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A hypothesis of a redistribution of North Atlantic swordfish based on changing ocean conditions



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ABSTRACT

Conflicting trends in indices of abundance for North Atlantic swordfish starting in the mid-to late 1990s, in the form of fleet specific catch-per-unit-effort (CPUE), suggest the possibility of a spatial shift in abundance to follow areas of preferred temperature. The observed changes in the direction of the CPUEs correspond with changes in trends in the summer Atlantic Multidecadal Oscillation (AMO), a long term mode of variability of North Atlantic sea surface temperature. To test the hypothesis of a relation between the CPUE and the AMO, the CPUEs were made spatially explicit by re-estimating using an “areas-as-fleets” approach. These new CPUEs were then used to create alternative stock histories. The residuals of the fit were then regressed against the summer AMO. Significant, and opposite, relations were found in the regressions between eastern and western Atlantic areas. When the AMO was in a warm phase, the CPUEs in the western (eastern) areas were higher (lower) than predicted by the assessment model fit. Given the observed temperature tolerance limits of swordfish, it is possible that either their preferred habitat, prey species, or both have shifted spatial distributions resulting in conflicting CPUE indices. Because the available CPUE time series only overlaps with one change in the sign of the AMO (~1995), it is not clear whether this is a directional or cyclical trend. Given the relatively localized nature of many of the fishing fleets, and the difficulty of separating fleet effects from changes in oceanography we feel that it is critical to create CPUE indices by combining data across similar fleets that fish in similar areas. This approach allowed us to evaluate area-specific catch rates which provided the power to detect basin-wide responses to changing oceanography, a critical step for providing robust management advice in a changing climate.

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1. Introduction

Swordfish (*Xiphias gladius*) is a highly migratory species found through the temperate waters of the Atlantic, Pacific and Indian Oceans and the Mediterranean Sea. Like many other highly migratory species, swordfish undertake seasonal migrations in search of food, reproductive success, or a hospitable habitat in which they can flourish for either the short or long term. Broad based physical oceanographic conditions in which the swordfish live, change on a temporal scale much faster than do the environmental preferences of swordfish. As a consequence, their

preferred habitat, and the location of this habitat, are not constant in time or space. Swordfish require huge amounts of prey intake to support their migratory and high energy life style and will travel thousands of miles north to higher latitudes within a year in search of their preferred prey. However, since the environmental conditions that are conducive to high prey densities are not the same as those for reproduction, they must then make southern migrations to the tropics in order to maximize their annual reproductive potential (Arocha and Lee, 1996).

Stock assessment models rely upon statistical fits to time series of landings and abundance indices and often age or length composition information to reconstruct historical stock abundance. Generally these time series of catch and indices of relative abundance are in the form of usually standardized catch-per-unit effort (CPUE) data from either fishery dependent data or scientific

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surveys. A fundamental assumption of standardized CPUE-based indices is that they are linearly related to actual abundance through a constant scaling parameter called catchability or the fraction of the population captured by a unit of fishing or survey effort (Arreguín-Sánchez, 1996). In most assessments, there are often multiple and sometimes conflicting indices available, presenting a dilemma as to which indices truly represent the population abundance. Often apparent conflicts can be rectified within age-structured models by allowing for differential selectivity by size or age (Quinn and Deriso, 1999) and by modeling of movement or complicated spatial structure (Cadrin and Secor, 2009).

However, most assessments do not explicitly model the usually time-varying spatial distribution of the stock and so assume that the stock is both homogeneous and time-invariant. It is further assumed that the catchability associated with the estimate of the CPUE is also constant over time and space. However as catchability is a function not only of the gear but also of the spatial availability of the fish, there are many factors that could alter the relationship between CPUE and fish abundance. For example, as fish migrate and redistribute themselves according to changes in preferred habitat, subsequent changes in their densities alter catchability. As a consequence, the observed CPUE in the preferred area can increase while those in the less preferred areas decrease due not to a change in overall stock size, but a change in area specific catchability caused by changes in local density. While it is sometimes possible to account for this phenomena in the CPUE standardization process with appropriate spatial or temporal structure, interannual variation in habitat is often completely confounded with the interannual abundance signal.

In the most recent stock assessment of North Atlantic swordfish conflicting CPUEs generated substantial discussion on how they should be treated and if these indices should be used in the assessment (Anonymous, 2014). The current Atlantic swordfish management units are separated into a north and a south stock delineated by a horizontal line at 5°N latitude, and we focus on the northern stock assessment for this paper.

CPUE time series from the northern stock showed conflicting trends in the past decade with indices from fisheries operating mostly in the northern latitudes (Canada, Morocco, Portugal) increasing at a relatively high rate while those operating in the more southern and central areas (U.S. and Japan) were decreasing or remained flat. Rather than confronting the assessment model with these conflicting indices, or attempting to determine which ones should be included/excluded in the assessment we sought a mechanistic reconciliation to these apparent contradictions.

In this paper we step through stage one of the swordfish stock assessment process that used CPUEs specific to the country flag of the fishing vessel (“flags-as-fleets”) to assemble the assessment model. We used the lack of fit of the estimated population trend to these CPUE indices to construct a hypothesis to explain the trend in the residuals of the fits in the western North Atlantic. Previous pop-up satellite tag (PSAT) studies have suggested that swordfish prefer water temperatures below 28 °C (Lerner et al., 2013; Abecassis et al., 2012; Dewar et al., 2011; Boyce et al., 2008; Sedberry and Loefer, 2001; Nakamura, 1985). This is the basis of the mechanism underlying the hypothesis. The Western Hemisphere Warm Pool (WHWP) is a region of sea surface temperatures (SST) warmer than 28.5 °C that develops west of Central America in the spring, then expands to the tropical Atlantic waters to the east. It has a distinct monthly trend as well as a low frequency cycle. Observing that the WHWP index went through a change in sign from negative (below average in areal size) to positive (above average in areal size) around 1995, we hypothesized that this increase in the area of water warmer than the preferred temperature of swordfish may have led to an increase in the rate or duration of the summer migration of swordfish into more northern regions. It was presumed that this led to a “crowding” effect

in the northern areas that could have increased the density and thus the catchability of the fish in those areas. We first step through our original hypothesis: the WHWP is a predictor of swordfish distribution and density in the western North Atlantic using “flags-as-fleets” CPUE’s. In step two we proceed to broaden our original hypothesis to one that uses the summer SST anomalies from the Atlantic Multi-decadal Oscillation (AMO), a spatially broader oceanographic indicator, coupled with a spatially explicit reanalysis of the CPUE data using an “areas-as-fleets” approach. Thus, the objective of this work was to use a hypothesis testing approach to quantitatively assess the likelihood of a null versus an alternative model configuration that represented two various possible states of nature, namely that the density, and thus the catchability, of northern swordfish has not (or has), changed over time and space in accordance with key environmental indicators.

2. Methods

2.1. “Flags-as-fleets” CPUE

We used standardized, flag-specific (i.e. “flags-as-fleets”) indices of abundance provided by the individual Contracting Party, Cooperating non-Contracting Party, Entity or Fishing Entity (CPC) during the ICCAT 2013 Atlantic swordfish data preparatory meeting (Anonymous, 2014a). The CPCs that provided vessel flag-specific indices that were used in the stock assessment included Canada (Andrushchenko et al., 2014), Japan (Yokawa and Kai, 2014), Portugal (Santos et al., 2014), Spain (García-Cortés et al., 2014), and the United States (Walter et al., 2014). The approximated areas that are fished by each CPC are shown in Fig. 1. Based on decisions made during the data preparatory meeting, the Japanese, Canadian, and United States data were each broken into two time stanzas that represented differences in that particular fleet’s fishing operations. In all cases, a Generalized Linear Model (GLM) procedure was used to standardize the nominal CPUE by factors found to be statically significant, however each CPC conducts an independent GLM analyses prior to presentation to the data preparatory meeting. So while CPUE standardization methods between CPCs are generally similar, they can differ in the specific covariates used across the participating CPC’s.

2.2. “Areas-as-fleets” CPUE

In addition to the flag-specific indices of abundance, a combined index of abundance (combined across all flags) was also created. Generalized Linear Modeling (GLM) procedures were used to standardize swordfish catch (biomass) and effort (number of hooks) data from the same longline fleets mentioned above with the addition of Morocco (Abid et al., 2014). Main effects included: year, area, quarter, a nation-operation variable accounting for gear and operational differences thought to influence swordfish catchability, and a target variable to account for trips where fishing operations varied according to the main target species. Interactions among main factors were also evaluated. For a complete description of how the CPUE indices were derived see Ortiz et al. (2014). The least square means of the year-area effects were used to estimate 14 individual CPUE indices, each corresponding to a unique area (Fig. 2).

2.3. Other observational data

Monthly values of the WHWP for the years 1948–present were available from the NOAA Earth System Research Laboratory website (<http://www.esrl.noaa.gov/psd/data/correlation/whwp.data>). A summer index of the WHWP was created by averaging the months August, September, and October, the months that coincide with the northernmost observations of swordfish from the

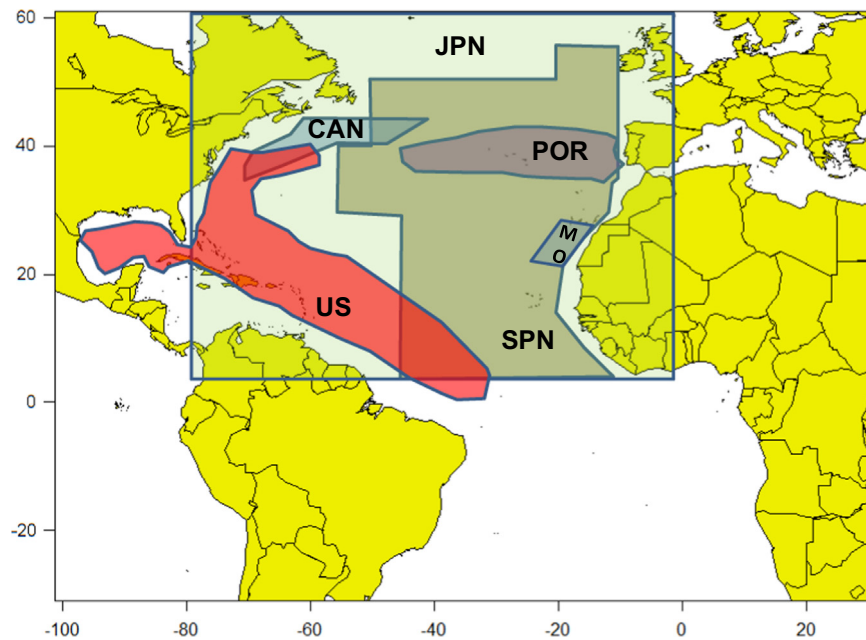


Fig. 1. Approximate areas that each ICCAT fleet fishes for swordfish with longline gear, 1960–2011; Japan (JPN), Canada (CAN), Portugal (POR), United States (US), Morocco (MO) and Spain (SPN).

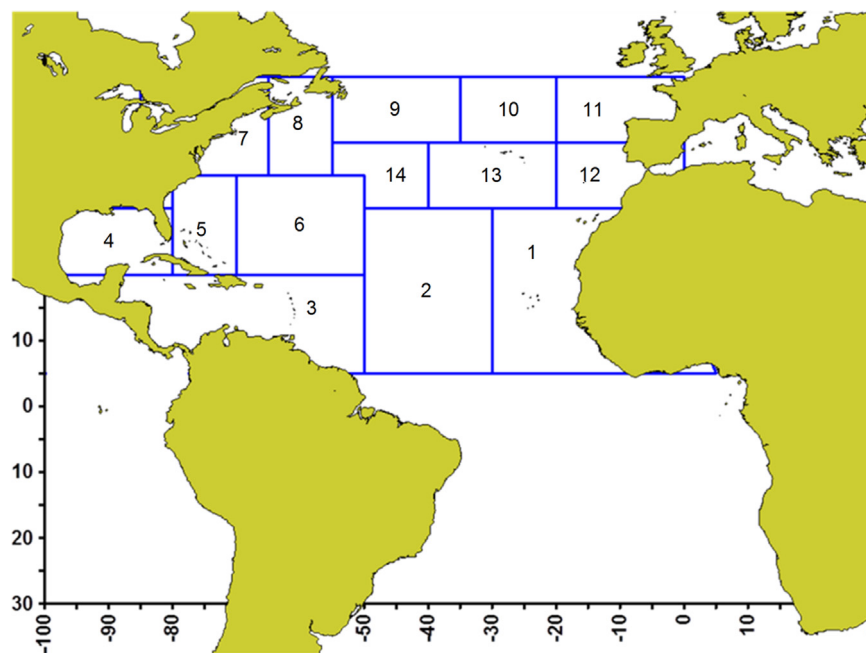


Fig. 2. Area designations used to produce the area-specific CPUEs, 1960–2011.

observer data as well as the peak size of the WHWP. The WHWP index was used in conjunction with the fully integrated model.

The Atlantic Multidecadal Oscillation (AMO) is an index of long duration changes in the sea surface temperature of the North Atlantic Ocean with cool and warm phases that may last for 20–40 years (Wang et al., 2008). It is highly correlated to the WHWP but covers a greater area. Monthly, unsmoothed values for the AMO were available from the NOAA Earth System Research Laboratory website (<http://www.esrl.noaa.gov/psd/data/correlation/amon.us.data>). The months of July, August, and September were averaged to arrive at a single value of summer SST anomalies. These months were chosen to coincide with the pattern of annual north/south migration of swordfish (see Section 3.1). Satellite imagery of the WHWP were available from 1992–2014 from the NOAA Fisheries webpage (<http://coastwatch.pfeg.noaa.gov/>

erddap/griddap/erdMH1sstmday.html. The index of summer SST anomalies was used in conjunction with the age-structured production model.

On board observer data of fishing activity and catch samples from United States flagged fishing vessels were available from 1996 onward. These data are collected from 5–8% subsample of randomly chosen trips from the U.S. fleet. These data were used to characterize the presence of swordfish off the U.S. east coast by month, latitude and sex.

2.4. Assessment model configuration 1: fully integrated model

For the first stage of hypothesis testing a fully integrated, age-structured model using the framework Stock Synthesis (Methot and Wetzel, 2013) was used to recreate the historic stock biomass

trend and assess the current status of the North Atlantic swordfish stock. This modeling platform was introduced for swordfish for the first time during the 2013 assessment and included data on landings, fleet-specific CPUE, growth, fecundity, sex ratio, and length compositions. All indices of abundance were given equal weighting in the fitting procedure. This modeling was done as an exploratory analysis but was also later considered for management advice. For a complete description of the assessment model see Schirripa (2014). The residual values between the observed CPUE and the estimated stock abundance trend were regressed against the summer WHWP values to determine if the WHWP might explain part of the lack of fit to the CPUEs. The residuals represent the lack of fit to the CPUE after accounting for annual changes in stock biomass.

2.5. Assessment model configuration 2: age-structured production model

For the second stage of hypothesis testing, Stock Synthesis was also used but configured as an age-structured production model approach. This model was constructed in a simpler manner than the fully integrated model, using one area, one sex, and one fishery and was fit to the fourteen area-specific CPUEs described above. This was done to accommodate the fact that it was not feasible to re-compile the length data by area, and thus the lengths could not be uniquely associated with the “areas-as-fleets” configuration. The fishery and all fourteen ‘surveys’ were assumed to have full

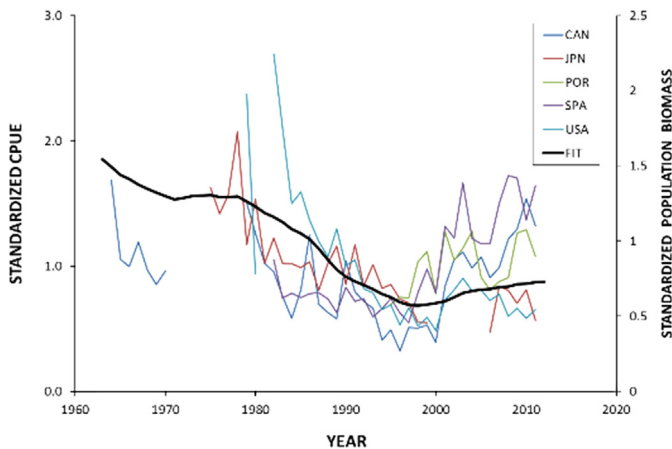


Fig. 3. Standardized longline CPUE by flag and estimated standardized swordfish population biomass from the fully integrated, “flags-as-fleets” stock assessment model.

and fixed (i.e. constant over time) selectivity. To make the model as similar to a traditional stock-production model as possible, all ages were put into one large plus group with all fish assumed to be mature. Natural mortality was fixed for each age at $M=0.20$. A Beverton–Holt stock-recruitment function was assumed with virgin recruitment (R_0) and steepness (h) being freely estimated (i.e. without any informative priors). Annual recruitment deviations were not estimated, also in keeping with the concept of an age-structured production model. A catchability coefficient was freely estimated for each of the fourteen surveys.

Two population models of this type were configured. The first model (NULL) represented the null hypothesis, that there was no relation between the annual values of the environmental covariate and the annual deviations in the observed and expected CPUE (e.g. no change in catchability over time and space). In this model no annual deviations in the catchability parameter (q) were allowed. The second model (ALT) represents the alternative hypothesis, that there is a significant relation between the summer AMO and the CPUE deviations, where the annual deviation in CPUE for each area is calculated as

$$Deviate_{ta} = \ln(CPUE.OBS_{ta}/CPUE.EXP_{ta})$$

where t is the annual time step, a is the area, $CPUE.OBS$ the observed CPUE and $CPUE.EXP$ is the expected CPUE from the model fit. The ALT model estimates the q for each survey (and thus each area), but allows annual deviations in this parameter as dictated directly by the deviations in the summer SST anomalies as follows:

$q_t = q_{base} * \exp(\beta * ENV_t)$ where for each survey q_t is the catchability at time step t , q_{base} is the estimated mean q value, ENV_t is the environmental data at time step t , and β is an estimated parameter depicting the sensitivity of q to ENV . While this method allows q to vary directly at each time step, it does so in a manner that assumes no observation error in the environmental data.

3. Results

3.1. CPUE analysis: “flags-as-fleets”

All of the flag-specific, or “flags-as-fleets”, CPUE time series generally agree on a downward trend in abundance from approximately 1980 to 1995. However, there is greater divergence in the trends after the mid 1990s (Fig. 3). The post-1995 trend in historical stock biomass estimated from the fully integrated assessment model resulted in a trend that fell between the two sets of divergent CPUEs. This result suggests that either the observation error of the indices of abundance changed after 1995 or that the assessment model was

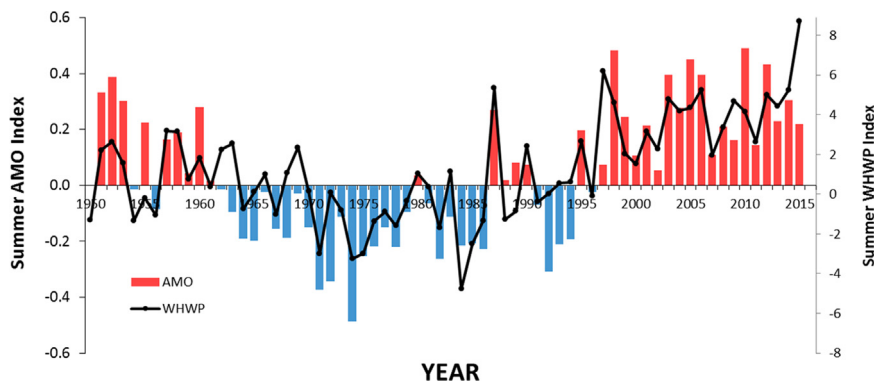


Fig. 4. Atlantic Multidecadal Oscillation for the summer (months June, July, and August) 1950–2015 (red bars indicate warm sea surface temperatures and blue bars represent cooler temperatures) and the area anomaly of the Western Atlantic Warm Pool for months of maximum observed swordfish northern migrations (September, October, and November) (positive values are years that are larger than average, negative are years that are smaller than average). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

misspecified after 1995. The divergence could also suggest that the distribution of the stock has become spatially more heterogeneous post-1995.

It was recognized that the period in the mid-1990s during which the trends in the flag-specific CPUE indices diverged coincided with the period when the sign of the WHWP summer anomaly changed from negative (below average in size) to positive (above average in size) (Fig. 4). From 1950 to 1970 the WHWP was in a positive phase, while from 1970 to 1995 it switched to a negative phase. In approximately 1995 the area of the WHWP switch again to positive and has maintained this positive phase up to 2015, the highest levels observed during the period shown.

Satellite images of the WHWP show the variation in the spatial extent of the 28.5 °C thermocline. In 1996 the WHWP was relatively small size (Fig. 5, top). Coincidentally, in 1996 the CPUE of the northern most CPC (Canada) was at its lowest level. Conversely, in August 2010 when the WHWP was anomalously large (Fig. 5, bottom), the Canadian CPUE was at a recent high. The anomalously large WHWP may have resulted in a latitudinal habitat compression situation where the swordfish were constrained to the northern most extent of their range, leading to increased density and thus an increased catchability.

Swordfish in the western North Atlantic begin an annual migration north in the spring, evidenced by the fact that no swordfish are observed above 40° latitude for the first five months of the year (Fig. 6, blocks). In May, the northern extent of swordfish observations begin to increase with a bias towards females. This movement north coincides directly with the beginning of the annual expansion of the WHWP (Fig. 6, line). The migration north increases in latitude each successive month with a peak in August, September and October. This peak corresponds very closely with the annual peak in the size of the WHWP. After October swordfish begin to migrate back to the southern areas, just when the WHWP begins an annual contraction. This annual migration pattern is presumably based on a search for sufficient food in the summer to support the next year's spawning activity. Swordfish spawning is strongly influenced by environmental factors, especially surface temperature. In the Atlantic, swordfish generally spawn ideally at temperatures from 23 to 26 °C (Beardsley, 1978; Rey, 1988). In the western North Atlantic, swordfish spawn all year round, with a peak in reproductive activity between December and June (Beardsley, 1978; Arocha, 1996). These observations lend support to our hypothesis that annual swordfish migration is triggered by the annual expansion and contraction of the WHWP. Furthermore, they suggest that annual variation in the size of the WHWP can lead to annual variations in the migration pattern.

The annual deviations in the fully integrated model fit to the Canada CPUE were positively correlated with the WHWP index ($R^2=0.33$) (Fig. 7). Thus, when the WHWP is larger (smaller) than average Canadian CPUEs are higher (lower) than expected by the assessment model. One explanation for these results is that the northern edge of the WHWP creates a thermal boundary of suitable swordfish habitat, increasing swordfish density to the north of the boundary and decreasing the density south of the boundary.

Conversely, the deviations to the Spain CPUE were shown to have a negative correlation ($R^2=0.39$) (Fig. 7). Thus, when the WHWP is larger (smaller) than average Spain CPUEs are lower (higher) than expected by the assessment model. However, Canada flagged vessels fish in the western North Atlantic while Spain flagged vessels fish in the eastern North Atlantic. So it was not clear how an index of suitable habitat confined mostly to the western North Atlantic would have an opposite effect in the eastern North Atlantic.

Annual deviations in the fit to the age-specific CPUE of Spain were shown to be positively correlated with the CPUEs of the younger ages (ages 1 and 2) and negatively correlated with the

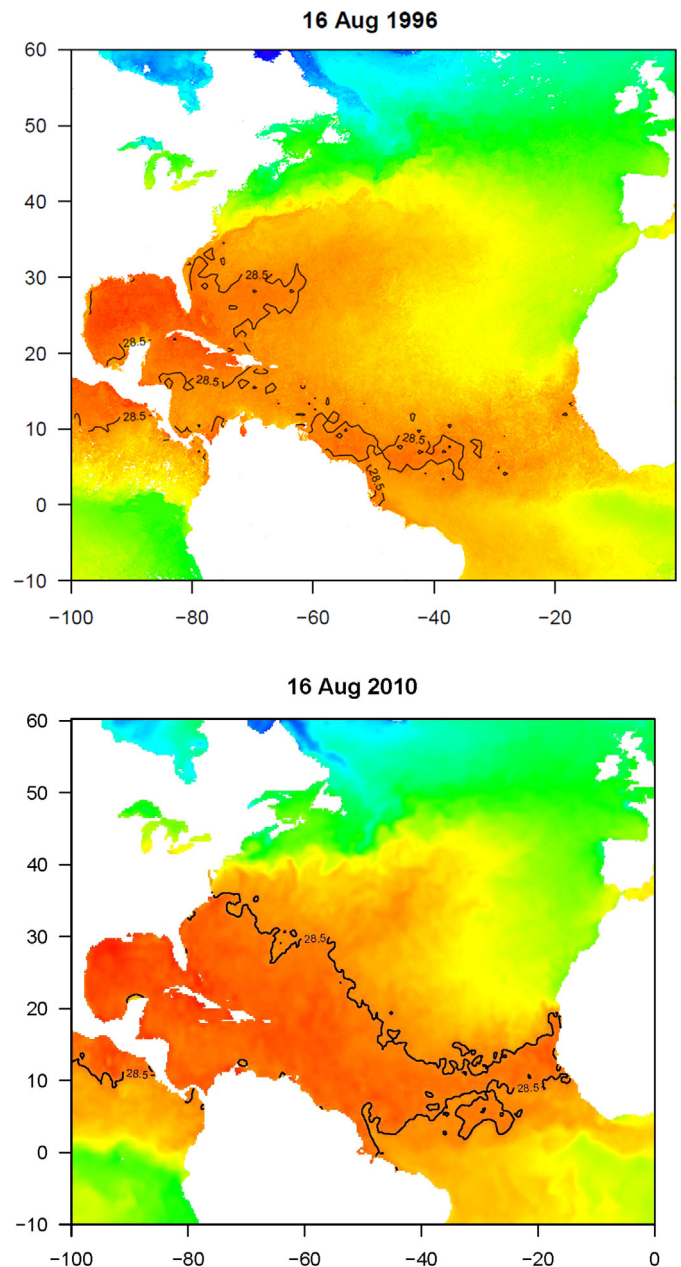


Fig. 5. Satellite imagery of sea surface temperatures with the Western Atlantic Warm Pool outlined (black contour) for the last anomalously small year (1996) and an anomalously large year (2010).

CPUEs of the older ages (age_4 and age_5) (Fig. 8). One possible explanation for this is that habitat preference and/or the ability to move to more preferred habitat differs between sizes and/or ages. This explanation is indirectly supported by the U.S. observer data that showed the shift in the sex ratio towards more females, which are larger than males, increased with increasing latitude (Fig. 6). Poisson and Fauvel (2009) also found seasonal patterns in swordfish size distribution in the Indian Ocean, suggesting sex and/or size specific habitat preferences.

Based on the above observations, we broadened our original hypothesis, which was based on observations of the CPUEs in only the western North Atlantic, to include the entire North Atlantic. To accomplish this, we needed to re-analyze the CPUE data to be more area specific rather than flag specific. Furthermore, we reasoned that the summer SST anomalies derived from the AMO, a geographically broader index of sea surface temperature than the

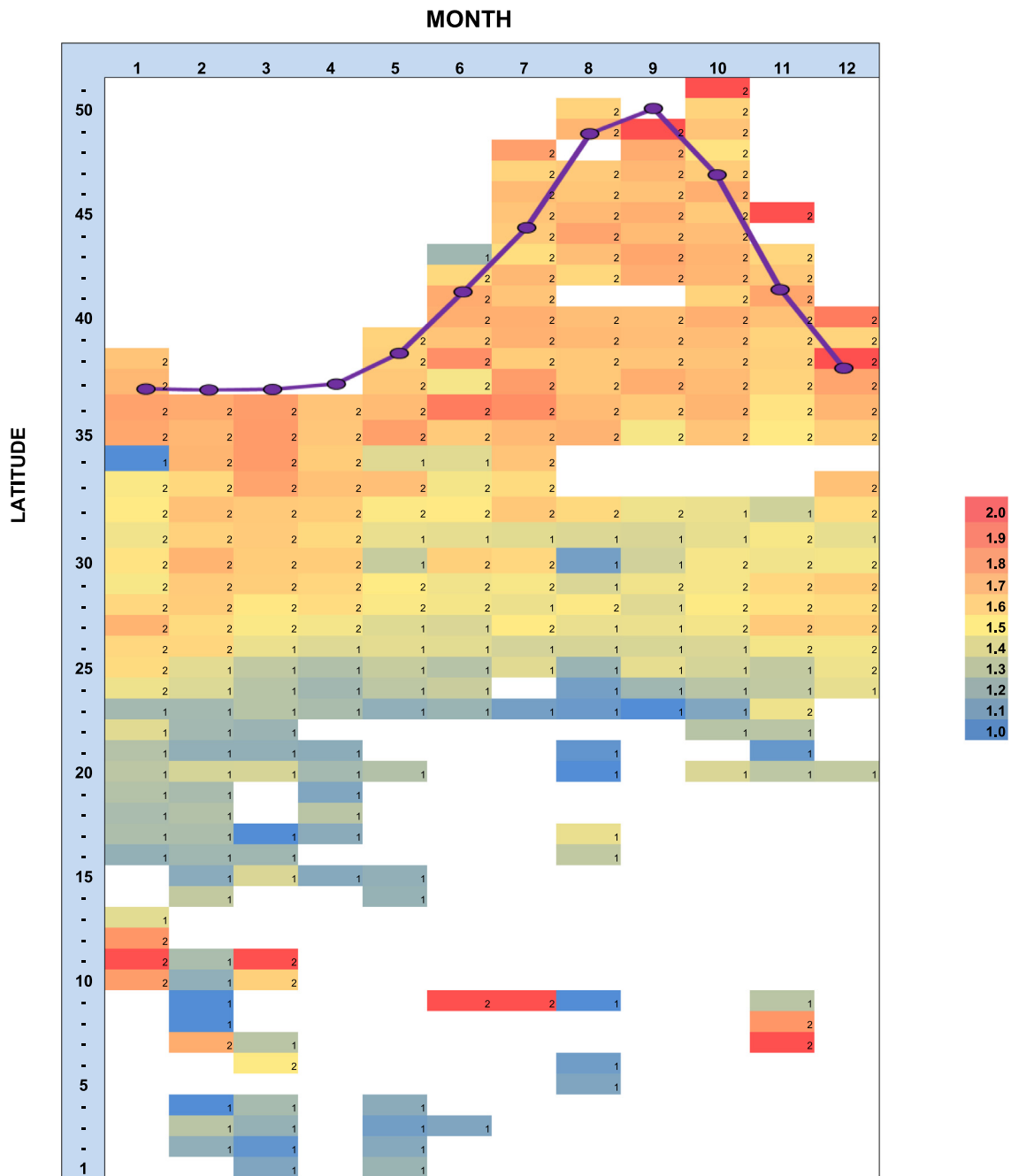


Fig. 6. Swordfish observations from U.S. fishery observers along the east coast of the U.S. by latitude and month, 1991–2011. Shading of cells and number within cells represent the average sex ratio of the observations across all years (1 and blue are males; 2 and females are red). The overlay line (purple) plot represents the monthly climatology of the size of the Western Hemisphere Warm Pool. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

somewhat more regionally confined WHWP, may be more appropriate for testing the broadened hypothesis β .

3.2. CPUE analysis: “areas-as-fleets”

Examination of the least squares means of the year-area effects from the combined GLM model suggested clustering between certain areas: areas 1–3, areas 4–6, areas 7–9, and areas 10–12 (Fig. 9). The areas within each cluster share at least one boundary and represent roughly the four quadrants of the North Atlantic. As a visual aid, these clusters were arranged within the figure to correspond to the four quadrants of the North Atlantic Ocean: the

northwest (upper left), northeast (upper right), southwest (lower left), and southeast (lower right) (Fig. 9). The trends in abundance in the southeast quadrant (areas 1, 2, 3) progressively decreased, while those in southwest corner (areas 4, 5, and 6) were more stable. The trends in abundance in the northwest quadrant (areas 7, 8, and 9) showed a marked increase starting in approximately 1995, while those in the northeast quadrant (areas 10, 11, and 12) decreased until approximately 2007, after which they began to increase. Based on these patterns in clustering and the differences between the four quadrants, we concluded that our original hypothesis of the environmental effects of the WHWP on the distribution of swordfish in the western North Atlantic may

actually be a geographically broader phenomenon. Because the WHWP index represents mostly the southwest quadrant of the North Atlantic, in step two we expanded our original hypothesis to consider the entire North Atlantic by using the summer SST anomalies from the AMO coupled with “areas-as-fleets” approach. The AMO is a geographically broader index of sea surface temperature than the somewhat more regionally confined WHWP, and thus was more appropriate for testing the modified hypothesis. Furthermore, the “areas-as-fleets” approach enabled us to make the CPUEs much more spatially explicit than the “flags-as-fleets” approach.

AMO warm phases (and by correlation the summer SST anomalies) occurred during 1860–1880 and 1940–1960, and cool phases during 1905–1925 and 1970–1990 (Enfield et al., 2001). Similar to the WHWP, the AMO switched signs in approximately 1962 and again in 1995 (Fig. 4). We plotted the residuals of the fit of the age-structured production model to the 14 year-area effects and found that some were positively correlated to the summer SST anomalies while other were negatively correlated (Fig. 10). We used ± 2 standard deviations of the estimate of the environmental link β parameter to derive approximate 95% confidence limits around each of the fourteen β estimates. Seven of the fourteen environmental link β parameters were found to have non-zero values (Table 1). Since the β parameter represents the slope of the line fit to the summer SST anomalies and CPUE residuals we treated non-zero values (i.e. values where zero was not contained within ± 2 standard deviations of the estimated value) as being significant at the $p < 0.05$ level. The residual mean square error for each of the fourteen fits either decreased with the addition of the summer SST anomaly data or stayed the same (Table 2). Using Akaike Information Criterion (AIC), a decrease of seventy-one likelihood units between the two models by the addition of the

fourteen environmental link β parameters justified the additional parameters (Anderson and Burham, 2002). Thus we concluded that the model incorporating the summer SST anomalies was superior to the model that did not.

Examination of the β parameter estimates show that neighboring areas were more similar than those further away (Fig. 11, top). If the areas of the CPUE analysis are colored according to the sign of the β parameter they follow very closely the stock boundaries suggested by genetic mapping (Bremer et al., 2005), as well as those from tagging (Neilson et al., 2014).

4. Discussion

This study sought to address three questions: (1) is there sufficient evidence to conclude that there has been a recent poleward shift in the Swordfish distribution in the North Atlantic; (2) if so, can this shift be quantified and are we making managerial progress by accounting for it within the stock assessment model; and (3) assuming number one is true, is this poleward shift unidirectional, or are we merely observing an abbreviated section of a reoccurring decadal cycle, the direction of which could change again sometime in the future. This investigation made a concerted effort to adhere as strictly as possible to the classic scientific method of “observation-hypothesis-test”. We first made the observation of the conflicting indices of abundance and developed the hypothesis and the mechanism behind it before attempting to statistically explain the deviations. In this way, we attempted to minimize the possibility of finding spurious correlations as a result of testing too many environmental time series. While the summer SST anomaly hypothesis does have a mechanistic underpinning, it was also noted that the time series of these anomalies only

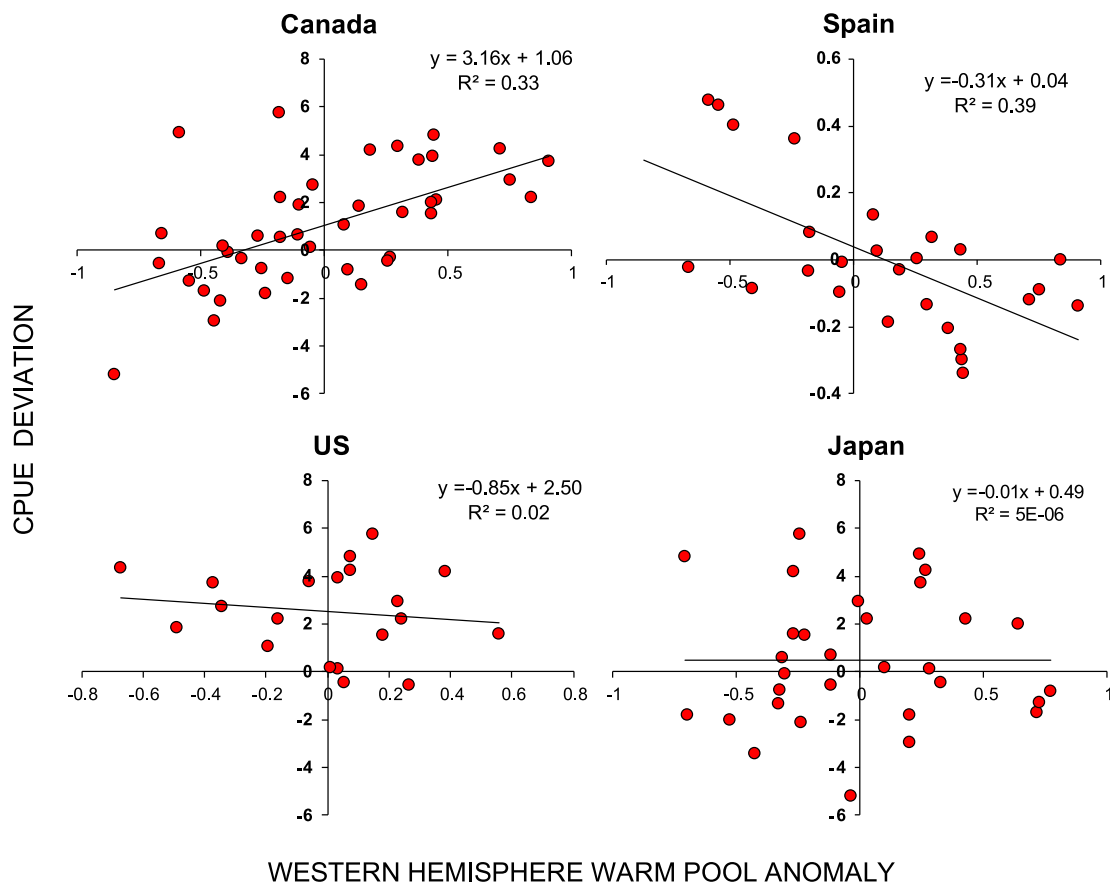
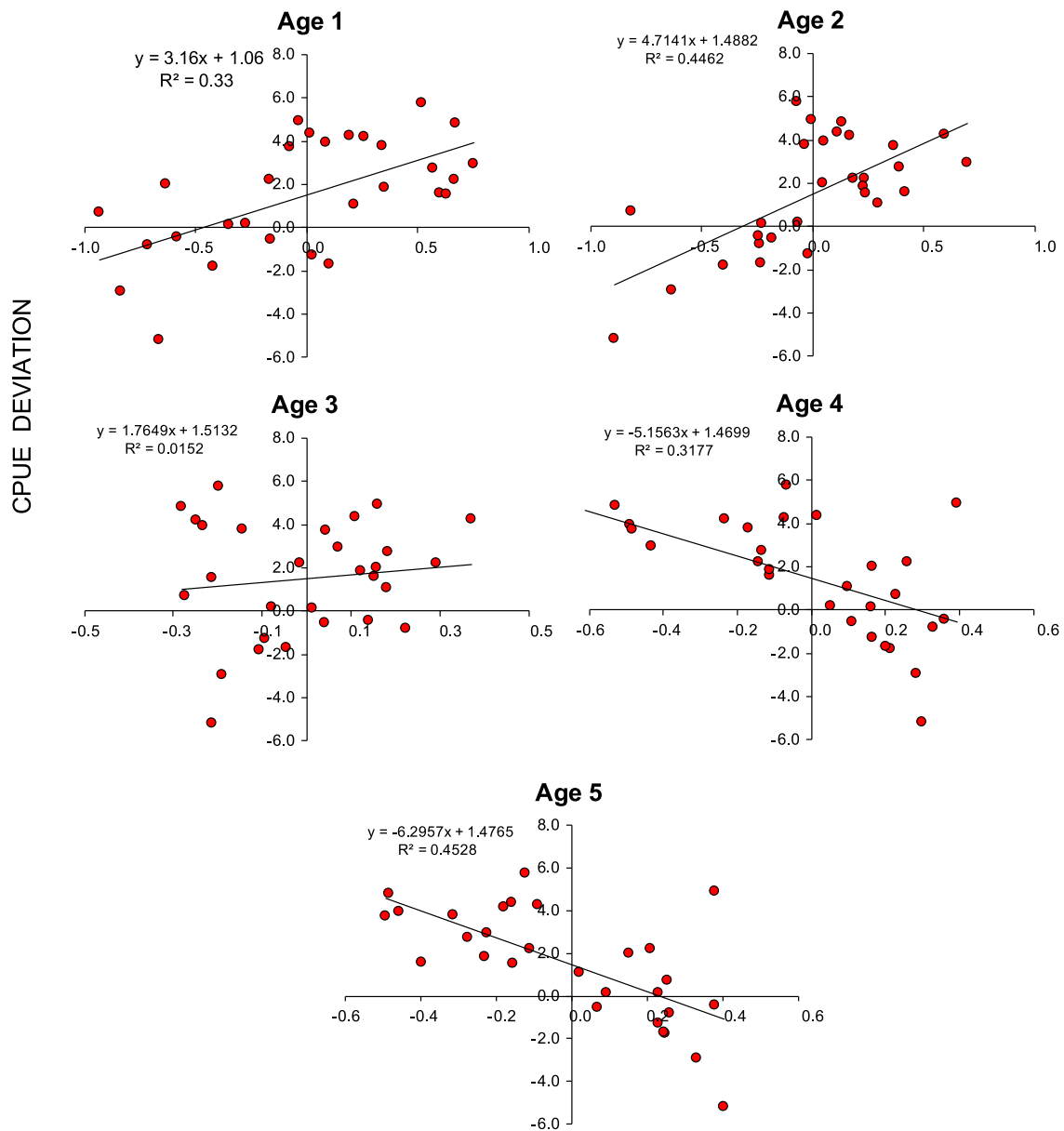


Fig. 7. Regression of the flag-specific CPUE deviations against the Western Hemisphere Warm Pool anomalies.



WESTERN HEMISPHERE WARM POOL ANOMALY

Fig. 8. Regression of the age-specific CPUE deviations from the Spanish longline fleet against the Western Hemisphere Warm Pool anomalies.

changed signs once during the time period covered in the investigation. A second change of the summer SST anomalies (i.e. back to a negative anomaly) would be the most effective way to determine if the hypothesis is correct.

The spatial pattern produced by shading the CPUE areas by the sign of the estimated environmental link parameter β (either positive or negative) bears some resemblance to the spatial pattern of the AMO described by Li et al. (2014, Fig. 1), which exhibits two warm centers, one south of Greenland and one in the tropics. These two warm centers nearly merge in the eastern North Atlantic, while in the western North Atlantic a cooler center is formed corresponding roughly to the Sargasso Sea. However, while there are some similarities in the two patterns, there are also some notable differences, such as can be seen in area 9. In this analysis it was not possible to determine if the summer SST anomalies were directly driving the distribution of swordfish through changes in water temperature, or whether it was merely a

proxy for some other mechanism, such as spatial distribution of prey or primary productivity. Lan et al. (2015) found that swordfish distribution in the Indian Ocean was related to the changes in net primary production and shallow mixed layer depth. Hence, changes in ocean temperature might change primary productivity, leading to distributional shifts in the swordfish prey such as pelagic fish and squid (Beardsley, 1978).

An alternative hypothesis that we did not test was that the ICCAT boundaries of the north and south Atlantic swordfish populations are incorrect and that the spatial pattern in CPUE deviations results from two separate stocks with different population trajectories. Recent work confirms the strong genetic differentiation between the stocks as currently defined by the ICCAT, but finds that the south Atlantic stock likely extends beyond the ICCAT 5°N latitude demarcation to 20°N–25°N and 45°W (Smith et al., 2015). Further support for this hypothesis is provided by the finding that swordfish tagged in the western North Atlantic tend

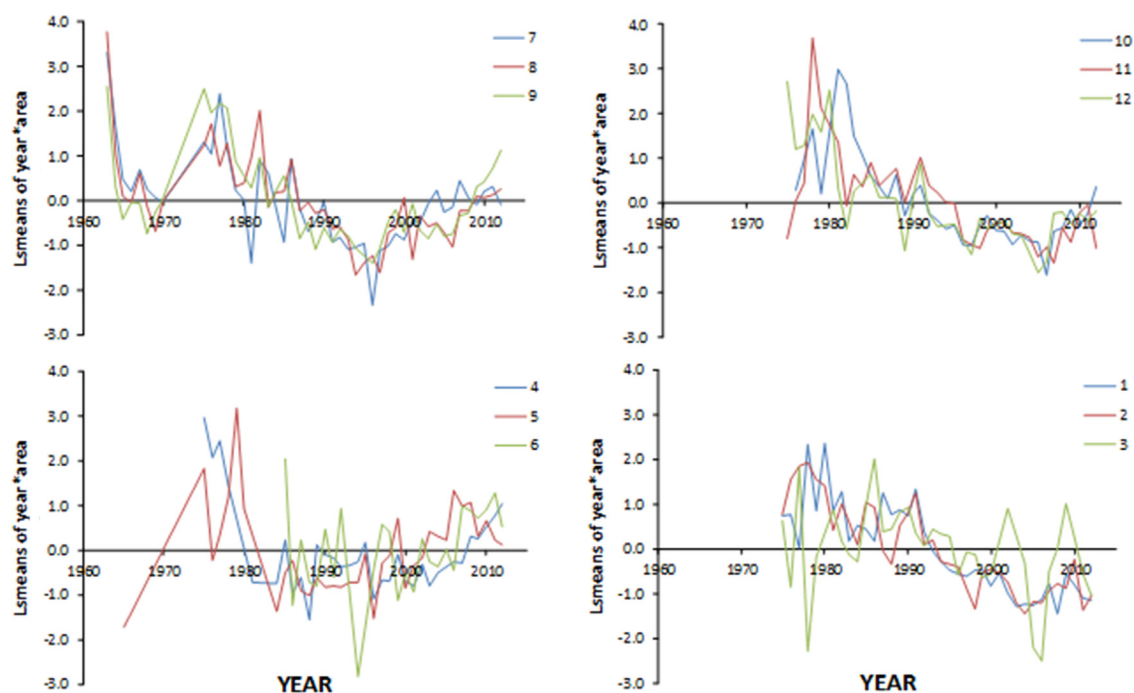


Fig. 9. Least square means of the year*area effects from the GLM model of area specific CPUEs grouped by similarities in trends, 1961–2011. The clusters were arranged within the figure to correspond to the four quadrants of the North Atlantic ocean; the northwest (upper left), northeast (upper right), southwest (lower left), and southeast (lower right).

to stay in that area and do not cross to the eastern side (Neilson et al., 2014). If the areas of the CPUE analysis from this study are colored according to the sign of the β parameter they follow very closely the stock boundaries suggested by genetic mapping (Smith et al., 2015), the reproductive areas (Bremer et al., 2015), as well as those from tagging (Neilson et al., 2014) (Fig. 11). Though similar, important differences still remain in the most northern areas (areas 10 and 11, but where few genetic samples were taken) as well as the southwest area (area 3) of this study. If, in fact, the south Atlantic population does extend north to 25°N to the north and west to 45°W as postulated by Smith et al. (2015), it would argue for moving the indices and landings from areas 1 and 2 (and possibly areas 11 and 12) from the North Atlantic to the South Atlantic stock assessments. However, the remaining residual patterns in indices for the other areas would likely remain unchanged, particularly the strong positive residuals in northern regions of the western side of the Atlantic where the sea surface temperatures in the WHWP have increased.

In this application we incorporated summer SST anomalies as an environmental index within the stock assessment model to reconcile conflicting CPUE indices following the general within-model approach of Maunder and Watters (2003). The assessment model construct that we used was a relatively simple one with a minimal number of estimated parameters. The addition of the deviations in the catchability directly accounted for at least some of the model process error and resulted in a better fit to the observational data. The additional process error resulted in the most improvement in the fit of the CPUEs from areas 2 and 5, the areas with the two largest β parameter estimates. Alternatively there is a substantial body of work that has taken a different approach by directly incorporating oceanography into the CPUE standardization process (Hinton and Nakano, 1996; Bigelow et al., 2002; Maunder et al., 2006). The choice of method will often be dictated by the resolution of the CPUE data or the resolution of the environmental process. In the case of a large-scale environmental index such as the AMO derived summer SST anomalies, it may not necessarily be possible to assign each catch record to an SST anomaly value, or the summer SST anomaly value would be the same for all observations within a

year and thus confounded with the year effect. In the current application the summer SST anomaly values would have been the same for all CPUE observations within a year. In other applications where it is possible to account for oceanographic processes that might affect CPUE on short time scales, such as proximity to an oceanographic front (Kleisner et al., 2004), sea surface temperature or fishing depth (Lynch et al., 2012) it is probably more appropriate to work directly with the CPUE data as these variables may not have meaningful interpretation on an annual time step. Lastly for certain processes such as warming sea surface temperatures as a result of climate change, it is currently unresolved whether it is more appropriate to account for these effects by operating directly on the CPUE data or to consider the process later in the assessment model.

Our hypothesis explicitly assumed that changes in the summer SST anomalies did not change overall productivity of the stock. Correlating the environment with catchability, or, as mentioned above, by incorporating the environmental covariate directly into the CPUE standardization, makes the implicit assumption that the environment is driving our interpretation of abundance, e.g., the CPUE and not abundance itself. Primarily we made this assumption from the necessity for a stock assessment to assume some level of temporal stationarity in productivity regimes to be able to estimate key quantities such as maximum sustainable yield but also due to the practical need to rectify the disparate CPUE indices. It is plausible that changes in oceanography may change productivity of the stock, particularly as the overall area of favorable habitat may change with the future climate (Muhling et al., 2015) or as species expand their range into more productive areas (Nye et al., 2009). Potentially there is some signal of this in the annual deviations in the fit to the age-specific CPUE of Spain that were shown to be positively correlated with the CPUEs of the younger ages (ages 1 and 2) and negatively correlated with the CPUEs of the older ages (age_4 and age_5). This could suggest that the WHWP could also affect productivity in addition to altering adult density and catchability. Alternatively we could have estimated whether the disparate CPUE indices reflect some change in the overall carrying capacity by allowing for time varying productivity parameters. This would test the hypothesis that there has

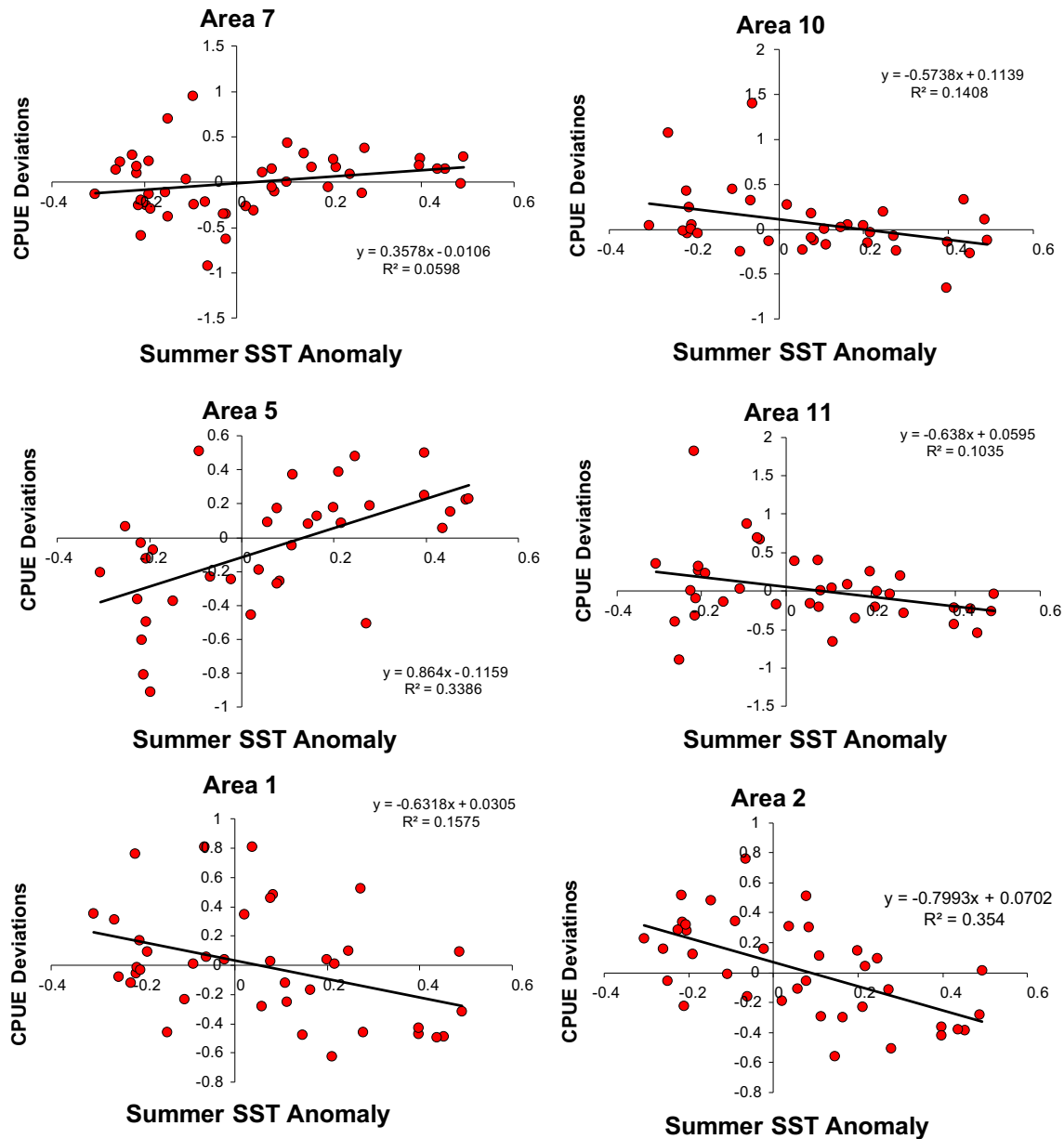


Fig. 10. Regression of the area-specific CPUE deviations against the Atlantic Multidecadal Oscillation.

been a change in productivity with environmental change. However separating the two hypotheses will be challenging, particularly as changing oceanography could affect both catchability and productivity.

The distinction between the two hypotheses, i.e., whether the environment changes catchability or productivity, is critical and will become increasingly relevant in the face of climate change (Stock et al., 2011). Currently our capacity to test for changes in productivity for highly migratory species remains limited, largely due to the limitations of fishery-dependent data coverage and quality, where time, fleet or spatial variation in catchability clearly limits the potential to detect changes in productivity. The combined fleet CPUE index used in this analysis (Ortiz et al., 2014) represents a key step forward in the ability to detect changes. The next critical step is to treat CPUE as a measure of total abundance calculated as the density (catch rate) multiplied by the area that this catch rate applies (Campbell, 2015). This differs from how most CPUE is treated in assessment models where different indices are often treated as equally plausible measures of overall

abundance. The approach proposed by Campbell (2015) to derive a single measure of total abundance has the desirable property of reflecting a conservation of mass. For example, if the population size was constant, but there was net movement from one region to another, the sum of the total abundance would remain constant but each region would have different apparent catch rates. Summing the catch rate \times area would maintain the same index of total abundance. Disentangling the productivity/catchability for highly migratory species will clearly require improved treatment of fishery dependent CPUE.

We believe there is sufficient evidence to conclude the distribution of northern swordfish has changed from what it was prior to 1996. Furthermore, we believe that this is likely due to a change in one or more environmental factors, be they related to habitat preference, prey distribution, or both. However, there remains the potential that environmental changes that appear to have altered swordfish distribution also may have altered productivity. We also conclude that attempting to account for this redistribution within the stock assessment model rather than on

Table 1

Estimated environmental link function (β) parameter (Value), standard deviation (Std Dev), approximate lower (LCI) and upper (UCI) 95% confidence intervals from the age-structured production assessment model. Asterisk are those β values that are non-zero estimates.

Area	Value	Std Dev	LCI	UCI	< > 0
1	-0.7021	0.1363	-0.9692	-0.4350	*
2	-0.8117	0.1449	-1.0957	-0.5277	*
3	-0.1594	0.1588	-0.4707	0.1518	
4	0.1538	0.1534	-0.1470	0.4545	
5	0.7665	0.1471	0.4782	1.0547	*
6	0.2781	0.2547	-0.2210	0.7773	
7	0.4436	0.1351	0.1787	0.7084	*
8	0.0799	0.1381	-0.1908	0.3505	
9	0.2014	0.1355	-0.0642	0.4669	
10	-0.4776	0.1716	-0.8139	-0.1412	*
11	-0.6721	0.1657	-0.9968	-0.3474	*
12	-0.1673	0.1415	-0.4447	0.1100	
13	-0.0480	0.1459	-0.3340	0.2380	
14	0.5052	0.2118	0.0900	0.9204	*

Table 2

Negative log-likelihood, residual mean square error (RMSE), mean CPUE input standard error, and variance adjustment from the age-structured NULL model and the ALT model incorporating the AMO.

AREA	-LOG (like)		RMSE		Mean Input SE	Variance adjustment	
	NULL	ALT	NULL	ALT		NULL	ALT
1	7.90	-4.33	0.37	0.34	0.20	0.17	0.15
2	-14.75	-30.10	0.32	0.25	0.21	0.10	0.04
3	-9.55	-10.59	0.42	0.42	0.24	0.17	0.17
4	-15.53	-16.24	0.39	0.39	0.23	0.16	0.16
5	-11.54	-28.28	0.36	0.28	0.24	0.12	0.04
6	-10.02	-11.05	0.41	0.40	0.29	0.12	0.11
7	-21.85	-29.22	0.33	0.32	0.22	0.11	0.10
8	-33.03	-33.50	0.31	0.31	0.23	0.09	0.09
9	-6.91	-8.86	0.43	0.43	0.23	0.20	0.20
10	-28.75	-31.93	0.37	0.35	0.28	0.09	0.07
11	-9.14	-16.60	0.47	0.45	0.29	0.18	0.16
12	-32.21	-32.72	0.26	0.26	0.21	0.06	0.06
13	-38.96	-38.69	0.24	0.24	0.22	0.02	0.03
14	-13.12	-16.51	0.44	0.45	0.34	0.10	0.11
SUM	-237.47	-308.62	5.12	4.89		1.70	1.47

individual CPUE may be the preferable approach given the large spatial extent of AMO changes. By incorporating an environmental linkage on catchability we reconciled conflicting indices and provided a more precise fit to the catch rate data. It is difficult to know if this shift is unidirectional. However, if it is in fact a function of the phase of the AMO or one of its correlated indices, such as the WHWP, then we may see the trend shift again as these indices change direction. Given the relatively localized nature of many of the fishing fleets, and the difficulty of separating fleet effects from changes in oceanography, we believe that it is critical to create CPUE indices by combining data across as many fleets as possible (Ortiz et al., 2014). This conclusion holds true regardless of which of the alternative hypotheses discussed here are controlling. Furthermore, because it is difficult to determine if changes in CPUE are due to changes in distribution or changes in productivity, we believe that applying the spatial summation approach of Campbell (2015) should be given consideration. Finally, we suggest that the current stock structure used in assessments conducted by the ICCAT be re-evaluated for consistency with the most recent literature. This approach allowed us to evaluate area-specific catch rates which provided

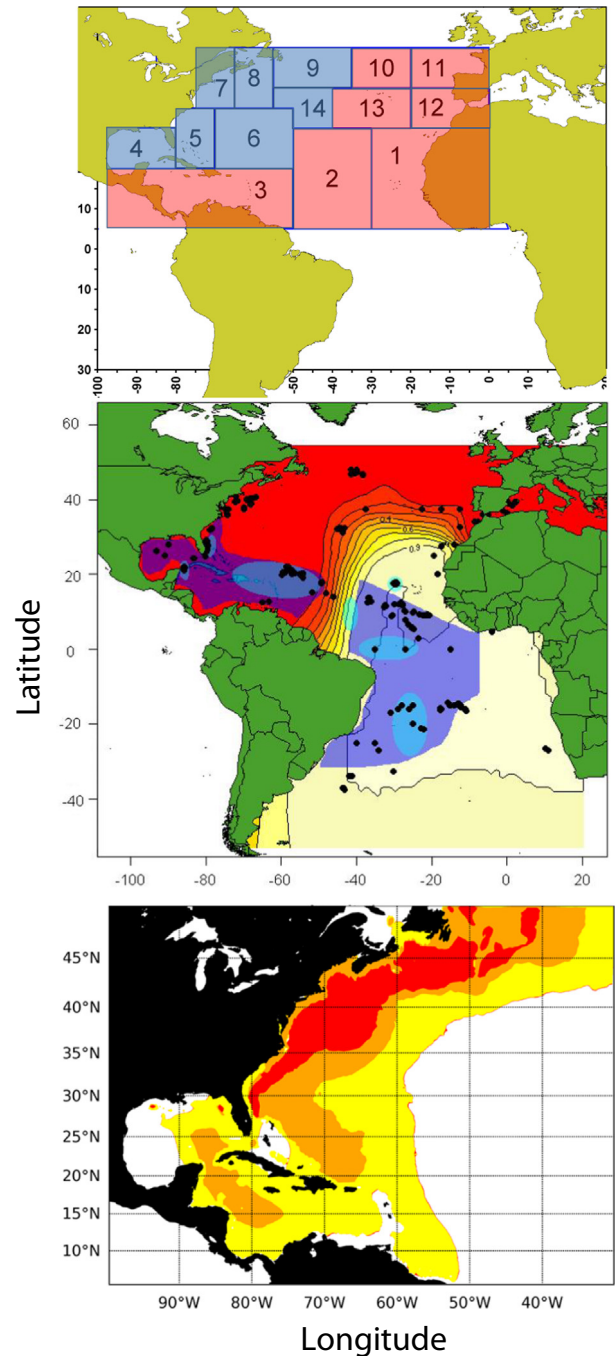


Fig. 11. Conclusions from various studies regarding Atlantic swordfish stock structure. Top: Depiction of the estimated environmental link parameter (β) value for each of the fourteen areas from the ALT model from this study. Blue colors are positive values (a positive correlation between CPUE residuals and the AMO), and red colors are negative values (a negative correlation between CPUE residuals and the AMO). Middle: GENELAND map of posterior probability of membership to the South Atlantic population reproduce from Smith et al. (2015), overlaid on the regions of reproduction of Atlantic swordfish summarized by Bremer et al. (2005), adopted from Smith et al. (2015). Bottom: Overall distribution of mature swordfish based on information from pop-up archival satellite results obtained by the National Marine Fisheries Service, South Carolina Department of Natural Resources and Fisheries and Ocean Canada, reproduced from Neilson et al. (2014). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the power to detect basin-wide responses to changing oceanography, a critical step for providing robust ecosystem based fisheries management advice in a changing climate.

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References

- Abecassis, M., Dewar, H., Hawn, D., Polovina, J., 2012. Modeling swordfish daytime vertical habitat in the North Pacific Ocean from pop-up archival tags. *Mar. Ecol. Progress. Ser.* 452, 219–236.
- Abid, N., Ayoub, M., El Omrani, F., 2014. Updated catch rates of swordfish from the Moroccan swordfish longline fishery in the north Atlantic, 2005–2012. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1721–1724.
- Anderson, D.R., Burnham, K.P., 2002. Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manage.* 66, 912–918.
- Andrushchenko, I., Hanke, A., Whelan, C.L., Neilson, J.D., Atkinson, T., 2014. A description of the Canadian swordfish fisheries from 1988 to 2012, and a candidate abundance indices for use in the 2013 stock assessment. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1679–1710.
- Anonymous, 2014. Report of the 2013 Atlantic swordfish stock assessment session. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1484–1678.
- Arocha, F., Lee, D.W., 1996. Maturity at size, reproductive seasonality, spawning frequency, fecundity and sex ratio in swordfish from the Northwest Atlantic. *Collect. Vol. Sci. Pap. ICCAT* 45 (2), 350–357.
- Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. *Rev. Fish. Biol. Fish.* 6 (2), 221–242.
- Beardsley, J.L., 1978. Report of the swordfish workshop held at the Miami laboratory southeast fisheries center, National Marine Fisheries Service Miami Florida. *Collect. Vol. Sci. Pap. ICCAT* 7 (1), 149–158.
- Bigelow, K.A., Hampton, J., Miyabe, N., 2002. Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). *Fish. Oceanogr.* 11, 143–155.
- Boyce, D.G., Tittensor, D.P., Worm, B., 2008. Effects of temperature on global patterns of tuna and billfish richness. *Mar. Ecol.—Progress. Ser.* 355, 267.
- Bremer, J.A., Mejuto, J., Gómez-Márquez, J., Boán, F., Carpintero, P., Rodríguez, J.M., Viñas, J., Greig, T.W., Ely, B., 2005. Hierarchical analyses of genetic variation of samples from breeding and feeding grounds confirm the genetic partitioning of northwest Atlantic and South Atlantic populations of swordfish (*Xiphias gladius* L.). *J. Exp. Mar. Biol. Ecol.* 327 (2), 167–182.
- Campbell, R.A., 2015. Constructing stock abundance indices from catch and effort data: Some nuts and bolts. *Fish. Res.* 16, 109–130.
- Dewar, H., Prince, E.D., Musyl, M.K., Brill, R.W., Sepulveda, C., Luo, J., Foley, D., Orbesen, E.S., Domeier, M.L., Nasby-Lucas, N., Snodgrass, D., 2011. Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fish. Oceanogr.* 20 (3), 219–241.
- Enfield, D.B., Mestas-Nunez, A.M., Trimble, P.J., 2001. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental U.S. *Geophys. Res. Lett.* 28, 2077–2080.
- García-Cortés, B., Ramos-Cartelle, A., Mejuto, J., 2014. Standardized catch rates in biomass for the north Atlantic stock of swordfish (*Xiphias gladius*) from the Spanish surface longline fleet for the period 1986–2011. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1792–1803.
- Hinton, M.G., Nakano, H., 1996. Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints and environmental data, with an application to blue marlin (*Makaira nigricans*) catch and effort data from Japanese longline fisheries in the Pacific. *Bull. Int.—Am. Trop. Tuna Comm. Bull.* 21, 171–200.
- Lan, Kuo-Wei, Lee, Ming-An, Wang, Sheng-Ping, Chen, Zhao-Yang, Environmental variations on swordfish (*Xiphias gladius*) catch rates in the Indian Ocean. *Fish. Res.* 166, 2015, 67–79.
- Lerner, J.D., Kerstetter, D.W., Prince, E.D., Talaue-McManus, L., Orbesen, E.S., Mariano, A., Snodgrass, D., Thomas, G.L., 2013. Swordfish vertical distribution and habitat use in relation to diel and lunar cycles in the western North Atlantic. *Trans. Am. Fish. Soc.* 142 (1), 95–104.
- Li, X., Holland, D.M., Gerber, E.P., Yoo, C., 2014. Impacts of the north and tropical Atlantic Ocean on the Antarctic Peninsula and sea ice. *Nature* 505 (7484), 538–542.
- Lynch, P.D., Shertzer, K.W., Latour, R.J., 2012. Performance of methods used to estimate indices of abundance for highly migratory species. *Fish. Res.* 125–126, 27–39.
- Maunder, M.N., Watters, G.M., 2003. A general framework for integrating environmental time series into stock assessment models: model description, simulation testing, and example. *Fish. Bull.* 101 (1), 89–99.
- Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., Harley, S.J., 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES J. Mar. Sci.: J. Du. Cons.* 63 (8), 1373–1385.
- Methot, R.D., Wetzell, C.R., 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fish. Res.* 142, 86–99.
- Nakamura, I., 1985. FAO 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 (5), 65.
- Neilson, J.D., Loefer, J., Prince, E.D., Royer, F., Calmettes, B., 2014. Seasonal distributions and migrations of Northwest Atlantic swordfish: inferences from integration of pop-up satellite archival tagging studies. *PLoS One* 9 (11), e112736. <http://dx.doi.org/10.1371/journal.pone.0112736>.
- Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Progress. Ser.* 393, 111–129.
- Ortiz, M., Mejuto, J., Andrushchenko, I., Yokawa, K., Walter, J., Santos, M.N., Abid, N., 2014. An updated combined biomass index of abundance for North Atlantic swordfish stock 1963–2012. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1912–1926.
- Poisson, F., Fauvel, C., 2009. Reproductive dynamics of swordfish (*Xiphias gladius*) in the southwestern Indian Ocean (Reunion Island). Part 1: oocyte development, sexual maturity and spawning. *Aquat. Living Resour.* 22 (01), 45–58.
- Rey, J.C., 1988. Comentarios sobre las áreas de reproducción del pez espada, (*Xiphias gladius*) en el Atlántico y Mediterráneo. *ICCAT, Collect. Vol. Sci. Pap.* 27, 180–193.
- Quinn, T.J., Deriso, R.B., 1999. Quantitative Fish Dynamics. Oxford University Press.
- Santos, M.N., Coelho, R., Lino, P.G., 2014. Standardized CPUE for swordfish (*Xiphias gladius*) caught by the Portuguese pelagic longline fishery in the north Atlantic. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1783–1791.
- Schirripa, M.J., 2014. North Atlantic swordfish 2013: stock synthesis configuration version 1.0. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1981–1997.
- Sedberry, G., Loefer, J., 2001. Satellite telemetry tracking of swordfish, *Xiphias gladius*, off the eastern United States. *Mar. Biol.* 139 (2), 355–360.
- Smith, B.L., Lu, C.P., García-Cortés, B., Viñas, J., Yeh, S.Y., Bremer, J.R.A., 2015. Multilocus Bayesian estimates of intra-oceanic genetic differentiation, connectivity, and admixture in Atlantic swordfish (*Xiphias gladius* L.). *PLoS One* 10 (6), e0127979.
- Stock, C.A., Alexander, M.A., Bond, N.A., Brander, K.M., Cheung, W.W., Curchitser, E. N., et al., 2011. On the use of IPCC-class models to assess the impact of climate on living marine resources. *Prog. Oceanogr.* 88 (1), 1–27.
- Walter, J., Lauretta, M., Hanke, A., Andrushchenko, I., Brown, C., 2014. Standardized catch rates of swordfish from the US dealer landings system with a preliminary consideration of a combined US-Canada pelagic longline fleet dataset. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1885–1911.
- Wang, C., Lee, S.K., Enfield, D.B., 2008. Atlantic warm pool acting as a link between Atlantic multidecadal oscillation and Atlantic tropical cyclone activity. *Geochim. Geophys. Geosyst.* 9, 5.
- Yokawa, K., Kai, M., 2014. Standardization of CPUE of swordfish caught by Japanese longliners in the north Atlantic. *Collect. Vol. Sci. Pap. ICCAT* 70 (4), 1843–1856.