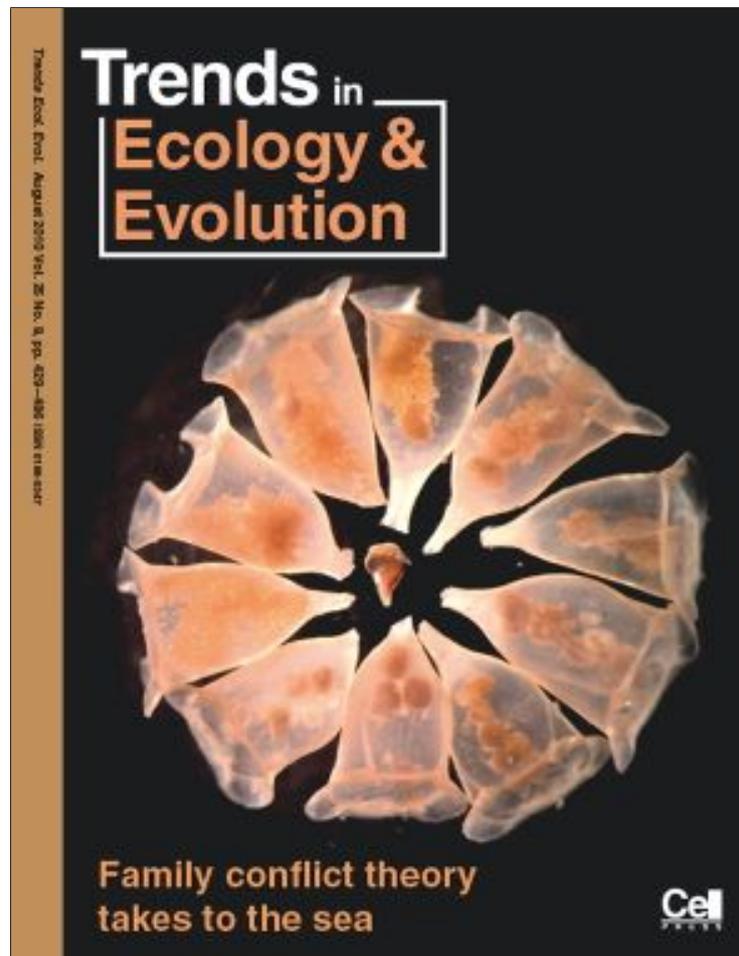


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# Family conflicts in the sea

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**In sexually reproducing organisms, conflicts of interest among family members are inevitable. The intensity of these conflicts depends upon the opportunities for parents and offspring to interact and the level of promiscuity. Despite the acknowledged role of family conflict in the evolutionary ecology of terrestrial organisms, its influence in the marine realm has largely been ignored. Nevertheless, marine organisms exhibit a wide range of reproductive and developmental modes through which sexual, sibling, and parent–offspring conflicts can manifest. Moreover, the existence of multiple mating in these species increases the likelihood, as well as the degree, of these conflicts. Consequently, many puzzling aspects of evolution in the sea, from life-history variation to diversification, could be clarified through the lens of conflict theory.**

## All in the family

The resolution of genetic conflicts of interest governs the evolution of all social relationships across the full range of biological organization, from genes to societies [1–2]. Lying in the middle of this spectrum, families represent a universal and especially intense arena for cooperation and conflict: fathers and mothers, sons and daughters, and brothers and sisters may sometimes die for each other, but given the right circumstances, they will also kill each other [2].

The classical view of the family unit, with all members harmoniously cooperating to maximize the number of surviving young, collapsed with the realization that the interests of interacting organisms are aligned only insofar as this reflects the degree to which they are related [2–5]. Mates, for instance, are rarely close kin and often have differing optima with respect to mating rate, sperm usage, parental care, and offspring provisioning [6]. Mothers are equally related to all of their offspring, but each offspring is more closely related to itself than to either its siblings or parents [3]. Finally, offspring can compete with both present and, indirectly, future siblings, who may or may not share the same father [4].

Pathways of family conflict often form a network of interactions among males and females, parents and offspring, and siblings that place constraints on conflict resolution and social behaviors in ways that are not readily apparent from simpler approaches based on pairwise interactions (Figure 1) [7,8]. For example, the degree of polyandry simultaneously governs the magnitude of sexual conflict and, through its influence on offspring

relatedness, the level of both parent–offspring and sibling conflict over resource allocation [3,4,9]. Indeed, experimental (e.g. [10]) and comparative (e.g. [11,12]) evidence from terrestrial organisms suggests that the degree of polyandry can be pivotal in regulating parental investment strategies [4,7,13]. For example, a comparative analysis of begging behavior across species of passerine birds shows that the loudness of nestling begging increases with levels of extra-pair paternity [12]. Similarly, there is a strong positive association in passerines between the rate of multiple paternity within broods and nestling growth rates [14] again confirming that, in birds at least, competitive interactions among siblings vary with mating system.

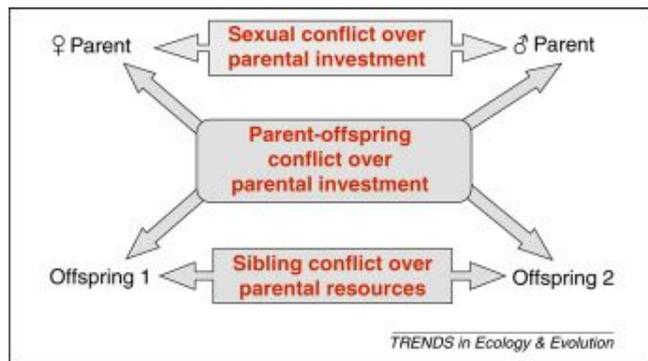
## Conflict in the sea

Much of the current thinking about the evolution of marine life histories is shaped by the theoretical work of Vance [15,16]. His model, based on a multi-way trade-off between egg size, larval duration, and offspring mortality, predicts that disruptive selection will favor either small, minimally provisioned, or large, well-provisioned eggs. Other factors (e.g. fertilization mode, benthic vs. planktonic development, post-settlement performance) have subsequently been shown to affect the evolution of offspring size and other life-history traits (reviewed in [17]).

However, despite the acknowledged role of family conflict in the evolution of life histories and behavior in terrestrial systems [3,4,6], similar studies in marine systems have proceeded largely without reference to conflict theory. This is presumably due to the perception that family members have limited opportunities to interact [18] (Box 1). Nevertheless, a growing number of studies are revealing genetic (especially kin) structure on surprisingly fine spatial scales (meters or less) [19,20]. In addition, there is consistent evidence for inbreeding [21], and a high prevalence of multiple paternity (see below). Moreover, marine organisms have the highest diversity of reproductive modes on the planet, from broadcast spawning eggs and sperm into the water column to internal fertilization with extensive post-zygotic care, and so provide unmatched opportunities for testing conflict theory (Table 1).

Here we explore some of the potential and realized impacts of multi-way family conflicts on the evolution and expression of life-history traits in marine organisms. Because of its critical role in regulating the magnitude of family conflict, we first consider the evidence for multiple mating in the sea. We then evaluate the opportunities and evidence for each of the classical pairwise conflicts (sexual,

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**Figure 1.** Pairwise interactions among family members: siblings compete with each other over parental investment (sibling conflict) while offspring have different interests from their parent(s) over investment (parent–offspring conflict). Where both parents invest, they are in conflict over the amount each should give (sexual conflict). Modified from [7].

parent–offspring, and sibling), highlighting how reproductive mode influences their expression. Finally, we consider how an improved understanding of family conflict might provide a general framework that allows for novel insights

### Box 1. Dispersal and the potential for sibling interactions

The remarkable dispersal potential of offspring in many marine species raises a fundamental question with respect to the influence of conflict: How likely are interactions among siblings (or between parents and offspring) after release from their mothers?

In organisms with direct development or extremely limited post-release dispersal, sibling interactions are probably common. For example, the alga *Mazzaella laminarioides* releases non-motile and negatively buoyant propagules during periods of low water movement, making dispersal in this species highly limited [84]. Similarly, some broadcast spawners release their offspring in a viscous matrix and, despite a development period of up to one day, embryos may be retained within this matrix and may even metamorphose on their mother's surface [85].

The prevalence of direct development and philopatric dispersal in a number of marine invertebrates also raises the possibility of extended sibling interactions after settlement [72]. Limited dispersal of progeny can even promote the evolution of true eusociality, as demonstrated in snapping shrimp [86]. These patterns may also increase opportunities for other forms of kin conflict and cooperation. For example, in the colonial ascidian *Botryllus schlosseri*, clonemates and closely related colonies often somatically fuse with one another, whereas more distantly related ones do not. Indeed, in many clonal invertebrates fusion frequencies decline with physical distance between tested colonies (reviewed in [73]). Johnson and Yund [87] further show that mating system also plays an important role in determining the outcomes of post-settlement fusion–rejection interactions; with increasing levels of multiple paternity within a brood, fusion frequencies decline.

For species with extended larval durations, post-settlement sibling interactions seem less likely but may still occasionally occur [88] through active larval behavior [72] and/or hydrodynamic effects that reduce the diffusion of larval ‘packets’ [89]. Further population genetic studies are needed to determine the extent of sibling aggregation at settlement; we predict that with the increasing use of highly polymorphic genetic markers, and growing emphasis on sampling individuals on finer spatial scales (within local populations), more examples of sibling association at settlement will emerge [90,91]. At present, the limited available data suggest that sibling interactions may be more pervasive than previously thought, and that planktonic development, even for days or weeks, does not preclude post-settlement interactions among kin. Thus, the interactions between mating systems and family conflict, and the consequences of these interactions, may extend throughout an organism's life cycle.

into an array of unresolved issues in marine systems, including questions of offspring size variation, parental allocation, and speciation.

### Mating systems and polyandry in the sea

The development of highly polymorphic genetic markers has revolutionized our understanding of mating systems in nature, and revealed unsuspected levels of polyandry, even in species once thought to be monogamous [22]. Nevertheless, despite the extensive potential for female promiscuity and polyandry in the sea, genetic analyses of mating systems in marine organisms are relatively uncommon.

In part because of their habit of packaging offspring in nurseries (e.g. brood chambers, egg masses, or capsules), marine mollusks provide some of the best systems for collecting genetic data on female promiscuity [23,24]. These studies repeatedly show that polyandry is common and that clutches, and even individual capsules, contain multiple patrilines. Studies on other groups, including porcelain and brachyuran crabs [25,26], lobsters [27], horseshoe crabs [28], sea urchins [29], squid [30], fish [31], colonial organisms (ascidians [32,33] and corals [34]), and red algae [35] also show that individual broods typically have multiple fathers.

The degree of polyandry can also vary substantially among females within a population, with some females apparently monogamous and others highly promiscuous. For example, in the lobster, *Homarus americanus*, Gosse-lin *et al.* [27] found both within- and among-population differences in the degree of polyandry. Taken together, the limited genetic data presently available show that polyandry is taxonomically widespread among marine organisms; polyandry can vary among females within a population, and the mating system can vary from population to population.

### Sexual conflict

Sexual conflict occurs when males and females have different optimal fitness strategies concerning reproduction, potentially leading to antagonistic selection [6]. Conflict between the sexes arises over optimal number of mates, mate choice, and parental care, and can be expressed at any stage of the male–female interaction from courtship and mating, through fertilization, to post-zygotic parental investment [6]. In many fish, sexual conflict can influence the occurrence and maintenance of alternative reproductive strategies, the co-evolutionary dynamic between courtship and coercion, and the persistence of both caring and non-caring males within a population [36].

Another pervasive source of conflict arises over optimal sperm release rates [37], with many examples coming from species that reproduce by broadcast spawning, i.e. releasing sperm and eggs into the sea [38]. Until relatively recently, it was generally assumed that virtually all eggs were fertilized during a spawning event, and that sperm rarely competed for such fertilizations, thereby limiting opportunities for sexual selection and conflict [38]. We now know that sperm limitation and sperm competition (with the associated threat of lethal polyspermy) are common in broadcast spawners and can also occur in spermcasting species that are internally fertilized [33,39]. These

**Table 1. Some effects of reproductive, fertilization, and developmental modes on the potential for multi-way family conflicts**

Reproductive mode	Fertilization	Development	Potential for conflict			Examples	
			Sexual	Parent–offspring	Sibling	Taxon	Refs
Broadcast spawning	External	Planktotrophic <sup>a</sup>	High: egg size, sperm release rates and other gamete traits	Limited	Some: if kin disperse together	Sea stars, sea urchins	[40,63]
	External	Lecithotrophic <sup>b</sup>	High: resource investment	Limited	Some: if kin disperse together	Corals, tunicates	[34]
Spermcasting	External (only sperm are released)	Planktotrophic <sup>a</sup>	High: gamete traits	High: resource allocation	High: space and parental resources	Colonial ascidians	[33,87]
Brooding	External	Direct <sup>c</sup>	High: resource investment	High: resource allocation	High: nutrients, oxygen, space	Sea spiders, pipefish	[44,98]
	Internal	Planktotrophic <sup>a</sup>	High: mating, sperm competition	Limited	High: oxygen, egg mass position	Crabs, barnacles	[25,99]
	Internal	Lecithotrophic <sup>b</sup>	High: mating, sperm competition, resource investment	High: resource allocation	High: nutrients	Bryozoans	[100]
	Internal	Planktotrophic <sup>a</sup> and direct <sup>c</sup>	High: mating, sperm competition	High: resource allocation	High: nutrients	Polychaetes	[57]
Encapsulating	Internal	Direct <sup>c</sup>	High: mating, sperm competition, resource investment	High: resource allocation	High: nutrients, oxygen	Gastropods, cephalopods	[30,58,64]

<sup>a</sup>Many eggs hatch out into free-swimming larvae and need to feed in the plankton in order to develop and undergo metamorphosis.

<sup>b</sup>Few large eggs (with large yolk reserves per egg) hatch into free-swimming larvae but do not need to feed in the plankton in order to undergo metamorphosis.

<sup>c</sup>Few large eggs that are brooded or released as small adults; there is no free-swimming larval stage.

represent potent, often conflicting selective forces acting on both egg and sperm traits, including egg size, sperm behavior, and the proteins that mediate gamete compatibility [40–43] (Box 2). In addition, sperm limitation can select for more efficient mechanisms of sperm capture, including egg retention which in turn could explain the evolution of internal brooding [42]. As we discuss in the next section, this (and other) derived forms of parental care enhance opportunities for parent–offspring and sibling conflict, and might thus act as important arbiters of sexual conflict [44].

### Parent–offspring conflict

There is growing evidence that, in many marine organisms, offspring size varies extensively within and among broods [17]. A key component of the hypothesis that parent–offspring conflict accounts for at least some of this variation is that offspring can influence parental investment after fertilization. In species that internally brood and nourish developing offspring (e.g. some echinoderms, cartilaginous fish, parasitic flatworms, tunicates, bryozoans, and cnidarians), or in taxa that provide post-zygotic parental care (e.g. teleost fish and crustaceans), parents and siblings directly interact [45,46]. These direct interactions can promote the evolution of behaviors like begging (reviewed in [4]), and structures such as placentas and plant endosperm that regulate nutritional flow from parent to offspring [46–48]. For example, viviparity is the dominant mode of reproduction among cartilaginous fishes, with the structure and complexity of the placenta varying greatly among species, perhaps resulting from differing degrees of conflict ([49] and see [50] for a review of conflict and placentation in the Poeciliidae).

Similarly, male pipefish brood their embryos in a pouch and nutrients cycle between father and offspring during pregnancy [51,52]. The brood pouch thus provides the venue for parental care, but recent work shows that it also plays a role in mediating conflict. For example, *Syngnathus scovelli* males invest fewer resources in broods

originating from smaller females, resulting in competition among siblings and lower survivorship [44]. Males also selectively abort smaller embryos and absorb the resulting nutrients at the expense of the female (a situation analogous to filial cannibalism in many externally fertilizing fish [53]). Although males of *S. scovelli* mate with a single female per pregnancy, other pipefish species (e.g. *Syngnathus typhle*) mate with several; in broods of mixed maternity, some sibships have higher survival than others, but it is unclear whether this results from differential competitive ability or differential parental provisioning [54].

### Sibling conflict

Even in the absence of direct interactions between parents and offspring, siblings may compete intensely with one another for limiting resources such as food and oxygen, when packaged in maternally provisioned nurseries. Offspring packaging is widespread in many aquatic animals (Figure 2), including amphibians [55], chondrichthyan fish [49], and mollusks [30,56], as well as many polychaete worms [57], and promotes various forms of sibling conflict, including the consumption of non-developing nurse eggs (oophagy), consumption of fertilized zygotes and embryos (adelphophagy), or viable siblings (cannibalism *sensu stricto*) [9].

Some of the most compelling evidence that encapsulation provides the requisite arena for conflict, and that the degree of polyandry modulates these conflicts, comes from studies of angiosperm seed development [9,13]. For example, many self-fertilizing plants have unimodal seed-weight distributions with little variance around the mean; in contrast, outcrossing plants have less symmetric distributions and significantly higher mean and variance of seed weights. Seed abortion rates also increase as polyandry increases and relatedness of siblings decreases [13]. While empirically unexplored, the parallels between fruits and pods on the one hand and egg masses and capsules on

### Box 2. Sexual conflict and the evolution of gamete interactions

For over thirty years, the prevailing explanation for anisogamy (large eggs and tiny sperm) has been that scramble competition for fertilizations leads to the evolution of increased sperm numbers at the expense of sperm size [92]. Theoretical models predict that, under sperm competition, males should release sperm as quickly as possible in order to increase their share of the fertilization 'raffle' [92]. In contrast, broadcast spawning males in many natural populations release their gametes slowly, spawning repeatedly over several days [93].

One explanation for this discrepancy is that fertilization failure can occur at both high and low sperm concentrations. When there are few males present at a spawning event, males should release fewer sperm than is optimal for females because, by doing so, they can maximize their number of spawning events, as well as minimize sperm wastage due to polyspermy [42]. Females can respond to this sperm limitation by adding accessory structures, such as jelly coats, that increase target size with minimal energetic investment [94]. They can also increase maternal allocation of yolk which may lead to the spawning of larger, but fewer, eggs than would be the maternal optimum in the absence of sperm limitation [40].

When many males are present, they will release more sperm than is optimal for females, since polyspermy will kill some of the females' eggs [42]. Females may then respond either by producing eggs that resist fertilization [95], or by producing smaller eggs than would be optimal for post-zygotic offspring performance [96]. Thus, sexual conflict could result in a co-evolutionary chase whereby eggs are selected to be harder to fertilize and sperm are selected to have greater fertilizing capacity [95], and might have played a role in the evolution of anisogamy and sperm-egg recognition proteins.

The strong effects of egg size on fertilization and subsequent offspring performance have manifold ecological and evolutionary implications. For example, egg size is often correlated with planktonic duration, so that species with small eggs and a planktonic larval stage should disperse considerably farther than species with large eggs [17]. These differences in dispersal distances should, in turn, influence the spatial scale and strength of demographic links between populations, genetic connectivity, the potential for local adaptation, and rates of speciation and extinction [97].

the other suggest that there should be comparable links between mating system and conflict in many marine organisms.

#### Competition for nutrients

There is tantalizing circumstantial evidence that sibling conflict over nutrients is rife, and that mating system may influence its magnitude and outcomes. In the snail *Nucella ostrina*, maternal resource allocation and, therefore, hatchling size vary between populations, habitats, individuals, and broods [58,59]. Mating aggregation densities also vary (e.g. [58,60]), potentially fueling differences in the degree of polyandry, and providing a conflict-driven explanation for within-population offspring size variation in this species.

Conflict may also occur among siblings competing for extracapsular resources. For example, sacoglossan mollusks deposit a string of eggs that are enclosed in an individual capsule and provisioned with nutritive albumen. Eggs are then encased within a protective tube and extracapsular yolk (ECY) is deposited throughout the egg mass. Veliger larvae consume this ECY until they exit the tube, and larval size depends more strongly on the amount of ECY available to and consumed by the embryos, rather than egg size *per se* [61].

Sibling conflict almost certainly occurs in many internally brooding species as well (Figure 2b), like the viviparous sea stars, *Parvulastra vivipara* and *Parvulastra parvivipara*, which incubate asynchronously developing young in their gonads [62,63]. In these species, juveniles prey on their siblings to varying degrees, which accounts for substantial differences in post-metamorphic size and growth. Interestingly, these species can both self-fertilize and outcross, but whether variation in rates of cannibalism correlates with the degree of relatedness among siblings remains to be examined.

#### Competition for oxygen

The low solubility and diffusibility of oxygen in water, combined with water's viscosity, present major constraints on the delivery of oxygen to embryos packaged in capsules or masses, and have undoubtedly influenced the evolution of numerous features of these nurseries [64,65]. While family conflict theory has yet to play a significant role in our understanding of competition for oxygen, the location of an embryo within an egg mass can be critical for that embryo's development and survival, and there is growing evidence that developing siblings compete for oxygen [64,65].

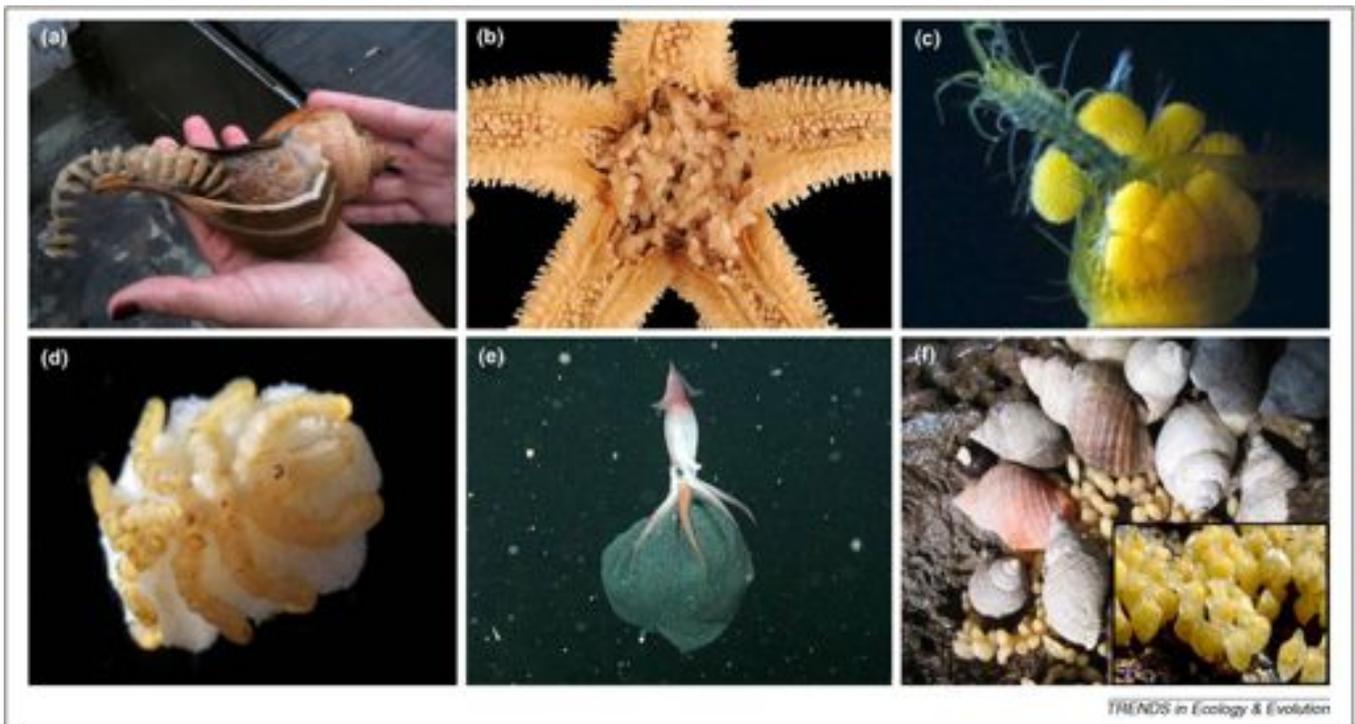
Embryos in the center of an aggregation are often exposed to longer periods of hypoxic conditions and have slower development times than embryos on the periphery, a situation that opens the door to sibling conflict over position within a mass [66]. In several direct-developing gastropod species, offspring cannibalize their siblings during development, an adjustment that seems to be related not only to nutritional needs but also to the regulation of oxygen availability. For example, in the predatory snail *Acanthina monodon*, sibling cannibalism increases as oxygen concentration decreases [67].

#### Where to from here?

Marine biologists are just beginning to consider the ramifications of family conflict for the evolution of life-history traits, and there is a vast amount of empirical work waiting to be done on quantifying these conflicts and their interactions with mating systems. Beyond this, there are several new frontiers, which we highlight below, that emerge from acknowledging that family conflict may be a pervasive selective force in the sea. [68]

#### Kin recognition

As the number of males fathering a brood increases, the inclusive fitness costs of harming a sibling will decline, and selfish behavior should increase [4,47,69]. Under these circumstances, kin selection will generally favor individuals that recognize and avoid harming full-siblings, or that limit destructive behavior in their presence [70]. For example, in spadefoot toads, young reared with full-siblings become cannibalistic less often than young reared in mixed sibships [71]. Several experimental studies on marine bryozoans [72] and ascidians [73] also suggest that offspring behavior toward siblings varies with relatedness in the direction predicted by kin selection theory. Further empirical work is needed to determine how often cannibalistic behaviors are directed away from close kin, and more



**Figure 2.** Various modes of offspring packaging and opportunities for sibling and parent-offspring conflict in marine organisms: (a) a female channeled whelk (*Busycon canaliculatum*) producing a string of egg capsules (Photograph by Eric Heupel); (b) a female sea star (*Diplasterias brandti*) brooding juveniles (Photograph by Adrian James; <http://invertebrates.si.edu/ANTIZ>); (c) external brooding of developing eggs in the planktonic polychaete worm *Autolytus* sp. (Photograph courtesy of Alexandra Bely, University of Maryland); (d) dorsal view of a live male pycnogonid (*Pycnogonum stearnsi*) carrying a large egg cluster (Photograph by P.J. Bryant); (e) egg-carrying in a female squid (*Gonatus onyx*), where the egg mass is suspended from hooks on the squid's arms. The female is using her arms to pump fresh water through the egg mass, causing it to inflate (Photograph courtesy of the Monterey Bay Aquarium Research Institute); (f) a group of whelks (*Nucella lapillus*) laying egg capsules on a rocky shore (Photograph by Judith Oakley; [www.oakleynaturalimages.com](http://www.oakleynaturalimages.com)). Inset: egg capsules in the intertidal predatory whelk, *Nucella ostrina* (Photograph by Eric Sanford, UC Davis).

generally whether there are associations between patterns of relatedness within broods, and overall tendencies to exhibit harmful behaviors.

#### Resource control

The outcomes of conflict are sensitive to assumptions regarding the ability of parents and offspring to develop counter-responses to novel tactics exhibited by the other party, both at ontogenetic and evolutionary timescales [74]. Consequently, empirical studies of proximate mechanisms, such as hormonal pathways, that mediate resource flow are essential steps toward understanding how such conflicts co-evolve [74]. For example, in a number of plant systems, hormones involved in resource uptake are exclusively synthesized by offspring tissue, whereas hormones involved in restricting transport of nutrients into the seeds are exclusively produced by maternal structures [75]. There are many opportunities to conduct analogous studies in marine organisms, especially among internal brooders.

Fusion between siblings, often seen in algae and colonial invertebrates, presents another promising area for future research. Fusion might allow siblings to regain control over resource allocation and provide a mechanism for increasing their size. This could be costly for mothers as it concentrates offspring in space and makes them more vulnerable to local disturbances. It might also result in offspring larger than the maternal optimum. Alternatively, sibling fusion may benefit the mother by increasing

the mean and/or variance of offspring size beyond that inherent in egg-size variation alone.

#### Conflict-mediation

How can females gain the direct and indirect genetic benefits of polyandry while minimizing the resulting increase in conflict among family members? One potential mechanism would be through cryptic choice of sperm: a female could regain control of the conflict by allocating patriline to particular broods, ensuring that interacting offspring will be full- rather than half-siblings [9].

Polyembryony, the splitting of a single sexually produced embryo into many clonal copies, represents another potential mechanism [76]. Although extremely rare in mammals, it is widespread in parasitoid Hymenoptera, internally fertilized cyclostome bryozoans, hydrozoans, and echinoderms [76]. Most hypotheses predict that polyembryony should evolve when offspring have more information regarding optimal clutch size than the parents [76]. An intriguing alternative is that it evolved as a means for mothers to reduce sibling, and consequently parent-offspring, conflict within a brood [13,77]. The diversity of marine invertebrates that exhibit polyembryony represents an entirely unexploited resource for testing this aspect of conflict theory.

#### Genomic imprinting

Parent-of-origin silencing of specific genes renders either the maternally or paternally inherited copy silenced while

the other copy is active in the embryo. Haig and colleagues initially proposed that such genomic imprinting could evolve from sexual conflict over offspring provisioning in species where offspring are directly nourished from maternal tissues (e.g. mammals and flowering plants) [48]. The recent discovery of a functional gene-silencing system in the social bee *Apis mellifera* underscores the potential importance of genomic imprinting in invertebrates [78]. In marine organisms, we might expect to see sex-specific differences in genes that regulate nutrient flow, or facilitate kin recognition among potentially cannibalistic offspring: maternal transcripts would block recognition (because all siblings are equally related to their mother), whereas paternal transcripts would favor consumption of half- vs. full-siblings. Recent genomic (e.g. high-throughput sequencing) and computational (e.g. bioinformatics) approaches should facilitate the acquisition and analysis of these types of data [79].

### Speciation

Several recent reviews have emphasized how sexual conflict in marine organisms affects the evolution of gamete-recognition proteins, reproductive divergence, and incipient speciation [43]. However, the role of conflict in promoting population divergence is not limited to inter-locus interactions. For example, growing evidence suggests that divergences in mating system can generate inter-population differences in both the magnitude of parent-offspring conflict, as well as the outcomes of selection to limit conflict, resulting in reproductive isolation [45,80]. These types of mismatches could be widespread, particularly among internally brooding marine organisms. In addition, comparative analyses across species could clarify how variation in mating systems influences patterns of evolutionary diversification.

### Why polyandry?

A wealth of recent studies, primarily on insects and birds, have documented the indirect benefits of polyandry, including enhanced fitness or genetic diversity of offspring and increased scope for cryptic female choice of genetically compatible sperm (reviewed in [22]). Several studies have extended this perspective into the marine realm, and suggest that polyandry can enhance fertilization success [81] and influence the expression of offspring traits related to juvenile performance [81,82]. Few studies, however, consider the latent indirect costs of polyandry (but see [83]), but these might play a role in the structuring of kin dynamics within a family.

### Conclusions

Family conflict theory has grown to provide a powerful and general framework that significantly extends previous approaches (i.e. pairwise conflicts and maternal effects) aimed at understanding the causes and consequences of inter-specific, intra-specific, and intra-individual variation in a broad array of life history traits, including mating behaviors, parental care, resource allocation, and dispersal. Such variation may also have profound macro-evolutionary consequences, influencing rates of speciation, extinction, and range sizes. Thus, across the full spectrum

of ecological and evolutionary timescales, marine organisms, with their unrivalled diversity of mating systems, fertilization, reproductive and developmental modes, offer a novel and compelling arena within which to examine all of these aspects of family conflict, many of which are just beginning to be investigated in terrestrial organisms.

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### References

- 1 Frank, S.A. (1998) *Foundations of Social Evolution*, Princeton University Press
- 2 Hamilton, W.D. (1964) Genetical evolution of social behaviour. *J. Theor. Biol.* 7, 1–52
- 3 Trivers, R.L. (1974) Parent-offspring conflict. *Am. Zool.* 14, 249–264
- 4 Mock, D.W. and Parker, G.A. (1997) *The Evolution of Sibling Rivalry*, Oxford University Press
- 5 Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*, Princeton University Press
- 6 Arnqvist, G. and Rowe, L. (2005) *Sexual Conflict*, Princeton University Press
- 7 Parker, G.A. *et al.* (2002) Intrafamilial conflict and parental investment: a synthesis. *Philos. Trans. R. Soc. Lond. B., Biol. Sci.* 357, 295–307
- 8 Morales, J. *et al.* (2009) Families on the spot: sexual signals influence parent-offspring interactions. *Proc. R. Soc. Lond., B Biol. Sci.* 276, 2477–2483
- 9 Elgar, M.A. and Crespi, B.J., eds (1992) *Cannibalism. Ecology and Evolution among Diverse Taxa*, Oxford Science Publications
- 10 Banuelos, M.J. and Obeso, J.R. (2003) Maternal provisioning, sibling rivalry and seed mass variability in the dioecious shrub *Rhamnus alpinus*. *Evol. Ecol.* 17, 19–31
- 11 Long, T.A.F. (2005) The influence of mating system on the intensity of parent-offspring conflict in primates. *J. Evol. Biol.* 18, 509–515
- 12 Briskie, J.V. *et al.* (1994) Begging intensity of nestling birds varies with sibling relatedness. *Proc. R. Soc. Lond., B Biol. Sci.* 258, 73–78
- 13 Shaanker, R.U. and Ganeshiah, K.N. (1997) Conflict between parent and offspring in plants: Predictions, processes and evolutionary consequences. *Curr. Sci.* 72, 932–939
- 14 Royle, N.J. *et al.* (1999) Sibling competition and the evolution of growth rates in birds. *Proc. R. Soc. Lond., B Biol. Sci.* 266, 923–932
- 15 Vance, R.R. (1973) On reproductive strategies in marine benthic invertebrates. *Am. Nat.* 107, 339–352
- 16 Vance, R.R. (1973) More on reproductive strategies in marine benthic invertebrates. *Am. Nat.* 107, 353–361
- 17 Marshall, D.J. and Keough, M.J. (2008) The evolutionary ecology of offspring size in marine invertebrates. *Adv. Mar. Biol.* 1–60
- 18 Palumbi, S.R. (1994) Genetic divergence, reproductive isolation, and marine speciation. *Annu. Rev. Ecol. Syst.* 25, 547–572
- 19 Sotka, E.E. *et al.* (2004) Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Mol. Ecol.* 13, 2143–2156
- 20 Calderon, I. *et al.* (2007) Finding the relevant scale: clonality and genetic structure in a marine invertebrate (*Crambe crambe*, Porifera). *Mol. Ecol.* 16, 1799–1810
- 21 Addison, J.A. and Hart, M.W. (2005) Spawning, copulation and inbreeding coefficients in marine invertebrates. *Biol. Lett.* 1, 450–453
- 22 Simmons, L.W. (2005) The evolution of polyandry: Sperm competition, sperm selection, and offspring viability. *Annu. Rev. Ecol. Syst.* 36, 125–146
- 23 Paterson, I.G. *et al.* (2001) Multiple paternity in *Littorina obtusata* (Gastropoda, Littorinidae) revealed by microsatellite analyses. *Biol. Bull.* 200, 261–267
- 24 Walker, D. *et al.* (2007) Multiple paternity and female sperm usage along egg-case strings of the knobbed whelk, *Busycon carica* (Mollusca; Melongenidae). *Mar. Biol.* 151, 53–61

- 25 Toonen, R.J. (2004) Genetic evidence of multiple paternity of broods in the intertidal crab *Petrolisthes cinctipes*. *Mar. Ecol. Prog. Ser.* 270, 259–263
- 26 Roy, N. (2003) Incidence de la polyandrie chez le crabe des neiges, *Chionoecetes opilio* (Brachyura, Majidae), MSc Thesis, Université du Québec à Rimouski, Rimouski.
- 27 Gosselin, T. *et al.* (2005) Geographic variation of multiple paternity in the American lobster, *Homarus americanus*. *Mol. Ecol.* 14, 1517–1525
- 28 Brockmann, H.J. *et al.* (2000) Paternity in horseshoe crabs when spawning in multiple-male groups. *Anim. Behav.* 60, 837–849
- 29 Levitan, D.R. (2005) The distribution of male and female reproductive success in a broadcast spawning marine invertebrate. *Integr. Comp. Biol.* 45, 848–855
- 30 Shaw, P.W. and Sauer, W.H.H. (2004) Multiple paternity and complex fertilisation dynamics in the squid *Loligo vulgaris reynaudii*. *Mar. Ecol. Prog. Ser.* 270, 173–179
- 31 Sogard, S.M. *et al.* (2008) Multiple paternity in viviparous kelp rockfish, *Sebastes atrovirens*. *Environ. Biol. Fish.* 81, 7–13
- 32 Johnson, S.L. and Yund, P.O. (2007) Variation in multiple paternity in natural populations of a free-spawning marine invertebrate. *Mol. Ecol.* 16, 3253–3262
- 33 Bishop, J.D.D. and Pemberton, A.J. (2006) The third way: spermcast mating in sessile marine invertebrates. *Integr. Comp. Biol.* 46, 398–406
- 34 Ayre, D.J. and Miller, K. (2006) Random mating in the brooding coral *Acropora palifera*. *Mar. Ecol. Prog. Ser.* 307, 155–160
- 35 Engel, C.R. *et al.* (1999) Performance of non-motile male gametes in the sea: analysis of paternity and fertilization success in a natural population of a red seaweed, *Gracilaria gracilis*. *Proc. R. Soc. Lond., B Biol. Sci.* 266, 1879–1886
- 36 Alonzo, S.H. and Warner, R.R. (2000) Female choice, conflict between the sexes and the evolution of male alternative reproductive behaviours. *Evol. Ecol. Res.* 2, 149–170
- 37 Warner, R.R. *et al.* (1995) Sexual conflict - males with highest mating success convey the lowest fertilization benefits to females. *Proc. R. Soc. Lond., B Biol. Sci.* 262, 135–139
- 38 Levitan, D.R. (2006) The relationship between egg size and fertilization success in broadcast-spawning marine invertebrates. *Integr. Comp. Biol.* 46, 298–311
- 39 Yund, P.O. and O'Neil, P.G. (2000) Microgeographic genetic differentiation in a colonial ascidian (*Botryllus schlosseri*) population. *Mar. Biol.* 137, 583–588
- 40 Levitan, D.R. (2008) Gamete traits influence the variance in reproductive success, the intensity of sexual selection, and the outcome of sexual conflict among congeneric sea urchins. *Evolution* 62, 1305–1316
- 41 Franke, E.S. *et al.* (2002) Sexual conflict and polyspermy under sperm-limited conditions: In situ evidence from field simulations with the free-spawning marine echinoid *Evechinus chloroticus*. *Am. Nat.* 160, 485–496
- 42 Bode, M. and Marshall, D.J. (2007) The quick and the dead? Sperm competition and sexual conflict in sea. *Evolution* 61, 2693–2700
- 43 Palumbi, S.R. (2009) Speciation and the evolution of gamete recognition genes: pattern and process. *Heredity* 102, 66–76
- 44 Paczolt, K.A. and Jones, A.G. (2010) Post-copulatory sexual selection and sexual conflict in the evolution of male pregnancy. *Nature* 464, 401–404
- 45 Zeh, D.W. and Zeh, J.A. (2000) Reproductive mode and speciation: the viviparity-driven conflict hypothesis. *BioEssays* 22, 938–946
- 46 Crespi, B. and Semeniuk, C. (2004) Parent-offspring conflict in the evolution of vertebrate reproductive mode. *Am. Nat.* 163, 635–653
- 47 Queller, D.C. (1984) Models of kin selection on seed provisioning. *Heredity* 53, 151–165
- 48 Haig, D. (1993) Genetic conflicts in human pregnancy. *Q. Rev. Biol.* 68, 495–532
- 49 Wourms, J.P. (1977) Reproduction and development in chondrichthyan fishes. *Am. Zool.* 17, 379–410
- 50 Pollux, B.J.A. *et al.* (2009) Evolution of placentas in the fish family poeciliidae: an empirical study of macroevolution. *Annu. Rev. Ecol. Syst.* 40, 271–289
- 51 Sagebakken, G. *et al.* (2010) Brooding fathers, not siblings, take up nutrients from embryos. *Proc. R. Soc. Lond., B Biol. Sci.* 277, 971–977
- 52 Ripley, J.L. and Foran, C.M. (2009) Direct evidence for embryonic uptake of paternally-derived nutrients in two pipefishes (Syngnathidae: *Syngnathus* spp.). *J. Comp. Physiol. B* 179, 325–333
- 53 Manica, A. (2002) Filial cannibalism in teleost fish. *Biol. Rev.* 77, 261–277
- 54 Ahnesjö, I. (1996) Apparent resource competition among embryos in the brood pouch of a male pipefish. *Behav. Ecol. Sociobiol.* 38, 167–172
- 55 Brown, J.L. *et al.* (2008) Phytotelm size in relation to parental care and mating strategies in two species of Peruvian poison frogs. *Behaviour* 145, 1139–1165
- 56 Gosselin, L.A. and Rehak, R. (2007) Initial juvenile size and environmental severity: influence of predation and wave exposure on hatching size in *Nucella ostrina*. *Mar. Ecol. Prog. Ser.* 339, 143–155
- 57 Gibson, G.D. (1997) Variable development in the spionid *Boccardia proboscidea* (Polychaeta) is linked to nurse egg production and larval trophic mode. *Invert. Biol.* 116, 213–226
- 58 Lloyd, M.J. and Gosselin, L.A. (2007) Role of maternal provisioning in controlling interpopulation variation in hatching size in the marine snail *Nucella ostrina*. *Biol. Bull.* 213, 316–324
- 59 Moran, A.L. and Emlet, R.B. (2001) Offspring size and performance in variable environments: field studies on a marine snail. *Ecology* 82, 1597–1612
- 60 Spight, T.M. (1982) Population sizes of 2 marine snails with a changing food supply. *J. Exp. Mar. Biol. Ecol.* 57, 195–217
- 61 Allen, R.M. *et al.* (2009) Larval size in *Elysia styliifera* is determined by extra-embryonic provisioning but not egg size. *Mar. Ecol. Prog. Ser.* 389, 127–137
- 62 Byrne, M. (1996) Viviparity and intragonadal cannibalism in the diminutive sea stars *Patriella vivipara* and *P. parvivipara* (family Asterinidae). *Mar. Biol.* 125, 551–567
- 63 Byrne, M. (2006) Life history diversity and evolution in the Asterinidae. *Integr. Comp. Biol.* 46, 243–254
- 64 Brante, A. *et al.* (2009) Limiting factors to encapsulation: the combined effects of dissolved protein and oxygen availability on embryonic growth and survival of species with contrasting feeding strategies. *J. Exp. Biol.* 212, 2287–2295
- 65 Lee, C.E. and Strathmann, R.R. (1998) Scaling of gelatinous clutches: effects of siblings' competition for oxygen on clutch size and parental investment per offspring. *Am. Nat.* 151, 293–310
- 66 Strathmann, R.R. (2000) Form, function, and embryonic migration in large gelatinous egg masses of arenicolid worms. *Invert. Biol.* 119, 319–328
- 67 Lardies, M.A. and Fernandez, M. (2002) Effect of oxygen availability in determining clutch size in *Acanthina monodon*. *Mar. Ecol. Prog. Ser.* 239, 139–146
- 68 Michiels, N.K. and Streng, A. (1998) Sperm exchange in a simultaneous hermaphrodite. *Behav. Ecol. Sociobiol.* 42, 171–178
- 69 Shaanker, R.U. *et al.* (1988) Parent-offspring conflict, sibling rivalry, and brood size patterns in plants. *Annu. Rev. Ecol. Syst.* 19, 177–205
- 70 Pfennig, D.W. (1997) Kinship and cannibalism. *Bioscience* 47, 667–675
- 71 Pfennig, D.W. and Frankino, W.A. (1997) Kin-mediated morphogenesis in facultatively cannibalistic tadpoles. *Evolution* 51, 1993–1999
- 72 Keough, M.J. (1984) Kin-recognition and the spatial distribution of larvae of the bryozoan *Bugula neritina* (L.). *Evolution* 38, 142–147
- 73 Grosberg, R.K. and Quinn, J.F. (1986) The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature* 322, 456–459
- 74 Uller, T. (2008) Developmental plasticity and the evolution of parental effects. *Trends Ecol. Evol.* 23, 432–438
- 75 Ravishankar, K.V. *et al.* (1995) War of hormones over resource-allocation to seeds - strategies and counterstrategies of offspring and maternal parent. *J. Biosci.* 20, 89–103
- 76 Craig, S.F. *et al.* (1997) The 'paradox' of polyembryony: a review of the cases and a hypothesis for its evolution. *Evol. Ecol.* 11, 127–143
- 77 Segoli, M. *et al.* (2009) Brood size in a polyembryonic parasitoid wasp is affected by relatedness among competing larvae. *Behav. Ecol.* 20, 761–767
- 78 Elango, N. *et al.* (2009) DNA methylation is widespread and associated with differential gene expression in castes of the honeybee, *Apis mellifera*. *Proc. Natl. Acad. Sci. U. S. A.* 106, 11206–11211
- 79 Yang, H.H. and Lee, M.P. (2004) Application of bioinformatics in cancer epigenetics. *Ann. N. Y. Acad. Sci.* 1020, 67–76

- 80 Schrader, M. and Travis, J. (2008) Testing the viviparity-driven-conflict hypothesis: parent-offspring conflict and the evolution of reproductive isolation in a poeciliid fish. *Am. Nat.* 172, 806–817
- 81 Marshall, D.J. and Evans, J.P. (2007) Context-dependent genetic benefits of polyandry in a marine hermaphrodite. *Biol. Lett.* 3, 685–688
- 82 Evans, J.P. and Marshall, D.J. (2005) Male-by-female interactions influence fertilization success and mediate the benefits of polyandry in the sea urchin *Heliocidaris erythrogramma*. *Evolution* 59, 106–112
- 83 Evans, J.P. and Kelley, J.L. (2008) Implications of multiple mating for offspring relatedness and shoaling behaviour in juvenile guppies. *Biol. Lett.* 4, 623–626
- 84 Santelices, B. *et al.* (2003) Field testing of inter- and intraspecific coalescence among mid-intertidal red algae. *Mar. Ecol. Prog. Ser.* 250, 91–103
- 85 Petersen, J.K. and Svane, I. (1995) Larval dispersal in the ascidian *Ciona intestinalis* (L) - evidence for a closed population. *J. Exp. Mar. Biol. Ecol.* 186, 89–102
- 86 Duffy, J.E. (1996) Eusociality in a coral-reef shrimp. *Nature* 381, 512–514
- 87 Johnson, S.L. and Yund, P.O. (2008) Multiple paternity and subsequent fusion-rejection interactions in a kin-structured population. *Mar. Ecol. Prog. Ser.* 364, 129–134
- 88 Veliz, D. *et al.* (2006) Genetic evidence for kin aggregation in the intertidal acorn barnacle (*Semibalanus balanoides*). *Mol. Ecol.* 15, 4193–4202
- 89 Vigliola, L. *et al.* (2007) Genetic identity determines risk of post-settlement mortality of a marine fish. *Ecology* 88, 1263–1277
- 90 Miller-Sims, V.C. *et al.* (2008) Dispersal in the spiny damselfish, *Acanthochromis polyacanthus*, a coral reef fish species without a larval pelagic stage. *Mol. Ecol.* 17, 5036–5048
- 91 Buston, P.M. *et al.* (2009) Genetic relatedness in groups of the humbug damselfish *Dascyllus aruanus*: small, similar-sized individuals may be close kin. *Mol. Ecol.* 18, 4707–4715
- 92 Parker, G.A. (1982) Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *J. Theor. Biol.* 96, 281–294
- 93 Marshall, D.J. and Bolton, T.F. (2007) Sperm release strategies in marine broadcast spawners: the costs of releasing sperm quickly. *J. Exp. Biol.* 210, 3720–3727
- 94 Podolsky, R.D. (2004) Life-history consequences of investment in free-spawned eggs and their accessory coats. *Am. Nat.* 163, 735–753
- 95 Levitan, D.R. and Ferrell, D.L. (2006) Selection on gamete recognition proteins depends on sex, density, and genotype frequency. *Science* 312, 267–269
- 96 Crean, A.J. and Marshall, D.J. (2008) Gamete plasticity in a broadcast spawning marine invertebrate. *Proc. Natl. Acad. Sci. U. S. A.* 105, 13508–13513
- 97 Sanford, E. and Worth, D.J. (2009) Genetic differences among populations of a marine snail drive geographic variation in predation. *Ecology* 90, 3108–3118
- 98 Barreto, F.S. and Avise, J.C. (in press) Quantitative measures of sexual selection reveal no evidence for sex-role reversal in a sea spider with prolonged paternal care. *Proc. R. Soc. B.* Published online 12 May 2010 doi:10.1098/rspb.2010.0311
- 99 Crisp, D.J. (1959) The rate of development of *Balanus balanoides* (L) embryos *in vitro*. *J. Anim. Ecol.* 28, 119–132
- 100 Allen, R.M. *et al.* (2008) Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am. Nat.* 171, 225–237