultaneous comparison of North Sea and Mediterranean populations. *Malacologia* **29**, 77–87.

Boyle, P. R. & Ngoile, M. A. K. 1993 Population variation and growth in *Loligo forbesi* (Cephalopoda: Loliginidae) from Scottish waters. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 49–59. Tokyo: Tokai University Press.

Boyle, P. R. & Pierce, G. J. (eds) 1994 Fishery biology of northeast Atlantic squid. *Fish. Res.* **21**, 1–314.

Boyle, P. R., Pierce, G. J. & Hastie, L. C. 1995 Flexible reproductive strategies in the squid *Loligo forbesi*. *Mar. Biol.* **121**, 501–508.

Bravo de Laguna, J. 1989 Managing an international multispecies fishery: the saharan trawl fishery for cephalopods. In *Marine invertebrate fisheries: their assessment and management* (ed. J. F. Caddy), pp. 591–612. New York: John Wiley & Sons.

Brierley, A. S., Rodhouse, G. G., Thorpe, J. P. & Clarke, M. R. 1993*a* Genetic evidence of population heterogeneity and cryptic speciation in the ommastrephid squid *Martialia hyadesi* from the Patagonian Shelf and Antarctic Polar Frontal Zone. *Mar. Biol.* **116**, 593–602.

Brierley, A. S., Thorpe, J. P., Clarke, M. R. & Martins, H. R. 1993*b* A preliminary biochemical genetic investigation of the population structure of *Loligo forbesi* Steenstrup, 1856 from the British Isles and the Azores. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 61–69. Tokyo: Tokai University Press.

Brierley, A. S., Thorpe, J., Pierce, G. J., Clarke, M. R. & Boyle, P. R. 1995 Genetic variation in the neritic squid *Loligo forbesi* (Myopsida: Loliginidae) in the northeast Atlantic Ocean. *Mar. Biol.* **122**, 79–86.

Brodziak, J. K. T. & Rosenberg, A. A. 1993 A method to assess squid fisheries in the north-west Atlantic. *ICES J. mar. Sci.* **50**, 187–194.

Caddy, J. F. 1983 The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In *Advances in assessment of world cephalopod resources* (ed. J. F. Caddy), pp. 416–452. *FAO Fish. Tech. Pap.* **231**. Rome: FAO.

Caddy, J. F. 1991 Daily rings on squid statoliths: an opportunity to test standard population models? In *Squid age determination using statoliths* (ed. P. Jereb, S. Ragonese & S. v. Boletzky), pp. 53–66. Mazara del Vallo: N. T. R.-I. T. P. P. special publication **1**.

Caddy, J. F. 1995 Cephalopods and demersal finfish stocks: some statistical trends and biological interactions. In *Squid 94 Venice. The 3rd International Cephalopod Trade Conference Proceedings*. London: Agra Europe.

Carvalho, G. R. & Loney, K. H. 1989 Biochemical genetic studies on the Patagonian squid *Loligo gahi* d'Orbigny. I. Electrophoretic survey of genetic variability. *J. exp. mar. Biol. Ecol.* **126**, 231–241.

Carvalho, G. R. & Pitcher, T. J. 1989 Biochemical genetic studies on the Patagonian squid *Loligo gahi* d'Orbigny. II. Population structure in Falkland waters using isozymes, morphometrics and life history data. *J. exp. mar. Biol. Ecol.* **126**, 243–258.

Carvalho, G. R., Thompson, A. & Stoner, A. L. 1992 Genetic diversity and population differentiation of the shortfin squid *Illex argentinus* in the south-west Atlantic. *J. exp. mar. Biol. Ecol.* **158**, 105–121.

Chotiyaputta, C. 1993 Cephalopod resources of Thailand. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 71–80. Tokyo: Tokai University Press.

Clarke, M. R. 1962*a* Significance of cephalopod beaks. *Nature, Lond.* **193**, 560–561.

Clarke, M. R. 1962*b* The identification of cephalopod 'beaks' and the relationship between beak size and total body weight. *Bull. Br. Mus. nat. Hist. (Zool.)* **8**, 419–480.

Clarke, M. R. 1977 Beaks, nets and numbers. *Symp. zool. Soc., Lond.* **38**, 89–126.

Clarke, M. R. 1983 Cephalopod biomass – estimation from predation. *Mem. Nat. Mus., Aust.* **44**, 95–107.

Clarke, M. R. 1986 *A handbook for the identification of cephalopod beaks.* Oxford: Clarendon Press.

Clarke, M. R. 1996 Cephalopods as prey. III. Cetaceans. *Phil. Trans. R. Soc. Lond.* B **351**, 1051–1063.

Coelho, M. L. & O'Dor, R. K. 1993 Maturation, spawning patterns and mean size at maturity in the short-finned squid *Illex illecebrosus*. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 81–91. Tokyo: Tokai University Press.

Coelho, M. L., Stobberup, K. A., O'Dor, R. & Dawe, E. G. 1994 Life history strategies of the squid, *Illex illecebrosus*, in the Northwest Atlantic. *Aquat. Living Resour.* **7**, 233–246.

Croxall, J. & Prince, P. A. 1996 Cephalopods as prey. I. Seabirds. *Phil. Trans. R. Soc. Lond.* B **351**, 1021–1041.

Dunning, M. C. 1993 Summer populations of *Ommastrephes bartramii* (Lesueur, 1821) and *Todarodes filippovae* Adam, 1975 (Cephalopoda: Ommastrephidae) from the Tasman Sea. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 97–118. Tokyo: Tokai University Press.

Ehrhardt, N. M., Jacquemin, P. S., Garcia, F. B. *et al.* 1983 On the fishery and biology of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico. In *Advances in assessment of the world cephalopod resources* (ed. J. F.Caddy), pp. 306–340. *FAO Fish. Tech. Pap.* **231**. Rome: FAO

Fields, W. G. 1965 The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. *Dept. Fish & Game, Fish. Bull.* **131**, 1–108.

Fogarty, M. J. 1989 Forecasting yield and abundance of exploited invertebrates. In *Marine invertebrate fisheries: their assessment and management* (ed. J. F. Caddy), pp. 701–724. New York: John Wiley & Sons.

Food and Agriculture Organisation (FAO) 1990 *Yearbook: catches and landings*, vol 72. Rome: FAO.

Food and Agriculture Organisation (FAO) 1992 *Yearbook: catches and landings*, vol 74. Rome: FAO.

Forsythe, J. W. 1993 A working hypothesis on how seasonal temperature change may impact the field growth of young cephalopods. In *Recent advances in cephalopod fisheries biology* (eds T. Okutani, R. K. O'Dor & T. Kubodera), pp. 133–143. Tokyo: Tokai University Press.

Forsythe, J. W. & Van Heukelem, W. F. 1987 Growth. In *Cephalopod life cycles*, vol. II (ed. P. R. Boyle), pp. 135–156. London: Academic Press.

Gabel-Deickert, A. 1995 Reproductive patterns in *Sepiola affinis* and other Sepiolidae (Mollusca, Cephalopoda). *Bull. Inst. oceanogr. Monaco*, **16** (Special), 73–83.

Garcia, S. 1989 The management of coastal penaeid shrimp fisheries. In *Marine invertebrate fisheries: their assessment and management* (ed. J. F. Caddy), pp. 281–306. New York: John Wiley & Sons.

Garthwaite, R. L., Berg, C. J. Jr. & Harrigan, J. 1989 Population genetics of the common squid *Loligo pealei* LeSeur, 1821, from Cape Cod to Cape Hatteras. *Biol. Bull. mar. biol. Lab., Woods Hole* **177**, 287–294.

Globefish 1994 World production and trade in cephalopods (1980–93). Statistical survey. *GLOBEFISH Research Programme*, **34**.

Hanlon, R. T. 1988 Behavioural and body patterning characters usefulin taxonomy and field identification of cephalopods. *Malacologia* **29**, 247–264.

Harman, R. E., Young, R. E., Reid, S. B., Mangold, K. M., Suzuki, T. & Hixon, R. F. 1989 Evidence for multiple spawning in the tropical oceanic squid *Stenoteuthis oualeniensis* (Teuthoidea: Omastrephidae). *Mar. Biol.* **101**, 513–519.

Hatanaka, H. 1988 Feeding migration of short-finned squid *Illex argentinus* in the waters off Argentina. *Nippon Suisan Gakkaishi* **54**, 1343–1349.

Hatanaka, H., Kawakara, S., Uozumi, Y. & Kasahara, S. 1984 Comparison of life cycles of five ommastrephid squids fished by Japan: *Todarodes pacificus*, *Illex illecebrosus*, *Illex argentinus*, *Nototodarus sloani sloani*, *Nototodarus sloani gouldi*. *NAFO Sci. Coun. Studies* **9**, 59–68.

Hatfield, E. M. C. & Rodhouse, P. G. 1991 Biology and fishery of the Patagonian squid *Loligo gahi* (d'Orbigny, 1835): a review of current knowledge. *J. Ceph. Biol.* **2**, 41–79.

Hatfield, E. M. C. & Rodhouse, P. G. 1994 Migration as a source of bias in the measurement of cephalopod growth. *Antarctic Sci.* **6**, 179–184.

Hilborn, R. & Walters, C. J. 1992 *Quantitative fisheries stock assessment: choice, dynamics & uncertainty.* New York: Routledge, Chapman & Hall Inc.

Hixon, R. F. 1983 *Loligo opalescens*. In *Cephalopod life cycles*, vol. I (ed. P. R. Boyle), pp. 95–114. London: Academic Press.

Hochberg, F. G. 1980 Cephalopoda: the squids and octopuses. In *Intertidal invertebrates of California* (ed. R. H. Morris, D. P. Abbott & E. C. Haderlie), pp. 429–444. Stanford University Press.

Ito, J., Shaw, W. & Burgner, R. L. (eds) 1993 Symposium on biology, distribution and stock assessment of species caught in the high seas driftnet fisheries in the North Pacific Ocean. *INPFC Bull.* **53**, 1–576.

Jackson, G. D. 1992 Seasonal abundance of the small tropical sepioid *Idiosepius pygmaeus* (Cephalopoda: Idiosepiidae) at two localities off Townsville, North Queensland, Australia. *The Veliger* **35**, 396–401.

Jereb, P., Ragonese, S. & Boletzky, S. v. (eds) 1991 *Squid age determination using statoliths.* Mazara del Vallo: N. T. R.-I. T. P. P. Special publication, vol. 1, pp. 1–127

Jones, J. B. 1992 Environmental impact of trawling on the seabed: a review. *N.Z. J. mar. Freshwat. Res.* **26**, 59–67.

Kashiwada, J. & Recksiek, C. W. 1978 Possible morphological indicators of population structure in the market squid, *Loligo opalescens*. *Cal. Dept. Fish & Game, Fish Bull.* **169**, 99–111.

Katugin, O. N. 1993 Genetic variation in the squid *Berryteuthis magister* (Berry, 1913) (Oegopsida: Gonatidae). In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 201–213. Tokyo: Tokai University Press.

Khromov, D. N., Lu, C. C., Guerra, A., Dong, Z. H. & Boletzky, S. v. 1996 A synopsis of Sepiidae outside Australian waters (Cephalopoda: Sepioidea). *Smiths. Contr. Zool.* (In the press.)

Kirkendall, L. R. & Steneth, N. C. 1985 On defining 'breeding once'. *Am. Nat.* **125**, 89–204.

Klages, N. T. W. 1996 Cephalopods as prey. II. Seals. *Phil. Trans. R. Soc. Lond.* B **351**, 1043–1050.

Klima, E. F. 1989 Approaches to research and management of U.S. fisheries for penaeid shrimp in the Gulf of Mexico. In *Marine invertebrate fisheries: their assessment and management* (ed. J. F. Caddy), pp. 87–113. New York: John Wiley & Sons.

LeGoff, R. & Daguzan, J. 1991 Growth and life cycles of the cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) in South Brittany (France). *Bull. mar. Sci.* **49**, 341–348.

Lewis, A. R. & Choat, J. H. 1993 Spawning mode and reproductive output of the tropical cephalopod *Idiosepius pygmaeus*. *Can. J. Fish. Aquat. Sci.* **50**, 20–28.

MacArthur, R. H. & Wilson, E. O. 1967 *Theory of island biogeography.* Princeton University Press.

Mangold, K. 1983 *Octopus vulgaris*. In *Cephalopod life cycles*, vol. I (ed. P. R. Boyle), pp. 335–364. London: Academic Press.

Mangold, K. & Hochberg, F. G. 1991 Defining the Genus *Octopus*: redescription of *Octopus vulgaris*. *Bull. mar. Sci.* **49**, 665.

Mangold, K. M., Young, R. E. & Nixon, M. 1993 Growth versus maturation in cephalopods. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 697–703. Tokyo: Tokai University Press.

May, R. M. (ed.) 1984 Exploitation of marine communities. In *Dahlem workshop reports: life sciences research report*, vol 32. Berlin: Springer Verlag.

Mayr, E. 1970 *Populations, species and evolution*. Cambridge: Harvard University Press.

McInnis, R. R. & Broenkow, W. W. 1978 Correlations between squid catches and oceanographic conditions in Monterey Bay, California. *Cal. Dept. Fish & Game, Fish Bull.* **169**, 161–170.

Mesnil, B. 1977 Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic. *ICNAF Sel. Papers* **2**, 55–69.

Murata, M. 1989 Population assessment, management and fishery forecasting for the japanese common squid, *Todarodes pacificus*. In *Marine invertebrate fisheries: their assessment and management* (ed. J. F. Caddy), pp. 613–636. New York: John Wiley & Sons.

Murata, M. 1990 Oceanic resources of squids. *Mar. behav. Physiol.* **18**, 19–71.

Naef, A. 1923 Die Cephalopoden. *Fauna Flora Golf Neapel.* **35**. (Monograph I/1.)

Natsukari, Y., Nakanose, T. & Oda, K. 1988 Age and growth of the loliginid squid *Photololigo edulis* (Hoyle, 1885). *J. exp. mar. Biol. Ecol.* **116**, 177–190.

Nesis, K. N. 1983 Dosidicus gigas. In *Cephalopod life cycles*, vol. I (ed. P. R. Boyle), pp. 215–231. London: Academic Press.

Nesis, K. N. 1987 *Cephalopods of the world*. Original Russian Edition, 1982, V.A.A.P. Copyright Agency of the USSR for Light and Food Industry Publishing House, Moscow. English translation, United States of America: T. F.H Publications, Inc., Ltd.

Nesis, K. N. 1993*a* Cephalopods of seamounts and submarine ridges. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 365–383. Tokyo: Tokai University Press.

Nesis, K. N. 1993*b* Population structure of oceanic ommastrephids, with particular reference to *Sthenoteuthis oualaniensis*: a review. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 375–383. Tokyo: Tokai University Press.

Nishiguchi, M. K., Ruby, E. G. & Mcfall-Ngai, M. J. 1995 Coevolution in a squid-luminous bacterium symbiosis; differentiation of sepiolid squids and their symbionts by molecular systematics and bacterial colonization. *Abstr. 12th Intern. malacol. Congr., Vigo.* 1995 (ed. A. Guerra, E. Rolan & F. Rocha), p. 316.

Norman, M. D. 1992*a* *Ameloctopus litoralis*, gen. et sp. nov. (Cephalopoda: Octopodidae), a new shallow-water octopus from tropical Australian waters. *Invertebr. Taxon.* **6**, 567–582.

Norman, M. D. 1992*b* Four new octopus species of the *Octopus macropus* group (Cephalopoda: Octopodidae) from the Great Barrier Reef, Australia. *Mem. Mus. Vict.* **53**, 267–308.

Norman, M. D. 1992*c* Ocellate octopuses (Cephalopoda: Octopodidae) of the Great Barrier Reef, Australia: description of two new species and redescription of *Octopus polyzenia* Gray, 1949. *Mem. Mus. Vict.* **53**, 309–344.

O'Dor, R. K. 1983 *Illex illecebrosus*. In *Cephalopod life cycles*, vol. I (ed. P. R. Boyle), pp. 175–199. London: Academic Press.

O'Dor, R. K. 1988 The energetic limits on squid distributions. *Malacologia* **28**, 113–119.

O'Dor, R. K., Durward, R. D. & Balch, N. 1977 Maintenance and maturation of squid (*Illex illecebrosus*) in a 15 metre circular pool. *Biol. Bull.* **153**, 322–335.

O'Dor, R. K., Durward, R. D., Vessey, E. & Amaratunga, T. 1980 Feeding and growth in captive squid, *Illex illecebrosus*, and the influences of food availability on growth in the natural population. *ICNAF Sel. Pap.* **6**, 15–21.

O'Dor, R. K. & Balch, N. 1985 Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. *NAFO Sci. Coun. Studies* **9**, 69–76.

O'Dor, R. K. & Webber, D. M. 1986 The constraints on cephalopods: why squid aren't fish. *Can. J. Zool.* **64**, 1591–1605.

O'Dor, R. K. & Wells, M. J. 1987 Energy and nutrient flow. In *Cephalopod life cycles*, vol. II (ed. P. R. Boyle), pp. 109–133. London: Academic Press.

O'Dor, R. K. & Coelho, M. L. 1993 Big squid, big currents, and big fisheries. In *Recent advances in cephalopod fisheries biology* (eds T. Okutani, R. K. O'Dor & T. Kubodera), pp. 385–396. Tokyo: Tokai University Press.

Ogawa, Y., Moriwaki, S., Yamada, H. & Okajima, Y. 1983 Migration patterns of *Loligo edulis* estimated from a joint tagging programme conducted by four prefectrues in the southwestern Japan Sea. *Coop. Invest. 'Shiro-ika'*, L. edulis *inhabiting western Japan Sea* **1**, 65–96.

Okutani, T. 1977 Stock assessment of cephalopod resources fished by Japan. *FAO Fish. Tech. Pap.* **173**.

Okutani, T. 1983 *Todarodes pacificus*. In *Cephalopod life cycles*, vol. I (ed. P. R. Boyle), pp. 201–214. London: Academic Press.

Okutani, T. 1990 Squids, cuttlefish and octopuses. *Mar. behav. Physiol.* **18**, 1–18.

Okutani, T. 1995 *Cuttlefish and squids of the world in color*. Tokyo: Natl. Cooperative Ass. Squid Processors.

Okutani, T. & Takayama, K. 1991 The *Sepiola parva* and *S. birostrata* Problem. *Bull. mar. Sci.* **49**, 666.

Orsi Relini, L. & Bertuletti, M. 1989 Sepiolidae (Mollusca, Cephalopoda) from the Ligurian Sea. *Vie Milieu* **39**, 183–190.

Osaka, M. & Murata, M 1983 Stock assessment of cephalopod resources in the northwestern Pacific. In *Advances in assessment of world cephalopod resources* (ed. J. F. Caddy), pp. 55–82. FAO Fish. Tech. Pap., vol. 231. Rome: FAO.

Packard, A. 1972 Cephalopods and fish: the limits of convergence. *Biol. Rev. Cambridge Philos. Soc.* **47**, 241–307.

Paine, R. T. 1974 Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* **15**, 93–120.

Pauly, D. 1979 Theory and management of tropical multispecies stocks: a review with emphasis on the Southeast Asian demersal fisheries. *ICLARM Stud. Rev.* 1.

Pauly, D. 1985 Population dynamics of short-lived species, with emphasis on squids. *NAFO Sci. Coun. Stud.* **9**, 143–154.

Pereiro, J. A. & Bravo de Laguna, J. 1979 Dinámica de la población y evaluación de los recursos del pulpo del Atlantíco centro-oriental. *Bol. Inst. Esp. Oceanogr.* **5**, 71–105.

Perez-Losada, M., Guerra, A. & Sanjuan, A. 1995 Allozyme electrophoretic technique and phylogenetic relationships in three species of *Sepia* (Cephalopoda: Sepiidae). *Comp. Biochem. Physiol.* (In the press.)

Pierce, G. J. 1995 Stock assessment with a thermometer: correlations between sea surface temperature and landings of squid (*Loligo forbesi*) in Scotland. ICES CM 1995/K **21**.

Pierce, G. J., Boyle, P. R., Hastie, L. C. & Key, L. 1994*a* The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fish. Res.* **21**, 17–41.

Pierce, G. J., Hastie, L. C., Guerra, A., Thorpe, R. S., Howard, F. G. & Boyle, P. R. 1994*b* Morphometric variation in *Loligo forbesi* and *Loligo vulgaris*: regional, seasonal, sex, maturity and worker differences. *Fish. Res.* **21**, 127–148.

Pierce, G. J., Boyle, P. R., Hastie, L. C. & Shanks, A. M. 1994*c* Distribution and abundance of the fished population of *Loligo forbesi* in UK waters: analysis of fishery data. *Fish. Res.* **21**, 193–216.

Pierce, G. J., Thorpe, R. S., Hastie, L. C. *et al.* 1994*d* Geographic variation in *Loligo forbesi* in the northeast Atlantic. *Mar. Biol.* **119**, 541–547.

Pierce, G. J. & Guerra, A. 1994 Stock assessment methods used for cephalopod fisheries. *Fish. Res.* **21**, 255–285.

Pierce, G. J. & Santos, M. B. 1996 Trophic interactions of squid in Scottish waters. *Proc. Roy. Soc. Edin.* (In the press.)

Rasero, M. 1994 Relationship between cephalopod abundance and upwelling: the case of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Galician waters (NW Spain). ICES CM 1994/K **20**.

Rathjen, W. F. & Voss, G. L. 1987 The cephalopod fisheries: a review. In *Cephalopod life cycles*, vol. II (ed. P. R. Boyle), pp. 253–275. London: Academic Press.

Richard, A. 1971 Contribution – l'étude expérimentale de la croissance et de la maturation sexuelle de *Sepia officinalis* L. (Mollusque, Céphalopode). Thèse de Doctorat d'âtat, Université de Lille (No.243).

Richardson, B. J. 1983 Protein variation in *Notodarus gouldi* from southeastern Ausralia. *Mem. Natl Mus. Victoria* **44**, 199–203.

Roberts, M. J. & Sauer, W. H. H. 1994 Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery? *Ant. Sci.* **6**, 249–258.

Rochebrune, A. T. de 1884 Etude monographique de la famille des Sepiadae. *Bull. Sci. Soc. Philom. Paris* **7**, 74–122.

Rodaniche, A. D. 1984 Iteroparity in the lesser striped octopus *Octopus chierchiae* (Jatta, 1889). *Bull. mar. Sci.* **35**, 99–104.

Rodhouse, P. G. & Hatfield, E. M. C. 1990 Dynamics of growth and maturation in the cephalopod *Illex argentinus* Decastellanos, 1960 (Teuthoidea, Ommastrephidae). *Phil. Trans. R. Soc. Lond.* **329**, 229–242.

Rodhouse, P. G., Croxall, J. P. & Prince, P. A. 1993 Towards an assessment of the stock of the ommastrephid squid *Martialia hyadesi* in the Scotia Sea: data from predators. In *Recent advances in cephalopod fisheries biology* (eds T. Okutani, R. K. O'Dor & T. Kubodera), pp. 433–440. Tokyo: Tokai University Press.

Rodhouse, P. G. & Nigmatullin, C. 1996 Cephalopods: role as consumers. *Phil. Trans. R. Soc. Lond.* B **351**, 1003–1022.

Rodhouse, P. G., Dawe, E. G. & O'Dor, R. K. (eds) 1996 *Squid recruitment dynamics*. Rome: FAO (In the press.)

Roper, C. F. E., Sweeney, M. J. & Nauen, C. E. 1984 FAO species catalogue, vol 3. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fish. Synop.* **125**. Rome: FAO.

Roper, C. F. E. & Hochberg, F. G. 1988 Behaviour and systematics of cephalopods from Lizard Island, Australia, based on colour and body patterns. *Malacologia* **29**, 153–193.

Rosenberg, A. A., Kirkwood, G. P., Crombie, J. A. & Beddington, J. R. 1990 The assessment of stocks of annual squid species. *Fish. Res.* **8**, 335–350.

Sahrhage, D. 1989 Antarctic krill fisheries: potential resources and ecological concerns. In *Marine invertebrate fisheries: their assessment and management* (ed. J. F. Caddy), pp. 13–33. New York: John Wiley & Sons.

Sanders, M. J. 1979 Preliminary stock assessmant for the cuttlefish *Sepia pharaonis* taken off the coast of the People's Democratic Republic of Yemen. *FAO RAB*/77/008.

Sauer, W. H. H., Smale, M. J. & Lipinski, M. R. 1992 The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape Coast, South Africa. *Mar. Biol.* **114**, 97–107.

Sauer, W. H. H. & Smale, M. J. 1993 Spawning behaviour of *Loligo vulgaris reynaudii* in shallow coastal waters off the south-eastern Cape, South Africa. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 489–498. Tokyo: Tokai University Press.

Schwerdtfeger, F. 1978 *Lehrbuch der Tieroekologie*. Hamburg & Berlin: Verlag Paul Parey.

Segawa, S., Hirayama, S. & Okutani, T. 1993 Is *Sepioteuthis lessoniana* in Okinawa a single species? In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 513–521. Tokyo: Tokai University Press.

Sinclair, M. 1988 *Marine populations: an essay on population regulation and speciation*. Seattle, London: University of Washington Press.

Smale, M. J. 1996 Cephalopods as prey. IV. Fishes. *Phil. Trans. Roy. Soc. Lond.* B **351**, 1065–1079.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.

Summers, W. C. 1983 *Loligo pealei*. In *Cephalopod life cycles*, vol. I (ed. P. R. Boyle), pp. 115–142. London: Academic Press.

Suzuki, H., Ichikawa, M. & Matsumoto, G. 1993 Genetic approach for elucidation of squid family. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 531–535. Tokyo: Tokai University Press.

Suzuki, T. 1990 Japanese common squid – *Todarodes pacificus* Steenstrup. *Mar. behav. Physiol.* **18**, 73–110.

Takeda, R. 1990 Octopus resources. *Mar. behav. Physiol.* **18**, 111–148.

Tranvouez, Y. & Boucher-Rodoni, R. 1990 Eye lens SDS-Page electrophoresis and the systematics of cephalopods. *Cah. Biol. Mar.* **31**, 281–289.

Vecchione, M. 1987 Juvenile ecology. In *Cephalopod life cycles*, vol. II (ed. P. R. Boyle), pp. 61–84. London: Academic Press.

Villanueva, R. 1994 Decapod crab zoeae as food for rearing cephalopod paralarvae. *Aquaculture* **128**, 143–152.

Voss, G. L. 1973 Cephalopod resources of the world. *FAO Fish. Circ.* **149**, 1–75.

Voss, G. L. 1974 On the absence of cuttlefish in the western Atlantic. *The Veliger* **16**, 367–369.

Voss, G. L. 1977 Present status and new trends in cephalopod systematics. *Symp. zool. Soc. Lond.* **38**, 49–60.

Voss, G. L. 1983 A review of cephalopod fisheries biology. *Mem. Nat. Mus. Victoria* 44, 229–241.

Wells, M. J. & Clark, A. 1996 Energetics: the costs of living and reproducing. *Phil. Trans. R. Soc. Lond.* B **351**, 1081–1102.

Yarnall, J. L. 1969 Aspects of the behaviour of *Octopus cyanea* Gray. *Anim. Behav.* **17**, 747–754.

Yeatman, J. M. & Benzie, J. A. H. 1993 Cryptic speciation in *Loligo* from Northern Australia. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 641–652. Tokyo: Tokai University Press.

Young, R. E. 1978 Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. *Fish. Bull.* **76**, 583–615.

Young, R. E. & Harman, R. F. 1988 'Larva', 'paralarva' and 'subadult' in cephalopod terminology. *Malacologia* **29**, 201–207.

Zuev, G. V. & Nikolsky, V. N. 1993 Ecological mechanisms related to intraspecific structure of the nektonic squid *Sthenoteuthis pteropus* (Steenstrup). In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 653–664. Tokyo: Tokai University Press.