



Habitat associations of dolphinfish larvae in the Gulf of Mexico

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ABSTRACT

The aim of this study was to investigate the role of the northern Gulf of Mexico (Gulf) as essential habitat of common dolphinfish (*Coryphaena hippurus*) and pompano dolphinfish (*C. equiselis*) during early life and to characterize conditions in which they were found. Eight ichthyoplankton surveys were conducted during the summer months from 2007 to 2010 in northern Gulf waters off Texas and Louisiana (26–28°N, 87–93°W), during which 1145 dolphinfish larvae were collected. *C. hippurus*, the dominant dolphinfish species, were collected in 57% of sampling sites with an overall mean density of 0.73 larvae 1000 m⁻³, whereas *C. equiselis* were only collected at 18% of sites with a mean density of 0.12 larvae 1000 m⁻³. Generalized additive models (GAMs) were used to examine the relationship between several environmental parameters and *C. hippurus* presence/absence and density. Both presence/absence and density GAMs indicated that catches of *C. hippurus* larvae increased near fronts and eddies and that increased abundances were most strongly associated with higher salinities and cooler temperatures. In addition, our models showed that *C. hippurus* larvae were positively associated with *C. equiselis* larvae, suggesting that *C. hippurus* and *C. equiselis* use similar habitats. Results of this study indicate that the Gulf may represent important spawning and/or nursery habitat of dolphinfishes and that mesoscale features and physicochemical conditions influence the distribution and abundance of *C. hippurus* larvae in this region.

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INTRODUCTION

Recruitment of marine fishes is highly variable and strongly influenced by the quality of habitats occupied during early life. Nurseries are typically regarded as habitats that support higher densities of larvae, often providing increased production of recruits due to enhanced growth and/or reduced mortality (Beck *et al.*, 2001). Growth and survival are heavily influenced by the environmental conditions experienced during early life, and as a result, habitat quality plays an important role in determining recruitment success and year class strength. The predominant biotic factors regulating the early life survival of fishes are prey quantity/quality (Cushing, 1975) and predation pressure (Paradis *et al.*, 1996). Physical processes such as freshwater inflow, upwelling and hydrodynamic convergence strongly affect ecosystem productivity and the transport/distribution of fish larvae and their prey (Bruce *et al.*, 2001). Thus, environmental conditions often play an important role in shaping spatiotemporal trends in early life habitat use and survival, and defining key attributes of productive nursery areas is needed in order to better understand the source of recruitment variability.

High rates of freshwater inflow from the Mississippi River and large-scale oceanographic features associated with the Loop Current (e.g., warm and cold core eddies) produce dynamic biotic and abiotic conditions in the Gulf of Mexico (Gulf). The combined effects of these features influence spatiotemporal variability in primary and secondary productivity, which in turn influence the distribution and abundance of larvae and fishery yields in the region (Govoni *et al.*, 1989). The Gulf is an important spawning and nursery ground for several species of pelagic fishes including billfishes, dolphinfishes and tunas (Ditty *et al.*, 1994; Richardson *et al.*, 2009; Rooker *et al.*, 2012), and an improved understanding of how these oceanographic features influence the early life ecology of these species is

necessary in order to forecast population trends and effectively manage adult stocks in this region.

Dolphinfishes are highly migratory epipelagic fishes that inhabit tropical and subtropical waters worldwide (Gibbs and Collette, 1959). The family Coryphaenidae is comprised of two species, *Coryphaena hippurus* (common dolphinfish) and *Coryphaena equiselis* (pompano dolphinfish). Both species support recreational and commercial fisheries throughout their global range (Oxenford, 1999). In spite of the considerable ecological and economic importance of these species and the value of early life history studies in evaluating population trends, our understanding of their distribution and habitat associations during early life is limited. In particular, little is known regarding the Gulf's role as a spawning and/or nursery habitat of either species. Here, we investigate the role of the northern Gulf as essential habitat of dolphinfishes and identify conditions that are associated with high occurrence and density of both species. We first characterize the distribution and abundance of dolphinfish larvae and early juveniles in the northern Gulf and then identify environmental conditions that are associated with increased abundances of dolphinfish larvae using generalized additive models (GAMs).

METHODS

Field work

Samples were collected during annual ichthyoplankton surveys in the northern Gulf in June and July from 2007 to 2010. Surveys were conducted in a region from 26 to 28°N and 87 to 93°W (Fig. 1). This sampling corridor varied slightly among years to encompass the

northwestern margin of the Loop Current and associated eddies in addition to open water sites, as these oceanographic features are thought to be important nursery habitats of marine fishes. In addition, this area is known to contain a high spawning biomass of other large pelagic species (Rooker *et al.*, 2007; Simms *et al.*, 2010). Approximately 60–70 stations were sampled during each survey from 2007 to 2009, with a smaller number of stations ($n = 48$) sampled in the 2010 surveys after the Deepwater Horizon oil spill. Stations were spaced approximately 15 km apart within each east-to-west running transect. Transects were spaced latitudinally at greater distances in order to provide comparisons from different regions of the continental margin (e.g., outer shelf versus slope). The specific number and latitudinal position of transects surveyed on each cruise was determined by the location of mesoscale features within the general sampling corridor. Paired neuston nets (2 m width \times 1 m height frame) equipped with 500 and 1200 μm mesh were towed through the upper meter of the water column at a speed of approximately 2.5 knots (1 knot = $\sim 1 \text{ m s}^{-1}$). Considering that neuston nets sample surface waters and are thus not completely submerged, abundance was calculated under the assumption that sampling was conducted at an average depth of 0.8 m (i.e., 80% net submersion). The duration of each tow was typically 10 min and tows were only conducted during daylight hours (beginning at sunrise and ending 30 min prior to sunset). Flowmeters (Model 2030R; General Oceanics Inc., Miami, FL, U.S.A.) were secured in the centre of the nets and were later used to determine the total surface area of water sampled during each tow.

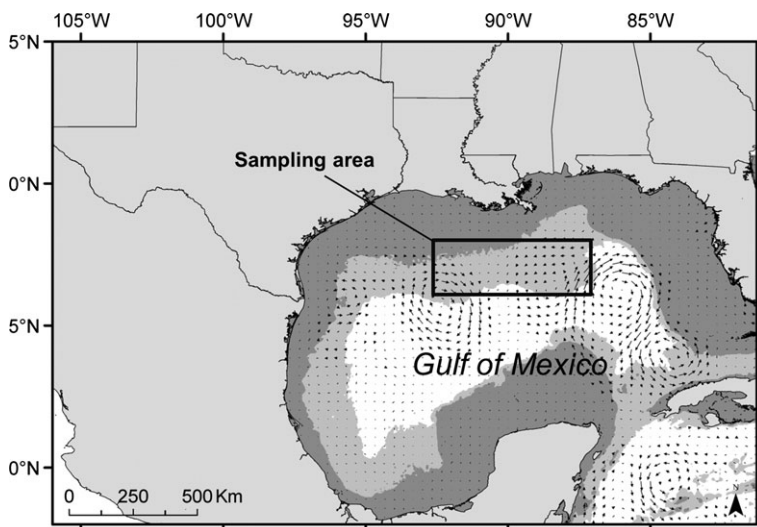


Figure 1. Map of the Gulf of Mexico with the location of the sampling area outlined in black. Dark gray areas represent depths < 1000 m, light gray regions represent depths of 1000–3000 m and white areas represent depths > 3000 m. Vector lines show general ocean current patterns (downloaded from the Aviso database using MGET).

Table 1. List of all environmental parameters obtained from remotely sensed datasets with descriptions and sources. Data for all variables except depth were obtained using the Marine Geospatial Ecology Toolbox version 0.8a42 (Roberts *et al.*, 2010).

Parameter	Sensor/model	Spatial resolution	Temporal resolution	Source
SSHA (cm)	Merged Topex/Poseidon, Jason-1, Jason-2, GFO, ERS-1, ERS-2. and EnviSat	1/3 degree	7 days	www.aviso.oceanobs.com
Feature classification	Merged Topex/Poseidon, Jason-1, Jason-2, GFO, ERS-1, ERS-2. and EnviSat	1/3 degree	6 weeks	www.aviso.oceanobs.com
Chlorophyll a (mg m ⁻³)	MODIS Aqua	1/24 degree	8 days	www.oceancolor.gsfc.nasa.gov
Depth (m)	U.S. Coastal Relief Model	3 arc-second	N/A	www.ngdc.noaa.gov/mgg/coastal/crm

Material captured by the nets was sorted and *Sargassum* biomass was recorded for each collection. All fish larvae were preserved onboard in 70% ethanol and later transferred into a 95% ethanol solution. Sea surface temperature (°C) and salinity were recorded at each sampling site using a YSI Sonde 6920 Environmental Monitoring System ($\pm 0.15^\circ\text{C}$, $\pm 1\%$ salinity; YSI Inc., Yellow Springs, OH, U.S.A.), and start and stop coordinates were obtained from a handheld GPS (Garmin International Inc., Olathe, KS, U.S.A.). Station coordinates were later inserted into ARCGIS (ESRI) and additional environmental datasets were downloaded and extracted from respective databases (Aviso, NOAA NGDC and NASA Ocean Color Group) for each sampling station (Table 1). The mean values of remotely sensed data were estimated from the smallest spatial and temporal resolution available for each sampling date and location.

In the lab, dolphinfish larvae were removed from ichthyoplankton samples and placed in separate vials containing a 70% ethanol solution. The standard length (SL) of each larva was then measured to the nearest 0.1 mm, and only larvae ≤ 25 mm SL were used in this study. Abundance of larvae (reported as larvae 1000 m⁻³) was calculated for each station by dividing the total number of larvae collected by the volume of water filtered during each tow. Although there is a possibility that recently hatched larvae were extruded from the 1200- μm mesh net, no significant differences were found between catch rates of 500- and 1200- μm nets so abundance measures account for total catches across both nets.

Molecular identification

Larger dolphinfish larvae and early juveniles were easily distinguished by species-specific differences in pigmentation, eye size, mouth size, body depth and spine counts (Ditty *et al.*, 1994). However, it is difficult to visually distinguish *C. hippurus* from *C. equiselis* larvae at sizes less than 8 mm SL. As a result, mitochondrial

DNA analysis was employed for smaller specimens (< 8 mm SL) according to the protocol of Rocha-Olivares and Chávez-González (2008). Briefly, DNA was first extracted from ethanol-fixed larvae through proteinase K digestion and ethanol precipitation. DNA samples isolated from larger juveniles of each species were used as positive controls. Multiplex haplotype-specific polymerase chain reactions (PCR) were then prepared with species-specific primers and thermal cycling was conducted using a Mastercycler (Eppendorf, Hauppauge, NY, U.S.A.). Next, PCRs were run on an agarose gel and results were read under a High-Performance Ultraviolet Transilluminator (Ultra-Violet Products Ltd., Upland, CA, U.S.A.).

Statistical analysis

Generalized additive models (GAMs) are a common method for modeling habitat use of fishes (Valavanis *et al.*, 2008) and were used here to model non-linear relationships between the response variable and multiple predictor variables (Hastie and Tibshirani, 1990). GAMs use non-parametric smoothing functions (Guisan *et al.*, 2002), allowing response curves (relationship between predictor and response variables) to be determined by the data rather than an *a priori* fitted parametric model. The use of GAMs in fish habitat modeling is valuable because fish abundances are generally not normally distributed and the relationship between species abundance and environmental predictors are often non-linear in nature (Oksanen and Minchin, 2002). GAMs were created to model spatial and temporal trends in the abundance of *C. hippurus* larvae to determine factors that influence their distribution in the northern Gulf. GAMs were not developed for *C. equiselis* due to small sample sizes (< 12 larvae in four out of the eight surveys); however, *C. equiselis* presence was used as a factor in the *C. hippurus* presence/absence model and *C. equiselis* density (larvae 1000 m⁻³) was used as a continuous variable in the *C. hippurus* density model. All GAMs were

developed using the 'mgcv' library (Wood, 2006) for R software packages (R Development Core Team, 2011). The general GAM structure is given by Eqn (1):

$$E[y] = g^{-1}(\beta_0 + \sum_k S_k(x_k)), \quad (1)$$

where $E[y]$ is the expected value of the response variable, g is the link function that defines the relationship between the response and additive predictors, β_0 is the intercept term, x is one of the k predictors, and S_k is the smooth function of each of the predictors (Hastie and Tibshirani, 1990). A cubic regression spline was used as the smoothing function for each predictor and smoothed responses were added together to form an additive model. Smoothing splines were restricted to a maximum of 3 degrees of freedom for all predictor variables to avoid overfitting.

Explanatory variables for GAM analyses included physicochemical (sea surface temperature and salinity), oceanographic (sea surface height anomaly, depth and feature classification), biological (chlorophyll *a*, *C. equiselis* presence/density and *Sargassum* biomass) and temporal (hours after sunrise, month and year) factors. Ocean depth data were retrieved from NOAA's NGDC U.S. Coastal Relief Model (www.ngdc.noaa.gov/mgg/coastal/crm.html) at a 3 arc-second resolution (Table 1). Sea surface height anomaly (SSHA) information was obtained from the Archiving, Validation, and Interpretation of Satellite Oceanographic data (Aviso) merged Topex/Poseidon, Jason-1, Jason-2, GFO, ERS-1, ERS-2, and EnviSat weekly dataset with a 1/3° resolution. The Okubo–Weiss algorithm (Okubo, 1970; Weiss, 1991) was used within the Marine Geospatial Ecology Toolbox (MGET) version 0.8a42 for ARCGIS (Roberts *et al.*, 2010) to locate eddy cores by estimating vorticity and strain from sea surface height images. Resulting polarity values (defining each site as being within a cyclonic/cold core feature, anticyclonic/warm core feature, or the open ocean) were used in the feature classification parameter. To prevent the detection of non-eddy features, only eddies that persisted longer than 6 weeks were selected. Chlorophyll *a* concentration was used as a proxy for food availability, and these data were taken from NASA OceanColor Group's Moderate Resolution Imaging Spectroradiometer (MODIS) on the Aqua satellite, generated every 8 days at a 1/24° resolution. Prior to model selection, all candidate variables were tested for collinearity using Spearman's correlation analysis and variables used in GAMs were not highly correlated ($\rho < 0.60$).

Data from ichthyoplankton surveys often include a large proportion of null-abundance data points; thus, two-strata GAMs are generally recommended for these

types of studies (Pennington, 1983). The first stratum models presence/absence as a binary process, whereas the second stratum models larval density conditional on presence. The presence/absence model was fitted with a binomial distribution using a logit link function, where local occurrence (0 = absent, 1 = present) was modeled against environmental variables across all years. Analysis of abundance data indicated overdispersion of larval density at non-null abundance stations; therefore, the density model was fit using a quasi-likelihood estimation of a Poisson distribution with a log link function.

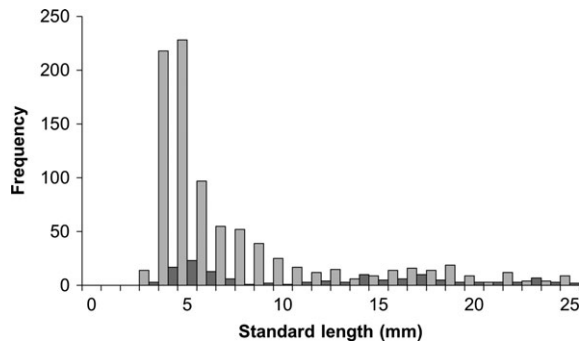
Final models were selected manually using a backwards stepwise procedure. Akaike Information Criterion (AIC) and quasi-Akaike Information Criterion (QAIC) values, which measure the goodness of fit for a model while accounting for degrees of freedom, were used to detect the relative importance of each variable in both presence/absence and density models, respectively. At each step of the selection procedure, AIC was calculated using the 'mgcv' package and QAIC was calculated using the 'MuMIn' package in R (Wood, 2006; Barton, 2011). The predictor with the highest P -value ($P > 0.05$) was removed to produce a reduced model and this variable was excluded from further analyses if its removal resulted in a lower AIC/QAIC (i.e., a better fitting model). Backwards selection continued until removal of additional variables yielded an increase in AIC/QAIC. The relative importance of each variable in final models was assessed by withdrawing individual retained variables and calculating the change in AIC/QAIC (Δ AIC/QAIC) and percent deviance explained (Δ DE) between the final and reduced models.

Additionally, a multivariate analysis of variance (MANOVA) was conducted to investigate size-specific *Sargassum* associations. Densities were calculated separately for small (< 8 mm SL) and large (> 8 mm SL) *C. hippurus* larvae and the MANOVA tested for differences in abundance between these size classes in relation to *Sargassum* biomass at each site.

RESULTS

Overall, 1145 dolphinfish larvae were collected across 558 sampling stations during the course of this 4-year study. The majority of larvae were very small with an overall mean standard length of 7.8 mm (Fig. 2). Visual identification was possible on 377 *C. hippurus* and 81 *C. equiselis* larvae, and all remaining larvae ($n = 687$) were genetically analyzed. Results revealed that *C. hippurus* was the more abundant of the two species, accounting for 87% of the total catch. Larvae

Figure 2. Standard length frequency of all *Coryphaena hippurus* (light gray) and *C. equiselis* (dark gray) larvae collected from the northern Gulf of Mexico from 2007 to 2010.



of both species were collected during each survey, and the percent frequency of *C. hippurus* ranged from 41.6% to 76.1% whereas occurrence of *C. equiselis* larvae was lower at 8.5% to 26.5% (Table 2). The overall mean density across the eight surveys for *C. hippurus* and *C. equiselis* ranged from 0.40 to 1.60 larvae 1000 m⁻³ and 0.02 to 0.20 larvae 1000 m⁻³, respectively. The mean density of larvae at stations where dolphinfish were present was 1.29 larvae 1000 m⁻³ (*C. hippurus*) and 0.66 larvae 1000 m⁻³ (*C. equiselis*). Although both species were present during both months in all years of this study, some temporal variability in abundance was observed. Peak density of

C. hippurus occurred in June 2007 (mean 1.06, max 20.99 larvae 1000 m⁻³), whereas the highest *C. equiselis* density occurred in July 2009 (mean 0.15, max 5.01 larvae 1000 m⁻³).

Dolphinfish larvae were collected throughout the extent of our sampling corridor and spatial variability in presence and abundance was observed for both species. Peak densities of *C. hippurus* larvae generally occurred in the eastern portion of our sampling corridor (Fig. 3). In contrast, *C. equiselis* larvae were more evenly distributed across the sampling corridor, although increased densities were observed south of 27°N and in areas affected by output from the Mississippi River.

Presence/absence model

The final presence/absence GAM for *C. hippurus* had an AIC of 693 with 11.6% of deviance explained (Table 3). Variables retained in the model included hours after sunrise, year, Sea Surface Temperature (SST), depth, *Sargassum* biomass, chlorophyll *a* concentration, feature classification, salinity and *C. equiselis* presence. All of these factors were significant except feature classification, *Sargassum* and salinity ($P > 0.05$). The most influential variables, which were significant variables whose removal from the model resulted in the largest Δ DE and/or Δ AIC, were hours after sunrise (Δ AIC = 16, Δ DE = 2.6%), SST

Table 2. Summary table of *Coryphaena hippurus* and *C. equiselis* larvae collected across eight surveys from 2007 to 2010 in the northern Gulf of Mexico. The number of stations sampled, total number of larvae collected, percent frequency (percent of stations in which larvae were found), overall larval density (number of larvae collected per 1000 m⁻³ of water sampled) and density at stations where larvae were present are shown.

Survey dates	# Stations	Species	# Larvae collected	% Frequency	Overall density	Density where present
6/20/2007–6/24/2007	59	<i>C. hippurus</i>	232	71.2%	1.60	2.24
		<i>C. equiselis</i>	6	8.5%	0.04	0.43
7/20/2007–7/24/2007	55	<i>C. hippurus</i>	61	50.9%	0.45	0.89
		<i>C. equiselis</i>	7	9.1%	0.02	0.43
6/9/2008–6/13/2008	72	<i>C. hippurus</i>	110	50.0%	0.60	1.20
		<i>C. equiselis</i>	30	22.2%	0.20	0.83
7/27/2008–8/1/2008	83	<i>C. hippurus</i>	91	53.0%	0.46	0.86
		<i>C. equiselis</i>	37	26.5%	0.15	0.68
6/3/2009–6/9/2009	92	<i>C. hippurus</i>	216	76.1%	1.02	1.34
		<i>C. equiselis</i>	29	22.8%	0.17	0.65
7/22/2009–7/29/2009	101	<i>C. hippurus</i>	150	41.6%	0.71	1.71
		<i>C. equiselis</i>	29	18.8%	0.15	0.75
6/15/2010–6/18/2010	48	<i>C. hippurus</i>	59	47.9%	0.40	0.83
		<i>C. equiselis</i>	8	10.4%	0.05	0.48
7/27/2010–7/30/2010	48	<i>C. hippurus</i>	69	66.7%	0.47	0.70
		<i>C. equiselis</i>	11	16.7%	0.09	0.44
Overall	558	<i>C. hippurus</i>	988	56.8%	0.73	1.29
		<i>C. equiselis</i>	157	18.1%	0.12	0.66

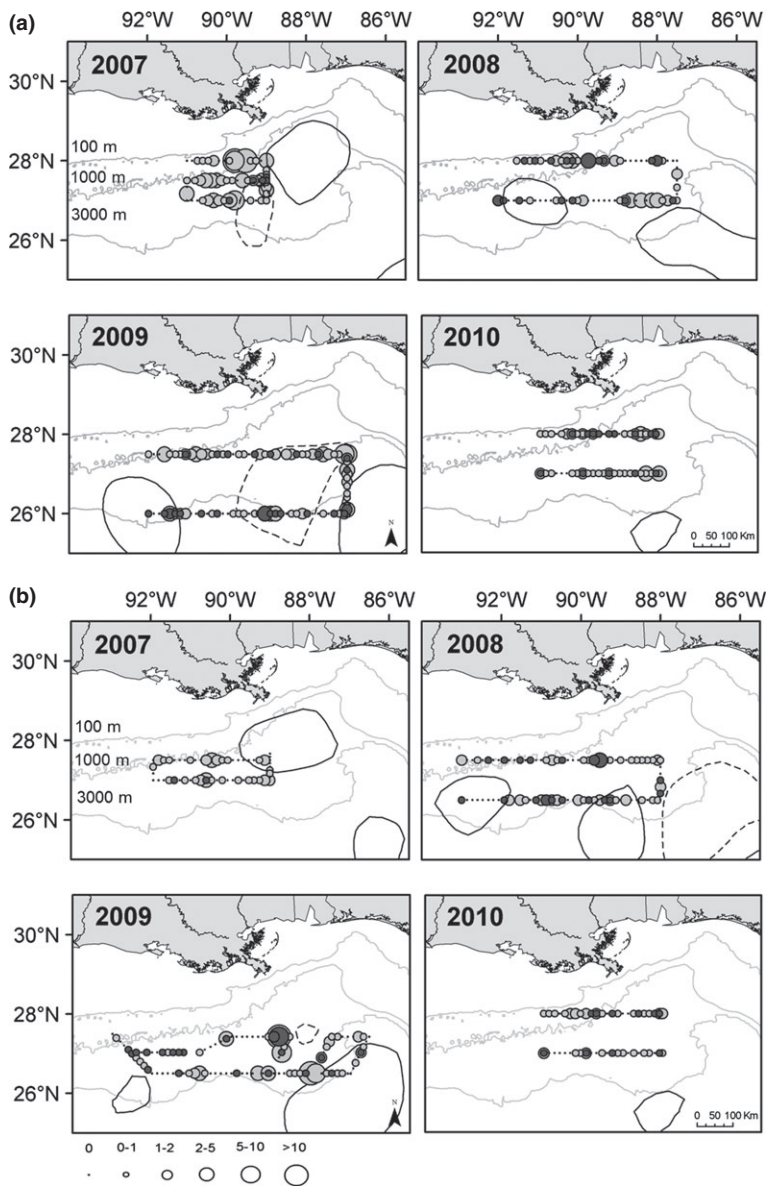


Figure 3. Map displaying the distribution and abundance of *Coryphaena hippurus* and *C. equiselis* larvae collected during (a) June and (b) July ichthyoplankton surveys in the northern Gulf of Mexico from 2007 to 2010. Bubble size is proportional to the density of larvae at each sampling location (measured in larvae 1000 m^{-3}), with light gray representing *C. hippurus* and dark gray representing *C. equiselis*. Solid contour lines delineate warm core features and dashed contour lines represent cold core features.

($\Delta\text{AIC} = 8$, $\Delta\text{DE} = 1.3\%$) and *C. equiselis* presence ($\Delta\text{AIC} = 7$, $\Delta\text{DE} = 1.2\%$). Presence of *C. hippurus* was highest in 2007 and lowest in 2008 surveys. Response plots revealed that occurrence of *C. hippurus* was higher > 8 h after sunrise, at depths > 2500 m, and at stations where *C. equiselis* larvae were present (Fig. 4). Additionally, GAMs showed a positive influence of SST $< 29^\circ\text{C}$ and chlorophyll *a* concentrations of $< 0.2\text{ mg m}^{-3}$ on *C. hippurus* presence. It should be noted that few sampling sites contained high chlorophyll *a* concentrations and variability of the additive effect in both models was high at those sites; thus, interpretation of chlorophyll *a* response plots should focus on concentrations $< 1.5\text{ mg m}^{-3}$.

Density model

The final density GAM for *C. hippurus* had a QAIC value of 324 and it explained 48.2% of deviance in abundance among stations where larvae were present (Table 3). The final model retained eight variables, including year, SST, SSHA, *Sargassum* biomass, chlorophyll *a*, salinity, hours after sunrise and *C. equiselis* density; all variables in the final model were significant. Analysis of ΔQAIC and ΔDE values revealed that *C. equiselis* density was one of the most influential parameters in this model ($\Delta\text{QAIC} = 2$, $\Delta\text{DE} = 13.9\%$), along with hours after sunrise ($\Delta\text{QAIC} = 2$, $\Delta\text{DE} = 13.8\%$) and salinity ($\Delta\text{QAIC} = 6$, ΔDE

Table 3. Retained variables, deviance explained (DE), and Akaike Information Criterion (AIC)/Quasi-Akaike Information Criterion (QAIC) for the final *Coryphaena hippurus* presence/absence and density generalized additive models. Δ DE, Δ AIC/ Δ QAIC and estimated *P*-values show the relative importance of individual variables in the model.

Model	Parameter	Δ AIC	Δ DE
Presence/absence Final AIC: 692.7 Final DE: 11.6%	Hours after sunrise**	15.7	2.6%
	Year*	3.1	1.2%
	SST*	8.0	1.3%
	Chlorophyll <i>a</i> *	5.8	1.8%
	Depth*	5.0	1.2%
	<i>Sargassum</i> biomass	4.2	0.6%
	Feature classification	14.6	2.6%
	Salinity	17.0	1.2%
	<i>C. equiselis</i> presence*	7.1	1.2%
Model	Parameter	Δ QAIC	Δ DE
Density Final QAIC: 324.3 Final DE: 48.2%	Hours after sunrise**	2.3	13.8%
	Year*	2.6	7.0%
	SST**	2.5	3.0%
	SSHA*	2.8	2.5%
	Chlorophyll <i>a</i> **	2.7	6.6%
	<i>Sargassum</i> biomass**	1.4	6.8%
	Salinity**	5.7	7.7%
	<i>C. equiselis</i> density**	1.9	13.9%

* $P < 0.05$, ** $P < 0.001$.

= 7.7%). Response plots showed that high salinities (> 36), high chlorophyll *a* concentrations ($> 0.2 \text{ mg m}^{-3}$), high SST ($> 31^\circ\text{C}$), and low SSHA (-10 to 5 cm) were associated with increased densities of *C. hippurus* (Fig. 5). Additionally, the few sites that contained high *C. equiselis* densities (> 2.5 larvae 1000 m^{-3}) had a strong positive influence on *C. hippurus* abundance. Conversely, *Sargassum* biomass had a negative influence on the density of *C. hippurus* larvae. GAM results also showed that densities of *C. hippurus* were highest in 2007 (overall mean: 1.04 larvae 1000 m^{-3}) and lowest in 2010 (0.40 larvae 1000 m^{-3}) surveys. Similar to the presence/absence model, high larval densities occurred later in the day ($> 10 \text{ h}$ after sunrise).

DISCUSSION

Larvae of both species were abundant and broadly distributed across our sampling area, suggesting that this region may be valuable spawning and/or nursery habitat of dolphinfishes. Both species were collected during all eight surveys from 2007 to 2010 with *C. hippurus* being more abundant and collected in more stations than *C. equiselis* in the northern Gulf, which is similar to findings from other ichthyoplankton surveys conducted in this region (Ditty *et al.*, 1994). Research on the abundance of dolphinfish

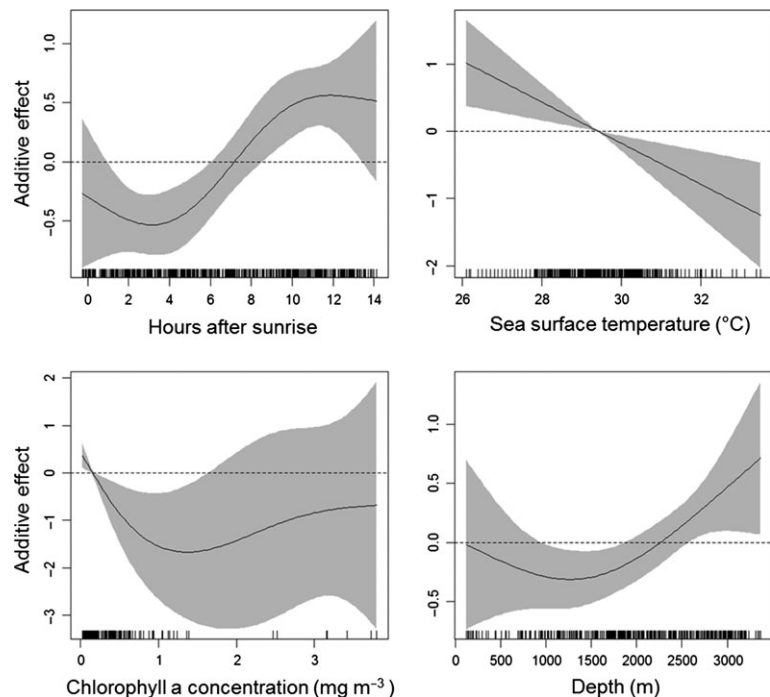
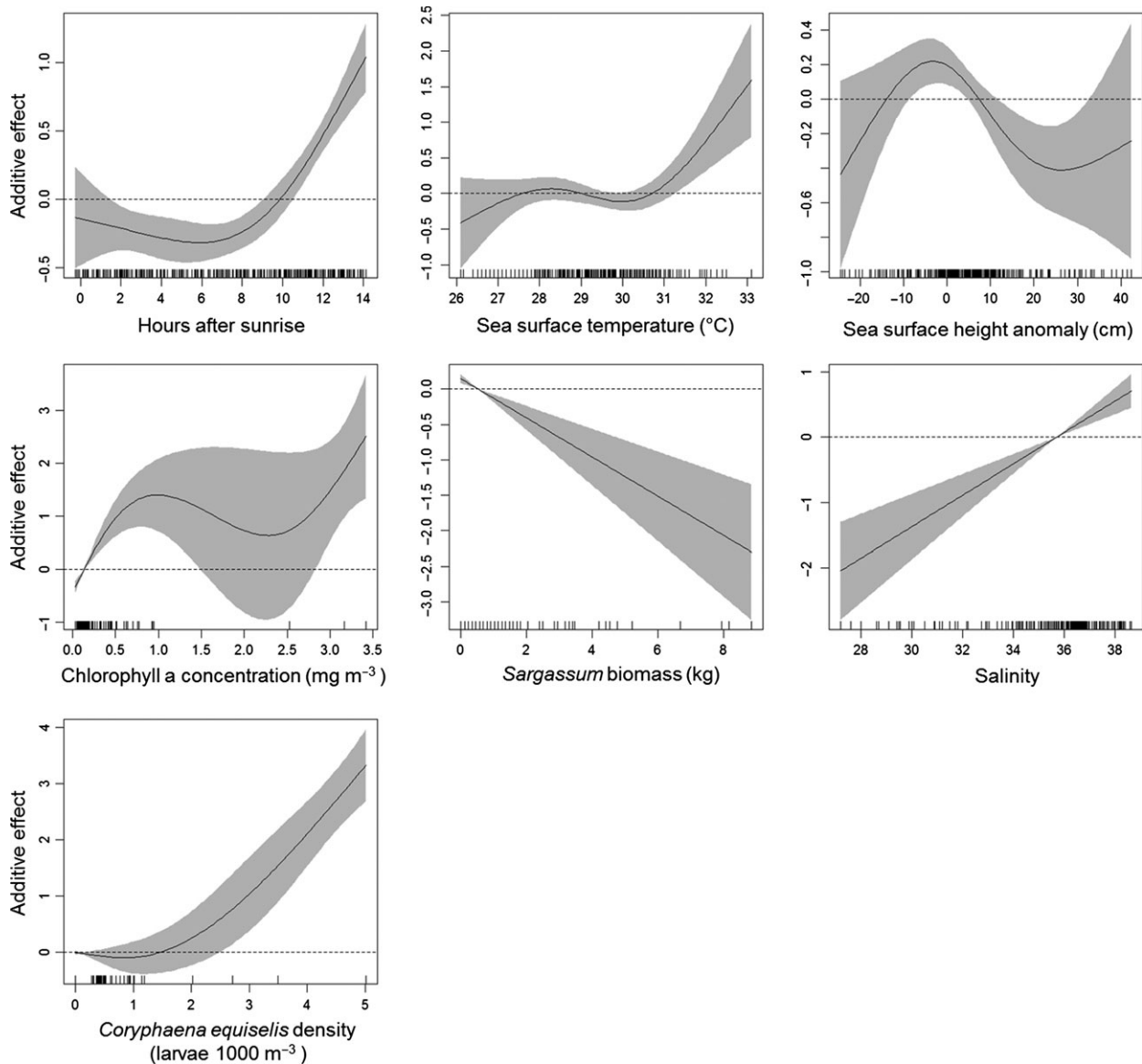


Figure 4. Smoothed response plots showing the effects of environmental variables on the presence or absence of *Coryphaena hippurus* larvae during the 2007–2010 surveys. The y -axis is the additive effect of each variable on *C. hippurus* presence, the tick marks along the x -axis show sampling intensity and the shaded areas represent 95% confidence intervals. All variables shown in this figure were retained in the final model and significant ($P < 0.05$).

Figure 5. Smoothed response plots showing the effects of environmental variables on *Coryphaena hippurus* density given presence during the 2007–2010 surveys. The y-axis is the additive effect of each variable on *C. hippurus* abundance, the tick marks along the x-axis show sampling intensity and the shaded areas represent 95% confidence intervals. All variables shown in this figure were retained in the final model and significant ($P < 0.05$).



larvae is limited and differences in the sampling protocols of other studies make it difficult to directly compare our larval catch numbers and densities. Regardless, we observed a higher frequency of occurrence of dolphinfish larvae (59% for *C. hippurus* and 17% for *C. equiselis*) than previously reported in the northern Gulf. Ditty *et al.* (1994) collected *C. hippurus* in only 11% and *C. equiselis* in 3% of sampling sites in June and July; however, lower catch rates may be due to the fact that summer sampling was

concentrated along the Mississippi Delta and in shelf waters affected by freshwater inflow. Additionally, the frequency of occurrence of *C. hippurus* in our study was high relative to larvae of other large pelagic fishes in the area collected during similar time periods, including bluefin tuna (21%), swordfish (17%), blue marlin (25%) and white marlin (5%) (Muhling *et al.*, 2010; Rooker *et al.*, 2012), revealing that this species is particularly widespread within this region of the northern Gulf. The northern Gulf is considered to be

important early life habitat of billfishes, tunas and swordfish. The mean densities of *C. hippurus* (ranging from 0.40 to 1.60 larvae 1000 m⁻³) were lower than that of blackfin tuna but comparable to sailfish and blue marlin (Simms *et al.*, 2010; Rooker *et al.*, 2012, 2013), whereas densities of *C. equiselis* (ranging from 0.02 to 0.20 larvae 1000 m⁻³) were comparable with swordfish and white marlin in the same region (Rooker *et al.*, 2012).

Significant inter-annual variation in dolphinfish catches from 2007 to 2010 was detected, whereas intra-annual differences (June versus July) were negligible. Year was an important variable in the presence/absence and density models with both models showing the highest *C. hippurus* abundances in 2007. The lowest observed densities for both species occurred in 2010 (annual mean: 0.40 *C. hippurus* larvae 1000 m⁻³ and 0.07 *C. equiselis* larvae 1000 m⁻³), but conditions were unique this year because oil from the Deepwater Horizon spill covered part of our sampling corridor. Although this gives some indication that the spill had a negative effect on the 2010 cohort, data from additional years after the spill are needed to account for inter-annual recruitment variability. Larval abundance may also be affected by temporal variability in the extent of frontal systems in the Gulf of Mexico, particularly the northern reach of the Loop Current, as this is thought to alter annual recruitment patterns of species associated with frontal features (Lamkin, 1997). Models did not detect any significant intra-annual variation and both *C. hippurus* and *C. equiselis* abundances were similar between months. Given that our sampling was limited to the months of June and July, the lack of a seasonal trend was not unexpected for either species. Ichthyoplankton surveys encompassing several seasons in the Gulf of Mexico were also unable to detect any significant seasonal variation in the abundance of *C. hippurus* or *C. equiselis* larvae (Ditty *et al.*, 1994) and *Coryphaena* spp. larvae were found to be present year-round in the Straits of Florida (Richardson *et al.*, 2010), which suggests that both species are protracted spawners.

Model results showed that both presence and density of *C. hippurus* larvae increased later in the day (close to sunset), indicating that larvae may migrate vertically in the water column. Vertical migratory behavior is common in marine fish and has been observed in the larval stages of several species (Leis, 2004; Llopiz and Cowen, 2008). The vertical distribution patterns of larvae are influenced by several factors, and similar to other species, *C. hippurus* larvae may have been responding to vertical differences in prey availability, predator avoidance, light intensity,

ultraviolet radiation, hydrostatic pressure, or turbulence (Munk *et al.*, 1989; Werner *et al.*, 2001; Browman, 2003; Huebert *et al.*, 2010). Additionally, larvae can control the distance and direction of horizontal dispersal by altering their vertical position in the water column (Fiksen *et al.*, 2007), and this type of behavioral response may therefore serve to facilitate transportation of *C. hippurus* larvae in water masses with vertically stratified current regimes. To date, information on the diel and vertical distribution patterns of dolphinfish larvae is limited and contradictory. Eldridge *et al.* (1977) observed significantly increased larval abundances of *C. hippurus* and *C. equiselis* at night during surface sampling, whereas Ditty *et al.* (1994) did not find a significant diel effect. Therefore, further investigation involving discrete depth sampling on a 24-h time scale is required to determine the degree of vertical movement by dolphinfish larvae. Additionally, a thorough understanding of vertical migratory behavior will allow for better interpretation of neuston net collections, as it is possible that the number of larvae collected from surface waters at a particular site could vary depending on the time of day during which sampling occurs.

Results indicate that the distribution of *C. hippurus* larvae in our 2007–2010 surveys was influenced by frontal zones and mesoscale eddies in the Gulf. Densities of *C. hippurus* were highest in areas with low or negative SSHA, suggesting that *C. hippurus* larvae were most abundant in cold core eddies (characterized by negative SSHA) or areas of confluence near eddy margins. In addition, model results revealed that feature class was an important predictor of larval presence. Lindo-Atichati *et al.* (2012) also found higher mean densities of *Coryphaena* spp. in cold core eddies in the northern Gulf, albeit densities were not significantly different across features. Frontal and eddy features are recognized as an important spawning habitat for many large pelagic fishes (Bakun, 2006), and the association between larval fish distribution and mesoscale oceanographic features has been widely documented (Richards, 1989; Richardson *et al.*, 2009; Rooker *et al.*, 2012). Frontal zones represent important nursery habitat because drifting animals and food particles accumulate along these areas of confluence, and therefore fish larvae have a greater probability of encountering prey in these regions (Bakun, 2006). Cold core features in the Gulf also represent important nursery grounds because cyclonic circulation causes upwelling of nutrient-rich waters from depth, resulting in enhanced primary productivity (Atkinson, 1985). In contrast, warm core features are zones of convergence where primary production levels and

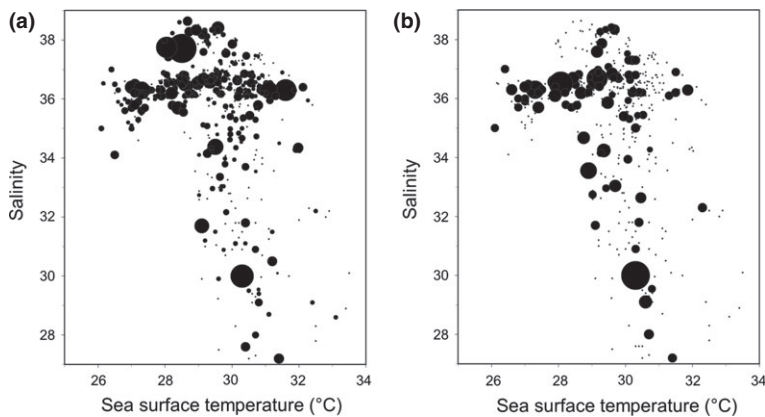


Figure 6. Temperature-salinity diagrams for all sites sampled from 2007 to 2010. Densities of (a) *Coryphaena hippurus* and (b) *C. equiselis* larvae (represented by bubble size) are shown here in relation to sea surface temperature and salinity data from each station, and small circles show temperature and salinity at sites where densities = 0 larvae 1000 m⁻³. Plots were developed using OCEAN DATA VIEW software (Schlitzer, 2012).

zooplankton biomass are depleted down to 100 m (Biggs, 1992), which is likely one of the reasons that abundance of *C. hippurus* larvae was lowest in this feature. While *C. hippurus* presence was highest in areas of low chlorophyll *a* concentrations, density was positively associated with increased chlorophyll *a* levels, potentially indicating that while *C. hippurus* catches are higher in offshore waters than enriched coastal regions, areas of enhanced food availability (e.g., in fronts and cold-core eddies) support increased larval densities within the sites where *C. hippurus* occur.

Spatial variability in the abundance of *C. hippurus* larvae was also associated with water temperature and salinity (Fig. 6). Temperature is a dominant environmental factor controlling growth and survival of fish larvae (Pepin, 1991), and SST was a significant factor in our presence/absence model for *C. hippurus*, with lower temperatures having a positive association with larval abundance. Eldridge *et al.* (1977) also found a significant negative relationship between SST and both *C. hippurus* and *C. equiselis* larval abundance. The density model showed a different trend, with high temperatures positively associated with larval abundance; however, this relationship was primarily driven by just a few instances of high abundance (up to 12 larvae 1000 m⁻³) in July 2009 at sites sampled within 2 h prior to sunset in the frontal zone near the periphery of the Loop Current. Regardless, the majority of *C. hippurus* larvae were collected in waters < 29 °C (Fig. 6), and these temperatures are typically observed in cold-core features in the Gulf of Mexico. Increased catches of *C. hippurus* occurred in waters with higher salinities; GAM results indicated that the density of *C. hippurus* larvae in our 2007–2010 surveys was positively associated with salinities > 36. Similarly, Ditty *et al.* (1994) reported that the majority of dolphinfish larvae collected in their Gulf surveys were at locations with lower SST and higher salinities, which are characteristics of offshore water masses in this region

during the summer. Thus, the relative abundance of *C. hippurus* larvae in the Gulf appears to be higher in offshore water masses and cold-core features outside the influence of coastal processes such as freshwater inflow from the Mississippi River.

The distribution and abundance of *C. hippurus* larvae was also significantly linked to biotic factors, including congener abundance and *Sargassum* biomass. Both presence and density of *C. hippurus* larvae were positively associated with the abundance of *C. equiselis* larvae, suggesting that these species use similar habitats. Adults of both species are known to occasionally school together (Beardsley, 1964), and thus it is possible that adults spawn in the same regions. We also observed a negative association between density of *C. hippurus* larvae and *Sargassum* biomass, and this finding is consistent with model results of blue marlin, white marlin and swordfish larvae collected in the same region (Rooker *et al.*, 2012). *Sargassum* is a floating brown alga commonly found throughout the Gulf that functions as valuable nursery habitat for several species of pelagic fishes (Wells and Rooker, 2004). However, *Sargassum* also tends to form large mat structures that attract many small fishes and invertebrates, possibly resulting in higher predation on fish larvae relative to open ocean habitats (Rooker *et al.*, 2012). The pigmentation of juvenile *C. hippurus* suggests that an association with *Sargassum* exists, with dark vertical bands on a yellow/orange background providing camouflage for the new recruits (Castro *et al.*, 2002). These bands are not present in small *C. hippurus* larvae (< 8 mm), and thus there appears to be an ontogenetic shift to *Sargassum* mats during the early juvenile period. MANOVA results indicated that significant differences exist between size classes of *C. hippurus* larvae in relation to *Sargassum* biomass, with highest densities of small larvae occurring at sites with no or small (< 2 kg) amounts of *Sargassum*, possibly because of the increased risk of predation-mediated mortality on

recently-hatched larvae near *Sargassum* mats. In contrast, larger *C. hippurus* were found in greatest abundance at sites with more than 6 kg of *Sargassum*; therefore, *Sargassum* does not appear to be essential habitat of *C. hippurus* during the larval stage but may provide valuable nursery habitat for juveniles.

Results of this study provide evidence that the northern Gulf may function as valuable spawning and/or nursery habitat of dolphinfishes. Additionally, model results clearly indicate that several physico-chemical and biological parameters influence the spatial distribution of *C. hippurus* larvae. In particular, peak abundances of *C. hippurus* larvae in this region appear to be associated with cold core eddies and fronts, suggesting that these features likely represent productive early life habitat of this species. Although the remaining unexplained variability in the models limits their predictive capabilities, GAMs developed in this study reveal important habitat associations of *C. hippurus* larvae which can be used to better understand recruitment variability of this species in the Gulf.

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