



## Survival of oyster larvae in different salinities depends on source population within an estuary

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### ABSTRACT

The role of environmental heterogeneity in limiting connectivity and shaping population structure continues to be a major question in evolutionary biology, particularly for high-dispersal species. Many marine species have a two part life cycle comprised of a sedentary adult phase and a dispersing larval phase. For estuarine species such as *Crassostrea virginica* (eastern oyster), larvae are often carried through very distinct water masses that can affect growth and survival prior to settlement, potentially impacting population connectivity. On the mesoscale of an estuary, gene flow may be a homogenizing force; however, for genomic regions experiencing strong differential selection along estuarine gradients, gene flow may be minimal if recurrent viability selection maintains functional genetic differentiation. Estuaries are defined by salinity gradients and many taxa rely on phenotypic plasticity to thrive there. Nonetheless, even euryhaline species like eastern oysters have their physiological limits, and this study tests whether survival of *C. virginica* larvae in different salinities depends on parental source reef and/or conditioning salinity. Oysters from high, intermediate and low salinities within Delaware Bay, New Jersey, were spawned in a common garden to test for differences in larval survival that have a genotypic basis. Under the null hypothesis of functional homogeneity among adult oyster populations we expected no difference in larval survival. Broodstocks were conditioned in low and high salinity common gardens for 4–6 weeks before spawning. Larvae from 56 pair-cross families were reared in low and high salinities for 13 days. Cox proportional hazard models were used to determine significant predictors of larval survival. Population source interacted with larval salinity treatments to significantly affect larval survival. This finding suggests that the larval pool of single estuaries contains abundant genetic variation for survival across different salinities, stemming in part from functional genetic differences among source reefs. Our results can help parameterize larval connectivity models that incorporate environment-dependent survivorship.

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### 1. Introduction

Understanding the degree of population connectivity, ranging from “closed” systems characterized by persistent genetic differentiation between populations to “open” systems showing broad-scale homogeneity, is vital to fishery management, restoration design and the designation of marine reserves (Cowen et al., 2007). Many marine species, particularly invertebrates, have a bipartite life cycle comprised of a sedentary adult phase and a dispersing larval phase. Planktonic larval stages can persist long enough for organisms to travel hundreds to thousands of kilometers; however, the connectivity of marine populations is often more restricted than predicted by the dispersal capabilities of migrants and the known hydrographic barriers (Koehn et al., 1980; Lewis and Thorpe, 1994). Two plausible and not exclusive explanations are physical barriers, such as isoclines and hydrographic fronts (Pineda et al., 2007), and biological barriers (Gaines et al., 2007; Grosberg and Cunningham, 2001). Physical explanations such as barriers to circulation

have successfully predicted patterns of larval transport (Gilg and Hilbish, 2003) but the effects of physical barriers are frequently hard to determine due to interactions with larval behavior (Shanks, 2009). Biological barriers may be particularly important in systems with environmental gradients or patchiness where strong selective pressures during and after dispersal both limit connectivity and shape population genetic variation among breeders. Salinity gradients from fresh to oceanic water define estuaries and provide an excellent system for measuring biological barriers to connectivity.

Biological barriers to connectivity can occur during both larval dispersal and post-settlement. A large percentage of mortality for high fecundity marine species occurs during dispersal (Thorson, 1950). Predation and starvation are spatially unpredictable circumstances for larvae leading to potentially high mortality rates over and above intrinsic factors stemming from genetic load. In contrast, physiological stress as larvae disperse across abiotic gradients may account for spatially non-random mortality that could shape population differentiation. Apart from dispersal, the ‘getting there’ part of connectivity, postsettlement survivorship further determines realized connectivity between populations in terms of adult abundance, and only with successful reproduction

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do immigrants have an evolutionary impact. Phenotypic plasticity is a common adaptation to habitat heterogeneity, but every trait has tolerance thresholds beyond which plasticity is no longer sufficient to acclimate to the environment (reviewed in Auld et al., 2010). These thresholds define habitat use boundaries below the spatial scale of dispersal.

To the extent that habitat heterogeneity occurs at scales below that of dispersal, a proportion of dispersal constitutes 'migrants' across different microhabitats. Immigrants to non-parental microhabitats can experience a phenotype–environment mismatch and low relative fitness (Marshall et al., 2010) resulting in spatially balanced polymorphisms (Sanford and Kelly, 2011). Along spatially stable environmental gradients, each generation of migrants will undergo recurrent viability selection resulting in persistent population differentiation among adults when the strength of selection is strong relative to  $N_e m$  (gene flow as measured by effective population size ( $N_e$ ) and migration rate ( $m$ )) (Alleaume-Benharira et al., 2006; Antonovics, 1968; Barton, 2001; García-Ramos and Kirkpatrick, 1997; Holt, 2003; Kirkpatrick and Barton, 1997). For species with sedentary adults and proximity-dependent mating (e.g. broadcast spawners), the recurrent functional population differentiation among adults can be translated into greater functional diversity among larvae than what is expected under panmixia. Alternatively, where the strength of selection on a trait is less than  $N_e m$ , but environmental stress is beyond plasticity thresholds, surviving immigrants can lower mean population fitness and constrain local adaptation such that no functional population differentiation would be observable (Hendry and Taylor, 2004; Nosil and Crespi, 2004; reviewed in Garant et al., 2007). The likelihood of these two outcomes depends on the degree of plasticity for a given trait, the strength of selection on that trait, and the distribution of gene effects underlying the trait (Yeaman and Whitlock, 2011). Thus, depending on the traits under investigation, populations compared across a gradient may exhibit different levels of connectivity and genetic differentiation related to these traits (Caillaud and Via, 2012).

One way to test for balancing selection is to measure population differentiation among adults for loci that are likely to be responding to selection gradients. Finding the relevant loci makes this classical population genetic approach challenging in non-model organisms, but with some luck and rigorous subsequent experiments, dramatic patterns of small scale genetic differentiation have been shown to result from post-settlement selection in several estuarine systems. One example is clinal variation at the *Lap* locus of *Mytilus edulis* (Koehn and Hilbish, 1987; Koehn et al., 1976, 1980). Among adult populations in the Atlantic Ocean and Long Island Sound a *Lap* allele decreased in frequency from 0.55 to 0.15 over a 10 mile distance with decreasing salinity (Koehn et al., 1976). In estuarine cohorts the oceanic allele was common in newly settled juveniles and progressively declined to the characteristic frequency found in local adults, consistent with recurrent post-settlement selection. Similarly, a strong selection gradient across the intertidal zone filters genotypes from the mixed larval pool in *Semibalanus balanoides* and maintains a stable polymorphism (Schmidt et al., 2000). These examples, along with other studies (rainbow smelt: Saint-Laurent et al., 2003; three-spined stickleback: Hendry et al., 2002, McCairns and Bernatchez, 2010), demonstrate the impact of a strong selection gradient on population differentiation in high gene flow systems.

An alternative approach is to experimentally test for genetically-based differences in survival limits for larvae derived from breeding populations experiencing different environments within a single estuary. If adults from different habitats are functionally differentiated as a result of recurrent selection then, after controlling for maternal effects, they should produce larval cohorts with distinct genotype-by-environment patterns of viability. Previous studies experimentally testing for genotype-by-environment effects on survival and growth of larvae have found phenotype–environment mismatches that suggest better survival and growth in the natal habitat than in other environments (eastern oyster: Newkirk et al., 1977; Newkirk, 1978; European oyster: Newkirk, 1986; hard clam: Knaub and Eversole, 1988; Manzi et al., 1991). In fact, larvae

have been shown to have narrower physiological tolerances than adults in several bivalve species (Bayne et al., 1976) facilitating this experimental approach. The strength of this approach is that no a priori knowledge of candidate loci or markers for population differentiation are needed. Additionally, differentiation is identified directly at the phenotypic level after accounting for plasticity and maternal effects, explicitly demonstrating the extent of phenotype–environment mismatch at the dispersal stage.

The goal of this study was to identify functional differentiation in *Crassostrea virginica* (eastern oyster) adults along a salinity gradient within a single estuary by experimentally measuring the impact of source location and broodstock conditioning salinity on larval progeny survivorship at low and high salinity treatments. In western North Atlantic estuaries the eastern oysters are ecosystem engineers (Lenihan and Peterson, 1998) whose complex reef systems provide habitat for over 300 species (Beck et al., 2011). Due to its diverse ecosystem services (reviewed in Constanza et al., 1997), the oyster is considered a keystone estuarine species (Barnes et al., 2007; Coen et al., 1999). With historic loss of 90% of eastern oyster reefs in North America (Jackson et al., 2001; Kirby, 2004), restoration of oyster populations is needed to realize these ecosystem services again. Many states are engaged in efforts to restore oysters (Beck et al., 2011), often through reef construction and planting of hatchery-produced oysters. It is this restoration objective that motivates a more rigorous examination of larval tolerances and the mechanisms that determine them.

A potentially valuable methodological advance in restoration planning is to couple hydrodynamic models with larval particle tracking and habitat heterogeneity to project the efficacy of different management and restoration procedures. The Oyster Restoration Optimization model (North et al., 2010) designed for the Chesapeake Bay and a model of oyster larval dispersal in the Delaware Bay (Narváez et al., 2012) are two such models. The integration of larval swimming behavior and environment-dependent mortality potentially increases the accuracy of source and sink relationships inferred from the models. By identifying sources and sinks, organizations can focus on the appropriate sites for their particular restoration goals such as constructing reefs at sink locations or enhancing stock at source locations. Currently, environment-dependent larval mortality is modeled based on species-specific thresholds. If functional genetic differentiation occurs among breeding oyster populations within single estuaries, and especially given that dispersal is predicted to be strongly asymmetric and downstream based on these models (North et al., 2010), then implementing population specific thresholds may improve the ability of models to accurately predict the realized connectivity resulting from differential larval and post-settlement survival.

## 2. Materials and methods

### 2.1. Sample collection

Two hundred adult oysters were collected from each of three sites with distinct salinity regimes within the Delaware Bay on April 18, 2011 (Fig. 1). Oysters from Cape Shore (39° 04.10' N, 74° 54.77' W; salinity range of 20–25; Narváez et al., 2012) were hand collected from intertidal reefs. Oysters from Arnolds reef (39° 23.055' N, 75° 27.002' W; salinity range of 6.5–14.5; Bushek et al., 2012) and New Beds reef (39° 14.518' N, 75° 15.071' W; salinity range of 9–16.5; Bushek et al., 2012) were collected by dredge from the NJ Fish and Wildlife vessel *Zephyrus*.

### 2.2. Adult oyster conditioning

The main objectives of adult oyster conditioning were to minimize the impact of maternal effects on larval survival and to have adults undergo gametogenesis under two different salinities (10 and 30). Half of the oysters were conditioned in recirculating tanks at Haskin Shellfish Research Laboratory (HSRL) of Rutgers University while the

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