Fisheries Research 102 (2010) 229–239

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data

Julia K. Baum[a,*], Wade Blanchard[b]

[a] Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada
[b] Department of Mathematics and Statistics, Dalhousie University, Chase Building, Halifax, Nova Scotia B3H 3J5, Canada

ARTICLE INFO

Article history:
Received 18 September 2009
Received in revised form
13 November 2009
Accepted 19 November 2009

Keywords:
Bycatch
Blue shark
Catch per unit effort
Generalized linear mixed models
Pelagic longline

ABSTRACT

We estimate recent (1992–2005) trends in relative abundance for Northwest Atlantic oceanic and large coastal sharks, using generalized linear mixed models to standardize catch rates of eight species groups as recorded by U.S. pelagic longline fishery observers. Models suggest precipitous (76%) declines in hammerhead (*Sphyrna* species) and large coastal (dusky, night, and silky shark, genus *Carcharhinus*) species, and moderate declines (53%) in blue and oceanic whitetip sharks over this period. In contrast, mako and thresher sharks appear to have stabilized, and the tiger shark population appears to be increasing. A comparison of nominal shark catch rates from this fleet's observer and logbook data (to evaluate the veracity of trends previously estimated from the latter) showed a high degree of concordance for each species group, both in individual sub-areas and overall. Models of these two datasets for the common time period (1992–2000) show that compared to the observer data the logbook data indicate greater declines for some species, but lesser declines for others. Signs of recovery for some shark species are encouraging, but must also be set in the context of the significant declines that occurred in previous decades.

1. Introduction

Concern about increased exploitation of sharks, coupled with the inherent vulnerability to overexploitation of many of these species, has brought this group of fishes to the forefront of marine conservation in recent years (FAO, 1998, 2000; Musick et al., 2000; ICCAT, 2004; CITES, 2006; Anon, 2009). Large pelagic sharks are circumglobally distributed top predators and among the most heavily exploited sharks (Camhi et al., 2008a; Dulvy et al., 2008). Species in this group, which includes wide-ranging oceanic sharks such as blue (*Prionace glauca*) and mako (*Isurus* species) and more coastal tiger (*Galeocerdo cuvier*) and hammerhead (genus *Sphyrna*) species, comprise the majority of those traded in Asia's shark fin trade (Clarke et al., 2006) and are also increasingly sought after for their meat (Hareide et al., 2007).

Quantifying the impacts of exploitation remains a challenge for most shark populations because of a paucity of data (Camhi et al., 2008a). Few stock assessments have been conducted for sharks, and results for many of those that have been were uncertain (e.g. ICCAT, 2008). Indices of abundance are key components of the complex population dynamics models used in stock assessments (Maunder and Punt, 2004), and also important indicators of the direction and magnitude of changes in abundance for the many shark species for which there are inadequate catch records and biological information to conduct stock assessments.

Estimating unbiased indices of abundance for large pelagic sharks is, however, complicated by several factors (Camhi et al., 2008b). Distributed in epipelagic and upper mesopelagic waters, these species are rarely caught in fishery-independent research surveys. Surveys that have sampled sharks often are limited by low sample size to provide estimates only for the most frequently caught coastal species. Conversely, fisheries sample intensely over large regions closer in size to the geographic ranges of shark populations, but are much more variable than designed research surveys making standardization of the catch rates a challenge (Maunder and Punt, 2004; Bishop, 2006). What is more, there is a dearth of long-term fishery-dependent data for sharks: most commercial fisheries began recording shark catches at the species level only in the 1990s, and reliable species identification remains a challenge. There also is a tradeoff between logbook data, which are self-reported by fishermen, and scientific observer data, which should be more accurate but often monitor only a small proportion of commercial fleets. The situation is exacerbated for oceanic sharks because much of their exploitation occurs on the high seas, where their catches are unrestricted and often un- or under-reported (Camhi et al., 2008b).

In the Northwest Atlantic Ocean, one of the most data-rich regions for sharks, many large pelagic shark species appear to

* Corresponding author at: National Center for Ecological Analysis and Synthesis, UCSB, 735 State St. Suite 300, Santa Barbara, CA 93101, USA.
Tel.: +1 805 892 2517, fax: +1 805 892 2510.
E-mail addresses: juliakbaum@gmail.com (J.K. Baum), wade.blanchard@dal.ca (W. Blanchard).

0165-7836/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2009.11.006

have declined significantly (Musick et al., 1993; Simpfendorfer et al., 2002; Baum et al., 2003; Ha, 2006; Myers et al., 2007; Aires-da-Silva et al., 2008). For example, two dedicated shark-targeted longline surveys conducted annually on the U.S. east coast since 1972 and 1974 respectively, have provided valuable multi-decadal records for many large coastal shark species; analyses of these data indicate substantial declines in dusky, tiger, blacktip and sandbar sharks (Ha, 2006; Myers et al., 2007). Examination of fisheries logbooks from 1986 to 2000 also suggested significant changes in large pelagic shark population abundance in this region, ranging from 40% declines for two mako shark species up to 89% declines for three hammerhead species (Baum et al., 2003). In those analyses, generalized linear models (GLM) were fitted to the non-zero catches with the truncated negative binomial distribution to avoid the potential bias of any change in fishermen's tendency to record shark catches over time (Baum et al., 2003). Six additional analyses using different statistical distributions and subsets of the data (based on the tendency of sharks to be recorded on different vessels) led to some quantitative differences in trends, but similar conclusions of significant declines in abundance (Baum et al., 2003, Supplementary Online Material). That research has, however, been criticized for inferring trends in abundance from a single data source, particularly since the data were from logbooks (Burgess et al., 2005, but see rebuttal in Baum et al., 2005, and analyses of additional data sources in Myers et al., 2007).

To address these concerns and to examine more recent changes, here we build upon this earlier research by using the U.S. Atlantic pelagic longline fishery's observer monitoring program data: (i) to describe the spatial distribution and concentrations of large pelagic sharks in the Northwest Atlantic Ocean, (ii) to estimate trends in their relative abundance using the most recent available observer data (1992–2005), (iii) to compare these data and estimates to those from the same fleet's logbook data, and (iv) to suggest improvements for future observer data collection and models.

2. Methods

2.1. Data and shark species

The U.S. Atlantic pelagic longline fishery is the major source of exploitation for large pelagic fishes off North America's east coast (Hoey and Moore, 1999; Beerkircher et al., 2002; Mandelman et al., 2008). The fleet primarily targets swordfish (*Xiphias gladius*) and yellowfin tuna (*Thunnus albacares*); substantial numbers of sharks are also caught, mainly as bycatch.

We obtained the observer and logbook data for this fleet, both of which include counts of the sharks caught per longline set. The logbook dataset used here is identical to that of Baum et al. (2003), spanning from 1986 to 2000, and comprising over 214,000 sets and 110 million hooks. Scientific sampling of the fleet was initiated in 1992 under the National Marine Fisheries Service's (NMFS) Pelagic Observer Program (POP), and observers have monitored between 2.2 and 11.5% of the sets (mean = 5.5%) in the fishery each year since (Beerkircher et al., 2004). We obtained the observer data from NMFS Southeast Fisheries Science Center (SEFSC), and met with and emailed POP staff to discuss the fishery, observer program, and dataset. These data were available from 1992 to 2005 and (excluding sets in the experimental fishery conducted to test measures for reducing sea turtle bycatch) totaled 6952 sets and over 4.8 million hooks. Detailed information on this observer program is available on the NMFS SEFSC website (http://www.sefsc.noaa.gov/pop.jsp).

Both datasets underwent extensive checks prior to analyses. Logbook data corrections and selection criteria are detailed in Baum (2002) and Baum et al. (2003); notable among these was the exclusion of sets that used bottom longline gear (to target large coastal sharks) or pelagic longline gear to directly target sharks. There were no bottom longline sets in the observer data, and we excluded the few shark-targeted pelagic sets ($n = 32$) because their uneven distribution in the time series and high shark catches could have biased conclusions about shark population trends. We performed summary statistics, plots, and range checks on all variables of interest in the observer data, and corrected obvious errors. For example, implausible dates and locations (e.g. on land) could often be corrected using information from other sets on the same fishing trips. Any outstanding queries were discussed with POP staff and corrected wherever possible.

Table 1

Total number of each shark species recorded in the U.S. Atlantic pelagic longline observer program between 1992 and 2005. Analyzed species are classified as either oceanic or large coastal sharks according to the U.S. Atlantic Highly Migratory Species Fishery Management Plan (NMFS, 2006). Species are grouped as in analyses. Species recorded fewer than 5 times not shown.

Species		Number caught
Common name	Latin name	
Oceanic sharks		
Blue	*Prionace glauca*	28,317
Mako sharks	*Isurus* species	3,433
Shortfin mako	*I. oxyrinchus*	2,705
Longfin mako	*I. paucus*	217
Unidentified makos	*I.* species	511
Thresher sharks	*Alopias* species	921
Bigeye thresher	*A. superciliosus*	627
Common thresher	*A. vulpinus*	148
Unidentified thresher	*A.* species	146
Oceanic whitetip	*Carcharhinus longimanus*	506
Porbeagle[a]	*Lamna nasus*	192
Large coastal sharks		
Hammerhead sharks	*Sphyrna* species	1,292
Scalloped hammerhead	*S. lewini*	742
Great hammerhead	*S. mokarran*	93
Smooth hammerhead	*S. zygaena*	15
Unidentified hammerhead	*S.* species	442
Tiger shark	*Galeocerdo cuvier*	1,190
Coastal group 1[b]	*Carcharhinus* species	7,212
Dusky shark	*C. obscurus*	1,924
Night shark	*C. signatus*	1,649
Silky shark	*C. falciformis*	3,639
Coastal group 2[b]	*Carcharhinus* species	9,799
Bignose shark	*C. altimus*	47
Blacktip shark	*C. limbatus*	125
Bull shark	*C. leucas*	42
Sandbar shark	*C. plumbeus*	550
Spinner shark	*C. brevipinna*	31
Sand tiger shark[a]	*Carcharias taurus*	6
Other shark species		
Atlantic sharpnose shark[a]	*Rhizoprionodon terraenovae*	20
Collared dogfish[a]	–	6
Crocodile shark[a]	*Pseudocarcharias kamoharai*	162
Reef shark[a]	–	7
Smooth dogfish[a]	*Mustelus canis*	59
Spiny dogfish[a]	*Squalus acanthias*	95
Unidentified dogfish[a]	–	38
		Unidentifiedsharks
Unidentified requiem sharks	*Carcharhinus* species	179
Unidentified sharks	–	1,613
Total (all sharks)		46,052

[a] Species not included in analysis because of small sample size.
[b] Coastal group 1 includes dusky, night, silky shark. Coastal group 2 includes Coastal group 1, plus bignose, blacktip, bull, sandbar, spinner and all unidentified sharks.

Observers have recorded over twenty-five shark species in this fishery (Table 1). Blue, tiger, and oceanic whitetip sharks are easily identified and were caught in sufficient numbers to model their catch rates (Table 1). Hammerhead (*Sphyrna* spp.), thresher (*Alopias* spp.), mako (*Isurus* spp.), and requiem (*Carcharhinus* spp.) sharks were modelled at the genus level, because observers identified a substantial proportion of them only to this taxonomic level (e.g. 34% of hammerhead sharks, 16% of thresher sharks, and 15% of mako sharks; Table 1). Reliable identification of species in these genera can be difficult during fisheries sampling even for trained observers because much fishing effort occurs at night and sharks are generally not brought onboard (L. Beerkircher, NMFS SEFSC, personal communication). In addition, a systematic bias occurred in observers' recording of requiem sharks (genus *Carcharhinus*) whereby night shark (*C. signatus*) was often recorded as 'unidentified shark' or misidentified as dusky (*C. obscurus*) or silky (*C. falciformis*) shark until species identification training improved in the late-1990s (L. Beerkircher, personal communication; Beerkircher et al., 2002). To address this problem, NMFS added a new species code, 'unidentified requiem shark', to the observer data collection system in 2004. Because trends for individual *Carcharhinus* species might reflect these trends in observers' recording tendencies rather than in the relative abundance of the species, we modelled them in two groupings encompassing the two extreme possibilities, first by including only the three most commonly recorded species (dusky, silky, and night sharks), and second by grouping these three species with other recorded *Carcharhinus* species and all unidentified sharks (Table 1). Herein, we use the word "species" to refer to species groups as well as to individual species.

We divided the sampled region of the Northwest Atlantic into the same nine areas as Baum et al. (2003) so the two could be easily compared, but excluded records from Area 9 because observer monitoring occurred there only from 1996 to 1999, on a few sets ($n = 62$).

2.2. Shark catch rates in U.S. pelagic longline observer and logbook data

We compared unstandardized shark catch rates among species and areas in the 1992–2005 observer data, and between the observer and logbook data for the common time period of available data,1992–2000. Comparisons of shark catch rates between these two data sources on a set-by-set basis would have required consistent 'trip' identifiers between the datasets, which were not available. Instead, for each species we compared the spatial distribution of catches by plotting maps of the catch rates for both datasets. We then made boxplots of the catch rates recorded in the two datasets for each species, in each of the nine areas and overall, including only the positive sets (i.e. sets in which recorded catch of the species was greater than zero) in order to evaluate the main assumption of Baum et al.'s (2003) analysis, that fishers had recorded positive shark catches approximately correctly.

2.3. Observer data models

For each shark species, we 'standardized' the catch rates (Maunder and Punt, 2004) by modelling the number caught per set using generalized linear mixed models (GLMM) with a negative binomial error distribution and a log link. GLMM are extensions of the GLMs commonly used to model fishery catch rates, which allow for correlated response data (Diggle et al., 2002; Venables and Dichmont, 2004; Bolker et al., 2009). Here, sets made on the same trip (and those made by the same vessel) can be thought of as repeated measures in a longitudinal analysis. In GLMs (which do not account for the correlations among observations) of these data, the standard errors of the trends in abundance were between 15% and 50% smaller than their GLMM counterparts, implying a false precision in the year estimates.

In the GLMMs, the expected mean catch μ is:

$$\log(\boldsymbol{\mu}) = \boldsymbol{X\beta} + \boldsymbol{Z\gamma} + \log(\boldsymbol{h})$$

Table 2
Variables included in initial models from the observed sets in the U.S. pelagic longline fishery between 1992 and 2005. Mean values ± 1 SD.

Variable	Description (mean ± 1 SD)/type
Temporal	
Year	1992–2005/continuous, categorical (separate models)
Season	Year-round/continuous (sines, cosines with periods of 1/2 and 1 year)
Time of fishing operation	Early morning, day, evening, night/categorical
Spatial/Environment	
Area*	Eight regions (see Figs. 2 and 3)/categorical
Ocean depth** (m below sea level)	−1924 ± 1441; range: −7996 to −10/continuous, quadratic
Surface water temperature (°C)	24.7 ± 4.1; range: 6.8–31.8/continuous
Operational	
Average hook depth (m)	45.8 ± 19.8; range: 6.4–182.9; continuous
Bait species	Mackerel (25%), herring (5%), squid (56%), artificial (1%), sardine (9%), scad (2%), other (<1%)/categorical
Hook type	J-hook (n = 77%), circle hook (n = 23%)/categorical
Number of light sticks	305 ± 277; range: 0 (24%)–1488/continuous
Hooks per set	702 ± 259; range: 10–1548/continuous, offset
Target species	Swordfish (43%), multiple spp. (26%), tuna spp. (15%), yellowfin tuna (14%), bigeye tuna (2%)/categorical

* Interactions with area × season, and area × year were also included.
** Data obtained from the International Research Institute for Climate and Society (http://ingrid.ldgo.columbia.edu/SOURCES/.WORLDBATH/.bath/) using the recorded latitudes and longitudes.

where $\boldsymbol{X}$ is a matrix of covariates, $\boldsymbol{\beta}$ is a vector of parameters (the fixed effects described below), $\boldsymbol{Z}$ is a matrix of random effect covariates, $\boldsymbol{\gamma}$ is a vector of random effect parameters, and $\boldsymbol{h}$ is a vector of the number of hooks that is known and treated as an offset. We fitted GLMMs with an exchangeable correlation among trips made by the same vessel (v), and a first-order autoregressive correlation structure (AR1) with trip (t) as the clustering variable. We refer to these models as GLMM-vt. To explore the sensitivity of shark trend estimates to this particular model formulation, we fitted two additional model types with the same error structure and link: generalized estimating equations (GEE) and GLMM in which we specified only the AR1 correlation structure for sets made on the same trip (see Appendix A for model results). We refer to this latter GLMM as GLMM-t.

For each model type, we began with a full model that included a suite of temporal, spatial, and operational variables that could affect shark catch rates (detailed in Table 2). To model the rate of change in catch rates (interpreted as the trend in relative abundance), we treated 'year' as a continuous variable. We also fitted separate models treating 'year' as a categorical variable to obtain individual year estimates. Although hook type was not always recorded (n = 5151; 74% of sets), and including this variable in models involved a tradeoff between modelling only the data subset for which it was recorded or missing potentially important sources of variation (Maunder and Punt, 2004), we felt that its potential impact on shark catch rates (e.g. Watson et al., 2005; Kaplan et al., 2007) coupled with a mandated change in 2004 to use only circle hooks, warranted investigation. We therefore fitted models for each species on the subset of data with hook type recorded including it as a model covariate, as well as on the full dataset without hook type as a covariate. The latter are presented for those species for which hook type was non-significant. For species for which it was significant, we also fitted models on the 'hook type' data subset without this variable to determine if the difference in year estimates between the full and hook type subsetted data was due to the inclusion of the hook type covariate or simply the difference in number of observations between the two. In each case the difference was indeed due to the inclusion of hook type in the model. Other potentially important operational variables had many missing values (e.g. leader material) and could not be included in the models.

All analyses were conducted in SAS v.9.1 (SAS Institute, 2004). GLMM-vt models were implemented using PROC GLIMMIX (SAS, 2005) by specifying the 'random' statement for vessel and the 'random _residual_' statement for trip. To fit these models, vessels with only one observed trip and trips with only one observed set had to be omitted. Starting parameter values also had to be provided for the vessel and trip variances, and either the AR(1) or the negative binomial parameter had to be held fixed.

For each species, we first fitted GLMM-vt using the 1992–2000 observer data in order to compare trend estimates between the observer and logbook data. Then, using the 1992–2005 observer data we fitted GLMM-vt (i) with year as a continuous variable, (ii) with year as a categorical variable, and (iii) with a year × area interaction, and the GLMM-t and GEE with year as a continuous variable. Since neither GLMM nor GEE are fitted using maximum likelihood, the Akaike Information Criteria (AIC) cannot be used to compare models. Instead, to select a final model for each of these model specifications we began with the full model containing all explanatory variables and used backward-selection by statistical significance testing of regression coefficients, with p-values at $\alpha = 0.1$.

3. Results

3.1. Shark catch rates in U.S. pelagic longline observer and logbook data

Fishing effort sampled by the observer program was concentrated from just inshore of the 200 m isobath out to the 1000 m isobath along the U.S. east coast, and beyond the 1000 m isobath in the Gulf of Mexico (Fig. 1), The fleet itself covered a larger offshore area of the Northwest Atlantic (see left column Figs. 2 and 3).

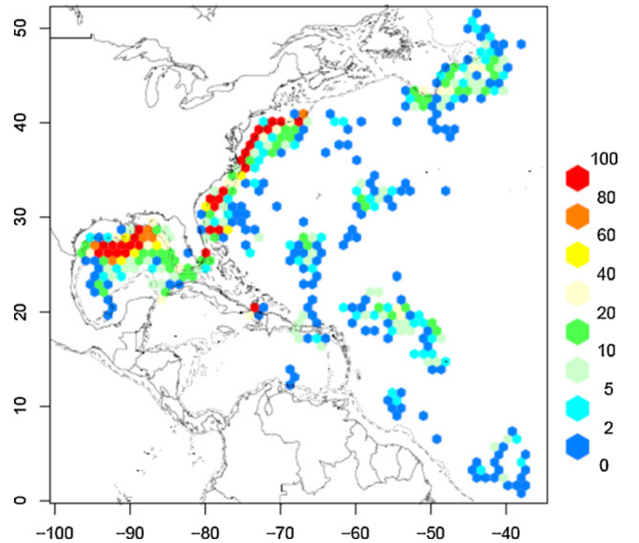

Fig. 1. Map of the Northwest Atlantic Ocean showing the distribution of effort in the U.S. pelagic longline fishery's observer program between 1992 and 2005, categorized by number of sets (0–100). The 200 m (dashed) and 1000 m (dotted) coastal isobaths are shown for reference.

3.1.1. Oceanic sharks

Blue shark had the highest shark catch rates, and accounted for 61% of all sharks recorded by observers (Table 1). Catches were concentrated off the Grand Banks (Area 7; Fig. 2b) where it was recorded on over 99% of observed sets. Between 1992 and 2005, observers recorded over 15,600 blue sharks in this area, with an average of 39 per 1000 hooks. This species was also caught frequently on the northeastern U.S. coast (Areas 5, 6; Fig. 2b) where it averaged just under 10 per 1000 hooks. Catch rates recorded by fishers were higher than those of observers in Area 7 (partially reflecting their tendency to round up the catch to even numbers on sets with many sharks), but otherwise similar between the datasets (Figs. 2a,b and 4).

Of the other oceanic sharks, makos also were commonly caught in the three northernmost areas (Fig. 2d), occurring on about half of those observed sets, with mean catch rates between 1992 and 2005 of 1.5 per 1000 hooks in Areas 5 and 6, and 3 per 1000 hooks in Area 7. Thresher sharks were caught infrequently (7.8% of observed sets) and in low numbers in all regions (overall mean catch rate = 0.24 per 1000 hooks between 1992 and 2005), except for rare, large offshore catches (Fig. 2f). Oceanic whitetips were caught on just over 5% of observed sets, with a mean catch rate of only 0.15 per 1000 hooks (Fig. 2h). Catch rates on non-zero sets were very similar in the two datasets for makos, and only slightly higher in the logbooks for thresher and oceanic whitetips (Fig. 4).

3.1.2. Coastal sharks

Although coastal sharks were seldom caught beyond the continental shelf, catch rates within the 200 m isobath often were high. Hammerhead sharks, for example, were recorded on 35% of observed sets (1992–2005) within or along the 200 m isobath of the southeast U.S. coast (Areas 3–5) and Gulf of Mexico (Area 2) (Fig. 3a,b), with a mean catch rate of 3 per 1000 hooks. Outside these areas, however, they were seldom caught (overall mean = 0.41 per 1000 hooks). Similarly, tiger sharks were caught on almost a quarter of observed sets along the southeastern U.S. coast (Areas 3, 4) at rates of about 1–3 per 1000 hooks (Fig. 3d), but their overall mean catch rate (0.31 per 1000 hooks) was much lower. Large coastal sharks of the genus *Carcharhinus* were recorded on 12% of observed sets, with a mean catch rate of 2.4 per 1000 hooks. This group's highest catch rates occurred in Areas 2–4, from the coast out to the 1000 m isobath (Fig. 3e,f), where observers recorded on average 7.9 per 1000 hooks. Recorded catch rates on positive sets for each of the coastal shark species was similar in the two datasets, in each area and overall, with only slightly higher rates recorded in the logbook data (Fig. 4).

3.2. GLMM estimates of 1992–2005 shark trends

We focus herein on the model-estimated year effects, but note that area, season, and ocean depth fished were significant for all of the modeled sharks, confirming the importance of modelling these data to account for these effects (Table A1). Examination of residuals indicated that the models tended to overfit some of the zero catches and underfit the rare, highest catches, but otherwise fit the data relatively well.

3.2.1. Oceanic sharks

Blue shark standardized catch rates have decreased by an estimated 53% (95% confidence interval (CI): 38–64%) between 1992 and 2005, based on an instantaneous decline rate of −0.057 (Fig. 5a). The individual year estimates, however, show high interannual variability, and while there appears to be a decline, the pattern is

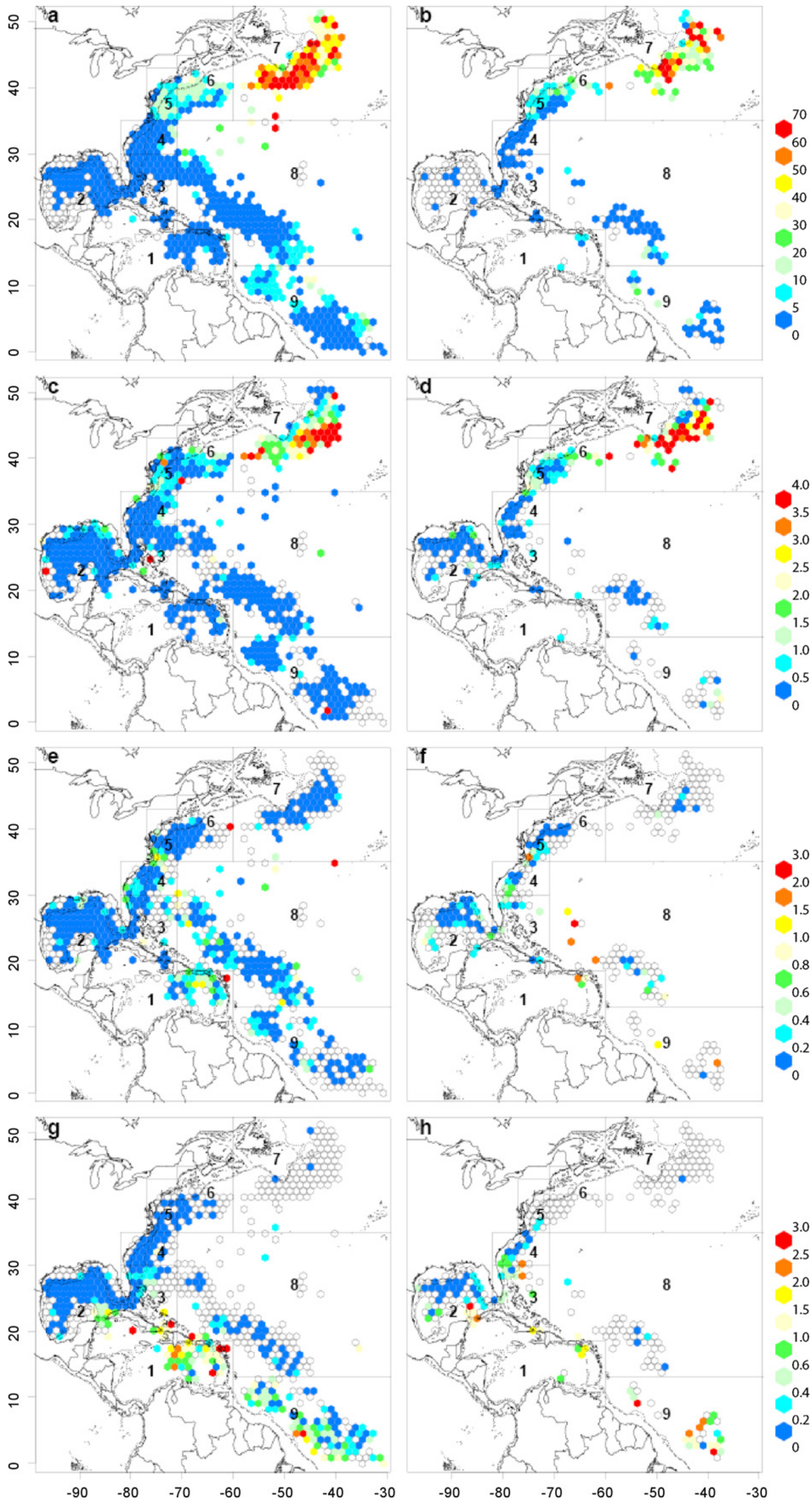

Fig. 2. Catch rates of oceanic sharks (blue (a,b), mako (c,d), thresher (e,f), oceanic whitetip (g,h)) in the Northwest Atlantic Ocean, as recorded in the U.S. pelagic longline logbook (left column) and observer (right column) data. The mean catch per 1000 hooks between 1992 and 2000 is plotted in each hexagon, and the scale differs among species to allow the greatest resolution of catch rates. Hexagons where no sharks of the plotted species were caught are displayed as empty. Areas (modified from the U.S. National Marine Fisheries Service's classification for longline fisheries): (1) Caribbean, (2) Gulf of Mexico, (3) Florida east coast, (4) South Atlantic Bight, (5) mid-Atlantic Bight, (6) northeast coastal, (7) northeast distant, (8) Sargasso/north central Atlantic, (9) tuna north and south. The 200 m (dashed line) and 1000 m coastal isobaths (dotted line) are shown for reference.

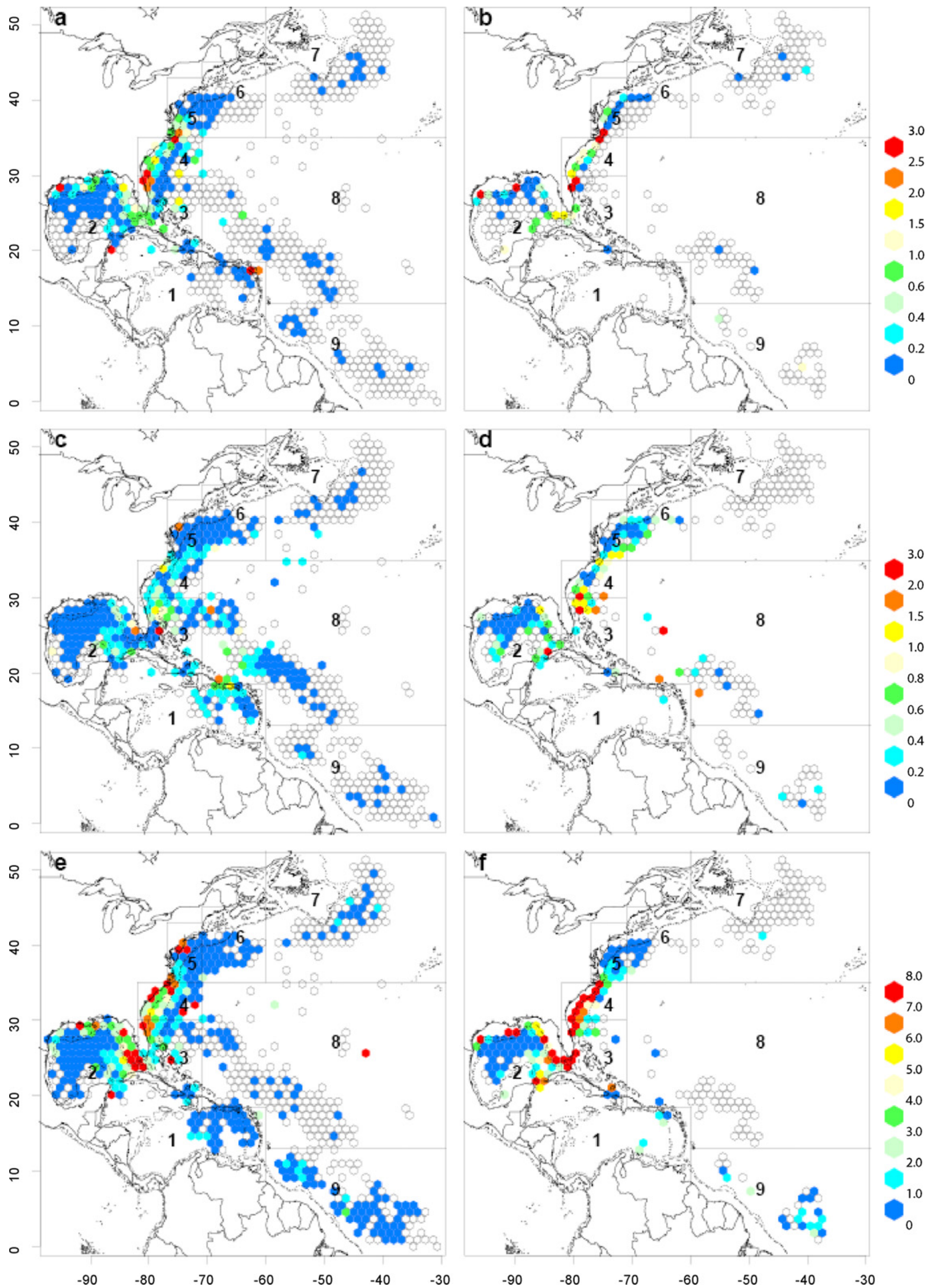

Fig. 3. Catch rates of large coastal sharks (hammerhead (a,b), tiger (c,d), large coastal sharks of the genus *Carcharhinus* (e,f)) in the Northwest Atlantic Ocean as recorded in the U.S. pelagic longline logbook (left column) and observer (right column) data. Plot details as in Fig. 1.

not well matched by the estimated trend (Fig. 5a). Examining the trend across areas, a strongly negative trend (−0.135) in Area 7, where blue shark was most frequently caught, was tempered by more moderate declines in other areas (Fig. 6a).

Mako shark standardized catch rates also are estimated to have declined, although the trend (instantaneous rate = −0.032) equating to a 34% decline (95%CI: 1–56%) between 1992 and 2005, was only marginally significant and imprecisely estimated (Fig. 5b). The estimated decline for shortfin mako, which accounted for 79% of all recorded mako sharks, was slightly greater (instantaneous rate = −0.040, 95% CI: −0.005 to −0.074, $p = 0.026$). Like blue sharks, the estimated rate of decline in mako sharks was significant and largest in Area 7 where they were most frequently caught (Fig. 6b).

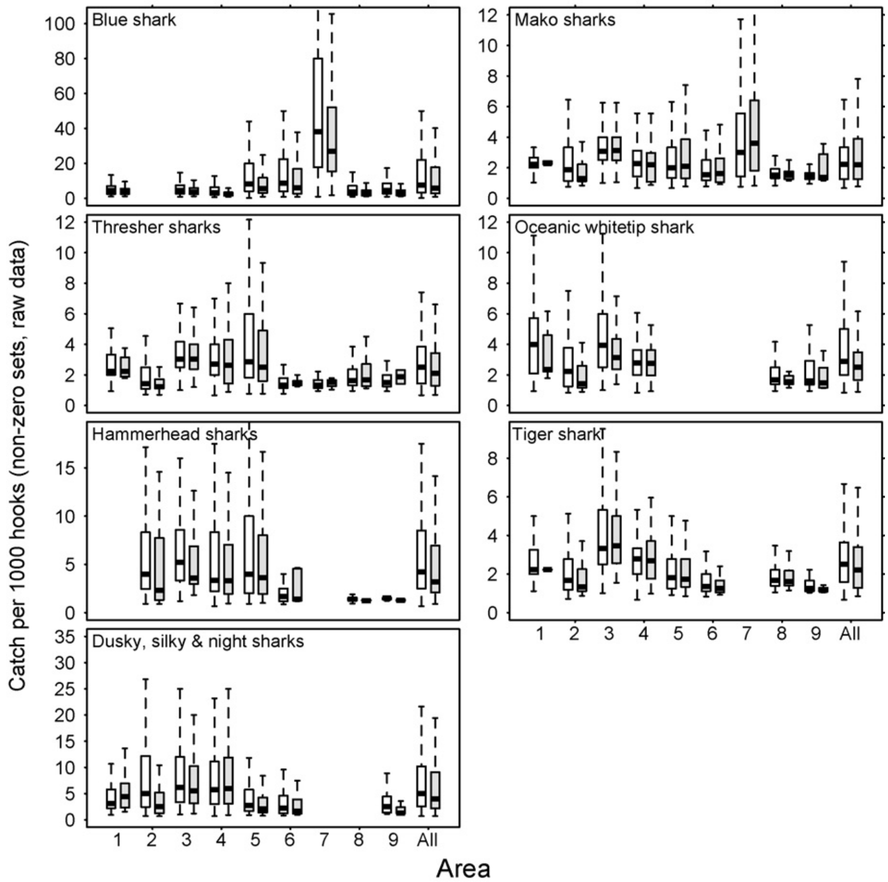

Fig. 4. Boxplots of catch per 1000 hooks on non-zero sets for modelled shark species in each area (for which observers recorded the species on > 1% of sets) and in all areas combined, according to the U.S. pelagic longline logbook (white bars, left) and observer (grey bars, right) data for 1992 to 2000.

Table A1
GLMMvt models for each species showing statistical significance of each covariate included in the final model (based on the Wald test): * = <0.1; ** = <0.01; *** = < 0.001; **** = < 0.00001, otherwise non-significant. - indicates variables that were dropped from the final model.

	Blue	Mako	Thresher	Oceanic whitetip	Hammerhead	Tiger	Coastal 1	Coastal 2
Year	****	*	*	**	****	*	****	***
Ocean depth	–	****	****	****	****	–	****	****
Ocean depth^2	**	****		****		*	****	****
Sine	*	*	**	–	****	–	***	****
Sine2	****	*			*		*	
Cos	**	–	–	–	**	*		
Cos2	–	–	–	–	**	*	*	
Soak time	****	**	*		***	***		
Temperature	****	*	*	**	***		*	*
No. light sticks	*				*			
Hook depth			***	**	*	*		
Area	****	****	****	****	****	****	****	****
Target species		****	***	**		*	****	***
Period	*		***		*		**	*
Hook type		*				*	****	**
Bait type		*		*		*		
Area × Sine	****	*	****	*	****	****		
Area × Sine2	****	*						
Area × Cos		*	****	**		****		
Area × Cos2	*	**	***	*	***	*		

The only nonsignificant trend was for thresher sharks, but the small estimated rate of decline (−0.024) masks differences in the trends among areas and over time (Figs. 5c and 6c). The problem arises because the change in catch rates was not monotonic over this time period, such that models underfit the earliest years, in order to better fit the data from recent years (Fig. 5c). Trend estimates for thresher sharks also varied significantly among areas: a decrease (−0.068) in the Mid-Atlantic Bight (Area 5), where thresher sharks were most commonly caught, contrasts with the increasing trend estimated in offshore Area 8 where they were seldom caught (Fig. 6c).

The estimated rate of change in oceanic whitetips was similar to that of blue shark, equating to a 50% decline (95%CI: 17–70%) between 1992 and 2005 (Fig. 5d). Differences in trends among areas were nonsignificant (Fig. 6d).

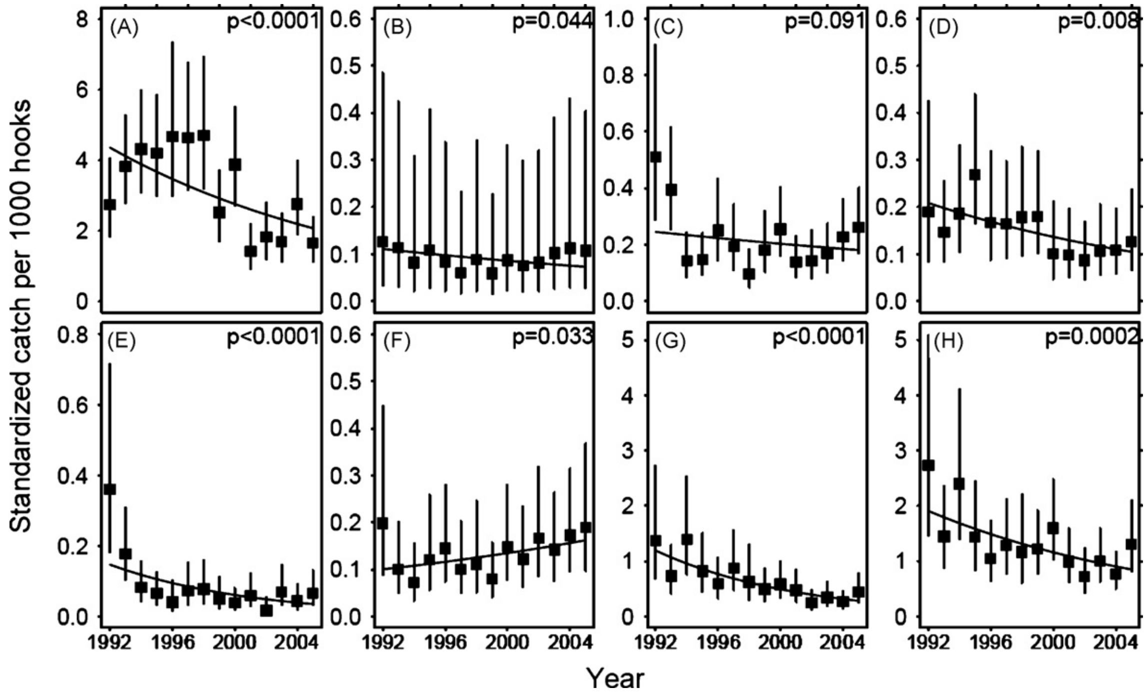

Fig. 5. Estimated change in relative abundance (standardized catch per 1000 hooks) between 1992 and 2005 based on the observer data for oceanic shark species: (A) blue, (B) mako, (C) thresher, (D) oceanic whitetip, and large coastal shark species: (E) hammerhead, (F) tiger, (G) coastal shark group 1, (H) coastal shark group 2. Plotted for each species are the overall trend (solid line) and the individual year estimates (■, ±95% CI) as estimated from generalized linear mixed models with vessel as a random effect and trip as a residual effect (GLMM-vt).

3.2.2. Coastal sharks

Both hammerhead sharks and coastal group 1 (dusky, silky, night shark) are estimated to have declined sharply, by 76% between just 1992 and 2005, and the trends match their respective individual year estimates well (Fig. 5e,g). Differences among areas were nonsignificant for hammerheads (Fig. 6e), while for coastal group 1 the estimated declines were significant in southerly areas (1–3) and non-significant in northerly areas (4–6) (Fig. 6 g; a statis-

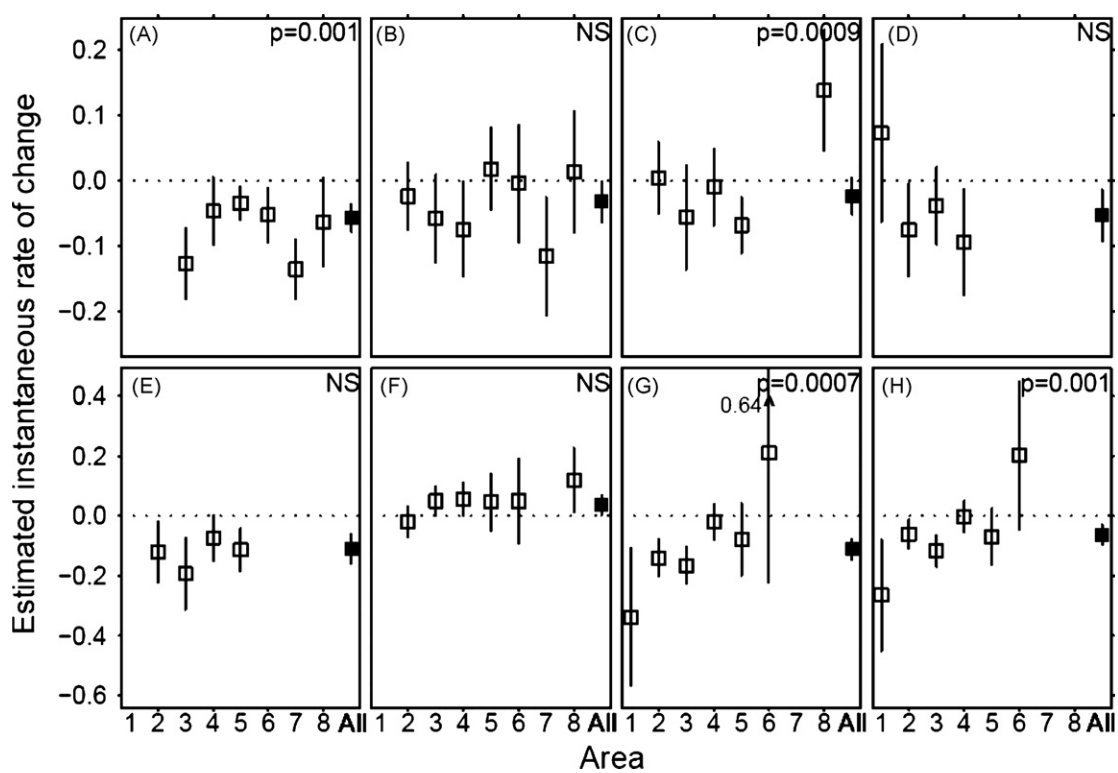

Fig. 6. Estimated instantaneous rate of change in abundance (i.e. the 'year' effect) in each area (□, ±95% CI) and in all areas combined (■, ±95% CI) between 1992 and 2005 based on the observer data for oceanic shark species: (A) blue, (B) mako, (C) thresher, (D) oceanic whitetip, and coastal shark species: (E) hammerhead, (F) tiger, (G) coastal shark group 1, (H) coastal shark group 2. Areas in which fewer than 50 individuals of the species (group) were caught in total are excluded.

tically significant difference in trends between Areas 1 and 6 may be an artifact of the small sample size for this group in these two areas). Models for coastal group 2 showed a less steep trend, equating to a 55% (95%CI: 32–71%) decrease (Fig. 5 h), but the same pattern among areas (Fig. 6 h) as coastal group 1.

In contrast, tiger shark did not decline throughout this period. Rather, the rate of change was non-constant as evidenced by individual year estimates, which suggests this species either declined slightly or was stable from 1992 to the late-1990s, and then began increasing back to the 1992 level (Fig. 5f).

4. Discussion

4.1. Shark catch rates in U.S. pelagic longline observer and logbook data

For wide-ranging species like large pelagic sharks, fishery-dependent data are typically the only source of time series data that samples intensively across a broad spatial scale similar to the range of the populations. As such, they can provide important information about the spatial distributions and hotspots of these species, which is complementary to the large body of data currently being collected from tagging programs for wide-ranging species (e.g. Weng et al., 2008).

Shark catch rates were highly variable among species, and for individual species among areas (Figs. 2–4). Given this variability, it is not surprising that some single locations (i.e. hexagons) with high catch rates differ between the two datasets. For each species group examined, however, the summarized catch rates from the observer and logbook datasets were similar overall and within each area; where discrepancies existed the tendency was for higher shark catch rates to be recorded in the logbook than the observer data (reflecting the tendency for fishermen to round up their catches). This suggests that overall the logbook data has provided a reasonable record of shark catches in the fishery (at least up until 2000), and can augment the more restricted observer dataset.

There are very few commercial fisheries datasets from years prior to the pelagic longline logbook and observer programs with which these recent catch rates can be compared. Apart from the exploratory research surveys analyzed by Baum and Myers (2004), the only data we know of is from Berkeley and Campos (1988). In that study, swordfish-targeted pelagic longline sets ($n = 111$) monitored on a single vessel off the east coast of Florida between 1981 and 1983 yielded an overall mean catch rate of 4.16 sharks per 100 hooks. Unfortunately, the original data from the study have been lost (S. Berkeley, personal communication, March 2007), precluding formal statistical comparison with more recent data. As a rough comparison, swordfish-targeted sets in the 1992–2005 observer data from the same area (part of Area 3) had an overall mean of only 1.03 sharks per 100 hooks, which is suggestive of a decline.

4.2. GLMM estimates of 1992–2005 shark trends

Models indicate substantial changes in standardized shark catch rates between 1992 and 2005, which by extension suggests there may have been corresponding changes in the relative abundance of these populations. From a conservation standpoint, the most important result is the precipitous decline estimated for hammerhead sharks (comprised primarily of scalloped hammerheads). The estimated rate of decline (−0.109) was less than that estimated in the logbook analysis (−0.158) for 1986–2000 (Baum et al., 2003), but similar to that estimated in the analysis of the 1972–2003 shark-targeted UNC research survey data (−0.127; Myers et al., 2007). Together, these three datasets provide consistent indication of marked declines in hammerheads. Large declines also were estimated for coastal shark group 1, but these must be balanced against the smaller decline estimated for coastal group 2 (55% in 14 years). Although frustrating that trends generally cannot be estimated from fishery-dependent data for individual *Carcharhinus* species, assessments that do so (e.g. Cortés et al., 2006), ignoring the propensity for fishermen and observers alike to misidentify these species, may produce biased results. Thus, there is at present a trade-off for this group between obtaining a single trend estimate for the genus across a broad geographic area (from fishery-dependent data) or obtaining species-specific trends for small single locations (from research surveys).

Although model estimates suggest significant declines in blue, mako, and oceanic whitetip sharks between 1992 and 2005, the high degree of interannual variability in the individual year estimates (especially for mako sharks; Fig. 5a,b,d) suggests that the catch rates have not been fully standardized (i.e. covariates that significantly influence catch rates of these species were not included in the models) and limits what can reasonably be inferred about the relative abundance of these species. Clearly, greater sampling effort and more complete recording of variables describing the fishing operation are required in the observer program to reduce this variability.

Interpretation of model estimates is complicated for thresher and tiger sharks because the changes between 1992 and 2005 do not appear to be monotonic for these species, as judged by their individual year estimates (Fig. 5c,f), and by the difference in estimated trends between the 1992–2000 and 1992–2005 observer data (Appendix A). Whereas models of the 1992–2005 observer data did not detect a trend for thresher sharks, models of the 1992–2000 observer and 1986–2000 logbook data showed almost exactly the same significant rate of decline (Appendix A), which equates to an 80% decrease from 1986 to 2000. Individual year estimates for thresher sharks suggest that this group has now stabilized (Fig. 5c). For tiger shark, the rate of increase estimated for 1992–2005 appears anomalously high when compared to its individual year estimates, which had high interannual variability but suggested that the population is at the same level now as it was in 1992. Even still, it seems that the tiger shark population has fared the best of all examined shark species over this fourteen-year period, which may be attributable to it being one of the most productive shark species (Cortes, 2002), having the highest survival rate among these sharks from being caught on the longlines (Beerkircher et al., 2002), and to recent management changes in the fishery (NMFS, 2006). Still, setting these changes in the context of tiger shark population declines that are estimated to have occurred in earlier decades (Musick et al., 1993; Ha, 2006; Myers et al., 2007) implies that these populations are stabilizing at greatly reduced levels of abundance.

4.3. Future research and recommendations

In future, alternative functional forms for 'year', or different model types may yield improved estimates of changes in relative abundance for sharks from these observer data. One possibility is to apply piecewise regression, in which separate trends are fitted to the data, one before and one after a breakpoint mid-way through the time series. We found, however, that at present there were too few years in the data after 2000 for these models to converge. A second possibility is to include a quadratic term for 'year' in the models. Such models were highly significant for mako, thresher, and tiger sharks, indicating that their trends do not follow a simple exponential model, and suggesting that there were significant increases in tiger sharks and significant declines in thresher sharks between 1992 and 2005.

Apart from the large number of variables to be included in models of observer data, two aspects of the data, its correlated structure

Table A2
Comparison of estimated instantaneous rates of change (±95% CI) amongst datasets and model types for each shark species (group). Estimates from models of the logbook data are from Baum et al., 2003Baum et al.'s (2003) analysis (models are of 1986–2000 or 1992–2000 data depending on the start date of recording for the species). Models of the observer data (described in detail in the Methods herein) are the GLMM-vt models of the 1992–2000 data for comparison to the logbook data, and of three different models (GLMM-vt, GLMM-t, GEE) for the 1992–2005 data.

Species	Trend/Year estimates					
	1986–2000	1992–2000		1992–2005		
	Logbook, GLM	Logbook, GLM	Observer, GLMM-VT	Observer, GLMM-VT	Observer, GLMM-T	Observer, GEE
Blue shark	−0.066 (−0.071 to −0.061)	–	0.005 (−0.034 to 0.044)	−0.057 (−0.078 to −0.037)	−0.063 (−0.085 to −0.041)	−0.052 (−0.072 to −0.032)
Mako sharks	−0.037 (−0.050 to −0.025)	–	−0.079 (−0.118 to −0.040)	−0.032 (−0.063 to −0.001)	−0.016 (−0.047 to 0.015)	−0.032 (−0.070 to −0.005)
Thresher sharks	−0.120 (−0.139 to −0.102)	–	−0.118 (−0.195 to −0.042)	−0.024 (−0.051 to 0.004)	−0.025 (−0.059 to 0.008)	−0.021 (−0.059 to 0.017)
Oceanic whitetip	–	−0.149 (−0.175 to −0.122)	−0.034 (−0.113 to 0.044)	−0.053 (−0.092 to −0.014)	−0.062 (−0.101 to −0.023)	−0.051 (−0.089 to −0.012)
Hammerheads	−0.158 (−0.172 to −0.143)	–	−0.223 (−0.300 to −0.150)	−0.110 (−0.157 to −0.062)	−0.097 (−0.140 to −0.053)	−0.144 (−0.198 to −0.090)
Tiger shark	−0.076 (−0.091 to −0.061)	–	0.001 (−0.049 to 0.051)	0.037 (0.003 to 0.071)	0.041 (0.007 to 0.074)	0.044 (0.009 to 0.080)
Coastal group 1	–	−0.117 (−0.134 to −0.101)*	−0.043 (−0.091 to 0.005)	−0.110 (−0.144 to −0.076)	−0.099 (−0.133 to −0.065)	−0.114 (−0.146 to −0.082)
Coastal group 2	–	−0.117 (−0.134 to −0.101)*	−0.040 (−0.092 to 0.011)	−0.062 (−0.095 to −0.030)	−0.061 (−0.088 to −0.034)	−0.062 (−0.088 to −0.035)

* *Note*: There was only one Coastal group in the logbook analysis.

and the high proportion of zeroes in the shark catches, present challenges for statistical modeling. In these analyses we focused on the first problem and modelled two levels of correlations (among sets on the same trip and among trips on the same vessel). In addition to these sources of variation, however, the high proportion of unidentified sharks and known reporting problem with night sharks suggests that observers' reporting tendencies may also cause correlations within sets reported by the same observer. It may therefore be worthwhile to investigate models with 'observer' as a random effect. Secondly, with the obvious exception of blue shark in Area 7, the catch data contain many zeroes. To better address the high proportion of zeroes, it may useful to implement models using the zero-inflated negative binomial (ZINB) distribution, which is a mixture of two distributions, one for the zeros and one that includes zeros and positive values (i.e. the negative binomial distribution). The ZINB has been applied recently to models of silky shark bycatch in an eastern Pacific Ocean purse-seine fishery (Minami et al., 2007). Models that can account for both the excessive zeros and correlations in the data (e.g. generalized linear mixed models with a ZINB distribution) would be a step forward.

Although observer data are generally considered to be an improvement over logbook data, in this case the high proportion of sharks identified only at the genus level, misidentified, or unidentified unfortunately precluded species-specific analyses for most sharks. The high variability in fishing areas, season, and gear in this fleet also leads to a large number of factors that can affect catch rates, underscoring the need for observers to provide complete and accurate records of the fishing operation, whereas at present some variables in the observer dataset have many missing values and cannot be modeled. Thus, in addition to increasing the percentage of the fleet monitored by observers, both improved species identification and data recording will improve the utility of observer data for monitoring sharks and other large pelagic fishes.

Acknowledgements

We thank the late Ransom A. Myers for inspiration and encouragement, G. Scott and G. Diaz at NOAA/National Marine Fisheries Service for providing the observer data, J. Cramer for providing the logbook data, L.R. Beerkircher and D. Lee for advice about the U.S. pelagic observer program and longline fishery, J. Mills-Flemming for statistical advice, and P. Ward for reviewing the manuscript. Many thanks to the longline fishers who provided their logbooks to NMFS. This research was funded by a Killam Trusts Pre-doctoral scholarship, a David H. Smith Conservation Research Fellowship, and a Natural Sciences and Engineering Research Council of Canada Fellowship to J.K. Baum, and a Pew Charitable Trusts grant to R.A. Myers. This is publication no. DHS2010-01 of the David H. Smith Conservation Research Fellowship Program.

Appendix A. Shark trends: comparison of logbook and observer models

Models of the observer data up to the year 2000 did not detect a trend in blue sharks, but the rate of decline for 1992–2005 was only slightly less than that estimated in the analysis of logbook data for 1986 to 2000 (−0.066; Table A2). Mako shark decline rates estimated from the observer data for 1992 to 2005 and the logbook data for 1986 to 2000 were very similar, while that estimated from the 1992–2000 observer data indicated a much greater decline (−0.079; Table A2). According to both the observer (1992–2000) and logbook (1986–2000) data, estimates from which were virtually identical (−0.118 vs. −0.120), thresher sharks declined sharply up to the year 2000 (Table A2). In contrast, models of the observer data between 1992 and 2000 failed to detect a significant trend for oceanic whitetip shark, which might be a result of its low sample size ($n = 358$), while the trend estimated from the logbook data for the same years based on over 8500 recorded individuals was significant and large (−0.145; Table A2)

For hammerhead sharks, the observer data model for 1992–2000 indicates a much larger decline rate ($p < 0.0001$) than the logbook data (Table A2), which is driven by the sharp decline in hammerhead catch rates in the early 1990s. The 1992–2000 observer data model failed to detect a trend for tiger sharks (Table A2). A significant decline in tiger shark abundance between 1986 and 2000 was estimated in the logbook analysis (Table A1): individual year estimates from these data suggest that tiger shark abundance declined from 1986 to 1992 and thereafter, as in the observer data, were stable (Baum et al., 2003). For the coastal shark groups, although the 1992–2000 observer data model suggested a smaller non-significant decline than in the logbook data, the 1992–2005 trends were very similar to that estimated in the 1992–2000 logbook data analysis suggesting that the latter estimates were not unrealistically large (Table A2).

Appendix B. Shark Trends: Comparison of GLMM-vt, GLMM-t, and GEE models

Estimated rates of change from the 1992–2005 observer data were very similar amongst the three model types for each of the modelled species (Table A2), suggesting that the simpler GEE models, although not common in the fisheries literature, may be as appropriate for these types of data as the more complex mixed models.

References

Aires-da-Silva, A.M., Hoey, J.J., Gallucci, V.F., 2008. A historical index of abundance for the blue shark (*Prionace glauca*) in the western North Atlantic. Fisheries Research 92, 41–52.

Anon, 2009. H.R. 81: Shark Conservation Act of 2009. http://www.govtrack.us/congress/bill.xpd?bill=h111-81.

Baum, J.K., 2002. Determining the effects of exploitation on shark populations using fishery-dependent data. M.Sc. thesis, Dalhousie University.

Baum, J.K., Myers, R.A., 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters 7, 135–145.

Baum, J.K., Kehler, D., Myers, R.A., 2005. Robust estimates of decline for pelagic shark populations in the Northwest Atlantic and Gulf of Mexico. Fisheries 30, 27–30.

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

Beerkircher, L., Cortes, E., Shivji, M., 2002. Characteristics of shark bycatch observed on pelagic longlines off the Southeastern United States, 1992–2000. Marine Fisheries Review 64, 40–49.

Beerkircher, L.R., Brown, C.J., Abercrombie, D.L., Lee, D.W., 2004. SEFSC pelagic observer program data summary for 1992–2002. Southeast Fisheries Science Center, Miami, p25.

Berkeley, S.A., Campos, W.L., 1988. Relative abundance and fishery potential of pelagic sharks along Florida's east coast. Mar. Fish. Rev. 50, 9–16.

Bishop, J., 2006. Standardizing fishery-dependent catch and effort data in complex fisheries with technology change. Reviews in Fish Biology and Fisheries 16, 21–38.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127–135.

Burgess, G.H., Beerkircher, L.R., Cailliet, G.M., Carlson, J.K., Cortes, E., Goldman, K.J., Grubbs, R.D., Musick, J.A., Musyl, M.K., Simpfendorfer, C.A., 2005. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? Fisheries 30, 19–26.

Camhi, M.D., Pikitch, E.K., Babcock, E.A., 2008a. Sharks of the Open Ocean: Biology, Fisheries and Conservation. Blackwell, Oxford.

Camhi, M.D., Lauck, E., Pikitch, E.K., Babcock, E.A., 2008b. A global overview of commercial fisheries for open ocean sharks. In: Sharks of the open ocean: Biology, fisheries & conservation. Blackwell, Oxford, pp. 166–192.

CITES, 2006. Implementation of CITES shark listings. In: Twenty-second meeting of the Animals Committee Lima, Peru, 7–13 July 2006. Convention on International Trade in Endangered Species of Wild Fauna and Flora, AC22 Doc. 17.2.

Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H., Shivji, M.S., 2006. Global estimates of shark catches using trade records from commercial markets. Ecology Letters 9, 1115–1126.

Cortes, E., 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conservation Biology 16, 1048–1062.

Cortés, E., Apostolaki, P., Brown, C.A., 2006. Stock Assessment of Dusky Shark in the U.S. Atlantic and Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City, USA, p. 155.

Diggle, P.J., Heagerty, P., Liang, K.-Y., Zeger, S., 2002. Analysis of Longitudinal Data, second edition. Oxford University Press, New York.

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D., Valenti, S., 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquatic Conservation: Marine and Freshwater Ecosystems 18, 459–482.

FAO, 1998. International plan of action for the conservation and management of sharks. Technical Document FI: CSS/98/3. Food and Agriculture Organization Fisheries Department, Rome.

FAO, 2000. Conservation and management of sharks. FAO Technical Guidelines for Responsible Fisheries. No. 4, Suppl. 1. Food and Agriculture Organization, Rome, 37pp.

Ha, D.S., 2006. Ecology and Conservation of Virginia Shark Species: Analysis of 30 Years of Virginia Longline Shark Census Data, 1974–2004. Virginia Institute of Marine Science, The College of William and Mary, Virginia, p. 198.

Hareide, N.R., Carlson, J.M.C., Clarke, S., Ellis, J., Fordham, S., Fowler, S., Pinho, M., Raymakers, C., Serena, F., Seret, B., Polti, S., 2007. European shark fisheries: a preliminary investigation into fisheries, conversion factors, trade products. In: markets and management measures. European Elasmobranch Association.

Hoey, J.J., Moore, N., 1999. Captain's Report: Multi-Species Catch Characteristics for the U.S. Atlantic Pelagic Longline Fishery. NMFS and the National Fisheries Institute, Inc, Silver Spring, MD and Arlington, VA, pp. 1–78.

ICCAT, 2004. Recommendation by ICCAT concerning the conservation of sharks caught in association with fisheries managed by ICCAT. BYC-04-10. http://www.iccat.int/Documents%5CRecs%5Ccompendiopdf-e%5C2004-10-e.pdf.

ICCAT, 2008. Report of the 2008 Shark Stock Assessments Meeting (SCRS/2008/017–SHK Assessment). ICCAT, Madrid, Spain. 89p.

Kaplan, I.C., Cox, S.P., Kitchell, J.F., 2007. Circle hooks for Pacific longliners: not a panacea for marlin and shark bycatch, but part of the solution. Transactions of the American Fisheries Society 136, 392–401.

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

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

Minami, M., Lennert-Cody, C.E., Gao, W., Roman-Verdesoto, M., 2007. Modeling shark bycatch: The zero-inflated negative binomial regression model with smoothing. Fisheries Research 84, 210–221.

Musick, J.A., Branstetter, S., Colvocoresses, J.A., 1993. Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic coast. In: Branstetter, S. (Ed.), Conservation Biology of Elasmobranchs. National Marine Fisheries Service, Seattle, WA, pp. 1–18.

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

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

NMFS, 2006. Final consolidated Atlantic Highly Migratory Species Fishery Management Plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MD. p. 1600.

SAS, 2004. SAS/STAT® 9. 1 User's Guide. SAS Institute Inc, Cary, NC.

SAS, 2005. The Glimmix Procedure, Nov. 2005. SAS. Available from http://support.sas/com/rnd/app/papers/glimmix.pdf.

Simpfendorfer, C.A., Hueter, R.E., Bergman, U., Conett, S.M.H., 2002. Results of a fishery-independent survey for pelagic sharks in the western North Atlantic, 1977–1994. Fisheries Research 55, 175–192.

Venables, W.N., Dichmont, C.M., 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70, 319–337.

Watson, J.W., Epperly, S.P., Shah, A.K., Foster, D.G., 2005. Fishing methods to reduce sea turtle mortality associated with pelagic longlines. Canadian Journal of Fisheries and Aquatic Sciences 62, 965–981.

Weng, K.C., Foley, D.G., Ganong, J.E., Perle, C., Shillinger, G.L., Block, B.A., 2008. Migration of an upper trophic level predator, the salmon shark Lamna ditropis, between distant ecoregions. Marine Ecology-Progress Series 372, 253–264.