

# Predicting the vertical distributions of reef fish larvae in the Straits of Florida from environmental factors

Klaus B. Huebert, Su Sponaugle, and Robert K. Cowen

**Abstract:** Three seasons of vertically stratified ichthyoplankton sampling at the edge of the Florida Current revealed consistent accumulations of some coral reef fish larvae under taxon-specific environmental conditions. Environmental variability ranging from predictable (seasonal differences in temperature, diel changes in light, and vertical gradients in many variables) to stochastic (changes in wind-driven turbulence and patchiness of zooplankton) was used to model larval distributions. In five taxa, including the commercially important Epinephelini (groupers), relative larval densities were predicted with significant accuracy based entirely on sampling depth. Models yielding these predictions were cross-validated among all seasons, indicating that larval vertical distributions were remarkably unaffected by other environmental factors, while revealing strong behavioral preferences for specific ranges of hydrostatic pressure. Pomacentridae (damselfish) larvae consistently occupied shallower depths at night than during the day, demonstrating diel vertical migrations. At the community level, depth and season were two major factors structuring larval coral reef fish assemblages. Predictable vertical distributions of larvae in the Straits of Florida can facilitate modeling the same taxa elsewhere in the Western Central Atlantic.

**Résumé :** Un échantillonnage stratifié verticalement de l'ichtyoplancton sur trois saisons à la marge du courant de Floride montre des accumulations régulières de larves de certaines espèces de poissons de récifs coralliens dans des conditions environnementales spécifiques à chaque taxon. Nous avons utilisé la variabilité environnementale allant de prévisible (différences saisonnières de température, changements diurnes de lumière et gradients verticaux de plusieurs variables) à stochastique (changements dans la turbulence sous l'effet du vent et répartition en taches du zooplancton) pour modéliser les répartitions des larves. Chez cinq des taxons, y compris les Epinephelini (les mérous) d'importance économique, la profondeur d'échantillonnage seule permet de prédire les densités relatives des larves avec une forte précision. Les modèles qui fournissent ces prédictions ont été soumis à une validation croisée sur toutes les saisons, ce qui indique que les répartitions verticales des larves sont remarquablement peu affectées par les autres facteurs du milieu et que les larves manifestent de fortes préférences comportementales pour des gammes spécifiques de pression hydrostatique. Les larves de Pomacentridae (demoiselles) se retrouvent de façon constante à des profondeurs moins grandes la nuit que le jour, ce qui démontre l'existence de migrations verticales diurnes. Au niveau de la communauté, la profondeur et la saison sont deux facteurs dominants dans la structuration des peuplements de larves de poissons de récifs coralliens. La répartition verticale prévisible des larves dans le détroit de Floride peut faciliter la modélisation des mêmes taxons ailleurs dans le centre de l'Atlantique de l'Ouest.

[Traduit par la Rédaction]

## Introduction

Marine fish larvae, like other zooplankton, rarely distribute randomly in the ocean water column. Instead, they assume distinct vertical distributions depending on the species and environment (reviewed in Heath 1992). Because the environmental conditions larvae experience vary considerably among different depths, vertical distributions can affect essential ecological processes such as feeding, transport, growth, and survival. Vertical gradients in physical factors

such as visible light (Forward et al. 1996), ultraviolet (UV) radiation (Browman 2003), pressure (Huebert 2008), turbulence (Werner et al. 2001), temperature (Olla et al. 1996), and salinity (Lougee et al. 2002) are thought to influence larval distributions. Vertical patterns of predators and prey are also considered important (Fortier and Leggett 1983; Fortier and Harris 1989). Some fish larvae actively seek out or avoid specific environmental conditions by vertical swimming (Olla et al. 1996; Huebert 2008), and those with physoclistic swimbladders can remain in a preferred environment

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**Table 1.** Sample sizes of coral reef fish larvae collected in spring, summer, and fall MOCNESS (Multiple Opening Closing Net with Environmental Sampling System) tows at a fixed station in the Straits of Florida over two diel cycles from 0 to 100 m depth.

Taxon	Spring	Summer	Fall
<b>Acanthuridae</b>	9	<b>45</b>	<b>129</b>
<b>Apogonidae</b>	<b>118</b>	10	<b>35</b>
Aulostomidae	—	—	2
Balistidae	41	23	17
Suborder Blennioidei	35	1	—
Callionymidae	14	20	49
Carapidae	12	15	41
Chaetodontidae	6	4	12
Cirrhitidae	—	—	9
Dactylopteridae	—	3	—
Diodontidae	—	6	—
Fistulariidae	1	—	1
Gerreidae	2	1	11
<b>Suborder Gobioidei</b>	<b>89</b>	<b>64</b>	<b>223</b>
Haemulidae	3	3	20
<b>Holocentridae</b>	<b>131</b>	<b>80</b>	<b>47</b>
Kyphosidae	—	2	4
Labridae <sup>a</sup>			
<i>Clepticus</i> spp.	2	1	8
<i>Decodon puellaris</i>	5	4	24
<i>Doratonotus megalepis</i>	1	1	18
<i>Halichoeres</i> spp.	11	6	9
<i>Lachnolaimus maximus</i>	4	—	—
<i>Thalassoma bifasciatum</i>	3	12	105
<i>Xyrichtys</i> spp.	1	25	265
<b>Lutjanidae</b>			
<b>Subfamily Etelinae</b>			
<i>Etelis oculatus</i>	1	1	48
<b><i>Pristipomoides</i> spp.</b>	1	<b>145</b>	<b>225</b>
Subfamily Lutjaninae			
<i>Rhomboplites aurorubens</i>	10	—	23
Other	9	25	34
Monacanthidae	76	15	18
Mullidae <sup>b</sup>	103	3	2
Opistognathidae	4	—	5
Ostraciidae	2	4	6
Pomacanthidae	—	27	22
<b>Pomacentridae</b>			
<i>Abudefduf</i> spp.	3	3	1
<i>Chromis</i> spp.	1	0	4
<b>Other</b>	<b>44</b>	<b>47</b>	<b>75</b>
<b>Priacanthidae</b>	<b>83</b>	<b>121</b>	<b>57</b>
<b>Scaridae</b>			
<i>Cryptotomus roseus</i>	5	9	32
<i>Scarus</i> spp.	1	1	4
<b><i>Sparisoma</i> spp.</b>	<b>31</b>	<b>47</b>	<b>171</b>
<b>Scorpaenidae</b>	<b>113</b>	<b>145</b>	<b>1014</b>

**Table 1 (concluded).**

Taxon	Spring	Summer	Fall
<b>Serranidae</b>			
<b>Subfamily Anthiinae</b>			
<i>Anthias nicholsi</i>	138	4	29
<i>Anthias tenuis</i>	5	—	—
<i>Anthias woodsi</i>	19	2	7
<i>Hemanthias leptus</i>	351	18	17
<b><i>Hemanthias vivanus</i></b>	<b>2070</b>	<b>37</b>	<b>62</b>
<i>Plectranthias garruppellus</i>	—	—	2
<i>Pronotogrammus martincenensis</i>	—	—	3
Unknown	7	—	—
<b>Subfamily Epinephelinae</b>			
<b>Tribe Epinephelini</b>	<b>33</b>	<b>30</b>	<b>242</b>
Tribe Grammistini	1	14	18
Tribe Liopropomini	—	10	52
<b>Subfamily Serraninae</b>	<b>154</b>	<b>33</b>	<b>115</b>
Sparidae	17	—	1
<b>Sphyraenidae</b>	<b>33</b>	<b>76</b>	<b>80</b>
Syngnathidae	13	3	3
Synodontidae	16	1	59
Tetraodontidae <sup>b</sup>	41	14	35

**Note:** Bold type indicates taxa included in vertical distribution models because of sample sizes of  $\geq 30$  in at least two seasons. Total volume sampled was highest in Fall (100%), lowest in summer (82%), and intermediate in spring (88%).

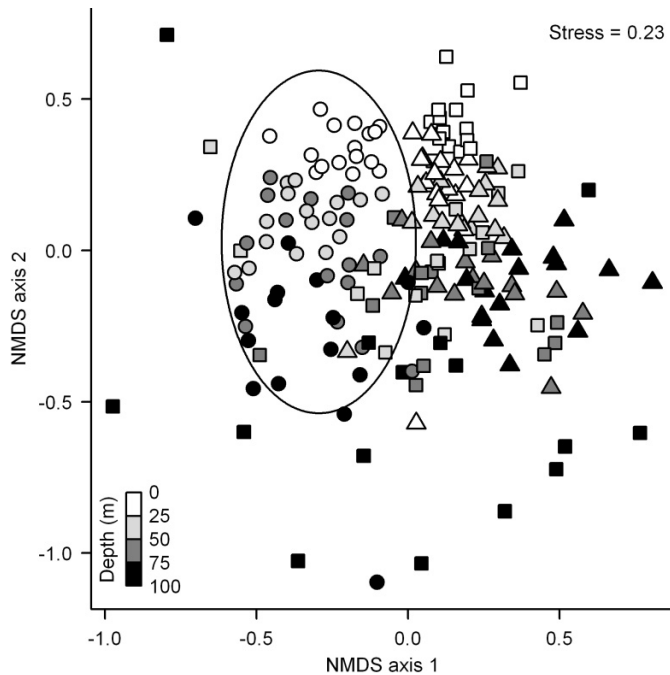
<sup>a</sup>Labridae were not pooled because different genera exhibited dissimilar vertical distributions.

<sup>b</sup>Mullidae and Tetraodontidae were caught in larger numbers in neuston net tows at <0.5 m depth than in MOCNESS tows and were excluded from analysis.

without expending the energy to swim by actively maintaining neutral buoyancy (Govoni and Hoss 2001). Coral reef fish larvae have physoclastic swimbladders and are fast swimmers relative to other fish larvae (Leis 2006), thus they may exercise a particularly high degree of control over their vertical distributions.

Previous studies of reef fish larvae have found significant differences in vertical distributions between day and night (Leis 1986, 1991b) and between early and late stage larvae (Cowen 2002), revealing the dynamic nature of vertical patterns. However, the role of specific environmental variables in influencing empirical larval reef fish distributions has not been examined quantitatively. The goals of the present study were to (i) measure the vertical distributions of coral reef fish larvae under a wide range of environmental conditions; (ii) develop statistical models that predict larval distributions based on environmental data; (iii) test the accuracy of model predictions; and (iv) use the accuracy of model predictions to estimate the importance of environmental factors in shaping larval vertical distributions. The focal data set of ichthyoplankton samples from the Straits of Florida represents one of the most extensive vertically stratified collections of reef fish larvae sampled at high temporal resolution. The analysis provides a novel quantitative approach to describe the influence of environmental conditions on larval fish distributions.

**Fig. 1.** Two-dimensional ordination of ichthyoplankton samples, using Kruskal's nonmetric multidimensional scaling of Bray–Curtis dissimilarity with respect to taxonomic composition across 30 coral reef fish families and the suborders Blennioidei and Gobioidae. Fish larvae were collected in the Straits of Florida during three seasons at four depth ranges. Two strong patterns are apparent: First, samples collected during spring (circles) cluster separately from summer (squares) and fall (triangles) samples, as illustrated by the ellipse. Second, samples collected at different depths form a distinct gradient from shallow (light) to deep (dark).



## Materials and methods

### Sampling

To characterize the vertical distributions of fish larvae in the Straits of Florida across a wide range of environmental conditions, three time series of biological and physical measurements were collected in spring, summer, and fall 2003. All time series involved repeated sampling of the water column every 3 h for two diel cycles. Sampling was conducted from the University of Miami's RV *F.G. Walton Smith*. During the spring time series from 7 April to 9 April and the fall time series from 30 September to 2 October, the vessel maintained position at a station ~30 km SSE of Miami (25.5°N, 80.06°W) with a bottom depth of ~130 m for 48 h of sampling. During the summer time series from 31 July to 2 August, the vessel maintained position at an adjacent station (25.5°N, 80.05°W) ~1 km farther offshore with a bottom depth of ~160 m for 42 h of sampling. Over the course of each time series, different parcels of water reflecting a variety of environmental conditions were transported past the sampling station by the Florida Current.

Ichthyoplankton samples were collected by towing a coupled asymmetrical Multiple Opening Closing Net with Environmental Sampling System (MOCNESS) (Guigand et al. 2005) obliquely from 100 m depth to the surface at a tow speed of 1.5 m·s<sup>-1</sup>. Two parallel sets of nets, one with 1 m<sup>2</sup> mouth opening and 150 μm mesh and one with 4 m<sup>2</sup>

**Table 2.** Diel variability in densities of common coral reef fish larvae collected in the Straits of Florida at 0–100 m depth in three seasonal 42–48 h duration time series of MOCNESS tows, expressed as percentages collected during the daytime (missing values (—) indicate sample sizes <30).

Taxon	Spring	Summer	Fall
Acanthuridae	—	51	52
Apogonidae	62	—	70
Epinephelini	46	41	42
Gobioidae	46	44	45
<i>Hemanthias vivanus</i>	41	38	73
Holocentridae	33	43	53
Pomacentridae <sup>a</sup>	51	52	51
Priacanthidae	41	48	62
<i>Pristipomoides</i> spp.	—	41	48
Scorpaenid	45	61	29
Serraninae	38	47	46
<b><i>Sparisoma</i> spp.</b>	<b>15</b>	<b>9</b>	<b>20</b>
Sphyraenidae	67	36	62

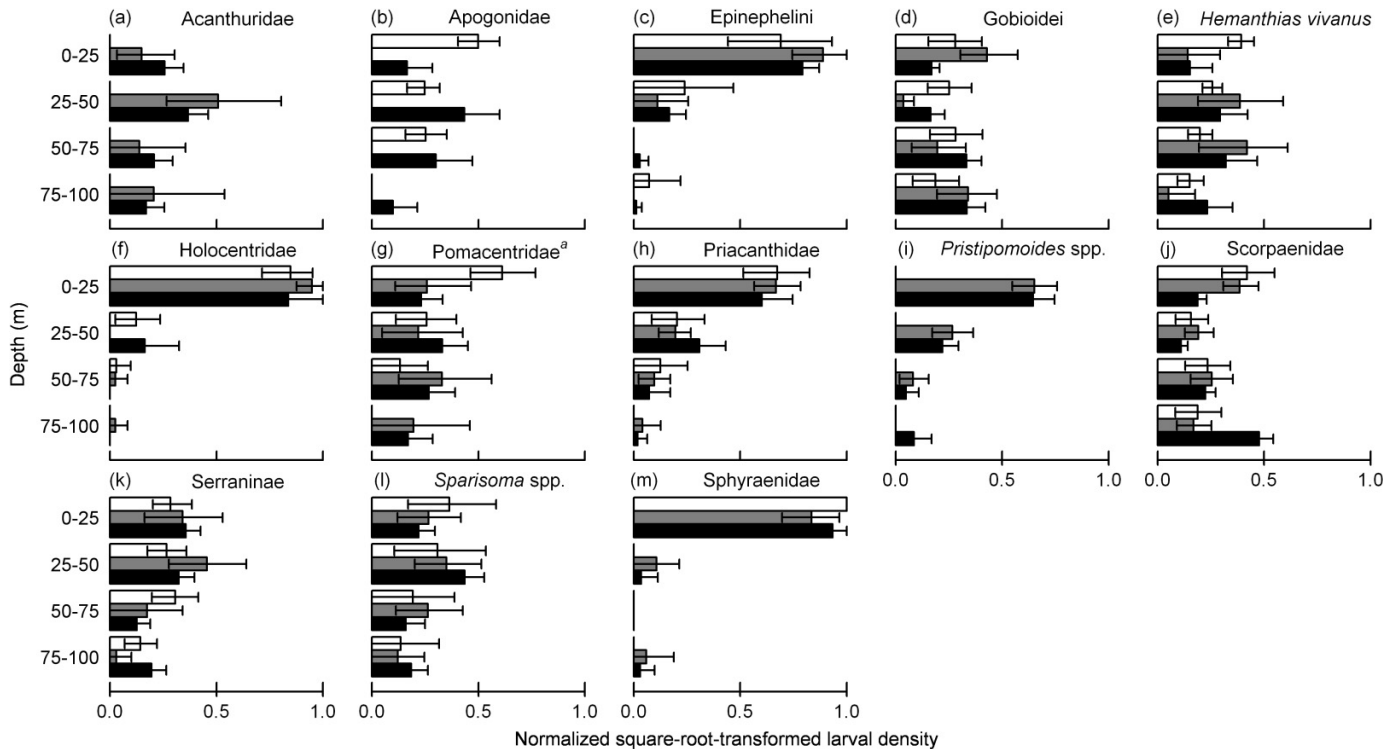
**Note:** <20% of *Sparisoma* spp. larvae (bold) were collected during the day and >80% during the night, revealing significant diel net avoidance (permutation test:  $p < 0.05$ ).

<sup>a</sup>Excluding the genera *Abudefduf* and *Chromis*.

mouth opening and 1 mm mesh, were opened and closed such that a different pair sampled from 100–75, 75–50, 50–25, and 25–0 m. The volume sampled by each net was calculated from flow through the net (MOCNESS flowmeter) and the mouth opening of the net corrected by its angle of attack (MOCNESS frame angle sensor). Additional sampling of the upper 0.5 m of the water column was conducted by towing adjoined neuston nets (0.5 m<sup>2</sup> with 150 μm mesh, 2 m<sup>2</sup> with 1 mm mesh) following each MOCNESS tow. Plankton samples were immediately fixed in 95% ethanol and later transferred to 70% ethanol for long-term storage. Larval fishes from only the 1 mm mesh nets were identified to family following Richards (2006). Larvae from the most abundant coral reef fish families were then further identified to the lowest possible taxonomic level. The settled plankton volume in samples from 150 μm mesh nets was used as a proxy for zooplankton biomass.

Physical measurements recorded by the MOCNESS included pressure, temperature, salinity, chlorophyll fluorescence (in summer and fall), and light (downwelling photosynthetically active radiation; in fall). Following each MOCNESS tow, a vertical profile of depth, salinity, temperature, fluorometry, oxygen saturation, and light transmission was collected with a CTD (conductivity–temperature–depth) instrument. In spring and summer, light-at-depth was calculated from shipboard radiometer and CTD transmissometer measurements. Light measurements were log-transformed. For all variables, the measurement taken closest to the midpoint of each sampled depth range, which generally corresponded to the median value (R.K. Cowen, unpublished data), was used to characterize the sample. Hourly wind speeds were obtained from the NOAA Fowey Rocks weather station, located 11 km to the northwest of the sampling station. Water level measurements at the NOAA Vir-

**Fig. 2.** Vertical distributions of larvae from 13 common coral reef fish taxa sampled at four different depth ranges in the Straits of Florida during three 42–48 h time series in spring (open), summer (grey), and fall (black) 2003. Error bars represent bootstrapped 95% confidence intervals. <sup>a</sup>In panel (g) for Pomacentridae, data excludes the genera *Abudefduf* and *Chromis*.



ginia Key station, 28 km to the northwest of the sampling station, were used as a tidal phase index. Mixed layer depth was defined as the depth above which no gradient in CTD temperature or salinity measurements was apparent. Under this definition, mixed layer depth captured the effects of recent turbulent mixing and was independent from and generally much shallower than the main (seasonal) pycnocline.

### Data analyses

Data analyses were focused on identifying ecologically meaningful and statistically robust relationships between vertical distributions of larvae and their environment. Given the large number of potentially correlated variables and the uncertain degree of statistical independence among larvae from the same net, adjacent nets from the same tow, and different tows from the same cruise, hypothesis testing required particular care. To reduce the chance of type I errors (incorrectly rejecting null hypotheses), associations between variables were only considered significant if they could be cross-validated (i.e., if consistent patterns were present in all analyzed sampling periods). Cross-validation also provided a safeguard against the misinterpretation of horizontal patterns (patchiness among larvae drifting past the station) as vertical patterns.

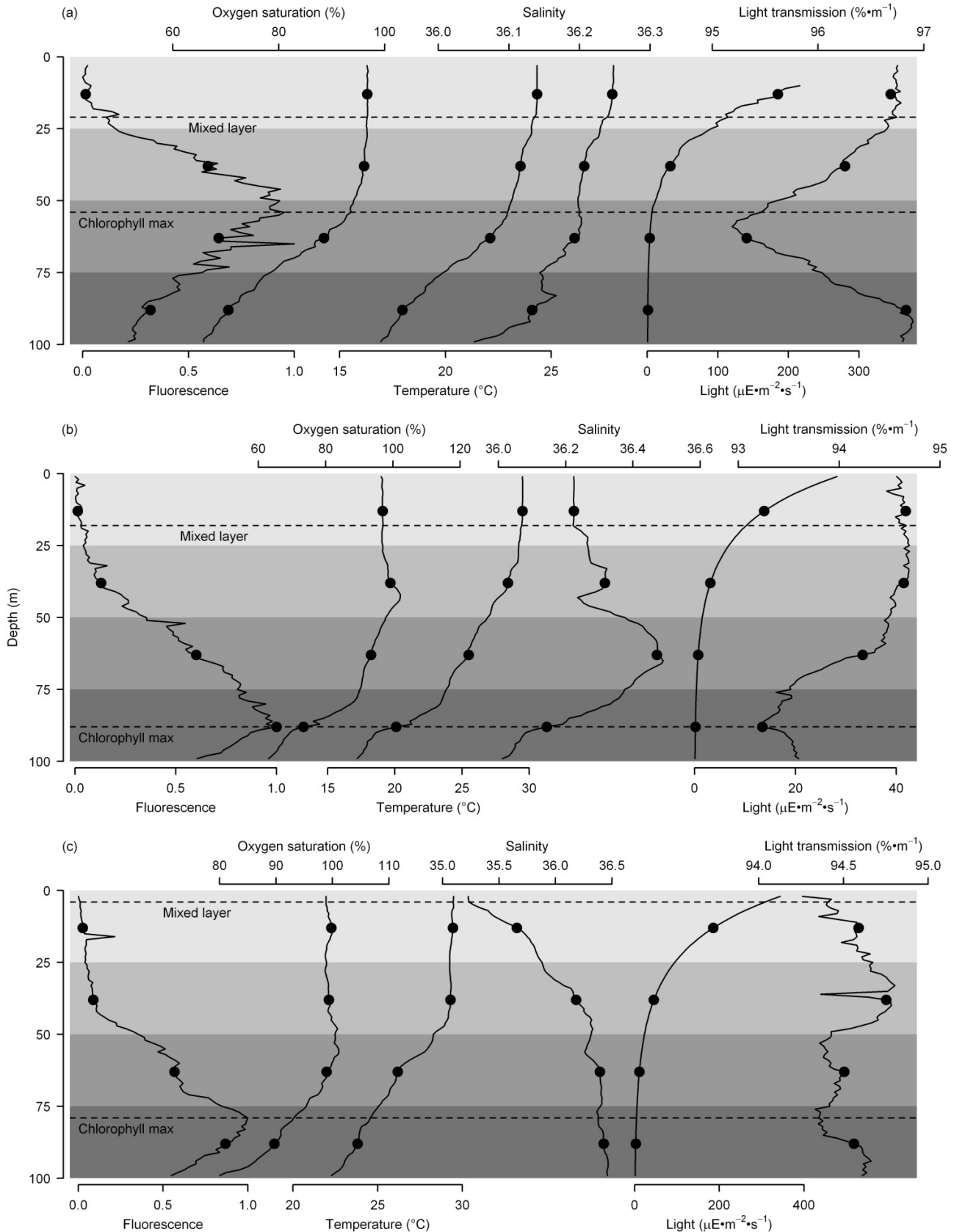
For each coral reef fish taxon, time series with sample sizes <30 larvae were considered insufficient for analysis and excluded. Further, cross-validation required analysis of at least two sampling periods; thus, taxa with sample sizes <30 in two time series were excluded entirely. Pomacentridae, except for the genera *Abudefduf* and *Chromis*, (hereafter referred to as pomacentrids) were pooled at the

family level. Labridae were excluded because the vertical distributions of different genera ranged from very shallow (*Lachnolaimus maximus*, *Doratonotus megalepis*) to very deep (*Decadon puellaris*), and no single genus was present in sufficient numbers. Tetraodontidae were excluded because MOCNESS samples alone were not considered representative of the population. All data from one net tow in spring were excluded because MOCNESS nets did not open and close at the correct depths.

Counts of larvae from each taxon in each sample were converted to densities per 1000 m<sup>3</sup> and square-root-transformed to reduce the effects of rare high counts (Sokal and Rohlf 1995). For statistical modeling, densities were then normalized such that the sum of all values for each taxon and cruise was equal to one. The resulting unitless “relative larval density” metric expressed the contribution of each sample to the total density in that particular time series. The use of relative density values allowed for meaningful comparisons of vertical distributions among seasons with different absolute densities.

Linear models and GAMLSS models (generalized additive model of location scale and shape) were fit to the data, with relative larval density as the dependent variable and environmental factors at depth (including interaction terms) as explanatory variables. GAMLSS fits specific families of statistical distributions to empirical data by simultaneously optimizing parameters for the location (e.g., mean), scale (e.g., variance), and shape (e.g., skewness) of the distributions (Stasinopoulos and Rigby 2007; Hernandez et al. 2009). Ecological density data sets have two properties that make fitting most types of distributions difficult: (i) negative

**Fig. 3.** Examples of (a) spring, (b) summer, and (c) fall depth profiles of environmental variables measured in the Straits of Florida. Depth profiles were collected every 3 h for 42–48 h, and the presented profiles are not intended to be representative of the entire period. Gray shading corresponds to nominal depth ranges at which discrete ichthyoplankton samples were collected. Points indicate measurements taken at the midpoints of depth ranges, which were used to characterize samples in statistical models. Conversion factor: 1  $\mu\text{E} = 1 \mu\text{mol}$  of photons.



**Table 3.** Range of environmental variables characterizing spring, summer, and fall ichthyoplankton samples collected every 3 h in the Straits of Florida over 42–48 h from 0 to 100 m depth and used to predict (i) relative larval fish densities and (ii) larval fish depth.

Factor	Unit	Source	Spring		Summer		Fall	
			Min.	Max.	Min.	Max.	Min.	Max.
<b>(i) Relative larval fish densities</b>								
Chlorophyll fluorescence	(Arbitrary units)	CTD	0.09	1.33	0.05	0.64	0.09	0.80
Chlorophyll (relative)	%	CTD	6	54	6	59	6	55
Light-at-surface	$\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Ship	<15	1035	<15	995	<15	550
Light-at-depth <sup>a</sup>	$\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Ship, CTD	<0.2	635	<0.1	474	<0.2	277
Oxygen saturation	%	CTD	66	98	60	99	80	100
Depth	m	MOCNESS	10	91	11	92	10	98
Salinity	(Unitless)	MOCNESS	35.9	36.3	35.6	36.6	35.3	36.4
Temperature	°C	MOCNESS	16.6	25.5	15.4	29.6	21.3	29.4
Light transmission	$\%\cdot\text{m}^{-1}$	CTD	94	97	93	95	94	95
Zooplankton settled volume	$\text{mL}\cdot 1000\text{ m}^{-3}$	MOCNESS	290	1140	190	800	260	1380
Zooplankton (relative)	%	MOCNESS	12	37	10	40	10	40
<b>(ii) Larval fish depth</b>								
Deep chlorophyll maximum	m	CTD	52	77	59	93	63	93
Light-at-surface	$\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Ship	<15	1035	<15	995	<15	550
Mixed layer depth	m	CTD	4	24	0	20	0	45
Oxygen saturation at 87.5 m <sup>b</sup>	%	CTD	66	90	60	96	80	96
Salinity at 12.5 m <sup>b</sup>	(Unitless)	MOCNESS	36.2	36.3	36	36.2	35.3	35.9
Temperature at 12.5 m <sup>b</sup>	°C	MOCNESS	24.5	25.5	29.3	29.6	29.0	29.4
Tidal phase index	(Unitless)	NOAA	-1.2	1.3	-1.2	1.2	-1.2	1.2
Wind speed	$\text{km}\cdot\text{h}^{-1}$	NOAA	1.5	21.7	2.2	15.6	2.6	17.7
Zooplankton center of mass	m	MOCNESS	44	56	43	54	39	53

**Note:** Factors included in models predicting relative larval fish density (i) represent individual samples, each measured at the mean depth of the sample (nominally 12.5, 37.5, 62.5, and 87.5 m). Factors included in models predicting larval fish depth (ii) characterize the state of the entire water column. CTD, conductivity–temperature–depth; MOCNESS, Multiple Opening Closing Net with Environmental Sampling System. Conversion factors: 1  $\mu\text{E}$  = 1  $\mu\text{mol}$  of photons.

<sup>a</sup> Light-at-depth was calculated from light-at-surface and light transmission at depth.

<sup>b</sup>Oxygen, salinity, and temperature measurements from depths with the greatest variability.

densities are meaningless, and (ii) densities of zero are common. To model these properties, we used zero-truncated  $t$  distributions and zero-inflated beta distributions in GAMLSS models. Nevertheless, the resulting GAMLSS models were generally driven by linear terms, and therefore equivalent to the much simpler linear models. Consequently, only the results of linear models are presented. Akaike's information criterion (AIC) was used as a guideline for selecting explanatory variables and interaction terms to include in the models. AIC expresses the degree to which a model captures the information contained in a data set while penalizing the model for each additional factor, thus limiting overparameterization. Since AIC does not measure the statistical significance of a model, the predictive value of models was tested by cross-validation. Samples from one season at a time were designated as "validation data," while samples from the remaining one or two seasons were used as "training data" for fitting a model. Each model was used to predict relative larval densities in the independent validation data, based on environmental variables only. Model significance was determined by a permutation test of the correlation between predicted and observed values (Hesterberg et al. 2005).

A second analysis was conducted with the depth at which larvae were collected as the response variable. This was accomplished by bootstrapping (drawing with replacement) samples of 10 000 larvae for each taxon from the original time series. The probability of drawing a larva from any particular sample was set to the square-root-transformed relative larval density, which is analogous to a square-root transformation of larval counts. The resulting bootstrapped samples were analyzed as described above by cross-validation of linear and GAMLSS models followed by permutation tests for significance testing. The strength of the second analysis was that variables characterizing the entire water column, as opposed to a specific sample, could be used as explanatory factors. Mixed layer depth, for example, could not have been used to predict larval densities in specific samples, but might nevertheless affect larval vertical distributions. The strength of the first approach was that the presence or absence of larvae from samples could be examined. In the second analysis this was impossible, because there was no way to calculate the depth of "absent fish."

Finally, to identify potential effects of environmental variability on ichthyoplankton assemblages, similarities in the taxonomic composition of samples were analyzed. Bray–

**Table 4.** Summary of linear models with significant (permutation test:  $p < 0.05$ ) cross-validated value for predicting relative larval density from environmental factors.

Taxon	Season(s) used to fit model	Predicted season	Factor	R <sup>2</sup>
Epinephelini	Spring and summer	Fall	Depth	0.50
	Spring and fall	Summer	Depth	0.39
	Summer and fall	Spring	Depth	0.15
Holocentridae	Spring and summer	Fall	Depth	0.31
	Spring and fall	Summer	Depth	0.44
	Summer and fall	Spring	Depth	0.36
Priacanthidae	Spring and summer	Fall	Depth	0.38
	Spring and fall	Summer	Depth	0.48
	Summer and fall	Spring	Depth	0.33
<i>Pristipomoides</i> spp.	Summer	Fall	Depth	0.40
	Fall	Summer	Depth	0.43
Sphyraenidae	Spring and summer	Fall	Depth	0.38
	Spring and fall	Summer	Depth	0.43
	Summer and fall	Spring	Depth	0.33
Apogonidae	Spring	Fall	Zooplankton	0.15
	Fall	Spring	Zooplankton	0.18
<i>Sparisoma</i> spp.	Spring and summer	Fall	Light-at-surface	0.10
	Spring and fall	Summer	Light-at-surface	0.23
	Summer and fall	Spring	Light-at-surface	0.10

Curtis dissimilarity matrices of square-root-transformed larval densities were used to perform Kruskal's NMDS (nonmetric multidimensional scaling). The Bray–Curtis index is widely used to measure ecological similarity across species and habitats, and NMDS is an ordination technique for visualizing the clustering of data in multidimensional space. A strength of NMDS is that unlike most ordination methods, NMDS neither requires that data meet restrictive parametric assumptions nor forces the clustering to conform to externally imposed explanatory variables (Legendre and Legendre 1998). This makes NMDS a powerful tool for exploratory data analysis of ichthyoplankton assemblages (e.g., Gray 1998). All data analyses were performed using the software package R (The R Project for Statistical Computing, <http://www.r-project.org/>).

## Results

### Larval composition

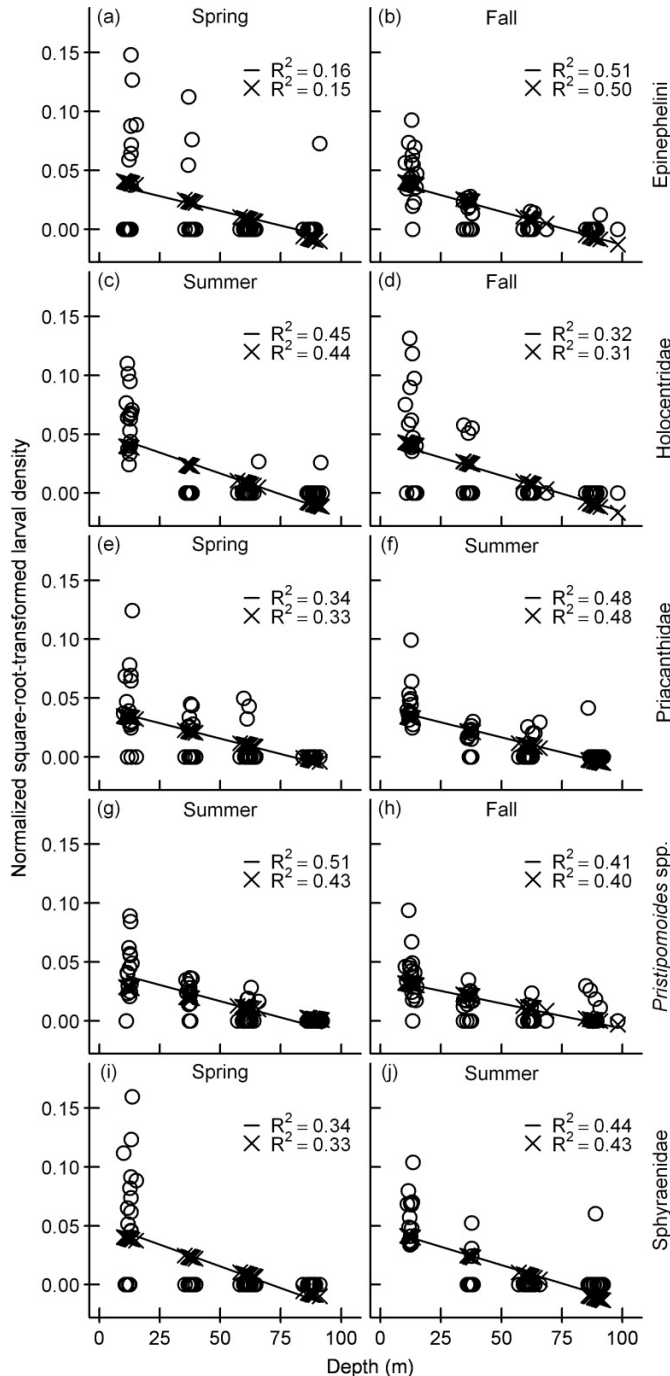
Over the course of three cruises, 8529 larvae representing at least 34 families strongly associated with coral reefs (Leis 1991a) were collected in MOCNESS samples (Table 1). Only larvae from the families Mullidae ( $n = 1279$ ) and Tetraodontidae ( $n = 315$ ) were collected in large numbers in neuston net samples, revealing that they aggregated at the surface of the water column. These two families were thus excluded from further analysis. Larvae from the most abundant groups could be identified to taxonomic levels ranging from 14 species identifications to one suborder. Most of these taxa are commonly observed on coral reefs in the Florida Keys (Bohnsack et al. 1999) and elsewhere in the Western Central Atlantic (Böhlke and Chaplin 1968). Various species in the subfamily Anthiinae, including the most abundant taxon of the study (*Hemanthias vivanus*), are common

on reefs deeper than 70 m (Hastings 1981), but are less well known. Most species of the family Scorpaenidae (the second most abundant taxon) are associated with reefs, but some inhabit other benthic habitats.

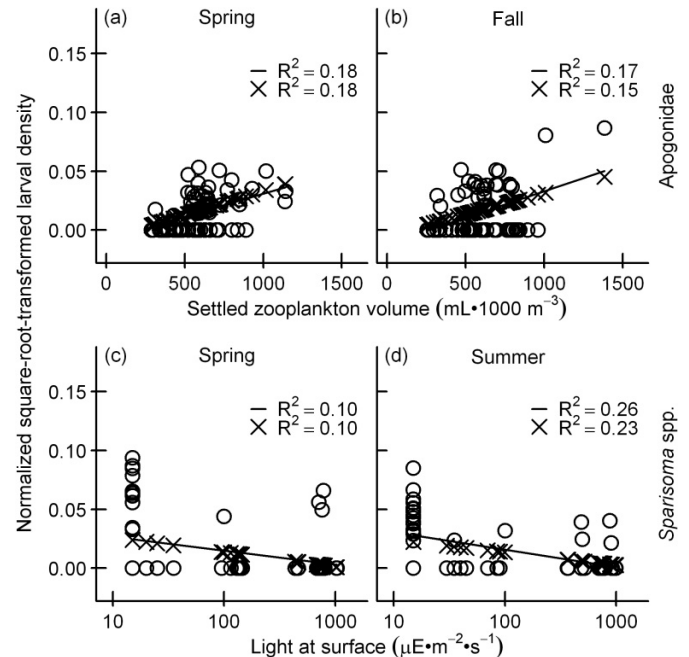
Samples collected in summer and fall were more similar to each other, in terms of taxonomic composition of reef fish larvae, than to samples collected in spring (Fig. 1). At the same time, samples formed clusters following an easily recognizable gradient in depth range from the deepest (75–100 m) to the most shallow (0–25 m) (Fig. 1). The combined density (untransformed) of reef fish larvae per 1000 m<sup>3</sup> of water in 1 mm mesh MOCNESS samples from all depth ranges was 58 in spring, 19 in summer, and 46 in fall. In several taxa, densities were much higher during either spring or fall than in the other two seasons. For example, *Hemanthias vivanus* made up 48% of the combined density in spring but only 3% in summer and 2% fall. Scorpaenids made up <1% of the combined density in spring, 1% in summer, and 31% in fall. Combined densities of larvae excluding the two above taxa were quite similar among seasons: 30, 18, and 31 larvae per 1000 m<sup>3</sup> in spring, summer, and fall, respectively.

Larvae from 13 taxa fulfilled the sample size requirements for further data analysis. In each time series, larvae from each analyzed taxon were present in >62% of MOCNESS tows. Approximately half of these larvae were collected during the day and half during the night (Table 2). However, the density of *Sparisoma* spp. larvae in the daytime samples accounted for <20% of the total, indicating diel net avoidance in this taxon. Among the 13 taxa analyzed, larval densities were frequently highest at 0–25 or 25–50 m and relatively low at 75–100 m depth (Fig. 2). The only group with highest densities at 75–100 m depth were scorpaenid larvae sampled during the fall time series.

**Fig. 4.** Observed and predicted relative densities of coral reef fish larvae (square-root-transformed and normalized such that the sum of all values equals one) at different sampling depths. In spring, summer, and fall, the upper 100 m of the water column in the Straits of Florida was sampled every 3 h for two diel cycles. Predicted densities for each season were generated by linear models fit to observed data in the other seasons. Titles indicate the taxon and season being predicted. Observed values ( $\circ$ ), lines, and associated  $R^2$  values illustrate significant regressions of larval densities and sampling depth (permutation test:  $p < 0.05$ ). Predicted values ( $\times$ ) and associated  $R^2$  values indicate the significant accuracy of models (permutation test:  $p < 0.05$ ). For each taxon, the seasons with highest and lowest model accuracy are shown.



**Fig. 5.** Observed and predicted relative densities of reef fish larvae (square-root-transformed and normalized such that the sum of all values equals one), collected in three seasonal 42–48 h time series in the Straits of Florida at 0–25, 25–50, 50–75, and 75–100 m depth. Predictions were generated by linear models fit to data excluding the season being predicted. Titles indicate the taxon and season being predicted. The  $x$  axis specifies the explanatory environmental variable. Observed values ( $\circ$ ), lines, and associated  $R^2$  values illustrate significant regressions in the observed data (permutation test:  $p < 0.05$ ). Predicted values ( $\times$ ) and associated  $R^2$  values indicate significantly accurate predictions (permutation test:  $p < 0.05$ ). For each taxon, the seasons with highest and lowest model accuracy are shown.

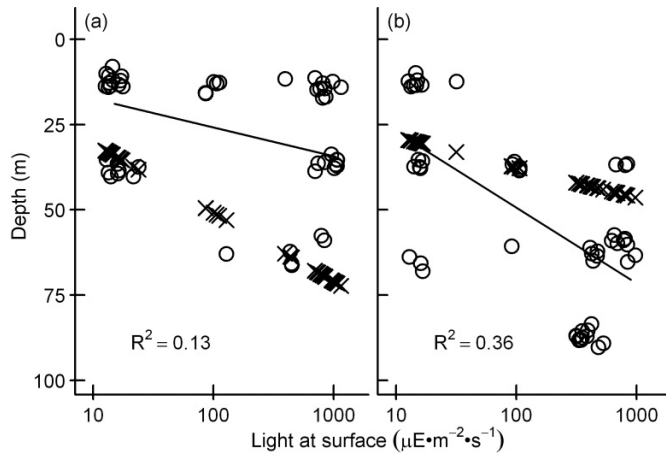


### Statistical models

The environmental conditions under which larvae were collected varied substantially both within and among cruises (Fig. 3, Table 3). Most models generated using AIC (one model was fit per taxon per season that could be used as validation data) included multiple factors and interaction terms that only described the training data, but did not improve predictions for the validation data. The best cross-validated predictions were generally achieved by models using only one explanatory factor.

Models with significant (permutation test:  $p < 0.05$ ) and cross-validated (at least two sampling periods) predictions for relative larval density were achieved in seven out of the 13 analyzed taxa (Table 4). Correlations were primarily driven by the presence or absence of larvae in different samples and to a lesser extent by differences among positive densities. Depth was the single most predictive factor for Epinephelini, Holocentridae, Priacanthidae, *Pristipomoides* spp., and Sphyraenidae, with all but one outlier having  $R^2 \sim 0.31$ – $0.50$  (Fig. 4). In some time series, relative densities of the above taxa were also related to other factors, such as oxygen saturation and light, but in all cases, the other factors were strongly correlated with depth (Supplemental Tables S1, S2<sup>3</sup>) and had less predictive value than depth.

**Fig. 6.** Random subset of bootstrapped observed ( $\circ$ ) and predicted ( $\times$ ) depths of pomacentrid (excluding the genera *Abudefduf* and *Chromis*) larvae sampled in the Straits of Florida in spring ( $n = 44$ ), summer ( $n = 47$ ), and fall ( $n = 75$ ) at 0–25, 25–50, 50–75, and 75–100 m depth. Regressions (lines) of surface light and observed depth were significant in each season (permutation test:  $p < 0.05$ ), the strongest and weakest relationships are shown: (a) spring, (b) summer. Data from each combination of two seasons were used to predict larval depth as a function of surface light in the third season. Models correctly predicted the direction of regression lines, but were not accurate in predicting observed values. Observed data were jittered to reveal individual data points (small random numbers were added to each coordinate).



Predictable correlations between relative larval densities and settled zooplankton volume (but not zooplankton normalized to the entire water column) were present for apogonids (Fig. 5; spring:  $R^2 = 0.18$ ; summer: no data; fall:  $R^2 = 0.15$ ). Relative densities of larval *Sparisoma* spp. were negatively correlated with surface light (Fig. 5; spring:  $R^2 = 0.10$ ; summer:  $R^2 = 0.23$ ; fall:  $R^2 = 0.10$ ), but not with light-at-depth, further indicating substantial diel net avoidance.

Cross-validated models accurately predicting larval depth were not achieved for any taxa. In the unique case of pomacentrids, the depth of larvae was significantly positively correlated with surface light in all three seasons (spring:  $R^2 = 0.13$ ; summer:  $R^2 = 0.36$ ; fall:  $R^2 = 0.18$ ; permutation test:  $p < 0.05$ ), revealing a diel vertical migration in this group (Fig. 6). Pomacentrid larvae consistently occupied shallower depth ranges during the night than during the day. However, both diel and nocturnal distributions were somewhat different in each season, causing model predictions to be inaccurate.

## Discussion

Vertical distributions are vital to the ecology of marine fish larvae because the biological and physical factors that define their environment change dramatically with depth. Since the early days of vertically stratified ichthyoplankton sampling (e.g., Ahlstrom 1959), it has been clear that larval vertical distributions can be dynamic yet somewhat predictable. Unfortunately, very few studies (e.g., Heath et al.

1988; Hernandez et al. 2009) have attempted to quantitatively predict distributions. All taxa in the present study have physoclastic swimbladders, which means that larvae can actively maintain neutral buoyancy at depth (e.g., Govoni and Hoss 2001), beginning at an early developmental stage (around yolk-sac absorption and first feeding) (Pelster 2004), while directly controlling their vertical movements by swimming (e.g., Leis 2004; Huebert and Sponaugle 2009). The degree to which different environmental variables are predictive of larval vertical distributions thus provides an empirical estimate for their importance in stimulating vertical swimming responses.

## Depth-regulating behavior

Of the environmental factors examined here, depth was the single best predictor of densities of reef fish larvae, resulting in significant cross-validated predictions for five taxa. Including other explanatory variables in addition to depth did not improve the precision of model predictions. All five depth – larval density relationships were quite stable in the face of substantial environmental variability, including seasonal changes in temperature, diel changes in light, and stochastic changes in turbulence. Among the taxa Epinephelini, holocentrids, priacanthids, *Pristipomoides* spp., and sphyraenids, depth models predicted a mean 35% of total variability in larval densities, including variability caused by horizontal patchiness among different parcels of water passing by the sampling station. It is possible to remove horizontal variability and focus entirely on vertical patterns by comparing predicted and observed proportions of larvae among each set of four net samples comprising one MOCNESS tow. Depth models of this kind predicted a mean 51% of vertical variability in larval proportions for the same five taxa.

Given accumulations of larvae at consistent depths in otherwise variable environments, which cues may be driving larval vertical orientation and swimming behavior? Our findings provide circumstantial evidence that larvae orient via hydrostatic pressure. While we treated depth and pressure as synonymous in our sampling and analyses, depth (distance from the surface) and pressure (force per area exerted by surrounding water) can be distinguished given proper ecological context. Pelagic fish larvae are frequently found at depths from which they cannot perceive the ocean surface, either by mechanoreception, vision (particularly at night), or any other known sense. However, larvae can sense hydrostatic pressure (Qasim et al. 1963; Govoni and Hoss 2001), and depth-regulating behavior of coral reef fish larvae in response to pressure cues has been demonstrated in controlled laboratory experiments conducted inside hyperbaric chambers (Huebert 2008). Larval behavioral preferences for specific levels of hydrostatic pressure thus present a parsimonious explanation for predictably stable larval vertical distributions.

All taxa with significant depth – larval density relationships accumulated at 0–25 m, with few larvae caught >50 m depth. This common pattern (Heath 1992) is often interpreted as an effect of the pycnocline (e.g., Palomera 1991; Coombs et al. 2001), sometimes without rigor-

<sup>3</sup> Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>).

ous hypothesis testing. While there is strong experimental evidence that some larvae avoid low temperature (Olla et al. 1996) or high salinity (Lougee et al. 2002), many larvae aggregate in the upper 50 m independent of the strength, location, or even presence of a pycnocline (Conway et al. 1997; Olivar and Sabates 1997). In our study, the main pycnocline started at a depth of ~70 m in spring, ~30 m in summer, and ~50 m in fall and continued past the 100 m limit of MOCNESS sampling in all seasons. No consistent effects of either temperature or salinity on larval distributions were apparent.

### Factors related to feeding and predation

Other environmental factors that are frequently used to explain larval vertical distributions in the sea include light, turbulence, and zooplankton concentration, all of which affect larval feeding. Obviously, high concentrations of zooplankton prey are favorable for feeding. As visual predators, larvae also depend on light to detect, pursue, and attack their prey (Blaxter 1986; Job and Bellwood 2000). Small-scale turbulence increases the rate of random prey encounters (Rothschild and Osborn 1988), but can interfere with successful prey capture when strong (MacKenzie and Kiorboe 2000). Given at least some light and some prey, vertical gradients in the above factors must cause a particular depth range to be most favorable for feeding. For example, in temperate continental shelf waters with strong seasonal stratification, the favorable range can correspond to the mixed layer (Buckley and Lough 1987), indicating once again the potential role of the pycnocline. In oceanic water around Barbados, the favorable range for *Thalassoma bifasciatum* is correlated with the deep chlorophyll maximum layer (Cowen et al. 2003). Similar logic can be applied to predation on larvae; thus, a particular depth range may also be most favorable for avoiding predators, and larvae may ultimately distribute in such a way as to optimize feeding and predation (Fortier and Harris 1989; Pearre 2003). Unfortunately, it has proven particularly difficult to obtain reliable measurements of predation (reviewed in Bailey and Houde 1989). Assuming that our measurements captured feeding and predation conditions, reef fish larvae did not generally adjust their vertical distributions in response to changing conditions within the three sampling periods.

The depth at which invertebrate zooplankton was most highly concentrated was not predictably related to the depth at which fish larvae were concentrated for any taxon. However, tows in which the concentration of zooplankton was unusually high across multiple depths were significantly and positively correlated with high relative densities of sampled apogonid larvae. In other words, while apogonid larvae did not accumulate at depths rich in zooplankton, they did accumulate in the entire water column under high zooplankton conditions. The observed relationship is therefore indicative of a horizontal as opposed to vertical pattern. Since our location was fixed for the duration of each sampling period, we sampled different water masses as they passed by the sampling station. Florida Current frontal eddies are known to accumulate both fish and invertebrate zooplankton off the Florida Keys (Limouzy-Paris et al. 1997; Lane et al. 2003; Richardson et al. 2009), and correlated fluctuations in zooplankton and apogonids may have been caused by pass-

ing water masses previously associated with eddies. This hypothesis does not explain why relative densities of other taxa were not predictably affected. Correlations between zooplankton and relative larval density were present in spring *Hemanthias vivanus* as well as spring and summer pomacentrids, but not in summer or fall *H. vivanus* or fall pomacentrids (thus not cross-validated).

Our only finding consistent with potential predator-prey-related vertical movements was a significant correlation between surface light and the depth at which we collected pomacentrid larvae in all three seasons. However, models did not accurately predict larval depths because of differences in vertical distributions among seasons. In other words, models predicted the presence and sign of a significant linear regression, but not the slope or intercept of the regression line. The pattern did not suggest behavioral preferences for specific light levels because relative pomacentrid densities were unrelated to light-at-depth. Instead, a transition between the daytime distribution and the nighttime distribution coincided with changes in light. Zooplankton (including fish larvae) commonly use dusk and dawn as cues for synchronizing vertical migrations thought to enhance feeding during the day (at the risk of increased predation) and reduce predation at night (Forward 1989; Neilson and Perry 1990; Richards et al. 1996). In our case study, pomacentrid densities increased at 50–75 m depth during the day and increased at 0–25 m depth during the night. Since pomacentrids require daylight to feed (Job and Bellwood 2000), the nocturnal distribution may be related to predator avoidance but not feeding. The diurnal distribution may be related to predator avoidance or prey densities or both.

### Net avoidance

The daytime net avoidance by *Sparisoma* spp., evident in the small percentage of larvae collected during the day, remains unexplained. There are two ways that larvae could have avoided capture during the day. Either *Sparisoma* spp. moved to depths that were not sampled by the MOCNESS, or they escaped the approaching sampling gear. *Sparisoma* spp. larvae were exceedingly rare in neuston net samples and thus did not avoid MOCNESS nets by accumulating at the ocean surface. Larval densities at 75–100 m depth were consistently low, including samples collected around dawn and dusk, suggesting that larvae did not migrate to deeper depths during the day. However, migrations to depths >100 m cannot be entirely ruled out since these depths were not sampled. The remaining explanation, visual net evasion, is common for some sampling methods (Ahlstrom 1959; Heath 1992), but surprising for a net with 4 m<sup>2</sup> mouth opening towed at ~1.5 m·s<sup>-1</sup>. While many settlement-stage reef fish larvae can swim at speeds of 0.4 m·s<sup>-1</sup> for short periods of time (reviewed in Leis 2006), swimming performance is related to the propulsive area of the fins (Fisher et al. 2000); thus, small larvae are much slower swimmers. *Sparisoma* spp. larvae were not larger or more developed than other larvae in our samples, and it seems unlikely that they consistently escaped nets when no other taxa did.

### Unexplained variability and limitations of the study

One of our most striking results was the amount of variability in larval distributions that was unrelated to a broad

range of environmental factors. Larvae almost certainly have sufficient swimming abilities (reviewed in Leis 2006) to assume vertical distributions matching their environmental preferences. However, for about half of the analyzed taxa, we found no compelling evidence that larvae sought out specific environmental conditions within the range encountered in the Straits of Florida. There are several possible explanations for this finding. First, it is possible that some exogenous factors did not repeatedly vary over sufficiently large ranges within our data set, limiting our ability to effectively cross-validate models. The presence of greater environmental extremes in more than one time series may have resulted in more predictable behavioral responses of larvae. Second, the 25 m vertical resolution of our samples may have been insufficient to detect some types of potentially important patterns. For example, the vertical distributions of phytoplankton (e.g., Rines et al. 2010) and invertebrate zooplankton (e.g., Young et al. 2009) can be patchy on much finer spatial scales (~1 m), and the effects of such thin layers of plankton on fish larvae would not have been detectable by our methods. Third, unpredictable vertical distributions may reflect behavioral preferences for environmental factors we did not address. For example, the vertical distributions of specific prey species were not resolved by our methods, and predators were not addressed at all. Fourth, larvae may exhibit seasonal variation in behavioral preferences. A multi-year data set would be required for cross-validations in this case. Finally, unpredictable vertical distributions may reflect behavioral plasticity within taxa, with different subsets of larvae exhibiting unique environmental preferences. Our study was limited to the detection of consistent environmental effects, but endogenous biological factors characterizing individual larvae may have caused the same environmental conditions to be favorable to some larvae and unfavorable to others.

Endogenous factors likely to interact with exogenous environmental variables in determining vertical orienting and swimming behavior include species, developmental stage, and satiation. With the exception of *H. vivanus*, the species composition within taxa analyzed in this study may have varied among seasons, and the presence of multiple species with different behaviors may have hindered the effectiveness of cross-validations. The lack of predictable patterns for pooled groups of multiple species is therefore inconclusive, and stronger patterns may emerge from species-level identifications, possibly by genetic techniques (e.g., Richardson et al. 2007). On the other hand, the presence of predictable patterns in some groups of larvae pooled at higher taxonomic levels indicates that closely related species often do behave similarly. Larval size and developmental stage also may be important. For example, postflexion larvae tend to occupy deeper depths than preflexion larvae around Barbados (Cowen 2002). Finally, even among individuals of the same species and size, variations in satiation may lead to different vertical behavior (Pearre 2003). With respect to our data, this aspect could perhaps be addressed by larval gut content analysis (e.g., Llopiz and Cowen 2009).

### Regional implications

Since the geographic ranges of reef fishes in the Western Central Atlantic generally span the entire Caribbean region

and beyond, it may be possible to extrapolate from our study in the Straits of Florida to other locations in the region. While it would be imprudent to expect vertical distributions elsewhere to exactly mirror those in the Straits of Florida, larval behaviors are likely to be equivalent, since gene flow among Caribbean reef fishes limits their potential for local adaptations (Planes 2002). Two patterns evident in our data set are likely to be of general regional importance. First, strong behavioral preferences for specific levels of hydrostatic pressure may be common among reef fish larvae. Specifically, preferences for relatively low levels of pressure in several taxa, including representatives of the commercially important grouper (*Epinephelini*) and snapper (*Pristipomoides* spp.), should result in predictable accumulations of larvae at <25 m depth. Second, within the range of environmental conditions addressed in our study, strong behavioral preferences for exogenous factors other than pressure (i.e., light, oxygen, phytoplankton, salinity, temperature, tidal phase, turbulence, water clarity, and zooplankton biomass) may generally be uncommon. However, this could change when the same larvae are exposed to more extreme conditions, both in the Straits of Florida and elsewhere in the Western Central Atlantic. For example, turbid freshwater intrusions associated with North Brazil current rings affect the vertical distributions of reef fish larvae in oceanic waters off Barbados (Cowen et al. 2003). With respect to more extreme environments, our measurements could be used to generate hypotheses for the range of conditions that fall within behavioral preferences as well as environmental tolerances of reef fish larvae.

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