Abstract—Ladyfish, Elops saurus, are recognized as an estuarine-dependent species, although no published study has described how ladyfish use estuarine habitats. This study found ladyfish to be common throughout Tampa Bay and Indian River Lagoon, Florida. In both estuaries, metamorphosing larvae were collected during several months of the year, but they were most abundant in spring. Length-frequency analyses suggested that age-0 ladyfish grew from 20–30 mm to 200–300 mm standard length during their first year and that at least three age classes were present throughout the year. Age-0 ladyfish followed an ontogenetic migration with regard to salinity. They entered estuaries as metamorphosing larvae and became concentrated in waters of lower than median salinity for both estuaries (23–25 ppt). In Tampa Bay, which had a greater range of salinity than the Indian River Lagoon, age-0 ladyfish were found principally in mesohaline and oligohaline areas; in the Indian River Lagoon, age-0 ladyfish were found in mesohaline and polyhaline waters. In autumn, age-0 ladyfish moved back to higher salinities, into lower parts of the estuaries, and even out to beaches along the Gulf of Mexico. These field observations are consistent with the hypothesis that ladyfish depend on estuaries, specifically positive estuaries, i.e. where freshwater input exceeds evaporative processes. However, published studies also demonstrate that larval ladyfish can metamorphose and juveniles can survive in hypersaline waters; therefore negative estuaries may also serve as suitable nursery habitats. It is not clear how salinity affects ladyfish growth and mortality, and further research should clarify how different types of estuaries (i.e. positive versus negative) contribute to maintaining populations of this fishery species.

Many fish species use estuaries of the southeastern United States as nursery habitats (e.g. Skud and Wilson, 1960; Gunter, 1967), but coastal habitat degradation threatens many of the economically important fisheries that rely on estuaries (Gilmour, 1995). There are many estuarine-dependent species (Hoss and Thayer, 1993). A simple approach to ranking relative habitat value is to compare specific fish distributions with respect to habitat in different estuaries. Associations between abundance and habitat can assist in predicting the response of coastal fish populations to changes in these habitats. Remarkably, such information is rarely available except for the most economically valuable species (Hedrich, 1983).

Freshwater inflows to estuaries of the southeast United States have been severely altered in the last 150 years and coastal development continues to divert more water away from estuaries (Stickney, 1984). The MSFCA’s Essential Fish Habitat mandate provides a policy framework for identifying the effects of reduced freshwater inflows on estuarine-dependent species. Yet researchers and managers often characterize species as estuarine-dependent more on intuition than rigorous examination of data. Able and Fahay (1998) outlined three criteria for defining estuarine-dependence: 1) predictable use of estuaries, 2) non-use of suitable alternative habitats, and 3) demonstrable effect on a fish population from a loss of estuarine habitat. The first two criteria are best addressed with field studies, but even such simple descriptions of habitat use at a landscape level are lacking for most estuarine fish species (Hoss and Thayer, 1993).

One example of this type of data gap is that for ladyfish, Elops saurus, a fishery species that inhabits coastal waters of Florida (Hildebrand, 1963; Murray et al., 1987; FMRI1). Ray (1997) listed ladyfish as an estuarine-dependent species but little is known about its use of habitat in coastal waters. Ladyfish are probably considered to be estuarine-dependent because they spawn in offshore waters and metamorphosing larvae and juveniles are found inshore (Hildebrand, 1943; Gehringer, 1959; Elbled and Lyons, 1966). However, ladyfish tolerate a wide range of salinities (Ali and Rao, 1951; Gunter, 1956; Gehringer, 1959; Bayly, 1972). Numerous studies have reported the occurrence of small juveniles in mesohaline or lower-salinity waters (< 18 ppt), which is consistent with an estuarine-dependent life history (Tagatz and Dudley, 1961; Gunter and Hall, 1965; Zillerberg, 1966; Tagatz, 1968; Tagatz and Wilkens, 1973; Sekavec, 1974; Govoni and Merriner, 1978 [and references within]; Thompson and Deegan, 1982; Peterson and Ross, 1991). Moreover, large ladyfish are present throughout

1 FMRI (Florida Marine Research Institute): www.floridamarine.org
the year in polyhaline and marine (>18 ppt) waters such as Florida Bay, Biscayne Bay, and the Indian River Lagoon (Low, 1973; Sogard et al., 1989a, 1989b; Tremain and Adams, 1995). Other studies, however, have reported presumptive age-0 juveniles (Harrington and Harrington, 1961; Kristensen, 1964), older subadults (Carles, 1967), or both (Simmons, 1957; Roessler, 1970; Brockmann, 1974) in hypersaline waters (>35 ppt). Thus, age-0 ladyfish may be seeking some condition other than specific salinities.

The purpose of our study was to determine whether age-0 ladyfish make predictable size-specific seasonal movements that would identify them as an estuarine-dependent species. Because salinity is part of the definition of an estuary (Pritchard, 1967), a landscape approach was used to follow ladyfish movements with respect to salinity within Tampa Bay and the Indian River Lagoon. If age-0 ladyfish select low-salinity waters, then we predicted that they would be found in lower than average salinity waters for each estuary. Furthermore, if age-0 ladyfish select low-salinity habitats, then we predicted that they would be more abundant in the lower salinity areas of Tampa Bay because this bay has a wider salinity range to select than that for the Indian River Lagoon. We also examined length-frequency data to make preliminary assessments of age-class composition and growth rates of ladyfish within estuaries. Although several publications have discussed the ecology of ladyfish in estuaries (e.g. Springer and Woodburn, 1960 and citations above), to our knowledge the data treatment in our study is the most comprehensive for this species.

Methods

Study sites

Data from Tampa Bay, on central Florida’s west coast, were compared with data from the Indian River Lagoon, on central Florida’s east coast (Fig. 1). Both water systems are located at similar latitudes, so they are subject to similar temperature cycles. Both systems are positive estuaries (i.e. freshwater input exceeds evaporative processes; Pritchard, 1967), but they have distinctive salinity regimes (Fig. 2). Tampa Bay is a drowned river system with considerable freshwater input and separate satellite barrier-island embayments, whereas the Indian River Lagoon is largely a series of barrier-island embayments with few inlets and no major rivers (Comp and Seaman, 1985).

Bay-wide survey—Tampa Bay We examined survey data for Tampa Bay fishes collected from 1989 to 1995 by staff of the Florida Marine Research Institute (FMRI). The sampling design incorporated both fixed sampling stations and locations assigned in a stratified random manner (McMichael et al., 1995). Tampa Bay was stratified into six major zones (Fig. 1A): the upper bay (A), the western bay (B),
the eastern bay (C), the satellite embayments (D), the lower bay (E), and the principal rivers (F). Each zone was stratified further by a 1-square-nautical-mile grid system. Sampling at fixed stations occurred monthly, but stratified random sampling was conducted principally in spring and autumn when many species recruit to Florida estuaries.

Sampling gear included seines, trawls, block nets, and gill nets (Table 1). A 21.3-m center-bag seine was deployed in one of three different ways: 1) it was hauled along the shoreline across an area of about 340 m² ("beach sets"); 2) it was deployed from a boat in a semicircular pattern in river zones and the mean area swept was 70 m² ("boat sets"); 3) or it was set away from the shoreline and hauled into the current across an area of about 140 m² ("offshore sets"). A much larger seine (183-m) was also deployed from a boat in a semicircular pattern. A 61-m block net was set against seawalls or mangroves of inundated shorelines at high tide, and fish were collected at the ensuing low tide. Otter trawls were towed for 10 min in bay zones (zones A–E) and for 5 min in river zones (zone F) at an approximate speed of 0.6 m/s. A 184-m gill net with four 46-m panels (75-, 100-, 125-, and 150-mm mesh) and a similar 198-m gill net that included a 15-m section of 50-mm mesh were used. These gill nets were set perpendicular to shore, four nets at a time, so that two nets with the larger mesh were oriented inshore and two nets were oriented in the opposite direction.

**Little Manatee River—Tampa Bay** In addition to sampling the Little Manatee River as part of the bay-wide survey, FMRI staff completed an independent survey of this river...
between January 1988 and December 1991 (Table 1; Fig. 1A). Samples were collected biweekly with a 22.9-m seine at six fixed shoreline stations located between the river mouth and the freshwater zone, with 2-3 seine hauls per station. Supplemental samples were collected with 9.1- and 22.9-m seines at two additional stations from January 1989 to June 1991 and with a 120-m seine at five fixed sites near the river mouth from March 1990 to November 1991.

**Gulf beaches—Tampa Bay** In a third independent survey by FMRI staff, two beach sites were sampled along the Gulf of Mexico coast of Pinellas County, FL (Table 1; Fig. 1A). Samples were collected biweekly with a 22.9-m seine from September 1992 to November 1994 at Treasure Island and from August 1993 to November 1994 at Indian Shores. Five hauls were made in the surf zone at each site during a single day; each haul began 50 m from the water’s edge and proceeded perpendicular to shore.

**Lagoon-wide Survey—Indian River Lagoon** We also examined data from an FMRI survey of the Indian River Lagoon fishes. The same general sampling design and gear were used in this survey and the bay-wide survey of Tampa Bay (see above; Tables 1–2; Tremain and Adams, 1995). Although the Indian River Lagoon survey started slightly later than the Tampa Bay survey, they were largely contemporaneous (1990-1995). The northern Indian River Lagoon system is a complex of the Indian River basin (zones A–C) and the Banana River basin (zones D–E; Fig. 1B). The sampling program in the Indian River Lagoon differed slightly from that in Tampa Bay. In the Indian River Lagoon, neither the 183-m seine nor block nets were used; gill nets were used at fixed stations and stratified-random locations, and fewer total hauls were made with most types of sampling gear because portions of this program started one or two years later than Tampa Bay’s program.

### Abundance and size of ladyfish

Monthly relative abundance was calculated as the mean number of ladyfish per haul (including hauls with no ladyfish) for each gear type used in each survey. Data from the stratified random programs were not included in calculations of monthly relative abundance because stratified...
random sampling did not occur in all months of the year. Geographic distributions of age-0 ladyfish were also plotted for each of four seasons. For such maps, relative abundance was calculated as the number of age-0 ladyfish per haul. Values for all positive catches were categorized into four quartile classes (≤25th, 26–50th, 51–75th, and >75th percentile) before plotting to standardize the data among gear types and estuary. Maximum size criteria were adjusted for each season to exclude fish older than age 0.

Fish size was measured and reported as standard length (SL) in mm. At least 20 randomly selected ladyfish per sample were measured and unmeasured fish were proportionally adjusted for the length-frequency plots to reflect the size structure of the entire sample(s). Sizes from the literature are also reported as SL and were converted when necessary by using the equations SL = -0.772 + 0.787 (total length), or SL = -2.46 + 0.943 (fork length); each equation was based on least squares regressions of measurements from 75 ladyfish that ranged from 39 to 475 mm SL (r²=0.99). Mean salinity at capture was calculated for each 25-mm-SL interval, and for each estuary separately, by using the weighted formula

\[ \bar{Y}_m = \frac{\sum_{i=1}^{n_m} w_i Y_i}{\sum_{i=1}^{n_m} w_i}, \]

where \( w_i \) = the number of ladyfish per 25-mm-SL interval for collection i; \( Y_i \) = the salinity measured for collection i; and \( n \) = the total number of collections with fish in that 25-mm-SL interval for that estuary.

We identified early life stages of ladyfish from their size and appearance. The following criteria and general terminology are from Gehring (1959). Early-metamorphic larvae have a leptocephalus form, with a clear and laterally compressed body. Early-metamorphic larvae shrink as they develop from about 45 to 25 mm SL. Mid-metamorphic larvae are generally less than 25 mm SL. Mid-metamorphic larvae shrink to about 18 mm SL and then grow to about 25 mm SL; they lose the leptocephalus form by the end of this stage. Late-metamorphic larvae have a juvenile form and grow from about 25 mm to 60 mm SL. After 60 mm the age-0 fish are referred to as juveniles. Older age classes (i.e. age-1 or age-2+) are defined by size, as inferred from length-frequency analysis. The complete size and age range of ladyfish in estuaries is not defined in Gehring or other published literature but appears to be largely restricted to immature fish.

### Results

#### Tampa Bay

In the bay-wide survey, 4422 ladyfish were captured in 7525 21.3-m-seine hauls, 458 183-m-seine hauls, 210

<table>
<thead>
<tr>
<th>Gear</th>
<th>Mesh (mm)</th>
<th>Zones</th>
<th>Period</th>
<th>Months</th>
<th>Years</th>
<th>C (c)(^4)</th>
<th>f</th>
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<tr>
<td>21.3-m seine (340 m(^2))(^1)</td>
<td>3.2</td>
<td>A, C-D</td>
<td>D</td>
<td>1-12</td>
<td>1991-95</td>
<td>273 (367)</td>
<td>619</td>
</tr>
<tr>
<td>21.3-m seine (70 m(^2))(^1)</td>
<td>3.2</td>
<td>B, C, E, E(^2)</td>
<td>D</td>
<td>(1-12)(^2)</td>
<td>1991-95</td>
<td>403 (67)</td>
<td>235</td>
</tr>
<tr>
<td>21.3-m seine (140 m(^2))(^1)</td>
<td>3.2</td>
<td>A, C-E</td>
<td>D, C(^2)</td>
<td>1-12</td>
<td>1991-95</td>
<td>42 (96)</td>
<td>668</td>
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<tr>
<td>6.1-m trawl</td>
<td>3.2(^3)</td>
<td>C-E</td>
<td>D</td>
<td>1-3 (4-5), 6-12</td>
<td>1991, 1992-95</td>
<td>7 (1)</td>
<td>617</td>
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<td>184-m gill net</td>
<td>75-150</td>
<td>A, D</td>
<td>C</td>
<td>(1-12)(^2)</td>
<td>1991-93, 1994(^2)</td>
<td>95</td>
<td>202</td>
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<tr>
<td>198-m gill net</td>
<td>50-150</td>
<td>A-D</td>
<td>C, N(^2)</td>
<td>(1-12)(^2)</td>
<td>1994-95</td>
<td>153</td>
<td>126</td>
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<tr>
<td>Total</td>
<td></td>
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<td></td>
<td></td>
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<td>2101 (815)</td>
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\(^1\) Value in parentheses indicates area swept by each haul; see text for further details.  
\(^2\) Less than 30 tows for this sampling unit.  
\(^3\) Minimum mesh size used.  
\(^4\) C = late-metamorphic, juvenile, and older stages; (c) = early- or mid-metamorphic (leptocephalus) larvae.
blocknet sets, 4787 trawl hauls, and 587 gillnet sets (Table 1). Generally, a new cohort of late-metamorphic larvae first appeared in April (Figs. 3 and 4A). Only 13 early- or mid-metamorphic larvae were collected (26–34 mm SL) in the bay-wide survey (n=14 for all Tampa Bay samples). Although the arrival of metamorphosing larvae (largely late-metamorphic stages) was concentrated in April, isolated individuals 26–41 mm SL were collected as early as February (1989) or March (1994, 1995) or as late as September (1994), October (1993), or

Figure 3
Monthly length-frequency of ladyfish, Elops saurus, in Tampa Bay. Early- and mid-metamorphic larvae were excluded because length decreases as they develop. Bay-wide data for all years (1989–95) from all zones (A–F) are plotted. n = number of fish sampled.
November (1990). All ladyfish ranged in length from 20 to 550 mm SL (Fig. 5). Length-frequency analyses suggested that there were three age classes: age-0 fish overwintering at 200–300 mm SL, age-1 fish overwintering at 300–400 mm SL, and age-2+ at sizes of 400 mm SL or larger (Fig. 3).

Nearly all ladyfish <200 mm SL were collected in mesohaline and oligohaline areas of rivers (zone F; Fig. 6). Early- and mid-metamorphic larvae were collected at polyhaline salinities (mean=20 ppt, Fig. 7); these larvae had probably entered Tampa Bay recently. In Little Manatee River, ladyfish were most common (59.7% of the total individuals) in the mesohaline zone (5.1–18 ppt), less common in the oligohaline zone (31.9%; 0.5–5.0 ppt), uncommon in the polyhaline zone (6.7%; 18.1–30 ppt), and rare in fresh water (1.7%; <0.5 ppt). Abundance in oligohaline waters peaked during June, about one month later than peak abundance in mesohaline waters.
During autumn, when age-0 fish were <300 mm SL, they began to move out of the rivers (Fig. 8). Fish measuring 170–360 mm SL (5–95 percentile; n=55 fish) were found at the mouth of the Little Manatee River during the winter. Large concentrations of age-0 ladyfish were also found at other river mouths, near the dredged (>12 m) portions of the Alafia River, and near the mouth of Tampa Bay. There was a sudden pulse of ladyfish along Gulf of Mexico beaches during September–October (Fig. 4B). These were juvenile age-0 ladyfish measuring 219–260 mm SL (5–95 percentile; n=126). Only 2 of 158 individuals collected at Gulf beaches were smaller than 178 mm SL. The absence of larval ladyfish in shallow Gulf beach habitats contrasted strongly with the abundance of larval ladyfish in riverine habitats of Tampa Bay.

**Indian River Lagoon**

A total of 2916 ladyfish were captured in 3791 21.3-m seine hauls, 2118 trawl hauls, and 815 gillnet sets (Table 2). The seasonal pattern of arrival was similar to that in Tampa Bay. Early- and mid-metamorphic larvae were much better represented (28% or n=815) in the Indian River Lagoon than in Tampa Bay (0.2% or n=14), and these leptocephali were present from at least December to May (Fig. 4C). Late-metamorphic larvae were found in many months throughout the year, but they were most abundant during spring (Figs. 4D and 9). All ladyfish collected in the Indian River Lagoon ranged from 20 to 600 mm SL. Age-0 fish reached a modal length during winter (i.e. 250–270 mm SL), similar to that observed in Tampa Bay. Age-1 ladyfish appeared to overwinter at a mode of about 350 mm SL, and a small number of age-2+ were probably present as postulated for Tampa Bay.

Ladifish <100 mm SL were more common in the Indian River basin than in the Banana River basin, and fish >300 mm SL were more common in the Banana River basin than in the Indian River basin (Fig. 10). Juveniles first occupied upper mesohaline and lower polyhaline salinities at sizes of about 75 mm SL, and they remained at such salinities until reaching about 300 mm SL (Fig. 7). In the Indian River Lagoon, the mean salinity occupied by ladyfish 75–125 mm SL was about 5 ppt higher than in Tampa Bay, but mesohaline and oligohaline habitats are less common in
Indian River Lagoon than in Tampa Bay. Overall, however, ladyfish were broadly distributed in both the Indian River and Banana River basins throughout the year (Fig. 11).

Discussion

Ladyfish were common, widely distributed, and fast growing in both Tampa Bay and the Indian River Lagoon. Metamorphosing larvae and overwintering juveniles were linked together in a single study by using multiple sampling gears. Ladyfish ages inferred from length frequencies indicated that few fish older than 2–3 years were present in either estuary. Over a thousand ladyfish gonads from Tampa Bay and the Indian River Lagoon were examined macroscopically, and nearly all fish were found to be immature (McBride, pers. obs.). Overall, our observations agree with previous reports that ladyfish arrive in coastal embayments as metamorphosing larvae and leave after about 2–3 years to mature and eventually spawn at sea. Carles’ (1967) samples from a hypersaline Cuban lagoon contained only immature age 1–3 fish (115–375 mm SL). Others who have suggested that ladyfish mature at sea, where they reach a maximum age of about 6 years and a maximum length of 570–660 mm SL, include Hildebrand (1963), Palko (1984), and Santos-Martinez and Arboleda (1993).
Ladyfish in both Florida estuaries followed a similar sequence of size-specific movements with respect to salinity. Soon after metamorphosis and for much of their first year, ladyfish occupied waters that were lower than the median salinity of each estuary. Following their first winter, ladyfish occupied higher than median salinities. The available salinity range was wider in Tampa Bay and ladyfish were found in a wider range of salinities in Tampa Bay than ladyfish in the Indian River Lagoon. Some details of these movements deserve further investigation. For example, as juveniles grew to about 150 mm SL during summer they were found in progressively lower salinities. However, they may have passively remained in shallow-water habitats where salinity was decreasing because of summer rains, instead of actively selecting lower salinity waters. We also did not examine other factors that may co-vary with salinity; therefore we cannot rank the effect of salinity in relation to other variables. In one such simultaneous analysis, Friedland et al. (1996) showed that juvenile menhaden (Brevoortia tyrannus) select waters of high chlorophyll-a levels more consistently than a specific salinity value.

Temperature presumably affects ladyfish distributions as well. During colder than average winters, ladyfish have experienced hypothermal mortality in both Tampa Bay (Springer and Woodburn, 1960) and the Indian River Lagoon (Snelson and Bradley, 1978). We observed ladyfish moving into deeper water, to river mouths, to the lower

![Figure 7](image_url)

**Figure 7**
Density-weighted mean salinity at capture for different sizes and stages of ladyfish, *Elops saurus*, in Tampa Bay (1989–95) and Indian River Lagoon (1990–95). Early- and mid-metamorphic larvae are indicated as "Lepto." Error bars represent 2 standard errors. The solid horizontal line represents the median salinity value, and the dotted horizontal lines represent the 10th and 90th salinity percentiles, based on all samples (with or without ladyfish) from each system.
part of Tampa Bay, and out into Gulf of Mexico waters during colder months. Ladyfish may be selecting these areas for overwintering because such areas are less affected by atmospheric cold fronts. The critical temperatures for ladyfish survival have not been examined in the laboratory, but the above field studies suggest that they could be as low as 10°C. Further work remains on the processes of habitat selection by ladyfish within estuaries.

This description of ladyfish early life history satisfies the first two of three predictions for an estuarine-dependent species: 1) predictable use of estuarine habitats, 2) absence of fish in suitable alternative habitats, and 3) demonstration of a negative population impact caused by the loss of estuarine habitats. Age-0 ladyfish followed an ontogenic migration along a salinity gradient and larval stages of ladyfish were absent from Gulf beaches. The third prediction, that of a negative impact on the population by the absence of habitat, was not supported by findings in our study. We anticipated that salinity differences between Tampa Bay and the Indian River Lagoon might affect growth rates, either due to osmoregulatory stress or perhaps to other correlated factors. Metamorphosing larvae moved into both estuaries at about the same time (i.e. in spring) but age-0 fish attained similar lengths.
(250–300 mm SL) by winter. In Florida Bay, age-0 ladyfish entered estuaries at similar stages during spring and reached similar overwintering sizes as well (Roessler, 1970). In contrast, Carles (1967) estimated much slower growth rates for ladyfish residing in hypersaline lagoons of Cuba, with sizes at annulus formation of 130 mm SL at annulus I, 195 mm SL at annulus II, and 247 mm SL at annulus III. If the growth increments observed by Carles (1967) are indeed annual (he used unvalidated scale annuli), then hypersaline (>35 ppt) conditions may

Figure 9

Monthly length frequency of ladyfish, Elops saurus, in the Indian River Lagoon. Early- and mid-metamorphic larvae were excluded because length decreases as they develop. Data from all years (1990–95), all gear types, and sampling zones (A–E) were plotted. n = number of fish sampled.
reduce ladyfish growth rates. The timing of ingress into the Cuban estuaries by metamorphosing larvae was not reported by Carles (1967); therefore it is not clear if overwintering sizes are comparable (i.e. if they represent the same seasonal growth period). If ingress into the Cuban estuaries occurred later than spring (i.e. when ladyfish entered Florida estuaries), then this would shorten the length of the growing season and could explain Carles’ (1967) results. This preliminary attempt to link salinity to growth rate, although suggestive, requires verification of reduced growth rates in hypersaline conditions. Experimental studies to determine the optimal salinity for ladyfish growth and survival will clarify whether ladyfish benefit by actively selecting low-salinity habitats. Such information would be the last step in demonstrating that ladyfish depend on estuaries and for showing the relative value of positive estuaries (with low salinity areas) to negative estuaries (with hypersaline conditions) for ladyfish populations. It would also be the next step for defining the essential fish habitat of ladyfish and for predicting the effects of changes in estuarine salinity on this fishery species.

Acknowledgments

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Dozens of anonymous and not so anonymous hands helped collect, sort, and identify fish. Valuable discussions or comments on earlier drafts were provided by R. Crabtree, K. Guindon-Tisdal, S. Kaiser, J. Levesque, K. Peters, R. Ruiz-Carus, and D. Winkelman. Editorial assistance was provided by L. French, J. Leiby, and J. Quinn. We thank all of the above.

Figure 11
Seasonal distribution plots for age-0 ladyfish, Elops saurus, collected in the Indian River Lagoon, 1991-95. Banana River and Indian River basins are identified in Figure 1B. Catch-per-unit-of-effort data from all positive catches of age-0 ladyfish were plotted as four quartile classes to standardize the data among gear types; increasing symbol size indicates higher catch per unit of effort. Smaller-size, age-1 ladyfish were excluded by increasing the size range for age-0, as indicated in each plot, from spring to winter.
Literature cited


