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REVIEW

MARINE MACROPHYSIOLOGY: STUDYING PHYSIOLOGICAL VARIATION ACROSS LARGE SPATIAL SCALES IN MARINE SYSTEMS

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ABSTRACT

A new approach toward understanding marine ecosystems has emerged through the integration of ecological physiology and macroecology. This multidisciplinary approach, titled here marine macrophysiology, facilitates unique insight into the foundation of macro-scale ecological patterns, such as biogeographic distributions, via examination of functional attributes of marine organisms across large spatial scales. For example, these broad-scale physiological inquiries confer the ability to directly assess the abundant-center hypothesis (aka Brown's principle) which proposes that species have decreased performance toward their ranges edges. By extension, the marine macrophysiological perspective also stands to clarify our understanding of more complex macro-scale phenomena such as biological invasions, the design of marine protected areas, and species' responses to global climate change. In this article, we review recent marine macrophysiology research and offer insights into future directions for this emerging field.

Key words: biogeography, environmental adaptation, marine, physiology, species range

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INTRODUCTION

Historically, understanding the determinants of species distribution patterns has been a central goal of marine ecology and ecological physiology (Valentine 1966, Gaston 2003, Somero 2005). A modern synthesis of this pursuit has emerged in the form of research focused on the underpinnings of species' range boundaries (e.g. Henderson and Seaby, 1999; Somero, 2002; Zacherl et al., 2003; Sorte and Hofmann, 2004; Osovitz and Hofmann 2005), abundance and distribution patterns (e.g. Sagarin and Gaines, 2002; Gilman, 2005; Rivadeneira and Fernández, 2005; O'Connor et al., 2007), and the analysis of large-scale community patterns (e.g., Broitman et al., 2001; Kinlan and Gaines, 2003; Sotka et al., 2004; Kinlan et al., 2005). Recently, a new emphasis has arisen in marine ecology and ecophysiology; namely, the call to understand and predict how species' will respond to climate change in marine ecosystems (e.g., Hoegh-Guldberg, 1999; Pörtner et al., 2001; Helmuth et al., 2002; Kennedy et al., 2002; Parmesan and Yohe, 2003; Stillman, 2003; Baker et al., 2004; Hassol 2004; Helmuth et al., 2005; Harley et al., 2006; Parmesan, 2007). In addition, marine invasions have highlighted the consequences of differential physiologies of marine organisms; specifically, invasive species often dominate via some element of enhanced performance in the invaded habitat that can span considerable geographic distances (Harris and Tyrrell, 2001; Grosholz, 2002). Given the significance of understanding species' responses to environmental change and ecosystem resilience to invasions, the need for studies that assess organismal condition and physiological performance across entire species' ranges has become heightened. In fact, a new subdiscipline, macrophysiology (see Chown et al., 2004 for definition of the term), is developing within marine ecophysiological research. These studies that measure physiological traits across large spatial scales are emerging as important contributors in the integrated efforts to understand the structure of geographic ranges and how species distribution and abundance patterns might shift in response to environmental change. In this article, we present an overview of marine macrophysiological research, highlighting studies in this growing experimental area within marine-focused ecological physiology.

OVERVIEW

Macrophysiological studies aim to determine how organisms are affected by the high levels of environmental variability encountered over large geographic distances by comparing physiological traits between individuals separated across geographic space. Using this strategy, researchers can begin to approach the functional foundation for community level dynamics, such as shifts in biogeographic ranges in response to climate change (Hawkins et al., 2003; Parmesan and Yohe, 2003; Root et al., 2004; Harley et al., 2006). For example, long-term sea surface temperature fluctuations were recently shown to correlate with changes in the distribution of several marine species (e.g. Perry et al., 2005; Rivadeneira and Fernández, 2005). However, developing accurate predictions regarding the biological effects of environmental variability is difficult without the use of a multidisciplinary approach that encompasses functional studies (Helmuth et al., 2005).

Although the integration of physiological studies with macroecology is critical, studies that utilize physiological approaches across large spatial scales are logistically challenging and thus have not been very common in the past, especially in aquatic ecosystems. Thus far, the majority of macro-scale physiological studies on have centered on terrestrial systems (see Gaston, 2003 for a review; Chown et al., 2004). Many of these studies have been concerned with either metabolic compensation in insects (e.g. Chown et al., 1999) or environmental tolerances of plants (e.g. Pither, 2003) with respect to large biogeographic zones. Traditionally, functional marine environmental studies have investigated the physiological effects of a single environmental parameter (e.g. hypoxia, heat, salinity) on small spatial scales (e.g. Bertness et al., 1999; Helmuth and Hofmann, 2001; Hochachka and Somero, 2002; Somero, 2002; Harley and Helmuth, 2003; Baker et al., 2004; Somero, 2005), overlooking large-scale signals. Additionally, the majority of marine functional studies that have examined physiology on large scales have done so using relatively basic organismal metrics such as growth rate (e.g. Levinton, 1983; Levinton and Monahan, 1983; Yamahira and Condover, 2002), body size (e.g. Roy and Martien, 2001), reproductive output (e.g. Lonsdale and Levinton, 1985; Lewis, 1986; Clarke, 1987; Leslie et al., 2005; Lovrich et al., 2005), and mortality (e.g. Ebert et al., 1999). One factor that has limited the application of more elaborate physiological techniques to large scales in marine systems is their cumbersome nature when employed in the study of natural populations. Collecting individuals or tissues from the ocean without disturbing their natural physiological state is very difficult, especially when collecting specimens from multiple distant, and sometimes remote, locations within a short period of time. Another challenge to this type of study is that natural systems are laden with variability (Helmuth et al., 2005), making the resultant data often complex and difficult to interpret. For example, variation within the physiology of natural populations can arise from time of day, season, age or size of individual (Chown et al., 1999; Helmuth et al., 2005). Thus, the degree of physiological or phenotyptic plasticity amongst individuals must be carefully considered when comparative studies are performed on populations separated by large distances.

Despite these challenges, a number of marine macrophysiological studies have been published in the last few years. Studies of this nature have varied considerably in their approaches, but can be roughly classified into two major categories: (1) investigations of variation of a trait in natural populations, and (2) comparative studies of species with different geographic ranges (e.g. Somero, 2005). The first group of studies focuses on measuring physiological traits in organisms in the field in order to assess performance at a specific window in time over macro-scales; the latter category uses biogeographic information to predict the different physiological tolerance of species understudy. Each approach has significant merit, however the studies of natural populations – a form of experimental biogeography – and not lab-based studies, is the approach that will help delineate how physiological plasticity interacts with environmental variation in space and time. The following sections review these trends in recent marine macrophysiological research and offer insight into its future.

INVESTIGATIONS OF VARIATION OF A TRAIT IN NATURAL POPULATIONS

Studies of this type are unique in that they focus on organisms' variable acclimatizational responses over great distances of the organism's natural range. Studying direct responses of organisms to the environment is ideal for investigating the mechanisms behind biogeographic patterns, as many believe that the direct effects of abiotic factors are a driving force in the establishment and maintenance of range boundaries (e.g. Brown, 1984; Dunson and Travis, 1991). A current paradigm in ecology is that species are more stressed toward the edges of their biogeographic range and that this environmental stress confines the borders of their ranges (e.g. Brown, 1984). Measuring plastic physiological traits in field-acclimatized organisms across large spatial scales, such as studying biogeographic stress profiles, is a valuable method to understand direct influences of environment on performance.

Macrophysiological studies of this type examine plastic traits, whose manifestations are very environmentally-dependant and may change on relatively short time scales (i.e. growth, fecundity), offering a means toward assessing an organism's or population's 'condition'. For example, Helmuth et al. (2002) showed that body temperatures of *Mytilus californianus* mussels during low tide differ significantly across the latitudinal cline of the west coast of North America. This result is obviously not a fixed adaptation to life at different latitudes, but a direct effect of the thermal variation across this expanse. Historically, very few marine studies have utilized the strategy of examining organism's natural states across large spatial scales. Many of those that have utilized this approach examined very basic traits; however, a small number of studies have employed more sophisticated physiological methods. For example, Hummel et al. (2000) showed that Baltic clams *Macoma balthica* translocated from the Netherlands to 200 km south of their distribution range edge in France had higher respiration rates and lower body weight indexes than clams that remained within their distribution range in the Netherlands. Also, Sorte and Hofmann (2004) showed that intertidal *Nucella canaliculata* dogwhelks living in their natural habitat near their southern range edge in California expressed higher levels of Hsp70 protein than those living near the center of their range in Oregon. Similarly, Osovitz and Hofmann (2005) found that the temperature that induced maximum *hsp70* mRNA expression in tube feet of purple sea urchins was higher in urchins existing in southern California than in those of urchins from Oregon populations. In an attempt to understand physiological variation among several biogeographic locations, Hsp70 protein expression was compared among 21 populations of the intertidal mussel *Mytilus californianus* and snail *Nucella ostrina* from Baja California to Vancouver, British Columbia (Sagarin and Somero, 2006). These authors discovered geographic variation in the Hsp70 protein expression in both species, although the pattern of expression was more complex than a simple correlation with latitude (Sagarin and Somero, 2006). Comparing different species, Lopez et al. (2002) likewise found natural variation in global protein expression between congeneric mussels *Mytilus edulis* on the coast of Netherlands and *M. galloprovincialis* on the east coast of Spain. Taken together, these studies suggest that environmental factors that vary across space directly affect marine organisms' performance and condition, lending empirical credence to traditional assumptions regarding these questions.

INFERRING THE BIOLOGICAL EFFECTS OF LARGE-SCALE GEOGRAPHIC SEPARATION THROUGH THE COMPARISON OF ENVIRONMENTAL TOLERANCES OF SPECIES WITH DISSIMILAR BIOGEOGRAPHIC RANGES

A much more common type of marine macrophysiological study involves the comparison of fixed physiological traits between differentially distributed organisms (e.g. Somero, 2005). In contrast to that of the previous section, this type of study focuses on the physiological tolerances of organisms from different geographic regions in order to make inferences regarding differential selective pressures of the environment. For example, after comparing the thermal acclimation capacity of several differently distributed species of *Petrolisthes* porcelain crabs, Stillman (2003) concluded that those species that inhabit lower latitudes and higher tidal zones should be substantially more susceptible to ocean warming. Historically, these types of studies have compared basic anatomical and physiological traits between geographically distinct taxa (e.g. Fox, 1936; Peiss and Field, 1950; Scholander et al., 1953; Wolcott, 1973), but recently, more sophisticated physiological techniques have been applied to the investigations of physiological variation across large geographic scales.

In order to investigate how large-scale geographic variation influences species performance, comparing traits between individual species is often useful, as no individual species boasts universal ranges (Brown and Lomolino, 1998). For example, species comparisons are often necessary to compare the physiologies of tropical and polar marine organisms because the ranges of very few single species encompass both regions. Such species comparisons have predominately examined adaptations that combat the direct physical effects of thermal variation (Q_{10} effects) in order to maintain characteristic rates of physiological systems (see Clarke, 2003). Conservation of metabolic rates is believed to be integral in the maintenance of biological function across the broad range of thermal habitat variation intrinsic to vast spatial distances (Clarke, 2003). Given that these physiological adaptations are usually discovered after identical long-term laboratory acclimation, observed trait variation is usually attributed to fixed genetic differences in these studies (e.g. Sokolova and Pörtner, 2001).

Pörtner (2002a) argued that the highest levels of biological organization should be examined when studying environmental tolerances, as a malfunction in any subsystem should also be apparent at higher levels. For example, Sokolova and Pörtner (2003) reported that unlike conspecifics from the sub-Arctic White Sea population, *Littorina saxatilis* from the temperate North Sea population experienced no down-shift in overall maximum critical temperature upon cold acclimation. This result suggests that the *Littorina* snail population living in the colder waters of the White Sea was adapted to that environment. Other investigators have shown similar results for marine invertebrates. Stillman and Somero (2000) demonstrated that the general upper thermal tolerance of 20 species of *Petrolisthes* porcelain crabs was correlated with the species' maximal habitat temperature, while dogwhelks of the genus *Nucella* displayed a similar pattern (Sorte and Hofmann, 2005). By demonstrating the existence of fixed physiological differences between species from different geographic regions, these and many other studies (e.g. Hummel et al., 1997; Van Dijk et al., 1999) have provided evidence that environmental adaptation on the whole organism level is important for the maintenance of dissimilar biogeographies.

Additionally, considerable marine macrophysiological research has focused on the conservation of muscle performance as a function of different habitat temperatures (Pörtner, 2002b for review; Guderley, 2004). Much of this research has been conducted on the ability of differentially distributed marine fishes to display comparable swimming performance at their respective habitat temperatures, despite the slowing metabolic effects of colder water (e.g.

Johnson and Johnston, 1991; Johnston et al., 1998). In particular, Johnson and Johnston (1991) reported that the temperature that induced maximum contractile tension of muscle fibers in tropical, temperate, and polar teleost fish species was highly correlated with habitat temperature. Metabolic enzyme activities in particular have been linked to fixed performance differences between biogeographically distinct species (e.g. Dalhoff and Somero, 1993; Lannig et al., 2003; Lucassen et al., 2003; Sommer and Pörtner, 2004). For example, Sokolova and Pörtner (2001) found that the activities of three of five metabolic enzymes constitutively differed between snails from the North Sea and White Sea populations of *Littorina saxatilis* and its congener *L. obtusata.* Fields (2001) argued that one of the ways that enzyme activities can be maintained across large spatial scales is through the adjustment of enzyme flexibility, since protein flexibility changes with temperature. Indeed, such differences in enzyme flexibility have been implicated in the adaptation to life at different latitudes (e.g. Holland et al., 1997; Fields and Somero, 1998). However, differences in enzyme activity due solely to disparities in concentration have also been discovered between differentially distributed marine organisms (e.g. Pierce and Crawford, 1997; Powers and Schulte, 1998; Schulte, 2001). Notably, Crawford and Powers (1989) found that higher activities of lactate dehydrogenase (LDH-B) within the tissues of *Fundulus heteroclitus* killifish from northern populations were largely a result of a higher frequency of a single more active promoter allele ($ldh\text{-}B^{b}$). Fixed differences between the expression levels of many other genes are thought to play a role in the maintenance of function across large spatial scales (e.g. Hofmann and Somero, 1996; Tomanek and Somero, 1999, 2002; Whitehead and Crawford, 2005). In one example, the transcript profiles of a Florida population of *Fundulus heteroclitus* was discovered to be more similar to that of the more distantly related Florida population of *F. grandis* than those of a New England population of *F. heteroclitus* after identical laboratory acclimation (Oleksiak et al., 2002). This trend suggests that the thermal variation encountered across the range from Florida to New England is sufficient to evoke differential thermal adaptations between individuals.

Many of these macrophysiological studies indeed found that, when exposed to a foreign set of environmental conditions, an organism's traits are often not able to function comparably to those of closely related organisms adapted to that environment. Various types of physiological adjustments appear to confer this ability to function in extremely dissimilar environments, including variation in gene expression and enzyme structure. Evolutionary adjustments in these traits are believed to be a means by which species maintain performance in the face of physiologically disruptive levels of environmental variation. If these irreversible functional adaptations are indeed necessary to preserve physiological performance across diverse environments, species ranges would likely be affected by environmental change. Inquiries into fixed adaptations between differentially adapted organisms have aided our understanding of how organisms successfully maintain large geographic ranges and our predictions regarding species responses to future climate change.

CONCLUSION AND FUTURE DIRECTIONS

As the macrophysiological approach gains momentum in marine systems, the pay-offs in this area will be substantial. These potential pay-offs range from the understanding of environmental adaptation (e.g. Pierce and Crawford, 1997; Fields and Somero, 1998) to biogeographic perspectives (e.g. Hummel et al., 1997, 2000; Sorte and Hofmann, 2004) to improved abilities to predict a species' responses to climate change based upon its plasticity and measured performance across its range (Helmuth et al., 2005). In addition, conservation efforts may also be supported by such studies; these include insights into the biology of marine invasions (e.g. Tyler et al., 2000; Lee and Peterson, 2002; Stachowitz et al., 2002; Cowling et al., 2003; Lee et al., 2003; Sax et al., 2005; Thieltges, 2005) and the consequences of marine protected area (MPA) establishment (Palumbi, 2004) (e.g., does the location of an MPA match well with the overall physiological "stress" signature of the populations that are being managed?). The studies that have directly measured physiological responses to environmental variation on large spatial scales reviewed in this paper have shown that natural levels of spatial and temporal environmental variation can have a great impact on the physical condition of individual marine organisms and species. This result is an important one, as the understanding of the impact of abiotic factors on species' distrubutions requires knowledge of such relationships between internal biological systems and the parameters of the ambient marine environment (Helmuth et al., 2005).

An important component of macrophysiology is the addition of a genetic perspective. This has been broached in the *Fundulus* studies (Powers and Schulte, 1998), for example and in other studies of local adaptation (e.g. Sanford et al., 2003) and is an essential step needed to understand the source of variation in physiological traits that may be revealed in macrophysioloigcal studies. Studies of population structure are relatively well-known in marine systems (e.g., Reeb and Avise, 1990; Hedgecock, 1994; Marko, 1998; Sotka et al., 2004; Ayers and Waters, 2005), but few couple the phenotype, in this case the physiological traits under study, to genotype in field studies (e.g. Lee and Peterson, 2002). The comparison of physiologies of organisms with distinct genotypes can offer an understanding of environmental tolerances conferred by differentially abundant genotypes. These comparisons can begin to address the question of whether individual genotypes will be differentially affected by climate change, perhaps leading to the elimination of genetic variation during environmental change.

Finally, on the technology front, the application of new techniques, such as cDNA microarrays in physiological (Gracey and Cossins, 2003) and ecological research (Thomas and Claper, 2004; Hofmann et al., 2005) is currently increasing the analytical power of marine macrophysiology (e.g. Oleksiak et al., 2002). Due to their enormous data output, these genomics-enabled techniques stand to enhance our understanding of many previously investigated large-scale physiological processes (e.g. Clark et al., 2004) as well as investigate new questions. On the whole, the macrophysiological approach has the potential to develop a global understanding of organismal function in the ocean in a way that will greatly inform the ecology of these systems. Insight into the relationship between marine species and habitats gained from the traditional ecological approach benefits greatly from the addition of the physiological perspective. This new multidisciplinary approach stands to uniquely advance the understanding of species responses to climate change, biological invasions, and the utility of MPAs in marine ecosystems.

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