Abstract—Extensive plankton collections were taken during seven September cruises (1990–93) along the inner continental shelf of the northcentral Gulf of Mexico (GOM). Despite the high productivity and availability of food during these cruises, significant small-scale spatial variability was found in larval growth rates for both Atlantic bumper (*Chloroscombrus chrysurus,* Carangidae) and vermilion snapper (*Rhomboplites aurorubens*, Lutjanidae). The observed variability in larval growth rates was not correlated with changes in water temperature or associated with conspicuous hydrographic features and suggested the existence of less-recognizable regions where conditions for growth vary. Cruise estimates of mortality coefficients (Z) for larval Atlantic bumper (*n*=32,241 larvae from six cruises) and vermilion snapper (*n*= 2581 larvae from four cruises) ranged from 0.20 to 0.37 and 0.19 to 0.29, respectively. Even in a subtropical climate like the GOM, where larval-stage durations may be as short as two weeks, observed variability in growth rates, particularly when combined with small changes in mortality rates, can cause order-of-magnitude differences in cumulative larval survival. To what extent the observed differences in growth rates at small spatial scales are fine-scale "noise" that ultimately is smoothed by larger-scale processes is not known. Future research is needed to further characterize the small-scale variability in growth rates of larvae, particularly with regard to microzooplankton patchiness and the temporal and spatial pattern of potential predators. Small-scale spatial variability in larval growth rates may in fact be the norm, and understanding the implications of this subtle mosaic may help us to better evaluate our ability to partition the causes of recruitment variability.

Small-scale spatial and temporal variability in growth and mortality of fish larvae in the subtropical northcentral Gulf of Mexico: implications for assessing recruitment success

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For many marine fishes year-class strength undergoes large fluctuations because of the inherent variability in larval, postlarval, and juvenile survivorship (Hjort, 1914; Cushing, 1975; Lasker, 1975; Hunter, 1982; Houde, 1987; Goshorn and Epifanio, 1991; Pepin and Myers, 1991). Understanding and quantifying recruitment variability remains one of the greatest challenges in fisheries science today (Fritz et al., 1990; Cushing and Horwood, 1994; Leggett and Deblois, 1994; Mertz and Myers, 1995). Early survival rates are influenced not only by predation pressure but also by growth rate which can alter the duration of the larval stage when larvae are exposed to accumulative high mortality rates (Houde, 1987; Chambers and Leggett, 1987; Anderson, 1988; Bailey and Houde, 1989). Pepin (1991) formalized this concept by depicting the cumulative mortality (*C*) of a population from stage *a* to older stage *b* as the direct function of the instantaneous growth (*g*[*x*]) and mortality (*M*[*x*]) rates such that

$$C = \int_a^b \frac{M[x]}{g[x]} \, dx,$$

where *x* are factors that influence the vital rates (*M* and *g*) such as food availability, temperature, and abundance of potential predators.

Many questions remain concerning the causes of recruitment variability. Reasons for variability include the following: the inherent variability in growth and mortality rates and resulting survivorship; difficulties in estimating mortality rates with sufficient accuracy and precision; and the complex interrelationships among factors that affect survivorship of larvae (Parrish, 1973; Laurence, 1979; Houde, 1987; Beyer, 1989; Pepin, 1991). Houde (1989) hypothesized that cohort survivorship is more sensitive to small changes in vital rates in high latitude systems than in tropical or subtropical systems because the colder temperatures cause slower growth rates and longer larval stage durations, i.e. up to 100 days.
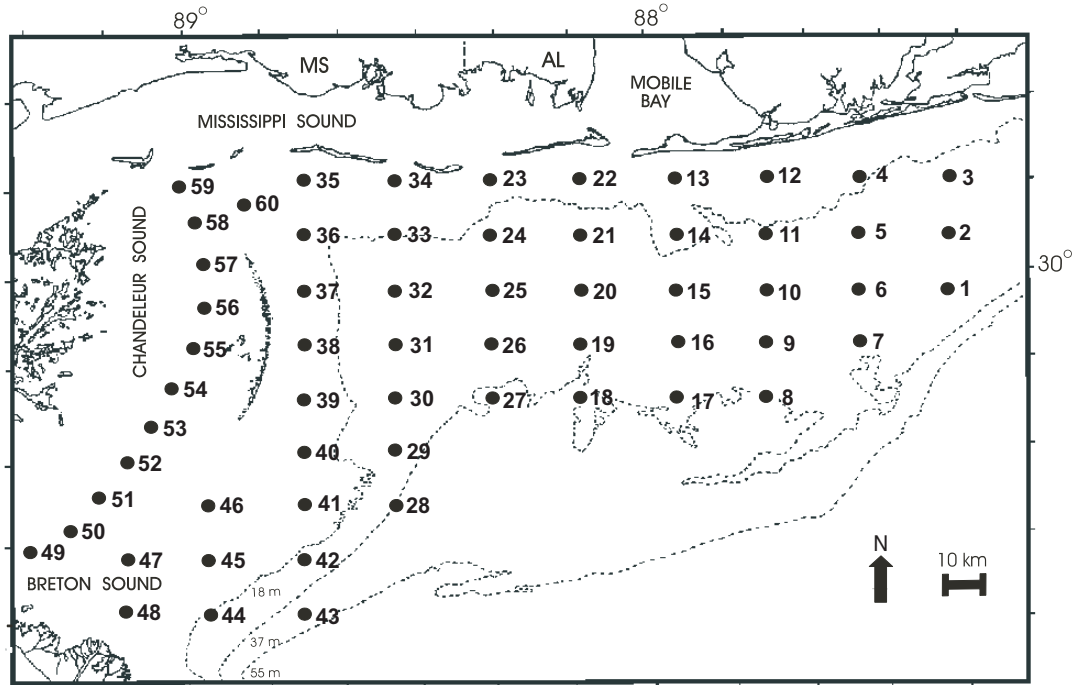
Figure 1

Station locations (•) of plankton collections in the northcentral Gulf of Mexico, September 1990 to 1993.

Pepin (1991) questioned this conclusion because he found no net effect of temperature on postlarval stage-specific mortality rates, although his study was based mainly on interspecific variation in mortality (Francis, 1994).

The objectives of our study were to determine if growth rates of Atlantic bumper (*Chloroscombrus chrysurus,* Carangidae) and vermilion snapper (*Rhomboplites aurorubens*, Lutjanidae) varied over small spatial scales in the northcentral Gulf of Mexico (GOM); determine the magnitude and variability of cruise estimates of larval mortality; and determine the potential influence of variability in these vital rates on cohort survivorship in a region where summer water temperatures approach 30°C and larval stage durations are as short as two to three weeks. Vermilion snapper is the most abundant species of snapper in the northern GOM (Goodyear and Schirripa[1]), and Atlantic bumper is the most abundant carangid.

Materials and methods

Sampling location and shipboard procedures

Seven, three-day cruises were conducted in inner-shelf waters of east Louisiana, Mississippi, and Alabama during

[1] Goodyear, C. P., and M. J. Schirripa. 1991. A biological profile for vermilion snapper with a description of the fishery in the Gulf of Mexico. Unpublished report CRD 87/88-16, 53 p. Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami FL 33149.

September 1990–93 (Fig. 1). Cruise estimates of larval mortality were determined by using data from all cruises during the four-year period. Specimens used for age and growth analyses were collected during 14–16 September 1991 when larvae of both vermilion snapper and Atlantic bumper were abundant.

Larvae were collected with a 1 m × 1.4 m Tucker trawl fitted with a 333-µm mesh nitex net and a mechanical flowmeter. Oblique tows were taken from the surface to within a few meters of the bottom and back to the surface at a speed of approximately two knots (1.0 m/s). Samples were concentrated and stored in 95% ethanol. At each sampling location surface, midwater and bottom measurements of temperature and salinity were obtained with water-bottle casts.

Laboratory procedures

Lengths of larvae were measured to the nearest 0.1 mm by using a stereomicroscope (12× or 25×) fitted with an ocular micrometer and the larvae were sorted into 0.5-mm size classes. Measurements were taken from the tip of the snout to the end of the notochord in preflexion larvae (notochord length), and from the tip of the snout to the end of the urostyle or hypural plate (whichever was more distal) in flexion or postflexion larvae (standard length). Larval shrinkage was not accounted for because between-station and between-cruise comparisons of growth rates were made with larvae that were preserved in the same concentration of ethanol and stored for approximately the same length of time. Shrinkage of ethanol-preserved

larvae is not large, e.g. 0 to 7% (Theilacker, 1980; Fowler and Smith, 1983; Kruse and Dalley, 1990). It is unlikely that size-related shrinkage effects would have biased our estimates of growth rate because these estimates were based on larvae in similar size classes. Additionally, Theilacker (1980) found that preserving northern anchovy larvae after they had died during net capture caused additional shrinkage, but this shrinkage was at a constant rate that was proportional to fish length. Catches of larvae were standardized to account for sampling effort and expressed as number of larvae under 10 m² of sea surface. This method of expressing the abundance of larvae more accurately reflects station differences in abundance than a mean density (number/m³) when fish larvae are not homogeneously distributed throughout the water column, as has been shown with other species from this area (Lyczkowski-Shultz and Steen, 1991), and when sampling (station) depths are variable, as they were in our study.

Dry weights of larvae were determined by rinsing specimens with distilled water, drying for 24 h at 60°C, and weighing to the nearest 0.1 µg. Both sagittal otoliths were removed following rehydration for 12 h. Otoliths were mounted convex side up on a glass microscope slide with a drop of Pro-Texx mounting medium and a cover slip. Otolith growth increments were counted in the sagittal plane under oil immersion (1250×).

A total of 140 Atlantic bumper larvae and 119 vermilion snapper larvae were selected for age analyses. Specimens were selected from stations where a wide size range of larvae were collected. Daily otolith increment formation has been validated for larval Atlantic bumper (Leffler and Shaw, 1992). Daily increment formation has not been validated for vermilion snapper; however, otolith increments observed in larval vermilion snapper were very similar in width and spacing to validated daily increments found in red snapper from this region (Szedlmayer, 1998; Lyczkowski-Shultz and Comyns[2]). Slopes of age-length regressions for larval vermilion snapper (n=11) and red snapper (n=25) collected during July 1992 in our study area were not significantly different, further indicating that vermilion snapper, like red snapper, form daily otolith growth increments.

Otolith growth increments were counted by using the sagitta (right or left) that provided the most distinct incremental zones. Paired t-test analyses showed no significant difference ($P \leq 0.05$) in diameters of left and right sagittae in both vermilion snapper (n=11) and Atlantic bumper (n=20). Daily increments were counted along the longest axis of the otolith from the core to the outer edge. Otoliths were read once by a single reader, and a random subsample of otoliths from vermilion snapper (n=30) and Atlantic bumper (n=30) was read a second time to examine within-

reader variability. Otolith increment counts differed by one day for only two of the 30 otoliths during the second reading for both species.

Data analysis

Age-length and age-weight relationships were described by using the exponential equation

$$L \text{ or } W = \exp(a + bt),$$

where, in its linearized form, L = notochord or standard length in mm;

W = dry weight in mg;
a = Y-intercept;
b = slope of regression line (instantaneous growth rate); and
t = age of larvae in days.

Values of a and b were calculated from the linearized form of the growth equation after the length or weight data were transformed to their natural logarithms. The instantaneous growth rate (b), i.e. the slope of the log-transformed, age-length or age-weight relationship, is also referred to as the growth coefficient. Caution must be exercised when making dry-weight comparisons because of preservation-induced weight loss. Kristoffersen and Salvanes (1998) found that body weight loss was as high as 37–39% in small ethanol-preserved mesopelagic fishes. Dry weight data were used only to determine whether relative changes in weight tracked trends found in age-length relationships. Analysis of covariance (ANCOVA) was used to determine if differences existed among station estimates of instantaneous growth coefficients (Sokal and Rohlf, 1969; SigmaStat, 1995). If differences were found (α=0.05), the simultaneous test procedure (STP; Sokal and Rohlf, 1969) was used as an *a posteriori* test to determine station differences.

Cruise estimates of total larval abundance for each size class (catch curves) were developed for Atlantic bumper and vermilion snapper by summing the abundance estimates of each size class under 10 m² of sea surface from each station. Length-frequency distributions were converted to age-frequency distributions by assigning ages to mid-points of the 0.5-mm size classes with the age-length relationship previously described. Age-class abundances were corrected for stage duration by dividing the abundance estimate of each age class by their respective durations (Houde, 1977). It is necessary to correct for stage durations of age classes if growth rates are nonlinear. Stage durations of age classes were determined by assigning ages based on previously determined growth equations to end-points of the 0.5 mm size classes. This customary method for constructing catch curves relies on the rarely examined assumption that larvae at different sampling locations are growing at similar rates. The high r^2 values of the age-length relationships (0.92 for Atlantic bumper; 0.84 for vermilion snapper) that resulted when aged larvae from all stations were combined indicated that growth

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[2] Lyczkowski-Shultz, J., and B. H. Comyns. 1992. Early life history of snappers in coastal and shelf waters of the north-central Gulf of Mexico late summer/fall months, 1983–1989, 12 p. + 9 tables, 17 figures. Technical Report submitted to the National Marine Fisheries Service, Southeast Regional Office, 9721 Executive Center Drive North, St. Petersberg, FL. 33702.

rates over the study area were similar enough to justify use of this technique.

Cruise estimates of larval mortality rates for Atlantic bumper and vermilion snapper larvae were estimated from catch curve analyses (e.g. Houde, 1977; Essig and Cole, 1986; Watanabe and Lo, 1988; Deegan, 1990; Comyns et al., 1991). The instantaneous mortality rate (Z) was estimated by the slope of the exponential function relating duration-corrected larval abundance and age (Ricker, 1975):

$$D_t = D_0 \exp (-Zt),$$

where D_t = total abundance of larvae at time t;
$\quad D_0$ = total abundance of individuals at time 0;
$\quad Z$ = instantaneous mortality rate; and
$\quad t$ = age of size class in days since spawning.

Age and abundance of size classes were fitted to this exponential function with a nonlinear least squares routine, and only the descending limb of the regression was used to estimate mortality rates. To reduce potential biases associated with 1) any trend of increasing variance in the length-at-age distribution with increasing age, and 2) net avoidance by larger larvae, only Atlantic bumper and vermilion snapper larvae smaller than 6.1 mm and 6.0 mm, respectively, were used to estimate mortality rates. Kolmogorov-Smirnov two-sample tests showed no significant differences ($P<0.05$) between size-frequency distributions for day versus night catches within this size range for vermilion snapper and Atlantic bumper larvae.

Results

Age and growth

Atlantic bumper larvae, which were commonly found throughout the study area, ranged from 2 to 14 days old, 1.4 mm to 8.1 mm in length, and 0.003 mg to 1.446 mg in dry weight. Estimates of age versus length growth coefficients were not similar for all stations (ANCOVA; $P=0.001$). The STP revealed no overlap in 95% confidence intervals around growth coefficients for larvae collected at station 42 and larvae collected at stations 41, 23, and 47 (Figs. 2A and 3). According to their respective growth equations, Atlantic bumper larvae at station 42 grew at approximately 0.43 mm/d and reached a length of 6 mm in approximately 13.3 days. Larvae collected at adjacent station 41 grew faster, approximately 0.63 mm/d, and reached a length of 6 mm in 10.4 days.
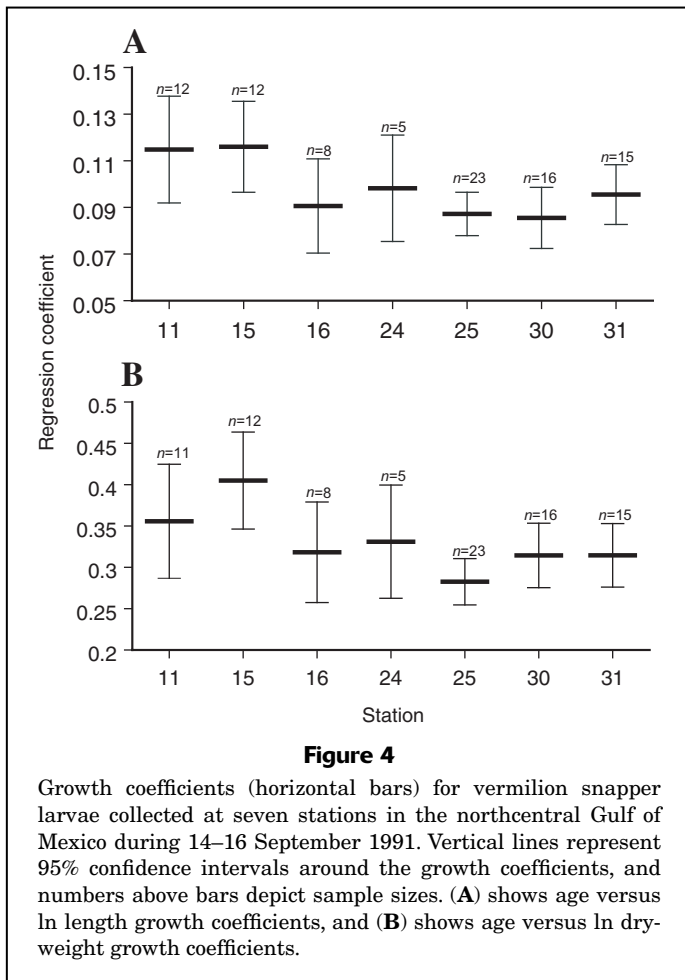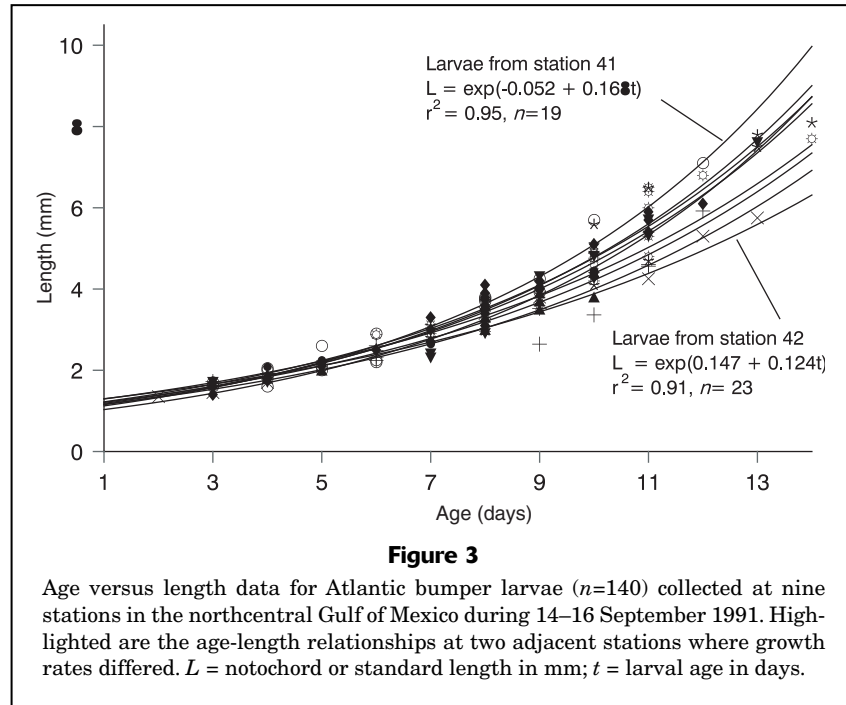
Similarly significant differences in station estimates ($n=9$) of age–dry-weight growth coefficients were also found (ANCOVA; $P=0.01$), and growth coefficients for larvae collected at station 42 were significantly different from larvae collected at stations 41 and 23 (STP; Fig. 2B). By 11 days, the estimated dry weight of an Atlantic bumper larva at station 42 was 0.38 mg, whereas at station 41 larvae gained weight faster and the estimated dry weight
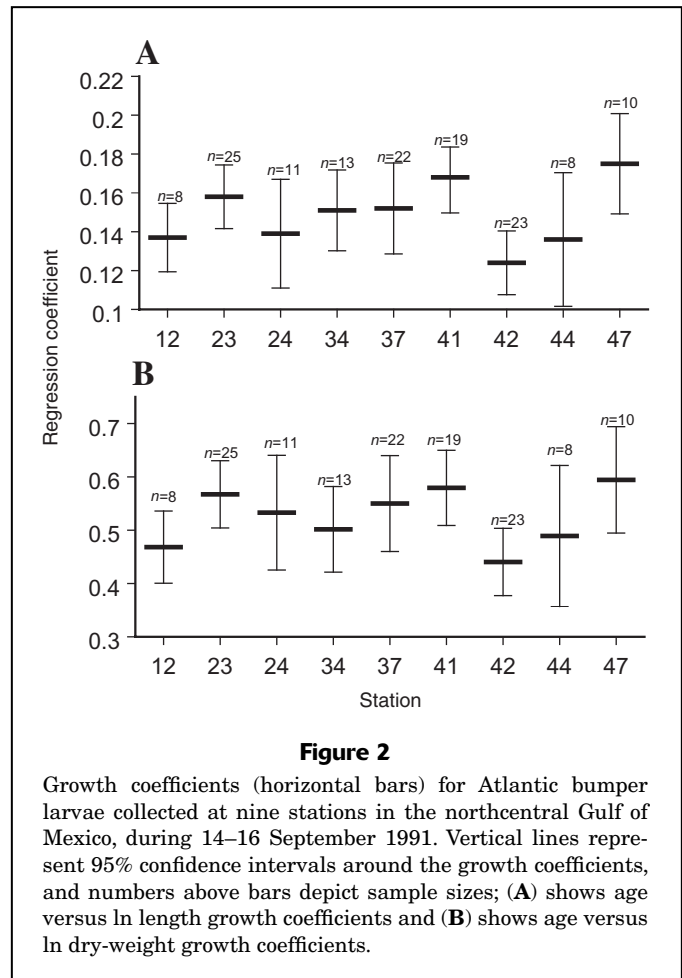
Figure 2

Growth coefficients (horizontal bars) for Atlantic bumper larvae collected at nine stations in the northcentral Gulf of Mexico, during 14–16 September 1991. Vertical lines represent 95% confidence intervals around the growth coefficients, and numbers above bars depict sample sizes; (**A**) shows age versus ln length growth coefficients and (**B**) shows age versus ln dry-weight growth coefficients.

of an 11-d-old larva was 0.58 mg. Adjacent stations 41 and 42 were 10 km apart, and water temperatures at these two locations were very similar. Surface temperatures varied by only 0.1°C (28.7°–28.8°C), and surface and midwater temperatures varied by only 0.5°C. Daily surface water temperatures recorded at a weather bouy within the study area showed that temperatures varied by less than 2°C during the 31-d period prior to our study.

Significant differences in station ($n=7$) growth rates of vermilion snapper larvae were also found in our 14–16 September 1991 cruise (ANCOVA; $P=0.03$). Vermilion snapper larvae ranged from 4 to 16 days old, 2.5 mm to 6.5 mm in length, and 0.014 mg to 0.696 mg in dry weight. Growth coefficients for larvae collected at stations 15 and 25 were significantly different (STP; Figs. 4A and 5). According to their respective growth equations, vermilion snapper larvae collected at station 15 reached a length of 5 mm in 10.7 days, whereas larvae collected at station 25 grew more slowly and did not reach a length of 5 mm until 12.6 days. Stations 15 and 25 were located 17 km apart on the inner shelf at water depths of 29–30 m. Surface water temperatures at these stations varied by 2.2°C, and both surface and midwater station temperatures differed by less than 2°C.
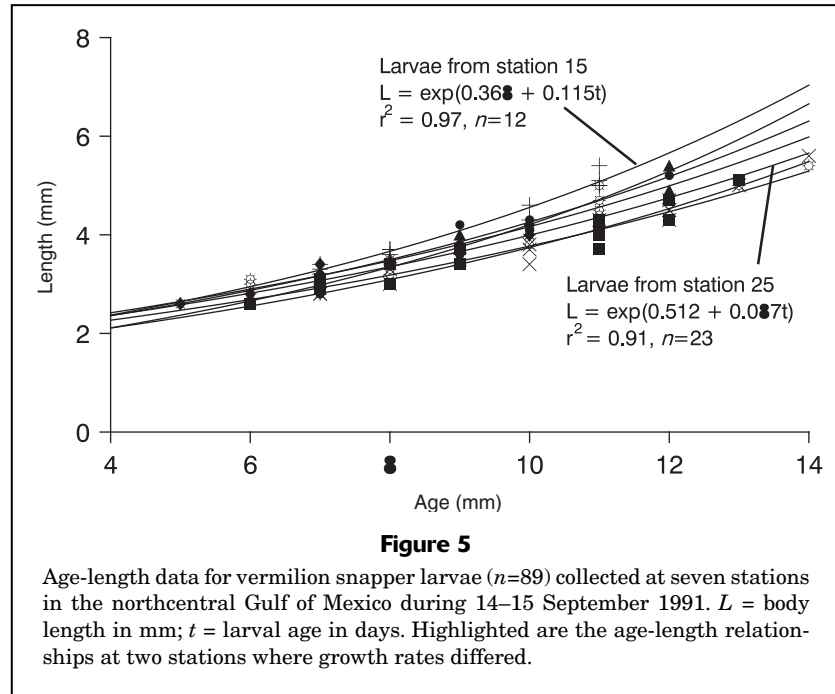
Figure 3

Age versus length data for Atlantic bumper larvae (*n*=140) collected at nine stations in the northcentral Gulf of Mexico during 14–16 September 1991. Highlighted are the age-length relationships at two adjacent stations where growth rates differed. L = notochord or standard length in mm; t = larval age in days.

Larvae from station 41
$L = \exp(-0.052 + 0.168t)$
$r^2 = 0.95$, $n=19$

Larvae from station 42
$L = \exp(0.147 + 0.124t)$
$r^2 = 0.91$, $n= 23$

Figure 4

Growth coefficients (horizontal bars) for vermilion snapper larvae collected at seven stations in the northcentral Gulf of Mexico during 14–16 September 1991. Vertical lines represent 95% confidence intervals around the growth coefficients, and numbers above bars depict sample sizes. (**A**) shows age versus ln length growth coefficients, and (**B**) shows age versus ln dry-weight growth coefficients.

Differences in age versus dry-weight growth coefficients were also significantly different (ANCOVA; *P*=0.03) and once again stations 15 and 25 (Fig. 4B) were significantly different (STP). Vermilion snapper larvae gained weight faster at station 15 where an 11.0-d-old larva had an estimated dry weight of 0.28 mg. At station 25 the estimated dry weight of this same larva was only 0.17 mg. Although vermilion snapper larvae were collected at most of the stations within the study area (Fig. 1), abundances were low at shallow (12–14 m depth) stations immediately south of the Mississippi–Alabama coast, and larvae were never collected at stations within Chandeleur Sound. These stations were very shallow (4–9 m).

Although our study did not assess microzooplankton prey availability, macrozooplankton dry-weight estimates varied widely over space and time. At the 33 stations east of Chandeleur Sound where larvae of vermilion snapper and Atlantic bumper used in our study were captured, macrozooplankton dry-weight estimates at 20 stations exceeded 3g/100 m^3, and at eight of those stations values exceeded 5g/100 m^3. Seven days later only at five of the 33 stations were macrozooplankton dry-weight estimates >3g/100 m^3 and at no station did estimates exceed 5g/100 m^3.

Mortality estimates

Atlantic bumper was generally the most abundant species in plankton collections; 32,241 larvae were collected during six cruises conducted in September of 1990, 1991, and 1993. Mortality rates were not estimated for Atlantic bumper larvae collected during the two cruises conducted in September 1992 because abundances of larvae were very low. When station abundance data were pooled for each of the six cruises, size-frequency distributions gener-

Figure 5

Age-length data for vermilion snapper larvae (n=89) collected at seven stations in the northcentral Gulf of Mexico during 14–15 September 1991. L = body length in mm; t = larval age in days. Highlighted are the age-length relationships at two stations where growth rates differed.
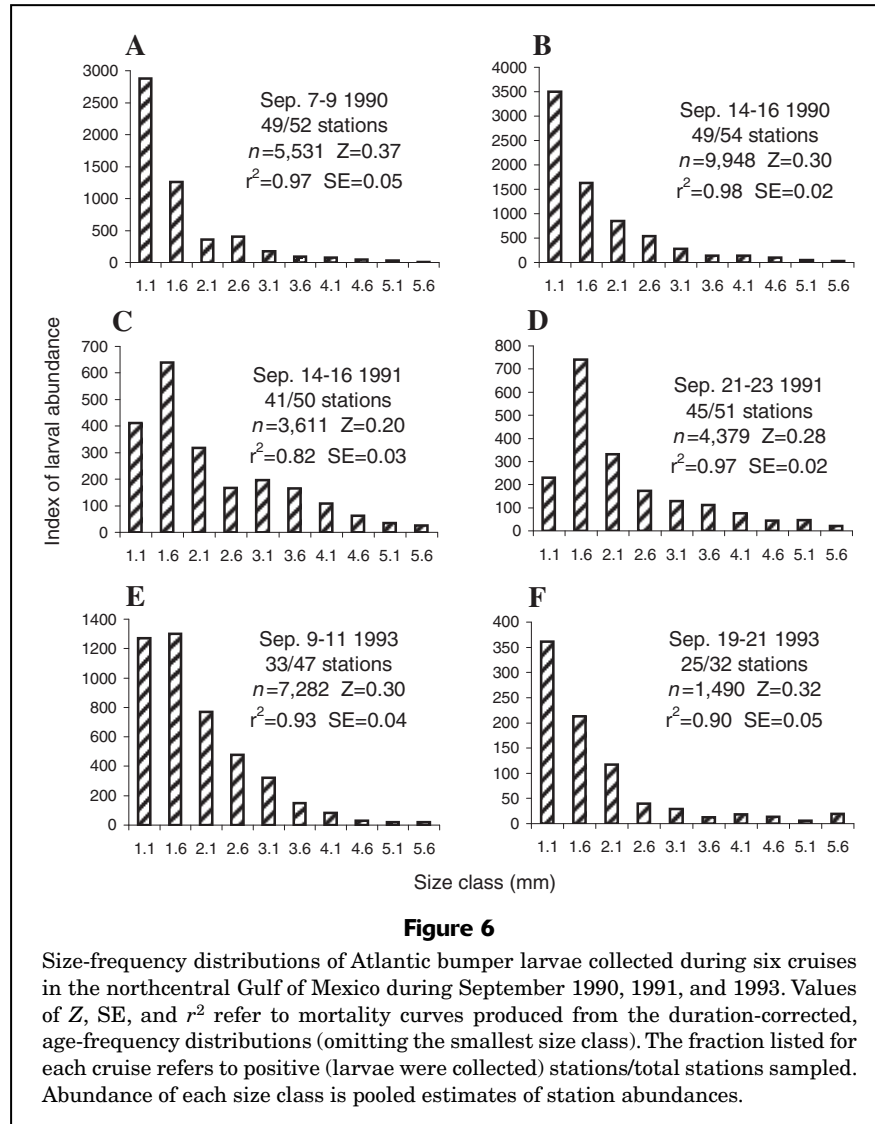
ally exhibited a similar decrease in abundance with successively larger size classes; however, the smallest size class (1.1–1.6 mm) was the most abundant in only three of the six cruises (Fig. 6, A, B, and F). This under representation of the smallest size class in several cruises was likely influenced by several potential factors, including a possible decrease in spawning prior to sampling and patchiness of eggs and newly hatched larvae caused by the aggregation of spawning adults. Cruise-estimates of mortality coefficients, which were derived by pooling data from all stations sampled during a cruise and omitting the smallest size class, ranged from 0.20 to 0.37 (Fig. 6). It is likely that mortality rates varied between stations, but as previously mentioned, an average cruise-estimate of mortality was determined to ascertain a realistic level about which the effects of small variations in growth rates could be assessed on the cumulative survival of larvae. Standard errors of Z estimates were low, ranging from 0.02 to 0.05.

Size-frequency distributions were derived for vermilion snapper larvae (n=2581) taken during two September 1991 cruises, and single late-September cruises in 1992 and 1993 (Fig. 7) when vermilion snapper larvae were abundant. Mortality estimates could not be estimated for five September cruises during the period 1990–93 because relatively few larvae were collected. Larvae collected during three of the four cruises when they were abundant showed a steady decrease in abundance of successively larger size classes (Fig. 7, A, C, and D). During the fourth cruise (late September 1991; Fig. 7B), the size-frequency distribution showed a distinct peak in abundance of intermediate-size larvae (4.0-mm size class). Mortality coefficients (Z) from the four cruises ranged from 0.19 to 0.30 and standard errors for the mortality coefficients were relatively low ranging from 0.02 to 0.05.

Discussion

Plankton collections taken in the northcentral GOM during September showed that growth and mortality rates did vary in time and space for Atlantic bumper and vermilion snapper larvae, and that these differences were great enough to significantly impact the cumulative survival of larvae in a subtropical climate where larval-stage durations are short (i.e. two weeks). Growth and mortality estimates of vermilion snapper larvae were previously unknown. Two previous studies of growth and mortality of Atlantic bumper larvae (Leffler and Shaw, 1992; Sánchez-Ramírez and Flores-Coto, 1998) provided no information on variability in growth rates at small spatial scales and no estimates of mortality during the period when our study was conducted.

Highly significant between-station differences in growth rates were observed for both Atlantic bumper and vermilion snapper larvae. The largest difference in age versus length growth coefficients for Atlantic bumper larvae was found at adjacent, inner-shelf stations located approximately 10 km apart. According to growth equations, the faster growing larvae grew to a length of 6 mm 2.9 days sooner than larvae at the adjacent station, and differences in larval weight gain as expressed by dry weight of 11-d-old larvae varied by over 30%. Water temperatures at these two stations were extremely similar; surface temperatures varied by only 0.1°C, midwater temperatures varied by 0.4°C, and surface and midwater temperatures varied by 0.5°C. It is likely that a similarly small temperature differential was present during the two-week period prior to this cruise, i.e. throughout the life of larvae used in our study because daily surface water temperatures recorded at a weather buoy within the study area during the previous month showed
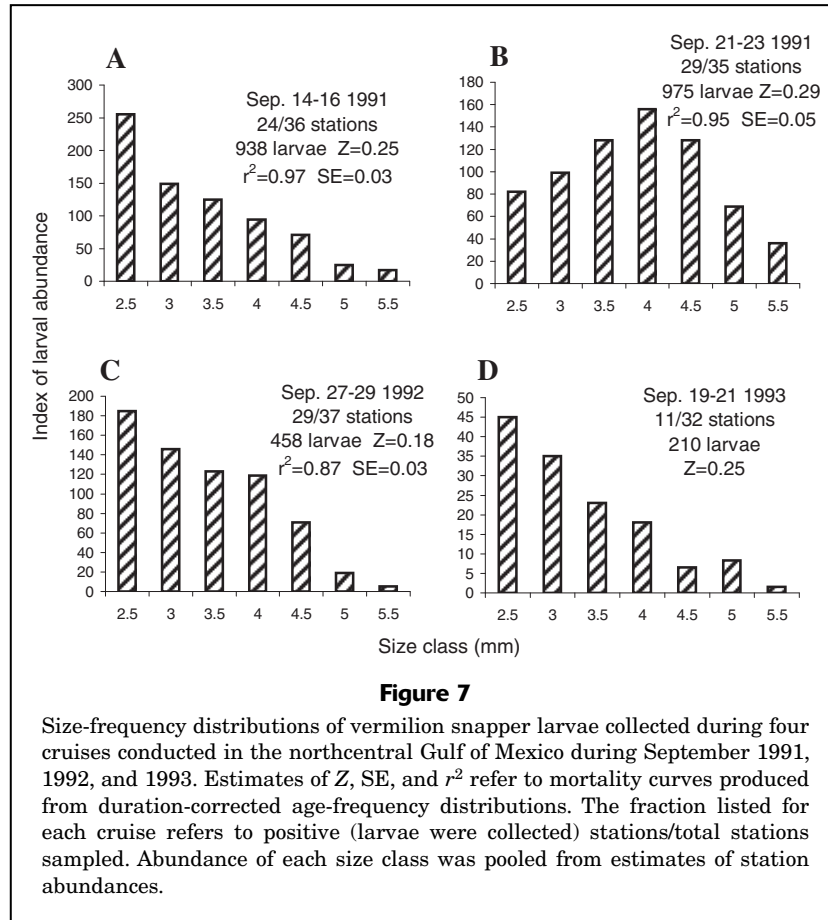
Figure 6

Size-frequency distributions of Atlantic bumper larvae collected during six cruises in the northcentral Gulf of Mexico during September 1990, 1991, and 1993. Values of Z, SE, and r^2 refer to mortality curves produced from the duration-corrected, age-frequency distributions (omitting the smallest size class). The fraction listed for each cruise refers to positive (larvae were collected) stations/total stations sampled. Abundance of each size class is pooled estimates of station abundances.

that temperatures varied by less than 2°C. Significant differences in both age versus length and age versus weight relationships were also found for vermilion snapper larvae collected at relatively close stations (i.e. 17 km apart). Water temperatures at these two stations were similar but differed by as much as 2°C. Faster growing larvae reached a length of 5 mm approximately 2 days sooner than larvae growing in nearby areas. Significant differences were also found in larval weight-gain; dry weight of 11-d-old larvae from different stations varyied by as much as 65%.

The variability in growth rates that we observed was likely caused by station differences in food availability and size-selective mortality, and to a lesser degree by water temperature. Unfortunately our data did not allow us to determine the individual effects of these factors on observed growth rates. At least for Atlantic bumper, the effects of temperature changes were probably minimal.

Larval survival is generally more influenced by factors other than temperature. Morse (1989) found a positive cor-

relation between length-dependent mortality and surface water temperature for 26 larval fish taxa and attributed this to increased predator consumption rates (caused by increased metabolic rates) at higher temperatures. He also concluded that increased growth due to increases in temperature alone would generally impart no advantage to reduce larval mortality because of the concomitant increased predatory consumption rates. Increased larval-stage duration at cooler temperatures is not necessarily associated with increased cumulative larval mortality because predation rates decline with decreasing temperature (Pepin, 1991; Francis, 1994). Methot (1981) concluded that after correcting for the effect of temperature on growth rates, the mean growth rate of larval fish is an indicator of the degree to which larval growth, and presumably survival, is food limited.

We acknowledge that size-selective predation, i.e. "culling out" the slowest (or fastest) growing larvae, could have produced the differences in size-at-age structure among

Figure 7

Size-frequency distributions of vermilion snapper larvae collected during four cruises conducted in the northcentral Gulf of Mexico during September 1991, 1992, and 1993. Estimates of Z, SE, and r^2 refer to mortality curves produced from duration-corrected age-frequency distributions. The fraction listed for each cruise refers to positive (larvae were collected) stations/total stations sampled. Abundance of each size class was pooled from estimates of station abundances.

stations that we observed. However, predation pressure seems unlikely to have been the primary cause of this variability. If among-station variability in size-selective mortality was largely responsible for the differences in larval growth rates, one would expect the variability in size-at-age at each station to be quite variable and this was not the case. Stations where the effects of size-selective mortality were minimal (or less) should have had both fast and slow growing larvae present; yet coefficients of determination (r^2) were ≥0.90 for age versus length regressions at all stations. Furthermore, there was no correlation between observed growth rates and r^2 values which would be expected if size selective predation was largely responsible for the variability in growth rates that we observed.

Many studies have shown that food availability has a large influence on growth rates of larvae (e.g. Houde and Schekter, 1981; Buckley et al., 1987; Pepin, 1991) and it is likely that station differences in food availability influenced our observed differences in larval growth rates. We did not collect the small size-fraction of prey eaten by fish larvae, but our data did reveal extensive spatial and temporal variability in the abundance of macrozooplankton. Macrozooplankton biomass at station 42, where relatively slow growth of Atlantic bumper occurred, was 2.6 mg/100 m^3 whereas at station 41, where larvae were growing

faster, macrozooplankton dry weight (3.9 g/100 m^3) was 50% higher. When all stations were considered, there was no correlation between macrozooplankton dry weight and growth coefficients of larvae, but macrozooplankton biomass was certainly very patchily distributed. For most stations there was at least a 50% difference in macrozooplankton dry weight between one of the adjacent stations. It is equally likely that the smaller size fraction of zooplankton that fish larvae eat were also very patchily distributed. In addition, several other studies have shown that primary production in the northern GOM is dynamic and spatially heterogenous (Lohrenz et al., 1990, 1994; Redalje et al., 1994), although these studies have focused on regions influenced by discharge from the Mississippi and Atchafalaya rivers.

In many studies the significant spatial variability in growth rates of field-caught larvae cannot be explained by changes in water temperature. These reported differences in growth rates have often been associated with factors such as storm events (Lasker, 1975; Maillet and Checkley, 1991), different geographical locations (Mokness, 1992; Nixon and Jones, 1997; Allman and Grimes, 1998;), or distinct hydrographic features such as tidal fronts (Munk, 1993) and riverine discharge plumes (Govoni et al., 1985; DeVries et al., 1990; Lang et al., 1994). All studies in the GOM that have reported spatial differences in larval

growth rates have involved comparisons in the vicinity of the Mississippi River discharge plume (Govoni et al., 1985; DeVries et al., 1990; Lang et al., 1994; Allman and Grimes, 1998). The observed variability in larval Atlantic bumper and vermilion snapper growth rates reported in our study was not associated with conspicuous hydrographic features (e.g. hydrographic convergence zones) and suggests the existence of less-recognizable regions where conditions for growth vary.

Cruise estimates of mortality were determined to ascertain a realistic level about which the effects of small variations in growth rates on the cumulative survival of larvae could be assessed. In order to do this, data from all stations sampled during a cruise were pooled. This provided the most reliable general estimate of mortality for each cruise despite likely site-specific differences in mortality rates that are extremely difficult to measure. Such pooling of data is not unusual; in fact Morse (1989) suggested that samples should be summed over the larval production cycle. Essig and Cole (1986) estimated mortality rates of larval alewives (*Alosa pseudoharengus*) by using both converted length-frequency distributions, as we did, and actual age-frequency distributions. They found no statistical difference between the two methods. Pepin and Miller (1993), however, warned that because variability in observed length-at-age increases with larval age (Chambers et al., 1988), analyses that use size in older fish to represent age may yield biased estimates of mortality rates. Yet, Pepin and Miller (1993) observed that their mortality rates, which were estimated by using size as a proxy for age, were consistent with mortality rates reported from other environments and species. Ideally, all fish would be aged, but for our study this was not possible because of the large sample sizes, multiple cruises, and the labor-intensive nature of otolith preparation for age determination.

Atlantic bumper larvae were extremely abundant (n= 32,241 for six cruises), and cruise estimates of age-frequency distributions showed consistent, well-defined descending limbs. Estimates of mortality coefficients (Z) for Atlantic bumper larvae were similar for September cruises conducted in the same year. For example, in 1990 the two cruise estimates of Z were 0.37 and 0.30, in 1991 the two Z estimates were 0.20 and 0.28, and in 1993 estimates of Z were 0.30 and 0.32. These mortality rates are similar to estimates reported by Leffler and Shaw (1992) during four September cruises in the same area during 1986–87 (Z=0.17–0.35) and by Sánchez-Ramírez and Flores-Coto (1998) in the southern Gulf (0.15–0.30). In addition, standard errors of the mortality estimates from our study were low, ranging from 0.02 to 0.05.

Cruise estimates of mortality rates for vermilion snapper were determined during four cruises when larvae were relatively abundant (n=2581). The descending limbs of three of the size-frequency distributions uniformly spanned all seven size classes, but during one cruise the middle size class was most abundant and the descending limb of this size-frequency distribution was restricted to four size classes. However, mortality rates were quite similar during all cruises (Z=0.19 to 0.30) and each had a low standard error (SE=0.02 to 0.05).

Collections of Atlantic bumper and vermilion snapper larvae were taken when water temperatures ranged from 25° to 30°C, and the mortality coefficients estimated from these collections were similar to those reported for other species under similar temperature regimes. Houde (1989) summarized vital rates of six species of larval fish as reported in seven studies where the mid-points of water temperatures at the time of collection ranged from 26° to 28°C. Most of these studies generated a range of mortality estimates, and the mid-points of the ranges reported in six of these studies varied from 0.21 to 0.38, values that are consistent with the mortality estimates (0.19 to 0.39) that we observed.

Our primary reason for estimating mortality rates was to ascertain a realistic level about which small variations could be assessed for potential effects on the cumulative survival of larvae, particularly in conjunction with variability in larval growth rates. Our method assumes a constant birth rate, or recruitment rate into the population, and assumes that fish leave the population only through death. There is clearly some expected variability in the degree to which these assumptions were met; however, based on the similarity of mortality estimates, not only between cruises but also to previously published estimates, it is concluded that our mortality estimates are biologically meaningful.

The well-accepted fisheries paradigm holds that changes in year-class strength are determined by variability in mortality during early life stages (Sissenwine, 1984; Houde, 1987; Bailey and Houde, 1989; Cushing and Horwood, 1994). Despite extensive efforts to understand the causes of recruitment variability, significant questions remain because the operant factors are likely to be interrelated parts of the ecosystem dynamics that comprise a multidimensional system (Ellersten et al., 1995). For example, it is not the mortality or growth rate alone that determines survival during the early life-stages, but the ratio M/G, the stage-specific mortality rate (Pepin, 1991). Examining previously published information, Houde (1989) found an exponential increase in predicted larval-stage duration with decreasing water temperature for 26 species of larval fishes and surmised that when temperature is low, small changes in growth rates can induce large changes in larval-stage duration that may significantly affect the recruitment process.

To determine the potential effects that variability in vital rates might have on the cumulative survival of larvae, hypothetical numbers of newly hatched Atlantic bumper were projected to a size of 6 mm under the influence of the growth and mortality rates we observed in the study area (Table 1). According to these vital rates, and a hypothetical initial cohort size of 1×10^6 individuals, 124,930 larvae survive to a length of 6 mm under the scenario of relatively fast growth and low mortality (G=0.61 mm/d; Z=0.20). If the growth rate is slowed (G=0.45 mm/d) and it takes approximately three days longer to reach a length of 6 mm, the number of larvae that survive to this length is reduced by 44%. If the slower growing larvae are exposed to the higher mortality rate (Z=0.37), cumulative survival of larvae decreases by an order of magnitude, and only

Table 1

Hypothetical survival of Atlantic bumper larvae to a size of 6 mm under the influence of growth and mortality rates observed in the study area.

Initial number in cohort	Instantaneous mortality coefficient (per day)	Age of 6-mm larva (d)	Number of 6-mm larvae
1×10^6	0.20	10.4	124,930
1×10^6	0.20	13.3	69,948
1×10^6	0.30	10.4	44,157
1×10^6	0.30	13.3	18,499
1×10^6	0.37	10.4	21,322
1×10^6	0.37	13.3	7292

7292 larvae survive to a length of 6 mm. Houde (1987) published a projection on the mortality of larvae exposed to hypothetical levels of mortality and growth rates, but the theoretical exercise used relatively long larval-stage durations (45–56 days). Results of our study show that even in a subtropical climate where larval stage durations may be as short as two weeks, relatively small changes in observed larval growth rates, particularly when combined with small differences in mortality, can have a large impact on cumulative larval survival. To what extent the observed differences in growth rates at small spatial scales are fine-scale "noise" that is ultimately smoothed by larger-scale processes is not known. Future research is needed to further characterize the small-scale variability in growth rates of larvae, particularly with regard to microzooplankton patchiness and the temporal and spatial pattern of potential predators. Small-scale spatial variability in larval growth rates may in fact be the norm, and understanding the implications of this subtle mosaic may help us to better evaluate our ability to partition the causes of recruitment variability.

Acknowledgments

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