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Larval assemblages of large and medium-sized pelagic species in the Straits of Florida

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ABSTRACT

Critical gaps in our understanding of the distributions, interactions, life histories and preferred habitats of large and medium-size pelagic fishes severely constrain the implementation of ecosystem-based, spatially structured fisheries management approaches. In particular, spawning distributions and the environmental characteristics associated with the early life stages are poorly documented. In this study, we consider the diversity, assemblages, and associated habitat of the larvae of large and medium-sized pelagic species collected during 2 years of monthly surveys across the Straits of Florida. In total, 36 taxa and 14,295 individuals were collected, with the highest diversity occurring during the summer and in the western, frontal region of the Florida Current. Only a few species (e.g. *Thunnus obesus, T. alalunga, Tetrapturus pfluegeri*) considered for this study were absent. Small scombrids (e.g. *T. atlanticus, Katsuwonus pelamis, Auxis* spp.) and gempylids dominated the catch and were orders of magnitude more abundant than many of the rare species (e.g. *Thunnus thynnus, Kajikia albida*). Both constrained (CCA) and unconstrained (NMDS) multivariate analyses revealed a number of species groupings including: (1) a summer Florida edge assemblage (e.g. *Auxis* spp., *Euthynnus alleterattus*, *Istiophorus platypterus*); (2) a summer offshore assemblage (e.g. *Makaira nigricans, T. atlanticus, Ruvettus pretiosus, Lampris guttatus*); (3) an ubiquitous assemblage (e.g. *K. pelamis, Coryphaena hippurus, Xiphias gladius*); and (4) a spring/winter assemblage that was widely dispersed in space (e.g. trachipterids). The primary environmental factors associated with these assemblages were sea-surface temperature (highest in summer-early fall), day length (highest in early summer), thermocline depth (shallowest on the Florida side) and fluorescence (highest on the Florida side). Overall, the results of this study provide insights into how a remarkable diversity of pelagic species spatially and temporally partition spawning within a region that is characterized by dynamic oceanography and strong habitat gradients.

1. Introduction

Large (>50 kg) and medium (1–50 kg) sized pelagic teleosts support many important fisheries around the world. During the past 60 years, the overcapitalization of fishing fleets and technological changes in fishing methods (reviewed in Sharp, 2001) have led to the depletion of this group as a whole and the reduction of many individual species to <10% of their pre-exploitation biomass (Sissenwine et al., 1998; Myers and Worm, 2003; Ward and Myers, 2005). In response to these system-wide population declines, and due to the recognition that the effects of overfishing extend beyond the targeted species, there have been a number of recent calls for ecosystem-based management approaches within pelagic fisheries (Botsford et al., 1997; Pauly et al., 2002; Pikitch et al., 2004). However for such management approaches to be effective, critical gaps must be filled in our understanding of the distributions, interactions, life histories, and preferred habitats of these species.

The study of the habitat associations and distributions of migratory pelagic fishes has traditionally focused on the distribution of forage species, regional hydrographic properties, and species-specific physiological capabilities (Sharp, 1978, 2001; Brill, 1994). Elevated concentrations of forage often exist at frontal zones and have been shown to support a higher abundance, and on a global scale, a higher diversity of apex pelagic predators (Worm et al., 2005). Similarly, locations where a vertical concentration of organisms exists also tend to support higher densities of pelagic species, both in the open ocean (Betrand et al., 2002) and where the depth range of vertically migrating mesopelagic species is compacted by bathymetry (Weaver and Sedberry, 2001). Within any one location, the accessibility of forage to a pelagic species is controlled by a combination of species-specific physiology and the temperature, dissolved oxygen, and light levels both in the surface layer and vertically in the water column (Brill, 1994; Betrand et al., 2002). This interaction of forage distribution, physiology and water column properties is considered to be primarily responsible for the

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prominent ocean-basin scale distributional differences among tuna species (Fonteneau, 1997; Worm et al., 2005).

With some exceptions, the influence of reproduction on the distribution of pelagic species has received less attention than the influence of feeding. Spawning habitat quality in all species is determined by how favorable a location is to the survival of larvae and how spawning in that area fits into the energy budget of the adult. For species such as the bluefin tuna (*T. thynnus*), where long-distance migrations are made to spawning grounds and residency times on the spawning ground are short (Block et al., 2005; Teo et al., 2007), specific oceanographic features appear to be chosen that are favorable to the survival of the larvae (Bakun, 1996). At the other extreme are species such as skipjack tuna that appear to spawn whenever and wherever sea-surface temperature (SST) exceeds a minimum level (Schaefer, 2001; Lehodey et al., 2003). As fish movement models advance and fish tagging data becomes more sophisticated, gaps in the understanding of spawning habitat characteristics have become more apparent and critical to fill.

In addition to influencing individuals' movement patterns, the oceanographic conditions within the primary spawning area of a species or population can strongly impact the recruitment dynamics of that species or population. These effects occur over a range of temporal scales, but are most dramatically illustrated by the synchronous multi-species fluctuations in recruitment over decadal time scales. For example, Pacific population cycles of skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) tend to fluctuate synchronously and in opposition to albacore tuna (*T. alalunga*). It is thought that multi-year climatic changes that positively affect the survival of early life stages in the shared skipjack and yellowfin tuna spawning habitat negatively affect survival in the albacore tuna spawning habitat (Bakun and Broad, 2003; Lehodey et al., 2003). Similar environmental controls on recruitment are most likely ubiquitous in pelagic fish populations (Sharp, 2001).

The collection and identification of the early life stages of fishes is one of the most tractable ways to obtain information on spawning patterns and recruitment dynamics. Such collections have been used to identify spawning areas for a range of large pelagic species including: bluefin tuna, swordfish (*Xiphias gladius*), blue marlin and white marlin (*Kajikia albida*; Richards, 1976; Govoni et al., 2003; Serafy et al., 2003; Prince et al., 2005), and on a more limited basis, have been used to identify oceanographic features associated with higher larval abundances (McGowan and Richards, 1989). To date, most studies have focused on either a single species or have made comparisons within a single family. This contrasts notably with the multi-species research on adult pelagic species (Block et al., 2003) and the long standing tendency in early life-history research to consider larval assemblages, or groups of co-occurring species (e.g. Cowen et al., 1993; Grothues and Cowen, 1999; Hare et al., 2001). Work on larval assemblages specifically has been useful in determining commonalities in the distribution of early life stages that reflect similarities in spawning strategies and in the processes that drive successful recruitment.

Here, we consider the diversity, assemblages, and associated habitat of the larvae of large and medium-size pelagic fishes collected during 2 years of monthly surveys in the Straits of Florida. This subtropical location encompasses the narrow (70–150 km) region between Florida and Cuba to the south, and the various banks of the Bahamas to the southeast and east. Within the Straits of Florida, the Florida Current dominates with maximum current speeds *ca.* 2 m s^{-1}, and eddies and strong frontal boundaries are common features (Leaman et al., 1987; Lee et al., 1994). The dynamic oceanography in the area and the strong spatial or seasonal gradients in key habitat features make it a particularly suitable region to explore the influence of the environment on the spawning and early life-history strategies of pelagic fish.

2. Materials and methods

2.1. Sampling protocol

During 2003 and 2004, surveys were performed using the R/V F.G. Walton Smith near the beginning of each month along a 17-station, 80-km long transect crossing the Straits of Florida at 25°30′N (Fig. 1). Stations were more tightly spaced along both edges of the transect than in the center (Fig. 1b). Biological sampling occurred during the day using a combined Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) equipped to simultaneously sample a 4-m^2 1000-μm mesh net and a 1-m^2 150-μm mesh net (Guigand et al., 2005) and a combined neuston net (1 × 2 m 1000-μm mesh net attached to a 0.5 × 1 m 150-μm mesh net); however for this study, only samples from the 1000-μm mesh nets were fully processed. The MOCNESS system contained temperature, salinity, fluorometry and light sensors, and measured the volume of water sampled by each net. Individual nets were triggered in 25-m depth intervals, and the entire system was deployed to 100 m at all but the first station where shallow bathymetry limited the tows to 50-m depth (Fig. 1b). The neuston net was towed with half of the frame out of the water, and the volume of water filtered was measured with a General Oceanics flowmeter.

At each station physical measurements were made through the entire depth of the water column using a CTD equipped with Seabird sensors measuring temperature, salinity, fluorescence, oxygen, beam transmission, and light levels. Surface temperature, salinity and fluorescence were measured continuously at <60 s intervals during the entire duration of each cruise via a flow-through system. Continuous measurements of the currents were also made using both a 600 kHz (2-m depth-bins from 4–40 m) and a 150 kHz (8-m depth-bins from 14–200 m) RDI Acoustic Doppler Current Profiler (ADCP).

Generally the entire transect was sampled within a 48-h period. The most common pattern of sampling involved net sampling along the western half of the transect during the first day, followed by CTD casts along the second half of the transect during the night. For the second day of sampling the boat proceeded in the opposite

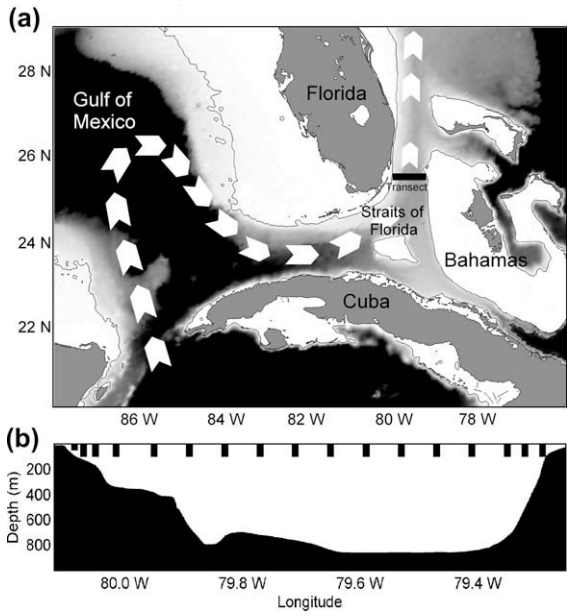

Fig. 1. Straits of Florida and adjacent regions. (a) The sampling transect and primary flow pattern are indicated. The 100 m isobath is marked by the contour lines, with the shallow banks and continental shelf in white. (b) The bathymetry across the Straits of Florida at the latitude of sampling (25.5°N). The locations of the 17 sampling stations are denoted with tick marks.

direction, sampling the second and first portions of the transect with the MOCNESS and CTD, respectively. This sampling strategy was extremely time efficient, but as with any ship-based sampling did not present a synoptic picture. Notably, near the center of the transect adjacent stations were sampled 24 h apart, and depending on the station, CTD casts and net tows were separated by 1–48 h. Because of the latter issue, if possible, physical data from the MOCNESS or the underway systems, rather than the CTD, were used when analyzing larval distributions.

For 21 of the 24 monthly cruises, biological sampling was successfully performed at $\geqslant$16 of the 17-stations. The exceptions were the December 2003 cruise (10 stations sampled), the January 2004 cruise (10 stations sampled), and the November 2004 cruise (seven stations sampled). Suspension of sampling during each of these three cruises was weather related. For 12 additional stations a single depth-bin of the large-mesh nets was not successfully collected, and the station was omitted from the analyses. In total, all depth-bins at 371 stations were successfully and completely sampled for this study.

2.2. Sample processing and larval identification

The targeted species for this study were oceanic pelagic species that exceed 1 kg in maximum adult weight. Additionally, all of the smaller species in the families Gempylidae and Scombridae were also included in the study. This more inclusive approach was taken because of within family morphological and trophic similarities of larvae, and the potential insights into the factors underlying patterns of spawning that can result from a comparison of phylogenetically related species that differ ecologically. Overall, 41 species were considered for the study, including 36 collected species (Table 1), and five additional species (*Thunnus alalunga*, *T. obesus*, *Tetrapturus pfluegeri*, *T. georgii*, *Masturus lanceolatus*) that were not collected.

Larval fish were first removed from all of the samples. All individuals were then identified morphologically following Richards (2006a). Identifications were generally to the family level, though if possible, the oceanic pelagic taxa were identified to species. Taxa considered in this study that could not be identified morphologically to species-level were identified molecularly following Richardson et al. (2007). This sequence-based identification methodology is based in concept on the barcode of life project (Hebert et al., 2003). More specifically, a high degree of automation is achieved in its use through a magnetic bead-based DNA extraction procedure and a MATLAB character-based bioinformatics script. Both the cytochrome-*b* primers described in Richardson et al. (2007) and the cytochrome oxidase subunit 1 primers listed in Ward et al. (2005) were used.

Table 1
Larval abundances of medium and large pelagic species in the Straits of Florida. Code corresponds to the identifier used in figures. Maximum weights are based on either the record size fish caught in the Atlantic recreational fishery (www.igfa.org) or Fishbase (Froese and Pauly, 2000). Abundance values indicated with a # are considered underestimates because of the likely occurrence of some individuals below the deepest sampled depth. Species included in the indirect gradient analysis are noted with a *. The method used to identify each taxon is also indicated (Morp = Morphological, Molec = Molecular, Sub = Subsampled). Relatively higher *n* values than abundance values occur for species frequently collected in the surface net tows.

Species	Common name	Family	Code	Max. weight (kg)	Abundance (individuals 100 m^{-2})	Positive stations	*n*	Identification method		
								Morph	Molec	Sub
Katsuwonus pelamis*	Skipjack tuna	Scombridae	Kpel	19	12.16	298	2130	2128	2	–
Thunnus atlanticus	Blackfin tuna	Scombridae	Tatl	20	11.05	213	3383	–	1037	2346
Nesiarchus nasutus	Black gemfish	Gempylidae	Nnas	3	9.25	202	1515	1515	–	–
Diplospinus multistriatus*	Striped escolar	Gempylidae	Dmul	1	#6.96	199	1002	1002	–	–
Euthynnus alletteratus*	Little tunny	Scombridae	Eall	12	5.17	69	1705	1705	–	–
Gempylus serpens*	Snake mackerel	Gempylidae	Gser	3	3.02	208	651	651	–	–
Bramidae*	Pomfrets	Bramidae	Bram		2.66	199	436	436	–	–
Auxis thazard*	Frigate tuna	Scombridae	Atha	1	2.19	97	549	456	63	30
Auxis rochei*	Bullet tuna	Scombridae	Aroc	1	1.81	79	586	176	196	214
Coryphaena hippurus*	Dolphinfish	Coryphaenidae	Chip	40	1.28	193	477	400	77	–
Coryphaena equiselis*	Pompano dolphinfish	Coryphaenidae	Cequ	5	0.67	129	204	166	38	–
Thunnus albacares*	Yellowfin tuna	Scombridae	Talb	176	0.67	46	181	–	84	97
Trichiuridae*	Cutlassfish	Trichiuridae	Tric		#0.60	52	97	97	–	
Neoepinnula americana*	American sackfish	Gempylidae	Name	1	0.46	47	83	83	–	–
Ruvettus pretiosus*	Oilfish	Gempylidae	Rpre	45	0.45	32	79	79	–	–
Makaira nigricans*	Blue marlin	Istiophoridae	Mnig	636	0.44	85	249	59	190	–
Istiophorus platypterus*	Sailfish	Istiophoridae	Ipla	61	0.44	92	310	240	70	–
Acanthocybium solandri*	Wahoo	Scombridae	Asol	67	0.28	36	56	56	–	–
Scomber colias*	Atlantic chub mackerel	Scombridae	Scol	1	0.28	14	99	99	–	–
Lophotidae/Re galecidae*	Unicornfish/Oarfish	Order: Lampridiformes	Lamp		0.27	35	48	48	–	–
Xiphias gladius**	Swordfish	Xiphiidae	Xgla	650	0.26	117	198	198	–	–
Scomberomorus cavalla*	King Mackerel	Scombridae	Scav	42	0.24	35	69	68	1	–
Lampris guttata*	Opah	Lampididae	Lgut	270	0.18	24	29	29	–	–
Nealotus tripes*	Black Snake Mackerel	Gempylidae	Ntri	1	0.17	24	32	32	–	–
Trachipteridae*	Ribbonfish	Trachipteridae	Trac		0.17	29	35	35	–	–
Prometichthys prometheus*	Roudi escolar	Gempylidae	Ppro	1	0.16	21	29	29	–	–
Lepidocybium flavobrunneum	Escolar	Gempylidae	Lfla	45	0.12	11	15	15	–	–
Alep isauridae	Lancetfish	Alepisauridae	Alep	5	#0.051	6	7	7	–	–
Ranzania laevis	Slender mola	Molidae	Rlae	20	0.05	8	9	9	–	–
Scomberomorus regalis	Cero	Scombridae	Sreg	8	0.04	7	8	8	–	–
Mola mola	Ocean sunfish	Molidae	Mmol	2000	0.02	2	2	2	–	–
Epinnula magistralis	Sackfish	Gempylidae	Emag	1	0.02	2	5	5	–	–
Thunnus thynnus	Bluefin tuna	Scombridae	Tthy	678	0.01	1	3	3	3	–
Luvarus imperialis	Louvar	Luvaridae	Limp	150	0.01	3	4	4	–	–
Kajikia albida	White marlin	Istiophoridae	Kalb	82	0.01	7	9	9	9	–
Scomberomorus maculatus	Spanish mackerel	Scombridae	Smac	5	0.00	1	1	1		–
			Total		61.63		14,295	9838	1770	2687

The extent to which molecular identification was employed varied by taxon. Molecular identification was used for all istiophorids not identifiable using lower jaw pigment patterns or snout length measurements (Luthy et al., 2005a), and coryphaenids not identifiable using characters in Ditty (2006). For the *Auxis* larvae, individuals <5 mm SL that lacked midlateral pigment in the caudal region required molecular identification. *Thunnus* larvae were only identified molecularly due to previous work suggesting that external morphological characteristics are not diagnostic (Richards et al., 1990). No attempts were made to molecularly identify a number of less common or less economically valuable families to species. These included trachipterids, trichiurids, bramids, alepisaurids, and a fifth grouping composed of lophotids and regalicids.

Due to the high abundance of *Thunnus* and *Auxis* larvae, a subsampling approach was instituted for molecular identification. Prior to this subsampling, all *Thunnus* larvae collected during the bluefin tuna (*T. thynnus*) spawning season (March–July) were screened for typical bluefin tuna pigment patterns (Richards et al., 1990), and all individuals with this pigment pattern were molecularly identified. The subsampling protocol for each station involved molecularly identifying five larvae plus an additional 10% of the remaining larvae. *Thunnus* and *Auxis* larvae not molecularly identified were assigned a species randomly based on the observed ratio of molecularly identified individuals at that station. In implementing this subsampling approach with *Thunnus,* all of the larvae from 50% of the stations were molecularly identified, and 50% of the larvae not identified molecularly came from 18 stations.

2.3. Abundance calculations

Abundances (individuals 100 m^{-2}) of each taxon were calculated for each station. Abundance calculations assume that the entire depth range of each taxon was sampled. For most taxa, this assumption appears to be valid. However, >20% of the individuals of three taxa, Alepisauridae (5 of 6 individuals), Trichiuridae (36 of 56), and *Diplospinus multistriatus* (158 of 311), occurred in the deepest depth-bin (75–100 m) that was sampled. The reported abundances of these taxa are considered to be underestimates though they were retained in the subsequent analyses nonetheless. The overall average abundance values reported for each species were based on a weighted mean in order to account for the influence of station spacing and cruise completeness. Within each cruise, each station was weighted based on the spacing between it and adjacent stations. Subsequently, each cruise was given the same weight to obtain an average abundance value.

2.4. Environmental data processing

The environmental parameters used in the analyses were: (1) sea-surface temperature (SST), (2) 100 m integrated fluorescence (a proxy for chlorophyll concentration), (3) depth of 20 °C isotherm, (4) depth of 3 mL L^{-1} oxygen isopleths, (5) day length, (6) sea surface density gradient (Δ sigma-t), and (7) horizontal current shear. At each station, SST was measured with the MOCNESS using values in the 3-m bin to ensure the sensor had equilibrated and to avoid the warmer surface skin that occurs during the day in low wind conditions. Integrated fluorescence values were also calculated from the MOCNESS. For the first five cruises, the MOCNESS did not contain a fluorometer, and thus CTD fluorescence measurements were used; however these measurements were not collected concurrently with the plankton tows. Analyses of the larval fish distribution data, both with and without these non-synoptic values, determined that this had little effect on the results. All fluorescence values were standardized to the CTD units of measurements using calibrations derived from stations where the CTD and MOCNESS were deployed sequentially.

Both the 20 °C isotherm and 3 mL L^{-1} oxygen isopleths were derived from CTD measurements. At the westernmost shallow (~70 m) station, the 3 mL L^{-1} oxygen level was frequently not reached and thus the bottom depth was used in analyses. Day length was determined using the time of sunrise and sunset provided by the US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.html). Sea surface density gradients were determined from the underway measurements using the Webster method of detecting discontinuities (Legendre and Legendre, 1998). Measurements were first averaged within 0.001° longitude (~100 m) bins. The gradient value was then calculated as the difference between the average value in 2-km windows on either side of the point.

Horizontal current shear was calculated using the 6-m depth-bin from the 600 kHz ADCP. One-minute average files were created using the WINADCP software. Subsequent processing removed data with Percent Good-4 (percentage of measurements with four beam solutions) values below 80%, or with boat speeds <2 m s^{-1}. Data collected when boat speeds were slow and the ship was on station tended to have higher errors, possibly due to the erratic cruise track during these times. Data were then averaged in 0.01° longitude (1 km) intervals, and smoothed using a 0.04° longitude moving average. Horizontal current shear was calculated as the difference in current speed in locations on 2 km of either side of the station.

2.5. Larval assemblage analysis

Species distributions and environmental data were evaluated using both indirect and direct gradient analysis. These approaches are complementary, as the unconstrained indirect ordination allows all the variability in species composition to be evaluated, including that not explained by environmental factors. On the other hand, the constrained direct gradient analysis restricts the ordination to axes that are a linear combination of the predetermined set of environmental variables, and thus only identifies variability associated with them. Concordance between the two approaches is indicative of strong support of species groupings and their relationship to measured environmental variables (Leps and Smilauer, 2003).

The indirect gradient analysis followed the methods outlined in Field et al. (1982) and the application of these methods to larval fish in Hare et al. (2001). Taxa were included in this analysis if $\geqslant$20 individuals were collected at $\geqslant$10 stations. Stations were excluded from analysis if all of the depth-bins were not completely sampled. This resulted in the inclusion of 26 species at 371 stations (Table 1). The analysis of larval fish assemblages used relativized larval fish abundances, a Bray-Curtis dissimilarity matrix, and hierarchical clustering using the weighted pair group method (WPGMA). Species were also ordinated using non-metric multidimensional scaling of this matrix with a designated two-dimensional solution.

For the direct gradient analysis, a Canonical Correspondence Analysis (CCA) was performed using the CANOCO software package (version 4.5, Microcomputer Power, Ithaca, NY) following the methods outlined in Grothues and Cowen (1999). All seven environmental variables were used in this analysis and all taxa were included, though rare species were downweighted. Larval abundances (individuals 100 m^{-2}) were ln (x + 1) transformed. Biplot scaling with a focus on interspecies distances was used. Environmental variables were kept in the model if their sequential addition was significant at $p < 0.01$ and we ran 4999 Monte Carlo simulations.

2.6. Diversity calculations

Measures of species-density were calculated using sample-based rarefaction curves (species accumulation curves). This

analytical technique provides a means to standardize species counts to a given level of sampling-effort (for comparisons between areas or times) and to evaluate the extent to which additional sampling would be expected to yield additional species. Rarefaction curves were computed using Estimate-S software (Colwell, 2006) which implements the algorithms of Colwell et al. (2004) rather than subsampling methodologies. For each calculation, stations were used as the unit of sampling-effort. A rarefaction curve was first calculated for the entire sampling-effort in the Straits of Florida. Subsequently, seasonal patterns of species-density were evaluated, with stations from both years for each month pooled. We report results for the number of species per 20 stations. Alternative standardizations of 5, 10, and 15 stations were qualitatively similar and are not reported here.

Cross-Straits patterns of diversity were also evaluated using rarefaction, with the number of species standardized to 20 stations reported. Alternative standardizations to 5, 10, and 15 stations (not reported here) were not qualitatively similar to the 20 station standardization. Because of this, an additional analysis was used to consider the persistence of spatial patterns of diversity over time. For this analysis, taxon counts at each station were transformed into *z*-scores (Legendre and Legendre, 1998) by subtracting the mean count for each cruise from count at each station and dividing by the cruise standard deviation. These *z*-scores were then averaged at each station across cruises. Excluded from the spatial diversity comparisons were the three cruises with <16 stations sampled, all the stations at which a single depth-bin was not successfully sampled, and the westernmost station at which a lesser volume of water was sampled due to the shallow depth of the tows.

3. Results

3.1. Environmental data

Peak SST ranged from 28–30 °C and extended from early June through early November. Low SSTs of 25–26 °C occurred from January to April, and coincided with increased spatial differences in SST (Fig. 2). Day length varied by approximately 3.5 h over the year with maximum day length preceding peak SST by about 2 months (Fig 3: bottom panel). The depth of the 20 °C isotherm and the 3 mL L^{-1} oxygen isopleths were consistently shallower on the Florida side of the transect. For the 20 °C isotherm this depth difference averaged 150 m, whereas for the 3 mL L^{-1} oxygen isopleth this difference was approximately 350 m (Fig. 2). Increased stratification on the western side of the transect during the summer months resulted in a shallower thermocline than during the winter months. Fluorescence measurements were most often higher on the Florida side of the transect, though patches of higher fluorescence also occurred offshore during many of the sampling periods (Fig. 2).

Steep gradients in sea surface density and northward current shear tended to occur most frequently on the western side of the transect (Fig. 2). This was most notable for the current shear,

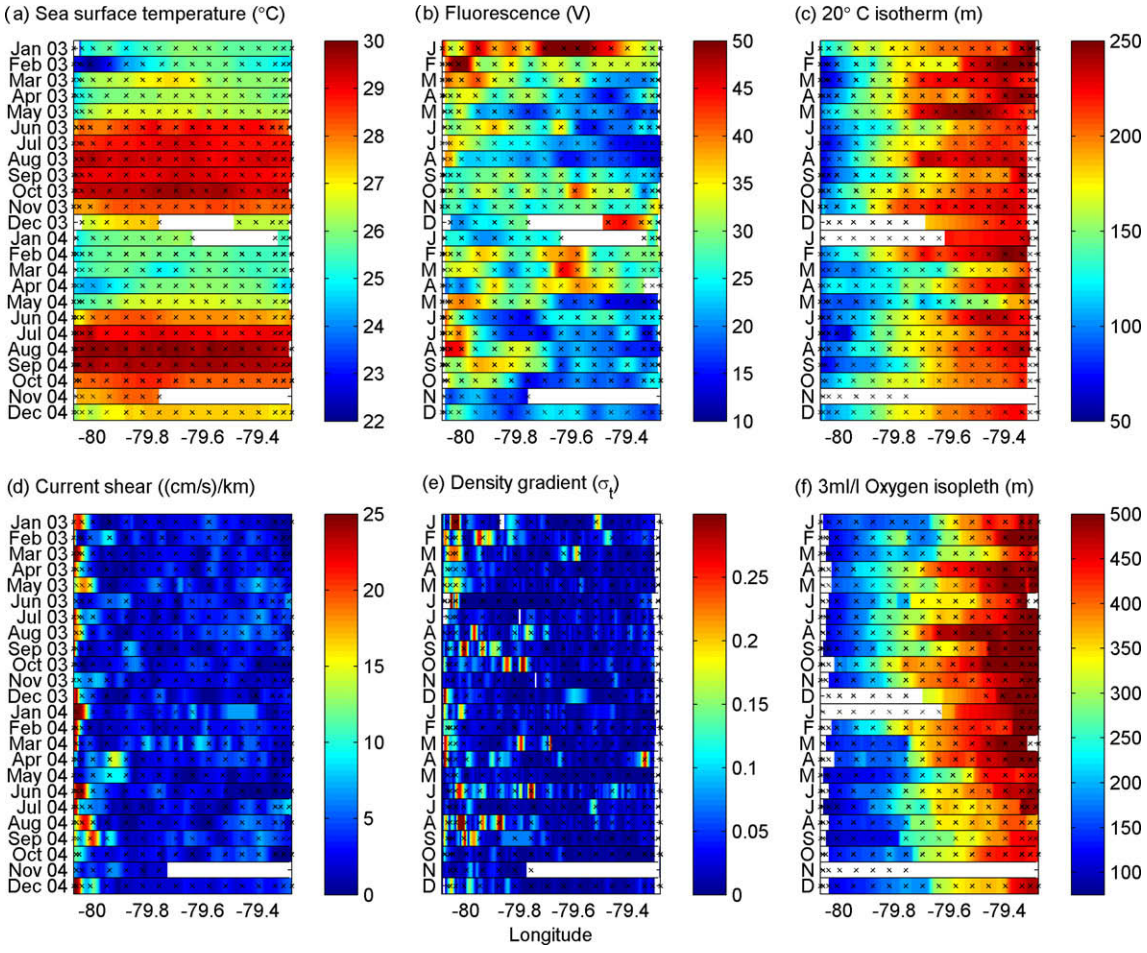

Fig. 2. Spatial and temporal patterns of environmental variables used in the Canonical Correspondence Analysis. Longitude of sampling is indicated on the *x*-axis, month of sampling along the *y*-axis. Stations sampled with the MOCNESS are indicated with an *X*. Gaps in the data indicate stations that were not sampled with either the MOCNESS or CTD. Fluorescence is the 100 m integrated measurements (V) from the CTD.

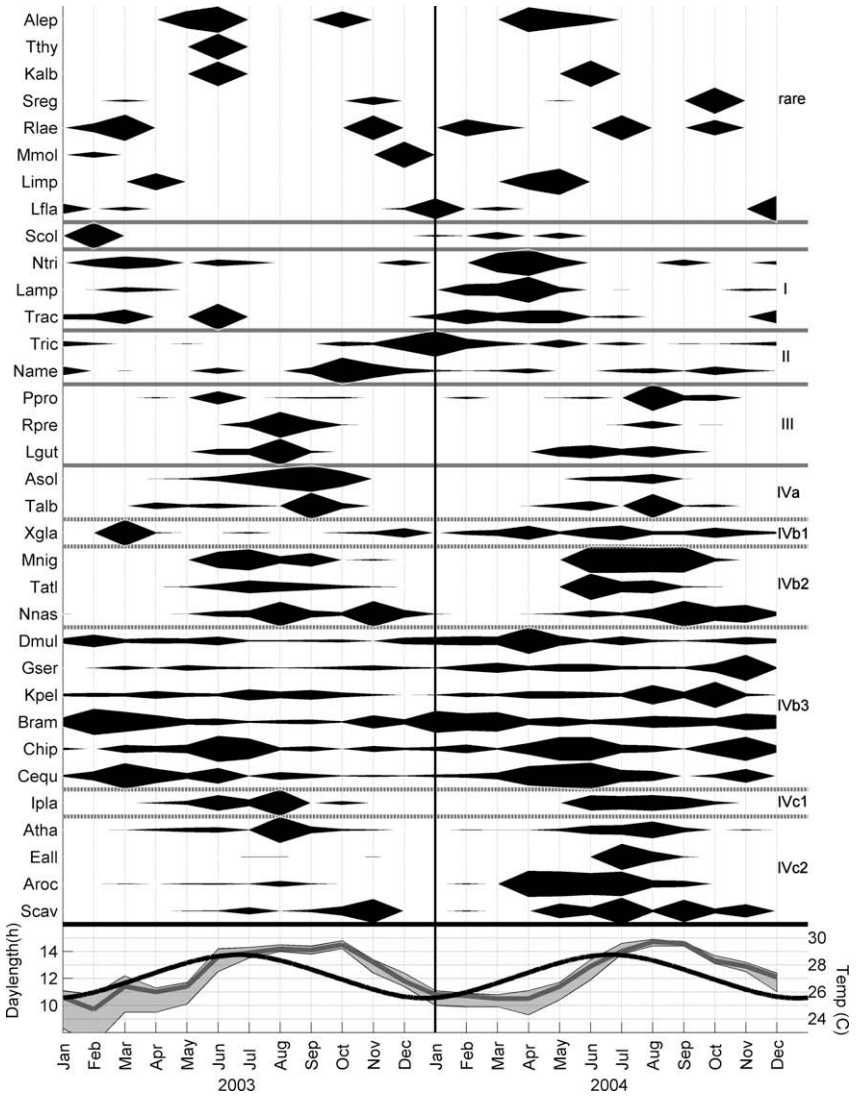

Fig. 3. Temporal patterns of larval occurrence of pelagic species during the 2 years of monthly sampling in the SF. Width of band is scaled to the maximum abundance (individuals 100 m^{-2}) of that species collected on any one cruise. Day length and SST mean and range for each cruise are plotted at the bottom of the figure. Species codes used in the labeling are in Table 1. Species are grouped and labeled based on the results of the cluster analysis.

which, except in the case of an offshore shift of the current axis, was always very high on the Florida side of the transect and low elsewhere. Density fronts often coincided with gradients of sea-surface temperature, or both sea-surface temperature and salinity. Additionally during some cruises in August–October, shallow bands of lower salinity (34.8–35.8) water occurred over the western half of the transect resulting in salinity-driven surface density fronts on both sides of the low salinity band.

3.2. Taxonomic composition

A total of 14 295 individuals representing at least 36 species of large or medium-size pelagic fishes were collected over the 2 years of sampling (Table 1). These individuals made up 8% of the 166 903 larval fishes of all taxa collected in the 1000-μm mesh neuston and MOCNESS nets. Five of the smaller scombrid species (*Thunnus atlanticus*, *Katsuwonus pelamis, Euthynnus alleteratus, Auxis thazard* and *A. rochei*), three of the smaller gempylid species (*Nesiarchus nasutus*, *Diplospinus multistriatus*, and *Gempylus serpens*) and unidentified bramids dominated the catch. Abundances of the larvae of large pelagic species, such as yellowfin tuna (*T. albacares*), bluefin tuna (*T. thynnus*), blue marlin (*Makaira nigricans*), sailfish (*Istiophorus platypterus*) and swordfish (*X. gladius*), were at least an order of magnitude lower than abundances of these smaller species. In aggregate, larvae of large pelagic species accounted for only 4.3% of the total abundance of pelagic species considered for this study. Absent from the samples were five species: albacore tuna (*T. alalunga*), bigeye tuna (*T. obesus*), longbill spearfish (*Tetrapturus pfluegeri*), roundscale spearfish (*Tetrapturus georgii*) and sharptail mola (*Masturus lanceolatus*), that would have been readily identified either molecularly or morphologically.

3.3. Larval assemblages

Distinct differences among species occurred in both the seasonality of larval occurrence (Fig. 3), and the spatial patterns of larval occurrence across the transect (Fig. 4). The cluster analysis and ordination identified four primary assemblages (I–IV) with the largest of these assemblages (IV) further dividing into a number of additional groupings (Fig. 5a). Species clustered based on the seasonality of larval occurrence (Fig. 3) and the relative abundance of larvae at stations nearest to the Florida coast versus offshore sta-

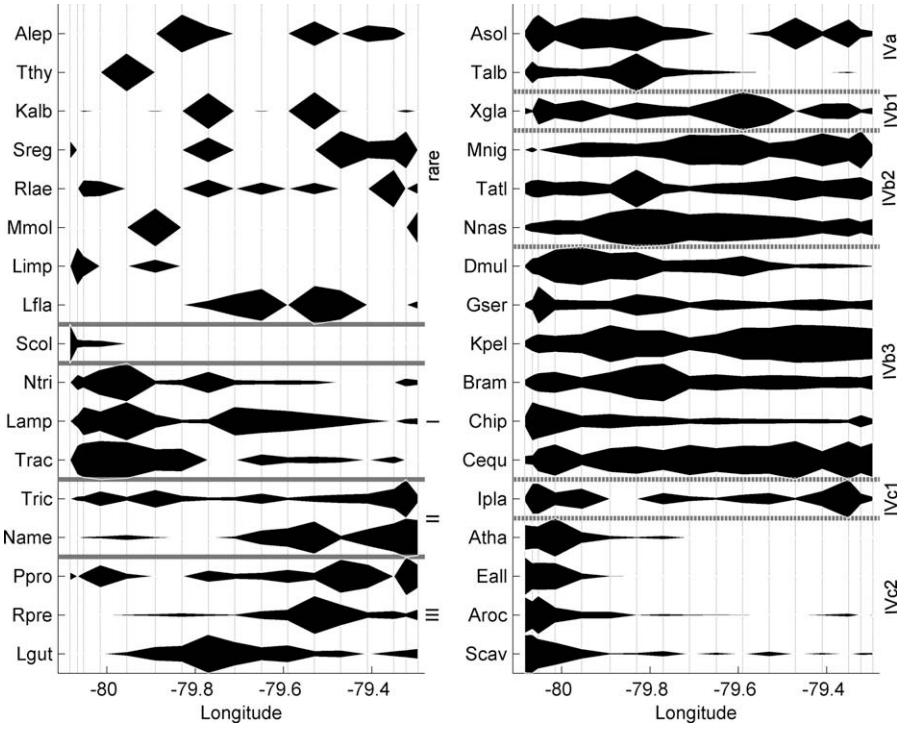

Fig. 4. Cross-Straits patterns of larval occurrence of pelagic species during the 2 years of monthly sampling in the Straits of Florida. Width of band is scaled to the maximum abundance (individuals 100 m^{-2}) of that species at a station averaged across cruises. Species codes used in the labeling are in Table 1. Species are grouped and labeled based on the results of the cluster analysis.

tions (Fig. 4). A single species, *Scomber colias*, was a distinct outlier from the remainder of the species (Fig. 5), as its larvae were caught only in the winter in nearshore waters. The first assemblage (I) encapsulated three taxa, *Neolatus tripes*, Regalicidae/Lophotidae and Trachipteridae that primarily spawn during winter and spring. The larvae of these taxa were primarily caught along the western half of the transect. Assemblage II contained only two taxa, Trichiuridae and *Neopinnula americana*, both of which had their highest abundance along the eastern half of the transect, and tended to occur year round with a fall to winter peak in abundance. The ordination supported these two species as distinct from most other species, but did not strongly support their grouping (Fig. 5b). Assemblage III, consisting of *Lampris guttatus*, *Ruvetus pretiosus* and *Promtichthys promethius* encompassed species collected in the summer at offshore locations.

The remaining 17 species grouped into assemblage IV and could be further subdivided. Within this assemblage, *Istiophorus platypterus* clustered (IVc1) distantly with the strongly supported grouping of *Auxis thazard*, *Euthynnus alluteratus*, *A. rochei* and *Scomberomorus cavalla* (IVc2). These species were all summer spawners. Larvae of the latter four were almost exclusively found on the Florida side of the transect, while larval *I. platypterus* abundance was highest on both edges of the transect. *Acanthocybium solandri* and *T. albacares* clustered together, and in the ordination diagram were close to the previous group (IVa). These species were also summer spawners with a majority of individuals collected on the western half of the transect, though not exclusively in the nearshore station as were members of the previous group.

The final grouping (IVb) within assemblage IV encompassed much more spatio-temporally ubiquitous species. *Diplospinous multistriaus*, Bramidae, *Gempylus serpens*, *Coryphaena equiselis*, *Katsuwonus pelamis* and *C. hippurus* larvae occurred year round and were spread out across the transect (IVb3). Similarly, *Xiphias gladius* (IVb1) was found in all seasons and along all portions of the transect. Finally, *T. atlanticus*, *Nesiarchus nasutus* and *Makaira nigricans* larvae were spread across the transect but were restricted to the summer months (IVb2).

3.4. Species–environment relationships

The first two canonical axes of the CCA explained 16.8% of the total variation in the distribution of species, with the third and fourth axes contributing an additional 3% combined (Table 2). The eigenvalues, which provide an indication of the influence of each axis on the ordination, were over fourfold higher for the second versus the third axis. The stepwise-forward selection indicated that all seven of the environmental variables contributed significantly ($p < 0.01$, Monte Carlo permutation test) to explaining species distributions. The first two canonical axes of the CCA explained 81.5% of the total variation in the environment-species relationship. Environmental gradients in the depth of the 20 °C isotherm, 3 mL L^{-1} oxygen isopleths, fluorescence, and to a lesser extent current shear and Δ sigma-t explained much of the variation along the first canonical axis. SST and day length contributed largely to the second canonical axis (Table 2) and there was a moderate correlation between SST and day length ($r^2 = 0.45$). We found a strong correlation between the 20 °C isotherm and 3 mL L^{-1} oxygen isopleth ($r^2 = 0.91$), and a moderate negative correlation between these variables and fluorescence ($r^2 = -0.50$ and -0.45, respectively; Table 3).

The broad grouping of taxa formed by the indirect NDMS analysis tended to also occur in the CCA analysis (Fig. 6). *Scomber colias* was again an outlier in the CCA biplot. Assemblage I in the cluster analysis and ordination also grouped together in the CCA. Species that occurred primarily on the western edge of the transect, and were contained in groups IVc and IVa in the cluster analysis, tended to separate out from the other species along the first axis. Along the second axis, year-round spawners (assemblages II, IVb1, IVb3) tended to separate out from the summer spawners (IVb2, IVa) and spring spawners (II). As with the NMDS ordination,

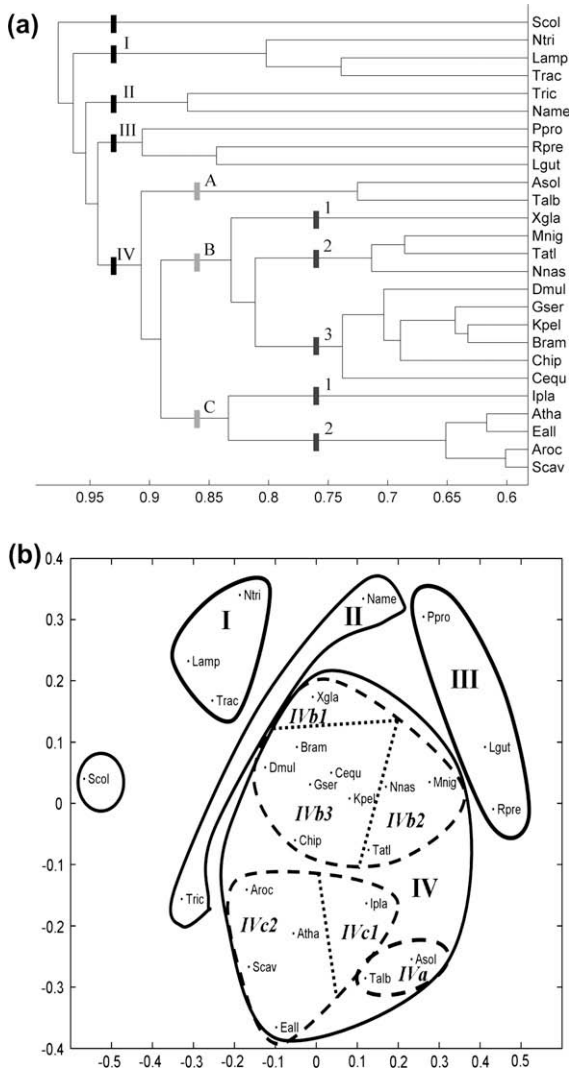

Fig. 5. Classification of larval fish assemblages using relativized larval fish abundances (individuals 100 m^{-2}) and a Bray-Curtis similarity matrix. (a) Results of the WPGMA (weighted pair group method with averaging) clustering. Four main assemblages and a number of groups and subgroups within assemblages were defined. (b) Non-metric multiple dimensional scaling ordination of the same matrix with assemblages and groups noted. Species codes used in the labeling are in Table 1.

the CCA revealed few clear discontinuities, but rather a gradient of species. Additionally, some assemblages tended to break down in the CCA, such as the separation of the assemblage III from group IVb2. Rare species not included in the indirect analysis occurred in a variety of locations in the CCA plots.

3.5. Species diversity and abundance

Sample rarefaction curves calculated across the entire dataset indicated a strong leveling off of taxon-counts between 100 and 200 sample stations (Fig. 7a). Seasonally, species-density reached a maximum in June, remained high through October, and then reached a minimum in January (Fig. 7b). Spatially, rarefaction of species counts to 20 stations did not reveal cross-Straits patterns in diversity (Fig. 7c); however, the alternative measure of diversity did reveal a strong spatial pattern (Fig. 7d). Diversity using standardized *z*-scores was highest 3–5 stations offshore of the western-most station and reached a minimum along the eastern half of the transect.

Table 2
Summary statistics for the Canonical Correspondence Analysis (CCA) of the larvae of 36 pelagic taxa collected at 371 stations in the Straits of Florida during 2 years of monthly sampling.

	AX1	AX2	AX3	AX4
Eigenvalue	0.234	0.204	0.046	0.031
Species–environment correlation	0.834	0.849	0.514	0.487
Cumulative percentage variance				
of species data	9.0	16.8	18.6	19.8
of species–environment relation	43.6	81.5	90.1	95.9
Inter-set correlations of environmental, variables with axes				
SST	0.14	−0.79	0.10	−0.09
20 °C isotherm	−0.70	−0.25	−0.02	0.19
3 mL L^{-1} oxygen isopleth	−0.60	−0.28	0.01	0.29
Day length	0.37	−0.49	−0.30	0.15
Fluorescence	0.52	0.40	0.20	0.15
Δ sigma-t	0.26	0.00	−0.05	0.06
Current shear	0.38	0.05	0.14	0.01

Table 3
Correlations of the seven environmental variables used in the CCA. Measurements were made over 2 years of monthly sampling along a transect crossing the Straits of Florida at 25.5 °N.

	SST	20 °C isotherm	3 mL L^{-1} oxygen isopleth	Day length	Fluorescence	Δ sigma-t
20 °C isotherm	0.07	–	–	–	–	–
3 mL L^{-1} oxygen isopleth	0.06	0.91	–	–	–	–
Day length	0.45	−0.06	0.07	–	–	–
Fluorescence	−0.25	−0.50	−0.45	−0.12	–	–
Δ sigma-t	−0.04	−0.21	−0.21	0.08	0.14	–
Current shear	−0.05	−0.35	−0.30	0.00	0.22	0.11

4. Discussion

4.1. Spawning strategies

Our aim was to determine the environmental properties associated with spawning and larval distributions across the spectrum of large and medium-size pelagic fishes. The results of both types of multivariate analyses (CCA and NMDS) revealed a continuum of patterns of larval distribution in space and time rather than clear discontinuities in species groupings. Additionally, the concordance of these analyses indicated that among species distributional differences were well explained by the seven environmental variables we used. In evaluating these results, it is important to note that comparisons of the relative importance of different, strongly correlated, environmental variables in observational data of this sort are not robust, nor do these correlations necessarily imply a causal relationship (Leps and Smilauer, 2003). On the other hand, when viewed in the context of previous work on these species, these results make it possible to infer how spatial and temporal patterns of spawning reflect the habitat preferences of adults and the suitability of an area for the survival of their offspring.

The seasonal component of spawning in fishes is most often related to photoperiod and temperature cues, a factor supported in this study by the strong role of both day length and SST in explaining the distribution of larvae. In more temperate latitudes, spawning in many species, while cued to these factors, may ultimately be timed to seasonal cycles of productivity (Cushing, 1975). This is likely not the case for pelagic species in the Straits of Florida and other subtropical locations, where specific oceanographic features (e.g. cyclonic eddies) rather than seasonal cycles most strongly influence patterns of productivity (Falkowski et al., 1991; McGillicuddy and Robinson, 1997; Hitchcock et al., 2005; McGillicuddy

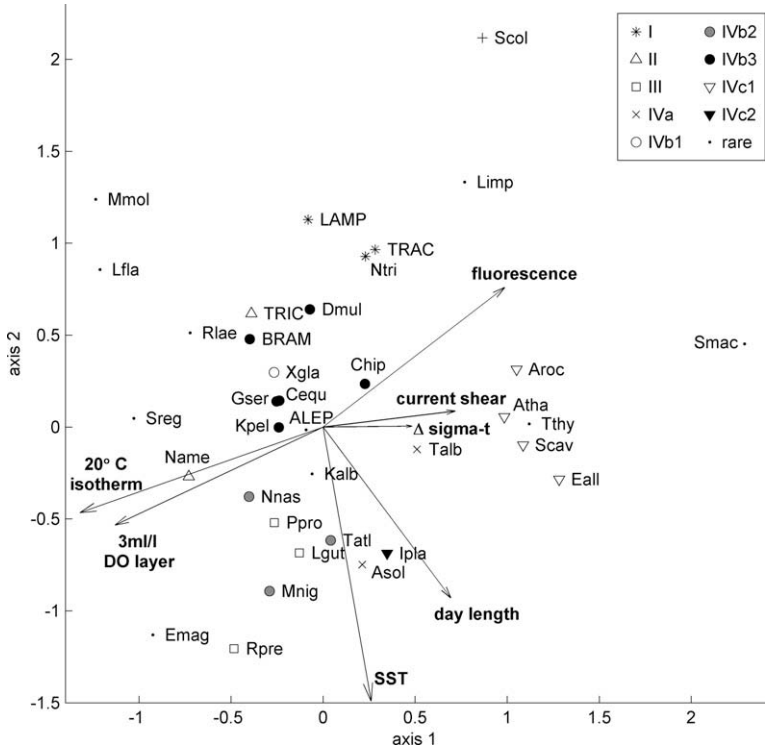

Fig. 6. CCA ordination of taxonomic groups and environmental variables. Groupings of larval taxa from the cluster analysis are indicated. Species codes used in the labeling are in Table 1.

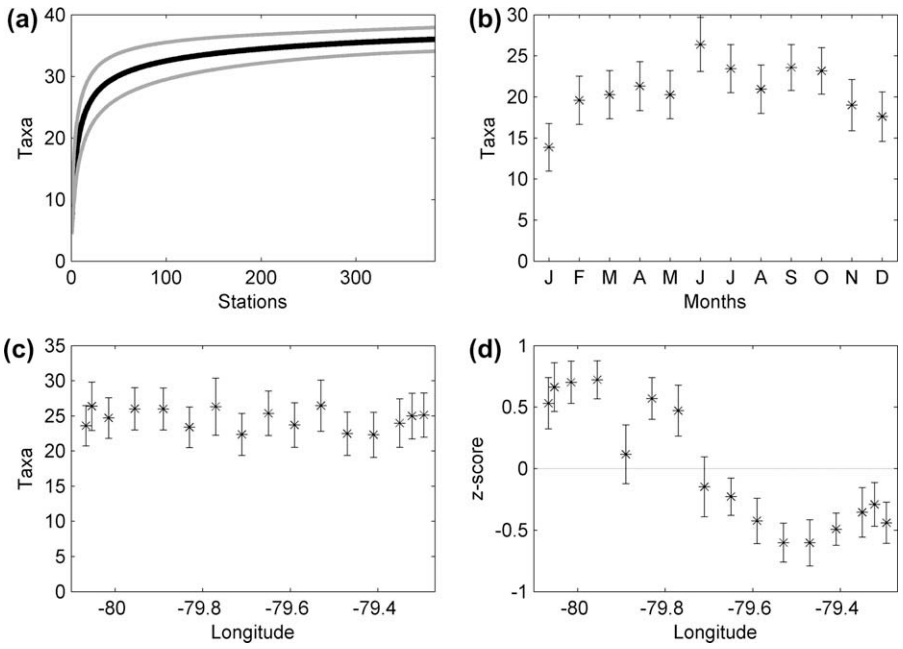

Fig. 7. Patterns of diversity of the larvae of large and medium size oceanic pelagic species in the Straits of Florida. (a) Rarefaction curve for entire sampling-effort, with mean and 95% CI, (b) Monthly rarefied diversity standardized to 20 stations (±SE), (c) cross-Straits rarefied diversity standardized to 20 station (±SE). (d) Cross-Straits diversity *z*-scores (±SE).

et al., 2007) and where productivity peaks in the winter (Hitchcock, *unpubl. data*). The occurrence of some primarily winter spawners may be attributed to this winter peak in productivity or to the seasonal occurrence of more northerly species in the study area during cooler months. However the predominance of summer or year-round spawning is likely due to the direct effects of day length and SST on rates of larval growth and development. Many taxa considered in this study exhibit extremely rapid larval growth (e.g., *Scomberomorus cavalla*: De Vries et al., 1990; *Xiphias gladius*: Govoni et al., 2003; *Istiophorus platypterus*: Luthy et al., 2005b; *Makaira nigricans*: Sponaugle et al., 2005), a strategy that is likely adapted to minimize the duration of the high mortality, larval stage. Spawning in higher temperature waters will positively affect rates of larval growth and development, assuming food is not

limiting (Houde, 1989; Pepin, 1991). Additionally, daily food intake increases with day length (Llopiz and Cowen, 2008), and energetics models in turn suggest that small increases in food intake have a disproportionate affect on growth rate (Feeley, 2006). On a basin-wide scale, a spawning strategy maximizing larval growth can account for the reduced seasonality of spawning (i.e. more protracted) in some tuna species at lower latitudes (Schaefer, 2001; Margulies et al., 2007). One further prediction of this spawning and life-history strategy is that in regions and at times where both day length and SST are maximized (i.e. summer in the subtropics), higher growth rates and possibly elevated spawning will occur.

The spatial patterns of larval occurrence observed in this study are affected by both the patterns of adult spawning and the subsequent modification of these patterns by larval transport. As such, it is important to consider the extent to which larval transport, a function of the age range of collected larvae (~4–12 d based on scombrid and istiophorid measurements) and current patterns, decouples the environmental characteristics of the spawning and larval collection locations. Within the Straits of Florida, the strongest component of flow is generally in the along-shore direction with flow in the across-shore direction often oscillatory due to its association with current meanders or eddies. An alternate way to view this issue is that current flow in the Straits of Florida is primarily parallel to isobaric surfaces, and in turn, parallel to isopleths of many of the variables considered in this study (20 °C isotherm, 3 mL L^{-1} oxygen isopleth and fluorescence). For these variables, the characteristics of larval collection sites should approximate the characteristics of the spawning locations. In contrast, notable decoupling would be expected for characteristics such as bottom depth or distance from shore due to the potential for larval transport around large current meanders, or into the narrower Straits of Florida from the wider expanses of the Gulf of Mexico. Both of these characteristics have previously been the focus of research on larval distributions of pelagic species (Leis et al., 1987, 1991; Boehlert and Mundy, 1994) but were not considered in this study.

The three correlated environmental characteristics, 20 °C isotherm, 3 mL L^{-1} oxygen isopleth and fluorescence that accounted for much of the spatial variability of larval distribution in the Straits of Florida may also structure the distribution of adult pelagic fishes (Sharp, 2001). The distribution of these variables in the Straits of Florida presents a unique tradeoff to pelagic species. In comparison to the eastern side, the western Straits of Florida is more productive but also characterized by vertical profiles of temperature and oxygen that should restrict the depth range of pelagic species and limit their access to deeper food resources. For many species, such as blue marlin, the benefits of being able to forage at deeper depths along the eastern edge of the Straits of Florida may offset the presumably higher food levels at the surface along the western edge (Prince and Goodyear, 2006). Conversely, restriction to the western edge of the Straits of Florida of the larvae of a number of smaller scombrid species (e.g. *Auxis* spp.), may be due to the high energy lifestyle of adults and their shallow distribution regardless of water column properties. Support for a similar mechanism controlling the distribution of tuna is provided by a consideration of ocean-basin-scale fisheries data (Sharp, 2001), and a more comprehensive study over a large (16° latitude × 20° longitude) area of the Pacific Ocean (Betrand et al., 2002). In the latter study, differences in regional abundances of tuna could be accounted for by a combination of species-specific physiological capabilities and the vertical profiles of oxygen, temperature and acoustically measured forage concentrations. Across the Florida Current, variability in the vertical profiles of temperature and dissolved oxygen exceeds that found in Betrand et al. (2002) and approaches longitudinal differences across ocean basins (Fonteneau, 1997). This makes the Florida Current and other western boundary currents a unique place to apply more process-oriented approaches to studying the combined effects of productivity and vertical habitat characteristics in structuring adult distributional differences. Such studies are necessary to verify the potential mechanism proposed here to account for the among-species differences in the spatial distribution of spawning.

Two other environmental variables that were also strongly patterned in space, density gradient and current shear had a comparatively small impact in explaining larval fish distributions. High current shear and steep density gradients are associated with the convergence of currents. Areas of high current shear are also associated with the generation of frontal eddies. As such, high current shear and strong density gradients generally lead to biological enrichment, and are predicted to be areas where spawning would occur or larvae would accumulate (Bakun, 2006). The relatively minor impact attributed to these two variables in the analysis, runs counter to the general biological importance attributed to these features. Methodological concerns associated with station spacing (~3–5 km) and the narrowness of fronts in the region (often <1 km) may explain some of the ambiguity that resulted from this analysis. Possibly, more important is the relatively crude measure (association between larval density and Δ sigma-t or current shear) that was used in an attempt to characterize what is a rather complex and time-varying biophysical process. In this region, multiple types of density fronts occur with each differing in their vertical extent, the mechanism that generated them, and their temporal evolution. A combination of issues such as these led Bakun (2006) to conclude that the systematic sampling designs that characterizes the majority of ichthyoplankton studies are poorly suited for addressing issues related to mesocale and submesoscale features such as fronts and eddies. This assertion is supported by the contrast between the results of this sampling and finer-scale Lagrangian-based sampling around a Florida Current frontal eddy that demonstrated elevated sailfish spawning in the front separating the interior of the eddy from surrounding waters (Richardson et al., 2009a). Illustrated by this contrast is the importance of recognizing the limitations of any single sampling strategy, and the need to integrate multiple forms of sampling into a study.

4.2. Regional diversity

Nearly all previous analyses of patterns of abundance and diversity of predatory oceanic species have relied on catch data from commercial fisheries. Ichthyoplankton studies, such as this one, while only characterizing the reproductively active component of the community, provide an alternative means of assessing these patterns. One remarkable result of this sampling is that the larvae of only 5 of 41 possible Atlantic pelagic taxa considered were not collected (*Thunnus alalunga*, *T. obesus*, *Tetrapturus pfluegeri*, *T. georgeii* and *Matsurus lanceolata*). Unfortunately, direct comparisons of this diversity to other studies are not possible, as this study has not been matched in the fine resolution of species identifications or the magnitude and temporal and vertical completeness of the sampling. Yet, even without a basis for comparison, the results of this study strongly suggest that the Straits of Florida is unique in the diversity of reproductively active large and medium-size pelagic species.

Numerous factors may drive the high diversity of larvae collected in the Straits of Florida including: (1) the western Atlantic bathymetry which makes the Straits of Florida a bottleneck for species migrating between the Atlantic and the Gulf of Mexico or western Caribbean, (2) the fast regional currents that may transport larvae spawned in distant locations to the Straits of Florida, (3) the persistence and predictable location in the Straits of Florida of a strong frontal zone and cyclonic eddies, both features considered favorable for spawning, and (4) the presence of strong

environmental gradients in both space and time allowing species with different optimum spawning habitats to occur in a constrained area. The importance of the last two factors is supported by the time-averaged peak in diversity in the most common location of the western Florida Current front. The assemblage analysis suggests that this peak in diversity may result from two faunas mixing at the frontal zone, though it is also likely that some species are specifically spawning at the front. Similarly, on a seasonal basis, the Straits of Florida supports species with different optimum temperatures for spawning, a factor which likely elevates larval diversity in this area above that in more temperate or tropical latitudes. Similar subtropical peaks in diversity have also been found in an analysis of commercial fishing data (Worm et al., 2005). However, in contrast to our study, in which diversity peaked through the summer months at SST > 28.5 °C, that study found a peak in adult diversity at intermediate SST of about 25 °C. This likely reflects the tendency of many species to spawn at the higher SST portion of their adult range.

One of the contentious debates with respect to pelagic fisheries concerns the extent to which industrialized fishing has resulted in a community-wide shift from large pelagic species, such as blue marlin, swordfish and bluefin tuna, to the smaller components of the community including bramids, *Auxis* spp., and snake mackerels (Ward and Myers, 2005). Myers and Worm (2003) asserted that 50 years of fisheries data indicate over 90% declines in large predators, a contention that has been strongly questioned (Hampton et al., 2005). The essence of this debate concerns the analysis of fisheries-dependent data, and how to account for the changing catchability of different species in light of constant changes in gear, techniques, targeted species and the spatial allocation of fishing operations. Highlighted by this debate is the undeniable need for fisheries-independent data in assessing fish stocks. On a community wide basis, the results of our study indicate that medium-size pelagic species are many times more abundant than large pelagic species. This may reflect the sampling location, but for many of the large pelagic species (e.g. swordfish, blue marlin) the abundances collected in the Straits of Florida were as high as or higher than have been reported elsewhere. Unfortunately, while ichthyoplankton samples have been collected in the region going back decades (Richards, 1976), the data on the full diversity of pelagic species remain unpublished, compromising our ability to address whether the regional species composition has changed.

One large pelagic species for which past ichthyoplankton sampling does allow decadal scale comparisons to be made in the Straits of Florida is bluefin tuna. Richards (1976) collected 123 bluefin tuna larvae while sampling (with a 333-μm mesh 1 m plankton net towed at the surface for 10 min) three stations on 31 different days from early April to early July of 1969–1971. Additionally, a five station cross-Straits transect was sampled 11 times in 1975 with a bongo net and a neuston net (with the same dimensions and mesh size used in this study) yielding 61 bluefin larvae. Both the 1969–1971 and the 1975 set of net tows had a similar magnitude of sampling during the bluefin spawning season as this study. Our collection of only three larvae thus stands in sharp contrast to these much higher numbers 30 years prior. It cannot be ruled out, but is considered unlikely, that the higher bluefin tuna numbers in the older studies resulted from morphological misidentifications. Specifically, the morphological identification criteria of Richards (2006b), the same author of this previous study, were applied in our study prior to molecular identification, without incorrectly identifying bluefin tuna. Such a contrast between the historical numbers and the more recent sampling thus likely reflects the precipitous decline in the western North Atlantic bluefin tuna spawning stock that has been seen across multiple datasets and is reflected in the stock assessments (Scott et al., 1993; Sissenwine et al., 1998). Interestingly, a similar comparison between historical swordfish collections and the recent sampling in the Straits of Florida does not show such a precipitous drop. Grall et al. (1983) reported a catch rate of 138 swordfish larvae at 263 stations in the Straits of Florida during sampling from 1953–1972. These numbers are comparable to the catch rate of 198 larvae at 371 stations in this study, though the early studies used such a range of gear (e.g. dip nets, conical nets, neuston nets) that more detailed comparisons are not possible. An extension of comparisons, such as these for bluefin tuna and swordfish, to components of the pelagic community that are not assessed but are taken in fisheries (e.g. opah, escolar), or are not targeted by fisheries but may have a substantial ecological role (e.g. *Auxis* spp.), could provide substantive evidence for or against broader community-wide changes in species abundance.

4.3. Conclusions

The dataset described herein provides the most complete description to date of the patterns of spawning across the suite of large and medium-sized pelagic species. Most previous studies have constrained their efforts to a select few targeted species, which while very useful, run in sharp contrast to the multi-species nature of pelagic fisheries, and by extension, the need for multi-species approaches in their management. Importantly, the benefits of this type of analysis will expand as more comparative and similarly comprehensive datasets from different regions become available. At the same time, it is important to recognize the limitations of the correlational approach with respect to addressing the critical questions concerning patterns of the movement and recruitment in pelagic species. Ongoing analyses of these collections with a focus on the feeding ecology (Llopiz and Cowen, 2008) and growth rates (Sponaugle et al., 2005) of larvae are better suited to exploring the mechanisms that underlie recruitment variability. Additionally, sampling focused on the temporal development of submesoscale features (Richardson et al., 2009a) and the tagging of adult fish during the spawning season (Richardson et al., 2009b) have provided additional information on finer-scale spawning habitat associations and individual-level spawning-related movements. In aggregate, these approaches can identify the mechanisms that link environmental conditions to the behavior and population dynamics of predatory pelagic species. This ultimately will provide useful information for the management of these species, and will represent a critical step towards predicting how these species will respond to changes in climatic conditions over the next decades.

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