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>>

**Week 2 – Local Adaptation (conceptual)**

**What are the implications for how we individually define local adaptation on how we study it and what we think about the processes that drive it?**

**Penn State:**

* Local adaptation is on level of demes, however many foundation fauna (grasses, corals) produce extensively via asexual reproduction whereby a particular multi-locus genotype becomes locally dominant. This makes this genet particularly fit in this location and we would want to consider that local adaptation. In general, population models count individuals which can be misleading for colonial organisms and species where organismal sizes vary over a large range.
* When observing clines in gene frequency, the challenge is to understand the forces that generate the pattern. If migration is limited than differentiation in spaces is due to drift, but if there is differentiation in space despite strong gene flow it would be a strong indicator of spatially varying selection.
* Some of the most interesting case entail species that are able to maintain physiological rates across huge environmental gradients – here a non-difference in phenotypes might mask a large difference in genotypes
* Lack of theoretical treatments of the evolutionary dynamics in general and local adaptation in particular between hosts and mutualists rather than hosts and parasites.

**Florida State:**

* Pattern of local adaptation does not always tell us about the process or spatial scale of local adaptation (acknowledged in the paper), and that patterns of GxE for fitness, including its spatial structure, are equally interesting because of the different processes that cause it. The Blanquart et al. 2013 metric is compelling for quantifying and comparing local adaptation as a property of multiple local populations across multiple environments. The onus then is on empiricists to choose demes carefully and to interpret the metric with respect to why demes were selected and how they were sampled, especially in terms of divergent phenotypes/genotypes, and the strength of divergent selection and gene flow.

**Rutgers:**

* Discussed how local adaptation is defined as both a pattern and as a process and how this is often confusing. As a process, what seems to be important is the relative strength of gene flow vs. selection. In cases of extensive gene flow but strong enough selection to result in balanced polymorphisms, should we call this local adaptation? As a pattern, yes. As a process, no.
* Local adaptation is difficult to measure and study because nature is not in equilibrium, and that the demographics and history of natural populations matter. It is also important to have some knowledge of the spatial extent of your species in order to be able to define a “deme”.
* Spent time going over theory behind why few loci of large effect (vs many loci of small effect) may promote local adaptation.
* Briefly talked about how local adaptation in the ocean may be different from that on land. Besides the high potential for dispersal in the ocean, assortative mating may be more important in the ocean than currently recognized.

**Hal-Dames Rule:**

* Three definitions were 1) Home vs. Away: local adaptation is recognized by better performance (fitness) in home environments compared to other environments (comparison across location). 2) Local vs. Foreign: defined as home genotypes performing better than infiltrating genotypes (comparison within location). 3) Sympatry vs. allopatry: at metapopulation scale, performance is better on average in home locations than away locations after habitat and genetic quality effects are removed (comparing average performances).
* Comparisons are helpful descriptions of systems, but utility depends on questions being asked. Local adaptation could determine which species persist in a changing climate. So we might ask if species X show local adaptation? In this question, sympatric vs. allopatric is best. Consider performance of species as whole for local adaptation. For questions about potential of mal-adaptation, potentially in the context of range expansion, we suggest using local vs. foreign definition. LvF seems to be more about the maladaptiveness of invading genotypes more so than local adaptation. For questions about specific sub-populations that have economic or conservation value, we suggest Home vs. Away approach, though it confounds habitat quality and local adaptation.
* For many of these definitions, there are logistical issues to consider. Maternal effects can be confounding, which can be tested in the lab. Constrains local adaptation questions to focus on short-lived or fast-reproducing species that can be reared in a lab.
* None of these definitions appear to incorporate the effects of population size, which is particularly important at the margins of species range and likely also influences local adaptation.

**Nicholls State:**

* Common garden experiments may replace transplants when working with animals, but does not always accurately represent what happens in natural systems.
* The scale of local was the most important aspect of the definition. May not be appropriate to decide on one definition to fit all study types but maybe more appropriate to discuss scale in manuscripts.
* Plasticity and local adaptation are not mutually exclusive. Plasticity can be a trait that becomes heritable and, especially in a stochastic environment, may actually be selected for as the fittest condition.
* Issues of local adaptation specific to Louisiana were discussed: Adaptation of fish and crayfish to hypoxic conditions, salt tolerant cypress trees, black mangroves along northern range edge, etc.

**UMass Amherst:**

* Considered local adaptation in terms of metapopulation. Both papers refer to local adaptation as a trait of a metapopulation, because in order for one deme to be locally adapted, it has to be compared to another deme. Therefore, the metapopulation itself has to be locally adapted. This seems to be slightly new to this group, since they had been thinking of local adaptation on the deme-level scale.
* A metapopulation is locally adapted when demes experience natural selection based on differences in environmental conditions, such that individuals in a specific deme experience higher fitness in their home environment.
* Kawecki et al. concluded the local vs. foreign definition is the correct one to use and this group agrees, because adaptation to anything requires present genotypes within a population or deme. Also discussed amount of genetic variation needed for local adaptation to occur. Seems there is a slim margin- just enough for beneficial genotypes to be present but not enough that these genotypes get drowned out by more generalized genotypes.
* Test for higher fitness is very important to the study of local adaptation. Paper gives three methods to evaluate fitness: 1) looking at competition between genotypes from different populations, 2) measuring population growth rate, 3) measurement of trait performance. Applied each of these to their own systems, found it useful in thinking about local adaptation in own systems. Survival could be tested for #1, #2 could possibly be tested using mark-recapture (but difficult to think of), #3 was most obvious such as growth rates, fecundity, etc.

**UGA/UNH:**

* Best way to measure local adaptation is habitat and organism specific. Cleared up debate important distinctions in the model given habitat variability in quality as well as metrics, and between populations in terms of “adapted” versus plasticity etc. With fitness costs to plasticity and genomic trade-offs being rampant, discussion centered around what systems were actually seeing local adaptation versus environmental filtering of immense amounts of genotypic diversity – thus the benefits of being marine in the Steele et al paper are that an organism can disperse huge quantities of cheap larvae and they will end up matching environmental heterogeneity with genetic heterogeneity – which is distinct from local adaptation and falls more into the microbe/fungal “everything is everywhere and the environment select” adage. Spent time talking about “reproductive waste” and that local adaptation may be persistent as a pattern but not through maintaining identity by descent rather than by fortune.

**Washington State:**

* This group is diverse, and had diverse perspectives of selective drivers and traits. For example, local-foreign evaluation is necessary for confirming local adaptation, since focal population may have similar fitness home and away, but other populations may have extremely low fitness in the local environment.
* Could it still be called local adaptation if your focal population had lower fitness overall (in context of foreign populations) but had highest fitness in home environment? Considering traits that are expressed on a gradient (or a more dynamic fitness landscape) everything becomes more blurry. Does it matter whether you are better than everyone else in your environment, or just that you do best in your own environment?
* Papers did not directly consider was the impacts of competition on relative fitness – when we import populations into a focal population’s environment, are we considering the effects of their interactions when evaluating fitness?
* Discussed assumption of branching phenotype and genotype and how we evaluate local adaptation. Have to be careful about how we look at phenotype and whether we actually know the underlying genetic drivers. Strictly speaking, local adaptation is on the genetic level.
* Discuss how individual definitions of phenomena often depend on how we obtain funding, and for some, a lack of clarity in field-wide definitions can lead to questionable ethics in grant language use. Therefore, we agree that defining local adaptation, at least within this group – can benefit our efforts at large to arrive on a field-wide consensus.

**Virtual Group:**

* Generally agreed that local-foreign and sympatric and allopatric definitions seemed most useful. N=1 sample size seemed not ideal, however N=1 could refer to single plankton culture or larval culture and not the growth of one larva.

**Louisiana State:**

* Questions are more complicated than a simple, “this is the best definition.” Discussed that definition used depends on question being asked, number of demes/habitats being examined, even stage of experiment (exploratory vs. secondary). Not prudent to pigeon-hole into one definition.
* In every scenario, could think of home vs. away as the least useful definition of local adaptation because it does not account for either genotypic differences or habitat suitability. Also determined that local vs. foreign model is most useful when you have a few demes. When you have few demes, the use of sympatric vs. allopatric unnecessarily hides the variation. Sympatric vs. allopatric model might be useful if you are examining many demes, but in general, the sheer experimental effort required to test local adaptation thoroughly with more than 4 demes/habitats is uncommon. Therefore, why not use local vs. foreign.
* Sketch 3-deme example that found useful in describing why it is easier to show local adaptation via a graph rather than a quantitative value. See example and accompanying text (writing stuff won’t help).
* Science community seems to be relying heavily on sequencing alone as a method for determining local adaptation. Can we truly use sequencing with no transplant to show local adaptation? Does difference in genotype really matter if it doesn’t correspond to increase in fitness?
* I the selection occurs at the larval stage, long before settlement, how does this impact our definition of and methods for studying local adaptation? If you cannot use transplant experiments on adults, and larval phases are often still a black box (not much known), what options are there?

**UC Santa Barbara:**

* Myriad of implications for inconsistent definitions of local adaptation in larger ecological/evolutionary framework (an impediment of meta-analyses across systems), determining generalized patterns of species adaptive capacity to climate change hinges on a unified definition of local adaptation. Local adaptation is important for RCN-ECU because it may allow for more resilient genotypes to persist under changing ocean conditions; demes harboring these resilient genotypes may then “seed” or rescue other populations in the future. Clearly defining local adaptation has salient management/conservation implications.
* Kawecki et al. reserved the term local adaptation for “patterns and processes observed across local populations of the same species connected, at least potentially, by dispersal and gene flow.” Want to clarify that local adaptation could occur within species connected by dispersal and/or gene flow. For example, sea urchin ranges in western coast. Dispersal ranges don’t overlap, but there is gene flow via intermediate populations.
* Appreciating multiple models of local adaptation summarized by Kawecki and Ebert and Blanquart can improve studies of local adaptation in the context of metapopulation resilience. Application and comparison of multiple local adaptation models to a given system is necessary for 1) understanding complexity of dynamics occurring in multiple locally adapted demes, 2) using studies of local adaptation to leverage conservation efforts. For example, use of home-away or sympatric-allopatric models alone to explain variation in fitness related traits across demes could ignore variation in genetic quality across them. The finding that local adaptation is nominally occurring in a species is often concluded to be evidence of its adaptive potential to environmental change. However, may not be true if a majority of demes exhibit poor genetic quality relative to a few demes that exhibit heightened fitness within their local habitat. In this case, measuring gene flow from high quality demes to low quality ones would be necessary for understanding the resilience of a metapopulation to environmental change.
* Tying local adaptation back into our discussion of eco-evolutionary processes in marine vs. terrestrial systems, we discussed how their patterns and impacts of local adaptation may vary. Wider dispersal neighborhoods and higher gene flow among marine populations may reduce the frequency of locally adapted demes. At the same time, a locally adapted deme of high genetic quality is likely to be of greater benefit to an entire metapopulations as this deme may have a wide dispersal neighborhood, facilitating the transmission of resilient genes that are capable of rescuing species. Is it possible that terrestrial systems have more frequent but weaker instances of beneficial gene flow from “rescuing” demes, while marine systems have less frequent but stronger instances of beneficial gene flow from rescuing demes?

**Northeastern:**

* Many systems do not allow for reciprocal transplant experiments. Limited to evaluating local adaptation using some combo of common garden experiments or even GxE studies that correlate fitness associated traits with environmental variables. These studies are often much more feasible and, although they may not directly measure local adaptation, give initial evidence towards demes being adapted to certain conditions.
* Also think it is important to remember that GxE interaction for FITNESS is key to defining local adaptation. For example, GxE interaction for trait such as growth, but the population may still be locally adapted because they would have higher fitness in sympatry than allopatry. In addition, many studies do not directly measure fitness and only measure traits that researchers believe to be associated with fitness. May not directly measure local adaptation, this work gives important insights for identifying populations harboring traits that correlate with certain environments. These studies become even more crucial when identifying the adaptive potential of a population to withstand future environmental conditions under climate change.
* Two limitations: Blanquart paper recommends measuring more demes than individuals with the highest power coming from one individual per deme. Again, difficult to measure multiple populations and studies often can focus on a few. Also felt that one individual would bias any results about local adaptation due to that individual not representing the deme as a whole.

**UC Davis:**

* Two main sets of definitions for local adaptation differ in scale at which they are quantified. Local vs. foreign and Home vs away define for individual populations while Sympatric vs. allopatric is averaged across meta-population. Which definition depends on what sort of question we are asking.
* What is important in climate change is species survival or extinction. Important when we decide what definition to use since sympatric/allopatric looks at metapopulation while LF and HA look at individual populations. Local adaptation may increase diversity at metapopulation level even if local populations might go extinct during the process. The species as a whole can be repopulated by individual deme/population. However, LF and HA might be more important if we were to decide on where to build marine protected area. Setting one or two definitions of local adaptation will help move the field forward by making it easier to look for broad patterns and conduct syntheses and meta-analyses.
* There are different implications whether you look at local adaptation involving single or multiple genes/traits. Polygenic traits might be subject to recombination and their expression might depend on their placement in the genome (e.g., linkage to other genes). This can impact the level of local adaptation and tradeoffs due to linked genes subject to opposing selection. We find it important to combine sequencing with experimental setups.
* Post-settlement mortality is important and it could drive patterns that appear to be local adaptation. Explicitly accounting for post-settlement mortality would be crucial for measuring LA rather than other processes like environmental filtering.
* We decided that dispersal was an important feature to study regarding LA. It seems that a dispersal kernel (harkening week 1) of a given species needs to be defined before proceeding. In the sea, this kernel can have very long tails. In contrast, the habitat might vary at a much finer scale. Does this still lead to local adaptation? Or will individuals just move instead of adapt. In panmixed meta-population with a lot of gene flow and a large dispersal kernel, you can move through different habitats without microadaptation. Hence, we might find a mix of genotypes that is conserved across a mosaic of habitats.
* What is a population/deme? Could not find consensus of one definition in the ocean. In theory, populations are units that show higher levels of gene flow within than between. However, where do we set the cut of? Can we split large demes into smaller demes based on location? Or would we lump all demes into one that show the same sign of local adaptation? Are populations in the ocean more of a continuum than distinct parts?

**Matt Hare:**

* Blanqart paper only varied spatial heterogeneity but marine systems have a lot of temporal variability. How might that change the results of the paper? Fluctuating environments may make local adaptation weaker and lower power to detect LA.
* Struck by metapopulation perspective, LA is not a property of a single population, but rather of a metapopulation where multiple environments and populations are sampled. Understands general sentiment, but wouldn’t we expect LA to be stronger in some places than others? If we are interested in that gradient or patchiness in evolutionary capacity or in strength of selection, then it would not be desirable to treat the metapopulation as a whole and test for local adaptation on average. Thus, agrees that working definition will depend on particular objectives, but perhaps experimental results can be presented in such a way as to allow later analysis/synthesis with different objectives.
* Greatest power with one individual hard to swallow. For one, density dependence of fitness is likely to be common whereby a genotype will have different fitness if alone vs. with others, all else being equal. Do simulations reflect the enormous intra-population variation so often occurring within marine populations. To the extent that genotypic diversity elevates mean population fitness because of microspatial heterogeneity and microspatial GxE, the simple ways that environments were simulated could have led to a result that would not have much practical relevance.
* Spatial scales with high fecundity and broad dispersal have a lot of selection going each generation at small spatial scales relative to average dispersal distance (match-mismatch, balanced polymorphism). This is not classical LA that is not progressive and multigenerational but increases mean population fitness all the same. As others have noted this dynamic would generate deme differences that potentially confound and amplify patterns consistent with LA depending on the life stage sampled. Is it important to include adaptation from within-generation selection into our definition of local adaptation? Or control for it? Or parse it out? Thinks yes if we want to understand how processes affect patterns.
* We should stay anchored to motivation for studying local adaptation under increasingly rapid environmental change. We need to understand processes and mechanisms that influence the capacity for adaptive response by a population. Severe experimental constraints exist, but vital rates and population growth are what matters in eco-evolutionary dynamics and this emphasizes the need to study components of fitness across life cycle.

**MSC:**

* Where we look for LA in the first place depends in large part on individual definitions of local adaptation, which can make it difficult to make comparisons or general patterns. We raised several issues during course of discussion including:
* Which traits do we measure, emphasizing importance of vital rates and components of fitness, but also recognizing that bigger does not always mean better.
* How definitions of LA may vary across life history stages and/or entire life cycle (high gene flow but strong limits on post-settlement establishment)
* The difficulty in assessing connectivity (including dispersal and actual vs. potential gene flow) between populations in marine systems and how this may affect predictions and interpretations given that restricted gene flow is expected
* The role of abiotic vs. biotic factors in LA. Biotic is not often couched as LA, the way reciprocal transplant experiments are done may minimize or eliminate effects of the biotic environment. Biotic interactions may result in more temporally variable selection, which may require consequent changes in dispersal and gene flow to detect LA

**Cal State Monterey Bay:**

* Discussed merits of studying traits vs. fitness and common garden vs. reciprocal transplant experiments. Some definitions of LA were difficult to assess. There was nostalgic affinity for home vs. away definition, though shortcomings were recognized. Reflected overall tension in group about the merits of theoretical consideration, but the challenges in assessing them in marine systems.
* Scale not a big point of concern as most agreed that LA would be variable depending on scale and system and question people were asking.
* Temporal variation and its possible effect on local adaptation was discussed. Generally favored the sympatry-allopatry definition based on it being more explicit as a model, but in hindsight, could have spent more time debating whether it was sufficient than just the best of the three. If temporal flux could be encompassed into either habitat or deme effects, it might not be that big of a deal. There are likely cases in which the assessment of plasticity evolving as a response to temporal fluctuation could be explored as another means of further isolating the effect of local adaptation.

**Cornell:**

* Most agreed that it is more intuitive and meaningful to think about whether specific populations, rather than every single deme within a meta population, is adapted to local conditions. Seems likely that for a species distributed over a vast range of environmental conditions, we might expect LA in the extreme habitat conditions, but not necessarily in more intermediate ones. If strictly applying SA concept, might in such a case conclude that the species does not show local adaptation, which would be misleading.
* Questioned general value of knowing whether species shows LA or not. Fitness discussed in theoretical terms, while of course the practical reality is that fitness is hard to measure. Even if we could measure fitness perfectly, how much insight would we gain from knowing that a species shows LA if we don’t know the particular mechanisms or traits through which this local adaptation is conferred?
* It is important to study putative fitness traits, but also gain an understanding of what different traits and tradeoffs are involved in the adaptation and how each of these traits interact to influence fitness.
* We can use insights about LA to predict responses to climate change and other rapid environmental shifts. Seems that LA within a species could both hinder and promote adaptive responses. If populations are closely adapted to current local environment, they may not be able to respond quickly enough to change. In that sense, a really resilient generalist population may fare much better (LA could be disadvantageous). Conversely, having a diverse set of populations pre-adapted to many different environmental conditions could also seed rapid adaption in a changing environment, or if the species is mobile, can facilitate spatial re-organization of genotype-environment matches.
* Provoked by suggestion in Blanqart to do single individuals. Beyond obvious logistical challenges, discussion pros and cons of design. None could think of a study that used this approach.

**What definition of local adaptation should we (the RCN-ECS) network use?**

**Penn State:**

* Using mathematical notation, HA and LF was an improvement over the first paper
* Recognize issues marine field has with measuring fitness and particularly agreed with reminder that bigger is not always better

**Florida State:**

* No consensus reached. Presence of dispersal between demes seems to always raise discussion and different perspectives on what is and is not local adaptation. For example, it is often noted that a balanced polymorphism, where there is high dispersal and where genetic differentiation is maintained by strong post-settlement selection against migrants acting each generation after dispersal, is not local adaptation, but could still give rise to a pattern of local adaptation.
* However, another perspective is that the sorting of genotypes after settlement still effectively reduces gene flow, and could still lead to the evolution of local adaptation if there is enough local retention for persistence and subsequent build up of locally adapted alleles. The proportion of recruits that are immigrants vs. local origin at the scale being studied, seems relevant.
* Recommend Conover et al. for when transplant experiments are not feasible.

**Rutgers:**

* Local adaptation is challenging to define because it depends on your system and how local is local. Our working definition has three criteria: 1) phenotype needs to be heritable, 2) phenotype needs to influence fitness, 3) GxE interaction within habitat range that is possible from dispersal over multiple generations. Many processes could result in patterns of local adaptation.

**Hal-Dames Rule:**

* Generally, for synthesizing data, the best way to ascertain species level adaptation effects was to utilize the approach laid out by Blanquart et al. isolating local adaptation effects from genetic or habitat quality effects. Orthogonal reciprocal transplant studies can be turned into allopatric vs. sympatric comparisons, and we can potentially combine studies of different, putatively connected populations to parse together a meta-population to ask broad questions if data within a study is sparse.

**Nicholls State:**

* Defining terms narrowly may be a hindrance to good science. Design of local adaptation studies may vary drastically when the environment varies drastically (coastal CA vs. coastal LA).

**Washington State:**

* Long discussion of metaphors in science. Big umbrella terms are metaphors because they are used by a wide variety of people for different reasons, making our work more connective and approachable (theoretically). When we try to define metaphors, however, groups of people separate out with different definitions and metaphor no longer holds same strength across field. Group did not agree on whether metaphors should be strictly defined or left open, as long as they are accompanied by definitions.
* To make a definition, have to realize it is more important to exclude than include things. To do this, we have to agree on whether local adaptation is a property of the metapopulation or the deme. Is something locally adapted or is local adaptation happening? What is our evolutionary unit? Who is selection acting upon? We would argue that selection is acting upon? We would argue that selection is acting up the population level in our definition, it has to be for W between different populations.
* Why would anyone care about the metapopulation? We disagree that metapopulation is a part of the definition of local adaptation. We study local adaptation in the context of demes and focal populations, what happens to other populations is somewhat irrelevant. We still need perspectives from the home-away and local foreign perspectives, but local adaptation as a property of the metapopulation is not necessarily relevant to focal populations that have lower fitness in their own and other habitats.
* Take home perspective is important. Sympatric-allopatric perspective is just rebranding of home-away but just controlling for habitat quality. We care about story of one population, which means that home-away is the best metric. However, need to know the context of other habitat quality, and therefore local-foreign is needed to be able to say a population is better in their home environment and others do in that same space.
* When you think you have a locally adapted population but don’t see a home vs. away differences because of limitations on measurements, we need extra inference from the local-foreign population.
* Argue for using more than one individual per population, which is obvious inclusion when you consider on the population instead of the metapopulation level.
* When measuring local adaptation, focus should be on repeatability of evolving those specific traits and think carefully about complex vs. mendelian traits.
* Thought process on defining local adaptation must be strict in considering which drivers of selection we consider, and how we incorporate (or not) potential interactions into the “habitat” variable.

**Virtual Group:**

* Emphasized importance of understanding local adaptation as process, not just a pattern. However, the definition will depend on the question and should account for: local adaptation in time (seasonal changes in phytoplankton), the role of post-settlement selection (LA isn’t happening if panmixia occurs in gametes/larvae every generation, but if only adults are sampled, could easily look like LA (pattern). The importance of genetic structure (though post-settlement selection can lead to genetic structure in sampled adults without LA). The importance of scale and patchiness of habitat (how do the definitions and practicalities of measuring LA change if you are considering patches vs. different ends of a cline)
* A flow chart might be a convenient way to summarize the best way to test for local adaptation given the particularities of the system at hand.
* How to test for LA? Discussed it can be unethical to do transplants if there will be gene flow into surrounding populations, particularly a concern for open systems. But, lab studies have obvious drawbacks discussed in readings. Also talked about role of molecular studies, which has changed a lot since 2004.

**Northeastern:**

* First thought to begin definition of local adaptation as needing genetic component but found in discussions that genetic component may not always be detectable, especially when many loci of small effect are responsible for a given phenotype and these may not be detectable by current statistical models. In addition, current literature around epigenetic shows epigenetic modifications do not change the underlying code but are heritable and potentially increases the fitness of offspring in a given environment. Therefore, if we cannot detect a genetic component to phenotypic differences when placed in different habitats can we not call that local adaptation?
* Rather discuss when home vs away or local vs foreign would be appropriate and/or useful ways of truly identifying local adaptation. Each definition is useful in its own right and can provide useful information. For example, the home vs. away comparison tells if deme is currently located in a habitat in which it displays highest fitness compared to other habitats. We could not conclude that a population is locally adapted in its “home environment” from this comparison. A deme may have highest fitness in its home habitat when comparing across habitats, but other allopatric demes may have higher fitness and be more adapted to that focal deme’s habitat. This comparison still gives important information about adaption in the focal deme and where it may survive and persist but may not always identify local adaptation.
* Local vs. foreign definition instead can tell us if the sympatric deme is more fit in the environment in which they are found when compared to all other allopatric demes. This can more often identify local adaptation because comparing a focal, sympatric deme to all other demes in the study and identifying the deme with the highest fitness. Again, able to think of scenarios which we would not detect local adaptation using this method, such as populations undergoing selection or historic bottlenecks.

**UC Davis:**

* We think one definition may not suffice. Since SA definition operates at the level of metapopulation and LF is best at the level of the deme, they can be used to address different questions depending on the scale of interest. Maybe best to calculate both metrics but rely on the definition that fits the study question. However, uses of the LF or HA should address their limitations (deme quality and habitat quality should be recorded/quantified).

**MSC:**

* There is value in considering multiple metrics of LA and thus found it difficult to choose one. SA lacks power to test a number of experimental designs that might provide valuable info on LA at population scale. Being able to make pairwise comparisons can be valuable and informative (as opposed to thinking only at a metapopulation scale). Similarly, being able to assess patterns at a population level is sometimes necessary as we seek to understand and predict the effects of climate change, but this isn’t possible using only the SA approach given the focus on average performance at the metapopulation scale. Additionally, SA approach doesn’t account for mortality, so how often this approach has been successfully applied in marine systems and how often mortality (and other realities of experimental manipulations) hindered applications of SA approach.

**Questions:**

It is important for RCN to come to consensus on language referring to the study of local adaptation.

* 22 Agree
* 0 Disagree

Local adaptation is not a property of a single population but a property of metapopulation.

* 17 Agree
* 0 Disagree

When studying local adaptation, the deme is the relevant unit of biological replication and more than 2 demes should be studied.

* 14 Agree
* 3 Question Mark
* Some discussion over what a deme is, but overall, none disagree.

A GxE interaction is a prerequisite for local adaptation.

* 23 Agree
* 0 Disagree

Local adaptation cannot be determined from a single population transplanted across multiple environments. Nor can it be determined by multiple populations grown in the same single environment/location.

* 17 Agree
* 1 Disagree
* One comment advising caution against using absolutist language or drawing lines in sand.

It is inappropriate to say “population/deme X is locally adapted to environment Y” because of the metapopulation context of local adaptation: it implies something about the fitness of other populations in that environment. Instead it would be more accurate to say, “population/deme X has evolved via natural selection to environment Y”

* 7 Agree
* 3 Disagree
* 5 Do not know
* 1 comment suggesting that it depends on why you want to know about population x.

We should be careful to use language that distinguishes between the extent of local adaptation of a metapopulation, the extent to which a deme has evolved (including processes of selection, mutation, drift, and gene flow) in response to local conditions and the extent to which that evolution is due to evolution by natural selection.

* 15 Agree
* 0 Disagree

The RCN should use the quantitative metric proposed and sympatric/allopatric statistical test by Blanquart et al to measure the extent of local adaptation of a metapopulation.

* 4 Agree
* 5 Disagree
* 6 Unsure

We need to come to a consensus on quantitative metrics that can be used to measure the extent to which a deme has adapted to local conditions.

* 22 Agree
* 0 Disagree

The RCN should use one of the three definitions proposed in the Blanquart paper: Quantitative definition 1 – a quantification of the proportion of spatial variation in mean fitness caused by adaptation to local conditions in a metapopulation. Quantitative definition 2 – the difference between fitness of populations in sympatry (eg transplanted back where they came from) and populations in allopatry (transplanted somewhere else). Quantitative definition 3 – the component of GxE interaction explained by sympatric vs. allopatric contrast.

* 6 Agree
* 2 express concerns that if we use this definition, previously published examples of local adaptation will no longer qualify as examples of local adaptation.

The definition of local adaptation that should be used is context dependent.

* 6 agree
* 6 disagree

**Week 3 – Local Adaptation, in practice**

**1.) When does landscape genomic data present good evidence of local adaptation (without experiments)?**

**Rutgers:**

* If local adaptation is a measurable increase in fitness, then no. Genomics in this sense can’t present conclusive evidence of LA. No quantitative measure of fitness based only on genetic differences.
* The question was raised whether you could have these genomic signals favoring spatially divergent selection when no LA is happening. A few examples of alternative explanations included allele-surfing and other genetic drift, error, and non-random mating. Matting success is part of a phenotype, even if it depends on the organism’s social environment.
* We ended up back at K’s statement that phenotype has too many dimensions to quantify in the same way as genomics. Genomics and transplants together, when appropriate for the same organism, highlight the genetic as well as phenotypic mechanisms behind apparent local adaptation.

**Univ. Southern California:**

* In an ideal scenario, such a study system has well-defined drivers for local adaptation, such as thermal cline of Australian Drosophila. In cases with well annotated genomes and large effective populations sizes, markers that strongly deviate from expected genetic variability offer a suite of potential regions under selection.
* Careful consideration of the ecologically relevant factors that may drive local adaptation and how an organism would account for deviations in factors physiologically can be used as a guide when analyzing genomic data from spatial regions in which LA may have occurred. A strong understanding of the potential selective pressures and how they could be solved genetically would be the strongest evidence for local adaptation.
* In the absence of this knowledge, we should be wary about constructing “just so” statements from genomic regions that segregate with each population. By integrating previous experimental data, and/or in-depth knowledge of the study system landscape genomic data can be used to generate and test hypotheses. Unfortunately, most study systems do not allow for genetic manipulation of candidate genes to assess functionality or the impact on fitness.

**CSU Northridge:**

* Not too many cases where genomic data can present good evidence for local adaptation.
* Two instances they came up with were when landscape genomic data could contribute evidence to (but not necessarily result in proof) of local adaptation would be if 1. These data were paired with environmental parameters that you could attribute to changes in genomic data, or 2. Identifying the phenotypes of genes that were different.
* Found fly paper interesting but failed to see how the authors concluded that there were “fundamental biological differences between flies from these two geographic regions”

**Virtual Group:**

* Most genomic data alone do not provide much evidence of local adaptation, though if there are very strong signals of selection, perhaps this could be suggestive. However, gene by environment interactions are the exception to this and are fairly compelling in identifying loci that are likely under selection due to the environment (so parallel mechanisms of local adaptation).
* Conclusion that integration of ecological/experimental approaches is best. Doesn’t make sense to do a bunch of sequencing if there is no evidence of interesting biology. The fly paper falls into this category in that a ton of work has been done indicating there is adaptation to temperature, the genomic follow up is a logical next step to get at mechanism.

**Washington State U:**

* Never. We need an assay of fitness (ecological context) to provide proof that differences at the genetic level actually manifest at the phenotypic level, where selection is acting.
* Also depends on your audience how important this is, but generally we expect some tie to fitness to be able to say something about local adaptation if it can be mapped to specific coding sequences, but that’s making assumptions about how selection works.
* Sometimes fine that even the most in-depth sequencing doesn’t provide with nucleotide that matters, especially in complex traits and environments. There are multiple ways to arrive at certain phenotypes on the genotype level, so it can be difficult to discern local adaptation even for a relatively simple phenotype or trait. Using just genetic sequencing, especially when we don’t have adequate knowledge of function, it is very difficult to label local adaptation for complex traits.

**Northeastern MSC:**

* Agreed that landscape genomics approach can provide good insight into novel system that perhaps does not have much a priori information.
* However, in the full absence of manipulative experimental procedure it generally should be relied upon more to provide indicators of local adaptation, as opposed to providing more conclusive evidence of it.
* With regard to local adaptation it is not enough to know an allele’s effect on a trait, but also that trait’s effect on fitness.

**Bodega/UC Davis/UC Santa Cruz:**

* Can present good evidence if you have several replicates of the same environmental cline and populations showing the same direction of allele frequency changes. However it will always be a correlation and not fully sufficient to demonstrate local adaptation.
* Comparison of various genomic metrics between populations can also provide insight into past selection, drift, or other demographic phenomena (e.g., using patterns of allelic diversity to infer selective sweeps).
* Economic motivation for comparing only the two endpoints of the drosophila range are understandable, we thought the study would benefit from the inclusion of an intermediate population to verify the progressive nature of allele frequency changes with latitude as opposed to geographic breaks.

**Nicholls State:**

* Genomic data provide valuable insights, specifically when researchers can link the genetics to the phenotype. Stronger cases can be made when additional data like transcriptomics, epigenomics, and proteomics. Pairing a study using multiple data types with experiments makes an even stronger case.
* We don’t believe that the discussion should be “genomics or experiments”. The question of local adaptation is too big to only use one tool. We should employ all tools when appropriate, which may vary based on the question (basic vs. applied science), the system, the scale, the organism, etc.
* When working with non-model and long-lived species, genomics can provide a good starting point to design an integrative approach to local adaptation.

**UMass Amherst:**

* Reminded that this is model based evaluation of adaptation, in which theory is used to describe what adaptation would look like, then actual genomes are examined for that pattern.
* Advantage of genomic approach is that markers of selection can be examined without phenotypes of selection. Also the direction of functional gain rather than neutral loss can be evaluated.
* Downside is that this approach requires good quality genomes to align reads against, which are not available for all organisms. Furthermore, deep insights and direct demonstration into what exactly the functional genes differing between organisms may do with respect to local adaptation is for the most part limited to model organisms and relatives.

**UConn/UT Arlington:**

* Phenotype is needed when analyzing genetic data. Therefore, experimentation is necessary at some point, especially because we can’t support that variances are due to selection and not drift without experimentation.
* If experimentation isn’t going to be carried out in a specific study, there would need to be very strong a priori information about fitness dynamics surrounding local adaptation.
* Felt that papers provided good general methods pipelines as Snail paper establishes that local adaptation exists within a species while the Fly paper seeks to explore the genetic basis for that adaptation.

**Old Dominion:**

* Depends on study system, which usually requires a biotic or abiotic gradient between populations that can produce differences in fitness such as temperature or prey availability.
* Also depends on which genes are under selection and the genomic techniques used to analyze local adaptation. For example, structural changes in genomic data can indicate divergence under environmental selection.
* Genome-environmental association analyses (GEAA) have become important for studies of local adaptation which are sensitive to gene variants associated with various environmental parameters. It is important to incorporate analysis of neutral genetic structure in studies of local adaptation as well.

**Cornell:**

* Highly dependent on study system, if good evidence of local adaptation can be presented without experiments and is dependent on conclusively linking genomic changes to phenotypic changes
* Not always possible for non-model systems for which we don’t know much about the functions of genes.
* However, if one can link genetic variation to phenotypic variation, particularly in populations along an environmental cline or across parallel cases of adaptation, then genomic data can provide good suggestive evidence of local adaptation.
* Genetic data are therefore most meaningful in the context of phenotypic information.
* Also discuss whether this would be conclusive proof for local adaptation since one wouldn’t know if these genetic changes really lead to higher fitness or not.
* In order to show local adaptation, one has to perform experiments.
* Even without experiments, genomic data can provide useful insights into the potential phenotypes under selection and thus provide a very good basis for experimental test of local adaptation. Experiments cannot be performed for many species, and genomic analyses can be the best evidence of local adaptation in these species.

**UConn Marine Science:**

* Landscape genomic data are useful in forming hypotheses about local adaptation, but insufficient to test for it.
* Not enough to determine how selection may be influencing certain genets, especially in non-model organisms without robust annotation or mapping data.
* Should be cautious in interpreting genomic differentiation if we are unsure of how those signatures relate to the environment.

**UC Santa Barbara:**

* Genomic data can suggest that local adaptation is occurring (but is not indicative of the degree to which fitness is changing) when genetic drift is controlled for.
* Changes in allele frequencies that are evident after controlling for genetic drift may be a smoking gun for selection on fitness-related traits. That said, measuring gene flow and/or dispersion is necessary for understanding genetic drift and therefore we agree that sequence data is not useful in this context purely on its own.

**UC Merced:**

* Landscape genomic data, such as differential population genetics and Fst values, is not sufficient for supporting local adaptation because of the difficulty in excluding other potential causes of differentiation.
* Genomic data may be more useful in assessing locally adapted alleles in high dispersing, well mixed populations (problem may be cryptic species).

**Northeastern**:

* Discussed that genomic data is more convincing when it is paired with experimental data, and evidence can be further improved by pairing it with clear morphological and environmental differences. For example, genetic loci putatively linked to selection along a gradient that also tracks changes in phenotypes along the same hypothesized selective gradient could be taken, in tandem, as good evidence of local adaptation.
* Acknowledge that this scenario would likely contribute to a bias towards genes of large effect.
* Also, genomic data linked to genes that implicate differences in fitness along this gradient could represent a compelling case for local adaptation, although identifying such links (functional pathways) requires that sufficient annotations be available for the species of interest.
* A particular shortcoming of the Fly study was its reliance on only the temperature cline endpoints, without any genomic data from the middle of the temperature range. Without a more complete characterization of genomic data along the temperature cline, it is difficult to make conclusions about local adaptation.

**Louisiana State:**

* Although genomic data may provide evidence for local adaptation, generally agreed that genomic data alone are insufficient for concluding that local adaptation has taken place. Differential genotypes do not necessarily indicate differential fitness and may not be result of adaptive processes.
* All available data should be included and used for comparison against a null model, which could be used to predict the selection necessary to establish the difference among genotypes. The fly study could’ve used a null model to predict the selection that would’ve been necessary to establish the cline and compared genomic data against the model.
* It is methodologically problematic to select the 1,2, and 5% outliers and consider them as a priori differentiated since there will always be outliers, yet they may not be significant for detecting local adaptation. If the outliers are always considered differentiated, and if differentiation is evidence for local adaptation, then by definition there will always be evidence for local adaptation.
* Instead, genes with known phenotypic correlates should be chosen for analyzing whether or not their differential distribution along a cline is adaptively significant.
* By limiting the Fst windows to 1-kb gradual adaptation driven by weak selection involving larger sections of the genome may be missed. A SNP analysis may provide additional insight, but in the absence of knowledge about the fitness differences of different genotypes, a genomic analysis alone is unable to conclusively demonstrate the presence of local adaptation.

**CSU Monterey Bay:**

* Landscape genomic approaches are most relevant for exploring genetic mechanisms that might underlie local adaptation. Evidence that landscape genomics is largely context dependent.
* What lead to these studies to have such compelling arguments for local adaptation was that in both cases there was a context where local adaptation made compelling sense. Possible adaptation had been established in the snail before transplant experiments and their dispersal capability is already somewhat limited as compared to other marine species and there had already been work on Drosophila in Australia to suggest genetic clines or patterns of local adaptation.
* It was pointed out that neither of these studies demonstrated local adaptation as described by Week 2’s papers, neither paper well demonstrated local adaptation. In snail study, you had one population outperforming the other in multiple environments and in neither did they test for actual fitness.

**Univ. Queensland:**

* Landscape genomics provides good evidence for local adaptation if the study is replicated across multiple landscapes of the same environmental gradient. If such replication recovers the same set of loci, then it might support the idea of the local adaptation.
* But recovering same loci across replicates will not reject local adaptation caused by similar factors. Because landscape genomics is correlative in nature, we think that inferring the particular causative factor is difficult even in well replicated study.
* Similarly, using the genomic information to identify cellular/physiological processes that are likely to be influenced by environmental factor of interest might post challenges as well due to the possible links of many cellular (metabolic/physiological) pathways.

**2.) How do the different research approaches (experimental vs. genomic) give different insights?**

**Rutgers:**

* Experimental approach allowed the identification and manipulation of selective pressures in a non-laboratory experiment. The group behind the whelk study has an incredibly detailed understanding of their study system, and between the foundations placed by their previous work and the differences in fitness of local and distant phenotypes in CA plots, they make a strong case for the existence and drivers of local adaptation in this species.
* This approach does not, however, reveal the genetic mechanisms behind the drilling adaptations of the California snails. If researchers used a genomics approach on this species without the same system knowledge, they may find plenty of positively selected genetic differences, but they may attribute them to the climatic gradient between CA and WA rather than to differences in prey recruitment.
* Genomics approach can be used to look for genetic differences relatively quickly and to avoid the confounding effects of plasticity and maternal effects. But you need the resources (annotated genomes) to know that the outliers they find are likely to result in phenotypic difference.
* In addition, this approach gives a deep time perspective that is impossible to achieve with transplant experiments. These genetic differences integrate over all past conditions and over whatever factors you didn’t’ measure in the field.
* You can look at a broader scale of genetic change without examining specific drivers or phenotypic mechanisms, but you still get very detailed information on the mechanisms of genetic change.

**Univ. Southern California:**

* Experimental approaches offer the ability to use a top-down method of hypothesis testing by manipulating specific ecological parameters of interest while still maintaining the complex environment available in situ that would be difficult to recapitulate in a lab setting.
* Genomic data employs a bottom up approach and allows for tracking of genetic information as the currency of evolution to ascertain if noted phenotypic differences appear in association with particular genotypes.
* Genomic information may also be acquired from a broad scale of organisms without direct manipulation in the field and such data is often relatively simple to generate and maintain, all the while knowing that it reflects the objective genetic character of natural populations (assuming adequate sampling).
* Coupling of the two approaches has the greatest potential to map ecologically applicable characteristics of the organism and their genotype to measurements of fitness to determine the validity of local adaptation in the system.

**William and Mary:**

* Question how much training across subdisciplines in biology matters here. If intro to adaptation is largely genomic/bioinformatic vs. natural historical, how does that drive the types of questions you’re asking?
* Both can be compelling but how do we bridge gap in training for students to appreciate and become adept at both if both are necessary?

**CSU Northridge:**

* After significant debate, concluded that experimental approaches provide ecologically-relevant insights into tangible implications such as management in response to changing environmental conditions, whereas genomic approaches give insights into detailed mechanistic aspects of adaptation.
* From experimental design standpoint, talked a lot about how to design experiments from both aspects that would target question of adaptation, and came to consensus that if the system was well studied, an experimental approach with targeted genomic data would be able to pinpoint both adaptation as well as mechanisms. However, if not much was known about a system, perhaps a “shotgun” approach of looking at a landscape genomic changes could be a good place to identify genes of interest then design ecological experiments around this.
* Also discussed – if we need genomic data to determine adaptation. If certain trait was being selected for and was identified, genetic data could provide a mechanistic cause, but perhaps would not be needed to prove adaptation.

**Hal-Dames Rule**:

* There are merits of incorporating both methods. Reciprocal transplant experiments can identify fitness differences which could show local adaptation, but genomic data is needed to show there is a genetic basis for the differences.
* For genomic studies, positive selection can be evaluated, but it does not necessarily mean the selected phenotypes are habitat specific; reciprocal transplant experiments are needed to evaluate habitat specificity.
* Alternatively, experiments are not always possible, and genomic studies can be insightful on their own if there are a-priori expectations of the region of the genome to target; candidate genes associated with traits expected to be under selection, complementary expression and trait data, and or clear phenotypic differences.
* For snails and flies, it is important to distinguish local adaptation from neutral processes like drift. Also, corridors connect subpopulations of both species. For flies, wind currents, human aided dispersal, and active flying and their range have the possibility of connecting the different populations. For the Snails, their movement across sites is primarily due to dispersal during the larval stage, so retention of larvae at a local site is needed to maintain adaptations.
* Comparing the two papers, the flies were also likely somewhat domesticated which can affect inference of what genes may be under selection.

**Virtual Group:**

* Think experimental work largely identifies patterns (local adaptation) while genomics gets us to the mechanism. Experimental work is fundamentally important to understand the drivers behind different performance of populations and which selective pressure may be driving adaptation. Genomics provides a nice way to identify the genes/mechanisms that may be responding to this selection.
* The issue with selection scans alone is linking the genotype to the phenotype that may be under selection, and how to avoid story telling with the results.
* Because environments are complex, it is unlikely that all selected regions are linked to temperature tolerance (or whatever trait), so parsing down the many regions identified as under selection to the set that drive temperature tolerance is important.
* One strategy is to use association mapping to link genotype to phenotype while simultaneously using selection scans. Then you can look for regions under selection that explain phenotypic variation in whatever trait.

**Washington State U:**

* The inference/result per dollar in these types of datasets are very different. Also, there are some systems where one or the other approach is not feasible (long generation times).
* Best and cheapest way to make inferences about local adaptation, if animal is tractable, is experimental approaches. But most can’t be investigated this way.
* If experiments aren’t feasible, you may need to make genetic correlations with environment. We do like that the genomic approach gives historical context but can’t say for sure whether this is specifically due to local adaptation.
* Lots of discussion around how value of insight between two approaches is organism-specific.

**Northeastern MSC:**

* Experimental approaches seemed to us to be the basis of all studies aiming for insights into fitness, which we agreed should be a focal point in any discussion of local adaptation. But additionally, experimental studies have the advantage of allowing for questions ranging from the limits of endurance to extreme values of environmental factors or identifying instances of phenotypic plasticity.
* Genomic approaches allow for broader evolutionary considerations, and in some ways can be necessary to perform prior to other experimental work in order to establish proper population structure or establishing genotype-phenotype-ecotype relationships and considering multivariate interactions between environmental variables in GxE studies.

**Bodega/UC Davis/UC Santa Cruz:**

* Experimental studies: common garden and reciprocal transplant experiments like Snail study provide strong evidence of fitness differences between demes, and are useful in making informed conclusions about the ecological effects of these fitness differences. In other words, they make possible the empirical leap from evolutionary to ecological processes. However, they provide very little insight into the direct mechanisms of selection.
* Genomic studies: Assist in building hypotheses for candidate genes and the physiological mechanisms through which adaptation may occur, and also provide a genetic context for understanding the present and historical constraints on local adaptation like gene flow, linkage, and genetic architecture, but are correlative and can’t directly measure differential fitness.
* Component missing from both is the physiological link from genetics and expression to ecology (what is happening in different tissues and how is it happening? They attack question from both sides but did not converge in the middle.

**Nicholls State:**

* Experimental approach was more elegant and the researchers were able to tie the information directly into the ecology of the system. However the experimental approaches do not provide insight into mechanism. Conversely, genomic studies provide info on a mechanism, but sometimes we struggle to connect that to the ecology.
* Fruit fly paper provided a wealth of data on the pathways potentially affected by genomic differences, which is valuable information and definitely shows more work should be done along this cline.
* Work with model organisms can lay groundwork to do more with non-model organisms, but this kind of study would not be possible with many other organisms.
* With right study design, molecular work can be used to understand how plastic an organism is, which may be more difficult with experimental approaches.
* Epigenomics/proteomics/transcriptomics combined with modeling can provide estimates of how well a population may acclimate/adapt in a changing environment. May also be less invasive especially if working with endangered animal.
* Using both together is most powerful way than either by itself.

**UMass Amherst:**

* Wondered about F2 generations. How do we avoid biasing the response of different populations when we transplant them out into the field by selecting a common lab environment?
* Why f2 and not f8? Just because everyone does it?
* How do we balance adaptation in the lab with too many generations vs. not enough to remove maternal effects? What if maternal effects are the adaptation?
* Genomics offers evolutionary directionality, hypothesis generation, and looking at mechanisms. The transplant approach offers testing of specific hypotheses, results of adaptation/phenotypes, and use of non-model organisms in complex environments they evolved in.

**Old Dominion:**

* The best approach depends on study system and study species. Fly paper was able to measure a swath of genomic indices that could indicate adaptation or divergence in part because the whole genome of D. melanogaster has been sequenced, making it a great candidate species.
* Experimental studies can observe how or if genetic differences show up in the study system, but it is important to understand the functional properties of the genes under selection. Measuring regulatory elements can provide information about the pathways that are under selection and gene knockouts can determine the functionality of genes supposedly responsible for local adaptation.
* Important for collaboration between different but complementary disciplines to emphasize effects of genetic changes on local adaptation.

**Cornell:**

* Experimental and genomic approaches give insights into different aspects of local adaptation and therefore the integration of both is very powerful.
* While experimental approaches, common garden, or reciprocal transplant experiments can teach us a lot about differences in fitness, the role of divergent phenotypes and the drivers of selective agents, they don’t provide insight into the genetic mechanisms of local adaptation and are often not feasible.
* The experimental snail study does a neat job of showing that fitness differs between populations but falls short of its potential as they did not further explore potential phenotypic differences between populations.
* Linking such an experimental study with landscape genomic analyses, particularly along the entire cline, could however provide more insights into the processes and mechanisms of local adaptation, such as the migration-selection balance and identifying genes underlying adaptive phenotypes.
* We think one approach should be followed up by the other, order unimportant, if one wants to provide evidence of local adaptation. Genomic approaches could first provide insights into mechanisms and potential phenotypes under selection, which are then tested through experiments, or experimental approaches can reveal the presence of local adaptation and identify adaptive phenotypes, and genomic approaches could be then used to investigate the underlying proximate and ultimate mechanisms of adaptation.

**UConn Marine Science:**

* Experiments test for local adaptation, genomics informs on mechanisms of adaptation. Both techniques must be executed in tandem and used to corroborate each other when assessing for mechanisms of adaptation.
* Must use experimental approaches to assess what traits are affected under certain environments, and must use genomics to understand how these traits are changing.
* Can also be subject to organism/habitat in question, which may help decide what analysis will produce the most impactful result.

**UC Santa Barbara:**

* Many of the major differences have already been brought up (transplantation studies provide quantitative insights into fitness differences, genomic approaches generate hypotheses about mechanisms of adaptation and they agree that integration of both approaches is ideal.
* Proposed following experimental design and wondered what info you could pull from this that you can’t determine using either on its own: Rear F2 hybrids of different demes under common garden conditions, outplant the F2 hybrids to home and away habitats where you measure fitness related traits in a large sample size of identifiable individuals and measure qtl associated with variation in fitness between both demes.
* If you could pull this off, you could understand what proportion of genetic divergence between demes is due to hybrid breakdown (which could be important in evaluating a high quality deme’s ability to rescue demes that are at risk.
* Limitations in this are fairly serious and we wondered to what extent this experiment would be possible in model marine systems.

**UC Merced:**

* Genomic and experimental research approaches can both show inherent population difference, but genomic approaches produce more mechanistic results, whereas ecological experimental approaches can give more general/holistic patterns.
* Linked to the aspect of scale incorporated in genomic and experimental approaches. For example, genomics provides smaller scaled insight for specific genes, while field experimentation can branch out showing organismal interactions and patterns in ecosystems. This suggests that both approaches are valid but become more useful when combined.

**Northeastern**:

* Genomic approaches can give insight into genetic differences, but not necessarily (directly) get at the agents of selection that are driving them. With experimental approaches, you can test hypothesized agents of selection.
* In general, genomic approaches may be more useful when an annotated genome is available for the organism of interest, as a way to make indirect inferences about function, which may limit the applicability of these approaches to non-model organisms.
* Spatial scope of inference is potentially much broader when using genomic techniques than that which is feasible through experiments. However, if the aim is to make associations between genetic and environmental differences across space, genome scan approaches would also require fine-scale characterization of the environment.
* Experimental approaches, alternatively, provide direct framework with which to test agents of selection, but require that the experimenter make a choice about the selective agent to test and the appropriate response variables to measure.
* A strength of experimental approaches like reciprocal transplant is that they often allow direct measurement of fitness (or traits that affect fitness) whereas a link to the relevant traits and organismal fitness is often missing from a purely genomic approach, even for those with well annotated genomes.

**Louisiana State:**

* Genomic approaches provide insight into allele frequency changes, whereas experimental approaches provide evidence for the adaptive significance of the allele frequency changes.

**CSU Monterey Bay:**

* Had debate on the nature and worth of deductive vs. inductive (abductive) reasoning. Experimental evidence is very convincing, but a strict deductive perspective is really one applicable to the scale of your experiment and the null hypothesis you are rejecting.
* The abductive/inductive approaches can be compelling in the context of the data presented and the authors seem to make good verbal argument for the expectation.
* One thing pointed out about landscape genomic approach is that the evidence identified based on the population allele frequencies would indicate a population-level response and possibly a metapopulation-level response, which is different than the experimental approach and its limited scale.
* People seemed to favor an approach that included both types of information is probably closest to an abductive reasoning model.

**Univ. Queensland:**

* The snail study allows us to infer particular phenotypes (or traits) that are likely underpinning fitness in some ways (phenotypes under selection).
* Experimental approach allows us to explicitly test for factors underlying local adaptation.
* Genomic approaches can possibly give us insights into the genetic underpinnings of local adaptation. Genomic studies may, however, give clues about genomic architecture underlying selection such as the number of loci involved, their sizes, etc.
* However, in the fly paper, the genomic approach is geared more toward generating hypotheses than inferring processes causing local adaptation.

**3.) How are the processes that drive local adaptation in the snail differ from the fly? How are they similar?**

**Rutgers:**

* Do we really know whats driving adaptation in the fly? In the snail paper, abiotic environmental factors drove changes in biotic distribution, which lead to local adaptation through predator-prey interactions. This could be happening in the flies too, but we can only hypothesize based on changes in protein structure and regulation that are impacted by the genetic differences that were found.
* In theory, doing genomics on the snails and experiments on the flies would allow researchers to make important connections between physical properties of chromosomes, likely mutations, and the effects of these mutations on phenotype.

**Univ. Southern California:**

* The snail system makes a cogent case for both biotic and abiotic determinants driving potential for local adaptation. In drosophila the cline was largely noted as being driven by climate and temperature without specific reference to biotic aspects.
* It is possible that populations of Drosophila across the cline experience drastically different biotic environments such as the predominant food item available especially in the case of agricultural products which may have different amounts of insecticide.
* In both systems there is a latitudinal gradient to the adaptation albeit that the determination of a cline in the snail population is difficult given data from four populations.

**CSU Northridge:**

* Discussed how differences in life history between the two species could drive local adaptation. With snails, processes of localized recruitment, shorter spatial dispersal, availability of prey could increase selective pressure for certain traits in microhabitats. In the fly system, we were unsure how the organismal interaction with the environment would affect its ability to adapt.
* Authors in the fly study identify differences in the genome across latitudinal clines, however there are many factors that may drive changes in the genome (temp, prey resources, habitat availability).
* Annotation of genes would be necessary to determine the processes that may drive local adaptation, and that a further ecological context is needed to interpret if this is in fact local adaptation.

**Virtual Group:**

* Lots of similarities between the systems, mainly nice clinal systems and large population sizes.
* Differences in life history may make the snails more likely to have local adaptation at small scales – short dispersal with very local recruitment. The main difference is that the snail system took the abiotic variation along the cline and identified the biotic consequences as compared to the rather straightforward abiotic focus in the flies. That extension is really nice and highlights how we need to focus on how abiotic parameters affect more than just physiological processes.
* Patterns of adaptation in snails very interesting. Because southern snails lack preferred prey, they have evolved to be able to consume a more broad array of prey than northern snails; their niche is expanded. This leads to an interesting reaction norm where southern snails have no change in fitness but northern snails have an adaptive pattern.
* We discussed for a while which population has actually adapted to their environment. On the surface it appears that the northern population has evolved, but probably the southern population has adapted to be able to consume larger prey? If this is true, then the population that has adapted shows no patterns of local adaptation.

**Washington State U:**

* Papers were too different to give a fair comparison. Question is not answerable based on these two papers alone, but thinking about general knowledge about these animals, we can say that the reproductive, environmental, dispersal, and many other processes are still so different they cannot be compared.

**Northeastern MSC:**

* The Nucella study was focused on prey availability and feeding behaviors of the Oregon and California populations. While some abiotic factors like temperature, were accounted for, other factors, like the long term shaping of population behavior by winter temperature differences couldn’t be explicitly considered. Experimental approach does require focusing on very explicit factors driving local adaptation.
* Drosophila study highlighted a range of factors potentially driving local adaptation, including thermal stress, insecticide resistance, circadian cycle differences, and mating behavior.
* Agreed that genomic approaches are very useful for hypothesis generation and can in fact generate multiple potential hypotheses per study while experimental approaches serve better to test explicit hypotheses and are by necessity only focused on a few factors.
* Wish that authors of snail paper had clarified terms instead of saying “show local adaptation” to “show signatures of local adaptation” since without knowing which population is ancestral, can’t say which is showing the adaptation.

**Bodega/UC Davis/UC Santa Cruz:**

* In both examples, local adaptation is driven by differences in environmental variables, but directly so in the case of drosophila, while there was no evidence that temperature differences were driving divergent selection in Nucella.
* However, regional differences in upwelling lead to changes in the strength of species interactions of Nucella with various prey species, driving differences in foraging pressures. Drosophila case, latitude factors. Snail, prey availability driven by differential recruitment.
* Nucella’s life history traits limit gene glow, but drosophila seem to have fewer physical boundaries to gene flow. Effective population size of drosophila also much greater, leading to a minimal impact of drift.

**Nicholls State:**

* Only discussed that snail is in an intertidal zone and the scale of the experiment was much smaller than the temperate versus tropical scale of the fruit fly.
* How can this be communicated to a broader audience? Is one type easier to communicate to the public when trying to explain importance of local adaptation to climate change?

**UConn/UT Arlington:**

* If local adaptation means increased fitness within an environment, got nitpicky that fitness wasn’t defined in the Fly paper. Drosophila altered development in response to abiotic forces, while Snails altered biology to deal with biotic forces (prey availability).
* Discussion that patterns in biology tend to be in response to abiotic forces (longitude and upwelling).

**Old Dominion:**

* Both papers investigate heterogenous environments with populations separated by geographic barriers resulting in restrictions of realized gene flow. Local adaptation in both examples are driven by abiotic processes, but biotic processes are also drivers of local adaptation in the snail.
* Biological processes under local adaptation at the genomic level were not as thoroughly analyzed in the fly paper.

**Cornell:**

* Ultimately, the processes driving local adaptation in both systems are directly or indirectly linked to differences in abiotic factors – either climate or upwelling.
* In the snail, differences in prey abundance, which are associated with abiotic differences are drivers of local adaptation, whereas in the fly paper, abiotic differences seem to directly be the driver of local adaptation.

**UConn Marine Science:**

* Obvious differences in the scope of both studies. Snail study uses system with similar climatic environments but different oceanographic contexts and prey availability. The fly paper uses a system that spans a larger geographic range with more distinct environmental differences.
* Comparing the two, one might interpret the lack of prey and difference in climates to drive adaptation for each respective study (how they are different), while both papers suggest that trait differentiation within the metapopulation seems to be the result of local adaptation (similarities).
* We are not convinced that either represents the local adaptation they seem to suggest. Both papers suggest evidence for some traits that are the result of adaptation, but without measuring fitness for each trait difference with respect to the environment, we cannot conclude that either the snails or the flies are locally adapted. This does not suggest that the information presented is invaluable, just suggests that that the way the data is presented leads the way for future studies.

**UC Santa Barbara:**

* Found snail paper unique in that both the selective pressures and the fitness-related traits being studied were directly linked to community level processes rather than purely organismal ones.
* Much of local adaptation literature is rooted in organismal processes, community- and ecosystem-level variation is crucial when considering how marine systems will be impacted by changing environmental conditions. In the case of flies, there are likely a myriad of selective pressures that differ between the two habitats that were studied, which were likely rooted in community and ecosystem processes and not just the physical environment.

**UC Merced:**

* Specific to these studies, it is difficult to define processes and compare the lines of evidence provided, because they are so different.
* Aside, transplants on ecosystems in the wild are approached with caution much more now than in the past.

**Northeastern**:

* Processes that drive LA in the snail are mediated by both biotic and abiotic processes, via spatially consistent differences in upwelling that lead to differences in prey recruitment. In contrast, the processes that drive LA in the flies are primarily abiotic.
* Both selective regimes were persistent in space.

**Louisiana State:**

* Do not agree the fly paper demonstrated presence of local adaptation in the fruit fly. Analysis of differential genotypes led to the detection of interesting patterns, which may be a good starting point for formulating hypotheses that should be methodically pursued, but patterns do not necessarily correspond with local adaptation.
* Paper on snails challenged to rethink definition of local adaptation, which they originally defined as reciprocity in fitness as a result of home/away comparison, because, on the one hand, we view the fitness differences (local vs foreign) between the CA and OR populations in the California sites as evidence for local adaptation, but on the other hand, we view the fitness differences between the populations in OR as fitness differences but not necessarily evidence of local adaptation.
* In the case of the snails, since there are many unknowns and variables to be considered such as the effect of drilling efficiency/likelihood of mussels on snail fecundity, concluded that Snail paper provided evidence for local adaptation in California sites, there was not enough to definitively determine that local adaptation was occurring. Not every population has to be locally adapted in their own locality.

**CSU Monterey Bay:**

* Didn’t spend much time, ultimately it was the same evolutionary forces at work here that we would see in any study, although of course, things like the nature of selection could definitely vary.

**Univ. Queensland:**

* In the snail experiment, biotic factors impose selection on the snails. In contrast, the fly study seems to examine the effect of physical factor, particularly temperature, in inducing local adaptation.
* Note that inferring spatial factors underlying local adaptation will be difficult with few populations

**Week 4: Evolution of genomic architecture**

**Summary**: Paper 1 – Chromosome inversions, Local adaptation and speciation. Kirkpatrick and Barton 2006 (Genetics). Paper 2 – Local adaptation by alleles of small effect. Yeaman 2015 (American Naturalist)

**1. What kind of genomic architecture to expect to evolve under high gene flow?**

**FSU:**

* Many quantitative phenotypes involved in local adaptation, so having many small effect alleles prone to swamping and high turnover is probably common.

**WSU:**

* Better appreciations for possibilities but haven’t been able to develop rule set for genomic architecture.
* Haldane’s rule balancing selection with migration is best null hypothesis.

**Cal State:**

* High gene flow favors genomic architecture with fewer, larger, and tightly clustered alleles.
* Small mutations may occur but expect larger alleles to have greater effect.
* Genetic redundancy, rate and size of mutation, and allele effect size will affect ability of gene to persist.

**UMass Amherst:**

* Inversions are maintained and spread primarily due to suppression of recombination, and if recombination were to occur, it would be lethal to the individual.
* Migration/selection balance – number of loci captured by inversion was driving factor in determining fate of inversion.
* If they are such powerful drivers, why don’t we detect them more often? Technological capacity?

**Uchicago**:

* Small effect loci depends on genome size/complexity. Most of results (yeoman) based on number of loci and genetic redundancy of trait. Finding these out is difficult, but perhaps feasible using combo of GWAS and quantitative genetic based approaches.
* Allelic patterns of divergence might change over time during local adaptation, where allele effect size might be most important at beginning of local adaptation.
* Common challenge – if patterns of adaptation we observe now are due to historical evolutionary processes, can we use them accurately to make future predictions?
* Time scale over which spatially fluctuating selection pressures drive local adaptation is distinct than rate at which adaptation to rapidly changing environmental conditions occur.

**USC:**

* Strongly differentiated motifs can withstand gene flow, while moderate or weakly differentiated more likely to be swamped.
* Inversions expected to become fixed – increased migration increases fixation because recombination with immigrants in the ancestral haplotype lowers the frequency of adaptive alleles.

**Nicholls:**

* It depends and its complicated. If organism has genome sequenced, then forward genetics are possible with more informative markers. Non model may be limited to just reverse genomics.
* May miss signal of if only using outlier SNPs if there is high gene flow, especially when considering alleles of small effect.
* Finding candidate genes/pathways may be only way to identify local adaptation in this case.
* Using markers beyond SNPs is highly exciting but marker choice comes down to question – do you want to prove local adaptation? May be impossible, but useful for management/conservation.
* Getting bogged down in mechanism may be informative for basic science but may not be useful in application.
* Combining genomics with epigenetics, transcriptomics, or proteomics may help.

**Rutgers**:

* How likely is it for beneficial inversions to occur?
* No single genomic architecture is likely to evolve under high gene flow but what emerges is highly context specific depending on system, traits under selection, degree of genetic variation already present in the genome, etc. \

**UCDavis:**

* Echoing Haldane, locally favored allele would be lost when immigration rate of maladapted genotype exceeds strength of selection against it.
* Echoing Felsenstein, At higher migration rates, locally adapted allele will spend a larger proportion of its evolutionary time in environments wehre it is disfavored, and above a critical migration rate it may have lower fitness than intermediate.
* Yeaman, if migration between difrerent environments, might predict that stable maintenance of allelic polymorphism would be effectively prevented by swamping if all genetic variants are of small effect relative to migration rate.
* Migration homogenizes populations which is gene swamping.
* Without change in environment, would expect constant molecular clock, Kimura suggests that most mutations are neutral.
* Maynard Smith, real adaptation occurs in sequence space that is discrete. Number of possible sequences for a gene is limited. Adaptive walk with different local optima, with too much migration, there is no walk.

**ODU:**

* Genomic architecture = non random arrangement of genome and can be seen in chromosomes, gene inversions, loci, genes, or number of copies.
* High gene flow, alleles are migrating from one population to another bringing in both adaptive, maladaptive, and neutral alleles.
* Gene swamping will flod the locally adapted alleles of original populations under certain circumstances.
* Genome architecture would likely be similar in population experiencing high gene flow.
* One-off events could create barrier to gene flow, making genome architecture more likely to be different.

**Hal-Dames:**

* Any genomic architecture that creates post zygotic barrier and or prevents recombination could be fixed in a population despite high rates of gene flow.
* Inversion and chromosome duplication good examples of genomic architecture that allow maintenance of fitness despite influx of maladaptive alleles.
* Alleles with small effect that are numerous/redundant may be more adaptable to changing environments. Alleles constantly being swamped by other alleles of small effect, which allows fitness of individuals in population to vary slightly. May mean that locally adapted alleles never reach fixation.
* Very difficult to detect “small” genes – transient nature means that It would be difficult to capture the exact snapshot in the population’s history where this suite of alleles is adaptive.
* Chromosome inversions seem easier to detect especially given whole chromosome sequencing.

**Cornell**:

* Might inversions be less favored when there is more complex fitness landscape?

**Northeastern**:

* Didn’t test whether inversions tend to evolve in high migration scenario, so it is difficult to know if they are likely to evolve under high gene flow.
* However, if you think of these as alleles of large effect, it is possible to rationalize, but needs to be tested.
* Yeaman showed how polygenic traits comprised of many alleles could evolve depending on migration/mutation rate. Demonstrating that even transient alleles could influence the adaptive divergence of a population when there was sufficient genetic redundancy and mutation.
* Did not find compelling evidence that specific architecture could broadly expected.

**CSU Monterey:**

* Large effect sizes in single celled organisms enhances purifying selection to such an extent that it eliminates non coding junk DNA.
* This selection yields efficient genomes with different architectures in multicellular orgs.
* But marine species often have large effective sizes and high gene flow, which tends to unify local populations. Larger effective size might have less junk dna as a result, but yet to look into it.
* An inversion that captures 2+ beneficial alleles will spread faster given high gene flow is interesting and plausible.

**LSU:**

* Interesting delineation between genetic and genomic. Paper suggests that genomic architecture describes potential loci that could result in adaptive trait, while genetic architecture is representative of currently variable loci contributing to adaptive trait.

**2. How does genomic architecture constrain adaptation?**

**WSU:**

* Depends on what is meant by genomic architecture, constrain, and adaptation. Definitions are context specific. Depends what system and what you measure. If it is context dependent, is it worth pushing for a general definition?

**Cal State:**

* If allele effects are large, could swamp out newer alleles even if they are adaptive. (does not consider fitness aspect of the population).
* Populations are never “stable” as conditions constantly change.
* In perfectly stable environment, would anything change? Theory based on stagnant environment.
* Philosophical conundrum that our understanding is from selective pressures of the environment.

**USC:**

* Redundancy and migration can limit fixation of alleles and constrain adaptation
* Inversions can capture locally adapted alleles but may also capture deleterious alleles at other loci, which may prevent fixation
* Inversions may fix advantageous alleles, but if the environment changes, these organisms cannot recombine with those who lack the inversion to adapt to new conditions.
* Small effect alleles may be more likely to contribute to local adaptation on a short term scale, but may not persist due to swamping.

**Rutgers:**

* Pace of adaptation may differ depending on if trait of interest is governed by mainly large or small effect alleles. If large, adaptation should be fast with larger jumps in fitness as beneficial alleles move to fixation then plateauing. Small effect = slower adaptation because of weaker selection. Transient nature of adaptive genomic architecture with small alleles may further slow this pace.

**UCDavis:**

* Linkage: when strength of divergent selection on linked locus is large relative to recombination rate between them.
* Only large effect alleles will contribute to divergence while quantitative genetic models predict that divergence will evolve as long as genetic variation is maintained.
* Quantitative genetics: standing genetic variation is due to many alleles of small effect. Fst would not pick up differences in alleles in second scenario.
* As # of loci contributing to trait increases, relative contribution of fst at individual loci decreases, while among population covariatnce in allele effect size tends to contribute more.
* Kimura: mutations must be beneficial but also to escape accidental loss when rare
* Welch and Waxman: cost of complexity is that distance traveled to optimum by a benefical mutation is smaller in a complex than simple species. Complexity = number of characters.

**ODU:**

* Constraint is high gene flow bc will homogenize.
* Not necessarily less genetic diversity. Barrier to genetic recombination necessary to lead to local adaptation, whether they be inversions, linkages, etc.
* How often to large effect genes lead to adaptation vs. small effect genes?
* Larger areas of genome likely to be linked than originally thought, which could reduce local adaptation.
* Length of sequence is limited, so effect of mutation on a specific gene limited.

**Hal-Dames:**

* Inversions may make populations more rigid in face of climate change.
* Altered genomic architectures may not be able to take advantage of new alleles delivered by gene flow. These pops may need to rely on new mutations.

**Northeastern:**

* Question could be interpreted different ways depending on how you define constraint.
* Could reduce number of ways adaptation could occur, or limit the rate or likelihood of adaptive evolution.
* Low mutation rates, minimal standing genetic variation, decreased genetic redundancy in polygenic traits.
* Inversions could also constrain adaptation when new adaptive inversions rapidly rise to fixation. Inversions are well adapted but have limited variation.
* Potential from underdominance or maladaptation due to recombination between inverted and non-inverted chromosomes might serve to further limit variation, so if environment were to shift, population of newly fixed inversion may be limited in response.
* Larger effect size might improve efficiency of selection on adaptive allele.
* If inversions are considered alleles of large effect size, then could facilitate faster rate of adaptive evolution, however highly context dependent.
* With poly genic traits, if variation is limited, there is limited potential fro adaptation.

**CSU Monterey:**

* Stumped, but hox genes, which must be kept in same order on chromosome – inversion in this region would not be beneficial.

**LSU:**

* If no linkage or proximity, adaptation can be constrained.
* With inversions, potential for propagation of both positive and negative alleles in a population.
* Inversions can present meiotic incompatibilities resulting in reduced fitness further constraining adaptation and possibly leading to speciation.
* Location of mutations as well as mutational target size can also constrain.
* Different areas of genome have different likelihoods of mutations (CpG islands have higher mutation rates) and size of mutation can influence persistence.

**3. What are the implications of different genomic architectures for our ability to study adaptation using genomic data?**

**FSU:**

* Ability to use genomic data depends on of unknown locus of transcience and allele turnover rate relative to recent history of ecological causes of divergent selection on phenotypes.

**UGH/UNH:**

* Focus on few, large effect vs. many, small effect and how to detect causal loci. Experimental design (cmg, rt) affects the ability to pinpoint candidate genes.

**Virtual Group:**

* Large effect genes have gotten most focus, but this is unwarranted.
* Genomic architecture has huge influence on how well we identify local adaptation.
* Standard measures of differentiation (Fst and GEA) rely on loci of large effect with little/no redundancy but miss class of polygenic traits driven by small effect loci.
* Polygenic signal likely to be common in physiological adaptation.
* How can we id polygenic stuff in non model? GWAS? New approaches?

**Cal State:**

* Complex orgs evolve slower bc mutations tend to be more deleterious for less complex organisms. Is this bc there are more genomic redundancies?
* Interesting to see how different lineages evolve due to genomic architecture.
* Papers mention that changes in genome structure don’t always scale to phenotype
* Not sure of next steps – what should we target? If we want to assess if a population is subject to gene swamping from high gene flow, how would we assess? Impractical to assess karyotype or determine standing gen. variation in non-model organisms- what alternative techniques are available?

**UMass Amherst:**

* Need to look at genes with small but significant effects, not just Fst outliers.
* Should also be considering how we study polygenic traits with differing levels of genetic redundancy.

**Uchicago:**

* Wish to know more about prevalence of inversions in marine species – data is sparse.
* Likelihoods of inversions probably different across species, depending on genome size/complexity, or structure of genome around trait of interest.
* Are larger genomes more susceptible? Are polygenic traits more likely to be affected by inversion?
* Determining species specific inversion rates and genomic architecture are critical steps.

**USC:**

* If working in marine systems with high gene flow, large effect alleles will likely be the ones contributing to local adaptation.

**Rutgers:**

* May need several different techniques to study local adaptation – as not all architectures result in equally detectable signatures of selection/adaptation.
* Small effect alleles may often go undetected while large effect likely to be identified via fst outliers.
* How do we detect inversion? Look for linkage blocks or by comparing gene positions in two populations of closely related species?

**UCDavis:**

* Large alleles have higher probabilities of establishing. What is large allele? Is size dependent on phenotype? Can we define it as proportion of phenotypic variance it can explain?
* Simulations show that local adaptation can occur when individual alleles underlying a trait are prone to swamping, given enough genetic variation.
* Genetic variation is key. Adaptation under migration selection balance cannot always be predicted by deriving traditional population genetic models for the maintenance of polymorphisms and extrapolating to the whole genome. Rather, adaptation is quantitative genetic phenomenon.
* If high genetic redundancy and variation, there can be high turnover in loci that contribute to divergence even when individual alleles are highly swamp-resistent.
* Adaptation via swamping prone genes can occur when selection acts on traits that are quantitative, but unlikely in traits with simple genetic basis.
* Solution to combine popgen with quantitative genetics approach. GWAS to estimate genotype values by taking frequency-weighted sum of individual SNP effects on trait of interest (Berg and Coop 2014).

**ODU:**

* Difficult to study underlying genomic architecture for most phenotypes. Difficult to know what is driving local adaption via observing changing phenotypes.
* Effect of genome architecture could be better understood with better sequencing technology that can identify structural changes in chromosomes.

**Hal-Dames:**

* Genetic mechanism underlying local adaptation could influence how organism responses to changing environment (rigid vs. pliable) so might be important for predictions. Just don’t know how to detect.

**Cornell**:

* Different constellations of alleles at many loci that can produce optimum phenotype. When this occurs, detectable fst outliers may be few. GWAS approach by Berg and Coop was mentioned, but It requires that a trait be identifyied and a large sample size, and may be prone to false positives.

**Northeastern:**

* If we expect small allele genes to drive adaptive divergence, we lack power to detect them.
* Methods that evaluate each locus individually biased towards individual alleles of large effect, due to expectation that they are more strongly correlated with phenotype or environment.
* Many small alleles under weak selection may not have dominant frequencies that are highly differentiated or corrupted beyond what we’d expect with null model. (below threshold of detection).

**CSU Monterey:**

* Curious about inability to detect many small genes.
* Encouraged by idea that at higher migration rates, more alleles would be swamping prone, but any alleles large enough to resist swamping would be more readily distinguished from neutrally evolving loci.
* GWAS an option, alternatively could look for difference in mutation rates estimated over temporal range of molecular clock calibrations. Time dependence hypothesis – genes that show rate in calibration time are likely experiencing mild purifying selection.
* Marine species have shallower decline in mutation rate than terrestrial species, probably due to larger effective population sizes.

**LSU:**

* May be detection bias for alleles of large effect, and easier detection doesn’t make them more common.
* Identifying Fst outliers may not be sufficient for detecting alleles of small effect.
* Would only be able to see it if more than one locally adapted alleles are caught in the inversion.
* Absence of identification of alleles of small effect not enough to claim absence.

**Week 5: Dispersal**

**Summary:** Groups discussed dispersal based on papers by Pringle and Wares (2009, *Marine Ecology Progress Series*) and Connolly et al. 2001 (*Ecology*)

**1. How might pelagic life histories with asymmetrical dispersal, coupled with genetic correlations between larvae and adult traits, constrain or promote adaptation?**

**RU:**

* Pelagic larvae constrain evolution. Things that enable adaptation increase the ratio of local to migrant settlers.
* Shorter pelagic duration could help or other larval behaviors that improve retention, especially if those are correlated with traits that promote adult fitness.
* Increased “pelagicity” would constrain ability to adapt by opening population.

**LSU:**

* Constrain: if there is a trait that is beneficial as larva but harmful as adult, would constrain adaptation.
* Promote: if there is trait correlated to success in both larval and adult.
* Difficult question – larval stage is where selection may be most important, but this stage is also hardest to research.

**NEU:**

* Easy to understand how adaptation may be promoted/constrained by genetic correlations between traits across stages, across different optima across stages, across traits adapting to different environments.
* Adding asymmetrical dispersal makes it difficult to predict.
* Important result – if allele is favored downstream (but not upstream), gene flow can swamp out this allele entirely unless there is barrier to larval transport.
* Huge implications for inferring adaptation from landscape genomic data, as clines may be established because of barriers to gene flow rather than an area where an allele is actually favored.
* Interesting how reproductive success can vary through space only due to variation in effective population size (good vs. bad habitat) and transport (migration).
* Results more broadly applicable to wind pollinated conifers, as wind can be asymmetric.

**WSU:**

* Depends on relative strength of selection in each life stage. Not as simple as beneficial vs. harmful in direct correlations.
* Relative strength of selection between life stages important, and distinction between trait that is expressed in one stage but affects all vs. distinct traits expressed in multiple life stages that have same function.
* Bet hedging is adaptive and can’t make simple connections between high fitness juvenile and adult phenotypes (and genotypes)
* Specific habitats may promote strong connections between life stages, but manifestation in that specific habitat complicates generalizable patterns.

**Hal-Dames:**

* If dispersal created unidirectional gene flow, cline will be transient unless differences are reinforced by selective pressure. (similar to polygenic traits from last week).
* Potentially redundant alleles could temporarily create a locally adapted genotype, but eventually be swamped out by high gene flow from up-current.
* If studies use pop genomics to identify local adaptation, researchers could detect false positives if transient differences are result of asymmetric dispersal in absence of selective pressure.
* Impact of isolation by distance would be difficult to distinguish from local adaptation using genetics alone. Should couple with experiments that connect genotypes to habitat-specific fitness.

**NoCal:**

* Likely to be other factors than upwelling that affect larval community composition.
* Any type of directional force moves genes in one direction- alleles adapted to upstream will be put downstream, leading to source-sink dynamics. Allelic diversity downstream is product of mutation and immigration
* In upstream population, allele frequencies will change like in population with symmetrical dispersal.
* In downstream populations, density dependence limits growth rates and takes a very large selection coefficient to maintain a new allele. Ultimately, this will constrain evolution.
* Another consequence of asymmetrical dispersal is that phenotypes will experience several different environments during different life stages. If there are genetic correlations between larval and adult traits, this can lead to phenotype-environment mismatches.
* Will differential gene expression of same genes in different environments/life stages a mechanism to counteract this disconnection
* RCN should focus on whole life stage view of evolution
* In the absence of quantitative genetics approaches, the heritability of allele frequency changes observed are unclear.

**MIT/Woods Hole:**

* Positive selection for a linked trait among life stages would promote local adaptation, especially in pops with high degree of self-recruitment via forces that limit the delivery and settlement of immigrants or promote retention of local genotypes.
* Coordination in direction of selection upon a trait may shift along species range. When coupled with asymmetrical dispersal, this could have interesting outcomes for establishment and maintenance of genetic differentiation.
* Difficult to assess though.

**FSU:**

* Asymmetric dispersal could lead to areas of the coast where post-settlement environments differ, but where migration > selection and where selected alleles cannot persist and avoid being washed out.
* Genetic correlations between larval and adult traits constrain adaptation when they cause reduced genetic variation along the axis that selection occurs.
* Could in theory, lead to areas of the coast where post-settlement environments differ but selection has removed the larval genotypes that would do best there as adults.

**UTA:**

* Adaptation might be constrained due to two life body plans in one genome. Beneficial traits to larvae may not be good for adults and vice versa but depends on environment.
* Asymmetrical dispersion could lead to rapid extinction of rescue depending on environmental factors.
* Strong selection means adaptation will be forced in one direction. In these cases, shorter larval life spans and production of more offspring would be more favorable to local adaptation.

**MSC:**

* Always returning to basics – tension between gene flow and selection, and how any oceanographic process or life history characteristic that shifts the balance will act to prevent or promote adaptation.
* Strong asymmetrical dispersal will constrain downstream adaptation by dragging allele frequencies away from downstream optimum – which can cause reduced reproductive output and render habitat a sink
* Any genetic correlations between adult and larval traits that would make the incoming larvae less fit in the downstream habitat would reduce their impact on the receiving population. Realized gene flow would be less than predicted based on oceanographic connectivity and dispersal potential.

**Katherine Silliman:**

* Interesting how clines can also arise due to other processes. Any interruption to gene flow (disruptions in larval transport, habitat availability).
* Clines may also shift downstream if mechanism maintaining them is removed. So cline may not be where it was originally described. Could mess with methods.
* Given sea level rise and even last ice age – possible that clines are moving or have moved from their origin.
* Should consider these factors as we consider adaptation in the future.
* Importance of regional variation in habitat quality/disruption of dispersal/larval retention on the strength of selection required for maintenance of adaptive divergence, should consider how these factors will change in the future and how that will alter our predictions for adaptation.

**USC Cee lab:**

* Asymmetrical dispersal would constrain adaptation to downstream but may yet still see adaptation due to constant influx of individuals from upstream.
* Locally adapted adults may produce larvae that are swept away from parental habitat and not larvae will not be adapted to environment it recruits to.
* This would reduce fitness and prevent successful gene flow/migration or depending on the number of larvae immigrating, generate a less adapted population.
* Genetic correlations could constrain or promote adaptation depending on the relationship of that correlation. For example, traits that are beneficial as larvae but not as adults will improve recruitment but hamper later life history stages.

**UCSB:**

* If asymmetric dispersal is causing one population to receive more propagules from the other it could reduce genetic diversity of the source relative to the sink.
* Whether or not asymmetrical dispersal can widen gaps in adaptive potential between populations may depend on a genetic correlation between stages, type and intensity of selective pressures across life history stages, and probability that larvae will experience selective pressures that exist in habitats within dispersal range.
* If there is poor genetic correlation between larvae and adults,, positive selection on larvae could mean that surviving larvae may not improve mean fitness if new population experiences same selection.
* Mating vs. spawning events could have effect on genetic diversity within larval cohort. More partners means more genetic diversity.

**Virtual Group:**

* Selection in the same direction on different stages amplifies selection, but if selection is in opposite directions at various stages, they can cancel each other out
* Selection can be very inefficient with traits on different stages, but depends on strength of selection. If they are opposite, never going to reach peaks at any stage.
* Maybe you can persist where you aren’t most favored, you can do it because larval stage is more favored increasing the spread of favorable allele.
* Could be differences between free and directed dispersal. More probable that different traits are selected in larvae and adults for free-living larval stage and they can have different feeding requirements but can that give more opportunity to persist at different habitats, why this happens so often for marine organisms?
* How about outcome if have two adult populations on two different selective habitats, and larvae only coming from one. Selection for larvae happens only in one habitat but selection on adults happens in both. Possible swamp out?

**CSU Monterey:**

* If adaptive alleles keep getting washed down stream, there may be selection for mechanisms that retain larvae like swimming or lecithorophic life histories, brooding, or shorter pelagic durations.
* Stronger current, the stronger the selection to keep adapted individuals close.
* Should see higher proportion of species with retention mechanisms in vicinity of boundary currents, but do not know if this is true.

**CSUN:**

* If there is strong connectivity between adult and larval populations, expect strong correlation between adult and larval traits, and less of an ability to adapt.
* High connectivity and high allele frequencies constrain local adaptation. Asymmetrical dispersal may promote adaptation. Larvae that come in waves with different genotypes could promote gene swamping thus leading to more adaptation potential over time.

**Cornell:**

* Multivariate breeders equation is good example of how evolution and adaptation in different stages can either be constrained or promoted.
* Dispersal period between the two stages and gauntlet that larvae experience can further complicate things.
* Where there is asymmetric dispersal due to, say advective current, simply having selective advantage is not enough to promote adaptation. Recruits must settle, survive, and reproduce. Selection coefficient alone is not enough to predict.
* How to detect adaptation in such systems? Focus on within-cohort patterns at different stages or with multiple populations at multiple loci over time.
* Under a linear model, also wondered what the implciations for adaptation were for the upstream source populations, assuming they are in marginal habitat.

**ODU:**

* When asymmetrical dispersal occur, there is a possibility of having a source sink type structure where crowding occurs downstream. In this situation, local adaptation is promoted but for migrating alleles, it might be more of a challenge to survive and adapt locally.
* Dispersal increases gene flow, but alleles of migrants migh be maladaptive locally possibly reducing their fitness and constraining adaptation for these alleles.

**UQ:**

* Oceanographic processes like upwelling can dictate where larvae settle. Distribution of alleles is further fine-tuned by a number of abiotic and biotic variables. Genetic clines are maintained if selection for downstream alleles is strong or variance in oceanographic processes is high, such that local recruitment is encouraged and outweighs L\_adv downstream.
* Balancing act between the strength of selection and environmental stochasticity also depends on other factors that modulate larval dispersal like currents and time of pelagic stage.
* These parameters are likely to be species specific, so can we expect to see consistency in where genetic structure forms and persists when different species are compared? Should carefully consider both oceanographic processes and larval behaviors that maximize Ldiff.

**2. When and where do we expect population genetic structure to be generated and/or maintained?**

**RU:**

* Tension between selection and dispersal, open and closed populations.
* Components that maintain differentiation are selection and environmental heterogeneity.
* If selection strong enough, downstream allele with fitness advantage could create genetic cline. Or a neutral allele could be maintained if there is some barrier. Either way, increased retention relative to immigration makes for a more closed population, enabling persistence.
* Real world probably in middle: traits with small selective advantage able to persist in the face of immigration because of environmental heterogeneity that increases larval retention.
* As barriers to dispersal decrease, strength of selection would need to increase, and this would be modulated by life history traits like pelagic duration, fecundity, agency of larvae, etc.

**LSU:**

* 3 criteria: 1. Gradient in selection for downstream allele, 2. Sufficient selection downstream of the cline to retain the downstream allele against advection, 3. Insufficient selection upstream of the cline to prevent the cline from moving upstream.
* May also be affected by habitat quality. If upstream is better quality, may prevent from moving upstream but could swamp out cline.

**NEU:**

* Need better understand the heterogeneous landscape of selection relative to migration across seascapes, the mean and stdev of dispersal distance, variation in effective population size, variation in habitat quality, and nature and strength of selection.
* Connelly paper saw strong patterns which highlights important role of competition when recruitment is high.

**WSU:**

* When there are barriers to dispersal and/or strong selection AND the phenotype is result of specific genotype.

**Hal-Dames:**

* Population structure depends on both pre and post recruitment barriers. Longer pelagic larval duration and more prominent headlands contribute to pre-recruitment barriers, local adaptation and historic effects (e.g. limited space availability) contribute to post-recruitment barriers.
* Distinctions are helpful if population mixing is constrained to one part of the life cycle
* Ability to adapt could be a trait that is under selection (plasticity vs. fixed traits)

**NoCal:**

* Pringle and Wares paper shows the effect of population dynamics on the retention of alleles, and one can discover how to define populations (demes) in a coastal system, id source/sink populations, and show how these populations are related to ocean circulation that drives dispersal.
* What is population (deme)? Can we label regions of relatively uniform allele frequency as a population? Any novel allelic diversity that arises will be swept downstream by currents and will not contribute to evolution of allelic diversity upstream.
* Including spatial structure of habitat and circulation will help define population genetic patterns.

**MIT/Woods Hole:**

* Genetic structure would be promoted by strong differential fitness across species range, especially when coupled with discontinuities in connectivity and/or heterogeneity in habitat quality.
* Very relevant given Connolly paper, interesting to compare with genetic studies.
* Differences in upwelling probably play some role, but wondered how differences in adult abundance between OR and CA may be responsible for differences in recruitment. Mention that magnitude of difference in recruitment vs. density is greater, but its possible its non-linear (possibly quadratic)
* Because difference in recruitment was mostly just across Cape Blanco and not gradual latitudinal pattern, could be any number of biogeographical differences that contribute to the observed difference in recruitment.

**FSU:**

* Important part of paper not only showing how alleles that are favored can persist without being washed out, but how asymmetric dispersal can keep an allele from being common in many places where it is selectively favored.
* Structure still generated by migration-selection balance, but in continuous space, oceanographic features may cause the break/cline to form in places not predicted by divergent selection or environmental differences.
* Could mean results from reciprocal transplant experiments might differ depending on where within the downstream region individuals were sampled and transplanted.

**UTA:**

* For genetic structure to be generated, there must be strong selection downstream relative to upstream or restricted gene flow from downstream to upstream.
* As selective pressures and dispersal types vary across a large range for species, can expect genetic structure to be generated.

**MSC:**

* Pringle and Wares demonstrates importance of barriers to gene flow – expect structure adjacent to such barriers.
* Interesting that geographical feature maintaining genetic cline may not be necessarily what generated it.
* Could be genetic cline that slides down coastline until they “catch” at a spot where the demography/geography shifts the gene flow/selection balance.
* Spent time on Fig. 7, could use reciprocal transplant to see GxE as source effect.

**USC Cee lab:**

* Should see genetic structure maintained when there is change in selection across dispersal range. Produce individuals more suited to local environment and thus local adaptation.
* Similar to last week’s discussion of local/microgeographic adaptation where selection must be large enough to outweigh gene flow.
* For asymmetrical dispersal, a break in larval dispersal would generate differentiation either by selection or drift between upstream and downstream populations.
* Where selection is not unidirectional, you would expect to see population genetic structure based on reduced gene flow such as with dispersal in Connolly paper.

**Virtual Group:**

* Connolly paper was purely ecological – patterns may look like selection but are actually due to dispersal currents.
* What is role of species evolutionary history/geologic history?
* Historic gene flow due to sea level leads to enough divergence to prevent mixing when oceanographic/sea level would permit.
* Secondary contact vs. selection patterns.
* Need to collaborate more with physical oceanographers, connect them to genetic people.

**CSU Monterey:**

* Absence of genetic structure does not necessarily indicate a high level of gene flow. Even in simple allopatric scenario, Fst will be 0 in 33% of replicates.
* Genetecists should take greater notice of coastal boundary layers that may decrease U and L\_adv while increasing L\_diff. Paper only discusses when L\_adv is greater than L\_diff, but opposite could be true, meaning dispersal against boundary current should not only be possible but perhaps common. Would lower threshold for selection to maintain cline or allow absence of habitat to more readily create structure.

**CSUN:**

* Expect it when there is some sort of gradient in abiotic or biotic conditions. These tend to be maintained when alleles are not swamped.
* In certain areas, larvae have larger impact on adult populations via influx of beneficial alleles.

**Cornell:**

* Structure could exist from simply neutral stochastic patterns and or from a spatial gradient in habitat selection.
* In terms of the Connolly paper, north and south seemed to have different selection pressures (space, recruitment, predation) and so there could be genetic structure and adaptive differences.
* Even with a gradient in recruitment along coast, was it truly local recruitment? How many were carried from north via current?
* Plasticity and responsiveness and sensitivity to environmental conditions/cues can lead to adjustments and fine tuning of the timing of recruitment. Predictability of such events would facilitate a response.

**ODU:**

* Genetic structure is expected to be generated in areas with barriers to gene flow. When and where depends on duration of barrier.
* Oceanographic events can both restrict and promote gene flow. Some of these have seasonal differences which can cause variation in gene flow depending on a species’ life history.

**UQ:**

* Strong links between larvae and adult phenotypes can influence the strength of selection required for structuring and adapting marine population with strong asymmetric dispersal.
* Selection against settling larvae manifests through habitat availability and competition, which does not capture selection acting on adult phenotypes and reproductive success.
* Given that strength and direction of selection can vary between life stages, question whether alleles favored in downstream environments at settlement would also be favored in adults if larval experiences in the plankton impose strong evolutionary constraints on adult populations.
* Knowing about such tradeoffs is central for understanding how selection operates across life cycles.

**Week 6 – Population Genetics**

**Summary:** Discussion based on papers that examined how coalescent theory (Eldon and Wakely, 2006 *Genetics*) and how continuous vs. discrete spatiatl distributions (Bradburd et al. 2018, *Genetics*) affect genetic structure and differentiation.

**1. What are the implications for sweepstakes reproduction on how we model evolutionary processes in the ocean?**

**WSU:**

* If SR is big term in model, wouldn’t be able to model evolutionary processes as we see them in lab/observations
* Need to track individuals through time to see if sweepstakes is truly random
* Looking at input/output distributions for mero/holoplanktonic larvae in the same environment, you can evaluate the relative importance of SR

**Hal-Dames:**

* Could cause population bottlenecks and impact signatures of local adaptation.
* Effective population size is not capturing the number of individuals that pass alleles to the next generation, so won’t scale with TMRCA and pops can diverge quickly.
* Evolutionary history of alleles may be difficult to detect due to repeat bottlenecks.
* How common is SR? Is it plastic?

**Rutgers:**

* SR can play large role.
* Creates large amounts of variability in number of viable offspring/recruits, which increases chances of multiple mergers in coalescent process.
* If variability is large or frequent enough, could cause uncertainty in the effectiveness of simpler models that estimate pop. Size or genetic diversity.

**NoCal:**

* SR can accelerate adaptation if nonrandom in regard to parental genotypes.
* In long term, might reduce genetic variation in populations and decrease adaptive potential.
* How common is SR? assume it is rare or may reduce genetic variation.

**Umass Amherst:**

* How does modeling SR differ between marine and terrestrial systems?
* SR can cause such extreme variance in reproductive success, and ultimately result in substantial temporal changes in allele frequencies in larval systems.
* Suggest sampling across size classes or age classes in addition to unbiased sampling to avoid inaccurate inferences.

**NEU:**

* Literature seems to focus on selection and drift lately, but there are other factors.
* Which dominates larval stage with genetic patchiness? Lately it is selection, earlier was drift.
* Both are at play, but still don’t know if one dominates.
* Should have strong considerations when applying moran model – most analyses assume wright fisher model which may cause erroneous conclusions if the species displays evidence of SR

**Cornell:**

* With SR, expect reduced genetic diversity, increased relatedness, and more rare variants.
* Could have implications for modeling evolutionary processes, especially given the assumptions of coalescent theory and wright-fisher model (assumes small variance in # of offspring, no sweepstakes).
* In Eldon + Wakeley’s model, extends coalescent, offspring of single individual can replace substantial fraction of population.
* Deals with variance in offspring, how much does it improve it compared to traditional methods? Is it closer to reality?
* How would this perform with nuclear markers?

**USC:**

* SR changes null expectations as previous coalescent methods estimate inaccurately low effective population size.
* Selection at larval stage could have implications for recruitment.
* Moran model probably always better as null model than wright-fisher coaslescent models.

**Laval:**

* SR is the chances of a highly fecund marine animal contributing offspring to a future pool of reproductively mature adults, a process envisioned to have few winners and many losers.
* In study, Eldon and Wakely highlight coalescent models for accounting for SRS parameters, which is substantial advance.
* Do we need to implement some intrinsic parameters relative to species of concern?

**MIT:**

* SR acts as bottleneck and can dramatically reduce genetic variation compared to what we would expect if every individual contributed to next generation.
* In coalescent, multiple mergers become important and coalescence events happen more quickly.
* Models that assume wright-fisher processes rather than accounting for rare reproductive eventus with a modified moran process will tend to underestimate the effective population size if SR is important.

**CSU MontBay:**

* In populations with high variance in reproductive success, coalescent process departs from Kinman coalescent so much that the concept of coalescent population size no longer holds. If this is true, can fit Moran model to a population that shows gamma between 1 and 2, then all bets are off with traditional pop gen.
* When family size of reproductive event is large (greater than 25%), then rule of thumb that sample size can be low for coalescent theory no longer applies. Doubt that it would ever be that large.
* In region of parameter space, multiple mergers can lead to star phylogenies and neutrality tests violated in the negative direction. Frequently happens and is usually interpreted as population expansion, selective sweep, or purifying selection. But may be none of the above!

**UT Arlington:**

* SR creates rush for resources, which could select for most advantageous traits (through bottleneck) and promote traits promoting resource attainment and management.
* Longer time scale, genetic diversity could be hindered.
* Depends on scenario and environmental variables on when it promotes or obstructs adaptation and how rapid adaptation comes at the expense of genetic variance in long term.

**MSC:**

* Commonly used models assume equal numbers of offspring and discrete populations, so violations like SR can lead to incorrect inferences.
* Authors say coalescent with multiple mergers is better, but even in this model simultaneous mergers are not allowed, so how important is that?
* Wondered how this would play out with nuclear markers.
* Discussed if SR is drift or selection and how it plays role in evolutionary processes.

**LSU**:

* Most models do not take SR into account.
* Source variation is layered, so genetic drift could potentially be misinterpreted with models not accounting for SR.
* Recency of common ancestor, allele frequency vs. kingman model could falsely conclude that an individual has high fitness among a population. So we need effective population size.
* How large of a sample size is sufficient?

**UQ:**

* SR is probably very important in how we model evolutionary processes in ocean.
* More interrogation into what data would look like with 0<gamma<2 would’ve been nice.
* Should be on lookout for multiple mergers and understand consequences on selection.

**2. Given the complexity of marine dispersal dynamics, do you think we as a field should adopt Bradburd et al. approach for characterizing population structure?**

**WSU:**

* No, need more information.

**Hal-Dames:**

* Might help extract the effect of space, help overcome some issues in detecting local adaptation vs. isolation by distance.

**Rutgers:**

* Can these programs resolve the clusters vs clines problem?
* Compelling way to look at population structure in systems where we think clines may be most responsible for shaping population structure, as ability to run both spatially explicit and non-spatial models gives a large degree of flexibility.

**NoCal:**

* What are assumptions of construct? What are effects of migration/dispersal on construct outcome?
* Does construct assume restricted dispersal?

**Umass Amherst:**

* Spatial components can be case specific. Temporary congregations of individuals can lead to inaccurate inference when identifying population structure. Another source of bias could be invasion populations.
* Adopting approach beneficial to characterizing pop. Structure, but agreed it’s a case-specific process and sampling scheme design is critical.
* Idenfiying populations and management units very important.

**NEU:**

* Bradbury approach is useful when analyzing pop structure in species with isolation by distance.
* STRUCTURE has been applied to many studies studying pop structure of species, but assumptions of model are not always considered carefully.
* Like idea of investigating few different K’s rather than picking single one – different k values can help identify large scale vs. smaller scale processes that might be shaping population structure.
* Limitation is that dispersal distance does not equal geographic distance, and membership in layers does not always reflect this.

**Cornell:**

* construct is expected to perform same as traditional methods when there is no IBD, we wish they had applied it to more no IBD species to confirm.
* Agree that tool is improvement, but may not be flexible enough to apply to marine systems with chaotic patchiness from sweepstakes could generate strongly non-IBD patterns.
* How prevalent is IBD in marine systems, and what spatial scale do we expect to see this pattern?
* Need to make sure construct is appropriate for species/distribution/sampling before we can sample it.

**USC:**

* Long dispersal distances may make it difficult to apply method that leans on spatial autocorrelation.
* But isolation by distance is observed in many marine systems so application of bradburd model is viable.
* We should account for migration and dispersal patterns within their system as strong currents can create areas of close relation across large spaces.
* Bradburd model has more conservative method for estimating number of clusters whereas STRUCTURE and its variants tend to overfit data.

**UChicago/UGA:**

* Bradbury approach useful for pop gen surveys in which interplay of both discrete and continuous components both important.
* construct requires subjective interpretation by the user (multiple K’s, not best K). Subjectivity is one of greatest issues for standardizing field and facilitating cross species comparisons.
* Perhaps instead of single option, validation through multiple agreed upon methods is best (each with different assumptions etc.).
* Approach could generate reproducible datasets along a species range to devise generalities for marine population structure across species range.
* May want to consider user friendly methods, well maintained by authors.
* Also need to find selectively neutral loci, which depends on robust filtering of putatively adaptive loci. Advancements here may be very useful because even small number of non-neutral loci can dramatically alter results.

**Laval:**

* Yes, until a certain level of genetic relatedness.
* Power of approach is that ultra high connectivity often leads to low Fsts.
* What is tradeoff between having many markers or just informative markers? What kind of markers should be used? Maximise number of markers or use only informatives (like Fst outliers?)

**MIT:**

* Continuous genetic variation is probably often important in marine systems so we think the approach of Bradburd would be a good way to generate hypothesise for organisms whose population structure is not known – but shouldn’t be only framework used.   
  Need to evaluate assumptions relative to the study system.
* Bradburd depends on spatial relationships between samples. But dispersal distance doesn’t always correspond to geographic distance. Further, pelagic organisms can have enormous ranges and it isn’t clear. Isolation by distance more important for certain species.

**CSU MontBay**

* Bradbury approach relevant but only relevant to extent.
* Most marine species in “waples zone” of high Ne and high migration, and don’t see evidence that this method will help work in this zone.
* Should be thinking about pop structure based on measured gene flow between populations rather than measured allele frequency differences.
* Coalescent sampler (migration – n) can differentiate populations and identify underlying metapopulation model when Nem is as high as 100 migrants per generation.

**UT Arlington:**

* Spatial model is interesting and will be better approach for some systems, but should not be used to generalize.
* Dispersal distance doesn’t always correlate with geographic distance.
* Model is good step but should be evaluated on system by system basis.

**MSC:**

* Bradbury approach useful in some situations, but not universal panacea.
* Could be modified to deal with other forms of spatial structure in addition to IBD. Best approach comes down to questions and resources.

**LSU**:

* Appropriate for statisticians. However, dispersal distance vs. geographic distance different and important to take barriers into account.
* Both STRUCTURE and ADMIXTURE are great tools, but shouldn’t be used alone. Other models should confirm results. As always, with population data, sample size is extremely important factor, so is question.
* Not 100% on accepting Bradbury approach as field.

**UQ:**

* Bradburd method is super cool but doesn’t help SR problem. Detecting lots of K’s with geographic restricted shifts in allele frequencies if sweepstakes is pervasive.

**3. Given the potential for high variance in reproductive success, overlapping generations, and a combination of continuous and discrete population structure, how should we sample for population studies? (Across space and cohorts)**

**WSU:**

* The more you know about your system, the more appropriate design you can implement.
* Important thing is variance structure in the data, not ecological/evol. Hypotheses.
* Different populations/questions will always differ in their approach, but may be able to address by understanding underlying variance structures in the data.

**Hal-Dames**:

* What about software to help figure out what sampling regime might overcome issues in your system?
* Difficulty in sampling makes overcoming some of these issues nearly impossible.
* Instead of increasing fine-ness of scale, adjust inference about data we have.
* Sampling design contingent on species, environment, and question.
* Simulations needed to determine sampling regime optimal – generate result or model that can be parameterized with system conditions (amount of variation in reproductive success) to determine targeted sampling regimes.

**Rutgerss:**

* Need for larger sampling efforts (more individuals/population) especially in SR systems.
* Systems in highly variable reproductive success will be comprised of individuals that will coalesce back to MRCA in a few generations, most of genetic diversity harbored in a few rare individuals. The more uncommon these individuals are, the larger the sampling effort will need to be to give them a fair chance of being sampled and better represent level of diversity actually present in study population.

**NoCal:**

* If SR has taken place and we use coalescent theory, most of alleles will trace back to same ancestor. If we want to learn about evolutionary potential of species, would have to include several populations and sample deeply to infer most recent common ancestory.
* For construct to pick up isolation by distance, would need to sample across distribution and not just at the extremes.
* How do offspring by SR distribute in space? Will there still be isolation by distance if sweepstaking in a population is strong?

**Umass Amherst:**

* Agree that this is case specific – biology should inform sampling design.
* Reducing geographic scope on a particular site should help reduce noise associated with high variance in reproductive success (in addition to assessing continuous vs. discrete population structure).
* Should consider applying eldon and wakely model to account for organisms that have overlapping generations as opposed to Wright-fisher model that doesn’t.
* To reduce bias in sampling, perhaps vary sampling sites over a temporal scale to cover both spatial and temporal scale – but longer lived organisms may not need temporal consideration.

**NEU:**

* Designing sampling scheme is complex and often limitations in how well you can sample.
* When researcher is trying to understand pop dynamics, important to know system and design study to sample across cohorts when possible.
* Even more critical in species with SR.
* Sampling should be more extensive across multiple years because most individuals could be highly related under SR.

**Cornell:**

* Sampling should be highly dependent on study system. More extensive spatial and/or temporal sampling may be needed in some scenarious.
* IBD is common at some scales, but may be at larger scales than is typical of terrestrial systems, so may need to sample more widely.
* Not clear whether random sampling is preferable to stratified sampling based on hypothetical barriers to dispersal.
* Sequencing pools may be better than sequencing individuals. If variation in pool, can we account for it using construct?

**USC:**

* Knowledge of system (life history) will yield best methods for distinguishing generations and variance in reproductive success.
* When there are overlapping generations, binning according to factors like size class could help disentangle separate generations.
* Genetic markers across multiple loci have power to determine population structure better than previous methods. Especially if this approach is combined with taxon specific knowledge could help with initial parsing of complex systems and could be used as scaffold of experimental design.

**UChicago/UGA:**

* High variance in reproductive success warrants investigation into the stability of inferred structure through time.
* Sampling method appropriate would be re-sampling over multiple (2-3) generations of a focal species and replicating computational methods to see how structure estimates vary.
* Sampling year/generation – need to standardize approximate age/life history stage of individuals
* Revised methods for field sampling may be useful: fine resolution around geographic breaks?
* Unclear how much bias will affect results, or if it would just improve defining fine-scale clusters.
* Within population sampling important where patterns of microgeographic adaptation are at play. Sampling across range of microhabitats within a population likely most robust means to correct for this. Sampling should be consistent across populations.

**Laval:**

* Impact of SRS could be different over time: population size fluctuations (temporal structure, bottlenecks, teLmporal seasonality) over different time-scales should be considered.
* Sampling over time and over cohorts seems a good approach to catch the SRS effect.
* However, no matter the sampling approach used (follow population through time or sit in one spot and study what is recruiting locally) – each is valid, and when combined, can provide powerful understanding of evolutionary change in marine populations.

**MIT:**

* Sampling regime should reflect biology of study system. Efforts should be made to sample across time and space, and sampling across cohors can become important with species with high variance in reproductive success.
* In marine systems, often critical to understand the physical oceanography of study system, especially for species that have current driven dispersal.

**CSU MontBay**

* Sampling depends on goal, but for coalescent studies, sampling should take place across cohorts present in population.
* Someone should design method based on Eldon and Wakeley to quickly determine whether sampled population sits in Moran space of 1 < gamma < 2 (SRS).
* Curious how frequently this happens in nature, not just in oysters.
* Noted that long generation times should even out generation to generation variance created by SRS.
* For studies based on coalescence, each genome is product of multiple coalescent processes, so large sample size may not be important if you sample widely across genome.

**UT Arlington:**

* Question depends on study system, questions, context.
* Range and dispersal should be weighed, while temporal parameters (gen time) must be accounted for.   
  Good to conduct preliminary study to look at pop structure and life history and discuss what definition of population is being used.

**MSC:**

* This may be productive discussion topic at working group meeting – because optimal sampling method will depend on question being asked and system, may be challenging to come up with guidelines.

**LSU**:

* Dynamic question that could be addressed a few different ways. Could sample across space and cohorts by using preserved historical samples. Could also give insight into historical sweepstakes events.
* Other way is to sample population studies given all of dynamic variables involved to ensure large sample size to account for rare alleles or events.

**UQ:**

* Time is as important as space. Not easy to do and hard to be funded.

**Week 7 – Group summaries**

**Summary:** Groups discussed papers about expansion load during range expansion (Gilbert et al. 2017, American Naturalist) and phenotype-environment mismatches in the sea (Marshall et al. 2009, Ecology Letters).

**1. What’s the relationships between phenotype-environment mismatches and genetic load?**

**Rutgers:**

* Hard to parse the connection. Most assumptions based on well-mixed populations.
* Might expect both maladaptation and expansion load to reduce fitness and limit range edges, but there is a lot of nuance.
* Expansion load could be reduced in environments under strong selection if alleles don’t surf to fixation. Selection would have to be stronger than what is in the Marshall paper.

**WSU:**

* No direct relationship
* There are other individuals of your type at the “new” environment, but what really matters is if one individual happens to get to this environment. As long as someone can get there, it’s still a random likelihood of high/low genetic load because of assumed connectivity.

**UMASS Amherst:**

* Including expansion load had smaller effect on expansion speed than difference in dispersal types.
* Discussed problem that models assume abundant center distribution which isn’t always the case

**LSU:**

* Genetic load is any deleterious allele that puts an individual at a fitness disadvantage (in specific environment or generally).
* 2 types of genetic load: expansion load where deleterious alleles get fixed from expanding population (allele surfing), and phenotypic environment mismatches, in which alleles are at a fitness disadvantage if they are in an environment the organism is not adapted to.

**NEU:**

* Can be interplay of phenotype environment mismatch and genetic load, they aren’t consistently linked in predictable fashion.
* Gilbert suggests increase in expansion load specifically could slow range expansion to point of overcoming local maladaptation, which could reduce instances of PEM. But loaded term was uniquely defined and not generally applicable to discussions of genetic load.
* Challenging to measure genetic load without strong contextual clarification. In absence of knowing true optimum, criteria for defining genetic load may be tricky.

**UC Davis:**

* Genetic load results from accumulation of maladaptive alleles in a population that reduces overall fitness relative to an optimum genotype. PEM occurs when individuals move from an environment in which they are well adapted to one in which they are poorly adapted. In these new environments, poorly adapted migrants have greater genetic load, resulting in high mortality rate.
* Genetic load relative to environment. Poorly adapted individual moves to another environment, previously maladaptive alleles may become useful phenotypic traits if genetic load was caused by outbreeding depression. Unlikely if genetic load is result of inbreeding depression.

**Virtual Group:**

* Complex. Marshall paper defines PEM very broadly, and Gilbert finds that maladaptation and load interact so each is less effective than expected when alone.
* Difference in outcome between a case where an allele is everywhere maladaptive vs allele that is adaptive in the core but maladaptive in the edge. Depend on demographics, but latter would correspond more closely with PEM.

**Uchic/UGA:**

* PEM could be selective agent shaping larval behavior, dispersal, and life history strategy. (produce behaviors that promote larval retention)
* Expansion load, local maladaptation, and potential interaction between two important for understanding impact of range expansion on genetic load.
* Challenging to test assumptions and hypotheses of model.

**USC:**

* During range expansion, PEM would slow expansion load and allow populations more time to adapt.
* Different environmental gradients would affect this though.
* With decreased environmental gradient, populations could expand further geographically and may lead to decreased PEM, but increase in genetic load.
* Multiple environmental gradients should also affect. Would there be more PEM causing slower range expansions?

**UCSB:**

* Genetic load can contribute to PEM at population levels, but maladaptive allele frequencies may not wholly determine PEM since plasticity may also contribute to PEM when transgenerational plasticity is mismatched with offspring experience.
* PEM linked to genetic variation can contribute to genetic load and other factors may contribute.
* Locally adapted population exhibiting mitochondrial traits that are maladaptive in a foreign environment (home to pop b) may increase genetic load to pop B following settlement and reproduction not only through PEM but potentially through mitochondrial incompatibility as well.
* Genetic load may increase after multiple generations- introgression of pop A into pop B could reduce offspring fitness via simultaneous PEM and hybrid breakdown.
* How do authors define PEM? Say that individuals that disperse suffer heightened mortality before reproduction relative to locally derived individuals, where others say it’s a reduction in fitness when an organism is specialized to one environment finds itself in another. Important because reduction in fitness may not necessitate mortality prior to reproduction. May simply be reduced reproductive success. Immigrant individuals capable of successful, even if reduced, reproduction will contribute to genetic load.
* Temporal env. Heterogeneity in which we might expect temporally variable environments to harbor genotypes associated with increased plasticity. Role of adaptive plasticity mentioned, but could allow propagules to survive settlement and eventual reproduction in foreign environments in spite of having suboptimal genotypes.

**Laval:**

* Genetic load is composed of many different loads. PEM cause one kind of load, but this is argued in Marshall that this shouldn’t happen in marine environment where consequences of PEM will appear before the reproduction of migrants. Suggest that PEM will cause reduction of connectivity in marine environments but no migration load
* Surfing alleles is another type of load, a drift load that appears when frequency of unfavorable or deleterious alleles increases due to stochasticity in small populations.
* Conclusion of Gilbert is that increased maladaptation due to environmental gradient from the center to the edges reduces expansion load and vice versa, increased expansion load will cause that locally adapted populations to have better chance of survival. Maladaptation due to PEM and expansion load at edges will appear negatively correlated.
* Genetic load and PEM relationship will be affected for all kinds of variables. Strength of connectivity between patches, sampling and time scales, kinds of dispersion, as well as environmental change and dynamics adding stress.
* PEM will cause migration load (=kind of genetic load) in terrestrial environments. In marine environments, PEM will reduce connectivity increasing the expansion load due to less migrants and drift load.

**Cornell:**

* Since PEM increase mortality in foreign migrant larval, gene flow is reduced. This could lessen genetic load by allowing local adaptation and inhibiting maladaptive alleles from continually being reintroduced by migrants (migrant load). Reduced gene flow leads to lower Ne, there may be less selection to purge linked deleterious variants.
* Important factor is migration at larval stage. Migration at adult stage could worsen genetic load by inhibiting local adaptation by swamping the migrant load.
* With MPAs, important to think of size and placement of MPAs. If MPAs are smaller than scale of environmental heterogeneity, may be ineffective due to PEM or may increase genetic load from migrant load. May be better to have many smaller MPAs for greater diversity of protected phenotypes.
* If goal is to reduce genetic load, MPA placement should be chosen according to environmental heterogeneity.

**MIT/WHOI:**

* PEM on broad scale would decrease genetic load as deleterious alleles are actively chosen against. Also produces bottleneck effect that could in the longer term allow for increases in the accumulation of deleterious alleles as drift occurs.
* Also consider innate patchiness of marine environment spatially and temporally – might encourage recruitment of organisms in other conditions would display a phenotype-environment mismatch. This would allow for an increase in allelic diversity, which might help act against genetic load accumulated from genetic drift.

**UQ:**

* Genetic load includes mutation load, expansion load, and migration load – latter two have geographic aspect.
* Expansion load could possibly contribute to PEM but main mismatch would most likely stem from maladaptation of migrants or colonizers.
* There are other sources of mismatch especially plastic phenotypes that match source of origin. Physiological debt from long or difficult larval phase could reduce fitness.

**MSC:**

* Equate PEM to post-settlement selection in marine systems and agree that migration load may be more prominent in terrestrial systems given the life history stage at which dispersal occurs.
* For long lived organisms that experience environmental change, end may be genetic load via a different process.

**2. How does dispersal scale and the scale of environmental heterogeneity contribute to genetic load?**

**Rutgers:**

* Marine species don’t have migration load or less if migrants aren’t able to establish and reproduce. But other components still apply.
* Components of genetic load still possible for marine species in the case where they are establishing new populations at the edge of their range (assuming they don’t go so far that there is no possibility of survival to reproduction).
* Higher load will impede success of high dispersers – if environment changes they will disperse further.
* Expansion load could be limiting the edge of a species’ range expansion, not dispersal, and slower expansions might allow enough time for selection to act enabling adaptation to the new environment.
* Depends on rate of migrant alleles from core, which could hinder local adaptation – would need to see how migration from core influences fitness at the edge.

**WSU:**

* Disparity in papers assuming linearity in environmental gradients (heterogeneity) and dispersal gradients – we know these factors aren’t linear, but models assume they are.
* Can we apply these concepts knowing this disconnect?
* Gibert argues increased slope of an assumed linear environmental gradient reduces genetic load. Means that selection takes a bigger role in the observed effects on the population on a range edge when you have steeper environmental gradient.
* Life history characteristics (broadcast), how can there be relationship with genetic load in adults if selection is happening in a completely different life stage with different selective pressures during larval dispersal?
* MPAs – should think about scale of dispersal and environments when designing ocean spatial management.
* Temporal considerations matter! Can’t just consider snapshots in time.

**UMASS Amherst:**

* Longer distance dispersal strategies may affect expansion load (not just expansion speed).
* Marine species relatively free of migration load due to mortality prior to reproduction.
* Marine species likely to suffer expansion load due to severe bottlenecking that occurs during sweepstakes and selection might outweigh expansion load in these taxa since they are able to persist despite the load.
* Many habitats follow this patchy pattern and apparent lack of connectivity across habitats might be the rule rather than the exception in aquatic environments. May compare with wind-dispersed terrestrial organisms.

**LSU:**

* Depends on organism and scale of dispersal relative to scale of environmental heterogeneity. Less genetic load if dispersal is large and environmental heterogeneity is small. If dispersal is small but env. Het. Is large, may be more genetic load.
* Steepness of environmental gradient slows range expansion, but more time for the core to adapt to the range edge and ameliorate the high genetic load.
* Assumes environmental heterogeneity in continuous landscape, not mosaic. In mosaic, if dispersal is short, high probability of staying in environment you’re adapted to.
* If you’re long range disperser, chance of getting to env. You’re adapted to is small.
* To link papers: local maladaptation and expansion may interact positively, each making the effects of the other more pronounced. Makes sense but model found opposite. They ameliorate each other, reducing genetic load.
* Could also be interpreted as PEM, all organisms are so maladapted at the range edge with such high genetic load that range edge populations quickly go extinct because they can be rescued by the core.
* Why do organisms disperse if PEM exists? Environments change through time, dispersal is not as random as we think, as way to increase genetic diversity?

**NEU:**

* Increased dispersal is associated with increased exposure to greater diversity of habitats, and migration load does impact local fitness of adaptive population, but evolutionary theory needed.
* Are orgs. Believed to be broadly dispersing more vagile or more plastic? Need to know fitness of genomes in different environments we won’t know the pressures that are driving them.
* Pressures could be represented in SNP data, but also indels and variation in genomic architecture.
* Discuss connection between genomic architecture and genetic load. Marine orgs have higher load than terrestrial as consequence of sweepstakes reproduction or increased germline mutation accumulation, possibly also due to PEM.
* Issue of MPAs – initial fecundity could be high but result in migration load. Load is context dependent, environmental heterogeneity can shift advantage/disadvantage of individual variants.
* What is feasibility in terms of planning MPAs? Systems aren’t static, heterogeneous environments shift with heterogeneous populations and it would be good to see more direct consideration of how managers can better account for this.

**UC Davis:**

* Environmental heterogeneity can be structured as continuous or discretely patchy. May affect genetic load differently depending on dispersal scale.
* When dispersal scales are large, cline will result in high genetic load because farther individuals disperse the more poorly adapted to their environment they are.
* In contrast, in patchy structure, long distance dispersal need not necessarily result in high genetic load bc far flung habitat patches are as likely to be suitable for dispersing individuals as sites near natal locations.
* Higher genetic load is more likely in a patchy structure where nearby sites are just as likely to be good habitats as they are to be poor habitat.
* Example is porcelain crab, which disperses across patchy environment of cobbles and mussel beds. Expect this species to have high genetic load as they are not thought to disperse far. No structure at Fst, maybe structure at Qst?

**Virtual Group:**

* Expect when scale of dispersal is larger than scale of heterogeneity, PEM (migrant load) will increase.

**USC:**

* If scale of dispersal is greater than scale of environmental heterogeneity, there will be increase in PEM which will slow down range expansions and decrease genetic load, as only those organisms with highest fitness in that environment are surviving to range edge.
* If dispersal is smaller than scale of environmental heterogeneity, genetic diversity will be maintained and there will be little or no genetic load.
* Need clarification of what environmental heterogeneity means.

**UCSB:**

* Increasing scale of dispersion increases the probability that an individual will encounter an environment in which its phenotype is mismatched, which could reduce genetic load by propagules onto new populations.
* This depends on environmental heterogeneity, because long distance dispersers in homogenous environments may contribute to genetic load compared to short distance dispersers settling somewhere across a more heterogenous environment.

**Laval:**

* When scale of dispersal is high, probabilistically fewer individuals will arrive (in and species with feeding larvae those who arrive will be disadvantageous) therefore decreasing likelihood of carrying deleterious alleles that can act as mutation load.
* Due to surfing alleles, deleterious mutations that arrive to range edge will increase frequency.
* Increased env. Heterogeneity will increase maladaptation due to PEM, maladaptation reduces the pace of expansion producing a reduction in expansion load and a number of migrants.
* In marine environments, the presence of environmental heterogeneity will reduce connectivity (due to PEM) could mean that expansion load will increase in this case too, because in small populations or edge populations drift load (surfing) will increase.

**Cornell:**

* Relationship of dispersal scale to scale of environmental heterogeneity is more important than the individual scales.
* Greater environmental heterogeneity, the lower we expect genetic load and expansion load, but less connected populations become.
* If dispersal scale is less than environmental heterogeneity we don’t expect migrant load. Clear that life history of species is important for management and evolutionary consequences of genetic load.

**MIT/WHOI:**

* With larger scale of dispersal, increased likelihood of mismatch between the arriving organisms and environment which would potentially contribute to a bottlenecking of survivors leading to increased genetic load.
* Takes broad scale view of environmental heterogeneity. On smaller scales, more likely that organism would encounter environment that matches its phenotype thus increasing diversity and decreasing genetic load.
* Then important to consider how fine-tuned the organisms have to be in order to for them to experience significant die-offs to result in a bottle neck.
* If dispersal is greater than scale of environmental heterogeneity, would result in decreased connectivity in ocean which favors local adaptation being predominant. Also favors increased genetic load as genetic drift occurs.

**UQ:**

* If organisms dispersal scale includes heterogeneous environments, then there will be migration load, unless phenotypic plasticity allows environmental matching post-settlement.
* Interesting situation would occur where environment changes rapidly (steep gradient) and therefore gene flow may be reduced due to post settlement mortality.

**MSC:**

* Environmental heterogeneity is primarily considered a gradient. But can also be patchiness. Patchiness could affect interaction of maladaptation and expansion load, as well as persistence of locally adapted populations.
* Non overlapping generations may affect predictions. How common are species with non-overlapping generations? May alter predictions especially for long lived species if individuals survive initial post-settlement selection and are more likely to reproduce.
* Interesting that gibert model included selfing, but what affect would this have on species that don’t self.
* Suggestion to follow Qst and Fst of cohort through life history, but wonder about feasibility. Anyone done this?

**Week 8 – Balancing Selection**

**1. What constitutes strong evidence for fluctuating selection, especially if the trait under selection is maintained by many loci with small effects?**

**UGA:**

* Discussion over how expectations play out over distinct life histories – gave example.

**WSU:**

* Presence of variability does not preclude alternative hypotheses of causation. We think you can’t separate phen. Plasticity from underlying genetic structure by looking at phenotype- just correlation at the phenotypic level is not strong evidence for fluctuating selection.
* Using definition of selection, have to have genetic info underlying the traits (census of the multiple loci that we think are driving the pattern. Also important to do this over long time period, not snapshot.

**UMass Amherst:**

* Does fluctuating selection require a temporal component? Yes.
* How do fluctuations in the ocean depart from seasonality? More rooted in large scale climate cycles (el nino) and changes in salinity, tide, environmental conditions.
* Fluctuating selection may contribute to greater diversity which would support higher adaptive capacity in response to changing environments.
* Appreciate isolating fluctuating selection as driver of season adaptive oscillations in drosophilocal adaptationespecially since presence of oscillations could reflect a myriad of ecological conditions.

**UCSB:**

* Clear that fluctuating selection was maintaining genetic variation among seasonal SNPs independent of other processes such as pleiotropic balancing selection.
* Evidence for fluctuating selection stronger when this pattern exists for multiple alleles that are not in linkage disequilibrium and when the phenomenon can be observed in multiple populations experiencing cyclical shifts in selection.
* Fluctuating selection may be more likely to maintain polymorphisms at multiple alleles of small effect rather than a few alleles of large effect, as fewer alleles are more likely to exhibit an “all or nothing” pattern that does not maintain variation under fluctuating selective pressures. If so, wonder if evidence of fluctuating selection at small number of alleles requires more investigation than what is present in Bergland paper.
* Fluctuations in direction of selection could simultaneously decrease certain alleles while increasing others. Why do seasonal patterns in bergland paper emerge (more seasonal SNPs in spring, decrease in fall).
* Some alleles should be under greater positive selection during fall and increase in abundance.
* But flies grow faster during warm seasons, so did this allow for beneficial alleles to propagate faster in the spring? Life cycles faster than the frequency of selection are the only cases that lend themselves to fluctuating selection and could be broadly important for ectotherms with rapid life cycles.

**Uchic/GaTech/Auburn:**

* Fluctuating selection pressures are likely prevalent in marine systems and the extent to which a fluctuating selection pressure produces and maintains genetic variation likely driven by the frequency/periodicity of selective regime relative to the species’ generation time.
* Species with shorter generation times amplify strength of divergent selection acting on a trait across generations. Species with generations that exceed periodicity of the fluctuations are likely to evolve a plastic response with regards to the stressor.
* Specific timing of an environmental fluctuation in respect to the life history stage of a species may also be an important consideration. (if sensitive stage occurs in different seasons).
* Identifying the presence of such temporally fluctuating selection difficult because they probably have polygenic basis, so the selective signature of which will be spread across several loci of small effect. Powerfully identifying loci involved in this process within a single population will therefore be difficult.
* Suggest following seasonal fluctuations in genetic variation across multiple “replicate” populations (separate populations exposed to the same fluctuating selective pressures). Allow for a more powerful way to identify small-effect loci that exhibit fine scale temporal fluctuations.

**Cornell:**

* Regarding the Bergland paper, the empirical case is strong. Recognized the interest in estimating the age of these seasonally cycling polymorphisms to address hypotheses about the importance of balancing selection for maintaining polymorphisms, and because it strengthens the balancing selection inference relative to alternative mechanisms.
* However, some thought that balanced polymorphisms needn’t be interspecific in age to be interesting and important for patterns of diversity.
* Adaptation to new environment might entail temporal fluctuations not experienced before, such that adaptation is via fluctuation of relatively new variants.
* Question whether old alleles should be a necessary criterion for demonstrating fluctuating selection.
* Short generation time of drosophila made it an excellent model for cycling adaptation to seasonal variation. What types of variation is periodic and regular enough to generate this dynamic for longer lived organisms? El-nino maybe, but these aren’t as symmetrical.
* How irregular can environmental flux be and still maintain diversity by fluctuating selection? Partially addressed in second paper, describing conditions for stable balanced polymorphisms in a polygenic model with reversal of dominance and diminishing returns of fitness.
* Curious about reversal of dominance beause it is crucial for model, but unfamiliar. Other papers have shown beneficial reversal of dominance for survival to adulthood in fresh vs. saline water. Dominance depends on environment, is an attribute of the favored allele in each environment. Need easier ways to screen for dominance!

**Laval:**

* We first discussed what we came up with from the readings of the two proposed papers. Wittman et al. showed that stable polymorphism at many loci is possible if currently favored alleles are sufficiently dominant (segregation lift), and Bergland paper revealed that typically revealed that typically variable selection contributes to repeatable adaptive oscillations at balanced polymorphisms.
* Showed that seasonal SNPs are enriched among functional genetic regions and present their association with variable phenotypes (starvation tolerance and disease recovery) so there is evidence of fluctuating selection.
* In marine environments, fluctuations are not necessarily representative of seasonality but correspond more to large scale changes like climate cycles. Even assuming seasonality in marine environment to be able to see evidence of Fluctuating selection the generation time should be shorter than the season length. So evidence of FS will be more plausible for organisms with rapid life cycles. Another point is that FS has to be stronger than stabilizing selection to persist.
* Finally, in marine environment, genetic drift is minimized (because of gene flow and generally high Ne) so natural selection is more efficient and more detectable (phenotypically talking) even with many loci of small effect involved.

**Rutgers:**

* Evidence is convincing to us (repeatable allele frequency variation by season, the time vs. space comparison, the links to fitness, plus the natural experiment with frost event).
* Many seem accepting of genomic evidence for fluctuating selection now, but we were relatively skeptical earlier about genomic evidence for local adaptation. Are they that different?
* Set up paper as if theory was established and all they needed was empirical support. Except Wittmann paper makes it clear that theory actually isn’t well developed. Bergland paper actually provided evidence for new theory.
* Severe limits in our ability to detect fluctuating selection that acts on many loci with small effects. If effects are small, the frequency changes will be small and/or identity of alleles changing frequency will change through time. Makes detection more difficult.
* Discussed segregation lift and mechanisms that could produce temporal changes in dominance. Thought of traits where plasticity is driven by gene expression, including cases in which one allele might be expressed in one environment but the other expressed in the other environment.

**MIT/WHOI:**

* Seems like actual phenotypic changes are needed to demonstrate strong evidence for fluctuating selection. Also seems like Bergland paper combined multiple lines of evidence to build convincing argument. Opportunistic experiment before and after frost event helped a lot with making it convincing.

**Virtual group:**

* This is the big question.
* Fundamentally, it is a question of detecting local adaptation to seasons
* Many loci of small effect, then signal may not be consistent through time, which makes things difficult. But if signal is consistent through time and across populations, the presence of fluctuating selection is fairly compelling.
* How might one experimentally reproduce the signal of seasonal selection?
* For marine organisms, especially planktonic species with rapid life cycles, there should be abundant seasons fluctuating selection
* Doing this in the lab might help parse down which environmental factors are the primary component to selection
* But also should figure out how widespread that mechanism is as contributor of genetic variation.
* Necessary to consider what types of organisms and fluctuations may be influenced by this – seasonality works with short lived species – what about el-nino? Upwelling? Etc.

**NEU:**

* Finding a simple allele frequency shift that correlates with some environmental variable is likely not sufficient evidence for selection. However, could be strengthened if found over several repeat measures (many seasons) or if the allele frequency shift is observed in different measurements of a particular environmental variable.
* For example, observing allele shifts correlated with season that are also correlated with latitudinal cline provides stronger evidence that these shifts may be the result of selection on temperature related traits.
* Linking genetic variation and allele frequency data with phenotypic variation could also bolster support of selection over drift. Correlations might be hard to find in highly polygenic traits.

**2. What are the benefits/consequences of fluctuating selection for long term changes in the environment?**

**WSU:**

* Maintaining variation is always good for pre-adaptation for future conditions, esp. under climate change.
* Maintenance of variation necessary but perhaps not sufficient if conditions are different from what has been experienced evolutionarily.
* Haven’t read much about seasonal maintenance of diversity.
* May also be relationships with generation time scales and time scales of fluctuation – are these papers relevant to marine organisms with seasonal reproductive events and/or generation times that span multiple seasons?

**UCSB:**

* Fluctuating selection during long-term changes in the environment maintains heterozygosity and increases standing genetic variation.
* Benefit of standing variation in a system where fluctuating selection occurs is unclear. On flip side, fluctuating selection has to be stronger than stabilizing selection may be capable of canalizing phenotypes that are adaptive under future conditions.
* Scale at which fluctuating selection is occurring relative to the scale at which long term changes in the environment are happening is a crucial consideration.
* Population subject adapted to annual fluctuating selection may not be able to sufficiently respond to an increase in the amplitude of monthly changes.

**Uchic/GaTech/Auburn:**

* Bergland paper presents comprehensive analytical framework for examining genome wide patterns of seasonal adaptation that may be useful for future empirical studies, although there were some elements that could be improved.
* To minimize variation, collection protocols should be standardized (same microhabitat, same timing).
* Like the comparison of seasonal SNPs with SNPs from diverged populations to test association with standing genetic variation, however, we felt this comparison would have been more meaningful if they had reported amount of overlap in seasonal SNPs and ancestral SNPs, and given more info on the environmental conditions and seasonality in the ancestral pops.
* Temporal variable selective pressures likely maintain variation within ecologically relevant traits. The standing variation provides raw fuel for adaptive response during a directional shift in the environment.
* Important that as environment shifts, previously adaptive variation for conditions that are becoming increasingly rare diminishes. Therefore, as long as variability continues during the directional shift, anomalous reversions back to previous conditions may induce sharp population declines.

**Cornell:**

* Argument that fluctuating environments are conducive to these mechanisms maintaining higher standing diversity, improving the odds of successfully weathering rapid environmental change.
* These ideas seem consistent with segregation lift models.

**Laval:**

* Preserving diversity baseline, fluctuating selection appears to be an advantage to keep stable polymorphism to keep pace with environmental change. FS and sweepstake reproductive success (i.e., context of overlapped generations or not).
* Evidence of FS should be more pronounced for discrete generations than overlapping generations.
* When there is balancing selection at a large number of loci genetic load is a potential concern but in the case of segregation lift with diminishing-returns epistasis, however, genetic load does not appear to play important role.
* Advantage/disadvantage of FS in invasive species. FS can play a role in invasive species expansion in a case of multi-invading events over time.

**Rutgers:**

* Biggest benefit we saw was the maintenance of polymorphisms in a population upon which selection could later act directionally. Summer fly pops look “southern” and so pops may be pre-adapted to more southern climates.
* Effects wouldn’t even have to be as well-balanced as in the fly example (old alleles) but could also be useful when they transiently prolong the survival of an allele.
* By increasing standing genetic variation, fluctuating selection can increase adaptive potential.

**MIT/WHOI:**

* Fluctuating selection is mostly beneficial. Requires species to balance decreased extinction risk with a decreased level of absolute adaptation or “optimality”.
* Consequences will rarely be realized because environment always fluctuates.
* Takes standing genetic variation that is likely to be beneficial for many species in the face of long-term changes in the environment.

**Virtual group:**

* Most important consequence is maintenance of genetic variation for traits under selection. I feel like there is a fair amount of hand waving about “temporal balancing selection” maintaining diversity without much elaboration.
* However, fluctuating selection on many different time scales is likely an important driver in this. Should increase adaptive potential and population resilience.

**NEU:**

* Benefit or consequence of fluctuating selection would in part depend on a few factors including the strength of selection, the magnitude of change in selection over a single fluctuation, the relative difference in selection strength among different events within a single fluctuation, and the relative length of an environmental fluctuation to the generation time of a species.
* In fly example, seasonal variation seems strong enough to see shifts in allele frequency between seasons, but not too strong as to drive a particular allele to fixation (or too weak to allow it to drift to fixation).
* Fact that several generations occur within each season may allow sufficient time for population wide shifts in allele frequency to occur (even if selection is not that strong). In this case, fluctuating selection may help maintain a larger amount of genetic variation and possibly contribute to increasing the adaptive capacity of a species if the environmental variables that are fluctuating are also those that are expected to undergo long term changes.

**Week 9: Plasticity**

**Summary:** Groups discussed phenotypic plasticity based on Waddington’s classic work (*Evolution* 1953) and Schaum and Collins 2014 paper on evolution in marine algae (*Proc. Of the Royal Society B*).

**1. Compare and contrast the two experiments. In what ways are they similar and different?**

**LSU:**

* Main difference is experiment itself. Waddington used artificial selection to select for particular trait, while Schaum paper enforced a stressful event and let natural selection take its course.
* Probably no mortality in flies, so no fitness disadvantage, while the strong selection event in algae does rely on fitness.
* Waddington paper was trying to demonstrate genetic assimilation via canalization of a trait, question whether it is actually shown.
* Would be interesting to see if flies become canalized for the veinlessness trait if they were heat shocked and then allowed to mate randomly (rather than with just other veinless). Certainly demonstrated canalization which was also observed in some of the Schaum paper.
* Schaum paper demonstrated that algae grown in stable high CO2 environments had higher growth at control levels of CO2. Algae grown in fluctuating environments had greater plasticity and were able to have normal growth rates under normal CO2 conditions demonstrating that a trait that is plastic under high CO2 scenarios can become canalalized if it is continuously exposed to these conditions.

**NEU:**

* Baseline difference was focus of Waddington on a purportedly non-adaptive variant through artificial selection vs. the direct focus on adaptive natural selection.
* While Waddington focused on stable exposure, Schaum focused on fluctuating vs. stable exposure.
* Both experiments highlight broad umbrella of cross-generational plasticity, Waddington paper focused on immediate responses of a stable temperature change as opposed to the effect of a fluctuating exposure.

**FSU:**

* Possible interpretation of waddington’s work is that the variation for that trait was in ancestral populations and that environmentally induced phenotype were actually present in the original wild stock and plastic phenotype was not actually plastic but rather a kind of threshold trait.
* Alleles for veinlessness are expressed after the heat shock exceeded some threshold for expression, then just increased in frequency over multiple generations of artificial selection for cross-veinlessness.

**UC Davis:**

* Schaum uses Ostreococcus which is large pop of marine microbes with short gen times and ample scope of evolution, while Waddington uses drosophila with smaller pop sizes and slower mutation rates.
* Schaum starts with 7 strains that differ in plasticity before the start of the experiment, Waddington uses one
* Schaum exposes both stressors and fluctuating environment, wadington only exposes one stressfull environment against ambient.
* Waddington’s trait not adaptive, Schaum saw adaptiveness
* Waddington did a lot of back crosses to fid genetic architecture which Schaum did not do.
* Waddington did no measure a fitness trait, do not kow whether mutated flies would survive or not. Schaum tested some fitness traits (baldwin’s).
* Waddington gives empirical evidence of a case where non-heritable environmentally induced variation is converted ito heritable variation. Initially this is cryptic genetic variation, will it become adaptive?
* Both have no idea about genetic architecture of the traits.
* Both investigate environmental drivers of phenotypic variation.
* Both show genetic assimilation

**UChicago:**

* Appreciate clear experimental design in waddingtons paper that first aimed to evolve plasticity and then test the extent that it augments evolution. Does seem difficult to be convinced that their metric of plasticity (o2 consumption in 2 environments) was able to resolve whether the phenotypic variation in the FA line was driven by increased genetic variation or plasticity.
* Revisited Botero et al. 2015. Model explored conditions under which plasticity is expected to evolve. Focal parameters of model were time scale of fluctuation and predictability of environmental switch.
* Environmental switch in schaum is not predictable and time scale is long relative to generation time.
* Under such scenarios, Botero predicts reversible plasticity is not favored but rather a diversified bet-hedging or adaptive in which phenotypic variation among individuals is fixed and genetic variation is maintained to facilitate adaptation to sudden and random shift in the environment.
* Hard to be certain this isn’t what happened in the FA line of the Schaum paper, as ultimate result of FA line evolving faster would be increased genetic variation in that line.
* More robust if they could track patterns of genetic variation in each lines to ensure that this metric did not accumulate disproportionately across treatments.

**UCSB:**

* Waddington paper selected arbitrary trait with no ecological relevance or fitness consequences. Schaum picked oxygen evolution rates as example of plastic trait with adaptive value as well as strong selective pressures on fitness related traits that are ecologically relevant.
* Two experiments used different selective pressures: Schaum used stable and fluctuating pCO2 treatments to drive selection rather than the artificial selection of crossveinless phenotype
* Direction of evolved trait differed between two experiments. Waddington demonstrated that genetic assimilation via canalization of phenotypic trait is unidirectional whereas in the case of Schaum et al the evolved trait was in the opposite direction of the evolved response.
* Schaum’s effort to raise 14 generations of variation adapted lines in static pco2 environment in order to rule out maternal effects as the driver of the adaptive pattern. While Waddington demonstrated the crossveinless was clearly heritable, we were not convinced that the increase in frequency of this phenotyp wasn’t tied to maternal effects.
* Acquired characters could have been cryptic genetic variation that manifested as a phenotype due to plasticity and increased in frequency across heat stressed generations via transgenerational effects.

**Rutgers:**

* Discussed how these two papers both investigate environmental drivers of phenotypic variation and in both cases how genetic architecture of trait is unknown.
* In both studies, genetic assimilation was observed.
* Classical paper such as waddingtons compared to newer paper – differences between two studies.
* Constrast between types of traits examined differed between papers (fitness vs. non fitness trait).
* Schaum demonstrates that evolutionary trajectory can be determined by ancestral plasticity. Agreed that in both papers, findings were close to proposed hypotheses.
* Plasticity and amount of plasticity required was addressed and how plasticity allows for flexible pathways which allow shifts in the default.

**2. How does plasticity in ancestral populations determine evolutionary trajectory?**

**LSU:**

* The more plastic the population, the more those populations seemed to evolve. Schaum paper clearly demonstrated that evolutionary trajectory can be determined by the ancestral plasticity.
* Wish there were more discussion on whether the evolutionary trajectory is always going to be beneficial for population.
* Lower growth rates might seem disadvantageous, authors do a nice job of explaining this can provide fitness advantage but want more empirical support.
* Don’t think the direction of evolution can be determined by plasticity and whether those changes will be beneficial or maladaptive.

**NEU:**

* Consider situations where plasticity is cyclical (or appears that way). In some environments, could be beneficial to be increasingly plastic while in others it may be beneficial to canalize around fixed phenotype.
* Discussed situation in which canalization may be a periodic point of evolution but there could be sufficient variation maintained around the canalized slope that could allow for plasticity to re-evolve if the environment changes and plasticity becomes adaptive again (sensu Lande et al. 2009).
* Consider how timing of environmental exposure can affect plasticity vs. canalization. Some traits can be developmentally plastic, but once induced, become fixed in the phenotype even if the environment changes.
* In contrast, some responses like gene expression are much more flexible and responsive to continual fluctuations in the environment. Differences could have important implications for the ultimate fitness and evolutionary trajectory of species.

**UC Davis:**

* More plastic lineages evolved faster than the less plastic ones.
* Why does plasticity in one trait make the population/strain evolve faster in another trait? Apparently two traits are correlated.
* Generally it would depend on strength and direction of selection as well as on the standing genetic variation in a population.
* If there is no underlying variation, a population might not adapt. I.E. adaptive plasticity can be so good it prevents adaptive evolution because the all purpose genotype produces an optimal phenotype in every environment.
* There is potential for adaptation, as long as the change in mean trait value goes into the same direction favored by selection in the new environment but below the adaptive peak.

**UCSB:**

* Results from schaum paper demonstrate that evolutionary trajectory can be determined by ancestral plasticity. Ostreococcus lineages founded from more plastic ancestors evolved more in high pCO2 environments than lineages founded from less plastic ancestors supporting the relationship between plasticity and evolution.
* With many ecological and evolutionary concepts, the adage “it depends” applies here. Plasticity does not always confer an adaptive benefit – in some cases, such as in a fluctuating environment, it benefits the population to maintain a degree of plasticity. In others, such as in a more stable environment, the costs outweigh the benefits of plasticity and the evolutionary trajectory leads in a direction away from the plastic population.
* Even in this scenario, it depends on generation time of focal organism, frequency and duration of environmental fluctuation, etc.

**3. Do empirical results agree or disagree with theoretical arguments?**

**LSU:**

* They agree.
* Past theoretical arguments converged on plasticity hindering a populations’ ability to evolve, more recent theoretical work seems to demonstrate the opposite.
* Plasticity enhances evolution/adaptation to new environments and Schaum paper results agree.

**NEU:**

* Plasticity should counteract true adaptive evolution and only if your plastic response happens to align with directional selection can in improve response rates to environmental stressors.
* Repeatedly refer back to fisher’s geometric model to visualize misaligned plastic potentials with adaptive gradients.
* The role of epigenetics in plasticity provides one particular mechanism of plasticity that requires more explicit study before broader theoretical models can be properly tested.
* Given theoretical predictions around genetic assimilation and plasticity, there are some theoretical scenarios that could only be supported once explicit mechanisms are more properly understood: with epigenetics being the elephant in the room.
* Relying too much on a single mechanistic determinant of plasticity can be a pitfall, and the theoretical value of work observing plastic responses, even in the absence of clear mechanisms is evident by the fact that we collectively read and compared a research article written almost 70 years ago to discuss the many still unsanswerd questions about plasticity.

**FSU:**

* Way authors define and use genetic assimilation seems to be slightly different to use Waddingtons version.
* Some definitions of GA are that it is a process that converts a plastic response into a genetically invariant one. If one considers plasticity itself (slope of reaction norm) as a quantitative phenotypic trait subject to selection and capable of evolving like any other quantitative trait.
* When viewing plasticity as quantitative trait, idea that responses to environmental change are through plasticity or evolution or the idea that plasticity promotes or affects evolution seem odd.
* Larger environmental changes could more easily be bridged by a plastic genotype. When environment is constant, there is no longer selection for plasticity so the reaction norm slope does not evolve or evolves to zero.
* Rate of environmental fluctuation was slow relative to generation time, so some environments were both variable and predictable and these treatments selected for plasticity.
* Results of schaum and Collins consistent with predictions from quantitative genetic theory that treats plasticity itself as a trait.

**UC Davis:**

* As Ghalambor points out: adaptive plasticity that places populations close enough to a new phenotypic optimum for directional selection to act is the only plasticity that predictably enhances fitness and is most likely to facilitate adaptive evolution on ecological time scales in new environments.
* This type of plasticity is likely to be the product of past selection on variation that may have been initially non-adaptive.
* Historically, theory suggested that selection acts on non-heritable phenotypic variation will not produce an evolutionary response is unimportant. (wtf)
* Environmentally induced variation might slow rate of adaptive evolution because it is shielding the genotype from the effects of selection.
* But west-eberhard showed that plasticity can become GA or speed up process of adaptive evolution. For this to work, there needs to be initial phenotypic variation/plasticity and the population needs to be faced with an environmental change following directional selection.
* May be disadvantageous at first to be plastic but the cost is not high relative to selective pressure. In other words, only those that are plastic can survive.
* But later directional selection will favor the new trait and genes coding for it will be under direct selection. Ultimately, selection might cause a variable trait to be fixed in the future. This depends on whether the environment changes to a new state or is fluctuating. Invasion bio is good place to study this.
* How likely is it? Will majority of populations die instead of resisting to new directional selection? Is maintaining phenotypic variation in a constant environment costly?
* As ghalambor points out: adaptations to new environments rarely involve single traits but rather suites of traits that respond to diverse selection pressures. Brings us back to week 5 where we discussed genetic correlations between different life stages of an organism. Might constrain potential for plasticity.

**UCSB:**

* Empirical results agree with more recent theoretical arguments regarding plasticity’s ability to reveal genetic variation at the phenotypic level, allow slection to occur across a greater number of otherwise cryptic genetic variants – plasticity promotes evolutionary innovation or adaptation and schaum paper demonstrates this.
* Previous evolutionary theories regarding plasticity have noted that it may limit adaptive potential. Schaum demonstrated that not all selective pressures result in adaptive responses by plastic populations. Can help synthesize competing theories regarding plasticity’s role in evolution.