Consensus and Contention: A Review of Topics

**Week 1: Spatial and Temporal scale of environmental variation**

**Discussion Questions:**

**1. Are marine systems more or less variable than terrestrial?**

**LSU:**

Variability is complex. Open ocean minimal variability coastal systems have high variability (related to latitude and depth), but perhaps not as high as terrestrial

Open ocean << coastal ocean << terrestrial

**Hal-Dames Rule:**

Water is natural buffer, so environmental variation should be greater in terrestrial systems especially at small temporal or spatial scales. Differences likely become smaller at larger spatial scales as environmental variation increase and approaches amount of variation present in terrestrial systems.

**MSC:**

Open ocean is temporally less variable than terrestrial, but coastal/intertidal systems could be as variable or more variable than terrestrial. Spatial variation is less clear because open ocean can be highly variable in light, temperature, etc. across depths and many species (zoop up to whales) will experience this variation daily. Predictability of variation is likely higher in ocean with exception of intertidal/estuarine. Would’ve like to see more data in the Steele et al. paper.

**NEU**:

Intuition is that marine systems are more variable, so surprised by Steele’s argument based on temperature data. Marine systems are more variable given stochastic ocean currents, upwelling, offshore advection, and possibly pathogens. Intertidal should be more variable given it is subject to stressors of both marine and terrestrial environments and can vary across small spatial scales. Steele downplayed the overlap in adaptive strategies (long life, many offspring, colonial vs. social systems) between marine and terrestrial species.

**UGA/UNH**:

Many exceptions to Steele’s generalizations that they focused on specific systems to make sense of it. It is a novel idea to consider marine life history diversity as the rule, not the exception, and terrestrial environments trying to survive a much more surprising environment. Conclusion of Steele is backward from argument, as marine organisms more likely to respond with differential population expansion/contraction to changing conditions, while possibly terrestrial organisms more likely to respond with plasticity.

**WSU:**

Oceans are more variable in a greater number of conditions (oxygen availability, salinity, pH, light attenuation, substrate stability, etc.) that are not considered when comparing marine and terrestrial systems. Usually these comparisons are biased toward temperature. Therefore, there may be more opportunities for selection/local adaptation/phenotypic plasticity to act in the marine environment that are under appreciated.

**USC:**

Over shorter time scales, terrestrial systems are more variable, but as you increase in scale, the two systems become closer in frequency and variance of environmental change. Land is less predictable and ocean systems are more predictable, but there are many marine systems that are not predictable. Perhaps a better focus is not variability but predictability of system. Oceans are more predictable. Mobility should be considered as strategy for animals to decouple from environmental variability. More sessile marine organisms have to rely on physiological means to deal with environmental changes that occur. Factors other than environmental variability could have strong impacts on reproductive systems that develop on land (no terrestrial equivalent to marine currents so different dispersal methods evolved to respond to different environment challenge, not necessarily the variability).

**RU:**

Agree that marine systems are generally “red noise” systems with variability occurring at longer time scales while terrestrial systems were generally more “white noise”. This is especially evident with thermal variability with marine species typically able to tolerate smaller range of temperatures than terrestrial species (with exception of intertidal species). It is difficult to categorize ocean currents as predictable sources of energy usable by dispersing larvae and argue that currents are more stochastic (especially smaller spatial scales) especially when considering the size of species impacted by those currents. Variability in the environment may act as a selective pressure, but at what level of organization does it act? Individual or higher? Not convinced that trees evolved longer lives as bet hedging strategy to spread out reproductive events and lessen chances of reproducing during bad period. If terrestrial systems are white noise systems, would the environment change quickly enough that organisms wouldn’t have to survive for very long to move past a bad period and into a period more suitable for offspring survival? Perhaps might be a better strategy to capitalize on good conditions when they occur. Also concerned with focus on invertebrate nesting as a way to mitigate environmental change, as eusociality is restricted to hymenoptera and is not dominant strategy.

**FSU:**

Too much variability in the extent of variability within each system to draw broad conclusions about average differences. Differences in the variability and the timescales of variability between habitats and according to species experiencing environment are more informative in studying rapid adaptation. For most examples of terrestrial life history, there are marine examples. Important to be clear on difference between variability and predictability, as these aspects of environmental fluctuations are key to understanding what “timescales of environmental variability” means for evolution and adaptation, and maybe not for explaining differences between land and sea. The Steele paper seems to focus on parental care and predictability – that there has been more transition to high fecundity/low parental care in the sea than land. Differences in parental care and other life history characteristics relates more to life in seawater vs. air, such as differences in density, viscosity, desiccation, movement, finding mates and food, etc. The trajectories of larvae in water currents are not as predictable as suggested in the paper, as currents may flow south at certain time of year but whether larvae will land in a good spot is mostly unpredictable from the parent’s point of view. Many bi-phasic marine life histories evolved to minimize the risks associated with stochastic currents.

**UCONN:**

Steele paper argues that terrestrial systems are more variable than marine systems on thousand-year time scales. However, there are important distinctions to make especially in an evolutionary context between variability and stochasticity of a system. Unpredictable variation would have a very different effect on the evolutionary dynamics in the system compared to predictable variation. It’s also unclear how well these conclusions extrapolate across latitude – would the same patterns hold for polar, temperate, and tropical systems? It is important to contextualize environmental variability. For example, while relatively unpredictable current movement may increase variability at one geographic point, characteristics of the water mass itself are fairly constant. The implication therefore being that the same environmental feature might have drastically different consequences on sessile benthic organisms vs. pelagic organisms entrained within the current.

**Bodega/UCDavis:**

Agree with Steel that small spatial scale temporal variability is more common on land than in sea due to the heat capacity of water dampening variability. However, Steele ignores or glosses over some variability in the oceans. The pelagic open ocean is subject to spatial variation in food availability. Phytoplankton are patchy and thus the pelagos isn’t necessarily the constant, predictable bath favoring larval development as Steele suggests. There is also variability in the chemical characteristics of the water (salinity, pH, DO) and nutrient concentrations that can vary unpredictably on short time scales due to freshwater outflow or upwelling. Coastal regions and particularly the intertidal are much more variable than the open ocean. However, the component of this variation due to tides is predictable and that predictability changes the nature of the variability from the organism’s perspective. In the water, a host is always exposed to and often in contact with potential pathogens. The microscale in the ocean might be more variable than on land, where pathogens may be selectively waterborne or passed through direct contact. Many researchers believe that marine larvae did not evolve to disperse but rather to exploit the resources and lower predator abundance of the pelagos. It could be that different life history strategies of the ocean vs. land was not driven by differences in variability but rather by differences in the physical properties of air vs. water.

**UCSB/UChicago:**

Among the variables that are shared between terrestrial and marine systems (especially temperature) we would agree with Steele that the magnitude of variation is often greater in terrestrial systems. However, the total number of fluctuating selection pressures is likely greater in marine systems (e.g., temperature, salinity, oxygen, light, pH, nutrients, etc.). What are the implications of coping/adapting to a greater number of fluctuating selection pressures that exhibit smaller amplitudes of variation versus coping with fewer with greater magnitude? For example, in marine systems, we might expect upwelling processes to cause greater co-variance in temperature, pH, oxygen, and nutrients. Therefore, while a single factor may have greater magnitude of variance in terrestrial systems, marine organisms may be more likely to experience the co-occurrence of multiple changing variables. Many studies have already recognized the importance of investigating multiple stressors within marine environments. Furthermore, the tendency for these variables to change together may result in greater predictability of the fluctuating selection pressures in marine systems (e.g., in upwelling systems, organisms may predict that temperature, pH, oxygen, and nutrients will change simultaneously. Could this lead to unique optimal adaptive strategies in marine vs. terrestrial systems?

**2. How can we link the scale of environmental variability to microgeographic adaptation in the ocean? Could other mechanisms be at play?**

**LSU:**

Linking scale of variability is dependent on what variable is being considered. (Example of microgeographic Killifish populations adapting to superfund contamination – Whitehead et al. 2017). Temperature variation more difficult to link but testable in systems like intertidal zones in which selection could occur every generation and remove individuals with low tolerance to increased temp or desiccation.

**Hal-Dames Rule:**

Microgeographic adaptation is likely prevalent and sometimes mistaken for phenotypic plasticity. Prevalence may depend on amount of environmental variability which also varies according to scale (temporal, spatial, organizational).

When are micro-adaptations vs. plasticity a better strategy? Benefit of each could depend on amount of variation experienced during lifetime of organism. To address this, could scale variation by lifetime to compare organisms with different life spans. Amount of variation depends on characteristics of habitat and species. Variation experienced by organism should conform to the variation of the environment if organism cannot move and is physiological conformer. Hypothesize that plastic phenotypes are more common when an organism moves relatively less but habitat varies on a temporal scale, while micro-adaptations are more common when organism moves less but habitat varies on spatial scale. Increases in mobility will increase plasticity relative to micro adaptations. If sea changes to become more variable through time, expect species with higher movement and higher capacity for plasticity to be more successful.

**MSC:**

The most critical thing in this context is environmental variability relative to dispersal and gene flow. Some mechanisms that promote or reinforce microgeographic divergence have little to do with environmental variation. Papers were disconnected because one focused on spatial variation while the other focused on temporal variation. Question claim in Steele et al. that dispersal and recruitment are predictable in marine environments.

**NEU**:

Better data is needed to fully understand scale of environmental variability from perspective of organism experiencing it. Most understanding of variability comes from ice cores, SST from buoys, nearshore data collected by individuals. Hard to determine microgeographic variation for many species due to logistical difficulty. Symbioses could be a mechanism that promotes microgeographic adaptation (e.g. if new coral symbiont allows coral to survive in different habitat, genotype could accumulate advantageous mutations over time).

**UGA/UNH**:

Recognition of scale (population, dispersal, symmetry, time, traits, genomic basis) needs to be more explicit in studies. Some suggest that “population” is a sloppy word to use in evolutionary science. Focused on examples of microhabitat variation in marine intertidal systems (Littorina saxitilis (low dispersal, strong environmental influence on shell shape and genetic composition) vs. Semibalanus balanoides (high dispersal, high environment-mediated mortality of microhabitat, no overall divergence of types). Need to think about scales important for abiotic and for the biotic (range, dispersal, abiotic variation) to be precise with contrasts.

**WSU:**

We need a way to know what phenotypic differences are relevant in order to address what scales of environmental variability are important to look at when addressing adaptation. We cannot link them until we know how and when and where selection is acting. If selection is acting upon one life stage or stress response, other environmental variability is irrelevant. The criteria to address this question vary depending on research bias. Richardson paper accentuated the point that all potential adaptations must be evaluated under common garden conditions and across multiple generations otherwise maternal effects may be playing large role.

Richardson paper sparked conversation about how to differentiate between phenotypic plasticity and micro adaptation and in which situations either of these would be advantageous. A dimensionless gradient metric between the two could be built using specific measurements outlined in Box 4 of the paper, and how this could help compare species that are dissimilar in life history strategy and scale of variation they are exposed to.

**USC:**

Marine dispersal kernels can be large, so does this mean microgeographic scales can be massive? Directed dispersal would incorporate environmental variability (i.e., habitat selection) at certain spatial scales. Is microgeographic variation based on genetic differences or trait differences? As long as you achieve the trait with optimum fitness, then is that considered micrographic adaptation or would there have to be distinct genetic differences (how do you define local adaptation?). Environmental variability would have to be on a scale smaller than the dispersal neighborhood in order to create the steep differential selection gradients needed for microgeographic adaptation (and these scales could be quite large in marine environments). Micro may be a misleading term given the dispersal range of many marine species, but adaptation is still evident over small spatial scales in marine systems even though range of gene flow is large. Does this mean that selection is increased in marine environments to produce this differentiation across smaller scales despite the high potential for gene flow? Other mechanisms at play include predation, sexual selection, genotypic variation, and habitat selection which were all mentioned in the paper.

**RU:**

Defining microgeographic adaptation in terms of dispersal ability is useful in creating a standard for comparing across systems, but the spatial scale of environmental variation may impact the likelihood/degree to which microgeographic adaptation may occur. Organisms in a heterogenous environment at small spatial scales may be more likely to experience microgeographic adaptation than those that inhabit more homogenous environments given equal dispersal ability. Organisms with high dispersal ability (like pelagic larval organisms) may encounter more varied environment as they can travel larger distances (but alternatively have more gene flow across these same distances). Landscape barriers may be less likely to play a role in local adaptation in the ocean, although currents, canyons, etc. likely reduce gene flow. Finally, mechanisms like frequency-dependent and spatially dependent selection might promote spatially balanced polymorphism and standing genetic variation of adaptive significance.

**UCONN:**

Discussion focused on requirements for adaptation. For example, if oceans are less variable than terrestrial, to what degree is this reflected in the evolution of marine performance curves? If this reduced temporal variability can be translated into decreased spatial variation and weaker gradients (horizontally, not with depth), this has the potential to weaken the selection needed to drive microgeographic adaptation. If marine organisms have relatively broad performance curves, the weaker environmental gradients may not represent strong enough selection to overcome migration. This reinforces that there is a significant need to characterize performance curves to diverse range of organisms before we can really define our expectations for the spatial scale of adaptation in marine systems. It is possible that narrower performance curves and increased dispersal capabilities may make micro-geographic adaptation more common in marine systems. Also highlights need to understand how migration differs between marine and terrestrial systems. For planktonic organisms in the open ocean, migration is a function of mixing and dispersal (mixing = eddy diffusion, dispersal = combined effect of eddy diffusion and advection) which result in a large potential trajectories and increased potential for migration, but also behavioral regulation of position in the water column and localized circulation patterns. The classic example is planktonic crab larvae in estuarine systems which have a large potential for dispersal, but which through control their vertical position in the water column may increase local retention in the estuary resulting in a significant difference between potential and realized dispersal. Defining the all-important dispersal kernels presents challenges for marine organisms (more for planktonic than benthic taxa) and likely relies heavily on modelling efforts. Determining an effective method of validating these modelling results is a crucial step.

A possible approach in studying this question of spatial scales in adaptation could focus on looking at intra- and inter-estuary divergence. The strong gradients in several different environmental conditions within estuaries could facilitate reduced migration, even at small spatial scales. Salinity gradients, for example, can be very strong in estuaries, moving from fresh, low salinities to marine, saline waters over a matter of kilometers. This may help facilitate divergence over small spatial scales even in planktonic organisms. Replicating studies across estuaries could therefore be extremely useful for a myriad of questions, including investigating parallel adaptation to similar environments and how these intra-estuarine gradients may facilitate inter-estuarine divergence and adaptation.

**Bodega/UCDavis:**

How can microgeographic adaptation be studied in the open ocean? How do you define dispersal kernels when everything (larvae and adults) is on the move? Strong currents can relocate pelagic organisms over great distances. Could these species locally adapt? Maybe we would be more likely to find local adaptation among retention zones like in the lee of headlands. If plankton are not caught in strong currents we might expect a gradient of allele frequencies rather than discrete subpopulations as we might expect along the coast where habitat types are patchily distributed. Selection against migrants leading to local adaptation could be especially important in the intertidal where larvae are subject to high post-settlement mortality. The evolvability of a population may depend on its adaptive genetic diversity. Individuals need to be able to acquire novel functions through genetic change that will help the organisms survive and reproduce. Further, it will depend on population size, mutation rate, sexual reproduction, and dispersal rates. Evolvability in bacteria has been shown to increase by generating more variation when populations are stressed. Large population sizes of pelagic fish increase threshold values of the selection coefficient above which selection (environmental variation) becomes an important player. Does the difference in spatial and temporal variation in the pelagic ocean compared to terrestrial systems affect the evolvability of populations living in them? It probably would with regard to dispersal, modes of reproduction, and population sizes, at least. Are populations in the pelagic marine realm generally bigger than populations on land? How does genetic variability compare in similar populations on land and in oceans? Examples in Richardson paper were mostly about strong environmental gradients (selective pressure) caused by humans. Are there good examples of strong environmental gradients not driven by humans causing micro-geographic adaptation? Do humans create sharper environmental gradients than exist naturally?

**UCSB/UChicago:**

Agree that the wide dispersal distances of many marine organisms may generally suppress microscale adaptation. However, we questioned to what extent wider dispersal ranges may also increase the probability that individuals will experience an instance or instances of high selective pressure across their distribution. The model for microscale adaptation described in Richardson paper proposed microscale adaptation as a function of dispersal distance, a variable that only has a suppressive effect on adaptation. We question whether wide dispersal distances can increase the potential to interact with different selective forces, thereby amplifying the likelihood of phenotype-environment mismatches and signatures of adaptation. Are species with wide dispersal ranges necessarily less likely to experience microscale adaptation? If not, should high potential for gene flow be reconciled with increased probability of experiencing high selective pressures when estimating occurrences of microscale adaptation?

**Discussion Points (Gathered by Molly)**

Temporal vs. spatial variation – are they the same?

Variation in terms of predictability – what is the driver, the amplitude of variability or the stochasticity of it?

Is there difference in plasticity vs. adaptation in marine vs. terrestrial?

What governs how selection is perceived: Is one strength of selection always going to produce the same fitness decline across marine/terrestrial and across scales and phenotypes? What might govern how selection is received

Passive vs. active dispersal. Have implications for adaptation/evolution?

<<Week 2 begins January 22>>