

TREATISE ONLINE

Number 23

Part M, Chapter 7:

Ecology and Mode of Life

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2011

KU PALEONTOLOGICAL
INSTITUTE

The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012 (online)
paleo.ku.edu/treatiseonline

PART M, CHAPTER 7: ECOLOGY AND MODE OF LIFE

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INTRODUCTION

Ecology is concerned with the relationships of living organisms to their surroundings, their habits, and their modes of life. The ecology of Recent coleoids is poorly known, and observations of their habits in relation to habitats is made difficult because many species are highly mobile, moving rapidly through considerable depths and even to more than one region of the marine environment (HEDGPETH, 1957) (Fig. 1). Each species has a living space defined by a unique complex of external factors forming its environment in the sea. Abiotic factors include salinity, temperature, pressure, oxygen tension, light intensity, currents, turbulence, water masses, sedimentary conditions, and seasonality; biotic factors include productivity and the availability of suitable prey, competition, predation, and migration. Changes in some or many of these factors may be encountered during the lifespan of a coleoid, and some of them even in a single day, by pelagic species that are capable of traversing considerable horizontal or vertical distances in a relatively short time. Other species are more restricted, as they remain largely in one region and in similar habitats throughout the life cycle. There are descriptions of the habitats and habits for a few, mostly shallow-living, coastal forms; only rarely are details included of the substrate, habitat, or associated plants and animals; quantitative data are even more scarce. Records from underwater cameras and submersibles are beginning to provide fascinating glimpses of the habits of nektonic and oceanic coleoids in their natural habitat. Indicative of the paucity of ecological studies is the scarcity of reviews on the subject (CLARKE, 1966; VECCHIONE, 1987).

Changes in habits during the lifespan of aquatic organisms were first recognized in 1828, when microscopic animals collected in a fine net bag towed behind a boat were identified as the young stages of otherwise bottom-living animals (HARDY, 1956). DARWIN (1840, p. 189) noted on December 6th, 1833, during his voyage on the *Beagle*, "I often towed astern a net made of bunting and thus caught many curious animals." A dredge appears to have first been used for obtaining marine organisms from shallow waters in the middle of the eighteenth century, and by the early nineteenth century the results from dredging along the coasts of Europe had been published (MURRAY & HJORT, 1912). Specimens dredged from the Aegean Sea in 1840 and 1841 showed each depth zone to be characterized by a special assemblage of species; their numbers apparently diminished with increasing depth to about 600 m, beyond which it was considered that no life existed (HARDY, 1956). Later expeditions found life to be abundant at much greater depths (THOMSON, 1877), and, in 1860, a telegraph cable 65 km long was raised from the bed of the Mediterranean Sea with attached mollusks, bryozoans, worms, alcyonarians, and hydroids, thus establishing beyond doubt that great depths are indeed inhabited by animals (MURRAY & HJORT, 1912).

Investigation of the distribution of species, including coleoids, with relation to salinity, temperature, and other abiotic conditions was instigated during expeditions in the last half of the nineteenth century (THOMSON, 1877; MURRAY & HJORT, 1912). Systematic records of the depths at which animals were captured also began at this time. HOYLE (1886) tabulated captures of coleoids in open nets from the surface to 6000 m during

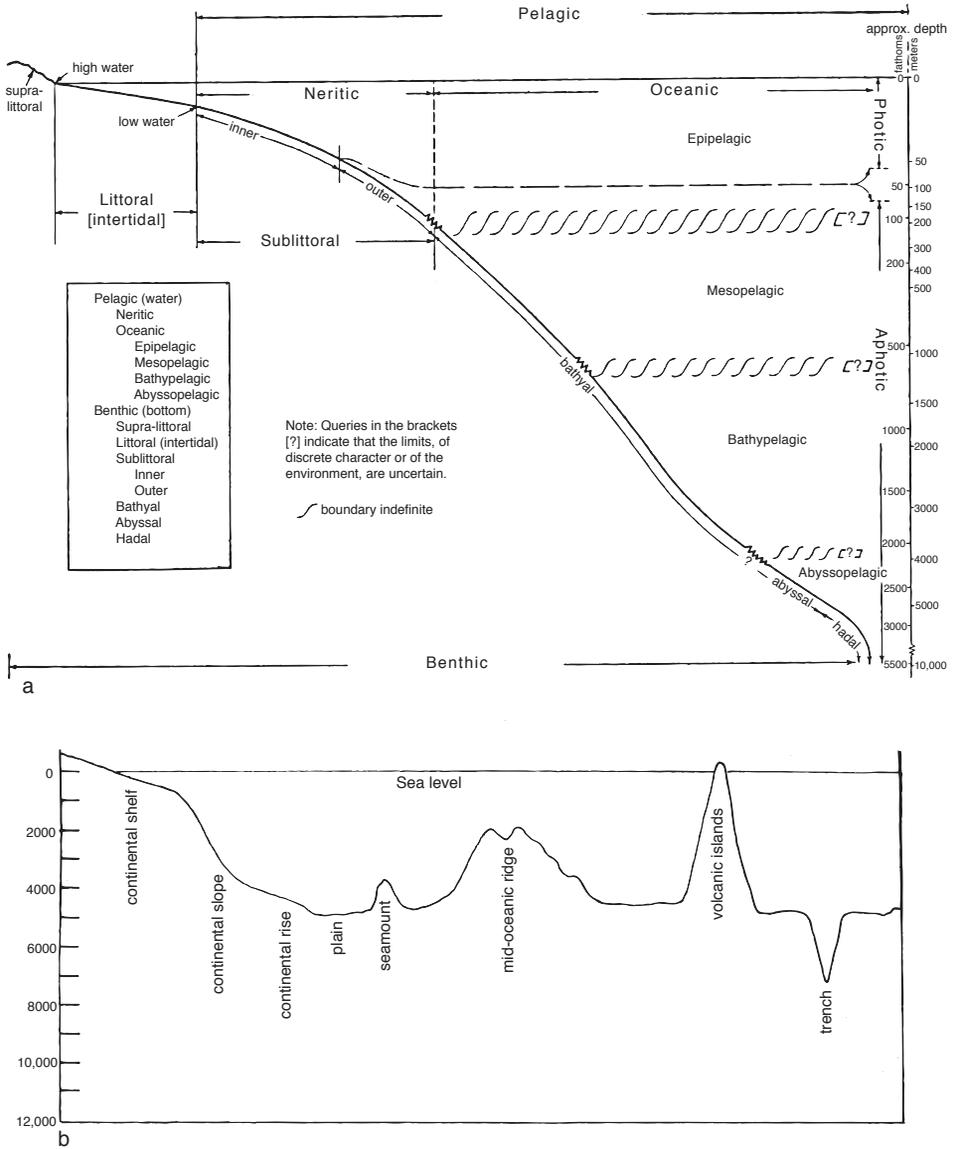


FIG. 1. Marine environments; a, classification; b, main topographic features of the ocean (Hedgpeth, 1957).

the voyage of HMS *Challenger* and also included those caught by other expeditions and vessels of the United States Commission of Fish and Fisheries (VERRILL, 1882). HOYLE (1886, p. 225) noted that the specimens captured did not necessarily inhabit the greatest depth reached by the dredge and that

too little material was “available for drawing any conclusions as to the Bathymetrical Distribution of the Cephalopods.” PFEFFER (1912) listed the species of coleoids and their depths of capture from the expedition of the Humboldt Foundation, and CHUN (1913) summarized the depth distribution of those

collected by the *Michael Sars*. The bathymetric distributions of *Vampyroteuthis infernalis* (Vampyromorpha) (PICKFORD, 1946), several octopods (THORE, 1949), and *Spirula spirula* (Spirulidae) (BRUUN, 1955) have been considered by these authors in relation to the conditions of the environments in which they were captured. ADAM and REES (1966) gave the vertical distribution of the members of the Sepiidae but considered the records imperfect. In 1966, CLARKE reviewed the distribution and ecology of oceanic squids and commented that (p. 93) "the taxonomic tangle prevents any but the most limited analysis of ecological data." In the following year, G. L. VOSS (1967, p. 515) described the bathymetric distribution of deep-sea cephalopods and commented, "It is still very difficult to arrive at definite conclusions concerning the depth inhabited by many species."

The habitats of coleoids in oceanic waters were poorly known until the late 1960s when opening-closing nets and depth monitoring devices were developed to give more precise information about the vertical distribution of these animals. The earliest studies with such sophisticated equipment were made in the North Atlantic Ocean near the southern end of Fuerteventura (Canary Islands) (CLARKE, 1969) and provided the first unequivocal evidence of diurnal vertical migration of oceanic coleoids. Other studies followed, and after capturing pelagic animals, some of which were caught in opening-closing nets, ROPER and YOUNG (1975, p. 37) noted, "Knowledge concerning the vertical distribution in cephalopods is rudimentary." CLARKE and LU (1974, 1975) and LU and CLARKE (1975a, 1975b) published a series of papers describing the distribution of oceanic coleoids captured at discrete depth horizons in opening-closing nets in the North Atlantic. Other techniques are now available to record the depths and habits of animals in the sea, including biotelemetry, underwater photography, television, and videotapes from manned and unmanned submersibles.

TABLE 1. Distribution of representatives of Recent Coleoidea in their habitats. Their presence is indicated by +; the numbers 1–3 show the inclusion of the three most speciose coleoid genera. The Sepiolida are coastal in habit, but one genus spends part of its life cycle in open waters (+) (new).

Order	Coastal waters	Oceanic waters
Spirulida		+
Sepiida	+1	
Sepiolida	+	(+)
Teuthida		
Myopsida	+2	
Oegopsida		+
Vampyromorpha		+
Cirroctopoda		+
Octopoda	+3	+

HABITATS

Recent Coleoidea inhabit all oceans and seas, except the Baltic and the Black Seas, from the shoreline to hadal depths. A small number of species are now known to tolerate estuarine or brackish waters, but none has colonized fresh water or land. Many undergo vertical, diurnal or diel, horizontal, seasonal, or ontogenetic migrations. Few studies even today are devoted to the ecology of living coleoids, but numerous investigations include some details of their natural history.

The species inhabiting the open waters of the oceans and seas belong to five of the seven orders of Recent Coleoidea (Table 1). The squids are divided into the oceanic Oegopsida, which is rich in families, a few species of which spend part of the life cycle in neritic waters, and the coastal Myopsida with two families. The orders Spirulida and Vampyromorpha are oceanic, and each includes only a single genus and species. The Cirroctopoda has three families with five genera; most are oceanic, but a few species are associated with the continental slope. The order Octopoda has families with species that inhabit open waters at all depths to 4000 m, and others that are coastal in habit. The Sepiolida are inhabitants of coastal waters, although one genus spends

TABLE 2. Recent coleoids, octopods, and myopsid squids, observed by skin and SCUBA divers in Greater Lameshur Bay, St John's, United States Virgin Islands (Hochberg & Couch, 1971).

Octopodinae	<i>Octopus vulgaris</i>	<i>Octopus briareus</i>	<i>Octopus macropus</i>
Number of specimens observed	4, and abundant young	14	12
Mantle length	20, 100 mm (early juveniles, immature)	70, 100 mm (no juveniles present)	20, 80, 180 mm (early juvenile to mature)
Activity	diurnal	nocturnal	nocturnal
Substrate	rock, coral reef, algae flat	coral reef	sand flats, coral reef
Den type	permanent, on reef face	semipermanent, reef-edge, coral-sand interface	semipermanent, blown out of sand under reef
Prey	bivalve and gastropod mollusks, hermit crabs	crabs, shrimps, and fishes	hermit crabs, crustaceans, and <i>O. macropus</i>
Myopsid squids	<i>Sepioteuthis sepioidea</i>	<i>Loligo plei</i>	<i>Pickfordiateuthis pulchella</i>
Number observed together on single occasions	4-6	20-30, and singly	30-60, and mate pairs
Period in water column	darkness	darkness	daylight

much of its life cycle in open waters. The genera *Sepia* (Sepiida), *Sepiolo* (Sepiolida), *Loligo* (Teuthida, Myopsida), and *Octopus* (Octopoda) are the most speciose of Recent Coleoidea, and the species of these genera all inhabit coastal waters, although after hatching, a number of species spend a period of time in the plankton of open waters.

COASTAL WATERS AND ISLANDS

Coastal waters are inhabited by sepiolids, sepiids, and octopods, which are mainly benthic or semibenthic in habit, and by loliginids, which are mostly neritic. Ecology of coleoids has been studied in a few and widely scattered parts of the world. These studies include observations in the sea by divers. Several have continued over long periods of time and revealed that subtle changes in habits and habitats take place during the lifetime of individuals of the investigated species.

Estuaries and brackish waters are inhabited by a few species that are able to tolerate reduced salinity for part or even most of their lives. One loliginid, *Lolliguncula brevis*,

lives in water of 17‰ to 30‰ salinity, primarily in bays and near the shore to a depth of 20 m, and from which it is periodically excluded by low temperatures and very low salinity during peak periods of freshwater runoff; it will also leave an area if the oxygen tension falls too low (HIXON & others, 1980).

In Greater Lameshur Bay, Saint John Island, United States Virgin Islands, the coleoid inhabitants were observed for six weeks by SCUBA divers (HOCHBERG & COUCH, 1971). Most were small; either early juvenile stages or species that are small as adults, one exception being a large and mature *Octopus macropus*, which is an inhabitant of very shallow water. The species living in this bay occupied various habitats, even in the small area under investigation (Table 2).

The coleoids of the intertidal zone of a continental, granitic island (30 km off the coast of Queensland, Australia, and 17 km inshore from the Great Barrier Reef) were observed by skin and SCUBA divers from December 2-14, 1975, and some specimens were observed subsequently in aquaria (ROPER & HOCHBERG, 1987, 1988). Most lived on or near the bottom, except two loliginids,

TABLE 3. Recent coleoids collected and/or observed in the intertidal zone of Lizard Island, Australia, December 2–14, 1975, and the substrate with which they were associated. In addition, the cuttlebones from a further three species of *Sepia* were collected from the beach, together with the internal shells of *Spirula spirula*; *ML*, mantle length (Roper & Hochberg, 1987, 1988).

Species	Substrate (habit) (depth at which observed or captured)
Sepiida	
<i>Sepia apama</i> (62 mm ML)	reef flat, coral, sand
<i>Sepia latimanus</i> (75 mm ML)	reef flat, coralline sand, rubble, algae
<i>Sepia mestus</i> (14–77 mm ML)	reef flat, coral, sand
<i>Sepia novaehollandae</i> (15–34 mm ML)	reef flat, coral, sand
<i>Sepia papuensis</i> (33–84 mm ML)	flat open sand, silt, algae, solitary corals (20–23 m)
<i>Sepia plangon</i> (16–23 mm ML)	sandy rubble (16 m)
<i>Sepia smithii</i> (53 mm ML)	sandy rubble (16 m)
<i>Metasepia pfefferi</i> (13–34 mm ML)	sand, silt mixture devoid rocks, sediment, algae (10–16 m)
Sepiolida	
<i>Sepiolo birostrata</i> (9 mm ML)	coral, sand
<i>Sepiolo tirostrata</i> (10 mm ML)	sandy (16 m)
<i>Euprymna stenodactyla</i> (1–20 mm ML)	sandy, coral rubble (16 m)
<i>Idiosepius pygmaeus</i> (5 mm ML)	coral, sand (1–15 m)
Octopoda	
<i>Hapalochlaena maculosa</i> (11–26 mm ML)	open sand or silt, coral rubble, coral, algae (10–22 m)
<i>Octopus ornatus</i> (33–73 mm ML)	reef flat, coarse coralline sand, sand, coral rubble (0–16 m)
<i>Octopus cyanea</i> (9–88 mm ML)	sandy rubble, coralline sand, rubble, reef flat (0–16 m)
<i>Octopus</i> sp. A	on reef, coral, sand (8–10 m)
<i>Octopus</i> sp. B	on reef, coral, sand (8–10 m)
Myopsida	
<i>Photololigo edulis</i> (88–98 mm ML)	pelagic
<i>Sepioteuthis lessoniana</i> (37–49 mm ML)	pelagic (1 m)
Oegopsida	
<i>Symplectoteuthis luminosa</i> (24 mm ML)	pelagic

Sepioteuthis lessoniana and *Photololigo (Loligo) edulis* (Table 3), and a small early juvenile of the ommastrephid squid, *Eucleoteuthis (Symplectoteuthis) luminosa*. Others were mostly small, either posthatchlings, early juveniles, or species that are small as adults. The area was richest in species of *Sepia*, as are the coasts of the mainland of Australia.

In one study lasting three years, *Sepioteuthis sepioidea* was observed in its natural habitat (San Blas Islands, off the Caribbean coast of northern Panama) by snorkel divers at various distances up to 20 km from the mainland (MOYNIHAN & RODANICHE, 1982). When newly hatched, this loliginid is semiplanktonic and lives in water 0.2 to 1.0 m deep, usually near or under floating vegetation and above a bottom of pure sand

or of sand, coral, and rubble mixture. With growth, the fins lengthen so that the young resembles a miniature adult. At this stage, it can swim rapidly yet spends less time in the plankton. The young congregate in shallow flats with turtle grass during the day, 25 to 30 cm below the surface, in water about 2 m in depth, moving into deeper water at night. Medium-sized and prespawning adults are nektonic and go to depths of 30 m or more, notably avoiding areas with turtle grass, preferring open water at night and inshore waters during the day. Courting and breeding adults are strongly attracted to coral reefs and concentrate in water 1.5 to 8.0 m deep. When fully mature, two individuals pair and remain together as they move to a site suitable for spawning. The

eggs are laid in strings and form clusters that are hidden from view, approximately 2.1 to 2.4 m down in water 2.7 to 3.3 m deep.

The coleoids of the Mediterranean Sea, especially along the European coasts, have been observed since classical times. One small area of the northwestern region of this sea has been the subject of several studies. Thus, it is feasible to follow the vertical distribution of coleoids from the surface to bathyal depths, on the sea floor, and in open waters (Table 4) (MANGOLD-WIRZ, 1963; ROPER, 1972, 1974; VILLANUEVA, 1992a, 1995; SARTOR & BELCARI, 1995; VOLPI, BORRI, & ZUCCHI, 1995). From the Catalan Sea (42°20' to 43°28' N and 2°50' to 3°50' E), specimens collected from or near the bottom, on various substrates, and from the water column between the surface and depths of 1000 m are listed (Table 4): each species is usually found between upper and lower depth limits (MANGOLD-WIRZ, 1963). Three species of *Sepia* inhabit these waters, and their cuttlebones have different characteristics as they implode at depths a little greater than those inhabited by each species (shown in parentheses in Table 4) (WARD & BOLETZKY, 1984); this demonstrates physiological constraints in the lives of these sepiids. In a bathyal basin (from 38°17' to 41°22' N and 1°12' to 3°36' E), coleoids were trawled from the bottom at depths from 628 m to 2208 m, mostly below 1000 m (VILLANUEVA, 1992a). In open waters (from 36°55' to 41°48' N and 0°35' to 13°08' E), various discrete depths were sampled between the surface and 1000 m (ROPER, 1972, 1974). *Heteroteuthis dispar* (Sepiolida) is usually caught in midwater trawls, but recent investigations indicate that the spawning females are associated with the sea floor, and so it is more like other members of the family than was previously supposed (RELINI, 1995).

The intertidal coleoids of California (eastern Pacific Ocean) are mostly benthic in habit; others enter this zone to spawn; and a few occur occasionally or are stranded (HOCHBERG & FIELDS, 1980). Five octopuses occu-

pying different niches are found along this coast. *Octopus bimaculoides* inhabits protected holes and crevices in pools of the middle and low intertidal zones and on mud flats. Older animals occupy kelp beds on rocks in subtidal waters to a depth of 20 m; the female lays eggs in clusters under the rocks and broods them, and the newly hatched young are benthic and often move into the intertidal zone. *O. bimaculatus* (a sibling species of *O. bimaculoides*) is found in the lowest intertidal zone and down to 50 m depth, where kelp, *Laminaria*, occurs. It deposits thousands of egg capsules and broods them until hatching; the hatchlings are planktonic. *Octopus rubescens* lives under stones in the low intertidal zone and in kelp beds offshore, where the bottom is sandy mud; the female spawns and broods the eggs in the intertidal or shallow subtidal zones. After hatching, the young are planktonic. Juveniles are found in kelp holdfasts when these are washed ashore. *O. micropysus*, one of the smallest octopus species known, inhabits empty gastropod shells or kelp holdfasts offshore. It occasionally enters the low intertidal zone and is often washed ashore with the kelp holdfasts. The eggs are laid in empty shells, under rocks, or in kelp holdfasts; and the young are planktonic. Only the young of *Enteroteuthis* (*Octopus*) *dofleini*, the giant Pacific octopod, occur occasionally in low intertidal pools on rocky shores; larger individuals generally live in the subtidal zone to depths of 100 m. The sepiolid *Rossia pacifica* is found in shrimp beds, where it digs shallow depressions in sand or muddy sand on the sea floor, usually in depths from 16 to 370 m. On rare occasions at night, it swims in the intertidal zone. The myopsid squid *Loligo opalescens* comes into shallow, inshore waters to spawn, where the bottom is muddy sand. It attaches its egg capsules to the substrate. Two large oegopsid squids are also encountered along the coast of California. *Moroteuthis robusta* is pelagic in coastal waters, at depths of 100 to 600 m, and is occasionally seen swimming near the surf line or even stranded ashore. *Dosidicus gigas* is abundant in some years when thousands come

TABLE 4. Recent coleoids recorded from three areas of the western Mediterranean and their habitats (Mangold-Wirz, 1963; Roper, 1972; Villanueva, 1992a) (*Posidonia* is a marine plant that forms undersea meadows). The depth of implosion of the cuttlebones from three species of *Sepia* are shown in parentheses (Ward & Boletzky, 1984).

Coleoidea	Substrate features	Catalan Sea	Bathyal basin	Open waters
		2°50'–3°50'N to 42°20'–43°28'E	38°17'–41°22'N to 1°12'–3°36'E	36°55'–41°48'N to 0°35'–13°08'E
		Depth m	Depth m	Depth m
Order Sepiolida				
<i>Sepiolo robusta</i>	sand, <i>Posidonia</i>	50–200		
<i>Sepiolo rondeletii</i>	sand, <i>Posidonia</i>	10–30		
<i>Sepietta obscura</i>	soft substrate	5–20		
<i>Sepietta oweniana</i>	mud	80–700	974	–
<i>Rossia macrosoma</i>	mud, coral	100–500	–	–
<i>Neorossia caroli</i>	mud	400–1000	661–1744	–
<i>Heteroteuthis dispar</i>	slope associate, open sea	–	980–1588	45–500
Order Sepiida				
<i>Sepia officinalis</i>	sandy mud (150–200 m)	10–100	–	–
<i>Sepia elegans</i>	sand, mud (400–600 m)	27–494	–	–
<i>Sepia orbignyana</i>	mud, sand (550–600 m)	33–512	–	–
Order Octopoda				
<i>Octopus macropus</i>	sand, rocks	5–10	–	–
<i>Octopus vulgaris</i>	sand, rocks	5–10	–	–
<i>Octopus salutii</i>	mud, sand	70–400	–	–
<i>Octopus defilippi</i>	mud, sand	100–200	–	–
<i>Octopus paralarva</i>		–	–	0–600
<i>Scaevurgus unicolor</i>		100–350	–	–
<i>Preoctopus tetracirrus</i>	mud	130–700	–	–
<i>Eledoone moschata</i>	sand, mud, gravel	10–90	–	–
<i>Eledone cirrhosa</i>	sand, mud, stones	10–400	–	–
<i>Bathypolypus sponsalis</i>	mud	200–900	628–1835	–
Order Cirroctopoda				
<i>Opisthoteuthis agassizii</i>		–	1204–2208	–
Order Teuthida				
Suborder Myopsida				
<i>Loligo vulgaris</i>		10–100	–	–
<i>Loligo forbesi</i>		150–400	–	–
<i>Alloteuthis subulata</i>		20–120	–	–
<i>Alloteuthis media</i>		20–300	–	–
Suborder Oegopsida				
<i>Illex coindetii</i>		40–500	–	–
<i>Todaropsis eblanae</i>		150–500	–	–
<i>Todarodes sagittatus</i>		200–1000	628	0–750
<i>Abraliopsis pfefferi</i>		–	–	25–600
<i>Onychoteuthis banksii</i>		–	–	0–250
<i>Ancistroteuthis lichtensteini</i>		–	1271	–
<i>Histioteuthis reversa</i>		–	628–1766	100–700
<i>Ctenopteryx sicula</i>		–	1099	–
<i>Ommastrephes</i> sp.		–	–	0–750
<i>Chroteuthis veranyi</i>		–	–	400
<i>Galiteuthis armata</i>		–	1007–2208	25–600

TABLE 5. The capture rate of two species of oegopsid squids near the Hawaiian Islands per 1000 m³ of water sampled; ND, no data (R. E. Young, 1978).

Depth m	Capture rate in daylight		Capture rate in darkness	
	<i>Pterygioteuthis microlampas</i>	<i>Pyroteuthis addolux</i>	<i>Pterygioteuthis microlampas</i>	<i>Pyroteuthis addolux</i>
0–50	ND	ND	15.2	1.5
50–100	ND	ND	62.1	6.5
100–150	ND	ND	23.3	7.3
150–200	0	0	14.1	15.9
200–250	0	0	0	3.1
250–300	ND	ND	1.0	6.5
300–400	2.3	6.9	0	0
400–500	42.3	14.1	4.9	4.9
500–600	72.2	20.7	6.9	5.1
600–700	8.7	14.9	1.4	0
700–800	5.3	3.2	0	0
800–900	8.5	1.2	0	0
900–1000	1.0	2.1	0	0
1000–1100	20.1	1.5	0	5.4

inshore in pursuit of spawning grunion, the fish *Leuresthes tenuis*, and, as a consequence, often become stranded.

Around the isolated, volcanic, oceanic islands of Hawaii (Pacific Ocean) there are many species of oegopsid squids. BERRY (1912, p. 267) indicated their richness and diversity: in a “single haul . . . between Oahu and Laysan Islands, where 11 specimens representing 1 species each of no less than 5 genera” were caught. In open waters, there is a broad peak in the species found between depths of 500 and 800 m in daylight, with an abrupt increase near 400 m, and in the upper few hundred meters in darkness (Table 5; R. E. YOUNG, 1978). Two species of the family Pyroteuthidae, *Pyroteuthis addolux* and *Pterygioteuthis microlampas*, have vertically separated habitats. Both species occupy depths around 500 m during the day, but at night, *P. microlampas* occurs at 50 to 100 m and *P. addolux* at 150 to 200 m (Table 5). Two species of cranchiid squids apparently inhabit different depths. *Liocranchia reinhardtii* has been found in near-surface waters at night and in upper mesopelagic depths during the day, whereas *L. valdiviae* has been caught in lower mesopelagic depths day and night (R. E. YOUNG, 1978). Three species of octopuses have been recorded

here, each being associated with different substrates. *O. ornatus* burrows under gravel; *O. cyanea* lives below large coral boulders; and an unnamed species is found along the undersurface of ledges in tide pools (HOUCK, 1982). *Euprymna scolopes*, a sepiolid endemic to these islands, spends the day buried in the sand, emerging at night to swim in intertidal waters (ANDERSON, 1997).

The isolated oceanic islands of Bermuda lie some 1000 km from the mainland coast of the western North Atlantic; the beaches are of coral sand and surrounded by reefs. The shells of *Spirula spirula* are commonly washed onto the beaches, as occasionally are the paper-thin shells of *Argonauta argo* (ROPER, 1986). Two areas (Coney Island Bridge and Whalebone Bay) were the sites for a series of observations of juvenile *Octopus vulgaris* over several years in water from intertidal to 2 m in depth. The octopuses lived where there was a mixture of rock and rocky rubble. They occupied a potential site and then removed sand and rocks to form a den (MATHER, 1994). The shallow-living *O. macropus* is also found here. Two loliginids inhabit these waters, and *Loligo plei* may form an isolated population (COHEN, 1976) that could have arrived via the Gulf Stream from the Caribbean (G. L. VOSS,

TABLE 6. The number of species caught at each of the horizons sampled in the North Atlantic, in daylight and darkness at six latitudes, all near 20° W; *broken lines*, no data (Clarke & Lu, 1974, 1975; Lu & Clarke, 1975a, 1975b).

Depth m	11° N day/dark	18° N day/dark	30° N day/dark	40° N day/dark	53° N day/dark	60° N day/dark	Total no. of species day/dark
0-100	69/58	30/47	9/7	3/5	4/6	3/3	118/126
100-200	17/12	8/11	10/8	2/2	3/4	2/2	42/39
200-300	5/21	20/9	5/9	2/0	1/2	0/1	33/42
300-400	13/3	6/5	3/4	0/2	2/2	0/1	24/17
400-500	6/5	5/15	1/3	1/1	1/1	1/2	15/27
500-600	21/10	6/9	5/2	0/1	2/0	1/1	35/23
600-700	14/17	5/2	3/2	0/1	1/0	0/0	23/22
700-800	12/8	17/7	4/1	1/0	0/1	1/0	35/17
800-900	11/9	6/3	2/3	0/1	0/1	0/1	19/18
900-1000	11/13	8/10	4/2	0/1	1/0	0/2	24/28
1000-1250	6/6	2/9	0/2	2/1	1/0	2/1	13/19
1250-1500	-/1	3/3	2/1	1/3	2/0	1/2	9/10
1500-2000	2/2	-/-	1/0	0/2	0/1	1/1	4/7

1960). The other, *Sepioteuthis sepioidea*, lives behind coral reefs, over reef flats, and above turtle grass beds, from the surface to depths of 20 m (ROPER, 1986). G. L. VOSS (1960) identified 14 new species of oceanic squids caught within 320 m of the islands and the young stages of 3 bathypelagic octopods and planktonic paralarvae of *Octopus* sp.

The margins of the seas and oceans, besides being inhabited by sepiids, octopods, and loliginids, provide shelter for some oceanic forms during the early part of their life cycles, as do seamounts and oceanic islands.

OCEANS AND SEAS

The use of opening-closing nets in the open waters of the North Atlantic Ocean provided the first unequivocal evidence of coleoids undergoing diurnal vertical migrations (CLARKE, 1969). This investigation was followed by a series of hauls in the eastern North Atlantic Ocean made at discrete depths from the surface to 2000 m depth, at about 10° intervals from 60° N to 11° N, all near 20° W. Some 3000 cephalopods were collected and their distribution described in four papers (Table 6; CLARKE & LU, 1974, 1975; LU & CLARKE, 1975a, 1975b). There is an apparent decline in the number of

species toward the poles, although catch per unit effort, sampling efficiency of the nets, net opening size, and the ability of the cephalopods to escape capture must also be considered. Table 6 gives the numbers of species represented in captures at each depth at the different latitudes in daylight and darkness. The trend is for a diminution in the number of coleoid species with increasing depth at most of the sampling sites, although some species are present at several depths. The near-surface waters (0 to 100 m) are inhabited by the largest number of species, and below 1250 m, the number is low and yet falls only slightly toward the poles. There is a notable change at about 40° N latitude, with a marked reduction in species. A similar change is reflected in fish and other groups of animals sampled at the same time and sites as the coleoids, and ANGEL (1992, p. 434) commented that "about 40° N latitude there is a sharp poleward reduction in species richness and a tendency for a limited number of species to dominate a community, and this is expressed at all depths down to at least 2000 m."

ROPER and YOUNG (1975) captured coleoids in opening-closing nets between the surface and 1000 m and a few to 5000 m in the open waters of the Pacific Ocean off California and Hawaii. These authors

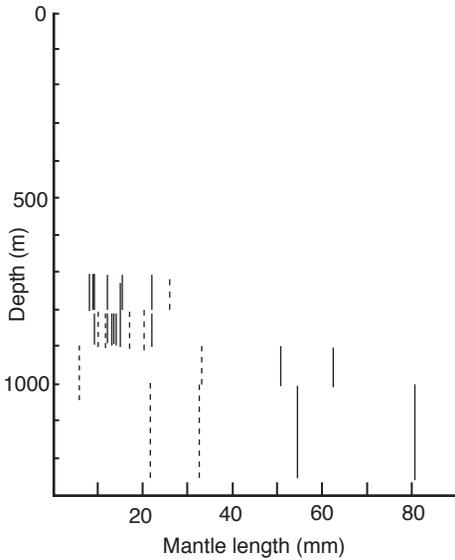


FIG. 2. The bathymetric distribution of *Vampyroteuthis infernalis* (Vampyromorpha) in the North Atlantic in relation to mantle length. The vertical lines represent the depth ranges in which the specimens were caught in daylight (broken lines) and darkness (solid lines) (Lu & Clarke, 1975b).

characterized five main patterns of movement. (1) The near-surface dwellers include such pelagic octopods as *Argonauta* sp., *Tremoctopus violaceus*, and *Ocythoe tuberculata* and one of the onychoteuthid squids, *Onykia caribaea*; this last species is regarded as a member of the neuston, in the topmost few centimeters of water (ROPER & YOUNG, 1975). Some teuthids can break clear of the surface, and VERRILL (1882, p. 323) commented that *Sthenoteuthis (Ommastrephes) bartrami* "is an exceedingly active species, swimming with great velocity, and not rarely leaping so high out of the water as to fall on the decks of vessels . . . it has been called the 'flying squid' by sailors." This species has been tracked with ultrasonic telemetry, and its average swimming speed was recorded as 250 cm/s (NAKAMURA, 1993). *Dosidicus gigas* was photographed emerging from the sea with a speed estimated to be 175 cm/s (COLE & GILBERT, 1970), and other squids have been recorded after landing on the decks of boats (REES, 1949). (2)

The diurnal vertical migrators, such as the enoploteuthid squids, are found from 300 to 600 m during the day and in the upper 200 m at night. (3) The diurnal vertical spreaders include *Octopoteuthis deletron*, found from 200 to 400 m during the day but from 0 to 500 m at night. (4) The vertical wanderers include the cranchiid squid, *Galiteuthis phyllura*, which is found below 900 m during the day and from 100 to 900 m at night (ROPER & YOUNG, 1975). (5) The nonmigrators, of which an example is *Vampyroteuthis infernalis* (Vampyromorpha), have been captured in opening-closing nets, mostly between 700 m and 1250 m with a peak in distribution between 800 to 900 m, both in daylight and darkness (Fig. 2) (LU & CLARKE, 1975b). *V. infernalis* lives within the oxygen minimum layer (SEIBEL & others, 1997). Its paralarvae, of less than 20 mm mantle length, have been captured off southern California deeper than 900 m, but larger specimens were shallower than 900 m (ROPER & YOUNG, 1975); and it is at 20 mm mantle length that it undergoes a morphological change as the two paralarval fins are resorbed to leave only the adult pair (PICKFORD, 1949a; and see *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan, and Chapter 6, Biogeography of Recent Forms).

POLAR SEAS

The polar regions are inhabited by a few species of coleoids for the whole of their life cycle. They are presumably adapted physiologically to low temperatures. Eight species of oegopsid squids from seven families inhabit Antarctic waters, and, in one bay, paralarvae of six of the eight species were caught (FILIPPOVA & PAKHOMOV, 1994; LU & WILLIAMS, 1994a). One of the squids, *Bathyteuthis abyssicola* (Bathyteuthidae), has a circumpolar distribution in the Southern Ocean, where it seldom approaches within 1000 m of the bottom or within 500 m of the surface, the major limiting factor apparently being organic productivity (ROPER, 1969). Seven species of benthic eledonines have been caught

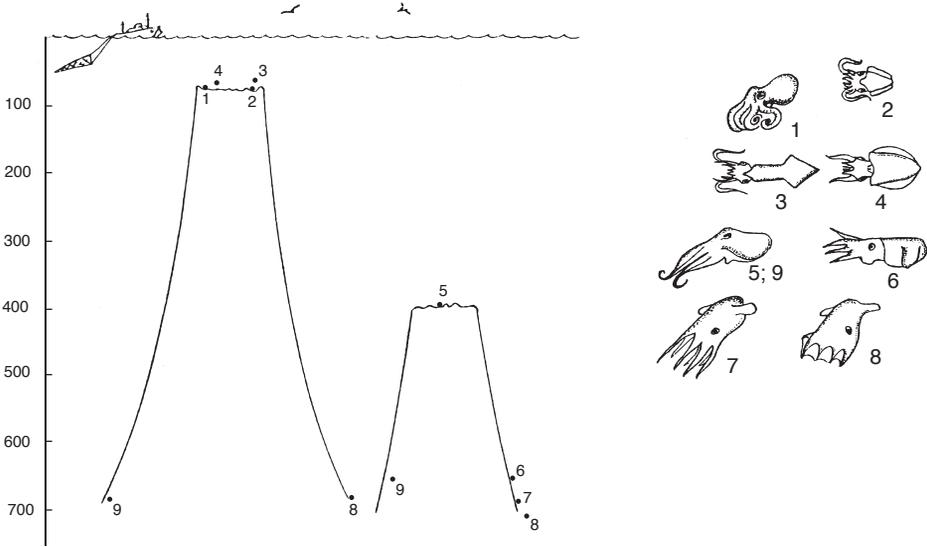


FIG. 3. Bottom- and near bottom-living coleoids of seamounts. Inhabitants of shallow-water banks belong to the following genera: 1, *Octopus*; 2, *Sepia*; 3, *Loligo*; 4, *Sepioteuthis*. Lower sublittoral and upper bathyal coleoids found predominantly on the tops of guyots and tablemounts belong to the following genera: 5, *Scaeurgus*, *Pteroctopus*, and *Danoctopus*. Middle and lower bathyal inhabitants found mainly on the slopes include: 6, *Neorossia*; 7, *Froekenia*; 8, *Grimpoteuthis*; *Opisthoteuthis*; 9, *Bathypolypus*, *Benthoctopus*; The ordinate shows the depth in meters (Nesis, 1993).

in bottom trawls (KUBODERA & OKUTANI, 1994). The records of coleoids in these waters are certainly incomplete, and those in Arctic waters are even less well known. Three species of oegopsid squid are found at 60° N, but there are few records from latitudes further north. One species, *Gonatus fabricii*, is the dominant squid in Arctic and sub-Arctic waters. Its young appear to hatch over a large area and are caught in swarms in the early summer months in the Davis Strait (Greenland) between 62° N and 70° N. The juveniles undergo vertical migrations to 70 to 80 m depth at night, at which time they appear to disperse (KRISTENSEN, 1984). Trawls in the Davis Strait captured two species of *Rossia* (Sepiolida), two species of *Bathypolypus* (Octopoda), and one cirrocotopod, *Cirrotheuthis* sp. (MUUS, 1962).

SEAMOUNTS AND GUYOTS

These are formed by isolated volcanic action, rise individually from the abyssal plain, and have various types of coleoids associated with them (NESIS, 1993, 1997;

PARIN, MIRONOV, & NESIS, 1997). There are bottom and near-bottom species, which live permanently on seamounts, and these are divisible into groups. On the Saya de Malha Bank (western Indian Ocean), there are shallow-water species, which include sepiids (*Sepia*), several species of which are considered endemic, a sepiolid (*Sepiolo*), loliginids (*Loligo*, *Sepioteuthis*), and octopods (*Octopus*). With the exception of *Sepia*, all the other species found here have a planktonic phase during their development when they drift passively (Fig. 3). Lower sublittoral and upper bathyal species are found predominantly on the tops of seamounts and include the octopods *Scaeurgus*, *Pteroctopus*, and *Danoctopus* and a sepiolid *Austrorossia*. Of these, only *Scaeurgus* has a pelagic paralarval stage. Middle- and lower-bathyal species inhabit the slopes of seamounts, and these include sepiolids (*Neorossia*), cirrocotopods (*Froekenia*, *Grimpoteuthis*, *Opisthoteuthis*), and deep-living octopods (*Benthoctopus*, *Bathypolypus*). There are near-bottom and benthopelagic species that spawn on the

bottom but subsequently are found in midwater over the seamount. These include typically micronektonic sepiolids of the subfamily Heteroteuthinae. Another group consists of neritooceanic species whose paralarvae and juveniles live in midwater, but as adults, they spawn on or near the bottom or near the surface of the tops or the slopes of seamounts. Others become associated accidentally with seamounts by passive advection. These include diel vertical migrators and nonmigrators. Species associated with seamounts and submarine ridges may spend only part of their life cycle there, as they are otherwise distributed in other and sometimes quite distant areas (PARIN, MIRONOV, & NESIS, 1997). Some of the large nektonic ommastrephids actively avoid areas over seamounts (NESIS, 1993).

ABYSSAL AND HADAL DEPTHS

Some coleoids have been found in abyssal depths and even hadal depths in deep trenches. One squid, *Promachoteuthis megaptera*, the only member of the Promachoteuthidae, lives at 1400 to 3500 m depth, mostly far above the bottom and at a greater depth than any other oegopsid squid (HOYLE, 1886; ROPER & YOUNG, 1968; OKUTANI, 1983b). Its body and fins are gelatinous, and the muscular system is poorly developed (ROPER & YOUNG, 1968). Cirroctopoda, the finned octopods, are mostly deep living, and one, *Grimpoteuthis* sp., was observed at more than 7000 m, currently a depth record for any living coleoid (G. L. VOSS, 1988b). Another, *Cirrothauma murrayi*, has been caught most commonly between 1500 and 5000 m (ALDRED, NIXON, & YOUNG, 1983). Several hundred photographs taken at depths of between 3480 m and 4020 m showed cirroctopods close to but above the bottom. The substrate ranged from boulders and coarse gravel to relatively fine sediment, consisting of fine and coarse fragmented foraminiferal sand of planktonic origin; fragments of coral, bivalves, gastropod

mollusks, sea urchins, and bryozoans; and volcanic and other terrigenous fragments (ROPER & BRUNDAGE, 1972). Associated with the cirroctopods were sea cucumbers, crustaceans, fishes, and plant detritus, including fragments of *Syringodinum*, *Thalassia*, and seaweed.

HYDROTHERMAL VENTS

Deep-living octopods, including *Granelledone* sp., *Benthoctopus*, and *Cirroteuthis magna*, have been observed near hydrothermal vents (TUNNICLIFFE, McARTHUR, & McHUGH, 1998); and a new genus and species, *Vulcanoctopus hydrothermalis*, has been collected from a vent (GONZÁLEZ & others, 1998). Cephalopods are probably visitors to vents, and the extent of their association with this habitat is not yet known.

MIGRATORY HABITS

Numerous migratory patterns exist among living coleoids. Many coastal species move onshore and offshore during their lifetime. Some oceanic coleoids migrate from open to neritic waters, others from current systems to open waters, and some show movements during ontogeny. Besides moving through horizontal and vertical distances, a number of species change their habits, for example, from planktonic to benthic or from pelagic to nektobenthic, as they develop and grow (LU & CLARKE, 1975b; ROPER & YOUNG, 1975; VECCHIONE, 1987; NIXON & MANGOLD, 1996).

Coastal and neritic coleoids may have one or more migratory patterns, the main one being to spawning grounds from which their young migrate in turn to the habitat of the juvenile and adult (MANGOLD, 1987). Some of the sepiids, sepiolids, loliginids, and octopods exhibit onshore and offshore migrations, related to sexual maturity, salinity, or temperature (MANGOLD-WIRZ, 1963; BOYLE, 1983a). *Loligo vulgaris* is mainly pelagic but moves inshore to spawn, when it becomes largely bottom living and attaches its egg strings to the substrate (WORMS, 1983). The horizontal speed of tagged loliginids

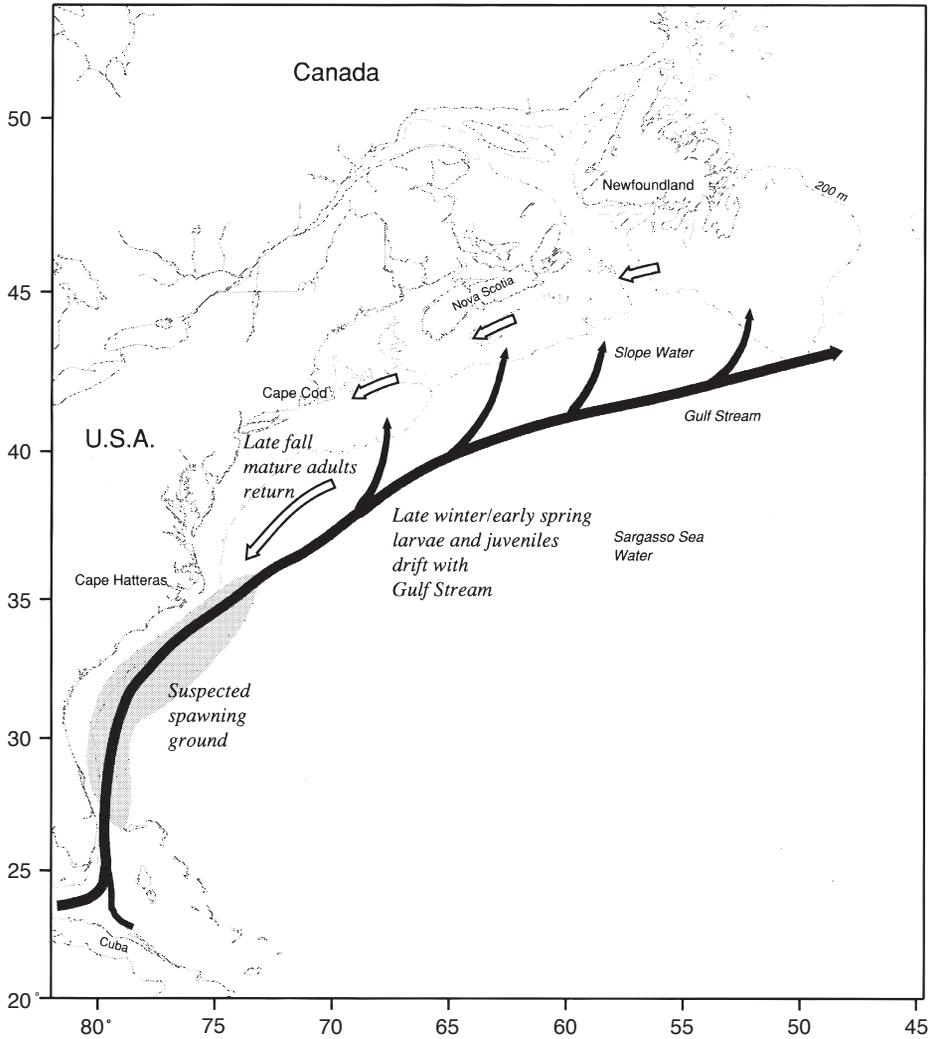


FIG. 4. The hypothetical migratory path of *Illex illecebrosus*. Transport to the northern feeding grounds is in the Gulf Stream and so is passive, but southward, it is active to the suspected spawning grounds (Black, Rowell, & Dawe, 1987).

off the coast of Japan was 0.2 to 0.6 km per hour (NATSUKARI & TASHIRO, 1991). In these waters, sepiids move inshore to spawn and offshore to winter, as they do in the Mediterranean Sea, where *Sepia officinalis* moves at about 0.23 km/day to its spawning grounds (EZZADINE-NAJAI, 1995; NIXON & MANGOLD, 1998). *Octopus vulgaris* shows rather similar migratory patterns, moving inshore to spawn and brood its eggs (NIXON & MANGOLD, 1996). Little is known of the

distances travelled, but off the coast of Japan, one tagged *O. vulgaris* had moved a horizontal distance of 48 km before being recaptured (NAGASAWA, TAKAYANAGI, & TAKAMI, 1993). The influence of abiotic factors on such movements is largely unknown, but there is evidence that salinity is important for some species (WORMS, 1983; PAULIJ, BOGAARDS, & DENUCÉ, 1990).

Migratory patterns of the muscular and fast-moving ommastrephid squids are

complex. *Illex illecebrosus* lives in the north-western Atlantic from latitude 25° N to 55° N, where it is primarily an inhabitant of the outer shelf and continental slope (Fig. 4) (COELHO, 1985; BLACK, ROWELL, & DAWE, 1987; O'DOR & COELHO, 1993). It is highly mobile, strong swimming, pelagic, and capable of moving through horizontal distances of more than 2000 km, averaging nearly 20 km/day, with a vertical range from the surface to depths of 1000 m or perhaps more; it is usually caught in water with temperatures of 0.5° C to 27.3° C and salinities of 30‰ to 36.5‰ (O'DOR, 1983). This squid spawns in midwater, and the egg mass sinks when released (O'DOR & BALCH, 1985). Paralarvae and hatchlings of this species are found concentrated along the central axis of the Gulf Stream (VECCHIONE & ROPER, 1986) and are transported north, following a wave of zooplankton productivity (O'DOR & COELHO, 1993), meanwhile growing from a fraction of a milligram to almost 2 kg in weight (O'DOR, 1983). In the northern feeding grounds, some move inshore and others remain in the water column between the surface and bathyal depths, surfacing at night to feed intensively before dawn, after which they descend several hundred meters. The squids actively migrate southward as they mature. The ecology of this squid is complex, as it passes through many different abiotic and biotic conditions during its various vertical and horizontal movements; its distribution off the eastern coast of Canada and the United States can vary from season to season and year to year (O'DOR & COELHO, 1993). Movements of another ommastrephid, *Todarodes pacificus*, off the coast of Japan are related to the prevailing currents and are complex because of the geography. *T. pacificus* migrates at speeds of 46.3 to 92.6 km/day, the figures being based on horizontal distances travelled by tagged animals (NAGASAWA, TAKAYANAGI, & TAKAMI, 1993).

Three females of the oceanic squid *Ommastrephes bartrami*, tagged with ultrasonic transmitters, had an average horizontal

speed of 0.7 to 0.9 km/h. The movements of one female were traced and can be compared with records of the light intensity at the surface and the temperature and salinity of the water at the same positions (Fig. 5). This individual moved constantly in a west-southwestern direction and travelled 21.9 km in 24 h at an average speed of 0.91 km/h. The two other females took rather tortuous courses (NAKAMURA, 1993).

The vertical migratory patterns of oceanic coleoids are varied. This became apparent when the mantle length of each specimen was measured of species collected in considerable numbers in the North Atlantic. Several distribution patterns were found, some being related to body size, others to diurnal changes (CLARKE & LU, 1974, 1975; LU & CLARKE, 1975a, 1975b). A diurnal vertical migratory pattern persists throughout the life of *Spirula spirula* (Spirulida) (CLARKE, 1969), from paralarval stage to adult (2.3 to 41 mm mantle length) (Fig. 6a), as all of the specimens were below 500 m in daylight hours and all but a few above 300 m in darkness (Fig. 6b). Three species, the octopod *Japetella diaphana* and two cranchiid squids, *Liocranchia reinhardti* and *Galiteuthis armata*, descend during growth. An octopod, *Vitreledonella richardi*, and an oegopsid squid, *Valbyteuthis danae*, extend their vertical limits as they grow (LU & CLARKE, 1975b).

DISPERSAL

Coleoids have recognizable patterns of distribution, although these are often imprecisely known, even for the better investigated species. Their boundaries can depend upon many factors, one or several of which may act as a barrier. Dispersal provides a vehicle for migration, but the establishment of a population is the key to extending the range of a species. The potential for dispersal is probably greatest during the early stages of life of many species of marine animals, including benthic forms, some of which have planktonic hatchlings. The larval stage, in theory, allows an organism to penetrate

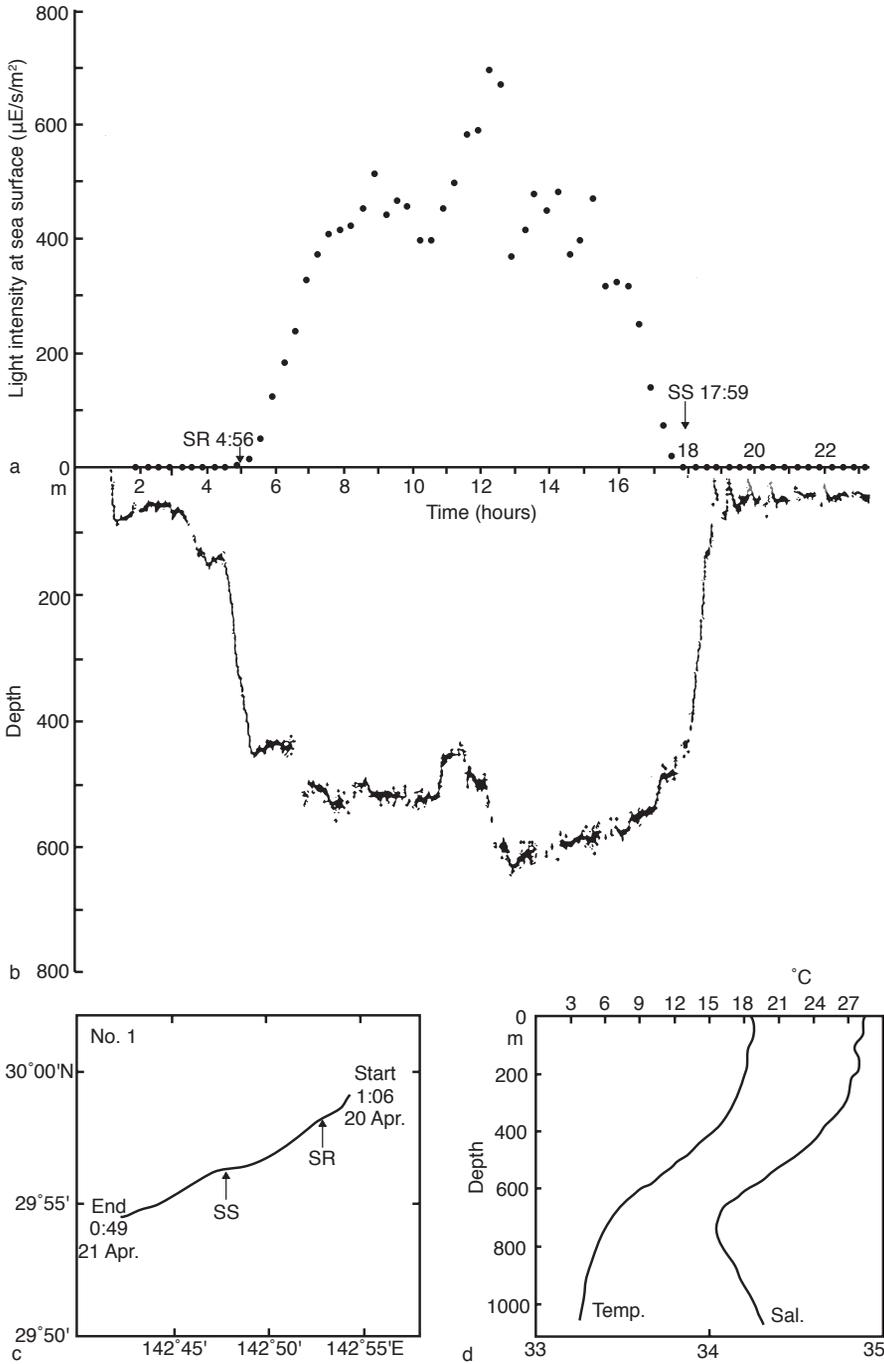


FIG. 5. Patterns of movement of *Ommastrephes bartrami* in the Pacific Ocean, near Japan, tracked by an attached ultrasonic transmitter. *a*, Change in light intensity at the sea surface, and *b*, vertical movements of the squid; *SR*, sunrise; *SS*, sunset; *c*, movement of squid No. 1, a copulated female of 46 cm, dorsal mantle length; *d*, vertical distributions of temperature and salinity at the point of termination of the track of the squid (Nakamura, 1993).

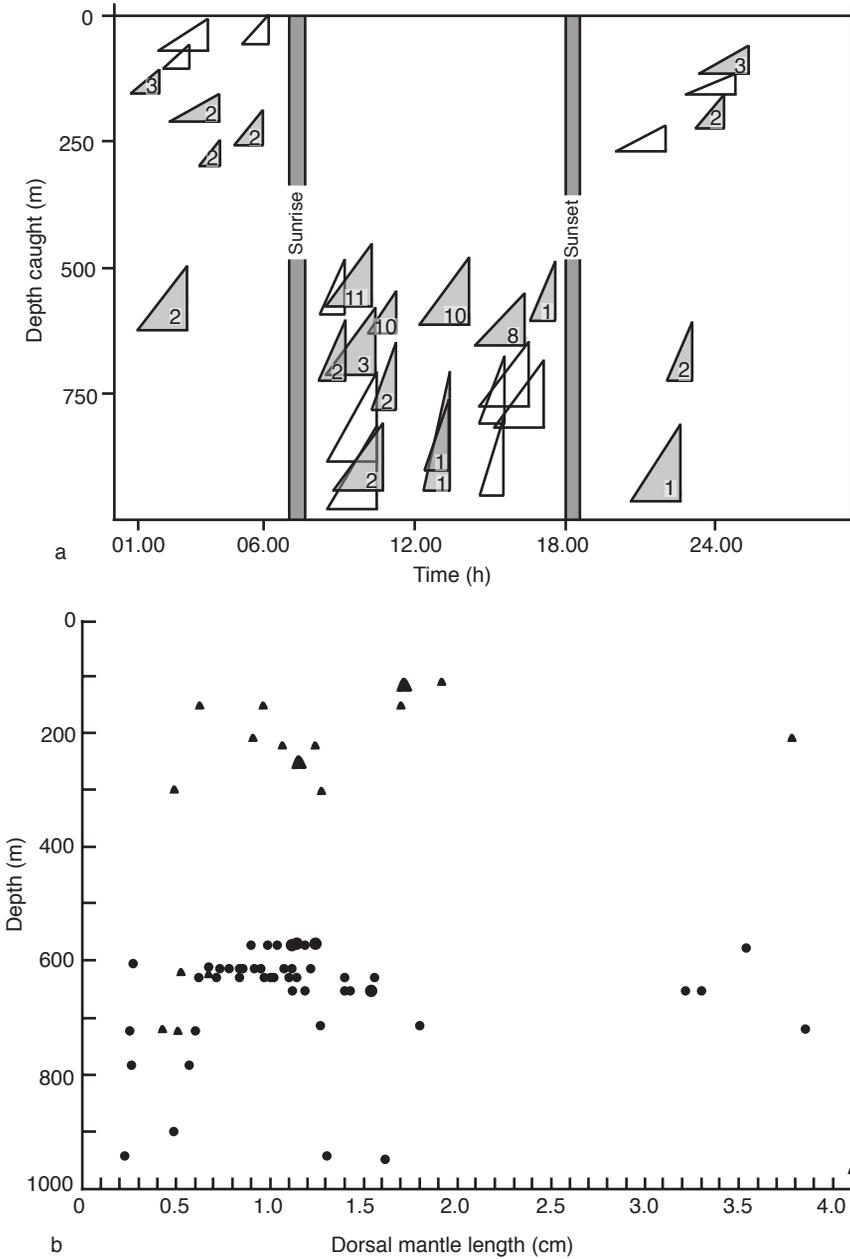


FIG. 6. *Spirula spirula* (Spirulida); a, depths and times of capture of the spirulid in the North Atlantic; lower left point of each triangle represents the opening time and maximum depth, the apical point the closing depth, the base line the duration of the horizontal part of the haul, and the vertical line the depth range from which the animals came; numbers in the triangles indicate number of specimens caught; unbatted triangles indicate the absence of *S. spirula* from hauls; stippled lines show variation in sunrise and sunset; b, size of the specimens is plotted against the maximum or fishing depth of the nets in which they were caught; animals taken in darkness (triangle) and in daylight (circles); the larger shapes indicate two specimens (Clarke, 1969).

TABLE 7. The number of paralarvae of four species of ommastrephid squids captured per 1000 m³, sampled in two layers of the Kuroshio Current, Japan (Saito & Kubodera, 1993).

Species	Depth in m					
	0–25	25–50	50–75	75–100	100–150	150–200
<i>Ommastrephes bartrami</i>	2.8		0.2			
<i>Symplectoteuthis oualaniensis</i>	6.0	2.0	1.0			
<i>Eucleoteuthis luminosa</i>	3.0	3.2	8.0	2.5	0.1	
<i>Ornithoteuthis volitans</i>			0.8	2.0	0.2	0.5

areas far removed from those of the adult and, in the process, traverse habitats unsuitable for the adult stages (MYERS, 1997). In many species, the early juvenile period is an ecologically distinct phase (GOSSELIN & QIAN, 1997). The phases of the life cycle that perhaps contribute most to dispersal are spawning and hatching. When eggs are shed singly or in large numbers directly into the sea (see *Treatise Online*, Part M, Chapter 5, Reproduction and Lifespan), they can disperse; and at hatching, the young, already in the water column, can further disperse. Hatchlings of some of the mainly benthic or benthopelagic forms enter the water column immediately after hatching; those of others settle to the bottom in the adult habitat but may be pelagic for part of the day. Females of pelagic octopods carry their eggs until hatching, which may take place at intervals; and so they disperse their own young.

The hatchlings of many species join current systems (e.g., OKUTANI & MCGOWAN, 1969; O'DOR, 1983; DUNNING, 1985). In the Kuroshio Current, with strong temperature and salinity fronts, the strange rhynchoteuthion paralarvae of two ommastrephid squids, *Eucleoteuthis luminosa* and *Ornithoteuthis volitans*, occur below the surface mixed layer; and those of two others, *Sthenoteuthis oualaniensis* and *Ommastrephes bartrami*, occur in the surface mixed layer (Table 7) (SAITO & KUBODERA, 1993). Entering such current systems greatly increases the potential for dispersal at the paralarval stage. Some paralarvae migrate vertically (VECCHIONE, 1987). The duration of the paralarval phase is not known for most coleoids, and it probably influences

the extent of their dispersal. The juvenile and maturing stages of some species may continue to move far away from the site of hatching, only to return as mature adults.

The normally accepted boundaries of a species are sometimes exceeded. For example, *Sepia officinalis* is rare off the coast of Scotland, yet in 1960 and 1961, it was recorded in such numbers as to constitute an invasion; some of the females contained eggs, but no evidence of spawning was found subsequently (RAE & LAMONT, 1963). Off the coast of southeastern Alaska, the range of *Loligo opalescens* was extended from 55° N to more than 58° N in two separate periods. These invasions were temporary, apparently associated with warmer than average temperatures; and there was no evidence subsequently of paralarval stages in the area (WING & MERCER, 1990), suggesting that the population had not become established. *Martialia hyadesi* (Ommastrephidae) has a circum-polar distribution related to the Antarctic polar front zone (PIATKOWSKI, RODHOUSE, & DUHAMEL, 1991), but it spreads northward sporadically over the Patagonian shelf associated with an unusually low sea-surface temperature (RODHOUSE, 1991).

As the oceans are essentially continuous, marine organisms with mobile stages have the theoretical potential to disperse around the world. Many coleoids are mobile at most stages of their life, and yet only a small number are found widely distributed. Somewhat surprisingly, the only living spirulid, *Spirula spirula* (see *Treatise Online*, Part M, Chapter 6, Biogeography of Recent Forms, Fig. 8) (BRUUN, 1943, 1955), and *Vampyroteuthis infernalis* (see *Treatise Online*,

TABLE 8. The estimated density of sepiolids caught in the northwestern Mediterranean Sea in trawls between 147 and 1156 m depth (Villanueva, 1995).

Subfamily and species	Estimates of number per km ²
Rossiinae	
<i>Rossia macrosoma</i>	60
<i>Neorossia caroli</i>	24
Heteroteuthinae	
<i>Heteroteuthis dispar</i>	98
Sepiolinae	
<i>Sepiola neglecta</i>	29
<i>Rondeletiola minor</i>	2109
<i>Sepietta oweniana</i>	2338

Part M, Chapter 6, Biogeography of Recent Forms, Fig. 9), the only member of the Vampyromorpha (PICKFORD, 1946), are widely distributed; yet neither species can be regarded as fast moving. The latter is apparently restricted to the oxygen-minimum

layer (PICKFORD, 1946, 1949a, 1949b; SEIBEL & others, 1997). Environmental barriers can prevent the passage of coleoids. Cold, oxygen-deficient water off the southern coast of Africa has existed for about 2.5 million years and is considered likely to have led to the divergence of a loliginid squid to two subspecies, *Loligo vulgaris vulgaris* and *L. v. reynaudii* (AUGUSTYN & GRANT, 1988). The genus *Teuthowenia* shows discrete, ecologically distinct distribution patterns in the three geographically isolated species living in the Atlantic Ocean; their distributions reflect the influence of biotic and abiotic factors, as the species occupy different ranges of salinity and temperature (N. A. VOSS, 1985) (see *Treatise Online*, Part M, Chapter 6, Biogeography of Recent Forms, Fig. 13–14).

GREGARIOUSNESS

Sociality was recognized by VERRILL (1882, p. 305) as he commented that *Illex illecebrosus* “occurs in vast schools when it

TABLE 9. The capture rate per hour of several species of Recent coleoids at various depths in the open waters of the Mediterranean Sea (Roper, 1972).

Species	No. collected per hour Daylight	No. collected per hour Darkness	Depth m
<i>Heteroteuthis dispar</i>		4	45
		4	50–100
	1.1		150–500
	5		200
	1		250
	3		400
<i>Onychoteuthis banksii</i>	1		410
		1	40
		6	0–45
		8	50
		1	80
	0.5		100
<i>Histioteuthis reversa</i>	0.3	0.3	375
<i>Brachioteuthis riisei</i>		1.0	150
<i>Todarodes sagittatus</i>		0.3	150
<i>Chiroteuthis veranyi</i>		0.3	400
<i>Galiteuthis armata</i>		0.5	400
<i>Pyroteuthis margaritifera</i>	1.3		400–600
		2	155
<i>Chtenopteryx sicula</i>		1.8	150–200
	5		50–100
		2.2	100–150
<i>Ommastrephes paralarva</i>		1	135
<i>Argonauta argo</i>		1	135

visits the coast." Aggregations of coleoids are best known among the teuthids but are occasionally recorded in other orders. The number of animals per unit area, volume, or time provides some indication of social structure, yet the density of coleoids is rarely recorded. Even when it is, various parameters have been used, so any comparison of the results is difficult. Numerous species occur in huge numbers and support fisheries of up to 2.7 million metric tons per year; fishing is mostly limited to the continental shelf areas, but their many predators consume many more metric tons in a year (CLARKE, 1983, 1996).

The ommastrephid *Illex illecebrosus* (MATHER & O'DOR, 1984) and a small loliginid, *Alloteuthis subulata*, both exhibit schooling behavior, the latter in daylight and darkness under experimental conditions (LIMA & others, 1995). Schools of the largest ommastrephid, *Dosidicus gigas*, can consist of some tens of widely spaced individuals or of hundreds or thousands of closely spaced individuals moving side by side night and day (NESIS, 1983). Aggregations of other species of squids occur as well.

Some coleoids are social only during courtship and mating. Loliginid squids exhibit various social habits, and *Sepio-teuthis sepioides* changes from nonsocial to highly social behavior during its lifetime (MOYNIHAN & RODANICHE, 1982). *Loligo vulgaris reynaudii* aggregates in shoals of separate sexes, often consisting of thousands of individuals and only mixing together on the spawning grounds (SAUER, SMALE, & LIPINSKI, 1992). A photograph of *Loligo opalescens* mating close to a ship shows a dense and milling mass of squids directly below a night light (LANE, 1957), which probably attracted the squids, as it does other coleoids (CLARKE & PASCOE, 1998). Spawning *L. opalescens* gather in huge numbers, and its spawning grounds off La Jolla, California, occupy an area of 1.6 km², of which 50 percent can be covered with their egg cases (FIELDS, 1965). After depositing eggs, the adults die, and their bodies litter the

spawning grounds, but no measures of their density are available. An estimated 4 to 16 paralarvae/1000 m³ of *L. opalescens* were collected from the plankton near the spawning grounds (OKUTANI & MCGOWAN, 1969). The density of paralarvae less than 4 mm in mantle length of ommastrephid squids in the Kuroshio region of Japan is shown in Table 7 (SAITO & KUBODERA, 1993).

In the northwestern Mediterranean, bottom trawls at various depths show coleoids to occur widely and in different densities. In a single trawl, a total of 1250 specimens of *Sepietta oweniana* (Sepiolida) were caught in one hour (BELCARI, BIAGI, & SARTO, 1989), and up to 77 were caught in the same period of time in other bottom trawls (VILLANUEVA, 1995). Some 5000 *Rondeletiola minor*, another sepiolid, were captured in a single haul in a bay on the Italian coast (NAEF, 1923), and more recently a bottom trawl caught 70 specimens of the same species in one hour (VILLANUEVA, 1995). Estimates show that *R. minor* and *Sepietta oweniana* have the highest density per km² among the sepiolid species living in one area of the Mediterranean (Table 8). In the open waters of this sea, coleoids were captured at between 0.3 and 5.0 per hour (Table 9) (ROPER, 1972).

Information is available about the numbers of some coleoids occupying a specific volume or area. From their capture in opening-closing nets in the North Atlantic, it was possible to estimate the numbers of several species present per 10,000 m³ (Table 10). The figures in this table are the corrected values for those recorded in the paper by LU and CLARKE (1975b) and given in a personal communication by M. R. CLARKE in 1996. Near the Canary Islands (North Atlantic), when *Spirula spirula* (Spirulida) was caught in hauls, it was present in pairs or in groups of 8 to 11 individuals (LU & CLARKE, 1975b), and off the coast of Natal, South Africa, 26 specimens of this species were captured in a single haul lasting 70 minutes (BRUUN, 1955). The

TABLE 10. The number of specimens belonging to five species of Recent coleoids filtered per 10,000 m³ to show their density and distribution in the water column, at the depths sampled day and night in the North Atlantic (Lu & Clarke, 1975b).

Depth in m	Oegopsida				Sepiolida		Vampyromorpha		Octopoda (pelagic)	
	<i>Bathyteuthis abyssicola</i>		<i>Mastigoteuthis schmidti</i>		<i>Heliocranchia dispar</i>		<i>Vampyroteuthis infernalis</i>		<i>Japetella diaphana</i>	
	day	night	day	night	day	night	day	night	day	night
0–100	–	–	–	0.29	0.07	0.04	–	–	0.76	0.04
100–200	–	0.27	–	–	0.64	0.20	–	–	0.36	0.60
200–300	–	0.23	–	0.05	0.28	0.11	–	–	0.14	0.28
300–400	0.05	–	–	–	0.09	0.06	–	–	0.05	0
400–500	–	0.06	–	0.06	–	–	–	–	0.04	0
500–600	0.38	0.06	0.54	0.47	–	–	–	–	0.09	0.06
600–700	0.17	0.46	1.21	1.85	–	–	–	–	0.17	0.35
700–800	0.65	–	0.42	0.69	–	–	0.13	0.28	0.26	0.23
800–900	0.23	0.48	0.33	0.59	–	–	0.23	0.32	0.23	0.27
900–1000	0.05	0.10	0.28	0.21	–	–	0.09	0.10	0.05	0.31
1000–1250	–	0.04	0.79	0.04	–	–	0.08	0.07	0.28	0.15
1250–1500	–	–	–	0.07	–	–	–	–	–	–
1500–2000	–	0.03	–	–	–	–	–	–	–	–

vertical distribution patterns for the most abundant species caught off the island of Oahu (Hawaii) are shown in Table 5.

Among benthic, coastal octopods, a monthly count of *Octopus briareus* ranged from 2 to 12 in an area of 810 m² (ARONSON, 1986); a single *O. joubini* occupied an area of 31 to 35 m² (MATHER, 1982); and *O. briareus*, living in a small saltwater pond (0.92 km²), had a density of 11 to 16 individuals in an area of 1000 m², depending on the presence of suitable sites for dens, the nearest neighbor distance being 80 cm (ARONSON, 1989). In the eastern Atlantic Ocean bottom, trawls, each swept for one hour, were made over an area of 138,000 to 150,000 m², in depths of 14 to 362 m, to capture *Octopus vulgaris* during October (Table 11). Most trawls were made in daylight, the time when this species is usually in its den. Of the octopuses caught, most (60.9 percent) were in water less than 30 m deep; with 17.6 percent between 30 and 40 m, and 20 percent between 40 and 100 m (GUERRA, 1981).

In the deep sea, the abundance of cirrocopods was estimated from several hundred photographs and found to range from 1.1 to

98/km²; where most abundant, the animals were in relatively organic-rich waters (ROPER & BRUNDAGE, 1972).

Mass occurrences are occasionally recorded when large numbers of one species invade a coastal area and are captured in a single haul in a short period of time or are stranded. Such occurrences are often termed plagues. There are several records of *Octopus vulgaris* invading the southern coast of England and the northern coast of France; along one shore of the Cherbourg peninsula (France), 68 octopuses were counted over a distance of 180 m (GARSTANG, 1900). Further invasions of this species have been recorded since, and in 1950 and 1951, it was unusually abundant along the English coast and entered harbors (REES & LUMBY, 1954). *O. vulgaris* was reported in large numbers on the coast of Japan; at the same time, the pearl-culturing bivalve was found to have cavities in its shell, and this was traced to the activities of the octopuses (FUJITA, 1916).

Reported mass strandings of the pelagic, oceanic octopod *Argonauta* date back to 1758. More recently, more than 6000 specimens were captured in one week in the Japan Sea, and large catches continued for months

(NISHIMURA, 1968; OKUTANI & KAWAGUCHI, 1983). *A. argo* and another pelagic oceanic octopod, *Tremoctopus violaceus*, appeared in huge numbers in the northern Adriatic Sea in 1936 (LANE, 1957).

VERRILL (1882) observed immense numbers of the ommastrephid *Illex illecebrosus* stranded on beaches on islands in the Bay of Fundy. A mass stranding of some 2000 specimens of the fast-moving ommastrephid *Martilia hyadesi* occurred on a stretch of beach about 400 m long on an island in the Southern Ocean (O'SULLIVAN & others, 1983); subsequent strandings of this species have been recorded (P. R. RODHOUSE, personal communication, 1993). The largest of the ommastrephids, *Dosidicus gigas*, sometimes occurs in large numbers stranded on the beaches of California, and mass invasions were recorded there in 1934, 1937, and 1974 (NESIS, 1983). Dead or dying *Ommastrephes (Todarodes) sagittatus* have been stranded along Scottish beaches, where the average number was up to 185 squids per 980 m along the shore (STEPHEN, 1937). The large oegopsid *Thysanoteuthis rhombus* appears regularly in the inshore waters of Japan, and after rough weather, many are barely alive when stranded (NISHIMURA, 1966). About 1000 specimens of the oceanic onychoteuthid *Chaunoteuthis mollis* were caught in one haul off Japan. Most were gravid females, probably forming a spawning population (OKUTANI & IDA, 1986). Even the giant squid, *Architeuthis*, has occurred in unusual numbers, as in October, 1875, when many were seen floating on the surface on the Grand Banks and a few were barely alive (VERRILL, 1882).

There are numerous reports of single strandings. STEENSTRUP (1898) wrote of gigantic cephalopods washed ashore and of strandings of ommastrephids and architeuthids dating back to the sixteenth century. The giant squid, *Architeuthis*, has been stranded off the coasts of Norway, the British Isles, Newfoundland, and America on many occasions, and these and other

TABLE 11. The highest numbers of *Octopus vulgaris* captured in trawls of one hour duration in October, off the coast of western Africa (26°N 23°N). The majority of the 53 trawls captured fewer than 10 specimens (Guerra, 1981).

Number captured per hour of trawling	Depth trawled in m
71	70-73
70	38-42
57	30
57	14
52	23-25

strandings have been tabulated (ALDRICH, 1991; ROELEVELD & LIPINSKI, 1991).

MORTALITY

Death can occur at any stage of the life cycle, and mortality is considered to be particularly high in the first moments of life in five orders of benthic marine invertebrates (GOSSELIN & QIAN, 1997). Mortality of the larvae of marine invertebrates is thought to be enormous among planktonic but lower in benthic larvae, although estimates are rare for any marine organism (C. M. YOUNG & CHIA, 1987). The relative importance of each potential source of mortality in larvae is little known (MORGAN, 1995) and is difficult to investigate in the sea, and for most coleoids, there is little or no information on the time, place, or manner of death. However, besides predation, mortality may be due to one or several natural causes, including changes in salinity, turbidity, pressure waves, starvation, diseases, natural chemical toxins, and pollution. Death can also result from chasing prey, such as the small silvery fish, the grunion *Leuresthes tenuis*, toward beaches in California. Furthermore, the tissues of several coleoids are known to disintegrate quite rapidly in warm temperatures, leaving behind only the hard tissues they possess (the beaks, radula, statoliths, gladii, stylets, cuttlebone, and internal chambered shell).

During the early stages of life, mortality can result from predation, including cannibalism, an inadequate supply of suitable

prey, parasites, disease, adverse abiotic conditions, transportation, and dispersal. For the planktonic paralarvae of benthic species, the inability to find a suitable site for settlement may prove fatal. The relative importance of such potential sources of mortality is barely known for cephalopods except for the early stages of life from laboratory mariculture. The coastal sepiid *Sepia officinalis* dies within three days of hatching if food is not available (BOUCHAUD, 1991). The ommastrephid squid *Illex illecebrosus* is estimated to have a mortality of 90 percent at the egg stage, 90 percent at the rhynchoteuthion paralarval stage, and 90 percent at four months of age (O'DOR, 1983). In another species of this family, *Todarodes pacificus*, mortality is more than 95 percent in paralarvae of 1.5 to 75 mm mantle length; this is attributable to translocation, starvation, and predation (OKUTANI & WATANABE, 1983). In laboratory-reared *Octopus vulgaris*, the mortality rate for the planktonic paralarval stage was 18.5 percent at 10 days, 67 percent at 20 days, 82 percent at 30 days, and 91 percent at 40 days (the time of settlement) (ITAMI & others, 1963; NIXON & MANGOLD, 1996). In another study of this species, a mortality rate of 91.1 percent from hatching to settlement was recorded (VILLANUEVA, 1994). The mortality of *Bathypolypus arcticus*, a bathy-benthic octopod inhabiting waters below 6° C, was 96 percent between hatching and adult (O'DOR & MACALASTER, 1983).

Spawning is terminal in some species and may result in mass death among these aggregations (BOYLE, 1983a; MANGOLD, YOUNG, & NIXON, 1993). Dead and dying males and females of the myopsid squid *Loligo opalescens* cover their egg masses on the spawning grounds (FIELDS, 1965). Concentrations of dead, mated females of the ommastrephid *Illex oxygonus* have been observed off the Florida coast (O'DOR, 1983). For most species, little or nothing is known of the nature of their death.

During the extremely cold winter of 1962–1963, large numbers of dead octopuses (*Octopus vulgaris*) were collected near the Channel Islands, and dead cuttlefish (*Sepia officinalis*) were seen floating among large patches of cuttlebones between Dover and Guernsey (WOODHEAD, 1964). The giant squid, *Architeuthis*, was recorded in unusual numbers on the Grand Banks by VERRILL in 1882. Dead octopuses of an unusually large size were seen floating on the surface (37°47' N, 74°15' W) as a steamer travelled a distance of some 290 km, and the specimens collected indicated that they were possibly the oceanic, pelagic *Alloposus mollis* (MURRAY & HJORT, 1912). The cuttlefish *Sepia officinalis* has been washed ashore in large numbers in Scotland, and its cuttlebones have been present in sufficient numbers to form long white bands on the beach (STEPHEN, 1944). A huge mass of cuttlebones covered a considerable area of a beach on the coast of Tunisia and made it appear white (author's personal observation, 1960). TOMPSETT (1939) recorded that the water and shores along parts of the Irish Sea are so covered by the buoyant cuttlebones that they resemble sea foam. Cuttlebones are carried long distances, as those identified as African and European species have been collected from the beaches of the Americas (G. L. VOSS, 1974). Of the shells cast ashore in the tropics, the white, chambered shells of the spirulid *Spirula spirula* are the most abundant; if such sediment became fossilized, then the shells of *Spirula* would be the most characteristic fossil (BRUUN, 1955). Examples of the so-called belemnite battlefields have been found in Antarctica and Britain; a cross section of mostly adult belemnites from Antarctica show the presence of *Belanopsis stephensoni* in very considerable numbers (DOYLE & MACDONALD, 1993), but comparison with the few recorded mass deaths of Recent Coleoidea is difficult in the absence of density measurements.

Note: this manuscript was initially submitted in 1999, and no new references have been added after that date.

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