Cannibalism in cephalopods

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Abstract Cannibalism refers to the action of consuming a member of the same species and is common in many taxa. This paper reviews the available literature on cannibalism in cephalopods. All species of the class Cephalopoda are predators and cannibalism is common in most species whose diet has been studied. Cannibalism in cephalopods is density-dependent due to their aggressive predatory and in case of the octopuses territorial nature. It also depends upon local and temporal food availability and of the reproductive season. Cannibalistic behaviour is positively related to the size of both cannibal and victim. It can affect population dynamics of cephalopods in periods of low food availability and/or high population abundance. Cephalopods are generally restricted in their ability to store energy. It is thus assumed that cannibalism is part of a population energy storage strategy enabling cephalopod populations to react to favourable and adverse environmental conditions by increasing and reducing their number. Finally, we propose five orientation points for future research on cannibalism in cephalopods.

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Introduction

To kill and eat a member of the same species is common in animals of various taxa and occurs for different reasons. Cannibalism can provide a competitive advantage among juveniles and/or adults and may be beneficial for survival in periods of food scarcity (Fox 1975; Polis 1981; Caddy 1983; Calow 1998). Cannibalism induced mortality can reach up to 95% of a particular age class (Fox 1975) and is often dependent on the size of the predator (Polis 1981; Amaratunga 1983; Sauer and Lipinski 1991; Claessen et al. 2000, 2002). It constitutes an important link between processes from the individual to the population level (Claessen et al. 2002). The size range of prey that a predator can capture has been defined as the window of predation and in case of cannibalism as the window of cannibalism (Claessen et al. 2000, 2002). Although cannibalism is size-specific, exceptions are known. Generally, the relative size difference between victim and predator is more important than the absolute size. Species that pass through ecdysis (the moult of the exoskeleton) periods, have pupae stages or are able to attack in groups show size-independent cannibalism that lead to the

conclusion that cannibalism in general is the result of physical dominance (Polis 1981).

Cannibalism is thought to be an important mechanism of density-dependent regulation in aquatic animals as fish (Laevastu and Favorite 1988; Smith and Reay 1991; Fortier and Villeneuve 1996; Wespestad et al. 2000; Claessen et al. 2000, 2002, 2004), cephalopods (Caddy 1983; Aronson 1986; Dawe 1988) and crustaceans (Fernández 1999; Moksnes 2004). It produces feedback mechanisms that can lead the population towards a determined density and in that way can be an important component of natural mortality (Polis 1981; Caddy 1983; Smith and Reay 1991; Claessen et al. 2004; Jurado-Molina et al. 2006). Different effects on the dynamics of a population can result: it may (1) force a population into population cycles, (2) destabilize it and create deterministic chaos, (3) stabilize it, (4) result in bi-stability and/or (5) have effects on the size distribution resulting in bi-stability of size distribution (see Claessen et al. 2004). Studies in marine fish have shown that cannibalism can control recruitment and produce cycles of different population densities (Ricker 1954; Uzars and Plikshs 2000; Wespestad et al. 2000; Claessen et al. 2000, 2002, 2004). In general, the behaviour of the victim (as that of the aggressor) can be the reason for cannibalism and as behaviour often is density-related, the rates of cannibalism are often related to the number of encounters (Fox 1975).

Intra-cohort and inter-cohort cannibalism can be distinguished (Wootton 1990). Intra-cohort cannibalism occurs between conspecifics of approximately the same age, and is common in fish and cephalopods (Smith and Reay 1991; Wootton 1990; Hanlon and Messenger 1996). Mortality caused by this type of cannibalism reduces intra-cohort competition and increases growth rates (Crowley and Hopper 1994; Claessen et al. 2000). Together with inter-cohort cannibalism that is inflicted by large specimens on smaller ones of—usually—younger cohorts it gives an opportunity to decrease competition by reducing density (Claessen et al. 2000).

Both types of cannibalism are usually hetero-cannibalism (i.e. cannibalism on unrelated conspecifics) in contrast to filial cannibalism—a special form of inter-cohort cannibalism—that relates individuals to their own offspring. Filial cannibalism usually reduces the fitness of an individual and this type of cannibalism occurs only when the benefits of cannibalism for the cannibal are high (Thomas and Manica 2003). A special form of intra-cohort cannibalism is sexual cannibalism where often the female devours the male (before, during, or after copulation) that in many cases is smaller than its female counterpart (Polis 1981; Elgar 1992). The benefits of this type of cannibalism are especially pronounced when two basic preconditions are met: (1) the females' fecundity increases with size or rather weight and (2) for the males it is unlikely that they have more opportunities to mate (Johns and Maxwell 1997). As cannibalism often is associated with an asymmetry between cannibal and victim, sexual cannibalism could be more common in animals with strong sexual dimorphism in size (Elgar and Crespi 1992).

In cephalopods, the taxonomic group of interest of the present review, both preconditions are met: fecundity is size-coupled and most species are monocyclic, i.e. senescence and rapid death strike after the first reproductive season. Semelparity is also common among cephaloods (Rocha et al. 2001). This and a number of other characteristic life history traits found in most cephalopod species make cannibalism especially beneficial for this taxon. They show high growth and metabolic rates (e.g. Rodhouse and Nigmatullin 1996; Boyle and Rodhouse 2005) and all living coleoid cephalopods (i.e. all modern cephalopods with the exception of the Nautilidae) are voracious carnivorous that consume a wide variety of available prey (Boyle and Rodhouse 2005). Cannibalism has been reported for many cephalopod groups of both octopus and squids like e.g. such of the genus *Illex*, *Octopus*, *Sepia*, *Dosidicus*, *Onychoteuthis*, *Todarodes*, *Ommastrephes* and *Loligo* (Caddy 1983; Roper et al. 1984; Hanlon and Messenger 1996; Boyle and Rodhouse 2005).

With the exception of short sections in Hanlon and Messenger (1996) and Boyle and Rodhouse (2005), a review on the subject does not exist and the effects of cannibalism on individual cephalopods and their populations are unknown. The present article reviews the available literature on cephalopod cannibalism to explore the patterns of different cannibal species and possible causes for it. It examines population densities, mating seasons, food shortages and the hierarchies of body size and between sexes, which all can be relevant factors in the cannibalistic strategies of cephalopods or be related to it. Publications on the diet of 34 species of cephalopods cannibals were

reviewed. The reported cannibalism was ranked in three arbitrary categories: (1) incidental with cannibalistic proportion of less than 1% of the diet, (2) common cannibalism with 1–10% of the diet, and (3) high with more than 10% of cannibalistic diet (Table 1). Where information was available cannibalism was classified into intra-cohort and inter-cohort predation of conspecifics. Further separation of the observed cannibalism considering biological and ecological reasons were made when possible.

Generalized patterns in cephalopod cannibalism

All cephalopods are carnivorous and they have probably been active predators since their appearance in the late Cambric as very early cephalopod fossils reveal (Boyle and Rodhouse 2005). We found 34 cannibals species of cephalopods in the literature, where 32.4% correspond to family Ommastrephidae, 26.5% Octopodidae, 20.6% Loliginidae, 8.8% Sepiidae, 5.9% Onychoteuthidae, 2.9% Nautilidae and 2.9% Architeuthidae (Table 1). In these 34 species cannibalism is incidental in 17.6%, common in 58.8% and high in 23.5% (Table 1). This pattern is unusual in animal kingdom and could be related to their voracious feeding behaviour, high metabolic demands, high abundances, and the absence of social behaviour.

In case of the squids, cannibalism in parts was thought be the result of stress rather than a result of feeding habits only (Ibáñez et al. 2008) and such stress-induced cannibalism has been described for a number of species during fishing operations (Hanlon and Messenger 1996; Markaida and Sosa-Nishizaki 2003). Starving experiments on *Illex illecebrosus* in captivity where cannibalism was provoked after about three days corroborate the view of stress-induced conspecific predation (O'Dor and Dawe 1998). Therefore, cannibalistic rates reported for commercial species of squids must be analysed with caution. Fishing inflicts stress and observed cannibalism or at least its intensity may be an artefact rather than real data (Table 1). An extreme example is *Dosidicus gigas*, a nerito-oceanic squid where high rates of cannibalism were observed (Ehrhardt 1991; Markaida and Sosa-Nishizaki 2003; Markaida 2006; Markaida et al. 2008; Ibáñez et al. 2008). Cannibalism in this species showed temporal variations related to migration and in relationship of body size (Ehrhardt 1991;

Markaida and Sosa-Nishizaki 2003). Additionally, fishing gear produces an artifact with respect to diet and the rate of cannibalism. Squids captured with jigs showed highest cannibalism, while squids captured with nets were less cannibalistic (Table 2). The observed bias is thought to be related with (1) the predation opportunity and (2) the predator density. In northern Chile in years of poor abundance of *D. gigas* its cannibalism is very low (Table 2). For octopus species such bias due to sample gear does not exist as octopus is solitary and is usually taken one by one.

Effects of cannibalism on population dynamics

Years of high density of the schooling squid *Illex illecebrosus* were associated with high rates of cannibalism suggesting density-dependent relationships (Dawe 1988). In contrast, the populations of *Loligo sanpaulensis* that do not form dense aggregations show low incidence of cannibalism (Santos and Haimovici 1998). Cannibalism has been observed for the jumbo squid (*Dosdicus gigas*) in years of mass strandings when its populations are forming large aggregations (Wilhelm 1951). Ommastrephid squids in general, show major abundance pulses related to interannual variations in environmental conditions (Anderson and Rodhouse 2001) and during episodes of high abundances population density cannibalism could be a regulating factor to reduce intra-specific competition.

When population density increases in case of octopuses (e.g. *Octopus briareus*) the territories must become smaller and subsequently the frequency of intra-specific encounters and the per capita rate of cannibalism increase (Aronson 1986). Similarly, for the octopus *Enteroctopus megalocyathus* and *Octopus vulgaris* a higher frequency of cannibalism has been reported in areas and periods where this species are more abundant (Chong et al. 2001; Oosthuizen and Smale 2003; Ibáñez and Chong 2008). Such situations theoretically generate a pattern in the structure of population sizes and/or impact stability of population cycles (Claessen et al. 2004). During El Niño-events the abundance of *Octopus mimus* increases in northern Chile which reflects in the catches (Castilla and Camus 1992; Defeo and Castilla 1998). This may provoke cannibalistic behaviour as a strategy of population regulation that can stabilize population

Table 1 Intensity and categories of cannibalism of cephalopod species

Species	Intensity	Category	Source
Order Nautiloida			
Family Nautilidae			
Nautilus sp.	Incidental	Inter-cohort	Arnold and Carlson (1986)[a]
Order Sepiida			
Family Sepiidae			
Sepia officinalis Linnaeus (1758)	Common	Intra-cohort	Castro and Guerra (1990)[b], Pinczon du Sel et al. (1997[c], 2000)[b]
Sepia australis Quoy and Gaimard (1832)	High		Mqoqi et al. (2007)[b]
Sepia pharaonis Ehrenberg 1831	Common		Roper et al. (1984)
Order Teuthida			
Family Ommastrephidae			
Todarodes pacificus Steenstrup (1880)	Common		Roper et al. (1984)
Todarodes sagittatus Lamarck (1798)	Common		Quetglas et al. (1999)
Todaropsis eblanae Ball (1841)	Common		Lordan et al. (1998)[b]
Ommastrephes bartrami Lesueur (1821)	High	Inter-cohort	Roper et al. (1984), Lipinski and Linkowski (1988), Ivanovic and Brunetti (2004)[d]
Sthenoteuthis pteropus Steenstrup (1855)	Common		Roper et al. (1984)
Nototodarus gouldi McCoy (1888)	High		Roper et al. (1984)
Dosidicus gigas d'Orbigny (1835)	High	Both	Wilhelm (1951)[e], Ehrhardt (1991)[d], Markaida and Sosa-Nishizaki (2003)[d], Markaida (2006)[d], Markaida et al. (2008)[d], Ibáñez et al. (2008)[c]
Illex coindetii Verany (1839)	Common	Inter-cohort	Lordan et al. (1998)[b]
Illex illecebrosus Lesueur (1821)	Common	Both	Dawe (1988)[d], Dawe and Brodziak (1998)[d]
Illex argentinus Castellanos (1960)	Common	Inter-cohort	Bazzino and Quiñones (2001)[d], Santos and Haimovici (1997[b], 2000)[b], Mouat et al. (2001)[d]
Martialia hyadesi Rochebrune and Mabile (1889)	Incidental	Inter-cohort	Rodhouse et al. (1992), González and Rodhouse (1998), Dickson et al. (2004)[d]
Family Loliginidae			
Sepioteuthis australis Quoy and Gaimard (1832)	Common		Roper et al. (1984), Steer et al. (2003)
Uroteuthis duvauceli d'Orbigny (1835)	Common		Roper et al. (1984)
Doryteuthis opalescens Berry (1911)	Common		Roper et al. (1984)
Doryteuthis pealeii Lesueur (1821)	Common		Roper et al. (1984), Maurer and Bowman (1985)
Loligo forbesi Steenstrup (1856)	Common	Inter-cohort	Roper et al. (1984), Rocha et al. (1994)
Loligo vulgaris Lamarck (1798)	Common	Inter-cohort	Roper et al. (1984), Sauer and Lipinski (1991), Rocha et al. (1994), Coelho et al. (1997)[b]
Loligo sanpaulensis Brakoniecki (1984)	Common	Both	Santos and Haimovici (1998)
Family Onycoteuthidae			
Onykia (Moroteuthopsis) ingens Smith (1881)	Common		Phillips et al. (2003)[b]
Onychoteuthis borealijaponica Okada (1927)	Common		Roper et al. (1984)
Family Architeuthidae			
Architeuthis dux Steenstrup (1857)	Incidental		Bolstad and O'Shea (2004)[e]
Order Octopodida			
Family Octopodidae			
Octopus vulgaris Cuvier (1797)	Common	Both	Guerra (1978)[f], Smith (2003)[f], Oosthuizen and Smale (2003)[f]
Octopus californicus Berry (1911)	Incidental	Inter-cohort	Hochberg (1997)[f]

Table 1 continued

Species	Intensity	Category	Source
Octopus bimaculatus Verrill (1883)	Incidental	Intra-cohort	Ambrose (1984)[f]
Octopus briareus Robson (1929)	Common	Inter-cohort	Roper et al. (1984)
Octopus maorum Hutton (1880)	High	Both	Grubert et al. (1999)[f], Anderson (1999)[f]
Octopus mimus Gould (1852)	Incidental		Cortez et al. (1995)[f]
Octopus tehuelchus d'Orbigny (1834)	High	Inter-cohort	Ré and Gómez-Simes (1992)[f]
Eledone massyae Voss (1964)	Incidental		Ré (1998)[f]
Enteroctopus megalocyathus Gould (1852)	High	Both	Ibáñez and Chong (2008)[f]

Classification based on Sweeney and Roper (1998)

[a] Direct observation; [b] trawls; [c] several methods; [d] jig; [e] stranded specimens; [f] scuba

Table 2 Frequency of occurrence of cannibalism in the diet of *Dosidicus gigas* in relation to method of capture

Cannibalism (%)	Sampling gear	Location	Year	Reference
5–30	Jigging	North Pacific	1980	Ehrhardt (1991)
1.3–26.3	Jigging	North Pacific	1995–1997	Markaida and Sosa-Nishizaki (2003)
0.3–22	Jigging	North Pacific	1998–2000	Markaida (2006)
29.7–58	Jigging	North Pacific	2005–2007	Markaida et al. (2008)
3.7–7.1	Jigging	South Pacific	1993–1994	Chong et al. (2005)
7.8	Purse-seine	South Pacific	2003–2004	Ibáñez et al. (2008)
34.3	Mid-trawl	South Pacific	2003	Ibáñez et al. (2008)
3.3	Trawl	South Pacific	2006	Ibáñez et al. (2008)
28.9	Jigging	South Pacific	2006	Ibáñez et al. (2008)

cycles (Claessen et al. 2004). However, in these periods high densities of bivalves, the main food of *O. mimus* (Cortez et al. 1995), were also found (Castilla and Camus 1992) which could keep the rate of cannibalism low.

It is assumed that cannibalism in case of cephalopods in general occurs mostly in populations with high densities. There the probability of conspecific encounters is elevated and the consumption of a member of the same species is more likely. However, it is difficult to conclude on this topic due to the limited number of studies and the fact of a bias due to sampling gear in case of squids (Table 1 and Table 2). Fluctuations in populations are the product of a number of factors that are either density-dependent or density-independent, and therefore it is of little value to test the existence of one type of factors exclusively (Lima 1995). Cannibalism could be a strategy of population regulation that leads to temporal fluctuations of this population (Fernández

1999; Claessen et al. 2004). Thus, the impact of cannibalism on population dynamics can be studied by comparing populations excluding cannibalism to population dynamics that result from different levels of cannibalism (Claessen et al. 2002).

The consideration of seasonal changes that occur especially in temperate environments can help to understand the mechanisms by which cannibalism can regulate a population in terms of productivity. The biomass of a population is determined by the carrying capacity of its ecosystem and the cannibalistic rate; the carrying capacity again is influenced by the varying productivity. In the months of increasing productivity a population of pelagic squids will increase its biomass. When productivity of the ecosystem declines the starving individuals increasingly feed on conspecifics that consequently decreases the biomass and results in population cycles (Fig. 1a). In summary, squids are cannibalistic when the food is scarce and the population abundance
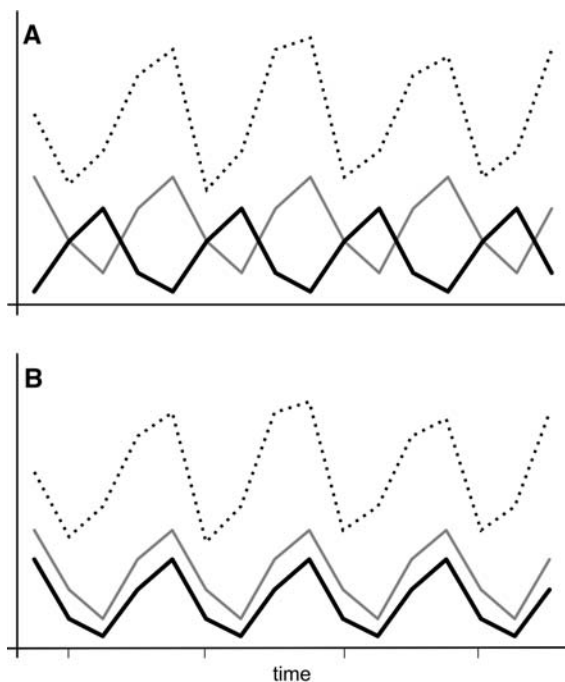
Fig. 1 Effects of cannibalism and productivity on population biomass over 3 years. **a** Pelagic squids; **b** Benthic octopuses; *dashed lines* productivity of ecosystem; *black lines* rate of cannibalism; *grey lines* squid/octopus biomass

is high. Cannibalism in this case acts density-dependent and occurs with a lag to the productivity of the ecosystem, i.e. in the example highest canni-balistic rate would occur in autumn/winter.

Squids living in shoals or groups have to be distinguished from the solitary and territorial octo-puses as the different lifestyles lead to different types of intra-specific interactions. In case of the benthic octopuses, periods with increasing productivity will lead to increasing biomass and an increasing rate of encounters between conspecifics. This will lead to more aggressive behaviour producing a higher per-centage of cannibals due to territoriality. As a result biomass will decrease immediately leading to popu-lation cycles different from those of squids (Fig. 1b). Here, cannibalism shows no lag to the environmental conditions and highest cannibalistic rate occurs in the period of highest productivity. It is assumed that inter-annual environmental variability, like e.g. observed during El Niño-event or the cool and warm regimes in the Eastern Pacific, can have similar effect on the cannibalistic rates as seasonal changes of productivity.

A modelling approach on the general effects of mortality on population dynamics showed that during periods of a reduced carrying capacity an extreme population reduction can be prevented by a rapid increase of mortality or a strong mortality pulses at or shortly after the appearance of adverse conditions. The abundance of a population then persists at higher levels than without the increased initial mortality (Hallett et al. 2004), i.e. the increased mortality stabilizes the population level. Cannibalism could be such a mechanism that provides the necessary mortality to stabilize a population during adverse conditions.

Cannibalism as a strategy when food is scarce

Cannibalistic behaviour has been suggested to be an indicator for limited food availability (Dawe 1988; Calow 1998). Ommastrephids and other squids are cannibalistic when they migrate in schools (O'Dor and Wells 1987; Rodhouse and Nigmatullin 1996; Mouat et al. 2001) and when food is scarce (Ennis and Collins 1979; O'Dor and Wells 1987). Cannibalism under such conditions can provide a mechanism for survival of at least parts of a school (O'Dor and Wells 1987) as it reduces competition for the limited resources and increases per capita consumption (Polis 1981; Calow 1998). Additionally, it can increase the ecosystem's carrying capacity (Polis 1981) by the indirect extension of the food size spectrum (Fox 1975). Larger speci-mens can access lower trophic levels when feeding on smaller conspecifics as shown in a population model for squids (Amaratunga 1983). This decreases the mean trophic level of the population and in that way makes it more efficient. Carrying capacity increases as does the survival rate of the larger individuals under otherwise insufficiently productive environments and secures reproduction (Keyl et al. 2008). Cannibalism in this sense has been coined life boat mechanism (van den Bosch et al. 1988; van den Bosch and Gabriel 1997). It has been assumed that cannibalistic popula-tions in such situations could apparently even grow since the selective removal of small individuals leads to an increase in average weight of the population even without individual growth. A starving population with a high cannibalistic rate could seem to grow faster than one that is able to keep up a moderate consumption (O'Dor and Dawe 1998).

In *Illex illecebrosus* cannibalism was not related to abundance and probably occurs according to the availability of prey only (Maurer and Bowman 1985). Moreover, no significant differences in cannibalism of the squid *I. argentinus* for different size classes exist (Bazzino and Quiñones 2001), suggesting that in the study area food is sufficiently available. In loliginid squids cannibalism generally has been associated with limited food resources (Santos and Haimovici 1998). Cannibalism in *Loligo vulgaris* of the Saharan Bank is related to the high abundance of juveniles that constitute an alternative prey when other food is scarce (Coelho et al. 1997). In years of food shortages higher cannibalistic behaviour were observed also for *I. illecebrosus* (Maurer and Bowman 1985) and *I. argentinus* (Santos and Haimovici 1997). In the Gulf of California, cannibalism of *Dosidicus gigas* can raise to over 30% of the diet in months of prey scarcity (Ehrhardt 1991). Under adverse environmental conditions where primary productivity is reduced, the rate of cannibalism of cephalopods is likely to increase with the consequence of decreasing biomasses due to the elevated level of cannibalism (Pecl and Jackson 2008).

Inter-cohort cannibalism

Adult cannibalism on juveniles is documented for several species of squid (Amaratunga 1983; Dawe 1988; Lipinski and Linkowski 1988; Sauer and Lipinski 1991; Rocha et al. 1994; Rasero et al. 1996; Santos and Haimovici 1997; Dawe and Brodziak 1998; Mouat et al. 2001; Markaida and Sosa-Nishizaki 2003) and octopus (Ré and Gómez-Simes 1992; Cortez et al. 1995; Anderson 1999; Grubert et al. 1999; Ibáñez and Chong 2008). Generally, cephalopods go through dietary changes during their ontogeny (Amaratunga 1983; Summers 1983; Rocha et al. 1994; Rodhouse and Nigmatullin 1996; Zuyev et al. 2002). From a crustacean diet during paralarvae and juvenile stages they switch to a diet consisting mostly fish and cephalopods in their adult stage (Rocha et al. 1994). In teleosts the ontogenic change from planktivorous to piscivorous was suggested to be the result of the interplay between size-dependent competition and cannibalism (Claessen et al. 2000). Physiological and behavioural restrictions make cannibalism inherently dependent

on the size of the victim and the cannibal (Claessen et al. 2000), increasing with age and depending on the size relation between both (Crowley and Hopper 1994; Claessen et al. 2000). In case of squids the results of a population model lead to the conclusion that cannibalism increases with age and promotes the transfer of energy from small individuals to larger ones (Amaratunga (1983).

Cannibalism is so common in adult squids that it was assumed that they are unable to maintain their daily consumption without a cannibalistic part in their diet, due to their high metabolic rates (O'Dor and Wells 1987). Juveniles and sub-adults of *Illex argentinus* (<20 cm) also consumed conspecifics of 19–70% of their own mantle length but the highest frequency of cannibalism occurred among individuals of sizes larger than 20 cm ML (Santos and Haimovici 1997). Mouat et al. (2001) found that cannibalism in *I. argentinus* squid occurs only in case of large specimens and tends to increase with increasing squid weight. The frequency of cannibalistic specimens of *Dosidicus gigas* increases with size and a significant positive relationship between the size of the cannibal and the victim is reported for this species (Markaida and Sosa-Nishizaki 2003). *Todaropsis eblanae*, an ommastrephid cephalopod shows high incidence of cannibalism in an area of high density of juveniles (Rasero et al. 1996) and similar behaviour is known for teleosts as e.g. *Gadus morhua*, *Theragra chalcogramma* and *Merluccius gayi gayi* (Uzars and Plikshs 2000; Wespestad et al. 2000; Cubillos et al. 2003).

As individuals of the first ontogenic stages do not have the physical dominance, i.e. capacity to kill and consume a conspecific, we propose that the relation between size of the victim and the predator is following a linear relationship and an upper and a lower size limit (Fig. 2). The resulting predation window (shaded area in Fig. 2) defines the size range of prey for a specifically sized cannibal (Claessen et al. 2000; 2002) that in case of cephalopods must be bigger than that of e.g. fish. Cephalopods have the capacity to prey on both relatively small and large prey due to the skilfulness of their arms and tentacles as well as the possibility to shred their food with their beaks (see Rodhouse and Nigmatullin 1996; Boyle and Rodhouse 2005).

As the cannibals increase in size the proportion of cannibalism in the diet is assumed to be not linear. Increasing size range of accessible victims together
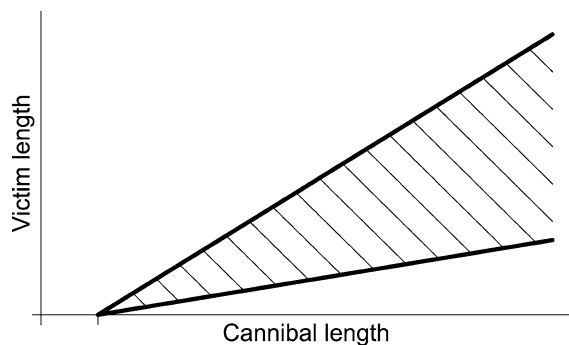
Fig. 2 Predation window; the relationship between cannibal length and victim length
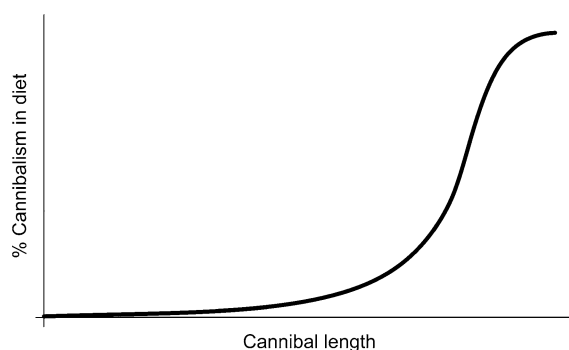

Fig. 3 Relationship between cannibal length and cannibalism proportion

with the size-related increase of energy requirements that additionally are augmented greatly during maturation are supposed to result in non-linear increase of the importance of cannibalism in the diet of the cephalopod cannibal (Fig. 3). Senescence at the end of a cephalopod's lifecycle (Anderson et al. 2002) as a consequence leads to lower energy intake of an individual and the here proposed sigmoid-like function. The cannibalism observed during this period is assumed to be primarily sexual (post-copulation) and in case of the octopuses additionally filial.

In *Octopus tehuelchus* cannibalism is important during the summer and autumn, when adults prey eggs and juveniles (Ré and Gómez-Simes 1992). A notable case of cannibalism is that of *O. maorum* in Tasmania, where cannibalism on small conspecifics and egg clusters (Anderson 1999) is second most important in the diet and has the highest weight percentage of all prey types (Grubert et al. 1999). Similarly, *Enteroctopus megalocyathus*, *O. tehuelchus*, *O. mimus* and

O. maorum feed on their juveniles and females cannibalize their eggs (i.e. filial cannibalism) during brood care (Ré and Gómez-Simes 1992; Cortez et al. 1995; Grubert et al. 1999; Ibáñez and Chong 2008). It was assumed that the reason for the latter behaviour is that they eat nonviable or sick eggs to prevent further infections, as observed in *Bathypolypus arcticus* (Wood et al. 1998). In other taxonomic groups like fish, birds or mammals filial cannibalism is more common (Fox 1975; Polis 1981) and a high intake of eggs as e.g. reported for anchovy, can affect the recruitment of juveniles and cause inter-annual or intra-annual population fluctuations (Hunter and Kimbrell 1980; Pájaro et al. 2007). Due to the monocyclic life-history of most cephalopods this type of cannibalism in cephalopods only occurs in case of brood-caring species of octopuses and polycyclic nautiluses (Arnold and Carlson 1986; Ré and Gómez-Simes 1992; Cortez et al. 1995; Wood et al. 1998; Grubert et al. 1999; Ibáñez and Chong 2008). It is not known how filial cannibalism affects the populations of species of these classes.

Intra-cohort cannibalism

Cannibalistic behaviour is affected by the sex of the cannibal and that of its victim as well as breeding related factors like e.g. the advance of reproductive season and individual maturity. It has been observed that adult females of *Octopus cyanea* try to kill and feed on the male during courtship (Hanlon and Forsythe 2008) perhaps as a means of assessing the quality of the male (Elgar 1992; Calow 1998). *Sepia officinalis* shows cannibalistic behaviour only during the breeding season and associated with fights during mating (Pinczon du Sel et al. 2000) and cannibalism in case of *Loligo sanpaulensis* intensifies during mating in summer and fall especially at night (Andriguetto 1989). In *Illex argentinus* it intensifies in adults during autumn, the pre-reproductive period (Koronkiewicz 1980; 1986). Cannibalism in general was thought to be a phenomenon associated with the concentration of squids in the spawning areas (Karpov and Caillet 1978; Ré 1998). In case of *Illex illecebrosus* an alimentary hierarchy and population control results from cannibalism as females usually reach larger sizes than the males (Dawe 1988; O'Dor and Dawe 1998). In octopuses similar consequences have been observed in

the laboratory and field, since the female of *Octopus maorum* and *O. cyanea* attack males after mating and even cannibalize them (Anderson 1999; Hanlon and Forsythe 2008). Small males of *Octopus vulgaris* are vulnerable to cannibalism by large females under laboratory conditions and the same was observed in their natural habitat (Hanlon and Messenger 1996).

The squids *I. illecebrosus* and *Dosidicus gigas* show marked sexual dimorphism with the females being larger than their males (O'Dor and Dawe 1998; Markaida 2001), a factor that can generate competitive hierarchies in cannibalistic behaviour, especially in mating season. In case of *D. gigas* cannibalism is intensified during reproductive period and consequently sex-ratios are changing, leading to a higher dominance of females in the population (Markaida 2001; Ibáñez and Cubillos 2007; Ibáñez et al. 2008). However, it was also proposed that changing sex-ratios could be a direct, phenotypic response to food availability in their ecosystems (Keyl et al. 2008; Tafur et al. submitted). In myopsid squids cannibalism occurs among males, while in oegopsid squid it is inflicted by the females over males. This corresponds to the observed sexual dimorphism of the two groups: while in myopsid squids males are larger than females, in oegopsid the females are larger (O'Dor 1998).

Other implications of cannibalism

Cannibalism has significant behavioural consequence as it affects the benefits of sociality (Hamilton 1964; Fox 1975; Polis 1981; Calow 1998). Cannibalistic behaviour is often directed at non-related individuals for this reason filial cannibalism and siblicide (i.e. to kill brothers and sisters often combined with feeding on them) may reduce inclusive the fitness of the cannibal and have important impacts on fitness and sociability (Hamilton 1964; Fox 1975; Smith and Reay 1991; Calow 1998; Thomas and Manica 2003). Recognition of familiarity in cephalopods is possible, but not certain (Boal 2006) and the possible lack of recognition could promote non hetero-cannibalism in cephalopods.

The existence of an individual storage organ of cephalopods is still discussed and the capacity of the digestive gland to store energy in the form of lipids was generally accepted. However, a number of studies found no evidence for this (Semmens 1998, 2002;

Moltschaniwskyj and Semmens 2000; Ibáñez et al. 2005) or found that the lipid metabolism of cephalopods is restricted (e.g. Phillips et al. 2001, 2002). For *Dosidicus gigas* a populational energy storage was suggested (Keyl et al. 2008); a feature that would enable the individuals of this species to shift energy storing from the individual to the population. During favourable conditions the population size increases rapidly in numbers and individual size. The resulting biomass could then be reduced again by cannibalism during unfavourable conditions ensuring the largest specimens (i.e. the reproductive part of the population) to survive. This strategy would allow avoiding loco-motory penalty due to large individual storage organs (O'Dor 1998) and nevertheless provides provision during fast migration (Bakun and Csirke 1998). Similar behaviour was suggested for *Illex illecebrosus* (O'Dor 1998) and may be more generally applicable for all cephalopods that are lacking a storage organ. Further advantages of cannibalism in this context are the high quality of the food and the fact that no energy is lost due to conversion of ingested proteins to storable substances (fat, lipids) which is known to lead to losses of over 30% of energy at least in case of ureotelic animals (Millward et al. 1976; Wieser 1994).

All forms of cannibalism may increase the risk of infestation with parasites reducing their fitness (Polis 1981; Calow 1998) although the transmission of disease via cannibalism is thought to be rare in natural populations due to more effective alternatives infection mechanisms (Rudolf and Antonovics 2007).

Discussion

Generally, an individual of a cannibalistic species that is physically more dominant or belongs to a group that ensures its physical dominance will be the cannibal. In many cannibalistic taxa an asymmetry exists in age, size or life history between the cannibal and its victim that generates the higher vulnerability of the victim (Elgar and Crespi 1992; Crowley and Hopper 1994; Claessen et al. 2000; 2002) and this also true in case of the cephalopods (e.g. Markaida and Sosa-Nishizaki 2003). The cannibalistic window of cephalopods is wider than e.g. in fish because their morphological adaptations to capture and kill prey—their arms, tentacles and beaks—increase the opportunities to find cannibalistic prey.

Cannibalism is not a rare and abnormal behaviour that is only found in highly stressed populations, but is a natural response to environmental factors and conditions (Fox 1975). Clearly there are advantages for cannibalistic individuals as e.g. reducing competition and access to food of high quality (Fox 1975; Polis 1981; Calow 1998). In contrast, disadvantages for cannibals also exist as it is more expensive to feed on less abundant prey and this also implies the elimination of individuals with a shared genotype (Polis 1981). Cannibalism has evolved in many different organisms—probably analogously—and therefore must have an evolutionary benefit, such as avoiding local extinction during resource scarcity (Bobisud 1976; Nishimura and Isoda 2004). Population regulation by cannibalism must base on the process of group selection which can be inefficient compared to individual selection even when food is scarce (Reed and Stenseth 1984). Adopting cannibalism for a population could convert to a mutant strategy in the context of evolutionarily stable strategies (ESS, Maynard-Smith 1982; Reed and Stenseth 1984). As cannibalism implies a high risk of reprisals by the victims it was assumed that cannibalism cannot be an ESS (Dawkins 1976) but considering that it is an asymmetric interaction it might be an ESS nevertheless (Smith and Reay 1991). It may have a genetic origin, since the occurrence of several adaptations that inhibit or promote cannibalism implies the presence of selection on genes that may regulate the expression (Fox 1975; Polis 1981) but no studies exist for cephalopods in this respect. However, not all types of cannibalism need to be adaptive and the product of natural selection. Cannibalistic behaviour is described as response to stress, accidents and variable feeding behaviour related to changing environmental conditions (Polis 1981) and all these factors have been assumed to be possible factors controlling cannibalism in cephalopods (e.g. Dawe 1988; Markaida and Sosa-Nishizaki 2003; Ibáñez et al. 2008).

The stabilizing effect of cannibalism on population dynamics has been found for many species (see examples in: Fox 1975; Polis 1981) and the underlying mechanism is supposed to be related to the inflicted mortality (e.g. van den Bosch and Gabriel 1997; Hallett et al. 2004). However, destabilizing effects are also possible (e.g. van den Bosch and Gabriel 1997; Claessen et al. 2004) dependent of the ecology and behaviour of a species. Although we assume that among cephalopod species it is more common that cannibalistic behaviour stabilizes population level further investigations would have to be conducted to conclude on this topic.

In summary, to study cannibalism in cephalopods—as in other taxa—possible environmental variations as well as population density, food availability, body size and sexual dimorphism must be considered. It is very important to work with time series and/or simulations that can incorporate different rates of cannibalism and variable environmental conditions. Furthermore, laboratory experiments should be conducted to study the behaviour of the cannibals in relation to the variables mentioned. Future research on cannibalism must be oriented on five points:

(1) Sampling should be carried out with different gear to avoid biases on stomach contents especially when relying on samples from fisheries. Methods like stable isotope, heavy metal, and fatty acid signature analyses should be used where possible.

(2) Cannibalism must be studied over longer periods to compare with environmental factors (e.g. temperature, primary productivity) and ecological factors (e.g. abundance, food availability).

(3) The asymmetry in size between cannibal and their victim must be explored by the search of cannibalistic window in an intra-cohort and inter-cohort approach.

(4) DNA fingerprinting on victims from stomach contents should be employed to understand the role of sexual and filial cannibalism and if the cephalopod cannibal is able to recognize closely related member.

(5) In an evolutionary context the origin of cannibalism in cephalopods must be identified by mapping cannibalistic and non cannibalistic species on phylogenies.

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