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Juvenile growth and mortality effects on white shrimp *Litopenaeus setiferus* population dynamics in the northern Gulf of Mexico

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ABSTRACT

Processes regulating juvenile growth and mortality of white shrimp *Litopenaeus setiferus* in coastal nurseries may be particularly important in regulating offshore adult population size and sustainability. To advance the integration of these processes into fishery stock assessments, and to provide a better understanding of the functional role of coastal nurseries for fishery species, we explored the potential effects of variable juvenile growth and survival on white shrimp population growth rate. We developed a population model that incorporates available information on vital rates (growth, mortality, fecundity) for each shrimp life stage. We used the model to explore the potential impacts of variability in juvenile growth and mortality rates on the overall population growth rate. Modest changes in juvenile growth and mortality rates were projected to have a greater impact on stock size than the full range in fishing mortality over the past few decades. These results suggest that variability in juvenile survival may be a strong driver of adult stock size and that the processes that regulate juvenile growth and mortality need to be properly understood for the effective management of coastal nurseries and shrimp stocks.

1. Introduction

Salt marshes and other shallow estuarine habitats are considered as critically important nurseries for many fishery species (Boesch and Turner, 1984; Beck et al., 2001). Like many species that use estuaries as nurseries, white shrimp *Litopenaeus setiferus* have a life cycle where the adults live and spawn in offshore waters, larvae move into coastal lagoons and estuaries where they settle for the juvenile phase, and sub-adults migrate back offshore to join adult stocks (Lindner and Cook, 1970). The early life stages of many nekton can suffer high levels of mortality (McGurk, 1986; Sogard, 1997), and small changes in juvenile survival can have a profound influence on ultimate cohort strength (Meyers and Cardigan, 1993; Levin and Stunz, 2005). The nursery paradigm thus implies that factors regulating juvenile growth and survival in coastal nurseries should have significant impacts on offshore adult stock size and population sustainability (Minello et al., 2003; Levin and Stunz, 2005; Sheaves et al., 2006).

Salt marsh habitats of the Gulf and Atlantic Coasts of the USA are believed to play important roles in regulating juvenile shrimp growth and mortality (Kneib, 1997; Zimmerman et al., 2000; Baker et al., 2013). The precise mechanisms are difficult to resolve, but the seasonally warm and highly productive waters of the salt marsh serve as nurseries for a great diversity of species, providing favorable conditions for growth and survival (Deegan et al., 2000). Comparisons of density estimates of organisms among particular habitats can provide a basic index of relative habitat quality (e.g. Rozas et al., 2007), and high densities of juvenile white shrimp within vegetated marsh habitats suggests marshes may be particularly important in the support of the fishery (Minello et al., 2008). However, to gain a true understanding of the relative importance of various habitats and processes to the persistence of populations, it is essential to place the value of individual habitats in the context of the entire life cycle (Beck et al., 2001), and to examine the processes regulating habitat value and functioning (Nagelkerken et al., 2013).

There are relatively few measures of white shrimp mortality in estuaries (Minello et al., 2003), largely due to the challenges in estimating mortality rates (Baker and Minello, 2010), and habitat-specific information on mortality is especially difficult to measure. The factors regulating juvenile shrimp growth, however, are better understood. White shrimp growth varies among habitat types

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(Shervette and Gelwick, 2008; Rozas and Minello, 2009), along salinity and temperature gradients (Zein-Eldin and Griffith, 1969; Rozas and Minello, 2011), and with landscape structure (Kneib, 2003; Webb and Kneib, 2004). Among marine organisms in general, growth and mortality rates are also intimately linked (Houde, 1997). While these relationships can be complex (Cowan et al., 1997), larger prey often experience lower rates of mortality, because they encounter fewer predators large enough to consume them (Peterson and Wroblewski, 1984; Minello et al., 1989; Sogard, 1997). Hence, faster growth allows individuals to pass through vulnerable early life stages more quickly, resulting in greater cohort survival (Yanez-Arancibia et al., 1994; Houde, 1997; Deegan et al., 2000; but see Anderson, 1988). Juvenile cohort survival, as a function of growth and mortality, may show substantial geographic and temporal variability (Rozas, 1995; Rountree and Able, 2007). For example, if direct access to the marsh surface provides any growth or survival advantage for white shrimp (Zimmerman et al., 2000), then significant temporal and geographic variability in marsh surface flooding and accessibility (Minello et al., 2012a) will translate into variable juvenile growth and survival (Kneib, 2003; Baker et al., 2013).

Traditional fishery management focuses on regulating inputs and outputs of the fishery, and mortality during early life history stages is often considered to be fixed. However, variations in nursery production may be a key driver of variable adult stock size (Barrett and Gillespie, 1973; Levin and Stunz, 2005). The generally poor spawner stock–recruitment relationship seen for white shrimp implies that processes regulating juvenile survival decouple parent stock size from subsequent recruitment of sub-adults back into the reproductive population (Belcher and Jennings, 2004; Nance, 2007). The importance of juvenile habitat has been recognized and incorporated in forecasting stock size for brown shrimp in Louisiana (Perret et al., 1993); however, the relative significance of survival in each life stage to overall population sustainability for white shrimp has not been evaluated.

The aim of this paper was to explore the potential effects of variable juvenile growth and survival on white shrimp stock size in order to advance the integration of processes regulating juvenile life stages into the fishery stock assessment, and to provide a better understanding of the functional role of coastal nurseries for fishery species. To address this aim we developed a population model that incorporates available information on vital rates (growth, mortality, fecundity) of each life stage, and allows us to model scenarios examining the potential impacts of variability in juvenile growth and mortality rates on the overall population growth rate. More specifically, we used the population model to examine the effects of known variability in juvenile growth rate on juvenile stage survival and population growth rate, based on the premise that faster growth allows juveniles to pass through vulnerable early life stages more quickly, hence enhancing survival rates. Further, we used estimates of the relative refuge value of marsh vegetation and interannual variations in marsh surface flooding to explore the impacts of variations in juvenile mortality driven by access to protective marsh vegetation. To place these model outputs in the context of fisheries management, we compared the projected effects of juvenile survival on population growth rate with those of variable adult mortality driven by natural fluctuations and by variations in fishing pressure.

2. Methods

2.1. Life table

We compiled existing data on vital rates (growth, mortality, fecundity) for white shrimp from published literature (Table 1). White shrimp complete their life cycle in 1 year, and based on the available data and understanding of habitat transitions during this year, we divided the life cycle into five stages; egg/larvae, early juveniles, late juveniles, bay sub-adult, and offshore adult (Fig. 1). The young shrimp occupying the shallow estuarine waters and the coastal marsh complex were divided into two stages, early juveniles (6–27 mm TL) and late juveniles (>27–70 mm), because previous work indicated that smaller juveniles suffer higher mortality than larger ones (Baker and Minello, 2010). Hereafter, we refer to early and late juveniles collectively as ‘juveniles’. The sub-adult bay stage was defined as shrimp from 70 to 100 mm migrating through bays from marshes to offshore habitats (Lindner and Anderson, 1956), while adults were larger shrimp (>100 mm TL) in offshore waters. Because the timing and size of individuals at migration are variable (Lindner and Anderson, 1956; Pullen and Trent, 1969), the boundaries of these life stages, although useful as a means for modeling, should be considered approximate. The graphical depiction of population size during the white shrimp migratory life cycle in Fig. 1 is based on the vital rates in Table 1.

2.2. Baseline population model

The annual population growth rate R_y between year y and $y+1$ is given as:

$$R_y = S_0 S_1 S_2 S_3 S_4 f_4 \quad (1)$$

where S_i is the survivorship of stage i over the duration of time spent in that stage and f_4 is the annual per-capita fecundity. Stage survivorship was derived from the vital rate estimates summarized in the life table by taking the exponential of the product of the daily instantaneous mortality rate (Z) and stage duration (in days). The survivorship gives the proportion of individuals surviving that life stage. Per-capita fecundity is the total number of eggs produced per female divided by 2, assuming the sex ratio of 1:1 (Lindner and Cook, 1970; Caddy, 1996).

For the baseline model, we refined the available estimates for juvenile shrimp by combining data from previously published studies. We combined data from the growth experiments of Rozas and Minello (2009, 2011) and Baker and Minello (2010) to estimate the mean growth rate for juvenile white shrimp. Growth rate estimates were needed to convert size-frequency distributions to age-frequency for the catch-curve analysis we used to refine available mortality estimates. The variability in juvenile growth among treatments in the growth experiments allowed us to explore the impact of variable juvenile growth on juvenile survivorship, which ultimately affects the population growth rate.

We refined juvenile mortality estimates by performing catch-curve analysis (Ricker, 1975) on the combined data sets from Rozas et al. (2007) and Baker and Minello (2010). The assumptions of catch-curve analysis are well known (Ricker, 1975), and interpretation of the models used here has been discussed at length (Baker and Minello, 2010). We combined the size frequencies by translating density estimates to numbers per hectare in the marsh complex based on the models of Rozas et al. (2007) and Minello et al. (2008). Although different sampling techniques were used to obtain the two data sets (drop sampling vs benthic sled), the two techniques give equivalent estimates of white shrimp density and size structure (Baker and Minello, 2011). We included only samples between July and September because this is the peak period of marsh occupation by all size-classes of juvenile white shrimp. This approach should minimize violations of the assumptions of catch-curve analysis caused by high abundances of new recruits and an absence of larger juvenile shrimp early in the season, and similarly, significant emigration of juveniles from the marsh following the cessation of new recruitment later in the season. The combined growth and catch-curve analysis together provided estimates of growth and