SYMPOSIUM

Reproductive Biology, Family Conflict, and Size of Offspring in Marine Invertebrates

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Synopsis All organisms face two fundamental trade-offs in the allocation of energetic resources: one between many small versus a few large offspring, and the second between present and future reproduction. Nowhere are these trade-offs more apparent than in the vast range of variation in the sizes of eggs and offspring exhibited among species of marine invertebrates. It has become increasingly clear that, in many taxa of marine organisms, there is also substantial intra-specific variation in the size of eggs and hatchings. This variation has largely been attributed to adaptive maternal effects. In theory, however, the inevitable conflicts of interest that arise in families of sexually reproducing organisms over the optimal distribution of parental resources among siblings could also account for much of this variation in egg and offspring size. Here, we explore the potential impacts of family conflict on offspring traits by comparing the life histories of two exemplar species of marine organisms, the polychaete *Boccardia proboscidea* and the gastropod *Solenosteira macrospira*, emphasizing how differences in modes of fertilization and parental care might influence the phenotype and, consequently, the fitness of offspring.

Introduction

The trade-off between size and number of offspring is the fundamental principle underlying virtually all of contemporary life-history theory (Vance 1973a, 1973b; Smith and Fretwell 1974). Since a mother can only allocate finite resources to her progeny, how those resources are partitioned among offspring both within and between clutches is a critical determinant of her fitness. Whether selection favors the production of a few large or many small offspring depends on the optimal balance between size and number of offspring, which in turn hinges on the relationship between the size of offspring and their fitness (Lack 1947; Smith and Fretwell 1974; Christiansen and Fenchel 1979; Lloyd 1987). Nowhere are these trade-offs more apparent than in the vast range of variation in the sizes of eggs, offspring, and clutches exhibited by marine invertebrates

(Thorson 1946; Strathmann 1985; Kohn and Perron 1994; McEdward 2000; Podolsky and Moran 2006).

Vance (1973a, 1973b) developed the theoretical framework that still guides much of our current thinking about parental investment and the evolution of egg size and offspring size in marine invertebrates (Strathmann 1985; Emlet and Hoegh-Guldberg 1997; Levitan 2000; McEdward and Miner 2003). His model, based on a multi-way energetic trade-off between egg size, duration of the larval stage, and offspring mortality, predicts that disruptive selection will favor either small, minimally provisioned, planktonic feeding offspring, or large, well-provisioned eggs and offspring. Subsequent work shows that factors other than energetics (e.g., fertilization mode, benthic versus planktonic development, post-settlement performance) affect the evolution of egg size, post-zygotic parental provisioning,

and hatchling size (Christiansen and Fenchel 1979; Perron and Carrier 1981; Grant 1983; Podolsky and Strathmann 1996; McEdward 1997; Levitan 2000; McEdward and Miner 2003; Marshall et al. 2006). These refinements, however, still largely focus on patterns of interspecific variation and generally assume that stabilizing selection on size of eggs or offspring should substantially limit intraspecific variation for these traits (reviewed by Kohn and Perron 1994; Marshall and Keough 2008).

Nevertheless, over the past decade it has become increasingly clear that, in many taxa of marine organisms, there is substantial intraspecific variation in size of eggs and hatchlings not only within and among populations, but also within and among broods of the same female (Gibson 1997; Ellingson and Krug 2006; Gosselin and Rehak 2007; Marshall and Keough 2007). Explanations for among-brood variation in the size of offspring often focus on the environmental factors influencing maternal investment (Bernardo 1996; Moran and Emlet 2001), or on variation in the availability of resources to planktonic larvae (Marshall and Keough 2007), whereas the causes of within-brood variation are virtually unexplored. The most common explanations ascribe such variation either to non-adaptive stochastic variation in provisioning (Rivest 1983) or to a maternal bet-hedging strategy in unpredictably varying environments (Geritz 1995; Marshall et al. 2008b).

The conflicts of interest that arise in families of sexually reproducing organisms over the optimal distribution of parental resources among siblings (Trivers 1974; Temme 1986; Mock and Parker 1997) represent an alternative, rarely considered, but potentially widespread source of variation in size of eggs, seeds, and offspring. These conflicts emerge from the asymmetries in relatedness that are inevitable consequences of sexual reproduction. Given that a female is equally related to all of her offspring, all else being equal, selection should favor a uniform allocation strategy (Parker et al. 2002). However, a given offspring is more closely related to itself than to either its siblings or to her, and would benefit from a greater share of parental resources (Parker et al. 2002). Thus, while maternal fitness might be optimized with an invariant size of eggs, seeds, or offspring, competition over resources between parent and offspring or among siblings can oppose this source of stabilizing selection and promote variation in size within and among populations, individuals, and broods (Queller 1984a, 1984b; Shaanker et al. 1988; Mock and Forbes 1992; Mock and Parker 1997). The mating system,

in turn, and especially the degree of multiple paternity within and among sibships, can further amplify the scope and magnitude of these conflicts, as it reduces the average relatedness among offspring and increases the incentive to harm siblings (Parker et al. 2002).

In contrast to several studies on mammals (Haig 1993), terrestrial plants (reviewed by Shaanker and Ganeshaiah 1997; Brandvain and Haig 2005) and marine (Paczolt and Jones 2010) and freshwater fishes (Schrader and Travis 2008), remarkably little empirical attention has focused on distinguishing whether intraspecific variation in size of eggs and offspring among marine invertebrates represents adaptive maternal effects (*sensu* Marshall et al. 2008b), or instead reflects family conflict (Kamel et al. 2010; see Parker et al. 2002; Royle et al. 2004; and Rowe and Arnqvist 2002 for more general reviews). This lack of attention may be due to the perception that mates, parents and offspring, and siblings have limited opportunities to interact in the sea. In this article, we re-consider this view by exploring the various ways that family conflict could influence the expression and evolution of variation in size of offspring in marine invertebrates, and by evaluating the limited empirical evidence that it does so.

Reproductive mode and arenas of conflict

Marine organisms exhibit an astonishingly diverse array of reproductive modes, broadly divided into differences in where fertilization occurs (external versus internal) and where and how offspring develop (planktotrophic, lecithotrophic, or direct). Broadcast spawners shed both eggs and sperm into the water; spermcasting species retain their eggs but release sperm; hence like copulating species, are usually internally fertilized. Regardless of whether fertilization occurs externally or internally, the larvae that develop after fertilization may either be feeding (planktotrophic) or non-feeding (lecithotrophic) as they disperse in the plankton before settling and metamorphosing into sessile or sedentary adults. However, in contrast to externally fertilized species, internally fertilized species can brood offspring until they emerge as fully developed juveniles (direct developers). Brooding, in turn, can be internal, with nutrient exchange occurring via placentas or analogous structures, or external, in egg masses, capsules or sacs (Thorson 1950).

These differences in reproductive mode fundamentally determine the arenas and opportunities for conflict among family members. In broadcast

spawners, for instance, parent–offspring and sibling conflict ought to be rare, because offspring will have little opportunity to influence parental allocation decisions, and siblings disperse sufficiently widely that they are unlikely to interact (for some exceptions see Keough 1984; Veliz et al. 2006). Family conflict will thus emerge primarily as an intersexual interaction, with males and females having different optima with respect to gametic traits such as egg size, sperm behavior, and the proteins that regulate fertilizability (Levitan 2006; Bode and Marshall 2007; Palumbi 2009). Conversely, in organisms that brood or encapsulate their offspring there are more extensive opportunities for family members to interact. For instance, encapsulation engenders some of the most extreme forms of parent–offspring conflict and sibling rivalry (Thorson 1950), including consumption of non-developing nurse eggs (oophagy), and of viable siblings (adelphophagy) (Elgar and Crespi 1992). Siblings not only compete for nutrients provided by their parents, but also for resources that are affected by the packaging *per se*, such as the availability of oxygen (Lee and Strathmann 1998; Strathmann and Hess 1999; Moran and Woods 2007; Brante et al. 2008).

The ubiquity of egg masses, capsules, and other forms of encapsulation in marine invertebrates suggests that competition among siblings will occur frequently. A recent meta-analysis, spanning a broad range of marine taxa, provided intriguing circumstantial evidence that encapsulation and internal brooding enhance opportunities for parent–offspring and sibling conflict to influence offspring size (Marshall and Keough 2007). In direct-developing species (many of which internally brood or encapsulate their offspring), the coefficient of variation (CV) in offspring size is ~14%, declining to 10% and 4% in lecithotrophic and planktotrophic developers, respectively (Marshall and Keough 2007). In addition, internally fertilized lecithotrophs (still more of which are brooders or encapsulators) exhibit a significantly higher within-population CV in offspring size than do externally fertilized lecithotrophs (none of which provide arenas for siblings to interact directly). What remains to be seen is the extent to which these correlations between variation in offspring size and developmental mode reflect various forms of environmentally modulated phenotypic variation (including adaptive maternal effects), or whether parent–offspring conflict and sibling conflict also play a central role in determining these correlations. We now turn to two case studies that illustrate how often-overlooked aspects of an organism's

reproductive biology can decisively affect the character and magnitude of family conflict.

Boccardia proboscidea

Ecology, reproduction, and development

Boccardia proboscidea (Hartman 1940) is a gonochoric spionid polychaete commonly found on the west Coast of North America, with a distribution extending from British Columbia to Baja California (Hartman 1941; F. Oyarzun, unpublished data). Its range also includes Japan, southern Australia, South Africa, and Hawaii, all places where it appears to have been introduced (Hartman 1941; Petch 1989; Sato-Okoshi and Okoshi 1997; Sato-Okoshi 2000; Simon et al. 2009). Individuals are small (~2 cm maximum length) and typically inhabit the high and middle intertidal zones, either in the upper 4 cm of sediments, or in crevices and between barnacles. Tubes consist of sand and mucus and can occur in aggregations as dense as 20,000 m^{-2}. The worms live ~12 months, and reproduce between March and September in the Northeast Pacific (F. Oyarzun, personal observations; Gibson 1997). Females can store sperm for months, and brood fertilized eggs in capsules that they attach to the inside wall of their tubes (Hartman 1941, F. Oyarzun, personal observations).

Some populations of *B. proboscidea* unambiguously exhibit poecilogonous development, in which conspecific females produce offspring that differ with respect to both trophic mode and, likely, dispersal potential (Gibson 1997; Gibson et al. 1999). Females have been categorized by the different proportions of offspring they produce (Gibson 1997). Type I females produce only planktotrophic offspring, dispersing larvae that feed on phytoplankton. Type III females produce capsules that contain unfertilized, non-developing nurse eggs (~90% of total egg production), and both planktotrophic and adelphophagic progeny (Fig. 1A–C). Adelphophages consume nurse eggs and can also cannibalize planktotroph siblings developing in the same capsule (F. Oyarzun, manuscript in review). Adelphophages spend little time on the plankton or recruit directly to the sediment after hatching. Type II females are extremely rare, and produce capsules in which most eggs develop as planktotrophs and the remaining ~15% are nurse eggs. Females of all types can reproduce multiple times within a season, producing ~30 capsules in a given event (F. Oyarzun, unpublished data). Egg capsules of Types I and II females contain ~40–50 larvae, and those of Type III females contain nurse eggs and, on average, five developing larvae (Gibson 1997).
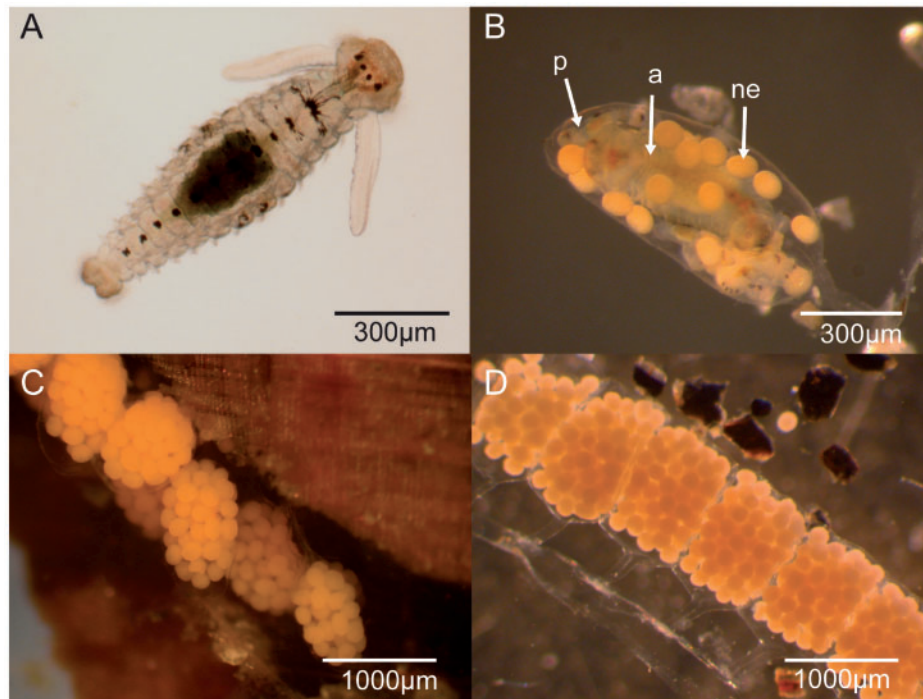
Fig. 1 (A) Adelphophagic larva of *B. proboscidea*. (B) Type III capsule of *B. proboscidea* containing adelphophagic (*a*) and planktotrophic (*p*) larvae and also several nurse eggs (*ne*). (C) Capsules of *B. proboscidea* still attached to parts of the mother's tube. (D) Capsules of *B. wellingtonensis*.

Sibling conflict

In *B. proboscidea*, the opportunities for sibling conflict depend on a female's reproductive type. Types I and II females produce dispersing larvae that feed in the plankton, limiting opportunities for competition among siblings for resources. Indeed, variance in offspring size, both within and among broods, is small for these types (Gibson 1997).

Numerous factors indicate that sibling conflict among offspring of Type III females should be high. Experimental manipulations show that adelphophages, the cannibalistic larvae that feed on nurse eggs and sibling planktotrophic larvae, grow faster at higher concentrations of nurse eggs. Given that the mean number of nurse eggs per embryo in a capsule is lower than the number of nurse eggs that results in the highest *in vitro* growth rates, sibling competition should be frequent (F. Oyarzun, manuscript in review). Indeed, the variance in offspring sizes is high among adelphophages (CV ~20%; Gibson 1997) and, within a given capsule, adelphophages can hatch out at different stages of development (F. Oyarzun, unpublished data). Adelphophages can also eat their planktotrophic siblings, which cannot defend themselves or escape from the capsule.

In *B. proboscidea*, mothers play an important role in mediating sibling conflict. First, they control the number of nurse eggs they allocate to capsules. Second, larval release requires maternal assistance. Females actively pull each capsule until it tears, expelling the contents of each capsule from the tube (F. Oyarzun, unpublished data), thus ending the opportunity for ongoing cannibalism.

Parent–offspring conflict

Parent–offspring conflict should arise in this system because the rate of cannibalism that maximizes maternal fitness is generally lower than the one that benefits individual cannibalistic offspring (Parker et al. 2002). Sibling cannibalism provides a net benefit to mothers if they gain in offspring number due to enhanced survival of cannibals as compared to the sibling victims that perish. Nevertheless in most circumstances, sibling cannibalism entails a high risk of direct fitness loss for the mother (Hamilton 1964). Selection should thus favor traits that control levels of sibling cannibalism (Schausberger and Hoffman 2008).

Given that females control the timing of hatching in *B. proboscidea*, the resulting phenotypes of the offspring (i.e., the proportion of planktotrophs

versus adelphophages; the size of adelphopages) may reflect the maternal optimum. At the least, mothers can limit the scope for sibling competition. The timing of hatching varies within and among females: some capsules are opened even though many nurse eggs still remain and offspring emerge at different sizes and at different developmental stages (F. Oyarzun, unpublished data). Early opening of capsules could provide both nutritional resources for the female (in the form of uneaten nurse eggs that she can ingest), as well as planktonically dispersing larvae, features that might be a response to locally unfavorable conditions. In any case, although there appears to be little opportunity for offspring to influence when they hatch they still could consume more of their siblings than would be the maternal optimum.

Maternal control of hatching is not ubiquitous in members of this genus, however. For example, females of the Southern-hemisphere species *Boccardia wellingtonensis* exhibit Type III reproduction, but mothers do not actively open capsules (F. Oyarzun, personal observations). Instead of discrete capsules, females produce strings of capsules linked by thin walls which, over time, can break down, permitting the offspring to escape (Fig. 1D; F. Oyarzun, personal observations). These connections also allow adelphophages to move to adjacent capsules and ingest other nurse eggs and planktotrophs. As a result, females may have less direct control over the size, number and dispersal of their offspring, although they might still be able to exert control over the types and sizes of offspring by modifying the distribution of nurse eggs and planktotrophs among individual capsules.

The contrasting opportunities for maternal control over sibling and parent–offspring conflict in *B. proboscidea* versus *B. wellingtonensis*, combined with extensive variation in the packaging of offspring in the *Boccardia–Polydora* complex (e.g., one large egg sac, interconnected capsules, separate capsules) (Blake 1969) raise the questions of whether this variation leads to predictable differences in levels of sibling and parent–offspring conflict, and how these reproductive traits evolve in a phylogenetic context. Is there a repeated evolutionary trend, both within and among clades, in the mode of encapsulation and resource control, or does the current distribution of traits reflect the present status of an ongoing, dynamic conflict between parents and offspring? The answers to such questions depend upon vastly improving our understanding not only of the phylogenetic relationships in taxa like *Boccardia*, but also on the phylogenetic distribution of the behaviors and life-history traits of parents and offspring.

Solenosteira macrospira

Ecology, reproduction, and development

Solenosteira macrospira (Berry 1957) is a gonochoric intertidal buccinid whelk native to the northern Gulf of California. Adult *S. macrospira* range from 35 to 45 mm in spire height (Brusca 1980), and live near rocks in sandy or muddy substrates in the middle to low intertidal zones (Gemmell et al. 1987). Buccinids are generally scavengers or saprophytes and can often be seen feeding on dead fish and invertebrates (Gemmell et al. 1987). Individuals of *S. macrospira* live for several years and reproduce between February and May in the northern Gulf of California.

Solenosteira macrospira females package large broods (more than 200 eggs) in durable chitinous capsules and then attach these capsules exclusively to the shells of male conspecifics during the course of mating (Fig. 2; Gemmell et al. 1987). Oviposition exclusively on males appears to be limited to some insects and amphibians in which males exhibit behaviors that bolster their confidence in paternity (Smith 1979a, 1979b). Based on sampling at three sites separated by up to 200 km of open water, *S. macrospira* appears to be one of the few species of gastropod in which females oviposit exclusively on males, despite sex ratios being nearly equal. Males also do not obviously guard females before, during, or after copulation (R.K. Grosberg and S.J. Kamel, unpublished data).

Females typically attach 4–31 ($x = 18.3$; SD $\pm$ 13.2) capsules per clutch. Laboratory studies show that inter-clutch intervals range from 2 to 14 days, and that well-fed females can produce as many as
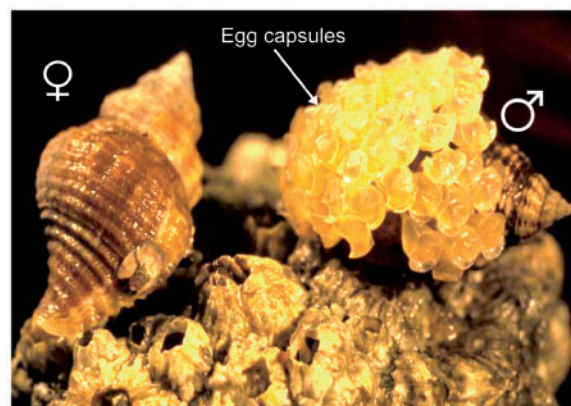

Fig. 2 Female (left) and male *S. macrospira* in the laboratory. Egg capsules nearly completely cover the male, barely visible on the right.

10 clutches ($x = 6.5 \pm 2.9$ SE) over a 2–3-month interval (R.K. Grosberg and S.J. Kamel, unpublished data). Virtually all of the eggs begin development synchronously; however, most are consumed by their capsulemates and, on average, 3–5 hatchlings emerge from the capsules and crawl off of the brooding male about a month after oviposition (R.K. Grosberg and S.J. Kamel, unpublished data). In contrast to evidence that *B. proboscidea* females cannibalize their offspring, neither female nor male *Solenosteira macrospira* engage in comparable behavior.

Sibling conflict

While parental protection increases offspring access to limiting resources and potentially reduces predation risk, offspring are nevertheless confined to a small space in which direct competition for resources can occur (Mock and Parker 1997; Strathmann and Strathmann 2006). Sibling cannibalism, the most extreme form of sibling conflict, is surprisingly common in animals that produce such nurseries (Elgar and Crespi 1992; Mock and Parker 1997). Killing a conspecific can reduce the intensity of competition for access to limited resources, whereas cannibalism provides additional nutrition.

Reduction in size of the brood in *S. macrospira* is severe, with only ~2.5% of the eggs surviving until hatching (R.K. Grosberg and S.J. Kamel, unpublished data). The size of the brood begins to decline by Day 7, with the highest rates of cannibalism taking place between Days 7 and 24. This occurs because some embryos within the case develop more rapidly than others, and consume many of the remaining eggs and more slowly developing embryos before exiting the case. Field and laboratory observations over the course of three breeding seasons show that cannibalism in *S. macrospira* occurs only within capsules, and does not extend to juveniles in other capsules (R.K. Grosberg and S.J. Kamel, unpublished data).

Rates of cannibalism and consequently growth within a capsule also vary across a season, resulting in substantial differences in the size and number of emerging hatchlings (Fig. 3; R.K. Grosberg and S.J. Kamel, unpublished data). We collected developmental data from newly laid, field-collected egg capsules deposited early and late in the breeding season that we reared in the laboratory at 18°C. We measured 15 embryos from four capsules of an individual female ($n = 5$ females) every three days using a calibrated ocular micrometer at 25× under a dissecting microscope. In clutches laid earlier in the reproductive season, embryos emerge sooner and at a smaller size, and levels of intracapsular cannibalism
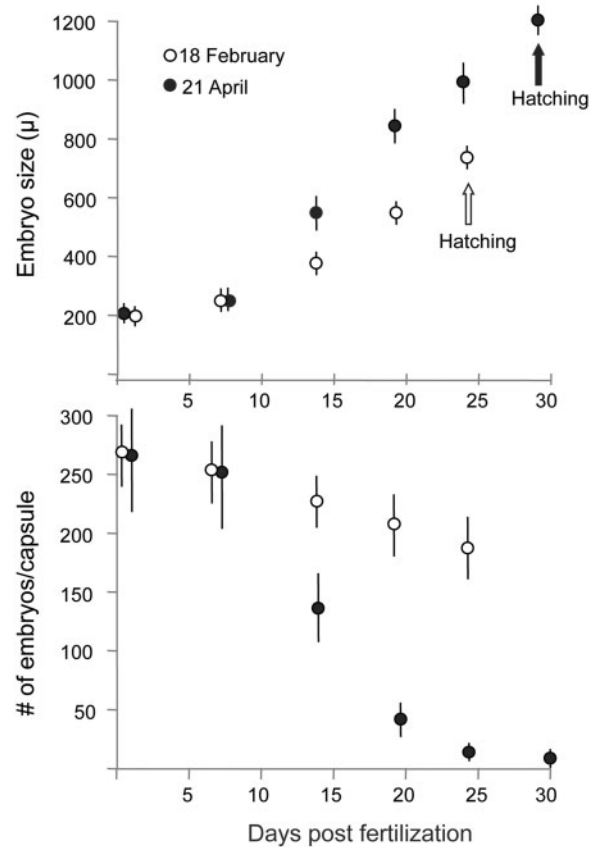

Fig. 3 Seasonal variation in (top) developmental rate and (bottom) cannibalism rate of *S. macrospira* based on newly laid, field-collected egg capsules reared at 18°C. Size estimates are pooled means ± SE of 15 offspring from four capsules from each of five field-collected females, sampled every third day.

are considerably lower than in clutches laid later on. The increase in rates of cannibalism could at least partly reflect changes in maternal allocation of resources to capsules. However, there are no obvious seasonal differences in patterns of maternal allocation, either in terms of egg size or number of eggs per capsule. Why then do late-season offspring emerge at a larger size than do offspring earlier in the season? Why are they more likely to cannibalize capsulemates? An intriguing possibility is that increases in cannibalism are driven by decreased relatedness of siblings within capsules, brought about by higher levels of polyandry and patrilineal diversity within a capsule later in the season. Explicit genetic tests of the incidence of polyandry in gastropods are rare (reviewed by Baur 1998); however, the few available data indicate that it may be common (Gaffney and McGee 1992; Paterson et al. 2001). In the case of *S. macrospira*, we assessed the incidence of polyandry by genotyping offspring at six microsatellite loci ($n = 228$ capsules and 1400 offspring), and inferred

the number of paternal genotypes within a capsule with the sibship reconstruction program COLONY (Wang 2004). Preliminary genetic analyses of embryos within field-collected *S. macrospira* egg capsules reveal more than four alleles at some microsatellite loci (the maximum number expected if a single male fathers the entire clutch), suggesting that multiple males sired the siblings within a capsule. Indeed, these analyses show that the mean number of patrilines per capsule is 2.9 (range 1–6) (Fig. 4; S.J. Kamel and R.K. Grosberg, unpublished data).

Parent–offspring conflict

Intrabrood sibling cannibalism represents a form of maternal investment subject to both parent–offspring and sibling conflict (Mock and Parker 1997; Parker et al. 2002). The magnitude of this conflict in part depends on the number of embryos a female places within a brood's nursery, whether offspring consume a fixed versus a variable number of siblings, and the relatedness of those offspring. Ecological context may also influence the fitness costs and benefits of cannibalism, and hence its expression (Elgar and Crespi 1992). For example, several studies show that the degree of cannibalistic behavior, and the extent to which cannibals discriminate among kin, varies with nutritional status, such that nutritionally stressed progeny are more willing to consume close relatives than when they are well fed (Pfennig et al. 1993).

Polyandry, through its effects on the relatedness of broodmates, also magnifies the scope for parent–offspring and sibling conflict over maternal allocation of resources as well as for rates of cannibalism
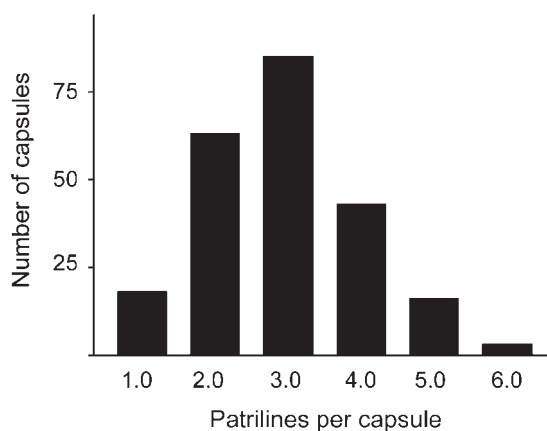
(Clutton-Brock 1991; Elgar and Crespi 1992; Mock and Parker 1997; Summers and Earn 1999; Loeb et al. 2000). A female is equally related to all of her offspring; however, when females use sperm from multiple males to fertilize a clutch, the average relatedness of siblings will decline below 0.5. If females mix sperm from different males, then the greater the level of polyandry, and the more likely it is that sibling interactions within a nursery or capsule will involve half-siblings, rather than full-siblings (McCauley and Odonnell 1984; Laurila and Seppa 1998). All else being equal, polyandry should favor the evolution and expression of sibling cannibalism, because the average inclusive fitness costs of consuming a capsulemate should decrease as the average relatedness among capsulemates declines, regardless of whether siblings can distinguish full- from half-siblings.

In *S. macrospira*, our preliminary data indicate that the seasonal increases in rate of cannibalism and in size at hatching are correlated with an increase in the number of patrilines represented within egg capsules. This increase may represent offspring acquiring more resources than the parental optimum later in the reproductive season, fueled by the declining inclusive fitness costs of consuming related capsulemates. Alternatively, the increasing levels of cannibalism may be consistent with a changing parental optimum, reflecting the increased efficiency that larger hatchlings might gain by attacking their preferred prey: barnacle spat that recruit early in the snail's reproductive season and continue to grow. Disentangling the relative winners and losers in this conflict remains a major challenge in this and other species subject to multiple conflicts of interest and will minimally entail characterizing how lifetime reproductive success in females varies as a function of offspring size.

Discussion

Egg size and offspring size have pervasive developmental, ecological, and evolutionary implications for marine invertebrates. For example, egg size is often correlated with duration of the planktonic phase, so that species with small eggs and a planktonic larval stage should disperse considerably farther than do species with large eggs (Kohn and Perron 1994; Collin 2004). Differences in dispersal abilities have been shown to influence population connectivity (Baskett et al. 2007), range size (reviewed by Lester et al. 2007), the potential for local adaptation (Sanford and Worth 2009; E. Sanford and

Fig. 4 Distribution of the number of patrilines within individual capsules of *S. macrospira* ($n = 228$ capsules). For each capsule, an average of 10 offspring was genotyped at six loci. Paternal genotypes were inferred using the sibship reconstruction program COLONY (Wang 2004).

M.W. Kelly, submitted for publication), as well as rates of speciation and extinction (Palumbi 1994).

Variation in egg size and offspring size both within and among populations may be caused by a variety of mechanisms. For instance, there is striking geographic variation in reproductive mode among populations of *B. proboscidea* (F. Oyarzun, unpublished data). All three types live in California; however, only Type III females (producing a mixture of planktotrophs and adelphophages) are abundant in Canada, Washington, Oregon, and Japan (Sato-Okoshi and Okoshi 1997; Sato-Okoshi 2000; F. Oyarzun, unpublished data). Several reproductive traits, such as the number of capsules deposited per female, the ratio of offspring types, and the number of nurse eggs per capsule, also vary geographically (Gibson et al. 1999; F. Oyarzun, unpublished data). Females in populations at higher latitudes spend more time with their capsules, brood for longer periods and produce more nurse eggs per capsule (F. Oyarzun, unpublished data). This intra specific pattern of latitudinal variation more-or-less corresponds to the interspecific pattern found in some (but by no means all) groups of marine invertebrates in which species living at higher latitudes tend to exhibit a higher incidence of direct development and invest more in protective structures such as capsules than do more temperate species (Thomson 1878; Thorson 1950; Pearse et al. 1991; Pearse 1994).

The sources and adaptive significance of this variation in *B. proboscidea* and many other species remain elusive. Most studies emphasize the roles of physiological stress, maternal size and nutritional state, and quality of habitats on the size of eggs and offspring, presumably reflecting changing, condition-dependent maternal optima (Marshall et al. 2008a). However, as we emphasize here, conflict between family members, especially between siblings and between parents and offspring over access to nutrients and other resources, can also generate variation in size of offspring. The jury is out as to whether the widely observed variation in size of offspring within and among broods represents adaptive adjustments on the part of parents, or is an outcome of an evolutionary tug-of-war among family members. Marine invertebrates, with their unmatched diversity of reproductive modes, provide incisive opportunities to investigate these complementary hypotheses.

Multiple mating, relatedness, and conflict

The role of mating system and family conflict as arbiters of offspring size has largely been ignored in marine organisms, in which most theoretical and empirical works have emphasized free-spawning species for which there is little opportunity for siblings to interact either with each other, or with their parents (e.g., abalones and sea urchins) (Levitan 1996; Swanson and Vacquier 1998). For many marine invertebrates, however, there is growing evidence that both polyandry and extended kin associations exist (Kamel et al. 2010). Thus, the conditions required for conflict to influence life-history evolution should be widely met in marine invertebrates.

In *B. proboscidea*, as in other spionids, males provide females with spermatophores, which can be stored for several months before use (Rice 1978, 1981; Söderström 1920). Although genetic data characterizing the mating system in *B. proboscidea* are not yet available, given its habit of living in very dense aggregations, sperm limitation seems unlikely, and multiple mating is probably common. Similarly, in *S. macrospira*, laboratory-reared females can deposit more than 10 clutches over a 2-month interval. The potential to lay multiple clutches, along with high population densities (>200 individuals/m^2), imply that females mate with different males during each mating event. Laboratory studies, in which individual females were placed with five males, confirm this prediction: females copulated with at least two, and sometimes all five, males over 5 days of observation (R.K. Grosberg and S.J. Kamel, unpublished data).

Polyandry in these systems would have further implications whereby the observed cannibalistic behaviors would be a vehicle for playing out genetic conflicts of interest. In polyandrous species, kin selection should favor cannibalistic individuals that can assess the degree of sibling relatedness resulting in an inverse correlation between the likelihood of cannibalism and the relationships between cannibal and victim (Pfennig 1997; Bilde and Lubin 2001). Thus, both *B. proboscidea* and *S. macrospira* provide ideal systems for studying the existence and mechanisms of kin recognition and its role in mediating family conflict.

Conclusions

In both terrestrial and marine systems, the expression and evolution of offspring size is subject to manifold conflicts, whose importance depends upon the venue for fertilization, developmental mode, and mating system. The degree of conflict also hinges on the ability of offspring to counteract parental strategies, as well as the discrepancy between the parental

optimum, and that of its offspring. Here, we have highlighted the biology of two species for which conflict might play an important, and novel, role in generating variation in offspring size. It remains to be seen whether such conflicts play a comparable role in other marine invertebrates, but the conditions essential for family conflict to influence the evolution and expression of life-history traits are far more pervasive than is presently assumed. To the extent that this is true, the current theoretical framework for interpreting both interspecific and intraspecific variation in marine invertebrate life histories should be expanded to recognize that neither father nor mother always knows best: sometimes the kids get their way.

Acknowledgments

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References

Baskett ML, Weitz JS, Levin SA. 2007. The evolution of dispersal in reserve networks. Am Nat 170:59–78.

Baur B. 1998. Sperm competition in molluscs. In: Birkhead TR, Møller AP, editors. Sperm competition and sexual selection. New York: Academic Press. p. 255–306.

Bernardo J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. Am Zool 36:216–36.

Berry SS. 1957. Notices of new eastern Pacific Mollusca I. Leaflets in Malacol 1:75–82.

Bilde T, Lubin Y. 2001. Kin recognition and cannibalism in a subsocial spider. J Evol Biol 14:959–66.

Blake JA. 1969. Reproduction and larval development of *Polydora* from northern New England (Polychaeta: Spionidae). Ophelia 7:1–63.

Bode M, Marshall DJ. 2007. The quick and the dead? Sperm competition and sexual conflict in sea. Evolution 61:2693–700.

Brandvain Y, Haig D. 2005. Divergent mating systems and parental conflict as a barrier to hybridization in flowering plants. Am Nat 166:330–8.

Brante A, Fernandez M, Viard F. 2008. Effect of oxygen conditions on intracapsular development in two calyptraeid species with different modes of larval development. Marine Ecol Progr Ser 368:197–207.

Brusca RC. 1980. Common intertidal invertebrates of the Gulf of California. Tucson, AZ: University of Arizona Press.

Christiansen FB, Fenchel TM. 1979. Evolution of marine invertebrate reproductive patterns. Theor Popul Biol 16:267–82.

Clutton-Brock TH. 1991. The evolution of parental care. Princeton, NJ: Princeton University Press.

Collin R. 2004. Phylogenetic effects, the loss of complex characters, and the evolution of development in calyptraeid gastropods. Evolution 58:1488–502.

Elgar MA, Crespi BJ. 1992. Cannibalism: ecology and evolution among diverse taxa. New York: Oxford University Press.

Ellingson RA, Krug PJ. 2006. Evolution of poecilogony from planktotrophy: Cryptic speciation, phylogeography, and larval development in the gastropod genus *Alderia*. Evolution 60:2293–310.

Emlet RB, Hoegh-Guldberg O. 1997. Effects of egg size on postlarval performance: experimental evidence from a sea urchin. Evolution 51:141–52.

Gaffney PM, McGee B. 1992. Multiple paternity in *Crepidula fornicata* (Linnaeus). Veliger 35:12–15.

Gemmell J, Myers BW, Hertz CM. 1987. A faunal study of the Bivalves of San Felipe and environs, Gulf of California, from the Gemmell collection (1965 to 1976). Festivus 18 (suppl.):1–72.

Geritz SAH. 1995. Evolutionary stable seed polymorphism and small-scale spatial variation in seedling density. Am Nat 146:685–707.

Gibson GD. 1997. Variable development in the spionid *Boccardia proboscidea* (Polychaeta) is linked to nurse egg production and larval trophic mode. Invert Biol 116:213–26.

Gibson G, Paterson IG, Taylor H, Woolridge B. 1999. Molecular and morphological evidence of a single species, *Boccardia proboscidea* (Polychaeta : Spionidae), with multiple development modes. Mar Biol 134:743–51.

Gosselin LA, 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 339:143–55.

Grant A. 1983. On the evolution of brood protection in marine invertebrates. Am Nat 122:549–55.

Haig D. 1993. Genetic conflicts in human pregnancy. Q Rev Biol 68:495–32.

Hamilton WD. 1964. The genetical evolution of social behaviour. J Theor Biol 7:1–52.

Hartman O. 1940. *Boccardia proboscidea*, a new species of spionid worm from California. J Washington Acad Sci 30:382–7.

Hartman O. 1941. Some contributions to the biology and life history of Spionidae from California. Allan Hancock Pac Exp 7:289–324.

Kamel SJ, Grosberg RK, Marshall DJ. 2010. Family conflicts in the sea. Trends Ecol Evol 25:442–449

Keough MJ. 1984. Kin recognition and the spatial distribution of larvae of the bryozoan *Bugula neritina*. Evolution 38:142–7.

Kohn AJ, Perron FE. 1994. Life history and biogeography. USA: Oxford University Press.

Lack D. 1947. The significance of clutch-size. Ibis 89:302–252.

Laurila A, Seppa P. 1998. Multiple paternity in the common frog (*Rana temporaria*): genetic evidence from tadpole kin groups. Biol J Linnean Soc 63:221–32.

Lee CE, Strathmann RR. 1998. Scaling of gelatinous clutches: Effects of siblings' competition for oxygen on clutch size and parental investment per offspring. Am Nat 151:293–310.

Lester SE, Ruttenberg BI, Gaines SD, Kinlan BP. 2007. The relationship between dispersal ability and geographic range size. Ecol Lett 10:745–58.

Levitan DR. 1996. Predicting optimal and unique egg sizes in free-spawning marine invertebrates. Am Nat 148:174–88.

Levitan DR. 2000. Optimal egg size in marine invertebrates: theory and phylogenetic analysis of the critical relationship between egg size and development time in echinoids. Am Nat 156:175–92.

Levitan DR. 2006. The relationship between egg size and fertilization success in broadcast-spawning marine invertebrates. Integr Comp Biol 46:298–311.

Lloyd DG. 1987. Selection of offspring size at independence and other size versus number strategies. Am Nat 129:800–17.

Loeb MLG, Diener LM, Pfennig DW. 2000. Egg-dumping lace bugs preferentially oviposit with kin. Animal Behav 59:379–83.

Marshall DJ, Allen RM, Crean AJ. 2008a. The ecological and evolutionary importance of maternal effect in the sea. Oceanogr Mar Biol 46:203–50.

Marshall DJ, Bonduriansky R, Bussiere LF. 2008b. Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. Ecology 89:2506–17.

Marshall DJ, Cook CN, Emlet RB. 2006. Offspring size effects mediate competitive interactions in a colonial marine invertebrate. Ecology 87:214–25.

Marshall DJ, Keough MJ. 2007. The evolutionary ecology of offspring size in marine invertebrates. Adv Marine Biol 53:1–60.

Marshall DJ, Keough MJ. 2008. The relationship between offspring size and performance in the sea. Am Nat 171:214–24.

McCauley DE, Odonnell R. 1984. The effect of multiple mating on genetic relatedness in larval aggregations of the imported willow leaf beetle (*Plagiodera versicolora*, Coleoptera, Chrysomelidae). Behav Ecol Sociobiol 15:287–91.

McEdward LR. 1997. Reproductive strategies of marine benthic invertebrates revisited: Facultative feeding by planktotrophic larvae. Am Nat 150:48–72.

McEdward LR. 2000. Adaptive evolution of larvae and life cycles. Semin Cell Dev Biol 11:403–9.

McEdward LR, Miner BG. 2003. Fecundity-time models of reproductive strategies in marine benthic invertebrates: fitness differences under fluctuating environmental conditions. Mar Ecol-Prog Ser 256:111–21.

Mock DW, Forbes LS. 1992. Parent offspring conflict - A case of arrested development. Trends Ecol Evol 7:409–13.

Mock DW, Parker GA. 1997. The evolution of sibling rivalry. Oxford: Oxford University Press. 464 p.

Moran AL, Emlet RB. 2001. Offspring size and performance in variable environments: Field studies on a marine snail. Ecology 82:1597–612.

Moran AL, Woods HA. 2007. Oxygen in egg masses: interactive effects of temperature, age, and egg-mass morphology on oxygen supply to embryos. J Exp Biol 210:722–31.

Paczolt KA, Jones AG. 2010. Post-copulatory sexual selection and sexual conflict in the evolution of male pregnancy. Nature 464:401–4.

Palumbi SR. 1994. Genetic divergence, reproductive isolation, and marine speciation. Ann Rev Ecol Syst 25:547–72.

Palumbi SR. 2009. Speciation and the evolution of gamete recognition genes: pattern and process. Heredity 102:66–76.

Parker GA, Royle NJ, Hartley IR. 2002. Intrafamilial conflict and parental investment: a synthesis. Philos Trans R Soc Lond Ser B-Biol Sci 357:295–307.

Paterson IG, Partridge V, Buckland-Nick J. 2001. Multiple paternity in *Littorina obtusata* (Gastropoda, Littorinidae) revealed by microsatellite analyses. Biol Bull 200:261–7.

Pearse JS. 1994. Cold-water echinoderms break ''Thorson's Rule''. In: Young CM, Eckelbarger KJ, editors. Reproduction, larval biology, and recruitment of the deep-sea benthos. New York: Columbia University Press. p. 26–43.

Pearse JS, McClintock JB, Bosch I. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes and timing. Am Zool 31:65–80.

Perron FE, Carrier RH. 1981. Egg size distributions among closely related marine invertebrate species - Are they bimodal or unimodal? Am Nat 118:749–55.

Petch DA. 1989. Variation in the spionid *polychaete Boccardia proboscidea*. PhD thesis. Melbourne: University of Melbourne. 136 p.

Pfennig DW. 1997. Kinship and cannibalism. Bioscience 47:667–75.

Pfennig DW, Reeve HK, Sherman PW. 1993. Kin recognition and cannibalism in spadefoot toad tadpoles. Animal Behav 46:87–94.

Podolsky RD, Moran AL. 2006. Integrating function across marine life cycles. Integr Comp Biol 46:577–86.

Podolsky RD, Strathmann RR. 1996. Evolution of egg size in free-spawners: consequences of the fertilization-fecundity trade-off. Am Nat 148:160–73.

Queller DC. 1984a. Models of Kin selection on seed provisioning. Heredity 53:151–65.

Queller DC. 1984b. Pollen-ovule ratios and hermaphrodite sexual allocation strategies. Evolution 38:1148–51.

Rice SA. 1978. Spermatophores and sperm transfer in spionid polychaetes. Trans Am Microscop Soc 97:160–70.

Rice SA. 1981. Spermatogenesis and sperm ultrastructure in three species of Polydora and in Streblospio benedicti (Polychaeta: Spionidae). Zoomorphology 97:1–16.

Rivest BR. 1983. Development and the influence of nurse egg allotment on hatching size in *Searlesia dira* (Reeve, 1846) (Prosobranchia, Buccinidae). J Exp Mar Biol Ecol 69:217–41.

Rowe L, Arnqvist G. 2002. Sexually antagonistic coevolution in a mating system: Combining experimental and comparative approaches to address evolutionary processes. Evolution 56:754–67.

Royle NJ, Hartley IR, Parker GA. 2004. Parental investment and family dynamics: interactions between theory and empirical tests. Popul Ecol 46: 231–41.

Sanford E, Worth DJ. 2009. Genetic differences among populations of a marine snail drive geographic variation in predation. Ecology 90:3108–18.

Sato-Okoshi W. 2000. Polydorid species (Polychaeta : Spionidae) in Japan, with descriptions of morphology, ecology and burrow structure. 2. Non-boring species. J Mar Biol Assoc UK 80:443–56.

Sato-Okoshi W, Okoshi K. 1997. Survey of the genera *Polydora*, *Boccardiella* and *Boccardia* (Polychaeta, Spionidae) in Barkley Sound (Vancouver Island, Canada), with special reference to boring activity. Bull Mar Sci 60:482–93.

Schausberger P, Hoffman D. 2008. Maternal manipulation of hatching asynchrony limits sibling cannibalism in the predatory mite *Phytoseiulus persimilis*. J Animal Ecol 77:1109–14.

Schrader M, Travis J. 2008. Testing the viviparity-driven conflict hypothesis: parent-offspring conflict and the evolution of reproductive isolation in a poecilid fish. Am Nat 172:806–17.

Shaanker RU, Ganeshaiah KN. 1997. Conflict between parent and offsrping in plants: predictions, processes and evolutionary predictions. Curr Sci 72:932–9.

Shaanker RU, Ganeshaiah KN, Bawa KS. 1988. Parent-offspring conflict, sibling rivalry, and brood size patterns in plants. Ann Rev Ecol Syst 19:177–205.

Simon CA, Thornhill DJ, Oyarzun F, Halanych KM. 2009. Genetic similarity between *Boccardia proboscidea* from Western North America and Cultures abalone, *Haliotis midae*, in South Africa. Aquaculture 294:18–24.

Smith RL. 1979a. Paternity assurance and altered roles in the mating behavior of a giant water bug, *Abedus herberti* (Heteroptera, Belostomatidae). Animal Behav 27:716–25.

Smith RL. 1979b. Repeated copulation and sperm precedence-Paternity assurance for a male brooding water bug. Science 205:1029–31.

Smith CC, Fretwell SD. 1974. Optimal balance between size and number of offspring. Am Nat 108:499–506.

Söderström A. 1920. Studien über die Polychätenfamilie Spionidae. Uppsala: Almquist and Wicksells. p. 1–286.

Strathmann RR. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Ann Rev Ecol Syst 16:339–61.

Strathmann RR, Hess HC. 1999. Two designs of marine egg masses and their divergent consequences for oxygen supply and desiccation in air. Am Zool 39:253–60.

Strathmann MF, Strathmann RR. 2006. A vermetid gastropod with complex intracapsular cannibalism of nurse eggs and sibling larvae and a high potential for invasion. Pac Sci 60:97–108.

Summers K, Earn DJD. 1999. The cost of polygyny and the evolution of female care in poison frogs. Biol J Linn Soc 66:515–38.

Swanson WJ, Vacquier VD. 1998. Concerted evolution in an egg receptor for a rapidly evolving abalone sperm protein. Science 281:710–2.

Temme DH. 1986. Seed size variability: a consequence of variable genetic quality among offspring? Evolution 40:414–7.

Thomson CW. 1878. Notice of some peculiariaties on the mode of propagation of certain echinocerms of the southern seas. Journal Linn Soc Zool 13:55–79.

Thorson G. 1946. Reproductive and larval development of Danish marine bottom invertebrates. Meddelelser fra Kommissionen for Havundersoegelser serie plankton 4:1–523.

Thorson G. 1950. Reproduction and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45.

Trivers RL. 1974. Parent-offspring conflict. Am Zool 14:249–64.

Vance RR. 1973a. More on reproductive strategies in marine benthic invertebrates. Am Nat 107:353–61.

Vance RR. 1973b. On reproductive strategies in marine benthic invertebrates. Am Nat 107:339–52.

Veliz D, Duchesne P, Bourget E, Bernatchez L. 2006. Genetic evidence for kin aggregation in the intertidal acorn barnacle (*Semibalanus balanoides*). Mol Ecol 15:4193–202.

Wang JL. 2004. Sibship reconstruction from genetic data with typing errors. Genetics 166:1963–79.