

Impact of environmental temperature on the lifespan of octopods

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ABSTRACT: Recent studies on the life history of cephalopods have challenged the paradigm that all coleoid cephalopods have a single reproductive cycle and a short lifespan. Although lifespan has been investigated in several octopod species, few studies have considered their life-history traits in relation to environmental conditions via a comparative approach. We tested the hypothesis that octopod lifespan is correlated with habitat characteristics. For that purpose, life history and environmental data of 25 incirrate octopod species and the vampire squid *Vampyroteuthis infernalis* were compiled from the literature. Regression analysis showed that the relationship between age at maturity and average habitat temperature was best described by a negative power function ($r^2 = 0.86$). The depth ranges of occurrence (minimum-midpoint-maximum) were positively correlated with time to reach maturity, with maximum depth showing the best fit ($r^2 = 0.47$). Using literature data and our analyses, we estimated that octopods living in polar and deep seas mature after 3 to 5 yr. The reviewed and estimated instantaneous relative growth rates ranged from 0.1 % body weight (BW) d^{-1} in the Antarctic species *Pareledone charcoti* to nearly 6 % BW d^{-1} in the temperate species *Macroctopus maorum*. Our analyses suggest that low water temperatures ($<5^{\circ}C$) result in an extended ontogenetic development, potentially as a result of reduced metabolic rates and constraints on protein synthesis, which increases the lifespan of octopods living in cold environments.

KEY WORDS: Cephalopoda · Incirrate octopods · Life-history traits · Temperature · Lifespan · Deep sea · Polar regions

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INTRODUCTION

A general trend in marine organisms is that the pace of life is reduced for species living in cold-water environments. Metabolic and growth rates are influenced by temperature, with organisms developing, growing, maturing and ageing faster at higher temperatures (Atkinson 1994, 1996, Angilletta et al. 2004). Marine poikilotherms such as fishes and invertebrates that live in polar and deep seas exhibit increased longevities when compared to their relatives living in temperate or warm waters (Cailliet et al. 2001, Young 2003). Research on various deep-sea taxa has revealed extreme longevities, including 11 000 yr for the deep-

sea sponge *Monorhaphis chuni* (Jochum et al. 2012), 4000 yr for proteinaceous corals (Roark et al. 2009), between 312 and 523 yr for the deep-sea oyster *Neopycnodonte zibrowii* (Wisshak et al. 2009), 507 yr for the ocean quahog *Arctica islandica* (Butler et al. 2013), 400 yr for Greenland sharks *Somniosus microcephalus* (Nielsen et al. 2016) and 200 yr for the rockfish *Sebastes aleutianus* (Cailliet et al. 2001). For most deep-sea taxa, information on longevity and other life-history characteristics is lacking, and hence it remains unknown how these parameters are related to habitat temperatures.

Cephalopods (e.g. squids and octopods) occur at all latitudes and inhabit all marine habitats, from tide

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[§]Corrections were made after publication. For details see www.int-res.com/abstracts/meps/v605/c_p151-164/
This corrected version: November 13, 2018

pools to abyssal depths (Boyle & Rodhouse 2005). As adults, most cephalopods are active carnivores that hunt for living prey, and typically they have one reproductive cycle (semelparity). Cephalopods are very abundant in the deep ocean, where large populations exist and where they show a great diversity at the family level (Rosa et al. 2008, Hoving et al. 2014). They are important in food webs as prey (e.g. marine mammals, top predatory fish, seabirds) and predators (e.g. on crustaceans, fishes and other molluscs) (Clarke 1996, Piatkowski et al. 2001, Villanueva et al. 2017). A recent study suggests that the overexploitation of finfish stocks may have favoured cephalopod populations, leading to regional increases in their biomass over the last 60 yr (Doubleday et al. 2016). Despite the pivotal role of cephalopods in the world oceans, knowledge on life histories is lacking for the majority of species that inhabit the deep sea.

Longevity studies on neritic cephalopods have consistently revealed short lifespans, rarely exceeding 3 yr (Arkhipkin 2004, Jackson 2004). The short lifespan is combined with a semelparous reproductive strategy. Semelparity in cephalopods means that all gametes are released during a single reproductive cycle, without a gonadal resting phase (Rocha et al. 2001). With the exception of the Antarctic giant warty squid *Kondakovia longimana* (Laptikhovskiy et al. 2013) and the vampire squid *Vampyroteuthis infernalis* (Hoving et al. 2015), all extant coleoid cephalopods that have been studied to date are semelparous. Within the borders of semelparity, the spawning strategies range from terminal synchronous spawning to the intermittent spawning of egg batches, with specific differences between cephalopods in fecundity, egg size, batch size, time and presence or absence of somatic growth between spawning events, mortality in ontogenetic phases and embryonic development time (Rocha et al. 2001, Hoving 2008).

Embryonic development in cephalopods ranges from a few days in coastal and tropical warm-water species to several months or even years in deep-sea and polar species (Boletzky 1994, Boyle & Rodhouse 2005, Robison et al. 2014). Intraspecific lifespan plasticity has been demonstrated for some species with wide distribution ranges, e.g. ommastrephids. In these species, the life cycle duration increases with latitude and adult size, varying from 5 mo in small-sized tropical forms to more than 1 yr in large animals that live in temperate and subpolar–polar latitudes (Arkhipkin 2004). Furthermore, cephalopods can adapt rapidly to local environmental and ecosystem changes by reaching full maturity at different

sizes and ages depending on the productivity of the environment (Pecl & Jackson 2008, Hoving et al. 2013, Schwarz & Perez 2013, Arkhipkin et al. 2015). Overall, there is evidence that the pace of life in cephalopod species is coupled strongly with the environment (Rodhouse et al. 2014, Hoving & Robison 2017).

Lifespan is also related to the reproductive strategy of cephalopods. Some deep-sea squids (e.g. *Gonatus onyx*, *Bathyteuthis berryi*) retain their eggs after spawning and brood in the bathypelagic zone, out of reach of bottom- and surface-dwelling predators (Seibel et al. 2005, Bush et al. 2012). In cold-water environments (<5°C), embryonic development is slow and may last for several months or even years (Boletzky 1994, Seibel et al. 2000). Using deep-sea observations from remotely operated vehicles, an extremely long brooding time was discovered for the deep-sea octopus *Graneledone boreopacifica* in the Monterey Submarine Canyon off California, USA. One brooding female was monitored from the first weeks when spawning of the eggs took place until the last weeks when the eggs hatched. The embryonic development lasted 53 mo, the longest brooding time ever recorded (Robison et al. 2014). Following the assumption that brooding time makes up 30% of the total life cycle (Boletzky 1987), this cold water octopus is expected to live >10 yr, a result that challenges the paradigm that cephalopods are short-lived animals. The few studies that investigated the lifespan of cold-water cephalopods including deep-sea species show increased longevity and reduced growth compared to warmer-water species (Arkhipkin 2004, Robison et al. 2014, Hoving & Robison 2017), but comparative studies on a wider range of species are still rare.

One of the first reviews on cephalopod growth and lifespan in relation to environmental factors was performed by Wood & O'Dor (2000). The authors investigated the effects of temperature and phylogeny on size at maturity and longevity, using literature data of 18 species from 5 cephalopod orders. The authors concluded that low temperatures delay the time to reach maturity and that larger cephalopods have longer life spans. However, the study was biased towards coastal cephalopods and included only 2 cold-water species, the North Atlantic octopus *Bathypolypus arcticus* and the giant Pacific octopus *Enteroctopus dofleini*. Seibel (2007) measured metabolic rates of pelagic cephalopod species from 8 families all inhabiting different environments. The study showed that the active and muscular coastal and epipelagic squid families Loliginidae and Ommas-

trephidae have the highest metabolic rates of all invertebrates, while the less active and gelatinous cold-water meso- and bathypelagic octopods (Boli-taenidae and vampire squids) had metabolic rates up to 200-fold lower than their shallow-living relatives. Since the high metabolic rates of ommastrephids are associated with a short life cycle, it may mean that cephalopods with low metabolic rates are longer lived, but data to support this notion are scarce.

In cephalopods, egg sizes and numbers, embryonic development time and the duration of the planktonic larval phase are dependent on habitat temperatures (Boletzky 1994, Voight & Drazen 2004, Laptikhovskiy 2006, Villanueva & Norman 2008), which together can be used to estimate lifespan (Robison et al. 2014). Incirrate octopods occur in all marine habitats and they provide post-spawning egg care, retaining the eggs during the entire development period (Boletzky 1992, Jereb et al. 2014). While incirrate octopods are a very suitable model group to investigate how environmental temperature may impact longevity, this has never been done in a comparative approach. We performed regression analysis of life-history data of incirrate octopods and the vampire squid to test the hypothesis that octopod lifespans are inversely correlated with habitat temperature, i.e. octopods living in cold-water habitats of the polar and deep seas have increased longevity compared to their shallow-water relatives.

MATERIALS AND METHODS

Data extraction from the literature

An extensive literature review resulted in life-history data for 25 species of incirrate octopods (Cephalopoda: Octopoda — Incirrata) as well as the vampire squid (Table 1). We used benthic and pelagic species with a distribution ranging from tropical waters to polar seas and from shallow coastal (0–15 m) to bathyal depths (3000 m). For 2 species (*Paraleledone charcoti* and *Bathypolypus arcticus*), we considered anecdotal data obtained from long-term husbandry of octopods under controlled laboratory conditions (Wood 2000, Daly & Peck 2000).

When a life-history trait (e.g. hatchling size) was available from more than one source for the same species (e.g. *Octopus vulgaris*), an average value for the species was calculated. When averages of biological and life-history traits (Table 1) were not explicitly listed, we calculated them by taking the midpoint between published minimum and maximum param-

eter values. For species where literature about life-history traits is scarce, we pooled information for the genus (e.g. *Graneledone boreopacifica* and *G. macrotyla*). We used the average value representative of the species or genus and followed the FAO taxonomic criteria for the latest taxonomic status of taxa (Jereb et al. 2014, Villanueva et al. 2016). All data values, with the exception of *P. charcoti*, refer to females.

Calculations

Life-history traits were quantified following the methodology applied by Wood & O'Dor (2000). Size at maturity was defined as the weight at full maturity (g), and age at maturity was noted in days. Instantaneous relative growth rate G (% body weight d^{-1}) was calculated from the formula:

$$G = \frac{\ln(W_2) - \ln(W_1)}{(t_2 - t_1)} \times 100 \quad (1)$$

where W_2 is the weight at maturity, W_1 is the weight at hatching, and $(t_2 - t_1)$ is the time interval between hatching and maturity (Forsythe & Van Heukelem 1987).

Embryonic development

Embryonic development times were taken as the average values obtained from experiments (Wood 2000, Iglesias et al. 2014). For species with no direct information on embryonic development, the values were estimated following the equation:

$$D = 10794T^{-1.79} \quad (2)$$

which predicts the embryonic developing time in days (D), based on the average habitat temperature in $^{\circ}C$ (T) (Robison et al. 2014). The authors compiled this equation using several sources of information including direct observations on embryonic development of *G. boreopacifica*, which lasted 1590 d at $3^{\circ}C$ (53 mo).

Unfortunately, there is a limitation when applying this equation to estimate embryonic development times for Antarctic octopods because they typically live in water temperatures ranging from -2° to $2^{\circ}C$ (Kuehl 1988). The equation does not process negative temperature values, and even at a water temperature of $1^{\circ}C$, the predicted time for embryonic development would be about 30 yr, which seems unrealistic. Since the egg dimensions of Antarctic

Table 1. Life history data and references for the octopod species analysed in the present study. Superscript numbers refer to literature from where the values were obtained (for references, see the Supplement at www.int-res.com/articles/suppl/m605p151_supp.pdf). Abbr: Abbreviation of the species names; Depth range: minimum and maximum depth for the species; Max ML: maximum mantle length; Emb.dev.: duration of the embryonic development; ~Emb.temp.: average temperature of egg incubation; Hatch.size: size at hatching (ML); Hatch.weight: weight at hatching; Mat.wt: weight at maturity; Mat.ML: ML at maturity; Age mat.: age at maturity; Average lifetime temp: temperature for the species; Lifespan: estimated in days; G: instantaneous relative growth rate; Method: method of age estimation, where L: laboratory, F: field experiments, B: beaks, St: stylets, Lp: lipofuscin concentration, eye: eye lenses, *In situ* observations and Rep: reproductive behaviour and time for egg incubation. Values in **bold italics** were estimated (see 'Materials and methods'). Genus (av.): average values obtained from different reference sources (see 'Data extraction from the literature' in 'Materials and methods')

| Species | Abbr. | Region | Depth range (m) | Max ML (mm) | Egg size (mm) | Emb. dev. (d) | ~Emb. Temp. (°C) | Hatch. size (mm) | Hatch. weight (g) | Mat. wt (g) | Mat. ML (mm) | Age mat. (d) | Average lifetime temp(°C) | Life span (d) | Method |
|---|-------|--|------------------------|----------------------|-----------------------|----------------------|-----------------------|------------------------|------------------------|--------------------------|----------------------|----------------------|---------------------------|-------------------|----------------------------|
| Octopodidae | | | | | | | | | | | | | | | |
| <i>Bathypolypus archicus</i> | Ba | North Atlantic | 20–1200 ^{1,4} | 70 ¹ | 18.0 ^{2,4} | 420 ² | 7.0 ² | 8.9 ² | 0.214 ² | 70 ¹ | 57 ³ | 1400 ¹ | 4.0 ¹ | 1820 | 0.41 ¹ L, F |
| <i>B. sponsalis</i> | Bs | Northeast Atlantic and Mediterranean | 930–1250 ⁴ | 100 ⁴ | 15.0 ⁵ | 126 | 12.0 ⁷ | 7.7⁸ | 0.151 | 150 | 58 ⁶ | 330 ⁶ | 12.0 ⁷ | 456 | 2.09 St |
| <i>Eledone cirrhosa</i> | Ec | Mediterranean and North Atlantic | 30–500 ^{4,10} | 250 ⁴ | 7.6 ⁹ | 110 ⁹ | 16.0 ⁹ | 4.5 ⁹ | 0.047 | 950 ¹⁰ | 174 ¹⁰ | 418 ¹⁰ | 16.0 ⁹ | 517 ¹⁰ | 2.37 L, St |
| <i>Eledone massyae</i> | Em | South America from Brazil to Argentina | 0–300 ⁴ | 90 ¹¹ | 12.0 ¹¹ | 96 | 14.0 ¹¹ | 10.5 ¹¹ | 0.296 | 108 ¹¹ | 90 ¹¹ | 540 | 14.0 ¹¹ | 720 | 1.09 Rep. |
| <i>Enteroctopus dofleini</i> | Ed | North Pacific (Alaska to Japan) | 0–1500 ⁴ | 600 ⁴ | 8.0 ⁴ | 180 ⁴ | 10.8 ⁸ | 5.4 ⁸ | 0.025 ¹ | 16300 ¹ | 600 ⁴ | 1019 ¹² | 10.7 ¹ | 1136 | 1.31 L, F |
| <i>E. megalocyathus</i> | Emg | South America (Chile to Argentina) | 15–170 ¹³ | 190 ⁴ | 10.7 ¹⁴ | 176 ¹⁵ | 12.0 ¹³ | 8.4 ¹⁴ | 0.111 ¹⁴ | 1613 ¹³ | 158 ¹³ | 558 ¹⁶ | 12.5 ¹⁵ | 734 | 1.72 L, Eye |
| <i>Graneleone boreopacifica</i> & <i>G. macrotyla</i> (av.) | Gr | Southern hemisphere and northern Pacific Ocean | 400–3000 ⁴ | 145 ¹⁷ | 15 ^{17–20} | 1590 ¹⁸ | 3.3 ¹⁸ | 28 ¹⁷ | 2.5 ¹⁷ | 811 ^{19–20} | 141 ^{18,20} | 3180 | 3.3 ¹⁸ | 4770 | 0.18 <i>In situ</i> , Rep. |
| <i>Macroctopus maorum</i> | Mo | Pacific Australia New Zealand | 0–50 ²¹ | 300 ⁴ | 7.0 ²¹ | 60 ²¹ | 18.0 ²¹ | 3.3 ²¹ | 0.009 ²² | 6000 ²² | – | 224 ²² | 18.0 ²¹ | 365 ²² | 5.97 St |
| <i>Pteroctopus tetricirrus</i> | Pt | Mediterranean and North Atlantic | 200–500 ²³ | 140 ²³ | 10 ^{24–25} | 90 ²⁴ | 12.0 ²³ | 8.3 ²⁶ | 0.178 | 476 ²⁵ | 122 ²³ | 365 ²³ | 12.0 ²³ | 455 | 2.16 Rep. |
| <i>Octopus bimaculoides</i> | Ob | Northeast Pacific, California | 0–20 ⁴ | 120 ²⁷ | 18 ⁴ | 46 ²⁷ | 23.0 ⁸ | 6.5 ⁸ | 0.070 ²⁷ | 597 ²⁷ | 120 ²⁷ | 370 ²⁷ | 23.0 ²⁷ | 416 | 2.45 L, F |
| <i>O. cyanea</i> | Oc | Tropical West Pacific East Africa to Hawaii | 0–25 ⁴ | 160 ⁴ | 2.8 ^{26,28} | 23 ^{26,28} | 26.0 ^{26,28} | 2.1 ²⁹ | 0.009 | 2883 ^{28,30,31} | 156 ^{30,31} | 250 ^{28–31} | 25.6 ^{28–31} | 411 | 5.09 L, F, St |
| <i>O. joubini</i> | Oj | Gulf of Mexico and Caribbean Sea | 0–15 ³² | 45 ⁴ | 3.5 ³² | 35 ³² | 25.0 ³² | 2.5 ³² | 0.003 ³² | 30 ³² | 45 ³² | 182 ³² | 25.0 ³² | 217 | 5.08 L, F |
| <i>O. maya</i> | Om | Gulf of Mexico (Yucatan; Campeche) | 0–50 ^{1,4} | 125 ^{4,33} | 17.0 ⁴ | 50 ³³ | 25.0 ³³ | 7.0 ³³ | 0.120 ^{1,33} | 1799 ^{1,33–34} | 126 ³³ | 234 ³³ | 25.0 ³³ | 284 | 4.12 L, F |
| <i>O. pallidus</i> | Op | Australia | 0–200 ^{35–40} | 150 ^{4,35} | 11.4 ^{37–38} | 136 ^{37,39} | 13.5 ^{35–40} | 6.5 ⁸ | 0.276 ³⁷ | 583 ^{35–40} | – | 246 ^{35–40} | 15.8 ^{35–37} | 437 | 3.12 L, St, Lp |
| <i>O. tetricus</i> | Ot | Australia | 0–50 ^{41,42} | 182 ⁴² | 2.6 ^{4,43} | 50 ^{41,43} | 16.0 ^{41,43} | 2.0 ^{41,43} | 0.008 | 2027 ^{41,42} | 155 ^{41,42} | 293 ^{41,42} | 19.0 ^{41–43} | 381 | 4.25 L, St |
| <i>O. vulgaris</i> | Ov | Worldwide tropical to temperate | 0–250 ^{1,4} | 200 ^{44–48} | 2.0 ^{4,8} | 30 ^{44,46} | 20.0 ^{44–48} | 2.0 ^{44,45} | 0.003 ^{44,45} | 2535 ^{44–48} | 188 ^{44–48} | 382 ^{44–48} | 20.0 ^{44–48} | 411 | 3.54 L, B, St |
| <i>Robsonella fontanians</i> | Rf | South America (Peru) to Subant. Chile | 0–200 ⁴ | 70 ^{4,49} | 5.2 ⁵⁰ | 74 ⁵¹ | 12.0 ⁵¹ | 3.0 ⁵⁰ | 0.019 | 82 ⁵⁰ | 62 ⁵⁰ | 280 ⁵¹ | 12.0 ⁵¹ | 424 ⁵¹ | 2.98 L |

(Table continued on next page)

Table 1 (continued)

| Species | Abbr. | Region | Depth range (m) | Max ML (mm) | Egg size (mm) | Emb. dev. (d) | ~Emb. Temp. (°C) | Hatch. size (mm) | Hatch. weight (g) | Mat. wt (g) | Mat. ML (mm) | Age mat. (d) | Average lifetime temp (°C) | Life span (d) | G | Method |
|----------------------------------|-------|---|------------------------|-------------------|--------------------|---------------|----------------------|-------------------|-------------------|----------------------|---------------------|-------------------|----------------------------|---------------|------|--------|
| Megaleledonidae | | | | | | | | | | | | | | | | |
| <i>Adeliedone polymorpha</i> | Ap | Antarctic–South Shetland Islands | 15–365 ⁵² | 105 ⁵³ | 16.5 ⁵³ | 1590 | 1.0 ⁵⁴ | 9.9 | 0.261 | 143 ⁵² | 73 ⁵² | 3180 | 1.0 ⁵⁴ | 4770 | 0.20 | Rep. |
| <i>Pareledone charcoti</i> | Pc | Antarctic–South Shetland Islands | 48–392 ⁵⁵ | 65 ⁵⁵ | 14.0 ⁵⁵ | 1590 | 1.0 ^{54,56} | 8.7 | 0.197 | 74 ⁵⁶ | - | 3996 | 1.0 ⁵⁴ | 3996 | 0.15 | L |
| <i>P. turqueti</i> | Ptu | Sub-Antarctic islands of South Georgia | 25–1000 ⁵⁷ | 96 ⁵³ | 19.0 ⁵³ | 1590 | 1.0 ⁵⁴ | 11.1 | 0.332 | 236 ⁵³ | 86 ⁵³ | 3180 | 1.0 ⁵⁴ | 4770 | 0.21 | Rep. |
| <i>P. aequipapillae</i> | Pa | Antarctic Peninsula | 110–465 ⁵⁵ | 70 ⁵⁵ | 14.0 ⁵⁵ | 1590 | 1.0 ⁵⁴ | 8.7 | 0.197 | 90 ⁵⁵ | 56 ⁵⁵ | 3180 | 1.0 ⁵⁴ | 4770 | 0.19 | Rep. |
| <i>Megaleledone setebos</i> | Ms | Circum-Antarctic | 32–850 ⁴ | 280 ⁴ | 41.5 ⁵⁸ | 1590 | 1.0 | 20.5 | 1.268 | 7800 ^{6,59} | 190 ^{6,59} | 1077 ⁶ | 1.0 | 2667 | 0.81 | St |
| Vampyromorpha | | | | | | | | | | | | | | | | |
| <i>Vampyroteuthis infernalis</i> | Vi | Tropical and temperate waters worldwide | 600–1500 ⁶⁰ | 210 ⁶¹ | 4.5 ⁶¹ | 731 | 4.5 ⁶¹ | 8.0 ⁶² | 0.164 | 448.0 ⁶⁰ | 102 ⁶⁰ | 1462 | 4.5 ⁶¹ | 2193 | 0.72 | Rep. |
| Bolitaenidae | | | | | | | | | | | | | | | | |
| <i>Japetella diaphana</i> | Jd | Tropical and subtropical waters worldwide | 200–1000 ⁴ | 85 ⁴ | 3.0 ⁶³ | 731 | 4.5 ⁶³ | 2.5 ⁶³ | 0.013 | - | 55 ⁶⁴ | 1462 | 4.5 ⁶³ | 2193 | - | Rep. |
| <i>Bolitaena pygmaea</i> | Bp | | 100–1400 ⁴ | 60 ⁴ | 2.0 ⁶³ | 731 | 4.5 ⁶³ | 2.0 ⁶⁵ | 0.008 | - | 45 ^{65,66} | 1462 | 4.5 ⁶³ | 2193 | - | Rep. |

octopods and those of *G. boreopacifica* are similar, we considered embryonic development time for octopod species brooding at water temperatures below 3°C to be 53 mo (sensu Robison et al. 2014). These estimates are conservative, since Antarctic octopods brood in an average temperature of 0°C (Kuehl 1988).

The hatchling size in relation to the adult size was also explored as a predictor for lifespan. We calculated the species hatchling size index (SHSI, %) as: (hatchling ML)/(maximum adult ML) × 100 (Villanueva et al. 2016), where ML is mantle length.

Age at maturity

Age at maturity was chosen as a lifespan indicator assuming that for the majority of species, growth is reduced or completely halted after spawning. With the exception of the vampire squid, all species included in this study are assumed to have one reproductive cycle and die shortly after the last eggs have been released or when the offspring hatches.

Age at size data were obtained from direct observations (e.g. laboratory or culture studies) and from estimates using indirect methods such as the interpretation of the growth increments in eye lenses, beaks and stylets, or the quantification of the lipofuscin concentration (Table 1). When data from 2 methods were available for the same species (e.g. beaks and stylets) an average value was used to estimate age.

We used the predicted embryonic development times (*D*) to estimate age at maturity for the deep-sea pelagic species *Vampyroteuthis infernalis*, *Bolitaena pygmaea* and *Japetella diaphana*, for the benthic deep-sea genus *Graneledone* (*G. boreopacifica* and *G. macrotyla*) and for the Antarctic species *Adeliedone polymorpha*, *Pareledone aequipapillae* and *P. turqueti*. The period of brooding in incirrate octopods, which brood large eggs (>10 mm) under low temperatures, may cover up to one-third of the female's life cycle (Boletzky 1987). Therefore, we estimated age at maturity as 2 times the predicted embryonic development duration (2×*D*) and the total lifespan as 3 times this period (3×*D*). For example, the vampire squid and bolitaenids were assumed to reach maturity after 4 yr (i.e. 2×*D* = 1462 d), and lifespan was calculated as 3×*D* (*D* = 731 d; lifespan = 3×731 d), which resulted in about 6 yr. These assumptions are based on the best data available, which are very limited and the lifespans proposed here will need to be validated or refuted in future studies.

To estimate lifespan for the Antarctic Charcot's octopus *Pareledone charcoti*, we used the average G (% body weight d^{-1}) values obtained from specimens that were collected in Antarctic waters and were kept in captivity for 21 mo (Daly & Peck 2000). In that study, one of the male octopods grew 10 g in 18 mo (from 64 to 74 g) and subsequently died after the release of one large spermatophore. The growth rate of that specimen was reported as 0.1% body weight d^{-1} . Assuming that G was constant since the hatching phase, the animal was about 11 yr old (i.e. 3996 d). Adult animals typically exhibit reduced growth rates compared to juveniles and this would explain such low values for G . Even though this value is a rough estimation, an octopus from the same genus and the same area was kept alive at the Alfred Wegner Institute in Bremerhaven, Germany, for about 8 yr (F. Mark unpubl. data). This lifespan also fits in the longevity expected for other cold-water octopods (Wood 2000, Robison et al. 2014). When age estimates were available in the literature, the lifespan was considered as the sum of the period to reach maturity and the embryonic development time.

Hatchling size and weight

For the Antarctic octopods *A. polymorpha*, *Megaleledone setebos* and *Pareledone* spp., data on hatchling sizes (HTs) and hatchling weights (HTw) are not available. To estimate hatchling sizes in these species, a model was fitted using data available for egg sizes (EgS) and hatchling size from 20 species used in the present study, including the pelagic deep-sea species *B. pygmaea*, *J. diaphana* and *V. infernalis*. The regression parameters were estimated by the minimization of the least squares error sum. The model that best described the relationship between egg size (EgS) and hatchling size (HTs) was expressed by a power function: $HTs = 1.086EgS^{0.788}$ ($r^2 = 0.70$, $p < 0.001$; Fig. 1). For *G. boreopacifica*, we used the egg size (15 mm) from the first observation made by Robison et al. (2014) and the hatchling size (ML = 28 mm) described by Voight & Drazen (2004). We used the size of ripe eggs (not the egg size at hatching), since the size of ripe eggs is available for more species, and can be obtained from mature pre-spawning females. Spawning eggs and egg size at hatching are still unknown for most cephalopod species, except for the unique case of *G. boreopacifica* where egg growth until hatching was observed using a submersible.

When hatchling weight was not available, the instantaneous growth rate (G) was calculated using derived data from the fitted relation between hatchling size and hatchling weight (HTw) of 10 benthic incirrate octopod species (Fig. 2). This relationship was best described by the power function: $HTw = 0.0018HTs^{2.174}$ ($r^2 = 0.93$; $p < 0.001$), where hatchling weight is in g and hatchling size is the mantle length in mm.

Regression analyses

We tested for correlations between age at maturity and growth rates, average temperature and species' depth of occurrence (Table 1). Our analyses were limited by the fact that population depth distributions/ranges are known, but not where the highest population density occurs. We therefore tested the relationship between age at maturity and growth rates with the minimum, average (midpoint) and maximum depths of the species' known distribution range.

When the conditions for independence, normality and equal variance were met, data were \log_{10} transformed to correct for non-linearity in the data and to prevent heterogeneity of variances. For the pelagic octopods *J. diaphana* and *B. pygmaea*, no information on weight at maturity was available. Therefore, these species were not included in the correlation between instantaneous growth rates (G) and environmental variables. We also analysed the relationships

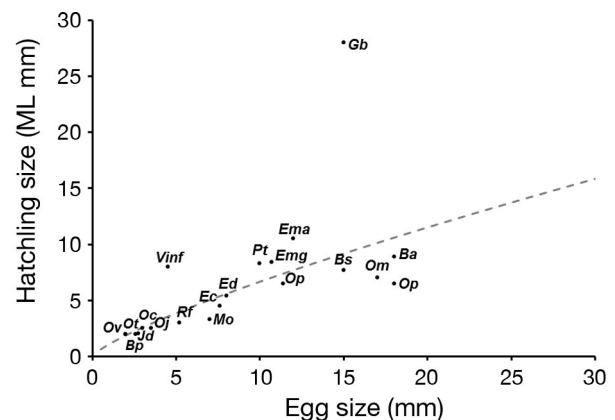


Fig. 1. Relationship between egg size (EgS) and hatchling size (HTs) for 20 species of octopods and *Vampyroteuthis infernalis*. The fitted model ($HTs = 1.086EgS^{0.788}$; $r^2 = 0.70$; $F = 42.7$, $df = 18$, $p < 0.01$) is influenced by the large hatchlings of *Graneledone boreopacifica* (*Gb*) (mantle length [ML] = 28 mm, Voight & Drazen 2004) at the top of the plot. For full species names, see Table 1

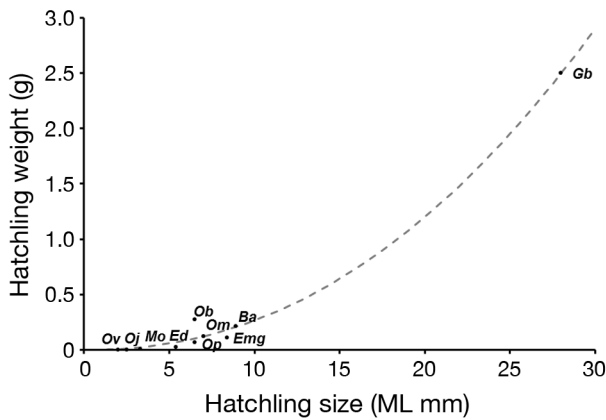


Fig. 2. Relationship between hatchling size (HTs) and hatchling weight (HTw) for 10 species of incirrate octopods. The power curve ($HTw = 0.0018HTs^{2.174}$, $r^2 = 0.93$) is influenced by the extremely large and developed hatchling of *Graneledone boreopacifica* (Gb) at the right end of the plot. For full species names, see Table 1

between age at maturity, growth rates and average lifetime temperature using the Arrhenius plot and by fitting linear regressions:

$$\ln Age \text{ or } \ln G = a - b(1000/T) \quad (3)$$

where T is the average lifetime temperature in degrees Kelvin, a is the intercept, and b is the slope of the linear regression. The Arrhenius plot aims to test how rates of biological processes function during an

increase in temperature (Peck et al. 2007, Peck 2016). All parameters were estimated using the functions lm and nls from the package 'stats' in the software R 3.5.0 (R Development Core Team 2018).

RESULTS

Life-history data in relation to environmental variables

Temperature

A strong negative relationship between average lifetime temperature and age at maturity was found (Table 2). Adjusting the power function ($Age = 3039Temp^{-0.61}$) heuristically showed that age at maturity increases one order of magnitude in species living at temperatures below $5^{\circ}C$ (Fig. 3A). Based on environmental temperature, octopods may be divided into 3 groups: species inhabiting waters between 10 and $25^{\circ}C$, pelagic deep-sea octopods and *Bathypolypus arcticus* clustering around $5^{\circ}C$, and benthic deep-sea and polar octopods living in temperatures below $3^{\circ}C$ (Fig. 3A). Since for some species age at maturity was calculated from their embryonic development time estimates (based on temperature), some of the data points are overlapping. This occurred for the pelagic species *Japetella diaphana*, *Bolitaena*

Table 2. Summary of the regression results for the comparisons. G : growth rate (%), $Temp$: average lifetime temperature ($^{\circ}C$); $Depth$ (m); Age (days); W : weight at maturity (g), $SHSI$: species hatchling size index

| Comparison | Model | Correlation (r^2) | F (df) | p |
|--|--|-----------------------|-----------|-------------------|
| Lifespan | | | | |
| Age at maturity vs Temp | $Age = 3039Temp^{-0.61}$ | 0.86 | 96.8 (23) | 0.01 |
| Age at maturity vs Depth (max.) | $\log [Age] = 1.70 + 0.46\log [Depth]$ | 0.47 | 20.3 (23) | 0.01 |
| vs Depth (average) | $\log [Age] = 1.89 + 0.49\log [Depth]$ | 0.45 | 18.7 (23) | 0.01 |
| vs Depth (min.) | $\log [Age] = 2.64 + 0.22\log [Depth]$ | 0.38 | 13.8 (23) | 0.01 |
| Growth rates | | | | |
| G vs Temperature | $G = 0.01 + 0.18Temp$ | 0.77 | 70.0 (21) | 0.01 |
| G vs Depth (max.) | $G = 7.51 - 2.2 \log [Depth]$ | 0.64 | 35.9 (21) | 0.01 |
| vs Depth (average) | $G = 6.69 - 2.08 \log [Depth]$ | 0.62 | 33.9 (21) | 0.01 |
| vs Depth (min.) | $G = 3.0 - 1.0 \log [Depth]$ | 0.44 | 16.2 (21) | 0.01 |
| Arrhenius plot relationship | | | | |
| Age at maturity vs Temp | $\ln Age = 5.97 - 3.42 (1000/T)$ | 0.30 | 5.6 (14) | 0.05 |
| G vs Temp | $\ln G = 17.95 - 4.90 (1000/T)$ | 0.47 | 11.4 (14) | 0.01 |
| Size vs lifespan - Do large octopods live longer? | | | | |
| Age at maturity vs weight at maturity | $\log [Age] = 3.22 - 0.15 \log_{10} [W]$ | 0.06 | 1.3 (21) | 0.27 ^a |
| Do species with large hatchlings live longer? | | | | |
| Age at maturity vs SHSI | $Age = 26.45 + 177.69 SHSI$ | 0.52 | 24.2 (23) | 0.01 |

^aAccept H_0 slope = 0, i.e. correlation not significant

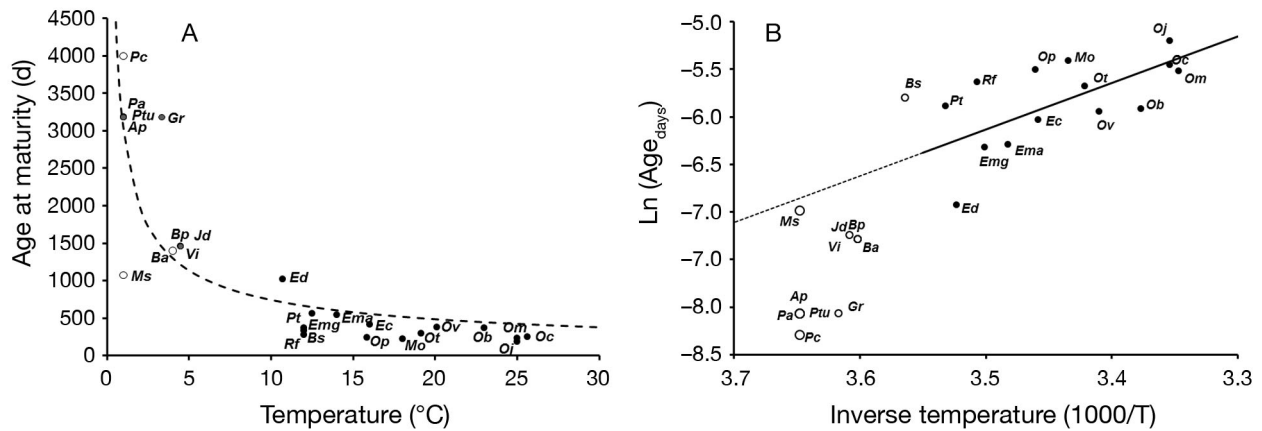


Fig. 3. Relationship between age at maturity and habitat temperature for 25 octopod species and *Vampyroteuthis infernalis*. (A) The dashed line shows the predicted model ($Age = 3039 Temp^{-0.61}$, $r^2 = 0.86$). White (open) circles represent deep-sea and Antarctic octopods ($<5^\circ C$), black circles represent temperate and tropical species ($>5^\circ C$). Grey circles indicate overlapped data points. (B) Arrhenius plot of the data used in (A). Solid line is the relationship for species living in temperatures above $5^\circ C$ ($Ln Age = 5.97 - 3.42(1000/T)$; $r^2 = 0.30$, $F = 5.58$, $df = 14$, $p < 0.05$). The dashed line represents an extension of the relationship to temperatures below $5^\circ C$. For full species names, see Table 1

pygmaea and *Vampyroteuthis infernalis* ($4.5^\circ C$); the benthic Antarctic species *Adelieledone polymorpha*, *Pareledone aequipapillae* and *P. turqueti* ($1^\circ C$), and for *Graneledone* spp. (see Table 1).

The Arrhenius plot for the same data revealed that temperate and tropical species follow a linear relationship with the inverse temperature values (Fig. 3B). These species are distributed along the regression line, while cold water species ($<5^\circ C$) aggregate far from the extrapolated fitted model ($Ln Age = 5.97 - 3.42(1000/T)$; $r^2 = 0.30$, $F = 5.58$, $df = 14$, $p < 0.05$). This pattern suggests that age at maturity in cold-water octopods cannot be solely predicted by environmental temperature. The values show that the time to reach maturity is delayed beyond the predicted effects of temperature on biological systems. While temperate and tropical species typically reach maturity in less than 2 yr, deep-sea species are predicted to mature after 4 yr, and Antarctic species inhabiting waters around $0^\circ C$ after 8 yr of age (Fig. 3A).

While lifespan tends to increase as habitat temperatures decrease, the growth rates (G) are positively correlated with temperature, with species growing faster at temperatures between 15 and $25^\circ C$ (Fig. 4A). An Arrhenius plot of the instantaneous relative growth rates showed a strong linear relationship for tropical and temperate species (Fig. 4B). As observed in the age at maturity plot, the estimated growth rates for polar and deep-sea species are much lower than the extrapolation of the relationship for temperate and tropical species ($Ln G = 17.95 - 4.90(1000/T)$; $r^2 = 0.47$, $F = 11.4$, $df = 14$, $p < 0.005$).

Depth of occurrence

The correlations between depth of occurrence (minimum, midpoint and maximum), age at maturity and growth rates were examined (Table 2). Although the regressions have non-zero slopes, the data were highly scattered around the fitted models (Fig. 5). The model which best described the relationship uses the maximum depths of occurrence, and it predicts ages at maturity close to the observed data (age estimated from increments in beaks, stylets and eye lenses) for species inhabiting shelf and slope depths shallower than 100 m (Fig. 5). Five of the 7 *Octopus* spp. and the Maori octopus *Macroctopus maorum* were placed close to the regression line, maturing before 2 yr. The long-lived Antarctic species, typically distributed over depths shallower than 500 m, were outliers and biased the correlation. The environmental conditions (e.g. temperature, hydrostatic pressure) for the Antarctic shelf and slope species can be similar to those experienced by cephalopods inhabiting the deep sea (>500 m) (Clarke 2003). The number of increments in the stylets of the deep-sea octopus *Bathypolypus sponsalis*, which occurs in water depths between 900 and 1250 m in the North-east Atlantic region, suggests that its lifespan is less than 1 yr (Barratt & Allcock 2010). All other species inhabiting water depths deeper than 1000 m were estimated to reach maturity after 3 yr (Fig. 5).

The regression analysis between instantaneous growth rates and maximum depth of occurrence shows again that species which occur in deep waters (>500 m), exhibited growth rates similar to species

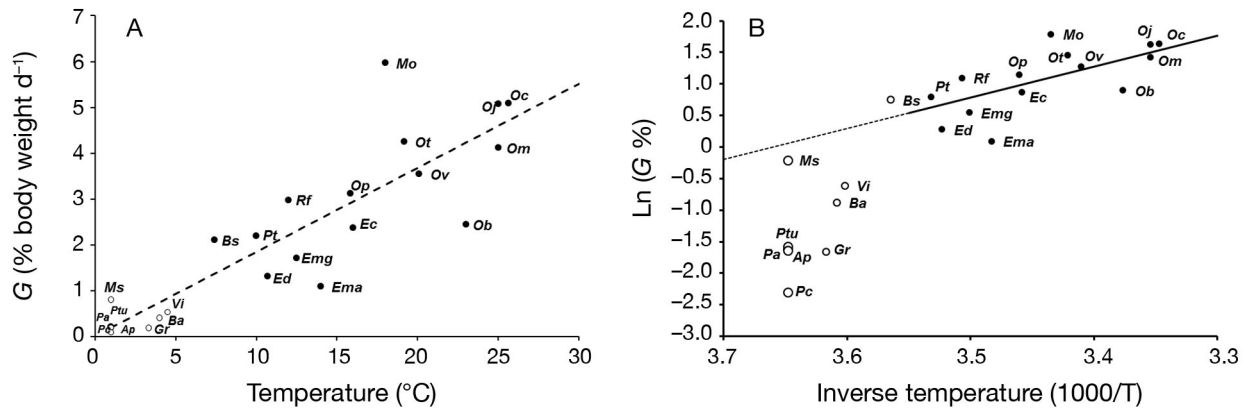


Fig. 4. Growth rates and average lifetime habitat temperatures. (A) Instantaneous growth rate G (% body weight d^{-1}) versus average habitat temperature of 24 octopod species (excluding bolitaenids). White circles represent deep-sea and Antarctic octopods ($<5^{\circ}C$), black circles represent temperate and tropical species ($>5^{\circ}C$). The dashed line is the adjusted linear regression [$G = 0.01 + 0.18Temp$, $r^2 = 0.77$]. (B) Arrhenius plot from same data. Solid line is the relationship for species living above $5^{\circ}C$ ($Ln G = 17.95 - 4.90(1000/T)$; $r^2 = 0.47$, $F = 11.4$, $df = 14$, $p < 0.01$). The dashed line represents an extension of the relationship to temperatures below $5^{\circ}C$. For full species names, see Table 1

living in polar regions ($G < 2\%$ body weight d^{-1}) (Fig. 6). For subtropical and temperate species inhabiting waters shallower than 500 m, growth rates ranged from 2.4 to 6% body weight d^{-1} . Other shallow-water octopods exhibited intermediate growth rates ranging between 4 and 5% (Fig. 6). Of the species that occurred deeper than 1000 m, *B. sponsalis* presented the fastest growth rates ($G = 2.1\%$), while the deep-sea genus *Graneledone* (*G. boreopacifica* and *G. macrotyla*), which can occur down to 3000 m, exhibited very low growth rates ($G = 0.2\%$).

Body weight and age at maturity

Our analyses covered a wide range in body sizes. The weight at maturity of the largest octopod species (*Enteroctopus dofleini*) was 500 times larger than the body weight of the smallest octopus, the Atlantic pygmy octopus *Octopus joubini* (Table 1). The slope of the correlation between age and weight at maturity ($\text{Log}[\text{Age}] = 3.22 - 0.15\text{Log}[W]$; $r^2 = 0.06$; $p > 0.27$) did not differ from 0 (Table 2). In our data set, *E. dofleini*, *Megaleledone setebos* and *Macroctopus*

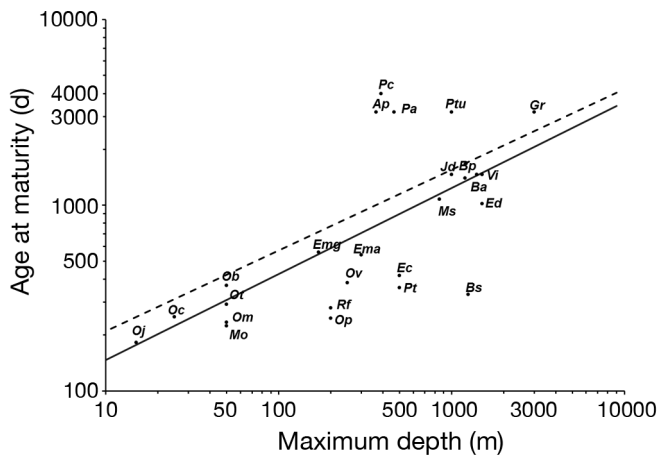


Fig. 5. Age at maturity related to maximum depth of occurrence for 26 octopod species, including *Vampyroteuthis infernalis*. Tick marks are displayed on a logarithmic scale. The continuous line shows the adjusted linear model ($\text{Log}[\text{Age}] = 1.70 + 0.46\text{Log}[\text{Depth}]$, $r^2 = 0.47$). The dashed line represents the same relationship but using average depths. For full species names, see Table 1

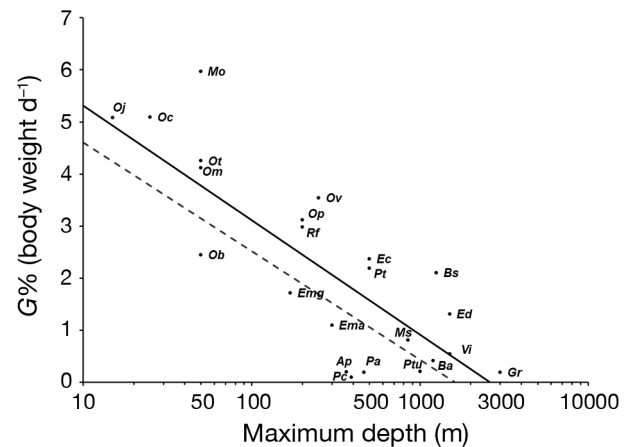


Fig. 6. Relationship between growth rates (G) and depth (m) for 24 octopod species. Tick marks are displayed on a logarithmic scale. Linear regression between growth rate G (% body weight d^{-1}) and maximum depth of occurrence for ($G = 7.98 - 2.37\text{Log}[\text{Depth}]$, $r^2 = 0.68$). The continuous line represents the relationship using maximum depth of occurrence, while the dashed line represents the relationship using average depths. For full species names, see Table 1

maorum were the only species that weighed on average more than 5000 g at maturity, and only *M. maorum* attains this body weight in less than 1 yr. The majority of the octopods with expected longevities exceeding 3 yr weighed less than 1000 g at maturity.

DISCUSSION

Growth rates, size at maturity and temperature

In this study we tested the hypothesis that lifespan in octopods is inversely correlated with temperature and depth distribution. We used published data from 26 species of octopods inhabiting water temperatures from -2 to 25°C , and found that species inhabiting colder waters have increased lifespans compared to warm-water species. The data analysis illustrates the diversity of life history strategies, even within the same order of cephalopods, and a tight coupling between longevity and environment. For ectotherms such as cephalopods, temperature controls the time required for embryonic development and maturation, which can consequently increase longevity (Table 2). Our results suggest that octopods living in polar and deep-sea habitats ($<5^{\circ}\text{C}$) reach maturity after 3 yr (~ 1000 d, Fig. 3A). The total lifespan of species for which the females brood the eggs after spawning can be considerably longer. The duration of the brooding time largely depends on the temperature at which the eggs have to develop.

Wood & O'Dor (2000) found a positive correlation between size and age at maturity. They noted that octopods typically mature at lower weights and have reduced growth rates compared to squids and cuttlefish. We did not find a significant correlation between age and weight at maturity (Table 2). The absence of such a correlation indicates that, at least for our data set, the octopods' body weight cannot predict age. This may be attributed to the fact that we included few large species, and many of the small species lack validation of the estimated lifespan (e.g. Antarctic octopods). For example, annual species of the genus *Octopus* reach maturity at an average weight of 2 kg within 1 yr, while most of the smaller Antarctic and deep-sea pelagic species (<1 kg) are predicted to reach maturity after 3 yr. Based on the available literature, the giant Antarctic octopus *Megaleledone setebos* (~ 8 kg) and the giant Pacific octopus *Enteroctopus dofleini* (16 kg) are estimated to reach maturity after 3 yr. However, *M. setebos* can grow up to 25 kg (Piatkowski et al. 2003) and *E. dofleini* was reported to reach 71 kg (Cosgrove &

McDaniel 2009), suggesting that these species can grow faster or live longer. Another large octopus which inhabits the cold waters of the meso- and bathypelagic zone is the benthopelagic giant deep-sea octopus *Haliphron atlanticus*. Females of this species brood their eggs, can grow up to 75 kg (O'Shea 2004) and prey on gelatinous zooplankton (Hoving & Haddock 2017). Although there are no age estimates for *H. atlanticus*, the lifespan may be comparable to that observed in *E. dofleini* or *M. setebos*.

Intermediate-size octopod species from tropical and temperate waters are fast-growing, with growth rates of 3–6% body weight d^{-1} (Forsythe & Van Heukelem 1987, Iglesias et al. 2014). However, those species can exhibit high intra-specific variation in growth, with animals that hatch with similar sizes (ML = 2–3 mm) reaching very different maturity sizes under the same temperature regimes. This is due to highly flexible life history strategies where size-at-maturity depends on genetics, environmental temperature, food availability and potentially a combination of these factors. Similar trends have been published for squids (e.g. Hoving et al. 2013, Arkhipkin et al. 2015, Takahara et al. 2017). Octopods from cold waters mature late and are typically of small to medium size, with the exceptions of *M. setebos* and *E. dofleini*. For *Bathypolypus sponsalis*, a small species usually inhabiting waters around 12°C (Quetglas et al. 2001), the predicted daily growth rate of 2% is 4 times higher than that estimated for *B. arcticus* ($G = 0.41\%$) living at average temperatures of 7°C . This illustrates the interspecific variation in growth rates of congeneric octopods, but the observed differences in growth rates may not solely be driven by environmental differences, but also by uncertainties related to age estimation. Age estimations based on the quantification of stylet increments in *B. sponsalis* suggest an annual lifespan with fast growth rates (2%); however, the periodicity of stylet increment deposition for this species is not validated (Barratt & Allcock 2010). Lower growth rates were measured for *B. arcticus* in experimental studies (Wood 2000, Wood & O'Dor 2000). The daily growth rate of 0.4% that was measured for *B. arcticus* reared at 7°C corresponds with a growth rate of 0.1% for the Antarctic octopod *Pareledone charcoti* kept at 0°C (Daly & Peck 2000), and fits in the life history trends observed in our study. For all octopods inhabiting water temperatures lower than 10°C , the instantaneous growth rates were less than 1%. The polar species *P. charcoti* ($G = 0.1\%$) grows 50 times slower than the similar-sized tropical pygmy octopus *O. joubini* ($G = 5\%$).

From an ecophysiological perspective, temperature seems to be the most important physical environmental factor affecting growth performance of ectotherms (Atkinson 1996), a trend that was confirmed in our analysis. For cephalopods, lower temperatures result in reduced growth rates and can increase size-dependent mortality by predation (Wood 2000). At higher temperatures, animals can grow fast, potentially to avoid predators, but mortality due to starvation will tend to increase if food is scarce and growth rates can be reduced if the temperatures surpass the optimum tolerance values (Rodhouse et al. 2014). The Arrhenius plots that test how rates of biological processes change during a temperature increase revealed that the effects of temperature on age at maturity and growth rates for polar and deep-sea species are slowed beyond the predicted relationship fitted for temperate and tropical species (Figs. 3B & 4B). The results presented here for octopods are congruent with those found for brooding in gastropod molluscs and growth rates in echinoids (Peck et al. 2007, Peck 2016). Evidence suggests that the low water temperatures of polar and deep-sea regions may exert a constraint on protein synthesis, and this may delay the processes involved in embryonic development and growth (Peck 2016).

Octopod age estimates derived from embryonic duration

Sizes of eggs and hatchlings are significant predictors of lifespan in cold-water octopods. The relationship between SHSI and the maximum adult size was positive, indicating that longer lifespans are expected for species producing large eggs and hatchlings with mantle lengths beyond 10–15% of the adult's size (Table 2). Among the incirrate octopods, egg sizes vary from 0.8 mm in the pelagic *Argonauta* spp. to more than 40 mm in the giant Antarctic octopus *M. setebos* (Boletzky 1992, Allcock et al. 2003). In all incirrate octopod species, egg brooding covers the embryonic development partially or completely. We used this aspect of the life cycle to estimate the longevity of some octopod species based on Boletzky's (1987) hypothesis which states that embryonic development in cephalopods may vary from a few percent to as much as one-third of the lifespan. Following this hypothesis, we conservatively assumed that brooding time in cold-water octopods is one-third of the total lifespan (Robison et al. 2014). Although this hypothesis remains to be tested, our calculations suggest a brooding period between 25

and 35% of the age at maturity for 7 octopus species (Table 1), corresponding well with Boletzky's assumptions. For the temperate species *Octopus pallidus*, which produces some of the biggest eggs in this genus, embryonic development can last up to 50% of the estimated age at maturity. Species living at temperatures above 15°C were estimated to have shorter brooding times lasting less than 20% of the age at maturity.

Following the above trends we may carefully infer brooding times for other cephalopod species. Vampire squid spawn batches of 10–100 eggs, where the spawning of each batch is separated by a gonadal resting phase (Hoving et al. 2015). Unlike incirrates, vampire squid release individual eggs of 4–5 mm that are believed to drift in the water column between 600 and 1500 m (Pickford 1949, Hoving et al. 2015), but spawning vampire squids have never been observed in their natural habitat. Gonatid and bathyteuthid squids spawn eggs of similar dimensions (>3 mm) as vampire squid do, and brood their egg masses in their arm crown (Seibel et al. 2005, Bush et al. 2012). Seibel et al. (2005) estimated that females of the squid *Gonatus onyx* brood eggs up to 9 mo in water temperatures of 1.7–3.0°C in the bathypelagic zone. Oogenesis in vampire squid takes place between 2 and 7°C, and the hatchling size is about 8 mm ML (Young & Vecchione 1999). This means that after spawning, the egg nearly doubles in size from 4.5 mm to ~8.0 mm before hatching occurs. Based on the egg development model in Robison et al. (2014), the development time of vampire squid eggs is approximately 2 yr. Pelagic incirrate bolidae live and brood eggs at depths similar to those at which vampire squids occur (Young 1972). By brooding, the female provides protection to the eggs and is able to control under which conditions (depth, temperature, salinity, and oxygen concentration) the eggs will develop, which may reduce offspring mortality. By being released into the water column, vampire squid eggs may suffer relatively high mortality rates, e.g. as a result of predation, fouling and hypoxia. On the other hand, the relatively high potential fecundity of up to 20 000 eggs (Hoving et al. 2015) may compensate for high mortality.

The environmental conditions under which the embryos of incirrate octopods develop may influence the hatchlings' early mode of life (benthic or pelagic) (Villanueva et al. 2016) and likely the life-cycle duration (Wood 2000, Robison et al. 2014). Although egg development times are extremely long for certain octopod species inhabiting water temperatures below 5°C (e.g. *G. boreopacifica*, 53 mo at 3°C; Robison

et al. 2014, Purser et al. 2016), such long development times are not uncommon for other marine invertebrates at high latitudes (Hain & Arnaud 1992, Peck et al. 2006). Hain & Arnaud (1992) investigated the reproductive strategy of 66 molluscan species from the Weddell Sea (Antarctica), and found that the intracapsular development of the gastropod species *Torellia mirabilis* and *Trophon scotianus* lasted up to 25 mo, a strategy that resulted in well-developed benthic juveniles. The authors concluded that gastropods from the Weddell Sea produce eggs that are 4 times larger and that the embryonic development can be up to 30 times longer than in related temperate gastropods (Hain & Arnaud 1992). The large egg cases of the Antarctic nudibranch *Bathydoris hodgsoni* are estimated to require up to 10 yr of embryonic development, which result in one of the largest mollusc hatchlings known to date (Moles et al. 2017). Investigations on the reproductive biology of various different taxa (Annelida, Arthropoda and Mollusca) inhabiting the deep seafloor revealed that brooding, large egg sizes and increased longevity are common specializations of the fauna living in these environments (Young 2003), which agrees with our results discussed here. Overall it seems evident that egg and larval development in Antarctic marine ectotherms is considerably slower than in temperate species (Peck 2002, Peck et al. 2006). This phenomenon is known as Thorson's rule (Mileikovsky 1971), which states that egg sizes and embryonic development duration in benthic ectotherms is positively correlated with latitude and depth. Thorson's Rule has been tested and confirmed for several taxa, including octopods (Ibáñez et al. 2018).

The methods presented in this study are limited by the high intraspecific variability of sizes at maturity in cephalopods, temperature regimes and depth distribution ranges, which all may confound the analysis. Another limitation of the method used here is that the life history traits of the analysed species may not be phylogenetically independent and require independent contrasts to eliminate phylogenetic bias (Harvey & Pagel 1991). Although the phylogenetic comparative methods are assumed as the most statistically correct, they also can present drawbacks. Cornwell & Nakagawa (2017) warned that inferring life history traits and environmental conditions of ancestral forms can induce more uncertainties in regression analysis in certain cases. Three main sources of uncertainty are pointed out by the authors: (1) wrong phylogenetic tree reconstruction based on limited data—where misplacement of species can result in wrong distances of the tree branches and the values in the tree nodes.

This is particularly important for our dataset since the phylogeny of the Octopoda is still not fully resolved (Strugnell et al. 2014); (2) trait uncertainty—traits may not be representative for the species as a whole, and frequently they are obtained from few observations or single populations; and (3) model uncertainty—the Brownian motion model of evolution may not apply in all cases. Due to these uncertainties, we consider further evolutionary analyses of our examined parameters beyond the scope of this paper since first more basic data on life history and octopod phylogeny is required.

Nevertheless, the theoretical approach using representatives of the order Octopoda living in a great variety of environments provides the first trends on how habitat characteristics may impact the life cycle of cold-water octopods, allowing the development of hypotheses and research questions for future research. New research should focus on obtaining life-history information (growth rate, age at maturity, longevity, spawning strategy) on abundant cold-water octopods which can be integrated in the models developed here. The advancement of deep-sea observational technology to study cephalopods in their natural habitat will further allow us to obtain new information on cephalopod biology, life cycles and behaviour (Hoving et al. 2014). The investigation of life cycle length and growth of cephalopods inhabiting cold water environments becomes important to evaluate how resilient these species can be against ongoing and future habitat disturbances (e.g. deep-sea mining, fisheries and predator removal).

Acknowledgements. We thank Dr. Felix Mark for the information about survival time of *Pareledone charcoti* in captivity. R.S. was funded by the National Council for Scientific and Technological Development (CNPq), Brazil (grant 201585/2015-4). H.J.T.H. received financial support from a grant (CP1218) of the Cluster of Excellence 80 'The Future Ocean', which is funded within the framework of the Excellence Initiative by the Deutsche Forschungsgemeinschaft (DFG) on behalf of the German federal and state governments.

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Rostock, Germany

Submitted: March 6, 2018; Accepted: September 5, 2018
Proofs received from author(s): October 6, 2018