FULL PAPER

Patterns of distribution and abundance of bonefish larvae *Albula* spp. (Albulidae) in the western Caribbean and adjacent areas

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Abstract Overall patterns of distribution and abundance of *Albula* spp. leptocephali larvae offshore in the western Caribbean Sea (CAS) and Gulf of Mexico (GOM), and in coastal waters of the Mexican Caribbean (MXC) were analyzed from: (a) cruise data available from the Academy of Natural Sciences of Philadelphia (CAS, GOM) and (b) coastal plankton surveys (1998–2002 and January 2004) (MXC). We found striking inshore-offshore differences in the larval catch and size structure. Offshore cruises yielded 57 leptocephali, mostly determined as early stage I (18.0 ± 8.2 mm SL, mean $\pm$ SD). In contrast, coastal samples yielded 2,466 larvae 51.4 ± 3.6 mm SL, mostly late stage I; of these, 2,345 (95%) were caught over 4 nights in January 2004. The relationship between the larval length (mm, SL) and the distance to the coastline (km) was best represented by the regression model $LENGTH_{ij} = 51.44 - 0.235 \cdot DISTANCE_{ij} + \varepsilon_{ij}$ with a distinct variance for each locality. To ascertain whether the coastal inflow of leptocephali follows a regular seasonal pattern or depends on episodic events will require further monitoring; available evidence suggests that the southern coast of the MXC offers favorable conditions for the recruitment of *Albula* spp. larvae.

Introduction

Bonefish are primitive forms of the Elopomorpha; they are being taxonomically reviewed (Colborn et al. 2001; Pfeiler et al. 2006; Adams et al. 2007; Bowen et al. 2007). For decades, one species, *Albula vulpes*, was thought to have a widespread distribution and was considered to be a circumtropical form (Briggs 1960; Alexander 1961). In the Western Atlantic region, only two species were known to occur: *A. vulpes,* distributed in Florida, the Gulf of Mexico, the Mexican Caribbean, and Belize (Hildebrand 1963; Schmitter-Soto et al. 2000), and *Albula nemoptera,* in the Greater Antilles, Belize, and Panama to Brazil (Rivas and Warlen 1967; Smith et al. 2003). This simplified view changed after a DNA comparative study, which revealed *A. vulpes* as a species complex including at least eight genetically distinct cryptic species (Colborn et al. 2001). This finding revealed the occurrence of a third species in the Caribbean region (*Albula* species B), known as *Albula garcia* (nomen nudum); its description is in progress (Adams et al. 2007; Bowen et al. 2007). Hence, in this paper we refer to bonefish larvae as *Albula* spp.

Species of *Albula* occur in the coastal and inshore waters of tropical seas worldwide. The life history of bonefish

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involves a larval stage called the leptocephalus. It is a transparent, ribbon-like larvae that can be easily distinguished from leptocephali of other families (Alexander 1961; Smith 1989). Larval bonefish development is characterized by three stages: two periods of length increase (stages I and III) separated by a period of length decrease (stage II). At the end of stage II, the leptocephalus acquires the appearance of a juvenile and starts growing again to the adult stage (Alexander 1961).

At the regional level, bonefish are a valuable target for sport fishing that supports an economically important recreational fishery, for instance, in Florida, USA, bonefish contribute nearly $1.5 billion every year (Ault et al. 2007). Just as with many tropical areas, in our study area of central and southern regions of Quintana Roo, Mexico, bonefish are also a highly appreciated target for catch-and-release sport fishing, representing additional income for coastal communities, although state-wide data on economic value and stock assessment are lacking (María del Carmen García, personal communication).

Ichthyological research previously conducted in the Mexican Caribbean is mostly descriptive, focused on lists of species occurring as adults. For bonefish there are also some records of larvae and juveniles (Vásquez-Yeomans et al. 1998; Vásquez-Yeomans and Richards 1999; Schmitter-Soto et al. 2000; Mora 2003; Ordóñez-López 2004; Herrera-Pavón and Arce-Ibarra 2004). In this paper, we review abundance data of *Albula* spp. leptocephali in open and coastal waters of the Mexican Caribbean, based on available information from: (A) the database of the Academy of Natural Sciences of Philadelphia (ANSP) from the research cruises MBI conducted in the Caribbean and the Gulf of Mexico and (B) coastal ichthyoplankton surveys along the central and southern coasts of the Mexican Caribbean during two periods: (B1) 1998 to 2002 and (B2) January 2004. We use these datasets (A, B1, and B2) to describe inshore-offshore patterns of distribution and abundance of leptocephali of *Albula* spp., and to model the relationship between larval length (mm SL) and distance to the coastline (km). We discuss these patterns in terms of habitat (coastal and offshore), sampling methodology, and seasonal occurrence.

Materials and methods

Study site. The Mexican Caribbean refers to the coast of Quintana Roo, a state of Mexico located on the westernmost sector of the Caribbean Basin (17°48′N, 21°10′W). Along this coastline is the northern end of the Meso-american Barrier Reef System (MBRS), which continues southward to Belize and Honduras. Between the reef crest and the coastline lies a shallow, narrow (250–1,000 m) reef lagoon, harboring beds of seagrasses (mainly

Thalassia testudinum) and coral patches. Two major bays are located on the central coast of the Mexican Caribbean, Bahia de la Ascensión (740 km^2) and Bahia del Espiritu Santo (350 km^2). Rio Huach, a lagoon complex to the south, is connected to the Caribbean Sea through a narrow channel. Bahia de Chetumal is the largest bay in the Mexican Caribbean and is connected to the ocean through two channels: the narrow and mangrove-bordered Bacalar Chico and the recently opened, manmade Zaragoza channel (Fig. 1).

Cruise documentation. At a regional level, important sources of information on *Albula* spp. leptocephali are the MBI research cruises, for which we consulted the records of the Philadelphia Academy of Natural Sciences [WWW.database] URL http://data.acnatsci.org/. These MBI collections originate from four main cruises made in the Yucatan Channel and the western Gulf of Mexico during the following time periods: 8–19 November 1975, 10–23 April 1976, 13 February–2 March 1977, and 20 July–5 August 1977. Two additional cruises were conducted off Cozumel in August 1975 and off Veracruz in August 1976. The number of cruise stations ranged from 10–13, between 180 to 1,800 m of depth, with each station consisting of five tows of a conical plankton net (2 m mouth diameter, 10 m length, and 0.570 mm mesh); most hauls were made at night (Smith 1989).

Coastal plankton surveys. Coastal ichthyoplankton samples were collected by our research group on the central and southern coast of the Mexican Caribbean during two periods: (1) 1998–2002 and (2) January 2004. The plankton surveys during 1998–2002 did not follow a strict sampling program. Larvae were collected in different months, except February and October, in four coastal systems: Punta Allen (19°48′N, 87°27′W), Rio Huach (18°25′N, 87°45′W), Xcalak (18°16′N, 87°49′W), and Bacalar Chico (18°11′N, 87°50′W) (Fig. 1). Most of the samples were taken with conventional gear: standard plankton net (0.5 m mouth opening, 0.5 mm mesh) towed for 10 min in a circular trajectory near the surface. Other sampling gear used included a sled sampler (0.7 m × 0.4 m, 0.5 mm mesh) towed for 15 min on a horizontal plume 25 cm above the bottom and a nightlight lift-net (0.5 m mouth-opening, 0.5 mm mesh) deployed at night (1900–0700 h) for 20-min periods, around the new moon (Rooker et al. 1996). Sea surface temperature averages during samplings varied between 26.3°C in December to 31.1°C in August. Mean values of salinity ranged from 24.5 psu in December to 35.2 psu in August.

In January 2004, plankton surveys were carried out during four consecutive nights around the new moon (23 January): January 22 and 23 on the reef off Punta Allen, and January 24 and 25 on the reef off Xcalak. In both areas samples were obtained using two moored channel nets

Fig. 1 Study location in the western Caribbean and adjacent areas. *Closed triangle* leptocephali collected by MBI cruises; *closed circle* leptocephali collected in coastal waters of Mexican Caribbean
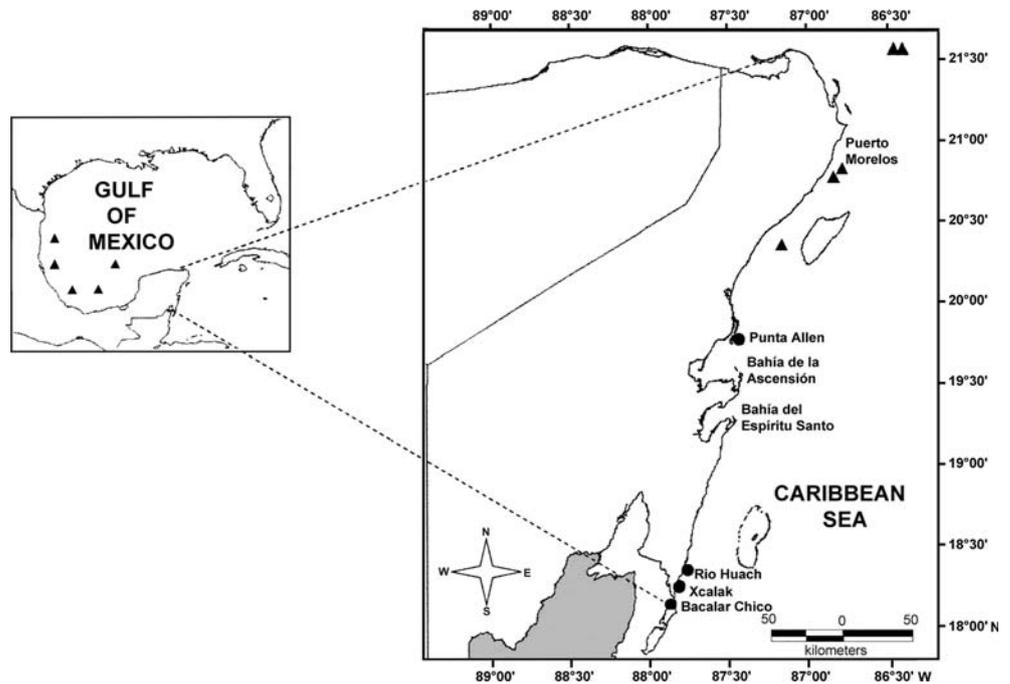
(1 mm mesh) suspended in two tidal passes on each reef (Shenker et al. 1993) and three light traps (Jones 2006) deployed in relatively protected waters inside the reef lagoon, before dusk (1900 h) and emptied after the following dawn (0600 h). Samples were fixed and preserved in 70% ethanol. All *Albula* spp. larvae were removed from the samples with the aid of a stereomicroscope and stages identified following current morphological criteria: stage I, has snout slightly hooked, spaced teeth extended in both jaws, and nostrils fused; early stage II, snout not hooked, teeth very small (reabsorbed) not spaced, numerous on both jaws, nostrils with signs of division (Alexander 1961; Eldred 1967). Specimens were deposited in the Collection of Fish Larvae of ECOSUR (ECO-CH LP) in Chetumal, Mexico.

Data analysis. The array of sampling gear used precludes expressing abundance data on absolute density. It must be stressed that it was not our goal to accomplish a direct quantitative comparison between larval catches from different sources, which requires data standardization. Instead, we used a simple index of relative abundance, i.e., number of larvae caught per sampling station, aiming to describe the range, average, and variability of observed values of the catch of leptocephalus larvae obtained using a diverse array of sampling gear across localities and habitats. Evidently, some combination of sampling gear, locality, and habitat yields higher catches compared to other combinations. This develops into a condition of "confounded effects," where the effect due to each factor cannot be assessed separately (Ramsey and Schafer 2002).

The standard length (SL) of all leptocephali from coastal samplings 1998–2002 and a subsample ($n = 430$) of the larvae captured in January 2004 were measured to the nearest 0.1 mm. These data, together with the size data from the ANSP's database, were related to the corresponding distance in km between the sampling station and the coastline using linear regression and additive models (Sokal and Rohlf 1995; Zuur et al. 2007). To represent the relationship between larval size and distance, several candidate models were considered, including conventional ones assuming a constant variance of residuals in addition to models having a distinct variance for each locality: two open ocean locations (Gulf of Mexico and Caribbean Sea) and three coastal locations (Punta Allen, Rio Huach, and Xcalak). The model selection procedure relied upon the AIC index from the information theoretic statistical framework (Burnham and Anderson 2002; Zuur et al. 2007). In the case of the larvae that we collected, we used both size and morphological criteria to determine the stage of the larvae; that most of our larvae were late stage I (preshrinkage) and early stage II. Thus, the misleading effect due to using only one size involves only a reduced part of the data ($n = 10$) from one MBI cruise (February–March 1977), with a mean size of 30.7 ± 5.8 mm, of which only length data were available.

To determine if mean size of larvae differed between reef lagoon and mangrove channels, sizes of larvae collected during 1998–2002 were examined with Student's test. All the above-mentioned statistical analyses and

procedures were performed using the R software platform (Ihaka and Gentleman 1996; http://www.cran.r-project.com).

Results

A total of 57 leptocephalus larvae of *Albula* spp. were found in 23 records of the ANSP database, corresponding to offshore stations (ca. 8 to 263 km) from the northern sector of the Mexican Caribbean (12) and the western Gulf of Mexico (45). Mean size (±SD) of these *Albula* spp. larvae was 18.0 ± 8.2 mm SL (Fig. 2a). One hundred twenty-one leptocephali from 1998–2002 collections in coastal localities of the central and southern Mexican Caribbean were larger, with a mean size of 55.3 ± 3.6 mm SL (Fig. 2b). Of a total of 2,345 larvae collected in Punta Allen and Xcalak during January 2004, a subsample (n = 430) had a relatively similar size (50.8 ± 2.9 mm SL) (Fig. 2c).
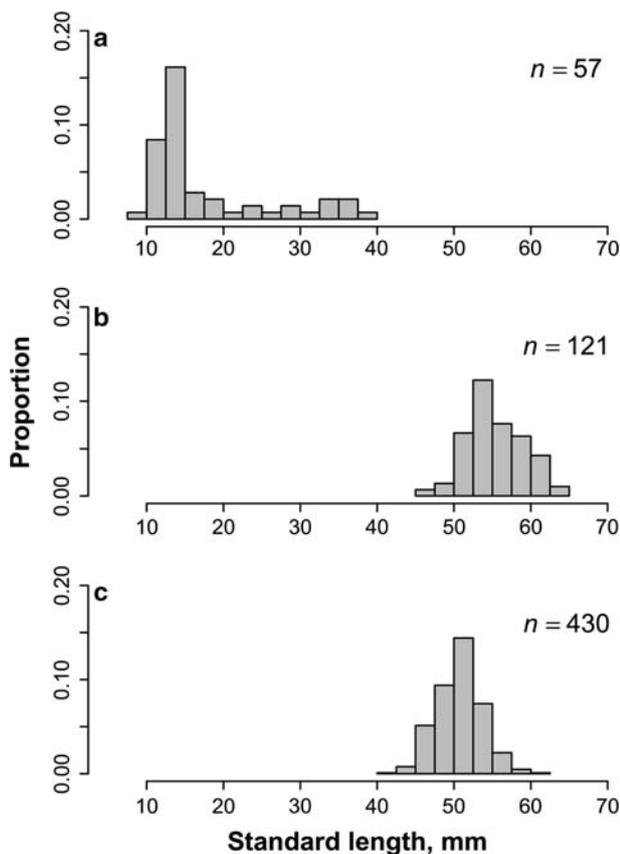

Fig. 2 Size distribution of *Albula* spp. larvae collected in different surveys: **a** total sample from cruises in offshore waters of the Gulf of Mexico and Caribbean Sea during 1975–1978; **b** total sample from coastal surveys at several localities of the Mexican Caribbean in the period 1998–2002; **c** subsample from coastal survey at two localities of the Mexican Caribbean during January 2004

Several models, linear and non-linear, were applied to examine the relationship between larval length (mm SL) and the distance to the coast in km (Table 1). Under the information-theoretic statistical framework (Burnham and Anderson 2002; Zuur et al. 2007), the model with the best fit (the minimum value of AIC index) was a regression model having a distinct variance for each locality or area (Table 2). This model corresponded to $LENGTH_{ij} = \alpha_0 + \beta \cdot DISTANCE_{ij} + \varepsilon_{ij}$, where the estimators and their standard error in parentheses were: $\hat{\alpha}_0 = 51.44$ (0.134), $\hat{\beta} = -0.235$ (0.024). The estimations of standard deviations are: $\hat{\sigma}_1 = 25.24$, $\hat{\sigma}_2 = 21.75$, $\hat{\sigma}_3 = 3.36$, $\hat{\sigma}_4 = 2.46$, $\hat{\sigma}_5 = 8.54$; for $n_i = 517$; and $j = 5$ localities or areas; 1 = offshore, Caribbean Sea; 2 = offshore, Gulf of Mexico; 3 = coastal, Punta Allen (January 2004); 4 = coastal, Xcalak (January 2004); 5 = coastal, Río Huach (1998–2002) (Fig. 3). This issue deserves further research, since it is very likely that the larval length vs. distance to the coast corresponds to a non-linear relationship; hence, our regression model must be viewed as a first approximation. This result perhaps is influenced by the available data, mostly from coastal waters, which overshadows the sparse data from offshore. The latter consideration gives rise to concerns of over-representation of coastal data driving the outcome of the fitted models, particularly the selected regression model. To address this over-representation, we remove the data from two coastal localities, Punta Allen (170) and Xcalak (260); then we fitted again the same type of model to the remaining subset of data (87), from open sea areas of the Mexican Caribbean (12) and Gulf of Mexico (45), and one coastal area, Rio Huach (30). As a result, we obtained again a statistically significant fitting, with intercept $\hat{\alpha} = 22.0027$ and slope $\hat{\beta} = -0.03342$ ($\beta \neq 0$, $ts = -2.449$, $P = 0.016$). Although the estimates of both intercept and slope varied with respect to the former model fitted to the full dataset, it must be noted that the selected model stands as a reasonable approximation of the relationship between larval length and distance to the coast.

A total of 2,466 *Albula* spp. leptocephali was collected in coastal waters of the Mexican Caribbean, with most of the 2,345 larvae (95% of the total catch) caught in January 2004 and the remaining 121 larvae caught on 12 nights at 7 sampling stations during the 1998–2002 sampling period. During the latter period, 61.2% of larvae were caught by light trap, 35.7% in the standard plankton net, and 3.1% by sled sampler (Table 2).

The outstanding number of *Albula* spp. leptocephali collected in 2004 is the highest record for so short a period of sampling (22–25 January) in the reef lagoon off Punta Allen and Xcalak. In both localities, the light traps caught all but one individual, which was collected by channel net.

Table 1 Models fitted to represent the relation between length of larvae (mm SL) and distance in km to the coastline from the sampling station

Model of length	Model type and assumptions	AIC	Notes
$\alpha_0 + \beta \cdot \text{DISTANCE}_i + \varepsilon_i$	Linear regression, conventional $\varepsilon_i \sim \text{N}(0, \sigma^2)$ σ^2 constant	3,615.3	α_0 intercept, β slope
$\alpha_0 + \beta \cdot \text{DISTANCE}_{ij} + \varepsilon_{ij}$	Linear regression $\varepsilon_i \sim \text{N}(0, \sigma^2_j)$ σ^2_j for each locality j	2,851.1	Locality or area was considered as factor to model the variance
$\alpha_0 + \text{s(DISTANCE)} + \varepsilon_i$	Additive model Smoother on distance $\varepsilon_i \sim \text{N}(0, \sigma^2)$ σ^2 constant	2,914.7	B-splines were the smoothers used
$\alpha_0 + \beta_1 \cdot x + \beta_2 \cdot x^2$	Non-linear model, quadratic curve σ^2 constant	3,387.0	x is DISTANCE
$\alpha \cdot e^{-\beta \cdot x}$	Non-linear model, negative exponential curve σ^2 constant	3,404.6	x is DISTANCE, α, β are constants

Table 2 Summary of previous and recent studies with results on larval *Albula* spp. in different localities

Reference	Locality	Date	Days	Gear	Stations	Min	Max	Total
Rooker et al. (1996)	Puerto Rico	June–July 1987	7	NLN (1)	9	2	49	203
		September–November 1987						
Mojica et al. (1995)	LSI, Bahamas	December 1990–February 1991	74	CN (6)	3	ND	60	316
		December 1991–February 1992	76	CN (6)	3	ND	30	467
		June–September 1992	73	CN (6)	3	ND	160	1,112
		December 1992–February 1993	76	CN (6)	3	ND	190	1,421
		December 1993–February 1994	76	CN (6)	3	ND	160	875
Anderson et al. (2002)	LSI, Bahamas	July–August 1997	13	CN (4)	2	ND	ND	17.2
		July–August 1997	13	LT (6)	2	0	0	0
Ordóñez-López (2004)	PM, Mexican Caribbean	September 1990–1991	48	NN (1)	2	1	13	59
This study	Sl, Mexican Caribbean	Sm 1998–2002	12	NLN (1)	5	1	30	74
		Sm 1998–2002	9	PN (1)	5	2	14	43
		Sm 1998–2002	9	SN (1)	2	1	3	4
	PA, Mexican Caribbean	22–23 January 2004	2	CN (2)	2	0	1	1
		22–23 January 2004	2	LT (3)	3	68	213	680
	XC, Mexican Caribbean	24–25 January 2004	2	CN (2)	2	0	0	0
		24–25 January 2004	2	LT (3)	3	72	807	1,665

LSI Lee Stocking Island, *PM* Puerto Morelos, *Sl* several localities, *PA* Punta Allen, *XC* Xcalak, *Sm* several months, *NLN* nightlight lift, *CN* channel net, *LT* light trap, *NN* Neuston net, *PN* plankton net, *SN* sled net, *ND* no data, number of sampling gear used in parentheses

In spite of sampling effort being the same, the numbers of larvae caught in 2004 varied between nights and localities: 680 (29%) in Punta Allen and 1,665 (71%) in Xcalak; however, this trend was not statistically supported ($F_{1,9} = 1.32$, $P = 0.27$) after a one-way ANOVA on square-root transformed abundance. Additionally, the relative abundance in Punta Allen was greater during the first night of sampling, while the opposite was observed in Xcalak (Fig. 4). Over 51% of all leptocephali caught in

January 2004 were obtained with one light trap during a single night (second night) in Xcalak.

Overall, with the exception of February and October when no samples were taken, leptocephali were collected year-round in coastal waters of the Mexican Caribbean (Fig. 5). MBI cruises caught a greater number of leptocephali in April (36), followed by February–March (16). Of those 52 leptocephali, only 9 were caught in the Mexican Caribbean. For the 1998–2002 coastal samplings, a
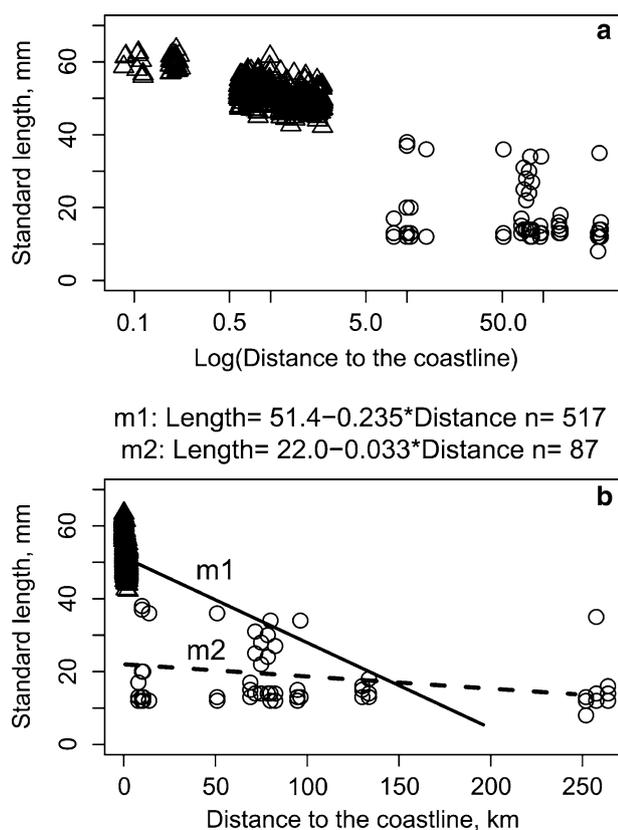
m1: Length= 51.4−0.235*Distance n= 517
m2: Length= 22.0−0.033*Distance n= 87

Fig. 3 Relationship between *Albula* spp. larval size (mm SL), and distance to the coast in km, only observations with x-axis log-scaled (**a**); comparison of model vs. observations (**b**). Data from coastal areas (*triangles*) and from cruises in open sea (*circles*). The selected model is fitted to both the full dataset (*m1*, *n* = 517) and a subset (*m2*, *n* = 87)
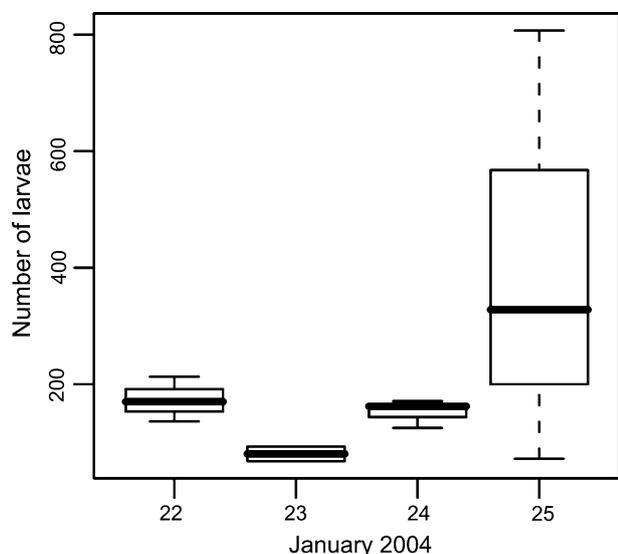

Fig. 4 Number of *Albula* spp. larvae caught in two coastal locations of the Mexican Caribbean: Punta Allen (22–23 January) and Xcalak (24–25 January). *Thick marks* inside the boxes are the medians of numbers recorded at three sampling sites, each one having a light trap. Sampling was performed around the new moon (23 January), with same effort in each location
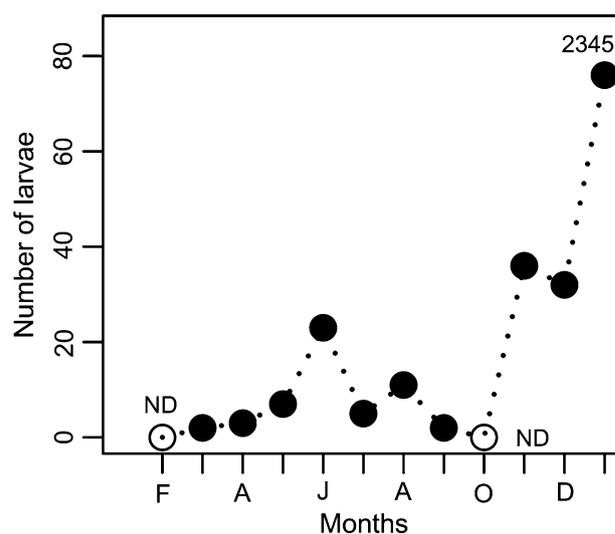

Fig. 5 *Albula* spp. larval catch in several locations of the central and southern coast of the Mexican Caribbean during 1998–2002, excepting the record catch of 2,345 larvae obtained in January 2004. *ND* No data, refers to months with no sampling

bimodal pattern of seasonal recruitment of larvae was observed; a peak of larval catch was detected from November to January, followed by a minor peak in June (Fig. 5). In January 2004, the total catch of leptocephali was noticeably high, and considerably higher than abundances reported from other Caribbean locations (Table 2).

For the coastal samples 1998–2002, a slightly greater proportion of larval bonefish (65, 53.7%) was collected in the mangrove channels compared to reef lagoon (56, 46.3%). However, mean size of larvae differed between these habitats ($ts = -4.02$, $g.l. = 119$, $P < 0.001$), with mean size greater in mangrove channels (mean ± SD = 56.64 ± 4.07; $n = 56$) than in the reef lagoon (54.06 ± 2.73; $n = 65$) (Fig. 6).

Discussion

A number of ichthyoplankton surveys have been made in the western central North Atlantic; however, only a few report leptocephali of *Albula* spp. (Alexander 1961; Hildebrand 1963; Richards et al. 1993; Mojica et al. 1995). Further, some cruises conducted in the Gulf of Mexico and the Caribbean Sea yield no records of *Albula* spp. leptocephali (Richards 1984; Richards et al. 1984). Other surveys have documented the wide distribution of these larvae in the Caribbean without providing abundance data (Hildebrand 1963), and a few have reported numerical data on leptocephalus abundance (Alexander 1961; Smith 1989; Richards et al. 1993; Mojica et al. 1995; Anderson et al. 2002). In this work we report high catches of *Albula* spp. leptocephali in coastal waters.
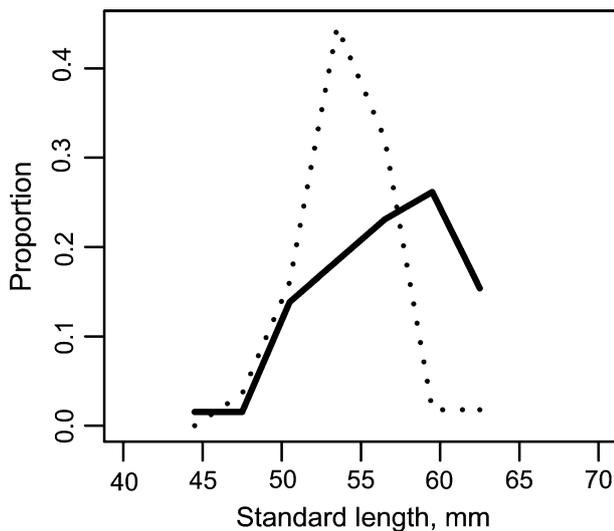
Fig. 6 Size frequency of *Albula* spp. larvae captured in two habitats, mangrove channels (*n* = 65, *solid line*) and reef lagoon (*n* = 55, *dashed line*). Data from coastal samplings 1998–2002 in the Mexican Caribbean

The capture of high numbers of *Albula* spp. leptocephalus larvae in coastal and offshore waters of the Mexican Caribbean indicates that this region provides adequate habitats for the reproduction and development of bonefish *Albula* spp. in two ways. Firstly, it is likely that the adjacent offshore waters are potential spawning grounds because the smallest larvae (ANSP data) were collected further offshore. This is similar to previous reports on premetamorphic bonefish larvae occurring in offshore waters (Alexander 1961; Pfeiler et al. 1988; Smith 1989). Furthermore, the significant difference in length between *Albula* spp. larvae caught in offshore waters (<40 mm SL) and those from coastal waters (>40 mm SL), as shown in this study, supports the hypothesis that the spawning grounds of bonefish are located offshore. Although direct otolith-based estimate of age would have been advantageous for determining the actual age (in days) of the larvae, the use of size in combination with morphology are sufficient to determine larval stage, which is a suitable proxy for age as used in this study. In addition, local fishermen have caught sexually mature females close to Xcalak (Nemesio Salazar, personal communication), where the continental shelf is narrow and open sea conditions are found within <2 km of the coastline. Second, since coastal habitats of this region were previously described as nursery areas for other fish species (Vásquez-Yeomans and Richards 1999), and metamorphic stage leptocephali (mainly in late stage I and early stage II) were in relatively high abundance in coastal habitats, it is inferred that some of these coastal habitats also function as nursery areas for *Albula* spp. An interesting finding was the size variation

across coastal habitats; although reef lagoon and mangrove channels frequently are close to each other, the larvae caught in mangrove channels were of greater mean size than those larvae captured in the reef lagoon (Fig. 6). More research on the role of nursery areas for the population of bonefish is needed in this region.

The highly complex early life history of *Albula* spp. is well known, comprising shrinkage in length during the transition between larval stages I and II, implying that each individual attains the same length three times (Alexander 1961)—once during initial larval growth, once during shrinkage between larval stages, and once during growth as an early juvenile. Nonetheless, despite the potential noise introduced into the model from these growth patterns, the regression model fits the relationship between larval size and distance to the coastline data relatively well compared to other models. Hence, although we suspected a non-linear relationship between these two variables, the available data provided an acceptable approximation using a linear model with a non-constant variance (Table 1).

As with most previous sampling efforts, use of different types of gear and sampling methodology prevents quantitative comparisons of *Albula* spp. larval abundance. Most of the previously reported data on catches of *Albula* spp. leptocephali are expressed as an unstandardized number of larvae, using different kinds of gear in different habitats and localities (Mojica et al. 1995; Rooker et al. 1996). Due to the high variability of larval abundance (Thorrold et al. 1994; Gray 1996; Hettler et al. 1997), our large catches of larvae on just a few dates do not necessarily indicate a regular pattern. It is likely we sampled during a massive episodic event of recruitment (Shenker et al. 1993; Danilowicz 1997; Dixon et al. 1999). Therefore, to ascertain whether the coastal inflow of leptocephali follows a regular seasonal pattern or depends on episodic events will require further monitoring.

The numerous types of gear used in this study did not sample with equal effectiveness. We sampled using light traps and channel nets, and found that the former were much more effective. However, other coastal surveys using light traps in the Caribbean failed to catch *Albula* leptocephali (Sponaugle and Cowen 1996; Hendricks et al. 2001; Wilson 2001; Anderson et al. 2002; Wilson 2003). Possible explanations for differences between those studies and this study include the sampling gear, differences in seasons sampled, the local hydrographic conditions, the presence of seed stock upstream or combinations of these factors. For example, Anderson et al. (2002) found that catch efficiency of channel nets and light traps were correlated to the current velocity: higher larval abundances of other taxa were obtained with channel nets deployed at sites with greater current velocity, whereas for light traps the higher larval catches occurred in low-flow sites.

Contrary to this, Mojica et al. (1995) using channel nets did not find a consistent correlation between the high abundance of *Albula vulpes* leptocephali and the meteorological conditions. However, another study including data for several sampling years evidenced that the number of larvae collected was correlated with the cross-shelf component of wind (Dahlgren et al. 2007). Unfortunately, we did not measure the winds during our coastal survey in January 2004, although calm conditions (no wind, slack currents) prevailed during the sampling period, particularly the second night in Xcalak (25 January). These results led to the initiation of a follow-up study to monitor leptocephalus abundance for 3 additional years (2005–2008), and these collections will be analyzed in the future (Vásquez-Yeomans et al., unpublished data).

In terms of the distributional patterns of bonefish, the larvae caught offshore (size <40 mm) suggest two alternative possibilities: (1) that spawning occurs offshore or (2) that spawning occurs at sites where the currents favor the offshore transport of eggs and larvae. Although these hypotheses have not been tested, it is presumed that leptocephalus bonefish spend the first weeks of life in a relatively stable pelagic environment (Alexander 1961; Pfeiler et al. 1988; Mojica et al. 1995; Friedlander et al. 2007). In any event, the physical transport of larvae by ocean currents will favor their return to nearshore nursery habitats.

The occurrence of leptocephali in every sampled month might suggest that spawning of bonefish occurs year-round in the Mexican Caribbean. Nevertheless, the long planktonic life [42–72 days, mean = 56 days (Mojica et al. 1995; Friedlander et al. 2007)] of bonefish leptocephali suggests that these findings must be considered cautiously. The low numbers of larvae during some months could be related to passive transport from other locations, near or far from our sites (Dahlgren et al. 2007), and from spawning events over a relatively long time period. Thus, it is difficult to determine the periodicity and duration of the reproductive activity of bonefish in our study area.

Regarding the reproductive season, in agreement with the results by Mojica et al. (1995), a bimodal pattern of seasonal recruitment of larvae was found in the Mexican Caribbean, with a major peak from November to January and a minor peak in June. This is consistent with the results of Crabtree et al. (1997), who reported major reproductive activity between November and June, and a smaller peak of activity in the summer. In contrast, according to a recent report, in coastal sampling off the Florida Keys during the period 1994–1997, *Albula* spp. leptocephali were caught only from December to April (Snodgrass et al. 2008).

Although the bimodal pattern is hard to interpret because the numbers of larvae caught are unstandardized, it

could also result from the local occurrence of two or more species of *Albula* with different spawning and/or recruitment seasonality patterns (Colborn et al. 2001; Adams et al. 2007). This pattern would follow that of another genus (*Elops*) that also has leptocephalus larvae, as reported for the Gulf of Mexico and western North Atlantic Ocean (McBride and Horodysky 2004). Furthermore, DNA barcode analysis based on the sequence diversity in the mitochondrial COI gene of leptocephali larvae of *Albula* spp. revealed the occurrence of three species of bonefish in coastal areas of the Mexican Caribbean (Valdéz-Moreno et al., unpublished data), further confounding patterns of seasonality. Moreover, most other studies cited herein were conducted prior to the identification of multiple species of *Albula* in the Caribbean (Colborn et al. 2001), so previous results for *A. vulpes* should be treated with caution.

In summary, the significant relationship between distance to the coast and larval length demonstrates offshore-inshore linkages, and suggests that *Albula* spp. spawn offshore and use coastal habitats as nurseries. However, temporal patterns of occurrence require further study. The use of size in combination with larval morphology is sufficient to determine larval stage, and the otolith-based estimate of age would contribute valuable information on the actual age (in days) of the larvae. The extremely high catch of *Albula* spp. leptocephali larvae that we reported in this study could be either a regular (recurrent) pattern of seasonally high influx or a non-regular, massive episodic event of recruitment, similar to previous findings for other fish (Shenker et al. 1993; Danilowicz 1997; Dixon et al. 1999). In addition, topics that also require further study include species-specific temporal and spatial patterns of abundance and determination of which environmental factors drive the recruitment process of *Albula* spp. larvae to the coastal habitats of the Mesoamerican Barrier Reef System.

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