Descriptive density models of scyphozoan jellyfish in the northern Gulf of Mexico

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ABSTRACT: Jellyfish play an important role in the food web of many coastal environments but are generally considered a nuisance to scientific fieldwork and industrial and economic trades. A better understanding of how jellyfish densities and distributions are affected by environmental parameters could elucidate population trends and provide assistance in ecological research and undesirable human interactions. In this study, abundance data for scyphozoan medusae, *Chrysaora* sp. and *Aurelia* spp., were extracted from Southeast Area Monitoring and Assessment Program trawling surveys for the northern Gulf of Mexico (nGoM) during the summer and fall months. Both *in situ* and satellite oceanographic measurements were obtained to coincide with the jellyfish data from 2003 to 2013. Data were separated into gulfwide seasonal models and regional (east, west) seasonal models. A generalized additive model was created for 3 methods (remote sensing, *in situ*, and all parameters) for all models. The regional models were more precise in replicating the observed data, and the all-parameter method produced the best-fit models. The oceanographic variables that were determined to be most descriptive for the nGoM were salinity, surface currents, temperature, chl *a* concentrations, and distance from shore. Understanding the dynamic relationship between jellyfish densities and oceanographic features in the nGoM is one step closer to better management of these species and the overall ecosystem.

KEY WORDS: Jellyfish · Descriptive model · Gulf of Mexico · GAM · Oceanographic measurements

INTRODUCTION

Jellyfish (cnidarian medusozoans) have existed in the world's oceans for approximately 500 million years (Cartwright et al. 2007), but only recently have they been studied for their involvement and importance to the structure and health of an ecosystem. As planktonic organisms, most horizontal movements are controlled by the flow of ocean currents; however, jellyfish are motile organisms that have the ability to perform directional movements with muscular contractions allowing them to migrate throughout the water column in search of prey (Hays et al. 2008, 2012). Jellyfish are primarily carnivorous, feeding on a diverse range of prey from protists to fish larvae, which enables them to live in a variety of environments (Richardson et al. 2009). Previous experimental and observational work has shown that the occurrence and distribution of jellyfish can be affected by water temperature, salinity, and dissolved oxygen as well as ocean currents, fronts, or other discontinuities such as thermoclines and pycnoclines (Decker et al. 2007, McClatchie et al. 2012, Purcell 2012, Lucas et al. 2014, Luo et al. 2014, Greer et al. 2015). Biological factors, such as primary production and zooplankton biomass (as food abundance), are also important for jellyfish development, growth, and reproduction (Purcell 2012, Lucas et al. 2014). Addressing the coupling of oceanographic features with the density distribution of jellyfish spe-

cies is necessary to describe their population dynamics and investigate favorable and detrimental interactions within the environment.

Jellyfish data are limited and inconsistent in most regions of the world (Brotz et al. 2012). The study and quantification of jellyfish is difficult because of their fragile bodies and high water content (Hamner et al. 1975, Remsen et al. 2004, Doyle et al. 2007). A few regions have time series data on jellyfish populations (Condon et al. 2013) where larger ecological questions are being addressed (Uye & Ueta 2004, Decker et al. 2014, Milisenda et al. 2014, Quiñones et al. 2015, Robinson et al. 2015). Continued monitoring and investigations on jellyfish are crucial to managing the health of the ocean's ecosystems (Richardson et al. 2009, Purcell 2011, Brodeur et al. 2016).

Most studies that address ecological interactions with jellyfish use remotely sensed surface chl *a* concentrations as a proxy for the presence of jellyfish (Hays et al. 2006, Fossette et al. 2010, Bailey et al. 2012); however, the surface signal of chl *a* may not always be valid. For example, trophic interactions with zooplankton may suppress the chl *a* signal in the location of the jellyfish, or a phytoplankton bloom may not overlap in time and space with zooplankton (Mackas & Boyd 1979, Lucas et al. 2012). Although no proxy is ideal, satellite-derived chl *a* concentrations only measure surface concentrations; however, phytoplankton blooms can occur subsurface out of the range of satellite instrumentation (Gould & Wiesenburg 1990, Richardson et al. 2000, Perry et al. 2008). Although remote sensing-based observations are widespread and easily accessible, they have limitations; therefore, a more comprehensive environmental approach that combines satellite and *in situ* data may produce a better representation of jellyfish distribution patterns.

Biophysical models that incorporate multiple parameters can provide a better prediction of the location and density of jellyfish where observational data are lacking. Several biophysical models have been developed to address the movement and abundance of jellyfish in terms of regime shifts and climate oscillations (Brodeur et al. 2008, Decker 2010). Decker et al. (2007) produced a jellyfish predictive model for the Atlantic sea nettle *Chrysaora quinquecirrha* based on temperature and salinity in Chesapeake Bay that is available on NOAA's National Weather Service Ocean Prediction Center website and was later included in the Chesapeake Bay Ecological Prediction System, which forecasts physical, biogeochemical, and organismal data (Brown et al. 2013). To date, a jellyfish biophysical model has not been developed for the Gulf of Mexico (GoM), possibly due to its large extent and dynamic ecosystems (Robbins et al. 2009, Salmerón-García et al. 2011).

In the northern Gulf of Mexico (nGoM), there is a distinct environmental shift around Mobile Bay, AL, and the submarine Desoto Canyon. In this area, the continental shelf shortens and the reach of the Mississippi River plume is lessened (Morey et al. 2003). From this point westward, the coastline contains many estuaries, marshes, and barrier islands and is dominated by riverine input. The consistent input of freshwater leads to a dynamic state of mixing water masses (Morey et al. 2003, Zavala-Hidalgo et al. 2003). Here the waters are turbid from the high amount of suspended particulate matter deposited from the Mississippi River system (Huh et al. 2001). The nutrient input from the Mississippi River supports high productivity, and its reach changes seasonally based on the prevailing winds and currents (Morey et al. 2003). Salmerón-García et al. (2011) showed distinct differences in the chl *a* concentrations between regions dominated by Mississippi River discharge and the eastern region in the nGoM in space and time. East of the Mobile Bay/Desoto Canyon divide, herein referred to as the eastern nGoM, the shelf is large and shallow and is influenced by the prevailing winds and the Loop Current circulation (Robbins et al. 2009). The nutrient levels are more oligotrophic compared to the western region. Seasonal changes that occur in the physical environment (e.g. temperature, salinity) also have an impact on the occurrence and distribution of jellyfish species. In the nGoM, the prevalent large medusae are *C. quinquecirrha* (sea nettle; herein referred to as *Chrysaora*) in the summer months and *Aurelia* spp. (moon jellyfish; herein referred to as *Aurelia*) in the fall (Graham 2001, Robinson & Graham 2013).

Due to the differing environmental conditions spatially and seasonally, and the importance of expanding the ecological knowledge of jellyfish in the productive waters of the nGoM, this study assessed density data for 2 jellyfish genera (*Chrysaora* and *Aurelia*) during the summer and fall seasons to determine the environmental parameters that can be used to model their distribution patterns within the nGoM. This investigation used multiple oceanographic datasets to determine how their changes affect jellyfish densities and to compare the descriptive power of satellite measurements versus *in situ* measurements. Knowledge of jellyfish densities can assist in management of the many anthropogenic interactions that occur in the nGoM.

METHODS

Data

Jellyfish data were assembled for the scyphozoan medusae, *Chrysaora* and *Aurelia,* collected during the groundfish survey cruises of the Southeast Area Monitoring and Assessment Program (SEAMAP) from 2003 to 2013 (Stunz et al. 1985). Data for the west coast of Florida began in 2008. Individual trawl specimen counts were converted to density measurements using the water column trawl depth and volume filtered to determine jellyfish density (ind. m^{-2}; Robinson & Graham 2013). The oceanographic *in situ* data collected concurrently with the groundfish trawls were also obtained from the SEAMAP database. Remote sensing data were gathered from NASA's OceanColor Web (oceancolor.gsfc.nasa.gov; MODIS-Aqua, L3, 4 km resolution, 8 d), the Physical Oceanography Distributed Active Archive Center (PO.DAAC; podaac.jpl.nasa.gov; OSCAR, L4, 1°), and the European Union's Copernicus Marine Environment Monitoring Service (CMEMS; marine.copernicus.eu; delayed time, global, allsat). The Open-source Project for a Network Data Access Protocol software framework (www.opendap.org) was used to acquire the data from the satellite databases mentioned. Due to the varying resolution scale of the satellite data obtained, the spatiotemporal satellite grid that contained the specific time and coordinates of the jellyfish collection was used. A variance inflation factor analysis was used to test for collinearity and eliminate any redundant variables. The only variables found to be correlated were the *in situ* environmental parameters measured at different depths (e.g. surface, mid-depth, and maximum-depth temperatures), but they were retained in the pool of variables to be used independent of each other to discern if different sections of the water column were more descriptive to the distribution of jellyfish and to help evaluate the comparison between the remote sensing and *in situ* models. To correct for the extreme skewness of certain data (Shapiro-Wilks and Kolmogorov-Smirnov tests), log(n + 1) transformations were applied to several environmental parameters (chl *a* concentrations, light attenuation, normalized fluorescent line height [standard measurement to discern living organisms from detritus; Gower & Borstad 1981], and distance from shore) as well as the response variable (jellyfish density). The jellyfish density calculated here differs from basic count data and had a high amount of variance. Therefore, a log transformation was applied to reduce the influence of outliers on the model fit. Not transforming the response variable can lead to adjusted R^2 values that are nonsensical. The complete list of oceanographic variables and their abbreviations are given in Table 1.

All data were sorted by month into 2 time windows, summer (June and July) and fall (October and November), due to the operation of the SEAMAP cruises. Using ArcGIS (v. 10.3; Esri), the jellyfish combined densities (herein referred to as the observed data) were mapped to a 25 × 25 km fishnet grid, and all oceanographic variables were averaged to within the grid cells. This grid size was chosen to correct for the inconsistent catch effort across the northern gulf yet still retain detailed local distributions. Jellyfish species data were included as a binary presence/absence variable for each grid cell. Two gulfwide seasonal models (summer and fall) were constructed that incorporated the entire continental United States coastline in the GoM. The data were then separated into the west region and east region at longitude 87.9° W, roughly Mobile Bay, AL, to account for the environmental shift across the nGoM. This separation led to the development of 4 distinct regional models: summer west (SumW), summer east (SumE), fall west (FallW), and fall east (FallE).

Model development

All of the following model development steps were completed independently for each of the 6 models described in the previous paragraph and were implemented in R (v. 3.2.4 revised; R Core Team 2016). The oceanographic variables were pre-screened for predictive power by calculating the information value (IV; Larsen 2016) utilizing the R package 'Information' (Larsen 2016). Briefly, the IV tests the univariate strength of the variable by calculating the weighted sum of all the weight of evidence (log odds + log density ratio) for each predictive variable. A negative IV result eliminated the variable from the analysis. The remaining predictive oceanographic variables were divided based on the collection method, remotely sensed (RS) or *in situ* (IS), and a third method which included both the RS and IS descriptive variables to produce an all-parameter (AP) method.

A generalized additive model (GAM; Hastie & Tibshirani 1990) was applied to describe the relationship between the oceanographic variables and the log density of jellyfish by using the R package 'mgcv' (Wood 2011). A GAM analysis is a nonparametric regression where cross-validation is included in the

Table 1. Description of all variables used in the generalized additive models, separated by collection method (remote sensing and *in situ*)

Variable name	Abbreviation	Unit
Remote sensing variables		
Chl *a* concentration	chlor_a	mg m^{-3}
Sea surface temperature	sst	°C
Colored dissolved organic matter	cdom	m^{-1}
Diffuse attenuation coefficient (@490 nm)	Kd	m^{-1}
Photosynthetically available radiation	par	E m^{-2} d^{-1}
Normalized fluorescence line height	nflh	mW cm^{-2} μm^{-1} sr^{-1}
Sea level height anomaly (positive, negative)	sla_pos, sla_neg	cm
Surface current velocities (zonal, meridional)	zonal, meridional	cm s^{-1}
Surface speed	surfspeed	cm s^{-1}
Eddy kinetic energy (positive, negative)	eke_pos, eke_neg	cm^2 s^{-2}
Distance from shore	shoredist	m
Sea surface temperature horizontal gradient	gsst	°C per degrees (north/west)
In situ variables		
Water temperature (surface, mid-depth, max-depth, and vertical gradient)	TEMPSURF, TEMPMID, TEMPMAX, VGTEMP	°C
Salinity (surface, mid-depth, max-depth, and vertical gradient)	SALSURF, SALMID, SALMAX, VGSAL	ppt
Oxygen (surface, mid-depth, max-depth, and vertical gradient)	OXYSURF, OXYMID, OXYMAX, VGOXY	ppm
Chl *a* (surface, mid-depth, max-depth, and vertical gradient)	CHLSURF, CHLMID, CHLMAX, VGCHL	mg m^{-3}
Turbidity (surface, mid-depth, max-depth, and vertical gradient)	TURBSURF, TURBMID, TURBMAX, VGTURB	Percentage (%)
Maximum water depth	DEPTHMAX	m

model selection and the functional relationships are determined by the data via smoothing. The restricted maximum likelihood (REML) optimizing method was used along with a thin plate regression spline and a Tweedie distribution. Forward selection was used to retain any descriptive variables that improved model performance (increased the deviance explained or decreased the REML value; Table S1 in the Supplement at www.int-res.com/articles/suppl/m591p071_supp. pdf). Descriptive variables were determined for each genera of jellyfish using a variable coefficient model (Hastie & Tibshirani 1990), which is commonly used in ecological studies to account for heterogeneity in species abundance (Zuur et al. 2009). Variable interactions [$f(x,y)$] were tested to further optimize the model fit and, finally, the best-fit GAM was chosen by the lowest Akaike's information criterion value. An RS, IS, and AP GAM was constructed for each model.

To test the descriptive power, each model was run for 500 iterations each time using a randomly selected 80% of the data to train the model, which described the remaining 20%. The selection of 500 iterations was based on the time to stability and an adequate predicted output for each grid cell. Any model density output greater than 50 log ind. m^{-2}

was flagged as an infinity value and removed from the analysis. The resulting density predictions, deviance explained (DE), R^2 values, estimated degrees of freedom (EDF), and residual sum of squares (RSS) were averaged and reported for each method to express the fit of each descriptive model. The overall average density and standard error of each model were calculated to compare the magnitude of the density provided by the models to the magnitude of the observed data. The descriptive models were mapped using the average predicted GAM log density from the 500 iterations. The jellyfish log density color scale was segmented in 0.25 ind. m^{-2} intervals with the initial segment between 0 and 0.0001, representing a value less than 1 jellyfish. Missing grid cells represent a location where data were missing and no density was calculated.

RESULTS

The general trend from the observed data shows a higher average density of jellyfish in the fall (0.58 ± 0.04 log ind. m^{-2}) compared to the summer (0.16 ± 0.01 log ind. m^{-2}) (Fig. 1). In both seasons, the abundance was greater closer to the shoreline and most

dense patches appear adjacent to freshwater inputs (Fig. 1). The regional division applied to the nGoM shows a difference in jellyfish density between the west and east region. The average regional densities for the summer were 0.26 ± 0.02 log ind. m^{-2} for the west and 0.03 ± 0.01 log ind. m^{-2} for the east, and the fall regional densities were 0.52 ± 0.04 log ind. m^{-2} for the west and 0.67 ± 0.07 log ind. m^{-2} for the east. In summer, the presence of *Chrysaora* (n = 127) was concentrated in the western region of the nGoM (Fig. 2A). The total presence of *Aurelia* (n = 136) in the summer was lower compared to *Chrysaora* in the west but was more abundant in the east (Fig. 2A). Less abundant in the fall season, *Chrysaora* (n = 93) were distributed throughout the nGoM but were clustered along the shoreline. *Aurelia* presence was dominant over the entire nGoM shelf during the fall (n = 268; Fig. 2B). The overall highly variable densities reported reflect the patchy distribution of jellyfish.

Gulfwide seasonal models had a lower descriptive fit than the regional models (Table S2 in the Supplement). These models were unable to predict any zero-density grid cells and underestimated the high-density grid cells seen in the observed data. The summer gulfwide model produced a nearly homogeneous distribution east of Louisiana (Fig. S1 in the Supplement), and the fall model used variables (Table S3 in the Supplement) that were descriptive in the western half of the nGoM and left a large number of missing grid cells in the eastern half (Fig. S2). These results support the notion that the high abundance of jellyfish in the west was driving the descriptive power of the models. This abundance difference seen in the observed density between the east and the west regions supports the application of regional models versus a gulfwide model. Therefore, because the gulfwide seasonal models pro-
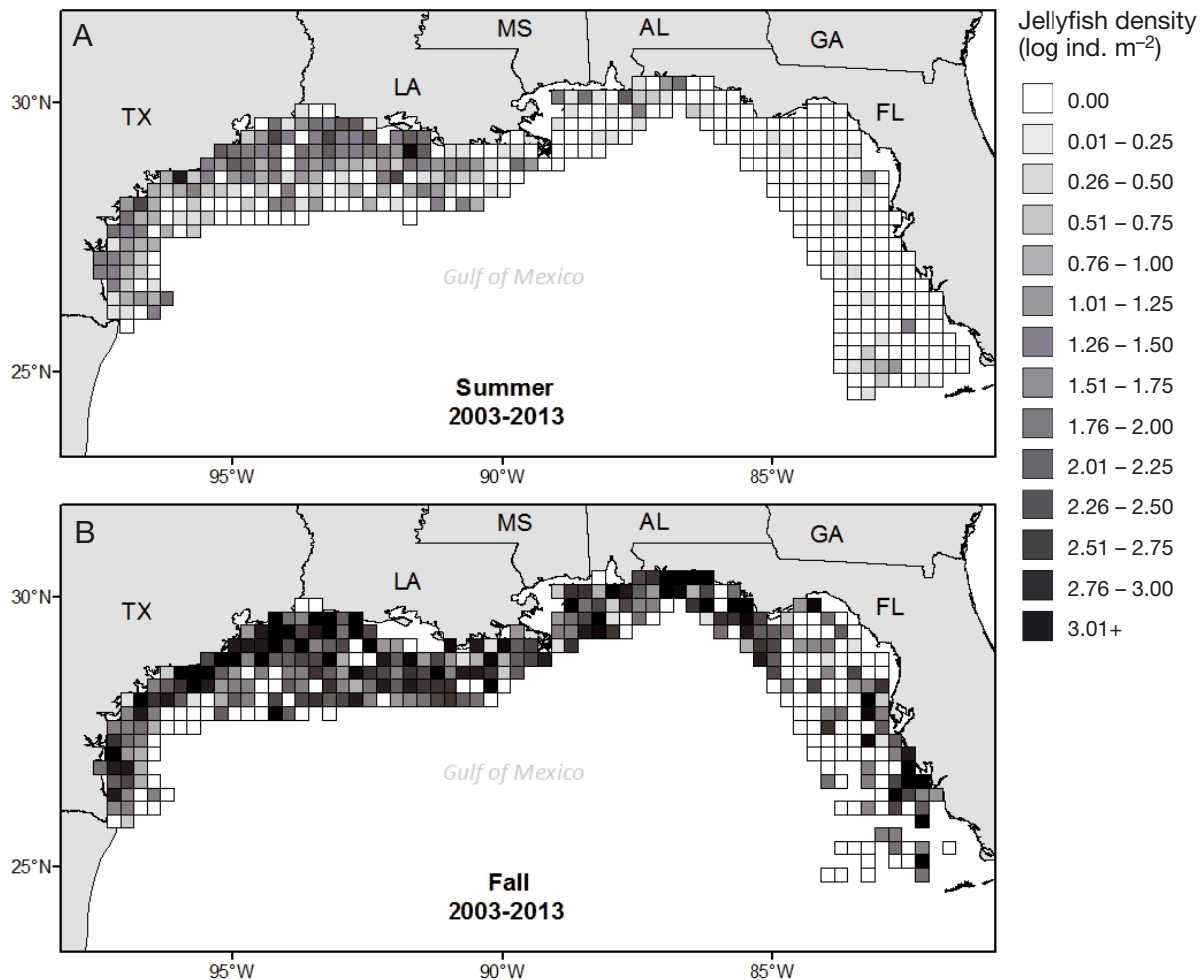

Fig. 1. Combined jellyfish densities (*Chrysaora* and *Aurelia*) from the Southeast Area Monitoring and Assessment Program survey database (averaged in 25 × 25 km grid) for (A) summer and (B) fall in the northern Gulf of Mexico
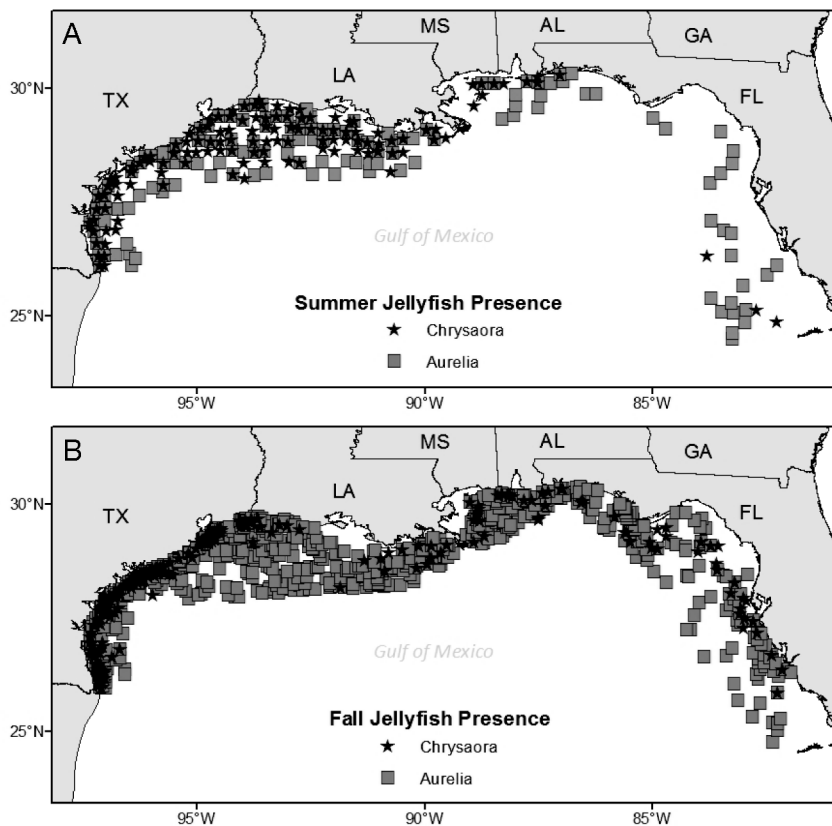
Fig. 2. Location of sampling presence for *Chrysaora* and *Aurelia* jellyfish between 2003 and 2013 during (A) summer and (B) fall

Descriptive variables

No single variable was found to be descriptive in every regional model; however, relationships with certain oceanographic features were apparent. A measurement of salinity was included in every model, and chl *a* concentration, surface currents, temperature, and distance from the shoreline were components in 3 of the 4 models (Table 2). Even though the specific variable changed (i.e. mid-depth salinity vs. vertical salinity gradient), the continuous presence of a feature was taken to show its importance to the distribution and abundance of jellyfish in the nGoM. All *in situ* variables found to be descriptive were measurements taken at depth (mid or maximum), with the exception of surface turbidity in the SumW model. Between the 2 jellyfish genera, distance to shore was exclusively used and chl *a* concentrations were dominant when describing *Aurelia* distributions. More variables were also required to describe the distribution of *Aurelia* compared to *Chrysaora* (Table 2).

duce results that were less descriptive than the regional models, they were excluded from the subsequent analysis.

Dynamic relationships were observed between the jellyfish density and the descriptive oceanographic variables (Fig. 3). Jellyfish density increased with

Table 2. Variables selected by the generalized additive models to describe the density distribution of jellyfish, separated by region, method (RS: remote sensing; IS: *in situ*; AP: all-parameter), and genera of jellyfish. () indicates interaction used between variables. * indicates smoother not factored by a genera of jellyfish. Variables defined in Table 1

	Aurelia	*Chrysaora*
Summer west		
RS	chlor_a, zonal*	eke_pos, chlor_a
IS	TEMPMAX, CHLMAX, SALMID	TEMPMAX, TURBSURF*
AP	chlor_a, zonal*, TEMPMAX, CHLMAX, SALMID	eke_pos, chlor_a, TEMPMAX, TURBSURF*
Summer east		
RS	zonal, shoredist, cdom,	zonal, cdom
IS	CHLMAX, SALMAX, DEPTHMAX	DEPTHMAX
AP	zonal, shoredist, cdom, CHLMAX, SALMAX	cdom, DEPTHMAX
Fall west		
RS	chlor_a, cdom, shoredist, sla_pos	par
IS	DEPTHMAX, CHLMID, SALMAX, OXYMID	VGOXY, TEMPMAX
AP	(chlor_a, CHLMID), cdom, shoredist, sla_pos, DEPTHMAX	TEMPMAX
Fall east		
RS	sst, shoredist, (zonal, eke_pos)	(zonal, eke_pos)
IS	VGSAL, TEMPMID	VGSAL
AP	sst, shoredist, TEMPMID	(zonal, eke_pos), VGSAL

salinity and steeper vertical salinity gradient. Zonal surface currents associated a higher density of jellyfish with westward currents. In the eastern region, distance from shore had a negative trend with the density of *Aurelia*; however, the west had an oscillating trend across the shelf. In the SumE model, the DEPTHMAX variable followed the same trend as the distance from shore for *Aurelia* but had a hump-shaped trend for *Chrysaora* with a peak in density around 50 m deep. Temperature had a positive effect on *Chrysaora* densities, suggesting their density increases with higher temperatures. The reverse occurred with temperature and the density of *Aurelia*. Chl *a* concentrations had a varying effect in the different regions as well as whether remotely sensed or measured *in situ*. Other relationships revealed included a positive trend with eke_pos for both species and a positive trend for *Aurelia* with sla_pos, suggesting mesoscale eddies are important for aggregated jellyfish in the nGoM (Fig. 3).

Model fitness

The AP method provided the best fit for each model, shown in the output values of average DE and adjusted R^2 (Table 3). The AP method used more independent variables than the RS and IS methods (ranged from 6 to 9) and therefore had a higher average EDF. In the fall, the AP method resulted in the

Table 3. Generalized additive model output results (mean ± SE) for deviance explained (DE), adjusted R^2, estimated degrees of freedom (EDF), and residual sum of squares (RSS) from 500 iterations of remote sensing (RS), *in situ* (IS), and all-parameter (AP) methods

	DE	R^2	EDF	RSS
Summer west				
RS	60.4 ± 0.12	0.54 ± 0.002	8.6 ± 0.04	3.4 ± 0.12
IS	65.6 ± 0.11	0.59 ± 0.001	10.7 ± 0.03	2.4 ± 0.18
AP	73.2 ± 0.12	0.75 ± 0.002	13.8 ± 0.07	6.1 ± 0.96
Summer east				
RS	92.7 ± 0.08	0.79 ± 0.004	6.7 ± 0.07	3.5 ± 1.3
IS	91.8 ± 0.07	0.71 ± 0.004	6.5 ± 0.05	5.3 ± 2.6
AP	96.6 ± 0.06	0.94 ± 0.002	9.5 ± 0.09	18.0 ± 5.8
Fall west				
RS	82.3 ± 0.11	0.58 ± 0.002	10.4 ± 0.04	7.9 ± 0.15
IS	82.4 ± 0.13	0.54 ± 0.002	12.1 ± 0.05	7.6 ± 0.19
AP	82.4 ± 0.09	0.67 ± 0.003	18.5 ± 0.08	6.7 ± 0.19
Fall east				
RS	70.3 ± 0.14	0.63 ± 0.002	5.2 ± 0.03	12.9 ± 0.20
IS	72.2 ± 0.13	0.63 ± 0.001	6.0 ± 0.03	13.8 ± 0.22
AP	76.8 ± 0.13	0.75 ± 0.001	7.2 ± 0.03	10.6 ± 0.19

lowest RSS, which expresses a better precision between the observed and predicted jellyfish densities. The higher RSS observed in the summer models, especially SumE, was most likely due to the limited number of non-zero data grid cells, which caused some iterations to be trained with or describe only all-zero grid cells. The IS method described the jellyfish densities slightly better in 4 of the 6 models and was within 1% DE of the RS method in the remaining 2 models (Table 3). However, no distinct trend was observed in the differences of the fit between regional or seasonal IS and RS methods. All models underestimated the observed extreme high densities and slightly overestimated the density of jellyfish in true zero-density grid cells (Figs. 4 & 5).

The regional models produced well-fit descriptions of the observed data based on the DE (73 to 96% for the AP method) and adjusted R^2 (0.67 to 0.94 for the AP method) (Table 3). The east models performed well in replicating the extreme variation of densities and describing the hotspots of high jellyfish density. The west models were adequate in describing zero-density grid cells but were unable to match the magnitude of high-density areas (Figs. 4 & 5). With a more evenly distributed density, the models had significantly different variances (*F*-test, $p < 0.05$) than the observed data, except in the SumW RS and AP models. Overall, the models produced significantly similar medians of density (Kruskal-Wallis test, $p < 0.05$) but lower total density for the regions, with the exception of SumE where a greater density was described due to the overestimation of the zero grid cells. Although models underestimated the magnitude of the observed high densities, they were able to describe the similar distribution trends within the regions (Fig. 6). The use of the consistent density scale, described in 'Methods', to visualize the data restricts the visualization of the trends in the model outputs because of their lower densities. Therefore, as an example, the model output densities for the fall AP method were scaled to the minimum and maximum densities reported, making the distribution trends visually apparent (Fig. 7).

DISCUSSION

The regional models determined that the most descriptive factors for describing the distribution of jellyfish in the nGoM were salinity, surface currents, temperature, chl *a* concentration, and distance from shore. Similar variables were used to describe the 2 jellyfish genera within each region (Table 2). The models were able to reproduce the distribution
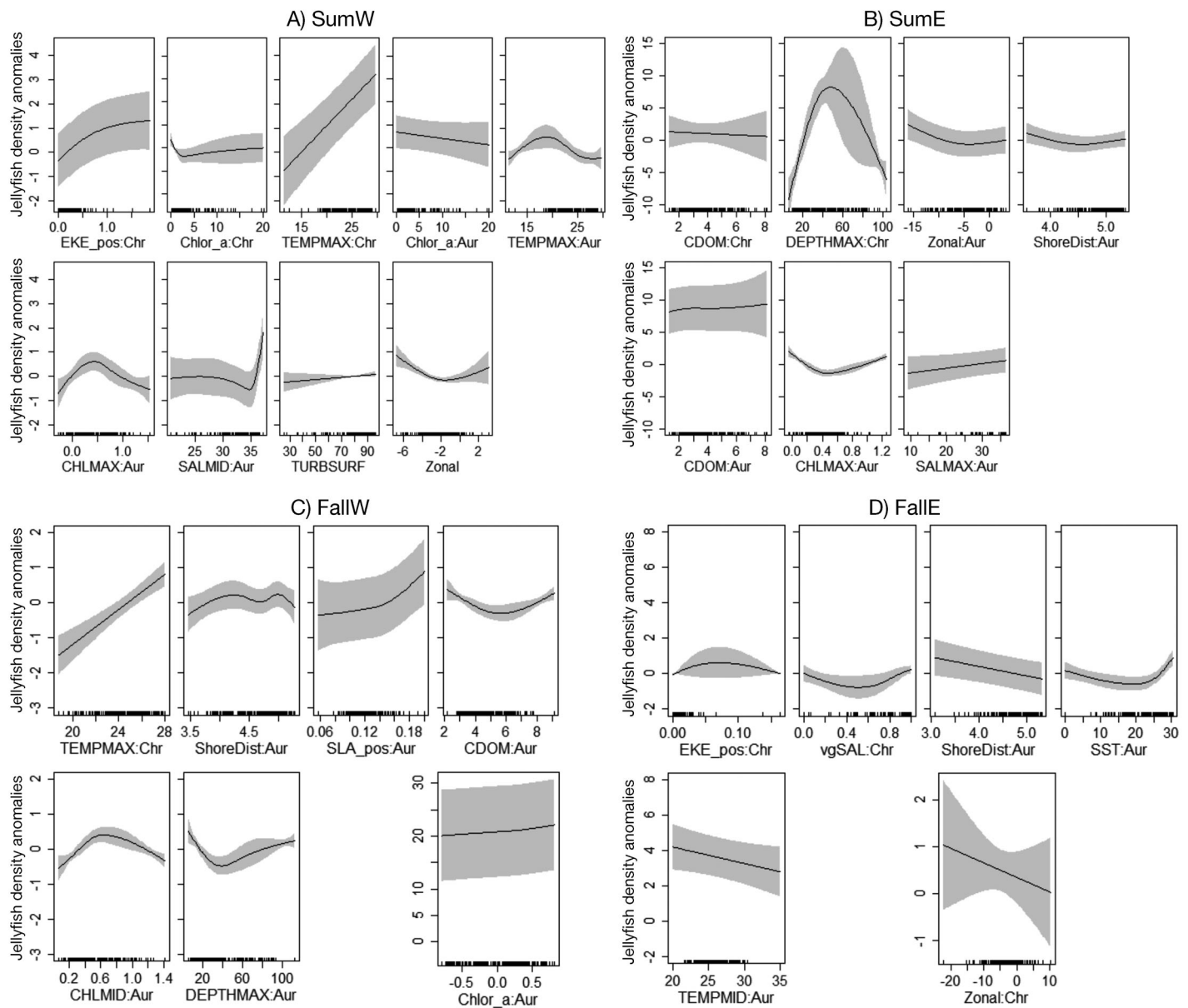
Fig. 3. Relationship between the changes in jellyfish log density and the descriptive variables used in the all-parameter method for the (A) summer west (SumW), (B) summer east (SumE), (C) fall west (FallW), and (D) fall east (FallE) regional models. Grey area indicates 95% CIs. Variables defined in Table 1, and :Chr and :Aur represent which genera the variable was applied to (Chr: *Chrysaora*; Aur: *Aurelia*)

trends seen in the observed data, specifically the locations of high density and the general increase of density closer to shore. However, the difference in the variance between the observed density and the regional model outputs resulted from the overall lower predicted densities.

Effects of oceanographic features

The influences of salinity, surface currents, temperature, chl *a* concentration, and distance from shore are consistent with current knowledge of jellyfish distribution drivers. Both salinity and temperature impact jellyfish density and distribution by regulating asexual reproduction, growth rates, and predator–prey interactions (Bamstedt et al. 1999, Purcell 2005, Lucas et al. 2014). Salinity and temperature were the only 2 predictive measurements used in the Chesapeake Bay jellyfish model (Decker et al. 2007), and temperature has been included in distribution models produced for the Bering Sea (Brodeur et al. 2008, Liu et al. 2011). Similar to the findings in these reports, salinity had a positive relationship with jelly-
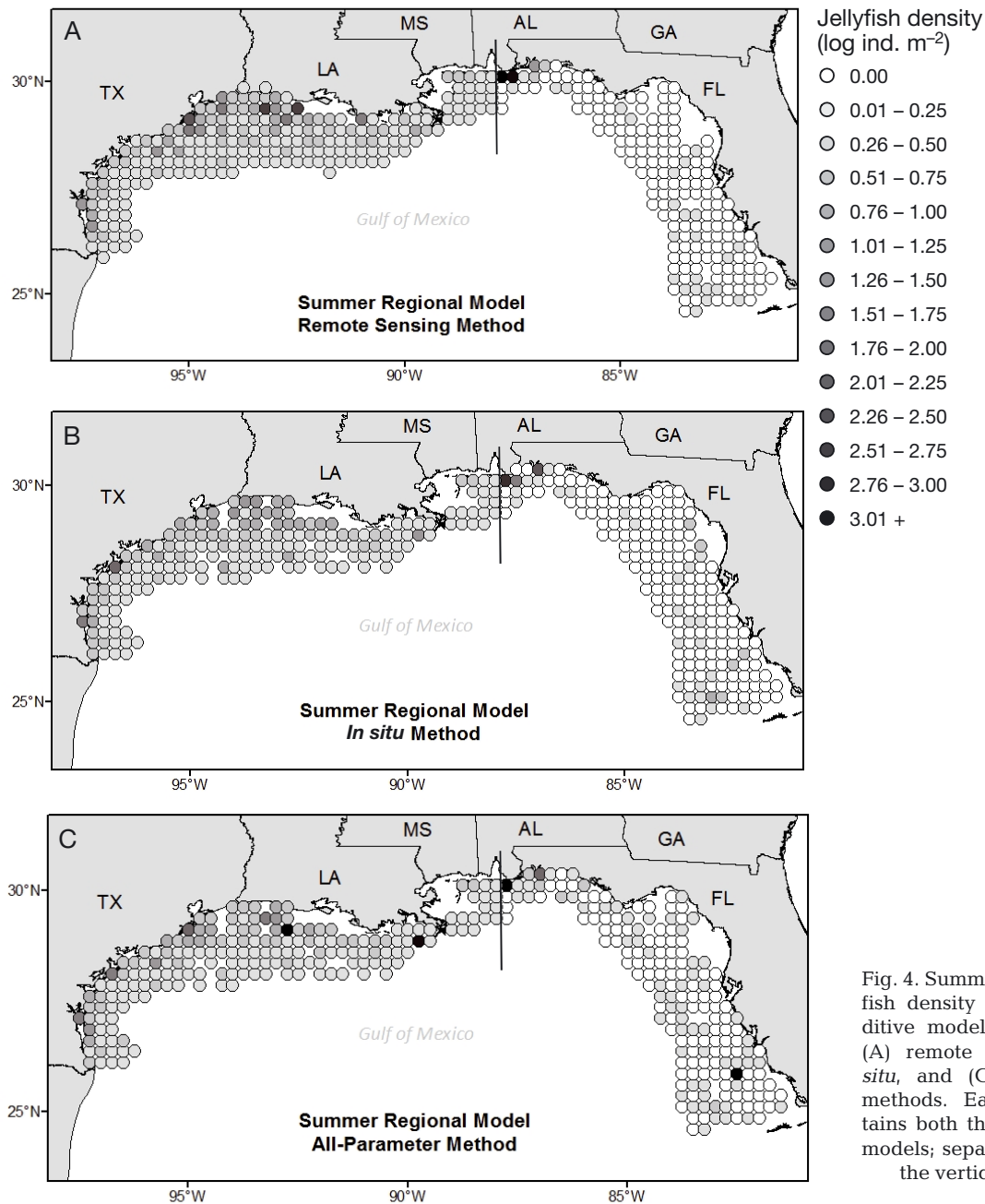
Fig. 4. Summer regional jelly-fish density generalized additive model results for the (A) remote sensing, (B) *in situ*, and (C) all-parameter methods. Each figure contains both the west and east models; separation shown by the vertical black line

fish in this study. The relationship with temperature was different between the 2 genera in the nGoM. An increase in temperature was associated with a greater density of *Chrysaora*, which supports their prevalence in the warmer summer season. Conversely, *Aurelia* were more abundant as temperatures decreased, which follows the cooling trend from summer to fall when *Aurelia* were dominant across the nGoM. The presence of chl *a* can affect the density and distribution of jellyfish by supporting the zooplankton biomass which is fed upon by jellyfish.

The chlorophyll variables were more descriptive for *Aurelia* than *Chrysaora* (Table 2) and varied depending on season and region. The descriptive power of chl *a* found here is not in agreement with the analysis of global cnidarian biomass predictors, nor was chl *a* concentration included in the Bering Sea or Chesapeake Bay biophysical model (Decker et al. 2007, Brodeur et al. 2008, Lucas et al. 2014). However, the resolution of data used in the global model was 5° grid cells, which could wash out the fine-scale patchy distribution of chl *a* (Lucas et al. 2014). Although
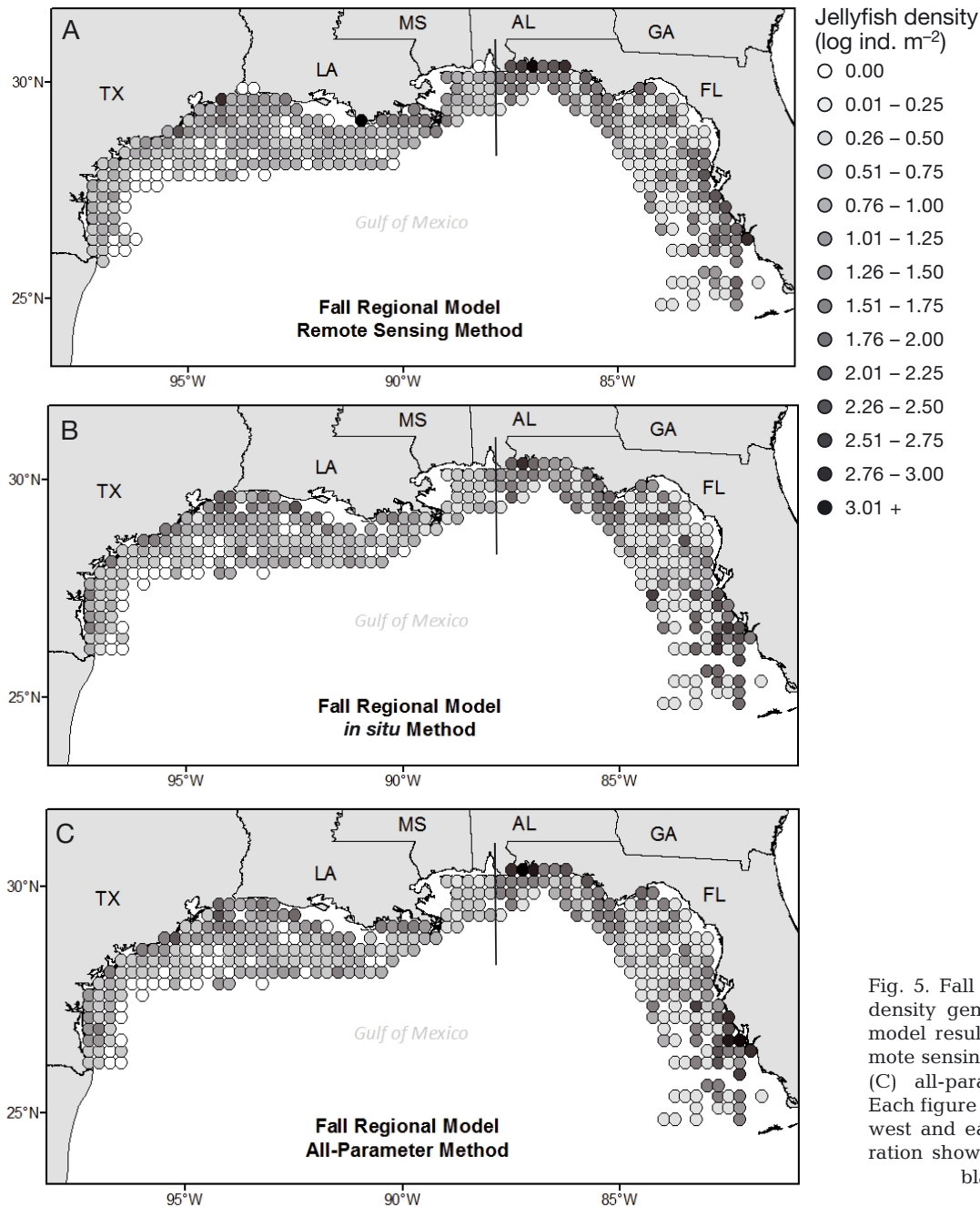
Fig. 5. Fall regional jellyfish density generalized additive model results for the (A) remote sensing, (B) *in situ*, and (C) all-parameter methods. Each figure contains both the west and east models; separation shown by the vertical black line

chl *a* was neglected in the Bering Sea model, zooplankton biomass, which has a closer trophic relationship to large jellyfish, was included and was determined to be predictive in the summer model (Brodeur et al. 2008). Several studies have shown the connection between chl *a* and zooplankton biomass throughout the water column (Grimes & Finucane 1991, Genin 2004, Greer & Woodson 2016) as well as the overlap between gelatinous zooplankton and chl *a* (Graham et al. 1992, Benson et al. 2007, Greer et al. 2015). Although chl *a* concentrations were found

to be descriptive variables in our model for the nGoM, the varying relationship between chlorophyll and jellyfish makes using the presence of chlorophyll as a proxy for the presence of jellyfish troublesome. A better alternative would be the combination of chlorophyll with additional parameters like salinity and temperature to signal the possible presence of jellyfish.

The distance to shore variable was only descriptive for *Aurelia*. The majority of the *Chrysaora* biomass was collected close to the shoreline (Fig. 2), so the
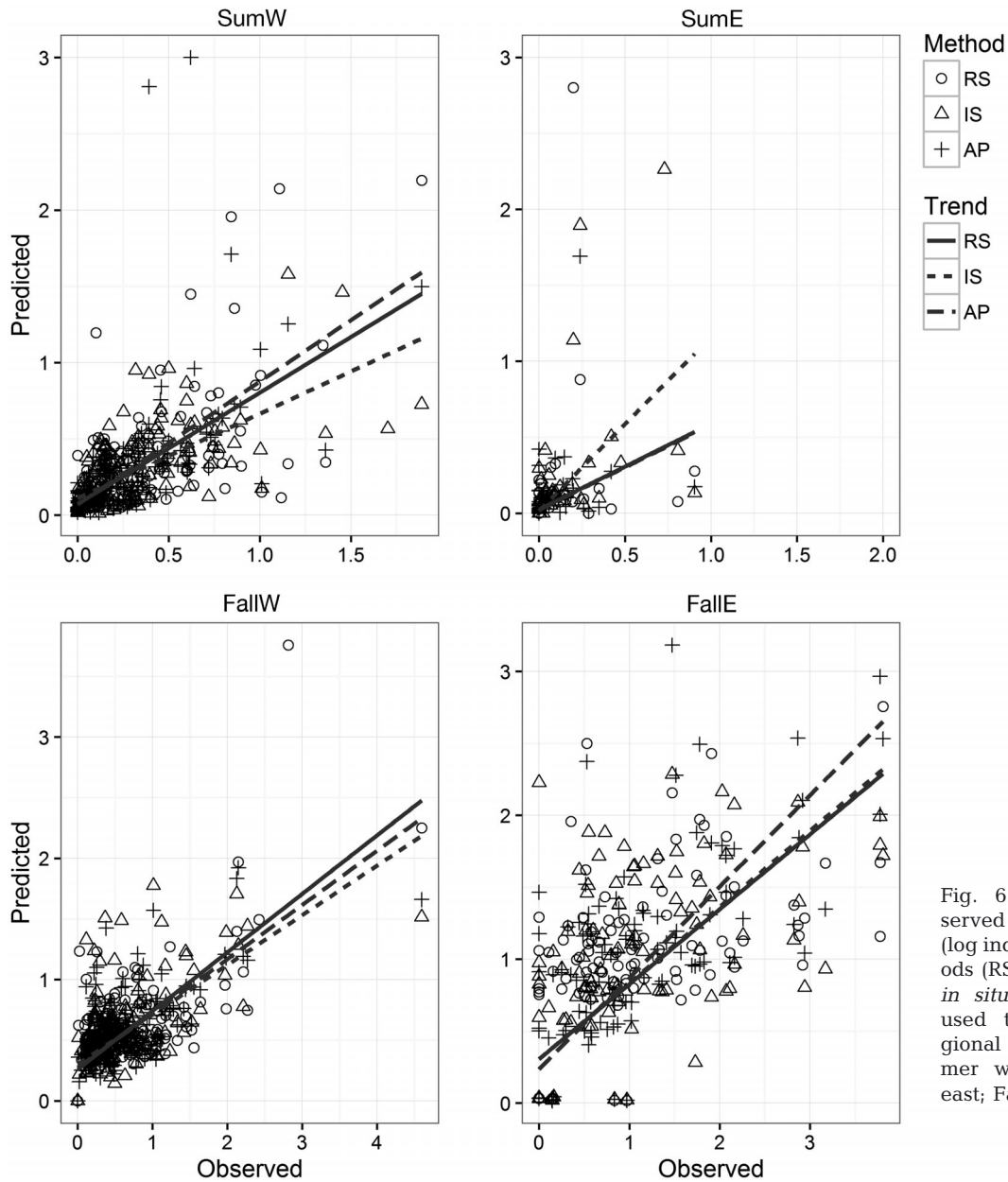
Fig. 6. Predicted vs. observed jellyfish densities (log ind. m^{-2}) for the 3 methods (RS: remote sensing; IS: *in situ*; AP: all-parameter) used to describe the regional models. SumW: summer west; SumE: summer east; FallW: fall west; FallE: fall east
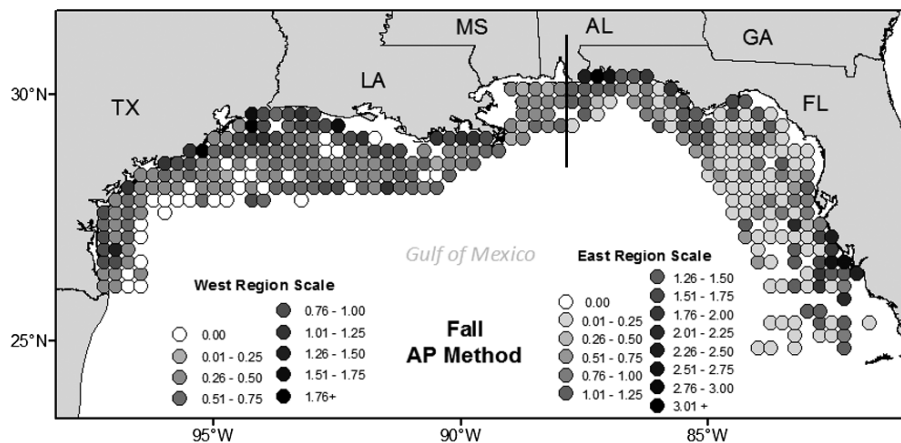

Fig. 7. Fall regional map for the all-parameter (AP) method with each region (west/east; separated by vertical black line) scaled to the highest predicted jellyfish density (log ind. m^{-2})

lack of variation in the observed distance to shore may have reduced its descriptive power for *Chrysaora*. Coastal hard substrate is the typical habitat for the polyp stage of development in these scyphozoan jellyfish; therefore, higher densities of medusae are often observed near the source of new biomass (Lucas et al. 2012, 2014). Further evidence to explain the differing jellyfish distributions observed between the seasons is the variation in the surface currents. Northerly (coastal) currents in the summer and southerly currents in the fall (Morey et al. 2003) could lead to the greater density observed across the continental shelf by *Aurelia* in the fall. The use of drifters among similar east and west regions of the nGoM showed high transport and retention time in the west (Morey et al. 2003). The higher density of jellyfish observed with westward currents is congruent with the prevailing westward flow across the Louisiana and Texas shelves (Zavala-Hidalgo et al. 2003) and the seasonal southwestern flow of the GoM in the fall (Morey et al. 2003). Large aggregations of jellyfish can be the result of advection and convergent currents (Graham et al. 2001), and longer residence time of a slow-moving water mass that contains jellyfish would lead to a higher local density (Graham et al. 1992). Such entrainment and advection of a jellyfish was modeled in the GoM when a large density of the invasive *Phyllorhiza punctata* was transported from the Caribbean Sea to the nGoM in 2000 (Johnson et al. 2005). Furthermore, the spawning of mesoscale eddies and subsequent interactions are a factor in both the western and eastern nGoM regions (Morey et al. 2003, Wang et al. 2003). Eddy circulations can entrain jellyfish and contribute to higher measured densities, which is seen in the presence of positive eddy kinetic energy (eke_pos) as a descriptive variable in the SumW and FallE models. The descriptive power of sla_pos in the FallW model also supports the presence of convergent mesoscale features that can aggregate jellyfish. Since these driving surface currents differ between the 2 spatial regions, their establishment as a descriptive variable was only observed when the nGoM was divided in the regional models and may be an essential factor in describing the distribution of jellyfish in the dynamic nGoM waters.

Model performance

Using oceanographic measurements to describe jellyfish density in the nGoM is complex due to the dynamic environmental conditions even with the spatial divide applied east of Mobile Bay, AL

(87.9° W), to separate the 2 overarching ecosystems on the shelf of the nGoM: the eutrophic river-dominated west and the oligotrophic oceanic east. A similar division of environments has also been applied to effectively address the oceanographic variables affecting jellyfish in the Bering Sea (Brodeur et al. 2008) and fishes in coastal Italy (Bonanno et al. 2016). Furthermore, a similar study investigated the influences of environmental factors on the distribution of shrimp in the nGoM with the development of gulf-wide GAMs and had a median of DE equal to 33.6% (Drexler & Ainsworth 2013), which is lower than our results for the gulfwide model. These investigations show that a universal model for a large area with different underlying abiotic conditions will not obtain the same level of precision as isolating the different environmental regimes. Therefore, understanding the basic environmental conditions and drivers and how they affect jellyfish is key to producing a proper model.

Our analysis showed that the combination of remote sensing and *in situ* measurements (i.e. the AP method) produced the best-fit models and were more descriptive than the RS and IS methods alone. The use of different methods (RS, IS, AP) to create the models was chosen to determine if there was a difference in the functionality of data sources and their potential for broader use. For example, if the RS method produced similar results to the IS and AP methods, then an RS model could be used more frequently and possibly on a wider area because of the availability of the data. The use of exclusively *in situ* variables could help determine the importance of below sea surface variables, which has been shown to be descriptive in jellyfish models, particularly in regions where stratification occurs (Liu et al. 2011).

The RS and IS methods produced comparable results among the models (Table 3). The IS method revealed the importance of the mid- and maximum-depth water column measurements, as they were found to be descriptive variables in all models. Although similar, the slight advantage seen in the fit of most IS methods could be explained by the fact that the IS measurements were taken at the time and location of the jellyfish collection. Therefore, they may be more relevant to the jellyfish distribution in the ever-changing waters of the nGoM than the satellite measurements, which may not capture the same trends due to the lower temporal and spatial resolution of the data. Nevertheless, the remote sensing or *in situ* data only can provide guidance to jellyfish distributions and density, but if both datasets are available, the AP methods are the most descriptive.

The descriptive models produced in this study have multiple applications for further research. These models help to detail the jellyfish distribution in the nGoM and could be used to investigate how changes in environmental conditions would affect jellyfish populations. Seasonally persistent jellyfish aggregations could be recognized with these models for large areas where public and industrial interactions may occur and should be monitored. Density data at this resolution could be used in predator–prey analyses to elucidate distribution overlaps. The output descriptions from this model could also be used to investigate the suggested association between persistent mesoscale eddies and jellyfish density. Conversely, at the resolution presented (25 × 25 km), this model would not be appropriate for subgrid-scale navigational avoidance or forecasting of jellyfish. At this time, it is not feasible to construct a predictive model of sufficient time or spatial resolution to be used in ecological management models for higher trophic levels.

Knowledge was gained on the nGoM oceanographic parameters that contribute to the density and distribution of jellyfish in the summer and fall, but continued work would be advantageous. Future improvements to the model could include a finer resolution of the spatial grid as well as the satellite data to alleviate some of the averaging in the distribution and could allow for the evaluation of smaller regions of the coastline. The addition of other oceanographic variables like zooplankton biomass and mixed layer depth, which were excluded from this analysis due to lack of data across the study area, could provide a better-fitting model. Lastly, with the collection of more data, models could be developed independently for specific jellyfish species or fit to include more species to investigate if certain oceanographic variables differently affect co-occurring jellyfish or jellyfish that are temporally separated.

CONCLUSIONS

The environmental factors that were found to be useful in describing the density distribution of jellyfish in the nGoM were salinity, surface currents, temperature, chl *a* concentration, and distance to shore. Additional descriptive variables were required to model the distribution of *Aurelia* compared to *Chrysaora*, but similar variables described both species within the same season and region, with the exception of distance from shore that was exclusively used with *Aurelia*. Descriptive models produced a better depiction of the observed data when the nGoM was divided into regions (east, west) to account for the difference in the underlying environmental conditions and drivers. The all-parameter descriptive models were a better fit than the remote sensing or *in situ* models alone, and variables representing measurements throughout the water column were found to be descriptive. As jellyfish are acknowledged for their key role in the ecosystem, the continuation of data collection and studies like this will provide critical information for environmental and industrial management.

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