Abstract.—The onshore movement of settlement-stage bonefish, *Albula vulpes*, leptocephali was monitored over four consecutive winters (1990–91 to 1993–94) and summer 1992 near Lee Stocking Island, Exuma Cays, Bahamas. Total catch over the four winters ranged from 316 to 1,421 fish per 70-day sampling period, whereas 1,112 were taken during the single 72-day summer sampling period. An analysis of otoliths from 87 fish collected during the last winter indicated continuous spawning activity during the fall and early winter and an estimated larval duration of 41 to 71 days. The collection of larvae in summer 1992 suggested that spawning continues until late spring. Virtually all recruiting leptocephali were collected at night and in the upper 1 m of the water column. Time-series analysis of the four winters linked together by lunar date revealed a strong cyclical pattern of recruitment, with a period of 30 days, and a strong association with the number of hours of flood tide occurring under dark, moonless conditions. The one major peak in the summer samples occurred during the first 12 days of sampling when the hours of dark flood tide was at its maximum level for the month; subsequent dark periods had low levels of recruitment. There were no strong associations between recruitment levels and wind and current patterns. These data suggest that the cyclical pattern in hours of dark flood tide creates "windows of opportunity" for the leptocephali to move onshore at times that minimize their vulnerability to visual predators in reefs and seagrass beds.

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Recruitment of bonefish, *Albula vulpes*, around Lee Stocking Island, Bahamas

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The bonefish, *Albula vulpes*, is found in the tropical western Atlantic and supports substantial recreational fisheries in south Florida, the Bahamas, and many Caribbean islands. Despite their importance as a sport fish, there is little quantitative information available about the abundance of adults in different locations, the temporal trends in population sizes, and the recruitment processes that may have a considerable influence on the size and spatial distribution of adult populations.

Adult bonefish typically inhabit shallow sand and seagrass flats, often in water less than half a meter deep, and feed on crabs, bivalves, shrimp, and small benthic fishes (Bruger, 1974; Colton and Alevizon, 1983). Some information on the seasonality of reproduction is available, but the temporal and spatial scales of spawning activity or spawning behavior itself have not been described. In the Florida Keys, spawning occurs from October to May.[1] Examination of gonads of fishes collected in the Bahamas indicated that fish in spawning condition also predominated between October and May, although some ripe fish were found throughout the year.[2]

In the pelagic environment, *Albula* leptocephalous larvae grow to lengths of up to 70 mm prior to settlement. On the basis of the temporal occurrence of ripe females and the subsequent appearance of metamorphosing leptocephali, Pfeiler et al. (1988) proposed a larval duration of six to seven months for *Albula* sp. from the Gulf of California. As the leptocephali move from offshore to the shallow nursery and adult habitats, their length decreases approximately 50% during their metamorphosis into juveniles. Pfeiler (1984) investigated the movement of *Albula* sp. leptocephali as they entered a hypersaline lagoon (estero) in the Gulf of California. Although sampling was limited to 15–20 minute periods of flood tide on 33 nights from February through May, Pfeiler suggested that larvae

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[1] Crabtree, R. E. 1994. Florida Department of Environmental Protection, Marine Research Institute, St. Petersburg, FL. Personal commun.

[2] Colton, D. E. 1994. 27395 Vista Del Toro Road, Salinas, CA. Personal commun.

moved into the lagoon during the first several hours of the flood tide and that there was no movement into or out of the lagoon during the ebb tide.

Although the leptocephali of *Albula vulpes* have been found throughout the Caribbean from Brazil to Bermuda and the southwestern Gulf of Mexico (Smith, 1989), few previous studies have investigated the larval biology of the species or their movement from the pelagic realm to the shallow juvenile habitat (e.g. Eldred, 1967; Thompson and Deegan, 1982). This study presents data on the recruitment of metamorphic *A. vulpes* in the Bahamas as they move from the deep pelagic Exuma Sound onto the shallow Great Bahama Bank near Lee Stocking Island (LSI). Data collected over four consecutive 70-day winter sampling seasons and one summer season were used to evaluate the effects of various environmental parameters that have been shown to influence recruitment of a variety of taxa (Shenker et al., 1993; Thorrold et al., 1994, a and b). The otoliths of 87 individuals that recruited during the 1993–94 winter season were examined to determine the presumed spawning (hatching) dates and to estimate the larval duration of *A. vulpes* in the Bahamas.

Materials and methods

Data collection

Larval bonefish were collected with moored channel nets suspended in two tidal passes on the western edge of Exuma Sound, Bahamas, immediately north of Lee Stocking Island (Fig. 1). Winter sampling was conducted from 17 December 1990 to 28 February 1991, 13 December 1991 to 26 February 1992, 12 December 1992 to 25 February 1993, and 10 December 1993 to 23 February 1994. Summer data were collected from 25 June to 4 September 1992. Station locations, net designs, and sampling protocols are detailed in Shenker et al. (1993) and Thorrold et al. (1994a). To summarize, each of three stations (corresponding to stations 1, 2, and 3 in Shenker et al., 1993) were equipped with both a surface net (mouth area=2 m wide ×1 m deep) and a midwater net (2 m×2 m) which fished the 2–4 m deep layer. Samples were removed from the 3-mm mesh nets after dawn and before dusk each day. In this study, we pooled catches among all six nets. Because less than 10% of the *A. vulpes* larvae were taken in the day samples, our analysis focuses on only the samples collected at night.

Wind speed and direction data during the first, third, and fourth winters, and the one summer were collected hourly at a Campbell Scientific weather station on LSI. During the second winter, the weather station was inoperative and measurements were recorded twice daily with a hand-held anemometer. After statistical analysis of a summer period when hand-held anemometer and weather-station data were recorded, it was determined that the hand-held anemometer data were consistent with those of the weather station (Thorrold et al., 1994b). No weather data were available for the month of December during the third winter or for the period from 1 through 10 January 1994.

Current patterns were monitored with a General Oceanics Mark II current meter moored on the shelf edge at a depth of 10 meters (Fig. 1). Hourly current data were recorded for one month during the first

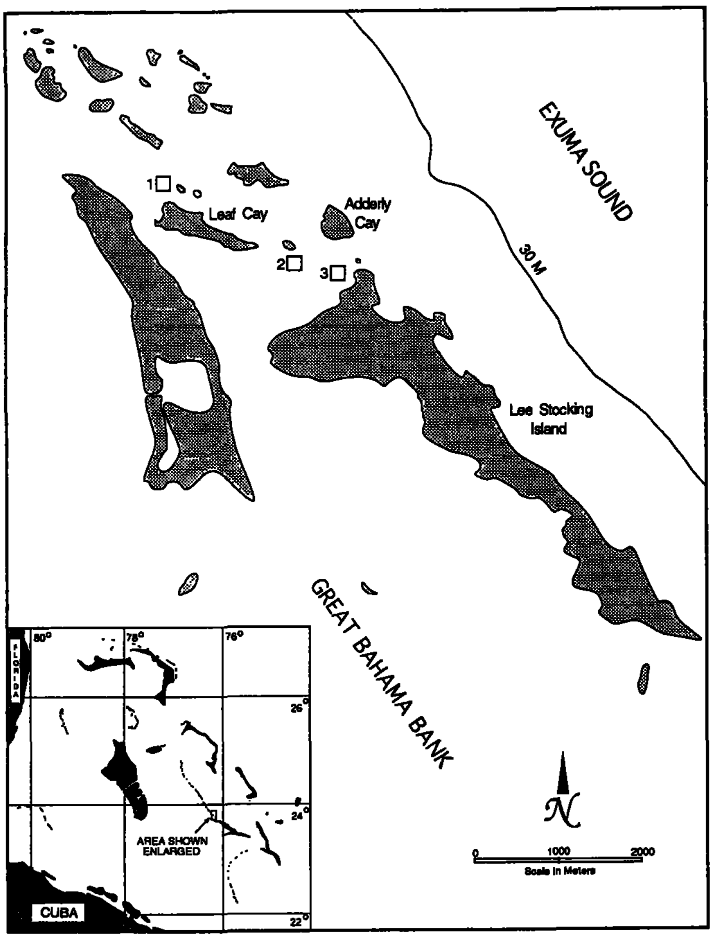

Figure 1
Location of Lee Stocking Island, Bahamas, and channel-net stations.

winter (23 January to 22 February), throughout the entire second and fourth winters, and for the one summer sampling period. Current meter data were not available for the entire third winter. For analysis, hourly wind and current data were averaged over 24 hours to generate estimates of mean flow, which were then decomposed into along-shore and cross-shelf components of motion.

Data analysis

The *A. vulpes* leptocephali from all six nets for each night during the winter sampling periods were summed for time-series analysis. To analyze the relationship between recruitment patterns and lunar phase, time series of fish abundances for the four winters were joined according to lunar month. Nine days were deleted from the beginning and six days from the end of 1991–92 (winter 2), and three days were deleted from the beginning of 1993–94 to ensure continuity with respect to the lunar month. Analyses were carried out on the resultant 277-day period. The time series was log 10 $(x+1)$ transformed to minimize the influence of several large peaks in the data. All time-series analyses were completed by using the statistical package Mesosaur (Kuznetsov and Khalileev, 1991).

A periodogram of the recruitment data was constructed to identify dominant periodicities within the 277-day time series. An autocorrelation function was then plotted to describe more accurately the cyclical patterns of the data. Finally a cross-correlation was run between the abundance time series and the corresponding "hours of dark flood tide" of each night, which previous studies had identified as an important variable affecting recruitment patterns of a number of taxa (Shenker et al., 1993; Thorrold et al., 1994b). The hours of dark flood tide is a measure of the total number of flood tide(s) that occur between sunset and sunrise under moonless conditions. This variable differs from lunar phase in a subtle but significant manner: as the time of moonrise becomes progressively later over consecutive nights, greater portions of the evening flood tide occur during darkness prior to moonrise. Because significant autocorrelations exist in both the larval abundance and the tidal time series, the resultant correlation coefficients could not be assigned statistical significance, and therefore confidence limits are shown only for reference. These plots can be used to center periodicities in recruitment with respect to the hours of dark flood tide.

Cross-correlations were used to examine responses of recruiting larvae to wind and current patterns. Because wind and current data were collected inconsistently over the four winters, each year was analyzed separately. Significant autocorrelations present in both recruitment and environmental data meant that standard correlation coefficients would be artificially high (Chatfield, 1979). To remove the effects of these autocorrelations, ARIMA (Auto Regressive Integrated Moving Average) models were fitted to all data. Residuals generated from the ARIMA models were then used in the cross-correlations. Only those correlations that identified a response of larvae to particular wind and current patterns on a lag of up to three days (i.e. fish moving onshore up to three days after a specific wind or current pattern) are presented. Occasional correlations at lags of greater than three days were observed but are difficult to interpret in a biological sense and may be statistical artifacts.

Although the one set of summer data was not long enough to permit rigorous analysis for cyclical patterns, and the level of recruitment was generally too low for correlation with environmental conditions, the data were examined for resemblance to patterns identified by the time series and correlation analyses of the winter data sets.

Otolith analysis

Otoliths were removed from 150 of the 875 larvae collected throughout the 1993–94 winter season. All fishes collected during this winter were preserved in 70% ethanol. Specimens selected for analysis were chosen from each day when recruits were captured. However, preservation problems in some larger samples prevented a more detailed examination of the hatching patterns of large pulses of recruits.

Sagittae were dissected and mounted in cyanurate glue on a labelled glass slide. After curing for 24 hours, otoliths were polished down to the midplane with a graded series of lapping papers with grits ranging from 9 to 0.3 microns. A circle etched into the slide with an electronic engraver prevented the cyanurate glue from dislodging from the slide during polishing. Prepared slides were projected onto a computer screen at 1000× by using a Sony TR81 camera integrated through a Macintosh 2CI computer equipped with Media-Grabber. This greatly facilitated counting and allowed two readers independently to view the otolith(s) back-to-back under similar lighting conditions. Otoliths were randomized and each otolith was read twice by each reader; if the different readers obtained mean counts within five increments of each other, the mean values were averaged and used for analysis. The otolith was discarded if differences in mean counts were greater than five increments. A total of 87 of the 150 mounted otoliths met this readability criterion.

Results

Winter environmental conditions

Winds in Exuma Sound during the four winters generally blew from the east or southeast; there is a considerable cross-shelf component of motion across the shelf edge that runs northwest-southeast (Fig. 2). The predominant along-shore component of the wind was towards the northwest. Passage of occasional storm fronts or cold fronts with winds from the northeast was characterized by cross-shelf winds at velocities exceeding 5 $m \cdot sec^{-1}$ and by along-shore flow to the southeast.

Currents on the outer edge of the shelf flowed predominantly along the shelf toward the northwest with only a weak cross-shelf component of motion (Fig. 2). Flow onto the shelf, and occasional current reversals along the shelf to the southeast were typically associated with the passage of storm fronts (Shenker et al., 1993).

The hours of dark flood tide cycled throughout the study, ranging from 0 to 7 hours per night (Fig. 3). The nights with 0 hours of dark flood tide occurred when the full moon was visible during the entire night flood tide. During the week after each full moon, moonrise became progressively later each night, and the amount of flood tide occurring between sunset and moonrise increased rapidly.

Temporal patterns of recruitment during winter

A total of 3,079 *A. vulpes* leptocephali were collected during the 277 nights of sampling over four winters (Fig. 3). Recruitment levels varied greatly among years; a low of 316 leptocephali were taken the first winter and 1,421 during the third winter. Several large peaks in recruitment, reaching a maximum of 190 fish/night, were detected during the third and fourth winters. Over all four years, 90.2% of the leptocephali were captured by the nets fishing the upper 1 meter of the water column.

Periodogram analysis of *A. vulpes* recruitment indicated a very strong cycle with a period of 30.7 days, which suggests a lunar or tidally influenced cycle (Fig. 4). Autocorrelation of recruitment data (Fig. 4) also identified cycling centered around 30 days. Cross-correlations between recruitment and hours of dark flood tide (Fig. 4) showed a strong positive association on nights with a high degree of flood tide occurring during moonless portions of the night and a negative relationship centered around the full moon.

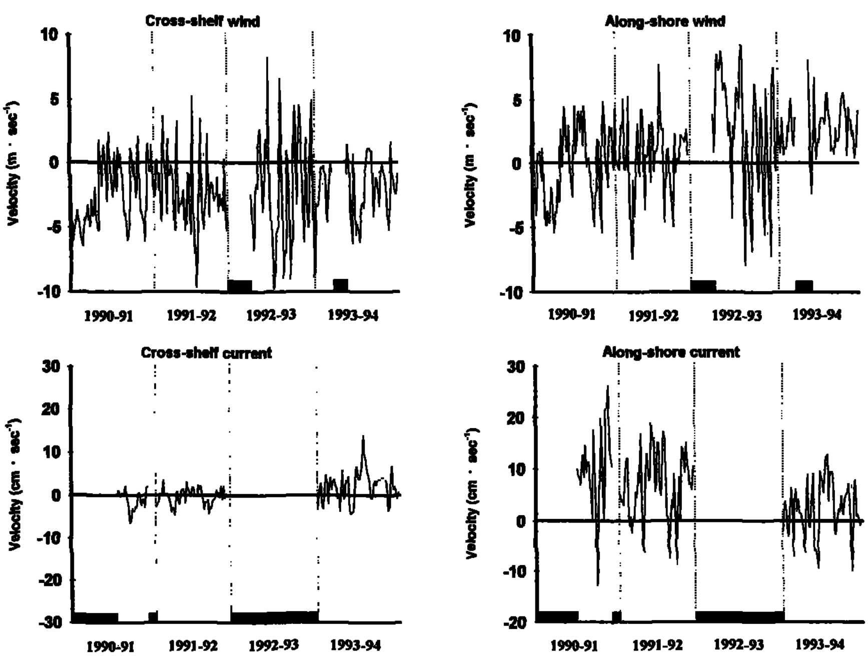

Figure 2

Cross-shelf (above line=movement offshore, below line=movement onshore) and along-shore (above line=to northwest, below line=to southeast) components of motion for wind and currents at Lee Stocking Island. Dotted vertical lines indicate where years are joined by lunar date. Solid bars on abscissae indicate when no data were available.

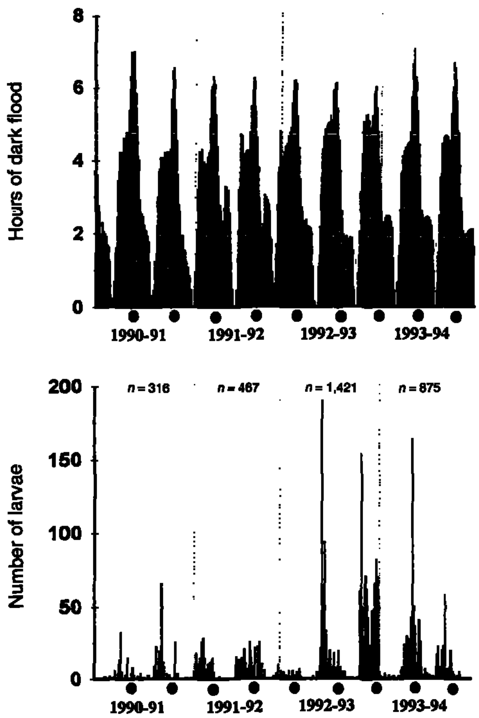

Figure 3

The total hours per night when the moon was below the horizon and the tide was flooding (hours of dark flood) throughout the four winter study periods (top graph). Dotted vertical lines indicate where years are joined by lunar date. Circles on abscissae indicate new moons. Total abundance of bonefish, *Albula vulpes*, larvae collected by channel nets during the four consecutive winters (bottom graph). Values above each year indicate total catch.

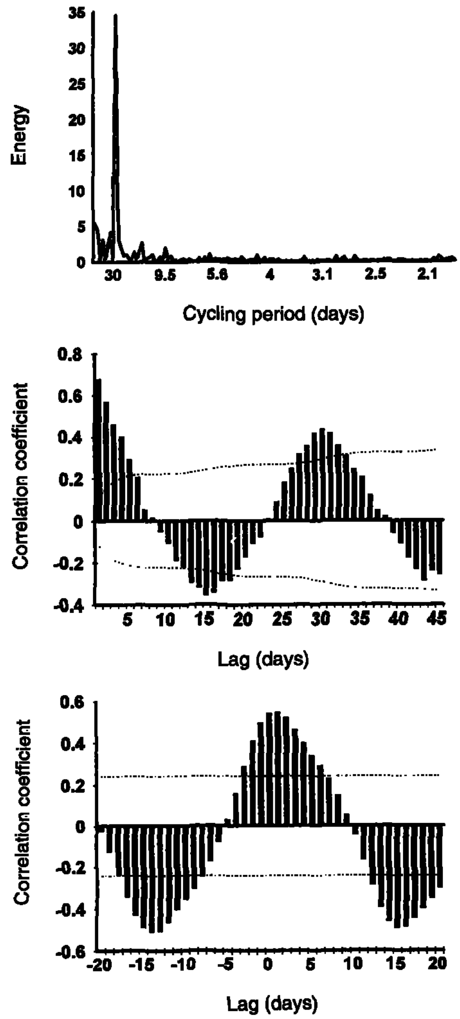

Figure 4

Periodogram plot of logged larval concentrations of bonefish, *Albula vulpes* (top graph), autocorrelation function of log $(n+1)$ larval abundance (middle graph) and cross-correlation function of log $(n+1)$ larval abundance with hours of dark flood tide (bottom graph). All analyses were conducted on the 277-day period which resulted from joining the four years of recruitment (and hours of dark flood) by lunar date. Dashed lines in autocorrelation and cross-correlation plots indicate approximate 95% confidence intervals. The cross-correlation plot coincides with lunar days starting with the new moon (lag of zero).

Few significant correlations between recruitment of bonefish and oceanographic or meteorological conditions were detected (Table 1). Recruitment was positively correlated with along-shore winds to the northwest with a lag of zero days for the 1991–92 season, whereas recruitment peaks the following winter lagged winds to the southeast by three days. No significant relationships between along-shore winds and recruitment were found during the other two winters, nor were relationships detected between recruitment and cross-shelf winds or either cross-shelf or along-shore currents.

Temporal patterns of recruitment during summer

A total of 1,112 *A. vulpes* leptocephali were collected during summer 1992. Over 76% of these fishes were taken during the first 12 days of the 72-day sampling season, and a peak of 160 leptocephali were taken during a single night (Fig. 5). Although this sampling period is too short for time-series analysis, recruitment appears to be limited to periods with relatively high amounts of flood tide occurring under moonless conditions (Fig. 5). The single peak in recruitment was not associated with specific wind or current patterns (data not shown); the very low numbers of fishes collected during following months precluded use of correlation analysis to examine the relationship between recruitment and environmental conditions.

Table 1

Results of cross-correlation analyses between recruitment of *A. vulpes* and along-shore and cross-shelf wind and current vectors for four winters. The table shows all significant correlation coefficients between larval recruitment and wind and current data, with a lag corresponding to the number of days indicated. Positive correlations indicate signficiant relationships with transport to the northwest (along-shore component) or offshore (cross-shelf component). Numbers below years in parenthesis indicate the number of days used in each analysis. NS = not significant (α=0.05). ID = insufficient current meter data for analysis.

	Wind		Current	
Year	Along-shore	Cross-shelf	Along-shore	Cross-shelf
1990–1991 (72)	NS	NS	ID	ID
1991–1992 (62)	0.28/0 days	NS	NS	NS
1992–1993 (55)	–0.22/3 days	NS	ID	ID
1993–1994 (58)	NS	NS	NS	NS

Larval ages and spawning patterns

Though the formation of daily otolith increments for *A. vulpes* has yet to be confirmed, the daily formation of increments in *Anguilla japonica* leptocephali has been verified (Umezawa et al., 1989). We thus assumed that increments are produced daily in bonefish and that deposition of increments begins at hatching. Given these assumptions, the average larval duration was 56 days, a range of 41–71 days (Fig. 6). Regression analysis of back-calculated hatching date and recruitment date revealed a strong relationship. Backcalculation of hatching dates from otolith data indicated continuous spawning from mid-October through early January (Fig. 6). The maximum number of otoliths examined per day was 7 for fish recruiting on 30 January. The back-calculated spawning dates of these fish ranged from 16 November to 27 December.

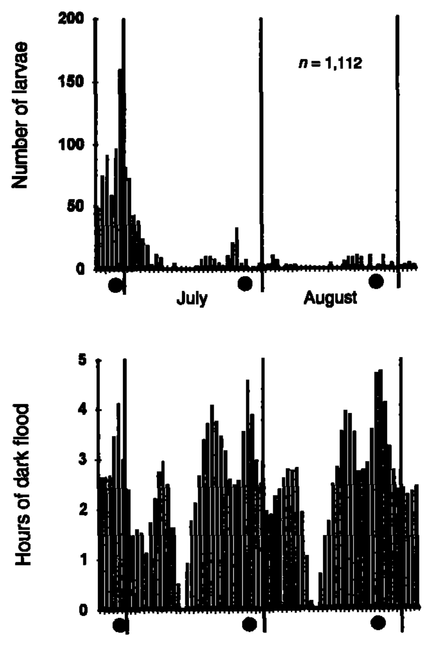

Figure 5

Abundance of bonefish, *Albula vulpes*, larvae collected each night from 24 June to 4 September 1992 (top graph) and hours of dark flood tide during the sampling period (bottom graph).

Discussion

Variation in the recruitment of tropical marine fishes is considered to be a dominant influence on the size and distribution of adult populations. Doherty and Fowler (1994) have shown that variations in the recruitment of a reef-dwelling territorial pomacentrid over a ten-year period could explain 90% of the variation in adult populations. Dramatic variability in larval recruitment has been detected by light trap surveys (e.g. Doherty, 1987; Milicich et al., 1992), visual surveys (e.g. Sale, 1980; Robertson et al., 1988; Robertson, 1992), and calculation of settlement patterns from otoliths (e.g. Thresher et al., 1989; Wellington and Victor, 1989). Recent work in the Bahamas (Shenker et al., 1993; Thorrold et al., 1994, a and b) and French Polynesia (Dufour and Gazlin, 1993) have shown that moored channel nets can be used to monitor onshore larval movement directly

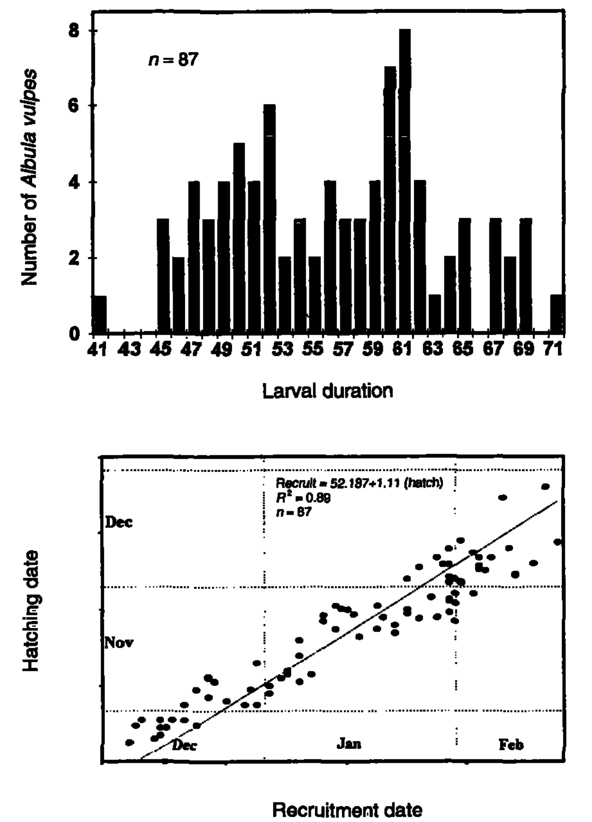

Figure 6

Frequency distribution of estimated larval duration (top graph) and relationship between estimated hatching date and recruitment date (bottom graph) of bonefish, *Albula vulpes*, collected during winter 1993–94.

through tidal passes and can help elucidate the patterns of recruitment and mechanisms driving transport. Although adult population sizes of highly mobile fishes such as *Albula vulpes* have yet to be measured, it is likely that whatever variation does occur in the abundance of adults is at least partially affected by recruitment variability.

A virtually universal pattern observed by studies on daily recruitment of tropical marine fishes is the association of peaks of recruitment with dark phases of the lunar cycle (Pfeiler, 1984; Robertson et al., 1988; Robertson, 1992; Dufour and Gazlin, 1993; Shenker et al., 1993; Thorrold et al., 1994, a and b). This pattern may be a function of a lunar spawning cycle, followed by a fixed larval duration. Alternatively, it may be an active response of fishes, enabling them to remain in the plankton until dark conditions permit them to move onshore, thus enabling them to avoid the "wall of mouths" of visual predators along reef edges (Hamner et al., 1988) and at settlement sites.

Our data suggest that *A. vulpes* follows the latter strategy. Analysis of larval otoliths of winter recruits (assuming that otolith increments are deposited daily, beginning at hatching) indicates that these fish spawn continuously from late October through December (Fig. 6). However, owing to preservation problems with some of the large recruitment pulses (>100 animals/night) in winter 1993–94, when otolith analyses were performed, we cannot exclude the possibility that the level of spawning activity varies over time. Significant spawning activity in the Bahamas probably extends until spring, with the large pulse of recruitment in late June 1992 presumably resulting from spawning in April and May.

After hatching, leptocephali remained in the pelagic environment of Exuma Sound for 41–71 days (with a mean of 56 d) in winter 1993–94. Despite this relatively broad range of larval duration, the metamorphosing larvae exhibited a very strong cyclical recruitment pattern (Fig. 4) that was not consistently related to meteorological conditions or currents measured along the shelf-edge seaward of the sampling stations (Table 1). This response supports the contention of Thorrold et al. (1994, a and b) that various species can actively control their onshore movements in certain environments, perhaps by delaying their metamorphosis until suitable environmental conditions or opportunities develop (Wellington and Victor, 1989). However, variable shrinkage of leptocephali, due to different times between capture, death in the nets, and preservation, prevented backcalculation of growth rates and a test of the ability of *A. vulpes* to delay metamorphosis.

In series of ichthyoplankton surveys from January through February 1991, *A. vulpes* leptocephali were found to be widely dispersed at night over a transect extending from the shelf edge near LSI to 24 km offshore (Drass, 1992), indicating that some larvae were always close enough to the shore so that they might become entrained in the flood tides crossing the narrow shelf. Despite the continuous presence of leptocephali close to the coast, however, their onshore movement was temporally restricted. The occurrence of favorable low nocturnal illumination levels may be the parameter that limits cross-shelf movement of larvae to specific "windows of opportunity." These windows of opportunity were defined by the relationship between lunar and tidal conditions. During bright, moonlit nights, recruitment levels were very low (Figs. 3 and 5); recruitment increased as larger amounts of night-time flood tide occurred prior to the progressively later moonrise. Extremely little recruitment occurred on nights when there were less than two hours of nocturnal flood tide under moonless conditions, whereas the

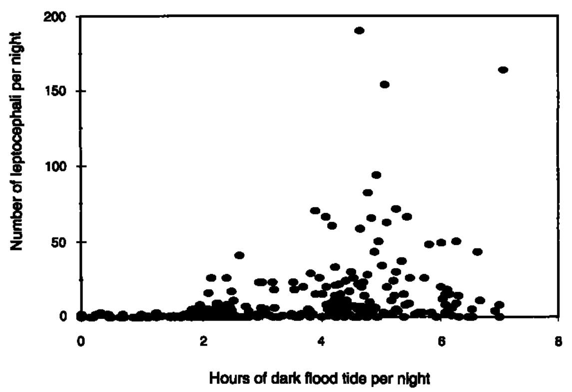

Figure 7

Number of bonefish, *Albula vulpes*, collected versus hours of flood tide occurring under moonless conditions. Most recruitment occurred on nights with >4 hours of flood tide under moonless conditions.

great majority of recruitment was observed on nights with more than four hours of dark flood tide (Fig. 7). The restriction of recruitment to these windows of opportunity may be responsible for the apparent bimodality in the age distribution of leptocephali (Fig. 6), although larger numbers of organisms need to be examined to test this possibility. Additional work is needed to determine whether onshore movement is concentrated in specific portion(s) of a flood tide and how cloud cover can affect lunar illumination and recruitment.

Active vertical migration may be the mechanism by which larvae influence the timing of onshore migration (Shenker et al., 1993). Early larvae were distributed through the pelagic environment of Exuma Sound to depths of 25–50 m (Drass, 1992). Migration of settlement-stage individuals toward the surface only under dark night conditions could enhance the entrainment of larvae into onshore tidal and wind-driven flow. The fact that over 90% of the *A. vulpes* larvae were taken by the channel nets in the upper 1 m of the water column during dark-night recruitment pulses, when only a relatively few larvae were found 2–4 m below the surface, indicates that these leptocephali do indeed selectively utilize the surface layer during their onshore movement.

The recruitment of *A. vulpes* leptocephali varied greatly among days, months, and years. This variability was generally not correlated with specific wind or shelf-edge current patterns (Table 1), unlike the very close association between a major settlement episode of Nassau grouper, *Epinephelus striatus*, and a storm event at LSI in February 1991 (Shenker et al., 1993). Recruitment of *A. vulpes* was thus more similar to that of other taxa recruiting near LSI (e.g. Bothidae and Labridae) that showed a lunar periodicity in recruitment but not a strong association with environmental parameters (Thorrold et al., 1994, a and b). The lack of strong correlation between environmental conditions and recruitment and the high degree of recruitment variability among months and years suggest that the processes controlling the supply of larvae are acting prior to their onshore movement in Exuma Sound. These processes span the range from spawning success to larval survival in the pelagic environment and will require additional sampling for evaluation of their potential roles as bottlenecks in the population of *A. vulpes* in the Bahamas.

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