Original Article

Abundance trends of highly migratory species in the Atlantic Ocean: accounting for water temperature profiles

Patrick D. Lynch[1]*,[‡], Kyle W. Shertzer[2], Enric Cortés[3], and Robert J. Latour[1]

[1]Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, VA 23062, USA
[2]National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Southeast Fisheries Science Center (SEFSC), 101 Pivers Island Road, Beaufort, NC 28516, USA
[3]NOAA, NMFS, SEFSC, 3500 Delwood Beach Road, Panama City, FL 32408, USA

*Corresponding author: tel: + 301 427 8151; fax: + 301 713 1875; e-mail: patrick.lynch@noaa.gov.

Relative abundance trends of highly migratory species (HMS) have played a central role in debates over the health of global fisheries. However, such trends have mostly been inferred from fishery catch rates, which can provide misleading signals of relative abundance. While many biases are accounted for through traditional catch rate standardization, pelagic habitat fished is rarely directly considered. Using a method that explicitly accounts for temperature regimes, we analysed data from the US pelagic longline fishery to estimate relative abundance trends for 34 HMS in the Atlantic Ocean from 1987 through 2013. This represents one of the largest studies of HMS abundance trends. Model selection emphasized the importance of accounting for pelagic habitat fished with water column temperature being included in nearly every species' model, and in extreme cases, a temperature variable explained 50–60% of the total deviance. Our estimated trends represent observations from one fishery only, and a more integrated stock assessment should form the basis for conclusions about stock status overall. Nonetheless, our trends serve as indicators of stock abundance and they suggest that a majority of HMS (71% of analysed species) are either declining in relative abundance or declined initially with no evidence of rebuilding. Conversely, 29% of the species exhibited stable, increasing, or recovering trends; however, these trends were more prevalent among tunas than either billfishes or sharks. By estimating the effects of pelagic habitat on fishery catch rates, our results can be used in combination with ocean temperature trends and forecasts to support bycatch avoidance and other time-area management decisions.

Keywords: billfish, catch per unit effort (CPUE), fish, index, longline, pelagic, population, shark, standardization, tuna.

Introduction

Fish stock assessments provide the quantitative basis for sustainable fisheries management. Assessment models typically rely on information about changes in stock abundance over time, and because it is impossible to conduct a census of most marine organisms, indices of relative abundance are often used to characterize population trends (Quinn and Deriso, 1999; Maunder and Punt, 2004). Within assessment models, indices are often treated as "observed" measures of relative abundance, thereby giving them substantial influence over assessment results. Unfortunately, relative abundance trends of highly migratory species (HMS) are rarely obtained through comprehensive, scientifically designed, survey programs (due to the high cost of implementation), but rather from fishery-dependent catch and effort data (Maunder and Punt, 2004; Lynch et al., 2011) (HMS in this study include fishes only [tunas, billfish, and sharks]). This poses a considerable challenge to estimating an accurate index of relative abundance, because fisheries frequently change their fishing

[‡]Present address: NOAA, NMFS, Office of Science and Technology, 1315 East West Highway, Silver Spring, MD 20910, USA.

practices in response to various socio-economic drivers. When fishery catch rates, or catch per unit effort (CPUE), are assumed to be proportional to stock abundance, changes in fishing practices need to be accounted for because they can cause the proportionality assumption to be violated (Maunder and Punt, 2004).

In the Atlantic Ocean, pelagic longline fisheries are responsible for the bulk of the fishing mortality experienced by many HMS. These fisheries have altered fishing practices over time by changing gear configurations, target species, and the spatio-temporal distribution of effort (Majkowski, 2007). Although contemporary statistical approaches to estimating HMS relative abundance trends do account for changes in fishing practices, ocean conditions are variable and pelagic habitats fished are related to both fishing practices and environmental conditions. While the distributions of HMS can be roughly characterized by depth and geography, temperature regimes are likely the main governing factor (Brill and Lutcavage, 2001; Bigelow and Maunder, 2007). Therefore, when estimating HMS relative abundance trends, it is important to consider pelagic habitats exploited (e.g. temperature regimes) in addition to fishing practices.

Temperature information is not straightforward to incorporate analytically when estimating relative abundance trends from pelagic longline fisheries data, because estimates of fishing depth and environmental conditions at depth are required. Longline fishing depths are notoriously difficult to estimate with accuracy (Ward and Myers, 2006; Rice et al., 2007) and environmental conditions at a given depth, time, and location are often not recorded, and can only be estimated through analysis of a global ocean database. Therefore, HMS relative abundance trends are typically estimated without accounting for the pelagic habitats exploited by the fishery, which inevitably vary over time.

Despite the challenges associated with accounting for pelagic habitat fished, Lynch et al. (2012) proposed a method for incorporating this information using a delta-generalized linear model (delta-GLM), and showed that it can improve the estimation accuracy of HMS relative abundance trends. The method is also relatively insensitive to errors in estimates of longline fishing depths, which is contrary to other methods that incorporate habitat, such as habitat-based standardization (HBS; Hinton and Nakano, 1996) and the statistical counterpart to HBS (statHBS; Maunder et al., 2006). The HBS and statHBS approaches have both demonstrated high sensitivity to model inputs, such as estimates of longline fishing depth (Goodyear, 2003; Lynch et al., 2012).

For fisheries stock assessments of Atlantic HMS, we are unaware of any occasions where the relative abundance trends used in the assessment incorporated detailed pelagic habitat information. Here, we accounted for temperature regimes in the application of delta-GLMs (some of which included mixed effects; i.e. delta-GLMMs) to fisher logbook data from the US pelagic longline fishery (USLL). These analyses resulted in new abundance trends for 34 HMS (Table 1) in the Atlantic Ocean. For comparison, we also analysed data collected by scientific observers aboard pelagic longline fishing vessels (US Pelagic Longline Observer Program). In general, relative abundance trends for species caught in the USLL are estimated by US members of the Standing Committee on Research and Statistics (SCRS), a committee within the International Commission for the Conservation of Atlantic Tunas (ICCAT). All of the 34 species analysed fall under the management purview of ICCAT, either as directly managed species or as bycatch species. However, not all species managed by ICCAT have been formally assessed using modern stock assessment methods. To our knowledge, only 13 of the 34 species (38%) have been assessed (Table 1).

With the exception of the incorporation of pelagic habitat fished, our relative abundance trends were estimated following an approach used for yellowfin tuna (*Thunnus ablacares*) by the SCRS (Walter, 2011). This framework represents the contemporary approach used by the SCRS, so our trends can be compared to those estimated by the SCRS with minimal concern over methodological differences. The independent variables included in our final models were objectively selected by considering the percent of total deviance explained by each variable. This allowed us to compare the importance of the temperature variables as related to the variables normally considered by the SCRS. Finally, we characterized general population trends by calculating instantaneous rates of change for each species. We used a flexible approach to detect measurable changes in relative abundance trends over time.

Methods

Fishery data

Relative abundance trends were generated for 34 HMS routinely caught by the USLL (Table 1). Fisher logbook and observer data for the USLL were obtained from the National Marine Fisheries Service. The logbook data contain longline set-specific information, including catches (numbers of individuals), effort (number of hooks), gear configurations, dates, time, and spatial locations (Figure 1). The primary target species of the USLL include swordfish (*Xiphias gladius*), yellowfin tuna, and bigeye tuna (*Thunnus obesus*); however, bycatch rates in this fishery are relatively high, particularly for sharks (Mandelman et al. 2008). While the USLL covers a large portion of the distributions of most species analysed, fishing effort is largely focused along the US east coast. The USLL in the early through mid-1970s was considered an "underground" fishery, and initially used a gear configuration similar to Japanese and Norwegian shark longline fisheries (Hoey and Bertolino, 1988). Between 1978 and 1983, various gear modifications occurred as the fishery evolved to using lighter monofilament line with increased hook spacing and depth, and chemical lightsticks. Other features of this fishery have been described in detail by Hoey and Bertolino (1988).

While fishers continually adjust their practices, the logbook and observer programs track this information on a set-by-set basis, allowing catch rates to be analysed and interpreted accordingly. The logbook program began in 1986, although data for that year are incomplete; thus, our analyses use data beginning in 1987. The major gear changes described by Hoey and Bertolino (1988) occurred before the start of the logbook program, so there is not a need to address those shifts in this study; however, we do account for the variety of fishing practices and time/area dynamics observed since 1987. There have been several time-area management measures imposed on the USLL, particularly since 2000 (Mandelman et al. 2008; Walter, 2011). Our treatment of the data, including data filtering is described in the Supplementary data.

Oceanographic data

Detailed oceanographic data were necessary for generating estimates of pelagic habitats fished. We designated temperature regimes as habitats; therefore, we assigned each longline set a

Table 1. Species for which abundance trends were generated using fisher logbook and pelagic longline observer program data from the USLL.

Species[a]	Logbook	Observer	Species	Logbook	Observer
Swordfish, *Xiphias gladius*	256643 (99.6%)	17496 (100.0%)	Silky shark, *Carcharhinus falciformis*	145539 (56.5%)	15333 (87.6%)
Yellowfin tuna, *Thunnus albacares*	255815 (99.3%)	17496 (100.0%)	Bigeye thresher, *Alopias superciliosus*	141026 (54.8%)	17496 (100.0%)
Dolphinfish, *Coryphaena hippurus*	253666 (98.4%)	—	Dusky shark, *Carcharhinus obscurus*	137124 (53.2%)	15333 (87.6%)
Bigeye tuna, *Thunnus obesus*	243036 (94.4%)	17496 (100.0%)	Blacktip shark, *Carcharhinus limbatus*	125346 (48.7%)	14460 (82.6%)
Wahoo, *Acanthocybium solandri*	233435 (90.6%)	—	**Spearfishes**, *Tetrapturus* spp.	105661 (41.0%)	—
Blue marlin, *Makaira nigricans*	221178 (85.9%)	—	Sandbar shark, *Carcharhinus plumbeus*	108111 (42.0%)	14235 (81.4%)
Albacore tuna, *Thunnus alalunga*	225525 (87.6%)	17496 (100.0%)	Oceanic whitetip shark, *Carcharhinus longimanus*	95149 (36.9%)	15333 (87.6%)
White marlin, *Kajikia albida*	220633 (85.7%)	—	**Skipjack tuna**, *Katsuwonus pelamis*	97107 (37.7%)	15333 (87.6%)
Atlantic bluefin tuna, *Thunnus thynnus*	218430 (84.8%)	17292 (98.8%)	Night shark, *Carcharhinus signatus*	71202 (27.6%)	14664 (83.8%)
Longfin mako, *Isurus paucus*	203654 (79.1%)	15333 (87.6%)	Scalloped hammerhead, *Sphyrna lewini*	54493 (21.2%)	15129 (86.5%)
Blue shark, *Prionace glauca*	198479 (77.1%)	17496 (100.0%)	Atlantic bonito, *Sarda sarda*	49258 (19.1%)	—
Tiger shark, *Galeocerdo cuvier*	193050 (74.9%)	17496 (100.0%)	Smooth hammerhead, *Sphyrna zygaena*	28920 (11.2%)	4072 (23.3%)
Hammerhead sharks, *Sphyrna* spp.	186753 (72.5%)	15333 (87.6%)	White shark, *Carcharodon carcharias*	34393 (13.4%)	—
Shortfin mako, *Isurus oxyrinchus*	186905 (72.6%)	17496 (100.0%)	Spinner shark, *Carcharhinus brevipinna*	34608 (13.4%)	11773 (67.3%)
Blackfin tuna, *Thunnus atlanticus*	188078 (73.0%)	—	**Porbeagle**, *Lamna nasus*	16384 (6.4%)	5739 (32.8%)
Oilfish, *Gempylidae* spp.	173749 (67.5%)	—	Bignose shark, *Carcharhinus altimus*	13527 (5.3%)	—
Sailfish, *Istiophorus albicans*	163142 (63.3%)	—			
Common thresher, *Alopias vulpinus*	166262 (64.5%)	11232 (87.6%)			

The number and percent of logbook and observer records analysed (of a potential 257581 logbook and 17496 observer records) after filtering the data to include only the regions and vessels with catch rates above predetermined thresholds. We did not have observer data for 11 of the species analysed. Species highlighted in bold text are those for which stock assessments are known to have been previously conducted.

[a]In addition to individual species, there were three species groups (i.e. identified to the genus level) included in the analyses: oilfish (*Gempylidae* spp.), spearfishes (*Tetrapturus* spp.), and hammerhead sharks (*Sphyrna* spp.). We use "HMS" and "species" throughout to collectively refer to individual species and species groups.
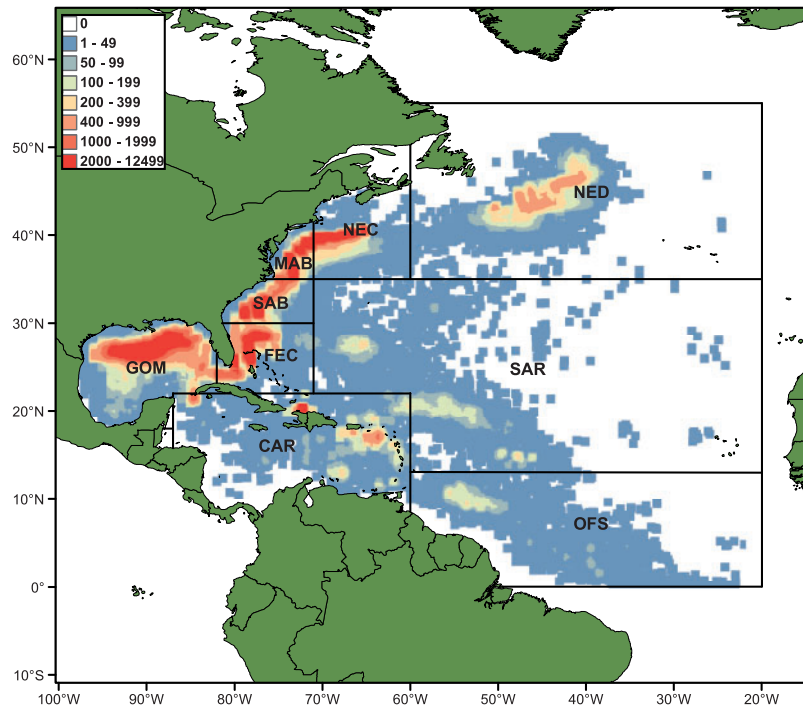

Figure 1. Map of the distribution of longline sets (total number per cell) between 1987 and 2010 for the USLL in the northwest Atlantic Ocean. The geographical regions used for classifying the fishery include the Caribbean Sea (CAR), Gulf of Mexico (GOM), Florida east coast (FEC), south Atlantic bight (SAB), mid-Atlantic bight (MAB), north-east coastal (NEC), north-east distant waters (NED), Sargasso Sea (SAR), and offshore waters (OFS).

fixed temperature-at-depth profile. Ocean temperature profiles were obtained from the National Oceanographic Data Center (www.nodc.noaa.gov) using the World Ocean Atlas (WOA) data series (Locarnini *et al.*, 2010). These data were available as average

monthly temperature profiles following 1° latitude by 1° longitude spatial resolution, covering a depth range of 0–1500 m over variable increments. The climatologies were derived from averaging decadal climatologies between 1955 and 2006

(Locarnini *et al.*, 2010). For the rare instances where temperature profiles were not available for a given combination of geographical location and month, the longline set record was removed entirely (<2% of the logbook records).

Pelagic habitat variables

To incorporate pelagic habitat fished, estimates of longline fishing depths and corresponding estimates of temperature at depth were required (Lynch *et al.*, 2012). See Supplementary data for a description of the methods used to calculate longline hook depths. Fishing depths for each longline set were related to temperature at depth for the corresponding month and geographical location of the set. Because temperatures were available at discrete depths, the temperature at the depth closest to estimated fishing depth was specified as the temperature fished for a given hook. Following Lynch *et al.* (2012), temperatures fished were converted to 1°C increments relative to surface temperature in the corresponding time/space. The maximum deviation from sea surface temperature (MaxΔT), or deepest, coldest pelagic habitat fished, was then assigned to each longline set as a single value (0°, ..., 15°C) thereby characterizing the contrast in temperatures fished for that set. For example, if surface water temperature is 25°C for a given longline set, and the temperature associated with the deepest hook fished in that set is 15°C, then the MaxΔT factor would have a value of 10°C for that set. In addition to MaxΔT, we evaluated a variable that characterized each longline set as the minimum temperature fished (Min$T$) in that set. This variable was specified as categorical with 5° temperature bins from 1°C to 30°C. In the example stated above, the Min$T$ variable would have a value of 15°C for that set. While MaxΔT directly accounts for the vertical distribution of the species being analysed, Min$T$ accounts for the distribution of the species geographically, as well as vertically.

The inclusion of temperature regimes fished is a non-trivial undertaking, but an important consideration. While temperature is likely related to depth, the correlation between these variables is not perfect due to dynamic ocean patterns. Furthermore, HMS distributions and behaviour are more a function of temperature than depth (Brill and Lutcavage, 2001). Thus, we concluded it was crucial to estimate temperature regimes fished, rather than depths, which would have been simpler.

The inclusion of these pelagic habitat variables represents the primary difference between our study and prior estimates of relative abundance for Atlantic HMS. Making only one change in methodology facilitated the comparison of results to previous work; however, it is important to consider if these new variables were correlated with any of the traditional variables (see Other variables), which may confound the comparisons. Because these habitat variables are included to account for potential biases due to the temperature-driven vertical distribution of HMS in the location of fishing, we conclude that the patterns in these variables are not captured by any of the traditional variables.

Other variables

A suite of additional explanatory variables was also considered in the analyses. These variables were modelled as categorical factors, and included Year (year in which the set occurred), Region (nine geographical regions commonly used to classify the longline fishery: Figure 1), Season (calendar quarters: January–March, April–June, July–September, October–December), Lightstick (the ratio

of lightsticks per hook categorized with four levels: 0, >0–0.4, >0.4–0.7, >0.7), hooks between floats (HBF) categorized with seven levels (0–3, 4–6, 7–9, 10–15, 16–21, 22–29, 30+), Time (time at the beginning of the set: a.m., p.m., or unknown), and Bait (type of bait used: live, dead, mixture, unknown). These variables are all thought to potentially affect catch rates of various species encountered by the USLL (Walter, 2011).

Modelling framework

We used a two-stage delta-GLM approach for estimating relative abundance trends (e.g. Aitchison, 1955; Lo *et al.*, 1992; Stefánsson, 1996; Maunder and Punt, 2004). A GLM is a linear model that can accommodate non-normal error structure using a link function to relate dependent and independent variables. The delta-GLM (also referred to as a hurdle model) accounts for zero-inflated data by combining two GLMs, one that models the probability of observing a zero catch as a function of predictor variables and a separate model of the non-zero catches. The delta-GLM is represented as:

$$\Pr(Y = y) = \begin{cases} w & y = 0 \\ (1 - w)f(y) & \text{otherwise} \end{cases} \quad (1)$$

where w is the probability of observing a zero for the response (CPUE) and $f(y)$ is a model of the mean of non-zero data (CPUE). Accordingly, our abundance trends were determined by combining two linear models, one of which modelled the presence/absence of a particular species as a linear function of explanatory variables, assuming a binomial error distribution (logit link function). The second modelled CPUE, calculated as numbers of individuals caught in a set per 1000 hooks. For this model, only the records with a positive catch rate (i.e. CPUE > 0) were included, and we assumed a lognormal error distribution by using log(CPUE) as the response variable (identity link function). For both models, explanatory variables and interaction terms were modelled as fixed effects, with the exception of interaction terms that included the Year variable, which were modelled as random effects to facilitate deriving abundance estimates using the year effects. Technically, when random effects were included, delta-GLMMs were applied, but we use the term "GLM" generally throughout to refer to our modelling framework.

Annual estimates of relative abundance were obtained by multiplying the probability of a positive catch rate $(1 - w)$ in a given year from the binomial GLM by the mean CPUE in that same year from the lognormal GLM. The probability of a positive catch was calculated as the back-transformed mean probabilities for each year, predicted when all factors other than Year were set to their mode level (Maunder and Punt, 2004). Mean CPUE for each year was calculated as back-transformed year means adjusted by an infinite series lognormal bias correction (Lo *et al.*, 1992), and standard errors of the annual abundance estimates were calculated using the delta method (Seber, 1982; Lo *et al.*, 1992).

Model selection

We based the selection of variables to include in our component GLMs on percent deviance explained with a threshold for inclusion of 5%. This mimics the approach commonly used when estimating relative abundance trends for HMS (Ortiz and Arocha, 2004; Walter, 2011; Supplementary data). By incorporating our

temperature variables (MaxΔT, Min$T$) into the established approach to model selection, we evaluated the importance of these variables relative to other variables commonly considered in these analyses. We considered all first-order interaction terms in our model selection exercise, but observed increasing model instability when multiple interaction terms were included. Thus, our final models only incorporated the interaction term that explained the highest percent of the total deviance (if the percent explained exceeded at least 5%).

General patterns

We used linear regression as a simple approach to characterizing the general patterns observed in our relative abundance trends (e.g. increasing/decreasing). Each trend was scaled to have a mean of one, and the general direction over time was estimated by regressing scaled relative abundance on Year (treated as a continuous variable). In addition to standard linear regression, we modelled each trend using piecewise, or segmented, regression with one breakpoint. We then used Akaike's Information Criterion, corrected for small sample size (Burnham and Anderson, 2002) to select between standard and segmented regression models. This provided an objective characterization of the general pattern in abundance as being either unidirectional over time, or one that exhibited a change in direction. There may have been cases where trends could have been characterized by more than two segments, but to avoid overparameterization, we did not fit these more complex models.

The slope parameters from the regression models represent instantaneous rates of change, and these were extracted for making comparisons across species. There were either one or two slope parameters for each species, depending on whether the standard or segmented regression model was selected for describing the abundance trend. We characterized the populations as stable over time when the slopes were not significantly different from zero, but when significantly positive or negative, we considered the populations to be increasing or decreasing, respectively. All quantitative analyses were implemented using the statistical programming language R (R Core Team, 2016).

Results

The USLL spatial coverage in the Atlantic Ocean can be characterized as broad with areas of concentrated fishing effort (Figure 1). Due to our data filtering technique (Supplementary data), we analysed a different number of USLL logbook records for each of the 34 HMS included in this study (Table 1). Observer data were not available for all species (Table 1), but when analysed, the number of available observer records was filtered by region (not by historical catches per vessel as with logbook records—Supplementary data). Species with more catch records (after data filtering was applied) tended to have a higher frequency of occurrence in the fishery (Figure 2a), but with the exception of swordfish and yellowfin tuna, positive catches were less frequent than catches equal to zero. Thus, most species we analysed were rarely encountered by the fishery. While our models accounted for excessive zeros in the data, the ability to infer population trajectories for rarely encountered species may be limited.

A wide variety of model structures was selected for the binomial and positive catch component models of the delta-GLMs (Supplementary Tables S1–S34). According to our selection criteria (at least 5% of total deviance explained by the variable), the Min$T$ habitat variable was selected for the binomial and/or positive models for almost every species (Figure 2c, Supplementary Tables S1–S35). This suggests that Min$T$ explained a substantial amount of the variability in the catch rates of target and incidentally captured species of the USLL. For several species, Min$T$ explained 50–60% of the total deviance.

In addition to Min$T$, we evaluated MaxΔT; however, this variable explained greater than 5% of the total deviance for only five species (wahoo, blackfin tuna, Atlantic bonito, white marlin, and night shark), and in these cases, the percent explained was only slightly above the threshold for inclusion (Figure 2b). Overall, at least one of our pelagic habitat variables was important to include when estimating abundance trends for all but five species (yellowfin tuna, swordfish, spinner shark, white shark, and bignose shark).

Estimates of Min$T$ explained substantial variability surrounding observed CPUE, and visualizing the influence of this variable on species-specific catch rates highlights behavioural patterns (Figure 3). Encounter rates (proportion of sets with positive CPUE) and median positive catch rates both exhibited variability across estimates of Min$T$. The highest encounter rates and median positive CPUE values were observed for swordfish and blue sharks when the coldest habitats were fished. In fact, the highest overall median CPUE corresponded with blue sharks at approximately 50 sharks per 1000 hooks. Other species with higher catch rates in cooler habitats include bluefin tuna, shortfin mako, hammerhead sharks, and porbeagle. The encounter rates of swordfish and yellowfin tuna (two important target species of this fishery) exhibited opposing gradients in response to Min$T$, with the highest rates for yellowfin tuna occurring when the warmest habitats were fished. Along with yellowfin tuna, wahoo, blackfin tuna, oilfish, skipjack tuna, dolphinfish, the billfishes (excluding swordfish), tiger shark, thresher sharks, and night shark had higher encounter and catch rates in the warmer habitats.

The majority of our relative abundance trends declined over the time series (Figure 4, Supplementary Tables S1–S35); however, the magnitude of change was highly variable. For instance, the declines observed for the primary target species, swordfish and yellowfin tuna, were much less severe than those observed for many of the sharks. When compared with relative abundance trends estimated from observer program data (Supplementary Figure S3), observer trends were more variable than those estimated from logbook data. Logbook and observer trends exhibited significant positive correlations for 57% of species (13 of the 23 species for which observer data were analysed). We also compared relative abundance trends estimated from logbook data to those previously estimated by the SCRS (Supplementary Figure S4), and 79% of these trends were significantly positively correlated.

General relative abundance patterns were characterized using either continuous or piecewise linear trends (Figure 4). Linear trends from the logbook analyses were compared with those estimated from observer data (Supplementary Figure S5), and in general, directionality was consistent across data sets, with obvious exceptions for blue shark, porbeagle, common thresher, scalloped hammerhead, smooth hammerhead, night shark, and spinner shark. As a measure of precision, the median of the annual coefficients of variation (MCV) was calculated for each relative abundance trend (Figure 4). According to MCV, eight
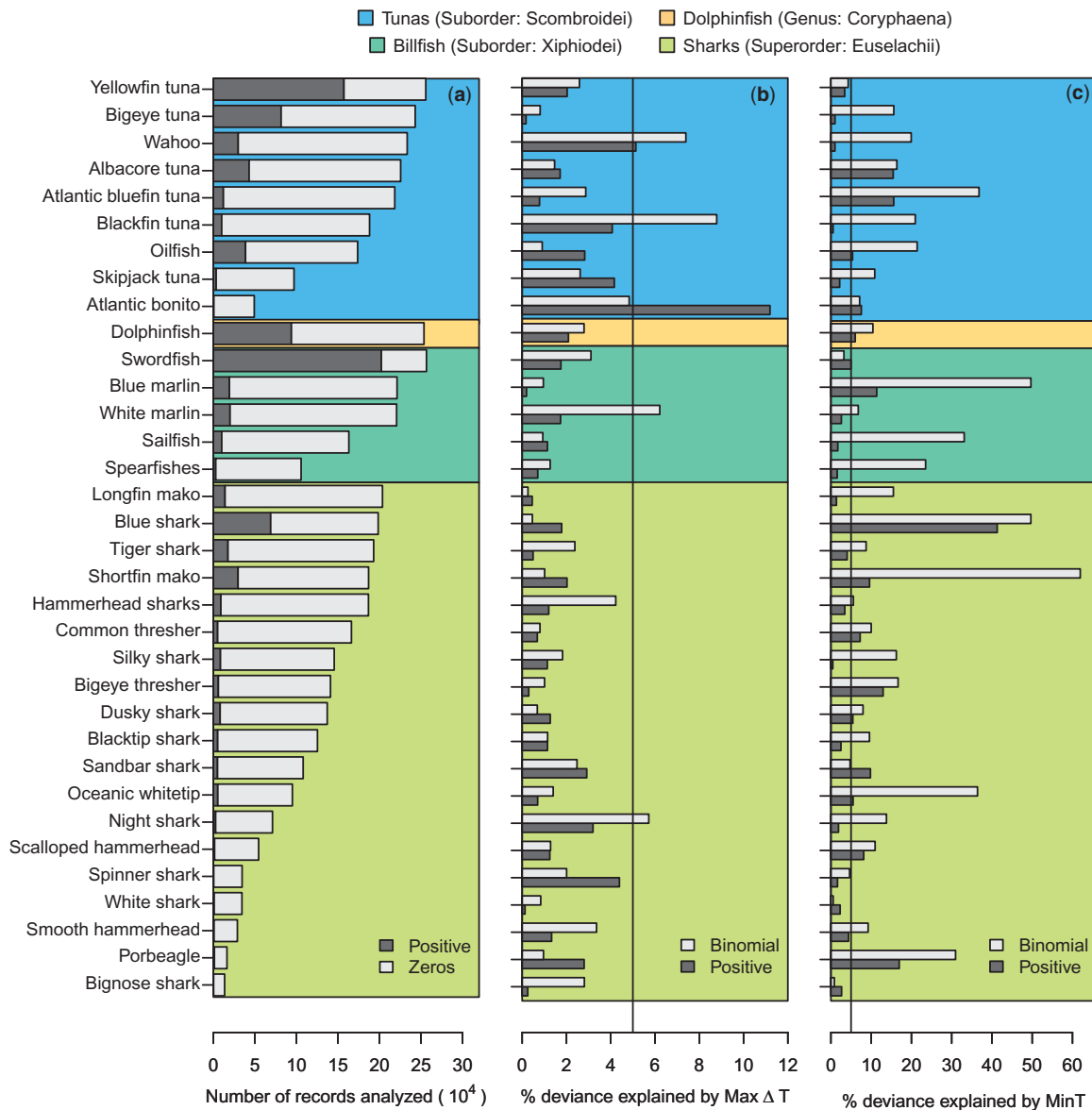
Figure 2. Number of logbook records analysed (a), including proportion of positive catch records for species captured in the USLL. Also, the percent of the total deviance explained by the habitat factors MaxΔT (b), and Min$T$ (c) for analysis of presence/absence of a given species (Binomial) or the positive catch records (Positive). The deviance threshold used for determining inclusion of the variable in the final model (5%) was provided for reference (black line).

(24%) of the trends were estimated with poor precision (i.e. MCV > 1), suggesting that the annual estimates of relative abundance for these particular trends should be interpreted with caution.

We further characterized relative abundance trends using instantaneous rates of change estimated from the logbook (Figure 5) and observer (Supplementary Figure S6) analyses. Strongly negative rates were most prevalent early in the time series, particularly for sharks, but most species with steep initial declines in abundance have either stabilized or are experiencing less severe declines in recent years. Eight patterns in instantaneous rates of change emerged from the logbook analyses: (1) decreasing (negative) throughout, (2) decreasing then stable (not significantly different from zero), (3) decreasing then increasing (positive), (4) stable throughout, (5) stable then increasing, (6) increasing

throughout, (7) increasing then stable, and (8) increasing then decreasing. A summary of these patterns (Table 2) indicated that approximately 71% of HMS analysed are either decreasing in recent years or have decreased without evidence of recovery (patterns 1, 2, and 5), while 29% exhibited other, more favourable trends (patterns 3, 4, and 6–8). These patterns were also summarized according to taxonomic grouping (Table 2), which emphasized that relative abundance trends are generally more favourable for tunas than for either billfishes or sharks. For tunas, 67% of the species fell into the favourable categories, whereas 20% of billfishes and 16% of shark species followed favourable patterns.

Discussion

In this study we estimated relative abundance trends (1987–2013) for 34 HMS in the western Atlantic Ocean using an approach that
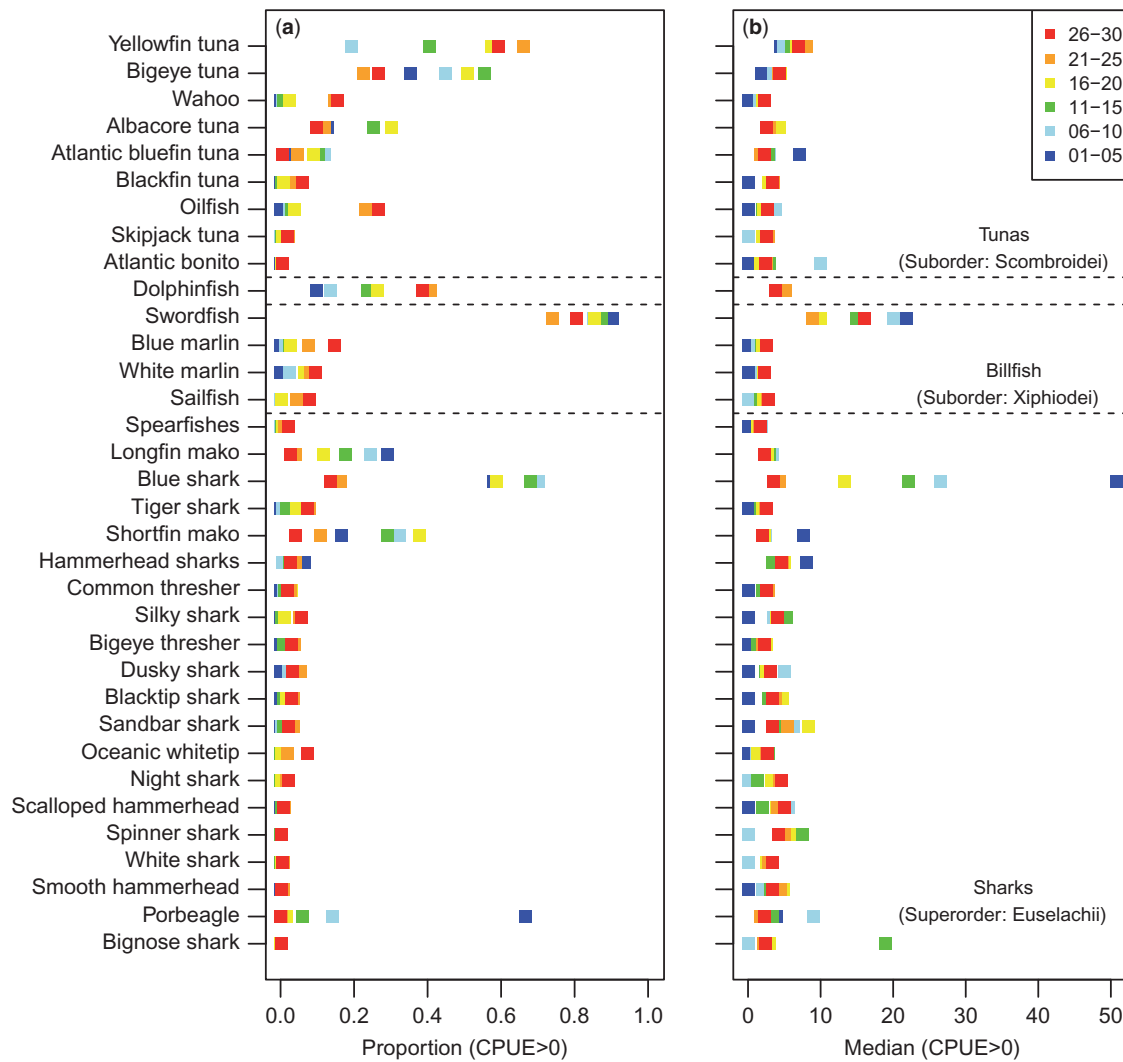
Figure 3. Catch rates (CPUE) by species from the USLL, presented as the proportion of positive catches (a) and the median of the positive catches (b) observed in 5°C temperature bins corresponding with the estimated minimum temperature fished per set.

accounts for pelagic habitat fished. This represents one of the most comprehensive analyses of HMS to date, and the individual species trends offer a variety of potential benefits. For the species that have previously been assessed by ICCAT (Table 1), our trends are useful in a comparative sense, because where available, stock assessment results should serve as the primary basis for understanding stock status and trends in abundance. However, our methodology may result in more accurate indices of relative abundance from the USLL fleet, which may improve the stock assessments of these species if our trends are incorporated. For the species that are not regularly assessed, including dolphinfish, wahoo, blackfin tuna, oilfish, spearfishes, and several sharks, we provide first-ever, or updated abundance trends that may well represent the best current understanding of their abundance trends. Overall, USLL abundance trends indicate population declines of varying degrees without noticeable recovery for most HMS analysed (71% of the species).

Declines in relative abundance of large predatory fishes have been cited as evidence of a global fisheries crisis (Jackson *et al.*, 2001; Baum *et al.*, 2003; Myers and Worm, 2003; Worm *et al.*, 2006;

Myers *et al.*, 2007; Ferretti *et al.*, 2008). While these studies have garnered considerable attention from the media, general public, and scientific community, many have been criticized for analytical flaws, some of which may have been critical to the conclusions (Walters, 2003; Burgess *et al.*, 2005; Hampton *et al.*, 2005; Polacheck, 2006; Wilberg and Miller, 2007). Examples of common criticisms include the use of aggregated CPUE (Walters, 2003), a failure to consider USLL observer data (Burgess *et al.*, 2005), and ignoring habitat, vertical distributions, and other factors that can bias trends in fishery CPUE (Burgess *et al.*, 2005; Hampton *et al.*, 2005; Polacheck, 2006). In our study, we did not aggregate CPUE across species or spatial cells, we included an analysis of USLL observer data, and we considered a full suite of variables (including habitats fished) that have been hypothesized to potentially bias CPUE trends. We fully recognize the difficulty in inferring population trends from fishery data, but given that there are no scientific monitoring programs operating at the population scale, fisheries offer the best available information. Thus, we have been careful to address many of the concerns associated with estimating relative abundance trends using fishery data.
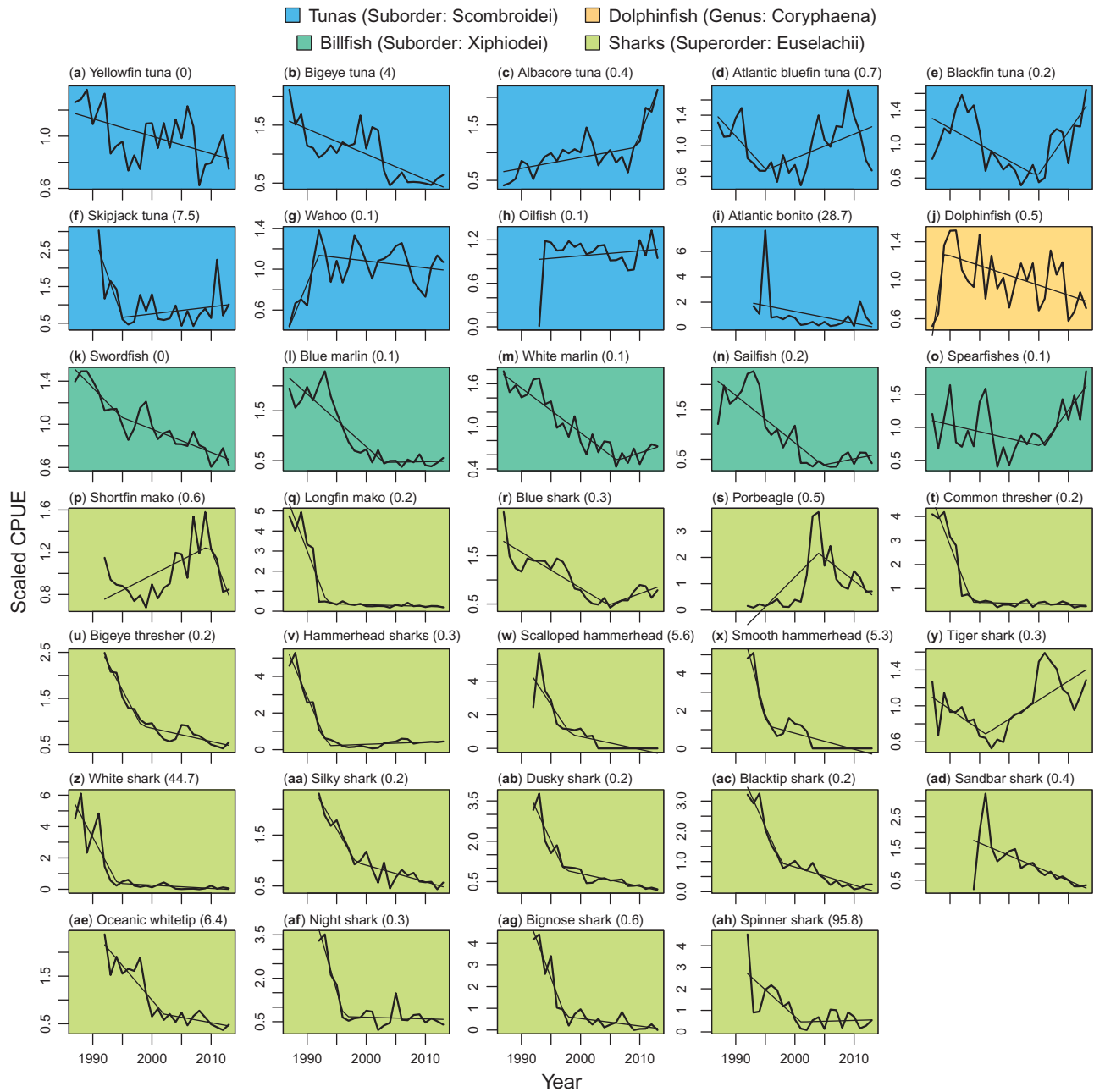
Figure 4. Abundance trends estimated for each species using fisher logbook data from the USLL (thick line), with linear trends fit to the abundance patterns (thin line). Each abundance trend was scaled to its mean value, and the corresponding median of the annual coefficients of variation was presented next to each species name in parentheses.

Using USLL-derived indices of abundance, we observed substantial declines for many species; however, complete extirpation of all large predators does not appear imminent unless several abundance trends suddenly decline. Approximately ten species (29%) did not show a statistically significant negative trend in relative abundance over the past several years (albacore tuna, bluefin tuna, blackfin tuna, wahoo, oilfish, Atlantic bonito, spearfishes, tiger shark, shortfin mako, and porbeagle), and some stocks showed signs of growth or recovery. It should be noted that while not statistically significant, shortfin mako and porbeagle appear to be declining in relative abundance. In contrast, if recent increases in blue shark relative abundance continue, we anticipate that our

analyses would identify a favourable change (i.e. significantly positive instantaneous rate of change) starting around 2005. While our results indicate that many HMS have declined in abundance over time, the species that exhibited favourable patterns suggest that either the purported demise of marine predators was overly pessimistic, or that some of these species began to rebuild since the earlier studies were conducted (we suspect both explanations to be true). The range of relative abundance patterns observed in this study support the conclusions of Worm *et al*. (2009), who, in a comprehensive analysis of global marine ecosystems, described a combination of overexploited and recovering fish stocks. Changes in fishing pressure, due to management actions or socio-economic
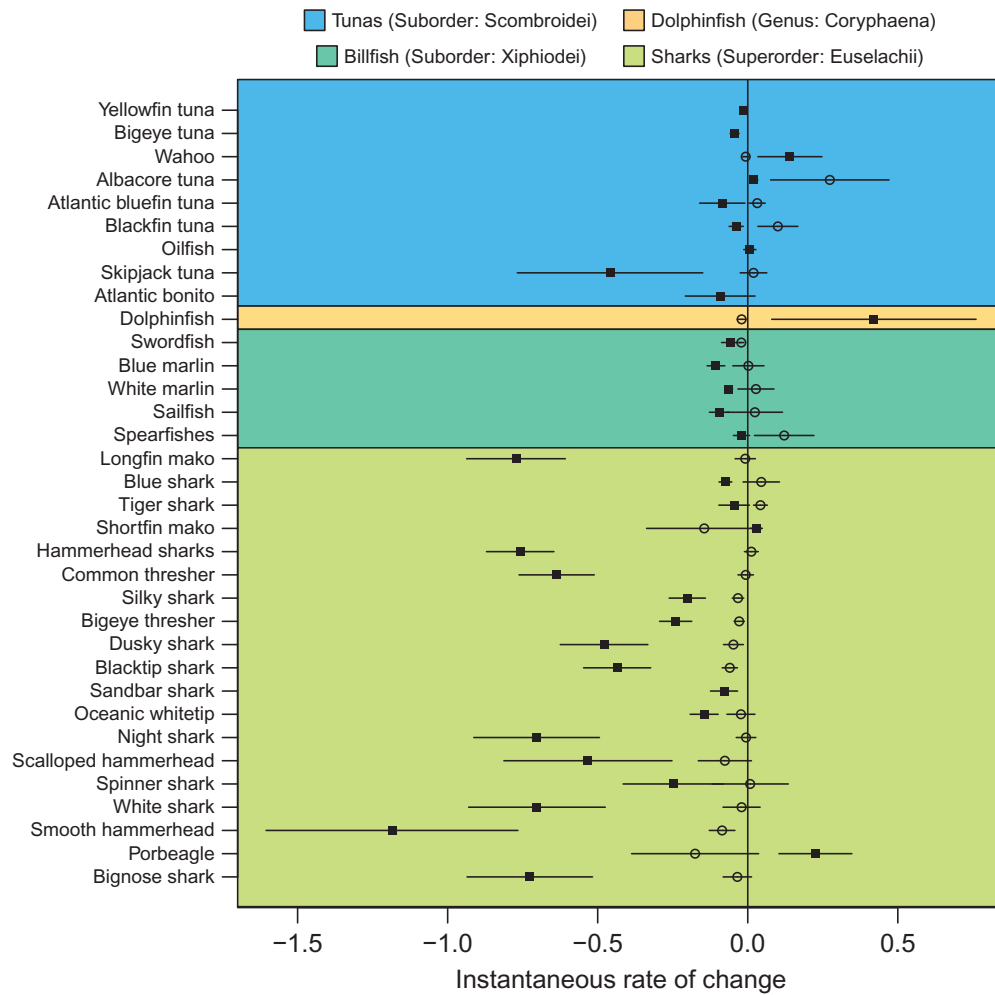
Figure 5. Instantaneous rates of change in relative abundance ±95% confidence intervals. A single or initial rate of change is presented for each species (■), and a second, more recent rate of change is presented for species where piecewise regression outperformed simple linear regression (○).

Table 2. Patterns observed for instantaneous rates of change in abundance estimated from the logbook analyses, presented as the total number and percent of species analysed corresponding to each pattern.

Pattern	All	Tunas	Billfish	Sharks
1. Decreasing	9 (26.5%)	2 (22.2%)	1 (20.0%)	6 (31.6%)
2. Decreasing then stable	14 (41.2%)	1 (11.1%)	3 (60.0%)	10 (52.6%)
3. Decreasing then increasing	2 (5.9%)	2 (11.1%)	0 (0.0%)	0 (0.0%)
4. Stable	2 (5.9%)	2 (11.1%)	0 (0.0%)	0 (0.0%)
5. Stable then increasing	2 (5.9%)	0 (0.0%)	1 (20.0%)	1 (5.3%)
6. Increasing	1 (2.9%)	1 (11.1%)	0 (0.0%)	0 (0.0%)
7. Increasing then stable	3 (5.7%)	1 (11.1%)	0 (0.0%)	2 (10.5%)
8. Increasing then decreasing	1 (2.9%)	0 (0.0%)	0 (0.0%)	0 (0.0%)

Patterns were summarized for all HMS analysed, tunas (Suborder: Scombroidei), billfish (Suborder: Xiphiodei), and sharks (Superorder: Euselachii). The single increasing then decreasing trend is associated with dolphinfish.

dynamics, are likely a strong driver of HMS abundance, but across all 34 species analysed, it would be very challenging to disentangle fishing effects from other potential drivers, such as climate change, environmental variability, and predator–prey dynamics.

The data used for our analyses comprise one of the best sources available for making inferences about HMS relative abundance in the Atlantic Ocean (Baum *et al.*, 2003). Pelagic longline fisheries typically cover a wide geographic range, and they have been operating in the Atlantic Ocean since the 1950s (Majkowski, 2007). Longline fleets from nations with a long-term presence in the Atlantic (e.g. Japan and Taiwan) are also potentially valuable sources of data for evaluating HMS abundance; however, to account for changing fishery dynamics, information about fishing practices must be available. When recorded, this information is often considered proprietary, and therefore can be difficult to obtain. We analysed fisher logbook data from the USLL, which includes detailed set-specific information concerning fishery dynamics. We encourage similar studies using pelagic longline data from other nations, such as Japan, if reliable data on fishing practices are available. Analyzing data from fisheries with longer time series may be most beneficial, because the first complete year of USLL logbook records was 1987, and relative abundance in the first year of our time series may have already been reduced following years of intense fishing pressure.

In general, stock assessments (Quinn and Deriso, 1999) that integrate multiple sources of information (including relative

abundance trends) provide a more complete evaluation of fish stock dynamics than simple trend analyses. For the few species that have been assessed, management decisions should be (and are) based on assessment results rather than fishery-derived relative abundance trends; however, our trends have the novelty of adjusting for exploited habitats and may be useful in future stock assessments.

Relative abundance trends previously estimated using logbook data from the USLL are available for species that have been assessed in a fishery stock assessment context or by individual research projects (e.g. Baum *et al.*, 2003). Our relative abundance trends are not completely divergent from those previously estimated for stock assessments, and they extend the estimates beyond the final year of the earlier time series (Supplementary Figure S4). We observed that previous relative abundance trajectories have continued for many species, while the direction of others has reversed (mainly those that exhibited signs of population growth in recent years). The relative abundance trends we estimated for swordfish and skipjack tuna are in contrast with previous estimates used in stock assessments. We showed a declining, rather than stable swordfish relative abundance over time, and we did not observe a sudden increase in skipjack tuna relative abundance as previously shown. An analysis of USLL observer data by Baum and Blanchard (2010) estimated relative abundance trends for many of the same shark species we analysed. Although Baum and Blanchard (2010) aggregated several of the shark species and conducted analyses at the genus or species group level, our estimated trends (Supplementary Figure S3) were similar to theirs through 2005 (the final year of data analysed by Baum and Blanchard [2010]).

When comparing and evaluating relative abundance trends for individual species, the population biology and fishery data collection for that species should be considered. For instance, estimates of relative abundance used in recent swordfish stock assessments relied on fishery weigh-out data to compute catches by age, and then aggregated catches over ages 3–10. We did not have weigh-out data available for our analyses, nor did we attempt to partition catches by age. Also, regulatory effects were considered when analysing the swordfish weigh-out data, and we did not explicitly consider species-specific regulations. These methodological differences between our analysis and the swordfish stock assessment may explain the divergent abundance trends. For billfishes, primarily white marlin, the recent validation of roundscale spearfish (*Tetrapturus georgii*) as a species (Shivji *et al.*, 2006) may have affected catch reporting accuracy by shifting catches that were historically reported as "white marlin" and other billfishes to "spearfishes." Abundance trends used in previous Atlantic bluefin tuna stock assessments were estimated using only records from the Gulf of Mexico during January–May (NMFS, 1993), yet we used data throughout the year.

There are also important considerations concerning the use of USLL logbook data to make inferences about the relative abundance of sharks (although these concerns may not apply to blue and shortfin mako sharks). Burgess *et al.* (2005) discussed regulatory changes in 1993 that might have contributed to false declines in catch rates of some sharks; however, we note that many of the shark species we analysed exhibited declines before 1993. Additional issues noted by Burgess *et al.* (2005) that may contribute significant errors to the logbook database include misidentification, errors in reporting, and failure to record bycatch species. However, random errors in identification and data recording are much less problematic than an unaccounted sudden change or systematic pattern in data recording. Although, for some species, such as white shark (*Carcharadon carcharias*), errors in the data may be substantial enough to make our relative abundance trends uninformative (most recorded white shark catches are likely the result of misidentification; Burgess *et al.*, 2005). Fishery observer data likely contain fewer issues related to misidentification or errors in reporting. Thus, positive correlations between abundance trends estimated from logbook data and those based on fishery observer data provide a degree of validation for 57% of the stocks with observer data (Supplementary Figure S3). For species with divergent logbook and observer trends, the trends based on logbook data should be interpreted with caution. Also, we recommend additional work to compare logbook and observer data collected on the same trip.

Catches observed in relation to the $\text{Min}T$ habitat variable (Figure 3) highlight the expected result that exploited pelagic habitats (which are a function of gear configuration, fishing location, and environmental conditions) largely govern the composition of species encountered. This conclusion provides strong support for including a temperature variable in models designed to estimate HMS relative abundance trends. Furthermore, the incorporation of pelagic habitat fished allows a post-hoc evaluation of the role of pelagic habitat on HMS catches. For instance, blue sharks exhibited a higher encounter rate when cooler habitats were fished. This is not necessarily surprising (Cortés *et al.*, 2007); however, when the fishery exploited the absolute coldest habitat (1–$5°C$) and blue sharks were encountered, their catch rates were higher than those for any other species caught by the fishery. Because blue sharks are a bycatch species in the USLL fishery, managers could use this information to impose time-area restrictions on certain gear configurations to avoid fishing the coldest habitat and possibly reduce overall bycatch of blue sharks. Evaluating habitat-specific catch rates would not only be useful for blue sharks, but potentially for all species analysed, especially those with high catch rates in specific habitats (e.g. shortfin mako shark, hammerhead sharks, sandbar shark, spinner shark, porbeagle, and bignose shark). Many shark species are particularly vulnerable to overfishing due to their relatively low fecundity, slow growth rates, and late maturity (Musick *et al.* 2000), and in fact, various stocks of scalloped hammerhead sharks are listed as either threatened or endangered under the Endangered Species Act (http://www.nmfs.noaa.gov/pr/species/esa/listed.htm#fish). Thus, our habitat-specific catch rates may facilitate conservation of many sharks and other species that are vulnerable to overfishing.

The pelagic habitat variables explained a relatively small amount of variance in catch rates of the primary target species, such as swordfish and yellowfin tuna (Figure 2). One explanation for this result is that, in order to maximize catch rates, fishermen purposefully deploy gear in the preferred habitats of their target species. Thus, variation in target species catch rates may be more related to changes in abundance and targeting practices than habitat-driven availability. For bycatch species, however, fishermen are not seeking to maximize their catch rates, and overlaps between fishing effort and their distributions are less frequent and likely more driven by incidentally fishing in their preferred habitats.

The relative lack of importance of $\text{Max}\Delta T$ was unexpected considering the results of a simulation study conducted by Lynch *et al.* (2012); however, that study was based on the dynamics of the Japanese pelagic longline fishery. The Japanese fishery has

substantially changed fishing practices over time, resulting in strong contrast in pelagic habitats exploited. The USLL has also exhibited systematic changes in fishing practices over the time period we analysed, but these changes did not occur on the temporal and spatial scales of the Japanese fishery. This does not suggest that relative temperature is not an important factor governing the population dynamics of HMS, but rather that the minimal contrast observed in $\text{Max}\Delta T$ precludes it from explaining considerable variability in USLL catch rates. We maintain that future efforts to estimate relative abundance trends from HMS fishery data consider both $\text{Min}T$ and $\text{Max}\Delta T$ in model development.

Several of our relative abundance trends were not estimated with high precision, and this uncertainty should be kept in mind when interpreting the patterns. In some cases, the inclusion of temperature variables may have increased uncertainty in relation to relative abundance trends previously estimated without these variables. However, increased uncertainty would be a poor justification for ignoring important dynamics, such as pelagic habitat fished, and in fact, our results suggest that pelagic habitat variables can explain substantial variability in HMS catch rates. Empirical evidence highlights the importance of temperature in governing HMS vertical distributions (Brill and Lutcavage, 2001), and our modelling exercises can be useful for understanding how HMS catch rates may respond to ocean dynamics. By including the temperature variables, our analyses may have placed a higher value on accuracy than precision, but we encourage that future studies seek to reduce uncertainty while maintaining the consideration of pelagic habitat. Also, to improve the characterization of habitats fished, we encourage enhanced sampling of oceanographic variables during fishing operations to be recorded in logbooks and by fishery observers.

In addition to precision, several underlying model assumptions warrant attention. For instance, to estimate the temperature fished in each longline set, we assumed that all sections of the gear were distributed identically throughout the water column. This is unlikely, because longline fishing depth is governed by numerous dynamic processes, including wind, hydrodynamics, and the behaviour of hooked organisms (Bigelow *et al.*, 2006; Ward and Myers, 2006; Rice *et al.*, 2007). Also, by relating fishing depth to temperature using average ocean temperatures we ignored interannual variability in temperature at depth for a given time and location. However, one benefit of ignoring interannual variability is that our analyses were not confounded by potential changes in stock productivity related to changing ocean temperature; rather, our temperature variables accounted for changes in availability due to monthly ocean dynamics. In the broader context of improving relative abundance estimates, future analyses might consider additional environmental factors, such as the oxygen minimum zone (Prince *et al.*, 2010), or other statistical treatments of spatio-temporal data (e.g. Thorson *et al.*, 2015).

Despite potential caveats, we believe this study advances the methodology for deriving fishery-dependent indices of abundance from HMS longline fisheries. Our habitat variables generally explained a substantial amount of deviation in catch rates. Thus, we recommend that these variables be considered in future stock assessments that incorporate estimates of relative abundance from longline catch rates. Further, the results of this study can help inform discussions about the health of global fisheries, particularly for species that are not regularly assessed. Overall,

we observed a mixture of declining, stable, and increasing trends in relative abundance, which indicates that global fisheries are not likely following a unidirectional pattern. However, in general terms, declines observed for bycatch species were more severe than those for target species. This may suggest that bycatch species of HMS fisheries are more susceptible to overfishing than target species. With this challenge in mind, the habitat-specific catch rates we observed (Figure 3) may serve as a valuable management tool for reducing fishing pressure on bycatch species.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

References

Aitchison, J. 1955. On the distribution of a positive random variable having a discrete probability mass at the origin. Journal of the American Statistical Association, 50: 901–908.

Baum, J. K., and Blanchard, W. 2010. Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. Fisheries Research, 102: 229–239.

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., and Doherty, P. A. 2003. Collapse and conservation of shark populations in the northwest Atlantic. Science, 299: 389–392.

Bigelow, K. A., and Maunder, M. N. 2007. Does habitat or depth influence catch rates of pelagic species? Canadian Journal of Fisheries and Aquatic Sciences, 64: 1581–1594.

Bigelow, K., Musyl, M. K., Poisson, F., and Kleiber, P. 2006. Pelagic longline gear depth and shoaling. Fisheries Research, 77: 173–183.

Brill, R., and Lutcavage, M. 2001. Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve stock assessments. *In* Island in the Stream: Oceanography and Fisheries of the Charleston Bump, Pp. 179–198. Ed. by G. R. Sedberry. American Fisheries Society, Bethesda, Maryland. 240 pp.

Burgess, G. H., Beerkircher, L. R., Cailliet, G. M., Carlson, J. K., Cortés, E., Goldman, K. J., and Grubbs, R. D. 2005. Is the collapse of shark populations in the northwest Atlantic Ocean and Gulf of Mexico real? Fisheries, 30: 19–26.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York, NY. 488 pp.

Cortés, E., Brown, C. A., and Beerkircher, L. R. 2007. Relative abundance of pelagic sharks in the western North Atlantic Ocean, including the Gulf of Mexico and Caribbean Sea. Gulf and Caribbean Research, 19: 37–52.

Ferretti, F., Myers, R. A., Serena, F., and Lotze, H. K. 2008. Loss of large predatory sharks from the Mediterranean Sea. Conservation Biology, 22: 952–964.

Goodyear, C. P. 2003. Tests of the robustness of habitat-standardized abundance indices using simulated blue marlin catch-effort data. Marine and Freshwater Research, 54: 369–381.

Hampton, J., Sibert, J. R., Kleiber, P., Maunder, M. N., and Harley, S. J. 2005. Fisheries: decline of Pacific tuna populations exaggerated? Nature, 434: E1–E2.

Hinton, M. G., and 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. Inter-American Tropical Tuna Commission Bulletin, 21: 171–200.

Hoey, J. J., and Bertolino, A. 1988. Review of the U.S. fishery for swordfish, 1978 to 1986. Collective Volume of Scientific Papers ICCAT, 27: 256–266.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., and Bradbury, R. H. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293: 629–638.

Lo, N. C. H., Jacobson, L. D., and Squire, J. L. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2515–2526.

Locarnini, R. A., Mishonov, A. V., Antonov, J. I., Boyer, T. P., Garcia, O. K., Baranova, O. K., and Zweng, M. M. 2010. World Ocean Atlas 2009, Volume 1: temperature. *In* NOAA Atlas NESDIS 68. Ed. by S. Levitus. U.S. Government Printing Office, Washington, DC. 184 pp.

Lynch, P. D., Graves, J. E., and Latour, R. J. 2011. Challenges in the assessment and management of highly migratory bycatch species: a case study of the Atlantic marlins, pp. 197–225. *In* Sustainable Fisheries: Multi-Level Approaches to a Global Problem. Ed. by W. W. Taylor, A. J. Lynch, and A. J. Schechter. American Fisheries Society, Bethesda, MD.

Lynch, P. D., Shertzer, K. W., and Latour, R. J. 2012. Performance of methods used to estimate indices of abundance for highly migratory species. Fisheries Research, 125-126: 27–39.

Majkowski, J. 2007. Global fishery resources of tuna and tuna-like species. FAO Fisheries Technical Paper 483. Food and Agriculture Organization of the United Nation, Rome. 54 pp.

Mandelman, J. W., Cooper, P. W., Werner, T. B., and Lagueux, K. M. 2008. Shark bycatch and depredation in the U.S. Atlantic pelagic longline fishery. Reviews in Fish Biology and Fisheries, 18: 427–442.

Maunder, M. N., Hinton, M. G., Bigelow, K. A., and Langley, A. D. 2006. Developing indices of abundance using habitat data in a statistical framework. Bulletin of Marine Science, 79: 545–559.

Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70: 141–159.

Musick, J. A., Burgess, G. H., Camhi, M., Cailliet, G., and Fordham, S. 2000. Management of sharks and their relatives (*Elasmobranchii*). Fisheries, 25: 9–13.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., and Peterson, C. H. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science, 315: 1846–1850.

Myers, R. A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature, 423: 280–283.

NMFS (National Marine Fisheries Service). 1993. Fishery management plan for sharks of the Atlantic Ocean. National Oceanic and Atmospheric Administration, Silver Spring, MD.

Ortiz, M., and Arocha, F. 2004. Alternative error distribution models for standardization of catch rates of non-target species from a pelagic longline fishery: billfish species in the Venezuelan tuna longline fishery. Fisheries Research, 70: 275–297.

Polacheck, T. 2006. Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? Marine Policy, 30: 470–482.

Prince, E. D., Luo, J., Goodyear, C. P., Hoolihan, J. P., Snodgrass, D., Orbesen, E. S., Serafy, J. E., *et al.* 2010. Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. Fisheries Oceanography, 19: 448–462.

Quinn, T. J., and Deriso, R. B. 1999. Quantitative Fish Dynamics. Oxford University Press, Oxford. 212 pp.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org/.

Rice, P. H., Goodyear, C. P., Prince, E. D., Snodgrass, D., and Serafy, J. E. 2007. Use of catenary geometry to estimate hook depth during near-surface pelagic longline fishing: theory versus practice. North American Journal of Fisheries Management, 27: 1148–1161.

Seber, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters, 2nd edn. Oxford University Press, New York. 654 pp.

Shivji, M. S., Magnussen, J. E., Beerkircher, L. R., Hinteregger, G., Lee, D. W., Serafy, J. E., and Prince, E. D. 2006. Validity, identification, and distribution of the roundscale spearfish, *Tetrapturus georgii* (Teleostei: istiophoridae): morphological and molecular evidence. Bulletin of Marine Science, 79: 483–491.

Stefánsson, G. 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. ICES Journal of Marine Science, 53: 577–588.

Thorson, J. T., Shelton, A. O., Ward, E. J., and Skaug, H. J. 2015. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES Journal of Marine Science, 72: 1297–1310.

Walter, J. 2011. Standardized catch rate in number and weight of yellowfin tuna (*Thunnus albacares*) from the United States pelagic longline fishery 1987–2010. Collective Volume of Scientific Papers ICCAT, 68: 915–952.

Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. Canadian Journal of Fisheries and Aquatic Sciences, 60: 1433–1436.

Ward, P. J., and Myers, R. A. 2006. Do habitat models accurately predict the depth distribution of pelagic fishes? Fisheries Oceanography, 15: 60–66.

Wilberg, M. J., and Miller, T. J. 2007. Comment on "Impacts of biodiversity loss on ocean ecosystem services". Science, 316: 1285b.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., *et al.* 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787–790.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., *et al.* 2009. Rebuilding global fisheries. Science, 325: 578–585.