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Mechanisms maintaining sympatric distributions of two ladyfish (Elopidae: *Elops*) morphs in the Gulf of Mexico and western North Atlantic Ocean

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Abstract

Two morphs of ladyfish exist in the western North Atlantic and adjacent waters: *Elops saurus,* a high-count morph (79–87 myomeres or vertebrae) in the north, and *Elops* sp., a low-count morph (73–78 myomeres or vertebrae) in the south. It has been proposed that these morphs are two allopatric species, but significant questions about their ecology remain. We examined 4,597 specimens and found that *E. saurus* was distributed principally in the western North Atlantic and Gulf of Mexico, whereas *Elops* sp. was distributed principally in the Caribbean Sea. Mixing of both morphs occurred along the east coast of the United States and the gulf coast of Mexico. Our results are consistent with the hypothesis that these meristic differences arise from latitudinal differences in temperature between spawning areas (i.e., Jordan's rule). Dispersal via the Gulf Stream System and associated mesoscale features appear sufficient to explain all areas of sympatric distribution. *Elops* larvae were found nearly year-round in Florida estuaries, but *E. saurus* larvae were dominant in winter and spring collections, and *Elops* sp. larvae were dominant in summer and autumn. Thus, juvenile *Elops* sp. experience a shorter growing season and a different suite of estuarine conditions than juvenile *E. saurus.* The low initial abundance and high mortality of *Elops* sp. reduce the potential for interbreeding with *E. saurus* where they are sympatric. Such ecological data uphold the postulation that the two morphs are different species and support the existence of macroscale biotic connectivity between the Caribbean region and North America.

Many marine larvae are capable of dispersing widely throughout the global oceans, affecting the zoogeographic patterns and population dynamics of marine species. Large current systems can transport larvae beyond faunal boundaries and facilitate colonization, at least temporarily (McBride and Able 1998), and trans-Atlantic dispersal of several marine species occurs (Scheltema 1968; Bowen et al. 2001). Within species' ranges, population structure is affected by their dispersal abilities (Waples 1987), and there is a long history of research acknowledging that dynamics of eggs and larvae can control the distribution and abundance of adult populations (Grosberg and Levitan 1992). Some researchers suggest that reproduction from 'upstream' islands is an important source of recruitment for some 'downstream' islands (Roberts 1997). In contrast, Cowen et al. (2000) found that by including larval mortality rates and accounting for vertical distribution of larvae in oceanographic models, the potential for the dispersal of a larval damselfish (Pomacentridae) between islands was significantly decreased. They concluded that realized connectivity had only a small influence on affecting the population dynamics of other island populations.

Tracking the dispersal of marine propagules and understanding their fates are important, but such processes are difficult to study directly. Tagging studies, which are used to provide direct evidence of animal movements, cannot easily be applied to larvae because of the small size and the dynamic nature of larval growth and mortality. Natural or biological marks exist, and they have been used in some cases. For example, the microstructure of otoliths can be used to age fish and thereby assign individuals to cohorts. In this manner, larvae or juveniles can be associated with specific—even distant—spawning events (Hare et al. 2002).

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In this study, we use a biological marker—myomere or vertebral counts—to examine larval dispersal and its consequences for ladyfish, *Elops saurus* Linnaeus, 1766, a coastal pelagic fish species.

Until recently, a single species of ladyfish (*Elops saurus*) was recognized in the western North Atlantic, ranging from Massachusetts and Bermuda southward to Rio de Janeiro, including the Gulf of Mexico and the Caribbean Sea. Smith (1989) postulates, however, that two morphs exist as allopatric species within this range. Each morph is distinguished by the number of myomeres, a larval characteristic. The specific pattern Smith measured was bimodal, with 79–86 total myomeres for the high-count morph, *E. saurus,* and 74–78 total myomeres for the low-count morph, *Elops* sp., which remains an unnamed species. The preanal myomere counts of these two morphs do not overlap (i.e., 76–80 vs. 68–72), which strongly indicates that these two morphs are separate species. However, this meristic variable also follows the expected pattern resulting from Jordan's rule (i.e., *Elops* larvae collected at southern latitudes have a lower myomere count than *Elops* larvae collected at northern latitudes). Therefore, these two morphs could be eco-phenotypes with little genetic differentiation, and temperature differences on southern versus northern spawning grounds could cause these meristic differences (Jordan 1891; Billerbeck et al. 1997).

The distribution of each *Elops* morph is not simply along a latitudinal gradient, but appears to be further influenced by regional hydrodynamics. Smith (1989) reports only low-count larvae for locations in the Caribbean Sea and only high-count larvae in the western and northern Gulf of Mexico, but larvae of both morphs occur in the eastern Gulf of Mexico and along the U.S. east coast from Florida to Virginia. This pattern can be explained if the two morphs spawn in different areas (i.e., low-count morph in the Caribbean Sea and the high-count morph in northern waters of the Gulf of Mexico and western Atlantic Ocean) and if low-count larvae are transported northward via currents, most notably the Gulf Stream System. Consistent with this hypothesis, there is no regular current flow to transport high-count morph larvae southward into the Caribbean Sea, and they are not seen south of Florida.

Elops species have leptocephalus larvae, which have a gelatinous, ribbon-shaped form (Gehringer 1959). The leptocephalus form is a specialized larval stage and is ubiquitous among—and defines in part—the superorder Elopomorpha (Obermiller and Pfeiler 2003). Leptocephalus larvae are associated with offshore spawning patterns and long planktonic durations. *Elops* are offshore spawners, and larval duration has been estimated to be 4–6 months, based on the time lag between the occurrence of the earliest-stage larvae and the arrival of most transforming juveniles into estuaries in the southeast United States (Gehringer 1959; Fahay 1975). *Elops* larvae move into estuaries, transform into juveniles, and reside for 2–3 yr in embayments before reaching maturity (McBride et al. 2001).

Smith (1989) only examined leptocephalus specimens, so he was unable to address the fate of the low-count morph as they ingress into North American estuaries. In this article we explore both the dispersal and fate of each *Elops* morph by examining leptocephalus larvae, transformed juveniles, and adults collected from Massachusetts (United States) to Brazil. We independently test if the geographic distribution of these life stages follows Jordan's rule (i.e., a latitudinal cline in myomere or vertebral numbers) and if sympatry corresponds to the regional hydrodynamics (i.e., more mixing of the two morphs in association with the Gulf Stream System). We do this using new samples, much larger sample sizes than used before, and samples that cover a greater geographic range than those used in previously published studies, particularly those involving the Caribbean Sea. Finally, we assess whether both morphs occur together at sexual maturity in regions of sympatry, which would be required if they interbreed.

By examining the processes and consequences of dispersal for *Elops* larvae, we address more than simply whether these two morphs are two species or just ecophenotypes. We use a biological marker to examine macroscale connectivity in aquatic systems. Further, we propose a hydrographic mechanism (i.e., seasonal fluctuations in water level) that appears to contribute substantially toward isolating the two *Elops* morphs by differential habitat use in areas of sympatry, ultimately leading to the disproportionally higher mortality of one of these morphs. Thus, we examine the combined role of macroscale and microscale processes maintaining sympatric distributions of two *Elops* morphs in the western North Atlantic Ocean.

Methods

A total of 4,597 specimens were obtained from a variety of sources. About 40% (n = 1,916) were collected during the period extending from 1994 to 2001 as part of a statewide sampling program by the Florida Marine Research Institute. Seine and gill nets were used, as described in McBride et al. (2001). Another 20% (n = 957) were collected in a salt-marsh impoundment of the Indian River Lagoon, Florida, during the period extending from 1980 to 1987 (i.e., impoundment No. 12, as described in Harrington and Harrington [1961], Gilmore et al. [1982], and Rey et al. [1991]). These fish were collected with pull nets and culvert traps on spring tides. For very large samples, the number of fish examined was limited to 30 randomly selected individuals. An additional 1,260 archived museum specimens (~27%) were examined from localities both within and outside of Florida. We also examined a summertime collection of 148 larvae from offshore and inshore locations of southwest Florida and 207 larvae collected during winter at Pivers Island, North Carolina. Finally, we included 109 miscellaneous individuals collected from both coasts of central Florida between 1982 and 1994.

We identified *Elops* life stages based on body size and gross morphology, following the descriptions of Gehringer (1959) and McBride et al. (2001). Fish length, reported as standard length (SL), was measured from the tip of the snout to the posterior end of the notochord in leptocephalus stages or to the posterior edge of the hypural plates in transformed stages. The early-life stages fell into four categories. In offshore collections, we encountered a few premetamorphic larvae, which had a distinct leptocephalus appearance (i.e., clear, laterally compressed body and a relatively small head). Most other larvae were metamorphic, which Gehringer further subdivided into three stages: the early-, middle-, and late-metamorphic stages. Early-metamorphic stages still have a leptocephalus appearance as they shrink in length from about 45 to 25 mm SL. Mid-metamorphic stages continue to shrink to about 18 mm SL and then grow to about 25 mm SL, losing their leptocephalus appearance by the end of this stage. Late-metamorphic stages generally have a juvenile appearance and grow from about 25 mm to 60 mm SL. After 60 mm, we referred to young-of-the-year (age-0) ladyfish as juveniles. Older age classes were characterized by seasonally specific size classes developed by McBride et al. (2001). Age-1 ladyfish were defined as 100–300 mm SL during winter (i.e., January–March), 200–325 mm SL during spring, 250–350 mm SL during summer, and 300–400 mm SL during autumn. Age-2 and older ladyfish were larger than the maximum sizes for age-1 cohorts.

Total myomere counts were recorded from leptocephali and total vertebral counts were made from transformed specimens (i.e., late-metamorphic fish, juveniles, and older age classes). Myomeres were counted using a compound microscope at 40× magnification, beginning with the first myomere behind the head and terminating with a patch of three myomeres adjacent to the caudal fin. Vertebrae were counted using one of two methods. For the first method, counts were made from radiographs using a binocular scope for small or archived specimens. Radiographs, original specimens, and voucher material have been distributed to depositary museums (*see* Acknowledgements). For the second method, large (>200 mm SL) frozen specimens from Florida locations were processed by filleting, steaming, scraping, and counting the vertebrae directly. Vertebral counts included all centra, from the proatlas to the urostyle.

Results

The myomere and vertebrae counts of all *Elops* examined for this study ranged from 73 to 87 (Tables 1, 2). Smith (1989) defined the low-count morph as having 74–78 myomeres and the high-count morph as having 79–86 myomeres. We regard the slightly wider range observed in our collections to have resulted from our survey of over 10 times more specimens than were examined by Smith (1989).

There were, as expected, marked differences in the frequency distributions of counts in the different geographic areas. Fish collected from the Caribbean basin featured a unimodal, ‘low-count’ distribution of myomeres and vertebrae. For the Caribbean samples, the modal myomere count was 75 or 77, and the modal vertebral count was 77. In contrast, these meristic characters were bimodally distributed for fish collected from North America. Myomere counts featured modes at 77 and 84 and an antimode at 80, whereas vertebral counts featured modes at 77 and 83 and an antimode at 79. The low-count individuals were a minority in North American sites (33.4% for leptocephalus-staged specimens and 9.6% for transformed specimens).

The geographic distribution of each morph was similar for both leptocephalus and transformed stages, demonstrating a disjunct distribution of low- versus high-count morphs between the Caribbean Sea and locations farther north (i.e., the Gulf of Mexico and the western North Atlantic Ocean; Fig. 1). Notable areas of sympatry are evident off the eastern coasts of Mexico and the continental United States. Minor mixing occurred in the northern and eastern Gulf of Mexico. Some individuals along the coasts of South America had one or two vertebrae more than the cut-off delineated by Smith (1989); we regard this slight difference as inconsequential to the interpretation of the disjunct distribution of the two morphs. A single, adult-sized (451 mm SL) individual attributed to Honduras had a vertebral count of 84, which was a rare and unexplained occurrence.

Larval dispersal occurs primarily during the pelagic, offshore, premetamorphic stage (Fig. 2). Larvae entering North Carolina and southwest Florida estuaries were all in the early metamorphic stage, and larval transformation of both *Elops* morphs was linked to the shift from oceanic to estuarine habitats. Larvae collected at locations well inshore of all Indian River Lagoon inlets were even smaller and more advanced in stage. Ingress into estuaries occurred nearly year-round, although the proportion of each morph was variable with respect to season. In the Indian River Lagoon, where the data was most complete, high-count larvae dominated winter and spring collections, and low-count individuals dominated summer and autumn larval collections (Fig. 3). In contrast, winter–spring data from North Carolina demonstrated that the monthly proportions of low-count larvae were without trend, varying between 35% and 68%. It is possible that the seasonality of ingressing *Elops* larvae of each morph in North Carolina may differ from that of Florida’s estuaries.

Early metamorphic larvae of both *Elops* morphs entered the Indian River Lagoon, where they remained sympatric for at least a couple of years (Fig. 4). High-count juveniles experienced a longer growing season than the low-count juveniles owing to their earlier season of ingress with respect to summer. Growth of the high-count juveniles could be readily tracked, from modal sizes of 70–80 mm SL in May–June to sizes of approximately 220–260 mm SL in September–October. Moreover, juvenile high-count fish grew largely as a single cohort. In contrast, the lengths of low-count juveniles were more variable but decidedly smaller, perhaps as a consequence of multiple age cohorts or variable growth rates. Regardless, the low-count morph reached only half the overwintering size of the juvenile high-count fish, and most low-count juveniles disappeared from the Indian River Lagoon after November. Low-count fish occurred among age-1 and older fish (approximately 300 mm SL and larger), but not in appreciable numbers. In general, although mixing of both morphs occurred in the Indian River Lagoon, the relative proportion of low-count individuals decreased significantly with age (i.e., from various larval stages to age-2 and older fish; Fig. 5).

Discussion

There are two allopatric morphs of ladyfish—a high-count morph (*E. saurus*) and a low-count morph (*Elops* sp.)—in

Table 1. Myomere frequency for staged (i.e., premetamorphic, early-metamorphic, and mid-metamorphic larvae) *Elops* leptocephali collected from nearshore and offshore waters of North America, Central America, the Bahamas, and in the Caribbean basin. Florida is divided into the following areas, by counties: northeast (Nassau–Volusia), east-central (Orange–Palm Beach), south (Broward–Monroe), southwest (Collier–Manatee), west-central (Hillsborough–Citrus). Number of fish = *n*.

	Total number of myomeres															
Geographic area	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	*n*
North Carolina–Massachusetts			38	17	37	20	16	10	22	12	14	22	15	2		225
Georgia–South Carolina		5	5	26	17	5	3	9	26	31	28	46	18	9	2	230
Florida-northeast coast									1	1	1	3	5	1		12
Florida–east-central coast		8	30	20	27	32	40	18	27	54	68	77	84	5		490
Florida-south coast										4	1	3	2	1		11
Bahamas			1	1	1											3
Florida-southwest coast		26	27	37	20	18		1		3	7	11	4	1		155
Florida–west-central coast								2		3	12	9	8	2		36
Alabama–Louisiana											2	1	2	2	1	8
Texas			2		4	13	8	17	16	10	21	22	26	2		141
Mexico					1	4		1		1	3	1	1			12
Total, North America	0	39	103	101	107	92	67	58	92	119	157	195	165	25	3	1,323
Greater Antilles			1	1	2	1	1	1								7
Lesser Antilles	1		6		4	1										12
Total, Caribbean basin	1	0	7	1	6	2	1	1	0	0	0	0	0	0	0	19

the western North Atlantic Ocean. Smith (1989; p. 962) regarded the meristic and geographic differences between these two morphs to be so distinct that while he did not name a second species owing to a lack of ecological data, ''they should probably be treated as separate species.'' Few taxonomic or ecological studies prior to that of Smith (1989) examined the meristics of more than 20 individuals, which presumably led to the failure to recognize a bimodal pattern of myomeres or vertebrae any earlier. In his seminal work, Smith (1989) examined 440 leptocephalus larvae, and we have examined 4,597 individuals.

Smith (1989) revealed that *E. saurus* and *Elops* sp. are distinguishable by at least one morphological character (i.e., total or preanal myomere counts); thus, they are not sibling species (sensu Knowlton 1993). The results presented here demonstrate that vertebrae followed a frequency distribution similar to that of larval myomere number. Other standard meristic and morphometric characters (e.g., Hubbs and Lag-

Table 2. Vertebral frequency for transformed (i.e., late-metamorphic, juvenile, and adult) *Elops* stages collected from nearshore and offshore waters of North America, Central America, and South America; the Bahamas; and in the Caribbean basin. Florida is divided into the following areas, by counties: northeast (Nassau–Volusia), east-central (Orange–Palm Beach), south (Broward–Monroe), southwest (Collier–Manatee), west-central (Hillsborough–Citrus), Big Bend (Levy–Wakulla), and Panhandle (Franklin–Escambia). Number of fish = *n*.

	Total number of vertebrae															
Geographic area	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	*n*
North Carolina–Massachusetts											5	6	2			13
Georgia–South Carolina				3	8	6	3		1	1	7	18	15	2	1	65
Florida-northeast coast										1	9	10	2			22
Florida-east–central coast	1	8	23	67	101	57	31	37	70	186	412	396	196	23	1	1,609
Florida-south coast				2	1	1		3	22	44	86	44	13	3		219
Bahamas			1													1
Florida-southwest coast						1	1		6	21	61	47	15	6	1	159
Florida–west-central coast				2		3		1	12	45	119	155	93	24	4	458
Florida–Big Bend region						1		1	10	10	17	14	6	1		60
Florida-Panhandle					3	2	1	4	9	46	58	44	9	5	1	182
Alabama–Louisiana			1	3	1	3	1	4	3	19	77	77	61	17	5	272
Texas								4	1	3	12	27	21	4		72
Mexico					2					2	4	6	3	1		18
Total, North America	1	8	25	77	116	74	37	54	134	378	867	844	436	86	13	3,150
Central America		1	1	5	5	6						1				19
Colombia–Venezuela			2	7	25	10	1	1								46
Guyana–Brazil				2	8	6	1									17
Greater Antilles			3	2	4	6										15
Lesser Antilles				2	5	1										8
Total, Caribbean basin	0	1	6	18	47	29	2	1	0	0	0	1	0	0	0	105

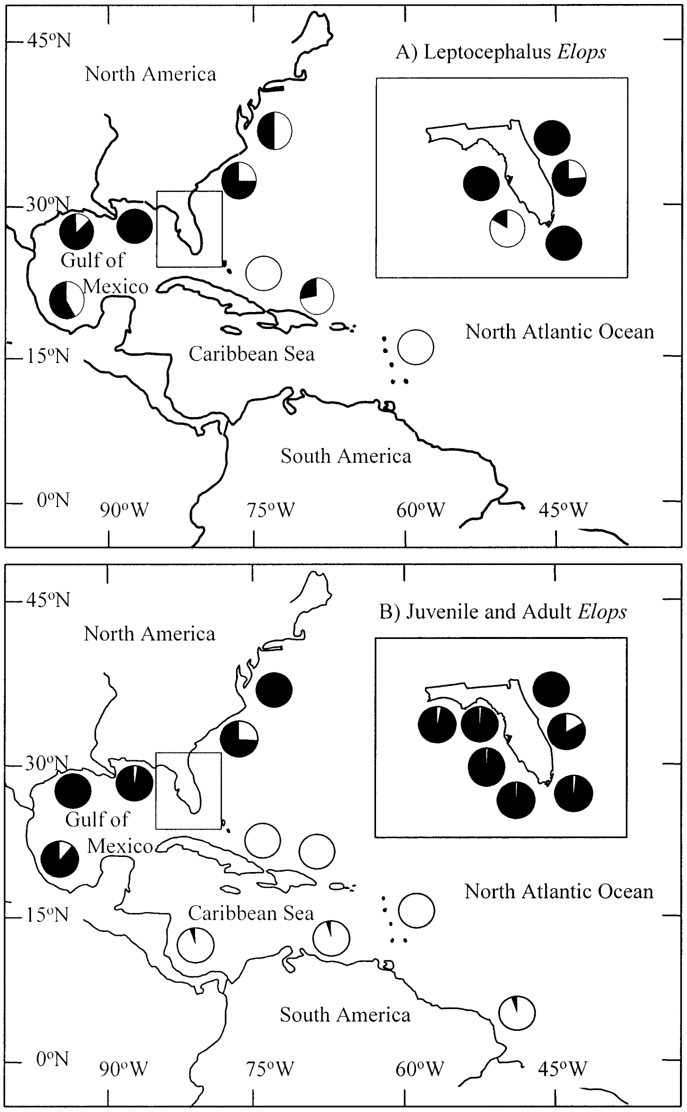

Fig. 1. Geographic distribution of A) *Elops* leptocephalus larvae and B) *Elops* late-metamorphosing larvae, juveniles, and adults. Pie figures identify the proportions of high-count (black, *Elops saurus*) and low-count (white, *Elops* sp.) morphs based on A) myomere or B) vertebral number. Data for regions within Florida are shown in inset (see Tables 1 and 2 for geographic breakdown and sample sizes).

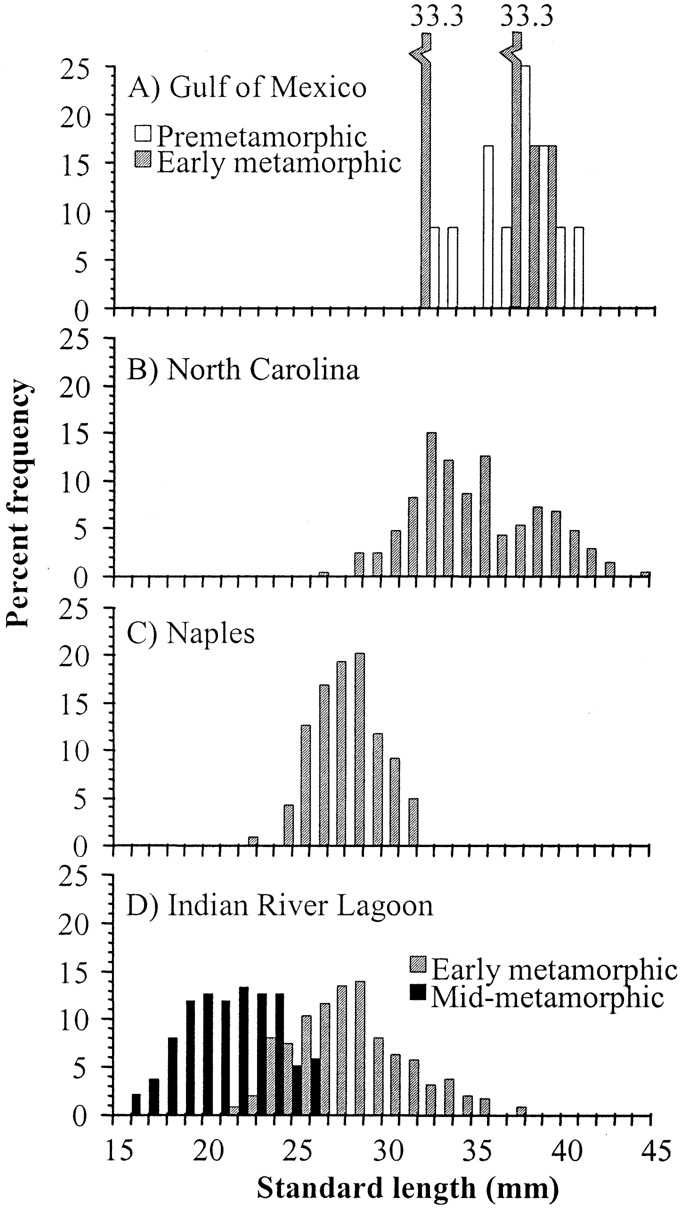

Fig. 2. Length–frequency distributions of *Elops* leptocephali from different habitats: A) premetamorphic ($n = 12$) and early-metamorphic ($n = 6$) larvae offshore of southwest Florida in the Gulf of Mexico; B) early-metamorphic larvae ($n = 207$) from Piver's Island, near Beaufort, North Carolina; C) early-metamorphic larvae ($n = 119$) from an oyster bar site near Naples, southwest Florida; D) and early-metamorphic ($n = 349$) and mid-metamorphic ($n = 135$) larvae from Impoundment No. 12 in the Indian River Lagoon, central-east Florida.

ler 1947) were examined, but none of these phenotypic characters distinguished the transformed *E. saurus* and *Elops* sp. (McBride unpubl. data). The number of myomeres, and eventually vertebrae, are set during embryogenesis and thereafter remain unchanged. Because many other meristic characters (e.g., scale number or fin rays) are set later in larval development, myomere and vertebrae counts better represent the environmental conditions of the spawning grounds. Thus, no phenotypic characters other than myomere or vertebrae appear to be useful for separating these two *Elops* species.

There are other data relevant for discriminating *Elops* sp. from *E. saurus*. *Elops* sp. are smaller at age-1 than are *E. saurus*. In Cuba, where Carles (1967) reported that *Elops* have 75–76 vertebrae (e.g., *Elops* sp.), juvenile ladyfish reach approximately 130 mm SL by their first winter—a small size that is very similar to that reported here for *Elops* sp. in the Indian River Lagoon. An appraisal of molecular genetic data supports the evolutionary divergence of *E. saurus* and *Elops* sp., consistent with the presence of two species (Bowen and McBride unpubl. data). Mitochondrial DNA partitions between each morph are in the range of 2–

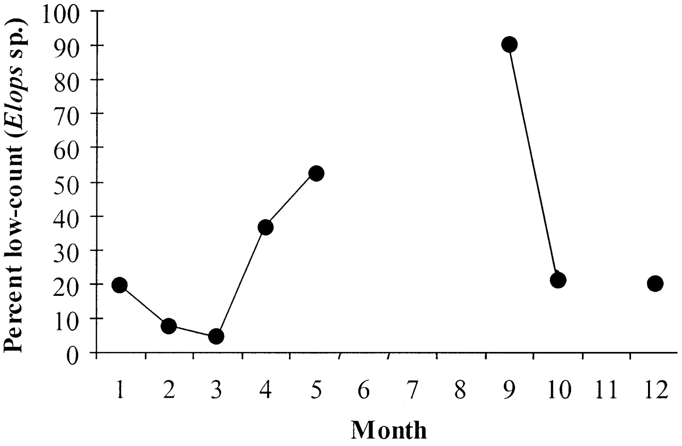

Fig. 3. Monthly proportions of the low-count morph (*Elops* sp.) versus the high-count morph (*Elops saurus*) as planktonic larvae (i.e., early and mid-metamorphic stages) from the Indian River Lagoon on Florida's east coast ($n = 504$). Data for months with <5 larvae collected were not included. January = 1.

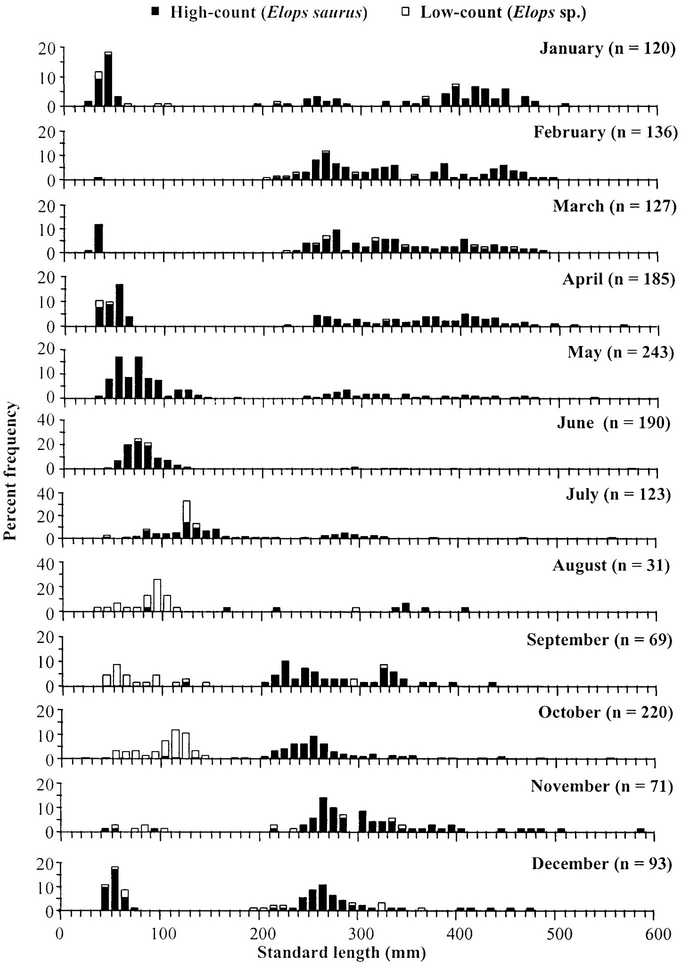

Fig. 4. Monthly length–frequencies of *Elops* late-metamorphic larvae, juveniles, and adults collected in the Indian River Lagoon on the east coast of Florida (multiple sampling years combined). Percentages of each morph are indicated separately: high-count, *Elops saurus* and low-count, *Elops* sp. Number of fish = *n*.

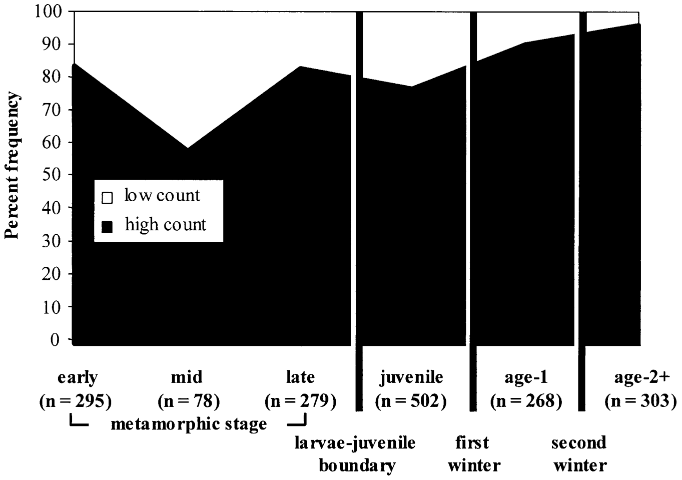

Fig. 5. Proportions of *Elops* by larval stages and age-classes for fish collected from the Indian River Lagoon, Florida ($n = 2{,}099$). The proportions of each morph were significantly different between all life stages (Chi-square test of independence: $\chi^2_{[5]} = 123.0$; $P < 0.001$). The proportions of each morph were also significantly different between just the juvenile and age-1 life stages (Chi-square test of independence: $\chi^2_{[1]} = 23.7$; $P < 0.001$).

3% sequence divergence, based on 470 base pairs of cytochrome b. Although this is on the low end of species-level divergences for fishes, it is similar to the genetic distances observed among other allopatric *Elops* species from the eastern Gulf of Mexico versus Hawaii (Obermiller and Pfeiler 2003).

Adult *E. saurus* have not been collected, and so presumably do not spawn, in the Caribbean Sea. Eldred and Lyons (1966) report the occurrence of premetamorphic *Elops* sp. larvae in the Yucatan Straits and of premetamorphic *E, saurus* in the eastern Gulf of Mexico and in the Florida Straits, which also indicates spatial separation of spawning areas. Smith (1989) reported an isolated premetamorphic (6 mm) *Elops* sp. larva from the Florida Straits, which indicates that only limited spawning by *Elops* sp. even occurs in the vicinity of Florida. The temporally distinct presence of larvae, with *E. saurus* dominating wintertime collections (data herein and Smith 1989), also indicate that spawning times are largely nonoverlapping. Fahay (1975) reported collecting premetamorphic larvae from the Straits of Florida to North Carolina, but he found *Elops* sp. offshore of Georgia and the Carolinas and *E. saurus* offshore of Florida. Nonetheless, the *Elops* sp. he observed were primarily collected during the summer, when *Elops* sp. is generally more abundant. Moreover, the *Elops* sp. collected by Fahay (1975) were large (>24 mm), which indicates that significant dispersal from the spawning grounds had occurred. More collections of premetamorphic stages will help characterize spawning by *Elops* species, particularly if larval duration could be known. Alternatively, collections of adults in spawning condition for various locations could identify the spawning areas of *E. saurus* and *Elops* sp. (McBride et al. 2003).

If the spawning grounds for *E. saurus* and *Elops* sp. are geographically isolated and temporally distinct, then how does sympatry occur? The most significant areas of sympatry occurred along the U.S. southeast coast and the Mexican gulf coast. *Elops* have a planktonic larval duration of several months, which presumably facilitates this widespread geographic distribution of Caribbean-derived *Elops* sp. larvae. Govoni and Merriner (1978) noted that *Elops* species are not known to spawn north of the Carolinas, and they proposed that the Gulf Stream System coupled with either Ekman transport or Gulf Stream eddies dispersed these larvae westward into the Chesapeake Bight. Recent studies by Hare et al. (2002) and Epifanio and Garvine (2001) review the evidence for dispersal of pelagic larvae via these cross-shelf transport mechanisms. In particular, Hare et al. (2002) include data for a holey-sock drogue that was released off of the Florida Keys and was transported for a few months northward, eventually becoming entrained in a warm core ring near the edge of the northeast U.S. continental shelf. Cyclonic spin-off eddies produced by wind-induced events are present along the southeast Florida shelf and northward to Cape Hatteras (Zantopp et al. 1987), and these also appear to be relevant for cross-shelf transport of larvae in this region. The periodic formation and persistence (~100 d) of anticyclonic gyres in the southern Straits of Florida (Lee et al. 1994) may be a temporary retaining mechanism amenable for the presumed long stage duration of *Elops* larvae. We also note that warm core rings spinning off of the Gulf of Mexico's Loop Current (e.g., Collard and Ogren 1990) may be the source for *Elops* sp. larvae entering into the northern and western Gulf of Mexico; again, the Gulf Stream System serves as the source of these larvae.

Although much of the above discussion is focused on physical transport mechanisms, we cannot rule out the possibility that metamorphosing *Elops* larvae are quite large and may be capable of swimming cross-shelf from pelagic offshore waters toward estuaries. Finally, although we cannot exclude contributions from other current features east of the Gulf Stream, we do not believe these are important sources for transporting *Elops* larvae to North America from the south. Colin (1995) notes that current flow within the Bahamas archipelago is largely localized, and Ingham (1975) concludes that the Antilles current does not add significantly to the Gulf Stream System. In summary, we believe that the Gulf Stream System is sufficient to explain the distributions of *Elops* larvae reported here and that this is the leading hypothesis to be tested more directly in the different regions adjacent to this western boundary current.

In regions of sympatry, do larval *E. saurus* and *Elops* sp. survive long enough to successfully interbreed? In the Indian River Lagoon, the strongly bimodal pattern of myomeres and vertebrae and corresponding lack of intermediates does not suggest interbreeding between *E. saurus* and *Elops* sp. To some extent the Indian River Lagoon is a unique estuary, with very high species diversity and a recognized flow of larvae via tropical currents from the Caribbean Sea (Gilmore 1995). Nonetheless, a strongly bimodal meristic pattern for *Elops* is also evident in the eastern and northern Gulf of Mexico (Thompson and Deegan 1982). Along Florida's coast, the seasonality of larval abundance is overlapping, but *E. saurus* is more concentrated in winter and spring and *Elops* sp. is more concentrated in summer and autumn (data herein, Thompson and Deegan 1982). The bimodal meristic pattern and separate seasons of larval ingress point to two distinct species of *Elops* in this region.

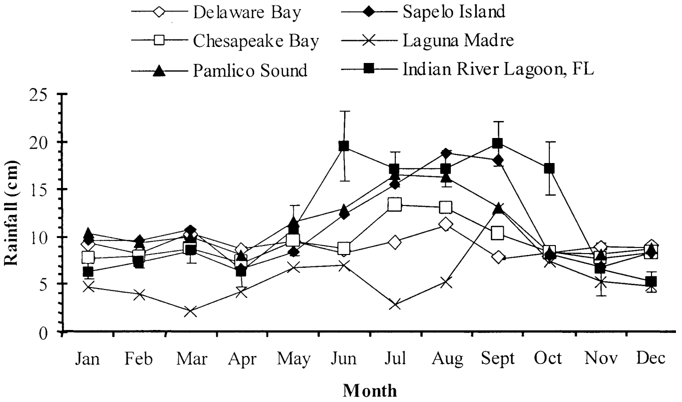

Fig. 6. Monthly mean rainfall for estuaries of middle Atlantic states (open symbols), south Atlantic states (filled symbols), and Texas (×). Error bars for Indian River Lagoon are 95% confidence limits. Means are calculated from monthly means for one rainfall gauge (Sapelo Island), two gauges (Delaware Bay, Chesapeake Bay, Pamlico Sound, Laguna Madre), or five gauges (Indian River Lagoon). (Data source: National Oceanic and Atmospheric Administration.)

In these areas of sympatry, how would interbreeding be prevented? The initial abundance of *Elops* sp. is low and the proportions of *Elops* sp. decline rapidly with age, so we postulate that *Elops* sp. does not survive to maturity in sufficient numbers to interbreed with *E. saurus* in Florida's waters. At sizes >400 mm SL, only 3.5% of the specimens were *Elops* sp. (i.e., 5 of 144 fish from Indian River Lagoon had <79 vertebrae). *Elops* are not believed to become sexually mature until they reach these sizes, which occurs at about 3 yr of age or older (McBride et al. 2001). We do not believe that *Elops* sp. has a different migratory pattern than *E. saurus,* an alternative mechanism that would explain their significant decline in abundance after their first winter.

Sources of high mortality for the smaller *Elops* sp. in Florida may be biotic (i.e., size-selective piscivory) or abiotic, such as from hypothermal conditions in shallow waters during winter. Although a variety of such processes deserve further attention, we draw attention to another source of mortality, albeit one that may be somewhat specific to the Indian River Lagoon. A strong seasonal pattern of rainfall (Fig. 6) in peninsular Florida significantly alters the water levels at specific estuarine locations during the autumn months, and metamorphosing *Elops* sp. arrive to find different—and ill-fated—microhabitats in this estuary relative to those microhabitats used by *E. saurus.* During autumn, increased rainfall inundates thousands of acres of otherwise unavailable ephemeral high-marsh habitats, leading to seasonal peaks in zooplankton densities in those new habitats (Rey et al. 1991). Newly ingressed metamorphosing *Elops* (nearly all *Elops* sp.) larvae enter these polyhaline habitats and feed on this abundance of copepods and *Aedes* larvae (Harrington and Harrington 1961). Late-metamorphic *Elops* larvae shift their diet to *Palaemonetes* shrimp and other fishes and grow quickly (Harrington and Harrington 1961). However, the marsh water levels recede drastically by January (Poulakis et al. 2002), and this climatological shift traps *Elops* sp. juveniles in ephemeral hypersaline ponds (Harrington and Harrington 1961). The decreasing water levels simultaneously exclude *E. saurus* larvae from the marsh habitat as they ingress into the Indian River Lagoon in winter and spring (*see* also McBride et al. 2001). Mortality rates of *Elops* sp. and other fish species trapped in the remnant ephemeral ponds are presumed to be high because individuals are subjected to a suite of increasingly harsher thermal, hypersaline, and predatory regimes (Harrington and Harrington 1961, Poulakis et al. 2002). Thus, although *Elops* sp. in Florida can take advantage of suitable summer and autumn conditions, they end up in unsuitable conditions during winter.

This hydrographic mechanism probably does not have as dramatic an effect on *Elops* sp. in estuaries outside of Florida for two reasons. First, rainfall levels in other estuaries (Fig. 6) do not show an autumn increase of similar duration or magnitude to the one observed in Florida. Second, winter conditions in estuaries north of Florida are increasingly colder, and tropically spawned *Elops* sp. larvae are unlikely to survive the typical winter temperatures encountered there. Hypothermal mortality of *Elops* juveniles in northern estuaries may be expected, as occurs for other subtropically spawned species (e.g., McBride and Able 1998). In this manner, the hydrographic mechanism proposed here (i.e., water level) would be the dominant abiotic mechanism driving overwinter survival of *Elops* sp. in Florida, and hypothermal mortality would be the dominant abiotic mechanism for *E. saurus* or *Elops* sp. in more northern estuaries.

In this study, we have used ecological data to address many of the questions posed by Smith (1989), namely: What are the geographic distributions of transformed *E. saurus* and *Elops* sp.?; What is the fate of *Elops* sp. larvae dispersed to Florida?; and Do *E. saurus* and *Elops* sp. interbreed? *E. saurus* and *Elops* sp. do have overlapping but distinct geographic distributions, and the seasonal distribution of juvenile *E. saurus* and *Elops* sp. within estuaries was also overlapping but distinct. This connectivity between Caribbean spawning areas and North American estuaries appears to have only limited impact on *Elops* population dynamics because so few *Elops* sp. dispersed to Florida survive to maturity. However, there may be some ecosystem effects of this biomass transport, and further genetic scrutiny of these fishes will clarify whether interbreeding of *E. saurus* and *Elops* sp. occurs.

Wide geographic distribution of marine species is often accepted, noncritically, as a consequence of the ability of marine organisms to disperse propagules in oceanic currents (Knowlton 1993). Larval duration of *Elops* appears to be several months, and *Elops* leptocephali are also good swimmers, so *Elops* should be more widely dispersed than many other marine fish species. Instead, we observed two disjunct geographic distributions of all stages of *Elops* species. This latitudinal separation of the *E. saurus* and *Elops* sp. is of particular interest because these latitudinal trends are interrupted by the regional hydrodynamics. Other species pairs have patterns of distributions similar to that identified here for *Elops* species. For example, *Serranus notospilus* features one population in the Gulf of Mexico and in the Florida Keys and another population in the Greater Antilles and southward to South America (Robins and Starck 1961). Also, Böhlke et al. (1989; p. 163) delineate similarly distinct geographic distributions for *Gymnothorax kolpos* and *G. conspersus.* Are more species pairs awaiting separation in this region? Knowlton's (1993) review of sibling species suggests that there are. Finding such species pairs will lead to a greater understanding of this region's biogeography and the associated ecological and evolutionary processes occurring in the oceans.

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