

ICHTHYOPLANKTON COMMUNITY STRUCTURE IN A SHALLOW SUBTROPICAL ESTUARY OF THE FLORIDA ATLANTIC COAST

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ABSTRACT

The northern Indian River Lagoon (IRL) system, Florida, possesses limited hydrologic connection to the Atlantic Ocean, a condition that dampens tidal flushing, with implications for both fish spawning behavior and subsequent larval recruitment. We conducted a 2-yr ichthyoplankton study of the northern IRL to document the abundance and distribution of individual larval taxa and assess spatio-temporal patterns in overall community structure. From August 2002 to July 2004, 48 surveys were performed in eight estuarine sub-basins. In total, 592,449 fish larvae from 58 identifiable taxa, and 6.1 million eggs were collected. Ichthyoplankton was numerically dominated by the families Engraulidae and Gobiidae, which comprised 74% and 17% of all larvae, respectively. The family Sciaenidae was the most speciose with eight taxa represented. Although community structure was similar throughout the region, temporal variation in ichthyoplankton abundance was pronounced with 85% of eggs and 94% of larvae collected during the May–October wet season. Marine-spawned larvae comprised < 0.2% of captures. Widespread estuarine spawning was apparent for red drum, *Sciaenops ocellatus* (Linnaeus, 1766), and southern kingfish, *Menticirrhus americanus* (Linnaeus, 1758), suggesting that northern IRL populations of these fishery species may be largely self-recruiting and do not depend on larval influx from shelf waters.

Estuarine fish faunas are comprised of species that demonstrate a broad array of reproductive strategies (Blaber et al., 1989; Able and Fahay, 1998; Whitfield, 1999; Able, 2005). Many are marine transients, species that spawn offshore but depend on estuaries (to varying degrees) as juvenile nurseries. Some are residents, completing their entire life cycle within the confines of the estuary, while still others are diadromous, utilizing estuaries during migrations between marine and freshwater habitats. The abundance and distribution of early stage fishes of each group within a specific estuary is known to depend on a variety of factors including seasonal temperature regimes (Witting et al., 1999; Avendaño-Ibarra et al., 2004), salinity (Locke and Courtenay, 1995; Berasategui et al., 2004), turbidity (Blaber and Blaber, 1980), food resources (Turner et al., 1983; Newton, 1996), and predator abundance (Cowan and Houde, 1993).

Ichthyoplankton assemblages within large and/or isolated estuaries are also strongly structured by their degree of connectivity to open marine habitats (Bennett et al., 1985; Neira et al., 1992; Russell, 1996; Strydom et al., 2003). Many coastal lagoons, for example, are characterized by narrow or intermittently closed ocean inlets which limit mixing with marine waters and result in long flushing times (Koutitonsky, 2005). This condition can curtail pelagic recruitment of marine-spawned fishes by providing only small passages for arriving individuals and by dampening astronomical tides necessary to drive selective tidal stream transport once inside the estuary (Neira and Potter, 1992). Theoretically, this physiography will also slow the dispersal potential of estuarine-spawned ichthyoplankton, especially for species which maintain discrete or widely spaced spawning sites. Of equal importance, reduced circu-

lation will mediate physico-chemical processes which also dictate survival success (Griffiths, 2001). Therefore, even within a single embayment, the ichthyoplankton assemblage may grade rapidly from a marine-dominated to estuarine or freshwater-dominated community in accordance with the size and spacing of inlets and distribution of suitable settlement substrates. Ichthyoplankton surveys which focus sampling near inlets to best resolve the mechanisms and seasons of recruitment of early stage fishes are unlikely to adequately characterize the community of more remote estuarine waters. Clearly, an understanding of the processes which influence assemblage structure in areas far removed from the marine environment is essential for proper management of coastal fisheries in relatively isolated systems.

The Indian River Lagoon (IRL) ecosystem, east-central Florida, possesses one of the most diverse ichthyofaunas of any U.S. estuary with nearly 400 fish species recorded to date (Gilmore, 1995). This richness is due to many factors including a transitional climate, several suitable habitat types, and a continuous supply of tropical fish larvae via the Gulf Stream (Gilmore, 1977, 1995; Snelson, 1983). The IRL is unique among Florida estuaries in that it maintains a very limited hydrologic connection with the Atlantic Ocean; lagoon-shelf circulation occurs through five narrow and widely spaced inlets. Areas distant from these inlets, especially in the northern IRL system, are microtidal and flushing with shelf water occurs over a timeframe of several months (Smith, 1987, 1993). Many investigators have concluded that this lack of tidal forcing contributes to the well documented south-north decline in species richness within the IRL by limiting recruitment of fish larvae arriving from offshore spawning sites (Snelson, 1983; Gilmore, 1988; Brown-Peterson and Eames, 1990; Kupschus and Tremain, 2001). Nonetheless, representatives from several marine-spawning families (e.g., Elopidae, Clupeidae, Gerreidae, Sparidae, and Mugilidae) are abundant and widely distributed throughout the northern IRL as juveniles and adults (Snelson, 1983; Tremain and Adams, 1995; Paperno et al., 2001). A better understanding of the abundance, size, and mechanism(s) of up-estuary recruitment strategies for these species is helpful when assessing the relative nursery function of the expansive IRL salt marshes and seagrass beds found in areas far from inlets. Such information is also of relevance to other regional estuaries (e.g., Laguna Madre, Texas; Pamlico Sound, North Carolina) with limited marine influence.

Evidence suggests that many of the region's economically valuable sciaenid sport-fishes (seatrouts, drums, and croakers) may be reproducing in estuarine areas far removed from ocean influence, including the red drum, *Sciaenops ocellatus* (Linnaeus, 1766), weakfish, *Cynoscion regalis* (Bloch and Schneider, 1801), and kingfish, *Menticirrhus* spp., which preferentially spawn at coastal inlets or along the continental shelf elsewhere in the west-central Atlantic. This behavior, which may also be related to the isolation of the northern IRL, has to date been inferred exclusively from passive acoustic techniques (Mok and Gilmore, 1983; Gilmore et al., 2003; Rydene, 2003) or qualitative field observations (Applied Biology et al., 1980; Murphy and Taylor, 1990; Johnson and Funicelli, 1991) which provide little insight as to resulting larval densities or distribution.

The specific goals of this study were to (1) define the spawning and recruitment seasons and reproductive strategies of individual estuarine fish species, and (2) employ non-metric multi-dimensional scaling (MDS) and related multivariate techniques to characterize the overall northern Indian River Lagoon ichthyoplankton community and identify how it changes in response to spatial and temporal fluctuations in habi-

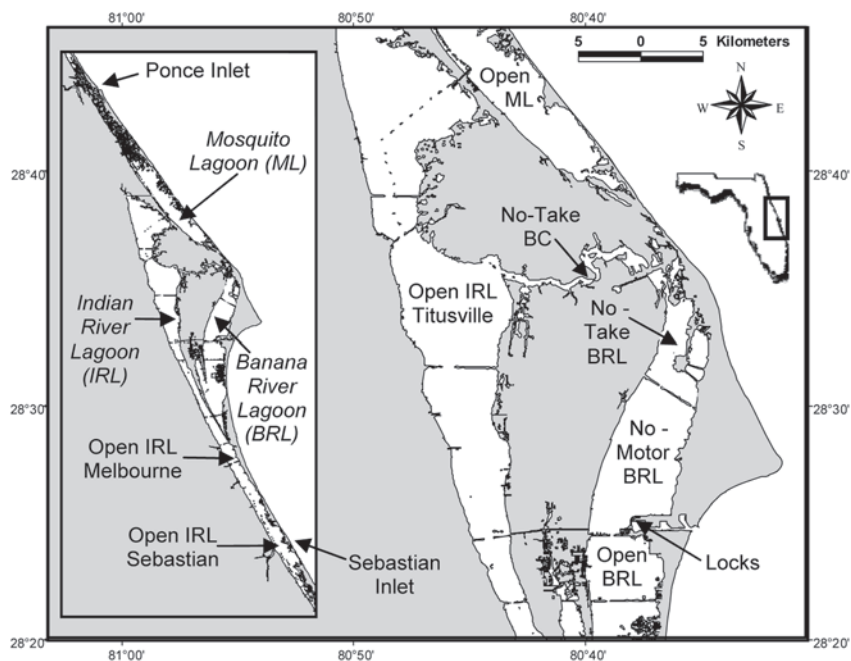


Figure 1. Map of the northern Indian River Lagoon system, east-central Florida. The system is composed of three semi-isolated estuarine basins including the IRL proper (IRL), Banana River Lagoon (BRL), and Mosquito Lagoon (ML). Sub-basins designated “No-Take” lack all public access. The sub-basin designated “No-Motor” has limited access due to motorized vessel restrictions and temporary security restrictions. All “Open” sub-basins have no restrictions on public access.

tat conditions. This effort, which represents the first multi-year quantitative ichthyoplankton survey of the region, is intended to serve as a benchmark at an important juncture in the history of this estuary, which is poised to undergo increasingly rapid change and further degradation in coming years due to unprecedented rates of human population growth.

MATERIALS AND METHODS

STUDY REGION.—The IRL system is a shallow bar-built estuary that extends 253 km from 26°30'N to 29°25'N along the central east coast of Florida and is composed of three semi-isolated water bodies: the Indian River Lagoon proper (IRL), the Banana River Lagoon (BRL), and Mosquito Lagoon (ML), with a combined surface area of 830 km². These basins are separated from each other and from the Atlantic Ocean by narrow barrier islands as well as the more expansive Cape Canaveral and Merritt Island landmasses. Five stabilized coastal inlets (Jupiter, St. Lucie, Fort Pierce, Sebastian, and Ponce) connect the IRL system with the Atlantic Ocean, and the Port Canaveral locks also allow for intermittent ocean water exchange with the BRL. The regional climate is subtropical with two general seasons; a warm humid rainy season from May to October and a cooler dry season from November to April. Details regarding the climate and physiography of the IRL watershed are provided by Woodward-Clyde (1994).

Sampling was confined to the northern half of the IRL system between Sebastian Inlet and southern Mosquito Lagoon (Fig. 1). Most of this area is far removed from the continental shelf (by up to 90 km) and is microtidal with astronomical tides from 0–5 cm in amplitude (Smith, 1987). Water level fluctuates slowly and horizontal circulation is weak, driven primarily by

wind (Pitts, 1989). Smith (1993) estimated that a 50% renewal with ocean water through the inlets took up to 230 d in some areas of the northern IRL. The region is typically polyhaline with a mean water depth of only 1.5 m (Snelson, 1983). Bottom substrates are composed of sand, mud, and shell, with prominent seagrass beds of *Halodule wrightii* Asch., *Ruppia maritima* L., and *Syringodium filiforme* Kütz (Dawes et al., 1995; Provancha and Scheidt, 1999).

Ichthyoplankton was collected from eight estuarine sub-basins of the northern IRL system which are compartmentalized to varying degrees by natural shorelines, shallow shoals, and/or manmade earthen causeways, features which further inhibit local intra-estuarine and ocean-shelf circulation processes (Evink, 1980; Morris et al., 2003; D. Christian, St. John's River Water Management District, unpubl. data). These sub-basins were selected both to (1) cover a wide geographic area, and (2) represent habitat on each side of the Kennedy Space Center (KSC) no-entry security zone (a de-facto no-take fisheries reserve) as a means of assessing sportfish ichthyoplankton density between areas experiencing differing levels of fishing harvest. Larvae of the family Sciaenidae, because of their regional economic value, were of particular interest in this regard. The distribution of sportfish larvae across the KSC boundary is presented in Reyier (2005).

Four of the areas sampled were considered primary sub-basins with ichthyoplankton collections made bi-weekly from August 2002 to July 2004. These are here named: (1) No-Take BRL, a largely undeveloped sub-basin at the northern terminus of the BRL which was established as a no-entry security zone for KSC and has been unfished since 1962; (2) No-Motor BRL, a federal manatee sanctuary south of No-Take BRL, also within KSC and largely undeveloped, whose public access is curtailed by a prohibition on motorized vessels; (3) Open BRL, the first fully public sub-basin south of the KSC whose watershed is largely urbanized, and (4) Open ML, a public but undeveloped sub-basin within KSC separated from No-Take BRL by < 3 km of wetlands. To expand the geographic scope of the study, three secondary sub-basins were sampled each March, June, September, and December. These included: (5) No-Take Banana Creek, a shallow mesohaline offshoot of the IRL proper also established as a KSC no-entry security zone; (6) Open IRL at Titusville, a partially urbanized sub-basin contiguous with No-Take BC, and (7) Open IRL at Melbourne, a fully urbanized sub-basin which consistently exhibits sub-optimal water quality and low seagrass coverage. Finally, an eighth sub-basin, Open IRL at Sebastian, was sampled in March and June 2004 to explore for latitudinal variations in fish spawning intensity (as suggested by preliminary data) and to provide for "snapshot" comparisons of species richness with an area with a stronger tidal influence. Important habitat characteristics of each sub-basin are listed in Table 1.

SAMPLING PROTOCOL.—Ichthyoplankton surveys commenced within 48 hrs of each new and full moon, periods of increased spawning for many fish including sciaenids in the southeastern US (Peters and McMichael, 1987; 1990; McMichael and Peters, 1989). Most surveys (44 of 48) were conducted at night because certain larvae, sciaenids included, exhibit a more uniform distribution in the water column at this time (Holt and Holt, 2000), and adults are actively spawning (Mok and Gilmore, 1983; Holt et al., 1985; Saucier and Baltz, 1993), potentially allowing for better identification of spawning sites. Bi-weekly surveys of primary sub-basins were typically completed within one night and expanded quarterly efforts (both primary and secondary sub-basins) within three nights. Eight ichthyoplankton tows were made within most sub-basins on each survey, with locations chosen using a random point generator in Arcview 3.2 GIS software. A ninth collection was made at IRL Sebastian to sample fish moving through the inlet proper, and only four samples per survey were made in No-Take Banana Creek due to its relative inaccessibility. All points occurring in water < 0.6 m were too shallow to sample and new random points were selected. Surface plankton tows were made with a 1 × 0.5 m rectangular neuston net with 500 µm mesh with a flow meter (General Oceanics 2030R) suspended across the net mouth to calculate water volume sampled. A mesh of this size extrudes some eggs and yolk sac larvae, resulting in underestimates of the density and size of certain species. This was a necessary protocol, however, because it minimized clogging from the ctenophore *Mnemiopsis mccradyi* Mayer, seagrass, and other debris, allowing for longer

Table 1. Physical and habitat characteristics of study sub-basins within the northern Indian River Lagoon system. Bathymetry and seagrass data provided by St. John's River Water Management District. Marsh area calculated from Rey and Kain (1990). BC = Banana Creek, BRL = Banana River Lagoon, ML = Mosquito Lagoon, PI = Ponce Inlet, SI = Sebastian Inlet.

Sub-basin	Public access	Sampling interval	Area (km ²)	Mean depth (m)	Area dredged %	Seagrass coverage %	Impounded salt marsh (km ²)	Min. distance to nearest inlet (km)
No-Take BRL	None	Bi-weekly	24.2	1.9	14.6	62.7	7.5	78.6 (SI)
No-Motor BRL	Limited	Bi-weekly	56.9	1.4	3.4	58.3	1.2	66.1 (SI)
Open BRL	Complete	Bi-weekly	25.3	1.5	3.2	36.9	0.0	60.8 (SI)
Open ML	Complete	Bi-weekly	38.3	0.9	0.0	52.2	11.7	42.1 (PI)
No-Take BC	None	Quarterly	9.2	0.5	0.0	NA	25.5	71.3 (PI)
Open IRL Titusville (T)	Complete	Quarterly	67.3	1.9	3.1	23.4	25.4	57.1 (PI)
Open IRL Melbourne (M)	Complete	Quarterly	16.3	1.9	2.3	28.6	0.0	29.9 (SI)
Open IRL Sebastian (S)	Complete	Twice	21.8	NA	6.3	NA	NA	0.0 (SI)

tow times necessary to collect rare or patchily-distributed larval taxa. The net was towed 20 m behind a 6 m skiff in a wide circle to avoid influence of prop wash on catch rates. Tow speed was 1 m s^{-1} for 4 min which typically resulted in filter water volumes $> 100 \text{ m}^3$. Since mean water depth of the region is only 1.5 m, it was assumed that surface tows would usually typify the entire water column so no attempts were made to step tows from near-bottom to surface. An exception to the sampling protocol was necessary in No-Take BC which is shallow and difficult to access. In this case, the net was fished passively in an area of localized wind-induced current generated by a culvert constructed within a narrow portion of central No-Take BC. Given its central location, this fixed sampling site is thought to typify Banana Creek.

At each collection site, water temperature ($^{\circ}\text{C}$), salinity, dissolved oxygen (mg L^{-1}), and pH were recorded with a YSI 6920 water meter, turbidity (expressed as nephelometric turbidity units, NTU) was measured with an ES&D 800 benchtop turbidity meter from water samples returned to the lab, and water depth (m) was measured using a handheld depth meter. The abundance of ctenophores, potential consumers of fish eggs and larvae, was measured by recording the displacement volume (i.e., biovolume) of collected animals using a graduated cylinder. Adult planktivorous fishes, also potential consumers of ichthyoplankton, were also removed and weighed to the nearest 0.1 g. Bioluminescence in the IRL is often pronounced due to the presence of the dinoflagellate *Pyrodinium* spp., and imparts a green glow to the net that may interfere with capture efficiency of larger, mobile larval fishes. Therefore, during each tow, bioluminescence was rated on a subjective scale of 0–5, with 5 representing the most intense glow.

Ichthyoplankton samples were preserved in 5% formalin and returned to the lab for sorting. For samples with many ctenophores, 50–100 ml of chlorine bleach was briefly added to sample bottles prior to rinsing to dissolve the ctenophores and allow for easier sorting. Larvae were removed from the sample, identified, and enumerated under a stereoscope. Notocord (NL) of preflexion larvae and standard length (SL) of flexion/postflexion fishes was recorded from a random sub-sample of most taxa (up to 10 individuals per sample for common species). When abundant, fish eggs, preflexion anchovies and gobies, and chaetognaths, *Saggita* spp. (another potential consumer of fish larvae) were sub-sampled with a Folsom plankton splitter. Eggs were tentatively classified based on published descriptions of estuarine spawning families who were also present in samples as yolk sac larvae. Several hundred preflexion gobies, and individuals of other taxa difficult to identify at small sizes, were cleared and stained following techniques outlined in Pothoff (1984) and assigned species affiliations based on meristic counts in agreement with regional species lists of Snelson (1983), Tremain and Adams (1995), and Paperno et al. (2001).

DATA ANALYSIS.—Multivariate statistical techniques were employed to discern spatio-temporal patterns in the ichthyoplankton community structure. First, to examine regional differences in species assemblages, the density of each taxon (larvae 100 m^{-3}) was averaged by sub-basin for each month of the 2-yr study and a sample similarity matrix was constructed using the Bray-Curtis similarity coefficient (Bray and Curtis, 1957). Density values were fourth-root transformed (Thorne et al., 1999) prior to constructing this matrix to down-weight the influence of abundant taxa (e.g., engraulids and gobiids), thus allowing less common species to contribute more fully to sample discrimination. Non-metric multi-dimensional scaling (MDS) was then employed to generate a low-dimensional ordination (map) of sample similarities across months and sub-basins, where interpoint distances are proportional to overall faunal similarity. To best resolve seasonal community changes within the region, these techniques were repeated by averaging all sample densities by month, irrespective of location. A two-way crossed analysis of similarities (ANOSIM) test with replication was then run for each of the four primary study sub-basins, averaged by month. An ANOSIM test is a non-parametric permutation procedure often used to test for differences in overall community structure between sites and times (Clark, 1993).

MDS was also employed to construct a species (as opposed to sample) ordination to determine if fish larvae were collected as discrete species groups or were occurring randomly

within samples. Larval counts were first standardized by total captures so that species ratios within samples (not absolute abundances) were used to construct the similarity matrix. Rare taxa are often distributed without pattern and disrupt species ordination (Clark and Warwick, 2001), so only the top 20 taxa (excluding those restricted primarily to Sebastian Inlet) were retained. A one-way ANOSIM was then used to test separation between (1) demersal and brooding estuarine-spawned, (2) pelagic estuarine-spawned, and (3) marine-spawned larvae. The degree to which measured habitat parameters were correlated to overall biotic structure was explored through the BIO-ENV procedure of Clarke and Ainsworth (1993) using all 10 habitat variables recorded at each site. These variables were $\log(1 + x)$ transformed when necessary to reduce skewness and then normalized to remove the effect of differing measurement scales. A sample similarity matrix based on Euclidean distance (appropriate for continuous environmental data containing few zero values) using habitat variables was then constructed and compared to the Bray-Curtis sample similarity matrix using the Spearman coefficient (ρ_s). The subset of variables most strongly correlated to the biotic pattern was selected. All multivariate procedures were performed with PRIMER 6.0 statistical software. Finally, all samples collected during each survey were averaged to allow determination of temporal fluctuations in species richness (taxa tow⁻¹), Shannon Diversity (H'), total fish egg and larval density, and densities of the 20 most abundant species (excluding those restricted primarily to Sebastian Inlet).

RESULTS

HABITAT CHARACTERIZATION—Mean water temperature ranged from 12 °C each winter to > 30 °C in summer and showed little spatial variation on any given survey (Fig. 2A). Most areas remained polyhaline and salinity rarely fluctuated by more than 10 in any sub-basin over the study duration (Fig. 2B). Open ML always exhibited higher salinity than the BRL and IRL, and the lowest salinity was consistently encountered in No-Take BC. Dissolved oxygen generally fluctuated from 5–10 mg l⁻¹, but on several occasions throughout the year concentrations dropped to < 4 mg l⁻¹ (Fig. 2C). pH showed little spatial or temporal variability, ranging between 7.8 and 9.2 (Fig. 2D). Turbidity fluctuated from < 1 NTU to nearly 20 NTU, but was < 7 NTU for most seasons and sampling locations (Fig. 2E). The highest turbidity was consistently recorded from No-Take BC and a consistent turbidity gradient was present in the BRL, with values increasing from north to south on most surveys. Mean water depth sampled on any given survey ranged from 1.5 to 3.5 m (Fig. 2F). The depth sampled was greatest in No-Take BRL (3.7 m) than in all other study areas (which ranged from 1.8–2.7 m) due to one or more samples collected each survey within dredged areas.

During both years, ctenophores were abundant during winter and spring but largely absent from samples collected between August and December (Fig. 2G). Mean densities during bloom periods exceeded 1000 ml 100 m⁻³ for several consecutive months, depending on location, and peaked near or above 4000 ml 100 m⁻³ early each spring. No-Take BC was the only sub-basin where ctenophores were common throughout the year, including summer, with mean abundance ranging from 500–18,500 ml 100 m⁻³ a condition which necessitated reduced tow times on most occasions. Chaetognath density peaked in summer and fall of both years, commonly averaging 15–40 individuals m⁻³, then declining to < 5 individuals m⁻³ during winter (Fig. 2H). Chaetognaths were occasionally found containing small larval fishes including atherinids, *Chasmodes* spp., gobiids, and *Sphoeroides* spp., although this consumption may be partly the result of cod-end predation. Adult planktivorous fishes were captured in 58% of tows. The bay anchovy, *Anchoa mitchilli* (Valenciennes, 1848), composed >

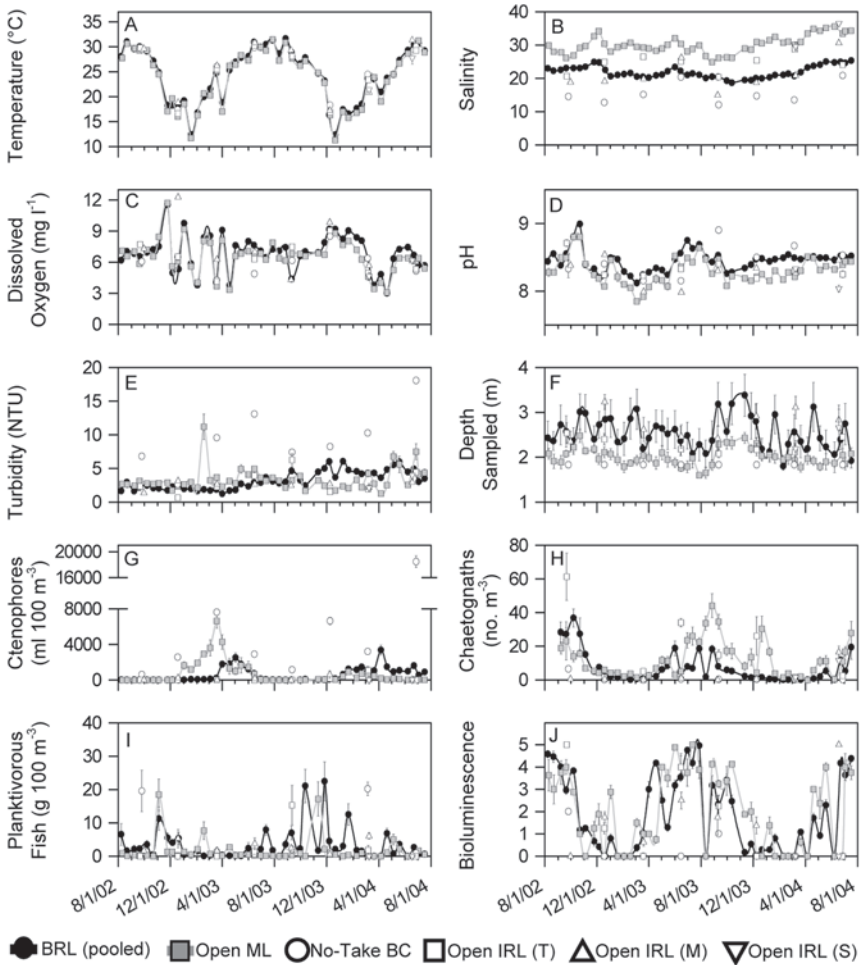


Figure 2. Temporal variation in habitat conditions (means \pm 1 SE) which may influence the distribution of ichthyoplankton in the northern Indian River Lagoon system. BC = Banana Creek, BRL = Banana River Lagoon, IRL = Indian River Lagoon, ML = Mosquito Lagoon. BRL data have been pooled.

98% of this biomass, with silversides, *Menidia* spp., and menhaden, *Brevoortia* spp., comprising the rest. Catch rates were highly variable but tended to be elevated in late fall and winter (Fig. 2I). Intensity of bioluminescence was highest from June to October but perceptible throughout the year (Fig. 2J). No tropical storms or hurricanes passed through the region during the study period.

ICHTHYOPLANKTON COLLECTIONS OVERVIEW.—Between August 2002 and July 2004, 592,449 larval fishes were collected in 1713 plankton tows. Fifty-eight distinct taxa in 28 families were recognized, although certain forms may represent two or more species (Table 2). Engraulids of the genus *Anchoa* were the most common, comprising > 74% of all fish larvae caught. These were almost exclusively *A. mitchilli*, based on examination of engraulid eggs (which are distinctive) as well as larvae > 10 mm SL. Gobiids, primarily of the genera *Gobiosoma* and *Microgobius*, based on identification of cleared and stained specimens, were also abundant, comprising an

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Table 2. Ichthyoplankton abundance (by sub-basin) collected from waters of the northern Indian River Lagoon system, August 2002–July 2004. (i) denotes immigrant (marine-spawned) larvae based on length and distribution information as well as known life history strategies. BC = Banana Creek, BRL = Banana River Lagoon, IRL = Indian River Lagoon proper, ML = Mosquito Lagoon. Taxa are listed phylogenetically.

Sub-Basin	No-Take BRL	No-Motor BRL	Open BRL	Open ML	No-Take BC	Open (T)	Open (M)	Open (S)	Total	% of Total
Ichthyoplankton Samples	384	384	383	384	32	64	64	18	1,713	
Surveys	48	48	48	48	8	8	8	2	—	
Total Water Filtered (m ³)	4.08 × 10 ⁴	3.70 × 10 ⁴	3.91 × 10 ⁴	3.94 × 10 ⁴	9.65 × 10 ²	6.15 × 10 ³	6.73 × 10 ³	1.97 × 10 ³	1.72 × 10 ⁵	
Mean Water Filtered (m ³)	106.2	96.3	102.1	102.6	30.1	96.1	105.2	109.4	—	
Larvae										
Elopidae										
<i>Elops saurus</i> , ladyfish ⁱ	2	1	6	3	1	1	1	14	29	0.005
<i>Elops</i> sp., ladyfish (undescribed) ⁱ	1	2	3	3	0	0	1	2	12	0.002
Megalopidae										
<i>Megalops atlanticus</i> , tarpon ⁱ	0	0	1	0	0	0	0	1	2	0.000
Ophichthidae										
<i>Myrophis punctatus</i> , speckled worm eel ⁱ	0	0	0	0	0	0	0	3	3	0.001
Clupeidae										
<i>Brevoortia</i> spp., Atlantic/yellowfin menhaden ⁱ	243	136	86	134	0	0	6	25	630	0.106
<i>Opisthonema oglinum</i> , Atlantic thread herring ⁱ	2	1	0	10	0	6	0	156	175	0.030
<i>Dorosoma cepedianum</i> , gizzard shad	0	0	1	0	0	0	0	0	1	0.000
Clupeidae (preflexion)	383	1	66	237	0	48	33	1,073	1,841	0.311
Engraulidae										
<i>Anchoa cubana/hepsetus</i> , Cuban/striped anchovy ⁱ	1	0	1	28	0	0	0	2	32	0.005
<i>Anchoa mitchilli</i> , bay anchovy	2,172	2,369	3,913	5,720	154	581	921	2	15,832	2.672
<i>Anchoa</i> spp. (preflexion)	34,977	112,701	139,928	97,517	161	14,489	21,705	1,287	422,765	71.359
Synodontidae										
Synodontidae sp. A ⁱ	0	0	0	0	0	0	0	1	1	0.000

Table 2. Continued.

Larvae	No-Take BRL	No-Motor BRL	Open BRL	Open ML	No-Take BC	Open IRL (T)	Open IRL (M)	Open IRL (S)	Taxon Total	% of Total
Gobiesocidae										
<i>Gobiesox strumosus</i> , skilletfish	9	19	41	16	0	17	31	1	134	0.023
Atherinidae										
Atherinidae sp. A	338	587	426	662	14	5	1	0	2,033	0.343
Atherinidae sp. B	42	18	12	59	0	6	0	0	137	0.023
<i>Membras martinica</i> , rough silverside	0	0	0	1	0	0	0	0	1	0.000
Fundulidae										
<i>Fundulus grandis</i> , gulf killifish	0	1	0	0	0	0	0	0	1	0.000
Poeciliidae										
<i>Gambusia holbrooki</i> , eastern mosquitofish	0	0	0	0	2	0	0	0	2	0.000
Cyprinodontidae										
<i>Cyprinodon variegatus</i> , sheepshead minnow	8	1	0	0	0	0	0	0	9	0.002
<i>Lucania parva</i> , rainwater killifish	101	28	3	34	1	0	0	0	167	0.028
Belontiidae										
<i>Strongylura notata</i> , redfish needlefish	0	0	2	0	0	0	0	0	2	0.000
<i>Strongylura timucu</i> , timucu	0	1	0	1	0	0	0	0	2	0.000
<i>Strongylura</i> spp.	2	2	0	4	0	0	0	0	8	0.001
Hemiramphidae										
<i>Hyporhamphus meeki</i> , American halfbeak	2	1	1	1	0	1	0	0	6	0.001
<i>Hyporhamphus</i> spp.	44	54	36	51	0	8	1	8	202	0.034
Syngnathidae										
<i>Hippocampus erectus</i> , lined seahorse	50	72	71	113	1	24	2	3	336	0.057
<i>Hippocampus zosterae</i> , dwarf seahorse	16	22	6	28	0	2	1	0	75	0.013
<i>Syngnathus louisianae</i> , chain pipefish	269	378	514	636	0	161	152	8	2,118	0.357
<i>Syngnathus scovelli</i> , gulf pipefish	562	434	313	671	7	222	104	17	2,330	0.393
Carangidae										
<i>Oligoplites saurus</i> , leatherjacket	26	91	382	238	0	22	6	2	767	0.129

Table 2. Continued.

Larvae	No-Take BRL	No-Motor BRL	Open BRL	Open ML	No-Take BC	Open IRL (T)	Open IRL (M)	Open IRL (S)	Taxon Total	% of Total
Gerreidae										
<i>Diapterus auratus</i> , Irish pompano ⁱ	0	8	4	1	0	0	3	0	16	0.003
<i>Eucinostomus</i> spp. ⁱ	0	5	10	1	0	0	0	23	39	0.007
Gerreidae ⁱ	0	0	0	0	0	0	0	7	7	0.001
Haemulidae										
<i>Orthopristis chrysoptera</i> , pigfish ⁱ	0	0	0	0	0	0	0	2	2	0.000
Sparidae										
<i>Lagodon rhomboides</i> , pinfish ⁱ	4	9	41	2	0	0	0	0	56	0.009
Sciaenidae										
<i>Bairdiella chrysoura</i> , silver perch	201	906	2,724	1,578	1	300	224	10	5,944	1.003
<i>Cynoscion arenarius/regalis</i> , weakfish	8	11	30	52	0	0	12	4	117	0.020
<i>Cynoscion nebulosus</i> , spotted seatrout	224	1,630	2,197	3,082	1	81	72	11	7,298	1.232
<i>Leiostomus xanthurus</i> , spot ⁱ	0	1	1	1	0	0	0	6	9	0.002
<i>Menticirrhus americanus</i> , southern kingfish	240	1,689	2,864	1,048	0	613	167	18	6,639	1.121
<i>Micropogonias undulatus</i> , Atlantic croaker ⁱ	2	2	4	13	0	0	0	2	23	0.004
<i>Pogonias cromis</i> , black drum	3	1	2	73	0	0	2	5	86	0.015
<i>Sciaenops ocellatus</i> , red drum	42	274	345	851	0	40	40	4	1,596	0.269
Sciaenidae (preflexion)	116	1,819	2,159	2,971	0	167	33	69	7,334	1.238
Ephippidae										
<i>Chaetodipterus faber</i> , Atlantic spadefish	0	2	0	1	0	1	0	0	4	0.001
Mugilidae										
<i>Mugil cephalus</i> , striped mullet ⁱ	7	10	6	1	0	0	0	0	24	0.004
Blennidae										
<i>Chasmodes</i> spp., Florida/striped blenny	1,124	1,622	1,123	1,762	15	1,349	139	1,306	8,440	1.425

Table 2. Continued.

Larvae	No-Take BRL	No-Motor BRL	Open BRL	Open ML	No-Take BC	Open IRL (T)	Open IRL (M)	Open IRL (S)	Taxon Total	% of Total
Blennioidei sp. A ⁱ	0	0	0	0	0	0	0	1	1	0.000
Blennioidei sp. B	0	0	0	0	0	0	0	180	180	0.030
Gobiidae										
<i>Ctenogobius</i> spp./ <i>Evorthodus lyricus</i> ^d	0	0	0	0	0	0	0	32	32	0.005
<i>Gobionellus oceanicus</i> , highfin goby	0	1	0	0	0	0	2	3	6	0.001
<i>Gobiosoma bosc</i> , naked goby	0	0	0	0	131	2	1	0	134	0.023
<i>Gobiosoma robustum</i> , code goby	18	45	159	0	6	196	143	0	567	0.096
<i>Gobiosoma</i> spp.	199	219	855	677	384	179	293	9	2,815	0.475
<i>Microgobius gulosus</i> , clown goby	19	11	15	0	14	30	0	0	89	0.015
<i>Microgobius</i> spp.	933	1,480	3,040	1,132	60	28	59	6	6,738	1.137
Gobiidae sp. A	2	0	0	2	0	0	3	0	7	0.001
Gobiidae sp. B ⁱ	0	0	0	0	0	0	0	5	5	0.001
Gobiidae (preflexion)	13,078	16,006	25,381	22,667	1,806	10,586	2,555	502	92,581	15.627
Achiridae										
<i>Achirus lineatus</i> , lined sole	70	129	232	257	1	5	19	30	743	0.125
Achiridae (preflexion)	7	40	82	68	0	0	3	2	202	0.034
Cynoglossidae										
<i>Symphurus</i> spp.	1	0	0	9	0	0	0	0	10	0.002
Pleuronectiformes sp. A	0	1	0	5	0	0	0	0	6	0.001
Pleuronectiformes (preflexion)	0	1	1	2	0	0	1	45	50	0.008

Table 2. Continued.

Larvae	No-Take BRL	No-Motor BRL	Open BRL	Open ML	No-Take BC	Open IRL (T)	Open IRL (M)	Open IRL (S)	Taxon Total	% of Total
Monacanthidae										
<i>Stephanolepis setifer</i> , pigmy filefish ¹	0	0	0	0	0	0	0	1	1	0.000
Tetraodontidae										
<i>Sphoeroides</i> spp.	267	123	154	62	0	113	173	22	914	0.154
Diodontidae										
Diodontidae sp. A	5	9	1	14	0	0	3	0	32	0.005
Perciformes sp. A	0	0	0	1	0	0	0	39	40	0.007
Perciformes sp. B	0	0	1	0	0	0	0	8	9	0.002
Sub-Basin Total	55,820	142,974	187,243	142,500	2,760	29,283	26,912	4,957	592,449	100.000
Eggs										
<i>Anchoa mitchilli</i> , bay anchovy	598,536	929,510	970,299	701,627	105	99,322	219,555	57,108	3,576,062	58.304
Sciaenidae	431,305	396,213	549,685	629,805	1	179,074	244,346	22,032	2,452,461	39.985
Pleuronectiformes	4,611	13,293	10,686	17,828	0	5,114	848	2,872	55,252	0.901
Other	24,969	492	1,227	9,786	0	7,352	5,504	328	49,658	0.810
Sub-Basin Total	1,059,421	13,339,508	1,531,897	1,359,046	106	290,862	470,253	82,340	6,133,433	100.000

additional 17% of fish larvae caught. The family Sciaenidae represented 5% of fish larvae and was the most speciose with eight species identified. An estimated 6.1 million fish eggs were also collected, 58% of which were *A. mitchilli*, 40% tentatively ascribed to the family Sciaenidae, and 1% to the order Pleuronectiformes. Greater detail on the abundance of individual egg and larval taxa are provided in Reyier (2005). Length data for all species are listed in Table 3.

ICHTHYOPLANKTON COMMUNITY STRUCTURE.—Ichthyoplankton abundance displayed marked seasonal variation with 85% of fish eggs and 94% of fish larvae collected during the May–October wet season (Fig. 3A,B). In all areas, total larval fish density peaked in late August or September during both years sampled. On many summer and early fall surveys, mean density exceeded 500 larvae 100 m⁻³ with the highest mean density reaching 4096 larvae 100 m⁻³ during September 2003 in No-Motor BRL. During October of both years, ichthyoplankton abundance dropped rapidly with density typically ranging from 1–100 larvae 100 m⁻³ from November through April. The number of species encountered also varied seasonally and was elevated during warmer months (Fig. 4A). Collections during summer and early fall contained representatives from a number of different families. In contrast, collections during winter and early spring were depauperate, characterized primarily by syngnathids and *Sphoeroides* spp. larvae as well as greatly reduced densities of engraulids and gobiids. But notably, this was the time when most marine-spawned larvae [e.g., *Elops* spp., *Brevoortia* spp., *Mugil* spp., *Lagodon rhomboides* (Linnaeus, 1766)] were encountered. Open IRL Sebastian had elevated species counts compared to other sub-basins when it was surveyed in March and June 2004. Eight taxa were taken here that were unique to the study, even though sampling effort was very limited. Species diversity was relatively stable across seasons and sub-basins (Fig. 4B). The lowest diversity was found in No-Take BC. The highest diversity was encountered at Open IRL Sebastian, due to the presence of unique species recruiting from marine waters.

Non-metric multidimensional scaling provided an adequate two-dimensional ordination of ichthyoplankton community structure. The considerable overlap of samples collected from the IRL, BRL, and ML demonstrate that the regional ichthyoplankton species assemblage was fairly uniform (Fig. 5). The two exceptions included No-Take BC, where both larval abundance and species richness were low, and Open IRL Sebastian, where species richness was highest. While statistically significant differences in community composition were noted between the four primary sub-basins (ANOSIM: Global R = 0.077, P = 0.007), low pairwise R values suggest these distinctions have little biological meaning and are likely due to high replication and quantitative differences in mutual species. Temporal variability in community structure was more pronounced and significant (ANOSIM: Global R = 0.584, P = 0.001). Changes in this species assemblage exhibited a strong seasonal cycle that was similar between years, partly because few new species were collected during year two of the study (Fig. 6). The greatest shifts in community composition occurred during late fall, when many taxa disappeared from the ichthyoplankton, and again in late winter/early spring, when reproduction of many estuarine-spawners resumed.

Fish larvae sharing similar dispersal strategies were typically collected together (Fig. 7). Taxa hatching from pelagic eggs such as *A. mitchilli*, sciaenids, the leather-jacket, *Oligoplites saurus* (Bloch and Schneider, 1801), and lined sole, *Achirus lineatus* (Linnaeus, 1758) were most abundant in deeper areas while those with demersal

Table 3. Lengths (in mm) of larval fishes collected in the northern Indian River Lagoon system, August 2002–July 2004.

Taxon	Mean \pm 1 S.D.	Min	Max	No. Measured	Taxon, continued	Mean \pm 1 S.D.	Min	Max	No. Measured
<i>Elops saurus</i>	36.7 \pm 5.3	24.0	45.0	27	<i>Eucinostomus</i> spp.	9.7 \pm 0.8	8.0	11.4	39
<i>Elops</i> sp. (undescribed)	33.1 \pm 5.2	26.0	43.0	12	Gerreidae	5.8 \pm 2.5	4.1	9.5	7
<i>Megalops atlanticus</i>	23.0 \pm 1.5	22.0	24.0	2	<i>Orthopristis chrysoptera</i>	18.2 \pm 11.1	10.4	26.0	2
<i>Myrophis punctatus</i>	50.0 \pm 1.0	49.0	51.0	3	<i>Lagodon rhomboides</i>	12.2 \pm 1.0	9.9	14.0	56
<i>Brevoortia</i> spp.	20.6 \pm 2.6	12.0	29.0	539	<i>Bairdiella chrysoura</i>	2.6 \pm 0.7	1.5	12.0	1,257
<i>Opisthonema oglinum</i>	18.1 \pm 4.4	12.0	28.0	73	<i>Cynoscion regalis</i>	2.4 \pm 0.6	1.7	4.8	78
<i>Dorosoma cepedianum</i>	24.0 \pm 0.0	—	—	1	<i>Cynoscion nebulosus</i>	2.6 \pm 0.8	1.5	12.0	1,480
<i>Anchoa hepsetus</i>	24.7 \pm 3.2	15.0	31.0	32	<i>Leiostomus xanthurus</i>	12.6 \pm 0.8	12.0	14.0	9
Synodontidae sp. A	8.1 \pm 0.0	—	—	1	<i>Menticirrhus americanus</i>	2.3 \pm 0.6	1.4	6.0	1,114
<i>Gobiosox strumosus</i>	4.4 \pm 1.9	2.0	9.5	121	<i>Micropogonias undulatus</i>	14.1 \pm 3.3	8.7	22.0	23
Atherinidae sp. A	4.9 \pm 2.2	2.4	23.0	838	<i>Pogonias cromis</i>	2.7 \pm 0.8	2.0	7.2	61
Atherinidae sp. B	4.6 \pm 1.6	3.0	14.0	95	<i>Sciaenops ocellatus</i>	2.5 \pm 0.6	1.6	6.5	466
<i>Membras martinica</i>	9.0 \pm 0.0	—	—	1	<i>Chaetodipterus faber</i>	2.6 \pm 0.9	2.0	3.8	4
<i>Fundulus grandis</i>	8.5 \pm 0.0	—	—	1	<i>Mugil cephalus</i>	20.6 \pm 1.4	19.0	23.0	21
<i>Gambusia holbrooki</i>	13.5 \pm 0.8	13.0	14.0	2	Chasmodes spp.	3.5 \pm 0.7	2.0	8.0	1,901
<i>Cyprinodon variegatus</i>	4.2 \pm 1.2	3.4	7.0	9	Blennoidei sp. A	6.7 \pm 0.0	—	—	1
<i>Lucania parva</i>	4.3 \pm 1.3	1.9	15.0	111	Blennoidei sp. B	2.8 \pm 0.4	2.0	3.7	62
<i>Strongylura notata</i>	33.7 \pm 10.1	23.0	43.0	3	<i>Ctenogobius/Evorthodus</i>	9.1 \pm 0.1	8.1	9.6	26
<i>Strongylura timucu</i>	44.0 \pm 0.0	—	—	1	<i>Gobionellus oceanicus</i>	12.3 \pm 0.5	12.0	13.0	4
<i>Strongylura</i> spp.	9.3 \pm 4.1	4.8	14.0	7	Gobiidae sp. A	3.0 \pm 0.6	2.0	3.5	5
<i>Hyporhamphus meeki</i>	26.7 \pm 6.9	19.0	38.0	7	Gobiidae sp. B	8.0 \pm 0.6	7.5	9.0	5
<i>Hyporhamphus</i> spp.	6.8 \pm 4.2	4.0	29.0	167	<i>Achirus lineatus</i>	2.3 \pm 0.8	1.5	9.0	329
<i>Hippocampus erectus</i>	14.7 \pm 5.5	7.0	35.0	216	<i>Symphurus</i> spp.	4.0 \pm 0.0	4.0	4.0	4
<i>Hippocampus zosterae</i>	16.1 \pm 6.3	5.0	30.0	56	<i>Stephanolepis setifer</i>	7.2 \pm 0.0	—	—	1
<i>Syngnathus louisianae</i>	15.6 \pm 6.0	8.0	50.0	944	<i>Sphoeroides</i> spp.	2.2 \pm 1.0	1.5	4.5	410
<i>Syngnathus scovelli</i>	15.4 \pm 4.0	7.5	47.0	972	Diodontidae sp. A	2.8 \pm 1.1	2.1	7.2	32
<i>Oligoplites saurus</i>	2.9 \pm 1.8	1.5	11.2	265	Perciformes sp. A	2.7 \pm 0.6	2.0	4.1	39
<i>Diapterus auratus</i>	14.8 \pm 3.3	10.4	23.0	16	Perciformes sp. B	2.4 \pm 0.3	2.1	2.7	9

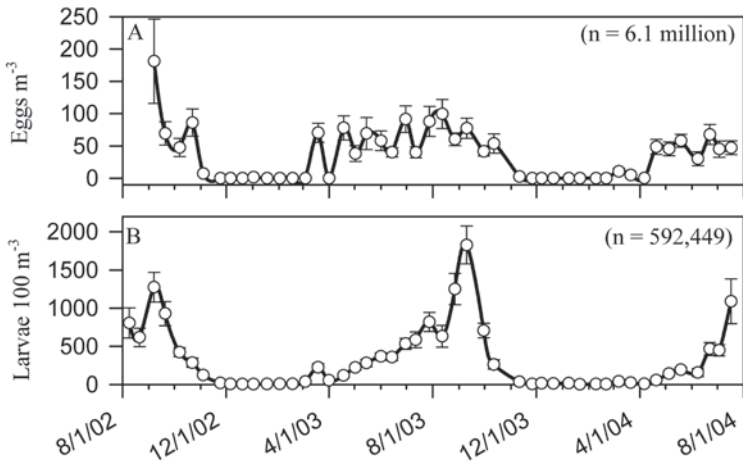


Figure 3. Regional density (mean \pm 1 SE), of (A) total fish eggs, and (B) larvae, in the northern Indian River Lagoon system, Florida, August 2002–July 2004.

eggs, including atherinids, halfbeaks, *Hyporhamphus* spp., blennies, *Chasmodes* spp., as well as brooding syngnathids, were collected more widely and were abundant over shallow seagrass. This separation was significant (ANOSIM: $R = 0.392$, $P = 0.003$), undoubtedly driven both by preferred adult spawning microhabitats as well as temporal differences in abundance. In general, species producing pelagic eggs had restrictive spawning seasons relative to brooders and demersal spawners. Results of the BIO-ENV procedure demonstrated that of the ten measured environmental variables, changes in water temperature alone most strongly correlated with changes in ichthyoplankton community structure through space and time (Spearman coefficient $\rho_s = 0.642$). All other variables had weak or no correlation to overall com-

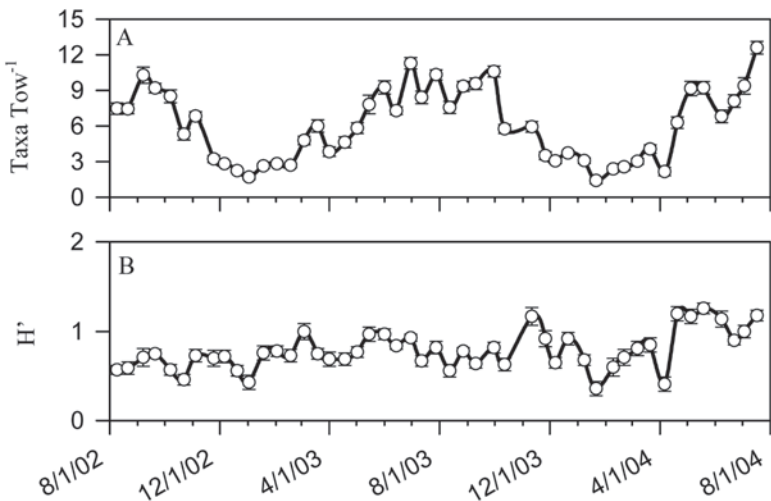


Figure 4. (A) Larval fish taxa per tow, and (B) Shannon Diversity (mean \pm 1 SE), in the northern Indian River Lagoon system, Florida, August 2002–July 2004.

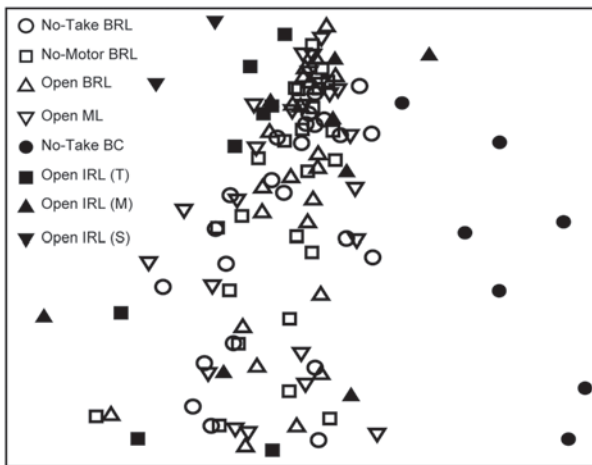


Figure 5. Spatial (sub-basin) differences in overall ichthyoplankton community structure within the northern Indian River Lagoon system, Florida, August 2002–July 2004, as demonstrated by non-metric multi-dimensional scaling. Each point represents overall fauna averaged by sub-basin for each month of the study. Open points indicate primary sub-basins, sampled bi-weekly. Solid points indicate secondary sub-basins sampled quarterly. Interpoint distances are proportional to overall faunal similarity. 2-D stress = 0.13.

munity structure, and combinations of environmental variables did not increase the explanatory value of the environmental data set (Table 4).

Larvae of species with known marine spawning requirements were uncommon, representing < 0.2% of captures when samples collected near Sebastian Inlet were excluded. Of this group, the majority were *Brevoortia* spp., with smaller numbers of *Elops* spp., *Mugil cephalus* Linnaeus, 1758, *L. rhomboides*, gerreids, and *Micropogonias undulatus* (Linnaeus, 1766). These larvae were widely distributed, however, and were commonly collected > 30 km away from oceanic ingress points and on the opposite side of earthen causeways or other potential physical barriers to pelagic dispersal. These were also the largest fish larvae present in samples, typically ≥ 10 mm SL.

For many common taxa, estuarine spawning began several weeks earlier in the southern half of the study area. Although sampling was limited outside of the BRL and ML, a survey in March 2003 at Open IRL Melbourne measured elevated egg densities relative to other sub-basins. Mean *A. mitchilli* egg density (219 m^{-3}) for example, was 15 and 79 times higher than in the BRL and ML, respectively, and sciaenid egg density (56 eggs m^{-3}) was 10 times higher than either the BRL or ML. Further, a survey in early March 2004 found low egg density throughout the IRL system with the exception of the newly added Open IRL Sebastian, where *A. mitchilli* and sciaenid eggs and many larval taxa were abundant. Densities within the BRL and ML did not approach similar levels until several weeks later each year. Temporal trends for the twenty most common larval taxa are provided in Figure 8.

DISCUSSION

The majority of the 400 fish species known from the IRL system have a pelagic larval dispersal stage; however, our study surveying all three lagoon basins (IRL proper, BRL, and ML) with good temporal replication, sampled only 50 larval taxa from 28

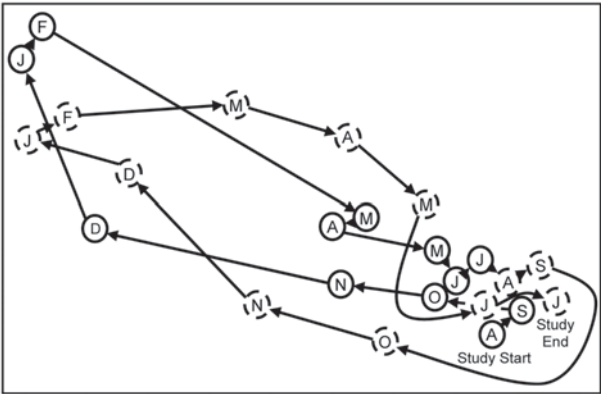


Figure 6. Seasonal shifts in overall regional ichthyoplankton community structure within the northern Indian River Lagoon system, Florida, as demonstrated by non-metric multi-dimensional scaling. Each circle represents the overall fauna averaged by month from August 2002–July 2004, irrespective of location. Solid circles represent the first year of the study and dashed circles represent the second year. Interpoint distances are proportional to overall faunal similarity. 2-D stress = 0.06.

families (representing no more than 75 discrete species) away from Sebastian Inlet. These findings demonstrate that the ichthyoplankton assemblage of the region is relatively depauperate, possessing only a small subset of the species which invariably occur in estuarine waters more proximate to the continental shelf. This pattern is further evident in a comparison with Ferrell (1999), who in a 1-mo period (September–October 1998) obtained 69 taxa from 40 families recruiting through Sebastian Inlet. Further, in only 18 collections near Sebastian Inlet during the current study (1% of total sampling effort), 40 larval taxa were recorded, greater than or equal to the number we collected within any other individual sub-basin over a 2-yr period.

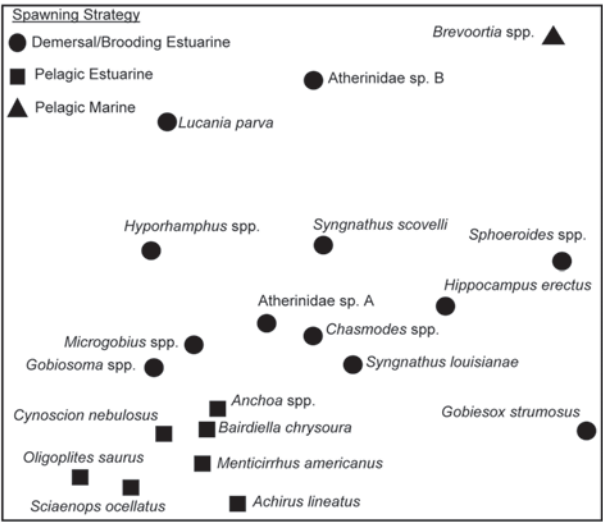


Figure 7. Ichthyoplankton species associations within the northern Indian River Lagoon system, Florida, August 2002–July 2004, as demonstrated by non-metric multi-dimensional scaling. Symbol shapes denote generalized reproductive strategies of the twenty most abundant species. Taxa closest together represent those most often collected together. 2-D stress = 0.13.

Table 4. Results of a Bio-Env procedure to determine which habitat factors, alone or in combination, are of greatest importance in structuring overall ichthyoplankton community composition.

Single habitat variables	Spearman rank correlation ρ_s
Water temperature	0.642
Bioluminescence	0.315
Chaetognaths	0.290
Dissolved oxygen	0.224
Turbidity	0.152
Ctenophores	0.140
Salinity	0.139
pH	0.006
Zooplanktivorous fishes	-0.020
Water depth	-0.032
Five best habitat variable subsets	Spearman rank correlation ρ_s
Water temperature	0.642
Water temperature, turbidity, chaetognaths	0.634
Water temperature, chaetognaths	0.625
Water temperature, dissolved oxygen, turbidity, chaetognaths, bioluminescence	0.623
Water temperature, turbidity, chaetognaths, bioluminescence	0.623

Our results were consistent with the conclusions of previous investigators (e.g., Snelson, 1983; Gilmore, 1988; Brown-Peterson and Eames, 1990; Kupschus and Tremain, 2001), who suggested that increasing distance from ocean inlets (and the concurrent reduction in tidal forcing) contributes to a latitudinal decline in ichthyofaunal richness by curtailing the pelagic supply of marine-spawned larvae. Given the microtidal conditions which prevail throughout most of the northern IRL system, fish larvae must instead rely on a combination of meteorological forcing, passive diffusion (neither of which offer consistent uni-directional transport vectors), or active swimming to drive dispersal. As a consequence, species which enter estuaries at small sizes or have a limited pelagic life span appear unable to reach the large expanses of otherwise suitable settlement habitat available in the study area. This restrictive distribution of marine-spawned ichthyoplankton, while likely atypical among most other Florida estuaries (all of which maintain wider connections to the continental shelf), may be emblematic of isolated coastal lagoons and has been previously documented from Laguna Madre, Texas (Holt et al., 1990), western Mexico (Flores-Coto et al., 1983), Australia (Neira and Potter, 1992), and South Africa (Strydom et al., 2003). Not surprisingly, larvae of the few marine-spawning species present in microtidal reaches of the northern IRL (e.g., *Elops* spp., *Brevoortia* spp., *M. undulatus*, *L. rhomboides*) were typically postflexion individuals (10–40 mm SL, depending on species), competent swimmers who can best sustain active up-estuary migrations.

A second factor that may contribute to limited penetration of marine-spawned larvae into the northern IRL is the diversity of settlement habitats near coastal inlets. Most notably, all five IRL inlets are proximate to freshwater rivers or large drainage canals. Many estuarine-dependent fishes favor reduced salinity nurseries to exploit abundant food and/or reduced predation rates, and as such, arriving larvae may pref-

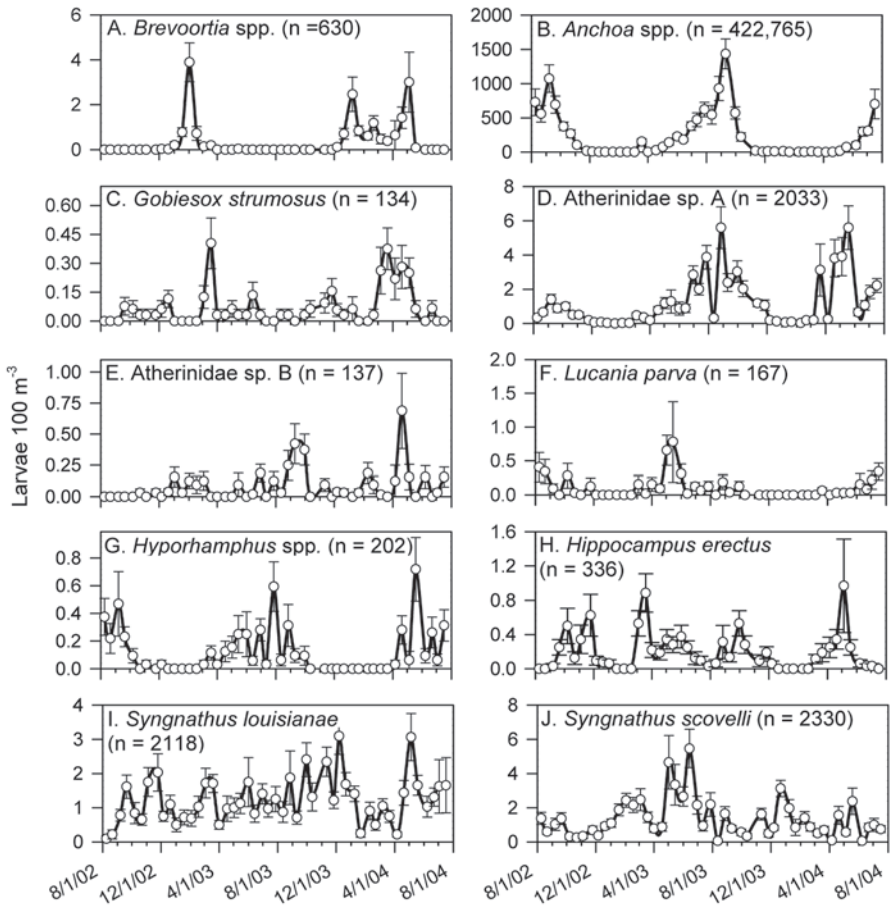
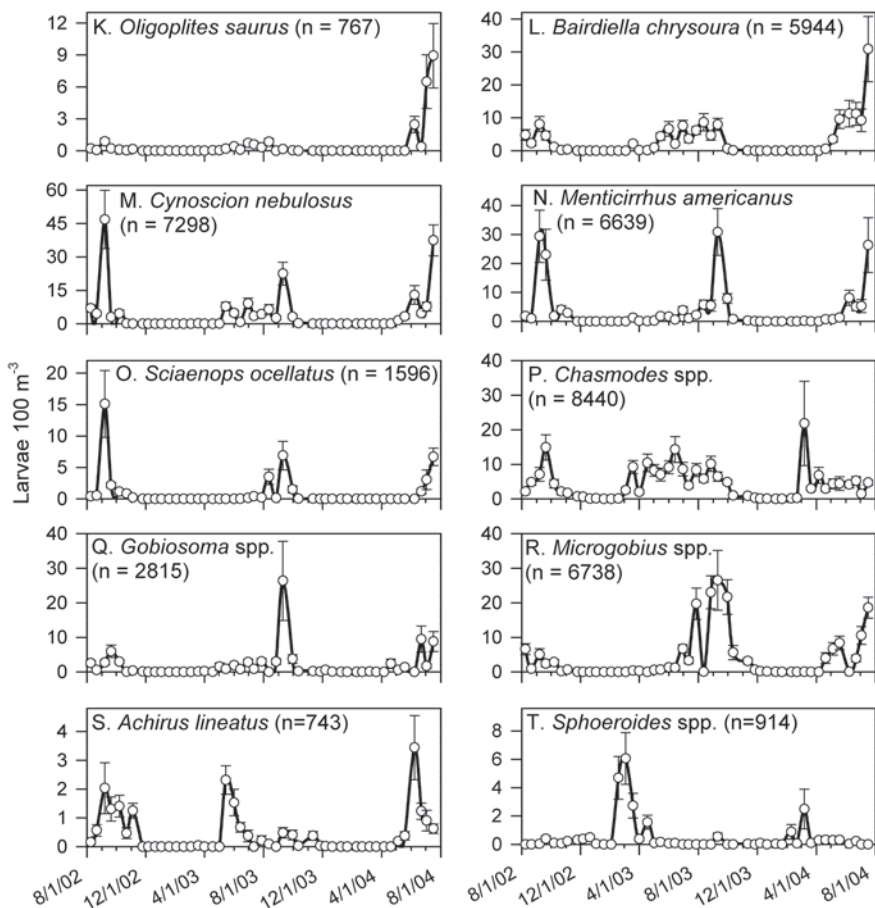


Figure 8. (*this and opposite page*) Regional density (mean \pm 1 SE) of common ichthyoplankton taxa of the northern Indian River Lagoon system, August 2002–July 2004. Note that y-axis scales differ among plots.

erentially settle near these freshwater outfalls. Surveys of both the Tomoka River (near Ponce Inlet) by Paperno et al. (2001) and St. Sebastian River (near Sebastian Inlet) by Paperno and Brodie (2004) demonstrate high juvenile densities of many marine-spawned fishes (e.g., clupeids, centropomids, gerreids, mugilids, certain sciaenids). Moreover, surveys of salt marshes and seagrass beds near IRL inlets also indicate heavy utilization by juveniles of many marine-spawning taxa (Gilmore, 1988; Wieher, 1995; Taylor et al., 1998; Poulakis et al., 2002). Combined, these habitats likely function as larval fish “filters”, retaining individuals which would otherwise reach alternate settlement substrates farther inside the estuary.

Despite low levels of pelagic recruitment of marine-spawned species to the region, many species are quite abundant as juveniles (Snelson, 1983; Tremain and Adams, 1995; Paperno et al., 2001) indicating that they do not adopt a “settle and stay” strategy but instead continue up-estuary migrations following transition to the juvenile form. Rooker et al. (1998b) documented this behavior for *Leiostomus xanthurus* Lacépède, 1802, and *M. undulatus* in Laguna Madre, Texas; larvae settled inside inlets at 10–14 mm SL but quickly shifted to alternate habitats. This strategy invariably



reduces competition for food and space near inlets and may be adopted by recruits of many marine-spawned taxa. In urbanizing estuaries like the IRL, such behavior may have management repercussions because while certain early stage fishes (e.g., clupeids and mugilids) are capable of quickly bypassing habitat of low suitability, others demonstrate specific habitat preferences following settlement to the benthos. One consequence of destruction and fragmentation of salt marshes (through impounding) or seagrasses (through eutrophication or dredging) is that important migratory pathways may be, or have already been, interrupted, curtailing up-estuary movement of post-settlement juveniles and thus reducing the nursery function and carrying capacity of more distant habitats.

The great distance between the northern IRL system and the Atlantic Ocean may also influence the reproductive behavior of adult fishes. Larvae of both *Menticirrhus* spp. [attributed to *Menticirrhus americanus* (Linnaeus, 1758) due to few local estuarine records of adult *Menticirrhus saxatilis* (Bloch and Schneider, 1801) or *Menticirrhus littoralis* (Holbrook, 1847)] and *S. ocellatus* were abundant and widely distributed throughout all three lagoon basins. Although there is some evidence that *S. ocellatus* will occasionally spawn within estuaries (Murphy and Taylor, 1990; Barrios, 2004), ichthyoplankton surveys along the U.S. east coast and Gulf of Mexico

suggest that both species preferentially spawn along the shelf or at tidal passes (to enhance dispersal and place eggs within preferred salinities) with larvae recruiting into estuaries during flood tides at > 3 mm (Springer and Woodburn, 1960; Darovec, 1983; Cowan and Birdsong, 1985; Holt et al., 1985, 1989; Smith and Wenner, 1985; Peters and McMichael, 1987; Setzler-Hamilton, 1987; Cowan and Shaw, 1988; Comyns et al., 1991; Rooker et al., 1998a). Sizes of *M. americanus* and *S. ocellatus* in this survey (mean NL = 2.5 and 2.3 mm, respectively) were smaller than that of *Cynoscion nebulosus* (Cuvier, 1830) and *Bairdiella chrysoura* (Lacépède, 1802), sympatric estuarine-spawning sciaenids. Given the considerable time (months) for marine water to filter into the study area from ocean inlets, the lack of astronomical tides to facilitate selective tidal stream transport, near-complete bottlenecks caused by earthen causeways, and the poor swimming ability of small sciaenids (Holt et al., 1989), it is difficult to envision that any of these preflexion sciaenids were passively transported or actively swam the necessary 30–90 km in such high numbers, especially when considering other marine-spawned taxa which enter estuaries at larger sizes were unable to do so. Instead, we believe these findings provide compelling evidence that a considerable proportion of IRL stocks of both *S. ocellatus* and *M. americanus* forego spawning migrations to instead reproduce within the estuary.

Our findings are not the first indication of local estuarine spawning for either species; Johnson and Funicelli (1991) hatched both species from eggs spawned within Mosquito Lagoon, a behavior they attributed to near marine salinity of the basin. Further, ripe adult *S. ocellatus* have been captured in the northern IRL (Murphy and Taylor, 1990) and spawning vocalizations have also been recorded locally (Gilmore et al., 2003). Our results are of interest primarily because they demonstrate that estuarine reproduction of *S. ocellatus* and *M. americanus* is a predictable yearly phenomenon over a wide geographic area, with preflexion larvae commonly found in salinity as low as 20. While the root cause(s) for this relatively novel strategy cannot be resolved with plankton collections alone, limited Atlantic Ocean access must impart considerable energetic costs to migrating adult fishes. Further, microtidal conditions and relatively weak salinity gradients (due to limited freshwater inputs in the region) may not provide adequate environmental cues necessary to easily direct inshore-offshore spawning migrations. Nonetheless, the high densities of small *S. ocellatus* and *M. americanus* larvae and concurrent presence of postflexion individuals indicate that these species have adapted to local conditions of the IRL and are not spawning unsuccessfully simply because they are trapped within an isolated lagoon.

The regional ichthyoplankton assemblage was dominated by estuarine residents (67% of species, $> 99\%$ of individuals) who spawn within the confines of the IRL. Community structure was spatially uniform throughout most of the study area but fluctuated dramatically over the year, as did the abundance of individual taxa. Assemblage shifts were strongly correlated with water temperature and weakly correlated with other measured physical or biotic variables. While often not the case in other estuarine settings, salinity, the only other measured habitat variable with the potential to preclude spawning of estuarine fishes over a wide geographic area, remained polyhaline and stable for the duration of the study in most sub-basins. Also of note, ctenophore density in the northern IRL, although quite high, peaked in winter and early spring. The low densities of pelagic fish eggs and larvae during these months, even in locations where ctenophores were scarce, suggests that few estua-

rine residents were actively spawning. Therefore, while these predators are renowned consumers of fish eggs and small larvae and are known to alter community composition in other areas, there is little evidence that they strongly influence northern IRL species diversity or the spawning success of most individual taxa except possibly for a brief period during late spring and early summer.

Despite such pronounced temporal fluctuations in ichthyoplankton abundance and composition, changes in the assemblage displayed a striking cyclicity, returning to a similar state each summer, and the rank abundance of numerically dominant taxa was similar from the first year to the second. This suggests that the northern IRL ichthyoplankton community is reasonably stable over annual cycles, with fish larvae appearing in samples in a predictable order and rank abundances, a pattern known to characterize other U.S. estuaries (Allen and Barker, 1990; Whitting et al., 1999). In fact, this assemblage may prove to be even more stable than most estuaries because marine-spawned larvae, whose recruitment success also depends on often variable conditions along the continental shelf, were so uncommon.

The northern Indian River Lagoon system is a rapidly urbanizing estuary whose constituent counties (Indian River, Brevard, and Volusia) are faced with human population growth in excess of 40% by 2030 (Florida Population Studies, 2004). Future anthropogenic alterations to the estuary may fundamentally alter the ichthyoplankton assemblage from its current state. Most notably, increases in freshwater inflow (which often characterizes urbanizing estuaries) may lead to persistent salinity reductions given the limited flushing of the region and preclude spawning of certain fishes, including important sciaenid sportfishes, over wide areas, as demonstrated by little evidence for spawning in mesohaline Banana Creek. Further, changes in ocean-estuary circulation rates, or even intra-estuarine circulation patterns, will also inevitably influence the recruitment success of marine-spawned fishes as well as spawning behavior and locations of estuarine residents. Actions which stand to alter hydrology and water quality in the IRL must account for the effects on fish early life history stages if the health of regional fisheries is to be maintained.

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