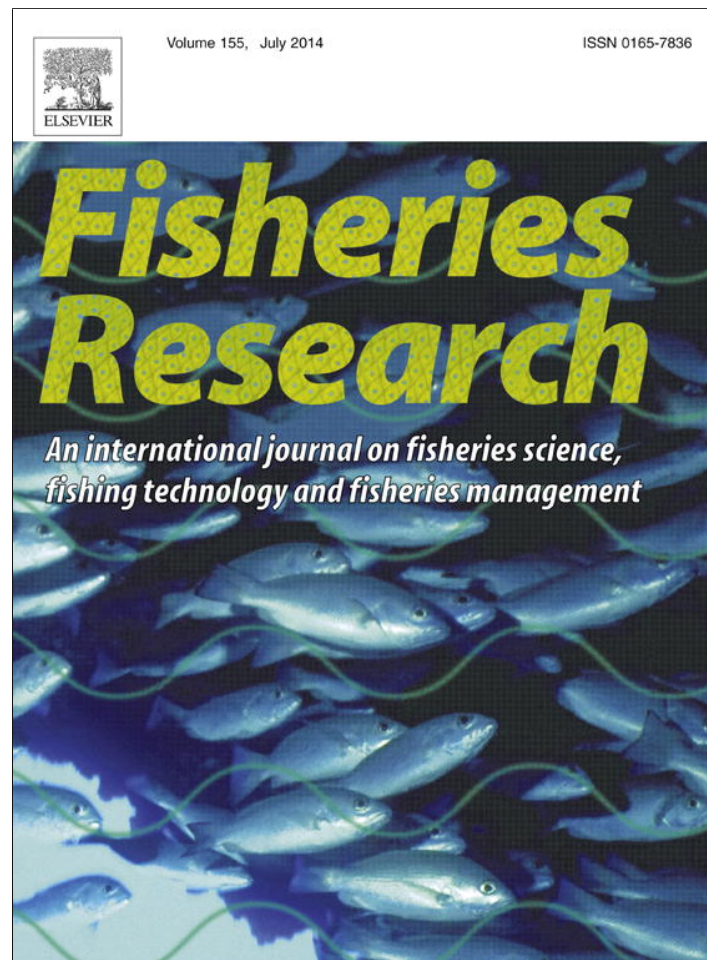


Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at ScienceDirect

Fisheries Research

journal homepage: [www.elsevier.com/locate/fishres](http://www.elsevier.com/locate/fishres)

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



Ronald Baker<sup>a,b,c,\*</sup>, Masami Fujiwara<sup>d</sup>, Thomas J. Minello<sup>a</sup>

<sup>a</sup> NOAA, National Marine Fisheries Service, SE Fisheries Science Center, Galveston Laboratory, 4700 Avenue U, Galveston, TX 77551, USA

<sup>b</sup> Centre for Tropical Water and Aquatic Ecosystems Research, School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia

<sup>c</sup> CSIRO Land and Water, Townsville Q 4811, Australia

<sup>d</sup> Texas A&M University, Department of Wildlife and Fisheries Sciences, College Station, TX 77843, USA

## ARTICLE INFO

### Article history:

Received 11 October 2013

Received in revised form 19 February 2014

Accepted 20 February 2014

Available online 21 March 2014

### Keywords:

Nursery

Salt marsh

Stock assessment

Life table

Sustainable fisheries

## 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.

© 2014 Elsevier B.V. All rights reserved.

## 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

\* Corresponding author at: Centre for Tropical Water and Aquatic Ecosystems Research, School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia. Tel.: +61 7 4753 8538.

E-mail address: [ronald.baker@jcu.edu.au](mailto:ronald.baker@jcu.edu.au) (R. Baker).

(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 inter-annual 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

**Table 1**  
Summary of white shrimp, *Litopenaeus setiferus* life stages and vital rates in the southeastern USA.

Stage	Habitat	TL (mm)	Duration (days)	Growth rate (mm/d)	Daily instantaneous mortality (Z)	Survivorship	Fecundity
Egg/larvae	Pelagic, offshore→marsh	<6	16 <sup>a,b</sup>	–	0.373 <sup>s</sup>	0.0026 ( $s_0$ )	0
Early juvenile	Salt marsh	6–27	26 <sup>c,d</sup>	0.6–1.2 (0.815) <sup>c,d</sup>	0.080–0.126 (0.0821) <sup>d,k</sup>	0.1183 ( $s_1$ )	0
Late juvenile	Salt marsh	>27–70	53 <sup>d</sup>	0.3–1.2 (0.815) <sup>d,e,f,g,h</sup>	0.014–0.091 (0.0312) <sup>a,d,g,k</sup>	0.1914 ( $s_2$ )	0
Subadult	Coastal bays	>70–100	33 <sup>b</sup>	0.4–1.5 (0.91) <sup>l,j</sup>	0.023–0.048 (0.0275) <sup>i</sup>	0.4035 ( $s_3$ )	0
Adult	Offshore	>100	237 <sup>r</sup>	0.4–1.0 <sup>l,q</sup>	0.004–0.034 (0.0104) <sup>l,m,n,o</sup>	0.0850 ( $s_4$ )	500,000 ( $f_4$ ) <sup>p</sup>
						$R_y$ :	1

Stage and size (total length) divisions are justified in the text. The growth rate and daily instantaneous mortality values shown in parenthesis, and the corresponding stage durations shown, are the values used to calculate survivorship for the baseline population model. The baseline model parameters are survivorship ( $s_i$ ) and fecundity ( $f_i$ ). Baseline annual population growth rate ( $R_y$ ) was derived from the population time series in Fig. 2.

- <sup>a</sup> Dall et al. (1990).
- <sup>b</sup> Lindner and Cook (1970).
- <sup>c</sup> Zein-Eldin and Griffith (1969).
- <sup>d</sup> Baker and Minello (2010).
- <sup>e</sup> Rozas and Minello (2009).
- <sup>f</sup> Rozas and Minello (2011).
- <sup>g</sup> Knudsen et al. (1996).
- <sup>h</sup> Webb and Kneib (2004).
- <sup>i</sup> Klima (1974).
- <sup>j</sup> Baxter and Holloway (1981).
- <sup>k</sup> Minello et al. (2008).
- <sup>l</sup> Hart (2012).
- <sup>m</sup> Nichols (1984).
- <sup>n</sup> Rothschild and Brunenmeister (1984).
- <sup>o</sup> Pauly et al. (1984).
- <sup>p</sup> Lindner and Anderson (1956).
- <sup>q</sup> Klima (1964).
- <sup>r</sup> Adult stage duration = remainder of 365 days.
- <sup>s</sup> Estimated from baseline population model as explained in Section 2.

mortality rates for juvenile shrimp based on larger sample sizes than the previously published values. For both early and late juvenile stages, the daily Z values used in the baseline model were derived from the catch–curve analysis of the pooled data sets, and are close to the lower range in available estimates (Table 1). This corresponds well to the distribution of available estimates, with most close to the minimum value and a few higher estimates (Baker and Minello, 2010).

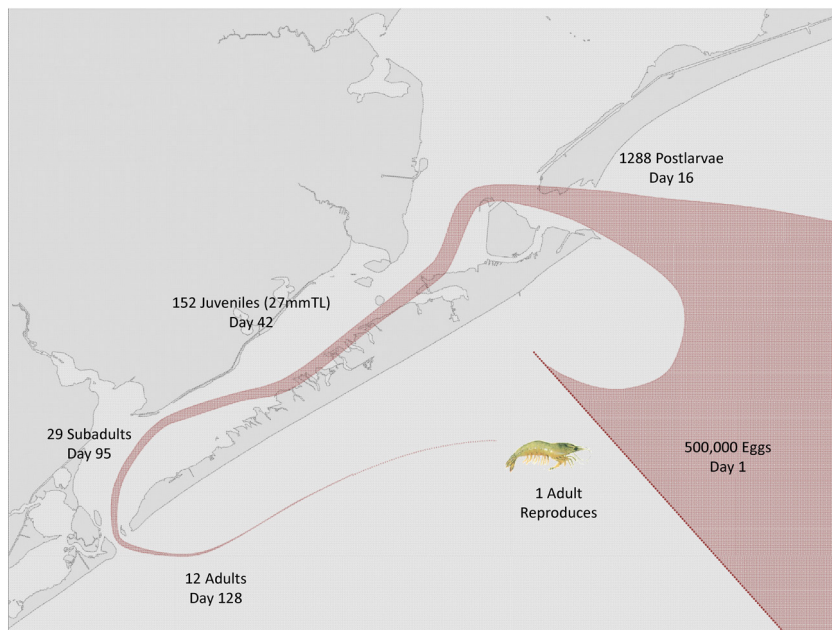
We estimated the survivorship of eggs and larvae from the estimates of all other vital rates and observed mean annual population

growth rate ( $R_y$ ), because no estimates are available for wild shrimp populations. By rearranging equation (1), the estimate of egg/larval survival ( $S_0$ ):

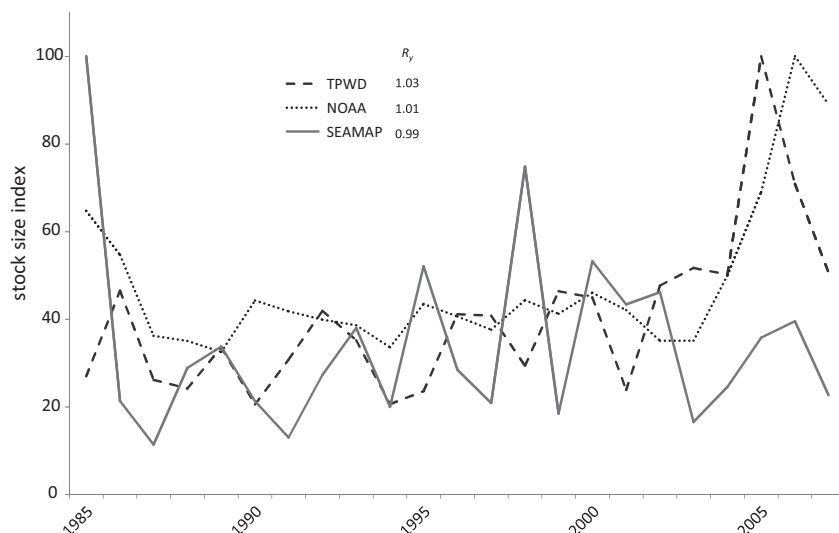
$$S_0 = \frac{\bar{R}_y}{\bar{S}_1 \bar{S}_2 \bar{S}_3 \bar{S}_4 \bar{f}_4} \quad (2)$$

where  $\bar{S}_i$  and  $\bar{f}_4$  are the estimated mean values.

We used three time series of indices of white shrimp stock size in the northern Gulf of Mexico (GoM) (Fig. 2) to estimate the



**Fig. 1.** Graphical depiction of the white shrimp life cycle in the northern Gulf of Mexico based on the vital rates in Table 1. The width of the line showing the migratory path corresponds to the population size indicated at each stage transition.



**Fig. 2.** Trends in white shrimp *Litopenaeus setiferus* stock size in the northern Gulf of Mexico between 1985 and 2007, based on three data sources; TPWD: Texas Parks and Wildlife Department gulf trawl surveys (described by Martinez-Andrade et al., 2005), NOAA stock assessments (Hart, 2012), and SEAMAP gulf trawl surveys (Nichols, 2004).  $R_y$  values in the legend are calculated mean population growth rates for each time series. These indicate that despite large interannual variations in stock size, the population was approximately stable during the period 1985–2007 (mean  $R_y = 1$ ).

mean annual population growth rate. The time series were derived from NOAA stock assessments (Hart, 2012), SEAMAP fishery-independent stock surveys (Nichols, 2004), and the Texas Parks and Wildlife Department (TPWD) gulf trawl surveys (Martinez-Andrade et al., 2005), which overlapped for the period from 1985 to 2007. For each time series an instantaneous population growth rate was estimated by taking the mean of  $\ln(n_{y+1}/n_y)$  where  $n_y$  is the index of abundance in year  $y$ . The exponential of the mean provides  $R_y$ , such that  $R_y = 1$  indicates a constant population size, while  $R_y > 1$  indicates an increasing population and  $R_y < 1$  a declining population. The three time series provided  $R_y$  estimates ranging from 0.99 (SEAMAP) to 1.03 (TPWD), with a mean close to 1. Hence,  $R_y = 1$  was used in the baseline population model, indicating a stable population over the period from 1985 to 2007, albeit with some large inter-annual fluctuations (Fig. 2).

### 2.3. Model scenarios

#### 2.3.1. Variable juvenile growth rate

Based on the premise that individuals make the transition from one stage to the next at a particular size, faster growth allows shrimp to grow through vulnerable early life stages more quickly, thereby increasing stage survivorship. Accordingly, we explored the relationship between juvenile shrimp growth rate and  $R_y$ . Variability in juvenile growth rates was derived from the field caging experiments of Rozas and Minello (2009, 2011) and Baker and Minello (2010). Variability among treatments in these experiments provides an estimate of the variability in mean juvenile growth associated with different environmental conditions, such as salinity, season, and habitat. For this scenario, we assumed constant and fixed juvenile mortality. We also assumed a constant growth rate in relation to juvenile size, because the growth experiments showed no consistent pattern of change in growth with size among juvenile shrimp. As such, varying the growth rate affected only a change in stage duration, thereby altering stage survival in the model. For this analysis, adult stage duration was allowed to vary such that the total lifespan remained 365 days, while all other parameters were held constant.

#### 2.3.2. Access to protective vegetated marsh habitat

We partitioned the combined early and late juvenile mortality rates into habitat-specific rates so that we could model the potential effects of variability in access to protective marsh vegetation on juvenile survival and the overall population growth rate. The combined mortality rate  $Z_{juv}$ , was derived as:

$$Z_{juv} = \ln \left( \frac{s_1 \times s_2}{d_1 + d_2} \right) \tag{3}$$

where  $s_i$  is the stage survivorship and  $d_i$  stage duration from Table 1; thus  $Z_{juv} = 0.048$ .

Our mortality estimates were derived from studies in Galveston Bay, TX, USA where 58.7% of the white shrimp population within the marsh complex is in the vegetation when it is flooded (Minello et al., 2008) and the marsh is flooded approximately 80% of the time (Minello and Webb, 1997; Minello et al., 2012a). This corresponds to 46.9% of juvenile mortality being experienced in marsh vegetation and 53.1% in open water. Mortality of juvenile brown shrimp in Galveston Bay has been attributed mainly to predation, and based on laboratory and field experiments, shrimp within protective marsh vegetation suffer about half the mortality rate as in adjacent open water (Minello et al., 1989; Zimmerman et al., 2000; Roth et al., 2008). Experimental data of this type on juvenile white shrimp is limited, but this species exhibits a similar distribution pattern as brown shrimp in relation to the marsh edge (Minello et al., 2008), and we assumed a similar refuge value of marsh vegetation for white shrimp, such that:

$$Z_o = 2Z_m \tag{4}$$

where  $Z_o$  is juvenile instantaneous mortality rate in open water and  $Z_m$  is the mortality rate in marsh vegetation. Therefore:

$$0.469 \times Z_m + 0.531 \times Z_o = Z_{juv} \tag{5}$$

By substituting equations (3) and (4) into equation (5), we derive habitat-specific mortality rates such that mortality in marsh vegetation ( $Z_m = 0.031$ ) is half that in open water ( $Z_o = 0.063$ ). Using information on variability in marsh flooding within Galveston Bay (Minello et al., 2012a), we could then calculate mortality rates for the juvenile stages under different durations of marsh flooding. The baseline values used in this analysis were specific to Galveston Bay. However, salt marshes across the northern GoM show

substantial inter-annual variability in flooding patterns (Minello et al., 2012a), so while the details of the model outputs are specific to the Galveston Bay baseline conditions (marsh configuration, shrimp distribution, and flooding durations), the shape and magnitude of the response of population growth rate to variability in marsh flooding should be broadly relevant.

### 2.3.3. Variable adult mortality

We compared the effects of variability in juvenile growth and survival on population growth rate with the effects of variability in adult mortality. For this comparison, we used estimates of variation in adult natural ( $M$ ) and fishing ( $F$ ) mortality rates from NOAA white shrimp stock assessments (Nichols, 1984; Hart, 2012).

### 2.3.4. Comparison among life stages

We investigated how sensitive  $R_y$  is to proportional changes in vital rates by varying each stage daily  $Z$  or adult fecundity by 10% while holding all other rates constant. In the absence of detailed data on variability in each vital rate for each life stage, this approach provides a simple way to examine the relative significance of variability in vital rates. To further clarify the relative effects of vital rates in different life stages on  $R_y$ , we also directly compared model scenarios. This analysis focused on marsh juveniles and offshore adults because these are the life stages that suffer perhaps the most direct threats (habitat loss, fishing) and are most amenable to management actions. We used combinations of adult natural ( $M$ ) and fishing mortality ( $F$ ) to calculate the range in  $R_y$  resulting from changes in adult survival, and then calculated the corresponding ranges in juvenile growth rates and durations of marsh flooding required to produce equivalent population growth rates.

## 3. Results

### 3.1. Effect of variable juvenile growth rate

Juvenile white shrimp growth rates were measured from 487 individual shrimp between 24 and 74 mm TL (mean  $\pm 1SE = 47.1 \pm 0.87$ ) during three caging experiments. The overall mean ( $\pm 1SE$ ) growth rate was  $0.815 \pm 0.02 \text{ mm d}^{-1}$ , with individual growth ranging from 0 to  $2.4 \text{ mm d}^{-1}$ . Baker and Minello (2010) reported that mean growth varied from 0.77 to  $0.91 \text{ mm d}^{-1}$  between summer and autumn, respectively, Rozas and Minello (2009) found mean growth rates ranged from 0.4 to  $1.2 \text{ mm d}^{-1}$  among marsh habitats, and Rozas and Minello (2011) measured mean growth rates from 0.4 to  $1.1 \text{ mm d}^{-1}$  along a salinity gradient from intermediate to saline marsh sites. With all other vital rates held constant, the mean annual population growth rate shows a sigmoidal response to variations in juvenile growth (Fig. 3a). The seasonal differences in mean juvenile growth reported by Baker and Minello (2010) translate into  $R_y$  values ranging from 0.84 to 1.36. Similarly, the variation in mean growth along the salinity gradient and among marsh habitats corresponds to  $R_y$  from 0.05 to 2.14 and 2.57, respectively. A mean juvenile growth rate of  $0.25 \text{ mm d}^{-1}$  would lead  $R_y$  close to 0, because so few individuals would survive the juvenile stages that almost none would survive to reproduce. Similarly, if the entire juvenile cohort grew at the maximum rate recorded for any individual in our growth experiments ( $2.4 \text{ mm d}^{-1}$ ), the modeled population increased almost 7-fold in a year ( $R_y = 6.99$ ) (Fig. 3a).

### 3.2. Variations in marsh access

The population growth rate shows an exponential increase with increasing duration of marsh flooding (Fig. 3b). If the marsh vegetation was not accessible at all, and all juvenile shrimp experienced

the open-water mortality rate for the entire duration of the juvenile phase, the model projects an  $R_y$  value of 0.31, or an almost 70% reduction in the shrimp population from one year to the next. For the scenario of a constantly flooded marsh, the model projects  $R_y$  of 1.34. The more modest effect of a constantly flooded marsh compared to no flooding reflects the baseline model conditions where the marsh is flooded for 80% of the time and 59% of shrimp occupy it when flooded. Minello et al. (2012a) estimated that annual marsh edge flooding durations in Galveston Bay ranged from 78% to 86% over the three years from 2006 to 2008. The model projects that the effects on juvenile survival of this range in flooding duration translates to a range in  $R_y$  from 0.97 to 1.09. At marshes throughout the southeast USA, mean annual flooding durations range from 54% in central Louisiana to 91.5% in central Texas (Minello et al., 2012a), which corresponds to  $R_y$  from 0.69 to 1.18.

### 3.3. Effects of natural and fishing adult mortality

Increasing adult daily instantaneous mortality rate produces an exponential decline in  $R_y$  in the population model (Fig. 3c). Removing all fishing mortality ( $F$ ), leaving just the mean natural mortality rate ( $M$ ) from Nichols (1984) as used in NOAA stock assessments ( $M = 0.009$ ) results in an  $R_y$  of 1.39, or a projected population increase of about 40% per year (Table 2). The  $M$  estimates from Nichols (1984) range from 0.004 to 0.014, which correspond to  $R_y$  of 4.56 to 0.43. Fishing mortality ( $F$ ) for the period 1985 to 2007 ranged from about 0.25 to 0.75 per year (Hart, 2012), or daily  $F$  of 0.0007 to 0.0021. Adding this range in  $F$  to mean  $M$  results in  $R_y$  ranging from 1.18 to 0.85 (Table 2).

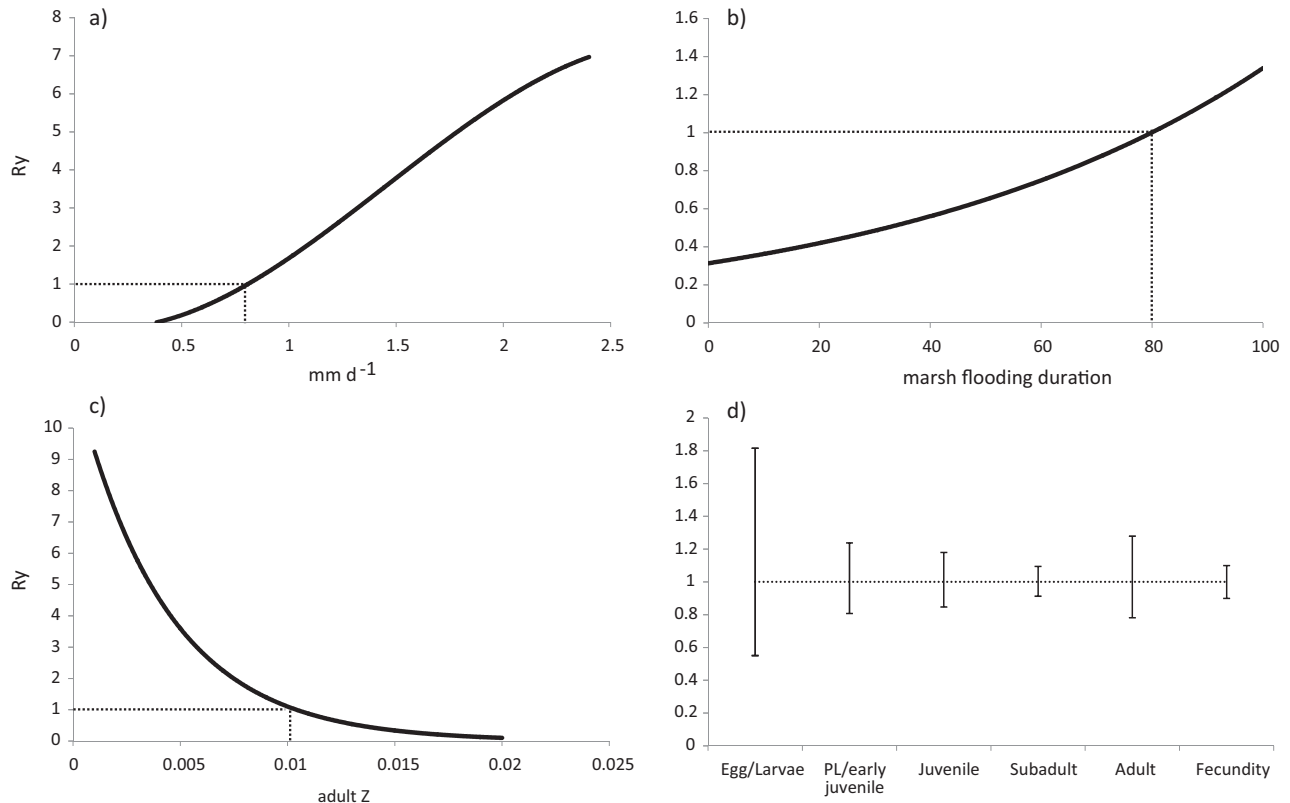
### 3.4. Comparison among life stages

$R_y$  was most sensitive to changes in egg/larval mortality rates, with a 10% increase or decrease in egg/larval daily  $Z$  producing  $R_y$  ranging from 0.55 to 1.82 (Fig. 3d).  $R_y$  was least sensitive to changes in sub-adult daily  $Z$  and adult fecundity, while early juvenile, late juvenile, and adult daily  $Z$  changes had intermediate effects on  $R_y$ . In comparing model scenarios, the effect on  $R_y$  of the full range in fishing mortality over the years 1985–2007 (i.e. mean  $M + \text{min or max } F$ ) is equivalent to the modeled effects of only modest ranges in either juvenile growth or duration of marsh flooding (Table 2). For example, a scenario where adults experience mean  $M$  and minimum  $F$  ( $Z = 0.0097$ ) produces  $R_y$  of 1.18, while the scenario of mean  $M$  plus maximum  $F$  results in an  $R_y$  of 0.85. The corresponding range in juvenile growth rates required to produce the same range in  $R_y$  is 0.77 to  $0.86 \text{ mm d}^{-1}$ . Hence, our model projects that the full range in fishing mortality rates reported by Hart (2012) for the years 1985 to 2007 could have a smaller effect on the overall population growth rate than would the seasonal range in juvenile growth rates reported by Baker and Minello (2010) ( $0.77\text{--}0.91 \text{ mm d}^{-1} = R_y$  of 0.85–1.36). Similarly, the effect of this range in fishing mortality is equivalent to the effect of access to protective marsh vegetation for juvenile shrimp ranging from 68 to 91% of the time (Table 2). Our model results indicate that variations in marsh flooding duration are unable to produce the same  $R_y$  values as the more extreme fishing or juvenile growth scenarios, where the duration of marsh flooding required is  $>100$  or  $<0\%$ .

## 4. Discussion

### 4.1. Population model outputs

Our population model indicates that the white shrimp population in the northern GoM is most sensitive to the survival rates of early life stages, in particular the egg/larval stage. This is typical for many marine organisms (Sogard, 1997, Levin and



**Fig. 3.** White shrimp *Litopenaeus setiferus* population model outputs projecting the relationship between mean annual population growth rate ( $R_y$ ) and; (a) juvenile growth rate (includes both early and late juveniles as defined in Table 1); (b) duration of flooding of the vegetated marsh surface assumed to provide refuge for juvenile shrimp; (c) adult mortality rates resulting from variable combinations of natural and fishing mortality; and (d)  $\pm 10\%$  variations in each life stage daily instantaneous mortality rate ( $Z$ ) or adult fecundity. Dotted lines indicate baseline model conditions;  $R_y = 1$ , juvenile growth rate =  $0.815 \text{ mm d}^{-1}$ , marsh flooding duration = 80%, and adult  $Z = 0.0104$ .

Stunz, 2005), especially among short-lived species like shrimp (e.g. Ramirez-Rodriguez and Arreguin-Sanchez, 2003). However, estimating vital rates for larval stages is challenging (Caddy, 1996; Ramirez-Rodriguez and Arreguin-Sanchez, 2003), and there are few options for any meaningful management efforts targeting this developmental stage (Gallaway, 2005). Traditional fishery management focuses on managing direct impacts on the fished stocks (Nance, 2007), while our model results indicate that the processes regulating juvenile survival in marsh habitats may be equally or more significant in regulating stock size and population sustainability. Together the marsh juvenile and offshore adult stages face perhaps the greatest direct threats, from habitat loss and fishing, and are most amenable to management actions aimed at sustaining the population into the future (Hart, 2012, Minello et al., 2012b).

The variation in annual population growth rate ( $R_y$ ) projected from the full range in fishing mortality over the past few decades (Hart, 2012) is less than that projected from the seasonal differences in juvenile growth rates recorded by Baker and Minello (2010).

This implies that if the mean growth rate of the entire juvenile cohort showed inter-annual variations equivalent to those measured among seasons within a year, then variable juvenile growth alone could be more influential on stock size than fishing pressure. Although the projected effects of variations in marsh flooding are more modest than those of juvenile growth rate, in reality, variable marsh flooding would affect growth rate as well as mortality because of differences in growth among habitats (Webb and Kneib, 2004; Shervette and Gelwick, 2008; Rozas and Minello, 2009). The model scenarios are necessary simplifications of population dynamics (Vetter, 1988); however, the outputs serve to highlight the relative significance of processes regulating survival in early life stages (Meyers and Cardigan, 1993; Levin and Stunz, 2005).

In order to interpret the drivers of variation in the overall annual population growth rate, it is important to consider how realistically the modeled variability reflects real temporal variation in the vital rates experienced by entire life stages among years. In our annual stage-based population model, each parameter represents

**Table 2**

Comparing the relative effects of adult mortality rates with equivalent range in juvenile growth and access to protective marsh vegetation on white shrimp population growth rate  $R_y$ .

Fishing scenarios	Adult daily Z	$R_y$	Corresponds to	
			Juvenile $\text{mm d}^{-1}$	% Marsh flooded
Min M	0.0004	4.56	1.68	184
Mean M	0.0090	1.39	0.92	103
Mean M + min F	0.0097	1.18	0.86	91
Mean M + mean F (baseline)	0.0104	1	0.815	80
Mean M + max F	0.0111	0.85	0.77	68
Max M + max F	0.0161	0.26	0.56	-12

Adult daily Z represents the combination of natural (M) and fishing (F) mortality scenarios indicated in the first column.

the mean value for an entire annual cohort passing through each life stage. However, the estimates of variation in vital rates were not all derived from comparisons of mean rates among years at the population level. For instance, while the estimates of annual adult natural and fishing mortality were derived at the stock-level, i.e. the adult population of the entire northern GoM (Nichols, 1984; Hart, 2012), the juvenile growth and mortality values were derived from site-, season-, or habitat-specific studies (e.g. Webb and Kneib, 2004; Shervette and Gelwick, 2008; Baker and Minello, 2010). If the mean growth rate of entire juvenile cohorts shows similar variation among years as the modest variations in juvenile growth rates measured among habitats and seasons, then variations in juvenile growth could match the modeled impact of variations in adult fishing mortality on population size. The physical drivers of variation in juvenile growth and mortality, such as salinity and temperature (Zein-Eldin and Griffith, 1969; Rozas et al., 1999) coupled with biological interactions including prey availability, competition, and predation (Beseres and Feller, 2007), quite likely show such variation at the scale of the entire juvenile cohort, driven by large-scale processes such as inter-annual variations in rainfall and climatic conditions (Rozas, 1995). Hence, despite the estimates of variation in vital rates being derived from studies at various spatial and temporal scales, we believe the model outputs are reflective of realistic variations in vital rates at the population level.

Density-dependent processes could modify the projected effects of variable vital rates (Rose et al., 2001), and this could be particularly important for variability in early life stages since there is a greater time period until reproduction in which such processes can act (Diop et al., 2007). For example, years of particularly high survival of juvenile shrimp in the marsh may be dampened by increased predation pressure on sub-adults migrating through estuarine passes and recruiting to offshore populations (Baker and Sheaves, 2009). Given the limited data on variability in vital rates for white shrimp, we were not able to incorporate density-dependent effects into our population model. So although our findings indicate juvenile growth and mortality may have similar or greater effects on population size as fishing pressure on the adult stocks, density-dependent effects on the intervening life stages until reproduction may serve to dampen or modify this effect (Rose et al., 2001).

In our analyses, white shrimp population growth rate was most sensitive to egg/larval survival. Although survival of this stage had to be estimated from the model since no vital rates are available for wild white shrimp, high larval mortality is typical for marine species (McGurk, 1986; Caddy, 1996), and our estimated values are similar to those for other penaeid shrimp (Dall et al., 1990; Ramirez-Rodriguez and Arreguin-Sanchez, 2003). Unless actual egg/larval mortality rates were substantially different from those estimated in our model, then the relative sensitivity of  $R_y$  to egg/larval survival would be similar. Despite some uncertainty in the other vital rates in Table 1, most come from multiple sources that are in broad agreement. For example, the estimated growth rates of juvenile white shrimp are similar from caging studies employing various cage designs in the central and western GoM (Rozas and Minello, 2009, 2011; Baker and Minello, 2010; Rozas et al., 2014) and measurements from free-ranging tagged shrimp in the marshes of Georgia (Webb and Kneib, 2004). Our white shrimp mortality rates are also similar to those estimated for pink shrimp *Farfantepenaeus duorarum* by Ramirez-Rodriguez and Arreguin-Sanchez (2003) using the gnomonic approach of Caddy (1996) (Fig. 4). A variety of models have been developed relating natural mortality with individual biomass of fishes and invertebrates. We compared the mortality rates for shrimp with rate estimates from the models of Peterson and Wroblewski (1984) for marine organisms in general, Lorenzen (1996) and McGurk (1986, 1987) for fish, and McGurk (1987) for planktonic marine crustaceans. Our mortality rates are similar to those predicted by several of these models (Fig. 4). Hence our

mortality rate estimates seem reasonable, and the model outputs should be robust.

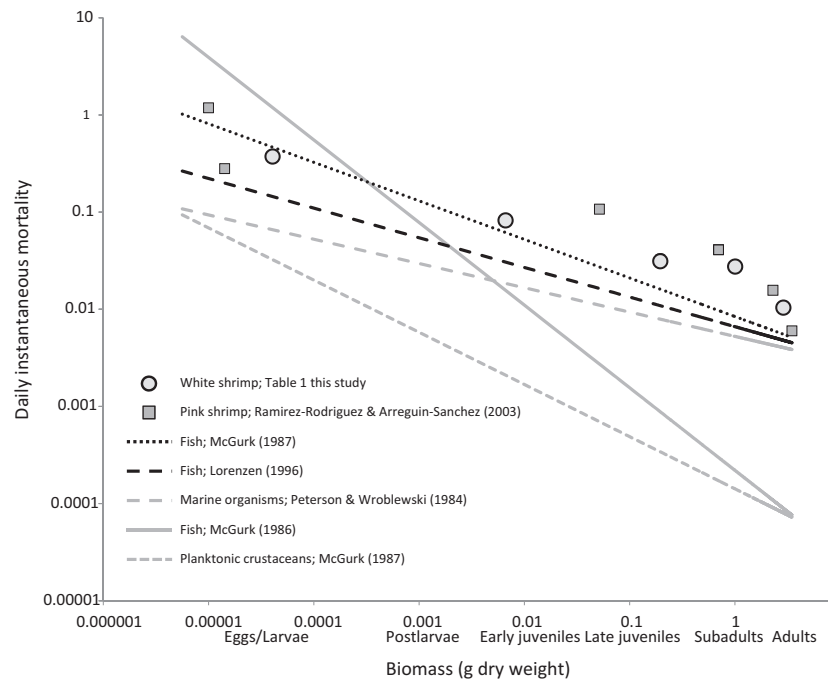
In our model we assumed that stage transition is a function of size and not age or season, i.e. that the movement of juvenile shrimp from marsh to bay, and bay to offshore habitats occurs at a particular size rather than age or time, and therefore that faster growth translates directly into shorter durations for that life stage. While most descriptions of the white shrimp life cycle imply that stage transitions are size-related (Lindner and Cook, 1970), there is evidence that specific events such as the passage of cold fronts or rapid changes in salinity may trigger migrations of shrimp from the estuarine nursery to deeper bay or offshore habitats (Pullen and Trent, 1969; Zein-Eldin and Renaud, 1986). Juvenile white shrimp occupy salt marshes along the Gulf and Atlantic coasts of the USA from early summer until early winter. The size of shrimp emigrating from coastal waters may decline with the onset of winter, and the coincidence of these migration events with the passage of cold fronts implies that shrimp spawned later in the season may migrate out of juvenile nursery habitats at smaller sizes due to unfavorable physical conditions within the nursery (Pullen and Trent, 1969). While a severe cold front may trigger the migration of all remaining shrimp out of the salt marsh at the onset of winter, these shrimp may represent only a small proportion of the juvenile shrimp population to have occupied the marsh during that year. So despite some uncertainty and variability in the timing, size, and age at transition from one life stage to the next, the overall finding that stock size is sensitive to changes in juvenile survival should be robust.

#### 4.2. Implications for fisheries management

The findings of the current study highlight the significance of processes regulating juvenile survival to population size and sustainability. However, there remain considerable challenges for integrating these processes into stock assessment and fishery management. To predict harvestable stock size, some state agencies use indices of the abundance of earlier life stages along with data on environmental variables such as salinity and temperature due to their effects on shrimp production, but these indices are primarily derived from late-stage sub-adults and the physical environment from which they are sampled (Belcher and Jennings, 2004). Our modeling results suggest that although such approaches may provide reasonable predictions of stock size, they fail to account for the processes regulating the critical early juvenile survival. Although the complexity of processes regulating juvenile survival makes their incorporation into stock assessment challenging (Diop et al., 2007), it may be possible where the areas of juvenile habitat most important for supporting adult stocks can be defined. For example, brown shrimp catches in Louisiana correlate with the amount of flooded marsh habitat above 10 ppt salinity (Perret et al., 1993). Much fishing effort in Louisiana is focused on sub-adults within coastal waters (Perret et al., 1993), and the link between juvenile habitat and subsequent stock size suggests an important role of flooded saline marshes for juvenile brown shrimp survival.

Our model suggests that indices of suitable juvenile habitat availability may aid in predicting white shrimp population size. Such indices would need to be developed at the stock scale (e.g., entire northern GoM), and this presents its own set of challenges. Habitat availability, in terms of access to flooded marsh and suitable salinity and temperature conditions (Perret et al., 1993), shows high geographic and temporal variability in the southeast USA (Rozas, 1995; Minello et al., 2012a). Models of habitat availability therefore need to incorporate the substantial spatial variation in processes regulating juvenile shrimp growth and survival (Baker et al., 2013). Landscape structure is also important in regulating juvenile shrimp populations and production, with the amount of marsh edge habitat being more important than the total area of marsh





**Fig. 4.** A comparison of white shrimp mortality estimates from Table 1 with rates published for pink shrimp *Farfantepenaeus duorarum* by Ramirez-Rodriguez and Arreguin-Sanchez (2003) and various modeled rates for marine organisms. Biomass of individual shrimp at different life stages indicated on the x-axis are approximate.

(Browder et al., 1989; Minello and Rozas, 2002). As such, metrics of available habitat that integrate landscape structure with the area of flooded marsh under suitable physical conditions may prove particularly useful in refining stock assessments for white shrimp in the northern GoM (Nance, 2007; Hart, 2012).

## 5. Conclusions

Our model results support the conclusion that variability in juvenile survival is potentially more important in regulating white shrimp population size than the full spectrum of fishing pressure. Despite the long-held beliefs about the roles of salt marsh habitats in regulating the growth and mortality of a great diversity of nekton species (Boesch and Turner, 1984; Zimmerman et al., 2000; Deegan et al., 2000), direct empirical evidence of the processes and mechanisms that underpin the functional value of these habitats remains elusive (Minello et al., 2003; Rountree and Able, 2007; Baker et al., 2013). Directly measuring growth and mortality rates of mobile aquatic organisms in intertidal and complex habitats is challenging (Webb and Kneib, 2004; Shervette and Gelwick, 2008; Mace and Rozas, in review), but further work to clarify spatial and temporal variability in the functional roles of salt marsh and other coastal nursery habitats is essential if we are to maintain the nursery function of these systems into the future, and sustainably manage the fisheries that rely on these nurseries.

## Acknowledgments

This research was initiated while RB held a post-doctoral associateship from the National Research Council with NOAA Fisheries in Galveston, TX, USA and completed during a post-doctoral fellowship from the Tropical Landscapes Joint Venture between the Commonwealth Scientific and Industrial Research Organisation and James Cook University in Townsville, Queensland, MF was funded by Texas Sea Grant (Grant #02-S120031). We thank Phil Levin, Lawrence Rozas, and Rick Hart (NOAA) for discussions on modeling and information on white shrimp vital rates and stock

assessments. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service.

## References

- Anderson, J.T., 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J. Northw. Atl. Fish. Sci.* 8, 55–66.
- Baker, R., Minello, T.J., 2010. Growth and mortality of juvenile white shrimp *Litopenaeus setiferus* in a marsh pond. *Mar. Ecol. Prog. Ser.* 413, 95–104.
- Baker, R., Minello, T.J., 2011. Trade-offs between gear selectivity and logistics when sampling nekton from shallow open water habitats: a gear comparison study. *Gulf Carib. Res.* 23, 37–48.
- Baker, R., Sheaves, M., 2009. Refugees or ravenous predators: detecting predation on new recruits to tropical estuarine nurseries. *Wetl. Ecol. Manag.* 17, 317–330.
- Baker, R., Fry, B., Rozas, L.P., Minello, T.J., 2013. Hydrodynamic regulation of salt marsh contributions to aquatic food webs. *Mar. Ecol. Prog. Ser.* 490, 37–52.
- Barrett, B.B., Gillespie, M.C., 1973. Primary Factors which Influence Commercial Shrimp Production in Coastal Louisiana. Louisiana Wildlife and Fisheries Commission, New Orleans.
- Baxter, K.N., Holloway, S.L., 1981. A summary of results of Louisiana white shrimp tagging experiments, 1977. NOAA Tech Memo NMFS-SEFC-72.
- Beck, M., Heck, K., Able, K., Childers, D., Eggleston, D., Gillanders, B., Halpern, B., Hays, C., Hoshino, K., Minello, T., Orth, R., Sheridan, P., Weinstein, M., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51, 633–641.
- Belcher, C.N., Jennings, C.A., 2004. Evaluation of stock–recruitment curves for white shrimp in Georgia. *N. Am. N. Am. J. Fish. Manag.* 24, 654–661.
- Beseres, J.J., Feller, R.J., 2007. Importance of predation by white shrimp *Litopenaeus setiferus* on estuarine subtidal macrobenthos. *J. Exp. Mar. Biol. Ecol.* 344, 193–205.
- Boesch, D., Turner, R.E., 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7, 460–468.
- Browder, J.A., May, L.N., Rosenthal, A., Gosselink, J.G., Bauman, R.H., 1989. Modeling future trends in wetland loss and brown shrimp production in Louisiana using thematic mapper imagery. *Remote Sens. Environ.* 28, 45–59.
- Caddy, J.F., 1996. Modeling natural mortality with age in short-lived invertebrate populations: definition of a strategy of gnomonic time division. *Aquat. Living Resour.* 9, 197–207.
- Cowan, J., Rose, K., Houde, E., 1997. Size-based foraging success and vulnerability to predation: selection of survivors in individual-based models of larval fish populations. In: Chambers, R.C., Trippel, E. (Eds.), *Early Life History and Recruitment in Fish Populations*. Springer, Netherlands, pp. 357–386.
- Dall, W., Hill, B.J., Rothlisberg, P.C., Staples, D.J., 1990. *The Biology of the Penaeidae*. Academic Press, London.
- Deegan, L.A., Hughes, J.E., Rountree, R.A., 2000. Salt marsh ecosystem support of marine transient species. In: Weinstein, M.P., Kreeger, D.A. (Eds.), *Concepts and*

- Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht, pp. 333–365.
- Diop, H., Keithly, W.R., Kazmierczak, R.F., Shaw, R.F., 2007. Predicting the abundance of white shrimp (*Litopenaeus setiferus*) from environmental parameters and previous life stages. *Fish. Res.* 86, 31–41.
- Galloway, B.J., 2005. Proposed revisions for the early life history parameters being used for red drum *Sciaenops ocellatus*, red snapper *Lutjanus campechanus* and penaeid shrimp in seawater-use assessments. Final Report for Pearl Crossing LNG Terminal LLC Project, LGL Ecological Research Associates.
- Hart, R., 2012. Stock assessment of white shrimp (*Litopenaeus setiferus*) in the U.S. Gulf of Mexico for 2011. NOAA Technical Memorandum NMFS-SEFSC-637, 36 p.
- Houde, E.D., 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. *J. Fish Biol.* 51 (A), 52–83.
- Klima, E.F., 1964. Mark-recapture experiments with brown and white shrimp in the northern Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute, 16th Ann Session, pp. 52–64.
- Klima, E.F., 1974. A white shrimp mark-recapture study. *Trans. Am. Fish. Soc.* 103, 107–113.
- Kneib, R.T., 1997. The role of tidal marshes in the ecology of estuarine nekton. *Oceanog. Mar. Biol. Ann. Rev.* 35, 163–220.
- Kneib, R.T., 2003. Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes. *Mar. Ecol. Prog. Ser.* 264, 279–296.
- Knudsen, E.E., Rogers, B.D., Paille, R.F., Herke, W.H., Geaghan, J.P., 1996. Juvenile white shrimp growth, mortality, and emigration in weired and unweired Louisiana marsh ponds. *N. Am. J. Fish. Manag.* 16, 640–652.
- Levin, P., Stunz, G., 2005. Habitat triage for exploited fishes: can we identify essential “Essential Fish Habitat?” *Estuar. Coast. Shelf Sci.* 64, 70–78.
- Lindner, M.J., Anderson, W.W., 1956. Growth, migrations, spawning and size distribution of shrimp *Penaeus setiferus*. *Fish. Bull.* 56, 555–645.
- Lindner, M.J., Cook, H.L., 1970. Synopsis of biological data on the white shrimp *Penaeus setiferus* (Linnaeus) 1767. FAO Fisheries Synopsis No. 101.
- Lorenzen, K., 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *J. Fish Biol.* 49, 627–647.
- Mace, M.M., Rozas, L.P., in review. Estimating natural mortality rates of juvenile white shrimp *Litopenaeus setiferus* using two different methods. *Estuaries and Coasts*.
- Martinez-Andrade, F., Campbell, P., Fuls, B., 2005. Trends in relative abundance and size of selected finfishes and shellfishes along the Texas coast: November 1975–December 2003. In: Management Data Series 232. Austin Texas, Texas Parks and Wildlife.
- McGurk, M.D., 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar. Ecol. Prog. Ser.* 34, 227–242.
- McGurk, M.D., 1987. Natural mortality and spatial patchiness: reply to Gulland. *Mar. Ecol. Prog. Ser.* 39, 201–206.
- Meyers, R.A., Cardigan, N.G., 1993. Density-dependent juvenile mortality in marine demersal fish. *Can. J. Fish. Aquat. Sci.* 50, 1576–1590.
- Minello, T.J., Rozas, L.P., 2002. Nekton in Gulf coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. *Ecol. App.* 12, 441–455.
- Minello, T.J., Webb, J.W., 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Mar. Ecol. Prog. Ser.* 151, 165–179.
- Minello, T.J., Zimmerman, R.J., Martinez, E.X., 1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. *Trans. Am. Fish. Soc.* 118, 693–708.
- Minello, T.J., Able, K.W., Weinstein, M.P., Hays, C., 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth, and survival through meta-analysis. *Mar. Ecol. Prog. Ser.* 246, 39–59.
- Minello, T.J., Matthews, G.A., Caldwell, P.A., Rozas, L.P., 2008. Population and production estimates for decapod crustaceans in wetlands of Galveston Bay, Texas. *Trans. Am. Fish. Soc.* 137, 129–146.
- Minello, T.J., Rozas, L.P., Baker, R., 2012a. Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. *Estuar. Coast.* 35, 501–514.
- Minello, T.J., Rozas, L.P., Caldwell, P.A., Liese, C., 2012b. A comparison of salt marsh construction costs with the value of exported shrimp production. *Wetlands* 32, 791–799.
- Nagelkerken, I., Sheaves, M., Baker, R., Connolly, R.M., 2013. The seascape nursery: incorporation of dynamic processes to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries*. DOI: 10.1111/faf.12057.
- Nance, J.M., 2007. Stock Assessment Report 2006 Gulf of Mexico Shrimp Fishery. NOAA NMFS, Galveston, Texas.
- Nichols, S., 1984. Updated assessments of brown, white and pink shrimp in the U.S. Gulf of Mexico. In: Stock Assessment Workshop, Miami, May 1984.
- Nichols, S., 2004. Derivation of Red Snapper Time Series from SEAMAP and Ground-fish Trawl Surveys. SEDAR-DW1.
- Pauly, D., Ingles, I., Neal, R., 1984. Application to shrimp stocks of objective methods for the estimation of growth, mortality, and recruitment-related parameters from length-frequency data (ELEFAN I and II). In: Gulland, J.A., Rothschild, B.J. (Eds.), *Penaeid Shrimps: Their Biology and Management*. Fishing News Books, Farnham, England, pp. 58–69.
- Perret, W.S., Bowman, P.E., Savoie, L.B., 1993. Louisiana’s brown shrimp monitoring and management program. *Proc. Ann. Conf. SE. Assoc. Fish. Wildl. Agencies* 47, 502–510.
- Peterson, I., Wroblewski, J.S., 1984. Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* 41, 1117–1120.
- Pullen, E.J., Trent, W.L., 1969. White shrimp emigration in relation to size, sex, temperature and salinity. *FAO Fish Rep.* 57, 1001–1014.
- Ramirez-Rodriguez, M., Arreguin-Sanchez, F., 2003. Life history stage duration and natural mortality for the pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) in the southern Gulf of Mexico, using the gnomonic model for time division. *Fish. Res.* 60, 45–51.
- Ricker, W., 1975. Computation and interpretation of biological statistics of fish populations, 191. Canadian Department of the Environment Fisheries and Marine Service Bulletin, Ottawa.
- Rosas, C., Ocampo, L., Gaxiola, G., Sanches, A., Soto, L.A., 1999. Effect of salinity on survival, growth and oxygen consumption of postlarvae (PL10-PL21) of *Litopenaeus setiferus*. *J. Crust. Biol.* 19, 244–251.
- Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2, 293–327.
- Roth, B.M., Rose, K.A., Rozas, L.P., Minello, T.P., 2008. Relative influence of habitat fragmentation and inundation on brown shrimp *Farfantepenaeus aztecus* production in northern Gulf of Mexico salt marshes. *Mar. Ecol. Prog. Ser.* 359, 185–202.
- Rothschild, B.J., Brunenmeister, S.L., 1984. The dynamics and management of shrimp in the northern Gulf of Mexico. In: Gulland, J.A., Rothschild, B.J. (Eds.), *Penaeid Shrimps: Their Biology and Management*. Fishing News Books, Farnham, England, pp. 145–172.
- Rountree, R.A., Able, K.W., 2007. Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. *Aquat. Ecol.* 41, 25–45.
- Rozas, L.P., 1995. Hydroperiod and its influence on nekton use of the saltmarsh: a pulsing ecosystem. *Estuaries* 18, 579–590.
- Rozas, L.P., Minello, T.J., 2009. Using nekton growth as a metric for assessing habitat restoration by marsh terracing. *Mar. Ecol. Prog. Ser.* 394, 179–193.
- Rozas, L.P., Minello, T.J., 2011. Variation in penaeid shrimp growth rates along and estuarine salinity gradient: implications for managing river diversions. *J. Exp. Mar. Biol. Ecol.* 397, 196–207.
- Rozas, L.P., Minello, T.J., Zimmerman, R.J., Caldwell, P., 2007. Nekton populations, long-term wetland loss, and the effect of recent habitat restoration in Galveston Bay, Texas, USA. *Mar. Ecol. Prog. Ser.* 344, 119–130.
- Rozas, L.P., Minello, T.J., Miles, M.S., 2014. Effect of Deepwater Horizon Oil on growth rates of juvenile penaeid shrimps. *Estuar. Coast.*, <http://dx.doi.org/10.1007/s12237-013-9766-1>.
- Sheaves, M., Baker, R., Johnston, R., 2006. Marine nurseries and effective juvenile habitats: an alternative view. *Mar. Ecol. Prog. Ser.* 318, 303–306.
- Shervette, V.R., Gelwick, F., 2008. Relative nursery function of oyster, vegetated marsh edge, and nonvegetated bottom habitats for juvenile white shrimp *Litopenaeus setiferus*. *Wetl. Ecol. Manag.* 16, 405–419.
- Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* 60, 1129–1157.
- Vetter, E.F., 1988. Estimation of natural mortality in fish stocks: a review. *Fish. Bull.* 86, 25–43.
- Webb, S., Kneib, R.T., 2004. Individual growth rates and movement of white shrimp (*Litopenaeus setiferus*) in a tidal marsh estuary. *Fish. Bull.* 102, 376–388.
- Yanez-Arancibia, A., Dominguez, A., Pauly, D., 1994. Coastal lagoons as fish habitats. In: B.K. (Ed.), *Coastal Lagoon Processes*. Elsevier, Amsterdam, pp. 363–376.
- Zein-Eldin, Z.P., Griffith, G.W., 1969. An appraisal of the effects of salinity and temperature on growth and survival of postlarval penaeids. *FAO Fishery Report* 57.
- Zein-Eldin, Z.P., Renaud, M.L., 1986. Inshore environmental effects on brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, populations of coastal waters, particularly of Texas. *Mar. Fish. Rev.* 48, 9–19.
- Zimmerman, R.J., Minello, T.J., Rozas, L.P., 2000. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. In: Weinstein, Kreeger (Eds.), *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer, Dordrecht, The Netherlands, pp. 293–314.