Question from Joth Davis: *Fundamental differences in life history strategy exist between cupped and flat oysters within the genus Crassostrea and Ostrea, respectively. Recall that both genera commonly have species that mainly dwell in intertidal habitats. Please describe 1. the differences in life history including reproductive strategy, evolutionary history and 2. how a changing climate including ocean conditions might differently impact populations of oysters within these two genera residing on intertidal beaches.*

The oyster genera *Crassostrea* (cupped oysters) and *Ostrea* (flat oysters) share a number of fundamental similarities, but significant divergences in some life history strategies have resulted in evolutionary differences, variation in response to anthropogenic exploitation, and probable differences in adaptation to climate change. Within the family of true oysters, Ostreidae, Crassostreinae are oviparous broadcast spawners and Lophinae and Ostreinae are brooders. These alternative reproductive strategies are the basis for divergences between the groups of oysters and are two legitimate ways of thriving in the marine environment. The brooding genus *Ostrea* has a longer history of exploitation in North America and Europe, which has greatly reduced natural populations, rendering them more vulnerable to future environmental change. The introduction of *Crassostrea* (mostly *C. gigas*) in the U.S. and Europe to revitalize the oyster industries may be contributing to difficulties in native oyster restoration efforts (A. Trimble, pers. comm.). A combination of differences in life history strategies, evolutionary trajectories, and histories of exploitation will make these two genera differentially susceptible to a changing climate.

The basic physiology of the oyster reproductive system is the same between *Crassostrea* and *Ostrea*, the contrasting elements being fertilization and larval development. Oysters have a paired gonad with profusely branching tubules in the connective tissue beneath the mantle (Galtsoff 1938). There are two genital canals and two gonoducts, one on each side of the body. Sperm and ova are discharged into the gonoduct via muscle contractions and then through the urogenital cleft to the suprabranchial chamber by ciliary action. Within the suprabranchial chamber, the gametes become entrained in the respiratory current from the gill cilia (Galstoff 1938). In female *Crassostrea*, eggs are expelled through the gills from the mantle cavity by rhythmic contractions of the adductor muscle and opening of the mantle (trans-ctenidial ovulation). In *Ostrea*, the eggs remain in the pallial chamber. Males of both genera expel sperm through the cloaca where they are washed away by seawater (Galstoff 1938). Male *Crassostrea* expel single spermatozoa, whereas male *Ostrea* expel spermatozeugmata (sperm packets or balls) that are not active until the individual sperm disassociate from the cluster (Ó Foighil 1989). This strategy may increase the likelihood of fertilization in species where individuals are far from each other and only one sex is a broadcast spawner (Ó Foighil 1989). Fertilization for *Crassostrea* occurs in the water column when gametes randomly come together; fertilization in *Ostrea* occurs internally when the female takes up sperm from the environment through the inhalant siphon. Both genera tend to be protandrous hermaphrodites, but *Ostrea* has more flexibility and can switch sexes yearly and even sometimes be a simultaneous hermaphrodite (Thompson et al. in *The Eastern Oyster*; Couch & Hassler 1989; Hopkins 1936).

Flat and cupped oysters seem to embody the trade-off between parental fecundity and investment in offspring. The hypothesis behind the evolutionary trade-off is that greater fecundity comes at the price of less investment in offspring and therefore greater offspring mortality. The eastern oyster, *Crassostrea virginica*, spawns between 10 and 50 million eggs per female. These eggs are approximately 50 um in diameter (Matthiessen 2001). The European flat oyster, *Ostrea edulis*, spawns fewer, larger eggs – approximately 1 million per female with 150 um diameter (Matthiessen 2001). *Ostrea* also generally have less reproductive output per gram body weight than *Crassostrea* (Thompson et al. *TEO*) and are smaller in size overall. Larvae in *Crassostrea* develop completely in the plankton, from fertilization through competence for settlement. The larval developmental process takes a few weeks as the fertilized egg develops into a D-hinge larva, a trocophore, a veliger, and then settles into its adult benthic lifestyle. The internal fertilization of *Ostrea*, however, allows for greater parental investment and brooding of the larvae. The fertilized eggs are incubated in the female’s pallial cavity for 10 to 12 days until they reach the veliger stage. Veliger larvae, about 250,000-300,000, are extruded at the end of incubation and complete development in the water column for 11-16 days (Hopkins 1936; Couch & Hassler 1989). For both *Crassostrea* and *Ostrea* spawning is temperature dependent, 200C and 150C, respectively (Matthiessen 2001). The number of eggs produced per female is also highly dependent on female size and nutrient reserves (Hopkins 1936; Thompson et al. *TEO*).

There are a number of environmental characteristics of the marine realm that allow for successful reproduction via planktonic larvae. Mostly simply, water is wet. Water allows for eggs and larvae to be freely cast out into the environment because there is no threat of desiccation, buoyancy keeps them all from falling back down directly to the benthos, and suspended plentiful food particles allow for long-term larval survival (Strathmann 1990). Dilution of the gametes in the water column can be problematic, but *Crassostrea* and *Ostrea* have both evolved different mechanisms to counterbalance this problem (Strathmann 1990). Both types of oyster synchronize spawning through conspecific cues from sperm. Female *C. virginica* do not spawn until they sense sperm in the water column and males of both *C. virginica* and *O. lurida* are stimulated to spawn similarly (Thompson et al. in *TEO*; Couch & Hassler 1989). The use of spermatophore-like structures by *Ostrea* spp. allows for sperm concentration until they are taken up by a female (Ó Foighil 1989).

The extensive similarities between *Crassostrea* and *Ostrea* reproduction suggest that one form, oviparity or larviparity, is the plesiomorphic mode of spawning and larval development. Through an analysis of the 28S rRNA gene in oyster species from both groups, Ó Foighil and Taylor (2000) resolved the debate over the original ancestral state in favor of oviparity. The common ancestor to the modern diverged oysters employed a combination of trans-ctenidial ovulation, broadcast spawning and planktotrophic larval development (Ó Foighil & Taylor 2000). Brooding in *Ostrea* is, therefore, a derived trait that evolved one in the common ancestor of Lophinae and Ostreinae and was retained in the descendents. The complete loss of an obligate feeding planktonic larval form is seen in only one very derived species, *Ostrea chilensis* (Ó Foighil & Taylor 2000). From these conclusions based on the phylogeny of oviparous and larviparous oysters, it can be hypothesized that the shared extended larval planktotrophy is a highly advantageous trait, whereas brooding may have evolved to allow expansion of oysters into novel habitats that were more hostile to vulnerable pre-veliger larvae. This would support the generalized trade-off of parental investment and offspring mortality because in a harsher environment, more energy would need to be invested to insure that offspring survive. Support for this hypothesis may be reflected in present-day ecology of *Ostrea* and *Crassostrea*. In a comparison of four brooding oyster species and three broadcast spawners, the larviparous oysters had a broader range of life history and genetic diversity values indicating a possible opportunity to evolve into a greater variety of ecological conditions (Buroker 1985). There was higher genetic diversity overall in the oviparous species, but a broader range of evolutionary patterns in the larviparous (Buroker 1985), indicating potential for two different kinds of environmental and evolutionary flexibility.

A noticeable trend across a number of marine taxa is the relatively smaller body size of brooders compared to non-brooders of related species. Even though this observation does not always hold true and there is little robust support for why brooders should have a smaller adult size (Strathmann & Strathmann 1982), it is still worth exploring for its potential evolutionary implications in the divergence of *Crassostrea* and *Ostrea*. There are three main hypotheses for the evolution of this pan-taxonomic trend. The first hypothesis is that the allometry of gamete production and brooding do not work for larger adults (Strathmann & Strathmann 1982). Specifically, larger organisms produce too many eggs to brood. This could be the case for oysters since *Crassostrea* not only produce a greater number of eggs, but also a greater number per gram body weight (Thompson et al. *TEO*). However, since oviparity is the plesiomorphic trait in Ostreidae and this hypothesis implied the contrary, allometry is probably not the reason why *Ostrea* are smaller, unless there was a concurrent reduction in body size when the trait evolved. The second hypothesis is that variability in recruitment is decreased with greater parental care (Strathmann & Strathmann 1982). Support for this hypothesis is contingent upon the assumption that a larger body size confers greater longevity and thus more breeding seasons to increase the chance of successful fertilization and development (Strathmann & Strathmann 1982). The second hypothesis basically follows the principle that with great risk comes great reward. However, this is not a direct argument for the evolution of small body size in brooders, but rather of larger body size in broadcast spawners. Lastly, the third hypothesis is that larvae will disperse greater distances with less parental care (Strathmann & Strathmann 1982). The verity of this hypothesis can be entirely environmentally dependent and vary inter-annually. Also, since *Ostrea* spp. have an extensive larval planktonic stage in addition to brooding, it is probably not directly relevant to oysters. In a much more simple hypothesis, Hopkins (1936) surmised that *O. lurida* brooding may have evolved so that larvae are not released until they are strong enough swimmers to escape the silt of the parental habitat that could smother them. This seems to be as likely an hypothesis as any and is consistent with the potential historic adaptive radiation of *Ostrea* into different habitats around the time that brooding evolved.

In looking forward to how future climate change will impact both *Crassostrea*  and *Ostrea*, it is important to consider how the intertidal environment will change. The Intergovernmental Panel on Climate Change (IPCC) predicts that by end of the 21st century the global mean temperature will increase 1.8-40C, the sea level will rise 0.18-0.59 m and the oceans will become more acidic by 0.14-0.35 pH units (IPCC 2007). These changes put 20-30% of currently extant plants and animals at risk of extinction (IPCC 2007). The resilience of many ecosystems will probably be exceeded by these changes and by associated disturbances from anthropogenic use of resources (IPCC 2007). On the west coast of the U.S. there is already evidence of increasingly acidic waters being upwelled on the coast (Hauri et al. 2009) and globally the aragonite and calcite (polymorphs of calcium carbonate) saturation horizons are shoaling (Feely et al. 2004). Both larval and adult oysters of both *Ostrea* and *Crassostrea* will be exposed to these changes. *C. virginica* larvae stay relatively close to the surface, above the halocline (Kennedy in *TEO*), which is where the majority of anthropogenic CO2 is taken up causing increased acidification (Sabine et al. 2004). Adults in the intertidal are also more exposed to warming air temperatures, as well as shallow waters that will become warmer and more acidic. Increased sea surface level may end up creating more usable habitat for *Ostrea* spp., which prefer more subtidal substrate, but will probably decrease available habitat for *Crassostrea* spp.

The divergent life histories and evolutionary trajectories of flat and cupped oysters may prompt them to respond differently to climate change effects on their habitat. In the larval stage, the incubation of *Ostrea* larvae until the veliger stage may shield developing larvae from harsh environmental conditions until they are a little more robust. If this strategy really is an adaptation for novel and potentially less hospitable environments, then it may serve the genus well in a changing environment. Lecithotrophy is the extreme form of brooding where fully developed non-feeding larvae are extruded from the parent to spend only hours to days in the plankton before settlement. It has been hypothesized that this strategy has developed for enhanced fitness in more hostile environments and may make lecithotrophs more fit in future climate change (Dupont et al. 2010). *Ostrea* brooding may be a less extreme form of lecithotrophy but for the same evolutionary reasons. Conversely, the greater number of larvae produced by *Crassostrea* may give them an advantage over *Ostrea* in terms of overall genetic variability. In broadcast spawning of both sexes, there is a greater chance that a larger number of crosses will occur, maximizing the genetic diversity in any one brood year. If there is sufficient genetic variability for traits that will be beneficial in a climate change scenario, then those larvae would have a greater chance of surviving through competency and reproducing. Both strategies have potential for larval propagation in a changing environment, but the extent of adaptation for the changes that will occur remains to be seen.

Temperature is projected to change significantly in future climate scenarios, which may prove to be detrimental for *Ostrea* spp. being more sensitive to temperature fluctuations. It is difficult to make direct comparisons in physiological response to climate change between *Ostrea* and *Crassostrea* because they are not congeneric. In congeneric species at different tidal zonations, a body of work has shown that there is a strong correlation between increasing tidal height and resistance to high temperatures (reviewed in Somero 2002). On the west coast of the U.S., *C. gigas* can be found higher in the intertidal than *O. lurida*. Species higher in the intertidal are generally considered to be living closer to their thermal limits, although in general they exhibit evidence of eurythermal function in heart rate, nervous system signaling, and mitochondrial respiration (Somero 2002). Exposure history may also affect how adeptly an organism is able to adapt to climate change, where organisms with a history of warmer temperature exposures are better able to survive in a warming climate (Somero 2002). These pieces of evidence from other intertidal species would indicate that *Crassostrea* may be able to better tolerate a warming climate. That is, of course, unless the thermal limits of *Crassostrea* are also breached. Even though *O. lurida* is sensitive to both high and low temperatures (Couch & Hassler 1989), *C. gigas* experiences high summer mortality even in its native habitat in the eastern Pacific (A. Trimble pers. comm.).

Ocean acidification (OA) goes hand in hand with warming temperatures from climate change and will most likely have detrimental impacts on all marine calcifiers in the intertidal. Less work has been done to determine the effects of OA on *Ostrea* spp., but in general their pH regulatory abilities and dependence on CaCO3 saturation state for shell formation are probably similar to those of *Crassostrea* spp. The main difference would lie in the potential sheltering of larvae during brooding until they are more robust to survive an acidified environment, as discussed above, but even larvae in the maternal brooding cavity come into contact with ambient seawater. Elevated pCO2 of 970 ppm, a realistic level for end-of-century predictions, caused decreased growth in larval and juvenile *O. lurida* (Hettinger et al. 2010). Adult and juvenile *C. virginica* also showed decreased growth at pH of 7.5 (3500 ppm of CO2; Beniash et al. 2010). *C. gigas* at pH of 7.68 demonstrated a decrease in hemolymph extracellular pH, coupled with increase in bicarbonate ion concentration and decreased body condition index (Lannig et al. 2010). The increase in bicarbonate is usually a sign of shell dissolution in an attempt to buffer internal pH changes. These findings together project nefarious effects of increased atmospheric CO2 on all life stages of oyster.

Cupped and flat oysters diverge in a number of important life history characteristics that may make them differentially susceptible to climate change; however, studies to date on the effects of ocean acidification imply universally detrimental effects on physiology and survival. Not all hope is lost in the face of OA since 100% mortality does not occur in any realistic scenario of future emissions. This means, that given the high fecundity of *Ostrea* and especially *Crassostrea*, oysters may experience population bottlenecks, but if enough larvae survive the adverse conditions the population could adapt over time. More work will need to be done on the synergistic effects of future climate scenarios and the heritability of traits for survival in each scenario. Differential historical exploitation could also affect how *Ostrea* and *Crassostrea* are able to respond to climate change. With a longer history of exploitation and dramatically decreased stocks of *O. edulis* in Europe and *O. lurida* in the U.S., the populations may be already too damaged to tolerate more stressors.

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