Chapter 8

Life-history reconstruction

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Abstract: An indirect reconstruction of squid life history has been attempted through interpretation of the accretive growth of two hard structures: the statolith and the gladius. The statoliths are paired calcareous structures situated in the squid's balance organs. Daily concentric rings, observed on the ground surface, have been directly validated in a few species including the ommastrephid *Illex illecebrosus*. The structure provides a reliable method of cohort analysis and estimates growth models, growth rates and life spans. Statolith rings have also been widely used to age important life-history events such as ecological transitions, sexual maturation, mating and spawning. Comprehensive applications in squid population ecology have derived from the comparison of age schedules estimated for these life-history events among different groups including species, sex groups, seasonal and geographic populations, and generations. The gladius is the squid's internal shell which grows by the accretion of chitin layers in three planes, all of them suitable for age and growth studies. The ostracum layer accounts for the longitudinal growth of the gladius and is normally the only layer available in loliginids and ommastrephids. Growth increments observed directly on the dorsal surface of the ostracum have not been directly validated but generally support comparisons with statolith daily rings. Due to structural change, early growth increments cannot be visualized and consequently, the layer does not provide an estimation of individual age. Nevertheless, because the ostracum correlates strongly with the mantle length, gladius growth increments are excellent estimations of somatic growth rates. The most important applications of gladius growth increment have been based on the estimation of mean size-specific growth curves and the reconstruction of individual growth histories. In *I. illecebrosus* and other ommastrephids, both approaches have assessed life-history transitions, differential growth between sexes and inter- and intra-populational growth variability, and addressed the impact of food and temperature gradients on squid growth. Age- and growth-related applications in population ecology, provided by statolith and gladius respectively, may yield important distinctions about population structure, biological attributes and selective pressures acting upon individuals, essential for the understanding of recruitment processes.

1   Introduction

Life-history studies of different species of squid are among the most important and interesting aspects of cephalopod ecology. In contrasto octopuses and cuttlefish, neritic and oceanic squids have only rarely been cultured in captivity throughout their life cycle, except for several species of inshore loliginids (*Loligo opalescens*, Yang *et al.* 1986; *Sepioteuthis lessoniana*, R. Hanlon, Marine Biomedical Inst. Galveston, Texas *unpubl. data*). The highly mobile nektonic life style and short life span (usually not exceeding one year) of commercial oceanic squids further impede direct investigations of their life history in the sea; it is difficult to organize large-scale surveys covering the entire population's distribution range during such a short ontogenesis.

Thus, it is valuable to study squid life history indirectly using hard structures that document and date the main patterns of their ontogenies. The presence of periodic (annual and subannual) features in the bony structures of various fishes distributed from polar to tropical waters is well known (reviewed by Campana

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Neilson 1985). Moreover, Panella (1971) and a number of subsequent researchers found daily periodicity in increment deposition within the otoliths of many teleost fishes. These findings allow estimation of age and daily growth with high accuracy.

During the past 30 years, growth increments have been found in almost all hard structures of cephalopods except horny sucker rings. Clarke (1965) was the first to examine the presence of narrow growth increments on mandibles of *Moroteuthis ingens* and within statoliths of some ommastrephid squids (Clarke 1966). Unfortunately, the periodicity of increment formation was not interpreted because the variables affecting growth increment deposition were unknown. Septa in the cuttlefish sepion seemed to be useful for age estimation (Choe 1963), but Richard (1967, 1969) revealed that internal septum formation was temperaturevariable. LaRoe (1971) observed growth increments in the gladius of *Sepioteuthis sepioidea*, but failed to assess their periodicity.

Although a number of cephalopod hard structures bear growth increments (gladius, sepion, statoliths, mandibles, crystalline lens), initially only statoliths were chosen for age and growth studies in squids (Lipinski 1978, Spratt 1978, Hurley and Beck 1979). Growth increments in the gladius are also currently being validated (Bizikov 1991, Perez *et al.* 1996). Successful indirect investigations of squid life histories by growth increment analysis should be possible after resolving the following questions:

1) When do the growth increments start to form?
2) What causes the formation of growth zones and checks, and how are they related to various ontogenetic stages?
3) Do the widths of growth increments correspond to the growth rates of the squid body?

In fish, all these questions must be addressed for each species or even population (Campana and Neilson 1985). This review focuses on application of analysis of statolith and gladius microstructure to life-history reconstruction in squids.

2   Statoliths

2.1 Statolith preparation and reading techniques

Statolith preparation for microstructure examination is multi-phasic, as has been thoroughly described and reviewed in recent works (Arkhipkin 1991, Dawe and Natsukari 1991). After extraction from the cartilaginous skull by either surgical or chemical methods, statoliths are stored in 95 percent ethanol or kept dry. Later, statoliths are attached to microscope slides with various mountants: Canada balsam (Lipinski 1978), thermoplastic cements (Hurley and Beck 1979) or polymerizing plastic media (Kristensen 1980, Rodhouse and Hatfield 1990a). Statoliths from larvae and juveniles may be examined intact after embedding in Eukitt (Lipinski 1978) or Canada balsam (Arkhipkin 1991) whereas larger statoliths are ground and polished from one or both sides with carborundum blocks or sandpaper (Dawe and Natsukari 1991). Thin sections of statoliths are embedded in Canada balsam or other mounting media, and become ready for examination under light microscopy with magnifications of 400–600x. Details of statolith microstructure and subsequent sections concerning statolith development are based largely on data collected from all three *Illex* species (Table 8.1).

2.2 Statolith structure and composition

Statoliths are calcareous structures situated within the squid equilibrium organs, or statocysts. Statolith shape is complicated and seems to be species-specific (Clarke 1978). Statoliths are composed of calcium carbonate ($CaCO_3$) in the form of aragonite crystals. Crystals of $CaCO_3$ (95 percent of statolith total weight)

lie within the mucoprotein matrix (the remaining 5 percent). An inverse relationship between the proportion of organic material in the statolith and size of squid exists such that the statolith becomes more calcified as body length increases. The protein matrix of the statolith consists predominantly of acidic amino acids and is high in aspartic acid, glutamic acid and glycine. This accounts for easy mineralization of the proteinaceous template. It has been suggested that the stable isotopic composition of oxygen and carbon of the statolith carbonate may provide information on past environmental conditions such as temperature for *Illex illecebrosus* (Radtke 1983). Similarly, statolith Ca:Sr ratios can be used for the same purpose; preliminary results have been presented for the ommastrephid *Martialia hyadesi* (Rodhouse *et al.* 1994). This is a new field in both fish and squid ecological studies and requires further investigation.

2.3 Nucleus and start of increment formation

Crystals of carbonate radiate from the initiation point of statoliths, termed the "focus" (Natsukari *et al.* 1988). As a rule, a single calcium concretion lies in the focus of a squid statolith (Fig. 8.1), whereas in fish otoliths there are often several or even numerous concretions (primordia) and the number of concretions may vary within a single brood of fish (Neilson *et al.* 1985). Rarely, an additional focus is seen within various growth zones of the statolith (Fig. 8.2). The origins remain unknown, but it may be that additional foci appear as a result of damage to the outer statolith covering and subsequent precipitation of carbonate concretion into the damaged site.

The nucleus surrounds the focus and the first growth increment is its outer border. In *Illex*, the nucleus is oval-shaped with a maximum diameter oriented in a plane toward the lateral dome. The nucleus is small with similar maximum diameter in all three species: 25–31 µm (Table 8.2).

Earlier, there were two alternate hypotheses concerning the time of nucleus formation. Radtke (1983) considered that the first growth ring appeared at hatching and used it as the starting point for counting subsequent growth increments in *I. illecebrosus*. Morris and Aldrich (1985) hypothesized that the nucleus appeared in early embryogenesis, and that *I. illecebrosus* hatched with statoliths consisting of the nucleus and a number of growth increments (about 40). Investigations of Dawe *et al.* (1985) and Balch *et al.* (1988) supported the first hypothesis; hatchlings of *I. illecebrosus* had oval statoliths with a diameter (20–23 µm) roughly corresponding to the diameter of the nucleus observed in statoliths of juveniles and adults. Moreover, statoliths of the largest larva hatched in captivity (42 µm in diameter, estimated age 1–2 days) bore the broad increment distal to the nucleus that was similar in width to the initial increments in statoliths of older larva (Balch *et al.* 1988). It was thus confirmed for *I. illecebrosus* that the nucleus represents a hatcWing statolith and the border of the nucleus represents the appropriate location from which to initiate counts (Balch *et al.* 1988).

Table 8.1. Statolith samples of three *Illex* species[a]

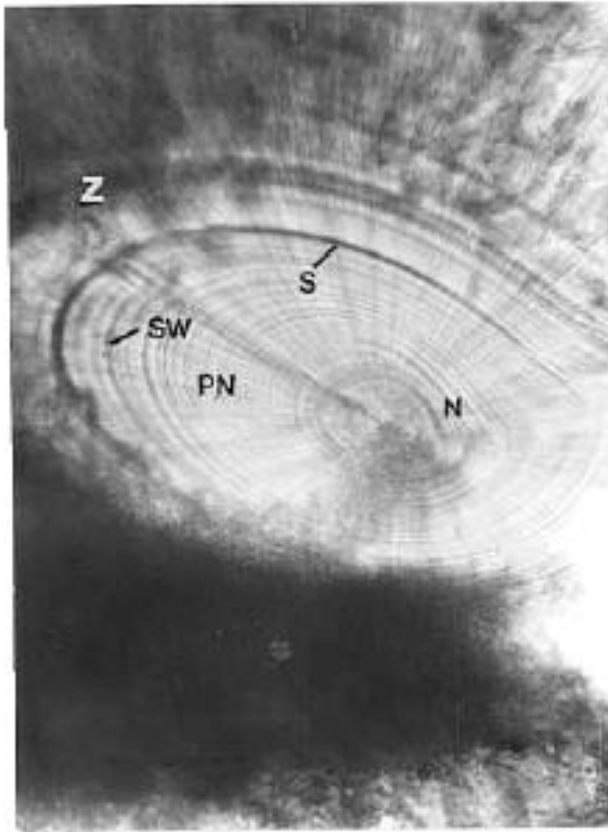| Species	Mantle length cm	Area	Sampling period	Number of statoliths
Illex illecebrosus	12.5-21.7	Scotian Shelf	1984	90
	1.9–12.8	oceanic waters off Scotian Shelf	1981	55
Illex argentinus	1.7–39.0	Patagonian Shelf	1982–90	3350
Illex coindetti	4.2–30.0	West Sahara Shelf	1987	112
	5.1–19.0	Sierra Leone	1987	60

[a] From Arkhipkin 1989

Figure 8.1. (above) Statolith microstructure of *Illex argentinus*; nucleus (N), postnuclear zone (PN), stress mark within PN (SW), stress mark on the border of the PN and dark zone (S), dark zone (Z)

Figure 8.2. (below) Statolith microstructure of *Illex argentinus*: focus (F) and additional focus (AF) in the postnuclear zone
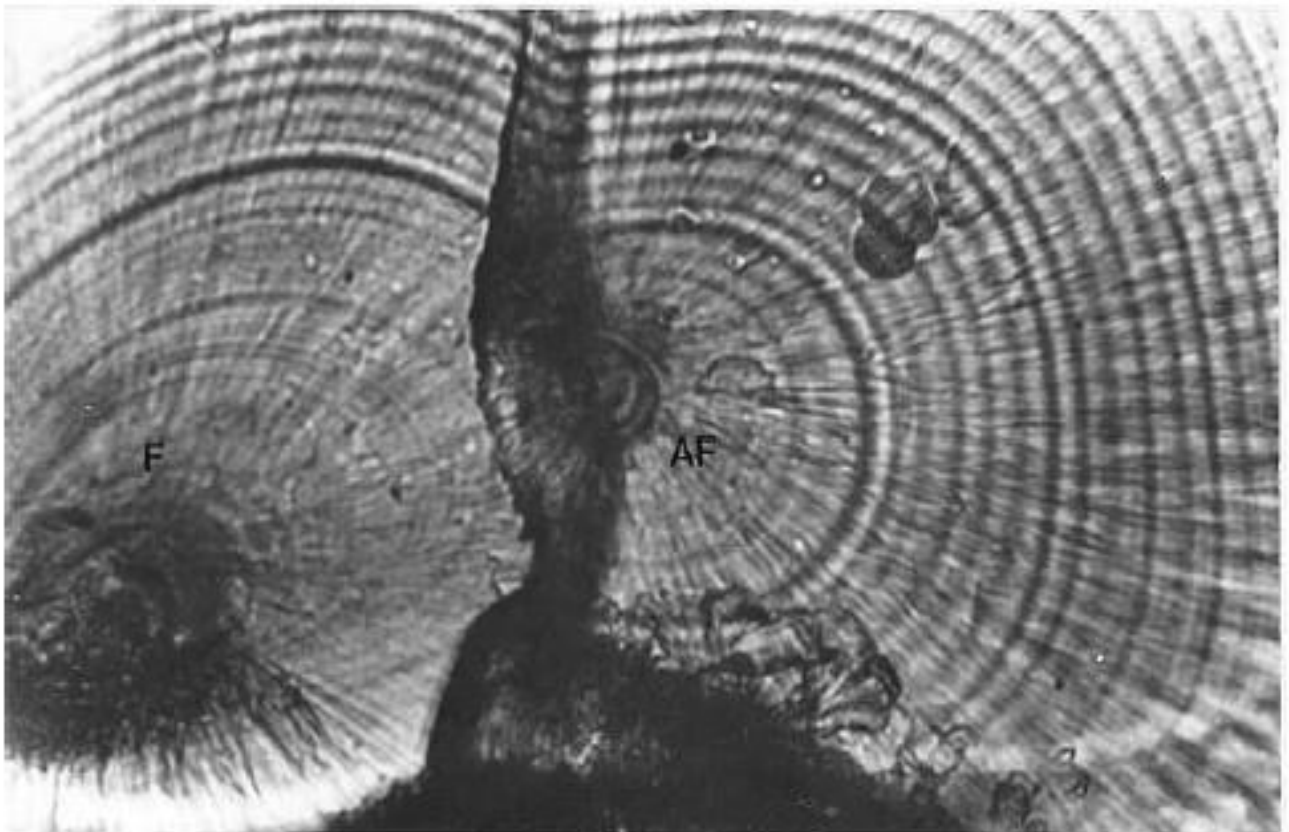
Table 8.2. Nucleus diameter (µm), mean number (N) and width (W) of growth increments within different growth zones of *Illex* statoliths[a]

Species	Nucleus	Postnuclear zone		Dark zone		Peripheral zone	
		N	W	N	W	N	W
Illex illecebrosus	25–28	37–43	2.5–3.5	120–130	2.5–5	1–30	2.0–2.8
Illex argentinus	28–31	38–42	1.5–3	145–195	2–5	1–120	1.5–3
Illex coindetii	25–28	36–40	2.4–2.8	63–98	4.5–7	5–131	2.4–3.5

[a] From Arkhipkin 1989

2.4 Growth increments and their interpretation

Outside the nucleus of ground statoliths of adult *I. illecebrosus*, there are numerous narrow growth increments forming three main growth zones (or regions): the postnuclear, dark and peripheral zones (R1, R2 and R3 regions of Morris and Aldrich 1985, respectively). Each growth increment consists of both a narrow, mainly protein, discontinuous ring and a wide, light, mainly aragonite ring (Kristensen 1980). Interpretation of the period of increment deposition has varied. The first researchers (Lipinski 1978, Spratt 1978) assumed that fine growth increments lying within the nuclear region ("juvenile" or postnuclear zone, Lipinski 1978) were daily, whereas increments in the peripheral zones were thought to be formed monthly. Later, Lipinski (1979) changed his opinion on the monthly periodicity of the outer growth increments and suggested they were also daily. However, clear evidence of daily periodicity of the statolith growth increments was required to confirm interpretations (Hurley and Beck 1979, Lipinski 1980).

The principal method for estimating the periodicity of increment formation is to rear squid from eggs and count growth increments in the statoliths of these animals of known age. A second method is to put "time" marks into the statoliths. Squid culture was used successfully with *Loligo opalescens* (Hixon and Villoch 1984, Yang *et al.* 1986), *S. lessoniana* (Jackson *et al.* 1993) and paralarvae of *Abralia trigonura* (Bigelow 1992), but its application to *I. illecebrosus* failed due to difficulties in maintaining larvae for more than a few days (O'Dor 1983, Balch *et al.* 1988). The "time"-marking method was used on adult *I. illecebrosus* in the Dalhousie University Aquatron Laboratory (Hurley *et al.* 1983). During the experiments, one animal was fed a shrimp stuffed with tetracycline HCI, and another specimen was fed two shrimps that had been soaked in a solution of strontium chloride. After feeding, the first animal lived 24 days and the second one 17 days. Statoliths of both squid were processed after death. Both substances were incorporated into the statoliths; the strontium mark was narrow, while the tetracycline mark spread over six or seven increments. Numbers of growth increments that could be counted from the mark to the outer edge of the statolith were 26 and 17, respectively. These counts closely corresponded with the differences between the time of marking and the death of the animals. Subsequently, a total of eight *I. illecebrosus* were administered statolith chemical markers; there was close agreement between the number of growth increments and the time (in days) elapsed after marking (Dawe *et al.* 1985). These investigations confirmed the hypothesized daily periodicity of growth increment formation in *I. illecebrosus*. This daily periodicity is likely to be true for congeneric *Illex argentinus* and *Illex coindetii* as well.

Environmental conditions influencing increment formation in squid statoliths remain unknown. The deposition of increments in statoliths may not depend on feeding regime and water temperature, and could be controlled by pH changes in the statocyst fluid, photoperiod and/or an intrinsic zeitgeber (Dawe *et al.* 1985, Morris 1991a,b, 1993, Lipinski 1993, Jackson 1994).

Stress marks, or checks, are often observed in ground statoliths. They are of two types, different in origin: complete (along the whole outline of the statolith) and incomplete (developed in some sections).

In some squids of the family Loliginidae (*Photololigo edulis*, Natsukari *et al.* 1988, *Loligo vulgaris*, Natsukari and Komine 1992), in *Gonatus fabricii* (Kristensen 1980) and in *Todarodes sagittatus* (Rosenberg *et al.* 1981), second-order bands have been noted consisting, on average, of 14 growth increments, corresponding to the lunar cycle. In *I. illecebrosus* (Morris and Aldrich 1985), *I. argentinus* and *I. coindetii* (Arkhipin *unpubl. data*), one particularly dark increment (a "check") is often followed by approximately seven or a multiple of seven lighter increments (Fig. 8.4). This pattern, however, is somewhat subjective and, consequently, it is not yet confirmed or interpreted for *Illex*.

2.4.1 Postnuclear zone and larval phase

The postnuclear zone lies outside the nucleus and has also been called the "juvenile zone" (Lipinski 1978), "the nucleus" (Hurley and Beck 1979) and R1 (Morris and Aldrich 1985). This zone is transparent in transmitted light, with narrow and nearly uniform growth increments. The number of growth increments in the postnuclear zone does not vary greatly among *Illex* species (Table 8.2), being approximately 38–40 increments. Usually, but not always, there is a prominent check on the outer border of the postnuclear zone (Fig. 8.1). Occasionally, checks (one, as a rule) appear within the zone (Fig. 8.1), reflecting a sharp delay in statolith growth and, probably, in growth of the larva itself, perhaps due to some dramatic change in environmental conditions. Morris and Aldrich (1985), inferring from data on *Alloteuthis subulata* and *Loligo* spp., which all had 18 or more increments in the statolith at hatching, suggested that the region R1 should be considered to be a pre-hatching zone. However, further investigations showed distinct differences in the time of formation of various zones between the families Loliginidae and Ommastrephidae. The small size of hatchling statoliths and obvious lack of any growth increments showed the assumptions of Morris and Aldrich (1985) to be incorrect (Dawe *et al.* 1985, Balch *et al.* 1988). Therefore, it is hypothesized that the postnuclear zone is associated with some other ontogenetic phase, most likely the larval stage. The transition between the postnuclear zone and dark zone might reflect the transition between larva and juvenile. Delay in statolith growth (reflected by the prominent check) and in body growth might be induced by starvation during the final splitting of the proboscis into two tentacles (Balch *et al.* 1988). This suggestion is supported by statolith analysis of other ommastrephid larvae, which had only the postnuclear zone in their statoliths during proboscis division (Arkhipin and Murzov 1986, *Dosidicus gigas*; Laptikhovsky *et al.* 1993, *Sthenoteuthis pteropus*).

Thus, the postnuclear zone corresponds with the larval phase of ommastrephid ontogenesis and the total number of its growth increments represents the duration of the larval phase in days. It is interesting that larvae of all *Illex* species develop at about the same rate - within 38 to 40 days (Table 8.2). Furthermore, the mean number of growth increments in the postnuclear zones in different monthly hatching groups of *I. argentinus* does not differ statistically (38 to 40 increments), despite the fact that larvae of these hatching groups foraged and grew in various seasons (Table 8.3). This phenomenon can probably be explained by similarity of environmental conditions (including temperature) in regions of *I. argentinus* spawning and larval development. Nektonic adults of *I. argentinus* could choose favourable conditions for spawning: either the whole Argentinean shelf in summer (Brunetti 1988) or only the northern part of the species range near the Brazil Current in winter (Haimovici *et al.* 1995).

2.4.2 Dark zone

The dark zone lying outside the postnuclear zone is brownish in transmitted light, milky opaque in reflected light, and contains the broadest growth increments. The total number of growth increments within the dark zone varies considerably among *Illex* species (Table 8.2). *I. coindetii* has only 63–98 growth increments in the dark zone, while *I. illecebrosus* may have 120–130 (Arkhipin 1989) or 97–140 (mean 127, Morris and Aldrich 1985) and *I. argentinus* has 145–195 growth increments.

Table 8.3. Growth increments (mean : ± SD) in the postnuclear and dark zones of males and females of different monthly cohorts of *Illex argentinus*[a]

Cohorts	Postnuclear zone		Dark zone	
	Female	Male	Female	Male
Jan	38.1 ± 1.2	38.7 ± 0.8	-	-
Feb	40.4 ± 0.6	40.3 ± 0.6	-	-
Mar	41.0 ± 0.7	38.8 ± 0.7	194 ± 5.4	-
Apr	41.8 ± 0.8	39.4 ± 0.9	182 ± 1.6	183 ± 4.3
May	39.0 ± 0.3	39.4 ± 0.5	175 ± 3.4	165 ± 2.5
Jun	39.1 ± 0.3	38.6 ± 0.3	162 ± 4.5	158 ± 1.9
Jul	39.9 ± 0.2	38.8 ± 0.2	155 ± 1.6	150 ± 3.2
Aug	39.2 ± 0.3	38.7 ± 0.3	148 ± 4.2	146 ± 2.8
Sep	39.5 ± 0.5	40.3 ± 0.6	151 ± 2.1	148 ± 1.9
Oct	38.4 ± 0.9	39.8 ± 1.2	157 ± 5.3	165 ± 5.5
Nov	42.0 ± 2.0	37.0 ± 1.1	-	-
Dec	38.2 ± 1.7	40.5 ± 1.5	-	-
Total	1959	982	1816	82

[a] From Arkhipkin 1989

Resolution and width of growth increments varies among and within species of *Illex*. Among juveniles of *I. argentinus* of the winter-spawning group, there are two statolith types differing with respect to dark-zone microstructure. The first type is characterized by well-distinguished, clear, narrow dark-zone increments (2–3 µm in width), numbering 150–200 (mean 165). Statoliths of that kind are observed in juveniles which feed in cold open waters of the Argentinean basin east of the Falkland (Malvinas) Current. The second type features poorly resolved broad-zone increments (up to 4–5 µm), with fewer increments (100–140 increments, mean 120) than in the first type. These statoliths were observed in juveniles which had fed in rather warm waters of the Patagonian Shelf (Arkhipkin and Scherbich 1991). The existence of these two types of dark zone microstructures in *I. argentinus* may be related to differences in life style between oceanic and shelf juveniles. Oceanic juveniles probably suffer from low prey availability in the open ocean, grow rather slowly and make deep vertical migrations (200–300 m, Parfeniuk *et al.* 1992), which causes an appearance of narrow, but prominent growth increments. Shelf juveniles experience higher prey availability, grow faster and make shallow vertical migrations (Brunetti 1988), resulting in the formation of wide, but relatively indistinct growth increments in the dark zone. This difference makes it possible to detect, by statolith examination, where winter-hatched adults have spent their juvenile stage -either in oceanic or in shelf waters (Arkhipkin 1993). It is notable that *I. illecebrosus* in our samples have statoliths of the first type and *I. coindetii* of the second type (Fig. 8.5). This is consistent, because *I. illecebrosus* has an oceanic juvenile phase, whereas *I. coindetii* spends the juvenile phase on the African shelf.

It is interesting to analyse the basis of formation of the dark zone within the statolith. In previous investigations it was suggested that such zones may be associated with decreased food intake and/or maturation (Kristensen 1980, Morris and Aldrich 1985). Table 8.4 relates changes in statolith microstructure to ontogenetic changes for several species of ommastrephids. The transition between the dark and peripheral zones is not obviously associated with the start of sexual maturation. The peripheral zone is absent in some mature specimens of *I. argentinus*, while the dark zone is complete in immature *D. gigas* and *S. pteropus*.
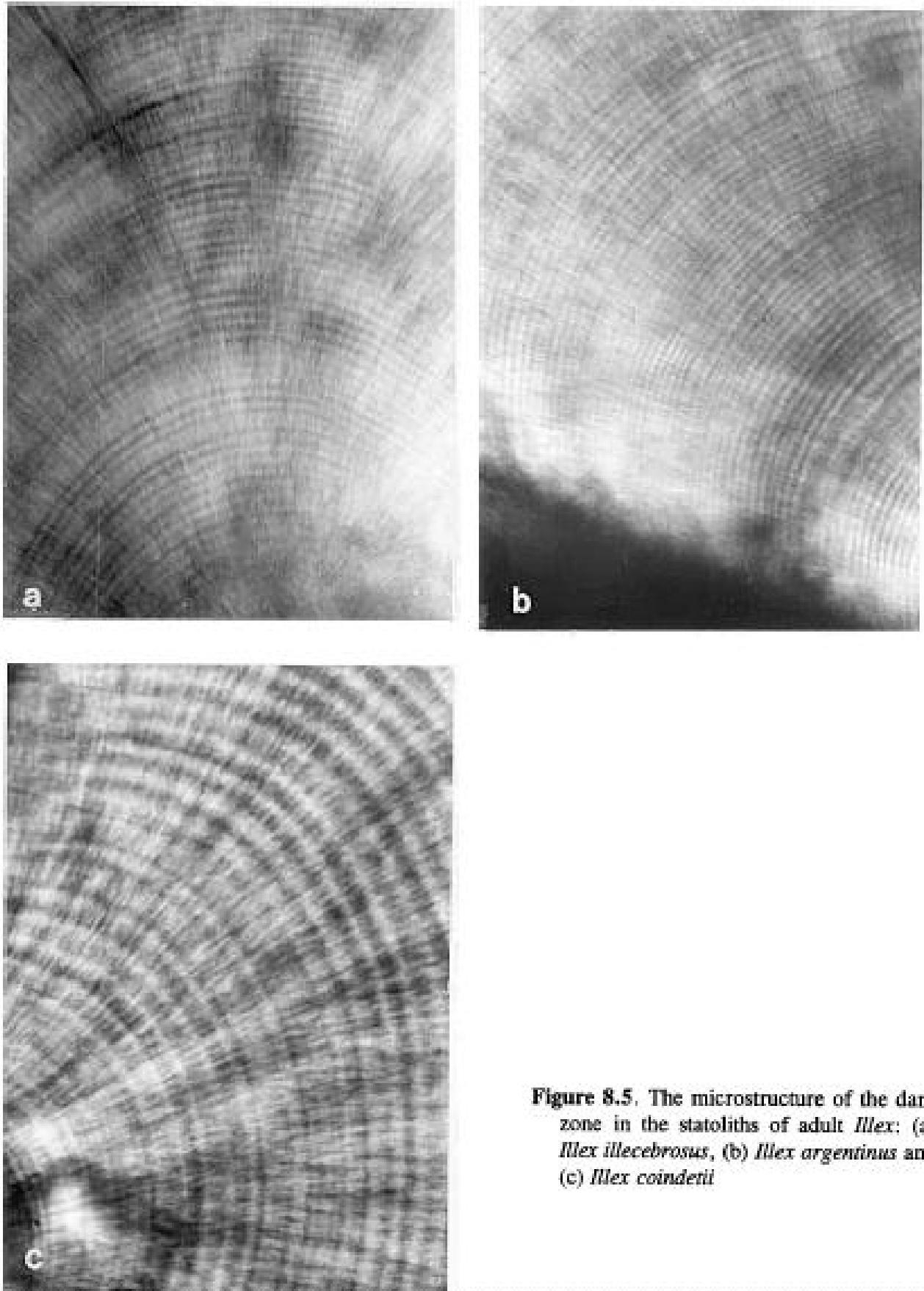
Figure 8.5. The microstructure of the dark zone in the statoliths of adult *Illex*: (a) *Illex illecebrosus*, (b) *Illex argentinus* and (c) *Illex coindetii*

Table 8.4. Ontogenetic shifts in statolith microstructure and ecology in different species of ommastrephids

| Character | *Illex* | | | *Sthenoteuthis* | *Dosidicus* |
	illecebrosus	*argentinus*	*coindetti*	*pteropus*	*gigas*
Mean total number of growth increments in the postnuclear and dark zones (age in days)[a]	157–173	183–237	99–130	130–140	70–82
Mean mantle length (ML) at completion of the dark zone[a]	155–190	190–248	75–125	160–180	110–130
ML at start of maturation[b]					
in males	150–200	140–250	100–150	120–140	150–300
in females	230–?[c]	180–340	130–250	150–440	270–600
ML at transition from crustacean to fish-feeding spectrum[b]	170–230	220–280	90–130	140–190	100–140

[a] Arkhipkin (1989)
[b] Ch. Nigmatullin, AtlantNIRO, Kaliningrad, Russia, *unpubl. data*
[c] Upper limit of ML in *I. illecebrosus* is unknown

Moreover, males of Ommastrephidae (including *Illex*) start maturing earlier than females (Arkhipkin 1989, 1990) and so would be expected to have fewer growth increments in the dark zone. However, no effect of sex on number of growth increments within the dark zone is evident in any monthly hatching group of *I. argentinus* (Table 8.3). Thus, maturation does not affect growth-zone formation in the statolith.

Among other factors which could affect the origin of the dark zone, changes in the feeding spectrum seem to be the most likely (Table 8.4). Juvenile and adult squids feed upon crustaceans (mainly euphausiids and amphipods) until they achieve some species-specific size, at which time they shift to feeding on fish and squid (Nigmatullin 1987). The dark zone may be associated with a predominantly crustacean diet in ommastrephids, and the outer peripheral zone with a fish and squid diet. The border between the outermost two zones is relatively poorly resolved because, in contrast to the shift from larva to juvenile, the transition from crustacean to fish diets is not abrupt and takes place within some particular size interval (usually within a 30–80 mm ML [mantle length] range, Nigmatullin 1987).

The number of growth increments in the dark zones of *I. argentinus* ranged from 149 in the August–hatched squid to 194 in the March-hatched squid (Table 8.3). The transition from a crustacean to a fish and squid diet depends on size, not age, of *I. argentinus* (A.S. Schetinnikov, AtlantNIRO, Kaliningrad, Russia, *unpubl. data*) and occurs in squid with ML ranging from 220–300 mm. By the average time of completion of postnuclear-zone formation, the March-hatched squid have achieved 190–200 mm ML (mean age 38 + 194 = 235 days), and the August-hatched squid have achieved 200–220 mm ML (mean age 39 + 148 = 187 days), sizes roughly corresponding to the beginning of the feeding transition. Because of their slower growth rate, the March-hatched and April-hatched squid may feed on crustaceans longer than the July and August-hatched squid.
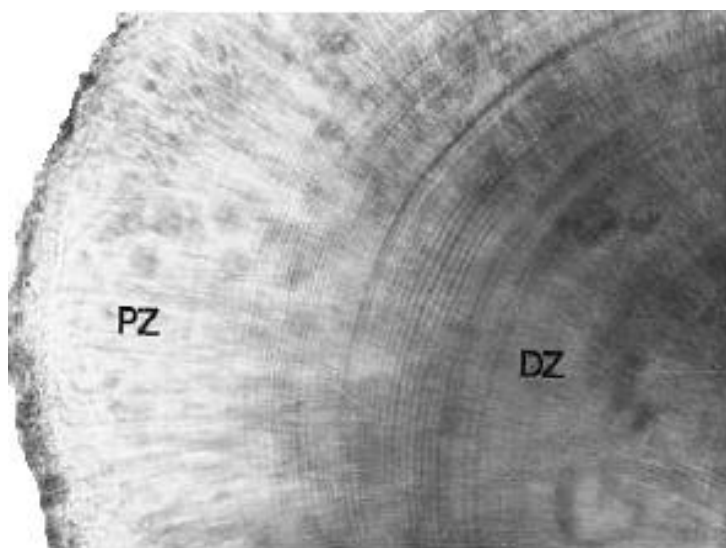
Figure 8.6. Statolith microstructure of *Illex argentinus*; the dark zone (DZ) and peripheral zone (PZ)

2.4.3   Peripheral zone

The peripheral zone appears in the statoliths of adult squids (Fig. 8.6). It is translucent, with narrow and rather regularly spaced growth increments (Table 8.2). In *I. illecebrosus*, it has been observed only in females which were found to have enlarged ovaries (Morris and Aldrich 1985). According to the data in Table 8.4, the peripheral zone may be associated with a fish and squid diet.

Checks or stress marks found in the peripheral zone of *D. gigas* could be associated with periods of multiple spawning (Arkhipkin and Murzov 1986). Unfortunately, spawning and spent *Illex* are rarely caught. Stress checks were not found in analysed statoliths from the six spawning and spent *I. argentinus* found to date. Females of *I. argentinus* spawn so quickly that they may not interrupt feeding as seriously as in *D. gigas* to induce the formation of stress marks. Further investigations are needed in this aspect.

2.5 Age detennination and growth rate estimation

As noted earlier, the start of growth-increment formation at hatching and the daily formation of increments in *Illex*, permit age determination of each individual. Longevity can be determined based on ages of fully mature squids of near maximum known size for the species, as well as on ages of spent animals. The life spans of the three *Illex* species do not exceed one year (Radtke 1983, Arkhipkin 1990). The only exception to the near one-year cycle was observed in the Sierra Leone populations of *I. coindetii*, which may have a half-year life cycle (Arkhipkin 1989).

It is not practical to use statolith microstructure (width of growth increments in particular) to back-calculate the growth rate of individual squid. Unlike fish scales and squid gladii, statoliths are not planar structures. The axis of maximum statolith growth changes with ontogenetic development, and ground statoliths show only projections, not real growth gradients. Grinding and viewing statoliths is very difficult due to their small sizes (in *Illex*, total statolith length usually does not exceed 1.3–1.5 mm in). Thus, only group growth rates can be estimated from size-at-age data. Other chapters of this volume discuss *Illex* growth at different ontogenetic stages.

Back-calculation of hatching dates makes it possible to investigate such population parameters as spawning periodicity, stock structure, age structure and migrations for any given species (Arkhipkin 1993, see also section 4.1).
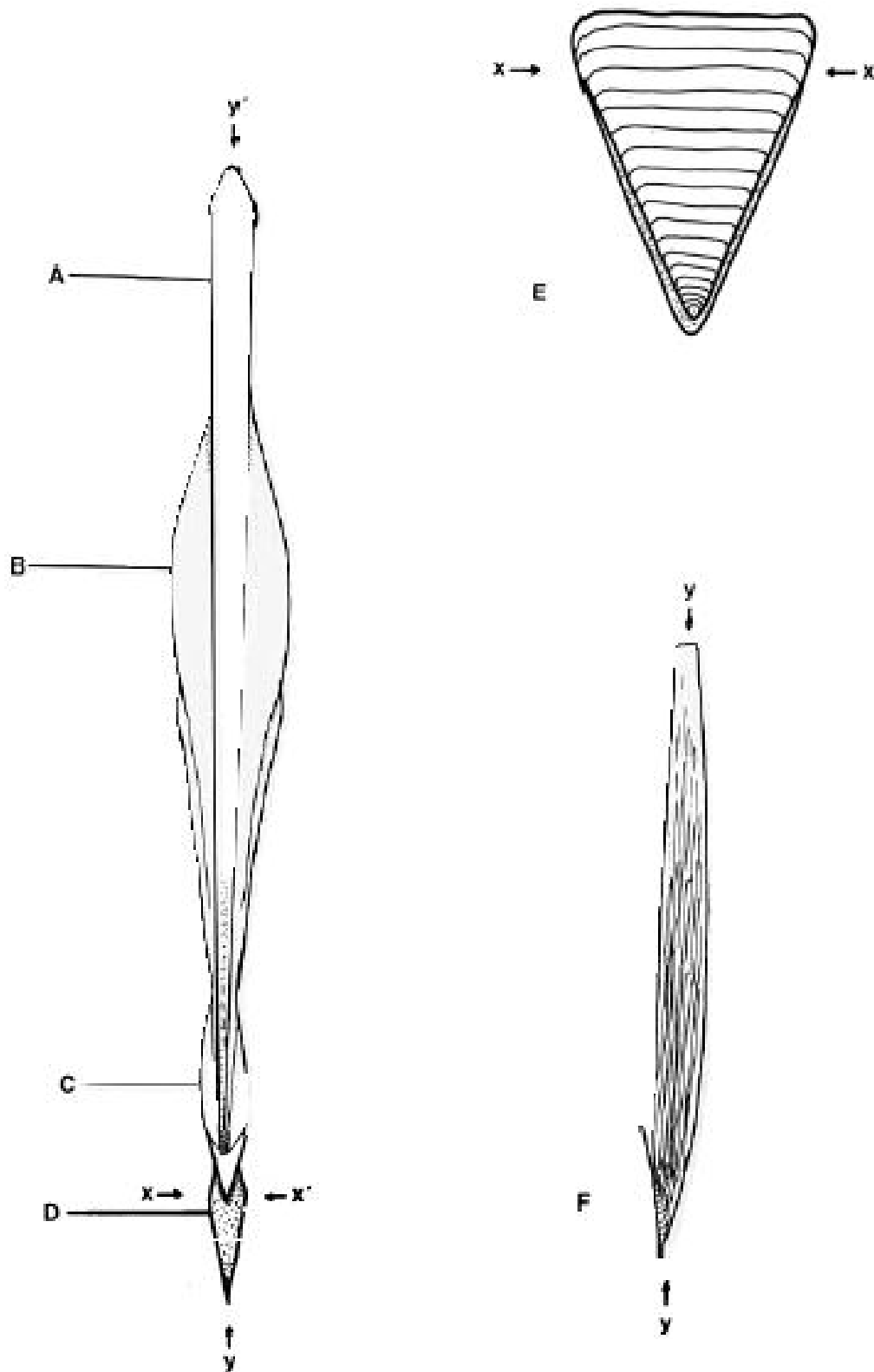
Figure 8.7. Dorsal surface of the squid gladius, general form; A = rachis, B = vane, C = conus, D = terminal spine, E = periostracum concentric growth as observed in the transversal section (xx') of the terminal spine, F = hypostracum lamellar growth as observed in the sagittal section (yy') of the gladius (Redrawn from Bizikov 1991)