Ingress of transformation stage gray snapper, *Lutjanus griseus* (Pisces: Lutjanidae) through Beaufort Inlet, North Carolina

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INGRESS OF TRANSFORMATION STAGE GRAY SNAPPER, *LUTJANUS GRISEUS* (PISCES: LUTJANIDAE) THROUGH BEAUFORT INLET, NORTH CAROLINA

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ABSTRACT

Ingressing transformation stage gray snapper (*Lutjanus griseus*) were sampled near Beaufort Inlet in 1993 and 1998. Gray snapper ingressed from July–October with a peak in September. Ingress occurred primarily during the new moon and secondarily during the full moon. Ingressing gray snapper were 11.3–15.8 mm standard length (SL), with a mean of 13.4 mm SL, and 21–34 d old, with a mean of 27 d. Estimated hatch dates ranged from June–September, with a peak in August. Hatching occurred throughout the lunar cycle with a peak during the new moon. Beaufort Inlet is 100s km north of known gray snapper spawning grounds; the mechanisms that result in yearly ingress in a predictable pattern have not been defined. Similarly, it is unknown whether juveniles that are resident in North Carolina estuaries successfully recruit to adult populations further south.

Most reef fish recruitment studies have focused on species that settle directly to adult reef habitats (pomacentrids, labrids, chaetodontids, acanthurids; Sale, 1991, 2002). However, a number of reef fish species settle to habitats within estuarine and nearshore environments before moving offshore to adult reef habitats (Lindeman et al., 2000). Specific settlement habitats include mangroves (Robertson and Duke, 1987; Thayer et al., 1987), seagrass (Carr and Adams, 1973; Baelde, 1990), macroalgae (Eggleston, 1995; Dahlgren and Eggleston, 2000) and nearshore reefs (Vigliola et al., 1998; Nagelkerken et al., 2000).

The relative importance of estuarine/nearshore juvenile reef fish nursery habitats in structuring reef fish populations is not well understood. Processes acting during settlement and residency in juvenile habitats may be important. In addition, variability in the movement from juvenile to adult habitats may control abundance. Processes acting after arrival of fish to adult habitats also may determine adult abundance.

The importance of nearshore nursery areas to reef fishes may be elucidated through comparison to estuarine use by non-reef fish species. Along the southeast U.S. continental shelf, a number of non-reef fish species use estuarine habitats as juvenile nurseries (Hoss and Thayer, 1993) and patterns of estuarine ingress are well documented (e.g., Norcross, 1991; Warlen, 1994; Hettler et al., 1997; Hettler and Hare, 1998). Modeling studies suggest that variability in the population abundance of Atlantic menhaden (*Brevoortia tyrannus*) is most likely driven by variability in the number of larvae surviving to enter estuaries, or the number of early juveniles surviving in estuaries (Quinlan and Crowder, 1999). There is also some evidence that abundance at ingress is linked to subsequent population abundance (Warlen, 1994). These studies suggest that for many estuarine-dependent species, ultimate adult abundance is strongly linked to estuarine larval supply and processes acting soon after ingress. Similarly, adult reef fish abundance is largely determined by larval supply (Doherty and Fowler, 1994) and post-settlement processes (Schmitt and Holbrook, 1999) as determined for reef fish species that settle directly to adult reef habitat.

In the Western Central Atlantic, several snapper species of the genus *Lutjanus* spawn on outer reefs, yet use nearshore habitats as juvenile nurseries, principally mangroves and seagrasses (Starck, 1971; Claro, 1981, 1982, 1983). Juvenile *Lutjanus* are often listed in fish surveys of southeast and mid-Atlantic estuaries along the east coast of the U.S. (Smith, 1902; Starck, 1971; Adams, 1976; Weinstein, 1979; Wenner et al., 1981; Ross and Epperly, 1985; Cuellar et al., 1996; Able and Fahay, 1998). In particular, juvenile gray snapper (*L. griseus*) are regularly found in Carolina estuaries (Cain and Dean, 1976; Weinstein, 1979; Manooch and Matheson, 1981; Wenner et al., 1981; Hettler and Barker, 1993) and may serve as a model for examining the importance of distinct, estuarine juvenile nursery habitats to the dynamics of reef fish populations.

The objectives of this study were to document the timing and magnitude of ingress, the age and size at ingress, and the hatch dates of gray snapper surviving to ingress. Insights gained into gray snapper life history are presented, and ingress patterns of gray snapper are compared to settlement patterns of other reef fish species and to ingress patterns of non-reef species that enter estuaries. The broader goal of this work is to provide a foundation for future studies aimed at developing a better understanding of the importance of estuarine juvenile habitats to the population ecology of gray snapper and other reef species with similar life histories.

METHODS

SAMPLE COLLECTION.—Sampling was conducted from a platform permanently installed under the bridge to Pivers Island near Beaufort, North Carolina, two kilometers inside of Beaufort Inlet (Fig. 1). During flood tides, water entering Beaufort Inlet passes through the channel spanned by the Pivers Island bridge before entering the Newport River Estuary. A 1 × 2 m neuston net frame fitted with a 0.947 mm mesh net was fished just below the surface (Warlen, 1994), and a flowmeter was attached to the net to determine current speed for calculation of water volume.

Samples were collected approximately weekly during maximum nighttime flood tides from June–November in 1993 and 1998. On a given date, three samples were collected sequentially with minimal time intervals between samples and immediately preserved in 95% ethanol. Between 200–500 m^3 of water were filtered per sample. Samples were sorted for fishes and all snapper were identified to species, counted, and measured for standard length (SL). Gray snapper were dominant, but mutton snapper (*Lutjanus analis*), schoolmaster (*Lutjanus apodus*), and lane snapper (*Lutjanus synagris*) were also collected in low numbers.

The sampling described above was preceded and followed by sampling for winter ingressing species using a slightly different protocol (Warlen, 1994); no gray snapper were collected during this November–May period and thus, only the June–November samples are considered here.

DETERMINATION OF AGE.—Age at ingress was determined through otolith microstructure analysis (Fig. 2). Otoliths from all fish were examined with two exceptions: 1) otoliths were not found or were damaged for nine individuals, and 2) on one sample date, 205 fish were collected, but otoliths were examined from only 37 randomly selected in one mm length classes over the size range collected (11–15 mm). Sagittae were extracted under a dissecting microscope, and one of each pair (the left one in most cases) was single polished (one face) for a transverse section (Secor et al., 1992). Prepared otoliths were examined with a compound light microscope under oil immersion using a 100× objective with a video camera that was connected to a computer running Optimas 6.0 image analysis software. Increments were counted from the center to the edge along the dorsal lobe (Fig. 2) unless prevented by preparation flaws. Blind counts were made by a single reader three times. If the coefficient of variation (CV) of the three counts exceeded 7.5%, a fourth and sometimes fifth count was made. The three counts that produced the lowest CV for each otolith were used in subsequent analyses. No otoliths were discarded from the analysis as after five counts, all CVs were less than 7.5%.

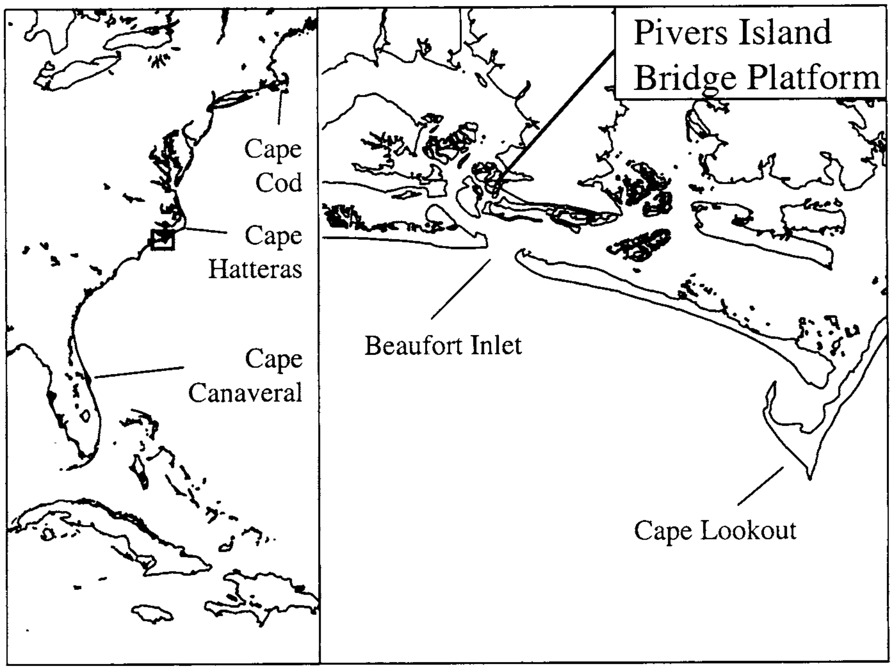

Figure 1. Map of study area showing the east coast of the U.S. and the vicinity of Beaufort Inlet, North Carolina.

Increment deposition rate was assumed to be daily, first increment formation was assumed to occur at hatching, and average increment count was used as an estimate of age in days. A laboratory validation study was conducted, but fish did not grow and the results were equivocal (Tzeng, 2000). Ahrenholz (2000) and Allman and Grimes (2002), however, found daily increment formation in juvenile gray snapper in North Carolina and Florida respectively, thereby validating the assumption of daily increment formation. The assumption that first increment formation occurs at hatching is supported by Thorrold and Hare's (2002) review of the application of otolith microstructure to the study of coral reef fish ecology.

DATA ANALYSIS

Gray snapper concentrations were calculated for each sampling date to examine the timing and magnitude of ingress. Sample concentration (C_S) was calculated as number of gray snapper/volume filtered. Sample date concentration (C_D) was calculated as the average of the three sample concentrations.

The relation between gray snapper ingress and lunar cycle was examined for four full lunar mo each yr: full moons of July 3–October 30, 1993, and July 9–November 4, 1998. Lunar day concentrations (C_{LD}) were calculated as the sum of sample date concentrations (C_D) from each given lunar day divided by the number of sampling dates included (a simple average, but the number of observations per lunar day varied). Third quarter moon was defined as lunar day 0, full moon as lunar day –7 and new moon as lunar day 7. Circular-linear correlations (Batschelet, 1981) were calculated on log-transformed lunar day concentrations to determine whether there were significant lunar patterns in ingress. Analyses were conducted for each yr separately (four lunar mo each) and both yrs combined (eight lunar mo).

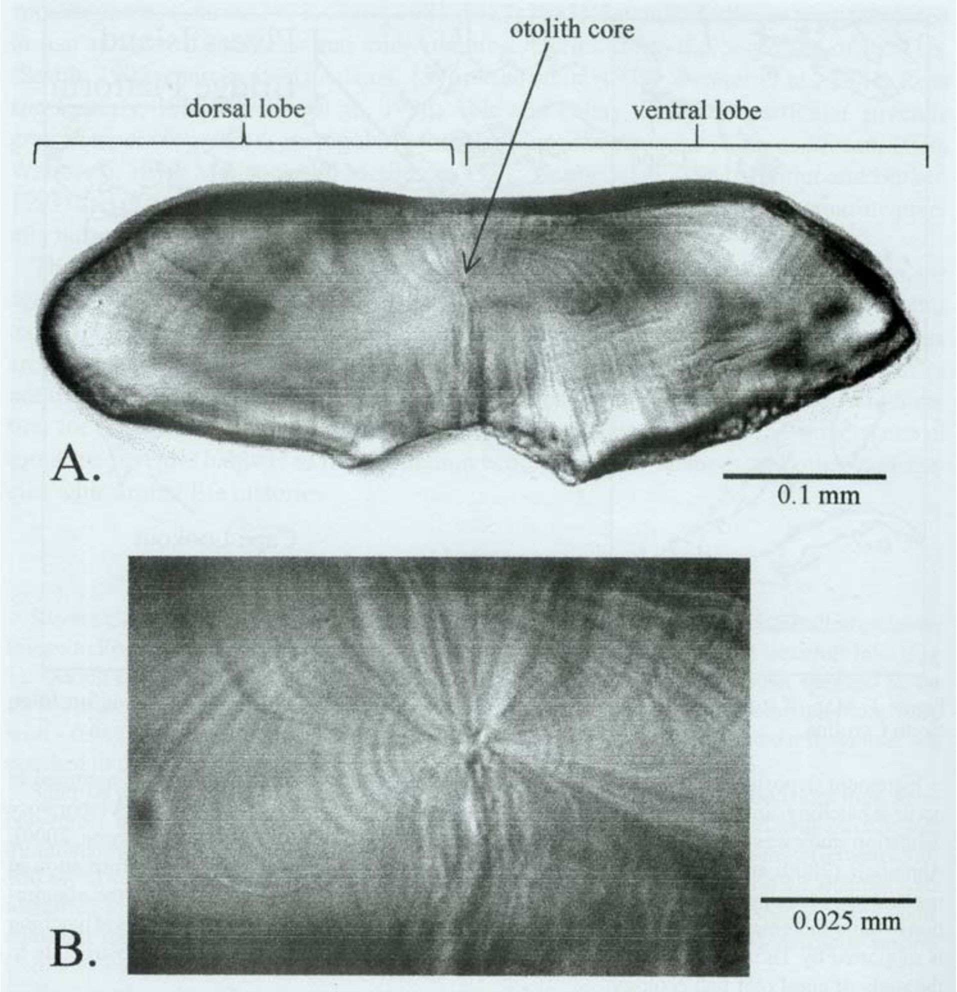

Figure 2. Polished transverse section of left sagitta from a 15.5 mm SL gray snapper (*Lutjanus griseus*). A) Entire section magnified at 200×. B) Otolith core magnified at 600×.

Concentrations of gray snapper of certain ages or hatch dates were determined by calculating a weighting factor for each fish aged: $W_{iS}=C_S/NA_S$ where W_{iS} is weight of fish i from sample S, C_S is the concentration of all fish in sample S and NA_S is the number of fish aged from sample S. Weighting was necessary because the volume filtered for each sample varied and not all gray snapper were aged due to subsampling (in one case), or the inability to extract otoliths from all individuals.

Estimated hatch dates were used to evaluate both spawning time and lunar patterns in spawning. Hatch dates were calculated for each aged fish by subtracting estimated age from capture date. Hatch dates were then combined with the individual weights (W_{iS}) to examine the time series of hatch dates. Individual weights of all fish hatched on a given lunar day were summed and circular-linear correlation was conducted for each year separately and both years combined (Batschelet, 1981).

Age and size at ingress were considered as a bivariate relation and examined using the framework developed by Chambers and Leggett (1992). Temporal cohorts were arbitrarily assigned based on natural gaps in the hatch date time series. A Multivariate Analysis of Variance (MANOVA) was used to compare the bivariate size and age at ingress data among cohorts, followed by a multivariate comparison between cohorts. Only those cohorts with > ten fish were included.

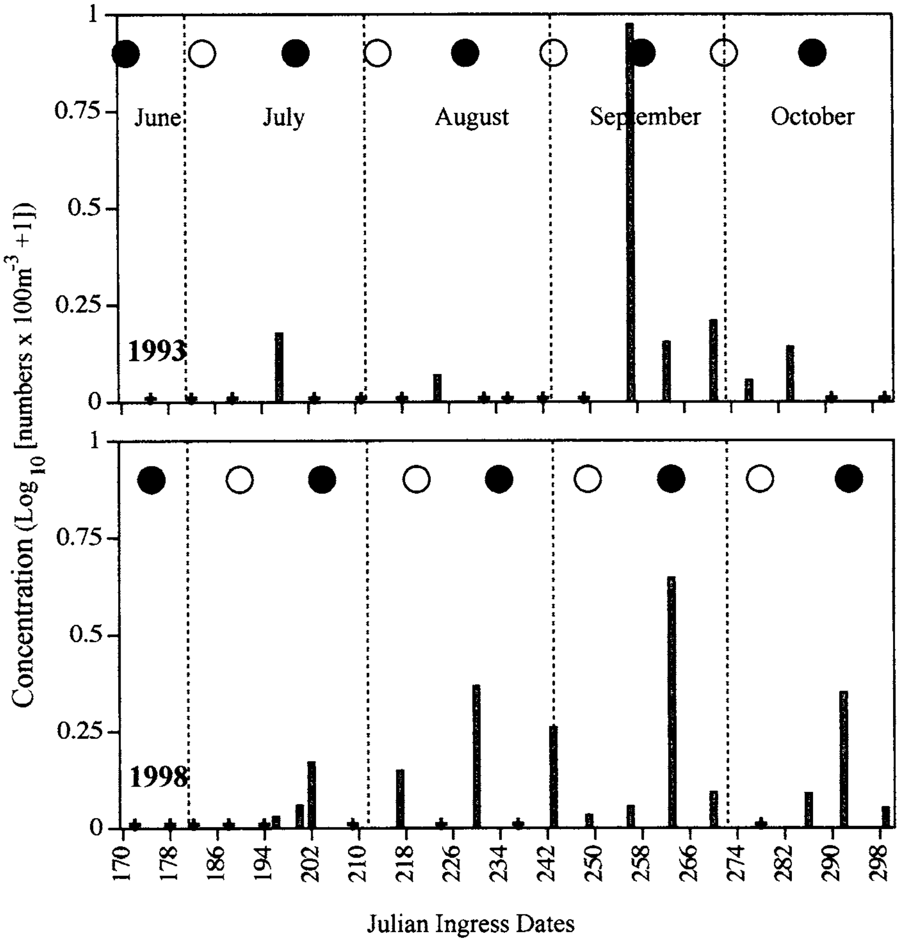

Figure 3. Timing and magnitude of ingress of gray snapper (*Lutjanus griseus*) through Beaufort Inlet, North Carolina in 1993 (July 16–Oct. 11) and 1998 (July 15–Oct. 26). Black crosses indicate sampling dates where no gray snapper were captured. Full and new moons are represented by white and black circles respectively. Dashed vertical lines represent month divisions.

Lunar patterns in age and size at ingress were examined. All age (size) data were pooled and a periodic regression was calculated between age (size) at ingress and lunar day (Batschelet, 1981). The model was: *age* = $M + A$ cos(T *lunar day* – w), where M is mean age (size), A is the amplitude of the lunar cycle, T is the period of the lunar cycle (28.5 d) in radians, and w is the phase of the relation between *age* and *lunar day*. The presence of a lunar cycle in *age* was evaluated by examining whether the amplitude term (A) was significantly different than 0.

RESULTS

Ingress of gray snapper into Beaufort Inlet occurred in late summer and early fall. In 1993 and 1998 gray snapper were collected from July–October with greatest concentrations observed in September (Fig. 3). Gray snapper were not collected from November–May, 1992–1999.

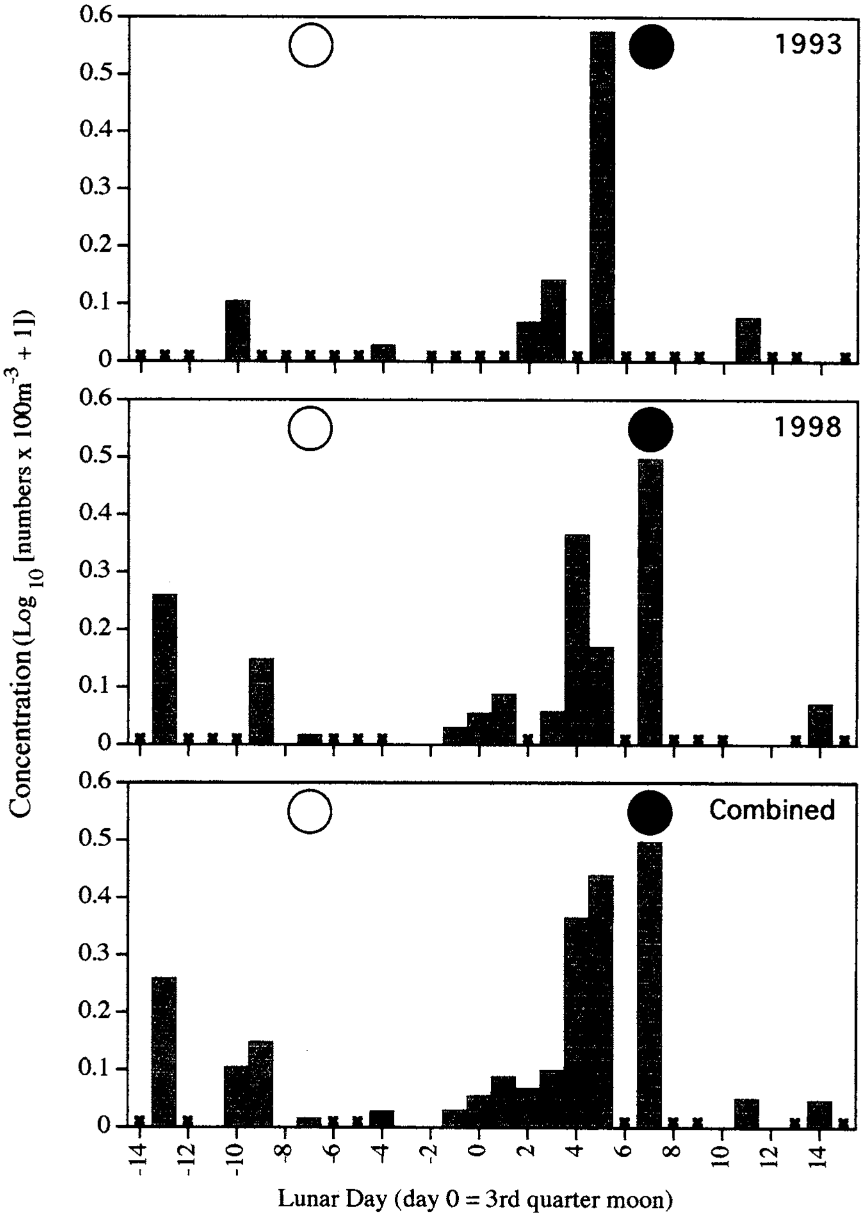

Figure 4. Lunar ingress date of gray snapper (*Lutjanus griseus*) at Beaufort Inlet in 1993, 1998 and both years combined. Lunar day portrayed as day from the third quarter moon. Black crosses indicate lunar days that were not sampled. Full and new moons are represented by white and black circles respectively.

Gray snapper were collected preceding every new moon from July–October in 1993 and 1998 (Fig. 3). Pooling ingress data by lunar day clearly showed peak ingress preceding the new moon during both yrs, but with some ingress at other times in the lunar cycle (Fig. 4). A significant correlation was found between gray snapper concentration and lunar day ($P < 0.05$) when yearly data was pooled, but correlations were not significant when yrs were analyzed separately ($P > 0.05$ in 1993 and 1998).

Estimated hatch dates ranged from mid-June–late-September, with the largest number hatched in August (Fig. 5). Distinct cohorts were evident in the hatch date time series and fish were assigned to four cohorts in 1993 and seven cohorts in 1998 for subsequent cohort-specific analyses (Fig. 5). Five cohorts had more than ten individuals: 1993C, 1993D, 1998C, 1998E, 1998G. There was no overlap in the timing of ingress of different cohorts (Fig. 5).

There was a clear lunar pattern to hatch dates. Gray snapper hatched around every new moon between June–September in both 1993 and 1998 (Fig. 5). Pooling hatch date data by lunar day showed that most hatching occurred at and just following the new moon, but some hatching occurred throughout the lunar cycle with a secondary peak around the full moon (Fig. 6). Hatch date and lunar day were significantly correlated in 1993 and for both yrs combined ($P < 0.05$, 1993; $P > 0.05$, 1998; $P < 0.05$, yrs pooled). Fish hatched during a given part of the lunar cycle tended to ingress during the same part of the cycle (Fig. 7).

Overall, age and length at ingress were positively correlated (Fig. 8A, $r = 0.45$, $P < 0.001$). Estimated age at ingress ranged from 21–34 d, and standard length at ingress ranged from 11.3–15.8 mm (Table 1). Variation in age was slightly greater than variation in length (CV_{age} 9.2 %, CV_{SL} 7.1 %).

The bivariate age and size relation differed significantly among the five cohorts with more than ten individuals (Fig. 8B, MANOVA: $q = 0.556$, $P < 0.0001$; see Chambers and Leggett, 1992). A multivariate multiple comparison found that age at ingress of the 1993C and 1993D cohorts differed from the 1998C cohort and age at ingress of these three cohorts differed from the 1998E and 1998F cohorts. Size at ingress differed between the 1998E cohort and the other four cohorts.

Small, but significant lunar patterns were found in both age and size at ingress (Table 2). Age varied by approximately two d over the lunar cycle and size varied by 1.6 mm (Table 2). Maximum age and length were predicted to occur at, or just following the new moon (Fig. 9). As the new moon approaches age (size) increases; however, these increases are small and most variability in age-at-ingress is not explained by lunar day; whether or not these patterns are biologically significant is uncertain.

DISCUSSION

Documented use of North Carolina estuaries by gray snapper over a number of years indicates that these habitats serve as juvenile nurseries. In this study, gray snapper entered Beaufort Inlet from July–October during both 1993 and 1998. Gray snapper juveniles have also been reported from southeast U.S. estuaries in numerous studies spanning a number of years (Smith, 1902; Adams, 1976; Cain and Dean, 1976; Weinstein, 1979; Manooch and Matheson, 1981; Wenner et al., 1981; Ross and Epperly, 1985; Hettler and Barker, 1993; Cuellar et al., 1996).

Although gray snapper juveniles inhabit southeast U.S. estuaries, the role of these habitats in supporting gray snapper populations is unclear. North of Florida, recreational fisheries rarely capture gray snapper (Chester et al., 1984; Burton, 2000) and adults are rare in visual censuses of reefs (Parker et al., 1994; Parker and Dixon, 1998). It is unknown whether juvenile gray snapper return from North Carolina estuaries to contribute to southern

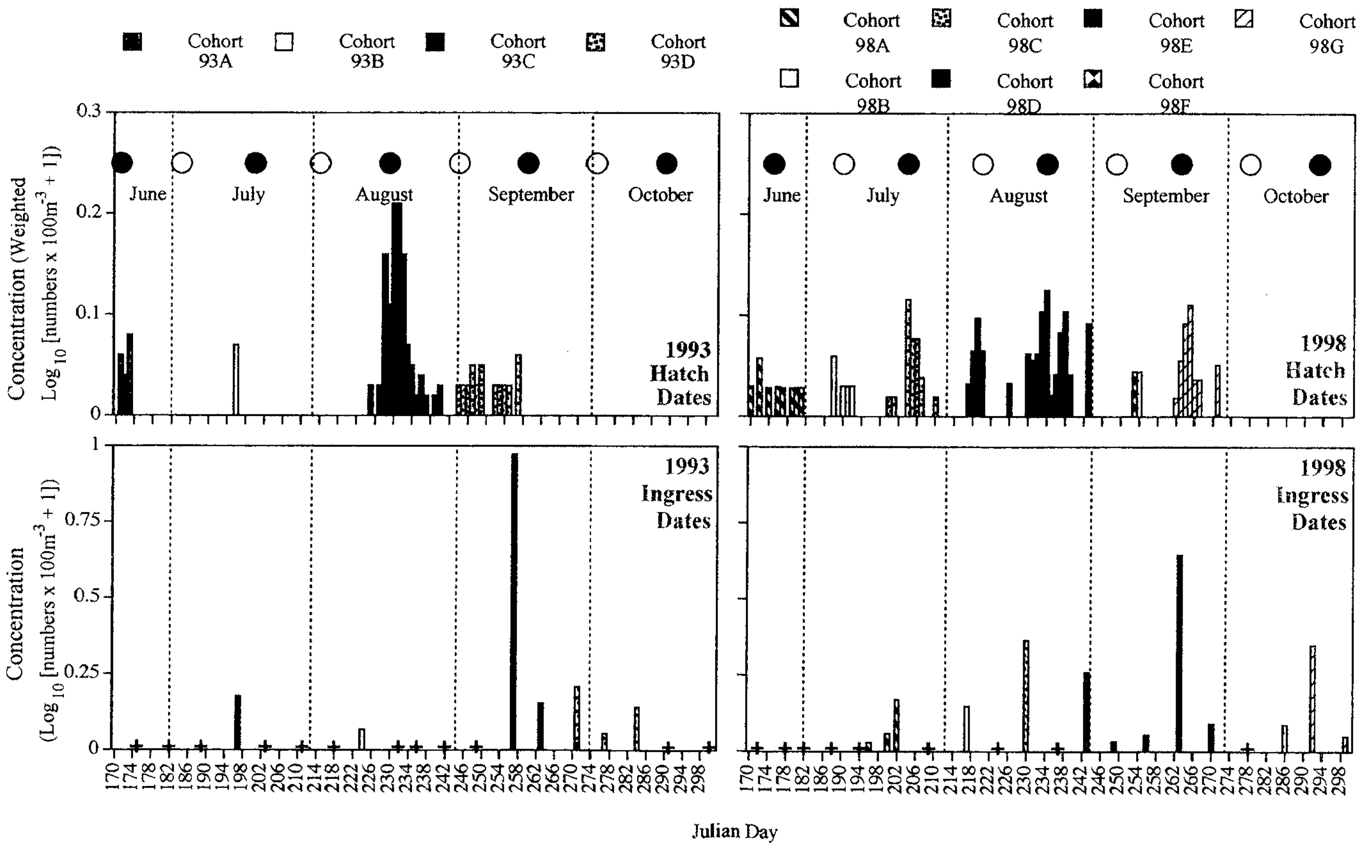

Figure 5. Timing and magnitude of estimated hatching for gray snapper (*Lutjanus griseus*) that entered Beaufort Inlet, North Carolina in 1993 and 1998. Full and new moons are represented by white and black circles respectively. Dashed vertical lines represent month divisions. Black crosses indicate sampling dates when no gray snapper were collected.

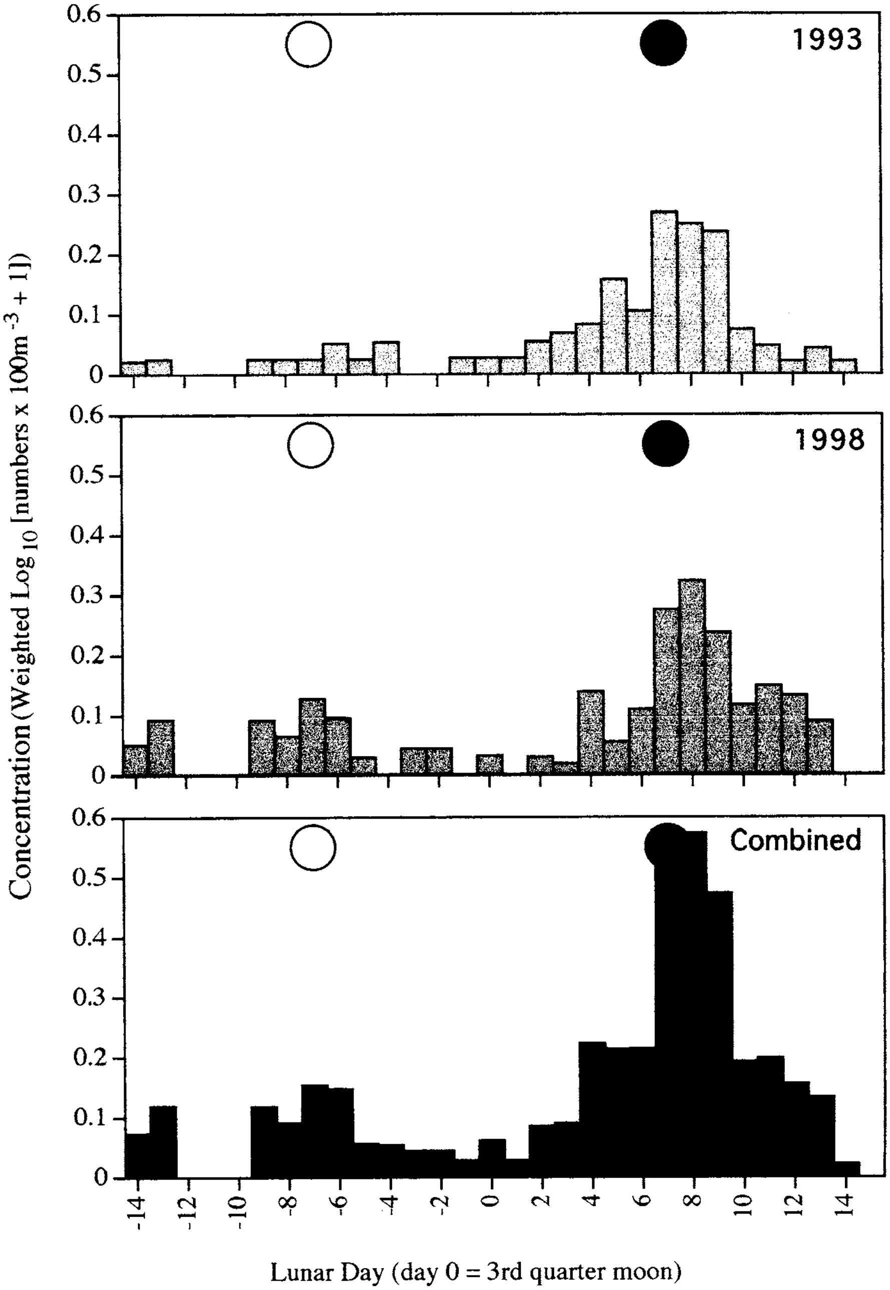

Figure 6. Lunar hatch date of gray snapper (*Lutjanus griseus*) ingressing through Beaufort Inlet in 1993, 1998 and both years combined. Lunar day portrayed as day from the third quarter moon. Full and new moons are represented by white and black circles respectively.

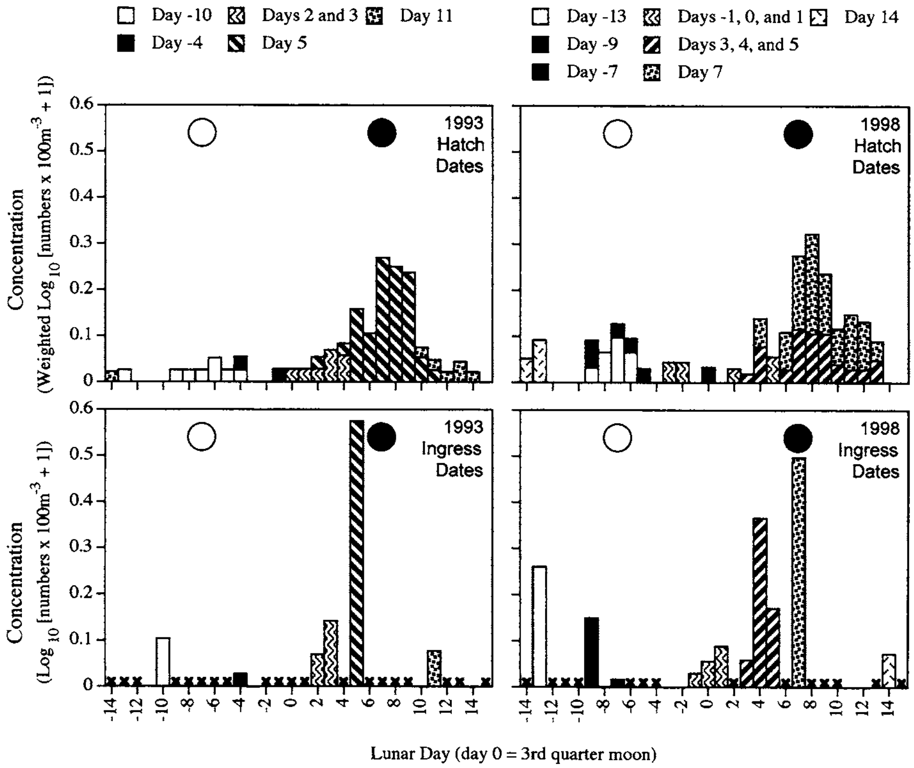

Figure 7. Lunar hatch date and lunar ingress date of gray snapper (*Lutjanus griseus*) ingressing through Beaufort Inlet in 1993, 1998. Fish identified on the basis of lunar ingress dates. Lunar day portrayed as day from the third quarter moon. Black crosses indicate lunar days that were not sampled. Full and new moons are represented by white and black circles respectively.

adult populations or perish, analogous to expatriated sub-tropical species found north of Cape Hatteras (Hare and Cowen, 1991; McBride and Able, 1998).

Similarly, the mechanisms of larval transport from spawning grounds (e.g., northern Florida and south) to North Carolina estuaries are unclear. Larvae could be transported northward along the shelf by wind-driven flows. Larvae could also be entrained into the northward flowing Gulf Stream and then advected across the North Carolina shelf (Govoni and Pietrafesa, 1994; Hare et al., 1999). In any case, the mechanism(s) of larval transport must act consistently to supply larvae over a similar four mo period with a similar lunar pattern in each of two years. Future study of northward transport of gray snapper larvae on the southeast U.S. continental shelf may lead to a better understanding of larval transport mechanisms in general, similar to the study of transport of sub-tropical species onto the northeast U.S. continental shelf (Hare and Cowen, 1991; Hare et al., 2002).

From adult biology studies, gray snapper spawning may begin as early as May (Domeier et al., 1996; Allman and Grimes, 2002) and end as late as October (Claro, 1983). Spawning peaks in July, based on analysis of gonad state (Starck, 1971), gonadosomatic index (Claro, 1983; Burton, 2000), and back-calculated hatch dates from Florida (Domeier et al., 1996; Allman and Grimes, 2002). The back-calculated hatchdate distribution of larvae entering Beaufort Inlet was from June–September, with a peak in August. The processes responsible for the apparent differences in observed spawning and hatchdates of

Table 1. Summary statistics of gray snapper age and size at ingress into Beaufort Inlet, North Carolina for distinct hatch date cohorts (see Fig. 5), pooled for each of the two years 1993 and 1998, and pooled for both years combined.

		Standard length (mm)				Age (d)				
Year	Cohort	Mean	SD	Max	Min	Mean	SD	Max	Min	Number
1993	A	12.8	1.0	14.3	11.5	25.0	1.1	26.3	23.7	9
1993	B	12.9	0.7	13.4	12.5	28.2	0.2	28.3	28.0	2
1993	C	13.1	0.7	14.5	11.8	26.9	1.8	31.7	22.7	45
1993	D	12.9	0.5	13.9	11.9	26.6	2.8	31.3	22.0	14
1998	A	12.8	0.8	14.0	11.3	25.4	2.9	30.0	21.5	9
1998	B	12.7	0.8	13.6	11.7	27.4	1.8	29.3	25.0	5
1998	C	12.6	0.6	13.7	11.5	25.2	2.0	29.7	20.5	19
1998	D	12.8	0.6	13.6	12.0	24.4	1.0	26.0	23.3	8
1998	E	14.2	0.8	15.8	12.7	28.0	2.8	33.5	23.0	35
1998	F	14.7	0.5	15.0	14.4	33.0	0.7	33.5	32.5	2
1998	G	13.2	0.8	14.6	11.7	27.8	1.3	29.7	25.3	20
1993	All fish	13.0	0.7	14.5	11.5	26.6	2.1	31.7	22.0	70
1998	All fish	13.4	1.0	15.8	11.3	27.0	2.7	33.5	20.5	98
Both years	All fish	13.2	0.9	15.8	11.3	26.8	2.5	33.5	20.5	168

larvae surviving to Beaufort Inlet are not known, but likely involve differential larval survival processes such as predation, successful transport, and the physiological effects of temperature.

Reports conflict on whether gray snapper spawning occurs primarily during the full or new moon. Starck (1971) and Claro (1983) reported peak spawning during full moons through observations of adult behavior, while Domeier et al. (1996) determined that spawning occurs primarily during new moons based on analysis of otoliths from juveniles. Allman and Grimes (2002) inferred peak spawning during both new and full moons, again from hatch date analysis of juveniles. Gray snapper surviving to ingress through Beaufort Inlet hatched primarily around new moons, with a secondary peak near full moons, yet some fish hatched throughout the lunar cycle. Thus, spawning occurs throughout the lunar cycle, with likely peaks near both full and new moons. However, the degree to which the appearance of lunar spawning patterns in hatchdates of surviving fish is caused by larval survival processes is unknown.

Ingress primarily occurred around each new moon, with smaller numbers arriving prior to each full moon and throughout the lunar cycle in September and October. Similar ingress patterns were found for snapper by Halvorsen (1994) and Smith (1995) from the Bahamas and east coast of Florida respectively, but both of these studies had problems with species identifications making direct comparisons with our study difficult. For gray snapper entering Beaufort Inlet, larval duration was relatively fixed (mean 26.8 d, standard deviation 2.5 d, Table 1) and lunar patterns in ingress likely resulted from lunar patterns in spawning, with the caveat that the influence of larval survival in modifying measured hatch date distributions at ingress was not quantified. A number of studies have observed lunar patterns in spawning and found lunar patterns in settlement of coral reef fish with relatively fixed larval durations (Robertson et al., 1988; Meekan et al., 1993; Colin et al., 1997). The remarkable point for gray snapper entering Beaufort Inlet is the consistent ingress near new moons to an estuary that is hundreds of km north of known spawning areas.

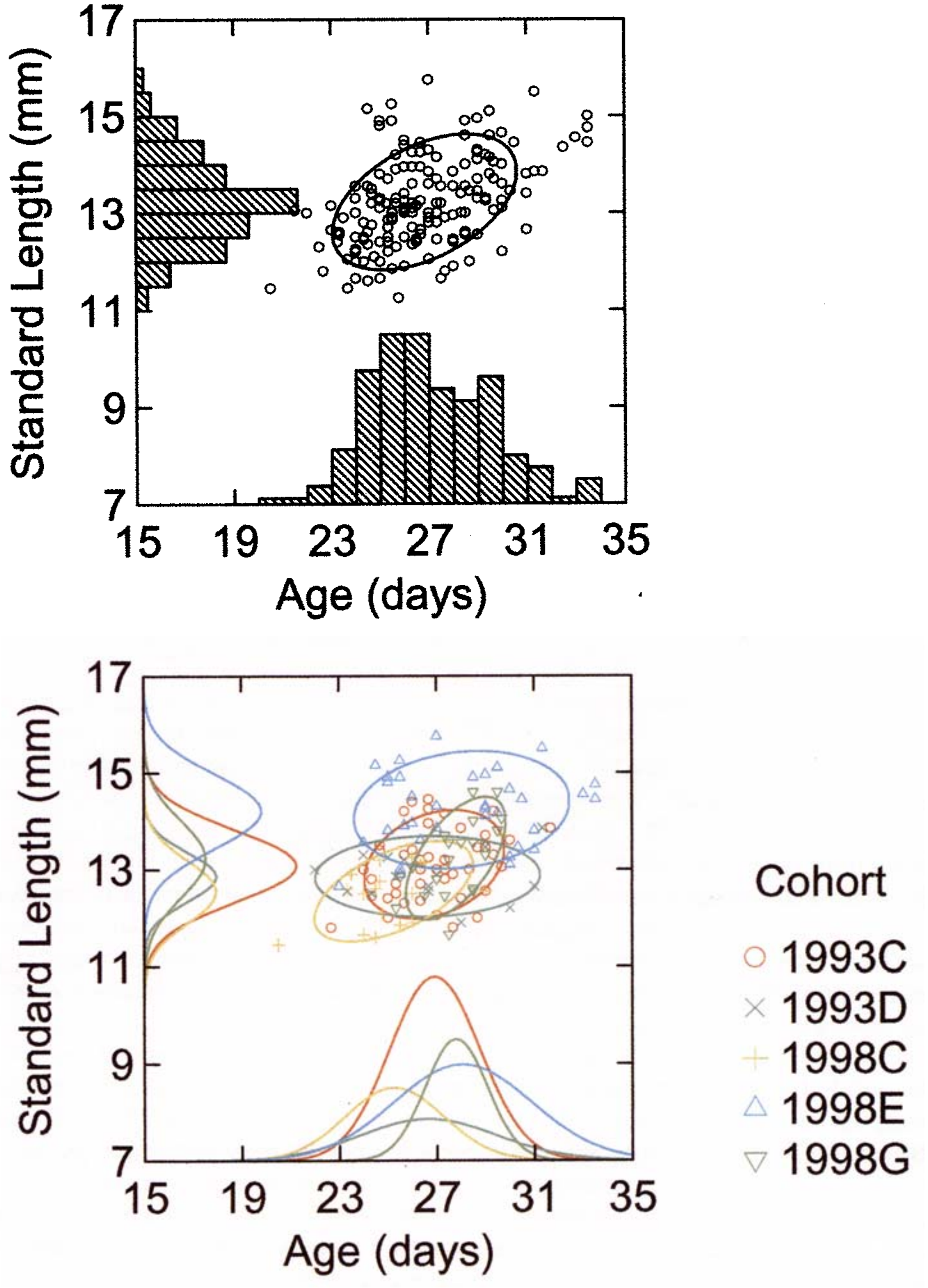

Figure 8. A) Bivariate age–size relation for gray snapper (*Lutjanus griseus*) ingressing through Beaufort Inlet. 95% confidence ellipse is shown. Univariate age and size at ingress frequency distributions are also provided on the x- and y-axes. B) Bivariate age-size relation for different cohorts of gray snapper ingressing through Beaufort Inlet. Each cohort is a different color and symbol. 95% confidence ellipse is shown for each cohort. Normal univariate distributions based on each cohort's age and size at ingress are shown on the x- and y-axes.

Table 2. Summary of periodic regression results that tested for lunar patterns in ingress size and age. Model is explained in the text and parameters are figuratively displayed in Fig. 9. Significance of amplitude term (indicated by *) determined by 95% confidence intervals for parameter not overlapping with 0.

Dependent variable	Parameter	Estimate	
Size	Mean	12.959	
	Amplitude	0.876	*
	Phase	102.857	
Age	Mean	26.288	
	Amplitude	−1.033	*
	Phase	11.294	

Cohort differences in age and growth may have consequences to the population dynamics of juvenile gray snapper in North Carolina estuaries. Size and age at ingress are determined by both environmental conditions (e.g., temperature, prey, transport) and maternal contribution (Chambers and Leggett, 1992). Growth rate and development rate affect larval survival (Chambers and Leggett, 1987; Meekan and Fortier, 1996; Hare and Cowen, 1997), thus variability in the age and size at ingress suggests that larval survival would be variable among cohorts. Similarly, differences in larval traits, evidenced by differences in the age and size at ingress (albeit small) may influence juvenile survival (Searcy and Sponaugle, 2000). Future work should examine the role of variable larval and juvenile size and growth on survival of gray snapper.

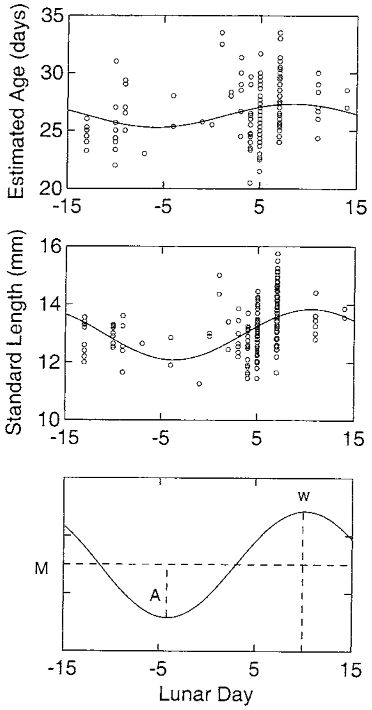

Figure 9. Age and size at ingress of gray snapper (*Lutjanus griseus*) pooled by lunar day. The estimated periodic regression function (see text) is also shown. Bottom panel provides an illustration of the terms of the model presented in Table 2 (M - Mean, A- Amplitude, w - phase).

Snapper ingress into Beaufort Inlet is unlike the ingress of a suite of winter-spawning groundfish (spot, Atlantic croaker, summer flounder) and is more similar to fish that settle directly to coral reefs. Winter spawning fish do not exhibit a pronounced lunar pattern in ingress (Hettler et al., 1997), and timing of ingress is related to wind and potentially Gulf Stream forcing (Stegmann and Yoder, 1996; Hare et al., 1999). Age and size at ingress increase during the ingress season of winter spawning fish and are quite variable on any given day (Warlen, 1994; Hettler et al., 1997). In contrast, ingress of gray snapper is largely predictable based on moon phase. Further age and size of gray snapper at ingress is relatively fixed. Many coral reef fish species exhibit lunar patterns in settlement and have relatively fixed larval durations (Robertson et al., 1988; Sponaugle and Cowen, 1994, 1997). These differences in timing of ingress and age and size at ingress between gray snapper and the suite of winter-spawning fishes indicate that ingress patterns are species dependent rather than a function of the physical properties of estuaries.

While the role of inshore areas as nursery habitats for temperate groundfish species has been studied extensively and is well documented (e.g., Zijlstra, 1972; Hoss and Thayer, 1993), studies on the use of inshore nursery habitats by reef fish have only recently begun (e.g., Able et al., 1995; Sheaves, 1995; Gillanders, 1997). Most coral reef fish research has focused on species that settle directly to reefs without making use of a separate nursery habitat (Sale, 1991, 2001). Many snappers and groupers, however, use a variety of inshore habitats as nurseries, including mangroves, seagrasses, estuaries and patch reefs (Keener et al., 1988; Dahlgren and Eggleston, 2000). To understand the dynamics of the recreationally and commercially important snappers and groupers, the processes related to survival during residency in distinct, juvenile habitats need to be elucidated; these processes include pelagic larval survival, mechanisms of ingress/settlement, juvenile survival in nursery habitats, and mechanisms by which juveniles move to adult habitats.

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