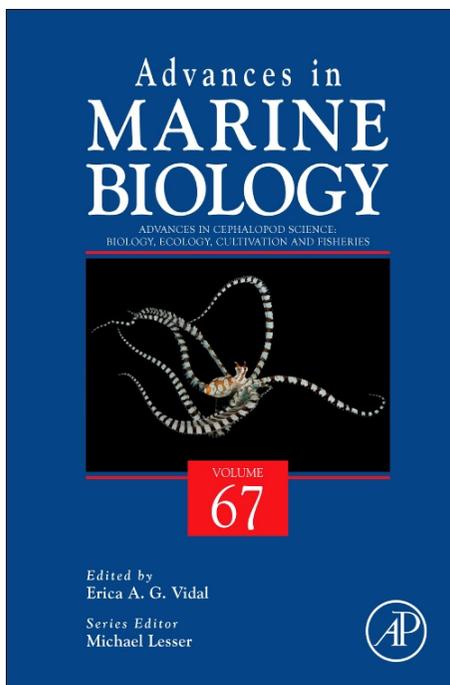


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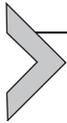
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# Transitions During Cephalopod Life History: The Role of Habitat, Environment, Functional Morphology and Behaviour

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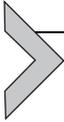
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## Abstract

Cephalopod life cycles generally share a set of stages that take place in different habitats and are adapted to specific, though variable, environmental conditions. Throughout the lifespan, individuals undertake a series of brief transitions from one stage to the next. Four transitions were identified: fertilisation of eggs to their release from the female (1), from eggs to paralarvae (2), from paralarvae to subadults (3) and from subadults to adults (4). An analysis of each transition identified that the changes can be radical (i.e. involving a range of morphological, physiological and behavioural phenomena and shifts in habitats) and critical (i.e. depending on environmental conditions essential for cohort survival). This analysis underlines that transitions from eggs to paralarvae (2) and from paralarvae to subadults (3) present major risk of mortality, while changes in the

other transitions can have evolutionary significance. This synthesis suggests that more accurate evaluation of the sensitivity of cephalopod populations to environmental variation could be achieved by taking into account the ontogeny of the organisms. The comparison of most described species advocates for studies linking development and ecology in this particular group.

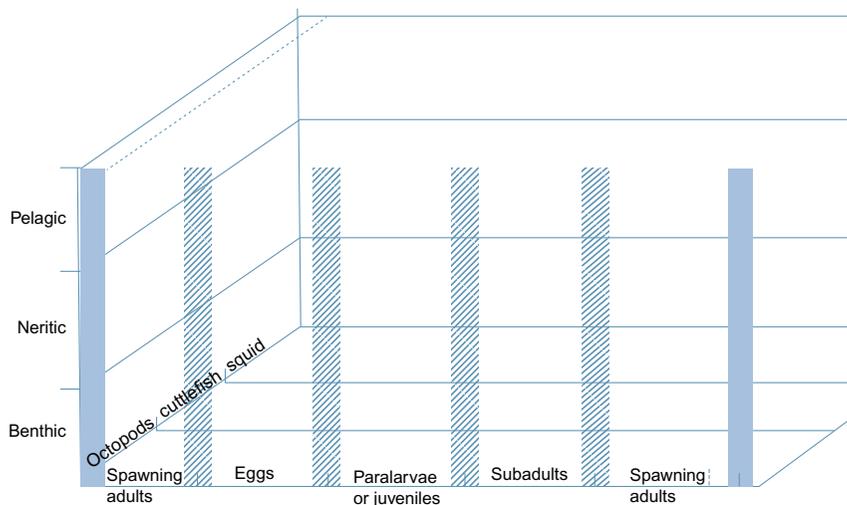
**Keywords:** Cephalopod ontogeny, Life stages, Morphological changes, Acquisition of behaviours, Habitat shifts, Environmental variability, Cohort survival, Paralarvae, Juvenile, Subadult, Adult



## 1. INTRODUCTION

A very common statement about cephalopod populations is that their abundance and dynamics are very variable and that this variability is due to the sensitivity of these organisms to environmental parameters and to their fluctuations. In fished species, the high productivity of cephalopod stocks is limited by variable recruitment (Boyle and Rodhouse, 2005; Rodhouse et al., 1998), but many noncommercial species are also spatially and temporally variable in their patterns of occurrence or distribution (Collins et al., 2001; Voss, 1988). A number of environmental parameters explain population variability; however, comparisons among species are often impaired by the fact that different life stages are considered. Although most cephalopods share common life traits, such as a relatively short life span and a fast growth rate, this group of molluscs is very diverse. Cephalopods have invaded almost all marine ecosystems, and there is diversity in life histories, from “big bang” spawners to “prolonged multiple” spawners (Boyle and Boletzky, 1996; Hoving, 2008; Hoving et al., 2013; Laptikhovsky et al., 2007, 2009; Rocha et al., 2001). A series of stages in an organism’s life represents in itself a range of adaptations to variable environments, and it is worth investigating in cephalopod life stages how the animal ecology changes between tiny eggs and large adults (Ebenman and Persson, 1988).

The main features of cephalopod life cycles were reviewed and described in detail three decades ago (Boyle, 1983b, 1987) and updated for some groups since Rosa et al. (2013). Our use of the terms embryo, paralarvae, juvenile, subadult and adult is consistent with those previously described by these authors and with Young and Harman (1988). From egg to spawning adult, a series of stages are undertaken (Figure 4.1) and are common to all coleoid cephalopods, with the exception of the “paralarvae”, which occur only in species in which the hatchlings show either discrete morphological differences from the adults (such as the rhyndoteuthis stage



**Figure 4.1** General framework for the transitional phases (shaded bars) between life stages for octopods, cuttlefish and squid for benthic, neritic and pelagic species. The scheme underlines common stages in cephalopod life cycles in spite of complex situations (change of habitats) and species differences.

of ommastrephids) or behavioural differences with planktonic posthatching versus nektonic or benthic adults (Boletzky, 1977). Life history theory (Stearns, 1992) suggests that the schedule and duration of key events in an organism's lifetime are shaped by natural selection to produce the largest possible number of surviving offspring and that these events depend on the ecological environment of the organism. The analysis of key events guided this chapter to explore how significant changes during ontogeny correspond to increased risks for a cohort's survival. While the life of an organism is a continuum of change, marine species often undergo a series of changes in life stage that can be characterised by either dramatic changes in shape and environment or subtle changes in behaviour and growth and development of internal organs. Each cephalopod life stage has its strengths and weaknesses and provides a response that fits best to the average environmental conditions. However, in a species life cycle, transitions need to be examined because they involve radical changes both in the organism and in its relationship to the environment. Transitions are critical to survival of cephalopod cohorts, and comparisons among groups of species or between ecosystems will be facilitated by looking at common transitions.

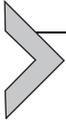
A transition refers to the time over which individuals move from one stage of their life cycle to the next (Figure 4.1). The rationale for introducing

the concept of “transitions” between cephalopod life stages lies in the idea that ontogenic stages are not artificial entities defined by the observer within a continuum, but rather, they result from interactions between the organism and its environment. Each life stage corresponds to a temporary, stable interaction of the organism with the environment that lasts for a measurable duration, and during which time, the individual adopts a mode of life. As individuals move from one stage to the next, there is a transition, usually short relative to the length of the stages they are transiting between, and the start and end of each transition are defined by the change in mode of life. During the transition, individuals undergo a suite of changes that permit a change in mode of life and that contribute to cohort success, if they occur under the best possible biotic and abiotic conditions. Some of these changes may be prepared during the previous stages as the whole development is governed by the activation of a set of genes. A series of four transitions common to most cephalopod groups is presented in [Figure 4.1](#) and will be referred to with the following headings:

1. Adult to egg: it is the transition from the mature egg inside the female to the release of the eggs, which is change in mode of life from inside the female to outside the female.
2. Egg to paralarvae: this transition is defined as the change in mode of internal to external sources of food and includes hatching that occurs during this transition.
3. First feeding to subadult: this transition is from the plankton mode of life to entering the nektonic or benthic mode of life, which involves adopting the adult lifestyle (will apply differently to species without a paralarval stage).
4. Subadult to adult: it is the transition from immature to mature adult mode of life.

This chapter examines the morphological, physiological, ecological and behavioural changes associated with each of the four transitions and their consequences at the population level. The objective of this analysis is not only synthesis but also extraction (when possible) unifying principles explaining which transitions are most critical and how transition success is related to habitats (or influenced by environmental variation). With this aim, this chapter does not intend to make a comprehensive list of all species whose life cycle changes were described, but rather to highlight phenomena of general interest. The scope of knowledge about each transition is inevitably limited by our capacity to sample and observe specimens at any stage of the life cycle. The bias related to sampling issues is mentioned in many

reviews (Boyle and Rodhouse, 2005). One should keep in mind that the species most studied are either abundant, supporting intensive fisheries, or easy to observe under rearing conditions.



## **2. TRANSITION #1: ADULT TO EGG (COMPLETE FERTILISATION OF EGG CLUTCH TO EGG LAYING)**

### **2.1. Introduction**

As stated by Young and Harman (1988), the adult phase in cephalopods is defined by individuals who are sexually mature and of adult size. Reproduction and spawning punctuate the final stage of the adult phase, which is terminated by senescence and death and results in the transfer of adult genetic material to a new generation. The transition from adult to egg (transition 1) is defined here as the time from complete fertilisation of the egg clutch to the release of the eggs, as a drifting mass, either attached to the benthos or retained within the arms of the female. This transition involves the change from the relatively well-protected adult stage to the relatively vulnerable stage of newly deposited or released eggs. Unlike in most marine invertebrates, this transition is critical for survival, both at the individual level (e.g. transfer of genes) and at the population level (e.g. successful annual recruitment), because the short lifetime of most cephalopods (Boyle, 1983a,b, 1987; Boyle and Rodhouse, 2005; Rodhouse, 2010) means that the majority of populations consist of only one generation and thus failure to spawn will result in recruitment failure and a subsequent population crash.

Cephalopods are not broadcast spawners; instead, the female fertilises each egg, using stores of sperm provided by the male, as she releases the egg from her oviduct and encases it in a protective layer. All cephalopod species provide a protective coat for the developing eggs, but there is a diversity of habitats that the protected developing embryos are released into and the degree to which the female uses the habitat to protect the eggs also varies. Eggs can be released into the water column to move with the currents, attached to sand or macroalgae or hidden within the matrix of corals or boulder habitats; it is only in octopuses and a few oceanic squid that protection of the developing embryos by the female is provided. This section will examine the fertilisation process, the timing of egg release and the changes that occur as the egg is released, the behaviours associated with spawning and postspawning and the habitats used for spawning.

## 2.2. Morphological, suborganismal and physiological changes during transition

The first transition begins with the fertilisation process, which is well described in *Sepia officinalis*, where sperm are stored in the mantle cavity or in the copulatory pouch and encapsulated eggs are fertilised by sperm externally (Boletzky, 1989). The sperm-attracting peptide SepSAP produced by eggs diffuses through the gelatinous layers, directing spermatozoa so that they can reach the egg while the female is holding the egg in her arms before attaching it to the substrate (Tosti et al., 2001; Zatylny et al., 2002). It is hypothesised that once fertilised, polymerisation of the egg capsule stops, and release of SepSAP from the oocyte prevents polyspermy (Zatylny et al., 2002). For species that store sperm in the ovary, for example, *Eledone*, fertilisation occurs as eggs leave the ovary and before encapsulation (Boyle and Rodhouse, 2005; Cuomo et al., 2005). Octopods are the only group of cephalopods where fertilisation is internal, occurring in most species in the oviducal gland (Hanlon and Messenger, 1998; Mangold, 1987). The only known exception is the genus *Eledone* in which fertilisation occurs in the ovary (Boyle, 1983a,b). Once fertilised, the egg undergoes cell division and embryonic development proceeds, which usually is after deposition, although eggs can go through cleavage stages while still inside the oviduct (*Argonauta* and *Tremoctopus*) (Boletzky, 1989). In the squid species *Doryteuthis opalescens*, an individual female was observed while laying an egg mass in the laboratory. During the process, a capsule sheath was produced within the mantle cavity of the female and then ejected out slowly through the siphon. The sheath was then manipulated within her arms so that the anchor strand was distal to her arms and the free-floating end was below her head. The female then pumped embryos into the capsule sheath from the top portion towards the end that would become the anchor (video: <http://gilly.stanford.edu/video/>; Zeidberg, 2009). Orientation of the capsule suggests that both locations of spermatophore placement, within the mantle of guarding males or in the seminal receptacle on the buccal membrane of guarding males, provide opportunities for fertilisation.

The physiological changes and processes that occur as eggs are released and leave the ovary are best described for *S. officinalis* but are unknown for other cephalopods. Storage of ovulated eggs in the oviduct is controlled by a suite of ovarian peptides, which prevent oviducal contractions (Bernay et al., 2004, 2005; Zatylny et al., 2000a,b); this allows eggs to be ready for

deposition once mating occurs. Once ready for release, oocytes of *S. officinalis* move from the oviduct to the funnel via oviduct contractions, modulated by neuropeptides, for example, FMRFamide-related peptides and APGWamide-related peptides (Henry et al., 1997, 1999), and ovarian peptides, for example, ILME and SepOvotropin (Bernay et al., 2006; Zatylny et al., 2000a,b).

The degree and nature of the encapsulation of the eggs vary among the cephalopod species, but in all cases, it is the role of the oviducal gland to produce the substances that surround the eggs, and without these gelatinous substances, fertilised eggs die several days later (Ikeda et al., 1993). The single (octopus) or paired (decapods) oviducal gland secretes the first gelatinous envelope enclosing the egg, while the cuttlefish and myopsid squid secrete a second layer of encapsulation provided by the nidamental gland (Boletzky, 1989). The cylindrical egg of *Octopus* lacks a gelatinous envelope, and the follicular tissue around the egg forms a stalk that thins out proximally (Boletzky, 1998; Naef, 1928). The eggs are coated with the encapsulation substances in the cavity of the oviducal gland after fertilisation and subsequently enter the distal oviduct before being released in a cluster (Froesch and Marthy, 1975). Like *Octopus*, the cuttlefish species deposit eggs singularly within a jelly-like substance; *S. officinalis* inserts a small quantity of ink into the egg capsule giving it the distinctive black colour. The loliginid squid deposit egg capsules that contain multiple eggs: three to eight eggs in the case of *Sepioteuthis australis* (Steer et al., 2003) to hundreds, for example, *D. opalescens* (Roper, 1965). Myopsid squid also encapsulate eggs in a sheath created by the accessory nidamental gland that is intercalated with bacteria transferred from the female (Biggs and Epel, 1991; Kaufman et al., 1998). The ommastrephid squids, for example, *Illex illecebrosus* and *Todarodes pacificus*, release the eggs within a fragile gelatinous matrix mass (O'Dor, 1983).

## 2.3. Ecological changes

### 2.3.1 Habitat and egg brooding

The first transition is complete when the adult female has deposited or released her eggs. The habitats used for egg deposition or release are diverse and range from inshore sites to open water. The squid egg masses of *Thysanoteuthis* are neustonic and thus are the most commonly observed oegopsid eggs. Eggs of the other non-deep-sea squid are found in mixed layer depths, for example, a *Dosidicus gigas* egg mass observed at 17 m depth (Staaf et al., 2008). Subsurface egg masses are laid by the female in the mixed

layer, but the egg mass has a greater ion content than sea water and is rapidly inflated via osmosis: the infusion of a sea water of a certain specific density enables the inflated egg mass to be neutrally buoyant at the depth of the water where it was laid (Rodhouse et al., 1998). The exact location and depth of egg mass release are unknown for many species. Hatching experiments determined that *D. gigas* eggs have a thermal limit of 15–25 °C (Staaf et al., 2011), suggesting that *D. gigas* could spawn 500 km offshore of California as far as 45°N assuming that egg masses float at the pycnocline (Staaf et al., 2011). Ommastrephid egg masses were first observed in the laboratory in 1981 (*I. illecebrosus*; O'Dor and Balch, 1985) and more recently *in situ*, for example, *D. gigas* in the Gulf of California (Staaf et al., 2008), *Nototodarus gouldi* in New Zealand (O'Shea et al., 2004) and *Thysanoteuthis rhombus* in the Sea of Japan (Miyahara et al., 2006a).

Egg capsules of the loliginid squid are negatively buoyant, and the female attaches the egg capsules to the substrate using a mucilaginous adhesive substance (Boletzky, 1998). The nature of the substrate used varies with species; for example, *D. opalescens* attaches eggs to sandy substrates in 10–12 °C water (Roper, 1965); *Doryteuthis gahi* attaches capsules to frondless kelp stipes 0.5–2.5 m from the benthos (Arkhipkin et al., 2000); *Doryteuthis pealeii* anchor eggs to seaweed, pilings or rocks (Summers, 1983); *Loligo vulgaris* eggs are found in 20–25 m on fixed or floating supports (Worms, 1983); *Loligo reynaudii* deposit eggs on sand or low-profile rock (Sauer et al., 1993); and *S. australis* attaches eggs onto the base of the sea grass *Amphibolis antarctica* (Moltschaniwskyj et al., 2002). Cuttlefish species tend to spawn relatively few, large eggs that the females attach in clusters to structures on the seabed including plants, submerged debris and rocks (Roper et al., 1984). The requirement to attach eggs to suitable structures may be a driving force for the inshore spawning migration (Hall and Fowler, 2003). *Sepia latimanus* attaches the eggs between the corallites of dead *Lobophyllia* colonies with females temporarily compressing and elongating the egg between their arms to deposit them through the opening (Corner and Moore, 1980). The eggs of *Sepia apama* (approximately 2 cm in diameter; Cronin and Seymour, 2000) are attached to the undersides of rocks, ledges and caves (Hall and Hanlon, 2002). Aggregative spawning activity may be facilitated by  $\beta$ -microseminoprotein found in the capsule sheath that stimulates males to engage in aggressive mating behaviours (Cummins et al., 2011). *S. officinalis* females use their tentacles to manipulate the basal ring of the egg's gelatinous envelope around a support (e.g. *Zostera marina*, *Sabella pavonina*, Porifera sp. and *Nemertesia* sp.) to fix it in place (Blanc, 1998;

Bloor, 2012; Boletzky, 1983). The majority of squid and cuttlefish species attach their eggs to the benthos and do not provide parental care to their offspring. However, brooding behaviour has been observed in at least one genus of oceanic squid *Gonatopsis* (Gonatidae) (e.g. Okutani et al., 1995; Seibel et al., 2000).

Female octopods are known to undertake parental care of their eggs, which they brood in a rocky or coralline overhang or within an enclosed space (Boyle and Rodhouse, 2005; Mangold, 1987; Voight and Grehan, 2000). Octopod eggs are deposited by two methods in the den: cemented individually in hard substrate and cemented in clusters where individual eggs are intertwined with each other (Hanlon and Messenger, 1998; Rocha et al., 2001). Alternatively, female octopods that occur in habitats without shelters or dens (e.g. sand or mud) will carry the developing eggs in the web of their arms, e.g. *Octopus burryi* and *Wunderpus photogenicus* (Miske and Kirchhauser, 2006), *Hapalochlaena* (Norman and Reid, 2000) and *Amphioctopus* (Huffard and Hochberg, 2005). Pelagic octopus females carry eggs in a range of different ways: attached to mineralised rods (family Tremoctopodidae), within elongated distal oviducts (family Ocythoidae), within the arm crown (families Amphitretidae, Bolitaenidae, Vitreledonellidae and Alloposidae) and within a thin calcareous chamber (family Argonautidae) (Boletzky, 1998). Bathybenthic cirrate octopuses such as *Opisthoteuthis* may represent an exception, since the female deposits her eggs freely and individually onto the seabed (Boletzky, 1982).

### 2.3.2 Mortality

The first transition involves the change from a relatively well-protected adult stage to the relatively vulnerable stage of newly deposited or released eggs. The eggs of cephalopods, compared with most marine invertebrates, are relatively well protected by encapsulation that provides a physical and chemical buffer (Boletzky, 2003). In some cephalopod species, for example, *Octopus*, parental care (Section 2.3.1) also helps increase the rate of survival and thus the success of the first transition, which is critical for survival of the population.

Incirrate benthic octopuses deposit their eggs in close spaces to protect them during brooding. Bathybenthic cirrate octopuses deposit their eggs individually on the seabed. Female pelagic octopuses carry their eggs in their arm crown while brooding (Boyle and Rodhouse, 2005). Predation pressure from conspecific and congeneric males is considerable (Anderson, 1997; Ibáñez and Keyl, 2010), although there is no relationship between octopus and potential reefal predators (eels) or reefal prey (crayfish) species

(Anderson, 1997). However, the consequences of predation on brooding females on the survival of the egg clutch are not known. No major predation pressures have been reported for the relatively large and well-protected, benthic egg capsules of cuttlefish (Guerra, 2006). The infusion of ink into the outer envelope of the egg capsule by female *S. officinalis* may aid in protection of embryos by camouflaging the eggs (Guerra and Gonzalez, 2011) and also potentially acting as a chemical deterrent to predators (Derby et al., 2007). Despite the intrinsic protection afforded to cuttlefish eggs, predation does occur in several species; for example, in Guam, butterfly fish (*Chaetodon ulietensis*) predate on and eat accessible eggs of *S. latimanus* (Corner and Moore, 1980). Predation on *S. officinalis* eggs does occur by the tompot blenny (*Parablennius gattorugine*) (Guerra and Gonzalez, 2011). While predators are seen on the grounds of spawning squid, it appears that the eggs are not the target, but spent females are targeted (Sauer et al., 1992). There is little in the literature to suggest that predation is a major source of mortality for either benthic squid or cuttlefish eggs.

### 2.3.3 Environmental variables

In general, the reproductive cycle of marine molluscs, such as cephalopods, is associated with nutrient storage and environmental parameters such as water temperature and food availability (Pliego-Cárdenas et al., 2011). Spawning sites are related to specific temperature zones, mainly because temperature regimes affect rates of embryonic development and success of hatching (Boletzky, 1974; Ortiz et al., 2011).

The eggs of most sepiolids, many octopods and myopsid squid are attached to fixed structures or substrates, and so, their successful embryonic development and survival are dictated almost entirely by biological and physical conditions encountered at the fixed spawning site. Eggs deposited at different times or locations will experience a variety of different environmental conditions including temperature, light intensity, oxygen saturation, pollution, salinity, photoperiod and predation. Bloor et al. (2013a) presented a detailed review of *S. officinalis* spawning, highlighting the importance of regulation of both temporal (e.g. timing of reproduction) and spatial (e.g. site and habitat selection) reproductive outputs of adult females to ensure successful regeneration of the spawning stock. Oceanic circulation can govern the distribution of spawning octopuses with pelagic paralarvae, for example, spawning *Octopus vulgaris* in the Strait of Sicily concentrate at the margin of eddies, favouring site retention and benthic settlement of the paralarvae (Garofalo et al., 2010).

## 2.4. Behavioural changes

### 2.4.1 Spawning patterns

Spawning patterns of cephalopods differ among species. Squid commonly form spawning aggregations with large groups of individuals at the surface or in the mid-water and smaller groups at the sea floor (Vaughan and Recksiek, 1978). Egg masses are deposited close to one another, for example, *S. australis* (Moltschaniwskyj et al., 2002), *L. reynaudii* (Sauer et al., 1992), *D. opalescens* (McGowan, 1954), *Loligo gahi* and *Loligo sanpaulensis* (Barón, 2001). Cuttlefish are generally considered solitary animals that do not shoal, but interaction between individuals does occur particularly during the reproductive period (Naud et al., 2004). In contrast, octopods are generally solitary animals with spawning also observed to be a solitary event with individuals displaying little or no courtship behaviour prior to mating (Hanlon and Messenger, 1998; Voight and Feldheim, 2009).

Female *D. opalescens* spawn 36% of their potential fecundity on the first day and 9% on each subsequent day (Macewicz et al., 2004). A small proportion of the population will continue to spawn for up to 6 days, depositing 78% of their total estimated potential fecundity, with, on average, females depositing eggs for 1.67 days on the spawning grounds before being lost from the population by natural or fishing mortality (Macewicz et al., 2004). In many squid species, the length of spawning events remains unknown. *L. reynaudii* tracked with acoustic tags were observed to perform daily migrations on and off the spawning grounds for up to 5 days (Sauer et al., 1997) and to migrate between spawning grounds for a mean of 43 km over 2 weeks (Sauer et al., 2000). This squid shows indications of atresia (degeneration and resorption of an oocyte and its follicle) that are absent in *D. opalescens* (Macewicz et al., 2004; Melo and Sauer, 1998; Sauer et al., 1999). However, serial spawning in *L. reynaudii* may occur quite rapidly, over several days to weeks (Melo and Sauer, 1999). Furthermore, individual *D. pealeii* produced multiple clutches in the laboratory over 3–6 weeks, often with several days between ovipositions (Maxwell and Hanlon 2000). Squids demonstrate a wide variety of reproductive patterns, simultaneous terminal spawning, multiple spawning, intermittent terminal spawning and continuous spawning (Rocha et al., 2001). *D. opalescens* has been described as simultaneous terminal spawner, but it seems the term “simultaneous” could range between 4 min (Hanlon et al., 2004) and 6 days (Macewicz et al., 2004) or possibly 42 days (Yang et al., 1986).

Several species of cuttlefish (e.g. *S. latimanus* and *S. officinalis*) are solitary for the majority of the year before aggregating in small loose associations (up

to five individuals) in shallow coastal waters during the reproductive period to compete for mates (Boletzky, 1983; Corner and Moore, 1980). Polypeptidic waterborne pheromones expressed and secreted by accessory sex glands may facilitate aggregative egg laying behaviour in *S. officinalis* (Boal et al., 2010; Enault et al., 2012). In the Spencer Gulf, Australia, the giant cuttlefish, *S. apama*, forms the only known large spawning aggregation of cuttlefish in the world, with up to 170,000 individuals recorded (Hall and Fowler, 2003). Adults migrate inshore to this area between April and July to mate and spawn over a restricted area of rocky reef (e.g. Hall, 2002; Naud et al., 2004). The cues or mechanisms responsible for the formation of these large spawning groups in cuttlefish remain largely unknown; however, the requirement for a specific rock-based spawning substrate, the availability of which is restricted within the area, may explain the large cuttlefish spawning aggregations that occur at this specific location (Naud et al., 2004).

Cuttlefish exhibit a high degree of flexibility in their spawning patterns (e.g. *S. officinalis*; Boletzky, 1986, 1987a), including spawning once (simultaneous terminal spawning) and spawning more than once, with multiple repeated spawning events over a period of several months (intermittent terminal spawning) (Rocha et al., 2001). In several species of *Sepia* (e.g. *S. officinalis*, *Sepia pharaonis*, *S. apama* and *Sepia dollfusii*), a range of developmental stages and egg sizes are found within the ovaries of sexually mature females during the spawning season, indicating that not all eggs mature simultaneously and that eggs are produced in multiple batches suggestive of an intermittent terminal spawning strategy in these species (Boletzky, 1987a; Gabr et al., 1998; Hall and Fowler, 2003). Telemetry studies of both *S. officinalis* (Bloor et al., 2013b) and *S. apama* (Hall and Fowler, 2003) indicate that females are present in the aggregation area over an extended period during which they are not continuously involved in oviposition, but are often relatively mobile with a high degree of plasticity in reproductive behaviour and general movement patterns. Postspawning mortality is substantial in all cuttlefish species (Roper et al., 1984).

Several species of octopods perform inshore–offshore migration associated with seasonal changes in temperature such as reported for *Enteroctopus dofleini* in Hokkaido waters (Rigby and Sakurai, 2004); others such as *O. vulgaris* and *Eledone cirrhosa* made onshore shallow–water migrations in spring to match with the breeding season (Mangold, 1987). Migration of medium and large octopuses to deeper water during periods of strong thermocline (e.g. summer) is suggested to be related with a reduction of energetic cost at colder temperature in *O. vulgaris* (Katsanevakis and

Verriopoulos, 2004a,b). Thus, suitable conditions for embryonic development under stable temperature may constrain breeding in octopods (Boletzky, 1987b). Spawning sites may vary within the same species depending on the region. Before reproduction, adult *O. vulgaris* from the Atlantic coast of Spain migrate to coastal waters. Breeding occurs mainly in summer; however, mature males can be found throughout the year (Rodríguez-Rúa et al., 2005). Shallow-water cephalopods tend to spawn in cold months, so the offspring hatch at warmer temperatures. In *Octopus pallidus*, maturation is faster when exposed to decreasing temperatures so that spawning occurs in cold months. However, it has been suggested that the spawning period for this species occurs in late summer–early autumn (Semmens et al., 2011). In *Octopus hubbsorum*, there have been reports of two different spawning seasons: for one region in autumn and for another region in winter–spring. Differences in spawning seasons within the same species may be due to the differences in regional environmental conditions (Pliego-Cárdenas et al., 2011).

### 2.4.2 Female choice

Copulation is often assumed the final criterion for female choice, but in animals that adopt internal fertilisation strategies, copulation seldom results in direct or inevitable fertilisation (Eberhard, 1985). Prior to the start of the first transition, processes that occur both before (e.g. direct female mate choice) and after (e.g. cryptic female choice) copulation can affect the chance of a copulation ending in fertilisation (Eberhard, 1996). The classic view of mate choice is that males compete for copulations and fertilisation but that females choose which males to mate with through assessment of some male secondary sexual trait or ornamentation, potentially preferring healthier males or those with good genes (Bateman, 1948).

#### 2.4.2.1 Direct female mate choice

Mate choice by females is known to occur in cuttlefish (e.g. *S. officinalis*; Boal, 1997), but the secondary traits or ornamentations used are not well defined. In the laboratory, Boal (1997) showed that while female *S. officinalis* did consistently prefer some males over others, these choices were not based on characteristics known to correlate with male dominance (e.g. body patterning or body size). In fact, Boal (1997) argued that female mate choice was more likely to be based on olfactory cues rather than visual cues. In *S. apama*, direct mate choice by females has also been observed, with females actively rejecting unwanted mating attempts. A total of 70% of

female rejection attempts were observed to be successful with only 3% resulting in forced copulations (Hall and Fowler, 2003). Females were not receptive to mating attempts while an egg was held in the arms, and one-third of the observed rejections occurred while females were holding an egg; the remaining two-thirds of the rejections were considered a result of direct choice by the female (Hall and Fowler, 2003).

Octopuses are presumed to be solitary and polygamous animals (however, see Huffard et al., 2008 for *Abdopus aculeatus*) resulting in no clear female choices (Hanlon and Messenger, 1998).

#### 2.4.2.2 Cryptic female choice

Observational studies of loliginids indicate that, despite arriving on the spawning ground with filled spermathecae, females copulate with multiple males (e.g. Hanlon et al., 2002) resulting in multiple paternity of eggs within the egg masses produced by loliginid squid (Buresch et al., 2001; Shaw and Boyle, 1997; Shaw and Sauer, 2004). DNA fingerprinting of *L. reynaudii* embryos indicates that four to five males can contribute their paternity with an emerging picture of complex genetic mating systems in squid that indicates potential for overt and cryptic female choice (Shaw and Sauer, 2004). Female cuttlefish are also polyandrous, accepting and storing sperm packages from multiple males. Females thus have access to sperm from two different sources: (1) sperm packages from recently mated males, which are deposited onto the buccal area (Naud et al., 2005), and (2) sperm from previous matings that are stored in their internal sperm-storage receptacles (copulatory pouch) located under the buccal mass (Hanlon et al., 1999). In *S. apama*, a study by Naud et al. (2005) confirmed that these two sperm stores contained sperm from between two and more than five males, indicating a high probability of sperm competition prior to fertilisation and highlighting a potential for stored sperm to be manipulated by females during fertilisation. This process could reflect the “cryptic female choice hypothesis” proposed by Eberhard (1996) that suggests that by actively influencing which sperm is utilised for fertilising eggs after copulation, polyandrous females who have mated with multiple males can still control which male ultimately sires her offspring. Naud et al. (2005) used microsatellite DNA analyses to determine the genetic diversity of the stored sperm in *S. apama* females and then compared it with that of their offspring. Their results indicated that fertilisation patterns with respect to the sperm stores used were not random (Naud et al., 2005). While these results represent the first account in cuttlefish of the use of sperm from multiple stores, it remains to be determined

whether this fertilisation bias results from active female manipulation of stored sperm (postcopulatory choice) or from simple physical constraints on sperm access to eggs (Naud et al., 2005).

While multiple paternity has also recently been confirmed in some species such as *Graneledone boreopacifica* (Voight and Feldheim, 2009) and *O. vulgaris* (Quinteiro et al., 2011), the hypothesis of cryptic female choice has yet to be tested for cephalopods. In a study by Quinteiro et al. (2011), analysis of two microsatellite loci of four females and their respective progeny revealed that two male contributors were inferred for all assayed offspring. The authors conclude that this reproductive pattern could originate from the differential use of sperm depositions (Shaw and Sauer, 2004; Walker et al., 2006) either through a process of sperm competition (Cigliano, 1995; Hanlon and Messenger, 1998) or mediated by a cryptic female choice (Quinteiro et al., 2011).

### 2.4.3 Sperm competition

In a promiscuous mating system, like that exhibited by many cephalopod species, the sperm from multiple males may compete for fertilisation of a given set of ova at the start of this first transition; this is known as sperm competition (Birkhead and Parker, 1997). To try and reduce the influence of sperm competition on their fertilisation success, male cuttlefish have developed a variety of mechanisms including agonistic behaviour (male–male aggression), pre- and postcopulatory mate guarding, sperm removal (flushing) and sneaker male mating and female mimicry.

#### 2.4.3.1 Male–male aggression

Aggression between males in competition for females has often been observed in cuttlefish species (e.g. *S. latimanus* (Corner and Moore, 1980) and *S. apama* (Hall and Hanlon, 2002; Norman et al., 1999)) and in octopus (e.g. *A. aculeatus* (Huffard et al., 2008)). In field observations of *S. latimanus*, aggression between males was often observed in competition for females (Corner and Moore, 1980). In *S. latimanus*, incidents of male–male aggression were observed to increase in frequency and intensity during the precopulatory patterns of females; typically, smaller males lost these interactions (Corner and Moore, 1980). Males dashed towards each other repeatedly; if neither backed away, then both males flared their arms upwards and outwards. If neither retreated, then the arms were extended to an umbrella pattern and the mouth exposed, which lead to submission of one combatant in six out of nine observed encounters. If the larger male

was unable to keep an opponent at bay, they resorted to an exaggerated umbrella pattern dashing in a side position towards the intruder with his arms twisted over the intruders head as if to bite him; this generally resulted in the intruder paling his body and retreating several metres (Corner and Moore, 1980). Ritualistic agonistic displays have also been observed to be used by large male *S. apama* in order to challenge consorts for female matings (Hall and Hanlon, 2002). In contests of disparate sized consorts, the agonistic display typically results in the loser submitting without physical contact, but in more even contests, battles can lead to biting and many males display scars or missing arm tips from such encounters (Norman et al., 1999). Male–male aggression has also been observed in the octopus species *A. aculeatus* almost exclusively while defending a female (26 of 29 male–male combinations) both at and away from the den (Huffard et al., 2008). Male aggression included behaviours such as chasing, touching and whipping with one straight arm and grappling (Huffard et al., 2008).

#### 2.4.3.2 Male mate guarding

Mate guarding is a form of resource defence in which males reduce the probability that a female will remate with other males, thereby increasing the chance of a newly mated male siring most of the next-laid eggs (Hall and Hanlon, 2002; Hanlon and Messenger, 1998; Naud et al., 2004). However, mate guarding can be time-consuming and reduces the available time that males have to seek out new mates (Huffard et al., 2008). Mate guarding has been observed in cuttlefish (e.g. *S. officinalis* (Boal, 1996; Hanlon et al., 1999) and *S. apama* (Hall and Hanlon, 2002)), benthic octopods (e.g. *A. aculeatus* (Huffard et al., 2008)) and squid (e.g. *D. opalescens* (Hurley, 1978)).

In cuttlefish, temporary postcopulatory mate guarding may serve to prevent the removal of the newly mated male's spermatangia on the buccal membrane during the brief period during which the spermatangia may be susceptible to removal or dilution by flushing (Hanlon et al., 1999). During this postcopulatory period, the sperm from several males may compete for entrance to the two pores of the seminal receptacle (Hanlon et al., 1999). A study by Naud et al. (2004) noted a correlation between the time that the egg was laid after mating and fertilisation success with eggs laid 20–40 min following copulation more often fertilised by the mated male than those laid before or after this time, and these results may explain the strong postcopulatory mate-guarding behaviour observed, such that by preventing the female from mating with another male for at least 40 min,

the newly mated male would gain more fertilisations (Naud et al., 2004). However, postcopulatory mate guarding has been observed to last for up to 90 min (*S. apama*; Hall and Hanlon, 2002), thereby also delaying their search for additional female copulations. Mate guarding has also been observed in squid in their natural environment; for example, large consort *Loligo* males were observed to guard their paired female mates as they descend towards the egg mass to deposit an egg capsule (Hanlon, 1998). During egg guarding, male squid were observed to touch the eggs with their arms, hover over the egg mass and display red coloration on their arms and pale coloration on their mantle and head to any other male that approached the egg mass (Hurley, 1978). If the second male did not retreat, the two males would line up parallel and perform agonistic behaviours including arm touching, pushing and occasionally biting that could result in severed arms and tentacles or scars on the mantle. The original guarding male would usually win these bouts, but if the challenger won, he would take up guarding the eggs. Artificial eggs made of silicon could stimulate females to lay eggs, but male agonistic behaviour could not be elicited until natural eggs were present. Contact with *Loligo*  $\beta$ -microseminoprotein (*Loligo*  $\beta$ -msp) immediately alters male squid, causing them to compete with agonistic behaviours even in the absence of females. *Loligo*  $\beta$ -msp is secreted by female exocrine glands and is embedded in egg capsule sheaths (Cummins et al., 2011). Large male and female pigmy octopuses (*A. aculeatus*) were found to occupy adjacent dens with copulation between the pair occurring frequently in mate-guarding situations over successive days (Huffard et al., 2008). Mate guarding in *A. aculeatus* was used by males as an effective tactic to temporarily monopolise mating with females (Huffard et al., 2008).

#### 2.4.3.3 Sneaker mating and female mimicry

Behaviours like sneaker mating and female mimicry have in theory evolved as a reaction to the other males with superior competitive abilities (Parker, 1990). Sneaker males and female mimics adjust their behaviour to procure copulations while reducing aggression from other males as a result of the prior knowledge they have of their (in)abilities compared with other individuals in a group (Parker, 1990).

Sneaker mating has been observed in cuttlefish, in squid and more recently in octopus. In the large spawning aggregations of the giant Australian cuttlefish (*S. apama*), sex ratios are skewed and can be as high as 11 males to 1 female (Hall and Hanlon, 2002). This leads to intense competition between males for copulation, and mate guarding occurs almost

continuously (Hanlon et al., 2005). In these aggregations, consort males were found to obtain approximately 64% of matings; the remainder are obtained by small, unpaired males, known as “sneakers”, which obtain extra pair copulations using open stealth (e.g. approaching a guarded female while the male is distracted), hidden stealth (e.g. meeting females under rocks) or female mimicry (e.g. mimicking the appearance and behaviour of females) (Hall and Hanlon, 2002; Hanlon et al., 2005; Norman et al., 1999). In aggregations of *S. apama*, smaller males have been observed to adopt a strategy of switching their appearance from that of a male to that of a female in order to foil the mate-guarding attempts of larger males. Single small males accompanied mating pairs while assuming the body shape and patterns of a female, thereby avoiding agonistic attacks by larger mate-guarding males. On more than 20 occasions, Norman et al. (1999) then observed these smaller males to change body pattern and behaviour to that of a male in mating display and attempt to mate with the female, often with success, while the larger male was distracted by another male intruder. Hanlon et al. (2005) verified the success of female mimicry by smaller *S. apama* males to obtain extra pair copulation (EPCs) and to successfully fertilise eggs. The authors observed five initiations of mating by mimics: One attempt was rejected by the female and another was interrupted by the consort male, and the remaining three attempts however all resulted in successful spermatophore transfer (Hanlon et al., 2005). Using DNA fingerprinting, they were able to verify that two sneaker EPCs by a small mimic male resulted in successful fertilisation of eggs (Hanlon et al., 2005), providing the first confirmed report of sneaker fertilisation in a cephalopod.

In squid, multiple paternity has been detected in the egg capsules of *L. reynaudii* (Shaw and Sauer, 2004), *Loligo forbesii* (Shaw and Boyle, 1997), *D. pealeii* (Buresch et al., 2001) and *Heterololigo bleekeri* (Iwata and Sakurai, 2007) with both guard males and sneaker males providing sperm for eggs within the same capsule. Guard or consort males clasp the mantle of the female from the ventral side and remain with her for minutes during egg laying. Guard males place their spermatophores inside the mantle cavity near the oviduct (Hanlon et al., 2002). Larger males are more likely to mate via guarding, and smaller males are more often sneakers (Hanlon et al., 2002; Iwata et al., 2005). In *H. bleekeri*, sperm size has been found to correlate to mating strategy. Sneaker males place their spermatophores in the seminal receptacle below the mouth of the female during very brief head-to-head contact. Spermatophores of sneaker males are larger but contained less spermatozoa. *In vitro* artificial fertilisation rates ranged from 70% to 98% in

sneaker males and 41% to 98% in consort males (Iwata et al., 2011). Egg capsule paternity tests suggest extra pair mating is successful <10% of the time (Iwata et al., 2005). Sperm differed in size and morphology in large and small mature *H. bleekeri*, and smaller sneaker males inserted smaller drop-like sperm in the seminal receptacle, and larger guard males inserted larger rope-like sperm in the mantle cavity (Iwata et al., 2008). Guard males had a greater success in paternity (Iwata et al., 2005). Conversely, in *L. reynaudii*, consort males sired 0–48% of the embryos examined in four egg capsules (Shaw and Sauer, 2004); in one capsule, a sneaker male or a prior consort male had 100% paternity, and the consort male captured at the time of egg deposition had zero paternity.

Sneaker mating is not well documented in octopus, a single example of sneaker mating has been reported in *Octopus cyanea* in the wild (Tsuchiya and Takashi, 1997) and more recently sneaker mating has also been observed in *A. aculeatus* during focal studies in the wild (Huffard et al., 2008). These studies demonstrate that natural history observations remain necessary for testing behavioural paradigms. A concerted effort is required to undertake further natural history observations of octopus in the wild in order to test behavioural paradigms and to document the mating behaviours of additional octopus populations (Huffard et al., 2008).

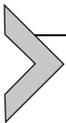
#### 2.4.3.4 Sperm removal or flushing

Sperm removal and flushing are behaviours that males of several species of cephalopods can incorporate into their reproductive repertoire in order to reduce sperm competition. These behaviours are known to occur in several cuttlefish species (e.g. *S. apama* and *S. officinalis*). Prior to sperm transfer, male cuttlefish repeatedly flush strong jets of water through their funnels towards the buccal area of the female; this action is thought to result in the removal of spermatangia from previous matings, thereby increasing the newly mated males' chance of reproductive success (e.g. *S. apama* (Hall and Hanlon, 2002) and *S. officinalis* (Hanlon et al., 1999)); however, to date, no significant relationship between flushing duration and fertilisation success has been found (Naud et al., 2004). However, it is possible that the effectiveness of this flushing mechanism may be dependent on the time elapsed since the prior mating (Hanlon et al., 1999). In octopus, the spoon-shaped tip of the male's hectocotyliised arm, known as the ligula, could function in the removal of stored sperm, from previously mated males and from within the spermatheca of the female's oviducal gland. This would function to try and ensure that the most frequently occurring paternal alleles

would be provided from the last copulation event (Hanlon and Messenger, 1998; Iwata et al., 2005; Quinteiro et al., 2011). However, to date, sperm removal and flushing behaviours in octopuses have not conclusively been demonstrated (Huffard et al., 2008). A study by Sato et al. (2013) using the Japanese pygmy squid (*Idiosepius paradoxus*) observed a spermatangium-removing behaviour by eating and blowing, which may be used by females for postcopulatory sexual selection. Using this process, females were able to remove the spermatangium following matings with unpreferred males before completing sperm transfer into their seminal receptacle.

## 2.5. Summary

During the transition from the fertilisation of eggs by spawning adults to egg release in the wild, a series of structures and phenomena are involved, which provide protection and shelter to the offspring. Fecundation and egg release are under the control of hormones and pheromones. The eggs are well protected either by encapsulation that provides a physical and chemical buffer or by parental care. Adult cephalopods have developed a wide array of behaviours, which contribute to the success of reproduction: Migrations to suitable habitats for egg release, courtship and mating optimise egg fertilisation and sneaker males maintain genetic diversity in size at maturity.



## 3. TRANSITION #2: EGG TO THE EXHAUSTION OF YOLK RESERVES

### 3.1. Introduction

The transition from egg to the exhaustion of maternally derived yolk reserves and first feeding is a critical phase within the early life history of cephalopods. This critical phase ends when individuals have survived the posthatching stage and are capable of obtaining and using external sources of energy in such a way it contributes to individual growth (Vidal et al., 2002a). It, thus, involves changes from the relatively protected environment within the egg to occupying the hatchling habitat and those occurring from dependence on maternally derived energy reserves to active predation.

Newly hatched cephalopods resemble miniature adults (Boletzky, 1974; Nesis, 1973) but do generally differ behaviourally, ecologically and morphologically from adults (Bartol et al., 2008). Across the cephalopod taxa, three different early life modes occur: (1) squid and a number of octopod (merobenthic) hatchlings are planktonic, referred to as paralarvae (Young and Harman, 1988); (2) the hatchlings of a number of benthic octopods display

nektonic–benthic behaviour before settling and adopting the benthic mode of life (Boletzky, 1977; Boletzky and Boletzky, 1973); and (3) all sepiids, most sepiolids and a number of octopod (holobenthic) species have hatchlings that immediately adopt the benthic mode of life (Boletzky, 2003; Young and Harman, 1988) observed in adults of these species. These large benthic hatchlings are referred to as juveniles (Naef, 1928).

This section will examine environmental factors, both within the egg capsule and in the surrounding oceanographic environment, that affect embryo survival; it will describe the conditions that determine hatching success and major changes occurring posthatching, from dependence on yolk reserves to a life stage of exclusive prey capture (Figure 4.3).

## 3.2. Hatching environment and key developmental milestones among cephalopod taxa

### 3.2.1 *The egg capsule environment and links to hatch initiation*

As a further result of ecological species adaptations, the size, structure and consistency of egg capsules vary considerably across taxonomic levels (Boletzky, 1989). Cephalopod embryos are encased in either an eggshell (cuttlefish) or a chorion, and within their encasings, all are bathed with perivitelline fluid (PVF). As such, PVF is in direct contact with the embryo and is considered important for the hatching process (Marthy et al., 1976). Perivitelline fluid enables a selective exchange between sea water and the embryo (Boletzky, 1987b). The buffering function of PVF implies a limited and selective exchange with sea water, specifically in terms of water, molecules (Gomi et al., 1986) and pollutants (Bustamante et al., 2004). Embryos therefore develop under abiotic conditions differing from those encountered as hatchlings. PVF is slightly hypertonic compared to sea water, enabling the swelling of cephalopods eggs, increasing surface area and decreasing capsule thickness (Cronin and Seymour, 2000). It has also been proposed that the osmoregulatory function of PVF could be closely coupled to physiological processes during embryonic development (Dorey et al., 2012). This fluid has also been suggested to act as a natural tranquilliser for embryos of loliginid squid, preventing premature hatching (Marthy et al., 1976).

The capsules and chorions act as a barrier to the diffusion of dissolved gases such as oxygen, resulting in dissolved oxygen levels within the egg capsules becoming a limiting factor towards the end of embryonic development. This has been observed in both benthic cuttlefish eggs (Cronin and Seymour, 2000; Gutowska and Melzner, 2009) and octopod eggs (Parra

et al., 2000; Uriarte et al., 2012). Low oxygen levels result from the metabolic demands during embryonic development leading to an accumulation of metabolic  $\text{CO}_2$  and a simultaneous drop in  $p\text{O}_2$  (reviewed recently by Marquez et al., 2013). Gutowska and Melzner (2009) found that PVF  $p\text{CO}_2$  increases as a function of embryo mass in cuttlefish. Both the postorganogenetic embryonic growth phase (Lacoue-Labarthe et al., 2010) and the hatching process (Parra et al., 2000) have been found to have a high energetic cost resulting in the rapid increase of oxygen consumption before and during hatching. The progressive depletion of oxygen at late embryonic stages may act as a hatching trigger in some species (Rosa et al., 2012).

Sea water properties such as pH and temperature also affect abiotic conditions of PVF, with important implications for cuttlebone calcification of embryonic and juvenile stages of the cephalopod *S. officinalis* (Dorey et al., 2012). Decreasing of sea water pH by 0.25–0.5 units resulted in hypercalcification by 17–80% of cuttlebone of cuttlefish embryos and juveniles (Dorey et al., 2012).

Elemental concentrations and requirements differ between eggshell-protected embryos (e.g. cuttlefish) and chorionic embryos (e.g. octopuses). The eggshell acts as a partially selective permeable barrier, depending on developmental stage, to both dissolved essential and nonessential trace elements (Bustamante et al., 2004; Lacoue-Labarthe et al., 2012), whereas in eggs surrounded by a chorion only, the uptake of elements is nonselective (further details in Villanueva and Bustamante, 2006). Despite the lack of information, particularly with regard to implications on the hatching process, a number of studies suggest that the bioaccumulation of trace elements influences embryonic development. Calcium reserves are needed for metabolic process being expected to be contained in yolk of cuttlefish eggs (Boletzky, 1989). Thus, calcium concentrations increased over the oocyte development of *O. vulgaris* suggesting the importance of sea water intake (Villanueva and Bustamante, 2006). Sea water properties such as  $p\text{CO}_2$  may affect this property (Lacoue-Labarthe et al., 2011). Abnormal hatchlings resulted from using artificial water without strontium in *O. vulgaris*, *L. vulgaris* and *S. officinalis* (Hanlon et al., 1989a). In addition, a high requirement of copper for hatchlings and juveniles was found in these species, particularly in octopus paralarvae, and is suggested to be related with haemocyanin requirements for oxygen transport (Villanueva and Bustamante, 2006). Not only is the environment within the egg capsule important, but also the conditions immediately surrounding the egg clutch

also influence mortality. The position of embryos within an egg clutch may lead to differences in hatchling traits such as developmental rate, survival and growth (Strathmann and Strathmann, 1995). Steer et al. (2003) found differences in the embryonic development rate within single egg strands of *S. australis*, with eggs situated at the fixed or proximal end developing more slowly than those situated at the free or distal end. It was also noted that embryos developing at the proximal end suffered higher mortalities. Differences in hatchling mantle length (ML) were found in *Illex coindetii* embryos incubated at different eggs densities during an *in vitro* experiment. Emergent hatchlings were larger at lower egg densities ( $\leq 5$  eggs  $\text{ml}^{-1}$ ) (Villanueva et al., 2011). Asynchronous development rates and variation in the size of hatchlings within a single egg strand or cluster have also been recorded for *Sepioteuthis sepioidea* and *Sepioteuthis lessoniana* (Chung, 2003; Ikeda et al., 1999; LaRoe, 1971). Strathmann and Strathmann (1995) suggested that the proximal embryos were not sufficiently oxygenated and/or accumulated excess excretory products and responded by either retarding or arresting development. Chung (2003) observed that large egg clusters tended to block the current causing less circulation within the clusters. This would indeed influence oxygenation. Pelagic eggs are extruded in a continuous fragile gelatinous mass, which, as a result of water absorption, has a neutral buoyancy. The absorption process increases the space between embryos and so allowing proper ventilation throughout the egg mass (Lee and Strathmann, 1998). The variability of hatchlings from the same egg strand can also be a result of multiple paternities (Buresch et al., 2001).

### **3.2.2 The changing oceanographic environment and effects on embryo survival and hatching**

Few studies have assessed how natural embryonic mortality results. Steer et al. (2002) found that natural mortalities of embryos of the southern calamari (*S. australis*) can vary between 4% and 20% in late November, decreasing to 10% until late December. In *D. gahi*, Arkhipkin et al. (2000) reported higher mortalities in winter, resulting in four times spring and summer mortalities. There is no clarity whether seasonal differences in embryo mortalities are related to thermal variations or other environmental conditions (e.g. rainfall (Steer et al., 2002) and salinity (Şen, 2005)). Recent studies in thermal tolerance in benthic octopus embryos have shown a higher thermal sensitivity in embryos than in preadults and adults (Uriarte et al., 2012). Cephalopod embryos are very vulnerable to thermal fluctuations, especially to extreme temperatures as those used in laboratory-based studies

(Oosthuizen et al., 2002a; Rosa et al., 2012; Uriarte et al., 2012). Furthermore, from embryo position studies, we know that oxygenation is important for embryo development and survival (Strathmann and Strathmann, 1995). Ocean pH effects on survival are also unknown for most species.

Cephalopods are well studied in terms of temperature effects on embryonic development and hatching. Results of those studies have important implications for the prediction of impacts of climate change (e.g. warming process). Thermal niche classification throughout embryonic stages has resulted in the potential to understand cephalopod distribution and the influence of oceanographic and physical conditions (e.g. *D. gigas* (StAAF et al., 2011)). A study on the effects of temperature on the embryonic development of this species found the upper temperature limit for successful embryonic development through hatching to be 25 °C (StAAF et al., 2011). Embryos experiencing temperatures outside the optimal thermal range resulted in mortalities by abnormal embryonic development in *L. reynaudii* (Oosthuizen et al., 2002a). A study by Rosa et al. (2012) investigated the effects of ocean warming (+2 °C) on *L. vulgaris* embryonic development. A metabolic suppression of embryos incubated at +2 °C of the optimal thermal range resulted in premature hatching under hypoxia.

Most cephalopod species are stenohaline with some exceptions (i.e. *Lolliguncula brevis*; Hendrix et al., 1981; Laughlin and Livingston, 1982) and are osmoconformers. Salinity was shown to affect the hatching rate, eggs size, first hatching time and dorsal ML of *L. vulgaris* under controlled conditions (Şen, 2005). Low salinity levels have been reported to have more severe effects on *S. lessoniana* embryonic development, in terms of abnormalities, compared to temperature (Chung, 2003). Very low salinity levels (20‰ and 25‰) were found to cause the death of *S. lessoniana* embryos, even at optimal temperatures (Chung, 2003). Similarly, the survival of loliginid embryos appears to be more affected by heavy rainfall and consequent reduction in salinity levels, rather than temperature changes (*S. australis*, Steer et al., 2002). Areas where salinity is expected to rapidly change (e.g. places with more frequent rain events) may negatively affect cephalopod inhabitants.

The global decrease of  $pO_2$  concentration in the ocean, deoxygenation, is caused by global warming and increased stratification (Keeling et al., 2010). Increasing declines in  $pO_2$  availability are predicted to affect cephalopod physiology, behaviour and demographics (Gilly et al., 2013; Pauly, 2010; Pörtner et al., 2005). The beginning of the transition, from hatch initiation to the exhaustion of yolk reserves, is especially susceptible to

deoxygenation as critical  $pO_2$  levels can be reached just prior to hatching in “normal” environmental conditions (Cronin and Seymour, 2000; Gutowska and Melzner, 2009). Although the metabolic demands differ among taxa, Pimentel et al. (2012) found that *L. vulgaris* had significantly higher demand than *S. officinalis*. They attributed this demand to reflect taxa differences in locomotion (Aitken and O’Dor, 2004), activity (Aitken et al., 2005), buoyancy (Denton and Gilpin-Brown, 1961) and oxygen extraction capabilities (Gutowska et al., 2010b; Strobel et al., 2012; Wells et al., 1988). In general, teuthiods have faster metabolic rates than octopods or sepiids throughout life stages including during the hatching process (Wells et al., 1988). Taxa with greater metabolic demands during embryogenesis may be especially vulnerable to asphyxiation or premature hatching in areas intensely impacted by deoxygenation.

To keep  $pO_2$  levels above critical low levels, hypoxia-induced metabolic suppression occurs until the embryo is mature enough to hatch, and it is suspected that this continues until a threshold of low  $pO_2$  ultimately triggers hatching (Pimentel et al., 2012). For loliginids, the PVF likely plays a key role during the transition by tranquillising near-hatch embryos, suppressing metabolic demand and allowing the embryo to fully develop (Marthy et al., 1976). *L. vulgaris* metabolic rate is more than doubled after hatching (Pimentel et al., 2012).

From what is known about cephalopods, teuthoids may be the most sensitive to deoxygenation with a broad spectrum of effects across species. These effects can be categorised as one of two types: lethal and sublethal. Lethal effects include underdevelopment or behavioural impairment preventing embryos from hatching, whereas sublethal effects include underdevelopment and/or malformations that carry over negative effects to later life stages (i.e. carry-over effects). Sublethal effects lower survivorship rates for paralarvae, reducing their abilities for feeding and/or for defence, and overall lower their fitness.

Ongoing anthropogenic  $pCO_2$  uptake by the ocean increases acidification of sea water and decreases global ocean pH (ocean acidification; Doney et al., 2009; Feely et al., 2004, Orr et al., 2005). Molluscs are vulnerable to acidification during larval stages (Bryne, 2011). Many invertebrate embryos exposed to global warming experience a mortality “bottleneck” leaving larval stages (and presumably the transition from hatch initiation to yolk exhaustion) vulnerable to acidification (Bryne, 2011). Gastropod embryos exposed to a pH of 7.6 exhibited “subtle” effects such as a slower heartbeats and reduced locomotion implicating lower survival rates in later life stages

including the larval stage (Ellis et al., 2009). Abalone and oyster were also found to be susceptible to acidification during the larval stage (Parker et al., 2013). Most mollusc ocean acidification studies have not focused on cephalopod embryos or young hatchlings (Bryne, 2011). Gutowska and Melzner (2009) showed that cuttlefish embryos experience low levels of pH naturally (i.e. 7.2). However, it is an open question whether low environmental pH interacts with PVF pH and, if so, whether the PVF is lowered by environmental pH. Large gaps remain in the study of ocean acidification effects on cephalopods; the effects of organisms exposed to increased concentrations of hydrogen ion and  $p\text{CO}_2$  (i.e. lower pH) are in their infancy.

Several burgeoning fields are developing in ecotoxicology and comparative physiology. Bioaccumulation of pollutants under low-pH conditions has been found for some species of sepiids (Lacoue-Labarthe et al., 2009, 2012) and teuthioids (Lacoue-Labarthe et al., 2011). Sepiids have been shown to calcify at higher rates having thicker densities possibly leading to negative effects on locomotion (Gutowska et al., 2008, 2010b). This likely impacts sensory abilities necessary for locomotion as has been found in fish. Sepiids could perform “normal” acid–base regulation under environmental pH below 7.2 (Gutowska et al., 2008, 2010a). Physiological study on gill membranes showed that late-stage embryos did experience significant reduction in somatic growth and incomplete development (Hu et al., 2011). Although some have suggested that cephalopods are “unscathed” by ocean acidification (Branch et al., 2013), we caution that many more studies across cephalopod taxa are needed to arrive at a clear understanding of the effects of high environmental  $p\text{CO}_2$  and associated low-pH exposure to cephalopods.

### 3.3. Hatching

Hatching conditions in cephalopods are flexible suggesting a phase of hatching competence rather than a well-defined hatching stage by morphological and/or physiological features (Boletzky, 2003). This flexibility is suspected to optimise posthatching survival (Boletzky, 2003). The timing of hatching, or hatching period, varies greatly across systematic groups, ranging from 2 days in *Octopus laqueus* (Kaneko et al., 2006) to 78 days in *E. dofleini* (Gabe, 1975). Villanueva and Norman (2008) undertook an extensive review of hatching times for many merobenthic octopods. They suggest that reported periods may be underestimated since observations likely come

from a single major hatching event. In *Octopus maya*, an observed variation in hatching time and size of emergent hatchlings from a single female implied a source of variation in initial conditions (e.g. initial size) (Briceño et al., 2010).

Mechanical stimulation, as well as biological and environmental factors, is suggested to trigger hatching (under wild and laboratory conditions). The mechanical stimulation of eggs, such as agitation or turbulence generated by a brooding octopus female, has also been suggested to promote or regulate the timing of hatching in benthic octopods (Villanueva and Norman, 2008). Octopus females are able to expel water forcibly over the eggs, aiding the ejection of hatchlings out of the den (Boletzky, 2003; Hanlon and Messenger, 1998). This behaviour has been largely observed at night, possibly enhancing hatchling survival (Hanlon and Messenger, 1998). The agitation of eggs incubated under artificial conditions (without parental care) was observed to promote hatching in *E. dofleini* (Snyder, 1986), *Octopus tetricus* (Joll, 1976) and *O. maya* (C. Rosas, personal observation).

Light has been proposed to modulate the hatching process in cephalopods, with most hatching events occurring during sunset and at night, which possibly minimises predatory risk (Rodrigues et al., 2011; Summers, 1985; Villanueva and Norman, 2008). Fields (1965) suggested that by emerging in darkness, hatchlings will be transported by tidal drift to clear spawning areas before light returns sight to any predators present in the vicinity of the spawning grounds. Under laboratory conditions, a majority of night-time hatchings were recorded for *O. vulgaris* (Villanueva and Norman, 2008), *Octopus briareus* (Hanlon and Wolterding, 1989), *S. pharaonis* (Nair et al., 1986) and *S. officinalis* (Paulij et al., 1991). In loliginid squid, such as *L. vulgaris*, hatching is influenced by light–dark transition, which is suggested to act as “zeitgeber” or synchroniser (Paulij et al., 1990). Other factors such as tidal and lunar rhythms, as well as external synchronisers and circadian rhythms in adults, are suggested to be associated with the hatching process (Villanueva and Norman, 2008). Variation in light regimes, the degree of exposure of study animals, observer behaviour, use of flash photography, mechanical vibrations and temperature fluctuations have been proposed as hatching stimuli under laboratory conditions (Villanueva and Norman, 2008).

Hatching success depends partially on the degree to which the chorion membrane swells (Villanueva et al., 2011). For example, the swelling process in *O. vulgaris* eggs has been found to occur in two distinct phases: first, an

initial slow swelling from Naef's stages 1 to 10–15 and, second, a subsequent accelerated swelling of the eggs (Marquez et al., 2013). Marquez et al. (2013) compared these two chorion swelling phases to a number of other studies and reported a second accelerated swelling process for loliginids, sepiolids, cuttlefish and octopods. Chorion expansion is essential to allow space for embryos to move and respire (Sakurai et al., 1995) and is said to be essential for successful hatching (Villanueva et al., 2011).

The hatching process begins with increased mantle contractions and fin movement by the embryo (Lee et al., 2009). Hoyle's organ, located at the distal tip of the mantle (Boletzky, 2003), and terminal spine are pushed directly against the inner wall of the chorion (Lee et al., 2009). This is thought to activate the secretion of enzymes from the hatching gland cells (Boletzky, 1987b; Villanueva and Norman, 2008). These enzymes digest the chorion membrane, while the terminal spine perforates the chorion and the enzyme-resistant outer capsule (Lee et al., 2009). Using mantle contractions and fin undulations, the embryo expels itself out of the opening (Lee et al., 2009).

### **3.4. From dependence on yolk reserves to exclusive prey capture**

#### **3.4.1 Changes from an internal to external energy source**

The yolk mass of late-stage cephalopod embryos is made up of the outer yolk sac, remaining outside of the embryo, and the inner yolk, the portion lying inside the embryo (Boletzky, 2002). The yolk neck connects the outer and inner yolk sacs (Boletzky, 2002). Towards the end of embryonic development, a shift in partial pressure, as a result of further development of the visceral mass, causes the yolk to “flow” from the outer to the inner sac (Boletzky, 2002). In cuttlefish *S. officinalis*, the transfer of yolk has been noted to take place during the final 2 weeks of embryonic development (Lacoue-Labarthe et al., 2010). The yolk volume inside the mantle cavity would peak around hatching, as has been observed in *T. rhombus* embryos (Miyahara et al., 2006b). These inner yolk reserves are essential to the survival of hatchlings during the first few days posthatching (Vidal et al., 2002a). As the outer yolk sac is normally shed after hatching (Boletzky, 2002), hatching before all the yolk has been transferred into the mantle cavity would limit the energy available (Boyle and Rodhouse, 2005).

After the yolk reserves are completely exhausted, hatchlings need to catch prey in order to survive (Vidal et al., 2002a). The switch from yolk utilisation to exclusive prey capture is a critical phase in the early life history

of cephalopods, and hatchlings are extremely sensitive to starvation during this period (Boletzky, 2003; Vidal et al., 2002a, 2006). The high mortality rates shortly after hatching, observed in numerous cephalopod rearing experiments (Boletzky and Hanlon, 1983; Vidal et al., 2002b; Villanueva, 2000; Yang et al., 1983), confirm this.

The rates of yolk utilisation in fed and starved laboratory-reared loliginid paralarvae suggest that yolk utilisation is dependent on feeding conditions, with fed paralarvae having lower utilisation rates (Vidal et al., 2002a). Initially, loliginid paralarvae undergo a no-net-growth phase as a result of the exponential rate of yolk utilisation to support the metabolic costs of maintenance (Vidal et al., 2002a, 2005). The weight lost is regained by feeding and the end of the no-net-growth phase reached when hatching weight is achieved (Vidal et al., 2002a, 2005). The no-net-growth phase shortly after hatching corresponds to the high mortality rates observed during this period (Vidal et al., 2002a, 2005). Loliginid statolith growth studies too indicate a period of no growth (Villanueva et al., 2007). This no-net-growth phase has also been observed in *O. maya* juveniles (Moguel et al., 2010). Analysis of RNA/DNA ratios in *D. opalescens* paralarvae confirms the poor nutritional condition of paralarvae during this period and their extreme sensitivity to starvation (Vidal et al., 2006). To survive the transition from yolk utilisation to exclusively prey capture, cephalopod hatchlings must not only initiate exogenous feeding but also find sufficient food to fuel metabolism and growth and improve prey-capture efficiency (Vidal et al., 2002a).

### 3.4.2 Hatchling morphology and prey capture

*O. maya* (Moguel et al., 2010) and *S. officinalis* (Darmaillacq et al., 2006) hatchlings do not immediately respond to or attack prey within the first few days posthatching. This lack of predatory behaviour has been attributed to the use of yolk reserves as the main energy source immediately after hatching (Moguel et al., 2010). Although hatchlings can survive on yolk reserves alone for a number of days (Miyahara et al., 2006b; Vidal et al., 2002a), yolk energy is used to fuel standard metabolism and activity and is quickly depleted (Vidal et al., 2005, 2006). The inner yolk reserve in cephalopods is separated from the digestive gland and is directly connected to the venous system (Boletzky, 2002). This enables simultaneous endogenous (yolk utilisation) and exogenous (prey-capture) feeding (Boletzky, 2002) and an opportunity to develop and improve prey-capture skills (Kier, 1996; Shea, 2005; Vidal et al., 2005). The capture and ingestion of prey at the first feeding induce the digestive process and the secretory activity

of the digestive gland (Boletzky, 2002; Boucaud-Camou and Roper, 1995; Mangold and Young, 1998; Moguel et al., 2010). Active feeding during the yolk utilisation phase has been observed in cuttlefish (Boletzky, 1975), *O. maya* (Moguel et al., 2010) and *D. opalescens* (Vidal et al., 2002a).

The first feeding depends on the cephalopod's ability to process visual and chemosensory information to recognise the sight or odour of potential prey (Romagny et al., 2012). This ability develops differently among cephalopod taxa. Young *S. officinalis* hatchlings innately prefer and target shrimplike prey (Darmaillacq et al., 2006). However, visually exposing embryos during late-stage embryonic development (Darmaillacq et al., 2008) or new hatchlings (Darmaillacq et al., 2006) of crab results in a preference for crab when active feeding commences a number of days later (Darmaillacq et al., 2006, 2008). Darmaillacq et al. (2006) also showed that the efficiency of this familiarisation in young hatchlings was dependent on the length of time and the number of crab that were visually exposed. The ability to learn the visual characteristics of prey in ova immediately after hatching facilitates imprinting and preference for prey abundant in the immediate area (Darmaillacq et al., 2008; Guerra and Gonzalez, 2011). This could have a beneficial effect during the transition from endogenous (yolk utilisation) to exogenous feeding (active predation), during which hatchlings are extremely sensitive to starvation (Vidal et al., 2006). Guerra and Gonzalez (2011) suggested that similarly late-stage embryos can recognise potential predators in ova and avoid them after hatching.

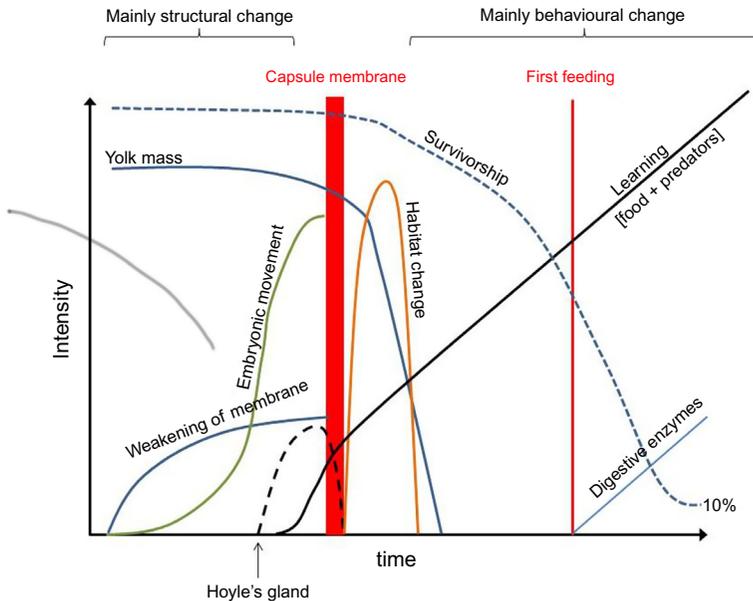
In contrast, prey selection experiments on *O. maya* suggest that preference in early juveniles (7 and 16 days posthatching) has a strong innate component that cannot be modified through imprinting or associative learning during the first weeks of life (Portela E., unpublished data). To preferentially attack prey that follow a predetermined search image of food may result in fast and successful foraging bouts that reduce both the time spent searching and testing alternative prey and the risk of failing to identify a deadly threat. In addition, to attack prey resembling a predetermined search image whenever it is present but readily to consume unfavoured prey when these are abundant would confer flexibility in foraging and allow predators to adjust to unpredictable changes in food quantity and quality.

Newly hatched cephalopods have a saclike mantle and a circular fin shape (Sweeney et al., 1992). Whether planktonic, nektonic–benthic or benthic, hatchlings swim by way of jet propulsion. Initially, the fins of squid paralarvae are small and rudimentary, and jet propulsion is the primary means

of locomotion (Bartol et al., 2008, 2009). After hatching, paralarvae immediately begin swimming within intermediate Reynolds numbers ( $Re$ ) (Bartol et al., 2008). The viscosity at this  $Re$  range prevents coasting, the continuous forward momentum observed in adults after the expulsion of water from the mantle (Bartol et al., 2008). As a result, paralarvae make use of pulse jet propulsion, with more rapid and frequent mantle contractions than observed in adults (Bartol et al., 2008; Thompson and Kier, 2001). Bartol et al. (2008) also noted that squid paralarvae swim predominately along a vertical axis, with sinking occurring as the mantle is refilled. Backward swimming is considered routine swimming and has been observed in planktonic squid (*L. vulgaris*, *L. forbesii* and *I. illecebrosus*) and octopus (*O. vulgaris*) hatchlings (Villanueva et al., 1997). Forward swimming forms part of predatory swimming behaviour (Villanueva et al., 1997).

Prey capture in cephalopods is both instinctive and experience-dependent (Messenger, 1977). In *D. opalescens* paralarvae, fundamental features of basic attack have been observed as early as the day of hatching (Chen et al., 1996). A rearing study has shown that the capture of copepods by squid paralarvae is a skill that must be acquired in an experience-dependent manner (Chen et al., 1996). Over the course of numerous unsuccessful attempts and the occasional successful capture, paralarva attacks become progressively more refined and complex (Chen et al., 1996).

Cephalopod hatchlings are visual predators (Boletzky, 1977; Villanueva and Norman, 2008) with prey capture achieved by a visual feedback system involving fixating the prey binocularly, assuming an attack position and striking the prey (Nair et al., 1986). According to Nair et al. (1986), it is essential that prey must be within the visual field of the hatchling in order for an attack to be initiated. Most teuthoids do not hatch with functional feeding tentacles, and the strike behaviour of young hatchlings differs from that of adults (Kier, 1996). In contrast, most sepiolids capture prey using the rapid tentacle elongation observed in adults (Boletzky 1987b; Boyle, 1983a,b). Kier (1996) noted that, considering the longer embryonic development phase in sepiolids compared with teuthoids, it appears that a longer developmental period is required for hatchlings to emerge with functional feeding tentacles. Changes in arm size relative to mantle size in early *O. maya* hatchlings suggest variations in attack success rate and prey capture as octopuses grow into full juveniles (Moguel et al., 2010). These changes together with those in the number (Boletzky and Boletzky, 1969) and structure of suckers (Kier and Smith, 1990) are believed to be in close correspondence with the transition from nektonic–benthic to fully benthic habits in octopuses.



**Figure 4.2** Overview of the main phenomena occurring to the organism during the transition from egg to paralarvae with qualitative indications of their intensity.

### 3.5. Summary

The numerous changes that occur during this transition are represented in a schematic diagram (Figure 4.2), which shows that some phenomena start before (and others continue after) the boundaries of this transition. Both the environment within the embryo and the surrounding oceanographic environment affect embryonic survival and hatching success. Once hatched, survival is largely dependent on passing through the critical transition from endogenous to exclusively exogenous feeding. Feeding and digestion of new items take part gradually. Brain development and learning start in the late embryo, and early acquisition of essential sequences such as feeding, swimming or predator escape might explain the high variability in the performance of specimens within the same cohort.



## 4. TRANSITION #3: FIRST FEEDING TO SUBADULT

### 4.1. Introduction

The transition from paralarva to subadult in cephalopods does not involve a metamorphosis as found in many other marine invertebrates (Boletzky, 1974). Paralarvae have, in general, similar morphology to subadult and adult

individuals. The changes occurring are subtle and concern the variation in growth rates, changes in body proportions or changes in the structure or function of specific organs, for example, the separation of the fused tentacles (proboscis) in ommastrephid rhynchoteuthion. In this respect, the transition from paralarva to subadult should be identified for each family or even for each species since the transition into a subadult is not followed by ecological or habitat changes in all species (Shea and Vecchione, 2010). For example, morphological aspects, such as the presence of a proboscis, have been used to identify ommastrephid squid paralarva (Froerman and Dubinina, 1984; Harman and Young, 1985; Wormuth et al., 1992), while for other oegopsid squid and sepiids, the differentiation of the tentacles has been also used as marker of the end of the paralarval stage (Kier, 1996). Both examples are not linked with changes in ecological function of tentacles but are used as keystone criteria to identify the transition between paralarva and subadult.

Obvious morphological changes during growth are characterised by discontinuities in relative growth that highlight crucial limits in stages of development (Nesis, 1979), and the first discontinuity seems to coincide with the transition from paralarva to subadult (Young and Harman, 1988). These changes in growth have been documented in many families including changes in body proportions in the Cranchiidae (Voss, 1980) and changes in chromatophore patterns in the Brachioteuthidae (Young et al., 1985). Many other examples can be found in Sweeney et al. (1992) and Vecchione (1983).

Shea and Vecchione (2010) examined the timing of ecological and morphological changes in oegopsid squids (*Chtenopteryx sicula*, *Mastigoteuthis magna* and *Brachioteuthis* sp.), and their results showed that the diel vertical migration (DVM) patterns are species-specific, and the end point of the paralarval stage cannot be defined ecologically in these three species. None of the three species examined had a sudden, obvious onset of DVM, and no clear pattern was found in the size of the specimens collected deeper than 250 m by day, the main benchmark for having left the paralarval stage (Young and Harman, 1988). In their work, Shea and Vecchione (2010) proposed a revised definition of paralarvae: “newly hatched cephalopods that have a distinctly different mode of life from the adults, with an endpoint identified by ecologically significant allometric changes in morphological characters”. After going through these significant changes in morphology, the subadults grow until the onset of the maturity process.

All stages of transition from one development stage to another are crucial to the survival of any animal, including cephalopods. The transition between

paralarva and subadult is not an exception. Mortality rates are higher during the early paralarval stages in many small-edged octopod species, and high peaks of mortality occur at settlement. Villanueva and Norman (2008) reviewed this aspect and showed that in laboratory experiments, the survival of benthic octopus at settlement is around 10% for individuals fed with crustacean zoeae. For species for which the transition from paralarva to subadult does not involve habitat changes as in oegopsid or myopsid squid, the survival numbers grow considerably. Using indirect mortality estimates, Bigelow (1992) estimated for *Abralia trigonura* an average instantaneous mortality rate of 7%, while González et al. (2010) using the same methodology estimated for *L. vulgaris* an instantaneous mortality rate between 5% and 10% depending on biotic and abiotic factors. In their study, González et al. (2010) showed that survival of paralarvae decreases with age and this trend is stronger between 40 and 50 days after hatching. The recruitment, which is an arbitrary measure of population breeding success, is also very dependent on the growth and survival of the paralarva to subadult stage (Boyle and Rodhouse, 2005).

Nixon and Young (2003) had provided an extensive range of examples in which one can observe changes in the nervous system and sense organs as animal transitions from a paralarva to a subadult and the consequences on behaviour. Therefore, this chapter will not discuss neurological underpinnings of this transition. Additionally, environmental factors evolved in this ecologically significant change in the mode of life can be quite diverse. The importance of each specific environmental factor in the transition from paralarva to subadult depends on the habitat occupied by the adult form of the species or group of species. For example, in the ommastrephid squid such as *Illex argentinus*, a significant change in feeding habitats marks the change in life stage (Vidal, 1994; Vidal and Haimovici, 1998). In others, as *O. vulgaris*, paralarvae become subadult when they settle to the benthic habitat (Villanueva and Norman, 2008). Thus, we have attempted to create a general synthesis of the broad morphological, physiological, ecological and behavioural changes associated with the transition from paralarva to subadult, but the specific context for groups and subgroups of cephalopods is equally important in our understanding of the importance of these changes.

## 4.2. Morphological, suborganismal and physiological changes during transition

Paralarvae exhibit distinct growth patterns that change as the animal transitions into subadulthood. The ML, the head length, the arm lengths and the

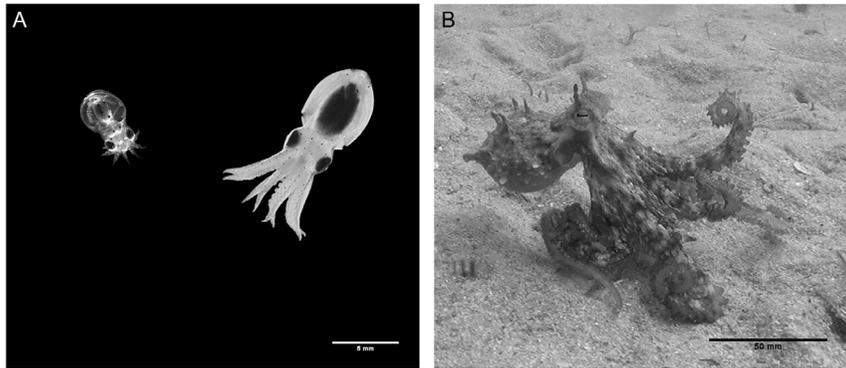
proboscis length of the paralarvae of the squids *I. illecebrosus* and *I. argentinus* grow allometrically (Froerman and Dubinina, 1984; Vidal, 1994).

The transition from paralarva to subadult often involves the modification, appearance or loss of the function of some organs. The newly hatched and paralarvae of all Ommastrephidae are known as rhynchoteuthions, in which both tentacles are fused into a “proboscis”. This organ becomes separated as individuals grow. The end of the rhynchoteuthion stage is marked by the complete separation of both tentacles, but the size at which this is completed is variable both within and between species (Okutani, 1987). The squid *I. argentinus* has three stages of growth during transition 3: (1) a rapid development of arms, suckers and fins with positive allometric growth (1–14 mm ML); (2) a rapid development of tentacles and clubs with isometric growth (14–28 mm ML); and (3) a greater increase in length relative to the other body parts with negative allometric growth (>28 mm ML) (Vidal, 1994). These shifts in growth pattern seem to be related to animal activity and food acquisition in different environments (Vidal et al., 2010).

In benthic octopuses with planktonic stages, the metamorphosis from paralarva to subadult occurs at settlement. Morphological changes associated with settlement include positive allometric arm growth; chromatophore, iridophore and leucophore geneses; the loss of Kölliker organs that cover the body surface; the loss of the “lateral line system”; and the loss of the oral denticles of the beaks (Villanueva and Norman, 2008). Changes in body proportions in *O. vulgaris* during this transition are shown in Figure 4.3.

According to Young and Harman (1988), the number of chromatophores on the dorsal surface of the mantle (and others body surfaces) varies during the transition between stages of paralarva and subadult. There is an increase in number and complexity of changes in the disposition of chromatophores. An increase in number of chromatophores and change in pigmentation pattern on the mantle were observed in three *Onychoteuthis* species at 12–16 mm dorsal ML (Young and Harman, 1987), between 14 and 17 mm ML for *I. argentinus* (Vidal, 1994), at 4.5 mm ML for *Doryteuthis pealeii* (Vecchione, 1981), between 7 and 10 mm ML for *S. lessoniana* (Segawa, 1987) and at 20 mm ML for *Gonatus madokai* (Kubodera and Okutani, 1977).

The size and shape of the eyes, especially in the oegopsid squids, vary widely within the paralarvae. Given that the major causes of mortality for the paralarvae are starvation and predation and that both depend critically



**Figure 4.3** Life cycle of *Octopus vulgaris* from hatching to settlement. Recently hatched *O. vulgaris* paralarvae have three suckers per arm (paralarvae on the left in A, 2.1 mm DML; photo by Jorge H. Urcera). After a period of constant swimming the planktonic octopuses undergo a transitional period from a pelagic lifestyle (juvenile on the right in A, 5.75 mm DML with 21 suckers; modified with permission from Iglesias et al., 2007) to the adult benthic life (subadult in B, 5 cm DML; photo by Manuel E. Garci). Figure composition by Alvaro Roura and Sílvia Lourenço.

on visual adaptations, it is likely that ocular specialisations that enhance visual efficacy have been favoured by evolution (Weihls and Moser, 1981). The two major limitations for foraging efficiency are the perception distance and the aperture of the visual field. Increasing the panoramic field of vision in cephalopod paralarvae has followed a progressive course. The first of these steps involves the possession of sessile eyes, round and firmly seated in their sockets. This type of eye is characteristic of loliginid paralarvae, paralarvae of some oegopsid squid species (e.g. the rhynchoteuthion of ommastrephids, *Onychoteuthis banksii* and/or *Gonatopsis borealis*) and species of octopuses with planktonic stages. The second stage involves the development of short eye-stalks, so that the eyes are directly in line with the outer margin of the head, such as in *Helicocranchia pfefferi* paralarvae. Such eyes rotate freely, allowing the animal to redirect the visual cone without moving the body. In the third stage, the eyestalks are arranged at different lengths. These eyes, besides allowing changes in the direction of the visual axis, increase visual perception of distance, so the volume of observable water from a given point becomes a sphere. Additionally, prey can be detected from farther away and with minimal movement of the paralarva. This is the case, for example, of the cranchiid squid *Bathothauma*, which stalked eyes may be connected with plankton feeding at great depths, perhaps improving distance judgement (Young, 1970). The disappearance of these eyestalks with growth could

be related to the different strategies of prey capture and predator avoidance for paralarvae and adults. For paralarvae, visual perception and immobility may be crucial, whereas in adults, these characteristics are less important (Guerra and Pérez-Gándaras, 1984).

In many cephalopods, the shape and features of the beak change during the transition from paralarva to subadult. In their planktonic stages, *L. vulgaris* and *D. pealeii* have teeth on the lower jaw, while the upper jaw is toothless (Boletzky, 1971). The beaks of the squid paralarvae also have a similar structure. Franco-Santos and Vidal (2014) observed that at hatching, the beak is rudimentary. Additionally, all beaks measured showed strong positive allometry in relation to ML, which has clear implications in a diet change as the animal grows. This character is found in both myopsid and oegopsid squids (Wakabayashi et al., 2005). In many species of incirrate octopods, such as *O. vulgaris*, *Octopus joubini*, *E. cirrhosa*, *Argonauta argo* and *Tremoctopus violaceus*, the anterior margin of both lower and upper beaks forms a row of relatively large teeth. This dentition is more important in species with planktonic paralarvae than in those whose offspring are benthic, like *O. maya* or *O. briareus*, in which the reinforced edges of the beaks seem more like the smooth cutting edges of the adult mandibles.

Although there is no direct evidence that toothed beaks are related to the planktonic life stages, this assumption is endorsed by the fact that teeth are present in common, newly hatched planktonic stages of different cephalopod groups: Octopoda with planktonic early life stages and paralarval Teuthida that are all planktonic. Whereas in all young Sepioidea, most of which are benthonic, the beaks are adult-like. The function of the teeth is possibly related to quick ingestion of planktonic prey (Boletzky, 1974). In consequence, this paralarval feature could be considered as a transitory formation in adaptation to the type of diet as the individual grows. Thus, the progressive strengthening of the jaws and teeth of planktonic larvae of cephalopods represents a change of role in the trophic web.

Photophore development can also mark the transition out of the paralarvae, especially in Myopsida and Oegopsida. Examples of photophore development have been shown in many oegopsid families, especially within Enoploteuthidae, Cranchiidae and Ommastrephidae, which are typically photophore-bearing squids (see Henning et al., 2002 and Okutani, 1987 for a review). Photophores develop on the ventral region of the eye in *Stenoteuthis oualaniensis* between the paralarval sizes of 1.8 and 6.3 mm (Ramos-Castillejos, 2007). Bykov and Dubinina (1984) examined the early

ontogenic stages of the squids of the families Enoploteuthidae. They identified successive development stages on the basis of the appearance of photophores on the ventral arms (*Abraliopsis morisii*) and intramantle photophores (*Pterygioteuthis giardi*) that defines roughly the morphological changes occurring during the transition from paralarva to subadult stage. Four stages were established for *A. morisii*: (1) stage without photophores (1.5–3.1 mm ML), (2) stage with one photophore on the ends of the ventral arms (2.7–3.8 mm ML), (3) stage with two photophores on the ventral arms (3.7–5.5 mm ML) and (4) stage with three photophores on the arms of the four pair; numerous photophores appear on the ventral surface of mantle, head and eyes (over 5.5 mm). Four stages were also established for *P. giardi*: (1) stage without photophores (ML is less than 1.9 mm); (2) stage with 1 pair of anal photophores, 1 photophore on each eye (ML 1.9–2.5 mm); (3) stage of branchial photophores, 3 photophores on each eye (ML 2.9–4.0 mm); and (4) stage of ventral photophores (ML more than 4.5 mm), 8 intramantle photophores—one paired anal, one paired branchial and four unpaired ventral—and 9–10 photophores on eyes.

An excellent example of the morphological changes with growth in paralarvae can be found with the diamond squid *T. rhombus* (Wakabayashi et al., 2005). Paralarvae with ML <3 mm possessed a round mantle with many chromatophores, long tentacles and small fins. At 3–6 mm ML, paralarval arms grew rapidly, and a primordial protective membrane developed simultaneously. By 15 mm ML, the shape of the mantle has become similar to that of the subadults, and fins were present along the entire length of the lateral mantle. Although arm suckers were present, they were not prominent and were absent from the distal third of the arms in specimens smaller than 6 mm ML. The development of protective membranes and the relatively long arms in the postlarval stage may be adaptations for floating in ocean currents rather than for active swimming and suggest that *T. rhombus* might have a long planktonic phase (Wakabayashi et al., 2005).

Arm and tentacle morphologies change to accommodate new methods of food acquisition (Kier, 1996; Messenger, 1977; Shea 2005). In cephalopod families such as Onychoteuthidae, Enoploteuthidae, Pyroteuthidae, Ancistrocheiridae, Octopoteuthidae, Gonatidae and Cranchiidae, some suction rings develop during ontogeny to form chitinous hooks, which facilitate grab and tighten the prey (Engeser and Clarke, 1988; Falcon et al., 2000; Kubodera and Okutani, 1977; Vecchione et al., 2001; Young and Harman, 1988). In other occasions, the transition between paralarva and subadult stages is marked by a loss. In *Taningia danae*, the tentacles are

reduced to minute appendages in young subadults, and they are absent in later stages, which influences hunting behaviour (Kubodera et al., 2007). Similar losses have been observed in *Octopoteuthis* and in *Chiroteuthis* spp., where the initial tentacular clubs are lost (Young, 1991).

Although only external morphological changes in the transition from paralarva to subadult stage have been discussed, there are also modifications in the functional morphology of some internal organs. However, these transformations mainly affect the size, growth and maturation of the gonads. No changes in the digestive tract were observed between paralarva and adult stages in many species, as cephalopods maintain carnivorous diet throughout their life (Boucaud-Camou and Roper, 1995). Nevertheless, the prey type proportion in the cephalopod diet changes ontogenically. While paralarvae fed mostly in larval stages of decapod crustaceans, subadult and adult shift their diet to larger crustacean life stages and species and to fishes and other cephalopods during growth (Rodhouse and Nigmatullin, 1996). *O. vulgaris* and *S. officinalis* clearly follow this trend (Nixon, 1985) with paralarvae feeding on large copepod and crustacean zoeae and changing gradually to bigger prey as arms grow and attack performance increases.

### 4.3. Ecological changes

It is widely recognised that cephalopods are highly sensitive to environmental conditions and changes at a range of spatial and temporal scales due to their short life cycles and rapid growth (Boyle and Rodhouse, 2005; Pierce et al., 2010). The specific environmental conditions that paralarvae and subadults are exposed to can affect the recruitment success and post-recruitment life history characteristics such as growth rate (Forsythe and Hanlon, 1988a), maturation (Boavida-Portugal et al., 2010; Forsythe and Hanlon, 1988b; Smith et al., 2005) and spawning (Lourenço et al., 2012; Otero et al., 2007).

Sea water temperature affects all phases of the life cycle, including paralarval growth and settlement of benthic species (Garofalo et al., 2010). Temperature directly affects growth in cephalopods (Forsythe, 1993; Forsythe, 2004; Forsythe and Hanlon, 1988a; Forsythe and Van Heukelem, 1987; Semmens et al., 2004) with increasing temperature (until reaching a threshold temperature value) positively affecting the growth rates in all cephalopod species. The initial exponential phase of growth is more strongly affected by temperature than the consequent phases of the growth curve (Briceño et al., 2010). This indicates that paralarvae experiencing

higher temperatures will transition into the subadult phase sooner. In *O. vulgaris*, the duration of the planktonic period lasted 47–54 days at 21.2 °C, 30–35 days at 23 °C and 40 days at 22.5 °C after which the octopuses started setting to the bottom (Iglesias et al., 2004; Imamura, 1990; Villanueva, 1995). *Octopus bimaculoides* grew from an approximate hatching size of 0.07 g to a mean of 619 g in 404 days at 18 °C. Growth was exponential from hatching until day 156 (21.18 g; 38.64 mm ML), with a mean relative growth rate of 3.56% of body weight per day. Growth was slower after day 156, becoming logarithmic. The weight data for the warm-water population (23 °C) revealed the same pattern of growth over slightly different time periods. The faster exponential growth phase lasted until day 142 (49.70 g; 51.83 mm ML) with an average growth rate of 4.5% of body weight per day. The slower logarithmic phase lasted from day 142 to day 324 (Forsythe and Hanlon, 1988a).

Nutrition is a key factor in octopus paralarval rearing success and, therefore, transition into a subadult. Comparisons of the effect of food type on paralarva survival when raised between 19 and 25 °C demonstrated that survival was more dependent on nutrition than on temperature (Iglesias et al., 2007). Meeting metabolic requirements is also important for the development of early stages of cephalopods. For most cephalopod species studied, the energetic requirement to grow depends on the protein degradation metabolic pathway (Lee, 1995), as several studies show on wild and captivity species where the availability or choice of a diet rich in protein or with a high ratio of protein/lipid content benefits the paralarva growth and survival (e.g. Rosas et al., 2013). Additionally, essential fatty acids also play an important role in the transition from paralarva to subadult. For *O. vulgaris*, prey rich in DHA (docosahexaenoic acid 22:6n-3), EPA (eicosapentaenoic acid 20:5n-3) and copper are required for optimal growth of the paralarvae (Navarro and Villanueva, 2000, 2003; Villanueva and Bustamante, 2006; Villanueva et al., 2004).

Changes in ocean currents, mixing, deepwater production and coastal upwelling will directly affect the distribution and abundance of plankton and of many fish and cephalopod species, as well as their migrations (e.g. González et al., 2005; Roberts and van den Berg, 2002; Waluda and Rodhouse, 2006). This, in turn, affects the temperature and nutritional options available to paralarvae as they transition to the subadult stage. Although oceanographic conditions are of particular significance for mobile pelagic species such as the ommastrephid squid, the less widely ranging demersal and benthic species may depend more on other physical habitat

characteristics (e.g. substrata and bathymetry). Coastal species may be affected by variations in water quality and salinity (related to rainfall and river flow) (Sobrino et al., 2002). In northwestern Atlantic Iberian upwelling system, the wind stress structure during the spring–summer (prior to the hatching peak) and autumn–winter (during the planktonic stage) was found to affect the early life phase of *O. vulgaris* and explains up to 85% of the total variance of the year-to-year variability of the adult catch (Otero et al., 2008). Despite this bottom-up modulation via environmental conditions, the results also provide evidence for a between-cohort density-dependent interaction, probably caused by cannibalism and competition for habitat (Otero et al., 2008). Moreover, Otero et al. (2009) suggested that the increase in *O. vulgaris* paralarval abundance and biomass was significantly correlated with the simultaneous decrease of water column integrated nitrate, ammonium and chlorophyll levels in the Ria de Vigo. These conditions occur during the early stage of the relaxation phase of coastal upwelling events, when nutrient salts are consumed to produce biogenic matter, which is retained in the system and transferred through the food web.

#### 4.4. Behavioural changes

For holobenthic octopus, prey capture by paralarvae is not fundamentally different from that of a subadult. The prey captured is smaller but the prey type stays relatively constant (Hanlon and Messenger, 1998). However, other cephalopod species, like pelagic squids with very characteristic paralarvae (e.g. the rhynchoteuthion in the ommastrephids) and the benthic octopods that do have a planktonic stage, differ in form and in size from the adults, and consequently, their feeding behaviour is substantially different.

Ontogenic changes in predatory behaviour are closely related to morphological changes in arms and tentacles of hatchlings. Newly hatched *D. opalescens* exhibit only one predatory behaviour: basic attack (BA). During BA, arms and tentacles were spread apart before being thrust forwards to make first contact with the prey. Forty days after hatchling, BA was replaced by arm net (AN) and tentacular strike behaviours (Chen et al., 1996).

Changes in the diet during development have been followed in several species of squids: together, they provide evidence that prey size, prey behaviour and prey density are critical. Vovk and Khvichiya (1980) recognised four stages of feeding in *D. pealeii*. Yang et al. (1983) followed these changes in *D. opalescens* reared in the laboratory and found that during the first

70 days, squid selected copepods less than 4 mm in length, as well as *Artemia* and chaetognaths; from day 60 to day 130, they ate mysid and shrimp larvae up to 10 mm long; and from day 100, they ate various shrimps (up to 25 mm) and specially fish (up to 70 mm). Three-week-old *S. sepioidea* stopped attacking mysids, and even before this stage, the young showed signs of selectivity. Mysids and juvenile fish were preferred over copepods, amphipods, polychaetes and zoeae of various crustacean species (LaRoe, 1971).

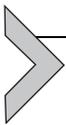
For many social species, the onset of social behaviour can indicate a transition to the subadult stage. The appearance of schooling behaviour, which depends partly upon size and swimming strength, was observed in *L. vulgaris*, *D. opalescens*, *D. pealeii* and *I. argentinus* 4–11 mm ML and 20–60 days old (Hanlon et al., 1987; Turk et al., 1986; Vidal et al., 2010; Yang et al., 1986). The schooling behaviour is associated with the increase of the swimming ability related to the onset of specific morphological features as improved vision, development of communication skills (chromatophores patterns) and the development of functional clubs (Vidal et al., 2010). This behaviour allows squid subadults to migrate vertically and explore more food resources, enhancing growth and survival (O'Dor, 1998). As the ability to swim against the current is crucial (Hurley, 1978), the formation of schools depends on size rather than age as proved for *D. opalescens* and *I. argentinus* (Vidal et al., 2010).

Transition between paralarva and subadult stages obviously implies the development and modification of some elements (chromatophores, iridophores, internal organs, muscles, photophores, etc.), units or groups of elements contributing to components, components or constituents of a pattern and the appearance of whole animal, which constitute the hierarchical categories of any behavioural pattern (Hanlon and Messenger, 1998). This transition also implies deep changes in the central nervous systems and receptors of the animal (Nixon and Young, 2003). However, little attention has been devoted to these aspects until present. The development of body patterning has been studied, at least, in *S. officinalis* (a species lacking paralarvae) and three octopus species (*O. vulgaris*, *Octopus rubescens* and *O. briareus*). Hanlon and Messenger (1998), compiling results of several researches, showed that in many cephalopods, new elements, units and components of body patterns develop in skin as the animal grows and that some adult body patterns and display are developed or refined during ontogeny. These changes in both enoploteuthid squids represent obvious modifications in behaviour of the animals. The acquisition of a complete set of

photophores means full development of behaviour in relation to intraspecific communication, between males and females, as well as the increased possibility of camouflage against predators.

#### 4.5. Summary

Planktonic paralarvae common in oegopsid squids, merobenthic octopods with small hatchlings and the exceptional pygmy cuttlefish *Idiosepius pygmaeus* (Boletzky, 1974) are not found in benthic octopods or cuttlefish of longer embryonic development and bigger hatchlings. Nevertheless, between the first feeding after hatch and the subadult phase, several important changes occur in morphology, ecology and behaviour in pelagic, benthic and merobenthic cephalopods. In species where this transitional stage is followed by migration to different habitats, important morphological, suborganismal and physiological changes occur. Examples of these changes are the separation of the rhynchoteuthis “proboscis” in two tentacles in the ommastrephid, the allometric growth in octopus paralarvae, the changes in chromatophore pattern in *T. rhombus* and the development of photophore patterns in oegopsid paralarvae. In all cases, the transition is associated with behavioural changes in diet, predation, migration and social patterns. In this, as in other transitional stages, environmental conditions play an important role in survival success. By finding the best environmental or nutritional conditions (e.g. primary production, water temperature and water column mixing), a quick transition can be achieved to the subadult stage where chances of individual survival are exponentially greater.



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## 5. TRANSITION #4: SUBADULT TO ADULT

### 5.1. Introduction

This chapter will examine the suite of changes that occur during the subadult phase and are directly associated with the transition to mature adult, including morphology, physiology, behaviour, diet and habitat. A subadult is an individual who, while appearing to be functionally and morphologically similar to an adult, is generally smaller than an adult and not yet reproductively mature, while an adult is an individual who is sexually mature and of adult size (Young and Harman, 1988). So effectively, we are examining the transition from being reproductively immature to mature; males will have spermatophores present and females will have mature ova in the ovary and are functionally mature (Arkhipkin, 1992). While there is a suite of

changes when individuals transition from subadult to adult, these changes are not as dramatic and rapid as other transitions in the cephalopod life cycle, yet they are crucial to reproductive success of the population. During this protracted transition, it is difficult for biologists to identify when this transition has been completed as there are no external signs of sexual maturation, which is first evident internally with the start of ova and sperm production. Furthermore, the size and age at which individuals start maturation are highly variable, both within and between populations of species, for example, *S. australis* (Pecl et al., 2004), *S. lessoniana* (Jackson and Moltschaniwskyj, 2002), *D. pealeii* (Macy and Brodziak, 2001) and *I. argentinus* (Arkhipkin and Laptikhovsky, 1994). Age and size at completion of the transition can differ between the sexes, with males usually maturing sooner than females, for example, *O. pallidus* (Leporati et al., 2008), *I. illecebrosus* (Rodhouse and Hatfield, 1990) and *D. gigas* (Liu et al., 2013); as a result, males may have a substantially longer reproductive life.

Given the absence of external characters indicating sexual maturation for most cephalopod species, especially in females, fisheries and population biologists identify the size and age at which subadults of a species become reproductively mature adults using logistic regression models. These models estimate the age or size that a specified percentage of the population has attained sexual maturity, usually 50%, and has finished the transition from subadult to adult. Although not usually reported, it is possible to use this approach to identify the age and size of the start of the transition, for example, size or age when 5% of the population are mature. If the presence of spermatophores or ovulated eggs defines the end point of the transition, then the best external indicators of the end of this transition for males are mating behaviour and the transfer of spermatophores to females. However, mating is not a good indicator of sexual maturation in females, as she is receptive to mating even when not fully reproductively mature and will store spermatophores until ready to fertilise eggs. For female cephalopods, the start of egg deposition may be the best external identifier of the transition end point. Not all species will have a subadult phase; if the acquisition of the adult morphology and diagnostic characteristics and the attainment of sexual maturity are almost simultaneous, the transition from a juvenile to adult effectively skips the subadult phase, for example. *Leachia pacifica* (Young, 1975).

Mortality estimates during this transition are not available in the literature, but it is assumed that most cephalopod species have a type III mortality pattern, with the highest mortality rates expected during the larval phase and following spawning. Therefore, the transition from subadult to adult most

probably has a relatively low mortality risks, although for species that undertake migrations (Section 5.5) during this transition, there are mortality risks associated with cannibalism and shifts in diet (Section 5.3). However, this transition is critical from an evolutionary biology perspective as the reproductive success of an individual determines its contribution to the next generation and the short life span of cephalopod means that the reproductive window is months not years. Delays in the start of the transition or extending the transition over a longer period can carry a risk of a shorter reproductive window once the adult phase begins. However, allocation of energy to reproduction and away from production of muscle tissue (Moltschaniwskyj and Carter, 2013) can influence capacity to escape predators and capture prey, affecting survival. Timing of the transition among individuals within a species is typically variable for cephalopods and is not necessarily directly a function of size or age (Pecl, 2001). Factors such as environmental and oceanographic conditions, food availability and behavioural interactions have the capacity to influence the timing of transition (Pecl et al., 2004, Pierce et al., 2005). Variability in size at maturity for squid is a function of the time of spawning and hatching occurring throughout the year, with individuals experiencing different growth rates dependent on environment conditions (Pecl et al., 2004). For *S. officinalis*, the length of time a subadult individual spends in optimal conditions (inshore summer) determines the speed and timing of maturation (Boletzky, 1983). For a few species, death occurs very shortly after completing the transition, for example, after ovulation in female *Onykia ingens* (previously *Moroteuthis ingens*; Jackson and Mladenov, 1994) and *Gonatus fabricii* (Arkhipkin and Bjorke, 1999), or shortly after sperm transfer, for example, in male epipelagic octopuses *Argonauta*, *Tremoctopus* and *Ocythoe* because they leave the hectocotylus in the female during sperm transfer (Mangold, 1987).

## 5.2. Morphological, suborganismal and physiological changes during the transition

Whole animal growth during the subadult stage is accompanied by allometric growth of external morphological structures, for example, *Photololigo* sp. (Moltschaniwskyj, 1995a) and *D. opalescens* (Zeidberg, 2004). Individuals reach their final body shape towards the end of the subadult phase with no evidence that further shape change occurs during the transition from subadult to adult. However, some morphological changes do occur during this transition. The males of most coleoid cephalopods develop a hectocotylus, a specialisation of one or more of the arm tip(s) used to transfer spermatozoa to

females. The number of modified arms and the nature of the specialisation are species-specific but can develop early in the reproductive maturation process, for example, *I. coindetii* (Zecchini et al., 2012). However, not all species use a hectocotylus for spermatophore transfer; for example, *Nautilus* have a large erectile mass known as a spadix (Arnold, 1987; Saunders and Spinosa, 1978), or there is no specialisation for spermatophore transfer, for example, cirrate octopods (Mangold, 1987). Females of some cephalopod species will develop secondary reproductive structures during the maturation phase; for example, female *Argonauta* develop specialised dorsal arms that secrete a calcareous brood chamber for her eggs. Epi-, meso- and bathypelagic octopuses (families Tremoctopodidae, Vitrellodellidae and Bolitaenidae) brood eggs in their arms, as do some deep-sea squid from the family Gonatidae (Seibel et al., 2000). However, we do not know if or when the development of the specialisations of the arms and suckers necessary to hold the eggs occurs. Additional secondary sexual characteristics that can develop during this transition are extra-large suckers on the second and third arms in mature males, for example, *O. cyanea* (Van Heukelem, 1973) and *Euprymna tasmanica* (Norman and Lu, 1997); mature male *Octopus* use them for displaying to conspecifics (Packard, 1961) and/or they may be used in chemoreception (Voight, 1991). Although *L. pacifica* has an abbreviated adult lifetime, immediately before sexual maturation, the female develops brachial photophores that may be used to attract mates (Young, 1975).

Hormones control the reproductive maturation process in most animals, and in *Octopus* spp., the optic glands secrete a small quantity of gonadotropin before the onset of sexual maturity (Wells and Wells 1959). The optic gland sits on the optic tract, which connects the optic lobes with the central regions of the brain, with its size, colour and structure changing with sexual development in a number of species, for example, *E. cirrhosa* (Boyle and Thorpe, 1984), *S. officinalis* (Koueta et al., 1995) and *S. sepioidea* (Arrieche, 1999). However, we know little about the endogenous and exogenous factors influencing optic gland secretory activity. It is possible that female *O. vulgaris* respond to cues from males, since females mature faster in the presence of males than when kept in isolation (Estefanell et al., 2010).

Attainment of sexual maturity involves growth and maturation of all the reproductive organs and is a consistent characteristic of the transition from subadult to adult. However, there is considerable variability in the nature and extent of changes to other organs, such as the digestive gland and mantle muscle, during the development and growth of reproductive tissue. If maturation, that is, transfer of sperm and egg deposition, occurs before final adult

size is attained, then energy is allocated to somatic and reproductive growth simultaneously, for example, *Photololigo* sp. (Moltschaniwskyj, 1995b); *S. lessoniana* and *S. australis* (Ho et al., 2004; Pecl, 2001); *I. argentinus* (Hatfield et al., 1992); *Octopus chierchiae* (Rodaniche, 1984), *O. vulgaris* (Otero et al., 2007; Rosa et al., 2004a) and *Octopus defilippi* (Rosa et al., 2004a); *E. cirrhosa* and *Eledone moschata* (Rosa et al., 2004b); and *S. dollfusii* (Gabr et al., 1999a) and *S. pharaonis* (Gabr et al., 1999b). These species show none of the dramatic changes in size or proximal composition of muscle tissue and digestive gland that are typical when stored energy reserves are mobilised; instead, individuals fuel reproductive growth directly from ingested food. However, somatic growth is affected, with specific growth rates of many cephalopod species slowing as individuals get older and larger, for example, *Photololigo* sp. (Moltschaniwskyj, 1995b), *S. lessoniana* and *S. australis* (Ho et al., 2004; Pecl, 2001), *O. chierchiae* (Rodaniche, 1984), *I. argentinus* (Hatfield et al., 1992), *D. gigas* (Mejía-Rebollo et al., 2008) and *N. gouldi* (Jackson et al., 2003). Slowing of somatic growth is due to slowing in the rates of both protein synthesis and degradation in the mantle muscle during reproductive maturation, allowing more energy to be allocated to reproductive growth (Moltschaniwskyj and Carter, 2013).

In contrast, some cephalopod species have dramatic changes in their digestive gland and/or muscle tissue size and composition during the transition from subadult to adult. Muscle tissue mass and integrity are lost as protein in the tissue is used as an energy source to fuel maturation, for example, *M. ingens* (Jackson and Mladenov, 1994; Jackson et al., 2004) and *G. fabricii* (Arkhipkin and Bjorke, 1999). Individuals mobilise energy from the mantle during reproductive growth either because they cease feeding as they reach sexual maturation or because they cannot catch sufficient food to support metabolism, movement and maturation.

### 5.3. Changes in feeding and diet

For many cephalopods, the transition from subadult to adult occurs while growing, and they may undertake a change in habitat at the same time (see section 5.5), both of these allow or necessitate a change in prey items. Cephalopods that are opportunistic predators change their diet based on the availability of prey items, for example, *I. argentinus* (Rodhouse and Nigmatullin, 1996), *I. coindetii* (Castro and Hernández-García, 1995) and *D. gigas* (Markaida and Sosa-Nishizaki, 2003). Increasing body size and associated changes in shape (see section 5.2) allow larger prey items to be

caught and consumed, although smaller prey are often retained in the diet, for example, *L. forbesii* (Collins and Pierce, 1996), which effectively increases the diversity of prey items consumed. A change in diet or increased prey diversity can be accompanied by a morphometric change in beak shape (Castro and Hernández-García, 1995). Differences in fatty acid profiles between mature and immature female *N. gouldi* suggest dietary differences during this transition, but it is likely that larger mature females are able to catch different prey as a function of their size, and there is no evidence that a change of diet directly contributes to the process of reproductive maturity (Pethybridge et al., 2012). Opportunistic use of prey species is critical to supporting fuelling of reproductive growth directly from ingested food (see section above) and maximises opportunities to reproduce regardless of nutritional history.

The risk of using income energy to fuel reproductive maturation in species that are relatively short-lived and have a short reproductive period is that insufficient energy is available to support all the biological demands at this time (Bonnet et al., 1998; Jonsson, 1997). One of the dietary options available, particularly to larger individuals in a population, is cannibalism, which increases during this transition (Ibáñez and Keyl, 2010). While there is a reproductive behavioural component to this (see Section 5.4), there is also evidence that this is a source of energy for individuals (Ibáñez and Keyl, 2010). Increased energy demands associated with reproduction and movement to spawning sites mean that cannibalism is important for many species, for example, *I. illecebrosus* (O'Dor, 1983) and *Sepioteuthis* spp. (Pecl, 2001).

#### 5.4. Behavioural changes

During the transition from subadult to mature adult, it is likely that individuals will need to learn and adopt new behaviours associated with courting and/or mating and also any new behaviours needed to use new habitats (see Section 5.5). Our knowledge of the acquisition or learning of new behaviours as individuals undergo the transition from subadult to adult is extremely limited; anecdotal evidence suggests that males become more active and females less as they approach maturity (Mather, 2006). While a body of research has described the behaviours during courting, mating and egg deposition, these descriptions of behaviours are in adults that have already undertaken the transition from subadult to adult. The changes in behaviour, how they are learnt and adopted and how they are mediated

hormonally warrant investigation (Hanlon and Messenger, 1998; Mather, 2006), as acquiring these behaviours is important for both survival and successful reproduction.

In some cephalopod species, the subadults are asocial and have limited interactions with conspecifics; this is particularly the case for *Octopus* species, many of the *Sepia* species and the sepiolids. Some of these species will continue a solitary existence as they transition from subadult to adult and will mate opportunistically when encountering the opposite sex. For species that show no evidence of courtship behaviours prior to copulation, for example, *I. paradoxus* (Kasugai, 2000), *Sepiolo atlantica* (Rodrigues et al., 2009) and *S. officinalis* (Hanlon et al., 1999), development of courtship behaviours will be absent. However, some species have extended and complex courtship behaviours that need to be developed and potentially learned by individuals during this transition, for example, *S. apama* (Norman et al., 1999), *S. australis* (Jantzen and Havenhand, 2003) and *L. reynaudii* (Hanlon et al., 1994). Males of species that school very early in their lifetime develop intraspecific aggressive behaviours that are expressed before, during and after mating, for example, *L. forbesii* (Hanlon et al., 1989b). For some species, for example, *S. australis* and *D. gigas*, subadults typically exist in small and socially loose aggregations; however, during the transition from subadult to adult, individuals experience great densities when individuals converge at a given location for spawning (Nigmatullin et al., 2001; Pecl et al., 2006; Schoen et al., 2002; Steer et al., 2005). The effect of aggregation on the timing of the transition from subadult to adult is unknown but is likely to promote a behavioural response that facilitates courtship and copulation. During the transition from subadult to adult, the reproductive behaviours of the adults develop and become apparent. Sexually mature female cuttlefish can distinguish between conspecific males and conspecific females (Palmer et al., 2006), while obviously an important element to reproductive behaviours, when this capacity develops, is unknown. Subadult *S. sepioidea* in the presence of reproductively mature adults display colour patterns out of normal sequence or to the wrong sex (Mather, 2006), suggesting that learning of some reproductive behaviours may occur as subadults join spawning aggregations.

The few studies that have examined ontogenic changes in behaviour in cephalopods have focused on the development of behaviours and learning. Cuttlefish (*S. officinalis*) significantly improve their learning ability during their transition from subadult to adult, and this improvement is correlated with the superior frontal and vertical lobe development (Agin et al., 2006; Dickel et al., 2001). Increased quality and complexity of the

surrounding environment at this time have a positive effect on the maturation of memory, highlighting the importance of habitat in the development of certain behavioural abilities (Dickel et al., 2000). Additionally, changes in individual personality occur at approximately the age that individuals start to undergo the maturation process (Sinn and Moltschaniwskyj, 2005), but there is no evidence of any further change at the time that mating and egg deposition occur. However, as this study described changes in personality in individuals held in isolation for their entire life, there is substantial scope to determine changes in behavioural interactions between males and females as individuals move from subadult to adult.

The use of visual displays and their importance changes as cephalopods transition from the subadult stage to the adult stage. Cuttlefish hatchlings are born with the ability to produce almost every adult body pattern; however, the visual displays shift from being used primarily for concealment and predator evasion to courtship and reproductive behaviours (Hanlon and Messenger, 1998). Body patterns beneficial for camouflage, such as light mottle or a disruptive pattern, are displayed more often in juvenile *S. officinalis*, and patterns associated with reproductive behaviours, like intense zebra, are developed around the time of sexual maturity (Hanlon and Messenger, 1998). The squid *S. sepioidea* present the first indications of sexual behaviour via visual displays (Mather, 2006). However, immature *S. sepioidea* males can mimic the displays of mature ones, making it difficult to use body patterns as indicators of the transition from subadult to adult. Regardless, the use and prevalence of reproductively associated visual displays are a key change during this transition, and the quality of these displays can affect the animal's fitness (Boal, 1997).

Cannibalism within a cohort, that is, among individuals of similar size and age, increases close to and during the reproductive season and changes with maturity status of individuals (Ibáñez and Keyl, 2010). This type of cannibalism appears to have both a strong element of behaviour, aggression and competition and also energy requirements (Ibáñez and Keyl, 2010). Where cannibalism is related to behaviours of aggression and competition, this occurs once maturation has occurred and often during courting and mating (see review by Ibáñez and Keyl, 2010).

## 5.5. Migration and habitat change during the transition

For many cephalopods, migration, large (thousands of kilometres) or small (tens–hundreds of kilometres), is a major event in the transition from subadult to adult and is commonly a prelude to mating and egg deposition.

Migrations can involve important changes in habitat, for example, from the continental slope to the shelf or vice versa, or migrations can occur along coasts or throughout oceans with little in the way of habitat change. Regardless of the magnitude of the migration, individuals will experience some changes in their physical and biological environment, including temperature, salinity, water chemistry, prey, predators and current systems. Although the nature and magnitude of migration during this transition vary among cephalopod species, migration appears to be associated with increasing the chances of finding a mate, finding and using habitats suitable for egg attachment or release. Formation of spawning aggregations, for example, *L. reynaudii* (Sauer et al., 1992), *S. apama* (Lu, 1998) and *Graneledone* sp. (Drazen et al., 2003), increases spawning potential, influences the number of offspring produced during spawning events and promotes genetic diversity within the population or stock (Naud et al., 2004).

Our knowledge of the distribution and abundance patterns of subadults is largely a function of methods of sampling and the nature of the data used to derive the pattern. If we derive our knowledge from fishery data, then the distribution of fishing effort and fishing technique will determine our capacity to track changes in the distribution patterns of subadults and adults. For *I. argentinus*, jigs catch larger squid than trawlers in similar regions (Koronkiewicz, 1995), so it is possible that the fishery catches a relatively greater proportion of larger subadults. Analyses of migration characteristics during this transition will require a sampling method, such as using fine mesh cod ends, that ensures all individuals in the population have equal chance of capture.

In some cases, the locations of the end point of migration are temporally and spatially predictable and stable, for example, southern calamari *S. australis* in Tasmania (Pecl et al., 2011) and *S. apama* in South Australia (Drazen et al., 2003). However, this is not always the case, and often, the location of the spawning grounds is strongly associated with characteristics of the physical environment (see review by Pierce et al., 2008). This association of distribution with environmental characteristics, such as temperature, may result in different migratory behaviours within a species; for example, Australian populations of *N. gouldi* migrate to the shelf waters of southern Australia to spawn (Green, 2011), but the New Zealand population does not undertake migrations to the shelf waters of New Zealand (Uozumi, 1998).

Whether cephalopods migrate between habitat types or within a habitat type will determine the magnitude of change in environmental and

oceanographic factors they experience, which in turn can affect the timing of transition. Shallow coastal habitats have greater spatial and temporal variability in biotic and abiotic factors, such as in temperature, salinity, nutrient load, current speed, turbidity, bottom types and food availability, compared with offshore waters (Boyle and Rodhouse, 2005). Species whose transition from subadult to adult occurs in a similar oceanographic realm experience relatively small changes in environmental and oceanographic conditions, for example, incirrate octopus and some benthic squid *Sepiadarium austrinum* (Norman and Reid, 2000). In contrast, species are likely to experience greater changes in habitat and environmental and oceanographic variables if they migrate between inshore and offshore habitats, for example, *L. gahi* (Arkhipkin et al., 2004); move in and out current systems, for example, *I. illecebrosus* (Falkland Current; Dawe et al., 2000) and *T. pacificus* (Kuroshio and Oyashio Currents; Sugimoto and Tameishi, 1992); or have significant inshore movements, for example, *S. australis* (Pecl et al., 2006). Changes in environmental conditions experienced by individuals undertaking migration are when energy and resources are being allocated to reproductive development and, as such, will have substantial influence on the size, age, growth and condition at maturity.

#### **5.5.1 Vertical migrations during transition: Change from well-lit, warm to cold, dark environment**

We are aware that some open-water cephalopod species undergo vertical migrations during the transition from subadult to adult, for example, *L. pacifica* (Young, 1975), *Eledonella pygmaea* (Voight, 1995) and *Gonatus onyx* (Hunt and Seibel, 2000). Collections of juveniles and mature adults with eggs indicate that individuals move to find a mate, with individuals moving from well-lit warm near-surface waters to dark and cold waters at depths of >1000 m. However, there are physiological impacts associated with this thermal change; in particular, metabolic rates decrease significantly for species that undertake vertical migrations associated with reproductive activities (Seibel et al., 1997). It is not clear what the biological implications are for these species, as slowing metabolic rates will affect locomotion and in turn activities such as finding mates and capturing prey (Seibel et al., 1997).

#### **5.5.2 Migrations between the offshore neritic and the inshore neritic**

Loliginids, sepiolids and octopods have a strong association with the sea bottom, where there is a diversity of habitats in this photic zone, with nutrients provided from terrestrial sources, and rich diversity of food resources, but

with large variations in environmental conditions (Boyle and Rodhouse, 2005). Many of these species do not migrate over long distances, preferring to deposit their benthic eggs in shallow waters (Boyle and Rodhouse, 2005). So, a common migration characteristic of neritic cephalopod species is for subadults to move from deeper offshore neritic waters to inshore shallower neritic waters, for example, *L. gahi* (Arkhipkin et al., 2004; Hatfield et al., 1990), *D. gigas* (Ibáñez and Cubillos, 2007; Nigmatullin et al., 2001), *D. pealeii* (Hatfield and Cadrin, 2002) and *S. officinalis* (Boucaud-Camou and Boismery, 1991; Le Goff, 1991). This may result in changes in the habitat that the individuals experience, as they move from bare low-profile sediment substrate to a more physically complex habitat, which supports marine plants and greater diversity of marine organisms, for example, *S. australis* who attaches eggs primarily to sea grass (Moltschaniwskyj and Pecl, 2003; Steer et al., 2007). In contrast, some species move inshore but remain on bare sediment and use this substrate to deposit their eggs, for example, *L. reynaudii* (Sauer et al., 1992). These shallower inshore habitats typically are warmer (Bettencourt and Guerra, 1999), which can potentially increase metabolic rates (Boucher-Rodoni and Mangold, 1995), but greater food intake needed to support this is readily available in these productive areas.

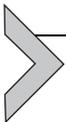
### 5.5.3 Migrations within habitats

There are groups of cephalopod species that display no dramatic shift in either habit or habitat during their transition from subadult to adult, but they may move within the habitat. The subadults occupy the same habitat as the adults, and it is here that they will become reproductively mature and start mating and deposit eggs, for example, *Photololigo* sp. (Moltschaniwskyj, 1995b). Some species such as *L. forbesii* have relatively short migrations where they make seasonal migrations along the coast of the United Kingdom (Waluda and Pierce, 1998), whereas *Uroteuthis edulis* and *H. bleekeri* have shown to prefer inshore continental shelf waters in the Sea of Japan (Natsukari and Tashiro, 1991, Semmens et al., 2007). For *O. vulgaris*, migration is on a very small scale from intertidal to the subtidal areas to spawn (Oosthuizen et al., 2002b). Depending on the population structure and dynamics, this transition may occur in the presence of adults, that is, overlapping generations when there are multiple spawning events or in the absence of adults when there is a single spawning event for an annual species. Fisheries stock assessment typically makes no distinction between subadult and adult, and size limits are not used as a management tool; as a result, these

individuals are treated as a single group irrespective to their status as a subadult or adult or if they are going through this transition.

## 5.6. Summary

The start and end of this transition is very difficult to identify because there are few external signs of sexual maturation, which is first evident internally with the onset of gonadal maturation. While the transition from subadult to adult occurs at a phase when mortality risks are relatively small, this transition is critical from an evolutionary biology perspective as the reproductive success of an individual determines its contribution to the next generation. Although allometric growth leads to changes in body proportions between subadults and adults, the main morphological change is the differentiation of mating structures in males. Most male coleoid cephalopods develop a hectocotylus, a specialisation of one or more of the arm tip(s) used to transfer spermatozoa to females. The main behavioural changes around the migration to spawning grounds, where known, occurs when there is differences in habitats; and this exposes individuals to challenges associated with new environmental factors and differences in prey. Those species that are generally solitary will experience behavioural changes associated with increased interaction with other adults during spawning, although these changes may be gradual.



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## 6. DISCUSSION

This description of four life stage transitions from morphological, ecological and behavioural perspectives gives us an opportunity to see how these transitions might be selected for, occur and vary within cephalopods. Transitions might be defined by major morphological change, habitat shift, shifts in energy allocation from growth to reproduction and internal changes such as hormone regulation (Bishop et al., 2006). In the four transitions undertaken by cephalopod species, morphological changes are present, but not extreme, for example, hatching gland development in transition 2, change in body proportions in transition 3 and growth of gonads in transition 4. Habitat shift is a common, though not universal, feature of these changes. Many cephalopod species seek specific sites for egg deposition during transition 1, they move from a benthic to pelagic habitat in transition 2, they transition from pelagic to benthic habitat in transition 3 and they may gather in specific locations during transition 4. There must be major epigenetic regulations during these changes; we know little about them, although we

know that hormonal influences on the optic gland trigger the transition from subadult to adult (transition 4).

If different stages of cephalopod life cycles occupy different niches, transitions may need to be rapid (Hadfield, 2000), so that each stage occupies the niche to which it is closely adapted for as long as possible and reduces the time taken to transition between the two niches (Moran, 1994). Our knowledge about the transitions from egg to the exhaustion of the yolk reserves (transition 2) and from paralarva to subadult (transition 3) identifies the major risk of mortality during these transitions. For both transitions, there are obvious changes in niche, and both are rapid relative to the time spent in each phase. In contrast, paralarvae, resembling the subadult more closely than many larvae of other marine animals, may delay their transition to subadult for some time until a suitable habitat has been found. Likewise, the transition from subadult to adult may be much longer as the search for suitable mates and appropriate habitat and the major morphological changes of the reproductive system take longer. Understanding the scope of transitions and the time over which they occur will assist in the management of many cephalopod species, as well as their cultivation in captivity. The challenges of quantitatively sampling cephalopods in every life stage are preventing us from defining “key” life stages (Yamamura, 1999). Nevertheless, this synthesis highlights the most critical transitions and more importantly identifies the factors known to be critical during the life history of cephalopod species.

Heyland and Moroz (2006) suggested a series of changes that must underlie any such transition. The first change necessarily prepares the animal for the new competence required of it, and Figure 4.2 demonstrates that the changes during hatching show this well. First, the membrane must weaken, the embryo begins to move, and Hoyle's gland develops—all before hatching. For the transition from paralarva to subadult, chromatophores increase in number and the relative size of arms to body changes before the paralarvae settle. Hadfield's (2000) next transitional step (for larval fishes) is the differentiation into structures appropriate for the next stage. Only after this should we see loss of the structures appropriate for the earlier stage and habitat change. Such a sequence is generally known for our transitions 2 and 3, much less so for 4 and 1, where many of the changes are behavioural. Major morphological changes, such as growth of gonads, are well described from dead animals, but behavioural changes and learning by individuals during the transitions require observations of live animals, preferably in their natural habitats, and this poses us with substantial challenges in most marine habitats

although there is a lot of ongoing work in this area (Hoving and Vecchione, 2012; Hunt and Lindsay, 2012).

This chapter has identified some critical questions about the transition from one life stage to the next. Early stages of development should be evolutionarily conservative, which suggests that transitions 1 and 2 should be more stereotyped than 3 and 4. Departures from the set four stages and transitions might occur in cephalopods. In stable environments, direct development, larger and fewer eggs, more yolk and longer embryonic development should occur—a pattern typical of deep benthic octopods. Such direct development should lead to fewer chromosomes, smaller geographic ranges and greater taxonomic diversity, which is a testable hypothesis. Another possible departure is neoteny, the adult retention of juvenile characteristics, which has been identified in some physiological characteristics of cephalopods (Rodhouse, 1998). Another departure from standard developmental patterns is found when larvae have accumulated enough stored energy that adults need neither feed nor grow, as is seen in many insects. Is this true for the adult cephalopod after transition 4 to the reproductive adult? Such a trend has been documented but not fully explored. Under what circumstances do cephalopods abandon semelparity?

Behind these descriptions is a deeper question, around the programming and control of saltatory development. The transitional stages are morphological, physiological and behavioural, a product of genes and environment. Development can be modelled as a sequential flow between stabilised states (stages) and relatively fast changes (transitions) (Balon, 2001); however, the induction of change must be the result of the activation of an array of genes at a particular time in the life cycle (Jackson et al., 2003). Many of the transitions may be brought on by specific environmental cues, such as temperature and light, and activated by external chemicals such as pheromones and internal ones such as hormones. Understanding the control of the transitions will take a mechanistic approach involving physiologists, behavioural ecologists, evolutionary biologists and molecular biologists with particular focus on developmental biology.

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## REFERENCES

- Agin, V., Poirier, R., Chichery, R., Dickel, L., Chichery, M.P., 2006. Developmental study of multiple memory stages in the cuttlefish, *Sepia officinalis*. *Neurobiol. Learn. Mem.* 86, 264–269.
- Aitken, J.P., O'Dor, R.K., 2004. Respirometry and swimming dynamics of the giant Australian cuttlefish, *Sepia apama* (Mollusca, Cephalopoda). *Mar. Freshw. Behav. Physiol.* 4, 217–234.
- Aitken, J.P., O'Dor, R.K., Jackson, G.D., 2005. The secret life of the giant Australian cuttlefish *Sepia apama* (Cephalopoda): behavior and energetics in nature revealed through radio acoustic positioning and telemetry (RAPT). *J. Exp. Mar. Biol. Ecol.* 320, 77–91.
- Anderson, T., 1997. Habitat selection and shelter use by *Octopus tetricus*. *Mar. Ecol. Prog. Ser.* 150, 137–148.
- Arkhipkin, A.I., 1992. Reproductive system structure, development and function in cephalopods with a new general scale for maturity stages. *J. Northw. Atl. Fish. Sci.* 12, 63–74.
- Arkhipkin, A.I., Bjorke, H., 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. *Polar Biol.* 22, 357–365.
- Arkhipkin, A., Laptikhovskiy, V., 1994. Seasonal and interannual variability in growth and maturation of winter-spawning *Illex argentinus* (Cephalopoda, Ommastrephidae) in the Southwest Atlantic. *Aquat. Living Resour.* 7, 221–232.
- Arkhipkin, A.I., Laptikhovskiy, V.V., Middleton, D.A.J., 2000. Adaptations for the cold water spawning in squid of the family Loliginidae: *Loligo gahi* around the Falkland Islands. *J. Molluscan Stud.* 66, 551–564.
- Arkhipkin, A.I., Grzebielec, R., Sirota, A.M., Remeslo, A.V., Polishchuk, I.A., Middleton, D.A.J., 2004. The influence of seasonal environmental changes on ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf. *Fish. Oceanogr.* 13, 1–9.
- Arnold, J.M., 1987. Reproduction and embryology of *Nautilus*. In: Saunders, W., Landman, N. (Eds.), *Nautilus: The Biology and Paleobiology of a Living Fossil*. Plenum Press, New York, pp. 353–372.
- Arrieche, D., 1999. Ultrastructure of the optic gland of the squid *Sepiotheutis sepioidea* (Cephalopoda: Loliginidae). *Rev. Biol. Trop.* 47, 831–842.
- Balon, E.K., 2001. Saltatory ontogeny and the life-history model: neglected processes and patterns of evolution. *J. Bioecon.* 3, 1–26.
- Barón, P.J., 2001. First description and survey of the egg masses of *Loligo gahi* (D'Orbigny, 1835) and *Loligo sanpaulensis* (Brakoniecki, 1984) from coastal waters of Patagonia. *J. Shellfish Res.* 20, 289–295.
- Bartol, I.K., Krueger, P.S., Thompson, J.T., Stewart, W.J., 2008. Swimming dynamics and propulsive efficiency of squids throughout ontogeny. *Integr. Comp. Biol.* 48, 720–733.
- Bartol, I.K., Krueger, P.S., Thompson, J.T., Stewart, W.J., 2009. Pulsed jet dynamics of squid hatchlings at intermediate Reynolds numbers. *J. Exp. Biol.* 212, 1506–1518.
- Bateman, A.J., 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2, 349.
- Bernay, B., Gagnon, J., Henry, J., 2004. Egg capsule secretion in invertebrates: a new ovarian regulatory peptide identified by mass spectrometry comparative screening in *Sepia officinalis*. *Biochem. Biophys. Res. Commun.* 314, 215–222.
- Bernay, B., Baudy-Floc'h, M., Zanuttini, B., Gagnon, J., Henry, J., 2005. Identification of SepCRP analogues in the cuttlefish *Sepia officinalis*: a novel family of ovarian regulatory peptides. *Biochem. Biophys. Res. Commun.* 338, 1037–1047.
- Bernay, B., Baudy-Floc'h, M., Gagnon, J., Henry, J., 2006. Ovarian jelly-peptides (OJPs), a new family of regulatory peptides identified in the cephalopod *Sepia officinalis*. *Peptides* 27, 1259–1268.

- Bettencourt, V., Guerra, A., 1999. Carbon- and oxygen-isotope composition of the cuttlebone of *Sepia officinalis*: a tool for predicting ecological information? *Mar. Biol.* 133, 651–657.
- Bigelow, K., 1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. *Mar. Ecol. Prog. Ser.* 82, 31–40.
- Biggs, J., Epel, D., 1991. Egg capsule sheath of *Loligo opalescens* Berry: structure and association with bacteria. *J. Exp. Zool.* 259, 263–267.
- Birkhead, T.R., Parker, G.A., 1997. Sperm competition and mating systems. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*. Blackwell, Oxford.
- Bishop, C.D., Erezylmaz, D.F., Flatt, T., Georgiou, C.D., Hadfield, M.G., Heyland, A., Hodin, J., Jacobs, M.W., Maslakova, S.A., Pires, A., Reitzel, A.M., Santagata, S., Tanaka, K., Youson, J.H., 2006. What is metamorphosis? *Integr. Comp. Biol.* 46, 655–661.
- Blanc, A., 1998. Recherches Bio-Écologique Et Ecophysiologique De La Phase Juvenile De La Seiche *Sepia officinalis* Linne (Mollusque, Cephalopod, Sepiidae) Dans Le Golfe Du Morbihan (Sud Bretagne). PhD Thesis, University of Rennes, France.
- Bloor, I.S.M., 2012. The Ecology, Distribution and Spawning Behaviour of the Commercially Important Common Cuttlefish (*Sepia officinalis*) in the Inshore Waters of the English Channel. Marine Institute and Marine Biological Association of the United Kingdom; Plymouth University, Plymouth.
- Bloor, I.S.M., Attrill, M.J., Jackson, E.L. (Eds.), 2013a. A Review of the Factors Influencing Spawning, Early Life Stage Survival and Recruitment Variability in the Common Cuttlefish (*Sepia officinalis*). Academic Press, Burlington.
- Bloor, I.S.M., Wearmouth, V.J., Cotterell, S.P., Mchugh, M.J., Humphries, N.E., Jackson, E.L., Attrill, M.J., Sims, D.W., 2013b. Movements and behaviour of European common cuttlefish *Sepia officinalis* in English Channel inshore waters: first results from acoustic telemetry. *J. Exp. Mar. Biol. Ecol.* 448, 19–27.
- Boal, J.G., 1996. Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda). *Anim. Behav.* 52, 529–537.
- Boal, J.G., 1997. Female choice of males in cuttlefish (Mollusca: Cephalopoda). *Behaviour* 134, 975–988.
- Boal, J.G., Prosser, K.N., Holm, J.B., Simmons, T.L., Haas, R.E., Nagle, G.T., 2010. Sexually mature cuttlefish are attracted to the eggs of conspecifics. *J. Chem. Ecol.* 36, 834–836.
- Boavida-Portugal, J., Moreno, A., Gordo, L., Pereira, J., 2010. Environmentally adjusted reproductive strategies in females of the commercially exploited common squid *Loligo vulgaris*. *Fish. Res.* 106, 193–198.
- Boletzky, S.V., 1971. Mandibules denticulées chez les larves des Teuthoïdés et des Octopodes (Mollusca: Cephalopoda). *C. R. Acad. Sci. Paris* 23, 2904–2906.
- Boletzky, S.V., 1974. The “larvae” of Cephalopoda: a review. *Thalass. Jugosl.* 10, 45–76.
- Boletzky, S.V., 1975. The reproductive cycle of Sepiolidae (Mollusca, Cephalopoda). *Pubbl. Staz. Zool. Napoli* 39, 84–95.
- Boletzky, S.V., 1977. Post-hatching behaviour and mode of life in cephalopods. *Symp. Zool. Soc. Lond.* 38, 557–567.
- Boletzky, S.V., 1982. Structure of the embryonic integument and its relation to the mode of hatching in cephalopods. *Bull. Soc. Zool. France* 107, 475–482.
- Boletzky, S.V., 1983. *Sepia officinalis*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles*. Academic Press, London.
- Boletzky, S.V., 1986. Reproductive strategies in cephalopods: variation and flexibility of life-history patterns. *Adv. Invertebr. Reprod.* 4, 379–389.
- Boletzky, S.V., 1987a. Fecundity variation in relation to intermittent or chronic spawning in the cuttlefish, *Sepia officinalis* L. (Mollusca, Cephalopoda). *Bull. Mar. Sci.* 40, 382–387.

- Boletzky, S.V., 1987b. Embryonic phase. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles. Volume II. Comparative Reviews*. Academic Press, London, pp. 5–31.
- Boletzky, S.V., 1989. Recent studies on spawning, embryonic development, and hatching in the Cephalopoda. *Adv. Mar. Biol.* 25, 85–115.
- Boletzky, S.V., 1998. Cephalopod eggs and egg masses. *Oceanogr. Mar. Biol. Annu. Rev.*, 36, 341–371.
- Boletzky, S.V., 2002. Yolk sac morphology in cephalopod embryos. In: Summesberger, H., Histon, K., Daurer, A. (Eds.), *Cephalopods—Present and Past*, vol. 57. *Abhandlungen der Geologischen Bundesanstalt*, Wien, pp. 57–68.
- Boletzky, S.V., 2003. Biology of early life stages in cephalopods molluscs. *Adv. Mar. Biol.* 44, 144–203.
- Boletzky, S.V., Boletzky, M.V.v., 1969. First results in rearing *Octopus joubini* Robson, 1929. *Verh. Naturforsch. Ges. Basel* 80, 56–61.
- Boletzky, S.V., Boletzky, M.V.v., 1973. Observations on the embryonic and early post-embryonic development of *Rossia macrosoma* (Mollusca, Cephalopoda). *Helgoländer Meeresun.* 25, 135–161.
- Boletzky, S.V., Hanlon, R.T., 1983. A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *Mem. Natl. Mus. Victoria* 44, 147–187.
- Bonnet, X., Bradshaw, D., Shine, R., 1998. Capital versus income breeding: an ectothermic perspective. *Oikos* 83, 333–342.
- Boucaud-Camou, E., Boismery, J., 1991. The migrations of the cuttlefish (*Sepia officinalis* L) in the English Channel. In: Boucaud-Camou, E. (Ed.), *The Cuttlefish, First International Symposium on the Cuttlefish Sepia*. Centre de Publications de l'Université de Caen, Caen.
- Boucaud-Camou, E., Roper, C.F.E., 1995. Digestive enzymes in paralarval cephalopods. *Bull. Mar. Sci.* 57, 313–327.
- Boucher-Rodoni, R., Mangold, K., 1995. Ammonia production in cephalopods, physiological and evolutionary aspects. *Mar. Freshw. Behav. Physiol.* 25, 53–60.
- Boyle, P.R., 1983a. *Eledone cirrhosa*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles. Volume I: Species Accounts*. Academic Press, London, pp. 365–386.
- Boyle, P.R. (Ed.), 1983b. *Cephalopod Life Cycles*. In: *Species Accounts*, vol. 1. Academic Press, London, p. 475.
- Boyle, P.R. (Ed.), 1987. *Cephalopod Life Cycles*. In: *Species Accounts*, vol. 2. Academic Press, London, p. 441.
- Boyle, P.R., Boletzky, S.V., 1996. Cephalopod populations: definitions and dynamics. *Philos. Trans. R. Soc. B* 351, 985–1002.
- Boyle, P.R., Rodhouse, P., 2005. *Cephalopods Ecology and Fisheries*. Wiley-Blackwell, Oxford, p. 472.
- Boyle, P.R., Thorpe, R., 1984. Optic gland enlargement and female gonad maturation in a population of the octopus *Eledone cirrhosa*: a multivariate analysis. *Mar. Biol.* 79, 127–132.
- Branch, T.A., DeJoseph, B.M., Ray, L.J., Wagner, C.A., 2013. Impacts of ocean acidification on marine seafood. *Trends Ecol. Evol.* 28, 178–186.
- Briceño, F., Mascaró, M., Rosas, C., 2010. GLMM-based modelling of growth in juvenile *Octopus maya* siblings: does growth depend on initial size? *ICES J. Mar. Sci.* 67, 1509–1516.
- Bryne, M., 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanogr. Mar. Biol. Annu. Rev.* 49, 1–42.
- Buresch, K.M., Hanlon, R.T., Maxwell, M.R., Ring, S., 2001. Microsatellite DNA markers indicate a high frequency of multiple paternity within individual field-collected egg capsules of the squid *Loligo pealeii*. *Mar. Ecol. Prog. Ser.* 210, 161–165.

- Bustamante, P., Teyssié, J., Danis, B., Fowler, S.W., Miramand, P., Cotret, O., 2004. Uptake, transfer and distribution of silver and cobalt in tissues of the common cuttlefish *Sepia officinalis* at different stages of its life cycle. *Mar. Ecol. Prog. Ser.* 269, 185–195.
- Bykov, A.N., Dubinina, T.S., 1984. Some peculiarities of larval development of squids of the family Enoploteuthidae from de Central-East Atlantic. *Malacol. Rev.* 17, 118.
- Castro, J., Hernández-García, V., 1995. Ontogenetic changes in mouth structures, foraging behaviour and habitat use of *Scomber japonicus* and *Illex coindetii*. *Sci. Mar.* 59, 347–355.
- Chen, D.S., Dykhuizen, G.V., Hodge, J., Gilly, W.F., 1996. Ontogeny of copepod predation in juvenile squid (*Loligo opalescens*). *Biol. Bull.* 190, 69–81.
- Chung, W.S., 2003. Effects of temperature, salinity and photoperiod on the deposition of growth increments in statoliths of the oval squid *Sepioteuthis lessoniana* Lesson, 1830 (Cephalopoda: Loliginidae) during early stages. MSc thesis, National Sun Yat-sen University, 65 pp.
- Cigliano, J.A., 1995. Assessment of the mating history of female pygmy octopuses and a possible sperm competition mechanism. *Anim. Behav.* 49, 849–851.
- Collins, L.A., Pierce, G.J., 1996. Size selectivity in the diet of *Loligo forbesi* (Cephalopoda: Loliginidae). *J. Mar. Biol. Assoc. U.K.* 76, 1081–1091.
- Collins, M., Yau, C., Allcock, L., Thurston, M., 2001. Distribution of deep-water benthic and benthopelagic cephalopods from the north-east Atlantic. *J. Mar. Biol. Assoc. U.K.* 81, 105–117.
- Corner, B.D., Moore, H.T., 1980. Field observations on the reproductive behavior of *Sepia latimanus*. *Micronesica* 16, 235–260.
- Cronin, E.R., Seymour, R.S., 2000. Respiration of the eggs of the giant cuttlefish *Sepia apama*. *Mar. Biol.* 136, 863–870.
- Cummins, S.F., Boal, J.G., Buresch, K.C., Kuanpradit, C., Sobhan, P., Holm, J.B., Degnan, B.M., Nagle, G.T., Hanlon, R.T., 2011. Extreme aggression in male squid induced by a  $\beta$ -MSP-like pheromone. *Curr. Biol.* 21, 322–327.
- Cuomo, A., Di Cristo, C., Paolucci, M., Di Cosmo, A., Tosti, E., 2005. Calcium currents correlate with oocyte maturation during the reproductive cycle in *Octopus vulgaris*. *J. Exp. Zool. A Comp. Exp. Biol.* 303, 193–202.
- Darmaillacq, A.S., Chichery, R., Dickel, L., 2006. Food imprinting, new evidence from the cuttlefish *Sepia officinalis*. *Biol. Lett.* 2, 345–347.
- Darmaillacq, A.S., Chichery, R., Dickel, L., 2008. Embryonic visual learning in cuttlefish, *Sepia officinalis*. *Anim. Behav.* 76, 131–134.
- Dawe, E.G., Colbourne, E.B., Drinkwater, K.F., 2000. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). *ICES J. Mar. Sci.* 57, 1002–1013.
- Denton, E.J., Gilpin-Brown, J.B., 1961. The buoyancy of the cuttlefish, *Sepia officinalis*. *J. Mar. Biol. Assoc.* 41, 319–342.
- Derby, C.D., Kicklighter, C.E., Johnson, P.E., Zhang, X., 2007. Chemical composition of inks of diverse marine molluscs suggests convergent chemical defences. *J. Chem. Ecol.* 33, 1105–1113.
- Dickel, L., Boal, J.G., Budelmann, B.U., 2000. The effect of early experience on learning and memory in cuttlefish. *Dev. Psychobiol.* 36 (2), 101–110.
- Dickel, L., Chichery, M.P., Chichery, R., 2001. Increase of learning abilities and maturation of the vertical lobe complex during postembryonic development in the cuttlefish, *Sepia*. *Dev. Psychobiol.* 39 (2), 92–98.
- Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., 2009. Ocean acidification: the other CO<sub>2</sub> problem. *Annu. Rev. Mar. Sci.* 1, 169–192.
- Dorey, N., Melzner, F., Martin, S., Oberhänsli, F., Teyssie, J.-L., Bustamante, P., Gattuso, J.-P., Lacoue-Labarthe, T., 2012. Ocean acidification and temperature rise: effects on calcification during early development of the cuttlefish *Sepia officinalis*. *Mar. Biol.* 160, 2007–2022.

- Drazen, J.C., Goffredi, S.K., Schlining, B., Stakes, D.S., 2003. Aggregations of egg-brooding deep-sea fish and cephalopods on the Gorda Escarpment: a reproductive hot spot. *Biol. Bull.* 205, 1–7.
- Ebenman, B., Persson, L. (Eds.), 1988. *Size-Structured Populations: Ecology and Evolution*. Springer-Verlag, Berlin, Germany.
- Eberhard, W.G., 1985. *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge, MA.
- Eberhard, W.G., 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton, NJ.
- Ellis, R.P., Bersey, J., Rundle, S.D., Hall-Spencer, J.M., Spicer, J.I., 2009. Subtle but significant effects of CO<sub>2</sub> acidified seawater on embryos of the intertidal snail, *Littorina obtusata*. *Aquat. Biol.* 5, 41–48.
- Enault, J., Zatylny-Gaudin, C., Bernay, B., Lefranc, B., Leprince, J., Baudy-Floc'h, M., Henry, J., 2012. A complex set of sex pheromones identified in the cuttlefish *Sepia officinalis*. *PLoS One* 7 (10), e46531. <http://dx.doi.org/10.1371/journal.pone.0046531>.
- Engeser, T.S., Clarke, M.R., 1988. Cephalopod hooks, both recent and fossil. In: Clarke, M.R., Trueman, E.R. (Eds.), *The Mollusca*, Vol. 12: Paleontology and neontology of Cephalopods. Academic Press, London, pp. 133–151.
- Estefanell, J., Socorro, J., Roo, F.J., Guirao, R., Fernández-Palacios, H., Izquierdo, M., 2010. Gonad maturation in *Octopus vulgaris* during ongrowth, under different conditions of sex ratio. *ICES J. Mar. Sci.* 67, 1487–1493.
- Falcon, L.I., Vecchione, M., Roper, C.F.E., 2000. Paralarval gonatid squids (Cephalopoda: Oegopsida) from the Mid-North Atlantic. *Proc. Biol. Soc. Wash.* 113, 532–541.
- Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero, F.J., 2004. Impact of anthropogenic CO<sub>2</sub> on CaCO<sub>3</sub> system in the oceans. *Science* 305, 362–366.
- Fields, W.G., 1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. *Fish. Bull.* 131, 1–108.
- Forsythe, J.W., 1993. A working hypothesis on how seasonal temperature change may impact the field growth of young cephalopods. In: Okutani, T., O'Dor, R.K., Kubodera, T. (Eds.), *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo, Japan.
- Forsythe, J.W., 2004. Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. *Mar. Freshw. Res.* 55, 331–339.
- Forsythe, J.W., Hanlon, R.T., 1988a. Behaviour, body patterning and reproductive biology of *Octopus bimaculoides* from California. *Malacologia* 29, 40–56.
- Forsythe, J.W., Hanlon, R.T., 1988b. Effect of temperature on laboratory growth, reproduction and life span of *Octopus bimaculoides*. *Mar. Biol.* 98, 369–379.
- Forsythe, J.W., Van Heukelem, W.F., 1987. Cephalopod growth. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles, Volume II, Comparative Reviews*. Academic Press, London.
- Franco-Santos, R.M., Vidal, E.A.G., 2014. Beak development of early squid paralarvae (Cephalopoda: Teuthoidea) may reflect an adaptation to a specialized feeding mode. *Hydrobiologia* 725, 85–103.
- Froerman, Y.M., Dubinina, T.S., 1984. Distribution and peculiarities of allometric growth of larval *Illex* in the Northwest Atlantic. *NAFO Scr. Doc.* 84/IX/115, 25 pp.
- Froesch, D., Marthy, H.J., 1975. The structure and function of the oviducal gland in octopods (Cephalopoda). *Proc. R. Soc. Lond. B Biol. Sci.* 188, 95–101.
- Gabe, S.H., 1975. Reproduction in the giant octopus of the North Pacific, *Octopus dofleini martini*. *Veliger* 18, 146–150.
- Gabr, H.R., Hanlon, R.T., Hanafy, M.H., El-Etreby, S.G., 1998. Maturation, fecundity and seasonality of reproduction of two commercially valuable cuttlefish, *Sepia pharaonis* and *S. dollfusi*, in the Suez Canal. *Fish. Res.* 36, 99–115.

- Gabr, H., Hanlon, R.T., El-Etreby, S., Hanafy, M., 1999a. Reproductive versus somatic tissue growth during the life cycle of the cuttlefish *Sepia pharaonis* Ehrenberg, 1831. *Fish. Bull.* 97, 802–811.
- Gabr, H., Hanlon, R.T., Hanafy, M., El-Etreby, S., 1999b. Reproductive versus somatic tissue allocation in the cuttlefish *Sepia dollfusii* Adam (1941). *Bull. Mar. Sci.* 65, 159–173.
- Garofalo, G., Ceriola, L., Gristina, M., Fiorentino, F., Pace, R., 2010. Nurseries, spawning grounds and recruitment of *Octopus vulgaris* in the Strait of Sicily, central Mediterranean Sea. *ICES J. Mar. Sci.* 67, 1363–1371.
- Gilly, W.F., Beman, J.M., Litvin, S.Y., Robison, B.H., 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* 5, 393–420.
- Gomi, F., Masamich, Y., Nakazawa, T., 1986. Swelling of egg during development of the cuttlefish, *Sepiella japonica*. *Zool. Sci.* 3 (4), 641–645.
- González, A.F., Otero, J., Guerra, Á., Prego, R., Rocha, F., Dale, A.W., 2005. Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain). *J. Plankton Res.* 27, 271–277.
- González, A.F., Otero, J., Pierce, G., Guerra, A., 2010. Age, growth, and mortality of *Loligo vulgaris* wild paralarvae: implications for understanding of the life cycle and longevity. *ICES J. Mar. Sci.* 67, 1119–1127.
- Green, C.P., 2011. Influence of environmental factors on population structure of arrow squid *Nototodarus gouldi*: implications for stock assessment. PhD Thesis, University of Tasmania, Hobart, Australia.
- Guerra, A., 2006. Ecology of *Sepia officinalis*. *Vie Milieu* 56, 97–107.
- Guerra, A., Gonzalez, J.L., 2011. First record of predation by a toplot blenny on the common cuttlefish *Sepia officinalis* eggs. *Vie Milieu* 61, 45–48.
- Guerra, A., Pérez-Gándaras, G., 1984. Larvas de cefalópodos. *Investig. Ciencia* 89, 6–15.
- Gutowaska, M.A., Melzner, F., 2009. Abiotic condition in cephalopod (*Sepia officinalis*) eggs: embryonic development at low pH and high pCO<sub>2</sub>. *Mar. Biol.* 156, 515–519.
- Gutowaska, M.A., Pörtner, H.O., Melzner, F., 2008. Growth and calcification in the cephalopod *Sepia officinalis* under elevated seawater pCO<sub>2</sub>. *Mar. Ecol. Prog. Ser.* 373, 303–309.
- Gutowaska, M.A., Melzner, F., Langenguch, M., Bock, C., Claireaux, G., Pörtner, H.O., 2010a. Acid-base regulatory ability of the cephalopod (*Sepia officinalis*) in response to environmental hypercapnia. *J. Comp. Physiol. B.* 180, 323–335.
- Gutowaska, M.A., Melzner, F., Pörtner, H.O., Meier, S., 2010b. Cuttlebone calcification increases during exposure to elevated seawater pCO<sub>2</sub> in the cephalopod *Sepia officinalis*. *Mar. Biol.* 157, 1653–1663.
- Hadfield, M.G., 2000. Why and how marine invertebrate larvae metamorphose so fast. *Semin. Cell Dev. Biol.* 11, 437–443.
- Hall, K.C., 2002. The Life History and Fishery of a Spawning Aggregation of the Giant Australian Cuttlefish *Sepia apama*. Department of Environmental Biology, University of Adelaide.
- Hall, K.C., Fowler, A.J., 2003. The fisheries biology of the cuttlefish *Sepia apama* Gray, in South Australian waters: Final Report to FRDC (Project No. 98/151). Adelaide.
- Hall, K.C., Hanlon, R.T., 2002. Principle features of the mating system of a large spawning aggregation of the giant Australian cuttlefish. *Mar. Biol.* 140, 533–545.
- Hanlon, R.T., 1998. Mating systems and sexual selection in the squid *Loligo*: how might commercial fishing on spawning squids affect them? *Calcofi Rep.* 39, 92–100.
- Hanlon, R.T., Messenger, J.B., 1998. *Cephalopod Behaviour*. Cambridge University Press, Cambridge, UK.
- Hanlon, R.T., Wolterding, M.R., 1989. Behavior, body patterning, growth and life history of *Octopus briareus* cultured in the laboratory. *Am. Malacol. Bull.* 7, 21–45.

- Hanlon, R.T., Turk, P.E., Yang, W.T., 1987. Laboratory rearing of the squid *Loligo pealei* to the juvenile stage: growth comparisons with fishery data. *Fish. Bull.* 85, 163–167.
- Hanlon, R.T., Bidwell, J.P., Tait, R., 1989a. Strontium is required for statolith development and thus normal swimming behaviour of hatchling cephalopods. *J. Exp. Biol.* 141, 187–195.
- Hanlon, R.T., Yang, W.T., Turk, P.E., Lee, P.G., Hixon, R.F., 1989b. Laboratory culture and estimated life span of the Eastern Atlantic squid, *Loligo forbesi* (Steenstrup, 1856) (Mollusca: Cephalopoda). *Aquac. Fish. Manag.* 20, 15–34.
- Hanlon, R.T., Smale, M.J., Sauer, W.H., 1994. An ethogram of body patterning behavior in the squid *Loligo vulgaris reynaudii* on spawning grounds in South Africa. *Biol. Bull.* 187, 363–372.
- Hanlon, R.T., Ament, S.A., Gabr, H., 1999. Behavioral aspects of sperm competition in cuttlefish, *Sepia officinalis* (Sepioidea: Cephalopoda). *Mar. Biol.* 134, 719–728.
- Hanlon, R.T., Smale, M.J., Sauer, W.H.H., 2002. The mating system of the squid *Loligo vulgaris reynaudii* (Cephalopoda, Mollusca) off South Africa: fighting, guarding, sneaking, mating and egg laying behavior. *Bull. Mar. Sci.* 71, 331–345.
- Hanlon, R.T., Kangas, N., Forsythe, J.W., 2004. Egg capsule deposition and how behavioral interactions influence spawning rate in the squid *Loligo opalescens* in Monterey Bay, California. *Mar. Biol.* 145, 923–930.
- Hanlon, R.T., Naud, M.J., Shaw, P.W., Havenhand, J.N., 2005. Transient sexual mimicry leads to fertilisation. *Nature* 433, 212.
- Harman, R.F., Young, R.E., 1985. The larvae of ommastrephid squids (Cephalopoda, Teuthoidea) from Hawaiian waters. *Vie Milieu* 35, 211–222.
- Hatfield, E., Cadrin, S., 2002. Geographical and temporal patterns in size and maturity of the longfin inshore squid (*Loligo pealeii*) off the northwestern United States. *Fish. Bull.* 100 (2), 200–213.
- Hatfield, E.M.C., Rodhouse, P.G., Porebski, J., 1990. Demography and distribution of the Patagonian squid (*Loligo gahi* d'Orbigny) during the austral winter. *ICES J. Mar. Sci.* 46, 306–312.
- Hatfield, E.M.C., Rodhouse, P.G., Barber, D.L., 1992. Production of soma and gonad in maturing female *Illex argentinus* (Mollusca: Cephalopoda). *J. Mar. Biol. Assoc. U.K.* 72, 281–291.
- Hendrix, J.P., McKinney, L.D., Salzer, R.R., Case, R.J., 1981. Salinity tolerance and the responses to hypo osmotic stress of the bay squid *Lolliguncula brevis*, a euryhaline cephalopod mollusk. *Comp. Biochem. Physiol.* 69A, 641–648.
- Henning, G.B., Bird, C.M., Wichmann, F.A., 2002. Contrast discrimination with pulse trains in pink noise. *J. Opt. Soc. Am. A* 19, 1259–1266.
- Henry, J., Favrel, P., Boucaud-Camou, E., 1997. Isolation and identification of a novel Ala-Pro-Gly-Trp-amide-related peptide inhibiting the motility of the mature oviduct in the cuttlefish, *Sepia officinalis*. *Peptides* 18, 1469–1474.
- Henry, J., Zatylny, C., Boucaud-Camou, E., 1999. Peptidergic control of egg-laying in the cephalopod *Sepia officinalis*: involvement of FMRamide and FMRamide-related peptides. *Peptides* 20, 1061–1071.
- Heyland, A.L., Moroz, L., 2006. Signaling mechanisms underlying metamorphic transitions in animals. *Integr. Comp. Biol.* 46 (6), 743–759.
- Ho, J.D., Moltschaniwskij, N.A., Carter, C.G., 2004. The effect of variability in growth on somatic condition and reproductive status in the southern calamary *Sepioteuthis australis*. *Mar. Freshw. Res.* 55, 423–428.
- Hoving, H.J.T., 2008. Reproductive biology of oceanic decapodiform cephalopods. PhD Thesis, University of Groningen, 184 pp.
- Hoving, H.J.T., Vecchione, M., 2012. Mating behavior of a deep-sea squid revealed by in situ videography and the study of archived specimens. *Biol. Bull.* 223, 263–267.

- Hoving, H.J.T., Gilly, W.F., Markaida, U., Benoit-Bird, K.J., Brown, Z.W., Daniel, P., 2013. Extreme plasticity in life-history strategy allows a migratory predator (jumbo squid) to cope with a changing climate. *Glob. Change Biol.* 19, 2089–2103.
- Hu, M.Y., Tseng, Y., Stumpp, M., Gutowska, M.A., Kiko, R., Lucassen, M., Melzner, F., 2011. Elevated seawater pCO<sub>2</sub> differentially affects branchial acid-base transporters over the course of development in cephalopod *Sepia officinalis*. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 300, R1100–R1114.
- Huffard, C.L., Hochberg, F.G., 2005. Description of a new species of the genus *Amphioctopus* (Mollusca: Octopodidae) from the Hawaiian Islands. *Molluscan Res.* 25, 113–128.
- Huffard, C.L., Cadwell, R.L., Boneka, F., 2008. Mating behavior of *Abdopus aculeatus* (d'Orbigny 1834) (Cephalopoda: Octopodidae) in the wild. *Mar. Biol.* 154, 353–362.
- Hunt, J.C., Lindsay, D.J., 2012. In situ behavioral observations of the mesopelagic squid *Stigmatoteuthis dofleini* (Cephalopoda: Histioteuthidae). *Am. Malacol. Bull.* 30, 335–338.
- Hunt, J.C., Seibel, B., 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): ontogenetic changes in habitat, behavior and physiology. *Mar. Biol.* 136, 543–552.
- Hurley, A.C., 1978. School structure of the squid *Loligo opalescens*. *Fish. Bull.* 76 (2), 433–442.
- Ibáñez, C.M., Cubillos, L.A., 2007. Seasonal variation in the length structure and reproductive condition of the jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) off central-south Chile. *Sci. Mar.* 71, 123–128.
- Ibáñez, C.M., Keyl, F., 2010. Cannibalism in cephalopods. *Rev. Fish Biol. Fish.* 20, 123–136.
- Iglesias, J., Otero, J.J., Moxica, C., Fuentes, L., Sánchez, F.J., 2004. The completed life cycle of the octopus (*Octopus vulgaris*, Cuvier) under culture conditions: paralarval rearing using Artemia and Zoeae, and first data on juvenile growth up to 8 months of age. *Aquac. Int.* 12, 481–487.
- Iglesias, J., Sánchez, F.J., Bersano, J.G.F., Carrasco, J.F., Dhont, J., Fuentes, L., Linares, F., Munoz, J.L., Okumura, S., Roo, J., van der Meeren, T., Vidal, E.A.G., Villanueva, R., 2007. Rearing of *Octopus vulgaris* paralarvae: present status, bottlenecks and trends. *Aquaculture* 266, 1–15.
- Ikeda, Y., Sakurai, Y., Shimazaki, K., 1993. Fertilizing capacity of squid (*Todarodes pacificus*) spermatozoa collected from various sperm storage sites, with special reference to the role of gelatinous substance from oviducal gland in fertilization and embryonic development. *Integr. Comp. Biol.* 23, 39–44.
- Ikeda, Y., Wada, Y., Arai, N., Sakamoto, W., 1999. Note on size variation of body and statoliths in the oval squid *Sepioteuthis lessoniana* hatchlings. *J. Mar. Biol. Assoc. U.K.* 79 (4), 757–759.
- Imamura, S., 1990. Larval rearing of Octopus (*Octopus vulgaris* Cuvier); the progress of technological development and some problems remained. *Collect. Breed.* 52, 339–343.
- Iwata, Y., Sakurai, Y., 2007. Threshold dimorphism in ejaculate characteristics in the squid *Loligo bleekeri*. *Mar. Ecol. Prog. Ser.* 345, 141–146.
- Iwata, Y., Munehara, H., Sakurai, Y., 2005. Dependence of paternity rates on alternative reproductive behaviors in the squid *Loligo bleekeri*. *Mar. Ecol. Prog. Ser.* 298, 219–228.
- Iwata, Y., Ito, K., Sakurai, Y., 2008. Effect of low temperature on mating behavior of squid *Loligo bleekeri*. *Fish. Sci.* 74, 1345–1347.
- Iwata, Y., Shaw, P., Fujiwara, E., Shiba, K., Kakiuchi, Y., Hirohashi, N., 2011. Why small males have big sperm: dimorphic squid sperm linked to alternative mating behaviours. *BMC Evol. Biol.* 11, 236.
- Jackson, G.D., Mladenov, P.V., 1994. Terminal spawning in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae). *J. Zool.* 234, 189–201.

- Jackson, G.D., Moltschanivskyj, N.A., 2002. Spatial and temporal variation in growth rates and maturity in the Indo-Pacific squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae). *Mar. Biol.* 140, 747–754.
- Jackson, G.D., McGrath Steer, B., Wotherspoon, S., Hobday, A.J., 2003. Variation in age, growth and maturity in the Australian arrow squid *Nototodarus gouldi* over time and space—what is the pattern? *Mar. Ecol. Prog. Ser.* 264, 57–71.
- Jackson, G.D., Semmens, J.M., Phillips, K.L., Jackson, C.H., 2004. Reproduction in the deepwater squid *Moroteuthis ingens*, what does it cost? *Mar. Biol.* 145, 905–916.
- Jantzen, T.M., Havenhand, J.N., 2003. Reproductive behavior in the squid *Sepioteuthis australis* from South Australia: interactions on the spawning grounds. *Biol. Bull.* 204, 305–317.
- Joll, L.M., 1976. Mating, egg-laying and hatching of *Octopus tetricus* (Mollusca: Cephalopoda) in the Laboratory. *Mar. Biol.* 36, 327–333.
- Jonsson, K.I., 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78, 57–66.
- Kaneko, N., Oshima, Y., Ikeda, Y., 2006. Egg brooding behavior and embryonic development of *Octopus laqueus* (Cephalopoda: Octopodidae). *Molluscan Res.* 26, 113–117.
- Kasugai, T., 2000. Reproductive behavior of the pygmy cuttlefish *Idiosepius paradoxus* in an aquarium. *Jpn. J. Malacol.* 59, 37–44.
- Katsanevakis, S., Verriopoulos, G., 2004a. Relative abundance of *Octopus vulgaris* on soft sediment. *Sci. Mar.* 68, 553–560.
- Katsanevakis, S., Verriopoulos, G., 2004b. Den ecology of *Octopus vulgaris* Cuvier, 1797, on soft sediment: availability and types of shelter. *Sci. Mar.* 68, 147–157.
- Kaufman, M.R., Ikeda, Y., Patton, C., Van Dijkhausen, G., Epel, D., 1998. Bacterial symbionts colonize the accessory nidamental gland of the squid *Loligo opalescens* via horizontal transmission. *Biol. Bull.* 194, 36–43.
- Keeling, R.F., Kortzinger, A., Gruber, N., 2010. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* 2, 199–229.
- Kier, W.M., 1996. Muscle development in squid: ultrastructural differentiation of a specialized muscle fiber type. *J. Morphol.* 229, 271–288.
- Kier, W.M., Smith, A.M., 1990. The morphology and mechanics of octopus suckers. *Biol. Bull.* 178, 126–136.
- Koronkiewicz, A., 1995. Size and maturity differences between trawl and jigger caught short-finned squid *Illex argentinus* (Cephalopoda: Ommastrephidae). *Acta Ichthyol. Piscat.* 25, 97–111.
- Koueta, N., Camou-Boucaud, E., Renou, A., 1995. Gonadotropic mitogenic activity of the optic gland of the cuttlefish, *Sepia officinalis*, during sexual maturation. *J. Mar. Biol. Assoc. U.K.* 75, 391–404.
- Kubodera, T., Okutani, T., 1977. Descriptions of a new species of gonatid squid, *Gonatus madokai*, n. sp., from the Northwest Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). *Jpn. J. Malacol.* 36, 123–151.
- Kubodera, T., Koyama, Y., Mori, K., 2007. Observations of wild hunting behaviour and bioluminescence of a large deep-sea, eight-armed squid, *Taningia danae*. *Proc. R. Soc. B* 274, 1029–1034.
- Lacoue-Labarthe, T., Martin, S., Oberhansli, F., Teyssie, J.L., Markich, S., Bustamante, P., 2009. Effects of increased pCO<sub>2</sub> and temperature on trace element (Ag, Cd and Zn) bioaccumulation in the eggs of the common cuttlefish, *Sepia officinalis*. *Biogeosciences* 6, 2561–2573.

- Lacoue-Labarthe, T., Le Bihan, E., Borg, D., Koueta, N., Bustamante, P., 2010. Acid phosphatase and cathepsin activity in cuttlefish (*Sepia officinalis*) eggs: the effects of Ag, Cd, and Cu exposure. *ICES J. Mar. Sci.* 67, 1517–1523.
- Lacoue-Labarthe, T., Reveillac, E., Oberhansli, F., Teysse, J.L., Jeffree, R., Gattuso, J.P., 2011. Effects of ocean acidification on trace element accumulation in the early-life stages of squid *Loligo vulgaris*. *Aquat. Toxicol.* 105, 166–176.
- Lacoue-Labarthe, T., Martin, S., Oberhansli, F., Teysse, J., Jeffree, R., Gattuso, J., Bustamante, P., 2012. Temperature and pCO<sub>2</sub> effect on the bioaccumulation of radionuclides and trace elements in the eggs of the common cuttlefish, *Sepia officinalis*. *J. Exp. Mar. Biol. Ecol.* 413, 45–49.
- Laptikhovskiy, V.V., Arkhipkin, A.I., Hoving, H.J.T., 2007. Reproductive biology in two species of deep-sea squids. *Mar. Biol.* 152, 981–990.
- Laptikhovskiy, V., Pereira, J., Salman, A., Arkhipov, A., Costa, A.M., 2009. A habitat-dependence in reproductive strategies of cephalopods and pelagophile fish in the Mediterranean Sea. *Boll. Malacol.* 45, 95–102.
- LaRoe, E.T., 1971. The culture and maintenance of the loliginid squids *Sepioteuthis sepioidea* and *Doryteuthis plei*. *Mar. Biol.* 9, 9–25.
- Laughlin, R.A., Livingston, R.J., 1982. Environmental and trophic determinants of the spatial/temporal distribution of the brief squid (*Lolliguncula brevis*) in the Apalachicola estuary (North Florida, USA). *Bull. Mar. Sci.* 32, 489–497.
- Le Goff, R., 1991. Biologie et Migration de la seiche *Sepia officinalis* L. (Mollusque, Cephalopode, Sepiidae) dans le secteur Morbraz-golfe du Morbihan (sud Bretagne). University of Rennes, Rennes, France.
- Lee, P.G., 1995. Nutrition of cephalopods: fuelling the system. *Mar. Freshw. Behav. Physiol.* 25, 35–51.
- Lee, C.E., Strathmann, R.R., 1998. Scaling of gelatinous clutches: effects of siblings' competition for oxygen on clutch size and parental investment per offspring. *Am. Nat.* 151, 293–310.
- Lee, P.N., Callaerts, P., de Couet, H.G., 2009. The embryonic development of the Hawaiian bobtail squid (*Euprymna scolopes*). *Cold Spring Harb. Protoc.* 4 (11), 1426–1435.
- Leporati, S.C., Pecl, G.T., Semmens, J.M., 2008. Reproductive status of *Octopus pallidus*, and its relationship to age and size. *Mar. Biol.* 155, 375–385.
- Liu, B., Chen, X., Chen, Y., Tian, S., Li, J., Fang, Z., Yang, M., 2013. Age, maturation, and population structure of the Humboldt squid *Dosidicus gigas* off the Peruvian Exclusive Economic Zones. *Chin. J. Oceanol. Limnol.* 31, 81–91.
- Lourenço, S., Moreno, A., Narciso, L., Gonzalez, A., Pereira, J., 2012. Seasonal trends of the reproductive cycle of *Octopus vulgaris* in two environmentally distinct coastal areas. *Fish. Res.* 127&128, 116–124.
- Lu, C.C., 1998. A synopsis of Sepiidae in Australian waters (Cephalopods: Sepioidea). In: Voss, N.A., Vecchione, M., Toll, R.B., Sweeney, M.J. (Eds.), *Systematics and Biogeography of Cephalopods*. Smithsonian Institution Press, Washington, pp. 159–190.
- Macewicz, B.J., Hunter, J.R., Lo, N.C.H., LaCasella, E.L., 2004. Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*). *Fish. Bull.* 102, 306–327.
- Macy, W.K., Brodziak, J.K.T., 2001. Seasonal maturity and size at age of *Loligo pealeii* in waters of southern New England. *ICES J. Mar. Sci.* 58, 852–864.
- Mangold, K., 1987. Reproduction. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles*, vol. 2. Academic Press, London, UK, pp. 157–200.
- Mangold, K.M., Young, R.E., 1998. The systematic value of the digestive organs. In: Voss, N.A., Vecchione, M., Toll, R.B., Sweeney, M.J. (Eds.), *Systematics and biogeography of cephalopods*. In: *Smithson. Contrib. Zool.*, 586, pp. 21–30.

- Markaida, U., Sosa-Nishizaki, O., 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *J. Mar. Biol. Assoc. U.K.* 83, 507–522.
- Marquez, L., Quintana, D., Lorenzo, A., Almanza, E., 2013. Biometrical relationship in developing eggs and neonates of *Octopus vulgaris* in relation to parental diet. *Helgol. Mar. Res.* 67, 461–470.
- Marthy, H.J., Hauser, R., School, A., 1976. Natural tranquilliser in cephalopod eggs. *Nature* 261, 496–497.
- Mather, J.A., 2006. Behaviour development: a cephalopod perspective. *Int. J. Comp. Psychol.* 19, 98–115.
- Maxwell, M.R., Hanlon, R.T., 2000. Female reproductive output in the squid *Loligo pealeii*: multiple egg clutches and implications for spawning strategy. *Mar. Ecol. Prog. Ser.* 199, 159–170.
- McGowan, J.A., 1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. *Calif. Fish. Game Bull.* 40, 47–54.
- Mejía-Rebollo, A., Salinas-Zavala, C.A., Quiñónez-Velázquez, C., Markaida, U., 2008. Age, growth and maturity of jumbo squid (*Dosidicus gigas* D'orbigny, 1835) off the western coast of the Baja California Peninsula. *Calif. Coop. Ocean. Fish. Invest. Rep.* 49, 256–262.
- Melo, Y.C., Sauer, W.H.H., 1998. Ovarian atresia in cephalopods. In: Payne, A.I.L., Lipinski, M.R., Clarke, M.R., Roeleveld, M.A.C. (Eds.), *Cephalopod Biodiversity, Ecology and Evolution*. In: *South African Journal of Marine Science*, vol. 20, pp. 143–151.
- Melo, Y.C., Sauer, W.H.H., 1999. Confirmation of serial spawning in the chokka squid *Loligo vulgaris reynaudii* off the coast of South Africa. *Mar. Biol.* 135, 307–313.
- Messenger, J.B., 1977. Prey capture and learning in the cuttlefish *Sepia*. *Symp. Zool. Soc. Lond.* 38, 347–376.
- Miske, V., Kirchhauser, J., 2006. First record of brooding and early life cycle stages in *Wunderpus photogenicus* Hochberg, Norman and Finn, 2006 (Cephalopoda: Octopodidae). *Molluscan Res.* 26, 169–171.
- Miyahara, K., Fukui, K., Nagahama, T., Ohatani, T., 2006a. First record of planktonic egg masses of the diamond squid, *Thysanoteuthis rhombus* Troschel, in the Sea of Japan. *Plank. Benth. Res.* 1, 59–63.
- Miyahara, K., Fukui, K., Ota, T., Minami, T., 2006b. Laboratory observations on the early life stages of the diamond squid *Thysanoteuthis rhombus*. *J. Molluscan Stud.* 72, 199–205.
- Moguel, C., Mascaró, M., Avila-Poveda, O.H., Caamal-Monsreal, C., Sanchez, A., Pascual, C., Rosas, C., 2010. Morphological, physiological, and behavioral changes during post-hatching development of *Octopus maya* (Mollusca: Cephalopoda) with special focus on the digestive system. *Aquat. Biol.* 9, 35–48.
- Moltschaniwskyj, N.A., 1995a. Changes in shape associated with growth in the loliginid squid *Photololigo* sp.: a morphometric approach. *Can. J. Zool.* 73, 1335–1343.
- Moltschaniwskyj, N.A., 1995b. Multiple spawning in the tropical squid *Photololigo* sp.: what is the cost in somatic growth? *Mar. Biol.* 124, 127–135.
- Moltschaniwskyj, N.A., Carter, C.G., 2013. The adaptive response of protein turnover to the energetic demands of reproduction in a cephalopod. *Physiol. Biochem. Zool.* 86, 119–126.
- Moltschaniwskyj, N.A., Pecl, G.T., 2003. Small-scale spatial and temporal patterns of egg production by the temperate loliginid squid *Sepioteuthis australis*. *Mar. Biol.* 142, 509–516.
- Moltschaniwskyj, N.A., Pecl, G., Lyle, J., 2002. An assessment of the use of short-term closures to protect spawning southern calamary aggregations from fishing pressure in Tasmania, Australia. *Bull. Mar. Sci.* 71, 501–514.
- Moran, N.A., 1994. Adaptation and constraint in the complex life cycles of animals. *Annu. Rev. Ecol. Syst.* 25, 573–600.

- Naef, A., 1928. Die Cephalopoden. Embryologie. Fauna Flora Golf Neapel 35, 1–357. English translation by Boletzky, S.V., 2001. The Cephalopoda—Embryology. Smithsonian Institution Press, Washington, District of Columbia, USA.
- Nair, K.P., Thomas, P.A., Gopakumar, G., Vincent, S.G., Omana, T.A., 1986. Some observations on the hatching and post-hatching behaviour of the cuttlefish *Sepia pharaonis* Ehrenberg. In: Silas, E.G. (Ed.), Cephalopod Bionomics. Fisheries and Resource of the Exclusive Economic Zone of India, vol. 37. Bulletin of the Central Marine and Freshwater Research Institute, pp. 157–159.
- Natsukari, Y., Tashiro, M., 1991. Neritic squid resources and cuttlefish resources in Japan. Mar. Behav. Physiol. 18, 149–226.
- Naud, M.J., Hanlon, R.T., Hall, K.C., Shaw, P.W., Havenhand, J.N., 2004. Behavioural and genetic assessment of reproductive success in a spawning aggregation of the Australian giant cuttlefish, *Sepia apama*. Anim. Behav. 67, 1043–1050.
- Naud, M.J., Shaw, P.W., Hanlon, R.T., Havenhand, J.N., 2005. Evidence for biased use of sperm sources in wild female giant cuttlefish (*Sepia apama*). Proc. R. Soc. Lond. B 272, 1047–1051.
- Navarro, J.C., Villanueva, R., 2000. Lipid and fatty acid composition of early stages of cephalopods: an approach to their lipid requirements. Aquaculture 183, 161–177.
- Navarro, J.C., Villanueva, R., 2003. The fatty acid composition of *Octopus vulgaris* paralarvae reared with live and inert food: deviation from their natural fatty acid profile. Aquaculture 219, 613–631.
- Nesis, K.N., 1973. Ecological classification (life forms) of cephalopods. Itogi Nauki Tekh. (Zool. Bespozv.) 2, 8–59, VINITI (in Russian).
- Nesis, K.N., 1979. Larvae of cephalopods. Biol. Morya 4, 26–37.
- Nigmatullin, C.M., Nesis, K.N., Arkhipkin, A.I., 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopods: Ommastrephidae). Fish. Res. 54, 9–19.
- Nixon, M., 1985. Capture of prey, diet and feeding of *Sepia officinalis* and *Octopus vulgaris* (Mollusca: Cephalopoda) from hatchling to adult. Vie Milieu 35, 255–261.
- Nixon, M., Young, J.Z., 2003. The Brain and Lives of Cephalopods. Oxford University Press, Oxford, 384 pp.
- Norman, M.D., Lu, C.C., 1997. Redescription of the southern dumpling squid *Euprymna tasmanica* and a revision of the genus *Euprymna* (Cephalopoda: Sepiolidae). J. Mar. Biol. Assoc. U.K. 77, 1109–1137.
- Norman, M., Reid, A., 2000. Guide to Squid, Cuttlefish and Octopuses of Australasia. CSIRO Publishing, Collingwood, Vic.
- Norman, M.D., Finn, J., Tregenza, T., 1999. Female impersonation as an alternative reproductive strategy in giant cuttlefish. Proc. R. Soc. B Biol. Sci. 266, 1347–1349.
- O'Dor, R.K., Balch, N., 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. NAFO Sci. Council Stud. 9, 69–76.
- O'Dor, R.K., 1983. *Illex illecebrosus*. In: Boyle, P.R. (Ed.), Cephalopod Life Cycles. Academic Press, London, pp. 175–200.
- O'Dor, R.K., 1998. Squid life history strategies. In: Rodhouse, P.G., Dawe, E.G., O'Dor, R.K. (Eds.), Squid Recruitment Dynamics. FAO Fisheries Technical Paper, 376, pp. 233–254.
- Okutani, T., 1987. Juvenile morphology. In: Boyle, P.R. (Ed.), Cephalopod Life Cycles. Volume II, Comparative Reviews. Academic Press, London, pp. 33–44.
- Okutani, T., Nakamura, I., Seki, K., 1995. An unusual egg-brooding behaviour of an oceanic squid in the Okhotsk Sea. Venus 54, 237–239.
- Oosthuizen, A., Roberts, M.J., Sauer, W.H., 2002a. Temperature effects on the embryonic development and hatching success of the squid *Loligo vulgaris reynaudii*. Bull. Mar. Sci. 71, 619–632.

- Oosthuizen, A., Smale, M.J., Sauer, W.H.H., 2002b. Aspects of biology, ecology and fishery potential of *Octopus* in the Eastern Cape, South Africa. *Bull. Mar. Sci.* 71, 1134–1135.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G., Rodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M., Yamanaka, Y., Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437, 681–686.
- Ortiz, N., Ré, M.E., Márquez, F., Glembocki, N.G., 2011. The reproductive cycle of the red octopus *Enteroctopus megalocyathus* in fishing areas of Northern Patagonian coast. *Fish. Res.* 110, 217–223.
- O'Shea, S., Bolstad, K.S., Ritchie, P.A., 2004. First records of egg masses of *Nototodarus gouldi* McCoy, 1888 (Cephalopoda: Ommastrephidae), with comments on egg-mass susceptibility to damage by fisheries trawl. *N. Z. J. Zool.* 31, 161–166.
- Otero, J., Gonzalez, A.F., Sieiro, M., Guerra, A., 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. *Fish. Res.* 85, 122–129.
- Otero, J., Álvarez-Salgado, X., González, Á.F., Miranda, A., Groom, S., Cabanas, J., Casas, G., Wheatley, B., Guerra, Á., 2008. Bottom-up control of common octopus *Octopus vulgaris* in the Galician upwelling system, northeast Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 362, 181–192.
- Otero, J., Álvarez-Salgado, X., González, Á.F., Gilcoto, M., Guerra, Á., 2009. High-frequency coastal upwelling events influence *Octopus vulgaris* larval dynamics on the NW Iberian shelf. *Mar. Ecol. Prog. Ser.* 386, 123–132.
- Packard, A., 1961. Sucker display of *Octopus*. *Nature* 190, 736–737.
- Palmer, M., Calve, M., Adamo, S.A., 2006. Response of female cuttlefish *Sepia officinalis* (Cephalopoda) to mirrors and conspecifics: evidence for signaling in female cuttlefish. *Anim. Cogn.* 9, 151–155.
- Parker, G.A., 1990. Sperm competition games: sneaks and extra-pair copulations. *Proc. R. Soc. Biol. Sci. B* 242, 127–133.
- Parker, L.M., Ross, P.M., O'Connor, W.A., Pörtner, H.O., Scanes, E., Wright, J.M., 2013. Predicting the response of molluscs to the impact of ocean acidification. *Biology* 2, 651–692.
- Parra, G., Villanueva, R., Yuféra, M., 2000. Respiration rates in late eggs and early hatchlings of the common octopus, *Octopus vulgaris*. *J. Mar. Biol. Assoc. U.K.* 80, 557–558.
- Paulij, W.P., Herman, P.M.J., Van Hannen, E.J., Denuce, J.M., 1990. The impact of photoperiodicity on hatching of *Loligo vulgaris* and *Loligo forbesi*. *J. Mar. Biol. Assoc. U.K.* 70, 597–610.
- Paulij, W.P., Herman, P.M.J., Roozen, M.E.F., Denuce, J.M., 1991. The influence of photoperiodicity on hatching of *Sepia officinalis*. *J. Mar. Biol. Assoc. U.K.* 71, 665–678.
- Pauly, D., 2010. Gaping fish and panting squids: oxygen, temperature and the growth of water-breathing animals. In: Kinne, O. (Ed.), *Excellence in ecology*, vol. 22. International Ecology Institute, Oldendorf/Luhe.
- Pecl, G., 2001. Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids. *Mar. Biol.* 138, 93–101.
- Pecl, G.T., Moltschanivskij, N.A., Tracey, S., Jordan, A., 2004. Inter-annual plasticity of squid life-history and population structure: ecological and management implications. *Oecologia* 139, 515–524.
- Pecl, G.T., Tracey, S.R., Semmens, J.M., Jackson, G.D., 2006. Use of acoustic telemetry for spatial management of southern calamary *Sepioteuthis australis*, a highly mobile inshore squid species. *Mar. Ecol. Prog. Ser.* 328, 1–15.

- Pecl, G.T., Tracey, S.R., Danyushevsky, L., Wotherspoon, S., Moltschanivskyj, N.A., 2011. Elemental fingerprints of southern calamary (*Sepioteuthis australis*) reveal local recruitment sources and allow assessment of the importance of closed areas. *Can. J. Fish. Aquat. Sci.* 68, 1351–1360.
- Pethybridge, H., Virtue, P., Casper, R., Yoshida, T., Green, C.P., Jackson, G., Nichols, P.D., 2012. Seasonal variations in diet of arrow squid (*Nototodarus gouldi*): stomach content and signature fatty acid analysis. *J. Mar. Biol. Assoc. U.K.* 92, 187–196.
- Pierce, G.J., Zuur, A.F., Smith, J.M., Santos, M.B., Bailey, N., Chen, C., Boyle, P.R., 2005. Interannual variation in life-cycle characteristics of the veined squid (*Loligo forbesi*) in Scottish (UK) waters. *Aquat. Living Resour.* 18, 327–340.
- Pierce, G.J., Valavanis, V.D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J.M., Katara, I., Piatkowski, U., Pereira, J., Balguerias, E., 2008. A review of cephalopod—environment interactions in European Seas. *Hydrobiologia* 612, 49–70.
- Pierce, G.J., Allcock, L., Bruno, I., Bustamante, P., Gonzalez, A., Guerra, A., Jereb, P., Lefkaditou, E., Malham, S., Moreno, A., Pereira, J. a, Piatkowski, U., Rasero, M., Sanchez, P., Santos, M.B., Santurtun, M., Seixas, S., Sobrino, I., Villanueva, R., 2010. Cephalopod Biology and Fisheries in Europe. Technical report, ICES Cooperative research report 303. Copenhagen, Denmark.
- Pimentel, M.S., Trubenbach, K., Faleiro, F., Boavida-Portugal, J., Repolho, T., Rosa, R., 2012. Impact of ocean warming on the early ontogeny of cephalopods: a metabolic approach. *Mar. Biol.* 159, 2051–2059.
- Pliego-Cárdenas, García-Domínguez, R.F.A., Ceballos-Vázquez, B.P., Villalejo-Fuerte, M., Arellano-Martínez, M., 2011. Reproductive aspects of *Octopus hubbsorum* (Cephalopoda: Octopodidae) from Espiritu Santo Island, southern Gulf of California, México. *Cien. Mar.* 37, 23–32.
- Pörtner, H.O., Langenbuch, M., Michaelidis, B., 2005. Synergistic effects of temperature extremes, hypoxia, and increases in CO<sub>2</sub> on marine animals: from Earth history to global change. *J. Geophys. Res.* 110, C09S10. doi:10.1029/2004JC002561.
- Quinteiro, J., Baibai, T., Oukhattar, L., Soukri, A., Seixas, P., Rey-Mendez, M., 2011. Multiple paternity in the common octopus *Octopus vulgaris* (Cuvier, 1797), as revealed by microsatellite DNA analysis. *Molluscan Res.* 31 (1), 15–20.
- Ramos-Castillejos J.E., 2007. Análisis morfológico y genético de las paralarvas Rhynchoteuthion del calamar gigante *Dosidicus gigas* (D'Orbigny, 1835) y del calamar púrpura *Sthenoteuthis oualaniensis* (Lesson, 1830). Master's thesis. Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S., Mexico, 135 pp.
- Rigby, R.P., Sakurai, Y., 2004. Temperature and feeding related to growth efficiency of immature octopuses *Enteroteuthis dofleini*. *Suisanzoshoku* 52, 29–36.
- Roberts, M.J., van den Berg, M., 2002. Recruitment variability of chokka squid (*Loligo vulgaris reynaudii*)—role of currents on the Agulhas Bank (South Africa) in paralarvae distribution and food abundance. *Bull. Mar. Sci.* 71, 691–710.
- Rocha, F., Guerra, A., Gonzalez, A.F., 2001. A review of reproductive strategies in cephalopods. *Biol. Rev.* 76, 291–304.
- Rodaniche, A.F., 1984. Iteroparity in the lesser Pacific striped octopus *Octopus chierchiai* (Jatta, 1889). *Bull. Mar. Sci.* 35, 99–104.
- Rodhouse, P.G., 1998. Physiological progenesis in cephalopod molluscs. *Biol. Bull.* 195, 17–20.
- Rodhouse, P.G., 2010. Effects of environmental variability and change on cephalopod populations: an introduction to the CIAC '09 Symposium special issue. *ICES J. Mar. Sci.* 67 (7), 1311–1313.
- Rodhouse, P.G., Hatfield, E.M.C., 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae). *Philos. Trans. R. Soc. Lond.* 329, 229–241.

- Rodhouse, P.G., Nigmatullin, C.M., 1996. Role as consumers. *Philos. Trans. R. Soc. B Biol. Sci.* 351, 1003–1022.
- Rodhouse, P.G., Dawe, E.G., O'Dor, R.K. (Eds.), 1998. Squid recruitment dynamics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability. FAO Fisheries Technical Paper, 376, p. 273.
- Rodrigues, M., Garci, M.E., Guerra, A., Troncoso, J.S., 2009. Mating behavior of the Atlantic bobtail squid *Sepioloideia atlantica* (Cephalopoda: Sepiolidae). *Vie Milieu* 59, 271–275.
- Rodrigues, M., Guerra, Á., Troncoso, J., 2011. The embryonic phase and its implication in the hatching size and condition of Atlantic bobtail squid *Sepioloideia atlantica*. *Helgol. Mar. Res.* 65, 211–216.
- Rodríguez-Rúa, A., Pozuelo, I., Prado, M.A., Gómez, M.J., Bruzón, M.A., 2005. The gametogenic cycle of *Octopus vulgaris* (Mollusca: Cephalopoda) as observed on the Atlantic coast of Andalusia (south of Spain). *Mar. Biol.* 147, 927–933.
- Romagny, S., Darmailacq, A.-S., Guibé, M., Bellanger, C., Dickel, L., 2012. Feel, smell and see in an egg: emergence of perception and learning in an immature invertebrate, the cuttlefish embryo. *J. Exp. Biol.* 215, 4125–4130.
- Roper, C.F., 1965. A note on egg deposition by *Doryteuthis plei* (Blainville, 1823) and its comparison with other North American loliginid squids. *Bull. Mar. Sci.* 15, 589–598.
- Roper, C.F.E., Sweeney, M.J., Nauen, C.E., 1984. Cephalopods of the World: an annotated and illustrated catalogue of species of interest to fisheries. FAO Fish. Synop., 125.
- Rosa, R., Costa, P.R., Nunes, M.L., 2004a. Effect of sexual maturation on the tissue biochemical composition of *Octopus vulgaris* and *O. defilippi* (Mollusca: Cephalopoda). *Mar. Biol.* 145, 563–574.
- Rosa, R., Costa, P.R., Pereira, J., Nunes, M.L., 2004b. Biochemical dynamics of spermatogenesis and oogenesis in *Eledone cirrhosa* and *Eledone moschata* (Cephalopoda: Octopoda). *Comp. Biochem. Physiol. B* 139, 299–310.
- Rosa, R., Pimentel, M.S., Boavida-Portugal, J., Teixeira, T., Tru'benbach, K., Diniz, M., 2012. Ocean warming enhances malformations, premature hatching, metabolic suppression and oxidative stress in the early life stages of a keystone squid. *PLoS One* 7(6). <http://dx.doi.org/10.1371/journal.pone.0038282>.
- Rosa, R., Pierce, G.J., O'Dor, R., 2013. *Advances in Squid Biology, Ecology and Fisheries*. Nova Science Publishers, Hauppauge, NY.
- Rosas, C., Valero, A., Caamal-Monsreal, C., Uriarte, I., Farias, A., Gallardo, P., Sanchez, A., Domingues, P., 2013. Effects of dietary protein sources on growth, survival and digestive capacity of *Octopus maya* juveniles (Mollusca: Cephalopoda). *Aquac. Res.* 44, 1029–1044.
- Sakurai, Y., Young, R.E., Hirota, J., Mangold, K., Vecchione, M., Clarke, M.R., Bower, J., 1995. Artificial fertilization and development through hatching in the oceanic squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* (Cephalopoda: Ommastrephidae). *Veliger* 38, 185–191.
- Sato, N., Kasugai, T., Munehara, H., 2013. Sperm transfer or spermatangia removal: post-copulatory behaviour of picking up spermatangium by female Japanese pygmy squid. *Mar. Biol.* 160, 553–561.
- Sauer, W.H.H., Smale, M.J., Lipinski, M.R., 1992. The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the eastern Cape coast, South Africa. *Mar. Biol.* 114, 97–107.
- Sauer, W.H.H., McCarthy, C., Smale, M.J., Koorts, A.S., 1993. An investigation of the egg distribution of the chokka squid, *Loligo vulgaris reynaudii*, in Krom bay, South Africa. *Bull. Mar. Sci.* 53, 1066–1077.
- Sauer, W.H.H., Koberts, M.J., Lipinski, M.R., Snide, M.J., Hanlon, R.T., Webber, D.M., O'Dor, R.K., 1997. Choreography of the squid's "nuptial dance". *Biol. Bull.* 192, 203–207.

- Sauer, W.H.H., Melo, Y., De Wet, W., 1999. Fecundity estimation in the chokka squid *Loligo vulgaris reynaudii*. Mar. Biol. 135, 315–319.
- Sauer, W.H.H., Lipinski, M.R., Augustyn, C.J., 2000. Tag recapture studies of the chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845 on inshore spawning grounds on the south-east coast of South Africa. Fish. Res. 45, 283–289.
- Saunders, W.B., Spinosa, C., 1978. Sexual dimorphism in *Nautilus* from Palau. Paleobiology 4, 349–358.
- Schoen, P.J., Sauer, W.H.H., Roberts, M.J., 2002. Environmental influences on spawning aggregations and jig catches of chokka squid *Loligo vulgaris reynaudii*: a 'black box' approach. Bull. Mar. Sci. 71, 783–800.
- Segawa, S., 1987. Life history of oval squid *Sepioteuthis lessoniana* in Kominato and adjacent waters central Honshu. Jpn. J. Tokyo Univ. Fish. 74, 67–105.
- Seibel, B.A., Thuesen, E.V., Childress, J.J., Gorodezky, L.A., 1997. Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. Biol. Bull. 192, 262–278.
- Seibel, B.A., Hochberg, F.G., Carlini, D.B., 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): deep-sea spawning and post-spawning egg care. Mar. Biol. 137, 519–526.
- Semmens, J.M., Pecl, G.T., Villanueva, R., Jouffre, D., Sobrino, I., Wood, J.B., Rigby, P.R., 2004. Understanding octopus growth: patterns, variability and physiology. Mar. Freshw. Res. 55, 367–377.
- Semmens, J.M., Pecl, G.T., Gillanders, B.M., Waluda, C.M., Shea, E.K., Jouffre, D., Ichii, T., Zumholz, K., Katugin, O.N., Leporati, S.C., Shaw, P.W., 2007. Approaches to resolving cephalopod movement and migration patterns. Rev. Fish Biol. Fish. 17, 401–423.
- Semmens, J., Doubleday, Z., Hoyle, K., Pecl, G., 2011. A multilevel approach to examining cephalopod growth using *Octopus pallidus* as a model. J. Exp. Biol. 214, 2799–2807.
- Şen, H., 2005. Incubation of European Squid (*Loligo vulgaris* Lamarck, 1798) eggs at different salinities. Aquac. Res. 36, 876–881.
- Shaw, P.W., Boyle, P.R., 1997. Multiple paternity within the brood of single females of *Loligo forbesi* (Cephalopoda: Loliginidae), demonstrated with microsatellite DNA markers. Mar. Ecol. Prog. Ser. 160, 279–282.
- Shaw, P.W., Sauer, W.H.H., 2004. Evidence for multiple paternity and complex fertilisation dynamics in the squid *Loligo vulgaris reynaudii*. Mar. Ecol. Prog. Ser. 270, 173–179.
- Shea, E.K., 2005. Ontogeny of the fused tentacles in three species of ommastrephid squids (Cephalopoda, Ommastrephidae). Invertebr. Biol. 124, 25–38.
- Shea, E.K., Vecchione, M., 2010. Ontogenetic changes in diel vertical migration patterns compared with known allometric changes in three mesopelagic squid species suggest an expanded definition of a paralarva. ICES J. Mar. Sci. 67, 1436–1443.
- Sinn, D.L., Moltshaniwskyj, N.A., 2005. Personality traits in dumpling squid (*Euprymna tasmanica*): context-specific traits and their correlation with biological characteristics. J. Comp. Psychol. 119 (1), 99.
- Smith, J.M., Pierce, G.J., Zuur, A.F., Boyle, P.R., 2005. Seasonal patterns of investment in reproductive and somatic tissues in the squid *Loligo forbesi*. Aquat. Living Resour. 18, 341–351.
- Snyder, S., 1986. Laboratory culture of *Octopus dofleini* from hatching to settlement. Am. Malacol. Bull. 4, 241.
- Sobrino, I., Silva, L., Bellido, J.M., Ramos, F., 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cádiz (SW Spain). Bull. Mar. Sci. 71, 851–865.
- Staaf, D., Camarillo-Coop, S., Haddock, S.H.D., Nyack, A.C., Payne, J., Salinas-Zavala, C.A., Seibel, B.A., Trueblood, L., Widmer, C., Gilly, W.F., 2008. Natural egg mass

- deposition by the Humboldt squid (*Dosidicus gigas*) in the Gulf of California and characteristics of hatchlings and paralarvae. *J. Mar. Biol. Assoc. U.K.* 88, 759–770.
- Staaf, D., Zeidberg, L.D., Gilly, W.F., 2011. Effects of temperature on embryonic development of the Humboldt squid *Dosidicus gigas*. *Mar. Ecol. Prog. Ser.* 441, 165–175.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford, p. 249.
- Steer, M.A., Moltschaniwskyj, N.A., Gowland, F.C., 2002. Temporal variability in embryonic development and mortality in the southern calamary, *Sepioteuthis australis*: a field assessment. *Mar. Ecol. Prog. Ser.* 243, 143–150.
- Steer, M.A., Moltschaniwskyj, N.A., Jordan, A.R., 2003. Embryonic development of southern calamary (*Sepioteuthis australis*) within the constraints of an aggregated egg mass. *Mar. Freshw. Res.* 54, 217–226.
- Steer, M.A., Fowler, A.J., Jackson, W.B., Jennings, P.R., 2005. *Southern Calamary (Sepioteuthis australis) Fishery*. SARDI Aquatic Sciences Publication, 135.
- Steer, M.A., Lloyd, M.T., Jackson, W.B., 2007. Assessing the feasibility of using 'by-product' data as a pre-recruit index in South Australia's southern calamary (*Sepioteuthis australis*) fishery. *Fish. Res.* 88, 42–50.
- Strathmann, R.R., Strathmann, M.F., 1995. Oxygen supply and limits on aggregation of embryos. *J. Mar. Biol. Assoc. U.K.* 75, 413–428.
- Strobel, A., Hu, M.Y.A., Gutowska, M.A., Lieb, B., Lucassen, M., Melzner, F., Pörtner, H.O., Mark, F.C., 2012. Influence of temperature, hypercapnia, and development on the relative expression of different hemocyanin isoforms in the common cuttlefish *Sepia officinalis*. *J. Exp. Zool.* 317A, 511–523.
- Sugimoto, T., Tameishi, H., 1992. Warm-core rings, streamers and their role on the fishing ground formation around Japan. *Deep Sea Research Part A. Oceanographic Research Papers*, 39, pp. S183–S201.
- Summers, W.C., 1983. *Loligo pealeii*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles*. Academic Press, New York, pp. 115–142.
- Summers, W.C., 1985. Ecological implications of life stage timing determined from the cultivation of *Rossia pacifica* (Mollusca: Cephalopoda). *Vie Milieu* 35, 249–254.
- Sweeney, M.J., Roper, C.F.E., Mangold, K.M., Clarke, M.R., Boletzky, S.V., 1992. "Larval" and juvenile cephalopods: a manual for their identification. *Smithson. Contrib. Zool.* 513, 282.
- Thompson, J.T., Kier, W.M., 2001. Ontogenetic changes in mantle kinematics during escape-jet locomotion in the oval squid, *Sepioteuthis lessoniana* Lesson, 1830. *Biol. Bull.* 201, 154–166.
- Tosti, E., Di Cosmo, A., Cumo, A., Di Cristo, C., Gragnaniello, G., 2001. Progesterone induces activation in *Octopus vulgaris* spermatozoa. *Mol. Reprod. Dev.* 59, 97–105.
- Tsuchiya, K., Takashi, U., 1997. Sneaker male in *Octopus*. *Jpn. J. Malacol.* 56, 177–181.
- Turk, P., Hanlon, R., Tanlon, R.T., Bradford, L.A., Yang, W.T., 1986. Aspects of feeding, growth and survival of the European squid *Loligo vulgaris* (Lamarck 1799), reared through the early growth stages. *Vie Milieu* 36, 9–13.
- Uozumi, Y., 1998. Fishery biology of arrow squids, *Nototodarus gouldi* and *N. sloanii*, in New Zealand waters. *Bull. Natl. Res. Inst. Far. Seas Fish.* 35, 1–111, Shimizu.
- Uriarte, I., Espinoza, V., Herrera, M., Zuñiga, O., Olivares, A., Carbonell, P., Pino, S., Farías, A., Rosas, C., 2012. Effect of temperature on embryonic development of *Octopus mimus* under controlled conditions. *J. Exp. Mar. Biol. Ecol.* 416 & 417, 168–175.
- Van Heukelem, W.F., 1973. Growth and life-span of *Octopus cyanea* (Mollusca: Cephalopoda). *J. Zool. (Lond.)* 169, 299–315.
- Vaughan, D.L., Recksiek, C.W., 1978. An acoustic investigation of market squid, *Loligo opalescens*. *Calif. Dep. Fish Game Fish. Bull.* 169, 135–147.

- Vecchione, M., 1981. Aspects of early life history of *Loligo pealei* (Cephalopoda: Myopsida). J. Shellfish Res. 1, 171–180.
- Vecchione, M., 1983. Proceedings of the International Squid Symposium. Trans. Am. Fish. Soc. 112, 731–732.
- Vecchione, M., Young, R.E., Guerra, A., Lindsay, D.J., Clague, D.A., Bernhard, J.M., Sager, W.W., Gonzalez, A.F., Rocha, F.J., Segonaz, M., 2001. Worldwide observations of remarkable deep-sea squids. Science 294, 2505–2506.
- Vidal, E.A.G., 1994. Relative growth of paralarvae and juvenile of *Illex argentinus* (Castellanos, 1960) in southern Brazil. Antart. Sci. 2 (6), 275–282.
- Vidal, E.A.G., Haimovici, M., 1998. Feeding and the possible role of the proboscis and mucus cover in the ingestion of microorganisms by rhyndoteuthion paralarvae (Cephalopoda: Ommastrephidae). Bull. Mar. Sci. 63, 305–316.
- Vidal, E.A.G., DiMarco, F.P., Wormuth, J.H., Lee, P.G., 2002a. Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. Bull. Mar. Sci. 71 (2), 915–931.
- Vidal, E.A.G., DiMarco, F.P., Wormuth, J.H., Lee, P.G., 2002b. Optimizing rearing conditions of hatchling loliginid squid. Mar. Biol. 140, 117–127.
- Vidal, E.A.G., Roberts, M.J., Martins, R.S., 2005. Yolk utilization, metabolism and growth in reared *Loligo vulgaris reynaudii* paralarvae. Aquat. Living Resour. 18 (4), 385–393.
- Vidal, E.A.G., DiMarco, P., Lee, P., 2006. Effects of starvation and recovery on the survival, growth and RNA/DNA ratio in loliginid squid paralarvae. Aquaculture 260 (1–4), 94–105.
- Vidal, E.A.G., Haimovici, M., Hackbart, V.C., 2010. Distribution of paralarvae and small juvenile cephalopods in relation to primary production in an upwelling area off southern Brazil. ICES J. Mar. Sci. 67, 1346–1352.
- Villanueva, R., 1995. Experimental rearing and growth of planktonic *Octopus vulgaris* from hatching to settlement. Can. J. Fish. Aquat. Sci. 52, 2639–2650.
- Villanueva, R., 2000. Effect of temperature on statolith growth of European squid *Loligo vulgaris* during the early life. Mar. Biol. 136, 449–460.
- Villanueva, R., Bustamante, P., 2006. Composition in essential and non-essential elements of early stages of cephalopods and dietary effects on the elemental profiles of *Octopus vulgaris* paralarvae. Aquaculture 261, 225–240.
- Villanueva, R., Norman, M.D., 2008. Biology of the planktonic stages of benthic octopuses. Oceanogr. Mar. Biol. Annu. Rev. 46, 105–202.
- Villanueva, R., Nozais, C., Boletzky, S.v., 1997. Swimming behaviour and food searching in planktonic *Octopus vulgaris* Cuvier from hatching to settlement. J. Exp. Mar. Biol. Ecol. 208, 169–184.
- Villanueva, R., Riba, J., Ruiz-Capillas, C., Gonzalez, A.V., Baeta, M., 2004. Amino acid composition of early stages of cephalopods and effect of amino acid dietary treatments on *Octopus vulgaris* paralarvae. Aquaculture 242, 455–478.
- Villanueva, R., Moltschanivskyj, N.A., Bozzano, A., 2007. Abiotic influences on embryo growth: statoliths as experimental tools in the squid early life history. Rev. Fish Biol. Fish. 17, 101–110.
- Villanueva, R., Quintana, D., Petroni, G., Bozzano, A., 2011. Factors influencing the embryonic development and hatchling size of the oceanic squid *Illex coindetii* following in vitro fertilization. J. Exp. Mar. Biol. Ecol. 407, 54–62.
- Voight, J.R., 1991. Enlarged suckers as an indicator of male maturity in *Octopus*. Bull. Mar. Sci. 49, 98–106.
- Voight, J.R., 1995. Sexual dimorphism and niche divergence in a mid-water octopod (Cephalopoda: Bolitaenidae). Biol. Bull. 189, 113–119.
- Voight, J.R., Feldheim, K.A., 2009. Microsatellite inheritance and multiple paternity in the deep-sea octopus *Graneledone boreopacifica* (Mollusca: Cephalopoda). Invertebr. Biol. 128 (1), 26–30.

- Voight, J.R., Grehan, A.J., 2000. Egg brooding by deep-sea octopuses in the North Pacific Ocean. *Biol. Bull.* 198, 94–100.
- Voss, N.A., 1980. A generic revision of the Cranchiidae (Cephalopoda: Oegopsida). *Bull. Mar. Sci.* 30, 365–412.
- Voss, G.L., 1988. The biogeography of the deep-sea Octopoda. *Malacologia* 29, 295–307.
- Vovk, A.N., Khvichiya, L.A., 1980. On feeding of long-finned squid (*Loligo pealei*) juveniles in Subareas 5 and 6. Northwest Atlantic Fisheries Organization (NAFO), SCR Doc. 80/VI/50. 9.
- Wakabayashi, T., Tsuchiya, K., Segawa, S., 2005. Morphological changes with growth in the paralarvae of the diamondback squid *Thysanoteuthis rhombus* Troschel, 1857. *Phuket Mar. Biol. Center Res. Bull.* 66, 167–174.
- Walker, D., Power, A.J., Sweeney-Reeves, M.J., Avise, J.C., 2006. Multiple paternity and female sperm usage along egg case strings of the knobbed whelk, *Busycon carica* (Molluscal; Melongenidae). *Mar. Biol.* 151, 53–61.
- Waluda, C.M., Pierce, G.J., 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. *S. Afr. J. Mar. Sci.* 20, 323–336.
- Waluda, C.M., Rodhouse, P.G., 2006. Remotely sensed mesoscale oceanography of the Central Eastern Pacific and recruitment variability in *Dosidicus gigas*. *Mar. Ecol. Prog. Ser.* 310, 25–32.
- Weihls, D., Moser, H.G., 1981. Stalked eyes as an adaptation towards more efficient foraging in marine fish larvae. *Bull. Mar. Sci.* 31, 31–36.
- Wells, M.J., Wells, J., 1959. Hormonal control of sexual maturity in *Octopus*. *J. Exp. Biol.* 36, 1–33.
- Wells, M.J., Hanlon, R.T., Lee, P.G., Dimarco, F.P., 1988. Respiratory and cardiac performance in *Lolligunclula brevis* (Cephalopoda, Myopsida): the effects of activity, temperature, and hypoxia. *J. Exp. Biol.* 138, 17–36.
- Worms, J., 1983. *Loligo vulgaris*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles*, Volume 1. Species Accounts. Academic Press, London, pp. 143–157.
- Wormuth, J.H., O'Dor, R.K., Balch, N., Dunning, M.C., Forch, E.C., Harman, R.F., Rowell, T.W., 1992. Family Ommastrephidae. *Smithson. Contrib. Zool.* 513, 105–119.
- Yamamura, K., 1999. Key-factor/key-stage analysis for life table data. *Ecology* 80 (2), 533–537.
- Yang, W.T., Hanlon, R.T., Krejci, M.E., Hixon, R.F., Hulet, W.H., 1983. Laboratory rearing of *Loligo opalescens*, the market squid of California. *Aquaculture* 31, 77–88.
- Yang, W.T., Hixon, R.F., Turk, P.E., Krejci, M.E., Hulet, W.H., Hanlon, R.T., 1986. Growth, behaviour and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. *Fish. Bull.* 84, 771–798.
- Young, J.Z., 1970. *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford, Clarendon, pp. 507–530.
- Young, R.E., 1975. *Leachia pacifica* (Cephalopoda, Teuthoidea): spawning habitat and function of the brachial photophores. *Pac. Sci.* 29, 19–25.
- Young, R.E., 1991a. Chiroteuthid and related paralarvae from Hawaiian waters. *Bull. Mar. Sci.* 49, 162–185.
- Young, R.E., Harman, R.F., 1987. Three species of larval *Onychoteuthis* from Hawaiian waters. *Veliger* 29, 313–321.
- Young, R.E., Harman, R.F., 1988. “Larva”, “paralarva” and “subadult” in cephalopod terminology. *Malacologia* 29, 201–207.
- Young, R.E., Harman, R.F., Mangold, K.M., 1985. The eggs and larvae of *Brachiotheuthis* sp. (Cephalopoda: Teuthoidea) from Hawaiian waters. *Vie Milieu* 35, 203–209.
- Zatylny, C., Gagnon, J., Boucaud-Camou, E., Henry, J., 2000a. The SepOvotropin: a new ovarian peptide regulating oocyte transport in *Sepia officinalis*. *Biochem. Biophys. Res. Commun.* 276, 1013–1018.

- Zatylny, C., Gagnon, J., Boucaud-Camou, E., Henry, J., 2000b. ILME: a waterborne pheromonal peptide released by the eggs of *Sepia officinalis*. *Biochem. Biophys. Res. Commun.* 275, 217–222.
- Zatylny, C., Marvin, L., Gagnon, J., Henry, J., 2002. Fertilization in *Sepia officinalis*: the first mollusk sperm-attracting peptide. *Biochem. Biophys. Res. Commun.* 296, 1186–1193.
- Zecchini, F., Vecchione, M., Belcari, P., Roper, C.F.E., 2012. Development of the hectocotylus in *Illex coindetii* (Verany, 1837) (Cephalopoda: Ommastrephidae). *Sci. Mar.* 76, 463–472.
- Zeidberg, L., 2004. Allometry measurements from *in situ* video recordings can determine the size and swimming speeds of juvenile and adult squid *Loligo opalescens* (Cephalopoda: Myopsida). *J. Exp. Biol.* 207, 4195–4203.
- Zeidberg, L.D., 2009. First observations of sneaker mating in the California market squid *Doryteuthis opalescens* (Cephalopoda: Myopsida). *J. Mar. Biol. Assoc. Marine Biodiversity Records* 2, e6. <http://dx.doi.org/10.1017/S1755267208000067>.