

# Chapter 1

## The genus *Illex* (Cephalopoda; Ommastrephidae): Characteristics, distribution and fisheries.

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**Abstract:** The genus *Illex* is representative of the family Ommastrephidae, which makes up most of world's tonnage of commercial squids. The ommastrephids, or "flying squids", are characterized by the smallest paralarva among the cephalopods, the rhynchoteuthion with tentacles fused into a proboscis, but grow rapidly into large powerful swimmers that range widely over the world's oceans. As this chapter illustrates, the genus is distributed throughout the Atlantic in a complex of closely related species that occupy diverse habitats along the continental margins. The relationships within this complex have long been debated by teuthologists and remain key to understanding the dynamics of recruitment to the highly productive but highly variable commercial stocks. This overview chapter gives a perspective for the next four chapters, which provide details of taxonomy and biology in the genus as a basis for the discussions of various aspects of recruitment in the rest of the volume.

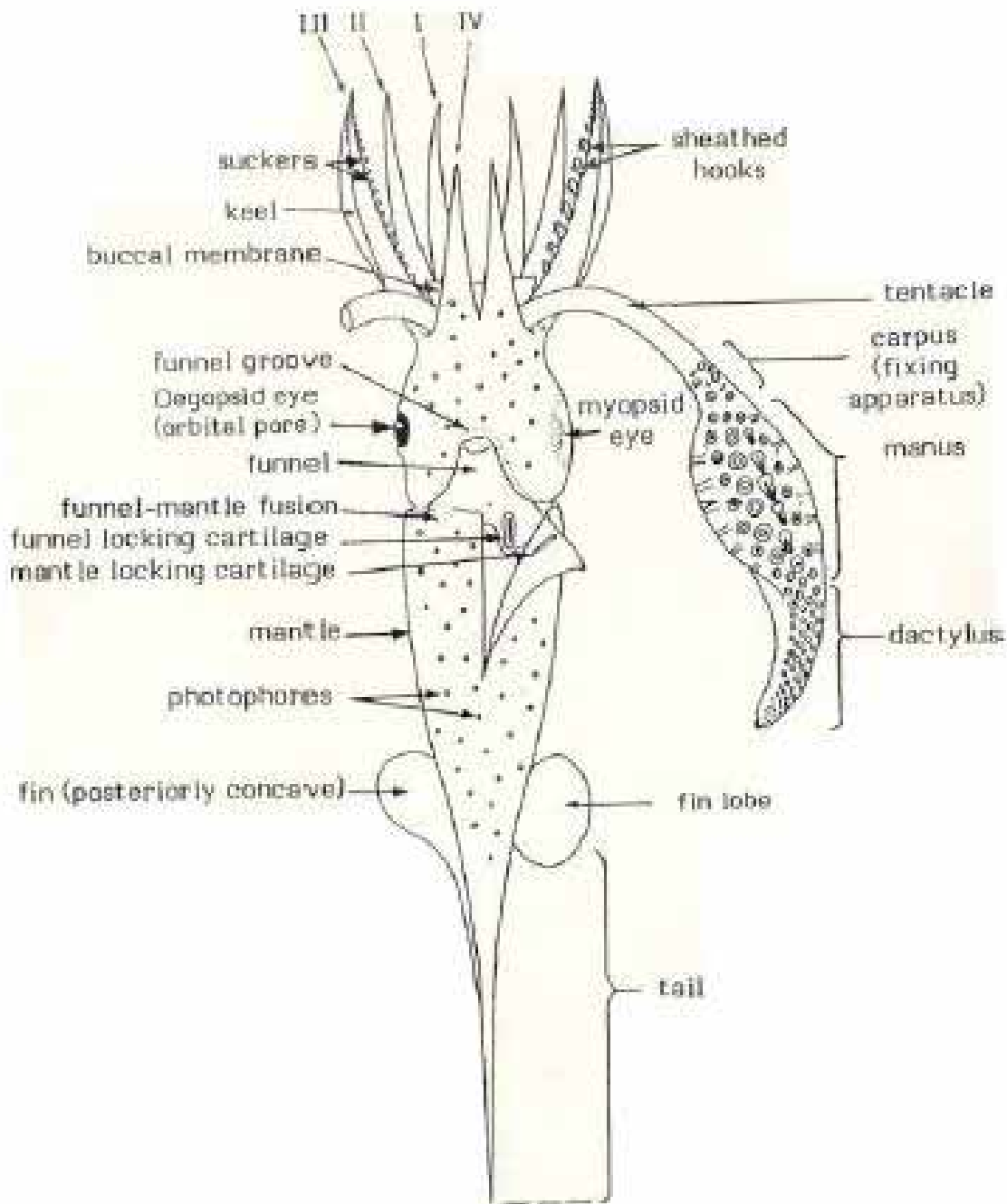
### 1 Introduction

The "flying squids" (Roper *et al.* 1984) of the family Ommastrephidae (suborder Oegopsida) account for about 65 percent of the world's commercial cephalopods (Brunetti 1990), which totalled 2.6 million t in 1991 (FAO 1993). Although perhaps less widely recognized than the inshore Loliginidae (suborder Myopsida), which are subjects of commercial and artisanal fisheries globally, ommastrephids are important in commerce and ecology. These oceanic/neritic squids were characterized by d'Orbigny for their powerful swimming and jumping and can be recognized by the open, cornea-less eyes, muscular, streamlined bodies and fins spanning less than 60 percent of mantle length (rarely >50 percent, Fig. 1.1). Also diagnostic and functionally important is the T-shaped funnel-locking apparatus (Fig. 1.2); this strong, efficient cartilaginous "snapfastener" holds the funnel and mantle together to maximize jet pressures (O'Dor and Webber 1991). The family can also be recognized in its unique "rhynchoteuthion" form as an embryo in egg masses or as a paralarva (this term is used by cephalopod biologists for hatchlings, acknowledging the fact that most cephalopods lack a distinct metamorphosis; Young and Harman 1988). In the rhynchoteuthion the tentacles are fused to form a characteristic trunk-like proboscis of unknown function.

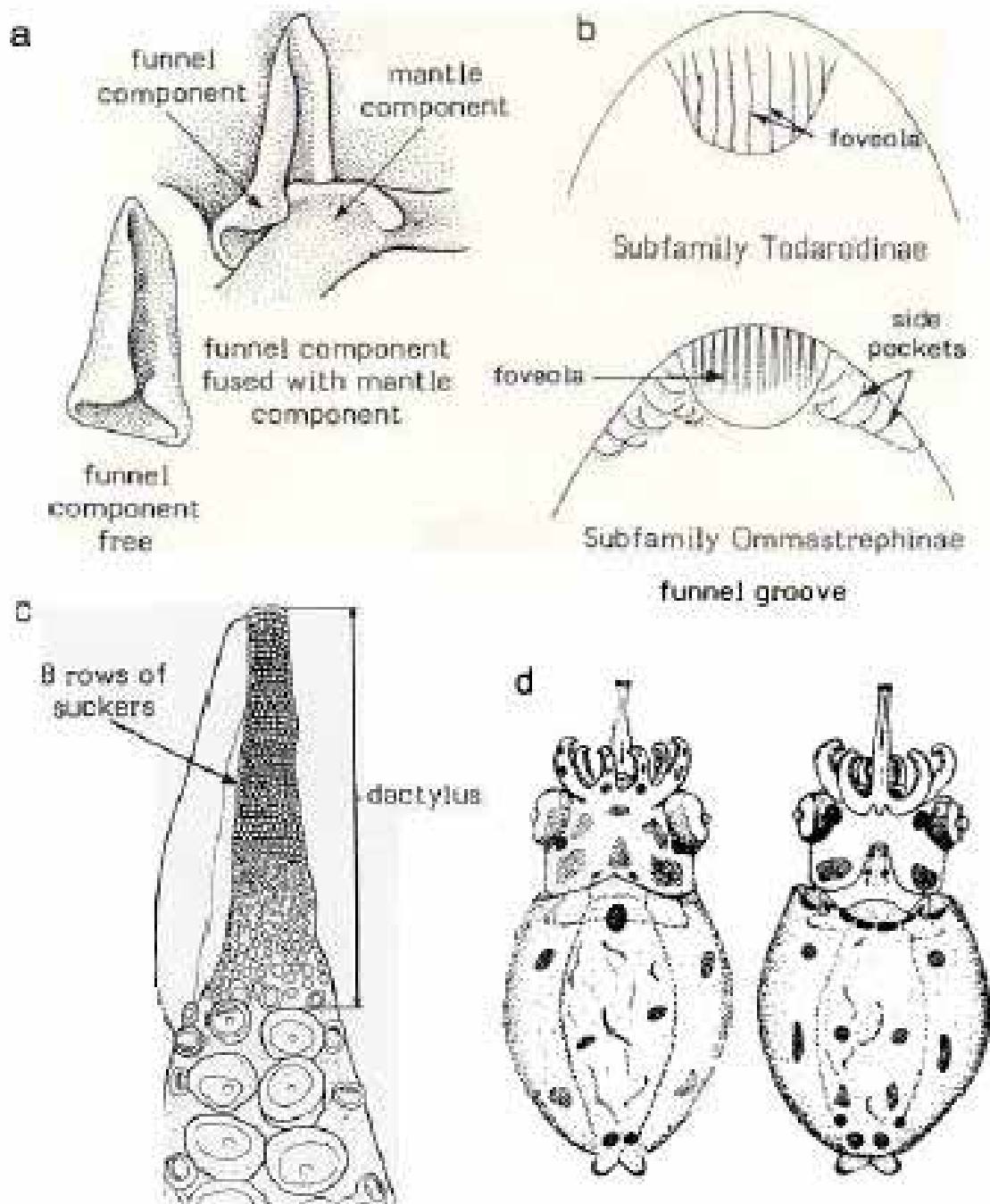
Nesis (1975, 1978, 1985) has argued that the major evolutionary trend among the Ommastrephidae (Steenstrup 1880) is from the neritic forms of the Illicinae and Todarodinae towards the more wide-ranging oceanic Ommastrephidae. Roeleveld's review (1988) generally supported this view and used the patterns of sucker teeth on the largest manus suckers, the handedness of the hectocotylyzed arm IV of the males (used in sperm transfer) and the structure of the three major elements of the hectocotylus as additional characters for distinguishing between members of this comparatively homogenous family. The need for locomotor optimization for an oceanic lifestyle may account for limited variation in general body form and the conservative nature of this family. If we view the success of the human fishery for the shelf-dependent neritic squids as a measure of their fitness failures, evolution towards a fully oceanic lifestyle certainly seems appropriate!

The annual yield from the subfamily Illicinae was 0.67 million t in 1991 (FAO 1993), representing 26 percent of the world's cephalopod catches and about 1 percent of the total world fishery. The Illicinae have eight rows of tiny suckers at the tip of the dactylus (Fig. 1.2c), rather than the usual four, and lack the central pocket (foveola) on the funnel groove that is diagnostic of the Todarodinae (Fig. 1.2b). Both lack the side

pockets and photophores of the third, more diverse subfamily Ommastrephinae. *Illex* is, at present, the only genus of subfamily Illicinae (Roeleveld 1988), and all species belong to the nektonic benthic-oceanic group in the ecological classification of Nesis (1985).



**Figure 1.1.** A composite diagram illustrating basic squid features used to identify *Illex* in the text, reproduced from Roper *et al.* (1984) with permission FAO



**Figure 1.2.** Details of squid features: (a) examples of the strong T-shaped locking cartilages diagnostic of the powerful swimmers of the family Ommastrephidae; (b) funnel grooves distinguish between subfamilies, ranging from the undifferentiated Illicinae (absent feature, not illustrated) to the complex Ommastrephidae; (c) tentacle dactylus characteristic of *Illex*; (d) rhynchoteuthion paralarvae of *Illex argentinus*; reproduced from Roper *et al.* 1984 with permission FAO, except (d) from Vidal 1994 with permission *Antarctic Science*.

The genus *Illex* is currently considered to include four closely related species, all limited to the Atlantic (Roper *et al.* 1969, Lu 1973, Roper *et al.* 1984, *see Chapter 2*). The species have oscillated between full and subspecies status since 1900 (Pfeffer), with Joubin (1924) considering them only local races, and Nesis (1985, 1987) the most recent to argue the subspecies case. Many workers have found the distinctions difficult to make (e.g. Cairns 1976, Laptikhovskiy and Nigmatullin 1993), particularly in an applied context, because the characters are highly variable and the best characters, associated with the hectocotylus, can only be used in mature males. This is of little value for monitoring recruitment of juveniles in an area of species overlap. Even allozymes indicate that *Illex* specimens from Europe, North and South America show fewer genetic differences than the two *Nototodarus* species from New Zealand (Yokawa 1994).

This volume is certainly not intended as a taxonomic work, but if we accept Mayr's (1942) definition of biological species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups", the question of whether these species interbreed becomes important to understanding recruitment variation and population dynamics in some of the world's largest squid fisheries. *Illex illecebrosus* (Lesueur, 1821) and *Illex argentinus* (Castellanos, 1960) have each produced over 100 000 t per year ( $> 10^9$  individual squid) in some years and appear to be confined to relatively limited ranges generally linked to the large Gulf Stream and Brazil Current western boundary systems, respectively (Fig. 1.3). *Illex coindetii* (Verany, 1837), in contrast, is distributed off four continents while *Illex oxygonius* Roper, Lu and Mangold, 1969 appears mainly along the southeast U.S. coast. It is the similarity of the animals and the diversity of habitats and population structures (Arkhipkin 1993) that make this group a good test case for a comparative approach to understanding recruitment.

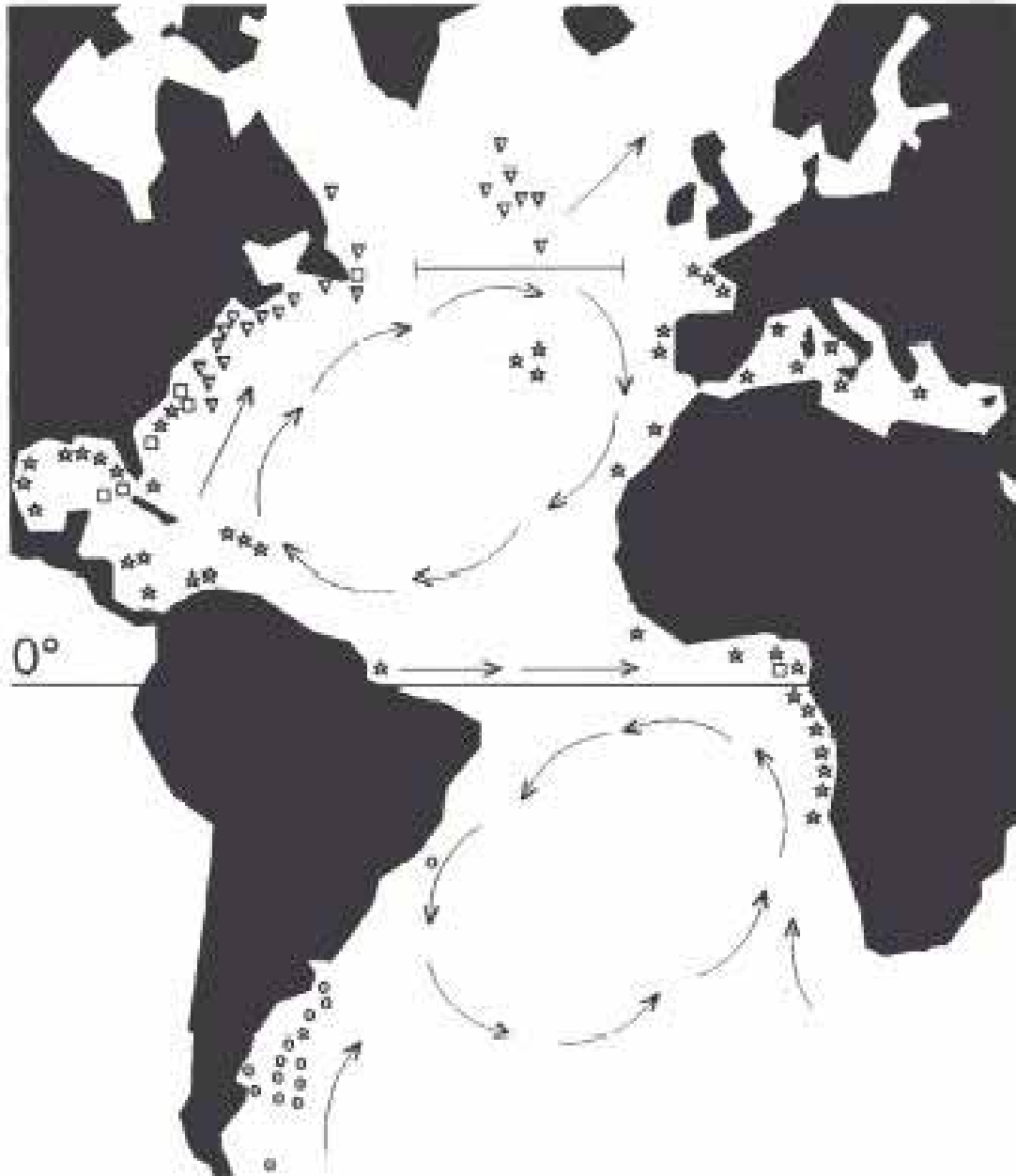
## 2 Distribution

Before focusing on the characters used to separate these species, let us consider what links them together. Figure 1.3 emphasizes the North and South Atlantic gyres, which can move objects, including animals, at remarkable speeds. Passive satellite-tracked drifters have travelled from Florida to the Azores in as little as four months (Kirwan *et al.* 1976). These squids can also swim actively at speeds averaging up to  $0.3 \text{ m s}^{-1}$  (O'Dor 1988). The bar on the map (Fig. 1.3) between the Flemish Cap, off Newfoundland, and Great Sole Bank, off Ireland, indicates the length (not the location) of the longest individual spawning migration of an *I. illecebrosus* recorded from tag recapture (Dawe *et al.* 1981). Given this adult mobility and the evidence that *Illex* eggs (O'Dor and Balch 1985), paralarvae and juveniles (Rowell *et al.* 1985, Rowell and Trites 1985, Dawe and Beck 1985) can be transported thousands of kilometres in these currents, one must wonder if any of these squids are really reproductively isolated? They are not really geographically isolated. Calculations indicate that it is not impossible for an individual squid to do a complete circuit of one of the gyres in less than the expected one year between being spawned and spawning. This is not likely, but even a half circuit would provide ample opportunity for gene flow.

Lu (1973) recognized that the oceanography of the North Atlantic favoured the westward movement of *I. coindetii* and might account for its occurrence in the Caribbean and the Gulf of Mexico. Is this a one-way gene flow or is there also a return? Is it possible that *I. coindetii*'s extensive distribution over  $80^\circ$  of latitude and  $120^\circ$  of longitude (*see Chapter 4*) is just part of a single interbreeding complex distributed over two gyres rather than a separate species? The evidence that even eggs in their large gel balloons (*see Chapter 5*) can drift in these gyres at speeds of up to 1 000 km/week (Rowell and Trites 1985) was not available to Lu, so total mobility was underestimated. Eggs, paralarvae and juveniles could cross the Atlantic in one direction in one generation and return in a second generation after breeding (or interbreeding, if the local population remains cross-fertile and there are no behavioural barriers to mating) as adults.

There is no direct evidence for movements on this scale as yet, although genetic or isotopic tags may eventually make such studies possible (Hatanaka *et al.* 1993). There is, however, some indirect support. Lu

(1973) examined *Illex* of 9–15 mm mantle length (ML) collected in the Azores (Degner 1925) that were assumed to be linked to European stocks of *I. coindetii* (there are no distinguishing characters at this size). The Azores are marginally closer to Europe than North America (the Grand Banks), but the warm surface waters that wash over them from the west are the most likely source of such small *Illex*. After the Gulf Stream bifurcates off the southern tip of the Grand Banks, its southern branch heads towards the Azores as the North



**Figure 1.3.** The known distribution of squid from the genus *Illex* according to Lu (1973), supplemented with data from Korzun *et al.* (1979) and Lipinski (1981); triangle = *I. illecebrosus* (Lesueur, 1821); star = *I. coindetii* (Verany, 1837); square = *I. oxygonius* Roper, Lu and Mangold, 1969; circle = *I. argentinus* (Castellanos, 1960); major ocean currents are indicated by arrows; the bar between Newfoundland and Ireland represents the length of the longest recorded migration of a tagged *I. illecebrosus* (2 300 km in 107 days, Dawe *et al.* 1981). (Modified from O'Dor 1995)

Atlantic Current moves off towards Britain. The core of the Gulf Stream has been characterized as a source of *Illex* paralarvae (Dawe and Beck 1985, Rowell and Trites 1985) and juveniles have been collected as far east as 40°W (Dawe *et al.* 1982). Korzun *et al.* (1979) reported collecting adult *I. illecebrosus illecebrosus* on banks of the mid-Atlantic ridge north of the Azores at 30°W. They suggested that these may be linked to "downstream" reports of *I. illecebrosus illecebrosus* in Iceland, Greenland (Irminger and West Greenland currents) and northern Europe. Although some of these reports are questionable (Lu 1973), the physical oceanography is consistent, and one of us (MRL) has recently re-examined Adam's (1952) specimens from the Bristol Channel and confirms his diagnosis as *I. illecebrosus*. Similar patterns have also been characterized in the South Atlantic for the larvae of less mobile animals like the spiny lobster (Pollock 1990).

### 3 Temperature variants

If *Illex* are transported east across the Atlantic, as speculated above, could *I. coindetii* segregate to the Azores and *I. illecebrosus* to the northern banks? Lu (1973) described *I. coindetii* as a warm-water form based on the water temperatures where it was found, and *I. illecebrosus* and *I. argentinus* as boreal and anti-boreal cold-water forms, respectively. We now know, however, that *I. illecebrosus* eggs develop and survive well at 26°C, require a minimum of 13°C to hatch (Balch *et al.* 1985), and that their paralarvae move out into cooler waters from the Gulf Stream as they grow during transport. Numerous newly hatched *Illex* rhynchoteuthion paralarvae have been collected in the Florida Current just north of Cape Canaveral, a suggested spawning area for *I. illecebrosus*, but some have also been collected as far south as Miami (Rowell and Trites 1985), which would make them *I. coindetii* based on adult distribution. We cannot be sure, as there are no characters that distinguish *Illex* species at the paralarval and juvenile stages, but it is possible that a preference for higher temperatures would lead to a natural separation of the two species as *I. illecebrosus* moves out into colder water and leaves *I. coindetii* in the southern branch of the Stream.

The above scenario for segregation of temperature "forms" assumes that genetic differences between species produce both physical character differences and temperature preferences. An alternate (and simpler) hypothesis is that temperature differences cause character differences by altering growth patterns. How can we tell whether all *Illex* that live in warm water are *I. coindetii* or whether any *Illex* that lives in warm water will grow to have the characters of *I. coindetii*? The best answers would come from rearing individuals from the same spawn in different temperature regimes, but this has so far proved impossible for ommastrephids (Balch *et al.* 1985). The alternative of looking at characters like RNA or DNA sequences that are not altered by temperature holds promise, but has not yet produced answers at this level (*see Chapter 10*). A third approach is to reconstruct the thermal history of individuals from analysis of statolith composition. O<sup>18</sup>/O<sup>16</sup> (Margosian *et al.* 1987) and Sr/Ca (Radtke *et al.* 1990) ratios both show potential for this approach, but applications to cephalopods have been limited (Rodhouse *et al.* 1994, Jackson 1993, Young 1993).

Why ask this question? There is clear evidence from Mediterranean *I. coindetii* individuals of known age that different seasons produce squid that differ in maximum size, weight-at-length and size at maturity (*see Chapter 4*). This probably reflects different temperature regimes, although squid could maintain constant temperatures by varying their depth distribution. Alterations in weight-at-length imply changes in robustness and width-to-length ratios, which are among the characters used to distinguish between *Illex* species. Size at maturity also likely influences the development and relative length of the modified part of the hectocotylus (Coelho *et al.* 1985), which are critical characters for this group.

These differences, of course, only suggest temperature-dependent variation in development, as does Coelho and O'Dor's (1993) evidence of a latitudinal cline in size at maturity in *I. illecebrosus*. The alternative is that the different seasonal spawning groups are sufficiently isolated genetically that they exhibit distinct growth and maturation patterns regardless of temperature. Carvalho *et al.* (1992) found evidence of sufficient microgeographic differentiation in *I. argentinus* allozymes to suggest that there may be subspecies or species

in the south Atlantic that have gone unrecognized on morphological bases but can be distinguished genetically. It is critical, from a management and recruitment perspective, to distinguish between stocks that look different but interbreed to return recruits to the fishery and those that look the same but are reproductively isolated and physiologically unique to the extent that they cannot be replaced from adjacent (in time or space) stocks once overfished (Sinclair 1988).

#### 4 Reproductive isolation

Genetic differentiation occurs either when there is strong selection for particular characters (genes resulting in characters, actually), as occurs when environmental conditions change, or when long isolation results in genetic drift of characters. Selection implies that in certain circumstances a particular character increases fitness, resulting in an increased proportion of offspring with that character to the eventual exclusion of alternate characters. Drift implies the exclusion by random chance of characters, which normally takes longer. Small populations offer fewer chances to avoid exclusion and therefore either selection or drift will occur faster when associated with a population "bottleneck". Sex-related characters, which alter the probability of reproductive success in some matings, can both increase selection and alter the effective population size, leading to rapid changes in the genetic composition of the population.

Speciation is the result of complete reproductive isolation and implies the absence of gene flow. This could occur if populations become (1) geographically, (2) temporally, (3) behaviourally or (4) physiologically isolated. Full geographic isolation requires that the ranges of the adult population never overlap (even in a second generation). Temporal isolation requires that adults from two populations never mature at the same time. Behavioural isolation might occur if two populations were gradually selected for different temperature preferences until they no longer occupied the same habitats at the same time or, more directly, if the mating behaviours of one sex no longer produced appropriate responses in the other. Infertility resulting from gamete incompatibility at the cellular or nuclear level are examples of the fourth category.

Given the properties of the gyres outlined above, geography does not appear to be a barrier to multigenerational gene flow in *Illex*, provided that drifting early life-history stages can interbreed with local stocks downstream. A model for the interaction of time, space and temperature in regulating life cycles, outlined in Chapter 11, indicates that there are constraints placed on migration routes by the spawning season and vice versa. These constraints may tend to reinforce some successful strategies and limit the success of stragglers, but it is hard to imagine that complete temporal isolation would arise in such a complex and variable environment.

Mating behaviour might be a serious barrier in loliginids, which spend long hours in complex mating rituals where one wrong move or colour pattern could result in exclusion from mating (Arnold 1962, Sauer *et al.* 1992), but this seems less likely among *Illex*. In several months of observation of spawning schools of *I. illecebrosus* in captivity, no distinctive mating rituals were observed (O'Dor 1983). Spermatophore transfer can occur in only a few seconds (Arnold 1984) and, in *I. illecebrosus*, almost without interrupting other activities (O'Dor 1983). Males have been observed transferring spermatophores to other males and to *Loligo pealei* in captivity (O'Dor *unpubl. data*), which suggests a fairly casual attitude to mate selection. Perhaps selectivity is sacrificed for speed when males mate with larger and potentially cannibalistic females.

There is almost no evidence for or against physiological isolation in ommastrephids because they are difficult to maintain in captivity. Thermal requirements for embryo development in *I. illecebrosus* and Mediterranean *I. coindetii* seem similar (Boletzky *et al.* 1973, O'Dor 1983), which would tend to bring the species together rather than isolate them. Given that temperature in most oceans varies vertically over tens of metres as much as it does over hundreds of kilometres horizontally, it seems unlikely to isolate squids, which have a strong diurnal vertical migration pattern at any age. Likewise, we are aware of no direct studies

of sperm and egg compatibility in any cephalopod, although this question could probably be tested through artificial fertilization techniques (Arnold and O'Dor 1990).

## 5 Species versus stocks

The current systematic view of *Illex* species seems rather asymmetric in relation to the fisheries. There are three identified species potentially involved in the North American fishery, and only one in the South American fishery. Both fisheries range over complex hydrographic features, including warm and cold currents and the runoff from major river systems. Both can produce at the  $10^5$  t level, although the southern fishery is larger and more stable. Since species diversity is usually associated with stability, one might have expected the reverse. The rest of the ocean contains only one species, which over its entire range sustains fisheries only at the  $10^4$  t level. What keeps *I. coindetii* from becoming abundant and *I. argentinus* from dispersing?

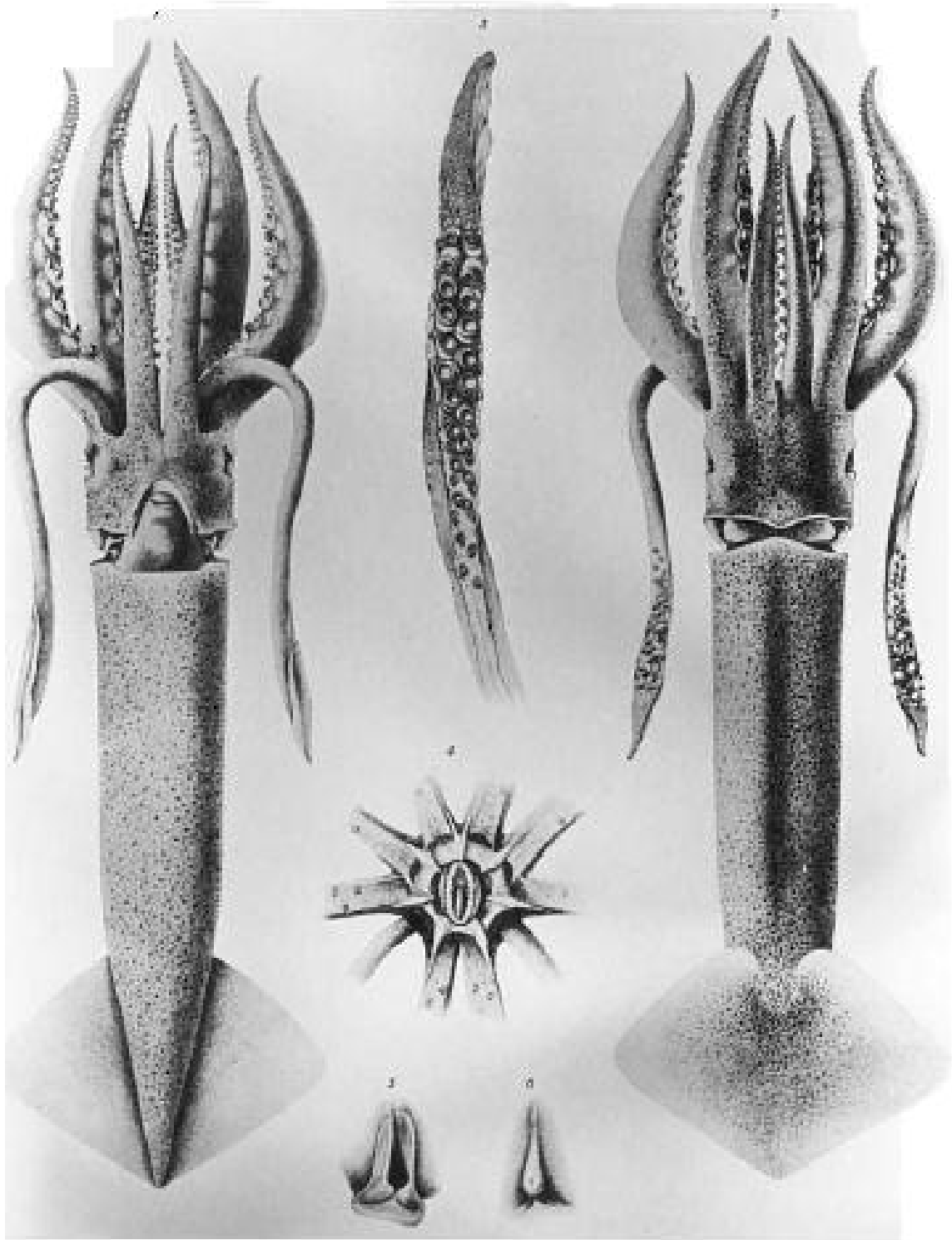
Several ommastrephid species have been characterized as having seasonal spawning groups, and for both *I. illecebrosus* and *Todarodes pacificus* major collapses of the fisheries have been associated with the disappearance of the winter-spawning groups which reach the highest latitudes. Such current-associated stocks have been suggested (Froerman 1984, O'Dor 1992, O'Dor and Coelho 1993) as the focus of the selection regimes for the evolution of oceanic squids (*sensu* Nesis 1978). Other spawning groups have maintained production at reduced levels, but in both cases the high-latitude stocks have not recovered in over a decade. Are these seasonal stocks reproductively isolated to the extent that there is little or no recruitment from other stocks? If the isolation is this complete are they separate species? Was it really *I. illecebrosus* that collapsed, while *I. coindetii* and/or *I. oxygonius* remained stable in their more southerly range? Would it clarify the fisheries management and recruitment problems to subdivide *T. pacificus*, *I. argentinus* and even *I. coindetii* to reflect cryptic population structure? Studies aimed at fisheries management or recruitment prediction must be designed in such a way that these fundamental questions about population dynamics are addressed. Systematic nomenclature is intended to describe natural relationships, but as commercial activity becomes a dominant component of "nature", it needs the flexibility to reflect changes in stocks, populations and "species" resulting from this impact. Such changes may be cryptic and best reflected in characters other than morphology.

## 6 *Illex* species

The general features of *Illex* are illustrated in Fig. 1.4 and a key to mature adults of the currently accepted *Illex* species is provided in the next chapter, but these species generally cannot be distinguished as juveniles. Despite some valuable new characters, *Illex* keys still depend heavily on relative dimensions in morphometric characters and statistical differences in meristic characters. Great care must be used in applying these to individuals of different sizes (Voight 1991a,b), maturities and coming from different regions (Roeleveld 1990). Since such characters may reflect seasonal growth, nutritional state and maturity, they may not be useful in attempts to understand population dynamics and recruitment. Correct species identity at all phases of the life cycle is a prerequisite for understanding population dynamics and recruitment and an aid to stock discrimination. Population variables such as maturity must be recognized and recorded correctly to maintain acceptable signal to noise ratios in stock data.

Schuldt (1979), for example, recommended using the percentage hectocotylus modified as an index of male maturity in *I. argentinus*, which suggests that this percentage changes as squids develop. Does the lack of modification in *I. illecebrosus* just reflect the fact that they are fished in feeding areas, in contrast to *I. argentinus* which were initially fished near spawning areas? The validity of such secondary sexual characters must be verified on large and diverse samples through the life cycle and, if possible, be correlated with age





**Figure 1.4.** Illustrations of *Illex illecebrosus coindetii* Verany specimens reproduced from Pfeffer (1912); (1,2) ventral and dorsal views at natural size of a female from Naples; (3) tentacle club from same specimen x 2.5; (4) buccal surface of a specimen from the Adriatic Sea x 2; (5,6) funnel and mantle cartilages of specimens from Messina

as well as size and other measures of maturity. Special care should be exercised when examining individuals from areas of overlapping species distributions. Lipinski (1981) has recorded an intermediate modification in an individual from the Cape Hatteras area – a hybrid or an environmental variant?

The available data do not resolve these questions, and it is clear that additional characters independent of sex and life-history stage are needed for population studies in areas of species overlap. These may include DNA sequences to resolve the more complex questions of cryptic species, hybridization and seasonal populations (*see Chapter 10*).

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