



Tuna and swordfish catch in the U.S. northwest Atlantic longline fishery in relation to mesoscale eddies

ANGO C. HSU,^{1,2*} ANDRE M. BOUSTANY,¹
JASON J. ROBERTS,¹ JUI-HAN CHANG² AND
PATRICK N. HALPIN¹

¹Marine Geospatial Ecology Lab, Nicholas School of the Environment, Duke University Marine Lab, A328, LSRC Building, Durham, NC 27708-0328, U.S.A.

²School of Marine Sciences, University of Maine, 5706 Aubert Hall, Orono, ME 04469-5706, U.S.A.

ABSTRACT

To analyze the effects of mesoscale eddies, sea surface temperature (SST), and gear configuration on the catch of Atlantic bluefin (*Thunnus thynnus*), yellowfin (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) and swordfish (*Xiphias gladius*) in the U.S. northwest Atlantic longline fishery, we constructed multivariate statistical models relating these variables to the catch of the four species in 62 121 longline hauls made between 1993 and 2005. During the same 13-year period, 103 anticyclonic eddies and 269 cyclonic eddies were detected by our algorithm in the region 30–55°N, 30–80°W. Our results show that tuna and swordfish catches were associated with different eddy structures. Bluefin tuna catch was highest in anticyclonic eddies whereas yellowfin and bigeye tuna catches were highest in cyclonic eddies. Swordfish catch was found preferentially in regions outside of eddies. Our study confirms that the common practice of targeting tuna with day sets and swordfish with night sets is effective. In addition, bluefin tuna and swordfish catches responded to most of the variables we tested in the opposite directions. Bluefin tuna catch was negatively correlated with longitude and the number of light sticks used whereas swordfish catch was positively correlated with these two variables. We argue that overfishing of bluefin tuna can be alleviated and that swordfish can be targeted more efficiently by avoiding fishing in anticyclonic eddies and in near-shore waters and using more light sticks and fishing at night in our study area, although further studies are

needed to propose a solid oceanography-based management plan for catch selection.

Key words: catch selection, eddy detection, mesoscale eddies, multivariate statistical models, pelagic habitat, sea surface temperature, swordfish, tuna, U.S. Atlantic longline fishery

INTRODUCTION

Spanning across tens to hundreds of kilometers and lasting months to years, mesoscale eddies play a vital role in the physical and biological environment of the world's major oceans. Eddies have higher kinetic energy than the mean ocean flow (Xu *et al.*, 2011), and they contribute to general circulation and the oceanic heat budget by transporting momentum (Morrow *et al.*, 1992; Iudicone *et al.*, 1998), heat (Volkov *et al.*, 2008), fresh water, and mass (Leach *et al.*, 2002).

Eddies are classified as having cyclonic or anticyclonic polarity, depending on the direction of their rotation. In the northern hemisphere, newly-formed cyclonic eddies and cyclonic eddies that are still intensifying (i.e., are in their spin-up phase) rotate in a counterclockwise direction. Cyclonic eddies upwell water at their center (the eddy core) and are thus also known as cold-core rings. Newly-formed anticyclonic eddies and anticyclonic eddies that are still intensifying rotate in a clockwise direction. Anticyclonic eddies downwell water at their center and are known as warm-core rings (Bakun, 2006; McGillicuddy *et al.*, 2007).

Because eddies effectively mix the water column both vertically and horizontally, they affect nutrient distribution (McGillicuddy and Robinson, 1997), regulate primary production (Oschlies and Garçon, 1998), and induce new production (McGillicuddy *et al.*, 1998) in the open ocean. Many studies have shown that eddies influence the behavior and distribution of every level of marine organisms, from plankton (Garçon *et al.*, 2001; Vaillancourt *et al.*, 2003) to top predators, such as seals (Campagna *et al.*, 2006), seabirds (Nel *et al.*, 2001; Cotté *et al.*, 2007), and sea turtles (Polovina *et al.*, 2004).

Eddies are also important oceanographic features for tuna and swordfish (*Xiphias gladius*) life cycles. Eddies

*Correspondence. e-mail: chentien.hsu@maine.edu

Received 8 June 2012

Revised version accepted 6 August 2015

create favorable spawning conditions for Atlantic bluefin tuna (*Thunnus thynnus*) (Teo *et al.*, 2007), albacore tuna (*Thunnus alalunga*) (Bakun, 2006), and Pacific bluefin tuna (*Thunnus orientalis*) (Satoh, 2010). In the Gulf of Mexico, eddy kinetic energy is one factor that significantly affects the location of bluefin tuna breeding grounds (Teo *et al.*, 2007). In the Mozambique Channel, tuna schooling is associated with cyclonic eddies and eddy edges, as the foraging conditions are more favorable in these areas (Tew-Kai and Marsac, 2010). In the Mediterranean, swordfish spawning and feeding grounds are surrounded by persistent eddies (Tserpes *et al.*, 2008).

The fact that pelagic longline fisheries in the north-west Atlantic Ocean are located in regions of high eddy activity (in particular, near the Gulf Stream), and the fact that eddies affect the distribution of large pelagic predators, provide us with an opportunity to test eddy activity as a criterion for selecting catch among different species of tuna and swordfish in the region. Using catch records from the U.S. pelagic longline fleet, we examined the effects of eddy presence and polarity on the catch of Atlantic bluefin tuna, yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), and swordfish. We also examined the effects of sea surface temperature (SST), another factor known to affect catch of these species.

The U.S. commercial pelagic longline fishery adopts different fishing strategies and gear configurations to target different species of tuna and swordfish in the North Atlantic Ocean (Witzell, 1999; Kot *et al.*, 2010). To account for the influence of fishing gear configuration on catch composition, we also modeled the effects of the number of light sticks used in a configuration and of the number of hooks between floats.

Our results demonstrate the patterns of tuna and swordfish catch in relation to mesoscale physical oceanographic features in the U.S. Atlantic longline fishery. In recent years, national quotas for bluefin tuna have been declining whereas quotas for swordfish have been increasing, leading the U.S. pelagic longline fleet to catch more than its allotted sub-quota for bluefin tuna, while struggling to catch its full swordfish quota (ICCAT, 2011). Our research may help improve this situation by providing useful information to fishers who wish to optimize catch of one or more species while avoiding others.

MATERIALS AND METHODS

Fishery data

We downloaded logbook records (NOAA, 2010) of pelagic longline hauls by the U.S. fishing fleet

covering a 13-year span (October 14, 1992 through December 31, 2005) in the region 30–55°N, 30–80°W. Each record specified the date and location of the haul and the count of each species of fish caught. We discarded potentially erroneous records—for example, records that have incomplete date information, a greater catch than the number of hooks set, or fewer than 100 hooks set. Using the remaining 62 121 records, we focused our analysis on three species of tuna (bluefin, yellowfin, and bigeye) and swordfish (Fig. 1).

To investigate the effects of fishing gear configuration on the catch, we extracted three gear characteristics for each haul: the numbers of hooks set, light sticks used, and hooks between floats. A light stick is a plastic tube containing chemiluminescent fluids. To attract fish to their gear, fishers sometimes affix light sticks on the fishing line above the hook, mainly while fishing at night. When more hooks are set between floats in a longline haul, the mainline is more likely to sag and thus fishes at a greater depth. In this paper, we treated the number of light sticks used as a proxy for set time and the number of hooks between floats as a proxy for fishing depth.

Eddy data

We downloaded 690 weekly sea level anomaly (SLA) images (AVISO global 1/3° gridded DT-MSLA Ref merged dataset; <http://www.aviso.oceanobs.com>) corresponding to the time period of the fishery data. Using the Marine Geospatial Ecology Tools (MGET) software (Roberts *et al.*, 2010), we developed an automated workflow for detecting eddies in the images using the Okubo–Weiss parameter.

The Okubo–Weiss parameter (Okubo, 1970; Weiss, 1991), W , has been used in a number of prior studies to identify eddy structures from sea surface height data (e.g., Isern-Fontanet *et al.*, 2004, 2006; Chelton *et al.*, 2007; Henson and Thomas, 2008). It is calculated using the following equation, which subtracts the square of vorticity (ω^2) from the sum of the square of the normal component of strain (s_n^2) and the square of the shear component of strain (s_s^2):

$$W = s_n^2 + s_s^2 - \omega^2 \quad (1)$$

To calculate the normal component (s_n) and the shear component (s_s) of strain and vorticity (ω), geostrophic velocities in x -direction (u) and y -direction (v) are calculated using sea level anomaly (h'), acceleration due to gravity (g), and Coriolis parameter (f):

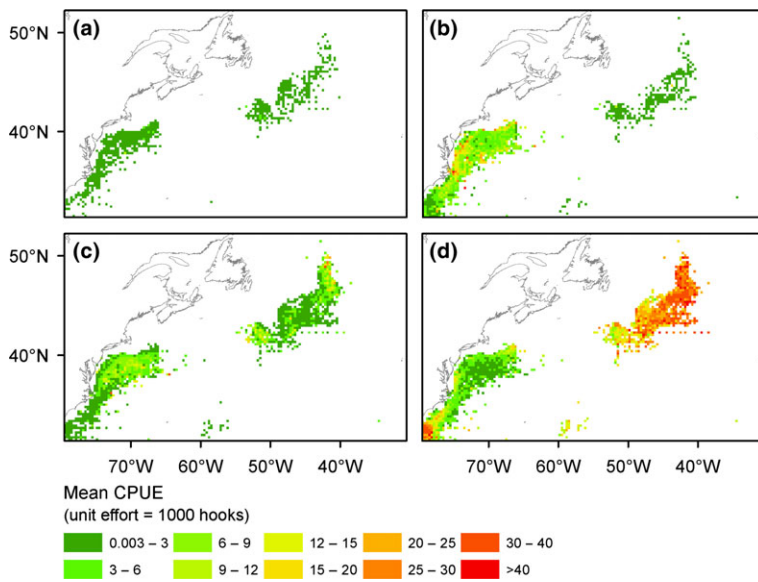


Figure 1. Mean catch-per-unit-effort (CPUE) for (a) bluefin tuna, (b) yellowfin tuna, (c) bigeye tuna, and (d) swordfish during the study period (1993–2005).

$$u = -\frac{g}{f} \frac{\partial h'}{\partial y} \text{ and } v = \frac{g}{f} \frac{\partial h'}{\partial x} \quad (2)$$

Then the strain components and vorticity are calculated:

$$s_n = \frac{\partial u}{\partial x} - \frac{\partial v}{\partial y} \text{ and } s_s = \frac{\partial v}{\partial x} + \frac{\partial u}{\partial y} \text{ and } \omega = \frac{\partial v}{\partial x} - \frac{\partial u}{\partial y} \quad (3)$$

According to Eqn (1), the eddy core, which has a relatively high vorticity and low strain rates, is characterized by a large negative value of the Okubo–Weiss parameter. In contrast, the eddy ring, which experiences relatively high rates of strain and low vorticity, has a large positive value of the parameter.

The MGET software labels eddy cores in a sea level anomaly image by calculating the Okubo–Weiss parameter for each cell of the image and then identifying coherent clusters of cells that are below the threshold value of the parameter. This threshold may be expressed as an absolute value of the parameter or as a difference, in standard deviations, from the mean value of the parameter for all of the cells. To be consistent with previous eddy identification studies (Isern-Fontanet *et al.*, 2006; Henson and Thomas, 2008), we used a threshold of -0.2 standard deviations.

Because hydrodynamic features such as Gulf Stream meanders can be mistakenly flagged as eddies by the Okubo–Weiss approach, MGET tracks eddies across successive images and provides mechanisms to filter the eddy core output according to eddy size, circularity, and duration. To reject oddly-shaped features that were not eddies, we set MGET's minimum area-

to-perimeter ratio to 0.4 (this ratio is normalized such that a perfect circle has the value 1.0).

Next, to identify the eddy rings, we first obtained the radius of each detected eddy core by assuming that the core was circular in shape and then calculating its radius from its surface area. Based on previous research, which indicated that the eddy core usually comprises ~ 50 to 60% of the diameter of an eddy, we buffered the detected eddy cores out to a distance equal to their radii. From the buffered areas, we then labeled cells with an Okubo–Weiss parameter greater than 0.2 standard deviations as eddy rings, because the eddy rings experience high rates of strain and, therefore, have a large positive Okubo–Weiss value (Henson and Thomas, 2008).

Finally, we combined the eddy rings and cores, labeled the resulting features according to the polarity of the eddy (anticyclonic or cyclonic), performed a spatiotemporal overlay of the longline haul records on the labeled images, and determined whether each haul occurred in an anticyclonic eddy, in a cyclonic eddy, or outside of eddies.

Sea surface temperature (SST) data

Prior research has shown that our focal species exhibit different tolerances for and adaptations to water temperature (Carey, 1982; Block *et al.*, 2001; Bertrand *et al.*, 2002a; Lawson *et al.*, 2010; Dewar *et al.*, 2011). To examine the possible influence of water temperature on the catch of these species and to provide a second environmental covariate to which eddies could be compared, we obtained SST estimates for the longline hauls extracted from the 8-day nighttime 4-km

AVHRR Pathfinder SST version 4.0 dataset (<http://po daac.jpl.nasa.gov>). SST at the set position was recorded for each set made within an 8-day period covered by any given satellite image. Due to cloud contamination, we were unable to obtain SST data for 6906 of our 62 121 logbook records. These records were excluded in the subsequent analysis.

Correlation of fish catch with eddies, SST, and gear characteristics

To investigate the effects of eddies, temperature, and gear configuration on the catch of three species of tuna and swordfish, multivariate statistical models were constructed. In these models, the response variable was equivalent to catch-per-unit-effort (CPUE). Although technically the catch of each of our focal species was used as the response variable, the models adjusted the difference in fishing effort of each longline haul by assigning the number of hooks set (H_i) to the offset of the models and by including this variable as one of the predictor variables and restricting its coefficient to 1. This approach is commonly used in statistical models to study the environmental preference of tuna and swordfish (Santos *et al.*, 2006; Mugo *et al.*, 2010; Teo and Block, 2010). To compare the number of fish caught in the anticyclonic eddy, cyclonic eddy, and non-eddy hauls, a categorical variable EDDY was constructed based on the eddy category of haul (i.e., anticyclonic, cyclonic, or non-eddy). To account for any unobserved events associated with a particular time of the year that might influence the number of fish caught, the year and month when each haul was made were included in our statistical models as two categorical variables YR and M. A detailed description of the predictor variables of our models was provided in Table 1. In the statistical models, the predicted number of fish caught (y_i) was estimated:

$$\begin{aligned} \log(y_i) = & \beta_0 + \sum_{j=1993}^{2005} \beta_{yr} YR_j + \sum_{k=1}^{12} \beta_m M_k \\ & + \sum_{l=1}^3 \beta_{EDDY} EDDY_l + \beta_{SST} SST_i + \beta_L L_i \quad (4) \\ & + \beta_{HBF} HBF_i + \beta_{LAT} LAT_i + \beta_{LON} LON_i \\ & + \log(H_i) + \varepsilon_i \end{aligned}$$

Our fishery data are count data (the number of fish caught), are overdispersed (the sample variance exceeds the sample mean), and contain a large number of zeros (hauls with no catch). Previous research has demonstrated that a zero-inflated negative binomial (ZINB) distribution is suitable for fitting this kind of data to environmental variables and variables that describe fishing effort and gear configuration (Minami *et al.*, 2007). A typical ZINB model has two portions, the zero-inflation portion and the count portion. In the zero-inflation portion, the model uses the predictor variables and negative binomial distribution to estimate the probability of a sample being one of the excess observed zeros. In the count portion, the model uses the predictor variables and, in our case again, negative binomial distribution to estimate the number of fish caught in a longline haul. Like the zero-inflation portion, the count portion can also predict zero fish catch in a longline haul, and the zeros predicted by the count portion are structural zeros, which refer to those longline hauls set in sub-optimal fishing grounds and caught no fish. Detailed descriptions of the ZINB model can be found in Zuur *et al.* (2009).

We built one ZINB regression model for each species. For each species, we first built an initial ZINB model by fitting the full model (Eqn 4) in both the count portion and the zero-inflation portion of the model. To examine the relative importance of the predictor variables in the initial model, we conducted a

Table 1. Predictor variables included in the regression models.

Variable	Abbreviation	Type	Description
Eddy presence and polarity	EDDY	Categorical	Anticyclonic hauls (A); cyclonic hauls (C); non-eddy hauls
Sea surface temperature	SST	Continuous	SST (°C) extracted from 8-day composite AVHRR satellite data
Number of light sticks used	L	Discrete	Total number of light sticks affixed to the longline
Number of hooks between floats	HBF	Discrete	Total number of hooks deployed between successive floats
Latitude	LAT	Continuous	Latitude of the longline hauls
Longitude	LON	Continuous	Longitude of the longline hauls
Number of hooks set	H	Discrete	Total number of hooks attached to the longline
Year	YR	Categorical	Year the longline hauls were made (1993–2005)
Month	M	Categorical	Month the longline hauls were made (1–12)

backward stepwise process, in which we successively remove one variable from each portion and compare the model with the initial model using likelihood ratio test. The variable that produces the least change in Akaike's information criterion (AIC) and the most insignificant Chi-square statistic in the likelihood ratio test was then removed from the initial model. We repeated the process until we reached a final model, in which removing any predictor variable produces a large change in AIC and is significant in the successive likelihood ratio test. For each species examined, a summary table of the final ZINB model is provided (Table S1–S4). The work was performed in the R statistical program (R Development Core Team, 2010) using the 'pscl' package and the 'MASS' package.

We reported the results using the count portion of our ZINB models. We reported a pattern for a species (i.e., that it responds to a certain variable in the ZINB regression models) if the variable has a coefficient significant at a 95% confidence level. By comparing which eddy category has the higher predicted number of fish caught, we summarized the responses of tuna and swordfish catch toward eddy presence and polarity. For latitude, longitude, SST, and the variables that describe gear configuration, we reported the sign of the coefficient of these variables in our regression models as our results for the direction of the variables' effects on the number of fish caught for a given species.

Sensitivity test

MGET provides mechanisms to filter the eddy core output according to eddy size and duration. To examine the relevance of both small, short-lived eddies and large, long-lived eddies, we used these mechanisms and conducted a sensitivity test that included six eddy-detecting scenarios. In these scenarios, we required eddy cores to be bigger than a specified area (4, 6, or 9 cells, corresponding to circles with approximate radii of 42, 51, and 63 km) and to persist for longer than a specified period of time (10 or 18 weeks). We omitted one scenario, in which we required eddy cores to be bigger than nine cells and to persist for longer than 18 weeks, because this eddy-detecting condition was too strict and too few eddy cores were detected for the downstream statistical analysis to be robust.

We repeated the above statistical analysis for each of the five eddy-detecting scenarios. Our results suggest that changing eddy size and duration does not affect the responses of tuna and swordfish catch to the predictor variables. For clear presentation, we only show the results of one scenario, in which we required eddy cores to have a radius greater than 51 km and to

persist for longer than 18 weeks, because this scenario contains large, long-lived eddies that are likely to be biologically relevant. The trends reported in this study are significant at a 95% confidence level in at least three eddy-detecting scenarios.

RESULTS

Spatial patterns in fishing effort and efficiency

To illustrate overall spatial patterns in fishing effort and efficiency, we derived mean CPUE maps for each focal species from the 62 121 hauls (Fig. 1). The hauls were distributed broadly across the study area but spatially clumped along the U.S. East Coast and in the Flemish Cap region. Cells with high mean CPUE concentrated in these two regions. For bluefin tuna and bigeye tuna, the mean CPUE was distributed relatively evenly across these two regions, whereas for yellowfin tuna and swordfish, the mean CPUE was higher in one region than the other. Mean CPUE was higher along the U.S. East Coast for yellowfin tuna and higher in the Flemish Cap region for swordfish. Overall, bluefin tuna had the lowest mean CPUE and swordfish had the highest mean CPUE among the four species (Table 4).

Spatial patterns in eddy activity

In this particular eddy-detecting scenario, in which eddy cores were required to have a radius of at least 51 km and to persist for longer than 18 weeks, 103 anticyclonic eddies and 269 cyclonic eddies were detected in our study area and period (Table 2). To illustrate overall spatial patterns in eddy activity, we aggregated the 690 weekly images showing eddy positions (e.g., Fig. 2) into climatological images that show the mean density of eddies over the study period (Fig. 3). In our study area, cyclonic eddies were more common than anticyclonic eddies, and anticyclonic eddies were concentrated

Table 2. The numbers of eddies detected and the numbers of longline hauls categorized to different eddy categories. In this eddy-detecting scenario, the minimum eddy radius and duration were required to be greater than 51 km and longer than 18 weeks, respectively.

	Number
Eddies	372
Anticyclonic eddies	103
Cyclonic eddies	269
Eddy hauls	2946
Non-eddy hauls	59 175
Anticyclonic eddy hauls	2695
Cyclonic eddy hauls	246

Figure 2. Example output from the eddy-detecting workflow, showing eddy cores detected on June 30, 2004. To illustrate the output in an oceanographic context, the detected cores are overlaid on contemporaneous images of (a) sea level anomaly (DT-MSLA Ref data from AVISO) and (b) sea surface temperature (GOES 10 SST data from NASA PO.DAAC).

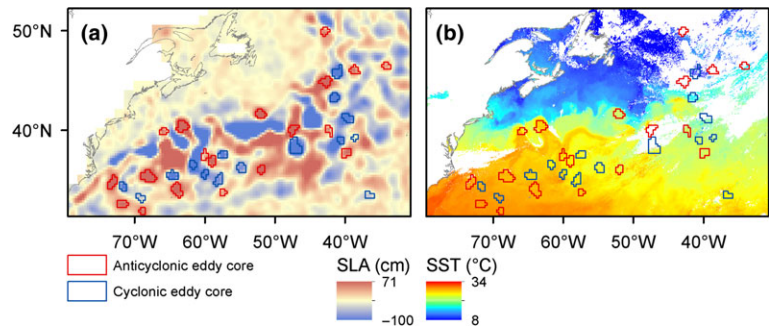
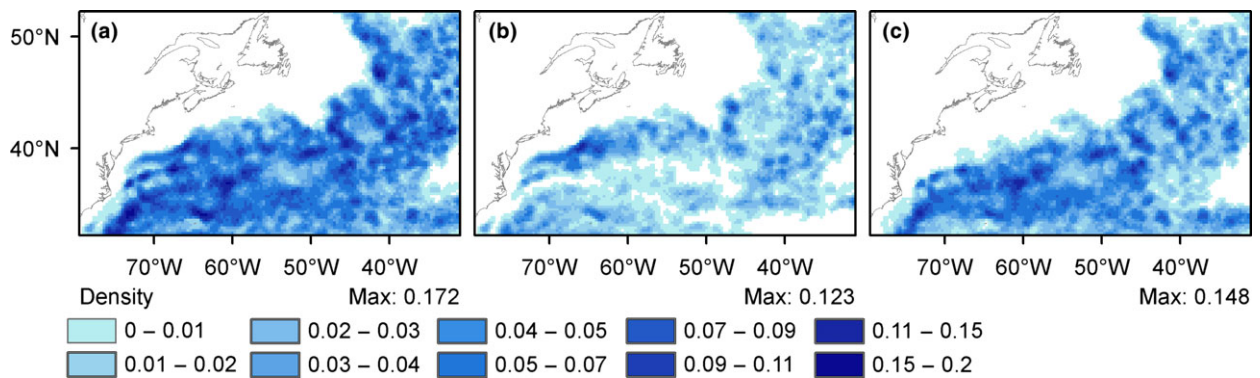


Figure 3. Density of (a) all eddy cores, (b) anticyclonic eddy cores, and (c) cyclonic eddy cores during the study period (1993–2005). The darker the color, the more frequently the grid cell was occupied by an eddy during the study period.



farther north than cyclonic eddies—especially along the northern edge of the Gulf Stream.

The number of longline hauls that belong to each eddy category was tallied in Table 2. Although many longline hauls occurred in eddies, most occurred outside of eddies (Table 2 and Fig. 4). This is because only a small portion of the study area is occupied by eddies at a given time (Fig. 2; also note values of density scale in Fig. 3). For hauls inside eddies, although cyclonic eddies were more prevalent in the overall study area, more hauls were located in anticyclonic eddies than in cyclonic eddies (Table 2), particularly along the portion of the Gulf Stream that veers away from the East Coast of the United States (Fig. 4). This is due to the fleet’s preference for fishing on the northern side of the Gulf Stream, where more anticyclonic eddies are generated than cyclonic eddies.

Correlation of fish catch with eddies, SST, gear characteristics, and spatial variables

We calculated the percentage of total variance explained by the final ZINB model for bluefin (66.88%), yellowfin (83%), and bigeye tuna (78.83%) and swordfish (81.26%). The models showed that eddy effects are statistically significant and that they display

distinct patterns for each of the focal species (Table 3). Bluefin tuna catch was higher in anticyclonic hauls than in non-eddy or in cyclonic hauls. For yellowfin tuna, the catch was highest in cyclonic hauls and lowest in anticyclonic hauls. Bigeye tuna catch was highest in cyclonic hauls, followed by anticyclonic hauls, and lowest in non-eddy hauls. Conversely, swordfish catch was highest in non-eddy hauls, followed by anticyclonic hauls, and lowest in cyclonic hauls.

For bluefin tuna and swordfish, catch increased with decreasing SST, whereas for yellowfin and bigeye tuna, catch increased with increasing SST. For all three species of tuna, the catch was negatively correlated with the number of light sticks used, whereas for swordfish, the catch was positively correlated with this variable. The number of hooks between floats is significant in determining the catch of bigeye tuna and swordfish. Bigeye tuna catch was positively correlated with the number of hooks between floats whereas swordfish catch was negatively correlated with this variable.

For swordfish, the catch was negatively correlated with latitude, whereas for bigeye tuna, the catch was positively correlated. For bluefin tuna, the catch was negatively correlated with the longitude, whereas for swordfish, the catch was positively correlated.

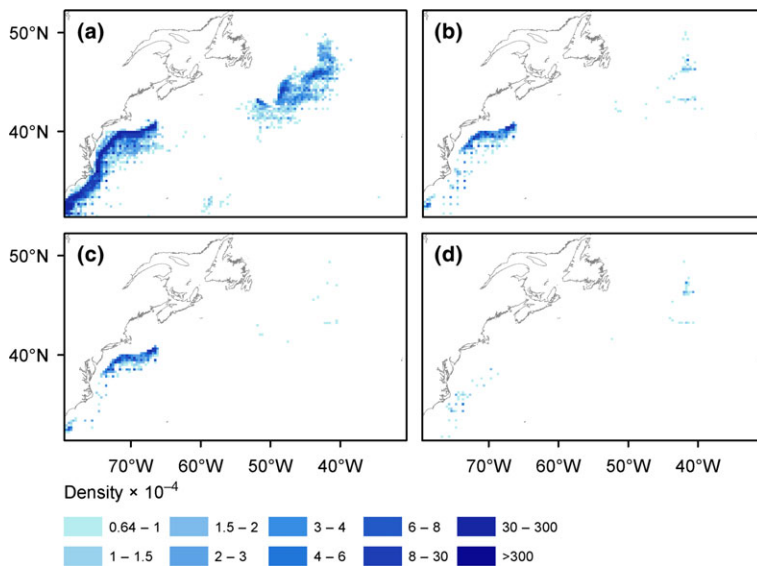


Figure 4. Density of longline hauls located (a) outside of eddies, (b) in eddies, (c) in anticyclonic eddies, and (d) in cyclonic eddies during the study period (1993–2005). For each gridded cell, haul density was calculated by dividing the number of hauls the cell contains by the total number of hauls (62 121) of the U.S. Atlantic longline fishery.

Table 3. The coefficients and the 95% confidence intervals of each predictor variable in the count portion of the final zero-inflated negative binomial (ZINB) models for each species. The models were fit using the eddy structures detected in the scenario, in which the eddy cores were required to be bigger than six cells (corresponding to a circle with a radius of approximately 51 km) and to persist for longer than 18 weeks. The predictor variables eliminated in the backward stepwise process were left blank.

Variable	Bluefin tuna	Yellowfin tuna	Bigeye tuna	Swordfish
EDDY (A)	0.4690 ± 0.2982**	−0.0803 ± 0.0706*	0.1327 ± 0.0721***	−0.1523 ± 0.0536***
EDDY (C)		0.2250 ± 0.2122*	0.7362 ± 0.2636***	−0.8068 ± 0.1452***
SST	−0.1873 ± 0.0262***	0.0471 ± 0.0089***	0.0983 ± 0.0096***	−0.0185 ± 0.0057***
L	−0.0012 ± 0.0003***	−0.0019 ± 0.0001***	−0.0007 ± 0.0001***	0.0012 ± 0.0001***
HBF			0.0106 ± 0.0089*	−0.0066 ± 0.0020***
LAT			0.0903 ± 0.0103***	−0.2459 ± 0.0078***
LON	−0.0860 ± 0.0094***			0.0801 ± 0.0025***

* P -value < 0.05; ** P -value < 0.01; *** P -value < 0.001.

Eddies are less important than the SST in determining tuna catch (Table S1–S3). In contrast, eddies have a larger effect than the SST in determining swordfish catch (Table S4). Of the two variables used to describe gear configuration, the number of light sticks used is more important than the number of hooks between floats in determining the catch of our focal species. Longitude is the most important variable in predicting bluefin tuna and swordfish catch, whereas the number of light sticks used and the SST is the most important variable in estimating yellowfin and bigeye tuna catch, respectively.

DISCUSSION

Spatial patterns in fish catch

The analysis of the NOAA logbook dataset reveals the catch distribution of our four focal species in the U.S.

Atlantic longline fishery (Fig. 1). Bluefin and bigeye tuna catches are distributed evenly in the main longline fishing regions across the North Atlantic Ocean. In contrast, yellowfin tuna and swordfish catches are more spatially aggregated. As a tropical tuna species with the narrowest tolerance for ambient water temperature among our focal species (Bertrand *et al.*, 2002a), yellowfin tuna were largely caught at lower latitudes along the East Coast of the United States.

In the North Atlantic, high swordfish catch appears in two areas. One high-catch area is located within a U.S. Atlantic longline fishing region known as the NED (Northeast Distant), which occupies the area 35–55°N, 20–60°W. The other high-catch area surrounds the Charleston Bump, a bottom topographic feature located approximately 90 miles southeast of Charleston, South Carolina (31°30'N, 79°W). Swordfish have evolved to adapt to extreme

environments of low temperature (Carey, 1982) and to thereby exploit resources at higher latitudes (Nakamura, 1985) and at great depths (Chancollon *et al.*, 2006). Neilson *et al.* (2009) showed that swordfish display a consistent pattern of seasonal migration, moving between the temperate waters north of 40°N and the Caribbean Sea. Swordfish usually reach the temperate waters in early June, stay until October, and then reside in the Caribbean Sea from early January through to April. Kot *et al.* (2010) analyzed the same logbook dataset and found swordfish catch in the NED increases in the fall. A swordfish tagging study shows that large females feed in cooler waters in higher latitudes in the NED during the summer and fall whereas smaller males stay in the lower latitudes (Sperling *et al.*, 2005). The other high swordfish catch area, the Charleston Bump, has been identified as a potential swordfish spawning and nursery ground (Sedberry and Loefer, 2001). In the western North Atlantic, swordfish spawn in different seasons in the Caribbean Sea, the Gulf of Mexico, and off the southeastern United States (Neilson *et al.*, 2009). At the Charleston Bump, the benthic structure deflects the Gulf Stream at the surface and creates abundant frontal eddies, gyres, and upwelling zones that are important to the life history of many marine species. Our statistical model suggests that swordfish catch increases with increasing longitude and with decreasing latitude; each corresponding with the two high swordfish catch areas, the NED and the Charleston Bump.

Fewer bluefin tuna were recorded than any of the other three species we examined (Fig. 1). The average CPUE of bluefin tuna is an order of magnitude lower than the CPUE of yellowfin and bigeye tuna and two orders of magnitude lower than the CPUE of swordfish (Table 4). This is likely due to the fact that the U.S. Atlantic longline fleet targets mainly swordfish and yellowfin and bigeye tuna, and that its fishing gear and fishing locations are likely optimized to maximize the catch of these three species (NMFS, 2002).

Table 4. Average catch-per-unit-effort (CPUE) (calculated as number of fish caught per thousand hooks) for the focal species in all 62 121 longline hauls made between 1993 and 2005 in the northwest Atlantic.

	Average CPUE
Bluefin tuna	3.39×10^{-4}
Yellowfin tuna	6.97×10^{-3}
Bigeye tuna	2.77×10^{-3}
Swordfish	1.47×10^{-2}

Spatial patterns in eddy activity

The eddy detecting algorithm was able to identify a large number of eddies in the study region (Fig. 3a), where eddy activity is known to be high (Chelton *et al.*, 2007). The anticyclonic eddies that pinch off from warm Gulf Stream water at the northern wall of the Gulf Stream, where the Gulf Stream meets with the cold Labrador Current and where the largest SST anomaly is found in the North Atlantic (Palmer and Sun, 1985; Hansen and Bezek, 1996), are especially obvious on SST images (Fig. 2b). In the subtropical region south of the Gulf Stream, where the contrast in SST is not as strong, our detected eddy structures are less easily discerned on SST images (Fig. 2b). The varying contrasts in SST between different regions of the North Atlantic make it less practical to develop an eddy-detecting workflow based on SST images. In addition, many SST products (including the GOES 10 SST image shown in Fig. 2b) suffer from severe cloud contamination, which requires an eddy-detecting workflow to use long SST composites that potentially smooth out eddy signals. In contrast, the eddy-detecting method that was applied in our research and various other studies (Isern-Fontanet *et al.*, 2004; Chelton *et al.*, 2007; Henson and Thomas, 2008) only requires SLA as the input, and the SLA images we used are not affected by clouds.

More cyclonic eddies than anticyclonic eddies were detected in our study area (Table 2). Many other studies have also shown that cyclonic eddies dominate in the western North Atlantic. Paillet (1999) reported that cyclonic eddies are more numerous than anticyclonic eddies in the western North Atlantic, and the dominance of anticyclonic eddies increases from west to east across the North Atlantic Ocean. By tracking the movement of buoyant floats, Shoosmith *et al.* (2005) recorded more cyclonic eddies than anticyclonic eddies in a region of the North Atlantic that is within our study area. In addition, anticyclonic eddies and cyclonic eddies are not distributed evenly in the North Atlantic. Both the climatological images of eddy density shown in Fig. 3b,c and Paillet's (1999) suggest that anticyclonic eddies are more often found in higher latitudes northwest of the Gulf Stream, whereas cyclonic eddies more often occupy lower latitudes southeast of the Gulf Stream. However, because of this regional distribution of eddies and because of the North Atlantic longliners' preference for fishing on the northern edge of the Gulf Stream, although cyclonic eddies dominate our study area, there are more anticyclonic hauls than cyclonic hauls (Fig. 4c, d). Similar to the distribution of anticyclonic eddies,

anticyclonic hauls are more likely than cyclonic hauls to be found near shore and at higher latitudes (Fig. 4c).

Fish catch in relation to oceanography

While many studies have shown that large pelagic predators have evolved various strategies to occupy different niches of the ecosystem (Chancollon *et al.*, 2006; Pusineri *et al.*, 2008; Young *et al.*, 2010), our statistical models demonstrate that responding to mesoscale eddies differently may be yet another strategy marine animals adopt for partitioning habitat use. Eddy presence and polarity have significant but different effects in determining the catchability of the species we analyzed. Cyclonic eddies are known to increase ocean primary productivity by upwelling nutrients at their interior, whereas anticyclonic eddies can aggregate marine organisms and attract consumers of different trophic levels by creating a convergent environment similar to the environments found in many frontal areas (Bakun, 2006).

As our species of interest mainly use our study area as feeding grounds and as research has related the catchability of longline fishery to prey abundance (Bertrand *et al.*, 2002b), it seems likely that the results of our statistical models can be explained by predator–prey relationships. The oceanographic preferences of our focal species are likely the result of the increased forage opportunities in these oceanographic features. In our study, tunas generally prefer eddy habitats over non-eddy habitats, whereas swordfish display the opposite preference. In addition, anticyclonic eddies and cyclonic eddies play different roles in the feeding activities of different tuna species.

The catchability of bluefin tuna in the U.S. Atlantic longline fishery was higher in anticyclonic eddies than in cyclonic eddies or in non-eddy habitats for our 13-year study period. Previous studies have found associations between anticyclonic eddies and marine predators, such as seabirds (Yen *et al.*, 2006), loggerhead sea turtles (*Caretta caretta*) (Polovina *et al.*, 2006; Howell *et al.*, 2010), and melon-headed whales (*Peponocephala electra*) (Woodworth *et al.*, 2011), and attributed these associations to the aggregation of mid-trophic-level fish and squid in convergence zones of anticyclonic eddies. Bluefin tuna display complex patterns of horizontal movements in the western North Atlantic. In the most noticeable pattern, they migrate seasonally between the Gulf of Mexico, their only confirmed spawning area in the western Atlantic, and their feeding grounds found on the continental shelf of the Gulf of Maine and Canada (Block *et al.*, 2005). Anticyclonic eddies (warm-core rings) are more often

found along the northern side of the Gulf Stream. Our results confirm bluefin tuna's use of this type of oceanographic structure. Anticyclonic eddies can aggregate bluefin tuna's prey, such as Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes* spp.), Atlantic mackerel (*Scomber scombrus*), squid, and crustaceans (Block *et al.*, 1998; Logan *et al.*, 2015). Tracking data for Atlantic bluefin tuna have recorded the animal's presence in warm-core rings on the northern edge of the Gulf Stream (Block *et al.*, 1998, 2001). By analyzing the movements of 35 electronically tagged Atlantic bluefin tuna, Lawson *et al.* (2010) reported that between March and April bluefin tuna move from coastal North Carolina to the northern wall of the Gulf Stream. After those waters warm in June, the fish move further north to forage in temperate waters. By studying 41 adult bluefin tuna using pop-up satellite archival tags, Galuardi *et al.* (2010) concluded that presumably mature bluefin tuna either do not spawn every year or spawn in places yet to be identified. They suggested that, by entraining the warm waters of the Gulf Stream, the warm-core rings have the potential to provide suitable conditions (temperature >24°C) for bluefin tuna spawning.

In our study, bluefin tuna catch occurred more frequently in lower SSTs. Unique endothermic physiology makes bluefin tuna more successful in conserving metabolic heat than other tuna species, allowing bluefin tuna to access cooler and generally more productive temperate waters (Carey and Lawson, 1973; Walli *et al.*, 2009).

Yellowfin tuna catch was highest in cyclonic eddies and lowest in anticyclonic eddies. Cyclonic eddies enhance the otherwise oligotrophic conditions found in the warm waters south of the Gulf Stream and are likely to improve yellowfin tuna's forage opportunity. Due to their narrow tolerance for ambient water temperature (Bertrand *et al.*, 2002a), yellowfin tuna were mainly caught at lower latitudes along the East Coast of the United States in the U.S. Atlantic longline fishery. This explains why yellowfin tuna catch was lower in anticyclonic eddies—anticyclonic eddies distribute further north in our study area (Fig. 3b). In contrast to yellowfin tuna, the catchability of bigeye tuna was higher in both types of eddy than in non-eddy habitats. Although yellowfin tuna and bigeye tuna are both tropical tuna species and the catches of both were correlated with higher SSTs, bigeye tuna do have a greater physiological tolerance for low temperatures (Brill, 1994), and more bigeye tuna were caught at higher latitudes in our study area than yellowfin tuna (Fig. 1). Our study shows that bigeye tuna catch was higher in both types of eddies, possibly due to the high

primary productivity found in cyclonic eddies and the high prey density found in anticyclonic eddies.

Swordfish catch distribution differed from those of the three tuna species. Swordfish catch was highest in non-eddy habitats, followed by anticyclonic eddies, and lowest in cyclonic eddies. Swordfish show less affinity to eddy structures than do tunas in our study area. This could be attributed to the fact that the diet and feeding ecology of swordfish differ from those of tunas in a number of ways. Swordfish are solitary, opportunistic feeders. In the North Atlantic, swordfish prey was dominated by both fish and cephalopods, while tuna prey tended to be dominated solely by fish (Chancollon *et al.*, 2006; Logan *et al.*, 2013). Swordfish generally occupy a higher trophic level than tunas and consume prey of larger body mass (Chancollon *et al.*, 2006). In the Indian Ocean, Potier *et al.* (2007) found that swordfish diet was dominated by larger, adult prey items, whereas the diet of yellowfin tuna was dominated by smaller, juvenile items. Swordfish also occasionally prey on tunas (*Thunnus* sp.) (Chancollon *et al.*, 2006). Compared to tunas, swordfish have lower energy needs and are better adapted to feed in the depleted parts of the ocean, such as the non-eddy habitats (Pusineri *et al.*, 2008). While our results suggest that swordfish catch was less associated with eddies, other studies have shown that swordfish are attracted to oceanographic structures, such as convergence zones, thermal fronts, and upwelling systems generated by the Gulf Stream (Sedberry and Loefer, 2001; Dewar *et al.*, 2011).

Similar to bluefin tuna catch, swordfish catch was correlated with lower SSTs. The oceanographic structures that attract swordfish, such as frontal areas and upwelling regions, are places where cold waters meet with warm waters and where large temperature contrasts are found (Sedberry and Loefer, 2001; Santos *et al.*, 2006). Swordfish can endure both extremely low temperatures (4°C) and rapid temperature changes (>20°C). This allows them to migrate between the deep cold waters during the day and the warm surface waters during the night. Swordfish sometimes break their typical diel pattern and return to the surface in daytime (Dewar *et al.*, 2011). This behavior, known as basking, is hypothesized to recharge the swordfish's thermal budget and to benefit the swordfish's foraging performance by providing a warm environment that facilitates swordfish's digestion (Dewar *et al.*, 2011).

Effects of fishing gear configuration on catch

Our statistical models show that tuna catch increases as fishers use fewer light sticks whereas swordfish catch increases as fishers use more light sticks. The number

of light sticks used is a good proxy for whether the longline set was a day set or a night set. Swordfish are active feeders at night, and the U.S. Atlantic longline fishery has learned to work at night and to use light sticks when targeting swordfish (Witzell, 1999). Conversely, tuna catch tended to increase as fewer light sticks were used. This is likely due to the fact that tunas tend to feed most heavily during the day, and fewer light sticks are used in day sets (Witzell, 1999; Walli *et al.*, 2009).

In addition to the different responses to the number of light sticks used, bigeye tuna and swordfish catches also display different responses to the number of hooks between floats. Bigeye tuna catch increases whereas swordfish catch decreases with increasing number of hooks between floats. Increasing the number of hooks between floats causes the fishing gear to fish deeper in the water, as the mainline can sag more between floats. Bigeye tuna are known to spend the majority of the day feeding actively in deep, oxygen-poor waters (Brill, 1994; Musyl *et al.*, 2003; Evans *et al.*, 2008), whereas swordfish stay closer to the surface at night (Dewar *et al.*, 2011). As a result, bigeye tuna (swordfish) were caught more frequently with fewer (more) light sticks used and with a greater (smaller) number of hooks between floats, suggesting that deep (shallow), day (night) sets were most effective at catching bigeye tuna (swordfish).

Bluefin and yellowfin tuna catches are significantly higher with decreasing number of light sticks used but have no significant correlation with the number of hooks between floats. For these two species, the number of light sticks used and, by proxy, whether the haul is a day set or a night set, is more important than the number of hooks between floats and, by proxy, fishing depth, in determining catch.

Implications for management

Our results regarding the distribution of fish species in relation to physical oceanography have potential implications for fisheries management. In the last several years, the U.S. pelagic longline fleet has exceeded their catch allocation of bluefin tuna, while being under their allotted swordfish catch. Bluefin tuna and swordfish catches display opposite responses to most of the predictor variables we analyzed using our statistical models. Among the three eddy categories present in our study area, the highest catch of bluefin tuna occurred in anticyclonic eddies, while eddy activity generally did not increase swordfish catch. Bluefin tuna catch was negatively correlated with longitude and the number of light sticks used whereas swordfish catch was positively correlated with these two

variables. According to these results, overfishing of bluefin tuna can be alleviated and swordfish can be targeted more efficiently in the northwest Atlantic by avoiding fishing in anticyclonic eddies and in near-shore waters and by using more light sticks and fishing at night. Although dynamic management based on oceanographic features is difficult to implement, this technique has been used or proposed in other regions and fisheries (Hobday and Hartmann, 2006; Howell et al., 2008; Teo and Block, 2010). To propose a solid oceanography-based management plan for selecting catch among our focal species in the northwest Atlantic fishery, further studies on the responses of these species to mesoscale oceanographic features are needed. Our research calls for studies that compare the different effects of eddies in different regions within our study area using different statistical approaches, different biological datasets, or a combination of both.

ACKNOWLEDGEMENTS

This research was supported by NASA grant NNX08AK73G. A.M.B. was partly supported by the NF-UBC Nereus Program. The altimeter products used in this study were produced by Ssalto/Duacs and distributed by AVISO, with support from CNES (<http://www.aviso.oceanobs.com/duacs/>). The authors thank the fishers and NOAA SEESC for providing logbook data and Connie Kot for processing and sharing logbook data. We wish to thank Edward Farrell for sharing his knowledge in applying ZINB models to fishery data. Helpful comments to an earlier version of this manuscript from four anonymous reviewers significantly improved this study. The authors also thank Jie-Sheng Tan-Soo for statistical advice and Tina Praprotnik for writing advice.

REFERENCES

- Bakun, A. (2006) Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Sci. Mar.* **70**(S2):105–122.
- Bertrand, A., Josse, E., Bach, P., Gros, P. and Dagorn, L. (2002a) Hydrological and trophic characteristics of tuna habitat: consequences on tuna distribution and longline catchability. *Can. J. Fish Aquat. Sci.* **59**:1002–1013.
- Bertrand, A., Bard, F.X. and Josse, E. (2002b) Tuna food habits related to the micronekton distribution in French Polynesia. *Mar. Biol.* **140**:1023–1037.
- Block, B.A., Dewar, H., Farwell, C. and Prince, E.D. (1998) A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proc. Natl Acad. Sci. USA* **95**:9384–9389.
- Block, B.A., Dewar, H., Blackwell, S.B. et al. (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* **293**:1310–1314.
- Block, B.A., Teo, S.L.H., Walli, A. et al. (2005) Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434**:1121–1127.
- Brill, R.W. (1994) A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fish Oceanogr.* **3**:204–216.
- Campagna, C., Piola, A.R., Marin, M.R., Lewis, M. and Fernandez, T. (2006) Southern elephant seal trajectories, fronts and eddies in the Brazil/Malvinas Confluence. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **53**:1907–1924.
- Carey, F.G. (1982) A brain heater in the swordfish. *Science* **216**:1327–1329.
- Carey, F.G. and Lawson, K.D. (1973) Temperature regulation in free-swimming bluefin tuna. *Comp. Biochem. Physiol. Part A Physiol.* **44**:375–392.
- Chancollon, O., Pusineri, C. and Ridoux, V. (2006) Food and feeding ecology of Northeast Atlantic swordfish (*Xiphias gladius*) off the Bay of Biscay. *ICES J. Mar. Sci.* **63**:1075–1085.
- Chelton, D.B., Schlax, M.G., Samelson, R.M. and de Szoeke, R.A. (2007) Global observations of large oceanic eddies. *Geophys. Res. Lett.* **34**:L15606. doi:10.1029/2007GL030812.
- Cotté, C., Park, Y.-H., Guinet, C. and Bost, C.-A. (2007) Movements of foraging king penguins through marine mesoscale eddies. *Proc. Biol. Sci.* **274**:2385–2391.
- Dewar, H., Prince, E.D., Musyl, M.K. et al. (2011) Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fish Oceanogr.* **20**:219–241.
- Evans, K., Langley, A., Clear, N.P. et al. (2008) Behaviour and habitat preferences of bigeye tuna (*Thunnus obesus*) and their influence on longline fishery catches in the western Coral Sea. *Can. J. Fish Aquat. Sci.* **65**:2427–2443.
- Galuardi, B., Royer, F., Golet, W., Logan, J., Neilson, J. and Lutcavage, M. (2010) Complex migration routes of Atlantic bluefin tuna (*Thunnus thynnus*) question current population structure paradigm. *Can. J. Fish Aquat. Sci.* **67**:966–976.
- Garçon, V.C., Oschlies, A., Doney, S.C., McGillicuddy, D. and Waniek, J. (2001) The role of mesoscale variability on plankton dynamics in the North Atlantic. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **48**:2199–2226.
- Hansen, D.V. and Bezdek, H.F. (1996) On the nature of decadal anomalies in North Atlantic sea surface temperature. *J. Geophys. Res.* **101**:8749–8758.
- Henson, S.A. and Thomas, A.C. (2008) A census of oceanic anticyclonic eddies in the Gulf of Alaska. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **55**:163–176.
- Hobday, A.J. and Hartmann, K. (2006) Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fish. Manage. Ecol.* **13**:365–380.
- Howell, E.A., Kobayashi, D.R., Parker, D.M., Balazs, G.H. and Polovina, J.J. (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endanger. Species Res.* **5**:267–278.
- Howell, E.A., Dutton, P.H., Polovina, J.J., Bailey, H., Parker, D.M. and Balazs, G.H. (2010) Oceanographic influences on the dive behavior of juvenile loggerhead turtles (*Caretta*

- caretta*) in the North Pacific Ocean. *Mar. Biol.* **157**:1011–1026.
- International Commission for the Conservation of Atlantic Tunas (ICCAT) (2011) Report of the Standing Committee on Research and Statistics (Madrid, Spain – October 4 to 8, 2010). *Report for biennial period 2010–2011, Part I (2010) Vol. 2*, 265 pp.
- Isern-Fontanet, J., Font, J., García-Ladona, E., Emelianov, M., Millot, C. and Taupier-Letage, I. (2004) Spatial structure of anticyclonic eddies in the Algerian basin (Mediterranean Sea) analyzed using the Okubo-Weiss parameter. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **51**:3009–3028.
- Isern-Fontanet, J., García-Ladona, E. and Font, J. (2006) Vortices of the Mediterranean Sea: an altimetric perspective. *J. Phys. Oceanogr.* **36**:87–103.
- Iudicone, D., Santoleri, R., Marullo, S. and Gerosa, P. (1998) Sea level variability and surface eddy statistics in the Mediterranean Sea from Topex/Poseidon data. *J. Geophys. Res.* **103**(C2):2995–3011.
- Kot, C.Y., Boustany, A.M. and Halpin, P.N. (2010) Temporal patterns of target catch and sea turtle bycatch in the US Atlantic pelagic longline fishing fleet. *Can. J. Fish Aquat. Sci.* **67**:42–57.
- Lawson, G.L., Castleton, M.R. and Block, B.A. (2010) Movements and diving behavior of Atlantic bluefin tuna *Thunnus thynnus* in relation to water column structure in the northwestern Atlantic. *Mar. Ecol. Prog. Ser.* **400**:245–265.
- Leach, H., Bowerman, S.J. and McCulloch, M.E. (2002) Upper-ocean eddy transports of heat, potential vorticity, and volume in the northeastern North Atlantic—'Vivaldi 1991'. *J. Phys. Oceanogr.* **32**:2926–2937.
- Logan, J.M., Toppin, R., Smith, S., Galuardi, B., Porter, J. and Lutcavage, M. (2013) Contribution of cephalopod prey to the diet of large fish predators in the central North Atlantic Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **95**:74–82.
- Logan, J.M., Golet, W.J. and Lutcavage, M. (2015) Diet and condition of Atlantic bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine, 2004–2008. *Environ. Biol. Fishes* **98**:1411–1430.
- McGillicuddy, D.J. and Robinson, A.R. (1997) Eddy-induced nutrient supply and new production in the Sargasso Sea. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **44**:1427–1450.
- McGillicuddy, D.J., Robinson, A.R., Siegel, D.A. et al. (1998) Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* **394**:263–266.
- McGillicuddy, D.J., Anderson, L.A., Bates, N.R. et al. (2007) Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. *Science* **316**:1021–1026.
- Minami, M., Lennert-Cody, C.E., Gao, W. and Román-Verdesoto, M. (2007) Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. *Fish. Res.* **84**:210–221.
- Morrow, R., Church, J., Coleman, R., Chelton, D. and White, N. (1992) Eddy momentum flux and its contribution to the Southern Ocean momentum balance. *Nature* **357**:482–484.
- Mugo, R., Saitoh, S.-I., Nihira, A. and Kuroyama, T. (2010) Habitat characteristics of skipjack tuna (*Katsuwonus pelamis*) in the western North Pacific: a remote sensing perspective. *Fish Oceanogr.* **19**:382–396.
- Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K. and Seki, M.P. (2003) Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fish Oceanogr.* **12**:152–169.
- Nakamura, Y. (1985) FOA species catalogue, vol. 5: billfishes of the world. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes and swordfishes known to date. *FAO Fish. Synop.* **125**:48–51.
- National Marine Fisheries Service (NMFS) (2002) Final Supplemental Environmental Impact Statement: Regulatory Adjustment 2 to the Atlantic Tunas, Swordfish, and Sharks Fishery Management Plan. Final Rule to Reduce Sea Turtle Bycatch and Bycatch Mortality in Highly Migratory Species Fisheries. Silver Spring, MD: National Marine Fisheries Service, 175 pp.
- Neilson, J.D., Smith, S., Royer, F., Paul, S.D., Porter, J.M. and Lutcavage, M. (2009) Investigations of horizontal movements of Atlantic swordfish using pop-up satellite archival tags. In: Tagging and Tracking of Marine Animals with Electronic Devices. J.L. Nielsen, H. Arribalaga, N. Fragoso, A. Hobday, M. Lutcavage & J. Sibert (eds) New York, NY: Springer, pp. 145–159.
- Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Anson, I.J., Ryan, P.G. and Klages, N.T.W. (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Mar. Ecol. Prog. Ser.* **217**:15–26.
- NOAA (2010) Fisheries Logbook System—Pelagic Logbook Data. Southeast Fisheries Science Center. National Oceanographic and Atmospheric Administration. URL <http://www.sefsc.noaa.gov/data/pelagiclogbook.htm>. [accessed 27 December 2007].
- Okubo, A. (1970) Horizontal dispersion of floatable particles in the vicinity of velocity singularity such as convergences. *Deep-Sea Res.* **17**:445–454.
- Oschlies, A. and Garçon, V. (1998) Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature* **394**:266–269.
- Paillet, J. (1999) Central water vortices of the eastern North Atlantic. *J. Phys. Oceanogr.* **29**:2487–2503.
- Palmer, T.N. and Sun, Z. (1985) A modeling and observational study of the relationship between sea surface temperature in the north-west Atlantic and the atmospheric general circulation. *Q. J. R. Meteorol. Soc.* **111**:947–975.
- Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P. and Dutton, P.H. (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central north Pacific Ocean. *Fish Oceanogr.* **13**:36–51.
- Polovina, J., Uchida, I., Balazs, G., Howell, E.A., Parker, D. and Dutton, P. (2006) The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **53**:326–339.
- Potier, M., Marsac, F., Cherel, Y. et al. (2007) Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fish. Res.* **83**:60–72.
- Pusineri, C., Chancollon, O., Ringelstein, J. and Ridoux, V. (2008) Feeding niche segregation among the Northeast Atlantic community of oceanic top predators. *Mar. Ecol. Prog. Ser.* **361**:21–34.
- R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL <http://www.R-project.org/> [accessed 31 May 2011].

- Roberts, J.J., Best, B.D., Dunn, D.C., Treml, E.A. and Halpin, P.N. (2010) Marine Geospatial Ecology Tools: an integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. *Environ. Model. Softw.* **25**:1197–1207.
- Santos, A.M.P., Fiuza, A.F.G. and Laurs, R.M. (2006) Influence of SST on catches of swordfish and tuna in the Portuguese domestic longline fishery. *Int. J. Remote Sens.* **27**:3131–3152.
- Satoh, K. (2010) Horizontal and vertical distribution of larvae of Pacific bluefin tuna *Thunnus orientalis* in patches entrained in mesoscale eddies. *Mar. Ecol. Prog. Ser.* **404**:227–240.
- Sedberry, G.R. and Loefer, J.K. (2001) Satellite telemetry tracking of swordfish, *Xiphias gladius*, off the eastern United States. *Mar. Biol.* **139**:355–360.
- Shoosmith, D.R., Richardson, P.L., Bower, A.S. and Rossby, H.T. (2005) Discrete eddies in the northern North Atlantic as observed by looping RAFOS floats. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **52**:627–650.
- Sperling, A.T., Neilson, J.D., Carruthers, E.H. and Stone, H.H. (2005) Compilation and analyses of Canadian conventional tagging data for swordfish (*Xiphias gladius*), 1961–2004. *Col. Vol. Sci. Pap. ICCAT* **58**:1483–1494.
- Teo, S.L.H. and Block, B.A. (2010) Comparative influence of ocean conditions on yellowfin and Atlantic bluefin tuna catch from longlines in the Gulf of Mexico. *PLoS ONE* **5**: e10756. doi:10.1371/journal.pone.0010756.
- Teo, S.L.H., Boustany, A.M. and Block, B.A. (2007) Oceanographic preferences of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Mar. Biol.* **152**:1105–1119.
- Tew-Kai, E. and Marsac, F. (2010) Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. *Prog. Oceanogr.* **86**:214–223.
- Tserpes, G., Peristeraki, P. and Valavanis, V.D. (2008) Distribution of swordfish in the eastern Mediterranean, in relation to environmental factors and the species biology. *Hydrobiologia* **612**:241–250.
- Vaillancourt, R.D., Marra, J., Seki, M.P., Parsons, M.L. and Bidigare, R.R. (2003) Impact of a cyclonic eddy on phytoplankton community structure and photosynthetic competency in the subtropical North Pacific Ocean. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **50**:829–847.
- Volkov, D.L., Lee, T. and Fu, L.L. (2008) Eddy-induced meridional heat transport in the ocean. *Geophys. Res. Lett.* **35**:L20601. doi:10.1029/2008GL035490.
- Walli, A., Teo, S.L.H., Boustany, A. et al. (2009) Seasonal movements, aggregations and diving behavior of Atlantic Bluefin Tuna (*Thunnus thynnus*) revealed with archival tags. *PLoS ONE* **4**:e6151. doi:10.1371/journal.pone.0006151.
- Weiss, J. (1991) The dynamics of enstrophy transfer in two-dimensional hydrodynamics. *Physica D* **48**:273–294.
- Witzell, W.N. (1999) Distribution and relative abundance of sea turtles caught incidentally by the US pelagic longline fleet in the western North Atlantic Ocean, 1992–1995. *Fish. Bull.* **97**:200–211.
- Woodworth, P.A., Schorr, G.S., Baird, R.W. et al. (2011) Eddies as offshore foraging grounds for melon-headed whales (*Peponocephala electra*). *Mar. Mamm. Sci.* **28**:638–647. doi:10.1111/j.1748-7692.2011.00509.x.
- Xu, C., Shang, X.D. and Huang, R.X. (2011) Estimate of eddy energy generation/dissipation rate in the world ocean from altimetry data. *Ocean Dyn.* **61**:525–541.
- Yen, P.P.W., Sydeman, W.J., Bograd, S.J. and Hyrenbach, K.D. (2006) Spring-time distributions of migratory marine birds in the southern California Current: oceanic eddy associations and coastal habitat hotspots over 17 years. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **53**:399–418.
- Young, J.W., Lansdell, M.J., Campbell, B.A., Cooper, S.P., Juanes, F. and Guest, M.A. (2010) Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Mar. Biol.* **157**:2347–2368.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M. (2009) Zero-truncated and zero-inflated models for count data. In: *Mixed Effects Models and Extensions in Ecology with R*. A. Zuur, E.N. Ieno, N. Walker, A.A. Saveliev & G.M. Smith (eds) New York, NY: Springer, pp. 261–293.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1–S4. Summary tables of the final zero-inflated negative binomial (ZINB) models that predict the catch of bluefin tuna (Table S1), yellowfin tuna (Table S2), bigeye tuna (Table S3), and swordfish (Table S4).