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Abstract. Explaining variability in offspring vs. adult size among groups is a necessary step to determine the evolutionary and environmental constraints shaping variability in life history strategies. This is of particular interest for life in the ocean where a diversity of offspring development strategies is observed along with variability in physical and biological forcing factors in space and time. We compiled adult and offspring size for 407 pelagic marine species covering more than 17 orders of magnitude in body mass including Cephalopoda, Cnidaria, Crustaceans, Ctenophora, Elasmobranchii, Mammalia, Sagittoidea, and Teleost. We find marine life following one of two distinct strategies, with offspring size being either proportional to adult size (e.g., Crustaceans, Elasmobranchii, and Mammalia) or invariant with adult size (e.g., Cephalopoda, Cnidaria, Sagittoidea, Teleosts, and possibly Ctenophora). We discuss where these two strategies occur and how these patterns (along with the relative size of the offspring) may be shaped by physical and biological constraints in the organism's environment. This adaptive environment along with the evolutionary history of the different groups shape observed life history strategies and possible group-specific responses to changing environmental conditions (e.g., production and distribution).

Key words: adult size; carbon mass; evolution; life history; marine animals; offspring size; reproductive strategy.

Introduction

Characterizing life history strategies among ecosystem players is a necessary precursor to determining ecosystem structure and function. Body size is an easily accessible trait that can be used to compare life history strategies among diverse groups and identify whether characteristics and strategies are shared or differ (Andersen et al. 2016). Identifying how life history processes differ among groups can help reveal the relevant forcing factors and adaptive environment shaping organisms and the overall community composition. When considering the evolutionary performance of a species, offspring size is of particular relevance, as it will evolve to maximize the reproductive potential of the adult with respect to physical and biological forcing factors. Thus, explaining variation in offspring size among organisms sheds light on underlying mechanisms

of selection and resulting adaptive strategies of the different ecosystem players.

Potential offspring size is constrained upwards by the size of the parent while the minimum possible size is determined by the physiological, ecological, and physical constraints on viability (e.g., Smith and Fretwell 1974, Strathmann 1985, Thygesen et al. 2005, Charnov and Ernest 2006, Caval-Holme et al. 2013; Fig. 1). Simple life history theory suggests that adults should maximize the number of surviving offspring by minimizing offspring size to optimize their lifetime reproductive success (or net reproductive rate, R_0; Andersen et al. 2008). Instead, we find variation in how relative offspring size varies among groups while constrained within the triangle in Fig. 1 (e.g., Levitan 2000, Falster et al. 2008). Such variability must be governed by differences in size-dependent survival (influenced by both mortality and growth) from birth to maturation. Thus, adult-offspring size patterns reflect the selection pressures affecting survival to maturation towards maximizing the reproductive potential of the adult within phylogenetic constraints (e.g., Smith and Fretwell 1974). Biological and physical factors influencing size-
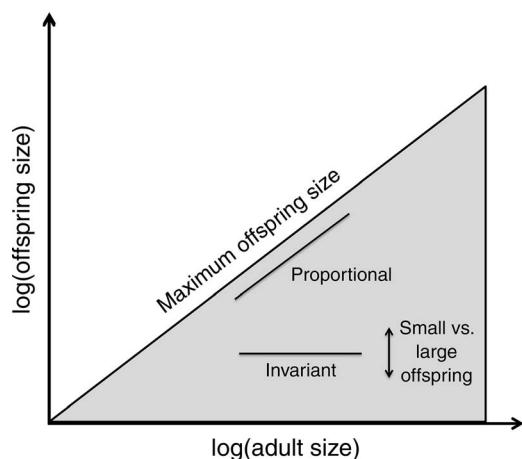
Fig. 1. Illustration of potential data distribution of adult and offspring sizes after Caval-Holme et al. (2013). Shown are possible proportional and invariant strategies, as well as variability in relative offspring size.

dependent offspring success include temperature, fertilization, consumption, mortality, competition, dispersal probabilities, and evolutionary history (Christiansen and Fenchel 1979, Levitan 1996, 2000, Andersen et al. 2008, Régnier et al. 2013). Therefore, explaining variation in offspring size strategies among groups will highlight some of the mechanisms affecting survival prior to maturation and resulting adult success.

We explore adult–offspring size relationships for life in the ocean spanning >17 orders of magnitude in body mass. The marine environment offers a diversity of larval development strategies and offspring sizes with which to explore the mechanisms of adult–offspring size patterns (e.g., Christiansen and Fenchel 1979). For example, work on fishes has identified two overall strategies with offspring size either invariant or proportional to adult size (Olsson 2015). We explore the ubiquity of these patterns for pelagic life in the ocean. We discuss how these patterns might emerge in the light of biological and physical factors affecting larval survival and how reproductive strategies mitigate environmental constraints to shape optimal offspring sizes among groups. Our results reveal macroecological patterns of offspring size strategies for life in the ocean, as well as identify mechanisms by which environmental changes may be expected to promote or suppress different groups via changes in optimal offspring size.
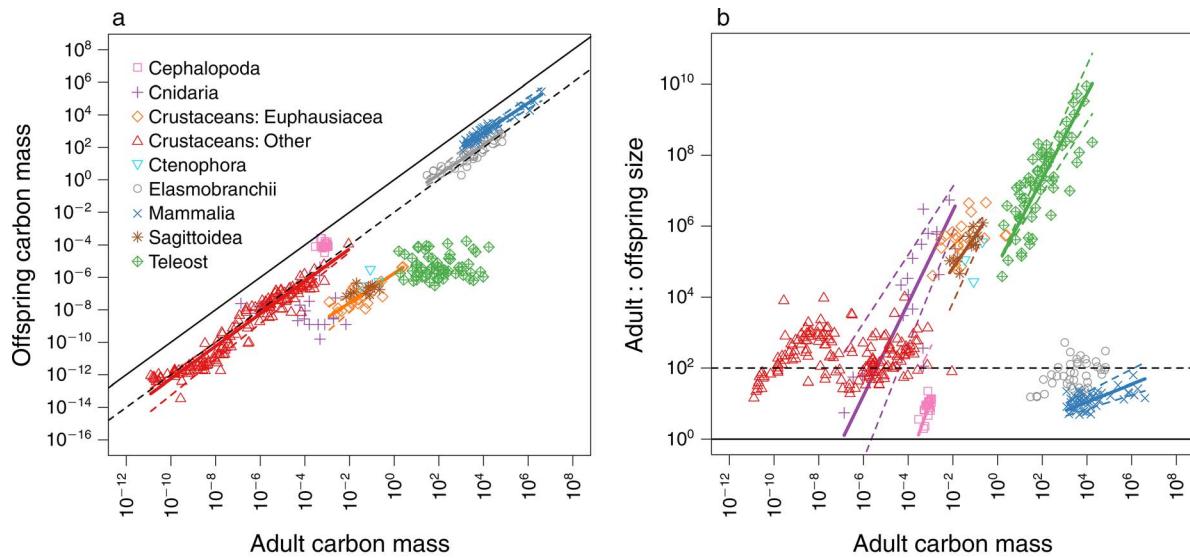
METHODS

Adult and offspring size estimates of 407 species were compiled from the literature covering >17 orders of magnitude in body mass and including Cephalopoda (ink fish), Cnidaria (jellyfish), Crustaceans, Ctenophora (comb jellies), Elasmobranchii (cartilaginous fish), Mammalia (mammals), Sagittoidea (arrow worms), and Teleost (i.e., Actinopterygii, bony fish) (A. B. Neuheimer, M. Hartvig, J. Heuschele, S. Hylander, T.

Kiørboe, K. H. Olsson, J. Sainmont, and K. H. Andersen, *unpublished manuscript*). Adult size was defined as either size at maturation, maximum size, or mean adult size depending on availability. This will introduce some noise, which, however, is insignificant considering the 17 orders of magnitude variation in body mass that was examined. Offspring size was defined as the smallest size at which offspring can be considered independent of the adult (Falster et al. 2008). Egg size was used in both broadcast spawning and egg-carrying invertebrates (e.g., crustaceans).

Individual size estimates were converted to standardized size estimates (carbon size, g) to allow for among-group comparisons. This required a number of size estimates to be converted. Conversion factors were compiled from the literature (A. B. Neuheimer, M. Hartvig, J. Heuschele, S. Hylander, T. Kiørboe, K. H. Olsson, J. Sainmont, and K. H. Andersen, *unpublished manuscript*). Conversions were made at the lowest available taxonomic level, e.g., when species-specific conversions were not available, genus-specific conversions were used; when genus-specific conversions were not available, family-specific conversions were used, etc. Multistep conversions were made where needed (e.g., length to wet mass to carbon mass). Depending on availability of conversion factors, general and/or adult conversions were used for both adult and offspring size estimates. Mean adult and offspring size was estimated for each species. Variability around conversion factors exists, introducing variability (measurement error) into our relationships. However, conversion factors with narrow confidence limits were found for broad groups including polychaetes, gastropods, bivalves, amphipods, and decapods (Ricciardi and Bourget 1998), and the introduced noise is expected to be insignificant relative to the large range in body sizes considered. For example, coefficients of variation of less than one order of magnitude were estimated for body size conversion factors for a range of pelagic organisms (Kiørboe 2013).

Linear dependencies of log-transformed mean offspring size on log-transformed mean adult size were made using standardized major axis (SMA) line-fitting (Warton et al. 2006, Falster et al. 2008). SMA line-fitting allows for error in both variables and is an appropriate method when there is interest in estimating the value of the slope parameter (e.g., for comparison to known values), as well as simply the dependency between two variables (Warton et al. 2006). A correlation between the two variables must be established before SMA line-fitting can be applied (Warton et al. 2006). Thus, dependencies of offspring size on adult size were first estimated by assessing correlations between log-transformed mean offspring size and log-transformed mean adult size. For groups demonstrating significant correlations (Pearson correlation coefficient, $P < 0.05$), relationships were then characterized using SMA line-fitting. Next, differences among significant relationships were examined by comparing adult–offspring relations

Fig. 2. Adult–offspring size comparisons (log-transformed carbon size measured in grams) for all groups with each point representing species-specific means as (a) adult vs. offspring and (b) adult vs. adult : offspring. Where significant, line-fits of estimates are given via standard major axis (SMA) line-fitting (solid colored lines with 95% CI around slope as dashed lines; see Table 1). Also shown are 1:1 (black solid line) and 100:1 (black dashed line) relationship lines.

using likelihood ratio tests (Warton et al. 2006). Slope comparisons to a known value (e.g., 1, from published values; see *Results* for mammals) were made by comparing residual and fitted axis scores using *b* as the slope (Warton et al. 2006). The fitted slope value is not significantly different from *b* when residual and fitted axis scores are uncorrelated (Warton et al. 2006).

Finally, relationships between the adult : offspring size ratio and adult sizes were estimated and explored via correlation, SMA, and likelihood ratio testing as above

for all groups demonstrating adult–offspring relations with slopes $\neq$ 1. All analyses were performed in R with base and smatr packages (Warton et al. 2006, 2012, R Development Core Team 2013).

RESULTS

Comparisons of offspring vs. adult size across our sampling range revealed two distinct patterns: (1) offspring size increasing with adult size or (2) offspring size independent of adult size (Fig. 2a, Table 1). The

TABLE 1. Statistical analysis of offspring vs. adult size (g carbon size) for a range of marine animals, based on $m_o = a \times m_a^b$, where m_o and m_a are offspring and adult size, respectively, with estimates and ranges for coefficients a and b.

		SMA line-fitting			
Group	P	Squared Pearson correlation coefficient	b	a (g C^{1-b})	Slope compare to 1, P
Cephalopoda (ink fish)	0.71	0.0063	NA	NA	NA
Cnidaria (jellyfish)	0.82	0.0028	NA	NA	NA
Crustaceans, Euphausiacea	<0.0001	0.60	0.91 (0.69–1.2)	1.8×10^{-6} (6.2×10^{-7}–5.2×10^{-6})	0.52
Crustaceans, other	<0.0001	0.93	1 (0.97–1.1)	0.0056 (2.9×10^{-3}–1.1×10^{-2})	0.49
Ctenophora (comb jellies)	0.83	0.071	NA	NA	NA
Elasmobranchii (cartilaginous fish)	<0.0001	0.77	0.91 (0.78–1.1)	3.2×10^{-2} (1.0×10^{-2}–1.0×10^{-1})	0.25
Mammalia (mammals)	<0.0001	0.94	0.90 (0.84–0.96)	2.1×10^{-1} (1.2×10^{-1}–3.7×10^{-1})	0.0015
Sagittoidea (arrow worms)	0.18	0.19	NA	NA	NA
Teleost (bony fish)	0.77	0.0013	NA	NA	NA

Notes: SMA is standardized major axis. See also Methods and Fig. 2a. NA denotes not applicable.

pattern of offspring size increasing with adult size was found in the Crustacean, Elasmobranchii, and Mammalia groups (Fig. 2a). All other groups showed no correlation between offspring and adult size (Table 1). Within the Crustacean group, Euphausiids were significant outliers, demonstrating a similar slope but different (lower) intercept than all other Crustacean groups (Table 1, Fig. 2; Appendix). Consequently, Crustaceans are treated as two groups: Euphausiacea and other.

Within groups showing offspring size increasing with adult size, the fitted SMA lines suggested that slopes were all close to 1 and offspring size is near proportional to adult size, in all but Mammalia (Table 1). The Mammalia group slope was slightly but significantly less than 1 (0.90; Table 1) and not significantly different from the slope of the relation for terrestrial mammals (0.95; Purvis and Harvey 1995, Falster et al. 2008; likelihood ratio testing, $P = 0.086$). For groups showing the proportional strategy, the average ratio of adult-to-offspring size mainly varied between 10^2 and 10^3, with the Euphausiids deviating significantly from this pattern by having much smaller eggs, relatively (ratio $\sim 10^5$; Tables 2 and 3). The ratio of adult-to-offspring size

increased with increasing adult size in the Mammalia group (from ~ 5 to 14; Fig. 2b).

Invariant offspring size was found in the Cephalopoda, Cnidaria, Sagittoidea, teleosts, and possibly Ctenophora, though the latter is data-limited with $n = 3$ (Tables 1 and 3; Appendix: Fig. A1). Average offspring sizes vary substantially among groups by more than four orders of magnitude, with Sagittoidea having the smallest offspring, the two gelatinous groups having intermediate but very different offspring sizes, and the teleosts and cephalopods having the largest offspring (Table 3).

Patterns among groups were consistent with the above when examining the ratio of adult-to-offspring size as a function of adult size (Fig. 2b). Groups demonstrating invariant offspring size showed an increasing adult : offspring size ratio with increasing adult size (Cephalopoda, Cnidaria, Sagittoidea, and teleost; Table 2). As above, the Mammalia adult vs. offspring slope differed from 1 and the group demonstrated increasing adult : offspring size ratio with increasing adult size (Fig. 2b, Table 2). Based on the statistical analyses in Tables 1 and 2, all groups were

TABLE 2. For all groups demonstrating adult–offspring size relationships (g carbon size) with slopes $\neq 1$ (including those not significantly different from zero, see Table 1), statistical analysis of adult : offspring vs. adult size based on $m_a/m_o = a \times m_a^b$, where m_o and m_a are offspring and adult size, respectively, with estimates and ranges for coefficients a and b.

		SMA line-fitting		
Group	P	R^2	b	a (g C^{1-b})
Cephalopoda (ink fish)	0.00088	0.39	1.8 (1.3–2.5)	3.1×10^6 (4.0×10^4–2.3×10^8)
Cnidaria (jellyfish)	<0.0001	0.68	1.3 (0.96–1.6)	1.1×10^9 (3.8×10^7–3.1×10^{10})
Ctenophora (comb jellies)	0.71	0.2	NA	NA
Mammalia (mammals)	<0.0001	0.26	0.25 (0.20–0.32)	1.1 (0.63–2.0)
Sagittoidea (arrow worms)	0.0015	0.69	0.91 (0.6–1.4)	4.4×10^6 (1.3×10^6–1.5×10^7)
Teleost (bony fish)	<0.0001	0.65	1.2 (1.0–1.4)	8.6×10^4 (3.4×10^4–2.2×10^5)

Notes: See also Methods and Fig. 2b. NA denotes not applicable.

TABLE 3. Categorization of offspring strategies based on the statistical analyses in Tables 1 and 2, as well as absolute and relative offspring sizes.

Group	Correlation offspring size vs. adult size	Correlation offspring : adult size vs. adult size	Offspring strategy	Offspring size, mean ± 1.96 × SD (g C)	Adult : offspring size ratio, mean ± 1.96 × SD
Cephalopoda (ink fish)	slope not different from zero	slope significant and in range 1.3–2.5	invariant	$1.0 \times 10^{-4} \pm 1.0 \times 10^{-4}$	NA
Cnidaria (jellyfish)	slope not different from zero	slope significant, not different from 1	invariant	$2.7 \times 10^{-7} \pm 1.9 \times 10^{-6}$	NA
Crustaceans, Euphausiacea	slope significant, not different from 1	NA	proportional	NA	$8.6 \times 10^{5} \pm 2.5 \times 10^{6}$
Crustaceans, other	slope significant, not different from 1	NA	proportional	NA	$580 \pm 2.5 \times 10^{3}$
Ctenophora (comb jellies)	slope not different from zero	slope not different from zero	NA	$1.3 \times 10^{-6} \pm 2.9 \times 10^{-6}$	$1.7 \times 10^{5} \pm 3.5 \times 10^{5}$
Elasmobranchii (cartilaginous fish)	slope significant, not different from 1	NA	proportional	NA	94 ± 194
Mammalia (mammals)	slope significant and in range 0.84–0.96	slope significant and in range 0.20–0.32	(proportional)	NA	NA
Sagittoidea (arrow worms)	slope not different from zero	slope significant, not different from 1	(invariant)	$2.0 \times 10^{-7} \pm 2.4 \times 10^{-7}$	NA
Teleost (bony fish)	slope not different from zero	slope significant and in range 1.0–1.4	invariant	$1.7 \times 10^{-5} \pm 6.5 \times 10^{-5}$	NA

Notes: Categories in parenthesis are based on non-significant relations. NA denotes not applicable.

classified to one or the other strategy (invariant vs. proportional) in Table 3.

DISCUSSION

Proportional vs. invariant offspring size strategy

Our analysis reveals that ocean life follows two distinct offspring-size strategies within major taxonomic groups: offspring size proportional to adult size or invariant offspring size, independent of adult size (Table 3). The analysis covers all major groups of multicellular life in the ocean spanning >17 orders of magnitude in adult size, from 1.2×10^{-11} g carbon (unidentified mysid) to 3.9×10^{6} g carbon (blue whale, *Balaenoptera musculus*). Groups that demonstrate the proportional offspring size strategy are Crustaceans, Elasmobranchii, and Mammalia (Table 3). In earlier work, offspring vs. adult size relationships significantly different from 0 were found for sharks (Freedman and Noakes 2002), foraminifera (Caval-Holme et al. 2013), and terrestrial mammals (Purvis and Harvey 1995, Falster et al. 2008). The offspring–adult slope for marine mammals (this study) was not different from that of terrestrial mammals (Falster et al. 2008) but was significantly less than 1. This implies a possible departure from a strictly proportional relationship between adult and offspring size with a decline in the relative investment in each individual offspring as adult size increases, a pattern also observed in Orders Calanoida and Mysida in the Crustacean group (see Appendix).

Groups demonstrating the invariant offspring size strategy are Cephalopoda, Cnidaria, Sagittoidea, Teleost, and possibly Ctenophora. Similar invariant egg size was found previously for teleosts (Duarte and Alcaraz 1989, Andersen et al. 2008; Olsson 2015), but not for other groups. The existence of a clear offspring size strategy (proportional or invariant) within each group requires a strong selective force acting to reinforce the strategy within the group. The pattern further suggests similarity in either the life history strategy or the environmental forcing among groups with the same strategy and consequently, a clear difference among groups with different strategies. In the following sections, we discuss existing theoretical life history explanations for offspring-size strategy followed by a detailed discussion of whether the general explanations are appropriate for each group.

Offspring size strategy explained by life history theory

Life history strategy theories are either optimization arguments that rely on finding the offspring size strategy with the highest lifetime reproductive outcome or they are game theoretic arguments predicting evolutionary stable strategies for offspring size. In both cases, the theories rely on a description of the trade-offs related to offspring size (Smith and Fretwell 1974). The benefit of small offspring size is an increase in the number of offspring at the cost of lower survival to adulthood due to higher mortality of smaller offspring and longer time to maturation (e.g., Peterson and Wroblewski 1984). The key metric is therefore the survival to maturation per biomass invested in reproduction. This can be calculated using theories of how growth and mortality vary as functions of size, e.g., from metabolic scaling assumptions (Brown et al. 2004, Andersen and Beyer 2006).

Optimization arguments based on metabolic scaling assumptions predict lifetime reproductive output being proportional to offspring size as m_o^{a-1}, where a is the ratio between mortality and weight-specific growth rate (Christiansen and Fenchel 1979, Thygesen et al. 2005,

Andersen et al. 2008) and o is offspring. The value of *a* is less than one (Andersen et al. 2008) so lifetime reproductive output increases if offspring size decreases. Therefore, optimization arguments predict that offspring size should be as small as possible. Small deviations from the metabolic scaling of mortality (i.e., deviations of the body size scaling exponent from −0.25) may lead to a specific offspring size being predicted as optimal (Kiflawi 2006, Jørgensen et al. 2011), but the argument will never predict offspring size proportional to adult size. Optimization arguments have been used to explain the offspring size in fish and marine benthic invertebrates (Christiansen and Fenchel 1979), but they obviously do not apply to the majority of metazoan marine life that follow the proportional strategy.

A weakness of optimization arguments is that they do not consider density-dependent effects on survival to maturation. When density-dependent survival occurs and it is influenced by offspring size, Falster et al. (2008) demonstrated a range of offspring-size strategies where offspring size related to adult size with an exponent that depended on adult reproductive output. Specifically, offspring size proportional to adult size was indeed an evolutionary stable strategy when adult reproductive output was proportional to adult size. Olsson (2015) applied a similar methodology to fish (teleosts and elasmobranchs) using observed scaling of growth and mortality, and demonstrated how the length of an early life density-independent period determined offspring size: if the period of density-independent survival in early life was sufficiently long, the evolutionary stable strategy was small offspring, just as predicted from the simple life history optimization. In contrast, early density-dependent survival led to the proportional strategy with an adult : offspring size ratio of around 100 (Olsson 2015). Thus, offspring size strategy depends on the nature of density dependence. Density-dependent survival that is influenced by offspring size selects for a proportional strategy, while density-independent survival selects for a small (invariant) offspring-size strategy. Applied to our observations, these theoretic results predict that offspring from the groups showing the invariant strategy have density-independent growth and/or mortality prior to maturation, while offspring in groups with the proportional strategy experience density-dependent growth and/or mortality prior to maturation.

Proportional offspring-size strategy

Groups with the proportional strategy have an adult : offspring size ratio of ∼100 (mammals ≈ 10); notable exceptions are the Ctenophores and the Euphausiids that have a much higher adult : offspring size ratio (10^5 and 10^6, respectively). The life history argument outlined previously indeed predicts a factor ∼100 of proportionality (Olsson 2015) with the exact value dependent on little-known parameters, such as the exact scaling of juvenile survival and the reproductive

efficiency. We hypothesize three other mechanisms that could lead to selection for a proportional offspring size strategy: parental care, a seasonal environment, and cannibalism. A proportional offspring-size strategy may be related to parental care strategies, where parental resources continue to be invested after the offspring are considered independent of the adult (Shine 1978). The addition of parental care increases the lower limit of offspring size relative to the size of the parent and may be responsible for proportional offspring–adult size patterns in mammals. This also fits with the observed pattern where mammals have the smallest adult : offspring ratio (∼10).

A strongly seasonal environment may induce an evolutionary drive for adults to produce offspring with a size sufficiently large to be able to mature within the season. This could be relevant for copepods or other smaller crustaceans with a life span comparable to the length of the season. This explanation implies that smaller adults should have relatively large offspring, which is not seen in the data. Thus, seasonality is not likely to be a strong driver shaping offspring size across these broad groups.

Most marine heterotrophs are cannibals and have a predator–prey mass ratio in the range $10–10^5$ with a mean ∼10^3 (Barnes et al. 2010). A strong density-dependent cannibalistic mortality induced by adults peaking at a factor 10^3 of adult size would induce a strong evolutionary drive for making offspring larger than the predator–prey size ratio; e.g., ∼10^2 found here. Examples of density dependence population regulation driven by egg cannibalism are well documented for pelagic copepods (Peterson and Kimmerer 1994, Ohman and Hirche 2001).

Invariant offspring-size strategy

Groups showing invariant offspring-size strategy (Cephalopoda, Cnidaria, Sagittoidea, Teleost, and possibly Ctenophora; Table 3) show considerable variability in the absolute offspring size observed ($10^{-7}–10^{-4}$ g C; Table 3). The life history arguments outlined previously provide strong support for a strategy with as small offspring as possible, but they do not predict the absolute offspring size. Only if the size-scaling of mortality is steeper than metabolic (i.e., with an exponent less than ∼−0.25; Jørgensen et al. 2011) do the arguments predict a specific offspring size (typically larger offspring the steeper the scaling of mortality). However, the predicted offspring size is very sensitive to model parameters. Thus, while these arguments predict variable offspring size among species, they are not sufficient to explain group-specific absolute values of offspring size, such as the well-defined mean offspring size of Teleosts (Fig. 2a). Mechanisms leading to the absolute offspring size should therefore be sought in factors not considered by the life history arguments. Specifically, current life history theory provides a selection response for smaller offspring size, but this

should be countered by a strong selective force acting in the opposite direction (toward larger sizes) at an offspring size around the observed size.

For Teleosts, we hypothesize that the selective force stems from the lower size limit of visual predation and from hydromechanical constraints to suction feeding. Most fish larvae are visual predators and their size is therefore limited by the smallest size of a functional camera eye, which has a diameter around 1 mm (Martens et al. 2015; an exception may include cave fish larvae that undergo eye degeneration as they develop; Yoshizawa and Jeffrey 2008). Organisms smaller than fish larvae, such as copepods, rely on tactile sensing to locate prey (Tiselius et al. 2013, Andersen et al. 2016). Similarly, fish larvae feed using suction, but due to scaling of the hydromechanics of suction-feeding at low Reynolds numbers, suction-feeding becomes ineffective for fish larvae smaller than about 1 cm (China and Holzman 2014). Taken together, we conclude that were fish to make smaller eggs, the larvae would be blind, unable to feed efficiently, and consequently outcompeted by the tactile sensing copepods. Similar developmental constraints may limit the lower offspring size of Cephalopods, also visual predators, and demonstrating direct development with offspring hatching as juveniles from large yolky eggs.

While Sagittoidea also have eyes, they are ambush feeders utilizing hydrodynamic disturbance to sense prey (Feigenbaum and Maris 1984). The minimum arrow worm offspring size may be limited by their strategy of rapid, direct development with no larval stages and offspring hatching as miniature adults after ~48 h of incubation (Margulis and Chapman 2010). Smaller offspring size may be gained through indirect development via larval stages (e.g., copepods), where size can be reduced if offspring occupy a different feeding niche than that of their parents. The lack of larval stages in arrow worms means offspring must quickly be able to fill the parental ambush predator role. Ambush feeding attacks in small pelagic animals is constrained by viscosity, and indeed, there is a minimum size below which predatory ambush feeding is not feasible (Kiørboe et al. 2009). This requirement may limit the lower offspring size that can be realized for arrow worms.

Cnidarian offspring typically undergo a number of stages before metamorphosing into sexually reproductive adults, beginning with fertilized eggs (which may be broadcast or brooded), free-swimming ciliated planula larvae, a sessile polyp stage, and a pelagic ephyra larval stage (Berrill 1949). Constraints (e.g., swimming and feeding) on any of these stages may limit the minimum offspring size observed. For example, planula larval stages must eventually settle out of the water column to the benthos. Settlement location has been shown to be nonrandom (e.g., Gröndahl 1989) with successful settlement dependent on swimming ability and larval (negative) buoyancy (Chia et al. 1984) both of which may limit the lower size limit of offspring.

Other drivers of offspring size

Oxygen limitation may influence offspring size, particularly in life forms where oxygen consumption is limited by diffusion (e.g., eggs). It was theorized that large eggs would be disadvantageous under hypoxic conditions as volume (and inferred oxygen demand) would increase with size faster than the surface area limiting oxygen uptake (e.g., Krogh 1959, Hendry et al. 2001, Kinnison et al. 2001, Rombough 2007). In practice, the opposite has been found: metabolic rate and oxygen consumption increase more slowly than surface area as egg size increases (Einum et al. 2002). This observation could be explained by the increase in egg volume being dominated by an increase in egg yolk, which is expected to respire at a lower rate than embryonic tissue (Hendry and Day 2003). In this case, oxygen limitation would not be limiting upper egg size and a larger egg size can evolve to, for example, allow eggs to be placed in lower oxygen environments that may represent refuges from predators (e.g., burying in nests, laying in guarded clutches; Hendry and Day 2003). Alternatively, oxygen may be limited by diffusion throughout the egg (vs. the surface; Munk and Riley 1952), leading to a scaling of oxygen supply rate with the diameter of the egg and not the square of the diameter as under surface limitation. If egg size is limited by oxygen supply, whether by uptake at the surface or by diffusion, a group may be limited to the invariant offspring size strategy, e.g., explaining invariance of fish egg size with respect to adult size. However, oxygen limitation alone cannot explain the production of larger eggs by some organisms (e.g., sharks and skates), without also requiring, for example, slower development of shark vs. fish eggs to allow for the lower oxygen supply per body mass. This hypothesis could be tested should, for example, development rate comparisons between fish and shark eggs become available.

The advective environment and relative benefit of retention vs. dispersal may also shape offspring size in either direction (Strathmann 1985, Falster et al. 2008). Large eggs hatch more quickly, which lowers the uncertainty of hatching location and makes it more likely that offspring will end up near the parents (Duarte and Alcaraz 1989). By contrast, small eggs are adapted for dispersal (Vance 1973, Strathmann 1985, Moran and McAlister 2009). An examination of larval physiology along with the advective environment may determine if the minimum size of offspring reflects morphological constraints associated with dispersal.

In areas where physical constraints reduce fertilization success (e.g., external fertilization in a highly advective environment), larger eggs may constitute a bigger target and therefore increase the chance of fertilization success (Levitan 1993). Indeed, minimum egg size may be dictated by the probability of contact with sperm in externally fertilizing organisms (Levitan 1996). Organisms can increase the chance of fertilization success by increasing egg size or with the use of accessory structures

(e.g., jelly coat, sperm attractive chemicals; Levitan 2006) that increase fertilization success. In particular, fertilization success may be increased in Euphausiid species through the use of spermatophores, which are packages of sperm that are transferred to the outside of the female's reproductive tract via a modified limb (e.g., Mauchline 1959). This may enable the relatively small egg size of the Euphausiid species we examined, where the adult : offspring ratio was estimated to be significantly larger than for any of the other groups with proportional strategy ($\approx 8.6 \times 10^5$). Determining whether fertilization limitation governs selection for offspring size requires knowledge of sperm production and size and such data are unavailable for the wide range of groups in this study.

Conclusion

We find that marine life exhibits either invariant or proportional offspring size with adult size. Superimposed on this is a range of offspring sizes both within and among groups that can be explained by examining the many different physical and biological factors shaping survival over the period of fertilization to maturation, as well as adult reproductive life span and the evolutionary history of the groups (e.g., Moles and Westoby 2006). Indeed, it may be possible to use variation in offspring size among related groups as a predictor of other life history parameters, including relative variation in fertilization success, dispersal, and mortality (Moran 2004). Mechanistic explanations of variability in adult–offspring size strategies are necessary (de Jong 2005) and will allow us to better predict how life histories may evolve under changing environmental conditions, as well as identify life history constraints that may mean group-specific distribution and production shifts under environmental change.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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