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## Habitat and Fish Population Dynamics: Advancing Stock Assessments of Highly Migratory Species

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**Habitat and Fish Population Dynamics: Advancing Stock  
Assessments of Highly Migratory Species**

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**A Dissertation**

**Presented to**

**The Faculty of the School of Marine Science  
The College of William and Mary in Virginia**

**In Partial Fulfillment  
of the Requirements for the Degree of  
Doctor of Philosophy**

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**By**

**Patrick D. Lynch**

**2012**

APPROVAL SHEET

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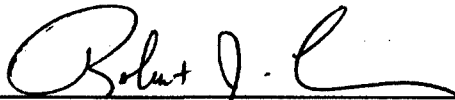
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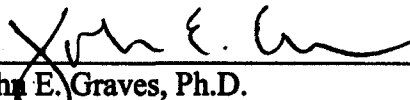


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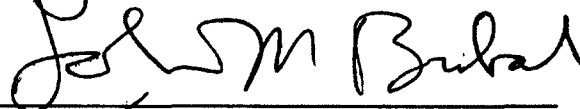
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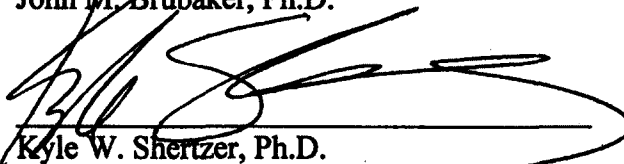
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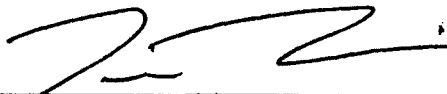
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## DEDICATION

To the memory of my grandfather, Dr. Howard E. Lynch.

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## ABSTRACT

Fisheries sustainability is inherently linked to an understanding of the population-level effects of fishing. With an accurate characterization of historical fish and fishery dynamics, management agencies are more equipped to create regulations that sustain fishery resources over the long term. The overarching goal of this dissertation is to contribute to the advancement of fisheries stock assessment and promote resource sustainability. My research focused on highly migratory species (HMS), particularly fishes that reside in the open ocean. These species constitute some of the highest valued global fisheries; however, numerous factors compromise HMS stock assessment and management. These challenges are fully described in Chapter 1, which also includes corresponding research and management recommendations. A key limitation in HMS assessments underlying my research is the lack of independent scientific monitoring programs. In the absence of research surveys, HMS stock assessments must rely on fishery catch and effort data. Therefore, special care is required to infer population dynamics from entities that were not established to monitor populations. In particular, the habitat in which fishing occurs largely dictates the amount and composition of fishes captured. Unfortunately, habitat effects on fishery-dependent data are not commonly accounted for in HMS assessments. Chapter 2 presents the results of a performance evaluation of methods used for estimating HMS abundance trends, including traditional generalized linear models (GLMs), an existing method that considers habitat (statHBS), and a proposed method that hybridizes traditional and habitat-based approaches (HabGLM). I demonstrate that HabGLM was most accurate of those evaluated, while exhibiting minimal sensitivity to errors in input data. I recommend the use of HabGLM in future HMS stock assessments; however, despite being most accurate, there were scenarios where HabGLM still did not sufficiently capture the true abundance pattern. In Chapter 3, the HabGLM was applied to 35 HMS in the Atlantic Ocean using fisher logbook data from the US pelagic longline fishery. This comprehensive analysis portrays an HMS community in the Atlantic as generally depleted, with current abundances of 76% of the species at less than half of their 25-year observed maxima. However, despite these depletions, 26% of the species exhibited population growth, suggesting recent fishing intensities may be adequate for sustaining or rebuilding certain populations. While interpretations of abundance trends can be informative, fisheries management is more often guided by the output of stock assessments. Thus, in Chapter 4, I present the results of a study that evaluated the effects of abundance index quality on the performance of a stock assessment model (Stock Synthesis), with a focus on Atlantic blue marlin (*Makaira nigricans*). In general, assessment model performance was superior when based on abundance indices estimated using HabGLM; however, the management quantities derived from this best case scenario were still overly optimistic, and when the fisheries were regulated accordingly, population biomass was projected to be well below the management target level. Overall, my research emphasizes that (1) habitat should be directly incorporated into HMS stock assessments, and (2) independent stock monitoring programs are essential for effective fisheries management.



## AUTHOR'S NOTE

The chapters that comprise this dissertation were written in manuscript format for a scientific publication. Thus, the formatting of each chapter follows the guidelines of the publication to which the manuscript was or will be submitted. At the time of writing, citations for individual chapters are as follows:

### CHAPTER 1

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### CHAPTER 2

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### CHAPTER 3

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### CHAPTER 4

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<sup>\*</sup>Coauthors to be determined

**Habitat and Fish Population Dynamics: Advancing Stock  
Assessments of Highly Migratory Species**

## **CHAPTER 1**

**Challenges in the assessment and management of highly migratory  
bycatch species: a case study of the Atlantic marlins**

## INTRODUCTION

In marine ecosystems, highly migratory species (HMS) are characterized as having vast geographical distributions, with extensive individual migrations often spanning entire oceans. Dispersal on this scale can promote ocean-wide population connectivity, resulting in many HMS exhibiting genetic homogeneity. From a biological perspective, these species often comprise a single unit stock within an ocean basin. Since single stocks can be distributed throughout multinational and international waters (as with the tunas [Family Scombridae]), sustainable management of these harvested stocks requires cooperation between all fishing nations. An international governing organization is imperative to ensure cooperation, and in the Atlantic Ocean, the member nations of the International Commission for the Conservation of Atlantic Tunas (ICCAT) are responsible for management of highly migratory fishes. The main objective of ICCAT is to maintain stocks at levels that produce maximum sustainable yield (MSY) (ICCAT 2007a), a goal that is likely shared among most fishing nations. However, numerous HMS exhibit spatial and temporal overlap, which creates management challenges since large quantities of nontarget HMS are often caught incidentally. The various HMS captured may not have the same intrinsic population growth rates or carrying capacities; therefore, their populations may not exhibit the same responses to a given level of fishing effort. Since fishers often seek productive stocks, nontarget species may be depleted at a rate faster than target species, thus sustainable management of all stocks may require a reduction of effort well below that which maximizes yield of the target species. For many fishing nations, this can result in substantial declines in commercial revenues. Since the overall importance of nontarget species inevitably varies between stakeholders, the international cooperation that is essential for management of HMS may break down when incidental catch is considered.

Numerous HMS and other large marine organisms are susceptible to incidental capture, including sea turtles (Family Cheloniidae), marine mammals (Order Cetacea), sharks (Superorder Euselachii), and billfishes (Family Istiophoridae). In the Atlantic, these species are most frequently encountered by fisheries that target tunas, swordfish *Xiphias gladius*, and sharks, with gears such as pelagic longlines, shark bottom longlines, and shark gill nets (NMFS 2007). For marine mammals, public disapproval of incidental fishing-induced mortality has been a powerful force in driving regulations (e.g., the Marine Mammal Protection Act of 1972 by the U.S. Congress) and adoption of new technologies that have reduced their respective fishing mortalities (Hall 1998; Hall et al. 2000). However, despite historically persistent overfishing (Restrepo et al. 2003), the excessive exploitation of Atlantic billfishes, such as blue marlin *Makaira nigricans* and white marlin *Kajikia albida*, has not invoked a similar reaction (Webster 2006). While the most recent regulations imposed by ICCAT for reducing Atlantic marlin mortality are surprisingly restrictive (see Governance section, this chapter), especially when considering ICCAT's goal of maximizing yield, it is uncertain that they are capable of rebuilding the stocks (ICCAT 2006; Webster 2006). Many of the challenges surrounding management of marlins are related to uncertainties in biological and fisheries data, resulting in uncertainties in the assessment process (Restrepo et al. 2003; Die 2006). Here, the focus is on Atlantic marlin populations and potential quantitative approaches to reduce uncertainty in their assessments, thereby promoting international cooperation and the implementation of sustainable management measures.

## IMPORTANCE

Globally, istiophorids comprise five genera and nine species (Collette et al. 2006). Of these, six species occur regularly in the Atlantic Ocean and its adjoining seas: blue marlin, white marlin, sailfish *Istiophorus platypterus*, longbill spearfish *Tetrapturus pfluegeri*, Mediterranean spearfish *T. belone*, and roundscale spearfish *T. georgii*. Blue marlin and white marlin are distributed throughout tropical and temperate waters of the Atlantic, ranging from Canada east to the Azores in the northern hemisphere to Argentina east to South Africa in the southern hemisphere (Figure 1). There is a temporal trend to their distribution, with presence in the higher latitudes typically occurring during warmer times of the year. Atlantic marlins tend to exhibit solitary behavior; however, small aggregations of white marlin have been observed (Nakamura 1985). As with all istiophorids, the marlins likely exhibit extremely rapid growth rates in early life (Sponaugle et al. 2005), but the average size of an adult blue marlin (100–175 kg) is much larger than that of a white marlin (20–30 kg) (NMFS 2007). Also, sexually dimorphic growth is common to both species (though much more pronounced in blue marlin), with females growing larger than males (Nakamura 1985; Wilson et al. 1991; Arocha and Bárrios 2009).

Marlins are apex piscivores that also consume invertebrates such as squid (de Sylva and Davis 1963; Nakamura 1985; Cox et al. 2002a; Júnior et al. 2004; Shimose et al. 2006). Apex predators are often considered ecologically important, as their depletion may impact food web structure through a trophic cascade (Paine 1969; Pace et al. 1999; Casini et al. 2009). However, Kitchell et al. (1999) demonstrated that the simulated removal of billfishes from the central North Pacific ecosystem had a minimal impact on trophic structure. In fact, in an assessment of importance, Kitchell et al. (2006) stated that the economic value generated by billfish angling is

far greater than their ecological value as apex predators. While the uncertainty associated with complex ecosystem models such as these can be overwhelming, it may be that healthy Atlantic marlin populations are not critical to maintaining ecosystem stability; however, it is certain that their sustainability is of significant economic importance for artisanal communities and countries with recreational fisheries.

Since its beginning in the late 1800s to early 1900s, the recreational billfish fishery has been an important component of the tourist industry in many parts of the world (Holder 1912; Jordan and Evermann 1923). Though difficult to calculate on a global scale, Ditton and Stoll (2003) estimated the economic impact of this fishery (for several countries combined) to be between US\$203.95 million and \$339.91 million, annually. Additionally, the economic importance of recreational billfish fisheries is emphasized by the regulatory actions of the United States. To reserve billfish for recreational fishing, commercial retention of Atlantic marlins has been prohibited in the United States since implementation of the 1988 Fishery Management Plan for Atlantic Billfish. Also, by law, the United States mandates a recreational fishing presence in the policy-making process by declaring that at least one of the U.S. commissioners to ICCAT must possess “knowledge and experience regarding recreational fishing in the Atlantic Ocean, Gulf of Mexico, or Caribbean Sea” (U.S. Congress 1975). This presence is critical to marlin recreational fisheries, as the interests of billfish anglers often differ from those of commercial fishers that target HMS.

In addition to the significant economic contributions, marlin recreational fisheries are also valued for their social and historical importance. In the mid-20th century, writers such as Zane Gray and Ernest Hemingway romanticized big game fishing, prompting a rapid increase in the popularity of angling for marlins (Peel et al. 2003). This popularity continues today, but the recreational fishing community has recognized that sustainability of marlin populations is imperative to preservation of their fishery. Thus, to minimize fishing mortality, recreational marlin fisheries have become primarily catch and release. An appreciable percentage of marlins

will likely survive this practice, but the rate of postrelease mortality may vary depending on fishing gear and other fishing characteristics (Serafy et al. 2009). While catch-and-release fishing began to take hold following years of substantial recreational landings, it does not represent a considerable sacrifice for most fishermen; it is the challenging fight that precedes capture rather than the capture itself that has drawn many people to the sport (Ditton and Stoll 2003).

Commercially, marlins are of lesser importance than many other HMS. They are landed as nontarget bycatch of fisheries that target tunas and swordfish because the amount of biomass landed and their value per kilogram are lower than these target species. While current ICCAT regulations require the release of any marlin caught alive (ICCAT 2007b, Rec. 2006–09), longline operations often land fish that are dead upon retrieval of the gear. These harvests represent the largest source of fishing mortality for the Atlantic marlins, with Brazil, Japan, and Chinese Taipei constituting the bulk of the landings (ICCAT 2006).

Following peaks in the 1960s, total marlin landings have fluctuated over time with decreasing trends exhibited in recent years (Figure 2). Historical oscillations in total landings essentially tracked longline effort (Restrepo et al. 2003). While recent declines in reported landings may be a result of live release from longline operations, further reduction of fishing mortality could be achieved through a decrease in overall effort or changes in fishing practices. However, given the potential resulting loss of target catch, either of these approaches would likely face substantial resistance by any ICCAT member nation that places a low value on recreational fisheries for marlins.

On a smaller scale, directed artisanal fisheries for Atlantic marlins are conducted by coastal nations, especially in the Caribbean Sea and off the coast of western Africa (ICCAT 2001a). These subsistence fisheries represent the only real reliance on marlins for their nutritional value (Peel et al. 2003). Thus, marlin stock collapses may have little impact on large commercial operations but could represent losses of valuable sources of protein for many developing coastal nations.



Another important group of stakeholders with an interest in Atlantic marlins is the environmental community. This constituency is most concerned with the existence and/or ecological values of the species. However, conservation of marlins has been a relatively low priority when considering the resources dedicated to preserving other charismatic marine megafauna such as bluefin tuna *Thunnus thynnus*, sea turtles, and marine mammals, but since recreational fishermen are also interested in healthy marlin populations, the messages and actions of the two groups are often aligned. A major exception to this collaboration occurred in 2001, however, when some conservationists petitioned to have white marlin listed as a threatened or endangered species under the U.S. Endangered Species Act (ESA; WMSRT 2002). If successful, a listing could have significantly impacted any recreational fisheries in the United States that have the potential to interact with white marlin. In 2002, the National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration determined that the petitioned action was “not warranted” despite concluding that the species was overexploited and that regulatory mechanisms implemented at that time were likely unable to prevent continued overfishing (WMSRT 2002). Subsequently, following further pressure from conservationist groups, NMFS agreed to reassess the species upon completion of the 2006 white marlin stock assessment conducted by ICCAT. After re-evaluation, NMFS maintained that the species did not warrant listing as threatened or endangered (WMBRT 2007).

Overall, the Atlantic marlins are most important to recreational and artisanal fisheries, and they are of relatively low commercial value. Their conservation hinges on an understanding of susceptibility to anthropogenic impacts, which is enhanced with knowledge regarding the sizes and distributions of marlin populations as related to habitat.

## POPULATIONS AND HABITATS

Starting in 2000, Atlantic blue and white marlins have been considered to comprise single unit stocks for assessment and management purposes (Restrepo et al. 2003; ICCAT 2006). Prior to this, it was assumed that the populations each contained northern and southern stocks separated at 58N (Restrepo et al. 2003). Recent genetic analyses supported the single unit stock approach for both populations (Graves and McDowell 2006; McDowell et al. 2007); however, Graves and McDowell (2006) identified significant spatial heterogeneity for white marlin, highlighting a potential need for continued research on their stock structure.

Current scientific understandings of population dynamics and stock status for marlins are entirely fishery-dependent, that is, independent research surveys are not used to monitor their populations. Therefore, estimates of historical biomasses are based on relative measures of catch per unit of effort (CPUE) obtained from the various fisheries, which are assumed proportional to exploitable abundance. Because the fisheries do not sample the populations in a random, unbiased fashion, a complete reliance on fishery-dependent data may introduce many potential sources of error. However, CPUE time series, and assessment models fitted to CPUE data are currently the best available estimates of historical relative abundance. Despite a potentially promising trend in recent years for white marlin, the relative biomasses estimated for each species have declined substantially from 1950s levels (Figure 3). In the context of MSY, these trends do not reflect sustainable harvests, but estimated biomasses may not be accurate because CPUE can be affected by changes in fishing practices regarding target species as well as changes in marlin abundance. Efforts to account for potential biases require an understanding of the relationship between marlin

habitat, susceptibility to capture, and the spatiotemporal dynamics of fishing effort (Maunder and Punt 2004; Bishop 2006).

As with the overlapping geographical distribution of Atlantic marlins, the vertical habitats utilized by these species are also similar. Valuable characterizations of vertical habitat utilization for large pelagic fishes have come from studies that used pop-up satellite archival tags (PSATs) to monitor animal behavior (Arnold and Dewar 2001; Luckhurst 2007; Hofmann and Gaines 2008). These tags record a nearly continuous stream of specified environmental parameters (temperature, pressure [depth], light, etc.), archive the data, and transmit the information via satellite after releasing from the organism and floating to the surface (Graves et al. 2002). There have been several studies in the Atlantic and adjacent seas that attached PSATs to blue marlin (Graves et al. 2002; 2003; Kerstetter et al. 2003; Saito et al. 2004; Prince et al. 2005; Luo et al. 2006; Prince and Goodyear 2006; Kraus and Rooker 2007; Goodyear et al. 2008) and white marlin (Horodysky and Graves 2005; Prince et al. 2005; Kerstetter and Graves 2006a; Horodysky et al. 2007; Graves and Horodysky 2008). The studies that made inferences about habitat utilization revealed similar trends; both species spent the majority of their time in warmer surface waters (<10 m) but made regular short-duration dives to deeper water (occasionally >100 m) (Graves et al. 2003; Kerstetter et al. 2003; Saito et al. 2004; Prince et al. 2005; Luo et al. 2006; Prince and Goodyear 2006; Horodysky et al. 2007; Kraus and Rooker 2007; Goodyear et al. 2008).

While depth can be an informative descriptor for habitat, it is more likely that sea surface temperature (SST) and relative deviations from SST govern marlin distributions through physiological pathways. Brill and Lutcavage (2001) suggested that cardiac function is compromised in billfish when they dive to cooler waters that exceed an 8°C deviation from SST. This implies that these fishes are constrained to a relative temperature-at-depth distribution. Additionally, in areas with a shallow thermocline above hypoxic water, dissolved oxygen concentrations can further limit billfish distributions (Prince and Goodyear 2006). Thus, an

understanding of marlin habitat is a key component to sustainable management. When evaluating vulnerability to fishing gear, it is not enough to simply consider the depth at which fishing effort is imposed, but the physical properties of the water column must also be incorporated.

Besides fishing, there are numerous human actions that may also affect marlin abundance. A review of anthropogenic impacts on billfish by de Sylva et al. (2000) highlighted a range of potential sources, including direct (e.g., fishing) and indirect (e.g., point and nonpoint sources of pollution) impacts that may degrade marlin habitats. Since marlins are distributed throughout relatively stable environmental conditions, they may be more susceptible to subtle ecological perturbations than coastal eurytopic organisms that experience variable conditions (de Sylva et al. 2000).

Given that Atlantic marlins are exploited across vast spatial scales, delineation of their habitats and the potential impacts of habitat degradation are crucial for conservation of these species. This is especially important since historical population trajectories indicate declines in abundance, raising concerns about the future for Atlantic marlins. There may be reason for cautious optimism, however, because relative biomass estimates from the 2000s suggest that the declines may have been arrested or, in the case of white marlin, the population may be in the early stages of a recovery (Figure 3). It is possible that these responses are the direct result of management measures, but there is little certainty in the trends in biomass, and several additional years of data are required to verify population responses (ICCAT 2006).

## FISHERIES

Fisheries targeting HMS have operated for many years, but until the 20th century, fishing was largely constrained to coastal waters (Majkowski 2007). In the early 1900s, a growing demand for canned tuna prompted the development of industrialized fisheries, including the Japanese longline fleet. By 1932, Japan had developed factory longline ships capable of canning tuna onboard (Morgan and Staples 2006). Following the elimination of post-World War II restrictions, this fleet expanded rapidly, eventually reaching the Atlantic Ocean in the late 1950s. Initially targeting yellowfin tuna *Thunnus albacares* and albacore *T. alalunga* in surface waters, the Japanese longline fishery was almost entirely responsible for the observed peak in Atlantic marlin landings in the late 1950s to early 1960s (Figure 2). Toward the end of the 1960s, developments in cold storage technology enabled Japanese fishermen to transition from the canned tuna market to a more lucrative sashimi market. This shift prompted a change in target species from yellowfin tuna and albacore to bigeye tuna *T. obesus* and bluefin tuna. By the early 1970s, the higher-valued target species dominated the catches in the Atlantic (Sakagawa et al. 1987). Since these species utilize deeper habitats, longline practices were altered to fish deeper in the water column (Majkowski 2007). Following this change, total landings of Atlantic marlins declined quickly, then fluctuated for many years before exhibiting further declines (white marlin, in particular) throughout the past decade (Figure 2).

Despite decreases in landings and potentially stabilizing biomass trajectories, the latest stock assessments concluded that Atlantic blue and white marlin stocks remain overfished and overfishing persists (ICCAT 2006). Given that ICCAT manages with respect to MSY, “overfishing” occurs when the fishing mortality rate ( $F$ ) exceeds the rate associated with

maximum sustainable yield ( $F_{MSY}$ ). Marlin stocks have been experiencing overfishing throughout much of the historical time series, but in recent years,  $F$  has drastically increased with respect to  $F_{MSY}$  (Figure 4). As relative biomasses have continued to decline (Figure 3), the reductions in landings necessary to rebuild the populations to MSY levels are greater than those observed. The recent changes in biomass trajectories may, in fact, be in response to management measures, but with lags in implementation and collection and reporting of data, the full effects of the measures may not be observed for several years. This delay could be detrimental to the species if the regulations prove inadequate for stimulating stock recoveries.

For many bycatch species, fishing mortality has been reduced through technological developments that attempt to improve survival of nontarget organisms while maintaining catch rates of target species. There have been relatively few developments that accomplished this for marlins; however, the use of circle hooks (as opposed to traditional J-style hooks) may show promise. In a review of studies that tested the effect of hook choice on billfishes, Serafy et al. (2009) determined that circle hooks are beneficial to billfish conservation efforts, and they recommended their use in commercial pelagic longline and recreational fisheries. However, when examining hook-induced mortality rates for blue and white marlins specifically, there are conflicting results among fisheries. For instance, in recreational fisheries for white marlin, circle hooks have been shown to significantly improve postrelease survival as compared to J hooks (Horodysky and Graves 2005). Yet, for pelagic longlines, white marlin mortality was slightly higher on circle hooks, though not significantly (Kerstetter and Graves 2006b). However, for most species analyzed, mortality rates were generally higher on J hooks than on circle hooks, and catch rates of the target species were not significantly impacted. It should be noted that mortality estimates in studies that used PSATs reflected postrelease mortality after a specified number of days, while in other studies mortality was the percentage of fish that were alive when brought alongside the boat (Serafy et al. 2009). There were not enough blue marlins captured ( $n = 1$ ) for

Kerstetter and Graves (2006b) to test the effects of hook type on survival, and there are currently ongoing studies comparing hook types in recreational fisheries for blue marlin.

In general, when compared to J hooks, circle hooks tend to reduce incidences of deep-hooking and bleeding in billfishes (Serafy et al. 2009). Thus, in the most recent stock assessment report, it was recommended that ICCAT consider encouraging the use of circle hooks to increase the chances of rebuilding Atlantic marlin stocks (ICCAT 2006). In the United States, the use of circle hooks has been mandatory in the pelagic longline fishery following the 2004 ESA section 7 consultation. This implementation was intended to minimize impacts on sea turtles, but marlin populations may also benefit. Also, circle hooks are currently required in all U.S. recreational Atlantic billfish tournaments when natural baits are used (NMFS 2006).

Recent stock assessments suggested that current fishery removals of Atlantic marlins are at levels too high to permit rebuilding to MSY levels. As relatively low value bycatch species of commercial fisheries, further depletion of marlin populations is not likely to substantially impact future commercial interests; however, recreational and artisanal fisheries will suffer in the absence of harvest policies that promote rebuilding. These trade-offs should be considered when management formulates recommendations, since international cooperation is required to attain sustainability. However, to rebuild populations to levels that support MSY, the main focus of management must be on the outcomes of stock assessments, which are scientific analyses of the status of the populations. Unfortunately, insufficient data result in numerous uncertainties in Atlantic marlin assessments (Restrepo et al. 2003; Die 2006), leading to disagreements over interpretations of assessment results, which serve as a basis for ICCAT member nations to object to further management restrictions. In fact, Webster (2006) identified uncertainty in the stock assessment process and the resulting lack of consensus regarding stock status as major factors preventing acceptance of more conservative international management measures for Atlantic marlins. Thus, identifying and accounting for assessment uncertainties is an important step in improving the management of blue and white marlins in the Atlantic.

## ASSESSMENT UNCERTAINTIES

Resource managers are faced with numerous sources of uncertainty, ranging from those analytical to those related to institutions and management (Hilborn 1987; Francis and Shotton 1997). While the consideration of management institutional uncertainties (i.e., uncertainties surrounding determination and implementation of management objectives and policies) is crucial for achieving sustainability, the focus here is on analytical uncertainties related to stock assessments and population dynamics (e.g., observation, model, and estimation uncertainty). Failure to address these sources of uncertainty can translate to errors in stock assessments, skepticism regarding stock status, and poor management advice; thus, the consideration of analytical uncertainties is an essential component of reliable sustainable resource management.

The importance of addressing analytical uncertainties in fisheries management is emphasized by the dynamics of the Atlantic herring (also known as the North Sea herring) *Clupea harengus* fishery. This stock has experienced two periods of severe overexploitation since the 1960s (Simmonds 2007). While warnings from scientists preceded the first decline, data at that time were insufficient to accurately determine stock status (i.e., observation uncertainty), and management action was resisted on this basis to preserve commercial profits. The stock eventually collapsed, moratoria were imposed, and a slow recovery followed. During the next period of overexploitation, the scientific understanding of the stock was more reliable, allowing management to take actions to successfully prevent a second total collapse. However, there were errors in the assessments during this decline, leading to an underestimation of exploitation rates. Had this not been the case, a second severe stock depletion may have been avoided altogether.



This example accentuates the importance of accounting for scientific uncertainty in fisheries management, and the lessons learned may translate to the management of many stocks, including Atlantic marlins. Similar to the tenor surrounding the initial decline in North Sea herring, Atlantic blue and white marlins are thought to be experiencing overfishing, but management measures are resisted, in part because of substantial uncertainties in the stock assessments. Delays in the enactment of management measures have been shown to increase the severity in the measures needed for stock rebuilding, the time required for rebuilding, and even the likelihood of stock collapse (Shertzer and Prager 2007). Therefore, unless the uncertainties are fully addressed and scientific advice is heeded, the management failures of the herring fishery may be repeated for Atlantic marlins.

The most recent stock assessments for Atlantic marlins were conducted by the Standing Committee for Research and Statistics (SCRS) of ICCAT in 2006. The assessments were performed using a Bayesian surplus production (BSP) model (McAllister et al. 2001; Babcock 2007) on catch data from 1990 to 2005, although catch data for 2005 were incomplete. The 2006 assessments seem to have improved scientific understandings of population dynamics in recent years; however, numerous sources of uncertainty remain.

#### *Catch-per-Unit-of-Effort Standardization*

Perhaps the most significant sources of debate and uncertainty in marlin assessments are CPUE standardization methods. The assessment models are “tuned” to CPUE time series, which represent indices of relative abundance under the assumption that catch (adjusted by effort) is proportional to abundance. However, numerous factors can impact catch that are not a result of changes in population size, including altering the temporal or spatial distribution of fishing effort, modifying fishing gear, and changing target species. If these factors are not accounted for, then the proportionality assumption is violated and CPUE no longer reflects relative abundance (Maunder and Punt 2004). This could introduce substantial error into the assessments.

There are two general approaches to standardizing marlin CPUE currently under consideration. The method used in the recent assessment is a traditional statistical approach using a generalized linear model (GLM; Nelder and Wedderburn 1972; McCullagh and Nelder 1989). As an extension of ordinary least squares linear regression, GLMs are capable of accommodating nonnormal error distributions by relating the expected value of the response variable to a set of predictor variables through a link function, where the link function is based on the assumed error distribution. Several CPUE time series were incorporated in the recent marlin assessments, each of which was standardized with some form of GLM (ICCAT 2006). For example, Diaz and Ortiz (2007) standardized catch rates from the U.S. pelagic longline fishery by accounting for factors such as year, area of fishing, gear characteristics, and fishing characteristics while also incorporating random interaction effects. The specification of random effects indicates that Diaz and Ortiz (2007) used a variant of GLM, referred to as a generalized linear mixed model (GLMM; Venables and Ripley 2002). While incorporating fishing characteristics can account for some of the variability caused by a change in target species, the GLMMs did not directly address the overlap between fishing effort and marlin distributions.

Another approach under consideration is habitat based standardization (HBS). This is a deterministic method that estimates effective fishing effort by incorporating information on the vertical distribution of the species in relation to the distribution of fishing effort (Hinton and Nakano 1996). Information on vertical distributions are typically derived from analyses of archival tagging data (e.g., PSATs), and the distribution of fishing effort is estimated based on characteristics of the gear. The HBS approach has been applied and incorporated into assessments of large pelagics in the Pacific Ocean (Bigelow et al. 2002; Maunder et al. 2002; Hinton and Maunder 2004; Maunder et al. 2006; among others); however, in the Atlantic, HBS has been applied but not used in stock assessments because of criticisms over the ambiguity surrounding the relationship of these species to the amount of fishing effort imposed on them (Yokawa et al. 2001; Goodyear et al. 2003; Yokawa and Takuchi 2003).

The merits of both approaches to CPUE standardization warrant thorough evaluation. Since the aforementioned shift in target species resulted in a change in the depth stratum exploited by the pelagic longline fishery, it is likely that marlin catch rates were impacted by factors other than changes in abundance. The HBS and GLM approaches can account for this variability as long as catchability ( $q$ ) is proportional to habitat type. However, it is difficult to effectively accommodate changes in exploited habitat if detailed information on habitat structure, marlin vulnerability as related to habitat, and the distribution of effort across habitats are unavailable. In the case of the 2006 marlin stock assessments, CPUE was standardized without directly considering changes in the habitats targeted by the fishery, resulting in steep declines early in the time series. These prominent features may be artifacts of a change in target species, yet they likely influence assessment results. The HBS approach can also be biased, however, because numerous factors can violate the assumption that  $q$  is proportional to habitat type. Some of these factors include inconsistent feeding behavior across vertical habitats, inconsistent fish behavior across time and space, inconsistent gear behavior with depth, and many others (Goodyear et al. 2003; Horodysky et al. 2004). Another drawback of HBS is that it is a deterministic approach and therefore does not allow a characterization of uncertainty. Since GLMs estimate parameters statistically, the error surrounding these estimates can be quantified.

In an effort to incorporate habitat information into CPUE standardization under a statistical framework, Maunder et al. (2006) described statHBS. This method estimates the habitat parameters of the original HBS method rather than deriving them from external data. This overcomes one of the main criticisms of HBS because depth and habitat utilization data do not determine vulnerability to fishing gear. Also, statHBS accommodates additional explanatory variables, as is possible with GLMs. The statistical nature of this model allows quantification of uncertainty and the application of model comparison and selection techniques. In fact, Maunder et al. (2006) compared various methods of CPUE standardization for bigeye tuna in the Pacific Ocean, and, through model selection, determined that the statHBS model fit best to the data. Also,

Bigelow and Maunder (2007) used statHBS and model selection to determine which explanatory variables are most important in understanding catch rates of bigeye tuna and blue shark *Prionace glauca* in the Pacific. They concluded that habitat parameters (those related to temperature and dissolved oxygen) are more reliable for predicting catch rates than depth. Nevertheless, statHBS and other approaches are not immune to shortcomings imposed by inadequate observations, which can violate assumptions and produce inaccurate trends in relative abundance.

Clearly, the methods of CPUE standardization mentioned here have unique advantages and drawbacks. Since a lack of consensus over the approach used in the last stock assessment of Atlantic marlins existed among the SCRS, it is important to fully evaluate and compare the available methods. Furthermore, Ortiz (2006) emphasized the need for additional comparisons of CPUE standardization techniques for blue and white marlins, specifically. Comparisons of GLM and HBS methods have been performed on simulated (Goodyear 2003a) and actual catch data (Maunder et al. 2006), but the conclusions of these studies were contradictory; HBS methods were favored by Maunder et al. (2006) and the GLM approach was determined most reliable by Goodyear (2003a). Since CPUE time series are fundamental to marlin stock assessments, it is imperative that the approaches to standardization are fully evaluated. Choosing between GLM and HBS standardizations can substantially influence the outcomes of assessments and, therefore, may have significant management implications. For example, the application of HBS in an assessment of Pacific blue marlin resulted in a stable, if not increasing, index of relative abundance and a completely different conclusion regarding stock status as compared to an assessment tuned to a GLM standardization, which produced a downward trend (Uozumi 2003).

#### *Habitat Utilization*

Whether entered directly (HBS) or estimated (statHBS), habitat parameters can substantially influence indices of relative abundance. Thus, prior to assessing the utility of these methods of CPUE standardization, it is important to thoroughly evaluate scientific understandings of Atlantic

marlin behavior and habitat utilization. Current knowledge regarding marlin habitats has, in large part, come from studies that used PSATs. Typically, these studies described habitat by reporting temperature and depth distributions for the tagged individuals. While this provides a valuable summary of habitat utilization, a thorough understanding of marlin distributions requires an explanation of the sources of variability within the populations. For instance, marlin habitats may vary ontogenetically, across regions and seasons, or in response to various environmental factors. In many ecological studies, the effects of these variables can be explained through statistical analyses, such as linear models. However, PSAT data present unique statistical challenges, causing a majority of studies to truncate the trends and report results as histograms representing mean behavior. This prevents the detection of significant sources of variation in the populations, which may substantially improve the accuracy of CPUE standardization methods that are habitat-based.

Determining an effective approach to the statistical analysis of PSAT data requires an understanding of the nature of the data. Since PSATs record numerous sequential measurements while attached to a fish, the measurements for one fish are likely more similar than those between fish, and measurements adjacent in time are likely more similar than those farther apart. As noted by Wilson et al. (2005), if the statistical method used for the analysis of PSAT data does not account for this autocorrelation, the power of a statistical test may be overinflated, potentially leading to erroneous conclusions that cannot be supported by the data. Typically, autocorrelated data resulting from multiple measurements within a single experimental unit are considered longitudinal data, and statistical methods capable of addressing their unique nature have been developed (Diggle et al. 2002). High frequencies of measurements obtained from PSATs, however, are considered intensive longitudinal data (ILD). The statistical methods developed for longitudinal data are designed for relatively few repeated measurements (roughly 10 or fewer) and may not be appropriate for ILD with multiple waves of measurements (Walls and Schafer 2006). Recently, statisticians in the social and health sciences developed statistical methods

designed to analyze ILD (Walls and Schafer 2006) that may have great potential for the analysis of archival tagging data.

There are several models reviewed by Walls and Schafer (2006) that may translate to PSAT data analysis. Those that show the greatest promise are essentially variations of the original multilevel linear model (MLM) developed for analysis of longitudinal data (Laird and Ware 1982). Li et al. (2006) described a variant of the MLM that may apply to PSAT data. Through the incorporation of local polynomial regression, their functional data analysis (FDA) techniques allow the fixed and random coefficients of the MLM to vary nonparametrically over time. This may provide more flexibility in the statistical analysis by accommodating the variability among dives often observed in PSAT data.

Along with random variation between dives, large pelagic fishes often exhibit periodic trends in their dive behavior (Horodysky et al. 2007). Fok and Ramsay (2006) built upon FDA techniques by incorporating Fourier basis functions and B-splines to analyze ILD with periodic and nonperiodic trends. Their approach may be effective in addressing the cyclic trends observed in many PSAT data streams (e.g., dives in relation to diel cycles).

Another analytical approach that shows promise for PSAT data analysis is state-space modeling. This method has been in use for some time (Jazwinski 1970; Anderson and Moore 1979) and has recently been described for application to longitudinal data in a regression model framework (Dethlefsen and Lundbye-Christensen 2006; Ho et al. 2006). When presented in this manner, state-space models represent an extension of generalized linear models where the parameters are allowed to vary over time (Dethlefsen and Lundbye-Christensen 2006). This flexibility may help to describe the complicated habitat utilization profiles typically observed in PSAT data.

The models described represent potential approaches to robust statistical analyses of PSAT data. These analyses may identify significant, presently unconsidered sources of variation in the habitats utilized by the Atlantic marlins, and may address several uncertainties surrounding

the relationships between marlin distributions and the distribution of commercial fishing effort. Since limited knowledge about fish (and gear) behavior has reduced confidence in CPUE standardization techniques that consider habitat (Goodyear et al. 2003; Horodysky et al. 2004), perhaps an improved understanding of habitat utilization would increase the value placed on these indices of abundance, potentially justifying their incorporation into stock assessments. It should be noted, however, that these methods still exclusively consider habitat and do not address the interaction between fish behavior and habitats. Thus, while understandings of marlin distributions may be improved, catchability is also a function of behavior, and this should be recognized when incorporating habitat into CPUE standardizations. Nonetheless, advancing knowledge regarding habitat utilization and potentially improving estimates of relative abundance may substantially improve the assessments.

#### *Assessment Model*

While the most recently applied stock assessment model (BSP) was useful for evaluating stocks in an entirely fishery-dependent context, there were potential sources of error that the model did not directly address. First, due to limited data, the BSP model relied solely on catch-and-effort data. This speaks to the importance of accuracy in estimating relative indices of abundance because changes in CPUE may considerably alter assessment results (Babcock 2007), especially when methods of standardization do not account for changes in target species (i.e., catchability). A sensitivity analysis using a range of indices of abundance may account for uncertainties associated with CPUE, but reliable indices facilitate accurate depictions of stock status. Furthermore, estimates of stock parameters in the recent assessments were constrained with prior distributions governed by the results of previous assessments. This biased the results and contributed to the uncertainty regarding stock status relative to MSY benchmarks (ICCAT 2006).

Also, the BSP model was relatively simple in that annual biomasses were aggregated across all ages in the population that were subject to exploitation. This assumed that, irrespective

of age, these individuals were equally vulnerable to incidental capture by the fisheries. Since this may be unlikely, evaluations of population dynamics could improve from better understandings of the age composition of marlin catches. Some marlin growth data are available, but validated aging methods do not exist for adult marlins (Drew et al. 2006), and this information was deemed insufficient for incorporating age structure into the most recent marlin assessments. Also, necessary additional biological information regarding ages at maturity and sex ratios of the catch was lacking (ICCAT 2006). It has been suggested, however, that despite the lack of confidence in the aging data, certain age-structured models may improve marlin assessments (Restrepo et al. 2003) since relatively simple production models capture net effects of fishing and not detailed historical trends of growth dynamics, selectivity-at-age, and other population impacts (Hilborn and Walters 1992; Walters and Martell 2004).

There are several existing age-structured assessment models that do not rely directly on detailed catch-at-age data, and therefore their application to Atlantic marlin stocks may be worth consideration. One mode of imposing age structure is through relating estimated growth models, such as length (or weight) at age, to length frequencies of the catch. These integrated assessment models, such as MULTIFAN-CL (Fournier et al. 1998), Stock Synthesis (Methot 2000; NOAA Fisheries Toolbox 2009), CASAL (C++ algorithmic stock assessment laboratory; Bull et al. 2005), and others have proven useful when applied to large pelagic fishes. Porch (2003) used a state-space age-structured production model to assess the Atlantic white marlin stock; however, his approach was purely heuristic and not meant to influence management decisions, largely due to limited information for estimating selectivity at age. Another assessment approach that has been attempted for marlins involves a delay-difference model in which age structure is imposed on immature individuals only, based on an assumed selectivity at age (Cox et al. 2002b). This model was applied to several stocks of large pelagic fishes in the central North Pacific Ocean. While the approach was relatively simple, the estimates were similar to those of more complex assessments. Typically, ideal model complexity for a stock assessment is ultimately related to the



data available (Walters and Martell 2004), yet, as exemplified by Cox et al. (2002b), additional complexity does not always result in a better understanding of stock status. In general, models that incorporate age/size structure are favored over less complex production models because they estimate trends in selectivity at age and can elucidate changes in growth patterns (Walters and Martell 2004). Thus, one or more of the proposed assessment models should at least be thoroughly evaluated and the results compared to those of the BSP model to see if increasing model complexity through the incorporation of age structure provides better information for managing Atlantic marlins.

#### *Catch Data*

In addition to addressing uncertainties pertaining to marlin habitats, CPUE standardization, and stock assessment models, there are numerous other sources of error that warrant attention. For instance, the historical catch database, which is the basis for marlin stock assessments, is incomplete (Restrepo et al. 2003). Since marlins are landed by commercial fisheries or directly by artisanal fisheries, they are difficult to monitor, causing many countries to inconsistently report landings or fail to report them altogether (WMBRT 2007). Gaps in the data are then filled in with estimated catches, which are based on the amount of target species landed. Also, landings typically do not include discards, a problem that may be exacerbated by regulations requiring live release. Individuals that were discarded dead were certainly subject to fishing mortality, and based on studies that estimated postrelease survival (Kerstetter et al. 2003; Kerstetter and Graves 2006b), a certain percentage of live releases also perish, depending on the species and gear used. Thus, any changes in release practices that are not documented further limit the ability to predict fishing-induced mortality rates. Atlantic marlins are subject to a range of illegal, unreported, and unregulated (IUU) fishing activities (for more on the complexities of IUU fishing, see Serdy 2011). While ICCAT has made recommendations to identify and combat IUU fishing (ICCAT 2004, Rec. 2003–16; ICCAT 2007b, Rec. 2006–12; ICCAT 2008, Rec. 2007–09), the practice

continues, thereby compromising the accuracy of the catch database. Each of these factors potentially results in underestimated landings. Since the degree of uncertainty surrounding the inadequacies in the catch data are difficult, if not impossible to quantify, accounting for underestimated landings in the assessment is a significant challenge. At the very least, sensitivity analyses using reasonable ranges of unreported landings, and live and dead discards are encouraged. Management decisions, therefore, could be based on a range of stock status predictions for Atlantic marlins rather than fixed estimates.

Another problem plaguing marlin assessments is billfish misidentification. There is misclassification between the marlins (WMBRT 2007), but awareness of the uncertainty in billfish classification has increased in recent years (ICCAT 2006). This may be due, in part, to the recent verification of the existence of roundscale spearfish *Tetrapturus georgii* in the Atlantic (Collette et al. 2006; Shivji et al. 2006). At first glance, this species can easily be confused with white marlin and other spearfish. Since roundscale spearfish has only recently been verified, it is impossible to estimate historical proportions of marlin landings comprised of roundscale spearfish. Uninformed estimates of these proportions could be generated and sensitivity analyses performed, but estimating proportions with confidence requires extensive research on landings, distribution, and habitat utilization of roundscale spearfish. While current estimates suggest that roundscale spearfish make up roughly 27% of the “white marlin” catch in the western Atlantic, simulated changes in the proportions over time were shown to substantially impact assessment results (Beerkircher et al. 2009). Furthermore, a portion of reported billfish landings are determined in port on fish that have already been processed for sale. Since billfishes are more difficult to distinguish when dressed, this represents a substantial source of uncertainty in the catch database. Unfortunately, without regular tissue sampling for genetic identification, the issues regarding classification in billfish landings will likely persist for some time.

### *Life-History Characteristics*

Finally, uncertainty regarding life-history characteristics can impact the accuracy of stock assessments and, as mentioned, has limited the choice of assessment models for Atlantic marlins. For example, sexually dimorphic growth (with females attaining larger sizes than males) is present in both species, especially blue marlin; therefore, it is likely that males and females differ in their susceptibility to fishing gear. Also, sexual dimorphism contributes to the difficulty of relating size and age in marlins, which further limits the ability to apply age-structured stock assessments. However, if unaccounted for, these growth dynamics could result in unforeseeable impacts to the populations. For instance, if the proportion of females (especially large females) removed from the population exceeds the proportional removal of males then overall reproductive output could be compromised (Luckhurst et al. 2006). This decreasing fecundity may be undetected in stock assessments that do not consider sex-specific effects, potentially resulting in overestimates of MSY, but if the impacts are well understood, management could enact measures designed to protect the most productive components of the population. At a minimum, an understanding of the sex ratios of the populations as well as of the catch would be required to estimate population impacts such as these. While sex ratios of samples of the populations and of the landings have been estimated in some areas (de Sylva and Davis 1963; Baglin 1977; Arocha and Bárrios 2009), a thorough sampling of the landings has not occurred; thus, historical trends in sex ratios would be difficult to determine. Despite these challenges, estimating the sex-specific impacts of fishing on the populations using the available data may be worth consideration. This could be attempted in an assessment context with sensitivity analyses, or through simulations similar to those performed by Goodyear (2003b). However, it should be noted that comprehensive size- or age-structured assessments of the populations may require information concerning age-specific sex ratios, maturity, fecundity, natural mortality rates, understandings of the stock–recruitment relationships, and any related density-dependent effects.

The aforementioned analytical uncertainties regarding Atlantic marlin population analyses (i.e., model and estimation uncertainties related to CPUE standardization and the stock assessment process and observational uncertainties surrounding habitat data, catch data, and life-history characteristics) limit the ability to manage these stocks sustainably. It may be that imposing relatively strict management measures can account for uncertainties indirectly and marlin populations can be conserved in this way, but informed management decisions based on assessments that directly address uncertainties are more likely to be broadly supported. While this is a difficult task, some of the suggestions provided may prove effective. Overall, it is critical to the sustainability of Atlantic marlins that attempts are made to address and account for uncertainties surrounding their assessments.

## GOVERNANCE

The Atlantic-wide stocks of blue marlin and white marlin are susceptible to multinational commercial, recreational, and artisanal fisheries. As mentioned previously, assessments and management of these stocks fall under the jurisdiction of ICCAT's member nations, a collection of contracting parties that represent national interests. Regulations by ICCAT are either in the form of nonbinding resolutions or binding recommendations, and passage of these measures typically involves consensus among member nations. In 1995, ICCAT passed their first resolution pertaining to billfish, which encouraged live release from commercial and recreational fisheries. Since this initial resolution, several recommendations and resolutions have followed (Peel et al. 2003; WMBRT 2007).

Currently, Atlantic marlins are in phase 1 of a two-part stock rebuilding program (ICCAT 2007b, Rec. 2006–09). This phase will apply through 2010, with regulations affecting commercial and recreational fisheries. For pelagic longline and purse-seine vessels, landings of blue and white marlins are restricted to 50% and 33%, respectively, of 1996 or 1999 landings (whichever year was greater). Also, all marlins caught alive are to be released, though successful live release from purse seines may be challenging. For U.S. recreational fisheries, total landings are not to exceed 250 individuals per year for blue marlin and white marlin combined, and other nations with recreational fisheries are encouraged to develop minimum size regulations. The remaining management measures associated with phase 1 mainly pertain to reducing uncertainties in stock assessments by encouraging continued research on Atlantic marlins and maintaining and improving fisheries data collection practices, especially for artisanal fisheries.

In addition to international regulations, member nations may choose to impose further management measures on their respective fisheries. For example, the United States prohibits all

commercial landings and trade of Atlantic marlins. This clearly emphasizes the value the United States places on its recreational fisheries; however, these fisheries are not immune to additional regulations. The annual allowable catch set by NMFS follows ICCAT's restriction at 250 blue and white marlins combined, and to attain this limit NMFS has established size limits for each species (2.51 and 1.68 m [99 and 66 in] lower jaw fork length for blue and white marlin, respectively). Furthermore, NMFS requires the use of circle hooks in natural baits for billfish tournaments and encourages the live release of all billfish caught recreationally, a practice favored by many billfish anglers.

Overall, the phase 1 regulations imposed by ICCAT will likely benefit Atlantic marlin populations to some degree. Increases in live-release practices are particularly promising, especially given that a substantial number of marlins are alive upon retrieval (haulback) of pelagic longline gear (Cramer 2000; Kerstetter and Graves 2006b). Also, when released from this gear, survival rates are likely to be high for both blue marlin (Kerstetter et al. 2003) and white marlin (Kerstetter and Graves 2006a). Furthermore, low postrelease mortality has been demonstrated in recreational fisheries for blue marlin (Graves et al. 2002) and white marlin, especially when circle hooks are used (Horodysky and Graves 2005; Graves and Horodysky 2008). Thus, when coupled with reduced landings, increased live-release practices should slow and possibly reverse downward population trajectories. If estimates of relative abundance are accurate, some evidence of population responses to these management strategies may already be observable (Figure 3), but stocks likely remain depleted and overfishing almost certainly continues.

The inability to eliminate or substantially reduce overfishing of Atlantic marlins has been considered a failure attributed to ICCAT (Peel et al. 2003). It should be noted, however, that due to overlapping distributions and differing biological characteristics, it is unlikely that ICCAT could ever achieve its goal of harvesting at MSY for all species under its purview. For instance, the fishing pressure associated with MSY for a target species may result in overfishing of

nontarget species. Conversely, ensuring sustainable harvests of nontarget species may lead to considerable underutilization of target species. The prior scenario reflects the relationship between the Atlantic marlins, whose estimated fishing mortality rates exceed  $F_{MSY}$ , and various target species (bigeye tuna, yellowfin tuna, and swordfish), whose rates are close to  $F_{MSY}$ . However, the latter scenario represents a form of precautionary management where effort is controlled to achieve MSY for the species most vulnerable to overfishing. Given the short-term declines in profits that would result from such an approach, it is unlikely that ICCAT could reach consensus on measures that ensure sustainability of bycatch species at the expense of commercial revenue.

While it is improbable that ICCAT will reduce fishing effort to the extent necessary for rapid rebuilding of marlin populations, further management actions may prove beneficial. Since ICCAT relies on self enforcement by member nations, full compliance with additional measures may be unlikely; nevertheless, these measures, including encouraging live release and the use of circle hooks, may substantially reduce fishing mortality rates. However, if marlin populations do not respond to additional management actions, external influences may be required to achieve reductions in fishing pressure. There are several options related to protected species management that may be applicable to marlins, including the Convention on International Trade in Endangered Species of Wild Fauna and Flora, the protocol on Specially Protected Areas and Wildlife of the Convention for the Protection and Development of the Marine Environment of the Wider Caribbean Region, and the U.S. Environmental Protection Agency (U.S. EPA; Peel et al. 2003). However, a petition to have white marlin listed as threatened or endangered under the U.S. ESA was not successful (see Importance section, this chapter). Beyond these management pathways, increased attention and interest by nongovernmental organizations, the public and the media could also be strong forces of influence over marlin bycatch. Thus far, these groups have expressed relatively little concern regarding the depleted biomasses and continued overfishing of marlins. If that changes, however, a successful campaign against products from fisheries that land

marlins incidentally could encourage the industry to minimize marlin bycatch or risk declining demand. The evolution to “dolphin-safe” tuna has already exemplified the utility of consumer activism as an effective strategy for reducing bycatch in these fisheries (Hall 1998; Hall et al. 2000). Perhaps consumer-driven sustainability for other bycatch species could be attempted by demanding a more comprehensive label for these fisheries, such as certification via the Marine Stewardship Council or other programs. This could provide an incentive for ICCAT’s member nations to abandon the status quo and enact holistic measures that promote ecosystem-wide sustainability.

In general, there has been relatively little action by ICCAT or external groups to ensure rebuilding of Atlantic marlins. Unfortunately, until management measures are designed to substantially improve the odds of rebuilding, the number of uncertainties surrounding marlin population assessments may actually facilitate inaction because it is difficult to confirm population responses with high certainty given the noise in the available stock indicators. Thus, marlin assessments may have produced overly optimistic or overly pessimistic portrayals of the stock conditions, rendering appropriate management actions difficult to discern unless uncertainties are addressed. However, even with improvements in data collection and statistical analysis, there will always be uncertainties surrounding assessment results. Such uncertainties should not be used to justify delayed management action.



## RECOMMENDATIONS

Following years of overfishing, Atlantic marlin populations appear to be severely depleted. Unfortunately, there are compounding limitations to successful rebuilding and management of these populations. First, the historical catch data are incomplete and potentially flawed. In combination with relatively poor understandings of marlin biology, ecology and behavior, these limitations compromise the accuracy of stock assessments. Also, uncertainties regarding quantitative approaches exist in the assessments, which further limit the willingness of ICCAT's member nations to make management decisions that constrain the fisheries, and result in a lack of consensus within ICCAT regarding the status of the stocks. Since these uncertainties represent a roadblock to effective management, it is important that they are addressed to ensure that management measures are based on the best possible characterizations of the stocks. Moreover, member nations are responsible for the development of management measures and enforcing compliance among their respective fisheries. However, full compliance is difficult to achieve, so management actions should be designed to accommodate implementation error.

Clearly there are many difficulties concerning management of Atlantic marlins. Nevertheless, with substantial international support, addressing and accounting for many of these issues may be possible. Uncertainties surrounding the catch data must be considered; major sources of error include unreported landings and discards from commercial, IUU, recreational, and artisanal fisheries, as well as misidentification of billfishes. Expanding the coverage and responsibilities of fisheries observers should be employed to address these limitations and improve the catch data. In addition to comprehensive monitoring of catch, landings, and number and condition of released bycatch species, observers could obtain valuable scientific information,

including sex ratios, removal of hard parts for aging purposes, tissue samples for genetic validation of species, and other potentially useful information (e.g., diet, maturity, etc.).

Beyond expanding observer coverage, there are further actions that should improve catch data. For instance, nations that fail to meet reporting obligations should be penalized, and in the cases where these nations lack a sufficient infrastructure to monitor their fisheries, appropriate assistance should be given to ensure that proper reporting can be achieved. For marlins in particular, documenting the status and biomass of discards is especially important because of recently imposed management measures requiring live release in longline fisheries. Previously, fish captured live may have been accounted for in total landings, but now that they are released, their encounter and fate must be documented or else CPUE time series and future assessments could be substantially biased. Also, since misidentification occurs not only at sea, but also in port, the establishment of a comprehensive port sampling program, where tissue samples are collected for genetic identification (verification) of species, would likely improve classification of billfish landings. Finally, concerted efforts to identify and quantify catches from IUU and artisanal fishing must be ongoing.

Additional uncertainties surrounding Atlantic marlins are related to the assessment process itself. Combined with improving the data, advancing quantitative approaches to population analyses will encourage international consensus over stock status determinations, thereby supporting the passage of sustainable management measures. With an initial focus on improving analyses of habitat utilization, evaluating methods for standardizing CPUE that appropriately consider habitat, and expanding the complexity of the current assessment approach, understandings of marlin populations should drastically improve. Without these advancements, a lack of consensus among ICCAT's member nations over the stock status of Atlantic marlins is likely to persist, and necessary management measures may be resisted on the basis of uncertainty. It should be noted, however, that expanding the complexity of assessment models may

substantially expand the data requirements; thus the suggested data collection improvements are a necessary first step.

Sustainability of Atlantic marlin populations is ultimately in the hands of the member nations of ICCAT. Many of the suggestions provided herein require management action, especially those related to improving the quality of the data. If enacted, these recommendations may improve the fisheries science and facilitate better understandings of Atlantic marlin populations, but their translation into sustainable management measures relies on the resolve of ICCAT's member nations. With many nations representing strong commercial interests, it seems unlikely that the contracting parties will manage for sustainability of bycatch species, such as Atlantic marlins, when commercial landings may suffer. Given this potential conflict of interest, it may behoove ICCAT to consider approaches such as time/area closures or alternative fishing strategies that minimize bycatch; otherwise, external pressure may be necessary to encourage precautionary management of all species under the purview of ICCAT.

Many of the world's fisheries that target HMS face bycatch problems similar to those described here. Therefore, a unified approach to monitoring, assessment, and management may increase the attention designated to bycatch and promote sustainability of these species. Globally, there are five regional fishery management organizations (RFMOs) that are responsible for international management of tuna and tuna-like resources, including billfishes. In addition to ICCAT, there is the Commission for the Conservation of Southern Bluefin Tuna, the Inter-American Tropical Tuna Commission (see Oh 2011), the Indian Ocean Tuna Commission, and the Western and Central Pacific Fisheries Commission. Currently, these RFMOs manage their respective fisheries independently; however, since each organization may be facing similar issues related to bycatch, coordinated efforts among the RFMOs may improve management efficiency and effectiveness. While previous collaborations have occurred (Majkowski 2007), we recommend that the five RFMOs collectively establish harmonized measures across the world's oceans that (1) improve reporting of landings, discards, and fishery practices and dynamics as

related to nontarget species; (2) expand fisheries observer coverage and responsibilities to fully monitor international fisheries and to collect valuable scientific information; (3) develop a comprehensive international port sampling program for identification and sample collection; (4) monitor IUU and artisanal fisheries to the extent possible; (5) encourage and support ongoing advancements in quantitative approaches to evaluating stocks that characterize and reduce uncertainties and fully utilize available data; and (6) with a focus on the results of stock assessments, follow a precautionary approach to fisheries management that considers the whole ecosystem and ensures the sustainability of target and nontarget species. Cohesive adoption of these recommendations by the tuna RFMOs would promote consistency and cooperation across international fisheries. This would encourage the sustainability of fisheries worldwide and would especially benefit bycatch species susceptible to overexploitation, such as the Atlantic marlins.

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**Yokawa, K., Y. Takeuchi, M. Okazaki, and Y. Uozumi. 2001. Standardizations of CPUE of blue marlin and white marlin caught by Japanese longliners in the Atlantic Ocean. Collective Volume of Scientific Papers ICCAT 53:345–355.**

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## FIGURES

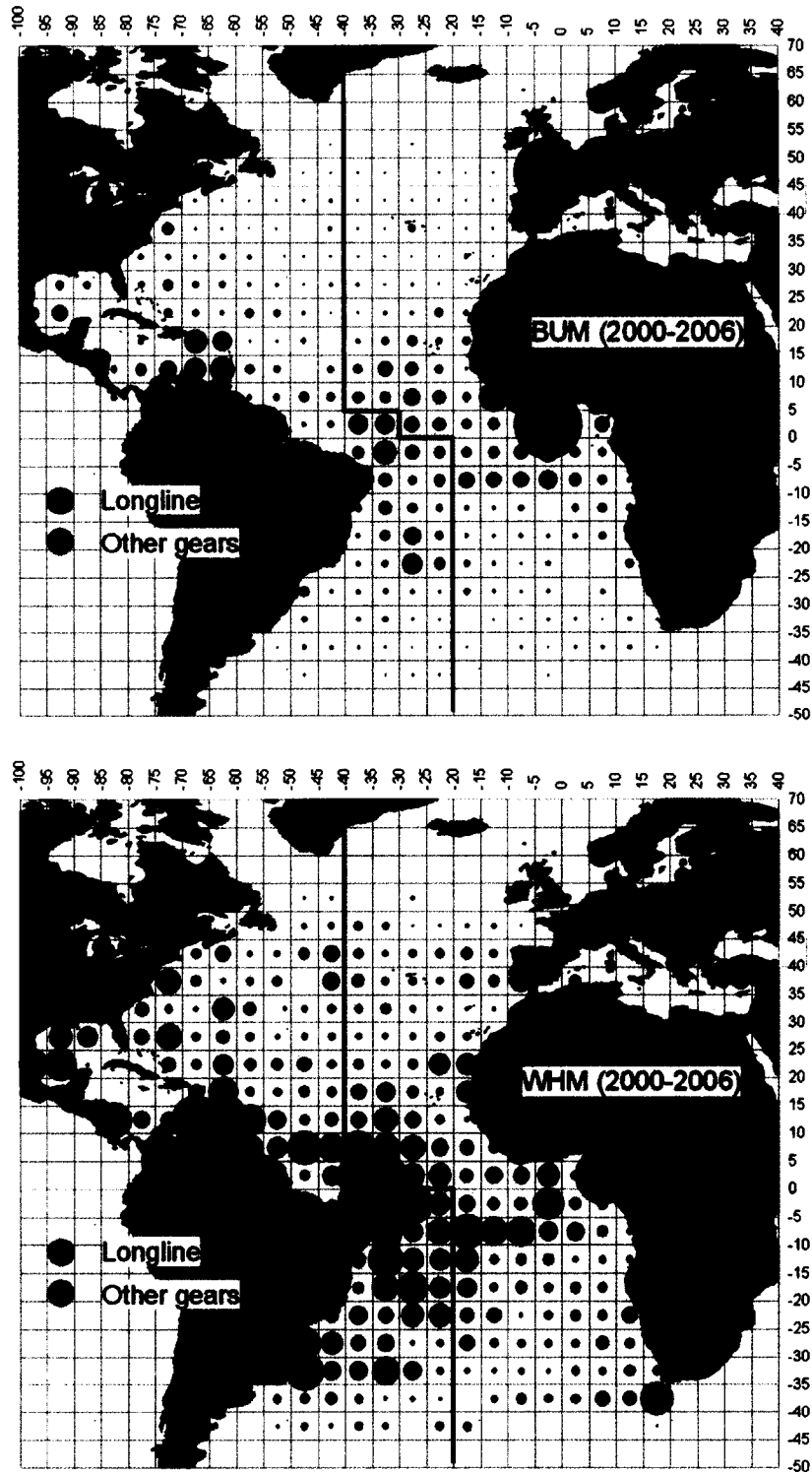


Figure 1. Distributions of blue marlin (BUM) and white marlin (WHM) in the Atlantic Ocean as determined from fisheries catch data from 2000 to 2006. The largest circles for BUM and WHM correspond to catches of 789 and 52 metric tons, respectively. Source: ICCAT (2009).

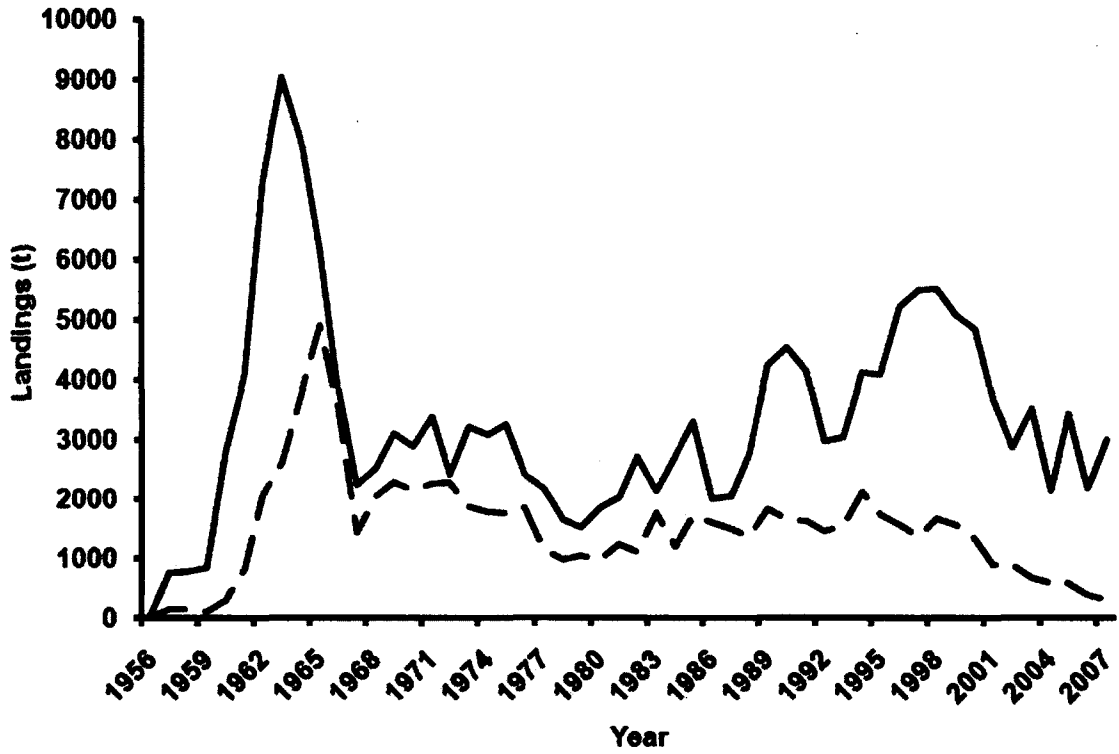


Figure 2. Total annual landings of blue marlin (solid line) and white marlin (dashed line) in the Atlantic Ocean. Data source: ICCAT online catch database ([www.iccat.int/en/accesingdb.htm](http://www.iccat.int/en/accesingdb.htm)). t = metric tons.

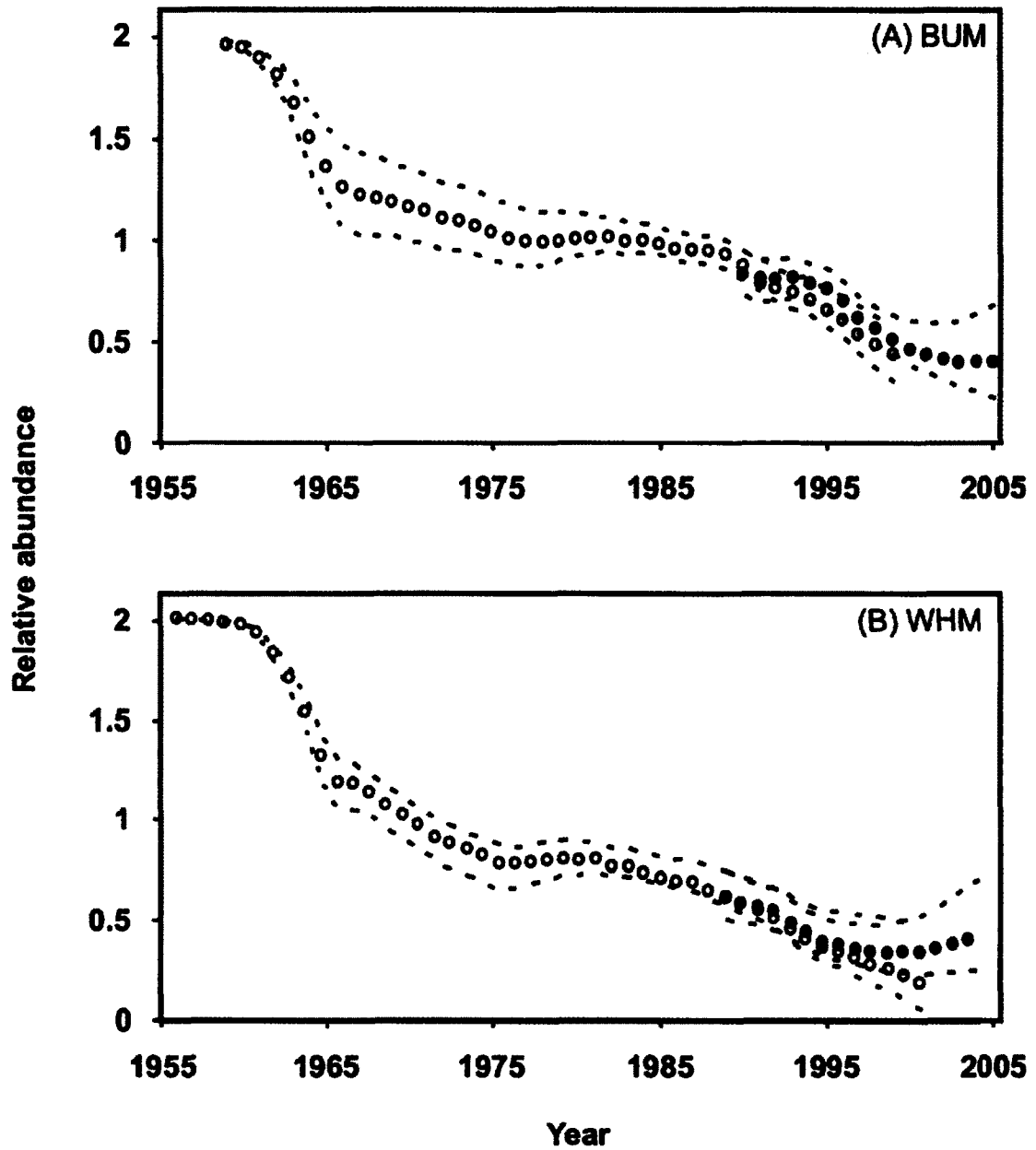


Figure 3. Estimated relative abundance of blue marlin (A: BUM) and white marlin (B: WHM), derived from production model fits to catch-per-unit-effort data from the most recent assessments (solid circles) and previous stock assessments in 2000 for BUM and 2002 for WHM (open circles). The models used in the assessments were similar, but the recent assessments were fit to all available catch-per-unit-effort time series separately, where the previous assessments considered a single composite index of abundance. Dashed lines represent 80% confidence intervals. Source: ICCAT (2007c).



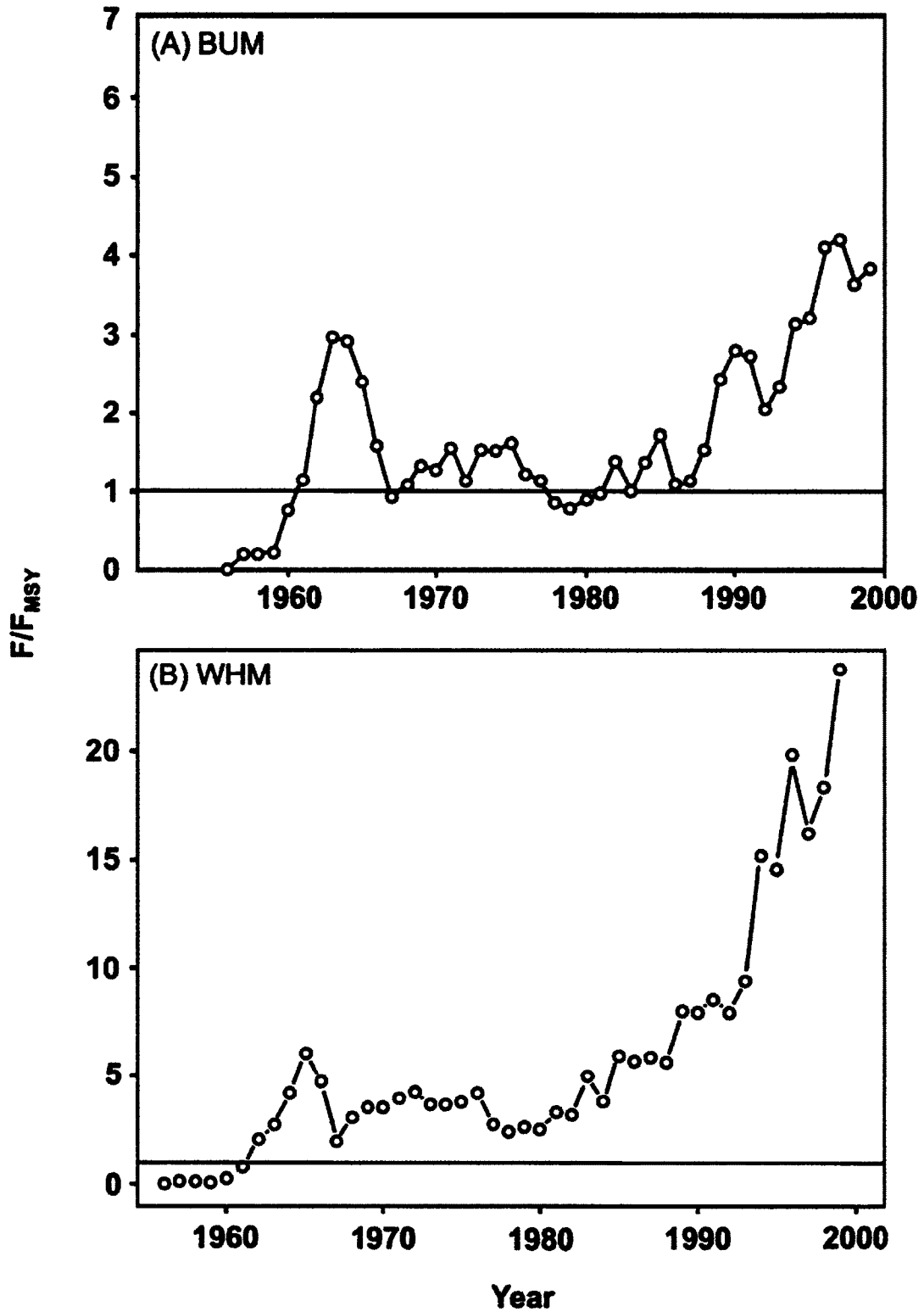


Figure 4. Historical trends in relative fishing mortality rate ( $F$ ) with respect to the rate at maximum sustainable yield ( $F_{MSY}$ ) for blue marlin (A: BUM) and white marlin (B: WHM) in the Atlantic Ocean. Estimates were generated in the 2000 stock assessments using a logistic production model. Points above the solid horizontal line represent years in which  $F > F_{MSY}$  trajectory. Source: ICCAT (2001b).

## **CHAPTER 2**

### **Performance of methods used to estimate indices of abundance for highly migratory species**

## ABSTRACT

Estimating indices of abundance from fishery-dependent data requires that catch-per-unit-effort (CPUE) be standardized to account for factors that may have affected CPUE but are not related to changes in abundance. Such standardization is particularly important for highly migratory species (e.g., tunas, pelagic sharks, and billfishes), because of time-varying mismatches between distributions of abundance and the distribution of fishing effort. Two commonly applied methods for standardizing CPUE are generalized linear models (GLMs), which can account for changes in fishing practices in a straightforward linear fashion, and habitat-based standardizations (e.g., statHBS), which use nonlinear analysis to relate the distribution of fishing effort to the species distribution. We evaluated the accuracy of these methods over three patterns in vertical catchability as related to ocean temperature profiles, and 50 possible biomass trajectories using a simulation framework that followed the general effort dynamics of the Japanese longline fishery in the Atlantic Ocean from 1956 to 2009. Additionally, we propose a method for directly incorporating vertical habitat information into the linear models. Overall, we found the most accurate approach to be a delta-lognormal GLM with our unique habitat factor. The statHBS approach was the most accurate when catchability was simulated to peak in surface waters. However, statHBS was much more sensitive to errors in estimates of longline hook depths (i.e., habitats exploited). Based on these results, we recommend that relative abundance be estimated for highly migratory species following a delta-GLM approach that considers vertical habitats fished.

## 1. INTRODUCTION

Management decisions in fisheries are often guided, at least in part, by the results of stock assessments. Therefore, in the interest of scientific integrity and sound management, it is important that scientists provide managers with accurate characterizations of stock dynamics and stock status. Assessment models often use fishery catch data and other inputs to estimate biomass trajectories and stock parameters by fitting predicted biomass to externally derived indices of relative abundance (Maunder and Starr, 2003). Such indices of abundance serve as ‘observed’ abundance trends and thus have an influence over the assessment results.

When derived from fishery-independent surveys that monitor the stock(s) being evaluated, indices of abundance may reliably depict abundance trends. However, many exploited species are either not monitored or not monitored comprehensively. For these organisms, information on distribution and abundance is primarily obtained through catch and effort data from fisheries that either target or incidentally catch these species. To estimate relative abundance from these data, it is common practice to adjust the catch by the corresponding amount of effort and assume a proportional relationship between catch-per-unit-effort (CPUE) and abundance. However, because fisheries are not designed to collect random unbiased samples of the harvested populations, fishery-dependent CPUE must be standardized to account for factors (e.g., changes in fishing practices) that may cause the proportionality constant (catchability) to be time-varying (Wilberg et al., 2010; Ye and Dennis, 2009), thereby violating the assumed relationship between CPUE and abundance. Numerous approaches are available for standardizing CPUE to estimate relative abundance (Maunder and Punt, 2004); thus, to promote confidence in stock assessment results it is important to evaluate proposed methods under various assumptions and real-world conditions.

Highly migratory species (HMS) represent valuable global resources, but the high cost associated with a large scale pelagic survey has prevented the development of comprehensive monitoring programs for HMS (Bishop, 2006). Therefore, estimated trends in abundance for HMS are typically derived from fishery-dependent data. Given the extensive spatial and temporal coverage of many HMS fisheries, such as the Japanese longline fishery (JLL), these time series, if appropriately standardized, may be capable of capturing true patterns in abundance. Longline data represent important sources for estimating indices of abundance for many HMS, but these data require careful consideration.

Changes in fishing practices within the JLL (Ward and Hindmarsh, 2007; Yokawa and Uozumi, 2001) have resulted in changes in vertical habitats exploited over time. Perhaps the most notable modification was a shift to deeper target habitats in response to a change in target species from yellowfin tuna, *Thunnus albacares*, and albacore, *Thunnus alalunga*, to bigeye tuna, *Thunnus obesus*, and bluefin tuna, *Thunnus thynnus*. While many HMS are known to exhibit vertical migrations, they have been shown to spend a large percent of their time in a relatively small depth or temperature (relative to the surface) range (Goodyear et al., 2008; Graves et al., 2002; Hoolihan et al., 2011; Horodysky et al., 2007; Kerstetter et al., 2003; Prince et al., 2010; among others). Considering the shift in JLL target habitat, the vertical distributions of HMS suggest that the proportion of their stocks removed by a given unit of effort (catchability) has not been homogeneous over time with respect to the vertical habitats exploited. This emphasizes the importance of including vertical fishing habitat in the CPUE standardization process when estimating relative abundance.

Historically, there have been two general classes of approaches to including vertical habitat information in CPUE standardization for HMS: generalized linear models (GLMs) and habitat-based standardization (HBS) (Goodyear, 2003; Hinton and Nakano, 1996; Maunder et al., 2006). In a GLM, environmental data are typically considered indirectly by including variables related to longline gear configurations as fixed effects to serve as proxies for habitats fished.

Habitats are directly included with HBS, and this approach has been used to estimate relative abundance for several HMS in the Pacific Ocean (Bigelow et al., 2002; Bigelow and Maunder, 2007; Hinton and Nakano, 1996; Langley et al., 2005; Maunder et al., 2006). The HBS approach was originally described as a deterministic model (Hinton and Nakano, 1996); however, the preferred method is cast in a statistical framework (statHBS; Maunder et al., 2006). In the statistical approach, the relative catchability from a given pre-specified vertical habitat is estimated by relating the total catch for a longline set to the amount of effort estimated to occur in each habitat for each set (see Section 2.2 for more details). The GLM approach is commonly used for Atlantic HMS; for example, blue marlin, *Makaira nigricans*, CPUE from the United States longline fishery was standardized using a delta-lognormal GLM with fixed effects for area, fishing characteristics, and gear characteristics (Ortiz and Hoolihan, 2010). The GLM and HBS approaches may provide different trends in abundance, which have been shown to affect assessment results (Uozumi, 2003). Accordingly, comparing and evaluating the accuracy of GLMs and HBS has been identified as an important research priority (ICCAT, 2004).

In addition to changes in exploited habitats, another common consideration is the proportion of records with zero catch (Maunder and Punt, 2004). For pelagic longline fisheries, this proportion can be relatively high, particularly for bycatch species. A high proportion of zero catches may violate the assumptions of the statistical analysis, and when the data are assumed to follow a lognormal probability distribution (a common assumption), computational issues arise because the natural logarithm of zero is undefined. These concerns are relevant for GLMs and HBS methods cast in a statistical framework (Section 2.2). One common approach to account for zeros is to add a small constant to all catch records before analysis (Maunder and Punt, 2004). Other approaches do not require the analyst to alter the data, such as using an assumed probability distribution that can include zero observations (e.g., Poisson or negative binomial), or modeling the proportion of zero observations and the observations with positive catches separately (i.e., the

delta-GLM approach; Aitchison, 1955; Lo et al., 1992; Maunder and Punt, 2004; Stefánsson, 1996; among others).

In this study, we simulated catch and effort data over a range of specified biomass trajectories and patterns in vertical catchability. We compared the indices estimated by statHBS and several formulations of GLMs, including delta-GLMs, when fit to the simulated data. The simulated catch data incorporated a trend in fishing effort that is similar to that of the JLL in the Atlantic Ocean from 1956 to 2009. Previous studies have compared similar approaches to standardizing indices of abundance (Bigelow and Maunder, 2007; Goodyear, 2003; Maunder et al., 2006); however none of these directly compared the commonly used models evaluated in this analysis.

## 2. METHODS

### 2.1. Data simulation

A simulation analysis is well suited for evaluating methods used to estimate relative abundance, because the true pattern in abundance is known. To simulate realistic catch data in this study, we specified fishing effort to follow the temporal dynamics of the JLL in the Atlantic Ocean. The change in target species and target fishing depth exhibited by this fishery highlights the importance of considering vertical habitats fished (e.g., depth) when estimating relative abundance from these data. Therefore, the data simulation propagated effort over a range of vertical habitats and specified catchability to vary by habitat.

It is common practice in fisheries to assume that CPUE is proportional to abundance ( $N$ ) using the following general relationship (Maunder and Punt, 2004):

$$CPUE = qN \tag{1}$$

where  $q$  represents catchability. This fundamental relationship served as the basis for data simulation, and by expanding it to incorporate a habitat-specific  $q$ , we simulated catch data per longline set following:

$$C_{y,s} = \left[ \sum_h q_h E_{y,s,h} B_y \right] e^{\varepsilon_{y,s}}, \quad \varepsilon_{y,s} \sim N(\mu = 0, \sigma = 2) \tag{2}$$

where  $C_{y,s}$  is the catch in biomass for longline set  $s$  in year  $y$ ,  $q_h$  refers to the catchability associated with vertical habitat  $h$ ,  $E_{y,s,h}$  is the total effort associated with habitat  $h$  in set  $s$  in year



$y$ ,  $B_y$  is the exploitable biomass in year  $y$ , and  $\varepsilon_{y,s}$  is a random deviation in catch for set  $s$  in year  $y$ . When generating random deviates, we selected a value for  $\sigma$  that enabled  $C_{y,s}$  to cover a realistic range as compared to many HMS caught by the JLL in the Atlantic. Overall, this simulation was relatively simple in that neither spatial structure nor population structure (size, age, sex, etc.) were considered; however, these simplifying assumptions are consistent with recent assessments of many HMS, such as Atlantic marlins, that used a single-stock approach without population structure (ICCAT, 2006).

We simulated catch data over a period of 54 years (1956–2009), a time-span during which the JLL operated continuously in the Atlantic Ocean (ICCAT, 2006; Uozumi and Nakano, 1994). Biomass trajectories were specified for this period by declaring an initial biomass in the first year ( $B_{1956} = 500,000$  t), with biomass in the following years determined as a random deviation from the previous year. The random deviates were derived from a normal distribution with a mean specified in each simulation as a random uniform number between  $-10,000$  and  $10,000$  and a standard deviation of  $10,000$ . Thus, the biomass trend followed a correlated random walk that increased when the mean of the normal distribution was large and positive, decreased when large and negative, and was stable when near zero. Also, a lower threshold of  $100$  t was imposed on  $B_y$  to prevent complete extirpation of the stock.

Fishing effort was specified as numbers of hooks, with one hook representing one unit of effort. Annual effort (total hooks fished per year) for the JLL in the Atlantic (Fig. 1) was determined using publically available catch and effort data from the International Commission for the Conservation of Atlantic Tunas (ICCAT)<sup>1</sup>. The number of longline sets per year (Fig. 1) was determined from these catch and effort data as the total number of records per year, and the number of hooks fished per longline set was then fixed for each year at the number of hooks per year divided by the number of sets per year. The total number of records in the ICCAT database may not be an accurate representation of total sets per year, because each record may represent

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<sup>1</sup> <http://www.iccat.int>; data accessed September 2011.

more than one set, but we feel this approach characterized the general pattern in sets per year for the JLL and improved efficiency in our simulation by reducing the total number of records (sets) generated.

To calculate the number of hooks from each set in each vertical habitat category, we specified a fishing depth for each hook in a set following catenary geometry (Bigelow et al., 2006; Yoshihara, 1951, 1954). These calculations required details pertaining to the configuration of longline gear over time, including the number of hooks per basket (HPB; i.e., hooks between floats), lengths of the branch-line ( $b$ ; connects the hook to the mainline; also called gangion), floatline ( $f$ ; connects the float to the mainline), mainline between floats ( $\ell$ ), and the angle ( $\varphi$ ) between horizontal and tangential of the mainline where it attaches to the floatline. The following equation was used to specify hook depths:

$$d_j = b + f + 0.5\ell \left\{ \left( 1 + \cot^2 \varphi \right)^{\frac{1}{2}} - \left[ \left( 1 - 2 \frac{j}{(\text{HPB} + 1)} \right)^2 + \cot^2 \varphi \right]^{\frac{1}{2}} \right\} \quad (3)$$

where  $d_j$  is the depth of hook  $j$  and  $j = 1$  to HPB for a given long-line set. The number of HPB is often considered representative of longline target fishing depth with smaller numbers (3–6) used in shallower sets and larger numbers (10–20) used in deeper sets. Corresponding to a shift in target species, the proportion of sets with a large number of HPB increased throughout the 1980s (Serafy et al., 2004; Uozumi, 2003; Ward and Hindmarsh, 2007; Yokawa and Uozumi, 2001). This simulation followed the proportions outlined by Uozumi (2003) for HPB from 1975–1998. For years prior to 1975, we used the proportion reported in 1975, and for years after 1998, we used the proportion reported for 1998 (Fig. 2). The angle  $\varphi$ , although variable in practice, was set to  $72^\circ$ , a conventional assumption in previous studies (Ward and Myers, 2006), and the lengths of the longline components  $b$  and  $f$  increased over time, following the historical trend in gear

configurations reported by Yokawa and Takuchi (2003) (Fig. 2). The value for  $\ell$  was determined by assuming a fixed distance between longline hooks (45 m) throughout the simulation (i.e.,  $\ell = 45[\text{HPB} + 1]$ ; Ward and Hindmarsh, 2007). Finally, we reduced calculated hook depths by 25% to account for shoaling of the gear (Ward and Myers, 2006). Actual hook depth is likely influenced by several dynamic processes, and it has been shown that catenary algorithms do not accurately estimate longline hook depth (Rice et al., 2007; Ward and Myers, 2006). Thus, hook depths from our simulation were reflective of a general pattern for the JLL over time, but are not necessarily an accurate characterization of each set.

While it is important to have an understanding of hook depth, the vertical distributions of HMS are likely governed by a physiological response to the thermal properties of the water column (Brill and Lutcavage, 2001). Because these properties are highly variable over time and space, fishing depth does not necessarily reflect habitat fished. Therefore, we declared 16 vertical habitats ( $h$ ) in which fishing effort could occur, each representing one degree deviations from sea surface temperature (i.e., 0 to  $-15$  °C). To simulate variability in the temperature at given hook depths, we randomly assigned each simulated longline set one of three possible temperature profile scenarios (i.e., relative temperature-at-depth): shallow, intermediate, or deep thermocline depth (Fig. 3). Relative temperature-at-depth was specified deterministically in each scenario to cover a range of possible temperature profiles. This effectively assigned each hook within each set to one of the 16 habitat categories and incorporated random variability between sets. Following the changes in longline gear configurations specified in the simulation, hook depths increased over time, which corresponded with deeper (cooler) habitats being fished (Fig. 2).

To relate habitat-specific fishing effort to vulnerability for the species being fished, we specified one of three potential scenarios for vertical habitat catchability (Fig. 3) in each simulation. The catchability in each habitat was influenced by relative temperature, and these scenarios were meant to cover the conceivable range for large pelagic fishes. While these

organisms may spend the majority of their time in a preferred thermal regime, their vertical movement is likely a foraging strategy; therefore, the likelihood of taking a baited hook may not be constant with depth, meaning the vertical trend in catchability may not be directly related to the vertical distribution of the species (Goodyear et al., 2003). To account for uncertainty in vertical catchability, the three scenarios evaluated included peaks in different thermal habitats, relative to sea surface temperature (SST): surface, intermediate, and deep (Fig. 3). Each scenario was specified to have the same total catchability over the vertical habitats ( $q_{total} = 2.5 \times 10^{-10}$ ), and  $q_h$  was determined as a proportion of total catchability allocated to each habitat using:

$$q_h = q_{total} P_h \quad h = 0, \dots, -15 \quad (4)$$

where in each scenario the proportion of total catchability for each habitat ( $P_h$ ) was specified using the normal probability density function (PDF). The parameters of the normal PDF ( $\mu$ ,  $\sigma$ ) varied between vertical catchability scenarios ( $\mu = 0, 3, 5$  and  $\sigma = 1.2, 1.5, 2.5$  for vertical catchability peaks at surface, intermediate, and deep habitats, respectively) and  $P_h$  was constrained to sum to one by dividing the probability densities in each habitat by the sum of the densities across  $h$ . We are unaware of any previously estimated patterns in vertical catchability for the JLL. The trends specified here allowed for the simulation of realistic catch data when following the effort dynamics of the JLL.

We repeated this simulation iteratively over 50 randomly determined biomass trajectories and the three possible scenarios for vertical catchability (Fig. 3) for a total of 150 simulated data sets. This captured the effects of a broad range of possible relationships between the abundance and vertical distribution of a large pelagic fish as related to the dynamics of the JLL. Also, to incorporate zeros in the catch data, sets with total catches less than 0.04 t were set to zero.

## 2.2. Approaches to estimating relative abundance

The 150 simulated datasets were used to compare the accuracy of indices of abundance estimated using three general approaches: the nonlinear statHBS model, GLMs, including delta-lognormal GLMs (delta-GLMs), and non-standardized ‘nominal’ CPUE (calculated as average annual CPUE). The statHBS model, as described by Maunder et al. (2006), models catch data ( $C$ ) from longline set  $i$  in a nonlinear framework as:

$$C_i = \hat{q}_{base} \hat{I}_t \sum_h \left( \hat{H}_h \sum_{i,j \in h} E_{i,j} \right) \quad (5)$$

where  $\hat{q}_{base}$  is overall catchability,  $\hat{I}_t$  represents the index of abundance over time  $t$ ,  $\hat{H}_h$  is the difference in catchability for habitat  $h$ , and  $E_{i,j}$  reflects the effort associated with hook  $j$  in set  $i$  (for this study each hook represented one unit of effort, so  $E_{i,j} = 1$ ). By multiplying the total number of hooks in habitat  $h$  by the change in catchability associated with that habitat ( $\hat{H}_h$ ), effective effort is calculated for each longline set, thereby directly accounting for changes in vertical habitats exploited over time. The number of hooks per habitat category was calculated using catenary algorithms and longline configurations to determine hook depth, and the thermal properties of the water column to relate fishing depth to temperature relative to the surface (categorized as one degree deviations from SST). Estimates of hook depth and temperature-at-depth relied on the values specified for gear configurations and temperature profiles in the simulation. The estimable parameters of this model are  $\hat{q}_{base}$  and elements of the vectors  $\hat{I}_t$  and  $\hat{H}_h$ . Overall catchability is confounded with  $\hat{I}_t$  and  $\hat{H}_h$ , so  $I$  in the first year is set to one, and  $\hat{H}_h$  is constrained to sum to one. These parameters were estimated by fitting this model to simulated  $C_i$  by minimizing the following negative log-likelihood function:

$$-\ln L(\theta | C_i) = \sum_i \ln(\sigma) + \left[ \frac{(\ln(C_i + \delta) - \ln(\hat{C}_i + \delta))^2}{2\sigma^2} \right] + \sum_h \left( \ln(\hat{H}_h) - \ln\left(\frac{1}{16}\right) \right)^2 \quad (6)$$

where  $\hat{C}_i$  is the predicted catch for longline set  $i$ ,  $\theta$  is a vector of parameters,  $\delta$  is a small constant (1) used to prevent taking the log of zero, and  $\sigma$  is the estimated standard deviation (in log space). The last term was included to improve convergence by penalizing deviation from a uniform distribution under the constraint that  $\hat{H}_h$  must sum to one.

The GLM-based approach to standardizing CPUE data has been used in stock assessments for many years (Maunder and Punt, 2004). A GLM can accommodate non-normal error structure by relating the expected  $i$ th value of a response variable to a set of predictor variables through a link function (McCullagh and Nelder, 1989; Nelder and Wedderburn, 1972). Since GLMs are linear models, a linear response is assumed between the function of the expected response and the explanatory variables as:

$$g(\mu_i) = \mathbf{x}_i^T \boldsymbol{\beta} \quad (7)$$

where  $g$  represents the link function,  $\mu_i$  is the predicted response,  $\mathbf{x}_i^T$  is a transposed vector of explanatory variables including an intercept and a categorical variable representing the time step (at a minimum), and  $\boldsymbol{\beta}$  is a vector of parameters. For the GLM, CPUE adjusted by a small number ( $1 \times 10^{-3}$ ) rather than catch (as with statHBS) was the response variable and lognormal error structure was modeled by taking the natural logarithm of CPUE (the identity link function was used). Annual estimates of relative abundance and their respective standard errors were

obtained as back-transformed year means with an infinite series lognormal bias correction following Lo et al. (1992).

The GLM is expanded in a delta-GLM, which models the probability of observing a zero catch as a function of the explanatory variables, and then separately fits a GLM to the non-zero catches (Aitchison, 1955; Lo et al., 1992; Maunder and Punt, 2004; Stefánsson, 1996; among others). This approach is represented by:

$$\Pr(Y = y) = \begin{cases} w, & y = 0 \\ (1-w)f(y) & \text{otherwise} \end{cases} \quad (8)$$

In Eq. (8),  $w$  is the probability of observing a zero for the response variable (CPUE) and  $f(y)$  is a model of the mean of the non-zero CPUEs. For our analyses, the proportion of sets with positive CPUE ( $1 - w$ ) was modeled using a binomial GLM with a logit link function, and the positive CPUEs were modeled with a lognormal GLM as previously described (though, without adjusting CPUE). Annual probabilities of positive catches from the binomial GLM were the back-transformed mean values for each year predicted when all additional factors were set to the level representing the observed mode (Maunder and Punt, 2004). Annual estimates of abundance were then obtained by multiplying the probability of positive observations for year  $y$  and the back-transformed bias corrected year means from the lognormal GLM of positive catches. To capture the precision of the abundance estimates, standard errors were calculated using the delta method (Lo et al., 1992; Seber, 1982).

It is important when evaluating the accuracy of GLMs and delta-GLMs to consider which explanatory variables should be included in the models. The year in which the catch occurred must be one of the variables, because the output of interest is relative abundance over time. The number of HPB is commonly used for longline catch and effort data as a proxy for fishing depth, so this factor was also considered in the analysis. Typically, when linear models are used to

estimate relative abundance from longline data, habitats exploited are not directly considered, because information cannot be summed over multiple habitats as with statHBS (Maunder et al., 2006). However, catenary geometry and water column temperature profiles can be used to combine fishing and environmental data into a single variable to be incorporated directly into the GLMs. For this type of variable, it is important to consider the degree of detail since a factor with numerous levels can result in an over-parameterized model. Thus, using the catenary algorithm (Eq. (3)) to estimate hook depths, and the simulated temperature profiles to relate depth to temperature, we created a factor that represents the largest change in temperature relative to SST (Max $\Delta$ T) for each longline set (i.e., deepest/coldest habitat fished per set).

To determine which predictor variables to include in the GLMs, a series of GLMs were evaluated using a range of configurations for the main effects of year, HPB, Max $\Delta$ T, and each possible first-order interaction (following convention, interactions with year were modeled as random effects). In practice, model selection techniques, such as Akaike's Information Criterion (AIC) or analyses of residual deviance, are often employed when selecting a model for generating a standardized index of abundance (Maunder and Punt, 2004). However, in a simulation analysis, estimated abundance trends can also be compared with the simulated 'true' pattern in abundance to determine model performance. Thus, we fit each proposed GLM configuration to all simulated datasets and recorded AIC, residual deviance, and a metric for model accuracy (Section 2.3). Selection via AIC was based on AIC for each model minus the minimum observed AIC ( $\Delta$  AIC). The model with  $\Delta$ AIC = 0 represented the 'best' model of those evaluated (Burnham and Anderson, 2002). For our deviance analyses, we calculated the percent of deviance explained by the stepwise addition of each factor (Ortiz and Arocha, 2004), and if the percent explained was less than the somewhat arbitrary cutoff value of 1%, then the model was rejected (Maunder and Punt, 2004). For comparisons made between different random effects, models were fitted using restricted maximum likelihood estimation, while standard maximum likelihood estimation was



used when comparing different configurations of fixed effects (Zuur et al., 2009). We conducted the analyses of model configurations using  $\ln(\text{CPUE} + 1 \times 10^{-3})$  as a response variable, then repeated the analyses using only the records with positive CPUEs (i.e.,  $\ln(\text{CPUE} > 0)$  was the response). We considered four configurations of fixed effects (FE1 = Year, FE2 = Year + Max $\Delta$ T, FE3 = Year + Max $\Delta$ T + HPB, and FE4 = Year + Max $\Delta$ T + HPB + Max $\Delta$ T  $\times$  HPB), and fit the candidate models to the 150 simulated datasets. To summarize the selection metrics across all scenarios, we recorded their median values and calculated the percent of times each model structure would have been selected following the three selection approaches. The summary statistics for model fit and model accuracy were then synthesized to select a single GLM structure for all simulated datasets. We did not allow the model structure to change during the simulations, because we did not want to introduce model selection as an additional level in our evaluations. The overall comparisons were then confined to five approaches: statHBS, a GLM and delta-GLM with the selected model structure, a delta-GLM without the Max $\Delta$ T factor (delta-GLM2) for evaluation of this unique variable, and nominal CPUE, because many studies (particularly meta-analyses) have used this approach to describe trends in abundance (e.g., Myers and Worm, 2003).

### *2.3. Model evaluation and comparison*

The GLMs and statHBS model were fit to different response variables (CPUE and catch, respectively); therefore, common statistical comparisons of model fit (e.g., AIC) could not be used to compare these models. However, this does not represent a substantial drawback, because these statistical metrics are typically concerned with balancing model fit and parsimony for a given dataset, and the most important aspect in this evaluation is the accuracy of the estimated trend in annual biomass. Because estimated trends were treated as relative indices, the estimates from the various models were scaled for comparison with the associated ‘true’ biomass. Model

comparisons were based on the annual percent difference in simulation scenario  $x$  for model  $m$  in year  $y$  (%  $D_{x,m,y}$ ) between true biomass and estimated biomass calculated as:

$$\% D_{x,m,y} = \frac{100 \left| B_{x,y} - \frac{\hat{I}_{x,m,y}}{\bar{I}_{x,m,y}} \bar{B}_{x,y} \right|}{B_{x,y}} \quad (9)$$

where  $\hat{I}_{x,m,y}$  refers to the index of abundance estimated in simulation  $x$  for model  $m$  in year  $y$ . To facilitate the comparison of methods, the median of the annual percent differences (MPD) was calculated for each model  $m$  to serve as a single metric of accuracy for each simulated time series  $x$  and the standard deviation (SDPD) was calculated to characterize the variability of %  $D_{x,m}$  across years. Our performance metrics compared the absolute value (magnitude) of the relative errors. To evaluate the pattern (directionality) in the errors, we analyzed overlaid plots of ‘true’ and estimated biomass across all scenarios.

#### 2.4. Sensitivity

The habitat variables specified in the GLMs and the statHBS model relied on estimates of hook depth for each longline set. By using the conditions described in the data simulation, these dynamics were known without error in the analyses. However, hook depth is notoriously difficult to estimate with accuracy (Rice et al., 2007; Ward and Myers, 2006), and uncertainty surrounding inputs for HBS methods have been shown to affect the accuracy of these approaches (Goodyear, 2003). Thus, we conducted a sensitivity analysis with a single simulated data set, assuming declining biomass over time and a peak in vertical catchability in surface waters. This scenario potentially reflects the vertical distribution and biomass trajectory of several HMS in the Atlantic Ocean. The statHBS model and a delta-GLM including the Max $\Delta$ T factor were then fit to the data

assuming different degrees of uncertainty regarding estimated hook depth. Because estimates of hook depth may be biased, three scenarios were considered in the sensitivity analysis (hook depths always underestimated, always overestimated, or randomly over/underestimated in each longline set), and hook depth errors were specified over a range of 5–50% (incremented by 5%) for each scenario. The model evaluation metrics (Section 2.3) were then compared across the range of errors specified.

### *2.5. Implementation*

With the exception of the statHBS model, the simulation and analyses were executed using the statistical programming language R (R Development Core Team, 2011). Due to increased model complexity, statHBS was implemented using AD Model Builder (ADMB Project, 2011), which was called from R.

### 3. RESULTS

The simulation model generated 150 separate catch and effort time series from 50 random biomass trends, each repeated three times to evaluate different profiles of vertical catchability. Of the 150 simulations, we highlighted nine as representative of the range of possibilities for patterns in relative abundance and vertical catch-ability (Fig. 4). When catchability was highest in surface waters (Fig. 4a–c), simulated catch peaked early in the time series, but then decreased as the fishery began targeting deeper habitats. When catchability was highest in intermediate and deeper habitats (Fig. 4d–i), simulated catches tracked the true trend in abundance more closely. Also, because one component of this study is the treatment of records with a total catch equal to zero (i.e., either add a constant or use the delta approach), we summarized the proportion of zeros across all simulation scenarios (minimum, mean, and maximum proportions were 0.02, 0.11, and 0.41, respectively). The highest proportions of zero catches occurred when catchability was simulated to peak in surface waters or when biomass was simulated to decrease over time.

Selection of a model structure for the GLMs and delta-GLMs was not straightforward, because the three selection metrics did not always lead to the same conclusion (Table 1). The AIC approach clearly favored FE3, while the deviance analysis selected FE2 and FE4 most frequently. However, the accuracy of the models is their most important attribute, and MPD indicated that FE3 and FE4 exhibited the greatest accuracy, with FE4 selected slightly more often, and a lower overall MPD for FE3. In fact, the AIC approach selected the most accurate configuration in only 19.3% of the scenarios, and the deviance analysis led to the most accurate model in only 10.7% of the scenarios. We decided to use FE3 rather than FE4 throughout the simulation runs, because it is a more parsimonious model, and also because the interaction term caused convergence issues

with the delta-GLM. We did not observe improved accuracy when the model contained random effects to describe interactions with the Year coefficient; thus, these interactions were not included in the analyses.

Indices of abundance were estimated for each simulated data set following five approaches (delta-GLM, delta-GLM2, GLM, nominal, and statHBS) and evaluation metrics were calculated for each approach. The overall comparison of MPD for all simulations (Fig. 5a) suggests that the delta-GLM that included detailed vertical habitat information provided the most accurate estimates of relative abundance (i.e., the lowest overall median of MPD), though the variability of this metric spanned a slightly larger range than that for GLM. When accounting for different patterns in vertical catchability across all biomass trends (Fig. 6a–c), delta-GLM was most accurate, except when vertical catchability peaked in surface waters (Fig. 6a). Comparison of MPD over different biomass trajectories across all catchability scenarios (Fig. 6d–f) suggested that delta-GLM was most accurate except when biomass increased over time (Fig. 6f). Overall variability in the accuracy of the estimates was lowest for delta-GLM2 (Fig. 5b), which exhibited the lowest SDPD when vertical catchability peaked in deep waters (Fig. 6i) and when biomass increased over time (Fig. 6l). However, in general, SDPD was relatively consistent across all approaches except when using nominal CPUE.

The nine highlighted simulation scenarios were used to visually evaluate estimated trends in abundance as compared to ‘true’ abundance trends (Fig. 7). The patterns in these plots were consistent across all simulated scenarios, and suggest that when vertical catchability peaked at the surface (Fig. 7a–c) all approaches over-estimated abundance early in the time series, but underestimated abundance when catches declined with changes in fishing strategy. These patterns were exacerbated for less accurate approaches, particularly nominal CPUE. For scenarios where vertical catchability peaked in intermediate and deep waters, there were no consistent patterns in the errors, irrespective of biomass trajectory (Fig. 7d–i).

Finally, the sensitivity analysis indicated that for the scenario evaluated, the statHBS model was sensitive to hook depth uncertainty, yet the delta-GLM with detailed habitat information was not particularly sensitive to this error (Fig. 8). Model evaluation metrics for statHBS and delta-GLM were compared with baseline metrics calculated assuming no error in estimated hook depth as well as delta-GLM2 which did not include the Max $\Delta$ T factor. The accuracy of statHBS was compromised when hook depths were always underestimated or randomly over/underestimated. When hook depths were always overestimated, accuracy did not decline until hook depth estimates were at least 30% different from actual fishing depths (Fig. 8a). For the delta-GLM, accuracy was not substantially reduced as hook depth uncertainty increased; though when hook depths were always overestimated, a relatively small amount of error caused delta-GLM to be less accurate than delta-GLM2, but larger errors in estimated hook depths actually improved accuracy (Fig. 8b). The statHBS model also appeared more sensitive than delta-GLM to hook depth uncertainty in terms of SDPD (Fig. 8c and d). For the delta-GLM, SDPD was relatively consistent across the range of hook depth uncertainty for all scenarios.

#### 4. DISCUSSION

There are numerous challenges surrounding the assessment and management of HMS (Lynch et al., 2011). Among these include a lack of fishery-independent scientific research, resulting in a reliance on fishery catch and effort data for making inferences about population dynamics. In this study, we evaluated common approaches to estimating indices of abundance for HMS from longline fishery data when the fishery exhibited a change in target fishing depth. This shift in the vertical distribution of effort is a common feature of many pelagic longline operations to which HMS are susceptible (Majkowski, 2007). Thus, we evaluated models that accounted for habitats exploited, such as statHBS and GLMs that included a unique habitat factor ( $\text{Max}\Delta T$ ). By including this habitat variable, we essentially created a bridge between statHBS and GLM approaches, because under both methods, estimates of vertical habitats exploited are derived by relating estimated longline hook depth to surrounding environmental conditions. Our overall conclusion from this study is that the most accurate approach was a delta-GLM that included the  $\text{Max}\Delta T$  habitat factor. Including this information improved the performance of the linear models tested, and to our knowledge, this type of detailed habitat factor has not previously been used for obtaining annual estimates of relative abundance from longline data. However, delta-GLM did not exhibit the lowest variability in the errors of the approaches evaluated. This suggests that while delta-GLM may provide more accurate estimates of abundance across a time series, the magnitude of the error is less consistent than that for other methods. Still, given that SDPD does not differ substantially across approaches, we maintain that delta-GLM is the preferred approach on the basis of MPD. It should be noted that we evaluated the base form of the statHBS model as described by Maunder et al. (2006). We did not consider alternative formulations; however, Maunder et al. (2006) suggested several that may improve the accuracy of the model.

While delta-GLM provided the most accurate estimates of abundance overall, other approaches provided the lowest MPD in several scenarios. For instance, when vertical catchability peaked at the surface, GLM and statHBS were generally more accurate than delta-GLM. However, it is important to recognize that under this catchability scenario all models provided relatively inaccurate estimates of abundance (Fig. 6a), even though the fishery and environmental data included in the analyses were known without error. A potential explanation for this phenomenon is that the shift by the fishery to deeper target habitats caused catches to decline over time to a level where there was no longer enough information to estimate annual biomasses with accuracy. This emphasizes the point that fisheries do not always sample populations effectively; thus, it is risky to rely on fishery-dependent data for making inferences about population dynamics, even when changes in fishing strategy are properly considered.

When indices of abundance fail to capture stock dynamics, it is important to determine if the estimated trends exhibit hyperstability (i.e., abundance decreases more rapidly than the index) or hyperdepletion (the index decreases more rapidly than abundance) (Hilborn and Walters, 1992). For scenarios with a peak in vertical catchability at the surface, we observed evidence of hyperdepletion in estimated trends in abundance (Fig. 7a–c). If these scenarios captured true patterns in vertical catchability for bycatch species, then our results support the assertion by Uozumi (2003) that assessments of bycatch HMS in the Atlantic have been overly pessimistic.

In general, the delta approach did not result in substantial improvements over the traditional GLM. This suggests that the treatment of zeros (i.e., longline sets with total catch equal to zero) constitutes another important aspect of our evaluations. The delta approach directly accounts for zero observations, and for statHBS and GLM the data are adjusted to accommodate zeros. Therefore, when the proportion of zero observations is relatively high, the delta approach would be expected to outperform methods that alter the data; however, statHBS and GLM performed better than delta-GLM in the scenario that resulted in the highest proportions of zeros (surface peak in catchability). Because the treatment of zeros was not the primary focus of our



analyses, this unexpected result warrants further evaluation of the influence of zero observations on methods used to estimate indices of abundance. Additional studies should also consider the choice of assumed error distribution, since discrete distributions (e.g., Poisson, negative binomial) would not require the data to be altered.

Another aspect of our study that could benefit from additional research is the application of model selection criteria when generating indices of abundance. For our simulated scenarios and model configurations, neither AIC nor deviance analysis were reliable for predicting the model that provided the most accurate index of abundance. Further studies are necessary, because these approaches are commonly used when selecting models to standardize CPUE. Alternative selection approaches to consider include cross-validation (Maunder and Punt, 2004) and consistent information criteria (Shono, 2005).

Our catch and effort simulation was based on the dynamics of the Japanese Atlantic longline fishery, partly because this fishery has been recommended in this context (ICCAT, 2004), but also because it captures a scenario when changes in the vertical distribution of fishing effort may have affected catchability. Because fisheries continually evolve in response to advances in technology and shifts in the global demand for resources, dynamic catchability is likely a common feature underlying the catch data of many species, especially HMS caught by longline fisheries that have changed targeting practices. Thus, the data simulated in this study incorporated a shift in the distribution of fishing effort across vertical habitats to reflect a change in target species. While this important feature was incorporated, the simulation did not consider other potentially important dynamics, such as the geographical distribution of fishing effort over time, or variability due to size, age, or sex in the fish population. In some cases, including such detail may be essential. For instance, Prince et al. (2010) demonstrated that catchability of bycatch HMS may be higher inside than outside the oxygen minimum zone of the eastern tropical Atlantic. Standardization of CPUE with GLMs could account for this by including an

appropriately defined area factor in the linear model, whereas statHBS could be expanded to include a GLM component with this area factor (Maunder et al., 2006).

While the incorporation of vertical habitats fished improved estimates of relative abundance, its main practical limitation is the ability to estimate hook depths with accuracy. Catenary algorithms are typically used to generate static estimates of hook depth for an entire longline set, yet numerous factors (wind, hydrodynamics, behavior of hooked organisms, etc.) can cause substantial deviations from predicted depth for a given hook position both within and between sets (Bigelow et al., 2006; Rice et al., 2007; Ward and Myers, 2006). By conducting a sensitivity analysis over a range of errors in estimated hook depths, we quantified the effects of this uncertainty on the performance of statHBS and a delta-GLM. The high sensitivity of statHBS is perhaps due to the reliance of this method on a detailed characterization of hook depth, whereas the less sensitive delta-GLM used a simple categorical variable to describe vertical habitats fished. Although the Max $\Delta$ T variable provided a simplistic depiction of habitats fished, its inclusion substantially improved the accuracy of the model (Table 1). Therefore, it is interesting that this influential factor was not particularly sensitive to error. In general, the sensitivity analysis provided a simple characterization of the influence of hook depth uncertainty. To provide a baseline evaluation, we selected a single simulated scenario that potentially reflects the vertical distribution and biomass trajectory of many HMS in the Atlantic Ocean (i.e., surface peak in catchability and declining biomass over time). For instance, stock assessments of Atlantic marlins indicated that their biomasses are in decline (ICCAT, 2006), and their vertical distributions have been characterized as surface oriented with occasional deep dives (Goodyear et al., 2008; Graves et al., 2002; Horodysky et al., 2007; Kerstetter et al., 2003; Prince et al., 2010). More comprehensive characterizations of hook depth uncertainty are warranted, and we encourage additional analyses that consider a variety of simulated scenarios. Additionally, our evaluations were conducted assuming no error in the catch data, gear dynamics, or oceanographic conditions. In practice there may be uncertainties surrounding each of these inputs, and a

characterization of their effects would be useful. For example, temperature profiles for each longline set would ordinarily be obtained from a global ocean database, which may require interpolation, and therefore may not reflect the true temperature profile for each set.

In addition to expanding the evaluation of the effects of hook depth uncertainty, the results of this study highlight the importance of several areas of research. For instance, the development of a more sophisticated approach to modeling longline gear behavior as a function of environmental conditions could be useful in these applications. Accordingly, increasing the detail of fishery data reporting to include catch by hook position and corresponding environmental conditions could foster a better understanding of catches by habitat. Additionally, we defined vertical habitat categories as 1°C deviations from SST, but decisions about how to partition habitat may influence estimates of abundance that include this information. This emphasizes the importance of continued research on behavior, physiology, and habitat use of fishes, and in future analyses, model performance may be further improved using model selection (e.g., AIC) to determine an appropriate degree of detail in the habitat factor. However, based on the results of our selection of a fixed structure for the linear models, caution should be exercised when using traditional model selection metrics for CPUE standardization. Furthermore, the methods evaluated are best suited for estimating historical trends in abundance, yet predictions about future patterns are also important for fisheries management. In reality, complex dynamics likely govern true abundance trends, and most approaches for estimating relative abundance do not incorporate these relationships. However, nonlinear forecasting may be a promising approach for predicting future abundance when the governing equations are unknown (Glaser et al., 2011).

The focus of our study was on estimating relative abundance in the presence of changes in the vertical distribution of fishing effort, but a change in the geographical distribution of effort is an equally important consideration (Walters, 2003). Fishery-dependent data provide information from areas fished, which typically represent areas of high profitability. Without accounting for abundance trends in areas that were not fished, there is an implicit assumption that

CPUE trends in areas fished are reflective of trends in areas that were not fished. In many cases this assumption may not be valid, and it has been shown to bias estimates of relative abundance (Campbell, 2004; Carruthers et al., 2010; Walters, 2003). To account for this source of bias in a CPUE standardization context, Carruthers et al. (2011) described a GLM approach to CPUE standardization that includes data imputation in unfished spatial cells. Their approach could easily be adapted to account for vertical habitats as described herein, thereby directly addressing effects on catchability due to changes in the distribution of effort in three dimensions.

Since the description of HBS by Hinton and Nakano (1996), the choice between using HBS or a GLM approach to estimating the relative abundance of HMS has been controversial (Bigelow and Maunder, 2007; Goodyear, 2003; Goodyear et al., 2003; Maunder et al., 2006; Prince and Goodyear, 2006; Ward and Myers, 2005). Debate over this choice could be expected given the potential influence on assessment results (e.g., Uozumi, 2003) and the fact that regulations aimed at conserving HMS affect highly valued international fisheries. Nevertheless, the controversy emphasizes the importance of comparing and evaluating these methods, and the results of our study should be interpreted in the context of previous research (i.e., Bigelow and Maunder, 2007; Goodyear, 2003). In a simulation study, Goodyear (2003) compared GLM with the original deterministic formulation of HBS, and concluded that both methods can be accurate, but HBS can be strongly biased when input assumptions were erroneous. Bigelow and Maunder (2007) however, modeled catch rates using statHBS and GLM when applied to real fisheries data and found that statHBS fit best to the data, though the focus of their conclusions was on the importance of considering vertical habitat, rather than depth, in CPUE standardization for HMS. Recognizing the significance of this conclusion, we decided to evaluate not only statHBS, but also GLMs that consider habitat. Furthermore, given that delta-GLMs are a popular approach to CPUE standardization, we thought it was important to evaluate this method of dealing with zeros in the catch data. Thus, this study is the first to compare delta-GLMs and statHBS in a simulation context. In agreement with previous work, we conclude that the incorporation of vertical habitats

exploited is important when estimating relative abundance of HMS from fishery-dependent data, specifically when there has been contrast in the habitats exploited over time. We further recommend that this information be included via delta-GLM rather than statHBS, unless there is substantial confidence in estimates of habitats exploited.

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TABLES

Table 1. Summary of linear model selection metrics for different fixed effect structures. The four hypothesized model structures were evaluated when fit to all catch data adjusted by a constant, and when fit to the positive catch records only. Median values across all 150 simulated datasets were presented for the change in Akaike’s Information Criterion from the minimum value ( $\Delta AIC$ ), the percent of the total residual deviation explained by the stepwise addition of each factor (% total dev.), and the median percent difference between estimated and true biomass (MPD). Also presented are the percent of times each model structure was selected by each corresponding selection metric (% S).

Model structure	$\Delta AIC$	% total dev.	MPD	% $S_{AIC}$	% $S_{Dev}$	% $S_{MPD}$
<i>Response: <math>\log(CPUE + 1 \times 10^{-3})</math></i>						
Year	1055.3	73.2	33.9	0.0	0.0	12.7
Year + Max $\Delta T$	21.7	24.6	12.2	19.3	47.3	10.7
Year + Max $\Delta T$ + HPB	0.0	1.0	9.7	62.0	5.3	27.3
Year + Max $\Delta T$ + HPB + Max $\Delta T$ x HPB	29.1	1.5	11.3	18.7	47.3	32.0
<i>Response: <math>\log(CPUE &gt; 0)</math></i>						
Year	762.1	75.6	35.0	0.0	0.0	8.7
Year + Max $\Delta T$	10.8	21.2	9.1	33.3	42.7	25.3
Year + Max $\Delta T$ + HPB	0.0	1.2	10.1	58.0	8.0	29.3
Year + Max $\Delta T$ + HPB + Max $\Delta T$ x HPB	37.5	1.9	11.1	8.7	49.3	30.0

FIGURES

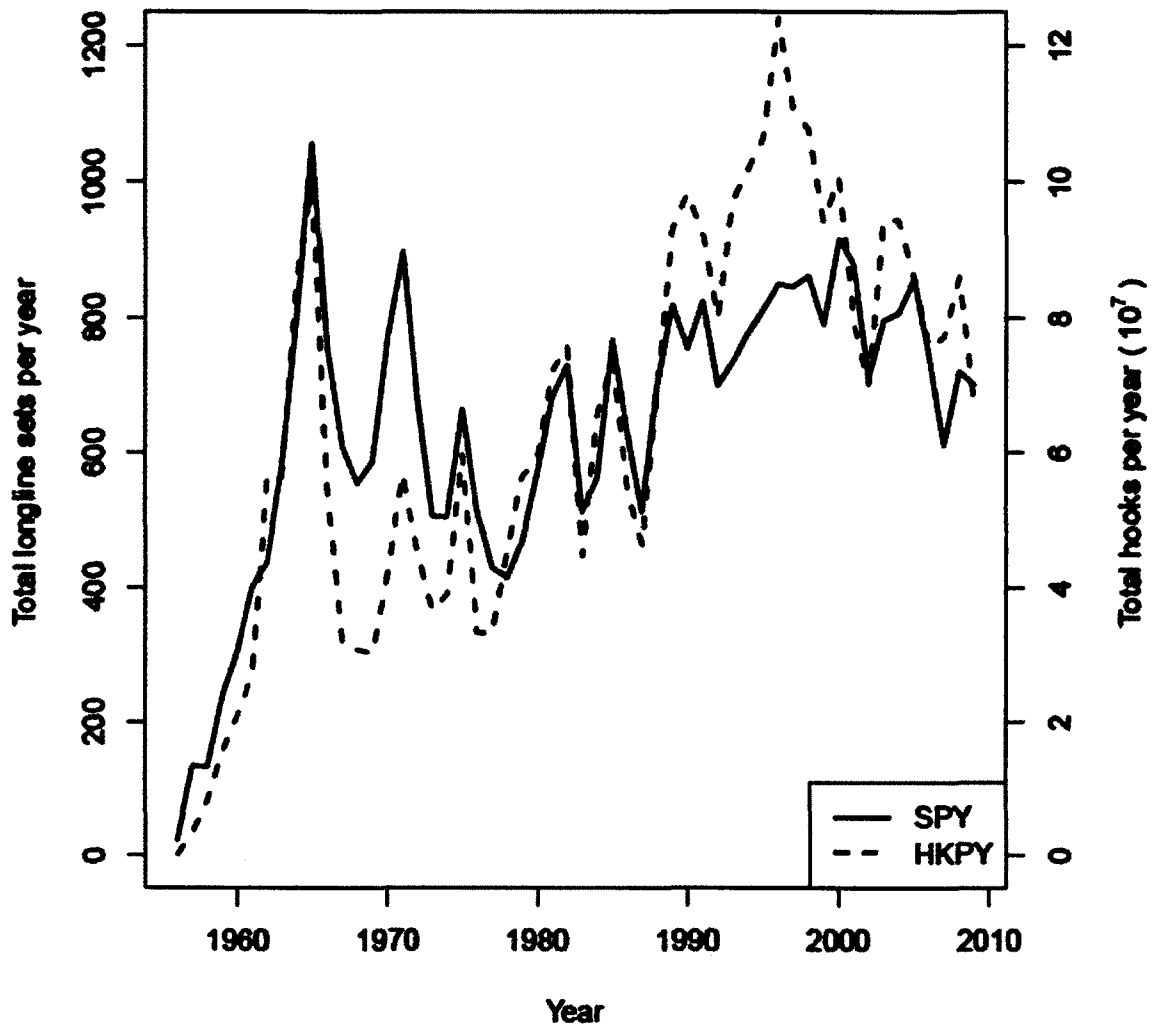


Fig. 1. Annual effort for the Atlantic Japanese longline fishery specified in the catch data simulation as total hooks and total sets per year (HKPY and SPY, respectively). The number of sets per year is an underestimate of the true number of sets for this fishery.

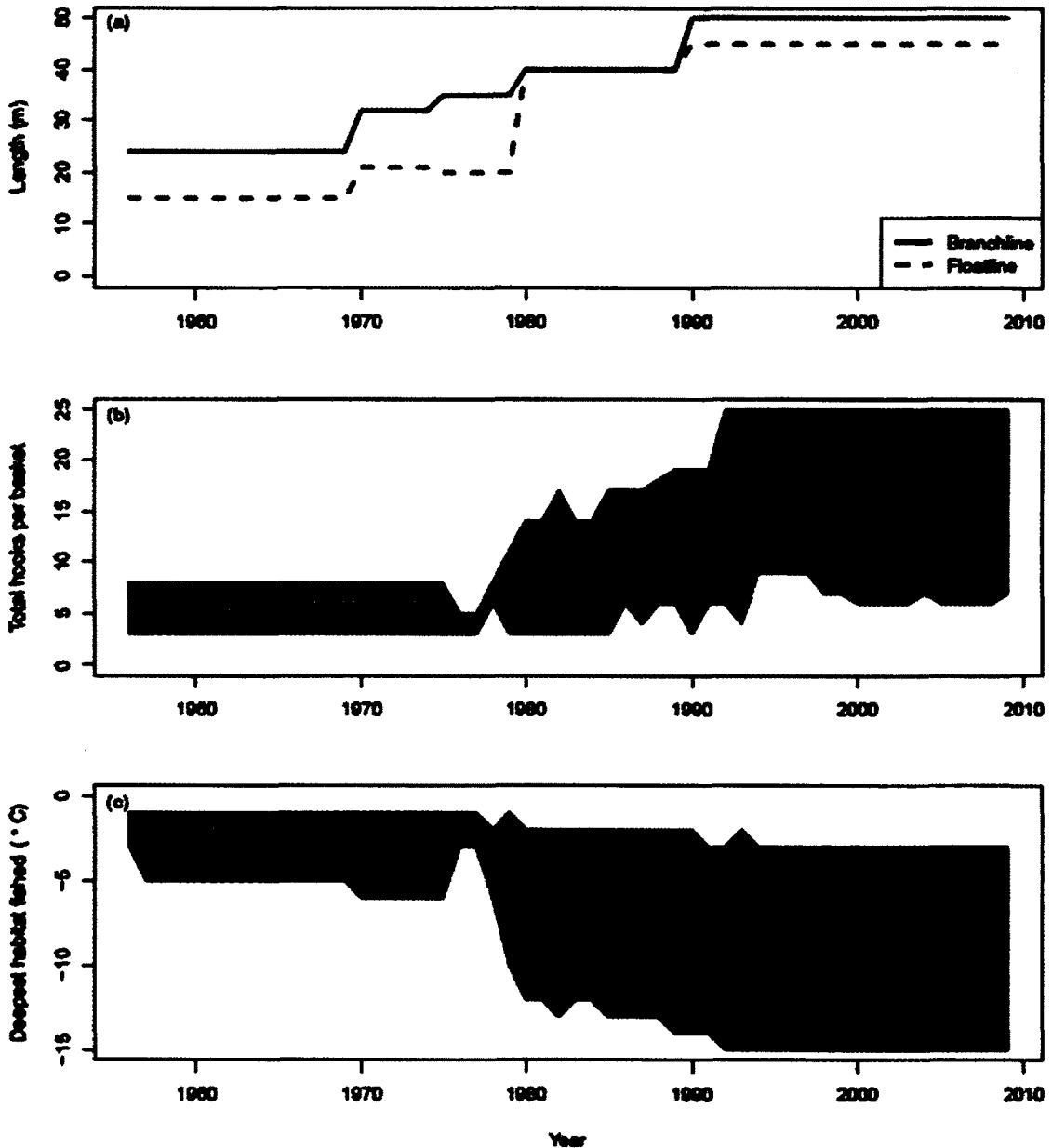


Fig. 2. Gear dynamics for the Atlantic Japanese longline fishery specified in the catch data simulation, including branchline and floatline lengths (a), and total hooks per basket (b) over time. Also, estimates of deepest habitats fished over time are presented (c). The total ranges (gray) and 95% confidence intervals (black) are presented for hooks per basket and deepest habitats fished.

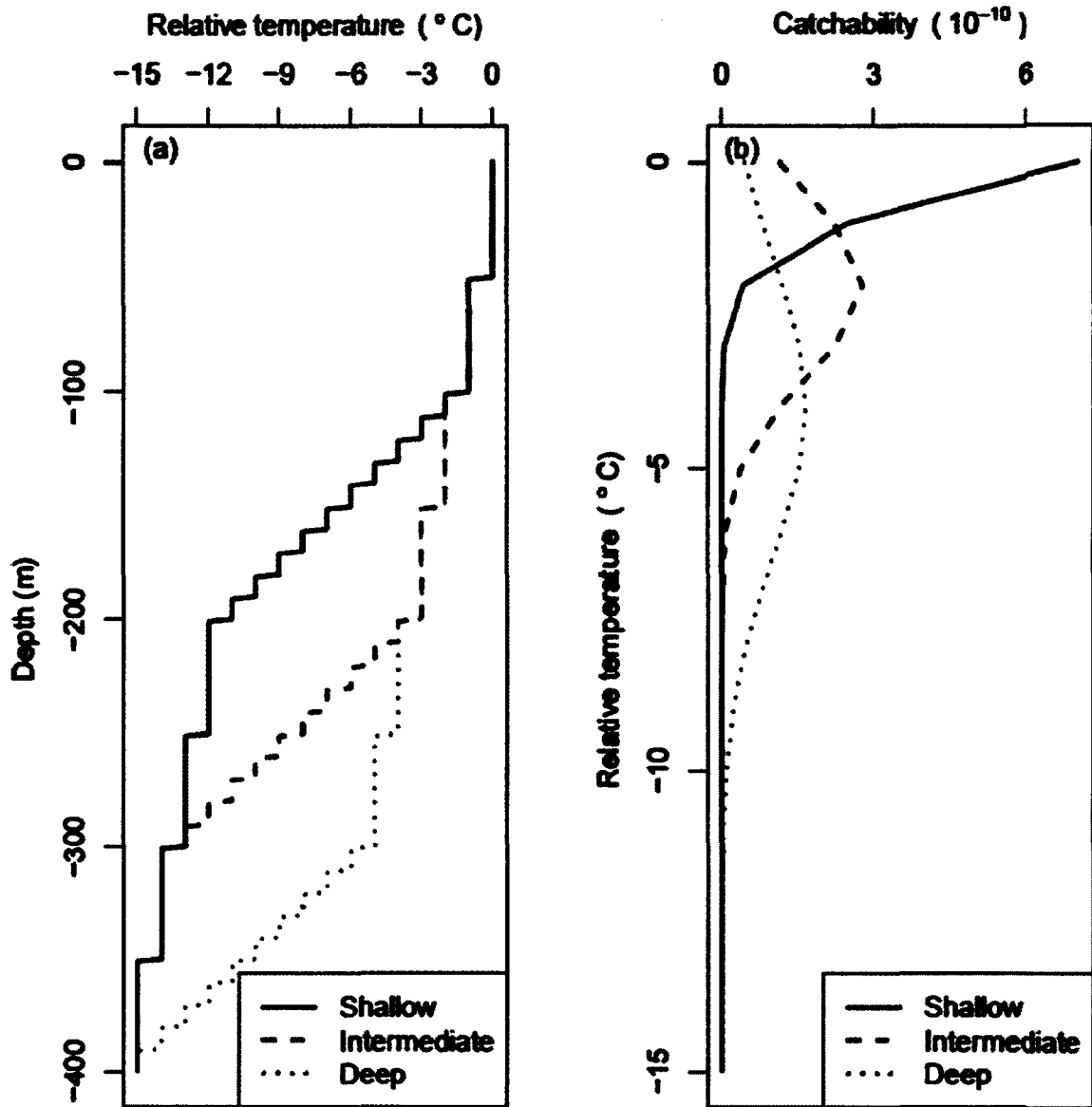


Fig. 3. Simulated ocean temperature profiles (a) and scenarios of vertical catchability (b). The temperature profiles were randomly assigned to simulated longline sets and were meant to reflect shallow, intermediate, and deep thermocline depths. The catchability scenarios exhibited peaks in surface (shallow), intermediate, and deep waters. The top of each panel represents the surface of the water with depth (a) and temperature (b) changing vertically.

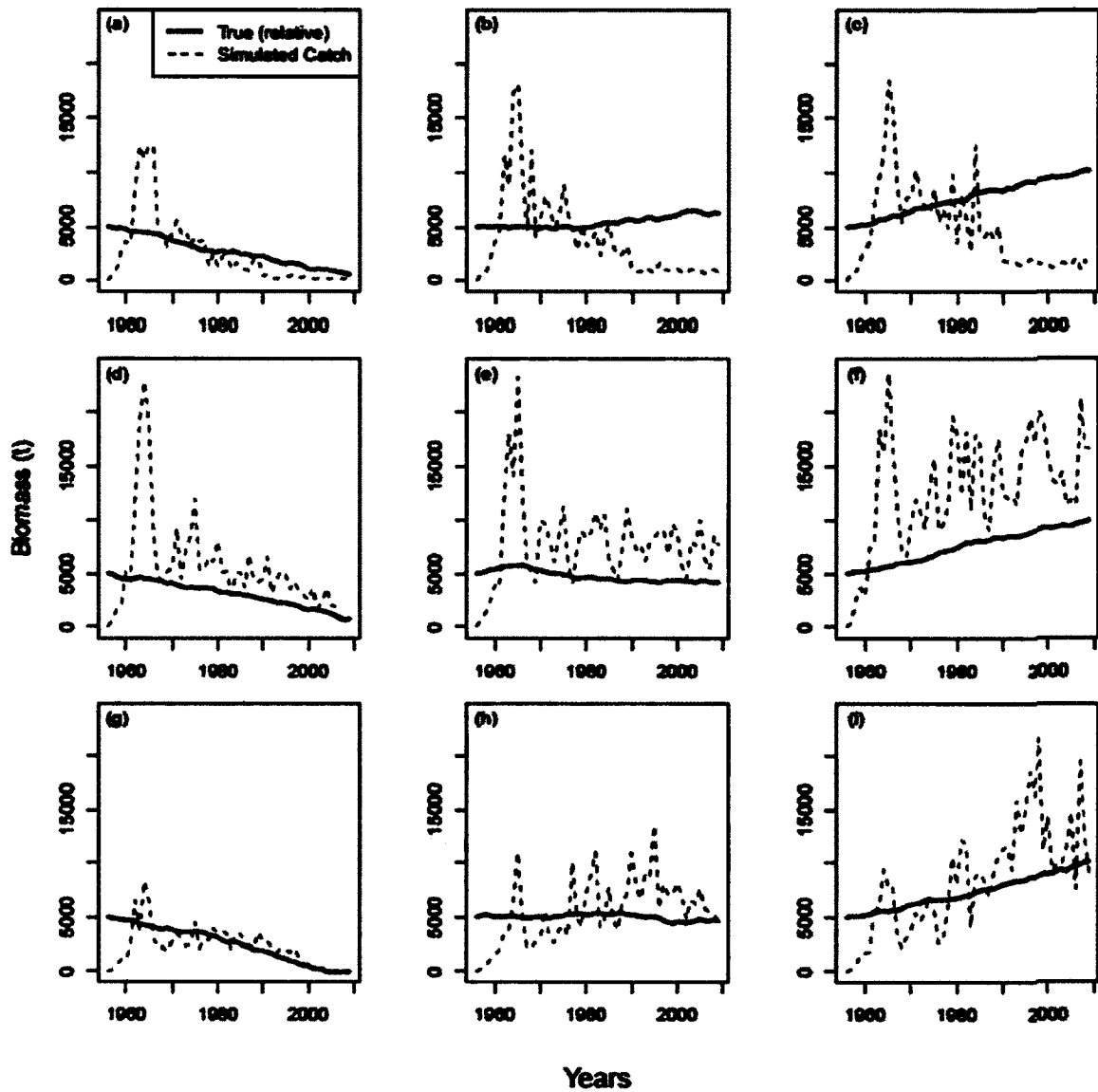


Fig. 4. Simulated catch data generated from a known underlying biomass trajectory for nine selected simulation scenarios where vertical catchability was assumed to peak in surface (a–c), intermediate (d–f), or deep waters (g–i), and the simulated ‘true’ biomass trajectory (scaled to total catch) was either decreasing (a, d, and g), stable (b, e, and h), or increasing (c, f, and i) over time.

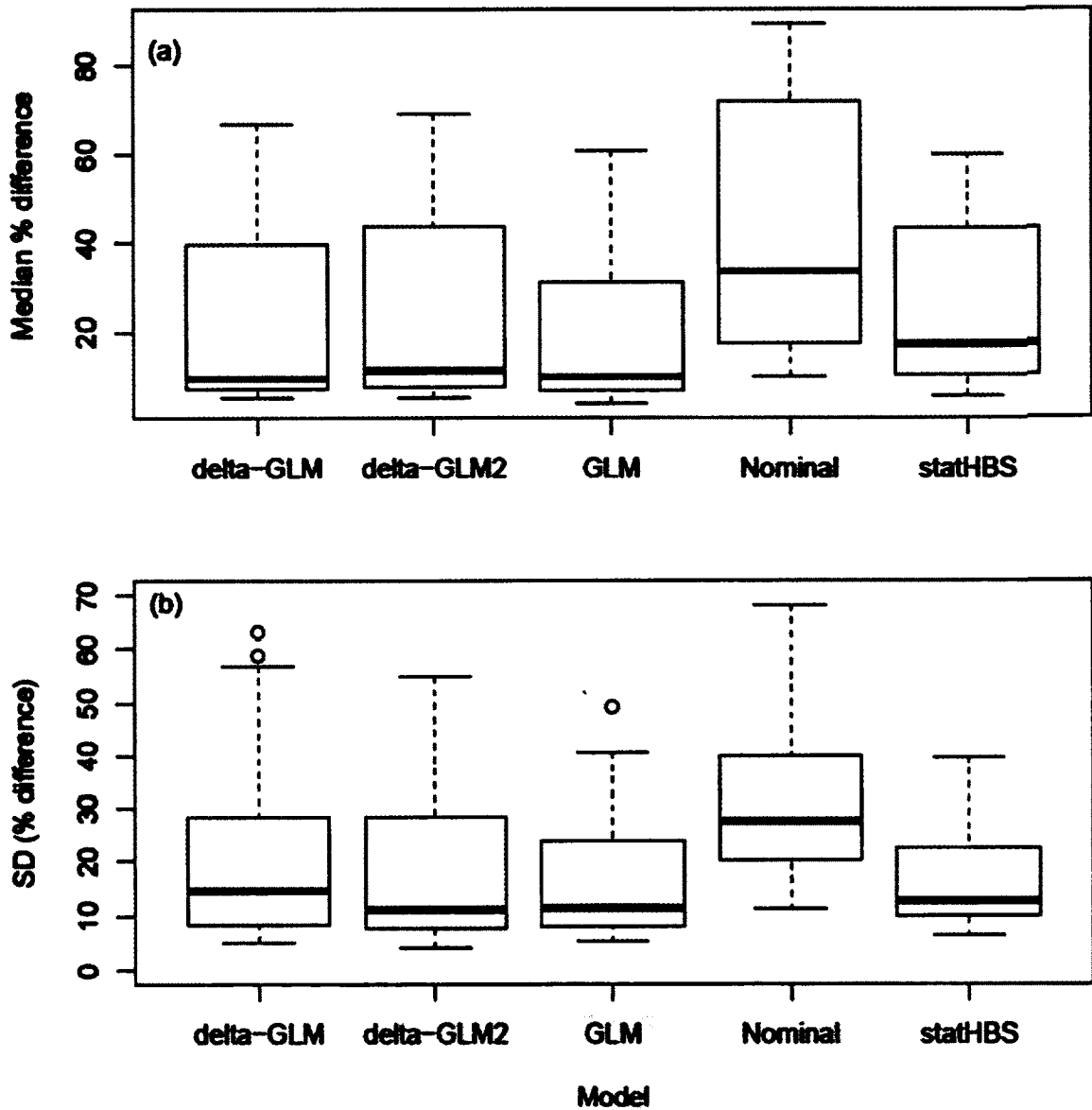


Fig. 5. Box and whisker plots of performance metrics, including median percent difference between estimated biomass and true biomass for a simulated dataset (a), and standard deviation (SD) of the percent differences (b) for five approaches to estimating an index of abundance. The solid line reflects the median, the box encompasses the interquartile range, the whiskers extend to the extreme values, and circles reflect potential outliers.



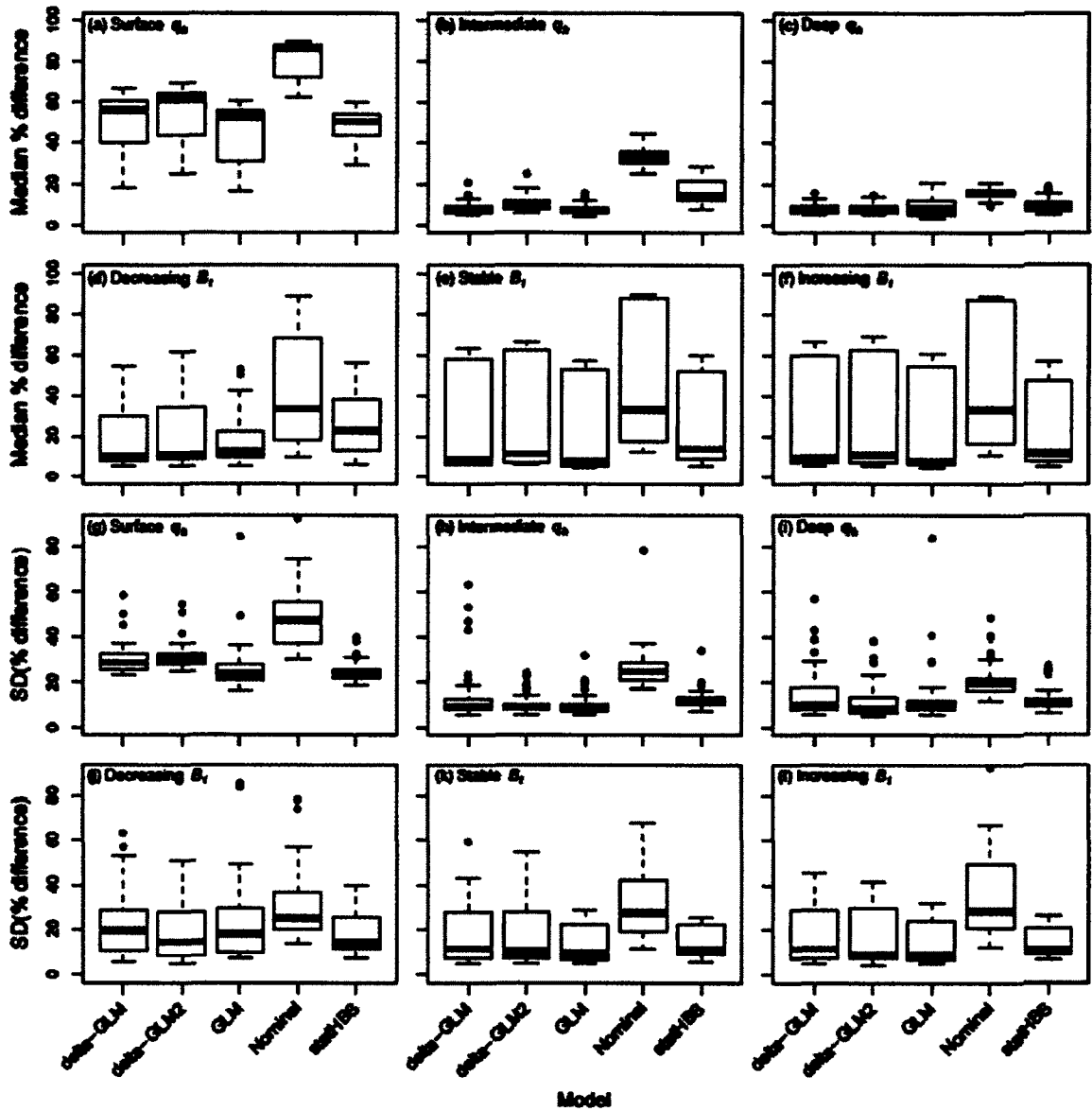


Fig. 6. Box and whisker plots of performance metrics, including median percent difference between estimated biomass and true biomass for a simulated dataset, and standard deviation (SD) of the percent differences for five approaches to estimating an index of abundance. The performance metrics were summarized for scenarios where vertical catchability ( $q_h$ ) was simulated to peak in surface (a and g), intermediate (b and h), or deep waters (c and i), and where biomass ( $B_t$ ) was simulated to decrease (d and j), remain stable (e and k), or increase (f and l) over time. The solid line reflects the median, the box encompasses the interquartile range, the whiskers extend to the extreme values, and circles reflect potential outliers.

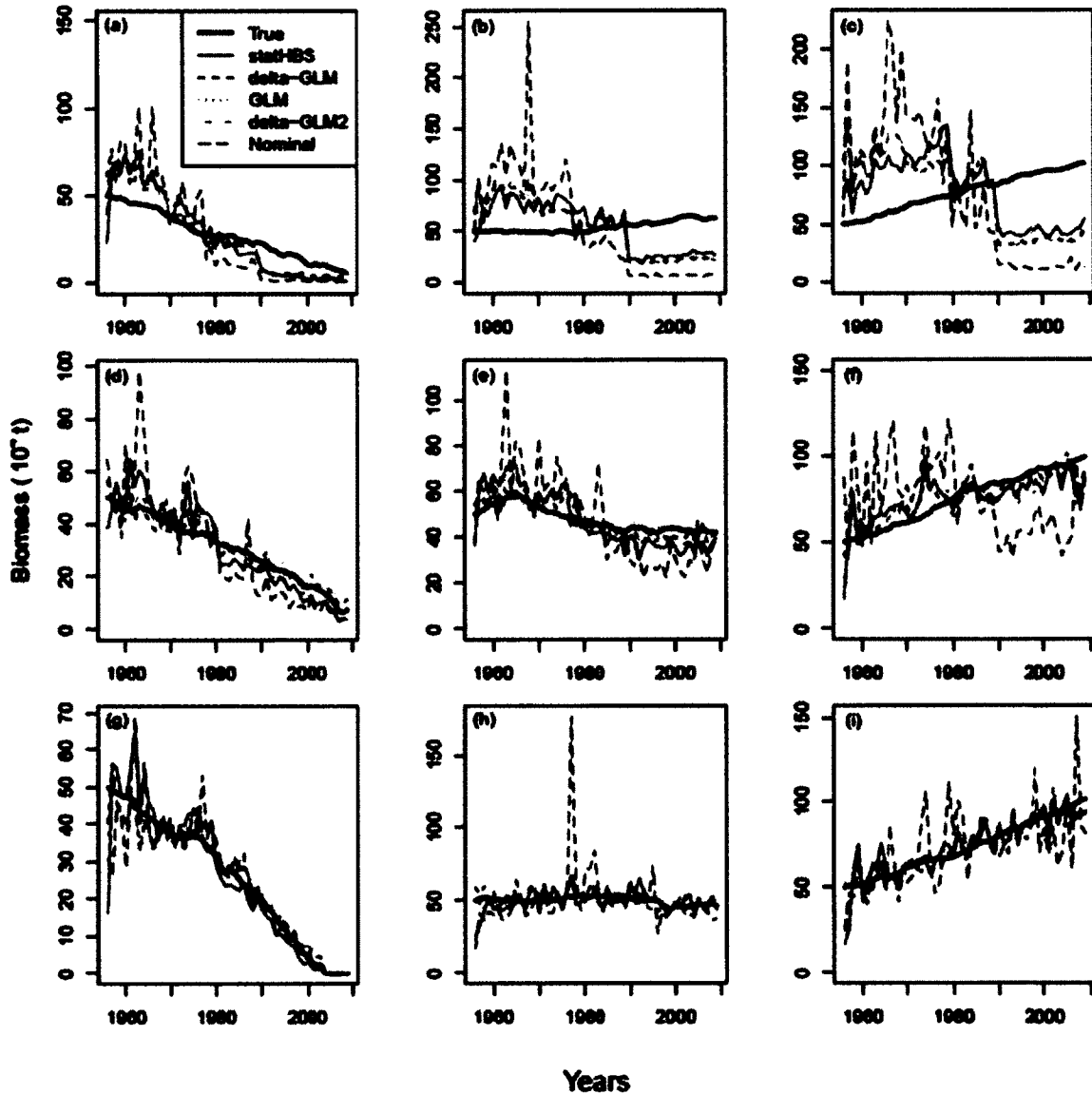


Fig. 7. Simulated 'true' biomass plotted against annual biomass from five approaches to estimating an index of abundance. Results are highlighted for nine selected simulation scenarios where vertical catchability was assumed to peak in surface (a-c), intermediate (d-e), or deep waters (g-i), and the known biomass trajectory was either decreasing (a, d, and g), stable (b, e, and h), or increasing (c, f, and i) over time.

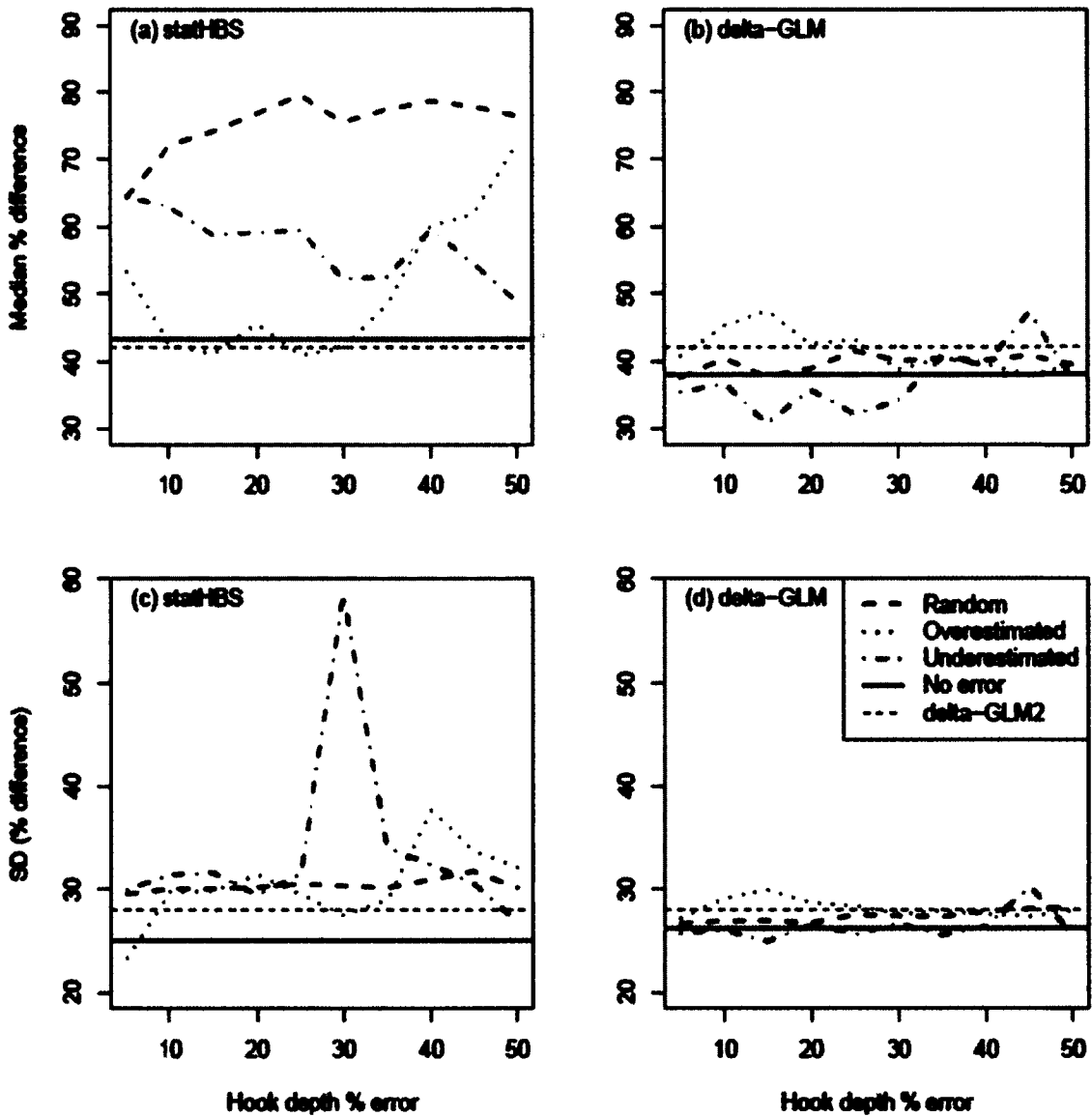


Fig. 8. Sensitivity plots for statHBS and a delta-GLM with an effect for habitats fished. These plots characterize the effect of hook depth uncertainty on the median percent difference between estimated and simulated biomass (a and b), and the standard deviation (SD) of the percent differences (c and d). The percent of error in estimated hook depth was applied as either overestimated (blue), underestimated (green), or with random directionality (black). The solid red line represents the result with no error in estimated hook depth, and the dashed line represents the result for a delta-GLM without an effect for habitats fished.

## CHAPTER 3

### Trends in abundance of highly migratory species in the Atlantic Ocean

## ABSTRACT

Declining populations of highly migratory species (HMS) have served as evidence of a global fisheries crisis. However, abundance trends have mostly been inferred from fishery catch rates, which are inherently biased. While many biases are accounted for through traditional catch rate standardization, habitats are often not directly considered. Using a method that explicitly accounts for habitats fished, we estimated abundance trends for 35 HMS in the Atlantic Ocean from 1987 through 2010. This represents one of the largest studies of HMS community dynamics. Overall, most populations appear to have declined over time with current abundances of roughly 76% of HMS analyzed at less than half of their 25-year observed maxima. However, 26% of the species exhibited signs of population growth, and in some cases, recovery. By including habitat in our analyses, we observed habitat effects on fishery catch rates; thus, our results can help guide management regulations aimed at reducing incidental catch of certain species, by avoiding the habitats in which these species catch rates were highest. Furthermore, we provide our abundance indices to facilitate their incorporation in fisheries stock assessments.

## 1. INTRODUCTION

Indices of abundance are necessary inputs for most fisheries stock assessment models. Within assessments, indices are treated as ‘observed’ abundance trends, thereby giving them substantial influence over assessment results. Unfortunately, abundance indices for highly migratory species (HMS) are not obtained through comprehensive, scientifically designed, monitoring programs (due to the high cost of implementation), but rather from fishery-dependent catch and effort data. This poses a considerable challenge to estimating an accurate index of abundance, because fisheries continually change their fishing practices in response to various socioeconomic drivers. It is common to assume that fishery catch rates are proportional to stock abundance, but 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 exhibited numerous changes in fishing practices over time, including changes in gear configurations, target species, and the spatiotemporal distribution of effort (Majkowski 2007). Although contemporary approaches to estimating indices of abundance for HMS do account for changes in fishing practices, ocean conditions are variable and 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 indices of abundance for HMS, it is important to consider habitats exploited (e.g., temperature regimes) in addition to fishing practices.

For longline fisheries, the incorporation of environmental information is not straightforward and is often not done in practice, primarily because estimates of fishing depth and environmental conditions at depth are required. It is notoriously difficult to estimate longline fishing depths with accuracy (Ward and Myers, 2006; Rice et al., 2007). Furthermore, environmental conditions at a given depth, time, and location are typically not recorded, and can only be estimated through interpolation from a global ocean database.

Despite the challenges associated with considering environmental information when estimating an index of abundance for HMS, it has been shown that this information can improve the accuracy of the index (Lynch et al., 2012). In fact, Lynch et al. (2012) proposed a method for incorporating habitat information using a delta generalized linear model (delta GLM) and found this approach to be relatively insensitive to errors in estimates of longline fishing depths. This is contrary to other index estimation methods that incorporate habitat, including 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 been shown to be highly sensitive to model inputs, such as estimates of longline fishing depth (Goodyear, 2003; Lynch et al., 2012).

For stock assessments of Atlantic HMS, we are unaware of any occasions where the abundance indices used in the assessment incorporated detailed habitat information. Here, we incorporate habitats fished into a delta GLM analysis of fisher logbook data from the US pelagic longline fishery (USLL) and derive new indices of abundance for a suite of HMS in the Atlantic Ocean. In general, indices of abundance for species caught in the USLL are generated 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). With the exception of our consideration of habitats fished, we estimated indices following the approach used by the SCRS (e.g., Walter, 2011). Walter (2011) provided indices of abundance for yellowfin tuna (*Thunnus albacares*), and we followed this

framework, not because yellowfin tuna represent a particularly strong candidate for incorporating habitat information, but rather because the framework reflects the contemporary approach used by the SCRS. Hence, we reduced confounding due to methodological differences, and our evaluation of the importance of including habitats fished is more robust.



## 2. METHODS

### 2.1. Fishery data

Indices of abundance were generated for 35 HMS<sup>2</sup> routinely caught by the US pelagic longline fishery (Table 1). Fisher logbook data for the US pelagic longline fishery were obtained from the National Marine Fisheries Service (NMFS) on November 21, 2011. The logbook database includes set-specific information, including catches (numbers of individuals), effort (number of hooks), gear configurations, dates, times, and spatial locations (Fig. 1). The primary target species of the US pelagic longline fishery include swordfish (*Xiphias gladius*), yellowfin tuna, and bigeye tuna (*Thunnus obesus*). Other features of this fishery have been described in detail by Hoey and Bertolino (1988).

Truncation of the dataset followed the restrictions imposed by Walter (2011). For instance, the logbook program began in 1986, but data for 1986 are incomplete; thus, our analyses used data from 1987 to 2010. Longline sets with fewer than 100 hooks in a set were excluded, and vessels that caught 10 or fewer individuals over the time series were excluded. Any records with incomplete catch, effort, time, or geographical information were removed, and records with more than one fish per hook were removed. Furthermore, sets occurring in areas that have been closed due to management restrictions, either before or after closure, were excluded. The time-area closures affecting the USLL were described in detail by Walter (2011). Finally, any sets occurring outside the regions commonly used in analysis of USLL data were not used.

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<sup>2</sup> There were two species groups included in the analyses (spearfish and hammerhead sharks). We use 'HMS' and 'species' throughout to collectively refer to individual species and species groups.

To estimate habitats fished, detailed longline gear information is required. Therefore, the indices that included habitat information required further data truncation. The main components of the longline gear used for estimating fishing depths include mainline length, the number of hooks between floats (HBF), branchline (or gangion) length ( $b$ ), and floatline length ( $f$ ) (see Maunder et al., 2006 for a description of these components). There were clear errors in the database associated with each of these components, and there were records that did not include data for one or more of the components. Thus, we excluded records where measurements of the gear components were either not reported, or fell within the upper or lower 0.5% quantiles of the data. For occasions where habitat information was not included in the analyses, the aforementioned data truncation procedure was used (Walter 2011).

## *2.2. Oceanographic data*

In addition to estimating fishing depth from longline gear information, estimates of habitats fished required detailed oceanographic data. We designated temperature regimes as habitats; therefore, we assigned each longline set a fixed temperature-at-depth profile. Ocean temperature profiles were obtained from the National Oceanographic Data Center<sup>3</sup> 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 to 1500 m over variable increments. For the rare instances where temperature profiles were not available for a given combination of geographical location and month, the set record was removed entirely.

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<sup>3</sup> [www.nodc.noaa.gov](http://www.nodc.noaa.gov): data accessed December 1, 2011.

### 2.3. Habitat variable

Incorporation of detailed habitat information requires estimates of longline fishing depths and corresponding estimates of temperature-at-depth (Lynch et al., 2012). Longline fishing depth (in meters) of hook  $j$  ( $d_j$ ) for  $j = 1$  to HBF was estimated using catenary geometry according to the following relationship (Bigelow et al., 2006; Yoshihara, 1951; 1954):

$$d_j = b + f + 0.5\ell \left\{ \left( 1 + \cot^2 \varphi \right)^{\frac{1}{2}} - \left[ \left( 1 - 2 \frac{j}{(\text{HBF} + 1)} \right)^2 + \cot^2 \varphi \right]^{\frac{1}{2}} \right\} \quad (1)$$

where  $\ell$  is the length of the mainline between floats, and  $\varphi$  is the angle between the horizon and the tangent of the mainline where it attaches to the floatline. We calculated  $\ell$  as the ratio of total mainline length to the number of panels fished, which was determined as the ratio of the total number of hooks fished in a set to HBF. There was insufficient information in the logbook database for estimating  $\varphi$ ; therefore, we used the average values reported by Bigelow et al. (2006). For shallow sets (2 – 6 HBF) we set  $\varphi$  to 56.40°, for deep sets (20+ HBF)  $\varphi$  was the average (61.45°) of the two deep fishing methods analyzed by Bigelow et al. (2006), and for intermediate sets (7 – 19 HBF) we averaged the deep and shallow set values (58.93°). Additionally, we corrected estimated fishing depths by the percent of shoaling of the longline gear using the following quadratic equations (Bigelow et al., 2006):

$$\% \text{ shoal} = \begin{cases} -36.562 + 0.9958d_j - 2.331 \times 10^{-3}d_j^2 & \text{for HBF} < 7 \\ -254.104 + 1.784d_j - 3.473 \times 10^{-3}d_j^2 + 2.184 \times 10^{-3}d_j^3 & \text{for HBF} > 19 \end{cases} \quad (2)$$

When  $HBF = 7$  to  $19$ , we averaged the components of Eq. (2), and when these equations resulted in estimates outside the range observed by Bigelow et al. (2006), the minimum or maximum value was used (0% or 87%, respectively).

Fishing depths for each longline set were then 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  $1^\circ$  increments relative to surface temperature in the corresponding time/space. The maximum deviation from sea surface temperature ( $Max\Delta T$ ), or deepest, coldest habitat fished, was then assigned to each longline set as a single value ( $0^\circ, \dots, 15^\circ$  C) characterizing the habitat fished for that set. In a simulation study based on the fishing dynamics of the Japanese longline fishery in the Atlantic Ocean, this variable was shown to improve the accuracy of indices of abundance for HMS (Lynch et al., 2012). The Japanese longline fishery however, has exhibited substantial changes in fishing techniques over its long time series, resulting in considerable contrast in  $Max\Delta T$  over time. The time frame for USLL logbook data is short by comparison, and gear configurations have been relatively consistent over the time series. This may limit the importance of  $Max\Delta T$  since minimal contrast would be expected for this variable. Thus, in addition to  $Max\Delta T$ , we evaluated a habitat variable that characterized each longline set as the minimum temperature fished ( $MinT$ ) in that set. This variable was specified as categorical with  $5^\circ$  temperature bins from  $1^\circ$  C to  $30^\circ$  C. While  $Max\Delta T$  directly accounts for the vertical distribution of the species being analyzed,  $MinT$  accounts for the distribution of the species spatially, as well as vertically.

#### *2.4. Other variables considered*

A suite of additional explanatory variables was also considered in the analyses. These variables were modeled as categorical factors, and included Year (year in which the set occurred), Region (nine geographical regions commonly used by to classify the longline fishery: Fig. 1), Season (calendar quarters: January – March, April – June, July – September, October – December), Lightstick (the number of lightsticks per hook categorized with four levels: 0, >0 – 0.4, >0.4 – 0.7, >0.7), 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 in the US pelagic longline fishery (Walter, 2011).

### *2.5. Index estimation*

We used a two-stage delta GLM approach to estimating indices of abundance (Aitchison, 1955; Lo et al., 1992; Maunder and Punt, 2004; Stefánsson, 1996; among others). Accordingly, each index of abundance was determined by combining two GLMs, one of which modeled the presence/absence of a particular species as a linear function of explanatory variables, assuming a binomial error distribution (logit link function). The second GLM modeled catch-per-unit-effort (CPUE), calculated as numbers of individuals caught in a set per 1000 hooks. For this GLM, 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 modeled as fixed effects, with the exception of interaction terms that included the variable Year, which were modeled as random effects.

Annual estimates of abundance were obtained by multiplying the probability of a positive catch rate 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). Standard errors of the annual abundance estimates were calculated using the delta method (Lo et al., 1992; Seber, 1982).

## *2.6. Model selection*

Selection of explanatory variables and interaction terms for the binomial and lognormal GLMs was based on the percent of overall deviance explained by the addition of each variable and the corresponding first-order interaction terms (Ortiz and Arocha, 2004). In maximum likelihood estimation, deviance is essentially the equivalent of sum of squares. This approach to model selection was employed by Walter (2011) and has been used to generate indices of abundance for numerous HMS in the Atlantic Ocean. By incorporating our habitat variables (Max $\Delta$ T, MinT) into the established approach to model selection, we evaluated the importance of these variables relative to other variables commonly considered in these analyses.

Typically, the statistical significance of each variable is considered in addition to the percent of the deviance explained (Ortiz and Arocha, 2004). However, we focused exclusively on percent deviance explained and only included variables or interactions that explained at least five percent (terms explaining this much deviance were always statistically significant). Percent deviance explained was calculated for each term as the decrease in deviance due to the addition of the term divided by the difference between the null model and the full model (Ortiz and Arocha, 2004). The null model only included the overall mean, and the full model included all variables and interaction terms that converged on a statistical solution (in our analyses interaction terms were evaluated individually to avoid convergence issues). For model selection, all variables and interaction terms, including interactions with

Year, were evaluated as fixed effects. Interactions with Year were only modeled as random effects when these terms were included in models used to generate indices of abundance (see Section 2.5). There were a few occasions where the selected model would not converge on a solution. This was mostly due to the models being rank deficient, and in these instances, all interaction terms were modeled as random effects.

### 2.7. Index comparison

In addition to evaluating the importance of including habitat information (Section 2.6), we used the selected models to generate indices of abundance for numerous HMS in the Atlantic Ocean. For several species, these may be the first ever estimated indices of abundance. For species previously analyzed, we compared our proposed indices to those most recently generated.

All abundance indices were standardized to their respective means for making species-specific comparisons. Visual comparisons were conducted using overlay plots for each species. Also, two metrics were used to characterize the relative difference between two indices, and the variability in the relative differences over time. The percent difference (% $D$ ) between any two indices ( $I_1, I_2$ ) in year  $y$  was calculated as (Lynch et al. 2012):

$$\%D_y = \frac{100 \left| \left( I_{1,y} / \sqrt{I_{1,y}} \right) - \left( I_{2,y} / \sqrt{I_{2,y}} \right) \right|}{I_{1,y}} \quad (3)$$

The median of the percent differences (MPD) was calculated to characterize the magnitude of the relative difference between indices, and the standard deviation (SDPD) was used to describe variability.

While our analytical approach is nearly identical to that used for yellowfin tuna (Walter, 2011), there may be small differences that confound the evaluation of the importance of the habitat variables. For instance, our analyses were conducted with the statistical programming language R (R Development Core Team, 2011) and Walter (2011) used SAS® (Littell et al., 1996; SAS Institute Inc, 1997). Also, we followed the approach to data truncation described by Walter (2011), but the original logbook data obtained may not be identical between studies. Therefore, to observe the potential effects of differences between studies, direct comparisons were made between analytical approaches and data truncation for yellowfin tuna, specifically.



### 3. RESULTS

Catch records for yellowfin tuna were used as a case study to evaluate our analytical approach as compared to that used by Walter (2011). Very slight differences between indices were observed between identical model structures and approaches to data truncation (Fig. 2a). These small differences may be attributed to differences between statistical packages (R versus SAS), or to slight discrepancies between data analyzed since logbook data were obtained at different times for the two studies, and the total number of records analyzed may not be consistent. Because the differences were minimal (MPD = 0.04, SDPD = 0.02) we are confident that meaningful comparisons can be made with previous indices generated from this dataset. Another comparison using yellowfin tuna suggested that removing additional records to generate detailed habitat variables (MinT, Max $\Delta$ T) had almost no effect (MPD = 0.01, SDPD = 0.01) on estimates of relative abundance (Fig. 2b). Also, the inclusion of MinT in the delta GLM minimally affected (MPD = 0.03, SDPD = 0.01) the index for yellowfin tuna (Fig. 2c). This is not a surprising result, because yellowfin tuna was the only species analyzed that was not a good candidate for including this variable (see below).

The detailed habitat variables MinT and Max $\Delta$ T were estimated for each longline set using information on longline gear configurations and local oceanographic conditions. The number of HBF is thought to be an important factor governing fishing depth and therefore habitats fished (Ward and Hindmarsh, 2007). We calculated annual means and 95% confidence intervals for HBF, Max $\Delta$ T, and MinT (Fig. 3). With such a large number of records in the logbook database, the range observed for these variables was much larger than the 95% confidence interval, but the overwhelming majority of records exhibited minimal variation in gear configurations over time. Despite only slight changes, the trends of

increasing HBF, Max $\Delta$ T, and MinT are apparent. It is surprising that MinT has increased with HBF since larger HBF should result in deeper, colder habitats exploited. Increases in MinT may be explained by changes in the spatial distribution of the fishery, and/or changing oceanographic conditions over time, such as ocean warming. Also, several gear variables in addition to HBF (e.g., branchline and floatline lengths, mainline tension, weights, etc.) influence fishing depth (Ward and Hindmarsh, 2007).

A different number of records was analyzed for each of the 35 HMS included in this study (Table 1), because data from vessels that caught fewer than 10 individuals over the time series were excluded. Species with more catch records (after truncation) tended to have a higher probability of being captured (Fig. 4), but with the exception of swordfish and yellowfin tuna, there were fewer instances of positive catches than catches equal to zero. This suggests that most species we analyzed were rarely encountered by the fishery, which may limit the ability to make inferences about population trends over time.

A wide variety of model structures was selected for the binomial and positive catch models (Appendix A). According to our selection criteria (at least 5% of total deviance explained by the variable), one of our proposed detailed habitat variables (MinT) was selected for the binomial and/or positive models for almost every species (Fig. 4, Appendix A). This suggests that MinT may explain a substantial amount of the variability in the catch rates of target and incidentally captured species of the USLL. For certain species, MinT explained over 40% of the total deviance. In fact, the only species for which MinT was not selected for either model was yellowfin tuna, which may explain why there was minimal difference between indices with and without MinT for this species (Fig. 2).

In addition to MinT, we evaluated Max $\Delta$ T, which has been shown to be a potentially important explanatory variable when estimating indices of abundance using data from a pelagic longline fishery (Lynch et al. 2012). However, there were only two species (wahoo, *Acanthocybium solandri*, and blackfin tuna, *Thunnus atlanticus*) for which this variable

explained a sufficient percent of the total deviance (Fig. 4b), and in these cases, the percent explained was only slightly above the threshold for inclusion.

Estimates of MinT were not only useful for generating indices of abundance, but also for observing the influence of this variable on species-specific catch rates (Fig. 5). Encounter rates (proportion of positive CPUE) and median positive catch rates both exhibited variability across estimates of MinT. The highest encounter rates and median positive CPUE values were observed for swordfish and blue sharks (*Prionace glauca*) when the coldest habitats were fished. In fact, the highest overall median CPUE corresponded with blue sharks at approximately 50 sharks per 1000 hooks. The encounter rates of swordfish and yellowfin tuna (two important target species of this fishery) exhibited opposing gradients in response to MinT, with the highest rates for yellowfin tuna occurring when the warmest habitats were fished. Numerous other species-specific patterns emerged (Fig. 5).

The majority of our abundance indices exhibited declines over the time series (Fig. 6, Appendix A); however, the magnitude of change was highly variable. For instance, when comparing current relative abundances of the primary target species, swordfish and yellowfin tuna are just below 50% of their observed maxima, where bigeye tuna have declined by more than 75%. For many of the bycatch species, particularly the sharks, the declines were more severe. A few species may have increased in abundance over the time series, such as northern bluefin tuna (*Thunnus thynnus*), albacore (*Thunnus alalunga*), porbeagle (*Lamna nasus*), spearfish (*Tetrapturus spp*), and shortfin mako sharks (*Isurus oxyrinchus*). For the select species with previously generated indices of abundance, our estimates are mostly consistent with the historical patterns, and extend the time series to provide an update of recent population dynamics (Fig. 6). However, the patterns for swordfish and skipjack tuna (*Katsuwonus pelamis*) are not consistent. As a measure of precision, the median of the annual coefficients of variation (MCV) was calculated for each index (Fig. 6). According to MCV,

many of the indices were estimated with very poor precision (i.e.,  $MCV > 1$ ), suggesting that these particular trends should be interpreted with caution.

#### 4. DISCUSSION

In this study we estimated trends in abundance for 35 HMS using a novel approach to account for habitats fished. This represents one of the most comprehensive analyses of HMS to date, and for some species (e.g., many of the sharks and other infrequently encountered fishes) these are the first ever estimated trends in abundance. For other species (e.g. blue shark and porbeagle), abundance indices have not been estimated in several years; thus, our indices provide an update of recent population dynamics. The remaining species have been evaluated recently (e.g., bigeye tuna and yellowfin tuna), meaning our indices are more useful in a comparative sense. Overall, population declines of varying degrees were observed for most HMS analyzed. Excluding the species group hammerhead sharks (due to redundant representation), the current relative abundances of 26 of the 34 species (76%) are less than 50% of their observed maxima (over the 25 year period), and 18 species (53%) are currently less than 25% of their observed maxima.

Declines in abundance of large predatory fishes have been cited many times as evidence of a global fisheries crisis (Jackson et al., 2001; Myers and Worm, 2003; Myers et al., 2007; Worm et al., 2006; Baum et al., 2003; Ferretti et al., 2008). While these studies have garnered considerable attention from the media, general public, and scientific community, many have been criticized due to analytical flaws, some of which may have been critical (Walters, 2003; Burgess et al., 2005; Hampton et al., 2005; Polacheck, 2006; Wilberg and Miller, 2007). We have been careful to address many of the concerns over the use of fisheries data (particularly pelagic longline logbook data) to infer population trends. Assuming our results generally reflect patterns in abundance (to the degree possible given the manner in which data were collected), substantial declines were observed for many species;

however, a trend toward complete extirpation of large predators was not evident.

Approximately nine species (26%) exhibited evidence of population growth (recovery in some cases) over the past several years, including northern bluefin tuna, albacore tuna, blackfin tuna, blue shark, porbeagle, tiger shark (*Galeocerdo cuvier*), spearfishes, escolar (*Gempylidae spp*), and shortfin mako shark. While our results show that many HMS may be at or approaching critically low population levels, the observed increases suggest that either the purported demise of marine predators was overly pessimistic, or several species began to rebuild since the earlier studies were conducted (we suspect both explanations to be true).

The range of abundance patterns observed in this study support the conclusions of Worm et al. (2009), who, in a comprehensive analysis of global fish stocks, described a combination of overexploited and recovering marine ecosystems.

The data used for our analyses is perhaps one of the best sources for making inferences about HMS population dynamics in the Atlantic Ocean (Baum et al., 2003). Given the vast distributions of HMS and the historical development of high seas fisheries, analysis of HMS populations is most robust using observations over a large spatial and temporal range (Uozumi, 2003). There are no independent scientific monitoring programs that have collected data on this scale; therefore, fishery-dependent sources may represent the best available information for capturing long-term changes in HMS abundance. Pelagic longline fisheries typically cover a wide geographic range, and they have been fishing 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) represent the most valuable sources of data for evaluating HMS dynamics; however, to account for changing fishery dynamics, information about fishing practices must be available. When recorded, this information is usually considered proprietary, and therefore can be difficult to obtain. We analyzed fisher logbook data from the USLL, which includes detailed set-specific information concerning fishery dynamics. When compared with the fisheries from Japan or Taiwan, the spatial and temporal

coverage of the USLL is limited. For instance, the first complete year of logbook records was 1987; meaning relative abundance in the first year of our time series may represent an abundance that has already been reduced following years of intense fishing pressure.

Despite efforts to account for factors that may have biased our results, a reliance on fishery-dependent data warrants a cautious interpretation of abundance trends. In a simulation study, Lynch et al. (2012) showed that, under certain scenarios, even when accounting for all potential sources of bias, the best performing model still may poorly estimate the true pattern in abundance. In general, comprehensive stock assessments (Quinn and Deriso, 1999) that incorporate multiple sources of information provide a more complete evaluation of fish stock dynamics. These types of analyses have not been conducted on many of the species we evaluated; thus, our results serve as best available characterizations of abundance trends. For the few species that have been assessed, management decisions should be (and are) based on assessment results rather than a single index of abundance; however, our indices have the advent of adjusting for exploited habitats and may be useful in future stock assessments.

Abundance trends previously estimated using fisher 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). In general, our abundance trends closely follow those previously estimated for stock assessments, and they extend the estimates beyond the final year of the earlier time series. We observe that previous population trajectories have continued for many species, while the direction of others has reversed (mainly those that are exhibiting signs of population growth). The abundance trends estimated for swordfish and skipjack tuna are clearly in contrast with previous estimates. We show a declining, rather than stable swordfish abundance over time, and we did not observe a sudden increase in skipjack tuna abundance as previously shown.

When comparing and evaluating abundance trends for individual species, the population biology and fishery data collection for that species should be considered. For

instance, previous estimates of abundance for swordfish used fishery weigh-out data to estimate 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. Furthermore, important considerations have been documented (Burgess et al., 2005) concerning the use of logbook data from the USLL to make inferences about the abundance of sharks (these concerns may not apply to blue and shortfin mako sharks). Misidentification, errors in reporting, and failure to record bycatch species contribute significant errors to the logbook database. 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 (*Carcharodon carcharias*), the error may be substantial enough to make our abundance trends uninformative (most recorded white shark catches are likely the result of misidentification; Burgess et al., 2005). While many of the criticisms by Burgess et al. (2005) concern the presence of random error in the logbook data, they discussed regulatory changes in 1993 that highlight a sudden change in shark reporting requirements. In response to the U.S. Atlantic Shark Management Plan (NMFS 1993), fishers in the directed shark fishery adopted a new logbook system. This migration may have removed fishers that were more likely to record shark catches from the logbook database we used, resulting in a false decline in catch rates starting in 1993; however, many of the shark species we analyzed exhibited declines before 1993. Overall, we maintain that our estimates of HMS abundance trends can be useful in an assessment and management context; however, we encourage critical evaluation of the applicability of our methods at the species-specific level.

Catches observed in relation to the MinT habitat variable (Fig. 5) highlight the expected result that, for a given longline set, the respective target species do not have equal probability of capture. Consequently, the habitats exploited (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 habitat variable in models designed to estimate indices of abundance. Furthermore, the incorporation of a habitat variable allows a post-hoc evaluation of the role of habitat on catches of HMS. For instance, blue sharks exhibited a higher probability of encounter when cooler habitats were fished. This is not necessarily surprising (see Cortes 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, fishery managers could use this information to impose restrictions 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 for all species analyzed.

The lack of importance of  $\text{Max}\Delta T$  may be unexpected considering the results of the simulation study conducted by Lynch et al. (2012); however, their 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 habitats exploited. The USLL has not exhibited systematic changes in fishing practices over the time period we analyzed, causing  $\text{Max}\Delta T$  to be relatively consistent (Fig. 2). This does not suggest that relative temperature is not an important factor governing the population dynamics of HMS, but rather that the minimal contrast in  $\text{Max}\Delta T$  precludes it from explaining considerable variability in USLL catch rates.

Many of our indices of abundance were not estimated with great precision, suggesting these indices be interpreted with caution. However, in addition to index precision, there are other concerns that warrant attention. For instance, our methodology was based on a commonly used approach described by Walter (2011) to facilitate the comparison of indices that consider habitats fished, but the approach itself is not evaluated in this study. In fact, the use of percent deviance for variable selection in these models may be unreliable for selecting

the most accurate model (Lynch et al. 2012). Furthermore, due to data limitations, estimates of habitats fished ignored potentially important sources of variation. By setting  $j = 1$  to HBF in Eq. (1), we made the assumption that in each longline set, 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 behavior of hooked organisms (Bigelow et al., 2006; Rice et al., 2007; Ward and Myers, 2006). Also, by relating fishing depth to temperature using average ocean temperatures we ignore interannual variability in temperature-at-depth for a given time/location. Finally, following the approach to data truncation used for yellowfin tuna, indices were estimated for each species using data from all times and areas available (with the exception of the closed areas). This comprehensive use of data may be appropriate for many HMS; however, unique considerations may be warranted for certain species. For example, previous indices of abundance for northern bluefin tuna from the USLL restricted the logbook data by only using records from the Gulf of Mexico during January to May (Cass-Calay, 2010). Many of the indices generated herein may be useful in a stock assessment context; however, species-specific considerations regarding distributions, population structure, and other treatments of the data should be taken into account.

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TABLES

Table 1. Species for which indices of abundance were generated using fisher logbook data from the U.S. pelagic longline fishery with corresponding species codes, and the number of records analyzed (out of a total of 292717) after removing records from vessels that caught less than ten individuals of a given species over the time period.

Species	Species code	Records analyzed	Species	Species code	Records analyzed
Swordfish <i>Xiphias gladius</i>	SWO	228596	Silky shark <i>Carcharhinus falciformis</i>	FAL	146503
Yellowfin tuna <i>Thunnus ablacares</i>	YFT	227784	Dusky shark <i>Carcharhinus obscurus</i>	DUS	144651
Dolphinfish <i>Coryphaena hippurus</i>	DOL	225738	Bigeye thresher <i>Alopias superciliosus</i>	BTH	140491
Bigeye tuna <i>Thunnus obesus</i>	BET	214539	Thresher <i>Alopias vulpinus</i>	ALV	137453
Wahoo <i>Acanthocybium solandri</i>	WAH	205132	Blacktip shark <i>Carcharhinus limbatus</i>	CCL	133756
Blue marlin <i>Makaira nigricans</i>	BUM	197412	Sandbar shark <i>Carcharhinus plumbeus</i>	CCP	117581
Alabacore tuna <i>Thunnus alalunga</i>	ALB	197216	Oceanic whitetip shark <i>Carcharhinus longimanus</i>	OCS	104673
Northern bluefin tuna <i>Thunnus thynnus</i>	BFT	195301	Spearfishes <i>Tetrapturus spp</i>	SPR	87513
White marlin <i>Kajikia albida</i>	WHM	194581	Skipjack tuna <i>Katsuwonus pelamis</i>	SKJ	85775
Shortfin mako <i>Isurus oxyrinchus</i>	SMA	190713	Night shark <i>Carcharhinus signatus</i>	CCS	78335
Escolars <i>Gempylidae spp</i>	OIL	184821	Scalloped hammerhead <i>Sphyrna lewini</i>	SPL	74137
Longfin mako <i>Isurus paucus</i>	LMA	181633	Atlantic bonito <i>Sarda sarda</i>	BON	47246
Tiger shark <i>Galeocerdo cuvier</i>	TIG	177109	White shark <i>Carcharodon carcharias</i>	WSH	40442
Blue shark <i>Prionace glauca</i>	BSH	173251	Smooth hammerhead <i>Sphyrna zygaena</i>	SPZ	40025
Blackfin tuna <i>Thunnus atlanticus</i>	BLF	168514	Porbeagle <i>Lamna nasus</i>	POR	37076
Hammerhead sharks <i>Sphyrna spp</i>	SPN	161941	Bignose shark <i>Carcharhinus altimus</i>	CCA	33945
Sailfish <i>Istiophorus albicans</i>	SAI	150602	Spinner shark <i>Carcharhinus brevipinna</i>	CCB	32684
King mackerel <i>Scomberomorus cavalla</i>	KGM	12042			

## FIGURES

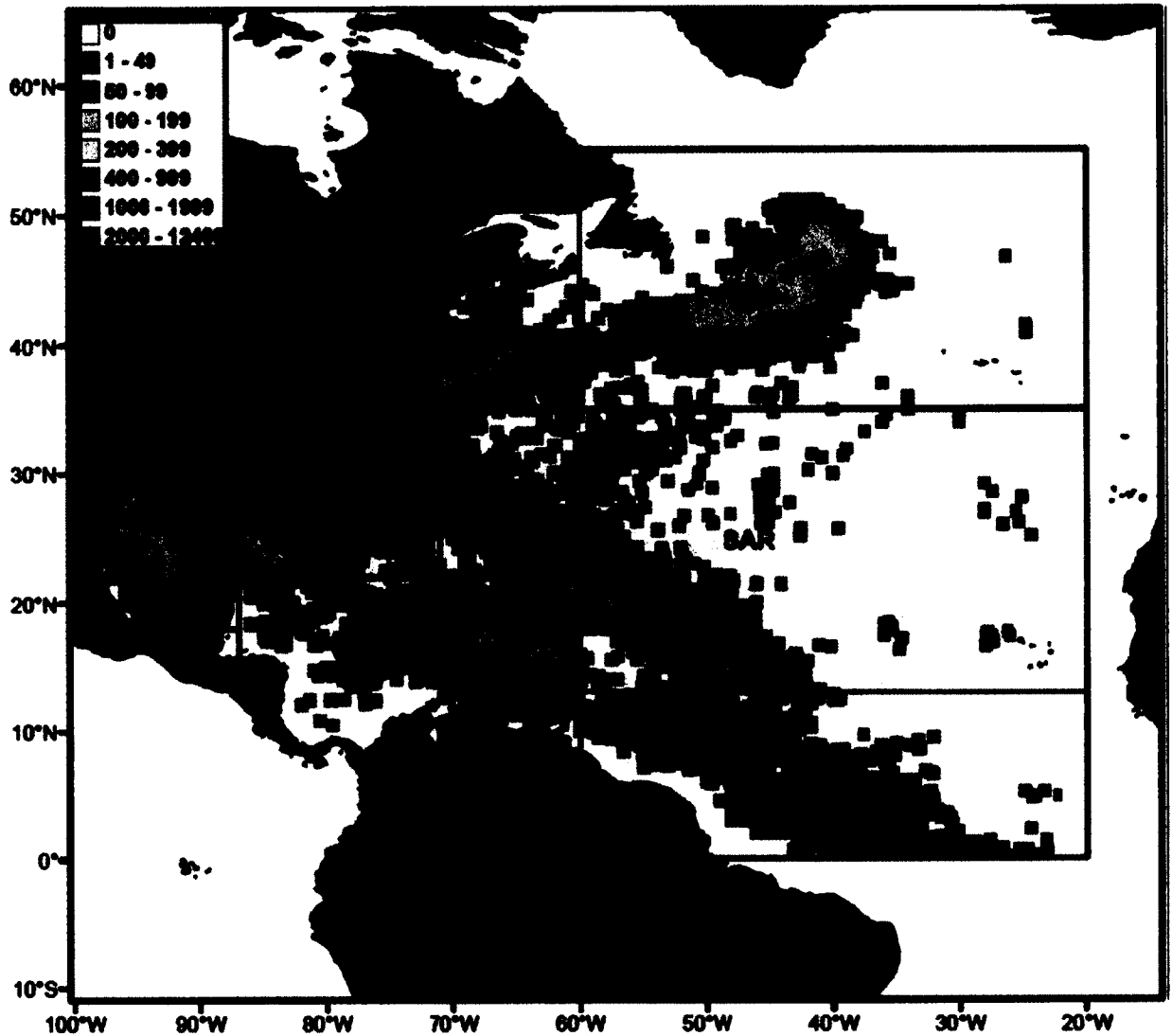


Fig. 1. Map of the distribution of longline sets (total number per cell) between 1987 and 2010 for the U.S. pelagic longline fishery in the Northwest Atlantic Ocean. The geographical regions used for classifying the fishery include the Caribbean Sea (CAR), Gulf of Mexico (GOM), Florida east coast (FEC),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



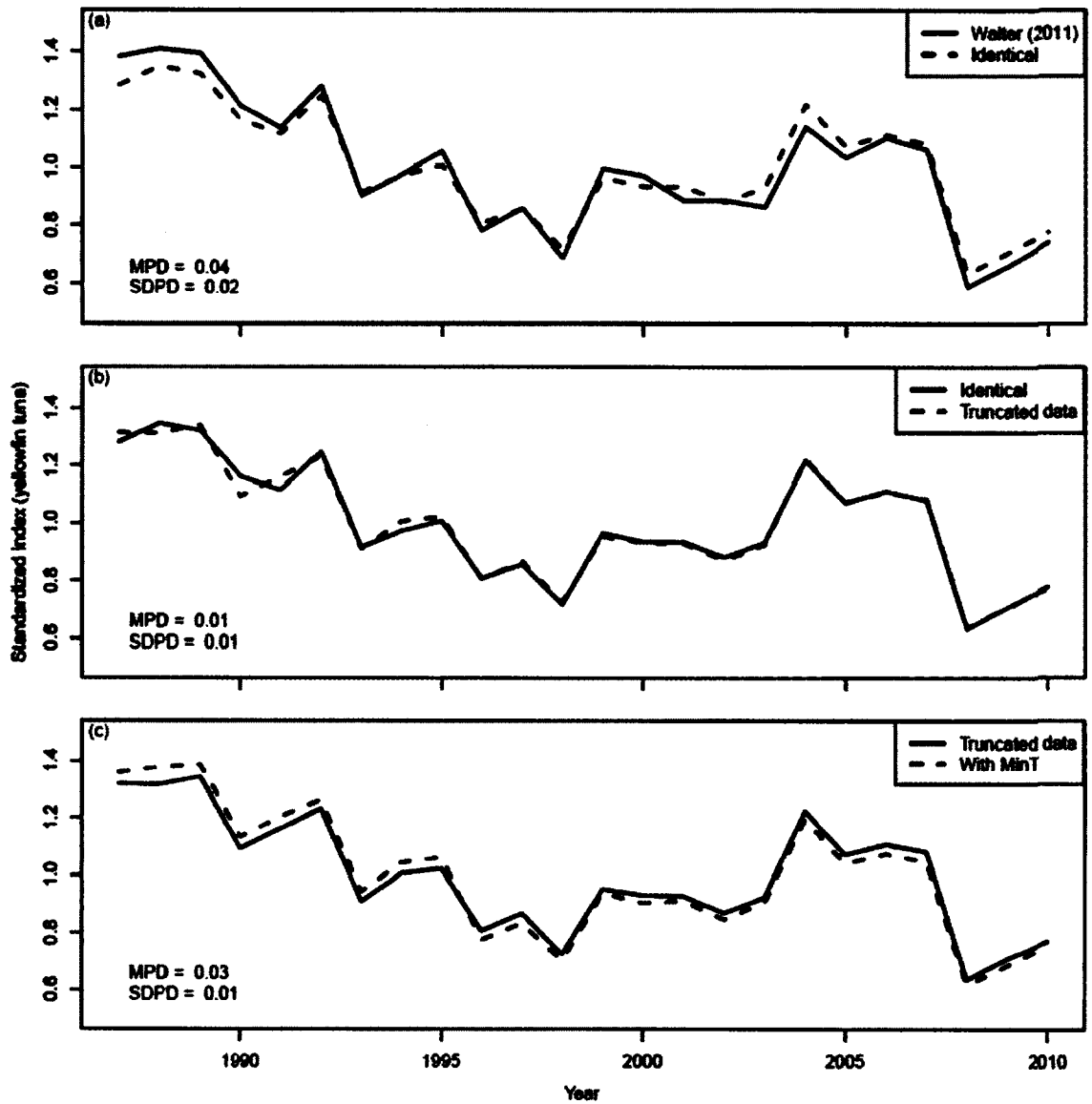


Fig. 2. Comparison between our approaches to data analysis and truncation, and those used by Walter (2011) to generate an index of abundance for yellowfin tuna. The standardized indices were compared between identical approaches (a), between an identical model structures but with further data truncation needed for calculating habitat variables (b), and between models with and without MinT (c). Median percent difference (MPD) and standard deviation of percent difference (SDPD) were calculated for each comparison.

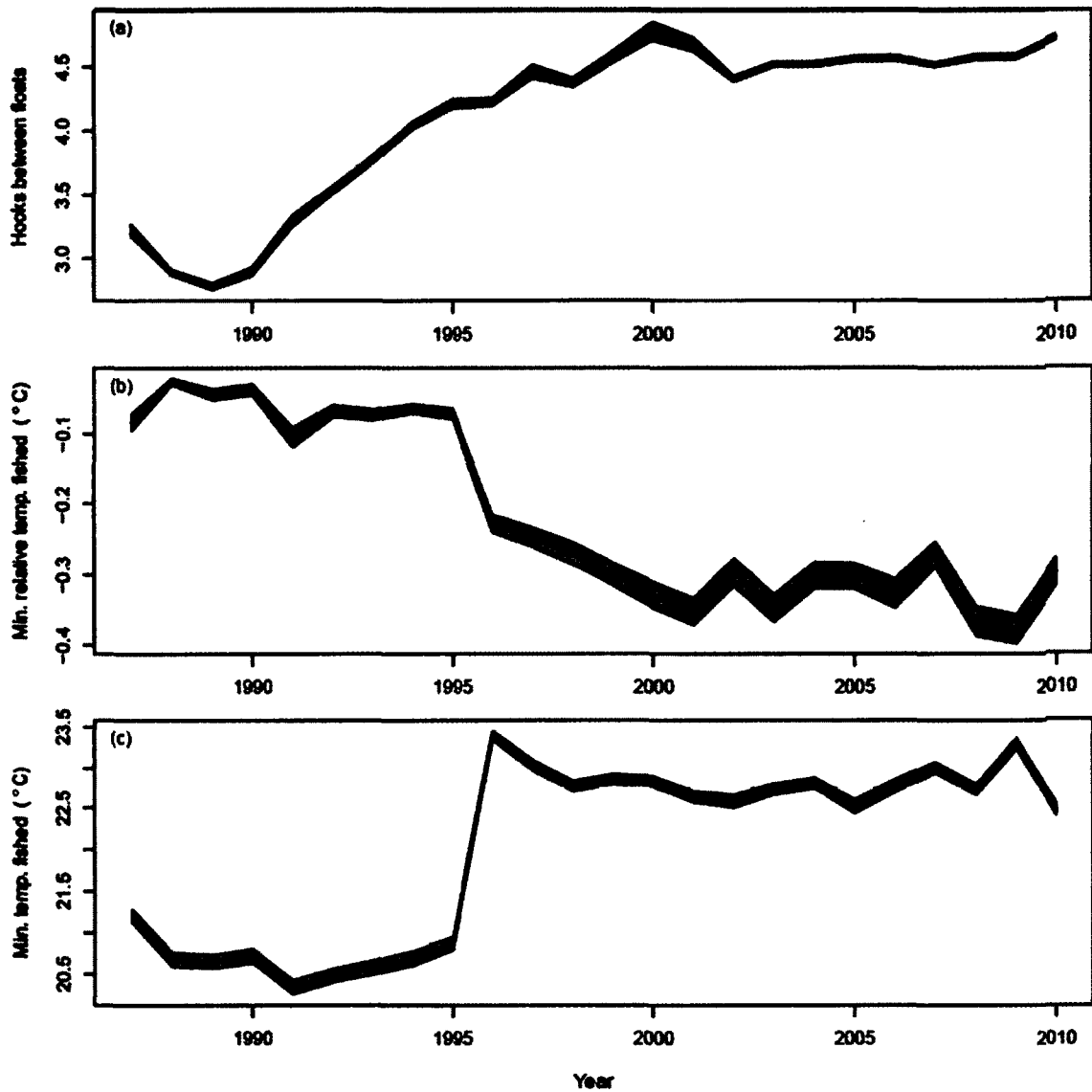


Fig. 3. Annual trends in the number of hooks between floats for the U.S. pelagic longline fishery (a), and estimated habitat variables including the minimum temperature relative to surface temperature ( $\text{Max}\Delta T$ ) fished per set (b), and the actual minimum temperature ( $\text{Min}T$ ) fished per set (c). The black line represents the mean and the grey area encompasses the 95% confidence interval.

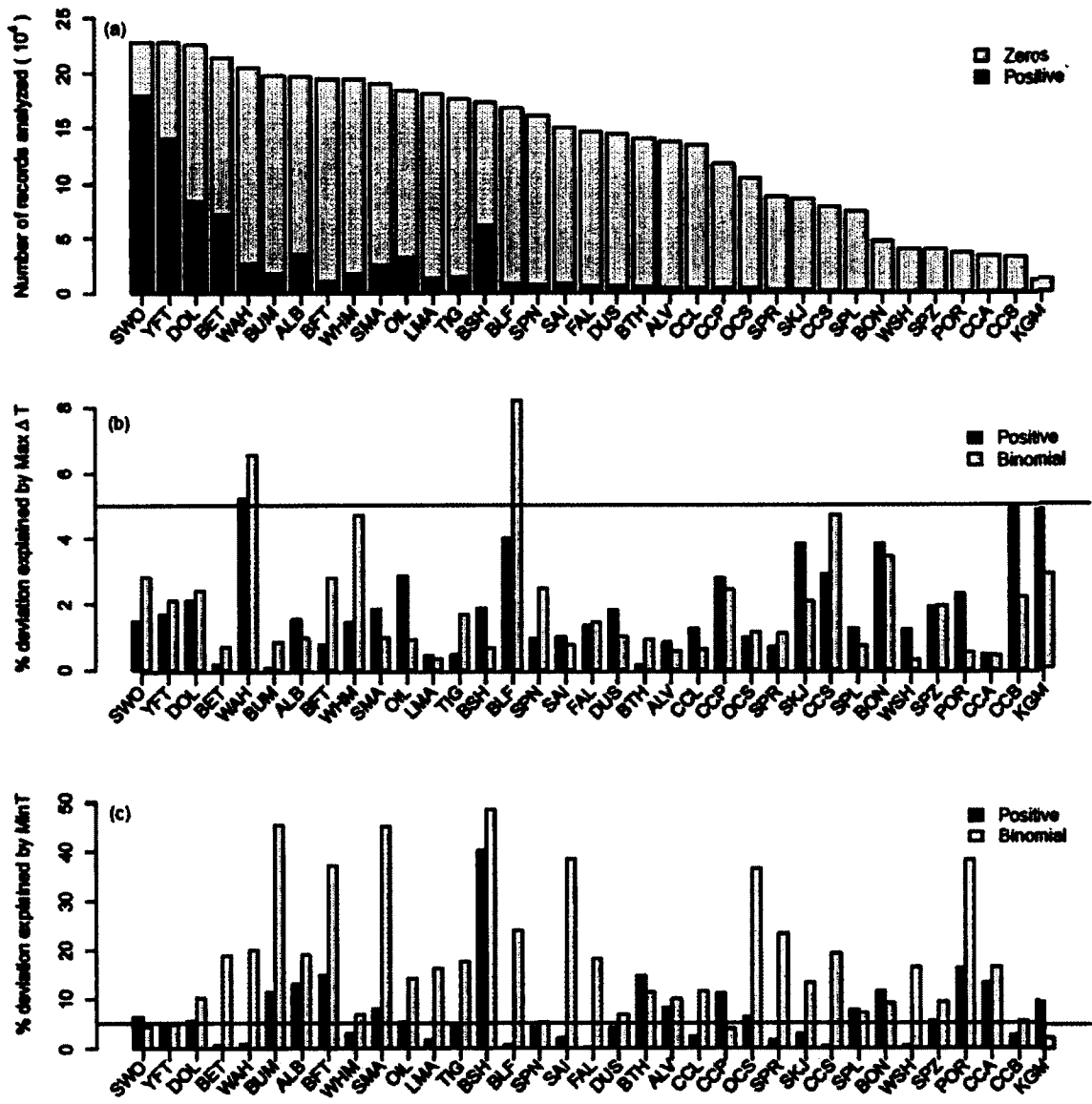


Fig. 4. Number of records analyzed (a), including proportion of positive catch records for species captured in the U.S. pelagic longline fishery (see Table 1 for definition of species codes). Also, the percent of the total deviance explained by the habitat factors Max $\Delta$ T (b), and MinT (c) for 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).

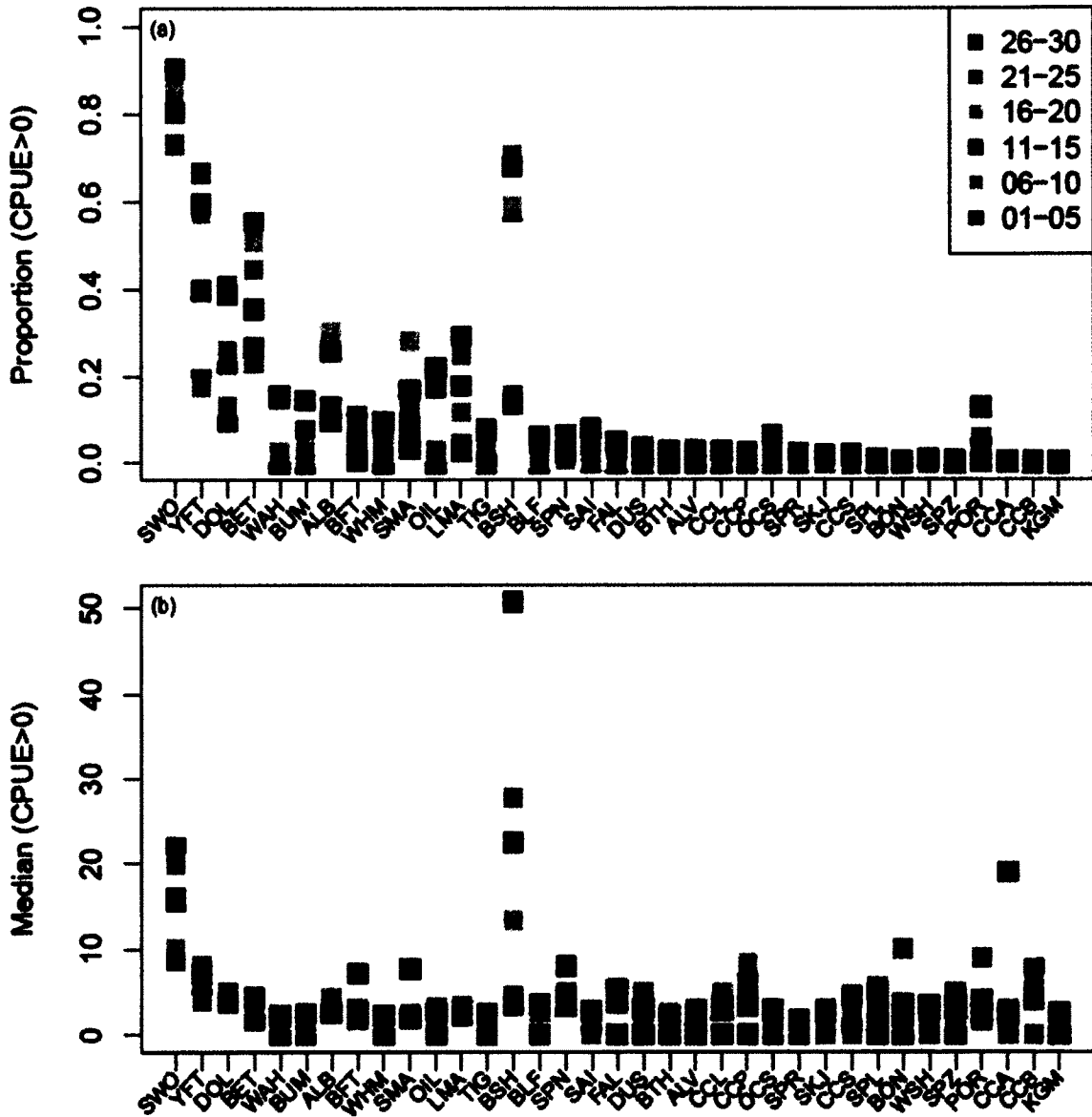


Fig. 5. Catch rates (CPUE) by species from the U.S. pelagic longline fishery (see Table 1 for definition of species codes), presented as the proportion of positive catches (a) and the median of the positive catches (b) observed in 5° C temperature bins corresponding with the estimated minimum temperature fished per set.

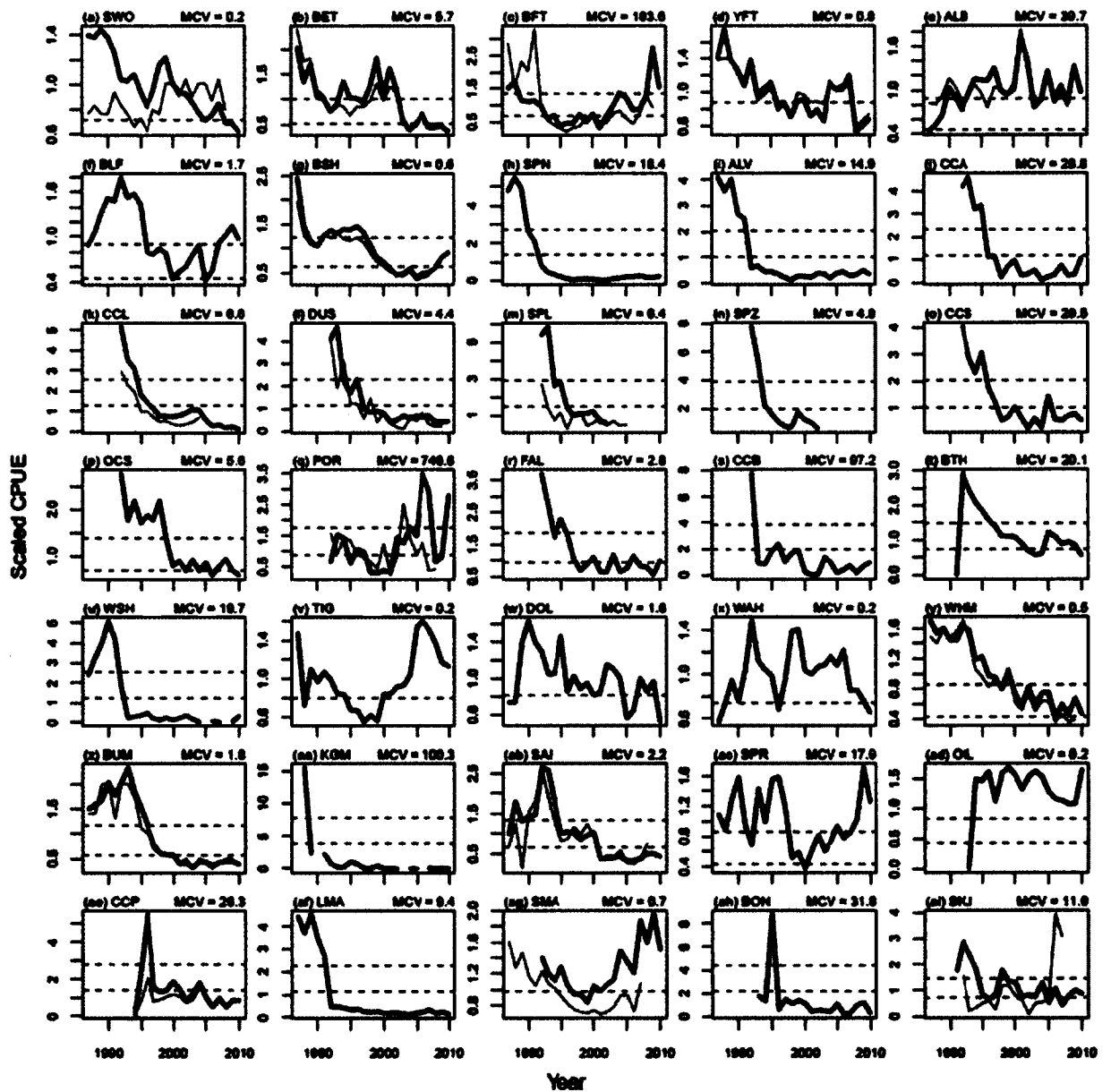


Fig. 6. Indices of abundance estimated for each species (see Table 1 for definition of species codes) using data from the U.S. pelagic longline fishery (black line), and indices estimated previously for select species (red line). Each index was scaled to its mean value, and the corresponding median of the annual coefficients of variation (MCV) was presented. Dashed lines represent 50% (top) and 25% (bottom) of observed maximum relative abundance.

APPENDIX A. INDICES OF ABUNDANCE

Table A1. Swordfish (SWO) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	8.867	1.699	1.399	0.192
1988	8.750	1.669	1.381	0.191
1989	9.162	1.741	1.446	0.190
1990	8.772	1.668	1.384	0.190
1991	8.011	1.522	1.264	0.190
1992	6.613	1.253	1.044	0.190
1993	6.537	1.240	1.032	0.190
1994	6.886	1.305	1.087	0.189
1995	6.028	1.141	0.951	0.189
1996	5.228	0.991	0.825	0.190
1997	6.010	1.139	0.948	0.190
1998	7.340	1.390	1.158	0.189
1999	7.759	1.471	1.224	0.190
2000	6.443	1.223	1.017	0.190
2001	5.964	1.133	0.941	0.190
2002	5.896	1.119	0.930	0.190
2003	5.437	1.037	0.858	0.191
2004	4.926	0.945	0.777	0.192
2005	4.528	0.862	0.715	0.190
2006	4.803	0.914	0.758	0.190
2007	5.376	1.030	0.848	0.192
2008	4.404	0.838	0.695	0.190
2009	4.385	0.837	0.692	0.191
2010	3.949	0.755	0.623	0.191

BFE: Year, Region, Time, Lightstick

BRE: NA

PFE: Year, MinT, Region, Lightstick

PRE: Year\*Region

Table A2. Yellowfin tuna (YFT) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	3.960	2.932	1.411	0.740
1988	4.913	3.259	1.751	0.663
1989	3.878	3.002	1.382	0.774
1990	3.566	2.755	1.271	0.773
1991	3.016	2.591	1.075	0.859
1992	3.905	2.756	1.391	0.706
1993	2.716	2.327	0.968	0.857
1994	2.936	2.475	1.046	0.843
1995	3.144	2.341	1.120	0.745
1996	2.390	2.016	0.852	0.843
1997	2.477	2.073	0.883	0.837
1998	1.988	1.776	0.708	0.893
1999	2.502	2.070	0.892	0.827
2000	2.559	2.023	0.912	0.790
2001	2.010	2.051	0.716	1.021
2002	2.218	1.768	0.790	0.797
2003	1.840	2.021	0.655	1.098
2004	3.093	2.606	1.102	0.842
2005	2.897	2.315	1.032	0.799
2006	2.908	2.366	1.036	0.814
2007	3.381	2.386	1.205	0.706
2008	1.497	1.515	0.533	1.012
2009	1.666	1.590	0.594	0.954
2010	1.899	1.702	0.677	0.896

BFE: Year, Region, Lightstick, Region\*Lightstick

BRE: Year\*Region

PFE: Year, Region, Time, Lightstick

PRE: Year\*Region

Table A3. Dolphinfish (DOL) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	1.534	3.766	0.740	2.455
1988	1.535	3.357	0.741	2.187
1989	2.887	4.439	1.393	1.537
1990	3.383	5.035	1.633	1.488
1991	2.896	4.081	1.397	1.409
1992	2.686	3.698	1.296	1.377
1993	2.169	3.424	1.047	1.579
1994	2.184	3.345	1.054	1.532
1995	3.040	4.190	1.467	1.378
1996	1.774	3.004	0.856	1.694
1997	2.134	3.513	1.030	1.647
1998	1.842	3.002	0.889	1.630
1999	1.974	3.160	0.952	1.601
2000	1.696	2.969	0.818	1.750
2001	1.766	2.956	0.852	1.674
2002	2.396	3.298	1.156	1.377
2003	2.296	3.418	1.108	1.489
2004	2.074	3.321	1.001	1.601
2005	1.164	2.345	0.562	2.014
2006	1.360	2.386	0.656	1.755
2007	2.077	3.128	1.002	1.506
2008	1.783	2.642	0.860	1.482
2009	2.013	2.872	0.971	1.427
2010	1.074	2.166	0.518	2.018

BFE: Year, MinT, Region, Season

BRE: Year\*Region, Year\*Season, MinT\*Region, MinT\*Season, Region\*Season

PFE: Year, MinT, Region, Season, Region\*Season

PRE: Year\*Region, Year\*Season



Table A4. Bigeye tuna (BET) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.693	2.781	2.027	4.014
1988	0.460	2.366	1.346	5.144
1989	0.578	2.338	1.692	4.042
1990	0.362	2.154	1.059	5.949
1991	0.345	2.007	1.010	5.816
1992	0.262	1.834	0.767	6.999
1993	0.302	1.918	0.883	6.353
1994	0.463	1.850	1.353	3.999
1995	0.353	1.716	1.031	4.866
1996	0.349	1.880	1.020	5.390
1997	0.323	1.815	0.944	5.626
1998	0.429	1.771	1.256	4.125
1999	0.625	2.229	1.829	3.566
2000	0.369	1.753	1.081	4.746
2001	0.553	1.916	1.618	3.464
2002	0.411	1.765	1.202	4.293
2003	0.195	1.458	0.570	7.486
2004	0.132	1.317	0.385	10.001
2005	0.173	1.387	0.505	8.034
2006	0.246	1.509	0.719	6.140
2007	0.151	1.316	0.441	8.726
2008	0.148	1.280	0.434	8.635
2009	0.162	1.286	0.473	7.964
2010	0.122	1.177	0.356	9.680

BFE: Year, MinT, Region, Season, Region\*Season

BRE: Year\*MinT, Year\*Region

PFE: Year, Region, Season, Region\*Season

PRE: Year\*Region

Table A5. Wahoo (WAH) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.733	0.149	0.570	0.203
1988	0.958	0.199	0.746	0.208
1989	1.226	0.250	0.954	0.204
1990	0.979	0.196	0.762	0.200
1991	1.339	0.225	1.042	0.168
1992	1.912	0.306	1.487	0.160
1993	1.447	0.246	1.126	0.170
1994	1.343	0.234	1.044	0.175
1995	1.270	0.204	0.988	0.161
1996	0.884	0.143	0.688	0.162
1997	1.230	0.196	0.956	0.160
1998	1.788	0.288	1.391	0.161
1999	1.812	0.284	1.410	0.157
2000	1.334	0.207	1.038	0.155
2001	1.293	0.197	1.006	0.153
2002	1.380	0.222	1.074	0.161
2003	1.402	0.231	1.091	0.165
2004	1.501	0.236	1.167	0.158
2005	1.395	0.229	1.085	0.164
2006	1.574	0.266	1.224	0.169
2007	1.105	0.186	0.860	0.168
2008	1.110	0.177	0.863	0.160
2009	0.987	0.160	0.768	0.162
2010	0.849	0.151	0.661	0.178

BFE: Year, MinT, Region, Season, Time

BRE: NA

PFE: Year, MaxΔT, Region, Season, Time, Lightstick, HBF

PRE: Year\*MaxΔT, Year\*Region, Year\*Season, Year\*Lightstick, Year\*HBF

Table A6. Blue marlin (BUM) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.577	0.761	1.500	1.319
1988	0.607	0.776	1.579	1.278
1989	0.636	0.765	1.654	1.202
1990	0.782	0.833	2.033	1.065
1991	0.679	0.739	1.765	1.088
1992	0.782	0.667	2.034	0.853
1993	0.892	0.670	2.318	0.751
1994	0.704	0.630	1.831	0.895
1995	0.583	0.568	1.517	0.973
1996	0.447	0.541	1.162	1.211
1997	0.298	0.454	0.775	1.521
1998	0.233	0.407	0.606	1.747
1999	0.223	0.422	0.580	1.894
2000	0.218	0.434	0.566	1.992
2001	0.154	0.390	0.400	2.535
2002	0.159	0.368	0.414	2.314
2003	0.123	0.372	0.319	3.035
2004	0.173	0.390	0.449	2.262
2005	0.165	0.412	0.430	2.492
2006	0.141	0.352	0.367	2.494
2007	0.163	0.403	0.424	2.475
2008	0.173	0.333	0.449	1.929
2009	0.172	0.358	0.446	2.085
2010	0.147	0.355	0.383	2.406

BFE: Year, MinT, Region, Season, Region\*Season

BRE: Year\*Region

PFE: Year, MinT, Region

PRE: Year\*Region

Table A7. Albacore tuna (ALB) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.019	2.046	0.429	107.747
1988	0.023	2.346	0.523	101.221
1989	0.029	2.290	0.658	78.587
1990	0.046	2.540	1.034	55.406
1991	0.040	2.125	0.896	53.502
1992	0.032	1.981	0.726	61.588
1993	0.041	1.903	0.928	46.297
1994	0.051	2.003	1.153	39.197
1995	0.050	2.011	1.139	39.837
1996	0.050	1.687	1.129	33.723
1997	0.058	1.655	1.314	28.429
1998	0.044	1.619	0.993	36.775
1999	0.042	1.713	0.939	41.177
2000	0.045	1.820	1.020	40.278
2001	0.078	1.773	1.760	22.728
2002	0.063	1.528	1.418	24.311
2003	0.034	1.474	0.760	43.768
2004	0.038	1.383	0.866	36.015
2005	0.056	1.658	1.267	29.532
2006	0.038	1.522	0.848	40.521
2007	0.047	1.521	1.065	32.204
2008	0.037	1.450	0.826	39.578
2009	0.059	1.501	1.338	25.311
2010	0.043	1.433	0.971	33.306

BFE: Year, MinT, Region, Season

BRE: Year\*Region, MinT\*Season, Region\*Season

PFE: Year, MinT, Region, Season

PRE: Year\*MinT, Year\*Region, Year\*Season, MinT\*Season, Region\*Season

Table A8. Northern bluefin tuna (BFT) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.023	2.995	1.513	128.529
1988	0.027	3.519	1.721	132.775
1989	0.018	3.098	1.160	173.384
1990	0.017	3.329	1.105	195.647
1991	0.017	3.208	1.131	184.078
1992	0.015	2.392	0.972	159.857
1993	0.009	2.075	0.592	227.360
1994	0.011	2.141	0.710	195.704
1995	0.006	1.975	0.366	350.469
1996	0.007	1.954	0.467	271.754
1997	0.007	1.523	0.453	218.328
1998	0.011	1.710	0.735	151.040
1999	0.008	1.682	0.495	220.453
2000	0.011	1.938	0.742	169.527
2001	0.005	1.570	0.309	330.036
2002	0.010	1.732	0.672	167.303
2003	0.015	1.941	0.962	131.040
2004	0.021	1.596	1.377	75.247
2005	0.019	1.832	1.241	95.844
2006	0.013	1.700	0.864	127.739
2007	0.013	1.994	0.872	148.426
2008	0.020	1.963	1.271	100.230
2009	0.042	2.097	2.739	49.705
2010	0.024	1.561	1.533	66.095

BFE: Year, MinT, Region, Season, Region\*Season

BRE: Year\*MinT, Year\*Region, Year\*Season

PFE: Year, MinT, Region, Season

PRE: Year\*MinT, Year\*Region, Year\*Season, MinT\*Season, Region\*Season

**Table A9. White marlin (WHM) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).**

<b>Year</b>	<b>Index</b>	<b>SE</b>	<b>Stdz. index</b>	<b>CV</b>
1987	1.148	0.427	1.705	0.372
1988	1.035	0.436	1.538	0.421
1989	1.080	0.459	1.605	0.425
1990	0.974	0.442	1.447	0.454
1991	0.970	0.416	1.442	0.428
1992	1.100	0.402	1.634	0.366
1993	1.065	0.390	1.582	0.366
1994	0.802	0.325	1.192	0.405
1995	0.827	0.322	1.229	0.389
1996	0.657	0.283	0.977	0.431
1997	0.642	0.279	0.954	0.434
1998	0.540	0.267	0.802	0.494
1999	0.692	0.307	1.029	0.444
2000	0.501	0.268	0.744	0.535
2001	0.384	0.249	0.571	0.648
2002	0.561	0.279	0.834	0.498
2003	0.395	0.237	0.586	0.601
2004	0.503	0.262	0.747	0.521
2005	0.511	0.298	0.760	0.583
2006	0.277	0.236	0.412	0.851
2007	0.401	0.245	0.596	0.611
2008	0.313	0.216	0.466	0.690
2009	0.457	0.240	0.680	0.525
2010	0.315	0.231	0.468	0.735

**BFE: Year, MinT, Region, Season, MinT\*Season, Region\*Season**

**BRE: Year\*MinT, Year\*Region, Year\*Season**

**PFE: Year, Region, Lightstick, HBF, Region\*Lightstick**

**PRE: Year\*Region, Year\*Lightstick**

Table A10. Shortfin mako shark (SMA) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.329	0.228	1.404	0.693
1993	0.281	0.195	1.201	0.693
1994	0.261	0.180	1.114	0.692
1995	0.301	0.208	1.289	0.691
1996	0.247	0.171	1.055	0.694
1997	0.220	0.153	0.941	0.694
1998	0.221	0.153	0.944	0.694
1999	0.195	0.136	0.835	0.697
2000	0.245	0.170	1.046	0.695
2001	0.230	0.160	0.982	0.696
2002	0.249	0.174	1.066	0.696
2003	0.264	0.184	1.127	0.697
2004	0.350	0.243	1.494	0.695
2005	0.318	0.222	1.359	0.697
2006	0.283	0.198	1.208	0.699
2007	0.439	0.305	1.878	0.695
2008	0.373	0.259	1.593	0.694
2009	0.458	0.318	1.959	0.694
2010	0.353	0.245	1.507	0.695

BFE: Year, MinT, Region

BRE: NA

PFE: Year, MinT, Region, Season, Lightstick, HBF

PRE: Year\*MinT, Year\*Region, Year\*Season, Year\*Lightstick, Year\*HBF, MinT\*Season, Region\*Season, Region\*Lightstick, Region\*HBF, Season\*Lightstick

Table A11. Escolars (OIL) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.021	0.025	0.014	1.158
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.000	0.000	0.000	NA
1993	0.015	0.009	0.010	0.572
1994	2.237	0.468	1.496	0.209
1995	2.197	0.450	1.469	0.205
1996	2.417	0.508	1.617	0.210
1997	1.675	0.351	1.121	0.210
1998	2.378	0.500	1.591	0.210
1999	2.528	0.525	1.691	0.208
2000	2.342	0.486	1.566	0.208
2001	1.979	0.413	1.324	0.209
2002	2.290	0.492	1.532	0.215
2003	2.435	0.523	1.629	0.215
2004	2.304	0.492	1.541	0.213
2005	1.916	0.425	1.282	0.222
2006	1.742	0.429	1.165	0.246
2007	1.699	0.411	1.137	0.242
2008	1.615	0.361	1.080	0.224
2009	1.624	0.383	1.086	0.236
2010	2.465	0.561	1.649	0.227

BFE: Year, MinT, Region

BRE: NA

PFE: Year, MinT, Region, Season, Lightstick, HBF

PRE: Year\*Region, Year\*Season, Year\*Lightstick, Year\*HBF, Region\*Season



Table A12. Longfin mako shark (LMA) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.814	0.764	4.425	0.939
1988	0.683	0.710	3.710	1.040
1989	0.834	0.746	4.534	0.894
1990	0.639	0.695	3.475	1.087
1991	0.500	0.666	2.718	1.331
1992	0.086	0.611	0.470	7.068
1993	0.087	0.599	0.475	6.857
1994	0.078	0.586	0.422	7.557
1995	0.063	0.500	0.344	7.905
1996	0.069	0.552	0.374	8.026
1997	0.048	0.519	0.259	10.884
1998	0.044	0.471	0.241	10.609
1999	0.050	0.447	0.274	8.870
2000	0.036	0.454	0.193	12.752
2001	0.037	0.408	0.202	10.955
2002	0.039	0.449	0.209	11.658
2003	0.030	0.396	0.164	13.122
2004	0.025	0.458	0.137	18.164
2005	0.038	0.404	0.208	10.562
2006	0.042	0.427	0.227	10.223
2007	0.065	0.460	0.354	7.061
2008	0.034	0.387	0.182	11.537
2009	0.045	0.448	0.244	9.958
2010	0.029	0.402	0.158	13.832

BFE: Year, MinT

BRE: Year\*MinT

PFE: Year, Region, Season, Lightstick, Region\*Season

PRE: Year\*Region

Table A13. Tiger shark (TIG) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.289	0.055	1.478	0.191
1988	0.141	0.027	0.723	0.190
1989	0.216	0.041	1.102	0.189
1990	0.190	0.036	0.971	0.189
1991	0.210	0.040	1.072	0.190
1992	0.193	0.036	0.988	0.188
1993	0.165	0.031	0.844	0.189
1994	0.164	0.031	0.838	0.188
1995	0.132	0.025	0.675	0.188
1996	0.132	0.025	0.672	0.189
1997	0.106	0.020	0.543	0.189
1998	0.122	0.023	0.622	0.190
1999	0.109	0.021	0.555	0.190
2000	0.165	0.031	0.842	0.189
2001	0.165	0.032	0.845	0.191
2002	0.180	0.034	0.920	0.189
2003	0.182	0.035	0.932	0.190
2004	0.205	0.039	1.047	0.190
2005	0.301	0.057	1.539	0.191
2006	0.314	0.060	1.603	0.191
2007	0.297	0.057	1.516	0.191
2008	0.268	0.051	1.370	0.191
2009	0.229	0.044	1.169	0.191
2010	0.222	0.042	1.133	0.190

BFE: Year, MinT, Region

BRE: NA

PFE: Year, Region, Lightstick, HBF

PRE: Year\*Region, Year\*Lightstick, Region\*Lightstick, Region\*HBF

Table A14. Blue shark (BSH) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	17.544	9.620	2.462	0.548
1988	10.391	6.504	1.458	0.626
1989	8.217	5.969	1.153	0.726
1990	7.442	5.360	1.044	0.720
1991	8.875	5.420	1.245	0.611
1992	9.778	5.317	1.372	0.544
1993	9.308	5.495	1.306	0.590
1994	9.955	4.866	1.397	0.489
1995	9.830	4.691	1.379	0.477
1996	10.403	4.874	1.460	0.469
1997	9.462	4.747	1.328	0.502
1998	7.675	3.788	1.077	0.494
1999	5.804	3.069	0.814	0.529
2000	5.098	3.013	0.715	0.591
2001	4.234	2.492	0.594	0.589
2002	3.155	2.076	0.443	0.658
2003	3.422	2.181	0.480	0.637
2004	4.145	2.474	0.582	0.597
2005	2.784	2.006	0.391	0.721
2006	3.436	2.352	0.482	0.684
2007	3.536	2.636	0.496	0.745
2008	4.212	2.489	0.591	0.591
2009	5.793	3.181	0.813	0.549
2010	6.554	3.431	0.920	0.523

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, MinT, Region, Season

PRE: Year\*Region

Table A15. Blackfin tuna (BLF) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.863	1.918	0.884	2.223
1988	1.034	2.234	1.060	2.161
1989	1.285	2.216	1.317	1.724
1990	1.483	2.062	1.520	1.390
1991	1.440	1.970	1.476	1.368
1992	1.749	2.017	1.792	1.153
1993	1.487	1.878	1.524	1.263
1994	1.542	1.869	1.580	1.212
1995	1.396	1.570	1.431	1.124
1996	0.775	1.338	0.795	1.725
1997	0.745	1.424	0.764	1.910
1998	0.823	1.356	0.843	1.647
1999	0.764	1.467	0.783	1.921
2000	0.429	1.339	0.440	3.120
2001	0.521	1.278	0.533	2.455
2002	0.586	1.236	0.601	2.109
2003	0.735	1.518	0.753	2.066
2004	0.868	1.456	0.889	1.678
2005	0.407	1.352	0.417	3.323
2006	0.529	1.472	0.542	2.781
2007	0.892	1.447	0.914	1.622
2008	0.998	1.198	1.023	1.200
2009	1.119	1.750	1.147	1.564
2010	0.949	1.499	0.973	1.580

BFE: Year, MinT, Region, Season

BRE: Year\*Region

PFE: Year, Region, Season, Lightstick

PRE: Year\*Region, Year\*Season, Year\*Lightstick, Region\*Season, Region\*Lightstick

Table A16. Hammerhead sharks (SPN) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	1.489	3.583	4.795	2.407
1988	1.707	3.473	5.497	2.035
1989	1.530	2.663	4.929	1.740
1990	0.822	2.331	2.646	2.837
1991	0.659	2.546	2.122	3.863
1992	0.256	1.891	0.825	7.383
1993	0.139	1.767	0.448	12.695
1994	0.109	1.574	0.350	14.461
1995	0.075	1.552	0.240	20.804
1996	0.040	1.350	0.130	33.475
1997	0.021	1.095	0.067	52.611
1998	0.031	1.065	0.099	34.623
1999	0.033	1.249	0.107	37.447
2000	0.027	1.086	0.087	39.971
2001	0.010	1.148	0.034	109.601
2002	0.009	0.923	0.030	97.744
2003	0.038	1.272	0.122	33.646
2004	0.044	1.351	0.143	30.408
2005	0.070	1.264	0.225	18.102
2006	0.066	1.465	0.213	22.200
2007	0.089	1.175	0.287	13.174
2008	0.059	0.962	0.192	16.161
2009	0.055	1.023	0.176	18.757
2010	0.073	1.134	0.234	15.577

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, Region

PRE: Year\*Region

Table A17. Sailfish (SAI) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.247	0.787	0.997	3.183
1988	0.446	0.725	1.797	1.626
1989	0.326	0.757	1.314	2.323
1990	0.354	0.722	1.427	2.039
1991	0.365	0.613	1.472	1.680
1992	0.655	0.654	2.642	0.998
1993	0.639	0.614	2.577	0.960
1994	0.441	0.563	1.778	1.276
1995	0.250	0.465	1.009	1.858
1996	0.261	0.450	1.053	1.724
1997	0.252	0.452	1.016	1.793
1998	0.208	0.385	0.838	1.854
1999	0.239	0.449	0.963	1.881
2000	0.256	0.470	1.032	1.836
2001	0.093	0.335	0.374	3.610
2002	0.097	0.389	0.393	3.991
2003	0.099	0.354	0.399	3.581
2004	0.114	0.338	0.461	2.954
2005	0.078	0.298	0.313	3.835
2006	0.082	0.340	0.329	4.157
2007	0.094	0.311	0.380	3.299
2008	0.125	0.333	0.502	2.671
2009	0.124	0.340	0.501	2.738
2010	0.107	0.329	0.432	3.072

BFE: Year, MinT, Region, Season

BRE: Year\*Region

PFE: Year, Region, Lightstick

PRE: Year\*Region

Table A18. Silky shark (FAL) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	1.408	2.226	3.693	1.580
1993	1.042	1.755	2.734	1.684
1994	0.649	1.409	1.701	2.172
1995	0.870	1.650	2.282	1.896
1996	0.697	1.717	1.828	2.463
1997	0.401	1.278	1.052	3.188
1998	0.259	1.097	0.679	4.232
1999	0.326	1.344	0.855	4.124
2000	0.417	1.338	1.093	3.208
2001	0.245	1.085	0.641	4.436
2002	0.241	0.860	0.633	3.563
2003	0.444	1.174	1.165	2.643
2004	0.245	0.697	0.643	2.841
2005	0.279	0.878	0.731	3.150
2006	0.434	0.951	1.138	2.193
2007	0.310	0.842	0.812	2.720
2008	0.299	0.881	0.784	2.947
2009	0.208	0.835	0.545	4.017
2010	0.377	0.949	0.989	2.516

BFE: Year, MinT, Region, Time, Lightstick

BRE: Year\*Region

PFE: Year, Region, Lightstick, Region:Lightstick

PRE: Year\*Region, Year\*Lightstick

Table A19. Dusky shark (DUS) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.351	0.746	4.080	2.129
1993	0.398	0.818	4.628	2.059
1994	0.193	0.462	2.247	2.394
1995	0.144	0.379	1.682	2.626
1996	0.198	0.460	2.309	2.317
1997	0.086	0.340	1.007	3.928
1998	0.073	0.306	0.846	4.212
1999	0.077	0.335	0.895	4.352
2000	0.070	0.286	0.811	4.101
2001	0.035	0.227	0.412	6.429
2002	0.042	0.234	0.493	5.525
2003	0.059	0.328	0.689	5.546
2004	0.052	0.326	0.601	6.307
2005	0.058	0.280	0.681	4.788
2006	0.055	0.252	0.640	4.583
2007	0.060	0.263	0.693	4.426
2008	0.036	0.231	0.423	6.349
2009	0.036	0.247	0.423	6.795
2010	0.038	0.254	0.440	6.731

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, Region, Lightstick, Region:Lightstick

PRE: Year\*Region, Year\*Lightstick



Table A20. Bigeye thresher shark (BTH) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	1.380	0.003	17625.917
1992	0.075	0.822	2.926	10.981
1993	0.063	0.631	2.473	9.980
1994	0.054	0.678	2.104	12.595
1995	0.048	0.557	1.862	11.695
1996	0.040	0.652	1.580	16.138
1997	0.036	0.619	1.393	17.371
1998	0.028	0.623	1.109	21.967
1999	0.028	0.626	1.111	22.022
2000	0.028	0.597	1.088	21.471
2001	0.023	0.603	0.906	26.003
2002	0.018	0.525	0.690	29.728
2003	0.015	0.478	0.572	32.691
2004	0.015	0.432	0.604	27.947
2005	0.031	0.540	1.224	17.247
2006	0.028	0.466	1.099	16.574
2007	0.023	0.424	0.889	18.662
2008	0.024	0.391	0.951	16.080
2009	0.022	0.510	0.865	23.045
2010	0.014	0.415	0.552	29.406

BFE: Year, MinT, Region, Season, MinT\*Season, Region\*Season

BRE: Year\*Region, Year\*Season

PFE: Year, MinT, Region, Lightstick

PRE: Year\*MinT, Year\*Region, Year\*Lightstick

Table A21. Thresher shark (ALV) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.397	0.896	4.097	2.259
1988	0.345	0.892	3.564	2.585
1989	0.390	0.876	4.028	2.246
1990	0.261	0.852	2.692	3.269
1991	0.242	0.798	2.502	3.296
1992	0.059	0.866	0.614	14.566
1993	0.066	0.653	0.684	9.871
1994	0.045	0.686	0.468	15.131
1995	0.044	0.697	0.456	15.797
1996	0.036	0.603	0.377	16.544
1997	0.023	0.552	0.237	24.071
1998	0.013	0.549	0.133	42.514
1999	0.028	0.582	0.288	20.888
2000	0.027	0.479	0.274	18.060
2001	0.023	0.439	0.236	19.251
2002	0.039	0.570	0.399	14.733
2003	0.036	0.582	0.373	16.104
2004	0.019	0.467	0.201	23.969
2005	0.039	0.534	0.399	13.837
2006	0.045	0.465	0.461	10.411
2007	0.030	0.516	0.310	17.203
2008	0.032	0.488	0.332	15.195
2009	0.050	0.501	0.512	10.112
2010	0.035	0.438	0.363	12.458

BFE: Year, MinT, Region, Season

BRE: Year\*MinT, Year\*Region, Year\*Season

PFE: Year, MinT, Region, Lightstick

PRE: Year\*MinT, Year\*Region

Table A22. Blacktip shark (CCL) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	1.474	2.061	5.156	1.398
1993	1.005	1.898	3.513	1.889
1994	0.886	1.964	3.099	2.216
1995	0.515	1.447	1.800	2.812
1996	0.407	1.339	1.424	3.288
1997	0.335	1.376	1.171	4.108
1998	0.219	1.149	0.765	5.253
1999	0.214	1.688	0.750	7.873
2000	0.210	1.556	0.735	7.406
2001	0.223	1.473	0.781	6.598
2002	0.263	1.933	0.921	7.341
2003	0.307	1.414	1.075	4.602
2004	0.306	1.668	1.071	5.446
2005	0.164	1.641	0.575	9.974
2006	0.081	0.859	0.284	10.561
2007	0.095	1.006	0.331	10.641
2008	0.054	0.708	0.189	13.065
2009	0.068	0.913	0.239	13.337
2010	0.035	1.526	0.121	44.229

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, Region, Season, Time, Lightstick, HBF

PRE: Year\*Region, Year\*Season, Year\*Lightstick, Year\*HBF, Region\*Season, Region\*Lightstick

Table A23. Sandbar shark (CCP) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.000	0.000	0.000	NA
1993	0.000	0.000	0.000	NA
1994	0.011	4.740	0.093	428.773
1995	0.296	4.015	2.480	13.572
1996	0.655	4.553	5.491	6.951
1997	0.185	3.390	1.549	18.347
1998	0.154	3.342	1.294	21.649
1999	0.165	4.477	1.384	27.126
2000	0.223	3.946	1.873	17.654
2001	0.171	3.409	1.430	19.989
2002	0.099	2.607	0.830	26.341
2003	0.139	3.575	1.166	25.706
2004	0.216	3.492	1.807	16.198
2005	0.118	3.120	0.993	26.340
2006	0.059	3.252	0.490	55.574
2007	0.115	3.885	0.960	33.918
2008	0.055	2.103	0.464	38.000
2009	0.102	3.161	0.859	30.853
2010	0.100	2.917	0.839	29.141

BFE: Year, Region, Season, Lightstick, Region\*Season, Region\*Lightstick, Season\*Lightstick

BRE: Year\*Region, Year\*Season, Year\*Lightstick

PFE: Year, MinT, Region, Season, Lightstick, HBF

PRE: Year\*Region, Year\*Season, Year\*Lightstick, Year\*HBF, Region\*Lightstick, Season\*Lightstick

Table A24. Oceanic whitetip shark (OCS) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.513	1.724	2.759	3.360
1993	0.325	1.691	1.747	5.203
1994	0.408	1.346	2.191	3.302
1995	0.317	1.248	1.703	3.938
1996	0.349	1.175	1.875	3.369
1997	0.328	1.143	1.764	3.484
1998	0.407	1.253	2.186	3.081
1999	0.254	1.179	1.367	4.635
2000	0.147	1.017	0.789	6.931
2001	0.166	1.002	0.890	6.052
2002	0.127	0.876	0.685	6.877
2003	0.170	0.959	0.914	5.641
2004	0.127	0.928	0.685	7.280
2005	0.160	0.947	0.859	5.926
2006	0.110	0.838	0.594	7.587
2007	0.143	0.858	0.769	5.997
2008	0.175	0.815	0.939	4.668
2009	0.129	0.734	0.692	5.705
2010	0.110	0.781	0.592	7.091

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, MinT, Region, Lightstick

PRE: Year\*Region, Year\*Lightstick, Region\*Lightstick

Table A25. Spearfishes (SPR) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.061	1.914	1.090	31.601
1988	0.049	2.059	0.879	42.163
1989	0.072	1.440	1.301	19.907
1990	0.088	1.328	1.583	15.094
1991	0.053	1.051	0.946	19.989
1992	0.038	1.171	0.682	30.895
1993	0.080	1.078	1.434	13.532
1994	0.055	0.985	0.992	17.869
1995	0.086	0.966	1.552	11.202
1996	0.088	1.086	1.583	12.344
1997	0.065	0.875	1.176	13.385
1998	0.029	0.778	0.515	27.222
1999	0.033	0.825	0.588	25.242
2000	0.021	0.736	0.375	35.365
2001	0.034	0.650	0.611	19.154
2002	0.045	0.817	0.816	18.021
2003	0.034	0.747	0.603	22.312
2004	0.041	0.815	0.729	20.098
2005	0.052	0.682	0.937	13.096
2006	0.043	0.721	0.771	16.829
2007	0.047	0.704	0.848	14.940
2008	0.057	0.627	1.027	10.982
2009	0.095	0.690	1.710	7.261
2010	0.070	0.801	1.255	11.490

BFE: Year, MinT, Region

BRE: Year\*MinT, Year\*Region, MinT\*Region

PFE: Year, Region

PRE: Year\*Region

Table A26. Skipjack tuna (SKJ) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.359	3.932	1.759	10.946
1992	0.591	4.231	2.892	7.163
1993	0.488	4.117	2.392	8.429
1994	0.374	2.806	1.833	7.495
1995	0.176	2.825	0.862	16.058
1996	0.132	1.869	0.649	14.110
1997	0.170	2.458	0.834	14.433
1998	0.363	2.547	1.777	7.018
1999	0.278	2.497	1.363	8.973
2000	0.268	2.411	1.313	8.988
2001	0.154	3.674	0.755	23.830
2002	0.168	2.288	0.823	13.614
2003	0.156	2.327	0.765	14.903
2004	0.263	3.044	1.286	11.591
2005	0.108	1.943	0.529	17.972
2006	0.220	2.086	1.076	9.499
2007	0.086	2.092	0.422	24.299
2008	0.163	1.899	0.799	11.634
2009	0.206	1.864	1.011	9.027
2010	0.176	2.080	0.862	11.813

BFE: Year, MinT, Region, Time, Lightstick

BRE: Year\*Region, Year\*Time, Year\*Lightstick

PFE: Year, Region, Time, Lightstick, HBF

PRE: Year\*Region, Year\*Time, Year\*Lightstick, Year\*HBF

Table A27. Night shark (CCS) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.195	2.923	4.050	14.984
1993	0.140	2.846	2.912	20.293
1994	0.111	2.540	2.305	22.880
1995	0.148	1.920	3.075	12.966
1996	0.085	1.965	1.766	23.101
1997	0.060	1.440	1.248	23.966
1998	0.026	1.668	0.549	63.130
1999	0.032	1.091	0.660	34.331
2000	0.051	1.505	1.058	29.546
2001	0.031	1.307	0.634	42.822
2002	0.011	1.186	0.238	103.618
2003	0.030	1.036	0.619	34.772
2004	0.013	1.169	0.271	89.604
2005	0.070	0.883	1.455	12.609
2006	0.028	0.893	0.584	31.717
2007	0.025	0.994	0.528	39.117
2008	0.034	0.682	0.710	19.946
2009	0.038	0.914	0.798	23.781
2010	0.026	0.960	0.540	36.916

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, Region

PRE: Year\*Region



Table A28. Scalloped hammerhead shark (SPL) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.153	0.494	5.384	3.220
1993	0.167	0.449	5.859	2.687
1994	0.075	0.311	2.631	4.152
1995	0.082	0.312	2.880	3.803
1996	0.042	0.260	1.460	6.248
1997	0.029	0.183	1.010	6.358
1998	0.031	0.303	1.098	9.683
1999	0.032	0.233	1.132	7.226
2000	0.036	0.270	1.247	7.603
2001	0.020	0.256	0.688	13.049
2002	0.017	0.247	0.611	14.182
2003	0.000	0.000	0.000	NA
2004	0.000	0.000	0.000	NA
2005	0.000	0.000	0.000	NA
2006	0.000	0.000	0.000	NA
2007	0.000	0.000	0.000	NA
2008	0.000	0.000	0.000	NA
2009	0.000	0.000	0.000	NA
2010	0.000	0.000	0.000	NA

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, MinT, Region, Season, Lightstick, MinT\*Season, Region\*Season, Region\*Lightstick, Season\*Lightstick

PRE: Year\*MinT, Year\*Region, Year\*Season, Year\*Lightstick

Table A29. Atlantic bonito (BON) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.000	0.000	0.000	NA
1993	0.353	3.929	1.788	11.120
1994	0.265	3.719	1.340	14.042
1995	1.746	5.560	8.833	3.185
1996	0.124	3.905	0.627	31.494
1997	0.299	4.570	1.511	15.297
1998	0.222	3.548	1.125	15.960
1999	0.281	5.268	1.419	18.782
2000	0.225	3.136	1.137	13.952
2001	0.087	2.446	0.439	28.211
2002	0.115	5.266	0.583	45.692
2003	0.098	4.118	0.494	42.196
2004	0.089	12.661	0.450	142.447
2005	0.221	9.203	1.117	41.670
2006	0.042	5.636	0.213	133.879
2007	0.068	4.638	0.343	68.440
2008	0.201	8.643	1.018	42.960
2009	0.247	7.909	1.248	32.058
2010	0.062	5.797	0.315	93.191

BFE: Year, MinT, Region, Season

BRE: Year\*MinT, Year\*Region, Year\*Season, Region\*Season

PFE: Year, MinT, Region

PRE: Year\*MinT, Year\*Region, MinT\*Region

Table A30. White shark (WSH) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.325	1.336	2.397	4.118
1988	0.445	1.829	3.284	4.113
1989	0.535	1.950	3.950	3.647
1990	0.690	1.364	5.096	1.976
1991	0.569	1.400	4.203	2.461
1992	0.238	1.216	1.760	5.100
1993	0.030	0.733	0.221	24.465
1994	0.041	1.179	0.300	28.984
1995	0.051	0.726	0.375	14.307
1996	0.067	0.652	0.497	9.699
1997	0.029	0.692	0.212	24.130
1998	0.016	0.642	0.120	39.657
1999	0.032	0.583	0.238	18.083
2000	0.016	0.759	0.118	47.619
2001	0.030	0.648	0.224	21.409
2002	0.049	0.545	0.362	11.132
2003	0.022	0.679	0.161	31.047
2004	0.003	0.810	0.019	314.410
2005	0.000	0.000	0.000	NA
2006	0.009	0.685	0.070	72.693
2007	0.001	1.011	0.009	804.345
2008	0.000	0.000	0.000	NA
2009	0.006	1.085	0.043	188.168
2010	0.046	0.648	0.342	13.997

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, Region, Lightstick

PRE: Year\*Region, Year\*Lightstick, Region\*Lightstick

Table A31. Smooth hammerhead shark (SPZ) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.504	0.932	7.804	1.849
1993	0.350	0.802	5.422	2.291
1994	0.141	0.490	2.185	3.474
1995	0.105	0.407	1.627	3.874
1996	0.068	0.417	1.059	6.102
1997	0.048	0.343	0.737	7.200
1998	0.042	0.457	0.657	10.784
1999	0.111	0.520	1.714	4.695
2000	0.079	0.381	1.224	4.820
2001	0.065	0.520	1.002	8.039
2002	0.037	0.375	0.569	10.209
2003	0.000	0.000	0.000	NA
2004	0.000	0.000	0.000	NA
2005	0.000	0.000	0.000	NA
2006	0.000	0.000	0.000	NA
2007	0.000	0.000	0.000	NA
2008	0.000	0.000	0.000	NA
2009	0.000	0.000	0.000	NA
2010	0.000	0.000	0.000	NA

BFE: Year, MinT, Region

BRE: Year\*Region

PFE: Year, MinT, Region, Lightstick, HBF

PRE: Year\*MinT, Year\*Region, Year\*Lightstick, Year\*HBF, Region\*Lightstick, Region\*HBF, Lightstick\*HBF

Table A32. Porbeagle (POR) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.003	4.213	0.635	1238.282
1993	0.008	4.824	1.527	589.494
1994	0.007	10.569	1.397	1411.869
1995	0.003	2.280	0.586	725.483
1996	0.006	5.499	1.058	969.518
1997	0.005	3.887	0.971	746.613
1998	0.002	3.679	0.305	2249.082
1999	0.002	3.324	0.286	2169.283
2000	0.002	4.052	0.369	2048.695
2001	0.002	3.209	0.312	1918.276
2002	0.008	2.785	1.433	362.556
2003	0.007	3.918	1.246	586.762
2004	0.009	4.608	1.765	487.168
2005	0.008	5.785	1.469	734.548
2006	0.019	6.330	3.486	338.753
2007	0.016	3.632	2.941	230.424
2008	0.003	3.905	0.629	1159.088
2009	0.004	3.493	0.797	817.795
2010	0.015	3.922	2.790	262.242

BFE: Year, MinT, Region

BRE: Year\*MinT, Year\*Region

PFE: Year, MinT, Region, Lightstick

PRE: Year\*MinT, Year\*Region, Year\*Lightstick

Table A33. Bignose shark (CCA) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.522	3.026	4.190	5.802
1993	0.572	3.139	4.598	5.486
1994	0.398	1.776	3.197	4.463
1995	0.422	1.656	3.387	3.928
1996	0.142	1.116	1.137	7.885
1997	0.143	1.470	1.150	10.268
1998	0.028	1.838	0.228	64.651
1999	0.088	1.287	0.707	14.617
2000	0.122	1.135	0.979	9.316
2001	0.040	1.331	0.324	33.011
2002	0.046	2.363	0.369	51.404
2003	0.067	2.829	0.539	42.147
2004	0.014	3.244	0.112	232.044
2005	0.030	5.388	0.239	181.451
2006	0.043	1.246	0.348	28.787
2007	0.094	1.816	0.759	19.234
2008	0.038	2.430	0.309	63.169
2009	0.044	7.288	0.356	164.696
2010	0.133	4.919	1.072	36.867

BFE: Year, MinT, Region

BRE: Year\*MinT, Year\*Region

PFE: Year, MinT, Region

PRE: Year\*MinT, Year\*Region

Table A34. Spinner shark (CCB) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	0.000	0.000	0.000	NA
1989	0.000	0.000	0.000	NA
1990	0.000	0.000	0.000	NA
1991	0.000	0.000	0.000	NA
1992	0.091	0.968	7.769	10.602
1993	0.010	0.835	0.887	80.146
1994	0.010	0.905	0.851	90.528
1995	0.021	0.724	1.804	34.180
1996	0.028	1.185	2.375	42.477
1997	0.012	1.383	1.005	117.121
1998	0.019	2.463	1.654	126.774
1999	0.023	1.784	1.920	79.091
2000	0.003	0.714	0.239	254.222
2001	0.000	0.223	0.027	692.961
2002	0.000	3.333	0.041	6974.026
2003	0.016	0.969	1.350	61.111
2004	0.012	2.071	0.997	176.837
2005	0.002	0.335	0.158	180.243
2006	0.005	0.646	0.403	136.604
2007	0.008	0.826	0.724	97.243
2008	0.002	0.784	0.155	431.524
2009	0.008	0.617	0.677	77.594
2010	0.011	0.686	0.965	60.521

BFE: Year, MinT, Region, Season, HBF

BRE: Year\*MinT, Year\*Region, Year\*Season, Year\*HBF, Season\*HBF

PFE: Year, Region, Season, Lightstick, Season\*Lightstick

PRE: Year\*Region, Year\*Season, Year\*Lightstick

Table A35. King mackerel (KGM) index of abundance, standard errors (SE), index standardized to mean (Stdz. Index), and coefficients of variation (CV). The components of the delta GLM with the factors (\* denotes interaction between factors) selected for generating the index are provided, including the binomial fixed effects (BFE), binomial random effects (BRE), positive fixed effects (PFE), and positive random effects (PRE).

Year	Index	SE	Stdz. index	CV
1987	0.000	0.000	0.000	NA
1988	4.756	7.613	15.499	1.601
1989	0.711	4.009	2.317	5.639
1990	0.000	0.000	0.000	NA
1991	0.694	8.500	2.263	12.244
1992	0.235	4.288	0.767	18.213
1993	0.073	4.313	0.239	58.757
1994	0.088	2.087	0.288	23.621
1995	0.327	1.443	1.066	4.413
1996	0.218	1.701	0.710	7.810
1997	0.012	1.755	0.040	141.794
1998	0.027	1.233	0.088	45.424
1999	0.139	1.821	0.454	13.067
2000	0.004	2.725	0.012	746.961
2001	0.002	1.410	0.005	848.663
2002	0.005	1.217	0.016	251.393
2003	0.000	0.000	0.000	NA
2004	0.002	2.201	0.008	934.077
2005	0.006	1.542	0.019	263.394
2006	0.000	0.000	0.000	NA
2007	0.039	28.764	0.128	733.616
2008	0.000	0.219	0.001	779.564
2009	0.022	18.150	0.072	819.905
2010	0.002	0.860	0.007	400.417

BFE: Year, Region

BRE: Year\*Region

PFE: Year, MinT, Region, Season, HBF

PRE: Year\*MinT, Year\*Region, Year\*Season, Region\*Season



## **CHAPTER 4**

**Performance of a fisheries stock assessment model as related to abundance index quality:  
an evaluation of the importance of habitat when assessing Atlantic blue marlin**

## ABSTRACT

Abundance indices are key inputs to fisheries stock assessments. For highly migratory species (HMS), abundance trends are estimated using fishery-dependent catch and effort data, which must be standardized to account for biases. However, despite being an important factor governing HMS catch rates, habitat effects are typically not directly considered in abundance index standardization. We used simulation to quantify the relative performance of a fisheries stock assessment model (Stock Synthesis) when different approaches to estimating abundance indices were used, including a method that explicitly accounts for habitats fished (HabGLM). We also considered a more traditional generalized linear modeling approach ( $GLM_T$ ), and nominal catch-per-unit-effort ( $CPUE_N$ ). While HabGLM has demonstrated superior abundance index accuracy over competing approaches, associated benefits to fisheries stock assessment have not been described. In general, there was less error associated with quantities output by the assessment model when abundance indices were estimated using HabGLM as opposed to  $GLM_T$  or  $CPUE_N$ . However, management quantities estimated in the HabGLM scenario were still overly optimistic, and performance regarding estimates of maximum sustainable yield (MSY) was best in the  $CPUE_N$  scenario. Additionally, estimates of the fishing mortality rates at MSY ( $F_{MSY}$ ) were nearly identical across scenarios. Because all scenarios overestimated  $F_{MSY}$ , when we projected spawning biomass (SB) after 50 years of fishing at  $F_{MSY}$ , the final value for all scenarios was approximately 28% of the supposed management target ( $SB_{MSY}$ ). We recommend the use of HabGLM in HMS stock assessments due to superior performance, but this study emphasized that the observed improvements would not likely overcome the limitations related to a reliance on fishery-dependent data. Consequently, independent scientific monitoring of HMS populations could substantially improve HMS assessment and management.

## INTRODUCTION

Fisheries stock assessment models provide understandings of fish population dynamics and the effects of fishing on those populations. Therefore, the ability for fisheries management to achieve its objectives directly relates to assessment model accuracy. A range of modeling options with differing data requirements are available to stock assessment scientists (Quinn and Deriso 1999), but one input common to nearly all approaches is a characterization of the historical pattern in abundance. Most assessment models estimate a biomass time series and other population parameters by fitting, or calibrating to observed changes in relative abundance (Maunder and Starr 2003). Given the role that indices of abundance play in stock assessments, it is important to characterize assessment model sensitivity to abundance index quality.

Evaluating the performance of a stock assessment model (or any statistical analysis) is best accomplished using simulation testing, where 'true' model parameters are known. Numerous studies have used simulation analyses to characterize assessment model performance as related to a range of data inputs and model assumptions (NRC 1998; Ianelli 2002; Punt 2003; Yin and Sampson 2004; Magnusson and Hilborn 2007; Wang et al. 2009; Conn et al. 2010; Wilberg and Bence 2010; Wetzell and Punt 2011; among others). Taken altogether, the affect of abundance index quality on assessment model performance is somewhat equivocal. A few studies emphasized the importance of a high quality index (NRC 1998; Wang et al. 2009; Conn et al. 2010; Wilber and Bence 2010), while Yin and Sampson (2004), for example, placed more of an emphasis on alternative inputs, such as increased age composition sampling. Most previous simulation analyses were configured such that they captured the dynamics of a wide range of species life histories, and population and fishery dynamics. This is a very useful attribute of these studies, because their results can then serve as general guidelines that are broadly applicable

across species. However, when conclusions are not entirely consistent across studies, such as those regarding the importance of abundance index quality, it may be necessary to conduct further studies that are more focused to address the model feature and/or species in question.

For many species, scientific programs have been developed to monitor population changes over time. In these cases, changes in abundance may be accurately characterized, resulting in less concern that corresponding indices of abundance will bias assessment results. However, for highly migratory species (HMS), monitoring programs are not in place and indices of abundance are typically derived from fisheries catch and effort data. To estimate trends in abundance, catch per unit effort (CPUE) time series from fisheries are 'standardized' to account for factors other than abundance that affect CPUE. There are numerous approaches available for standardizing CPUE (Maunder and Punt 2004), including habitat-based models (Hinton and Nakano 1996; Maunder et al. 2006). Habitat-based standardization, as opposed to a more traditional linear modeling technique, has been proposed for HMS, because the fisheries responsible for a majority of HMS fishing mortality (longline fisheries) have changed target species and target habitats over time (Majkowski 2007). These changes highlight the need to include habitat when estimating the abundance of target and bycatch species from longline fisheries, because neither species group is caught randomly across their respective habitats. However, the application of habitat-based methods in real fisheries stock assessments has been resisted (particularly for Atlantic HMS), because associated assumptions and data inputs are considered highly uncertain (Goodyear et al. 2003; Ward and Myers 2006).

Lynch et al. (2012) introduced a hybrid approach to CPUE standardization that incorporated habitat information into a generalized linear modeling framework (HabGLM). Through simulation analysis they demonstrated that HabGLM produced more accurate indices of abundance than other models tested, and was less sensitive to errors surrounding estimates of habitats fished. When the HabGLM was applied to fisher logbook data from the U.S. pelagic longline fishery, the habitat variable explained a significant portion of the variability in CPUE for

34 out of 35 HMS analyzed (Chapter 3), further emphasizing the importance of including habitat in the standardization process. While the indices produced by HabGLM have been shown to be more reliable than those from competing methods, it is unclear to what degree these indices improve assessment model performance.

In this simulation study, we evaluate the influence of indices of abundance developed using HabGLM on the performance of a statistical model commonly applied in modern fisheries stock assessments (Stock Synthesis; Methot 2005; 2009). Stock Synthesis (SS) is considered an integrated analysis, or statistical-catch-at-age assessment model. We use this framework, in part because it is a flexible, widely applied, contemporary approach, but also because we are particularly interested in understanding how our results apply to the assessment of Atlantic blue marlin (*Makaira nigricans*). Blue marlin is an HMS that is incidentally captured in high seas tuna fisheries, and is a target of recreational and artisanal fisheries. The most recent blue marlin assessment (ICCAT 2012) was conducted using SS, and indices of abundance for that assessment were estimated using fishery-dependent CPUE. Based on the results of Lynch et al. (2012), HabGLM would likely provide the most accurate indices of abundance derived from longline fisheries; however, the indices for these fisheries in the blue marlin assessment did not incorporate habitat information (ICCAT 2012). By creating a simulation model with realistic blue marlin population and associated fishery dynamics, we are able to characterize the error surrounding select management quantities estimated by SS when different approaches to estimating abundance indices, including HabGLM, are used.

## MATERIALS AND METHODS

The simulation framework used for testing assessment model performance consisted of several steps (Fig. 1). Initially, we developed an operating model with known parameters, and used that model to simulate population and fisheries data. Using the simulated longline fishery data, we estimated indices of abundance following three approaches: HabGLM, traditional GLM, and nominal CPUE (total annual CPUE). We established three stock assessment scenarios using the simulated data, changing only the indices of abundance. Each assessment scenario resulted in several estimated parameters and management quantities, and we used Markov Chain Monte Carlo simulation (MCMC) to capture their associated uncertainty. Finally, we compared the estimated quantities to the values specified in the operating model, and calculated performance metrics for each quantity in each assessment scenario. Generally, our experimental design was inspired by several previous simulation analyses (NRC 1998; Ianelli 2002; Punt 2003; Yin and Sampson 2004; Magnusson and Hilborn 2007; Wang et al. 2009; Conn et al. 2010; Wilberg and Bence 2010; Wetzell and Punt 2011). One aspect of this study that differs from many simulation analyses is that we used the estimation model (SS) under a deterministic configuration that replicates the operating model to calculate the ‘true’ fishing mortality rates and management quantities. This was done to prevent any issues related to how these quantities are defined by SS, and to quantify differences solely due to the indices of abundance.

### *Operating model*

A comprehensive model was developed to simulate a single Atlantic blue marlin population. The simulation incorporated general spatial dynamics, age and sex structure, and catches from

multiple fisheries using customary relationships defined for population (Table 1) and fishery (Table 2) dynamics (Quinn and Deriso 1999). In an attempt to simulate population dynamics that are most reflective of the actual blue marlin population over time, input parameters (Table 3) were obtained from multiple sources, including primary literature, secondary literature, and stock assessment reports. The simulation was initiated approximately one generation before fishing began (1935) and continued through 2010.

Spatial dynamics were simulated over seven defined regions ( $r$ ) in the Atlantic Ocean (Fig. 2), including west tropical (WT), east tropical (ET), southwest subtropical (SW), southeast subtropical (SE), northwest subtropical (NW), northeast subtropical (NE), and Caribbean Sea/Gulf of Mexico (CG). Temporal dynamics were simulated by defining four seasons ( $S$ : January – March, April – June, July – September, October - December). The spatiotemporal distribution of blue marlin was specified as the proportion of the population at age  $a$  in region  $r$  during season  $S$  ( $P_{a,r,S}$ : Table 4). The values for  $P_{a,r,S}$  were qualitatively determined, but generally followed seasonal population concentrations as defined by Nakamura (1985), and 27 – 28°C surface water isotherms (Goodyear 2003, Goodyear et al. 2008) using seasonal water temperatures from the National Oceanographic Data Center (NODC)<sup>4</sup>.

Our simulated population was subjected to fishing by five separate fisheries that operate in the Atlantic Ocean and adjacent seas: the pelagic longline fisheries from Japan (JAPLL) and the US (USLL), the gillnet fisheries from Venezuela (VENGN) and Ghana (GHAGN), and the US recreational fishery (USREC). We excluded other fisheries that capture blue marlin (and other HMS) in the Atlantic, to maintain model efficiency. Fishing effort ( $E$ ) varied over years, seasons, and regions according to catch and effort dynamics reported for each respective fishery considered. With the exception of the USLL, effort data were obtained from the International

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<sup>4</sup> [www.nodc.noaa.gov](http://www.nodc.noaa.gov); data accessed September 20, 2011.

Commission for the Conservation of Atlantic Tunas (ICCAT)<sup>5</sup>. For the USLL, we used fisher logbook data obtained from the National Marine Fisheries Service on November 21, 2011.

Catches were determined by specifying catchability ( $q$ ), and relating effort dynamics to population dynamics within the appropriate year, region, and season. For all fisheries,  $q$  was specified in the first year of fishing by taking the average of the first three years of each fishery's observed CPUE divided by the total biomass in those years estimated by the 2011 blue marlin stock assessment (ICCAT 2012) in the corresponding years. Initial  $q$  was then subjected to small random annual proportional increases to incorporate stochasticity, fisher experience, and technological improvements as demonstrated by Ward (2008). For the longline fisheries, catches were also related to the habitats fished by each hook within each set as a function of fishing depth. Habitat categories ( $H$ ) were defined as temperature zones relative to sea surface temperature, binned by 1°C intervals. Therefore, fishing depth and temperature profiles in the area of fishing determined the habitats exploited per set (Fig. 3), and  $q$  was adjusted by summing over the habitat-specific catchabilities (Table 2). For gillnet and recreational fisheries, effort was assumed to be distributed in surface waters; therefore, catches for these fisheries were related to a single annual  $q$  and the spatiotemporal overlap between fishing effort and the distribution of blue marlin.

We used catenary algorithms (Bigelow et al., 2006; Yoshihara, 1951; 1954) and followed the approach described by Lynch et al. (2012) to specify fishing depths for the JAPLL. Longline gear components necessary for determining fishing depths included the number of hooks between floats (HBF), lengths of the branchline, floatline, and mainline between floats, and the angle between the tangent of the mainline where it attaches to the floatline and the horizon (catenary angle). Lynch et al. (2012) assumed a fixed value for the catenary angle; however, in this study, angles were specified as a normal random variable based on the number of hooks between floats (HBF) and the corresponding means and standard deviations observed by Bigelow et al. (2006).

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<sup>5</sup> www.iccat.int; data accessed September 23, 2011.



Otherwise, gear measurements were identical to those used by Lynch et al. (2012). For the USLL, catenary algorithms were also used, but we relied on fisher logbook data to specify measurements of the gear components. The hook depths specified for each set from the USLL and JAPLL were both reduced by a random proportion due to shoaling [ $N(\mu = 0.75, \sigma = 0.05)$ ].

To relate fishing depth to temperature at depth, we used the temperature profile data obtained from NODC<sup>4</sup> (e.g., Fig. 3). Each spatial region was equally divided into six sub-regions, and average temperature at depth was determined for each sub-region in each season. This resulted in 168 available temperature profiles (7 regions x 6 sub-regions x 4 seasons), and each longline set was randomly assigned one of the six available profiles corresponding to the region/season in which the set occurred (interannual variability was not incorporated). To assign a habitat category to each hook, temperature at fishing depth was specified as the value relative to surface water temperature, rounded to the nearest degree.

High resolution catch data were simulated according to the specified fishery/population dynamics and structure. For the gillnet fisheries, we assumed that captured individuals did not survive; thus, total catch equaled true removals (*TR*). However, a proportion of the catch was assumed to survive capture in the longline and recreational fisheries, and the year of fishing determined the live discard (*LD*) proportion for each fishery (Table 3). Furthermore, based on studies of post-release survival for Atlantic marlins caught in longline and recreational fisheries (Kerstetter et al., 2003; Graves and Horodysky, 2010), a proportion of *LD* was simulated to survive (*DS*). In the recreational fishery, *DS* was further related to the type of gear used (Table 3).

#### *Abundance index scenarios*

The goal of this study was to quantify the importance of using HabGLM when estimating indices of abundance for stock assessments of HMS (Atlantic blue marlin in particular). Thus, we evaluated the performance of the assessment model when HabGLM (Lynch et al. 2012; Chapter 3) was used, but for comparative purposes, we used two additional approaches: traditional GLM

without habitat information ( $GLM_T$ ), and nominal CPUE ( $CPUE_N$ ). Since habitat information has been demonstrated to be important when estimating abundance indices from pelagic longline data (Lynch et al. 2012), we evaluated indices from the longline fisheries only (JAPLL and USLL).

The only difference between HabGLM and  $GLM_T$  was that a habitat explanatory variable was included in HabGLM and not  $GLM_T$ . Otherwise, indices of abundance were estimated for these methods using a delta-lognormal generalized linear model (Aitchison 1955; Lo et al. 1992; Maunder and Punt 2004; Stefánsson 1996). The delta-lognormal GLM is a combination of two GLMs; one models the presence/absence of a species as a function of explanatory variables, assuming a binomial error distribution (logit link function), and the other models the log of positive CPUE as a function of explanatory variables, assuming Gaussian errors (identity link function). A categorical measure of time (usually expressed as years) is included in the explanatory variables for each model component of the delta GLM, and the product of the back-transformed, bias-corrected (Lo et al. 1992) time effects from each model is the index of abundance.

In addition to the year in which fishing occurred, we identified three other variables to be considered for constructing the GLM components of HabGLM and  $GLM_T$ . These variables were all specified in the operating model and included Region, Season, and HBF (categorized with seven levels: 0 – 3, 4 – 6, 7 – 9, 10 – 15, 16 – 21, 22 – 29, 30+). These are common variables to consider when generating indices of abundance for HMS from longline data (e.g., Walter 2011). We did not include other variables commonly considered in these types of analyses (e.g., bait type, time of day, etc.), because these complexities were not included in the operating model. For the HabGLM, there were two habitat variables also considered: the minimum temperature fished by the longline (MinT), and the temperature associated with the deepest hook, relative to surface temperature, or maximum deviation from surface temperature (Max $\Delta$ T). We treated both habitat variables as factors in the HabGLM, categorizing MinT with six levels (1 – 5, 6 – 10, 11 – 15, 16 – 20, 21 – 25, and 26 – 30 °C), and rounding Max $\Delta$ T to the nearest degree (see Fig. 3 for a

visualization of the habitat variables). The Max $\Delta$ T and MinT variables have both shown promise for improving abundance estimates from the JAPLL (Lynch et al. 2012) and the USLL (Chapter 3).

All variables used in the HabGLM and GLM<sub>T</sub> were specified in the operating model to affect catch rates to differing degrees. When incorporating these variables into our models, we used the true simulated values corresponding to each longline set. In practice, there would be error surrounding some of these variables; therefore, the abundance indices used in our evaluation represent best case scenarios.

For selecting variables to include in the binomial and positive components of the delta GLMs, we followed an approach commonly used when estimating abundance indices for HMS in the Atlantic Ocean (e.g., Walter 2011; Chapter 3). We evaluated each variable and corresponding first order interaction term in the context of deviance explained. Variables (and interaction terms) that explained at least 5% of the total deviance were included in the final models, and all others were excluded. Interaction terms selected for the final models were treated as random effects when they included the Year variable, or when they were determined to be rank deficient.

To evaluate how well each index of abundance tracked the pattern specified in the operating model, the performance metrics used by Lynch et al. (2012) were calculated. The accuracy of each index was quantified as the median of the annual percent differences between ‘true’ and estimated abundance. This median percent difference (MPD) is akin to another commonly used performance metric, the median of the absolute values of the relative errors (e.g., Punt 2003), but expressed as a percentage. Finally, to quantify variability in the error, the standard deviation of the percent differences (SDPD) was calculated.

### *Estimation model*

We evaluated the performance of SS (version 3.23b) as obtained from the NOAA Fisheries Toolbox<sup>6</sup>. The SS program represents a contemporary, and extremely flexible approach to fisheries stock assessment, offering a range of complexity over which models can be configured (Methot 2005; 2009). As mentioned, we used SS to ‘calculate’ the fishing mortality rates and management quantities corresponding to the dynamics specified in the operating model. These ‘true’ values, which form the basis of the performance evaluation, were obtained by running SS under a deterministic configuration, where all parameters were fixed to the values specified in the operating model (for the most part, one of the growth coefficients of variation was estimated using a strong prior).

In general, the operating model was formulated to resemble the component models of SS to prevent confounding in the performance evaluation; however, there were a few discrepancies (e.g., the equations for length-at-age differed). Where there were discrepancies between formulations, the ‘true’ values of the parameters required by SS were estimated externally, by optimizing the sum of the squared differences between the dynamics (e.g., growth) specified in the operating model, and those predicted by the respective SS formulation. Furthermore, we configured SS to model a two-sex, age-structured population as specified in the operating model, but for simplicity, only one season and one area were specified, and rather than entering each fishery separately, total annual landings were aggregated into three gear groups: longline, gillnet, and sport.

Once true management quantities were calculated in the deterministic configuration, we fit SS using the three abundance index scenarios (HabGLM, GLM<sub>T</sub>, and CPUE<sub>N</sub>). For the deterministic configuration, two indices of abundance were specified: the total biomass and total age-0 recruitment time series from the operating model. For the index scenarios, we included only

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<sup>6</sup> NOAA Fisheries Toolbox. 2012. Stock Synthesis, Version 3.23b . [<http://nft.nefsc.noaa.gov>].

the indices estimated using JAPLL and USLL data. Despite the JAPLL time series beginning in 1956, we maintained initiation of the assessment model in the first year specified in the operating model (1935). Assessment models based on fishery-dependent data are often initiated in the first fishing year, but our goal was to quantify differences strictly due to the indices, not to the indices and the shortened assessment time series. We also ran the assessments following a more traditional approach that began in the first year of fishing, but we did not present these results because the relative comparisons were identical, yet the overall performance of SS in all scenarios was degraded due to the shortened time series.

In addition to using fishery-dependent indices of abundance, we specified the stock-recruitment parameters (steepness and virgin recruitment) to be freely estimated. This was important, because derived management quantities are strongly informed by steepness and virgin recruitment; thus, fixing or imposing strong priors on these parameters is essentially no different than predetermining the management quantities output by the assessment (Brooks et al. 2010). Furthermore, we did not include length or age composition data in the assessment evaluation, because fishery selectivity parameters were not estimated, and the inclusion of composition data caused model instability. Aside from these changes, SS was configured identically to the original deterministic run to directly quantify effects due to the abundance indices (note: the inclusion or exclusion of age/length composition data did not affect the output of the deterministic configuration).

### *Model performance*

The parameters used in our performance evaluation included steepness ( $h$ ), virgin recruitment ( $R_0$ ), maximum sustainable yield (MSY), fishing mortality rate at MSY ( $F_{MSY}$ ), spawning biomass at MSY ( $SB_{MSY}$ ), fishing mortality rate in the final year ( $F_{2010}$ ), spawning biomass in the final year ( $SB_{2010}$ ), and fishing mortality and spawning biomass ratios in the final year ( $F_{2010}/F_{MSY}$  and  $SB_{2010}/SB_{MSY}$ ). For each abundance index scenario, parameter vectors were resampled using

MCMC with  $5 \times 10^4$  iterations, a thinning interval of 50, and a 10% burn-in period. We calculated the mean of the posterior distribution for each parameter to serve as the estimate, and we characterized uncertainty using the 95% highest posterior density interval (HDPI). The error surrounding parameter  $\theta$  ( $E_\theta$ ) was calculated as the posterior mean minus the corresponding 'true' value specified in the operating model. The magnitude and direction of the error are captured by  $E_\theta$ , but we also calculated  $\%E_\theta$  to quantify relative error.

### *Management implications*

One aspect of the stock assessment process that is particularly important to fisheries management is the determination of population (stock) status in the final (current) year of the assessment. Using MSY-based management quantities, a population is considered to be experiencing overfishing when the fishing mortality rate in the final year (in this case,  $F_{2010}$ ) exceeds  $F_{MSY}$ , and the population is labeled overfished when spawning biomass in the final year is less than  $SB_{MSY}$  (or  $B_{Final} < B_{MSY}$ ). Thus, our final assessment year ratios ( $F_{2010}/F_{MSY}$  and  $SB_{2010}/SB_{MSY}$ ) were used as indicators of final year stock status in each assessment scenario, and comparisons were made to the true stock status extracted from the operating model.

Furthermore, we evaluated the potential effects of error in management quantities on a projected future population. We used the deterministic configuration of SS to project spawning biomass for 40 years (2011 – 2050) using the  $F_{MSY}$  estimated in each scenario. The projection assumed that, following the final assessment year, the management body fixed fishing mortality at the estimated  $F_{MSY}$  without error. Then, to quantify management implications associated with each scenario, we calculated the ratio of spawning biomass in 2050 ( $SB_{2050}$ ) to the true  $SB_{MSY}$ .

### *Implementation*

With the exception of SS, the operating model and all analyses were coded using the statistical programming language R (R Core Team 2012). For efficient optimization, the SS program is

coded in AD Model Builder (ADMB Project, 2011); however, we ran SS by generating input files and calling the program using R.

## RESULTS

### *Abundance indices*

The operating model simulated realistic fishery data that were used to estimate indices of abundance for the JAPLL and USLL following three approaches (HabGLM, GLM<sub>T</sub>, CPUE<sub>N</sub>). The abundance trends estimated by these methods characterized the true biomass pattern with differing degrees of accuracy (Fig. 4, Table 5). For both longline fisheries, the HabGLM provided the best representation of true abundance, while GLM<sub>T</sub> offered the worst. For the JAPLL, all indices exhibited hyperdepletion (i.e., were overly pessimistic) due to the change in fishing depth. By contrast, the USLL indices exhibited hyperstability. The USLL indices tracked the true pattern in abundance more closely than JAPLL indices; however, the USLL time series was much shorter.

### *Assessment model performance*

Of the parameters and derived quantities estimated in the three stock assessment scenarios, nine were selected for the performance evaluation. The posterior mean and HDPI associated with these quantities were compared with the simulated true values from the operating model (Table 6). For most quantities, estimates from the HabGLM scenario were closer to the true values than those from the GLM<sub>T</sub> or CPUE<sub>N</sub> scenarios. Furthermore, true values for the quantities were contained within the HDPIs from the HabGLM scenario, while most were not surrounded by the HDPIs from the other scenarios. There were two clear exceptions to this general result; the CPUE<sub>N</sub> scenario provided the best estimate of MSY overall, and the GLM<sub>T</sub> scenario provided the best estimate of  $SB_{2010}/SB_{MSY}$ . The estimate of  $R_0$  from the GLM<sub>T</sub> scenario was closest to the true value, but the associated HDPI did not contain true  $R_0$ .



In general, plots of posterior distributions of the quantities further demonstrate that the HabGLM scenario performed better than the other scenarios (Fig. 5). For instance, the posterior distributions from the HabGLM scenario surrounded the true values of the quantities, where the true values were mostly outside the distributions from the other scenarios. The only exceptions to this were associated with  $F_{2010}$  from the GLM<sub>T</sub> scenario, MSY from the CPUE<sub>N</sub> scenario, and the stock status indicators from all scenarios.

We quantified the performance of each stock assessment scenario by calculating error, and % error for the select quantities (Table 7). Estimates from the HabGLM scenario exhibited the least amount of error on absolute and relative scales for most quantities. As previously observed (Table 6, Fig. 5), the HabGLM scenario performed best regarding  $F_{MSY}$ ,  $F_{2010}$ ,  $SB_{MSY}$ ,  $SB_{2010}$ ,  $F_{2010}/F_{MSY}$ , and  $h$ , while CPUE<sub>N</sub> performed best with MSY and GLM<sub>T</sub> provided the best estimate of  $SB_{2010}/SB_{MSY}$ . The error surrounding  $R_0$  was lowest in the GLM<sub>T</sub> scenario, but recall that the posterior distribution for  $R_0$  from the GLM<sub>T</sub> scenario did not contain true  $R_0$ , while the posterior from the HabGLM scenario did (Fig. 5). In general, the direction of the error surrounding MSY-based management quantities from all scenarios would encourage regulations that may be detrimental to the population (i.e., MSY and  $F_{MSY}$  were overestimated and  $SB_{MSY}$  was underestimated); however, MSY from the CPUE<sub>N</sub> scenario was slightly underestimated. While estimates for most MSY quantities were overly optimistic, all scenarios presented an overly pessimistic characterization of stock status in the final assessment year (i.e.,  $F_{2010}$  was overestimated and  $SB_{2010}$  was underestimated). The % error for management quantities from the HabGLM scenario was relatively low (< 20%) for MSY,  $F_{2010}/F_{MSY}$  and  $SB_{2010}/SB_{MSY}$ , moderate (20 – 50%) for  $F_{2010}$ ,  $SB_{MSY}$ , and  $SB_{2010}$ , and was high (> 50%) for  $F_{MSY}$ . For the GLM<sub>T</sub> scenario, % error was low for  $SB_{2010}/SB_{MSY}$ , moderate for MSY,  $F_{2010}$ ,  $SB_{MSY}$ ,  $SB_{2010}$ , and  $F_{2010}/F_{MSY}$  and was also high for  $F_{MSY}$ . For the CPUE<sub>N</sub> scenario, % error was low for MSY, moderate for  $SB_{2010}/SB_{MSY}$ , and the remaining quantities were not estimated accurately, with the highest % error associated with  $F_{2010}$ .

### *Management implications*

Based on the true values specified in the operating model our simulated population was subjected to overfishing in the final year ( $F_{2010}/F_{MSY} = 1.83$ ), but was not overfished ( $SB_{2010}/SB_{MSY} = 1.31$ ). The results of the HabGLM and GLM<sub>T</sub> assessment scenarios lead to the correct characterization of stock status in the final year with less error surrounding the F ratio from the HabGLM scenario, and less error surrounding the SB ratio from the GLM<sub>T</sub> scenario (Table 7). Stock status from the CPUE<sub>N</sub> scenario was overly pessimistic, because in addition to severely overestimating the degree of overfishing, the population would be considered overfished.

Using estimates of  $F_{MSY}$  from the three assessment scenarios, we projected spawning biomass and compared  $SB_{2050}$  from each  $F_{MSY}$  with true  $SB_{MSY}$ . While most quantities exhibited variability across assessment scenarios,  $F_{MSY}$  was relatively constant and overestimated (the small differences in  $F_{MSY}$  are not realized in Table 6 due to rounding). Thus, SB was projected to decrease substantially in all assessment scenarios, stabilizing well below  $SB_{MSY}$ . The percent of true  $SB_{MSY}$  projected in 2050 for the HabGLM, GLM<sub>T</sub>, and CPUE<sub>N</sub> scenarios was 28.21, 27.87, and 27.98 %, respectively. Therefore, in terms of  $F_{MSY}$ , the HabGLM scenario offers the most accurate management advice, but the realized differences among the three scenarios are negligible.

## DISCUSSION

Stock assessments of HMS rely, almost exclusively, on fishery-dependent data. To support effective HMS management and promote confidence in assessment model output, it is important to (1) understand what inherent biases may be present in the data, (2) develop methods that account for these biases, and (3) evaluate assessment model performance when different approaches are taken. Due to changes in fishing practices over time, nominal (raw) fishery-dependent CPUE does not likely capture true HMS abundance patterns; thus, numerous approaches to CPUE standardization have been developed to correct for biases in CPUE and extract an index that is proportional to abundance (Maunder and Punt 2004; Maunder et al. 2006; Lynch et al. 2012). Our results demonstrate superior assessment model performance when HabGLM is used to estimate indices of abundance from pelagic longline data as opposed to  $GLM_T$  or  $CPUE_N$ . The assessment scenario that incorporated the HabGLM index led to the correct determination of current stock status (overfishing occurring, but not overfished), the least amount of error surrounding most management quantities, and posterior distributions and HDPIs that surrounded the true values of all quantities evaluated.

It is not unexpected that assessment model performance in the HabGLM scenario was better overall than in other scenarios. Several previous studies have demonstrated a relationship between abundance index quality and assessment model performance (NRC 1998; Wang et al. 2009; Conn et al. 2010; Wilberg and Bence 2010). The HabGLM index has been shown to provide better abundance indices from pelagic longline fisheries than  $GLM_T$  or  $CPUE_N$  (Lynch et al. 2012), and in this study, HabGLM provided the most accurate reflection of true biomass over time. Thus, it stands to reason that the HabGLM assessment scenario was superior to those that

relied on lower quality abundance indices. However, in addition to simply ranking the scenarios evaluated, our goal was to quantify their influence on assessment model performance.

Understanding the effects of different approaches to estimating abundance is particularly important for HMS assessments, because of the international approach utilized by the regional fishery management organizations (RFMOs) responsible for setting most HMS regulations. With ICCAT, stock assessments are conducted by scientists from various member nations, and some contribute indices of abundance from their respective fisheries. Without a formal process in place, it is up to each scientist to determine how their abundance index is estimated, and due to their proprietary nature, the raw fishery data used for their analyses are typically not available for error checking or reanalysis by the assessment committee. Inevitably, indices of varying quality are contributed, and the committee is faced with the difficult decision of determining which indices to include in the assessment, and how to do so. Therefore, studies such as ours can help guide discussions among assessment committees, and provide scientific justification for the exclusion, inclusion, or weighting of various indices.

In addition to our study (and others that underscore the importance of abundance index quality), there are a number of simulation analyses that offer other useful guidelines for implementing statistical catch-at-age assessment models. For example, reliability of productivity estimates is related to several variables (Ianelli 2002; Conn et al. 2010), length and/or age composition data have been highlighted as important inputs (Yin and Sampson 2004; Wetzel and Punt 2011), and the safest assumption regarding catchability may be that it varies over time (Wilberg and Bence 2010). Overall, these previous simulation studies evaluated effects of numerous assumptions and data inputs over a wide range of theorized population and fishery dynamics. This general approach makes the results broadly applicable; however, a common conclusion of most studies is that additional analyses are required to test specific questions, or to quantify effects for a particular stock. This led many studies to include specific test cases. Our

results may well extend to HMS worldwide, but our study was specifically configured to quantify the performance of the Atlantic blue marlin stock assessment as related to indices of abundance.

Overall, the case to be made for using HabGLM in blue marlin and other HMS stock assessments is strong, but we did not observe superior performance for every aspect of the assessment model. For instance, the GLM<sub>T</sub> scenario provided estimates of  $R_0$  and  $SB_{2010}/SB_{MSY}$  with the least amount of error, and the error surrounding MSY was lowest in the CPUE<sub>N</sub> scenario. While  $R_0$  from the GLM<sub>T</sub> scenario is closest to the true value, the corresponding HDPI and posterior distribution did not contain the true value. Since true  $R_0$  was contained in the HDPI and posterior distribution from the HabGLM scenario, there is some probability that an assessment using HabGLM would arrive at the true estimate, and we maintain that HabGLM is superior to GLM<sub>T</sub> for HMS assessments. However, the estimate of MSY from the CPUE<sub>N</sub> scenario is clearly superior to MSY estimates from the other scenarios. This quantity can be of particular importance to management agencies, but we were unable to determine why the CPUE<sub>N</sub> scenario performed so well with regard to MSY. Nevertheless, the CPUE<sub>N</sub> scenario did not perform well overall (largest % error for most quantities and incorrectly declared the population overfished); hence, we would not recommend the use of fishery-dependent nominal CPUE as index of abundance in any assessment.

While the HabGLM scenario performed best of those evaluated, this study raises concerns surrounding HMS stock assessments in general. As with many assessment model performance evaluations, the population and fishery dynamics specified in the estimation model were identical to those in the operating model, with the exception of the variable of interest (the abundance indices, in this case). This approach is important for evaluating effects due to a specific attribute of an assessment model, because incorporating multiple sources of variability may confound the analyses. However, accurate knowledge of all aspects (except one) of a population and associated fisheries is unrealistic in a real-world assessment. A typical stock assessment would likely be faced with substantial parameter and model misspecification (Yin and

Sampson 2004; Conn et al. 2010). Thus, the performance quantified for the various assessment scenarios likely represents their best case. Unfortunately, the scenario that performed best overall (HabGLM), still exhibited large relative errors for all quantities (Table 7). In fact, if the management agency implemented regulations (without implementation error) that fixed fishing mortality at  $F_{MSY}$  estimated by the HabGLM scenario, spawning biomass would decline over the subsequent 40 year period to a level that is 28.21% of their target spawning biomass ( $SB_{MSY}$ ). Consequently, even when the best available approach to index standardization is used without error in input data, and when an accurate characterization of population and fishery dynamics is specified in the assessment model, derived management quantities may still be overly optimistic. Hence, in the best case scenario, there exists the potential for inadvertent mismanagement and substantial decline of an important natural resource. We believe that this is the consequence of a strict reliance on fishery-dependent data; therefore, we cannot overemphasize the importance of independent research and monitoring programs for all exploited organisms. For HMS, comprehensive monitoring programs are considered cost prohibitive due to the geographic scale over which these programs would need to be conducted; however, if sustainable HMS management is a high priority, these investments are crucial.

Further evaluation is required to understand why estimates of MSY-based quantities from all scenarios were overly optimistic. Estimates of steepness were overestimated across all scenarios, which likely caused the overly optimistic management quantities (Conn et al. 2010), but we were unable to determine how the abundance indices led to overestimates of steepness. The JAPLL index offered a longer time series than the USLL index, deviated more from the true biomass pattern, and exhibited hyperdepletion, where the USLL index exhibited hyperstability. Since the two indices were equally weighted in the assessment, we would suspect that the length of the JAPLL time series would have caused it to be more influential over assessment results, and given that the JAPLL index exhibited hyperdepletion, we would expect steepness to be underestimated rather than overestimated. While we are not certain of the exact cause of

steepness overestimates, it may be due to the relative influence of the USLL index or the fact that true steepness was close to the lower bound for this parameter. Additionally, the degree to which  $F_{MSY}$  estimates were overestimated was similar across scenarios. Thus, the importance of abundance index quality is not realized with regard to  $F_{MSY}$ .

The results of our study are partially conditioned on one important feature: in the operating model, we specified a vertical catchability profile that followed thermal habitats. This profile caused catches to be partitioned by habitat, thereby driving the importance of the habitat variables included in HabGLM. In general, we configured the operating model to follow a contemporary understanding of the population dynamics of Atlantic blue marlin, and there is a wealth of information to suggest that catchability for blue marlin (and other HMS) is not constant over vertical temperature regimes. Archival tagging studies have demonstrated that HMS are not homogeneously distributed across vertical habitat, and Brill and Lutcavage (2001) assert that HMS depth distributions are governed by the relative change in water temperature with depth. In other words, HMS are physiologically confined to a thermal envelope irrespective of absolute temperature. It is for this reason that we specified our vertical catchability profile according to relative temperature. A valid argument has been made that catchability does not necessarily correlate with a species' vertical distribution, because vertical migrations are likely motivated by feeding (Goodyear et al. 2003). While we agree it is unlikely that blue marlin vertical catchability is linearly related to their vertical distribution, we contend that the catchability profile specified in our operating model (highest probability of capture in surface waters) is a best approximation of the true profile. Many archival tagging studies have demonstrated that blue marlin distribute predominately in surface waters with occasional deep dives (Graves et al. 2002; Kerstetter et al. 2003; Saito et al. 2004; Kraus and Rooker 2007; Goodyear et al. 2008; Dutton 2010). Furthermore, the recreational fishery catches blue marlin in surface waters. Based on the fact that blue marlin spend the majority of their time in surface or near-surface waters, and will take a

baited hook in surface waters, we maintain that catchability is likely highest at the surface, and may indeed follow a profile similar to that specified in the operating model.

Our study emphasizes the importance of implementing HabGLM when using pelagic longline data to estimate HMS abundance for stock assessments; however, there are several limitations that should be considered. Despite our attempts to replicate true population and fishery dynamics, the operating model is inherently a simplification of extremely complex processes. This is true of all modeling efforts, and while results may vary over differing levels of complexity, it is difficult, if not impossible, to identify the ideal level for a given study. Secondly, the effects of abundance index quality were evaluated in isolation. There are many unknowns in fish stock assessments (e.g., growth dynamics, natural mortality rates, fishery selectivity, etc.), but in our estimation model, these were fixed at their known values. In reality, additional uncertainties may combine to obscure effects due to abundance indices quantified herein. Next, slight inconsistencies between operating and estimation models may have contributed a small amount of error to the performance evaluation, but we feel our approach to correcting for inconsistencies drastically minimized any error. Additionally, the catchability profile specified in the operating model was strictly related to relative temperature, but Prince et al. (2010) demonstrated that the dissolved oxygen content of the water by depth may also influence HMS catch rates in the Atlantic Ocean. Dissolved oxygen limitation is most relevant in the eastern tropical Atlantic, but we did not incorporate this attribute in any region. Finally, the fishery and oceanographic data used in the HabGLM index estimation were incorporated without error. However, these uncertainties may not drastically affect the results, because Lynch et al. (2012) showed that HabGLM was not particularly sensitive to error in estimates of fishing depth. Given the complexity of fishery stock assessments, there are many potential sources of uncertainty. While numerous studies have been conducted, we recommend continued research to quantify effects of multiple inputs and assumptions in isolation, in combination, and for general and specific scenarios.



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TABLES

Table 1. Formulation of the population dynamics component of the operating model.

Quantity	Symbol	Definition
Length at age by sex	$L_{a,x}$	$L_{a,x} = L_{\infty,x}(1 - e^{-k_x(a-t_0)})$
Weight at age by sex	$W_{a,x}$	$w_{a,x} = (\alpha_x L_{a,x}^{\beta_x})$
Proportion mature at age by sex	$m_{a,x}$	$m_{a,x} = \frac{1}{1 + e^{-\eta(a-a_{m50,x})}}$
Natural mortality rate at age by sex	$M_{a,x}$	$M_{a,x} = M_u W_{a,x}^b$
Total mortality rate at age by sex and year*	$Z_{a,x,y}$	$Z_{a,x,y} = M_{a,x} + F_{a,x,y}$
Abundance at age by sex and year	$N_{a,x,y}$	$N_{1,x,1935} = R_0/2$ $N_{a+1,x,1935} = N_{a,x,1935} e^{-M_{a,x}} \quad \forall a \in (0, \dots, A-1)$ $N_{A,x,1935} = N_{A-1,x,1935} \frac{e^{-M_{A-1,x}}}{1 - e^{-M_{A,x}}}$ $N_{1,x,y+1} = 0.5 \left( \frac{0.8R_0 h SB_y}{0.2SB_0(1-h) + (h-0.2)SB_y} e^{e_y^R - 0.5\sigma_R^2} \right)$ $N_{a+1,x,y+1} = N_{a,x,y} e^{-Z_{a,x,y}} \quad \forall a \in (0, \dots, A-1)$ $N_{A,x,y} = N_{A-1,x,y-1} e^{-Z_{A-1,x,y-1}} + N_{A,x,y-1} e^{-Z_{A,x,y-1}}$
Biomass at age by sex and year	$B_{a,x,y}$	$B_{a,x,y} = N_{a,x,y} w_{a,x}$
Spawning biomass of females by year	$SB_y$	$SB_y = \sum_a B_{a,female,y} m_{a,female}$

\* $F_{a,x,y}$  was zero in years with no fishing (1935 – 1955).

Table 2. Formulation of the fishery dynamics component of the operating model.

Quantity	Symbol	Definition
Selectivity at age by sex and fishery	$s_{a,x,f}$	$s_{a,x,f} = \frac{1}{1 + e^{-\eta_f(a-a_{50,x})}}$
Catchability by fishery and fishing year	$q_{f,fy}$	$q_{f,1} = \sum_{fy=1}^3 \left( \frac{nCPUE_{f,fy}}{\hat{N}_{fy}} \right) / 3$ $q_{f,fy} = q_{f,fy}(1 + \varepsilon_{f,fy}^2) \quad \forall fy \in (2, \dots, FY)$
Longline catchability by fishery and habitat	$q_{LL,H,fy}$	$q_{LL,H,1} = q_{LL,1} * p_H$
Proportion of overall catchability by habitat	$p_H$	$p_H = \frac{PD_H}{\sum_H PD_H} \quad \forall H \in (0, \dots, 26)$
Catch at age by sex, fishery, effort unit, region, season, and year	$C_{a,x,f,Eu,r,S,y}$	$C_{a,x,f,Eu,r,S,y} = s_{a,x,f} \left[ \sum_H q_{f,H,y} E_{f,Eu,r,S,H,y} \right] P_{a,r,S} B_{a,x,y} e^{[e_{a,x,f,Eu,r,S,y}^c - 0.5(\sigma_f^2)]}$
True removals at age by sex, fishery, effort unit, region, season, and year	$TR_{a,x,f,Eu,r,S,y}$	$TR_{a,x,f,Eu,r,S,y} = C_{a,x,f,Eu,r,S,y} (1 - LD_{f,Eu,r,S,y} DS_{f,Eu,r,S,y})$
Reported landings at age by sex, fishery, effort unit, region, season, and year	$RL_{a,x,f,Eu,r,S,y}$	$RL_{a,x,f,Eu,r,S,y} = C_{a,x,f,Eu,r,S,y} (1 - LD_{f,Eu,r,S,y})$
Fishing mortality rate by age, sex, and year	$F_{a,x,y}$	<p>Calculated as the value for <math>F_{a,x,y}</math> that optimizes the following:</p> $\sum_{f,s,r,S} TR_{a,x,f,Eu,r,S,y} = B_{a,x,y} \left( \frac{F_{a,x,y}}{F_{a,x,y} + M_{a,x}} \right) [1 - e^{(-F_{a,x,y} + M_{a,x})}]$
Annual fishing mortality rate	$F_y$	<p>Calculated as the value for <math>F_y</math> that optimizes the following:</p> $\sum_{a,x,f,s,r,S} TR_{a,x,f,Eu,r,S,y} = \left( \sum_{a,x} B_{a,x,y} \right) \left( \frac{F_y}{F_y + \bar{M}_y} \right) [1 - e^{(-F_y + \bar{M}_y)}]$

Table 3. Input variables for the operating model.

Variable	Definition	Value(s)
$a$	Discrete ages ( $A$ : beginning of plus group)	0 – 19+
$x$	Sex categories	Male, female
$y$	Discrete years	1935 – 2050
$L_{\infty,x}$	von Bertalanffy asymptotic size*	178.64 ( $x$ = male) 247.07 ( $x$ = female)
$k_x$	von Bertalanffy growth rate*	0.90 ( $x$ = male) 0.78 ( $x$ = female)
$t_0$	von Bertalanffy age at size 0*	-0.2
$\alpha_x$	Length-weight constant <sup>†</sup>	$2.47 \times 10^{-6}$ ( $x$ = male) $1.90 \times 10^{-6}$ ( $x$ = female)
$\beta_x$	Length-weight constant <sup>†</sup>	3.22 ( $x$ = male) 3.28 ( $x$ = female)
$\eta$	Slope parameter for logistic maturity function <sup>‡</sup>	1.0
$a_{m50,x}$	Age at 50% maturity <sup>‡</sup> ( $\bar{M}$ = natural mortality rate averaged over ages)	$a_{m50,x} = \frac{1}{k_x} \log \left( \frac{3k_x + \bar{M}_x}{\bar{M}_x} \right)$
$M_u$	Natural mortality rate at unit weight (1 g) <sup>§</sup>	3.69
$b$	Allometric scaling factor <sup>§</sup>	-0.31
$R_0$	Asymptotic recruitment at $F = 0$ *	$1.80 \times 10^5$
$h$	Steepness*	0.36
$\varepsilon_y^R$	Recruitment deviations <sup>†</sup>	$N(\mu = 0, \sigma_R = 0.4)$
$f$	Fishery	Longline (LL) from US or Japan, gillnet (GN) from Venezuela or Ghana, US recreational (REC)
$\eta_f$	Slope parameter for logistic selectivity function*	2.0 ( $f$ = LL) 2.5 ( $f$ = GN) 1.8 ( $f$ = REC)
$\alpha_{s50,x}$	Age at 50% selectivity*	6.0 ( $x$ = male) 5.5 ( $x$ = female)
$f_y$	Counter for fishing year per fishery	1 – final $f_y$
$nCPUE_f$	Nominal catch-per-unit-effort observed per fishery	Data obtained from <a href="http://www.iccat.int">http://www.iccat.int</a> <sup>¶</sup>
$\hat{N}_{fy}$	Total estimated abundance per fishing year*	Variable, depending on fishing year per fishery
$\varepsilon_f^q$	Catchability deviations per fishery	$N(\mu = 5 \times 10^{-3}, \sigma_R = 1 \times 10^{-3})$
$H$	Temperature change relative to surface in 1°C bins	1 – 26
$PD_H$	Value of probability density function (PDF) per $H$	$PDF[N(\mu = 0, \sigma = 1.2)]$
$Eu$	Effort units per fishery	Individual set ( $f$ = LL) Sets per year, region, season ( $f$ = GN) Fishing hours per year, region, season ( $f$ = REC)
$S$	Season (calendar quarter)	Jan-Mar, Apr-Jun, Jul-Sep, Oct-Dec

$E$	Effort	Per hooks ( $f = LL$ ) Per set ( $f = GN$ ) Per hour ( $f = REC$ )
$\varepsilon^C$	Process error to model stochastic fishing: $N(\mu = 0, \sigma_f^C)$	$\sigma_{LL}^C = 0.05$ $\sigma_{GN}^C = 0.025$ $\sigma_{REC}^C = 0.06$
$LD_f$	Proportion of catch discarded alive* ( $LD_{GN} = 0$ )	$LD_{JAPLL} = \begin{cases} 0 & \forall y < 2001 \\ N(0.3, 0.02) & \forall y \in (2001, \dots, 2050) \end{cases}$ $LD_{USLL} = \begin{cases} 0 & \forall y < 1988 \\ N(0.3, 0.02) & \forall y \in (1988, \dots, 2003) \\ N(0.47, 0.02) & \forall y \in (2004, \dots, 2050) \end{cases}$ $LD_{REC} = \begin{cases} e^{0.1y-199.9} & \forall y < 1999 \\ N(0.97, 0.01) & \forall y \in (1999, \dots, 2050) \end{cases}$
$DS_f$	Proportion of discards that survive from LL**, and REC	$DS_{LL} \sim N(0.99, 5 \times 10^{-3})$ $DS_{REC} \sim N(\mu_{hk,y}, 5 \times 10^{-3})$
$\mu_{hk,y}$	Weighted mean proportion of discards that survive based on REC hook type	$\mu_{hk,y} = 0.5[PC_y \mu_C + (1 - PC_y) \mu_J]$
$\mu_C, \mu_J$	Mean proportion of discards that survive in the REC fishery caught on circle (C) or J-style (J) hooks <sup>††</sup>	$\mu_J = 0.93, \mu_C = 0.99$
$PC_y$	Proportion of circle hook use	$\begin{cases} 0 & \forall y < 2006 \\ 0.05, 0.1, 0.2 & \text{for } y = 2007, 2008, 2009 \\ 0.25 & \forall y > 2009 \end{cases}$

\*Based on the results of the 2011 Atlantic blue marlin stock assessment (ICCAT 2012).

†Obtained from Prager et al. (1995).

‡Following Conn et al. (2010).

§Following mortality at age for oceanic fishes from Lorenzen (1996).

¶Value for  $\sigma_R$  reflects a relatively low estimate considering Beddington and Cooke (1983).

¶Data accessed September 27, 2011.

\*Based on Diaz (2008) for longlines.

\*\*Obtained from Kerstetter et al. (2003).

††Obtained from Graves and Horodysky (2010).



Table 4. Proportional distribution of Atlantic blue marlin by age, region and season assumed in the operating model.

Age	WT	ET	SW	Region			
				SE	NW	NE	CG
<i>Season: Jan - Mar</i>							
0	0.25	0.75	0	0	0	0	0
1	0.1	0.4	0.3	0.05	0.05	0	0.1
2	0.1	0.3	0.3	0.05	0.05	0.05	0.15
3+	0.05	0.25	0.3	0.05	0.1	0.05	0.2
<i>Season: Apr - Jun</i>							
0	0.25	0.75	0	0	0	0	0
1	0.1	0.3	0.25	0.05	0.1	0.05	0.15
2	0.1	0.25	0.25	0.05	0.1	0.05	0.2
3+	0.05	0.2	0.25	0.05	0.2	0.05	0.2
<i>Season: Jul - Sep</i>							
0	0.25	0.75	0	0	0	0	0
1	0.1	0.4	0.05	0	0.3	0.05	0.1
2	0.1	0.3	0.05	0.05	0.3	0.05	0.15
3+	0.05	0.25	0.1	0.05	0.3	0.05	0.2
<i>Season: Jul - Sep</i>							
0	0.25	0.75	0	0	0	0	0
1	0.1	0.3	0.15	0.05	0.2	0.05	0.15
2	0.1	0.25	0.15	0.05	0.2	0.05	0.2
3+	0.05	0.2	0.2	0.05	0.25	0.05	0.2

Table 5. Summary of models from the abundance index scenarios used in the performance evaluation. Three scenarios were used to generate abundance indices from data simulated for the pelagic longline fisheries of Japan (JAPLL) and the US (USLL). The explanatory variables for the binomial (B) and positive (P) components of the delta-lognormal GLMs were provided, as well as median percent difference (MPD) and standard deviation of percent difference (SDPD) for each index relative to simulated biomass.

Fishery	Index scenario	Explanatory variables	MPD	SDPD
JAPLL	HabGLM	B: Year, Area, MaxDT P: Year, Area, Season, MaxDT	16.44	28.16
	GLM <sub>T</sub>	B: Year, Area, Season, *Year*Area, *Area*Season P: Year, Area, Season, *Year*Area, *Year*Season, *Area*Season	98.05	129.92
	CPUE <sub>N</sub>	NA	52.08	31.20
USLL	HabGLM	B: Year, Area, Season, MaxDT P: Year, Season, MaxDT	8.80	12.86
	GLM <sub>T</sub>	B: Year, Area, Season P: Year, Area, Season, *Year*Season, *Area*Season	95.55	36.49
	CPUE <sub>N</sub>	NA	57.00	29.30

\*Interaction term fitted as random effect

Table 6. Posterior mean values for select parameters and management quantities estimated by Stock Synthesis (SS), including maximum sustainable yield (MSY), the fishing mortality rate (F) and spawning biomass (SB) at MSY and in the final assessment year (2010), final assessment year status indicators ( $F_{2010}/F_{MSY}$  and  $SB_{2010}/SB_{MSY}$ ), steepness ( $h$ ), and virgin recruitment ( $R_0$ ). Values were provided for scenarios where SS was fitted using abundance indices that were estimated following three approaches (HabGLM, GLM<sub>T</sub>, and CPUE<sub>N</sub>). The true values from the operating model are also included. Uncertainty was characterized using the 95% highest posterior density interval (HPDI).

Quantity	True value	Scenario 1: HabGLM (HPDI)	Scenario 2: GLM <sub>T</sub> (HPDI)	Scenario 3: CPUE <sub>N</sub> (HPDI)
$F_{MSY}$	0.04	0.07 (0.02, 0.11)	0.07 (0.06, 0.09)	0.07 (0.05, 0.10)
$F_{2010}$	0.06	0.09 (0.05, 0.12)	0.09 (0.07, 0.13)	0.18 (0.11, 0.27)
$SB_{MSY}$ ( $10^4$ t)	3.21	1.99 (0.92, 3.37)	1.90 (1.61, 2.25)	1.45 (0.96, 1.98)
$SB_{2010}$ ( $10^4$ t)	4.21	2.95 (1.68, 4.41)	2.62 (1.59, 3.58)	1.30 (0.72, 1.88)
$MSY$ ( $10^3$ t)	1.96	2.31 (1.58, 3.31)	2.68 (2.50, 2.89)	1.91 (1.67, 2.23)
$F_{2010}/F_{MSY}$	1.83	1.50 (0.53, 2.58)	1.25 (0.89, 1.74)	2.69 (1.32, 4.39)
$SB_{2010}/SB_{MSY}$	1.31	1.56 (0.95, 2.47)	1.38 (0.91, 1.85)	0.92 (0.50, 1.46)
$h$	0.36	0.50 (0.28, 0.68)	0.53 (0.48, 0.59)	0.52 (0.42, 0.65)
$R_0$ ( $10^5$ n)	1.81	1.30 (0.95, 1.87)	1.35 (1.24, 1.50)	1.00 (0.83, 1.28)

Table 7. Performance of the Stock Synthesis (SS) assessment model expressed in terms of select parameters, including maximum sustainable yield (MSY), the fishing mortality rate (F) and spawning biomass (SB) at MSY and in the final assessment year (2010), final assessment year status indicators ( $F_{2010}/F_{MSY}$  and  $SB_{2010}/SB_{MSY}$ ), steepness ( $h$ ), and virgin recruitment ( $R_0$ ). Performance metrics include error, and % error. For the assessment scenarios, SS was fitted using abundance indices that were estimated following three approaches (HabGLM, GLM<sub>T</sub>, and CPUE<sub>N</sub>). Assessment scenarios corresponding to the best performance metric are highlighted (grey).

Quantity	Error			% error		
	HabGLM	GLM <sub>T</sub>	CPUE <sub>N</sub>	HabGLM	GLM <sub>T</sub>	CPUE <sub>N</sub>
$F_{MSY}$		0.04	0.04		105.81	99.06
$F_{2010}$		0.03	0.12		40.18	179.60
$SB_{MSY}$ (t)		$-1.31 \times 10^4$	$-1.76 \times 10^4$		40.80	54.81
$SB_{2010}$ (t)		$-1.59 \times 10^4$	$-2.91 \times 10^4$		37.72	69.08
MSY (t)	350.53	726.74		17.92	37.16	
$F_{2010}/F_{MSY}$		-0.58	0.86		31.68	46.86
$SB_{2010}/SB_{MSY}$	0.25		-0.39	19.18		29.56
$h$		0.17	0.16		47.77	44.38
$R_0$ (n)	$-5.08 \times 10^4$		$-8.05 \times 10^4$	28.10		44.55

FIGURES

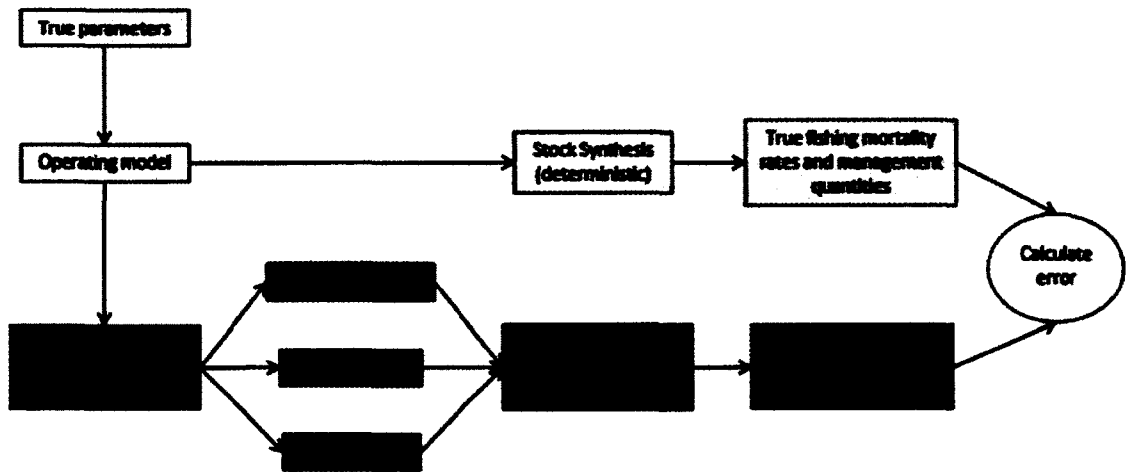


Fig. 1. Overview of the simulation procedure.

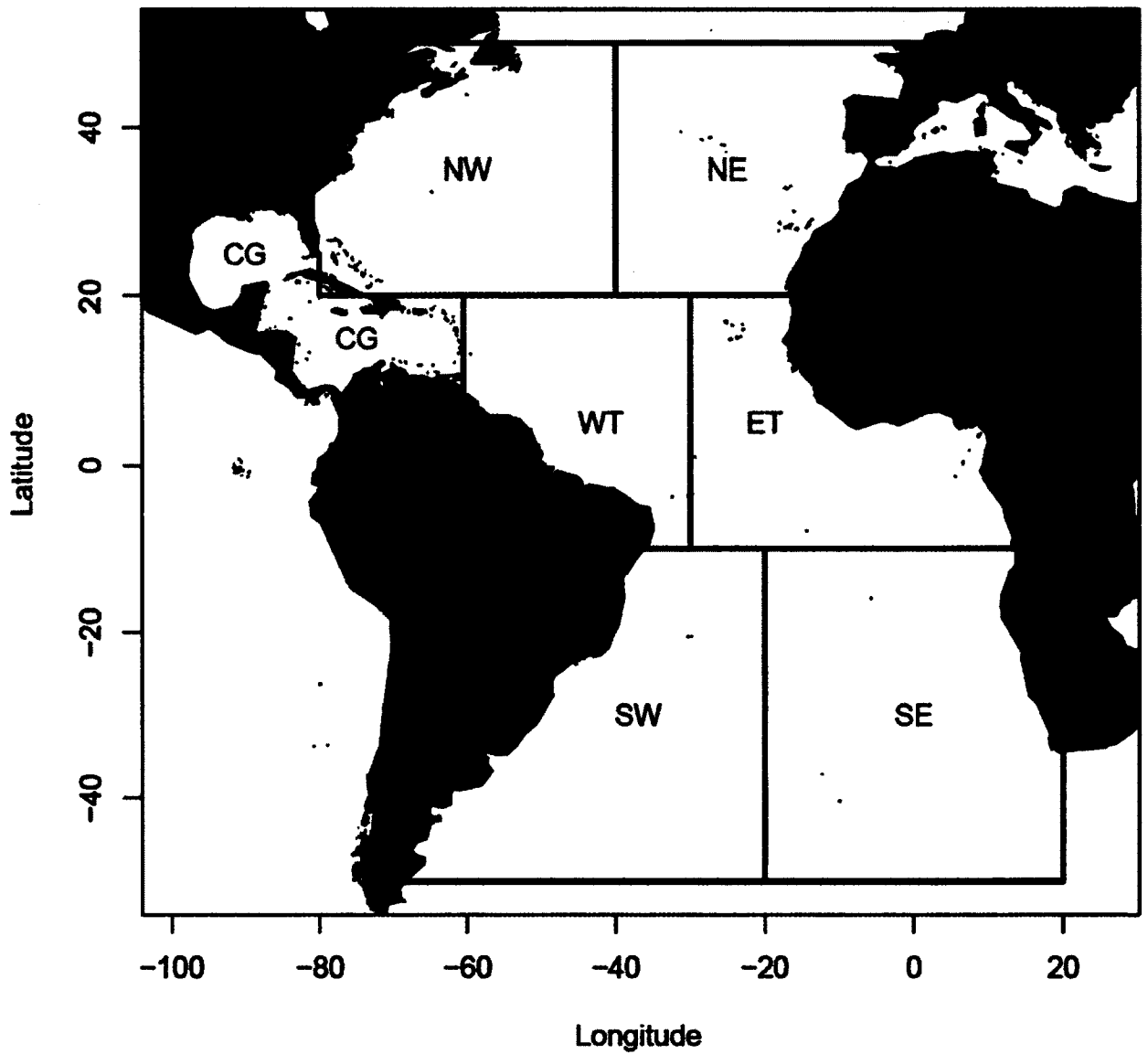


Fig. 2. Map of regions defined in the operating model for simulating fishery and population dynamics related to blue marlin in the Atlantic Ocean and adjacent seas. Regions include northwest (NW), northeast (NE), Caribbean Sea/Gulf of Mexico (CG), western tropical (WT), eastern tropical (ET), southwest (SW), and southeast (SE).

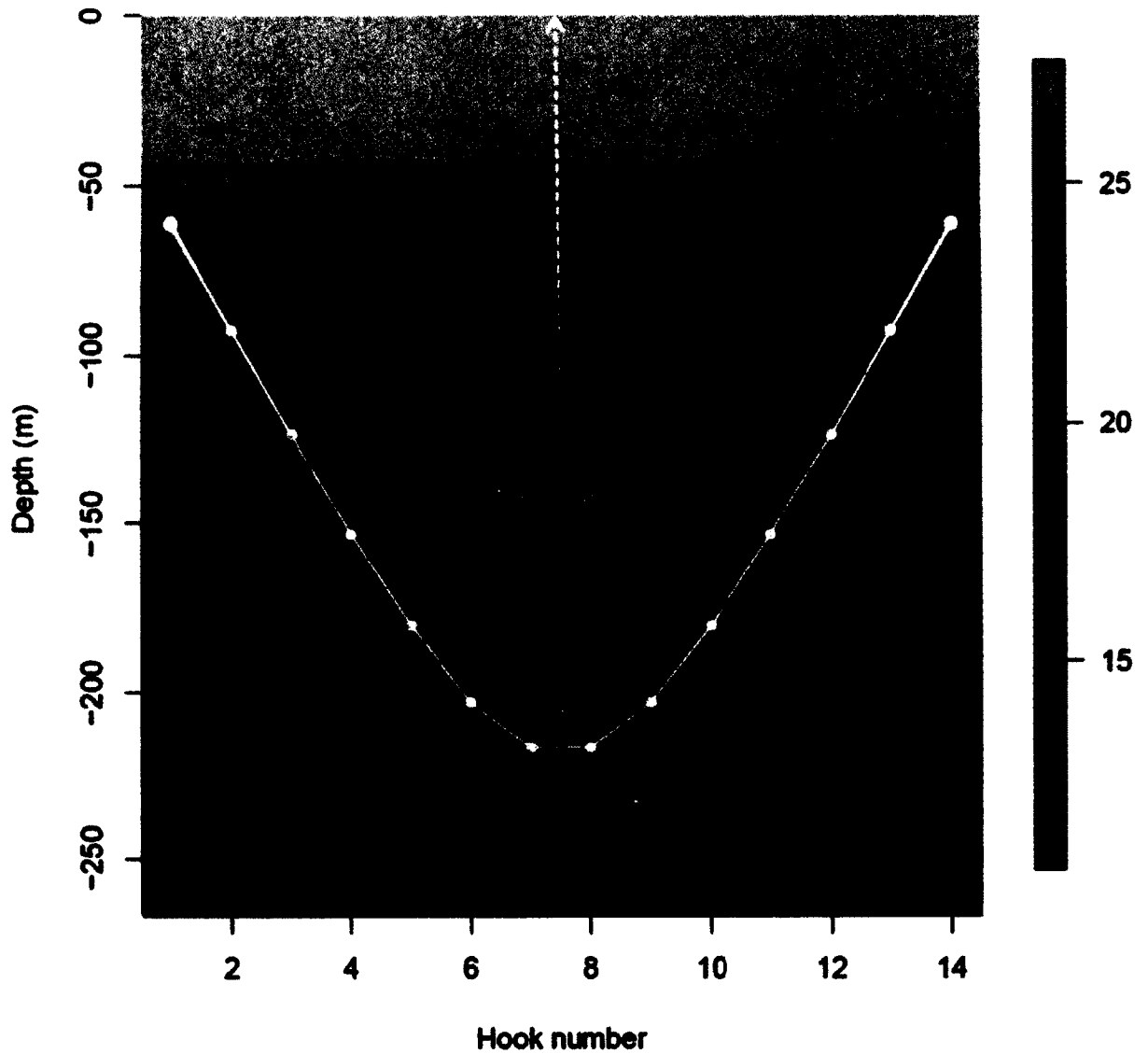


Fig. 3. Visualization of a longline set, depicting the fishing depth of each hook (filled circles) in a single panel, predicted using catenary algorithms and realistic gear dimensions for a moderately deep set (14 hooks between floats). A temperature profile (gradient, ° C) was assigned to this example, demonstrating one potential relationship between fishing depth and temperature. Also, the HabGLM habitat variables, including minimum temperature fished (MinT) and maximum deviation from surface temperature (Max $\Delta$ T) that would be extracted for this longline set are displayed.

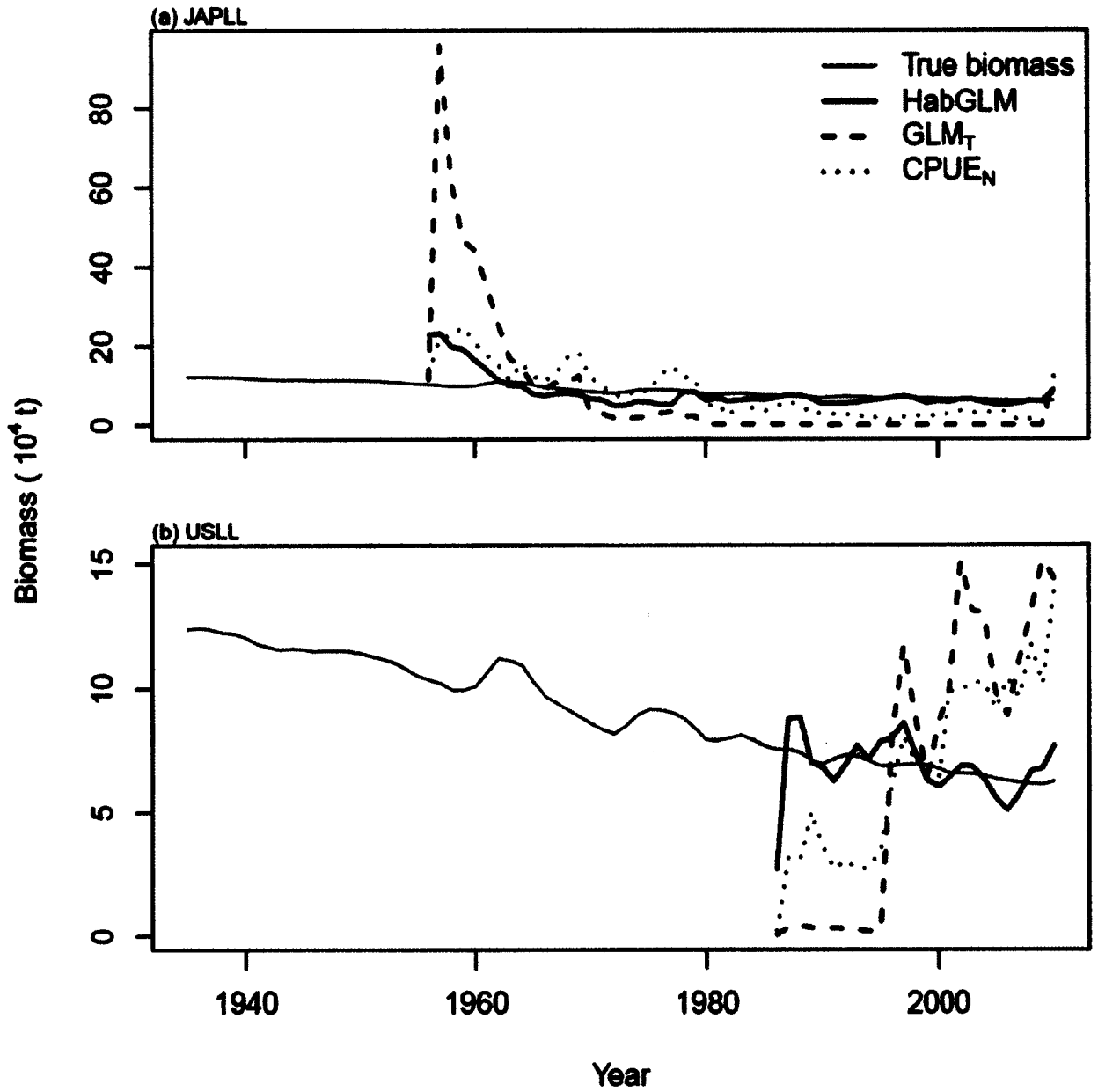


Fig. 4. Indices of abundance estimated from simulated data for the Japanese longline (a, JAPLL), and US longline (b, USLL) fisheries, following three approaches (HabGLM, GLM<sub>T</sub>, and CPUE<sub>N</sub>). The indices are scaled for comparison with the simulated true biomass pattern.



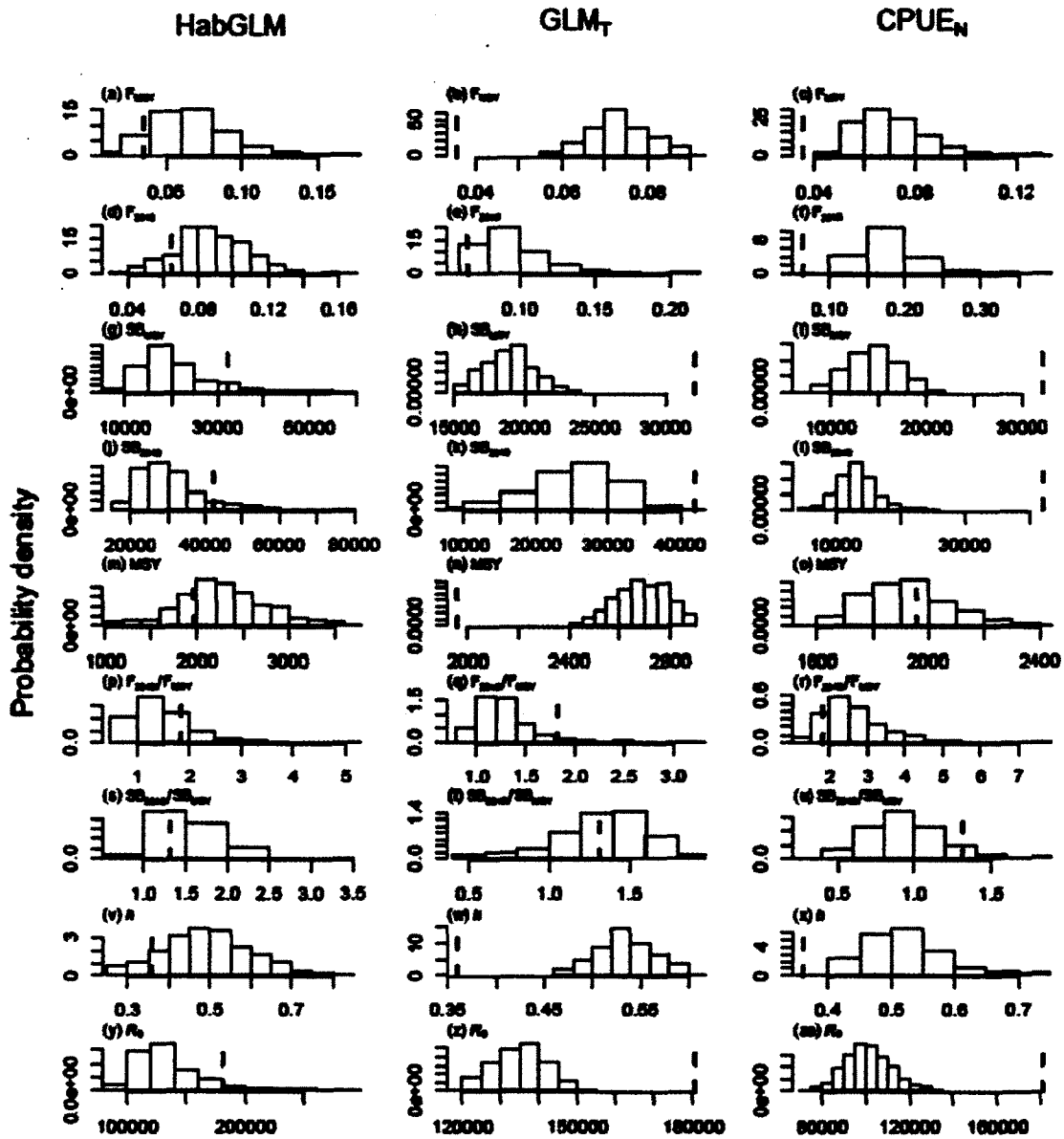


Fig. 5. Posterior distributions of select parameters and derived quantities estimated by Stock Synthesis (SS), including maximum sustainable yield (MSY), the fishing mortality rate ( $F$ ) and spawning biomass (SB) at MSY and in the final assessment year (2010), final assessment year status indicators ( $F_{2010}/F_{MSY}$  and  $SB_{2010}/SB_{MSY}$ ), steepness ( $h$ ), and virgin recruitment ( $R_0$ ). For the assessment scenarios, SS was fitted using abundance indices that were estimated following three approaches (HabGLM,  $GLM_T$ , and  $CPUE_N$ ). Vertical dashed lines represent the simulated true value of the quantities.

## CONCLUSIONS

The research studies that comprise this dissertation focused on the role of habitat in understanding the population dynamics, and assessing the stocks of highly migratory species (HMS). The results of each study have direct implications for HMS management. For instance, when habitat was directly incorporated into methods used for estimating abundance, the accuracy of abundance estimates improved. Accordingly, higher quality abundance indices resulted in enhanced performance of a stock assessment model. Therefore, these studies suggest that when habitat is accounted for in HMS assessments, management agencies are more equipped to enact measures that promote sustainability.

Additionally, when estimated abundance trends incorporated habitat, the Atlantic HMS community was portrayed as generally depleted. Conversely, substantial decreases in abundance were not observed for several species, while others exhibited signs of growth and/or recovery. These mixed results align with those of Worm et al. (2009), who posited that the current status of global fisheries is transitioning from being mostly overexploited to being managed sustainably.

While habitat considerations advance the stock assessment and management of HMS, the advancements, unfortunately, do not necessarily lead to adequate results. Even when accounting for all sources of bias, including habitat, indices of abundance estimated from fishery-dependent catch rates still may not reflect true abundance trends. Thus, bias may persist in the stock assessments even in best case scenarios. This clearly emphasizes that independent stock monitoring programs are essential for effective fisheries management. Given vast spatial distributions, the cost of monitoring programs for HMS would be substantial. However, it is reckless to exploit renewable resources when there is no reason to suggest that management regulations can reliably achieve their goals. Therefore, nations with an interest in harvesting these

important internationally-shared resources should collaborate to support implementation of comprehensive scientific monitoring programs.

Unfortunately, the establishment of HMS monitoring programs is a nontrivial enterprise that would require significant time and resources. Thus, it is unlikely that HMS will be extensively monitored in the near future. Moreover, given a long history of exploitation without scientific monitoring, any established programs would be most useful for characterizing future population dynamics, while fishery-dependent data would continue to serve as the basis for understanding historical abundance patterns.

A projected reliance on fishery-dependent data highlights the relevance of this dissertation research, and emphasizes the importance of continuing and expanding the research. For instance, it would be fairly straightforward to incorporate additional considerations in the method proposed for estimating HMS abundance trends (HabGLM; Chapters 2, 3, and 4). Fisheries that catch HMS do not distribute randomly over space; therefore, abundance patterns estimated using catches from select geographic areas may not reflect abundance trends in areas that were not fished. Hence, failure to account for dynamics in unfished spatial cells can bias abundance estimates (Walters 2003). An analytical approach has been described that utilizes data imputation to account for biases due to spatial dynamics (Carruthers et al. 2011), and since this approach was cast in a linear modeling framework, it could easily be merged with the HabGLM.

The HabGLM could be further expanded to incorporate habitat variables, in addition to temperature, that may influence fishery catch rates. For example, HMS habitat compression has been linked to oxygen limitation in areas with relatively shallow oxygen minimum zones (OMZs), such as the eastern tropical Atlantic Ocean (Prince et al. 2010). This localized habitat compression likely causes spatial variations in catchability, and therefore should be accounted for when estimating HMS abundance trends. To incorporate oxygen limitation in the HabGLM when using pelagic longline data, either the corresponding OMZ depth could be estimated and categorized for each set, or spatial regions with similar OMZ depths could be defined. There are

many additional habitat/environmental variables worth researching to determine their effects on HMS populations. A subset of these relevant variables includes phytoplankton biomass (chlorophyll *a* concentration), salinity, predator/prey biomass, solar radiation, lunar phase, and sea surface height.

Beyond expanding the HabGLM, there are several areas of more general research that I am particularly interested in pursuing. For one, I hope to continue investigating environmental influences on fish populations, and how to incorporate those influences into fishery stock assessments. Secondly, relating natural influences to population dynamics facilitates a transition from single-species stock assessments to more holistic ecosystem assessments. This transition may be imminent, because living resources affect, and are affected by various ecosystem features. I would like to contribute to the development of ecosystem assessments in the context of marine resource management by researching the influences of habitat on fish community dynamics. Finally, the goal of my research was to advance HMS stock assessments by improving methods used to understand historical population trends. With improved assessment accuracy, fishery managers can use historical stock assessments to set future harvests at levels that promote long-term sustainability. However, given changing environments, harvest levels may need to vary over time to meet management objectives. Fortunately, global climate models can be used to project future habitat; thus, if habitat is incorporated in stock assessments, population projections could simultaneously account for the effects of climate change, climate variability, and harvesting. It is my goal to research the coupling of fishery stock assessment models/ecosystem assessment models and global climate models to further advance fishery stock assessments and projections under various management scenarios.

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