COMMENTARY

Love, not war, drove the Mesozoic marine revolution

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To be *in flagrante delicto* requires a sophisticated sensory and anatomical toolkit. Substantial musculature and an active metabolism are required to roam about “on the hunt.” Advanced sensory systems and neurological processing are needed to locate and recognize mates from among the wide gamut of other organisms in one’s habitat, some of which are prey, some predators, but few potential mates. Copulatory organs (if present) also must be physically compatible when successfully transferring gametes. In many species, mating is preceded by complex courtship rituals involving careful selection among potential mates, or by physical combat among rivals. These abilities are not that far removed from those required for a predator or omnivore to successfully detect, hunt down, and capture prey. In PNAS, Bush, Hunt, and Bambach (1) recognize the dual-function of this sophisticated toolkit and argue that the mating function better explains the diversification in marine predators starting ~200 million y ago, a transition widely termed the “Mesozoic marine revolution” (2) that continues to shape the modern world.

The power of predators to shape communities has been long acknowledged (3, 4). Vermeij’s hypothesis of escalation (5, 6) formalized this concept across geological time, arguing that ecological history is shaped by coevolutionary arms races, in which predators exert powerful selection pressures on prey, which respond in kind with their own defensive adaptations. This competitive milieu has been invoked to explain a variety of ecological trends spanning marine animal history, but especially those involving increases in more powerful predators, durophagous-resistant shell defenses, colonization of infaunal habitats, more active metabolisms, and greater mobility (see recent summaries in refs. 6 and 7). Although these basic coevolutionary dynamics have likely always been in effect (8–11), the pace of escalation appears to have accelerated in the Mesozoic (12–14), triggered largely by increased global productivity in the oceans and on land (13, 15) that permitted energetically costly lifestyles.

Until the present study (1), however, a compelling explanation for why predators became more diverse (taxon-rich) during escalatory intervals has remained elusive. The most common argument has been that productivity

permits ecological expansion via novel predatory strategies (4, 16), especially energy-intensive ones that were previously untenable. Able to specialize in individual prey using more precise hunting strategies, these advanced predatory species are better able to survive with smaller geographic ranges, a factor often associated with increased speciation rates (17, 18). However, an ecologically permissive environment, by itself, ought to not automatically ratchet up speciation rates (19, 20). Bush et al. (1) offer a more direct causation, in which copulation (and other forms of mating involving significant behavioral or anatomical interaction) becomes the primary pump for diversification.

Bush et al. (1) arrive at this conclusion by coding marine fossil occurrences from the Paleobiology Database into one of three categories based on fertilization strategy. Broadcasters (Fig. 1B), sometimes termed external fertilizers, shed gametes (or at the very least, sperm) directly into the water column and lack direct interaction between adult sexual partners. Contact-maters (Fig. 1A)—termed “nonbroadcasters” in the article (1)—encompass a wide range of behaviors, including internal deposition of gametes during copulation and external fertilization during close physical contact, but in all cases, successful fertilization requires sexual rendezvous between partners or small groups. Bush et al. also recognized a third category of intermediate fertilizers that may aggregate in large numbers before broadcast spawning, but these taxa were of minor numerical importance compared with the other two categories. Because these fertilization strategies are highly phylogenetically conserved, the authors were able to infer them reliably for ancient relatives.

For broadcasters (Fig. 1C), diversity has remained relatively steady during the past 450 million y, with a brief downturn and recovery during the end-Permian mass extinction. Aided by statistical maximum-likelihood models, Bush et al. (1) interpret this pattern as being consistent with diversity dependence. During the Paleozoic and early Mesozoic, contact-maters shared a similar stability in diversity, but starting around 150 million y ago, animals that reproduced in this more active manner have diversified at a constant exponential rate, such that they

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Fig. 1. (A) Mating slender crabs *Metacarcinus gracilis* in precopulatory embrace, an example of contact-mating animals. Image courtesy of Ken Kurtis. **(B)** Broadcast-spawning flower coral *Eusmilia fastigiata*. Image courtesy of Ned DeLoach. **(C)** Diversity curve of marine animals since the Ordovician Period, categorized according to fertilization mode. Units of geological time (MA) means millions of years ago. Data taken from Bush et al. (1); see Bush et al. for details on data standardization methods.

account for nearly 75% of marine genera today, an approximately threefold increase in 150 million y.

Given that copulation has probably existed since the late Neoproterozoic, the delayed diversification begs explanation. Bush et al. (1) attribute the onset to increased productivity beginning in the Jurassic (12, 13). The more energetically intensive contact-maters were preadapted to active lifestyles and were able to capitalize on the

increased trophic flexibility by specializing in new ecological ways. That they also copulate (or otherwise transfer sperm between adults) has allowed for smaller viable population sizes, resulting in increased diversification rates. In contrast, speciation rates for broadcast spawners—most of which are constrained to suspension-feeding, given their lack of mobility—were unable to capitalize in the same way (4). Broadcast spawning has had little influence on global diversity since the Ordovician radiation.

It remains difficult to disentangle correlation from causation in these data because of the high phylogenetic correlation between fertilization mode and predatory habit in most marine animal taxa (21). However, Bush et al. (1) use caenogastropods (which are contact-maters that include both predatory and nonpredatory habits) to demonstrate that contact-mating is an essential ingredient in diversification. The authors note that sea stars (which are externally fertilizing predators) also provide consistent support for this interpretation, but their much poorer fossil record precludes a strong test (22). Extant annelids (23) and fishes (24) could prove especially worthwhile for future analysis, given their wide variety of reproductive and feeding strategies.

This underpinning of evolutionary pattern with reproductive causation has broad support in biology. Animal-pollinated angiosperms offer a direct analogy (13, 25), in which reproductive specialization for increased pollen transmission allows populations to inhabit smaller geographic ranges and greater efficiency in gamete transmission, facilitating increased rates of speciation (26). The fact that diversification in angiosperms—which are ecologically so different from marine animals—is also attributed to reproductive biology, suggests that fertilization mechanism, not ecology, should be considered the primary factor promoting diversification. Genetic surveys of marine invertebrates demonstrate that copulating species have greater genetic diversity and less inbreeding than broadcast spawners (21). Sexually selected and courting animal species are well established to have higher speciation rates relative to other lineages (27). But active selection of sexual partners has been demonstrated to not be sufficient, by itself, to result in increased speciation rates (20, 28); additional factors are required to prime the diversity pump, including ecological specialization and environmental opportunity. In a world of low productivity, such as is thought to have occurred throughout much of the Paleozoic and early Mesozoic, anatomically and behaviorally complex sexual predators could never sustain their energy-intensive physiological requirements across sufficiently broad geographic regions to lead to rampant speciation and increased specialization on prey, habitats, and other resources. However, when productivity increased, beginning in the Mesozoic, constraints on the Allee effect diminished, allowing the macroevolutionary pump to drive up diversity in concert with more selective mating strategies. Reproductive mode thus assumes dominance as the main evolutionary driver of the Mesozoic marine revolution, with predation the passenger. Increased ecosystem productivity still appears to play a critical role in the timing of the Mesozoic marine revolution (13, 15, 29), but the study by Bush et al. (1) provides a more fundamental underpinning in reproductive biology that may turn out to be more important than energetics or predation alone in explaining the cause of the evolutionary diversification.

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