

2.22 **Family OMMASTREPHIDAE** Steenstrup, 1857 by Clyde F.E. Roper, Chingis Nigmatullin and Patrizia Jereb

Ommastrephidae Steenstrup, 1857c, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1857(1/2): 11–14 [12].

Type Genus: *Ommastrephes* d'Orbigny, 1834.

FAO Names: En – Flying squids; Fr – Encornet, Calmar; Sp – Jibia, Pota, Volantes.

Diagnostic Features: The mantle is cylindrical or conical; **densely muscular**. Fins terminal, transversely rhomboidal or heart-shaped. Head and eyes are large. **Arms strong with well-developed protective membranes and swimming keels**. Suckers biserial with denticulate rings. **Tentacles with well-defined stalk, carpus, manus and dactylus**. Manus and dactylus bear 4 series of suckers, except *Illex* which has 8 series of suckers on the dactylus. The suckers of the 2 median series on the manus are larger than those on the marginal series. The large sucker rings on the manus have sharp teeth, low broad plates, or are smooth (last 2 conditions mainly in *Illex*). The special fixing apparatus with knobs and opposing smooth-ringed suckers occurs on the carpus only in Ommastrephinae. **One or both ventral arms hectocotylized**. If one arm is hectocotylized, it may be longer than the adjacent non-modified ventral arm, or both arms are equal-sized. **Three types of hectocotylization distinguish the subfamilies according to differences in the distal protective membranes. Buccal membrane connective formula is DDVD**. The funnel groove is deeply recessed, distinct, triangular, either smooth, without a foveola (Illicinae, *Todaropsis*), or with a foveola, with either; 1) an arched transverse fold (pocket) of skin (other Todarodinae), or 2) a foveola with additional small, arched, cutaneous pockets situated on each side of the funnel groove (Ommastrephinae). **Funnel-locking cartilage with 2 deep grooves joined to each other in the form of an “inverted-T” shape: this form is the principal family characteristic**, and it is present and stable throughout ontogenesis from the earliest paralarval stage. Mantle-locking cartilage consists of 2 merging ridges (horizontal and vertical) that correspond to the form of the funnel cartilage grooves. The funnel- and mantle-locking cartilages are fused in 2 species, beginning at the end of the paralarval stage in *Sthenoteuthis oulaniensis* and *Euclideanoteuthis luminosa*. The nuchal cartilage is a relatively long, narrow ridge and groove plate with rounded ends; the mantle component conforms to fit into the nuchal component. The gladius is narrow and sword-shaped, consists mainly of rachis; vanes absent. The rachis is supported by 3 rigid ribs: the median rib and 2 marginal ribs. Lateral plates are extremely narrow, transformed into rigid ribs on each side of the rachis. The posterior part of the gladius, anterior to the cone flags, is transformed into a narrow, flexible, supportive stem. The vanes (wings) are absent. The conus is small and the rostrum on the apex of the cone is reduced to a minute cup, which usually is distinguished only with a microscope. The morphology of the beaks is typical for an oegopsid squid. The lower beak is most suitable for identification with the following characters: a tooth on its shoulder, a transparent strip below the jaw angle in young and some adults, a low wing fold (or no wing fold), a broad hood with notch, a relatively long rostral edge compared with the wing, a rather square profile, the hood in the midline about as long as the rostral edge, and a lateral wall fold that extends to a point about half-way between the crest and the free corner of the lateral wall (or no fold at all). The regression of the lower rostral length in millimetre (r) against wet weight in grams (w) for the family is: $\ln w = 2.714 + 293 \ln r$. Radula consists of 7 rows of teeth: the central (rachidian) row of trident-shaped teeth, 2 lateral rows of bicuspid teeth flanking it on each side, then 2 rows of canine-like unicuspid marginal teeth on each side. Marginal plates present, reduced. Light organs (photophores) are absent in Illicinae and Todarodinae and present in Ommastrephinae, either as small, subcutaneous granules, or as round, oval, or longitudinal, reflective, cutaneous photophores. Ocular and intestinal photophores also can be present. Spermatozoa possess 2 flagella (*Illex*) or 1 flagellum (all other Ommastrephidae).

Size: Minimum adult size is 80 to 100 mm mantle length and 10 to 13 g in weight (*Hyaloteuthis*), and maximum adult size extends to 1.2 m mantle length, and to 55 to 65 kg in weight (*Dosidicus*).

Geographical Distribution: The family has representatives in all oceans of the world.

Habitat and Biology: Ommastrephid squids are the most abundant, widely distributed and ecologically active family of cephalopods. They are strong, muscular, active, nektonic, small, medium- and large-sized squids that are distributed throughout the World Ocean from sub-Arctic seas to sub-Antarctic seas. They inhabit waters of the shelf, slope and open ocean, from the surface to depths that range to 2 000 m. Almost all species, particularly the oceanic ones, are abundant and widely distributed. As a rule the range of populations has a complex spatial structure and it is subdivided into reproductive zones and spatial feeding areas. Three main ecological groups (life forms) are distinguished among ommastrephids by characteristics of habitat, especially spawning habitat, which includes the degree of relationship with the bottom. 1) Slope-shelf group: the main habitats are the waters of the continental slope and shelf; *Illex*, *Todaropsis*, *Todarodes pacificus*, *T. angolensis*, *T. sagittatus* (the North African coast population), *Nototodarus sloanii*, *N. gouldi*. 2) Nerito-oceanic group: the main habitats are the waters of the continental slope, oceanic seamounts and islands, and adjacent oceanic waters; *Todarodes sagittatus* (the North Atlantic population), *T. filippovae*, *Nototodarus hawaiiensis*, *Martialia*, *Ornithoteuthis*, *Dosidicus*. 3) Oceanic group: the entire life cycle takes place only in oceanic waters and no connections or relationships ever exist with the bottom; *Ommastrephes*, *Sthenoteuthis*, *Euclideanoteuthis*, *Hyaloteuthis*. The majority of ommastrephids are among the fastest growing squids. The maximum relative daily growth rates (RDGR) of body weight were observed in paralarvae at 15 to 20% body weight. RDGR in juveniles of fast-growing species (e.g. *Dosidicus*, *Sthenoteuthis*) are high, up to 10 to 12% body weight, while those of slow-growing (e.g. summer-spawning *Illex argentinus*) are 3 to 4% body weight. Immature and maturing subadults exhibit 2 to 3% body weight. The maximum absolute daily growth rate observed in large-form females of *Dosidicus* at 350 days old was 104 g/day (about 0.8% body weight). Somatic growth of mature shelf-slope ommastrephids (*Illex*, *Todaropsis*, *Todarodes*) sharply decreased to 0.3 to 0.6% body weight, then ceased during the spawning period when feeding activity ceased.

completely. Mature and spawning oceanic squids (*Dosidicus*, *Ommastrephes*, *Sthenoteuthis*) demonstrated slow growth at a level of 1.5 to 2% body weight while active feeding continued. Considerable variation of adult sizes exists in large, medium-sized and dwarf ommastrephids basically dependant on the differences of RDGR at the larval and juvenile stages. Usually males are smaller than females due to earlier maturation and consequent earlier decrease of somatic growth. Individual and group phenotypic variability of growth and maturation rates with regard to intraspecific structure and year-round spawning with high fecundity (from 0.1 to 35 million ova) enables ommastrephids to maintain stability of their populations under considerable variation in numbers. In spite of differences in growth rates, adult size (e.g. mantle lengths from 80 to 120 mm up to 600 to 900 mm), as well as ecological and zoogeographic life styles, life cycles of almost all ommastrephids are one year. However, some tendencies exist to shorten the life cycle to half a year, e.g. in some tropical populations of *Illex coindetii* and *Todaropsis eblanae*, the dwarf form of *Sthenoteuthis oualaniensis* and *Hyaloteuthis pelagica*. The length of spermatophores formed by ommastrephid males ranges between 5 and 53 mm (4.4 to 27% mantle length), depending on the species, mantle length and stage of spermatophorogenesis. Minimum male fecundity ranges from 100 spermatophores (*Hyaloteuthis*), through 600 to 1 800 (*Illex*) up to 1 000 to 2 500 (*Dosidicus*, *Ommastrephes* and *Sthenoteuthis*). Spermatophores are transferred to the mantle cavity (*Illex*) or to the buccal membrane where 7 to 265 seminal receptacles are situated (all other Ommastrephidae). Ommastrephid squids mate in the "male-parallel" or "head to head" position. Mating is quick, not more than 1 to 2 minutes, and promiscuous, with both sexes accepting multiple partners. The oocyte stock development is asynchronous throughout the entire ontogenesis with constant predominance of the small protoplasmic oocytes. The ripe egg size varies in different species from 0.75 to 1.2 mm (*Illex*, *Todaropsis*, some *Todarodes*, *Nototodarus*, *Ornithoteuthis*, Ommastrephinae) to 1.6 mm (*Martialia*) and to 2.4 mm (North Atlantic and Mediterranean *Todarodes sagittatus*). The range of female potential fecundity varies from 40 thousand to 35 million oocytes depending on species and adult mantle length. Maximum egg number in oviducts varies from species to species from 50 up to 1.2 million eggs. Ommastrephids are intermittent spawners with multiple filling and evacuation of the oviducts, with up to more than 10 cycles.

Two strategies of spawning exist: the coastal type and the oceanic type. The coastal type is characteristic of Illicinae and Todarodinae (potential fecundity is 0.04 to 2.5 million). After maturation and initiation of spawning activity, females cease to feed. During the spawning period of life, with continuous oocyte maturation and periodical laying of egg-masses, the main source of energy is the digestive gland and mantle tissue. This is called the descending type of spawning, during which initial egg masses laid are the largest with the greatest number of eggs, then in subsequent egg masses, the number of eggs gradually decreases due to reduction of the female energetic reserves. Consequently, the somatic growth becomes negative and by the end of the spawning period the female's body proportions are significantly changed. The oceanic type is characteristic for the Ommastrephinae (potential fecundity is 0.1 to 35 million). During the spawning period a significant number of oocytes mature, periodical laying of egg masses of approximately the same size exists, active feeding between egg-laying events continues and appreciable somatic growth occurs. Total post-spawning mortality occurs in all ommastrephid species. Large, pelagic, gelatinous, egg masses either float near the surface or at the near-bottom habitat depending on the species. Egg masses are slightly more dense than seawater and they mostly inhabit the near-surface or midwater pycnoclines. Duration of embryonic development in species for which data are available, with egg sizes of 0.75 to 0.9 mm varies from 3 to 22 days; duration depends mostly on water temperature. post-embryonic development is achieved with a unique paralarval stage (rhynchoteuthion) that is characterized by the tentacles fused together to form a trunk-like proboscis with a few suckers on the distal tip. The proboscis is present at hatching, and by the end of the paralarval stage, between 6.5 and 10 mm mantle length, the proboscis progressively splits, starting from the proximal base, and soon the tentacles are separated.

Ommastrephids exhibit the following ecological traits of r-strategies: monocyclia (a complete life cycle within one year), small eggs, very high fecundity, prolonged intermittent multi-batch individual spawning and prolonged population spawning, presence of the planktonic rhynchoteuthion paralarvae and juveniles, very high growth rates, complex intraspecific spawning structure with presence of different seasonal spawning groups, significant long-term fluctuations of abundance (by an order of magnitude or more), and complete annual renewal of the population composition. The most important factor that determines the pattern of abundance, dynamics and distribution of exploitable ommastrephid populations is the availability of planktonic paralarvae and juveniles that inhabit subsurface depths for about 2 to 2.5 months. These stages are characterized by a high mortality rate. Therefore, spawning success and paralarval survival rates constitute the principal factor that determines recruitment level. Another important ecological-population feature of these squids is their 1-year life cycle. These 2 key factors govern the problems and specifics of ommastrephid fishery biology and the annual abundance dynamics. All ommastrephids are obligate shoaling and schooling animals from the young juvenile stages. The number of individual squid in schools ranges from 2 to 5 up to some hundreds, even thousands, generally of equal-sized individuals. Most ommastrephid species are characterized by long daily vertical migrations (hundreds of metres) and ontogenetic seasonal horizontal migrations, both parallel to the coastline, up to 1 000 to 1 500 miles long, and perpendicular (bathymetric) migrations from 10 to 50 miles and even to 150 miles offshore. During these migrations squids traverse the boundaries of a diversity of climatic zones and ecosystems. Throughout the life cycle, with continuous body size increases, most ommastrephids "permeate" the trophic pyramid, consecutively transferring from consumers of II to III orders to consumers of IV to VI orders and respectively changing the taxonomic and ecological spectrum of their food organisms (prey), enemies (predators) and parasites. In some oceanic communities, large-sized adult ommastrephids actually are the top-level predators. Ommastrephids are strongly active predators. Their food composition depends on their mantle length: in young small-sized squid, prey consist predominantly of meso- and macroplanktonic crustacea and juvenile fishes; in middle-sized squid prey consists of micronektonic fishes (mainly myctophids) and macroplanktonic euphausiids and shrimps; and in large-sized individuals prey are only fishes, squids and to a lesser degree, shrimps. Cannibalism is common. Ommastrephids have a high general and active metabolism, and a daily food consumption rate of 6 to 12% of the body weight of adult squids. Protein is the main substrate for energy metabolism. The unique combination of ecological and physiological traits confirms that ommastrephid squids are one of the most important elements in the "rigid framework" of highly mobile predators that unites local ecosystems into ecosystems of the next higher rank, and they function as "ecosystem enzymes": they significantly accelerate all ecosystem-related processes. The total instantaneous ommastrephid

biomass is around 55 million tonnes on average; the total yearly production is about 400 million tonnes (production/biomass coefficient is $P/B = 5$ in inshore species and $P/B = 8$ in oceanic species), and the total annual food consumption is around 1 000 million tonnes. Ommastrephids are food for numerous animals – sea birds, marine mammals and especially large predacious teleosts (alepisaurids, gempilids, coryphaenids, tunas, billfishes, swordfishes, etc) and sharks.

Interest to Fisheries: The Ommastrephidae are the most important commercial fishery group among cephalopods. **During the last decade (1997–2007) the annual world catch of ommastrephids varied between 1 and over 2 million tonnes, which represents 50% of the total world cephalopod catch.** The most important species in terms of catch tonnage were *Todarodes pacificus* in the northwestern North Pacific Ocean, *Nototodarus sloanii* in New Zealand waters and *Dosidicus gigas* in the eastern Pacific Ocean. The current level of exploitation of inshore ommastrephids, principally species of *Illex*, *Todarodes* and *Nototodarus*, is close to the maximum calculated yield and any significant increase in the catch of these ommastrephids seems unlikely in principle. Of the oceanic species group, only *Ommastrephes bartramii* in the northwestern Pacific Ocean and *Dosidicus gigas* in the Gulf of California and off Peru are exploited commercially. The bulk of populations of the oceanic squids *Ommastrephes* and *Sthenoteuthis* are widely scattered, consequently are not easily captured in large numbers. The combined potentially fishable aggregations of *Dosidicus*, *Ommastrephes* and *Sthenoteuthis* are calculated to be about 4 to 7 million tonnes. The total world fishery potential for all exploitable ommastrephid species is estimated at 6 to 9 million tonnes, while the total for all cephalopods combined is considered to be 6 to 12 million tonnes. In general, oceanic ommastrephids are considered the only remaining abundant underexploited fishery resource in the World Ocean that could provide an increase in world commercial catch of high-quality food protein. Oceanic ommastrephid stocks may be exploited on a year-round basis if the following problems can be solved: 1) optimization of search methodologies for fishery aggregations; 2) methods of artificial aggregation techniques for targeted squid species; 3) development of more effective, efficient fishing methods, tactics and gear; 4) wasteless utilization of total catch. Certainly, in order to solve these problems, considerable financial support and scientific effort will be required. Jigging with light attraction and trawling currently are the main fishing methods for ommastrephids. Jigged squid command the highest prices because they are the highest quality of marketable product. The main edible parts of squid, the mantle, fins, arms and tentacles, have the best quality for culinary presentation and they are a highly nutritious food. The common types of product on the market are frozen whole squid, processed/cleaned “tubes” (mantle) and arms; more rarely are squid available in fresh condition as sashimi. In Japan, however, about 70% of *Todarodes pacificus* is consumed as sashimi. The remaining 30% is comprised of processed squid products, such as, dried, smoked, salted, salted-fermented, canned, paste products, breaded rings or steaks, as ingredient in seafood cocktail, and pickled digestive gland (“liver”). Moreover, the viscera (principally digestive gland, then reproductive organs, inc sac, gladius, optical lobes of brain) are a source for production of important and promising biologically active substances that include anti-tumor, anti-shock, anesthetic and anti-parasitic drugs, cytostatics, powerful toxins, chitin, chitosan, squid-liver oil with wound healing properties, bactericidal and detoxification activity among others. The development of numerous and varied squid products on the premise of wasteless catch utilization will significantly increase the cost efficiency of ommastrephid fisheries and supply a high quality, abundant stock for the pharmaceutical and biochemical industries. Finally, squids are used extensively as bait mainly for tunas, billfishes, swordfishes and in the cod longline fishery. Many species of ommastrephids are used extensively as experimental animals in studies that examine care and maintenance, feeding, rearing (eggs, embryos, juveniles), treatment of disease, tagging and tracking, collecting, handling and transport, and anesthetics and euthanasia.

Remarks: Since the mid-twentieth century the traditional classification of the Ommastrephidae consisted of 3 subfamilies: Illicinae, Todarodinae and Ommastrephinae (e.g. Roeleveld, 1988; Guerra, 1992; Wormuth, 1998; Young *et al.* 2009). Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayshi *et al.*, 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodinae). The subfamilial classification has been further subdivided with the addition of 2 new subfamilies, Tदारopsinae and Ornithoteuthinae (Nigmatullin, 1979, 1992 [1991], 2000). In this presentation we choose to use the more conservative system with the 3 traditional subfamilies.

A complete list of the recognized genera and species is reported below. From the phylogenetic point of view, *Illex* and *Todaropsis* are the 2 most primitive ommastrephid genera, and the Ommastrephinae is the most advanced subfamily. In general, evolution within the family from the morpho-functional aspect (i.e. the development of active nektonic swimmers) and the ecological aspect (i.e. the shift from shelf-slope to oceanic realms), there are 3 basic stages: 1) the shelf-slope Illicinae, 2) the nerito-oceanic Todarodinae, and 3) the true oceanic Ommastrephinae.

Due to the paramount relevance of this family to the world fishery, a particularly detailed treatment has been given to it in this Catalogue. However, such an extensive literature exists on most Ommastrephid species, that only those publications considered comprehensive of biological and fisheries information are quoted in the main literature sections below. Many others are reported in the Appendices.

Literature: Wormuth (1976), Nigmatullin (1979), Roper *et al.* (1984), Guerra (1992), Dunning (1998b,c,f), Wormuth (1998), Dunning and Wormuth (1998), Dunning *et al.* 1998d, Nigmatullin (2004), Sweeney and Young (2003u), Wakabayshi *et al.* (2006), Young *et al.* (2009).

Family Ommastrephidae Steenstrup, 1857

Classification

(Species listed in **bold type** are the type species of the indicated genus)

1. Subfamily **ILLICINAE** Posselt, 1891
 - Genus *Illex* Steenstrup, 1880: 82
 - I. illecebrosus*** (Lesueur, 1821: 95)
 - I. argentinus* (Castellanos, 1960: 55)
 - I. coindetii* (Verany, 1839: 94)
 - I. oxygonius* Roper, Lu and Mangold, 1969a: 299

2. Subfamily **OMMASTREPHINAE** Posselt, 1891
 - Genus *Ommastrephes* d'Orbigny, 1834: 45 [in 1834–1847]
 - O. bartramii*** (Lesueur, 1821: 90)
 - Genus *Dosidicus* Steenstrup, 1857a: 120
 - D. gigas*** (d'Orbigny, 1835: 50 [in 1834–1847])
 - Genus *Eucleoteuthis* Berry, 1916: 60
 - E. luminosa*** (Sasaki, 1915b?: 144)
 - Genus *Hyaloteuthis* Gray, 1849: 63
 - H. pelagica*** (Bosc, 1802: 46)
 - Genus *Ornithoteuthis* Okada, 1927c: 15
 - O. volatilis*** (Sasaki, 1915b: 138)
 - O. antillarum* Adam, 1957: 3
 - Genus *Sthenoteuthis* Verrill, 1880b: 222
 - S. pteropus*** (Steenstrup, 1855: 200)
 - S. oualaniensis* (Lesson, 1830–1831: 240)

3. Subfamily **TODARODINAE** Adam, 1960b
 - Genus *Todarodes* Steenstrup, 1880: 83
 - T. sagittatus*** (Lamarck, 1798: 130)
 - T. angolensis* Adam, 1962: 32
 - T. filippovae* Adam, 1975: 3
 - T. pacificus* (Steenstrup, 1880: 79)
 - T. pusillus* Dunning, 1988b: 149
 - Genus *Martialia* Rochebrune and Mabille, 1889: H8
 - M. hyadesi*** Rochebrune and Mabille, 1889: H9
 - Genus *Nototodarus* Pfeffer, 1912: 434
 - N. sloanii*** (Gray, 1849: 61)
 - N. gouldi* (McCoy, 1888: 255)
 - N. hawaiiensis* (Berry, 1912: 434)
 - Genus *Todaropsis* Girard, 1890: 204
 - T. eblanae*** (Ball, 1841: 364)

Key to the subfamilies and genera of Ommastrephidae

- 1a. Photophores present **Subfamily Ommastrephinae → 2**
- 1b. Photophores absent → 7

- 2a.** Mantle narrow, elongate, posteriorly drawn out into a pointed tail; funnel groove side pockets often obscure; tentacle fixing apparatus without tubercle-like knobs; rings of large club suckers with 15 to 25 equal-sized pointed teeth; no external photophores, nor any small subcutaneous photophores; 1 photophore on each eyeball, 2 intestinal photophores; in adults a narrow pinkish photogenic band extends along viscera from rectum to near posterior end of mantle cavity with 2 gaps ***Ornithoteuthis***
- 2b.** Mantle wide, end of mantle without pronounced tail; funnel groove side pockets clearly defined; tentacle fixing apparatus with 1 or several knobs alternating with smooth ringed suckers; rings of large club suckers with either 1 large median tooth in distal part of ring, or with 4 large teeth, 1 at each quadrant; small yellow subcutaneous photophores (like short rice grains) on head, mantle, fins and arms; some species may have arrangement of different form (large mantle photophores) with reflective subjacent layer; 1 ocular and 1 or 2 intestinal photophores present → **3**
- 3a.** Tips of all arms in adults thin and very attenuate, bearing numerous, minute, densely packed suckers; arms have up to 200 pairs of suckers; large mantle photophores absent, small, scattered subcutaneous photophores present; 1 ocular and 2 intestinal photophores present in juveniles and subadults ***Dosidicus***
- 3b.** Tips of arms not attenuate; arms have about 32 to 35 pairs of suckers; large cutaneous mantle photophores present; ocular and intestinal photophores present or absent → **4**
- 4a.** No large cutaneous photophores in form of spots and stripes on ventral surface of mantle; small subcutaneous photophores present; no or 2 intestinal photophores; rings of large club suckers with 4 large teeth, 1 at each quadrant → **5**
- 4b.** Large cutaneous photophores of spot or stripe-like form occur on ventral surface of mantle; 1 intestinal photophore; rings of large club suckers with 1 large medial tooth in distal part of ring → **6**
- 5a.** Large, compound, subcutaneous photophore absent on anterodorsal part of mantle; no ocular or intestinal photophores; 1 wide gold or silvery longitudinal, cutaneous, bioluminescent stripe extends along ventral midline of mantle from near mantle edge to beginning of fin; end of fin slightly attenuate posteriorly; 4 to 7 suckers with denticulate rings in carpal part of club proximal to first knob ***Ommastrephes***
- 5b.** Squid of mantle length greater than 140 mm with single, large, oval, compound, subcutaneous photophore on anterodorsal part of mantle; 1 ocular and 2 intestinal photophores present; no longitudinal, cutaneous, bioluminescent stripe on ventral side of mantle; fin rhomboidal, not attenuate posteriorly; not more than 2 suckers with denticulate rings in carpal part of club proximal to first knob . . ***Sthenoteuthis***
- 6a.** Pair of long stripes of cutaneous, bioluminescent tissue (large elongate photophores) extends along ventral side of mantle, 1 on each side of midline, each stripe broken posteriorly by gap at level of maximum width of fin; 2 oval bioluminescent patches on head near anterior margin of mantle aligned with base of each ventral arm ***Eucleoteuthis***
- 6b.** Nineteen round, cutaneous, bioluminescent patches arranged in a fixed pattern on ventral side of mantle that form converging or separated pairs; cutaneous, bioluminescent patches at base, in middle and near tip of each ventral arm ***Hyaloteuthis***
- 7a.** Eight longitudinal series of small to minute suckers on dactylus of tentacular club . . **Subfamily Illicinae** → ***Illex***
- 7b.** Four longitudinal series of small suckers on dactylus of tentacular club **Subfamily Todarodinae** → **8**
- 8a.** Funnel groove smooth, without foveola ***Todaropsis***
- 8b.** Funnel groove with foveola → **9**
- 9a.** Biserial row of finger-like projections extends from first suckers almost to base of tentacular stalk; finger-like cirri project beyond protective membranes along both sides of arms and tentacular clubs ***Martialia***
- 9b.** Finger-like projections and cirri absent on arms and tentacular clubs → **10**
- 10a.** One ventral arm hectocotylized, usually right, rarely left; species distributed in all 3 oceans, mainly in temperate and cold waters ***Todarodes***
- 10b.** Both ventral arms hectocotylized: 1 arm in proximal and distal parts, other arm only in proximal part; species distributed in tropical, subtropical and partly temperate waters of Indo-Pacific region and Australian-New Zealand area ***Nototodarus***

Table 5

Character states within genera of the Ommastrephidae

Character State	<i>Illex</i>	<i>Todaropsis</i>	<i>Martalia</i>	<i>Todarodes</i>	<i>Nototodarus</i>	<i>Ornithoteuthis</i>	<i>Dosidicus</i>	<i>Ommastrephes</i>	<i>Sthenoteuthis</i>	<i>Eucoleoteuthis</i>	<i>Hyaloteuthis</i>
Funnel groove:											
a) smooth	X	X									
b) with foveola			X	X	X	X	X	X	X	X	X
c) with side pockets						X ^{1/}	X	X	X	X ^{1/}	X ^{1/}
Tentacular carpal-fixing apparatus:											
a) absent	X	X	X	X	X	X					
b) present							X	X	X	X	X
Central club sucker ring dentition:											
a) smooth or bluntly crenulated	X										
b) uniform-sized pointed teeth		X		X ^{2/}	X ^{4/}	X					
c) 1 pointed distal tooth larger			X	X ^{3/}	X ^{5/}					X	X
d) 4 large teeth, one at each quadrant			X				X	X	X		
Hectocotylization of ventral arms:											
a) both	X	X	X	X	X	X	X	X	X	X	X
b) one											
Hectocotylization, distal membrane:											
a) absent	X										
b) ventral enlarged											
c) thickened trabeculae		X	X	X	X	X	X	X	X	X	X
Photophores on intestine:											
a) absent	X	X	X	X	X			X			
b) present						X	X-juv.		X	X	X
Photophores on eyeball:											
a) absent	X	X	X	X	X						
b) present						X	X-juv.		X	X	X
Small subcutaneous mantle photophores:											
a) absent	X	X	X	X	X	X					
b) present							X	X	X	X	X
Large mantle photophores:											
a) absent	X	X	X	X	X	X	X	X	X	X	X
b) present											

^{1/} side pockets often obscure; ^{2/} in *T. pacificus* including *T. pusillus*; ^{3/} in rest *Todarodes*; ^{4/} in *N. gouldti* and *N. sloani*; ^{5/} in *N. hawaiiensis*.

FAO English names for Ommastrephidae

Flying Squids

Dosidicus

D. gigas Jumbo flying squid

Eucleoteuthis

E. luminosa Luminous flying squid

Hyaloteuthis

H. pelagica Glassy flying squid

Illex

I. argentinus Argentine shortfin squid

I. coindetii Broadtail shortfin squid

I. illecebrosus Northern shortfin squid

I. oxygonius Sharptail shortfin squid

Martialia

M. hyadesi Sevenstar flying squid

Nototodarus

N. sloanii Wellington flying squid

N. gouldi Gould's flying squid

N. hawaiiensis Hawaiian flying squid

Ommastrephes

O. bartramii Neon flying squid

Ornithoteuthis

O. volatilis Shiny bird squid

O. antillarum Atlantic bird squid

Sthenoteuthis

S. pteropus Orangeback flying squid

S. oualaniensis Purpleback flying squid

Todarodes

T. angolensis Angolan flying squid

T. filippovae Antarctic flying squid

T. pacificus Japanese flying squid

T. pusillus Little flying squid

T. sagittatus European flying squid

Todaropsis

T. eblanae Lesser flying squid

2.22.1 Subfamily ILLICINAE Posselt, 1891

Illicinae Posselt, 1891, *Videnskabelige Meddelelser fra den Naturhistoriske Forening i København*, 1890: 301–359.

Type Genus: *Illex* Steenstrup, 1880.

Diagnostic Features: Ommastrephids with **smooth funnel groove, without foveola or side pockets; 8 longitudinal series of small to minute suckers on dactylus of tentacular club;** rings of large manal suckers smooth or with flattened small teeth or low broad plates; **photophores absent;** tentacular stalks **without carpal-fixing apparatus;** either right or left arm IV hectocotylized (papillary type).

Remarks: The Illicinae formerly included *Illex* and *Todaropsis*, but the latter genus has been shifted to the Todarodinae as a better phylogenetic fit. While the relationships among the ommastrephid subfamilies remain unresolved, there seems little doubt that *Illex* is distinctive with several apomorphic characters, e.g. club sucker dentition and arrangement, absence of protective membranes on the hectocotylized tip, and secondary modifications on the medial portion of the hectocotylus. Some species of *Illex* have been or currently are the target of extremely important fisheries. Formerly *I. illecebrosus* supported a significant fishery that produced catches in excess of 100 000 tonnes (up to 160 000 tonnes) for several years. But probable overfishing and changing environmental factors drove the unmanaged fishery into a total collapse from which it has not recovered in more than 20 years. *Illex argentinus* on the other hand, after a marked negative fluctuation in the years 2004–2005, continues to support an extremely productive fishery that consistently produces catches of around 700 000 tonnes. This fishery is the object of a very comprehensive management system based on pre-assessed and constantly monitored biological factors and real-time catch statistics. *Illex coindetii* represents a reasonably significant bycatch in the Mediterranean fin-fish trawl fishery.

Illex Steenstrup, 1880

Plate IX, 52

Illex Steenstrup, 1880, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1880: 73–110 [82].

Type Species: *Illex illecebrosus* (Lesueur, 1821).

Diagnostic Features: The **funnel groove is smooth, without foveola or sidepockets.** No photophores present; no carpal-locking apparatus occurs on the tentacular stalk. Tentacular club moderately to broadly expanded. The dactylus of the tentacular club has 8 rows of small to minute suckers. Manus tetraserial; rings of largest medial suckers on manus have smooth, bluntly crenulate or flattened small teeth or low broad plates; lateral suckers of manus small. Carpal suckers are small, biserial. **Either right or left arm IV hectocotylized by the papillary type with equal frequency;** dorsal and ventral protective membranes of hectocotylus terminate near base of distal modified tip; secondary modification present on medial part of hectocotylized arm. The gladius has wide, long, cone flags that do not bear radial creases. The greatest width of the cone flags is roughly equal to that of the rachis. The marginal rigidity ribs of the rachis are doubled, and the axial rigidity rib of the rachis is T-shaped in cross-section. The lateral plates of the gladius adhere entirely to the dorsal surface of the rachis. The stem is short and pince-nez-shaped in cross-section. The cone is narrow, slightly compressed laterally; the rostrum is absent. The alveola is thick, and its surface bears tiny thorns. Each spermatozoum has 2 flagellae.

Remarks: Four species of *Illex* are recognized, initially based on morphological characters. While *Illex argentinus* is geographically isolated, thus easily identified, the remaining 3 species, *I. coindetii*, *I. illecebrosus* and *I. oxygonius* can be difficult to identify in areas where their distributions overlap. The systematics and distribution sections confirm the valid specific status of all 4 nominal species, provides distinguishing morphological characters, enumerates detailed geographic distribution, presents tables of meristic characters, a table of comparative morphological features and a key to species. Adults of the 4 species of *Illex* can be distinguished principally on the basis of the **hectocotylus, dentition of largest medial manal suckers, and morphological and meristic characters of the head, mantle, fins, arms, beaks and spermatophores.** *Illex argentinus* is the southernmost species but is rather broadly distributed from off Rio de Janeiro southward to the tip of the continent off Argentina and well offshore around the Falkland Islands. *Illex coindetii* is a single, variable, widely distributed species, morphotypes of which occur throughout the Mediterranean Sea, the eastern Atlantic from the North Sea to Namibia and the western Atlantic from the southeastern Caribbean, the Gulf of Mexico and the southern Straits of Florida. *Illex illecebrosus* is highly seasonally distributed, from off northern Florida, along the entire east coast of the United States of America and Canada to Newfoundland, the Labrador Sea, perhaps occasionally to Iceland. *Illex oxygonius* is the most restricted of the 4 species in its distribution, as it occurs from off New Jersey and the middle Atlantic states southward into the eastern Gulf of Mexico. Discriminate analysis of large suites of morphometric data on body and beaks can yield positive species identifications up to 90% correct for the 3 dominant species of *Illex*. Genetic analysis of the 4 nominal species of *Illex* using allozyme polymorphisms (Martinez *et al.* 2005a, b), confirms their valid specific status and reveals that *I. illecebrosus* and *I. oxygonius* are sister species, with a close relationship to *I. argentinus*, while *I. coindetii* forms a more remote, different lineage.

Definitions of Hectocotylus Features

- HAb** (length of) suckerless area at base of hectocotylized arm measured from V-notch between arms IV to first sucker.
- HALs** length of hectocotylized arm measured from most proximal sucker to distal tip (equivalent to HcA in Roper and Voss, 1983).
- HALt** total length of hectocotylized arm measured from V-notch between arms IV to distal tip.
- HA1** (length of) proximal sucker-bearing section on hectocotylized arm with normal-sized, graded suckers.
- HA2** (length of) medial section of hectocotylized arm (distal sucker-bearing section) with suckers of reduced diameter, fringed trabeculae, or other modifications.
- HA3** (length of) modified distal tip of hectocotylus characterized by absence of protective membranes and replacement of suckers with lamellae and papillae.

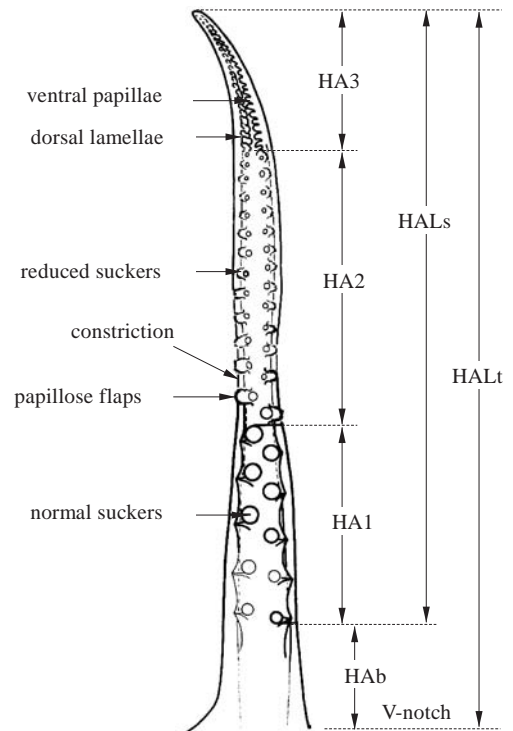


Fig. 281 Diagram of *Illex* hectocotylus showing morphological features, proportions and measurements

Table 6

Hectocotylized arm length^{1/} indices (HALsI) and hectocotylized tip length^{2/} indices (HAsSI) for mature specimens of the four *Illex* species (from Roper and Mangold, 1998).

	Mean	Range	Standard deviation	No.
HALI:				
<i>I. illecebrosus</i>	53.0	(39.7–66.0)	7.9	27
<i>I. coindetii</i>	63.7	(42.3–87.1)	9.9	65
<i>I. argentinus</i>	67.6	(49.5–82.0)	7.4	68
<i>I. oxygonius</i>	51.5	(40.6–59.9)	5.7	10
HA3LI:				
<i>I. illecebrosus</i>	22.1	(13.0–30.3)	4.6	27
<i>I. coindetii</i>	25.1	(17.1–30.0)	2.7	65
<i>I. argentinus</i> ^{3/}	50.3	(19.8–70.3)	11.0	68
<i>I. oxygonius</i>	28.8	(23.8–32.0)	2.7	10

^{1/} Length of hectocotylized arm measured from most proximal sucker to arm tip.

^{2/} Length of hectocotylized tip measured from most distal sucker to arm tip.

^{3/} Includes HA2, which loses suckers at full maturity, making it difficult to determine the junction point of HA2 and HA3.

Table 7Head length indices (HLI) and head width indices (HWI) for males and females of the four species of *Illex*^{1/}

	Male		Female	
	Mean	Range	Mean	Range
HLI:				
<i>I. illecebrosus</i>	16.4	(10.6–24.7)	15.7	(11.4–22.6)
<i>I. coindetii</i>	21.8	(13.7–29.6)	19.0	(10.0–23.6)
<i>I. argentinus</i>	19.5	(16.0–23.9)	16.8	(14.3–19.7)
<i>I. oxygonius</i>	18.2	(15.0–21.3)	16.3	(12.9–18.6)
HWI:				
<i>I. illecebrosus</i>	17.0	(10.0–21.8)	16.3	(12.9–18.6)
<i>I. coindetii</i>	21.1	(13.2–29.1)	18.4	(12.9–25.1)
<i>I. argentinus</i>	17.8	(11.8–21.1)	16.0	(11.7–18.8)
<i>I. oxygonius</i>	20.0	(18.2–22.9)	17.5	(14.7–19.7)

^{1/} Based on Roper *et al.* (1969a) and Lu (1973).**Table 8**Fin length indices (FLI), fin width indices (FWI) and fin base length indices (FbLI) for males and females of the four species of *Illex*^{1/}

	Male		Female	
	Mean	Range	Mean	Range
FLI:				
<i>I. illecebrosus</i>	43.8	(31.3–49.3)	44.1	(38.1–53.5)
<i>I. coindetii</i>	39.2	(31.3–46.4)	39.4	(29.4–46.2)
<i>I. argentinus</i>	41.9	(36.3–47.2)	42.3	(37.3–45.2)
<i>I. oxygonius</i>	45.0	(42.0–47.9)	45.0	(42.5–48.1)
FWI:				
<i>I. illecebrosus</i>	55.4	(43.0–64.2)	54.6	(40.9–65.8)
<i>I. coindetii</i>	56.4	(45.7–66.5)	53.7	(37.0–65.9)
<i>I. argentinus</i>	58.0	(51.9–66.3)	56.4	(52.2–64.2)
<i>I. oxygonius</i>	51.5	(43.8–62.4)	50.5	(43.1–56.9)
FbLI:				
<i>I. illecebrosus</i>	39.5	(28.4–44.3)	39.5	(33.8–50.3)
<i>I. coindetii</i>	33.9	(19.3–40.7)	34.5	(25.0–41.6)
<i>I. argentinus</i>	37.5	(35.2–43.0)	37.8	(34.4–40.3)
<i>I. oxygonius</i>	40.2	(35.8–42.4)	40.0	(37.9–43.2)

^{1/} Based on Roper *et al.* (1969a) and Lu (1973).

Table 9Arm length indices (ALI) (hectocotylus not included) for males and females for the four species of *Illex*^{1/}

Arm	<i>I. illecebrosus</i>		<i>I. coindetii</i>		<i>I. argentinus</i>		<i>I. oxygonius</i>	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Males:								
I	39.1	(25.5–56.0)	47.4	(27.1–77.4)	55.6	(45.8–65.0)	43.9	(35.2–53.3)
II	48.2	(32.4–70.0)	62.5	(37.4–96.6)	70.2	(57.9–84.2)	54.8	(45.0–64.2)
II	48.2	(32.4–70.3)	61.0	(37.6–95.9)	71.2	(52.5–86.4)	54.7	(43.8–63.0)
IV	43.0	(27.5–62.9)	54.1	(29.3–87.8)	61.6	(42.6–74.4)	47.9	(39.4–60.6)
Females:								
I	36.5	(29.2–49.3)	37.6	(25.0–56.1)	46.2	(39.3–53.7)	34.3	(27.9–39.3)
II	44.5	(35.3–56.8)	48.7	(36.4–67.1)	57.4	(48.5–66.5)	42.9	(34.7–50.9)
III	44.5	(34.7–57.6)	48.3	(36.4–67.1)	58.5	(47.1–70.0)	43.4	(36.5–54.0)
IV	40.4	(29.4–52.6)	42.4	(25.0–63.5)	52.0	(43.4–59.7)	38.1	(31.9–46.0)

^{1/} Based on Roper *et al.* (1969a) and Lu (1973).**Table 10**Comparison of the beaks of the four *Illex* species^{1/}

Feature	<i>I. illecebrosus</i>	<i>I. coindetii</i>	<i>I. argentinus</i>	<i>I. oxygonius</i>
Upper Beak:				
Hood	long, strong	long, strong	long, strong	short, weak very thin
Shoulder	serrated	smooth	serrated	smooth, straight or slightly curved
Jaw angle	large notch, with tooth	small notch	large, notch with tooth	small notch
Rostrum	long	long	long	short
Lateral wall	short, shallow; crest curved	short, shallow; crest curved	short, shallow; crest curved	long, deep; crest straight
Wing	short	short	short	short
Lower Beak:				
Jaw edge	straight, short	straight, long	curved, long	curved, long
Wing	long, wide, no lobe; regular outline	long, wide, no lobe; slightly irregular outline	long, wide, no lobe; regular outline	short, narrow lobate; irregular outline
Lateral wall	short, blunt	short, blunt	short, blunt	long, pointed
Rostral width	narrow	narrow	narrow	wide

^{1/} Based on Roper *et al.* (1969a) and Lu (1973).

Literature: O'Dor (1983), Rodhouse *et al.* (1998a), Roper *et al.* (1998), Roper and Mangold (1998), Martinez *et al.* (2005a,b) Carlini *et al.* (2006).

Key to the species of *Illex* (from Roper *et al.* 1998)

- 1a.** Proportional length (ALI) of all arms long (e.g. 8 to 10% larger than in other species); tentacular club not broadly expanded, medial manal suckers exceptionally enlarged, lateral manal suckers extremely small; distal modified portion of hectocotyized arm >50% of total arm length (=HA2 + HA3); distribution restricted to western South Atlantic Ocean, 23°S–55°S. ***Illex argentinus***
- 1b.** Proportional length (ALI) of all arms moderate to short (e.g. 8 to 23% smaller than in *I. argentinus*); tentacular club expanded, medial manal suckers enlarged, lateral manal suckers small (not so markedly disproportionate as above); distal modified portion of hectocotyized arm (HAS) <33% of total arm length; distribution North Atlantic, Caribbean, Gulf of Mexico, or Mediterranean → **2**
- 2a.** Distal enlarged manal-sucker rings notched, 7 or 8 low, broad, flat, plate-like teeth; relative lengths of fins and fin bases short; relative length of head (HLI) long; relative length of arms (ALI) long; base of hectocotyized arm (HAb) devoid of suckers for 13% of total arm length; trabeculae on hectocotylus midsection (HA2) modified to papillose, fringed flaps; distribution pan-Atlantic, only *Illex* species in eastern Atlantic and Mediterranean ***Illex coindetii***
- 2b.** Distal enlarged manal-sucker rings smooth, toothless, rarely with 1 or 2 notches; relative lengths of fins and fin bases long; relative length of head (HLI) short; relative length of arms (ALI) short; base of hectocotyized arm (HAb) devoid of suckers for 4 to 6% of total arm length; trabeculae on hectocotylus midsection (HA2) not modified; distribution restricted to western North Atlantic → **3**
- 3a.** Relative width of fins broad, 55% of mantle length; head length and width indices relatively low, 16 to 17% of mantle length; arm lengths relatively short in males, 39 to 48% of mantle length; arm sucker diameter indices relatively small, 1.02 to 1.75; hectocotyized arm equal to or slightly shorter than opposite arm IV and of equal thickness; lower beak jaw edge straight, short; wing long, wide; lateral wall short, blunt; rostral width narrow ***Illex illecebrosus***
- 3b.** Relative width of fins narrow, 51% of mantle length; head length and width indices relatively high, 16 to 20% of mantle length; arm lengths relatively long in males, 44 to 55% of mantle length; arm sucker diameter indices relatively large, 1.12 to 2.47, especially in males; hectocotyized arm relatively long, more robust than opposite arm IV; lower beak jaw edge curved, long; wing short, narrow; lateral wall long, pointed; rostral width wide ***Illex oxygonius***

Illex illecebrosus (Lesueur, 1821)**Fig. 282; Plate IX, 53**

Loligo illecebrosus Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101, pl. 11. [95]. [Type locality: Isles of Shoals, New Hampshire, USA, western North Atlantic Ocean].

Frequent Synonymy: *Illex illecebrosus illecebrosus* (Lesueur, 1821); *Loligo illecebrosus* Lesueur, 1821; *Loligo piscatorum* La Pylaie, 1825; *Illex coindetii* (Veranyi, 1839); *Ommastrephes illecebrosus* Verrill, 1880a,b; non *Illex illecebrosus*, Adam, 1952 (= *Illex coindetii* Veranyi, 1839).

FAO Names: **En** – Northern shortfin squid; **Fr** – Encornet rouge nordique; **Sp** – Pota norteña.

Diagnostic Features: The mantle is robust, widest at midpoint between anterior end and beginning of fins; tail not sharply pointed. Fin angle mostly 45° (40° to 50°) never greater than 50°; fin width greater than fin length. Head small, short, narrow; head width index low: 16.3 to 17.0. Arms relatively short, about equal length in both sexes. Right or left arm IV hectocotyized with distal hectocotyized portion limited to about 22% (13 to 30%) of total arm length; papillae and lamellae weakly developed; basal (proximal) suckerless part of hectocotyized arm short, about 4 to 6% of total arm length; proximal sucker-bearing part with 7 or 8 pairs of normal suckers that increase in diameter distally; distal sucker-bearing part with slight secondary modification of one-quarter reduction in sucker diameter compared to normal proximal suckers; oral surface of arm IV not expanded, sucker rows not abnormally separated; very slight muscular constriction in transition zone between proximal and distal sucker-bearing parts; trabeculae not

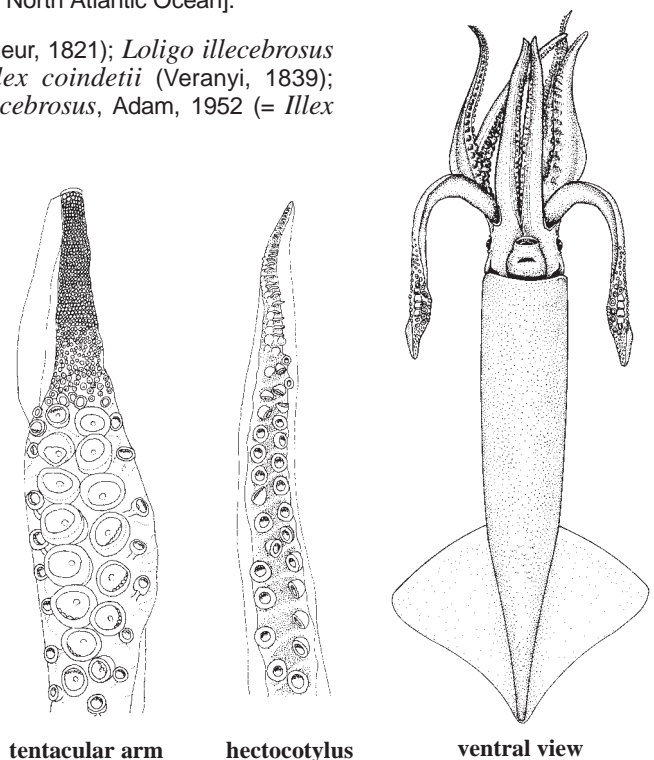


Fig. 282 *Illex illecebrosus*

modified as papillose fringed lobes; hectocotylized arm shorter than or equal to its opposite arm in length and always equal in thickness. One or 2 knobs present on dorsal row of lamellae on modified arm tip. Tentacular club expanded; largest distal medial mantle sucker rings smooth, only rarely with crenulations or notches. Lower beak with jaw edge straight, short; wing long, wide, no lobe; rostral width narrow; lateral wall short, blunt. Upper beak with long, strong hood; shoulder serrated; rostrum long; wing short; jaw angle with large notch, with tooth; lateral wall short, shallow; crest curved. Spermatophore cone at oral end of cement body a low, right-isosceles triangle with rounded corners in outline; oral tube long, narrow; aboral neck long, narrow. **Colour:** reddish brown to deep purple, more intense on head, arms and dorsal surfaces of mantle and fins; a dark purple stripe extends along dorsal midline of mantle; paler on ventral surfaces; a brilliant yellowish green tint.

Size: Maximum mantle length 340 mm in females and 270 mm in males in the northern part of its distributional range, but 200 mm in females and 180 mm in males in the southern part. Weight to 1 kg.

Geographical Distribution: Northwestern North Atlantic Ocean off the east coast of North America from about 26°N to 29°N off the east coast of Florida to 66°N (Iceland, southern Greenland, Baffin Island) (Fig. 283).

Habitat and Biology: The northern shortfin squid principally is a neritic species that inhabits continental shelf and upper slope waters, associated with the high-velocity Western Boundary Current (Florida Current, Gulf Stream) and nutrient-rich upwellings. The Blake Plateau is a major spawning area for the species in Slope Water shoreward of the Gulf Stream Frontal Zone. The Gulf Stream system entrains, transports and disperses paralarvae and juveniles during their current-assisted northern migration toward the feeding grounds in late spring and early summer. *Illex rhynchoteuthion* paralarvae are concentrated where water temperatures converge at 13° to 18°C at 150 to 200 m depth between the water mass known as the slope-water thremostad and the Gulf Stream water. In the area of distributional overlap of

I. illecebrosus and *I. oxygonius*, from Cape Hatteras to south of Cape Canaveral, *Illex rhynchoteuthion* paralarvae are taken only in the slope water/Gulf Stream interface; and further southeastward, off Fort Pierce, Florida, only in the narrow band of "transitional water" just shoreward of the Florida Current (Gulf Stream). The interactions between the slope water and the Gulf Stream seem to be of critical importance to *Illex* spawning, paralarval distribution and recruitment. Because the physical characteristics of the slope-water thremostad-Gulf Stream water mass remain relatively constant year-round, prolonged or "non-seasonal" spawning by *I. illecebrosus* seems quite possible. The vertical distribution of *I. illecebrosus* extends over a broad range of depth depending on season, size/age, and time of day. For example, subadults/adults generally concentrate on or near the bottom during the day then disperse into the water column at night, based on benthic and midwater trawling and *in situ* observations from submersibles. During spring, the 15°C isotherm lay between 80 and 150 m where only juvenile and paralarval *I. illecebrosus* specimens were caught; in the autumn, the isotherm was at less than 200 m (temperatures of 12° to 13°C) and only maturing and large mature specimens were caught. During winter the isotherm was at 25 to 0 m, where only paralarval and juveniles (6 to 18 mm mantle length) specimens were captured. No specimens were caught in the summer because they migrate to northern inshore waters in time for intensive feeding. Seven survey cruises (1986–1989) conducted with pelagic trawls over bottom depths from 169 to 4 800 m in slope waters off Nova Scotia revealed that *I. illecebrosus* was by far the most abundant species overall (nearly twice as numerous as the secondmost abundant species), and it also constituted the most specimens taken in a single trawl. The minimum bottom depth above which the species was captured was 497 m. Six exploratory pelagic and benthic trawling surveys to the Bear Seamount off New England, western North Atlantic Ocean, found *I. illecebrosus* to be the most abundant species in all habitats sampled. During the years of high to peak landings by East Asian squid jigging vessels off Newfoundland and Nova Scotia, the largest catches were taken in the region of the confluence of the warm, northward-flowing Gulf Stream (the western boundary current of the northwestern North Atlantic Ocean) and the cold, southward-flowing Labrador Current. Numerous *in situ* observations have been made from submersibles on *I. illecebrosus* in continental slope waters of the western North Atlantic Ocean. *Illex illecebrosus* was observed both in midwater and on the bottom, where it rests on its arm tips with its head, mantle opening and funnel raised off the substrate. Resting sites apparently are selected because of their paucity of epibenthic fauna as potential predators. Feeding behaviour was observed in midwaters. *In situ* observations from submersibles have documented high concentrations in association with strong daytime Deep Scattering Layer (DSL) recordings at 12 kHz in midwater at 220 to 250 m and 490 to 510 m off Cape Hatteras. Numerous observations show *I. illecebrosus* "resting" on the bottom, as well as in midwater, actively swimming, capturing prey, in large aggregations and small groups, or just "hanging" diagonally head-down and motionless in the water in the "J" posture, with arms and tentacles held together and arched dorsally over the head and anterior mantle.

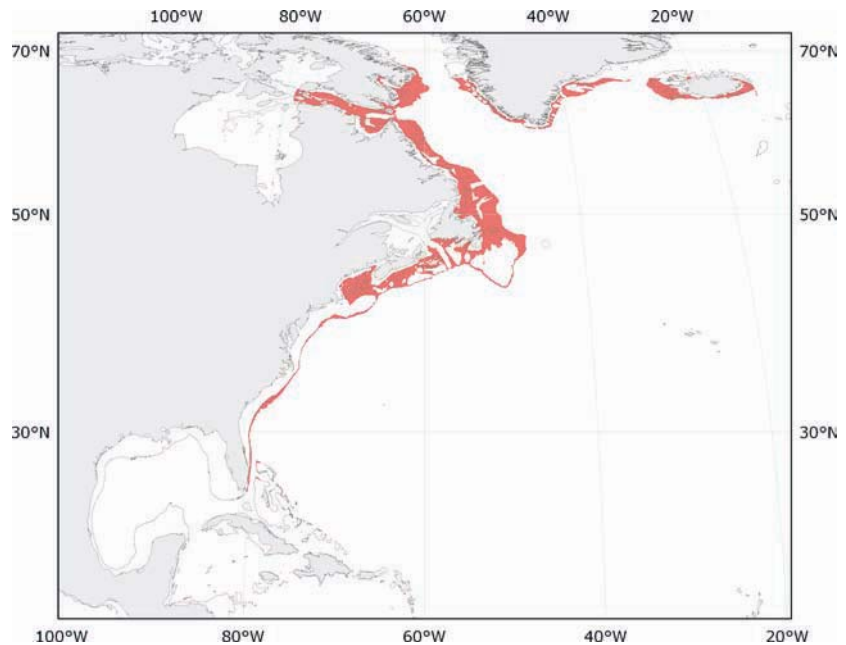


Fig. 283 *Illex illecebrosus*

Known distribution

Illex illecebrosus serves as a biological pump that transfers energy/biological production gained on the feeding grounds back to the spawning grounds over 1 000 km to the south. These fast-acting biological pumps between ecosystems, spawning grounds to feeding grounds and back to spawning grounds, is possible because of semelparity, low levels of predation on paralarval and juvenile stages during northward transport in the Gulf Stream, relatively low mortality on the feeding grounds because rapid growth enables individuals to outgrow most predators, high food conversion rates that convert most of the biological production on the shelf into body mass, and one-way transfer of production from feeding grounds to spawning grounds in a short period of time. Interannual variations in abundance and size of *I. illecebrosus* seem to be associated with the variations in the latitudinal position of the Shelf-Slope Front. These variations affect the efficiency of downstream dispersal by the Gulf Stream and consequently the survival of paralarvae and young forms.

Feeding strategies of *I. illecebrosus* differ according to the size of the targeted fish prey. Squid attack their prey head first, initially with their arms and tentacles (brachial crown) held closely together in a hydrodynamic cone. Just prior to impact with the prey, the arms and tentacles splay widely, effectively creating a disproportionately huge mouth that captures the prey and manipulates it to the beaks, where it is subdued and consumed. The functional result of the arm crown serving as the mouth enables squid to capture prey much larger than their piscine competitors of equivalent size. During experiments, attacks on trout (large prey) are characterized by rotation from tail-first to head-first swimming, rapid acceleration toward the prey, slow tracking of the prey, accelerated attack. No tracking phase occurs in attacks on mummichogs (small prey). Fishes are captured by a quick headfirst attack with rapidly out-thrust tentacles, which then withdraw the fish into the open arm crown; the entire process is accomplished in less than 2 seconds. When swarms of pelagic crustaceans euphausiids, for example, are encountered, the squid rapidly flares and expands its arms to create an in-flowing turbulence in which to trap, then encircle the prey. The rate of digestion of *I. illecebrosus* is very rapid at first, then slows progressively, but it is not phased. Although this species lives in relatively cold water, its digestion is quite rapid and very efficient (0.6% of body weight digested per hour). Starvation of female *I. illecebrosus* in the laboratory induces significant increases in weight and volume of the ovary and the nidamental gland. Causal factors are thought to be the size of the females and their stage of maturity, the season and duration of starvation exposure. During jetting locomotion, *I. illecebrosus* demonstrates very high-power consumption rates, exceeded only by some terrestrial animals at much higher temperatures.

Fishes are the most nutritious prey for promoting growth, whereas crustaceans are the least suitable. High weight at length in July in years of high squid abundance is related to a high level of predation on fish. After July in years of high squid abundance the incidence of cannibalism increases dramatically as predation on fish declines sharply. In years of low squid abundance, no seasonal dietary shifts occur, diet remains mixed all season and cannibalism remains at relatively low levels.

Several models using 75-year and 25-year time series of environmental parameters and *I. illecebrosus* annual abundance data indicate that squid abundance is positively related to a favourable oceanographic regime associated with a negative North Atlantic Oscillation Index (i.e. weak winter northwesterly winds), high water temperatures and a southward shift in the position of fronts within the Gulf Stream System.

Recruitment of juvenile *I. illecebrosus* to the adult feeding ground on the continental shelf off eastern Canada constitutes an important transition from warm, food-limited Gulf Stream waters to cold, productive slope and coastal waters. Young *Illex* are energetically expensive and food-limited in Gulf Stream waters, their hatching environment. Growth conditions improve inshore, where metabolic costs are reduced and more food is available. Juvenile onshore migration is driven by elevated food requirements, but it involves physiological adaptations to compensate for decreased temperatures. Ultimate success in terms of growth and survival depends on access to patches of concentrated food, which is determined by timing and transport dynamics of the main water masses.

Total population size or year class strength is affected predominantly by the winter spawning group, the paralarvae of which are transported into the northern grounds by the Gulf Stream in synchrony with the spring/summer productivity peak. This strategy is highly adaptive because environmental conditions that promote strong year classes also favour population expansion via expedient advection of young stages and a favourable oceanographic regime in the northernmost area. This high-productivity area assures rapid growth and maturation to support the subsequent long southern migration to the spawning grounds. This migration is supported in part by the high concentration of lipids stored in the digestive gland during the intensive feeding phase inshore.

Mean mantle length increases from the offshore transport water masses toward the inshore cooler feeding grounds. Intensive feeding and rapid growth occur in the northern waters in summer, then maturing squid migrate back to southern waters to spawn.

During late autumn squid from all subareas in Newfoundland waters move off the shelf and begin their southward migration.

Back-calculated hatching dates from statoliths for Newfoundland squid indicate hatching from December to June, predominantly March to May. Females grow faster than males and for the March to May hatchlings, length at age and growth rate increased with hatching month. Positive effects of late hatching dates also occur in growth in mass, gonad development and sexual maturation. Recruitment to all fishing areas for *I. illecebrosus* is adversely affected by cold-water events associated with the Labrador Current. Off Newfoundland, the northernmost area, warm intrusions related to a strong Gulf Stream influence are associated with high recruitment levels, but particularly cold-water events, induced by cold-water intrusions of the Labrador Current, have a dominant adverse effect that is independent of Gulf Stream variability. The life history strategy of *I. illecebrosus* ensures survival of the species by stabilizing recruitment in at least one of its several population areas through protracted spawning, complex population structure and interaction of spawning components.

The population structure of *I. illecebrosus* in the waters off Newfoundland is extremely complex. Three maturing groups occur there that result in 3 spawning groups far to the south in winter, spring and summer. Significant inter-annual variation occurs in maturation and size composition of each group, but this variation is compounded by intermixing among groups in the southern population. Mean size at maturity also varies, both geographically and annually. *Illex illecebrosus* is primarily an annual species, so the population can achieve diversity and stabilization only by spawning multiple micro-cohorts throughout most of the year to ensure broad dispersal throughout its range into equally variable micro-habitats. This behaviour links recruitment more rigidly to environmental variability. The population dynamics of *I. illecebrosus* and the strategies employed to maintain them are quite complex and may include kinship, school cohesion and cannibalism. Spawning occurs throughout the year over the Blake Plateau, south of Cape Hatteras, North Carolina (34°N). Eggs enclosed in neutrally buoyant gel masses are carried north by the Gulf Stream, where embryonic development and hatching takes place. The early life is spent along the meandering northern boundary of the Gulf Stream and the slope waters, and it ends when the offspring reach the adult habitat on the continental shelf. During this transition, offspring are subject to important temperature and food availability gradients, as determined by their encountering distinct water masses.

Gametogenesis in *I. illecebrosus* reveals that the development of the gonads is monocyclic. Increased day length accelerates maturation of the gonads while the squid are on the feeding grounds in preparation for their migration to the spawning grounds. During ontogeny the spermatophores grow to 18.0 to 26.0 mm (mean 23.5 mm); the total fecundity in Needham's sac during successive matings is about 1 800 spermatophores (mean 300 to 700). During copulation spermatophores are transferred via the male's hectocotylus into the female's mantle cavity, where they are implanted near the oviducal gland, attached to the interior mantle, base of the gills or the oviducal gland itself. Spermatophore implantation provides the stimulus for spawning to commence within a few days. Spawning occurs on the bottom (based on 2 *in situ* observations), where the female is in the traditional "resting position" on the bottom and the chromatophores are totally retracted so the female appears nearly pure white, with a sharply contrasting dark band near the mantle opening and very dark zones near the fin tip and arm tips. The egg mass is extruded by very strong, rapid contractions of the mantle which presumably squeeze the ova out of the oviducts, extrude the gelatinous matrix out of the nidamental glands and break off the implanted spermatophores, all components to be mixed with water and incorporated into the egg mass. Females produce nearly spherical egg masses that absorb water and swell to about 1 m in diameter; each mass contains about 100 000 eggs in the homogenous, tenuous gelatinous mass.

Spawning occurs in midwaters where temperatures exceed about 12° to 13°C. At 13°C full development to hatching requires 16 days; development is more rapid at increased temperatures. A trend exists in which spawning occurs earlier in years of high stock abundance and later in years of low abundance. This species is a batch spawner, releasing egg masses sequentially over a short period of time. The death of males and females occurs immediately following copulation and sequential egg mass laying, respectively. Laboratory culture of *Illex illecebrosus* rhynchoteuthions was accomplished by obtaining egg masses from captive females and incubating them under controlled conditions. Factors critical for rearing success include tank size, captive population density, turbulence, light levels and periodicity, food type and concentration. Rhynchoteuthions survived for 9 days after hatching. In nature paralarvae hatch at about 1.1 mm mantle length as the rhynchoteuthion-stage, defined by the tentacles being fused into a single "proboscis". The proboscis divides into discrete tentacles at about 8 to 10 mm mantle length to form the juvenile stage. The juveniles grow to about 100 mm mantle length, at which time habitat and food preferences (availability) change and rapid growth towards mature adulthood ensues.

Statoliths and gladii are used to determine many phases of the life history of *I. illecebrosus* through analyses of accretive growth lines, e.g. ecological transitions, age, growth rates, sexual maturation, mating and spawning, as well as more comprehensive applications to sex groups, seasonal and geographic populations and generations. Unfortunately biases exist between preparation techniques and the age interpretation and enumeration of increments. These biases greatly affect estimates of growth and age. Therefore a higher level of standardization at the international level is required in order to derive accurate, comparable age and growth data.

Growth increments on the gladius of *I. illecebrosus* approximate those on statoliths, confirming the daily nature of the depositions during adulthood (early growth increments are masked by growth of the gladius). These increments are highly correlated with mantle growth and reflect early life cycle growth events. Studies on gladii of juvenile and young squid collected in the Slope Water/Gulf Stream front and the Scotian Shelf indicate that offshore growth is exponential and at least 6 size-specific growth stages are distinguished. Paralarval growth is completed by 10 mm gladius length (GL). At 30 to 40 mm GL a significant growth change is associated with the shift from macroplanktonic to micronektonic habitats and the transition from Gulf Stream to Slope waters. The approximation to the Shelf/Slope Water front is reflected by a growth transition at 68 mm GL. The change to linear growth occurs at 90 mm GL after the nektonic lifestyle is attained over shelf waters.

Illex illecebrosus preys on a broad spectrum of bony fishes based on studies of fish otoliths collected from squid stomachs. In Newfoundland waters most abundant prey are young-of-the-year Atlantic cod after July. Adult capelin are common early in the season, while juvenile sand lance are common later in the season. Other fishes include Arctic cod, Atlantic herring, redfish and hake. Otolith data do not reflect the entire species diversity of *Illex* prey because squid tend not to consume the heads (and otoliths) when they prey on larger fishes and because the residence time for otoliths to remain in stomachs varies considerably depending on their size and shape. Total prey of adults extends over a broad range of species, for example, other fishes: myctophids, rattails; crustaceans: amphipods, copepods, decapods, euphausiids, isopods, mydocopids; cephalopods: *I. illecebrosus*, *Gonatus fabricii*, histioteuthids; gastropods: limacinid snails. It also preys on *Doryteuthis pealeii* in submarine canyons on the continental shelf edge in wintertime. Larger juveniles of about 45 to 94 mm mantle length prey on amphipods, mysids, copepods and are cannibalistic on other juveniles. Euphausiids (*Thysanoessa* and *Meganyctiphanes*) are common prey of juveniles.

The predators of *I. illecebrosus* are numerous. Certain size ranges of *I. illecebrosus* are most vulnerable to predation, and predation on the squid varies ontogenetically among predators such as finfishes, elasmobranchs and marine mammals. *Illex illecebrosus* is a significant prey of the cod fish (*Gadus morhua*), swordfish (*Xiphias gladius*), other billfishes and tunas, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), summer flounder (*Paralichthys dentatus*), shortfin mako shark (*Isurus oxyrinchus*) and bigeye thresher shark (*Alopias superciliosus*); seabird predators include: northern gannet, *Morus bassanus*, greater shearwaters (*Puffinus gravis*), sooty shearwaters (*P. griseus*), fulmars (*Tulmarus glacialis*), and the larger gulls, e.g. black-backs.

Illex illecebrosus was the nearly exclusive prey of the long-finned pilot whale (*Globicephala malaena*) in Newfoundland inshore waters into the mid-1970s (up to 10 million tonnes annually); their distributions and seasonal movements coincide in time and space. Peaks in landings were coincident and the availability of pilot whales in shore was dependant on *I. illecebrosus* abundance. Annual squid production (biomass), based on consumption of *I. illecebrosus* by pilot whales, was in the order of several hundred thousand tonnes.

Other mammals predators include the white-sided dolphins (*Lagenorhynchus acutus*), the "squid hound" (*L. albirostris*) and the harbor seals (*Phoca vitulina*). As a consequence, the international fishery for *I. illecebrosus* captures marine mammals as incidental catch; pilot whale species (*Gloubicephala* spp.) and common dolphin (*Delphinus delphis*), together comprising 93% of incidental catch in Canadian and the United States waters, southward into the mid-Atlantic Bight. These species are known to be major predators on *I. illecebrosus*, so quite naturally are foraging in the squid concentrations during trawling operations.

Natural mortality through predation by marine homeotherms can be substantial and should be taken into account in management schemes. Parasites include pleroceroidean cestodes and nematodes.

Interest to Fisheries: The short-finned squid *I. illecebrosus* has sustained a valuable but highly unpredictable fishery in the Northwest Atlantic, that collapsed after intense, widely distributed exploitation (1976–1981). Domestic fisheries for *I. illecebrosus* have occurred at least since the mid-1800s, probably much earlier, primarily to supply bait for the tub trawl/long line fisheries, principally, though not exclusively, on the Grand Banks off Newfoundland. Catches were about 1 000 tonnes per year until the early 1970s when a major Japanese vessel-based fishery developed for the human consumption market. Catches expanded greatly through the 1970s. In United States waters catches peaked at 24 700 tonnes in 1976, while the primarily distant water fleets off Nova Scotia and Newfoundland landed sharply increasing catches through the 1970s to a peak of 180 000 tonnes in 1979. During peak years of the fishery well in excess of 100 000 tonnes were landed annually, over 1 million tonnes in a decade (1971–1981, mostly 1976–1981). The fishery totally collapsed thereafter. The decadal average for 1992–2002 was 13 197 tonnes, declined sharply in 2002, to increase again in the last years (i.e. over 10 000 tonnes in 2007). Population levels and catch productivity since 1970 have shown high variability in Newfoundland waters and the periods of highest productivity occurred between 2 periods of low productivity.

The jigger used in the traditional squid fishery in Newfoundland has taken several forms over the years, but once the Japanese exploitation began in the 1970s the jigs used in that fishery have become standard, even in the inshore artisanal fishery. Significant catches also are made with benthic otter trawls, particularly on the Grand Banks and along the eastern seaboard southward to the mid-Atlantic around Cape Hatteras, North Carolina. In trawl surveys with large pelagic trawls set at depths of 169 to 4 800 m off Nova Scotia, *Illex illecebrosus* was the most abundantly caught species by nearly 2:1 over the next most abundant species, *Abrialiopsis hoylei*.

The "boom and bust" type of fishery exemplified by the *I. illecebrosus* fishery in eastern Canada, principally Newfoundland waters, could be mitigated by creation of reserve areas that would minimize recovery time and maximize long-term production.

The principal product of *I. illecebrosus* for human consumption remains the muscle tissue of the mantle, fins, head and arm crown, that are marketed fresh, frozen and canned, as well as in various value-added preparations. The muscle tissue contains an extremely active family of proteases that are responsible for rapid degradation of quality in postmortem tissue and also are important during frozen storage. In an effort to utilize more fully the remaining tissue, a number of products have been developed. For example, formerly underutilized parts of the squid are made into squid patties with the addition of starch and egg white albumin heat-set binders. Application of aminopeptidase from *I. illecebrosus* digestive glands accelerates the ripening process of cheddar cheese. Squid protein extracted from arms and tentacles of *I. illecebrosus* are used as an additive to gels of Atlantic pollack surimi to improve texture and impart a darker red pigmentation. Extracts from the digestive gland of *I. illecebrosus* are used as a supplement to develop the most desirable taste characteristics in fermented squid and herring products. Proximate composition and fatty acids of total lipids from processed viscera yield residual protein with high levels of essential amino acids that are a good source of protein supplement for animal feed.

Local Names: JAPAN: Kanadairekkusu, Taiseiyoirekkususurume, Taiseiyosurume; USA: Northern shortfin, Short-finned squid.

Remarks: Adam (1952) reported *I. illecebrosus* from the Bristol Channel off southwestern England, but a re-examination of Adam's specimens confirmed that they clearly were *I. coindetii* based on the hectocotylus, and body meristics, especially fin angle (Roper *et al.* 1998). Genetic analysis of the 4 nominal species of *Illex* using allozyme polymorphisms confirms their valid specific status and reveals that *I. illecebrosus* and *I. oxygonius* are sister species, with a close relationship to *I. argentinus*, while *I. coindetii* forms a more remote, different lineage (Martinez *et al.* 2005a,b; Carlini *et al.* 2006).

Literature: O'Dor (1983), Roper *et al.* (1984), Aldrich (1991), Dawe *et al.* (1992), Dawe and Hendrickson (1998), Vecchione *et al.* (1998a), Roper and Mangold (1998), Roper *et al.* (1998), Martinez *et al.* (2005a,b), Carlini *et al.* (2006), Coehlo and O'Dor (1993), Dawe *et al.* (2007).

Illex argentinus (Castellanos, 1960)

Fig. 284

Ommastrephes argentinus Castellanos, 1960, *Neotropica*, 6(20): 55–58, figs 1–5. [55].
[Type locality: Patagonia, western South Atlantic Ocean].

Frequent Synonyms: *Ommastrephes argentinus*, Castellanos, 1960.

Misidentification: *Ommastrephes bartramii* (Angelescu et al., 1958).

FAO Names: **En** – Argentine shortfin squid; **Fr** – Encornet rouge argentin; **Sp** – Pota argentina.

Diagnostic Features: Mantle long, muscular, widest at midpoint. Fins muscular, relatively short (length 42% of mantle length) and broad (width 57% of mantle length); fin angle broad, 45° to 55° (90° to 110° both fins).

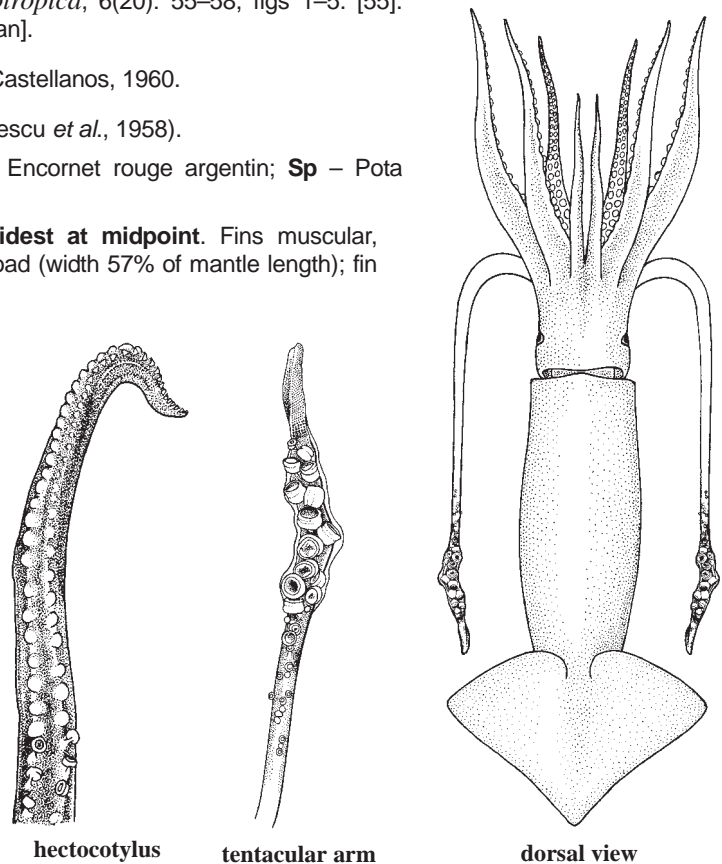
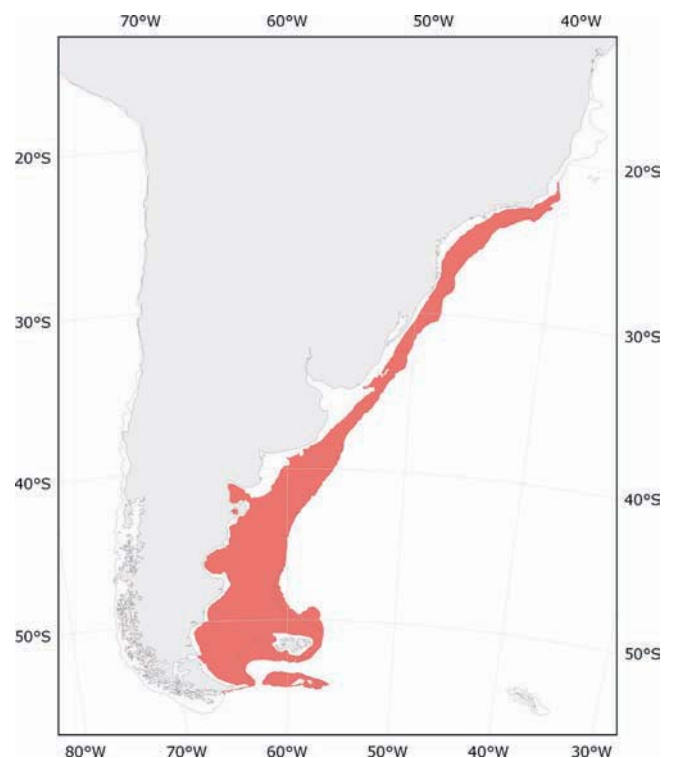
Arms very long for the genus, up to 72% of mantle length for arms III in males; all arms of males significantly longer than in females.

Hectocotylus with distal hectocotylyzed portion of right (or left) arm IV (HA3) and modified HA2 greater than 50% (up to 70%) of total arm length (HALt); distal tip with 18 to 22 large, truncate or rounded lamellae on dorsal row and numerous small, indistinct, narrow lamellae on ventral row to tip; medial modified part of hectocotylyzed arm (HA2) with 10 to 16 enlarged, rounded, suckerless knobs on dorsal row and 7 to 10 low, suckerless knobs followed by 7 to 12 nipple-like papillae on ventral row; proximal sucker-bearing part (HA1) with 8 to 13 normal suckers; basal, suckerless part (HAb) of hectocotylyzed arm about 10% of total arm length; hectocotylyzed arm longer and more robust than opposite arm. Club only slightly expanded; **distal medial manal suckers very enlarged, lateral manal suckers extremely small; largest medial manal-sucker rungs smooth or notched with few, low, broad crenulate plates.** Head-width index low, 16.0 to 17.8. Lower beak with jaw edge curved, long; wing long, wide, no lobe; rostral width narrow, lateral wall short, blunt. Upper beak with hood long, strong shoulder serrated; rostrum long; wing short; jaw angle with large notch, with tooth; lateral wall short, shallow; crest curved. Spermatophore cone at oral end of cement body, flat, low, lens-shaped in outline; oral tube broad; aboral neck broad, distinct.

Size: Maximum mantle lengths are around 380 to 400 mm.

Geographical Distribution: Western South Atlantic Ocean from about 22°S, around Rio de Janeiro and Cabo Frio, Brazil, southward to about 55°S, including the Falkland Islands, the tip of Tierra del Fuego, Staten Island (Isla de los Estados) and Burwood Bank. Greatest abundance occurs south of about 40°S (Fig. 285).

Habitat and Biology: *Illex argentinus* is the most abundant species of Ommastrephidae that occurs in the southwestern South Atlantic Ocean. It is a nerito-oceanic species that is broadly distributed from southern Brazil off Uruguay, and to southern Argentina, but it is most abundant between 35°S and 52°S at depths from 80 to 400 m. The adults are concentrated in shelf waters of subantarctic origin (8° to 12°C), mostly the cold waters of the Falkland (Malvinas) Current, while the embryos and paralarvae develop in the warmer waters to the north in the meanderings of the Brazil Current.

Fig. 284 *Illex argentinus*Fig. 285 *Illex argentinus*

Known distribution

This species supports one of the most productive cephalopod fisheries in the world, ranking among the top 3 species for several decades. This abundance derives from its habitat in association with the most extensive open continental shelf area in the world. The Patagonian Shelf is 1 700 km long; it extends from 39°S to 55°S, and it averages over 400 km wide off mainland Uruguay and Argentina, then bulges to nearly 900 km wide around the Falkland (Malvinas) Islands. Oceanographic conditions drive the high productivity of marine life in these waters, just as they do in the western North Atlantic habitat of *I. illecebrosus*. The southwestern South Atlantic waters are under the influence of the strong western ocean boundary currents, similar to the Gulf Stream off North America. The southward flowing Brazil Current dominates the northern portion of the range, while the southern region is dominated by the northward flowing Falkland (Malvinas) Current. The 2 currents merge off Rio de la Plata, where the Falklands Current remnant component continues northward nearer the coast and the Brazil component sets offshore. These current components result in a highly developed shelf-break upwelling accompanied with strong tidal mixing that combine to create a region of very high primary and secondary productivity.

While the species range is widely distributed in the southwestern Atlantic, 4 more or less geographically distinct subpopulations, occur. Each one is characterized by its specific spawning area, spawning season, size at maturity and ontogenetic distribution.

These following subpopulations occur from north to south:

- 1) **The Summer Spawning Stock (SSS)** spawns principally on the intermediate and outer shelf at 80 to 150 m (range 50 to 200 m) during December to February (summer) at about 42°S to 45°30'S; they are mature and spawn at a small size, 140 to 250 mm mantle length, in the stratified shelf waters. Spawning is completed during one short period of 30 to 60 days. Late embryonic stages and rhynchoteuthion paralarvae occur in the upper warm layer in water temperatures above 13°C. Paralarvae occur near the surface from December to March over the intermediate Patagonian shelf along the tidal frontal system that develops between the shelf stratified waters and the well-mixed coastal waters. They are concentrated in the upper waters along the stratified side of the system, where abundance increases from the surface to a maximum at 40 m near the thermocline.
- 2) **The South Patagonic Stock (SPS)** spawns in autumn (April–May to July) in the southern shelf ecosystem along the Falkland (Malvinas) Current (45°S to 48°S), over the outer shelf and upper continental slope, when adults are 180 to 350 mm mantle length. Eggs and paralarvae are swept northwards by the current into warmer waters where development is enhanced.
- 3) **The Bonaerensis-North Patagonic Stock (BNPS)** that occurs between 35°S and 38°S, spawns in near-oceanic waters in winter (July–August) along the western boundary of the Brazil-Falkland (Malvinas) Current Confluence, at a size of 180 to 350 mm mantle length. Eggs and paralarvae are carried northward by the current into warmer waters where their development is enhanced.
- 4) **The Spring Spawning Stock (SpSS)** with adults of 230 to 350 mm mantle length, spawns in stratified shelf waters of the inner to intermediate shelf (50 to 100 m) at around 38°S to 40°S in the spring, September to November. Late embryonic stages and rhynchoteuthion paralarvae occur in the upper warm waters at greater than 13°C.

Juveniles 10 to 100 mm mantle length from the **SPS** and **BNPS** populations are pelagic and occur on the Bonaerensis-North Patagonic shelf during August through September. The SPS forms then migrate southward to the region of 45°S to 49°S, while the BNPS juveniles remain in the Bonaerensis-North Patagonic shelf area. Both stocks, then in their breeding grounds, recruit to the bottom by late spring. Other juveniles, 10 to 50 mm mantle length and 2 to 3 months old, occur in the oceanic region off coastal Argentina, mostly in the meanders and eddies formed in the Brazil–Falkland Confluence, while smaller numbers occur in the sub-Antarctic waters of the Falkland (Malvinas) Current during August through September. These juveniles probably had been transported as paralarvae from their spawning grounds into the oceanic region by the eastward shift of the Brazil current.

The vertical distribution pattern of *I. argentinus* is essentially one of ontogenetic descent. Smallest juveniles inhabit the epipelagic layer. Then, along with other forms of sub-Antarctic macrozooplankton, they move into the 25 to 40 m zone where they feed intensively and grow rapidly. Following this period they begin their recruitment into the final phase of their ontogenetic descent through the water column and recruit to the bottom when they are larger than 180 mm mantle length. From this point on they undergo daily migrations and disperse at night into the water column where they feed. They return to the vicinity of the bottom, or onto the bottom, during the daylight hours, descending to depths of 125 to 850 m.

Maturation of subadults to reproductive condition occurs relatively quickly, generally as the squids undergo their migrations to their respective spawning grounds. The biochemical composition and energy content of the gonads differs between males and females. Whereas they remain relatively constant during sexual maturation of the testis in males, the composition of the ovary changes significantly in mature females, with the concomitant development of the nidamental glands and oviducal glands. The nidamental glands of female *Illex argentinus* can account for more than 7% of body weight.

Individuals of the winter–spawning stock grow and mature on feeding grounds on the southern Patagonian Shelf, then migrate northward to the spawning grounds. They prey on rich zooplankton stocks and grow rapidly as they mature. The majority of tissue growth goes into somatic tissue; in females, 23% goes into the mantle, 17% to arms, tentacles and head, and 46% to the digestive gland, while only 16% goes into reproductive tissue; males grow significantly slower, mature at a smaller size and only 6% of accumulated energy goes into reproductive tissue. This strategy, while differing from many other squids, directs a large proportion of the energy budget into somatic tissues required to conduct the long migration to the spawning grounds. Once the spawning grounds are reached it is not yet known whether somatic reserves are then converted for gonadal production, as occurs in other squid species, e.g. *Moroteuthis ingens*.

The total fecundity of oviduct eggs of females from the Summer Spawning Stock averages 18 854 ova, while that of females from the Bonaerensis-North Patagonic Stock averages 59 644. The individual fecundity of fully mature females (240 to 270 mm mantle length) from the South Patagonic Stock is 113 835 to 246 098 mature oocytes from the ovary and oviducts. An estimate of total fecundity based on oviduct eggs and previtellogenic oocytes in the ovary, that would eventually mature and be spawned, ranges from 75 000 (150 to 170 mm mantle length) to 1 200 000 (360 to 380 mm mantle length).

The reproductive strategy in males involves the slowing of growth at maturity of the accessory reproductive organs (that function to manufacture and store spermatophores). The size of spermatophores that accumulate in Needham's sac increases slowly and modal sizes of spermatophores produced at different times usually are the same. Males produce relatively smaller spermatophores than other ommastrephids, but they are more numerous. Male fecundity depends on the volume of Needham's sac and on the number of periods of active formation of spermatophores between copulations, which are more numerous in the larger males. The goal of the reproductive strategy is to maximize effective sperm production (the number of sperm packaged in proper spermatophores during ontogeny). In Illicinae the mechanisms to attain this goal are an increase in the relative volume of Needham's sac and an increase in the number of periods of formation and accumulation of spermatophores between matings. In males of 164 to 290 mm mantle length, spermatophores vary from 16.4 to 36.0 mm (mean 26.0 mm) and average about 11.5% of mantle length; the fecundity can be up to 1 600 spermatophores.

The nutritional value of *I. argentinus* for predators is high, because it is very muscular, thus rich in protein, and its large digestive gland is rich in lipids. Fresh Argentine shortfin squid are composed of 78 to 80% water (typical for marine invertebrate soft tissue), 10 to 17% protein, 12% lipid and minor carbohydrate content. The total proximate biochemical composition of the squid tissue does not alter during the life cycle, but a proportional shift in composition and mass of various organs and tissues occurs with sexual maturation, especially of the gonads and digestive gland.

Illex argentinus is preyed upon by a broad spectrum of predators, based on stomach content analyses. These include marine mammals, fishes, birds and conspecifics. Among major predators there are the Argentine hake (*Merluccius hubbsi*), the Patagonian hake (*Merluccius australis*) the Patagonian whiphake (*Macrouronus magellanicus*) and the southern blue whiting (*Micromesistius australis*). All these fishes probably are both prey and competitor of *I. argentinus*. Other predators on this squid, and probable competitors for fish prey, are the southern cod (*Notothenia ramsayi*), elasmobranchs (skates and dogfish sharks), including the picked dogfish (*Squalus acanthias*), lings (*Genypterus blacodes*) and, probably, *Loligo* squid. Also, *I. argentinus* is ranked as very frequent in the diets of the bigeye tuna (*Thunnus obesus*), swordfish (*Xiphius gladius*), wreckfish (*Polyprion americanus*), hammerhead shark (*Sphyrna lewini*), yellowfin tuna (*Thunnus albacares*), and the albacore tuna (*Thunnus alalunga*). Other fishes that feed less frequently on *I. argentinus* include bluefish (*Pomatomus saltatrix*), red porgy (*Pagrus pagrus*), cutlassfish (*Trichiurus lepturus*), billfishes, (Istiophoridae) and shortfin mako shark (*Isurus oxyrinchus*).

Additional predators from off southern Brazil include the São Paulo squid (*Loligo sanpaulensis*), the Argentine angel shark (*Squatina argentina*), the skate (*Squatina ocula*), channel seabarrfish (*Evoxymetopon taeniatus*), the school shark (*Galeorhinus galeus*), the blackbelly rosefish (*Helicolenus d. lahillei*), the polkadot catshark (*Scyliorhinus besnardi*), the common dolphinfish (*Coryphæna hippurus*), the Atlantic sailfish (*Istiophorus albicans*), skipjack tunas (*Katsuwonus pelmas*), pilotfishes (*Naucrates ductor*), blue sharks (*Prionace glauca*) and white marlins (*Tetrapturus albidis*). Several marine birds prey on *I. argentinus*, including the magellanic penguin (*Sphesnisus magellanicus*), the wandering albatrosses (*Diomedea exulans*) and white-chinned petrels (*Procellaria aequinoctialis*). Marine mammal predators include pygmy sperm whales (*Kogia breviceps*), sperm whales (*Physeter macrocephalus*), common dolphins (*Delphinis* sp.), longfinned pilot whales (*Globicephala melas*), southern elephant seals (*Mirounga leonina*) and sub-Antarctic fur seals (*Arctocephalus tropicalis*).

A complex trophic system exists among *I. argentinus*, the Argentine hake (*M. hubbsi*) and the Argentine anchovy (*Engraulis anchoita*), in the demersal-pelagic community: squid and hake prey on anchovy, squid prey on young pelagic hake, and older hake prey on all sizes of squid. Consequently, hake are prey, predator and competitor of *I. argentinus*; they feed more intensely on squid in the southern part of its range from January to July and in the northern part from April to June. Clearly the total contribution of *I. argentinus* to the overall trophic system is highly significant throughout its range in waters of the Patagonian shelf, slope and adjacent oceanic region. Rough estimates indicate that it comprises between 40 and 75% by weight of the diet of predatory fishes.

Illex argentinus is an opportunistic predator that preys mainly on zooplankton when young, but fishes and squids can represent a significant proportion of the diet in some areas and with increasing age. The principal prey for squids less than 200 mm mantle length are crustaceans. Cannibalism occurs throughout the range, but it is more prevalent north of 42°S.

Generally, adults feed on large prey, such as fishes and squids, but occasionally, large squids in the Patagonian shelf area prey mainly on crustaceans, which are available in great abundance. Feeding behaviour is reflected in the diel vertical migration habits of *I. argentinus*. Two patterns exist: 1) immature and maturing squid feed on the bottom during the day then vertically migrate to near the surface to feed at night; 2) prespawning and spawning squid feed near the bottom at night and in the water column during the day, up to 200 to 300 m, preying on myctophid fishes in the acoustic scattering layer. The prey of *I. argentinus* generally are those that have a high lipid content, such as crustaceans (euphausiids, amphipods) and mesopelagic fishes (myctophids), and they accumulate high levels of lipid in their digestive gland, which grows at a considerably higher rate than the rest of the somatic tissues. This suggests a role as energy storage, or possibly increased buoyancy, in preparation for the long spawning migration. However, if spawning migrations are long, as in the case of the winter spawning population that feeds around the Falkland Islands, the squid must migrate to spawning grounds 1 000 km to the north. In this

case the somatic energy reserves are insufficient to fuel the entire migration. Consequently, cannibalism occurs on smaller individuals during the journey, and on juveniles of earlier-spawned individuals on the spawning grounds.

Major prey items include copepods (*Oncaea media*), peneids, mysids, young Argentine hakes (*Merluccius hubbsi*), Argentine anchovies (*Engraulis anchoita*), macrourids, myctophids (*Diaphus dumerilii*), scianids, sternoptychids (*Maurolicus muelleri*) and cephalopod such as *Argonauta* sp., enoploteuthids, *Spirula spirula*, loliginid squid and conspecifics (*I. argentinus*). *Illex argentinus* is host to a broad range of parasites, including cestodes (*Phyllobothrium* spp., *Pelichnibothrium speciosum* I, and *Hepatoxylon trichiuri*), trematodes (*Derogenes varicus*, *Hirudinella ventricosa*) and nematodes (*Porrocaecum* sp. I, *Contracaecum* sp. I, *Anisakis simplex* I, *Anisakis* sp. I (II), *Hysterothylacium* sp. I, *Spinitectus* sp. I). Trophic relations can be inferred from the existence and intensity of parasites. For example, throughout the squids' geographical range, the cartilaginous fishes, the final hosts for cestodes, and marine mammals, the final hosts of nematodes, are the main predators of *I. argentinus*. While further north in its distribution, tunas and xiphoid fishes, the final hosts of didymozoids, are the most significant predators. The different spawning groups of *I. argentinus* are not distinguishable by their parasite fauna, because, while they spawn at different times, they all are caught in the same regions and their parasitic composition is similar, not cohort-specific. However, in the northern part of the range, off southern Brazil, immature and maturing squid caught in all seasons frequently are infected by didymozoids, which are absent in the colder waters south of the subtropical convergence. Of all the mature specimens, only those caught in autumn are infected with didymozoids, while large mature and spawning specimens caught in winter and spring, had no didymozoid parasites. This suggests that most of the winter and spring spawners off Brazil are migrants that feed and grow in colder southern waters, then migrate north to the Brazil Current to spawn.

Interest to Fisheries: The development of the fishery for *I. argentinus* in the southwestern South Atlantic Ocean occurred relatively recently in comparison to its congeners in the North Atlantic (*I. illecebrosus*, *I. coindetii*) and Mediterranean (*I. coindetii*). Before the species was named and described, its ecological importance in the Argentine shelf waters was already recognized, as *Ommastrephes bartramii*, during a studies of the biology and trophic relations of the common hake (*Merluccius hubbsi*). The Argentine shortfin squid was landed in small numbers only as bycatch from the then developing bottom trawl fishery for hake. In 1966, an extensive bottom trawl survey on the shelf by the FRV Walther Herwig indicated that an estimated catchable stock size of several hundred thousand tonnes existed in those waters. A small directed bottom trawl fishery developed in 1973, and combined bycatch and directed catch remained less than 6 000 tonnes through 1977.

The collapse of the *I. illecebrosus* fishery led to the rapid shift of the international jigging fleet in the late 1970s and early 1980s to the southwestern South Atlantic to pursue the *I. argentinus* fishery. This has been the most important squid fishery in the world, overall, since the early 1980s. By 1990 the catch had grown to 410 000 tonnes and continue to increase to peak in the late 1990s (over 1 million tonnes in the 1999); an important decrease (actually a collapse) was registered in the years 2004–2005, then catch values arose again to over 950 000 in 2007.

Squid fisheries have represented an extremely important resource in the southwest Atlantic Ocean, and *I. argentinus* represents its dominant species. However, since the inception of the directed fishery began in the late 1970s, both total abundance and total catches have been very variable. The most severe decline was the system-wide collapse of the *I. argentinus* stock in 2004. Both the shelf summer and autumn spawning stocks, as well as the winter spawning slope-oceanic stock experienced sharp declines. Two main factors are attributed to the collapse: 1) environmental changes, due mainly to the water dynamics of the Falkland–Brazil Current system with consequent high mortality of the paralarval stage; 2) overfishing. Retrospective analyses of catch data show correlations with various spatio-temporal patterns and explain interannual variations in catches with effects of year, month, latitude, position on continental shelf and body size.

Stock abundance has a non-linear relationship with SST so that the highest CPUE occurs at SST temperatures of 13° to 14°C. The years of collapse in the fishery, particularly 2004, were defined by low SSTs, around 10°C.

An analysis of the spatio-temporal distribution of *I. argentinus* based on over 11 000 trawl and jig haul records placed the areas of maximum abundance in deeper waters of the high seas between 44.5°S and 47°S outside the Argentine Exclusive Economic Zone (EEZ) and northwest of the Falkland (Malvinas) Islands. The jigging and trawling fishery is conducted by long range fleets from Argentina to southern Brazil, but a major portion of the catch is taken by the international fleet under a well-regulated management system. The principal fishing nations with the longest participation in the fishery are: Japan, Korea, Portugal, Spain and Taiwan Province of China. Other jigging fleets have been from Chile, Falklands, France, Italy, Poland and the United Kingdom. The greatest tonnage has been taken, in descending order by: Korea, Japan, Taiwan Province of China, Poland, Spain, China, Brazil, Falklands, Cambodia and Honduras. In general, the jigging fishery is conducted by the Asian-country fleets, while the trawling fishery is executed by the European and South American participating countries. While the trawl fishery off southern Brazil in the Exclusive Economic Zone (EEZ) concentrates on 3 species of fish (Gulf hake, Argentine hake and monkfish) a significant bycatch of *I. argentinus* is taken, principally in the winter over the upper slope at 250 to 500 m. Trawling peaked in 2002, and has steadily declined since: the “gold rush” development of the slope fishery with such high fishing capacity is incompatible with a sustainable fishery. The fishery operates in coastal and shelf waters, mostly along the edge of the shelf break north of 52°S where a well-defined frontal boundary zone persists along nearly the entire length of the shelf.

The fishery developed so rapidly during its early years that considerable concern existed over the condition and sustainability of the full stock of *I. argentinus*, as well as the potential of overexploitation of the 3 or 4 component populations that had been distinguished. However, under the supervision of the South Atlantic Fisheries Commission, Argentina and the United Kingdom collaborated since 1990 in joint or coordinated research and management efforts that led to rational assessment, monitoring and management of the fishery, both by local and the international fleets. Under this management regimen, the Argentine shortfin squid is considered to be fully exploited in spite of the very high year-to-year variability in recruitment, abundance and

harvests. Through this collaborative management, virtually real-time monitoring of the stock and the ability to coordinate management action exists. In spite of close management the fishery continues to undergo annual declines. The short life span and semelparous life style of *I. argentinus* makes it difficult to manage the fishery, because, once the spawners of one generation have reproduced and died, it is extremely difficult to assess the potential recruitment strength and resultant stock size of the next generation. A biologically rational quota for the harvest can not be established until the new generation is recruited into the fishery. Consequently, the fishery is managed by effort limitation and assessed in real time. Effort is established prior to the new jigging season based on historical information on putative stock size. Then, once the fishery opens for that year, the stock is continuously assessed using the Leslie-Delury depletion analysis; the fishery is closed once the CPUE estimates indicate that the remaining biomass corresponds to the precalculated target spawning escapement. This management approach was introduced in 1987 when the target escapement was established as 40% of the numbers of squid recruited into the fishery. Subsequently, the escapement target has been determined as an absolute year-to-year value in order to stabilize the size of the spawning population, regardless of the annually variable recruitment. The 40% proportional escapement policy was later refined to require an absolute minimum escapement of 40 000 tonnes, which insures a precautionary limit in a year of poor recruitment. A further refinement involves pre-recruitment surveys that improve the initial assessment of catch effort prior to the opening of the fishing season. Empirical modelling to predict the level of recruitment for the next season employs predictive variables of the environmental conditions on the spawning grounds off the Plate River during the previous year. Recognition and incorporation of the strong association of oceanographic parameters to recruitment is necessary. The sustainability of the multi-cohort stocks depends on the ability of the management approach to respond to changing environmental conditions, both between years (response to variable recruitment by in-season management of single-age cohorts) and to long-term periods of oceanographic regime shifts.

Regional sea surface temperature data taken by remote sensing over the southwestern South Atlantic indicate that about 55% of the recruitment variability in *I. argentinus* in the Falkland (Malvinas) Islands fishery is created by area changes in the optimum temperature for larval development on the spawning grounds during the spawning season prior to recruitment of that year class.

The sea surface temperature conditions that predict strong recruitment also are associated with a reduction in horizontal temperature gradients (3°C over a 15 km span) in the spawning grounds. Such effects in the South Atlantic are associated with sea surface temperature anomalies that occur in the El Niño Southern Oscillation (ENSO) system in the southeastern South Pacific Ocean; these variations stimulated by the ENSO cycle eventually affect the recruitment, population size and fishery catches of *I. argentinus* in the Patagonian Shelf/Falkland Islands fishery 2 to 5 years later. Knowledge about the variability and behaviour of the ENSO each year ultimately can help to predict environmental variability on the spawning grounds in subsequent years, thus to forecast recruitment and population levels and enable a management system to more precisely establish sustainable catch levels in the fishery. The Southern Oscillation Index (SOI) and sea surface temperatures (SSTs) on southern and northern parts of the Patagonian Shelf have different effects on *I. argentinus* abundance. SSTs in both areas show a link with the SOI at lag times of 2 and 3 years, respectively. No significant correlation exists between the SOI and squid abundance, or between SSTs of the southern portion of the shelf and squid abundance within a 10 year lag time. However, SSTs in the northern portion of the shelf correlate negatively with squid abundance with a 1-year lag time. Consequently, cold events in this region in the previous year could cause high squid abundance in the current year. In any case, the distribution patterns of *I. argentinus* on the Patagonian Shelf are influenced locally by the thermal fronts, which in turn depend on the intensity and distribution of the cold currents. Catch rates vary monthly with peak catches in February and March. SSTs of 7° to 14°C are suitable for catching *I. argentinus*: 11° to 12°C in February, 10° to 12°C in March, 8° to 9°C in April and 7° to 8°C in May. Catches are best where SSTs are slightly higher than the historical average level.

In addition to known effects of environmental factors on survival, growth, recruitment, abundance and availability of *I. argentinus*, commercial exploitation also should be expected to have discernible effects. The short life span of squids makes them highly susceptible to the selective effects of commercial exploitation. Life history characteristics can be altered and there exists a strong selection for an even earlier age of maturation than has already been demonstrated, as well as the potential loss of a migratory component of the population (migrations from feeding grounds to spawning grounds and return are critical components of the life history cycle).

As with any well-managed squid fishery, sound management of the *I. argentinus* resource ultimately requires a full understanding of the life cycle of the species.

Remarks: In studies off the central South Brazilian Bight on cadmium concentrations in marine fishes and cephalopods, the mean cadmium concentration in *I. argentinus* digestive gland was 1002.9 µg/g wet weight (Dorneles *et al.*, 2007). This represents the highest cadmium level ever recorded in a cephalopod. Causative factors for such remarkable cadmium levels include anthropogenic action from coastal industrial and urban development, upwelling systems and cannibalism.

Local Names: ARGENTINA: Calmar; JAPAN: Argentina matsu ika; URUGUAY: Calmar.

Literature: Roper *et al.* (1984), Nigmatullin (1989b), Brunetti *et al.* (1998a,b), Barton *et al.* (2004), Boyle and Rodhouse (2005), Chen *et al.* (2005b), Martinez *et al.* (2005a,b), Chen *et al.* (2007a,b).

Illex coindetii* (Verany, 1839)*Fig. 286; Plate VIII, 50–51**

Loligo coindetii Verany, 1839, *Memorie della Reale Accademia delle Scienze di Torino*, Series 2, 1: 91–98. [94, pl. 4]. [Submitted in 1837]. [Type locality: off Port Vendres, France, northwestern Mediterranean Sea].

Frequent Synonyms: *Loligo brogniartii* Blainville, 1823; *L. coindetii* Verany, 1839; *L. pillae* Verany, 1851; *L. sagittata* Verany, 1851; *Illex illecebrosus coindetii* Pfeffer, 1912.

Misidentifications: *Illex illecebrosus*, Adam, 1952.

FAO Names: En – Broadtail shortfin squid; Fr – Encornet rouge; Sp – Pota voladora.

Diagnostic Features: Mantle moderately long and narrow, widest at anterior end (except in fully ripe females); tail pointed. Fins rhomboidal, fin angle >50%. Head wide and robust, especially in mature males; head-width index high, 23 (19 to 26) in mature males, 19 (15 to 22) in mature females. Funnel groove smooth, without foveola or side pockets. Dactylus of tentacular club with 8 longitudinal rows of small suckers. Club expanded; largest distal manal sucker rings notched in distal half or all around with low crenulations, not smooth. Arms relatively long and robust, especially in males. Either left or right ventral arm hectocotylized, with distal hectocotylized portion of the arm (HA3) relatively short, about 25% (17 to 30% on fully mature males) of total arm length (HALt); basal, suckerless part (HAb) of hectocotylized arm about 13% (10 to 14%) of total arm length; proximal sucker-bearing part (HA1) with 5 to 7 (mostly 5 or 6) pairs of normal suckers, increasing in diameter distally; distal sucker-bearing part (HA2) starts with a pair of suckers immediately decreased in diameter by one-half or more in comparison with the proximal adjacent pair on HA1; rows widely separated, suckers in both rows remain small; oral surface of arm constricted in transition zone between HA1 and HA2; at proximal origin of HA2, trabeculae distal to largest normal suckers (HA1) transformed into distinctive fringed flaps; modified distal portion (HA3) bears fully developed truncate lamellae on dorsal rows and digitate papillae (no lamellae) on ventral row.

Size: Maximum mantle length recorded is 379 and 279 mm respectively, for a female and a male from Spanish Atlantic waters. Common at 200 to 250 m throughout its distributional range.

Geographical Distribution: *Illex coindetii* has an unusual widespread, disjunct, distribution for a neritic cephalopod. It occurs in the eastern Atlantic, from as far north as the Oslo Fjord, off the Norwegian coast (i.e. 60°N), throughout the North Sea and southward, along the Atlantic European and African coasts, southward to the Namibian waters at 19°S to 20°S. It is distributed throughout the Mediterranean Sea, from the western to the eastern ends; Aegean and lower Adriatic Seas; absent from the upper Adriatic Sea and the Black Sea, but it has been reported from the Sea of Marmara. In the western Atlantic its northernmost records are from off the Virginia coast (i.e. 37°N); it is distributed southward, in association with the Gulf Stream and the Florida Current, in the Gulf of Mexico and the Caribbean Sea, and it has been reported from the French Guiana waters, so it probably extends to 3°N, but the exact extent of its southern distribution remains undetermined (Fig. 287).

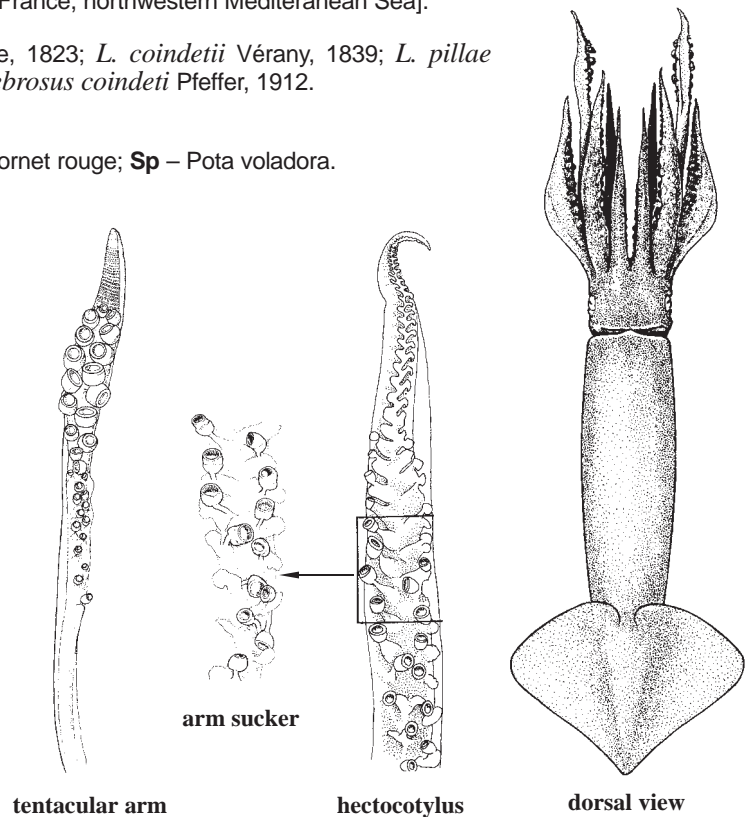


Fig. 286 *Illex coindetii*

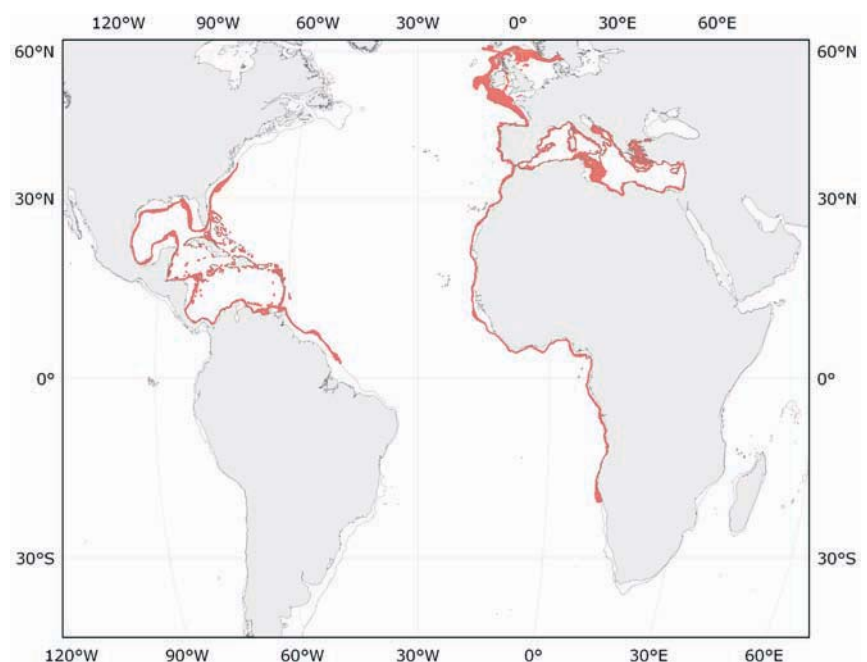


Fig. 287 *Illex coindetii*

Known distribution

Habitat and Biology: A demersal, neritic species of the continental shelf and upper slope, *Illex coindetii* occurs from the surface down to over 1 000 m, with maximum concentrations between 50 and 100 m and 400 to 600 m, depending on geographical location. For example, in the Mediterranean Sea, peak concentrations are at 60 to 400 m, the eastern Atlantic 150 to 300 m, the western Atlantic 200 to 600 m and the Caribbean Sea 180 to 450 m. It is found commonly on sandy and muddy bottoms typically covered by seapens (*Funiculina* spp.) asteroids and ophiuroids, often associated with fishes and crustaceans targeted by commercial fisheries, such as the giant gamba prawn (*Aristaeomorpha foliacea*), the deep-water rose shrimp (*Parapeneus longirostris*), the Norway lobster (*Nephrops norvegicus*), the European hake (*Merluccius merluccius*) and the blue whiting (*Micromesistius poutassou*) and with the lesser flying squid (*Todaropsis eblanae*). Mature squids are distributed over the whole depth range and adults undergo vertical migrations, living close to the bottom during the day, then they ascend towards the surface at night. Seasonal migrations also have been observed, at least in some areas of the distribution, e.g. the western and central Mediterranean Sea. Sex ratio usually is 1:1; significant deviations from this value were recorded in the Spanish (Galician) waters, eastern North Atlantic and Ionian populations of central Mediterranean, but such differences are attributed to ecological and/or morphological constraints rather than to actual genetic differences.

Changes in general morphology do occur with sexual maturity and can be quite dramatic in the last stages of maturation, when the relative dimensions of head and arms lead to a distinct sexual dimorphism, with males conspicuously more robust and heavier than females. Size at maturity varies significantly, but generally males mature at a smaller size than females. Also, a west–east gradient of decreasing values in mantle length at 50% maturity occurs in *I. coindetii* populations from the Atlantic to the eastern Mediterranean.

Reproduction and spawning extend throughout the year, with peaks in different seasons/months, depending on geographic location. Fecundity varies with the size of females and spermatophore number with size of males. A potential fecundity of more than 700 000 oocytes was estimated for females from the northwest African waters. Recorded spermatophore length varies between 11 and 38 mm and the maximum number reported is slightly more than 1 500. Spermatophores are deposited in bunches into the female mantle cavity and usually more than one bunch occurs in mated females, suggestive of multiple mating events; the probability that females mate with different males seems high; this behaviour would promote increased genetic exchange. Eggs are small (0.8 to 1.3 mm), embedded in a transparent egg jelly that forms floating egg masses. This gelatinous mass functions as a buoyancy mechanism which prevents eggs from sinking; the equilibration of density between egg masses and sea water, in fact, requires many days under most conditions. Therefore, if spawning occurs in the pelagic domain, the egg masses can remain suspended in the mesopelagic zone for a relatively long time. Such a mechanism would allow pelagically-spawned eggs to take advantage of temperature and other oceanographic conditions most beneficial for embryonic development. *Illex* egg masses have not been recorded in the natural environment, but observations in the laboratory of *I. illecebrosus*, showed that this species produces gelatinous egg masses while swimming in open water. Embryonic development in the laboratory requires between 10 and 14 days at 15°C; this value probably reflects the period under natural conditions. Rhynchoteuthion hatchlings are about (1.4 mm), and the rhynchoteuthion-phase probably constitutes the most delicate time of the entire life cycle; since these paralarvae seem unable to attack prey, they probably feed on suspended particulate material. Favourable environmental conditions during this phase of embryonic development may cause recruitment peaks and, ultimately, may influence recruitment success. An unusually high abundance of *I. coindetii* paralarvae and juveniles in the Evoikos Gulf off central Greece seems related to the convergence of currents in an area of upwelling that resulted in a high concentration of nutrients, thus high productivity that was conducive to aggregations of cephalopod paralarvae and larval fishes.

Growth is rapid; females have higher growth rates than males and several groups with different growth rates usually are detectable within a population; animals hatched in spring–summer have a higher growth rate than those hatched in autumn–winter. Growth differs between sexes, being positively allometric in males and isometric or negatively allometric in females, because of the morphometric dimorphism already mentioned. The only exception to this rule is the positive allometric growth recorded for females from northwestern Spanish waters; also in this case, however, “b” value was lower than that computed for males. Recent observations indicate that parasites can negatively affect growth, as well as the general condition of the animals. Length frequency distributions in ommastrephids usually are polymodal and difficult to use to investigate growth; also, different results generally are obtained when estimating life cycle duration by direct age investigation (i.e. statolith analysis). Duration of the life cycle of *I. coindetii* based on length frequency analysis was estimated to range between 12 and 18 months and 24 months for populations from the eastern Atlantic and the Mediterranean Sea. However, studies on age determination based on statolith investigations, have revealed a shorter life span, such as 12 to 15 months in the eastern Atlantic, 16 months in the western Mediterranean and an even shorter life span (6 to 7 months) for individuals from the waters of Sicily (central Mediterranean). Spawning represents the terminal phase of the life cycle, but it lasts longer than previously thought; many observations indicate that *I. coindetii* females are “intermittent spawners” that spawn several times during a period of time ranging between a few days and a few weeks.

As is the case for cephalopods in general, and for ommastrephids in particular, *I. coindetii* is a voracious and opportunistic predator. It feeds on a wide spectrum of prey, including fishes, crustaceans and other cephalopods, depending essentially on those prey most available and on the size of the predators. Changes in the diet composition with growth have been noted, with smaller squids preying more intensively on crustaceans, while larger, adult animals seem to prefer fishes and other cephalopods, but these changes have been related to important changes in mouth structure of the squid and consequent foraging behaviour, and they were not considered proof of prey selection. Stomach content analysis supports a more pelagic habitus in young squids (a higher proportion of euphasiids in the diet) while adults feed both on the bottom (i.e. amphipods, cephalopods and benthic fishes) and in the water column (a wide variety of pelagic species, such as myctophids, clupeids, gadids). Cannibalism does occur, but probably it is an occasional phenomenon, related to situations of unusually high squid abundance and/or scarcity of other prey. A significantly higher number of mature females with prey remains in their stomach has

been recorded, indicating an increased level of feeding in females, probably due to the higher energy required for maturation and egg production; this surplus of energy would be obtained mainly by direct feeding, since evidence seems to indicate that storage reserves are not transferred from internal tissue to gonadal tissue.

Illex coindetii is preyed upon by a wide variety of predators, including cetaceans such as common dolphins (*Delphinus delphis*), pilot whales (*Globiocephala melas*), Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*), bony and cartilaginous fishes such as sharpnose sevengill sharks (*Heptranchias perlo*), swordfishes (*Xiphias gladius*), yellowfin tunas (*Thunnus albacares*), blue whittings (*Micromesistius poutassou*), greater forkbeards (*Phycis blennoides*) and conger eels (*Conger conger*) and other cephalopods, such as larger squids like the European flying squid (*Todarodes sagittatus*) and the European squid (*Loligo vulgaris*).

Interest to Fisheries: Taken mainly as a bycatch by bottom trawl fisheries throughout its distributional range, *I. coindetii* also is fished by trammel and gillnets; it is caught at night by encircling seiners in the Catalan Sea and was caught by experimental jigging. Specific statistics do not exist, since the species generally is marketed along with the sympatric ommastrephid *Todaropsis eblanae* and occasionally with *Todarodes sagittatus*. However, it is likely to constitute a conspicuous fraction of the annual ommastrephid squid catches both in the Mediterranean Sea and in the Atlantic waters. In the last decades landings in European waters ranged from 3 000 tonnes to more than 7 000 tonnes, the most conspicuous fraction of which was caught in Italian waters of the central Mediterranean. Catches of *I. coindetii* in this area may represent a valuable resource based on tonnages recorded. A marked seasonality in the landings occurs in various areas of the species distribution in the central Mediterranean and North East Atlantic. For example, *I. coindetii* is periodically very abundant in coastal waters of the eastern North Atlantic off Scotland, Ireland and Spain, where it supports opportunistic fisheries. The oceanographic and biological factors that drive this phenomenon, however, currently are not known. Along the Spanish Catalan coast the species is taken mainly as bycatch, and landings have increased steadily since 1987. The spawning season is protracted with maximum peaks in autumn and spring, represented as well by the period of maximum abundance. Large individuals occur year-round, but are most abundant and concentrated during the spawning seasons, spring and autumn, while juveniles are most commonly caught in winter and summer.

Local Names: GREECE: Kokkino, Thrapsalo; ITALY: Totano, Todaro; PORTUGAL: Pota voladora.

Remarks: The remarkable morphological variation observed throughout the distributional range of the species (characterized by a number of more or less distinct morphotypes), along with its disjunct occurrence on both sides of the Atlantic, has led to the suggestion of the existence of a multiple species complex. Recent studies, both on systematics, morphometry and genetics of *I. coindetii* from across the distributional areas, seem to reject this hypothesis (Martinez *et al.*, 2005a,b, Carlini *et al.*, 2006). However, the high variability observed, along with the confirmed existence of at least 2 basic distinct morphological forms, 1 inhabiting the Mediterranean Sea the other inhabiting the Atlantic Ocean, support the need for further morphological and genetic studies.

With regard to the broad variation in results of various age analyses we offer a strong cautionary note: in spite of the recognized validity of age estimation by statolith analysis, several studies suggest that values should be regarded as estimates, not absolutes.

Literature: Mangold-Wirz (1963), Roper *et al.* (1984), Guerra (1992), Jereb and Ragonese (1995b), Rasero *et al.* (1996), Lordan *et al.* (1998a), Roper and Mangold (1998), Roper *et al.* (1998), Sanchez *et al.* (1998b), Belcari (1999c), Arvanitidis *et al.* 2002, Martinez *et al.* (2005a,b), Ceriola *et al.* (2007), Hastie *et al.* (2009).

Illex oxygonius Roper, Lu and Mangold, 1969

Fig. 288

Illex oxygonius, Roper, Lu and Mangold, 1969a, *Proceedings of the Biological Society of Washington*, 82: 295–322. [299]. [Type locality: 24°13'N, 81°58'W, western Central Atlantic Ocean].

Frequent Synonyms: None.

Misidentifications: Non *Illex illecebrosus* (Lesueur, 1821), in part; *I. coindetii* (Verany, 1839), in part.

FAO Names: **En** – Sharptail shortfin squid; **Fr** – Encornet rouge à pointe; **Sp** – Pota puntiaguda.

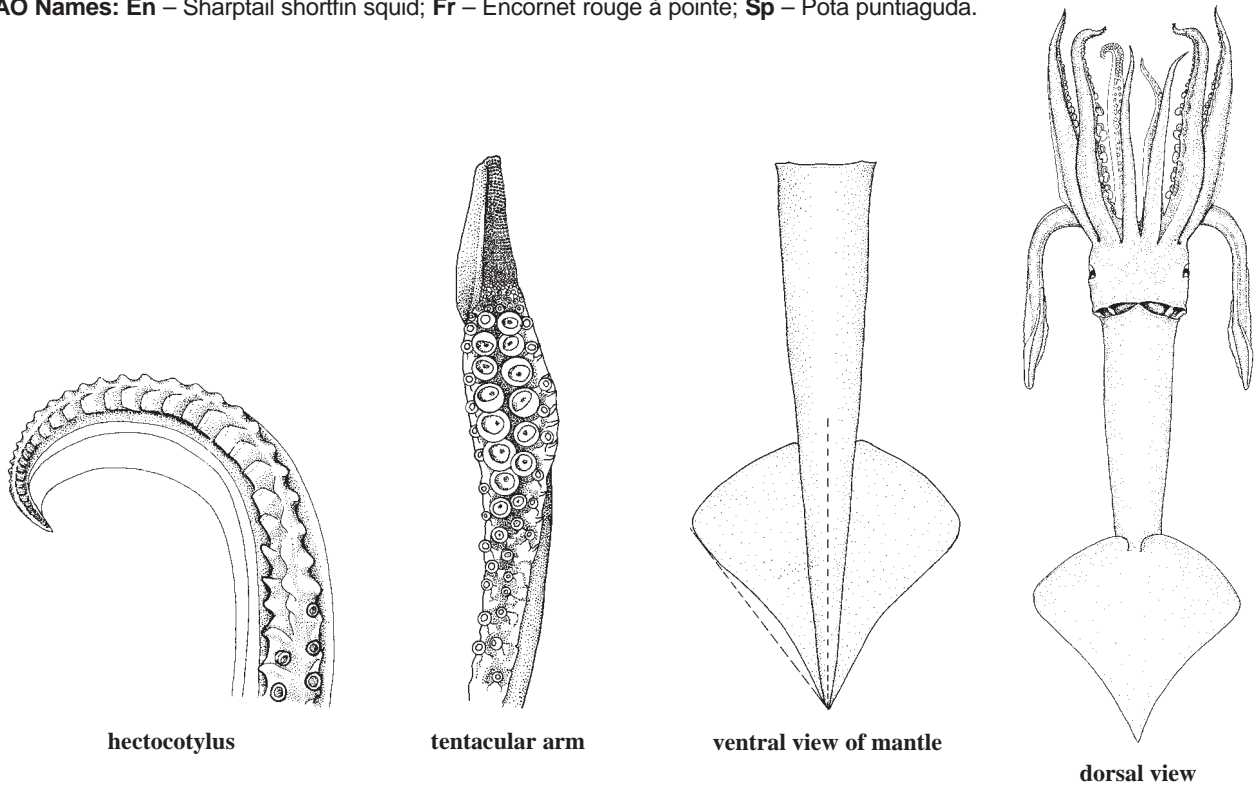


Fig. 288 *Illex oxygonius*

Diagnostic Features: Mantle widest at anterior end, long and narrow; tapers gradually to elongate point posteriorly; males with sharp triangular dorsal lobe at mantle opening. The hectocotylus with distal hectocotyliized portion of arm IV (HA3) moderately long, about 29% (24 to 32%) of total arm length (HALt); 3 knobs and 2 slightly flattened papillae proximal to well-developed lamellae in dorsal row; basal, suckerless part (HAb) of hectocotyliized arm 4% of total arm length; proximal sucker-bearing part (HA1) with 7 pairs of normal suckers; distal sucker-bearing part (HA2) with sucker diameters reduced in size by about one-quarter on both rows. Rows normally separated; oral surface of arm constricted slightly in transition zone between HA1 and HA2, but with no distinct reduction of arm musculature between normal and reduced sucker areas; trabeculae not modified as fringed lobes; **hectocotyliized arm longer and more robust than opposite arm in fully mature animals. Club-sucker rings of largest distal medial manal suckers smooth, without crenulations or notches.** Head-width index high, 20.7 (19 to 23) in mature males, 17.8 (16 to 20) in mature females. Arms long, robust, especially Arms II and III in males. Lower beak with jaw edge curved, long; wing short, narrow, lobate; rostral width wide; lateral wall long, pointed. Upper beak with hood short, very thin, weak; shoulder smooth, straight or slightly curved; rostrum short; wing short; jaw angle with small notch; lateral wall long, deep; crest straight. **Fin angle in mature males acute, 25° to 35°, occasionally 40°; fin width equal to fin length.** Spermatophore cone at oral end of cement body, funnel-shaped, with sides equal, broadly triangular in outline; oral tube relatively broad; aboral neck moderately short, narrow. The colour of the live animal is reddish to reddish brown, more vivid on dorsal head and mantle; more pale, yellowish ventrally.

Size: Maximum mantle length 230 mm in males, 210 mm in females.

Geographical Distribution: Western North Atlantic, off mid-Atlantic United States from off New Jersey, the Chesapeake Bight, southward through the Florida Current and into southeastern Gulf of Mexico; Gulf of Guinea, eastern Atlantic, single record. Limits of geographical distribution of species not well defined because of lack of comprehensive collections (Fig. 289).

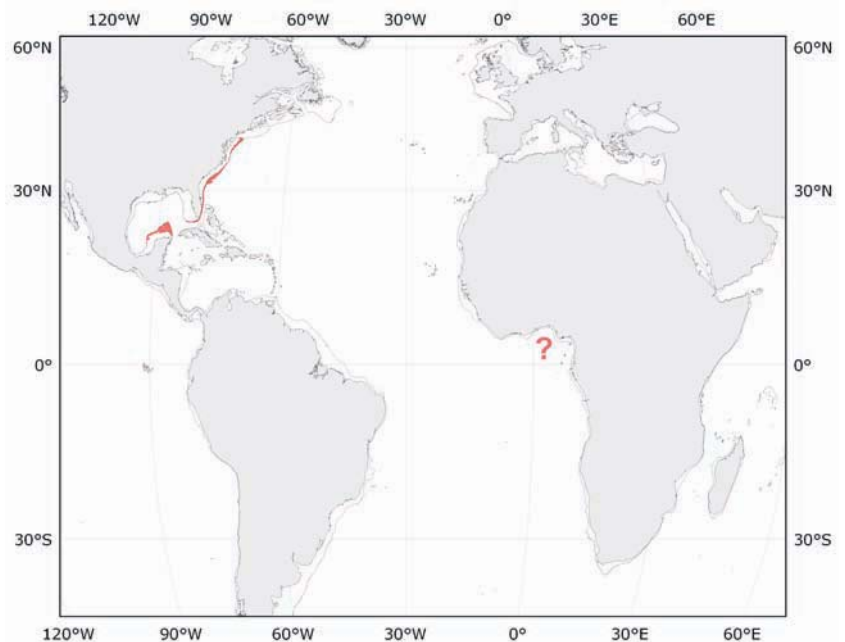


Fig. 289 *Illex oxygonius*

Known distribution

Habitat and Biology: *Illex oxygonius* is primarily a neritic species that occurs at depths between 50 and 550 m within a temperature range from 6° to 13°C. It is associated with the bottom during daylight hours but disperses into the water column at night. Its biology, abundance and total distribution, are largely unknown. It is believed to feed on crustaceans and fishes, similar to its congeners. It is sympatric with both *I. illecebrosus* in the northern parts of its range and *I. coindetii* in the southern parts. All 3 species appear to co-occur in the Straits of Florida, but this needs to be confirmed with more precisely located collections.

Interest to Fisheries: At present, the species is taken only as bycatch in bottom trawl fisheries. When concentrations are discovered, the species would be a valuable fishery resource because its size and consistency are excellent for human consumption, just as with its congeners.

Remarks: Nigmatullin (1989) suggested that *I. oxygonius* was an example of advanced spawning and spent squid traits typical of final life stages of small-sized mature squids of the 2 other species of *Illex*. Subsequently, however, 2 significant genetic studies (Martinez *et al.* 2005a,b, Carlini *et al.* 2006) have confirmed the existence of 4 species of *Illex*, including verification of the distinct species status of *I. oxygonius*. The 2 different techniques used, allozyme polymorphisms (from purpose-caught, freshly prepared specimens) and cytochrome C oxydase subunit I (from formalin-fixed museum specimens), differed somewhat in results and cohesion. Consequently, especially in areas where distributions overlap, specific identification of some specimens remains tenuous until further research clarifies the situation.

Local Names: USA: Sharptail shortfin squid.

Literature: Roper *et al.* (1969a), Roper *et al.* (1998), Vecchione (2002), Martinez *et al.* (2005a,b), Carlini *et al.* (2006).

2.22.2 Subfamily OMMASTREPHINAE Posselt, 1891

Ommastrephinae Posselt, 1891, *Videnskabelige Meddelelser fra den Naturhistoriske Forening: Kjøbenhavn*, 1890: 301–359.

Type Genus: *Ommastrephes* d'Orbigny, 1834 in 1834–1847.

Diagnostic Features: **Small yellow subcutaneous photophores** (similar to short grains of rice) **on mantle, fins, head and arms**; some species may have different arrangement and form of photophores, e.g. large mantle photophores with reflective subjacent layer; **1 ocular and 1 or 2 intestinal photophores present**. Mantle wide, posterior end without pronounced pointed tail; **funnel groove with clearly defined side pockets**; tentacle fixing apparatus with one or several knobs that alternate with smooth-ringed suckers; rings of large suckers on manus with either one large median tooth in distal part of ring, or with 4 large teeth, 1 at each quadrant.

Table 11
Comparison of genera of Ommastrephinae^{1/}

	Largest manus sucker	Visceral photophores	Enlarged, easily visible, subcutaneous photophores	Hectocotylus with lateral pores	Arm tips
<i>Dosidicus</i>	Toothed, enlarged tooth in each quadrant	2 round organs, no streaks	None	Yes	Attenuate at >350 mm ML, with 200–500 small suckers
<i>Eucleoteuthis</i>	Smooth except 1 tooth	1 round organ, no streaks	Circular pads and streaks	No	Normal
<i>Hyaloteuthis</i>	Smooth, sometimes 1 tooth	1 round organ, no streaks	circular pads	No	Normal
<i>Ommastrephes</i>	Toothed, enlarged tooth in each quadrant	None	None	No	Normal
<i>Ornithoteuthis</i>	Toothed, no enlarged teeth	1 or 2 round organs, streak	None	Yes	Normal
<i>Sthenoteuthis</i>	Toothed, enlarged tooth in each quadrant	2 round organs, no streaks	None	Yes; No in early maturing form	Normal

^{1/} from Young and Vecchione (2008g)

***Ommastrephes* d'Orbigny, 1834 in 1834–1847**

Ommastrephes d'Orbigny, 1834 in 1834–1847. Mollusques. *Voyages dans l'Amerique Meridional*, 5(3): 1–758, 85 pls. [45].

Type Species: *Ommastrephes bartramii* (Lesueur, 1821).

Diagnostic Features: The funnel groove has a **foveola with 5 to 8, occasionally 9, longitudinal folds and 2 to 5 (mainly 3 or 4) distinct side pockets. External light organs present**, including small, scattered, subcutaneous photophores embedded in the tissue of the mantle, head and ventral arms, **but no large dorsal mantle photophore is present**. No ocular nor intestinal photophores present. **A long, wide, silvery or golden opalescent strip extends along the ventral midline from just posterior to the mantle opening to the level of the anterior edge of the fins**. Similar silvery or golden tissue occurs on the ventral surface of the head and ventral arms. A relatively dense aggregation of small subcutaneous photophores is concentrated under this opalescent tissue. The **dactylus** of the tentacular club **has 4 rows of small suckers**. The carpal-locking apparatus on the tentacular stalk has 2 to 5 knobs and 2 to 4 smooth-ringed suckers; 4 to 7 suckers with denticulate rings occur on the carpus proximal to the first knob. **The largest medial suckers on the manus of the tentacular club have 4 large pointed teeth, 1 at each quadrant**. The tips of all arms are not attenuate. The arms have 24 to 35 pairs of suckers. The tips of the trabeculae of the protective membranes do not project beyond the edge of the membrane. **The ventral protective membranes of arms III are very wide, and in adult females they expand into a large, triangular, membranous lobe**. Right or left ventral arm is hectocotylized with the smooth type of modification, without suckers. Fins rhomboidal, slightly attenuate posteriorly; fin length 40 to 50% and width 60 to 85% of mantle length; fin angle 46° to 65°. The cone flags of the gladius are short, rhomboidal, with distinct radial creases. The greatest width of the cone flags is about 56% of the width of the rachis. The marginal rigidity ribs of the rachis are doubled; the axial rigidity rib of the rachis is wide, rounded-rectangular in cross-section. The lateral plates of the gladius do not adhere to the dorsal surface of the rachis but form wide free folds over the rachis. The stem of the rachis is short, reminiscent of a mammalian vertebra in cross-section. The width of the stem is slightly greater than its thickness. The cone is short, flattened laterally. A rostrum is absent. The alveola is thick, covered with tiny ribs and thorns. Spermatozoa have 1 flagellum.

Geographical Distribution: Widely distributed in subtropical and partly temperate waters of both hemispheres in the Atlantic, Indian and Pacific Oceans.

Remarks: Monotypic: a single oceanic species is recognized. Restriction profiles of 2 endonucleases, Alu I and Tsp509 I are diagnostic for species identification.

Ommastrephes bartramii* (Lesueur, 1821)*Fig. 290**

Loligo bartramii Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2 (1): 86–101. [90, pl. 7]. [Type locality: Not designated].

Frequent Synonyms: *Loligo bartramii* Lesueur, 1821; *Stenoteuthis bartramii* (Lesueur, 1821); *Loligo vitreus* Rang, 1835 in Ferrussac and d'Orbigny, 1834–1847; *Ommastrephes cylindraceus* d'Orbigny, 1835 in Ferrussac and d'Orbigny, 1834–1847; *Loligo pironneauii* Souleyet, 1852; *L. pironneauii* Souleyet, 1852; *Onychoteuthis brevimanus* Gould, 1852; *Loligo touchardii* Souleyet, 1852; *Ommatostrephes bartrami* Steenstrup, 1880; *Sthenoteuthis bartramii* Verrill, 1880; *Ommastrephes ensifer* Owen, 1881; *O. caroli* Furtado, 1887; *Sthenoteuthis bartramii caroli* Pfeffer, 1900; *Ommastrephes caroli stenodactyla* Rancurel, 1976b.

FAO Names: En – Neon flying squid; Fr – Encornet volant; Sp – Pota saltadora.

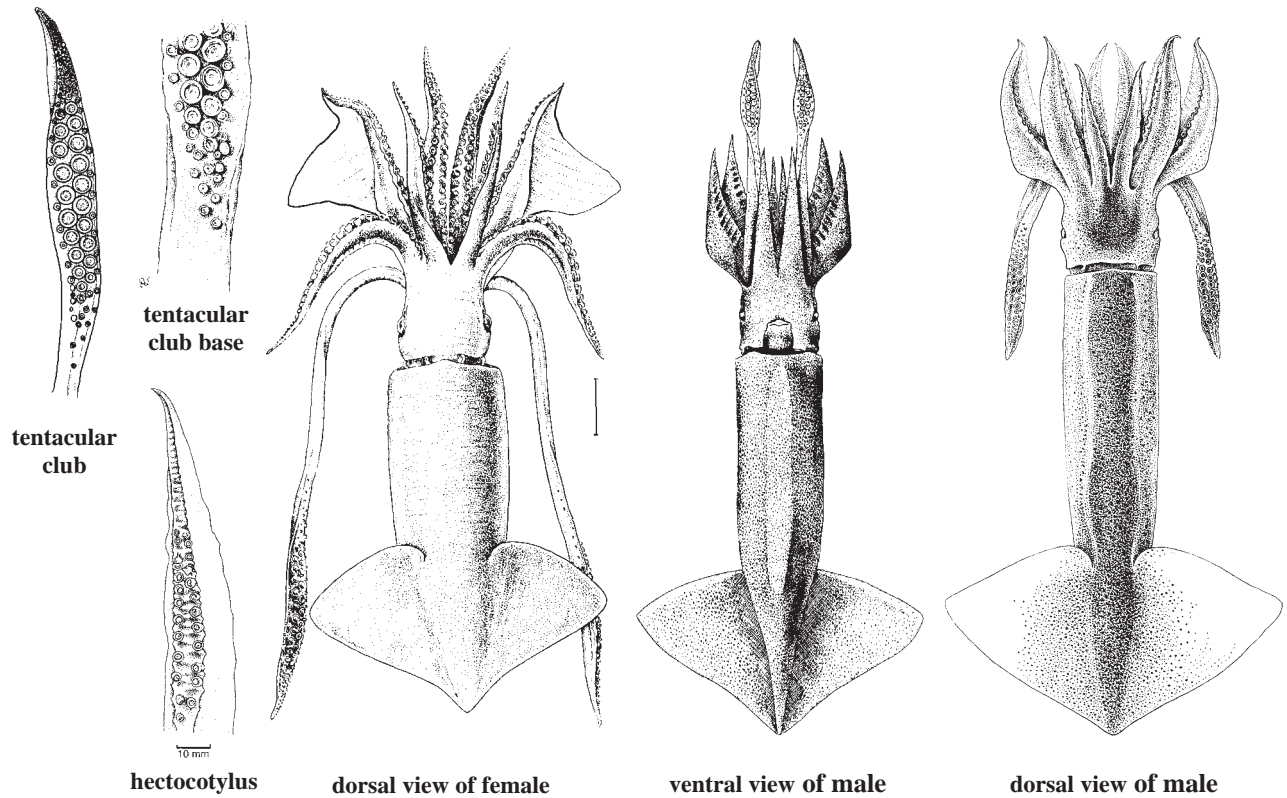


Fig. 290 *Ommastrephes bartramii*

Diagnostic Features: The same as those given for the monotypic genus.

Size: In the North Atlantic Ocean and the Southern Hemisphere the maximum mantle length of females is 800 to 900 mm (body weight 20 to 25 kg) and of males it is 400 to 420 mm (body weight 2 to 2.2 kg), and in the North Pacific the maximum mantle length of females is 500 to 600 mm (body weight about 6 kg) and of males it is 400 to 450 mm (body weight 2 kg to about 2.9 kg).

Geographical Distribution: *Ommastrephes bartramii* is an extremely widely distributed ommastrephid species with an oceanic bi-subtropical (anti-tropical) worldwide distribution. It inhabits the great subtropical ocean gyres in subtropical and partly temperate oceanic waters, but it is excluded from the equatorial waters of all 3 oceans (Fig. 291).

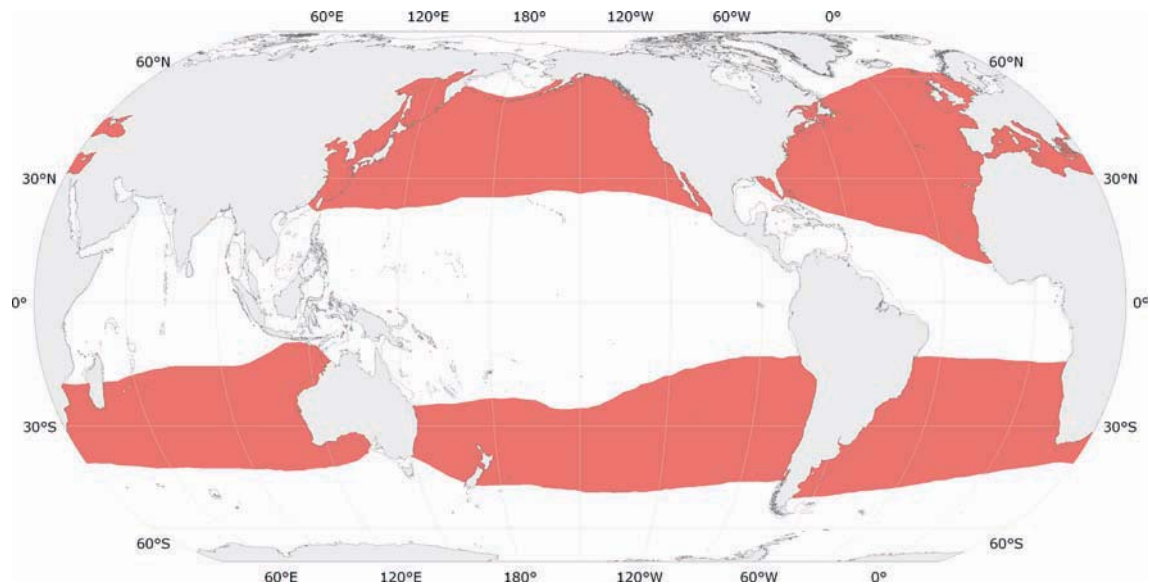


Fig. 291 *Ommastrephes bartramii*

Known distribution

Habitat and Biology: *Ommastrephes bartramii* principal (nuclear) part of distributional range is in subtropical water masses. In the temperate and partly tropical zones *O. bartramii* penetrates into warm and cold boundary currents, respectively. It occurs at sea surface temperatures from 10° to 25°C, generally over bottom depths greater than 200 m. Three major populations, or subspecies, not yet formerly described, inhabit 3 massive, but isolated, regions of the species range.

- 1) The North Atlantic subspecies** is distributed in the Northern Hemisphere from the North Sea and the Shetland Islands (60°N) to the Grand Banks of Newfoundland (48°N), and southward from Mauritania (commonly to 18°N but sometimes to 9°N) to the southern part of the Sargasso Sea and south Florida (23°N to 25°N). Occasionally it penetrates into the most eastern part of the Gulf of Mexico.
- 2) The Southern Hemisphere conspecific group** is distributed in a broad circumglobal band in subtropical waters of all 3 oceans. In the South Atlantic its range extends from 13°S to 46°S, rarely to 50°S in the western part, and from 14°S to 40°S in the eastern part. In the southern part of the Indian Ocean this subspecies is distributed between 20°S and 40°S to the Australian coast in the north and to the Great Australian Bight (135°E) in the south. Its range in the South Pacific extends from the Australian and Tasmanian coasts between 20°S and 46°S in the eastern part, between 25°S and 48°S in the central part, and between 12°S (commonly from 16°S to 18°S) and 46°S eastward to 78°W in the western part, where the natural boundary of its habitat probably is the core waters of the Peruvian Current.
- 3) The North Pacific subspecies of *Ommastrephes bartramii*** is distributed in the same broad band that extends from east of the southern Kurile Islands (47°N) (in some years it penetrates further north to the Commander Islands (55°N)), and the western Aleutian Islands (53°N) to Taiwan Province of China and the Bonin Islands (23°N) in the western part, and from southern British Columbia (50°N) to the middle coast of Mexico (20°N) in the eastern part of the North Pacific Ocean. Occasionally it penetrates into the Sea of Japan. The North Pacific population is represented by 2 seasonal cohorts (autumn and winter-spring) and 4 stocks, each defined geographically and seasonally. Paralarvae from northern Hawaiian waters have been identified by diagnostic restriction profiles of 2 endonucleases.

This abundant oceanic/nektonic species inhabits open waters over depths greater than 200 to 400 m, and it is not associated in any way with the bottom, to the extent that it appears to actively avoid areas over seamounts. It inhabits the entire water column through epipelagic, mesopelagic and upper bathypelagic zones from 0 to 1 500 m and it has a true oceanic distribution and life style strategy, different from the “offshore” squids more associated with the continental shelf break with its upwellings, convergent flow patterns, frontal formations, etc. (e.g. *Illex illecebrosus*, *I. argentinus*, *Todarodes pacificus*, *Nototodarus* spp.). For example, *O. bartramii* inhabits the unique frontal areas between the Southern Ocean and the areas to the north, where they effectively occupy the ecological niche normally associated with fishes in the epipelagic zone.

The planktonic paralarvae, post-paralarvae and juveniles up to 100 to 150 mm mantle length inhabit 0 to 100 m in surface waters during day and night. Squids of 60 to 150 mm mantle length may burst through the surface and glide through the air when they are threatened and pursued by predators. At night most juveniles of 60 to 150 mm mantle length descend from the surface layers to depths of about 40 to 100 m. Subadults and adult squids up to 600 to 650 mm mantle length undergo daily vertical migrations through a significant depth range. At night they concentrate for active feeding mostly in surface and subsurface layers between 0 and 100 m to 150 m (mainly 0 to 40 m or 30 to 70 m), but some portion of the population may remain in the deep layers of the daytime habitat. About an hour before the morning sunrise period they begin to migrate from surface waters to depths of 150 to 600 m in the higher latitudes of their geographical range and to depths from 400 to 1 500 m (mainly 600 to 800 m) in the lower latitudes; both populations remain at their depths during the daytime, principally in a state of low activity. Squids of 100 to 650 mm mantle length (modal size 150 to 350 mm) are fished in the surface layers during the night. Large females of more than 650 mm mantle length do not migrate to the surface at all, but permanently inhabit depths of 300 to 800 m throughout the 24-hour day.

The structure of *O. bartramii* populations (2 cohorts, 4 stocks) is complex in the most intensively studied part of the species' North Pacific range. The area for reproduction is located in the subtropical waters to the south of 35°N to 40°N, while active feeding and somatic growth occur in high latitude temperate areas occupied by migrating squid.

Spawning occurs almost year round in the **North Pacific**. **Two principal intraspecific groups**, cohorts, are distinguished by the time reproduction occurs: **1) a fall or autumn cohort** that spawns in autumn with the hatching period from September to February, and **2) and the winter-spring cohort** that spawns in winter with the hatching period principally from January to May and sometimes to August. Both groups have a 1-year life cycle. These 2 cohorts each are subdivided into 2 subgroups (stocks) by size composition, paralarval distribution and parasitic helminth infection rates (Fig. 292).

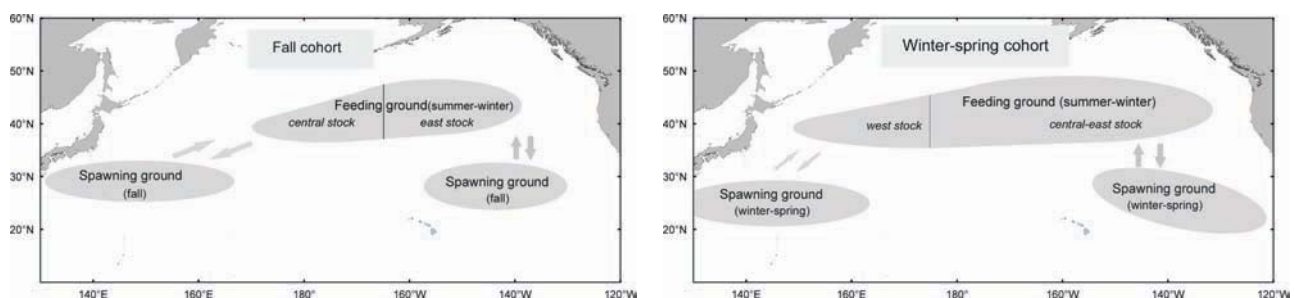


Fig. 292 Migration patterns of the autumn and winter-spring cohorts of red flying squid (*Ommastrephes bartramii*) in the North Pacific (from Bower and Ichii, 2005)

The size of mature females of the autumn spawning group is greater than 460 mm mantle length, while the size at maturity of the winter-spring spawning group of mature females is smaller than 490 mm mantle length. The size of squid of the autumn group during the summer period is much larger than that of the winter-spring group (380 to 460 mm mantle length and 160 to 280 mm mantle length, respectively), and they also differ by maximum size (600 and 490 mm mantle length, respectively). Males are non-migratory; they remain in subtropical waters and do not migrate to the northern grounds. Migrating squid are capable of covering 5 to 10 km per day. It has been observed that the parasite load of *O. bartramii* is sufficiently different geographically as to differentiate between populations associated with eastern and western Pacific feeding grounds.

The North Atlantic reproductive/spawning area is located in the subtropical waters to the south of 45°N to 50°N. The more high-latitude temperate areas of these ranges are used by migrating squid, mainly females, as foraging zones in summer and early autumn. In the northeast Atlantic, after the summer feeding migration of large immature females into high latitudes, including the North Sea, some specimens (600 to 800 mm mantle length) remain in this feeding part of the range. Some of these non-migrating, large squid are stranded during strong winter storms onto the shores of the British Isles, Faeroe Islands, Denmark, Germany and Holland, and these "sea monsters" stirred the imagination of the coastal inhabitants in early times.

In the Southern Hemisphere the latitudinal, feeding and spawning structure of the population probably is similar to that in the Northern Hemisphere: the reproductive/spawning area is in subtropical waters (mainly between 20°S and 30°S to 35°S) and the foraging area occurs in temperate waters (35°S to 50°S) that are used in the southern summer period.

The North Atlantic and Southern Hemisphere males start to mature at 270 to 300 mm mantle length and all males larger than 320 mm mantle length are mature. Two groups are distinguished among females by their size at maturation: 1) females of the middle-sized group mature at 360 to 600 mm mantle length, and 2) females of the large-sized group mature at greater than 650 to 700 mm mantle length.

The life span of males and middle-sized females is 1 year; the life span of the large female group is not known.

Spawning in the North Atlantic and the Southern Hemisphere occurs throughout the year, with some seasonal activity from spring to the beginning of autumn in the corresponding hemisphere. Potential fecundity varies from 3 to 8 million oocytes in females of the middle-sized form and from 12 to 18 million in the large-sized group. Relative fecundity is 900 to 1 500 oocytes per gramme.

The size of ripe eggs is 0.9 to 1.2 mm. The maximum number of eggs in the oviducts of mature females varies between 0.5 and 2 million eggs, depending on the size of the mature females. *Ommastrephes bartramii* females are intermittent, multibatch spawners. After the first spawning, they continue to feed and grow in order to mature the next portions of oocytes for subsequent spawnings. Spermatophore morphometry, length and numbers are different in same-sized males from the North Atlantic and from those in the other parts of the species range. The length of spermatophores in the North Atlantic males varies between 32 and 53 mm (10.3 to 14.7% mantle length, and in other regions it is 22 to 41 mm (7.6 to 10.7% mantle length). The number of spermatophores in the Needham's sac of mature males is 500 to 800 in North Atlantic males and 900 to 1 700 in males from the Southern Hemisphere and the North Pacific. Mass mating occurs in surface layers at night in the "head to head" position, and probably promiscuity occurs. Duration of copulation is 1 to 2 minutes. Spermatangia are attached to the buccal cone and membrane. Between 115 and 160 seminal receptacles occur on the buccal membrane.

As with its subfamilial relatives, *O. bartramii* is a high speed, manoeuvrable and powerful squid that reacts very quickly to any change in its surroundings. Juveniles up to 120 to 160 mm mantle length are able to "fly": they burst from the surface and glide in the air some tens of metres when they are endangered by attacking predators. This species is a powerful, epipelagic, jet-propelled swimmer equipped with a strongly muscular mantle for maximum thrust and short, muscular, triangular fins for stabilization and manoeuvring. The measured horizontal sustained speed of adult squid (370 to 530 mm mantle length) in the sea varies between 6 and 17.6 km per hour, while the burst speed is greater. During evening and morning vertical migrations the swimming speed is less and varies on average from 3 to 5 km per hour. The species is an obligate shoaling squid throughout ontogenesis. Distinct shoals (schools) are comprised of uniform-sized squid. Shoal size varies from 2 to about 150 individuals, sometimes more. At the low-latitude periphery of the geographic range, this species may form joint schools with same-sized *Dosidicus gigas*, *Sthenoteuthis oulaniensis* and *S. pteropus*.

Ommastrephes bartramii is an active predator throughout all ontogenetic stages; this requires periodic changes in prey selection. Paralarvae feed on micro- and mainly mesozooplankton (copepods, juveniles of euphausiids and amphipods). Post-paralarvae and juveniles of 10 to 120 mm mantle length feed on meso- and macroplanktonic invertebrates, mainly euphausiids, amphipods, chaetognaths, heteropods, thecosome pteropods and the larvae and small juveniles of fishes and squids. Squid of 120 to 180 mm mantle length sharply increase their predation on planktivorous teleosts (mainly myctophids and sauries) and small squids. Feeding of subadult and adult squid of 500 to 600 mm mantle length takes place during night time in surface layers from 0 to 70 m, and feeding activity is significantly reduced during daytime at the greater depths of the mesopelagic zone. The broad spectrum of prey for this adult size group of squid is relatively similar in the different parts of the vast geographical range of the species. These squid feed principally on myctophids (*Electrona*, *Myctophum*, *Hygophum*, *Diaphus*, *Symbolophorus*, *Lasmpanyctus*, *Protomyctophum*, *Ceratoscopelus*, etc.), sternoptychids (*Mauroliticus*, *Argyropelecus*), sauries (*Gololabis saira*, *Scomberesox saurus*), and to a lesser degree on juveniles of predatory fishes (chauliodontids, paralepidids, gempylids, etc), flying fishes, squids (mainly *Onychoteuthis borealijaponica* and spp., *Berryteuthis anonychus*, *Gonatus berryi* and spp., *Abraliopsis* spp., histioteuthids, enoploteuthids, conspecific juveniles) and on pelagic shrimps, amphipods and euphausiids. Large females larger than 650 to 700 mm mantle length feed at mesopelagic

depths on middle-sized, mesopelagic non-migratory predatory fishes, (e.g. myctophids: *Bathylagus ochotensis*, *Lampanyctus regalis*, *Protomyctophum thompsoni* and *Stenobrachius nannochir*), squids and to a lesser degree on large shrimps.

In geographical areas where the distribution of *O. bartramii* overlaps with other oceanic ommastrephid squid in the same ecosystem, a niche separation occurs; for example, when it overlaps with *Todarodes pacificus*, it feeds principally on crustaceans, while *T. pacificus* preys on fishes.

The main predators of *O. bartramii* also change during ontogenesis. Paralarvae and post-paralarvae are eaten by small squids, as well as plankton-eating and small carnivorous teleosts, including juveniles and subadults of tunas. Juveniles (3 to 14 mm mantle length) are the prey for large squids (mainly conspecific adults), cod (*Gadus morhua*), lancet fishes (*Alepisaurus ferox*), and tunas (*Thunnus alalunga*, *T. obesus*, *T. albacares*, *T. thynnus*, etc). The Pacific pomfret (*Brama japonica*) is an important predator of *O. bartramii* juveniles in the central part of North Pacific. In addition, they are eaten by sea birds: black-browed albatross (*Diomedea melanophris*), shy albatross (*Diomedea cauta*), cape gannet (*Morus capensis*) near South Africa, red-footed boobies (*Sula sula*) near the Hawaiian Islands, Parkinson's petrel (*Procellaria parkinsoni*), Herald petrel (*Pterodroma heraldica*), Kermadec petrel (*Pterodroma neglecta*), Murphy's petrel (*Pterodroma ultima*) in the South Pacific near the Pitcairn Islands, and seabirds breeding in the Hawaiian Islands. The major predators of subadult and adult *O. bartramii* are swordfish (*Xiphias gladius*), blue marlin (*Makaira mazara*), some active species of sharks (*Prionace glauca*, *Sphyrna zygaena*, *S. lewini*, *Carcharhinus longimanus*, etc.) and sperm whales (*Physeter macrocephalus*). *Ommastrephes bartramii* is a dominant squid species in the diets of yellowfin tuna (*Thunnus albacares*) and especially of swordfish (*Xiphias gladius*) off eastern Australia. Swordfish and sperm whales are common important predators on adult mature squid in all parts of the species range, mainly on females of 300 to 600 mm mantle length and possibly to the maximum size. Other representatives of marine mammals also are known as significant predators: northern fur seal (*Callorhinus ursinus*), cape fur seal (*Arctocephalus pusillus*), sub-Antarctic fur seal (*Arctocephalus tropicalis*), northern elephant seal (*Mirounga angustirostris*), short-beaked common dolphin (*Delphinus delphis*), Cuvier's beaked whale (*Ziphius cavirostris*), killer whale (*Orcinus orca*), false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Kurioshio Current*) and Baird's beaked whale (*Berardius bairdii*). Remains of subadult *O. bartramii* of 360 mm mantle length were found in stomach contents of giant squid, *Architeuthis*, in southern African waters.

An helminth fauna parasitic on *O. bartramii* of 14 species of larval trematodes, cestodes, nematodes and acanthocephalans has been described. Two species of nematodes affect commercial utilization and value. Larvae of *Anisakis* sp. are mortally dangerous to humans; however, they are localized in the ovaries and encysted in coelomic membranes, neither of which is used for human food, so the danger largely is eliminated. Thousands of larvae of *Porrocaecum* sp. may be encysted on the internal mantle wall, and they may reduce the quality of the marketable product with high levels of infestation.

Interest to Fisheries: In spite of its worldwide distribution, *Ommastrephes bartramii* is fished commercially only in the North Pacific Ocean where its populational structure and abundance seem to be maximized for exploitation. Fisheries have not developed in other parts of its distributional range, although several studies suggest that a fishery might be sustainable in the Atlantic. Experimental fisheries were carried out in the Tasman Sea and the slope waters off the coast of Uruguay without successful commercial results. However, continued demand for squid products, steady to elevated price structures, and increased knowledge about the biology and populational structure of the species may lead to geographically expanded fishery exploitation.

The total, instantaneous biomass of *O. bartramii* is about 10 to 13.5 million tonnes, including 8 to 10 million tonnes outside the national Exclusive Economic Zones (EEZs). The total tonnage is distributed in the different parts of the species geographic range as follows: North Pacific – 3 to 3.5 million tonnes, South Pacific – 2 to 2.5 million tonnes, North Atlantic – 2 to 2.5 million tonnes, South Atlantic – 2 to 3.5 million tonnes, Indian Ocean – 1 to 1.5 million tonnes.

The fishery in the North Pacific is seasonal; it begins in June and lasts through December. In recent years the fishery has continued through February off northeastern Honsu. The most productive period is July to August when about 50% of the total annual catch is harvested. The fishery is based on the location of squid feeding concentrations. The fishing grounds are situated in a wide belt between 30°N and 45°N from Japan to the American west coast, i.e. throughout the full extent of the feeding grounds. Regions of high biological productivity are conducive for concentrations of feeding *O. bartramii* and, consequently for fishing effort. Such areas where warm-core rings and *O. bartramii* fisheries exist are in the Kurushio Current system off Japan and the East Australia Current off southeastern Australia. Sea surface temperatures for optimal catches range between 12° and 22°C depending on season (month) and locality on the broad fishing grounds.

Ommastrephes bartramii was first commercially fished in the North Pacific by Japanese jig vessels off the Pacific coast of Japan in 1974, and the fishery rapidly developed. The driftnet fishery was introduced for this species in September 1978 and due to overexploitation by both fisheries on the stock, serious competition developed between the driftnet and jig fisheries. To calm this conflict, the Japanese Government separated the fishing grounds for these fisheries in 1979: the jig fishery was limited to waters west of 170°E longitude and the driftnet fishery was restricted to the waters east of 170°E. longitude. Subsequently, South Korean driftnet vessels, Taiwan Province of China jig and driftnet vessels and Chinese jigging fleet also joined the fishery. Since 1993 the fishery has been limited to a jigging fishery only, due to the moratorium on the commercial use of large-scale driftnets introduced into practice by the 45th United Nations General Assembly in 1991.

Rough estimations by Japanese investigators suggest limits of 300 000 to 700 000 tonnes for the possible sustainable annual catch rate of *O. bartramii*. However, a decreasing trend in the catches for the last years is shown by the FAO statistics (i.e. to about 18 500 tonnes in 2007).

The huge number of squid throughout the remaining part of species range is scattered over vast areas. However, potential fishery areas exist where squid concentrations are sufficiently high to warrant an experimental fishery to be carried out. These areas include: the southwestern Pacific Ocean near Australia and New Zealand and the southeastern part of the Indian Ocean near Australia; the slope and adjacent open waters around South Africa, far southeastern South Atlantic Ocean, the Brazil-Falkland Confluence area between 34°S and 44°S, as well as on the warm side of the Brazil Current between 32°S and 25°S in the southwestern Atlantic Ocean; the area between Cape Blanc (21°N near northwest Africa) and the Canary Islands; near the Azores Islands; around the North sub-Arctic Frontal Zone in the North Atlantic Ocean.

Local Names: ARGENTINA: Calamar rojo; AUSTRALIA: Red ocean squid; CANADA: Red flying squid, Neon flying squid; CHINA: rÓu-yú, bá-shì-rÓu-yú, qíang-rÓu-yú; FRANCE: Encornets rouges, Calmars rouges; GERMANY: Pfeilkalmar, Flugkalmar; ITALY: Totano nero; JAPAN: Aka-ika (Red squid), Murasaki-ika (Purple squid), Baka-ika (shortened form of Baka ni ookii ika (very large squid), Kuro-ika, Goudou-ika; KOREA: Bbal-gang-O-jing-eo; PORTUGAL: Pota de orelhas, Pota saltadora; ROUMANIA: Calmarul zburator; RUSSIA: Kal'mar bartrama, Neonovyj kal'mar, Letaujschij kal'mar; SPAIN: Pota saltadora; TAIWAN PROVINCE OF CHINA: Chì-yÓu; UK: Large squid; URUGUAY: Calamar rojo; USA: Neon flying squid, Red flying squid, Webbed flying squid.

Remarks: Three subspecies of *Ommastrephes bartramii* inhabit the North Atlantic, the North Pacific and the circumglobal Southern Hemisphere, but they have not yet been formerly described. These 3 geographically isolated populations are differentiated by spermatophore morphology, by their size structure (Zalygalin *et al.*, 1983; Nigmatullin *et al.*, 2003) and by substrate-inhibitory traits of optic ganglia cholinesterases (Shevtsova *et al.*, 1979). It is critically necessary that a special taxonomic revision of this species be undertaken in order for the 3 subspecies to be officially established and named, based on well-founded systematic analyses and descriptions. This is necessary not only for systematic and nomenclatural purposes, but it is important for biological and, especially, fishery-oriented management reasons.

Literature: Wormuth (1976), Roper *et al.* (1984), Dunning (1998a,b,f), Yatsu and Mori (2000), Bower and Ichii (2005), Brunetti *et al.* (2006), Wakabayashi *et al.* (2006).

Dosidicus Steenstrup, 1857

Dosidicus Steenstrup, 1857a, *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobenhavn*, 1856–1857: 120–121. [120].

Type Species: *Dosidicus gigas* (d'Orbigny, 1835).

Diagnostic Features: Funnel groove deeply excavated in **foveola**, rounded anteriorly, **with average of 7 longitudinal ridges and 4 or 5 side pockets**; carpal-locking apparatus present on tentacular club; medial suckers on manus with 4 large teeth, 1 in each quadrant; dactylus of tentacular club with suckers in 4 longitudinal rows; **small subcutaneous photophores on ventral surface of mantle, head and arms III and IV**, 2 intestinal photophores (in juveniles/subadults); photophore present on ventral surface of eyeballs (in juveniles/subadults); no large mantle photophores; **right or left arm IV hectocotylized, modified section smooth; tips of all arms in adults very attenuate, thin**, with numerous, minute, densely-packed suckers; longitudinal ridge of mantle component of locking cartilage with anterior bifurcation; cross-section A of gladius with 3 lateral lobes.

Remarks: Monotypic.

***Dosidicus gigas* (d'Orbigny 1835)**

Ommastrephes gigas d'Orbigny 1835, in 1834–1847, *Voyage dans l'Amerique.Meridionale*, 5(3): 1–758 [50, pl 4]. [Type locality: 40°S to 60°S Valparaiso, eastern South Pacific Ocean].

Frequent Synonymys: *Ommastrephes gigas* d'Orbigny 1835; *O. giganteus* d'Orbigny, 1839–1842, in Ferussac and d'Orbigny, 1834–1848; *O. giganteus*, Gray, 1849; *Dosidicus eschrichtii* Steenstrup, 1857a; *D. steenstrupi* Pfeffer, 1884.

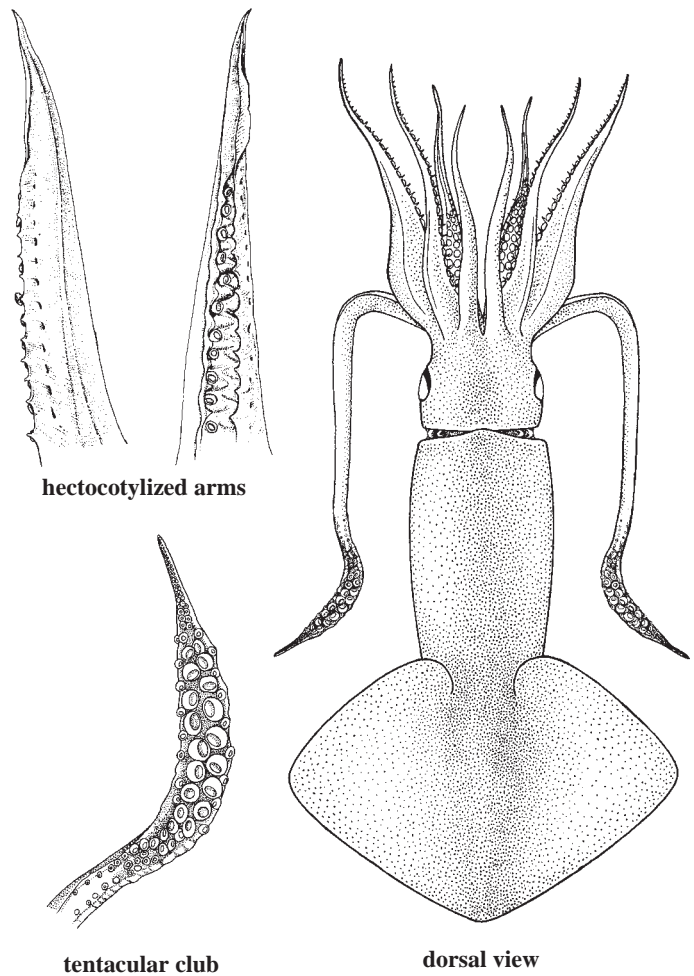
FAO Names: En – Jumbo flying squid; Fr – Encornet géant; Sp – Jibia gigante.

Diagnostic Features: The mantle is large, robust, thick-walled. The fins are rhomboidal, very muscular, broad, width 56% of mantle length (49 to 65%), length 45% (41 to 49%) of mantle length, single fin angle 57° (50° to 65°). The funnel groove is deeply excavated in the foveola, rounded anteriorly, with an average of 7 cutaneous longitudinal ridges and 4 or 5 lateral side pockets. The dactylus of the tentacular club has suckers in 4 longitudinal rows. The carpal-locking apparatus has 1 to several knobs that alternate with smooth-suckered rings. The largest suckers on the manus of club have 1 enlarged central tooth distally and 3 smaller enlarged teeth in the other quadrants. Small subcutaneous photophores occur on the ventral surfaces of the mantle, head and arms III and IV; 2 small intestinal photophores exist. These are visible in juveniles and young individuals but are obscure in adults. The longitudinal ridge of the mantle component of the locking cartilage has an anterior bifurcation. The distal tips of the arms, especially in adults, are drawn out into very long, attenuate tips with 100 to 200 minute, closely packed suckers; dorsal protective membrane on arms very weakly developed, but the trabeculae are well developed, muscular, exposed papillae; either right or left arm IV is hectocotylized (not both on the same specimen) by absence of suckers and stalks at arm tip, and expanded and perforated protective membranes. The anterior section of the gladius is tri-lobed or A-shaped in cross-section; the gladius lacks vanes, is very narrow, rod-like, then widens slightly posteriorly into a small terminal conus.

Size: Large-sized species: maximum total length approaches 2.5 m, with a maximum mantle length of 1.2 m (off Chile); maximum weight to 50 kg. Attains about 1 m mantle length in the northern population; common mantle length to about 500 to 800 mm; common weight to about 20 to 30 kg.

Geographical Distribution: *Dosidicus gigas* exhibits a broad and variable range in the eastern Pacific Ocean: from approximately 22°N to 22°S, limited approximately by the 20°C isotherm. Unusual periodic extensions of range reach into the 50° North and South regions; records are confirmed from 59°N in Alaska, and from 53°S, approaching Tierra del Fuego. The longitudinal range westward into the open equatorial Pacific Ocean probably extends to 125°W, but the full extent is not clearly known (fishing has been successful in waters 1 000 km off the Peruvian coast) (Fig. 294).

Fig. 293; Plate IX, 54

Fig. 293 *Dosidicus gigas*Fig. 294 *Dosidicus gigas*

Known distribution

Habitat and Biology: *Dosidicus gigas* is one of the largest and most abundant nektonic squids in the epipelagic zone of the world oceans; it is endemic to the eastern Pacific Ocean and its distribution seems to be limited by the isoline of phosphate of 0.8 mg. concentration and by the 20°C surface isotherm. During the El Niño event of 1997–1998 that affected coastal oceanographic conditions as far north as northern California and Oregon, associated with the advection of anomalously warm water into inshore waters, *D. gigas* was reported in Oregon for the first time and was caught in large numbers. A similar, though much more wide-spread and invasive El Niño event in 2002–2006 carried *D. gigas* into Alaskan waters for the first reported time as far north as 59°N. This species has undergone a sustained range extension into central and northern California waters. This invasion has impacted the ecosystem dynamics in Monterey Bay where it has established permanent residence since 2002 in coincidence with climate-linked oceanographic conditions and a consequent reduction in competing top-level predators. The abundance of Pacific hake (*Merluccius productus*), a principal prey of the Humboldt squid and the most important commercial groundfish species, has declined markedly in coincidence of the establishment of *D. gigas* in the region.

The jumbo flying squid is known to descend to depths in excess of 1 000 m. An ultrasonic telemetry system was employed to track vertical and horizontal movements of 3 *D. gigas* off the Costa Rica Dome and in Peruvian waters. Squid were tagged and released after sunset and tracked for 8 to 14 hours. Swimming activity generally was above 200 m at night; then the squids dived to bathypelagic depths (greater than 1 000 m) during the day. Most daytime hours were spent deeper than 250 m in the oxygen minimum layer (OML) or hypoxic zone; then the squid migrated to near-surface waters at night. Feeding occurs both at night and during the day in the OML below 300 m.

During El Niño years *D. gigas* exhibits a high abundance in association with the well-developed countercurrent “ridge”, or upwelling, off the Costa Rica Dome, but during La Niña years when the upwelling is less developed, abundance is low. Two factors associated with the well-developed upwelling probably account for the higher abundance of *D. gigas*: 1) subsurface phytoplankton, *Chlorophylla maxima*, form there to provide high productivity, many species of which become prey for jumbo flying squid; 2) a strong salinity front forms along the North Equatorial Countercurrent to serve as a barrier to entrain the squid. The abundance of *D. gigas* in the eastern central Pacific during October to December is higher in areas of upwelling. Squids migrate periodically northwest to southeast and back, in association with the changing divergence zones. Off Peru where a significant fishery occurs, adult squid abundance is positively associated with sea surface temperatures (SST) of 17° to 22°C in July, the peak of the fishery season. In the presumptive hatching area off the Costa Rica Dome high abundance is associated with SST of 24° to 28°C. These patterns are associated with the mesoscale variability of the El Niño Southern Oscillation (ENSO).

The size at first maturity for females in Peruvian waters is 240 to 320 mm mantle length; mature adults occur throughout the year but the principal spawning period is spring/summer (October to January), with a secondary peak in July/August. Spawning occurs along the entire coast of Peru with greatest concentrations in the north between 03°S to 08°S and in the central zone between 12°S and 17°S.

A large-scale artisanal fishery for *D. gigas* occurs in the central Gulf of California in 2 areas of alternate seasonal upwelling. Two distinct cohorts of *D. gigas* occur in that area: a large, late-maturing cohort and a medium-sized early-maturing cohort. Large females mature late at age 1 year and 730 mm mantle length, large males mature at 10 months and 600 mm mantle length. Females of the medium-sized cohort mature at 7 months, 370mm mantle length and males at 7 months and 340 mm. Predominant catches consist of large mature females, 750 mm mantle length and males, between 530 and 670 mm mantle length. The intra-annual cohorts of *D. gigas* forage in alternate upwelling seasonal areas during their respective life histories.

Growth of *D. gigas* in equatorial waters is rapid and the life span of most is about 1 year; however the largest specimens of the large cohort probably live to 2 years.

Reproduction takes place year-round. Spermatophore total and component lengths, and sperm volume increase remarkably with growth of the male. Female *D. gigas* have the highest potential fecundity known among cephalopods, up to 32 million oocytes.

Mature eggs from oviducts of females are transparent, amber-yellow, slightly ovoid, 0.9 mm to 1.1 mm long. The hatchlings are about 1 mm mantle length. The paralarva is a typical rhynchoteuthion type with a well-developed tentacular proboscis that is quite thick and much longer than the arms in the early stages; eventually it can be up to 80% of mantle length. The process of separation of the proboscis begins at 5 to 6 mm mantle length and is complete by about 10 mm mantle length.

Paralarvae are planktonic and the smallest ones (1.2 to 1.6 mm mantle length) normally are found over the continental slope and up to about 300 nautical miles offshore in the epipelagic waters, mostly from the surface to 100 m. However, extraordinarily high abundance of *D. gigas* rhynchoteuthion paralarvae have been caught in a band parallel to the coast, 740 to 900 km offshore from Central America. Captures were coincident with the 29°C surface isotherm and maximum abundance (>12 000 rhynchoteuthions per 15-minute tow) was 4 orders of magnitude greater than any other report of paralarval cephalopod abundance. This extraordinary abundance may have been created by the interactions of warm El Niño waters and the aggregation by convergence of surface currents. Paralarval and juvenile *D. gigas* (1 to 10 mm mantle length) have been positively identified, using mitochondrial gene sequencing, in the central Gulf of California, Mexico. Since the smallest paralarvae of 1 mm mantle length are the size expected for *D. gigas* hatchlings, spawning must take place in the area of San Pedro Martin Basin.

Artificial fertilization of *D. gigas* eggs from Peruvian waters produced 167 hatchlings that were maintained at 18°C. Hatching occurred 6 to 9 days after fertilization and the rhynchoteuthion paralarvae survived for up to 10 days following hatching. Size at hatching was 0.9 to 1.3 mm mantle length (mean 1.1 mm) and mantle length increased to 1.1 to 1.5 mm (mean 1.4 mm) 7 days post-hatching.

Dosidicus gigas progresses through a spectrum of prey organisms during ontogenesis. Ontogenetic stages alternate with critical transitional periods during which squids change their mode of life and progress to the next higher trophic level. A principal prey of adults is the California sardine (*Sardinops sagax caerulea*) and in years of high population density the squid consume up to 60 000 tonnes of sardines during their 9-month residence in the Gulf. Such an intense predation, when 80% of the squid diet is sardines, negatively impacts the landings in the sardine fishery. Also in the Gulf of California, as well as in the open ocean, large and medium-sized *D. gigas* prey significantly on epipelagic/mesopelagic fishes, principally myctophids, e.g. *Hygophum atratum*, *Myctophum aurolaterdatum*, *Lampanyctus parvicauda*, *Diogenichthys laterdatum*, *Benthosema panamense*, *Triphoturus mexicanus*; also *Vinciguerria lucetia*, *Symbolophorus* spp. and other small pelagic fishes (e.g. northern anchovy and Pacific sardine species, saury-pike (*Scomberesox saurus*), flying fishes (Exocoetidae). Secondary, though significant, prey consists of micronektonic squids (principally ommastrephids, including cannibalism on smaller conspecific specimens), pelagic red crab (*Pleuroncodes planipes*), pteropods, megalopae and euphausiids. In its expanded range in the California Current off Monterey, California, *D. gigas* feeds on Pacific hake (*Merluccius productus*), shortbelly rockfish (*Sebastes jordani*) and other species with semi-pelagic life histories. Large migratory squids off the coast of Chile consume congrijo (*Genypterus*), hake (*Merluccius gayi*), sardines, squids, decapod and stomatopod crustaceans. A dramatic decrease in catch of hake, the main demersal fishery resource in central Chilean waters, resulted in a total allowable catch in 2005 of 70 000 tonnes, about one-half that of 2004. Since *D. gigas* is a known major predator on hake, a multispecies model was conducted which estimated that the Humboldt squid biomass of 300 000 tonnes removed a biomass of hake of 150 000 tonnes, slightly in excess of the total commercial hake landings in 2004. Coupled with estimates of overfishing, squid predation is the principal cause of the serious hake decline.

Adult *D. gigas* squid were observed to attack captive skipjack tuna (*Katsuwonus pelamus*) and yellowfin tuna (*Thunnus albacores*) when inside the purse seine, causing significant bite damage. This unnatural condition begs the question of which species is predator and which is prey. Normally, *D. gigas* hunts in near-surface waters with peak intensity at dawn and a secondary peak in the evening. While they probably prey on small tunas, it seems most likely that the netted tunas prey on the aggregated squid, and bite damage on the fish is the result of opportunism or defense by the squid. The adult *D. gigas* occasionally is captured in the purse-seine fishery for tunas in only about 2% of the sets. The interactions between tunas and *D. gigas* demonstrate considerable plasticity in the schooling behaviour of the squid. *Dosidicus gigas* is very aggressive and cannibalistic on smaller individuals and readily attacks conspecific individuals that have been captured on jigs. Occasionally the attack behaviour is so strong that many individuals will attack others that have attacked jigged specimens, so that a large "squid ball" is formed. Several reports exist of attacks on humans by large *D. gigas*, including at least one death. Scuba divers working among large feeding *D. gigas*, usually at night and separated from dive buddies, have been attacked by single or multiple individuals, that sometimes attempt to pull them into deeper water, or sometimes inflict deep lacerations through wet suits and dive skins.

A major prey of sperm whales stranded in Peru and Chile, *Dosidicus gigas* was the second most important species in terms of weight, 32% in one study. Abundance of sperm whales in Peruvian waters is positively associated with high CPUE in the *D. gigas* fishery. In the Humboldt Current sperm whales (*Physeter macrocephalus*) prey almost exclusively on *D. gigas*, consuming what was estimated between 6.7 and 20.1 million tonnes per year, which represented 34 times the highest catch of squid reported in the Peruvian fishery. Sperm whales in the Gulf of California prey extensively on *D. gigas* every spring/summer season, regardless of the inter-annual variations in squid populations. Various species of beaked whales also prey on *D. gigas*, as do the inshore and offshore forms of bottlenose dolphin in the Gulf of California, Mexico. *Dosidicus gigas* is among the 3 most-captured prey species that constitute 90% of the diet of blue marlin (*Makaira nigricans*) caught off Cabo San Lucas, Gulf of California, Mexico; it is prey of the striped marlin (*Tetrapturus andax*) in southern Gulf of California, Mexico and it constitutes the principal prey of swordfish (*Xiphias gladius*) and sailfish (*Istiophorus platypterus*) at lower its distributional range. Other pelagic fish predators include the dolphinfish or mahi mahi (*Coryphaena hippurus*), the yellowfin tuna (*Thunnus albacares*), juvenile hammerhead shark (*Sphyrna lewini*) and silky sharks (*Cercharhinus falcifer*).

The jumbo flying squid releases prodigious quantities of ink when threatened by potential predators. The ink contains free amino acids and ammonium which serve as a chemical defense by disrupting sensory detection and by phagomimicry.

The parasites of *D. gigas* include 9 to 12 species of nematodes, cestodes, trematodes and the ciliate, *Chromidina*. All parasites occur in their larval stages. Infection rates and species compositions are similar for males and females of similar mantle length, as well as geographically across the sampling range. Parasites are acquired progressively during ontogeny and the formation of the helminth fauna proceeds in definite ecological patterns typical for particular size-age groups of hosts.

Interest to Fisheries: The significant fishery for *D. gigas* is linked to the major coastal upwelling ecosystem associated with the low velocity eastern boundary current system, the Peru or Humboldt Current. Exploratory fishing for this species was initiated in the early 1970s in several Pacific areas off the western Americas. Most of the fishery was carried out by Japanese jigger boats under a joint venture scheme and by Mexican shrimp fishermen that switch to squid fishing during the closed season for shrimp fishing. The best catches are obtained during the summer months, but the season has been progressively expanded, so that fishing now occurs throughout the year. Reduced catches in some areas coincide with increased catches in other parts of the species range: so a decreased abundance in Peruvian waters coincided with increased catches principally in the Gulf of California, Mexico and off Central America, in the Costa Rica Dome region.

The fishery for *D. gigas* in the Gulf of California developed very rapidly during 1978–1980, attaining 22 400 tonnes; it collapsed entirely for several years after 1981, then it rebounded again in the 1990s.

In Chilean waters catches of *D. gigas* occur year-round, concentrated mainly off central Chile. Chinese jigging vessels in offshore waters of Chile recorded maximum catches concentrated around 28°30'S, 76°78'W; average CPUE was in excess of 10 tonnes/day, with sea surface temperatures mainly 17° to 19°C. The principal gear for the *D. gigas* fishery is the jigging machine.

Jigging is the main fishing activity in Peruvian waters as well. The multinational jigging fleet active off Peru is so extensive and concentrated, that the light emission from the jigging vessels is detectable from space via satellite imagery. Fishing grounds are concentrated off the coast of Peru at 02°S to 10°S; jigging grounds on the high seas were located off Peru at 03°S to 18°S and off Central America at 05°N to 10°N. These localities were associated with areas of upwelling events in the eastern Pacific rather than with bathymetry or proximity to coastal regions, and they occurred over depths of 200 to 4 500 m between 30 and 400 nautical miles offshore.

With extensive knowledge of the El Niño/southern oscillation cycle and increasing knowledge of the life cycle of *D. gigas*, recruitment can be predicted and appropriate management schemes can be applied.

The total instantaneous biomass of *D. gigas* is estimated to be 7 million to 10 million tonnes, of which 2 million to 4 million tonnes occur in the open ocean, beyond the EEZs (Exclusive Economic Zones). With catches values close to 700 000 tonnes in 2007, this species alone accounted for about 21% of the total squid world catch in that year.

Dosidicus gigas tissues are rich in essential amino acids and the species is consumed fresh and frozen. Hydrolyzed protein of *D. gigas* is an excellent supplement to the feed of farmed shrimps. Squid meal made from different body parts were tested as food for cultured shrimp, with positive results.

Local Names: JAPAN: Amerika-ooakaika, Amerika-oosurume, Jumbo squid; MEXICO: Pota; USA: Humboldt squid.

Literature: Nesis (1983), Roper *et al.* (1984), Ehrhardt *et al.* (1986), Roper *et al.* (1995), Hernandez-Herrera *et al.* (1998), Wormuth (1998), Nigmatullin *et al.* (2001), Nigmatullin *et al.* (2002a), Markaida (2006a,b), Rodhouse *et al.* (2006), Waluda *et al.* (2006), Gilly *et al.* (2006a,b), Field *et al.* (2007b).

Euclidean Berry, 1916

Euclidean Berry, 1916, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68: 45–66. 4 plates. [60].

Type Species: *Euclidean luminosa* (Sasaki, 1915).

Diagnostic Features: The funnel groove has **foveola with 4 to 9 longitudinal folds and 1 to 3 side pockets**, often obscure. **External photophores include** small, scattered, subcutaneous photophores on mantle, head, arms and tentacles and **large cutaneous mantle photophores that consist of a pair of long yellowish strips** that extend **along the ventral surface of the mantle**, one on each side of the midline; each strip interrupted posteriorly by a gap at the level of maximum fin width; **2 oval bioluminescent patches near anterior margin of mantle** anterior to each strip; 2 patch-like photophores at base and in middle on ventral surface of each ventral arm. **A single, round photophore on ventral surface of each eye and 1 round photophore on intestine.** Dactylus of tentacular club with 4 series of small suckers; carpal-locking apparatus on tentacular stalk with 1 to 4 knobs and 1 to 3 smooth-ringed suckers. Two to 4 suckers with denticulate rings are located on carpus proximal to first knob. Largest medial suckers on manus of club with 1 large, pointed tooth at distal margin of ring. Tips of all arms not attenuate. Arms have 19 to 32 pairs of suckers. **Left ventral arm hectocotylized by smooth type (suckers absent).** Fins heart-shaped with attenuate tail; fin length 41 to 50% and width 50 to 65% of mantle length; fin angle 35° to 50°. **Mantle-funnel locking cartilage fused after paralarval stage.** The cone flags of the gladius are short, rhomboidal, with distinct radial creases. The greatest width of the cone flags is about 56% of that of the rachis. Marginal rigid ribs of the rachis are simple; axial rigidity rib of the rachis is trapezoid-like in cross-section. Lateral plates of the gladius do not adhere to the dorsal surface of the rachis but form wide free folds over the rachis. The stem is short, reminiscent of a mammalian vertebra in cross-section. Width of the stem is approximately equal to its thickness. Cone is short, flattened laterally. Rostrum is drop-shaped, its apex is curved ventrally. Alveola is thin; its ventral and lateral walls are thin, smooth, while the dorsal wall is ribbed. Spermatozoa with 1 flagellum.

Geographical Distribution: High tropical and subtropical areas in the southern sectors of the Atlantic, Indian and Pacific oceans and northern sector of the Pacific Ocean.

Remarks: Monotypic genus that contains 1 oceanic species. Restriction profiles of 2 endonucleases, AluI and Tsp509I are diagnostic for species identification.

Eucleoteuthis luminosa (Sasaki, 1915)**Fig. 295**

Symplectoteuthis luminosa Sasaki, 1915b, *Journal of College of Agriculture, Tohoku Imperial University, Sapporo*, 6(6): 131–150. [144, fig. 4, pl. 4, figs 7–13]. [Type locality: Sagami Bay, Japan, western Pacific Ocean].

Frequent Synonyms: *Symplectoteuthis luminosa* Sasaki, 1915b.

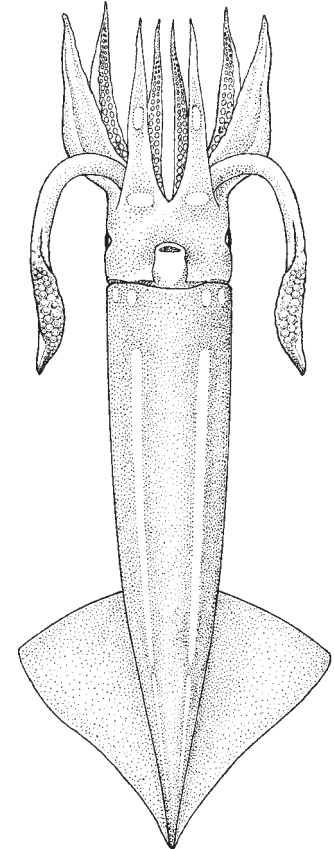
FAO Names: **En** – Luminous flying squid; **Fr** – Encornet lumineux; **Sp** – Pota luminosa.

Diagnostic Features: The same as those given for the genus.

Size: Maximum mantle length 227 mm and body weight about 235 g.

Geographical Distribution: True bi-peripheral oceanic species with ranges in the North Pacific Ocean and the Southern Hemisphere. Distributed in the North Pacific Ocean from the southern Kurile Islands and Japan (from 25°N to 45°N) to California and western Mexico (from 10°N to 40°N); in the southern South Pacific Ocean between 20°S and 35°S in the west and between 13°S and 43°S in the east; in the southern Indian Ocean between 15°S and 34°S and in the southern Atlantic Ocean between 10°S and 36°S. Absent in the North Atlantic Ocean (Fig. 296).

Habitat and Biology: *Eucleoteuthis luminosa* is the least studied species among ommastrephids. It is an epipelagic and upper mesopelagic species distributed from the surface to 400 m. It inhabits open waters mostly over great depths of more than 200 m, and it is neither associated with the bottom nor slope habitats. Subadult and adult squids can be observed at the surface at night, but only infrequently. During the day they inhabit the depths greater than 50 to 100 m. The abundance is low or moderate locally (especially in the South Pacific Ocean between 30°S and 40°S). The maximum mantle length in males is 207 mm and in females 227 mm. Males reach maturity at 95 to 185 mm mantle length (age 180 to 270 days), and females mature at 102 to 200 mm mantle length (age 220 to 240 days). Geographical variability of size at maturity and size morphology is pronounced. Maximum size and size at maturity increases from the low latitudes to the high latitudes. Life span is a maximum of 1 year. In the lower latitudes spawning occurs throughout most of the year, and in the higher latitudes spawning occurs in the spring and summer seasons. Spermatophore lengths are 11.2 to 15.8 mm, and their numbers in Needham's sac of mature males reach up to 150, mostly between 70 and 100. Egg size is 0.8 to 1.0 mm, and potential fecundity of mature females varies between 300 000 and 625 000 ova. The oviducts of mature females contain about 17 000 ripe eggs, probably more.



ventral view

Fig. 295 *Eucleoteuthis luminosa*

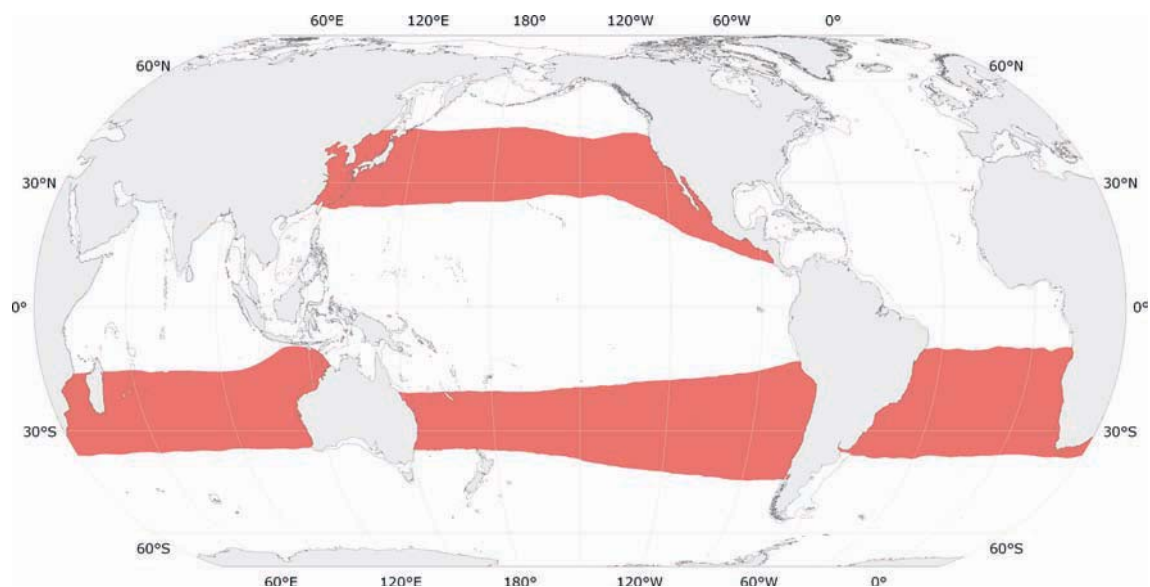


Fig. 296 *Eucleoteuthis luminosa*

■ Known distribution

This species is an intermittent, multibatch spawner. Paralarvae can be distinguished from other confamilial paralarvae by their specific chromatophore pattern on the surface of the mantle and head.

Prey organisms for *Eucleoteuthis luminosa* include many species of pelagic crustaceans, heteropod molluscs and larvae and juveniles of teleost fishes and squids. The known predators include lancetfish (*Alepisurus ferox*), shark (*Sphyrna zygaena*), different species of tunas, the trichichthyid fish, orange roughy (*Haplostethus atlanticus*), sea birds and northern fur seal. Off eastern Australia *E. luminosa* is preyed upon by yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*) in the warmer surface waters associated with the East Australia Current. Most subadult and adult squids are infested with helminth parasites: larvae of nematodes and cestodes and metacercariae of trematodes of the family Didymozoidae. All forms of parasites mainly are localized on the inner wall of the stomach.

Interest to Fisheries: The species is not fished commercially due to its low abundance and widespread population structure. However, in Japanese waters from time to time it may be captured as bycatch during the jigging fishery for *Todarodes pacificus*.

Local Names: AUSTRALIA: Striped squid; JAPAN: Suji-ika; RUSSIA: Kal'mar-ljuminosa, Polosatj kal'mar; TAIWAN PROVINCE OF CHINA: Guang-tiáo -yóu; USA: Luminous flying squid.

Literature: Young (1972a), Zuev *et al.* (1975), Alexeyev (1994a), Roper *et al.* (1995), Mori *et al.* (2002), Okutani (2005).

Hyaloteuthis Gray, 1849

Hyaloteuthis Gray, 1849: *Catalogue of the Molluska in the British Museum*. I. Cephalopoda Artepedia, pp. 164 London [63].

Type Species: *Hyaloteuthis pelagica* (Bosc, 1802).

Diagnostic Features: The funnel groove has a **foveola with 7 to 9 longitudinal folds and 0 to 3 side pockets**, often obscure. **Large cutaneous photophores present** on the ventral surface of the mantle and arms in the form of round, yellow, reflective patches: **3 situated along each ventral arm and 19 arranged in a fixed pattern on the ventral surface of the mantle**, where they form pairs, either closely set or well-separated. **A single, round photophore on ventral surface of each eye and 1 round photophore on the intestine**. Dactylus of tentacular club with 4 series of small suckers. Carpal-locking apparatus on tentacular stalk with 1 knob and 1 smooth-ringed sucker. Largest medial suckers on manus of club with 1 large, pointed tooth at distal margin. Protective membrane of tentacular club very poorly developed. Tips of all arms not attenuate. Arms have 15 to 22 pairs of suckers. **Right, or rarely left, ventral arm has a hectocotylus of the smooth type**, with the absence of suckers on the modified portion. Fins rhomboidal with straight or very slightly convex posterior edges. Fin length 35 to 40% and fin width 55 to 62% of mantle length; fin angle 45° to 55°. Mantle-funnel locking cartilage not fused. The cone flags of the gladius are short, rhomboidal, with minute radial creases. The greatest width of the cone flags comprises 57 to 87% of that of the rachis. Marginal rigid ribs of the rachis are simple, and the axial rigid rib of the rachis is low, rounded in cross-section. Lateral plates of the gladius adhere to the dorsal surface of the rachis. The stem is roughly triangular in cross-section; width of the stem is slightly greater than its thickness. The cone is short, rounded in cross-section. Rostrum is absent. Alveola is very thin and smooth. Spermatozoa with 1 flagellum.

Geographical Distribution: Tropical waters in the Atlantic and Pacific Oceans.

Remarks: *Hyaloteuthis* is monotypic, comprised of 1 oceanic species. The restriction profiles of 2 endonucleases, AluI and Tsp509I, are diagnostic for species identification.

Hyaloteuthis pelagica* (Bosc, 1802)*Fig. 297**

Sepia pelagica Bosc, 1802, *Histoire Naturelle Coquilles*, I: pp. 324. [46, pl. 1, figs 1–2]. [Type locality: “Trouvee en pleine mer, par Bosc dans l'estomac d'une dorade”].

Frequent Synonyms: *Sepia pelagica* Bosc, 1802; *Ommastrephes pelagicus* d'Orbigny, 1834–1848; *Ommatostrephes pelagicus* Steenstrup, 1880.

FAO Names: En – Glassy flying squid; Fr – Encornet vitreux; Sp – Pota estrellada.

Diagnostic Features: The same as those given for the genus.

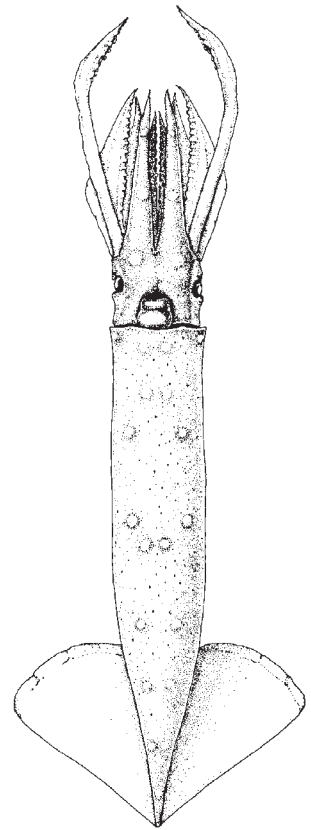
Size: Maximum mantle length 105 mm and body weight 35 g.

Geographical Distribution: A truly bicentral oceanic species; in the north Atlantic Ocean from 10°N to 28° N in the eastern part and to 40°N in the western part; in the South Atlantic Ocean from 5°S to 15°S in the eastern part and to 23°S in the western sector; in the North Pacific Ocean from 10°N to 35°N off Japan and to 25°N off California; its range in the South Pacific Ocean includes oceanic waters from 0°S to 36°S off Australia and to 20°S off southern Chile; mostly absent from the equatorial zones of both oceans. It was not found to occur in the open waters of the Indian Ocean (Fig. 298).

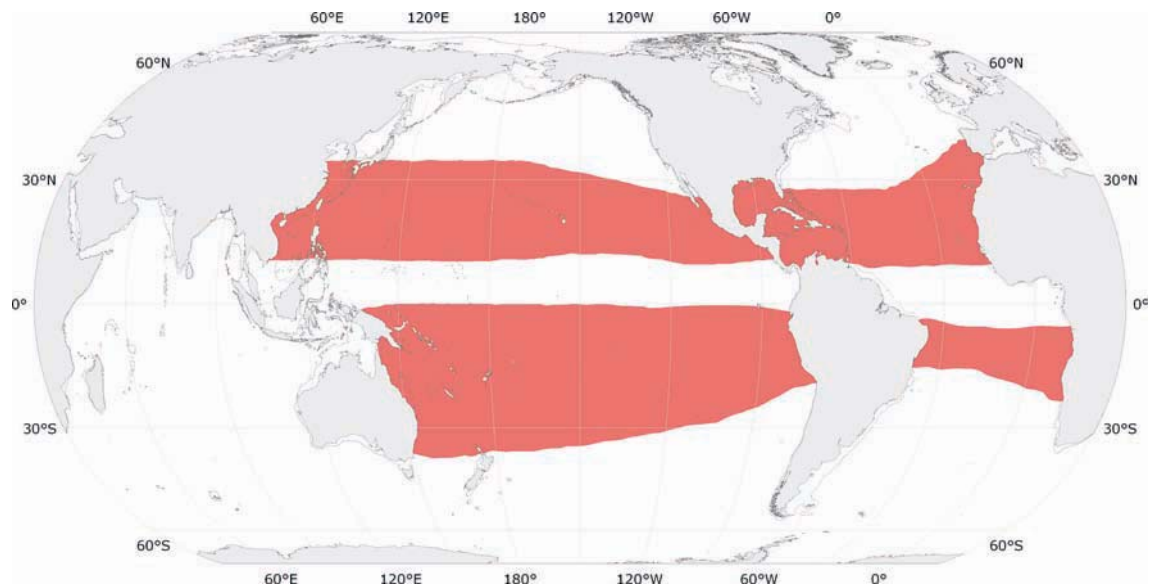
Habitat and Biology: *Hyaloteuthis pelagica* is distributed mainly in zones of trade-wind currents and adjoining parts of the central waters of the cyclonic circulations; it is absent from zones of equatorial divergence. This epipelagic to mesopelagic and upper bathypelagic species inhabits open waters over great depths of more than 400 m, and it is not related in any biological or oceanographic way to bottom and slope waters. Paralarvae and juveniles inhabit the upper 50 m at night and from 100 to 200 m during the day. Subadult and adult squids inhabit subsurface layers from 15 or 20 m to 150 m at night. They also have been observed at night at the surface but only infrequently. During daytime they inhabit the depths from 200 to 800 m. The population numbers are low or moderate locally. The maximum male mantle length is 81 mm and the maximum female mantle length is 105 mm. Males reach maturity at 50 to 65 mm mantle length (age 80 to 100 days), and females mature at from 50 to 90 mm (age 80 to 135 days). No pronounced geographical variability exists for size at maturity or size morphology. The life span is half a year. Spawning occurs throughout the year with some seasonal variability in activity. Spermatophores attain lengths of 5 to 11.5 mm, and their numbers in Needham's sac of mature males reach a maximum of 120, but normally they vary between 50 and 80 total. Egg size is 0.9 to 1.0 mm, and female potential fecundity varies between 30 000 and 100 000 ova. Oviducts of mature females contain a



tentacular club



ventral view

Fig. 297 *Hyaloteuthis pelagica***Fig. 298** *Hyaloteuthis pelagica*

■ Known distribution

maximum of 500 ripe eggs. The species is an intermittent, multibatch spawner. It feeds mainly on juvenile teleosts and squid, hypereid amphipods, crab larvae, chaetognaths and to a lesser degree on copepods, shrimps, euphausiids and teleost larvae. Its predators include several oceanic species of ommastrephid squids, dolphinfish (*Coryphaena*), lancet fish (*Alepisurus*), bonito (*Sarda*), different species of tunas and sea birds. *Hyaloteuthis pelagica* is preyed upon by yellowfin tuna (*Thunnus albacares*) off eastern Australia and it is an important prey of several fishes in the tropical Atlantic Ocean, such as albacore (*Thunnus alalunga*), yellow fin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), sailfish (*Istiophorus albicans*), blue marlin (*Makira nigricans*), white marlin (*Tetrapturus albidus*) and longbill spearfish (*Tetrapturus pfluegeri*). Most subadult and adult squids are infested by helminth parasites, principally metacercariae of trematodes of the family Didymozoidae, that are localized in cysts on the inner wall of the stomach.

Interest to Fisheries: The species is not fished commercially due to its small size and low, local area abundance.

Local Names: JAPAN: Shirahoshi-ika; RUSSIA: Kal'mar-gjalotevtis, Kal'mar-svetljach'ek.

Literature: Wormuth (1976), Nesis and Nigmatullin (1979), Young and Hirota (1990), Roper *et al.* (1995), Vecchione *et al.* (1998a), Okutani (2005).

Ornithoteuthis Okada, 1927

Ornithoteuthis Okada, 1927c, *Bulletin de l'Institut Oceanographique de Monaco*, 494: 13–16. [15].

Type Species: *Ornithoteus volatilis* (Sasaki, 1915b).

Frequent Synonyms: *Ommastrephes* Sasaki, 1915b.

Diagnostic Features: Mantle narrow, drawn out posteriorly into long, pointed tail; fins long, narrow, strongly pointed posteriorly, their length 50 to 60% and width about 45 to 52% of mantle length; fin angle 20° to 35°; funnel groove smooth with foveola with 7 to 9 longitudinal folds and a few side pockets (often obscure); small tetraserial suckers on dactylus of tentacular club; tentacular club moderately expanded but without carpal-locking apparatus; carpal sucker area reduced, tubercle-like knobs absent; largest medial suckers on manus with 15 to 25 equal-sized pointed teeth; no enlarged teeth; no external photophores, nor subcutaneous photophores exist; a single, round photophore evident on ventral surface of each eye and 2 round photophores on ventral surface of intestine in paralarvae and a narrow, pinkish photogenic strip, with 2 interruptions, extends along the ventral midline of viscera in adults; right (or very rarely left) arm IV hectocotylized in mature males with papillose type (distal modified section bears papillae formed from sucker stalks) and with a honey-comb sculptural formation along the midpart of ventral surface of arm. Protective membranes of arms and tentacles normally developed. Cone flags of the gladius very long (about 25% of the gladius length), without radial creases; greatest width of the cone flags about two-thirds that of the rachis. Marginal rigidity ribs of rachis simple; axial rigidity rib rounded-rectangular in cross-section. Lateral plates of gladius adhere to dorsal surface of rachis by their proximal parts. Distal parts of lateral plates free, form longitudinal fold over hanging rachis. Ventral stem very long, with high dorsal keel, anchor-like in cross-section; stem width less than its thickness. Cone very short, round in cross-section; rostrum absent. Alveola thin, film-like, smooth. Spermatozoa with 1 flagellum.

Size: Small- to medium-sized squid; maximum reported mantle length 310 mm.

Geographical Distribution: Indo-West Pacific and tropical-subtropical Atlantic Ocean.

Habitat and Biology: Epi-mesopelagic, lower sublittoral and bathyal squids. Adults occur in the lower epipelagic and mesopelagic zones and to the bottom in the bathyal realm. Paralarvae and juveniles occur in midwater and into the near-surface epipelagic waters.

Remarks: The 2 nerito-oceanic species in the genus are quite similar in appearance and habitat in their respective oceans, the Indo-West Pacific (*Ornithoteuthis volatilis*) and the tropical-subtropical Atlantic (*O. antillarum*). Historically the distributional ranges of these 2 now-distinct species probably were continuous, but biogeographic divergence resulted in the formation of the separate, closely-related species recognized currently. The 5 syntype specimens from Sagami Bay and off Atami are extant in the Museum of Tokyo University, Zoology Department.

Literature: Nesis (1979a,c), Nesis and Nigmatullin (1979), Hochberg (1983), Bizikov (1996), Dunning (1998b,c), Nesis (2003), Nigmatullin *et al.* (2003).

Key to the species of *Ornithoteuthis*

- 1a.** Sessile arm sucker ring dentition without sexual dimorphism on arms II; hectocotyzed right arm IV with honeycomb-like cutaneous sculpturing on the midventral surface comprised of 2 or 3 longitudinal rows of small depressions, with 10 to 15 depressions (pits or pores) in each row
 ***Ornithoteuthis volatilis***
- 1b.** Sessile arm sucker ring dentition with sexual dimorphism on arms II; rings on dorsal row with 2 small plate-like lateral teeth and 1 distal, central, sharply pointed, enlarged tooth; rings on ventral row with 2 small, medial plate-like distal teeth and 2 small plate-like lateral teeth; hectocotyzed right arm IV with honeycomb-like cutaneous sculpturing on the midventral surface comprised of 4 or 5 longitudinal rows of depressions, with 20 to 25 depressions (pits or pores) in each row
 ***Ornithoteuthis antillarum***

Ornithoteuthis volatilis* (Sasaki, 1915)*Fig. 299**

Ommastrephes volatilis Sasaki, 1915b, *Journal of the College of Agriculture, Tohoku Imperial University, Sapporo*, 6(6): 131–150. [138, text fig. 3, pl. 4, figs 1–6]. [Type locality: off Atami, Sagami Province, Japan, western Pacific Ocean].

Frequent Synonyms: *Ommastrephes volatilis* Sasaki, 1915.

Misidentifications: *Ornithoteuthis volatilis*, Silva-Mello, 1998 (see Remarks).

FAO Names: **En** – Shiny bird squid;
Fr – Encornet planeur; **Sp** – Pota plane adora.

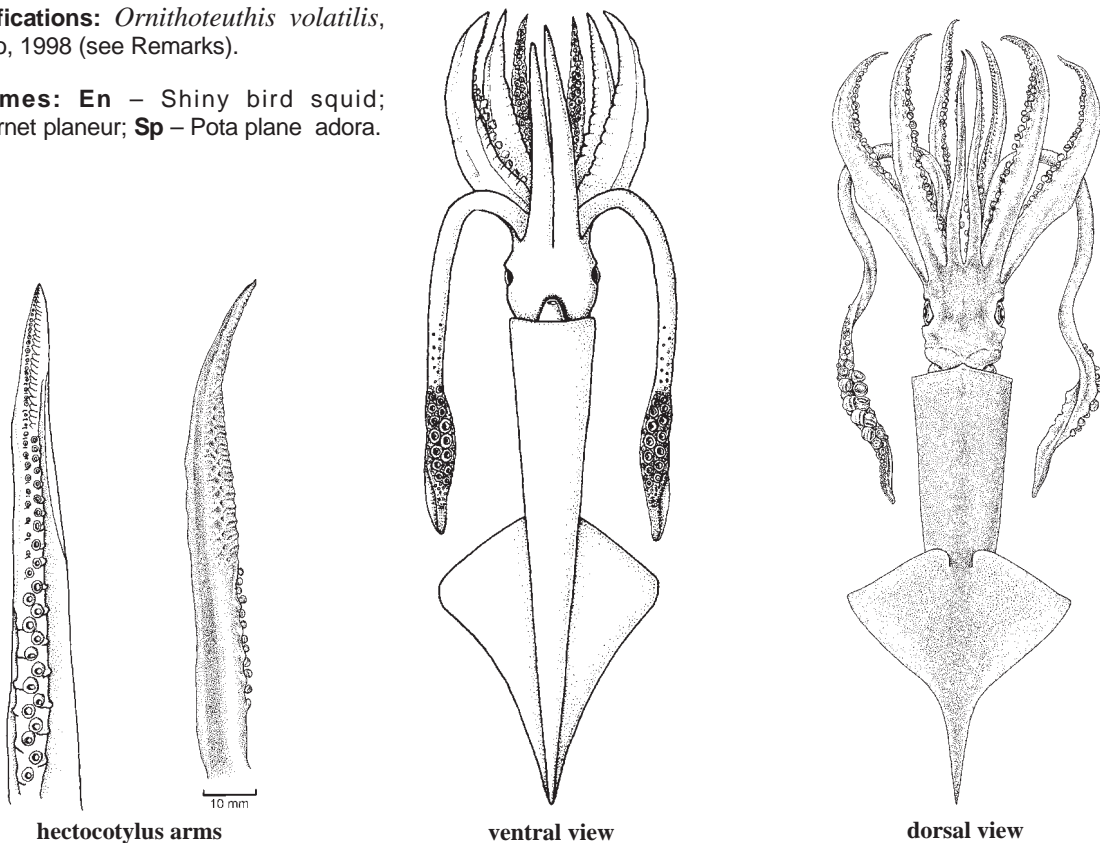


Fig. 299 *Ornithoteuthis volatilis*

Diagnostic Features: Mantle very narrow, muscular, drawn out posteriorly into a long pointed tail. Fins long, sagittate, sharply lanceolate posteriorly, posterior margins concave; fin length 55% (51 to 59%) of mantle length; fin width 47% (45 to 51%) of mantle length; single fin angle 27% (20 to 35%). Head broad, considerably broader than mantle width. Tentacular club expanded with very large medial manal suckers, their rings with 18 to 21 evenly-spaced, equal-sized (not enlarged), sharply-pointed teeth, occasionally interspersed with low, flat platelets. Arm sucker rings with 10 to 14 sharp teeth on distal margin and with smooth proximal rim; rings without sexual dimorphism. Right arm IV hectocotyzed with papillose type modification; distal half with reduced-sized suckers, sucker stalks modified into papillae, particularly in dorsal row, and a honeycomb sculpturing with lateral pores along the midventral surface with 2 or 3 longitudinal columns of depressions and swollen ridges, and with 10 to 15 depressions (pits or pores) in each column. A single, round photophore patch occurs on the ventral surface of each eye; on viscera one large, round photophore occurs near the anus and one small oval photophore occurs at the posterior end of the intestine; a narrow strip of pinkish bioluminescent tissue extends from the small photophore to the posterior tip of the mantle cavity, interrupted by 2 gaps where arteries intervene. These round photophores persist from the paralarval stage to fully mature adults.

Paralarvae with 2 round, unequal-sized intestinal photophores that are evident at about 3.5 mm mantle length; the larger, anterior one ventral to the intestine near the anus; the smaller, posterior one ventral to the intestine just anterior to its descent from the ceacum; a single, ovoid photophore patch on the ventral surface of each eye at about 4.0 mm mantle length; a proboscis typical of the ommastrephid rhynchoteuthion-stage with a length of 50 to 75% of the mantle length at less than 4.0 mm mantle length; proboscis length approximately equal to longest arms; the 2 lateral distal suckers on tip of proboscis up to 150% larger than remaining 6 suckers; dorsal mantle chromatophore pattern of 5 oblong chromatophores in a +-shape and a single small chromatophore between the minute fins; ventral mantle chromatophore pattern form a side-to-side oblong of 6 rectangular chromatophores and 2 very small, roundish chromatophores at the posterior tip of the mantle.

Size: The maximum mantle length reported is 250 mm in females and 310 mm in males.

Geographical Distribution: Indo-West Pacific, tropical to subtropical oceans. In the western Pacific from 36°15'N to 40°S; off southwestern Japan, the Ogasawara Islands, off Sanriku and Joban districts, northeastern Japan, and in the South China Sea; New Caledonia; eastward to the Line Islands, to 140°W, where its latitudinal range is quite restricted, roughly 5°N to 15°S. In the Indian Ocean *O. volatilis* occurs from the Arabian Sea to south of Madagascar in the west to about 30°S, and eastward into the Timor Sea; Coral Sea. Off the eastern Australian coast its distribution extends to 40°S, off the northwestern Australian coast it occurs in continental slope waters between 13°50'S and 18°37'S. The species apparently does not occur in the central and eastern North Pacific and it is absent from Hawaiian waters. *Ornithoteuthis volatilis* has been reported in the far southeastern Atlantic off South Africa and Namibia, but whether a permanent, self-perpetuating population exists in the Benguela Current presently is not verified (Fig. 300).

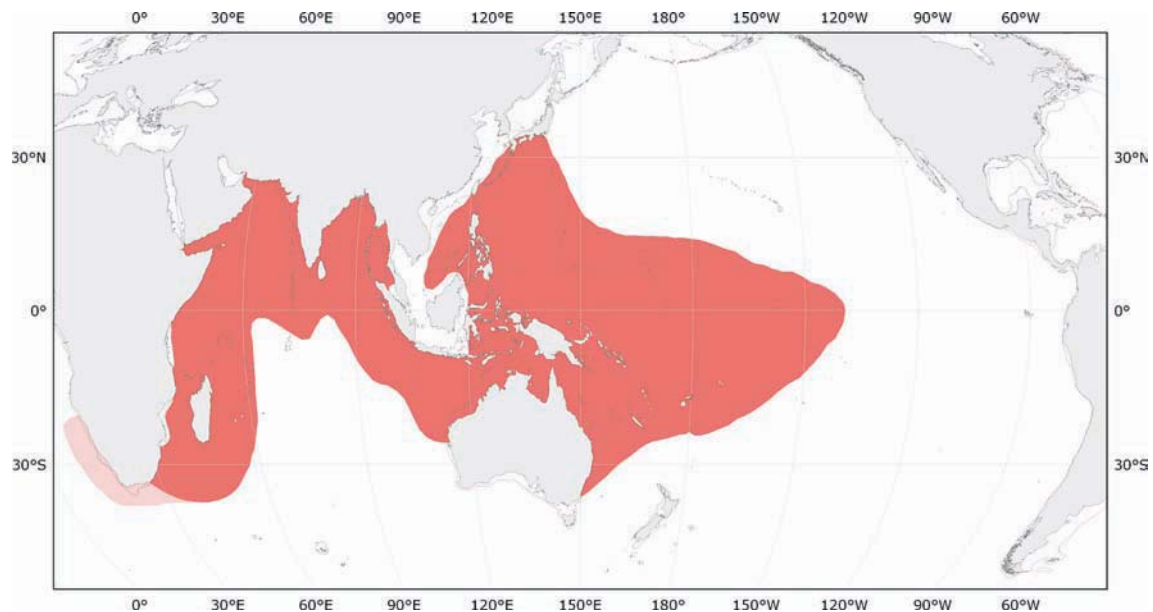


Fig. 300 *Ornithoteuthis volatilis*

■ Known distribution ■ Probable presence

Habitat and Biology: *Ornithoteuthis volatilis* is a tropical/subtropical species, widely distributed in the Indo-Pacific Ocean. It occupies tropical slope and oceanic waters from the surface (paralarvae; adults at night) to moderate depths, at the bottom in bathyal zone and in midwater above the slope (lower epipelagic, mesopelagic). Paralarvae and juveniles also occur in the equatorial zone in midwater above great oceanic depths. Specimens of 180 to 200 mm mantle length have been captured in trawls fished at 500 to 770 m in the South China Sea. The abundance (density index) on the continental slope of the South China Sea is highest at 400 to 600 m. In the western Indian Ocean the species is recorded off Kenya (1°S to 6°S, 46°E to 52°E) and around Saya-de-Malha Bank (8°30'S to 11°S, and 56°E to 60°E). *Ornithoteuthis volatilis* is commonly captured in trawl catches in Australian slope waters. While identification of adults is relatively easy because of the slender body and long, attenuate fins, traditionally the identification of ommastrephid paralarvae has been challenging in areas where multiple species co-occur. Recent studies, however, have demonstrated positive identification techniques using chromatophore patterns. The colour of the mantle of live adults is dark reddish brown, with a bright strip along the ventral midline produced from the intestinal photophores. Adults are captured principally in midwater and demersal trawls in continental slope waters and near seamounts but rarely are caught at the surface. On the other hand, several specimens have been inadvertently captured when they broke the sea surface and "flew" aboard vessels. It has been suggested that *O. volatilis* undergoes diel vertical migrations, just as its congener, *O. antillarum*, does in the North Atlantic.

In the South China Sea *O. volatilis* is most abundant in May and June and during the day than at night. Size at maturity varies significantly in both sexes, depending on season and locality. For example, mature females have been observed at 150 mm mantle length, while other females up to 270 mm mantle length were still maturing in winter. Also, mature males were caught in southeastern Australia in summer, at 160 to 240 mm mantle length, while other males were still immature at 180 to 200 mm mantle length.

The reproductive strategy of *O. volatilis* adheres to the "*Sthenoteuthis*-type" for r-strategists. They have very small eggs (0.7 to 1.0 mm, mostly 0.75 to 0.85 mm), and the total of vitelline oocytes in the ovary plus ripe eggs in the oviducts usually represents 10 to 15% of the potential fecundity. Females have an asynchronous type of oocyte stock (fecundity) formation by which oogenesis occurs by continuous asynchrony. Spawning is intermittent (batch, pulse) with several egg masses produced over a more or less extended period of time. The intensity of spawning and average egg numbers in these sequential egg masses is approximately constant during the spawning period. Spermatophores from a mature male of 93 mm mantle length from the western Indian Ocean averaged 9.6 mm long, about 10.3% of mantle length; the number of spermatophores (fecundity) was about 100 with a total sperm reservoir volume of 0.1 cm³. The reproductive strategy of males belongs to the "intermediate type" for effective sperm production in which there is an ontogenetic increase in the volumes of both the Needham's Sac and the seminal reservoirs of the spermatophores.

As a neritic-oceanic species, *O. volatilis* lives near or over slopes; paralarvae, juveniles and subadults live in midwater in the epi- and mesopelagic zones over the slopes and oceanic depths, as well as above the tops and slopes of seamounts and midocean ridges; they spawn near the bottom around seamounts and ridges, some after long migrations to these localities. Spawning of *O. volatilis* off southeastern Australia occurs in the deeper shelf and upper continental slope waters that comprise the warm East Australian Current of tropical origin. Size distribution analysis of paralarvae and adults suggests that spawning in this region occurs year-round. In the northern South China Sea the spawning season is from June to October. In the western North Pacific Ocean *O. volatilis* spawns in the summer and its paralarvae are distributed in the Kuroshio Current off Japan. Division of proboscis begins at about 4.0 to 5.0 mm mantle length and separation of tentacles is complete by about 6.5 to 7.0 mm mantle length. The hunting strategy of *O. volatilis* is the actively browsing predator type in which prey consists of many different food component species, each of relatively small individual size and weight. Predators of *O. volatilis* include yellowfin tunas (*Thunnus albacares*), longnose lancetfishes (*Alepisaurus ferox*), dolphinfishes (*Coryphaena hippurus*), swordfish (*Xiphias gladius*) and numerous other species of pelagic fishes throughout the tropical Indo-Pacific and eastern Pacific Oceans; also, sperm whales prey extensively on this species, as do the South African fur seals (*Arctocephalus pusillus pusillus*) and several shark species, such as the tiger shark (*Galeocerdo cuvier*), the scalloped hammerhead shark (*Sphyrna lewini*) and the smooth hammerhead shark (*Sphyrna zygaena*). *Ornithoteuthis* species are host to the diagenetic trematode parasites.

Interest to Fisheries: While *O. volatilis* is a widely distributed species in tropical/ subtropical Indo-West Pacific waters, to date adults have not been captured in large numbers. The mean instantaneous biomass for harvest-sized *O. volatilis* is estimated to be 1 million tonnes. However, if concentrations of this species can be found, they will provide a potentially desirable product because both the size and texture of the flesh are suitable. In the northern South China Sea, a study indicated that the stock was over 550 tonnes in the survey area. The same study also determined that the nutrient composition of the flesh will make a fishery worth developing.

Local Names: AUSTRALIA: Long-tailed flying squid; JAPAN: Tobi-ika, yase-tobi-ika; RUSSIA: Letajuschij kal'marptica.

Remarks: The reference to *O. volatilis* by Silva-Mello (1998) from pelagic fish stomach contents is considered a misidentification. *Ornithoteuthis volatilis* never has been reported in the western Atlantic Ocean, and the very few records in the far southeastern Atlantic Ocean are considered incidental occurrences, not established populations. *Ornithoteuthis antillarum* is the only Atlantic species in the genus and it is common in the tropical/subtropical western Atlantic, as identified in Silva-Mello's report. Consequently, Silva-Mello's reference to *O. volatilis* is a misidentification.

Literature: Nesis (1993a), Dunning (1998b,c), Nesis (2002), Okutani (2005).

***Ornithoteuthis antillarum* Adam, 1957**

Fig. 301; Plate IX, 55–57

Ornithoteuthis antillarum Adam, 1957, *Bulletin de Institut Royal Science Naturelle Belgique*, 33(7): 1–10. [3, pl. 1 figs 1–4]. [Type locality: Basse Terre (Guadeloupe), Antilles, West Indies, western central Atlantic Ocean].

Frequent Synonyms: None.

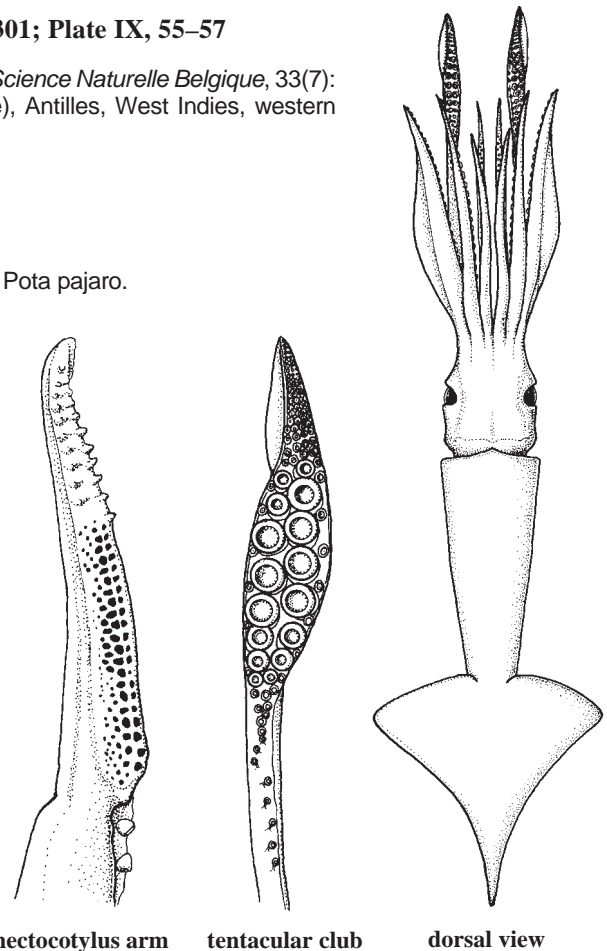
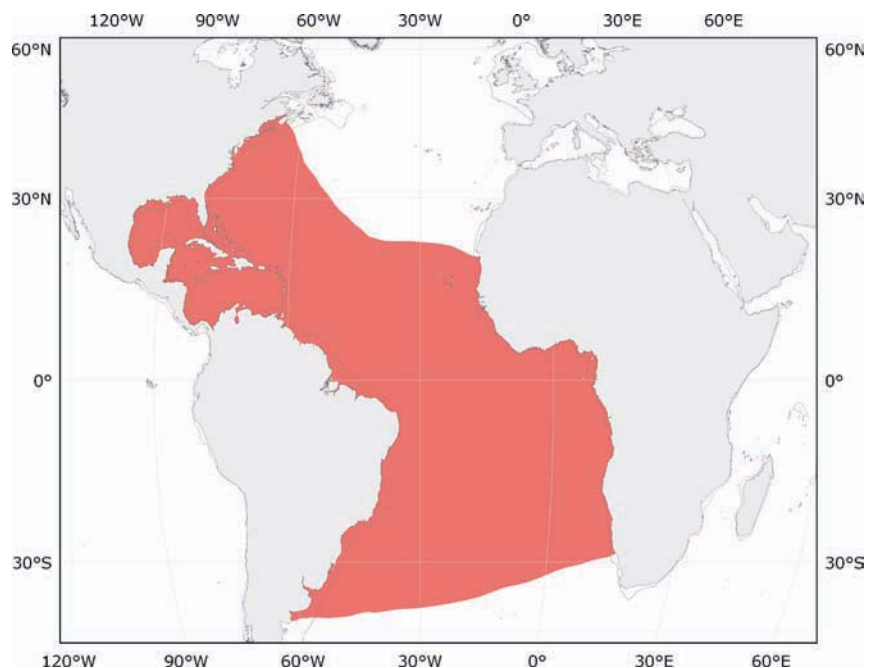
Misidentifications: *Ornithoteuthis volatilis*, Silva-Mello, 1998.

FAO Names: En – Atlantic bird squid; Fr – Encornet oiseau; Sp – Pota pajaro.

Diagnostic Features: Mantle muscular, very narrow, drawn out posteriorly into a long, thinly-pointed tail. Fins elongate, sagittate to lanceolate, very sharply pointed posteriorly; posterior margins concave; anterior margins convex; fin length greater than 50% of mantle length. Head broad, equal to or greater than maximum mantle width. Funnel groove with foveola with 7 to 12 indistinct folds, side pockets frequently obscure or absent. Tentacular club moderately expanded with 12 to 14 enlarged medial club suckers; sucker rings with about 20 nearly equal-sized, sharp teeth, occasionally interposed with low, flat platelets; no enlarged teeth. Carpal-locking apparatus weakly developed with few suckers and without knobs. Arm sucker rings with 15 sharply-pointed teeth; sexual dimorphism on rings of arms II: rings on dorsal row have 2 small plate-like lateral teeth and 1 distal, central, sharply-pointed enlarged tooth; rings on the ventral sucker row have 2 small, medial, pointed distal teeth and 2 small plate-like lateral teeth on each side. **Right arm IV hectocotylized** with reduced distal suckers and honeycomb-like cutaneous sculpturing on the midventral surface comprised of 4 or 5 longitudinal columns of depressions with 20 to 25 pits or pores in each column. **A single elongate photophore patch** occurs on the ventral surface of each eye. In the mantle cavity 1 relatively large round photophore lies near the anus and 1 smaller oval photophore lies on the posterior end of the intestine. **A narrow strip of pinkish bioluminescent tissue** extends along the ventral midline from the posterior oval photophore to the posterior tip of the mantle cavity. The morphology of the gladius at various growth stages also may be diagnostic. Proboscis length in paralarvae is 25 to 50% of mantle length, thick and longer than the arms at less than 4 mm mantle length. Then they become equal to or shorter than the arms for a period of time. The 2 lateral (distal) suckers on the tip of the proboscis are 2 times larger than the remaining 6 suckers. A single, oblong photophore occurs on the ventral surface of each eye, developed at 4.0 to 4.5 mm mantle length, and 2 unequal-sized, round photophores are on the ventral surface of the intestine: the anterior one larger, near the anus, yellowish, developed at 3.0 to 3.5 mm mantle length; the posterior one, smaller, later-developing, whitish, developed at 8 mm mantle length. A visceral luminous strip develops on juveniles larger than 30 mm mantle length. Mantle covered with densely crowded, large brown chromatophores.

Size: The maximum mantle length recorded is 300 mm on a specimen from the northern end of the species' distributional range.

Geographical Distribution: An amphi-Atlantic tropical/subtropical species that has been recorded in the eastern Atlantic Ocean from 20°N to 28°S and in the western Atlantic Ocean from 45°N to 40°S (Fig. 302).

Fig. 301 *Ornithoteuthis antillarum*Fig. 302 *Ornithoteuthis antillarum*

Known distribution

Habitat and Biology: This species is a nerito-oceanic form that occurs throughout the water column over slope and oceanic depths. In the western North Atlantic it is common in slope waters off New England and southeastern Canada. Paralarvae and adults are relatively abundant in the Gulf of Mexico, the Straits of Florida and the Gulf Stream, as well as southward into the Caribbean and further southward into slope waters off Brazil. While it appears not to be a schooling species, experimental trawling in the western Atlantic Ocean off northern New England, as well as numerous observations from submersibles, indicate that it is common in midwater to just above the bottom. It has never been observed sitting on the bottom. It has been reported at the surface at night in the Caribbean, and many specimens were captured at night over deep bottom depths in large midwater Engel trawls in the eastern South Atlantic at 100 to 600 m. In the eastern Gulf of Mexico (27°N 86°W) extensive opening-closing net (Tucker trawl) samples determined the diurnal vertical distribution of micronektonic *O. antillarum* to be only 200 to 400 m during the day, with a few specimens at 100 to 200 m. The population occurred at 0 to 100 m exclusively at night, while some were at 100 to 200 m. The significant preponderance of captures from daytime bottom trawls versus night trawls and the occurrence in midwater and at the surface at night suggests that *O. antillarum* is a modified diel migrator that lives above the bottom during the day and disperses into mid-depths at night. Daytime depths of capture on the slope range from 450 to 1 100 m.

This species is a fast swimmer, so frequently is able to avoid capture by nets. Observations and video imagery from submersibles are recorded from off Key West, Florida, the Lesser Antilles, the Louisiana/Texas slope, the Northwest Providence Channel, Bahamas, and off New England where it was captured at depths of 100 to 893 m, water temperatures of 7.4 to 15°C, and with mantle lengths of 90 to 153 mm. On dives in the Bahamas in 2 consecutive years during autumn, *O. antillarum* was the most commonly observed squid. A typical position in the water column observed for this species at rest is the "J" posture, in which the animal hangs roughly head-down with the arms and tentacles curled and slightly splayed dorsally back over the head and anterodorsal mantle. This behaviour has been observed in several ommastrephid species.

Maximum mantle length of mature adults varies over the range of the species. In tropical waters some specimens of both sexes mature at 80 to 90 mm mantle length, while further north and south some specimens are still immature at greater than 100 mm mantle length.

Statolith analysis of a population of small-sized, early-maturing squids from the tropical central-east Atlantic Ocean indicates the species is fast-growing and does not exceed 182 days old. Growth rates for juvenile and immature individuals are high but decrease significantly with onset of maturity. It is thought that spawning migrations occur as populations mature and move into waters associated with sea mounts. Paralarvae, juveniles and subadults occupy midwater in epipelagic to mesopelagic zones over slopes, tops and oceanic depths, then with onset of maturity migrate to seamounts and ridges to spawn on or near the bottom, for example on the equatorial Atlantic seamounts along the mid-Atlantic Ridge.

Maturation of males follows the intermediate strategy of simultaneous ontogenetic increase in the volumes of both Needham's sac and the seminal reservoirs of spermatophores. Spermatophore length averages 9.0 mm, or about 6% of mantle length and the fecundity is quite low for a nerito-oceanic ommastrephid, about 100. The mean volume of seminal reservoirs is 0.15 mm³, while the volume of the total sperm reservoirs is 0.1 cm³. Reproduction-type in *O. antillarum* is the r-strategy, characterized by very small eggs (0.7 to 1.0 mm, mainly 0.75 to 0.85 mm). The total of vitellin oocytes in the ovary and ripe eggs in the oviducts generally represents 10 to 15% of potential fecundity in pre-spawning females. Oocyte stock formation (fecundity) is asynchronous, where oogenesis occurs by continuous asynchrony.

Spawning is intermittent (pulse, batch) with several egg masses spawned over an extended time; the intensity of spawning and the average number of eggs per mass are approximately constant during the spawning period. Females from a small-sized, early maturing population from the tropical central-east Atlantic have a potential fecundity of 50 000 to 220 000 oocytes and is a multiple (intermittent) spawner and frequently releases small egg masses of fewer than 1 500 eggs.

Young paralarvae can retract completely into their mantle cavity. Proboscis fusion begins to separate at about 4 mm mantle length and division into 2 separate tentacles is complete at 6 mm mantle length. Paralarvae are abundant in the summer in Gulf Stream waters from west of Key West, Florida northwards, concentrating along the Gulf Stream front at 75 to 100 m.

Ornithoteuthis antillarum exhibits the actively browsing type of hunting strategy in which prey represents many different species, each with low individual weight. As a browsing predator it feeds on all available small prey, principally on amphipods, as well as on larvae and fry of carnivorous fishes and on small squids, both in and below the thermocline. One specimen of 140 mm mantle length was observed and photographed from a submersible at 684 m (10.7°C) in the Bahamas feeding on an adult midwater fish, *Gonostoma elongata*. The prey of micronektonic *O. antillarum* in the eastern Gulf of Mexico (27°N 86°W) changes during ontogeny.

While copepods are numerically dominant at the smaller size classes (less than 4.0 mm mantle length) (of these the metridiid *Pleuromamma* is the major prey item), the less frequent euphausiids probably are more important energetically because of their larger size and morphology; decapod crustaceans and cephalopods are the most abundant prey at larger size classes (more than 4.0 mm mantle length).

Predators on *O. antillarum* include epipelagic and mesopelagic fishes. A study off northeastern Brazil revealed that the diet of 4 species of billfishes, Istiophoridae, consisted mainly of *O. antillarum* and the ocean pomfret (*Brama brama*). In upper slope and adjacent oceanic waters off Brazil *O. antillarum* and *Illex argentinus* are the most important links in the trophic relations, the former a major component in the diets of the smaller tunas (*Thunnus alalunga* and *T. albacares*), as well as billfishes. Other species of fishes and cetaceans predators on *O. antillarum* include: common dolphinfishes (*Coryphaena hippurus*), Atlantic sailfishes (*Istiophorus albicans*), skipjack tunas (*Katsuwonus pelamis*), white marlins (*Tetrapturus albidus*),

albacore tunas (*Thunnus alalunga*), yellowfin tunas (*Thunnus albacares*), bigeye tunas (*Thunnus obesus*), swordfishes (*Xiphias gladius*), pygmy sperm whales (*Kogia breviceps*) and orca whales (*Orcinus orca*). A seasonal study on yellowfin tuna (*Thunnus albacares*) off southern Brazil showed that *O. antillarum* and teleost fishes are the most important dietary components in winter. The parasites of *O. antillarum* are primarily didymozoid trematodes, at infection intensity of 10 to 50 times less than in same-sized specimens of *Sthenoteuthis pteropus*.

Interest to Fisheries: *Ornithoteuthis antillarum* is similar to all other species of ommastrephids in that its flesh is firm, muscular and palatable. Tests on its congener, *O. volatilis*, have confirmed its qualities and acceptability as a potentially viable commodity. Its size of 80 to 120 mm mantle length is adequate for fishery purposes. In the higher latitudes of its range, *O. antillarum* attains a very desirable size of 250 to 300 mm mantle length. Observations from submersibles indicate it is a common species in slope waters of the tropical/subtropical western Atlantic. Its abundance in stomach contents of many species of large oceanic and neritic predatory fishes and cetaceans also suggests an abundant resource. However, it does not appear to assemble in large schools, as do *Illex* species, and it never has been observed to rest or reside on the bottom, where it would be more readily available to commercial trawls. An approximation of the instantaneous biomass of *O. antillarum* suggests a value of 500 000 tonnes. If an efficient fishing technique can be developed, this species could provide an important fishery product.

Local Names: USA: Atlantic bird squid.

Remarks: This species was misidentified as *O. volatilis* (Silva-Mello, 1998) in stomach contents of pelagic fishes from the southwestern equatorial Atlantic Ocean. *Ornithoteuthis antillarum* is a very abundant prey in this region and *O. volatilis* does not occur in these waters.

Literature: Roper and Young (1975), Vecchione and Roper (1992 [1991]), Passarella and Hopkins (1992 [1991]), Arkhipkin *et al.* (1998c), Dunning (1998b,c), Vecchione *et al.* (2001), Nesis (2002, 2003).

Sthenoteuthis Verrill, 1880

Sthenoteuthis Verrill, 1880, *Transactions of the Connecticut Academy of Sciences*, 5(5): 177–257. [222].

Type Species: *Sthenoteuthis oualaniensis* (Lesson, 1830)

Diagnostic Features: Funnel groove has a **foveola with 5 to 9 longitudinal folds and 4 to 6 distinct side pockets**. The **external light organs present**, including small subcutaneous photophores, are scattered on mantle, head and ventral arms. Large dorsal mantle photophores present: **large, yellow, oval photophore located anteriorly on dorsal part of mantle in squid greater than 140 mm mantle length** (observed to shine constantly in live squid). The photophore consists of numerous, densely packed, small, yellow, subcutaneous photophores, 1.0 to 2.5 mm in diameter, embedded in the mantle musculature, beneath which is a white reflective layer. **A single round photophore occurs on the ventral surface of each eye and 2 round photophores occur on the ventral surface of the intestine**. The dactylus of the tentacular club has 4 rows of small suckers. Carpal-locking apparatus on tentacular stalk with 2 to 5 knobs and an equivalent number of alternating smooth-ringed suckers. Zero to 2 suckers with denticulate rings occur on the carpus proximal to the first knob. **The largest medial suckers on the manus have 4 large, pointed teeth, one at each quadrant. Tips of all arms not attenuate**. Arms have 26 to 35 pairs of suckers. Tips of trabeculae of protective membranes do not project beyond the edge of the membrane. Ventral protective membranes of arms III subequal to arm width. Right or left ventral arm hectocotylized by smooth type. Fins rhomboidal, not attenuate posteriorly. Fin length 40 to 50% and fin width 70 to 88% of mantle length; fin angle is 58° to 72°. Mantle funnel-locking cartilage may be fused or not fused. The cone flags of the gladius are short, rhomboidal, with distinct radial creases. The greatest width of the cone flags ranges between 55 and 60% of the width of the rachis. The marginal rigid ribs of the rachis are doubled (with the exception of the giant form of *Sthenoteuthis oualaniensis*), axial rigid rib of the rachis is wide, rounded-rectangular in cross-section. The lateral plates of the gladius do not adhere to the dorsal surface of the rachis, but form wide, free folds over the rachis. The anterior stem is short, reminiscent of a mammalian vertebra in cross-section. The width of the stem is equal to, or slightly greater than, its thickness. The cone is short, compressed laterally. The rostrum is absent. The alveola of the gladius is thick, covered with tiny ribs and thorns. Spermatozoa have 1 flagellum.

Size: Large-sized squid; mantle length up to 650 mm.

Geographical Distribution: It occurs in tropical and partly subtropical waters of the Atlantic, Indian and Pacific Oceans.

Remarks: *Sthenoteuthis* includes 2 oceanic species. Two endonucleases, AluI and Tsp509I, are diagnostic for species identification.

Literature: See species accounts.

Key to the species of *Sthenoteuthis*

- 1a. Mantle and funnel cartilages fused at post-paralarval stages; 6 to 8 pairs of suckers on hectocotylyzed arm; distributed in the Pacific and Indian Oceans ***Sthenoteuthis oualaniensis***
- 1b. Mantle and funnel cartilages not fused; 11 to 13 pairs of suckers on hectocotylyzed arm; distributed in the Atlantic Ocean ***Sthenoteuthis pteropus***

***Sthenoteuthis oualaniensis* (Lesson, 1830)**

Fig. 303; Plate X, 58

Loligo oualaniensis Lesson, 1830, *In 1830–1831, Zoologie*, 2(1): 471 pp. [24, pl. I, fig. 2]. [Type locality: Oualan Island, Caroline Archipelago, Micronesia, western Central Pacific Ocean].

Frequent Synonyms: *Loligo oualaniensis* Lesson, 1830; *L. vanicoriensis* Quoy and Gaimard, 1832; *L. brevitentaculata* Quoy and Gaimard, 1832; *Ommastrephes oualaniensis* d'Orbigny, 1834–1848; *Ommatostrephes oualaniensis* Steenstrup, 1880; *Symplectoteuthis oualaniensis* Pfeffer, 1900.

FAO Names: En – Purpleback flying squid; Fr – Encornet bande violette; Sp – Pota cárdena.

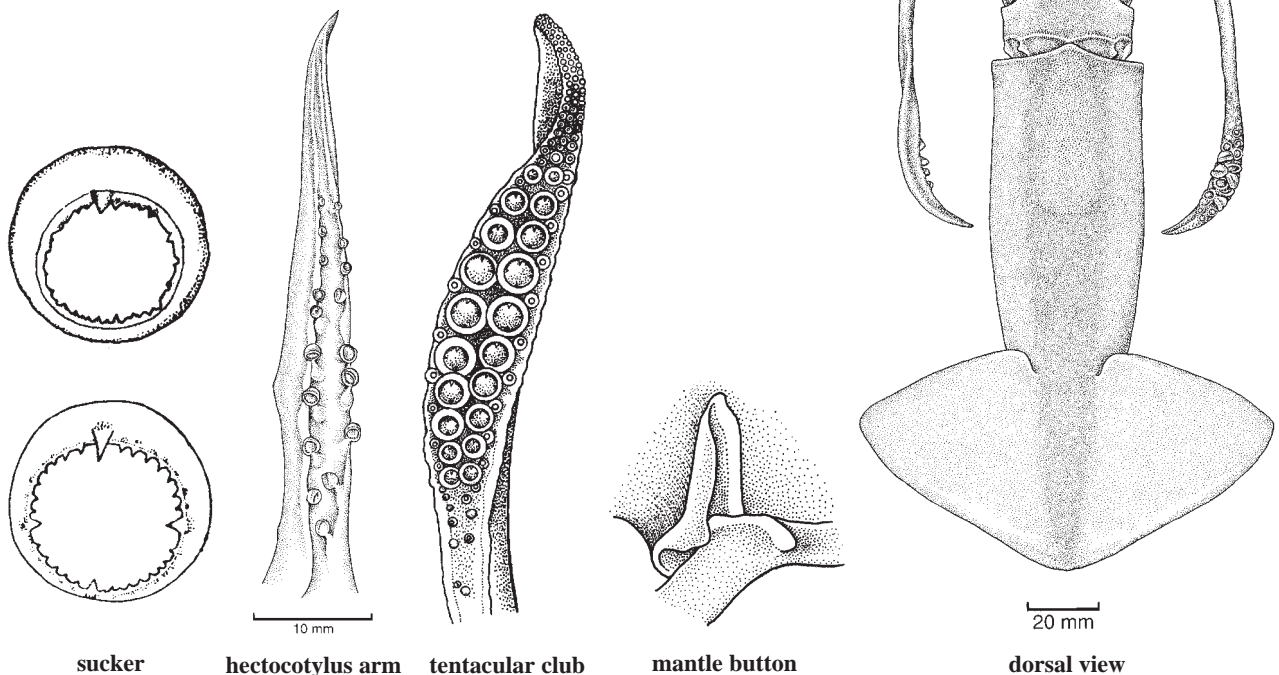


Fig. 303 *Sthenoteuthis oualaniensis*

Diagnostic Features: Mantle and funnel cartilage fused at post-paralarval stage by 9 to 12 mm mantle length. The large dorsal mantle photophore begins to develop in immature squid of 100 to 120 mm mantle length, but in maturing and mature squid of this same size it is not quite developed; **6 to 8 pairs of suckers occur on the hectocotylyzed arm of mature males.**

Size: Maximum mantle length 650 mm and body weight 8.5 kg.

Geographical Distribution: Indo-Pacific, tropical, oceanic species; its range extends in a broad band that stretches throughout the open waters of the tropical zone of the Indian and Pacific oceans and the Red Sea, generally where bottom depths exceed 200 m. It enters into subtropical zones where warm currents occur near Japan, the eastern Australian coast and South Africa (Fig. 304).

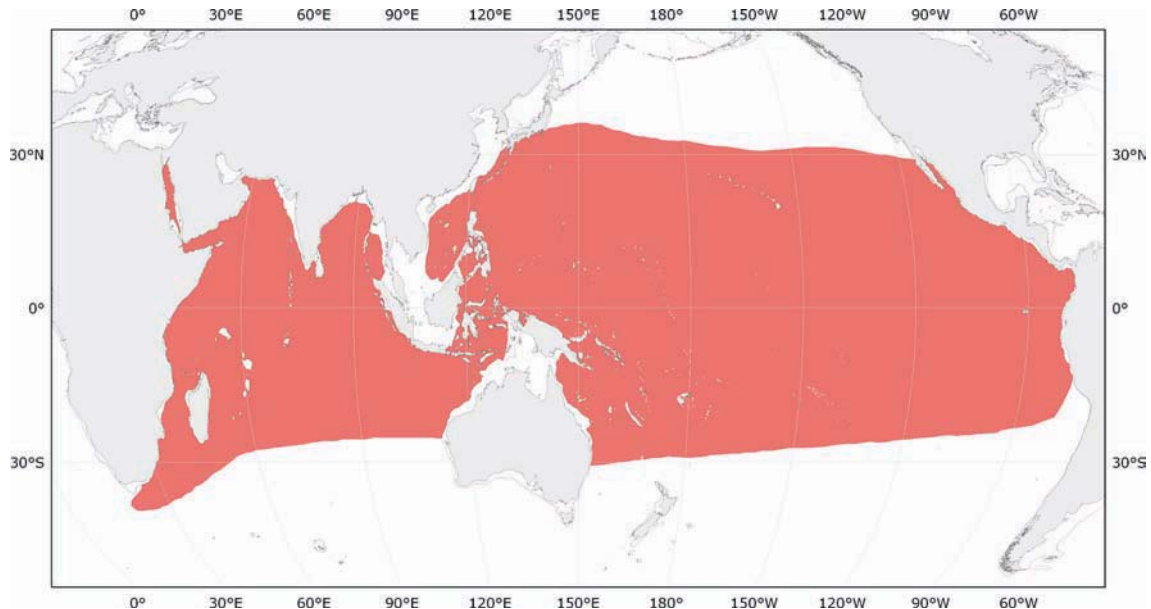


Fig. 304 *Sthenoteuthis oualaniensis*

■ Known distribution

Habitat and Biology: *Sthenoteuthis oualaniensis* is a widely distributed, abundant and highly productive, epipelagic to mesopelagic and upper bathypelagic species that inhabits open waters over great depths of more than 200 to 400 m, at sea surface temperatures from 16° to 32°C, but usually above 20° to 22°C.

The Asian continent limits the northern boundary of its range in the Indian Ocean. The southern boundary reaches to the southernmost point of Africa to about 35°S, and in some years even to 39°S (commonly it is located in the Natal area and in some warm years even up to the Agulhas Bank); then it continues eastward approximately along the longitudes 25°S to 30°S, then to 35°S near the western Australia coast. In the Pacific Ocean it is widely distributed from the Pacific coast of central Honshu, Japan (about 36°N to 38°N) to the central part of the California Peninsula (about 25°N); in the Southern Hemisphere it extends from the southern part of the Australian coast (38°40'S) eastward to northern Chile (18°S to 22°S). The reproductive area of the species is located in the Indian Ocean northward of 18°S to 22°S, in the North Pacific Ocean between 20°N to 25°N and in the South Pacific Ocean from 16°S to 25°S. The more high-latitude areas of the species range is used by migrant squid as foraging zones, mainly by the females of the middle-sized form. Squid migrate to high latitudes with seasonal warming during summer in their appropriate hemisphere along the shift of surface isotherms of 20° to 22°C; then they move to lower latitudes with the seasonal autumn of water temperature. This species is truly pelagic, not associated with the bottom.

The planktonic paralarvae and juveniles usually live in the homogenous surface layer above and near the gradient layer (0 to 75 m and 100 m). Diurnal vertical migrations by paralarvae and juveniles are absent or very short in distance. During daytime the main bulk of juveniles occurs near the surface from 0 to 30 m, while at night they descend deeper, between 25 and 75 m, moving out of the zone of maximum numbers of conspecific predatory adult squids. Subadult and adult squids are interzonal animals. At night they inhabit surface and subsurface layers from 0 to 150 m to feed, with maximum numbers between the surface and about 25 m. In the morning they descend to depths of 200 to 1 100 m and remain there during the day.

The species is in the process of intensive adaptive radiation. On the basis of size differences of mature squid, as well as dorsal photophore and gladius morphology, 5 forms of undetermined status are distinguishable. At least the dwarf (1), middle-sized (3) and giant (5) forms probably are species in *statu nascenti*. **1) The dwarf form without a dorsal photophore;** the morphology of the gladius is variable. It is a common inhabitant of the equatorial waters of the Indian and Pacific Oceans mainly between 15°N and 15°S, but with locally warm currents it extends to 20°N to 26°N and 20°S to 27°S. The mantle length of mature males is 75 to 130 mm and of mature females 80 to 150 mm. The life cycle is about a half-year. **2) The dwarf form with a dorsal photophore;** the morphology of the gladius is unknown. The abundance of this form is very low. It has been recorded in the Red Sea, Mozambique Channel and Costa Rica Dome area. The mantle length of mature females is 90 to 150 mm. Duration of the life cycle is unknown. Probably this form is not a separate group, but, rather, it may represent the earliest maturing stage of both middle-sized groups (3 and 4). **3) The middle-sized, typical form** has a **dorsal photophore and double axes on the gladius**. This is the most abundant and widely distributed form. Its range coincides with the range of *S. oualaniensis* except it is absent in the Red and Arabian Seas and the Gulf of Aden. The mantle length of mature males is 120 to 240 mm and of females

150 to 400 mm. The life cycle is 1 year. **4) The middle-sized not typical form** has a **dorsal photophore and a single axis on the gladius**. This form is relatively abundant but it is narrowly distributed in the Red and Arabian Seas and the Gulf of Aden. The mantle length of mature males is 160 to 260 mm and of females 200 to 320 mm. The life cycle is 1 year. Probably this form and the giant form are parts of a united stock. **5) The giant form** has a **dorsal photophore and a single axis on the gladius**. This form is very abundant, an inhabitant of the Red Sea, the Arabian Sea and the Gulf of Aden northward of 12°N, but 2 large mature females of 725 and 820 mm mantle length were captured in an equatorial area (5 September 1991; 00°58'8"N, 2°06'8"E). The mantle length of mature males is 240 to 320 mm and of females it is 360 to 650 mm and even to 820 mm. The life cycle is 1 year, but its duration in very large specimens (greater than 700 mm mantle length) is unknown.

The species is very fast growing: by the age of 300 days specimens can reach 550 to 600 mm mantle length and 8 to 9 kg body weight; the largest daily increment in length is 1.0 mm for dwarf and middle-sized forms and 3.8 mm for the giant form. *Sthenoteuthis oualaniensis* is a typical monocyclic r-strategist. Potential fecundity varies from 300 000 to 350 000 oocytes in the dwarf form, from 0.7 to 8.5 million in the middle-sized form and from 6 to 22 million in the giant form. The relative fecundity is 3 000 to 7 000 oocytes per gram. The ripe eggs are small, 0.75 to 1.0 mm in diameter. Spermatophore lengths depend on the mantle length of mature males, and it varies from 8.8 to 11.7 mm in the dwarf form, from 16 to 32 mm in the middle-sized form, and from 40 to 50 mm in the giant form. The number of spermatophores in the Needham's sac of mature males can reach 300, but mainly it varies between 100 and 200. Mating occurs in surface layers at night in the "head to head" position without preliminary rituals; probably promiscuity is common. Duration of copulation is short, only 0.5 to 2 minutes. Copulation results in up to 150 spermatangia being attached to the buccal cone and membrane of females, and then the viable sperm are stored in 70 to 120 seminal receptacles that are situated on the buccal membrane. At the species level, spawning takes place all year round, with the duration of the spawning season for individual females up to 1 to 3 months. The spawning peak of the dwarf form is in the summer, of the middle-sized form in the northern part of its range it is in autumn to winter and in its southeastern Pacific range it is during the warm season (December to February); the spawning season of the giant Arabian form is in the spring. Spawning takes place in the epipelagic zone at night. This squid is an intermittent, multibatch spawner. After spawning once, females continue to feed and grow, while the next portion of oocytes matures; then spawning begins again. Each subsequent batch is quasi-equal in number of eggs. In the giant form, the maximum measured volume of egg mass is about 25 litres with a density of about 1 or 2 eggs per cubic centimetre. Egg masses are pelagic, and they float above the upper pycnocline layer. The duration of embryogenesis in water temperatures of 20° to 25°C is 3 to 6 days. Hatching size is about 1.0 mm mantle length. Paralarvae have the typical ommastrephid rhynchoteuthion-stage defined by the tentacles being fused into a trunk-like proboscis. During growth the proboscis gradually separates and in *S. oualaniensis* this separation is complete by 7.0 to 8.0 mm mantle length, signalling the end of the rhynchoteuthion-stage. Molecular genetics sequencing of the mitochondrial gene cytochrome c oxidase I discriminates 1 to 10 mm mantle length paralarvae from other rhynchoteuthions, e.g. *Dosidicus gigas*.

Sthenoteuthis oualaniensis is a fast-swimming, highly manoeuvrable nektonic squid that reacts very quickly to any change in its surroundings. Juveniles are capable of "flying" during daytime. Under threat from pursuit of predators they can reach a high speed and then glide above the surface of the sea some tens of meters. The cruising speed of adult squid is about 3 to 10 km per hour, but the burst speed reaches greater than 25 to 35 km per hour. During the day at depth, squids are nearly non-active, and either "hang" in the water or move slowly with a speed of only 1 to 1.5 km per hour, propelled by the undulating fins. The species is an obligate shoaling (schooling) squid throughout ontogenesis. Usually, shoals consist of squid of uniform size. Shoal size is highly variable and depends on the productivity of the area and the density of the squid population: it varies from 2 to about 800 individuals, occasionally more. At the periphery of its geographical range, this species may form joint schools with same-sized *Dosidicus gigas* and *Ommastrephes bartramii*.

Sthenoteuthis oualaniensis is an active predator with a very wide spectrum of food organisms. Paralarvae feed on micro- and mainly mesozooplankton (copepods, amphipods, etc). Post-paralarvae and juveniles (10 to 80 mm mantle length) feed on meso- and macroplanktonic invertebrates, mainly copepods, euphausiids, amphipods and chaetognaths, as well as on juvenile fishes and squids. In squid from 90 to 150 mm mantle length, the role of fishes and squids increases as food preference. Active feeding of middle-sized squid (150 to 350 mm mantle length) takes place in the evening, night and early morning at the surface, and to 50 and 75 m. The middle-sized squid feed predominantly on micronektonic plankton-eating fishes (mainly myctophids, juveniles of flying fishes and the oceanic lightfish *Vinciguerrria nimbaria*), juveniles of predatory fishes (paralepidids, gempylids, etc), squids (mainly the common clubhook squid *Onychoteuthis banksii*, different species of enoploteuthids and conspecific juveniles) and pelagic shrimps and crabs. The adult females of the giant form (greater than 400 mm mantle length) in the Arabian Sea feed mainly on myctophids, that occur in very dense concentrations in the layer of 100 to 200 m. The duration for complete digestion of food is 3 to 6 hours in juveniles and 5 to 8 hours in adult middle-sized squid.

The predators of this species (all forms) are very diverse. For paralarvae and juveniles they include large chaetognaths, jellyfishes, small squids, planktivorous and small carnivorous teleosts. Juveniles (3 to 12 mm mantle length) are the prey for large squids (conspecific adults and the Humboldt squid *Dosidicus gigas*), both species of dolphinfishes (*Coryphaena hippurus*, *C. equisetis*), snake mackerel (*Gempylus serpens*), lancet fish (*Alepisaurus ferox*), and different species of tunas (*Thunnus alalunga*, *T. obesus*, *T. albacares*, etc). Off eastern Australia, *S. oualaniensis* is common prey of yellowfin tuna (*T. albacares*) and swordfish (*Xiphias gladius*). Many species of sea birds are significant predators on juveniles, especially around the numerous oceanic islands. The main predators of middle-sized and large squid include swordfishes (*Xiphias gladius*), striped marlins (*Tetrapterus audax*), several species of sharks, such as the frill shark (*Chlamydoselachus anguineus*), the blue shark (*Prionace glauca*), the dusky shark (*Carcharhinus obscurus*), the oceanic whitetip shark (*Carcharhinus longimanus*), the smooth hammerhead (*Sphyrna zygaena*, etc), marine mammals such as the striped and the spotted dolphins (*Stenella caeruleoalba*, *S. attenuata*), the sperm whale (*Physeter macrocephalus*) and, locally, the Galapagos fur seal (*Arctocephalus galapagoensis*). In the Arabian Sea, adults of the giant form are their principal predator.

The helminth fauna of this squid consists of 12 species of larvae of trematodes, cestodes, nematodes and acanthocephalans, among which are 2 representatives of nematodes that have significant negative impact on the commercial importance of the species. Larvae of *Anisakis* sp. are a mortal danger to humans, but they are localized in the ovaries and encysted in the coelomic membranes, neither of which is used for human food. Larvae of *Porrocaecum* sp. are encysted on the internal mantle wall and they may significantly degrade the quality of the marketable components of the infested squid.

The total instantaneous biomass of *S. oualaniensis* is estimated to be at the level of 8 to 11.2 million tonnes, including 3 to 4.2 million tonnes in the Indian Ocean and 5 to 7 million tonnes in the Pacific Ocean. In general, the areas of dense concentrations coincide with dynamically active feeding zones and oceanographic fronts. In the open waters of the Peruvian region (5°S to 25°S and from the Exclusive Economic Zone (EEZ) boundary to 95°W) it forms dense concentrations together with *Dosidicus gigas*.

Interest to Fisheries: *Sthenoteuthis oualaniensis* is not fished commercially on an industrial level mainly due to the absence of effective fishery methods and to the relatively poor quality of the meat (at least for Asian consumers in comparison with *Todarodes pacificus*). Local artisanal fisheries for this species carried out in the last 40 years by dipnet and hand jigs were conducted from near Okinawa, Taiwan Province of China and Hawaii. The catches are used mainly as bait for the tuna fishery. Many attempts to use jigging machines to fish for the species in different parts of the species range were not effective. However, this species has great potential for a future significant fishery with about 3 million tonnes of stock in dense concentrations and a potential catch on the level of about 300 000 to 500 000 tonnes or more. The main prospective areas for fishery development are the Arabian Sea, the Gulf of Aden and the adjacent open waters to 12°N; the southern part of the equatorial zone of the Indian Ocean between 4°S and 10°S and between 65°E and 95°E; the area of Mozambique between Madagascar and the edge of the Mozambique shelf; the equatorial zone of the Pacific Ocean between 2°N and 2°S and between 95°W and 110°W; the oceanic part along the Peruvian Exclusive Economic Zone (EEZ) boundary between 6°S and 18°S (mixed concentrations with *Dosidicus gigas*); and areas near the Hawaiian Islands, Taiwan Province of China and Okinawa. The most promising area for the development of a large-scale fishery for *S. oualaniensis* is the Arabian Sea. The giant form of this species of 300 to 650 mm mantle length (mode 480 to 540 mm mantle length) inhabits this area. More than 200 000 tonnes were captured in the northwestern part of the Arabian Sea in dense concentrations of more than 10 tonnes per square km. The potential average catch is estimated at about 100 000 tonnes. The optimal fishing season for this squid is September to May, with the peak in March to May. The most effective gears are the wide-cut pelagic trawl and the mechanized vertical lines with large blinking jigs. The meat of the giant form of greater than 350 mm mantle length tastes acidic because of the presence of large quantities of urea (49.1±1.52 mg/100 g); special treatment with citric acid is required for this species to be utilized as food.

Local Names: AUSTRALIA: Yellow-backed squid; CHINA: Yuán-wū-zēi; JAPAN: Tobi-ika; PERU: Pota cárdena; RUSSIA: Kal'mar-ualanienis, Purpurnyj kal'mar (purple squid); TAIWAN PROVINCE OF CHINA: Nán-yóu; USA: Purpleback flying squid.

Literature: Zuev *et al.* (1975), Wormuth (1976), Roper *et al.* (1984), Nigmatullin *et al.* (1991b), Nesis (1993b), Roper *et al.* (1995), Bower *et al.* (1999c), Nigmatullin *et al.* (2002c), Zuev *et al.* (2002), Nixon and Young (2003), Okutani (2005), Gilly *et al.* (2006b), Parry (2006), Wakabayashi *et al.* (2006).

Sthenoteuthis pteropus (Steenstrup, 1855)

Fig. 305

Ommastrephes pteropus Steenstrup, 1855, in *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1855(5/6): 199–200. [199]. [Type locality: St Croix Island, Caribbean Sea, western Central Atlantic].

Frequent Synonyms: *Ommatostrephes pteropus* Steenstrup, 1855; *Architeuthis megaptera* Verrill, 1878; *Sthenoteuthis megaptera* Verrill, 1880.

FAO Names: **En** – Orangeback flying squid;
Fr – Encornet orange; **Sp** – Pota naranja.

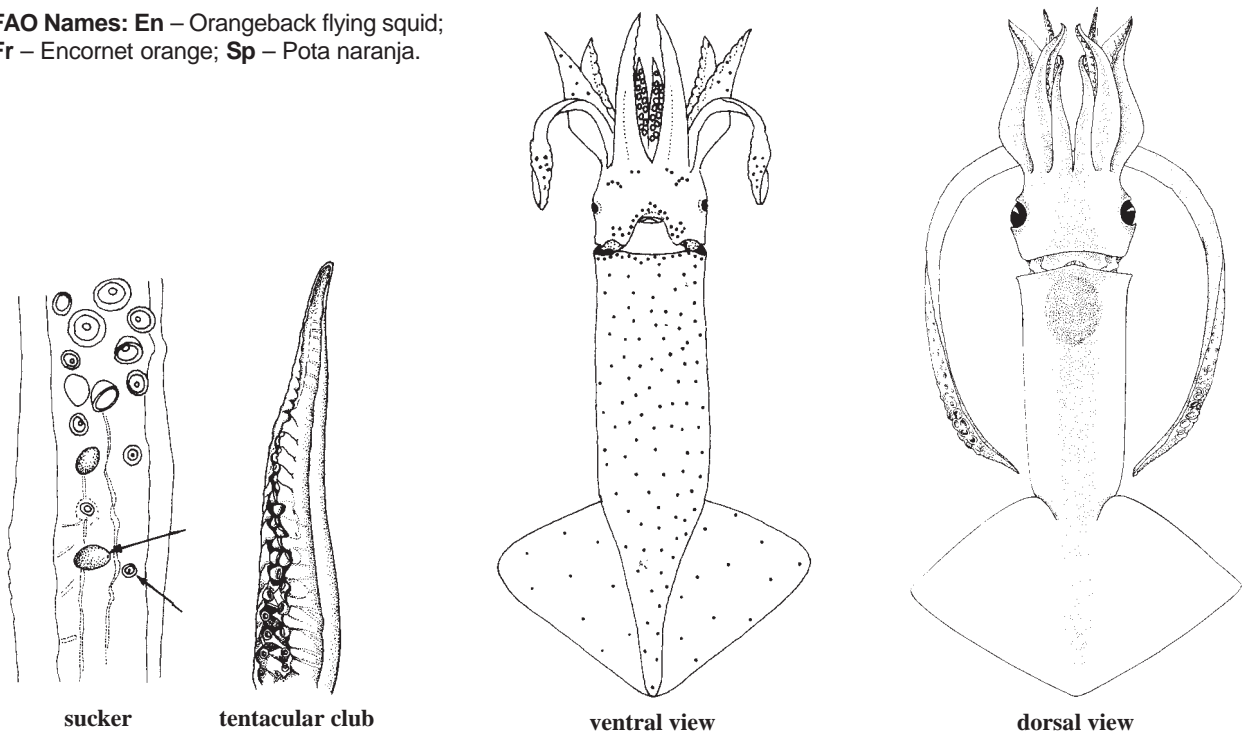


Fig. 305 *Sthenoteuthis pteropus*

Diagnostic Features: Mantle and funnel cartilage not fused during entire ontogenesis (only 2 specimens recorded with fused funnel cartilage among many thousands studied). Large dorsal mantle photophore begins to develop in immature and maturing squid of 90 to 110 mm mantle length; all adult specimens have this photophore; **11 to 13 pairs of suckers on hectocotylized arm.**

Size: Maximum mantle length 650 mm; body weight 7 kg.

Geographical Distribution: Tropical Atlantic Ocean. The extreme limits of its northern distribution lie at the latitude of New York (42°N) and Madeira (34°N); in some years north to 36°N near the Strait of Gibraltar. Its southernmost limits extend to southern Brazil (30°S to 32°S) and South Africa (36°S). The boundaries of the species range in the central part of the ocean coincide approximately with the Tropics of Cancer and of Capricorn (Fig. 306).

Habitat and Biology: *Sthenoteuthis pteropus* occurs at sea surface temperatures from 16° to 32°C, usually above 20° to 22°C. Squid migrate to high latitudes with seasonal warming of the appropriate hemisphere in harmony with the shift of the surface isotherms of 20° to 22°C; then they return to lower latitudes in the autumn in coincidence with the seasonal drop in water temperature. Significant seasonal shifts occur at the boundaries of the range. During summer in the Northern Hemisphere (July to October) the northern boundary is displaced to the northern limits of the species distribution, whereas the southern boundary displaces approximately to 23°S near Brazil and Namibia and about 10°S in the central part of ocean. During winter (February to March) the northern boundary shifts to the south to about 20°N to 22°N near Cuba and northern Mauritania, while the southern boundary is displaced to the southern limits of the species range. The reproductive region occupies the equatorial zone, including the Caribbean Sea and Gulf of Mexico between 20°N and 20°S near the continents and between 10°N and 10°S in the central part of the ocean. The higher latitudes in both hemispheres are the principal feeding zones of the species range; they also are occupied seasonally, mainly by immature females of the large form.

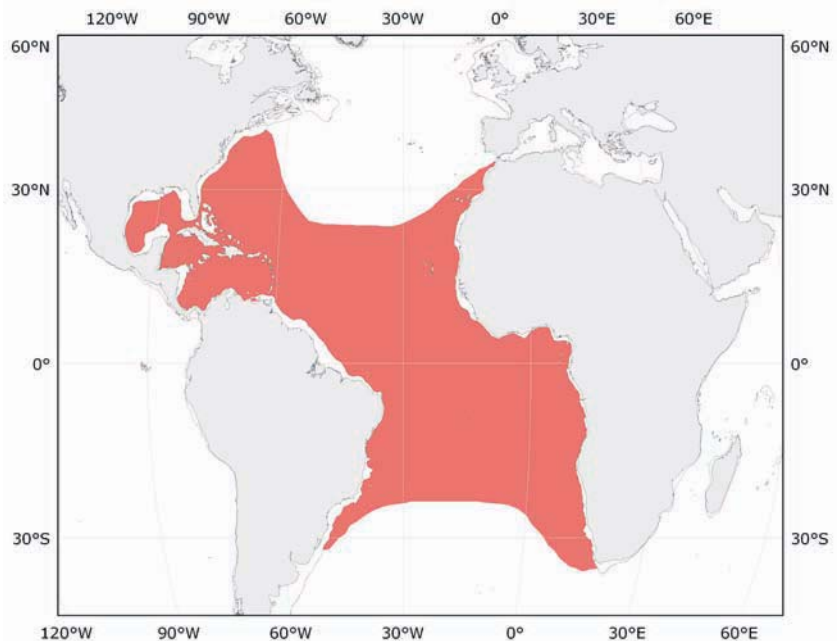


Fig. 306 *Sthenoteuthis pteropus*

■ Known distribution

Sthenoteuthis pteropus is an abundant, highly productive species that dwells in epipelagic to mesopelagic and upper bathypelagic zones. It inhabits open waters over great depths in excess of 200 to 400 m, and this species is not associated with the bottom. In general, squid of this species live in the oceanic pelagic zone from the surface to 1 200 m. Paralarvae, post-paralarvae and early juveniles up to 90 mm mantle length as a rule live in the homogenous surface layer from the surface to between 50 and 75 m. Diurnal vertical migration in paralarvae and post-paralarvae is minimal to absent, and in juveniles it is a very short range. During daytime, juveniles principally inhabit the surface layer from the surface to about 30 m, and at night their habitat extends to depths of 30 m to between 75 and 100 m. Squids larger than 120 to 150 mm mantle length undergo the typical diurnal vertical migration: they rise to the surface layers at night for active feeding, then descend to daytime depths in the morning. On moonless nights most squids are concentrated near the surface between 0 and 30 m, while on moonlit nights they are more widely dispersed in somewhat deeper water, between 10 and 50 m. During about a 1-hour period at dawn, squid descend to the depth of their daily habitation, with the maximum concentration at depths of 600 to 850 m. In the twilight crepuscular period – before sunrise and sunset-squid occur in the 150 to 400 m range.

Sthenoteuthis pteropus is represented by 2 intraspecific forms of undetermined systematic status. 1) **A small, early-maturing, equatorial form**; it lives only in the equatorial zone and its most adjacent waters between 10°N to 15°N and 8°S to 15°S in the eastern Atlantic, while it occupies nearly the entire range of the species distribution (*sensu lato*) in the central and western Atlantic, including the Caribbean Sea and the Gulf of Mexico. These squids are relatively stable in that they do not undergo long distance migrations at any time during their life cycle. Spawning takes place all year round. The mantle length of the mature male of the small form is 110 to 200 mm and of the mature female 150 to 320 mm (mode 210 to 250 mm). 2) **A large, late-maturing, mostly peripheral form**; this is distributed throughout the entire range of the species (*sensu lato*) in the eastern Atlantic, less broadly in the central part of the ocean to 20°W to 25°W; probably it occurs in the peripheral parts of the species range (*sensu lato*) in the western Atlantic. In the eastern Atlantic the main concentrations of this large form of squid are distributed in waters to the north of 8°N to 12°N and to the south of 6°S to 10°S, as well as along the south tropical front. Two allopatric populations occur in the open waters along the African coast; they differ by distribution, spawning season and direction of ontogenetic migrations. These squids are northern and southern populations that are confined to northern and southern African upwelling zones respectively. These populations spawn in the equatorial zone. Then the developing immature females greater than 200 to 250 mm mantle length migrate during the warm season in their given hemisphere, to the north (northern population) and the south (southern population) to foraging grounds that are located in both peripheral zones of the species range (*sensu lato*). After active feeding and somatic growth they migrate back to the equatorial zone to complete maturation and to spawn. However, no morphological differences exist to differentiate between these forms.

Spawning is seasonal, and it takes place in the autumn period of each particular hemisphere. The mantle length of the mature male of the large form is 180 to 280 mm and of the female 300 to 650 mm.

In the most intensively studied area, the eastern Atlantic, *S. pteropus* appears to be subdivided into 3 groups that probably have populational status: the northern large squid, the equatorial small squid and the southern large squid. They differ ecologically and genetically, and their ranges overlap to a small degree (the 2 populations of the large form) or to a considerable degree (both large squid populations with the equatorial form).

The reproductive biology of *S. pteropus* is very similar to that of *S. oualaniensis*. The potential fecundity of mature pre-spawning females varies from 0.5 to 1.5 million oocytes at 160 to 180 mm mantle length and from 6 to 18 million oocytes at 400 to 540 mm mantle length. These same mean values for females of the small early-maturing form are about 2 to 3 million oocytes, and for the large late-maturing females it is 8 to 10 million oocytes. The relative fecundity is 2 000 to 5 200 oocytes per gram.

Ripe eggs are small, 0.75 to 1.0 mm in diameter. The oviducts contain from thousands to 1 million eggs depending on the size of mature female and the stage of the infilling process. Spermatophore lengths are proportional to the mantle length of the mature male and they vary from 15 at 107 mm mantle length to 42 at 240 mm mantle length. The number of spermatophores in the Needham's sac of mature males less than 160 mm mantle length is 100 to 300, while at greater than 170 mm mantle length there are 200 to 500 spermatophores. Promiscuous mating takes place in the surface layers at night in the "head to head" position. The duration of copulation is 0.5 to 1 minute. Each copulation results in up to 180 spermatangia being attached to the buccal cone and buccal membrane of females, and then the viable sperm are stored in 57 to 154 seminal receptacles that are situated on the buccal membrane.

Spawning occurs in the epipelagic zone at night. *Sthenoteuthis pteropus* is an intermittent, multibatch spawner. After the first spawning, females continue to feed and grow, while the next portion of oocytes matures; then they spawn again. Each subsequently spawned batch of eggs is subequal in number of eggs. Large females presumably release at least more than 50% of their total oocyte stock.

In total, during the individual spawning period of at least the large females, 5 or 6, and probably more, egg masses are produced. Egg masses are pelagic, and they float above the upper pycnocline layer. The size of embryos at hatching is about 1.0 mm mantle length. The duration of the paralarval stage is 32 to 38 days.

The majority of males become mature at 120 to 150 days, and almost all males older than 180 days are fully mature. The life span of males is completed by age 270 to 280 days. Females begin to mature at the age of 200 to 220 days, and the maximum maturation takes place at 240 to 300 days. All females are in full spawning condition at ages over 300 to 320 days. The maximum age of a spent male is 305 days and of a spawned-out female it is 372 days. The life cycle of females of both small and large forms seldom exceeds 1 year, and the life cycle of males is 1 to 2 months shorter.

This species is a very fast-swimming and highly manoeuvrable nektonic squid that reacts very quickly to any change in its surroundings. Occasionally, under threat from potential predators, juveniles may break through the sea surface and soar into

the air for some tens of metres. The cruising speed of adult squid is about 3 to 10 km per hour, and burst speed is more than 30 km per hour. During the day at depth these squid are nearly inactive, and they either “hang” or move very slowly with undulating fins at a speed of about 1.5 km per hour. Throughout ontogenesis, shoaling (schooling) is the obligate behaviour of this squid. Usually, shoals consist of uniform-sized individuals. The size of shoals is highly variable, from 2 to about 1 000 specimens. At the periphery of its distributional range, *S. pteropus* may form joint feeding schools with same-sized *Ommastrephes bartramii*.

Sthenoteuthis pteropus is an active predator that undergoes gradual changes in its food spectrum during ontogenesis. Paralarvae feed on micro- and mainly mesozooplankton (copepods, juveniles of euphausiids and larvae of fishes and squids). Post-paralarvae and juveniles (10 to 80 mm mantle length) feed on meso- and macroplanktonic invertebrates, mainly copepods, euphausiids, amphipods and chaetognaths, as well as juvenile fishes and squids. In squid from 90 to 150 mm mantle length, the role of myctophid fishes and small squids as food sharply increases, while the role of crustaceans is minimized. Active feeding of subadult and adult specimens takes place in the evening, night and early morning hours at the surface down to 50 to 75 m. Squid 150 to 350 mm mantle length feed predominantly on micronektonic plankton-eating fishes. These are mainly myctophids (principally species of *Myctophum*, *Hygophum* and *Vinciguerria nimbaria*) and to a lesser degree juveniles of predatory fishes (paralepidids, gempylids, etc), as well as flying fishes, squids (mainly *Onychoteuthis banksii*, different species of enoploteuthids and juveniles of their own species) and pelagic shrimps. Large females of 360 to 650 mm mantle length feed mainly on squids (mostly *Onychoteuthis banksii* and their own species) and to a lesser degree on flying fishes and middle-sized predatory fishes. The duration for full digestion of food is 3 to 6 hours in juveniles and 5 to 8 hours in adults. Correspondingly, the values of daily food ration for these 2 ontogenetic groups is 8 to 27% of body weight and 7 to 10% of body weight, respectively.

The known predators of this squid include the following groups: paralarval and post-paralarval predators include jellyfishes, small squids, plankton-eating and small carnivorous teleosts; juveniles (3 to 14 mm mantle length) are the prey for large squids (mainly conspecific adults), dolphinfishes (*Coryphaena hippurus*, *C. equisetis*), snake mackerel (*Gempylus serpens*), lancet fishes (*Alepisaurus ferox*, *A. brevirostris*), and several species of tunas (e.g. *Thunnus alalunga*, *T. obesus*, *T. Albacares*); locally, sea birds also are predators on juveniles; the main predators of subadult and adult *S. pteropus* are swordfishes (especially important is *Xiphias gladius*), some active species of pelagic sharks, such as the blue shark (*Prionace glauca*), the bigeye thresher (*Alopias superciliosus*), the great white shark (*Carcharodon carcharias*), hammerheads (*Sphyrna* spp.) and requiem sharks (*Carcharhinus* spp), dolphins (including *Steno bredanensis*) and very rarely, sperm whales.

The parasitic helminth fauna of this squid consists of 13 species of larvae of trematodes, cestodes, nematodes and acanthocephalans. Two nematode species have negative implication for the commercial importance of *S. pteropus*. The larvae of *Anisakis* sp. cause death to humans, but they are localized in the ovaries and encysted in coelomic membranes that are not used for food. The larvae of *Porrocaecum* sp. are encysted locally on the internal mantle wall; they may reduce the quality and value of the marketable product of infested squids.

The total instantaneous biomass of *S. pteropus* is estimated at the level of 4.2 to 6.5 million tonnes. More than half of this standing stock is concentrated in the eastern tropical Atlantic Ocean in 3 macroscale areas of dense concentrations (see below). The annual total biomass production for *S. pteropus* is estimated at 34 to 52 million tonnes.

Interest to Fisheries: *Sthenoteuthis pteropus* currently is not intensively fished commercially, but it represents a significant potentially valuable fishery resource in the open Atlantic Ocean. The mantle and the appendages are well suited for human consumption, and the viscera are excellent raw materials for the production of biologically active substances. A seasonal, artisanal fishery occurs near Madeira with very small catches. In the 1970s to 1980s Soviet investigators attempted to develop commercial exploitation of this species in the eastern tropical Atlantic Ocean, experimenting with wide-cut pelagic trawls, twin trawls, automatic jigging machines and mainly individual hand jigs. Jigging machines were not effective because the feeding behaviour of this oceanic squid is more complicated in comparison with that of inshore and neritic species of *Illex*, *Todarodes* and *Nototodarus* that are very efficiently fished by this gear. To increase the fishing efficiency for this species, the complicated lifting movement of a longline is required. The use of the wide-cut pelagic trawl from large-capacity trawlers also was unsuccessful. The catches did not exceed tens of kilograms. Likewise, the catches of twin trawls in surface waters (0 to 15 m) in the equatorial eastern Atlantic Ocean, as a rule, did not exceed 200 kg. At some lighted drift stations where dense concentrations of large squid (280 to 450 mm mantle length) occurred in areas near the Angola and Namibia Exclusive Economic Zone (EEZ) boundaries, catches were on the level of 3 to 8 tonnes. Collectively, these data are evidence of the potential for a viable fishery for this species. The total annual fishery potential is 1.9 to 2.9 million tonnes. The possible annual potential catch inside Exclusive Economic Zones (EEZs) is about 0.5 to 0.8 million tonnes. The 3 principal potential fishery grounds are located in the eastern Atlantic Ocean eastwards from 20°W between 15°N and 22°N and 25°S: 1) northeast area between 10°N and 20°N, from the African coast to 25°W; 2) equatorial area between 5°N and 10°S and from 0° to 20°W; 3) Angolan area between 5°S and 20°S, from the African coast to 5°E. Two smaller areas of high squid concentrations occur in the open waters of the Gulf of Guinea between 2°N and 3°S, and in the Caribbean Sea and western Atlantic near the Lesser Antilles. Because *S. pteropus* is so widely distributed and is subdivided into geographic populations that undergo sequential seasonality of growth and reproduction, it is possible to maintain a year-round fishery. The main impediment to the development of a viable commercial fishery for this species is the development of optimal fishing gear and the establishment of consistent, reliable fishery methods.

Local Names: COLUMBIA, CUBA, MEXICO, VENEZUELA: Lomo aranjado; JAPAN: Nise-akaika; MADEIRA: Pota de limao, Lula de limao; PORTUGAL: Pota laranja, Pota limão; RUSSIA: Krylorukij kal'mar (wing-armed squid), Kal'mar pteropus; USA: Orangeback flying squid, Yellowback squid.

Literature: Roper (1963), Roper *et al.* (1984), Arkhipkin *et al.* (1988), Zuev *et al.* (1992 [1991]), Dunning (1998b), Nigmatullin (2002a), Zuev *et al.* (2002), Laptikovsky and Nigmatollin (2005), Okutani (2005).

2.22.3 Subfamily **TODARODINAE** Adam, 1960

Todarodinae Adam, 1960b, *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 36(19): 1–10 [2].

Type Genus: *Todarodes* Steenstrup, 1880.

Diagnostic Features: Ommastrephids with **funnel groove and foveola present** (except *Todaropsis*), **side pockets absent**; left tentacular club with 2 pairs of carpal suckers; tentacles without carpal-locking apparatus; **suckers on dactylus of tentacular club quadriserial**; medial manus sucker rings with 20 or fewer long, pointed teeth, with single, large, pointed tooth distally (in some species); right or left or both arm(s) IV hectocotylized in mature males; ocular, visceral and mantle photophores absent.

Table 12
Comparison of genera of Todarodinae^{1/}

	Hectocotylus	Funnel groove with foveola	Tentacular stalks with free trabeculae	Largest manus sucker with teeth	Largest manus sucker with teeth
<i>Martialia</i>	left or right arm IV	Yes	Yes	1 tooth enlarged	linked by intermediate ridges or plates
<i>Nototodarus</i>	both arms IV	Yes	No	1 tooth enlarged or subequal teeth	linked by intermediate ridges or plated
<i>Todarodes</i>	right arm IV	Yes	No	generally subequal teeth	linked by intermediate ridges or plated
<i>Todaropsis</i>	both arms IV	No	No	subequal teeth	without intermediate ridges of plates

^{1/} From Young and Vecchione (2008k).

Todarodes Steenstrup, 1880

Todarodes Steenstrup, 1880, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1880: 73–110, 12 figs, 1 pl. [83].

Type Species: *Todarodes sagittatus* (Lamarck, 1798).

Diagnostic Features: **Funnel groove with foveola, side pockets absent.** Tentacular club with 2 pairs of carpal suckers, tentacles without fixing apparatus; suckers on dactylus of tentacular club quadriserial; medial manus sucker rings with 20 or fewer long, pointed teeth with a single larger tooth distally in some species. **Only right arm IV hectocotylized** in mature males. **Ocular, visceral and mantle photophores absent.**

Remarks: The genus *Todarodes* is represented in the Mediterranean Sea, the North and South Atlantic Ocean, the northwestern and southwestern Pacific Ocean, Indo-Pacific waters, northeastern Indian Ocean, and the Southern Ocean and its northern meanders. Traditionally, the genus consists of 4 species, one of which, *T. pacificus*, contained 2 subspecies. While these former subspecies of *T. pacificus*, namely *pacificus* and *pusillus*, are similar in several respects, it is now considered that their morphological differences are sufficiently broad as to consider them separate species. This distinction has been recognized by Okutani (2005), a designation with which we concur. Some species of *Todarodes*, particularly *T. pacificus* and less so *T. sagittatus*, support among the largest fisheries in the world.

Todarodes sagittatus (Lamarck, 1798)

Fig. 307

Loligo sagittata Lamarck, 1798, *Bulletin des Sciences par la Société Philomatique de Paris*, 2(5): 129–131. [130]. [Type locality: “sur les côtes de l’Océan de l’Europe et de l’Amérique”, fide Lamarck (1799: 14)].

Frequent Synonyms: *Loligo sagittata* Lamarck, 1798; *Ommastrephes sagittatus* Lamarck, 1798; *Ommatostrephes sagittatus* Lamarck, 1798; *Loligo todarus* Verany, 1851; *L. aequipoda* Rüppell, 1844; *Sepia media* Barbut, 1783; *Loligo brasiliensis* Férussac, 1823; *Sepia loligo* Gmelin, 1789.

Misidentifications: None.

FAO Names: En – European flying squid; Fr – Toutenon commun; Sp – Pota europea.

Diagnostic Features: Mantle strong, muscular, long and slender; fins wide and strong, fin length up to 45% mantle length. Funnel groove with foveola, without side pockets. Entire club relatively very long, extends along stalk; club suckers on elongate carpus in 10 to 12 pairs; medial manus sucker rings with 17 to 20 long pointed teeth; manus with 14 to 18 quadriserial sucker rows; club suckers on dactylus in 4 rows. Arm suckers with enlarged central tooth, 7 to 9 regular teeth and virtually no small alternating teeth. No light organs on viscera. **Right arm IV hectocotylized in males**, by the modification of terminal suckers into fleshy papillae. Dark purplish in colour.

Geographical Distribution: Eastern North and South Atlantic Ocean: from the lower Barents and Kara Sea (Arctic Ocean) southward to about 13°S (south of the Gulf of Guinea), including the North Sea, the Mediterranean Sea and the Marmara Sea. In the North Atlantic it extends to the mid-Atlantic Ridge (Fig. 308).

Size: Large-sized species: maximum reported size 750 mm mantle length for an unsexed specimen, probably a female, 640 mm mantle length for a male, both in North Atlantic waters. Common size between 250 to 350 mm mantle length.

Habitat and Biology: A neritic and oceanic species that occurs from the surface to well over 1 000 m, having been captured in British waters to a depth of 4 595 m. Occasionally associated with the shelf and upper slope bottom communities, e.g. North African population, typically it inhabits lower slope waters, between 350 and 700 m.

Todarodes sagittatus undergoes important trophic and ontogenetic migrations in the North Atlantic Ocean. In early summer large schools appear off the south and southwest coast of Iceland, the Faeroe Islands, Norway and, in some years, Scotland, where they remain until the beginning of winter. Coastal strandings of great numbers of squid are relatively common during this period. As winter arrives, the squid migrate into deeper offshore waters for the duration of winter. The populations of the northwestern African waters and the western Mediterranean are rather stationary in comparison. This species is found in large numbers from March to May on the fishing grounds around Madeira and other parts of the eastern central Atlantic Ocean. Here ontogenetic movements occur as well, from the shelf to the slope and deep waters. *Todarodes sagittatus* is known to carry out diel vertical migrations between the surface and near-surface waters at night and in proximity to bottom waters during the day. However, night catches in deeper waters indicate that a portion of the population may not adhere to this general pattern. This species may occur alone or in small groups; then individuals form into very large congregations during its trophic movements on the North Atlantic and north African shelves.

With the exception of some geographic areas and seasons, the sex ratio is usually biased towards females in all the populations investigated to date, with relatively few, under-represented males in the captures. Numerous observations indicate that this is due mainly to ecological factors, since males and females inhabit different feeding grounds and get together during the mating/spawning seasons. Males may remain on the spawning grounds without

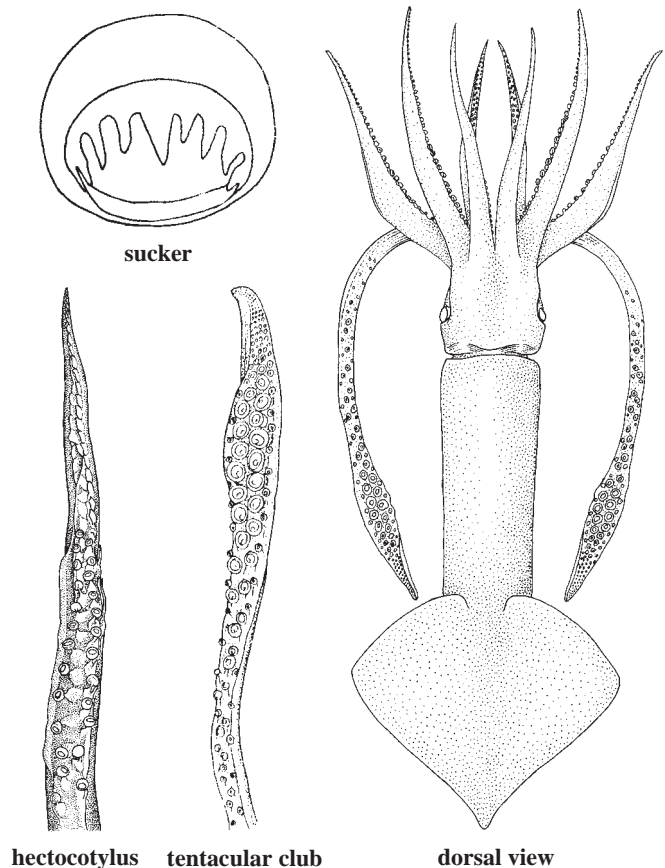


Fig. 307 *Todarodes sagittatus*

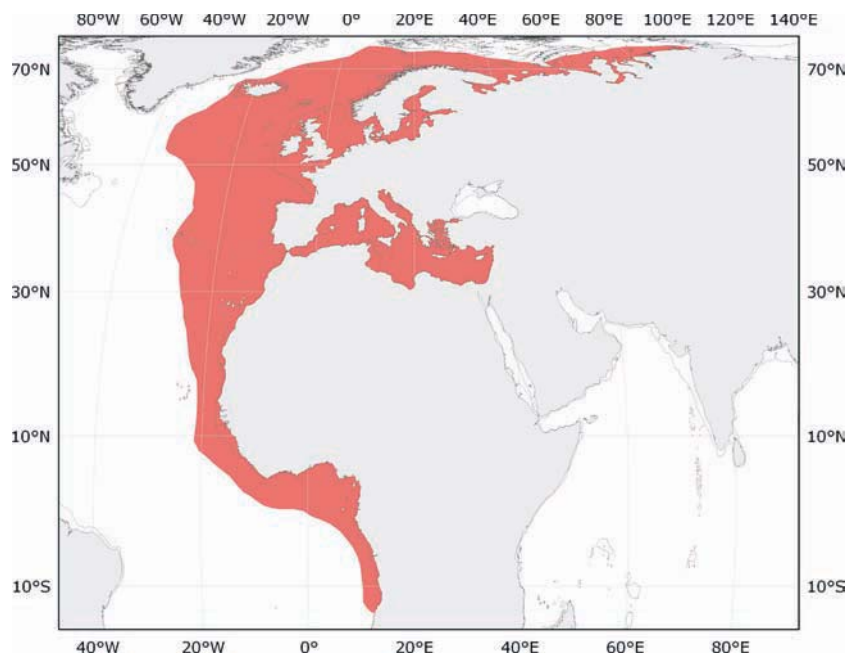


Fig. 308 *Todarodes sagittatus*

Known distribution

taking part in the feeding migrations, which may explain why they inhabit different depths than females and would account for their relative scarcity in the sampling captures. Males mature earlier and at smaller sizes than females. The smallest mature males from the northern African waters measured 170 to 180 mm mantle length, while the smallest mature females were 200 to 210 mm mantle length. These sizes are comparatively smaller than those of squids in the Mediterranean Sea and in the North Atlantic Ocean. In the Mediterranean Sea, the smallest mature males measured 196 mm mantle length, but the bulk of the population matures at 230 mm mantle length; females start to mature from 300 mm mantle length onwards. In the North Atlantic, males start to mature at 280 mm mantle length and females (mantle length at 50% maturity between 460 and 480 mm) may remain immature until 500 mm mantle length. Spawning probably occurs throughout the year on the continental slope, with pronounced seasonal peaks that occur in late winter or early spring off northern Europe and North Africa, and between September and November in the western Mediterranean Sea (Catalan Sea and Balearic Islands). Spermatophore length varies depending on male size and geographic area; comparatively larger spermatophore sizes of 48 to 54 mm occur in squid from the Catalan Sea (western Mediterranean Sea), followed by North Atlantic males (38 to 44 mm) and North African populations (20 to 29 mm). Egg sizes also vary; with the exception of the Irish Sea populations (where mature eggs in female oviducts measure 1 to 4 mm; maximum diameter; preserved material), larger egg sizes are recorded in the North Atlantic and in the Mediterranean Sea (fresh material; 2.4 to 2.6 mm) than in the North African waters (preserved material; 1.0 to 1.2 mm). These differences may be related to the use of fresh material versus preserved samples, but this is not clear without additional observations. As in most ommastrephids, fecundity is high (up to several hundred thousand ova) and varies depending on the size of females; a potential fecundity up to 950 000 eggs was reported for females from northwestern African waters. *Todarodes sagittatus* females decrease feeding activity prior to spawning, and they are likely to undergo the "descending" type of spawning, characterized by intermittent activity, with a decrease of egg number per egg mass, as described for other members of the subfamilies Illicinae and Todarodinae. Spawning occurs in deep waters (200 to 800 m) apparently close to the bottom. No information is available on egg masses and embryonic development, nor are early life stages well known, partly because youngest paralarvae often are confused with or mixed with those of other ommastrephids. Observations on juveniles over the mid-Atlantic Ridge indicate that they are transported by currents and distributed in the upper layer of the water column (50 to 150 m), perhaps descending somewhat deeper during the day. Paralarvae off the North African coastal waters rise to the subsurface layers over the slope to forage, then they migrate later to the shelf edge as juveniles. Growth rate is high, especially in the early life phase, then slows with the onset of sexual maturity. A life cycle of about 1 year or slightly more is estimated based on statolith analysis after indirect validation, but a longer life span (from 1 and a half to 2 years) is considered likely for animals larger than 500 mm mantle length. Geographical area and environmental conditions *sensu lato* also may affect age and growth. A 600 mm mantle length female (plus several other specimens larger than the normal median size of 300 mm mantle length) was caught in the waters off Sardinia, central Mediterranean. Such records indicate that *T. sagittatus* in the Mediterranean can reach sizes comparable to the maximum reported size of the species in the North Atlantic waters. The peculiar small modal sizes of mature squid (250 to 300 mm mantle length) of the North African population off western Sahara, compared with those of their northern counterparts (350 to 420 mm mantle length), is thought to be caused by early maturation and subsequent decrease of somatic growth rates.

Todarodes sagittatus feeds on fishes, crustaceans and cephalopods, in decreasing order of importance; in northern waters the main prey are small herrings (*Clupea harengus*) and cod (*Gadus morhua*). In turn, it is preyed upon by several top-level predators, such as tunas, swordfish, sharks, seals and cetaceans, both dolphins and whales, for which, in some species, *T. sagittatus* constitutes the most important food item. This is particularly relevant since *T. sagittatus*, along with *Illex coindetii* and *Todaropsis eblanae*, is the most important paratenic host for Anisakid nematods. A better understanding of parasitic transfer and parasite-induced diseases through the food web will aid the management of marine resources in general, as well as the safer human consumption of raw marine products in particular.

Interest to Fisheries: *Todarodes sagittatus* currently is taken mainly as a bycatch of trawl fisheries, but it may occur in sufficient densities in Norway to support a moderate, targeted fishery. In the Mediterranean, the main fishery is conducted by Italian vessels. A seasonal targeted fishery occurs during summer in southern Italy by commercial as well as sport fishermen; here, as in some other Mediterranean countries, the commercial value of this species is relatively high, although the flesh of large individuals is described as tough. This squid is consumed fresh or boiled and also it is marketed frozen, salted or dried, and it is used as bait in the cod and halibut fisheries. Apart from large-scale predation on commercial finfish species, occasionally it has been considered a nuisance because of its competition with finfishes in the baited hooks (long line) fisheries. Common fishing methods other than trawling are jigging and purse seining. Separate fishery statistics do exist, but the quality of fishery data reporting on this species is poor, since *T. sagittatus* often is mixed in catches with other short finned squid species.

Local Names: CYPRUS: Thrapsallo; FRANCE: Calmar; GREECE: Kalamari; ITALY: Totano viola, Totano selvaggio; JAPAN: Hokkaisurumeika, Taiseiyosurume, Yoroppasurumeika; MALTA: Totlu bajdani; MOROCCO: Passamar; RUSSIA: Kalmar; SPAIN: Pota; YUGOSLAVIA: Lignjun.

Remarks: Observations on several population parameters, along with peculiarities in the open-water distribution and certain morphological-ecological traits, support the existence of different populations in the Atlantic Ocean and the Mediterranean Sea (e.g. Nigmatullin, 1989b, Borges and Wallace, 1993, Borges, 1995, Nigmatullin *et al.*, 2002b). Further studies and observations are required, especially considering that such morphological and geographical differences are considered definitive at a subspecific level by some authors (i.e. Nigmatullin and Laptikhovskiy, 1999). Mass strandings of the species have been observed in several areas of its distribution, e.g. Iceland, Scotland, Italy, but no sound explanation for these events is available to date.

Literature: Mangold-Wirz (1963), Clarke (1966), Wiborg and Gjørseter (1981), Roper *et al.* (1984), Shimko (1984), Wiborg and Beck (1984), Guerra (1992), Piatkowski *et al.* (1998), Quetglas *et al.* (1998), Arkhipkin *et al.* (1999), Belcari (1999g), Lordan *et al.* (2001a), Nigmatullin *et al.* (2002b), Cuccu *et al.* (2005), Hastie *et al.* (2009).

Todarodes angolensis* Adam, 1962*Fig. 309**

Todarodes angolensis Adam, 1962, *Memorias da Junta de Investigações do Ultramar*, 2(33): 9–64, 2 pls. [32, text-fig 4, pl 2, figs 1–3]. [Type locality: Baía dos Elefantes, Angola, eastern South Atlantic Ocean].

Frequent Synonyms: None.

Misidentifications: *Todarodes sagittatus* Sanchez (1981, 1982, 1988), Sanchez and Moli (1984).

FAO Names: **En** – Angolan flying squid; **Fr** – Toutenon angolais; **Sp** – Pota angolense.

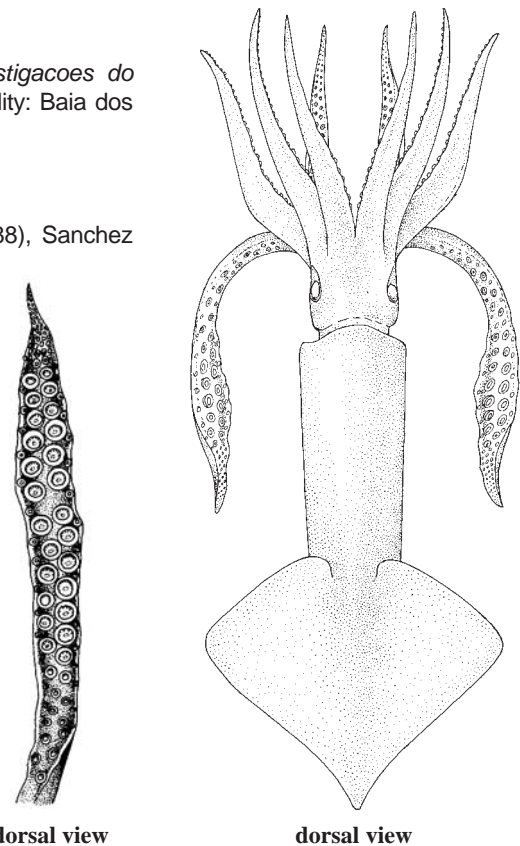
Diagnostic Features: Mantle cylindrical, typical for *Todarodinae*, fins sagittate. **Funnel groove with foveola, no side pockets**; no light organs on viscera. Carpal area of club very short; **4 pairs of suckers only (only 2 pairs in *Todarodes filippovae*; 10 to 12 in *T. sagittatus*)**; **medial manus sucker rings with 13 to 16 long, pointed teeth**; **largest sucker diameter <2.6% mantle length**; **manus with 14 to 18 quadriserial sucker rows**. Tentacular suckers in 4 rows; large sucker rings with 14 to 17 conical teeth alternating with square plates. Arm sucker rings with large distal teeth alternating with very small teeth; distal 40% of **right arm IV of male hectocotylized** with suckerless, thick pedicels nearly completely connected by the ventral protective membrane; dorsal row of pedicels flattened. Body dark purplish brown in colour.

Size: Large-sized squid; maximum mantle length 433 mm in females.

Geographical Distribution: Eastern South Atlantic Ocean, south of 13°S; occurs around South Africa and reaches into the Indian Ocean. Limits unknown (Fig. 310).

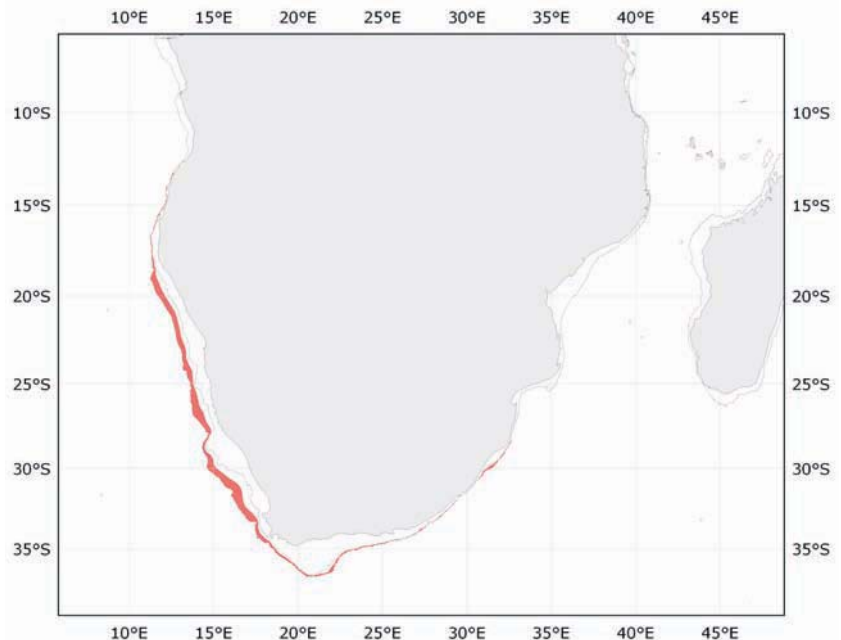
Habitat and Biology: On the South African continental slope, *T. angolensis*, along with *Todaropsis eblanae*, is an indicator species for the upper slope benthic habitat, from 300 to 500 m. During daylight adult squids occur only near the bottom, whereas juveniles occur in the water column but avoid the surface layer. At night, adult squids are dispersed throughout all the horizons except the surface layer, and juveniles are concentrated in the upper 60 to 80 m layer. Generally speaking, however, young squid prefer epipelagic waters, a habitus also reported for the Mediterranean *T. sagittatus*. The sex ratio in the studied population of Namibian waters shows a clear predominance of females, as observed for the congener species *T. sagittatus* in other areas, a phenomenon explained by several authors with the assumption that

females and males inhabit different grounds and depths except during the mating/spawning seasons. The smallest mature male measured 240 mm mantle length; the smallest mature female 250 mm mantle length. However, observations on the length and indices of the nidamental glands, the size-range of immature females (not exceeding 350 mm mantle length) and the presence of spermatangia on the buccal membrane of females of 300 mm mantle length, suggest that 300 to 350 mm is the size range corresponding to the onset of sexual maturity in the population. Southern Hemisphere spring (e.g. October to December) is the period of greatest abundance of maturing and mature squid. Growth studies based on statolith analysis indicate that the life span is about 1 year; however, a longer life span is possible, as hypothesized for its northern congener *T. sagittatus*. Growth



dorsal view

dorsal view

Fig. 309 *Todarodes angolensis***Fig. 310 *Todarodes angolensis***

Known distribution

rates are subject to considerable individual variation and highly related to the environmental variability in the northern Benguela Upwelling System. The species feeds opportunistically on a variety of fishes and it is known to prey upon the Cape hake, *Merluccius capensis*, in the northern Benguela Current. In turn, it is preyed upon by several fishes, sharks and marine mammals, for some of which it constitutes the most common food item.

Interest to Fisheries: Currently there is no directed fishery for this species. It is caught as bycatch in otter trawl fisheries, but separate statistics are not reported.

Local Names: None available.

Remarks: The history of the nomenclature of *T. angolensis* and its congener, *T. filippovae*, was outlined by Roeleveld (1989). *Todarodes angolensis* was first described by Adam (1962) as a subspecies of the northeastern Atlantic Ocean *Todarodes sagittatus* (Lamarck, 1798) and raised to the status of full species by Nesis (1973). In 1975, Adam described *T. filippovae*, on the basis of the specimens first recorded by Filippova (1968b) from the southern Indian Ocean and originally identified as *T. sagittatus angolensis*. Subsequently, Nesis (1979c) synonymised *T. filippovae* as described by Adam (1975) with *T. angolensis*, on the basis of other specimens from the Australia-New Zealand region (2 immature females and 1 juvenile). Afterwards, Russian scientists referred all *Todarodes* (adults and paralarvae) caught in Southern Hemisphere waters to *T. angolensis*. Therefore, the species is reported to occur from off New Zealand, the Auckland and Campbell Islands and in the area west and south of Tasmania. However, this synonymy was not generally accepted and other cephalopod systematists continued to treat the 2 species as distinct taxa (e.g. Okutani, 1980, 1990, 2005, Roper *et al.*, 1984, Dunning and Brandt, 1985). Further morphological and genetic studies fully supported the separation of the 2 species (e.g. Dunning and Wormuth, 1998, Roeleveld, 1989, Yokawa, 1994), which are clearly associated with different water masses in the Benguela system (Roeleveld, 1989). Okutani (2005), considered *T. angolensis* restricted to the South African coastal waters, while *T. filippovae* has a circum-subantarctic distribution. We support this view; however, further studies and observations are necessary to help clarify the status of the distribution of *Todarodes* species in the Southern Hemisphere. Special attention is necessary when species distribution is based on identification of stomach contents: due to the potential overlapping of *Todarodes* species in the area, identification to species level from beaks remains, especially in absence of flesh, must be considered with caution.

Literature: Adam (1962), Nesis (1973, 1979b), Roper *et al.* (1984), Roeleveld (1989), Villanueva and Sanchez (1989), Dunning and Wormuth (1998), Okutani (2005).

***Todarodes filippovae* Adam, 1975**

Fig. 311

Todarodes filippovae, Adam 1975, *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 50(9): 1–10. [3]. [Type locality: 35–38°S, 66–77°E, southern Indian Ocean].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Antarctic flying squid; Fr – Toutenon antarctique; Sp – Jibia antártica.

Diagnostic Features: Mantle muscular, long, narrow (width 16 to 24% of mantle length); tapers to a pointed tail. Fins saggittate; length and width about 50% of mantle length; single fin angle about 30° to 35° (60° to 70° both fins). Tentacles very large and robust. Clubs very expanded occupying nearly entire length of tentacles; only 2 pairs carpal suckers at base of club (4 pairs in *Todarodes angolensis*; 10 to 12 pairs in *T. sagittatus*); medial manus sucker rings with 7 to 13 long, pointed teeth; largest sucker diameter 2.7 to 4.5% mantle length manus with 12 to 14 quadriserial sucker rows. Arms relatively short; sucker rings with 10 sharp teeth; right

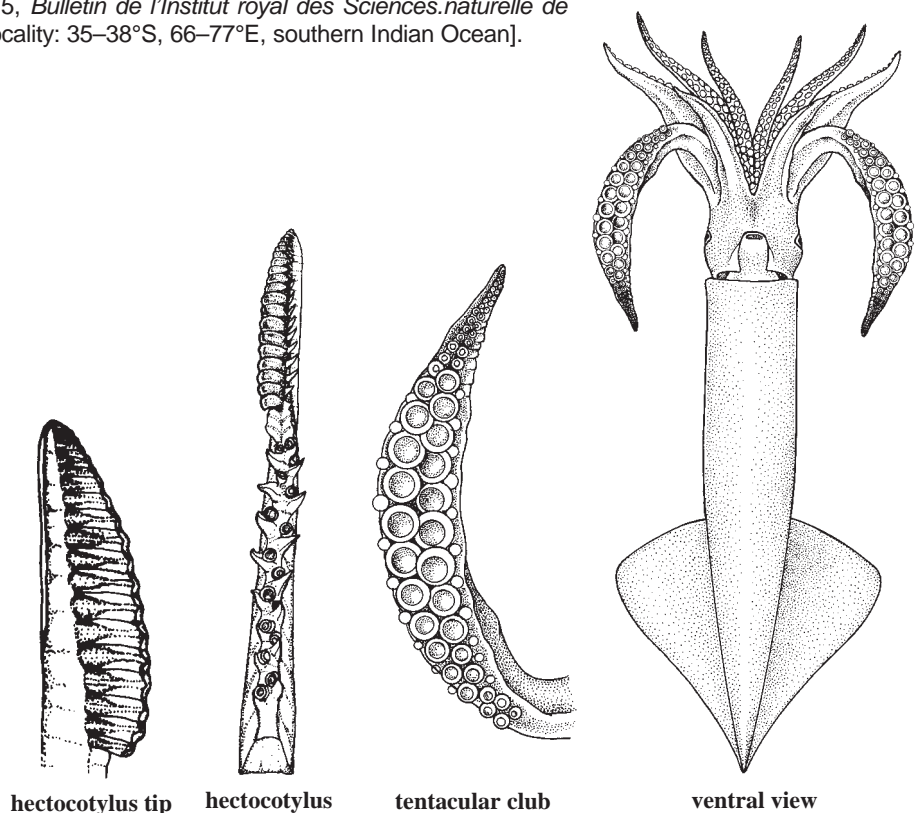


Fig. 311 *Todarodes filippovae*

arm IV hectocotylized along the distal 21 to 36% (up to distal 60%, Dunning, 1993) of the arm, with suckers transformed to papillae and tubercles, with the ventral protective membrane and trabeculae very expansively developed.

Size: Large-sized squid; maximum reported size 540 mm mantle length, 4.7 kg for a female, about 400 mm mantle length for males; common between 200 and 400 mm mantle length.

Geographical Distribution: Circumpolar in the Southern Ocean; south of approximately 35°S; common in the Antarctic Convergence zone. The northernmost occurrence of the species is the record of 2 juveniles caught at 16°46' S, close to the economic zone of Peru, most likely as a result of the Peru Current transportation (Fig. 312).

Habitat and Biology: An oceanic species, *Todarodes filippovae* extends from the surface to about 1 200 m depth; it inhabits open waters or slope locations, very rarely, if ever, extending over the continental shelf. With the exception of the low velocity Peru Current off the southeastern Pacific coast of South America, all other areas where the species has been collected are associated with high velocity current systems, i.e. the Antarctic Circumpolar Current, the Falkland Current, the Benguela Current and the East Australia Current.

Positive links between species life cycles and these high velocity systems are likely to occur, both in the transport of planktonic eggs and paralarval stages, as well as in the adult feeding ecology, as already described for other ommastrephids (e.g. *Illex argentinus*).

No clear relationship is apparent between the species distribution and water temperature: *T. filippovae* is found associated with cold, Antarctic Intermediate Water (3° to 3.8°C), as well as warm superficial streams (up to 24°C). These observations suggest the presence of either a cryptic complex of species with different temperature requirements or a single, eurythermal species. While the species is widely distributed in the Southern Hemisphere, most information on its biology comes from the Tasman Sea (southern Australia) and South Africa. In Australian waters during summer *T. filippovae* occurs from central New South Wales to southwestern Western Australia and it is the most abundant ommastrephid squid in the subtropical convergence zone of the Tasman Sea and in the slope waters along the southeastern Australian coast. Juveniles as well as large adult individuals are most abundant in the upper, surface layer of the water column, where they are caught by jigs and driftnets in surface water temperatures between 11.5° and 24.7° C and at 250 m between 9.7°C and 11.9°C. No mass migration in a north-south direction nor across the Tasman Sea has been observed. However, mature specimens of both sexes move to the continental slope waters during summer months, prior to spawning. The spawning season occurs between December and August. Mature males represent a higher proportion of the population off southern New South Wales (38° to 32° S), suggesting that mating and spawning probably occur towards the northern boundary of the species distribution in this area. Spermatophores are evident in males at 260 mm mantle length, and at 320 mm mantle length all males have fully formed spermatophores. The smallest mature female observed with eggs in the oviduct was 380 mm mantle length. Observations from South African waters suggest a similarly long spawning period (February to August). Also, data on specimens from stomachs of commercially caught sperm whales off Durban suggest that these squid spawn off the southeast African coast. Few data exist on early life stages and rhynchoteuthion paralarvae are unknown. A few juveniles between 40 and 80 mm mantle length were caught off eastern Tasmania during midaustral summer and juveniles of unreported length were collected in the southern Pacific in autumn. Growth is rapid, as in most ommastrephids, with females generally growing faster than males and reaching larger sizes, while males mature earlier. Based on estimated growth rates of the summer Tasman Sea population, as well as on assumed daily periodicity in statolith increments, the life cycle is about 1 year or slightly more. In contrast with other ommastrephid species, but similar to its congener *T. angolensis*, *T. filippovae* appear to grow faster in cooler oceanographic conditions. The species feeds on fishes, crustaceans and cephalopods. Crustaceans dominate in the diet of smaller squids (< 200 mm mantle length), while cephalopods are the more abundant prey items in stomachs of larger squids (>200 mm mantle length). In turn, *T. filippovae* is preyed upon by several fish species and top predators such as seals, albatrosses and sperm whales. Adults of this species may be infested with large numbers of encysted nematodes and cestodes in their mantle tissue.

Interest to Fisheries: This species is taken as bycatch to the jig fishery for *Nototodarus sloanii* off New Zealand and southern Australia; also it is caught as bycatch by trawlers around most of its distributional range. Listed among the 6 most abundant squid species in the South West Atlantic, it has been reported among the jig catches off the Falkland Islands, but there are no records of the species in the *Illex argentinus* or *Loligo gahi* squid fisheries on the shelf around the Falkland Islands since the establishment of the Falkland Islands Government Fisheries Department in 1987. Defined as 1 of the 2 “encroaching species” (along with *Martialia hyadesi*) of the targeted ommastrephid fisheries in the in the Southern Hemisphere, *T. filippovae* likely is a candidate for future exploitation.

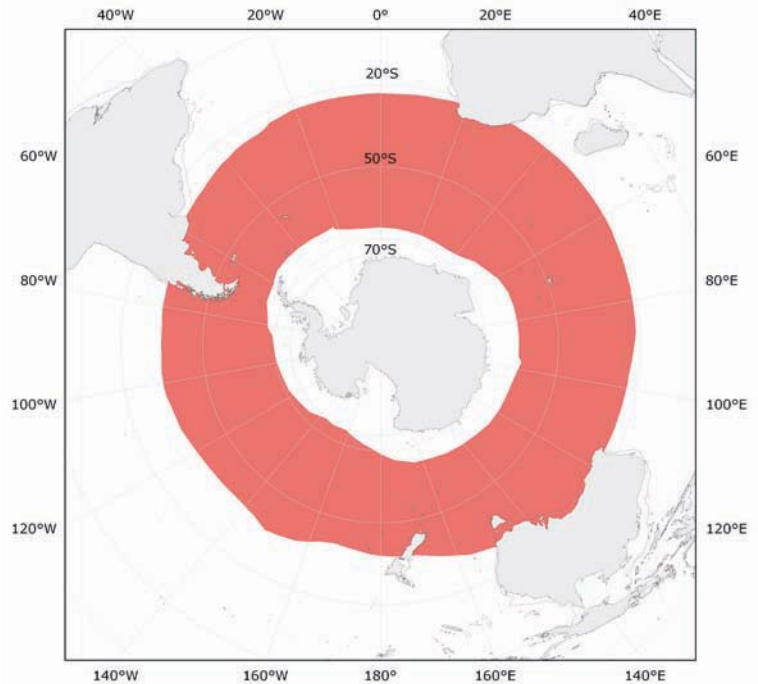


Fig. 312 *Todarodes filippovae*

Known distribution

Local Names: AUSTRALIA: Southern Ocean arrow squid.

Remarks: *Todarodes filippovae* was described by Adam (1975), on the basis of specimens from the southern Indian Ocean originally identified as *T. sagittatus angolensis* by Filippova (1968b). Subsequently, Nesis (1979b) synonymised *T. filippovae* with *T. angolensis*, and most Russian scientists then referred all *Todarodes* (adults and paralarvae) caught in Southern Hemisphere waters to *T. angolensis*. Therefore, many records of *Todarodes* squid off New Zealand, the Auckland and Campbell Islands and in the area west and south of Tasmania were considered to belong to *T. angolensis* (e.g. Korzun *et al.*, 1979, Nesis, 1979b, 1982, 1987). However, this synonymy was not widely accepted by the cephalopod community and other cephalopod systematists continued to treat the 2 species as distinct taxa (e.g. Okutani, 1980, 1990, 2005, Roper *et al.*, 1984, Dunning and Brandt, 1985). Additional morphological and genetic studies fully support the separation of the 2 species (e.g. Dunning and Wormuth, 1998, Roeleveld, 1989, Yokawa, 1994), which are clearly associated with different water masses in the Benguela system (Roeleveld, 1989). Okutani (1980), considered *T. filippovae* to have a circumsubantarctic distribution, potentially overlapping with that of *T. angolensis* in southern Africa waters. We support this view, while recognizing that further studies and observations are necessary to help clarify the status of the *Todarodes* species distributions in the Southern Hemisphere. Because of its broad circumpolar distributional range and the propensity for crypsis among ommastrephid and loliginid squid (e.g. Smith *et al.*, 1981, Brierley *et al.*, 1993, Yeatman and Benzie, 1993), possibly more than one species is represented by *T. filippovae*. For example, Roeleveld, (1995) suggested that *T. filippovae* from off Chile is a distinct species. Consequently, the entity currently identified as one species, possibly represents a *T. filippovae* species complex (Rodhouse, 1998).

This species may prove to be important in the circumpolar Antarctic ecosystem, both because of its abundance and its trophic links with other organisms, as already evidenced for some areas of the distribution (e.g. the Benguela system Lipinski, 1992). When a fishery develops for this species, fundamental research focused on precise specific/subspecific/populational identification and stock structure will be required. Also, considering the role of *T. filippovae* in the food web, any future fishery will need to be rationally managed so that prey/predator relationships are not negatively impacted.

Literature: Adam (1975), Nesis (1979b), Roper *et al.* (1984), Dunning and Brandt (1985), Dunning (1998c), Roeleveld (1989), Dunning and Wormuth (1998), Rodhouse (1998), Jackson *et al.* (2007a).

***Todarodes pacificus* (Steenstrup, 1880)**

Fig. 313

Ommatostrephes pacificus (Steenstrup, 1880). *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1880: 73–110, 12 figs, 1 pl. [79]. [Type locality: Hakodate, Japan, western Pacific Ocean].

Frequent Synonyms/Misidentifications: *Ommatostrephes pacificus* Steenstrup, 1880: 79, fig. 5 (misspelling); *Ommastrephes sloani pacificus* Sasaki, 1929; *Nototodarus philippinensis* Voss, 1962a (= *N. hawaiiensis* (Berry, 1912)); *Todarodes pacificus pacificus* Dunning, 1988a.

FAO Names: En – Japanese flying squid; Fr – Toutenon japonais; Sp – Pota japonesa.

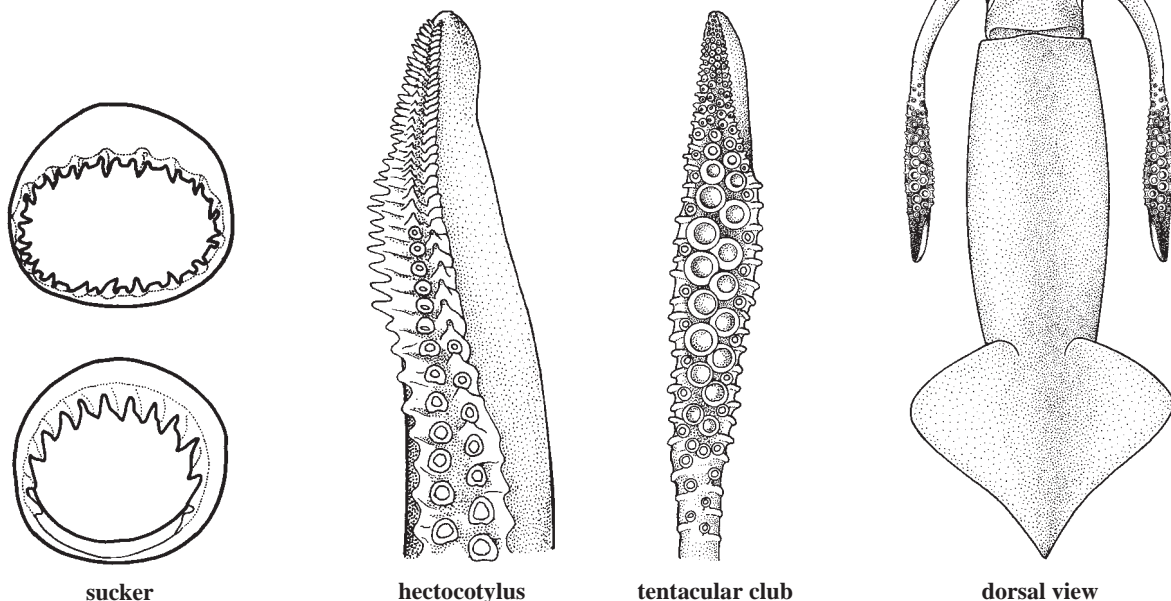


Fig. 313 *Todarodes pacificus*

Diagnostic Features: Mantle cylindrical, slender, moderately muscular, with abrupt taper in the caudal area; fins short, rhombic, sagittate; fin length 35 to 45% of mantle length. Head large, only slightly narrower than mantle width. Mantle element of inverted T-shaped locking apparatus with straight ridge; no muscular fusion to funnel element of locking apparatus; funnel groove present with foveola but no side pockets. Arms subequal and long, the longest slightly less than half the mantle length; swimming keels well developed; largest arm sucker rings with 9 to 11 sharp, subequal, then somewhat flattened, teeth that gradually diminish in size to the smooth proximal rim; protective membranes and their supports (trabeculae) of uniform height, not higher than suckers. Only the **right ventral arm (IV) is hectocotyized in males**; right arm IV slightly thicker and shorter than left arm IV; 44 to 48 normal arm suckers present proximally; approximately 20 pairs of trabeculae present in the modified distal section that form an undulating spatula on the dorsal edge; the hectocotyized portion on the distal arm IV represents about 30% of the total arm length. Tentacular club long, expanded. Medial suckers on the tentacular club manus in 6 to 8 tetraserial, transverse rows; largest medial manus sucker rings with 16 to 28 moderately large, subequal, conical teeth interspersed with low, horny plates. **Light organs absent.** **Colour:** dorsal mantle brown with a distinct, deep blue-black stripe along the dorsal midline of the mantle that broadens on the dorsal surface of the head and extends anteriorly as thin stripes along the aboral edges of dorsal and dorsolateral arms (I and II). Rhynchoteuthion paralarvae have no ocular or visceral photophores; chromatophores on the ventral surface of the mantle are in 3 transverse rows of 4, with a single row of 2 at the posterior tip; a single small chromatophore lies at the posterior end of the dorsal mantle between the bases of the very small fins. The length of the proboscis usually is slightly longer than the longest arms, and the 8 minute suckers on the tip of the proboscis are nearly equal in size. The division of the proboscis begins at about 4 mm mantle length and the tentacles usually are separate 7 to 9 mm mantle length, occasionally up to 15 mm mantle length.

Size: The maximum mantle length of *Todarodes pacificus* is reported to be 500 mm, commonly 300 mm in temperate Japan, less than 200 mm off Hong Kong and in the South China Sea.

Geographical Distribution: This nerito-oceanic species is widespread in continental shelf and upper slope waters of the northwestern Pacific Ocean, from north of Japan into the Sea of Okhotsk at 52°N (reported to 60°N) and in the North Pacific to 49°N, eastward into the open Pacific to the region of about 45°N 170°E. The distribution continues southwestward through the western North Pacific, the Sea of Japan and the East China Sea to Hong Kong to around 18° to 19°N. Rarely, the species occurs in the eastern North Pacific to the northern coast of Canada, its northernmost record (Fig. 314).

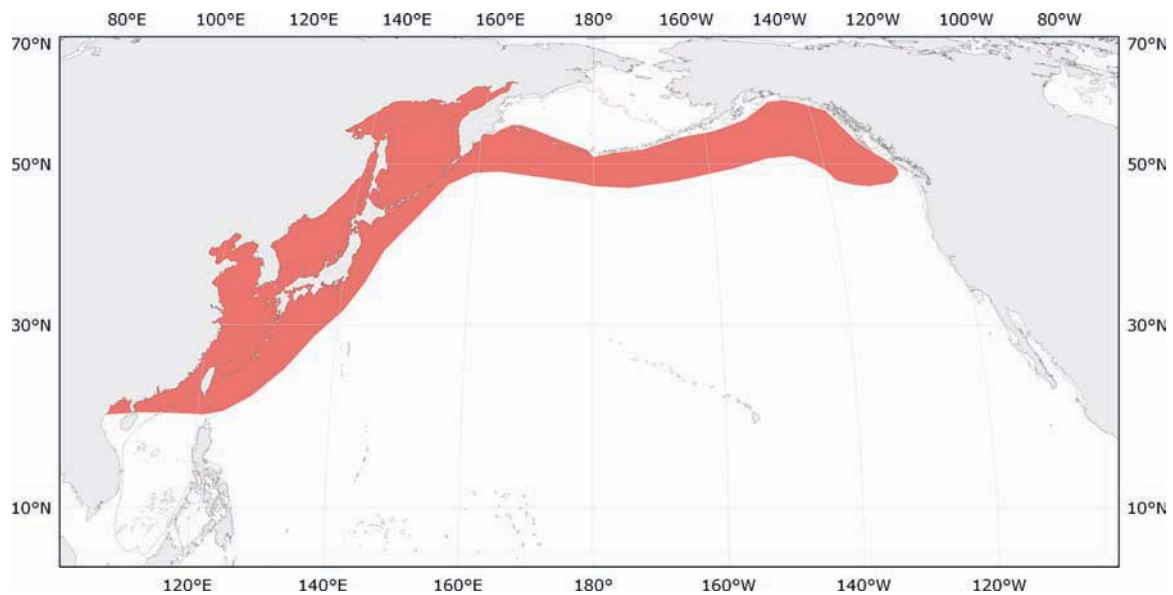


Fig. 314 *Todarodes pacificus*

■ Known distribution

Habitat and Biology: *Todarodes pacificus* is a nerito-oceanic species in the low boreal to subtropical realm in the western North Pacific Ocean. It is a species characteristic of the high-velocity Western Boundary Current System with its nutrient-rich upwellings and vertical mixings in the continental shelf-slope zone. It inhabits the zoogeographic shelf provinces designated as north Japanese, south Japanese and Indo-Malayan. Populations are highly migratory and occur in large aggregations around oceanic fronts, seamounts and gyres where food is abundant. Three subpopulations, cohorts or stocks, defined by their spawning season, are recognized. The winter spawning population, with its centre of distribution north of 45°N, spawns from December to April, and the summer spawning population spawns from April to August. The autumn population usually is located south of 44°N and spawns from April to December.

The diel vertical distribution follows a typical nerito-oceanic species pattern. Both males and females inhabit the midwaters and near the bottom during the day, where they descend to or close to the bottom to feed on benthic and epibenthic prey at 150 to 200 m. At night the population ascends the water column to the upper 50 m and even to near the surface, principally to feed. While mating behaviour occurs above the bottom in midwater, the females descend to the bottom to rest, then to spawn on the

continental shelf and upper slope at depths of 100 to 500 m. The sex ratio in exploited stocks is females greater than males, to a small degree. Sexual maturity in males usually occurs 4 to 6 months earlier than it does in females, so the males are considerably smaller at maturity than the females. Generally, females are slightly larger than the males.

Size differences occur between different geographical areas. The size at maturity for the summer spawning population is 230 to 270 mm mantle length, and that for the winter and autumn spawning populations is 240 to 330 mm mantle length. In immature females the GSI is <1.0% and m is <0.21; maturing females have a GSI of 1.0 to 2.6% and an m of 0.21 to 0.29, and mature females have a GSI of >2.6% and an m of >0.29. Oocyte development is asynchronous. Spermatophores are among the smallest in the Ommastrephidae, second only to those of *Ornithoteuthis antillarum*.

In situ field observations and laboratory experiments have led to the proposal of a working hypothesis for the reproductive strategy of *T. pacificus*. Eggs are laid into a gelatinous, balloon-shaped, nearly neutrally buoyant mass where they develop at 15 to 23°C for 4 to 9 and a half days. Hatchlings develop in water temperatures of 17° to 23°C. Spawning occurs on the bottom of the continental shelf and upper slope, where bottom trawls frequently collect exhausted, spent females at 100 to 500 m depth. *Todarodes pacificus* belongs to the offshore type ("type *Illex*") of reproductive strategy, which is evolutionarily less advanced than the oceanic strategy ("type *Sthenoteuthis*"). Adult females of the offshore type have specific potential fecundity and growth rate characteristics that define their strategy as r-strategists: shelf-living species with very small eggs (0.70 to 0.95 mm); oocyte stock (fecundity) production is continuously asynchronous, where several egg masses are spawned intermittently over a period of time (also called pulse or batch spawning) and subsequent egg masses contain about the same number of eggs, rather than continuously diminish. These females continue to feed and grow during the intermittent spawning process, and they stop feeding only when an egg mass is being spawned; they do not undergo a gelatinous degeneration of muscular tissue, e.g. of mantle, arms, etc. The fecundity in the oviducts of pre-spawning females is between 320 000 and 470 000 ripe ova. Total fecundity, however, is much greater, because oocytes in all stages of development, from yolkless to mature stages, occur in the ovary of spawning females. Exhausted females with thin mantles have ovaries and oviducts that comprise 28% of the total body weight. Post-spawning, dead females have oviducts that still contain many ova, indicating that many more ova are produced than are laid. The reproductive strategy of male *T. pacificus* belongs to the "intermediate type" that is characterized by increased volumes of Needham's sac and of the seminal reservoirs of spermatophores to insure the maximization of effective sperm production.

Mating and spawning have not been observed in nature, but a series of experiments and observations in the laboratory have been successful in defining these behaviours. Immature squid were captured in inshore waters off southern Hokkaido, Japan, and maintained in a large tank, where their maturation, mating and spawning were recorded. Males matured earlier than females, and they began mating with immature females about 2 to 3 weeks before the females matured, with ripe ova in their oviducts; after mating, the females spawned, then died. To mate, the male approaches the female rapidly from below and behind, grasps her around the head and mantle with his arms and tentacles; the hectocotylus (right arm IV) picks up a bundle of spermatophores as they are passed from the funnel opening, then quickly and firmly inserts them into the buccal membrane of the female. The spermatophores penetrate into the membrane tissue, now free of the ejaculatory apparatus, and the resulting sperm bulbs, or spermatangia, transfer spermatozoa into the seminal receptacles that encircle the buccal membrane of the female. Spermatozoa remain viable for several weeks until spawning takes place. In captive experiments females stop feeding and move to the bottom of the tank to rest about 2 days before spawning. The female supports herself on the bottom with the tips of the second and third pairs of arms, the tentacles and the posterior tip of the mantle. Once the female is at rest, the chromatophores begin to flash rapidly over the entire surface of her body, a signal that spawning is about to occur. While eggs have not been found in the natural habitat, eggs taken from the ripe ovary measure 0.78 mm in greatest diameter and 0.75 mm in smallest diameter, and up to 0.90–0.92 mm by 0.77–0.80 mm. Eggs are laid in a large gelatinous ball, up to at least 800 mm in diameter.

Just prior to spawning, the arms become flattened and lowered for about 1 minute, then they open gradually to envelop the small egg mass that is extruded through the funnel. The egg mass gradually swells into an enlarged mass, similar to a balloon being inflated, nearly neutrally buoyant, and requires about 7 minutes to be completed and then to be released and float near the surface. The external surface of the egg mass is formed by a thin layer of gelatinous, water-soluble mucosubstance, secreted by the nidamental glands, while the interior is another type of jelly with fibrils, an insoluble fraction of mucosubstance, presumably secreted by the nidamental glands (or the oviducal glands). The external layer serves as a protective shield that prevents crustaceans, protozoans and bacteria from invading and infecting the interior and the eggs and embryos. The mass contains about 200 000 eggs, each about 0.9 mm in diameter; greater than 90% of the eggs are fertilized. The chorion around each egg swells its diameter to 1.9 to 2.3 mm.

Paralarvae hatch in 4 to 6 days at 18° to 19°C and are immediately active, many swimming toward the surface. Once hatching is complete, the egg mass deteriorates. Hatchlings, at 0.95 mm mantle length, feed for about 7 days on the internal yolk until it is resorbed, then they begin to feed on their own, at 1.25 mm mantle length. The vertical distribution of hatchlings and paralarvae is associated with mantle length (age) and a general ontogenetic descent occurs. Most hatchlings (in the Sea of Japan near Oki Island) of less than 1.0 mm mantle length occur at 0 to 25 m; smallest paralarvae, 1 to 2 mm mantle length are concentrated at 0 to 50 m (90%); paralarvae of 2 to 3 mm mantle length (71%) concentrate at 25 to 75 m; and those paralarvae from >3 to 6.7 mm mantle length also occur principally at 25 to 75 m. The temperature range in the zone of capture is 15° to 22.3°C, conditions considered ideal for paralarval survival and development; the pycnocline occurs below 50 m, slightly deeper than the majority of paralarval captures. Largest catches are made in the frontal or mixing zone of cool water from the northwest and warm water in the Oki Strait.

Young juveniles are transported by oceanic currents from their hatching grounds to their feeding grounds. Their early distribution includes most of the waters that surround the Japanese Islands, except off the Pacific coast of northeastern Honshu and Hokkaido and the northernmost region of the Sea of Japan. The geographical and temporal distributions can vary significantly depending on the seasonal brood and the local subpopulation.

Paralarvae and juveniles of the autumn spawning population (the fishery for adults is mainly in the offshore waters in the Sea of Japan) are spawned principally in the area from the eastern East China Sea to the western sector of the Sea of Japan. Autumn-spawned juveniles are densely distributed during October through December, with peak abundance in November, along the west coast of Kyushu. Hatchlings and juveniles of the winter-spawned population (the fishery for adults occurs principally to the south of Kyushu) occur in abundance during November through April in waters to the south of Kyushu. Winter population juveniles are restricted to water temperatures above 18°C and over 19.20 parts per thousand chlorinity, with peak abundance at 20° to 22°C and 19.25 to 19.35 ppt chlorinity.

During the paralarval and juvenile periods, mortality is about 94%, caused by starvation, transport into unfavourable environmental conditions and predation, principally by scombroid fishes and later by tunas. The abundance of juveniles can predict the eventual stock size of adults. The values of strontium to calcium ratios (Sr:Ca) in the statoliths of *T. pacificus* can reveal the different spawning grounds and migration routes of the different populations of squid. Age data from statoliths analysis indicate that growth in *T. pacificus* can be represented by a sigmoid curve. The first 4 months after hatching are a relatively gentle slope, followed by a steep growth rate for the next 3 months and finally by a more gentle curve, to nearly flat, during the final 5 months of life. Growth rates can vary depending on the seasonal population and local environmental conditions, particularly the temperature regime. From hatching to 15 mm mantle length takes 0.5 months, to 120 mm mantle length requires 3 months, to 190 mm mantle length 6 months, and to 260 mm mantle length, about the maximum size, 12 months.

Recent research predicts the short- and long-term fluctuations in stock size by factors of wind stress, air temperature, sea surface temperature (SST), and mixed layer depth (MLD) during the spawning period (weak winds, warm air and SST positively affect recruitment and stock size). The spawning grounds are mapped with SST (19° to 23°C) over water depths of 100 to 500 m and the combination of factors determines stock success and abundance.

Years of poor recruitment correspond closely to years of lower than normal SST in the winter and spring, and cold winters influenced by strong northwesterly winds also are associated with lower recruitment levels. Significant changes in aspects of growth, size and maturity occur between the periods of high stock levels versus periods of low stock level. The mantle lengths of squid taken during the low stock period were smaller during June to early August than those taken during the high population period, but they were larger from mid-September to December. The mean proportions of mature males caught in low stock years sharply increased in mid-August and were consistently higher than the levels during high stock years, and gradually increased from mid-September onwards. Also, the squid matured earlier in low stock years than in high stock years. *Todarodes pacificus* life span is about 1 year.

Predators of *T. pacificus* are numerous, including many species of marine mammal such as the short-finned pilot whale (*Globicephala macrorhynchus*), other toothed whales, baleen whales, northern fur seal, rays, dolphin fish (*Coryphaena hippurus*), chub mackerel, jack mackerel (*Tracurus japaonicus*), skipjack tuna (*Katsuwonus pelamis*).

The prey of subadult and adult *T. pacificus* varies, depending on age and locality, as they tend to be opportunistic feeders, including on fishes and cephalopods when they are available. Juveniles and subadults feed mainly on planktonic crustaceans, notably euphausiids (e.g. *Thermisto* sp.), gastropod larvae, chaetognaths and nectonic fishes, such as Myctophidae, sardines, anchovies (*Engraulis japonica*) and other small species and squids, including cannibalism. Adults prey mostly on nectonic species. When subadults and adults feed along the shelf-slope interface, they prey heavily on myctophid fishes. The feeding rate is greatest at around 18.00 to 20.00 hours, then gradually decreases towards dawn. Adults feed more actively during the daytime near the bottom than they do at night near the surface.

Niche separation occurs when the distributions of 2 ommastrephid species overlap; for example, *T. pacificus* and *Ommastrephes bartramii* are sympatric in some areas of their distributions, but in these areas *T. pacificus* preys on crustaceans, while *O. bartramii* feeds on fishes.

Experiments on the visual attack system of *T. pacificus* showed that attacks on slowly-introduced bait were made by the arms, not the tentacles; this conforms to observations on *Loligo*, *Illex* and *Sepia*. Similarly, slower moving hauling speeds on jigging machines catch more squid because the squid attack and are hooked by the arms, not the more fragile tentacles. Other behavioural experiments on visual discrimination revealed that *T. pacificus* can not discriminate between blue, green or white light. The positive cues for correct responses are intensity of the light, not the colour. This has important consequences for the fishery in eliminating the practice/expense of manufacturing and using coloured-lighted jigs, which are no more effective than white-lighted jigs.

Interest to Fisheries: For more than a century *T. pacificus* has supported a major fishery that nearly always has been in the top 2 or 3 in total annual landings of cephalopods in the world. It is the largest single cephalopod fishery resource over time on record. Fluctuations in landings are attributed to fluctuations in optimal oceanographic conditions as well as to over fishing. Estimates of instantaneous biomass, fishery production and potential catches are informative, both from the current levels as well as from anticipated future production. The estimated instantaneous biomass for *T. pacificus* is 2 to 5 million tonnes.

The fishery for *T. pacificus* has been conducted in Japanese waters for well over a century, and catch statistics have been compiled since prior to 1910. Since that time, fishery biology studies have been conducted, based on catch record analyses and exploratory fishing. The first comprehensive study on the life history of *T. pacificus* with an interest to the fishery was published in 1921. The earlier fishing grounds before the 1940s were centred in the neritic waters along the coasts of southern Hokkaido and northeastern Honshu. Following the second world war the fishery expanded dramatically with the development of technology and gear, the increase in the size of the jigging boats, and the expansion of the fishing grounds. So important were the general fisheries, including the squid fisheries, that at least 8 regional fisheries research laboratories were established in 1948. The fishery access to major concentrations of the squid occurs during the periods of their migrations to, at, and from the feeding grounds. Catches of *T. pacificus* climbed to a maximum of 768 000 tonnes in 1968. Even though new stocks and grounds have been discovered and developed since then, the catches remained in the 300 000 tonne range for many years. During the 1980s the annual catch averaged 267 000 tonnes. Then in the 1990s, with significantly increased effort and improved oceanographic conditions (a shift from a cool to a warm regime), the annual catches began to rise until 1996 when another peak catch was achieved (716 000 tonnes). Catches during the 1990s fluctuated between 280 000 tonnes to the peak in 1996, then dropped to 379 000 in 1998. Since then, through 2007, catches have averaged around 400 000 to 500 000 tonnes.

While purse seine and bottom trawl fisheries are conducted, the major portion of the fishery is conducted from jigging vessels using lights and continuous line jigging machines. Both the size and power of the boats, the intensity of the lights and the efficiency of the machines have increased drastically in recent years. With these increases, the costs of conducting the fishery have risen sharply. The concentration of vessels on the fishing grounds and the intensity of their lights are easily seen from satellites in space, a phenomenon that enables real-time knowledge of the spatial and temporal location of the fleet. This remote sensing technology also allows the repositioning of the fleet into water masses that influence the accumulation of the squid. The biomass of aggregations of squid on the continental shelf edge and the upper slope, as well as on any other potential fishing grounds, can be assessed directly by utilization of the echo integration method following rationalization with normalized target strength measurements and purse seine CPUE data. The fishing concentrations take place in the warm core eddies and streamers that spin off from the Kuroshio Current system at its confluence with the Oyashio Current off the east coast of Japan, as well as in mixed waters of the warm Tsushima Current and cold Liman Current in the Sea of Japan. Warm core rings can be up to 200 km in diameter and have a life span of a few months to 1 to 2 years. The squid fisheries always develop in the warm rings, never in the cold rings, and once started, productive jigging in the ring can last up to 2 months. The large autumn spawning population supports the major offshore fishery in the Sea of Japan. Many years of accumulated data from paralarval surveys show that when paralarval distributions are expanded over a broader geographic range, the resulting adult stock is high; conversely, a more restricted range of paralarval distribution results in a low population size in the adults from that brood. Thus, stock size can be predicted based on the extent of the distribution of the paralarvae that constitutes that year class.

Efforts to employ stock assessment models for management purposes have produced poor or inconsistent results. Clearly, when the spawning stock in any population gets too low, recruitment will be adversely affected. Most efforts at fishery management concentrate on limitation or control of the period and scale of fishing effort in an effort to be consistent with sustainable catch levels. However, in the case of the *T. pacificus* fishery, the prevention of fishing disputes and maintenance of catch prices also are objectives. Prior to 1998 fishing effort control was through vessel licensing. Then the Japanese government introduced a TAC (total allowable catch) system to manage the fishery based on an estimation of the allowable biological catch (ABC). Each of the 2 main stocks (spawning groups; Japan Sea, Pacific) is located in a separate area and fished at a different season (autumn, winter, respectively). Pre-season scientific surveys assess the distribution of the stocks, the number of recruits and specific biological parameters. Catches from previous years are used to calculate the allowable biological catch for the current year.

Squid are eaten in many different preparations as fresh, frozen, dried, fermented, etc. products. *Todarodes pacificus* often is eaten raw by humans as "sashimi" and "sushi", and sometimes the squid are infected with helminth parasites that are pathogenic to humans. These parasites are 3 species of larval anisakid nematodes (*Anisakis simplex*, *A. physeteris* and *Pseudoterranova decipiens*) and 1 species of larval trypanorhynch cestode (*Nybelinia surmenicola*). Humans are not final or definitive hosts of these parasites, but they are considered as accidental hosts. In addition to the importance of squid as human food, it is important as bait for many species of fishes. Researchers have developed an artificial bait produced from the liver (digestive gland) retrieved from the waste products of processed squid. The artificial bait has the same hooking ratio as natural squid, but the bycatch of the artificial bait is much reduced.

Local Names: CHINA: Yat boon yau yue (Japanese softfish); JAPAN: Akaika, Ganzeki, Matsuika, Mugiika, Surumeika, Tonkyu.

Remarks: Despite clear differences in some morphological characters, genetic analyses indicate that the 3 seasonal groups are separate ecological populations that maintain genetic exchange (Kidokoro and Mori, 2004) Also, genetic analyses show that 2 major genetically distinct successive breeding groups exist in the Sea of Japan. One group consists of the squid from the autumn spawning aggregations, while the second group contains squid from the winter, summer and spring spawning cohorts (Kumagai *et al.*, 2006). Analysis of 13 trace elements in squid tissues reveals that concentrations in *T. pacificus* were within international standards for 9 elements. In addition, Co, Zn, Ag and Cd (cobalt, zinc, silver, cadmium) were concentrated in the liver (digestive gland) at high levels (Oikawa *et al.*, 2003). Mitochondrial DNA sequencing suggests that *Nototodarus sloanii* and *N. gouldi* are more closely related to *T. pacificus* than to *N. hawaiiensis* (Wakabayashi *et al.*, 2006). The most effective preservatives for fixing and maintaining paralarval chromatophore patterns and mantle size are 5% hexamine-buffered formalin and 99% ethanol.

Literature: Roper *et al.* (1984), Okutani *et al.* (1993), Nigmatullin and Laptikhovskiy (1999), Kidokoro and Mori (2004), Kumagai *et al.* (2006), Kishi *et al.* (2007), Sakurai and Kishi (2007).

Todarodes pusillus* Dunning, 1988*Fig. 315**

Todarodes pusillus Dunning, 1988b, *Memoirs of the Museum of Victoria*, 49(1):149–157, 4 figs. [149]. [Type locality: 13°48'S, 124°19'E, Timor Sea, northeast Indian Ocean].

Frequent Synonyms: *Todarodes pacificus pusillus* Dunning, 1988b.

Misidentifications: None.

FAO Names: **En** – Little flying squid; **Fr** – Petit encornet volant; **Sp** – Pequeña pota saltadora.

Diagnostic Features: Fin length 25 to 31% of mantle length; largest medial manus sucker rings with 16 to 18 long, pointed teeth interspersed with low chitinous plates; manus with 6 to 8 quadriseriate sucker rows. The mantle is slender, moderately muscular, with abrupt taper posteriorly ventral to the fins; fins very short, small, rhombic; head slightly narrower than the mantle opening; mantle element of T-shaped locking apparatus with straight ridge, no muscular fusion to funnel element; funnel groove with foveola, but no side pockets. Arms subequal and large, the longest slightly less than 50% of the mantle length, with well-developed swimming keels. Largest arm sucker rings with 9 to 11 subequal, somewhat flattened teeth. Right ventral arm (IV) in males hectocotylied, slightly shorter and thicker than left ventral arm IV; 11 to 13 normal proximal arm suckers; about 20 pairs of trabeculae present on modified distal section that form an undulating spatula on the dorsal edge; hectocotylied portion occupies about 45 to 57% of the arm length. Arm I has 12 to 17 suckers. **Colour:** dorsal mantle dark to brown with a distinct blue-black stripe along the dorsal mantle midline that broadens on the head, then extends anteriorly along the dorsal surfaces of arms I and II.

Size: A very small-sized species: the largest female reported is 74 mm mantle length and the largest male is 68 mm mantle length. Maximum size certainly less than 100 mm mantle length.

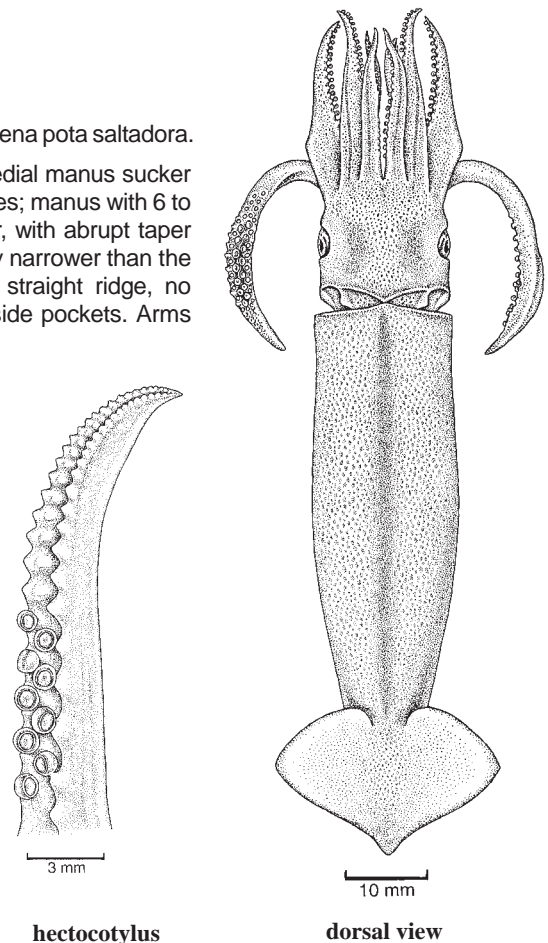
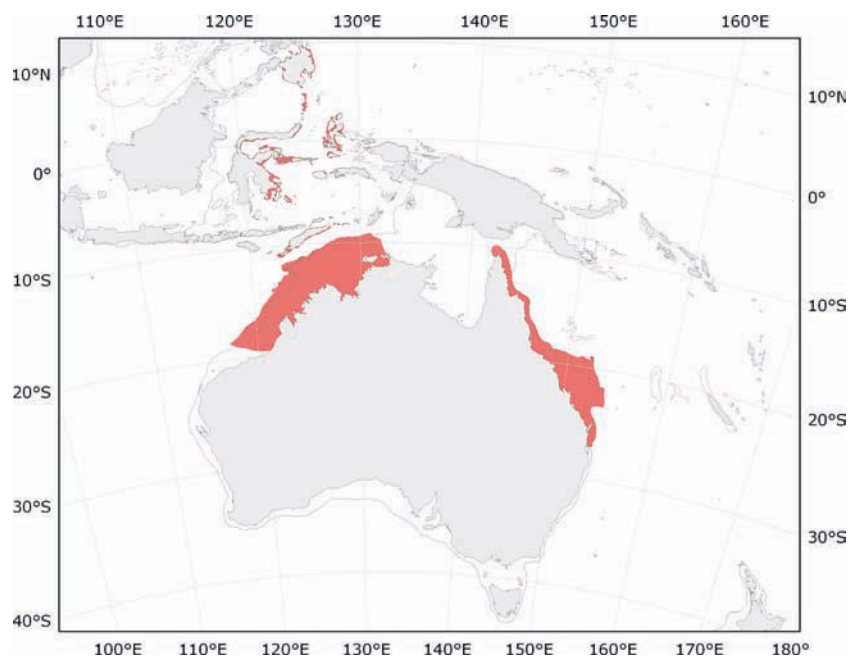
Geographical Distribution: This species inhabits the continental shelf and upper continental slope of northern Australia, from the Timor Sea between 8°53'S and 19°31'S on the Northwest Shelf, and off the east coast of Australia, from the Torres Strait to off Brisbane. It also is reported in a narrow band from the Timor Sea through Indonesian waters to Mindanao in the southern Philippines (Fig. 316).

Habitat and Biology: To date, all recorded specimens were captured in demersal trawls at water depths between 78 and 357 m. The temperature at 50 m in the areas of capture is in excess of 23°C and surface temperatures reach 29°C in summertime. Up to 54 individuals have been caught in a single trawl tow, which suggests that this species is a schooling form. All females larger than 60 mm mantle length are sexually mature, with eggs in the oviducts; all males larger than 50 mm mantle length carried fully formed spermatophores.

Interest to Fisheries: None at present. Currently this species is so poorly known that it is difficult to predict its potential value in a fishery. While it is very small, with a maximum mantle length of perhaps 80 mm, its flesh seems to be a desirable consistency, comparable to juveniles of other *todarodine* species. If large concentrations occur, this species might support a limited fishery.

Local Names: None available.

Literature: Dunning (1988b), Dunning and Wormuth (1998), Okutani (2005).

**Fig. 315 *Todarodes pusillus*****Fig. 316 *Todarodes pusillus***

Known distribution

***Martialia* Rochebrune and Mabile, 1889**

Martialia Rochebrune and Mabile, 1889, *Mission Scientifique du Cap Horn, 1882–1883*, 6(2) (*Zoologie*): H1–H143. [8].

Type Species: *Martialia hyadesi* Rochebrune and Mabile, 1889.

Diagnostic Features: Mantle robust, tapers to a somewhat elongated tail. Funnel groove with foveola possesses 7 longitudinal folds; no side pockets. Photophores absent throughout life cycle. Tentacular clubs occupy almost entire length of tentacles; not expanded. Carpal-locking apparatus absent on tentacular club/stalk. Dactylus of tentacular club with 4 rows of small suckers. Largest medial suckers on manus with 15 relatively large, sharp teeth (1 conical tooth usually larger than others) alternate with 15 small flat plates or blunt teeth. Protective membranes of arms and tentacular clubs low, poorly developed; trabeculae strongly developed, prominent, like cirri. Arm suckers (stalks) attached at bases of trabeculae. Arm suckers proportionally small; rings with 5 pointed teeth in distal half, central 1 conical, lateral ones become truncated; proximal half of ring smooth. Right (rarely left) ventral arm (IV) hectocotylized by papillary type; trabeculae on distal one-third of arm modified as rounded flaps on ventral row; flaps reduced then absent distally on dorsal row. Fins rhomboidal and elongated posteriorly to small tail; fin length 38 to 46% and fin width 54 to 66% of mantle length; fin angle 45° to 55°. The cone flags of the gladius are narrow, with indistinct radial creases in anterior part; greatest width about 50% rachis width. Marginal rigidity ribs of rachis simple; axial rigidity rib of rachis round-rectangular in cross-section. Lateral plates of gladius adhere to dorsal surface of rachis proximally. Distal ends of lateral plates free, form 2 longitudinal lobes above rachis; stem short, anchor-like in cross-section, width greater than thickness. Cone narrow, laterally compressed. Rostrum small, dorsoventrally compressed, curved ventrally. Alveola thick, with ribbed surface. Spermatozoa with 1 flagellum.

Remarks: The genus is monotypic.

***Martialia hyadesi* Rochebrune and Mabile, 1889**

Fig. 317

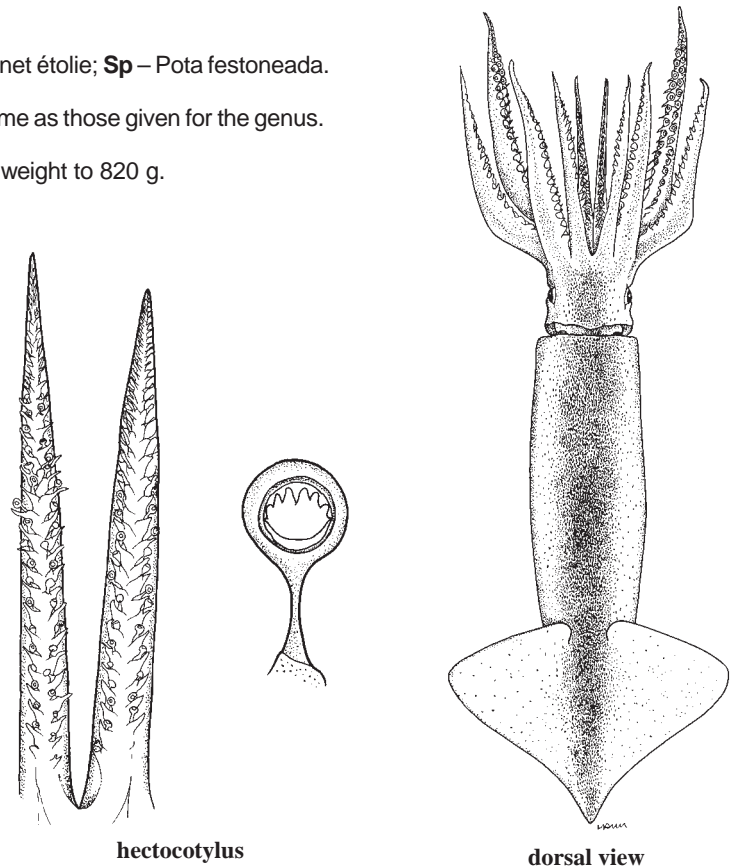
Martialia hyadesi Rochebrune and Mabile, 1889, *Mission Scientifique du Cap Horn, 1882–1883*, 6(2) (*Zoologie*): H1–H143. [H9]. [Type locality: Orange Bay (Isla Navarino), Chile, eastern South Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Sevenstar flying squid; Fr – Encornet étoilie; Sp – Pota festoneada.

Diagnostic Features: Specific characters are the same as those given for the genus.

Size: Maximum mantle length to 400 mm and body weight to 820 g.

Fig. 317 *Martialia hyadesi*

Geographical Distribution: Circumglobal in cool temperate waters of the Southern Ocean; a neritic-oceanic slope species associated with high velocity cool waters of the Antarctic Circumpolar Current, especially along the Antarctic Polar Frontal Zone; southern Patagonian Shelf edge, Scotia Sea, New Zealand waters south of the subtropical convergence zone; sub-Antarctic islands (Fig. 318).

Habitat and Biology: Adults are oceanic-neritic in slope waters, seldom penetrating into waters where bottom depths are less than 200 m. *Martialia hyadesi* is classified as a Notalian-Antarctic species, endemic to the circumpolar zone bounded roughly by the subtropical southern boundary and the Antarctic Polar Front. Small juveniles, less than 10 mm mantle length, have been found in southern New Zealand waters south of the Subtropical Convergence, indicating spawning in the region of the Auckland Island Shelf. Paralarvae and juveniles occur in the Falklands Islands Shelf water mass in spring. The very distinctive tentacular club is evident on juveniles of 19 mm mantle length, while the distinctive arm trabeculae first appear at 40 to 50 mm mantle length. The size of ripe eggs is 0.7 to 2.4 mm and the potential fecundity of 20 000 to 2.5 million. Mature males of 233 to 260 mm have spermatophores 25 mm long with a fecundity of 500. Growth in *M. hyadesi* is characterized by slow juvenile growth (less than 100 mm mantle length), rapid growth in immature squids, and a sharp decrease in growth rate during maturation. The species matures later than other temperate ommastrephids (greater than 270 days), but final maturation is quite rapid, 2 to 3 months. Statolith analysis indicates an age of 12 to 13 months, but other life cycle data suggest a life span that approaches 2 years. In spite of its oceanic habitat, occasionally this species will undergo mass strandings, as occurred in the Falkland Islands in 1997, when more than 3 000 immature *M. hyadesi* (220 to 270 mm mantle length) forcibly drove ashore; 61% were females. Such strandings are believed to be related to temporal shifts in frontal zones that affect behaviour, range and environment of foraging squids. Parasites include a coccidian that occurs in 96.5% of the digestive tracts of the host specimens.

Martialia hyadesi is an active predator with a broad range of prey that includes the hyperiid amphipods, especially krill components (mainly *Euphausia superba*, occasionally *Thermisto gaudichaudi*), mesopelagic fishes (up to 90% myctophids, mainly lanternfishes (*Krefflichthys anderssoni* and *Electrona carlsbergi*) and squids, mainly cannibalism on small juveniles and immatures (20 to 102 mm mantle length). *Martialia hyadesi* is an extremely important prey species for many species of sub-Antarctic vertebrates; it is the most important single prey species for juvenile and adult southern elephant seals (*Mirounga leonina*) and it is preyed upon by the Antarctic fur seal (*Arctocephalus gazella*) and the sub-Antarctic fur seal (*Arctocephalus tropicalis*), the Patagonian toothfish (*Dissostichus eleginoides*) and the slender tuna (*Allothenus fallai*). *Martialia hyadesi* is an important prey for the false killer whales (*Pseudorca crassidens*) and it is important to dominant (up to 89% biomass) in the diets of both adults and chicks of numerous oceanic birds (e.g. grey-headed albatross, black-browed albatross, light-mantled albatross, wandering albatross, white-chinned petrel) and the king penguins (*Aptenodytes patagonicus*).

Interest to Fisheries: While the dominant cephalopod fishery in the southwestern South Atlantic Ocean has been conducted on *Illex argentinus*, for several decades, accumulated data on and assessment of the circumantarctic population of *M. hyadesi* indicate a very significant biomass of this species, with high potential for supporting a managed fishery. Commercial catches generally occur as by catch in the *I. argentinus* fishery in the southwestern South Atlantic Ocean, on the edge of the southern Patagonian Shelf, and catches vary significantly and do not reflect actual population abundance. This is demonstrated by the fact that the estimated annual consumption of this species by known predators in the Scotia Sea is higher than total catches values. An estimation of the instantaneous biomass of *M. hyadesi* is 1 to 3 million tonnes. Acoustical survey techniques offer potential for more accurately assessing stock abundance within proscribed areas. An assessment of stocks in the waters of South Georgia, south of the Antarctic Polar Front, in the austral winter, suggested a potential jig fishery on the stock of feeding *M. hyadesi* (1-year-old mature males, 220 mm to 350 mm mantle length, and the same aged, but immature, females, 212 mm to 370 mm mantle length). Exploratory fishing and predator catch analysis revealed the presence of significant stocks of cephalopods along the Antarctic Polar Frontal Zone in the Scotia Sea. The largest and most abundant species was *M. hyadesi* and mesoscale features suggest this is an area of foraging locations, thus accessible for fishery development. Variations in population structure, distribution and abundance correspond to variations in inter-annual oceanographic conditions in the West Wind Drift; such variations will affect the location, timing and productivity of fishing efforts.

Local Names: None available.

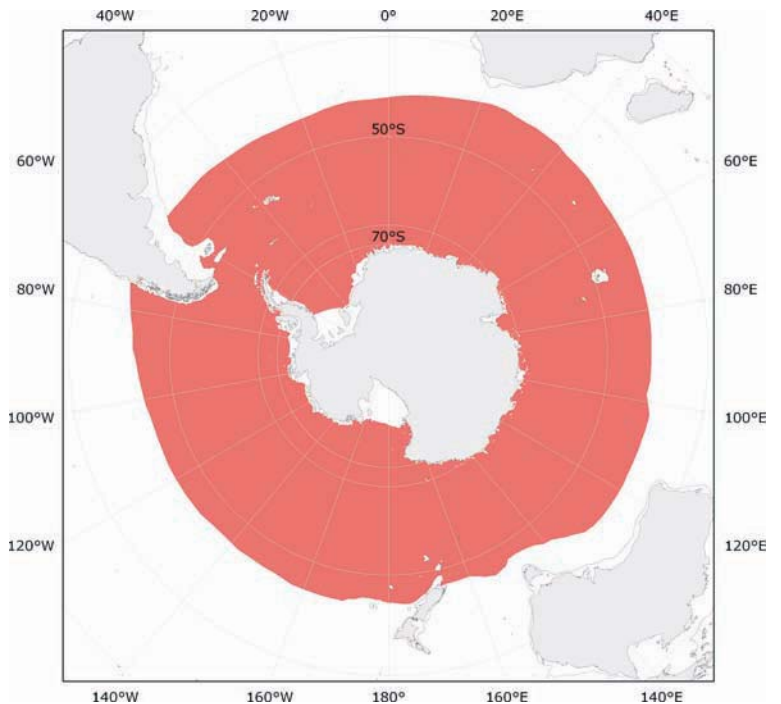


Fig. 318 *Martialia hyadesi*

Known distribution

Remarks: An analysis of systematics and phylogenetic relationships of ommastrephid squids indicates that *M. hyadesi* is in the more primitive range of evolutionary development, more advanced than Illicinae and Todarodinae, but less advanced than the Ommastrephinae (Nigmatullin, 1992 [1991]). Genetic studies indicate considerable genetic differentiation across the circum-antarctic range of the species, suggesting the possibility that sibling or cryptic congeneric entities might exist (Brierley, *et al.*, 1993).

Literature: Rodhouse (1992 [1991]), Nigmatullin (1992 [1991]), Brierley *et al.* (1993), Gonzalez *et al.* (1997b), Lipinski *et al.* (1998b), Wormuth (1998), Anderson and Rodhouse (2001), Nigmatullin (2002a), Nesis (2003), Okutani (2005).

Nototodarus Pfeffer, 1912

Nototodarus Pfeffer, 1912, *Ergebnisse der Plankton Expedition der Humboldt-Stiftung*, 2: 1–815 + Atlas. [434].

Type Species: *Nototodarus sloanii* (Gray, 1849)

Diagnostic Features: The funnel groove has foveola, but it lacks side pockets. Photophores are absent in all life stages. The carpal-locking apparatus is absent on the tentacular stalk. The dactylus of the tentacular club has 4 rows of small suckers. The largest medial suckers on the manus of the club has teeth of equal size, or 1 sharply pointed tooth larger than the other teeth (*N. hawaiiensis*). The protective membranes of the arms and tentacles are normally developed, without exposed trabeculae. Both ventral arms are hectocotylized by the aberrant type, with the right arm modified completely and the left arm partially; at the distal part of the right arm are papillae and in the proximal part of both arms is a very unusual sculptured structure of hyaline integuments. The fins are rhomboidal, slightly attenuate posteriorly; fin length varies between 36 and 50% and fin width between 50 and 61% of mantle length; fin angle is 40° to 57°. The cone flags of the gladius are relatively narrow, with feeble radial creases in the anterior part. The greatest width of the cone flags ranges between 58 and 65% of that of the rachis. Marginal rigidity ribs of the rachis are simple; axial rigidity rib of the rachis is wide, rounded-rectangular in cross-section. Lateral plates of the gladius adhere to the dorsal surface of the rachis by their proximal parts. Distal parts of the lateral plates are free, forming 2 longitudinal flaps above the rachis. The stem is very short, anchor-like in cross-section. The width of the stem is approximately equal to or less than its thickness. The cone is short, narrow; it is flattened laterally. A rostrum is absent. The alveola is thin, smooth; it has broad wing-like longitudinal folds on the dorsal side. Spermatozoa with 1 flagellum.

Size: Medium-sized squid; maximum recorded mantle length about 420 mm.

Geographical Distribution: Distributed in tropical, subtropical and temperate waters of the Indian and Pacific oceans.

Habitat and Biology: *Nototodarus* species form a significant part of the diet of pygmy sperm whales (*Kogia breviceps*) stranded on New Zealand shores. Long-finned pilot whales in New Zealand feed exclusively on cephalopods, of which *Nototodarus* species are predominant. The diet of orange roughy (*Hoplostethus atlanticus*) has changed over time with a progressive decline in the occurrence of squid, principally *Nototodarus* species. *Nototodarus* species comprise major populations in the shelf-break zone where enriched food supplies are created by eastern and western boundary currents and their associated mesoscale and downwelling features, such as upwelling cells and eddies. Young of the species congregate seasonally over the continental shelf in large schools, feeding on the rich food supplies to foster growth and maturation.

Remarks: An analysis of morphological characters among ommastrephid species, in order to determine morphological evolution and phylogenetic relationships, indicated that *Nototodarus* (Todarodinae) is more advanced than the most primitive group, the Illicinae, but it is more primitive than the remaining genera in the Ommastrephinae (Nigmatullin, 1992 [1991]).

The number of specific and subspecific taxa had been in a confused state for decades, with several combinations of specific and subspecific entities in use. Finally Dunning and Förch (1998) concluded that the basic specific composition within *Nototodarus* is *Nototodarus sloanii* (Gray, 1849), *N. gouldi* (McCoy, 1888) and *N. hawaiiensis* (Berry, 1912) and reviewed the systematics, distribution and biology of the 3 species. Table XX provides a comparison of characters for these 3 species.

Recent mitochondrial DNA analyses indicate that *Nototodarus gouldi* and *N. sloanii* are sister species and that they are more closely related to *Todarodes pacificus* than to *Nototodarus hawaiiensis*. These results suggest that the form of the hectocotylus, currently a major morphological distinguishing character in *Nototodarus*, may not be a reliable character (Wakabayashi *et al.* 2006).

Literature: Dunning and Förch (1998), Wakabayashi *et al.* (2006).

Table 13

Comparison of species characters in *Nototodarus* (see Roper, 1983, for explanation of indices) (from Dunning and Förch, 1998)

Character	<i>Nototodarus sloanii</i> ^{1/}	<i>Nototodarus gouldi</i> ^{1/}	<i>Nototodarus hawaiiensis</i> ^{2/}
Arms I sucker count	>60	28–50	19–28
Head-length index	<20	16–20	19–31
Head-width index	<24	18–22	21–30
Arms I sucker index	<1.5	<1.5	1.5–2.3
Tentacle-sucker index	<2.5	<3.0	2.8–3.7
Fin-length index	>42	>40	35–43
Arm and tentacular sucker teeth	~equal	~equal	1 tooth much larger
Teeth on largest medial manus sucker	12–15	12–15	14–18
Quadriseserial rows of manus	12–13	12–13	10–11
Skin	smooth	smooth	smooth
Hectocotylus			
Proximal-sucker bases enlarged as cushions	~10 pairs	~5–6 pairs	~4–5 pairs
Normal sucker rows (right arm)	~5	~5	1–6
Ventral protective membrane (right arm)	present only on distal 1/5 of arm	wide, with attenuated supports to arm tip	wide, with attenuated supports to arm tip
Ventral-sucker bases (right arm)	rapidly diminish in height distally	rapidly diminish in height distally	modified as thin papillae
Dorsal-sucker bases modifications (right arm)	distally flattened papillae extend to arm tip	broad-based papillae extend to arm tip	broad-based papillae extend to arm tip, equal in length to ventral papillae

^{1/} Syntheses of values from Kawakami and Okutani (1981) and Dunning (1988c).^{2/} Syntheses of values from Wormuth (1976) and Dunning (1988c).***Nototodarus sloanii* (Gray, 1849)**

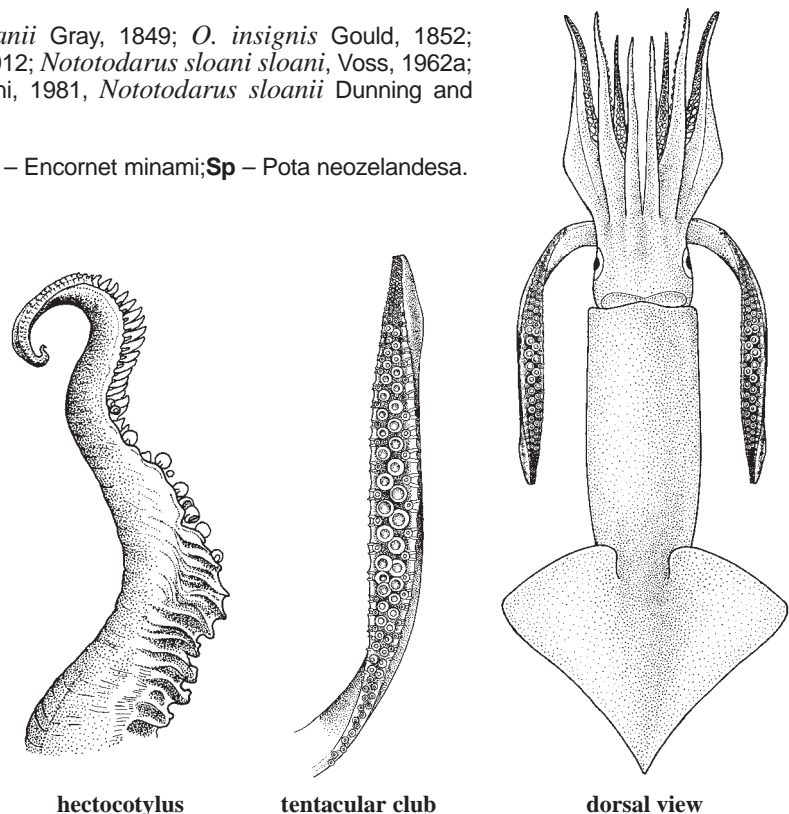
Fig. 319

Ommastrephes sloanii Gray, 1849, *Catalogue of the Mollusca in the British Museum, Part I. Cephalopoda artepedia*. 164 p. [61]. [Type locality: Waitemata Harbour, New Zealand, Tasman Sea, western South Pacific Ocean].

Frequent Synonyms: *Ommastrephes sloanii* Gray, 1849; *O. insignis* Gould, 1852; *Ommatostrephes sloanei sloanei*, Pfeffer, 1912; *Nototodarus sloani sloani*, Voss, 1962a; *Nototodarus sloani*, Kawakami and Okutani, 1981, *Nototodarus sloanii* Dunning and Förch, 1998.

FAO Names: En – Wellington flying squid; Fr – Encornet minami; Sp – Pota neozelandesa.

Diagnostic Features: Arms I have more than 60 pairs of suckers. Mantle muscular, tapers to pointed tail. Fins broad, sagittate; length 42 to 48% of mantle length; single fin angle 44° (40° to 50°). Funnel groove with foveola and 10 to 13 longitudinal ridges. **Tentacular club occupies much of tentacle length;** protective membranes very low, weak; largest sucker rings with 11 to 13 conical teeth around entire ring, interspersed with low truncate platelets; distal central tooth not enlarged. Arm sucker rings smooth proximally, grading to truncate teeth laterally, then to about 11 to 15 short, triangular teeth distally; the central tooth is enlarged. **Both arms IV in males hectocotylized basally** with modification of protective membranes and trabeculae into large, ridged, saw-tooth processes; **suckers absent; about 10 proximalmost pairs of suckers modified into large, swollen tubercles.** The hectocotylized right arm IV has a single row of slender, conical papillae distally; the ventral protective membrane has expanded supports only opposite to the extreme tip of the arm.

Fig. 319 *Nototodarus sloanii*

Size: Maximum mantle length about 420 mm, maximum weight 1.8 kg in the western, South Island, New Zealand population, but 320 mm and 0.6 kg in the warmer waters of northeastern New Zealand.

Geographical Distribution: *Nototodarus sloanii* occurs in New Zealand continental shelf waters off and around South Island, southward from the northern boundary of the Subtropical Convergence Zone (about 41°S to the Auckland Islands, 51°S) and the Campbell Islands (53°S) at bottom depths that vary from 50 to 500 m; it extends eastward to the southeast of the Chatham Islands (175°40'W). It also occurs along the west coast of New Zealand's South Island from off Cook Strait southward along the narrow continental shelf to merge with the southeastern subpopulation south and east of South Island (Fig. 320).

Habitat and Biology: *Nototodarus sloanii* is a neritic-oceanic species that occurs from near the surface to about 500 m depth; occasionally it forms large aggregations down to 300 m. It is most abundant on the continental shelf in depths of less than 200 m. At the northern end of its range it overlaps with its congener, *N. gouldi*, while in the southern part it co-occurs with *Todarodes filippovae*, where the 2 species are caught together in the jig and trawl fisheries.

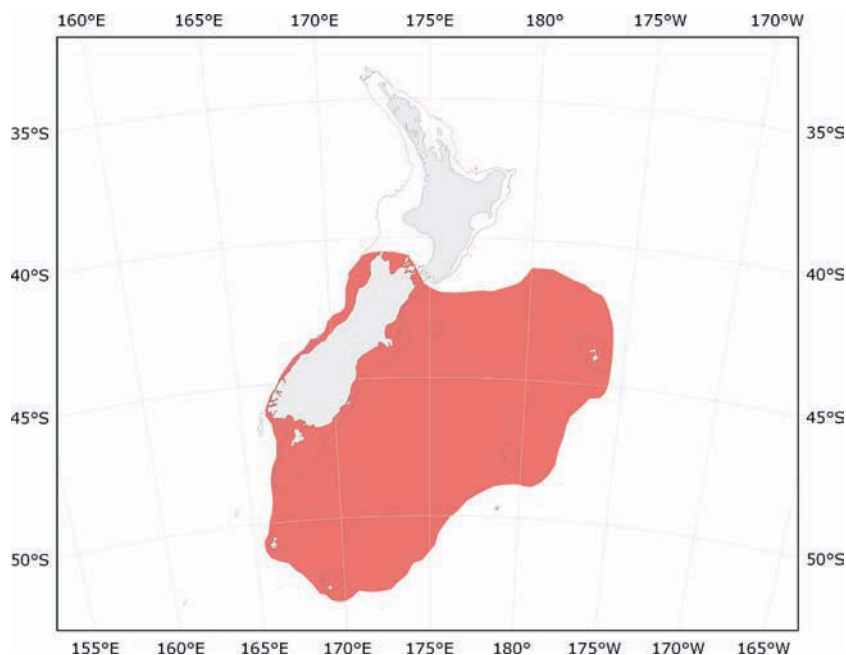


Fig. 320 *Nototodarus sloanii*

Known distribution

The Antarctic Circumpolar Current that enriches New Zealand waters northward to about 41°S provides oceanic primary productivity that drives the flow of energy and material into the extensive ranges of secondary producers and predators, that, in turn, are preyed upon by *N. sloanii*. Consequently, *N. sloanii* is an important member of the mid-to-outer continental shelf species assemblage. It occurs over a broad range of temperatures but seems to be either more abundant or more vulnerable to fisheries activities in colder waters.

Geographical subpopulations exist that vary in size and season of maturity and spawning. These groups are distinguished by minor morphometric features, biology and geography. Two major subpopulations exist, 1 north of the subtropical convergence zone and 1 within and south of the convergence. The northern group occurs in 2 "cohorts": 1 off eastern South Island, New Zealand, and through Cook Strait; the second cohort occurs in the upwelling region along the western coast of South Island over the narrow continental shelf; it grows to larger sizes than the eastern cohort. The second major subpopulation occurs south of the subtropical convergence and is associated with high velocity, cool waters of the Antarctic Circumpolar Current/sub-Antarctic Front. The interannual abundance of populations is correlated with environmental changes associated with the Southern Oscillation Index and the Trans-Polar Index. Small-scale environmental factors influence fluctuations in each seasonal cohort.

Spawning occurs throughout the year, mainly on the continental shelf throughout the adult life span. Each of the 2 northern populations has 2 peak spawning seasons: autumn (March and April) and spring (September to November) for the northwestern population, and July and December for the northeastern population. Eggs, paralarvae, sometimes juveniles, are transported by the current from the spawning grounds to the feeding grounds. Some inshore-offshore migration exists of older stages.

Testis somatic index (TSI) shows males begin to mature at 200 days and reach a maximum maturity at 270 days. Females start to mature when the maximum TSI in males is achieved. Development of the ovary, oviduct and nidamental glands occurs simultaneously, and copulation with spermatangia implantation around the buccal membranes occurs at this time, followed 2 months later by spawning, thus completing the 1-year life span.

Paralarvae of *N. sloanii* are distributed over the continental shelf and banks shallower than about 150 m; juveniles are distributed over the continental shelf along the east and south coasts of South Island, on the Auckland Islands shelf and around the Chatham Islands. Adult distribution patterns are very similar to those of the paralarvae and juveniles.

Hatching occurs principally in April to June, the austral autumn. Paralarvae are most abundant off eastern South Island, New Zealand, south of the subtropical convergence in sub-Antarctic waters. The size and age of the winter-spawned group is larger than the summer group at about 100 to 230 days, but the trend is reversed by about 250 days.

Nototodarus sloanii grows to a maximum mantle length of 420 mm but can be mature at 260 mm mantle length; fully mature females weigh 1.8 kg. Growth rates vary with size: smaller squid (180 to 240 mm mantle length) grow 25 to 40 mm per month,

and larger squid (240 to 330 mm mantle length) grow 15 to 30 mm per month. Thus growth over the exploited size range from 7.5 to 11 months suggests a life span of 1 year. Parasites of *N. sloanii* include *Anasakis* nematodes that infest the visceral organs and membranes, rarely the muscular tissues. The prey of *N. sloanii* is varied and consists of crustaceans (euphausiids, amphipods, crab zoea), fishes (myctophids, saury) and squids, including conspecific and congeneric forms. *Nototodarus sloanii* is preyed upon by seabirds such as the Southern Buller's albatross, fiordland crested penguin (*Eudyptes pachyrhynchus*), yellow-eyed penguin (*Megadyptes antipodes*) and little blue penguins, marine mammals, e.g. New Zealand fur seals (*Arctocephalus forsteri*), which prey predominantly on *N. sloanii* during summer and autumn, and Hooker's (or New Zealand) sealions (*Phocarctos hookeri*) around the Auckland Islands. Interestingly, neither *N. sloanii* nor *N. gouldi* appear to be prey of sperm whales (*Physeter catodon*), probably because they live in the shallower waters over the continental shelf, where sperm whales generally do not feed. However, *N. sloanii* formerly was abundant (18.5%) in the stomachs of sperm whales stranded on New Zealand coasts. In recent years, however, beaks of these species have been entirely absent. A second very large predator is the giant squid, *Architeuthis*. The lengths of upper and lower rostra of the beaks taken from predators can predict both mantle length and wet weight of the squid consumed.

Interest to Fisheries: *Nototodarus sloanii* is fished in the sub-Antarctic waters south of the Subtropical Convergence Zone, about 44°S, over the continental shelf of South Island, New Zealand. It is the major squid fishery in New Zealand. The species may be represented by multiple cohorts, but insufficient biological data are available to confirm this; thus the entire stock is managed as a single cohort. The instantaneous biomass of both *Nototodarus* species is estimated to be 2 to 3 million tonnes of which 1 to 2 million tonnes are *N. sloanii*, so the potential for a managed sustainable fishery is high. The fishery first developed in 1972 and landings continued to increase, with variability, including the exceptionally good landings in 2004 of a little over 108 000 tonnes. The catch recorded for 2007 was about 74 000 tonnes. The annual *N. sloanii* total landings accounts for about 2 to 4% of the total world cephalopod landings. Annual fishery statistics, catch per unit effort (CPUE), joint ventures and foreign vessel data are available in the Occasional Publication Data Series, Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington, New Zealand. Interannual variability in fishery catch demonstrates 2 peaks of abundance during good years, in mid-February and late March, and 1 peak during poor years, in mid-February. CPUE is higher when sea-surface temperature is greater than 16°C in mid-February; and higher in late March with temperatures less than 14°C. Peak catches occur in January-February, east of South Island within the 200 m isobath where surface temperature is 13° to 15°C. Catches are related to moon phase: full yields lower, new yields higher. This is typical for oceanic species that undergo diel vertical migration. The light intensity during full moon is sufficient to limit the extent of migration into shallower depths. Fishing at greater depths during full moon might increase otherwise reduced catches.

The fishery for *N. sloanii* in New Zealand's Economic Zone is dominated by foreign vessels that operate under government licenses, joint ventures and charter agreements. *Nototodarus sloanii* is taken by both jigging and trawling, with jigging often being more productive, as well as being more "resource friendly", because it does not produce unwanted, destructive incidental catches. Furthermore, jigging is selective on the size of squid it captures, produces a high-quality product that can be processed at a steady rate and it does not destructively interfere with benthic fauna and habitat. Japanese and South Korean jigging vessels, operating under joint-venture schemes with New Zealand, take about half the total catch, but they land only a fraction in New Zealand. This squid also is taken in trawling operations of foreign licensed vessels from the former USSR countries, Japan and the Republic of Korea. The fishery is regulated through a quota system. The vessels usually operate during a 90 to 120 day fishing season extending from December to April. The Total Allowable Catch is established annually, and this tonnage normally seems not to be achieved; TACs have ranged from 90 000 tonnes to 166 250 tonnes, but the combined total catch of both species, *N. sloanii* and *N. gouldi*, seldom has exceeded 50 000 tonnes. Frozen and processed squids are exported to various countries. Domestically caught squid are marketed fresh or processed. The majority of the squid is processed for human consumption, but viscera also are used for other purposes. Biochemical analysis of proximate composition and fatty acid compositions of viscera shows the residual protein has high levels of essential amino acids that provide a good source of protein supplement for domestic animal feed.

The trawl fishery for *N. sloanii* inadvertently captures sea lions (*Phocarctos hookeri*), a threatened species. An annual catch limit is imposed on the squid fishery in order to stimulate healthy recovery of the sea lion.

Local Names: JAPAN: Minamisurumeika, Nyujirando-minamisurumeika, Nyujirandosurumeika; NEW ZEALAND: New Zealand arrow squid, Wellington flying squid.

Remarks: Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayashi *et al.*, 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodanae). However, within Todarodinae, *Nototodarus* appears to be paraphyletic under all analyses done: *N. sloanii* was shown to be a sister species of *N. gouldi*, and these 2 species appear to be more closely related to *Todarodes pacificus* than to their congeneric entity, *N. hawaiiensis*. Ultimately, this study was not able to resolve the phylogenetic relationships within the Ommastrephidae because of the significant genetic divergence among species. The identification of the sympatric species, *N. sloanii* and *N. gouldi*, is difficult in areas of geographical overlap. The key distinguishing features are: the **number of suckers on right arm I** (greater than **60** versus **28** to **50**, respectively), the number of **proximal enlarged sucker bases/cushions** (**10** versus **5** or **6**, respectively) and the **morphology of the distal part of hectocotylized arm** (flattened papillae versus broad-based papillae, respectively) (Smith *et al.*, 1987).

Literature: Saito *et al.* (1974), Smith *et al.* (1981), Förch (1986), Smith *et al.* (1987), Nesis (1993a), Dunning and Förch (1998), Waluda *et al.* (2004a), Wakabayashi *et al.* (2006).

Nototodarus gouldi* (McCoy, 1888)*Fig. 321**

Ommastrephes gouldi McCoy, 1888, *Prodromus of the Zoology of Victoria, Decade*, 17: 255–257, 2 pls. [255, pl. 169]. [Type locality: Hobson's Bay, Victoria, southern Australia (fide Dunning and Förch, 1998: 397)].

Frequent Synonyms: *Nototodarus sloani gouldi* (McCoy, 1888); *Ommastrephes gouldi* McCoy, 1888; *Ommatostrephes sagittatus sloanei* Pfeffer, 1900; *O. sloanei sloanei* Pfeffer, 1912; *Nototodarus sloani gouldi* Voss, 1963a.

FAO Names: En – Gould's flying squid, Gould's arrow squid; Fr – Encornet éventail; Sp – Pota australiana.

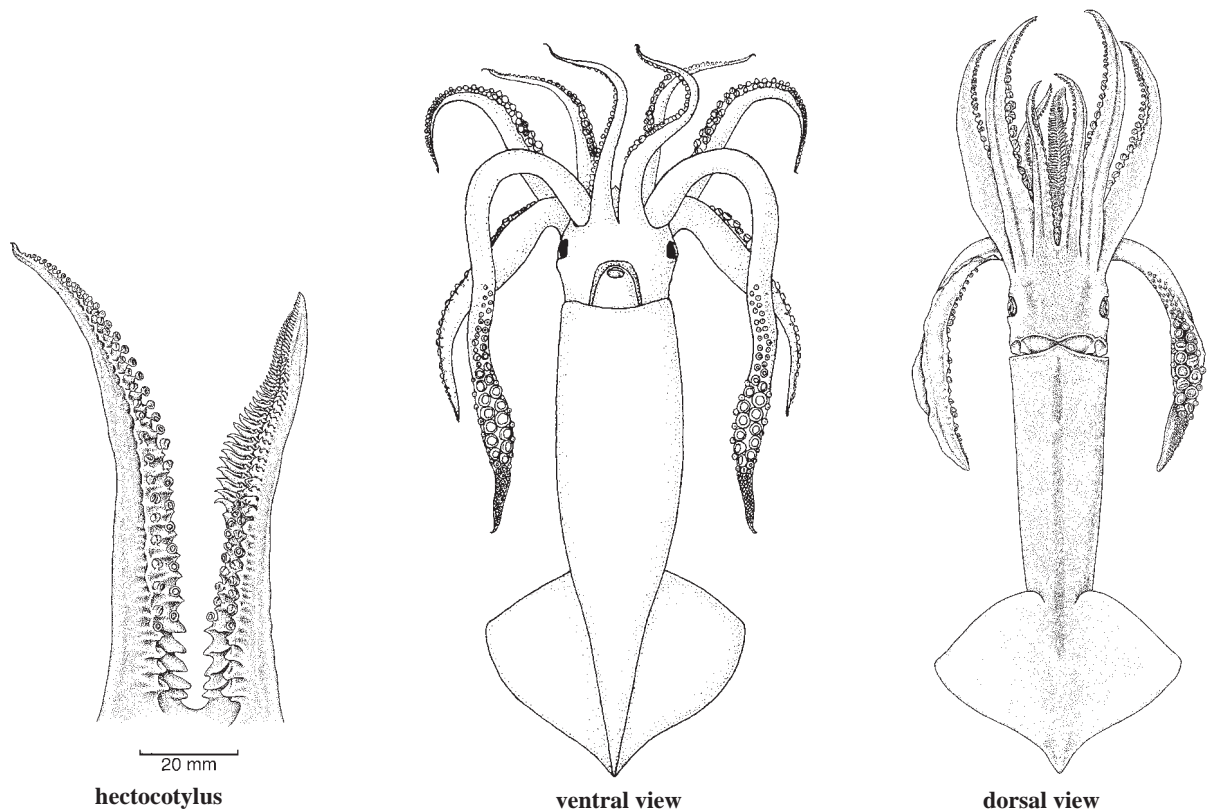


Fig. 321 *Nototodarus gouldi*

Diagnostic Features: Arms I have **28 to 50 pairs of suckers**. Mantle robust, heavily muscled, tapers gradually then very acutely to a point posteriorly. Fins strong, about 45% as long as mantle length; angle broad, 90° to 110° (45° to 55° single fin). Funnel groove with foveola and 6 to 8 low longitudinal ridges anteriorly. **Tentacular club long, 60 to 70% of tentacle length;** about 8 pairs of enlarged manal suckers in median rows, marginal suckers small, subequal; largest sucker rings toothed all around with 15 separated, stout, triangular, pointed teeth interspersed with low, side platelets. Arm sucker rings with 12 or 13 sharp, triangular teeth graded to a single large central tooth distally; proximal one-third smooth, without teeth or denticles; **both ventral arms (IV) in males hectocotylized:** the right arm with a heavily tuberculate basal region, a narrow sucker-bearing midpart, and a distal part with very broadly expanded, pectinate protective membrane; **the left ventral arm one-fourth longer than right IV, about 5 proximalmost pairs of suckers modified into large, swollen tubercles.**

Size: Maximum mantle length 420 mm in females, 350 mm in males; weight to about 1.2 kg in females.

Geographical Distribution: Temperate to subtropical areas off Australia: from south of 27°S off the east coast (Queensland), southward around Tasmania through the Bass Strait, westward along the south coast, then northward off Western Australia to about 25°S off Shark Bay; off the northern and central coasts of New Zealand, principally off North Island (Fig. 322).

Habitat and Biology: *Nototodarus gouldi* is sympatric with *N. sloanii* where the area of overlap occurs between 40° and 44°S and in the northern extreme of its range of eastern Australia it overlaps in slope waters with *N. hawaiiensis*.

It is a neritic and oceanic, mostly epipelagic species, that occurs from the surface to about 500 m depth. Its abundance in surface waters is correlated with the lunar cycle; in full moon nights the squids tend to remain in deeper waters where they are less vulnerable to the fishing gear.

The principal oceanographic feature that supports and sustains the *N. gouldi* populations is the productivity of the Antarctic Circumpolar Current through the distribution and dispersal of energy flow into the region of secondary producers and predators that form their prey.

Nototodarus gouldi is a dominant species in the mid to outer continental shelf species assemblage in New Zealand waters. While its greatest abundance is over shelf waters at 50 to 200 m (300 m), *N. gouldi* occasionally is abundant in shallow coastal waters in the summer in Australian waters. The distribution of paralarval and juvenile *N. gouldi*, 20 to 40 mm mantle length, in New Zealand occurs principally in continental shelf waters off the east and west coasts of North Island and to the northwest of South Island. This distributional pattern is very similar to that of the adults, so the entire life cycle is spent in continental shelf waters.

Age at sexual maturation has been determined using statolith aging techniques. Males start to mature at about 200 days, and the testis somatic index (TSI) reaches its maximum at about 270 days. Females begin to mature as the TSI reaches its maximum in males. The rapid development of the ovary, oviducts and nidamental glands occurs simultaneously, and copulation takes place during this period, as well. Spawning occurs about 2 months after copulation, completing the slightly less than 1 year life cycle, based on statolith analysis.

Males exhibit no seasonal differences in growth rates, but females do: females hatched in summer have significantly higher growth rates than those hatched in winter, autumn or spring. During cool months females are larger, have slower lifetime growth, lower gonadic investment and better somatic condition than those caught in warm months, representing a trade-off between gonadic investment and somatic condition. Males have a tight coupling between gonadic investment and somatic condition throughout the seasons, with gonadic and somatic tissues growing concurrently. This strategy of “using” monthly variations in ambient conditions to govern egg production and spawning would have positive effects to maximize reproduction and survival. Studies over a broad range of southeastern Australian localities confirm complex variations in size, age, growth and maturation among sites, where life span is slightly less than 1 year. Considerable genetic mixing occurs across all sites, that allows a possibility of populational substructures and suggests the existence of more than 1 stock in Australian waters. However, an allozyme electrophoresis study of squid from the same geographical area revealed no evidence to support the existence of separate stocks.

Females grow larger than males, but males tend to be heavier at a given mantle length, until females surpass them at maturity. Across the range of the species in southeastern Australian waters considerable variation exists in size, growth rates and maturity between sites, seasons and years. The age of mature squid varies by over 100 days from youngest to oldest. Interannual variations in the Southern Oscillation Index (SOI) and the Trans Polar Index (TPI) affect the environment and abundance of *N. gouldi*: juveniles are affected mainly by the SOI at lower latitudes, while the adults are affected by the TPI in higher latitudes. This mechanism influences recruitment and stock abundance. *Nototodarus gouldi* exhibits the multiple-spawning strategy whereby eggs are laid in discrete batches during the course of the spawning period. Mature ovaries contain oocytes with a range of sizes with discrete peaks. The life cycle generally is related to warm currents and eggs, paralarvae, occasionally juveniles, are transported by the current from the spawning grounds to the feeding grounds, where they become available to the fishery. Following mating and spawning, the muscular tissues of spent individuals begin to degrade and become weakened and flaccid. Probably the very rapid disposition of somatic protein into protein-rich yolk during

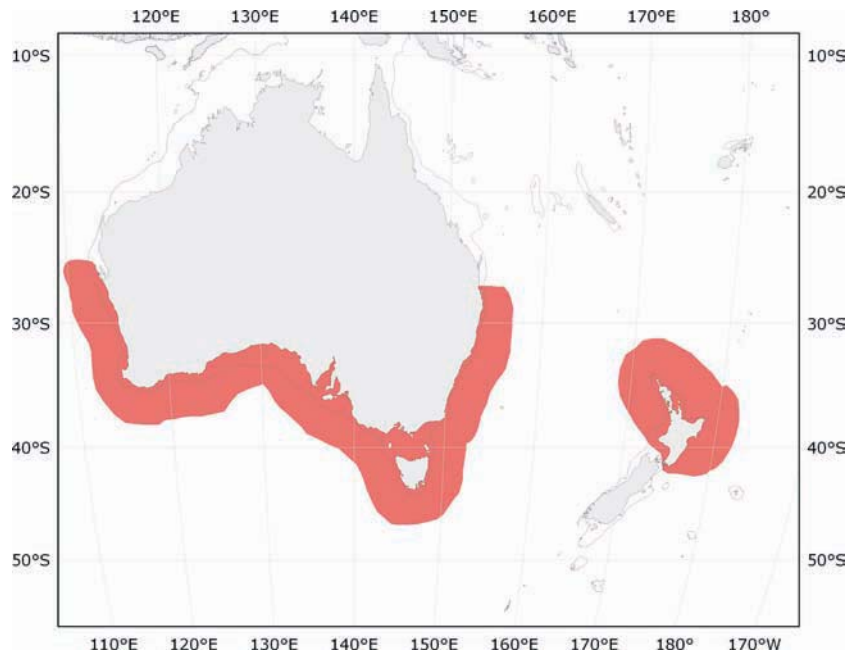


Fig. 322 *Nototodarus gouldi*

■ Known distribution

vitellogenesis in the ovary, coupled with reduced or ceased feeding, leads to the somatic degradation after spawning, soon followed by death.

Nototodarus gouldi is an opportunistic predator that preys on planktonic/nektonic crustaceans, fishes and cephalopods. The incidence of crustaceans in the diet decreases with growth, while the incidence of cephalopods, including *N. gouldi* and other ommastrephids, increases. Feeding occurs mainly at night and at dawn and digestion is rapid. Fishes *Sardinops pilchardus* and *Leionura auntae* and the crustacean *Leptochela sydniensis* and *Cirolana*, and some isopods and amphipods are the most common prey. Ommastrephids made up most of the cephalopod component: frequently smaller *N. gouldi* and *Todarodes filippovae*; other squids: occasionally *Onychoteuthis* sp., *Brachioteuthis* sp. and *Sepioteuthis* sp. The quantity of each main food group varies monthly, depending on the availability of preys. The digestive gland of *N. gouldi* accululates high levels of trace metals (cadmium, copper, zinc, polonium-210).

The predators of *N. gouldi* vary widely and include seals, dolphins, tuna, as well as pelagic, benthic and bathypelagic fishes. This species is a significant prey of pygmy sperm whales in New Zealand waters. Larger *N. gouldi* are a dominant prey of swordfish (*Xiphias gladius*) off eastern Australia, as well as important in the diet of yellowfin tuna, school shark (*Galeorhinus australis*) and gummy shark (*Mustelus antarcticus*). Other species of sharks from eastern Australian waters preying on *N. gouldi* include the smooth hammerhead shark (*Sphyrna zygaena*), the scalloped hammerhead shark (*S. lewini*), the blue shark (*Prionace glauca*) and the shortfin mako (*Isurus oxyrinchus*). Examination of stomach contents revealed that the giant squid, *Architeuthis*, preys on *Nototodarus* species; undoubtedly that would include *N. gouldi*. Among marine mammals, *N. gouldi* is a dominant prey of Australian fur seals (*Arctocephalus pusillus*) which are attracted to squid jigging operations where they prey upon *N. gouldi*. The Gould's squid is the most abundant cephalopod in the diet of the shy albatross on Albatross Island, Tasmania, of juvenile southern bluefin tuna in the waters off coastal southern Western Australia and of short-tailed shearwater in Tasmanian waters. This species also is the most frequent cephalopod prey of the little penguin (*Eudyptula minor*) at Phillip Island, Victoria, Australia. *Nototodarus gouldi* was a significant prey of sperm whales stranded in New Zealand in the 1960s, but these species have been entirely absent from stranded sperm whales in recent years.

Interest to Fisheries: Prior to the development of a directed fishery, the species was only taken as by catch in the Australian prawn fishery. Feasibility fishing started in the summer 1978/1979, with 19 Japanese jigger vessels operating in southeast Australian waters. In the light of promising catch rates, exploratory fishing was subsequently expanded. Chinese jigging vessels (from Taiwan Province of China) operate intermittently in the area. Catches are best in the waters around Tasmania and the western Bass Straits, particularly from December to March. In early years, the annual catch fluctuated between 4 000 and 5 000 tonnes. An active fishery then developed for *N. gouldi*, principally around southern Australia and Tasmania in temperate waters, then in subtropical waters north to 27°S off the east coast, and to 25°S along the west coast.

A smaller stock of *N. gouldi* is fished in subtropical waters around North Island, New Zealand, north of the Subtropical Convergence Zone. There, the major fishing grounds are off southwestern North Island and off northwestern South Island over a broad area of the shelf in waters of the Westland/D'Urville Current system at temperatures greater than 18°C. Fishing is conducted by a New Zealand fleet, as well as by an international fleet, using a combination of gears: jigging machines on specialized jigging vessels, and bottom otter trawls and pelagic trawls on large stern trawlers.

The instantaneous biomass of *Nototodarus* species throughout their ranges has been estimated at 2 to 3 million tonnes of which 0.5 to 1 million tonnes are *N. gouldi*.

The principal goal in management of a fishery on squid with an annual life cycle is to enable a sufficient number of spawning individuals to escape. In the case of *N. gouldi*, regulation of effort is the best tool to manage the fishery, regardless of the fishing area. Clearly, knowledge of the timing of spawning, the ecology of hatchlings, the larval distribution and the growth dynamics of juveniles are critical to understand the location and life cycle of the adults in order to sustain a well-managed, consistent fishery.

Echo sounding and sonar surveys were conducted to determine the suitability of alternative fishing techniques for *N. gouldi*. This species forms demersal aggregations during daylight hours. Around dusk, squid leave the bottom, and disperse into the water column to feed at night. This behaviour is conducive for bottom and midwater trawling. Purse seining was suggested as an alternative technique for capturing squid attracted by lights at night and clustered in demersal aggregations during daylight hours.

During the week of full moon, catch rates are about 25 to 50% lower than during darker weeks. Catch rates generally are greatest during the days following new moon. Commercial jigging operations are conducted both during the day and at night, but nighttime catches are greater, probably because the diel vertical migration pattern brings the squid off the bottom layer and closer to the surface at night. In the developing squid fishery off New South Wales, *N. gouldi* is the most abundantly caught species.

The fishery for *N. gouldi* at present is managed as one stock.

Local Name: AUSTRALIA: Gould's squid; NEW ZEALAND: Gould's arrow squid.

Remarks: Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayashi *et al.*, 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodinae). However, within Todarodinae, *Nototodarus* appears to be paraphyletic under all analyses done: *N. sloanii* was shown to be a sister species of *N. gouldi*, and these 2 species appear to be more closely related to *Todarodes pacificus* than to their congeneric entity, *N. hawaiiensis*. Ultimately, this study was not able to resolve the

phylogenetic relationships within the Ommastrephidae because of the significant genetic divergence among species. *Nototodarus gouldi* and *N. sloanii* are closely-related, similar-looking species that are difficult to discriminate. The following distinguishing characters aid in specific identification: *N. gouldi* has **28 to 50 suckers** on arms I versus **60 suckers** on *N. sloanii*; *N. gouldi* has about **5 or 6 pairs** of proximal sucker bases enlarged as cushions on the hectocotylus, versus **10 pairs** on *N. sloanii*; *N. gouldi* has dorsal sucker bases on right arm IV modified as **broad-based papillae** that extend to the tip of the arm, versus distally flattened papillae to the arm tip in *N. sloanii* (Smith *et al.*, 1987).

Literature: Thrower (1978), Roberts (1983), Hatanaka *et al.* (1985), Smith *et al.* (1987), Gibson (1995), Dunning and Förch (1998), McGrath and Jackson (2002), Stark (2006b), Wakabayashi *et al.* (2006).

***Nototodarus hawaiiensis* (Berry, 1912)**

Fig. 323; Plate X, 59

Ommastrephes hawaiiensis Berry, 1912, *Proceedings of the Academy of Natural Sciences Philadelphia*, 64(2):434–437 [434]. [Type locality: off Oahu Island, Hawaiian Islands, North Pacific Ocean].

Frequent Synonyms: ?*Ommatostrephes sloanei sloanei* Pfeffer 1912; *Ommastrephes hawaiiensis* Berry, 1912; *Nototodarus sloani philippinensis* Voss, 1962c; *Nototodarus sloani hawaiiensis* Voss, 1962c; *Nototodarus nipponicus* Okutani and Uemura, 1973; *Nototodarus philippinensis* Roper *et al.* 1984; *Nototodarus sloanii philippinensis* Dunning, 1988c.

FAO Names: **En** – Hawaiian flying squid; **Fr** – Encornet bouquet; **Sp** – Pota hawaiana.

Diagnostic Features: **Mantle cylindrical, muscular;** it tapers to a narrow, conical tip posteriorly. **Fins muscular, broad, short; fin length 35 to 43% of mantle length;** single fin angle (50° to 57°); a dark stripe of thickly set chromatophores occurs along dorsal midline of mantle and fins. Arms I have fewer than 30 pairs of suckers (18 to 28); head length index high (19 to 31). **Funnel groove with foveola, without side pockets.** Tentacular club with 4 rows of suckers on dactylus; **carpal area occupies most of tentacle length along stalk (about 70%);** about 12 medial manus suckers are 3 to 4 times larger than the lateral suckers; largest medial manus sucker

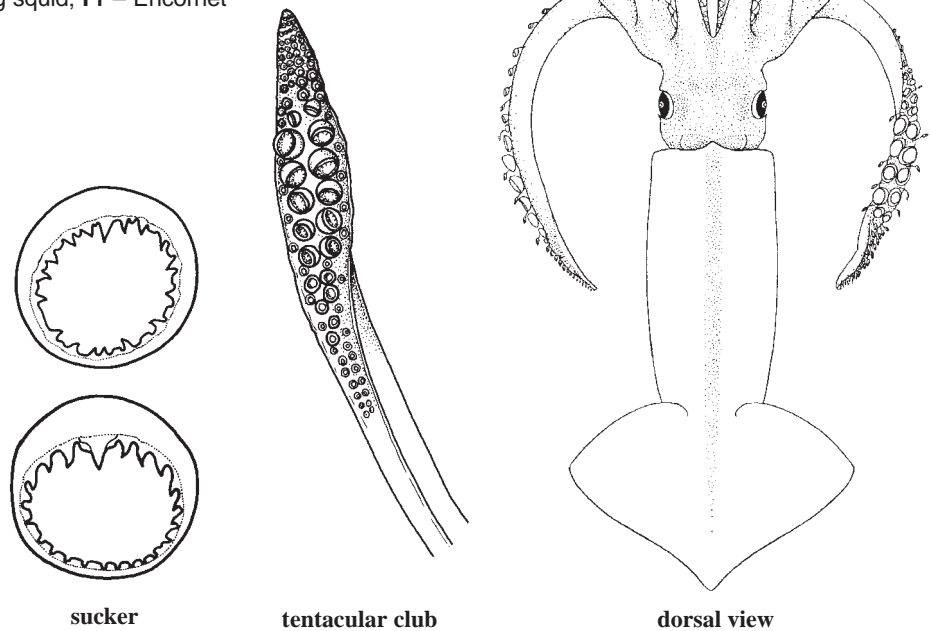


Fig. 323 *Nototodarus hawaiiensis*

rings have 14 or 18 large conical, pointed teeth with low, truncated platelets between each tooth; distal, central tooth much enlarged. Arm sucker rings toothed all around with 19 to 21 small, conical (distally) to rounded (proximally) teeth; distal, central tooth much enlarged; small denticles between some distal teeth. **Both arms IV hectocotylized in males, right especially so;** it is longer and larger than the left and has a double row of slender, conical papillae and expanded protective membrane distally; **proximal one-quarter of each arm IV has 4 or 5 enlarged cushion-like trabeculae** and wide protective membranes (a saw-like or comb-like appearance) that have attenuated supports that extend to arm tip; dorsal and ventral distal right arm trabeculae, sucker stalks and suckers modified by enlargements, reductions, etc.

Size: Maximum mantle length varies according to locality: off southern Queensland, Australia, males 215 mm, females 248 mm; western Indian Ocean, males 290 mm; southeastern Pacific Ocean, 318 mm; Philippine waters, 180 mm; total weight 0.5 kg or more in large specimens.

Geographical Distribution: *Nototodarus hawaiiensis* has a very broad, disjunct distribution in tropical to subtropical waters of the Pacific and Indian Oceans: Hawaiian Islands to Midway Island, South China Sea, Japanese waters (south of 35°N), Hong Kong, Philippine and Vietnamese waters, northeastern Australia, Northwest Shelf of Western Australia, Andaman Sea, Bay of Bengal, Hawaiian Ridge, Sala y Gomez Ridge to Nazka Ridge, Saya de Malha Bank, off Somalia, Madagascar, Seychelle Islands, Mozambique, KwaZulu-Natal, Southern African waters. It also has been reliably reported from a seamount in the far southeastern South Pacific Ocean off Chile, 35°39'S, 85°31'W (Fig. 324).

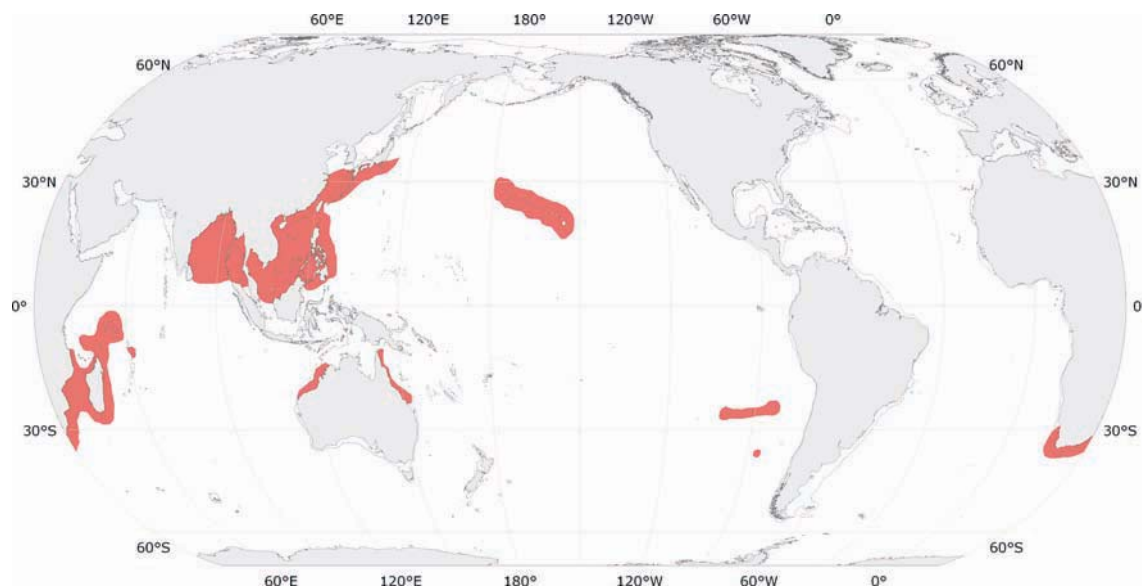


Fig. 324 *Nototodarus hawaiiensis*

Known distribution

Habitat and Biology: *Nototodarus hawaiiensis* is a pan-tropical nerito-oceanic species associated with continental shelf and slope waters, oceanic seamounts, ridges and banks. Distributed down to depths of 650 m, it also occurs in shallower waters where it is an important food item in the diet of seabirds and fishes. This species occupies the mesopelagic-boundary region in Hawaiian waters where it is both epipelagic and demersal, as evidenced by *in-situ* observations from a submersible. During the daytime *N. hawaiiensis* "sits" on the bottom on its arm tips and posterior mantle tip, a common behaviour in ommastrephids, then it disperses into midwaters at night to forage. Paralarvae, juveniles and subadults inhabit midwaters in the epi- to upper mesopelagic zones over the tops of sea mounts, slopes and oceanic depths, and the adults spawn near or on the bottom. *Nototodarus hawaiiensis* occupies this niche in the Indian Ocean: Saya de Malha Bank; Pacific Ocean: Hawaiian Ridge; Sala y Gómez Ridge; transitional zone between Sala y Gómez and the Nazca Ridge. Adults of *N. hawaiiensis* do not occur in the open ocean, but they always remain near oceanic seamounts, ridges and banks, in spite of significant expatriation of young stages into the open ocean. The dispersal of paralarvae and juveniles by oceanic currents supports the very broad distribution of most species that spawn at or near the bottom; this occurs with *N. hawaiiensis* that is dispersed across the Indo-Pacific realm from Somalia and Mozambique to Hawaii and Sala y Gómez. Interestingly, in spite of the very extensive range of *N. hawaiiensis* throughout the Indo-Pacific region, it does not occur in the Gulf of Aden nor on the Nazca Ridge eastward of 85°W. *Nototodarus hawaiiensis* is considered a very rare epipelagic species in the Sea of Japan, where it occurs south of 35°N latitude and specimens are considered to be strays from other communities. Its biology is little known. A survey of egg size and fecundity in selected species in the Todarodinae revealed that *N. hawaiiensis* is characterized in the group that has ripe egg sizes on the order of 0.7 to 2.4 mm and low to medium fecundity of 20 000 to 2.5 million oocytes. The spermatophoric organ in mature males of about 150 mm mantle length contains around 2 700 developing spermatophores at an average length of 18 mm and a fecundity of 1 000 spermatophores. Paralarvae are caught at or near the surface year-round in the South China Seas, where they are spatially concentrated in a particular area in Vietnamese waters. Paralarval distribution patterns of squid species in Hawaiian waters are divided into 2 assemblages: island-associated and oceanic. A large range in age at maturity exists in individuals of a similar size depending on locality and season. For example, off western Australia males of 98 mm and females of 100 mm are mature.

Interest to Fisheries: *Nototodarus hawaiiensis* is common in bottom trawls over the slope at 200 to 620 m off Mozambique and KwaZulu-Natal, north of Durban, South Africa and it is the predominant cephalopod species caught as bycatch in the shrimp and prawn demersal trawl fishery on the Northwest Slope off Western Australia, principally in the Ramkin Bank area. Its abundance in these fisheries and the quality of its muscular tissues indicate a high potential as a fishery resource (Australia, Hawaii, Philippines, Mozambique, South Africa), even though its occurrence in relatively deep waters may limit access by common trawling techniques. An artisanal fishery exists off Hawaii (Big Island) out of the Port of Hilo. Exploratory fishing was conducted with jigs and gillnets and the species is believed to have sufficient potential for an expansion of the fishery. An estimate of the instantaneous biomass of *N. hawaiiensis* is 0.5 million tonnes. The species is used for human consumption and as bait.

Local Names: AUSTRALIA: Hawaiian arrow squid; FRANCE: Encornet fuiripin; INDO-PACIFIC: Hawaiian arrow squid; JAPAN: Fuiripinsurumeika; NEW ZEALAND: Hawaiian arrow squid; PHILIPPINES: Philippine flying squid; SPAIN: Pota Filipina.

Remarks: Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayashi *et al.*, 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodanae). However, within Todarodinae, *Nototodarus* appears to be paraphyletic under all analyses done: *N. sloanii* was shown to be a sister species of *N. gouldi*, and these 2 species appear to be more closely related to *Todarodes pacificus* than to their congeneric entity, *N. hawaiiensis*. Ultimately, this study was not able to resolve the phylogenetic relationships within the Ommastrephidae because of the significant genetic divergence among species. *Nototodarus nipponicus* Okutani and Uemura, 1973 was described from Japanese waters off southern Honshu, but its differentiating characters were shown to merge within the range of variation with those of *N. sloanii philippinensis* Voss, 1962, so it was considered a junior synonym of this subspecies (Okutani and Kuroiwa, 1985). Subsequently, *N. sloanii philippinensis* Voss 1962 was demonstrated to be a junior synonym of *N. hawaiiensis* by Dunning (1988c), so continued use of the trivial name *philippinensis* is untenable.

Literature: Smith *et al.* (1987), Young (1995), Dunning and Förch (1998), Bower *et al.* (1999c), Nateewathana *et al.* (2000), Wakabayashi *et al.* (2006).

***Todaropsis* Girard, 1890**

Todaropsis Girard, 1890. *Journal de Ciencias Mathematicas, Physicas e Naturaes*, (series 2)1(3): 200–205. [204].

Type Species: *Todaropsis eblanae* (Ball, 1841).

Diagnostic Features: Dactylus of tentacular club with 4 rows of longitudinal suckers; medial manus sucker rings with 30 or more, evenly spaced, approximately equal, long, pointed teeth; both arms IV hectocotyzed in mature males; cross-section A of gladius with 2 lateral lobes. Monotypic.

***Todaropsis eblanae* (Ball, 1841)**

Fig. 325

Loligo eblanae Ball, 1841, *Proceedings of the Royal Irish Academy*, 1 (19): 362–364. [362]. [Type locality: Dublin Bay, Ireland, Irish Sea, North Atlantic Ocean].

Frequent Synonyms: *Loligo eblanae* Ball, 1841; *Loligo sagittata* Verany, 1851; *Todaropsis veranii* Nobre, 1936; *Todaropsis veranyi* Girard, 1890.

Misidentifications: None.

FAO Names: En – Lesser flying squid; Fr – Toutenon souffleur; Sp – Pota costera.

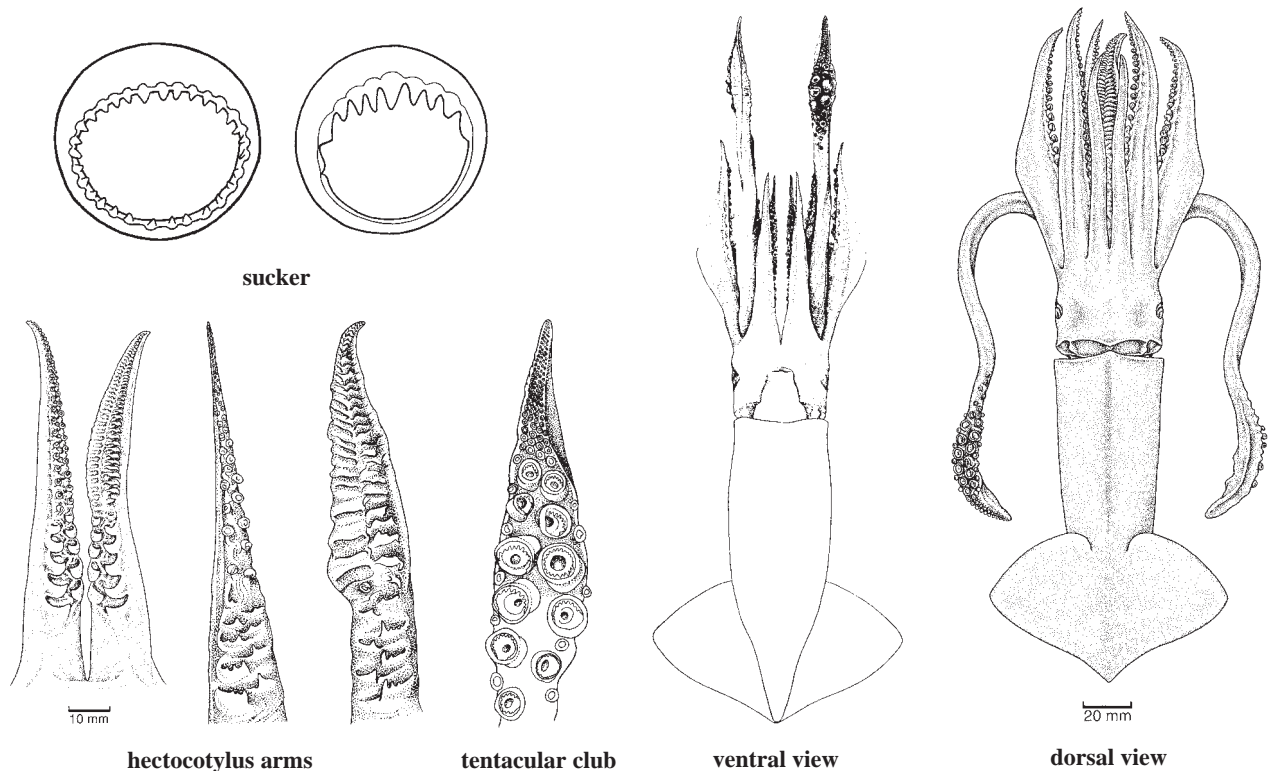


Fig. 325 *Todaropsis eblanae*

Diagnostic Features: Mantle robust, stout; head large, broad, 4 nuchal folds on posterior of head (neck); funnel groove without foveola or side pockets. Fins broad, anterior border more convex than posterior border; fins length less than 50% of dorsal mantle length, combined fin width equal to 90% of dorsal mantle length. Dactylus of tentacular club with **4 longitudinal rows of small suckers; manus of club with 6 transverse rows of 4 suckers, each with median pairs up to 4 times larger in diameter than lateral suckers.** Sucker rings of largest median club suckers with about 30 short, pointed teeth, occasionally alternating with minute teeth. Left and right ventral arms (IV) hectocotylized by modification of suckers into cirrated lappets and with transverse lamellae and expanded protective membrane; sucker rings of largest arm suckers with 1 large pointed median tooth and 3 or 4 smaller pointed teeth.

Size: Medium-sized species; maximum recorded size 290 mm mantle length for females and 220 mm mantle length for males (North Atlantic).

Geographical Distribution: This species exhibits a very disjunct distribution, as follows: Eastern Atlantic Ocean from 61°N (Shetland Islands) to 36°S (Cape of Good Hope, Cape Town, South Africa [Adam, 1952]), including the British Isles and the entire Mediterranean Sea; western Indian Ocean (Saya de Malha and Nazareth Banks, Mascarene Ridges); western Pacific Ocean, South China Sea and Australian waters: the Timor Sea (northern Australian coast), along the western and eastern Australian coasts, to Tasmania on the eastern side (Fig. 326).

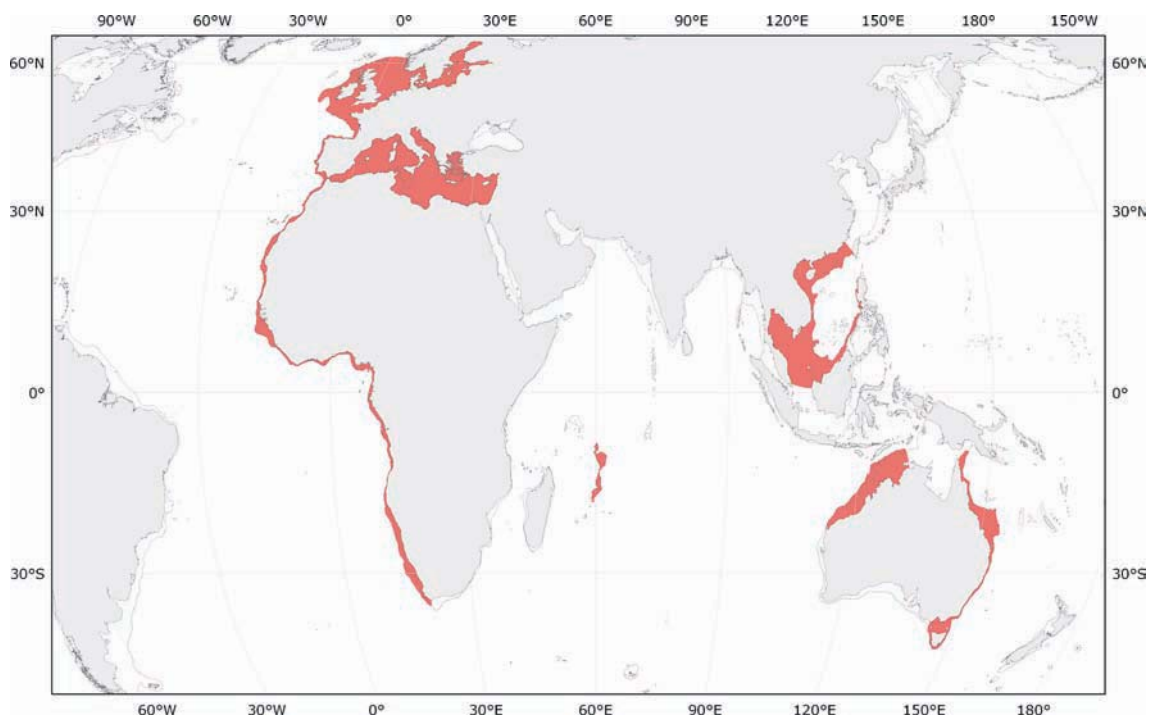


Fig. 326 *Todaropsis eblanae*

■ Known distribution

Habitat and Biology: This demersal species usually is associated with sandy and muddy bottoms, within a temperature range from 9° to 18°C in depths between about 20 and 850 m, but it is confined to depths less than 200 m in the North Sea. Typically it is associated with the shelf break zone where boundary currents and associated mesoscale oceanographic events such as downwelling eddies and upwelling cells promote rich food supplies. No clear evidence exists of seasonal migrations or any other type of major migration. *Todaropsis eblanae* probably is the least mobile of the ommastrephid squids in terms of migratory habits, and it tends to behave like a neritic loliginid squid species. The sex ratio is usually 1:1 in all the populations studied to date, in contrast to the female dominated sex-ratio observed in the more oceanic ommastrephids; slight deviations to that condition usually are caused by ecological and/or fishery related constraints than to genetic differences in population structure. Females grow larger than males, but no other sexual dimorphism is evident. Smallest mature males from the central Mediterranean Sea measured 100 mm mantle length, while smallest mature females were 120 mm mantle length (Tyrrhenian Sea), similar to what occurs in Atlantic populations. The western Mediterranean and the Australian populations, however, begin to mature at a slightly larger size (males at 160 mm mantle length, and females at 120 to 150 mm mantle length). Generally, size at 50% maturity is estimated to be 120 to 130 mm mantle length for males and 160 to 170 mm mantle length for females. The spawning season probably extends year-round in both the Atlantic Ocean and the Mediterranean Sea, with seasonal spawning peaks that depend on geographic area. In eastern Australian waters spawning occurs from late summer until early winter. Fecundity varies greatly, depending on size of females and specific populations; total fecundity ranges between a few thousand to over 250 000 ova. Evidence suggests that the energy for egg production is taken directly from food, rather than from stored products. The number and the size of spermatophores increase with the size of the males; spermatophore length

ranges between 11 and 30 mm, and their numbers range between 10 and 20 in excess of 250. The final maturation phase is rapid, and spawning constitutes the terminal phase of the life cycle. Intermittent terminal spawning is possible, but the degeneration process after the last spawning event must be rapid, since spent females are seldom found. Immature oocytes are pale yellow in colour, while mature oocytes are bright orange and measure from 0.8 to 2.5 mm in diameter. Eggs are laid in a large capsule secreted by the greatly enlarged nidamental glands. No *in situ* observations on egg deposition are available, although they probably are laid in floating masses, as observed for many other ommastrephids in the natural environment and in captivity. No information exists on the embryonic development nor on the newly hatched squids. Growth is rapid, especially in the initial phase, with females growing faster than males. Length-weight relationships differ between geographical regions; for example, males from the Spanish Atlantic waters are comparatively more robust than those from other areas. In both sexes growth is allometric, at least until maturity is reached. Observations from Italian waters show that growth in mature females is isometric, indicating a change in the growth performance once maturity is achieved. The duration of the life cycle determined by statolith analysis is about 1 year, a little shorter than that suggested by indirect observations on females of the western Mediterranean, for which a second year of life was hypothesized. *Todaropsis eblanae* preys on fishes, crustaceans and other cephalopods, in decreasing order of importance. Anatomical and behavioural changes occur in the diet, during ontogeny.

The lesser flying squid is a typical opportunistic predator that feeds on its principal available prey species depending on geographical area and other environmental factors. Analyses of stomach contents show a predominance of pelagic and nektonic species, such as myctophid, clupeid and gadoid fishes. The absence of sympatric benthic organisms in stomach contents indicates that *T. eblanae* feeds mainly in the water column. Cannibalism also occurs, but it is mainly an occasional phenomenon associated with anomalous concentrations of conspecific squid and/or scarcity of commonly available prey. No differences in the diets of males and females have been observed; however, mature females with food in their stomachs outnumbered feeding males, confirming that mature females continue feeding actively, i.e. that reproductive investment is mainly dependent on food intake and that spawning is protracted over an extended time period. *Todaropsis eblanae* is preyed upon by a variety of fishes and cetaceans, for some of which this squid constitutes an important component in the diet. Recent observations indicate that *T. eblanae*, along with *Illex coindetii* and *Todarodes sagittatus*, is the most important paratenic host for anisakid nematods. A better understanding of parasitic transfer and parasite-induced diseases throughout the food web will help in a better management of marine resources in general as well as of human consumption of raw marine food in particular.

Interest to Fisheries: *Todaropsis eblanae* is taken mainly as bycatch in otter trawl fisheries throughout its distributional range. In the Mediterranean and the eastern Atlantic, *T. eblanae* also is caught by artisanal fisheries. This species exhibits a highly irregular and discontinuous abundance in some areas of its distributional range, e.g. in the North Sea and in Spanish Atlantic waters. However, it is a constant and consistent component of the catches in other areas, where it is of significant commercial interest. These areas include the western Irish waters, the southern African Atlantic waters, and the Sicilian Channel (Central Mediterranean). Separate statistics are not reported for this species.

Local Names: AUSTRALIA: Golden arrow squid; ITALY: Totano tozzo.

Remarks: Roeleveld (1988) reviewed the importance of the characteristics of the funnel groove as a primary taxonomic character within the family Ommastrephidae and reassessed the placement of *Todaropsis* within the subfamily Illicinae. Consequently, she placed this species within the subfamily Todarodinae, in a monophyletic group with *Nototodarus*. Nigmatullin (1992 [1991]), based on the analysis of variability of 18 morphological characters, distinguished directions and stages of morpho-functional evolution of ommastrephids. He presented the recognized taxa in phylogenetic order ranging from primitive to more advanced forms in terms of evolutionary development. In his interpretation, 5 subfamilies are considered, 3 basic, Illicinae, Todarodinae and Ommastrephinae and 2 intermediate ones, Todaropsinae, monotypic for *Todaropsis*, and Ornithoteuthinae. He considered *Todaropsis eblanae* more closely related to the Todarodinae than to the Illicinae, without, however, belonging to either subfamily, a point of view repeatedly stressed (Laptikhovskiy and Nigmatullin, 1999, Nigmatullin and Laptikhovskiy, 1999, Nigmatullin *et al.*, 2003). This peculiar isolation of *Todaropsis* with respect to the other species of the family is supported to a degree by a genetic study carried out on 16 ommastrephids species by Yokawa (1994). Recent studies on *T. eblanae* from the Atlantic and the Mediterranean (Dillane *et al.*, 2005) indicate the existence of at least 3 genetically isolated populations in the eastern Atlantic. This finding, along with the broad and unusually disjunct geographical distribution of the species, supports the need for further detailed studies on its identity and systematic status throughout its world wide range.

Literature: Mangold-Wirz (1963), Clarke (1966), Lu (1982), Roper *et al.* (1984), Roeleveld (1988), Nigmatullin (1992 [1991]), Gonzalez *et al.* (1994), Hastie *et al.* (1994), Yokawa (1994), Lordan *et al.* (1998a), Wormuth (1998), Laptikhovskiy and Nigmatullin (1999), Nigmatullin and Laptikhovskiy (1999), Hernandez-Garcia (2002b), Robin *et al.* (2002), Nigmatullin *et al.* (2003), Dillane *et al.* (2005), Okutani (2005), Hastie *et al.* (2009).