

Evaluating Adaptive Processes for Conservation and Management of Estuarine and Coastal Resources

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Abstract This special feature: *Genetic Structure and Adaptation in Coastal Ecosystems* emphasizes the importance of research focused on population genetic structure and evolutionary change for understanding estuarine and coastal communities. Many studies have examined the effect of environmental gradients on community-level patterns in estuarine habitats; however, relatively little is known about the role of genetically based adaptation (the heritable response to these environmental gradients) in these organisms. This special feature presents 11 studies that use a variety of approaches including ecophysiology, ecological genetics, molecular markers, and patterns of gene expression occurring within these populations. These studies provide examples of the role of genetic diversity and adaptation across a diversity of estuarine and coastal environments, and highlight the temporal and spatial scales at which adaptation impinges upon management. This collection of papers is especially timely, given the increasing importance of understanding and predicting the response to global climate change in order to effectively manage these communities.

Keywords Adaptation · Climate change · Ecological genetics · Ecological genomics · Environmental gradient · Evolution · Genetic structure · Global climate change · Invasive species · Microarrays · Next-generation technology · Phenotypic plasticity · Phylogeography · Physiological stress · Pollutants · Salt marsh · Seagrass

Introduction

Rocky intertidal and shallow soft-bottom estuarine communities are models for exploring physiological stress (Bertness and Ellison 1987; Bertness and Hacker 1994; Stillman and Somero 1996) because organisms must cope with daily and seasonal shifts in temperature, salinity, exposure, sunlight, and a number of other stresses in a very narrow habitat. Considering predicted sea level rise and shifts in temperature and salinity (IPCC 2007), estuarine and coastal systems are also an obvious immediate target ecosystem for exploration of how species adapt to the stress associated with global climate change. These stresses include not only the long-established problems of nutrient loading and contamination from urban development (Gedan et al. 2009), but also rapidly changing abiotic conditions (Chevin et al. 2010; Rohr and Raffel 2010) and competition from invasive species (Freeman and Byers 2006; Richards et al. 2008; Kettenring et al. 2010). Understanding the evolutionary basis of trait response will be critical for predicting how organisms will respond to the challenges of anthropogenic alteration of the global environment. While many studies in estuarine habitats have examined the effect of salinity and water-logging gradients, as well as disturbance, nutrient flows, and freshwater inputs on community-level patterns, relatively little is known about the role of

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heritable adaptation in these organisms. Much estuarine research has been done without considering significant genetic structure within and among populations. Long-term viability of populations, design of reserves and protected areas, and success of restoration projects depends on conserving sufficient and/or appropriate genetic material to increase the probability that populations are able to adapt to pathogens, compete with invasive species, and survive erosion, storm regimes, and changing climatic conditions.

This special feature showcases several studies that highlight the importance of evolutionary concepts and approaches for understanding the genetic composition of populations in estuarine and coastal habitats. These studies incorporate a wide variety of tools and approaches including ecophysiology, ecological genetics, molecular markers, and genomics. Linking these concepts with estuarine science is a powerful way to understand ecological response in these habitats, particularly in the face of rapidly changing local and global conditions. These approaches should therefore become more commonly used to inform researchers, managers, and policy makers as they begin to unravel the potential impacts of global climate change on these critical communities.

How is Genetic Variation Relevant to Estuarine Science?

A central question in marine science is to understand factors that contribute to healthy estuarine and coastal systems. Most species consist of genetically variable individuals that express variation in ecologically important traits (Linhart and Grant 1996; Clark 2010). Several recent studies on introduced species in particular have indicated that species can evolve rapidly in response to novel conditions (Maron et al. 2004; Freeman and Byers 2006; Bossdorf et al. 2008). Likewise, understanding the contribution of genetic variation and genetically based response to environment is critical to basic ecological research (e.g., Whitham et al. 2006; Johnson and Stinchcombe 2007) as well as for ecological restoration (Hufford and Mazer 2003; Rice and Emery 2003; Bischoff et al. 2006; Mackie et al. 2010), and the response of ecological communities to global environmental change (Davis and Shaw 2001; Davis et al. 2005; Jump and Pañuelas 2005; Parmesan 2006).

An important first step in understanding the potential role of genetic variation in estuarine systems is documenting the level of overall genetic variation and how it is structured across the landscape. In this issue, Wyllie-Echeverria et al. (2010) use molecular markers to identify unique multi-locus genotypes or clones of the seagrass *Zostera marina* (eelgrass) in the San Juan Archipelago. They show a broad range of diversity across sites, but find that many sampled locations

have very few unique genotypes and are largely comprised of ramets of the same clone. A common assumption is that populations of limited diversity may be more susceptible to disease or changing conditions, which is of concern since these eelgrass beds provide spawning sites for commercially important fisheries. Other studies have found both a positive (Hughes and Stachowicz 2004; Reusch et al. 2005; Ehlers et al. 2008) and a negative relationship (Diaz-Almela et al. 2007; Arnaud-Haond et al. 2010) between genetic or clonal diversity and resilience to environmental stress depending on local conditions and community dynamics. The work by Wyllie-Echeverria et al. (2010) may therefore provide a foundation for making predictions about the effects of disease and other impacts in monitoring-based science in these communities. Similarly, in another study using molecular markers, Díaz-Ferguson et al. (2010) use a phylogeographic approach with six invertebrates of the Atlantic salt marshes to confirm limited genetic structure across a broad landscape. In addition, they found that shifts in ecological interactions in these salt marsh systems are likely to be environmentally driven, rather than due to historical differentiation and adaptation. These two studies demonstrate how documenting patterns of neutral genetic variation informs us not only of levels of genetic diversity, migration, and genetic drift, but also lends insight into timescales that may be of greatest relevance for understanding adaptation and interactions among species in an ecosystem.

While patterns of migration and drift are important forces shaping genetic structure, natural selection also shapes populations by acting on functional or potentially adaptive traits. Considering the strong environmental gradients and traits that allow organisms to deal with environmental variation, estuarine organisms provide a unique opportunity to study the process of adaptation. Evolutionary theory predicts that, if a species has heritable phenotypic variation for traits that are associated with differences in fitness, selection should act to match the traits to the environment, which would lead to locally adapted populations. However, few studies have addressed these types of questions in estuarine systems. It remains unresolved, for instance, whether the extreme differences in plant phenotypes at the ends of salt marsh gradients are due to phenotypic plasticity in response to environmental variation or to specialized traits that have resulted from natural selection (Pennings and Bertness 2001). Richards et al. (2010) address this type of question in a dominant salt marsh plant on Sapelo Island, Georgia, the Sea Ox-eye daisy, *Borrchia frutescens*. Using replicates of genetically different individuals in a greenhouse experiment, they found that trait response was due largely to phenotypic plasticity in every trait measured, and, in general, they found no evidence for adaptation to salt content alone. In contrast, Nacci et al. (2010) show that populations of the

non-migratory estuarine fish, *Fundulus heteroclitus*, vary widely in their sensitivity to pollutants, and that variation in this trait is genetically based and correlates to the magnitude of contamination at their residence site. Mancina et al. (2010) asked similar questions using genomics tools to look at expression patterns across the genome of bottlenose dolphins and found that gene expression reflects the environment—including pollutant levels—but that there may also be effects based on gender, indicating the degree of care necessary in interpreting variable gene expression across environments.

Recently, several studies have recognized the role of genetic diversity in processes at the community level and that genetic diversity may play an equivalent role to species or functional group diversity in ecosystem functioning (Vellend and Geber 2005; Whitham et al. 2003, 2006; Crutsinger et al. 2006; Reusch and Hughes 2006; Lankau and Strauss 2007). Robinson et al. (2010) test whether genetic diversity within species is correlated to species diversity within salt marsh communities. They found a strong positive relationship between overall genetic diversity and species richness within these communities. Furthermore, they used a model selection procedure (Akaike Information Criteria) to identify larval influx as a stronger predictor of within-site genetic diversity than either productivity of *Spartina alterniflora* or abiotic factors (temperature and salinity). These findings should assist in the management of marine reserves because they inform how best to focus limited resources to preserve these communities.

Global Change Biology in Estuarine Studies

The studies in the previous section provide examples of how a variety of ecological genetics tools can contribute to our understanding of estuarine and coastal systems at the genetic level, but they also provide a baseline of information to compare with future studies that can document how populations are responding to climate change. Our special feature also includes three studies that specifically address questions related to response or resilience to the changing estuarine environment (Arnaud-Haond et al. 2010; Proffitt and Travis 2010; Walls 2010). It may be intuitive that organisms will rapidly respond to novel or changing environments through phenotypic plasticity, but adaptation might also play an important role. For example, Walls (2010) found that plasticity was important for *Fallopia* species (Japanese knotweed) invading on Long Island, NY. However, she also reports that selection for increased specific leaf area may have contributed to differentiation of the plants found in the novel beach habitat. Similarly, Proffitt and Travis (2010) show that *Rhizophora mangle* (red mangrove) demonstrated plasticity in several traits in

response to transplantation in the field but that some genotypes were clearly more able to survive at different elevations in the intertidal zone. These studies offer insight into how organisms might be able to adapt to future climate change scenarios since some genotypes in each case were more able to survive novel habitat.

Using surveys of natural populations instead of manipulative experiments, Arnaud-Haond et al. (2010) collected repeated demographic measures of 30 populations of *Posidonia oceanica* (seagrass) to assess how clonal diversity and genetic diversity might contribute to the resilience of these populations to disturbance. In contrast to some previous work in eelgrass that found a positive relationship between genetic or clonal diversity and resilience to environmental stress (Hughes and Stachowicz 2004; Reusch et al. 2005; Ehlers et al. 2008), Arnaud-Haond et al. (2010) provide evidence of a negative relationship and suggest that certain genotypes might be more resilient and therefore survive to be bigger clones. Their work supports another study that showed *P. oceanica* meadows made up of larger clones and with lower allelic diversity were more resilient to heavy mortality induced by fish farm effluents (Diaz-Almela et al. 2007).

Genomics and Bioinformatics in Estuarine Studies

While most of these studies have used classic approaches, the development of genomic technologies is expanding beyond the traditional model systems into a wide range of wild species and will be powerful for understanding response to global change. For example, Mancina et al. (2010) present an overview of a new genomic tool in dolphins. They explain how microarray chips can be used in natural field settings and that the application of this technology can lead to understanding changing patterns in populations of these organisms that are otherwise difficult to study. In addition to the application of microarrays to understanding natural patterns in this species, there are several examples in the recent literature demonstrating that researchers can increasingly use genomic tools initially developed for model organisms to study processes in closely related wild organisms of interest (Slotte et al. 2007; Travers et al. 2007; Morinaga et al. 2008). For example, Horvath et al. (2003) used *Arabidopsis thaliana* microarrays to analyze gene expression in several distant species, including leafy spurge and poplar.

For organisms that are much more distantly related to any of the model systems that have commercially available microarrays or in research programs without the resources to develop their own, several researchers have turned to developing expressed sequence tag (EST) libraries (Bouck and Vision 2007). Although this approach has limitations

because it assays expressed genes and therefore is dependent on sample tissue and timing, ESTs provide a molecular snapshot of the *functional* component of the genome, which is therefore exposed to selection and potentially of adaptive importance (Bouck and Vision 2007). Reitzel et al. (2010) present the results of such a library developed for *Nematostella vectensis* (starlet sea anemone). This library is an example of how the latest technology can provide not only molecular markers to document genetic diversity and structure, but also how expression varies in response to the wide variety of natural habitats that this organism occupies. Previous research with AFLPs (Reitzel et al. 2008) and microsatellites (Darling et al. 2009) in *N. vectensis* has also shown a substantial amount of population genetic structure throughout this species' range. By finding SNPs that result in changes in proteins, researchers can begin to correlate population-specific polymorphisms in coding regions of genes with local phenotypic differences to link genotype with phenotype across the landscape (Reitzel et al. 2010).

Using yet another application of genomics technology, Jones (2010) introduces next-generation sequencing tools to examine community structure of microbes. This approach does not rely on microarrays or ESTs but instead on direct sequencing of samples taken from natural settings using 454 high-throughput sequencing technology. With appropriate experimental design and sample collection, estuarine scientists can now identify a broad array of organisms in any given sample. Jones (2010) in combination with Mancía et al. (2010) and Reitzel et al. (2010) demonstrate that the increasing number and applications of microarrays and the availability of massively parallel sequencing machines allow for genomics approaches that reveal ecologically important changes in gene expression in an increasing number of important taxa (Bonneau et al. 2007; Bouck and Vision 2007; Chapman et al. 2009; Richards et al. 2009).

When Are Evolutionary Phenomena Influential to Management?

A primary mission of the Coastal and Estuarine Research Federation and of estuarine science in general is to advance understanding and stewardship of coastal and estuarine systems. As such, this series of articles highlight the importance of understanding genetic structure and adaptation in these systems and how these approaches will be powerful tools in understanding response to global change. An important next phase of estuarine research is to apply our findings to management and conservation of these systems. Each of the papers discusses the potential impact of evolutionary studies on the methods employed in management practices and how these approaches should be implemented in policy making. As evidence of rapidly

changing climatic conditions accumulates, it has become an important agenda to identify what the future impacts will be on our biological systems. Coastal systems in particular are recognized as important buffers from storm and wave action, serve as vital nursery grounds for many economically important fisheries, and could be among the first to be impacted by rising global temperatures and sea level.

On a final note, while estuarine science has a lot to gain from incorporating concepts and experimental design of evolutionary ecology, evolutionary biology and functional genomics could also benefit from studies done in the natural context of coastal or estuarine systems (Richards et al. 2009; Franks 2010). A large portion of evolutionary theory stems from studies under controlled laboratory settings in model organisms. However, complex natural environments are the norm, and it is in this context that developmental pathways and physiological states of organisms actually function and evolve. It remains unclear how fluctuating environmental signals interact with each other and with an organism's genotype to fine-tune phenotypic response; but, clearly, the next step in evolutionary biology and functional genomics is to determine how gene expression is modulated in ecologically relevant organisms and conditions in the wild (Travers et al. 2007; Richards et al. 2009).

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