CEPHALOPOD BIOLOGY AND EVOLUTION

Evolution of development type in benthic octopuses: holobenthic or pelago-benthic ancestor?

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Abstract Octopuses of the family Octopodidae are singular among cephalopods in their reproductive behavior, showing two major reproductive strategies: the first is the production of few and large eggs resulting in well-developed benthic hatchlings (holobenthic life history); the second strategy is the production of numerous small eggs resulting in free-swimming planktonic hatchlings (pelago-benthic life history). Here, we utilize a Bayesian-based phylogenetic comparative method using a robust molecular phylogeny of 59 octopus species to reconstruct the ancestral states of development type in benthic octopuses, through the estimation of the most recent common ancestors and the rate of gain and loss in complexity (i.e., planktonic larvae) during the evolution. We found a high probability that a free-swimming hatchling was the ancestral state in benthic octopuses, and a similar rate of gain and loss of planktonic larvae through evolution. These results suggest that in benthic octopuses the holobenthic strategy has evolved from an ancestral pelago-benthic life history. During evolution, the paralarval stage was reduced to well-developed benthic hatchlings, which supports a "larva-first" hypothesis. We propose that the origin of the holobenthic life history in benthic octopuses is associated with colonization of cold and deep sea waters.

Keywords Life history evolution · Phylogenetics · Octopodidae · Comparative method · Dollo's law

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Introduction

Life history theory is mainly based on optimization models used to explain variation in size at birth, growth rates, age and size at maturity, clutch size and reproductive investment, as well as mortality rates and lifespan (Stearns, 1992; Roff, 2002). Optimization models predict that life history traits are adapted to local environmental conditions, not considering an historical explanation (Stearns, 1992). In the case of

the evolution of life history traits, the use of phylogenetic comparative methods can help estimate whether the pattern is attributable to the history of the lineages or adaptation processes (Stearns, 1992; Stearns & Hoekstra, 2005). To analyze comparative data among species and correctly infer evolutionary patterns, the phylogenetic history of the study group should be considered (Felsenstein, 1985; Harvey & Pagel, 1991). Until now, most comparative studies of life history evolution in marine invertebrates have detected a parallel evolution pattern, based on multiple switches observed in closely related taxa (McHugh & Rouse, 1998; Duda & Palumbi, 1999; Hart, 2000; Byrne, 2006; Collin et al., 2007; Keever & Hart, 2008; Kerr et al., 2011), while few studies have found strong phylogenetic signals that explain the distribution of life history traits in taxonomic groups (e.g., Jeffery et al., 2003).

Benthic octopuses of the family Octopodidae comprise over 200 species that inhabit all oceans of the world including tropical, temperate and polar regions, from the intertidal to 4,000 m depth (Nesis, 2003). These animals, of which life history trait evolution is poorly understood, are characterized by fast growth, early maturity, high fertility, and short life span (Boyle & Boletzky, 1996). Post-mating females care for their eggs until hatching, and then die (Hanlon & Messenger, 1996). Male octopuses package sperm into spermatophores which they transfer to females via a modified arm, the hectocotylus (Wodinsky, 2008). Both sexes are promiscuous and sperm competition in octopuses has been frequently described (Hanlon & Messenger, 1996; Voight, 2009). Benthic octopuses exhibit two main reproductive strategies: The first corresponds to the production of few large eggs resulting in well-developed benthic hatchlings (Villanueva & Norman, 2008), and a holobenthic life history; the second strategy consists of the production of numerous small eggs hatching into free-swimming planktonic paralarvae (Villanueva & Norman, 2008). The term paralarvae is an ecological term to define a young cephalopod that inhabits the epipelagic area in the pelagic zone (Young & Harman, 1988), and consequently this second strategy implies a benthic–pelagic habitat alternation during ontogeny. The origin of this pelago-benthic life history requires knowledge of the ancestral state, and two hypotheses dominate current opinion about the ancestral life cycle of bilaterians: the "larva-first" and the "intercalation"

hypotheses (Nielsen, 2009; Page, 2009). Until recently, the larva-first hypothesis was preeminent; however, the intercalation hypothesis may be a better model for interpreting the development of mollusks and other lophotrochozoans (Page, 2009). This hypothesis proposes that larval stages (planktotrophic or lecithotrophic) have evolved as specializations from the ancestral, direct life cycle (Nielsen, 2009). Consequently, the "intercalation" hypothesis suggests that the two contrasting life strategies in benthic octopuses went from benthic-hatching larvae to the free-swimming planktonic larvae directionally during evolution. If this (intercalation) hypothesis is true, the evolution of life history in benthic octopuses has occurred by increasing the complexity of the life cycle in an irreversible way, given that the re-evolution of complex traits has been considered unlikely (e.g., Dollo's law, Gould, 1970). Boletzky (1992) proposed that the pelagic life style was ancestral, because most incirrate octopods are pelagic (e.g., *Argonauta*, *Ocythoe*, *Japetella*, *Tremoctopus*), and this phase probably has been eliminated in bentho-pelagic species of benthic family Octopodidae.

In this study, we evaluate these hypotheses of evolution of reproductive strategies in benthic octopuses, assessing the evolutionary pattern of the reproductive life history strategies, through estimation of the most recent common ancestors and the rate of gain and loss complexity (i.e., planktonic larvae) in a phylogenetic framework. For this purpose, we constructed a molecular phylogeny of octopuses and used phylogenetic comparative methods to reconstruct ancestral states of development type in the phylogenetic tree.

Materials and methods

We used 59 octopus species for which information on holobenthic and pelago-benthic reproductive strategy was obtained from an extensive review of the literature (Sweeney et al., 1992; Norman 2000; Villanueva & Norman, 2008; and unpublished data of the authors). For phylogenetic reconstruction purposes, we retrieved sequences of rRNA (16S) and cytochrome oxidase III (COIII) for 50 of these species from Genbank and we sequenced the other 9 (Table 1).

Total DNA was extracted from 9 species following the saline extraction protocol (Aljanabi & Martinez,

Table 1 Species studied and information about the sequences

Species	16S rRNA	COIII
Vampyroteuthis infernalis	DQ280043	GU288521
Abdopus aculeatus	GQ900717	AB573185
Amphioctopus aegina	FJ800371	AB573189
Pareledone aequipapillae	EF102201	EF102160
Pareledone albimaculata	EF102203	EF102162
Pareledone aurata	EF102199	EF102158
Octopus berrima	AY545105	AJ628218
Octopus bimaculoides[a]	KC792308	KC792299
Graneledone boreopacifica	EU071435	EU071460
Octopus californicus	HM572164	HM572187
Pareledone charcoti	EF102197	EF102156
Eledone cirrhosa[b]	KC792309	KC792300
Octopus conispadiceus	AB191116	AB573222
Pareledone cornuta	EF102207	EF102165
Octopus cyanea	GQ900721	AB573224
Enteroctopus dofleini	AY545109	AB573211
Muusoctopus eureka	HM572155	HM572191
Amphioctopus fangsiao	AJ252747	AB573188
Hapalochlaena fasciata	GQ900711	AB573212
Pareledone felix	EF102205	EF102163
Robsonella fontaniana[c]	KC792310	KC792301
Thaumeledone gunteri	AF299266	EU148470
Vulcanoctopus hydrothermalis	HM572163	HM572200
Cistopus indicus	AJ252744	AB573210
Octopus insularis	AJ390315	AJ012123
Amphioctopus kagoshimensis	AJ311108	AB573193
Octopus kaurna	AY545106	AJ628227
Octopus laqueus	AB302177	AB573215
Muusoctopus longibrachus[c]	KC792311	KC792302
Callistoctopus luteus	GQ900707	AB573208
Hapalochlaena maculosa	AY545107	AB573214
Macroctopus maorum	AJ311110	AJ628231
Amphioctopus marginatus	GQ900709	AB573195
Octopus maya[a]	KC792312	KC792303
Enteroctopus megalocyathus[c]	KC792314	KC792304
Octopus mimus[c]	KC792313	KC792305
Callistoctopus minor	AB191110	AB573201
Amphioctopus mototi	AJ252752	AJ628233
Muusoctopus normani	HM572153	HM572188
Octopus oliveri	GQ900712	AB573226
Muusoctopus oregonensis	FJ603543	FJ603538
Callistoctopus ornatus	GQ900705	AB573209
Octopus pallidus	AJ252754	AJ628236
Pareledone panchroma	EF102214	EF102172

Table 1 continued

Species	16S rRNA	COIII
Octopus parvus	EF102211	AB573216
Thaumeledone peninsulae	EU148474	EU071458
Adelieledone piatkwoski	EU071431	EU071455
Adelieledone polymorpha	EF102194	EF102153
Muusoctopus rigbyae	FJ428011	FJ603528
Octopus rubescens[a]	AJ252755	KC792306
Sasakiopus salebrosus	GQ900705	GQ226028
Octopus salutii	AJ390323	AJ250484
Pareledone serperastra	EF102209	EF102167
Megaleledone setebos	EF102195	EF102154
Bathypolypus sponsalis	EF016338	FJ603530
Pareledone subtilis	EF102210	EF102169
Scaeurgus unicirrhus	AJ390324	AJ012129
Octopus variabilis	FJ800368	FJ800369
Graneledone verrucosa	AY545111	EU071462
Octopus vulgaris[b]	KC792315	KC792307

V. infernalis was used as outgroup

[a] Mexico

[b] France

[c] Chile

1997). PCR amplifications were carried out using for each sample 2.5 μl of 10× Taq DNA polymerase buffer, 2.0 μl of dNTPs (2.5 mM), 1 and 1.5 μl MgCl₂ (50 mM) for 16S and COIII respectively, 0.3 μl (16S) and 0.5 μl (COIII) Platinum®Taq DNA polymerase (Invitrogen) and 0.5 μl of each primer (CO3F and CO3R for COIII and 0.5 μl of 16SF and 16SR primers for 16S rRNA (all primers were used at a final concentration of 10 pmol) (see primers in Allcock et al., 2008). After an initial denaturation (3 min at 94°C), the reaction mixtures were subjected to 35 cycles of 94°C (40 s), 40°C (40 s) for COIII and 55°C (40 s) for 16S rRNA, and 72°C (60 s) followed by a final extension at 72°C (10 min), using a thermal cycler. PCR products were sent to Macrogen Inc. for sequencing. Sequences were aligned in the software Clustal W, implemented in MEGA 5.0 (Tamura et al., 2011).

Phylogenetic reconstruction was inferred from a matrix including the concatenated dataset (CO-III + 16S rRNA). To evaluate evolutionary relationships, we used a phylogenetic hypothesis based on a Bayesian framework using Mr. Bayes v3.2 (Ronquist et al., 2012) to obtain a sample of trees. For this

analysis, we used four models of branch length priors (unconstrained: uniform, unconstrained: exponential, clock: uniform, clock: birth–death) and compared these models with Bayes Factor (BF, Kass & Raferty,

1995) in the software Tracer v1.5 (Rambaut & Drummond, 2009). These prior settings gave us a better estimation of phylogenetic trees because branch length priors influence the posterior probability (PP) of
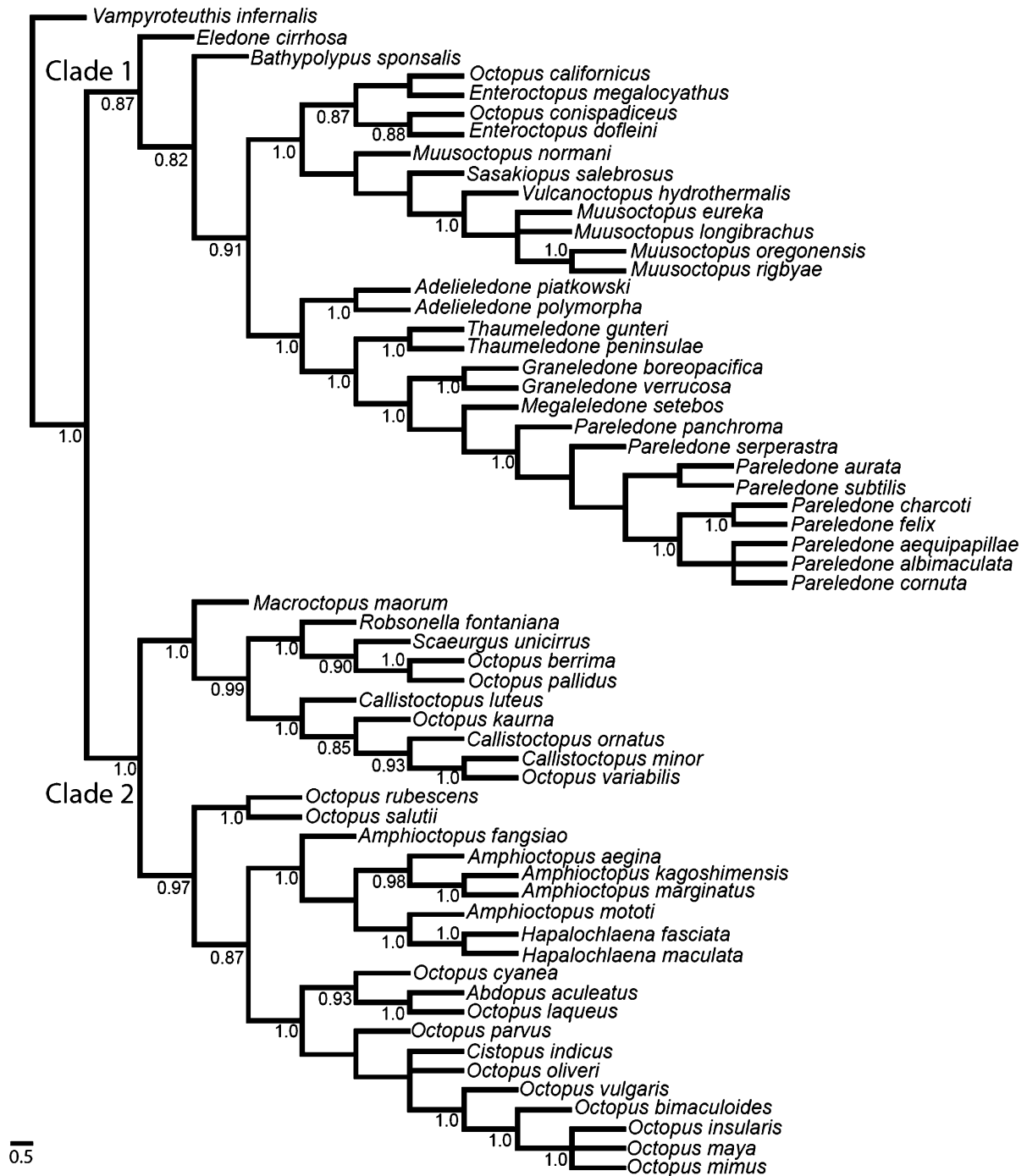

Fig. 1 The majority rule consensus tree of 4,500 phylogenetic trees obtained from the Bayesian analysis in Mr. Bayes

Table 2 Median values of PP in bayesian phylogenetic ancestral reconstruction of the development type in the benthic octopuses

	PP (0) pelago-benthic	PP (1) holobenthic
Root	0.72 (0.64–0.79)	0.28 (0.21–0.36)
Clade 1	0.42 (0.28–0.48)	0.58 (0.52–0.72)
Clade 2	0.92 (0.91–0.99)	0.08 (0.01–0.09)
Clade 3	0.85 (0.78–0.96)	0.15 (0.04–0.22)
Clade 4	0.93 (0.92–0.99)	0.07 (0.01–0.07)
Clade 5	0.10 (0.06–0.10)	0.90 (0.89–0.99)
Clade 6	0.04 (0.01–0.05)	0.96 (0.95–0.99)

In parenthesis are the HPD (95%). Clades as in Fig. 2

phylogenies (Yang & Rannala, 2005). The best model of the concatenated data set (COIII + 16S rRNA) selected by jModeltest v 2.1.1 (Darriba et al., 2012) was TrN + I + G ($-$lnL = 13641.4, BIC = 28146.8). This model is not implemented in Mr. Bayes and for this reason, we used the most complex model (GTR + Γ + I) to reduce the chance that the method would concentrate too much probability in too few trees (Huelsenbeck & Rannala, 2004). We ran four chains with 5,000,000 iterations of MCMCMC (Metropolis Coupling Monte Carlo Markov Chains) sampling parameters and trees every 1,000 iterations. This analysis was performed at least twice to check the convergence of the chains. We rooted the trees using *Vampyroteuthis infernalis* (Vampyromorpha) as outgroup, previously described as the sister group of the Octopodiformes (Young & Vecchione, 1996; Young et al., 1998; Carlini et al., 2001). Finally, 500 first trees (10%) were burned in Mr Bayes after checking the PP of trees in BayesTrees v1.3 (Meade, 2011) and the likelihood trace in Tracer.

Evolution between holobenthic and pelago-benthic life history was evaluated using the multistate model of the software BayesTraits in a Bayesian framework (Pagel et al., 2004), estimating the rate of gain (q01) and loss (q10) of the pelago-benthic life style in each branch of the 500 phylogenetic random trees selected from the sample of trees of Mr Bayes using the software BayesTrees. We used exponential hyperprior for q10 and q01. In these analyses, we calculated the most recent common ancestors assessing the PP of each reproductive strategy (P(0) = free-swimming planktonic, P(1) = benthic hatchling) for the basal
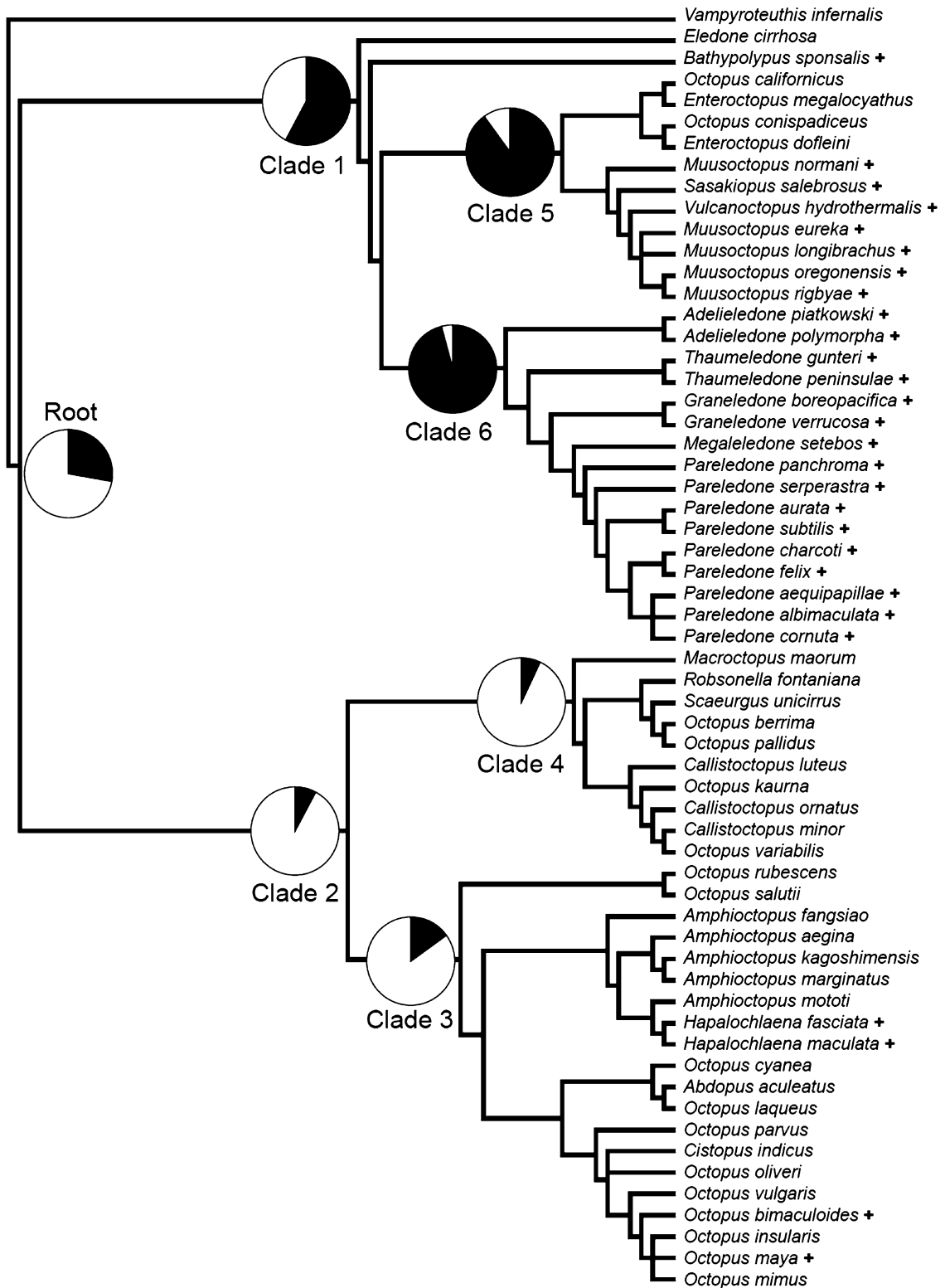
nodes of the trees. In the Bayesian analysis of character evolution, we ran 10,000,000 iterations by means of MCMC, sampling parameters every 1,000 iterations with the first 20% of the parameters discarded as burn-in, over 500 phylogenetic trees.

Results

The value of the Bayes factor comparing the four branch length priors indicated very strong evidence against the birth–death prior on branch lengths (log-BF > 7.0). Therefore, the node support obtained by the birth–death prior was greater.

Two principal clades were retrieved from the phylogenetic reconstruction: Clade 1 composed principally of cold water and deep sea species, and Clade 2 with tropical-temperate and shallow water species (Fig. 1). This clade topology is similar to previous studies (e.g., Strugnell et al., 2005; Lindgren et al., 2012). The consensus of 4,500 phylogenetic trees showed high PP values (>0.8) for most of the nodes (Fig. 1). In this tree, we can see that the genus *Octopus* is polyphyletic, probably related to the fact that many *Octopus* species are poorly described and are in unplaced genera (sensu Norman & Hochberg, 2005). As suggested by previous authors (Gleadall, 2004; Kaneko et al., 2011), *Octopus* systematics needs deep revision and therefore several species included in our study may not belong to the genus *Octopus* (e.g., *O. californicus*, *O. rubescens*, *O. salutii*, *O. conispadiceus*, *O. variabilis*, *O. berrima* and *O. pallidus*).

Ancestral reconstructions of reproductive strategies by the Bayesian approach were supported by adequate values of acceptance (median = 0.20, highest posterior density [HPD] 95% 0.13–0.27). We found a high probability that free-swimming hatchling was ancestral at the root of the tree (Table 2) and that the rates of gain and loss the pelago-benthic strategy through evolution were similar and greater than zero (q01 = 2.69, HPD = 0.52–3.07, q10 = 2.70, HPD = 0.46–3.13), rejecting Dollo's law (law of irreversibility) in benthic octopuses. In the phylogenetic tree, we found four nodes with greater PP of a free-swimming hatchling ancestor (root and Clades 2, 3 and 4) and three nodes with greater PP of a benthic hatchling ancestor (Clades 1, 5 and 6) (Table 2; Fig. 2).

Vampyroteuthis infernalis
Eledone cirrhosa
Bathypolypus sponsalis +
Octopus californicus
Enteroctopus megalocyathus
Octopus conispadiceus
Enteroctopus dofleini
Muusoctopus normani +
Sasakiopus salebrosus +
Vulcanoctopus hydrothermalis +
Muusoctopus eureka +
Muusoctopus longibrachus +
Muusoctopus oregonensis +
Muusoctopus rigbyae +
Adelieledone piatkowski +
Adelieledone polymorpha +
Thaumeledone gunteri +
Thaumeledone peninsulae +
Graneledone boreopacifica +
Graneledone verrucosa +
Megaleledone setebos +
Pareledone panchroma +
Pareledone serperastra +
Pareledone aurata +
Pareledone subtilis +
Pareledone charcoti +
Pareledone felix +
Pareledone aequipapillae +
Pareledone albimaculata +
Pareledone cornuta +
Macroctopus maorum
Robsonella fontaniana
Scaeurgus unicirrus
Octopus berrima
Octopus pallidus
Callistoctopus luteus
Octopus kaurna
Callistoctopus ornatus
Callistoctopus minor
Octopus variabilis
Octopus rubescens
Octopus salutii
Amphioctopus fangsiao
Amphioctopus aegina
Amphioctopus kagoshimensis
Amphioctopus marginatus
Amphioctopus mototi
Hapalochlaena fasciata +
Hapalochlaena maculata +
Octopus cyanea
Abdopus aculeatus
Octopus laqueus
Octopus parvus
Cistopus indicus
Octopus oliveri
Octopus vulgaris
Octopus bimaculoides +
Octopus insularis
*Octopus maya* +
Octopus mimus

Discussion

Ancestral reconstruction of development types showed high probability of a planktonic paralarvae strategy in the ancestral octopus. These results suggest that in benthic octopuses, the holobenthic life history evolved as a specialization from the ancestral pelago-benthic life history. Moreover, the results showed that octopuses evolved to benthic hatchlings from species with a planktonic paralarvae strategy in separate clades, supporting the idea of parallel evolution in these taxa. Free-swimming paralarvae as the ancestral life history trait, as well as repeated rounds of evolution from indirect to direct development, has been proposed in several other marine invertebrate groups (Strathmann, 1993; McHugh & Rouse, 1998; Jeffery et al., 2003; Sly et al., 2003). Moreover, studies based on phylogenetic reconstructions have shown that changes in life history traits appear several times and independently along the trees (e.g., echinoderms, polychaetes, corals, Hart et al., 1997; McHugh & Rouse, 1998; Jeffery et al., 2003; Byrne, 2006; Keever & Hart, 2008; Kerr et al., 2011). Our results suggest that during the evolution of life history strategies of the benthic octopuses, in the pelago-benthic life style the pelagic paralarvae stage was reduced or lost and evolved to well-developed benthic hatchlings (holobenthic life style). This evidence supports the "larva-first" hypothesis or that the original indirect life cycle included a planktonic larva followed by a benthic adult (Page, 2009).

Most of the evolutionary shifts found in this study from one strategy to another in benthic octopuses occurred in the tropical and temperate clade, while only a single shift was associated with deep-sea and cold water clades. If evolutionary shifts between these strategies occurred in all tropical, temperate and cold waters, benthic hatchlings seem to have been more successful in cold and deep-sea waters at an evolutionary scale. In this context, the predominance of benthic hatchling species in deep and cold water would be associated with diversification processes

after colonization of these habitats rather than recurrent adaptive processes in divergent lineages. Octopuses with different development strategies may have colonized deep-sea and polar habitats but only species with holobenthic life history would have had evolutionary success through radiation processes (e.g., *Pareledone* spp.) (Clade 1, Fig. 3). In tropical and temperate areas, octopus species generally maintained bentho-pelagic development and the few species that made an evolutionary shift to holobenthic development (e.g., *Octopus maya*, *O. bimaculoides*, *Hapalochlaena* spp.) do not exhibit evolutionary success in term of diversification processes (Clade 2, Fig. 3). This new hypothesis implies a differential diversification rate in different marine ecosystems, which is probably mediated by local environmental conditions such as temperature and environmental stochasticity. We propose that in low temperature conditions and low environmental stochasticity (i.e., deep-sea and polar habitats), to stay alive the octopuses produced few large eggs and well-developed benthic hatchlings that improved the chance of survival and reproduction in the same area (i.e., benthic); this would increase the speciation rate in holobenthic life history and would increase the extinction rate in the pelago-benthic life cycle (Fig. 3). On the other hand, in high temperature conditions and high environmental stochasticity (i.e., tropical and temperate habitats), to stay alive the octopuses produced numerous small eggs which hatched into free-swimming planktonic paralarvae that improved the chance of survival and reproduction using the transient opportunities of the environment (benthic or pelagic); this would increase the speciation rate in the pelago-benthic life history and would increase the extinction rate in the holobenthic life history (Fig. 3). These hypotheses need to be evaluated in future research. Moreover, phylogenetic evidence suggests that polar and deep-sea octopuses originated from shallow water forms, showing a rapid diversification in both habitats associated with Southern Ocean cooling during the Miocene (Strugnell et al., 2008, 2011). These results support the hypothesis of differential extinction/speciation rates that has been previously proposed to explain the predominance of brooding among Antarctic invertebrates (Poulin & Féral, 1996; Pearse et al., 2007).

Alternatively, the evolution of life history in benthic octopuses could occur decreasing the complexity of development strategies in a reversible way;

Fig. 3 Hypothesis development mode evolution of benthic octopuses of the family Octopodidae. *Branch lengths* represent the speciation rate process and *dotted lines* the extinction events
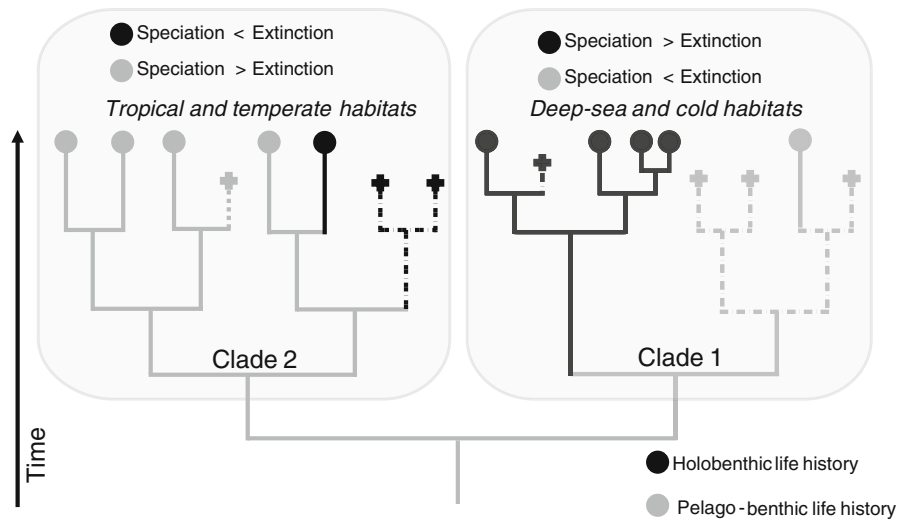
this evolution from pelago-benthic to holobenthic contrasts with the re-evolution from direct to indirect development which is much less frequent among marine benthic invertebrates (McEdwards, 1992; Collin et al., 2007). Consequently, we did not find evidence for Dollo's law (law of irreversibility) in benthic octopuses based on our results on transition rates. According to this hypothesis a trait that has been lost through evolution will not reappear in exactly the same form of the ancestral species (Gould, 1970; Goldberg & Igić, 2008). In benthic octopus species, however, this re-evolution would have occurred only twice and only in Clade 1, almost exclusively composed of polar and deep-sea species. Such a shift back to planktonic paralarvae occurred in the ancestor species of four octopuses distributed currently in cold-temperate waters of the continental shelf of the north Pacific and Atlantic regions and Patagonia. The other shift was detected for *Eledone cirrhosa*, found along the Mediterranean Basin and northeast Atlantic from sea level to 800 m depth (Belcari et al., 2002). It is worth mentioning that its sister species, *E. moschata*, has a benthic hatchling mode. However, based on plankton sampling along the Iberian shelf, Roura (2013) never found *E. cirrhosa* paralarvae and suggested that the recently hatched are not truly pelagic but associated with the sea bottom. The unique report of recently hatched of *E. cirrhosa* (4–5 mm ML) was informed from around the Shetland Islands and off the west coast of Scotland (Collins et al., 2002). Our phylogenetic results could be confirming

that *E. cirrhosa* has a holobenthic life style. It is expected that species that re-evolve to a benthic hatchling mode will exhibit a modified larva characterized by numerous apomorphic characters. This transformation has been described in echinoderms, where larvae of the sea star *Pteraster tesselatus* exhibit a unique morphology and embryonic development compared to the classical bipinnaria architecture (McEdwards, 1992). Because octopus paralarvae are morphologically similar to juvenile forms, such dramatic evolution in larval architecture would not occur in case of re-evolution to benthic hatchlings. However, paralarvae of octopus species that showed a return to a planktonic strategy in our phylogenic reconstruction (Clade 1) had the largest sizes among the family and ambiguous swimming behavior between benthic and planktonic (Sweeney et al., 1992; Villanueva & Norman, 2008); these characteristics could reflect their past development mode or an intermediate strategy. These re-evolutions from holobenthic to pelago-benthic life history are few probably because rates of gain and loss the pelago-benthic strategy in octopuses are similar and the hypothesis of differential extinction/speciation rates (Fig. 3) is more probable in the light of our phylogenetic results.

Finally, our study gives support to the idea of that the easy access to new tools for evaluating evolutionary patterns (i.e., evolution of reproductive strategies) makes it possible to build more complete scenarios using available evidence from extant taxa to complement (or in the absence of) information from the fossil

record (Avaria-Llautureo et al., 2012; Hernández et al. 2013).

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