Genotype-specific growth of hard clams (genus *Mercenaria*) in a hybrid zone: variation among habitats

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Abstract Shell growth rate is an important component of fitness in bivalve molluscs. Using the \( \omega \) parameter computed from the von Bertalanffy growth equation, we quantitatively compared rates of annual shell growth among the hard clams *Mercenaria mercenaria*, *M. campechiensis*, and their hybrids sampled from a variety of habitats in the Indian River lagoon, Florida, USA, a zone of species overlap and natural hybridization. Our results indicate that the classical paradigm describing hard clam growth, in which growth rate is fastest in *M. campechiensis*, intermediate in hybrids, and slowest in *M. mercenaria*, is not supported in the Indian River lagoon. Instead, *M. campechiensis* has a growth advantage in deep-water habitats in the northern section of our study area. In the central and southern sections of our study area, hybrids have a growth advantage over *M. mercenaria* in shallow-water habitats, but *M. mercenaria* has a growth advantage over hybrids in deep-water habitats. In all other sampled habitats, either growth rate among genotype classes is equal, or *M. mercenaria* has a growth advantage. This complex relationship between genotype and habitat-specific growth provides a mechanism for selection to act on hard clams in the Indian River.

Introduction

Shell growth rate is an important component of fitness in bivalve molluscs because the bivalve shell provides a defense against many potential predators. The mechanical force required to crush a bivalve shell is positively correlated with shell size (Blundon and Kennedy 1982), so the shell becomes a more effective predator-defense mechanism as shell size increases (Whetstone and Eversole 1981; Arnold 1984; Juanes 1992). Other components of fitness, including sedimentation-induced mortality, maturation and fecundity, and competitive interactions, may also be directly or indirectly size-dependent (Bricelj and Malouf 1980; Peterson 1983; Rawson and Hilbish 1991). As a result, the fitness of individuals having rapid growth rates may be enhanced compared to that of slower-growing individuals.

Hard clams of the genus *Mercenaria* are a commercially important and ubiquitous component of shallow-water estuarine and marine benthic communities along the Atlantic and Gulf of Mexico coasts of the USA. Two species, *M. mercenaria* and *M. campechiensis*, occur within that range (Abbott 1974). Along the Atlantic coast, the two species are generally parapatrically distributed (*M. mercenaria* occurs inshore and *M. campechiensis* occurs offshore), but in the Indian River lagoon on the east-central coast of Florida, the two species occur sympatrically and hybridize extensively (Dillon and Manzi 1989; Bert et al. 1993; Bert and Arnold 1995).

Previous controlled field studies of hard clam growth in the southeastern USA indicated that the mean annual shell growth rate (hereafter termed “growth”) of *Mercenaria campechiensis* was faster than that of *M. mercenaria* and that the growth of their reciprocal hybrids was generally intermediate between that of the parental species (Chesnut et al. 1956; Haven and Andrews 1956; Menzel 1961, 1962). However, recent research on growth of natural populations of hard
clams from nearshore waters of the Atlantic and Gulf of Mexico coasts of Florida suggests that comparisons of the relative growth of the two species are more complex than first perceived. In Florida, growth of *M. mercenaria* along the Atlantic coast was similar among locations, but growth of *M. campechiensis* from the Gulf of Mexico was highly variable among locations (Jones et al. 1990). Growth of some Gulf of Mexico *M. campechiensis* populations was faster than that of Atlantic *M. mercenaria* populations, but growth of other Gulf of Mexico *M. campechiensis* populations was slow compared to that of Atlantic *M. mercenaria*.

Whether these observed differences in growth among natural hard clam populations are genotype-specific or reflect differences in relative growth among habitats is not clear. To differentiate between these alternatives, it is necessary to compare growth among the two species and their hybrids within similar habitats. The Indian River lagoon provides an ideal location for such a comparison. Both species and their hybrids occur in the lagoon (Dillon and Manzi 1989; Bert and Arnold 1995). Furthermore, the benthic structure of the lagoon is composed of a variety of microhabitats (Arnold et al. 1991a), and various combinations of the two species and their hybrids occur in each of those microhabitats. This offers a unique opportunity to compare growth among genotypes within a diverse array of habitat types.

In this study, we compare the growth of three genetically identified genotype classes (*Mercenaria mercenaria*, *M. campechiensis*, and hybrids of the two species) collected from a variety of locations in the Indian River lagoon. We have previously reported the habitat-specific nature of the growth of *M. mercenaria* in the lagoon (Arnold et al. 1991a). We now extend our analysis to include *M. campechiensis* and hybrids. We compare growth between pairwise combinations of the genotype classes within and between representative habitats within the lagoon. The complex genotype-specific and habitat-specific growth relationships we observed provide a potential mechanism for selection to contribute toward the maintenance of the *Mercenaria* hybrid zone in the Indian River.

**Materials and methods**

**Sample collection**

Our study area, comprising Shellfish-Harvesting Areas C, D, E, and F of the Indian River lagoon, is bordered on the north by State Road 405 and on the south by Sebastian Inlet (Fig. 1). Water depth within the study area averages 1.5 m; maximum depths of 4 m are found in the Intracoastal Waterway, which roughly bisects the Indian River throughout its length, and in areas around Eau Gallie and Melbourne (White 1986). The Indian River lagoon is "microtidal" (Smith 1991). Within the study area, tidal range is ≤ 5 cm (Smith 1993).

During July and August 1986, we collected all hard clams (*Mercenaria* spp.) ≥ 40 mm shell length from each of 75 randomly allocated, 1 m² quadrats located in each of the four shellfish-harvesting areas. Prior to collecting the clams, we recorded water depth at each station, extracted triplicate 2.5 cm-diam × 5 cm-deep sediment cores from within each quadrat, and visually determined the presence or absence of submerged aquatic vegetation (SAV) within the quadrat. The SAV was generally composed of various proportions of the seagrasses *Syringodium filiforme* and *Halodule wrightii* or of the marine alga *Caulerpa prolifera* (Rice et al. 1983). In the laboratory, we determined sediment composition (percentage of gravel, sand, silt-clay, and organic matter) following the methods of Folk (1974), except that sediments were wet-sieved. We analyzed pooled sediment samples from each station for percent composition of gravel (grain size ≥ 2.00 mm), sand (grain size 0.06 to 2.00 mm), and silt-clay (grain size < 0.06 mm). Percent organic matter was determined by ignition at 550 °C for 6 h. The clams were returned alive to the laboratory, where samples of gill and mantle tissue were dissected, quick-frozen in liquid nitrogen, and stored at −80°C for protein electrophoresis. The shell valves were cleaned and stored for subsequent age determination.

From 20 October 1987 through 30 August 1988, we monitored salinity (%) biweekly at each of eight sampling stations (two stations per shellfish-harvesting area) within the study area (Fig. 1). Salinity was measured 0.5 m above the sediment–water interface using a YSI Model 33 salinity–conductivity–temperature meter. Salinity was compared among stations using the nonparametric Kruskal–Wallis test (Sokal and Rohlf 1981). Significant differences in mean salinity among stations were determined using the simultaneous test procedure for unplanned multiple comparisons with equal sample sizes (Sokal and Rohlf 1981).